

Apparent resource partitioning and trophic structure of large-bodied marine predators in a relatively pristine seagrass ecosystem

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ABSTRACT: Large predators often play important roles in structuring marine communities. To understand the role that these predators play in ecosystems, it is crucial to have knowledge of their interactions and the degree to which their trophic roles are complementary or redundant among species. We used stable isotope analysis to examine the isotopic niche overlap of dolphins (*Tursiops cf. aduncus*, large sharks (>1.5 m total length), and smaller elasmobranchs (sharks and batoids) in the relatively pristine seagrass community of Shark Bay, Australia. Dolphins and large sharks differed in their mean isotopic values for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and each group occupied a relatively unique area in isotopic niche space. The standard ellipse areas (SEAc; based on bivariate standard deviations) of dolphins, large sharks, small sharks, and rays did not overlap. Tiger sharks *Galeocerdo cuvier* had the highest $\delta^{15}\text{N}$ values, although the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of pigeye sharks *Carcharhinus amboinensis* were similar. Other large sharks (e.g. sicklefin lemon sharks *Negaprion acutidens* and sandbar sharks *Carcharhinus plumbeus*) and dolphins appeared to feed at slightly lower trophic levels than tiger sharks. In this seagrass-dominated ecosystem, seagrass-derived carbon appears to be more important for elasmobranchs than it is for dolphins. Habitat use patterns did not correlate well with the sources of productivity supporting diets, suggesting that habitat use patterns may not necessarily be reflective of the resource pools supporting a population and highlights the importance of detailed datasets on trophic interactions for elucidating the ecological roles of predators.

KEY WORDS: Food webs · Predator–prey interactions · Stable isotope · Niche overlap · Elasmobranchs · Sharks · Cetacean · Trophic redundancy · Niche partitioning

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INTRODUCTION

Large-bodied marine predators, especially sharks and odontocete cetaceans (toothed whales), can play important roles in coastal marine communities through

both consumptive and non-consumptive effects on their prey (e.g. Williams et al. 2004, Heithaus et al. 2008, 2010, Wirsing et al. 2008). In many cases, however, our understanding of the ecological role of these taxa is hindered by a lack of information on

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their trophic interactions and the degree of resource partitioning or trophic redundancy that may exist within this guild of large marine predators (e.g. Kitchell et al. 2002, Heithaus et al. 2008, Ferretti et al. 2010). Often, this lack of information can be attributed to the difficulty in obtaining adequate sample sizes for stomach content analysis. Yet, understanding the trophic interactions and positions of large-bodied predators is an important step in elucidating the dynamics of marine communities (e.g. Williams et al. 2004, Lucifora et al. 2009) and the potential for top predators to couple various trophic pathways (e.g. Rooney et al. 2006).

In many systems, there is a high degree of interspecific differentiation in the diets and trophic interactions of sympatric species of large-bodied sharks and odontocetes. For example, in the southwest Indian Ocean, sympatric species of small odontocetes forage at different trophic levels or from different food web modules (Kiszka et al. 2011). Off the coast of South Africa, most species of dolphins and sharks show relatively low dietary overlap (Heithaus 2001a). Resource partitioning, however, is not ubiquitous, and substantial dietary overlap has been documented among sympatric large shark species as well as between shark and dolphin populations. For example, off the coast of South Africa, there is significant dietary overlap between several species of large sharks and common dolphins *Delphinus delphis* (Heithaus 2001a). Also, off the Pacific coast of Costa Rica, silky sharks *Carcharhinus falciformis* and common bottlenose dolphins *Tursiops truncatus* compete for fish prey (Acevedo-Gutiérrez 2002). Gaining further insights into potential overlap or divergence in trophic interactions of upper trophic level predators is important because the degree of trophic redundancy and intraguild predation (when predator and prey also compete for resources) play important roles in community stability (e.g. Bascompte et al. 2005, Kondoh 2008).

In the absence of extensive stomach content data, stable isotopes can provide important insights into variation in trophic interactions both within and among species (e.g. Bearhop et al. 2006, Quevedo et al. 2009, Layman et al. 2012), albeit over different temporal scales and with different resolution than information derived from stomachs. We used stable isotopes to investigate the trophic relationships of large-bodied sharks and a resident odontocete cetacean within a relatively pristine coastal seagrass ecosystem—Shark Bay, Australia—that has been used as a model system for understanding the ecological role of large marine vertebrates. Specifically,

we investigated (1) trophic positions and isotopic niches (see Newsome et al. 2007) of the common large-bodied (>1.5 m) predators, (2) overlap of isotopic niches among species and higher-order taxa (i.e. the potential for resource partitioning), (3) the relationships between body size and relative trophic position, and (4) the possibility for individual level dietary specialization in trophic interactions within populations of common species.

MATERIALS AND METHODS

Study site

Shark Bay is a ca. 13000 km² subtropical embayment along the central coast of Western Australia. The bay contains ca. 4000 km² of seagrass beds and is perhaps one of the most pristine seagrass ecosystems left in the world (e.g. Heithaus et al. 2008). In addition to seagrasses, the primary sources of productivity that support food webs in Shark Bay include plankton and macroalgae (e.g. Burkholder et al. 2011, Heithaus et al. 2011). The bay contains substantial populations of large vertebrates, including herbivorous green turtles *Chelonia mydas* and dugongs *Dugong dugon* and predators such as loggerhead turtles *Caretta caretta*, Indo-Pacific bottlenose dolphins *Tursiops cf. aduncus*, and a variety of sharks. The shark fauna is dominated numerically by tiger sharks *Galeocerdo cuvier* (Heithaus 2001b, Wirsing et al. 2006), which account for >90% of captures of sharks over 1.5 m total length (Heithaus et al. 2012). Tiger sharks in Australia consume a wide range of prey, including teleosts, cephalopods, sea snakes, sea turtles, marine birds, and marine mammals (Simpfendorfer 1992, Heithaus 2001a, Simpfendorfer et al. 2001). The proportion of large-bodied prey in tiger shark diets increases with shark size (Simpfendorfer 1992, Simpfendorfer et al. 2001). Other species of large sharks in Shark Bay are primarily from the genus *Carcharhinus*. In locations where their diets have been studied, these species feed primarily on teleosts and cephalopods (Cortés 1999). The pigeye shark *Carcharhinus amboinensis*, however, tends to include a high proportion of elasmobranchs in its diet (Cortés 1999), as does the occasionally encountered great hammerhead shark *Sphyrna mokarran* (Stevens & Lyle 1989, Cortés 1999). Smaller sharks and dolphins in the study area are largely piscivorous (e.g. Cortés 1999, Heithaus & Dill 2002, White et al. 2004).

