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#### **ORIGINAL ARTICLE**

# New insights on the trophic ecology of blue (*Prionace glauca*) and shortfin make sharks (*Isurus oxyrinchus*) from the oceanic eastern South Pacific

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#### **ABSTRACT**

The blue shark (*Prionace glauca*) and the shortfin mako shark (*Isurus oxyrinchus*) are two large and highly migratory sharks distributed in most oceans. Although they are often caught in the south Pacific Ocean long-line fisheries, their trophic ecology is poorly understood. Stable isotopes with Bayesian mixing and dependence concentration models were performed to determine the diet and trophic differences between the two species in the South-eastern Pacific Ocean. According to the mixing models, fishes are the most important prey of these sharks. Dolphin calves and remains were found in the stomachs of both species, which represents a novel finding in trophic ecology of South Pacific sharks. Intra-specific differences were found in *P. glauca*, but not in specimens of *I. oxyrinchus*. The two sharks showed a high degree of diet overlap (73%), primarily over mackerel and dolphin carcasses. Our results indicate that blue and shortfin mako sharks have a generalist feeding strategy in the eastern Pacific Ocean, with a strong preference for teleost fishes and also for dolphin carcasses. Therefore, trophic studies are useful to understand energy flow through the food web, and the trophic position of key species.

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### Introduction

Changes in ecological interactions and abundances of marine species require understanding of the trophic connections and similarities among species. Trophic ecology studies not only deal with the diet composition of a given organism, but also provide important information on the structure of the food web (Baum & Worm 2009; Hussey et al. 2012; Preti et al. 2012). This is especially apparent in predators at the top of trophic networks, such as some shark species (Grubbs et al. 2016; Roff et al. 2016). Indeed, the removal of predators resulting from human activities, such as fisheries and habitat destruction, has been suggested as a substantial factor in the disruption of population size in sharks (e.g. Stevens et al. 2000;

Friedlander & DeMartini 2002; Myers & Worm 2003; Hutchings & Reynolds 2004; Polovina et al. 2009; Clarke et al. 2013).

The blue shark (*Prionace glauca*) and shortfin mako shark (*Isurus oxyrinchus*) are commonly caught in the pelagic longline and driftnet fisheries, particularly by countries with high-seas fleets (e.g. Watson et al. 2004; Pauly et al. 2005; Gilman et al. 2007; Nakano & Stevens 2009; Stevens 2009). Due to heavy fishing pressure around the world, the populations of both species have declined, as evidenced by reports of decreasing catch rates (e.g. North Atlantic Ocean) (Cortés 2013). However, these catch levels could be underestimated because of illegal and unreported

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catches of pelagic sharks, which have been captured due to the high economic value attained by their fins (Clarke et al. 2013). In Chile, both species are taken as by-catch from the swordfish fisheries, where they constitute up to 70% of the total catch, and their fins are sold in Asian markets, where they are in high demand (Acuña et al. 2001; Hernández et al. 2008, 2009).

Given that the removal of large predators has the potential to disrupt ecosystem function, by causing top-down cascade effects (Dobson & Frid 2009), knowledge of the trophic ecology of sharks is crucial for both species to help preserve pelagic ecosystem functioning and for the species' conservation themselves. The combination of data from long-term monitoring programmes with new methodologies to study animal trophic ecology and its interactions is an effective tool to develop modern management approaches. The analysis of natural biological tracers such as stable isotopes is a robust way to trace energy flow through food webs. This approach is based on the fact that stable isotope ratios of carbon ( $^{13}\text{C}/^{12}\text{C} = \delta^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}/^{14}\text{N} = \delta^{15}\text{N}$ ) in predator tissues reflect those of their prey in a predictable way (Cabana & Rasmussen 1996; Post 2002; Hussey et al. 2014). Carbon isotope ratios ( $\delta^{13}$ C) stay relatively constant from prey to consumers, whereas  $\delta^{15}N$  values commonly increase by 2 to 4‰ (Post 2002; Hussey et al. 2012). Hence, the  $\delta^{15}N$  value mostly indicates trophic position (Post 2002; Hussey et al. 2012), while the  $\delta^{13}$ C values reveal foraging habitats and movements of consumers and prev (e.g. Cabana & Rasmussen 1996; Domi et al. 2005; MacNeil et al. 2005; Kerr et al. 2006; Hussey et al. 2012). The stable isotope approach can complement and expand on common means of stomach content analyses since both techniques are required to observe diet shifts (Harvey et al. 2002). Isotopic mixing models can assess the relative contribution of each potential prey to the diet based on the stable isotopic values of the consumers and their potential prey (Jackson et al. 2009; Hussey et al. 2012).

