

Cephalopod prey of two demersal sharks caught in the Aegean Sea (eastern Mediterranean)

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*This study concerns the cephalopod species that are part of the diet of the small-spotted catshark *Scyliorhinus canicula* and the longnose spurdog *Squalus blainville* sampled by commercial trawlers in the Aegean Sea from 2005 to 2012. Based on the examined cephalopod beaks, 15 species were identified belonging in six families of Teuthida, one of Sepiida and two of Octopoda. The diversity of cephalopod prey species was higher for *S. canicula* ($N = 15$) than for *S. blainville* ($N = 10$). Nektonic cephalopods comprised the majority (>72%) of the preyed species by both sharks, among which about 55% inhabit the demersal zone and 45% the mesopelagic. In the diet of *S. canicula*, the demersal squid *Illex coindetii* and the pelagic sepiolid *Heteroteuthis dispar* were equally represented composing 20% of prey specimens, followed by the small-sized squid *Abralia veranyi* and the demersal sepiolid *Rossia macrosoma*. The latter species was substituted in the diet of *S. blainville* by the demersal medium-sized octopod *Scaevargus unicolor*, which with the equally represented three other species, composed 50% of the cephalopod prey. Differences observed between *S. canicula* and *S. blainville* in the condition of beaks retained in their stomach contents and in the variation of prey species diversity by predator specimen size, may imply differences in their foraging tactics (hunting for prey vs scavenging on the bottom), habitats and stomach evacuation frequency.*

Keywords: stomach content, cephalopods, *Scyliorhinus canicula*, *Squalus blainville*, Mediterranean Sea

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INTRODUCTION

Defining diet is a crucial first step to better understanding of trophic interactions and building robust marine food web models (Murphy *et al.*, 2012). Cephalopods constitute a significant prey for larger fish, seabirds and marine mammals and as such, they hold a pivotal role in structuring of marine ecosystems. Their importance as prey is enhanced by their very high growth rates, which, together with other life cycle characteristics (exclusively carnivorous diet, short lifespan and semelparity) lead to high biomass turnover rates or productivity (P/B ratio) (Boyle, 2002).

Despite the ecological and economic key positions of cephalopods, there is limited information about their overall role in the marine environment, i.e. their significance as food resources for higher trophic levels and their impact as predators of finfish and invertebrates (Clarke, 1996). The reason for this is that several cephalopods, particularly the pelagic ones, are not widely fished and conventional gears, used in monitoring other pelagic taxa, usually collect juveniles, since adult specimens generally avoid being captured (Clarke, 1996; Piatkowski *et al.*, 2001). Therefore, diet composition

analysis of various top predators, such as cetaceans, seabirds, sharks and large pelagic finfish, is a standard technique that provides valuable information on their ecology, geographic distribution, abundance and seasonal fluctuations (Clarke, 1986; Xavier *et al.*, 2014).

In the Mediterranean Sea, cephalopods are significant for the diet of several marine predators (e.g. Blanco & Raga, 2000; Salman *et al.*, 2001; Madurell, 2003; Salman, 2004; Romeo *et al.*, 2012; Dede *et al.*, 2016). Nevertheless, in the Hellenic waters (eastern Mediterranean), data on the cephalopod prey-specific composition is still poor regarding whales, finfish and sharks, and research has focused on the Aegean (Peristeraki *et al.*, 2005), Ionian (Lefkaditou & Pouloupoulos, 1998; Lefkaditou *et al.*, 2016) and Libyan Seas (Roberts, 2003).

This study focuses on cephalopod species that are part of the diet of two demersal sharks, the small-spotted catshark *Scyliorhinus canicula* (Linnaeus, 1758) and the longnose spurdog *Squalus blainville* (Risso, 1826), captured in the Aegean Sea. Both species inhabit the Mediterranean Sea and the eastern Atlantic Ocean (Compagno, 1984a, b). They are considered small-sized sharks (maximum length = 1 m), with *S. canicula* exhibiting philopatric behaviour (Kousteni *et al.*, 2015) and *S. blainville* showing high dispersal potential and the ability to cross open water masses (Kousteni *et al.*, 2016b).

