

# Isotopic niches of the blue shark *Prionace glauca* and the silky shark *Carcharhinus falciformis* in the southwestern Indian Ocean

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**ABSTRACT:** In the Indian Ocean, the blue shark *Prionace glauca* and the silky shark *Carcharhinus falciformis* represent the 2 main shark bycatch species in pelagic longline and purse seine fisheries, respectively. With the increasing market demand for fins, catches may increase in the future, with potential effects on ecosystem trophic functioning through top-down cascading effects. Knowledge of the species' trophic ecology is therefore crucial but is limited by the lack of data from the Indian Ocean. Stable isotope analysis was therefore performed on muscle tissues ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) of these 2 shark species from the western Indian Ocean. Our study showed that body length, season, and zone effects were relatively small for the 2 species. However, significant  $\delta^{13}\text{C}$  differences between the 2 species suggest niche partitioning, with silky sharks having a more inshore foraging habitat than blue sharks. Finally, lower muscle  $\delta^{15}\text{N}$  values were observed in juvenile silky sharks caught by purse seiners around fish aggregating devices (FADs) compared to juveniles caught by longliners. One hypothesis is that FADs could act as an ecological trap for juvenile silky sharks, leading to a position at lowest trophic level for these individuals. However, different foraging habitats could also explain the observed patterns between juveniles. Although preliminary, our results provide a basis for the implementation of species-specific protection and management strategies.

**KEY WORDS:** Stable isotopes ·  $\delta^{13}\text{C}$  ·  $\delta^{15}\text{N}$  · Trophic ecology · Niche partitioning · Foraging habitat · Sharks

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## INTRODUCTION

Pelagic sharks, which are among the largest predators in the ocean, play an important ecological role in open-sea ecosystems through predation effects on community structure (Estrada et al. 2003, Heithaus et al. 2008, Ferretti et al. 2010). Large pelagic sharks are sometimes the only consumers of a range of meso-predators (Heithaus et al. 2008) such as small

elasmobranchs (Wetherbee & Cortés 2004) or some marine mammals. Most shark populations are intensively exploited by large-scale pelagic fisheries (Baum et al. 2003, Campana et al. 2008), leading to marked and rapid declines of the less resilient species, such as carcharhinids. Worldwide, 700 000 to 850 000 t of sharks are caught annually as target species or bycatch, and landings increase at an annual rate of ca. 2% (Camhi et al. 2009, Lucifora et

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al. 2011). This value is an underestimation (Clarke et al. 2006) because of non-reported and illegal catches of pelagic sharks for their fins, for which there is a high demand in Asian markets. Such a removal of large predators could initiate trophic cascades (Heithaus et al. 2008). The loss of top-down forcing could have unanticipated impacts such as modifying biogeochemical cycles or favoring invasive species (Estes et al. 2011). Knowledge of the trophic ecology of sharks, which is limited by the lack of data in most regions of the world oceans (Matich et al. 2011), is therefore crucial for their conservation but also to preserve pelagic ecosystem functioning. The blue shark *Prionace glauca* and the silky shark *Carcharhinus falciformis* are 2 of the most intensively exploited pelagic sharks in the world (Bonfil 2008, Stevens 2010).

Stable isotope analysis has been increasingly applied to a variety of organisms and has proven particularly useful in the study of animal trophic ecology, trophic interactions, habitat use, and movements of mobile organisms (Cherel et al. 2007, Hobson 2007). Depending on the tissues studied, the non-lethal biopsy punch technique is particularly useful when studying endangered species. The approach is based on the fact that stable isotope ratios of carbon ( $^{13}\text{C}/^{12}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N}$ ) in predator tissues reflect those of their prey in a predictable manner (DeNiro & Epstein 1978, Peterson & Fry 1987). While carbon isotope ratios are fairly constant from prey to consumers (Peterson & Fry 1987, Hobson & Welch 1992),  $\delta^{15}\text{N}$  values usually increase by 2 to 4‰ (DeNiro & Epstein 1978, Post 2002). Thus,  $\delta^{15}\text{N}$  measurements mostly serve as indicators of trophic level (Rau et al. 1983, Vanderklift & Ponsard 2003), while  $\delta^{13}\text{C}$  values are used to identify sources of primary production in the trophic network. In particular,  $\delta^{13}\text{C}$  values can serve to define a consumer foraging habitat, e.g. inshore versus offshore, or pelagic versus benthic, with inshore and benthic habitats being enriched in  $^{13}\text{C}$  when compared to offshore or pelagic habitats (Cherel et al. 2007, Hobson 2007). Stable isotope analysis can therefore provide qualitative information on both resource and habitat, 2 components commonly utilized to define ecological niche space. The concept of isotopic niche has indeed emerged as a key tool for ecologists to study ecological niche at a given time, through ontogeny, or intra- and inter-individual degree of specialization in individuals and populations (Newsome et al. 2007). However, prey size and trophic level generally increase with increasing predatory

body length (e.g. Jennings et al. 2002). In addition, baseline isotopic variations (variations of the stable isotope values at the base of the food web; see Graham et al. 2010) can be conserved through several trophic levels (e.g. Ménard et al. 2007). These spatial differences together with differences in body length should, then, be taken into account when comparing isotopic signatures of different species or populations.

