

# Species diversity, abundance, biomass, size and trophic structure of fish on coral reefs in relation to shark abundance

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**ABSTRACT:** Theory predicts that loss of gape-limited sharks should lead to increases in the abundance and biomass of smaller size classes of prey. We used stereo-baited remote underwater video stations (stereo-BRUVS) and stereo diver-operated video systems (stereo-DOVS) to characterise the shark and fish assemblages on 2 remote, atoll-like reef systems in northwestern Australia, the Rowley Shoals and the Scott Reefs. Whereas the Rowley Shoals is a marine protected area, sharks have been removed from the Scott Reefs for over 3 centuries. We found that sharks were significantly more diverse, more abundant, larger in size and greater in biomass in the marine reserve relative to the Scott Reefs. Consistent with *a priori* hypotheses, bony fishes displayed greater species diversity, abundance and biomass where sharks were common relative to the predator-depleted location. The size and trophic structure of bony fish assemblages also differed between locations. Our results provide large-scale evidence consistent with the hypothesis that reef-associated sharks are gape-limited trophic omnivores that impose top-down effects on medium sized (<50 cm), low- to mid-trophic level fishes. On stereo-BRUVS, for example, prey in the 0 to 29.99 cm size class had 203% more biomass at the predator-depleted reef relative to the location where sharks were abundant. As body size is an important determinant of ecological role and fitness in fishes, these findings suggest that the rapid and ongoing loss of sharks from reefs globally may have important implications for reef management and investigations into the effect of fishing on reef systems.

**KEY WORDS:** Apex predator · Mesopredators · Herbivores · Food web · Lethal effects · Ecosystems · Natural experiments

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## INTRODUCTION

Body size is one of the most influential factors governing the fitness of animals (Peters 1983). It has been shown to influence mortality rate, reproductive fitness, diet, trophic level and competitive interactions (Jennings et al. 2001, Bonaldo & Bellwood 2008). As a result, size distributions provide unique insights into the structure and function of communities (Woodward et al. 2005). Body size also influences vulnerability to predation, particularly in marine systems where many predators are gape-limited (Scharf et al. 2000). Indeed, many piscivores

are limited to eating prey less than approximately 40% of their own length (Olson 1996, Bethea et al. 2004).

Gape-limitation has been implicated in increases in the abundance and biomass of certain size classes of prey fishes following loss of predators in both temperate ecosystems and on tropical reefs (Carr & Hixon 1995, Daskalov et al. 2007). However, other studies have failed to find evidence for increases in prey abundance and/or biomass following removal of marine predators on coral reefs (Jennings & Polunin 1997). In addition, the impact of gape-limited predators on species richness on reefs is poorly understood,

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with some studies suggesting that they promote diversity while others indicate that they reduce diversity overall (Terborgh 2015). The absence of strong evidence for trophic cascades on coral reefs has been attributed to high levels of functional redundancy and omnivory in reef assemblages (Roff et al. 2016).

The majority of studies on the effect gape-limitation on reef fishes have examined piscivores in general, with the result that relatively little is known explicitly about the ecological role of reef sharks (Roff et al. 2016). However, there is growing evidence that reef sharks should be downgraded in status from apex predators to mid-trophic 'mesopredators' that primarily influence other carnivorous fishes such as lethrinids and lutjanids via competition exclusion rather than predation (Frisch et al. 2016, Roff et al. 2016). Removal of a predator can lead to breakdown of niche partitioning between the predator and competitors, leading to increased access to formerly rare, shared prey and niche expansion to include novel prey items (Schuette et al. 2013). Some insight into the 'apex' versus 'in the pack' question can be gathered by comparing locations where sharks have been removed with those where populations of the predators remain intact. Such large-scale, natural experiments provide an important means of gathering evidence at ecologically relevant scales yet cannot fully control against alternative explanations of patterns (Barley & Meeuwig 2016). In particular, reef comparisons are complicated by the fact that fishermen typically target multiple components of fish communities, such that a reduction of shark-induced effects is compounded by the imposition of a new type of mortality and a loss of selected species within the food web.

The Scott Reefs and the Rowley Shoals offer a rare opportunity to examine the impact of shark overfishing on otherwise unexploited fish assemblages (Ruppert et al. 2013). These remote, atoll-like reefs lie approximately 300 km off the coast in northwestern Australia and are similar with respect to productivity, habitat structure, composition of benthic communities, average coral cover, shelf position and total reef size (Ruppert et al. 2013). The primary difference between the 2 locations is the fishing regime. The Rowley Shoals is a marine protected area established in 1990, containing both no-take zones and zones where minimal, highly regulated charter fishing is allowed. In contrast, sharks have been removed by Indonesian fishers from the Scott Reefs for over 300 yr (Russell & Vail 1988). The fishers target high-

value sharks, trochus and bêche-de-mer, catching reef fishes for subsistence and otherwise leaving the bony fish assemblage largely intact (Milton 1999, Nowara & Newman 2001). The use of traditional fishing methods at the Scott Reefs was legalised by a memorandum of understanding (MOU 74) between the Australian and Indonesian governments in 1974 (Russell & Vail 1988).

Due to historic differences in fishing pressure, the shark assemblages at the 2 locations are significantly different. Whereas the Scott Reefs shark assemblage is characterised primarily by 'mesopredatory' species such as grey reef *Carcharhinus amblyrhynchos* and white tip *Triaenodon obesus*, the Rowley Shoals assemblage additionally contains larger, 'apex' species such as tiger *Galeocerdo cuvier* and scalloped hammerhead *Sphyrna lewini* (Meekan et al. 2006). Moreover, shark populations are 4 to 17 times smaller at the Scott Reefs than at the Rowley Shoals, with some species that are targeted by fishers absent altogether (Meekan & Cappo 2004). Consistent with the hypothesis that loss of sharks can trigger trophic cascades on coral reefs, Ruppert et al. (2013) found that mesopredatory teleosts were more abundant at the shark-depleted Scott Reefs than at the Rowley Shoals, while herbivores were rarer.

Ruppert et al. (2013), however, did not examine whether sharks as gape-limited predators alter the size structure of reef fish assemblages. Here, we tested the hypothesis that a reduction in the number of sharks at the Scott Reefs has led to an increase in the abundance and biomass of fishes belonging to size classes, trophic levels and dietary guilds typically targeted by reef sharks. We also examined evidence for competitive release following declines in sharks at the Scott Reefs and predicted that bony fish assemblages at this location would display lower species diversity than predator-rich reefs due to the beneficial effects of predation on prey coexistence, consistent with Terborgh (2015).

## MATERIALS AND METHODS

We compared shark and fish assemblages between the Scott Reefs and the Rowley Shoals using stereo diver-operated video systems (stereo-DOVS) and stereo-baited remote underwater video systems (stereo-BRUVS). See the 'Supplementary methods' in the Supplement at [www.int-res.com/articles/suppl/m565p163\\_supp.pdf](http://www.int-res.com/articles/suppl/m565p163_supp.pdf) for details of the system design.

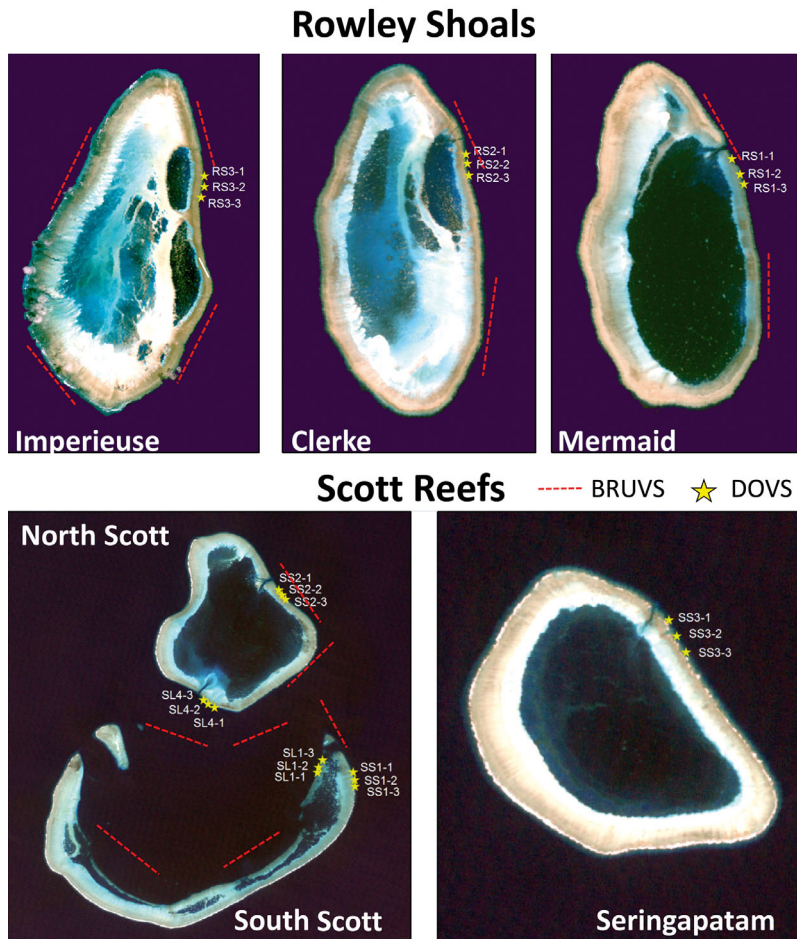


Fig. 1. The Scott Reefs, where sharks are targeted by Indonesian fishermen, and the Rowley Shoals, where sharks are protected, in northwestern Australia. Also shown are the locations of sampling for stereo-BRUVS and stereo-DOVS samples at the Rowley Shoals ( $n_{BRUVS} = 64$  and  $n_{DOVS} = 9$ ) and the Scott Reefs ( $n_{BRUVS} = 56$  and  $n_{DOVS} = 15$ ). Each red dashed line is equivalent to 8 stereo-BRUVS samples, and each yellow star comprises 1 stereo-DOVS sample composed of 5 transects. Fine-scale maps provided by the Australian Institute of Marine Science

