

Reassessing the trophic role of reef sharks as apex predators on coral reefs

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Abstract Apex predators often have strong top-down effects on ecosystem components and are therefore a priority for conservation and management. Due to their large size and conspicuous predatory behaviour, reef sharks are typically assumed to be apex predators, but their functional role is yet to be confirmed. In this study, we used stomach contents and stable isotopes to estimate diet, trophic position and carbon sources for three common species of reef shark (*Triaenodon obesus*, *Carcharhinus melanopterus* and *C. amblyrhynchos*) from the Great Barrier Reef (Australia) and evaluated their assumed functional role as apex predators by qualitative and quantitative comparisons with other sharks and large predatory fishes. We found that reef sharks do not occupy the apex of coral reef food chains, but instead have functional roles similar to those of large predatory fishes such as snappers, emperors and groupers, which are typically regarded as high-level mesopredators. We hypothesise that a degree of functional redundancy

exists within this guild of predators, potentially explaining why shark-induced trophic cascades are rare or subtle in coral reef ecosystems. We also found that reef sharks participate in multiple food webs (pelagic and benthic) and are sustained by multiple sources of primary production. We conclude that large conspicuous predators, be they elasmobranchs or any other taxon, should not axiomatically be regarded as apex predators without thorough analysis of their diet. In the case of reef sharks, our dietary analyses suggest they should be reassigned to an alternative trophic group such as high-level mesopredators. This change will facilitate improved understanding of how reef communities function and how removal of predators (e.g., via fishing) might affect ecosystem properties.

Keywords Elasmobranch · Food web · Stable isotope analysis · Top-down control · Trophic ecology

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Introduction

Apex predators are species that occupy the top trophic level in a community (Ritchie and Johnson 2009). In many cases, apex predators have profound top-down effects on prey demography, habitat structure and ecosystem productivity (Estes et al. 2011; Ripple et al. 2014) and thus are regarded as a key functional group and a high priority for conservation and management. However, in some ecosystems, it is unclear which species function as apex predators due to the complexity of food webs (e.g., Bascompte et al. 2005; Hussey et al. 2015) and intra-specific variation in functional role. For example, coyotes (*Canis latrans*) often function as apex predators, but they can also function as mesopredators (intermediate predators consumed by apex predators) in ecosystems where larger carnivores (e.g.,

wolves) exist (Roemer et al. 2009). These problems and inconsistencies often lead to misclassification of apex predators, which impedes our ability to understand the drivers of community structure, predict the ecological effects of predator removal, and manage resources at the ecosystem level (Heithaus et al. 2008; Rizzari et al. 2015).

Sharks are commonly regarded as apex predators in marine ecosystems (Heithaus et al. 2008; Rizzari et al. 2014c), and their populations are rapidly declining due to the combination of intense fishing pressure and *K*-selected life-history traits (Dulvy et al. 2014; Rizzari et al. 2014a). This is worrisome because altering the density of sharks may invoke community-wide trophic cascades that have far-reaching, detrimental consequences for marine ecosystems and the human livelihoods that depend on them (Myers et al. 2007; Heithaus et al. 2008). Therefore, a better understanding of sharks and their trophic functions is imperative for guiding management actions that aim to preserve or enhance ecosystem services.

On coral reefs, sharks can be grouped into two broad categories: (1) true reef sharks, which are most often found on or near coral reefs and tend to be conspicuous (e.g., whitetip reef shark, *Triaenodon obesus*, blacktip reef shark, *Carcharhinus melanopterus*, grey reef shark, *C. amblyrhynchos*); and (2) ‘other’ sharks, which occupy a broad range of habitats, but visit or inhabit coral reefs opportunistically and tend to be inconspicuous or rare (e.g., tiger shark, *Galeocerdo cuvier*, dusky shark, *C. obscurus*, silvertip shark, *C. albimarginatus*, sicklefin lemon shark, *Negaprion acutidens*, tawny nurse shark, *Nebrius ferrugineus*; Ceccarelli et al. 2014; Heupel et al. 2014). Reef sharks have a strong affinity for reefs with high coral cover and structural complexity (Espinoza et al. 2014; Rizzari et al. 2014b), presumably because these reefs provide the necessary habitat requirements and/or food resources. Knowledge of how reef sharks use these components is important for understanding their vulnerability to climate change, which is predicted to modify the structure and productivity of coral reefs (Hoegh-Guldberg et al. 2007). Hence, it is critical to identify the sources of primary production that support reef shark populations to accurately predict and mitigate the response of reef sharks to environmental change.

Reef sharks are typically assumed to be apex predators (e.g., Friedlander and DeMartini 2002; Sandin et al. 2008; Rizzari et al. 2014c) but this assumption is generally based on their relatively large body size and conspicuous predatory behaviour rather than on detailed knowledge of their diet and trophic ecology. Indeed, preliminary observations suggest that reef sharks may be more aptly described as mesopredators than apex predators (Mourier et al. 2013; Hilting et al. 2013; Heupel et al. 2014). If so, conclusions about trophic structure and food web dynamics of coral

reefs may be biased (Trebilco et al. 2013; Hussey et al. 2014a, 2015; Rizzari et al. 2015), which has important implications for how reef communities are studied and managed. Hence, a reassessment of the trophic ecology and functional role of reef sharks is warranted.

Several previous studies have generated considerable information about reef sharks’ diet and trophic position (TP). The general consensus is that reef sharks eat mostly teleosts, cephalopods and crustaceans (in decreasing order of importance), and all have a similar TP (~3.7–4.3) (Randall 1977; Stevens 1984; Wetherbee et al. 1997; Cortés 1999; Papastamatiou et al. 2006; Speed et al. 2012). Combined, these studies suggest that reef sharks may share a common trophic niche, although there may be a high degree of resource partitioning and geographic separation among species (McCauley et al. 2012; Rizzari et al. 2014b; Hussey et al. 2015). To better understand trophic interactions between reef shark species, and to resolve the controversy surrounding their functional role, more detailed studies of reef shark diet are required, particularly in places where multiple reef shark species co-exist.

In this study we used stable isotope analysis (SIA) and stomach content analysis (SCA) as complementary methods to investigate the trophic ecology of reef sharks. In particular, we sought to (1) estimate the TP of reef sharks and, by comparison to a guild of mesopredatory reef fishes (snapper, emperor, grouper), assess their assumed status as apex predators, (2) define the trophic niche of reef sharks and thus evaluate the potential for dietary overlap among species, and (3) estimate the contributions of pelagic versus reef-based sources of primary production that support reef shark populations. Integration of this information provides insights into the functional role of reef sharks and their dependency (or lack thereof) on reef-based primary producers which are forecasted to undergo substantial demographic changes in the near future due to climate change (Hoegh-Guldberg et al. 2007). Target species were *T. obesus*, *C. melanopterus* and *C. amblyrhynchos*, as these are the dominant reef shark species on Indo-Pacific coral reefs (Ceccarelli et al. 2014; Rizzari et al. 2014b). For comparison, we also present limited data for other sharks (e.g., *G. cuvier*), but results for this group are only indicative of trends rather than conclusive (due to small sample sizes).