In sharks, stable isotope ratios of carbon and nitrogen have already been used to investigate feeding habits, movements (Fisk et al. 2002, Estrada et al. 2003, Kerr et al. 2006), and trophic levels (Rau et al. 1983, McMeans et al. 2009). Diet–tissue discrimination factors (i.e. the difference between the isotopic composition of an animal's tissue and its diet) have been shown to be lower than those reported for teleost fish, i.e. close to 2.3‰ and 0.9‰ for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively, in large sharks such as sand tiger and lemon sharks (Hussey et al. 2010a,b). However, to date, only few studies have used stable isotopes as a tool to investigate the foraging ecology of *Prionace glauca* and *Carcharhinus falciformis*, and these have provided limited data (Rau et al. 1983, Estrada et al. 2003, MacNeil et al. 2005, Revill et al. 2009). In the western Indian Ocean, *P. glauca* and *C. falciformis* constitute the main shark bycatch for industrial pelagic longline and purse seine fisheries, respectively. In addition, both species are intensively exploited by several artisanal fisheries (Sri Lanka, Yemen, and Maldives). However, the reported catches of these artisanal fisheries decreased from 36 290 t in 2000 to 16 350 t in 2009 ([www.fao.org/fishery/statistics/global-capture-production/query/](http://www.fao.org/fishery/statistics/global-capture-production/query/)), demonstrating the recent decline of the Indian populations. Despite the threat to these sharks, the trophic ecology and the foraging habitats of these 2 species are poorly known in this region. In this context, our goal was to examine interspecific, spatial, and size differences in stable isotope values of muscle tissues of these 2 top predators in the western Indian Ocean and thus to define their isotopic niches.

## MATERIALS AND METHODS

### Shark species

The blue shark *Prionace glauca* is an oceanic species found worldwide in temperate and tropical waters. It is the most abundant pelagic shark (Nakano & Stevens 2008). Temporal and geographic patterns of size and sexual dimorphism have been described for this species. Reported full sexual matu-

rity is between 144 and 184 cm fork length (FL), corresponding to ages of 4 to 6 yr old (Stevens 1975, Pratt 1979, Aires-da-Silva 1996). Gravid females in the Indian Ocean have been observed between 2° N and 6° S. Longevity is estimated at 20 to 26 yr, and maximum size is around 308 cm FL (Nakano 1994). The silky shark *Carcharhinus falciformis* is an oceanic warm water species also found over continental shelf areas (Compagno 2001). Individuals spend most of their time in the surface layer (or in the upper 100 m). Newborns with some early juveniles could have demersal habits. Maximum age is estimated to be >20 yr, and maximum size >280 cm FL (Compagno 1984, Bonfil et al. 2005).

### Sample collection

The study was carried out around Madagascar in the southwestern Indian Ocean. Blue and silky sharks were caught in 2009 and 2010 during the northeast (NE) and southwest (SW) monsoons (Table 1). The oceanic circulation in the western Indian Ocean is strongly related to the wind monsoon regime (Schott & McCreary 2001). The NE monsoon extends from December to March corresponding to boreal winter, and the SW monsoon from June to September corresponding to boreal summer. The inter-monsoon May and October were included in the data for the SW monsoon, and April and November in the data for the NE monsoon, according to the dominant direction of the wind regime (Tomczak & Godfrey 1994). Individuals of *Carcharhinus falciformis* and *Prionace glauca* were collected from both research and commercial pelagic longline fishing operations targeting swordfish at night. Sampling was performed west of Madagascar in the Mozambique Channel from 11° 00' S to

13° 54' S, and from 43° 10' E to 49° 04' E, and along the east coast of Madagascar from 15° 34' S to 27° 31' S and from 45° 54' E to 53° 51' E (Fig. 1). West of Madagascar, 17 additional samples were collected in 2010 from silky sharks caught by purse seiners around fish aggregating devices (FADs) during the NE monsoon to detect a possible gear effect (longline

