

Title: The 'resort effect': can tourist islands act as refuges for coral reef species?

Authors and affiliations:

Charlotte Moritz^{1,2,3,4}, Frédéric Ducarme⁵, Michael J. Sweet⁶, Michael D. Fox⁷, Brian Zgliczynski⁷, Nizam Ibrahim⁸, Ahmed Basheer¹, Kathryn A. Furby⁷, Zachary R. Caldwell⁹, Chiara Pisapia^{1,10}, Gabriel Grimsditch¹, Ameer Abdulla^{1,11}.

1 IUCN Maldives, H. Merry Rose 2nd Floor, Filigas Magu, 20006 Malé, Maldives

2 CMOANA consulting, BP1105, 98703 Punaauia, French Polynesia

3 PSL Research University: EPHE-UPVD-CNRS, USR 3278 CRIOBE, BP 1013 Papetoai, 98729 Moorea, French Polynesia

4 Laboratoire d'Excellence « CORAIL »

5 Centre d'Ecologie et des Sciences de la Conservation, UMR 7204, Muséum National d'Histoire Naturelle, Paris.

6 Environmental Sustainability Research Centre, College of Life and Natural Sciences, University of Derby, derby, DE22 1GB

7 Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA, USA

8 Marine Research Center, H. White Waves, Moonlight Hingun, Malé, 20025, Republic of Maldives

9 The Nature Conservancy, Hawaii, Honolulu, Hawaii, United States of America

10 Department of Biology California State University Northridge, California 91330-8303

11 Global Change Institute and Center for Biodiversity and Conservation Science, University of Queensland, Australia

Corresponding author: Charlotte Moritz, c-m.moritz@laposte.net

Ameer Abdulla and Gabriel Grimsditch should be considered joint senior author.

E-mail addresses (co-authors): frederic.ducarme@ens-lyon.fr; m.sweet@derby.ac.uk;
fox@ucsd.edu; brian.zgliczynski@gmail.com; nibrahim@mrc.gov.mv; ahmed.basheer@iucn.org;
kfurby@ucsd.edu; zcaldwell@tnc.org; chiara.pisapia.1@gmail.com; a.awad.abdulla@uq.edu.au;
gabriel.grimsditch@iucn.org

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Abstract

Aim: There is global consensus that Marine Protected Areas offer a plethora of benefits to the biodiversity within and around them. Nevertheless, many organisms threatened by human impacts also find shelter in unexpected or informally protected places. For coral reef organisms, refuges can be tourist resorts implementing local environment-friendly bottom-up management strategies. We used the coral reef ecosystem as a model to test whether such practices have positive effects on the biodiversity associated with *de facto* protected areas.

Location: North Ari Atoll, Maldives.

Methods: We modelled the effects of the environment and three human management regimes (tourist resorts, uninhabited and local community islands) on the abundance and diversity of echinoderms and commercially important fish species, the percent cover of reef benthic organisms (corals, calcareous coralline algae, turf, and macroalgae), and the proportion of coral disease. We used multivariate techniques to assess the differences between reef components among the management regimes.

Results: Reefs varied between the management regimes. A positive 'resort effect' was found on sessile benthic organisms, with good coral cover and significantly less algae at resort islands. Corals were larger and had fewer diseases in uninhabited islands. Minor 'resort effect' was detected on motile species represented by commercial fish and echinoderms.

Main conclusions: In countries where natural biodiversity strongly sustains the tourist sector and where local populations rely on natural resources, a balance between tourism development, local extraction practices, and biodiversity conservation is necessary. The presence of eco-friendly managed resorts, which practices would need to be certified on the long term, is beneficial to protect certain organisms. House reefs around resorts could therefore provide areas adding to

existing marine protected areas, while marine protection efforts in local community islands should focus on improving fishing management.

Keywords: coral reefs, echinoderms, generalised linear mixed-effect models, human impact, Maldives, management, reef fish, refuge, tourist resort.

(A) Introduction

The effect of human impacts on Earth's ecosystems can now be seen on a global scale and has been shown to influence a wide variety of organisms (Halpern *et al.*, 2015; Lewis & Maslin, 2015). State-run protected areas, although increasing in size and shielding habitats from destructive use, are still regarded as being unable to effectively protect the vast majority of the wildlife and the ecosystems as a whole (Rodrigues *et al.*, 2004; Venter *et al.*, 2014). One of the largest issues facing the protection of specific species is illegal or destructive extraction of individuals (Kelleher *et al.*, 1995; Francis *et al.*, 2002; McClanahan *et al.*, 2005; Campbell *et al.*, 2012; Biggs *et al.*, 2013). However, even outside of state-run protected areas, many organisms can and do find shelter in unexpected or informally protected places. Such locations include artificially created habitats (Rosenzweig, 2003), houses (Bertone *et al.*, 2016), and even militarised zones (Martin & Szuter, 1999; Stein *et al.*, 2008). Furthermore, distance from population centres and the remote geography of ecosystems can, in some instances, serve as coincidental protection from direct human influence (McCauley *et al.*, 2013). Together, these factors can contribute to protecting species or habitats in places that serve as *de facto* refuges, and that are increasingly being recognised as of great importance in global conservation efforts (Kantsa *et al.*, 2013; Bertone *et al.*, 2016). Additionally, the economic incentives associated with ecotourism can lead to increased conservation and management efforts. For example, in some geopolitical regions, coral reef ecosystems are popular tourist attractions, and local bottom-up management strategies are increasingly being implemented in order to protect biodiversity and marine resources (Christie & White, 2007; Mills *et al.*, 2010; Cinner & McClanahan, 2015; Bambridge, 2016).

In the Maldives archipelago, many islands are leased to foreign investors to develop and manage resorts for the lucrative tourism industry. More than one hundred three to five star resorts have been built on available islands that were previously uninhabited or barely used due

to the lack of ground freshwater (Rufin-Soler, 2005), but on which modern desalination technologies allowed resort development as early as the 1970's (Domroes, 2001; Scheyvens, 2011). Regulation under the Maldives Tourism Act (MoTAC 2008) allows such islands to be leased for up to 99 years for the sole purpose of tourism, and allows resorts to exclude extractive activities such as fishing in 500 to 1000 m radius (depending on their lease). Therefore, these resorts, where some activities are regulated and managed (e.g. light tourist and staff night fishing is allowed inside resort boundaries), offer the possibility of efficient protection for the associated marine life, contrary to the current state-run MPAs that often implement no specific management strategy nor enforce laws to protect biodiversity (Rasheed *et al.*, 2016).

Over the past decades, the Maldives have become a popular destination for tourists and the resorts scattered across the archipelago welcome approximately 1 million foreign tourists every year, placing tourism as the main economic sector (25.3% of GDP: MoTAC, 2015; US\$2.6 billion in revenue: Maldives Monetary Authority, 2015). Tourists travelling to the Maldives expect to see healthy coral reefs and associated fish communities. However, these same visitors expect to dine on local fare including fish and crustaceans collected from coral reefs adjacent to the resorts. Fisheries in the Maldives is a millennium-old practice, which underwent a boom in the 1970's and 1980's with the beginning of international exports including tuna, live grouper and sea cucumbers to various countries throughout East Asia (Risk & Sulka, 2000). Several species of near shore reef fishes are both targeted for bait fishing (to sustain the offshore tuna fishery) and for local and tourist consumption (Risk & Sluka, 2000; AUSAID, 2005; McClanahan, 2011; see Table S1 in Supporting Information). Bait fishing in the Maldives is a universal right of every Maldivian and allowed on all reefs in the Maldives. The sea cucumber (*Holothuroidea deBlainville 1834*) fishery began in the mid 1980's due to increased demand in Asian markets. The lack of regulation and use of unsustainable fishing practices led to the fishery becoming overexploited by the early 1990's (Joseph, 1992), with the depletion of most high-value species

(James & Manikfan, 1994). In 2013, a FAO synthesis reported a worrying state of sea cucumber populations, pointing to systematic overfishing, absence of enforcement of the weak regulations, and massive poaching (Eriksson *et al.*, 2013), which made the main commercial species only rarely observed by scientific missions (Ducarme, 2016). Therefore, increased tourism, limited regulation, and overfishing the marine resources may threaten coral reefs of the Maldives if not sustainably managed.

