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Trophic ecology of the blue shark (*Prionace glauca*) based on stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and stomach content

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*Occupying the upper levels of trophic webs and thus regulating prey at lower levels, sharks play an important role in the trophic structure and energy dynamics of marine ecosystems. In recent years, the removal of these individuals from upper trophic levels as a result of overfishing has negatively affected ecosystems. We analysed the diet of blue sharks (*Prionace glauca*) caught off the west coast of Baja California Sur, Mexico, during the months of February–June in 2001, 2005 and 2006. We employed both stomach content and stable isotope analyses as each method provides distinct yet important information regarding the role of blue sharks in marine food webs, allowing us to estimate the relative contribution of different prey items to this predator's diet. Of the 368 stomachs analysed, 210 contained food (57%) and 158 (43%) were empty. Based on stomach contents and the index of relative importance (IRI), the pelagic red crab (*Pleuroncodes planipes*) was the most important prey, followed by the squids* Gonatus californiensis *(34.1%) and* Ancistrocheirus lesueurii *(10.4%). The mean (±SD) values for $\delta^{15}N$ (16.48 ± 0.94‰) and $\delta^{13}C$ (−18.48 ± 0.63‰) suggest that blue sharks prefer feeding in oceanic waters. The trophic level based on stomach content analysis was 4.05, while that based on the stable isotope analysis was 3.8, making blue sharks top consumers in the marine ecosystem of Baja California Sur, Mexico.*

Keywords: Food habits, sharks, stomach contents, stable isotopes, Mexican Pacific

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INTRODUCTION

The blue shark (*Prionace glauca*) is an oceanic species distributed globally in temperate and tropical waters (Nakano & Stevens, 2008). Worldwide, it is one of the shark species most frequently captured by fisheries, directly and as bycatch (Stevens, 1976). Due to the nature of this particular fishery and this species' distribution, the blue shark is one of the most studied species (Nakano & Stevens, 2008). Its feeding habits are no exception: studies have been conducted off the coasts of Santa Catalina Island, California (Tricas, 1979), and Baja California, Mexico (Markaida & Nishizaki, 2010), as well as in the north-east (Kubodera *et al.*, 2007; Preti *et al.*, 2012) and southern Pacific (Hoyos *et al.*, 1991; Pardo-Gandarillas *et al.*, 2007; López *et al.*, 2010) and in the Atlantic Ocean (Vaske-Junior & Rincón-Filho, 1998; Henderson *et al.*, 2001; McCord & Campana, 2003; Bornatowski & Schwingel, 2008). Based on stomach content analysis (SCA), the previously cited studies found that blue sharks feed on a wide variety of cephalopods and fishes, suggesting opportunistic behaviour.

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Providing taxonomic information on recently consumed prey, SCA offers a window onto the diet of the predator over the short-term. In contrast, stable isotope analysis (SIA) provides insights regarding long-term patterns of trophic interactions (from days to months) (DeNiro & Epstein, 1978; Fry & Parker, 1979; Michener & Schell, 1994; Fry, 2006). The most commonly examined isotopes in trophic studies are $\delta^{13}C$ and $\delta^{15}N$ (Niño-Torres *et al.*, 2006); $\delta^{13}C$ values help identify the carbon source in a trophic web (coastal *vs.* oceanic habitats) as the consumer's isotope ratio is typically similar to that of its diet (DeNiro & Epstein, 1978), while $\delta^{15}N$ values facilitate estimation of the predator's trophic level. If the prey and their corresponding isotopic $\delta^{15}N$ and $\delta^{13}C$ values are known, SIA can be a useful tool for reconstructing diets, characterizing trophic relationships and constructing food webs (Boecklen *et al.*, 2011). Stable isotope analysis has previously been used to examine blue sharks in Mexican waters (Polo-Silva *et al.*, 2012); the authors argue that analysing the stable isotopes in teeth is appropriate for inferring dietary change over a short time period. Polo-Silva *et al.* (2012) found no significant difference in the isotopic signatures of mature and immature females; the opposite was true among males, where significant differences were observed in the isotopic signatures of juvenile and adult males. In the Indian Ocean, Rabehasago *et al.* (2012)

argue that body size is one of the most common sources of intraspecific variation in the *P. glauca* isotopic signature, as large sharks have access to larger prey.