Since 1997, we have used the Eastern Gulf of Shark Bay, along the eastern coast of Peron Peninsula, as a

model system for understanding the behavior and ecological role of large marine vertebrates, particularly tiger sharks and large grazers (see Heithaus et al. 2008, 2009). This area has also been the site of long-term research on the behavior and ecology of Indo-Pacific bottlenose dolphins (Connor & Smolker 1985, Smolker et al. 1992). Large sharks tend to be seasonally abundant in the study area, with high densities found in the warm months (September to May) and lower densities in winter (June to August) (Heithaus 2001b, Wirsing et al. 2006). Bottlenose dolphins are year-round residents of the Eastern Gulf of Shark Bay with individual home ranges up to ca. 50 m² (females) to 145 km² (males) (Watson-Capps 2005, Randic et al. 2012).

Field methods

Tissue samples were collected from sharks during drumline fishing from 2005 to 2011 (see Heithaus 2001b, Wirsing et al. 2006 for details). Although analyzing samples over many years brings in potential bias due to temporal variation in signatures of prey and resource pools, such an approach can allow for detection of robust patterns that transcend short-term and small-scale isotope variation (e.g. Layman et al. 2005). When a shark was captured, it was brought alongside the research vessel to be tagged and measured (total length [TL]). During handling, a small amount of tissue was collected from the trailing edge of the first dorsal fin using clean scissors. The tissue was immediately placed on ice and stored at -20°C upon returning to shore. Sharks captured by drumline fishing generally were relatively large, from 1.4 to 4.4 m TL. Smoothnose wedgefish *Rhynchobatus laevis*, a large-bodied and highly mobile ray species with a shark-like body, were collected via strike-netting from 2007 to 2011, and we collected tissue samples from their dorsal fins (see Vaudo & Heithaus 2011 for details). We compared these results to smaller-bodied elasmobranchs (sharks < 1.5 m TL and batoids) captured in the study area using other methods and published previously (Vaudo & Heithaus 2011) as well as other upper trophic level predators (e.g. teleosts, sea birds, and sea snakes) sampled opportunistically. Virtually all of the samples were collected during the warm season (September to May; Heithaus 2001b; Table 1).

Dolphin tissue samples were obtained during cold and warm seasons (Table 1) from 1997 to 2004 using a remote biopsy system constructed for small cetaceans (Krützen et al. 2002). Samples were preserved

in a saturated NaCl and 20% dimethyl-sulfoxide (DMSO) solution (Amos & Hoelzel 1992) at -20°C in the field and -80°C in the laboratory. Prior to stable isotope analysis, the epidermal skin was removed from each sample. Lipid extraction of cetacean skin samples stored in DMSO is a commonly used method for removing the effect of DMSO preservation on isotopic signatures (Todd et al. 1997, Marcoux et al. 2007). Accordingly, dolphin skin was washed with distilled water and lipid extracted by several rinses with a 2:1 mixture of chloroform and methanol for 24 h before further processing. Such processing removes any influence of the DMSO on isotopic values (Lesage et al. 2010).

Stable isotope analysis

Samples were thawed and washed in distilled water before being dried for at least 48 h and then ground into a fine powder. Samples were analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at stable isotope facilities at the Yale Earth System Center, Florida International University, and the University of Western Australia. Homogenized trout standards analyzed at the same time as our samples had standard deviations ranging from 0.10 to 0.19‰ for $\delta^{13}\text{C}$ and 0.02 to 0.08‰ for $\delta^{15}\text{N}$. Because elasmobranch samples had low C:N ratios (2.69 ± 0.26 , mean \pm SD) and previous studies have found that elasmobranch body tissue has low lipid content (Devadoss 1984, Hussey et al. 2010) and changes in $\delta^{13}\text{C}$ after lipid extraction tend to be relatively small (Hussey et al. 2012), we did not correct $\delta^{13}\text{C}$ values for the effects of lipids.

We used ANOVA to explore variation in mean isotopic values among species for which we obtained adequate sample sizes. We supplemented these analyses by exploring overlaps using standard ellipse areas corrected for sample size (SEAc), developed by Jackson et al. (2011). The SEAc are the equivalent of a bivariate standard deviation and are a measurement of isotopic dispersion. In addition to species-specific analyses, we explored overlap in ellipses calculated for the major large-bodied predator groups in Shark Bay: dolphins, large sharks (>1.5 m), small sharks (<1.5 m), and batoids (data on batoids from Vaudo & Heithaus 2011 with additional samples collected during the present study).

Because measures of central tendency, like mean isotopic values and SEAc, can disguise ecologically important variation within species and potential individual level overlap in resource use (Layman et al. 2012), we also used 2 quantitative metrics from Lay-

Table 1. Stable isotope values and measures of trophic diversity. TL: mean total length of individuals sampled; CD: mean centroid distance (values with different upper-case letters in superscript are significantly different based on post-hoc Tukey's tests). The TA (total area) column includes the p-value of a regression through the final 4 points of rarefaction analysis. $p > 0.05$ suggests that the TA of a species has been sampled adequately. 'Unique area' is the area of a taxon's TA that does not overlap with the TA of any other taxon. 'Unique points' is the number of individual isotopic values for a taxon that do not fall within the TA of any other taxon. Unique area and unique points are based on TA analysis

