



Abstract—The blue shark (*Prionace glauca*) is the most landed shark species in Peruvian shark fisheries, representing 42% of total landings. Despite its importance for fisheries, the ecological role of the blue shark in Peruvian waters remains poorly understood. Therefore, in this study, we aimed to assess the food habits of blue sharks off northern Peru through stomach content analysis. Between February and December of 2015, 143 stomachs were collected and 28 found to be empty. Individuals measured from 110.0 to 299.4 cm in total length. The results indicate that blue sharks have epipelagic and mesobathypelagic feeding habits, preying upon a wide number of prey taxa (42 species) but with a diet dominated by cephalopods, especially *Argonauta* spp. and *Ancistrocheirus lesueurii*. Diets differed by size class and location, suggesting that longitudinal movements are related to increments in body size. In addition, we propose that blue sharks scavenge for food on the basis of finding the cyprid larval stage and juvenile cosmopolitan duck barnacle (*Lepas anatifera*) associated with the prey item ‘unidentified cephalopods.’ The present study contributes new information on the diet of blue sharks.

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Food habits of the blue shark, *Prionace glauca* (Linnaeus, 1758), in waters off northern Peru

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In the southeastern Pacific Ocean, the area off northern Peru is an important area of convergence between temperate (Humboldt Current) and tropical (South Equatorial Current) waters (Spalding et al., 2007). This particular area hosts a diversity of marine species (Chirichigno and Cornejo, 2001), including a large number of sharks (Cornejo et al., 2015). One of these is the blue shark (*Prionace glauca*), which is considered a key cosmopolitan pelagic species that exerts top-down control on community structure (Stevens et al., 2000).

On a global scale, the blue shark is the most landed shark species (as target and nontarget catch) and the major component of the international shark fin trade (Clarke et al., 2006; Nakano and Stevens, 2008). It is also the most landed species by Peruvian shark fisheries, representing 42% of total landings (Gonzalez-Pestana et

al.,¹ 2016). Seventy percent of blue shark landings come from the small-scale longline fishery operating along the coast (Doherty et al., 2014), especially off southern Peru where cold to temperate waters support higher abundances of pelagic sharks (Adams et al., 2016). Likewise, it is one of the most frequently species caught in Peruvian small-scale drift-net shark fisheries (Alfaro-Shigueto et al., 2010). However, despite its importance for fisheries, biological studies describing the ecological role of blue sharks in Peruvian waters are few.

There have been several studies regarding the diet of blue sharks in

¹ Gonzalez-Pestana, A., C. Kouri, and X. Velez-Zuazo. In review. Shark fisheries in the southeast Pacific: a 61-year analysis from Peru. *F1000Research* 3:164. [Available at [website](https://www.f1000research.com/10.1099/f1000research.2014.00164).]

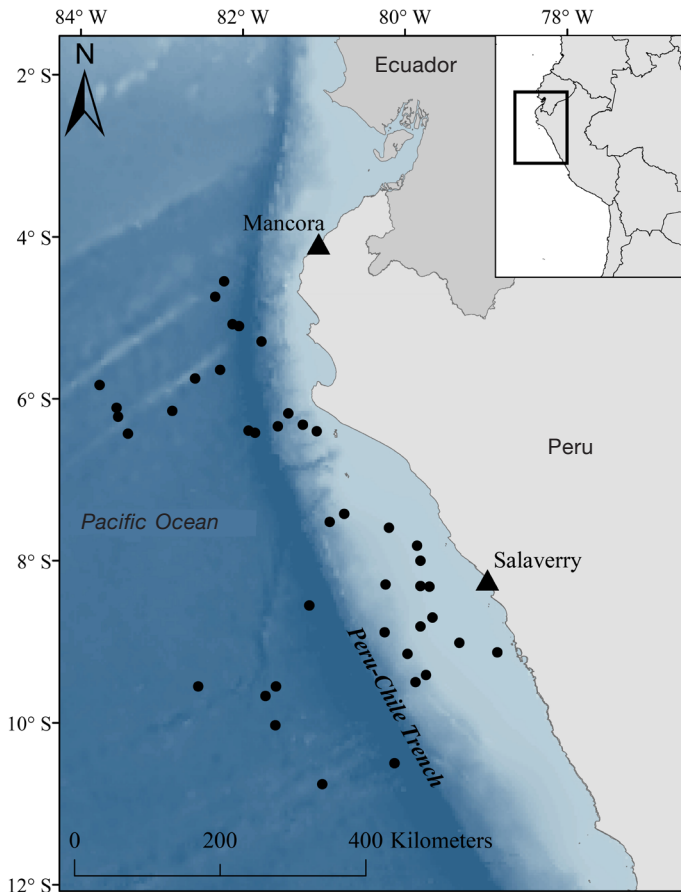


Figure 1

Map of locations where blue sharks (*Prionace glauca*) were collected in northern Peru between February and December 2015. The blue vertical gradient defines the position of the Peru–Chile Trench (with an average distance from shore of 130 km or 70 nautical miles).

the eastern Pacific Ocean. For example, Tricas (1979) and Harvey (1989) reported that blue sharks consume euphausiids (mostly *Thysanoessa spinifera*), small fish (e.g., the northern anchovy, *Engraulis mordax*), and a variety of cephalopods (e.g., Loliginidae and Histioteuthidae). Studies from the Mexican Pacific Ocean have revealed a high consumption of the pelagic red crab (*Pleuroncodes planipes*), as well as a variety of squid, including *Histioteuthis heteropsis*, *Gonatus californiensis*, and *Ancistrocheirus lesueurii* (Markaida and Sosa-Nishizaki, 2010; Hernández-Aguilar et al., 2016). Lóor-Andrade et al. (2017) showed that *A. lesueurii*, *Stigmatoteuthis hoylei*, and the jumbo squid (*Dosidicus gigas*) were the most consumed species off Ecuador. In Chilean waters, prey species included a variety of fishes: mackerels (*Trachurus murphyi* and the Pacific chub mackerel, *Scomber japonicus*) and tunas (*Thunnus* spp.), as well as jumbo squid (Lopez et al., 2010; Klarian et al., 2018).

