



A taste for squid: the diet of sperm whales stranded in Greece, Eastern Mediterranean

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ABSTRACT

Sperm whales (*Physeter macrocephalus*) inhabiting the world's oceans, prey mainly on cephalopods, but also feed on fish when found in higher latitudes. However, the feeding habits of endangered Mediterranean sperm whales have received little attention with thus far only two individuals analysed for their stomach contents. This study expands the available knowledge using analysis of the stomach contents from nine individuals stranded in Greece between 2005 and 2014. 48,166 prey remains were examined in total and 28,258 of them were identified to show that sperm whales fed on 18 prey species (17 cephalopods and one teleost) from 14 different families. 15 of these species were deep-sea squids, which are not presently targeted by fisheries. The most important prey species, both in terms of numerical abundance (%N) and abundance by weight (%W), was the oceanic squid *Histioteuthis bonnellii* (%N = 48.4, %W = 66.3) followed by *H. reversa* (%N = 28.4, %W = 13.8) and *Octopoteuthis sicula* (%N = 8.5, %W = 17.2). Calf sperm whales consumed smaller cephalopods of these three prey species than non-calves, probably because larger cephalopods are more difficult to catch. The vast majority of ingested cephalopods were gelatinous, slow-swimming and small. Therefore, sperm whales inhabiting the Greek Seas and likely the whole eastern Mediterranean Sea, appear to target prey that are easy to catch, but need to be consumed in great numbers to fulfil the energy requirements of the whales.

1. Introduction

The study of trophic ecology is essential for understanding ecosystem dynamics and how human-induced ecosystem alterations influence species' conservation status (Pauly et al., 1998; Polis, 1994). Nevertheless, the feeding habits of several endangered species are often understudied. Surprisingly, this is even the case for large oceanic predators such as the toothed whales (Cetacea, Odontoceti) and especially their deep-diving representatives (Kogiidae, Physeteridae, Ziphiidae and some members of the Delphinidae). These predators, notably the larger species, collectively play a major role in deep-sea energy turnover (Lavery et al., 2010). Their habitual behaviour of feeding at depth and defecating at the water surface can result in increased primary production by reallocating iron and nitrogen in the water column (Lavery et al., 2010; Roman and McCarthy, 2010). However, their elusive lifestyle does not allow *in situ* and direct observations of feeding and makes any diet study challenging (but see Aoki et al., 2015; Mathias et al., 2009).

Fortunately, the operation of several cetacean stranding networks during recent decades has provided the opportunity to exploit stomach contents of dead, stranded animals over large geographical ranges. Visual identification of musculoskeletal remains and indigestible prey remnants (e.g., fish otoliths and cephalopod rostra or "beaks", Clarke et al., 1993) found in these stomachs provides information on the diet of stranded whales. Important drawbacks of stomach content analysis include: (1) the potential retention of cephalopod beaks in the stomach for a long period leading to overestimation of these species' contribution to diet (Bigg and Fawcett, 1985; Pitcher, 1980); (2) the differential excretion of some cephalopod beaks which in turn will be underestimated in the diet (Smith and Whitehead, 2000); and (3) the bias towards sick animals whose feeding habits may not be representative of their population (Santos et al., 2001a). However, it is the only method that simultaneously allows for species identification and quantification of prey importance and size (Clarke, 1986; Clarke et al., 1993).

The largest living odontocete species, the sperm whale *Physeter macrocephalus* Linnaeus, 1758, regularly dives to between 500 and

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1000 m to search for prey (Teloni et al., 2008; Watwood et al., 2006). In this dark environment, sperm whales navigate and track their prey via echolocation with little competition from visual predators (Madsen et al., 2007, 2002). The consensus about their diet is that in most examined areas, they mainly feed on mesopelagic and bathypelagic cephalopods (Mollusca, Cephalopoda), especially squids (Oegopsida, Kawakami, 1980). Fish can be an important dietary component for male sperm whales in high-latitude areas (Clarke and MacLeod, 1976; Gaskin and Cawthorn, 1967; Martin and Clarke, 1986; Rice, 1989). Although sperm whale diet varies significantly with time (Kawakami, 1980; Smith and Whitehead, 2000) and geographical location, squid families such as Architeuthidae, Cranchiidae, Histioteuthidae, Gonatidae, Octopoteuthidae, Ommastrephidae, Onychoteuthidae and Pholidoteuthidae are the most important worldwide (Clarke, 1996). The activity of these families of squid is rather diverse, ranging from highly mobile and muscular (ommastrephids) to sluggish and gelatinous (histioteuthids) (Clarke, 1980). Surprisingly, the majority of squid that sperm whales consume are small (<3% of whale body length, MacLeod et al., 2006) and not particularly nutritious. Accordingly, to consume a food mass equivalent to 3% of their body weight per day (Lockyer, 1981), sperm whales feed routinely during both day and night (Best, 1999). For a 30-tonne whale, this mass corresponds to about 1000 medium-sized squids per day (Clarke et al., 1993), which exceeds the 18–20 prey capture attempts per hour indicated by records of echolocation buzzes (Miller et al., 2004a; Watwood et al., 2006). Intraspecific partitioning of food resources is probably mediated by females and smaller males feeding on smaller squid species and smaller members of the same species than that consumed by adult male sperm whales (Best, 1999; Clarke, 1980; Clarke et al., 1993).

Total global food consumption by sperm whales is estimated to be 100 million tonnes/year (Clarke, 1977), exceeding the total annual catch of both marine and freshwater organisms harvested by humans (90 million tonnes/year, FAO, 2018). Available knowledge about deep-sea cephalopods is extremely limited because they are particularly difficult to catch, requiring specialised gear and dedicated surveys. Conversely, predators of these cephalopods are capable of capturing a great abundance and a high diversity of these squids, including large and sexually mature individuals, which are rarely caught by humans (Clarke, 1977; Xavier et al., 2003). Therefore, the sperm whale diet can offer valuable data for these understudied and elusive cephalopods.

The sperm whale population in the Mediterranean Sea is genetically differentiated and isolated from conspecifics in the Atlantic Ocean by the Strait of Gibraltar (Engelhaupt et al., 2009). Individuals of this population are found in both the eastern and western basins of the Mediterranean Sea, with their numbers likely being in the low to mid hundreds (Notarbartolo di Sciara, 2014). Unsustainable bycatch in drift nets and ship strikes have driven the classification of this population as Endangered by the IUCN (Notarbartolo di Sciara, 2014). In Greece, sperm whales can be found in both the Aegean Sea and the Hellenic Trench (Frantzis et al., 2003), with the latter being the core habitat for the entire population of the eastern Mediterranean Basin (Frantzis et al., 2014; Lewis et al., 2018). Sperm whales along the Hellenic Trench are usually found close to the 1000 m depth contour where they dive to catch their prey (Frantzis et al., 2014). In spite of the 'Endangered' conservation status of the Mediterranean sperm whales, little is known about their feeding habits. To date, all published data have come from the stomach contents of two adult males stranded in Crete, Greece (Roberts, 2003) and the Ligurian Sea, Italy (Garibaldi and Podestà, 2014). Although it is difficult to draw any general conclusions from such a small sample size, both studies found that oceanic cephalopods were the sole prey of sperm whales and overall identified eight prey species (Garibaldi and Podestà, 2014; Roberts, 2003). A common finding between these two studies was that the oceanic deep-sea squid *Histioteuthis bonnellii* (Férussac, 1834) was the most important prey, both in terms of numerical abundance and abundance by weight, and had a small mean dorsal mantle length (DML) (162 mm, Garibaldi and Podestà, 2014;

192 mm, Roberts, 2003).