There are few reports on blue shark and shortfin mako diets from the South-eastern Pacific Ocean, even though these sharks are the most abundant bycatch species in the Chilean long-line fisheries (López et al. 2009, 2010, 2012). In northern Pacific and Atlantic Ocean waters, trophic studies of the blue shark and shortfin make based on stomach contents show that both sharks feed on tuna, squid and small teleost fishes (e.g. McCord & Campana 2003; Vetter et al. 2008; López et al. 2009, 2010, 2012; Markaida & Sosa-Nishizaki 2010). However, these results can be biased by opportunistic feeding by the predator and differing

rates of digestion of each prey. It is often necessary to analyse great numbers of stomachs across different seasons of the year, fishing areas and size-classes to have a general understanding of the feeding habits and diet of predators.

Here, our aim was to analyse the diet and feeding habits of P. glauca and I. oxyrinchus in the open ocean of the South-eastern Pacific using a combined analysis of stable isotope and stomach content data, which allows for the estimation of the contribution of those prey types using Bayesian isotope models.

#### **Materials and methods**

# Field and laboratory work

Individuals of blue shark (n = 69) and make shark (n = 69)98) were collected as by-catch of the long-line swordfish commercial fisheries between 23°-33°S and 77°-83°W from January 2013 to November 2013. Onboard, muscular tissues from the dorsal part of the animal and stomachs were removed and frozen at  $-20^{\circ}$ C.

In order to elucidate the stomach contents (SCA), prey items were sorted, counted (N), weighed (W), and identified to the lowest possible taxonomic level. Tissue samples of fresh prey (i.e. low digestive stages and almost intact) were frozen for further analysis, whereas for stable isotope analysis (SIA),  $\sim$  1 mg of tissues from predators and their prey were dissected and washed with milli-Q water. Due to the high lipid and urea content in sharks, the former was removed using a solution of chloroform:methanol (2:1) and shaking it for 30 minutes (Hussey et al. 2010). Tissues were then rinsed with milli-Q water and dried in an oven (40°C) for 12 hours. Tissue samples were ground with an agate mortar; small amounts of this tissue powder (~ 0.5 mg) were placed in pre-weighed tin capsules and stored in a desiccator. The isotope composition was analysed at the Laboratorio de Análisis Isotópico, Universidad Andrés Bello, Viña del Mar, using a Eurovector elemental analyser coupled with a continuous flow (CF) 'Nu-Instruments' isotope ratio mass spectrometer. Stable isotope ratios were reported in the  $\delta$  notation as the deviation from standards (atmospheric N for  $\delta^{15}N$  and Pee Dee Belemnite for  $\delta^{13}$ C); therefore,  $\delta^{13}$ C or  $\delta^{15}$ N = [(R<sub>sample</sub>/R<sub>standard</sub>)- $1] \times 10^3$ , where R is  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ , respectively. Typical precision of the analyses was  $\pm 0.5\%$  for  $\delta^{15}N$ and  $\pm 0.2\%$  for  $\delta^{13}$ C.

