



Variation in size frequency distribution of coral populations under different fishing pressures in two contrasting locations in the Indian Ocean



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ARTICLE INFO

Article history:

Received 5 November 2016

Received in revised form

17 September 2017

Accepted 21 September 2017

Available online 23 September 2017

Keywords:

Coral reefs

Fisheries

Ecosystem management

Coastal waters

Effects-population

ABSTRACT

This study aimed to assess how the size–frequency distributions of coral genera varied between reefs under different fishing pressures in two contrasting Indian Ocean locations (the Maldives and East Africa). Using generalized linear mixed models, we were able to demonstrate that complex interactions occurred between coral genera, coral size class and fishing pressure. In both locations, we found *Acropora* coral species to be more abundant in non-fished compared to fished sites (a pattern which was consistent for nearly all the assessed size classes). Coral genera classified as ‘stress tolerant’ showed a contrasting pattern i.e. were higher in abundance in fished compared to non-fished sites. Site specific variations were also observed. For example, Maldivian reefs exhibited a significantly higher abundance in all size classes of ‘competitive’ corals compared to East Africa. This possibly indicates that East African reefs have already been subjected to higher levels of stress and are therefore less suitable environments for ‘competitive’ corals. This study also highlights the potential structure and composition of reefs under future degradation scenarios, for example with a loss of *Acropora* corals and an increase in dominance of ‘stress tolerant’ and ‘generalist’ coral genera.

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1. Introduction

Many biological processes associated with clonal animals such as corals have been argued to be related to size rather than age (Connell, 1973; Loya, 1976; Hughes and Jackson, 1980; Hughes and Connell, 1987; Szmant, 1991; Soong, 1993). In corals, survival, growth and fecundity are strongly size-dependent (Hughes and Jackson, 1980, 1985) and consequently the size structure of coral populations is an important driver of their dynamics (Bak and Meesters, 1998). Assessing size structures of coral populations can provide information about important ecological processes such as coral survivorship, recruitment, fecundity, mortality and community responses to various stress events such as mass coral bleaching

or *Acanthaster planci* outbreaks (Meesters et al., 2001; McClanahan et al., 2008). Records of coral size class distributions and frequencies can provide an in-depth understanding of trends in the condition and resilience of reef ecosystems, rather than the data offered from more simplified metrics such as coral cover or diversity (Bak and Meesters, 1998; de Barros and Pires, 2006; Meesters et al., 2001).

Indeed, numerous studies have already started to take coral size class distribution into account, for example when surveying reefs subjected to variable stressors such as in areas with high human population densities, increased urbanization and higher fishing pressures (Meesters et al., 2001; Vermeij and Bak, 2003; Adjeroud et al., 2007; McClanahan et al., 2008). For example, Meesters et al. (2001) showed that reefs closer to heavily urbanized coastal areas contained relatively fewer colonies in smaller size classes but more colonies in larger size classes. Coral reefs in such areas are often classed as degraded due to the higher levels of pollution and sediment loads coupled with an increase in fishing pressure. In

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contrast to Meesters et al. (2001), McClanahan et al. (2008) illustrated that in areas where fishing pressure increased, a reduction in coral size across all genera was observed. In this instance, the findings were linked with increased rates of partial mortality or through the removal of functionally important herbivorous fish that are a key resource in regulating coral-algal competition and in maintaining resilience of coral populations against disturbances and mortality events (McClanahan et al., 2008).

Both studies illustrate the role of herbivorous fish in influencing coral population demographics. Herbivorous fish have been shown to be beneficial to coral populations as they provide key ecosystem functions that influence benthic communities (Folke et al., 2004), principally by reducing levels of macroalgae and promoting benthic organisms such as turf algae and crustose coralline algae that in turn provide suitable substrate for the settlement and growth of coral larvae (Harrington et al., 2004). Loss of herbivorous fish can result in an increase in macroalgae, which can out-compete corals for space and light and lead to reduced chances of survival for coral recruits (Birrell et al., 2005; Mumby et al., 2007; Hughes et al., 2007). The literature, highlighted above, illustrates that we still do not fully understand the true impacts fishing activity can have on coral size class frequencies and coral species with varying life history strategies.

Here we aimed to assess how the size-frequency distributions of coral genera varied between reefs under different fishing pressures in two contrasting locations in the Indian Ocean. We surveyed reef sites in East Africa (Kenya and Tanzania) and compared them to reef sites in Maldives (North Ari Atoll). Together they represent distinct biogeographical regions (Obura, 2012), with varying levels of anthropogenic pressures (McClanahan, 2011). East African fringing reef systems are subject to a high-pressure subsistence fishery, with moderately-sized and well-enforced non-fished Marine Protected Areas (McClanahan, 2011). Such fishing practices are routinely carried out using basket traps, hand lines, spear guns, beach seines and gill nets. Commonly targeted species include Lethrinidae, Scaridae and Siganidae. In contrast, Maldivian atoll reef systems are subject to lighter reef fishing and bait fishing pressure on community reefs with smaller de facto no-take areas in the reefs surrounding tourist resort islands (Jaleel, 2013; Pisapia et al., 2017a,b; Moritz et al., 2017). 'Bait fishing' is defined as the targeting of species of reef fish that are captured and kept alive to be used as live bait for pelagic tuna fishing and is carried out using nets to capture schools of bait fish species, for example *Spratelloides*, *Caesonidae*, *Pomacentridae* and *Apogonidae* (Adam, 2006). In contrast, reef fishing (targeting *Serranidae*, *Carangidae* and *Lutjanidae* among others) in the Maldives is generally carried out using handline. Differing fishing regimes in the Maldives and East Africa could potentially affect coral demographics in both regions.

