

Stomach contents of three deep-diving toothed whale species stranded in Greece, eastern Mediterranean

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Abstract

Understanding trophic ecology is essential for assessing the role of top predators in marine food webs. In the Mediterranean Sea, toothed whales are key components of megafauna and for this reason, we investigated the diets of nine deep-diving odontocetes stranded along the Greek coastline: five Risso's dolphins (*Grampus griseus*), three goose-beaked whales (*Ziphius cavirostris*) and one sperm whale (*Physeter macrocephalus*). A total of 17 cephalopod species were identified and quantified via percentage by number (%N) and by weight (%W). For Risso's dolphins, *Histioteuthis reversa* was the most important prey item (%N=24.7, %W=27.3), while *Histioteuthis bonnellii* dominated the diets of goose-beaked whales (%N=32.3, %W=34.1) and the sperm whale (%N=86.8, %W=99.8). We report, for the first time for *G. griseus* in the eastern Mediterranean, *Illex coindetii* as a rather important prey and the beltfish *Trichiurus lepturus* as an unusual prey. Our findings underscore the ecological importance of the *Histioteuthis* genus in the diets of deep-diving toothed whales in the Mediterranean. Risso's dolphins exhibited the most diverse diet, indicative of a generalist foraging strategy, whereas goose-beaked whales and the single sperm whale displayed more specialized feeding habits focusing on mesopelagic and bathypelagic prey. The finding of macroplastics in the sperm whale highlights a widespread threat to this species in the region. Despite the small sample size and the opportunistic nature of stranding events, our findings align with previous evidence of species-specific dietary patterns and emphasize the importance of conserving deep-sea foraging habitats in the eastern Mediterranean.

Keywords: cephalopod; diet; odontocetes; teuthophagous; trophic ecology; plastic debris.

Introduction

Marine top predators such as large fish, seabirds, seals and cetaceans play a crucial role in regulating ecosystems through top-down control of prey populations and nutrient cycling (Curry *et al.*, 2011; Lynam *et al.*, 2017; Aarts *et al.*, 2019; Rupil *et al.*, 2022). Understanding their trophic ecology is therefore essential for interpreting predator-prey dynamics, identifying critical habitats, and assessing the potential impacts of human activities on these species (Harkonen *et al.*, 2012; Maxwell *et al.*, 2013; Roff *et al.*, 2018).

Several species of marine top predators inhabit both basins of the Mediterranean Sea. In the eastern basin, the narrow continental shelf and steep deep-sea trenches form important habitats for deep-diving toothed whales (Frantzis *et al.*, 2003; Frantzis, 2009; Frantzis *et al.*, 2014). These geomorphological features act as biological hotspots by concentrating prey, such as deep-sea cepha-

lopods and fish, along slope-associated fronts, thereby facilitating efficient foraging during prolonged, breath-hold dives (Aïssi *et al.*, 2012).

Three deep-diving odontocete species are regularly observed in the eastern Mediterranean: sperm whales (*Physeter macrocephalus* Linnaeus, 1758), goose-beaked whales (*Ziphius cavirostris* Cuvier, 1823), and Risso's dolphins [*Grampus griseus* (G. Cuvier, 1812)]. These species inhabit both pelagic and slope-associated habitats (Frantzis *et al.*, 2003; Frantzis, 2009; Frantzis *et al.*, 2014). According to the IUCN Red List of Threatened Species, the Mediterranean subpopulations of sperm whales and Risso's dolphins are currently classified as Endangered (EN) (Lanfredi *et al.*, 2021; Pirotta *et al.*, 2021), while goose-beaked whales are listed as Vulnerable (VU) (Cañadas & Notarbartolo Di Sciara, 2018). Although the ecology of these three species has been studied in other regions (Clarke *et al.*, 1993; West *et al.*, 2017; Bloch *et al.*, 2012), caution must be exercised when extrapolating

such findings to the isolated Mediterranean subpopulations, which are genetically distinct from their Atlantic counterparts (Dalebout *et al.*, 2005; Gaspari *et al.*, 2007; Violi *et al.*, 2023).

Stomach content analysis of stranded animals has long served as a valuable tool for investigating the trophic ecology of deep-diving toothed whales, whose elusive behaviour makes direct observation of feeding nearly impossible (Clarke, 1980). This method allows for accurate species-level identification of prey remains and estimation of prey size, enabling a quantitative assessment of each prey's relative importance in the predator's diet (Pierce & Boyle, 1991). However, because it relies on opportunistic samples, stomach content analysis may disproportionately reflect the most recent feeding events of stranded individuals, which might not be representative of the broader population.