The identification of cephalopod species found in the stomach contents of the examined sharks was achieved through the taxonomic classification of their beaks, as being

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quite resistant to digestive processes (Clarke, 1962). The cephalopod prey species diversity was examined for each predator by sampling depth and size, and further compared with the findings of similar studies in the Mediterranean Sea and the eastern Atlantic Ocean. Finally, the mantle length of the consumed cephalopods was reconstructed and the relationship of prey-predator size was investigated in relation to the maximum size known for the cephalopod species.

MATERIALS AND METHODS

A total of 432 and 212 individuals of *Scyliorhinus canicula* and *Squalus blainville*, respectively, were incidentally captured by commercial trawlers in the Aegean Sea from November 2005 to January 2012 at depths of 101–513 m (Figure 1). Individuals were immediately frozen at sea and transported in ice boxes to the laboratory, where total length (TL) was measured to the nearest millimetre (mm), from the tip of the snout to the tip of the upper caudal lobe.

The digestive tract of each specimen was removed and the stomachs were isolated and fixed in a 10% formalin solution. Cephalopod prey items, including flesh, eye lenses and beaks that were either loose or embedded in buccal mass remains, were isolated during stomach content examination. Cephalopod beaks were cleaned, separated into upper and lower ones, and preserved in 70% ethanol. They were then assigned to species using taxonomic keys and illustrations by Naef (1923), Clarke (1986) and Xavier & Cherel (2009), and after being compared with the beaks of the IMBRIW-HCMR reference collection. Although beaks can be retained in the stomachs of marine predators for a long

time, they are affected by chemical and mechanical digestion processes. According to the level of erosion, beaks were categorized into three types with type A representing 'fresh' beaks still bearing intact wings and cartilages covering the front edge of the lateral wall; type B including beaks still uneroded but not possessing cartilages while wings might be broken; and type C representing abraded, very darkened beaks with rounded rostrum, as suggested by Piatkowski & Pütz (1994).

To facilitate identification and measurement of beak remains, calibrated digital images of their lateral view were obtained through a stereoscope connected to the image analysis system of HCMR. Standard dimensions of the beak's rostrum, crest and hood, following Clarke's (1986) definitions, were measured using Image PRO-Plus algorithms. Specifically, upper rostral length (URL) and lower rostral length (LRL) in squids and sepiolids, and lower crest length (LCL) and lower hood length (LHL) in octopuses were measured to the nearest 0.01 mm. The mantle length (ML in mm) of each cephalopod prey individual was estimated using previously established allometric equations relating ML with LRL for squids and with LCL or LHL for octopus species (Table S1).

The identified cephalopod species were characterized based on their habitat as demersal (d), epipelagic (e) and mesopelagic (p). In demersal species, squid species closely associated to the bottom that are supposed to undergo vertical migrations at night, such as *Illex coindetii* and *Abralia veranyi* (Roper & Young, 1975; Rodhouse *et al.*, 1998), were also included.

Percentage (%) frequency of cephalopod prey species occurrence was estimated for the total number of specimens of each predator and also for two groups of predator specimens considered in relation to their sampling depth



Fig. 1. Map of the study area indicating the sampling locations (north Aegean Sea, north Evoikos Gulf, Cyclades Islands, Cretan Sea and Saronikos Gulf) of 432 individuals of *Scyliorhinus canicula* and 211 individuals of *Squalus blainville* captured by trawlers and included in the present study. The locations where *S. blainville* individuals were captured are indicated with a white asterisk. An average geographic position is presented.

