Quantifying the biodiversity and biomass of mesopredatory reef fishes on Laamu Atoll

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Abstract

The ecological importance of mesopredators is increasingly recognized and has been demonstrated on coral reefs. However, they are particularly vulnerable to overexploitation by commercial and artisanal fisheries. The Maldivian grouper fishery is already overfished but it is not known how mesopredatory reef fishes, including groupers, are faring outside of the central atolls. This study provides baseline population data for grouper, snapper and sweetlips populations in Laamu Atoll and explores the pressures they face. Underwater Visual Census surveys conducted by scuba divers revealed a high biodiversity of groupers, snappers and sweetlips on Laamu's reefs, including five nearly threatened or vulnerable grouper species. Key factors have been identified which influence mesopredator abundance (the type of reef, depth and current strength) but high levels of unexplained variability within and between sites suggests that additional variables must be included in future research. Hithadhoo Corner was identified as a particularly ecologically significant site, due to the high biomass of mesopredatory fish present on coral bommies. Interviews with local fishermen suggest that several reef fish species are already in decline, supporting the need for improved fisheries management. As a result of these findings, I call for improved monitoring of commercially targeted species and the ecological factors that influence them, and recommend that more robust fisheries management be enacted, including designation of a protected area at Hithadhoo Corner.

Introduction

Made up of 1,190 coral islands (McClanahan & Muthiga 2014), the Maldives relies on coral reefs for a wide range of goods and services (Moberg & Folke 1999). The fisheries and tourism industries deliver 89.2% of the Maldives' GDP (Emerton et al. 2009) but there is often conflict between these pillars of the Maldivian economy (Sattar & Adam 2005). Pressure on marine resources is ever increasing and has changed considerably in recent decades.

From the 1970s onwards, the Maldivian economy has undergone significant change, particularly regarding tourism and fisheries (Shakeel & Ahmed 1997). The population has almost tripled since 1970, from 114,469 to 341,256 in 2014 (Table 3.1, NBS 2015). Within that timeframe the size and nature of the country's fisheries and tourism have changed dramatically. The first tourist resort was opened in 1972 (Sathiendrakumar & Tisdell 1989) and the number of tourists arriving in the Maldives soared from 42,007 in 1980 to 1,125,202 in 2013 (NBS 2015, Sathiendrakumar & Tisdell 1989). Although the dominant fishery is tuna, a commercial reef fishery has developed in recent decades due to demand from tourists (Shakeel & Ahmed 1997) and the development of a grouper export market in the early 1990s (Sattar et al. 2011).

These inshore fisheries were initiated in the central atolls but have now spread farther south to more remote atolls (Sattar et al. 2011). One such atoll is Laamu, which has avoided the high intensity pressure from tourism and fisheries documented in the central atolls until relatively recently (Scheyvens

2011; Shakeel & Ahmed 1997). This provides a crucial opportunity to determine the state of fish populations there, before further exploitation takes place. Located in the southern third of the Maldives Archipelago, Laamu Atoll is the 5th most populous atoll with the 5th largest industrial area, despite only being the 11th largest atoll and having the 7th largest reef area (Table 1.6, NBS 2015). Although it did not have a burgeoning commercial reef fishery as early as the central atolls, it is now a prominent fishing site and a grouper cage was constructed there in 2003 (Sattar et al. 2011; Sattar & Adam 2005). It is clear that overfishing now affects the Maldivian grouper fishery (Sattar et al. 2011), but little research has addressed fisheries in southern atolls.

Laamu atoll is currently home to one resort, Six Senses Laamu, which is incredibly popular and maintains a pro-sustainability ethos (Six Senses, 2011). This approach involves reducing the resort's consumption and waste, selecting sustainable brands for purchased products, and encouraging environmental awareness and social responsibility in their operations (Six Senses, 2011). Despite these efforts, luxury tourism carries significant concerns regarding environmental, economic and socio-cultural sustainability (Scheyvens 2011). Furthermore, a much larger resort is currently under construction (F. Westraadt, 2015, pers. comm., 17 August) so pressure from tourism will undoubtedly increase in future years.

Although fisheries and tourism are intrinsically linked and essential to the atoll's economy, providing significant employment opportunities, there is clearly tension between them, regarding their uses of marine resources. Six

Senses relies on local fishermen to supply tuna and reef fishes (M. van Well, 2015, pers. comm., 6 Aug), but also uses the reefs for several non-consumptive activities that can conflict with fishing practices. These tensions are widespread in the Maldives and exist within and between the fishing and tourism industries (Shakeel & Ahmed 1997). For example, reef fishing is driven by demand from resorts (Shakeel & Ahmed 1997) but dive-tourists wish to see these species their natural habitat. Indeed, the influence that the size and abundance of grouper has on diver satisfaction has been shown to increase sites' non-extractive economic value (Rudd & Tupper 2010). In return, fishermen complain that divers are a disturbance to reef and bait fishing (Shakeel & Ahmed 1997). Furthermore, sport fishing tourists may have an underestimated influence on fish stocks due to the sector's lack of regulation compared to commercial fisheries (Cooke & Cowx 2004).

The Maldivian reef fishery targets a range of predatory fishes, including several mesopredators. The definition of what constitutes a mesopredator is fairly vague and context-dependent, with a particular species sometimes occupying the role of top predator, depending on which other species are present (Ritchie & Johnson 2009). Therefore, this study will focus on three commercially significant mesopredatory groups; Epinephelinae, Lutjanidae and the genus Plectorhinchus. Members of these groups that occupy higher trophic levels will be included due to their ecological and commercial significance, and the lack of a concrete definition for mesopredators.

Mesopredators play an important role within coral reef food webs and are involved in numerous trophic interactions (Boaden & Kingsford 2015). The mesopredator release hypothesis states that the abundance of these smaller predators will increase as their competition with apex predators is reduced (Soulé et al. 1988). This phenomenon has been illustrated in coral reef ecosystems (Ruppert et al. 2013) and, more commonly, amongst terrestrial mammals (Boaden & Kingsford 2015). However, other studies emphasise the complexity of trophic interactions on coral reefs and argue that factors other than top-down control may be more prominent in determining community assemblages (Rizzari et al. 2015). Multiple factors may inhibit top-down effects. For example, coral reefs generally exhibit high functional redundancy so when a predator is removed, another may occupy its role (Shurin et al. 2010). Variations in benthic habitat and structural complexity may also mediate predator-prey interactions (Jones 2004).

Removal of top predators can also release mesopredators from fear-driven behaviour responses, which may impact their prey species (Palacios et al. 2015). Although mesopredatory species have a strong influence on herbivorous fish, they can be responsible for other aspects of ecosystem functioning. The tendency of some mesopredatory species to form aggregations can cause nutrient hotspots which influence benthic community structure (Shantz & Ladd 2015). Mesopredators play an important role in coral reef ecosystems but monitoring of their populations, behaviour and trophic interactions is needed to improve our understanding of their true significance.

