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The "resort effect": Can tourist islands act as refuges for coral reef species?

Charlotte Moritz[1,2,3,4] | Frédéric Ducarme[5] | Michael J. Sweet[6] | Michael D. Fox[7] | Brian Zgliczynski[7] | Nizam Ibrahim[8] | Ahmed Basheer[1] | Kathryn A. Furby[7] | Zachary R. Caldwell[9] | Chiara Pisapia[1,10] | Gabriel Grimsditch[1,*] | Ameer Abdulla[1,11,*]

[1]IUCN Maldives, Malé, Maldives

[2]CMOANA Consulting, Punaauia, French Polynesia

[3]USR 3278 CRIOBE, PSL Research University: EPHE-UPVD-CNRS, Moorea, French Polynesia

[4]Laboratoire d'Excellence "CORAIL", Moorea, French Polynesia

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

[6]Environmental Sustainability Research Centre, College of Life and Natural Sciences, University of Derby, Derby, UK

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

[8]Marine Research Center, Malé, Maldives

[9]The Nature Conservancy of Hawaii, Honolulu, HI, USA

[10]Department of Biology, California State University, Northridge, CA, USA

[11]Global Change Institute and Center for Biodiversity and Conservation Science, University of Queensland, Brisbane, QLD, Australia

Correspondence
Charlotte Moritz, IUCN Maldives, Malé, Maldives.
Email: c-m.moritz@laposte.net

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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 per cent 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, generalized linear mixed-effect models, human impact, Maldives, management, reef fish, refuge, tourist resort

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

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1 | 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 (Biggs, Courchamp, Martin, & Possingham, 2013; Campbell et al., 2012; Francis, Nilsson, & Waruinge, 2002; Kelleher, Bleakley, & Wells, 1995; McClanahan, Davies, & Maina, 2005). 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 (Pryke & Samways, 2009; Rosenzweig, 2003), houses (Bertone et al., 2016) and even militarized zones (Dudley et al., 2002; Martin & Szuter, 1999; Stein, Scott, & Benton, 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 recognized as of great importance in global conservation efforts (Bertone et al., 2016; Kantsa, Tscheulin, Junker, Petanidou, & Kokkini, 2013). 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 to protect biodiversity and marine resources (Bambridge, 2016; Christie & White, 2007; Cinner & McClanahan, 2015; Mills, Pressey, Weeks, Foale, & Ban, 2010).

In the Maldives archipelago, many islands are leased to foreign investors to develop and manage resorts for the lucrative tourism industry. More than 100 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 1970s (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 500–1,000 m radius (depending on their lease). Therefore, these resorts, where some activities are regulated and managed (e.g., light tourist and staff night fishing are allowed inside resort boundaries), offer the possibility of efficient protection for the associated marine life, contrary to the current state-run marine protected areas (MPAs) that often implement no specific management strategy nor enforce laws to protect biodiversity (Rasheed, Abdulla, & Zakariyya, 2016).

Over the past decades, the Maldives have become a popular destination for tourists and the resorts scattered across the archipelago welcome approximately one 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 1970s and 1980s 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 (AUSAID, 2005; McClanahan, 2011; Risk & Sulka, 2000; see Table S1). 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 1980s 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 1990s (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, Purcell, Conand, Muthiga, & Lovatelli, 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 characterized 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 & Sulka, 2000).

Here, we aimed to characterize 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 localized 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; Brown, Turner, Hameed, &

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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

Bateman, 1997; Domroes, 2001; Price & Firaq, 1996; 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 characterized benthic communities (per cent of coral, crustose coralline algae (CCA), turf and macroalgae), along with the assessments of coral health and size structure.

2 | METHODS

2.1 | Study site and survey methodology

The Republic of Maldives is a coral island nation of the central Indian Ocean, composed of ≃1,200 islands scattered among 25 reef structures (16 atolls, five oceanic faros and four oceanic platform reefs: Naseer & Hatcher, 2004; Risk & Sulka, 2000; Figure 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 north-east 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 km^2, 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 because 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 (Figure 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.

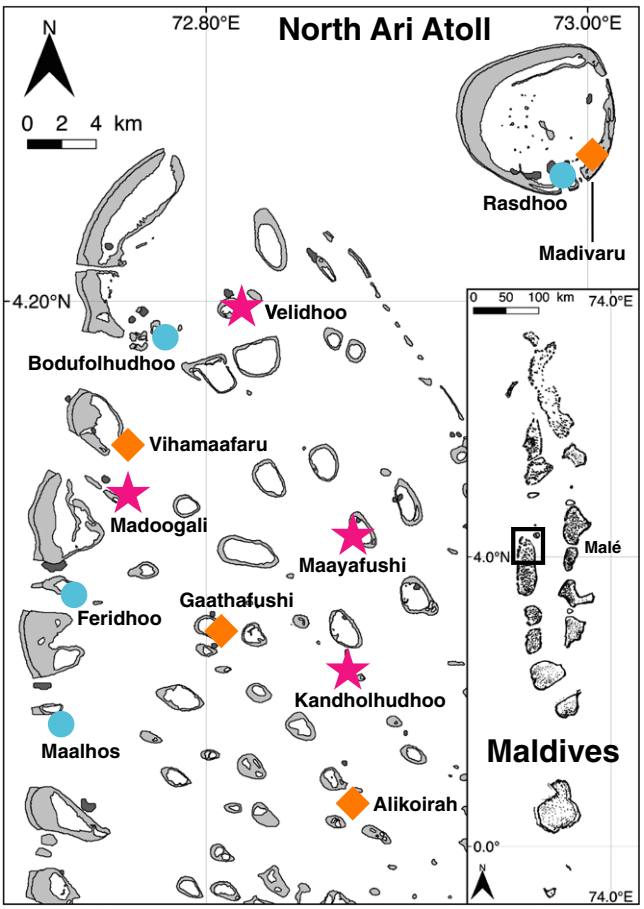

FIGURE 1 Location of islands sampled in North Ari Atoll. Stars represent resort islands, circles represent community islands, and diamonds represent uninhabited islands. Map projection: WGS 1984 UTM 43N. [Colour figure can be viewed at wileyonlinelibrary.com]