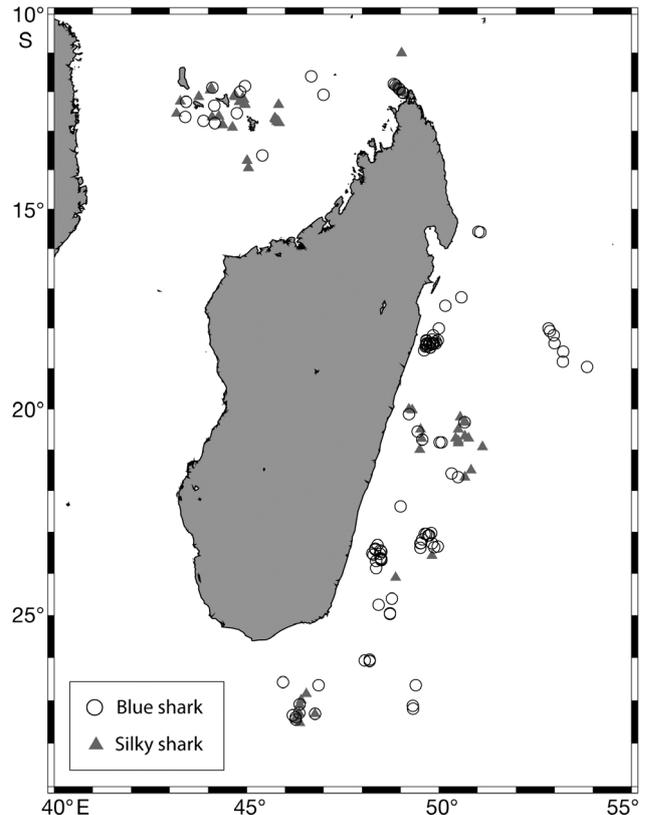


Fig. 1. Locations where muscle tissue was sampled from blue sharks *Prionace glauca* (circles) and silky sharks *Carcharhinus falciformis* (triangles) east and west of Madagascar

Table 1. *Prionace glauca* and *Carcharhinus falciformis*. Sample characteristics with mean  $\pm$  SD of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and C:N ratios of blue and silky sharks. Shark body length was measured as fork length (cm)

Species Zone	Group	Year	n	Body length (m)		Latitude (°S)		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N
				Min	Max	Min	Max			
<b>Blue shark</b>										
Madagascar west	NE monsoon	2008–09	10	165	260	12.55	11.80	$-17.6 \pm 0.6$	$12.7 \pm 0.9$	$2.41 \pm 0.16$
Madagascar west	SW monsoon	2009	8	181	304	13.63	11.61	$-17.7 \pm 0.6$	$12.8 \pm 0.7$	$2.47 \pm 0.12$
Madagascar east	NE monsoon	2009–10	55	130	252	27.45	15.57	$-17.8 \pm 0.5$	$12.1 \pm 0.6$	$2.46 \pm 0.09$
Madagascar east	SW monsoon	2009	48	110	242	27.20	20.13	$-17.8 \pm 0.5$	$12.3 \pm 0.7$	$2.40 \pm 0.12$
<b>Silky shark</b>										
Madagascar West	NE monsoon	2009–10	19	64	197	12.80	11.00	$-16.4 \pm 0.5$	$12.4 \pm 0.5$	$2.66 \pm 0.08$
Madagascar West	SW monsoon	2009	23	76	168	13.95	12.10	$-16.7 \pm 0.3$	$11.3 \pm 0.5$	$2.65 \pm 0.06$
Madagascar East	NE monsoon	2009–10	18	68	148	27.53	23.57	$-16.3 \pm 0.2$	$12.2 \pm 0.4$	$2.66 \pm 0.05$
Madagascar East	SW monsoon	2009	22	81	144	27.67	20.00	$-16.4 \pm 0.3$	$11.8 \pm 0.6$	$2.68 \pm 0.09$

versus purse seine individuals aggregated around FADs) on stable isotope values.

Onboard, all shark individuals caught by longline set were measured in FL to the nearest 0.5 cm. To allow comparisons with other studies, relationships between total length (TL) and FL were used as follows:  $TL = 1.1436 \times FL + 10.1367$  for blue sharks and  $TL = 1.2060 \times FL + 1.5174$  for silky sharks (Ariz et al. 2007). White muscle samples were collected from the dorsal region in front of the first dorsal fin from freshly caught sharks, and were immediately frozen at  $-20^{\circ}\text{C}$  until further processing. Isotopic analysis was performed on 203 specimens ( $n = 121$  for blue sharks and  $n = 82$  for silky sharks) of various body lengths collected during these cruises (Table 1).

### Sample preparation and analysis

Muscle samples were freeze-dried and ground into a homogeneous powder. Lipids were removed using 4 ml of cyclohexane on powder aliquots of about 0.1 g (Kojadinovic et al. 2008). As the C:N ratio in soft tissues is positively related to their lipid content (Post et al. 2007), the extent of lipid extraction was checked through the C:N mass ratio of the samples. Lipid-extracted samples were dried at  $50^{\circ}\text{C}$  before processing, then 300 to 400  $\mu\text{g}$  of homogenized powder were packed into  $8 \times 5$  mm tin containers. Isotopic ratios were determined by a continuous flow mass spectrometer coupled online to an elemental analyzer. Replicate measurements of internal laboratory standards indicated measurement errors less than 0.15‰ for  $\delta^{13}\text{C}$  and 0.20‰ for  $\delta^{15}\text{N}$ . Triplicate measurements performed on some samples confirmed that analytical reproducibility was very good (0.2‰ maximum variation). Isotopic ratios are expressed in the conventional  $\delta$  notation as parts per thousand (‰) deviations from the international standards: atmospheric nitrogen ( $\text{N}_2$ ) for  $\delta^{15}\text{N}$  and Vienna Pee Dee Belemnite for  $\delta^{13}\text{C}$ :

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000 \quad (1)$$

where  $X$  is  $^{15}\text{N}$  or  $^{13}\text{C}$ , and  $R$  is the corresponding ratio  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$ .

