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The importance of oceanic atoll lagoons for coral reef predators

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Abstract

Predators on coral reefs play an important ecological role structuring reef fish communities and are important fishery targets. It is thought that reef predator assemblages increase in density and diversity from inner lagoonal to outer edge reefs. Oceanic atolls may differ though, as nutrients are available throughout. Reef predator populations are declining, but there is little known about how their distributions may vary across oceanic atolls. Using a combination of underwater visual census and baited remote underwater video, this study aimed to compare reef predator populations between inner and outer reefs of North Malé Atoll (Maldives) and determine which reef metrics may drive any differences in assemblage structure. We found that predator assemblages were significantly different between inner and outer atoll. Body sizes of several predator families were consistently larger in the outer atoll, however, abundance, biomass and species richness were similar between outer edge reefs and inner lagoonal reefs suggesting atoll lagoons may be undervalued habitats. Depth and complexity were consistently important predictors of the predator assemblage. Inner atoll lagoonal habitat is equally as important for reef predator assemblages as outer reef slopes, although the dominant species differ. This study provides important information on reef predator populations in the Maldives, where detailed assessments of the reef predator assemblage are lacking but the reef fishery is thriving and annual catch will continue to increase.

Introduction

Coral reef predators play an important role in structuring reef fish communities (Clark et al. 2009; Roff et al. 2016). They regulate the composition and dynamics of prey assemblages, directly through predation and indirectly through the modification of prey behaviour (Ceccarelli and Ayling 2010; Roff et al. 2016). Locally abundant teleosts such as snappers, emperors and groupers are an important part of the reef predator assemblage, making regular movements between hard and adjacent soft bottom habitats (Berkström

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et al. 2012; Green et al. 2015). They also substantially contribute to coral reef fishery yields, providing livelihoods to millions of people globally. Currently, populations of sharks and other reef fishes are experiencing worldwide decline (Graham et al. 2010; Roff et al. 2016), but their removal can result in community-wide impacts which may destabilise the food web (Bascompte et al. 2005).

In both terrestrial and marine systems, predators show a preference for edge habitats (Phillips et al. 2004; Heithaus et al. 2006), such as forest grassland edges (Svobodová et al. 2011), forereef ledges (Papastamatiou et al. 2009) and outer shelf areas (Cappo et al. 2007). Consequently, reef predators may increase in density and diversity from shallow, lagoonal habitats to outer reef slopes (Friedlander et al. 2010; Dale et al. 2011). Outer reef habitats may provide a greater availability of resources, for example they host aggregations of planktivorous fishes (Hamner et al. 1988, 2007) that take advantage of increased plankton prey abundance (Wyatt et al. 2013) and sustain reef predators (Frisch et al. 2014; Matley et al. 2018).

In the Maldives, atolls are characterised by an oceanic outer reef slope with deep channels separating inner shallow, lagoonal reefs from the adjacent open ocean. A range of hydrodynamic processes such as equatorial currents and

local upwelling facilitate water mixing within the Maldivian archipelago (Sasamal 2007), enhancing biological productivity. Consequently, unlike more closed systems, nutritional resources are available throughout the atolls and into the lagoons due to the extensive water circulation (Radice et al. 2019). Furthermore, tourist resort islands, often located inside atoll lagoons, act as refuges for reef fish communities, because fishing is often prohibited there. As such, resort islands support a higher diversity of commercial fish species, such as groupers, than other permanently inhabited islands (Moritz et al. 2017). Inner lagoonal reef habitats may thus be equally as important to reef predator assemblages as outer edge reefs (Skinner et al. 2019).

Fisheries in the Maldives traditionally focused on tuna, but the annual reef fishery catch has increased (Sattar et al. 2014) due to a growing demand for reef fish from tourists (Ministry of Tourism 2018). Moreover, the 2009–2013 Maldives Strategic Action Plan identified expansion and diversification of the fisheries sector as a national priority (Adam and Sinan 2013), signifying further development and exploitation of the reef fish fishery. Although the Maldives was classified as one of the most underexploited fisheries in the Indian Ocean (Newton et al. 2007; MacNeil et al. 2015), there are no unfished or historically "pristine" coral reef ecosystems in the region (McClanahan 2011). In addition, current estimates suggest that the reef fishery is approaching the limit of its maximum sustainable yield (Sattar et al. 2014) and prior to 1998 sharks were intensively fished (Ushan et al. 2012). There is thus an urgent need to assess abundance and distribution of reef predator populations to determine which atoll habitats are important.

All survey methods for assessing abundances of fishes have their strengths and weaknesses, so, to accurately assess predator populations, multiple methods are desired that take into account inherent interspecific differences in body size, habitat association, aggregative or schooling behaviour, mobility (particularly in the case of elasmobranchs), or the response to the presence of divers or various types of equipment (Kulbicki 1988; Willis and Babcock 2000; White et al. 2013). Underwater visual census (UVC) allows a comprehensive sampling of smaller, resident species that are harder to detect, however time underwater is limited and high replication is required to detect rarer (or more mobile) species (Dulvy et al. 2003). Conversely, baited remote underwater video (BRUV) offers a non-invasive and non-destructive technique that can cover a wide geographic area, depth range and number of habitats (Harvey et al. 2013). BRUV is particularly useful in assessing occurrences of larger, more mobile species (Willis and Babcock 2000; Cappo et al. 2003; Harvey et al. 2012; White et al. 2013). However, it can be difficult and time consuming to identify species from the video footage and there is a potential bias arising from attracting species to the bait (Willis and Babcock

2000; Cappo et al. 2003; Harvey et al. 2012; Espinoza et al. 2014). By combining these two survey methodologies, a more comprehensive estimate of reef predator abundances and distributions can be achieved.

This study aimed to assess coral reef predator assemblages across an oceanic atoll using both BRUV and UVC. We sought to determine if there were: (1) differences in the abundance, size, biomass, and diversity of predators between the inner and outer atoll, and (2) what habitat characteristics help explain the differences?

Materials and methods

Study site

The Maldives is an archipelago of 16 atolls and is the historical archetype of a coral reef province (Naseer and Hatcher 2004). The coral reef area is 8920 km^2 (Spalding et al. 2001), while the EEZ covers almost 1 million km^2 (FAO 2006). The north–south extent cuts across the equator and is subject to equatorial currents transporting high concentrations of nutrients (Sasamal 2007). Fieldwork was conducted in North Malé Atoll (4°18′34.5 N, 73°25′26.4 E) from January to April 2017. North Malé Atoll is located in the centre of the double chain of the Maldivian archipelago, on the eastern side. It has an atoll perimeter of 161 km, 117.9 km of which is shallow edge reef while 43.1 km is deeper channels (Beetham and Kench 2014), promoting water exchange between the adjacent open ocean and the atoll lagoon. The atoll has 189 reef platforms, covering 22.3% of its surface area (Naseer and Hatcher 2004). The atoll was divided into two areas: (1) inner: enclosed lagoonal reef platform sites, and (2) outer: outer reef slope sites.

Underwater visual census (UVC)

UVC was carried out at 40 sites, 20 in the inner atoll and 20 in the outer atoll (Fig. 1). A total of 200 transects were surveyed, 100 within each area. At each site, five 50×5 m transects were laid parallel to the forereef habitat at 2.5–15 m depth. A minimum of 5 m was left between transects. Abundance and size to the nearest centimetre of all reef predator species were recorded (here predators at assumed trophic levels 3.5 and above, species list in Appendix Table S1). Predators were characterised as either mobile and highly visible or cryptic and site attached based on their behaviour (Brock 1982). Two observers recorded the predatory fish assemblage. The first observer laid the transect while recording all mobile, highly visible predators, and the second searched the benthos for cryptic, site-attached predators. Percent cover of branching, massive and table coral, and algae was estimated for each transect in the
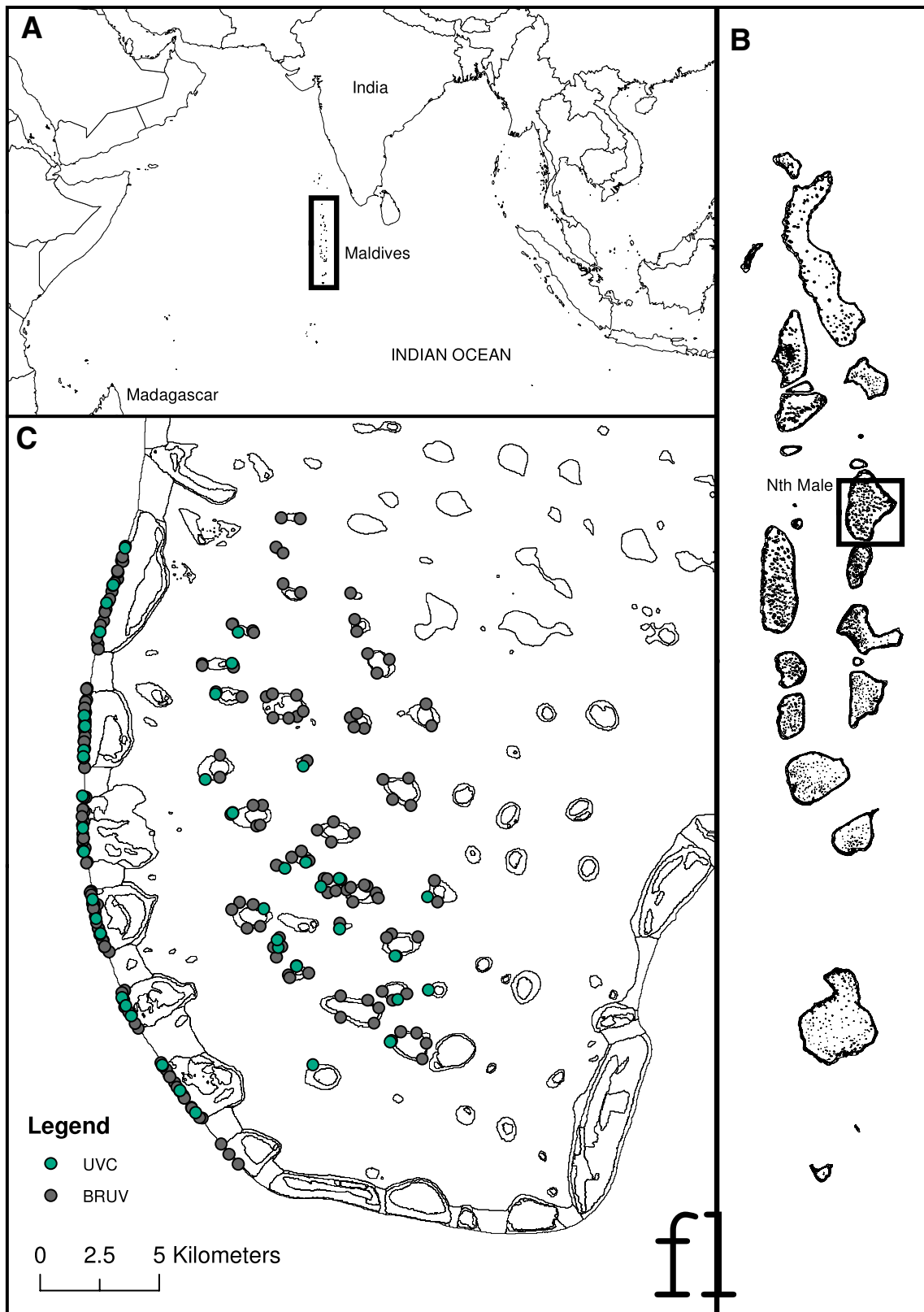
Fig. 1 Underwater visual census (UVC) and baited remote underwater video (BRUV) survey locations. **a** Maldives location in the north Indian Ocean (3.2028° N, 73.2207° E), **b** North Malé Atoll in the central Maldives archipelago (4.4167° N, 73.5000° E), and **c** the UVC and BRUV inner and outer survey locations in North Malé Atoll