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 m × 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 m × 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

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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 × 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 categorized 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 categorized according to Coral Reef targeted research-Disease Working guidelines as in Miller, Sweet, Wood, and Bythell (2015). Close-up photographs were taken of each disease enabling later verification and standardization of disease identification.

2.2 | 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, Guillemot, & Amand, 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. As *Chromis viridis* Cuvier 1830 and *Chromis atripectoralis* Welander 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, Cheal, Ryan, Williams, & Mc, 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). Per cent 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 ($p < .05$) among the management regimes.

Because human and environmental factors can both interact to drive variable response of coral reef species (Heenan, Hoey, Williams, & Williams, 2016), a series of generalized 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 per cent 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 per cent 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), per cent deviance explained (%De) to provide an index of the model's goodness of fit (Crawley, 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-standardized, that is, transformed according to rows and columns to homogenize 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-standardized 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-standardized data matrix to highlight which reef descriptor was typical of each management regime. Reef descriptors contributing significantly ($p < .05$) to each management regime were represented on the RDA ordination diagram.

All analyses were conducted with the free statistical software R version 3.1.2 (R Development Core Team, 2014). 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, Maechler, Bolker, & Walker, 2015), and model performance descriptors were calculated using AICCMODAVG (Mazerolle, 2016) package.

3 | RESULTS

The generalized linear mixed-effect models, accounting for nested structure of the data and both human management and environmental

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TABLE 2 Summary of generalized linear mixed-effect model comparisons using Akaike's information criterion corrected for small sample sizes (AICc) for commercial and bait fish abundance and diversity

	Abundance				Diversity		
Model	LL	%De	ΔAICc	Model	LL	%De	ΔAICc
Commercial fish				*Commercial fish*			
~ site(island) + Manage × Exp	−2,328	0	0	~ site(island) + Manage × Exp	−239	11.3	0
~ site(island) + 1	−2,334	0	1.33	~ site(island) + Pos + Manage × Exp	−239	11.4	2.38
				~ site(island) + 1	−248	0	6.68
Baitfish				*Baitfish*			
~ site(island) + 1	−11,041	0	0	~ site(island) + 1	−107	0	0

ΔAICc scores indicate the difference between the candidate model and the best-fitting model. Only models outperforming the null model and with a ΔAICc value <4 when compared with the best model are presented.
LL, log-likelihood; %De, per cent deviance explained by the model; Manage, management regime; Pos, island position in the atoll; Exp, site exposure.

TABLE 3 Summary of generalized linear mixed-effect model comparisons using Akaike's information criterion corrected for small sample sizes (AICc) for echinoderm abundance and diversity

	Abundance				Diversity		
Model	LL	%De	ΔAICc	Model	LL	%De	ΔAICc
Holothurids				*Holothurids*			
~ site(island) + Pos	−173	0.8	0	~ site(island) + 1	−99	0	0
~ site(island) + Pos × 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

ΔAICc scores indicate the difference between the candidate model and the best-fitting model.
Only models outperforming the null model and with a ΔAICc value <4 when compared with the best model are presented.
LL, log-likelihood; %De, per cent deviance explained by the model; Pos, island position in the atoll; Exp, site exposure.

variables, showed that management regime and site exposure outperformed the null for commercial fish descriptors, with a ΔAICc<4 when predicting abundance, but >4 when predicting diversity (Table 2). No model outperformed the null or had a ΔAICc> 4 when predicting bait fish abundance and diversity (Table 2) and echinoderm diversity and abundance (Table 3). Per cent reef builder cover was better predicted by site exposure, but with a ΔAICc < 4 compared to the null, whereas per cent 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 the 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 ($p < .05$ and $p < .01$, respectively; Figure 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 ($p < .001$ and $p < .01$ respectively; Figure 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 ($p < .001$), and large coral colonies (21–40 and >41 cm) were more abundant in uninhabited than in community islands ($p < .01$; Figure 2a,d). Medium-sized coral colonies (6–20 cm) were equally abundant among the three management regimes ($p > .05$; Figure 2b,c). Commercial fish diversity was higher in resorts than in the other types of islands ($p < .001$ and $p < .01$), and the same result was found when considering groupers only ($p < .05$, Figure 3b,d). There were, however, no significant differences in commercial fish biomass and in bait fish biomass and diversity among the three management regimes ($p > .05$; Figure 3a,c,e,f). Sea cucumbers and starfish were significantly less diverse in community islands than in either resort or uninhabited islands ($p < .001$ and $p < .05$, respectively; Figure 4b,f). Resort islands also had a higher abundance of starfish than community islands ($p < .05$; Figure 4e). Commercial sea cucumbers tended to be more abundant in resorts (Figure 4c,d).