Under 'healthy' reef conditions, it would be expected that coral reefs harbour a population structure consisting of many small colonies and fewer large colonies (Bak and Meesters, 1998). In this study, we hypothesized that coral size class frequencies and distributions would vary between the different fishing regimes studied i.e. 'fished' and 'non-fished' areas. More specifically, it was expected that lower densities of larger coral size classes would be found in fished areas, especially in East Africa where fishing pressure is generally higher, compared to non-fished areas where larger coral size classes were expected to be more frequent (Adam, 2006; McClanahan, 2011; Samoilys et al., 2017). Intraspecific and interspecific variation in size-structure responses to fishing pressure were also expected, with some taxa being more susceptible to changes in coral size class frequencies and distributions than others, especially when taking coral life history strategies into account. Corals can be classified as having 'competitive' life-history strategies when they grow quickly, shade out other genera and can dominate communities in ideal non-

stressed environments, for example tabular and branching *Acropora* coral species (Darling et al., 2012). However, these corals are also usually highly sensitive to breakage, thermal stress and other local stressors on the reef. Corals classified as 'stress tolerant' include species that have massive domed morphologies, large corallites, high fecundity, slow growth rates and are usually broadcast spawners - all advantageous traits for conserving energy and surviving in more stressed environments (Darling et al., 2012). Corals classified as 'weedy' tend to be small, have brooding reproductive strategies, fast growth rates and high population turnover. Corals classified as 'generalists' exhibit traits of all the previous three life-history strategies (Darling et al., 2012). In this study, it was expected that coral genera categorized as 'stress tolerant' would exhibit a higher frequency of colonies, of larger sizes, in higher fishing pressure reefs when compared to non-fished reefs. In contrast, coral genera categorized as being 'competitive' would exhibit the opposite trend i.e. a lower frequency of colonies of larger sizes in areas with higher fishing pressure.

2. Materials and methods

2.1. Study sites

The study was conducted in two distinct biogeographic locations: North Ari Atoll, in the central Maldivian archipelago, and along the East African coast from Mombasa in Kenya, to Pemba in Tanzania (Fig. 1). Overall, 31 sites were surveyed (Table 1). In 2009, 10 sites in East Africa were selected and surveyed. These included four in Marine Protected Areas (MPAs), that are closed to fishing and heavily enforced, three sites open to fishing and therefore potentially subjected to high levels of subsistence fishing, and three sites open to fishing but with gear restrictions in place (classified as marine reserves). In 2015, 21 sites in North Ari Atoll were also surveyed. These included nine in resort islands, which were classed as 'de facto' marine protected areas as they are effectively 'closed' from fishing activities, and 12 sites associated with community islands, where the reefs are open to light subsistence reef fishing pressure and the practice of bait fishing.

2.2. Survey methodology

At each reef site, three replicate 10 m × 1 m belt transects were laid lengthwise along the reef slope at 10 m depth, with a minimum of 3 m separating each transect. All living corals within the belt transect were identified to genus level and for each colony the longest diameter was recorded. A total of 6178 coral colonies of 11 genera were counted in the Maldives and a total of 2693 coral colonies of the same 11 genera were counted in East Africa. These 11 genera were chosen as they were the most abundant across the sites in both regions. The colonies were classified in predetermined size classes: 0–5 cm, 6–10 cm, 11–20 cm, 21–40 cm and >40 cm following Obura and Grimsditch (2009). The corals sampled here have contrasting morphologies and life history strategies, and therefore were classed in different categories following Darling et al. (2012): *Acropora* sp. was categorized as 'competitive'; *Porites* massive sp., *Favia* sp., *Favites* sp., *Galaxea* sp., *Goniastrea* sp., and *Platygyra* sp. as 'stress tolerant'; and *Echinopora* sp. and *Pavona* sp. as 'generalist'. There are, however, some genera which do not easily fit into these three main categories and as such were given proportional values to account for the different life history strategies they exhibit. This is calculated from the number of species that is 'typical' for any given site; see Keith et al. (2013). Thus, *Pocillopora* was classed as being 25% 'weedy' and 75% 'generalist' and *Montipora* was classed as being 25% 'competitive', 58% 'generalist' and 17% 'stress tolerant'. For these two genera any total frequencies

