

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/318823218>

# Trophic ecology of the smooth hammerhead shark (*Sphyrna zygaena*) off the coast of northern Peru

Article in *Fishery Bulletin- National Oceanic and Atmospheric Administration* · July 2017

DOI: 10.7755/FB.115.4.2

CITATIONS

5

READS

249

7 authors, including:



**Adriana Gonzalez Pestana**

James Cook University

22 PUBLICATIONS 34 CITATIONS

SEE PROFILE



**Javier Jesús Coasaca-Céspedes**

Universidad Científica del Sur

9 PUBLICATIONS 9 CITATIONS

SEE PROFILE



**Francisco Córdova-Zavaleta**

Pro Delphinus

7 PUBLICATIONS 9 CITATIONS

SEE PROFILE



**Joanna Alfaro Shigueto**

ProDelphinus

100 PUBLICATIONS 1,632 CITATIONS

SEE PROFILE

Some of the authors of this publication are also working on these related projects:



Southern Right Whale population of Peru/Chile: why no firm signs of recovery? [View project](#)



Biology and conservation of cetaceans in Peru [View project](#)



**Abstract**—The smooth hammerhead (*Sphyrna zygaena*) is the third most captured shark species in Peru, a nation with one of the largest shark fisheries in the Pacific Ocean. We sought to better understand the trophic ecology of this shark in northern Peru by analyzing stomach contents. From 2013 through 2015, we collected 485 samples of gut contents from sharks measuring 53–294 cm in total length. Our results show that the smooth hammerhead is a top predator with a diet dominated by jumbo flying squid (*Dosidicus gigas*) and the Patagonian squid (*Doryteuthis (Amerigo) gahi*). Smooth hammerheads displayed different diets with different body size, and this finding indicates that sharks change their distribution and habitat during development. This study represents the most comprehensive investigation to date of the trophic ecology of smooth hammerhead in waters off Peru. We propose that these waters represent an important eastern Pacific Ocean feeding ground for smooth hammerhead. Because this species is commercially important and also preys upon other commercial species, these findings could contribute to the design and implementation of plans for ecosystem-based fisheries management.

Manuscript submitted 14 October 2016.  
Manuscript accepted 7 June 2017.  
Fish. Bull. 115:451–459 (2017).  
Online publication date: 31 July 2017.  
doi: 10.7755/FB.115.2

The views and opinions expressed or implied in this article are those of the author (or authors) and do not necessarily reflect the position of the National Marine Fisheries Service, NOAA.

## Trophic ecology of the smooth hammerhead shark (*Sphyrna zygaena*) off the coast of northern Peru

Adriana Gonzalez-Pestana (contact author)<sup>1,2,3</sup>

Nicolas Acuña-Perales<sup>1,4</sup>

Javier Coasaca-Cespedes<sup>1,2</sup>

Francisco Cordova-Zavaleta<sup>1,5</sup>

Joanna Alfaro-Shigueto<sup>1,2,6</sup>

Jeffrey C. Mangel<sup>1,6</sup>

Pepe Espinoza<sup>2,7</sup>

Email address for contact author: [adriana@prodelphinus.org](mailto:adriana@prodelphinus.org)

<sup>1</sup> ProDelphinus  
Calle Jose Galvez 780-e  
Lima 18, Peru

<sup>2</sup> Universidad Científica del Sur  
Panamericana Sur Km 19  
Villa El Salvador, Lima 42, Peru

<sup>3</sup> James Cook University  
1 James Cook Dr.  
Townsville City, Queensland 4811, Australia

<sup>4</sup> Universidad Ricardo Palma  
Avenida Alfredo Benavides 5440  
Santiago de Surco, Lima 33, Peru

<sup>5</sup> Universidad Nacional Agraria La Molina  
Avenida La Molina s/n  
La Molina, Lima 12, Peru

<sup>6</sup> Center for Ecology and Conservation  
College of Life and Environmental Sciences  
University of Exeter, Penryn Campus  
Penryn, Cornwall TR10 9FE, United Kingdom

<sup>7</sup> Instituto del Mar del Perú  
Esquina Gamarra y General Valle s/n  
Chucuito, Callao 05, Peru

The smooth hammerhead (*Sphyrna zygaena*) is distributed from California to Chile within the eastern Pacific Ocean. This species reaches a maximum size of 370–400 cm in total length (TL), and is one of the largest fishes in the southeast Pacific Ocean (Fowler et al., 2005). At birth, neonates measure 50–61 cm-TL (Fowler et al., 2005). Neonate and juvenile smooth hammerheads use shallow coastal waters as nursery grounds and as they grow larger they move to more offshore oceanic waters (Smale, 1991; Diemer et al., 2011; Francis, 2016). The distribution of adults worldwide, however, is still unknown (Francis, 2016).

Abundance of this species is decreasing and the species is classified as vulnerable in the IUCN Red List of Threatened Species (Casper et al., 2005). As of September 2014, the spe-

cies has been included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (<https://cites.org/eng/app/appendices.php>). Smooth hammerhead fins are prized in Asian markets and sharks are increasingly targeted in some areas. Peru is one of the top 12 countries that supply shark fins to Asian markets (Cheung and Chang, 2011). The smooth hammerhead is commonly caught in the southeast Pacific Ocean but the impact of these fisheries on its population is unknown (Fowler et al., 2005). Peru also reports the highest accumulated historical shark landings in the Pacific Ocean and smooth hammerhead is identified as the third most captured shark species by the fisheries of Peru and the most frequently captured shark species off northern Peru (Gonzalez-Pestana et

al., 2016). However, the fisheries lack robust monitoring and management, and species biology and ecology remain poorly understood, both locally and worldwide (Fowler et al., 2005; Cortés et al., 2010).