In the present study, we analysed the stomach contents of nine sperm whales originating from all seasons and various age classes in order to better understand the trophic ecology of sperm whales in Greece and the eastern Mediterranean Sea. Prey species, size and importance in the sperm whale diet were used to elucidate how the largest toothed predator on the planet makes a living in a small and oligotrophic sea.

2. Materials and methods

2.1. Collection of samples

Stomach contents of sperm whales were collected by the Pelagos Cetacean Research Institute between 2005 and 2014 from nine individuals stranded along the Greek coasts (Table 1 and Fig. 1). The length and sex of each animal were recorded along with the cause of death when possible (Table 1). Whales of total length below 6 m were classified as calves according to Frantzis et al. (2014). The group of whales with total length ≥ 6 m were classified as either juveniles or sub-adults/adults (hereafter collectively termed non-calves).

All stomach contents were carefully removed *in situ* from the sperm whales. In one case following a ship strike (Pm10, Table 1), the stomach was already torn apart and part of the stomach contents was lost at sea. All prey remains (including cephalopod beaks, eye lenses and fish jawbones and vertebrae) were preserved in 70% ethanol.

2.2. Analysis of stomach contents

Cephalopod beaks, eye lenses and musculoskeletal remains along with fish remains and marine debris were sorted from every sample. We used beaks as the main diagnostic morphological structures and sorted them into lower and upper rostra. The identification of cephalopod prey to species level was based on lower beaks using published guides (Clarke, 1986; Lu and Ickeringill, 2002; Xavier and Cherel, 2009) and the reference collection of Dr Evgenia Lefkaditou at the Hellenic Centre for Marine Research in Agios Kosmas, Athens, Greece. Damaged lower beaks were identified to the lowest taxon possible and only used in determining the total number of prey. Identification of fish jawbones was also based on published information (Dalyan and Eryilmaz, 2008). The number of fish was estimated from the number of dentary bones and that of cephalopods from the number of lower beaks. Since the upper beaks of some cephalopod species are also diagnostic, like those of *Octopoteuthis sicula* Rüppell, 1844, *Todarodes sagittatus* (Lamarck, 1798) and *Ommastrephes bartramii* (Lesueur, 1821) (Lefkaditou et al., 2011), the estimated number of cephalopods was revised when upper beaks were more numerous than lower beaks. Although *Ommastrephes* d'Orbigny, 1834 has been long considered a monotypic genus (Zuev et al., 1975), recent molecular data suggest that it is a complex of species whose taxonomic status is currently under review (Fernández-Álvarez et al., 2018). Therefore, any prey remains belonging to the *Ommastrephes* genus are hereafter referred to as *Ommastrephes* sp.

Several damaged lower beaks belonging to the genus *Histioteuthis* d'Orbigny [in Férussac & d'Orbigny], 1841, could not be assigned into any of the two species known to occur in the Mediterranean Sea: *H. bonnellii* and *Histioteuthis reversa* (Verrill, 1880). We thus used the percentage of these two species in each stomach to proportionally assign these unidentified beaks to one of the two *Histioteuthis* species.

Standard measurements of undamaged cephalopod lower beaks and fish dentary bones were taken with a digital Vernier caliper (± 0.02 mm). Wet weight (W) and dorsal mantle length (DML) were estimated for each individual cephalopod from standard regressions (Table S2) relating prey body length and weight to lower beak rostral length (LRL) for squids or lower beak hood length (LHL) for octopodids and sepiolids. We obtained these regressions from the literature, preferentially from Mediterranean prey populations when available (Table S2). The total weight represented by the beaks of a given cephalopod species was

Table 1

Information about the stranded sperm whales included in this study. L and U: lower and upper cephalopod beaks respectively. For the purposes of this study, juvenile, sub-adult and adult sperm whales were collectively grouped together as non-calves. The Pm1 code corresponds to the sperm whale stranded in Loutro, Chania and analysed by Roberts (2003).

Identification code	Stranding date	Stranding location (Latitude, Longitude)	Total length (m)	Sex	Age class	Cause of death	Number of cephalopod beaks (L, U)	Number of cephalopod species	Presence of fish remains
Pm2	15/04/2005	Tholo, Ieia (37° 24' 50" N, 21° 39' 49" E)	5.4	F	Calf	Ship strike	109, 83	6	+
Pm3	25/02/2006	Parisaina, Magnisia (39° 27' 52" N, 23° 06' 52" E)	9.7	M	Sub-adult	Ship strike	3531, 1493	9	–
Pm4	18/04/2006	1 nm off Armenistis lighthouse, Mykonos (37° 30' 00" N, 25° 23' 15" E)	5.4	M	Calf	Gastric blockage	12943, 6790	11	–
Pm5	20/06/2007	Chrysoskalitissa, Chania (35° 18' 46" N, 23° 31' 38" E)	6.8	M	Juvenile	Ship strike	4668, 3757	14	–
Pm6	11/11/2007	Lefkos, Karpathos (35° 35' 12" N, 27° 04' 06" E)	8.0	F	Sub-adult	Unknown	6555, 5252	14	+
Pm7	15/05/2010	Psara, Chios (38° 33' 26" N, 25° 33' 54" E)	5.9	M	Calf	Ship strike	373, 334	6	–
Pm8	16/01/2011	Livadia, Chania (35° 21' 35" N, 23° 31' 52" E)	7.9	F	Sub-adult	Unknown	1321, 764	11	+
Pm9	30/06/2011	Potisiaes, Lefkada (38° 48' 06" N, 20° 37' 48" E)	3.6	M	Newborn	Unknown	0	0	–
Pm10	15/02/2014	Agia Kiriaki, Messinia (37° 07' 22" N, 21° 34' 25" E)	10.5	M	Adult	Ship strike	143, 40	6	–

