



Trophic ecology of the dusky catshark *Bythaelurus canescens* (Günther, 1878) (Chondrichthyes: Scyliorhinidae) in the southeast Pacific Ocean

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Summary

Feeding and stable isotope analyses for *Bythaelurus canescens* individuals were conducted to describe the diet of *B. canescens* as well as infer their potential prey species in the community. Stomach content analysis and mixing models by ratio isotopes composition were used to infer the food habits and calculate the trophic level of the dusky catshark, *B. canescens*. The results showed siphonophores and cephalopods as the most important food in the diet (67.9 and 20.2%, respectively). Calculated trophic level was 3.9, indicating that *B. canescens* is a meso-predator in the upper continental slope communities off Chile. By mixing models based on isotope data it can be inferred that the probabilities of the consumption cephalopods and siphonophores would be 36.7 and 15.2%, respectively.

Introduction

The dusky-catshark *Bythaelurus canescens* (Günther, 1878) is a deep-sea scyliorhinid shark, endemic to southeastern Pacific waters. Inhabiting the upper continental slope, its geographic range stretches from southern Perú to the southernmost coast of Chile (Compagno et al., 2005), reaching a maximum length of 70 cm and inhabiting depths between 250–700 metres (Compagno, 1984). This species is commonly caught as by-catch in the nylon shrimp trawl fishery in northern and central Chilean coasts and can constitute as much as 20.3% of the total catch (Acuña and Villarroel, 2002; Lamilla et al., 2008; Valenzuela et al., 2008). Despite this, the biology of deep-sea sharks off Chile is poorly known, although recent efforts have been made to study their trophic relationships and reproductive biology (Acuña and Villarroel, 2010; Concha et al., 2010; Hallet and Daley, 2011; Pethybridge et al., 2011).

Many chondrichthyes occupy an important ecological role as top predators in the marine environment, potentially regulating through predation the size and dynamics of prey species populations (Cortés, 1999). Therefore, trophic studies are useful to contribute to ecosystem analyses and consequently infer biological processes and fisheries interactions (Lopez et al., 2010). This in turn can be used to estimate food consumption and biomass of different species, quantify predator-prey relationships, and analyze energy flow between the elements of ecosystems in order to assess the impact of resources in the community structure, which subsequently are used in the integrated management of marine ecosystems (Lopez et al., 2012).

Stomach content analysis is the most widely used method in tropho-dynamics, although it can be biased by opportunistic

feeding and differing digestion rates by the predator of the prey. Often great numbers of stomachs from different seasons of the year, fishing areas, and size classes are necessary to obtain a general overview of the predator diet. The analysis of natural biological tracers, such as the stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), is often employed for trophic ecology studies, constituting a robust approach regularly used to trace energy flow pathways through the food webs (Cabana and Rasmussen, 1996; Post, 2002). The $\delta^{15}\text{N}$ value of a predator when compared with the trophic level of a primary consumer, provides a general and integrated view of the trophic position at which the species feeds, although it does not stipulate specific dietary information (Post, 2002). Meanwhile, the habitat and movements in the water column of predators as well as their prey can be inferred with $\delta^{13}\text{C}$ analysis (Cabana and Rasmussen, 1996; Domi et al., 2005; MacNeil et al., 2005; Kerr et al., 2006). However, stable isotopes analyses alone are not sufficient because without stomach-content analyses of the prey, the study is incomplete. Moreover, poor agreement between stable isotope analysis and stomach-content observations suggests the simultaneous use of both techniques to observe the diets shifts (Harvey et al., 2002). Thus, the purpose of this study was to describe the feeding habits of *B. canescens* in central-southern Chilean waters inferred from stomach contents and stable isotopes.

Materials and methods

A total of 50 individuals of *B. canescens* were collected as by-catch of industrial hake demersal fisheries middle-water long-line at a depth range of 270–550 m, between 35°–42°S and 73°–74°W, during the spring and summer of 2010. Total length was measured on board and the stomach removed and immediately stored in formalin-ethanol solution. Kaehler and Pakhomov (2001) proved that the preservation method is suitable for stable isotope analysis since it does not alter isotopic ratios significantly. Three specimens were sampled for isotopic analyses whereby the muscular body tissues were frozen at -80°C .

Stomach content analyses

The stomachs were analysed at the Laboratorio de Biología Marina, UNAB, Santiago, Chile. Each sample was weighed and its contents extracted. Prey items were identified to the lowest possible taxonomic level, weighed and counted and tissue samples of the most important prey (determined from subsequent data analyses) were stored in ethanol (70%).