Analyses of stomach contents from Mediterranean sperm whales, goose-beaked whales and Risso's dolphins have revealed an almost exclusive reliance on mesopelagic and bathypelagic squids as their primary prey (Tables S1, S2 and S3). Although deep-sea squids are important prey for these predators, their biological and ecological characteristics remain poorly understood due to limitations of standard sampling methods (Hoving *et al.*, 2014). For sperm whales, the deep-sea squid *Histioteuthis bonnellii* (A. Féruccac, 1834) has been consistently identified as the most important prey species in their diet (Roberts, 2003; Garibaldi & Podesta, 2014; Mazzariol *et al.*, 2018; Foskolos *et al.*, 2020a; Tonay *et al.*, 2021). In contrast, goose-beaked whales and Risso's dolphins appear to have broader dietary niches. The diet of *Z. cavirostris* includes a range of deep-sea squid species from the families Chiroteuthidae, Cranchiidae, Histiocteuthidae, and Octopoteuthidae (Blanco & Raga, 2000; Kovačić *et al.*, 2011; Pedà *et al.*, 2015; Tonay *et al.*, 2025). *G. griseus*, on the other hand, preys on squids from the families Histiocteuthidae, Ommastrephidae, and Onychoteuthidae (Würtz *et al.*, 1992; Bello & Bentivegna, 1996; Blanco *et al.*, 2006; Öztürk *et al.*, 2007; Pedà *et al.*, 2015; Milani *et al.*, 2018; Luna *et al.*, 2021).

Across the Mediterranean, stomach content analyses have been conducted on 28 individuals of *G. griseus* and 14 individuals of *Z. cavirostris*, with only three and eight individuals, respectively, originating from the eastern basin (Würtz *et al.*, 1992; Bello & Bentivegna, 1996; Blanco & Raga, 2000; Orsi Relini & Garibaldi, 2005; Blanco *et al.*, 2006; Öztürk *et al.*, 2007; Kovačić *et al.*, 2011; Pedà *et al.*, 2015; Milani *et al.*, 2017; Luna *et al.*, 2021; Tonay *et al.*, 2025). In contrast, 11 of the 12 *P. macrocephalus* individuals examined to date were stranded in the eastern Mediterranean (Roberts, 2003; Foskolos *et al.*, 2020a; Tonay *et al.*, 2021). Despite these efforts, the total number of stomachs analysed for all three species remains too limited to support robust assessments of spatial, interspecific, or intraspecific variations in their diet.

To expand the limited dataset for the eastern Mediterranean basin, we analysed the stomach contents of nine individuals stranded along the Greek coastline: five Risso's dolphins, three goose-beaked whales, and one sperm

whale. Although the sample size is small, our results indicate that squids of the genus *Histioteuthis* represent a key dietary component for all three species. These findings therefore offer valuable insights into the trophic ecology of these elusive deep-diving cetaceans across a region increasingly affected by anthropogenic pressures.

Materials and Methods

Sample collection

Stomach contents of five Risso's dolphins and three goose-beaked whales stranded along the Greek coastline were collected by the Pelagos Cetacean Research Institute (PCRI) between 1994 and 2012 (Table 1, Fig. 1). In addition, we included the stomach contents of a single sperm whale stranded in 2019 (Table 1, Fig. 1). Stomach contents from other sperm whales stranded in Greece between 2005 and 2014 were excluded, as they have been already reported in a previous study (Foskolos *et al.*, 2020a). For each individual, the length, sex and -when possible- the cause of death were recorded (Table 1).

Stomach contents were carefully extracted *in situ* from all toothed whales. For one Risso's dolphin (Gg1 in Table 1), the stomach contents were only photographed while for all other specimens, prey remains were preserved in 70% ethanol. As most of these stomach contents had already been analysed for debris items in a previous study (Alexiadou *et al.*, 2019), we only washed and dried the debris found in specimen Pm11 (Table 1) for further analysis.

Analysis of stomach contents

Cephalopod beaks, eye lenses and musculoskeletal remains, fish bones and other invertebrate remains were sorted from each sample. Beaks served as the primary diagnostic morphological structures and were categorized into lower and upper. Cephalopods were primarily identified to the species level using lower beaks, following the identification guide by Pedà *et al.* (2022). Damaged lower beaks were identified to the lowest possible taxonomic level and were used solely to estimate the total number of prey. Fish and crustacean remains were identified using published references (Dalyan & Eryılmaz, 2008; Fischer *et al.*, 1987; Nakamura & Parin, 1993). Abundance was then estimated based on the number of dentary bones for fish and telsons for crustaceans. Similarly, cephalopod abundance was estimated by counting lower beaks. However, since upper beaks of certain species -such as *Octopoteuthis sicula* Rüppell, 1844 and *Argonauta argo* Linnaeus, 1758- can also be diagnostic, the estimated number of cephalopods was revised whenever upper beaks outnumbered lower ones.

Standard measurements of undamaged cephalopod lower beaks were taken using a digital Vernier calliper (± 0.02 mm accuracy). For each individual cephalopod, total wet weight (W) and mantle length (ML) were

Table 1. Details of the stranded Risso's dolphins (*Gg*), goose-beaked whales (*Zc*) and the single sperm whale (*Pm*) included in this study. “L” and “U” refer to lower and upper cephalopod beaks, respectively. The identification codes for the sperm whales follow the numbering system used by Foskolos *et al.* (2020a). All stomach contents, except for that of *Pm11*, were previously analysed for debris items in Alexiadou *et al.* (2019).