Mixing models have recently been used to estimate the contribution of different prey to a given consumer's diet by assessing the isotope values of the predator and its potential prey species (Phillips & Gregg, 2003; Caut *et al.*, 2008). This combination of methods provides a more detailed description and a more accurate estimation of the relative contribution of different food sources to the diet of a particular predator. In the present study, two complementary techniques (SIA and SCA) were used to describe the trophic ecology of blue sharks off the west coast of Baja California Sur, including information on diet composition and possible variations based on sex and ontogenetic development.

MATERIALS AND METHODS

Samples were obtained from artisanal fisheries at three locations off the west coast of Baja California Sur: Las Barrancas (26°04′N 112°16′W), Punta Belcher (24°15′N 112°05′W), and Punta Lobos (23°25′N 110°15′W) (Figure 1). Sampling was conducted during different years at the three locations: Punta Belcher (February and May 2001), Las Barrancas (May and June 2005) and Punta Lobos (May and June 2006).

Shark captures were made from *pangas* (motorboats) using simple longline fishing lines equipped with a single hook; mackerel (*Scomber japonicus*) and *Auxis* spp. were used as bait. The sex and total length (TL) of each organism were recorded; the stomach was extracted and its contents were fixed in a 10% formaldehyde solution. Muscle tissue from the anterior-dorsal region was recovered, labelled and frozen for isotopic analysis.

Adults (males ≥180 cm TL, females ≥200 cm TL) and juveniles (males <180 cm TL, females <200 cm TL) were identified following Carrera-Fernández *et al.* (2010).

Stomach content analysis

Each prey item was identified to the lowest possible taxonomic level. Back-calculations were used to estimate cephalopod weights (Kubodera *et al.*, 2007). Other species of relative importance in the diet showed a minimal digestion state (e.g. *Pleurocondes planipes*). Diet analysis involved calculating the frequency of occurrence (%FO = number of stomachs containing prey *i*/total number of full stomachs × 100), the percentage of numerical abundance (%N = number of prey *i*/total number of prey × 100), and weight percentage (%W = weight of prey *i*/total weight of prey × 100) (Hyslop, 1980). Once these values were obtained, we calculated the IRI [IRI = (%N + %W)* %FO] (Pinkas *et al.*, 1971), which incorporates the previous indices to evaluate the importance of each item in the species' trophic spectrum (Liao *et al.*, 2001). This index is expressed as a percentage following Cortés (1997).

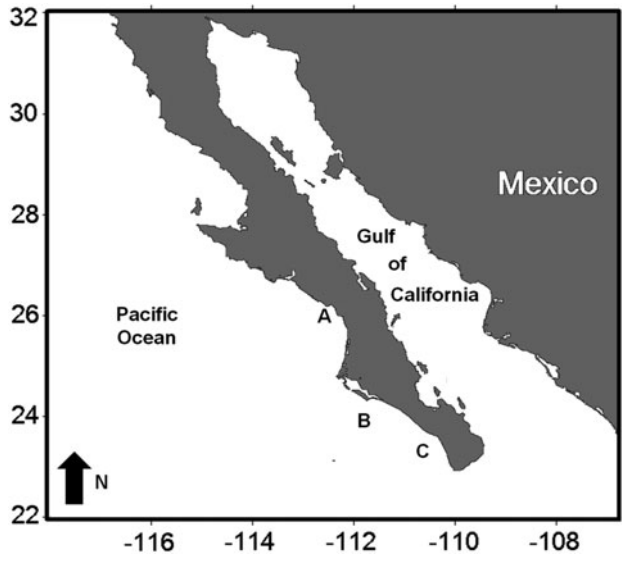

Fig. 1. The study area, the shark fishing zone in Baja California Sur, Mexico: A. Las Barrancas, B. Punta Belcher and C. Punta Lobos.

To determine the diet breadth, Levin's standardized index (Krebs, 1989) was calculated using the following equation:

$$Bi = \frac{1}{n} - 1\left[\left(\frac{1}{\sum pij^2}\right) - 1\right]$$

where Bi = Levin's index, Pij = proportion of prey j in the diet of predator i, and n = number of components in the diet. The values for this index range from 0 to 1. When Bi values are close to zero, the predator is considered a specialist; when Bi values are close to 1, the predator is considered a generalist.

