



Isotopic niche partitioning of co-occurring large marine vertebrates around an Indian ocean tropical oceanic island

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ABSTRACT

Tropical oceans host a high diversity of species, including large marine consumers. In these oligotrophic ecosystems, oceanic islands often favour the aggregation of species and biomass as they provide feeding opportunities related to the mechanisms of island mass effect. As such, the waters surrounding La Réunion (Southwest Indian Ocean) host seabirds, large pelagic teleosts, elasmobranchs, delphinids and sea turtles. Isotopic niche partitioning and comparison of trophic levels among these species ($n = 21$) were investigated using stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis. Overall, $\delta^{13}\text{C}$ values were highly variable among taxa, indicating that the species exploit multiple foraging habitats along a coast-open ocean gradient. Overlap in $\delta^{15}\text{N}$ values was limited, except for teleost species, the two species of sea turtles and two species of delphinids, the Indo-pacific bottlenose dolphin (*Tursiops aduncus*) and the Spinner dolphin (*Stenella longirostris*). Stable isotope analyses of samples collected over a 9-years period on different tissues with different integration times provide a consistent picture of the structure of the community of large marine vertebrates species around La Réunion and highlight the underlying mechanisms to limit the competition between species. The wide range of isotopic values confirms that large marine vertebrates have different trophic roles in coastal marine food webs around this oceanic island, which limits their potential of competitive interactions for resources.

1. Introduction

Large vertebrates fulfill important and diverse set of roles in marine ecosystems (Heithaus et al., 2008; Estes et al., 2016). They can exert top-down controls through consumptive and non-consumptive effects, but also stimulate bottom-up processes through the translocation of nutrients within and across ecosystems (Helfield and Naiman 2006; Schmitz et al., 2010). Changes in the abundance and distribution of large marine vertebrates can affect the structure and functioning of food webs, particularly in coastal marine ecosystems (Jackson et al., 2011; Estes et al., 2016). In ecosystems in which resources are limited, the coexistence of sympatric predatory species with similar trophic roles requires some degree of habitat and trophic resource partitioning (Pianka 1974; Kiszka et al., 2011; Matich et al., 2017). Ecological niche theory states that each ecological niche is multidimensional,

encompassing a species habitat, use, trophic interactions and their temporal variability (Grinnell 1917). A shared resource with a limited supply will result in competition between members of the same species (intraspecific competition) or between individuals of different species (interspecific competition) (Roughgarden 1976). Assessing the extent of trophic redundancy within predator guilds (i.e., whether the role of a particular species can be filled by another) is particularly important to predict the potential impacts of changes in predator abundance on the functioning and the resilience of ecosystems (Peterson et al., 1998; Mouillot et al., 2013).

Around oceanic islands, the high diversity of the marine megafauna can be explained by both the presence of a wide range of marine habitats that occur in close proximity to each other (Kiszka et al., 2011) and the island-mass effect that enhances marine productivity (Doty and Oguri 1956; Hernandez-Leon, 1991; Martinez and Maamaatauaiahutapu 2004;

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Hasegawa et al., 2008). Oceanic islands act as discontinuities where primary production is usually higher compared to the surrounding oceanic habitat, which promotes higher abundances of low and intermediate trophic level organisms (Benoit-Bird and Au 2006), and ultimately provides foraging opportunities for high trophic level predators (Piontovski, 1995; Bakun 2006). These islands are also important for large grazers since macrophyte communities usually develop in coastal waters (Zubia et al., 2018a, b).

Numerous studies have investigated the trophic ecology within large marine vertebrate communities using several methods, including direct observations, stomach content and feces analysis, or fatty acid and stable isotope analysis (e.g., Cortes 1999; Simpfendorfer et al., 2001; Matich et al., 2010; Linchant et al., 2015; Navia et al., 2017; Dicken et al., 2017; Meyer et al., 2021). The use of stable nitrogen and carbon isotopes has allowed increasing our understanding of the trophic structure and roles of many marine predator communities (Cherel et al., 2008; Gross et al., 2009; Kiszka et al., 2015; Burkholder et al., 2011; Li et al., 2016a). The carbon and nitrogen isotope ratios ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$, hereafter expressed as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ respectively) of a consumer reflect those of their diet in a predictable manner (Das et al., 2003). While many studies have used stable isotopes at the species level (Graham et al., 2007; Jaquemet et al., 2008; Vander Zanden et al., 2013, Dicken et al., 2017), taxonomic communities (Cherel et al., 2008; Kiszka et al., 2014; Pratte et al., 2019) or guilds (Kitchell et al., 2002; Heithaus et al., 2013; Kiszka et al., 2015; Li et al., 2016a), few have attempted to compare isotopic niches and trophic levels within assemblages of large marine vertebrates. The examination of specific interactions and the degree to which the trophic roles are complementary or redundant among species is, however, fundamental to understand the effects of exploitation, anthropogenic threats, and global environmental changes on the structure and function of communities (Heithaus et al., 2013; Whalen et al., 2020). In this context, the objective of the study was to investigate the trophic relationships among large marine vertebrates co-occurring in

the waters of the oceanic island of La Réunion, Southwest Indian Ocean, using stable carbon and nitrogen values collected from multiple tissues.

2. Materials & methods

2.1. Study area

La Réunion (21°07' S, 55°32' E) is an oceanic island of volcanic origin located in the Southwest Indian Ocean, 800 km east of Madagascar (Fig. 1). The insular shelf is narrow (up to 5 km) and deep open-ocean waters are in close proximity to the coastline (McDougall 1970). Fringing coral reefs are distributed along the west coast of the island and the shelf is the most developed in the northwestern part of the study area (Tessier et al. 2008). The waters around the island are oligotrophic (Jena et al., 2013), yet a wide range of large marine vertebrates are permanently present in these waters, including cetaceans (Dulau-Drouet et al., 2008), large pelagic teleosts (Le Manach et al., 2015), sea turtles (Jean et al., 2010, Chassagneux et al. 2013), elasmobranchs (Trystram et al., 2017; Guyomard et al., 2019), and seabirds (Jaquemet et al., 2004).

2.2. Sample collection and preparation

Between October 2010 and November 2019, a total of 1568 samples from 7 species of sharks, 7 large pelagic teleosts, 4 delphinids, 2 sea turtles and 1 seabird were collected mainly off the west coast of the island (Table 1, Fig. 1). Shark samples were mostly collected from individuals caught during dedicated shark population control operations off La Réunion, either as target or by-catch species (Guyomard et al., 2019). A portion of white muscle was sampled from the back of each individual, below the first dorsal fin. For Bull shark (*Carcharhinus leucas*) and Tiger shark (*Galeocerdo cuvier*), the target species of these control operations, blood and skin samples were additionally collected during

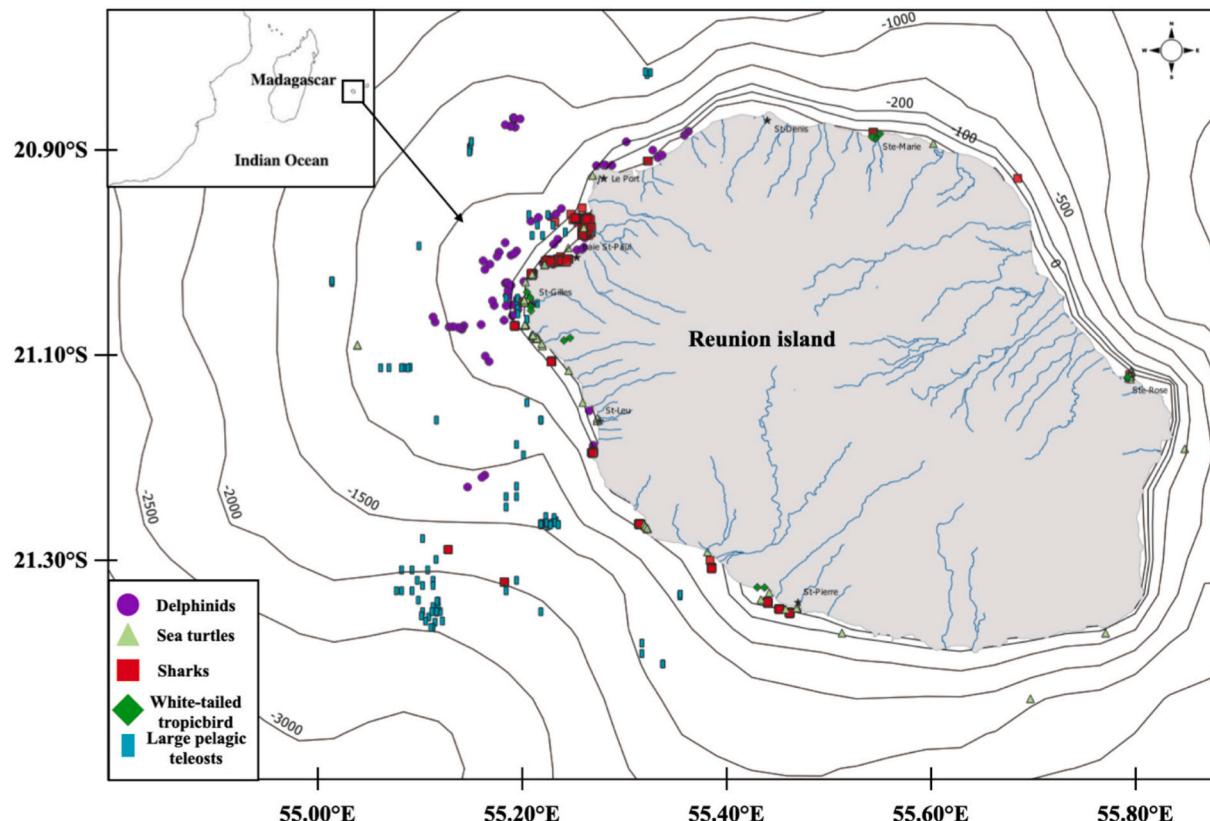


Fig. 1. Map of the study area with samples location by main taxonomic groups of species.