In addition to resort islands where extractive activities are limited, there are two further management regimes associated with islands in the Maldives, hereafter characterised as community islands and uninhabited islands (Table 1). Community islands contain Maldivian villages, which are subject to construction and pollution (sewage) pressure, and surrounding reefs are fished by the local island community and potentially other Maldivian fishers. Uninhabited islands have some fishing regulations such as restrictions on gear and species, but due to their proximity to inhabited community islands they are not off limits to fishing. Therefore, they often experience unregulated fishing pressure but are relatively free of pollution or construction (Risk & Sluka, 2000).

Here, we aimed to characterise the coral reef ecosystem associated with the three island management regimes (resort, community, and uninhabited), with a focus on commercially important species. Given the varying level of management across these islands (i.e. the level of unregulated fishing pressure), we expect that resort islands may offer the highest level of protection from fishing, while community and uninhabited islands may represent the lowest level (Table 1). We also predicted that the uninhabited islands and then the resorts may offer the least amount of direct human impact to the reef (Table 1), despite the localised impacts associated with resort islands, including habitat loss and damage through initial construction, sewage and waste discharge, sedimentation from sand pumping, and general reef damage through water sport recreational activities and increased use by numerous tourists (Allison, 1996; Price &

Firaq, 1996, Brown *et al.*, 1997; Domroes, 2001; Scheyvens, 2011). To address this, we analysed the variation in diversity and abundance of echinoderms (sea cucumbers and starfish), and the variation in diversity, abundance and biomass of commercial and bait fish (see Table S1). We also characterised benthic communities (percent of coral, crustose coralline algae (CCA), turf, and macroalgae), along with the assessments of coral health and size structure.

(A) Methods

(B) Study site and survey methodology

The Republic of Maldives is a coral island nation of the central Indian Ocean, composed of ≈ 1200 islands scattered among 25 reef structures (16 atolls, five oceanic faros, and four oceanic platform reefs: Risk & Sluka, 2000; Naseer & Hatcher, 2004; Fig. 1). Ari Atoll, 90 km long and 32 km wide, is located in central Maldives along the western line of the double chain of atolls of the Maldives archipelago, and is composed of three natural units: Ari Atoll, Rasdhoo Atoll (a small circular atoll) and Thoddoo Island (a small oceanic platform), both located northeast of the main Ari Atoll, separated by deep channels. These geographical units were originally managed as one administrative unit but were subdivided into North Ari (Alifu Alifu) Atoll (including the northern half of Ari Atoll, Thoddoo Island and Rasdhoo Atoll) and South Ari Atoll in the 1980s. North Ari comprises about 80 reef systems, covering 170 km², and is a popular atoll for tourists due to its proximity to Malé and its 13 resort islands. It is a well-representative atoll of the Maldives since all coral reef habitats are present, and it contains a balanced number of islands belonging to each management regimes.

In North Ari Atoll, 12 islands were surveyed using a stratified sampling technique (Fig. 1). Islands were chosen according to their management regimes and their position in the atoll: four resort islands, four community islands, and four uninhabited islands were surveyed; six of these islands were located inside the atoll lagoon and six on the atoll rim. No state-designated or

formal MPAs were surveyed as they are not managed and mainly located around popular deep dive sites away from islands. A total of three independent sites were surveyed at each island by SCUBA diving. At each site, three 50 m transect tapes were laid lengthwise parallel to the reef slope at 10 m depth, with a minimum of 3 m separating each tape to ensure sample independence. Commercial and bait fish (see Table S1 for species list established by Maldivian fishery experts from the Marine Research Center and the IUCN-Maldives) were identified to the species level and tallied within a fixed area (50 x 4 m) along the three transects. The size of individual fishes was estimated to the nearest 5 cm total length. Sea cucumbers and starfish were identified to the species level and counted in three 50 x 2 m belt transects at 10 m depth (except for two islands where only one transect was sampled). All echinoderm surveys were carried out by searching under crevices and rocks. Benthic cover was estimated using the Point Intercept Transect method ("PIT", Hill & Wilkinson, 2004) along the 50 m tape, with points separated by 50 cm. Benthic taxa were recorded at the functional group level (hard coral, CCA, turf, macroalgae, sponge, soft coral, and non-biological substrate; Hill & Wilkinson, 2004). Coral colonies were counted in three 10 x 1 m belts at the beginning of each transect tape, with ≈ 40 m in between consecutive belts. These colonies were measured at their widest diameter and categorised into 5 cm size class bins from 0-5 to >65 cm. Health states associated with all the corals in these belt transects were assessed, and incidences of diseases recorded and categorised according to Coral Reef targeted research-Disease Working guidelines as in Miller *et al.* (2015). Close up photographs were taken of each disease enabling later verification and standardisation of disease identification.

(B) Data analysis

We used a variety of reef biological descriptors to estimate whether reefs were healthier in resort, community, or uninhabited islands. Biomass of commercial and bait fish (see Table S1) was calculated by applying the length-biomass relationship to each fish species (Kulbicki *et al.*,

2005): $B = (a \times TL^b) \times A$, where B is the biomass, TL the total length, A is the abundance, and a and b are taxon-specific length-weight coefficients found in the literature or obtained from online resources (i.e. www.fishbase.org). If taxon-specific coefficients were unavailable, we used the coefficients from congener species. Since *Chromis viridis* Cuvier 1830 and *Chromis atripectoralis* Welanders and Schultz 1951 (Pomacentridae Bonaparte 1832, see Table S1) only account for 1% of the bait fish catch in the Maldives (Anderson, 1994; AUSAID, 2005), we discarded these two species to avoid bias associated with the bait fish analysis regarding management regime, given their tight relationship with benthic biological components of the reef (Halford *et al.*, 2004). Echinoderm abundance was used, instead of biomass as individual sizes were not recorded, and taxon diversity was calculated from these values. The number of coral colonies falling into four size classes (<5 cm, 5 to <20 cm, 20 to <40 cm, and ≥ 40 cm) and the proportion of coral disease according to live coral cover were calculated. Reef benthic descriptors were combined into "reef builders" for hard corals and CCA and into "fleshy algae" for turf and macroalgae, based on their specific functional role within reefs (Smith *et al.*, 2016). Percent cover was calculated at each transect for each of these categories.

To provide an overall picture of reef descriptors among the different management regimes, regardless of other environmental conditions and assuming independence between transects, sites, and islands as detailed in the sampling methods, statistical t -tests were conducted averaging all transects and all sites for community-resort, community-uninhabited, and resort-uninhabited pairs to assess whether there were significant differences ($p < 0.05$) among the management regimes.