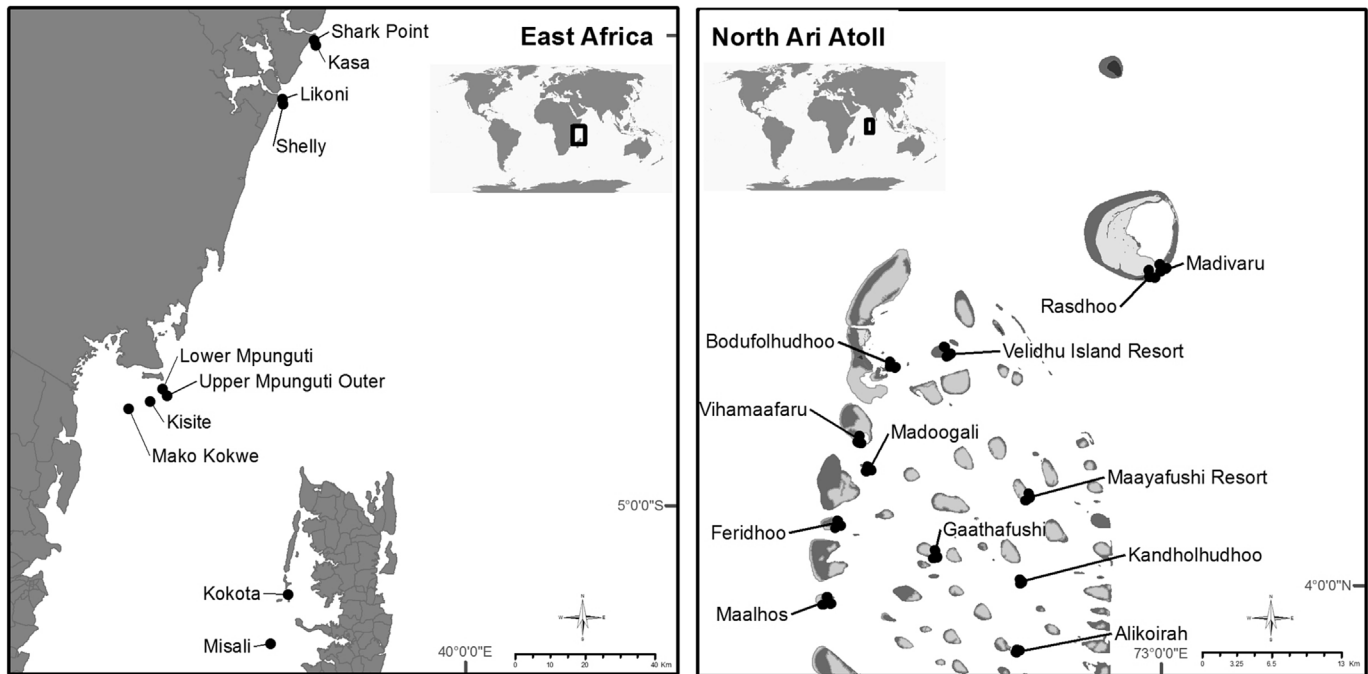


Fig. 1. Map of the study sites in North Ari Atoll, in the central Maldivian archipelago, and along the East African coast from Mombasa in Kenya, to Pemba in Tanzania.

were split up as stated, which allows for a more realistic frequency for each of the representative life history strategies highlighted (Keith et al., 2013).

2.3. Data analysis

Since for each site we had data for various coral genera or life history strategies, and for up to five size classes per genus, site was considered a random factor to account for multiple data points per site. Preliminary exploration of the data (comparing the histograms of the original data set with a simulated data set from various distributions with the same parameters) suggested that coral numbers followed a negative binomial distribution that was not further zero inflated. Therefore, a generalized linear mixed effects model was used with a negative binomial distributed error structure, using the package glmmADMB vs. 0.8.3.2 in R vs. 3.2.2 (Fournier et al., 2012; R Core Team, 2015; Skaug et al., 2015). The full

model included the four-way interaction term of the fixed independent categorical variables 'area' (East Africa or Maldives), 'fishing' (present or absent), 'life history strategy' (three types: competitive, generalist, and stress tolerant), and 'coral size' (five size classes: 0–5 cm, 6–10 cm, 11–20 cm, 21–40 cm, and >40 cm). 'Study site', nested within 'life history strategy', was treated as a random factor, and 'counts of corals' was treated as a dependent variable. For model simplification, and to compare between, for example, zero-inflated and non-inflated models, the Akaike Information Criterion (AIC) was used (Zuur et al., 2009). Additionally, the overall significance value for the three way interactions was determined by comparing the model including all three-way interactions against models that removed in turn each of these interactions using a log-likelihood ratio test. Finally, a generalized linear model was used for each genus separately, allowing determination of whether or not 'fishing' had a significant effect on the frequency of different size classes of specific coral genera.

Table 1
Management and fishing regimes of 31 surveyed sites in East Africa and the Maldives.

Site	Region	Management	Fished?	Gear restrictions?
Shark Point	East Africa	Marine Protected Area	No	Yes
Kasa	East Africa	Marine Protected Area	No	Yes
Likoni	East Africa	Open	Yes	No
Shelly	East Africa	Open	Yes	No
Lower Mpunguti	East Africa	Marine Reserve	Yes	Yes
Upper Mpunguti Outer	East Africa	Marine Reserve	Yes	Yes
Kisite	East Africa	Marine Protected Area	No	Yes
Mako Kokwe	East Africa	Marine Reserve	Yes	Yes
Kokota	East Africa	Open	Yes	No
Misali	East Africa	Marine Protected Area	No	Yes
Rasdhoo (3 sites)	Maldives	Open	Yes	No
Velidhu (3 sites)	Maldives	Resort	No	Yes
Bodufolhudhoo (3 sites)	Maldives	Open	Yes	No
Feridhoo (3 sites)	Maldives	Open	Yes	No
Maalhos (3 sites)	Maldives	Open	Yes	No
Maayafushi (3 sites)	Maldives	Resort	No	Yes
Kandholhudhoo (3 sites)	Maldives	Resort	No	Yes

3. Results

3.1. Life history strategy responses to fished vs non-fished sites

When assessing coral life history strategies and response under different fishing pressures, the minimal adequate model (with the lowest AIC of 4998.6) included all three-way interactions but not the four-way interaction (see summary Table 2). Removing the interaction 'area:life history strategy:size class' resulted in a significantly worse model (log-likelihood ratio test: deviance = 33.5, $p < 0.001$), as was the case when removing 'area:fishing:size class' (deviance = 11.2, $p = 0.024$), and 'area:fishing:life history strategy' (deviance = 15.1, $p = 0.002$). This indicates that the reaction to fished and non-fished sites did not only differ between different size classes and life history strategies, but also between East Africa and the Maldives. Corals which were classified as having a 'generalist' life history strategy were generally more abundant in East Africa compared to the Maldives, especially in fished conditions, except for in the case of 0–5 cm sized corals under non-fished conditions (Fig. 2a–b). 'Weedy' corals were more abundant in smaller size categories (0–5 cm and 6–10 cm) in East Africa compared to Maldives, but otherwise showed similar trends with overall low numbers (Fig. 2c–d). Corals classified as 'competitive' showed a higher abundance in the Maldives compared to those sites in East Africa – a pattern which was found in nearly all size categories. 'Competitive' corals were also generally more abundant in non-fished sites, especially in the 0–5 cm category in the Maldives and in corals larger than 20 cm in both regions (Fig. 2e–f). 'Stress tolerant' corals were more abundant in fished compared to non-fished sites, across most size classes and in both regions, except for the size category of 0–5 cm sized corals which were more abundant in non-fished sites in East Africa (Fig. 2g–h).