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TABLE 4 Summary of generalized linear mixed-effect model comparisons using Akaike's information criterion corrected for small sample sizes (AICc) for reef builder and fleshy algae per cent cover

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

ΔAICc scores indicate the difference between the candidate model and the best-fitting model. Only models outperforming the null model and with a ΔAICc value <4 when compared with the best model are presented.
LL, log-likelihood; %De, per cent deviance explained by the model; Pos, island position in the atoll; Exp, site exposure.

TABLE 5 Summary of generalized 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

	Coral		
Model	LL	%De	ΔAICc
Disease			
~ site(island) + 1	−164	0	0
Number of colonies ≤5 cm			
~ site(island) + Manage × Exp	−4,314	3.68	0
~ site(island) + Pos + Manage × Exp	−4,302	3.68	0.99
~ site(island) + 1	−4,445	0	274.66
Number of colonies >5 and ≤20 cm			
~ site(island) + Manage × Pos + Exp	−3,569	0.29	0
~ site(island) + Pos × Exp	−3,573	0.29	1.06
~ site(island) + Exp	−3,576	0.29	2.62
~ site(island) + 1	−3,585	0	17.22
Number of colonies >20 and ≤40 cm			
~ site(island) + Manage × Exp	−1,486	0.04	0
~ site(island) + Pos × Exp	−1,489	0.04	0.53
~ site(island) + Exp	−1,492	0.04	0.99
~ site(island) + Pos + Manage × Exp	−1,486	0.04	2.36
~ site(island) + 1	−1,525	0	67.28
Number of colonies >40 cm			
~ site(island) + Manage × Exp	−1,264	0	0
~ site(island) + Pos + Manage × Exp	−1,263	0	2.27
~ site(island) + 1	−1,285	0	31.54

ΔAICc scores indicate the difference between the candidate model and the best-fitting model.
Only models outperforming the null model and with a ΔAICc value < 4 when compared with the best model are presented.
LL, log-likelihood; %De, per cent deviance explained by the model; Manage, management regime; Pos, island position in the atoll; Exp, site exposure.

Analysis of similarity (ANOSIM) on the standardized matrix of reef descriptors showed significant differences ($R = .1$, $p < .001$) associated with the three management regimes. Ordination diagram of partial RDA removing the effects of the environment ($p_{RDA} = .001$, $p_{RDAaxis1} = .001$, $p_{RDAaxis2} = .009$) showed distinct standard deviation ellipses around the centroid of each management regime group (Figure 5). The factor *management regime* was significant ($p < .01$) 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 characterized by reef builders and especially by medium-sized coral colonies, whereas the number of small and large coral colonies increased at uninhabited islands (Figure 5). Community islands were characterized by two species of grouper (Serranidae Swainson 1839 recognized as commercially important species) and cardinal fish (Apogonidae Günther 1859, important as bait species). Uninhabited islands were characterized by starfish such as *Acanthaster planci* Linnaeus 1758, the lined unicornfish *Naso brevirostris* 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.

4 | DISCUSSION

This study highlights that reef communities can be characterized across islands exposed to varying levels of management, that is, 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 above average per cent 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, Bianchi, Chiantore, Morri, & Montefalcone, 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

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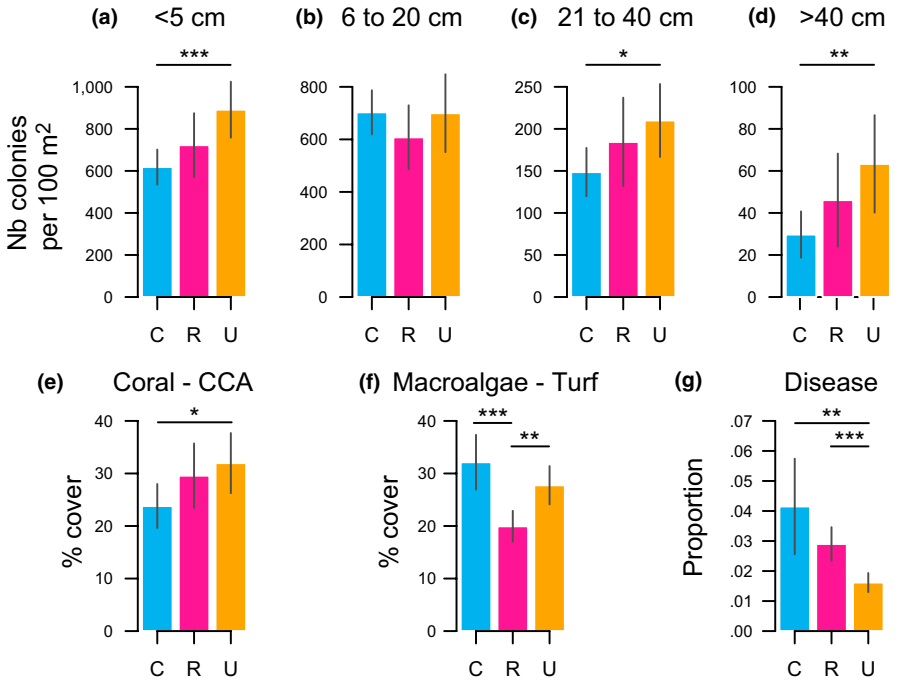