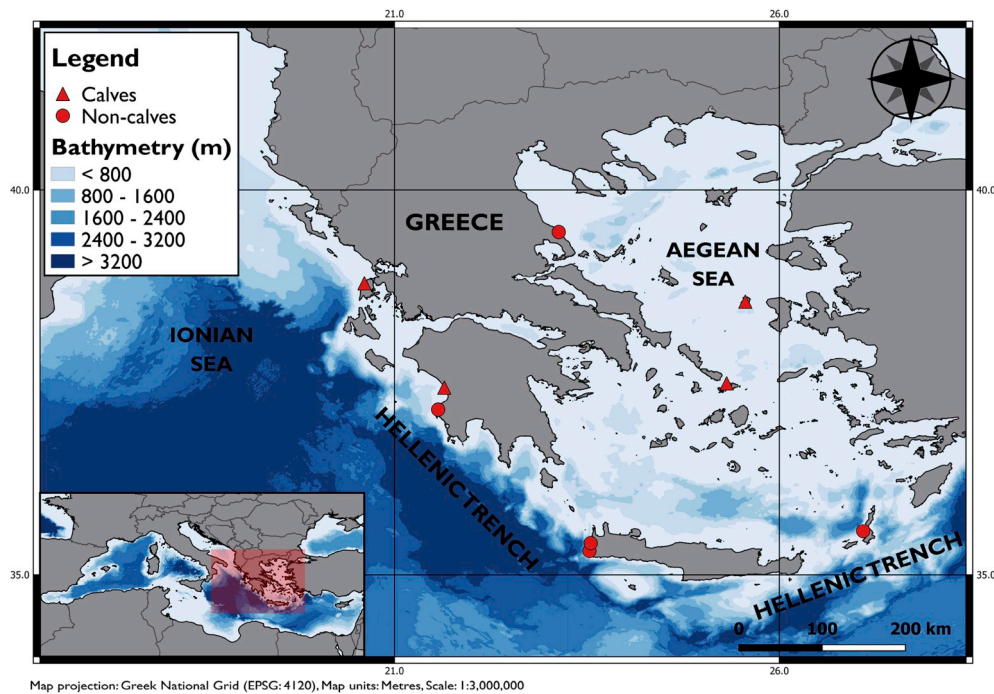


Fig. 1. Stranding locations of sperm whales from which stomach contents were analysed. Triangles: calves; circles: non-calves, i.e., juveniles and sub-adults/adults.

estimated as (sum of weights represented by beaks measured)/(proportion of individuals measured) (Santos et al., 2001b). Fish length was estimated from the length of dentary bones (Table S2).

We used three indices to describe the sperm whale diet: frequency of occurrence, average percentage abundance, and prey-specific abundance (Amundsen et al., 1996). Indices were calculated as following:

$$\text{Frequency of occurrence} : FO_i = \frac{n_i}{n}$$

$$\text{Average percentage abundance} (\%N_i, \%W_i) : \%A_i = \frac{\sum_{j=1}^n \%A_{ij}}{n}$$

$$\text{Prey – specific abundance} (\%PN_i, \%PW_i) : \%PA_i = \frac{\sum_{j=1}^n \%A_{ij}}{n_i}$$

where n_i is the number of stomachs containing prey i , n the total number of stomachs, A_{ij} the abundance (number or weight) of prey i in stomach j , $\%PN$ the percentage prey-specific number and $\%PW$ the percentage prey-specific weight. We then calculated the Prey-Specific Index of Relative Importance (PSIRI; Brown et al., 2012) for each prey species to determine its overall significance in the diet:

$$PSIRI_i = FO_i \cdot (\%PN_i + \%PW_i)$$

We did not calculate PSIRI for one fish species whose weight could

not be estimated. Values are expressed as %PSIRI, which was calculated by dividing the PSIRI for prey i by the sum of all PSIRI values and multiplying by 100. Important prey items were defined as species with %PSIRI > 5 (Harvey et al., 2014). The stomach contents from Pm9 and Pm10 (empty and partly lost respectively; Tables 1 and S1) were not included in the calculation of any dietary index.

Trophic niche width was estimated with PSIRI using the standardised version B_{st} (Hurlbert, 1978) of Levin's index B (Levins, 1968):

$$B = \frac{1}{\sum PSIRI_i^2}$$

$$B_{st} = \frac{B - 1}{k - 1}$$

where k is the number of prey species for which PSIRI was calculated. B_{st} ranges from 0 (specialist) to 1 (generalist predator, Krebs, 1999).

Two linear mixed-effects models were used, for each cephalopod species with %PSIRI > 5, to investigate the effect of (1) sperm whale age class (calves and non-calves) and (2) season, on the DML of the cephalopods. We defined the four seasons as following: winter (December–February), spring (March–May), summer (June–August) and autumn (September–November). For every season, we compared the DML with that of all the other seasons combined. Within-whale correlation was treated with a random intercept and the 0.05 criterion was used for statistical significance. Goodness of fit was evaluated with marginal $R^2_{(m)}$ and conditional $R^2_{(c)}$ (Nakagawa and Schielzeth, 2013). Marginal R^2 describes the proportion of variance in the response variable that is explained by the fixed variables only, while conditional R^2 describes the one explained by the entire model (fixed plus random effects). The $R^2_{(m)}$ for the null model (i.e., the model with the same random structure but no fixed effects) was also computed to describe the proportion of variance that is explained by the random variables only. Lastly, we used the Hartigans' Dip test to assess the bimodality in the DML distributions of the cephalopod species with %PSIRI > 5 (Hartigan and Hartigan, 1985). Statistical analyses were conducted in RStudio.

3. Results

Detected prey items consisted almost exclusively of cephalopod beaks: 18,513 upper and 29,643 lower beaks, along with 23,672 rostral tips (from either upper or lower beaks) and many hundreds of cephalopod eye lenses were recovered from all stomach contents, with the exception of the newborn sperm whale (Pm9, Table 1). This stomach contained only a white creamy substance resembling milk and a few leaves of the seagrass *Posidonia oceanica* (Linnaeus) Delile, 1813. Other cephalopod remains (i.e., radulae, gladii, sucker rings and arm hooks) were present in four out of eight stomachs (Pm2, 5, 6 & 8), while cephalopod musculoskeletal remains (i.e., buccal masses, crowns, mantles and one whole squid of *H. bonnellii*) were infrequent and only found in three stomachs (Pm2, 7 & 8). Fish skeletal remains (i.e., vertebrae, premaxillae, maxillae and dentaries) were found in three stomach contents (Pm2, 6 & 8). Tens of nematodes were recovered from two stomachs (Pm4 & 7) and have already been identified as the species *Anisakis physeteris* (Baylis, 1923) (Mattiucci et al., 2014). Megaplastic and macroplastic material was also found in five stomach contents (Pm4, 5, 6, 8 & 10, Fig. 2, Alexiadou et al., 2019), with the stomach of the individual stranded in Mykonos (Pm4) containing nearly 100 pieces (Alexiadou et al., 2019).