3.2. Genera-specific responses to fished vs non-fished sites

Some genera such as *Goniastrea*, *Pavona*, and *Pocillopora* follow the predicted pattern of highest frequency for smallest size classes, and lowest for largest, while others show more variable patterns (Figs. 3 and 4). When assessing the individual genera separately, distinct interactions can be observed regarding fishing pressure, potentially highlighting vulnerability of some genera to this stress (Figs. 3 and 4). For example, more *Acropora* colonies were found associated with reefs with less fishing pressure. Furthermore, there was also a notable decrease in colony numbers for the larger size classes in reefs under fishing influence compared to those non-fished (Figs. 3 and 4). In contrast, some of the more stress tolerant genera showed a pattern whereby more corals of all size classes were associated with fished reefs than non-fished reefs (Fig. 3). These included *Favia* and *Favites*, for example (Fig. 4). The majority, however, showed no effect of fishing, in particular *Echinopora* and *Galaxea*. While the remaining genera showed little effect of fishing pressure, some caveats were associated with certain genera: *Goniastrea* and *Montipora*, for example, showed somewhat lower numbers under non-fished areas. For *Pocillopora* a trend was observed that under fishing pressure there were more small corals than in non-fished reefs, whereas for other size classes there was less difference between the two conditions (Figs. 3 and 4).

4. Discussion

The results highlight complex interactions associated with coral size class data and fishing pressure over two distinct geographical regions. While some corals such as *Echinopora* and *Galaxea* did not seem to be affected by fishing pressure, others showed a noticeable trend. Analysing the data in two different ways (via general

variation and life history strategy) highlighted certain contrasting trends and some similarities. Here we argue that there will likely be some genera which could be classed as 'winners' in the face of certain stressors like fishing pressure, whilst others are more likely to be classed as 'losers'. It is now widely accepted that anthropogenic impacts will, and indeed already are having, a major effect on the composition of coral assemblages by disturbing the critical ecological processes which occur on reefs. However, it should be noted that in this study we have only measured the impact of fishing practices on coral age-size class, and other anthropogenic impacts such as water quality, for example, were not accounted for. That said, the available literature shows that both these regions have relatively good water quality in the reef sites sampled; for instance, in the Maldivian sites water quality was consistently good regardless of management regime (Pisapia et al., 2017a,b). However, it is difficult to compare the two geographic regions from available data sets (Mwangi et al., 2001; Pisapia et al., 2017a,b) and further research should be conducted with water quality measured as a factor. Regardless, some trends are apparent. For example, the genus *Acropora* was more abundant in nearly all colony size classes in areas that were non-fished compared to those that were fished both in East Africa and the Maldives. This is no surprise, as *Acropora* corals have often been shown to be highly susceptible to a range of stressors including rises in sea surface temperature and coral bleaching (Loya et al., 2001; McClanahan et al., 2004; Obura, 2001), mechanical damage (Riegl and Velimirov, 1991), and algal competition (Birrell et al., 2005; Birrell et al., 2008a; 2008b; Swierts and Vermeij, 2016), particularly as juveniles. This latter stress (increased competition from macroalgae) is one potential driver of the trends observed here as reefs that have reduced fishing pressures have been shown to have higher biomass of herbivorous fish in both locations (McClanahan and Arthur, 2001; Muthiga et al., 2003; McClanahan et al., 2007; Munga et al., 2012; Pisapia et al., 2017a,b). Fishing can also have a more direct effect on the success of corals by causing trophic changes in coral predators and grazers; and this is thought to be particularly the case for 'competitive' genera such as *Acropora* and even more so for the recruits and juveniles of these species (Dulvy et al., 2004; Mumby et al., 2007; O'Leary et al., 2012). For example, in East Africa overfishing has caused a shift from fish to sea urchins as the main grazers on many reefs, and sea urchins reduce the survival changes of coral recruits, again, appearing to affect *Acropora* sp. disproportionately when compared to other genera (O'Leary and McClanahan, 2010; O'Leary et al., 2012; Darling et al., 2013). Furthermore, direct physical impact on corals caused by fishing gear can also have a negative impact on corals, and in particular *Acropora* species (Marshall, 2000; Cros and McClanahan, 2003; Mangi and Roberts, 2006).

In contrast to Acroporids, coral genera which were classified as being more stress tolerant, such as *Favia* and *Favites*, showed a higher abundance of colonies in fished coral reefs compared to non-fished reefs in both East Africa and Maldives and across nearly all size classes. Corals from these two genera are generally encrusting or massive, and have been shown to be more resistant to the same stressors noted above (Loya et al., 2001; Obura, 2001; Swierts and Vermeij, 2016). Members of these genera may therefore take advantage of the open substrate left by the reduction in number of Acroporids, for example, and their life history strategies including massive domed morphologies, larger corallites, higher fecundity, slower growth rates and broadcast spawning means they are more suited to these 'stressed' environmental conditions (Darling et al., 2012). Reefs where such shifts in coral demographics have already occurred may offer us a glimpse into the future, regarding the shape and structure of reefs across the Indian Ocean. Fished sites also had a significantly higher abundance of juvenile *Pocillopora* coral colonies, smaller than 5 cm in diameter. *Pocillopora*

Table 2
 Summary statistics for generalized linear mixed model using negative binomial distribution for all three-way interaction terms of the variables Area (A: two levels: East Africa, Maldives), Fishing (F: two levels: Fishing, Non-fished), Life history group (LH: three levels: Competitive, Generalist, Stress tolerant), and Size Class (SC: five levels: 0–5, 6–10, 11–20, 21–40, >40 cm). AIC = 4998.6 (AICs of other models going up to 5014.9 for the null model and 5788.0 for the model including only the intercept). It should be noted that significance levels of all factors and combinations nested within the significant higher-level interactions are not meaningful. Significance levels: < 0.1; * < 0.5, ** < 0.01; *** < 0.001.