Species	TL (cm) Mean (range)	N (summer, winter)	$\delta^{15}\text{N}$ Mean \pm SD (‰)	$\delta^{13}\text{C}$ Mean \pm SD (‰)	TA (units ²) (p)	Unique area (%)	Unique points (%)	CD \pm SD
Marine mammals								
<i>Tursiops cf. aduncus</i>	200 ^a	36 (17, 19)	10.6 \pm 0.4	-14.0 \pm 1.1	5.3 (0.09)	3.9 (74.0)	25 (69.4)	1.01 \pm 0.63 ^{AB}
Sharks								
<i>Carcharhinus amboinensis</i>	188 (173–203)	8 (6, 2)	11.5 \pm 0.6	-11.6 \pm 0.8	2.5 (0.07)	0	0	0.86 \pm 0.48 ^{AB}
<i>Carcharhinus brachyurus</i>	227 (185–269)	2 (2, 0)	10.6, 11.0	-10.8, -14.0	–	–	–	–
<i>Carcharhinus brevipinna</i>	270 (259–280)	2 (2, 0)	11.1, 11.2	-13.5, -14.1	–	–	–	–
<i>Carcharhinus cautus</i> ^b	82 (50–117)	6 (4, 2)	8.7 \pm 0.6	-9.7 \pm 0.3	1.7	1.5 (89.7)	5 (83.3)	0.72 \pm 0.56
<i>Carcharhinus plumbeus</i>	179 (164–189)	19 (16, 3)	11.1 \pm 0.5	-11.1 \pm 0.7	2.8 (0.37)	0.4 (15.0)	3 (15.8)	0.77 \pm 0.33 ^B
<i>Carcharhinus sorrah</i>	131 (96–154)	3 (3, 0)	10.9 \pm 0.7	-12.8 \pm 1.0	0.44	–	–	–
<i>Chiloscyllium punctatum</i> ^b	69 (59–82)	23 (21, 2)	8.7 \pm 0.6	-12.2 \pm 0.8	6.7 (0.08)	4.1 (61.6)	21 (91.3)	0.87 \pm 0.42 ^B
<i>Negaprion acutidens</i>	224 (94–261)	6 (6, 0)	11.3 \pm 0.7	-10.1 \pm 1.2	2.0	0.2 (11.2)	2 (33.3)	1.13 (0.51)
<i>Orectolobus hutchinsi</i>	75 (61–90)	3 (3, 0)	9.3 \pm 0.3	-10.7 \pm 2.1	1.1	–	–	–
<i>Galeocerdo cuvier</i>	285 (156–417)	166 (145, 21)	11.9 \pm 0.7	-11.8 \pm 1.3	16.1 (0.18)	10.4 (64.4)	80 (48.2)	1.31 \pm 0.74 ^A
<i>Sphyrna mokarran</i>	377	1 (1, 0)	9.4	-9.0	–	–	–	–
Batooids ^c								
<i>Rhynchobatus laevis</i>	212	6 (6, 0)	8.7 \pm 0.7	-11.5 \pm 0.7	1.0	–	–	0.76 \pm 0.69
Group-level								
Large sharks		199			17.7	16.1 (91.0)	179 (89.9)	
Dolphins		36			5.3	3.9 (74.0)	25 (69.4)	
Small sharks ^b		29			7.2	0.9 (13.0)	3 (10.3)	
Batooids ^b		211			34.4	27.8 (80.8)	184 (87.2)	

^aMean total length is based on sizes of several stranded adult dolphins within the study area; samples taken by remote biopsy during the present study were all from adult-sized animals, which exhibit relative little variation in body length compared to sharks.

^bIncludes individuals from Vaudo & Heithaus (2011)

^cIncludes individuals not included by Vaudo & Heithaus (2011); not included in analyses of species-level overlap (included with batooids in group-level analyses)

man et al. (2007) for comparisons among species. Total area (TA) can be used as a proxy for the isotopic trophic diversity within a species over the timescale at which tissues assimilate isotopic values from diets. It is calculated as the area of the convex hull encompassing all individuals of that species. The convex hull approach is powerful because it incorporates each individual sampled and thus includes information about every part of isotopic niche space occupied (Layman et al. 2012). Mean distance to the centroid (CD) provides a proxy for the degree of trophic diversity among individuals of a species and was calculated using the distances of each individual from the mean of all individuals. We calculated all distances and areas using the Animal Movement Analyst Extension (AMAE) (Hooge & Eichenlaub 2000) for ArcView GIS 3.2a.

To assess whether we had adequately sampled the intraspecific variability and therefore the full isotopic niche space used by each species, we used AMAE to conduct bootstrap analyses ($n = 250$) examining the mean TA across varying sample sizes. We considered TA to be adequately sampled if the slope of a linear regression on the final 4 endpoints of the curve relating sample size to TA was not significantly different from zero (Bizzarro et al. 2007). Total areas were also calculated for both taxonomy- and size-based groups. We assessed the unique area occupied by each species TA by determining the total area in biplot space occupied only by that species' TA. Similarly, we calculated the proportion of individual isotopic values for each species that did not fall within any other species' TA.

We used the relative value of $\delta^{13}\text{C}$ as a proxy for the importance of seagrass-based productivity to sharks and dolphins. In Shark Bay and other coastal ecosystems, seagrasses tend to have more enriched ^{13}C values (mean \pm SD $\delta^{13}\text{C} = -9.4 \pm 1.3\text{‰}$) compared to their epiphytes and macroalgae (mean \pm SD $\delta^{13}\text{C} = -15.5 \pm 2.6\text{‰}$) (Vaudo & Heithaus 2011). A dugong and herbivorous isopods, 2 consumers that feed primarily on seagrass, had $\delta^{13}\text{C}$ values near -10‰ (Burkholder et al. 2011). Filter feeding bivalves (which can be used to infer isotope values of sestonic primary producers) are more ^{13}C -depleted (mean \pm SD $\delta^{13}\text{C} = -17.49 \pm 1.70\text{‰}$; Vaudo & Heithaus 2011), as are the leaves of fringing mangroves ($\delta^{13}\text{C}$ ca. -23‰ Heithaus et al. 2011). Inputs of mangrove-derived productivity to lower trophic levels in the study area appear to be minimal (Heithaus et al. 2011), and there are no significant terrestrial or freshwater inputs of basal resources (e.g. Kendrick et al. 2012).

RESULTS

We collected tissue samples from 239 sharks, representing 11 species, between 2005 and 2012 (Table 1). Relative sample sizes of sharks over 1.5 m TL reflected the relative abundance of sharks captured on drumlines, with the exception of tiger sharks, for which only a subset of samples were analyzed. In addition, we obtained isotopic values from 36 Indo-Pacific bottlenose dolphins that were sampled during 1997 to 2004 and 6 samples from smoothnose wedgefish collected between 2007 and 2011. Across isotopic values of all individuals, there was no relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ($F_{1,279} = 0.82$, $p = 0.37$, $R^2 < 0.01$). There was, however, a weak ($R^2 = 0.07$) but significant negative relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ for tiger sharks ($F_{1,167} = 13.1$, $p = 0.0004$). No significant relationships were found within other taxa.