In Peru, three studies of blue shark diet have revealed that they feed on jumbo squid, Peruvian anchoveta (*Engraulis ringens*), Pacific sardine (*Sardinops*

sagax), Peruvian hake (*Merluccius gayi peruanus*), and eggs from flying fish (Exocoetidae) and Chilean silverside (*Odontesthes regia*) (Hoyos et al., 1991; Elliot et al., 1995, 1996). Although these previous studies provide valuable insights into prey species of blue sharks off the coast of Peru, their results have been limited by sample size, time series, and size classes. Therefore, to determine the ecological role of blue sharks in the Peruvian marine ecosystem, we focused on providing broader information on blue shark food habits off northern Peru by analyzing stomach contents and assessing diet variability by sex, size class, season, and fishing ground.

Materials and methods

Sampling and stomach content analysis

Stomach contents of blue sharks were collected between February and December 2015 by onboard observers during small-scale driftnet and longline fishing trips that landed in Mancora and Salaverry ports in northern Peru (Fig. 1). Sex of each shark was determined and total length (TL) was measured to the nearest centimeter (Bigelow and Schroeder, 1948). Stomachs were extracted and preserved in 10% formalin for analysis (Galván-Magaña et al., 1989). Stomach samples were examined at the Laboratorio de Recursos Hidrobiológicos of the Universidad Nacional Agraria la Molina, where prey items were identified to the lowest possible taxon and weighed (wet weight) to the nearest 0.01 g. Fish items (entire specimens and skeletons) were identified according to Chirichigno and Velez (1998) and Clothier (1950), and fish otoliths were identified according to Rivaton and Bourret (1999) and García-Godos (2001). Cephalopods were identified by examination of beaks (Wolff, 1982, 1984; Clarke, 1986; Xavier and Cherel, 2009). Crustaceans and marine mammals were identified according to Moscoso (2013) and Jefferson et al. (2015), respectively. Reconstruction of cephalopod weights by regression equations was based on measurements of the lower rostral length of cephalopod beaks (Wolff, 1982, 1984; Clarke, 1986; Smale et al., 1993; Xavier and Cherel, 2009), whereas reconstruction of fish weights was based on the relationship of length to weight (Fernández, 1987; IMARPE²) and the relationship of otolith radius to total length (Goicochea and Arrieta, 2008) when possible.

To assess whether the sample size collected was appropriate to describe the diet of blue sharks, we constructed a cumulative prey curve at the family level from the total number of prey species identified, excluding ‘unidentified remains’ (i.e., cephalopod, fish, and crustacean) prey items by using the software Es-

² IMARPE (Instituto del Mar del Peru). 2012. Crucero 1202-04 de “Evaluación hidroacústica de los recursos pelágicos.” Inst. Mar Peru, Inf. Ejec., 49 p. [Available from [website](#).]

estimateS, vers. 9.1.0 (Colwell, 2013). The order of samples was permuted 1000 times to reduce bias. Following the method of Jiménez-Valverde and Hortal (2003), we plotted the results to analyze the suitability of the sample size. When the curve approaches the asymptote (slope < 0.1), the number of samples is deemed to be sufficient to describe the diet (Soberón and Llorente, 1993). Furthermore, we used the calculation method proposed by Bizzarro et al. (2007) to reinforce the sampling assessment. This method states that the slope of the line generated from the curve endpoints (mean cumulative number of prey taxa generated for the final 4 stomach samples) should be compared to a line of 0 slope to establish whether a cumulative prey curve has reached an asymptote. Slopes are compared by using Student's *t*-test, where slopes that are not significant ($P > 0.05$) indicate that the curve has reached an asymptote (Bizzarro et al., 2007).

The relative importance of each prey species to the diet of the blue shark was established by the prey-specific index of relative importance (%PSIRI) (Brown et al., 2012), by using the equation:

$$\%PSIRI = 0.5\%FO_i \times (\%PN_i + \%PW_i), \quad (1)$$

where %FO_{*i*} = the number of stomachs containing prey category *i*, divided by the total number of stomachs *n*;

%PN_{*i*} = prey-specific numeric abundance; and

%PW_{*i*} = prey-specific wet-weight abundance.

Prey-specific abundance (%PA_{*i*}) was calculated by

$$\%PA_i = \sum_{j=1}^n \%A_{ij} n_i^{-1},$$

where %A_{*ij*} = the abundance (by counts [%PN_{*i*}] or weight [%PW_{*i*}]) of prey category *i* in stomach sample *j*; and

n_i = the number of stomachs containing prey *i*.

The %PSIRI, is a modification of the index of relative importance (%IRI [Cortés, 1997]) that avoids %FO redundancies taken in the %IRI and is additive with respect to taxonomic levels. As a result, the %PSIRI of a family will be equal to the sum of the %PSIRI of the species within the taxon (Brown et al., 2012).

Niche breadth was calculated according to Levin's standardized index by using %PSIRI converted to proportions at the family level (Krebs, 1999). The index values ranged between 0 and 1, where values closer to 0 indicate a diet dominated by few prey species (i.e., by a greater degree of specialization) and values closer to 1 indicate a lesser degree of specialization (Munroe et al., 2014). In addition, the graphical analysis proposed by Amundsen et al. (1996) was performed to explore prey importance at the family level and predator feeding strategy. The analysis is based on a 2-dimensional graph representation of prey-specific abundance (%PA_{*i*}) in relation to the frequency of occurrence of the different prey types in the diet (%FO_{*i*}).

Trophic position was calculated based on percent weight values of the prey species identified with the equation proposed by Christensen and Pauly (1992):

$$TP = 1 + \left(\sum_{j=1}^n DC_{ij} \right) \times (TP_j), \quad (2)$$

where DC_{*ij*} = the composition of the prey *j* in the diet of the predator *i*;

TP_{*j*} = to the trophic level of prey *j*; and

n = the number of prey species in the diet of predator *j*.

Values of trophic position for fish prey were obtained from Froese and Pauly³ and Espinoza (2014); and for cephalopod prey from Cortés (1999) and Espinoza (2014).