Identification code	Stranding date	Stranding location	Total length (m)	Sex	Cause of death	Number of cephalopod beaks (L/U)	Number of cephalopod species	Presence of non-cephalopod prey remains	Presence of debris items
Gg1	08/01/1994	Gythio, Laconia	2.95	F	Deliberate killing	3/7	1	+	-
Gg2	29/04/2006	Megas Gialos, Siros	3.15	M	Unknown	1/0	1	-	-
Gg3	07/06/2008	Gira, Lefkada	2.91	F	Ingestion of macroplastics	464/405	9	-	+
Gg4	04/04/2011	Tsoukalia, Paros	3.06	M	Unknown	2/7	3	-	-
Gg5	18/10/2012	Zacharo, Ilia	3.13	F	Unknown	169/94	8	-	-
Zc1	12/05/1996	Kartelas, Messinia	4.50	M	Military sonar	180/162	7	+	-
Zc2	30/11/2011	Arillas, Kerkyra	4.88	M	Military sonar	126/167	6	+	-
Zc3	01/12/2011	Kontogialos, Kerkyra	4.33	M	Military sonar	134/134	7	-	-
Pm11	27/10/2019	Keratea, Attica	12.1	M	Ship strike	1300/332	6	-	+

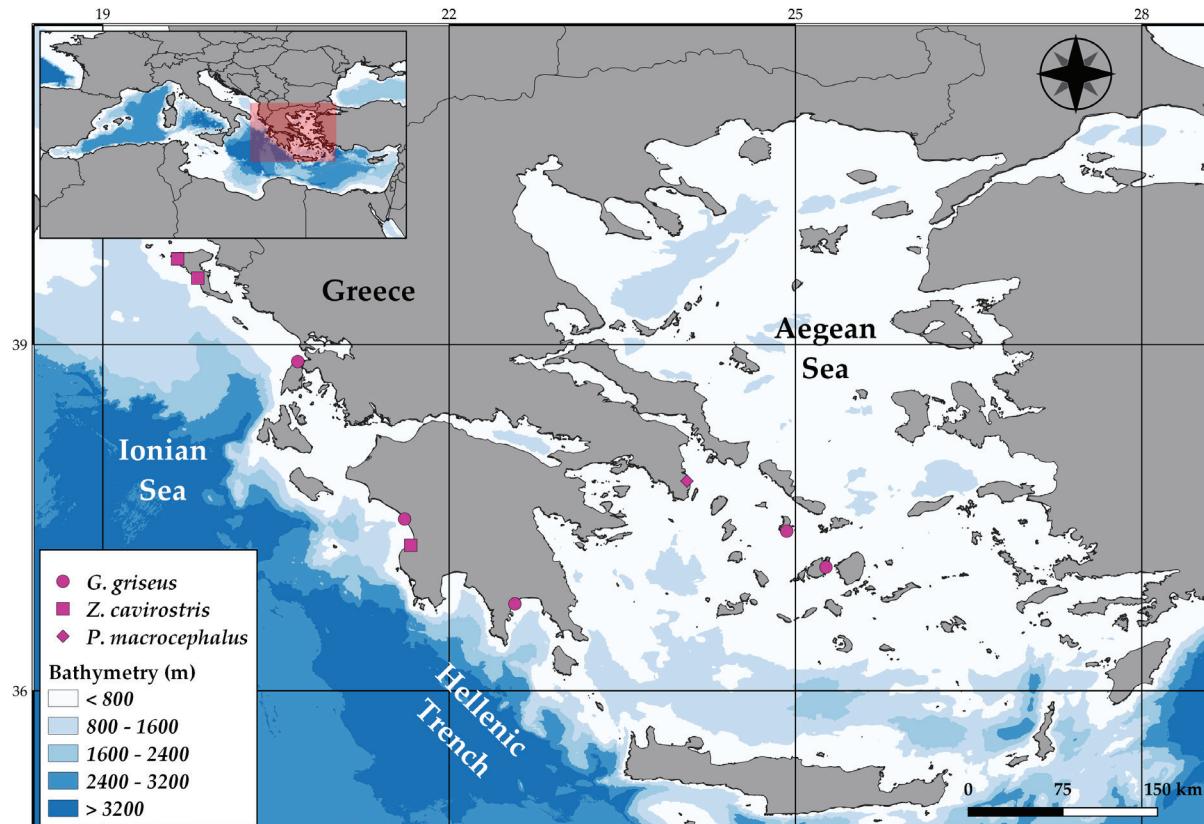


Fig. 1: Stranding locations of deep-diving toothed whales whose stomach contents were analysed for this study (Table 1). The map was created using QGIS (<https://www.qgis.org>), with data sourced from the following: coastline (<https://www.eea.europa.eu/data-and-maps/data/eea-coastline-for-analysis-2/gis-data/eea-coastline-polygon>), country borders (<https://gadm.org>), and bathymetry (<https://www.emodnet-bathymetry.eu/>).

estimated using established regression equations (Table S4); these equations relate body size and weight to either the lower beak rostral length (LRL) of squids or lower beak hood length (LHL) for octopodids. We obtained these regressions from the literature, with preference given to studies based on Mediterranean populations when available (Table S4). Beaks for which the estimated ML and W were not within the range of values used in the selected regressions were not included in the analysis. The total biomass represented by the beaks of a given cephalopod species was estimated by dividing the summed estimated weights of the measured beaks by the proportion of individuals measured, following the method of Santos *et al.* (2001).