Term	Estimate	SE	Z-value	p-value	Significance
(Intercept)	4.53	0.33	13.7	<0.001	***
Single factors					
A = Maldives	0.38	0.38	1.0	0.31	
F=Non-fished	0.48	0.43	1.1	0.27	
LH = Generalist	0.16	0.38	1.4	0.68	
LH = Stress tolerant	0.52	0.38	-1.4	0.17	
LH = Weedy	-1.14	0.39	-2.9	0.003	**
SC = 6-10	-0.59	0.29	-2.0	0.044	*
SC = 11-20	-1.15	0.30	-3.9	<0.001	***
SC = 20-40	-2.08	0.31	-6.7	<0.001	***
SC=>40	-3.23	0.35	-9.4	<0.001	***
Two-way interactions					
A = Maldives:F=Non-fished	0.74	0.50	1.5	0.14	
A = Maldives:LH = Generalist	0.21	0.43	1.2	0.23	
A = Maldives:LH = Stress tolerant	0.51	0.43	1.2	0.23	
A = Maldives:LH = Weedy	-1.06	0.44	-2.4	0.016	*
A = Maldives:SC = 6-10	-0.60	0.32	-1.9	0.062	
A = Maldives:SC = 11-20	0.58	0.33	1.8	0.077	
A = Maldives:SC = 20-40	0.80	0.34	2.4	0.017	*
A = Maldives:SC=>40	0.23	0.38	0.6	0.55	
F=Non-fished:LH = Generalist	0.15	0.47	0.3	0.76	
F=Non-fished:LH = Stress tolerant	1.11	0.47	2.4	0.018	*
F=Non-fished:LH = Weedy	0.05	0.49	-0.1	0.91	
F=Non-fished:SC = 6-10	0.42	0.34	1.3	0.21	
F=Non-fished:SC = 11-20	-0.08	0.33	-0.2	0.82	
F=Non-fished:SC = 20-40	1.07	0.35	3.1	0.002	**
F=Non-fished:SC=>40	1.61	0.39	4.1	<0.001	***
LH = Generalist:SC = 6-10	0.89	0.38	2.3	0.020	*
LH = Stress tolerant:SC = 6-10	0.44	0.39	1.1	0.26	
LH = Weedy:SC = 6-10	0.34	0.41	0.8	0.40	
LH = Generalist:SC = 11-20	0.53	0.38	1.4	0.17	
LH = Stress tolerant:SC = 11-20	0.85	0.39	2.2	0.029	*
LH = Weedy:SC = 11-20	0.37	0.41	0.9	0.36	
LH = Generalist:SC = 20-40	0.60	0.40	1.5	0.13	
LH = Stress tolerant:SC = 20-40	0.86	0.40	2.2	0.031	*
LH = Weedy:SC = 20-40	-0.25	0.45	-0.6	0.58	
LH = Generalist:SC=>40	0.26	0.44	0.6	0.56	
LH = Stress tolerant:SC=>40	0.83	0.45	1.9	0.063	
LH = Weedy:SC=>40	-2.77	1.03	-2.7	0.007	**
Three-way interactions					
A = Maldives:F=Non-fished:LH = Generalist	-0.41	0.49	-0.8	0.41	
A = Maldives:F=Non-fished:LH = Stress tolerant	-1.91	0.50	-3.8	<0.001	***
A = Maldives:F=Non-fished:LH = Weedy	-0.60	0.53	-1.1	0.25	
A = Maldives:F=Non-fished:SC = 6-10	-0.18	0.30	-0.6	0.55	
A = Maldives:F=Non-fished:SC = 11-20	0.27	0.30	0.9	0.37	
A = Maldives:F=Non-fished:SC = 20-40	-0.56	0.31	-1.82	0.069	
A = Maldives:F=Non-fished:SC=>40	-0.75	0.37	-2.0	0.041	*
A = Maldives:LH = Generalist:SC = 6-10	-0.32	0.40	-0.8	0.43	
A = Maldives:LH = Stress tolerant:SC = 6-10	0.24	0.41	0.6	0.56	
A = Maldives:LH = Weedy:SC = 6-10	-0.62	0.44	-1.4	0.17	
A = Maldives:LH = Generalist:SC = 11-20	-1.36	0.41	-3.3	<0.001	***
A = Maldives:LH = Stress tolerant:SC = 11-20	-0.46	0.41	-1.1	0.26	
A = Maldives:LH = Weedy:SC = 11-20	-1.05	0.44	-2.4	0.018	*
A = Maldives:LH = Generalist:SC = 20-40	-1.45	0.42	-3.5	<0.001	***
A = Maldives:LH = Stress tolerant:SC = 20-40	-0.66	0.42	-1.6	0.12	
A = Maldives:LH = Weedy:SC = 20-40	-0.23	0.42	-0.5	0.62	
A = Maldives:LH = Generalist:SC=>40	-0.84	0.46	-1.8	0.070	
A = Maldives:LH = Stress tolerant:SC=>40	-0.47	0.47	-1.0	0.31	
A = Maldives:LH = Weedy:SC=>40	1.46	0.96	1.5	0.13	
F=Non-fished:LH = Generalist:SC = 6-10	-1.1	0.38	-2.9	0.004	**
F=Non-fished:LH = Stress tolerant:SC = 6-10	-0.48	0.38	-1.3	0.21	
F=Non-fished:LH = Weedy:SC = 6-10	-0.83	0.44	-1.9	0.059	
F=Non-fished:LH = Generalist:SC = 11-20	-0.32	0.38	-0.8	0.40	
F=Non-fished:LH = Stress tolerant:SC = 11-20	-0.34	0.38	-0.9	0.37	
F=Non-fished:LH = Weedy:SC = 11-20	-0.15	0.43	-0.4	0.72	
F=Non-fished:LH = Generalist:SC = 20-40	-0.88	0.39	-2.2	0.025	*
F=Non-fished:LH = Stress tolerant:SC = 20-40	-0.92	0.39	-2.4	0.018	*
F=Non-fished:LH = Weedy:SC = 20-40	-0.08	0.45	-0.2	0.86	
F=Non-fished:LH = Generalist:SC=>40	-1.09	0.44	-2.5	0.012	*
F=Non-fished:LH = Stress tolerant:SC=>40	-1.93	0.44	-4.4	<0.001	***
F=Non-fished:LH = Stress tolerant:SC=>40	0.09	0.85	0.1	0.92	