To identify possible differences in diet, individual sharks were analyzed according to 5 factors: sex, season, size class, latitude of fishing ground, and longitude of fishing ground. The analysis by sex was performed to clarify whether the composition of diets of females and males is related to the reported spatial segregation by sex (Nakano and Stevens, 2008). Specimens analyzed per season were grouped into warm (February–May and December) and cold (June–November) seasons according to established patterns of sea-surface temperatures (SST) (Flores et al., 2013). Cluster analysis was employed with 20-, 30-, and 40-cm-TL intervals to define size classes (Markaida and Sosa-Nishizaki, 2010) by using the numeric abundance (at family levels) of identified preys. Calculations were performed by the unweighted pair-group method with arithmetic mean and by using the Bray–Curtis index as a measure of dissimilarity. A 50% of dissimilarity distance indicated major divisions between size classes (Ebert and Bizzarro, 2007). Fishing grounds based on latitude were grouped into 2 biogeographical marine provinces, where 'northern' corresponds to the Tropical Eastern Pacific marine province and 'Northern–Central' to the Warm Temperate Southeastern Pacific marine province (Spalding et al., 2007). Fishing grounds based on longitude were grouped into 'coastal' and 'oceanic' groups, with the Peru–Chile Trench (which occurs at an average distance from the coast of 130 km or 70 nautical miles) as the boundary between these 2 groups (Macharé et al., 1986) (Fig. 1).

Statistical analysis

To assess differences in the diet of blue sharks by factors, we performed two multivariate techniques: non-metric multidimensional scaling (MDS) ordinations and analysis of similarity (ANOSIM). These techniques were conducted with the Bray–Curtis index of dissimilarity generated from the numeric abundance of each prey grouped by family (Mendoza-Ávila et al., 2016), pretreated by fourth-root transformation and standardized to percentages. The stress value generated by the nonmetric MDS model indicates the reliability of the representation, where values closer to 0 indicate excellent representation and values larger than 0.2 indicate that interpretation of the data is unreliable (Clarke,

³ Froese, R., and D. Pauly (eds.). 2018. FishBase, vers. 02/2018. World Wide Web electronic publication. [Available from [website](http://www.fishbase.org).]

Table 1

Diet composition of blue sharks (*Prionace glauca*), based on analysis of stomach contents collected between February and December 2015 off northern Peru, by percent frequency of occurrence (%FO), percent prey-specific number (%PN), percent number (%N), percent prey-specific weight (%PW), percent weight (%W) and the prey-specific index of relative importance (%PSIRI).

Prey species	%FO	%N	%PN	%W	%PW	%PSIRI
CEPHALOPODA						
Decapodiformes						
Oegopsida	4.35	0.27	6.18	<0.01	<0.01	0.13
Ancistrocheiridae						
<i>Ancistrocheirus lesueurii</i>	14.78	5.07	34.31	7.37	49.86	6.22
Chiroteuthidae						
<i>Chiroteuthis veranyi</i>	3.48	1.45	41.83	0.93	26.85	1.19
<i>Grimalditeuthis bonplandi</i>	11.30	1.88	16.66	<0.01	<0.01	0.94
Cranchiidae						
<i>Galiteuthis pacifica</i>	2.61	1.14	43.63	0.88	33.55	1.01
<i>Leachia danae</i>	4.35	1.06	24.34	0.24	5.42	0.65
Enoploteuthidae						
<i>Abraliopsis affinis</i>	1.74	0.51	29.35	0.28	16.34	0.40
Gonatidae						
<i>Gonatus antarcticus</i>	11.30	4.06	35.90	5.88	51.98	4.97
<i>Gonatus</i> sp.	0.87	0.87	100.00	0.87	100.00	0.87
Histiototeuthidae						
<i>Histiototeuthis cerasina</i>	0.87	0.14	16.67	0.05	6.00	0.10
<i>Stigmatoteuthis hoylei</i>	6.96	2.12	30.44	2.91	41.83	2.51
Mastigoteuthidae						
<i>Mastigoteuthis dentata</i>	2.61	1.53	58.59	0.88	33.64	1.20
Octopoteuthidae						
<i>Octopoteuthis sicula</i>	6.09	1.65	27.15	1.30	21.35	1.48
Ommastrephidae						
<i>Dosidicus gigas</i>	6.09	1.58	26.03	4.03	66.17	2.81
<i>Ommastrephes bartramii</i>	1.74	0.61	35.00	1.22	70.40	0.92
Onychoteuthidae						
<i>Onychoteuthis banksii</i>	4.35	0.89	20.46	0.07	1.72	0.48
Pholidoteuthidae						
<i>Pholidoteuthis massyae</i>	3.48	0.27	7.74	0.11	3.05	0.19
Thysanoteuthidae						
<i>Thysanoteuthis rhombus</i>	12.17	5.53	45.41	6.43	52.79	5.98
Myopsida						
Loliginidae						
<i>Doryteuthis (Amerigo) gahi</i>	2.61	0.49	18.88	1.39	53.43	0.94
Octopodiformes						
Argonautidae						
<i>Argonauta</i> spp.	26.09	17.60	67.46	14.52	55.65	16.06
Bolitaenidae						
<i>Japetella diaphana</i>	7.83	3.61	46.18	3.15	40.21	3.38
<i>Japetella heathi</i>	1.74	0.34	19.64	<0.01	<0.01	0.17
Enteroctopodidae						
<i>Muusoctopus</i> sp.	0.87	0.14	16.67	0.01	0.73	0.08
Octopodidae						
<i>Eledone</i> spp.	0.87	0.05	5.71	<0.01	<0.01	0.02
Tremoctopodidae						
<i>Tremoctopus violaceus</i>	1.74	0.10	5.72	0.01	0.77	0.06
Vitreledonellidae						
<i>Vitreledonella richardi</i>	1.74	0.07	4.26	<0.01	0.00756	0.04
Vampyromorphida						
Vampyroteuthidae						
<i>Vampyroteuthis infernalis</i>	6.96	2.42	34.82	2.96	42.55	2.69
Unidentified cephalopods	33.04	29.57	89.47	33.04	99.98	31.30