There are limited studies from Mexico, Ecuador, and Peru on the diet of smooth hammerhead in the Pacific Ocean. Research shows that the diet of this shark in waters off Mexico is composed of fishes and cephalopods (e.g., California needlefish [*Strongylura exilis*]; common clubhook squid [*Onychoteuthis banksia*]) (Galvan-Magaña et al., 1989; Ochoa-Díaz, 2009; Galvan-Magaña et al., 2013). In waters off Ecuador, information suggests that the diet is composed mainly of cephalopods (e.g., jumbo flying squid [*Dosidicus gigas*]; purpleback flying squid [*Sthenoteuthis oualaniensis*]; whip-lash squid [*Mastigoteuthis dentata*]; and sharpnose squid [*Ancistrocheirus lesueurii*]) (Castañeda and Sandoval, 2004; Estupiñan-Montaño and Cedeño-Figueroa, 2005; Bolaño Martínez, 2009). In one study in Peru, the diet of smooth hammerhead was analyzed and smooth hammerheads were found to feed primarily on fishes (Pacific sardine [*Sardinops sagax*]; Peruvian hake [*Merluccius gayi peruanus*]; and Peruvian anchoveta [*Engraulis ringens*]), as well as on cephalopods (*Loligo* spp., and jumbo squids) (Castañeda<sup>1</sup>). Although this study in Peru had an adequate sample size, time series, and size distribution for the smooth hammerhead, it is more descriptive than analytical and is limited to a seasonal comparison.

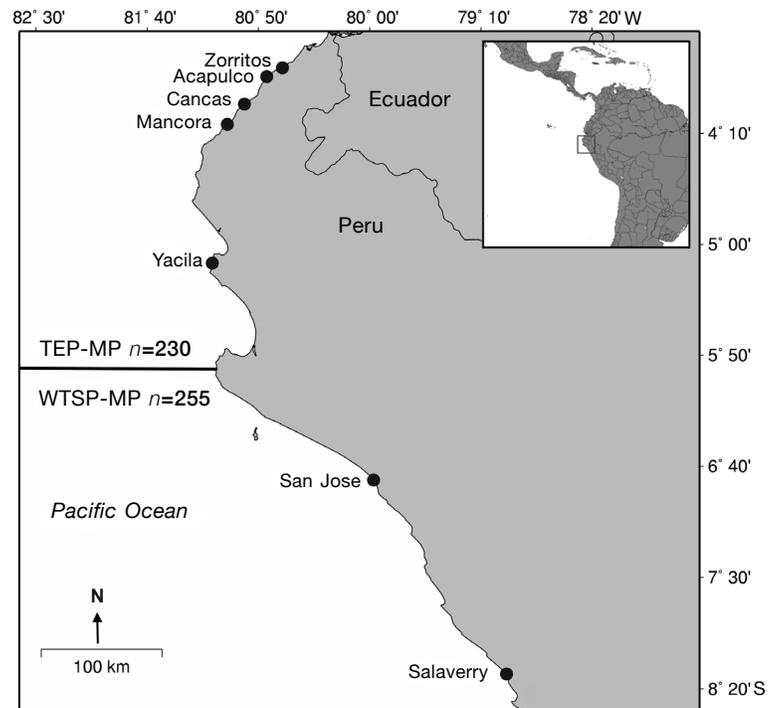
We sought to better understand the trophic ecology of smooth hammerhead off the coast of northern Peru by analyzing stomach contents. We assessed diet variability by sex, body size, location, season, year, and environmental conditions.

## Materials and methods

### Collections, storage, and analysis of samples

Samples were collected from a small-scale driftnet fishery from December 2012 through June 2015 at 7 landing sites along the coast of northern Peru: Zorritos, Acapulco, Cancas, Mancora, Yacila, San Jose, and Salaverry (Fig. 1). Nets in this fishery are typically set at the time of sunset and retrieved the following morning for an average set length of ca. 14 h (Alfaro-Shigueto et al., 2010). Sharks were measured (total length) and sex was determined. Stomachs were extracted and preserved in 10% formalin solution.

<sup>1</sup> Castañeda, J. 2001. Biología y pesquería del “tiburón martillo” (*Sphyrna zygaena*) en Lambayeque, 1991–2000. Inst. Mar Perú Inf. Prog. 139:17–32. [Available from [website](#).]



**Figure 1**

Map of the study area and the 7 landing sites where smooth hammerhead (*Sphyrna zygaena*) were collected off northern Peru from December 2012 through June 2015. The black line defines the division between the Tropical East Pacific Marine Province (TEP-MP) and the Warm Temperate Southeastern Pacific Marine Province (WTSP-MP),  $n$ =number of stomachs collected from each marine province. This map was created with Seaturtle.org Map-tool (Seaturtle.org Inc. [website](#), accessed January 2017).

### Analysis of stomach contents

Prey items from stomach contents were analyzed at the Laboratorio de Ecología Trófica of the Instituto de Mar del Perú,<sup>2</sup> and identified to the lowest possible taxon, counted, and weighed (wet weight). For identification of fishes and cephalopods, and their hard parts (otoliths and beaks), the following identification guides were used: Iverson and Pinkas (1971); Wolff (1982, 1984); Clarke (1986); Chirichigno and Cornejo (2001); Garcia-Godos (2001); Lu and Ickeringill (2002); and Xavier and Cherel (2009). Cephalopod beaks were used to reconstruct total mass at ingestion, by using regression equations (Lu and Ickeringill, 2002). Values for stage of digestion were allocated to each prey item and ranged from 1 (little or no digestion) to 4 (advanced state of digestion) (Bolaño Martínez, 2009).

Diet was quantified by using percentage of prey, by number (%N), weight (%W), and frequency of occurrence (%O) (Hyslop, 1980). The index of relative importance (IRI) was calculated as  $IRI = \%O (\%N + \%W)$ . It was then divided by the total IRI for all items to express the

<sup>2</sup> and at the Laboratorio de Biología Marina of the Universidad Científica del Sur.

IRI as a percentage (%IRI; Cortés, 1997). Items rarely found in stomachs (e.g., rocks, snails) and parasites (e.g., isopoda) were not included in the analysis.

### Statistical analysis

Cumulative prey curves were constructed to determine whether an adequate number of stomachs had been collected to accurately describe the diet of smooth hammerhead (Jimenez and Hortal, 2003). The order in which stomachs were analyzed was randomized 1000 times to eliminate bias. The number of stomachs analyzed is considered sufficient in describing the diet when a cumulative prey curve reaches an asymptote. Therefore, a slope value less than 0.1 indicates a good representation of diet (Soberón and Llorente, 1993).