The 28,248 intact lower beaks were attributed to 17 cephalopod species from 13 different families (Table 2). The prey families in declining frequency of occurrence were: Ancistrocheiridae, Chiroteuthidae, Histioteuthidae, Octopoteuthidae (100%), Onychoteuthidae (85.7%), Cranchiidae, Ommastrephidae (71.4%), Ctenopterygidae (57.1%), Enoplateuthidae (42.9%), Brachioteuthidae, Pyroteuthidae, Sepiolidae (28.6%) and Octopodidae (14.3%). The species with the



Fig. 2. The entire stomach content of a sperm whale (Pm8) stranded in West Crete, Greece. It included cephalopod musculoskeletal remains (top right), eye lenses (bottom right), beaks (bottom left) and a large plastic bag.

highest numerical abundance was *H. bonnellii* (48.4%), followed by *H. reversa* (28.4%) and *O. sicula* (8.5%) while all the remaining prey species had a combined numerical abundance of ca. 6%. These three most abundant species comprised more than 95% of the total reconstructed weight, with *H. bonnellii* constituting 66.3% of this total. According to %PSIRI, the most important prey species (%PSIRI > 5) in the sperm whale diet were *H. bonnellii* (60.2%), *H. reversa* (22.2%) and *O. sicula* (13.5%). The standardised Levin's index B_{st} was equal to 0.08 indicating a specialised diet. Fish remains could be only identified in one stomach content (Pm6) and belonged to Sloane's viperfish *Chauliodus sloani* Bloch and Schneider, 1801, whose numerical abundance was negligible (Table 2).

The eight stomachs combined (Pm2–8 & Pm10) contained a total estimated ingested biomass of 15621 kg. This biomass ranged from 78 to 4700 kg for these eight stomachs (Table S1). The estimated DML of all cephalopods for which beaks could be measured ranged from 8 to 511 mm (mean = 117 mm, sd = 48 mm, $n = 18545$). The species with the smallest mean DML was *Heteroteuthis dispar* (Rüppell, 1844) (21 mm). The smallest prey consumed was an enoplateuthid, *Abralia veranyi* Rüppell, 1844 (DML = 8 mm) while the largest one was an individual of *Ommastrephes* sp. (DML = 511 mm). The estimated DMLs of *H. bonnellii*, *H. reversa* and *O. sicula* are shown in Fig. 3 and were between 17 and 266 mm (median = 108 mm, Q1 = 68 mm, Q3 = 143 mm, *H. bonnellii*), 20 and 160 mm (median = 106 mm, Q1 = 89 mm, Q3 = 118 mm, *H. reversa*) and 99 and 263 mm (median = 164 mm, Q1 = 151 mm, Q3 = 208 mm, *O. sicula*) respectively. According to Hartigans' Dip Test, the distributions of estimated DML were clearly bimodal for *H. bonnellii* ($p < 0.001$, modes at 61 and 132 mm) and *O. sicula* ($p < 0.001$, modes at 152 and 212 mm), but not for *H. reversa* ($p = 0.08$).

Age class was found to have a strong effect on the DML of *H. bonnellii* ($p = 0.004$) and *O. sicula* ($p = 0.004$) but not of *H. reversa* ($p = 0.06$, Fig. 4, Table A1). On average, calves consumed smaller individuals of the first two species (*H. bonnellii*: 85 mm [48–122 95% CI], *O. sicula*: 136 mm [130–196]) than non-calves (*H. bonnellii*: 133 mm [120–145], *O. sicula*: 207 mm [196–217]). Differences were also found for the DML of all three species between spring and all the other seasons combined (Fig. 5, Table A2). These species had a smaller DML in spring (*H. bonnellii*: 85 mm [52–119], *H. reversa*: 87 mm [62–113], *O. sicula*: 163 mm [130–197]) than in summer, autumn, and winter combined (*H. bonnellii*: 135 mm [124–146], $p = 0.001$, *H. reversa*: 107 mm [99–115], $p = 0.03$ & *O. sicula*: 210 mm [200–221], $p = 0.002$).

Table 2

Diet composition of stranded sperm whales (Pm2-8) by percentage frequency of occurrence (%FO), percentage prey-specific number (%PN), percentage number (%N), percentage prey-specific weight (%PW), percentage weight (%W), and prey-specific index of relative importance (%PSIRI). The mean and standard deviation of LRL/LHL (mm), mean and maximum DML (mm) and total weight (g) are also provided for every prey species. A value of NA is shown where weight and %PSIRI were not estimated. *For *Chauliodus sloani* only.

Class	Order	Family	Species	%FO	%PN	%N	%PW	%W	%PSIRI	LRL/LHL (mm)		DML or TL* (mm)		Total weight (g)
										Mean	SD	Mean	Max	
Cephalopoda	Oegopsida	Ancistrocheiridae	<i>Ancistrocheirus lesueurii</i>	100	1.6	1.6	1.8	1.8	1.8	6.2	0.9	213	280	$2.5 \cdot 10^5$
		Brachioteuthidae	<i>Brachioteuthis riisei</i>	28.6	0.1	<0.1	<0.1	<0.1	<0.1	1.2	0.6	37	66	17
		Chiroteuthidae	<i>Chiroteuthis veranyi</i>	100	0.8	0.8	0.1	0.1	0.5	4.6	0.7	123	165	$8.9 \cdot 10^3$
		Chtenopterygidae	<i>Chtenopteryx sicula</i>	57.1	<0.1	<0.1	<0.1	<0.1	<0.1	1.4	0.2	59	69	130
		Cranchiidae	<i>Galiteuthis armata</i>	71.4	3.3	2.4	0.5	0.4	1.4	5	1	218	299	$15.4 \cdot 10^3$
		Enoploteuthidae		42.9	<0.1	<0.1	<0.1	<0.1	<0.1	–	–	–	–	–
			<i>Abralia veranyi</i>	28.6	<0.1	<0.1	<0.1	<0.1	<0.1	1.3	0.7	30	52	35
			<i>Abraliopsis morisii</i>	28.6	<0.1	<0.1	<0.1	<0.1	<0.1	1.1	0.3	44	54	7
		Histoteuthidae		100	76.9	76.9	80.1	80.1	82.4	–	–	–	–	–
			<i>Histoteuthis bonnellii</i>	100	48.4	48.4	66.3	66.3	60.2	6	2.3	109	266	$11.8 \cdot 10^6$
			<i>Histoteuthis reversa</i>	100	28.4	28.4	13.8	13.8	22.2	3.6	0.7	103	160	$1.6 \cdot 10^6$
		Octopoteuthidae		100	8.5	8.5	17.2	17.2	13.5	9.7	2.2	178	263	$1.8 \cdot 10^6$
			<i>Octopoteuthis sicula</i>											
				71.4	0.2	0.1	0.7	0.4	0.2	–	–	–	–	–
		Ommastrephidae		28.6	<0.1	<0.1	0.2	<0.1	<0.1	11.9	–	511	–	$6.5 \cdot 10^3$
			<i>Ommastrephes</i> sp.											
			<i>Todarodes sagittatus</i>	71.4	0.1	<0.1	0.5	0.3	0.2	11.3	1.4	387	454	$61.3 \cdot 10^3$
		Onychoteuthidae		85.7	0.2	0.1	<0.1	<0.1	<0.1	–	–	–	–	–
			<i>Ancistroteuthis lichtensteinii</i>	71.4	0.1	<0.1	<0.1	<0.1	<0.1	5.6	1	178	209	$1.9 \cdot 10^3$
			<i>Onychoteuthis banksii</i>	57.1	<0.1	<0.1	<0.1	<0.1	<0.1	2.5	0.6	84	107	238
		Pyroteuthidae		28.6	<0.1	<0.1	<0.1	<0.1	<0.1	1.2	0.2	39	43	20
			<i>Pyroteuthis margaritifera</i>											
		Unidentified	Unidentified	–	–	–	–	–	–	–	–	–	–	–
		Broken beaks		85.7	11.1	9.5	–	–	–	–	–	–	–	–
	Sepiida	Sepiolidae		28.6	<0.1	<0.1	<0.1	<0.1	<0.1	1	0.1	21	22	5
			<i>Heteroteuthis dispar</i>											
Actinopterygii	Octopoda	Octopodidae	<i>Octopus vulgaris</i>	14.3	<0.1	<0.1	<0.1	<0.1	<0.1	1.1	–	–	–	7
	Stomiiformes	Stomiidae	<i>Chauliodus sloani</i>	14.3	<0.1	<0.1	NA	NA	NA	–	–	80	110	–