Materials and methods

Study sites and sample collection

The study was conducted in February and June 2013 on coral reefs adjacent to Lizard and One Tree islands in the northern and southern regions of the Great Barrier Reef

(GBR), respectively (Fig. 1). To enable capture of the three target shark species, which have slightly different habitat preferences (Ceccarelli et al. 2014; Rizzari et al. 2014b), it was necessary to sample each region at multiple sites (within 5–30 km of each other; Fig. 1). Although analysing samples over several sites introduces potential bias due to spatial variation in isotopic signatures of prey and resource pools, any such bias was probably very small because the study sites were within the recorded movement distances of reef sharks (Heupel et al. 2010; Whitney et al. 2012; Chin et al. 2013). Furthermore, a multi-site approach allows for detection of robust patterns that transcend small-scale isotopic variations. At all sites, fishing pressure and other anthropogenic influences were low or absent and faunal communities were largely intact, suggesting that trophic interactions and energy pathways were suitably representative of functional coral reefs. For detailed descriptions of the structure and diversity of fish communities on the GBR, see Williams and Hatcher (1983) and Newman et al. (1997).

Sharks were captured using a semi-benthic longline that was positioned 2–5 m above the seafloor on reefs that were 3–25 m deep. The longline was deployed for periods of 1–1.5 h between 0800 and 1800 h and fishing effort was distributed across all major habitat types (reef slope, lagoon, back reef). The longline consisted of ten circle hooks (Mustad, size 14/0) attached to a 50-m rope with 1 m of multistrand wire. Each hook was baited with randomly selected pieces of common reef fishes (scarids, lutjanids, lethrinids, epinephelids, caesionids and carangids) that were cut into squares to enable differentiation of ingested bait and prey. Upon capture, sharks were restrained on the

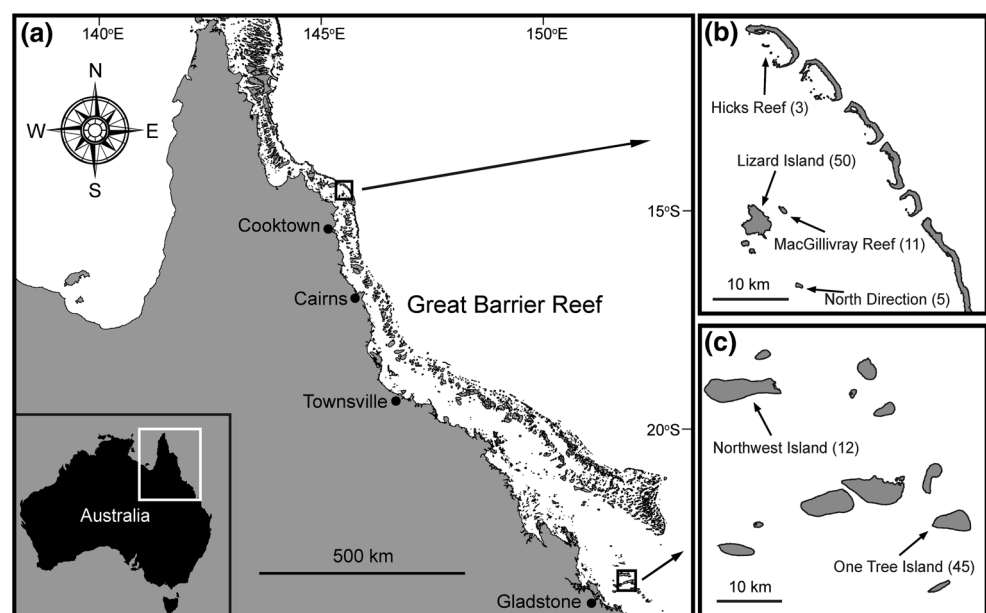
deck, seawater was applied to the gills, and total length (L_T) was recorded using a flexible tape. Approximately 0.5 cm³ of white muscle tissue was collected from the anterior dorsal region and then stored frozen (−20 °C) until further analysis. Stomach contents were extracted by gastric lavage, i.e., seawater was pumped into the stomach using an orally inserted PVC pipe (20 mm diameter). Expelled items were collected in a bucket for later identification in the laboratory. To comply with ethical standards, sharks were released alive and in good condition, except for a subsample of 14 individuals that were dissected to determine the success rate of gastric lavage.

Stable isotope analysis

All samples were oven-dried (60 °C for 48 h) and ground to a fine powder using a mortar and pestle. Samples were weighed to the nearest 0.001 g, and isotope content (¹³C, ¹²C, ¹⁵N, ¹⁴N) was measured using a continuous-flow, isotope ratio, mass spectrometer (Delta-V Plus, Thermo Finnigan, Australia) coupled with an elemental analyser (ECS410, Costech Analytical Technologies, U.S.A.). Results are expressed as parts per thousand (‰) deviation from Pee Dee Belemnite (vPDB) and atmospheric nitrogen standards for $\delta^{13}\text{C}$ (ratio of ¹³C to ¹²C) and $\delta^{15}\text{N}$ (ratio of ¹⁵N to ¹⁴N), respectively. Experimental precision (standard deviation of replicates of internal standard) was 0.1 ‰ for $\delta^{13}\text{C}$ and 0.2 ‰ for $\delta^{15}\text{N}$.

The relative influence of region, species, sex and total length on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were evaluated using boosted regression trees (BRT). For this analysis, tree complexity was restricted to five, learning rate was kept low (0.005),

Fig. 1 a Map of Australia showing the location of study sites: reefs surrounding Lizard Island (b) and One Tree Island (c). Numbers in parentheses are sample sizes (all species combined)



optimal tree number was kept close to 1000, and bag fractions were tested between 0.5 and 0.8 (Elith et al. 2008). The relative influence of predictor variables was calculated as the percentage reduction in sum-of-squared-error at each iteration, and results were validated using ten-fold cross-validation (CV) methods (Elith et al. 2008). All BRT models were fitted with R software (R Core Team 2012) using the package *dismo* and additional custom code (Elith et al. 2008).

Isotope data were pooled across regions because there were no significant geographic differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (tested using stable isotope Bayesian ellipses in R, SIBER). Species-specific isotope data were then compared by analysis of variance (ANOVA) and Tukey's HSD post hoc test. The effects of body size on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures were evaluated by model II linear regression (ranged major axis) using the package *Imodel2* in R (R Core Team 2012).

Trophic position of reef sharks was estimated in two ways. Firstly, TP was estimated assuming constant diet-tissue fractionation:

$$\text{TP}_{\text{constant}} = \lambda + (\delta^{15}\text{N}_{\text{shark}} - \delta^{15}\text{N}_{\text{base}}) / \Delta_n$$

where λ is the TP of a known base group, $\delta^{15}\text{N}_{\text{shark}}$ and $\delta^{15}\text{N}_{\text{base}}$ are the direct estimates of mean $\delta^{15}\text{N}$ in each shark species and base group, respectively, and Δ_n is the diet-tissue discrimination factor. The latter was assumed to be constant at 2.3 ‰ based on the mean fractionation of $\delta^{15}\text{N}$ in white muscle tissue of large sharks held in captivity (Hussey et al. 2010). Secondly, TP was estimated using a scaled fractionation approach:

$$\text{TP}_{\text{scaled}} = \log_e(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{base}}) - \log_e(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{shark}}) / k + \lambda$$

where $\delta^{15}\text{N}_{\text{lim}}$ is the saturating isotope limit and k is the average rate at which consumer isotope values approach $\delta^{15}\text{N}_{\text{lim}}$ per trophic step. $\delta^{15}\text{N}_{\text{lim}}$ and k were assumed to be 21.9 ‰ and 0.137, respectively, following meta-analysis of experimentally derived Δ_n in fish (Hussey et al. 2014a, b).