# Isotopic mixing model analysis

The analysis of isotope data was performed with the package MixSIAR in R (Stock & Semmens 2013). The dietary habits of the predators were fitted using a Bayesian mixing model based upon a Gaussian likelihood, with a Dirichlet-distributed mixture prior to obtain the means of the organisms. Additionally, we incorporated concentration dependence models [%N: %C] to obtain the probability of prey consumption by predators. Also, the following equation allowed us to use the stomach content values as prior information in the form of % of importance called PSIRI (Brown et al. 2012), which is a standardization of IRI:

$$PSIRI = \%FO \times (\%PN + \%PW)/2$$

where %FO is the percentage of the frequency of occurrence. %PN and %PW are number and weight corrected by FO. PSIRI was expressed on a percent basis, such that %PSIRI for a specific food category i (PSIRIi) becomes:

$$\%PSIRIi = 100\%PSIRIi/\sum PSIRIi$$

The R package 'SIBER' (Stable Isotope Bayesian Ellipses) was used to study dietary overlap (Layman et al. 2007; Jackson et al. 2011; Parnell et al. 2012). According to Bustamante & Bennett (2013), each shark was assigned to one of three size groups: for blue sharks, small  $(\leq 170 \text{ cm}; n = 12), \text{ medium } (>170 \text{ cm and } \leq 195; n = 100)$ 25) and large (>195 cm; n = 32); and for shortfin mako sharks, small ( $\leq$ 180 cm; n = 42), medium (>180 cm and  $\leq$ 285; n = 27) and large (>285 cm; n =29). Following Fry (2013), prey species were grouped

into major categories; for instance, the category 'squid' was Dosidicus gigas + Todarodes filippovae (Table I). Following Quinn & Keough (2002), a oneway permutational multivariate analysis of variance (PERMANOVA) was used to detect trophic overlap. and one-way ANOVA was used to infer changes in  $\delta^{15}N$  and  $\delta^{13}C$  between both sharks (Clarke & Warwick 2001). All statistical analyses were performed with R statistical software (R Development Core Team 2013).

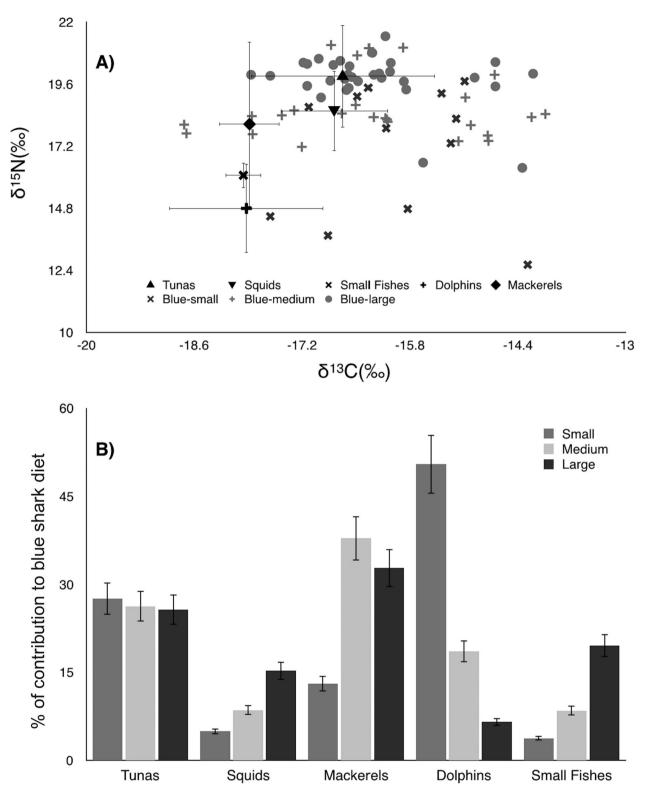
### Results

 $\delta^{15}$ N and  $\delta^{13}$ C mean values were similar between blue and shortfin make sharks (i.e. -16.0%  $\delta^{13}$ C and 19.0% $\delta^{15}$ N; Table I). In particular,  $\delta^{15}$ N values varied among sizes in both sharks (F = 16.2, P < 0.01 for blue shark; F = 23.6, P < 0.01 for make), large sharks had a higher mean value of nitrogen than small/medium sized ones. In contrast, there were no statistical differences among  $\delta^{13}$ C values of the species studied (F = 0.37, P = 0.68 for blue shark; F = 0.92, P = 0.39 for make). The isotopic values for all species are summarized in Table I. The small blue sharks had mean  $\delta^{13}$ C values of  $-16.0 \pm 1.0\%$ , and mean  $\delta^{15}N$  values of 17.1  $\pm$ 2.5% (Figure 1A). Meanwhile the medium size of P. glauca showed values of  $\delta^{13}$ C and  $\delta^{15}$ N in a range of  $-16.2 \pm 1.3\%$  and  $18.7 \pm 1.2$ , respectively, whereas large specimens of this shark had mean values of

Table I. Stable isotopes values for predators and prey species/groups used in the mixing model analysis for the eastern South Pacific.