We used 2 indices to evaluate trophic niche width of prey taxa: Levin index and Berger–Parker index. The Levin index was based on %N values. The index values range from 0 to 1: low values (<0.6) indicate a diet dominated by few prey items (specialist predator) and higher values (>0.6) indicate a generalist diet (Labropoulou and Eleftheriou, 1997). The Berger–Parker index uses the formula of Magurran (1988),  $d=(n_i \text{ max})/N$ , where  $N$  represents the number of all recorded food components (taxa) and  $n_i$  max represents the number of specimens from taxon  $i$  (the most numerous taxon in the diet). This index ranges between  $1/N$  and 1: values closer to 1 represents a specialist feeder and a value closer to  $1/N$  indicates a generalist feeder.

We calculated trophic position on the basis of %IRI values of the prey species presented in the stomach content. We used the following equation:

$$TL=1+ (\sum DC_{ij}) \times (TL_j) \quad (1)$$

(Christensen and Pauly, 1992),

where  $DC_{ij}$  = the composition of the diet in which  $j$  is the proportion of preys in the diet of the predator  $I$ ; and

$TL_j$  = the trophic level of the preys.

The trophic level of the fishes were taken from Froese and Pauly<sup>3</sup> and Espinoza (2014) and the trophic level of the cephalopods were taken from Cortés (1999) and Espinoza (2014).

We analyzed differences in diet according to 6 factors: body size and sex of sharks, location of capture, season, year, and environmental conditions (El Niño–Southern Oscillation event: November 2014 to December 2015). For body size we divided the sharks into size classes. This division was based on analyses of similarities (ANOSIM) where we chose the size classes that showed the highest  $R$ -statistic and the lowest  $P$ -value (Clarke, 1993). The division of the locations (north: Zorritos, Acapulco, Cancas, Mancora, and Yacilla; south: San Jose; and Salaverry) was justified be-

cause of biogeographic characteristics of the Tropical East Pacific and Warm Temperate Southeastern Pacific marine provinces where the collection sites were located (Spalding et al., 2007) (Fig. 1). The division of the seasons was based upon the seasonality of chlorophyll- $a$  concentration and primary production; for which the highest levels occurred during the austral summer and fall (Pennington et al., 2006). Therefore, we divided the data into 2 seasons: season 1 (austral summer and fall) and season 2 (austral winter and spring).

Nonmetric dimensional scaling (nMDS) ordinations generated from a Bray–Curtis similarity matrix on numeric abundance of prey (%N) was used to determine whether sex, body size, capture location, season, year, or environmental conditions exerted the greatest overall influence on the dietary composition of smooth hammerhead. ANOSIM was used to test whether dietary compositions differed significantly, by generating a  $R$ -statistic, stress value, and a  $P$ -value.  $R$ -statistic values describe the extent of similarity (Clarke, 1993), with values near 1 indicating that the 2 groups are entirely separate and values close to 0 indicating that there are no differences between the 2 groups. Stress value measures the goodness-of-fit of the nMDS model to the data, where values closer to zero indicate excellent representation (without risk of misinterpretation) and values larger than 0.2 indicate that the interpretation is unreliable (Clarke, 1993). Similarity percentages (SIMPER) were employed to determine the dietary categories that typified particular groups or contributed most (or typified a combination of both categories) to the similarities between groups (Clarke, 1993). If significant differences existed in the diets by factors (e.g., sex), then trophic niche width, degree of overlap (based on the Bray–Curtis index) and trophic position were calculated for each factor.

Statistical analyses were performed by using RStudio, vers. 0.96.122 (RStudio, 2012) with R, vers. 3.2.2 (R Core Team, 2016).

## Results

A total of 485 samples of gut contents were collected. Individual smooth hammerheads measured between 53 and 294 cm TL. The slope value of 0.002 (less than 0.1) for the cumulative prey curve showed that sufficient stomach contents were examined to adequately and reliably describe the diet of smooth hammerhead. With the cumulative prey curve, we calculated that the contents from 39 stomachs would be needed to accurately analyze the diet of smooth hammerhead.

Food items were found in 78% of the stomachs. Of these, 92% were in an advanced state of digestion (stages 3 and 4). Prey composition comprised 25 prey items: 14 teleosts and 11 cephalopods (Table 1). According to %IRI values, the most important prey species were Patagonian squid (*Doryteuthis (Amerigo) gahi*) (37%) and jumbo squid (27%). These 2 species comprised more than 60% of the diet. The trophic position was high

<sup>3</sup> Froese R., and D. Pauly. 2012. FishBase, vers. 02/2012. [World Wide Web electronic publication; available from <http://www.fishbase.org>]

**Table 1**

Composition of prey identified in stomachs of smooth hammerhead (*Sphyrna zygaena*) collected from December 2012 through June 2015 in northern Peru: %N=percentage by number; %W=percentage by weight; %O=percentage by frequency of occurrence, %IRI=index of relative importance, and SD=standard deviation.

Prey category	%W	%N	%O	%IRI (SD)
<b>Chordata</b>				
Teleostei				
Fish remains	2.7		12.9	
<i>Scomber japonicus</i>	0.3	0.2	0.4	0.3 (3.72)
<i>Odontesthes regia</i>	0.0	0.0	0.2	0.0 (0.13)
<i>Peprilus</i> sp.	3.2	3.3	4.0	3.3 (16.24)
<i>Opisthonema libertate</i>	0.4	0.5	0.9	0.5 (6.16)
<i>Sardinops sagax</i>	0.3	0.1	0.2	0.2 (3.87)
<i>Selene brevoortii</i>	0.1	0.2	0.2	0.0 (0.86)
<i>Scomberesox saurus scombroides</i>	0.1	0.1	0.2	0.1 (2.55)
<i>Trachurus murphyi</i>	0.1	0.1	0.2	0.1 (1.64)
<i>Hemanthias peruanus</i>	0.2	0.1	0.2	0.1 (2.74)
<i>Merluccius gayi peruanus</i>	1.7	1.4	2.2	1.9 (11.80)
Engraulidae	0.6	0.4	0.9	0.5 (6.10)
<i>Engraulis ringens</i>	0.0	0.4	0.7	0.2 (2.34)
<i>Anchoa nasus</i>	0.3	0.3	0.2	0.3 (5.42)
Fistulariidae	0.1	0.1	0.2	0.1 (2.15)
<b>Mollusca</b>				
Cephalopoda				
Teuthoidea				
<i>Octopoteuthis sicula</i>	1.2	1.3	5.1	1.3 (7.33)
<i>Gonatus antarcticus</i>	7.5	6.6	17.3	7.1 (18.44)
<i>Stigmatoteuthis hoylei</i>	2.2	1.3	4.7	1.8 (9.05)
<i>Mastigoteuthis dentata</i>	9.1	12.2	20.9	10.9 (25.18)
<i>Dosidicus gigas</i>	30.5	23.8	30.9	26.6 (36.28)
<i>Ommastrephes bartramii</i>	1.0	1.2	2.4	1.1 (9.08)
<i>Doryteuthis (Amerigo) gahi</i>	34.5	38.4	44.0	37.5 (41.56)
<i>Ancistrocheirus lesueurii</i>	1.6	3.5	12.0	2.3 (7.96)
<i>Architeuthis dux</i>	0.1	0.6	2.2	0.4 (5.55)
Octopodea <sup>1</sup>	2.1	4.1	9.8	3.4 (14.28)

<sup>1</sup>*Argonauta* spp., *Tremoctopus violaceus*

(4.3), indicating that the smooth hammerhead is a top predator.