Table 1. Number of samples (n) collected at each site and location, and range of depths surveyed, with mean in parentheses. Each stereo-DOVS sample represents the mean of 5 transects, whereas each stereo-BRUVS sample represents a single drop of a camera

Method	Location	Site	n	Depth (m)
Stereo-DOVS	Scott Reefs	North Scott	6	9–11 (10)
		South Scott	6	9–11 (10)
		Seringapatam	3	9–11 (10)
	Rowley Shoals	Clerke	3	9–11 (10)
		Imperieuse	3	9–11 (10)
		Mermaid	3	9–11 (10)
Stereo-BRUVS	Scott Reefs	North Scott	16	34.8–58.0 (42.5)
		South Scott	40	33.2–75.5 (53.4)
	Rowley Shoals	Clerke	16	54.4–71.1 (63.7)
		Imperieuse	32	50.2–91.1 (68.7)
		Mermaid	16	60–76.4 (67.1)

### Sampling techniques

Stereo-DOVS and stereo-BRUVS are non-destructive, camera-based methods that can be used to estimate fish abundance, length and biomass (Schobernd et al. 2014). While stereo-DOVS may provide better abundance estimates for small, rare, cryptic and site-attached species, stereo-BRUVS are more effective at sampling sharks and mesopredatory teleosts (Watson et al. 2010). Stereo-BRUVS capture up to 40% greater species diversity overall than stereo-DOVS and sample herbivores as effectively (Watson et al. 2010). Where length–weight relationships are known, stereo configurations of DOVS and BRUVS allow the lengths of fishes and therefore population biomass to be estimated (Harvey et al. 2012). See the ‘Supplementary methods’ in the Supplement for more information on the relative benefits of the 2 techniques.

### Survey design

The Scott Reefs and the Rowley Shoals were defined as locations (Fig. 1). Each location was composed of 2 to 3 sites and site was nested in location for all analyses (Table 1). Both stereo-DOVS and stereo-BRUVS sampled outer reef slope and lagoonal habitats. In total, 15 stereo-DOVS samples were collected at the Scott Reefs from 3 sites (North Scott, South Scott and Seringapatam). Nine stereo-DOVS samples were also collected at the Rowley Shoals from 3 sites (Clerke, Imperieuse and Mermaid; Fig. 1, Table 1). For stereo-BRUVS, we collected 56 samples at the Scott Reefs from 2 sites (North Scott and South Scott) and 64 samples at the Rowley Shoals (Clerke, Imperieuse and Mermaid reefs). Stereo-BRUVS were deployed in February 2014 at the Scott Reefs and in November 2013 at the Rowley Shoals. Stereo-BRUVS sampled a greater

range of locations and habitats than stereo-DOVS due to the fact that the latter were constrained to pre-designated Australian Institute of Marine Science (AIMS) sites.

### **Fish identification, abundance and length measurements**

Footage from the left camera of the stereo-DOVS and stereo-BRUVS was analysed using the Event-Measure™ software package ([www.seagis.com.au](http://www.seagis.com.au)) and a custom interface (BRUVS1.5.mdb, AIMS 2006). Species were identified to the lowest taxonomic level possible. Analysis of each stereo-BRUVS sample began when the rig settled on the sea floor and continued for 60 min. Abundance was estimated as total abundance per transect (250 m<sup>2</sup>) on stereo-DOVS. On stereo-BRUVS, abundance was estimated as the maximum number of individuals of a given species observed at any one time on a video (MaxN; hereafter referred to as abundance). This approach avoids double counting of individuals, providing a conservative estimate of the relative abundance of species (Letessier et al. 2013). All length measurements were made using EventMeasure™ following the uploading of a CAM calibration file unique to each rig. Footage from the left and right cameras was synchronised using the flashing diode and the length of fishes was measured from snout to fork. For the stereo-DOVS samples, all individuals were measured where possible, whereas on the stereo-BRUVS videos, lengths were only measured at time of MaxN, following Watson et al. (2010).

### **Habitat**

Stereo-DOVS surveys were conducted in comparable, highly rugose reef habitats. However, as stereo-BRUVS were deployed remotely from a boat, there was inevitably some variation in habitats sampled. A still image from the start of each stereo-BRUVS sample was used to classify habitat as dominated by (1) high-profile massive, tabular or branching hard coral, (2) solitary or detached corals, (3) barrel sponges or filterers, (4) rubble with encrusting organisms or (5) soft coral. We further classified habitat as either high complexity (hard coral, barrel sponge or filterer and rubble substrates with encrusting organisms) or low complexity (solitary or detached hard corals, open sandy seabed and soft coral).

### **Data analysis**

Statistical analyses were performed using R software (R Core Team 2015).

### **Length estimation**

Where the length of a fish could not be measured, we developed a number of techniques to estimate it (see 'Supplementary methods' and Tables S1–S3 in the Supplement). In the first instance, length was estimated by taking the mean of conspecific lengths from the same sample. Where no individuals of a given species were measured in a sample, the mean length for the species from the same location was used. If a fish was identified to genus or family but not to species, its length was estimated using a weighted mean of the lengths of all species belonging to that genus or family observed at the location. In the rare instances where no measurements were available for a species from 1 or either location, alternative methods were used ('Supplementary methods' in the Supplement).

### **Weight and biomass**

The weight of each individual was calculated using the allometric relationship between weight ( $W$ ) and length ( $L$ ) where  $W = a \times L^b$  and  $a$  and  $b$  are constants available on FishBase (Froese & Pauly 2015). Where species-specific coefficients were unavailable, the relationship for a similarly sized and/or shaped congener was used (Table S9 in the Supplement). Where no suitable congener was available, we used the relationship for the family or body shape ('Supplementary methods' in the Supplement). To estimate total biomass of a species per sample we summed the individual weights by species.

### **Depth and habitat**

All stereo-DOVS transects were sampled at a mean depth of 9 m at both locations along the outer reef slope or in the lagoon, as per standard protocols used by the AIMS. For the stereo-BRUVS, we tested if depth varied between locations using a 1-tailed  $t$ -test assuming unequal variances. A  $2 \times 2$  chi-square contingency table with no fixed margin was used to determine whether the 2 locations differed in habitat complexity.

### Shark and fish assemblages

The shark and bony fish data were divided into 2 separate datasets. Average values of species diversity, abundance, length and biomass were calculated for both datasets, with site nested in location. Due to lack of independence between stereo-DOVS transects, data were calculated for each of the 5 transects and then averaged to yield a final estimate for the sample. For the stereo-BRUVS, each deployment of a rig constituted a sample because transects were separated by >450 m. Site-level averages were then used to estimate a location-level mean value. To test whether mean values of species diversity, abundance, length and biomass differed by location, we used 1-tailed *t*-tests assuming unequal variance. Differences in the composition of assemblages between locations were tested using permutational multivariate ANOVA (PERMANOVA), using the R function *adonis* (package 'vegan') on a Bray-Curtis dissimilarity matrix of  $\log(x + 1)$  transformed species' abundance and biomass data (9999 permutations [perms]), with site nested in location.

#### Sharks

We defined the 'encounter rate' of sharks as the number of samples in which sharks were present divided by the total number of samples. To test whether the encounter rate differed between locations, we used a  $2 \times 2$  chi-square contingency table with no fixed margin and a Yates correction on the uncorrected counts. Shark species with low sample sizes ( $n = 1$ ) were excluded from the PERMANOVA analysis. We also used similarity percentage analysis (R function *SIMPER*; package 'vegan') to determine the contribution of each species of shark to differences in abundance and biomass between locations on stereo-BRUVS, but not on stereo-DOVS due to a lack of sharks on the latter.