The Morisita-Horn index ($C\lambda$) was used to evaluate diet overlap between sizes (juveniles-adults) and sexes (males-females) (Smith & Zaret, 1982). This index ranges from 0 (completely different diets) to 1 (similar diets). A biologically significant diet overlap occurs when values are over 0.60; meanwhile, values from 0.30 to 0.59 indicate intermediate overlap, and those ranging from 0.1 to 0.29 reflect minimal overlap (Langton, 1982). The Morisita-Horn index is calculated using the following formula:

$$C\lambda = \frac{2\sum_{i=1}^{n}(P_{xi} \times P_{yi})}{(\sum_{i=1}^{n} P_{xi}{}^2 + \sum_{i=1}^{n} P_{yi}{}^2)}$$

where $C\lambda$ is the Morisita–Horn index, P_{xi} is the proportion of the ith prey item of all prey items consumed by predator x, P_{yi} is the proportion of the ith prey item of all prey items consumed by predator y, and n is the total number of prey.

The trophic level based on stomach contents was calculated using Christensen & Pauly's (1992) equation:

$$TL_{sc} = 1 + \sum_{i=1}^{n} DC_{ij} \times TL_j$$

where TL_{sc} is the predator's trophic level, DC_j is the proportion of prey j in the diet, and TL_j is the standardized trophic level of the jth prey. Trophic levels for the different prey species are from Dambacher *et al.* (2010).

Stable isotope analysis

Muscle samples were collected from Punta Belcher (N = 17; February–July 2001; February, April and May 2002), Punta Lobos (N = 3; December 2000 and June 2001) and Las Barrancas (N = 3; July 2002). Twenty-three sharks of different sizes and both sexes were sampled: seven females, 15 males, one unidentified; 15 juveniles, eight adults. The samples were dried at 45°C and 24–27 × 10^{-3} MBAR for

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24 h using a LABCONCO dry freezer; lipid extraction was carried out using a 1:1 chloroform-methanol solution in a Mars X microwave digestion oven at controlled temperature and pressure for 20 min. Dried samples were then homogenized using an agate mortar and pestle; an analytical balance was used to weigh 0.001 g of the homogenized sample, placed in 8 × 5 mL tin capsules. Stable isotope analysis was carried out at the University of California, Davis, USA, using a mass spectrometer (EMRI) (20–20 mass spectrometer, PDZ Europe, Scientific Sandbach, UK).

The $\delta^{15}N$ and $\delta^{13}C$ values were calculated using the following equation:

$$\delta^{15}N \text{ or } \delta^{13}C(‰) = [(R_{sample}/R_{standard}) - 1] \times 1000$$

where R_{sample} is the ratio of $^{15}N/^{14}N$ for $\delta^{15}N$, or the ratio of $^{13}C/^{12}C$ for $\delta^{13}C$. The standards used for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were Pee Dee Belemnite limestone (PDB) and atmospheric nitrogen (AIR), respectively.

Isotope values for the blue shark's main prey were also included in the analysis. These values are from studies carried out in the same area (Velasco-Tarelo, 2005; Richert, 2007; Ochoa-Díaz, 2009).

We calculated the relative trophic level (TL_p) based on isotope values was using the following equation proposed by Post (2002):

$$TL_p = \lambda + \frac{\delta^{15}N_{secondary\ consumer} - \delta^{15}N_{base}}{\Delta n}$$

where λ is the trophic position of the prey used as $\delta^{15}N_{base}$, and Δn is the enrichment in $\delta^{15}N$ per trophic level. In this case, we assumed an isotopic enrichment of 3.7‰ for ^{15}N, following Kim *et al.* (2012). The organism used as $\delta^{15}N_{base}$ should be an abundant prey species that shares the same habitat as the predator and integrates the isotopic signature of the food web at a time scale large enough to minimize the effects of short-term variation (Post, 2002). *P. planipes* ($\delta^{15}N$ = 9.3‰; value obtained from Dambacher *et al.*, 2010) was used as $\delta^{15}N_{base}$ as this prey meets the criteria proposed by Post (2002).