Stable isotopes analyses

Tissue samples (1 mg) from *B. canescens* individuals and their prey were dissected and washed with mili-Q water. Samples were later oven-dried (60°C) for 12 h. Due to the high lipid content in the fish tissues, they were removed using a chloroform: methanol (2 : 1) solution and shaken for 30 min (Bligh and Dyer, 1959; Hussey et al., 2010). This procedure was repeated at least three times, until a clear solution was reached. The tissue samples were then rinsed with mili-Q water and oven-dried (40°C) for 12 h and ground with an agate mortar into a fine powder. Small amounts of the tissue powder (0.5 mg) were placed in pre-weighed tin capsules and stored in a desiccator. The isotope composition was analyzed at the School of Biological Sciences, Washington State University, USA using a Euro-vector elemental analyzer coupled to a Micromass Isoprime isotope ratio mass spectrometer. Stable isotope ratios were reported in the δ notation as the deviation from the standard (Pee Dee Belemnite for $\delta^{13}\text{C}$ and atmospheric N for $\delta^{15}\text{N}$), therefore $\delta^{13}\text{C}$ or $\delta^{15}\text{C}$ or $\delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}})-1] \times 10^3$, where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. Typical precision of the analyses was $\pm 0.5\text{‰}$ for $\delta^{15}\text{N}$ and $\pm 0.2\text{‰}$ for $\delta^{13}\text{C}$.

Data analysis

Common indices were used for stomach-content analyses and the percentage of number (%N), frequency of occurrence (%F) and weight (%W) were calculated for major and specific prey categories. The generalised index (GI) was calculated (Assis, 1996): $\text{GI} = (\%N + \%F + \%W)/\sqrt{3}$. Following Cortés (1997), the percent of GI was estimated: $\% \text{GI} = \text{GI}_i / \sum \text{GI} \times 100$. The analysis of isotope data was made with the SIAR package (Stable Isotope Analysis in R) (Parnell et al., 2010; Parnell and Jackson, 2011) using the options of the dietary habits of dusky cat-shark fitted using a Bayesian mixing model based upon a Gaussian likelihood with a mixture 'dirichlet-distributed' prior to obtaining the mean of the organism (predator and prey). In order to achieve the probability of prey consumed by *B. canescens* (400 days), Gaussian likelihood was used for $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ and $\text{TL}_{15\text{N}}$; for the Bayesian model (95% confidence interval) the data was randomized with the 1000 bootstrapping method, followed by a principal component analysis (PCA) and convex hull method of polygon. The trophic level was estimated from two methods: firstly, by the raw $\delta^{15}\text{N}$ values (Post, 2002): $\text{TL}_{15\text{N}} = \text{TL}_{\text{base}} + (\delta^{15}\text{N}_{\text{predator}} - \delta^{15}\text{N}_{\text{base}})/3.4$; and secondly, inferred from stomach-content analyses (Cortés, 1999): $\text{TL} = 1 + (\sum \text{GI}_i \times \text{TL}_i)$, where i was the prey item. According to the scale given by Cortés (1999), the nylon-shrimp *Heterocarpus reedi*, a benthodemersal shrimp distributed off central and northern Chile, has a trophic level (TL_{base}) of 2.52, which was used as the base for $\text{TL}_{15\text{N}}$ estimations. The mean enrichment of $\delta^{15}\text{N}$ per trophic level was assumed to be 3.4 (Post, 2002). On the other hand, the trophic level of prey found in the stomach-content analyses was taken from the scale given by Hobson et al. (1994), Pauly and Christensen (1995) and Pauly et al. (1998). For all analyses, each shark was assigned to one of three groups based on size: Group 1 (G1): ≤ 55 cm total length (TL), Group 2 (G2): >55 and ≤ 65 cm TL, and Group 3 (G3): >65 cm TL. This allowed a comparison between the present study and a previous report by Acuña and Villarroel (2010) on the diet of *B. canescens*. The Mann-Whitney U -test was used to compare differences in diet between size classes of *B. canescens* from both stomach-contents and isotopic analyses.