(<250 m over the continental shelf; >250 m over the slope). To establish a probable foraging zone in the plot of prey species occurrence by predator group, cephalopod species, except for the epipelagic octopod *Argonauta argo*, were ranked according to the depth of their maximum abundance in the Hellenic waters as estimated by Lefkaditou (2007) by the 'centre of gravity' (GOC) method (Moranta *et al.*, 1998). Furthermore, the prey species contribution by ML class was shown by ranking prey species according to their ML_{max} (Table S1). Finally, the ML size of each cephalopod prey vs the TL of each predator was plotted in a graph.

RESULTS

Cephalopod flesh, eye lenses and beaks were found in 118 out of the 314 non-empty stomachs of *Scyliorhinus canicula* and in 55 out of the 147 non-empty stomachs of *Squalus blainville*, representing about 37% of stomachs analysed by predator species. Identified cephalopod beaks (Figure S1) occurred in 36 and 19 individuals with non-empty stomachs of *S. canicula* and *S. blainville*, respectively.

Both predators preyed upon Teuthida, Sepiida and Octopoda. Higher cephalopod species diversity was recorded in *S. canicula* (N = 15) compared with *S. blainville* (N = 10). Specifically, representatives of six families of cephalopods (Enoploteuthidae, Pyroteuthidae, Ommastrephidae, Onychoteuthidae, Sepiolidae and Octopodidae) were common in the diet of the examined predators, while species belonging to Histioteuthidae (*Histioteuthis bonnellii*), Loliginidae (*Loligo forbesii*) and Argonautidae (*Argonauta argo*) were found in *S. canicula* stomach contents only (Table 1, Figure 2).

Nektonic cephalopods consisted the major part (>72%) of preyed species by both sharks, out of which about 55% inhabit the demersal zone and 45% the mesopelagic. In the diet of

S. canicula, the demersal squid *Illex coindetii* and the pelagic sepiolid *Heteroteuthis dispar* were equally represented composing 45% of prey specimens, followed by the small-sized squid *Abralia veranyi* and the demersal sepiolid *Rossia macrosoma* representing 25%. The latter species was substituted in the diet of *S. blainville* by the demersal medium-sized octopod *Scaevargus unicolorrhus*, which with the almost equally represented *A. veranyi*, *H. dispar* and *I. coindetii*, composed 50% of cephalopod prey specimens (Table 2).

The majority of beaks obtained from the stomach content of *S. blainville* were fresh (type A), usually extracted from remains of buccal masses, whereas beaks of type B were dominant in the stomach of *S. canicula* (Table 2).

Based on the cephalopod prey species occurrence in the diet of the predator specimens caught over the continental shelf (<250 m) and slope (>250 m), it was shown that cephalopod species distributed over shelf-break and upper slope were identified in the stomach contents of both predators and regardless of the depth zone of their capture (Figure 3). The presence of cephalopod prey species distributed mainly over the continental slope in the stomach content of specimens caught over the shelf, was more frequently observed in *S. canicula*.

Ommastrephids dominated among larger prey specimens (ML > 100 mm) of both predators, whereas smaller prey-specimens (ML < 40 mm) belonged mainly in small-sized cephalopod species and only among those consumed by *S. canicula* juveniles of *H. bonnellii* and *Todaropsis eblanae* were recorded. According to the estimated ML values, the size range of the cephalopod prey was wider in *S. canicula* than *S. blainville* (Table 2). This is probably due to the larger sample of *S. canicula* examined. However, the limited number of the identified beaks could not allow for between-species comparisons. Finally, based on the cephalopod ML–predator TL relationships (Figure 4), both predators showed an increasing cephalopod species diversity as they became

Table 1. Characterization of the cephalopod species identified in the stomach contents of *Scyliorhinus canicula* and *Squalus blainville* sampled in the Aegean Sea based on their habitat.

