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ORIGINAL ARTICLE

Pelagic cephalopods of the central Mediterranean Sea determined by the analysis of the stomach content of large fish predators

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Abstract The pelagic cephalopod fauna of the central Mediterranean Sea was investigated through stomach content analyses of large fish predators. A total of 124 *Xiphias gladius,* 22 *Thunnus thynnus,* 100 *Thunnus alalunga,* and 25 *Tetrapturus belone* were analyzed. Overall, 3,096 cephalopods belonging to 23 species and 16 families were identified. The cephalopod fauna in the study area is dominated by Sepiolidae, Ommastrephidae, and Onychoteuthidae. The sepiolid *Heteroteuthis dispar* was the most abundant species ($n = 1{,}402$) while the ommastrephid *Todarodes sagittatus* showed the highest biomass. They can be considered key-species in the pelagic food web of the study area. The neutrally buoyant *Histioteuthis bonnellii, H. reversa,* and *Chiroteuthis veranyi* seem to characterize the deeper water layers. Given the difficulty in sampling pelagic cephalopods, the presence of cephalopod beaks in the stomach of predators represents a fundamental tool to assess the biodiversity and the ecological importance of these taxa in the marine ecosystem.

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Introduction

Knowledge of the pelagic cephalopod community has increased over the last decades thanks to improved techniques. However, there is still a significant lack of information on these animals' biology, distribution, and importance in the food web. This is mainly due to the difficulties associated with sampling, as conventional gears used in monitoring of the pelagic environment usually collect juvenile cephalopods, while adult specimens generally avoid being captured (Clarke 1996a).

Despite the difficulties in sampling, the ecological importance of cephalopods in the marine ecosystem has already been emphasized by several authors (Clarke 1996b; Bustamante et al. 1998; Piatkowski et al. 2001; Velasco et al. 2001). In particular, muscular squids are able to quickly convert their food into biomass and to grow rapidly. They, therefore, represent a significant source of energy for predators. Moreover, while most mid-water fishes do not grow bigger than 200 mm in length, many pelagic cephalopods grow up to larger sizes. They thus fill the gap between small fishes (i.e., myctophids, etc.) and large pelagic organisms, linking secondary production with higher trophic levels, as reported in energetic models of pelagic food webs (Clarke 1996b; Olson and Watters 2003).

Studies on the feeding habits of oceanic predators, including marine mammals and sea birds, revealed the actual role played by cephalopods in the pelagic food web (Amaratunga 1983; Clarke 1996b; Santos et al. 2001; Cherel et al. 2004). The identification of this taxon in the stomach content of top predators is often achieved via a taxonomic classification of their beaks, because these are quite resistant to digestive processes (Clarke 1962a, b). In this way, it is possible to describe the occurrence of pelagic cephalopods in an area and to obtain precious information on the ecology and behavior of cephalopods (Bello 1996; Tsuchiya et al. 1998; Cherel et al. 2004; Lansdell and Young 2007). Although several studies underlined the significant presence of cephalopod prey in the diet of large Mediterranean pelagic fishes (Bello 1991; Bello 1999; Salman 2004; Sinopoli et al. 2004; Peristeraki et al. 2005; Sarà and Sarà 2007; Castriota et al. 2008; Consoli et al. 2008; Karakulak et al. 2009; Salman and Karakulak 2009; Romeo et al. 2009), data on the specific composition and distribution of pelagic cephalopod communities in the Mediterranean are still poor.

In the present paper, stomach content analyses of large predators were performed to assess the occurrence and distribution of cephalopods in the Central Mediterranean Sea (southern Tyrrhenian Sea and Strait of Messina). To select for the most effective "cephalopod collectors," data on the species' different ecology and feeding strategy were considered. Large pelagic species usually hunt across a specific water layer at varying—although sometimes overlapping—depth levels. Considering differences between species in diving behavior, feeding strategies, and occurrence in the study area, the following top predators were selected: (1) swordfish, *Xiphias gladius* Linnaeus 1758; (2) blue-fin tuna, *Thunnus thynnus* (Linnaeus 1758); (3) albacore, *Thunnus alalunga* (Bonnaterre 1788); and (4) Mediterranean spearfish, *Tetrapturus belone* Rafinesque 1810.