#### Bony fishes

All individuals were divided into 10 cm size classes ranging from 0–9.99 to 180–189.99 cm. Species were assigned trophic levels following Froese & Pauly (2016) and then divided into 6 levels of 0.49 trophic units each, ranging from 2.00 to 4.99. Mean abundance, length and biomass were estimated by taking the average value for all fishes in a size class or trophic level per sample. We also calculated mean

species diversity by trophic level. Relative differences between the 2 locations, the Scott Reefs (S) and the Rowley Shoals (R), in each size class in terms of abundance ( $\% \Delta A$ ) and biomass ( $\% \Delta B$ ) were calculated using the following equation and substituting *B* for *A* for biomass:

$$\% \Delta A = 100 \times \frac{[A_S - A_R]}{A_R} \quad (1)$$

Values were  $\log_{10}(x + 1)$  transformed using the R function *log1p()*. A similar approach was used to estimate relative differences between locations in each trophic level in terms of species diversity ( $\% \Delta SpD$ ).

Differences between the assemblages in terms of the abundance, length and biomass of fishes in each size class and trophic group were tested using PERMANOVA with the R function *adonis*. The analysis was based on a Euclidian distance matrix (Watson et al. 2007), treating trophic level or size class as factors. The contribution of each size class and trophic level to differences in locations was determined using the R function *SIMPER*. Unconstrained principal coordinates analysis was performed (function *CAPSCALE*, package 'vegan') on Bray-Curtis dissimilarity matrices calculated using log-transformed mean values of abundance and biomass by size class and trophic level at each location. The results were visualised using a biplot.

In order to understand whether prey respond differently to removal of sharks based on diet, we also assigned fishes to 8 dietary guilds ('Supplementary methods' in the Supplement for classification system).

#### Estimation of size refuge

Reef sharks typically eat prey with lengths that are 20 to 36% of their own body length (Bethea et al. 2004). We multiplied 0.36 by the mean of the maximum lengths of the 2 most common species of gape-limited shark to estimate the 'absolute' size refuge available to prey, and by the mean length of the 2 species to estimate the 'partial' size refuge. The latter was considered to be the size at which prey would escape predation by the most common size of shark.

## RESULTS

### Shark assemblage

Stereo-DOVS recorded no sharks at the Scott Reefs. At the Rowley Shoals, stereo-DOVS recorded

Table 2. Summary statistics for the fish assemblages at the Scott Reefs and the Rowley Shoals. One-tailed *t*-tests assumed unequal variance and unequal sample sizes. All values are presented as mean ( $\pm$ SE) values per sample, with site nested in location. PERMANOVAs (*F*-statistic) were conducted on mean abundance and biomass values by size and trophic level (in parentheses). Mean values were log-transformed for PERMANOVA (9999 permutations with Euclidean distances). NA: not applicable. \* $p < 0.05$ , \*\* $p < 0.001$

Parameter	Scott Reefs	Rowley Shoals	n	<i>F</i>	<i>t</i>	p
<b>Stereo-DOVS (n = 24)</b>						
Total species	131	115	NA	NA	NA	NA
Species richness	20.3 $\pm$ 1.34	26.6 $\pm$ 1.87	6	–	2.62	0.029*
Abundance	71.2 $\pm$ 15.9	185.6 $\pm$ 26.4	6	–	3.47	0.0011*
			24	7.61 (17.3)	–	0.0003** (9.9 $\times 10^{-4}$ **)
Length (cm)	19.6 $\pm$ 0.51	18.6 $\pm$ 0.59	6	–	1.75	0.22
Biomass (kg)	25.2 $\pm$ 0.54	28.1 $\pm$ 2.77	6	–	2.13	0.37
			24	8.12 (6.06)	–	0.003* (0.0014*)
<b>Stereo-BRUVS (n = 120)</b>						
Total species	161	135		NA	NA	NA
Species richness	21.4 $\pm$ 1.67	14.0 $\pm$ 1.32	5	–	6.31	0.20
Abundance	72.9 $\pm$ 7.83	56.3 $\pm$ 17.4	5	–	0.21	0.209
			120	24.6 (16.1)	–	0.0001** (0.0001**)
Length (cm)	25.5 $\pm$ 1.02	36.3 $\pm$ 1.08	5	–	6.31	0.088
Biomass (kg)	24.5 $\pm$ 4.96	34.5 $\pm$ 4.33	5	–	2.92	0.015*
			120	18.4 (11.7)	–	0.0001** (0.0001**)

0.22  $\pm$  0.22 (mean  $\pm$  SE) species of shark and 0.56  $\pm$  0.56 individuals per sample (all *Carcharhinus amblyrhynchos*, n = 4). Mean shark length and biomass at the Rowley Shoals were 72.2 cm and 2.34  $\pm$  2.34 kg, respectively, and the encounter rate of sharks was 22.2% of samples (Table 2).

Stereo-BRUVS recorded a higher shark species richness per sample at the Rowley Shoals than at the Scott Reefs (1.19  $\pm$  0.06 vs. 0.72  $\pm$  0.10 species per sample;  $t$ [n = 5] = 5.25,  $p = 0.0172$ ; Fig. 2). Sharks were more abundant at the Rowley Shoals than at the Scott Reefs (1 [n = 5]  $\pm$  0.29 vs. 0.73  $\pm$  0.17 sharks per sample; 1-tailed *t*-test assuming unequal variance and unequal sample sizes,  $t$ [5] = 2.92,  $p = 0.014$ ). Encounter rate was significantly higher at the Rowley Shoals compared to the Scott Reefs (74% vs. 55%; 2  $\times$  2 contingency table with no fixed margins and Yates correction,  $\chi^2_{adj} = 6.998$ ,  $p < 0.01$ ). Length per sample was also significantly higher at the Rowley Shoals compared to the Scott Reefs (129.6  $\pm$  8.52 vs. 102.1  $\pm$  3.05 cm;  $t$ [5] = 1.67,  $p = 1.78 \times 10^{-3}$ ). Shark biomass per sample was approximately 13 times greater at the Rowley Shoals than at the Scott Reefs (130.7  $\pm$  22.7 vs. 10.1  $\pm$  1.4 kg per sample;  $t$ [5] = 5.30,  $p = 0.0169$ ). See Table S4 for a summary of values by species and Table S5 for a summary for the entire shark assemblage at each location (both in the Supplement at [www.int-res.com/articles/suppl/m565p163\\_supp.pdf](http://www.int-res.com/articles/suppl/m565p163_supp.pdf)).

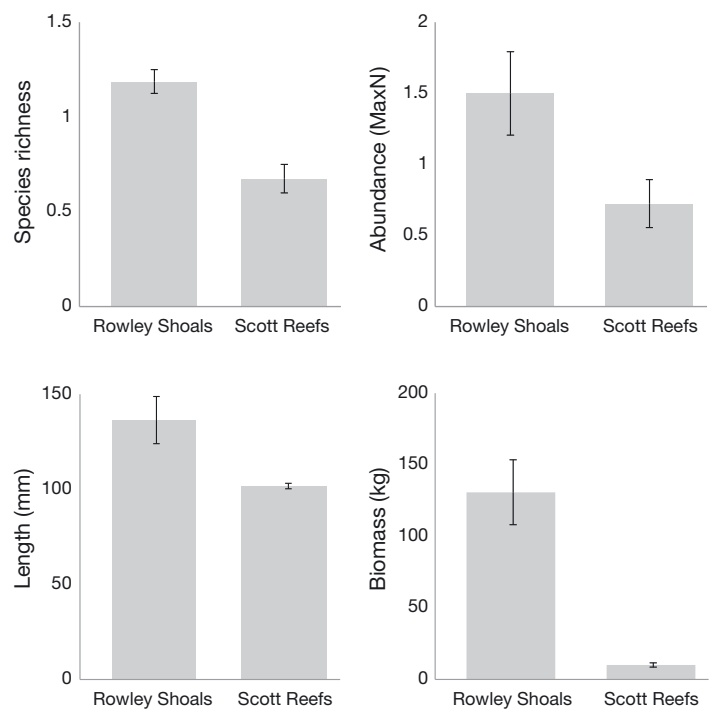


Fig. 2. Characteristics of the shark assemblage (species richness, abundance, length and biomass) for the stereo-BRUVS at the Rowley Shoals (n = 64 samples) and the Scott Reefs (n = 56 samples). All values were calculated as means ( $\pm$ SE) per sample, with site nested in location. Abundance and biomass were, respectively, calculated as the mean MaxN and mean total biomass (kg) per sample site

The composition of the shark assemblage differed significantly in terms of abundance (n = 74,  $F = 12.6$ ,  $p < 0.0001$ , 9999 perms; Fig. 3, Fig. S1 in the Supple-

ment) and biomass ( $n = 120$ ,  $F = 11.3$ ,  $p < 0.0001$ , 9999 perms) by location. SIMPER analysis showed that *C. amblyrhynchos*, *C. albimarginatus* and *Triaenodon obesus* were the main determinants of differences in abundance in the shark assemblages (total contribution 78.4%).