following categories: 0% = absent, > 0 and < 25% = low, > 25 and < 50% = fair, > 50 and < 75% = good, > 75% = excellent (Chou et al. 1994). Reef habitat structural complexity was visually assessed on a 6-point scale from 0 to 5, where 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex and 5 = exceptionally complex (Polunin and Roberts 1993). Abundance of crown of thorns (*Acanthaster planci*) and pin cushion starfish (*Culcita novaguineae*) starfish were also recorded by the second observer. The same observers were used throughout the surveys to prevent observer bias (Willis and Babcock 2000). A training period was carried out prior to data collection to ensure accurate species identification and size estimates (Wilson et al. 2007).

Baited remote underwater video (BRUV)

Overall, 205 BRUVs were deployed, 102 in the inner atoll and 103 in the outer atoll (Fig. 1). BRUV deployments were restricted to depths of 2.5–15 m to sample the same habitat as the UVC surveys and set ≥ 600 m apart (Cappo et al. 2003). For each BRUV, a single GoPro Hero 4 camera with a red filter was attached to a stainless steel frame with a detachable bait arm holding a bait bag. Bait bags were made out of 12 mm wire mesh encased in 15 mm plastic mesh. These were attached to 160 cm lengths of 22 mm plastic PVC pipe using cable ties and a metal pin. Bait consisted of ~ 1 kg of guts and discards from a range of oily fish species: bonito (*Sarda orientalis*), rainbow runner (*Elagatis bipinnulata*) and great barracuda (*Sphyraena barracuda*). BRUVs were deployed with 6 mm polypropylene ropes and surface marker buoys and set manually on coral rubble or sand. For each BRUV, the time deployed and the depth were recorded. Cameras were only deployed during daylight hours (09:00–17:00) to avoid bias from changes in feeding behaviour (Willis and Babcock 2000) and left to record for approximately 70 min to ensure there was 60 min of analysable footage.

During video processing, 25 deployments were excluded from analysis as (1) the field of view was blocked by upright substrate or (2) the camera angle had moved and was facing straight up or straight down (Asher et al. 2017). Consequently, only 180 deployments were included, 90 from each atoll area. Habitat was classified into one of nine categories: (1) aggregate reef, (2) dead boulder coral/rock, (3) entirely reef rubble, (4) rubble/reef, (5) rubble/sand, (6) sand flat, (7) sand with reef in view, (8) sand with scattered coral/rock and (9) spur and groove, the first habitat type being the most dominant of the two identified (Asher et al. 2017). Reef habitat structural complexity was visually assessed using the same 6-point scale of vertical relief as for the UVC surveys (see above) (Polunin and Roberts 1993). Analysis of footage was focused solely on fish predators, i.e. all sharks,

Aulostomidae, Carangidae, Fistulariidae, Scombridae and Serranidae species and larger bodied, more mobile Lutjanidae and Lethrinidae species (see Table S1 for full species list). Predators were identified to the lowest taxonomic level of species in most cases, but where species could not be identified, individuals were pooled at the genus level (Espinoza et al. 2014). For each species, the maximum number seen at any one time on the whole video (MaxN) was recorded (Harvey et al. 2012). Video analysis began after a settlement period (min 02:00–max 08:00 min) had elapsed (Kiggins et al. 2018). The settlement period was characterised as over when all sand or sediment had settled and visibility returned to normal and at least a minute had passed since the BRUV was moved or repositioned.

Data analysis

The following statistical procedures were carried out for both UVC and BRUV data using PRIMER 6 (v. 6.1.15) with the add-on PERMANOVA+ (v. 1.0.5) (Anderson et al. 2008) and R version 3.5.2 (R Core Team 2017) linked with R Studio version 1.1.463 (RStudio Team 2012).

Species richness for each dataset was determined using the species accumulation curve in the vegan R package (Oksanen et al. 2018). Curves were generated using 100 permutations and the "exact" method, which finds the expected mean species richness. 95% confidence intervals were calculated from standard deviations. Only individuals identified to species level were included.

Spatial variation in predator populations

UVC assemblage data were analysed at the transect level and BRUV assemblage data at the BRUV level. Where BRUV sites were repeat sampled on different days, each deployment was counted as an independent sample. Predator abundance data were square root transformed and a resemblance matrix was created based on Bray–Curtis similarity measures. Using the R vegan package (Oksanen et al. 2018), data were graphically compared using non-metric multidimensional scaling (nMDS) with a Kruskal fit scheme set to 3 and a minimum stress level of 0.01. If there were clear outliers that were entirely distinct from the other points, these were removed and an additional nMDS plot was carried out on a subset of the data (see supplemental material for all MDS plots, Fig S1 and S2). Significantly correlated species were extracted and overlaid on the nMDS plots as vectors. Differences in the predator assemblage occurring between atoll areas and among sites were investigated using a nested model in PERMANOVA+ (Type III sum of squares, under a reduced model with 9999 permutations), where site (UVC: 40 levels and BRUV: 39 levels) was a random factor nested within the fixed factor area (two levels). Species contributing

to between-area dissimilarity and within-area similarity were identified using the SIMPER function (Clarke and Warwick 2001).

UVC predator biomass data were calculated using length–weight relationships available on FishBase (https://fishbase.org) with the exception of *Aethaloperca rogaa* where length–weight relationships were taken from Mapleston et al. (2009). Spatial differences in UVC predator biomass were investigated using a generalized linear model (GLM) with transect level biomass as the response variable and site nested within area as the predictor variable. Model normality and homogeneity assumptions were assessed by plotting predicted values against residuals, predicted values against standardised residuals, and q–q plots of standardised residuals. Biomass data were $\log_{10}$ transformed to satisfy model assumptions. An analysis of variance (ANOVA) was applied to determine whether effects were significant ($p < 0.05$). A second GLM was run with the same parameters but without the nurse shark, *Nebrius ferrugineus*, as three large (1.9–2.5 m) individuals were recorded on only one transect in the inner atoll.

Variation in predator body size between atoll areas was investigated for each predator family individually using a linear mixed effects model with the R package lme4 (Bates et al. 2015). Body size (cm) was the response variable, area was a fixed effect and species was a random effect. Model assumptions were checked as above and data were log transformed to meet assumptions when necessary. When the predator family only had one recorded species (Aulostomidae, Carcharhinidae, Scorpaenidae), an ANOVA with body size (cm) as the response variable and area as the predictor variable was used. Size data were checked for normality and homogeneity of variances using a Shapiro–Wilk's test and a Levene's test, respectively. When data did not conform to these parameters, a non-parametric Kruskal–Wallis test was used. Although two species of Carangidae were recorded, *Caranx ignobilis* was only observed once in the inner atoll. This observation was removed from analysis and an ANOVA was used. Fistulariidae and Ginglymostomatidae were only recorded in the inner atoll so no size-based comparisons were made.

Correlation with environmental variables

Using PRIMER, environmental data were normalised. For each entry of a variable, the mean of the variable is subtracted and the value is divided by the standard deviation for that variable (Clarke and Gorley 2006). UVC environmental variables consisted of depth, complexity (Comp), branching coral cover (BC), massive coral cover (MC), table coral cover (TC), algal cover (AC), abundance of crown of thorns starfish (COTS) and abundance of pin cushion starfish (PIN), while BRUV environmental variables consisted

of depth, complexity and habitat type. Data were compared using principal coordinate analysis (PCO) based on Euclidean distance similarity measures with overlaid vectors of Pearson's correlated environmental variables. Differences in environmental variables between inner and outer atoll were investigated using a nested model in PERMANOVA+ (Type III sum of squares, under a reduced model with 9999 permutations), where site (UVC: 40 levels and BRUV: 39 levels) was a random factor nested within the fixed factor area (two levels).