			δ <sup>13</sup> C			$\delta^{15}N$		
Major group	Species	Mean	SD	%C	Mean	SD	%N	n
Predators								
	Prionace glauca	-16.2	1.1	_	18.9	1.7	_	69
	Isurus oxyrinchus	-16.8	1.5	_	19	1.4	_	98
Prey								
Tuna	Auxis thazard	-17.5	_	_	19.3	_	_	1
	Gasterochisma melampus	-15.9	0.5	_	14.8	2.2	_	3
	Katsuwonus pelamis	-16.5	1	_	19.8	1	_	6
	Lepidocibyum flavobruneum	-17.3	1.3	_	20.1	1	_	16
	Ruvettus pretiosus	-15.6	0.6	_	22.3	0.7	_	5
	Thunnus alalunga	-18.1	0.8	_	18.9	0.3	_	2
	Thunnus albacares	-16.7	0.7	_	20	1.9	_	8
	Thunnus obesus	-15.8	0.9	_	19.4	1.3	_	6
Tuna summary	_	<b>-16.7</b>	1.2	19.5	19.9	2	2.1	47
Squid	Dosidicus gigas	-16.7	0.7	_	18.7	1.4	_	20
·	Histioteuthis sp.	-16.8	0.7	_	18.2	1.9	_	18
	Todarodes filippovae	-16.8	0.7	_	18.3	1.4	_	28
Squid summary	_	<b>-16.8</b>	0.7	15.5	18.6	1.5	5.7	66
Mackerel	Trachurus murphyi	-17.7	0.4	_	18.4	1.6	_	6
	Scomber japonicus	-18.2	0.3	_	13.8	2.6	_	6
Mackerel summary	_	-18	0.4	22.1	16.1	3.2	4.9	12
Marine mammals	Tursiops truncatus	<b>–17.9</b>	2.4	16.2	14.8	3.7	6.6	5
Small fishes	Scomberesox saurus	-18	0.4	_	18.9	1.3	_	11
	Cubiceps pauciradiatus	-17.8	0.7	_	17.3	1.9	_	37
Small fishes summary		<b>-17.9</b>	0.2	20	18.1	0.5	6	48
Total individuals analysed								345

SD = standard deviation, n = number of specimens sampled.



**Figure 1.** (A) Biplot of  $\delta^{15}N$  and  $\delta^{13}C$  values (mean  $\pm$  SD) and (B) diet proportion inferred from mixing models for blue sharks in the eastern South Pacific waters.

 $\delta^{13}C$   $-16.3\pm0.9\%$  and  $\delta^{15}N$   $19.8\pm1.0\%$ . Small short-fin make sharks had mean values of  $\delta^{13}C$   $-17.1\pm1.8$  and  $\delta^{15}N$   $18.8\pm1.5\%$ , the medium size values of

 $\delta^{13}C$   $-16.6\pm1.4$  and  $\delta^{15}N$   $18.0\pm0.9\%$  and large specimens had mean values of  $\delta^{13}C$   $-16.7\pm0.9$  and  $\delta^{15}N$   $20.2\pm0.8\%$  (Figure 2A).