Due to uncertainty in the suitability of any particular base group, we estimated $\text{TP}_{\text{constant}}$ and $\text{TP}_{\text{scaled}}$ using three different base groups that encompass a broad range of λ , i.e., herbivore (*Siganus doliatus*), small demersal predator (*Thalassoma lunare*), and large pelagic predator (*Scomberomorus commerson*). Base trophic position (λ) of herbivores was assumed to be two, and λ of *T. lunare* (3.65) and *S. commerson* (4.47) were derived from Farmer and Wilson (2011). Direct estimates of $\delta^{15}\text{N}_{\text{base}}$ for each of the three groups at the study site were 6.59, 9.35 and 11.80, respectively (Frisch et al. 2014). To calculate mean TP of sharks, each estimate of $\text{TP}_{\text{constant}}$ was weighted according to λ (rounded down to the nearest integer), because

uncertainty increases with each trophic step due to potential error in estimates of diet-tissue fractionation (Hussey et al. 2014a). To calculate mean $\text{TP}_{\text{scaled}}$, the arithmetic mean was used.

To evaluate whether reef sharks are apex predators, their TPs and isotopic niches were compared to those of other sharks and large predatory fishes. The latter consisted of leopard coral grouper (*Plectropomus leopardus*), bar-cheek coral grouper (*P. maculatus*), red-throat emperor (*Lethrinus miniatus*) and stripey snapper (*Lutjanus carponotatus*), which are the most abundant high-level mesopredators on the GBR (Newman et al. 1997; Frisch et al. 2014). All data for predatory fishes originate from the GBR and are reported by Frisch et al. (2014).

Isotope data were plotted in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space, and isotopic niches were quantified using Bayesian standard ellipse areas (SEA_B) and small sample size-corrected standard ellipse areas (SEA_C), which were calculated using the SIBER component of the *SIAR* package (Stable Isotope Analysis in R; Jackson et al. 2011). Total size of SEA is a proxy for isotopic trophic diversity within a species, and the extent of overlap of SEA among species indicates the likelihood of inter-specific competition for prey.

To estimate the contributions of pelagic versus reef-based sources of primary production that support reef sharks, we used a two-source mixing model (Frisch et al. 2014). End members were (1) the most ^{13}C -depleted *S. commerson* (Spanish mackerel; $\delta^{13}\text{C} = -17.69$), which is a well-known pelagic piscivore that predominantly eats pelagic fishes such as engraulids and clupeids (Blaber et al. 1990; Farmer and Wilson 2011), and (2) the most ^{13}C -enriched *P. maculatus* ($\delta^{13}\text{C} = -8.96$), which is a coral reef piscivore whose distribution is strongly linked to live coral cover (Evans et al. 2010; Frisch et al. 2012).

Stomach content analysis

Stomach contents of reef sharks were identified to the lowest possible taxonomic level. Species-specific distributions of prey taxa were compared by χ^2 tests, and species-specific mean weights of stomach contents were compared by ANOVA. Inter-specific dietary overlap (D) was quantified using Schoener's (1968) index:

$$D = 1 - 1/2 \left(\sum |p_{xi} - p_{yi}| \right)$$

where p_{xi} and p_{yi} are the relative proportions of prey taxa i for species x and y , respectively. The index ranges from 0 (no overlap) to 1 (complete overlap), and values >0.6 are considered to indicate significant dietary overlap (Schoener 1968). Assumptions of statistical tests were checked a priori, and heteroscedastic data were transformed

Table 1 Summary of isotopic metrics for reef sharks and 'other' sharks (*)

Species	n	Sex ratio (% f:m)	Mean size ($L_t \pm SE$)	Size range (cm L_t)	Mean $\delta^{13}C$ (‰ $\pm SE$)	$\delta^{13}C$ range (‰)	Mean $\delta^{15}N$ (‰ $\pm SE$)	$\delta^{15}N$ range (‰)	Pelagic source ^a (%; mean $\pm SE$)	Reef source ^a (%; mean $\pm SE$)	Ellipse area ^b	Unique area ^c (%)
<i>Triakonodon obesus</i>	31	55:45	125.6 \pm 3.4	80–151	-12.0 \pm 0.3	6.8	9.6 \pm 0.1	3.2	34.6 \pm 3.3	65.4 \pm 3.3	3.7	34.9
<i>Carcharhinus melanopterus</i>	45	73:27	128.0 \pm 2.7	68–153	-11.4 \pm 0.2	4.5	10.4 \pm 0.1	3.5	28.2 \pm 2.0	71.8 \pm 2.0	2.7	38.6
<i>Carcharhinus amblyrhynchos</i>	32	72:28	114.9 \pm 5.6	70–158	-14.0 \pm 0.2	5.2	10.8 \pm 0.1	2.2	57.8 \pm 2.3	42.2 \pm 2.3	1.9	69.3
<i>Nebrius ferrugineus*</i>	7	86:14	198.0 \pm 19.3	121–256	-12.7 \pm 0.3	2.0	9.9 \pm 0.4	2.9	42.7 \pm 3.3	57.3 \pm 3.3	2.5	15.5
<i>Negaprion acutidens*</i>	6	33:67	193.0 \pm 23.3	95–250	-11.4 \pm 0.4	2.9	11.2 \pm 0.3	1.9	27.7 \pm 4.6	72.3 \pm 4.6	2.2	67.7
<i>Galeocerdo cuvie*</i>	4	50:50	241.0 \pm 44.8	164–370	-14.8 \pm 0.7	2.8	11.9 \pm 0.3	1.5	67.3 \pm 8.1	36.7 \pm 8.1	3.3	92.1
<i>Carcharhinus obscurus*</i>	1	100:0	270.0	–	-13.8	–	13.0	–	55.9	44.1	–	–

^a End members for the two-source mixing model were the most ^{13}C -depleted *Scomberomorus commerson* (a pelagic specialist) and the least ^{13}C -depleted *Plectropomus maculatus* (a coral reef specialist; data from Frisch et al. 2014)

^b Ellipse area refers to the corrected standard ellipse area (SEAC) and is dimensionless

^c Unique area refers to non-overlapping ellipse area (see Fig. 4; excludes large predatory fishes)

($\log_x + 1$). All data are expressed as mean \pm standard error of untransformed data unless otherwise noted.

Results

Stable isotope analysis

One hundred and twenty-six individuals from three species of reef shark and four species of other shark were analysed for isotopic composition (Table 1). The size range of these sharks was very broad (68–158 cm L_t for reef sharks and 95–370 cm L_t for other sharks), although most individuals were of adult size [see Last and Stevens (2009) for sizes at maturity]. For reef sharks, the majority of sampled individuals were female (55–73 % per species; Table 1); however, this had little or no effect on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios (see below).