Table continued

Table 1 (continued)

Prey species	%FO	%N	%PN	%W	%PW	%PSIRI
TELEOSTEI						
Clupeiformes						
Engraulidae						
<i>Engraulis ringens</i>	2.61	1.12	42.91	1.52	58.43	1.32
Gadiformes						
Macrouridae						
<i>Coryphaenoides</i> sp.	0.87	0.02	2.86	<0.01	<0.01	0.01
Merlucciidae						
<i>Merluccius gayi peruanus</i>	0.87	0.05	6.25	0.56	63.94	0.31
Myctophiformes						
Myctophidae						
<i>Myctophum aurolaternatum</i>	0.87	0.09	10.00	<0.01	0.03	0.04
Perciformes						
Coryphaenidae						
<i>Coryphaena hippurus</i>	1.74	0.43	25.00	1.65	94.84	1.04
Scombridae						
<i>Auxis thazard</i>	0.87	0.08	9.09	0.02	2.87	0.05
Sphyraenidae						
<i>Sphyraena idiaestes</i>	0.87	0.11	12.50	<0.01	<0.01	0.05
Unidentified fishes	22.61	8.71	38.53	3.51	15.51	6.11
MAMMALIA						
Cetacea						
Delphinidae						
<i>Delphinus capensis</i>	0.87	0.29	33.33	0.25	28.61	0.27
CRUSTACEA						
Decapoda						
Galatheidae						
<i>Pleuroncodes monodon</i>	0.87	0.84	97.14	0.81	92.64	0.83
Unidentified crustaceans	5.22	0.70	13.42	<0.01	0.06	0.35
AVES						
Unidentified bird	0.87	0.11	12.50	<0.01	0.31	0.06
EGGS						
Exocoetidae eggs	7.83	2.17	27.76	2.25	28.75	2.21

1993). The R -statistic values from ANOSIM describe the extent of similarity, where $R=0$ refers to an identical diet and $R= \pm 1$ is indicative of the most divergent diet (Clarke, 1993). Similarity percentages (SIMPER) were used, as well, to determine the prey categories, by family, that typified particular groups, or contributed most to the similarities between groups, or both (Clarke, 1993). Finally, the semiparametric permutation multivariate analyses of variance (PERMANOVA) test on the Bray–Curtis index of dissimilarity (based on numeric abundance) was used to test whether an interaction was present between factors that were significant according to the pairwise tests (ANOSIM).

Statistical analyses were conducted with the software RStudio, vers. 1.1.453 (RStudio, 2018) with R, vers. 3.5.0 (R Core Team, 2018). Descriptive statistics are presented with mean standard deviations (SDs).

Results

A total of 143 stomachs of blue sharks were obtained from the ports of Mancora ($n=43$) and Salaverry ($n=100$).

Of these, 115 (80.4%) had food remains and 28 (19.6%) were empty. Of those individuals with food remains, 47 were female (range: 165–293 cm TL; mean: 214 cm TL [SD 35]) and 68 were male (range: 110–288 cm TL; mean: 220 cm TL [SD 41]). A cumulative prey curve was constructed on the basis of 74 stomach contents because 41 stomachs containing only ‘unidentified remains’ were excluded. The curve slope was 0.9, indicating that the sampling size was sufficient to describe the diet of blue sharks. However, according to the Bizzarro’s et al. (2007) method, the curve did not reach an asymptote ($P<0.05$), and therefore suggests that the results presented here do not fully describe the blue shark diet.

Prey comprised 42 taxonomic levels (Table 1). Cephalopods represented the main prey group (87.4% PSIRI), followed by fishes (8.5% PSIRI), flying fish eggs (2.1% PSIRI), crustaceans (1.1% PSIRI), and marine mammal and bird remains (0.8% and 0.1% PSIRI, respectively). The prey item ‘unidentified cephalopods’ (represented by flesh, gladii, and eye lenses) was the most important (31.3% PSIRI) in the overall analysis, followed by *Argonauta* spp. (16.1% PSIRI) and *A. lesueurii* (6.2% PSIRI) (Table 1; Fig. 2).