Materials and methods

Study area

This study was carried out between 2002 and 2008 in the central Mediterranean Sea (southern Tyrrhenian Sea and Strait of Messina) (Fig. 1). A very small continental shelf and the presence of important fish resources (Palko et al. 1981; Di Natale et al. 2005; Andaloro 2006; Battaglia et al. 2010) consolidated a fishing tradition targeting large pelagic species, which use these areas for reproduction and nursery purposes (Palko et al. 1981; De Metrio et al. 2005). In fact, since ancient times this area has represented an important fishing ground for the local populations, where several types of fisheries have been employed: harpoon, hand lines, tuna traps, and in the last decades also driftnets and longlines (Lentini and Romeo 2000; Di Natale and Mangano 2008; Battaglia et al. 2010). The Strait of Messina, in particular, is well known as an important migration and feeding area of large pelagic species, where upwelling phenomena result in high nutrient concentrations and prey biomass (Guglielmo et al. 1995).

Data collection

Stomachs were collected during commercial fishing activities within different research projects between 2002 and 2008 aboard boats using drifting long-lines (three different types of equipment targeting *T. alalunga*, *T. thynnus,* and *X. gladius*, respectively) and harpoon ("feluca" boats targeting *X. gladius* and *T. belone*). Each predator specimen

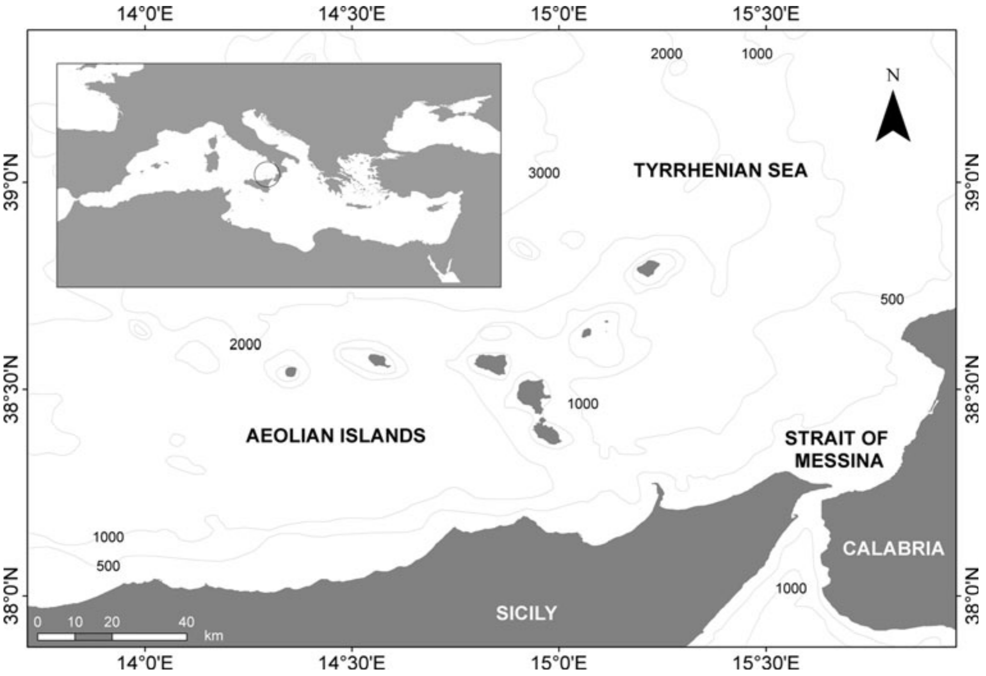

Fig. 1 Study area in the central Mediterranean Sea

was measured and weighed (TW = total weight in kg) on board. Lower jaw fork length (LJFL, expressed in cm) was recorded for swordfish and Mediterranean spearfish, while fork length (FL, expressed in cm) was recorded for blue-fin tuna and albacore. Stomachs were immediately removed from the fish specimens and preserved in order to stop the digestion process, using three methods: (1) preservation in formalin/sea water solution for 24 h and subsequent transfer into 80% ethanol; (2) conservation in 70% ethanol; (3) freezing at −20°C.