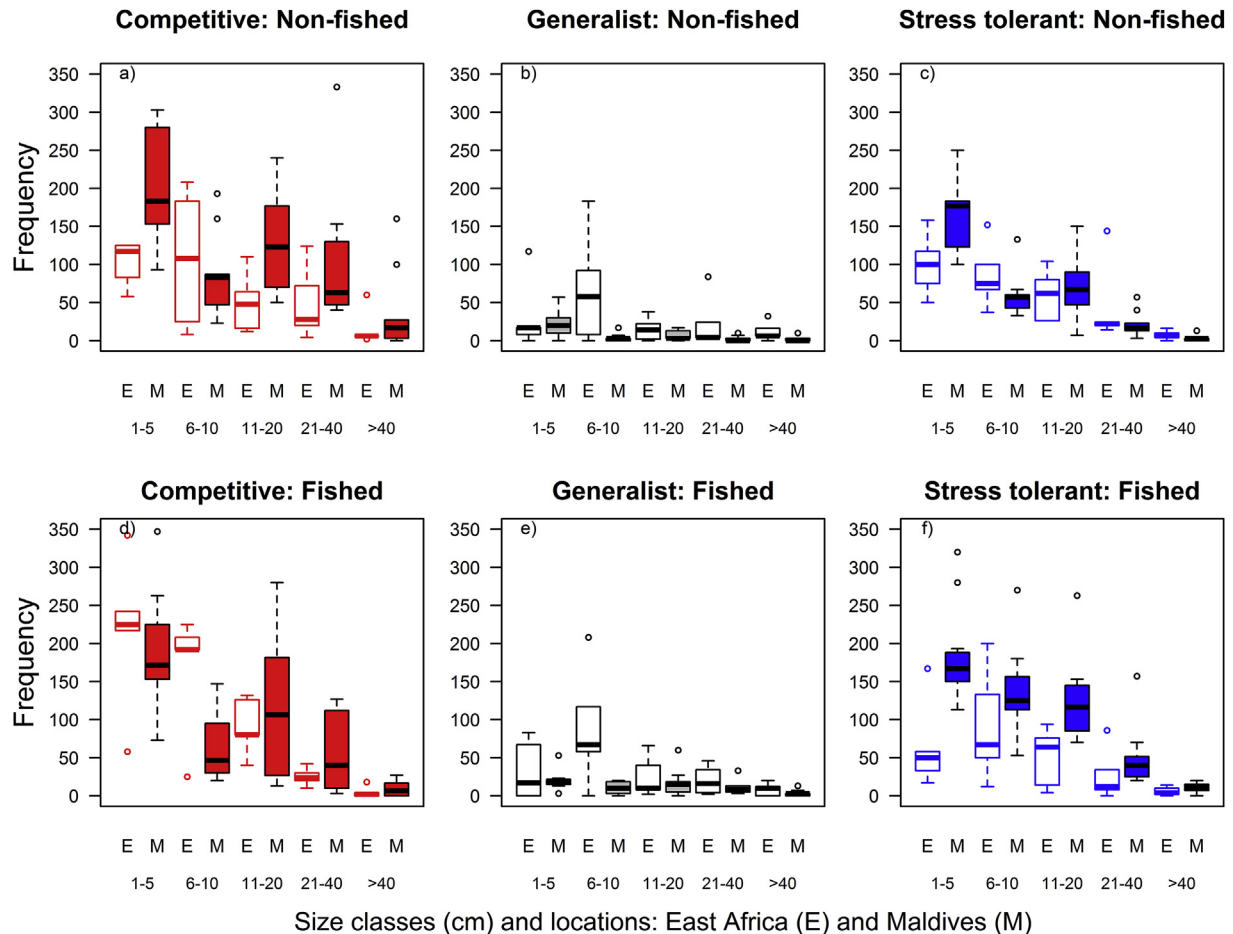


Fig. 2. Frequencies of different size classes of four natural history classes in non-fished (left panels) and fished areas (right panels) for generalist (grey; a, b), weedy (green; c, d), competitive (red; e, f) and stress tolerant (blue; g, h) corals in East Africa (E; open boxes) and the Maldives (M; filled boxes). Note: In order to allow using the same scale for all panels a few outliers with frequencies >300 were classed as 300 to create Fig. 2 e and f. A full figure including these outliers can be found in the [Electronic Appendix](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species are known to have high reproductive capacity, and can reproduce sexually by brooding and broadcast spawning (Ayre et al., 1997; Combosch and Vollmer, 2013; and Sier and Olive, 1994; Kruger and Schleyer, 1998; respectively), as well as asexually through fragmentation (Highsmith, 1982). *Pocillopora* species tend to be opportunistic, indeed some species are even classified as 'weedy' due to this trait, and therefore they tend to be the first corals to colonize newly available substrates, thus being common in frequently disturbed environments (Tomascik et al., 1996). Interestingly, other than those stated above, the majority of coral genera analysed did not show a significant preference for either fished or non-fished sites. Overall our findings are consistent with those reported in other studies spanning a wide range of different geographical locations and therefore these trends are likely to be seen on a global scale (McClanahan et al., 2000; Pratchett et al., 2011; Graham et al., 2014; McClanahan and Muthiga, 2014).