To investigate the relationships between the predator assemblage and the respective environmental variables (Table S2), the RELATE function in PRIMER 6 (v. 6.1.15) with a Spearman's rank correlation coefficient and 9999 permutations (Clarke and Warwick 2001) was used. These correlations were further tested using a distance-based multiple linear regression model (DISTLM) in PERMANOVA+ (v. 1.0.5) (Anderson et al. 2008), which models the relationship between a multivariate distance-based dataset, as described by a resemblance matrix, and the variables (Anderson et al. 2008) using distance-based redundancy analysis (dbRDA) (Legendre and Anderson 1999). Relationships were first analysed using marginal tests. No starting terms were specified for the model. The Best selection procedure was used as it incorporates and examines the selection criterion for all possible combinations of predictor variables, with an AICc selection criterion and 9999 permutations of the raw data to obtain p values for each individual predictor variable (Anderson et al. 2008). AICc values indicate the goodness of a model fit to the data and the model with the lowest AICc value was considered the most parsimonious (Symonds and Moussalli 2011).

Results

A total of 6524 predators of 47 species and ten families were recorded from the 200 transects that surveyed 50,000 m^2 of reef (Fig. 2a) and the 10,800 min of examined footage from 180 BRUVs (90 in each area) (Fig. 2b). Species accumulation plots showed similar patterns and indicated that the sampling effort of each method was sufficient to record most of the predators occurring in the area surveyed (Fig. 3). However, both methods showed higher predator species richness in the inner atoll compared to the outer atoll, and this difference was greatest for the BRUVs.

Spatial variation in predator populations

Similar numbers of species were recorded in each atoll area (Table 1), although five species were only recorded in the inner atoll (*Carcharhinus falciformis*, *Elagatis bipinnulata*, *Epinephelus ongus*, *Lethrinus harak* and *Lethrinus microdon*),
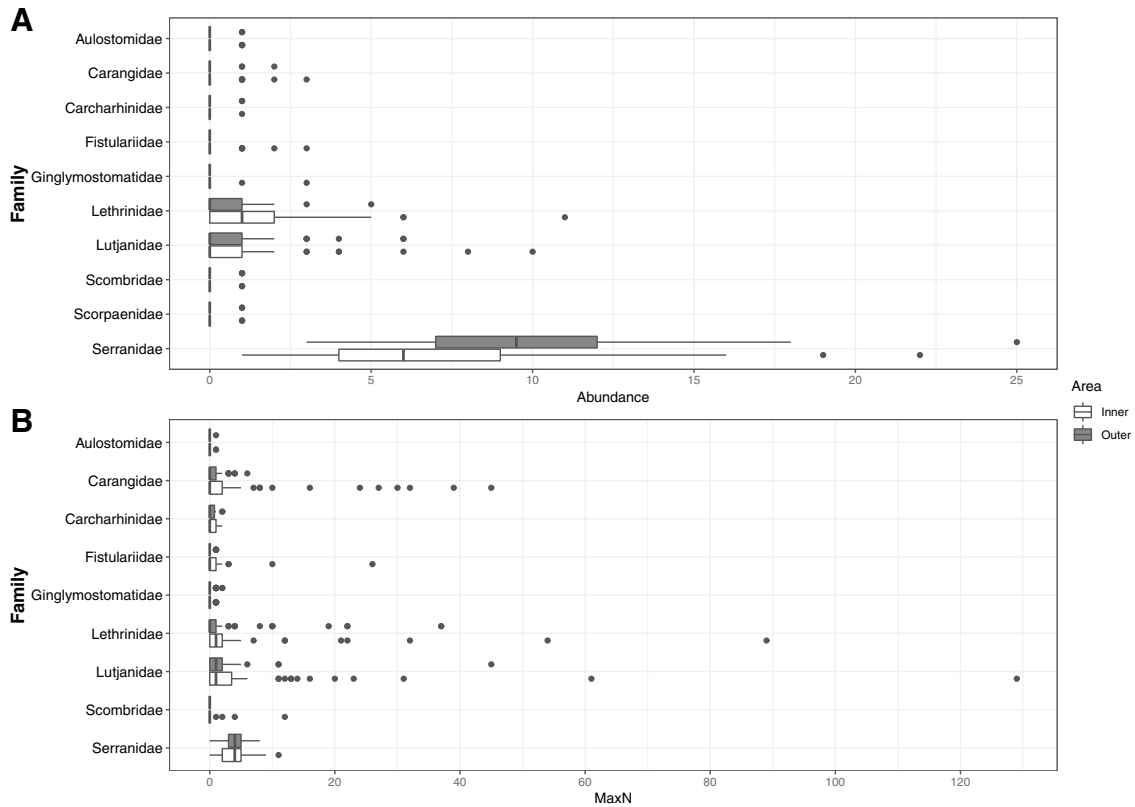
Fig. 2 a Abundance from underwater visual census (UVC) and **b** MaxN from baited remote underwater video (BRUV) of predator families in inner and outer atoll. Individual points are **a** 250 m^2 transects and **b** BRUV deployments
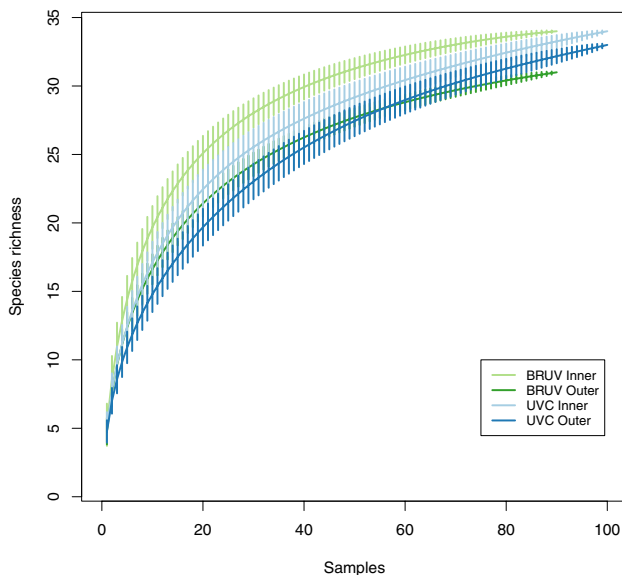

Fig. 3 Species accumulation curves derived from the cumulative number of underwater visual census (UVC) transects and baited remote underwater video (BRUV) deployments in both inner and outer atoll. Bars represent 95% confidence intervals derived from standard deviation

while seven species were only recorded in the outer atoll (*Carcharhinus amblyrhynchos*, *Epinephelus malabaricus*, *Epinephelus tauvina*, *Lutjanus decussatus*, *Lutjanus fulvus*, *Macolor macularis* and *Negaprion acutidens*; Table S1).

Total recorded predator biomass was 0.29 t ha^{-1} in the inner atoll and 0.25 t ha^{-1} in the outer atoll. The biomass of Carcharhinidae, Lethrinidae, Lutjanidae and Serranidae was greater in the outer atoll, while biomasses of Aulostomidae, Carangidae and Scombridae were greater in the inner atoll (Fig. 4). There was no significant difference in total predator biomass between areas (ANOVA, $p < 0.05$), but there was a highly significant difference in biomass among sites within areas (ANOVA, $F (1,39) = 2.08$, $p \leq 0.001$). When *Nebrius ferrugineus* was removed from biomass calculations, total predator biomass was significantly greater in the outer atoll (ANOVA, $F (1) = 4.51$, $p \leq 0.05$) and there were still significant differences among sites within each area (ANOVA, $F (1,39) = 1.82$, $p \leq 0.05$).

The size of Aulostomidae (ANOVA, $p > 0.05$), Carcharinidae (ANOVA, $p > 0.05$) and Scorpaenidae (Kruskal–Wallis, $p > 0.05$) did not differ between atoll areas, but Carangidae were larger in the outer atoll (mean inner: 28.56 cm; outer: 39.75 cm; ANOVA, $F (1,11) = 12.68$, $p \leq 0.001$). Linear mixed effects models suggested no difference in mean size

of Scombridae between atoll areas (mean inner: 49.67 cm; outer: 49.00 cm), but Lethrinidae (mean inner 21.79 cm; outer: 24.74 cm), Lutjanidae (mean inner: 23.04 cm; outer: 30.46 cm), and Serranidae (mean inner: 18.81 cm; outer:

18.99 cm) were all significantly larger in the outer atoll (Table 2; Fig. 5).

The nMDS plot of the UVC predator data revealed relatively distinct inner and outer atoll predator assemblages, while that of the BRUV data suggested greater

Table 1 Summary of recorded predator data

	Inner			Outer		
	UVC	BRUV	Both	UVC	BRUV	Both
Individuals (mean ± sd)	9.56 ± 6.01	16.97 ± 24.72	13.07 ± 17.90	10.81 ± 4.04	9.69 ± 10.42	10.28 ± 7.75
Species	33	34	39	33	31	41
Species unique to method	5	6		10	8	
Families	10	8	10	8	8	10

Summary of collected reef predator data in inner and outer atoll areas by underwater visual census (UVC) and baited remote underwater video (BRUV)

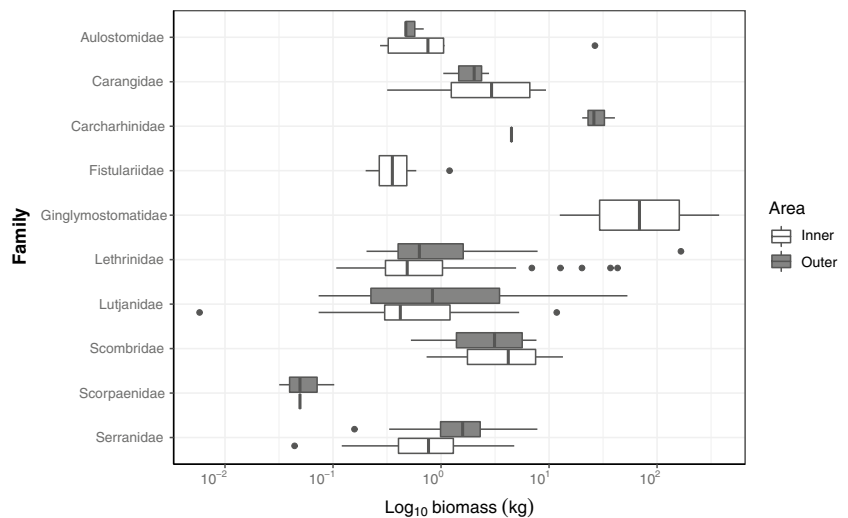**Fig. 4** Biomass (kg) of predator families recorded by underwater visual census (UVC). Values are on a $\log_{10}$ scale