Laboratory analyses

Stomachs were dissected in the laboratory, and their content was examined under a stereomicroscope. Entire specimens or partially digested cephalopods were identified to the lowest possible taxa, following taxonomic features reported by Roper et al. (1984), Jereb and Roper (2005), and Guerra (1992). When classification turned out to be difficult, beaks were taken as the best means to identify the species. A large portion of cephalopods was determined by lower beak identification, since the beaks were often the only structures found in stomachs. Their classification was performed by identification keys (Wolff 1982, 1984; Clarke 1986; Lu and Ickeringill 2002) and by comparison with beaks of the ISPRA reference collection (Pedà et al. 2009).

The identified preys were counted and weighed; entire specimens were preserved in 70% ethanol, while beaks were immersed in a mixture of ethanol, glycerin, and water.

Data analyses

In order to trace back cephalopods' size and fresh weight, the lower rostrum length (LRL) for Teuthida and the lower hood length (LHL) for Sepiolidea and Octopoda were measured to the nearest 0.1 mm. When the wet mass of prey was not available (i.e., when it had already been more or less digested), this value was calculated using equations available from Wolff (1982, 1984), Clarke (1962a, 1986), Lu and Ickeringill (2002), Zumholz and Piatkowski (2005) or calculated from specimens preserved in the ISPRA reference collection (Table 1).

To assess the cephalopod abundance in the study area through diet information, the percent abundance ($\%N =$ number of prey i/total number of prey $\times$ 100), estimated weight percentage ($\%eW =$ weight of prey i/total weight of prey $\times$ 100), and frequency of occurrence ($\%F =$ number of stomachs containing prey i/total number of stomachs containing prey $\times$ 100) were calculated for each cephalopod prey taxon (Pinkas et al. 1971; Hyslop 1980), and for each predator species.

Finally, in order to evaluate the importance of the prey mass for the diet of each predator, all cephalopods were grouped into four weight classes (small = 0–50 g; medium/small = 51–100 g; medium = 101–300 g; large $\geq$ 300 g) and also into the following categories: muscular squids, buoyant squids, sepiolids, pelagic octopuses, and demersal octopuses. The percentage of each category per each mass group was calculated for each predator diet.

Results

Overall, 3,096 cephalopods belonging to 16 families and 23 species (Table 2) were identified through the analysis of the stomach content of 124 swordfishes (LJFL range 65–225 cm), 22 blue-fin tunas (FL range 45–270 cm), 100 albacores (FL range 48–91 cm), and 25 Mediterranean spearfishes (LJFL range 120–189 cm). In terms species number, the most represented families in the study area were the Ommastrephidae (4) and the Octopodidae (3). With 1,402 specimens, the sepiolid *Heteroteuthis dispar* (Rüppell, 1845) was the most abundant species in the area, although its biomass was low due to the small maximum size of this species. Ommastrephidae, especially *Todarodes sagittatus* (Lamarck 1798) and *Illex coindetii* (Vérany 1839), and Onychoteuthidae as *Onychoteuthis banksii* (Leach 1817) and *Ancistroteuthis lichtensteinii* (Férussac and d'Orbigny 1835) represented a consistent part of the local cephalopod fauna. The highest values of biomass were estimated for *T. sagittatus* (46,098.2 g). Similar values were reached by *Thysanoteuthis rhombus* Troschel 1857, but these resulted from just a few ($n = 6$) large individuals (Table 2).