The trophic niche width was narrow with a low Levin index value (<0.6) for the 2 groups of prey taxa: cephalopods and fishes. Also the value of *d* for the Berger–Parker index was closer to 1 than 1/N for both groups. This value means that the diet of smooth hammerhead is dominated by few prey species (Table 2). Moreover, the average frequency of occurrence of cephalopods (89%) in gut contents was higher than the average frequency of occurrence of fishes (11%). The most common number of prey species per stomach was 1, followed by 2 prey species (41% of stomachs contained 1 prey species, and 26% of the stomachs had 2 prey species) (Fig. 2). For stomachs that contained 1 prey species, the single prey species was the Patagonian squid in 60% of stomachs and the jumbo squid in 20% of the cases.

The average number of prey items per stomach was 5.3 with a mode of 1 and a maximum value of 74. The

greatest number of prey items was found in a shark that measured 230 cm TL which contained 74 pairs of squid beaks (equivalent to 74 cephalopods).

#### Comparisons of dietary composition

There were statistically significant differences in diet based upon body size. For this analysis, we divided the sharks into 4 size classes: I (53–70 cm TL, *n*=40), II (71–100 cm TL, *n*=175), III (101–190 cm TL, *n*=111) and IV (191–294 cm TL, *n*=10). The stress value (0.11) of the nMDS plot indicated that this plot provides an accurate representation of the data, and an overall ANOSIM showed significant differences among the size classes (*R*-statistic=0.4, *P*<0.001). The nMDS plot and the overall *R*-statistic indicate that the diet of the size classes overlap but are clearly distinct.

By analyzing each of the pairwise comparisons, we found that all size classes had significant differences (*P*<0.05), except size classes III and IV. Among the size

**Table 2**

Trophic niche width of 2 groups of taxa in the diet of smooth hammerhead (*Sphyrna zygaena*) collected from December 2012 through June 2015 in northern Peru, according to Levin and Berger–Parker indices. The Berger–Parker index uses this formula:  $d=(n_i \max)/N$ , where  $N$ =the number of all recorded food components and  $n_i \max$ =the number of specimens with the most numerous taxon in the diet.

	Levin index	Berger–Parker index	
		$d$	$1/N$
Cephalopods	0.24	0.31	0.0102
Fish species	0.30	0.39	0.0005
Total	0.27	0.38	0.0005

classes that presented a significant difference, size classes I–III had the highest  $R$ -statistic and the lowest overlap, and therefore their diets are well separated. Size classes II and III had the lowest  $R$ -statistic and the highest overlap; therefore their diets were minimally separated (Table 3).

According to analysis with SIMPER, the prey species that most contributed to the diet in size class I are *M. dentata*, teleosts and the Patagonian squid; in size class II they were the Patagonian squid, the jumbo flying squid, and *M. dentata*; in size class III they were the jumbo flying squid and Patagonian squid; and in size class IV they were the jumbo flying squid, sharp-ear enope squid, *Gonatus antarcticus*, and giant squid (*Architeuthis dux*) in order of importance. The IRI showed a similar trend. Sharks in size class I fed chiefly on Patagonian squid (31% of IIR), teleosts (26%) and whip-lash squid (25%); whereas sharks in size class II fed chiefly on Patagonian squid (49%), whip-lash squid (13%) and jumbo squid (13%); sharks in size class III fed chiefly on jumbo flying squid (54%) and Patagonian squid (24%); and sharks in size class IV fed chiefly on jumbo flying squid (62%), giant squid (15%) and sharp-ear enope squid (9%) (Fig. 2).

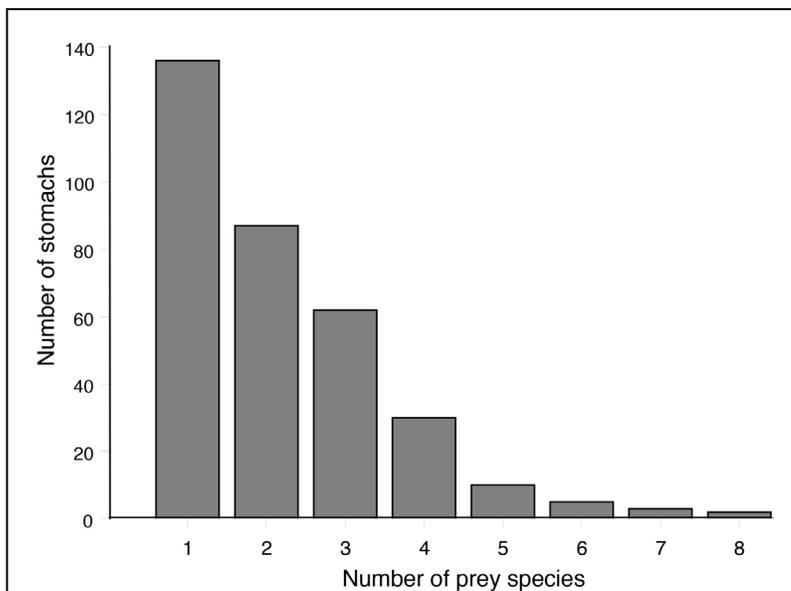
We were also able to identify some general trends in the diet as sharks increased in size, such as, a reduction in the consumption of teleosts and whip-lash squid and an increase in the consumption of jumbo flying squid and sharp-ear enope squid. The giant squid was present only in the diets of sharks in size class IV (Fig. 3). Sharks in size classes II and III were the most specialized feeders, whereas sharks in size class I were the least specialized. Sharks in size class II (mean trophic position: 4.34 cm TL) had the lowest trophic position, and

sharks in size class IV had the highest trophic position (mean trophic position: 4.63 cm TL). As an overall trend, sharks increased their trophic position as they increased in size.