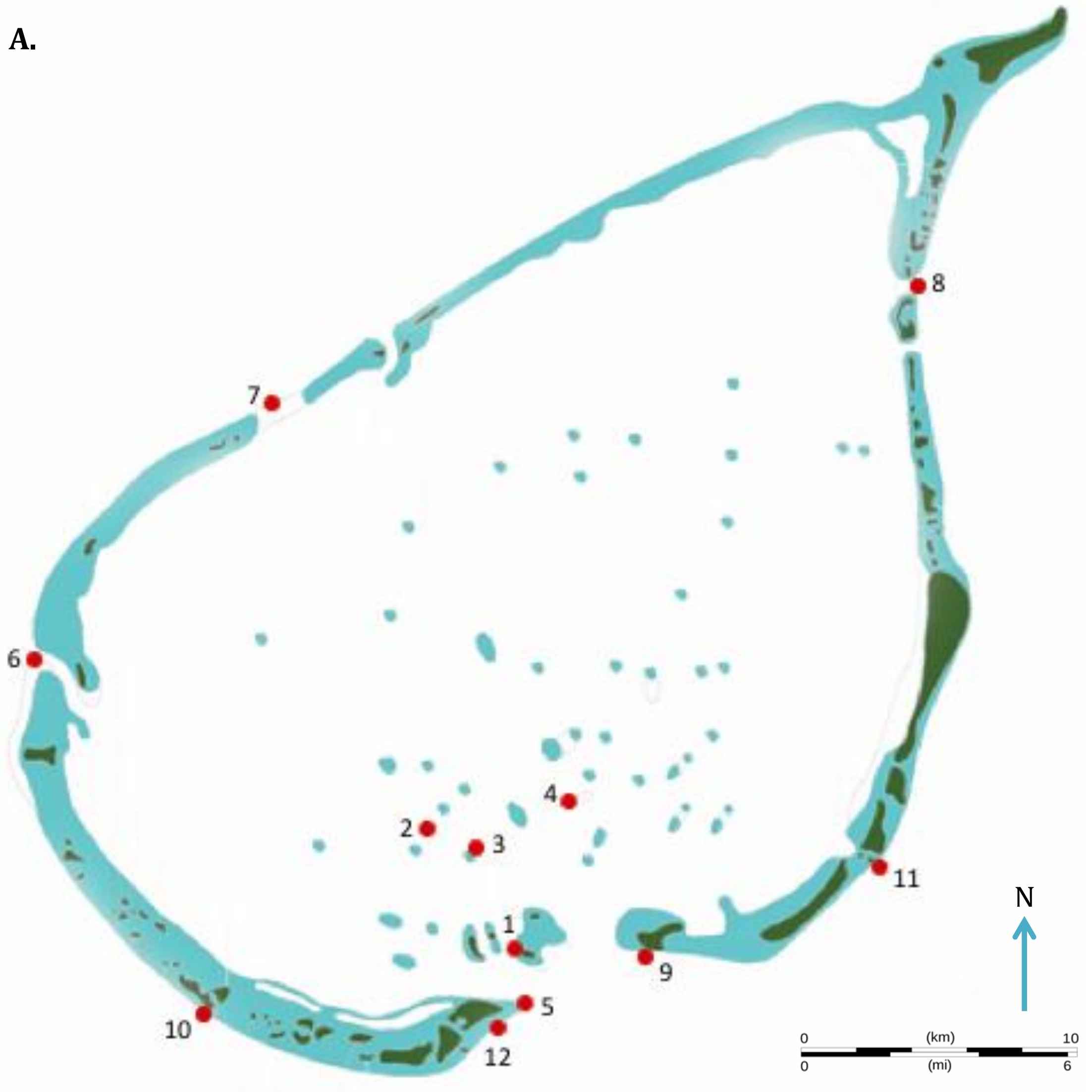
Using SCUBA-based fish survey methods, this study aims to quantify the biodiversity, density and biomass of mesopredatory reef fish on Laamu Atoll, focusing on groupers, snappers and sweetlips. Interviews will also be conducted to gather qualitative information regarding reef fishing practices on the atoll, how reef fishing has changed in recent decades and fishermen's perspectives on fisheries management. It is hoped that this will improve insight into the status of mesopredatory reef fish on Laamu Atoll and thus provide guidance for future management strategies.

Methodology

Study sites

Research was carried out on Laamu Atoll (2.0°N, 73.5°E), Maldives from 1st July-3rd September 2015. Twelve study sites, as shown in Figure 1, were selected to maximise geographic coverage of the atoll. Reefs on the outside of the atoll, channels and reefs within the atoll lagoon were selected. The sites' depth ranges, use levels by divers or fishers and exposure to possible future impacts were taken into account. The Six Senses resort Housereef was included due to the high level of pressure the resort exerts. Hitadhoo Corner was included because it is a manta ray cleaning station (Six Senses, 2013).

A.



B.

Site number	Site name	Site type	GPS coordinates
1	Six Senses Housereef	Inner reef	1°49'14"N 73°24'07"E
2	Haleema Haa	Inner reef	1°49'51"N 73°22'46"E
3	Laama Faru Haa	Inner reef	1°51'05"N 73°23'10"E
4	Gadhoo Kandu Haa	Inner reef	1°50'47"N 73°23'34"E
5	Hithadhoo Corner	Channel	1°48'02"N 73°24'38"E
6	Maava Kandu	Channel	1°54'37"N 73°14'28"E
7	Muniya Fushi Kandu	Channel	1°59'54"N 73°19'10"E
8	Fushi Kandu	Channel	2°02'38"N 73°32'12"E
9	Gadhoo Out	Outer reef	1°48'40"N 73°27'03"E
10	Fares Out	Outer reef	1°47'37"N 73°17'52"E
11	Boduguraa Out	Outer reef	1°50'24"N 73°31'10"E
12	Hithadhoo West	Outer reef	1°47'14"N 73°23'38"E

Figure 1: A) Laamu Atoll with the twelve study sites marked in red. B) Study site name, reef type and GPS coordinates.

Fish survey techniques

Prior to data collection, training exercises were undertaken to improve accuracy and reduce inter-observer bias when estimating fish length. Observers were required to estimate the lengths of several pieces of wood of differing sizes (16-100cm) underwater until their estimates were no longer significantly different ($p>0.05$) from the correct lengths or each other's estimates, according to a paired t-test (Bell et al. 1985). Several practice surveys were conducted with an observer who ensured that there were no methodological differences between the two researchers.

Underwater visual census (UVC), a widely used and effective survey method (Dickens et al. 2011), was used to assess the abundance and biomass of grouper, snapper and sweetlips. A roving diver survey (Hill & Wilkinson 2004) was used to gain additional information regarding species richness. Where conditions and reef topography allowed, study dives were carried out at 3-8m, 10-15m and 17-22m at each site. Each dive was conducted as shown in Figure 2, beginning where the divers reached the appropriate depth range. Divers conducted the UVC by laying individual 30m by 4m belt transects within the appropriate depth range whilst ensuring there was no overlap between the two transects. To reduce the effects of disturbance caused by laying the transect, a five minute acclimatization period was allowed before beginning observations (Irigoyen et al. 2013; Sano 2000). The surveyors swam at a constant speed (average speed was 5.13 minutes/transect) against the current, recording the presence of groupers, sweetlips and snappers. Fish were identified to species level and their length was estimated to the nearest centimeter. Environmental variables were recorded at each transect; current strength, weather conditions, depth, temperature and visibility.

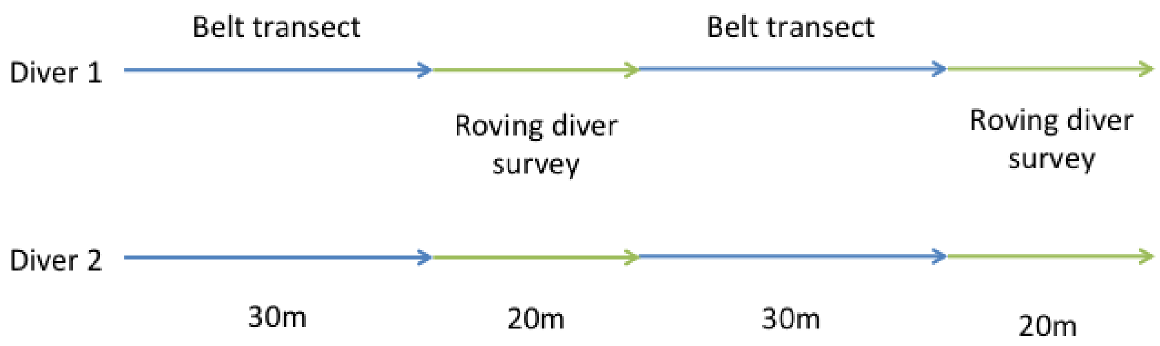


Figure 2: Survey dive protocol per dive. Belt transects are shown in blue and roving diver surveys in green.

