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Food and feeding habits of the blue shark *Prionace glauca* caught off Ensenada, Baja California, Mexico, with a review on its feeding

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*Stomach contents of 893 blue shark (*Prionace glauca*) caught off Ensenada, Todos Santos Bay, Baja California, from 1995 to 1997 were analysed. 614 had identifiable food remains. A large variety of pelagic cephalopods occurred in 55.5% of all stomachs and accounted for 46.2% of all prey and 84% by estimated weight of stomach contents. The most abundant (17%) and frequent (32%) was* Histioteuthis heteropsis *and the most important by estimated weight (22%) was* 'Gonatus californiensis'. Argonauta *spp. and* Vampyroteuthis infernalis *were also abundant prey. A pair of beaks of giant squid* Architeuthis *sp. constitutes the first record for Mexican waters. Feeding habits and the probability of scavenging on mesopelagic cephalopods is discussed. The single most abundant prey was the pelagic, red crab* Pleuroncodes planipes *(41.7%). Other prey included teleost fish, amniotes and floating items. Diet varied greatly between months with no clear seasonal pattern. Tiny diet differences due to shark size or sex were inconclusive. A thorough review of studies on blue sharks stomach contents analysis is given. Blue shark feed on a large variety of passive pelagic prey, mainly mesopelagic cephalopods, that could be preyed upon as well as scavenged. Depletion of this predator due to overfishing may be leading to unknown cascading top-down effects in the mesopelagic realm.*

Keywords: blue shark, *Prionace glauca*, Baja California, stomach contents, feeding habits, shark trophic studies, mesopelagic cephalopods, *Pleuroncodes planipes*

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INTRODUCTION

The blue shark *Prionace glauca* L. is the most abundant pelagic shark worldwide in tropical and subtropical seas, distributed over oceanic as well as neritic waters, and is commercially caught elsewhere (Strasburg, 1959; Nakano & Stevens, 2008). It is the main target of the artisanal fishery for pelagic sharks off the western Baja California coast, of which 1000 annual tons are landed. This fishery faces management problems with overfishing, as catches are dominated by immature sharks, motivating the need for further research (Sosa-Nishizaki *et al*., 2008).

Sharks are abundant marine apex predators, and play a major role in the exchange of energy between upper trophic levels in the marine environment. Studies of consumption and feeding ecology of sharks are few, and knowledge of their role in marine ecosystems is limited (Wetherbee *et al*., 1990). Previous works on blue shark diet elsewhere reported fish, cephalopods, crustaceans, and miscellaneous items as the most common food, although they were largely unidentified to lower taxonomic levels (Strasburg, 1959; LeBrasseur, 1964; Capapé, 1975; Gubanov & Grigor'yev, 1975; Stevens, 1984). Prey identification in later studies revealed a remarkable difference in diet between sharks from offshore and inshore waters. The diet of blue shark caught over deep waters (>200–500 m) is dominated by mesopelagic cephalopods (and a large variety of teleosts such as myctophids), whereas shark from shallow waters (<200–500 m) feed mainly on fish (gadoids, scombrids and clupeoids) and neritic cephalopods (Table 1). This pattern has been observed particularly in blue shark from the Mid-Atlantic Bight (Kohler & Stillwell, 1981; Kohler, 1987), off the south-west British Isles (Stevens, 1973; Clarke & Stevens, 1974; Henderson *et al*., 2001), Azorean waters (Clarke *et al*., 1996), Adriatic Sea (Politi, 1997) and New South Wales (Stevens, 1984; Dunning *et al*., 1993) (Table 1).

Few studies have been made on blue shark diet in the California Current. Most of these observations have been made on sharks from shallow water (<500 m) indicating that blue shark feed on neritic prey (Table 1). This work describes the diet of blue sharks caught over the deep waters of the continental slope off Todos Santos Bay, Baja California, Mexico, testing for seasonal and shark size and sex differences. A global review of studies on blue shark feeding is considered.

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Table 1. Worldwide studies of blue shark stomach contents in which some kind of quantification is reported.

Area	Gear[1]	N	% empty (% everted)	Main prey[2]	Bottom depth (m)	Reference
South-western Atlantic						
North-eastern Brazil	LL	90	37 (35)	Cephalopods, teleosts	>2000	Hazin *et al.*, 1994
South Brazil	LL	68	41.2	*Chiroteuthis*, oceanic squid, *Lepidocybium*	500–3500	Vaske-Júnior & Rincón-Filho, 1998
North-eastern and South Brazil	LL	122	32 –38	*Arioma, Histioteuthis* oceanic teleost and squid	–	Vaske *et al.*, 2009
North-western Atlantic						
Nova Scotia	RR	706	19 (43)	Scombrids, clupeids, *Cyclopterus*	Nearshore	McCord & Campana, 2003
Mid-Atlantic Bight	LL	17	0	*Histioteuthis*, cephalopods, fish	>1000[3]	Casey & Hoenig, 1977[4]
Mid-Atlantic Bight	RR, LL	863	51.4	Gadids, clupeids, scombrids Oceanic cephalopods	<91 ≥91	Kohler & Stillwell, 1981[4]
Mid-Atlantic Bight	RR, LL	1199	47.6	Gadids, *Pomatomus* *Haliphron*, Cephalopods, *Alepisaurus*	≤183 >183	Kohler, 1987
North-eastern Atlantic						
Southern Ireland	H	7	0	*Cyclopterus*, *Enterulus*	<100[3]	Dorman, 1987
South-western Ireland	GN	248	19.4	*Histioteuthis*, *Halipron*	>1000[3]	Macnaughton *et al.*, 1998
South-western Ireland	GN	159	21	*Histioteuthis*, *Halipron*	>200–3000[3]	Henderson *et al.*, 2001
English Channel	RL	98	39	Scombrids, clupeids	70	Stevens, 1973
English Channel	LT, HG	151	32–43	Fish, *Sepia*	70	Clarke & Stevens, 1974
Bay of Biscay		12	0	Cranchiids, *Histioteuthis*	>500	
English Channel	RL	16	25	*Trachurus*, *Scomber*, *Sepia*	Nearshore	Fergusson, 1994
Azores	LL	195	42.8	*Capros*, *Histioteuthis*	Inshore/offshore	Clarke *et al.*, 1996
Mediterranean						
Ligurian Sea	LL	85	16.5	*Histioteuthis*, cephalopods	1000–2500	Garibaldi & Orsi Relini, 2000
Gulf of Taranto	LL	5	0	*Histioteuthis*, *Todarodes*	500–1700	Bello, 1990
Jonian and Adriatic Seas	LL	139	28	*Histioteuthis*, *Sepia*, *Ancistrocheirus*, *Chiroteuthis*		Clò & Bianchi, 1997
Adriatic Sea	RR	75	1.3 (22.6)	Sepiidae, Clupeidae, Gadidae	<60, 100–200	Politi, 1997
Pacific Ocean						
Pacific	LL	140	54.3	Unidentified fish and cephalopods, squid, sardines	Oceanic	Strasburg, 1959
North-west Pacific Transition	GN	70	18.6	*Chiroteuthis*, oceanic squid, octopods, myctophids	>4000[3]	Kubodera *et al.*, 2007
Frontal Zone Subartic	GN	72	55.5	Myctophids, *Ommastrephes*, Gonatidae	>4000[3]	Seki, 1993
New South Wales, Eastern Australia	RR	128	15.6 (60.1)	*Ancistrocheirus*, *Argonauta*, fish	Inshore to >200	Stevens, 1984; Dunning *et al.*, 1993
South Pacific	GN	60	30	Cephalopods, *Trachurus*, fish	>3000[3]	Yatsu, 1995
Northern Australia	LL	9	55 (33)	Unknown teleost	212–920	Stevens & McLoughlin, 1991
Central-north Chile	LL	228	27.2	*Cubiceps, Alepisaurus, Dosidicus*	>3000[3]	López, 2007
Central-south Chile	PS	13	23	*Engraulis*, *Dosidicus*		Pardo-Gandarillas *et al.*, 2007
California Current						
Gulf of Alaska	GN	29	17.2	Fish, squid	>2000[3]	LeBrasseur, 1964
Oregon—Washington	PS	14	14.2	*Merluccius*, *Engraulis*	≤200	Brodeur *et al.*, 1987
Monterey Bay	H	150	15.3	Euphausiids, *Engraulis*	≤500	Harvey, 1989
Santa Catalina Island	H	81	6	*Engraulis*, *Loligo* *Histioteuthis*	<500 >500	Tricas, 1979
South California Bight	GN	16	6.2	Squid, *Pleuroncodes*		Mearns *et al.*, 1981
South California Bight	GN	97	30.9	*Argonauta*, *Gonatus*		Preti *et al.*, 2006
Indian Ocean						
Equatorial Indian Ocean	LL	256	59 (11.7)	*Alepisaurus*, squid, octopus	Oceanic	Gubanov & Grigor'yev, 1975

[1]Gear: LL, longline; RR, rod & reel; H, hook; GN, gillnet; RL, rod & line; LT, light tackle; HG, heavy gear; PS, purse seine; [2]quantification method greatly differs between authors. Prey number, frequency of occurrence or weight were mostly used; [3]depth estimated from bathymetric maps; [4]samples from these works were included in Kohler (1987).

MATERIALS AND METHODS

Study area and sampling

Shark fishermen based in the harbour of Ensenada, Baja California, Mexico, fish for shark in an area typically comprising 10 to 50 km off Todos Santos Bay, on the continental slope over >800 m bottom depth (Figure 1). Blue shark, the main targeted species, is common year-round in the area, although they are more abundant during summer months further north off California (Harvey, 1989).

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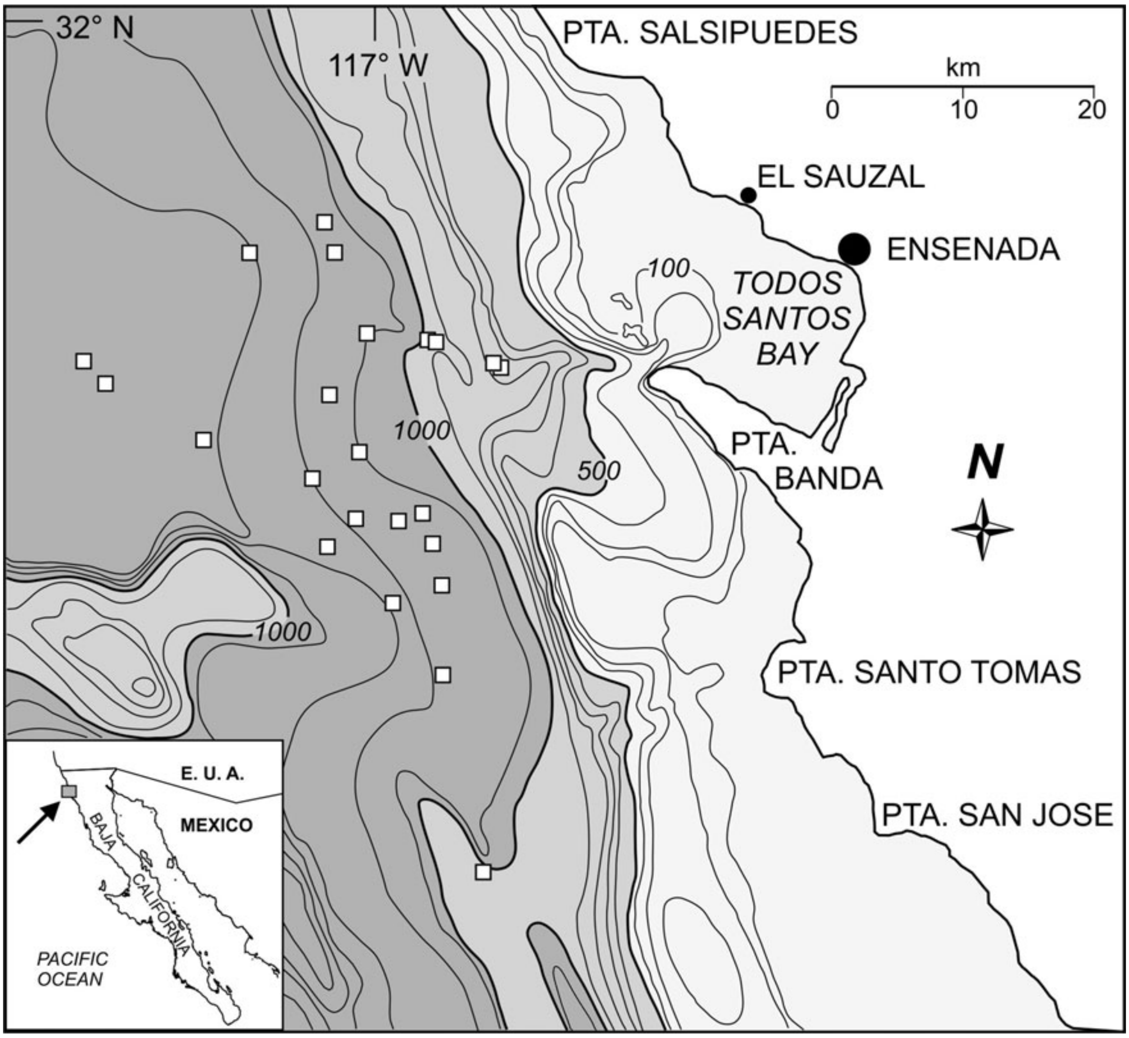

Fig. 1. Artisanal shark longline set-retrieval positions for 13 fishing nights between June 1995 and May 1996 off Ensenada, Baja California. Depth in 100 m isobaths.