In general, reef sharks and other sharks were broadly distributed throughout $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space (Fig. 2), indicating a broad range of trophic diversity. *Triaenodon obesus* had the largest range of $\delta^{13}\text{C}$ (6.8 ‰) and potentially the broadest range of carbon sources, while *C. melanopterus* had the largest range of $\delta^{15}\text{N}$ (3.5 ‰) and potentially feeds over the broadest range of TPs (Table 1; Fig. 2). Species-specific mean $\delta^{13}\text{C}$ values ranged from -14.8 ± 0.7 ‰ (*G. cuvier*) to -11.4 ± 0.4 ‰ (*N. acutidens*) and mean $\delta^{15}\text{N}$ values ranged from 9.6 ± 0.1 ‰ (*T. obesus*) to 11.9 ± 0.3 ‰ (*G. cuvier*), although the single sample of *C. obscurus* measured 13.0 ‰ (Table 1; Fig. 2). According to the mixing model, *C. amblyrhynchos* and *G. cuvier* derive the majority (>50 %) of their food sources from pelagic-based food webs, which are driven by primary producers such as phytoplankton. In contrast, *T. obesus*, *C. melanopterus*, *N. acutidens* and *N. ferrugineus* derive the majority (>50 %) of their food sources from reef-based food webs, which are driven by benthic primary producers such as coral and algae (Table 1).

Boosted regression trees indicate that species identity had the highest relative influence on both $\delta^{13}\text{C}$ (64.5 %) and $\delta^{15}\text{N}$ (42.1 %), followed by (in decreasing order) L_t ($\delta^{13}\text{C} = 22.5$ %; $\delta^{15}\text{N} = 33.1$ %), region ($\delta^{13}\text{C} = 9.1$ %; $\delta^{15}\text{N} = 17$ %) and sex ($\delta^{13}\text{C} = 3.9$ %; $\delta^{15}\text{N} = 7.8$ %) (Fig. 3). Specifically, mean $\delta^{13}\text{C}$ was significantly more depleted in *C. amblyrhynchos* than in *C. melanopterus* and *T. obesus* (ANOVA, $F_{2,105} = 38.9$, $p < 0.001$; Tukey's HSD, $p < 0.001$), while $\delta^{15}\text{N}$ was significantly more enriched in *C. amblyrhynchos* and *C. melanopterus* than in *T. obesus* (ANOVA, $F_{2,105} = 23.9$, $p < 0.001$; Tukey's HSD, $p < 0.001$; Fig. 3a). The total deviance explained by BRT models of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ was 46 % and 55 %, respectively, and the overall predictive performance of BRT models (CV Spearman correlation) was 0.69 ± 0.04

and 0.72 ± 0.08 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Linear regression analysis found no relationship between $\delta^{13}\text{C}$ and L_t for any species of reef shark, and only a weak relationship between $\delta^{15}\text{N}$ and L_t for *T. obesus* ($r^2 = 0.16$, $p = 0.03$) and *C. melanopterus* ($r^2 = 0.27$, $p < 0.001$), suggesting that size has little influence on TP and no influence on food sources within the range of sizes that we examined (Electronic Supplementary Material, ESM, Fig. S1). We did not examine relationships between variables in other sharks due to small sample sizes.

Using a constant discrimination factor (2.3 ‰) and a variety of base groups, mean $\text{TP}_{\text{constant}}$ of reef sharks (3.8–4.1) was similar to mean $\text{TP}_{\text{constant}}$ of large predatory fishes (4.0–4.1) but less than mean $\text{TP}_{\text{constant}}$ of other sharks such as *N. acutidens*, *G. cuvier* and potentially also *C. obscurus* (4.5–5.1) (Table 2). Estimates of TP changed little when the scaled approach was used, except that mean $\text{TP}_{\text{scaled}}$ of *G. cuvier* and *C. obscurus* increased to 5.0 and 5.9, respectively.

Isotopic niches of reef sharks differed in size and position, indicating a moderate to high degree of trophic diversity (Figs. 4, 5). Ellipse area (SEA_C) was smallest for *C. amblyrhynchos* (1.9 units) and largest for *T. obesus* (3.7 units), with a significant difference between species (SIBER, $p = 0.01$; Table 3). Isotopic niche overlap (a proxy for trophic competition) was moderate between *T. obesus* and *C. melanopterus*, minimal between *T. obesus* and *C. amblyrhynchos*, and absent between *C. amblyrhynchos* and *C. melanopterus* (Fig. 4; Table 3). When considered at the group level, however, there was isotopic niche overlap between reef sharks and some species of other sharks and large predatory fishes (Fig. 4).

Stomach content analysis

Gastric lavage was demonstrably successful at extracting stomach contents from reef sharks, since only one of 14 dissected sharks retained any stomach contents after being lavaged, and this particular individual was one of the first to be sampled (i.e., before we perfected the lavage technique). Other sharks tended to be much larger than reef sharks, so it was often impossible to restrain (and subsequently lavage) them, which resulted in small sample sizes. Therefore, stomach content data are omitted for other sharks.

One hundred and seven reef sharks were subjected to gastric lavage. Stomachs were empty in 42.2, 67.7 and 71.0 % of *C. melanopterus*, *T. obesus* and *C. amblyrhynchos*, respectively (Table 4), and differences between species were statistically significant ($\chi^2 = 7.94$, $p = 0.019$). Stomachs in the remaining individuals were found to contain a wide range of prey species, including several species of reef-dwelling herbivores (e.g., parrotfish,

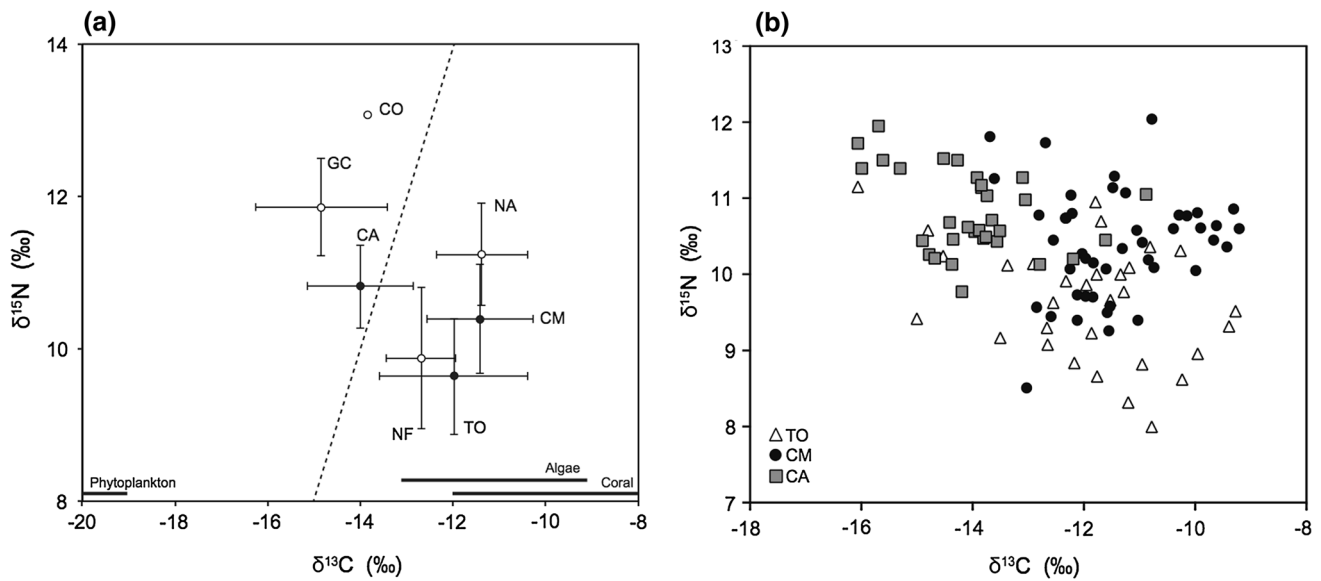


Fig. 2 **a** Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (\pm SD) of reef sharks (TO, CM, CA) and other sharks (NF, NA, GC, CO). White circles indicate species with small sample sizes ($n = 1-7$), which are shown for comparison. Horizontal lines depict range of $\delta^{13}\text{C}$ values for common primary producers (see Frisch et al. 2014) and oblique line depicts hypothesised division between pelagic and reef-based food webs (slope of