After each belt transect, a roving diver survey was carried out to gain a better representation of site species richness and ensure independence between transect locations. The roving diver survey was conducted for a distance of 20 fin cycles. It was determined prior to data collection that 20 fin cycles was approximately equal to 20m under average conditions. This survey was carried out at the same depth as the UVC and divers recorded the presence of any species of grouper, snapper or sweetlips.

Four UVCs and four roving diver surveys were conducted per dive. Since 3-8m surveys were not possible at all sites, a total of 30 study dives were carried out, generating 116 transects. These were conducted between 9:00am and 4:30pm to ensure there was no shift between nocturnal and diurnal fishes (English et al. 1994).

The sites generally consisted of a fairly uniform reef wall with some sandy patches but Hithadhoo Corner had a unique topography with consisting of a sandy bottom with coral bommies (pers. obs.). Since transects were located at haphazardly determined points wherever the divers reached the correct depth range, the intitial transects at the site completely avoided these bommies, where the majority of fish life is located. To improve representation of the site's ecology, four additional transects were conducted that focused on the bommies. Although not included in the main analysis, these data provide valuable insight.

Interviews with fishermen

Semi-structured interviews were carried out with 6 local reef fishermen from 2 islands; 3 from Maavah and 3 from Maamendhoo. Since interviewees were selected based on their experience level, only a small sample size was available. Fishermen who began reef fishing following the increase in demand driven by the resort where not consulted because they may contribute to a shifting baseline effect (Pauly 1995) and would not provide the insight afforded by more experienced individuals. The two islands were selected because their reef fisheries have distinctive characteristics due to their differing proximities to the resort.

The interviews mainly consisted of open-ended questions and addressed several themes; the interviewee's experience levels, which species they target and the methods they use, how catches and techniques have changed, and their views on fisheries management and protection (see Appendix 1 for questionnaire). The interviews were conducted separately and only comments made by the interviewee were included in analysis (if somebody else was present). An interpreter translated between Dhivehi and English, and notes were kept throughout the interviews to ensure all details were included. It is acknowledged that the language barrier between the interviewer and interviewee, even when mediated by an interpreter, can be problematic (Edwards 1998). This, coupled with the small sample size, meant only broad thematic analysis was conducted.

Scuba intensity

The level of scuba diving at each site was determined by asking instructors (n=5) at the resort's dive centre how often they lead dives at each site, see Appendix 2. Sites were rated on a 5-point scale. This result was averaged and converted into an ordered factor, such that intensity 1 was the most dived site and intensity 9 is never dived (Rstudio statistical package 2013). Information regarding safari dive boats visiting the atoll was not available.

Data analysis

Biomass was estimated for each fish by using length-weight relationships ($W=aL^b$) to convert length estimates to estimates of body mass. Constants (a,b) for each species were obtained from Fishbase (Froese & Pauly 2000). Where no constants were available for a species, the most closely related species with a similar body size, shape and ecology was used.

Generalised Linear Models (GLMs) were used to examine the relationship between 6 predictor variables and total species richness, biomass and abundance, as described in Table 1 (Rstudio 2013). Temperature was not included because the variation appeared to result from poor calibration of the observers' dive computers. In some cases, data could not be transformed for appropriate use with Guassian or Poisson distributions. Therefore, several distributions were used. To avoid intercorrelation between predictor variables confounding the results (Crawley 2005), the variables were assessed to ensure that Pearson's coefficient remained below $r < 0.7$ (Dormann et al., 2013) and the Variance Inflation Factors were below 2 (Zuur et al., 2010). This process created full models for the response variables, as described in Table 2.

Table 1: The predictor (marked *) and response variables included in the GLM analysis and descriptions of each variable.

Variable	Description
Total species richness*	Number of grouper, snapper and sweetlips species
Total biomass*	Biomass of groupers, snappers and sweetlips (kg)
Total abundance*	Number of grouper, snapper and sweetlips individuals
Depth	Survey depth range e.g. 3-8m, 10-15m, 17-22m
Type	Reef type; inside the atoll, outside the atoll or in a channel
Scuba	Rating of pressure from scuba divers. The lower the number the higher the intensity (1-9)
Visibility	Distance observers could see (m)
Lunar	Whether or not the date according to the Islamic calendar was at a time of month that the fishermen identified as important for aggregations of groupers or snappers.
Current	Strength of current during transect

Table 2: Response and predictor variables for the three GLMs used in this study, and the distribution used in each model.

Response variable	Distribution used in GLM	Predictor variables
Total species richness	Poisson	Type, depth, scuba, visibility, lunar, current
Total abundance	Negative binomial	Type, depth, scuba, visibility, lunar, current
Total biomass	Binomial-gamma hurdle model	Type, depth, scuba, visibility, lunar, current

A log link function and Poisson error distribution was used to predict species richness. A negative binomial distribution was used to model abundance because of the numerous zeros and overdispersion. To improve model parsimony, Akaike's information criterion (AIC) was used to carry out backward and forward stepwise reduction. Analysis of deviance tests ensured that the reduced models were representative of the full model (Crawley 2005). Since appropriate handling of zeros in ecological data is so important (Martin et al. 2005), the Vuong non-nested test (Vuong 1989) was used to compare the negative binomial model's fit with the equivalent zero-inflated model. The AIC correction, which addresses concerns regarding the Vuong test's assumptions (Desmarais & Harden 2013), revealed that the negative binomial distribution was more suitable ($z= -4.89x10^3$, $p<0.001$).

Since biomass was skewed towards zeros and small values, a binomial-gamma hurdle model. Without further study, it is difficult to determine whether these zeros are true (Martin et al. 2005). Although zero-inflated models for continuous data exist (Syrjala 2000), little literature examines the strengths of different approaches. Given the distribution of the biomass data, the best option was to deperate the model into a presence-absence model and one which predicts each occurrence's value (Fletcher et al. 2005). This approach is usually involves a binomial or Poisson distribution (Martin et al. 2005), but a binomial-gamma hurdle model was selected because the data are continuous. The approach used for the previous models was employed to generate the minimum adequate model.. The False Discovery Rate (FDR) criterion (García 2004) was used to conduct endpoint adjustment. This revealed which variables (and conditions) have a significant influence on mesopredator abundance, richness and biomass.

Spatial heterogeneity at Hithadhoo Corner was examined by comparing the initial transects collected at 17-22m with those focussing on the coral bommies. Fisher's exact test was used to compare total abundance and a Welch Two Sample t-test (Crawley 2005) was used to compare the biomass.

Results

Fish surveys

Overall 29 species were observed, as described in Table 3. Table 4 shows the small proportion of the species that were very common, but the majority were relatively rare. 1790 individual fish were observed in total but, as Table 3 shows, snappers had the highest mean abundance. However, relatively few sites hosted most of the individuals, resulting in a disparity between the median and mean abundance, see Table 3. This effect was particularly pronounced for snappers. The mean biomass was more consistent between groups but snappers were still the highest.

Table 3: Descriptive statistics regarding the populations of groupers, snappers and sweetlips at the 12 study sites. Transects were 30m by 4m.

	Species richness	Number of individuals	Mean abundance per transect	Median abundance	Mean biomass per transect (kg)
Groupers	17	468	4.03±3.98	3	1.61±2.98
Snappers	9	1211	10.4±34.1	1	2.06±5.31
Sweetlips	3	111	0.957±4.02	0	1.02±4.05

Table 4: The five most ubiquitous species observed at the study sites. The proportion of locations occupied reveals the percentage of the 29 available locations (12 sites with multiple depths at each site) within which each species was observed. These occurrences include both the belt transects and roving diver survey data.

