Evidence for dynamic resource partitioning between two sympatric reef shark species within the British Indian Ocean Territory

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Stable-isotope analyses (δ13C, δ15N and δ34S) of multiple tissues (fin, muscle, red blood cells and plasma), revealed ontogenetic shifts in resource use by grey reef sharks *Carcharhinus amblyrhynchos* and resource partitioning with silvertip sharks *Carcharhinus albimarginatus* within the British Indian Ocean Territory marine protected area (MPA). Resource partitioning varied temporally, with *C. albimarginatus* feeding on more pelagic prey during October to January, potentially attributable to an influx of pelagic prey from outside the MPA at that time. Reef sharks may therefore be affected by processes outside an MPA, even if the sharks do not leave the MPA.

KEYWORDS
British Indian Ocean Territory, reef shark, resource partitioning, stable isotope, δ13C, δ15N, δ34S

Sharks are believed to play an important role in structuring marine communities and consequently contribute to ecosystem productivity (Heithaus et al., 2008). However, the ecological role of reef sharks has been at the forefront of recent debate (Heupel et al., 2014; Rizzari et al., 2014; Roff et al., 2016) as they often share similar habitats and trophic roles (Speed et al., 2012), but have been shown to exhibit resource partitioning (Rizzari et al., 2014). Some authors have classified reef sharks as top predators (Friedlander & DeMartini, 2002), whereas others suggest they are mesopredators (Heupel et al., 2014) with a high degree of functional redundancy within the guild (Frisch et al., 2016b). To understand these relationships and their ecological importance better, interactions such as resource partitioning need to be examined.

Stable-isotope analysis (SIA) of nitrogen (δ15N) and carbon (δ13C) provide insights into trophic interactions and resource partitioning (Papastamatiou et al., 2006; Plumlee & Wells, 2016), which are key for understanding how ecological communities are structured. Previous studies of sharks have shown that the turnover rates of stable isotopes in muscle and fin tissue are relatively slow, incorporating dietary information over more than a year (MacNeil et al., 2006). In contrast, red blood cells (RBC) turnover faster (minimum 95% turnover rate estimates of 258 days for δ15N and 405 days for δ13C) and plasma quicker still (170 days for δ15N and 252 days for δ13C for plasma; Caut et al., 2013) and thus represent diets over shorter time scales. Thus, SIA can reveal temporal changes in the trophic ecology of organisms if multiple tissue types are sampled (Hussey et al., 2012).

In this study, SIA was used to examine resource partitioning and seasonal variation in resource use, specifically if dynamic resource partitioning occurs between two sympatric reef sharks, the grey reef shark *Carcharhinus amblyrhynchos* (Bleeker 1856) and the silvertip shark *Carcharhinus albimarginatus* (Rüppell 1837), within the British Indian Ocean Territory (BIOT) marine protected area (MPA). To
sampling five teleost families (barracuda, Sphyraenidae; grouper, Serpaelegonidae; snapper, Lutjanidae; trevally, Carangidae; tuna, Scombridae; wahoo, Scombridae; Table 1). Mean (± SD)