Fishing is done in small open boats with outboard engines called *Pangas*. Trips last two nights offshore. A rudimentary longline with 400–500 hooks is set all night long (Sosa-Nishizaki *et al.*, 2008). Bait available at the local market are mackerel *Scomber japonicus*, bullet tuna *Auxis* spp., Pacific sardine *Sardinops caeruleus* or jumbo squid *Dosidicus gigas*.

Samples were collected every three or four weeks from April 1995 to May 1997. They were collected by us on board from May 1995 to April 1996 (except December to February when they were sampled by fishermen). During this time, sharks were measured for total length (TL, cm) and sexed, and shark weight was calculated through a length–weight relationship (Harvey, 1989). Fishermen continued sampling for stomachs from May 1996 to May 1997 (except August, October and February). No data on TL or sex are available for these samples. Monthly sample size ranged between 13 and 88 stomachs (Table 2).

Stomach contents analysis

Stomachs were analysed or frozen immediately after arriving to harbour. Stomach contents were weighed to the nearest 0.1 g. Stomach fullness was expressed as a percentage of shark weight. Stomach contents were screened through a 0.5 mm mesh sieve to retain prey remains useful for identification. Cephalopod beaks were identified using available guides (Wolff, 1984; Clarke, 1986) and reference collections at the Santa Barbara Museum of Natural History, California, and at CICESE, Baja California. Fish were identified from available keys for external features (Miller & Lea, 1972), vertebrae (Clothier, 1950) or otoliths (Harvey *et al.*, 2000). Unidentified fish were subsequently identified at the Marine Vertebrate Collection of the Scripps Institution of Oceanography. Marine mammal remains were identified according to the descriptions of Stevens (1973).

The number of consumed cephalopods or fish was estimated as the maximum number of upper or lower cephalopod beaks, or right or left fish otoliths. Due to the advanced degree of digestion of stomach contents only the most conspicuous prey items were weighed to the nearest 0.1 g. No attempt was made to weigh prey traces, such as cephalopod beaks.

Data analysis

The monthly minimum sample size required to adequately describe the diet of blue shark was determined using the graphic method proposed by Hoffman (1979) which used Pielou's method to calculate dietary diversity (H_k).

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Table 2. Summary of blue shark stomachs collected off Ensenada, Baja California, analysed in this study.

Date[1]	Stomach					Sex		TL[2] (cm)
	Food	Just bait	Empty	Everted	Total	Male	Female	
3 April 1995	14		4		18	3		203.5 ± 18.2
2 May 1995	56	6	7		69	26	16	133.8 ± 39.0
12 May 1995	10		3		13			
29 June 1995	26	1	1		28	10	18	111.0 ± 21.7
25 July 1995	27		5	1	33	28	5	119.6 ± 33.0
17 August 1995	16	3	5	2	26	18	8	161.5 ± 39.7
25 September 1995	20		18	1	39	37	2	170.4 ± 27.9
24 October 1995	56	8	24		88	34	43	153.1 ± 21.3
20 November 1995	19	1	6	1	27	9	17	142.0 ± 17.5
21 December 1995	22	2	1		25			
27 December 1995	30	1	3	1	35			
12 February 1996	40	1	5	1	47			
11 March 1996	17	2			19			
28 March 1996	31	16	15	3	65	46	19	115.1 ± 20.2
15 & 30 April 1996[3]	23		4	1	28	17	4	142.2 ± 34.7
13 & 22 May 1996[3]	35		13		48			
24 June 1996	27	3	9	4	43			
18 July 1996	21	1			22			
24 & 27 September 1996[3]	10	4	3	2	19			
1 November1996	11		10	4	25			
19 November 1996	14	3	7	1	25			
31 December 1996	4	1	1		6			
29 January 1997	35	5	7	1	48			
25 & 30 March 1997[3]	29	6	17	1	53			
23 April 1997	9	4	6		19			
10 May 1997	12	3	9	1	25			
Total	614	71	183	25	893	228	132	139.2 ± 34.2

[1]Samples were also taken the day after every given date; [2]TL, total length (mean ± SD); [3]samples pooled because of temporal proximity.

Frequency of occurrence, numeric and gravimetric (volumetric) methods were used to quantify the diet. Frequency of occurrence (%FO) was calculated as the percentage of blue shark that consumed certain prey. Number (%N) is the number of individuals of a certain prey relative to the total number of individual prey. Weight (%W) is defined as the weight of a certain prey relative to the total weight of all prey, expressed as a percentage (Cortés, 1997). The index of relative importance (IRI) = (%N + %W) × (%FO) was plotted to illustrate monthly diet composition (Pinkas *et al.*, 1971). Only prey species or taxa with IRI values >1% were included in plots.

A log-linear analysis was performed with measured shark to test for the significance of the interaction terms (prey number by season, shark sex, size and food type) (Cortés, 1997). Stomach contents were grouped by season (spring, summer and autumn 1995 and spring 1996), shark size (< 120, 120–160 and >160 cm TL), and food type (Vampyromorpha, squids, octopods, crustaceans, fish, and miscellaneous items (mammals, floating objects and trash)).

The effect of each of these variables on shark diet (same 6 food types) was tested. Differences in prey numbers among shark groupings were analysed by building $R \times C$ contingency tables and calculating G-statistics. This statistic has a Chi-square distribution with $(R\text{-}1) \times (C\text{-}1)$ degrees of freedom. *Post-hoc* comparisons were performed by removing the variable with largest G marginal value and testing again for differences with the remaining variables (Cortés, 1997).

Frequency of occurrence values among different shark groupings were compared by transforming them to proportions and performing a comparison of two or more proportions (Zar, 1999). Statistical analyses were considered significant ($P < 0.05$), very significant ($P < 0.01$) and highly significant ($P < 0.001$).

Cephalopod mantle length (ML) and weight were estimated from lower beak rostral or hood lengths (measured to the nearest 0.1 mm), using available relationships for squids and vampyromorphs (Wolff, 1984; Clarke, 1986; Kubodera, 2005) and pelagic octopods (Smale *et al.*, 1993; Lu & Ickeringill, 2002; Santos *et al.*, 2002). Cephalopod standard lengths (from arm tip to mantle tip) were estimated from ratios obtained from drawings in Young (1972) and Nesis (1987), as suggested by Clarke *et al.* (1996).

The total carapace length (CL) of pelagic red crabs was measured from the tip of the rostrum to the posterior midpoint. Relationships between CL and standard carapace length (SCL, from the base of subrostral spines of the rostrum to the posterior midpoint) and length of pelagic crab (TL, from the end of the tail to the tip of extended claws) were obtained from individuals (22.7–31.8 mm CL) stranded in Todos Santos Bay during the 1998 El Niño (all measurements in mm):

$$SCL = 0.186 + 0.766CL, N = 61, r^2 = 0.88.$$

$$TL = 6.544 + 2.943CL, N = 61, r^2 = 0.68.$$

An average TL to weight relationship for both sexes was taken from Gómez-Gutiérrez & Sánchez-Ortíz (1997). Fish standard lengths were estimated from otolith lengths using available relationships (Harvey *et al.*, 2000).

RESULTS

Samples structure

A total of 893 blue shark stomach were collected, of which 614 (68.7%) had food, 254 (28.4%) were completely empty (20.4%) or had just bait remains (7.9%), and 25 (2.8%) were everted. Measured shark accounted for 364 (40.7%) of the total collected, of which 132 were females, 228 males and four unsexed (Table 2). Sharks ranged 64–240 cm TL. Males were larger than females (mean cm TL 157.9 ± 24.4 SD versus 104.2 ± 11.0; Mann–Whitney *U*-test $U = -15.8$, $P < 0.001$). Mean shark total length and sex-ratio both significantly changed by month (Table 2), although no correlation was found between TL and sex-ratio ($r = 0.4$, N = 10, $P > 0.05$).

Stomach contents

Bait remains were readily identifiable by their fresh appearance and knife cuts (McCord & Campana, 2003). They were found in a third (33.1%) of all stomachs, and they accounted for a majority by weight of stomach contents pooled together, totalling 32.7 kg (61.5%). Bait and parasites were not considered when describing diet.

Stomach contents (excluding bait) were generally highly digested and usually only hard parts of prey remained. Almost half (44%) of the 614 stomachs with contents were represented only by traces (cephalopod beaks and lenses) <1 g in weight. Stomach contents weighing >100 g were rare (7.5%) (Figure 2A). Mean stomach content weight was 33.3 ± 102 g, with a maximum of 1141 g. Stomach fullness was determined for 239 measured sharks with stomach contents. This index averaged 0.28 ± 0.78%, with a maximum of 5%. Stomach fullness showed no correlation with shark weight ($r = 0.04$, N = 239, $P > 0.05$) (Figure 2B).

Cephalopods were identified by beaks belonging to at least 1897 individuals. Unidentified cephalopods (3.6% of all cephalopods) consisted of flesh remains of 35 cephalopods in 32 stomachs and another 35 lens pairs in 17 stomachs. Fish were mainly identified by their external features and vertebrae. Otoliths only accounted for 31 identified fish, most of them belonging to the Pacific hake *Merluccius productus* (28 otoliths in 12 stomachs). Almost half of the fish remains—185 (47%)—were unidentified. These consisted of 144 fish lens pairs found in 51 stomachs, and vertebrae and otoliths of another 41 fish in 39 stomachs. Lenses associated with identifiable remains were not taken into account when quantifying the diet. Cephalopod lenses accounted for twice the number and occurrence of fish lenses.

General description of diet

The main prey items of blue sharks were cephalopods, pelagic crustaceans and teleost fish. A large variety of oceanic cephalopods were found in 55.5% of stomachs, representing three coleoid orders and belonging to at least 34 species in 21 families. The most frequent cephalopods were histioteuthid squid, mainly *Histioteuthis heteropsis*, which occurred in one-third of stomachs. The next most frequent were gonatid and cranchiid squid, with 18 and 9%FO respectively. Pelagic octopods, dominated by *Argonauta*, accounted for 17%FO and *Vampyroteuthis infernalis* was found in 12% of stomachs. Crustaceans, mainly the pelagic red crab *Pleuroncodes planipes* occurred in almost one-third of stomachs. Teleosts occurred in one-fifth of stomachs; other than hake they were dominated by scombrids, engraulids and clupeids. Diet was numerically dominated by the pelagic red crab (41%N). All cephalopods accounted for 46%N but the most numerous species, *H. heteropsis*, was 17%N (Table 3). Teleosts accounted for only 9%N, although they comprised over a third of stomach contents weight. Cephalopods and crustaceans were 20%W each. Marine mammal remains accounted for 12%W and these were represented by remains of skin, hair, flesh and blubber. Three birds were found. A variety of floating items were also found in the stomachs including thaliaceans, algae and flying fish eggs. Human solid debris included food remains and plastic packing.

Hoffman's method (not shown) suggested a monthly sample size from 30 to 40 stomachs. Almost half of our samples reached that number of stomachs. Dietary diversity was high ($H_k = 0.8–1.0$) for all samples, indicating a generalist habit in the diet.

Interactions between sex, size and season

Interactions were tested between factors considering four seasons (spring, summer and autumn 1995 and spring 1996), sex, three size-groups (>160, 140–160 and <120 cm TL) and six food types: Vampyromorpha, squid, octopods, crustaceans, fish and miscellaneous items (mammals, floating objects and trash). The log-linear analysis showed that the three factor interactions between season, sex and size ($\chi^2 = 63$,

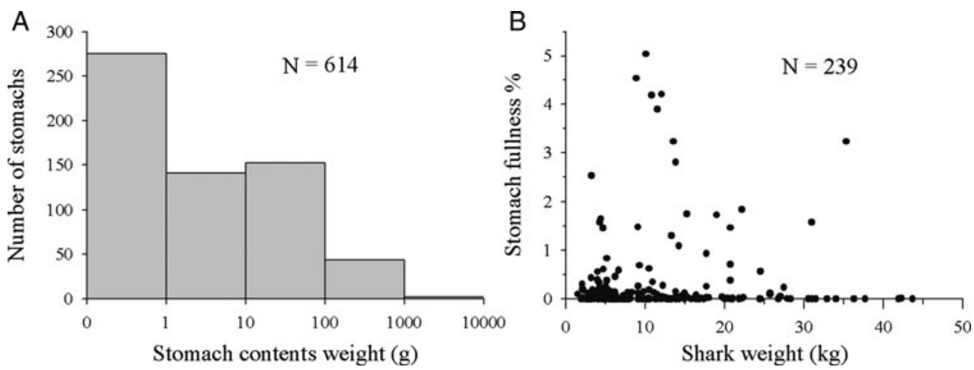

Fig. 2. (A) Frequency distribution of stomach contents weight and (B) relationship between stomach fullness and blue shark weight. Empty or everted stomach and bait remains were not included in these calculations.