Table 2 Linear mixed effects model of differences in predator body sizes between areas

Formula: size ~ area + (1|species)			df	t	p value	
	Estimate	SE				
Lethrinidae						
Intercept	21.87	1.32	1.51	16.56	0.01	*
Area	2.96	0.78	174.66	3.79	0.00	***
Lutjanidae						
Intercept	25.69	2.61	4.43	9.83	0.00	***
Area	6.39	1.59	129.76	4.01	0.00	***
Scombridae						
Intercept	45.76	12.48	1.08	3.67	0.16	
Area	-2.62	4.51	4.00	-0.58	0.59	
Serranidae						
Intercept	20.28	1.72	11.98	11.77	0.00	***
Area	2.30	0.28	1631.84	8.13	0.00	***

Separate models were run on each individual family with body size as the response variable, area as a fixed factor and species as a random factor
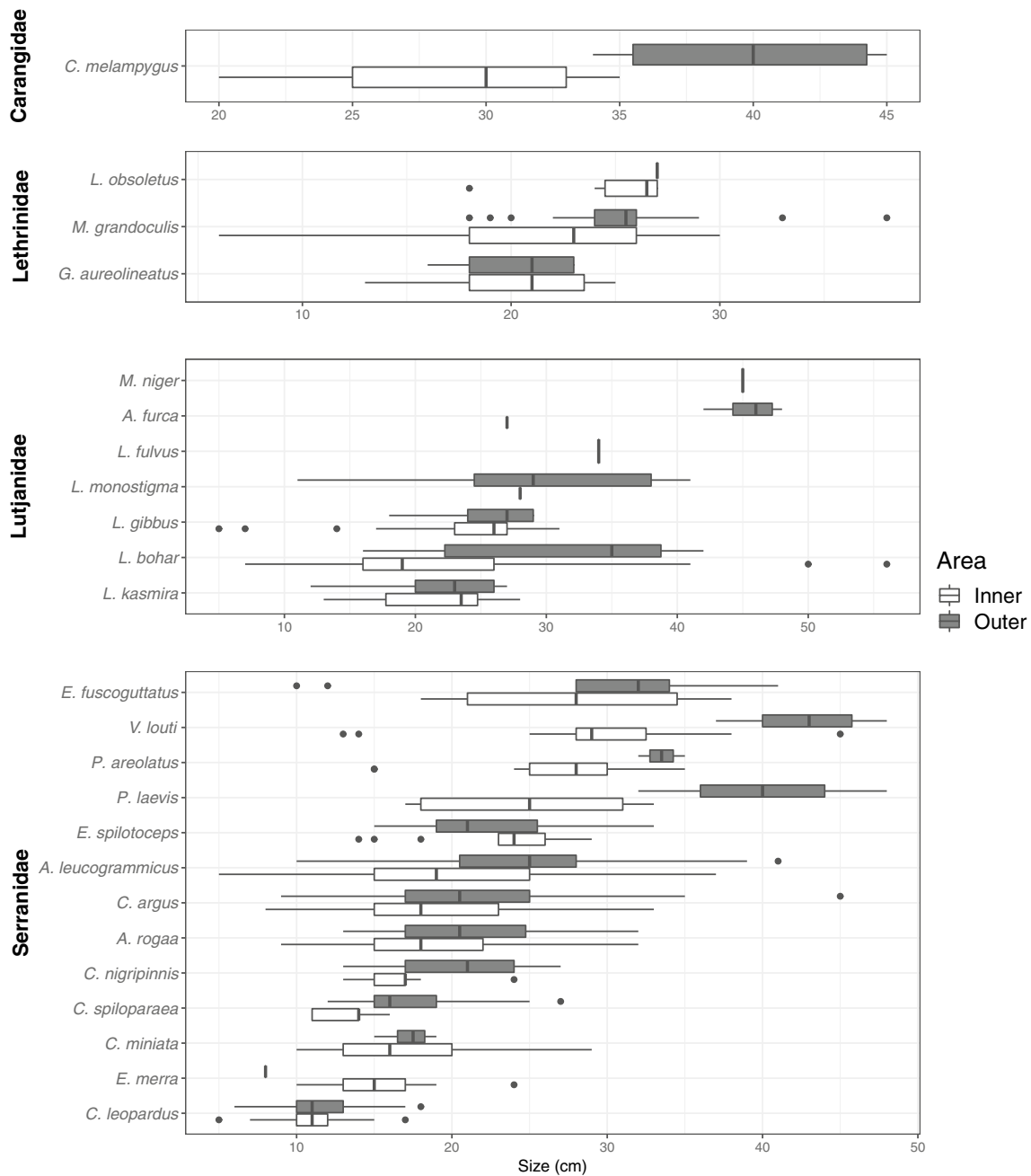
Fig. 5 Total length (cm) of predators belonging to four families where there were significant differences between inner and outer atoll, as indicated by ANOVA and linear mixed effects models. Vertical bars represent the median

overlap between areas (Fig. 6). There were highly significant differences in the predator assemblage between atoll areas (Nested PERMANOVA, UVC = $F(1) = 17.57$, $p \leq 0.001$; BRUV = $F(1) = 4.07$, $p \leq 0.001$) and among sites (Nested PERMANOVA, UVC = $F(38) = 2.21$, $p \leq 0.001$; BRUV = $F(37) = 1.40$, $p \leq 0.001$). SIMPER analysis revealed a high level of dissimilarity in biota between atoll areas (SIMPER UVC = 63.94%, driven by *Cephalopholis leopardus*, *C. argus*, and *Anyperodon leucogrammicus*;

BRUV = 74.11%, driven by *Caranx melampygus* and *C. argus*; Table 3). Within areas, similarity of predator assemblages recorded using UVC was moderate (SIMPER, inner: 41.10%, driven by *C. argus*, *A. leucogrammicus*, and *Monotaxis grandoculis*; outer: 49.12%, driven by *C. argus* and *C. leopardus*), while similarity of those recorded using BRUV was low (SIMPER, inner: 29.07%, driven by *Aethaloperca rogaa*, *Lutjanus bohar*, and *C. argus*; outer: 33.37%, driven by *C. argus*, *A. rogaa*, and *L. bohar*; Table 3).
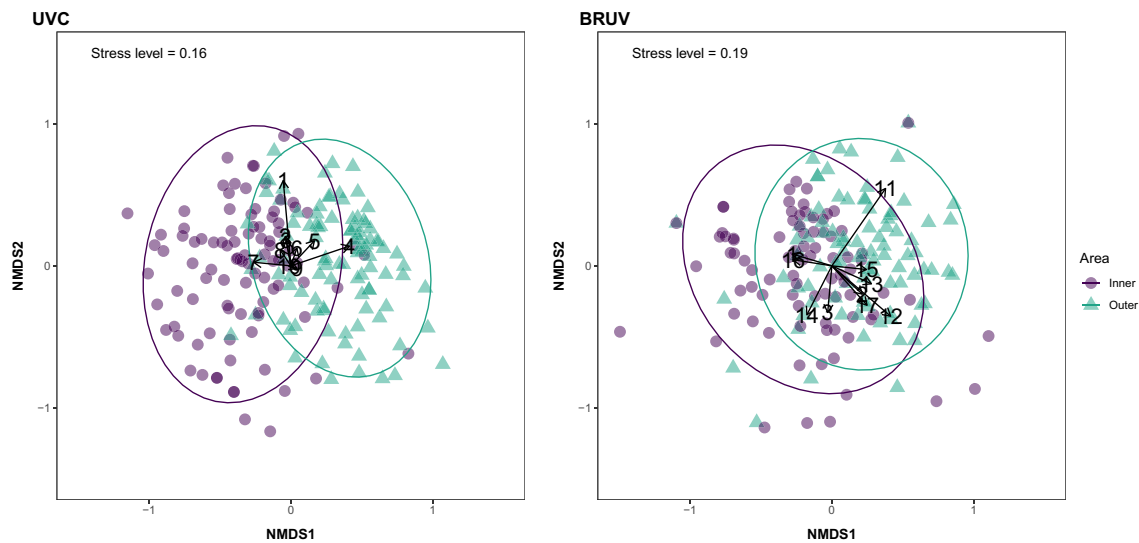
Fig. 6 Non-metric multidimensional scaling (nMDS) of predator abundance data from **a** underwater visual census (UVC) and **b** baited remote underwater video (BRUV). Species that are significantly correlated ($p < 0.05$) are overlaid as vectors. UVC (1–10) and BRUV (1–3, 11–17): 1: *Aethaloperca rogaa*; 2: *Aprion virescens*; 3: *Caranx melampygus*; 4: *Cephalopholis spiloparaea*; 5: *Epinephelus fasciatus*; 6: *Epinephelus malabaricus*; 7: *Epinephelus merra*; 8: *Gnathodentex aureolineatus*; 9: *Macolor niger*; 10: *Pterois antennata*; 11: *Cephalopholis argus*; 12: *Cephalopholis leopardus*; 13: *Cephalopholis nigripinnis*; 14: *Cephalopholis* spp.; 15: *Epinephelus spilotoceps*; 16: *Lutjanus bohar*; 17: *Nebrius ferrugineus*

Table 3 Main species contributing to between area and within area dissimilarity using both UVC and BRUV abundance data. Species contributing below 9% are not shown

Species	Dissimilarity between Areas (%)	Similarity within Inner (%)	Outer (%)
UVC			
Cephalopholis leopardus	13.73	–	30.41
Cephalopholis argus	11.22	34.62	40.56
Anyperodon leucogrammicus	10.04	18.44	–
Aethaloperca rogaa	9.97	15.39	12.39
Monotaxis grandoculis	9.17	19.35	–
BRUV			
Caranx melampygus	9.95	–	–
Cephalopholis argus	9.08	12.07	32.23
Aethaloperca rogaa	–	30.63	17.64
Lutjanus bohar	–	20.86	14.67
Monotaxis grandoculis	–	10.30	–
Cephalopholis nigripinnis	–	–	12.31

Correlation with environmental variables

Environmental data varied significantly between areas (Nested PERMANOVA, UVC $= F(1) = 11.95$, $p < 0.001$; BRUV $= F(1) = 15.99$, $p < 0.001$) and among sites (Nested PERMANOVA, UVC $= F(38) = 5.89$, $p < 0.001$; BRUV $= F(37) = 1.58$, $p < 0.05$). The first two axes of a PCO explained 82.88% of the total variation in the BRUV environmental data and showed areas to be relatively distinct (Fig. S3). There was similar separation between atoll areas in the UVC environmental data, but the first two axes of the PCO only explained 43.1% of the total variation in the data and the points were more clustered (Fig. S3).