Mixing model

To determine the contribution of each prey item to the predator's diet, we compared the $\delta^{13}C$ and $\delta^{15}N$ values of the predator and its prey using the SISUS program's mixing model (http://statacumen.com/sisus) (Erhardt, 2009). This routine is based on a Bayesian approximation, determining the probabilistic distributions of the proportion each prey (source) contributes to the predator's diet (mix). These distributions range from 1 to 99%. To eliminate the effect of the metabolic fractionation that occurs from one trophic level to the next, we employed the isotopic fractionation value proposed by Kim *et al.* (2012): 3.7‰ enrichment in $\delta^{15}N$ values. The prey taxa chosen (*Argonauta* spp., N = 3; *Pleuroncodes planipes*, N = 1; *Gonatus californicus*, N = 1; *Scomber japoncus*, N = 1; *Ancistrocheirus lesueurii*, N = 1; *Dosidicus gigas*, N = 1) for incorporation into the mixing model were the most important prey in the predator's diet based on the IRI (primary and secondary prey).

RESULTS

Stomach content analysis (SCA)

A total of 368 blue shark samples were collected from three fishing locations off the west coast of Baja California Sur; the vast majority (314) was obtained from Punta Belcher, while 37 were obtained from Punta Lobos and 17 from Las Barrancas. Of the 368 blue sharks analysed, 225 were juvenile males, 36 were adult males, 86 were juvenile females and 21 were adult females (Table 1). The minimum and maximum TL recorded were 99 and 269 cm, respectively. Of the 368 stomachs analysed, 57% (N = 210) contained food.

A total of 27 different prey items were identified: 13 cephalopods, eight fish, three crustaceans, one bird, one macroalga and one chondrichthyan (Table 2). In total, 736 prey items were recorded: the pelagic red crab *P. planipes* constituted 52.0% of all prey by number, followed by the cephalopods California armhook squid *Gonatus californiensis* (11.4%) and *Argonauta* spp. (8.9%). The prey items that made up most of the biomass were *G. californiensis* (36.7%), the sharpear enope squid *Ancistrocheirus lesueurii* (22.4%), and the seven-arm octopus *Haliphron atlanticus* (18.0%), which together accounted for nearly 80% of the biomass found in stomachs. The total biomass of the recorded prey items was 92,760.86 g. The items most frequently encountered in stomachs were *P. planipes* (24.3%), *G. californiensis* (22.9%), *Argonauta* spp. (17.6%) and *A. lesueurii* (11.9%).

Based on the IRI, the three most important items in the diet were: *P. planipes* (IRI = 40.0%), *G. californiensis* (IRI = 34.1%) and *A. lesueurii* (IRI = 10.4%). The species identified as secondary prey include *Argonauta* spp. (IRI = 5.1%), *H. atlanticus* (IRI = 4.5%) and *Dosidicus gigas* (IRI = 1.6%) (Figure 2).

Table 1. Number of blue shark stomachs analysed by location, month, sex and stage of sexual maturity. Juveniles (J), Adult (A).

	Punta Belcher 2001				Las Barrancas 2005				Punta Lobos 2006			
	Male		Female		Male		Female		Male		Female	
Month	J	A	J	A	J	A	J	A	J	A	J	A
February	34	11	22	4								
March	55	2	17	5								
April	43	7	14	4								
May	61	5	26	4	3	1	2		8	3	1	1
June					8	1	2		13	6	2	3
Total	193	25	79	17	11	2	4		21	9	3	4

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Table 2. Diet of the blue shark *Prionace glauca* caught off the western coast of Baja California Sur, Mexico, in percentage values by number (N), weight (W), frequency of occurrence (FO) and Index of Relative Importance (IRI).