Of all the other factors assessed (sex, location, season, year, and environmental conditions), ANOSIM showed that the dietary composition of smooth hammerhead differed significantly only between location and year. However, these differences were small ( $R$ -statistic < 0.25,  $P < 0.05$ ) and an overlap exists between the dietary composition of these factors (Clarke, 1993). We therefore concluded that the diet of smooth hammerhead did not show variability according to the sex, location, season, year, or environmental conditions.

## Discussion

Our analyses indicate that the smooth hammerhead has a narrow trophic niche width and a high trophic position and can therefore be considered a specialized top predator. These results complement the findings from other diet studies of smooth hammerhead in the eastern Pacific Ocean (Ecuador and Baja California) and southeastern Africa—studies in which this shark species was found to feed mainly on cephalopods (e.g., jumbo squid, Patagonian squid, whip-lash squid, and sharp-ear enope squid) (Smale, 1991; Smale and Cliff, 1998; Castañeda and Sandoval, 2004; Estupiñan-Montaña and Cedeño-Figueroa, 2005; Galvan-Magaña et al., 2013). Studies from Ecuador and Baja California showed that the smooth hammerhead is a specialist predator with a trophic level between 4 and 4.5,

**Figure 2**

Number of prey species in stomachs of smooth hammerhead (*Sphyrna zygaena*). Smooth hammerheads were collected off northern Peru from December 2012 through June 2015.

**Table 3**

Comparison of prey items in the diet of smooth hammerhead (*Sphyrna zygaena*) collected from December 2012 through June 2015 in northern Peru, generated from a Bray–Curtis index that is based on the percentage by number of prey (%N) and from *R*-statistics and *P*-values generated from analysis of similarities. Size classes of sharks: I (53–70-cm-TL), II (71–100 cm TL), III (101–190 cm TL) and IV (191–294 cm TL). An asterisk (\*) indicates comparisons for which differences were significant ( $P < 0.001$ ). “Overlapping” indicates that the diet of smooth hammerhead overlaps for the 2 size classes in each paired comparison (of horizontal and vertical values).

	Size class I		Size class II		Size class III	
	Overlapping	<i>R</i>	Overlapping	<i>R</i>	Overlapping	<i>R</i>
Size class II	33	0.47*	—	—	—	—
Size class III	25	0.71*	66	0.27*	—	—
Size class IV	36	0.29*	26	0.6*	32	0.2

similar to the result of 4.3 that we found in this study (Castaneda, 2004; Estupiñan-Montaño and Cedeño-Figueroa, 2005; Bolaño Martínez, 2009; Galvan-Magaña et al., 2013). Additionally, the fact that 92% of stomach contents examined were in an advanced state of digestion indicates that smooth hammerhead is an intermittent feeder. Stomach contents of a continuous feeder would have food items at different stages of digestion (Medved et al., 1985).

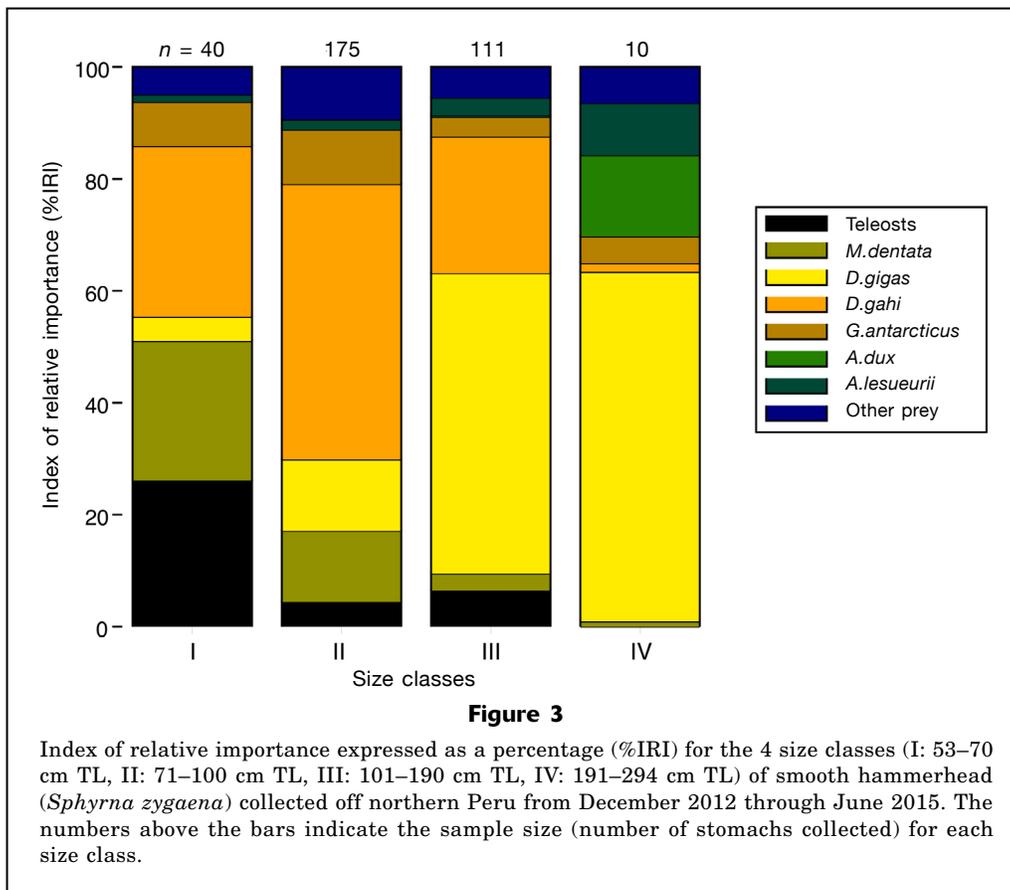
Although we were able to analyze the contribution of cephalopods in the diet, we were limited in our ability to quantify the contribution of fish in the diet. According to the percentage of prey by frequency of occurrence, 12.9% of the diet was composed of fish that could not be identified at a species level owing to their advanced state of digestion. Otoliths are often used to identify species because they resist the digestive process. However, in our study, smooth hammerhead preyed upon pelagic fishes with small and expellable otoliths, often preventing species identification (Lombarte et al., 2010). Conversely, the hard structures of squid beaks were easier to detect owing to their larger sizes and resistance to digestion (Braccini et al., 2005). Despite these challenges, although fish as prey may be underestimated, we were still able to identify otoliths and it is clear that fish comprise an important component of the diet of the smooth hammerhead. Future studies could better refine these estimates with the use of complementary methods, such as molecular analysis, that are helpful in identifying taxonomic groups with precision (King et al., 2008). Moreover, future studies should emphasize the collection of samples from sharks greater than 200 cm TL. We were able to collect only 10 samples for size class IV (191–294 cm TL). Therefore our results more accurately represent the diet of neonates and juveniles.