Because human and environmental factors can both interact to drive variable response of coral reef species (Heenan *et al.*, 2016), a series of generalised linear mixed-effect models (GLMMs) were used to assess the effect of island management regime (three levels: *resort*, *community*, *uninhabited*), position in the atoll (two levels: *inner*, *outer*), and exposure to

prevailing conditions at each site (two levels: *exposed, sheltered*) on the reef descriptors (*i.e.* commercial and bait fish abundance and species richness, sea cucumber and starfish abundance and species richness, reef builder and fleshy algae percent cover, number of coral colonies in each size class, and proportion of disease). Appropriate error distributions and link functions were chosen for each response variable: Poisson and log for abundance, species richness and number of colonies by size class (counts), and binomial and logit for substrate percent cover and proportion of disease (values bounded between zero and one). Management regime, island position in the atoll, and site exposure were included as fixed effects. All combinations of one, two, and three of these fixed effects, as well as their interactions, were tested. Island was included as a random factor with site nested within island. GLMM performance was assessed using log-likelihood (LL), percent deviance explained (%De) to provide an index of the model's goodness of-fit (Crawley *et al.*, 2005), and Akaike's information criterion corrected for small sample sizes (AICc), providing an index of Kullback–Leibler information loss (Burnham & Anderson, 2002). AICc favours more complex models (*i.e.* with higher predictive capacity) when tapering effects exist and sample sizes are large (Link & Barker, 2006). Models were ranked by AICc. Models outperforming the null and with a ΔAICc value < 4 when compared with the best model (*i.e.* the model with the smallest AICc) were retained.

Finally, multivariate techniques were used to test the assemblage structure among the management regimes. The data matrix containing fish, echinoderms and benthic descriptors was Wisconsin-standardised, *i.e.* transformed according to rows and columns to homogenise data expressed in different metrics. An analysis of similarity (ANOSIM) was performed to compare the variation in species abundance and composition among the management regimes. A partial redundancy analysis (RDA), used to assess the effects of a set of variables on community structure conditioned by another set of variables, was carried out on the Wisconsin-

standardised data matrix. This allowed evaluating the relationship between management regimes and reef descriptors while controlling for island position in the atoll and site exposure. Point biserial correlation coefficients, used for determining the ecological preferences of reef descriptors among the management regimes, were calculated on the Wisconsin-standardised data matrix to highlight which reef descriptor was typical of each management regime. Reef descriptors contributing significantly ($p < 0.05$) to each management regime were represented on the RDA ordination diagram.

All analyses were conducted with the free statistical software R (R Development Core Team, 2016). Multivariate analyses were performed using the 'vegan' (Oksanen *et al.*, 2016) and 'indicspecies' (De Caceres & Legendre, 2009) packages. GLMMs were implemented using function 'glmer' from the package 'lme4' (Bates *et al.*, 2015), and model performance descriptors were calculated using 'AICcmodavg' (Mazerolle, 2016) package.

(A) Results

The generalised linear mixed-effect models, accounting for nested structure of the data and both human management and environmental variables, showed that management regime and site exposure outperformed the null for commercial fish descriptors, with a $\Delta AICc < 4$ when predicting abundance, but > 4 when predicting diversity (Table 2). No model outperformed the null or had a $\Delta AICc > 4$ when predicting bait fish abundance and diversity (Table 2) and echinoderm diversity and abundance (Table 3). Percent reef builder cover was better predicted by site exposure, but with a $\Delta AICc < 4$ compared to the null, whereas percent fleshy algae cover was better predicted by island position in the atoll (best-fitting model compared to the null) and by site exposure (Table 4). Proportion of coral disease was not predicted by any of the variables (Table 5). The best-fitting model predicting small (< 5 cm), medium, and large-sized (21-40 and

>40 cm) coral colony abundance included management regime and site exposure (and their interaction), and island position was also retained in the second-best model. The three variables were retained in the best-fitting model predicting abundance of number of coral colonies sized >5 and ≤20 cm.

T-tests based on all sites, testing for the management regime, showed that reef builder cover was higher and proportion of disease was lower in uninhabited islands compared to both community and resort islands ($p < 0.05$ and $p < 0.01$ respectively; Fig. 2e,g). A large percentage of massive *Porites* Link 1807 was affected by *Porites* White Patch Syndrome (PWPS) at one community island housing a fish processing factory. Fleshy algae cover was lower in resort islands than in community and uninhabited islands ($p < 0.001$ and $p < 0.01$ respectively; Fig. 2f). No coherent patterns were observed in the other benthic categories (see Fig. S1). Small coral colonies (<5 cm) were more numerous in uninhabited islands than in community and resort islands ($p < 0.001$), and large coral colonies (21-40 and >41 cm) were more abundant in uninhabited than in community islands ($p < 0.01$; Fig. 2a,d). Medium-sized coral colonies (6 to 20 cm) were equally abundant among the three management regimes ($p > 0.05$; Fig. 2b,c). Commercial fish diversity was higher in resorts than in the other types of islands ($p < 0.001$ and $p < 0.01$), and the same result was found when considering groupers only ($p < 0.05$, Fig. 3b,d). There were however no significant differences in commercial fish biomass, and in bait fish biomass and diversity among the three management regimes ($p > 0.05$; Fig. 3a,c,e,f). Sea cucumbers and starfish were significantly less diverse in community islands than in either resort or uninhabited islands ($p < 0.001$ and $p < 0.05$ respectively; Fig. 4b,f). Resort islands also had a higher abundance of starfish than community islands ($p < 0.05$; Fig 4e). Commercial sea cucumbers tended to be more abundant in resorts (Fig. 4c,d).

Analysis of similarity (ANOSIM) on the standardised matrix of reef descriptors showed significant differences ($R = 0.1$, $p < 0.001$) associated with the three management regimes.

Ordination diagram of partial redundancy analysis (RDA) removing the effects of the environment ($p_{RDA} = 0.001$, $p_{RDAaxis1} = 0.001$, $p_{RDAaxis2} = 0.009$) showed distinct standard deviation ellipses around the centroid of each management regime group (Fig. 5). The factor *management regime* was significant ($p < 0.01$) and explained 4.13% of variance in the reef descriptor data. Results of analysis of point biserial correlation coefficients plotted on the RDA ordination diagram revealed that community islands, showing the largest variability, were characterised by reef builders, and especially by medium-sized coral colonies, whereas the number of small and large coral colonies increased at uninhabited islands (Fig. 5). Community islands were characterised by two species of grouper (Serranidae Swainson 1839 recognised as commercially important species) and cardinal fish (Apogonidae Günther 1859, important as bait species). Uninhabited islands were characterised by starfish such as *Acanthaster planci* Linnaeus 1758, the lined unicornfish *Naso Breviceps* Cuvier 1829 (a commercially important fish species), and the neon fusilier *Pterocaesio tile* Cuvier 1830 (an important bait fish), whereas the bluefin trevally *Caranx melampygus* Cuvier 1833 (commercial fish) and *Fromia indica* Perrier 1869 (another starfish species) were more commonly associated with resort islands.

(A) Discussion

This study highlights that reef communities can be characterised across islands exposed to varying levels of management, *i.e.* whether the islands house resorts, communities, or are uninhabited. We found that the diversity of commercially important reef fish is higher, echinoderms are in general more abundant and diverse, reef building corals have a good percent of cover, and fleshy algae are less abundant at resort islands. This suggests *de facto* environmental management of these islands may be offering a level of protection for important groups of reef organisms. However, this level of protection may vary between sessile and motile species and can depend on the natural ecological and environmental conditions associated with

each island, with some differences depending on island location (on the inside of or on the atoll rim) and site exposure to strong currents (Nepote *et al.*, 2016).