### Statistical analyses

Shark samples were grouped by species, zone, year, and season. Analyses were first conducted for each species. Different statistical models on the  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  data allowed us to test factors of interest (i.e. zone, season, body length), taking into account the

unbalanced sampling scheme. The year factor was investigated for blue sharks only, as data on silky sharks were too unbalanced. In addition, robust regressions were used to test the body length effect. Then we combined data of both species and fitted univariate regression trees to explain the variation of  $\delta^{15}\text{N}$  using several explanatory variables (season, zone, body length, species). This method partitions the dataset into mutually exclusive groups by growing a tree (repeated binary splitting of the data). All data are represented by a single node at the top of the tree. The tree is then built by repeatedly splitting the data, and each split is defined by a simple rule based on a single explanatory variable. Splits are chosen to maximize the homogeneity of the resulting 2 nodes. Each final group is characterized by mean values of  $\delta^{15}\text{N}$  or  $\delta^{13}\text{C}$ .

## RESULTS

FL ranged from 110 to 304 cm for blue sharks (mean  $\pm$  SD =  $189 \pm 3$  cm) and from 64 to 197 cm (mean  $\pm$  SD =  $111 \pm 27$  cm) for silky sharks (Fig. 2).  $\delta^{13}\text{C}$  values ranged from  $-18.7$  to  $-15.8$ ‰ for blue sharks and from  $-18.0$  to  $-15.7$ ‰ for silky sharks. The 2 shark species were significantly segregated by their carbon isotopic signatures (means  $\pm$  SD of  $-17.8 \pm 0.5$ ‰ versus  $-16.5 \pm 0.4$ ‰ for blue and silky sharks, respectively,  $p < 0.001$ ; Fig. 3). The  $\delta^{15}\text{N}$  values ranged from 10.9 to 14.4‰ for blue sharks and from 10.5 to 13.2‰ for silky sharks, and differed significantly ( $12.3 \pm 0.7$ ‰ versus  $11.9 \pm 0.7$ ‰ between blue and silky

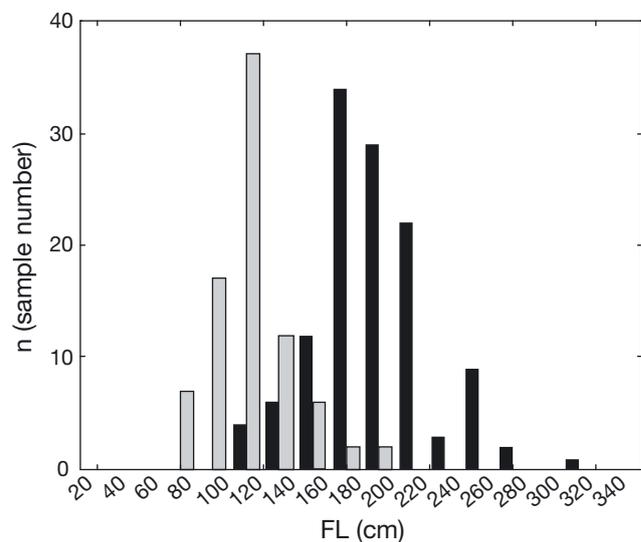


Fig. 2. *Prionace glauca* and *Carcharhinus falciformis*. Distribution of the fork length (FL, cm) of blue sharks (black bars) and silky sharks (grey bars)

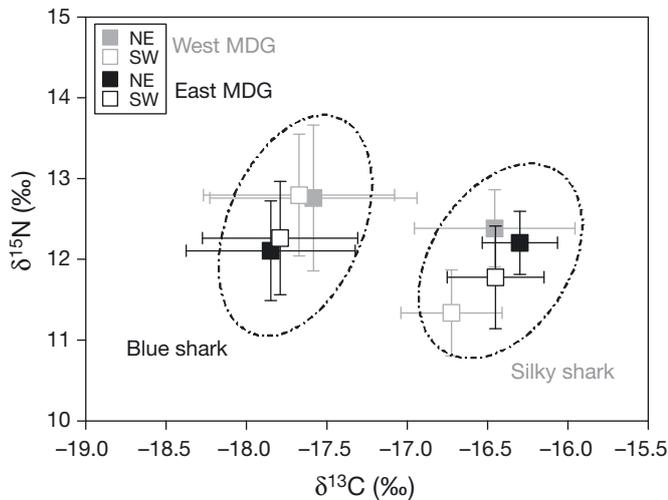


Fig. 3. *Prionace glauca* and *Carcharhinus falciformis*. Mean  $\pm$  SD seasonal  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for muscle samples of blue sharks and silky sharks west (grey symbols) and east (black symbols) of Madagascar (MDG). Open symbols correspond to the southwest monsoon and filled symbols to the northeast monsoon

sharks, respectively,  $p < 0.01$ ). The year effect on  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data of blue sharks collected east of Madagascar during the NE season was not significant ( $p > 0.05$ ).  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  data of both species were consequently grouped by season (NE and SW monsoons) and by zone (west and east of Madagascar), independent of the sampling year (Table 1, Fig. 3)