That said, it should be noted that the importance of location is also apparent in our results and therefore some level of caution should be taken in generalizing findings if a study only looks at one site or even one country. For example, reefs in the Maldives exhibited a significantly higher abundance in all size classes of corals that were classed as 'competitive', such as *Acropora*. This may be due to biogeographical variation, but it could also indicate that East African reefs are, or have been, subject to higher levels of stress and are less suitable environments for *Acropora* corals to grow and survive. Indeed, East African reefs are subject to more intense

artisanal fishing pressure than those of the Maldives archipelago (McClanahan, 2011; Samoilyis et al., 2017; Adam, 2006). For example, fishers in Kenyan lagoons use destructive gear such as beach seines, which impact the benthos. Average catch rates and species-richness have declined dramatically in Kenya since the 1980s (Samoilyis et al., 2017). Maldivian reefs in contrast have historically used 'less destructive' fishing gear such as nets for live bait fish, or hand line for reef fish and over-exploitation has, until recently, been reportedly less (Adam, 2006).

Another possible reason for the observed geographical variation could be the six-year gap between the surveys conducted in East Africa and the Maldives (2009–2015). Mortality events have been recorded throughout this time-period and prior to this (1998) both areas witnessed a dramatic loss of coral cover, which would have affected the corals in both locations. Although such global climatic events (driven by El Niño and climate change) likely affected the coral assemblages in both regions, when the corals were surveyed in the Maldives they had six more years to recover. Furthermore, recovery rates and coral survivorship in these regions may well have varied due to the observed thermal regimes in each location. The Maldives appears to be more thermally stable, whilst East Africa has been characterized as thermally more dynamic and variable (McClanahan et al., 2007).

Interestingly, one further observation of note is that coral colonies in the size class of 0–5 cm in East Africa appear to show a marked decline compared to what would have been expected. This

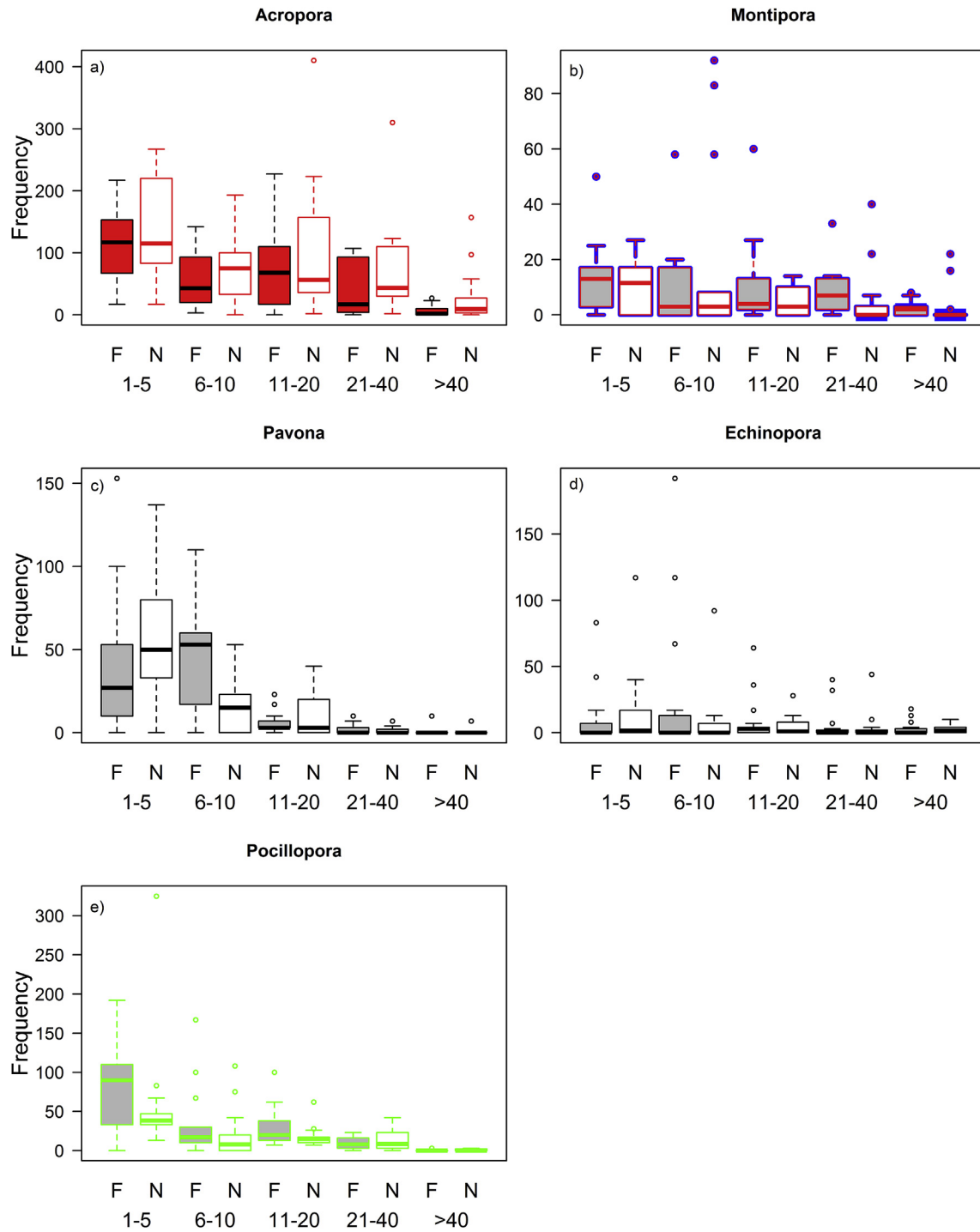


Fig. 3. Frequencies of different size classes under different fishing regimes for competitive coral genus *Acropora* (a), *Montipora* (b; partly competitive partly generalist, partly stress tolerant), generalist genera *Pavona* (c) and *Echinopora* (d), and *Pocillopora* (e; partly generalist, partly weedy).

may be indicative of a poor survival year or failure in recruitment in the past. Similarly, in the Maldives, *Acropora* colonies in the size class of 5–10 cm showed a marked decline to what we were originally expecting. This similarly indicates a potential poor survival year or failure in recruitment of *Acropora* corals. Assessing reef condition in this way can therefore provide us with better insights into coral population dynamics and highlight changes in community structure and threats to corals that would be missed if only simple metrics such as coral cover were measured. This result,

along with the three-way interactions reported, highlight the overall importance of assessing colony size in future studies and that simply assessing coral cover will likely miss important ecological function patterns.