FIGURE 2 Bar plots of mean and 95% confidence interval for different management regimes (C: community; R: resort; U: uninhabited) across all transects (n = 108) for number of colonies of four coral size classes (a–d), reef builder per cent cover (e), fleshy algae per cent cover (f) and proportion of disease (g) (*p<0.05, **p<0.01, ***p<0.001). [Colour figure can be viewed at wileyonlinelibrary.com]

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" deigned 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, Morat, Galzin, & Sasal, 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 (Almany et al., 2007; Palumbi et al., 2004), and similar to the spillover effect of an MPA (Russ & Alcala, 1996; Goñi, Hilborn, Díaz, Mallol, & Adlerstein, 2010). Islands in North Ari are indeed close to each other (a few hundred metres to a couple of kilometres) and reef systems in the atolls exhibit increased connectivity due to strong inner currents (Lüdmann, Kalvelage, Betzler, Fürstenau, & Hübscher, 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 whose 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 per cent 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; Bruno, Petes, Harvell, & Hettinger, 2003; Domroes, 2001; Kaczmarsky, Draud, & Williams, 2005; Nepote et al., 2016; Redding et al., 2013; Vega Thurber et al., 2014). 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

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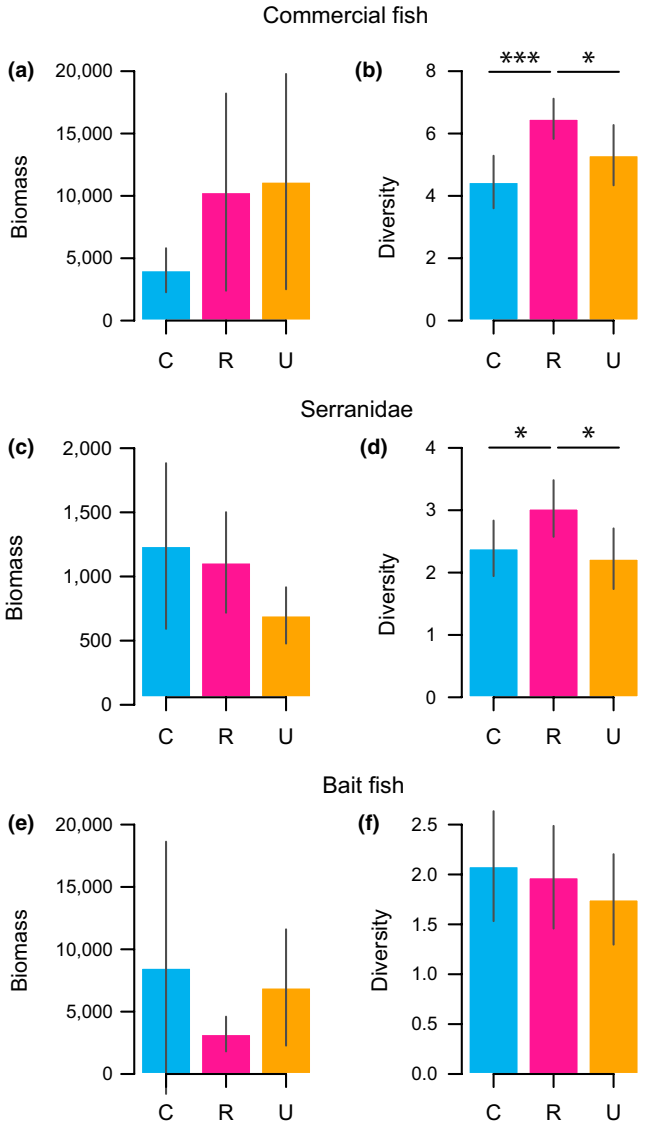

FIGURE 3 Bar plots of mean and 95% confidence interval for different management regimes (C: community; R: resort; U: uninhabited) across all transects (n = 108) for biomass and diversity of commercial fish (a, b), Serranidae Swainson 1839 (c, d) and bait fish (e, f) (*p<0.05, ***p<0.001). [Colour figure can be viewed at wileyonlinelibrary.com]