### Blue shark

The body length effect was significant for both  $\delta^{13}\text{C}$  ( $p < 0.002$ ,  $R^2 = 0.08$ ) and  $\delta^{15}\text{N}$  ( $p < 0.001$ ,  $R^2 = 0.1$ ) values (Fig. 4). However, both estimated slopes were low, 0.0069 (SE = 0.0018) for  $\delta^{15}\text{N}$  and 0.0044 (SE = 0.0014) for  $\delta^{13}\text{C}$ , indicating small increases of isotopic values as size increased (Fig. 4). The linear predicted isotopic differences between small (150 cm) and large (300 cm) blue sharks were approximately 1‰ for  $\delta^{15}\text{N}$  and 0.7‰ for  $\delta^{13}\text{C}$ . Season and zone were never selected as additional explanatory variables once shark size was included in the models. However, for the  $\delta^{15}\text{N}$  model, the p value ( $p = 0.075$ ) of the zone effect was close to 5%, showing a systematically slightly higher value (around 0.6‰) west of Madagascar (Fig. 3).

### Silky shark

Size was never significant (robust linear regressions,  $p > 0.05$  for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  data) for the silky shark. The more parsimonious linear model for  $\delta^{15}\text{N}$  selected the interaction between season and zone as the only significant covariate ( $p < 0.05$ ,  $R^2 = 0.37$ ). The difference between NE and SW monsoons was about 1‰ (12.4 versus 11.3‰, respectively) west of Madagascar, and less than 0.5‰ (12.2 versus 11.8‰, respectively) east of Madagascar (Fig. 3). For  $\delta^{13}\text{C}$  data, both season and zone were significant factors, but the

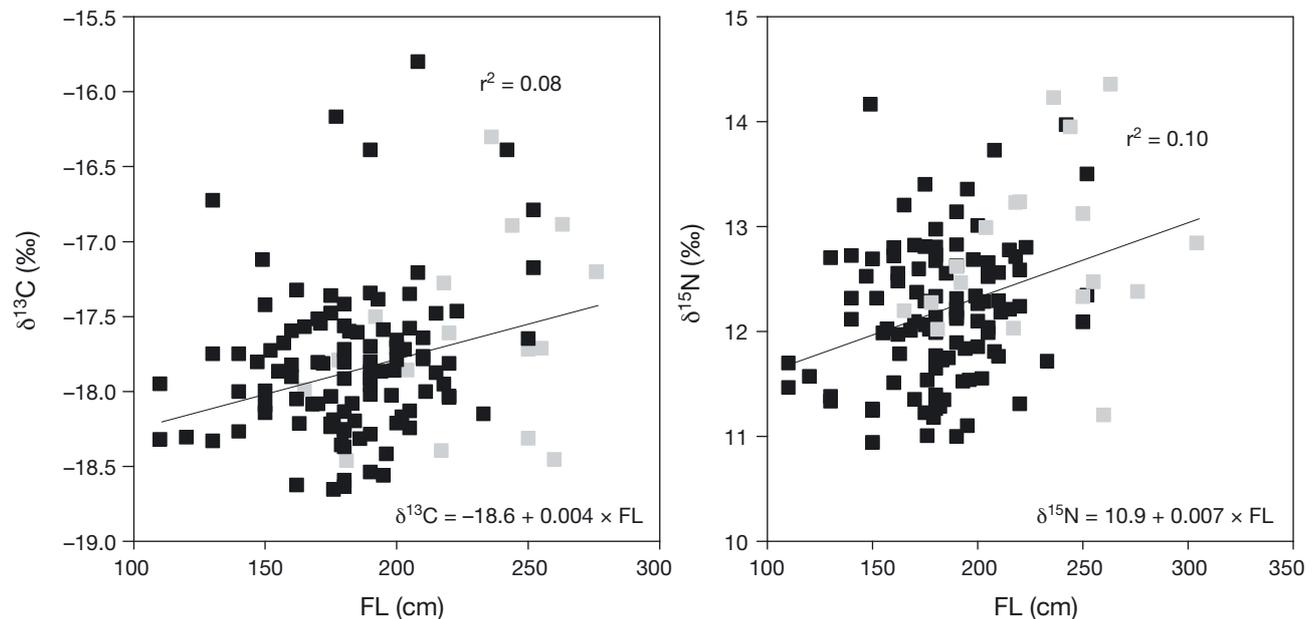


Fig. 4. *Prionace glauca*. Relationship between  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values and body length (fork length, FL, in cm) for blue sharks. Individuals were sampled east (black squares) and west (grey squares) of Madagascar

model did not select their interaction as a significant variable ( $p > 0.05$ ,  $R^2 = 0.15$ ). West of Madagascar,  $\delta^{13}\text{C}$  predicted values were always lower by 0.2‰ compared to the east coast, independent of the season. The same difference was observed between NE and SW monsoons, independent of the sampling zone.