Table 1

Trophic discrimination values ($\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$ in ‰) and turnover rates of studied species based on controlled feeding studies. (a) [Turner Tomaszewicz et al., 2017](#); (b) [Pajuelo et al., 2012](#); (c) [Pajuelo et al., 2010](#); (d) [Vander Zanden et al., 2014a,b](#); (e) [Gimenez et al., 2016](#); (f) [Bearhop et al., \(2002\)](#); (g) [Madigan et al., 2012](#); (h) [Hussey et al., 2010](#); (i) [Malpica-Cruz et al. \(2013\)](#).

Taxonomic groups	Tissue	$\Delta^{13}\text{C}$	$\Delta^{15}\text{N}$	$\delta^{13}\text{C}$ half-life	$\delta^{15}\text{N}$ half-life
Sea-turtles	Epidermis	2.3 (a)	4.1 (a)	45 days to 2 months (b,c,d)	45 days to 2 months (b,c,d)
Delphinids	Epidermis	1.01 (e)	1.57 (e)	24.16 ± 8.19 days (e)	47.63 ± 19 days (e)
Sea-birds	Whole blood	1 (f)	3 (f)	14.4 days (f)	15.7 days (f)
Large pelagic teleosts	Muscle	1.9 (g)	1.8 (g)	255 days (g)	167 days (g)
Elasmobranchs	Muscle	0.90 (h)	2.29 (h)	130–180 days (h)	80–100 (h)
Elasmobranchs	Skin	0.90 (h)	2.29 (h)	several months	several months
Elasmobranchs	Blood	2.9 (i)	2.6 (i)	45 days (i)	51 days (i)

necropsies. Sea turtle samples were taken from free-ranging individuals caught by hand while scuba diving. By-caught sea turtles in good body condition were also sampled. Skin samples were taken at the junction of one of the posterior flippers, in the scaleless part, using a sterilized scalpel and stored in a hypersaline solution ([Barrow et al., 2008](#)). Dolphin samples were collected using a crossbow (BARNETT Phantom® Class, 60 lb draw weight) with Finn Larsen (Ceta-Dart, Copenhagen, Denmark) bolts and tips (25/7 mm). Samples of ~0.5–1 cm³ were exclusively collected from adult individuals (based on relative body size). Seabird blood samples were directly collected from the heart using a single-use syringe on dead specimens recovered by the local bird conservation organization (SEOR) and kept frozen at –20 °C. Large pelagic teleost white muscle samples were collected from professional fishermen. All samples were kept frozen at –20 °C shortly after sampling until further analyses.

All frozen samples were freeze-dried at –50 °C for 48 h using a CRIOS Cryotec freeze dryer. Dry samples were reduced by milling for 3 min to a homogeneous powder using a Mixer Mill Retsch MM400 at 30 Hz. Between 0.1 and 1.5 mg of powder was packed in tin capsules. Samples were weighed using a precision balance to the nearest 0.1 mg. Capsules were then folded into small spheres, placed in a 96-sink plate and sent to the IRMS platform, University of La Rochelle, France. Reference standards for carbon and nitrogen were VPDB and AIR, respectively, and internal standards (caffeine, USGS-61 and USGS-63). Repeated analyses of internal standards yielded a precision of 0.1‰ for nitrogen and 0.15‰ for carbon. Some studies have highlighted the presence of biases in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values due to lipids and urea in the white muscles ([Hussey et al., 2010](#); [Li et al., 2016b](#)). Lipids present in the tissues of species studied cause a decrease in $\delta^{13}\text{C}$ values. Urea and trimethylamine oxide (TMAO) present in elasmobranch muscles, and used to maintain the osmotic balance, are ¹⁵N-depleted, which may result in lower $\delta^{15}\text{N}$ values. To limit these biases, we applied arithmetic corrections to muscle isotope values implemented by [Li et al. \(2016b\)](#) for elasmobranchs, except the Bull shark (*Carcharhinus leucas*) and the Tiger shark (*Galeocerdo cuvier*), for which we used the arithmetic corrections published by [Martin and Jaquemet \(2019\)](#). For delphinids, isotopes values were measured in epidermis (hereafter skin) samples. Because lipids are ¹³C-depleted relative to other tissue components and are abundant in delphinids' skin, lipid-extractions were performed. For lipid-extractions, an aliquot of approximately 100 mg of fine powder was stirred with 4 mL of cyclohexane for 1 h at room temperature, this operation being repeated three times. Then, the sample was centrifuged for 5 min at 4000 g and the supernatant containing lipids was discarded. The sample was dried in an oven at 45 °C for 48 h, and 0.35 ± 0.05 mg subsamples of lipid-free powder were then weighed in tin cups for stable isotope analyses. For all other samples, C:N ratios were <3.5, which is considered as an indicator of low lipid contents and as such lipid extraction was not required ([Post et al., 2007](#)).

2.3. Data analysis

In addition to species-specific differences in turnover rates, isotopic discrimination values (i.e., enrichment or depletion between trophic

steps) also vary across species and tissues, necessitating adjustments to stable isotope values prior to comparisons across taxa (reviewed by [McCutchan et al., 2003](#); [Vanderklift and Ponsard 2003](#)). Therefore, the tissues collected from each species for stable isotope were adjusted for differences in discrimination values prior to statistical analyses (Table 1).

Statistical analyses were performed using R (Version 4.0.2; R Development Core Team, 2014). All statistical analyses were carried out for species with sample size >3. Mean stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) values for each species were investigated using the Ward's hierarchical clustering analysis ([Ward and Hook 1963](#)). To investigate differences between clusters obtained with the Ward's method, a Multivariate Analysis of Variance (MANOVA, Wilk's lambda) was performed using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of each species, followed by Tukey's HSD (Honestly Significant Difference) paired comparisons. To investigate isotopic niche space and isotopic niche overlap among species and the distance to the centroids, we used a Bayesian approach based on multivariate ellipse metrics (SIBER – Stable Isotope Bayesian Ellipses within the R-package siar; [Jackson et al., 2011](#)). Standard ellipses are a representation of the core area of the population in the isospace, enclosing 40% of the bivariate data.. This analysis generates standard ellipse areas corrected for small sample sizes (SEAc), which can be compared among species to determine differences in core isotopic niche space and core niche overlap ([Jackson et al., 2011](#)). The degree of niche overlap among species was calculated using the OVERLAP function. The percentage overlap between two standard ellipse areas (SEAc) was calculated as follows:

$$\left(\frac{\text{Overlap}}{\text{SEAc}} \right) \times 100$$

2.4. Trophic levels (TL)

The trophic level (TL) of individual species was estimated from nitrogen stable isotope values following the scaled $\Delta^{15}\text{N}$ framework approach based on a dietary $\delta^{15}\text{N}$ value-dependent $\Delta^{15}\text{N}$ model ([Hussey et al., 2014a, b](#)).