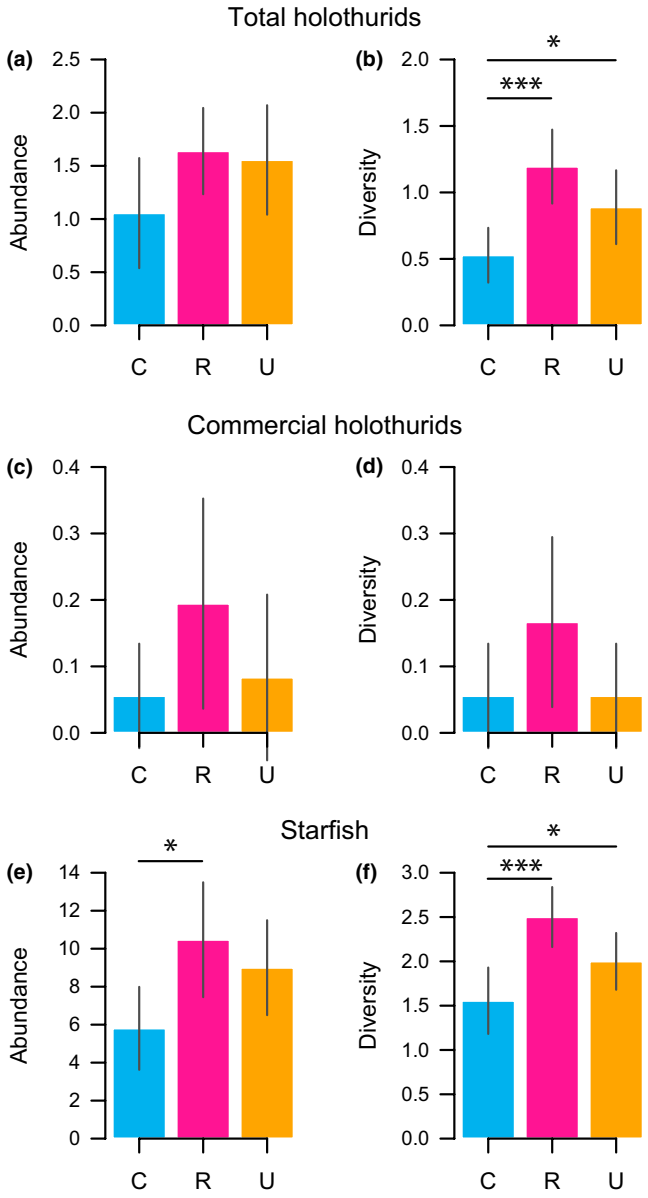

FIGURE 4 Bar plots of mean and 95% confidence interval for different management regimes (C: community; R: resort; U: uninhabited) across all transects (n = 108) for abundance and diversity of total holothurids (a, b), commercial holothurids (c, d) and starfish (e, f) (*p<0.05, ***p<0.001). [Colour figure can be viewed at wileyonlinelibrary.com]

Porites white patch syndrome (PWPS). Incidentally, this was the first recording of this disease within the Maldives archipelago. A pathogen, *Vibrio tubiashii* has been proposed as the causal agent of PWPS (Séré et al., 2015), and further work should be conducted to see whether 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 (Fabricius et al., 2005; McClanahan et al., 2002; Szmant, 2002), 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 (Carpenter & Williams, 2007;

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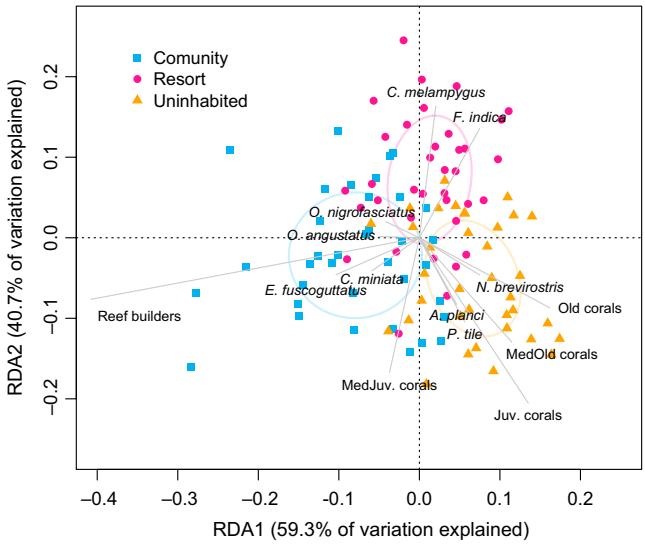

FIGURE 5 Ordination diagram of partial redundancy analyses (RDA removing environmental effects) on Wisconsin-standardized fish (commercial and bait), echinoderm and substrate (substrate categories and coral size classes) data. Ellipses represent standard deviation around the centroid for each management regime (p = .001). RDA axis 1: p = .001, 1.99% explained variance, RDA axis 2: p = .019, 1.45% explained variance. [Colour figure can be viewed at wileyonlinelibrary.com]

Williams & Carpenter, 1998). 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, Jennings, MacNeil, Mouillot, & Wilson, 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 (Fabricius et al., 2005; Hughes et al., 2007; McClanahan et al., 2002; McCook et al., 2001; Szmant, 2002), 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 *Holothuria nobilis* Selenka 1867 have been shown to have nurseries in resorts (Sweet, Ducarme, & Conand, 2016). We therefore suggest that, when governments design protected areas, either in the terrestrial or in 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 implementing fishing regulations so as not to impact local communities' fishing spots and practices (Rasheed et al., 2016).

Risk and Sulka (2000) suggested that pollution from sewage from Maldivian resort 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 (Erftemeijer, Riegl, Hoeksema, & Todd, 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, that is, 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, Haider, Williams, & Englund, 2007; Kim, Palakurthi, & Hancer, 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 follow environmental best practices (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, that is, 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

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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, such as groupers for example, already shows 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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REFERENCES

Allison, W. R. (1996). Snorkeler damage to reef corals in the Maldive Islands. *Coral Reefs*, *5*, 215–218.

Almany, G. R., Berumen, M. L., Thorrold, S. R., Planes, S., & Jones, G. P. (2007). Local replenishment of coral reef fish populations in a marine reserve. *Science*, *316*, 742–744.

Anderson, R. C. (1994). The size of the Maldivian tuna live bait fishery. *Rasain*, *3*, 178–181.

Ashourian, M. H., Cherati, S. M., Mohd Zin, A. A., Niknam, N., Mokhtar, A. S., & Anwari, M. (2013). Optimal green energy management for island resorts in Malaysia. *Renewable Energy*, *51*, 36–45.

AUSAID (2005). An assessment of damage to Maldivian coral reefs and baitfish populations from the Indian Ocean tsunami. Prepared by an Australian Government Mission and the Maldives Marine Research Centre. ISBN 1920861319 (A37). 67pp.