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Table 3. Stomach contents quantification for 893 blue shark caught off Ensenada, Baja California.

Prey	Frequency of occurrence		Number		Weight	
	Frequency of occurrence	%	N	%	g	%
CEPHALOPODA	496	55.54	1940	46.24	4243.2	20.64
TEUTHIDA	425	47.59	1477	35.20	3244	15.78
Histioteuthidae	300	33.59	743	17.72	412.3	2.01
Histioteuthis heteropsis	286	32.03	712	16.98	263.3	1.28
Histioteuthis hoylei	30	3.36	31	0.74	149	0.72
Gonatidae	159	17.80	280	6.65		
Gonatus berryi	59	6.61	89	2.12		
'Gonatus californiensis'	51	5.71	102	2.43		
Gonatus onyx	41	4.59	44	1.05		
Gonatus pyros	40	4.48	43	1.03		
Gonatopsis borealis	2	0.22	2	0.05		
Cranchiidae	84	9.41	147	3.51	17.9	0.09
Leachia sp.	55	6.16	99	2.36		
Cranchia scabra	16	1.79	21	0.50	17.9	0.09
Liocranchia reinhardti	12	1.34	16	0.38		
Taonius sp.	7	0.78	7	0.17		
Unidentified Cranchiidae	2	0.22	4	0.10		
Planctoteuthis sp. A	32	3.58	36	0.86		
Planctoteuthis sp. B	1	0.11	1	0.02		
Grimalditeuthis bomplandii	29	3.25	32	0.76		
Chiroteuthis sp.	28	3.14	43	1.03		
Octopoteuthis deletron	28	3.14	31	0.74	491.8	2.39
Mastigoteuthis sp. A	26	2.91	29	0.69		
Mastigoteuthis sp. B	7	0.78	7	0.17		
Moroteuthis robusta	17	1.90	18	0.43	4.3	0.02
Onychoteuthis borealijaponicus	8	0.90	8	0.19	52.6	0.26
Onychoteuthis cf *'banksii'*	2	0.22	2	0.05		
Ancistrocheirus lesueuri	23	2.58	24	0.57	349.4	1.70
Dosidicus gigas	15	1.68	24	0.57	1915.7	9.32
Unidentified Ommastrephidae	1	0.11	1	0.02		
Loligo opalescens	12	1.34	46	1.10		
Unidentified Enoploteuthidae	2	0.22	2	0.05		
Neoteuthis?	2	0.22	2	0.05		
Architeuthis sp.	1	0.11	1	0.02		
OCTOPODIDA	154	17.24	242	5.76	113.7	0.55
Argonauta spp.	94	10.53	145	3.46	27.7	0.13
Japetella sp.	48	5.38	53	1.26	5	0.02
Haliphron atlanticus	23	2.58	24	0.57	81	0.39
Ocythoe tuberculata	13	1.46	17	0.41		
Octopus rubescens (juv.)	3	0.33	3	0.07		
VAMPYROMORPHIDA						
Vampyroteuthis infernalis	108	12.09	151	3.60	122.7	0.60
Unidentified Cephalopoda	49	5.49	70	1.67	762.85	3.71
CRUSTACEA	274	30.68	1750	41.74	4410.8	21.46
Pleuroncodes planipes	261	29.23	1727	41.19	4385.9	21.33
Gnatophausia zoea	9	1.01	9	0.21	18.7	0.09
Cancer oregonensis	1	0.11	1	0.02	0.1	<0.01
Unidentified Decapoda	1	0.11	1	0.02	1	<0.01
Idotea resecata	7	0.78	7	0.17	5.1	0.02
Euphausiiacea	3	0.34	3	0.07		
Amphipoda	1	0.11	1	0.02		
Unidentified Crustacea	1	0.11	1	0.02		
TELEOSTEI	191	21.389	382	9.10	7467.3	36.32
Scomber japonicus	33	3.70	43	1.03	1041.9	5.07
Auxis sp.	1	0.11	1	0.02		
Unidentified Scombridae	1	0.11	1	0.02	6.6	0.03
Sardinops caeruleus	28	3.14	37	0.88	381.7	1.86
Merluccius productus	21	2.35	37	0.88	1685.2	8.20
Engraulis mordax	16	1.79	38	0.91	138.3	0.67
Unidentified Myctophidae	6	0.67	8	0.19	7.3	0.04
Triphoturus mexicanus	1	0.11	1	0.02	1.5	0.01

Continued

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Table 3. Continued

Prey	Frequency of occurrence		Number		Weight	
	Frequency of occurrence	%	N	%	g	%
Lampanyctus sp.	1	0.11	1	0.02	3.2	0.02
Trachurus symmetricus	6	0.67	6	0.14	92.9	0.45
Sternoptychidae	4	0.45	4	0.10	3.5	0.02
Mola mola	3	0.34	3	0.07	1900.2	9.24
Sebastes spp.	3	0.34	3	0.07	410	1.99
Idiacanthus antrostomus	2	0.22	2	0.05	6	0.03
Pseudobathylagus milleri	1	0.11	3	0.07	102	0.50
Scorpaenichthys marmoratus	1	0.11	2	0.05	455	2.21
Mugil cephalus	1	0.11	1	0.02	450	2.19
Cubiceps sp.	1	0.11	1	0.02	164	0.80
Strongylura exilis	1	0.11	1	0.02	77	0.37
Cololabis saira	1	0.11	1	0.02	8	0.04
Zaniolepis frenata	1	0.11	1	0.02	1.5	0.01
Porichthys notatus	1	0.11	1	0.02	1.3	0.01
Unidentified Stomiiformes	1	0.11	1	0.02	1	<0.01
Unidentified Teleostei	90	10.08	185	4.41	528.3	2.57
OTHER VERTEBRATA	26	2.91	26	0.62	2720.1	13.23
Elasmobranquia	3	0.34	3	0.07	61.1	0.30
Aves	3	0.34	3	0.07	88.2	0.43
Feathers	4	0.45	4	0.10	0.1	0.00
Delphinus	8	0.90	8	0.19	1518.4	7.39
Unidentified Mammalia	6	0.67	6	0.14	600.2	2.92
Blubber	2	0.22	2	0.05	452.1	2.20
FLOATING ITEMS	59	6.60	63	1.50	160.2	0.77
Thaliacea	4	0.45	4	0.10	2.5	0.01
Pyrosoma	5	0.56	5	0.12	11	0.05
Algae	39	4.37	40	0.95	120.7	0.59
Philospadix	4	0.45	4	0.10	2.9	0.01
Exocoetid eggs	10	1.12	10	0.24	23.1	0.11
Human waste	29	3.25	32	0.76	1556.5	7.57
Total	893	100	4195	100	20558.15	100

df = 6, $P < 0.001$) and season, size and food type ($\chi^2 = 73$, df = 30, $P < 0.001$) were highly significant. All two factor interactions were significant ($P < 0.05$).

Temporal variation in diet

The diet of blue shark varied greatly by month (Figure 3). No clear pattern for the %FO of the most frequent prey (*H. heteropsis*, *P. planipes*, *Argonauta* spp. or *V. infernalis*) was found. Testing between the four seasons in prey numbers for the aforementioned six food types yielded highly significant differences ($G = 172$, df = 15, $P < 0.001$). *Post-hoc* tests confirmed significant differences between any pair of seasons when all prey groups were considered ($P < 0.001$), but showed no significant differences between all seasons for vampyromorphs, squids and miscellaneous items ($G = 8.3$, df = 6, $P > 0.05$).

Sexual variation in diet

Empty stomachs (31%) were equally distributed between both sexes ($Z = 0.15$, $P > 0.05$). Males had a higher occurrence of *Leachia* ($Z = 2.1$, $P < 0.05$), while females had a higher occurrence of all fish ($Z = 2.2$, $P < 0.05$). There were no significant differences in the occurrence of all other prey between sexes, including individual fish species ($Z \leq 1.25$, $P > 0.05$). Considering prey numbers by the six large groups, males ingested more crustaceans than females ($G = 66.3$, df = 7, $P < 0.001$). No differences were found for the rest of the prey groups ($G = 9.2$, df = 6, $P > 0.05$).

Shark size variations in diet

Smaller sharks (<120 cm TL) had a higher occurrence (%FO) of squid in general and *H. heteropsis* in particular ($\chi^2 = 14.1$, df = 2, $P < 0.001$), as well as teleosts ($\chi^2 = 6.2$, df = 2, $P < 0.05$), than the other two size-groups. The medium size-group (120–160 cm TL) had a higher occurrence of *Argonauta* (and octopods) in the diet ($\chi^2 = 12.8$, df = 2, $P < 0.01$). No differences were found for the rest of prey with shark size ($\chi^2 \leq 5.7$, df = 2, $P > 0.05$). Variation of prey %FO by shark size is shown in Figure 4.

Differences in the diet between sharks of three sizes-classes for numbers of six main prey categories were tested, yielding significant differences ($G = 58.2$, df = 10, $P < 0.001$). *Post-hoc* tests showed that there were no significant differences in prey number between medium (120–160 cm TL) and large (>160 cm TL) size-groups ($G = 8.14$, df = 5, $P > 0.05$). Variation of prey number by shark size is shown in Figure 5.

Prey dimensions

The most numerous cephalopod beak dimensions and pelagic red crab carapace lengths are shown in Figure 6. *Histioteuthis heteropsis* beak sizes almost did not overlap with those of