### Fish assemblage

#### Length estimation

Length measurements were available for 29.4% of fishes recorded on stereo-DOVS and 37.6% of all fishes on stereo-BRUVS. We estimated the lengths of an additional 21.1% ( $n = 6945$ ) of all fish counted on stereo-DOVS and 31.0% ( $n = 5050$ ) of all fish observed on stereo-BRUVS by taking the mean of the lengths of conspecifics in the same sample and of 3.48% and 28.9% of fishes on stereo-DOVS and stereo-BRUVS by taking the average of conspecifics at the same location (Table S1 in the Supplement).

#### Species diversity, abundance, length and biomass

On stereo-DOVS, fish were identified to species level for 98.7% of observations (vs. 97.1% of observations on stereo-BRUVS). The total number of species recorded by stereo-DOVS at the Scott Reefs was

131 compared to 115 at the Rowley Shoals. On stereo-BRUVS, 161 species were recorded at the Scott Reefs versus 135 species at the Rowley Shoals. Species richness per sample on stereo-DOVS was significantly lower at the Scott Reefs than at the Rowley Shoals ( $20.3 \pm 1.34$  vs.  $26.6 \pm 1.87$  species per sample; 1-tailed  $t$ -test assuming unequal variance,  $t[6] = 2.62$ ,  $p = 0.0295$ ), but there was no significant difference between locations on stereo-BRUVS (1-tailed  $t$ -test assuming unequal variance,  $t[5] = 6.31$ ,  $p = 0.20$ ; Table 2). All trophic groups had significantly higher species diversity at the Rowley Shoals relative to the Scott Reefs except trophic level 4–4.49, for which there was no significant difference (Table S8 in the Supplement).

Total fish abundance was significantly lower at the Scott Reefs than at the Rowley Shoals on stereo-DOVS ( $71.2 \pm 15.9$  vs.  $185.6 \pm 26.4$  fishes per sample; 1-tailed  $t$ -test assuming unequal variance,  $t[6] = 3.47$ ,  $p = 1.05 \times 10^{-3}$ ) but there was no difference in abundance between the locations based on stereo-BRUVS observations ( $t[5] = 0.21$ ,  $p = 0.209$ ). Fork length did not differ significantly between locations based on stereo-DOVS ( $t[6] = 1.75$ ,  $p = 0.223$ ) or stereo-BRUVS ( $t[5] = 6.31$ ,  $p = 0.088$ ). Biomass did not differ between locations on stereo-DOVS ( $t[6] = 2.13$ ,  $p = 0.374$ ) but was lower at the Scott Reefs than at the Rowley Shoals on stereo-BRUVS ( $24.5 \pm 4.96$  vs.  $34.5 \pm 4.33$  kg per sample,  $t[5] = 2.92$ ,  $p = 0.0149$ ; Table 2).

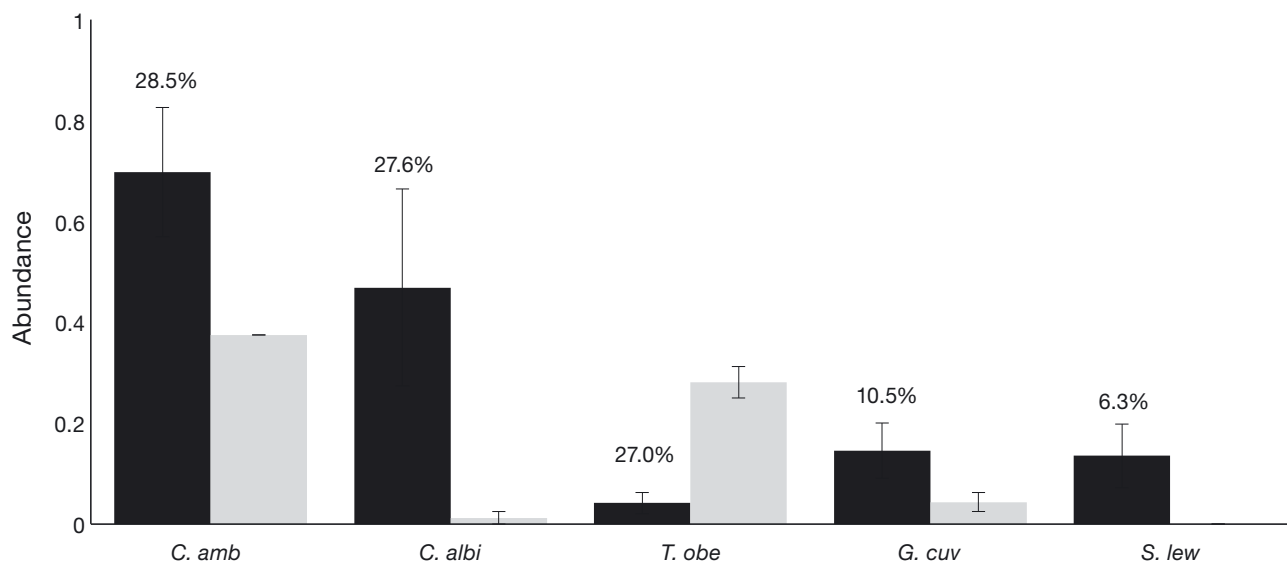


Fig. 3. Abundance on stereo-BRUVS for shark species at the Rowley Shoals (dark,  $n = 64$ ) and the Scott Reefs (light,  $n = 56$ ), with standard error bars. All values were calculated as means (MaxN,  $\pm$ SE) per sample, with site nested in location. The species of shark, from left to right, are *Carcharhinus amblyrhynchos* (*C. amb*), *C. albimarginatus* (*C. albi*), *Triaenodon obesus* (*T. obe*), *Galeocerdo cuvier* (*G. cuv*) and *Sphyrna lewini* (*S. lew*), ordered in descending order according to the % contribution to difference between location as estimated by SIMPER, with the corresponding value given above each bar

## Size classes

PERMANOVA results (Table 2) showed that the fish assemblages at each location differed in size structure with respect to both abundance ( $F[24] = 7.61$ ,  $p = 0.0003$ , 9999 perms) and biomass ( $F[24] = 8.12$ ,  $p = 0.003$ , 9999 perms) on stereo-DOVS. SIMPER analysis showed that the size class 20.00–29.99 cm was the main determinant of differences in abundance between assemblages (24.4%), with fishes in this class 61.7% less abundant at the Scott Reefs than at the Rowley Shoals. The size class 30.00–49.99 cm contributed a further 29.7% of the differences in abundance between the assemblages, with 23.3% more fish of this size on average at the Scott Reefs than the Rowley Shoals. The size class 30–49.99 cm was the main determinant of differences in biomass between assemblages (32.7%) and fishes in this size class had 37.6% more biomass at the Scott Reefs than at the Rowley Shoals (Fig. 4, Table S6 in the Supplement).

The size structure of fish assemblages recorded on stereo-BRUVS was significantly different both in terms of abundance (PERMANOVA,  $F[120] = 24.6$ ,

$p = 0.0001$ , 9999 perms) and biomass (PERMANOVA,  $F[120] = 18.4$ ,  $p = 0.0001$ , 9999 perms) between the 2 locations (Table 2). The main size class on stereo-BRUVS determining differences in the abundance of fish assemblages was 10.00–19.99 cm, with 190.5% more fish of this size at the Scott Reefs than at the Rowley Shoals. The size class 20.00–29.99 cm contributed a further 13.1% of the differences in abundance between assemblages and there were 133.5% more fishes in this group at the Scott Reefs than at the Rowley Shoals. In terms of biomass, the size class 50.00–59.99 cm was the main driver of differences between assemblages, and fish in this category had 64.4% less biomass at the Scott Reefs than at the Rowley Shoals. Almost a third (32.1%) of the difference in biomass between assemblages was due to small fishes (0.00–29.99 cm) and the biomass of fishes in this size class was on average 203.4% higher at the Scott Reefs than at the Rowley Shoals. Fish in the size class 90–109.99 cm were 898% more abundant and had 230% greater biomass at the Scott Reefs than at the Rowley Shoals, with this size class contributing 1.6 and 3.9% of the difference between the 2 assemblages, respectively (Fig. 4, Table S6).