Bambridge, T. (2016). *The Rahui: Legal pluralism in Polynesian traditional management of resources and territories*. Australia: ANU Press.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Bertone, M. A., Leong, M., Bayless, K. M., Malow, T. L. F., Dunn, R. R., & Trautwein, M. D. (2016). Arthropods of the great indoors: Characterizing diversity inside urban and suburban homes. *PeerJ*, *4*, e1582. https://doi.org/10.7717/peerj.1582

Biggs, D., Courchamp, F., Martin, R., & Possingham, H. P. (2013). Legal trade of Africa's rhino horns. *Science*, *339*, 1038–1039.

Brown, K., Turner, R. K., Hameed, H., & Bateman, I. (1997). Environmental carrying capacity and tourism development in the Maldives and Nepal. *Environmental Conservation*, *24*, 316–325.

Bruno, J. F., Petes, L. E., Harvell, C. D., & Hettinger, A. (2003). Nutrient enrichment can increase the severity of coral diseases. *Ecology Letters*, *6*, 1056–1061.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information theoretic approach*. New York, NY: Springer-Verlag.

Campbell, S. J., Hoey, A. S., Maynard, J., Kartawijaya, J., Cinner, J., Graham, N. A. J., & Baird, A. H. (2012). Weak compliance undermines the success of no-take zones in a large government-controlled marine protected area. *PLoS ONE*, *7*, e50074. https://doi.org/10.1371/journal.pone.0050074

Carpenter, R. C., & Williams, S. L. (2007). Mass transfer limitation of photosynthesis of coral reef algal turfs. *Marine Biology*, *151*, 435–450.

Christie, P., & White, A. T. (2007). Best practices for improved governance of coral reef marine protected areas. *Coral Reefs*, *26*, 1047–1056.

Cinner, J. E., & McClanahan, T. R. (2015). A sea change on the African coast? Preliminary social and ecological outcomes of a governance transformation in Kenyan fisheries. *Global Environmental Change*, *30*, 133–139.

Crawley, M. J. (2005). *Statistics: An introduction using R*. New York, NY: John Wiley & Sons Ltd.

De Caceres, M., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, *90*, 3566–3574. http://sites.google.com/site/miqueldecaceres/

Domroes, M. (2001). Conceptualising state-controlled resort islands for an environment-friendly development of tourism: The Maldivian experience. *Singapore Journal of Tropical Geography*, *22*, 122–137.

Ducarme, F. (2016). Field observations of sea cucumbers in Ari Atoll, and comparison with two nearby atolls in Maldives. *SPC Beche-de-Mer Information Bulletin*, *36*, 9–14.

Dudley, J. P., Ginsberg, J. R., Plumptre, A. J., Hart, J. A., & Campos, L. C. (2002). Effects of war and civil strife on wildlife and wildlife habitats. *Conservation Biology*, *16*, 319–329.

Erftemeijer, P., Riegl, B., Hoeksema, B. W., & Todd, P. A. (2012). Environmental impacts of dredging and other sediment disturbances on corals: A review. *Marine Pollution Bulletin*, *64*, 1737–1765.

Eriksson, H., Purcell, S., Conand, C., Muthiga, N., & Lovatelli, A. (2013). Report on the FAO Workshop on Sea Cucumber Fisheries: An Ecosystem Approach to Management in the Indian Ocean (SCEAM Indian Ocean), Mazizini, Zanzibar, the United Republic of Tanzania, 12–16 November 2012. *FAO Fisheries and Aquaculture Report No. 1038*, p. 92.

Fabricius, K., Death, G., McCook, L., Turak, E., & Williams, D. Mc B (2005). Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin*, *51*, 384–398.

Francis, J., Nilsson, A., & Waruinge, D. (2002). Marine protected areas in the eastern African Region: How successful are they? *Ambio*, *31*, 503–511.

Goñi, R., Hilborn, R., Díaz, D., Mallol, S., & Adlerstein, S. (2010). Net contribution of spillover from a marine reserve to fishery catches. *Marine Ecology Progress Series*, *400*, 233–243.

Graham, N. A. J., Jennings, S., MacNeil, M. A., Mouillot, D., & Wilson, S. K. (2015). Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, *518*, 94–97.

Green, A. L., Maypa, A. P., Almany, G. R., Rhodes, K. L., Weeks, R., Abesamis, R. A., … White, A. T. (2015). Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. *Biological Reviews*, *90*, 1215–1247.

Halford, A., Cheal, A. J., Ryan, D., Williams, D., & Mc, B. (2004). Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology*, *85*, 1892–1905.

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., … Walbridge, S. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications*, *6*, https://doi.org/10.1038/ncomms8615

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Heenan, A., Hoey, A. S., Williams, G. J., & Williams, I. D. (2016). Natural bounds on herbivorous coral reef fishes. *Proceedings of the Royal Society B*, *283*, 20161716.

Hill, J., & Wilkinson, C. (2004). *Methods for ecological monitoring of coral reefs. A resource for managers*. Townsville, Australia: Australian Institute of Marine Science.

Hughes, T. P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., … Willis, B. (2007). Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology*, *17*, 360–365.

Ibrahim, N., Mohamed, M., Basheer, A., Ismail, H., Nistharan, F., Schmidt, A., … Grimsditch, G. (2017). *Status of coral bleaching in the Maldives in 2016*. Malé, Maldives: Marine Research Centre.