Seasonal comparisons were only possible for dolphins and tiger sharks. There was no effect of season on $\delta^{15}\text{N}$ values for tiger sharks ($F = 0.20$, $p = 0.84$) or dolphins ($F = 0.91$, $p = 0.37$). Similarly, there was no effect of season on $\delta^{13}\text{C}$ values of dolphins ($F = 0.62$, $p = 0.54$), but $\delta^{13}\text{C}$ values of tiger sharks were slightly higher in the cold season (mean \pm SD = $-11.24 \pm 1.15\text{‰}$) than the warm season (mean \pm SD = $-11.89 \pm 1.37\text{‰}$; $F = 2.1$, $p = 0.04$). We did not detect significant effects of year on dolphin $\delta^{13}\text{C}$ ($F_{6,18} = 0.6$, $p = 0.72$) or $\delta^{15}\text{N}$ ($F_{6,18} = 0.7$, $p = 0.64$) values or isotopic values of sandbar sharks ($\delta^{13}\text{C}$: $F_{3,35} = 0.5$, $p = 0.67$; $\delta^{15}\text{N}$: $F_{3,35} = 0.2$, $p = 0.91$). For tiger sharks, there were no changes in $\delta^{15}\text{N}$ across years ($F_{6,167} = 1.9$, $p = 0.08$), but $\delta^{13}\text{C}$ varied among years ($F_{6,167} = 10.02$, $p = 0.0001$). Values of $\delta^{13}\text{C}$, however, did not change consistently through time. The highest mean (\pm SD) value was in 2006 ($-10.7 \pm 1.06\text{‰}$), and the lowest was in 2009 ($-12.6 \pm 1.09\text{‰}$).

The isotopic values of the large predators we sampled exhibited a wide range of $\delta^{13}\text{C}$ (-15.2 to -8.6‰) and $\delta^{15}\text{N}$ (9.5 to 14.1‰) values (Fig. 1). Among species with at least 6 individuals sampled, however, there was significant variation in mean isotope values ($F_{7,270} = 106.2$, $p < 0.001$ for $\delta^{15}\text{N}$; $F_{7,270} = 20.8$, $p < 0.0001$ for $\delta^{13}\text{C}$; Fig. 2, Table 2). Tiger sharks and pigeye sharks were similar in both mean $\delta^{15}\text{N}$ and mean $\delta^{13}\text{C}$ (Table 1, see Table 2 for pair-wise post-hoc tests). Sandbar sharks *Carcharhinus plumbeus* were lower in mean $\delta^{15}\text{N}$ than tiger sharks, but not pigeye sharks. Sicklefins *Negaprion acutidens* had the highest mean $\delta^{13}\text{C}$ of the large-bodied sharks and were similar to other large sharks in mean $\delta^{15}\text{N}$ (Table 1). Both smaller sharks—nervous sharks *Carcharhinus caudatus* and brown-banded

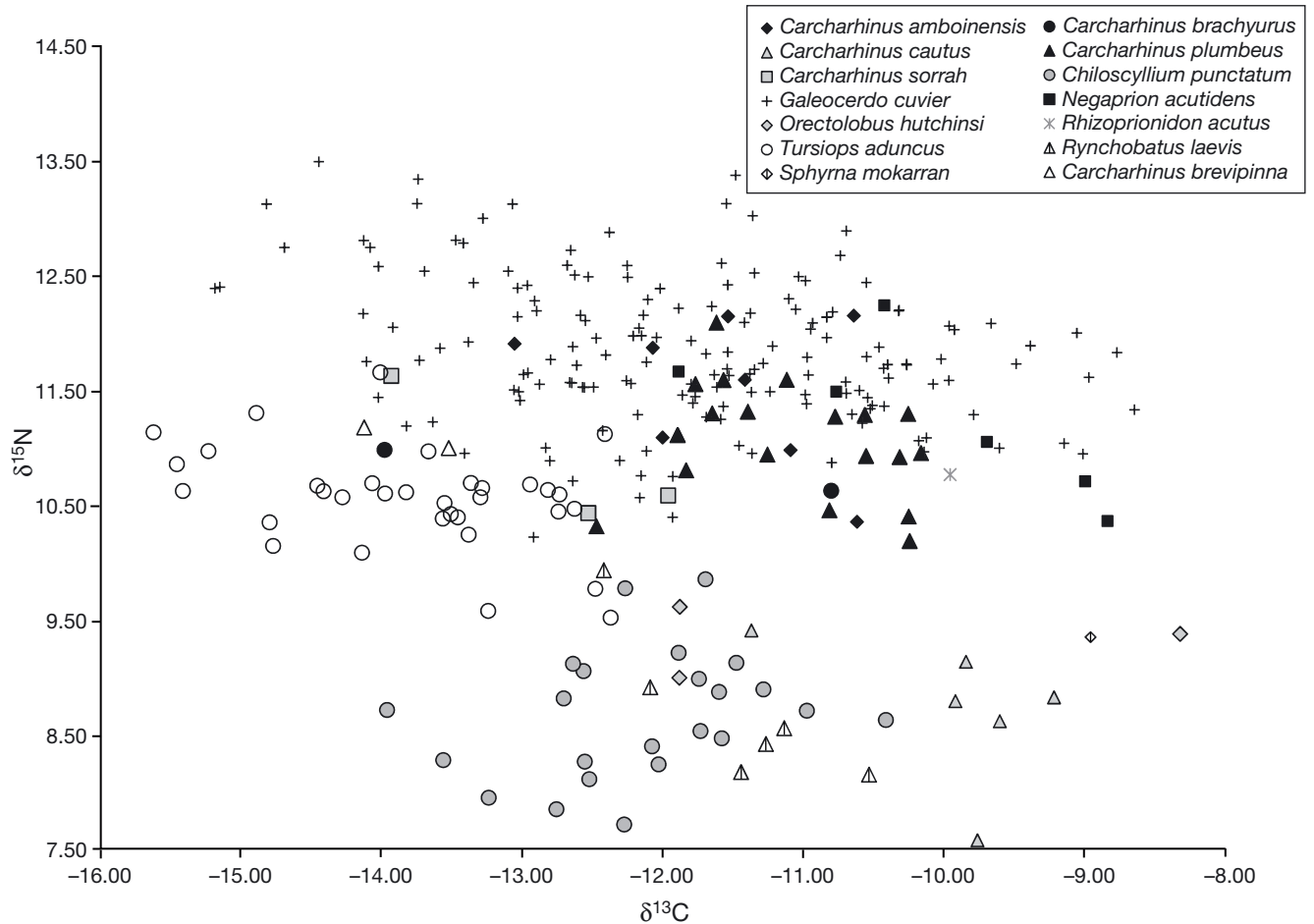


Fig. 1. Isotope values of all individual sharks and dolphins sampled in the Eastern Gulf of Shark Bay, Australia

bamboo sharks *Chiloscyllium punctatum*—had lower mean $\delta^{15}\text{N}$ than larger sharks, and nervous sharks had higher mean $\delta^{13}\text{C}$ values than brown-banded bamboo sharks. Smoothnose wedgetfish were similar in mean $\delta^{15}\text{N}$ to these 2 smaller shark species and slightly more C^{13} -depleted than bamboo sharks. Bottlenose dolphins exhibited very different isotopic values than all sharks, especially in mean $\delta^{13}\text{C}$. Dolphins had a lower mean $\delta^{13}\text{C}$ value than all shark species examined. There were, however, several species of rarely encountered sharks, which thus could not be included in analyses, with $\delta^{13}\text{C}$ values that were similar to those of dolphins (Figs. 1 & 2, Table 2).