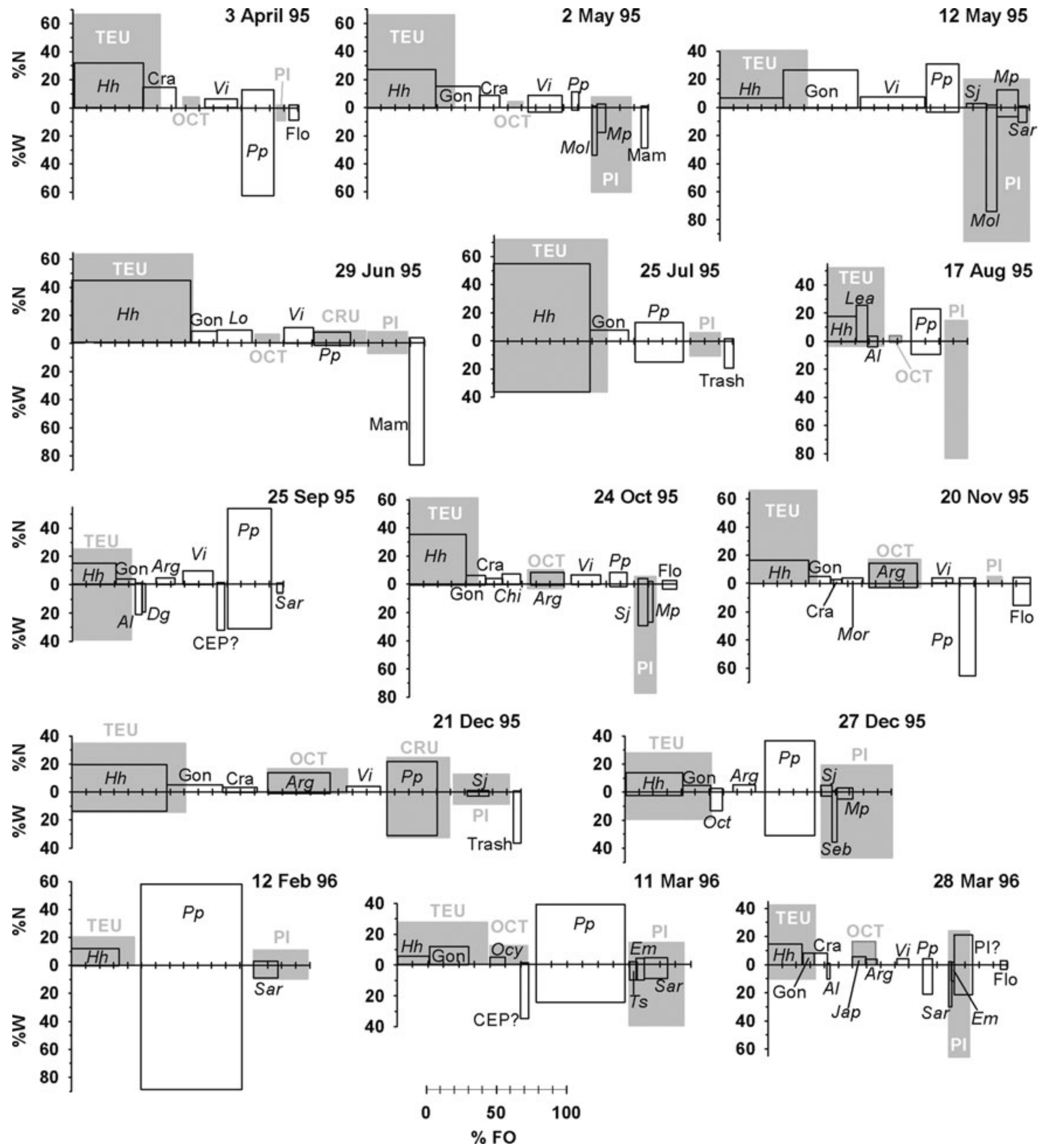

Fig. 3. Periodical composition by percentage number (%N), weight (%W) and frequency of occurrence (%FO) of those prey found in stomach contents of 893 blue sharks collected off Ensenada from April 1995 to May 1997. *Hh*, *Histioteuthis heteropsis*; *Hd*, *Histioteuthis hoylei*; *Lea*, *Leachia*; Cra, Cranchiidae; Gon, Gonatidae; *Al*, *Ancistrocheirus lessueuri*; *Lo*, *Loligo*; *Dg*, *Dosidicus gigas*; *Chi*, *Chiroteuthis*; *Mor*, *Moroteuthis*; *Oct*, *Octopoteuthis*; *Arg*, *Argonauta*; *Jap*, *Japetella*; *Ocy*, *Ocythoe tuberculata*; *Vi*, *Vampyroteuthis infernalis*, CEP?, unidentified cephalopods; *Pp*, *Pleuroncodes planipes*; *Sj*, *Scomber japonicus*; *Mp*, *Merluccius productus*; *Mol*, *Mola mola*; *Sar*, *Sardinops caeruleus*; *Em*, *Engraulis mordax*; *Seb*, *Sebastes*; *Ts*, *Trachurus symmetricus*; *Scor*, *Scorpaenichthys marmoratus*; *Aux*, *Auxis*; *Por*, *Porichthys*; PI? Unidentified fish; Mam, marine mammals; Av, birds; and Flo, floating debris. Large prey groups in grey: TEU, Teuthida; OCT, Octopodida; CRU, Crustacea; PI, Pisces. Monthly sample size as given in Table 2. Stomach contents of six sharks taken in December 1996 are not shown.

H. hoylei. Among gonatids, *'Gonatus californiensis'* beaks are distinctively larger than other species, and show darkened wings. Next in size was *G. berryi*. The pelagic red crab mean SCL measured 20.3 mm and ranged from 11.3 to 26.3 mm.

Estimated MLs of the 1092 squids eaten by blue sharks averaged 109 ± 92 mm ML. These varied from a mean of 52 mm ML for *H. heteropsis* to 332 mm ML for *'G. californiensis'*; *V infernalis* measured 82 ± 20 mm ML while *Argonauta* spp. were 35 ± 16 mm ML. The pelagic red crab measured 83 ± 9 mm TL and 56 fish were 203 ± 118 mm in standard length (Figure 7) (Table 4).

With an estimated mean weight of 156 g, cephalopods accounted for 84.5% of estimated weight of prey found in blue shark stomach contents. Gonatid squid alone, mainly *'G. californiensis'*, accounted for 25%. Despite being the most numerous cephalopods, histioteuthids accounted for only 15% by weight, as did vampyromorphs. Twenty beaks of the large pelagic octopod *Haliphron atlanticus* yielded an estimated mean weight of 1.6 kg, accounting for 11.5% of total weight. Although numerous, crustaceans represented a negligible portion of diet as estimated weight (2.2%). Teleosts accounted for 12% by estimated weight. The largest fish were the ocean sunfish *Mola mola*, two of which were represented by pieces of 750 and 1100 g (Table 4).

No correlation was evident between shark size and estimated cephalopod and crustacean sizes (Figure 8A–E, G).

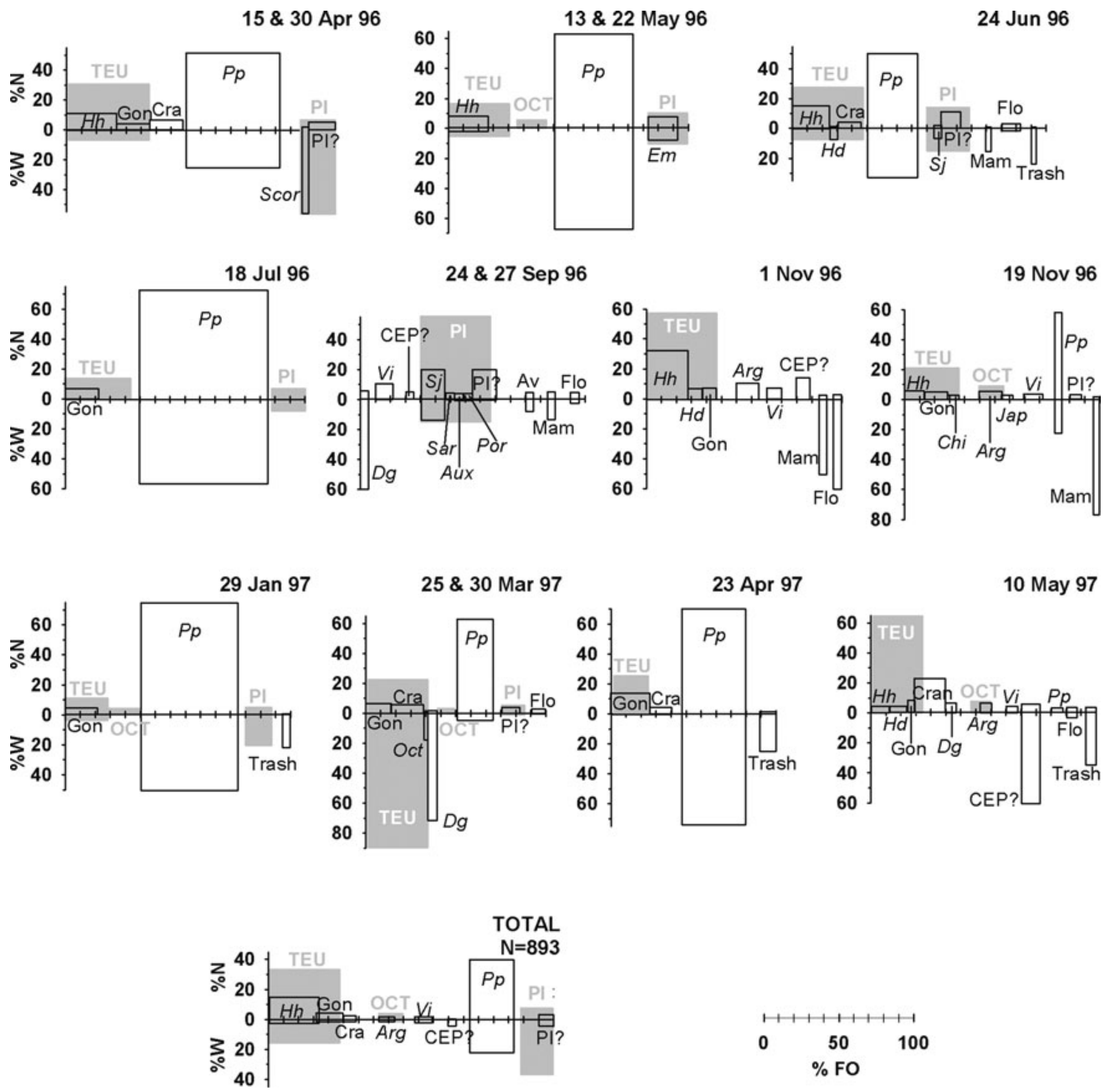

Fig. 3. Continued.

Thus *H. heteropsis* standard length relative to shark total length decreased from 17% TL in sharks <100 cm TL to 5% for shark >180 cm TL. *'Gonatus californiensis'* relative size decreased from 19 to 11%TL in sharks from <120 to >180 cm TL. Only for teleosts did prey size correlate with shark size ($r = 0.62$, N = 14, $P < 0.05$; Figure 8F).

DISCUSSION

Stomach contents

A high incidence of empty stomachs is common in blue shark diet studies (see Table 1) and largely depends on fishing gear (Hazin *et al.*, 1994). Shark caught at night, when most of their feeding occurs, may show a higher frequency of empty stomachs (Henderson *et al.*, 2001). Well-fed sharks are less interested in bait (Stevens, 1973; McCord & Campana, 2003; Wetherbee & Cortés, 2004) or they may vomit while on hook (Stevens, 1973). A high incidence of empty stomachs may also reflect a long time between capture and examination (Hazin *et al.*, 1994; Henderson *et al.*, 2001; McCord & Campana, 2003). Although some degree of digestion will take place owing to the very acidic pH of shark stomachs, there is no evidence that post-mortem digestion would significantly affect stomach contents. Stomach eversion may be the result of stress at capture or a natural process for removing undesirable ingested items (Kohler, 1987).

Stomach contents with food from previous studies averaged 480 g (Clarke *et al.*, 1996), 360 cc (McCord & Campana, 2003) or 172 cc to 146 g when including empty stomachs (Kohler, 1987; Garibaldi & Orsi Relini, 2000). These figures are larger than the 32 g mean found in this study (still only 80 g when excluding stomach contents <5 g). The average stomach fullness of our study, 0.18% of body weight, is also lower than those reported elsewhere, 0.9% to 0.30–0.49% (Kohler, 1987; Garibaldi & Orsi Relini, 2000). The subjective index indicates that mean fullness and digestion were half (Brodeur *et al.*, 1987) and stomachs with contents were usually less than half full and not recent (Harvey, 1989; Vaske *et al.*, 2009). No relationship has been found between stomach fullness and shark length (Kohler, 1987; Kubodera *et al.*, 2007).

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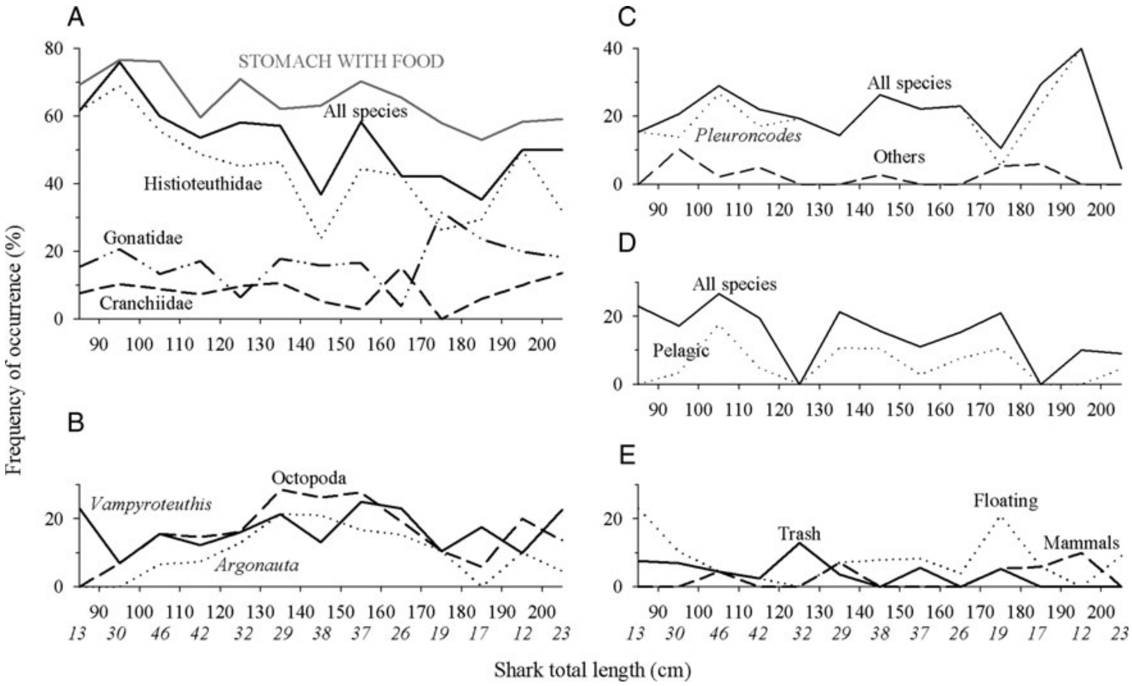

Fig. 4. Variability of the frequency of occurrence for (A) squid, (B) other cephalopods, (C) crustaceans, (D) teleost fish and (E) miscellaneous items found in 364 blue sharks (including empty stomachs) caught off Ensenada for each 10 cm total length. Numbers in italics refer to samples size for each shark size interval.