Jamaludin, M., & Yusof, Z. B. (2013). Best practice of Green Island resorts. *Procedia - Social and Behavioral Sciences*, *105*, 20–29.

James, D. B. B., & Manikfan, M. A. (1994). Some remarks on the present status of beche-de-mer industry of Maldives and its lesson for the Lakshadweep. *Bulletin of the Center for Marine Fishery Resources Institute*, *46*, 101–105.

Joseph, L. (1992). *Review of the Bêche-de-mer (Sea Cucumber) Fishery in the Maldives*. Bay of Bengal Programme Technical Report 79. Chennai, India: Food and Agriculture Organization of the United Nations.

Kaczmarsky, L. T., Draud, M., & Williams, E. (2005). Is there a relationship between proximity to sewage effluent and the prevalence of coral disease? *Caribbean Journal of Science*, *41*, 124–137.

Kantsa, A., Tscheulin, T., Junker, R., Petanidou, T., & Kokkini, S. (2013). Urban biodiversity hotspots wait to get discovered: The example of the city of Ioannina, NW Greece. *Landscape and Urban Planning*, *120*, 129–137.

Kaunda-Arara, B., & Rose, G. A. (2004). Homing and site fidelity in the greasy grouper *Epinephelus tauvina* (Serranidae) within a marine protected area in coastal Kenya. *Marine Ecology Progress Series*, *277*, 245–251.

Kelleher, G., Bleakley, C., & Wells, S. (1995). *Global representative system of marine protected areas*. Washington, DC: The World Bank.

Kelly, J., Haider, W., Williams, P. W., & Englund, K. (2007). Stated preferences of tourists for eco-efficient destination planning options. *Tourism Management*, *28*, 377–390.

Kim, Y. J., Palakurthi, R., & Hancer, M. (2012). The environmentally friendly programs in hotels and customers' intention to stay: An online survey approach. *International Journal of Hospitality & Tourism Administration*, *13*, 195–214.

Kulbicki, M., Guillemot, N., & Amand, M. (2005). A general approach to length-weight relationships for New Caledonian lagoon fishes. *Cybium*, *29*, 235–252.

Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, *519*, 171–180.

Link, W. A., & Barker, R. J. (2006). Model weights and the foundations of multimodel inference. *Ecology*, *87*, 2626–2635.

Lüdmann, T., Kalvelage, C., Betzler, C., Fürstenau, J., & Hübscher, C. (2013). The Maldives, a giant isolated carbonate platform dominated by bottom currents. *Marine and Petroleum Geology*, *43*, 326–340.

Maldives Monetary Authority (2015). *Annual report 2014*. Malé, Republic of Maldives: Maldives Monetary Authority.

Martin, P. S., & Szuter, C. R. (1999). War zones and game sinks in Lewis and Clark's west. *Conservation Biology*, *13*, 36–45.

Mazerolle, M. J. (2016). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c)*. R package version 2.0-4. http://CRAN.R-project.org/package=AICcmodavg.

McCauley, D. J., Power, E. A., Bird, D. W., McInturff, A., Dunbar, R. B., Durham, W. H., … Young, H. S. (2013). Conservation at the edges of the world. *Biological Conservation*, *165*, 139–145.

McClanahan, T. R. (2011). Coral reef fish communities in management systems with unregulated fishing and small fisheries closures compared with lightly fished reefs – Maldives vs. Kenya. *Aquatic Conservation: Marine and Freshwaer Ecosystems*, *21*, 186–198.

McClanahan, T. R., Cokos, B. A., & Sala, E. (2002). Algal growth and species composition under experimental control of herbivory, phosphorus and coral abundance in Glovers Reef, Belize. *Marine Pollution Bulletin*, *44*, 441–451.

McClanahan, T., Davies, J., & Maina, J. (2005). Factors influencing resource users and managers' perceptions towards marine protected area management in Kenya. *Environmental Conservation*, *32*, 42–29.

McCook, L. J., 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.

Miller, J., Sweet, M. J., Wood, E., & Bythell, J. (2015). Baseline coral disease surveys within three marine parks in Sabah, Borneo. *PeerJ*, *3*, e1391. https://doi.org/10.7717/peerj.1391

Mills, M., Pressey, R. L., Weeks, R., Foale, S., & Ban, N. C. (2010). A mismatch of scales: Challenges in planning for implementation of marine protected areas in the Coral Triangle. *Conservation Letters*, *3*, 291–303.

Morri, C., Montefalcone, C., Lasagna, R., Gatti, G., Rovere, A., Parravicini, V., … Bianchi, C. N. (2015). Through bleaching and tsunami: Coral reef recovery in the Maldives. *Marine Pollution Bulletin*, *98*, 188–200.

MoTAC (Ministry of Tourism and Civil Aviation) (2015). *Tourism Yearbook 2015*. Malé, Republic of Maldives: MoTAC.

MoTCA (Ministry of Tourism and Civil Aviation). (2008). *Maldives Tourism Act (Law No. 2/99)*. http://www.tourism.gov.mv/downloads/Tourism_Act(Law2-99).pdf

Naseer, A., & Hatcher, B. G. (2004). Inventory of the Maldives' coral reefs using morphometrics generated from Landsat ETM+ imagery. *Coral Reefs*, *23*, 161–168.

Nepote, E., Bianchi, C. N., Chiantore, M., Morri, C., & Montefalcone, M. (2016). Pattern and intensity of human impact on coral reefs depend on depth along the reef profile and on the descriptor adopted. *Estuarine, Coastal and Shelf Science*, *178*, 86–91.