#### Life stages

Shark species change their diet over the course of their life (Lowe et al., 1996; Wetherbee and Cortés,

2004). In Ecuador, as smooth hammerhead grew, Patagonian squid decreased proportionally in the overall diet composition; whereas jumbo flying squid increased (Bolaño Martínez, 2009). Similarly, in South Africa, juveniles fed on loliginids and adults fed on *Ancistrocheirus* sp. and red flying squid (*Ommastrephes bartramii*) (Smale and Cliff, 1998). Our results are consistent with those reported for Ecuador and South Africa. We found that all size classes had statistically significant differences, except for size classes III and IV, which could be explained by the low sample size of size class IV. Moreover, our samples were composed mainly of neonates and juveniles and included only a small sample size of adults. Therefore, further studies, should include a wider range of sizes to assess fully the trophic ecology of smooth hammerhead over its entire size range.

We found that neonates and small juveniles consumed coastal species (i.e., Patagonian squid, *Peprilus* sp.; Jereb and Roper, 2010), and larger juveniles and adults consumed oceanic species (i.e., jumbo squid, *Ancistrocheirus lesueurii*; Nigmatullin et al., 2001; Jereb and Roper, 2010). These diet habits suggest a change of habitat and distribution. Sharks of size class IV were the only individuals that consumed giant squid, which is a deep-sea species with a vertical distribution range of 200–1000 m (Landman et al., 2004; Jereb and Roper, 2010). In New Zealand, an electronically tagged smooth hammerhead measuring 160 cm TL gave evidence of vertical migrations and a maximum depth recorded at 144 m (Francis, 2016). This finding suggests that larger sharks may be migrating vertically to capture prey. Furthermore, the change in diet from coastal to oceanic prey species can be explained partly by the need to consume prey species of greater biomass and energy content (Navia et al., 2007). The Patagonian squid, for example, provides 3.1 kJ/g, whereas jumbo flying squid provides 6.6 kJ/g (Croxford and Prince, 1982; Abitia-Cardenas et al., 1997). Trophic position of this species rises to a higher level in the food chain as the sharks increased in size, and this has also been ob-



served in other studies of smooth hammerhead (Bolaño Martínez, 2009; Ochoa-Díaz, 2009).

#### Foraging grounds and predator–prey relations

Populations of jumbo flying squid can impact the dynamics of marine ecosystems, owing in part to the rapid growth characteristics of the species (e.g., rapid growth rate, short life span) (Gilly et al., 2006). For example, an increase in the jumbo flying squid population resulted in population declines of Chilean hake (*Merluccius gayi*) and Pacific hake (*Merluccius productus*), and affected the catches of commercial fisheries for these species along Chile and California (Arancibia and Neira<sup>4</sup>; Jereb and Roper, 2010). In the eastern Pacific Ocean, this study, and previous studies, have identified smooth hammerhead as an important predator of jumbo flying squid and one of the main predators of cephalopods in the eastern Pacific Ocean (Galvan-

Magaña et al., 1989; Castañeda and Sandoval, 2004; Estupiñan-Montaño and Cedeño-Figueroa, 2005; Bolaño Martínez, 2009; Ochoa-Díaz, 2009; Galvan-Magaña et al., 2013). It is likely, therefore, that the smooth hammerhead plays an important role as a biological control of cephalopods, and, as a result, has important direct and indirect effects on the viability of multiple fisheries. Furthermore, the high abundance of jumbo flying squid (Nesis, 1983; Nigmatullin et al., 2001; Argüelles et al., 2008) and massive smooth hammerhead fishery landings in northern Peru (Bonfil, 1994; Fischer et al., 2012; Gonzalez-Pestana et al., 2016) make clear that this ocean region represents an important feeding area for smooth hammerhead in the eastern Pacific Ocean. This study contributes to the basic understanding of the trophic ecology of smooth hammerhead and provides information that can also contribute to the design and implementation of national or regional conservation plans for the smooth hammerhead.

<sup>4</sup> Arancibia, H., and S. Neira. 2006. Assessing the potential role of predation by jumbo squid (*Dosidicus gigas*) and fishing on small pelagics (common sardine *Strangomera bentincki* and anchovy *Engraulis ringens*) and common hake (*Merluccius gayi*) in central Chile, 33–39°S. In The role of squid in open oceans ecosystems. Report of a GLOBEC-CLIoTOP/PFRP workshop, 16–17 November 2006, Honolulu, HI, USA (R. J. Olson and J. W. Young, eds.), p. 68–70. GLOBEC Rep. 24. [Available from [website](#).]

#### Acknowledgments

The authors thank the following institutions who funded this study: Fondo para la Innovación, la Ciencia y la Tecnología (PIBA-369-2014), Rufford Foundation, PADI Foundation, Whitney Fund for Nature, and Darwin Initiative. They thank A. Jiménez, S. Pingo, J. Xavier, S.

Kohatsu, A. Sánchez, and A. Arévalo for assistance in collecting, analyzing, and identifying samples, and B. Ramsby for assistance in designing the figures.