Stable isotope values suggest considerable differentiation in trophic interactions among large predator groups. There was no overlap in SEAc of any group (i.e. dolphins, large sharks, small sharks, and rays) pairings, suggesting that the positions of the groups in isotope niche space are distinct (Fig. 3). Furthermore, none of the species-specific SEAc's of large sharks overlapped the SEAc of dolphins or

those of the 2 smaller-bodied shark species. Within the large shark group, there was general differentiation of SEAc areas among species, with the exception of tiger sharks and pigeye sharks (Fig. 3). About 72% of the pigeye SEAc was contained within the SEAc of tiger sharks.

There were several instances in which shark species rarely encountered in Shark Bay (and, therefore, not included in the calculation of the group SEAc) had isotopic values that fell within or near the SEAc of other groups. Two individual spottail sharks *Carcharhinus sorrah* (a small shark) and 1 bronze whaler *Carcharhinus brachyurus* (a large shark) had isotope values that overlapped those of dolphins. The isotopic values of a 377 cm TL great hammerhead *Sphyrna mokarran* were more similar to those of small sharks (Fig. 1).

To further explore the potential for overlap in isotopic niches of species, we used the TA metric (Layman et al. 2007). TA provides for more conservative assessment of niche partitioning (i.e. more likely to detect niche overlap) because it incorporates every

sampled individual from the populations. Considering the isotopic values of all individuals sampled, dolphins occupied a relatively large area of unique isotopic space, as did large sharks, with more than 60% and 85% of individuals, respectively, falling outside the TA of other groups. Overlap between large sharks and dolphins was moderate, but <40% of dolphin individuals were within the TA of large sharks, and only ca. 10% of individual large sharks fell within the dolphin TA. There was no overlap in TAs of large sharks and the small sharks included in analyses (Fig. 1).

Mean body size of species sampled explained a considerable amount of variation in mean $\delta^{15}\text{N}$ of dolphins and sharks, with increasing $\delta^{15}\text{N}$ as mean body

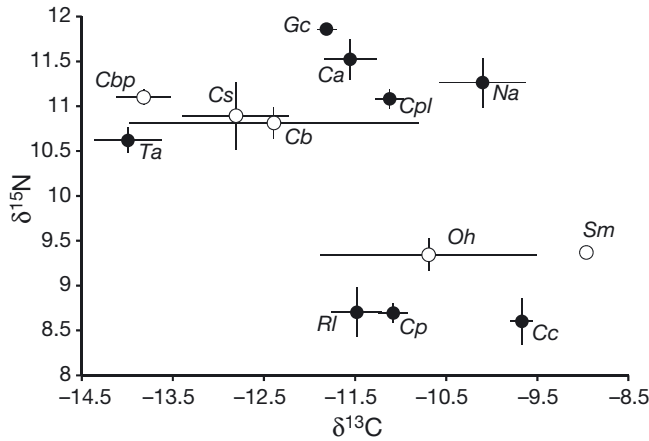


Fig. 2. Mean isotope values (± 1 SE) for sharks, dolphins, and 1 species of large ray in Shark Bay, Western Australia. Filled circles are species with samples sizes adequate for analysis. Species represented by open circles were not included in analyses. For species codes and Tukey's test results, see Table 2

Table 2. Species codes with the results of Tukey's post-hoc tests for the mean isotope values presented in Fig. 2. Species with the same letter are not significantly different based on Tukey's test

Scientific name (figure code)	Common name	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
<i>Galeocerdo cuvier</i> (Gc)	Tiger shark	B	A
<i>Carcharhinus amboinensis</i> (Ca)	Pigeye shark	AB	AB
<i>Carcharhinus plumbeus</i> (Cpl)	Sandbar shark	AB	BC
<i>Negaprion acutidens</i> (Na)	Sicklefin lemon shark	A	ABC
<i>Carcharhinus brachyurus</i> (Cb)	Bronze whaler	-	-
<i>Carcharhinus sorrah</i> (Cs)	Spottail shark	-	-
<i>Tursiops cf. aduncus</i> (Ta)	Bottlenose dolphin	C	C
<i>Orectolobus hutchinsi</i> (Oh)	Wobbegong	-	-
<i>Rynchobatus laevis</i> (Rl)	Smoothnose wedgefish	AB	D
<i>Chiloscyllium punctatum</i> (Cp)	Bamboo shark	B	D
<i>Carcharhinus cautus</i> (Cc)	Nervous shark	A	D
<i>Carcharhinus brevipinna</i> (Cbp)	Spinner shark	-	-
<i>Sphyrna mokarran</i> (Sm)	Great hammerhead	-	-