West of Madagascar, 17 additional samples were collected in 2010 from silky sharks caught by purse seiners on FADs during the NE monsoon. We therefore tested a gear effect between individuals caught by pelagic longline ( $n = 19$ ) and aggregated individuals on FADs caught by purse seine ( $n = 17$ ) in that zone and for that season. A significant difference in  $\delta^{15}\text{N}$  values was observed between silky sharks caught by longliners and purse seiners west of Madagascar (medians of 12.5 and 10.3‰, respectively; i.e. a 2.1‰ difference between the 2 medians). The gear effect was highly significant for  $\delta^{15}\text{N}$  ( $p < 0.0001$ ), with higher  $\delta^{15}\text{N}$  values for individuals caught by pelagic longline (Fig. 5) compared to aggregated individuals on FADs, and not significant for  $\delta^{13}\text{C}$  ( $p = 0.10$ , data not shown). As size ranges differed between longline individuals (median = 109 cm FL) and purse seine individuals (median = 64 cm FL), we also compared  $\delta^{15}\text{N}$  values for the same size class (<90 cm), and found that a significant 2.0‰ nitrogen difference remained between the 2 fishing gears.

### Global analyses of both species

Fig. 6 displays both regression trees fitted to  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively. For  $\delta^{15}\text{N}$ , 6 groups were

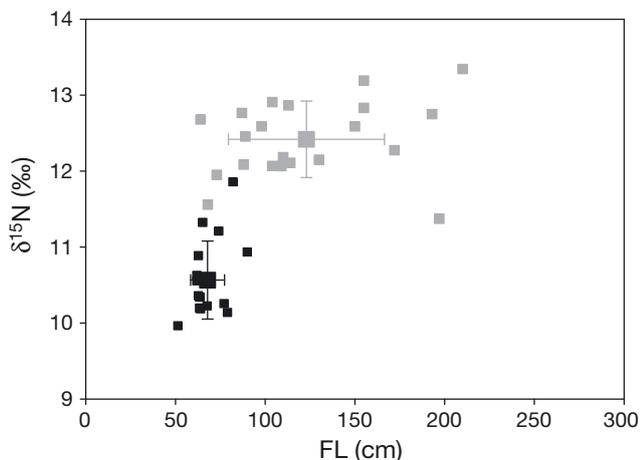


Fig. 5. *Carcharhinus falciformis*. Muscle  $\delta^{15}\text{N}$  values versus fork length (FL, cm) for silky sharks collected in 2010 west of Madagascar during the northeast monsoon by purse seiners (black squares,  $n = 17$ ) and longliners (grey squares,  $n = 19$ ). Means  $\pm$  SD are also shown (enlarged squares with error bars)

selected by the model. Size was the most important variable explaining the different splitting, followed by season and zone. Three groups clustered individuals of the same species (*Carcharhinus falciformis* or *Prionace glauca*). The 3 extra groups combined individuals from both species, but each group was dominated either by *C. falciformis* or by *P. glauca* (4, 2 and 11 misclassified individuals of 25, 32 and 91 individuals, respectively; Fig. 6). Therefore, species and size were mainly surrogate covariates for species in the regression tree based on the  $\delta^{15}\text{N}$  values. The regression tree fitted to the  $\delta^{13}\text{C}$  data fully segregated the 2 species. Three groups were selected, 1 grouping all silky sharks and the 2 others grouping 2 size classes of blue sharks.

## DISCUSSION

Our results showed that body length, season, and zone effects were relatively small for both blue and silky sharks. Stable isotope signatures enabled us to identify differences in trophic ecology and foraging habitats of the two species, but additional information would be needed to provide information on the underlying ecological processes that could determine these patterns. Here, we examine some hypotheses supported by our results, taking into account the sampling scheme.

### Size effect

The body length effect was significant for both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values for blue sharks only, although the relation was weak. In marine ecosystems, predator–prey relationships are often related to body length (Scharf et al. 2000, Ménard et al. 2007, Costa 2009). Large blue sharks can predate both small and large prey items, while small blue sharks most likely feed on small prey only. Mouth-gape size limitation is usually the main cause supporting this hypothesis (Tricas 1979, Scharf et al. 2000). The increase in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values for a doubling of the blue shark body length is not equivalent to 1 trophic level change. Predicted rates between small and large blue sharks are below recent diet–tissue discrimination factors estimated for lipid-extracted muscle of sharks (2.3‰ and 0.9‰ for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , respectively; Hussey et al. 2010a). Large blue sharks, which can feed on a large prey size spectrum, most likely have a larger dietary niche breadth than small blue sharks (Costa 2009), although Markaida & Sosa-Nishizaki (2010)