Latin name	Common name	Proportion of locations occupied
Cephalopholis argus	Peacock grouper	89.7%
Aethaloperca rogaa	Redmouth grouper	86.2%
Lutjanus bohar	Red snapper	75.9%
Lutjanus gibbus	Humpback snapper	58.6%
Anyperodon leucogramma	Slender grouper	51.7%

The GLMs, shown in Table 5, illustrate that the most important variables in predicting the biomass, species richness and abundance of grouper, snapper and sweetlips are the type of reef, depth, scuba diving intensity and current strength, although visibility was also found to be significant for biomass. For species richness, as shown in Figure 3, the greatest values are at 17-22m in the channels but this pattern does not hold overall. Of the three response variables, species richness exhibits the most uniformity across all sites, excluding the bommies at Hithadhoo Corner. The model predicting species richness is the best of the three models because it explains the most variability, 59.5%. The GLM revealed that depth explains the highest proportion of the deviance (17.2%).

Figure 4 shows that mean abundance is fairly consistent across the study sites (excluding the Hithadhoo Corner bommies). However, the 95% confidence intervals illustrate the high variability within sites. Abundance is the response variable most poorly explained by this study, with only 29% deviance accounted for. However, of the variables within the model, depth is by far the most important, explaining 10% of the deviance.

Biomass is generally higher in the channels but, as Figure 5 shows, there is high variability between and within sites. Assuming mesopredators are present, the gamma model (described in Table 5) reveals that current strength and scuba intensity predict the most of this variability (14.6% and 13.5% respectively). Biomass was greatest where scuba intensity was rated 1-2, i.e. always dived – sometimes dived. Current strength did not have a consistent trend but the highest mean biomass was for weak current.

Table 5: The full models and minimum adequate models used to predict total species richness, biomass and abundance of groupers, snappers and sweetlips. The minimum adequate models contain variables determined by Akaike's information criterion (AIC) and the percentage of the deviance (%D) explained by each variable (as well as the overall model) is listed for each. Since the predictor variables are factors, the significance of each level (p) was calculated based on a reference level (as selected by default in R). Those that remained significant following FDR correction (α shown for each model) are illustrated here. The probability of decreased deviance compared to the full model is also provided (*p*[D]). See methods for variable descriptions. All values reported to 3 significant figures.

Full model	Minimum adequate model
Model A – Poisson GLM Response: Total species richness Predictors: Type, depth, scuba, visibility, lunar, current	Type: %D= 2.77 Depth: %D= 17.2 - 3-8m: p= 0.0110, α = 0.0375 Scuba: %D= 13.2 - Intensity 3: p = 0.00101 - Intensity 4: p = 0.01694 Current: %D= 5.36 - Weak: p= 0.0327 Type:depth - Inner : Middle p= 0.0236 (Overall: AIC = 568.58, %D = 59.5, p[D]=0.0925)
Model B – Negative binomial GLM Response: Total abundance Predictors: Type, depth, scuba, visibility, lunar, current	Type: %D= 4.83 - Outer reefs: p= 0.00473, α = 0.03 Depth: %D=10.0 - 10-15m: p= 0.00496 - 3-8m: p<0.001 Scuba: %D= 2.75 Current: %D= 5.63 - Weak: p<0.001 - Strong: p<0.001 (Overall: AIC = 744.63, %D = 29.0, p[D]= 0.454)
Model C – Binomial gamma hurdle model Response: Biomass Predictors: Type, depth, scuba, visibility, lunar, current NB: According to the binomial model, the probability of encountering a non-zero value is 0.903 (95% CIs = 0.838-0.948). The minimum adequate model determined by the gamma portion of the model is described in the following cell and reveals which variables influence mesopredator biomass, given a situation where they are present.	Type: %D= 5.90 - Outer reefs: p <0.001, α = 0.0206 Depth: %D= 11.5 - Shallow: p= 0.00473 Scuba: %D= 13.5 - Intensity 2: p <0.001 - Intensity 3: p= 0.00166 - Intensity 5: p= 0.0169 - Intensity 6: p <0.001 Current: %D= 14.6 - Weak: p <0.001 - Weak-medium: p <0.001 - Medium: p <0.001 Visibility: %D= 6.97 - p= 0.0194 Type:depth - Outer : Middle p <0.001 (Overall: AIC = 1822.4, %D = 51.3, p[D]= 0.543)

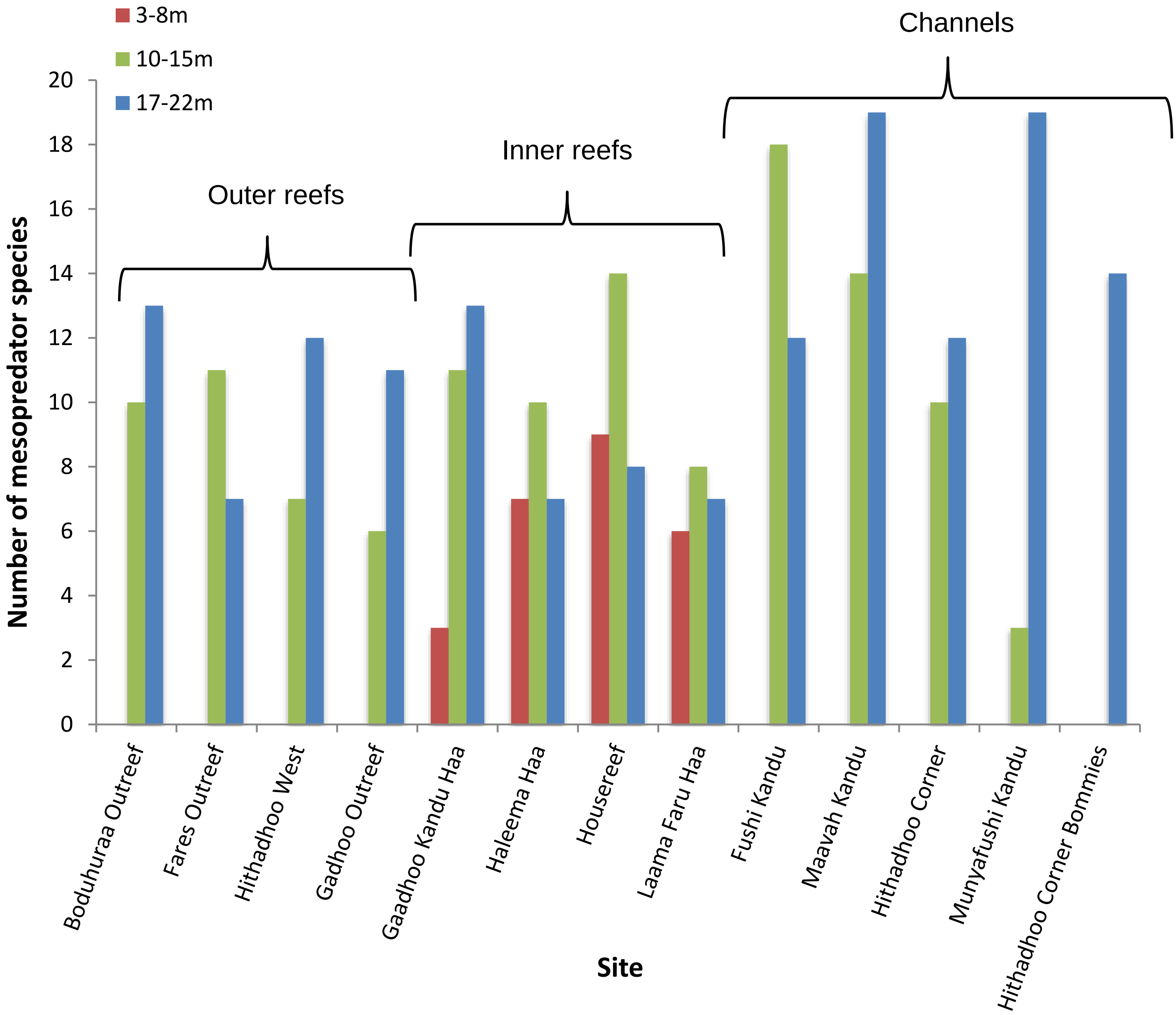


Figure 3: Species richness of grouper, snapper and sweetlips found at three depth ranges (3-8m shown in red, 10-15m shown in green, 17-22m shown in blue) at 12 sites around Laamu Atoll. The sites are arranged by reef type; inside the atoll, outside the atoll or channel reef. The species richness is the combined species count from all four belt transects and roving diver surveys at each depth.