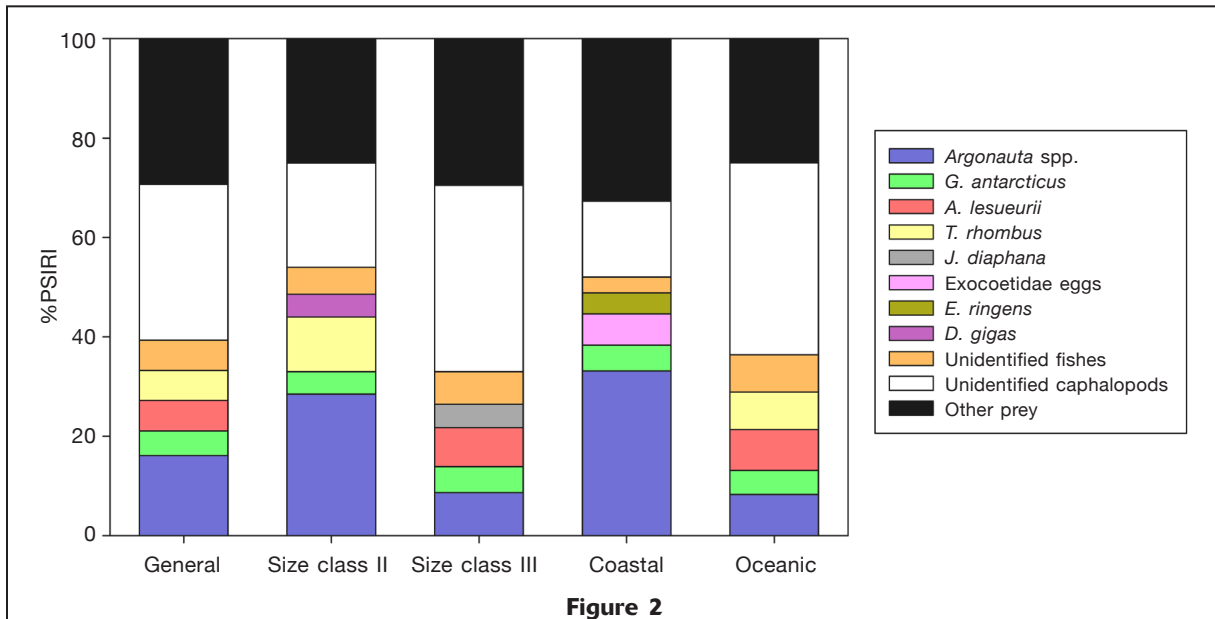


Figure 2

Prey-specific index of relative importance (%PSIRI) of the overall diet of blue sharks (*Prionace glauca*) sampled in northern Peru between February and December 2015, by size class and longitude of fishing ground. Size class II represents fish 150.0–229.9 cm in total length (TL) and size class III represents fish 230.0–309.9 cm TL; size class I had only 2 samples and was excluded from most analyses. Two regions were used for analyses with longitudes: coastal and oceanic, delineated by the Peru–Chile Trench (which has an average distance from shore of 130 km or 70 nautical miles). Taxa include *Argonauta* spp., *Gonatus antarcticus*, *Ancistrocheirus lesueurii*, the diamond squid (*Thysanoteuthis rhombus*), *Japetella diaphana*, flying fish (Exocoetidae) eggs, the Peruvian anchoveta (*Engraulis ringens*), and the jumbo squid (*Dosidicus gigas*).

Table 2

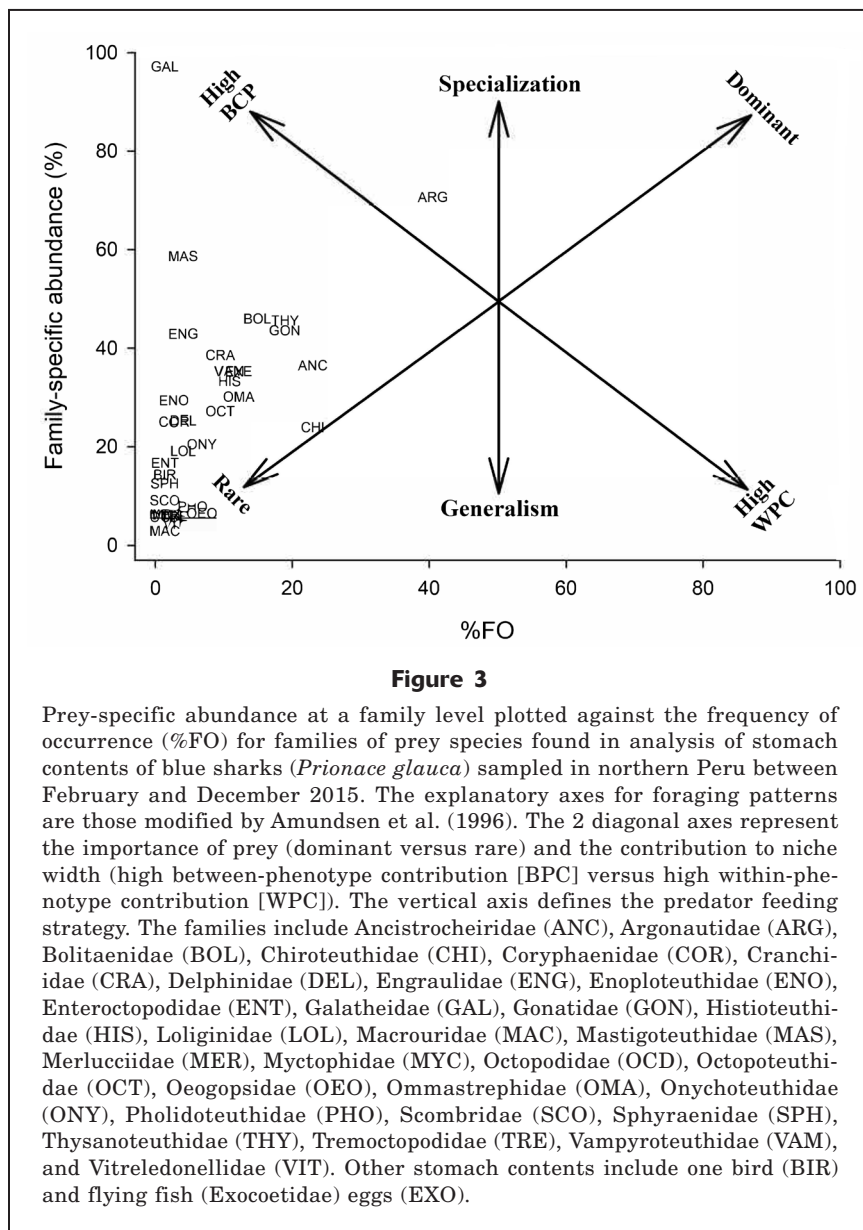
Levin's standardized index (B_i), analysis of similarity (ANOSIM), and trophic position (TP) of blue sharks (*Prionace glauca*) from which stomach contents were collected between February and December 2015 off northern Peru, by size class and longitude of fishing ground. Size class II represents fish 150.0–229.9 cm in total length (TL) and size class III represents fish 230.0–309.9 cm TL; size class I had only 2 samples and was excluded from most analyses. Two regions, coastal and oceanic, were used for the analyses with longitudes of fishing grounds: these regions are separated by the Peru–Chile Trench (which has an average distance from shore of 130 km or 70 nautical miles). General=overall analysis.

Factor	Subfactor	ANOSIM	B_i	TP
General	–	–	0.26	4.4
Size class	II	II vs III ($R=0.05$; $P<0.05^*$)	0.19	4.4
	III		0.42	4.4
Fishing ground longitude	Coastal	Coastal vs. oceanic ($R=0.10$; $P<0.01^*$)	0.18	4.4
	Oceanic		0.40	4.4

The niche breadth of the blue shark was considered narrow according to Levin's standardized index (Table 2), indicating a higher degree of specialization. The graphical analysis suggests a similar feeding pattern, with a clear dominance of the Argonautidae family (Fig. 3). Additionally, the trophic position of the blue shark was calculated as 4.4, indicating that the blue

shark is a high trophic-level consumer within the food web off northern Peru.