Management regime appeared to be a good predictor of abundance and diversity in mobile reef organisms such as commercial reef fish species, and the significant difference associated with species diversity, also observed for less mobile echinoderms, suggests that resorts have the potential to protect biodiversity to some degree. The general observation of higher fish and echinoderm biomass at resort islands supports previous observations that fishing pressure would be reduced in resort islands compared to uninhabited and community islands (Domroes, 2001; McClanahan, 2011; and the few broken fishing lines observed during the surveys). However, the lack of significant signals may be caused by the fishing pressure exerted specifically on predatory species such as groupers (Serranidae) around resorts. Building on these results, assessing how the size structure and biomass spectra differ between management regimes can be an interesting perspective to further examine the effects of fishing and levels of protection (Zgliczynski & Sandin, 2017). Furthermore, unbalanced fishing pressure across islands will undoubtedly have a knock-on effect in resort reefs with close proximity to other island types, either by reducing overall biomass of species (especially highly motile fish) that move over greater spatial scales from resorts to other fished islands where they get caught, or by attracting species searching for shelter from fishing and as a direct result of 'fish feeding' designed to encourage them to stay in the vicinity for the tourists. For example, large schools of jacks and snappers, known to exhibit site fidelity (Kaunda-Arara & Rose, 2004; Vignon *et al.*, 2008), were encountered at resort islands. Analysis of commercially important fish species may however be skewed by these schooling species which may aggregate around resorts. Regardless of these specific trends, resorts acting as a refuge for some fish species may serve as important sources of fish larvae, juveniles, and adults able to disperse to neighbouring islands (similar to the spill-over effect of an MPA: Russ & Alcala, 1996; Goni *et al.*, 2010). Islands in

North Ari are indeed close to each other (a few hundred meters to a couple of kilometers) and reef systems in the atolls exhibit increased connectivity due to strong inner currents (Lüdmann *et al.*, 2013). In this context, combining island connectivity and home ranges of fish species, which varies among and within species, time, and habitat (Green *et al.*, 2015) could provide insights on the way that fish species are distributed and potentially move among Maldivian islands to escape fishing pressure or look for suitable habitats. Interestingly, there were no significant differences for either biomass or diversity of bait fish between the management regimes, which may be due to their planktonic feeding behaviour (with the exception for Apogonidae, see Table S1, which are also more active at night and therefore which abundance could have been underestimated) and more important factors such as deep ocean currents, upwelling, and nutrient content which were not included in our analysis. This would likely mean that many of these bait species are independent of the variables such as coral and algae cover, and more affected by seasonal fluctuations and oceanographic conditions (AUSAID, 2005).

In contrast, benthic species such as corals and algae were shown to be strongly impacted by management regimes. In general, corals appeared to be in better condition in uninhabited islands compared to both resort and community islands in terms of percent cover, colony size, and prevalence of disease, and corals around resort islands were also better than around community islands. This is likely due to the reduced levels of pollution and physical damage associated with uninhabited areas, shown to affect corals in many ways, and which are higher in the two latter management regimes highlighted here (Brown *et al.*, 1997; Domroes, 2001; Bruno *et al.*, 2003; Kaczmarzsky *et al.*, 2005; Redding *et al.*, 2013; Vega Thurber *et al.*, 2014; Nepote *et al.*, 2016). Indeed, one of the locations where coral disease was prevalent was a community island housing a fish processing factory. At this site, the majority of massive corals (from the genus *Porites*) were observed to be afflicted by *Porites* White Patch Syndrome (PWPS). Incidentally, this was the first recording of this disease within the Maldives archipelago.

A pathogen, *Vibrio tubiashii* Dubert *et al.* 2016 has been proposed as the causal agent of PWPS (Sere *et al.*, 2015) and further work should be conducted to see if the pathogen is linked to the runoff from the fish processing factory. Interestingly, for size class of the corals, trends could also be observed with regard to the management regimes. Small (i.e. recruits <5 cm) and very large colonies appeared to be more numerous in islands where pollution and physical damage (either from building works or breakage by tourists) could be lower (i.e. uninhabited islands; Allison, 1996; Brown *et al.*, 1997; Domroes, 2001). Interestingly, we found a gradient in abundance of small coral colonies from community (highly impacted: building and fishing activities) to resort (medium impacted: building and tourist activities) and uninhabited (not impacted: no building) islands (Table 1). Despite the effect of pollution over a range of depths was recently examined (Nepote *et al.*, 2016), the extent to which anthropogenic pollution can spread across connected Maldivian islands remains to be assessed.

We observed less abundant fleshy algae, which are sometimes indicative of higher nutrient levels (McClanahan *et al.*, 2002; Szmant, 2002; Fabricius *et al.*, 2005), in resorts compared to both community and uninhabited islands. Algal abundance also appeared to be more abundant in the outer reefs surveyed when compared to those more inside the atoll ring (Nepote *et al.*, 2016). This could be due to higher water flow, which enhances algal growth (Williams & Carpenter, 1998; Carpenter & Williams, 2007). Although algal cover in the Maldives archipelago is often thought of as being a less dominant part of the reef structure (Morri *et al.*, 2015), with recent bleaching events and coral die off (Ibrahim *et al.*, 2017) algae may bloom and become increasingly more common (Graham *et al.*, 2015). In resorts, fleshy algae cover was lower than reef builder cover, suggesting that the ecosystem was overall in good health. These levels are likely to be natural for the reefs in the Maldives, however little work has been undertaken to assess macroalgae cover throughout the archipelago. Furthermore, the low level of fleshy algae is likely to result from a high herbivory pressure (McCook *et al.*, 2001;

McClanahan *et al.*, 2002; Szmant, 2002; Fabricius *et al.*, 2005; Hughes *et al.*, 2007), but further analyses focusing specifically on herbivore species are required.

Taking all the factors above together, this study highlights some interesting possible ecological effects that have occurred as a result of the various usages of islands throughout the Maldives. *De facto* protected areas, represented here by resort islands, do appear to offer some level of protection for certain species, which we named the 'resort effect'. This effect seems to be more commonly associated with the diversity of motile species, showing that resorts can indeed provide refuge for fished, rare or endangered species. As an example, some of the rarer commercially important echinoderms such as *Holothurianobilis* Selenka 1867 have been shown to have nurseries in resorts (Sweet *et al.*, 2015). We therefore suggest that, when governments design protected areas, either in the terrestrial or marine environment, or if these protected areas fail in implementing long-term management plans, *de facto* protected areas will be beneficial in the protection of certain species. Resources used to implement other strict no-take areas aiming at protecting the more motile species would need to be allocated efficiently. In the Maldives, MPAs would require sound management plans and could be based around currently uninhabited islands where reefs are in good condition. However, consideration needs to be taken when designing these areas and implement fishing regulations so as not to impact local communities' fishing spots and practices (Rasheed *et al.*, 2016).

Risk & Sluka (2000) suggested that pollution from sewage from Maldivian resort islands can be relatively limited compared to that found in some community islands. This is especially the case where requirements are in place to install sewage systems, when regular inspections are enforced by government officials, and when beaches are cleared from garbage (Domroes, 2001). However, these man-made *de facto* protected areas rarely come with a high understanding of the strong environmental impact they have during initial implementation (Scheyvens, 2011). Sediments produced during construction affect coral adult reproductive

success and recruit settlement (Erfteemeijer *et al.*, 2012), which may alter the coral community renewal over the following years and have indirect, cascading effects on the other ecosystem groups (e.g. fish, echinoderms). Therefore, positive resort effects on biodiversity appear only once the reef recovers from destructive constructions, *i.e.* several years later (Nepote *et al.*, 2016). A true resort effect is also only likely to be detectable if the resorts are operated in an environmentally sensitive and sustainable manner. Resorts around the world are increasingly using eco-friendly practices (Ashourian *et al.*, 2013; Jamaludin & Yusof, 2013) that have the potential of attracting tourists (Kelly *et al.*, 2007; Kim *et al.*, 2012) and raise their awareness of ecological tipping points (Suutari & Marten, 2007) for reef protection by avoiding some common damaging practices (e.g. trampling and use of sunscreen). Such examples should be used as models in the Maldives where only a few resorts do (e.g. Veligandu Island Resort, Jamaludin & Yusof, 2013). Environmental schemes such as ISO 14001:2015, not compulsory in the Maldives, would also help if implemented in the resorts.