A high incidence of empty stomachs and few food items support the conclusion that sharks are intermittent rather than continuous feeders (Wetherbee & Cortés, 2004). Telemetered blue sharks revealed extensive dives of hundreds of metres during the daytime and smaller vertical excursions to the thermocline depth at night. This diel difference in shark diving behaviour may be a response to the diel vertical migration of its prey (Carey & Scharold, 1990). However, it is believed that blue sharks take most prey at night in near surface waters (Sciarrotta & Nelson, 1977; Harvey, 1989; Seki, 1993; Henderson *et al.*, 2001). Flesh remains were eaten the night of capture, while the most digested remains

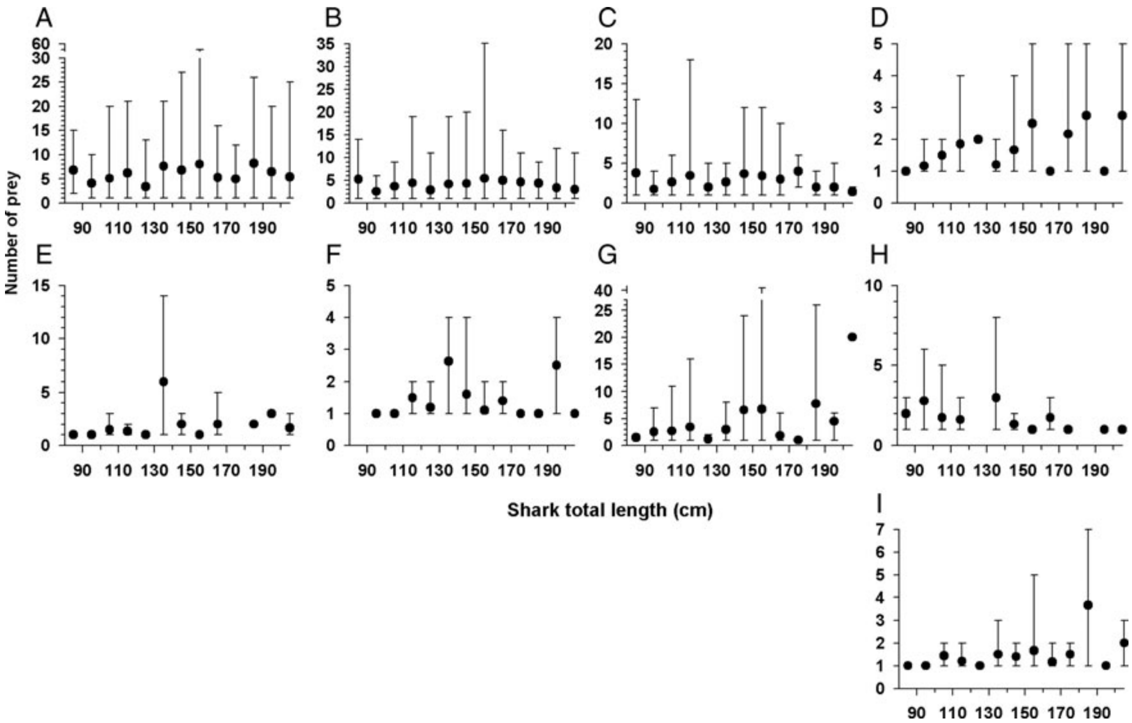

Fig. 5. Variability of the average and range in number for (A) all prey, (B) squid, (C) *Histioteuthis heteropsis*, (D) gonatids, (E) cranchiids, (F) octopods, (G) pelagic red crab, (H) fish and (I) *Vampyroteuthis infernalis* in occurrences of 364 blue sharks caught off Ensenada for each 10 cm total length. Samples size for each shark size interval as in Figure 4.

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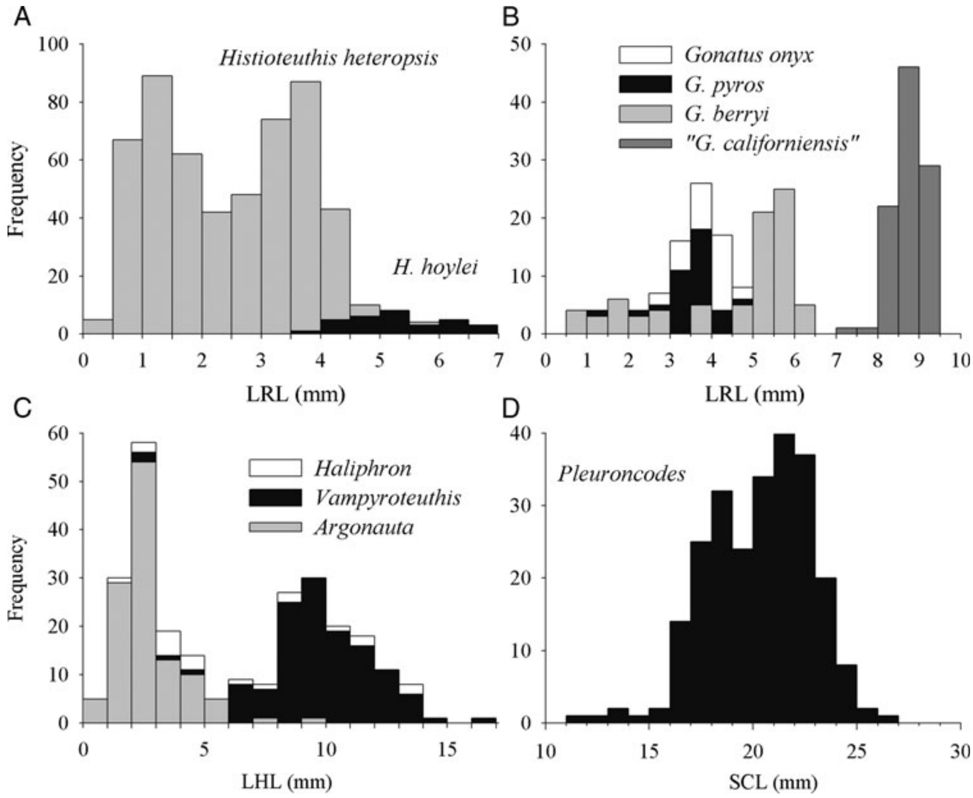

Fig. 6. Size distribution of hard remains of most numerous prey found in the stomach of 893 blue sharks caught off Ensenada: lower rostral length (LRL) for histioteuthid squid (A), gonatid squid (B), lower hood length (LHL) for octopods and vampyromorphs (C), and standard carapace length (SCL) for pelagic red crab (D). Prey number as in Table 4.

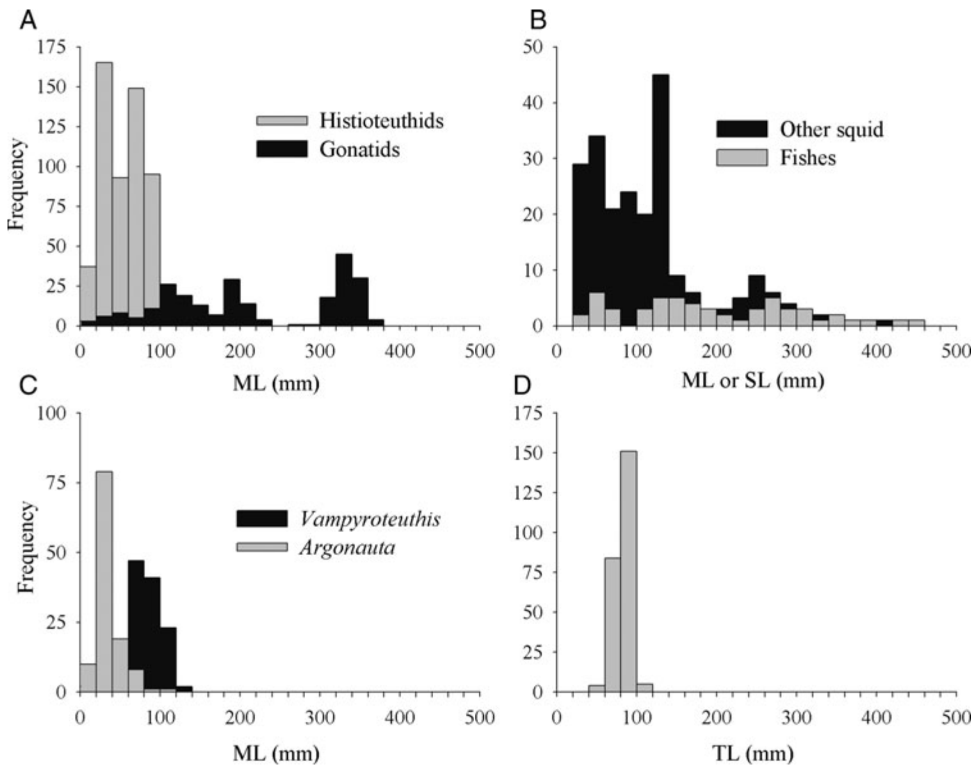

Fig. 7. Lengths of the most numerous prey found in the stomach of 893 blue sharks caught off Ensenada: (A) mantle length for histioteuthid and gonatid squid, (B) for other squid and standard length for fish, (C) mantle length for other cephalopods and (D) total length for pelagic red crab. Prey number as in Table 4.

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Table 4. Sizes of hard remains and dimensions estimated from them for preys of 893 blue shark caught off Ensenada, Baja California.

Prey	Number	Lower rostral length, mm			Estimated prey dimensions: Mantle length, mm			Weight, g				
		Mean	SD	Range	Mean	SD	Range	Mean	SD	Range	Total[1]	%
Squid											193066	57.58
'Gonatus californiensis'	99	8.77	0.40	7.4–9.5	332.7	17.1	273–363	724.2	107.7	407–936	73868	22.03
Gonatus berryi	81	4.50	1.66	0.7–6.3	125.4	51.6	12–183	75.5	42.0	0.1–134	6720	2.00
Gonatus onyx	30	3.90	0.53	2.5–4.8	123.5	22.0	67–160	69.8	21.0	24–111	3071	0.92
Gonatus pyros	32	3.53	0.63	1.1–4.5	107.3	27.7	24–153	37.9	18.3	1.3–82	1630	0.49
Gonatopsis borealis	2	3.75	0.28	3.5–3.9	147.7	9.0	141–154	114.5	20.5	100–129	229	0.07
Histioteuthis heteropsis	516	2.45	1.17	0.3–5.6	52.4	24.1	8–118	61.5	59.1	0.1–378	43788	13.06
Histioteuthis hoylei	31	5.35	0.78	4–6.8	85.5	11.4	65–106	237.6	84.9	112–414	7366	2.20
Architeuthis sp.	1	13.44			741.5			24365.0			24365	7.27
Dosidicus gigas	19	6.38	1.46	3.3–9.4	272.5	52.5	165–381	585.7	311.9	111–1410	14057	4.19
Ancistrocheirus lesueuri	20	4.70	1.20	2.9–7.3	150.2	49.1	80–259	271.1	288.8	40–1018	6506	1.94
Moroteuthis robusta	14	4.03	1.67	1.1–7.2	217.0	101.9	39–410	208.1	243.6	1–935	3746	1.12
Onychoteuthis borealijaponicus	8	4.08	0.79	3.1–5.3	220.0	48.3	160–294	133.1	76.3	53–265	1065	0.32
Octopoteuthis deletron	24	6.30	1.91	1.8–8.2	108.9	33.2	30–141	93.8	48.1	4–152	2908	0.87
Loligo opalescens	38	1.38	0.31	0.6–1.8	116.3	19.2	72–142	25.6	7.6	9–36	1178	0.35
Mastigoteuthis sp. 1	27	2.77	1.03	1.1–5.4	77.9	30.2	30–156	30.9	37.6	1–158	896	0.27
Mastigoteuthis sp. 2	7	4.11	0.43	3.2–4.4	117.8	12.7	91–127	72.5	19	34–88	508	0.15
Leachia sp.	80	1.49	0.19	0.9–1.9	120.0	13.5	79–147	5.0	1.5	1–8	495	0.15
Taonius sp.	7	3.87	0.71	2.9–5.0				44.2	18.0	22–76	309	0.09
Cranchia scabra	14	1.22	0.25	0.8–1.6	51.9	7.0	40–62	7.2	2.4	3–11	151	0.05
Liocranchia reinhardti	12	0.97	0.36	0.5–1.7	77.1	29.6	39–135	7.0	5.4	1–19	112	0.03
Chiroteuthis sp.	33	1.27	0.58	0.5–2.8	42.6	14.4	23–80	2.3	3.1	0.1–12	99	0.03
Other cephalopods		**Lower hood length, mm**									90241	26.91
Vampyroteuthis infernalis	126	9.77	2.19	2.4–16.0	82.3	19.7	15–138	328.2	249.7	1–1647	49558	14.78
Haliphron atlanticus	20	6.45	3.89	1.9–13.9				1607	2385	14–7728	38568	11.50
Argonauta spp.	118	2.75	1.31	0.5–9.5	34.9	16.4	6–119	13.2	54.5	1–585	1914	0.57
Ocythoe tuberculata	13	3.83	1.18	1.4–5.6	24.5	6.8	10–39	11.8	7.5	0.8–26	201	0.06
Crustaceans		**Total carapace length, mm**			**Total length, mm**							
Pleuroncodes planipes	244	26.2	3.27	14–34	83.8	9.6	49–106	4.3	1.4	0.7–8.7	7426	2.21
Fish		**Otolith length, mm**			**Standard length, mm[2]**						40149	11.97
Scomber japonicus	2				258	172.5	136–380	456.7	605.9	28–885	19638	5.86
Merluccius productus	27	10.71	5.05	5.2–26.6	237.7	107.4	115–552	162.1	242.1	11–1190	5998	1.79
Mola mola	2							942		753–1141	2826	0.84
Sardinops caeruleus	2				118.5	75.6	65–172	40.6	33	17–64	1502	0.45
Sebastes spp.	2				214	19.7	200–228	260.8	59.8	218–303	782	0.23
Scorpaenichthys marmoratus	1				300			227.5			455	0.14
Mugil cephalus	1				335			450			450	0.13
Engraulis mordax	1				111			16.4			623	0.19
Cubiceps sp.	1				250.0			164.0			164	0.05
Trachurus symmetricus	2	3.8			92.5	45.9	60–125	24.6	22.3	8–40	148	0.04
Porichthys notatus	1	7.6			186.9			105.6			106	0.03
Strongylura exilis	1				450			77			77	0.02
Myctophidae	3				59	20	57–60					
Unidentified fish								~82			7380	2.20
Marine mammals					150[3]						2570	0.77
Trash											1556	0.46
Others											310	0.09
Total											335317	100.00