Oksanen, J., Blanchet, G. F., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., … Wagner, H. (2016). *vegan: Community ecology package*. R package version 2.3-4. http://CRAN.R-project.org/package=vegan

Palumbi, S. R. (2004). Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. *Annual Review of Environmental Resources*, *29*, 31–68.

Price, A. R. G., & Firaq, I. (1996). The environmental status of reefs on Maldivian resort islands: A preliminary assessment for tourism planning. *Aquatic Conservation*, *6*, 93–106.

Pryke, J. S., & Samways, M. J. (2009). Recovery of invertebrate diversity in a rehabilitated city landscape mosaic in the heart of a biodiversity hotspot. *Landscape and Urban Planning*, *93*, 54–62.

R Development Core Team. (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org.

Rasheed, A. R., Abdulla, A., & Zakariyya, N. I. (2016). Vulnerability of different types of fishers to potential implementation of a management plan in a Marine Protected Area (MPA) in the Maldives. *Marine Policy*, *74*, 195–204.

Redding, J. E., Myers-Miller, R. L., Baker, D. M., Fogel, M., Raymundo, L. J., & Kim, K. (2013). Link between sewage-derived nitrogen pollution and coral disease severity in Guam. *Marine Pollution Bulletin*, *73*, 57–63.

Risk, M. J., & Sulka, R. (2000). The Maldives: A nation of atolls. In T. R. McClanahan, D. Obura, & C. R. C. Sheppard (Eds.), *Coral reefs of the Indian Ocean: Their ecology and conservation* (pp. 325–352). New York, NY: Oxford University Press.

Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., … Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, *428*, 640–643.

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Rosenzweig, M. L. (2003). Reconciliation ecology and the future of species diversity. *Oryx*, *37*, 194–205.

Rufin-Soler, C. (2005). Les politiques de gestion insulaire dans l'archipel des Maldives. *Cybergeo: European Journal of Geography, Espace, Société, Territoire*, *322*, https://doi.org/10.4000/cybergeo.23381

Russ, G. R., & Alcala, A. C. (1996). Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series*, *132*, 1–9.

Sattar, S. A., & Adam, M. S. (2005). *Review of grouper fishery of the Maldives with additional notes on the Faafu Atoll Fishery*. Malé, Maldives: Marine Research Centre.

Scheyvens, R. (2011). The challenge of sustainable tourism development in the Maldives: Understanding the social and political dimensions of sustainability. *Asia Pacific Viewpoint*, *52*, 148–164.

Séré, M. G., Tortosa, P., Chabanet, P., Quod, J. P., Sweet, M. J., & Schleyer, M. H. (2015). Identification of a bacterial pathogen associated with *Porites* white patch syndrome in the Western Indian Ocean. *Molecular Ecology*, *24*, 4570–4581.

Smith, J. E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., … Sandin, S. (2016). Re-evaluating the health of coral reef communities: baselines and evidence for human impacts across the central Pacific. *Proceedings of the Royal Society B*, *283*, 20151985.

Stein, B. A., Scott, C., & Benton, N. (2008). Federal lands and endangered species: The role of military and other federal lands in sustaining biodiversity. *BioScience*, *58*, 339–347.

Suutari, A., & Marten, G. (2007). Eco tipping points: How a vicious cycle can become virtuous. *Earth Island Journal*, Summer, *2007*, 26–31.

Sweet, M. J., Ducarme, F., & Conand, C. (2016). Juvenile "black teatfish" in Maldives. *SPC Beche-de-Mer Information Bulletin*, *36*, 82–83.

Szmant, A. M. S. (2002). Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? *Estuaries*, *25*, 743–766.

Vega Thurber, R., Burkepile, D. E., Fuchs, C., Shantz, A. A., McMinds, R., & Zaneveld, J. R. (2014). Chronic nutrient enrichment increases prevalence and severity of coral disease and bleaching. *Global Change Biology*, *20*, 544–554.

Venter, O., Fuller, R. A., Segan, D. B., Carwardine, J., Brooks, T., Butchart, S. H. M., … Watson, J. E. M. (2014). Targeting global protected area expansion for imperiled biodiversity. *PLoS Biology*, *12*, e1001891.

Vignon, M., Morat, F., Galzin, R., & Sasal, P. (2008). Evidence for spatial limitation of the bluestripe snapper *Lutjanus kasmira* in French Polynesia from parasite and otolith shape analysis. *Journal of Fish Biology*, *73*, 2305–2320.

White, A. T., & Vogt, H. P. (2000). Philippine coral reefs under threat: Lessons learned after 25 years of community-based reef conservation. *Marine Pollution Bulletin*, *40*, 537–550.

Williams, S. L., & Carpenter, R. C. (1998). Effects of unidirectional and oscillatory water flow on nitrogen fixation (acetylene reduction) in coral reef algal turfs, Kaneohe Bay, Hawaii. *Journal of Experimental Marine Biology and Ecology*, *226*, 293–316.

Zgliczynski, B. J., & Sandin, S. A. (2017). Size-structural shifts reveal intensity of exploitation in coral reef fisheries. *Ecological Indicators*, *73*, 411–421.

BIOSKETCH

This study is part of the broader Project Regenerate, a partnership project between the International Union for the Conservation of Nature, the Government of Maldives and USAID, 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. organized the scientific expedition. All authors participated in the data collection (except N.A.) and in manuscript editing.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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