| Species | LCS (cm) | Lf (cm) | n | Fin | Muscle | SBC | Pre-caudal length; Lf, fork length; n, the numbers of animals sampled with shark sex ratios (M:F); RBC, red blood cells. | Plasma |
|---------|----------|---------|---|-----|--------|-----| RBC samples were for 5 C. amblyrhynechos and 7 C. ambimarginatus only. Plasma samples were collected for 5 C. amblyrhynechos and 7 C. ambimarginatus only. Morphometric measurements of one male C. ambimarginatus were not recorded. Sulphur data were not available for one tuna. | |
| Sharks | C. amblyrhynchos | 102.4 (55-125) | 113.5 (58-138) | 15 (0:15) | -12.2 ± 1.1 | 12.3 ± 0.4 | -13.4 ± 1.7 | 14.0 ± 0.6 | 17.5 ± 0.9 | -14.0 ± 1.3 | 13.7 ± 0.4 | -13.7 ± 0.3
| C. ambimarginatus | 111.4 (91-141) | 124.5 (103-156) | 11 (7:4) | -13.7 ± 0.3 | 12.0 ± 0.4 | -14.6 ± 1.0 | 13.3 ± 0.8 | 17.0 ± 2.4 | -16.2 ± 0.2 | 13.2 ± 0.2 | -15.6 ± 0.2 | 12.4 ± 0.2
| Teleosts | Barracuda, Sphyraenidae | 57.7 (45.5-72) | 10 | -17.0 ± 0.5 | 13.6 ± 0.5 | 15.0 ± 1.7 | -15.3 ± 0.8 | 13.7 ± 0.4 | 13.9 ± 0.4 | -16.8 ± 0.2 | 13.1 ± 0.2 | 16.2 ± 1.8d
| Grouper, Serpaenidae | 61.5 (21-95) | 4 | -13.6 ± 2.0 | 13.7 ± 0.1 | 17.2 ± 0.8 | -17.1 ± 0.5 | 13.1 ± 1.1 | 16.6 ± 2.8 | -16.7 ± 0.2 | 12.5 ± 0.7 | 17.1 ± 1.0
| Snapper, Lutjanidae | 36.3 (21-59) | 3 | -15.3 ± 0.8 | 13.7 ± 0.4 | 13.9 ± 0.4 | -16.8 ± 0.2 | 13.1 ± 0.2 | 16.2 ± 1.8d | -16.7 ± 0.2 | 12.5 ± 0.7 | 17.1 ± 1.0
| Trevally, Carangidae | 54.0 (51-57) | 2 | -13.6 ± 2.0 | 13.7 ± 0.1 | 17.2 ± 0.8 | -17.1 ± 0.5 | 13.1 ± 1.1 | 16.6 ± 2.8 | -16.7 ± 0.2 | 12.5 ± 0.7 | 17.1 ± 1.0
| Tuna, Scombridae | 52.6 (30-70) | 12 | -15.3 ± 0.8 | 13.7 ± 0.4 | 13.9 ± 0.4 | -16.8 ± 0.2 | 13.1 ± 0.2 | 16.2 ± 1.8d | -16.7 ± 0.2 | 12.5 ± 0.7 | 17.1 ± 1.0
| Wahoo, Scombridae | 110.5 (94-133) | 6 | -15.3 ± 0.8 | 13.7 ± 0.4 | 13.9 ± 0.4 | -16.8 ± 0.2 | 13.1 ± 0.2 | 16.2 ± 1.8d | -16.7 ± 0.2 | 12.5 ± 0.7 | 17.1 ± 1.0

C. amblyrhynchos L - 102.4 ± 22.23 cm; all individuals were female. C. ambimarginatus L - 111.4 ± 21.02 cm; 28 males and 31 females. C. albimarginatus L - 111.4 ± 21.02 cm; 28 males and 31 females.
L_{PC} = 111.4 ± 18.18 cm and included seven males and four females (Table 1). L_{PC} correlated positively with δ^{13}C in C. amblyrhynchos fin (P < 0.05, r^2 = 0.44) and muscle tissue (P < 0.05, r^2 = 0.55) and δ^{15}N of fin tissue (P < 0.05, r^2 = 0.61), indicating an ontogenetic shift in foraging location and trophic position, respectively (Table 2 and Supporting Information Figures S1, S2). In contrast, no significant relationships were found between length and δ^{13}C or δ^{15}N in C. albimarginatus for any tissue type suggesting that neither foraging location nor trophic position were influenced by body size (Table 2 and Supporting Information Table S2). This supports previous studies that have found these two species feed at a similar trophic level (Cortés, 1999). C. amblyrhynchos also had significantly higher δ^{15}N values than C. albimarginatus in all tissues (+1.2–2.2‰; Table 1 and Supporting Information Table S2). This indicates that while these species co-exist and feed at a similar