## Literature cited

- Abitia-Cardenas, L. A., F. Galvan-Magaña, and J. Rodríguez-Romero.  
1997. Food and energy values of prey of striped marlin, *Tetrapturus audax*, off the coast of Mexico. *Fish. Bull.* 95:360–368.
- Alfaro-Shigueto, J., J. C. Mangel, M. Pajuelo, P. H. Dutton, J. A. Seminoff, and B. J. Godley.  
2010. Where small can have a large impact: structure and characterization of small-scale fisheries in Peru. *Fish Res.* 106:8–17. [Article](#)
- Argüelles, J., R. Tafur, A. Taípe, P. Villegas, F. Keyl, N. Domínguez, and M. Salazar.  
2008. Size increment of jumbo flying squid *Dosidicus gigas* mature females in Peruvian waters, 1989–2004. *Prog. Oceanogr.* 79:308–312. [Article](#)
- Bolaño Martínez, N.  
2009. Ecología trófica del tiburón martillo *Sphyrna zygaena* (Linnaeus, 1758) en aguas Ecuatorianas. M.S. thesis, 140 p. Instituto Politécnico Nacional, Centro Interdisciplinario de Ciencias Marinas, La Paz, Mexico.
- Bonfil, R.  
1994. Overview of world elasmobranch fisheries. FAO Fish. Tech. Pap. 341, 119 p. Rome, Italy.
- Braccini, J. M., B. M. Gillanders, and T. I. Walker  
2005. Sources of variation in the feeding ecology of the piked spurdog (*Squalus megalops*): implications for inferring predator–prey interactions from overall dietary composition. *ICES J. Mar. Sci.* 62:1076–1094. [Article](#)
- Casper, B. M., A. Domingo, N. Gaibor, M. R. Heupel, E. Kotas, A. F. Lamónaca, J. C. Pérez-Jimenez, C. Simpfendorfer, W. D. Smith, J. D. Stevens, A. Soldo, and C. M. Vooren.  
2005. *Sphyrna zygaena*. The IUCN Red List of Threatened Species 2005: e.T39388A10193797. [Available from [website](#), accessed June 2016.]
- Castañeda, J., and L. Sandoval.  
2004. Hábitos alimentarios de los tiburones martillo *Sphyrna lewini* y *Sphyrna zygaena* en el Pacífico Ecuatoriano. Bachelor's thesis, 138 p. Univ. Jorge Tadeo Lozano, Bogotá, Colombia.
- Cheung, G. C. K., and C. Y. Chang.  
2011. Cultural identities of Chinese business: networks of the shark-fin business in Hong Kong. *Asia Pac. Bus. Rev.* 17:343–359. [Article](#)
- Chirichigno, N., and M. R. Cornejo.  
2001. Catálogo comentado de los peces marinos del Perú, 314 p. Publ. Espec. Inst. Mar Perú, Callao, Peru.
- Christensen, V., and D. Pauly.  
1992. ECOPEATH II—software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Model.* 61:169–185. [Article](#)
- Clarke, M. R. (ed.).  
1986. Handbook for the identification of cephalopod beaks, 273 p. Clarendon Press, Oxford, UK.
- Clarke, K. R.  
1993. Non-parametric multivariate analysis of changes in community structure. *Aust. J. Ecol.* 18:117–143. [Article](#)
- Cortés, E.  
1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* 54:726–738. [Article](#)
1999. Standardized diet compositions and trophic levels of sharks. *ICES J. Mar. Sci.* 56:707–717. [Article](#)
- Cortés E., F. Arocha, L. Beerkircher, F. Carvalho, A. Domingo, M. Heupel, H. Holtzhausen, M. N. Santos, M. Ribera, and C. Simpfendorfer.  
2010. Ecological risk assessment of pelagic sharks caught in Atlantic pelagic longline fisheries. *Aquat. Living Resour.* 23:25–34. [Article](#)
- Croxall, J. P., and P. A. Prince.  
1982. Caloric content of squid (Mollusca: Cephalopoda). *Br. Antarct. Surv. Bull.* 55:27–31.
- Diemer, K. M., B. Q. Mann, and N. E. Hussey.  
2011. Distribution and movement of scalloped hammerhead *Sphyrna lewini* and smooth hammerhead *Sphyrna zygaena* sharks along the east coast of southern Africa. *Afr. J. Mar. Sci.* 33:229–238. [Article](#)
- Espinoza, P.  
2014. Trophic dynamics in the northern Humboldt Current system: insights from stable isotopes and stomach content analyses. Ph.D. diss., 131 p. Univ. Bretagne Occidentale, Brest, France.
- Estupiñán-Montaño, C., and L. Cedeño-Figueroa.  
2005. Estudio de los hábitos alimenticios mediante el análisis del contenido estomacal del tollo mico *Carcharhinus falciformis* (Bibron, 1839) y los tiburones martillo *Sphyrna lewini* (Griffith & Smith, 1834) y *Sphyrna zygaena* (Linnaeus, 17758) en el área de Manta—Ecuador. Bachelor's thesis, 133 p. Univ. Laica Eloy Alfaro, Manabí, Ecuador.
- Fischer, J., K. Erikstein, B. D'Offay, S. Guggisberg, and M. Barone.  
2012. Review of the implementation of the International Plan of Action for the conservation and management of sharks. FAO Fish. Aquat. Circ.1076, 120 p. FAO, Rome.
- Fowler, S. L., R. D. Cavanagh, M. Camhi, G. H. Burgess, G. M. Cailliet, S. V. Fordham, C. A. Simpfendorfer, and J. A. Musick (eds.).  
2005. Sharks, rays and chimaeras: the status of the chondrichthyan fishes, 481 p. Status survey. IUCN/ SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.
- Francis, M. P.  
2016. Distribution, habitat and movement of juvenile smooth hammerhead sharks (*Sphyrna zygaena*) in northern New Zealand. *N. Z. J. Mar. Freshw. Res.* 50:506–525. [Article](#)
- Galvan-Magaña, F., H. J. Nienhuis, and A. P. Klimley.  
1989. Seasonal abundance and feeding habits of sharks of the lower Gulf of California, Mexico. *Calif. Fish Game* 75:74–84.
- Galvan-Magaña, F., C. Polo-Silva, S. B. Heránandez-Aguilar, A. Sandoval-Londoño, M. R. Ochoa-Díaz, N. Aguilar-Castro, D. Castañeda-Suárez, A. Cabrera Chavez-Costa, Á. Baigorri-Santacruz, Y. E. Torres-Rojas, et al.  
2013. Shark predation on cephalopods by sharks in the Mexican and Ecuadorian Pacific Ocean. *Deep-Sea Res. II* 95:52–62. [Article](#)
- García-Godos Naveda, I.  
2001. Patrones Morfológicos del otolito sagitta de algunos peces óseos del mar Peruano. *Bol. Inst. Mar Perú* 20(1–2):1–61.