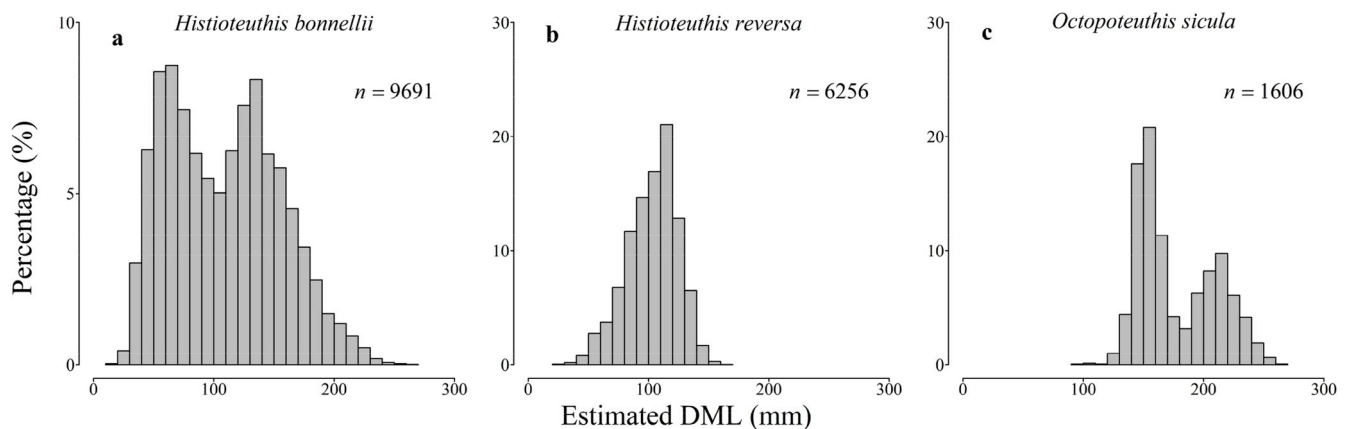


Fig. 3. Histograms of estimated dorsal mantle length (DML) for the most important prey species in the sperm whale diet (%PSIRI>5). Both *Histoteuthis bonnellii* and *Octopoteuthis sicula* are characterized by clear bimodal distributions. Data from sperm whales Pm2-8 only are used. *n*: number of measured lower beaks.

4. Discussion

Visual analysis of stomach contents is a valuable method for elucidating the diet of deep-diving predators such as sperm whales whose foraging behaviour is nearly impossible to directly observe (Clarke, 1996, 1962). Stomach content analysis provides a temporal and spatial snapshot of an individual's diet (Santos et al., 2001a). Stomach contents analysed in this study originated from various geographical locations

and across all seasons. This heterogeneous sampling potentially mitigated the effect that stranding location and season can have on the dietary results. Additionally, the stomach contents examined came from independent and single (i.e., not mass) stranding events.

Caution is required to avoid extensive inference when examining potentially sick and/or starved animals, whose feeding habits may be atypical and not representative of healthy individuals (Santos et al., 2001a). In this study, cephalopod musculoskeletal remains were present

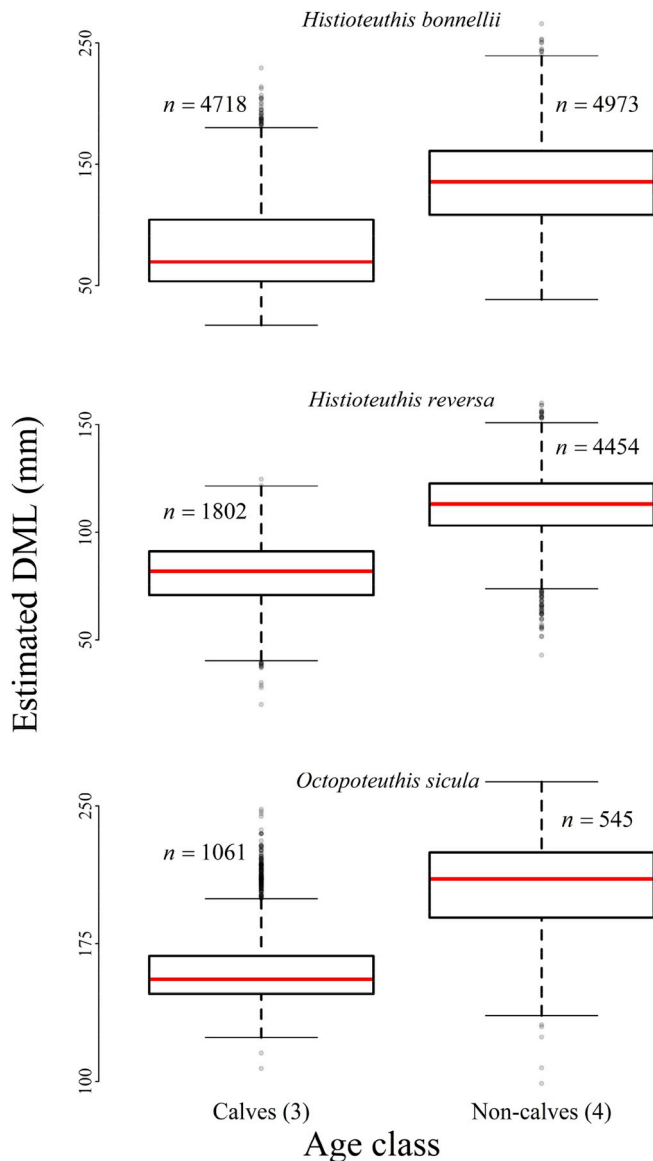


Fig. 4. Boxplots of estimated dorsal mantle length (DML) for the three prey species with %PSIRI > 5 in two sperm whale age classes. For all three species, calves (Pm2, 4 & 7) consumed individuals of smaller dorsal mantle length than non-calves (Pm3, 5, 6 & 8). The boxes show the 25th, 50th (median) and 75th percentile (lower, mid and upper lines in the box) of DML, while whiskers denote the lowest and highest datum within 1.5 interquartile range. Data from sperm whales Pm2–8 only are used. *n*: number of measured lower beaks.

in the stomachs of three sperm whales (Pm2, 7 & 8, Table 1), two of which died from ship collisions and were probably feeding just before their death. However, poor health may predispose an animal to death from a ship strike. It is therefore possible that our samples are biased towards animals that were in poor health. Nevertheless, the similarity between the disparate samples in terms of dominant prey species suggests that they accurately reflect the natural variation in the diet of sperm whales found in Greece.