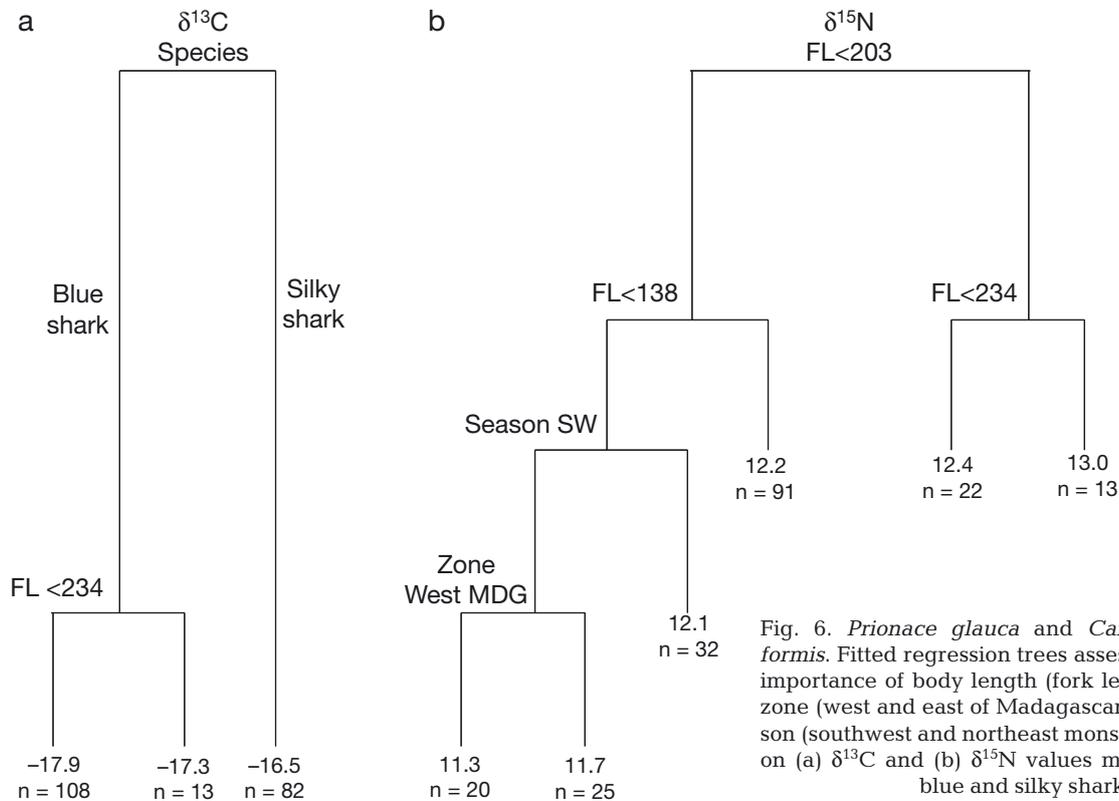


Fig. 6. *Prionace glauca* and *Carcharhinus falciformis*. Fitted regression trees assessing the relative importance of body length (fork length, FL, in cm), zone (west and east of Madagascar, MDG) and season (southwest and northeast monsoon, SW and NE) on (a)  $\delta^{13}\text{C}$  and (b)  $\delta^{15}\text{N}$  values measured on both blue and silky sharks

reported no clear difference in diet among various sizes of blue sharks in Baja California (total length ranging from 64 to 240 cm), which supports the small increase in both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values with size in our study. Conversely, isotopic patterns did not provide evidence of any dietary change with increasing silky shark body length. However, these results need to be confirmed as (1) we sampled a very low number of adult silky sharks in this study, and (2) stomach content analyses have not yet been carried out to investigate blue and silky sharks in the western Indian Ocean.

#### Gear effect for silky sharks

A 2.0‰  $\delta^{15}\text{N}$  difference was observed between silky shark individuals of the same size class (<90 cm) caught by 2 different fishing gears (purse seiners versus longliners). These 2 fishing gears catch sharks in different pelagic trophic habitats. Indeed, FAD-associated catches of purse seiners generate bycatch of juvenile silky sharks trapped in the very upper surface waters (Filmlalter et al. 2011). Conversely, longliners targeting large pelagic fish capture incidentally 'free' silky shark individuals, at depths up to 100 m. Two hypotheses can therefore

support our results. First, the lower  $\delta^{15}\text{N}$  values for aggregated juvenile silky sharks caught by purse seiners on FADs could reflect a lower trophic level due to possible detrimental effects of FADs on food quality, according to the ecological trap hypothesis (Marsac et al. 2000, Hallier & Gaertner 2008). Alternatively, variation in the  $\delta^{15}\text{N}$  values of these sharks may result from different foraging habitats, with silky sharks caught by longliners foraging in other water masses or in deeper water, for example. Prey from deep waters (100 to 200 m) has indeed been proposed to have higher  $\delta^{15}\text{N}$  values than similar prey in surface waters (Graham et al. 2006). Higher  $\delta^{15}\text{N}$  values for silky sharks caught by longliners would then reflect foraging on prey at a similar trophic level but at greater depths compared to juveniles of the silky shark aggregated at the sea surface around FADs. Nevertheless, both trophic level and nitrogen isotopic variations at the base of the food web could act at the same time.