line is approximately 2.3/1.1 due to differential fractionation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). **b** $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of individual reef sharks. TO, *Triaenodon obesus*; CM, *Carcharhinus melanopterus*; CA, *C. amblyrhynchus*; NF, *Nebrius ferrugineus*; NA, *Negaprion acutidens*; GC, *Galeocerdo cuvier*; CO, *C. obscurus*

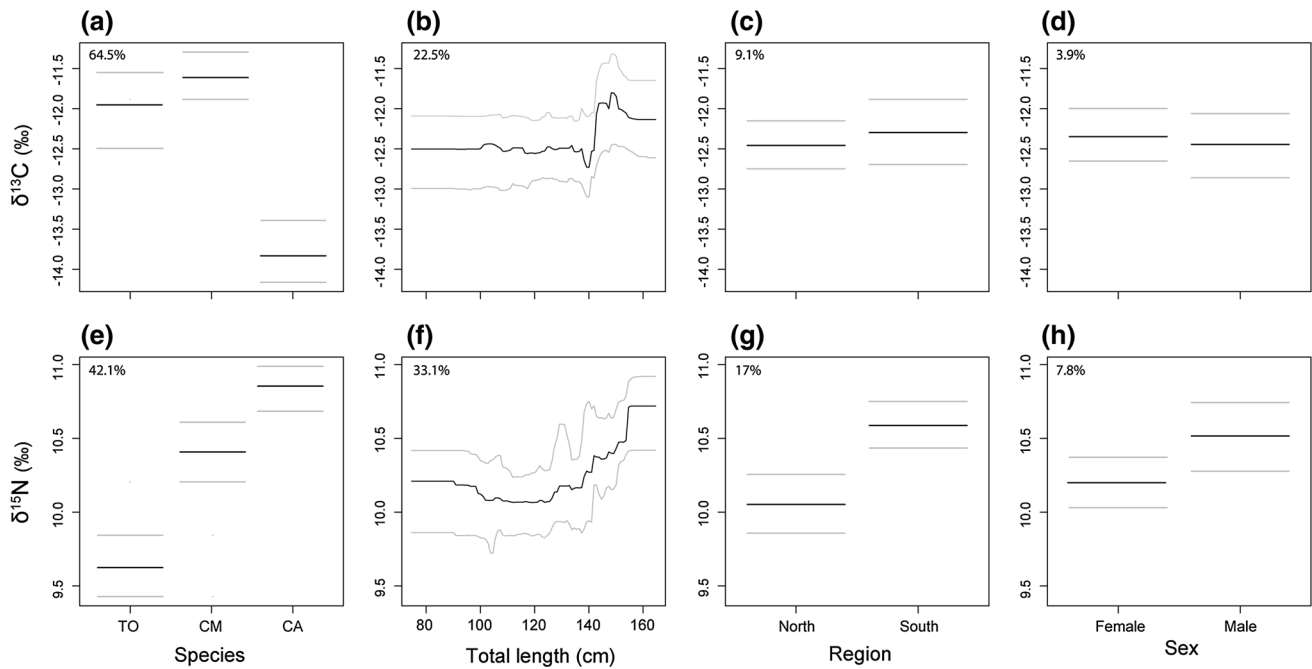


Fig. 3 Partial dependence plots of **a, e** species, **b, f** total length, **c, g** region, and **d, h** sex in boosted regression tree models for predicting $\delta^{13}\text{C}$ (**a-d**) and $\delta^{15}\text{N}$ (**e-h**). Fitted lines represent the mean estimate (black) and 95 % confidence intervals (grey) based on 500 bootstrap

replicates. Relative influence (%) of each variable on isotope models is shown in the top left corner of each panel. TO, *Triaenodon obesus*; CM, *Carcharhinus melanopterus*; CA, *C. amblyrhynchus*. Other species are not included due to small sample sizes

surgeonfish, tropical abalone), pelagic planktivores (e.g., hardyheads, fusiliers) and low-level mesopredators (e.g., octopus, wrasse, sea snake), but high-level mesopredators

were rare or absent (only one small *L. carponotatus* was found in 107 reef sharks). Some prey taxa (e.g., octopus, wrasse, parrotfish) were found in two or more species of

Table 2 Trophic position (TP) of reef sharks relative to the TP of different base groups, assuming constant and scaled (in parentheses) diet-tissue fractionation (as per Hussey et al. 2010, 2014b, respectively)

Species	Base group ^a			Mean TP (\pm SE) ^b
	Herbivore ($\lambda = 2$)	Small demersal predator ($\lambda = 3.65$)	Large pelagic predator ($\lambda = 4.47$)	
<i>Triaenodon obesus</i>	3.3 (3.6)	3.8 (3.8)	3.9 (3.1)	3.8 \pm 0.1 (3.5 \pm 0.2)
<i>Carcharhinus melanopterus</i>	3.6 (4.1)	4.1 (4.3)	4.3 (3.5)	4.1 \pm 0.1 (4.0 \pm 0.2)
<i>Carcharhinus amblyrhynchos</i>	3.6 (4.3)	4.1 (4.5)	4.3 (3.8)	4.1 \pm 0.1 (4.2 \pm 0.2)
<i>Nebrius ferrugineus</i> *	3.3 (3.8)	3.8 (4.0)	4.0 (3.2)	3.8 \pm 0.1 (3.6 \pm 0.2)
<i>Negaprion acutidens</i> *	4.0 (4.6)	4.5 (4.8)	4.7 (4.1)	4.5 \pm 0.1 (4.5 \pm 0.2)
<i>Galeocerdo cuvier</i> *	4.0 (5.1)	4.5 (5.3)	4.7 (4.5)	4.5 \pm 0.1 (5.0 \pm 0.2)
<i>Carcharhinus obscurus</i> *	4.6 (6.0)	5.1 (6.2)	5.3 (5.4)	5.1 \pm 0.1 (5.9 \pm 0.2)
<i>Plectropomus leopardus</i> **	3.4 (4.9)	4.2 (5.1)	4.5 (4.4)	4.1 \pm 0.3 (4.8 \pm 0.2)
<i>Plectropomus maculatus</i> **	3.4 (4.3)	4.2 (4.5)	4.5 (3.7)	4.1 \pm 0.3 (4.1 \pm 0.2)
<i>Lethrinus miniatus</i> **	3.2 (4.6)	4.1 (4.8)	4.4 (4.0)	4.0 \pm 0.3 (4.5 \pm 0.2)
<i>Lutjanus carponotatus</i> **	3.3 (4.2)	4.1 (4.4)	4.4 (3.7)	4.0 \pm 0.3 (4.1 \pm 0.2)