Resort implementation on new islands reduces potential fishing grounds from local communities, which may cause conflict, all the more that the presence of more resorts would increase the demand for reef fish from surrounding reefs. As such, resort *de facto* protected area status may well be seen as controversial, and a balance has to be struck between tourism development, environmental conservation, and local social considerations before resorts are advocated as a solution. An important development question for the Maldives is to understand the "socio-ecological breaking points" and carrying capacity of tourism or limits of acceptable change, *i.e.* the threshold above which the number of resorts might be too high, inducing too many impacts on the ecosystem and conflicts with the local communities. There are indeed reported incidences where resorts and local fishermen have violent conflicts as some fishermen enter into resort boundaries to harvest bait and other resources such as sea cucumbers, without resort approval. More socio-ecological work is still required to appropriately document these

issues in order to advise development policy. Even if resorts are beneficial for the economy of the Maldives and for some species by creating *de facto* no-take zones, too many resorts could lead to a situation of overfishing and reduced resilience, pushing surrounding reefs past their ecological tipping points. A 'carrying capacity' based on available fishing areas and biomass fished in surrounding reefs should be carefully investigated, as some fisheries like the grouper one shows evidence of decline in some atolls (Sattar & Adam 2005). Finally, community islands, despite showing very little waste management, should not be ignored with regard to their potential to develop locally managed protected areas. In this context, community-driven marine protection efforts could be associated with efforts from resort islands like in other parts of the world (e.g. Apo Island, White & Vogt, 2000) and seasonal closure of fishing grounds as is common in other countries reliant on reefs for income and food (Bambridge *et al.*, 2016).

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Biosketch

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aiming to understand the impacts of climate change and anthropogenic stressors on coral reef ecosystems in the Maldives, as well as factors that contribute to social and ecological resilience.

Author contributions: C.M. and F.D. conceived the study and conducted data analysis. C.M., F.D., M.S., and G.G. wrote the manuscript. A.A., C.P., and G.G. organised the scientific expedition. All authors participated in the data collection (except N.A.) and in manuscript editing.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. List of commercial and bait fish species in the Maldives.

Figure S1. Percent cover of reef benthic components for the three management regimes.

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Tables

Table 1. Summary of *de facto* status of community, resort, and uninhabited islands and the potential effects on reef descriptors.

	Community	Resort	Uninhabited
Anthropogenic presence	Village, limited sewage and waste management, harbour	Hotels, waste management, sewage treatment plants with discharge pipes	None
Reef structure /corals	Not protected	Protected for aesthetic values but presence of divers - snorkellers (possible physical damage on corals)	Not protected but only occasional presence of divers - snorkellers
Fish	Not protected - fished	Protected but some light line fishing by tourists and staff	Not protected - fished
Echinoderms	Not protected - fished	Protected - unfished	Not protected - fished

Table 2. Summary of generalised linear mixed-effect model comparisons using Akaike’s information criterion corrected for small sample sizes (AICc) for commercial and bait fish abundance and diversity. Δ AICc scores indicate the difference between the candidate model and the best-fitting model. Only models outperforming the null model and with a Δ AICc value < 4 when compared with the best model are presented. LL: log-likelihood; %De: percent deviance explained by the model; Manage: management regime; Pos: island position in the atoll; Exp: site exposure.

Abundance				Diversity			
Model	LL	%De	Δ AICc	Model	LL	%De	Δ AICc
Commercial fish:				Commercial fish:			
~ site(island) + Manage x Exp	-2328	0	0	~ site(island) + Manage x Exp	-239	11.3	0
~ site(island) + 1	-2334	0	1.33	~ site(island) + Pos + Manage x Exp	-239	11.4	2.38
				~ site(island) + 1	-248	0	6.68
Baitfish:				Baitfish:			
~ site(island) + 1	-11041	0	0	~ site(island) + 1	-107	0	0

Table 3. Summary of generalised linear mixed-effect model comparisons using Akaike's information criterion corrected for small sample sizes (AICc) for echinoderm abundance and diversity. Only models outperforming the null model and with a $\Delta AICc$ value < 4 when compared with the best model are presented. $\Delta AICc$ scores indicate the difference between the candidate model and the best-fitting model. LL: log-likelihood; %De: percent deviance explained by the model; Pos: island position in the atoll; Exp: site exposure.

Abundance				Diversity			
Model	LL	%De	$\Delta AICc$	Model	LL	%De	$\Delta AICc$
Holothurids:				Holothurids:			
~ site(island) + Pos	-173	0.8	0	~ site(island) + 1	-99	0	0
~ site(island) + Pos x Exp	-171	2.1	0.28				
~ site(island) + 1	-175	0	0.54				
Starfish:				Starfish:			
~ site(island) + 1	-326	0	0	~ site(island) + 1	-108	0	0

Table 4. Summary of generalised linear mixed-effect model comparisons using Akaike's information criterion corrected for small sample sizes (AICc) for reef builder and fleshy algae percent cover. Δ AICc scores indicate the difference between the candidate model and the best-fitting model. Only models outperforming the null model and with a Δ AICc value < 4 when compared with the best model are presented. LL: log-likelihood; %De: percent deviance explained by the model; Pos: island position in the atoll; Exp: site exposure.

Reef builder % cover				Fleshy algae % cover			
Model	LL	%De	Δ AICc	Model	LL	%De	Δ AICc
~ site(island) + Exp	-469	0	0	~ site(island) + Pos	-414	0.1	0
~ site(island) + 1	-470	0	0.25	~ site(island) + Pos x Exp	-412	0.3	1.26
				~ site(island) + 1	-416	0	2.21

Table 5. Summary of generalised linear mixed-effect model comparisons using Akaike's information criterion corrected for small sample sizes (AICc) for coral colony size classes and proportion of disease. Only models outperforming the null model and with a ΔAICc value < 4 when compared with the best model are presented. ΔAICc scores indicate the difference between the candidate model and the best-fitting model. LL: log-likelihood; %De: percent deviance explained by the model; Manage: management regime; Pos: island position in the atoll; Exp: site exposure.

Coral			
Model	LL	%De	ΔAICc
Disease:			
~ site(island) + 1	-164	0	0
# colonies ≤ 5 cm:			
~ site(island) + Manage x Exp	-4314	3.68	0
~ site(island) + Pos + Manage x Exp	-4302	3.68	0.99
~ site(island) + 1	-4445	0	274.6
# colonies >5 and ≤ 20 cm:			
~ site(island) + Manage x Pos + Exp	-3569	0.29	0
~ site(island) + Pos x Exp	-3573	0.29	1.06
~ site(island) + Exp	-3576	0.29	2.62
~ site(island) + 1	-3585	0	17.22
# colonies >20 and ≤ 40 cm:			
~ site(island) + Manage x Exp	-1486	0.04	0
~ site(island) + Pos x Exp	-1489	0.04	0.53
~ site(island) + Exp	-1492	0.04	0.99
~ site(island) + Pos + Manage x Exp	-1486	0.04	2.36
~ site(island) + 1	-1525	0	67.28
# colonies >40 cm:			
~ site(island) + Manage x Exp	-1264	0	0
~ site(island) + Pos + Manage x Exp	-1263	0	2.27

~ site(island) + 1	-1285	0	31.54
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Figure legends

Figure 1. Location of islands sampled in North Ari Atoll. Stars represent resort islands, circles represent community islands, and diamonds represent uninhabited islands. Map projection: WGS 1984 UTM 43N.

Figure 2. Barplots of mean and 95% confidence interval for different management regimes (C: community; R: resort; U: uninhabited) across all transects (n=108) for number of colonies of four coral size classes (a to d), reef builder percent cover (e), fleshy algae percent cover (f), and proportion of disease (g).

Figure 3. Barplots of mean and 95% confidence interval for different management regimes (C: community; R: resort; U: uninhabited) across all transects (n=108) for biomass and diversity of commercial fish (a, b), Serranidae Swainson 1839 (c, d), and bait fish (e, f).

Figure 4. Barplots of mean and 95% confidence interval for different management regimes (C: community; R: resort; U: uninhabited) across all transects (n=108) for abundance and diversity of total holothurids (a, b), commercial holothurids (c, d), and starfish (e, f).