| Species               | r^2  | P     | slope | r^2  | P     | slope | r^2  | P     | slope |
|-----------------------|------|-------|-------|------|-------|-------|------|-------|-------|
| **C. amblyrhynchos**  |      |       |       |      |       |       |      |       |       |
| Fin                   | 0.48 | 0.01  | 0.06  | 0.64 | <0.001| 0.03  | 0.16 | 0.16  | −0.02 |
| Muscle                | 0.58 | <0.001| 0.09  | 0.01 | 0.81  | 0.00  | 0.01 | 0.02  | 0.66  |
| RBC                   | 0.85 | 0.08  | 0.19  | 0.46 | 0.32  | 0.03  | 0.32 | 0.44  | 0.02  |
| Plasma                | 0.76 | 0.13  | 0.13  | 0.32 | 0.44  | 0.02  | 0.32 | 0.44  | 0.02  |
| **C. albimarginatus** |      |       |       |      |       |       |      |       |       |
| Fin                   | 0.08 | 0.36  | 0.00  | 0.17 | 0.16  | −0.01 | 0.10 | 0.39  | 0.04  |
| Muscle                | 0.06 | 0.50  | 0.01  | 0.02 | 0.66  | −0.01 | 0.02 | 0.66  | −0.01 |
| RBC                   | 0.01 | 0.87  | 0.00  | 0.46 | 0.14  | 0.01  | 0.46 | 0.14  | 0.01  |
| Plasma                | 0.34 | 0.22  | −0.01 | 0.10 | 0.55  | 0.00  | 0.10 | 0.55  | 0.00  |

Bold denotes significant relationships with PCL at P ≤ 0.05.

FIGURE 1 Bayesian isotope mixing models were used to determine the extent that *Carcharhinus amblyrhynchos* and *Carcharhinus albimarginatus* were reliant on reef (blue) or pelagic (red) resources. End members were set as the most δ^{13}C depleted (pelagic) and most δ^{13}C enriched (reef) of the teleosts sampled (trevally (Carangidae) for reef, tuna (Scombridae) for pelagic). Posterior probability distributions indicate model predictions of reliance on a given source with higher values indicating greater reliance.
FIGURE 2  (a) Maximum likelihood standard ellipse areas (σ, 40% of the data) for isotopes δ13C v. δ15N in fin, (b) muscle, (c) red blood cell, (d) plasma and for isotope δ34S v. δ13C (e) and δ15N (f) of Carcharhinus amblyrhynchos (♂) and Carcharhinus albimarginatus (♀). Convex hulls (—-.) are drawn between the centers of each group. Overlapping values, if present, are the proportion of overlapping area of the two ellipses. Potential competitor–prey teleost data are shown (●) with associated error bars (± 1 SD). Ellipses for red blood cell and plasma presented for reference but represent small sample sizes (< 10) and therefore come with lower confidence.
trophic level, there is a degree of resource partitioning. Overall, δ15N values of teleosts sampled were similar to those of both C. amblyrhynchos and C. albimarginatus, suggesting these species may not represent direct prey for reef sharks and feed at similar trophic levels. These data broadly support observations of Roff et al. (2016) who classify C. amblyrhynchos as mesopredators that occupy a similar trophic level to large piscivorous fishes. Owing to restrictions in the BIOT MPA, it was not possible to sample lower trophic level species that have been shown to contribute significantly to the diet of reef sharks (Frisch et al., 2016b). Tunas have the lowest mean δ13C values and therefore the strongest pelagic signal (mean ± SD = –17.1% ± 0.5); whereas the highest mean δ13C values were found in reef associated trevally (–13.6% ± 2.0; Table 1).