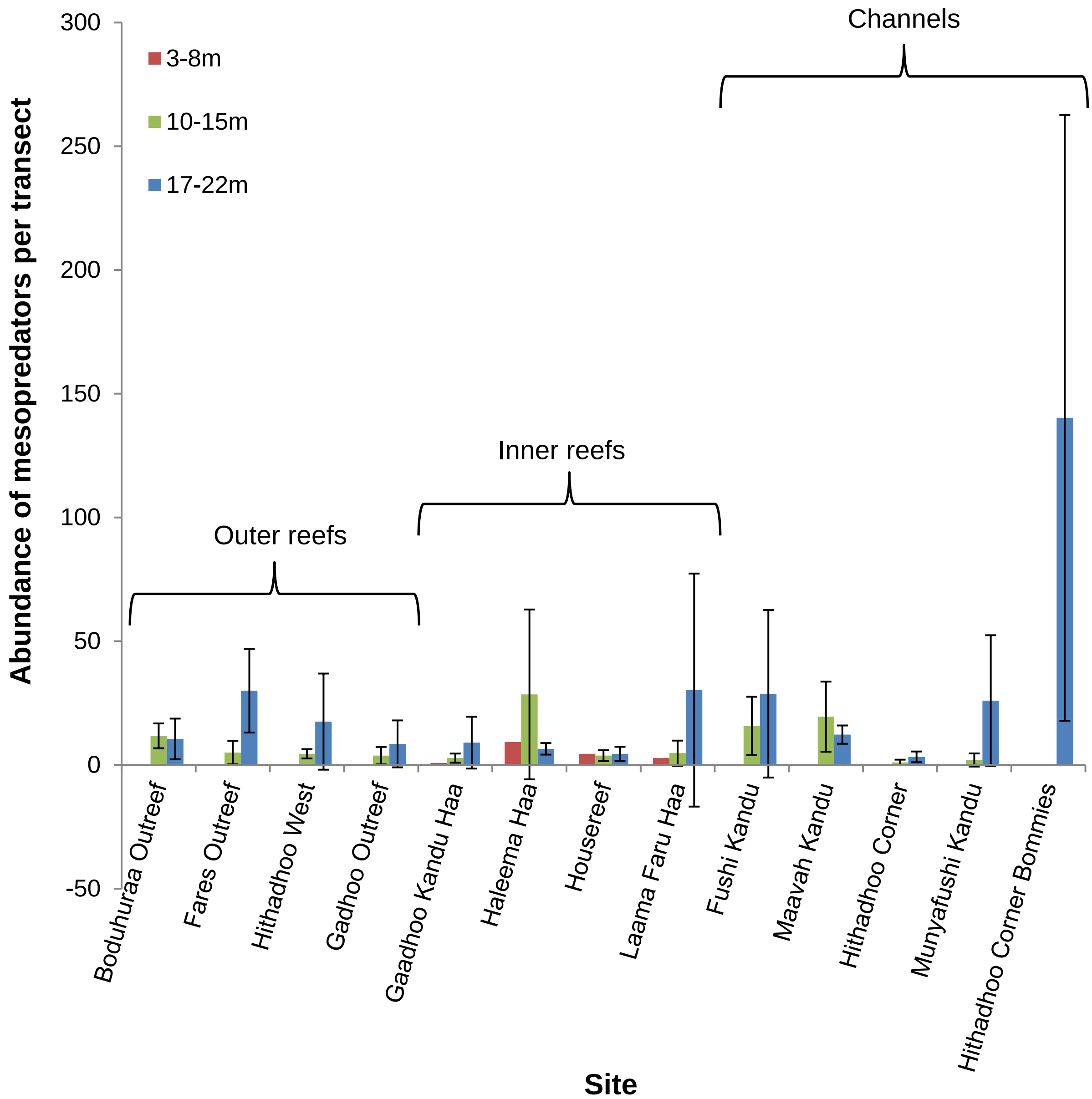


Figure 4: Mean abundance of grouper, snapper and sweetlips found at three depth ranges (3-8m shown in red, 10-15m shown in green, 17-22m shown in blue) at 12 sites around Laamu Atoll. The sites are arranged by reef type; inside the atoll, outside the atoll or channel reef. 116 transects were conducted and n=4 for each bar. Error bars indicate 95% confidence intervals.