To describe the diet composition of each toothed whale species, we used three indices: frequency of occurrence, average percentage abundance, and prey-specific abundance (Amundsen *et al.*, 1996). These indices were calculated as follows:

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

Average percentage abundance (% N_i , % W_i): &

$$\%A_i = \frac{\sum_{j=1}^n \%A_{ij}}{n}$$

Prey-specific abundance (% PN_i , % PW_i):

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

Here, n_i represents the number of stomachs containing prey i , and n is the total number of stomachs analysed. A_{ij} denotes the abundance (by number or weight) of prey i in stomach j . % PN refers to the prey-specific percentage by number, and % PW to the prey-specific percentage by weight. To assess the overall dietary importance of each prey species, we calculated the prey-specific index of relative importance (PSIRI; Brown *et al.*, 2012) as follows:

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

We did not calculate PSIRI for two fish species (*Chauliodus sloani* Bloch & Schneider, 1801 and *Trichiurus lepturus* Linnaeus, 1758) and one crustacean species [*Aristaeomorpha foliacea* (Risso, 1827)] for which weight could not be estimated. All values are expressed as %PSIRI, calculated by dividing the PSIRI for prey item i by the sum of PSIRI values for all prey items, then multiplying by 100. Prey species with %PSIRI > 5 were considered important dietary components (Harvey *et al.*, 2014). Stomach contents from three Risso's dolphins (Gg1, Gg2 and Gg4, Tables 1 and S5) contained only a few prey items and were therefore excluded from all dietary index calculations.

Each debris item found in the stomach of Pm11 was labelled, weighed, photographed and measured using a measuring tape. All debris consisted of plastic, particularly user plastics -non-industrial remnants of plastic products-. These were classified into five main categories proposed by Provencher *et al.* (2017) and into commonly used size categories (Barnes *et al.*, 2009): megoplastics

(>100 mm), macroplastics (>20-100 mm), mesoplastics (5-20 mm) and microplastics (<5 mm). We also categorized plastic items into eight broad colour groups based on Verlis *et al.* (2013).

Results

With the exception of Gg2, Gg4 and Pm11 (Table 1), all toothed whales had stranded alive. The identified prey items consisted almost exclusively of cephalopod beaks: 2379 lower beaks and 1308 upper beaks (Table 1), along with 341 rostral tips from either upper or lower beaks. Cephalopod eye lenses were present in most stomachs (i.e., Gg1, Gg3, Gg5, Zc1, Zc2, Zc3 and Pm11), whereas cephalopod gladii were only found in Gg1 and Zc1. Cephalopod flesh remains were even rarer, limited to Gg1, which contained three mantles, two buccal masses and four crowns of arms. Fish remains were infrequent and included a complete skeleton of *T. lepturus* (total length 81 cm) in Gg1 and a dentary bone of *C. sloani* in Zc1. Crustacean remains were also rare, represented by an abdomen of *A. foliacea* in Zc1. A few nematodes were recovered from Zc2 and Zc3. Macroplastic debris was found in Pm11 as well as in Gg3 (see Alexiadou *et al.*, 2019).

A total of 2162 intact lower beaks were identified, corresponding to 17 cephalopod species across 12 different families. These included 14 species in Risso's dolphins, 10 species in goose-beaked whales, and six species in the single sperm whale respectively (Tables 2, 3, 4). In Risso's dolphins, the most frequently occurring cephalopod families were (in descending order): Chiroteuthidae, Histiotheuthidae, Octopoteuthidae, Ommastrephidae, Onychoteuthidae, Ancistrocheiridae, Argonautidae, Brachiotheuthidae, Ctenopterygidiae, Cranchiidae, and Loliginidae. For goose-beaked whales, the dominant families were: Histiotheuthidae, Octopoteuthidae, Ancistrocheiridae, Chiroteuthidae, Cranchiidae, Onychoteuthidae, Ctenopterygidiae and Ommastrephidae (Table 3). The most numerically abundant prey species were *Histioteuthis reversa* (A.E. Verrill, 1880) for Risso's dolphins (24.7%), and *Histioteuthis bonnellii* for goose-beaked whales (32.3%) and the single sperm whale (86.8%) (Tables 2, 3, 4). These species contributed the largest proportion of total reconstructed biomass for each predator species, accounting for 27.3% (Risso's dolphins), 34.1% (goose-beaked whales) and 99.8% (sperm whale), respectively (Tables 2, 3 and 4). Based on the %PSIRI index, the most important prey species (%PSIRI > 5) were the following (Tables 2, 3, 4): *H. reversa* (27%), *Illex coindetii* (Vérany, 1839) (22.6%), *Argonauta argo* Linnaeus, 1758 (11.5%), *Todarodes sagittatus* (Lamarck, 1798) (8.2%), *Onychoteuthis banksii* (Leach, 1817) (5.4%), and *Octopoteuthis sicula* Rüppell, 1844 (5.1%) for Risso's dolphins; *H. bonnellii* (33.3%), *Galiteuthis armata* Joubin, 1898 (22.3%), *H. reversa* (16.9%), *O. sicula* (12.9%), and *Chiroteuthis veranii* (A. Féussac, 1835) (7.8%) for goose-beaked whales; and *H. bonnellii* (99.4%) for the sperm whale. The combined stomach contents yielded an estimated in-