Order	Family	Cephalopod species	<i>S. canicula</i>	<i>S. blainville</i>	Habitat	
TL range of specimens (mm)			144–517	182–759		
Number of stomachs examined			432	211		
Number of non-empty stomachs			314	147		
Number (and percentage) of stomachs with cephalopod remains			118 (37.58)	55 (37.41)		
Number (and percentage) of stomachs with cephalopod beaks			35 (11.15)	19 (12.93)		
Teuthoidea	Enoploteuthidae	<i>Abralia veranyi</i>	+	+	d	
		<i>Pyroteuthis margaritifera</i>	+	+	p	
	Histioteuthidae	<i>Histioteuthis bonnellii</i>	+		p	
		<i>Loligo forbesii</i>	+		d	
	Ommastrephidae	<i>Illex coindetii</i>	+	+	d	
		<i>Todarodes sagittatus</i>	+	+	p	
		<i>Todaropsis eblanae</i>	+	+	d	
		<i>Onychoteuthis banksii</i>	+	+	p	
	Sepioidea	Sepiolidae	<i>Heteroteuthis dispar</i>	+	+	p
			<i>Neorossia caroli</i>	+		d
<i>Rossia macrosoma</i>			+	+	d	
<i>Sepietta oweniana</i>			+		d	
<i>Scaevargus unicolorrhus</i>			+	+	d	
Octopoda	Argonautidae	<i>Argonauta argo</i>	+		e	
	Octopodidae	<i>Octopus salutii</i>	+	+	d	

d, demersal zone; e, epipelagic zone; p, mesopelagic zone; +, present.

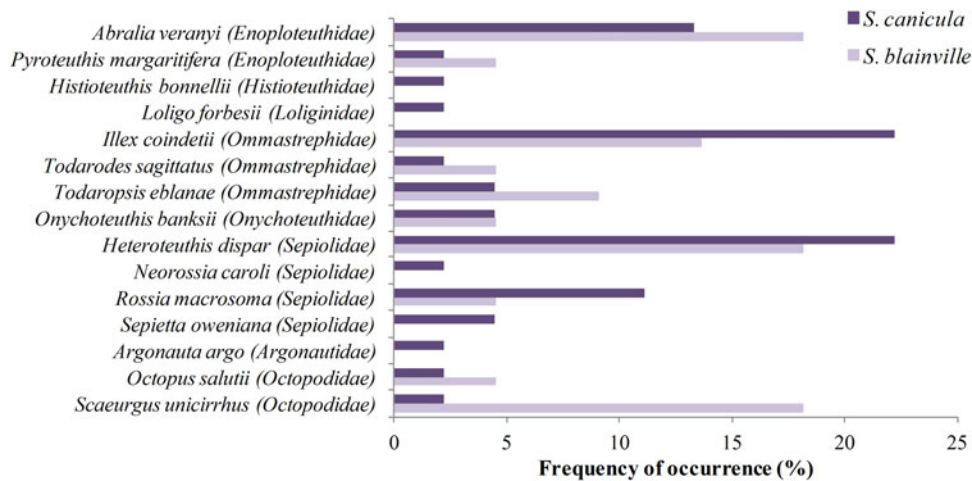


Fig. 2. Percentage (%) frequency of cephalopod prey species occurrence in the stomach contents of *Scyliorhinus canicula* and *Squalus blainville* that were identified based on the beaks (N = 45 and 22, respectively).

larger in size. An increasing trend of ML with TL size was evident only for the demersal ommastrephids *I. coindetii* and *T. eblanae* consumed by *S. blainville* (Figure 4).

DISCUSSION

The present study examines the cephalopod prey species diversity and contribution in the diet of *Scyliorhinus canicula* and *Squalus blainville* in the Aegean Sea, two demersal sharks that consume cephalopods in large quantities, although they are both characterized as generalist predators, and contributes to the existing knowledge about the diet of these predators from the Hellenic waters (Kousteni, 2015; Kousteni et al., 2016a, 2017).