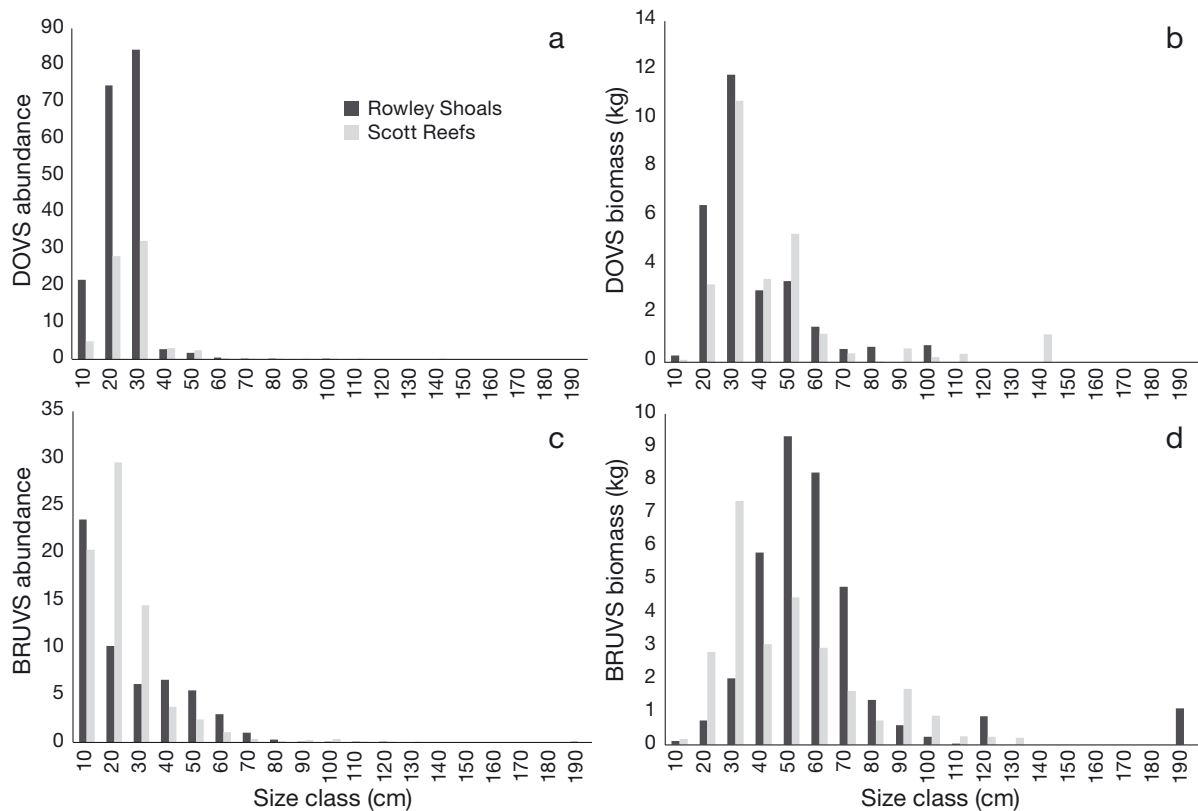


Fig. 4. Size class distributions for fishes by (a,c) abundance and (b,d) biomass on (a,b) stereo-DOVS and (c,d) stereo-BRUVS at the Rowley Shoals (dark) and the Scott Reefs (light). Site was nested within location to derive average values. Abundance and biomass were, respectively, calculated as the mean MaxN and mean total biomass (kg) per sample site. Note that y-axis scales differ



### Trophic level

PERMANOVA results from stereo-DOVS showed that fish assemblages differed in trophic structure with respect to abundance ( $F[24] = 17.3$ ,  $p = 9.9 \times 10^{-4}$ , 9999 perms) and biomass ( $F[24] = 6.06$ ,  $p = 0.0014$ , 9999 perms; Table 2). SIMPER analysis showed that trophic level 3.00–3.49 was the main driver of differences between assemblages in terms of abundance, with fish in this level less abundant at the Scott Reefs than at the Rowley Shoals (Table S7 in the Supplement). Trophic level 4.00–4.49 drove a further 17.2% of the differences between assemblages in terms of abundance, with 191.1% more fish in this trophic level at the Scott Reefs than at the Rowley Shoals. In terms of biomass, trophic level 4.50–4.99 was the most important contributor to differences between assemblages (29.6% of differences), with less biomass in this category at the Scott Reefs than at the Rowley Shoals. Trophic level 3.50–4.49 drove 34.9% of the difference between assemblages, with on average 88.2% greater biomass in this category at the Scott Reefs than at the Rowley Shoals (Table S7).

The trophic structure of fish assemblages recorded on stereo-BRUVS was significantly different both in terms of abundance (PERMANOVA,  $F[120] = 16.1$ ,  $p = 0.0001$ , 9999 perms) and biomass (PERMANOVA,  $F[120] = 11.7$ ,  $p = 0.0001$ , 9999 perms; Table 2). The main trophic level driving differences in abundance between assemblages was 3.00–3.49 (30.0% of differences), with 21.1% more fishes in this category at the Scott Reefs than the Rowley Shoals. Together, trophic level 2.00–4.49 contributed 85.8% of the differences in abundance between fish assemblages, with 116.4% more fishes in this category on average at the Scott Reefs than at the Rowley Shoals (Table S7). Differences in biomass between locations were driven by fishes in trophic level 2.00–2.49 (23.6% of differences), with 62.7% more biomass in this level at the Scott Reefs than at the Rowley Shoals. Overall, trophic level 2.00–3.49 contributed 63.7% of the differences between assemblages, with 111.4% more biomass in this trophic level at the Scott Reefs than at the Rowley Shoals on average (Table S7). See Fig. 5 for plots of the relative abundance and biomass of trophic levels at the Scott Reefs relative to the Rowley Shoals.

Differences in dietary structure were confirmed using Eq. (1) (Fig. 6). Differences in both trophic and dietary structure between the Scott Reefs and the Rowley Shoals were confirmed using redundancy analysis of a distance matrix based on abundance

and biomass per sample of fishes in each trophic level (Figs. 7 & 8).

### Habitat

Mean depth in the stereo-BRUVS videos at the Scott Reefs and the Rowley Shoals ( $51.4 \pm 1.44$  vs.  $66.5 \pm 1.06$  m, respectively) differed significantly (2-tailed  $t$ -test assuming unequal variances and unequal sample sizes,  $t[120] = 1.66$ ,  $p = 1.78 \times 10^{-15}$ ). Habitat did not differ between the 2 locations ( $2 \times 2$  contingency table with no fixed margins:  $\chi^2 = 3.841$ ,  $\chi_{\text{obs}}^2 = 2.036$ ,  $0.1 < p < 0.5$ ). See Table S10 in the Supplement for habitat complexity data.

### Size refugia

Grey reef *C. amblyrhynchos* and silvertip *C. albimarginatus* sharks dominated the shark assemblage. The 2 dominant shark species had a combined mean length of 101.5 cm and a mean maximum length of 152 cm. We therefore estimated that a size refuge from the most common size of the most common predators would begin at roughly 36.5 cm. We also predicted that size refuge from the biggest sharks, however, would start at approximately 54.7 cm.

## DISCUSSION

Our results confirm that the diversity, abundance and biomass of sharks at the Scott Reefs were significantly different to those at the Rowley Shoals. At the Rowley Shoals, sharks were almost twice as speciose, over twice as abundant, over 20% longer and had almost 13 times as much biomass per sample, with this pattern evident in both stereo-DOVS and stereo-BRUVS. The 2 most common species of shark, *Carcharhinus amblyrhynchos* and *C. albimarginatus*, were approximately 3 times more abundant at the Rowley Shoals than at the Scott Reefs, suggesting that levels of shark fishing at the Scott Reefs have remained constant over the last decade (Ruppert et al. 2013). High-value species that are the primary target of the shark finning trade, such as *Sphyrna lewini*, *C. albimarginatus* and *Galeocerdo cuvier*, were greatly reduced in number at the Scott Reefs relative to the Rowley Shoals, suggesting that fishing is the main driver of variation in the shark abundance.