The predator assemblage was correlated with the environmental data collected using UVC (RELATE, $Rho = 0.115$, $p < 0.05$) and BRUV (RELATE, $Rho = 0.157$, $p < 0.05$). With the UVC data, marginal tests showed that depth (Pseudo-$F = 25.73$, $p < 0.001$, Prop. variation $= 0.12$), BC (Pseudo-$F = 7.10$, $p < 0.001$, Prop. variation $= 0.3$), MC (Pseudo-$F = 8.12$, $p < 0.001$, Prop. variation $= 0.04$), TC (Pseudo-$F = 2.73$, $p < 0.05$, Prop. variation $= 0.01$), complexity (Pseudo-$F = 3.57$, $p < 0.005$, Prop. variation $= 0.02$)

and PIN (Pseudo-$F = 5.18$, $p < 0.001$, Prop. variation = 0.03) had a significant interaction with the predator assemblage. The most parsimonious model included depth, BC, MC and complexity (DISTLM; AICc = 1479.1), which when visualised using a dBRDA explained 87.2% of the variation in the fitted data but only 13.6% of the total variation in the data (Fig. 7a). For the BRUV data, marginal tests showed that complexity (Pseudo-$F = 3.18$, $p < 0.005$, Prop. variation = 0.02), depth (Pseudo-$F = 3.26$, $p < 0.001$, Prop. variation = 0.02) and habitat type (Pseudo-$F = 2.31$, $p < 0.05$ Prop. variation = 0.01) had a highly significant correlation with the predator assemblage, but the final best model included only depth and complexity (DISTLM; AICc = 1377.8). Results visualised using a dbRDA explained 100% of the variation in the fitted data but only 3.7% of the total variation in the data (Fig. 7b).

Discussion

There were several distinct differences between the inner lagoonal and outer edge reef habitats. In contrast to previous studies, density and diversity of predators were similar between the inner lagoonal and outer forereef slopes (Friedlander et al. 2010; Dale et al. 2011), but there were significant differences in species composition. Furthermore, when the rarely recorded *Nebrius ferrugineus* was omitted, biomass was significantly greater along the outer reef slopes. Lethrinidae, Lutjanidae, and Serranidae, were also significantly larger in the outer atoll, so despite being more numerically abundant in the inner atoll, their mean biomass was greater along the outer reef slopes. Schooling species belonging to these families (e.g. *Gnathodentex aureolineatus* and *Lutjanus kasmira*) were more frequently recorded in the outer atoll (Table S1) and several large bodied species of Lutjanidae and Serranidae were also uniquely recorded in the outer atoll (e.g. *Epinephelus malabaricus*, *Lutjanus decussatus*, *Lutjanus fulvus*, and *Macolor macularis*).

These findings are consistent with shifts in habitat usage related to ontogeny. Although teleost reef predators often have relatively small home ranges (Nash et al. 2015), some species of Lutjanidae, Lethrinidae and Serranidae may move tens to hundreds of kilometres between habitat types as they undergo ontogenetic shifts, moving from juvenile nurseries such as mangroves and seagrasses to their adult habitat on coral reefs (Williams 1991; Green et al. 2015). The presence of juvenile nursery habitats close to coral reefs increases adult biomass (Mumby et al. 2004; Nagelkerken 2007), while a lack of nursery habitats has been linked to lower adult densities and the absence of some species (Olds et al. 2012; Wen et al. 2013). The significant differences in predator sizes and abundances between inner and outer atoll found here are consistent with ontogenetic habitat shifts, and indicate that the inner atoll lagoon may be an important nursery habitat for many of these predator species. In the British Virgin Islands, nearly half the reef fishes exhibited ontogenetic shifts between lagoons and forereefs and almost all species were significantly larger in the reef habitat than in the lagoon (Gratwicke et al. 2006). Furthermore, even isolated nursery habitats are utilized by juvenile emperors, suggesting that ontogenetic migrations of these species act to connect adult and juvenile habitats (Nakamura et al. 2009). In North Malé Atoll, the proximity of the edge and lagoonal reefs to each other, in addition to the relatively shallow nature of the lagoon, may facilitate a high degree of mobility and connectivity between inner and outer atoll (Berkström et al. 2013).
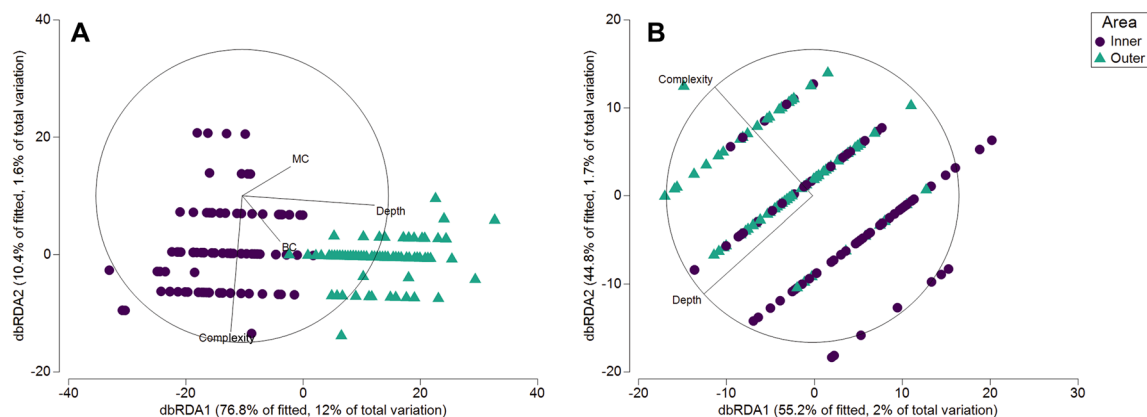

Fig. 7 Distance-based redundancy analysis (dbRDA) of Bray–Curtis dissimilarities calculated from square root transformed abundance of reef predator species vs. environmental predictor variables. The most parsimonious model was chosen using the AICc selection criterion and included **a** complexity, depth, branching coral (BC), and massive coral (MC) for the underwater visual census (UVC) predator data, and **b** depth and complexity for the baited remote underwater video (BRUV) predator data

Differences in the reef habitat between atoll areas may also play a role. The outer reef slopes provide a larger, more continuous reef area compared to the shallow inner reefs, where soft bottom habitat is extensive. Large piscivorous fish are more abundant in areas of higher live coral cover with greater habitat structural complexity (Connell and Kingsford 1998), and growth rates and abundances of predatory fishes tend to be higher when prey densities are greater (Beukers-Stewart et al. 2011). Higher prey availability is also a key driver of ontogenetic emigrations of snappers and emperors from nearshore to coral reef habitats (Kimirei et al. 2013). The larger body sizes and school sizes in the outer atoll, in addition to the unique occurrence of several of these species, suggest that this habitat may be of a higher quality, providing sufficient food and space to fit the requirements of these predator species. However, only a detailed assessment of the available habitat and prey assemblages will help determine the factors influencing predator distributions.

Several families had a greater biomass in the inner atoll, including Aulostomidae, Carangidae, Fistulariidae and Ginglymostomatidae. Aulostomidae were rarely recorded along the outer reef slopes, although their habitat preferences include reefs extending to the continental slope (Bowen et al. 2001). Competition from the greater numbers of Lutjanidae and Serranidae may play a role in limiting their numbers in the outer atoll. Higher numbers of the bluefin trevally, *Caranx melampygus*, were the main contribution to the greater biomass of Carangidae. *C. melampygus* is an important mobile predator that is prominent in nearshore waters (Hobson 1979; Sancho 2000). Their diet consists of diurnally active prey, predominantly from shallow-water habitats (Sudekum et al. 1991), which suggests they may enter the lagoon during the day to hunt. The lagoon may also represent an important nursery ground for this species, as juvenile *C. melampygus* occupy shallow-water protected environments, such as lagoons and estuaries (Smith and Parrish 2002). As no UVC surveys or BRUV deployments were conducted at night, it is not certain whether their numbers would increase along the outer reef slopes after dark. Fistulariidae and Ginglymostomatidae had a greater biomass in the inner atoll, but only because biomass estimates were derived solely from UVC. Fistulariidae prefer coastal areas with soft bottoms (Fritzsche 1976) and were recorded in both atoll areas with BRUVs, but the UVC surveys were conducted solely on hard reef substrate. Ginglymostomatidae were frequently recorded in both inner and outer atoll on BRUVs, but biomass estimates came from the occurrence of several large *N. ferrugineus* on two transects in the inner atoll, while none were recorded during UVC in the outer atoll. Future work would benefit from the inclusion of biomass estimates from several survey methods and from conducting surveys at night.