Considering previous dietary studies of *S. canicula* and *S. blainville* (e.g. Capapé, 1975; Kabasakal, 2002; Özütemiz et al., 2009; Gravino et al., 2010; Karachle & Stergiou, 2010; Martinho et al., 2012; Kousteni, 2015; Kousteni et al., 2016a,

2017), cephalopods are one of the three most consumed prey groups, among fish and crustaceans, confirming the general view that predator fish that consume cephalopods have a broad diet spectrum that includes other groups (Smale, 1996). In the area of study, cephalopods seemed to be an important prey group for both predators with a higher contribution to the diet of *S. blainville* (%W = 51.2) compared with that of *S. canicula* (%W = 30.8), thus characterizing it as a teuthophagus species (Kousteni, 2015; Kousteni et al., 2016a, 2017). However, cephalopods have not always contributed significantly to the diet of *S. canicula* (Olaso et al., 1998, 2005; Serrano et al., 2003; Valls et al., 2011; Martinho et al., 2012; Mnasri et al., 2012; Šantić et al., 2012) and *S. blainville* (Kabasakal, 2002; Martinho et al., 2012), which might be spatio-temporal specific (Hanlon & Messenger, 1996). It should be noted that the cephalopods found in stomach contents would not necessarily come from the area where the predator was caught. Beaks of cephalopods are known to remain undigested for longer periods than fish bones and otoliths (Clarke, 1996) and as *S. blainville* has been assumed to

Table 2. Descriptive statistics (mean value, SD and range) of the estimated ML of the cephalopod species identified in the stomach contents of *Scyliorhinus canicula* and *Squalus blainville* sampled in the Aegean Sea.

Cephalopod species	<i>S. canicula</i>				<i>S. blainville</i>			
	N (N _{A,B,C})	Mean	SD	Range	N (N _{A,B,C})	Mean	SD	Range
<i>Abralia veranyi</i>	6 (0, 6, 0)	39.5	18.2	25.9–75.2	4 (4, 0, 0)	29.8	3.09	26.8–33.0
<i>Pyroteuthis margaritifera</i>	1 (0, 1, 0)	28.5			1 (0, 1, 0)	30.9		
<i>Histioteuthis bonnellii</i>	1 (0, 1, 0)	9.66						
<i>Loligo forbesii</i>	1 (0, 1, 0)	124						
<i>Illex coindetii</i>	10 (1, 6, 3)	144	36.8	67.6–178	3 (3, 0, 0)	120	62.5	48.0–163
<i>Todarodes sagittatus</i>	1 (0, 0, 1)	203			1 (0, 1, 0)	136		
<i>Todaropsis eblanae</i>	2 (0, 2, 0)	39.0	19.7	25.1–53.0	2 (1, 1, 0)	90.2	34.5	65.8–115
<i>Onychoteuthis banksii</i>	2 (0, 2, 0)	68.1	25.1	50.3–85.9	1 (1, 0, 0)	115		
<i>Heteroteuthis dispar</i>	10 (0, 1, 0)	18.3	5.51	13.4–20.0	4 (1, 3, 0)	15.4	4.40	11.1–19.9
<i>Neorossia caroli</i>	1 (0, 0, 1)	54.9						
<i>Rossia macrosoma</i>	5 (0, 4, 1)	38.9	13.3	20.5–57.6	1 (1, 0, 0)	36.7		
<i>Sepietta oweniana</i>	2 (0, 2, 0)	26.6	2.77	24.7–28.6				
<i>Argonauta argo</i>	1 (0, 1, 0)	34.3						
<i>Octopus salutii</i>	1 (0, 1, 0)	46.6			1 (1, 0, 0)	75.2		
<i>Scaevurgus unicirrhus</i>	1 (0, 1, 0)	57.8			4 (3, 1, 0)	51.2	2.46	48.7–54.6

N, number of individuals; N_{A,B,C}, number of type A, B and C beaks according to Piatkowski & Pütz (1994); SD, standard deviation; all measurements in mm.