Prey item			%FO	%N	%W	%IRI
CEPHALOPODA	ANCISTROCHEIRIDAE	*Ancistrocheirus lesueurii*	11.9	5.8	22.4	10.4
	ALLOPOSIDAE	*Haliphron atlanticus*	6.7	3.7	18.0	4.5
	CRANCHIIDAE	*Liocranchia reinhardti*	1.0	0.4	0.3	0.0
	GONATIDAE	*Gonatus californiensis*	22.9	11.4	36.7	34.1
	HISTIOTEUTHIDAE	*Histioteuthis dofleini*	6.2	1.8	1.5	0.6
	OMMASTREPHIDAE	*Dosidicus gigas*	5.2	1.9	7.9	1.6
	ONYCHOTEUTHIDAE	*Onychoteuthis banksii*	1.9	0.8	0.7	0.1
	PHOLIDOTEUTHIDAE	*Pholidoteuthis boschmai*	3.3	1.2	0.4	0.2
	THYSANOTEUTHIDAE	*Thysanoteuthis rhombus*	0.5	0.1	5.5	0.1
	VAMPYROMORPHA	*Vampyroteuthis infernalis*	1.9	0.5	0.0	0.0
		Rest of cephalopoda	10.5	3.0	3.3	2.0
OCTOPODA	ARGONAUTIDAE	*Argonauta* spp.	17.6	9.0	0.3	5.1
	BOLITAENIDAE	*Japetella heathi*	6.7	2.7	0.0	0.6
OSTEICHTHYES	CARANGIDAE	*Selar crumenophthalmus*	0.5	0.1	0.0	0.0
	SCOMBRIDAE	*Scomber japonicus*	5.2	2.2	0.7	0.5
		Auxis thazard	0.5	0.1	0.0	0.0
	ECHENEIDAE	*Remora remora*	0.5	0.1	0.0	0.0
	TRACHIPTERIDAE	*Zu cristatus*	0.5	0.1	0.0	0.0
	ENGRAULIDAE	*Engraulis* spp.	1.0	0.3	0.0	0.0
	MERLUCCIIDAE	*Merluccius productus*	1.0	0.3	0.0	0.0
		unidentified fishes	1.4	0.4	0.2	0.0
CHONDRICHTHYES	CARCHARHINIDAE	*Prionace glauca*	2.4	0.7	0.8	0.1
BIRDS	CINCLIDAE	*Cinclus mexicanus*	0.5	0.1	0.0	0.0
CRUSTACEA	GALATHEIDAE	*Pleuroncodes planipes*	24.3	52.0	1.2	40.0
	SQUILLIDAE	*Squilla biformis*	0.5	0.1	0.0	0.0
	LOPHOGASTRIDA	LOPHOGASTRIDAE	0.5	0.1	0.0	0.0
ALGAE	LAMINARIALES	*Macrocystis pyrifera*	2.9	0.8	0.0	0.1

The most important prey items in the diet of males and females were similar; the trophic overlap between the sexes was intermediate ($C\lambda$) of 0.35, with the IRI of some prey items varying by sex (Figure 3). The trophic overlap between juveniles and adults was significant ($C\lambda = 0.95$), as the main prey items were consumed in similar proportions (i.e. *Pleuroncodes planipes, Gonatus californiensis* and *Ancistrocheirus lesueurii*) (Figure 3). Levin's index indicated a narrow trophic breadth; therefore, this shark may be categorized as a specialist predator ($Bi = 0.08$).

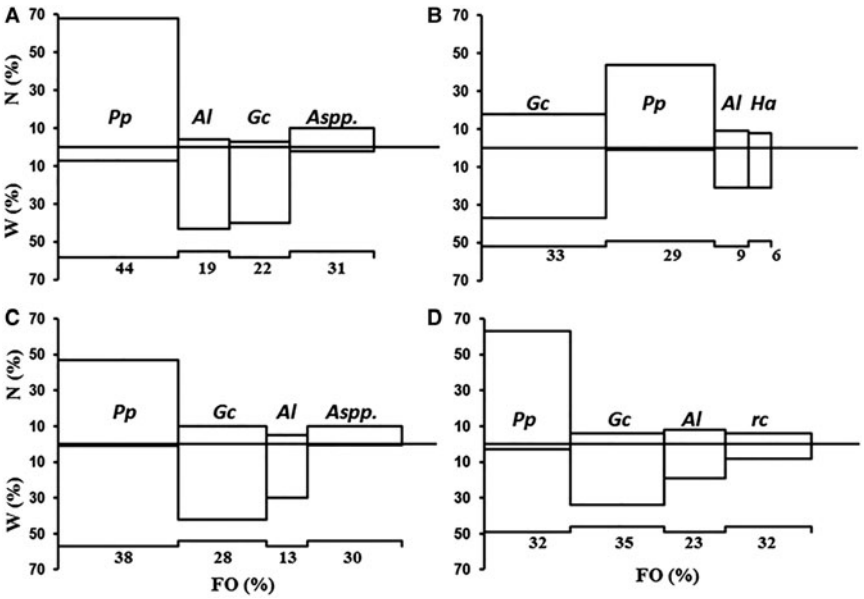

Fig. 2. Variation in the prey species consumed by blue sharks based on the index of relative importance (IRI); (A) females, (B) males, (C) juveniles, (D) adults. Prey items: (Pp) *Pleuroncodes planipes*, (Al) *Ancistrocheirus lesueurii*, (Gc) *Gonatus californiensis*, (Aspp.) *Argonauta* spp., (Ha) *Haliphron atlanticus* and (rc) cephalopod remains.