[1]Multiplying the total number for each prey in Table 3 by its mean weight; [2]those not estimated from otoliths were found whole in the stomach; [3]fork wide of a *Delphinus* sp. foetus?

were taken the previous nights (Clarke *et al.*, 1996). This could be the case for cephalopods, as lack of flesh in the stomach contents indicates that they were mostly taken quite some time before being caught, perhaps the night before.

Differential digestion between teleosts and cephalopod prey as a bias in the study of shark diet has been stressed (Trikas, 1979; Kohler, 1987; Harvey, 1989; Hazin *et al.*, 1994; Clarke *et al.*, 1996; Garibaldi & Orsi Relini, 2000; McCord & Campana, 2003; Kubodera *et al.*, 2007). Cephalopod flesh particularly that of mesopelagic species is digested more quickly than firm fish. On the other hand, cephalopod beaks may stay longer than any other prey

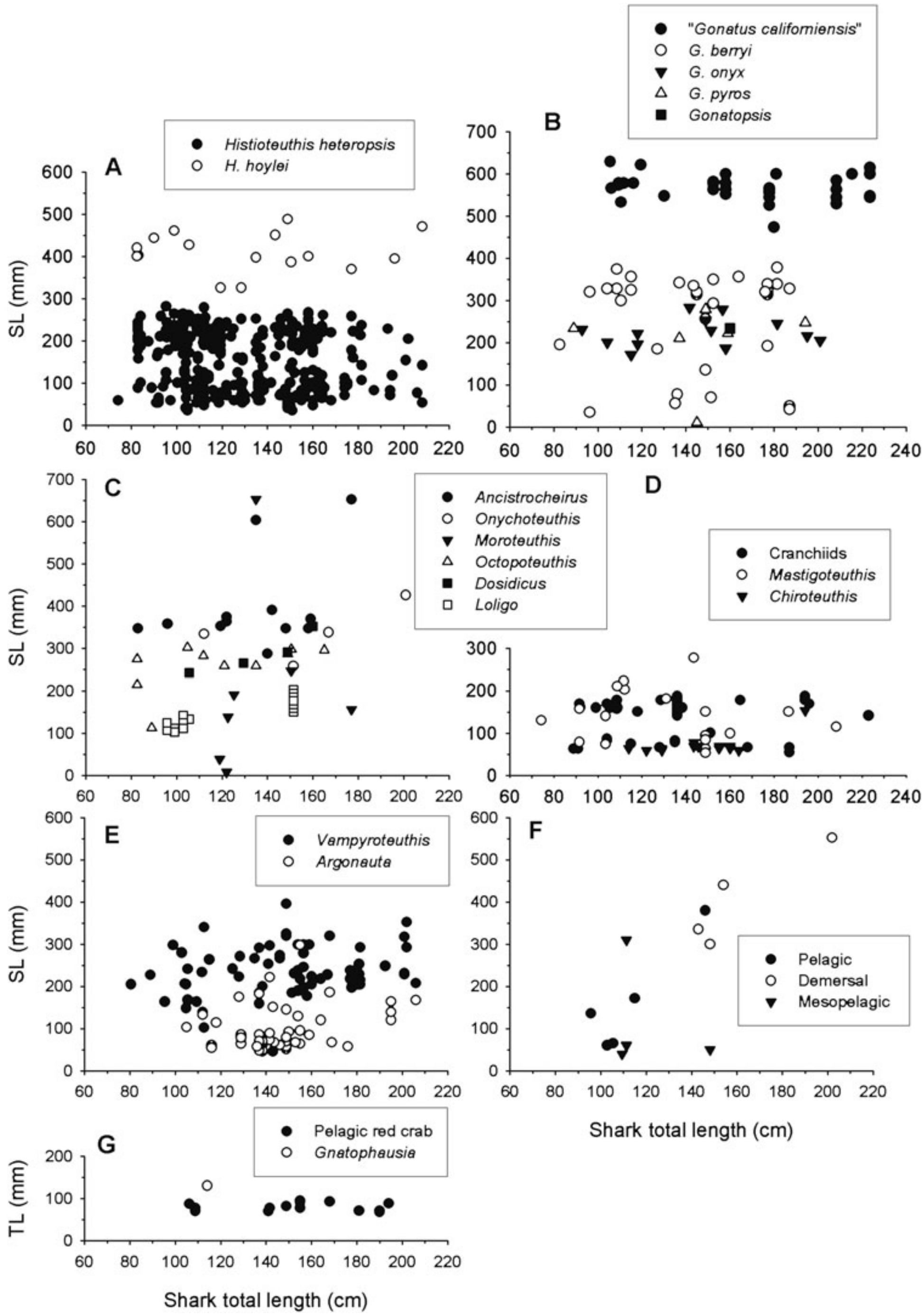

Fig. 8. Relationship between prey standard length (SL) or total length (TL) and blue shark size for 364 sharks: (A) histioteuthids, (B) gonatids, (C) and (D) other squid, (E) other cephalopods, (F) teleosts and (G) total length of crustaceans.

remains in the digestive tract (Harvey, 1989; Clarke *et al.*, 1996). This is reflected by the fact that sometimes teleosts comprise most of the stomach contents by volume, even when cephalopod beaks are more numerous (Casey & Hoenig, 1977; Clarke *et al.*, 1996). Our estimation of prey biomass in blue shark diet may have been largely biased toward pelagic squid and octopods.

Cephalopods

Blue shark caught off Ensenada preyed on a large variety of pelagic cephalopods from the upper continental slope. Up to 21 species of squid and 5 of octopods in Young's (1972) checklist for southern California were found. Not found in blue shark diet were families Enoploteuthidae, Brachiteuthidae and Bathyteuthidae, and seven species of ommatrephids and cranchiids, and the pelagic octopod *Eledonella*. However, other species such as *Ancistrocheirus lesueuri* absent from the checklist and seldom reported in the California Current (Markaida & Hochberg, 2005), were found in blue shark stomachs.

Preference for mesopelagic cephalopods of families Histioteuthidae, Gonatidae and Cranchiidae indicates the slow, low-activity nature of this predator. Histioteuthid squid were the most frequent and numerous prey of blue

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shark in most offshore areas near continental slope, although in some regions cranchiids, *Ancistrochierus* or *Chiroteuthis* were most important (Table 1).

The most important prey by estimated weight in the diet of blue shark, *'Gonatus californiensis'*, was identified by unchecked beaks (Markaida & Hochberg, 2005) and tentatively named after a species whose adults are yet unknown. Walker considers these beaks to be *Galiteuthis*? sp. A (e.g. Pitman *et al*., 2004). Our findings suggest that this is a common squid in the area and underline the importance of studying stomach contents of marine predators to determine cephalopod distribution and biology. Blue shark stomach contents have yielded little known cephalopods (Nigmatullin, 1976; Roper & Vecchione, 1993; Bello, 1994; Clò & Bianchi, 1997; Macnaughton *et al*., 1998) and it is probably the fish that a largest variety of cephalopods consumes.

Vampyroteuthis infernalis is seldom reported as prey of blue sharks from other seas (Clarke *et al*., 1996), but our results suggest that it is a common species in the California Current. By contrast, the large pelagic octopod *Haliphron atlanticus* has greater importance in the diet of blue shark from other areas (Kohler & Stillwell, 1981; Kohler, 1987; Clarke *et al*., 1996; Macnaughton *et al*., 1998; Henderson *et al*., 2001; Kubodera *et al*., 2007) than from the California Current. *Argonauta* is also abundant in the diet of sharks from subtropical seas (Dunning *et al*., 1993).

A pair of giant squid *Architeuthis* sp. beaks were found in a stomach collected on the 19 November 1996. This discovery represents the southernmost record of this species in the California Current and the first record for Mexican waters, although it could have been taken by the shark somewhere else (Clarke & Stevens, 1974). The dimensions of these beaks are similar to those found in a blue shark from the Eastern Equatorial Atlantic (Nigmatullin, 1976), suggesting a ML of 74 cm and a weight of 24.3 kg (Table 4), the largest prey found in this study.

Many mesopelagic cephalopods undertake diel migrations (Roper & Young, 1975) and blue shark may feed on them throughout the water column (Kohler, 1987). Some midwater cephalopods visit surface waters at night (Roper & Young, 1975) where blue shark could take them (Trikas, 1979; Harvey, 1989). However, the vertical distribution of other mesopelagic cephalopod prey suggest that blue shark might forage at depths of over several thousand metres (Kubodera *et al*., 2007), or at least deeper than 500 m (Clarke *et al*., 1996). The deepest blue shark telemetered dives surpass 600 m depth in the Sargasso Sea and eastern Australia but reach only 275 m depth off California (Carey & Scharold, 1990; Nakano & Stevens, 2008). In the California Current a well developed oxygen minimum layer occurs below 500 m depth, and it could limit blue shark diving depth, while cephalopod prey such as *V. infernalis* are thought to live below those depths (Roper & Young, 1975). Occurrences of some mesopelagic prey in the blue shark diet are difficult to explain owing to predation. Blue shark telemetry studies currently underway could determine their vertical migration range off California and clarify this question.

Most families found in this study are neutrally buoyant cephalopods such as ammoniacal squid (Histioteuthidae and Cranchiidae; Voight *et al*., 1994), lipid rich gonatids and pelagic octopods (Alloposidae and Boliteanidae; Nesis, 1996) already noted in other studies (Table 1). Spent females of these mesopelagic cephalopods float passively to the surface and die (Nesis, 1996). This could be the case for gonatids like *'G. californiensis'* whose beaks show pigmented wings, indicating a mature squid. Blue shark might easily scavenge on these dead buoyant cephalopods floating in upper waters. This possibility has only been considered once (Garibaldi & Orsi Relini, 2000), despite the knowledge that blue sharks are active scavengers (see Other prey below). This feeding behaviour has been widely discussed for sea birds (Croxall & Prince, 1994). In fact, histioteuthid gonatid and cranchiid squid were also the most abundant cephalopod prey eaten by Laysan albatrosses from the neighbouring Guadalupe Island (Pitman *et al*., 2004). All but three of the 22 species of pelagic cephalopods identified in that study were found also in the blue shark diet. The most abundant and frequent species in albatross pellets (*Histioteuthis hoylei*, *Taonius borealis* and *Gonatus pyros*), except *Galiteuthis*? sp. A = *'G. californiensis'*, were rare in blue shark, although that could be an artefact of the small sample size of bird pellets. The most important prey items in the blue shark diet were also common in albatross pellets, except for the notable absence of *V. infernalis* and *Argonauta* spp. Ingested cephalopod lower beak dimensions are strictly similar in range and mean for many species in both predators. If albatrosses scavenge squid prey (Croxall & Prince, 1994; Pitman *et al*., 2004) it is hard to believe that an active scavenger like the blue shark would not profit from such an abundant food source as well, even if they could also catch those prey alive. This comparison suggests that many squid taken by blue sharks could have been scavenged. It would explain the predominance of midwater cephalopod beaks over mesopelagic fish remains. This possibility is important to note in trophic modelling that includes an abundant pelagic predator like the blue shark.