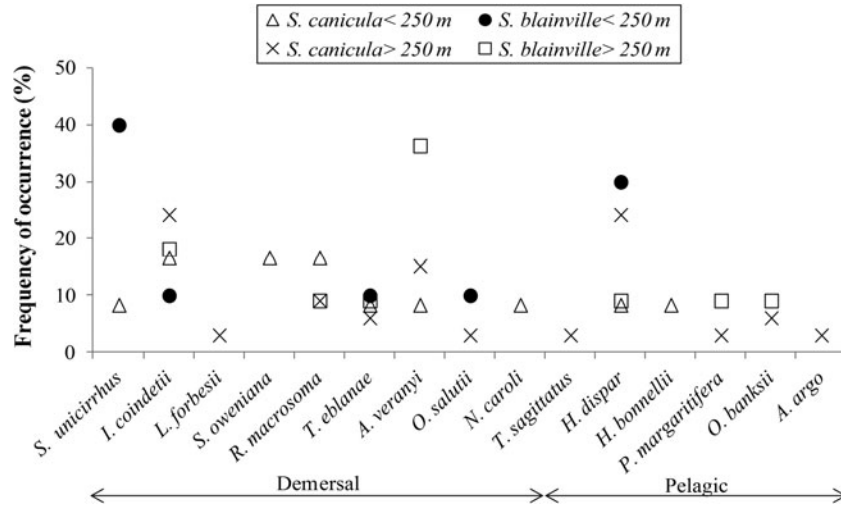


Fig. 3. Percentage (%) frequency of cephalopod prey species occurrence in the diet of the predator specimens caught by trawl over the continental shelf (<250 m) and slope (>250 m) in the Aegean Sea. Cephalopod species are ranked following their depth distribution in the Hellenic waters (Lefkaditou, 2007).

move long distances (Kousteni *et al.*, 2016b), the region from which the cephalopods originate probably cannot be precisely determined. This assumption, however, does not stand for *S. canicula*, a species with philopatric behaviour that tends to

form distinct stocks on small geographic scales (Kousteni *et al.*, 2015).

With regard to cephalopod prey species levels, initial records in the diet of *S. canicula* derived from the present