In conclusion, we highlight complex interactions between coral genus, size class and fishing pressure over two distinct geographical areas that have been historically managed in different ways. Such data could be utilized in reef management strategies and reserve design. Continued monitoring in the same manner allows us to

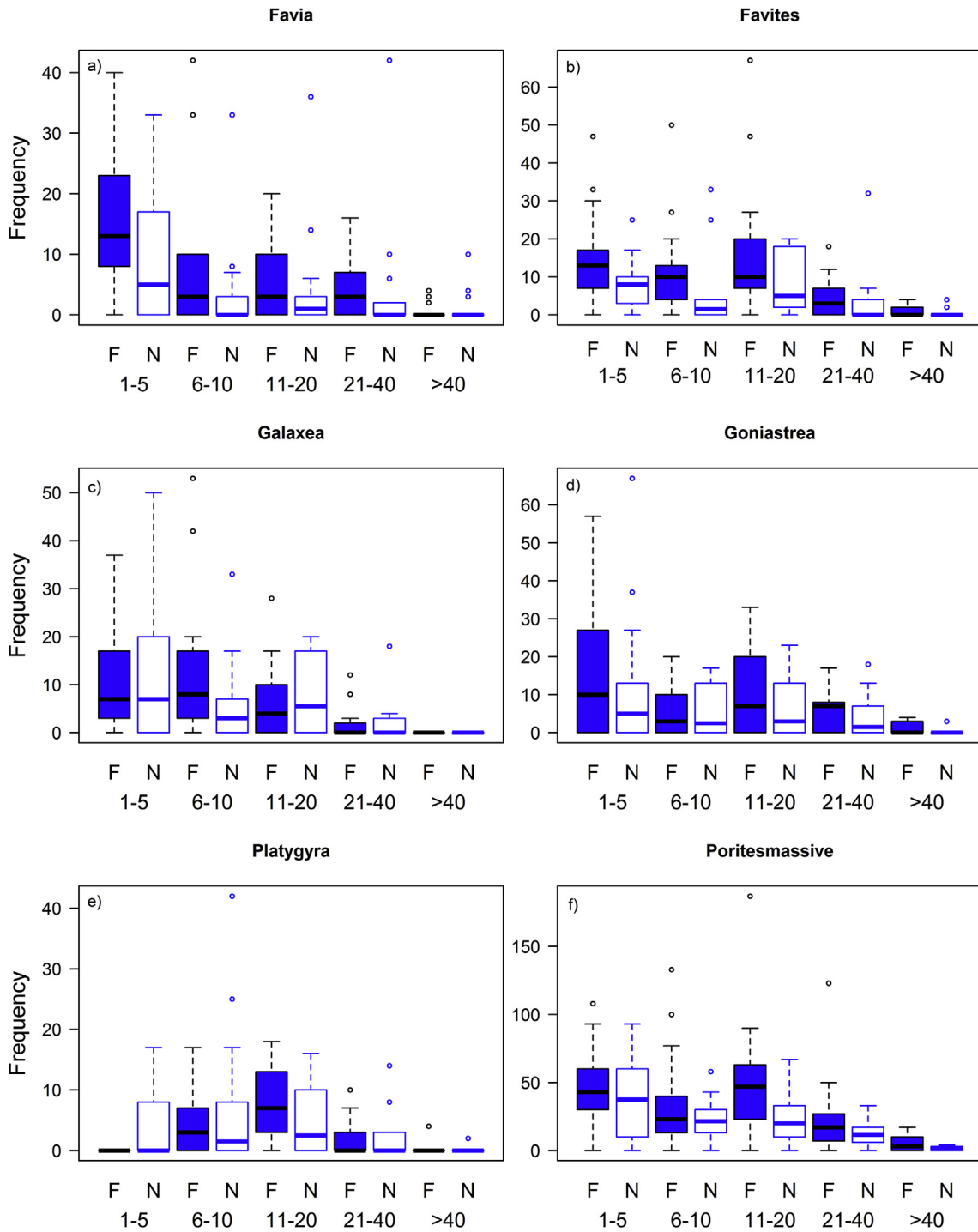


Fig. 4. Frequencies of different size classes under different fishing regimes for stress tolerant genera *Favia* (a) and *Favites* (b), *Galaxea* (c), *Goniastrea* (d), *Platygyra* (e), and *Poritesmassive* (f).

monitor changes in the community composition of coral reefs, with implications for understanding coral reef condition and resilience with more precision. Furthermore, studies such as this potentially highlight the structure and composition of what reefs may look like under future “business-as-usual” or further degradation scenarios with loss of major reef building corals such as those from the genus *Acropora* and an increased dominance of stress tolerant or generalist genera.

Acknowledgements

This work was supported and made possible by USAID, MacArthur Foundation, Project Regenerate, CORDIO East Africa, International Union for the Conservation of Nature, Kenya Wildlife Service, Maldives Marine Research Centre, Maldives Ministry of Fisheries and Agriculture, and the Zanzibar Marine Conservation Unit. Special thanks to Fathimath Nistharan of IUCN-Maldives for

providing GIS support and making the maps, to Dr Emily Darling of Wildlife Conservation Society for advice on coral life history strategies and analysis, and to the reviewers of the manuscript. The data are being used with permission from the Government of Maldives. The views expressed in the article are those of the authors and do not reflect the views of the Government of Maldives.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.marenvres.2017.09.017>.

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