Table 1

Diet of *Bythaelurus canescens* inferred by stomach content analyses, off Central Chile, spring and summer 2010

Item	%N	%F	%W	GI	%GI
Siphonophora					
<i>Agalma elegans</i>	1.11	2.13	1.11	4.60	0.41
<i>Chelophyes appendiculata</i>	1.11	2.13	5.42	12.39	1.09
<i>Diphyes dispar</i>	5.56	6.38	6.63	52.40	4.61
<i>Muggiea atlantica</i>	5.56	6.38	12.24	76.34	6.72
<i>Lensia</i> sp.	2.22	2.13	2.87	9.15	0.81
<i>Lensia hotspur</i>	2.22	4.26	4.42	21.32	1.88
<i>Lensia hardy</i>	6.67	4.26	3.52	29.53	2.60
<i>Lensia conoidea</i>	3.33	2.13	1.11	7.33	0.65
<i>Rosacea</i> sp.	1.11	2.13	0.93	4.27	0.38
<i>Rosacea plicata</i>	3.33	2.13	0.83	6.83	0.60
<i>Sulculeolaria quadrivalvis</i>	7.78	6.38	15.59	98.79	8.70
<i>Sulculeolaria chumi</i>	5.56	6.38	4.78	44.54	3.92
<i>Siphonophore</i> sp. '1'	1.11	2.13	0.49	3.48	0.31
Siphonophore remains	12.22	23.40	12.58	355.97	31.33
Fishes					
<i>Coelorhynchus fasciatus</i>	8.89	4.26	14.98	69.74	6.14
Macrouridae sp. '1'	1.11	2.13	0.75	3.94	0.35
Gadiformes remains	1.11	2.13	0.09	2.75	0.24
Cephalopods					
<i>Loligo gahi</i>	27.78	14.89	8.01	320.93	28.25
<i>Moroteuthis</i> sp.	1.11	2.13	1.75	5.75	0.51
Ommastrephidae sp. '1'	1.11	2.13	1.89	6.02	0.53
Total	100	100	100	1136.06	100
Siphonophora	58.9	72.3	72.5	117.65	67.92
Cephalopods	30.0	19.1	11.7	35.10	20.27
Fishes	11.1	8.5	15.8	20.46	11.81
Total	100	100	100	173.2	100

%N: percentage of number, %F: percentage of occurrence, %W: percentage of weight, GI: generalized index of food.

Results

Only 37 out of 50 stomachs sampled (74%) contained food. Of these, 10 were in G1 (27%), 16 in G2 (43.2%) and 11 in G3 (29.7%).

The squid, *Loligo gahi*, was the most important prey in the *B. canescens* diet, with 28.3% of GI. In second place was the siphonophore *Sulculeolaria quadrivalvis* with 8.7% of GI, followed by *Muggiea atlantica* and rattail fish *Coelorhynchus fasciatus* (6.7 and 6.1% of GI, respectively). In terms of the major categories of prey (Table 1), the siphonophores were the most important group in the dusky catshark diet with 67.9% of GI, followed by cephalopods and bony fishes (20.2 and 11.8% of GI, respectively). Figure 1 shows that the distribution of prey items was similar among the size groups, with siphonophores being the most important category followed by cephalopods. Indeed, there was no statistical difference in stomach-content composition among the three size groups ($U = 14.6$; $P = 0.73$, Table 2).

The isotopic values for all species (sharks and prey) are summarized in Table 3. The most important prey groups indicated by the isotopic analyses were the octopuses with CI (Bayesian mixing models) = 36.0–37.3%, followed by siphonophores with CI = 14.6–15.8%. The remaining prey items were considered incidental or rare food in the diet (Table 4) and did not exceed 10%. When considering the different size groups, octopus was also the dominant food with CI = 40–42% in G1, CI = 24–25% in G2 and CI = 44–45% in G3. The siphonophores were the second group of food in G1 and G3 with CI = 33–38% and CI = 8.6–9.4%, respectively, while G2 showed squid and gadiform with CI = 21–22% as the secondary food (Table 4). When