We used the δ13C of potential competitor–prey teleost species to assess the relative importance of different food webs (pelagivorevs. reef) to sharks. To do this we used a δ13C discrimination factor of 0.000‰ and a standard deviation of ± 0.33 (Hussey et al., 2010). Bayesian mixing models indicate that C. amblyrhynchos derive c. 78% of their biomass from reef sources compared with just c. 60% for C. albimarginatus (Figure 1). Interestingly, while the relatively increased dependence of C. amblyrhynchos on reef resources presented here are broadly consistent with findings for C. amblyrhynchos in the Great Barrier Reef (Frisch et al., 2016b), they are in contrast to C. amblyrhynchos in Palmyra Atoll (5° 53′ 01″N, 162° 04′ 42″W) which derive the majority (c. 86%) of their biomass from pelagic sources (McCaulley et al., 2012). These data suggest significant ecological variability within a reef-shark species dependent on location.

Here, some of the first δ34S data examining trophic interactions and resource partitioning among sharks on remote coral reefs is presented. No significant difference in δ34S values was observed between shark species, but both exhibited large ranges (C. amblyrhynchos 15.4–18.6‰; C. albimarginatus 11.8–19.0‰; Table 1 and Figure 2e,f). Mean δ34S values for reef sharks (17.0–17.5‰) suggest they are heavily dependent on pelagic productivity (Gajdzik et al., 2016). However, the wide ranges suggest they have diverse intraspecific feeding strategies, especially C. albimarginatus, verifying previous dietary studies (Cortés 1999). Teleosts had similar δ34S values when compared with reef sharks, again suggesting a strong dependence on pelagic prey items (Table 1). Interestingly, epinephelids had the lowest mean δ34S value (13.9 ± 5.4‰) and the largest range (Table 1). This is consistent with their broad diet across benthic and pelagic sources (Frisch et al., 2016a).

For all tissue types, SEAc for δ13C and δ15N values were considerably larger in C. amblyrhynchos (fin = 1.26; muscle = 3.30; RBC = 1.75; plasma = 1.18) than C. albimarginatus (fin = 0.36; muscle = 1.57; RBC = 0.08; plasma = 0.12; Figure 2a–d and Supporting Information Table S3), suggesting C. amblyrhynchos have a larger isotopic niche and a more generalised feeding ecology than C. albimarginatus. Overall, very little isotopic niche overlap occurred between the two species with only muscle tissue showing a small degree of overlap (0.02; Figure 2b, but note small sample sizes). These data indicate clear niche partitioning between these two closely related species. Our findings also support the categorization proposed by Frisch et al. (2016b) that C. amblyrhynchos are true reef sharks but C. albimarginatus are less dependent on reef-based resources. Furthermore, it appears that this partitioning of resources varies temporally. While muscle isotope data indicate that these sharks exploit different resources over long time frames, niche partitioning was most evident in tissues with faster turnover rates (Figure 2a–d). Though our sample size was limited, we postulate that this may be driven by seasonal increases in the use of pelagic resources by C. albimarginatus relative to C. amblyrhynchos. As sampling occurred in January, this would suggest that C. albimarginatus increased their use of pelagic resources in prior months (c. October–December). This timeframe matches the historical peak pelagic fishing season (October–January) within BIOT when a purse-seine fishery targeted migrating yellowfin tuna Thunnus Albacares (Bonnaterre 1788) (Mees et al., 2009). Recent tagging studies have shown that C. albimarginatus remain within the BIOT MPA boundaries (A Carlisle unpubl. data) and are therefore directly spatially protected from the effects of legal fishing vessels, although the illegal poaching of sharks occurs within the MPA (Ferretti et al., 2018). Such findings are important to consider when establishing and managing protected areas, which are usually focused on protecting intrinsic characteristics of a species such as home ranges or important life cycle events (e.g., spawning grounds; Green et al., 2014). However, it is clear that relative to C. amblyrhynchos, C. albimarginatus are more dependent on pelagic prey, some of which may migrate into BIOT MPA from outside. Thus, sharks, particularly C. albimarginatus, within the MPA may therefore be indirectly affected by processes such as fisheries beyond its borders.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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