A third way to obtain mesopelagic cephalopods might be to take them secondarily from cetaceans (Stevens, 1973). However, Kohler (1987) did not find a relationship between marine mammals and cephalopod occurrences in blue shark stomachs. Furthermore, large differences have been found between cephalopods from sperm whales and blue sharks taken off the Azores regarding species composition, estimated sizes and depth distribution (Clarke *et al*., 1996). Seventeen out of 27 species of pelagic cephalopods taken by sperm whales off California (Fiscus *et al*., 1989) were found in the blue shark diet. Both predators feed heavily on gonatids, histioteuthids and cranchiids, although onychoteuthids and octopoteuthids, abundant in sperm whale stomachs, are rarely consumed by blue sharks. Feeding on sperm whale regurgitations is unlikely because the most abundant species in this predator (*Gonatopsis borealis*, *Moroteuthis robusta*, *Octopoteuthis deletron*, *H. hoylei*, *Galiteuthis* spp. *Mastigoteuthis* sp., *Taonius* sp. and *V. infernalis*) (Fiscus *et al*., 1989) are rare or absent in blue shark stomachs and/or their beaks are much larger.

The squid composition of the blue shark diet significantly differs from that of swordfish, who take mainly muscular ommastrephids and the gonatid *Gonatus berryi* of western Baja California (Markaida & Hochberg, 2005). This difference in consumption has been also documented for the Mediterranean (Bello, 1996; Garibaldi & Orsi Relini, 2000) and for Azorean waters (Clarke *et al*., 1996). Both predators are common catches in the pelagic fisheries of the California Current (Sosa-Nishizaki *et al*., 2008) and their cohabitation can thus be understood on the basis of different feeding habits that reduce competition for food resources. The same difference has been found when comparing blue shark and lamniid shark diets (Kohler, 1987; Kubodera *et al.*, 2007).

Pelagic red crab

Predation on pelagic red crab *Pleuroncodes planipes* has been previously documented in the Southern California Bight (Bane, 1968; Mearns *et al.*, 1981). Only once have crustaceans been observed as the most numerous prey; Harvey (1989) reported direct feeding on euphausiids, although we found them as secondary prey from mackerel stomachs. We also found pelagic red crab and juvenile *Octopus rubescens* beaks from the stomachs of two cabezon *Scorpaenichthys marmoratus* from a shark stomach, so smaller prey may have been secondarily ingested.

The centre of the pelagic distribution of the pelagic red crab is the continental shelf of western Baja California south of Punta San Antonio, although it extends north into California waters during El Niño warm events (Longhurst, 1966; Boyd, 1967). However, most of the sampling period comprised a La Niña event (September 1995 to February 1997; Schwing *et al.*, 2002) and not until August during the 1998 El Niño were stranded crabs observed in Todos Santos Bay (U. Markaida, personal observation). Recently it has been found that pelagic red crab is abundant over the shelf and the shelf break southward, near the studied area (Robinson *et al.*, 2004). The size distribution of pelagic red crabs ingested by blue sharks is comparable to the pelagic form sampled near the surface in that study (mean SCL = 17.7 mm, range 7.7–28.2 mm) (Robinson *et al.*, 2004), and those stranded in Todos Santos Bay in 1998 (mean SCL = 21.7 mm, range 18.3–24.5 mm). During their pelagic phase, they perform vertical migrations between the bottom and the surface, and thus they may have been taken by blue sharks throughout the water column. Crabs >26 mm SCL become exclusively benthic (Boyd, 1967) and thus might be out of the blue shark reach.

Other prey

Both neritic and pelagic fish (mainly scombrids, gadoids and clupeoids) are not uncommon in the blue shark diet, suggesting that blue shark feed at all depths (Stevens, 1973; Kohler & Stillwell, 1981; Harvey, 1989; Henderson *et al.*, 2001; McCord & Campana, 2003). Remains of neritic fish almost whole or with flesh, in sharks caught off Ensenada suggest a recent movement from inshore waters. Blue sharks perform both diel and seasonal offshore–inshore movements (Sciarrotta & Nelson, 1977). Anchovies were the most common fish prey in nearshore waters of California (Tricas, 1979; Harvey, 1989), while myctophids and gonostomatids were the most abundant in the oceanic areas of the Pacific (Seki, 1993; Kubodera *et al.*, 2007).

Marine mammal and bird remains were evidently scavenged rather than taken alive (Stevens, 1973; Kohler & Stillwell, 1981; Kohler, 1987; Macnaughton *et al.*, 1998; Garibaldi & Orsi Relini, 2000; Vaske *et al.*, 2009). Predation on netted dolphins has been proposed as an explanation for their occurrence in blue shark stomach contents (Henderson *et al.*, 2001). Shark fishermen harpooned dolphins in Todos Santos Bay for use as bait when other sources are scarce, as was observed once during this study (U. Markaida, personal observation).

Although anthropogenic material found in blue shark stomach contents is uncommon (1 to 5.9%FO; Stevens, 1973; Kohler & Stillwell, 1981; Kohler, 1987; Macnaughton *et al.*, 1998; Garibaldi & Orsi Relini, 2000; McCord & Campana, 2003; Vaske *et al.*, 2009), it does reflect the impact of human activities on the distant epipelagic environment. Trash of anthropogenic origin found in this study reflects the intense maritime traffic in the area.

Variations in blue shark diet

Although blue sharks are more abundant during summer and autumn farther north off California waters (Harvey, 1989), they are abundant off Ensenada all year around. Few studies have focused on temporal variation in blue shark diet in a given area. Clarke & Stevens (1974) found that a monthly decrease in cephalopod beak occurrence in sharks was due to decreasing shark size as the season advances in the English Channel. Cephalopods, teleosts and alepisuriids increased their frequency from spring to winter in the stomach contents of shark caught offshore Mid-Atlantic Bight, while miscellaneous food and marine mammals decreased (Kohler, 1987). Blue sharks during their seasonal appearance in Monterey Bay fed on northern anchovy, euphausiids and market squid (Harvey, 1989). Interannual differences in blue shark diet have been also documented off Nova Scotia (McCord & Campana, 2003). For a given area, the largest variability in shark diet is temporal and we found large monthly differences. This would be most likely due to large variability in availability and patchy distribution of pelagic prey. No clear tendency in seasonality was found in %FO of most frequent prey (Figure 3). These results suggest that feeding studies based on a few sample collections without covering the whole season must be taken with caution.

Spatial variation in the diet has been extensively documented and mainly explained by changes in potential prey availability (Tricas, 1979; Kohler & Stillwell, 1981; Kohler, 1987; McCord & Campana, 2003; Vaske *et al.*, 2009). As mentioned before, diet variation is remarkable between sharks taken from inshore and offshore waters (Table 1). Our results generally differ from other studies in the California Current (Tricas, 1979; Harvey, 1989; Table 1) due to covering deeper waters, where mesopelagic cephalopods are available, and more southern waters, where other prey such as pelagic red crab are known to be more common. The only similarity found with the aforementioned studies is the predominance of *H. heteropsis* as the most frequent squid off Santa Catalina I (Tricas, 1979).

No differences have been found in food groups between the sexes in blue shark (Kohler & Stillwell, 1981; Kohler, 1987; Clarke *et al.*, 1996; this study). Differences in diet by sex and maturity stage have been related to spatial segregation of sexes caused by differing habits, including feeding and reproductive behaviour (Politi, 1997; McCord & Campana, 2003).

No differences in diet were found between sharks of different sizes (Kohler, 1987; Clarke *et al.*, 1996). However, Seki (1993) found that sharks of ≤65 cm precaudal length consumed more micronektonic myctophids and gonatids whereas sharks of >65 cm length ingested more neon flying squid and other fish. Differences between several shark sizes for a few prey were found in this study, but no clear tendency was seen along the shark size gradient for any prey.

Cephalopod dimensions estimated in this study were comparable to those found in other areas for cephalopods (Bello,

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1990; Dunning *et al.*, 1993; Clarke *et al.*, 1996; Macnaughton *et al.*, 1998; Kubodera *et al.*, 2007) and fish (Harvey 1989). Overall no relationship has been found between blue shark and prey sizes (Kohler, 1987). In a few cases a positive correlation has been shown for some squids (Garibaldi & Orsi Relini, 2000), anchovies (Pardo-Gandarillas, 2007) and teleosts (this study).

CONCLUSIONS

Blue shark feed on a large variety of passive prey, mainly mesopelagic cephalopods. This predator could have a more important role as scavenger of the world oceanic ecosystem than previously thought. Blue sharks are heavily fished worldwide and a growing body of evidence on population declines has been documented (Nakano & Stevens, 2008), including in Mexican waters (Sosa-Nishizaki *et al.*, 2008). Removal of this predator from oceanic ecosystems might impact their structure and functioning through changes in top-down control. Short-life, fast-growing prey such as cephalopods might proliferate with depleting shark populations, triggering unknown cascading effects in the poorly understood mesopelagic ecosystem. On the other hand, these effects could be minimized if they were compensated by the proliferation of more productive predators such as tuna (Baum & Worm, 2009), or protected scavengers such as sea birds. In any case we cannot expect the release of any potential mesopredatory shark (Baum & Worm, 2009), as they were absent in the blue shark diet.

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REFERENCES

Bane G.W. (1968) The great blue shark. *California Currents* 1, 3–4.

Baum J.K. and Worm B. (2009) Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology* 78, 699–714.

Bello G. (1990) Cephalopod remains from the blue sharks, *Prionace glauca*, caught in the Gulf of Taranto. *Rapports Commission Internationale pour l'Exploration Scientifique de la Mer Méditerranée* 32, 242.

Bello G. (1994) *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae) in the Adriatic Sea: evidence from predator stomachs contents. *Bollettino Malacologico* 30, 43–48.

Bello G. (1996) Teuthophagous predators as collectors of oceanic cephalopods: the case of the Adriatic Sea. *Bollettino Malacologico* 32, 71–78.

Brodeur R.D., Lorz H.V. and Pearcy W.G. (1987) Food habits and dietary variability of pelagic nekton off Oregon and Washington, 1979–1984. *NOAA Technical Report NMFS* 57, 1–31.

Boyd C.M. (1967) Benthic and pelagic habitats of the red crab, *Pleuroncodes planipes*. *Pacific Science* 21, 394–403.

Capapé C. (1975) Observations sur le régime alimentaire de 29 sélaciens pleurotrêmes des côtes tunisiennes. *Archives de l'Institut Pasteur de Tunis* 4, 395–414.

Carey F.G. and Scharold J.V. (1990) Movements of blue shark (*Prionace glauca*) in depth and course. *Marine Biology* 106, 329–242.

Casey J.G. and Hoenig J.M. (1977) Apex predators in deepwater dumpsite 106. *NOAA Dumpsite Evaluation Report 77–1. Baseline Report of Environmental Conditions in Deepwater Dumpsite 106. Volume II. Biological Characteristics*. US Department of Commerce NOAA, pp. 309–376.

Clarke M.R. (1986) *A handbook for the identification of cephalopod beaks*. Oxford: Clarendon Press, 273 pp.

Clarke M.R. and Stevens J.D. (1974) Cephalopods, blue sharks and migration. *Journal of the Marine Biological Association of the United Kingdom* 54, 949–957.

Clarke M.R., Clarke D.C., Martins H.R. and Da Silva H.M. (1996) The diet of the blue shark (*Prionace glauca* L.) in Azorean waters. *Arquipelago Life Marine Sciences. Bulletin of the University of the Azores* 14A, 41–56.

Clò S. and Bianchi I. (1997) Osservazioni sul comportamento alimentare della verdesca, *Prionace glauca* (Linnaeus, 1758) (Chondrichthyes: Carcharhinidae). *Quaderni della Civica Stazione Idrobiologica di Milano* 22, 79–93. [In Italian with English abstract.]

Clothier C.R. (1950) A key to some southern California fishes based on vertebral characters. *California Department of Fish and Game Fish Bulletin* 79, 1–83.

Cortés E. (1997) A critical review of methods studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 726–738.

Croxall J.P. and Prince P.A. (1994) Dead or alive, night or day: how do albatrosses catch squid? *Antarctic Science* 6, 155–162.

Dorman J. (1987) Notes on the stomach contents of some blue sharks (*Prionace glauca*, L.) caught in Courtmacsherry Bay, County Cork. *Irish Naturalists' Journal* 22, 207.

Dunning M.C., Clarke M.R. and Lu C.C. (1993) Cephalopods in the diet of oceanic sharks caught off Eastern Australia. In Okutani T., O'Dor R.K. and Kubodera T. (eds) *Recent advances in cephalopod fisheries biology*. Tokyo: Tokai University Press, pp. 119–131.

Fergusson I.K. (1994) Further observations on the diet of blue sharks, *Prionace glauca* (Linnaeus, 1758) from the English Channel. In Fowler S.L. and Earll R.C. (eds) *Proceedings of the 2nd European Shark & Ray Workshop*. Peterborough: Joint Nature Conservancy Council (JNCC), pp. 47–48.