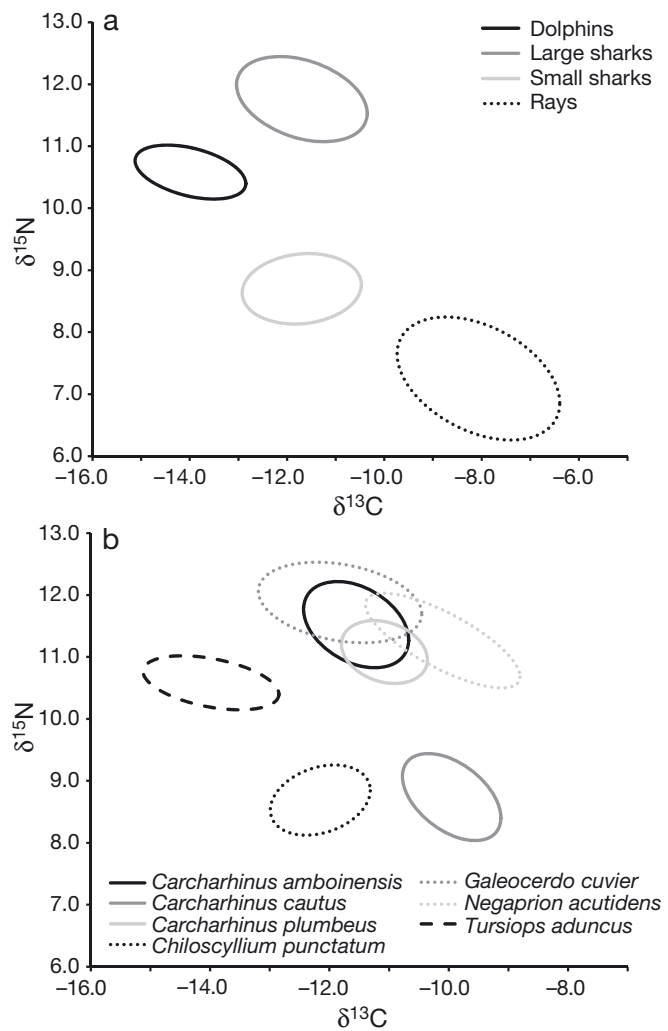


Fig. 3. Standard ellipse areas corrected for sample size (SEAc) of large predators based on (a) guild-level and (b) species-level analyses

size increased ($F_{1,9} = 18.0$, $p = 0.003$, $R^2 = 0.69$, Fig. 4). There were no trends between body size and $\delta^{13}\text{C}$ ($F_{1,9} = 0.9$, $p = 0.38$; $R^2 = 0.10$). Relationships between body length and isotope values within species differed from species-level patterns. There was a no significant relationship between tiger shark total length and $\delta^{15}\text{N}$ ($F_{1,165} = 3.31$, $p = 0.07$, $R^2 = 0.02$). There was a weak ($R^2 = 0.04$) but statistically significant decrease in $\delta^{13}\text{C}$ with increasing tiger shark length ($F_{1,165} = 6.54$, $p = 0.01$). There was no relationship between total length and $\delta^{15}\text{N}$ ($F_{1,7} = 0.57$, $p = 0.48$, $R^2 = 0.08$) or $\delta^{13}\text{C}$ for pigeye sharks ($F_{1,7} = 3.9$, $p =$

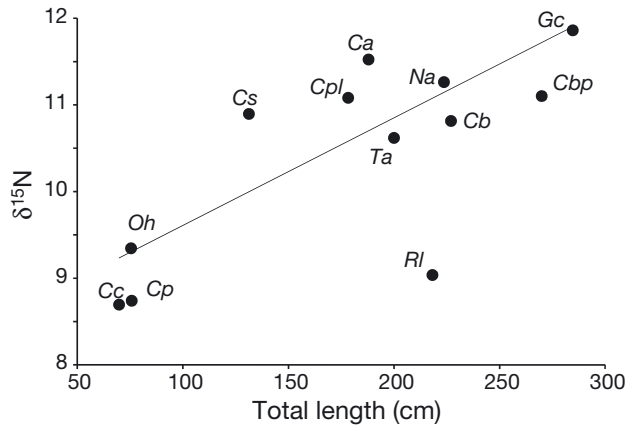


Fig. 4. Relationship between mean $\delta^{15}\text{N}$ and mean total length. See Table 2 for species codes

0.09, $R^2 = 0.39$). No relationship between body size and $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ was found for sandbar sharks. Relationships between body size and isotope variation could not be evaluated within dolphins because of little size variation in the sampled individuals (i.e. all were adult animals near maximum lengths).

Considerable intraspecific variation in isotopic values was found for several species. Tiger sharks showed the largest range in isotopic values for $\delta^{13}\text{C}$ (-15.1 to -8.6% ; Fig. 1). Dolphin $\delta^{13}\text{C}$ ranged from -12.4 to -16.3% . Like $\delta^{13}\text{C}$, the $\delta^{15}\text{N}$ of tiger sharks varied widely, from 10.2 to 14.1% , which may be up to 2 trophic levels based on previous studies of fractionation in elasmobranchs (Hussey et al. 2010). In contrast, pigeye sharks, which had a similar mean $\delta^{15}\text{N}$ to tiger sharks, had a relatively narrow $\delta^{15}\text{N}$ range of 1.8% (Table 1).

CD, a measure of average trophic diversity within a population, varied among those species ($F_{4,251} = 5.5$, $p = 0.003$) for which sample sizes were relatively large ($n \geq 8$). Tiger sharks had significantly higher CDs than sandbar and bamboo sharks. There were no statistically significant differences in CDs of other species (Table 1).

Isotope values of other taxa support the notion that large sharks and dolphins are upper-trophic level predators (Tables 1 & 3, Fig. 5). Their $\delta^{15}\text{N}$ values are considerably higher than rays, 2 species of sea turtles, and many teleosts. However, the $\delta^{13}\text{C}$ values of 2