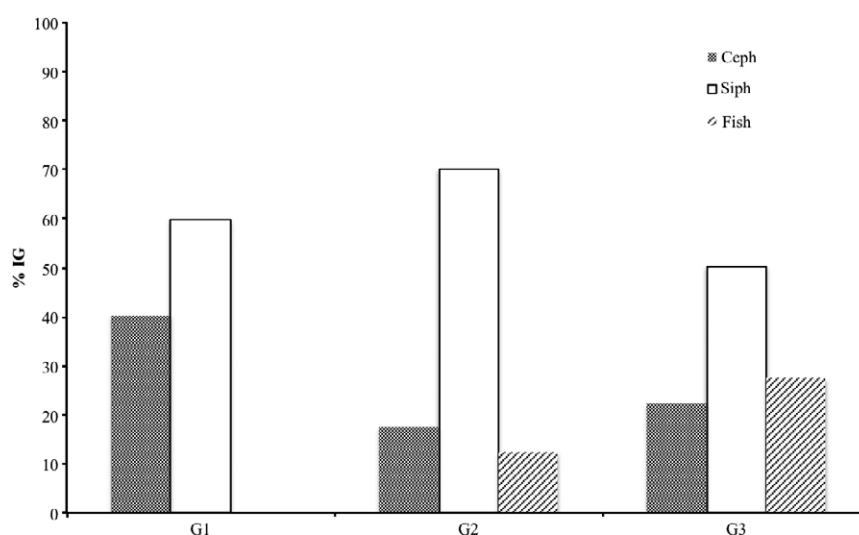


Fig. 1. Main food item variations in *B. canescens* diet corresponding to different size-group classes off central Chile. Ceph: Cephalopods, Siph: Siphonophores and Fish: Fishes. G1 (n = 10), G2 (n = 16) and G3 (n = 11)

Table 2

Mann-Whitney *U*-test values for comparisons among size-class groups of *B. canescens* off Chile, spring and summer 2010. Above the diagonal *p* values and below number of *U*-test. Group 1 (G1): ≤ 55 cm LT, Group 2 (G2): between > 55 and ≤ 65 cm, and Group 3 (G3): > 65 cm

	G1	G2	G3
G1	–	0.8701	0.8686
G2	16	–	0.4307
G3	16	12	–

Table 3

Stable isotopic compositions of dusky catshark *B. canescens* and stomach contents off central Chile, spring and summer 2010 (\pm standard deviations). Within parentheses = number of specimens sampled

Species	Mean $\delta^{13}\text{C}$	Mean $\delta^{15}\text{N}$
Predators	–	–
<i>Bythaelurus canescens</i> (3)	-16.3 ± 1.5	20.6 ± 3.1
Prey	–	–
Squid	–	–
<i>Logigo gahi</i> (5)	-19.0 ± 0.6	13.6 ± 0.7
Octopus	–	–
<i>Benthoctopus</i> sp. (6)	-17.2 ± 1.6	18.0 ± 2.1
Siphonophores (4)	-19.2 ± 0.3	4.0 ± 0.6
Gadiform	–	–
<i>Coelorinchus fasciatus</i> (2)	-15.1 ± 0.4	20.8 ± 1.5
Myctophidae (1)	-15.7	18.0
Crustacea	–	–
<i>Heterocarpus reedi</i> (3)	-16.9 ± 1.1	16.0 ± 0.3

comparing feeding by size, there were no statistical differences ($U = 14$; $P = 0.5693$); therefore the diet among groups was similar.

The trophic levels (TL) calculated from stomach contents were 4.1 and TL_{15N} were 3.9. Figure 3 shows no variations in TL from the stomach content analyses among different sizes, with 3.8, 3.7 and 3.9 in G1, G2 and G3, respectively. Values of TL_{15N} in sizes were 2.9, 4.6 and 4.1 in G1, G2 and G3, respectively, showing a wider variation (Fig. 2a). Although our TL values were higher than those of Acuña and Villarroel (2010) (Fig. 2b), the Mann-Whitney *U*-test revealed no significant differences in diets between the two studies ($U = 23$, $P = 0.3293$). Similarly, there was no difference in the diet inferred from the stomach contents and stable isotope analyses ($U = 18$, $P = 0.4435$).

The PCA results (Fig. 3) showed that the octopus group and siphonophores could be consumed by as much as 36.7 and 15.2%, respectively, by *B. canescens*. The remaining prey appearing in the PCA such as squid, crustacean or Myctophidae could be inferred as incidental food and their capture by the dusky catshark would depend on the environmental availability.