Fiscus C.H., Rice D.W. and Wolman A.A. (1989) Cephalopods from the stomach of sperm whales taken off California. *NOAA Technical Report NMFS* 83, 1–21.

Garibaldi F. and Orsi Relini L. (2000) Summer abundance size and feeding habits of the blue shark, *Prionace glauca*, in the pelagic sanctuary of the Ligurian Sea. *Biologia Marina Mediterranea* 7, 324–333. [In Italian with English abstract.]

Gómez-Gutiérrez J. and Sánchez-Ortíz C.A. (1997) Larval drift and population structure of the pelagic phase of *Pleuroncodes planipes* (Stimpson) (Crustacea: Galatheidae) off the southwest coast of Baja California, Mexico. *Bulletin of Marine Science* 61, 305–325.

Gubanov Y.P. and Grigor'yev V.N. (1975) Observations on the distribution and biology of the blue shark *Prionace glauca* (Carcharhinidae) of the Indian Ocean. *Journal of Ichthyology* 15, 37–43.

Harvey J.T. (1989) Food habits, seasonal abundance, size, and sex of the blue shark, *Prionace glauca*, in Monterey Bay, California. *California Fish and Game* 75, 33–44.

Harvey J.T., Loughlin T.R., Perez M.A. and Oxman D.S. (2000) Relationship between fish size and otolith length for 63 species of fishes from the Eastern North Pacific Ocean. *NOAA Technical Report NMFS* 150, 1–36.

Hazin F., Lessa R. and Chammas M. (1994) First observations on stomach contents of the blue shark, *Prionace glauca*, from southwestern Equatorial Atlantic. *Revista Brasileira de Biologia* 54, 195–198.

Henderson A.C., Flannery K. and Dunne J. (2001) Observations on the biology and ecology of the blue shark in the North-east Atlantic. *Journal of Fish Biology* 58, 1347–1358.

Hoffman M. (1979) The use of Pielou's method to determine sample size in food studies. In Lipovsky S.J. and Simenstad C.A. (eds) *Gutshop '78, Fish food habits studies. Proceedings of the Second Pacific Northwest Technical Workshop, October 10–13, 1978, Maple Valley, WA.* Seattle: Washington Sea-Grant Publications, University of Washington, pp. 56–61.

Kohler N.E. (1987) *Aspects of the feeding ecology of the blue shark,* Prionace glauca *in the western North Atlantic.* PhD thesis. University of Rhode Island, USA.

Kohler N.E. and Stillwell C.E. (1981) *Food habits of the blue shark (*Prionace glauca*) in the Northwest Atlantic.* International Council for the Exploration of the Sea (CM Papers and Reports), CM 1981/H:61, 7 pp., 3 figs., 2 tables.

Kubodera T. (2005) *Manual for the identification of cephalopod beaks in the Northwest Pacific.* National Museum of Nature and Science, Tokyo. Available at http://research.kahaku.go.jp/zoology/Beak-E/index.htm. Accessed 5 November 2009.

Kubodera T., Watanabe H. and Ichii T. (2007) Feeding habits of the blue shark, *Prionace glauca*, and salmon shark, *Lamna ditropis*, in the transition region of the Western North Pacific. *Reviews in Fish Biology and Fisheries* 17, 111–124.

LeBrasseur R.J. (1964) Stomach contents of blue shark (*Prionace glauca* L.) taken in the Gulf of Alaska. *Journal of the Fisheries Research Board of Canada* 21, 861–862.

Longhurst A.R. (1966) The pelagic phase of *Pleuroncodes planipes* Stimpson (Crustacea, Galatehidae) in the California Current. *California Cooperative Oceanic Fisheries Investigations Reports* 11, 142–154.

López S. (2007) *Alimentación y relaciones trófica del azulejo* Prionace glauca *(Linneaus, 1758) (Chondrichthyes: Carcharhiniformes: Carcharhinidae), frente a Chile Centro-Norte durante el año 2005*. In Libro de resúmenes ampliados Primer Encuentro de Estudiantes de Ciencias del Mar EECMAR, 30 July–3 August 2007, Santiago, Chile. 500 pp. Available at http://www.aqua.cl/zona_u/uploads/13639116394741ef5171569.doc Accessed 5 November 2009. [In Spanish.]

Lu C.C. and Ickeringill R. (2002) Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of southern Australian finfishes. *Museum Victoria Science Reports* 6, 1–65.

Macnaughton R., Rogan E., Hernández-García V. and Lordan C. (1998) *The importance of cephalopods in the diet of blue shark* (Prionace glauca) *south and west of Ireland*. International Council for the Exploration of the Sea (CM Papers and Reports), CM 1998/M:07, 12 pp.

Markaida U. and Hochberg F.G. (2005) Cephalopods in the diet of swordfish (*Xiphias gladius* Linnaeus) caught off the west coast of Baja California, Mexico. *Pacific Science* 59, 25–41.

McCord M.E. and Campana S.E. (2003) A quantitative assessment of the diet of the blue shark (*Prionace glauca*) off Nova Scotia, Canada. *Journal of Northwest Atlantic Fishery Science* 32, 57–63.

Mearns A.J., Young R.D., Olson R.J. and Schafer H.A. (1981) Trophic structure and the cesium–potassium ratio in pelagic ecosystems. *California Cooperative Oceanic Fisheries Investigations Reports* 22, 99–110.

Miller D.J. and Lea R.N. (1972) Guide to the coastal marine fishes of California. *California Department of Fish and Game Fish Bulletin* 157, 1–249.

Nakano H. and Stevens J.D. (2008) The biology and ecology of the blue shark, *Prionace glauca*. In Camhi M.D., Pikitch E.K. and Babcock E.A. (eds) *Sharks of the open ocean: biology, fisheries and conservation*. Oxford: Blackwell Publishing Ltd, pp. 140–151.

Nesis K.N. (1987) *Cephalopods of the world*. Neptune City: T.F.H. Publications, 351 pp.

Nesis K.N. (1996) Mating, spawning, and death in oceanic cephalopods: a review. *Ruthenica* 6, 23–64.

Nigmatullin Ch.M. (1976) Discovery of giant squid *Architeuthis* in equatorial waters of the Atlantic Ocean. *Biologiya Morya* 4, 29–31. [In Russian with English abstract.]

Pardo-Gandarillas M.C., Duarte F., Chong J. and Ibáñez C.M. (2007) Dieta de tiburones juveniles *Prionace glauca* (Linnaeus, 1758) (Carcharhiniformes: Carcharhinidae) en la zona litoral centro-sur de Chile. *Revista de Biología Marina y Oceanografía* 42, 365–369. [In Spanish with English abstract.]

Pinkas L., Oliphant M.S. and Iverson L.K. (1971) Food habits of albacore, bluefin tuna, and bonito in California waters. *California Department of Fish and Game Fish Bulletin* 152, 1–105.

Pitman R.L., Walker W.A., Everett W.T. and Gallo-Reynoso J.P. (2004) Population status, foods and foraging of Laysan albatrosses *Phoebastria immutabilis* nesting on Guadalupe Island, Mexico. *Marine Ornithology* 32, 159–165.

Politi E. (1997) Analysis of stomach contents of *Prionace glauca* in the northern and central Adriatic Sea. *Quaderni della Civica Stazione Idrobiologica di Milano* 22, 65–78 & 147–150.

Preti A., Smith S.E., Ramon D.A. and Kohin S. (2006) Diet differences among 3 species of pelagic sharks inhabiting the California Current: the shortfin mako (*Isurus oxyrinchus*), blue (*Prionace glauca*), and thresher (*Alopias vulpinus*) sharks. In *Proceedings of the 57th Annual Tuna Conference. Lake Arrowhead, California, May 22–25, 2006.* p. 45. Available at http://www.tunaconference.org/PDFfiles/57th-Tuna-Conference-Proceedings.pdf. Accessed 5 November 2009.

Robinson C.J., Anislado V. and Chaparro P. (2004) The pelagic red crab (*Pleuroncodes planipes*) related to active upwelling sites in the California Current off the west coast of Baja California. *Deep-Sea Research II* 51, 753–766.

Roper C.F.E. and Vecchione M. (1993) A geographic and taxonomic review of *Taningia danae* Joubin, 1931 (Cephalopoda: Octopoteuthidae), with new records and observations on bioluminescence. In Okutani T., O'Dor R.K. and Kubodera T. (eds) *Recent advances in cephalopod fisheries biology*. Tokyo: Tokai University Press, pp. 441–456.

Roper C.F.E. and Young R.E. (1975) Vertical distribution of pelagic cephalopods. *Smithsonian Contributions to Zoology* 209, 1–51.

Santos M.B., Pierce G.J., García Hartmann M., Smeenk C., Addink M.J., Kuiken T., Reid R.J., Patterson I.A.P., Lordan C., Rogan E. and Mente E. (2002) Additional notes on stomach contents of sperm whales *Physeter macrocephalus* stranded in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 82, 501–507.

Schwing F.B., Murphree T., deWitt L. and Green P.M. (2002) The evolution of oceanic and atmospheric anomalies in the northeast Pacific during the El Niño events of 1995–2001. *Progress in Oceanography* 54, 459–491.

Sciarrotta T.C. and Nelson D.R. (1977) Diel behaviour of the blue shark, *Prionace glauca*, near Santa Catalina Island, California. *Fishery Bulletin* 75, 519–528.

Seki M.P. (1993) The role of neon flying squid, *Ommastrephes bartrami*, in the North Pacific pelagic food web. *International North Pacific Fisheries Commission Bulletin* 53, 207–215.

Smale M.J., Clarke M.R., Klages N.T.W. and Roeleveld M.A.C. (1993) Octopod beak identification resolution at a regional level (Cephalopoda, Octopoda: Southern Africa). *South African Journal of Marine Science* 13, 269–293.

Sosa-Nishizaki O., Márquez-Farías J. and Villavicencio-Garayzar C.J. (2008) Case study: pelagic shark fisheries along the west coast of Mexico. In Camhi M.D., Pikitch E.K. and Babcock E.A. (eds) *Sharks of the open ocean: biology, fisheries and conservation*. Oxford: Blackwell Publishing Ltd, pp. 275–282.

Stevens J.D. (1973) Stomach contents of the blue shark (*Prionace glauca*, L.) off south-west England. *Journal of the Marine Biological Association of the United Kingdom* 53, 357–361.

Stevens J.D. (1984) Biological observations on sharks caught by sport fisherman off New South Wales. *Australian Journal of Marine and Freshwater Research* 35, 573–590.

Stevens J.D. and McLoughlin K.J. (1991) Distribution, size, and sex composition, reproductive biology and diet of sharks from northern Australia. *Australian Journal of Marine and Freshwater Research* 40, 129–146.

Strasburg D.W. (1959) Distribution, abundance, and habits of pelagic sharks in the central Pacific Ocean. *US Fishery Bulletin of the Fish and Wildlife Service* 58, 335–361.

Tricas T.C. (1979) Relationship of the blue shark, *Prionace glauca*, and its prey near Santa Catalina Island, California. *Fishery Bulletin* 77, 175–182.

Vaske-Júnior T. and Rincón-Filho G. (1998) Stomach content of blue sharks (*Prinace glauca*) and anequim (*Isurus oxyrinchus*) from oceanic waters of southern Brazil. *Revista Brasileira de Biologia* 58, 445–452. [In Portuguese with English abstract.]

Vaske Jr T., Lessa R.P. and Gadig O.B.F. (2009) Feeding habits of the blue shark (*Prionace glauca*) off the coast of Brazil. *Biota Neotropica* 9, 55–60.

Voight J.R., Pörtner H.O. and O'Dor R.K. (1994) A review of ammonia-mediated buoyancy in squids (Cephalopoda: Teuthoidea). *Marine and Freshwater Behaviour and Physiology* 25, 193–203.

Wetherbee B.M. and Cortés E. (2004) Food consumption and feeding habits. In Carrier J.C., Musick J.A. and Heithaus M.R. (eds) *Biology of sharks and their relatives*. Boca Raton, FL: CRC Press, pp. 223–244.

Wetherbee B.M., Gruber S.H. and Cortés E. (1990) Diet, feeding habits, digestion and consumption in sharks, with special reference to the lemon shark, *Negaprion brevirostris*. *NOAA Technical Report NMFS* 90, 29–47.

Wolff G.A. (1984) Identification and estimation of size from the beaks of 18 species of cephalopods from the Pacific Ocean. *NOAA Technical Report NMFS* 17, 1–50.

Yatsu A. (1995) The role of slender tuna, *Allothunnus fallai*, in the pelagic ecosystems of the South Pacific Ocean. *Japanese Journal of Ichthyology* 41, 367–377.

Young R.E. (1972) The systematic and areal distribution of pelagic cephalopods from the seas off Southern California. *Smithsonian Contributions to Zoology* 97, 1–159.

and

Zar J.H. (1999) *Biostatistical analysis*. 4th edition. Upper Saddle River, NJ: Prentice-Hall.

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