Figure 5. Ordination diagram of partial redundancy analyses (RDA removing environmental effects) on Wisconsin-standardised fish (commercial and bait), echinoderm, and substrate (substrate categories and coral size classes) data. Ellipses represent standard deviation around the centroid for each management regime ($p=0.001$). RDA axis 1: $p=0.001$, 1.99% explained variance, RDA axis 2: $p=0.019$, 1.45% explained variance.

Figure 1

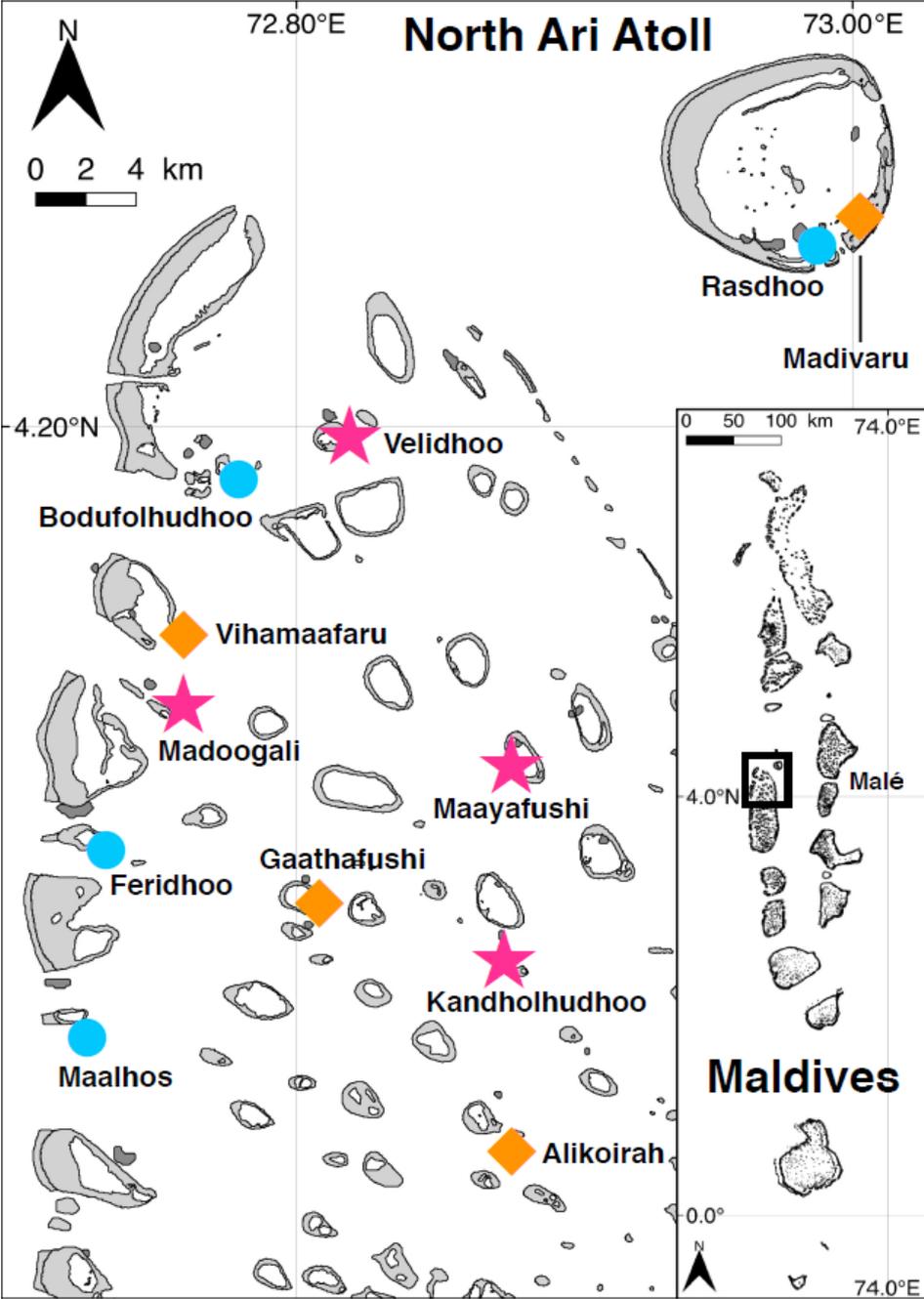


Figure 2

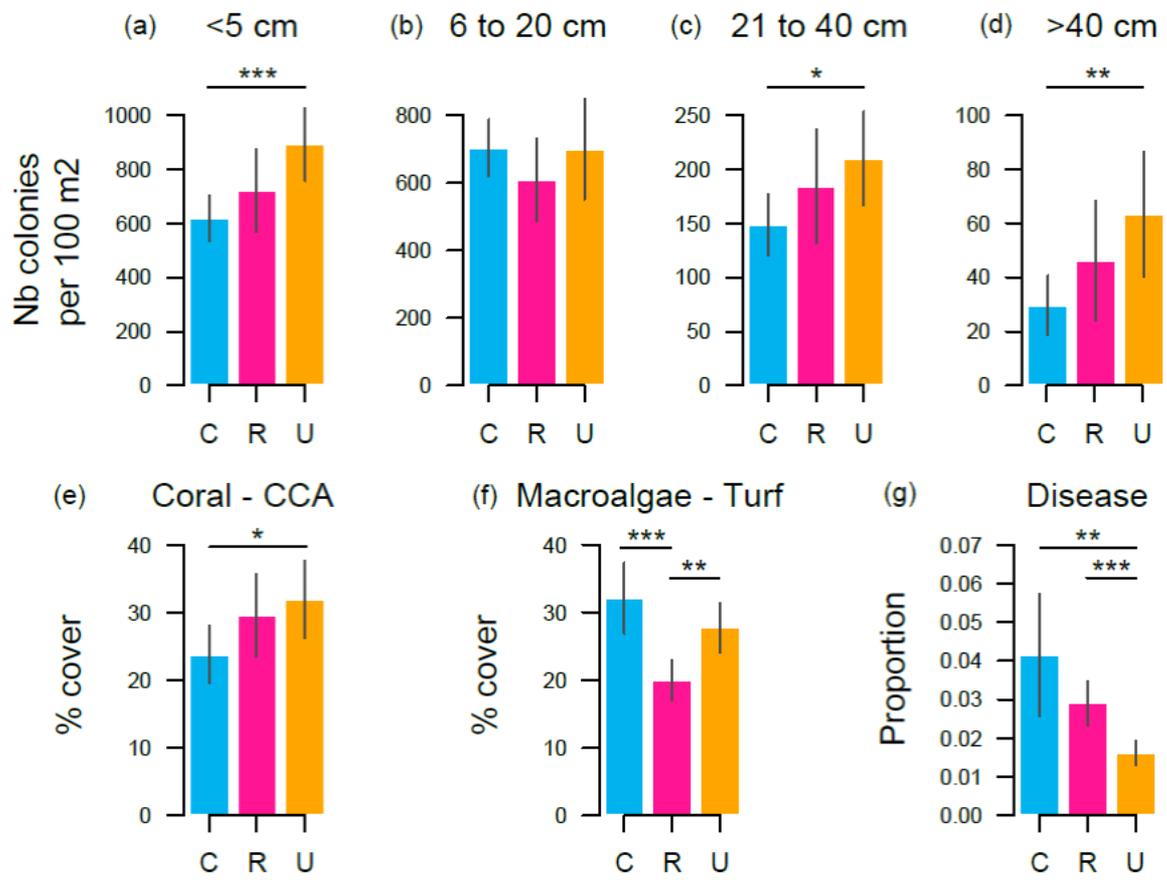


Figure 3

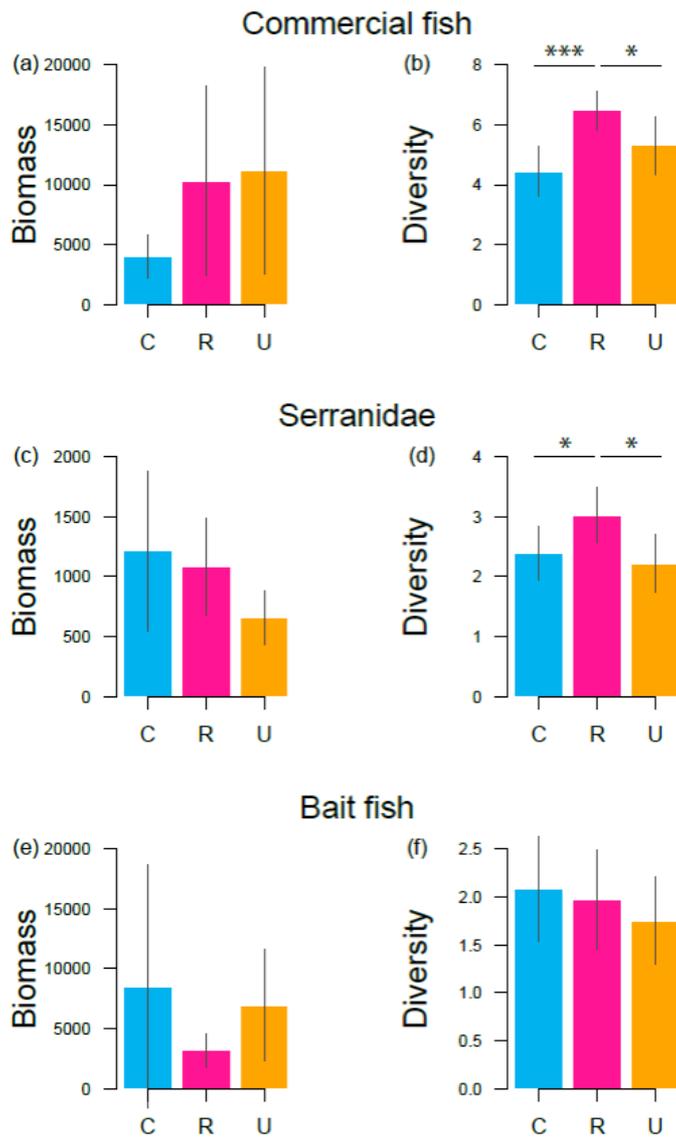


Figure 4

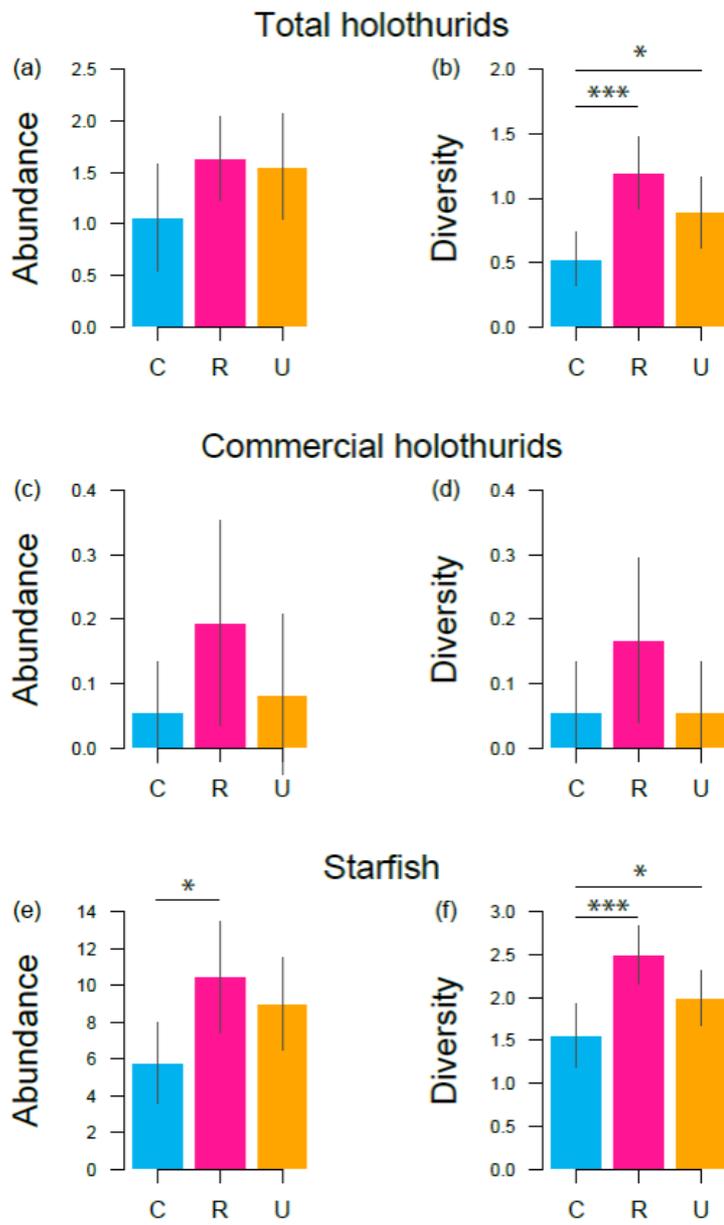
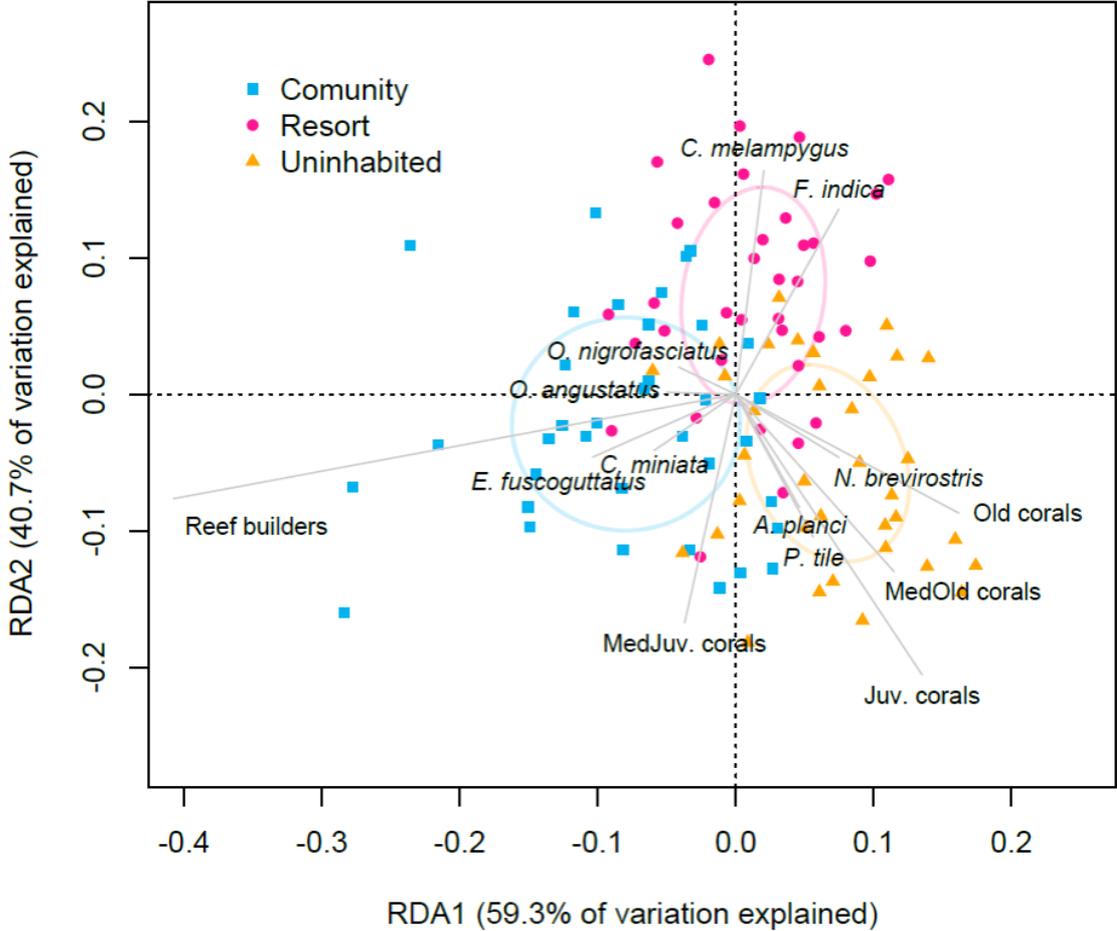