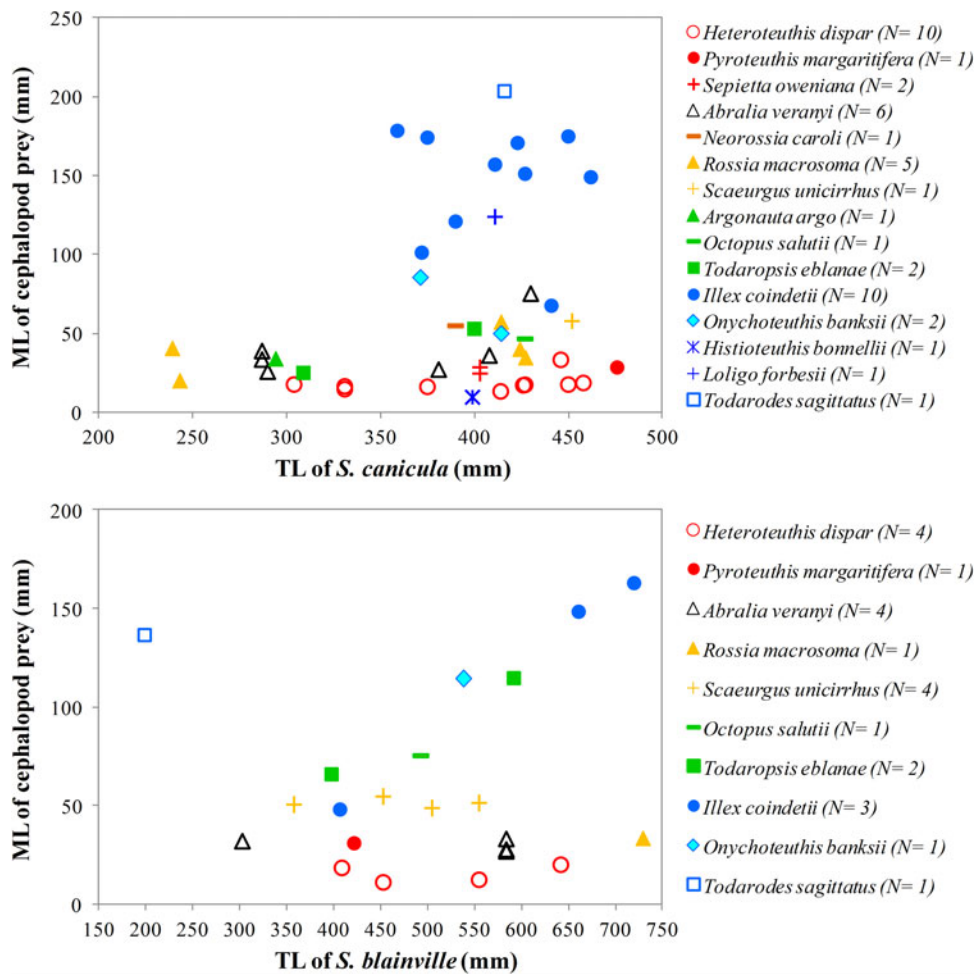


Fig. 4. Relationship between the estimated mantle length (ML) of the cephalopod prey and total length (TL) of *Scyliorhinus canicula* and *Squalus blainville* individuals sampled in the Aegean Sea. Cephalopod species are ranked in relation to their ML_{max} recorded in the Mediterranean Sea (Table S1).

study represent 2/3 of the identified cephalopod prey species, resulting in a higher diversity compared with that reported in other studies (Table S2). In the case of *S. blainville*, seven out of the 10 identified cephalopod prey species in the present study have not been previously reported (Table S3). In general, the diversity of cephalopod prey species was lower in *S. blainville* (N = 10) compared with *S. canicula* (N = 15), but similarly to *S. canicula* higher than that reported in other studies (Table S3), despite the few cephalopod beaks recovered from their stomach contents. This could reflect either the higher cephalopod species diversity in the Aegean Sea, the wider bathymetric range of the sampling procedure compared with previous studies (e.g. <70 m in Martinho *et al.*, 2012; 90–130 m in Šantić *et al.*, 2012) or the difficulty of assigning the beaks to species (Romeo *et al.*, 2012). It is also possible that the few recovered cephalopod beaks compared with the total sample size could be attributed to evacuation phenomena during sharks' ascent from great depths (Yano & Tanaka, 1984), a feature which was also reflected in the relatively high numbers of empty stomachs that were recorded in *S. canicula* and *S. blainville* (27.3 and 30.3% respectively).

In the Aegean Sea, members of Ommastrephidae (*Illex coindetii*, *Todarodes sagittatus* and *Todarodes eblanae*) were prominent in the diet of *S. canicula* and *S. blainville* (N = 13 and 6, respectively), highlighting the potential importance of the arrow squid family within the study area as a food supply. This is consistent with previous dietary results of other predators (Lansdell & Young, 2007). The pelagic squid *T. sagittatus* is an important energy source because of its size (ML_{max} = 780 mm, common ML = 250–350 mm; Wood & Day, 1998) and particularly its muscular body composition in contrast with the ammoniacal body of *Histioteuthis* species (Clarke *et al.*, 1979). The most consumed Ommastrephidae species was the demersal *I. coindetii*, which could also be considered as a significant dietary source given its recorded ML_{max} of 320 mm (González *et al.*, 1996).

Considering the habitat of the preyed cephalopods, demersal species dominated in the diet of both sharks. This could imply that any change in their communities caused by intense fishing could affect the predator-prey relationships and should be considered when developing management plans for sustainable fisheries. Mesopelagic Histioteuthidae, neritic Loliginidae and epipelagic Argonautidae species participated only in *S. canicula* stomach contents. On the other hand, *Heteroteuthis dispar* was the most consumed pelagic cephalopod prey species in both examined predators. *Heteroteuthis dispar*, although very rarely caught by bottom trawl, seems to be quite abundant over the upper slope of the Mediterranean Sea, as it is among the most frequently found cephalopods in the diet of demersal chondrichthyans (Bello, 1997; Lefkaditou, 2007), large pelagic fish (Bello, 1991, 1999; Salman & Karakulak, 2009) and dolphins (Orsi Relini & Relini, 1993), as well as among catches of experimental mesopelagic trawls and macroplankton devices (Roper, 1974; Lefkaditou *et al.*, 1999). The presence of *H. dispar* in the stomach contents of predators coming from different depth zones corresponds to its high tendency for vertical migrations (Roper, 1974).