Several species were recorded solely in one atoll area. Two of the species unique to the outer atoll were the grey reef shark, *Carcharhinus amblyrhynchos*, and the lemon shark, *Negaprion acutidens*. Grey reef sharks prefer forereef habitats over lagoons (Papastamatiou et al. 2018) and although juvenile lemon sharks are atoll lagoon residents (Filmalter et al. 2013), adults move to deeper coastal reef habitats (Compagno 1984). Conversely, the silky shark, *Carcharhinus falciformis*, and the rainbow runner, *Elagatis bipinnulata*, were recorded exclusively in the inner atoll by the BRUVs; these are not typically reef-associated species (Bonfil 1993) but the BRUVs were effective in recording their use of the channels between the shallow inner reefs. Channels act as important habitat corridors, enhancing connectivity between the inner lagoonal and outer reef slopes, with energy moving from one area to another through a range of hydrodynamic processes (Sasamal 2007; Rogers et al. 2017; Green et al. 2019). These corridors also facilitate movement of mobile marine species, with marine predators taking advantage of them for foraging (Hastie et al. 2016). The thumbprint, *Lethrinus harak,* and smalltooth, *L. microdon*, emperors were also only observed in the inner atoll on BRUVs. Emperors forage extensively over sandy bottoms where they predate on less mobile prey (Kulbicki et al. 2005). While the BRUVs were deployed over a range of hard and soft bottom substrates, the UVC surveys were conducted solely on hard bottom reef substrate. In addition, BRUVs will attract these species to the bait, while UVC typically requires high replication to record such species (Dulvy et al. 2003). These discrepancies between the survey methods may explain the absence of the emperors from the UVC dataset. Moreover, these species are not necessarily exclusive to one area. The 1-h BRUV soak time and lack of long-term and night time sampling are likely to lead to underrepresentation or absence of rarer species (Asher et al. 2017).

The asymptotes of the species accumulation plots suggested that the BRUV and UVC surveys were sufficient to obtain an accurate measure of species richness and, although actual values varied, predator family abundance patterns were similar for both methods between areas. However, several species uniquely recorded with either UVC or BRUV underline the importance of using more than one survey methodology when assessing fish populations. For example, sharks were almost exclusively recorded with BRUVs. BRUVs are more effective at recording carnivores (Langlois et al. 2010) and heavily exploited species that are wary of divers (Lindfield et al. 2014). The teleost predators identified through the BRUV footage have small home ranges (Nash et al. 2015) and will not travel far in response to a bait plume, but sharks, being more mobile, may follow bait plumes to investigate the origin of the scent. This is one of the biases of this methodology (Willis and Babcock 2000; Cappo et al.

2003; Harvey et al. 2012), but it is also why BRUVs are effective in tandem with UVC, which underrepresents more mobile, transient species (MacNeil et al. 2008). In contrast, the species recorded solely during UVC, such as the strawberry grouper, *Cephalopholis spiloparaea*, the honeycomb grouper, *Epinephelus merra* and the spotfin lionfish, *Pterois antennata*, are more cryptic and wary. These species may be near the BRUV but their cryptic nature, the habitat complexity and the angle of the camera mean they may be missed.

Our analysis found a clear interaction of the predator assemblage data with live branching and massive coral cover, which accords with previous studies (Bell and Galzin 1984; Komyakova et al. 2013). Depth and complexity were important variables for models of both the UVC and the BRUV assemblage data. Structural complexity on reefs provides important habitat structure and refuge for prey assemblages and is linked to increased fish biomass and abundance (Rogers et al. 2014). While structural complexity is also important for predator assemblages, reefs of intermediate complexity are most suitable for their productivity, as the increased refuge space on higher complexity reefs allows more prey to hide, thereby reducing available food (Rogers et al. 2018). The relationship between predator assemblage data and structural complexity is complicated, but its inclusion in both models reinforces its importance in structuring predator assemblages (Ferrari et al. 2017). Depth was the second predictor included in both models. Reef fish communities vary dramatically with depth (Friedlander et al. 2010; Schultz et al. 2014; Jankowski et al. 2015), as predator abundances and species compositions change (Asher et al. 2017; Tuya et al. 2017). Its inclusion in both models is further evidence that it also plays a key role in structuring predator assemblages.

Total biomass of all recorded predators (inner atoll 0.29 t ha^{-1}, outer atoll 0.25 t ha^{-1}) was similar to that found at other remote but inhabited and exploited atolls (Kiritimati ~ 0.2 t ha^{-1}, Tabuaeran ~ 0.3 t ha^{-1} (Sandin et al. 2008)), and it was considerably lower than at unfished, uninhabited atolls and islands (Palmyra ~ 1.8 t ha^{-1}, Kingman ~ 5.2 t ha^{-1} (Sandin et al. 2008); Chagos Archipelago ~ 3–7.75 t ha^{-1} (Graham et al. 2013)). Although the Maldives are considered underexploited (Newton et al. 2007), this indicates that these predator species are likely overfished. Reef fisheries provide an important source of food to both tourists and increasingly locals, and the rise in reef fish catch is evidence of a growing demand for these resources (Sattar et al. 2014). Reef predators typically dominate the reef fish catch with fishermen targeting Carangidae, Lutjanidae and Serranidae using handlines (Sattar et al. 2011, 2012, 2014). Although more recent information on the status of the reef fishery is lacking, significant declines in the mean length of the ten most

exploited grouper species (Sattar et al. 2011) and of key target species *Lutjanus bohar* and *L. gibbus* (Sattar et al. 2014) suggest the fishery is already overexploited.

In addition to the outer reef slopes, reef fisherman in Baa Atoll, North and South Ari Atoll, and Vaavu Atoll target patch reef edges and small isolated submerged reefs (locally known as *thila*) in the lagoon, but there is little information available on which habitats fishers target in North Malé Atoll (Sattar et al. 2012). Furthermore, although resort islands within atoll lagoons often prohibit fishing on their house reefs (Domroes 2001; Moritz et al. 2017), they organise regular recreational fishing trips to reefs nearby. Catches from these recreational trips are also dominated by upper level reef predators (e.g. *C. melampygus*, *Cephalopholis miniata*, *L. bohar*, *L. gibbus*, *Lethrinus olivaceus*), with an estimated 68,000 individuals caught on an annual basis, often of a small size (Sattar et al. 2014). Currently, recording of resort landings data is voluntary (Sattar et al. 2014), so the full impact of these trips has not been accurately quantified, despite the fact that they occur at a national scale. Given the consistent removal of reef predators through both commercial and recreational fishing, it is likely that lagoonal reefs are being substantially exploited yet their predator populations are largely unstudied. While predators were recorded throughout the sites surveyed, the relatively low total biomass recorded here is indicative of an exploited system (Friedlander et al. 2010). Recovery of exploited systems to intact (or nearly intact) conditions and a high biomass of apex predators is estimated to take decades and involve large area closures (Myers and Worm 2003; Robbins et al. 2006). While this may be unrealistic to achieve, careful management of the reef fish populations in the Maldives is required to prevent irreversible loss of these key predatory species.

Globally reef predator populations are declining and species richness is being lost due to climate change and a range of direct anthropogenic stressors (Friedlander and DeMartini 2002; Hempson et al. 2017; Hughes et al. 2017). To date, little information exists on reef predator assemblages and their distributions in the Maldives. Evidently, lagoonal reefs are important habitats hosting diverse and abundant reef predator populations which may have been previously undervalued. Predator assemblages are important in terms of biodiversity and available resources, so there is an urgent need to manage them carefully in the face of climate change, rapidly increasing tourism, and fisheries expansion to prevent future declines in their populations.

Author contributions CS, ACM, SPN and NVCP conceived the ideas and designed the methodology. CS and SNA collected the data and CS processed and analysed the data. CS wrote the first draft of the manuscript and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

References

Adam MS, Sinan H (2013) Coastal and marine fisheries management in the Maldives. SAARC Agriculture Centre (SAC), Bangladesh

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Asher J, Williams ID, Harvey ES (2017) An assessment of mobile predator populations along shallow and mesophotic depth gradients in the Hawaiian Archipelago. Sci Rep 7:3905. https://doi.org/10.1038/s41598-017-03568-1

Bascompte J, Melian CJ, Sala E (2005) Interaction strength combinations and the overfishing of a marine food web. Proc Natl Acad Sci 102:5443–5447. https://doi.org/10.1073/pnas.0501562102

Bates D, Maechler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48. https://doi.org/10.18637/jss.v067.i01

Beetham EP, Kench PS (2014) Wave energy gradients and shoreline change on Vabbinfaru platform, Maldives. Geomorphology 209:98–110. https://doi.org/10.1016/j.geomorph.2013.11.029

Bell K, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. Mar Ecol Prog Ser 15:265–274

Berkström C, Gullström M, Lindborg R, Mwandya AW, Yahya SAS, Kautsky N, Nyström M (2012) Exploring 'knowns' and 'unknowns' in tropical seascape connectivity with insights from east African coral reefs. Estuar Coast Shelf Sci 107:1–21. https://doi.org/10.1016/j.ecss.2012.03.020

Berkström C, Lindborg R, Thyresson M, Gullström M (2013) Assessing connectivity in a tropical embayment: fish migrations and seascape ecology. Biol Conserv 166:43–53. https://doi.org/10.1016/j.biocon.2013.06.013

Beukers-Stewart BD, Beukers-Stewart JS, Jones GP (2011) Behavioural and developmental responses of predatory coral reef fish to variation in the abundance of prey. Coral Reefs 30:855–864. https://doi.org/10.1007/s00338-011-0792-9

Bonfil R (1993) The biology and ecology of the silky shark, Carcharhinus falciformis, from the Campeche Bank. México NOAA/NMFS, Silver Spring

Bowen BW, Bass AL, Rocha LA, Grant WS, Robertson DR (2001) Phylogeography of the trumpetfishes (Aulostomus): ring species complex on a global scale. Evolution 55:1029–1039

Brock RE (1982) A critique of the visual census method for assessing coral-reef fish populations. Bull Mar Sci 32:269–276

Cappo M, De'ath G, Speare P (2007) Inter-reef vertebrate communities of the Great Barrier Reef Marine Park determined by baited remote underwater video stations. Mar Ecol Prog Ser 350:209–221