Figure 5



Supporting information

Table S1. List of commercial and bait fish species used in this study, implemented using AUSAID-MRC document (2005) and expert knowledge from IUCN-Maldives and Marine Research Center (see affiliations and main text).

	Family	Scientific name	English name	Dhivehi name
Commercial fish	Acanthuridae	<i>Nasobrevirostris</i>	Spotted unicornfish	Thunbi
	Acanthuridae	<i>Nasoelegans</i>	Orange-spine unicornfish	Ran geri
	Acanthuridae	<i>Nasovlamingi</i>	Big-nose unicornfish	Vaalanmas
	Carangidae	<i>Carangoidesferdau</i>	Banded trevally	Dhanbaruhandhi
	Carangidae	<i>Carangoidesorthogrammus</i>	Island trevally	Thunbahandhi
	Carangidae	<i>Caranxignobilis</i>	Giant trevally	Muda handhi
	Carangidae	<i>Caranxmelampygus</i>	Blue-fin jack	Fanihandhi
	Carangidae	<i>Caranxsexfasciatus</i>	Big-eye trevally	Haluvimas
	Haemulidae	<i>Plectorhinchusalbovittatus</i>	Giant sweetlips	Maaguruva
	Haemulidae	<i>Plectorhinchuschaetodonoides</i>	Harlequin sweetlips	Galuguruva
	Haemulidae	<i>Plectorhinchusvittatus</i>	Oriental sweetlips	Kan'duguruva
	Holocentridae	<i>Myripristisberndti</i>	Yellow-fin soldierfish	Kothari reendhoodhanbondu
	Holocentridae	<i>Neoniphonsammara</i>	Spotfinsquirrelfish	Raiyythikiraiverimas
	Holocentridae	<i>Sargocentroncaudimaculatum</i>	White-tail squirrelfish	Asdhaanuraiverimas
	Holocentridae	<i>Sargocentronspiniferum</i>	Sabre squirrelfish	Raiverimas
	Kyphosidae	<i>Kyphosuscinerascens</i>	Snubnose rudderfish	Kirulhiyamas
	Lethrinidae	<i>Lethrinusharak</i>	Black-blotch emperor	Lahfilolhu
	Lethrinidae	<i>Lethrinusmicrodon</i>	Small-tooth emperor	Thundhigufilolhu
	Lethrinidae	<i>Lethrinusolivaceus</i>	Long-noseemperor	Filolhu
	Lethrinidae	<i>Monotaxisgrandoculis</i>	Large-eye bream	Dhongu
	Lutjanidae	<i>Aprienvirescens</i>	Green jobfish	Giulhu
	Lutjanidae	<i>Lutjanusbohar</i>	Red bass	Raiyymas

	Lutjanidae	<i>Lutjanusfulvus</i>	Black-tailsnapper	Dhonmas
	Lutjanidae	<i>Lutjanusgibbus</i>	Humpback snapper	Ginimas
	Lutjanidae	<i>Lutjanuskasmira</i>	Blue-striped snapper	Dhonreendhoomas
	Lutjanidae	<i>Lutjanusmonostigma</i>	One-spot snapper	Filolhu
	Scombridae	<i>Euthynnusaffinis</i>	Mackerel tuna	Latti
	Scombridae	<i>Gymnosarda unicolor</i>	Dogtooth tuna	Voshi mas
	Serranidae	<i>Anyperodonleucogrammicus</i>	White-lined grouper	Boalhajehifaana
	Serranidae	<i>Cephalopholisargus</i>	Peacock rock cod	Mas faana
	Serranidae	<i>Cephalopholisboenak</i>	Dusky-banded rock cod	Faana
	Serranidae	<i>Cephalopholisleopardus</i>	Leopard rock cod	Raithikifaana
	Serranidae	<i>Cephalopholisminiata</i>	Vermilion rock cod	Kovelifaana
	Serranidae	<i>Cephalopholissexmaculata</i>	Six-spot rock cod	Landaafaana
	Serranidae	<i>Epinepheluscaeruleopunctatus</i>	Small-spotted grouper	Hudhulahfaana
	Serranidae	<i>Epinephelusfuscoguttatus</i>	Flower grouper	Kasfaana
	Serranidae	<i>Epinepheluslongispinis</i>	Long-spined grouper	Koorufaana
	Serranidae	<i>Epinephelusmerra</i>	Honeycomb grouper	Lahfaana
	Serranidae	<i>Epinepheluspilotoceps</i>	Foursaddle grouper	Asdhaanufaana
	Serranidae	<i>Epinephelustauvina</i>	Greasy grouper	Londhifaana
	Serranidae	<i>Gracilalbomarginata</i>	White-square grouper	Boakudafaana
	Serranidae	<i>Plectropomuslaevis</i>	Black-saddlecoral grouper	Kula olhufaana
	Serranidae	<i>Plectropomuspessuliferus</i>	Indiacoral grouper	Dhonolhufaana
	Serranidae	<i>Variolalouti</i>	Lunar-tailed grouper	Kanduhaa
	Siganidae	<i>Siganuslineatus</i>	Sri Lankan rabbitfish	Thammas
Baitfish	Apogonidae	<i>Cheilodipterusarabicus</i>	Tiger cardinalfish	Boadhi / Fatha
	Apogonidae	<i>Cheilodipterusisostigmus</i>	Toothy cardinalfish	Boadhi / Fatha
	Apogonidae	<i>Ostorhinchusangustus</i>	Narrow-striped cardinalfish	Boadhi / Fatha
	Apogonidae	<i>Ostorhinchusnigrofasciatus</i>	Black-striped cardinalfish	Boadhi / Fatha
	Balistidae	<i>Odonusniger</i>	Blue triggerfish	Vaalanrondu
	Caesionidae	<i>Caesiocaerulea</i>	Gold-band fusilier	Muguraan
	Caesionidae	<i>Caesio lunaris</i>	Moon fusilier	Muguraan

Caesionidae	<i>Caesiovarilineata</i>	Thin-lined fusilier	Muguraan
Caesionidae	<i>Caesioxanthonota</i>	Yellow-back fusilier	Muguraan
Caesionidae	<i>Pterocaesio chrysozona</i>	Yellow-stripe fusilier	Muguraan
Caesionidae	<i>Pterocaesio lativittata</i>	Broad-stripe fusilier	Muguraan
Caesionidae	<i>Pterocaesio pisang</i>	Banana fusilier	Muguraan
Caesionidae	<i>Pterocaesio tile</i>	Blue-dash fusilier	Muguraan
Caesionidae	<i>Pterocaesiotrilineata</i>	Striped fusilier	Muguraan

Figure S1. Barplots of mean and 95% confidence interval for different management regimes (C: community; R: resort; U: uninhabited) across all transects (n=108) for non-biological reef components (a), soft corals (b), sponge (c), and other categories (d) percent cover.