Trophic positions of other sharks (*) and large predatory reef fishes (**) are also shown for comparison (fish data are from Frisch et al. 2014)

^a Base $\delta^{15}\text{N}$ values were derived from Frisch et al. (2014) and base trophic positions (λ) were derived from Farmer and Wilson (2011)

^b Means derived using a constant discrimination factor were weighted according to λ

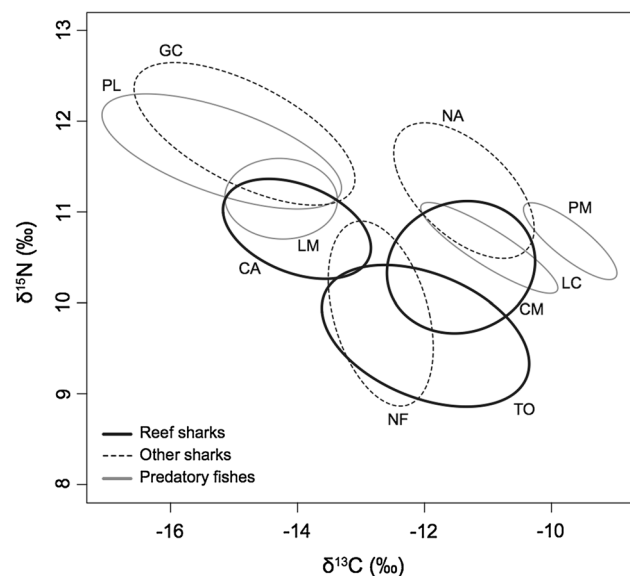


Fig. 4 Isotopic niche space of reef sharks (black lines), ‘other’ sharks (dashed lines) and large predatory fishes (grey lines) presented as Bayesian ellipses. Note that ‘other’ sharks had small sample sizes ($n = 4-7$) and are shown only for comparison. *Carcharhinus obscurus* is not included as only a single individual was sampled. Fish data are from Frisch et al. (2014). TO, *Triaenodon obesus*; CM, *C. melanopterus*; CA, *C. amblyrhynchos*; NF, *Nebrius ferrugineus*; NA, *Negaprion acutidens*; GC, *Galeocerdo cuvier*; PL, *Plectropomus leopardus*; PM, *Plectropomus maculatus*; LM, *Lethrinus miniatus*; LC, *Lutjanus carponotatus*

reef shark, but the majority of prey taxa were found in only a single species of reef shark (Table 5). Mean weight of stomach contents (per shark) was very small

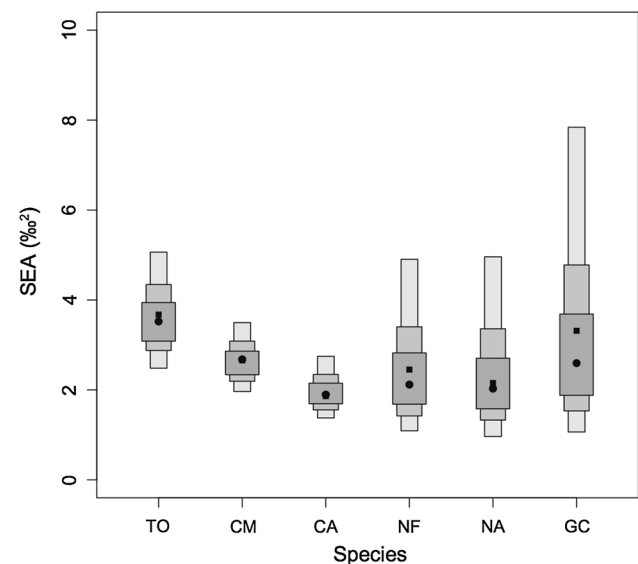


Fig. 5 Density plots showing the credibility intervals of Bayesian standard ellipse areas (SEA_B). Black circles and squares indicate mode SEA_B and small sample size-corrected SEA (SEA_C), respectively. Shaded boxes indicate the 50, 75 and 95 % credibility intervals for each species. TO, *Triaenodon obesus*; CM, *Carcharhinus melanopterus*; CA, *C. amblyrhynchos*; NF, *Nebrius ferrugineus*; NA, *Negaprion acutidens*; GC, *Galeocerdo cuvier*. *Carcharhinus obscurus* is not included as only a single individual was sampled

(82.1 ± 20.6 g for all reef sharks combined; Table 4), and there were no significant differences among species (ANOVA). For all three species of reef shark, fish were the

Table 3 Interspecific overlap (%) of Bayesian standard ellipse areas (SEA_B) and probability that the SEA_B of one species is larger than the SEA_B of another species (in parentheses)

Species 2	Species 1					
	<i>Triaenodon obesus</i>	<i>Carcharhinus melanopterus</i>	<i>Carcharhinus amblyrhynchos</i>	<i>Nebrius ferrugineus</i>	<i>Negaprion acutidens</i>	<i>Galeocerdo cuvier</i>
<i>Triaenodon obesus</i>	–	32.58 (0.08)	0 (0.90)	14.66 (0.56)	32.34 (0.57)	0 (0.32)
<i>Carcharhinus melanopterus</i>	23.56	–	0.60 (0.99)	73.47 (0.81)	0 (0.81)	0 (0.57)
<i>Carcharhinus amblyrhynchos</i>	0.31	0	–	12.2 (0.27)	0 (0.30)	7.88 (0.14)
<i>Nebrius ferrugineus</i>	49.03	13.53	16.06	–	0 (0.52)	0 (0.32)
<i>Negaprion acutidens</i>	0	26.19	0	0	–	0 (0.31)
<i>Galeocerdo cuvier</i>	0	0	14.03	0	0	–

Data should be interpreted as the percentage of SEA_B of Species 1 that is occupied by the SEA_B of Species 2. Bold text indicates a significant difference in SEA_B between two species when $\alpha = 0.05$

Table 4 Summary of stomach contents of reef sharks

Species	No. of sharks lavaged	% of sharks with empty stomach	No. of sharks with stomach contents	Total no. of prey items	Mean weight of each prey item (g ± SE)	Mean weight of stomach contents (g ± SE)
<i>Triaenodon obesus</i>	31	67.7	10	11	90.0 ± 74.6	99.0 ± 78.3
<i>Carcharhinus melanopterus</i>	45	42.2	26	40	51.4 ± 15.6	79.0 ± 19.3
<i>Carcharhinus amblyrhynchos</i>	31	71.0	9	13	50.0 ± 20.4	72.2 ± 24.5
All reef sharks	107	57.9	45	64	57.7 ± 17.3	82.1 ± 20.6

Other sharks are not included due to small sample sizes

dominant prey (64.1 %) followed by molluscs (26.5 %), and the distribution of major prey types (fish, molluscs and ‘miscellaneous’) was not significantly different among shark species (χ^2 ; Table 5). Schoener’s diet overlap index was 0.38 (*C. melanopterus* vs *T. obesus*), 0.33 (*C. melanopterus* vs *C. amblyrhynchos*) and 0.44 (*T. obesus* vs *C. amblyrhynchos*), indicating low to moderate levels of dietary overlap.