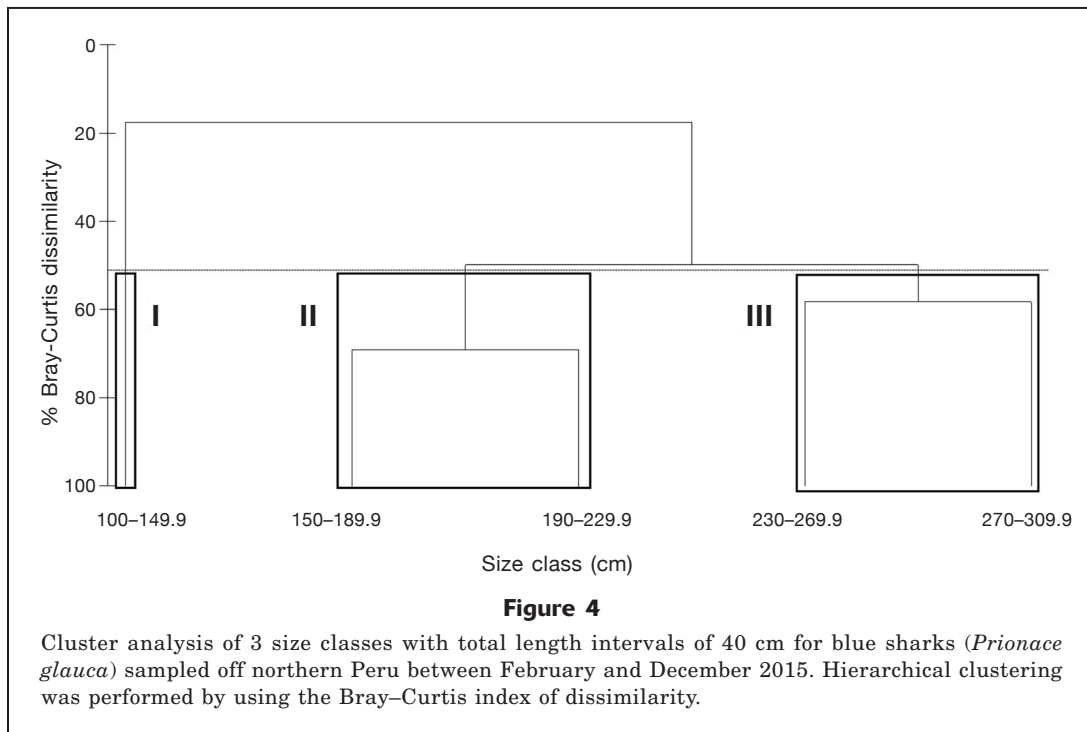
Size class groups were evaluated at 20- and 30-cm-TL intervals and showed no clear organization of size classes. Nevertheless, cluster analysis with a 40-cm-TL interval showed positive results, with 3 size classes identified at 50% of Bray–Curtis dissimilarity (Fig. 4).



However, because size class I (110.0–149.9 cm TL) was represented by only 2 samples, only size class II (150.0–229.9 cm TL, $n=32$) and size class III (230.0–309.9 cm TL, $n=40$) were considered for subsequent analyses.

From all the factors assessed (sex, season, size class, and fishing ground [by latitude and longitude]), ANOSIM showed a significant difference in the diet by size class and fishing ground longitude. These differences were small (Table 2), but indicated that an overlap exists between the composition of dietary factors (Clarke, 1993). A small difference in diet composition existed between size class II and III (Table 2). The nonmetric MDS plot showed that this small difference is explained by an overlap of diets (Fig. 5A). According to SIMPER analysis, in order of importance, the prey families that most contributed to the diet of size class II were Argo-

nautidae and Thysanoteuthidae, whereas in size class III they were Argonautidae and Ancistrocheiridae. The %PSIRI for size classes showed a similar trend (Fig. 2). *Argonauta* spp. represented the main prey taxon for both size classes, although a considerable decrease in this taxon was observed from size class II (28.5%) to size class III (8.6%). Furthermore, larger size individuals (size class III) exhibited a tendency to forage on other prey species such as *A. lesueurii* (7.8%) and *Japetella diaphana* (4.7%), in addition to an increase in the importance of ‘unidentified cephalopods’ in the diet. Niche breadth analysis revealed that both groups had high degrees of specialization, even though higher values were estimated for size class III (Table 2). Blue sharks of both groups were considered top predators (Table 2).



The nonmetric MDS ordination for fishing ground longitude showed that the diets of both groups overlapped (Fig. 5B). This overlap explains the small difference calculated with ANOSIM (Table 2). SIMPER analysis revealed that, in order of importance, Argonautidae and Chiroteuthidae contributed more to the diet of blue sharks in the coastal zone, whereas Ancistrocheiridae and Argonautidae contributed more to the diet of individuals in the oceanic zone. Trophic positions in both longitudinal zones were similar and Levin's standardized index revealed that blue sharks had a higher degree of diet specialization in both zones, although higher values were estimated for the oceanic zone (Table 2). Values of %PSIRI for longitudinal zones (Fig. 2) showed that the coastal zone diet ($n=36$) was predominated by *Argonauta* spp. (33.2%), flying fish eggs (6.3%), *Gonatius antarcticus* (5.2%), and Peruvian anchoveta (4.2%). In contrast, the oceanic zone ($n=79$ stomachs) had a much lower percentage of *Argonauta* spp. (8.3%), in addition to *A. lesueurii* (8.2%) and diamond squid (*Thysanoteuthis rhombus*, 7.6%). Furthermore, 'unidentified cephalopods' varied greatly between coastal (15.3%) and oceanic (38.6%) zones.

Finally, the PERMANOVA test (pseudo- $F=0.7961$, $P>0.05$) indicated no interaction between the 2 size classes and coastal and oceanic fishing grounds.