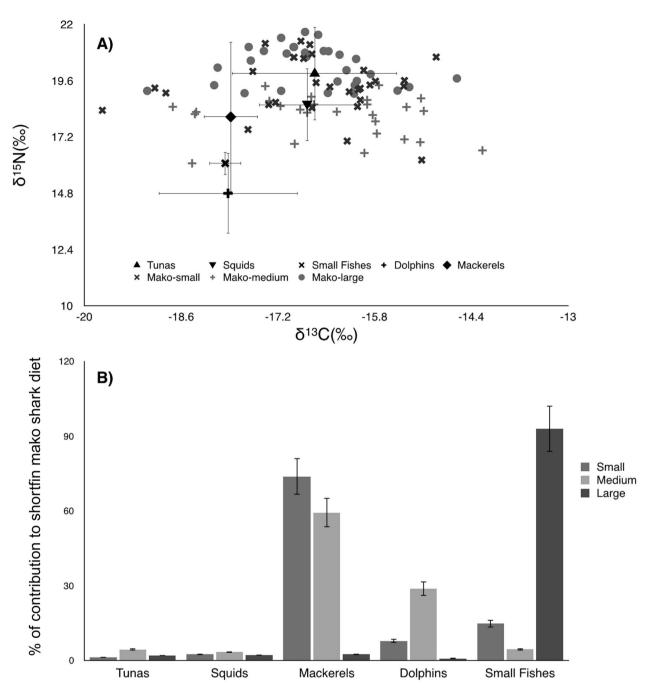


Figure 2. (A) Biplot of  $\delta^{15}N$  and  $\delta^{13}C$  values (mean  $\pm$  SD) and (B) diet proportion inferred from mixing models for shortfin make sharks in the eastern South Pacific waters.

# Feeding ecology

A total of 167 stomachs of both species of sharks were examined. The diet of blue and shortfin make sharks was composed mostly of mackerel (26.7% for blue shark and 47.4% for shortfin make). Interestingly, remains and carcasses of the dolphin Tursiops truncatus were found in the stomachs of both species (Figure S1, supplementary material). Dolphins represented 10.2% and 21% of the stomach contents for shortfin mako and blue sharks respectively, representing an

important food item for blue sharks (Table II). When both techniques were combined, MixSIAR model revealed that the stomach contents of blue sharks included mackerel (27.9%), tuna (26.5%) and then dolphin (25.2%), whereas for the diet of shortfin makos, the main items were mackerel (45.2%), small fishes (37.3%) and dolphin (12.4%). Both sharks showed that squids do not exceed 10% of the contribution. In general terms, there were no inter-specific differences, resulting in 73.3% of similarity between

Table II. Diet data for shortfin make and blue shark in the South-eastern Pacific.

	Mako shark						Blue shark							
Prey Group	%N	%FO	%W	PN	PW	PSIRI	%PSIRI	%N	%FO	%W	PN	PW	PSIRI	%PSIRI
Mackerel	36.36	45.16	8.93	0.81	0.20	219.79	47.36	31.25	18.75	22.20	1.67	1.18	26.72	26.72
Dolphin	3.03	3.23	28.47	0.94	8.83	47.44	10.22	10.42	18.75	31.64	0.56	1.69	21.03	21.03
Small fishes	30.30	29.03	2.28	1.04	0.08	48.18	10.38	34.72	43.75	7.54	0.79	0.17	21.13	21.13
Squid	27.27	19.35	4.50	1.41	0.23	57.14	12.31	16.67	12.50	3.08	1.33	0.25	9.87	9.87
Tuna	3.03	3.23	55.83	0.94	17.31	91.56	19.73	6.94	6.25	35.55	1.11	5.69	21.25	21.25
Total	100	100	100			464.11	100	100	100	100			100	100

%N = percentage of number. %FO = percentage of occurrence. %W = percentage of weight. PN = prey-specific abundance. PW = prey-specific weight. PSIRI = standardized importance.

diets, which is confirmed with a non-significant PERMA-NOVA test (F = 15.4; P = 0.421).

# Intra-specific dietary relationships

## Prionace glauca

All size groups of blue sharks were found to scavenge on dolphins of different sizes (Figure S1), with 50.5%  $\pm 0.23$  in small,  $18.6\% \pm 0.15$  in medium and  $6.6\% \pm$ 0.07 in large sharks (Table III). It is interesting how the different groups of sizes differ in the way they use dolphin carcasses. Indeed, small blue sharks appear to scavenge more than those of larger size (Figure 1B). Additionally, small blue sharks exhibited a similar preference for other prey (Table III) when disaggregated by size and thus can be classified as generalists. Mackerels and tunas (Table III) were the primary prey in the diet of medium- and large-sized specimens. No statistical differences were found within the diet of observed sizes. Furthermore, all sizes of blue shark showed a high degree of feeding overlap, with 89.8% and 81.6% of similarity for small/medium and medium/large sizes, respectively. This high overlap was in accordance with the significant PERMANOVA; small vs medium (F = 22.1, P = 0.997), small vs large (F = 29.9, P = 0.999) and medium vs large (F = 62.4, P = 0.492).