Cappo M, Harvey ES, Malcolm H, Speare P (2003) Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas. In: Beumer JP, Grant A, Smith DC (eds) Aquatic protected areas what works best and how do we know?. University of Queensland, Queensland, pp 455–464

Ceccarelli D, Ayling T (2010) Role, importance and vulnerability of top predators on the Great Barrier Reef—a review. Great Barrier Reef Marine Park Authority

Chou LM, Wilkinson CR, Licuanan WRY, Alino P, Cheshire AC, Loo MGK, Tangjaitrong S, Sudara S, Ridzwan AR, Soekarno SS (1994) Status of coral reefs in the ASEAN region. In: Wilkinson CR, Sudara S, Chou LM (eds) Third ASEAN-Australia Symposium on Living Coastal Resources. Chulalongkorn University, Bangkok, pp 1–10

Clark RD, Pittman S, Caldow C, Christensen J, Roque B, Appeldoorn RS, Monaco ME (2009) Nocturnal fish movement and trophic flow across habitat boundaries in a coral reef ecosystem (SW Puerto Rico). Caribb J Sci 45:282–303. https://doi.org/10.18475/cjos.v45i2.a15

Clarke K, Warwick R (2001) Change in marine communities: an approach to statistical analysis and interpretation. PRIMER-E, Plymouth

Clarke KR, Gorley RN (2006) PRIMER v6: user manual/tutorial. PRIMER-E Ltd, Plymouth

Compagno LJV (1984) Sharks of the world: an annotated and illustrated catalogue of shark species known to date. FAO, Rome

Connell SD, Kingsford MJ (1998) Spatial, temporal and habitat-related variation in the abundance of large predatory fish at One Tree Reef, Australia. Coral Reefs 17:49–57. https://doi.org/10.1007/s003380050094

Dale JJ, Meyer CG, Clark CE (2011) The ecology of coral reef top predators in the Papahānaumokuākea Marine National Monument. J Mar Biol 2011:1–14. https://doi.org/10.1155/2011/725602

Domroes M (2001) Conceptualising state-controlled resort islands for an environment-friendly development of tourism: the Maldivian experience. Singap J Trop Geogr 22:122–137. https://doi.org/10.1111/1467-9493.00098

Dulvy NK, Sadovy Y, Reynolds JD (2003) Extinction vulnerability in marine populations. Fish Fish 4:25–64

Espinoza M, Cappo M, Heupel MR, Tobin AJ, Simpfendorfer CA (2014) Quantifying shark distribution patterns and species-habitat associations: implications of marine park zoning. PLoS ONE 9:e106885. https://doi.org/10.1371/journal.pone.0106885

FAO (2006) Review of the state of world marine capture fisheries management: Indian Ocean, Rome

Ferrari R, Malcom HA, Byrne M, Friedman A, Williams SB, Schultz A, Jordan AR, Figueira WF (2017) Habitat structural complexity metrics improve predictions of fish abundance and distribution. Ecography 41:1077–1091. https://doi.org/10.1111/ecog.02580

Filmalter JD, Dagorn L, Cowley PD (2013) Spatial behaviour and site fidelity of the sicklefin lemon shark Negaprion acutidens in a remote Indian Ocean atoll. Mar Biol 160:2425–2436. https://doi.org/10.1007/s00227-013-2237-1

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: the effects of fishing down apex predators. Mar Ecol Prog Ser 230:253–264

Friedlander AM, Sandin SA, DeMartini EE, Sala E (2010) Spatial patterns of the structure of reef fish assemblages at a pristine atoll in the central Pacific. Mar Ecol Prog Ser 410:219–231. https://doi.org/10.3354/meps08634

Frisch AJ, Ireland M, Baker R (2014) Trophic ecology of large predatory reef fishes: energy pathways, trophic level, and implications for fisheries in a changing climate. Mar Biol 161:61–73. https://doi.org/10.1007/s00227-013-2315-4

Fritzsche RA (1976) A review of the cornetfishes, genus *Fistularia* (Fistulariidae), with a discussion of intrageneric relationships and zoogeography. Bull Mar Sci 26:196–204

Graham NAJ, Pratchett MS, McClanahan TR, Wilson SK (2013) The status of coral reef fish assemblages in the Chagos Archipelago, with implications for protected area management and climate change. In: Sheppard C (ed) Coral reefs of the United Kingdom overseas territories. Springer, Dordrecht

Graham NAJ, Spalding MD, Sheppard CRC (2010) Reef shark declines in remote atolls highlight the need for multi-faceted conservation action. Aquat Conser Mar Freshw Ecosyst 20:543–548. https://doi.org/10.1002/aqc.1116

Gratwicke B, Petrovic C, Speight MR (2006) Fish distribution and ontogenetic habitat preferences in non-estuarine lagoons and adjacent reefs. Environ Biol Fishes 76:191–210. https://doi.org/10.1007/s10641-006-9021-8

Green AL, Maypa AP, Almany GR, Rhodes KL, Weeks R, Abesamis RA, Gleason MG, Mumby PJ, White AT (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev 90:1215–1247. https://doi.org/10.1111/brv.12155

Green RH, Jones NL, Rayson MD, Lowe RJ, Bluteau CE, Ivey GN (2019) Nutrient fluxes into an isolated coral reef atoll by tidally driven internal bores. Limnol Oceanogr 64:461–473. https://doi.org/10.1002/lno.11051

Hamner WM, Colin PL, Hamner PP (2007) Export-import dynamics of zooplankton on a coral reef in Palau. Mar Ecol Prog Ser 334:83–92. https://doi.org/10.3354/meps334083

Hamner WM, Jones MS, Carleton JH, Hauri IR, Williams DM (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bull Mar Sci 42:459–479

Harvey ES, Newman SJ, McLean DL, Cappo M, Meeuwig JJ, Skepper CL (2012) Comparison of the relative efficiencies of stereo-BRUVs and traps for sampling tropical continental shelf demersal fishes. Fish Res 125–126:108–120. https://doi.org/10.1016/j.fishres.2012.01.026

Harvey E, McLean D, Frusher S, Haywood M, Newman SJ, Williams A (2013) The use of BRUVs as a tool for assessing marine fisheries and ecosystems: a review of the hurdles and potential. University of Western Australia, Perth

Hastie GD, Russell DJF, Benjamins S, Moss S, Wilson B, Thompson D (2016) Dynamic habitat corridors for marine predators; intensive use of a coastal channel by harbour seals is modulated by tidal currents. Behav Ecol Sociobiol 70:2161–2174. https://doi.org/10.1007/s00265-016-2219-7

Heithaus MR, Hamilton IM, Wirsing AJ, Dill LM (2006) Validation of a randomization procedure to assess animal habitat preferences: microhabitat use of tiger sharks in a seagrass ecosystem. J Anim Ecol 75:666–676. https://doi.org/10.1111/j.1365-2656.2006.01087.x

Hempson TN, Graham NAJ, MacNeil MA, Williamson DH, Jones GP, Almany GR (2017) Coral reef mesopredators switch prey, shortening food chains, in response to habitat degradation. Ecol Evol 7:2626–2635. https://doi.org/10.1002/ece3.2805

Hobson ES (1979) interactions between piscivorous fishes and their prey. In: Clepper HE (ed) Predator-prey systems in fisheries management. Sport Fishing Inst, Washington, pp 231–242

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017) Coral reefs in the Anthropocene. Nature 546:82–90. https://doi.org/10.1038/nature22901

Jankowski MW, Graham NAJ, Jones GP (2015) Depth gradients in diversity, distribution and habitat specialisation in coral reef fishes: implications for the depth-refuge hypothesis. Mar Ecol Prog Ser 540:203–215. https://doi.org/10.3354/meps11523

Kiggins RS, Knott NA, Dvis AR (2018) Miniature baited remote underwater video (mini-BRUV) reveals the response of cryptic fishes to seagrass cover. Environ Biol Fishes 101:1717–1722

Kimirei IA, Nagelkerken I, Trommelen M, Blankers P, van Hoytema N, Hoeijmakers D, Huijbers CM, Mgaya YD, Rypel AL (2013) What drives ontogenetic niche shifts of fishes in coral reef ecosystems? Ecosystems 16:783–796. https://doi.org/10.1007/s10021-013-9645-4

Komyakova V, Munday PL, Jones GP (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. PLoS ONE 8:e83178. https://doi.org/10.1371/journal.pone.0083178

Kulbicki M (1988) Correlation between catch data from bottom longlines and fish censuses in the SW lagoon of New Caledonia. In: 6th International Coral Reef Symposium, Townsville, pp 305–312

Kulbicki M, Bozec Y-M, Labrosse P, Letourneur Y, Mou-Tham G, Wantiez L (2005) Diet composition of carnivorous fishes from coral reef lagoons of New Caledonia. Aquat Living Res 18:231–250. https://doi.org/10.1051/alr:2005029

Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects. Aquat Biol 9:155–168

Legendre P, Anderson M (1999) Distance-based redundancy analysis: testing multispecies hypotheses responses in multifactorial ecological experiments. Ecol Monogr 69:1–24

Lindfield SJ, Harvey ES, McIlwain JL, Halford AR (2014) Silent fish surveys: bubble-free diving highlights inaccuracies associated with SCUBA-based surveys in heavily fished areas. Methods Ecol Evol 5:1061–1069. https://doi.org/10.1111/2041-210x.12262

MacNeil MA, Graham NAJ, Cinner JE, Wilson SK, Williams ID, Maina J, Newman S, Friedlander AM, Jupiter S, Polunin NVC, McClanahan TR (2015) Recovery potential of the world's coral reef fishes. Nature 520:341. https://doi.org/10.1038/nature14358

MacNeil MA, Graham NAJ, Conroy MJ, Fonnesbeck CJ, Polunin NVC, Rushton SP, Chabanet P, McClanahan TR (2008)

Detection heterogeneity in underwater visual-census data. J Fish Biol 73:1748–1763. https://doi.org/10.1111/j.1095-8649.2008.02067.x