In the present study, cephalopod prey size showed a wide range (ML = 10–207 mm), but ML values between 10–60 mm were the most frequent in both shark species. This is consistent with the fact that small- or medium-sized predators

cannot capture large cephalopods and so prey on smaller ones, as was assumed by Velasco *et al.* (2001) after examining the role of cephalopods as forage in 27 demersal fishes. In general, cephalopods are difficult to catch and can avoid predators using various mechanisms (Clarke & Merrett, 1972).

Differences observed between *S. canicula* and *S. blainville* in the condition of beaks retained from their stomach contents may mirror differences in their foraging tactics (hunting vs scavenging behaviour) and habitats. The majority of beaks found in the stomach content of *S. blainville* were fresh, probably implying that this predator has a more effective hunting ability or preys mainly in the benthopelagic zone. Nevertheless, scavenging behaviour of this predator can be demonstrated by identifying a large *T. sagittatus* specimen (ML = 136 mm) as prey of a small-sized individual (TL = 199 mm). On the contrary, the dominance of worn beaks in the stomach content of *S. canicula* could imply that its cephalopod prey are the result from scavenging on the bottom, a behaviour that has previously been reported (Olaso *et al.*, 1998, 2005). This species is known to use its olfactory lobes to detect the lifeless prey (Dijkgraaf, 1975). Nevertheless, it should be noted that the level of beak erosion could be related to the fact that beaks can be retained in the stomach of marine predators for a long time (Piatkowski & Pütz, 1994).

Finally, both predators showed higher cephalopod species diversity when becoming larger in size, corresponding to a food selectivity attitude, probably related to an increase in gape size. It was apparent that *S. canicula* showed a sudden increase in cephalopod prey species diversity with the onset of maturity (total length at 50% maturity; L_{50} = 397 and 382 mm for females and males, respectively; Kousteni, 2015), as well as a preference for cephalopod species of larger size, such as *Loligo vulgaris*, *I. coindetii*, *T. sagittatus* and *Octopus salutii*. The greater energy expenditure of the larger, and thus mature, individuals may also explain the observed ontogenetic shift in the cephalopod forage of *S. canicula*. Rodríguez-Cabello *et al.* (2007) observed that this shift to larger prey in the diet of *S. canicula* reflects its transition from the immature to mature state. In the case of *S. blainville*, there was a clear correlation between the increase of Ommastrephid prey species (*I. coindetii* and *T. eblanae*) ML and the predator's size, whereas a clear dietary cephalopod prey species diversity pattern in relation to *S. blainville* body size was not observed.

With the increasing focus on fishing impacts, environmental change and the development of ecosystem-based management strategies, understanding the ecological role of cephalopods could contribute to our understanding of these changes (Lansdell & Young, 2007). The central role of cephalopods in marine food chains is underlined in the many pelagic ecosystem models being currently developed (e.g. Olson & Watters, 2003), while understanding their trophic inter-relationships will help to elucidate cephalopod ecology and form the basis for further ecosystem modelling. Considering the frequent loss of food in sharks as they are being hauled up from great depths (Yano & Tanaka, 1984) in combination with the sampling difficulties of cephalopods themselves (Piatkowski *et al.*, 2001), further sampling is needed to fully elucidate their predation upon cephalopods, which would provide at the same time data on the distribution and abundance of cephalopods in new, unexplored habitats.

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SUPPLEMENTARY MATERIAL

The supplementary material for this article can be found at <https://doi.org/10.1017/S002531541700159X>.

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