Relative TL was calculated as follows:

$$TL = \frac{\log(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{base}}) - \log(\delta^{15}\text{N}_{\text{lim}} - \delta^{15}\text{N}_{\text{TL}})}{k} + TL_{\text{base}}$$

Where TL_{base} is the TL of the baseline species, $\delta^{15}\text{N}_{\text{lim}}$ the saturating isotope value, k represents the rate at which $\delta^{15}\text{N}_{\text{TL}}$ approaches $\delta^{15}\text{N}_{\text{lim}}$ and $\delta^{15}\text{N}_{\text{TL}}$ is the $\delta^{15}\text{N}$ value of the large marine vertebrates species. The baseline was established using POM, SOM and seagrass isotopic values from La Réunion ([Kolasinski et al., 2011](#); [Cuvillier 2016](#)). To estimate the potential contributions of the different sources to the diet of each species, we applied stable isotope analysis in R (MixSIAR) Bayesian isotopic mixing models ([Stock et al., 2018](#)). This model estimates the relative contribution of each source item to the diet of the consumer based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the consumer and its potential source. This model allows the inclusion of variability in the stable isotope ratios of the predator and the potential prey isotopic discrimination factors

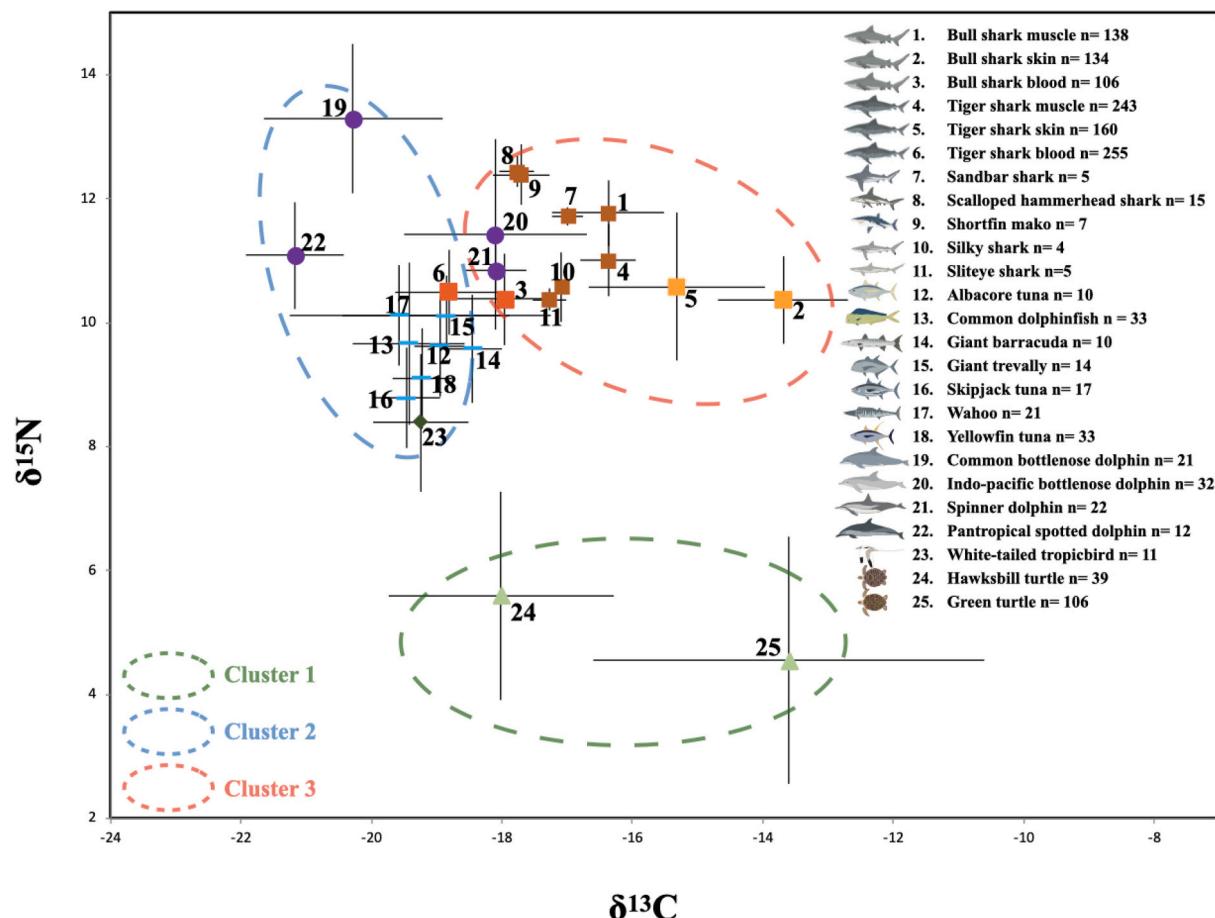


Fig. 2. Biplot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean \pm SD). Sharks skin (orange square), Sharks blood (red square), Sharks muscle (dark orange square), delphinids (purple circle), sea turtles (green triangle), White-tailed tropicbird (green diamond) and large pelagic teleost (blue stick). Illustrations: ©Guillaume CHANDELIER.

(Stock et al., 2018). The baseline was calculated as follows:

$$\delta^{15}\text{N}_{\text{base}} = \sum_k^n (\mathbf{S}_k * \mathbf{P}_k)$$

Where \mathbf{S}_k is the $\delta^{15}\text{N}$ values of source and \mathbf{P}_k is the proportion of the source. The $\delta^{15}\text{N}_{\text{lim}}$ and k values of 21.93 and 0.14 respectively were derived from a meta-analysis of experimental isotope data (Hussey et al., 2014a). To analyze the differences of trophic level between studied groups (sharks, large pelagic teleosts, delphinids, turtles and seabirds), an Analysis of Variance (ANOVA) was performed on the trophic level values followed by Tukey's HSD (Honestly Significant Difference) paired comparisons.

2.5. Trophic level ($\delta^{15}\text{N}$) and habitat ($\delta^{13}\text{C}$) ontogenetic profiles

Ontogenetic changes in relative trophic level ($\delta^{15}\text{N}$) and foraging habitat ($\delta^{13}\text{C}$) were investigated for species where the size was available (Curved Carapace Length for turtles and Total Length for other species). Cook's test was used to identify outliers, each tissue comparison regression model slope was tested to determine if it deviated significantly from a slope of one, and paired difference models were tested as linear and polynomial models to identify the best fitting model.

3. Results

The Ward's method classified the studied species into three distinct clusters (Fig. 2) with significant differences in their overall stable isotopic ratios (MANOVA, Wilk's lambda $F_4, 2896 = 901.93, p < 0.0001$). Stable carbon isotope values of cluster 2 were significantly lower than those of both clusters 1 and 3 (post hoc Tukey honest significant difference multiple comparison tests, all $p < 0.05$, Appendix 1). There was no significant difference between cluster 1 and 3 for $\delta^{13}\text{C}$ ($p = 0.46$). Stable nitrogen isotope values of the three clusters were significantly different. Cluster 1 had the lowest values, followed by cluster 2 and cluster 3 (all $p < 0.05$, Appendix 1). Within each cluster, significant differences in isotopic values were observed (MANOVA, lambda de Wilk's, $F_{2,143} = 3.41, F_{10,850} = 35.25, F_{22,1712} = 117.26$ for clusters 1, 2 and 3 respectively, all $p < 0.005$). Cluster 1 ($\delta^{13}\text{C} = -16.88 \pm 3.86\%$ and $\delta^{15}\text{N} = +4.84 \pm 2.28\%$) included the Green turtle (*Chelonia mydas*)

and the Hawksbill turtle (*Eretmochelys imbricata*), species with the lowest $\delta^{15}\text{N}$ values of all species investigated and a wide range of $\delta^{13}\text{C}$ values (Fig. 2). Tukey tests showed that the Hawksbill turtle had significantly higher $\delta^{15}\text{N}$ values and significantly lower $\delta^{13}\text{C}$ values than the Green turtle ($p = 0.01$ and $p = 0.01$, respectively). Cluster 2 ($\delta^{13}\text{C} = -19.05 \pm 1.04\%$ and $\delta^{15}\text{N} = +10.28 \pm 1.21\%$) included 12 species, all large pelagic teleosts, the White-tailed tropicbird (*Phaeton lepturus*), the Tiger shark (*Galeocerdo cuvier*, samples of blood) and two species of delphinids, the Common bottlenose dolphin (*Tursiops truncatus*) and the Pantropical spotted dolphin (*Stenella attenuata*). This cluster was characterized by some of the highest $\delta^{15}\text{N}$ and the lowest $\delta^{13}\text{C}$ values of all species (Fig. 2). Overall there was no significant difference for $\delta^{13}\text{C}$ values between the large pelagic teleosts (Appendix 1). Tukey tests showed that the Giant trevally had significantly higher $\delta^{13}\text{C}$ values than the other species of cluster 2 (Appendix 1), with the exception of the Giant barracuda (*Sphyraena barracuda*, $p = 0.07$). For $\delta^{15}\text{N}$, the Common bottlenose dolphin showed highest $\delta^{15}\text{N}$ values than all other species of the cluster (Appendix 1). Cluster 3 ($\delta^{13}\text{C} = -16.49 \pm 1.49\%$ and $\delta^{15}\text{N} = +10.93 \pm 0.85\%$) included 7 species of sharks and two species of delphinids, the Indo-pacific bottlenose dolphin (*Tursiops aduncus*) and the Spinner dolphin (*Stenella longirostris*). Tukey tests showed that the Shortfin mako (*Isurus oxyrinchus*) and the Scalloped hammerhead shark (*Sphyrna lewini*) had $\delta^{13}\text{C}$ values significantly lower and $\delta^{15}\text{N}$ values significantly higher than all others species of the cluster with the exception of blood samples of the Bull shark and the Sliteyes shark (*Loxodon macrorhinus*) for $\delta^{13}\text{C}$ and the Sandbar shark (*Carcharhinus plumbeus*) for $\delta^{15}\text{N}$ (Appendix 1). Tukey tests showed also that skin samples of Bull and Tiger sharks had significantly higher $\delta^{13}\text{C}$ values than all the other species (Appendix 1).