A total of 1,032 cephalopods were recorded from swordfish (8.3 prey/predator), 131 from bluefin tuna (5.9 prey/predator), 1,876 from albacore (18.8 prey/predator), and 57 from Mediterranean spearfish (2.3 prey/predator) (Table 3). The cephalopods *T. sagittatus*, *O. banksii*, *I. coindetii*, *Histioteuthis reversa* (Verrill 1880), *Ancistrocheirus lesueurii* (Férussac and d'Orbigny 1842), and *Argonauta argo* (Linnaeus 1758) were preyed by all pelagic fish species studied. In contrast, some taxa were found only in the stomachs of a single predator species: *Abralia veranyi* (Rüppell 1844), *Galiteuthis armata* (Joubin 1898), and *Octopoteuthis* cfr. *sicula* (Rüppell 1844) in swordfish; *Todaropsis eblanae* in bluefin tuna; *Alloteuthis subulata* (Lamarck 1798) and *Scaeurgus unicirrhus* (Delle Chiaje 1840) in albacore. Table 3 also shows the average values of beak size (LRL or LHL in mm) and body mass (*eW* in g) for each cephalopod.

The abundance percentage (%*N*), estimated weight percentage (%*eW*), and frequency of occurrence (%*F*) of cephalopod species and families are listed in Table 4.

Table 1 Equations used to rebuild body mass from beak size (LRL or LHL) for each species

Superorder and order	Family	Species	Equation	References	No. of individuals
Octopodiformes					
Octopoda	Octopodidae	*Eledone cirrhosa*	$\ln W = 1.68 + 2.85 * \ln \mathrm{LHL}$	Clarke (1986)	214
		Pteroctopus tetracirrhus	$W = 0.951 + 0.928 * \mathrm{LHL}$	Present paper (only juveniles)	11
		Scaeurgus unicirrhus	$W = 0.943 + 0.937 * \mathrm{LHL}$	Present paper (only juveniles)	6
	Argonautidae	*Argonauta argo*	$\ln W =- 0.545 + 3.26 * \ln \mathrm{LHL}$	Present paper	10
	Ocythoidae	*Ocythoe tuberculata*	$\ln W = -1.05 + 2.51 * \ln \mathrm{LHL}$	Lu and Ickeringill (2002)	16
	Tremoctopodidae	*Tremoctopus violaceus*	$\ln W = 0.390 + 2.829 * \ln \mathrm{LHL}$	Present paper	8
Decapodiformes					
Oegopsida	Brachioteuthidae	*Brachioteuthis riisei*	$\ln W = -0.81 + 2.94 * \ln \mathrm{LRL}$	Lu and Ickeringill (2002)	25
	Chiroteuthidae	*Chiroteuthis veranyi*	$\ln W = -0.241 + 2.7 * \ln \mathrm{LRL}$	Clarke (1980)	14
	Cranchiidae	*Galiteuthis armata*	$\ln W = 0.700 + 2.233 * \ln \mathrm{LRL}$	Present paper	5
	Ancistrocheiridae	*Ancistrocheirus lesueurii*	$\ln W = -0.194 + 3.56 * \ln \mathrm{LRL}$	Clarke (1980)	21
	Enoploteuthidae	*Abralia veranyi*	$\ln W = 0.979 + 2.304 * \ln \mathrm{LRL}$	Present paper	5
	Histioteuthidae	*Histioteuthis bonnellii*	$\ln W = 1.594 + 2.31 * \ln \mathrm{LRL}$	Clarke (1986)	–
		Histioteuthis reversa	$\ln W = 1.41 + 2.35 * \ln \mathrm{LRL}$	Lu and Ickeringill (2002)	10
	Octopoteuthidae	*Octopoteuthis cfr sicula*	$\ln W = 0.23 + 2.54 * \ln \mathrm{LRL}$	Lu and Ickeringill (2002)	9
	Ommastrephidae	*Illex coindetii*	$\ln W = 1.174 + 2.47 * \ln \mathrm{LRL}$	Clarke (1962a, b)	14
		Ommastrephes bartrami	$\ln W = 1.834 + 2.07 * \ln \mathrm{LRL}$	Wolff (1982)	–
		Todarodes sagittatus	$\ln W = 0.783 + 2.83 * \ln \mathrm{LRL}$	Clarke (1962a, b)	–
		Todaropsis eblanae	$\ln W = 1.066 + 2.724 * \ln \mathrm{LRL}$	Zumholz and Piatkowski (2005)	313
	Onychoteuthidae	*Ancistroteuthis lichtensteinii*	$\ln W = 0.09 + 3.23 * \ln \mathrm{LRL}$	Lu and Ickeringill (2002)	18
		Onychoteuthis banksii	$\ln W = 0.58 + 3.7 * \ln \mathrm{LRL}$	Wolff (1984)	–
	Thysanoteuthidae	*Thysanoteuthis rhombus*	$\ln W = 2.855 + 3.06 * \ln \mathrm{LRL}$	Clarke (1962a, b)	7
Myopsida	Loliginidae	*Alloteuthis subulata*	$\ln W = 2 + 2.75 * \ln \mathrm{LRL}$	Clarke (1986)	116
Sepioidea	Sepiolidae	*Heteroteuthis dispar*	$\ln W = 1.033 + 2.527 * \ln \mathrm{LRL}$	Present paper	14