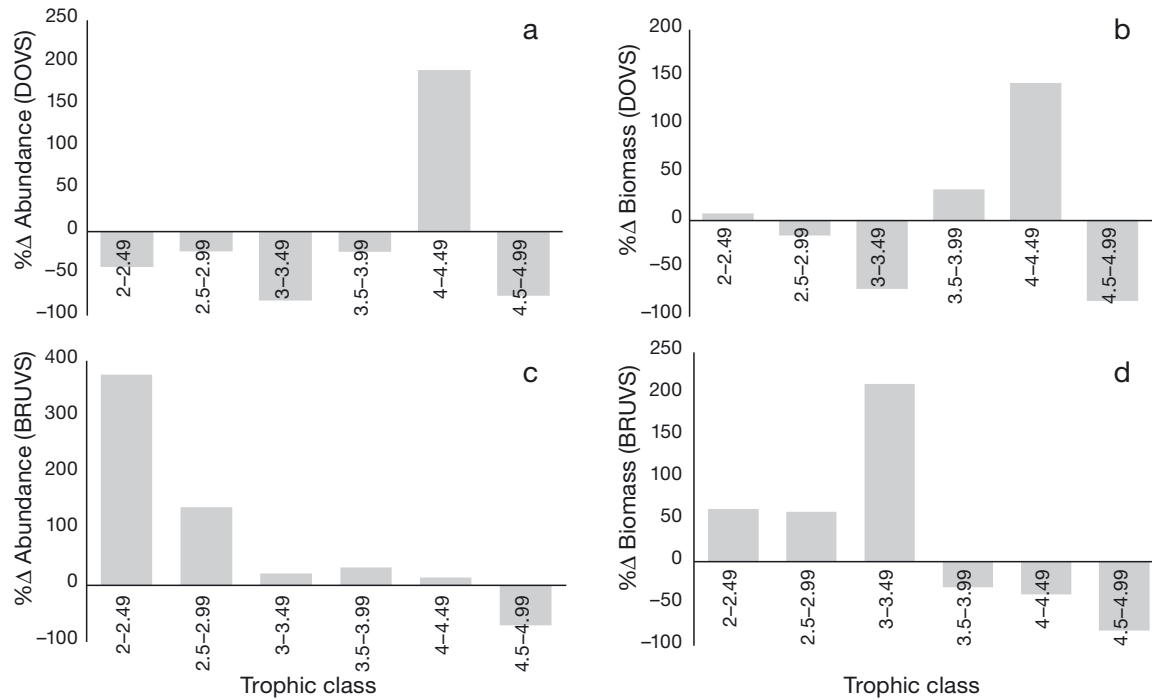


Fig. 5. Relative (a,c) abundance (% $\Delta A$ ) and (b,d) biomass (% $\Delta B$ ) per sample for trophic levels at the Scott Reefs compared to the Rowley Shoals (see Eq. 1) for (a,b) stereo-DOVS and (c,d) stereo-BRUVS. All values were calculated as means per sample, with site nested in location. Note that y-axis scales differ

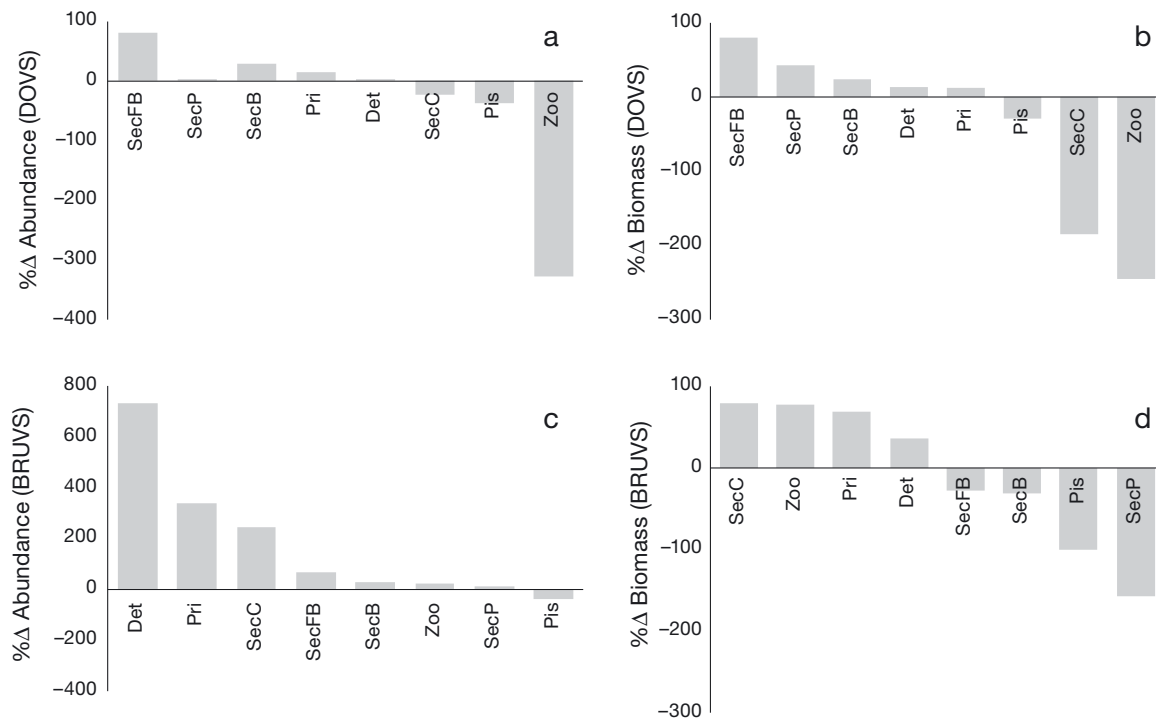


Fig. 6. Relative (a,c) abundance (% $\Delta A$ ) and (b,d) biomass (% $\Delta B$ ) per sample for fish guild at the Scott Reefs compared to the Rowley Shoals (see Eq. 1) for (a,b) stereo-DOVS and (c,d) stereo-BRUVS. The guilds included Pis (piscivores), SecFB (secondary consumers of fishes and benthos), SecP (secondary consumers of parasites), SecB (secondary consumers of benthos), SecC (secondary consumers of coral), Zoo (zooplanktivores), Pri (primary consumers) and Det (detritivores). All values were calculated as means per sample, with site nested in location. Note that y-axis scales differ

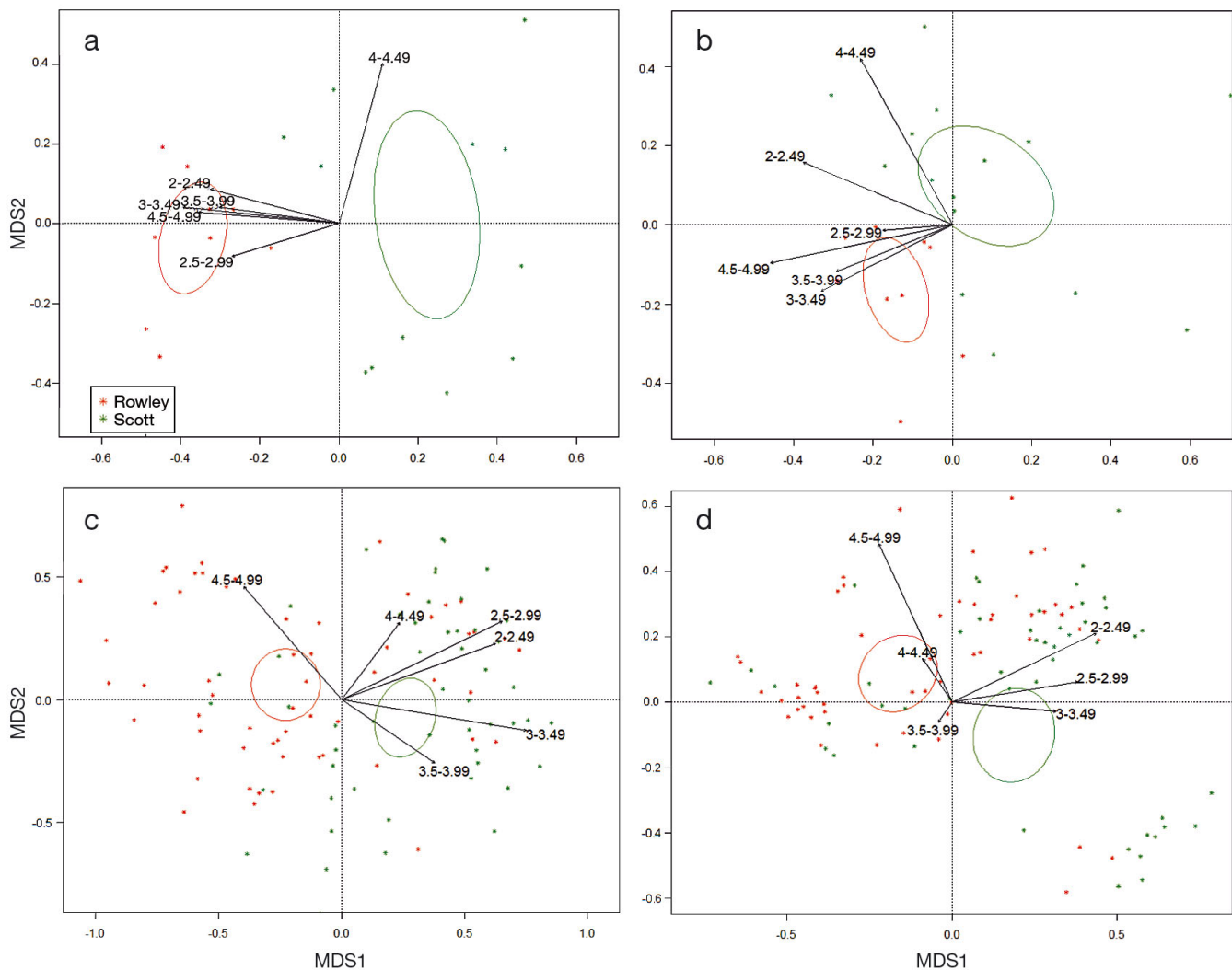


Fig. 7. Unconstrained ordination biplots of redundancy analysis results for (a,c) abundance and (b,d) biomass of fish assemblages at the Rowley Shoals (red) and the Scott Reefs (green) for trophic levels (black arrows) on (a,b) stereo-DOVS and (c,d) stereo-BRUVS

*Triaenodon obesus* was the only shark species to be more common at the Scott Reefs than at the Rowley Shoals, with approximately 570% higher abundance and 190% greater biomass at the former location (Table S4). This may reflect natural variation in abundance; however, a more plausible explanation is that *T. obesus* is not as vulnerable to long-lines set by fishers at the Scott Reefs in the waters off the reef, which are far more likely to capture *C. amblyrhynchus* and other larger species. Furthermore, *T. obesus* is a low-value species that is not typically targeted by commercial fisheries (Whitney et al. 2012) and as a result, it may not be retained by fishermen even if it has been caught. In addition, reduction in large 'apex' sharks such as *G. cuvier* (maximum

length: 750 cm; Froese & Pauly 2016), *C. albimarginatus* (300 cm) and *C. amblyrhynchus* (255 cm) may have led to predatory and/or competitive release in the smaller-bodied *T. obesus* (213 cm) at the Scott Reefs. Large sharks are a significant source of predation for smaller sharks and their removal can lead to increases in the numbers of juvenile conspecifics and smaller species (van der Elst 1979). As the isotopic niches of *T. obesus* and other reef-associated sharks such as *C. amblyrhynchus* differ significantly (Frisch et al. 2016), competitive release in *T. obesus* may be suggestive of breakdown in niche partitioning.