For species with ≥ 5 individuals, estimates of corrected standard $\delta^{15}\text{N}-\delta^{13}\text{C}$ ellipses areas (SEAc) ranged from 0.14 for the Sandbar shark to 19.3 for the Green turtle (Fig. 3, Table 2). Overall, a high isotopic niche overlap occurred between species of the same taxonomic groups (sharks, delphinids, sea turtles, large pelagic teleosts; Fig. 3, Appendix 2). For example, the isotopic niche (SEAc) of the Indo-pacific bottlenose dolphin (fully overlapped that of the Spinner dolphin (Fig. 3, Appendix 2). Similarly, the isotopic niche (SEAc) of the Scalloped hammerhead shark fully overlapped that of the Shortfin mako (Fig. 3, Appendix 2). A significant overlap of the isotopic niche (SEAc) of the Green turtle with that of the Hawksbill turtle (Fig. 3, Appendix 2) occurred. In addition,

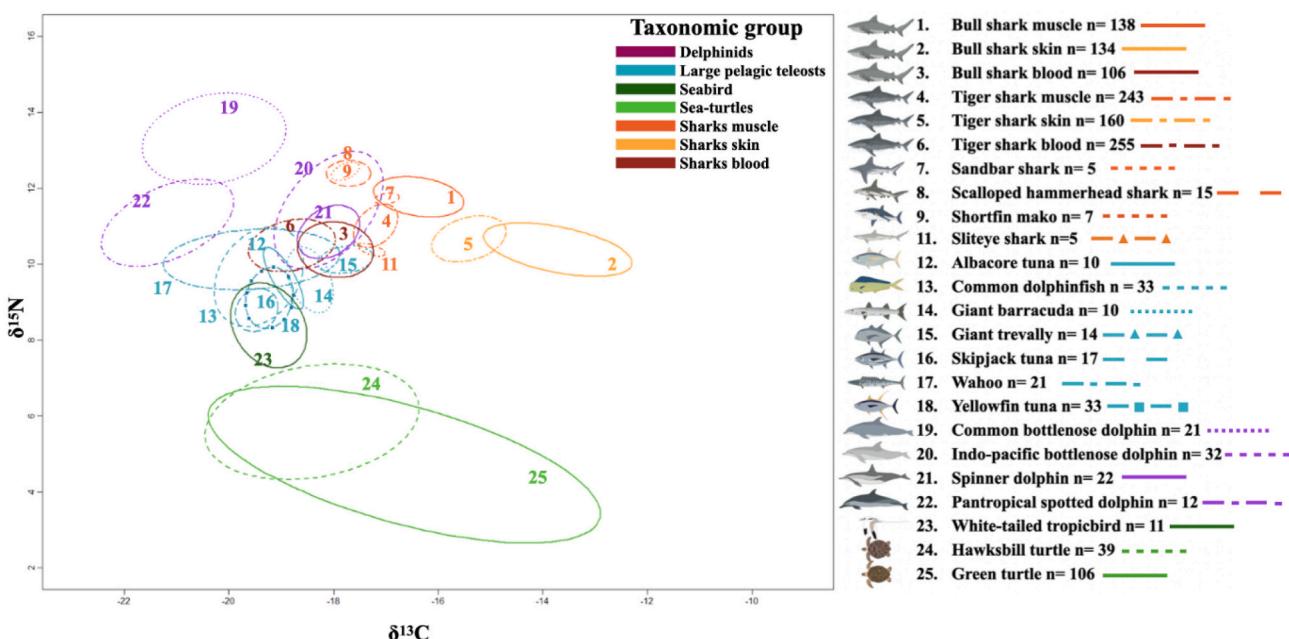


Fig. 3. Stand ellipse areas corrected for sample size (SEAc) of studied species. Illustrations: ©Guillaume CHANDELIER.

Table 2

Characteristics of the large marine vertebrates species sampled around La Réunion. Stable isotope values are displayed as mean (\pm standard deviation). n = number of samples, TL = trophic level, SEAc = corrected standard ellipses areas, CD = centroid distance.

Taxonomic group	Species	Common name	Sampling tissue	n	Mean size \pm standard error (cm)	Range size (cm)	Cluster	n° Fig. 1	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Mean trophic level \pm standard error	SEAc (‰ ²)	CD = distance to the centroid
Delphinids	<i>Stenella attenuata</i>	Pantropical spotted dolphin	Skin	12	NA	NA	2	22	-19.60 (± 0.74)	+12.10 (± 0.86)	3.48 (± 0.36)	4.48	1.32
	<i>Stenella longirostris</i>	Spinner dolphin	Skin	22	NA	NA	3	21	-16.59 (± 0.51)	+11.75 (± 0.65)	3.78 (± 0.25)	1.68	0.93
	<i>Tursiops aduncus</i>	Indo-pacific bottlenose dolphin	Skin	32	NA	NA	3	20	-16.50 (± 1.03)	+12.42 (± 1.51)	4.06 (± 0.28)	4.54	1.26
	<i>Tursiops truncatus</i>	Common bottlenose dolphin	Skin	21	NA	NA	2	19	-18.71 (± 1.37)	+14.30 (± 1.20)	4.23 (± 0.46)	5.36	1.48
Large-pelagic teleosts	<i>Acanthocybium solandri</i>	Wahoo	Muscle	21	108 (± 9)	97–142	2	17	-17.77 (± 1.68)	+12.01 (± 0.80)	3.27 (± 0.21)	3.94	1.37
	<i>Caranx ignobilis</i>	Giant trevally	Muscle	14	102 (± 14)	83–135	2	15	-15.97 (± 0.52)	+12.01 (± 0.36)	3.26 (± 0.09)	0.73	0.52
	<i>Coryphaena hippurus</i>	Common dolphinfish	Muscle	33	96 (± 13)	69–114	2	13	-17.62 (± 0.85)	+11.56 (± 1.31)	3.16 (± 0.33)	3.61	1.41
	<i>Katsuwonus pelamis</i>	Skipjack tuna	Muscle	17	59 (± 13)	39–90	2	16	-17.66 (± 0.40)	+10.68 (± 0.56)	2.92 (± 0.13)	0.74	0.57
	<i>Sphyraena barracuda</i>	Giant barracuda	Muscle	10	110 (± 29)	64–138	2	14	-16.64 (± 0.44)	+11.48 (± 0.86)	3.12 (± 0.23)	1.25	0.80
	<i>Thunnus alalunga</i>	Albacore tuna	Muscle	10	99 (± 3)	95–104	2	12	-17.15 (± 0.38)	+11.52 (± 0.81)	3.13 (± 0.2)	0.68	0.70
	<i>Thunnus albacares</i>	Yellowfin tuna	Muscle	33	77 (± 23)	50–145	2	18	-17.42 (± 0.45)	+11.006 (± 0.80)	3.0 (± 0.20)	1.14	0.78
Sea turtles	<i>Chelonia mydas</i>	Green turtle	Skin	106	58 (± 18)	34–119	1	25	-14.53 (± 2.94)	+8.85 (± 1.59)	2.09 (± 0.38)	19.32	3.86
	<i>Eretmochelys imbricata</i>	Hawksbill turtle	Skin	39	49 (± 12)	31.5–85.5	1	24	-16.19 (± 1.49)	+9.93 (± 1.17)	2.29 (± 0.30)	9.32	2.20
Seabird	<i>Phaethon lepturus</i>	White-tailed tropicbirds	Blood	11	NA	NA	2	23	-18.24 (± 0.72)	+11.39 (± 1.11)	2.76 (± 0.26)	2.76	1.11
Sharks	<i>Carcharhinus falciformis</i>	Silky shark	Muscle	4	138 (± 13)	120–149	3	10	-16.19 (± 0.058)	+12.86 (± 0.56)	3.43 (± 0.15)	0.11	0.47
	<i>Carcharhinus leucas</i>	Bull shark	Skin	106	252 (± 54)	95–327	3	2	-12.79 (± 1.41)	+12.66 (± 0.70)	3.35 (± 0.21)	2.75	1.26
	<i>Carcharhinus leucas</i>	Bull shark	Blood	134	257 (± 47)	104–327	3	3	-15.06 (± 0.72)	+12.98 (± 0.62)	3.16 (± 0.19)	1.71	0.86
	<i>Carcharhinus leucas</i>	Bull shark	Muscle	138	254 (± 49)	101–325	3	1	-15.47 (± 0.86)	+14.05 (± 0.53)	3.74 (± 0.17)	1.39	0.80
	<i>Carcharhinus plumbeus</i>	Sandbar shark	Muscle	5	174 (± 38)	176–203	3	7	-16.09 (± 0.23)	+14.01 (± 0.14)	3.75 (± 0.04)	0.14	0.24
	<i>Galeocerdo cuvier</i>	Tiger shark	Skin	160	301 (± 66)	130–415	3	5	-14.51 (± 0.71)	+12.96 (± 0.61)	3.44 (± 0.75)	1.32	0.80
	<i>Galeocerdo cuvier</i>	Tiger shark	Muscle	243	310 (± 60)	130–429	3	4	-16.30 (± 0.42)	+13.30 (± 0.57)	3.52 (± 0.16)	0.71	0.60
	<i>Galeocerdo cuvier</i>	Tiger shark	Blood	255	310 (± 60)	130–429	2	6	-15.90 (± 0.82)	+13.09 (0 ± .68)	3.16 (± 0.19)	1.77	0.87
	<i>Isurus oxyrinchus</i>	Shortfin mako	Muscle	7	NA	NA	3	9	-16.87 (± 0.26)	+14.73 (± 0.24)	3.99 (± 0.08)	0.21	0.31
	<i>Loxodon macrorhinus</i>	Sliteye shark	Muscle	5	97 (± 3)	93–102	3	11	-16.38 (± 0.25)	+12.67 (± 0.17)	3.36 (± 0.04)	0.14	0.25
	<i>Sphyraena lewini</i>	Scalloped hammerhead	Muscle	15	270 (± 24)	64–315	3	8	-16.96 (± 0.2)	+14.65 (± 0.38)	3.96 (± 0.11)	0.49	0.42