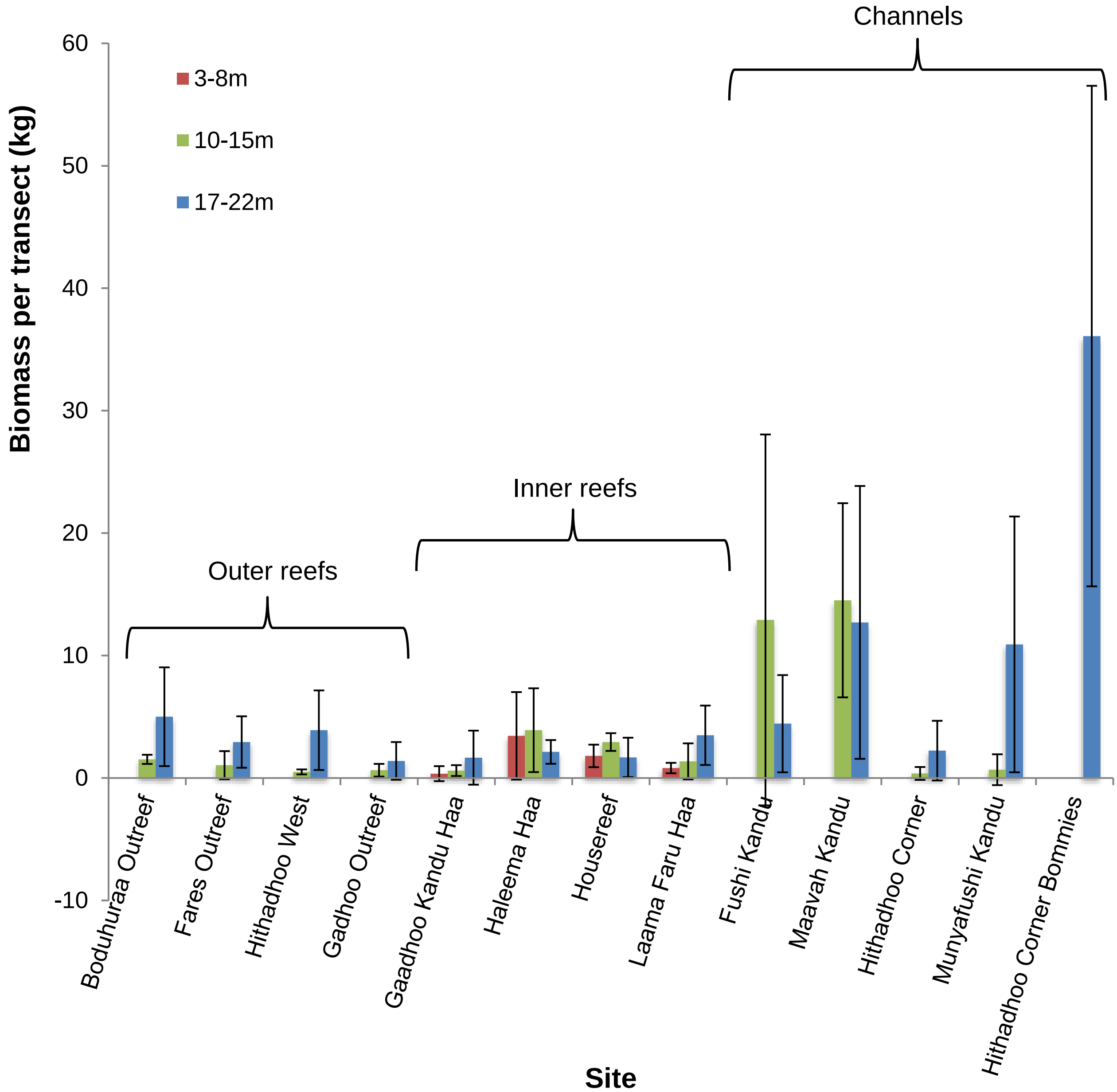


Figure 5: Mean biomass (kg) of grouper, snapper and sweetlips found at three depth ranges (3-8m shown in red, 10-15m shown in green, 17-22m shown in blue) at 12 sites around Laamu Atoll. The sites are arranged by reef type; inside the atoll, outside the atoll or channel reef. 116 transects were conducted and n=4 for each bar. Error bars indicate 95% confidence intervals.

Figure 4 & 5 illustrate the comparatively high levels of biomass and abundance at the coral bommies at Hithadhoo Corner. The biomass and abundance of groupers, snappers and sweetlips was significantly greater (p=0.0466 and p=0.00710 respectively, n=8) on the bommies than the initial transects, as shown in Figure 6.

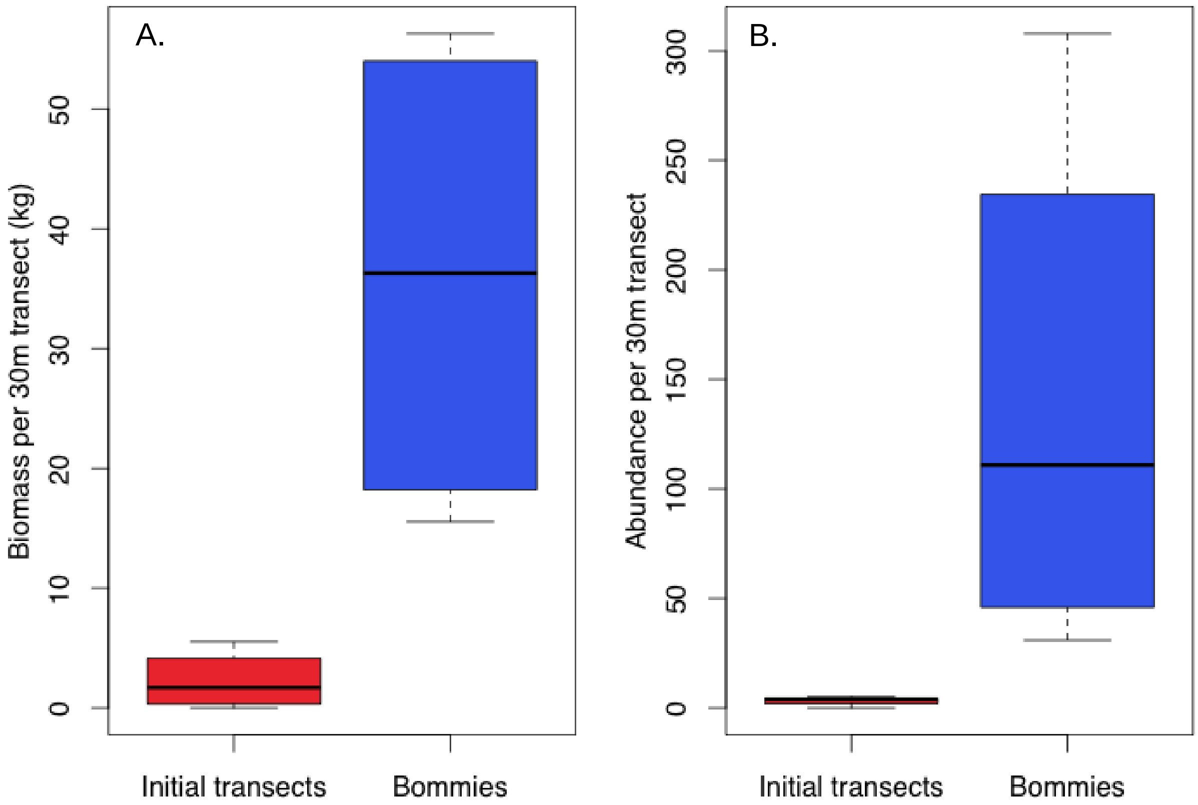


Figure 6: The A) biomass (kg) and B) abundance of groupers, snappers and sweetlips from 17-22m at Hithadhoo Corner recorded by the initial, haphazardly located transects (shown in red) and when the transects were located on the coral bommies (shown in blue). The difference between the initial transects and the bommies is significantly different for both biomass (p=0.0466, n=8) and abundance (p=0.00710, n=8).

Interviews with fishermen

The interviewees had a mean age of 53 years, ranging from 48-57 years. The mean experience level was 33.3 years, ranging from 13-43. All participants are actively involved in fishing but 4 of them mentioned that they have an additional job. When asked about seasonal variation of their catch, everyone mentioned the importance of the lunar cycle (Hijri calendar) and the monsoons or currents. Overall, three times of the Hijri month were identified as providing better catches, 1-7th, 14-18th, 26-30th, the characteristics of which are described in Table 6. The variation associated with monsoons was attributed to differing weather conditions. Interviewees agreed that the northeast monsoon had calmer weather and one mentioned that the currents were better. However, another stated that the southwest monsoon was better for some channels.

Table 6: Times of the month that fishermen identified as having higher productivity.

Date according to the Hijri calendar	Features of the catches at the specified times
1-7th	Particularly good time for snappers, especially • Red snapper (*Lutjanus bohar)* • Humpback snapper (*Lutjanus gibbus*) • Midnight snapper (*Macolor macularis*).
14-18th	Consistently described as the best days for fishing, especially • Red snapper • Emperors (Lethrinidae) • Jacks (Carangidae), when there is a particularly bright moon
26-30th	Good catches associated with grouper spawning behaviour. They are thought to move to the channels on the 22nd-24th, spawn on the 26-28th and leave the channels on the 30th.

The target catches were red snapper, jacks, emperors, jobfish (especially *Aprion virescens*), humpback snappers, midnight snapper and grouper. Fishermen from Maavah put more emphasis on groupers than those from Maamendhoo. There is little incentive for Maamendhoo fishermen to target groupers because their main market is Six Senses, which does not buy groupers.

Five participants described catch declines since their career began. The individual who disagreed attributed this to the efficacy of modern methods and technology. In contrast, two interviewees argued that catches are insufficient, despite adopting better technology, such as GPS and Fishfinders. One stated that, although the cost is high and the catch is low, they remain in business because of high demand. Specifically, they have observed decreases in groupers, jobfish and red snapper. Five participants discussed red snapper's changing spatial distribution; it used to be "everywhere" but now only particular locations have sufficient stocks. However, there is disagreement over the timescale of these declines. Maavah fishermen noticed changes much earlier (25 or 9 years ago) than on Maamendhoo, where the declines seem result from increased local fishing pressure due to the resort's demand for reef fish.

The participants all use several methods but focus on trolling, jigging and handlining. Although hooks, lines and baits have improved during their careers, the techniques have not changed. A major change that influenced the most experienced fishers was shifting from sailing to dhonis with engines. One participant said that this happened in 1978.

Reef fishing is widespread, but popular locations vary depending on the island (see Figure 7). An attempt was made to collate this information into a map of fishing intensity but it was not clear how often each site was visited and how the preferences of participants compared to the practices of the whole atoll.