The importance of cephalopods and especially oceanic squids (Oegopsida) for sperm whales in Greece is highlighted by our findings. It must be noted though that since cephalopod beaks are resistant to digestion, stomach content analysis can introduce a bias towards a diet based on cephalopods. While *Ommastrephes* sp. can also be found in the neritic zone, the remaining squids are deep-sea cephalopods inhabiting the mesopelagic or the bathypelagic zone and only visiting the lower epipelagic zone during the night (Jereb and Roper, 2010). At the present

time, none of the squid species we found is targeted by fisheries in the Mediterranean Sea (except *T. sagittatus*, Katsanevakis et al., 2008 for which %PSIRI was only equal to 0.2).

While cephalopods are known to be the most important prey for sperm whales, fish can form a considerable proportion of their diet in high latitudes such as New Zealand and the northern parts of the Pacific and Atlantic oceans (Clarke and MacLeod, 1976; Gaskin and Cawthorn, 1967; Martin and Clarke, 1986; Rice, 1989). In some of these areas, sperm whales even remove catch from longlines (Hucke-Gaete et al., 2004; Nolan et al., 2000). The very low number of fish remains in the stomachs of this study suggests that fish are of relatively low dietary importance for sperm whales in Greece but caution is required when interpreting such results due to the high susceptibility of fish bones to chemical degradation in the stomach (Harvey, 1989). Mediterranean sperm whales have not been reported to attack longlines but entanglements in them (Di Natale and Mangano, 1983; Mussi et al., 1998) and anecdotal reports of presence of hooks in their stomachs (Mazzariol et al., 2011) suggest feeding attempts on hooked fish or cephalopods may occur (Bearzi, 2002).

The stomach of Pm9 belonged to a newborn (3.6 m long) that was only a few weeks old (Table 1). His stomach contained only milk and no hard prey remains, indicating that this whale had not started ingesting solid food before the stranding. Milk has also been found in the stomach of a sperm whale calf stranded in Co Clare, Ireland (Santos et al., 2006). This calf was 5.8 m long and several cephalopod beaks were found in his stomach, which is consistent with the findings from similarly sized sperm whales in this study (Pm2, 4, 5 & 7, Table 1).

The stomach of a 5.4 m long calf stranded in Mykonos (Pm4) contained a very high number of worn cephalopod beaks (ca. 13,000 lower beaks, Table 1). We were unable to locate any reference regarding the stomach of a single sperm whale that was close to the number of lower beaks found in this stomach. This stomach was completely full with nearly 100 megaplastic and macroplastic pieces (Alexiadou et al., 2019). Accordingly, the gastric blockage caused by the ingestion of plastic was probably the reason behind this great number of cephalopod beaks that were “trapped” in the stomach and probably represented an accumulation of many days of feeding.

Our study revealed ten prey species not previously reported for sperm whales in the Mediterranean Sea (nine cephalopods and one teleost): *Brachioteuthis riisei* (Steenstrup, 1882), *Chtenopteryx sicula* (Vérany, 1851), *Abralia veranyi*, *Abraliopsis morisii* (Vérany, 1851), *Ommastrephes* sp., *T. sagittatus*, *Pyroteuthis margaritifera* (Rüppell, 1844), *Heteroteuthis dispar*, *Octopus vulgaris* Cuvier, 1797 and the fish *Chauliodus sloani*. This is probably due to the greater number of stomachs that we analysed compared to the two previously analysed from the Mediterranean Sea (Garibaldi and Podestà, 2014; Roberts, 2003). In addition to the low %FO and %PSIRI, these new species represented small-bodied taxa (except *Ommastrephes* sp. and *T. sagittatus*). Although their presence might be the result of secondary ingestion by the larger squid sperm whales consume (González et al., 1994), mastication of prey consumed by squid renders this scenario unlikely.

Despite the fact that around one third of cephalopod species found in the Greek Seas (18/49 or 36.7%, Lefkaditou, 2006; Lefkaditou et al., 2012, 2011) were identified as prey species, the sperm whale diet is specialised (niche breadth = 0.08), with the umbrella squid *H. bonnellii* being unequivocally the most important prey. This squid is considered a common bathypelagic cephalopod at 800–2000 m depth (Bello, 2000; Voss et al., 1992) and is the largest species of its genus with some individuals reaching 6 kg in total weight (Garibaldi and Podestà, 2014; Jereb and Roper, 2010). Its high significance in the sperm whale diet has already been emphasized in the two previous Mediterranean studies (Garibaldi and Podestà, 2014; Roberts, 2003) with its high %PSIRI stemming from both its high numerical abundance and abundance by weight. Nonetheless, in the present study, *H. reversa* and *O. sicula* are also shown to be important prey of sperm whales in the Mediterranean Sea. Despite its smaller size (Fig. 3b), the reverse jewel squid *H. reversa*