Table 2. Diet composition of stranded Risso's dolphins (*Gg3* & *Gg2*), presented as percentage frequency of occurrence (%FO), percentage prey-specific number (%PN), percentage number (%N), percentage prey-specific weight (%PW), and the prey-specific index of relative importance (%PSIRI). For each prey species, the mean and standard deviation (sd) of lower rostral length (LRL) or lower hood length (LHL) in millimeters (mm), as well as the mean and maximum mantle length (ML, mm) and total weight (g), are also reported. Prey species with %PSIRI>5 are marked with **bold** since they were considered important dietary components (Harvey *et al.*, 2014). The total number of prey items are presented in Table S5.

Class	Order	Family	Species	%FO	%PN	%N	%PW	%W	%PSIRI	LRL/LHL (mm)	ML (mm)	Total weight (g)		
										Mean	sd	Mean		
Cephalopoda	Bathyteuthida	Ctenopterygidae	<i>Ctenopteryx sricula</i>	50	2.7	1.4	1	0.5	1	1.2	0.2	50	67	154
Myopsida	Loliginidae	<i>Loligo vulgaris</i>	50	4.6	2.3	12.6	6.3	4.4	3.1	0.2	262	291	$3 \cdot 10^3$	
Oegopsida	Ancistrocheiridae	<i>Ancistrocheirus alessandrinii</i>	50	1	0.5	9.8	4.9	2.8	5	1.2	162	206	$1.5 \cdot 10^3$	
	Brachioteuthidae	<i>Brachioteuthis riisei</i>	50	2.3	1.2	0.2	0.1	0.6	1.2	0.2	34	45	23	
	Chiroteuthidae	<i>Chiroteuthis veranii</i>	100	6.2	6.2	3.4	3.4	5	3.4	0.8	94	157	$1.1 \cdot 10^3$	
	Cranchiidae	<i>Galiteuthis armata</i>	50	0.6	0.3	0.9	0.4	0.4	3.9	1	338	407	135	
	Histioteuthidae	<i>Histioteuthis reversa</i>	100	24.7	24.7	27.3	27.3	27	2.5	0.7	68	105	1.2 \cdot 10^4	
	Octopoteuthidae	<i>Octopotethis sricula</i>	100	4.1	4.1	5.8	5.8	5.1	5.7	1.4	120	150	2.1 \cdot 10 ³	
	Ommastrophidae	<i>Illex coindetii</i>	100	21.3	21.3	22	22	22.6	3.6	0.6	162	207	5.7 \cdot 10^3	
	Todaridae	<i>Todaropsis ebolliae</i>	50	10.3	5.2	8.7	4.3	4.9	3.8	0.5	132	176	$2.1 \cdot 10^3$	
		<i>Todarodes sagittatus</i>	50	5.2	2.6	26.4	13.2	8.2	7.7	0.9	287	326	6.4 \cdot 10^3	
	Onychoteuthidae	<i>Ancistroteuthis lichtensteini</i>	50	3.8	1.9	-	-	1	-	-	-	-	-	
		<i>Onychoteuthis banksii</i>	100	4.6	4.6	5.7	5.7	5.4	2.4	0.1	117	129	$1.8 \cdot 10^3$	
Octopoda	Argonautidae	<i>Argonauta argo</i>	50	32.8	16.4	11.5	5.8	11.5	3	0.7	41	82	$1.7 \cdot 10^3$	
Broken beaks		-	100	7.3	7.3	-	-	-	-	-	-	-	-	

Table 3. Diet composition of stranded goose-beaked whales (*Zel-3*), expressed as percentage frequency of occurrence (%FO), percentage prey-specific number (%PN), percentage number (%N), percentage prey-specific weight (%PW), percentage weight (%W), and the prey-specific index of relative importance (%PSIRI). For each prey species, the mean and standard deviation (sd) of lower rostral length (LRL) in millimeters (mm), as well as the mean and maximum mantle length (ML, mm) and total weight (g), are also reported. Prey species with %PSIRI > 5 are marked with **bold** since they were considered important dietary components (Harvey *et al.*, 2014). The total number of prey items are presented in Table S5.