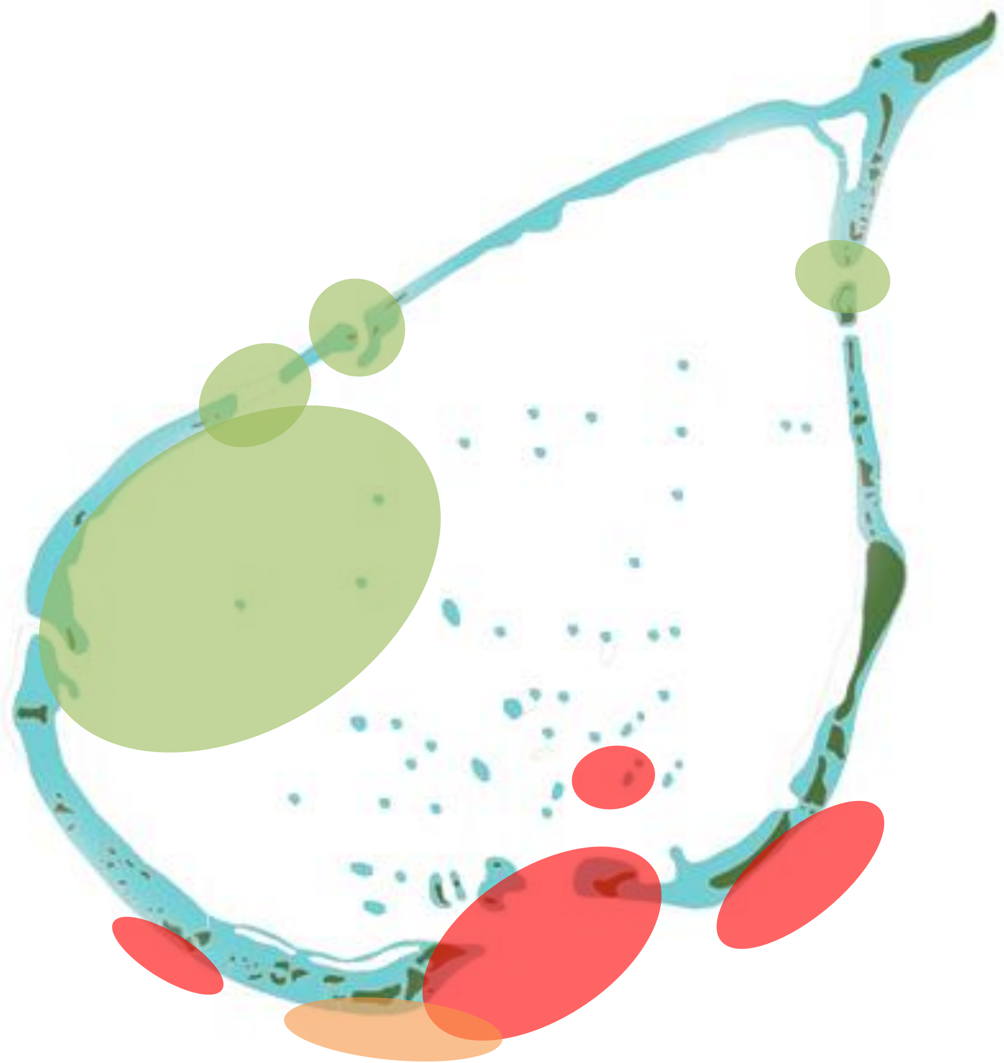


Figure 7: Primary fishing locations of interviewed fishermen from Maavah and Maamendhoo (n=6). Green indicates areas mentioned by Maavah fishermen, red corresponds to Maamendhoo fishermen and both groups mentioned the orange area. These codes give an indication of the areas described in the interviews. The boundaries are not exact, nor are they to scale.

The bans on catching napoleon wrasse (*Cheilinus undulates*), sharks, eels and turtles were well known, with 5/6 mentioning them. However, there was confusion regarding grouper regulations. One respondent believed catching groupers below 9 inches is prohibited, two stated that only suppliers are subject to regulations and another explained that the resort determines the target species.

When asked about fisheries management, the fishermen emphasized the importance of enforcement and awareness. One participant stated that management is important because many people rely on the industry. However, there was confusion about what management exists. For example, fishing with nets is prohibited but a participant said that poor enforcement results in poor compliance. Nevertheless, it was believed that the government knows what is required and will adopt necessary changes. Two participants believe the practice of catching small fish is unsustainable. Another discussed the importance of keeping the marine environment clean. One fisherman suggested that less effective bait (e.g. frozen) could be used to reduce catch per unit effort and that weaker lines could be used to avoid catching large, fecund individuals.

Although there was not full agreement, several people thought that protection could be a constructive fisheries management tool. Table 7 outlines the recommendations made by the interviewees. Clearly reasons for these comments vary, with some individuals focusing more on fisheries, others on tourism and one commenting on the ecosystem services provided by particular species.

Table 7: Fishermen's views and recommendations for protection of particular areas of reef or species of fish (n=6).

Type of protection	Summary of opinion
Locations	Protection for fishing purposes is not needed, but important areas for tourism will be protected
	Temporary closures of grouper aggregations would be valuable
	Hithadhoo to Gaadhoo should be closed to protect sheltering groupers
	Hitadhoo to Fonadhoo should have extra protection for turtles
	There are no areas where additional protection would improve the fishery.
	The government will carry out research and decide what is needed. Fishermen will respect this.
Species	Blacksaddle grouper (*Plectropomus laevis*), due to its rarity
	Lunar-tailed coral trout (*Variola louti*) and mixed groupers (*Cephalopholis argus* and *Cephalopholis miniata*) because they bring baitfish to the surface
	The species that the tourists want to see
	Napoleans and sharks are already protected so no more species-specific protection is needed.

Discussion

This study reveals novel information about populations of mesopredators on Laamu atoll and the pressures they face. It also identifies areas that should be addressed in future studies. These results should be seen as a basis for establishing monitoring in the future, rather than a comprehensive review of ecosystem health.

There is clearly high variability between and within sites, with no model explaining over 60% of this variability. This may be due to spatial and temporal heterogeneity (Sluka 2000; Grünbaum 2012) so additional research is needed to determine the causes of such high intra-site variation. Furthermore, due to zero-inflation in the data, analysis was carried out with groupers, snappers and sweetlips combined. Analysis of these groups or species individually may reveal clearer patterns. For example, reef type (inner, outer or channel reef) influences the mean abundance of some species of grouper (*P. pessuliferus* and *V. louti*) but not others (*P. areolatus* and *P. laevis*) (Sluka 2000).

Despite high levels of variability, several key variables emerge from the models; reef type, depth, scuba diving intensity and current strength. Interpreting the implications of this is challenging, but some conclusions can be drawn. The relationship with scuba intensity may be because divers seek out sites with healthy reefs, high biodiversity and high fish abundance. The influence of current strength may be related to the ecological functions that currents provide, particularly in channels (McClanahan & Karnauskas 2010). The data suggest that a weak current is beneficial, perhaps improving food availability, but above a certain level fish seemed to have moved or were taking shelter and so were no longer visible. Depth was the most important variable in predicting biodiversity, biomass and abundance. The 17-22m depth range was particularly significant in the channels, revealing the importance of studying communities at this depth. This is often overlooked by monitoring programmes such as Reef Check, which has a maximum depth of 12m (Hodgson et al, 2006).

Although this study addressed several significant variables, some important subjects were not included., Although the importance of top-down control exerted by predatory fish on coral reefs is recognized (Dulvy et al. 2004; Mumby & Steneck 2011), the control that prey abundance has on the biomass of piscivorous fish is increasingly acknowledged (Beukers-Stewart et al. 2011; Stewart & Jones 2001). For example, the abundance of prey influences the abundance, development and growth rate of mesopredatory groupers (Beukers-Stewart et al. 2011). Incorporating prey abundance into future studies will enable more ecological interactions within the environment to be taken into account.