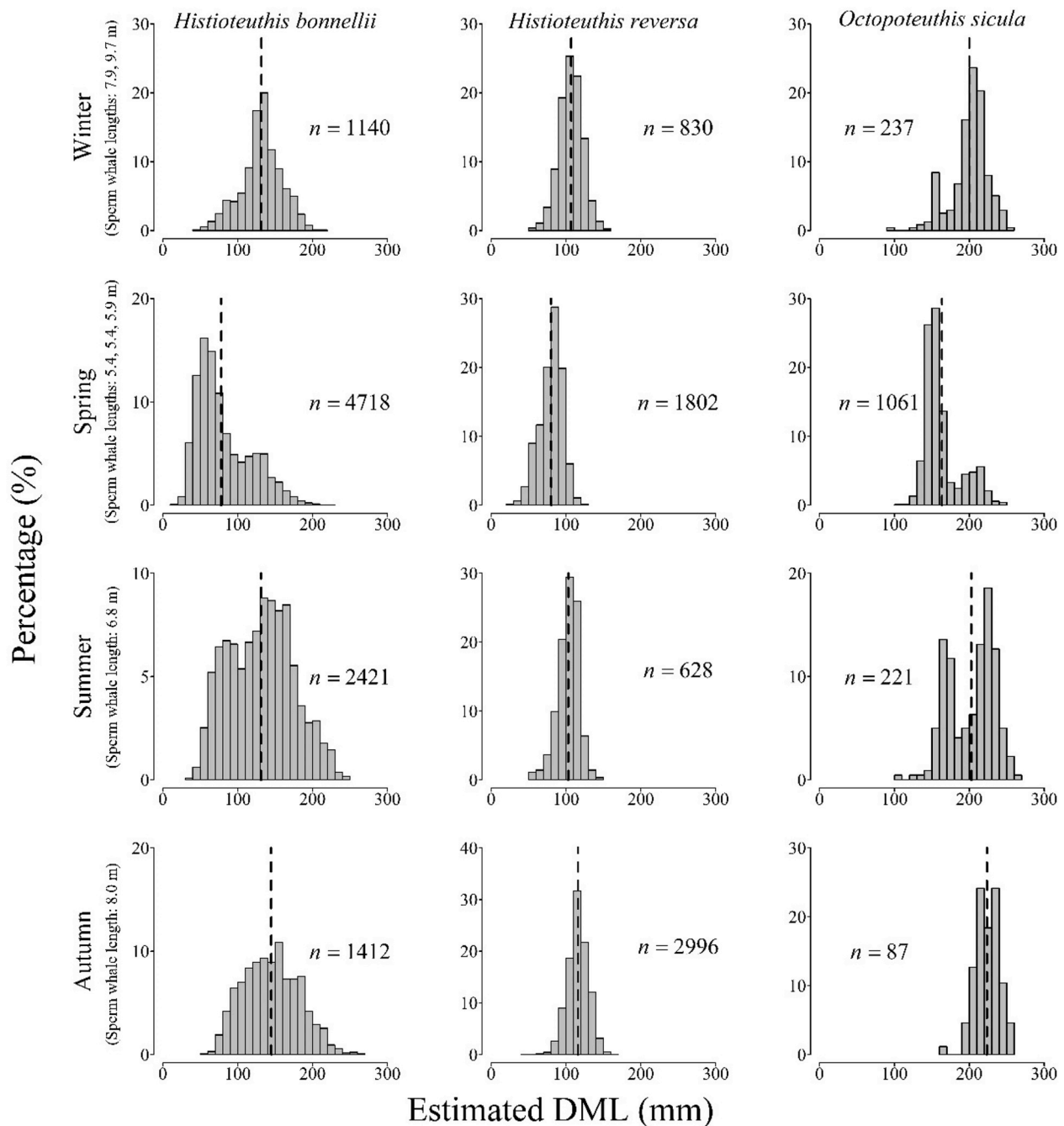


Fig. 5. Histograms of estimated dorsal mantle length (DML, dashed line: mean) for the three prey species with %PSIRI > 5 between the four different seasons. For all three cephalopod species, DML is smaller in spring suggesting a possible recruitment of juvenile cephalopods between winter and spring. Data from sperm whales Pm2-8 only are used. The total length of the sampled sperm whales is presented as subtitle on the y-axis of each season, with calves defined as whales of total length < 6 m. n: number of measured lower beaks.

was consumed in great numbers while the Rüppell's octopus squid *O. sicula* had a large %PSIRI due to its high abundance by weight. Both species share similar depth ranges with *H. bonnellii* and are characterized by diurnal vertical migration to mesopelagic (*Histioteuthis* spp.) or epipelagic waters (*O. sicula*; Jereb and Roper, 2010). This type of migration and the possible schooling behaviour of *H. bonnellii* (Jereb and Roper, 2010) may allow sperm whales to consume these cephalopods in great numbers.

The stomach content analysis in this study can shed light on the life cycles of the three main prey species, which are currently poorly known. For both *H. bonnellii* and *O. sicula*, a bimodal DML distribution was apparent (Fig. 3a, c). This may result from sperm whales feeding on two

different cohorts (Huston and DeAngelis, 1987) in spring and summer (Fig. 5). These bimodal DML distributions could be also attributed to sexual dimorphism (Hoving et al., 2008; Jereb et al., 2016; Mereu et al., 2011). A second interesting finding is the smaller DML of all three prey species in spring compared with all the other seasons combined (Fig. 4, Table A2). This may result from the recruitment of young squid along with the subsequent death of post-spawning sexually mature individuals (Nesis, 1987) between winter and spring. However, due to the limited sample size of this study, definitive explanations regarding the change in squid size over the year cannot be provided, and further analysis of more stomach contents is required to explain these findings.

The high significance of *Histioteuthis* genus as prey of sperm whales is

not only a Mediterranean phenomenon. In New Zealand, Iceland and other Atlantic areas contiguous to the Mediterranean Sea (e.g., Madeira, Vigo, the Azores, the Canary Islands and Bay of Biscay), species of this genus are the first or second most important prey of sperm whales (Clarke, 1962; Clarke et al., 1993; Clarke and MacLeod, 1976, 1974; Fernández et al., 2009; Gómez-Villota, 2007; González et al., 1994; Spitz et al., 2011). In spite of the small to medium body size of *Histioteuthis* species, their ingested biomass among non-calves was observed to range from 2648 kg to 4100 kg (Table S1). The simultaneous importance of this genus for other apex oceanic predators such as albacores *Thunnus alalunga* (Bonnaterre, 1788), blue sharks *Prionace glauca* (Linnaeus, 1758), Risso's dolphins *Grampus griseus* (G. Cuvier, 1812) and Cuvier's beaked whales *Ziphius cavirostris* Cuvier, 1823 (Bello, 1999, 1990; Blanco and Raga, 2000; Würtz et al., 1992) is a strong indication of the pivotal role of *Histioteuthis* in deep-sea food webs.

Besides the relative importance of each prey in the sperm whale diet, the dietary data also provide evidence for the whales' feeding strategy. Given the large disparity in size of sperm whales and their prey (MacLeod et al., 2006), the whales showed a clear preference towards small squid (median DML of all cephalopods: 11.3 cm) verifying the quote of the late Malcolm Clarke that "[the sperm whale's diet] is comparable to a 90 kg man aiming to sample food the size of a walnut" (Clarke et al., 1993, p. 81). In addition to their small size, the most important squid families sperm whales consumed (i.e., Ancistrocheiridae, Chiroteuthidae, Cranchiidae, Histioteuthidae, and Octopoteuthidae with overall %PSIRI = 99.6, Table 2) were neutrally buoyant, not muscular, and by extension slow-swimming and poor in calorific value (Clarke et al., 1985, 1979). In contrast, muscular and fast-swimming squids with high energy content (i.e., *Ommastrephes* sp., *T. sagittatus*, *Ancistroteuthis lichtensteinii* (Férussac [in Férussac & d'Orbigny], 1835) and *Onychoteuthis banksii* (Leach, 1817)) were insignificant prey since they had a cumulative %PSIRI of ca. 0.3 (Table 2). This 'appetite' for a narrow range of relatively small, low-quality and slow-swimming prey is probably a foraging strategy that fits the low metabolic cost of living (Spitz et al., 2012) and slow swimming speed (<2 m/s) of these whales (Miller et al., 2004b). A similar foraging strategy has been observed for sperm whales in Norway, which are known to mainly feed on *Gonatus fabricii* (Lichtenstein, 1818) (Bjørke, 2001) and switch to less active prey capture attempts with fewer maneuvers when attempting to target sedentary life stages of this squid (Isojunno and Miller, 2018). This specialisation on organisms of specific size and mobility could be also linked to the deep-diving behaviour of air-breathing mammals that need to operate under tight energy budgets during long foraging dives (MacLeod et al., 2006). The large %PSIRI (60.2) of *H. bonnellii* could thus be related to the combined effect of its ease of capture and high abundance (Bello, 2000). Although large squid have been reported from sperm whale stomachs in other areas (e.g., the Azores, Clarke et al., 1993), there was an underrepresentation of such sizes in this study. This finding may be due to both the foraging strategy of sperm whales and the lack of very large oceanic cephalopods in Greece (Lefkaditou, 2006; Lefkaditou et al., 2011).