Results from both stereo-DOVS and stereo-BRUVS were consistent with the hypothesis that

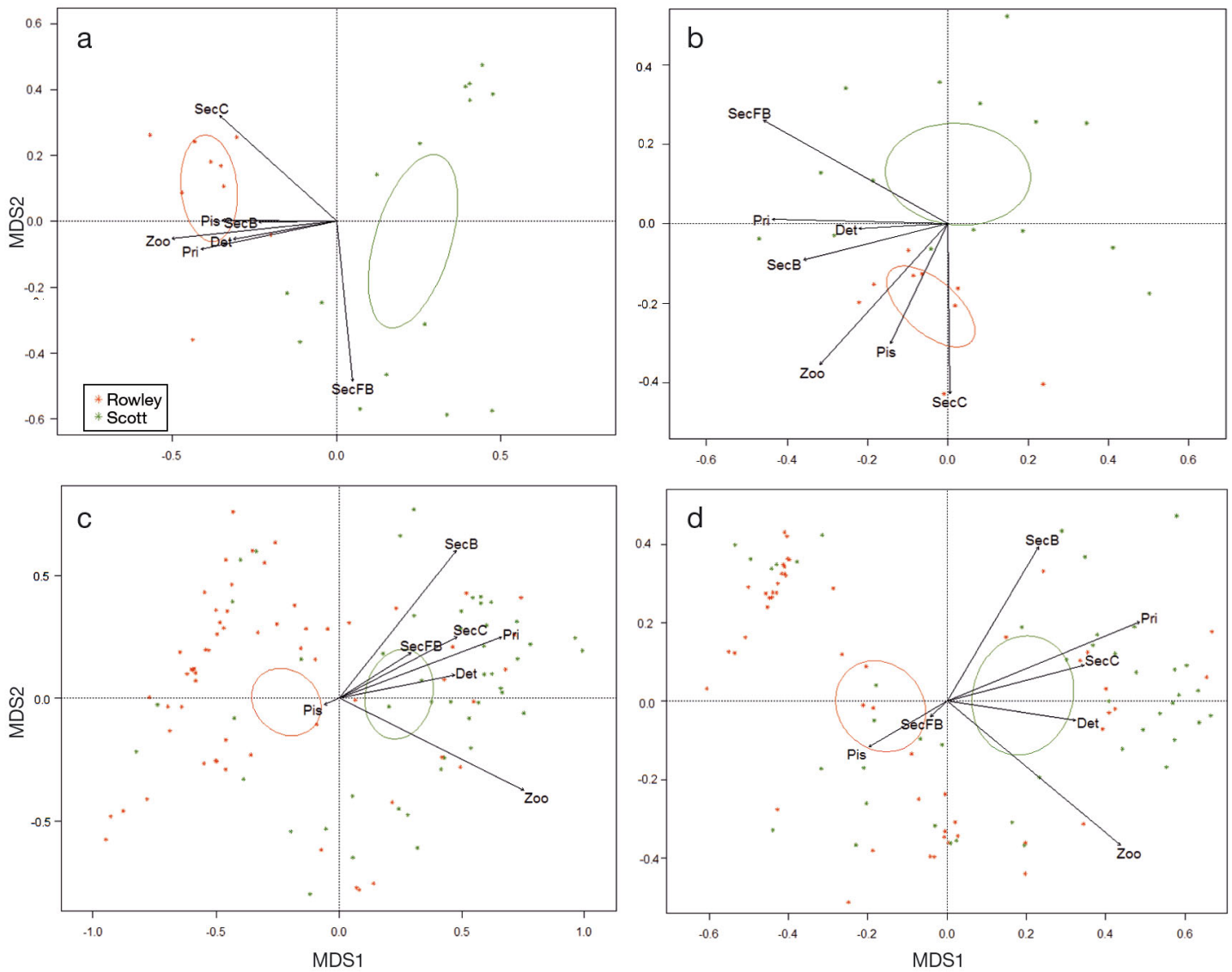


Fig. 8. Unconstrained ordination biplots of redundancy analysis results for (a,c) abundance and (b,d) biomass of fish assemblages at the Rowley Shoals (red) and the Scott Reefs (green) for dietary guilds (black arrows, see Fig. 6 for abbreviations) on (a,b) stereo-DOVS and (c,d) stereo-BRUVS

sharks are gape-limited predators that alter the size structure of prey populations. Fishes that were 30–50 cm in length were more abundant (+23%) and had greater biomass (+38%) at the Scott Reefs relative to the Rowley Shoals on stereo-DOVS. The stereo-BRUVS also suggested increases in smaller fishes (<30 cm), with the 20–30 cm size class experiencing the greatest relative increase in biomass (+274%) at the Scott Reefs relative to the Rowley Shoals. This result is consistent with but greater in magnitude than that of Dulvy et al. (2004), who reported a 17% increase in the biomass of the 21–25 cm size class of teleosts in response to pred-

ator removal. Both the stereo-DOVS and stereo-BRUVS results support the hypothesis that gape-limited predators create size refugia but that the refugia are defined not by the largest, rarer sharks, but by the most common size class of shark. Our results suggest that a size refuge may exist at 30–50 cm, which is lower than a size refuge based on the mean maximum length of the 2 dominant species of shark (55 cm) and more consistent with that predicted from the mean lengths of the 2 species (36 cm). This is consistent with research showing that while rare species can be important regulators of ecosystem function, the importance of

common species to the structure of assemblages is often overlooked (Gaston & Fuller 2008).

Our results suggest that removal of sharks may lead to an increase in the abundance and biomass of mesopredatory teleosts ('mesopredator release', sensu Crooks & Soulé 1999), consistent with Ruppert et al. (2013). Mesopredatory teleosts, defined here as omnivorous consumers of fish and benthos belonging to trophic level 4–4.49, were more abundant at the Scott Reefs than at the Rowley Shoals on both stereo-DOVS and stereo-BRUVS, although the magnitude of the observed difference was larger on stereo-DOVS (+191 vs. +14.3%, respectively). The few gut contents analyses that have been conducted on reef-associated sharks suggest that they consume a diverse array of teleosts that includes both mesopredatory teleosts such as lethrins, serranids and lutjanids, and herbivores including scarids and acanthurids (Papastamatiou et al. 2006). Therefore, the observed 'release' in the abundance and biomass of mesopredatory teleosts may be due to a reduction in predation pressure, as suggested by several previous studies (e.g. Casini et al. 2009).

However, increases in mesopredatory teleosts at the Scott Reefs relative to the Rowley Shoals may also be due to competitive release. There can be significant trophic overlap between reef-associated sharks such as *C. amblyrhynchos* and mesopredatory teleosts such as lethrins, lutjanids and serranids (Frisch et al. 2016). Increased abundance in these teleosts at the Scott Reefs compared to the Rowley Shoals may therefore be due to reductions in competitive exclusion, leading to increased consumption of shared prey items, dietary expansion via breakdown of niche partitions and a range of other fitness-promoting behavioural changes. Indeed, bony fishes in the same size class as the 2 most common shark species (90–109.99 cm) were 898% more abundant and had 230% greater biomass at the Scott Reefs than at the Rowley Shoals. However, if competitive release were an important driver of our results, one might also expect relative increases at the Scott Reefs in trophic level 4.5–4.99 fishes, which overlap trophically with the larger sharks *G. cuvier* and *S. lewini*. However, trophic level 4.5–4.99 fishes were 73% more abundant and had 83% more biomass at the Rowley Shoals than at the Scott Reefs on both stereo-DOVS and stereo-BRUVS, suggesting that they have not undergone competitive release at the latter location in response to reductions in the number of large sharks.