#### Niche partitioning between the two species

$\delta^{13}\text{C}$  values track productivity at relatively small scales within oceanic basins, with higher values in productive nearshore regions, such as upwelling

zones, compared to less productive offshore regions (see Graham et al. 2010).  $\delta^{13}\text{C}$  values of consumers have therefore been previously used to differentiate between inshore ( $^{13}\text{C}$  enriched) versus offshore ( $^{13}\text{C}$  depleted) carbon sources (Cherel & Hobson 2007). Muscle  $\delta^{13}\text{C}$  values of blue and silky sharks were very well discriminated by the regression tree (Fig. 6), with significantly higher  $\delta^{13}\text{C}$  values for silky sharks compared to blue sharks regardless of season or zone (average difference of 1.3‰), which suggests that these species were exploiting different sources of dietary carbon. Using carbon isotopic values as a proxy for inshore versus offshore foraging habitat, lower  $\delta^{13}\text{C}$  values of blue sharks would correspond to foraging in more oceanic regions, while silky sharks would feed more inshore. The blue shark is a typical pelagic species (Compagno 1984, Casey 1985, Brooks et al. 2005) and mostly feeds in offshore waters on teleost fishes and cephalopods (Vaske-Júnior et al. 2009), even if some seasonal inshore migrations and subsequent feeding have been observed (Markaida & Sosa-Nishizaki 2010). Although essentially pelagic, the silky shark, in contrast to the blue shark, is not restricted to the open ocean (Compagno 1984, Branstetter 1987, Joung et al. 2008); its range also includes shallow waters in inshore areas and waters near the edges of continental shelves and over deepwater reefs (Bonfil et al. 1993). In our study, silky sharks were captured offshore. However, these highly mobile predators have the potential to forage at a great distance from sites where they spend considerable amounts of time (Matich et al. 2011), and their carbon isotope values indeed suggest that they forage at least in part in inshore waters with  $^{13}\text{C}$  enriched values.

Interestingly, the carbon isotope difference we found between blue and silky sharks was also observed in other studies but in different oceans, with silky sharks having higher  $\delta^{13}\text{C}$  values than blue sharks. Blue sharks in the Atlantic Ocean near the coast of Brazil had  $\delta^{13}\text{C}$  values of  $-17.4 \pm 0.5\text{‰}$  (Bugoni et al. 2010) and at Cape Cod and Martha's Vineyard (USA) they had values of  $-16.9 \pm 0.1\text{‰}$  and  $-17.4 \pm 0.2\text{‰}$  (Estrada et al. 2003, MacNeil et al. 2005). In the Pacific Ocean, in oceanic waters off eastern Australia, mean  $\delta^{13}\text{C}$  values of blue sharks were  $-17.2 \pm 0.3\text{‰}$  (Revill et al. 2009), while our mean  $\delta^{13}\text{C}$  value was about  $-17.8 \pm 0.5\text{‰}$  in the western Indian Ocean. For the silky shark, 2  $\delta^{13}\text{C}$  values are available in the Pacific Ocean:  $-15.8\text{‰}$  (Rau et al. 1983) and our mean value of  $-16.4\text{‰}$ . The same pattern of higher  $\delta^{13}\text{C}$  values for silky sharks compared to blue sharks seems to be conserved through

oceans, reinforcing the idea that the 2 species have different foraging habitats.

### Trophic level difference between blue and silky sharks

Stable isotopes of nitrogen provide an important tool to examine relative trophic position (Vanderklift & Ponsard 2003). In the present study,  $\delta^{15}\text{N}$  values were slightly higher for blue sharks than for silky sharks west of Madagascar ( $12.5 \pm 0.7\text{‰}$  versus  $11.9 \pm 0.5\text{‰}$ ). The 2 species occupied the same trophic level because the  $\delta^{15}\text{N}$  difference is less than the 2.3‰ required for detecting 1 trophic level difference in sharks (Hussey et al. 2010a). This tiny difference is mainly explained by body length. A regression tree on  $\delta^{15}\text{N}$  values evidenced that species and size were surrogate factors explaining the splitting at 6 nodes (Fig. 6). Silky sharks sampled in this study were smaller than the blue sharks sampled (Fig. 2). Once the body length effect is removed for blue sharks,  $\delta^{15}\text{N}$  values of both species become very close (around 11.8‰ for a FL of 120 cm). Preferences in prey size and composition could differ between the 2 species, but silky and blue sharks are clearly in the same top predator category.

To summarize, the most important result of our study is the consistent significant  $\delta^{13}\text{C}$  difference between the 2 species due to different foraging habitats (niche partitioning, with silky sharks having a more inshore foraging habitat than blue sharks, i.e.  $\delta^{13}\text{C}$  values were highest for silky sharks). This result provides the basis for developing future satellite tagging programs in order to validate movement and foraging strategies of the species, which is critical for shark protection and management. Secondly, lower muscle  $\delta^{15}\text{N}$  values were observed in juvenile silky sharks caught by purse seiners around FADs compared to individuals caught by longliners. Networks of FADs deployed by the purse seiners could, then, act as an ecological trap for juveniles, with the result that FAD individuals are at lower trophic levels compared to free ones. A caveat of our study is the lack of baseline isotopic data for this region. Stomach content analyses and particulate organic matter (POM) analyses in the southwestern Indian Ocean, together with extra analyses on larger specimens of silky sharks, are needed to confirm or reject our hypotheses.

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