Mapleston A, Currey LM, Williams AJ, Pears R, Simpfendorfer CA, Penny AL, Tobin A, Welch D (2009) Comparative biology of key inter-reefal serranid species on the Great Barrier Reef. Project milestone report to the marine and tropical sciences research facility. Reef and Rainforest Research Centre Limited, Cairns

Matley JK, Maes GE, Devloo-Delva F, Huerlimann R, Chua G, Tobin AJ, Fisk AT, Simpfendorfer CA, Heupel MR (2018) Integrating complementary methods to improve diet analysis in fishery-targeted species. Ecol Evol 8:9503–9515. https://doi.org/10.1002/ece3.4456

McClanahan TR (2011) Coral reef fish communities in management systems with unregulated fishing and small fisheries closures compared with lightly fished reefs—Maldives vs. Kenya. Aquat Conserv Mar Freshw Ecosyst 21:186–198. https://doi.org/10.1002/aqc.1172

Ministry Of Tourism (2018) Tourism yearbook 2018. Statistics & Research Section, Ministry of Tourism, Republic of Maldives

Moritz C, Ducarme F, Sweet MJ, Fox MD, Zgliczynski B, Ibrahim N, Basheer A, Furby KA, Caldwell ZR, Pisapia C, Grimsditch G, Abdulla A, Beger M (2017) The "resort effect": can tourist islands act as refuges for coral reef species? Divers Distrib 23:1301–1312. https://doi.org/10.1111/ddi.12627

Mumby PJ, Edwards AJ, Ernesto Arias-González J, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CC, Llewellyn G (2004) Mangroves enhance the biomass of coral reef fish communities in the Caribbean. Nature 427:533–536. https://doi.org/10.1038/nature02286

Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. Nature 423:280–283

Nagelkerken I (2007) Are non-estuarine mangroves connected to coral reefs through fish migration? Bull Mar Sci 80:595–607

Nakamura Y, Horinouchi M, Sano M, Shibuno T (2009) The effects of distance from coral reefs on seagrass nursery use by 5 emperor fishes at the southern Ryukyu Islands, Japan. Fish Sci 75:1401. https://doi.org/10.1007/s12562-009-0163-4

Naseer A, Hatcher BG (2004) Inventory of the Maldives coral reefs using morphometrics generated from Landsat ETM+ imagery. Coral Reefs 23:161–168. https://doi.org/10.1007/s00338-003-0366-6

Nash KL, Welsh JQ, Graham NA, Bellwood DR (2015) Home-range allometry in coral reef fishes: comparison to other vertebrates, methodological issues and management implications. Oecologia 177:73–83. https://doi.org/10.1007/s00442-014-3152-y

Newton K, Cote IM, Pilling GM, Jennings S, Dulvy NK (2007) Current and future sustainability of island coral reef fisheries. Curr Biol 17:655–658. https://doi.org/10.1016/j.cub.2007.02.054

Oksanen J, Blanchet GF, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) vegan: Community ecology package. R package version 2.5-2

Olds AD, Connolly RM, Pitt KA, Maxwell PS (2012) Habitat connectivity improves reserve performance. Conserv Lett 5:56–63. https://doi.org/10.1111/j.1755-263X.2011.00204.x

Papastamatiou YP, Bodey TW, Friedlander AM, Lowe CG, Bradley D, Weng K, Priestley V, Caselle JE (2018) Spatial separation without territoriality in shark communities. Oikos 127:767–779. https://doi.org/10.1111/oik.04289

Papastamatiou YP, Lowe CG, Caselle JE, Friedlander AM (2009) Scale-dependent effects of habitat on movements and path structure of reef sharks at a predator-dominated atoll. Ecology 90:996–1008. https://doi.org/10.1890/08-0491.1

Phillips ML, Clark WR, Nusser SM, Sovada MA, Greenwood RJ (2004) Analysis of predator movement in prairie landscapes with contrasting grassland composition. J Mammal 85:187–195. https://doi.org/10.1644/1545-1542

Polunin NVC, Roberts CM (1993) Greater biomass and value of target coral-reef fishes in 2 small Caribbean marine reserves. Mar Ecol Prog Ser 100:167–176. https://doi.org/10.3354/meps100167

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Radice VZ, Hoegh-Guldberg O, Fry B, Fox MD, Dove SG, Dorrepaal E (2019) Upwelling as the major source of nitrogen for shallow and deep reef-building corals across an oceanic atoll system. Funct Ecol 33:1120–1134. https://doi.org/10.1111/1365-2435.13314

Robbins WD, Hisano M, Connolly SR, Choat JH (2006) Ongoing collapse of coral-reef shark populations. Curr Biol 16:2314–2319

Roff G, Doropoulos C, Rogers A, Bozec YM, Krueck NC, Aurellado E, Priest M, Birrell C, Mumby PJ (2016) The ecological role of sharks on coral reefs. Trends Ecol Evol 31:395–407. https://doi.org/10.1016/j.tree.2016.02.014

Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. Curr Biol 24:1000–1005. https://doi.org/10.1016/j.cub.2014.03.026

Rogers A, Blanchard JL, Newman SP, Dryden CS, Mumby PJ (2018) High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. Ecology 99:450–463

Rogers JS, Monismith SG, Fringer OB, Koweek DA, Dunbar RB (2017) A coupled wave-hydrodynamic model of an atoll with high friction: mechanisms for flow, connectivity, and ecological implications. Ocean Model 110:66–82. https://doi.org/10.1016/j.ocemod.2016.12.012

RStudio Team (2015) RStudio: integrated development for R. RStudio, Inc., Boston, MA. http://www.rstudio.com/

Sancho G (2000) Predatory behaviors of *Caranx melampygus* (Carangidae) feeding on spawning reef fishes: a novel ambushing strategy. Bull Mar Sci 66:487–496

Sandin SA, Smith JE, DeMartini E, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh SM, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the northern line islands. PLoS ONE 3:e1548. https://doi.org/10.1371/journal.pone.0001548.g001

Sasamal SK (2007) Island wake circulation off Maldives during boreal winter, as visualised with MODIS derived chlorophyll—a data and other satellite measurements. Int J Remote Sens 28:891–903. https://doi.org/10.1080/01431160600858459

Sattar SA, Najeeb A, Afzal MS, Islam F, Wood E (2011) Review of the Maldivian grouper fishery and export industry. Darwin Reef Fish Project/Marine Research Centre/MCS UK. Male, Republic of Maldives

Sattar SA, Andrefouet A, Andréfouët S, Ahsan M, Adam MS, Anderson CR, Scott L (2012) Status of the coral reef fishery in an atoll country under tourism development: the case of central Maldives. Atoll Res Bull 590:163–186

Sattar SA, Wood E, Islam F, Najeeb A (2014) Current status of the reef fisheries of Maldives and recommendations for management. Marine Research Centre/Marine Conservation Society, UK

Schultz AL, Malcolm HA, Bucher DJ, Linklater M, Smith SD (2014) Depth and medium-scale spatial processes influence fish assemblage structure of unconsolidated habitats in a subtropical marine park. PLoS ONE 9:e96798. https://doi.org/10.1371/journal.pone.0096798

Skinner C, Newman SP, Mill AC, Newton J, Polunin NVC (2019) Prevalence of pelagic dependence among coral reef predators

across an atoll seascape. J Anim Ecol 88:1564–1574. https://doi.org/10.1111/1365-2656.13056

Smith GC, Parrish JD (2002) Estuaries as nurseries for the jacks *Caranx ignobilis* and *Caranx melampygus* (Carangidae) in Hawaii. Estuar Coast Shelf Sci 55:347–359. https://doi.org/10.1006/ecss.2001.0909

Spalding M, Ravilious C, Green EP (2001) World atlas of coral reefs. University of California Press, Berkeley

Sudekum AE, Parrish JD, Radtke RL, Ralston S (1991) Life history and ecology of large jacks in undisturbed, shallow, oceanic communities. Fish Bull US 89:493–513

Svobodová J, Kreisinger J, Šálek M, Koubová M, Albrecht T (2011) Testing mechanistic explanations for mammalian predator responses to habitat edges. Eur J Wildl Res 57:467–474. https://doi.org/10.1007/s10344-010-0455-0

Symonds MRE, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol 65:13–21

Tuya F, Herrero-Barrencua A, Bosch NE, Abreu AD, Haroun R (2017) Reef fish at a remote tropical island (Principe Island, Gulf of Guinea): disentangling taxonomic, functional and phylogenetic diversity patterns with depth. Mar Freshw Res 69:395. https://doi.org/10.1071/mf17233

Ushan M, Wood E, Saleem M, Sattar S (2012) Maldives sharkwatch report for 2009–2010. In: 12th International Coral Reef Symposium, Cairns, Australia.

Wen CKC, Almany GR, Williamson DH, Pratchett MS, Mannering TD, Evans RD, Leis JM, Srinivasan M, Jones GP (2013) Recruitment hotspots boost the effectiveness of no-take marine reserves. Biol Conserv 166:124–131. https://doi.org/10.1016/j.biocon.2013.06.017

White J, Simpfendorfer CA, Tobin AJ, Heupel MR (2013) Application of baited remote underwater video surveys to quantify spatial distribution of elasmobranchs at an ecosystem scale. J Exp Mar Biol Ecol 448:281–288. https://doi.org/10.1016/j.jembe.2013.08.004

Williams DM (1991) Patterns and processes in the distribution of coral reef fishes. In: Sale PF (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, pp 437–474

Willis TJ, Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. Mar Freshw Res 51:755–763. https://doi.org/10.1071/mf00010

Wilson SK, Graham NAJ, Polunin NVC (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Mar Biol 151:1069–1076

Wyatt ASJ, Lowe RJ, Humphries S, Waite AM (2013) Particulate nutrient fluxes over a fringing coral reef: source-sink dynamics inferred from carbon to nitrogen ratios and stable isotopes. Limnol Oceanogr 58:409–427. https://doi.org/10.4319/lo.2013.58.1.0409