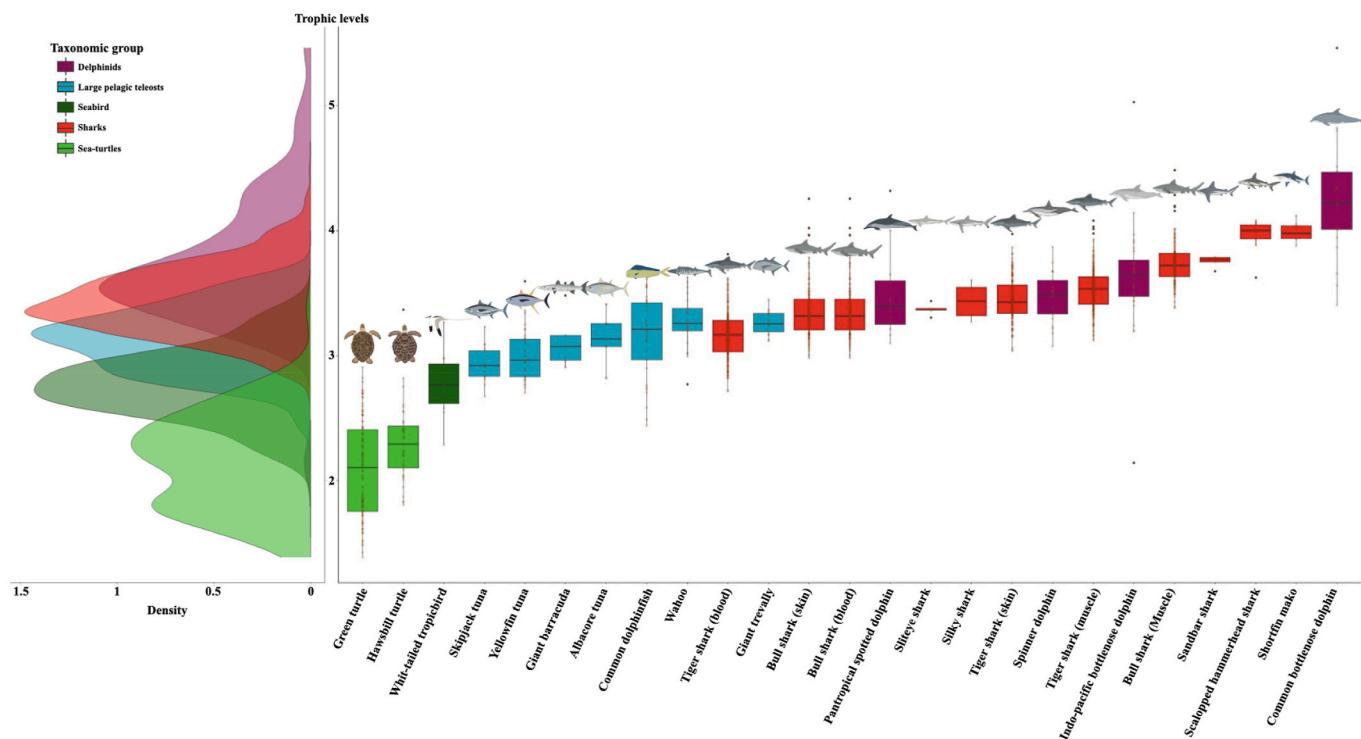


Fig. 4. Trophic level estimation of the species using $\delta^{15}\text{N}$ values. Illustrations: ©Guillaume CHANDELIER.

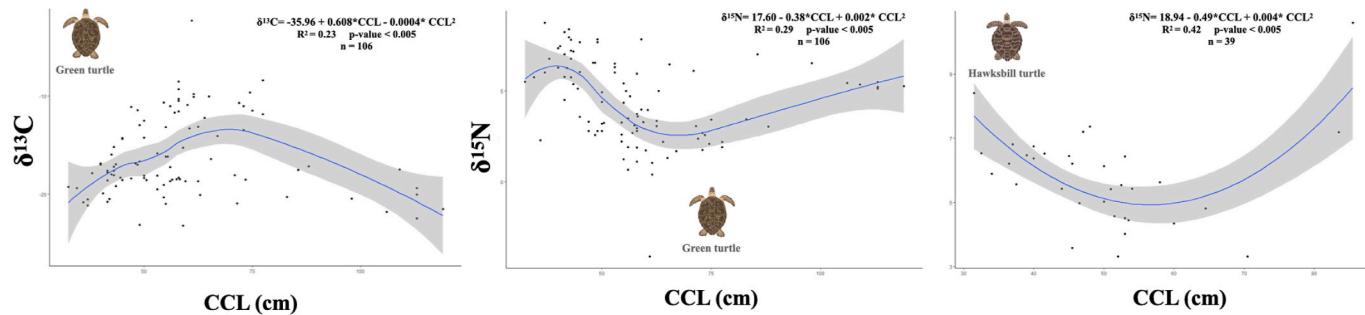


Fig. 5. Regression of the relationship between stable isotopes $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and size = CCL = curved carapace length (cm).

the isotopic niche (SEAc) of the Wahoo (*Acanthocybium solandri*) significantly overlapped with the niches of many large pelagic fish species such as the Albacore tuna (*Thunnus alalunga*), the Giant barracuda, the Giant trevally (*Caranx ignobilis*) and the Common dolphinfish (*Coryphaena hippurus*). Finally, the isotopic niche of the Common dolphinfish overlapped significantly with those of the Skipjack (*Katsuwonus pelamis*) and the Yellowfin tuna (*Thunnus albacares*) (Fig. 3, Appendix 2). A high isotopic niche overlap occurred between species of different taxonomic groups (Fig. 3, Appendix 2). For example, the isotopic niche (SEAc) of the Indo-pacific bottlenose dolphin fully overlapped that of the Shortfin mako and the Scalloped hammerhead shark, and largely overlapped those of the Tiger and Bull shark blood samples (Fig. 3, Appendix 2). The isotopic niche of the Wahoo also overlapped significantly with those of the Tiger and Bull shark blood samples and the Giant trevally with the Bull shark blood. Finally, the isotopic niche (SEAc) of the White-tailed tropicbird showed a significant overlap with several large pelagic teleosts such as the Common dolphinfish, the Yellowfin tuna and the Skipjack tuna (Fig. 3, Appendix 2).

Trophic levels were significantly different (one-way ANOVA: $F_{4, 1473} = 657.80$, $p < 0.0001$), with dolphins and sharks species with the highest trophic levels, followed by large pelagic teleosts, the seabird

species and sea turtles. At the species level, trophic levels ranged between 2.09 ± 0.38 for the Green turtle to 4.06 ± 0.28 for the Common bottlenose dolphin (Fig. 4, Table 1). The Common bottlenose dolphin has significantly higher trophic level than all species with the exception of the Shortfin mako, the Scalloped hammerhead shark and the Bull shark (Blood and skin samples, Appendix 2). The Green and Hawksbill turtle have significantly lower trophic levels than all other species (Appendix 2). The lowest and highest mean distances to centroid were 0.2 and 3.9 for the Sandbar shark and the Green turtle respectively (Table 1).

Six species showed a significant relationship between size and $\delta^{13}\text{C}$ though the coefficient of determination R^2 is weak for most of them, indicating that the size of the individuals has a limited influence on the variability of $\delta^{13}\text{C}$ values (Appendix 3). For the Bull shark, the relationship between the individual size and the $\delta^{13}\text{C}$ values is significant and positive for the three tissues, while only the skin is significant for the tiger shark. The Albacore tuna and the Yellowfin tuna showed positive and significant relationships between the size and the $\delta^{13}\text{C}$ values, while for the Wahoo no clear trend emerged. For the Green turtle, $\delta^{13}\text{C}$ values increased until $LCC = 75$ cm then decreased. Four species showed a significant relationship between size and $\delta^{15}\text{N}$, and these relationships

were overall stronger than with $\delta^{13}\text{C}$. For the Albacore tuna and the two sea turtle species, the relationship showed similar patterns with smaller and larger individuals with higher $\delta^{15}\text{N}$ values than intermediate size individuals (Fig. 5).