Class	Order	Family	Species	%FO	%PN	%N	%PW	%W	%PSIRI	LRL (mm)	ML (mm)	Total weight (g)
Cephalopoda	Bathyteuthida	Ctenopterygidae	<i>Ctenopteryx sicula</i>	33.3	8.9	3	2.8	0.9	2	1.4	0.2	58
Oegopsida	Ancistrocheiridae	<i>Ancistrocheirus alessandrinii</i>		66.6	1.1	0.7	2.1	1.4	1.1	6.3	0.3	214
	Chiroteuthidae	<i>Chiroteuthis veranii</i>		66.6	12.9	8.6	10.4	6.9	7.8	5.1	0.7	135
Cranchiidae	Galeiidae	<i>Galeiuthis armata</i>		66.6	45	30	21.9	14.6	22.3	3.5	0.8	313
Histioteuthidae		<i>Histioteuthis bonnellii</i>		100	32.3	32.3	34.1	34.1	33.3	4.5	1.5	81
		<i>Histioteuthis reversa</i>		100	15.1	15.1	18.7	18.7	16.9	2.8	0.6	77
Octopoteuthidae		<i>Octopoteuthis sicula</i>		100	5.3	5.3	20.5	20.5	12.9	8.2	1.6	157
Ommastrephidae		<i>Ommastrephes caroli</i>		33.3	0.5	0.2	5.7	1.9	1.1	10	-	447
		<i>Todarodes sagittatus</i>		33.3	1.1	0.4	-	-	0.2	-	-	-
Onychoteuthidae		<i>Ancistrotethis lichtensteini</i>		66.6	6.1	4	1.6	1	2.5	3.3	0.4	106
Malacostraca	Decapoda	Aristeidae	<i>Aristaeomorpha foliacea</i>	33.3	-	-	-	-	-	-	-	-
Actinopterygii	Stomiiformes	Stomiidae	<i>Chauliodus sloani</i>	33.3	-	-	-	-	-	-	-	-

Table 4. Diet composition of the stranded sperm whale (*Pm/I*), expressed as percentage frequency of occurrence (%FO), percentage prey-specific weight (%PW), and the prey-specific index of relative importance (%PSIRI). For each prey species, the mean and standard deviation (sd) of lower rostral length (LRL) in millimeters (mm), as well as the mean and maximum mantle length (ML, mm) and total weight (g), are also reported. Prey species with %PSIRI > 5 are marked with **bold** since they were considered important dietary components (Harvey *et al.*, 2014). The total number of prey items are presented in Table S5. Percentage number (%N) and percentage weight (%W) are not reported since they are equal to %PN and % PW respectively.

Class	Order	Family	Species	%FO	%PN	%PW	%PSIRI	LRL (mm)	ML (mm)	Total weight (g)
Cephalopoda	Oegopsida	Brachioteuthidae	<i>Brachioteuthis riisei</i>	100	0.1	-	0	1.5	-	41.1
	Chiroteuthidae	<i>Chiroteuthis veranii</i>		100	0.1	-	0	3.9	-	106.1
	Enoploteuthidae	<i>Abrolia veranyi</i>		100	0.1	-	0	-	-	-
	Histioteuthidae	<i>Histioteuthis bonnellii</i>	100	86.8	99.8	99.4	6.8	1.2	126.5	195.5
		<i>Histioteuthis reversa</i>	100	0.5	0.1	0.3	3.3	0.3	93.1	106.3
	Octopoteuthidae	<i>Octopoteuthis sicula</i>	100	0.2	0.1	0.2	6.7	5.3	135	190.4
			100	12.2	-	-	-	-	-	-
		Broken beaks								

gested biomass of 34 kg for Risso's dolphins, 75 kg for goose-beaked whales, and 912 kg for the sperm whale (Tables 2, 3, 4, S5). The measurable beaks from which we could reliably estimate ML ($n=1329$) gave estimates that ranged from 24 mm for *A. argo* to 461 mm for *G. armata* (mean=129 mm, median=119 mm, $sd=71$ mm). ML estimates for *H. reversa* and *H. bonnellii* in each predator species are presented in Figure 2, while estimates for other key prey species are shown in Figure S1.

All 50 debris items found in Pm11 were plastic, the majority of which were sheet plastics (43 items), including 38 plastic bags (Table 5). The total weight of the debris was 3.7 kg, with a combined surface area of 23.1 m² (Table 5, Fig. 3). Most items were classified as megaplastics (95.4%), while only 4.6% were macroplastics. Although 58.8% of the items appeared blackened due to squid ink staining, their original colour was predominantly off/white-clear (76.5%). The remaining items were originally blue-purple (8.8%), grey-silver (5.9%), black (5.9%), or orange-brown (2.9%).

Discussion

Despite recent scientific advances, the inaccessibility of deep-sea habitats continues to make stomach content analysis a valuable tool for investigating the diets of deep-diving predators and the ecosystems they inhabit. In this study, we analysed the stomach contents of nine stranded individuals from three deep-diving toothed whale species to identify key prey taxa and contribute new dietary data for the eastern Mediterranean, a region where such information remains scarce. However, given the limited sample size, our findings should be interpreted with caution when making inferences about population-level dietary patterns.

The individuals included in this analysis stranded across a broad geographic area, over different seasons and years, introducing potential confounding factors related to prey availability. Nevertheless, the diet of all three species was consistently dominated by cephalopods, supporting previous studies that characterise them as teuthophagous (Clarke, 1996). In particular, our results underscore the central role of *Histioteuthis* spp. in the diets of deep-diving odontocetes in the Mediterranean Sea (Bello, 2000), with *H. reversa* identified as the primary prey of Risso's dolphins, and *H. bonnellii* predominating the diets of both goose-beaked whales and the sperm whale. This prevalence of deep-sea cephalopods in the diets of all three whale species highlights the ecological significance of poorly studied deep-sea habitats, such as submarine canyons, and underscores the need to prioritize these areas in future conservation efforts targeting deep-diving toothed whales. In these habitats -especially in extensive regions like the Hellenic Trench- seismic exploration for oil and gas is both ongoing and planned. In addition to the direct acoustic impact on cetaceans (Duarte *et al.*, 2021), evidence indicates that anthropogenic noise from such activities may also significantly disrupt cephalopod populations (Solé *et al.*, 2017). This disrupt-