Table 2 Total number (*N*) and estimated weight (*eW*) of each cephalopod species identified from the stomach contents of large pelagic predators caught in the central Mediterranean, together mean values of beak size (LRL or LHL in mm) and estimated cephalopod weight (*eW*)

Superorder and order	Family	Cephalopod species	*N*	*eW* (g)	LRL/LHL (mm)		*eW* (g)	
					Mean	SD	Mean	SD
Octopodiformes								
Octopoda	Octopodidae	*Eledone cirrhosa* (Lamarck, 1798)	2	4.8	0.8	–	2.4	–
		Pteroctopus tetracirrhus (Delle Chiaje, 1830)	67	104.2	0.7	0.2	1.6	0.2
		Scaeurgus unicirrhus (Delle Chiaje, 1840)	30	45.1	0.6	0.1	1.5	0.1
	Argonautidae	*Argonauta argo* Linnaeus, 1758	47	456.2	2.1	1.5	8.6	12.2
	Ocythoidae	*Ocythoe tuberculata* Rafinesque, 1814	18	106.7	2.1	1.8	5.5	7.5
	Tremoctopodidae	*Tremoctopus violaceus* Delle Chiaje, 1830	81	11,192.6	2.5	1.5	138.2	509.9
Decapodiformes								
Oegopsida	Brachioteuthidae	*Brachioteuthis riisei* (Steenstrup, 1882)	6	38.8	2.4	0.4	6.5	2.7
	Chiroteuthidae	*Chiroteuthis veranyi* (Férussac, 1835)	20	260.1	2.4	1.1	13.0	18.6
	Cranchiidae	*Galiteuthis armata* Joubin, 1898	16	178.1	2.6	0.9	11.1	17.4
	Ancistrocheiridae	*Ancistrocheirus lesueurii* (Férussac and d’Orbigny, 1842)	16	1,493.7	2.0	2.1	92.9	189.5
	Enoploteuthidae	*Abralia veranyi* (Rüppell, 1844)	4	8.7	1.5	0.4	2.2	1.2
	Histioteuthidae	*Histioteuthis bonnellii* (Férussac, 1835)	21	797.4	2.1	1.0	38.0	52.3
		Histioteuthis reversa (Verrill, 1880)	27	1053.2	2.9	0.7	55.7	29.8
	Octopoteuthidae	*Octopoteuthis cfr sicula* Rüppell, 1844	1	935.3	–	–	–	–
	Ommastrephidae	*Illex coindetii* (Vérany, 1839)	152	11,259.8	3.1	1.6	74.1	65.2
		Ommastrephes bartrami (Lesueur, 1821)	39	6,611.5	4.2	2.5	169.5	256.9
		Todarodes sagittatus (Lamarck, 1798)	565	46,098.2	2.7	1.8	81.6	122.5
		Todaropsis eblanae (Ball, 1841)	2	273.8	3.7	–	136.9	–
	Onychoteuthidae	*Ancistroteuthis lichtensteinii* (Férussac and d’Orbigny, 1835)	302	11,335.0	2.4	1.2	37.5	53.5
		Onychoteuthis banksii (Leach, 1817)	270	2,587.1	1.2	0.6	9.6	22.5
	Thysanoteuthidae	*Thysanoteuthis rhombus* Troschel, 1857	6	45,192.0	5.6	3.7	7,532.0	11,263.5
Myopsida	Loliginidae	*Alloteuthis subulata* (Lamarck, 1798)	2	7.7	0.8	–	3.9	–
Sepioidea	Sepiolidae	*Heteroteuthis dispar* (Rüppell, 1845)	1,402	1,317.9	0.9	0.2	0.8	1.3