All age and sex classes of sperm whales use the Hellenic Trench, the core habitat for the eastern Mediterranean sperm whale subpopulation, for vital life functions such as feeding, breeding, calving and nursing (Frantzis et al., 2014). A potential consequence of this lack of segregation in habitat use is the increased intraspecific competition for the same

trophic resources between sperm whales of different size. Although the sample size of stomach contents was inadequate for inferring any differences in prey composition among the age and sex classes, the data on the DML of *H. bonnellii* and *O. sicula* suggest that calves consume smaller squid than non-calves (Fig. 4, Table A1). This difference, albeit not large, has been observed for *H. bonnellii* from sperm whales in the Azores (Clarke et al., 1993) and may emerge from the interaction of three different factors: (1) the lesser diving capacity of calves (Gannier et al., 2012; Noren and Williams, 2000; Tønnesen et al., 2018); (2) the ontogenetic migration of some deep-sea squids to greater depths as they mature (e.g., *H. reversa*, Voss et al., 1998); and (3) the greater difficulty of capturing bigger squid. As a result, large squid may be too difficult to catch and/or inaccessible to calves; especially during the day when the squid avoid the upper mesopelagic and epipelagic zone (Jereb and Roper, 2010).

Whether sperm whales consume ca. 3% of their body weight in squid per day (Lockyer, 1981) largely remains a mystery. However, the stomach contents analysed in this study reveal that sperm whales in Greece, and likely the whole eastern Mediterranean Sea, may have a narrow dietary niche primarily feeding all year-round on three oceanic bathypelagic squids that play a key role in the deep-sea food web. Specialisation to target small, slow-swimming and low calorific-value prey may be related to biomechanical and bioenergetic constraints during long breath-hold dives.

Commercial fish and cephalopod species were not found in the sperm whale stomachs suggesting that direct competition with fisheries may not currently affect the conservation of sperm whales in this region. Despite this, there are many other anthropogenic activities that undermine their survival and make their future uncertain in the eastern Mediterranean Sea (e.g., ship-strikes, oil and gas exploration, and plastic debris pollution, Alexiadou et al., 2019; Frantzis et al., 2019; Madsen et al., 2006).

Declaration of competing interest

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix B. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2019.103164>.

Appendix A

Table A.1

Summary of the fixed, random effects and the goodness of fit for the three age class models of each important prey species (%PSIRI>5). Est: mean DML (mm); CI: confidence intervals; σ_e^2 and σ_k^2 the variance within and between sperm whales respectively. *P* values below 0.05 are shown in bold.

Fixed effects	<i>Histioteuthis bonnellii</i>		<i>Histioteuthis reversa</i>		<i>Octopoteuthis sicula</i>	
	Calves	Non-calves	Calves	Non-calves	Calves	Non-calves
Est [95 %CI]	85 [48–122]	133 [120–145]	88 [58–117]	106 [96–116]	163 [130–196]	207 [196–217]
<i>p</i>		0.004		0.06		0.004
σ_e^2		13·10 ²		206		634
			Random effect (σ_k^2)			
Est [95% CI]		151 [39–579]		101 [28–364]		108 [24–487]
			Goodness of fit			
$R_{(m)}^2$		0.26		0.18		0.36
$R_{(c)}^2$		0.34		0.45		0.45
$R_{(n)}^2$		0.35		0.47		0.48

Table A.2

Summary of the fixed, random effects and the goodness of fit for the four season models of each important prey species (%PSIRI>5). Est: mean DML (mm); CI: confidence intervals; σ_e^2 and σ_k^2 the variance within and between sperm whales respectively. *P* values below 0.05 are shown in bold.

Fixed effects	<i>Histioteuthis bonnellii</i>		<i>Histioteuthis reversa</i>		<i>Octopoteuthis sicula</i>	
	Winter	Non-winter	Winter	Non-winter	Winter	Non-winter
Est (95 %CI)	134 [62–205]	107 [83–130]	105 [69–142]	97 [85–109]	209 [142–277]	186 [164–208]
<i>p</i>		0.22		0.41		0.26
σ_e^2		1.4·10 ³		206		629
			Random effect (σ_k^2)			
Est (95% CI)		710 [227–2.2·10 ³]		184 [59–576]		616 [195–1.9·10 ³]
			Goodness of fit			
$R_{(m)}^2$		0.04		0.02		0.05
$R_{(c)}^2$		0.36		0.48		0.52
$R_{(n)}^2$		0.36		0.46		0.51
Fixed effects	Spring	Non-spring	Spring	Non-spring	Spring	Non-spring
Est (95 %CI)	85 [52–119]	135 [124–146]	87 [62–113]	107 [99–115]	163 [130–197]	210 [200–221]
<i>p</i>		0.001		0.03		0.002
σ_e^2		1.3·10 ³		206		629
			Random effect (σ_k^2)			
Est (95% CI)		152 [43–531]		89 [27–213]		134 [36–530]
			Goodness of fit			
$R_{(m)}^2$		0.29		0.21		0.39
$R_{(c)}^2$		0.36		0.45		0.50
$R_{(n)}^2$		0.37		0.46		0.51
Fixed effects	Summer	Non-summer	Summer	Non-summer	Summer	Non-summer
Est (95 %CI)	131 [31–232]	115 [93–137]	103 [55–151]	99 [89–110]	203 [109–296]	194 [173–215]
<i>p</i>		0.62		0.82		0.77
σ_e^2		1.3·10 ³		206		629
			Random effect (σ_k^2)			
Est (95% CI)		895 [286–2.8·10 ³]		205 [199–213]		767 [587–2.4·10 ³]
			Goodness of fit			
$R_{(m)}^2$		0.02		2·10 ^{−3}		6·10 ^{−3}
$R_{(c)}^2$		0.40		0.50		0.55
$R_{(n)}^2$		0.37		0.46		0.51
Fixed effects	Autumn	Non-autumn	Autumn	Non-autumn	Autumn	Non-autumn
Est (95 %CI)	145 [89–200]	113 [52–241]	116 [92–140]	97 [41–154]	224 [175–273]	191 [76–241]
<i>p</i>		0.33		0.20		0.26
σ_e^2		1.3·10 ³		206		629
			Random effect (σ_k^2)			
Est (95% CI)		785 [249–2.4·10 ³]		153 [48–492]		617 [193–1.9·10 ³]
			Goodness of fit			
$R_{(m)}^2$		0.05		0.20		0.04
$R_{(c)}^2$		0.40		0.54		0.52
$R_{(n)}^2$		0.36		0.46		0.51

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