Discussion

Analyses of stomach contents and stable isotopes revealed subtle inter-specific differences in the trophic role of reef sharks (*T. obesus*, *C. melanopterus* and *C. amblyrhynchos*), but also inter-group trophic overlap between reef sharks, other sharks and large predatory fishes. Previously, reef sharks were explicitly or implicitly assumed to be apex predators (Friedlander and DeMartini 2002; Sandin et al. 2008; Rizzari et al. 2014c). However, results from the

present study provide multiple lines of evidence that challenge this assumption. Firstly, $\delta^{15}\text{N}$ values reveal that reef sharks occupy a similar TP to large predatory fishes (putative mesopredators) but a lower TP than other sharks such as *G. cuvier*, *N. acutidens* and potentially also *C. obscurus* (Table 2; see also Speed et al. 2012; Hilding et al. 2013). Secondly, stomach contents of reef sharks consisted primarily of small or juvenile fishes (herbivores, planktivores, low-level mesopredators) and molluscs, with few or no large piscivores (Tables 4, 5; see also Randall 1977; Stevens 1984; Wetherbee et al. 1997; Papastamatiou et al. 2006). Thirdly, reef sharks and large predatory fishes (e.g., *Lethrinus miniatus*, *Lutjanus carponotatus*) have broadly similar diets (cf Table 5; Connell 1998; Kulbicki et al. 2005) and occupy a similar band of isotopic niche space (Fig. 4). In addition, reef sharks are known to be eaten by larger sharks such as *G. cuvier* and *Sphyrna mokarran* (great hammerhead shark) (Lowe et al. 1996; Mourier et al. 2013). Collectively, these results provide strong evidence that reef sharks do not occupy the apex of coral reef food

Table 5 Diet composition of reef sharks

Prey taxa	<i>Triacnodon obesus</i>	<i>Carcharhinus melanopterus</i>	<i>Carcharhinus amblyrhynchos</i>	All reef sharks
Teleost fish (total)	(90.9)	(52.5)	(76.9)	(64.1)
Wrasse (Labridae)	9.1	7.5	0	6.3
Flutemouth (Fistulariidae)	0	7.5	0	4.7
Hardyhead (Atherinidae)	0	5.0	0	3.1
Parrotfish (Scaridae)	27.3	2.5	0	6.3
Eel (Muraenidae)	0	2.5	7.7	3.1
Angelfish (<i>Centropyge bicolor</i>)	0	2.5	0	1.6
Snapper (<i>Lutjanus carponotatus</i>)	0	2.5	0	1.6
Lizardfish (Synodontidae)	0	2.5	0	1.6
Surgeonfish (<i>Naso unicornis</i>)	9.1	0	0	1.6
Fusilier (<i>Pterocaesio marri</i>)	9.1	0	0	1.6
Cardinalfish (Apogonidae)	0	0	7.7	1.6
Unidentifiable fish	36.4	20.0	61.5	31.3
Mollusc (total)	(9.1)	(35.0)	(15.5)	(26.5)
Tropical abalone (<i>Haliotis</i>)	0	25.0	0	15.6
Octopus (Octopodidae)	9.1	7.5	7.7	7.8
Squid (Loliginidae)	0	2.5	0	1.6
Cuttlefish (Sepiidae)	0	0	7.7	1.6
Other vertebrates (total)	(0)	(7.5)	(7.7)	(6.2)
Sea snake (Hydrophiinae)	0	2.5	7.7	3.1
Bird (Sternidae)	0	5.0	0	3.1
Crustacea				
Crab (Brachyura)	0	2.5	0	1.6
Other				
Coral (Scleractinia)	0	2.5	0	1.6

Data are expressed as per cent frequency of pooled stomach contents. See Table 4 for sample sizes. Other sharks are not included due to small sample sizes

chains, at least on reefs where predator communities are intact, but instead occupy trophic niches similar to those of large predatory fishes. These findings have important implications for interpreting the structure and function of coral reef communities and for predicting the effects of predator removal.

Assignment of species into discrete trophic groups is standard protocol in community ecology and has facilitated unique insights into ecosystem function and alternative management scenarios, which are ultimately used to guide policy decisions. At present, reef sharks are typically assigned to the apex of food webs (e.g., Bozec et al. 2004; Bascompte et al. 2005; Sandin et al. 2008), but our results indicate that this practice misrepresents trophic structure among high TP species. Hence, we advocate a reassignment of reef sharks to an alternative trophic group (such as high-level mesopredators) that better reflects trophic similarities between reef sharks and large predatory fishes. This change is expected to refine our understanding of how reef

communities function, and ultimately, improve management of reef sharks.

If indeed reef sharks are high-level mesopredators, who then are the apex predators on coral reefs? Given their superior size and ability to eat reef sharks, we hypothesise that the role of apex predator is fulfilled by large, roving sharks such as *G. cuvier*, *C. obscurus*, *C. albimarginatus*, *N. acutidens* and *S. mokarran*. Although large roving sharks are seldom seen during visual surveys of coral reefs (e.g., Rizzari et al. 2014b) and thus are typically considered rare, their actual abundances may be much higher than currently believed, since they accounted for ~9 % of all sharks captured by long-lining at our study sites (excludes *N. ferrugineus*; Table 1) and they comprise a high proportion of sightings by baited remote underwater videos on the GBR (Espinoza et al. 2014). Therefore, it is plausible that large roving sharks are present in sufficient numbers to potentially exert top-down control of reef sharks and other high-level mesopredators on coral reefs (see also Heupel et al. 2014).

Removal of apex predators such as wolves, lions and dingoes can invoke trophic cascades due to release of numerous prey species and subsequent flow-on effects to lower trophic levels (Estes et al. 2011; Ripple et al. 2014). However, trophic cascades induced solely by removal of reef sharks are rare, subtle and/or equivocal (Heithaus et al. 2010; Ruppert et al. 2013; Rizzari et al. 2015), implying that reef sharks have relatively weak effects on community structure and function. A potential explanation is that functional redundancy exists among large piscivores, such that equivalent species compensate for any loss of reef sharks and thus buffer potential trophic cascades. This hypothesis is supported by our results, which indicate that (1) reef sharks and large predatory fishes are functionally similar (based on equivalent mean TPs and overlapping isotopic niches; Tables 2 and 3), and (2) these two groups of predators are dietary generalists (Table 5; Connell 1998; Kulbicki et al. 2005) and potentially consume prey in proportion to availability (Kingsford 1992), thereby compensating for loss of species-level interactions. It is also noteworthy that large predatory reef fishes are highly diverse (>20 species on the GBR) and probably encompass a broader range of trophic niches than those of the four species considered here. In view of these results, we contend that functional redundancy exists among large piscivores and is sufficiently high on the GBR to stabilize community structure despite moderate to high fishing pressure and depletion of reef sharks in some areas (Rizzari et al. 2015).