- Gilly, W. F., U. Markaida, C. H. Baxter, B. A. Block, A. Boustany, L. Zeidberg, K. Reisenbichler, B. Robison, G. Bazzino, and C. Salinas.  
2006. Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Mar. Ecol. Progr. Ser.* 324:1–17. [Article](#)
- Gonzalez-Pestana, A., J. C. Kouri, and X. Velez-Zuazo.  
2016. Shark fisheries in the Southeast Pacific: a 61-year analysis from Peru. *F1000Research* 3:164. [Article](#)
- Hyslop, E. J.  
1980. Stomach content analysis—a review of methods and their application. *J. Fish Biol.* 17:411–429. [Article](#)
- Jereb, P., and C. F. E. Roper (eds.).  
2010. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date, vol. 2: myopsid and oegopsid squids. *FAO Species Catalogue for Fisheries Purposes* 4, vol. 2, 605 p. FAO, Rome.
- Jimenez-Valderde, A., and J. Hortal.  
2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. *Rev. Ibérica Aracnología* 8:151–161.
- King, R. A., D. S. Read, M. Traugott, and W. O. C. Symondson.  
2008. Molecular analysis of predation: a review of best practice for DNA-based approaches. *Mol. Ecol.* 17:947–963. [Article](#)
- Iverson, L. K., and L. Pinkas.  
1971. A pictorial guide to beaks of certain eastern Pacific cephalopods. *In* Food habits of albacore, bluefin tuna, and bonito in California waters, p. 83–105. *Calif. Dep. Fish Game, Fish Bull.* 152.
- Labropoulou, M., and A. Eleftheriou.  
1997. The foraging ecology of two pairs of congeneric demersal fish species: importance of morphological characteristics in prey selection. *J. Fish. Biol.* 50:324–340. [Article](#)
- Landman, N. H., J. K. Cochran, R. Cerrato, J. Mak, C. F. E. Roper, and C. C. Lu.  
2004. Habitat and age of the giant squid (*Architeuthis sanctipauli*) inferred from isotopic analyses. *Mar. Biol.* 144:685–691. [Article](#)
- Lombarte, A., M. Palmer, J. Matallanas, J. Gómez-Zurita, and B. Morales-Nin.  
2010. Ecomorphological trends and phylogenetic inertia of otolith sagittae in Nototheniidae. *Environ. Biol. Fish.* 89:607–618. [Article](#)
- Lowe, C. G., B. M. Wetherbee, G. L. Crow, and A. L. Tester.  
1996. Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. *Environ. Biol. Fish.* 47:203–211. [Article](#)
- Lu, C. C., and R. Ickeringill.  
2002. Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of southern Australian finfishes. *Mus. Vic. Sci. Rep.* 6, 65 p. *Mus. Vic., Fish. Res. Dev. Corp., Melbourne, Australia.*
- Magurran, A. E.  
1988. Ecological diversity and its measurement, 179 p. *Princeton Univ. Press, Princeton, NJ.*
- Medved, R. J., C. E. Stillwell, and J. J. Casey.  
1985. Stomach contents of young sandbar sharks, *Carcharhinus plumbeus*, in Chincoteague Bay, Virginia. *Fish. Bull.* 83:395–402.
- Navia, A. F., P. A. Mejía-Falla, and A. Giraldo.  
2007. Feeding ecology of elasmobranch fishes in coastal waters of the Colombian Eastern Tropical Pacific. *BMC Ecol.* 7:8. [Article](#)
- Nigmatullin, C. M., K. N. Nesis, and A. I. Arkhipkin.  
2001. A review on the biology of the jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae). *Fish. Res.* 54:9–19. [Article](#)
- Nesis, K. N.  
1983. *Dosidiscus gigas*. *In* Cephalopod life cycles, vol. 1: species accounts (P. R. Boyle, ed.), p. 215–231. *Academic Press, London, UK.*
- Ochoa-Díaz, M. R.  
2009. Espectro trófico del tiburón martillo *Sphyrna zygaena* (Linnaeus, 1758) en Baja California Sur: aplicación de  $\delta^{13}\text{C}$  y  $\delta^{15}\text{N}$ . M.S. thesis, 90 p. *Cent. Interdiscip. Cienc. Mar., Inst. Politéc. Nac., La Paz, Mexico.*
- Pennington, J. T., K. L. Mahoney, V. S. Kuwahara, D. D. Kolber, R. Calienes and F. P. Chavez.  
2006. Primary production in the eastern tropical pacific: a review. *Prog. Oceanogr.* 69:285–317. [Article](#)
- R Core Team.  
2016. R: a language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria.* [Available from [website](#), accessed October 2016.]
- RStudio.  
2012. RStudio: integrated development environment for R. *RStudio Inc., Boston, MA.* [Available from [website](#), accessed May 2012.]
- Smale, M. J.  
1991. Occurrence and feeding of three shark species, *Carcharhinus brachyurus*, *C. obscurus* and *Sphyrna zygaena*, on the Eastern Cape coast of South Africa. *S. Afr. J. Mar. Sci.* 11:31–42. [Article](#)
- Smale, M. J., and G. Cliff.  
1998. Cephalopods in the diets of four shark species (*Galeocerdo cuvier*, *Sphyrna lewini*, *S. zygaena* and *S. mokarran*) from KwaZulu-Natal, South Africa. *S. Afr. J. Mar. Sci.* 20:241–253. [Article](#)
- Soberón, J., and J. Llorente.  
1993. The use of species accumulation functions for the prediction of species richness. *Conserv. Biol.* 7:480–488. [Article](#)
- Spalding, M. D., H. E. Fox, G. R. Allen, N. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, et al.  
2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* 57:573–583. [Article](#)
- Xavier, J. C., and Y. Cherel.  
2009. Cephalopod beak guide for the southern ocean, 129 p. *Br. Antarct. Surv., Cambridge, UK.*
- Wetherbee, B. M., and E. Cortés.  
2004. Food consumption and feeding habits. *In* Biology of sharks and their relatives. (J. A. Carrier, J. C. Musick, and M. R. Heithaus, eds.), p. 225–246. *CRC Press, Boca Raton, FL.*
- Wolff, G. A.  
1982. A beak key for eight eastern tropical Pacific cephalopod species with relationships between their beak dimensions and size. *Fish. Bull.* 80:357–370.
1984. Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean. *NOAA Tech. Rep. NMFS* 17, 50 p.