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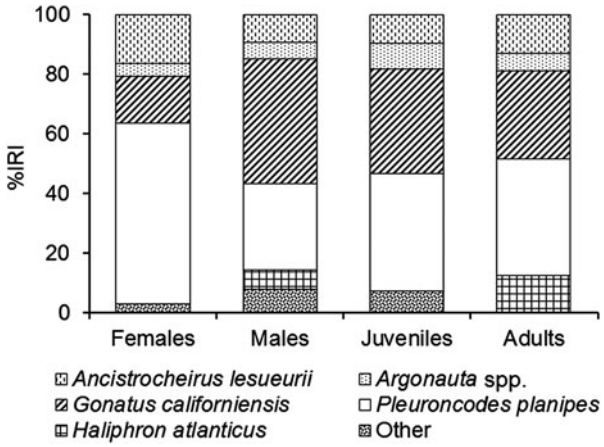

Fig. 3. Percentage of main prey items (IRI >5%) consumed by blue sharks by sex and maturity stage.

Stable isotope analysis (SIA)

Blue shark $\delta^{15}N$ values were normally distributed and ranged from 15.24 to 18.84 ($\mu = 16.48‰ \pm 0.94‰$); while $\delta^{13}C$ values ranged from −19.37 to −17.22‰ ($\mu = -18.48 \pm 0.63‰$) (Figure 4). Similar isotope values were found for males ($\delta^{13}C$ $\mu = -18.66 \pm 0.66‰$, $\delta^{15}N$ $\mu = 16.45 \pm 1.03‰$), females ($\delta^{13}C$ $\mu = -18.27 \pm 0.38‰$, $\delta^{15}N$ $\mu = 16.48 \pm 0.95‰$), juveniles ($\delta^{13}C$ $\mu = -18.60 \pm 0.65‰$; $\delta^{15}N$ $\mu = 16.42 \pm 1.16‰$) and adults ($\delta^{13}C$ $\mu = -18.40 \pm 0.54‰$; $\delta^{15}N$ $\mu = 16.53 \pm 0.49‰$).

The isotopic contribution of different prey items to the diet ranged from 0% to 60%. *Argonauta* spp. made the greatest contribution to the blue shark diet (11–41%; $\delta^{13}C$ $\mu = -19.6‰$; $\delta^{15}N$ $\mu = 15.9‰$), while the contributions of *G. californiensis* (0–26%; $\delta^{13}C = 16.3‰$; $\delta^{15}N = 15.6‰$), *P. planipes* (0–60%; $\delta^{13}C = -19.0‰$; $\delta^{15}N = 12.3‰$), *A. lesueurii* (0–57%; $\delta^{13}C = -18.0$; $\delta^{15}N = 12.7‰$), *D. gigas* (0–34%; 0–29%; $\delta^{13}C = -16.7‰$; $\delta^{15}N = 13.5‰$) and *S. japonicus* (0–29%; $\delta^{13}C = -16.5‰$; $\delta^{15}N = 19.7‰$) were lower and not delimited as they were not present in all stomachs (Figure 5).

Trophic level

The blue shark's trophic level was estimated using both SCA and SIA, obtaining levels of 4.05 and 3.9, respectively. The SIA value (3.9) was obtained using the 3.7‰ $\delta^{15}N$ enrichment factor proposed by Kim *et al.* (2012).

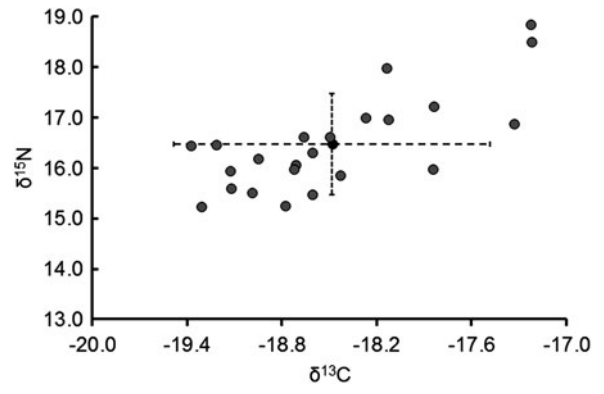

Fig. 4. Distribution of $\delta^{15}N$ and $\delta^{13}C$ values for blue sharks caught in Mexican waters.