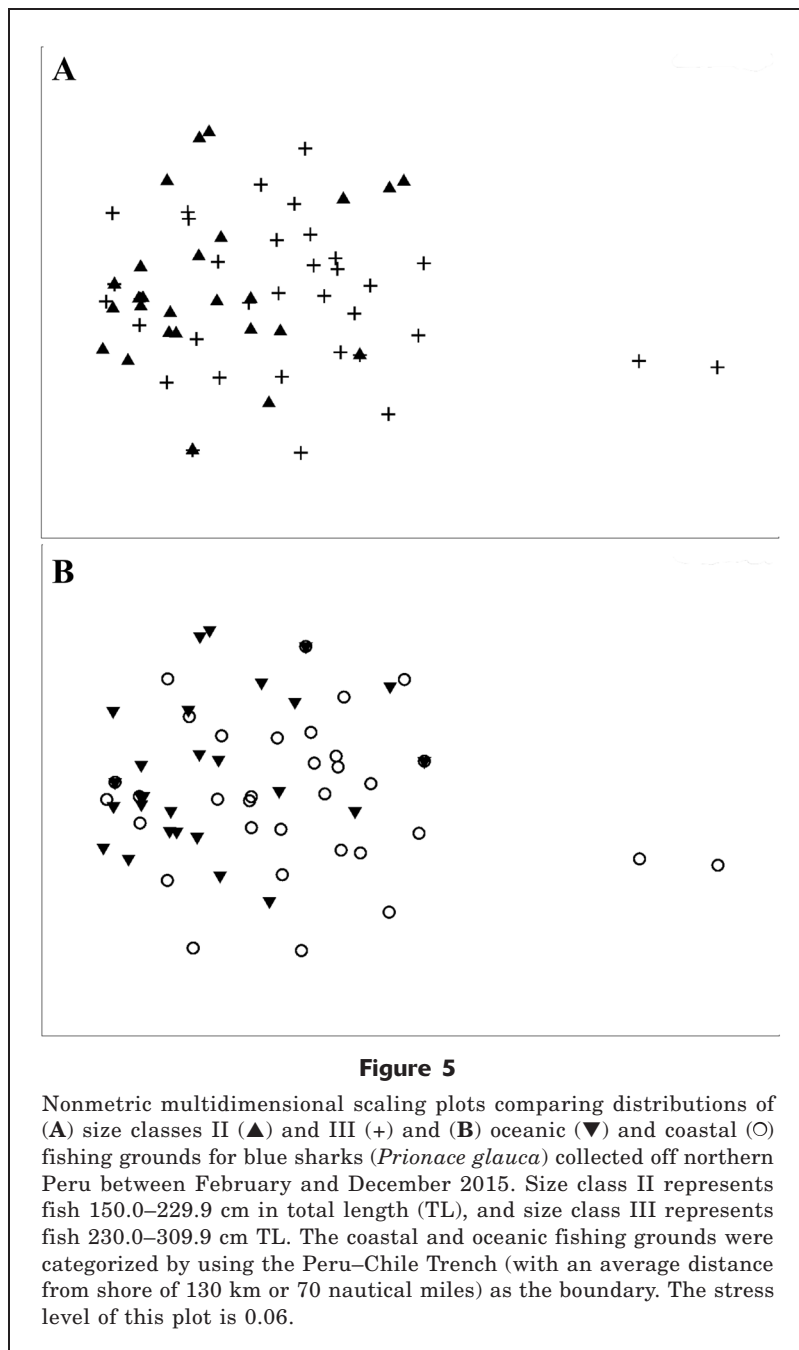
Discussion

The present study provides important new information on the diet of blue sharks in Peruvian waters. In this

study, cephalopods represented 87.4% PSIRI of overall diet, and 66.7% of total prey species identified. These results validate, for Peruvian waters, the preference of blue sharks to prey on squid in the eastern Pacific Ocean (Markaida and Sosa-Nishizaki, 2010; Looor-Andrade et al., 2017). Furthermore, our results showed that small quantities of fish were consumed (8.5% PSIRI). It is important, however, to note that fish consumption is likely underestimated because both fish flesh and otoliths degrade faster than cephalopod flesh and beaks (Tricas, 1979; Hernández-García, 1995).

Blue sharks have been described as meso- and bathypelagic predators (Clarke et al., 1996). They are known to swim at depths near the thermocline at night, whereas during daylight hours, they prefer to dive and complete long incursions to great depths (Carey and Scharold, 1990). Campana et al. (2011) stated that this behavior was highly related to the diel vertical migrations of their preferred prey (i.e., cephalopods), which feed in the epipelagic zone at night and move to greater depths during daylight hours. Our identification of mesopelagic (e.g., Ancistrocheiridae, Histioteuthidae, Gonatidae cephalopods) and bathypelagic (i.e., *Vampyroteuthis infernalis*) prey in significant quantities, suggests that, at least for the area studied, they also completed vertical migrations to feed on preferred or available prey, or both (Roper and Young, 1975).

Argonauta spp. off the coast of northern Peru have been studied little and have been described only as fauna associated with prospectations associated with the Peruvian anchoveta fishery in the northern Humboldt ecosystem (between 4–16°S and 0–148 km from shore)



(IMARPE⁴) and as a component of the diet of dolphin-fish (*Coryphaena hippurus*) (Solano et al., 2015). However, recent investigations have begun to assess basic aspects of its ecology. Orosco-Montenegro (2016) reported that the abundance of larvae of *Argonauta* spp. is higher during the summer (318 individuals/m²) than during the fall (9 individuals/m²) along the Peru-

⁴ IMARPE (Instituto del Mar del Peru). 2015. Crucero 1502-04 de “Evaluación hidroacústica de los recursos pelágicos.” Inst. Mar Peru, Inf. Ejec., 42 p. [Available from [website](#)]

vian coast, while Sajinez et al. (2016) mentioned that *Argonauta* spp. abundance is highly related to SST, with increased abundance during positive anomalies. During the sampling year, an SST positive anomaly of 1.7°C (SD 1.2) (DHN⁵) was reported for the Niño 1+2 region (in the eastern equatorial Pacific Ocean between 0–10°S and 90–80°W). Therefore, the elevated consumption of *Argonauta* spp. that we observed (16.1% PSIRI) may have been a response to higher abundances of this species during the SST positive anomaly if we consider the opportunistic foraging behavior of the blue shark upon abundant available prey (Stevens, 1973). The elevated consumption of *Argonauta* spp. is what most makes the blue shark a consumer with a high degree of specialization. However, further investigations are needed to further confirm this feeding pattern and to evaluate how this degree of specialization varies during La Niña periods.