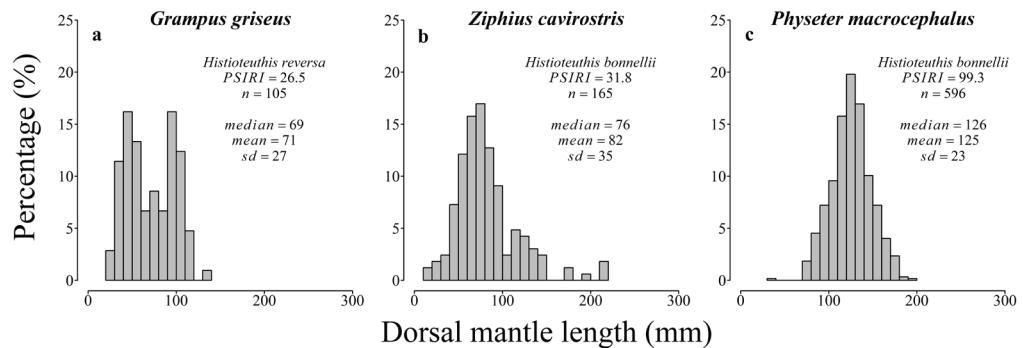


Fig. 2: Histograms of estimated mantle length for the prey species with the highest prey-specific index of relative importance (PSIRI) in the diet of the three toothed whale species. *n*: number of measured lower beaks, *sd*: standard deviation. This figure was created using RStudio (<https://posit.co/download/rstudio-desktop/>).

Table 5. Data on debris items found in the stomach of the stranded sperm whale *Pm11*. *sd*: standard deviation, *se*: standard error. Plastic debris was categorized into sheet plastics (including bags, sacks and other), threads (including rope) and miscellaneous items, following the classification system of Provencher *et al.* (2017).

Debris items	Number	Weight (g)		Total weight (g)	Total surface area (m ²)		
		Mean (sd/se)	Median				
all plastics	bags	38	62 (76/13)	27	5-350	2355	20.1
	sheets	4	239 (53/26)	247	160-300	955	3
	other	1	25 (0/0)	25	-	25	-
	threads	4	42 (0/0)	42	-	170	-
	miscellaneous	-	87 (98/56)	20	15-225	260	-



Fig. 3: Plastic debris recovered from the stomach of the stranded sperm whale *Pm11*. (a-e) Plastic sheets (bags and sacks) as well as threads (b) appeared blackened due to staining from squid ink. (f) Unusual plastic items, from left to right: a fragment of a bucket, pot or similar item; a spray can cap; and a thick tube. Scale bar: 10 cm.

tion could reduce prey availability, thereby indirectly threatening the survival of these teuthophagous predators.

Risso's dolphins exhibited the most diverse diet among the three species analysed, with 14 cephalopod species identified across 11 families. The most important prey, in decreasing order of importance, were *H. reversa*, *I. coindetii*, *A. argo*, *T. sagittatus*, *O. banksii* and *O. sicula*. Notably, the broadtail shortfin squid (*I. coindetii*) is reported here for the first time in the diet of *G. griseus* in the eastern Mediterranean. Additionally, this study provides the first record of the largehead hairtail (*T. lepturus*) in the stomach contents of Risso's dolphins in the Mediterranean Sea. The dominance of the reverse jewel squid (*H. reversa*) in the diet aligns with previous findings from the western Mediterranean (Würtz *et al.*, 1992), suggesting that this species is a key prey resource throughout the basin. The presence of vertically migrating species (e.g., *O. banksii*), the epipelagic *A. argo* and more strictly bathypelagic taxa (e.g., *C. veranii*) indicates that Risso's dolphins forage across a range of depths, reflecting a broad trophic niche and an opportunistic foraging strategy. Taken together, these results suggest that *G. griseus* in the eastern Mediterranean functions as a generalist predator that primarily consumes deep-sea cephalopods, while maintaining the flexibility to exploit a diverse array of prey. Strandings like those of the three Risso's dolphins with stomachs that contained only a few prey items are rarely documented in the literature and may indicate compromised feeding, underscoring the need for caution when interpreting dietary data from stranded individuals.

Goose-beaked whales had a more selective diet than Risso's dolphins, with ten cephalopod species identified, largely dominated by deep-water taxa. The umbrella squid (*H. bonnellii*) was the most important prey species, followed by *G. armata*, *H. reversa*, *O. sicula*, and *C. veranii*, all characteristic of mesopelagic and bathypelagic habitats. This prey composition indicates a clear foraging preference for deep-sea cephalopods, aligning with the extreme diving behaviour of *Z. cavirostris*, known to exceed depths of 1000 meters (Schorr *et al.*, 2014). These findings are therefore consistent with previous studies in the Mediterranean (Pedà *et al.*, 2015; Blanco & Raga, 2000; Tonay *et al.*, 2025), while also providing new dietary data for the eastern basin, where empirical evidence on the species' feeding ecology remains limited. Although the giant red shrimp (*A. foliacea*) and Sloane's viperfish (*C. sloani*) are reported for the first time in the stomachs of goose-beaked whales in the Mediterranean, their presence likely reflects secondary ingestion, as their small size and low abundance suggest they were consumed by the whales' cephalopod prey rather than directly targeted.