4. Discussion

Stable isotope analyses of samples collected over a 9-years period provide a consistent picture of the structure of the community of large marine vertebrates species around La Reunion (Dulau-Drouot et al., 2008; Jaquemet et al., 2011; Le Manach et al., 2015; Trystram et al., 2017). The range of carbon and nitrogen isotopic values measured in the 21 studied species demonstrates that these species exploit different resources along a coastal-offshore gradient, thus limiting habitat and trophic redundancy between species. Differences in isotopic niche widths indicate that some species have either high inter-individual variability (Burkholder et al., 2011) and/or that some species rely on multiple carbon sources. Interestingly, species known to forage on oceanic resources such as large pelagic teleosts showed intermediate carbon values between oceanic and coastal carbon sources (Kolasinski et al., 2011; Cuvillier 2016). This supports the idea that some oceanic predators link spatially distinct habitats and use peri-insular waters where feeding opportunities could be higher than in the open ocean (Bakun et al. 2006). This is consistent with a higher exploitation of coastal resources for Yellowfin tuna and Skipjack tuna caught around La Reunion compared to individuals caught further offshore (Jaquemet et al., 2011).

4.1. Foraging habitats

Carbon isotope values showed a coast-open ocean gradient of foraging habitats for the studied species. In addition, the wide range of intra and inter-specific $\delta^{13}\text{C}$ values suggests that the studied species likely use several foraging habitats. The Green turtle and the Bull shark showed a strong preference for coastal foraging habitats as indicated by their higher $\delta^{13}\text{C}$ values compared to other species. For the Bull shark, it seems to have an ontogenetic change in the habitat use, with juveniles more inshore than adults, as already shown (Trystram et al., 2017). The Shortfin mako, the Scalloped hammerhead shark, the White-tailed tropicbird, the Pantropical spotted dolphin, the Common bottlenose dolphin and the large pelagic teleosts had relatively lower $\delta^{13}\text{C}$ values, indicating that they mostly rely on oceanic resources. Nevertheless, for most species, $\delta^{13}\text{C}$ values were intermediate to those habitats, suggesting that they forage in both coastal and oceanic habitats (Hussey et al., 2011) or at least derive their carbon sources from both habitats. Export of coastal material offshore and enrichment of the oligotrophic oceanic ecosystems is typically associated to island mass effect (Bakun 2006). Such process could explain the fact that most species have intermediate $\delta^{13}\text{C}$ values between coastal and oceanic sources (Kolasinski et al., 2011). Some species, particularly the two sea turtle species, all delphinids except the Spinner dolphin and 2 species of large pelagic teleosts, the Wahoo and the Common dolphinfish, showed a high intraspecific variability of $\delta^{13}\text{C}$ values. This high variability can be explained by either a strong inter-individual difference of foraging habitat use and/or a dependency to multiple carbon sources, as documented in other ecosystems for the Green turtle (Burkholder et al., 2011). For the two latter species, the dependency to multiple carbon sources could be explained by different duration of residency in the vicinity of the island, as these species are known to exhibit seasonal patterns of abundance in relation with environmental conditions (Marinez-Enriquez et al. 2017).

4.2. Trophic levels and trophic redundancy

Results from this study reveal considerable intraspecific variation in $\delta^{15}\text{N}$, suggesting some level of individual dietary-specialization in several of the studied species, consistent with the intraspecific

variability of foraging habitat use suggested by the $\delta^{13}\text{C}$. For the studied species, trophic levels were similar to studies using stable isotope method (Kiszka et al., 2015; Dicken et al., 2017), and were also comparable to studies that use stomach content analysis (Cortes 1999). Our results showed that, around La Reunion, large marine vertebrates have a wide range of trophic levels, from primary consumers to apex predators (Roger 1994; Ménard et al., 2006; Kojadinovic et al., 2008; Kiszka et al., 2014; Li et al., 2016a; Trystram et al., 2017; Figgener et al., 2019). Overall, the two species of sea turtles have the lowest trophic levels, which is consistent with a diet composed mainly of organisms at the base of food webs (e.g. algae, sponges, zoantharia). (León and Bjorndal 2002; Burkholder et al., 2011; Di Benedetto et al., 2017).

Although there is no study on the trophic ecology of sea turtles using stable isotopes in La Reunion, their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values fall within the range of known values for the two species at the global scale (Figgener et al., 2019) but also at the Indian Ocean scale (Burkholder et al., 2011). Their isotopic niches were the largest of all studied species, showing extreme variations in isotopic values between individuals in the population. The green turtle is known to exhibit significant ontogenetic dietary changes (Reich et al., 2007; Cardona et al., 2009). Although the turtle population in Reunion Island is mainly composed of juveniles at the neritic stage, the results of our study show an important variation of isotopes according to the size (CCL). Indeed, small (CCL<50 cm) and larger (CCL>80 cm) individuals showed the highest $\delta^{15}\text{N}$ and the lowest $\delta^{13}\text{C}$ values compared to intermediate size (CCL = 50–80 cm). The $\delta^{15}\text{N}$ values of small individuals could be explained by either the fact that they still rely on oceanic zooplankton and micro-nektonic prey despite being in the neritic zone or they recruit recently in their juvenile neritic habitat and still exhibit the signature of their carnivorous oceanic stage of development. These typical oceanic life-phase isotopic signatures related to sampling in the coastal environment could represent a key moment in the life cycle of juvenile green turtles (Hamabata et al., 2015). However, isotopic signatures would show that juvenile green turtles would not make a feeding change directly after settling in the neritic environment (Cardona et al., 2009) but would go through a transition period where they depend on both coastal and offshore resources. Another hypothesis would be that the change in diet of juvenile green turtles in the coastal environment of Reunion is rapid but that isotopic assimilation is asynchronous due to an enzymology not adapted to plant resources in the first months of ontogenetic change (Cardona et al., 2010). For adults (largest size), the similar isotopic signatures to juveniles could reveal that they feed on animal sources in addition to algae and sea grasses, leading to an increase in their $\delta^{15}\text{N}$ value. This feeding behaviour could be implemented to counter the low availability of resources related to the small size of the neritic zone present in La Reunion. In a less marked way, our results showed the same trend for Hawksbill turtles. In addition to the isotopic differences between the different size classes, it is possible to observe a large variability of isotopic values for individuals of the same size class. This high variability in individual isotopic values can be driven by the exploitation of a wide range of feeding resources across multiple foraging habitats (Burkholder et al., 2011; Haywood et al., 2019; Figgener et al., 2019), but also short-term differences in diet, or even a long-term specialization on a subset of resources in a population that vary in isotopic composition ('individual specialization') and finally by individual differences in physiology (Hobson and Clark 1992; Bearhop et al., 2004; Barnes et al., 2008). The extreme dispersion of isotopic values observed in the turtles in this study suggests that the narrow neritic habitat likely limit food availability for sea turtles, forcing individuals to forage more efficiently on a narrow set of resources to limit the competition with congeners (Bolnick et al., 2003). This hypothesis can be confirmed by the high variability of carbon sources (e.g. algae, sea grasses, sponges and zoantharia) founded in the stomach contents of both species (C. Jean unpubl. data).

The White-tailed tropicbird and the large pelagic teleosts had similar trophic levels, higher than sea turtles but lower than sharks and

delphinids indicating that they are mesopredators. Dolphins and sharks have relatively similar trophic levels with the exception of the Shortfin mako, the Scalloped hammerhead shark, and the Common bottlenose dolphin that exhibited significantly higher positions in the food web (Cortes 1999; Maia et al., 2006; Hernandez-Milan et al. 2015). Variations in the use of the oceanic and coastal ecosystems could partially explain the difference of trophic positions, which limit the comparison between species that do not gather to the same clusters (Fig. 2) Some studies have suggested partial (Li et al., 2016a) or high (Kitchell et al., 2002) functional redundancies among oceanic sharks, tunas and billfish in the offshore Pacific. Other studies have suggested resource partitioning through dietary divergence in space and time to reduce inter-specific competition, as is the case for cetaceans in coastal ecosystems (Pinela et al., 2010; Browning et al., 2014; Matich et al., 2017). Overall, our results confirm a high degree of isotopic niche overlap among large pelagic fishes around La Réunion, which is consistent with previous studies carried out in the region (Kojadinovic et al., 2008), but also for other oceanic predator guilds, such as tropical seabirds in the western Indian Ocean (Cherel et al., 2008). This high overlap between large pelagic teleost could be due to either a low variability of carbon sources in oligotrophic offshore ecosystems, characterised by low productivity and seasonality (Cherel et al., 2008), a strong trophic plasticity (Kiszka et al., 2015) or a high diversity of foraging locations for these highly mobile species. However, this overlap can also be explained by the fact that long-term tissues mask patterns of habitat and resource partitioning, especially by averaging intra-specific variability.