We recorded higher abundances of herbivores and benthic invertivores at the Scott Reefs relative to

the Rowley Shoals on stereo-DOVS, in addition to a greater biomass of detritivores. This finding was echoed by the stereo-BRUVS, which demonstrated that the abundance and biomass of herbivores and detritivores were greater at the shark-depleted location relative to the Rowley Shoals. Moreover, fishes in trophic level 2–3.49 were characterised by 99% greater biomass at the former location relative to the latter on stereo-BRUVS. Gut contents analyses have demonstrated that reef sharks are trophic omnivores (Wetherbee et al. 1997). Yet, in contrast to our results, many large-scale studies have failed to detect increases in the abundance of lower trophic level fishes following reductions in predator number (Stevenson et al. 2007). Some studies have argued that this lack of evidence is due to mesopredator 'release' suppressing lower trophic groups (Ruppert et al. 2013). However, others have argued that the positive correlation between herbivore and shark abundance is an artefact of fishing at multiple trophic levels and that herbivore abundance should theoretically increase in response to loss of sharks via trophic cascades (Stevenson et al. 2007). Consistent with the latter, this study suggests that removal of sharks can lead to increases in fish abundance and biomass at multiple trophic levels.

An implication of these findings is that removal of sharks may not lead to classic 'top-down' trophic cascades (in which loss of a top predator leads to outbreaks of prey which, in turn, suppresses their own food supply) but may instead alter the system from the 'bottom up' and 'middle out' via multiple trophic levels. The latter is more consistent with more recent definitions of trophic cascades by e.g. Pace et al. (1999), who described cascades as 'strong interactions within food webs that influence the properties of the system (p. 484).' Changes in the abundance of low-trophic level fishes can influence reef systems via diets of algae, sea urchins and coral, both dead and alive (Harborne et al. 2009). In particular, benthic excavators, grazers and scrapers may influence recovery rates on coral reefs following disturbance events by cropping algae and eroding dead coral (Bellwood et al. 2004). A second implication of our results is that the removal of sharks may ultimately influence the stability of reef communities. Lower trophic level fishes are faster growing, more fecund and have shorter life spans than higher trophic fish, which means that they also experience greater fluctuations in recruitment and population size (Planque et al. 2010).

Our results are consistent with Terborgh's (2015) conclusion that loss of predators can lead to loss of

biodiversity. There is a large body of evidence that predators promote species co-existence via density-dependent prey switching, preventing any one species from gaining dominance or being extirpated (Terborgh 2015). Yet studies have also found evidence to the contrary, concluding that predators reduce fish recruit and adult diversity on coral reefs by excluding the rarest species (Almany & Webster 2004). Our results show that species diversity was higher where sharks were relatively abundant. In addition, all trophic levels had significantly higher species diversity at the Rowley Shoals relative to the Scott Reefs, aside from trophic level 4–4.49, for which there was no significant difference. These results are consistent with Terborgh (2015), suggesting that sharks favour species diversity among prey, leading to declines in diversity when predators are reduced in number. However, the results also suggest that, to some extent, competitive release in mesopredatory teleosts may preserve species diversity in trophic level 4–4.49 following reductions in shark numbers.

As is the case with all natural experiments, the differences in the fish assemblages that we observed may be influenced by more factors than just the loss of predators. The sometimes conflicting results from the stereo-DOVS and stereo-BRUVS likely reflect differences in the designs of the techniques (Watson et al. 2010). However, there are also potential environmental reasons for why the results of the stereo-DOVS and stereo-BRUVS diverged during this analysis. The former technique occurred at depths of approximately 10 m, while the latter were deployed at a mean depth of 60 m. Shark distribution—and therefore the ‘seascape’ of fear that they create—may be biased towards depths of 30 to 60 m (Vianna et al. 2013), suggesting that habitats surveyed by stereo-BRUVS may better reflect prey assemblages exposed to lethal and risk effects than the habitats captured by stereo-DOVS.

Depth was not a factor influencing our stereo-DOVS results, as the mean depth of this technique was the same at both locations. Depth did vary for stereo-BRUVS, with mean ( $\pm$ SE) rig depth shallower at the Scott Reefs than at the Rowley Shoals ( $51.4 \pm 1.44$  vs.  $66.5 \pm 1.06$  m, respectively). Depth can influence the abundance and diversity of shallow water fish assemblages (<15 m; Jankowski et al. 2015). However, Brokovich et al. (2008) found no evidence for changes in teleost abundance along a 0 to 65 m depth range. Similarly, depth did not influence shark abundance in a comparison of 2 depth ranges (0–30 vs. 40–70 m) by Meekan et al. (2006) at our study locations. These authors also

failed to document consistent responses in mesopredatory teleosts with depth. It is therefore unlikely that the discrepancy in mean depth between our 2 locations (~51 vs. 67 m) had an ecologically meaningful effect on shark and teleost populations, although it is impossible to exclude this possibility due to the nature of large-scale natural experiments (Barley & Meeuwig 2016).

Natural disturbance events can alter the trajectories of reef systems, causing variable responses in fish populations via erratic recruitment, ecological plasticity and changes in growth, feeding behaviour and condition (Nyström et al. 2000). For example, Roff et al. (2016) suggested that the increase in herbivores reported by Ruppert et al. (2013) at the Rowley Shoals relative to the Scott Reefs might be due to loss of coral and a concomitant increase in algae due to cyclone activity, rather than a shark overfishing-triggered trophic cascade. Due to the nature of large-scale natural experiments, it is impossible to rule out the possibility that the observed results were confounded by disturbance history (Barley & Meeuwig 2016). However, AIMS has collected annual data on fish abundance and benthic cover on the outer reef slopes of both locations since 1994, showing that although coral cover was reduced from approximately 60 to <10% by disturbance events in 1996 to 1998 at both locations, both reefs recovered to pre-disturbance levels over the following decade (Ruppert et al. 2013). Furthermore, Ruppert et al. (2013) demonstrated that while the abundance of planktivores and corallivores fluctuated in accordance with disturbance events such as bleaching or cyclones at both locations, ‘bottom-up’ effects did not influence the density of mesopredatory teleosts, which remained constant within each system over a period of over 15 yr.

In addition, Ruppert et al. (2013) found that the 2 systems were similar with respect to productivity, habitat structure, benthic communities and average coral cover over a 15 yr period, with shelf position and total reef size also similar. One important difference between the 2 locations is that the Scott Reefs includes both open, deep lagoons and shallow lagoonal habitat, while the Rowley Shoals is characterised by only the latter. It is possible that this difference in habitat may have contributed to our results. However, there is significant overlap between fish assemblages within lagoons and on outer reef slopes due to diurnal and other migrations (McKibben & Nelson 1986, Economakis & Lobel 1998, Nagelkerken et al. 2008, Chateau & Wantiez 2009). As a result, we would argue that while differences in lagoon

morphology cannot be ruled out as a factor contributing to our results, it is unlikely to have had a significant effect.

The structure of fish assemblages can also be influenced by a number of environmental factors such as habitat complexity (Carreiro-Silva & McClanahan 2001). Although our data suggests that there was no significant difference in habitat complexity between locations, it is impossible to exclude the possibility that subtle variations in habitat contributed to the observed patterns in the data. Differences in temperature are also unlikely to be a factor, as temperature regimes are not significantly different between the locations (Barley et al. in press). Although it is possible that the differences we observed between the 2 locations were due to fish immigrating or emigrating, this is unlikely as there is good evidence that the fish populations in this region are self-recruiting (Underwood et al. 2012). Variable recruitment may be a factor contributing to differences in abundance of small size classes between assemblages (Doherty 2002); however, it is unlikely that assemblage metrics would have been consistent across different guilds and trophic levels if recruitment were the key driver of the trends. Differences in seasons, tidal state and time of day of sampling may also have influenced the results, although sampling was conducted during the same time window each day at both locations. Finally, it is possible that the results in terms of species diversity were influenced by resource quality and stochastic processes such as extinction and speciation (Diamond 1988).

Like all natural experiments, there are limitations to what conclusions can be drawn from our study about the ecological role of sharks on reefs. Our results must be viewed in the context of mesocosms, other small-scale experiments and models, as large-scale natural experiments can only indicate correlation rather than causation (Barley & Meeuwig 2016). In light of these caveats, we found evidence for increases in the abundance and biomass of mesopredatory teleosts at the Scott Reefs relative to the Rowley Shoals that were consistent with the effects of predatory and competitive release. Regardless of mechanism, our results also suggest that removal of sharks can drive release at multiple, lower trophic levels including herbivores, detritivores and zooplanktivores. Moreover, our results suggest that removal of sharks may drive increases in small to medium size classes (20–50 cm) of fishes, but that these increases are not compensatory, leading to overall declines in biomass within the system. In contrast to studies that have suggested that trophic cascades in

marine systems are weak (Shurin et al. 2002), loss of sharks as gape-limited predators on coral reefs may therefore have the potential to significantly alter food web interactions.

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