Discussion

B. canescens feeds on a variety of species of siphonophores, whereby none of these prey species reached 10% of GI (Table 1), suggesting that the dusky shark is an opportunistic forager. In fact, some authors have reported opportunistic behaviour in the feeding habits of other deep-sea sharks (Carrason et al., 1992; Ebert et al., 1992; Bergstad et al., 2003). On the other hand, the importance of *L. gahi* and *C. fasciatus* could be attributed to the energetic demand of the predator, since the high energetic value of cephalopods and fishes as prey is well known (Smale, 1996; Halver and Hardy, 2002; Rossano et al., 2005). The Mann-Whitney *U*-test revealed no statistical differences between our results and those of Acuña and Villarroel (2010) for the diet. Despite this, the latter authors reported a high incidence of the benthic Pandalidae crustacean *Heterocarpus reedi* (>45%) compared with there being no occurrence in the present study. This may be due to two reasons: firstly, the different years in which samples were taken, as it is well known that the diet of any predator could change due to variable prey availability as a result of environmental dynamics (Wootton, 1999); the second explanation could be attributed to the sharks eating the nylon shrimp while caught in the nets, thus causing a bias in a posterior analysis.

The $\delta^{13}\text{C}$ values (Table 3) showed that *L. gahi* (-19.0‰) and siphonophores (-19.2‰) are benthic-pelagic, while *H. reedi* (-16.9‰), *Benthoctopus* sp. (-17.2‰), Myctophidae fishes (-15.7‰) *C. fasciatus* (-15.1‰), and *B. canescens* (-14.8‰) are benthic-demersal species. This conclusion is consistent with the known habitats of these species, except for the myctophid fishes, which are indicated as being meso-pelagic species (Wisner, 1974; Acuña and Villarroel, 2010). The results from mixing models (Table 4) provide a general and good view of the *B. canescens* diet in which octopus and siphonophores were probably the most important foods, which is consistent with inferences as to stomach contents. As a result, the dusky shark

Table 4

Mixing models result in 95% likelihood for % GI composition of *B. canescens* diet off central Chile. Values are analogous to GI% values in stomach contents

	General			Group 1			Group 2			Group 3		
	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper	Lower	Mean	Upper
Squid	—	—	—	—	—	—	—	—	—	—	—	—
<i>Logigo gahi</i>	2.3	5.9	9.4	2	2.3	2.7	21	21.5	22	2.9	3.7	4.4
Octopus	—	—	—	—	—	—	—	—	—	—	—	—
<i>Benthoctopus</i> sp.	36.0	36.7	37.3	40	41	42	24	24.5	25	44	44.5	45
Siphonophores	15.8	15.2	14.6	33	35.5	38	1	1.2	1.4	8.6	9	9.4
Gadiform	—	—	—	—	—	—	—	—	—	—	—	—
<i>Coelorinchus fasciatus</i>	7.5	7.8	8.1	0.7	0.8	0.9	21	21.5	22	0.9	1.1	1.3
Myctophidae	7.2	7.5	7.8	0.7	0.8	0.9	20	20.5	21	1	1.2	1.4
Crustacea	—	—	—	—	—	—	—	—	—	—	—	—
<i>Heterocarpus reedi</i>	3.7	4.1	4.6	1.4	1.7	1.9	7.3	8	8.7	2.3	2.9	3.4