#### Isurus oxyrinchus

Small specimens of shortfin make feed mostly on mackerel, with a mean value of  $73.8\% \pm 0.33$  (Figure 2B). Small fishes, such as *Scomberesox saurus* 

and Cubiceps pauciradiatius, were found as secondary prey in the diet with a mean of  $14.7\% \pm 0.22$ . In third place, dolphins appeared with 7.8% ± 0.18. Nevertheless, it is possible that small shortfin makes do not actively prey on dolphins, according to the remains found in the stomachs (Figure S1). Therefore, they were designated as a rare prey item. Individuals of medium size scavenge more frequently on dolphins  $(28.7\% \pm 0.4)$ , contrasting with the rest of the sizes (Table III). However, mackerel were still the preferred prey item with  $59.3\% \pm 0.5$ . Large specimens of shortfin make showed different feeding habits – with respect to small/medium size - with small fishes as the most important prey item with  $92.9\% \pm 0.17$ , reflecting an active feeding on nomeids and sauries. Thus, small and medium size showed a diet overlap of 38.8% of similarity (F = 13.6; P = 0.692). Medium and large size showed a low overlap with 16.8% of similarity and different diet (F = 67.4; P < 0.05). The greatest distinction in diet occurred between small and large individuals with <1% of similarity and highly significant values (F = 11.4; P < 0.01).

# Discussion

The results of the combination of mixing models and stomach contents provide a general and clear view of the diet of sharks. Since prey were studied and identified from stomachs of the sharks, high levels of precision were obtained for our inferences. In fact, some authors recommend performing diet studies with fresh prey and low degree of digestion (<3 hours)

**Table III.** Estimated proportional prey inputs (95%) of shortfin make and blue shark from stable isotope mixing models from the eastern South Pacific.

		Mako ( $n = 98$ )		Blue ( <i>n</i> = 69)				
Prey	Small (n = 42) Mean	Medium (n = 27) Mean	Large ( <i>n</i> = 29) Mean	Small (n = 12) Mean	Medium (n = 25) Mean	Large (n = 32) Mean		
Tuna	1.2 ± 0.04	4.3 ± 0.1	1.9 ± 0.05	27.6 ± 0.19	26.3 ± 0.15	25.7 ± 0.16		
Squid	$2.4 \pm 0.07$	$3.3 \pm 0.1$	$2.1 \pm 0.07$	$5 \pm 0.07$	$8.6 \pm 0.11$	$15.3 \pm 0.16$		
Mackerel	$73.8 \pm 0.33$	$59.3 \pm 0.5$	$2.4 \pm 0.09$	$13.1 \pm 0.16$	$37.9 \pm 0.23$	$32.8 \pm 0.21$		
Marine mammals	$7.8 \pm 0.18$	$28.7 \pm 0.4$	$0.7 \pm 0.04$	$50.5 \pm 0.23$	$18.6 \pm 0.15$	$6.6 \pm 0.07$		
Small fishes	$14.7 \pm 0.22$	$4.4 \pm 0.1$	$92.9 \pm 0.17$	$3.8 \pm 0.06$	$8.5 \pm 0.13$	$19.6 \pm 0.22$		

from stomachs to obtain better resolution of their diet (Caut et al. 2009; Wyatt et al. 2010). Moreover, Phelps et al. (2009) reported that no statistical differences were found in stable isotope signatures among hard structures of prev from stomachs of Micropterus salmoides.

The results of this study provide new data on the diet composition of P. alauca and I. oxvrinchus in the South-eastern Pacific, with marine mammal carcasses as prey. Indeed, the discovery of dolphins inside the stomachs of blue and shortfin make sharks is not new. For instance, in Mediterranean waters, Porsmoguer et al. (2014) found that the short-beaked dolphin Delphinus delphis are prey for shortfin mako sharks, while in South-eastern Pacific waters, López et al. (2012) found small Tursiops truncatus in both blue and shortfin make sharks, and recently, Loor-Andrade et al. (2017) found remains of an unidentified dolphin in these sharks in the central Pacific. However, all of these works reported dolphins in low frequencies and just as a rare prey item.