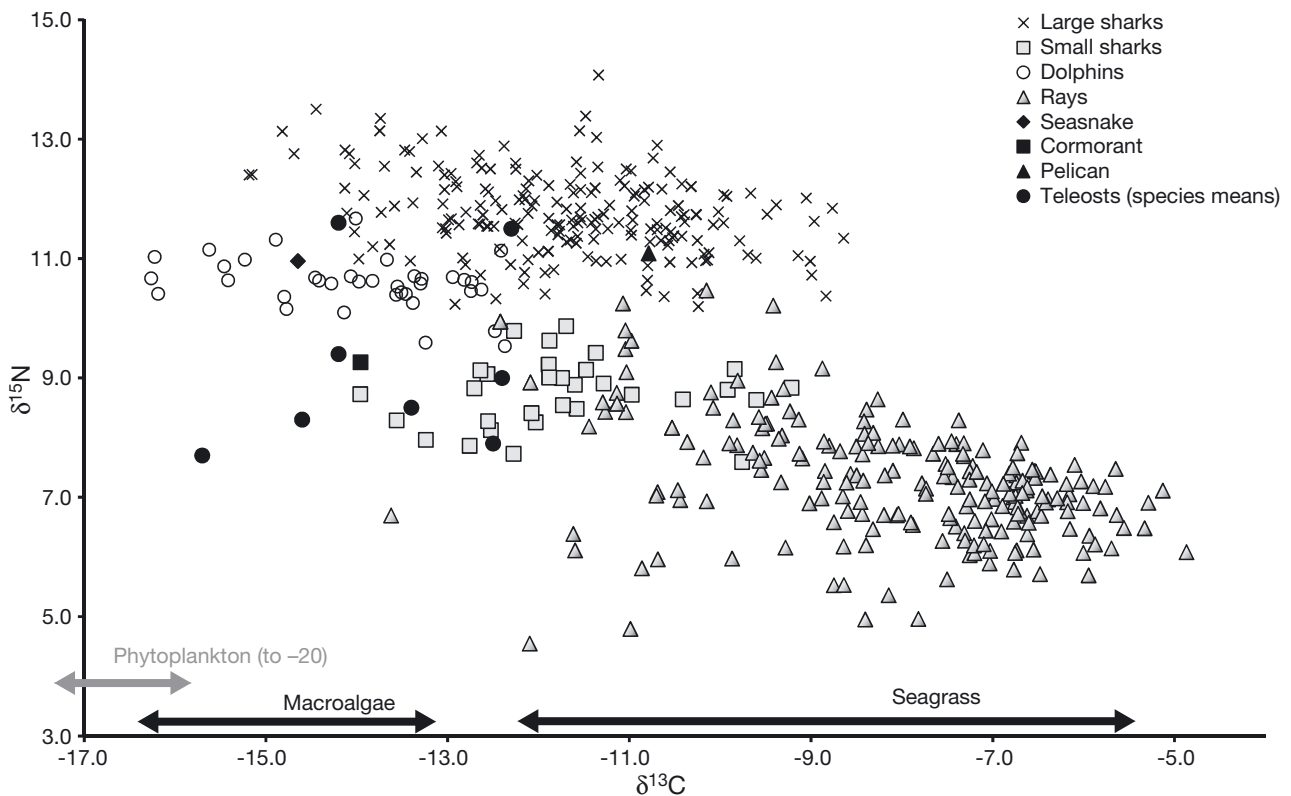


Fig. 5. Isotopic values of large predators (individual values) and representative teleosts (species means) collected from the Eastern Gulf of Shark Bay. Ranges of $\delta^{13}\text{C}$ for seagrasses, macroalgae, and plankton (based on $\delta^{13}\text{C}$ of filter feeders) are given along the $\delta^{13}\text{C}$ axis (see Burkholder et al. 2011). Only individuals of species included in analyses are given for the large predator groups

Table 3. Stable isotope values of other consumers in Shark Bay, Australia. Values are based on muscle samples obtained from within the primary study site

Species	TL (cm)	N	$\delta^{15}\text{N} \text{‰}$ (mean \pm SD)	$\delta^{13}\text{C} \text{‰}$ (mean \pm SD)
Teleosts				
Emperor <i>Lethrinus laticaudus</i>	20.8	5	9.4 \pm 0.13	-14.2 \pm 0.59
Mackerel <i>Scomberomorus semifasciatus</i>	72.5	2	11.6 \pm .40	-14.2 \pm 0.08
Butterfish <i>Pentapodus vitta</i>	19.5	9	8.5 \pm 0.55	-13.4 \pm 1.08
Fan-bellied leatherjacket <i>Monacanthus chinensis</i>	14.2	3	7.7 \pm 0.45	-15.7 \pm 0.27
Tailor <i>Pomatomus saltatrix</i>	34.5	2	11.5 \pm 0.51	-12.3 \pm 1.45
Tarwhine <i>Rhabdosargus sarba</i>	16	5	7.9 \pm 1.08	-12.5 \pm 2.05
Striped trumpeter <i>Pelates octolineatus</i>	21.6	45	8.3 \pm 0.67	-14.6 \pm 2.16
Yellowtail trumpeter <i>Amniataba caudovittata</i>	18.8	6	9.0 \pm 0.29	-12.4 \pm 0.42
Reptiles				
Sea snake <i>Disteria major</i>		1	11.0	-14.6
Birds				
Pied cormorant <i>Phalacrocorax varius</i>		2	10.1 \pm 1.24	-14.2 \pm 0.29
Australian pelican <i>Pelecanus conspicillatus</i>		1	11.1	-10.8

seabirds, a sea snake *Disteria major*, and 2 piscivorous teleosts (mackerel *Scomberomorus semifasciatus* and tailor *Pomatomus saltatrix*) were similar to those of dolphins and several species of large sharks (Tables 1 & 3). The common teleost species that may be prey for large predators all had lower $\delta^{15}\text{N}$ values (Table 3).

DISCUSSION

We found considerable variation in isotopic values within species of upper trophic level predators in Shark Bay. Yet, there appears to be considerable differentiation in resource use among major groups of large-bodied predators in this ecosystem. Given that different diets can result in similar isotopic values, it was surprising that there was no overlap of SEAc, which encompasses 1 standard deviation from the group bivariate means (i.e. the isotopic area that the bulk of individuals occupy), of major groups. Furthermore, even using the TA metric, which encompasses all individuals sampled, there was surprisingly little overlap among these groups.

Although sampling took place over multiple years and across seasons, it is unlikely that these temporal factors explain the distinct patterns that were observed. First, the vast majority of samples were collected during the warm season. For the 2 species with adequate samples in the cold season, the variation in isotope values between winter and summer was small or in the case of dolphins, which had the largest proportion of samples from cold seasons, non-significant. Furthermore, variability across seasons might

be expected to enhance variation within groups and lead to greater overlap between species or groups. Concurrent studies within our study area failed to detect seasonal changes in $\delta^{13}\text{C}$ values of seagrass and macroalgae, and seasonal shifts in $\delta^{13}\text{C}$ of planktonic consumers were not sufficient to impact general interpretations of our results (Burkholder et al. 2011). Also, because isotopes are integrated over periods of weeks to months in marine mammal skin and shark fins (e.g. Hicks et al. 1985, Matich et al. 2010), isotope values in the present study are likely to incorporate foraging over multiple seasons and minimize impacts of seasonal variation in isotopic values at the base of the food web. There were no detectable changes in $\delta^{15}\text{N}$ among years for the 3 species tested, nor was there interannual variation in $\delta^{13}\text{C}$ values of sandbar sharks and dolphins. Although $\delta^{13}\text{C}$ varied across years in tiger sharks, this variation likely enhances overlap with other taxa rather than lessens it.

Bottlenose dolphins showed substantial isotope differences from large shark species. Although they appear to feed at a similar trophic level as the similarly sized sicklefin lemon and sandbar sharks (as inferred from $\delta^{15}\text{N}$), dolphin $\delta^{13}\text{C}$ values were substantially lower than those of all other large predator species for which adequate sample sizes were available. There was individual variation in $\delta^{13}\text{C}$ values within dolphins and tiger sharks, in particular, but the generally higher $\delta^{13}\text{C}$ values of large sharks suggest that they are obtaining more of their energy from seagrass-based food webs, while dolphins are obtaining more of their resources from plankton- or macroalgae-derived food webs. It is also possible that dolphins are obtaining energy from mangrove-derived food webs

($\delta^{13}\text{C}$ ca. -23‰ ; Heithaus et al. 2011). However, we consider this scenario to be unlikely because of the relatively restricted spatial extent of mangroves in this system and the finding that invertebrates and fishes within mangrove habitats near our study site in Shark Bay appear to derive little energy from mangroves (Heithaus et al. 2011). The pathways through which seagrass-derived carbon supports elasmobranch populations are yet to be resolved but may include direct-grazing pathways (e.g. Burkholder et al. 2012) or, perhaps more likely, detrital ones (Vaudo & Heithaus 2011, Belicka et al. 2012).