The consumption of flying fish eggs (in patches) recorded in this study may suggest, as Nakano and Seki (2003) proposed, the ingestion of prey (or objects) whose silhouettes are detected against light from the sea surface. However, the maximum number of individuals of certain small-size species (e.g., *Argonauta* spp.=102, *P. monodon*=34, *Doryteuthis (Amerigo) gahi*=25, Peruvian anchoveta=24, *Grimalditeuthis bonplandi*=14) reported in different samples may also reflect a habit of foraging upon shoals of small-size species (Tricas, 1979). Furthermore, Tricas (1979) indicated that blue sharks benefit from schools of spawning squid, such as those of the opalescent inshore squid (*Loligo opalescens*). Therefore, *Argonauta* spp. could be prey of blue sharks within spawning areas of *Argonauta* spp. off northern Peru, as well, especially considering that abundant fertilized and nonfertilized Argonautidae eggs were found in 21 stomachs.

Scavenger behavior

Blue sharks are considered active scavengers in the open ocean (Garibaldi and Orsi Relini, 2000). However, this behavior has only been discussed because of the discovery of cephalopod and marine mammal parts in stomachs of blue sharks (Markaida and Sosa-Nishiza-

⁵ DHN (Dirección de Hidrografía y Navegación). 2015. Anomalías de la temperatura superficial del mar en el Pacífico ecuatorial. Bol. Oceanogr., December 2015, 9 p. [Available from [website](#)]

ki, 2010; Klarian et al., 2018). In this study we sought to reinforce these studies with a new approach, i.e., with the consideration of the cosmopolitan duck barnacle (*Lepas anatifera*) as a bioindicator of scavenging behavior.

The duck barnacle is a cosmopolitan species that as an adult is commonly found attached to floating objects (Hinojosa et al., 2006). Its cyprid larval stage denotes the shift from a free-swimming organism to a sessile organism. During this stage, cyprid larvae are forced to find a favorable place to settle and metamorphose into juvenile duck barnacles (Høeg et al., 2012). The most common substrate used by cyprid larvae are animals and floating objects, such as boats, buoys (Snelli, 1983), wood (Minchin, 1996), macroalgae (Hinojosa et al., 2006), turtles (Casale et al., 2012), and even fish (Zevina and Memmi, 1981). However, we believe that other substrates could be used by duck barnacle in the open ocean, for example, moribund spent females of many deep-water cephalopods that float passively to the ocean surface and die (Nesis, 1996). Indeed, Markaida and Sosa-Nishizaki (2010) stated that blue sharks may easily scavenge on these dead buoyant cephalopods. In our study, two stages of duck barnacle—cyprid larvae (60.1%, range: 1–200 individuals) and juveniles (9.1%, range: 1–3) (Suppl. Fig.)—were found in stomachs containing only the prey ‘unidentified cephalopods’ ($n=40$). We believe that at least some of the ingestion of cephalopods was the result of scavenging behavior. The possible scavenging behavior of blue sharks is also reinforced by findings of duck barnacle cyprid larvae in samples containing skin, blubber, muscle tissue, and dorsal fin of marine mammals, and in the keeled sternum of an ‘unidentified bird’ (Klarian et al., 2018).

Dietary variability by ontogenetic factors

Ontogenetic shifts have been described in the diets of several shark species—shifts that are mainly due to energetics, metabolism, or changes in foraging ability (Grubbs, 2010). In the case of blue sharks, some studies have tried to prove these ontogenetic shifts, however, with no success (Markaida and Sosa-Nishizaki, 2010; Hernández-Aguilar et al., 2016).

Length at first maturity of blue sharks in the southeastern Pacific Ocean has been reported to be around 200 cm TL (Bustamante and Bennett, 2013). Therefore, size class II in our study was considered to comprise both juvenile and small adults, with a large predominance (82%) of juveniles. Juvenile blue sharks (TL < 200 cm) have a narrow coastal distribution before they take part in larger-scale migrations (Vandeperre et al., 2014). Litvinov (2006) supported the idea that this spatial isolation of juvenile blue sharks is caused by limitations on prey consumption at the earliest age, specifically during the period of development of teeth cusps. In addition, Vandeperre et al. (2014) stated that coastal areas may provide juvenile blue sharks (fork length < 185 cm) with optimal growth conditions because of the availability of food resources that are

associated with the diversity of topographic features (seamounts and islands), and localized oceanographic processes. In our study, the large abundance of small-size octopods, such as *Argonauta* spp., in the diet of individuals from size class II and in the diet of those captured in the coastal zone (Fig. 2), reaffirms the hypothesis that small-size blue sharks occur in coastal areas and feed upon available prey items.

Vertical and horizontal movements of blue sharks expand progressively as body size increases, and according to migratory patterns throughout their life history (Nakano and Stevens, 2008). The smaller quantities of *Argonauta* spp. and the appearance of the oceanic squid *A. lesueurii* in the diet of individuals from size class III (100% adults) and from oceanic areas (Fig. 2) may indicate longitudinal movements of larger blue sharks from coastal to oceanic areas (Vögler et al., 2012). Moreover, the presence of cephalopods from deeper depths, such as *J. diaphana* or *V. infernalis*, in the diet of size class III may indicate progressive dives to greater depths by larger individuals (Roper and Young, 1975).

In this article we have provided important new information about the food habits of blue sharks off northern Peru. Blue sharks feed on small-size (*Argonauta* spp.) and larger size (*A. lesueurii*) prey species, which indicate a surface and mesobathypelagic foraging behavior. In addition, we identified prey items with commercial importance, such as jumbo squid, *D. gahi*, Peruvian anchoveta, and flying fish eggs in the diet of blue sharks, which highlight the importance of the results from this study for Peruvian ecosystem management.

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