Thus, this work presents new findings: first, our results showed a higher frequency of this prey in the stomachs when compared with previous reports, especially in blue sharks, where the %FO reached 18.7%, and second, we were able to establish that these sharks are consistent scavengers. Blue sharks exhibited ontogenetic shifts in their scavenger behaviour, feeding largely on dolphin remains (e.g. fins, tails), but also calves. These results raised questions about how these sharks acquired these prey items. Perhaps some juvenile dolphins live briefly or died after birth, which could be supported by the low levels of  $\delta^{15}N$  found in this work. Moreover, these findings may also be attributed to the spontaneous abortion shown by dolphins, which is caused by infectious diseases (Woodhouse & Rennie 1991; O'Brien & Robeck 2012). However, whatever the case, these newborns are left to drift in open waters, making them easy prey for these sharks. Therefore, we hypothesize that sharks of the southern Pacific may choose to scavenge on mammals as a strategy to improve their diet quality and energy intake. In fact, prey with a high content of energy provide sharks with more capacity to synthesize new tissue and major swimming resistance (Wootton 1999).

Shark feeding on fishes - mainly on mackerel and tuna - in this study confirms that they play a key role in the ecosystems of the open sea in the Southeastern Pacific Ocean. This approximation is relevant for the management of open ocean fisheries, given that tuna and mackerel are fishes with a high economic value. In fact, understanding the role of species and trophic interactions in the ecosystem is crucial for a good, sustainable and integrative fishery programme (Brown et al. 2007; Michener & Kaufman 2007; Vetter et al. 2008; Gascuel et al. 2011: Malpica-Cruz et al. 2013: Maya et al. 2016). For instance, previous reports show blue and shortfin mako shark as piscivorous predators, which is supported by our data, confirming this type of feeding behaviour for the South-eastern Pacific Ocean (Cortés 1999; McCord & Campana 2003; Domi et al. 2005; Wood et al. 2009; Markaida & Sosa-Nishizaki 2010; Brunnschweiler et al. 2011; López et al. 2012).

In the California current, Maya et al. (2016) suggested that these sharks presented a low feeding overlap with no ontogenetic differences. One of the possible reasons for this pattern of differential feeding habits may be due to differences in hunting grounds. For example, these shark populations hunt their prey at different depths (Maya et al. 2016). The South-eastern Pacific populations differ from this, exhibiting a high degree of overlap and ontogenetic dietary shifts. Indeed, larger sharks tend to have higher metabolic requirements than smaller ones, and therefore the extent of their habitat may increase as they grow (Kim et al. 2012; Espinoza et al. 2015). In this case, sharks of open waters use a broad range of habitats with access to a multiplicity of prey resources, resulting in an increase in metabolic activity. Some authors reported different reasons for ontogenetic driven shifts in the diet. For instance, Lucifora et al. (2008) inferred that large sharks can feed on large prey. In addition, older and more experienced specimens may be faster and more efficient at capturing bigger prey, which are a more valuable source of energy (Espinoza et al. 2015). The morphology of the cranium and apparatus in elsamobranchs typically changes throughout ontogeny, which is presumed to enhance the ability to exploit a wider range of resources and facilitate access to a more diverse diet (Dean et al. 2007; Lowry et al. 2007). In the South-eastern Pacific region, commercial long-line fisheries are not well studied or are poorly regulated. Many aspects of ecological structure of oceanic communities still remain uncertain, and this is why ecosystem-based fisheries management is needed. Although it is still unclear how the fisheries affect marine populations (Espinoza et al. 2015), shifts in abundances and species composition are expected to have an effect on the trophic structure and function of open ocean food webs. Therefore, trophic studies are useful to understand food webs, trophic positions of key species, and how energy flows through marine



communities, informing fishery managers to attain more sustainable fisheries.

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## **Disclosure statement**

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