That elasmobranchs appear to be obtaining a greater proportion of their energy from seagrass-based food webs than dolphins is somewhat surprising. Dolphins are often found foraging over seagrass banks (Heithaus & Dill 2002, 2006) and are year-round residents. Shark species show considerable variation in their abundance across seasons, and large species can move long distances away from Shark Bay (e.g. Heithaus 2001b, White & Potter 2004, Wirsing et al. 2006, Heithaus et al. 2007). Because stable isotopic values are a time-integrated reflection of foraging, the isotopic values of highly mobile sharks certainly reflect foraging that occurs both inside and outside the study area. However, the warm season in the study area lasts ca. 9 mo, and data from acoustic monitoring and satellite tracking indicate that tiger sharks can remain within Shark Bay for extended periods of time (months; Heithaus 2001b, M. R. Heithaus unpubl. data). Therefore, their isotopic values are likely reflective of at least some foraging within Shark Bay. Furthermore, the basal resource pools (and the $\delta^{13}\text{C}$ values of these resource pools) that coastal shark species are likely to encounter outside of Shark Bay are similar to those inside the bay (e.g. Borrell et al. 2011, Kiszka et al. 2011). Thus, even though sharks may move long distances (even into pelagic waters; Heithaus et al. 2007), they are likely still feeding largely in coastal benthic food webs derived from seagrasses. Indeed, sharks (*Carcharhinus melanopterus*, *C. amblyrhynchos*, *Triaenodon obesus*, and *Negaprion acutidens*) from Ningaloo Reef, >300 km north of Shark Bay, also showed $\delta^{13}\text{C}$ values suggestive of foraging in seagrass-derived food webs (Speed et al. 2012). While it is not possible to fully address the role of long-distance movements in shaping isotopic signatures of large sharks sampled in Shark Bay, it is likely that isotope values reflect real differences in the food webs in which large predator diets are based. Differences in isotopic values of dolphins and many ray and small shark species likely reflect differences in foraging ecology within Shark Bay (e.g. Vaudo & Heithaus 2012).

There are several possible explanations for dolphins apparently foraging little in seagrass-derived food webs. First, dolphins may feed on fishes that, although they inhabit seagrass beds, do not feed directly on seagrasses or invertebrates that use seagrass-derived resources. Based on limited sample sizes, Belicka et al. (2012) used fatty acid analysis to show that several species of potential dolphin prey do not appear to feed in seagrass-derived food webs in Shark Bay. Second, many individual dolphins largely abandon seagrass habitats during the 9 mo of the year that tiger sharks are abundant (Heithaus & Dill 2002, 2006), while others forage almost exclusively in channel habitats throughout the year (Mann & Sargeant 2003), where seagrass cover is sparse (Burkholder et al. 2013). We sampled individual dolphins that foraged over seagrass banks as well as those that primarily, or exclusively, use deep-water foraging tactics. However, larger sample sizes of individual dolphins with known foraging histories may help to determine the overall importance of seagrass-based food webs to dolphins in the study area.

In other areas of the world, dolphins and sharks can exhibit considerable overlap in diets. For example, in South Africa, stomach content analysis revealed substantial overlap in the fish component of the diets of inshore dolphins and sharks, but diets diverged because sharks also included elasmobranchs in their diets, while dolphins consumed more squid (Heithaus 2001a). Off Costa Rica, there is interference competition between silky sharks and common bottlenose dolphins (Acevedo-Gutiérrez 2002). Partitioning in Shark Bay may be more likely than in South Africa or Costa Rica, where an abundance of schooling fish forms the basis of dietary overlap between dolphins and sharks. The pattern of niche separation among upper level marine predators that we documented is similar to that observed in other systems among large sharks (Papastamatiou et al. 2006), among dolphins (Kiszka et al. 2011), among sharks, dolphins, and piscivorous fishes (Pusineri et al. 2008), and between seabirds and piscivorous fishes (Cherel et al. 2008).

The $\delta^{15}\text{N}$ values of tiger and pigeye sharks suggest they are the top predators in the Shark Bay ecosystem and that other large sharks (>1.5 m TL) and bottlenose dolphins feed at slightly lower trophic levels. Tiger sharks and pigeye sharks appear to fit a classic example of a top predator that integrates multiple trophic channels (e.g. Rooney et al. 2006). Interestingly, $\delta^{15}\text{N}$ values suggest that smaller predators in Shark Bay may feed at trophic levels similar to dolphins and some large sharks. For example, a ca.

70 cm mackerel and a 35 cm tailor as well as a sea snake and seabirds had $\delta^{15}\text{N}$ values that were similar to dolphins. In contrast, the relatively large smooth-nose wedgetfish appears, based on $\delta^{15}\text{N}$ values, to feed relatively low in the food web. This result is consistent with studies of congeners, which reveal diets composed primarily of crustaceans (Darracott 1977). Similarly, the one great hammerhead we sampled had a relatively low $\delta^{15}\text{N}$ for its body size. This finding, combined with a high $\delta^{13}\text{C}$, may be a result of foraging heavily on rays (e.g. Stevens & Lyle 1989, Vaudo & Heithaus 2011).

Overall, we found that Shark Bay's large predators display clear separation in isotopic space on the basis of taxonomic group and size. Such separation among the large primarily piscivorous species examined comes as somewhat of a surprise because isotopic similarities can be observed despite dramatically different diets and, given the tissues examined, could reflect differences in long-term movement patterns or habitat use (i.e. how the species use resources when outside of the study area). Additional research that integrates stable isotope analysis with diet and behavioral data is required to further elucidate the functional roles played by these predator groups in Shark Bay. Seagrass-derived carbon appears to be important to elasmobranchs in the Shark Bay ecosystem, but much less important to dolphins, despite their frequent use of seagrass habitats. This suggests that habitat use patterns may not necessarily be reflective of the resource pools supporting a population and highlights the importance of detailed datasets on trophic interactions for elucidating the ecological roles of predators.

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