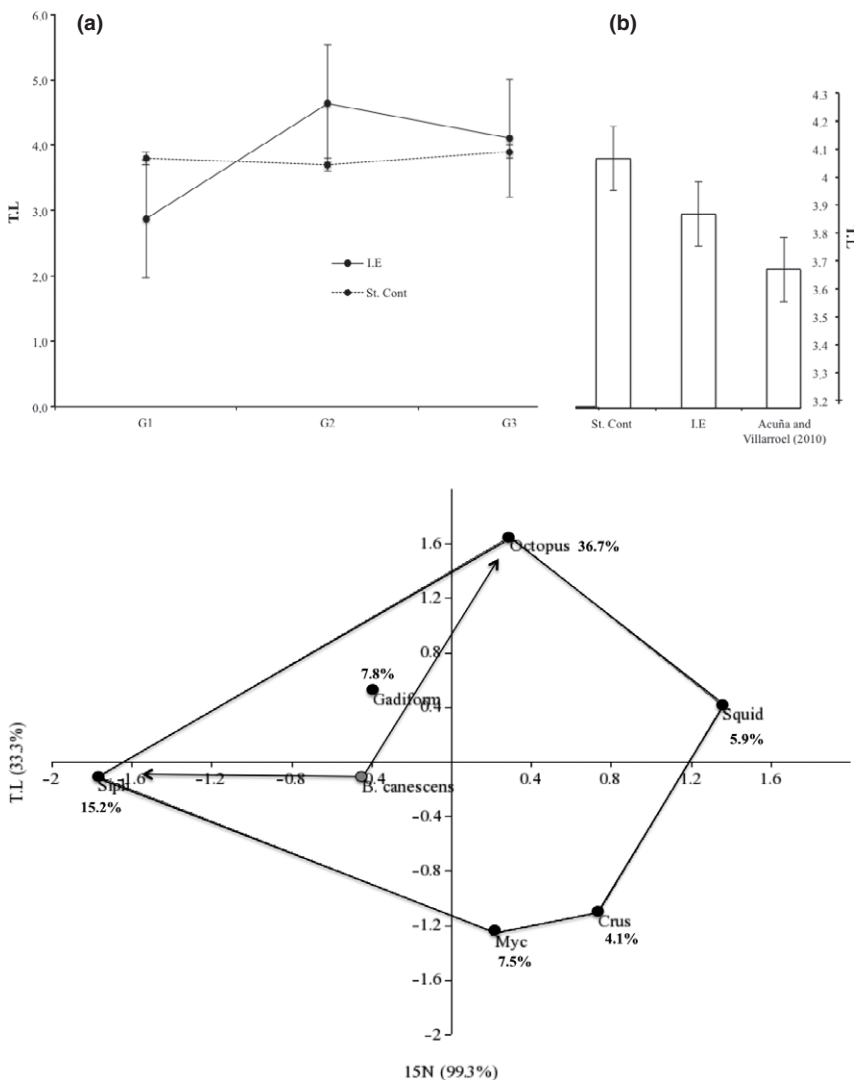


Fig. 2. (a) Trophic levels of different sizes and (b) all sizes of *B. canescens* off central Chile. Panel b also compares data from stomach contents (St. Cont.) and stable isotopes (I.E) in the present study to data from Acuña and Villarroel (2010)

Fig. 3. PCA of potential *B. canescens* prey off central Chile. Percentages in parentheses of axes are the variance. Percentages next to prey are mixed model outputs

B. canescens, could be considered as a generalistic and opportunistic benthic-demersal predator. The occurrence of pelagic and benthic prey could therefore be due to the feeding behaviour exhibited by *B. canescens*. For instance, the sharks could undertake daily vertical migration to search for food, show seasonal feeding variability or reproductive aggregations (Abrams, 2000). This behaviour has been reported in other deep-sea fishes. For example, the southern hake *Merluccius australis*, shows daily vertical migration and sexual aggregations (Lillo et al., 2004).

According to stomach content analyses, the calculated trophic level of *B. canescens* was 4.1, similar to those reported by Cortés (1999) for other Scyliorhinidae sharks such as *Halaehurus hispidus* and *H. natalensis*, both of which have trophic levels of 4.2, corroborating their roles as top predators in the central Chilean deep-sea ecosystem.

No statistical differences were found when comparing the diet among size groups using the stomach content method, showing siphonophores as the most important prey in them all (Fig. 1). Similarly, when using this method there were also no

differences in trophic levels among size groups (Fig. 3), which could be due to the number of stomachs used in each size sample that then produced a bias in the analyses. On the other hand, mixing the model analyses showed differences among size groups (Table 4), with G1 and G3 showing diets dominated by octopus and siphonophores (41 and 35.5%, respectively), in contrast to G2 with a heterogeneous diet including four prey species of up to 20%. In fact, differences in feeding habits among sizes or between sexes could be linked to the reproductive stages of the predator. Lopez et al. (2012) showed feeding changes according to maturity stages of *Prionace glauca* and *Isurus oxyrinchus*, showing several differences in the diet among immature, in maturation, and mature individuals. Unfortunately, the link between sizes and maturity stages for dusky sharks is not known, and thus the changes could be attributed simply to the supply of prey in the environment.

With respect to the possible prey, this is the first approach to infer potential prey for the populations of the *B. canescens* off Chile. The PCA analysis showed two important prey groups, the octopus and siphonophores, consistent with current stomach content analyses, mixing models and the probabilities to show that potential feeding will include octopus and siphonophores at 36.7 and 15.2%, respectively. These values could indicate the high variability of prey abundance in the deep-sea ecosystems. The convex hull polygon showed a wide trophic spectrum, with squids, Myctophidae fishes and crustaceans as incidental foods. Finally, the results reflect *B. canescens* as a meso-predator and opportunistic shark with a heterogeneous feeding strategy in Chilean deep-sea ecosystems and also show the importance of these studies of sharks for fisheries management.

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