Secondly, coral reef structural complexity is known to have a positive relationship with fish biomass and density (Graham & Nash 2013) and groupers have been shown to exhibit preferences for particular microhabitats (Sluka 2000). Personal observations revealed that sandy patches or reefs with low structural complexity had relatively small mesopredator populations but this was not corroborated with quantitative data. Future studies should include analysis of structural complexity, benthic substrate and the potential preference for particular microhabitats.

Fishing intensity was not fully addressed, which is concerning because predatory reef fish are especially vulnerable to overfishing as they are the main target for artisanal and commercial fisheries (Stallings 2009). Unsuccessful attempts were made to gather information regarding this issue during the interviews, Characterising the catches from a multi-gear, multi-species, small-scale tropical fishery is notoriously difficult and requires a specialist methodology (White et al. 2014). Nevertheless, the interviews suggest that reef fishermen in Laamu are already witnessing declines.

Temporal heterogeneity driven by the lunar cycle has already been identified for groupers in Laamu (Sluka 2001). Fishermen also described predictable patterns based on the Hijri calendar. Other studies have described the view amongst fishermen that daily fish productivity depends on the lunar cycle, which is related to the Hijri calendar (Muchlisin et al. 2011). This study examined the effect of whether the survey was carried out during a time of the lunar calendar that the fishermen had identified as having higher catch levels. However, as this carried out *post hoc,* further research is needed in this area, particularly since divers observed seasonal aggregations of *Epinephelus fuscoguttatus* and *E. polyphekadion* at Hithadhoo Corner. Highly conspicuous behaviour, which was only observed during these times, may influence the probability of individuals being spotted by observers when conducting transects.

In addition to these neglected variables, future studies should address some methodological issues. Despite the training exercises undertaken prior to data collection, observer bias may have contributed to intra-site variability. If this is the case, it is likely that biomass will be more heavily biased than abundance (Edgar et al. 2004). If future monitoring will be carried out by pooling data collected by two divers, it is suggested that a double-observer method (Jenkins & Manly 2008) be used to ensure consistency between divers in all aspects of the survey technique, rather than just for length estimation.

Another source of bias is that the disturbance caused by laying the transect tape may have scared skittish species away. There is evidence that a 5 minute acclimatization period, as used in this study, reduces this effect (Dickens et al. 2011) but there is disagreement in the literature about the extent of this problem. Some argue that the presence of the divers significantly reduces the accuracy of UVCs (Dickens et al. 2011), but others disagree that this problem has a significant effect (Dearden et al. 2010). However, to avoid potentially underestimating the biomass or abundance of fish it is suggested that future studies use a protocol that involves laying the transect tape behind the observer (Fulton et al. 2001) in order to minimize disturbance.

Regardless of these limitations, it is clear that a number of vulnerable species are found in Laamu Atoll; *E. polyphekadion, E. fuscoguttatus, P. areolatus, P. laevis* and *P. pessuliferus* are all rated Near Threatened or Vulnerable by the IUCN Red List (IUCN 2015). Therefore, it is important that pressure from fisheries and tourism is managed appropriately and monitoring is carried out to track the response of the ecosystem, and these species in particular, to future changes.

Due to its ecological significance as a manta cleaning station and an important site for vulnerable grouper species, it is believed that Hithadhoo Corner should be declared a protected area. There is an obvious need for additional baseline data but this study provides a solid indication of the site's importance. Assessment of the channels around the atoll to determine the location and scale of grouper spawning aggregations would also be valuable. Several fishermen favour the idea of protecting

Hithadhoo Corner and the surrounding area. Although not all agreed with this, there was a general acceptance of the idea that environmental research or government work may result in recommendation for the site to be protected, and that such a designation would lead to benefits for the tourism industry. Further work with stakeholders is needed to develop the high levels of community engagement needed in order to ensure success in this endeavor (Pollnac et al. 2001).

In conclusion, this study establishes a baseline to which future studies of mesopredatory fish populations can be compared and makes recommendations for future projects in this area. The results suggest that improved fisheries management is needed before the atoll's marine resources become overexploited. The only way to maintain the atoll's main industries is to protect marine ecosystems, and increasing protection of a valuable site, Hithadhoo Corner, would be an important contribution to this effort.

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Appendix 1: Interview Questionnaire

<u>Introduction:</u>

We are Jenny, Beth and Adam, staff from the Manta Trust - a global organisation working heavily in the Maldives. We are currently working in Laamu on a brand new project and we would like to understand what the fishing here is like. From the outset it is very important for you to understand that everything that we discuss today will be completely confidential and all information will be anonymous.

Before we begin I would like to tell you a little about this study, why we are asking these questions and what we hope to find out. We would like to learn about your fishing experiences, especially what you catch and how you do so. The reason for this is that we are studying the presence of important fish species at Laamu Atoll and your knowledge and experience may help us to understand them better.

If you do not understand anything or want to ask any questions during the interview, please stop me at any time. It is crucial that you answer each question as accurately as possible. If you are not sure of the answer to a question, please state this as your answer.

Right, let us begin:

Interview

<u>A. Fishing experience</u>

1. How many years have you been fishing for? (Open)
2. How old are you?
3. Are you still actively involved in fishing? (Yes/No)

4. Does your catch vary on a seasonal basis? If so, how?

5. What do/did you fish for? (Open)

6. Has your target catch changed since you began fishing? (Yes/No)

7. If yes, then:
    a. When did this change occur? (Open)
    b. Why did it change? (Open)

8. Has the amount you catch changed since you began fishing? (Yes/No)

9. If yes, then:
    a. When did this change occur? (Open)
    b. Why did it change? (Open)

10. What is your method of fishing? (Open)

11. Has your method of fishing changed since you began fishing (Yes/No)

12. If yes, then when did you change the way you fished (Open)

13. Which types of fish do you catch the most? (this will be asked with visual aids to illsutrate potential target species)

To gauge the trustworthiness of the respondent's answers, they were asked to answer a couple of questions on pictures of different fish species some of which are known ***not*** *to exist or be of great abundance in the Maldives (eg. Nassau grouper).*

14. Please show on this map which areas you go fishing (a map will be provided so they can mark the areas they use the most)

B. Fishery management

15. Are you aware of any rules and regulations about fishing in the Maldives? (Yes/No)?

16. How do you feel about fisheries management?
    (It's good/it's bad/don't know)
    a) Why: ____

17. What changes, if any, would you make to fisheries management? (Open)
    Prompts may be given: less restriction/more restriction/fishing methods

18. Do you think any species of fish should be protected? (Yes/No)
    b) Why: ____

19. Do you think any areas of reef should be protected? (Yes/No)
    a. Why: ____

Appendix 2: Diving questionnaire

How often do you dive on the following sites?

1. **House Reef**

   Always Often Sometimes Rarely Never

2. **Haleema Haa**

   Always Often Sometimes Rarely Never

3. **Laama Faru Haa**

   Always Often Sometimes Rarely Never

4. **Gaadhoo Kandu Haa**

   Always Often Sometimes Rarely Never

5. **Hithadhoo Corner**

   Always Often Sometimes Rarely Never

6. **Maavah Kandu**

   Always Often Sometimes Rarely Never

7. **Munyafushi Kandu**

   Always Often Sometimes Rarely Never

8. **Fushi Kandu**

   Always Often Sometimes Rarely Never

9. **Gaadhoo Out**

   Always Often Sometimes Rarely Never

10. **Fares Out**

    Always Often Sometimes Rarely Never

11. **Boduhuraa Out**

    Always Often Sometimes Rarely Never

12. **Hithadhoo West**

    Always Often Sometimes Rarely Never