Bivariate isotope data (Fig. 2) and stomach contents (Table 5) indicate subtle inter-specific differences in diet and low to moderate inter-specific competition for prey among reef shark species. Limited or incomplete trophic overlap is thought to be a prerequisite for competitor coexistence and has been previously documented within predatory communities of a broad range of animal taxa (Woodward and Hildrew 2002; Heyward and Kerley 2008), but only rarely in predatory communities where species show strong morphological, taxonomic and habitat similarities. Total area of isotopic niche space was substantially larger for *T. obesus* than for *C. melanopterus* and *C. amblyrhynchos* (Table 1), indicating that *T. obesus* is more generalist in its diet and is perhaps more resilient to environmental disturbances that alter the composition of reef fish communities.

Mean $\delta^{13}\text{C}$ (an indicator of food source) of reef sharks indicates that they participate in multiple food webs and are sustained by multiple sources of primary production. According to the mixing model, *C. amblyrhynchos* derives the majority (58 %) of their carbon from pelagic sources such as phytoplankton, whereas *T. obesus* and *C. melanopterus* derive the majority (65 and 72 %, respectively) of their carbon from benthic reef-based sources such as coral

(Table 1; see also McCauley et al. 2012). Due to the effects of climate change, the abundance of corals and coral-dependent fishes is expected to decline during the next century (Hoegh-Guldberg et al. 2007), with unknown but potentially severe consequences for reef sharks. Vulnerability to climate-related stressors is predicted to be highest for *C. melanopterus* and lowest for *C. amblyrhynchos* due to differential use of benthic reef-based sources of production, although further research is needed to confirm this hypothesis.

Although pelagic production has long been known to play an important role in sustaining coral reef food webs, the ultimate sources of carbon available to reef sharks are poorly understood (Bozec et al. 2004; Hilding et al. 2013). Our results demonstrate that planktonic producers contribute substantially to reef shark production, with planktonic carbon contributions as high as 57.8 % in the case of *C. amblyrhynchos* (Table 1; see also McCauley et al. 2012). Protection of pelagic habitats is therefore an important component of reef shark conservation. However, despite the importance of pelagic production to *C. amblyrhynchos* (Table 1; McCauley et al. 2012), surprisingly few pelagic prey were identified in their stomach contents (Table 5; see also Wetherbee et al. 1997; Papastamatiou et al. 2006). It is possible, therefore, that planktonic production is linked to *C. amblyrhynchos* via reef-based planktivores (or consumers of reef-based planktivores). It is also possible that SCA underestimated the consumption of pelagic prey, potentially because common pelagic fishes such as clupeids and engraulids are small, soft-skinned and thus rapidly digested (relative to coral reef prey). Differential digestion is a fundamental problem with SCA (Cortés 1997) and highlights the utility of stable isotope analyses as a complementary method for investigation of trophic ecology.

It is noteworthy that herbivores such as parrotfish and unicorn surgeonfish (*Naso unicornis*) were found in the stomachs of *T. obesus* (Table 5; Randall 1977) and that both predator and prey have closely matching $\delta^{13}\text{C}$ signatures (Table 1; Frisch et al. 2014). Reef-based herbivorous fishes, particularly *N. unicornis*, have keystone characteristics and are thought to be critical for maintaining the competitive balance between corals and algae (Hoey and Bellwood 2009). Due to direct (consumptive) and indirect (behavioural) effects of reef sharks on herbivorous fishes, a primary concern is that reef sharks may suppress recovery of degraded coral reefs (Rizzari et al. 2014c). However, reef shark prey is typically small (Table 4), so it is likely that most species of herbivorous fishes achieve a size refuge and escape the risk of predation at a relatively early age (Mumby et al. 2006). Build-up of reef sharks in marine reserves is therefore unlikely to reduce net grazing capacity of herbivorous fishes to the extent that it threatens the overall health of coral reefs.

An alternative and widely-held hypothesis is that reef sharks have positive effects on coral reefs by suppressing high-level mesopredators (groupers, snappers, emperors), which, in turn, enhances herbivory via a trophic cascade (Bascompte et al. 2005; Ruppert et al. 2013). If this hypothesis were true, one would expect to find mesopredators in the diet of reef sharks. However, we found little evidence that reef sharks consume mesopredators; only one small snapper (*L. carponotatus*) was found in the stomachs of 107 reef sharks (Table 5), and species-specific estimates of TP (Table 2; see also Cortés 1999; Speed et al. 2012) suggest that reef sharks and mesopredators feed at approximately the same trophic position. Although these results cast doubt on the mesopredator-suppression hypothesis (Bascompte et al. 2005; Ruppert et al. 2013), it remains possible that reef shark-induced trophic cascades occur via behavioural effects, which are driven by fear rather than consumption (Heithaus et al. 2008). Clearly, further research is needed to elucidate the effects of reef sharks on fish community structure and to evaluate the overall importance of reef sharks to coral reef health. In the meantime, reef shark populations should be managed with high regard for the precautionary principle.

The interpretations and predictions presented thus far are dependent on two key assumptions. Firstly, we assumed that the reef- and pelagic-based sources of production that we represented with end members in the mixing model were the key sources of production that sustain reef sharks, i.e., that reef sharks primarily rely on a combination of reef and pelagic production and not on additional or alternate sources such as deep-water inter-reef food webs. Although the selected end members almost certainly do not represent the complete isotopic signature of reef and pelagic food webs, concordance between the isotopic signatures of end members and relevant producers (Frisch et al. 2014) suggests that the selected end members do indeed serve as suitably accurate isotopic proxies for reef and pelagic systems. Secondly, we assumed that the high proportion (42–71 %) of reef sharks with empty stomachs was not caused by regurgitation during capture on the longline. This assumption is supported by three lines of evidence: (1) a high proportion of diver-speared reef sharks have empty stomachs (authors' pers. obs.); (2) no reef sharks were seen to regurgitate voluntarily, either in the water or on deck; and (3) some reef shark stomachs contained square pieces of bait, indicating that recently ingested food was not regurgitated (see “Materials and methods”). A high proportion of empty stomachs is common in reef sharks (Randall 1977; Stevens 1984; Wetherbee et al. 1997) and highlights the utility of a dual approach (SCA and SIA) to estimate diet and associated trophic metrics of reef sharks.

In summary, it is apparent that reef sharks do not occupy the apex of coral reef food chains. Instead, they have

functional roles similar to those of large predatory fishes such as snappers, emperors and groupers, which are typically regarded as high-level mesopredators. Hence, there is probably a degree of functional redundancy in this guild of large predators, potentially explaining why shark-induced trophic cascades are rare or subtle on coral reefs. It is also apparent that reef sharks participate in multiple food webs and are sustained by multiple sources of primary production, some of which (e.g., corals) are particularly susceptible to climate-related stressors. We assert that large conspicuous predators, be they elasmobranchs or any other taxon, should not axiomatically be regarded as apex predators without thorough analysis of their diet. In the case of reef sharks, which were previously assumed to be apex predators, our dietary analyses suggests they should be reassigned to an alternative trophic group such as high-level mesopredators. This change will facilitate improved understanding of how reef communities function and how removal of predators (e.g., via fishing) might affect ecosystem properties, ultimately leading to improved reef shark conservation and management. This is imperative and urgent given the recent declines in reef shark populations (see Rizzari et al. 2014a and references therein) and the intensifying threats they will face in the future.

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