The single sperm whale examined in this study displayed a highly specialized diet, with a marked predominance of *H. bonnellii*. This finding is consistent with previous research from both the western and eastern Mediterranean (Roberts, 2003; Mazzariol *et al.*, 2011; Foskolos *et al.*, 2020a; Tonay *et al.*, 2021). The near exclusivity of *H. bonnellii* in the stomach contents of this apex predator suggests a strong prey specialization, likely driven by the energetic efficiency of targeting relatively

small, neutrally buoyant, slow-swimming cephalopods in deep waters -species that are not subject to commercial exploitation. Other prey species found in this individual were negligible in biomass and occurred at very low abundances, further supporting the conclusion that sperm whales in the eastern Mediterranean exhibit a narrow trophic niche, relying heavily on a small number of key prey species (Foskolos *et al.*, 2020a). Additionally, the presence of debris in this individual provides further evidence that sperm whales in Greece regularly ingest macroplastics, often with fatal consequences (Alexiadou *et al.*, 2019; Foskolos *et al.*, 2020b).

Despite the limited sample size, our results are consistent with recent findings, suggesting that dietary niche segregation among deep-diving odontocetes is influenced not only by prey taxonomic composition but also by differences in prey size and, by extension, ontogenetic stage (Visser *et al.*, 2021). Although Risso's dolphins, goose-beaked whales and the sperm whale all consumed cephalopods from the same families, the dominance of different prey species and size classes likely reflects variation in prey selection and foraging depth. These differences are, in turn, shaped by species-specific physiological constraints, such as diving capacity and biosonar characteristics. Notably, *H. bonnellii*, a dominant prey species for both goose-beaked whales and sperm whales, was not detected in the diet of Risso's dolphins. While this prey species has been reported in previous dietary studies of Risso's dolphins in the Mediterranean (Würtz *et al.*, 1992; Blanco *et al.*, 2006; Öztürk *et al.*, 2007; Pedà *et al.*, 2015; Milani *et al.*, 2017; Luna *et al.*, 2021), its absence here may reflect regional or/and seasonal variation in foraging behaviour and prey availability.

While this study provides valuable insights into the trophic ecology of deep-diving cetaceans in the eastern Mediterranean, it also underscores the urgent need for the analysis of additional stomach contents from these predators. Due to the opportunistic nature of data derived from strandings, only a larger sample size can support population-level generalizations and enable meaningful inter-basin comparisons across species. As anthropogenic pressures on the marine environment continue to intensify, addressing these data gaps is essential for understanding how deep-diving cetaceans interact with their prey, and how their ecological roles may shift in a rapidly changing sea.

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Supplementary Data

The following supplementary information is available online for the article:

Fig. S1: Histograms of estimated mantle length for the prey species with the highest prey-specific index of relative importance (PSIRI) in the diets of Risso's dolphins (a-e) and goose-beaked whales (f-i). *n*: number of measured lower beaks, *sd*: standard deviation. This figure was created using RStudio (<https://posit.co/download/rstudio-desktop/>).

Table S1. Prey species identified in the stomachs of Risso's dolphins from the Mediterranean Sea, along with ecological information obtained from the literature. Data sources include Guerra *et al.* (2014), FAO (2016), Jereb & Roper (2005, 2010), and the online databases FishBase (www.fishbase.se) and SeaLifeBase (www.sealifebase.se), accessed in May 2025. Reported depth ranges are indicative and may be updated as new data become available.

Table S2. Prey species identified in the stomachs of goose-beaked whales from the Mediterranean Sea, along with ecological information obtained from the literature. Data sources include Guerra *et al.* (2014), FAO (2016), Jereb & Roper (2005, 2010), and the online databases FishBase (www.fishbase.se) and SeaLifeBase (www.sealifebase.se), accessed in May 2025. Reported depth ranges are indicative and may be updated as new data become available.

Table S3. Prey species identified in the stomachs of sperm whales from the Mediterranean Sea, along with ecological information obtained from the literature. Data sources include Guerra *et al.* (2014), FAO (2016), Jereb & Roper (2005, 2010), and the online database FishBase (www.fishbase.se), accessed in May 2025. Reported depth ranges are indicative and may be updated as new data become available.

Table S4. Regression equations used to estimate cephalopod mantle length and weight based on standard measurements of their beaks. Length and weight are reported in millimeters (mm) and grams (g), respectively. Abbreviations: LHL - lower hood length; LRL - lower rostrum length; ML - mantle length; TW - total (wet) weight.

Table S5. Number of prey items (N) and total weight (W, in g) for each prey species identified in the stomach contents of individual whales. Weight estimation was not possible for the prey species found in individuals Gg1 and Gg2. See Table 1 for whale identification codes.