DISCUSSION

Both the stable isotope analysis (SIA) and stomach content analysis (SCA) indicated that blue sharks from oceanic waters consumed organisms associated with the pelagic food chain, mainly epipelagic cephalopods; they may also consume mesopelagic and bathypelagic cephalopods. The SIA and SCA provided different types of information regarding the contributions of different prey items to the blue shark diet. The SCA indicated that the pelagic red crab *P. planipes* was the most important prey (IRI = 40%), whereas mixing models based on a probabilistic approach to isotope analysis indicated that the prey item most assimilated by blue sharks was the cephalopod *Argonauta* spp. These contrasting results reflect the variety of possible diet combinations.

Relative to other food components (i.e. cephalopods and fishes), the pelagic red crab *P. planipes* does not provide much energy (Abitia-Cárdenas *et al.*, 1997); however, it represents an abundant and available food source, as reflected by the mass strandings of these organisms off the west coast of the Baja California Peninsula (Aurioles-Gamboa *et al.*, 1994). The feeding strategy of blue sharks is therefore influenced by the abundance of different prey items, as confirmed by the relatively narrow breadth of their trophic niche. This phenomenon has been observed in other sharks, where the dominance of one species in the predator's diet is closely related to the abundance of that species in the ecosystem (Escobar-Sánchez *et al.*, 2006; Blanco-Parra *et al.*, 2011). Blue sharks consumed the most abundant and available prey during winter in the study area, indicating an opportunistic strategy. A greater abundance of squid has been reported at the start of the warm season (Galván-Magaña *et al.*, 2013); blue sharks may take advantage of the abundance of different food items; thus, their trophic behaviour may be related to natural fluctuations in the abundance of potential prey.

Other researchers have characterized blue sharks as teutophagous, due to both the large number of cephalopods they consume and the considerable biomass these prey items represent in this predator's diet (Vaske-Junior & Rincón-Filho, 1998; Henderson *et al.*, 2001; Kubodera *et al.*, 2007). In the present study, cephalopods were an important group in the stomach contents of blue sharks (~10 cephalopod species). They are considered an important food source for large predators in marine environments, including other shark species and billfish (Amaratunga, 1983; Galván-Magaña *et al.*, 2013).

Similar values were observed by category (sex and size) using both methods. SCA indicated that blue sharks of both sexes and of different sizes preyed on the same species: *P. planipes, G. californiensis* and *A. lesueurii*. Although the same food components were recorded for males and females, the proportion of each prey item consumed varied by sex (IRI). This translated to moderate trophic overlap as females fed mostly on the crustacean *P. planipes*, while males preferred the squid *G. californiensis*. Sex and size segregation has been suggested for elasmobranchs (Blanco-Parra *et al.*, 2011); however, the blue sharks sampled in this study were caught in the same area. Thus, we argue that the presence of the same prey items in the diet of both sexes and in individuals of different sizes may be associated with prey abundance.