In contrast to what Kiszka et al. (2015) observed for pelagic sharks in the oceanic western tropical Indian Ocean, isotopic niche estimates did not show strong overlap among sharks, indicating low functional redundancy in accordance with what Li et al. (2016a) observed in the central Pacific Ocean. This can be explained by the discontinuity produced by the island in the homogeneous oceanic masses, leading to strong coastal-open ocean gradient of carbon and nitrogen in comparison to the open ocean. Among delphinids, only the Indo-pacific bottlenose dolphin and the Spinner dolphin exhibited significant isotopic overlap, whereas the Pantropical spotted dolphin and the Common bottlenose dolphin were both significantly different from one another and with the two other species. The lack of differences between the Indo-pacific bottlenose dolphin and the Spinner dolphin was unexpected since these two species are known to use different foraging habitats and feed on different prey in other locations, including in the western Indian Ocean (Kiszka et al., 2011, 2014). This might indicate that the foraging habitat of the Spinner dolphin around La Réunion is more coastal than expected, and closely related to their coastal resting habitat, which is consistent with recent information on their afternoon distribution and diel movements (Condet and Dulau-Drouot 2016; Globice, Unpub. data). Finally, it should also be considered that defining trophic redundancy using isotopes remains incomplete. Further investigations would help to better understand the foraging ecology of these species.

4.3. Relationships within trophic guilds

The results showed an important overlap between the isotopic niches of the two marine turtles in Réunion Island. Indeed, the isotopic niche of hawksbill turtles is enclosed in that of green turtles. Hawksbill turtles seem to use the same resources consumed by green turtles. However, green turtles have a much broader isotopic niche and appear to rely primarily on resources not consumed by hawksbill turtles. Stable isotope values alone cannot explain whether this significant overlap is an indicator of competition between these species. However, it would appear that in Réunion Island these two species have a similar diet composed mostly of red algae (C. Jean, unpublished data). Indeed, unpublished data on stomach contents of the two species showed that the share of red algae in stomach contents is about 80% for the green turtle ($n = 14$) and 50% for hawksbill turtles ($n = 5$), which supports the hypothesis of a possible trophic competition between these two species for some

carbons sources. The narrow neritic habitat and the low abundance of the sea grass in the lagoon (Cuivillier, 2016), likely limit the availability of food resources and the opportunities of dietary differentiation for these two species, thus increasing their trophic competition.

Previous studies have shown that seabirds/delphinids and seabirds/large pelagic teleosts foraging associations occur off La Réunion (Jaquemet et al., 2004; Kojadinovic et al., 2008). These foraging associations suggest that both seabirds and surface predators feed on similar prey. The significant overlap of isotopic area between the White-tailed tropicbird and some species of large pelagic teleosts support this statement, in contrast to the lack of overlap between the White-tailed tropicbird and the delphinids. As these associations are mostly ephemeral and tropical seabirds have very limited diving abilities (Sommerfeld and Hennicke, 2009), the overlap of isotopic niches indicates that either the large teleosts derived a small part of their food only during these surface feeding events or that seabirds' access on a small portion of the prey only therefore acting as true commensals of their associated surface predators. Although the predation by the sharks on sea turtles, dolphins, pelagic fish and seabirds is documented (Dicken et al., 2017; Heithaus et al., 2017), including off Réunion Island (Trystram et al., 2017), the stable isotope values alone do not clearly depict such relationships between species in our study. This highlights the limits of stable isotopes and the necessary use of complementary methods (e.g., fatty acids, compound-specific stable isotopes, stomach content analysis, Shipley & Matich, 2020) to evaluate more precisely isotopic niche partitioning and comparison of trophic levels between marine species in complex environments such as around oceanic islands.

5. Conclusion

To conclude, the results of this study suggest that the close proximity of the inshore and offshore habitats around La Réunion promotes movements of marine predators among these habitats. Similar to Hawaii (Benoit-Bird and Au 2006), the topography of La Réunion could promote horizontal movements of micronektonic organisms during the diel migration, thus leading to an increase of the forage biomass near the coast, which would ultimately provide higher feeding opportunities in the vicinity of the island for both coastal and oceanic predators (Heywood et al., 1990; Signorini et al., 1999). The aggregation of forage organisms around La Réunion associated to export of organic matter and nutrients from the island could promote the co-existence of large marine vertebrates in the vicinity of the island, by producing strong coastal-open ocean gradient of matter and energy. The large range of carbon and nitrogen isotopic values and trophic levels of the studied species confirm that they have different trophic positions in the ecosystem and limited functional redundancy.

Ethical statement

Delphinid samples were collected by GLOBICE and OFB/BNOI, under programs with research permits delivered by the French Ministry for Environment (2009-336 and 2016-04) and the Ministry for Research (#6197-2016071511066393). Turtles samples were collected under the Ethical approval code provided by La Réunion Environment, Planning and Housing Direction (DEAL/CNPN) from the Ecological and Solidarity Transition French Ministry (MTES): CHARC (n°19/12/2012) EGETOMER DA n° 2014-03 et 2014-06 and project authorization 03866.01 21/08/15 - MEN/ESR HATOCAM (n° 2017-01) and project authorization (09-14-05/SG/DRCTCV) (Turtle Care Centre of Kelonia). All sharks were caught as part of the local shark control program organized since 2012 by the French government around the island. This program aims at reducing the shark risk close to nautical activities and all catches are done by professional fishermen. Réunion Island University takes the opportunity of these catches to organize the dissection of the sharks captured to improve knowledge of the local biology and ecology of the species. As the death of the sharks is not primarily related to the

gathering of scientific knowledge and samples or data are only taken from already dead animals, no ethical agreement is needed to conduct this research.

Author statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix 1. P-value from MANOVA showing differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between and among clusters. *: p-value <0.05, **: p-value <0.01, ***p-value <0.001, **** p-value <0.0001

$\delta^{13}\text{C}$		Cluster 1						Cluster 2		
$\delta^{13}\text{C}$	Cluster 1									
	Cluster 2									
	Cluster 3									
$\delta^{15}\text{N}$	Cluster 1									
	Cluster 2									
	Cluster 3									
Cluster 1										
$\delta^{13}\text{C}$										
Green turtle										Hawksbill turtle
$\delta^{15}\text{N}$										
Green turtle										Hawksbill turtle
Cluster 2										
$\delta^{13}\text{C}$	Wahoo	Common dolphinfish	Giant trevally	Tiger shark blood	Skipjack tuna	White-tailed tropicbird	Pantropical spotted dolphin	Giant barracuda	Albacore tuna	Yellowfin tuna
Common dolphinfish	1									
Giant trevally	**	****								
Tiger shark blood	0.59	**	***							
Skipjack tuna	1	1	****	***						
White-tailed tropicbird	0.99	1	***	0.67	0.99					
Pantropical spotted dolphin	0.12	*	****	***	*	**				
Giant barracuda	0.19	**	0.07	0.46	***	0.16	***			
Albacore tuna	0.87	0.34	****	0.97	0.09	0.98	**	0.25		
Yellowfin tuna	0.99	0.97	****	***	0.71	1	**	**	0.71	
Common bottlenose dolphin	0.91	0.31	****	***	0.31	0.2	0.72	***	*	0.07
$\delta^{15}\text{N}$	Wahoo	Common dolphinfish	Giant trevally	Tiger shark blood	Skipjack tuna	White-tailed tropicbird	Pantropical spotted dolphin	Giant barracuda	Albacore tuna	Yellowfin tuna
Common dolphinfish	0.88									
Giant trevally	1	0.76								
Tiger shark blood	0.61	*	0.06							

(continued on next page)

(continued)

Cluster 2											
$\delta^{13}\text{C}$	Wahoo	Common dolphinfish	Giant trevally	Tiger shark blood	Skipjack tuna	White-tailed tropicbird	Pantropical spotted dolphin	Giant barracuda	Albacore tuna	Yellowfin tuna	
Skipjack tuna	****	0.06	****	****							
White-tailed tropicbird	0.01	0.12	0.01	**	0.98						
Pantropical spotted dolphin	0.32	0.05	0.25	0.76	***	***					
Giant barracuda	0.84	1	0.74	0.15	0.33	0.24	0.06				
Albacore tuna	0.86	1	0.76	0.14	0.22	0.19	0.06	1			
Yellowfin tuna	**	0.59	****	****	0.85	0.66	**	0.88	0.78		
Common bottlenose dolphin	****	****	****	****	****	****	***	***	***	***	***

Cluster 3											
$\delta^{13}\text{C}$	Silky shark	Bull shark muscle	Bull shark skin	Bull shark blood	Sandbar shark	Tiger shark muscle	Tiger shark skin	Shortfin mako	Sliteye shark	Scalloped hammerhead shark	Spinner dolphin
Bull shark muscle	****										
Bull Shark skin	****	****									
Bull shark blood	****	****	****								
Sandbar shark	0.99	*	***	**							
Tiger shark muscle	0.34	****	****	****	0.72						
Tiger shark skin	****	****	****	****	***	***					
Shortfin mako	**	****	****	0.98	**	**	****				
Sliteye shark	0.86	**	****	*	0.76	0.99	***	0.08			
Scalloped hammerhead shark	***	****	****	0.64	*	**	***	0.99	0.29		
Spinner dolphin	****	****	****	0.99	***	***	***	0.88	**	0.5	
Indo-pacific bottlenose dolphin	***	****	****	1	***	**	***	0.98	*	0.81	1