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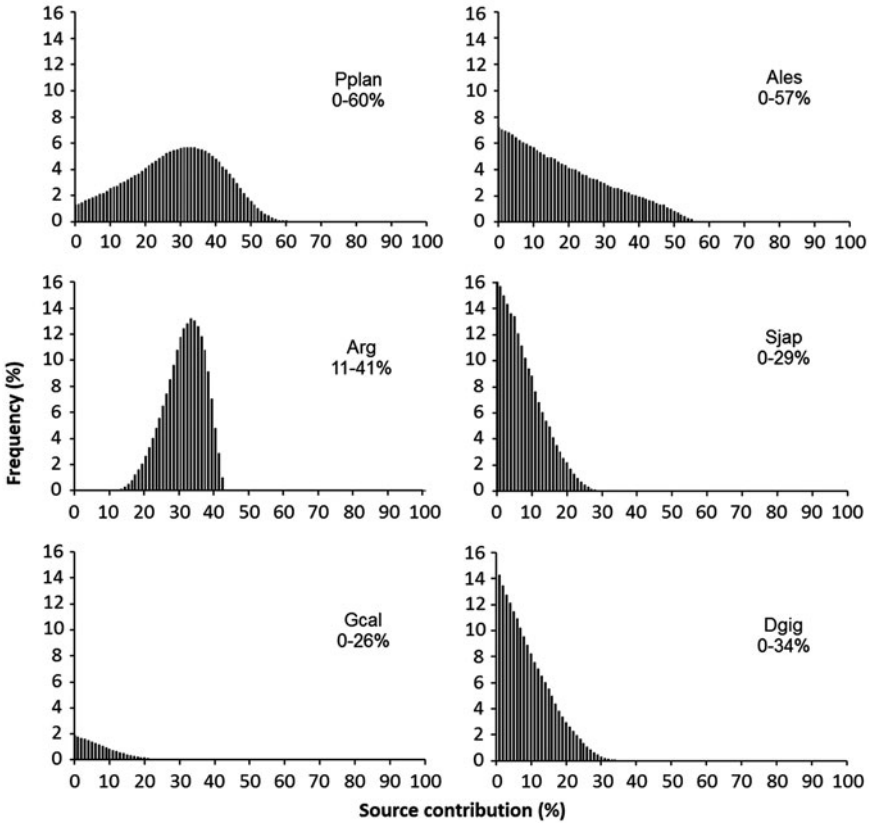

Fig. 5. Contributions of six food sources to the *Prionace glauca* diet based on the results of the mixing models, showing the per cent of each food source (range: 1–99%): Pplan (*P. planipes*), Ales (*A. lesueurii*), Arg (*Argonauta* spp.), Sjap (*S. japonicus*), Gcal (*G. californiensis*), Dgig (*D. gigas*).

The lack of differences between categories in the isotopic analysis may mean that the same prey items were assimilated. Polo-Silva *et al.* (2012) report that males and females feed on prey with similar isotope values, as reflected in the lack of variation in the SIA. In the present study, some shark categories (e.g. adults) were represented by small sample sizes; therefore, it is difficult to determine the influence of sex or maturity on dietary habits.

The results obtained from the mixing model were variable, likely due to the fact that different prey species from the same area with similar feeding habits tend to have similar isotope values, leading to inconclusive mixing model results (Newsome *et al.*, 2007). However, the mixing model supported the SCA results; the most important prey items identified by the SCA were within the range of viable contributions of each prey identified by the mixing model. Histograms of the distributions of feasible contributions suggest that the cephalopod *Argonauta* spp. should be the prey most assimilated by blue sharks; other prey items did not display a restricted distribution in the mixing model.

The mixing model results were not conclusive due to the probabilistic approach distributions of some blue shark prey species, namely *P. planipes* and *G. californiensis*, the most important prey based on stomach contents. The relatively small contribution by pelagic red crab to blue shark muscle growth was also observed by Kim *et al.* (2012) using isotopic analysis.

The blue shark's trophic levels based on both the SIA ($TL_p = 3.9$, interval 3.6–4.6; using the 3.7‰ enrichment value published by Kim *et al.*, 2012) and the SCA were similar ($TL_{sc} = 4.05$), making blue sharks tertiary consumers. This value is slightly lower than that reported by Froese & Pauly (2015) on the Fishbase website ($TL_{sc} = 4.4$), but close to that reported by Cortés (1999) for the Atlantic Ocean ($TL_{sc} = 4.1$). In the present study, blue sharks also consumed carnivorous prey (squid), but there was a high prevalence of pelagic red crabs, a prey with a low trophic level that may have influenced the overall trophic level. In a study in the Atlantic Ocean, Estrada *et al.* (2003) assigned a trophic level of 3.8 (TL_p) to blue sharks based on stable isotopes (with a range of 3.7–4.0), which is in accordance with the present study in the Mexican Pacific.

SIA has proven particularly useful in the study of animal trophic ecology, trophic interactions, habitat use and movements (Rabehagasoa *et al.*, 2012). The stable isotope composition of an organism depends on its diet; thus, SCA is a useful tool that provides taxon-specific sources for the most important prey, providing the biomass, abundance and frequency of occurrence for each prey item. The importance of both complementary techniques allows the integration of information on the trophic ecology of a particular species, in this case blue sharks. Although a considerable number of samples are necessary to correct for bias and further elucidate variation by category or season.

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