$\delta^{15}\text{N}$	Silky shark	Bull shark muscle	Bull shark skin	Bull shark blood	Sandbar shark	Tiger shark muscle	Tiger shark skin	Shortfin mako	Sliteye shark	Scalloped hammerhead shark	Spinner dolphin
Bull shark muscle	0.18										
Bull Shark skin	0.99	****									
Bull shark blood	0.99	****	1								
Sandbar shark	0.19	1	****	****							
Tiger shark muscle	0.87	****	****	****	***						
Tiger shark skin	1	****	*	*	****	****					
Shortfin mako	*	*	****	****	*	**	***				
Sliteye shark	0.99	****	1	1	****	**	0.2	***			
Scalloped hammerhead shark	0.05	****	****	****	***	***	***	1	***		
Spinner dolphin	0.99	***	0.23	0.23	***	0.99	0.99	***	0.27	***	
Indo-pacific bottlenose dolphin	0.61	0.98	*	*	0.99	0.93	0.28	0.06	*	0.07	0.8

Appendix 2. Overlap of SEAc (available in excel file)

Overlap (SEAc)	Bull shark blood	Bull shark muscle	Bull shark skin	Sandbar shark	Scalloped hammerhead shark	Shortfin mako	Sliteye shark	Tiger shark blood	Tiger shark muscle	Tiger shark skin
Bull shark blood	0	0	0	0	0	57.8	33.1	16.7	0	
Bull shark muscle	0	0	0	0	0	0	0	0	1.4	0
Bull shark skin	0	0	0	0	0	0	0	0	0	16.6
Sandbar shark	0	0	0	0	0	0	0	33.1	0.4	0
Scalloped hammerhead shark	0	0	0	0	100	0	0	0	0	0
Shortfin mako	0	0	0	43.7		0	0	0	0	0
Sliteye shark	5	0	0	0	0	0	0	0	4.2	0
Tiger shark blood	34.5	0	0	0	0	0	0	0	0	0
Tiger shark muscle	7.14	0.7	0	2.1	0	0	21.4	0		0
Tiger shark skin	0	0	7.2	0	0	0	0	0	0	0
Albacore tuna	0	0	0	0	0	0	0	13.7	0	0
Common dolphinfish	1.7	0	0	0	0	0	0	56	0	0
Giant barracuda	16	0	0	0	0	0	0	18.8	0	0
Giant trevally	36.9	0	0	0	0	0	30.7	1.8	0	0
Skipjack tuna	0	0	0	0	0	0	0	0	0	0
Wahoo	39.2	0	0	0	0	0	0	80.5	0	0
Yellowfin tuna	0	0	0	0	0	0	0	1.7	0	0
Common bottlenose dolphin	0	0	0	0	0	0	0	0	0	0
Indo-Pacific bottlenose dolphin	61.3	5.3	0	21.4	100	100	0	70.2	26.7	0
Pantropical potted dolphin	0	0	0	0	0	0	0	0	0	0
Spinner dolphin	50	0	0	0	0	0	0	33.7	5.6	0
Green turtle	0	0	0	0	0	0	0	0	0	0
Hawksbill turtle	0	0	0	0	0	0	0	0	0	0
White tailed tropicbird	0	0	0	0	0	0	0	0	0	0

Albacore tuna	Common dolphinfish	Giant barracuda	Giant trevally	Skipjack tuna	Wahoo	Yellowfin tuna	Common bottlenose dolphin	Indo-Pacific bottlenose dolphin	Pantropical potted dolphin	Spinner dolphin	Green turtle	Hawksbill turtle	White tailed tropicbird
0	1.03	21.6	98.4	0	15	0	0	22.3	0	64.1	0	0	0
0	0	0	0	0	0	0	0	1.6	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0.8	0	0	0	0	0
0	0	0	0	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	0	4.5	0	0	0	0	0
0	0	0	6.8	0	0	0	0	0	0	0	0	0	0
35.2	28.8	26.4	5.2	0	32.7	1.7	0	26.6	0	45	0	0	0
0	0	0	0	0	0	0	0	4.1	0	3	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	16.1	13.6	0	0	10	23.9	0	0	0	0	0	0	4
82.3		26.4	0	88.15	50.7	88	0	9.9	0	1.3	0	0	39.2
25	9.5		7.9	0	13.6	1.7	0	7.5	0	6.8	0	0	0
0	0	4		0	4.5	0	0	3.4	0	6.8	0	0	0
0	19.3	0	0		0.2	46.1	0	0	0	0	0	0	27.6
63.2	64.2	48	31.7	1.18		0	0	22.3	6.7	33.5	0	0	4.7
41.1	29.6	1.6	0	71.05	0		0	0	0	0	0	0	32.3
0	0	0	0	0	0	0		0	3.6	0	0	0	0
4.4	13.2	28	25.3	0	23.4	0	0		0	100	0	0	0
0	0	0	0	0	0	0	2.9	0		0	0	0	0
0	0.5	7.2	14.2	0	10	0	0	28.4	0		0	0	0
0	0	0	0	0	0	0	0	0	0		75.1	0	
0	0	0	0	0	0	0	0	0	0	0		38.4	0
16.1	31.1	0	0	100	2.9	76	0	0	0	0	0	0	0

Appendix 3. Regression equations displaying the relationship between stable isotopes and size. Shown in gray are equations that have significant p-values <0.05 and R² > 0.1

Species	Isotopes	Tissue	Equation	P-value	Adjusted R-Squared
Tiger Shark	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -17 - 0.006 * \text{TL}$	0.1631	0.003939
		Blood	$\delta^{13}\text{C} = -19.1 + 0.0008 * \text{TL}$	0.1887	0.003091
		Skin	$\delta^{13}\text{C} = -16.17 + 0.002 * \text{TL}$	0.003165	0.04781
	$\delta^{15}\text{N}$	Muscle	$\delta^{15}\text{N} = 11.17 - 0.0005 * \text{TL}$	0.3778	-0.000907
		Blood	$\delta^{15}\text{N} = 9.2 - 0.004 * \text{TL}$	5.291e-08	0.1139
		Skin	$\delta^{15}\text{N} = 10.33 - 0.001 * \text{TL}$	0.1257	0.008542
Bull shark	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -17.49 + 0.012 * \text{TL} - 0.00005 * \text{TL}^2$	0.0004346	0.0965
		Blood	$\delta^{13}\text{C} = -17.17 - 0.002 * \text{TL}$	0.0231	0.03168
		Skin	$\delta^{13}\text{C} = -20.55 + 0.055 * \text{TL} - 0.0001 * \text{TL}^2$	0.0001495	0.1421
	$\delta^{15}\text{N}$	Muscle	$\delta^{15}\text{N} = 11.82 - 0.0002 * \text{TL}$	0.767	-0.006801
		Blood	$\delta^{15}\text{N} = 10.03 - 0.001 * \text{TL}$	0.3719	-0.001507
		Skin	$\delta^{15}\text{N} = 10.27 + 0.0004 * \text{TL}$	0.7111	-0.008358
Albacore tuna	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -24.40 + 0.05 * \text{TL}$	0.0008599	0.8395
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 437.31 - 8.52 * \text{TL} + 0.04 * \text{TL}^2$	0.00111	0.9079
Giant trevally	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -17.34 + 0.05 * \text{TL}$	0.7729	-0.09041
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 9.62 + 0.005 * \text{TL}$	0.06307	0.3386
Wahoo	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -101.4 + 1.324 * \text{TL} - 0.005 * \text{TL}^2$	0.001264	0.4707
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 6.40 + 0.03 * \text{TL}$	0.06933	0.1192
Common dolphinfish	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -18.53 - 0.009 * \text{TL}$	0.4166	-0.01017
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 9.82 - 0.001 * \text{TL}$	0.9241	-0.03195
Skipjack tuna	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -19.48 + 0.0002 * \text{TL}$	0.9734	-0.06658
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 8.18 - 0.001 * \text{TL}$	0.3449	-0.003063
Yellowfin tuna	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -19.83 + 0.007 * \text{TL}$	0.01709	0.1433
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 9.03 + 0.0008 * \text{TL}$	0.8845	-0.03154
Giant barracuda	$\delta^{13}\text{C}$	Muscle	$\delta^{13}\text{C} = -17.96 - 0.003 * \text{TL}$	0.6673	-0.1283
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 9.03 + 0.0008 * \text{TL}$	0.763	-0.1476
Hawksbill turtle	$\delta^{13}\text{C}$	Skin	$\delta^{13}\text{C} = -17.36 - 0.02 * \text{CCL}$	0.4182	-0.01002
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 18.94 - 0.49 * \text{CCL} + 0.004 * \text{CCL}^2$	0.00006	0.42
Green turtle	$\delta^{13}\text{C}$	Skin	$\delta^{13}\text{C} = -35.969 + 0.608 * \text{CCL} - 0.0004 * \text{CCL}^2$	0.000001	0.23
	$\delta^{15}\text{N}$		$\delta^{15}\text{N} = 17.60 - 0.38 * \text{CCL} + 0.002 * \text{CCL}^2$	0.00000002	0.29

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