T. sagittatus ($\%N = 30.52$; $\%eW = 36.53$; $\%F = 62.9$) and *A. lichtensteinii* ($\%N = 19.57$; $\%eW = 8.69$; $\%F = 48.4$) were the most important cephalopods detected in swordfish stomachs, whereas blue-fin tuna preyed mainly on *Tremoctopus violaceus* Delle Chiaje 1830 ($\%N = 36.64$; $\%eW = 37.86$; $\%F = 36.4$) and *T. sagittatus* ($\%N = 19.85$; $\%eW = 6.80$; $\%F = 59.1$). *H. dispar* ($\%N = 65.03$; $\%eW = 24.04$; $\%F = 66.0$) was found to be the preferential prey for albacore, followed by *T. sagittatus* ($\%N = 11.78$; $\%eW = 24.10$; $\%F = 46.0$) and *O. banksii* ($\%N = 9.65$; $\%eW = 24.43$; $\%F = 57.0$). Mediterranean spearfish preyed mostly on the epipelagic cephalopod *T. violaceus* ($\%N = 24.56$; $\%eW = 22.29$; $\%F = 1.8$) and the ommastrephid *I. coindetii* ($\%N = 22.81$; $\%eW = 23.08$; $\%F = 1.5$).

The analysis of cephalopod body mass in predator diet shows a clear dominance of muscular squids of all weight classes (0–50 g; 51–100 g; 101–300 g; >300 g) in swordfish and blue-fin tuna food items (Fig. 2). These cephalopods were less represented in samples collected from Mediterranean spearfish, as this fish also preyed on pelagic octopuses and buoyant squids. The pelagic octopuses constituted a consistent part of blue-fin tuna prey for all weight classes. The albacore showed selective feeding on small prey (99.6% of total prey), in particular sepiolids (65.0%). Moreover, this predator is able to collect also juvenile specimens of demersal octopuses (5.1%), which have not yet settled on the bottom.

Discussion

The present study investigated the presence and distributional patterns of pelagic cephalopods by assessing the importance of these species in the diet of large predatory fish, which are considered efficient “cephalopod collectors.” In fact, the analysis of the stomach content of apex

Table 3 Number of specimens (*N*) and total and mean estimated weight (*eW*) of each cephalopod species identified from the stomach contents of large pelagic predators caught in the central Mediterranean (SWO = Swordfish; BFT = Bluefin tuna; ALB = Albacore; MSP = Mediterranean spearfish), together mean values of beak size in mm (LRL or LHL)

Superorder and order	Family	Cephalopod species	SWO						BFT					
			N	LRL/LHL (mm)		*eW* (g)			*N*	LRL/LHL (mm)		*eW* (g)		
				Mean	SD	Tot	Mean	SD		Mean	SD	Tot	Mean	SD
Octopodiformes														
Octopoda	Octopodidae	*Eledone cirrhosa*	1	–	–	2.1	–	–	0			0		
		Pteroctopus tetracirrhus	3	0.8	0.1	5.2	1.7	0.1	0			0		
		Scaeurgus unicirrhus	0			0			0			0		
	Argonautidae	*Argonauta argo*	14	2.5	1.2	124.3	8.9	11.9	4	3.8	0.9	86.9	21.7	12.0
	Ocythoidae	*Ocythoe tuberculata*	11	2.9	1.9	96.4	8.8	8.2	0			0		
	Tremoctopodidae	*Tremoctopus violaceus*	19	2.7	2.2	4,979.8	262.1	901.1	48	2.5	1.3	5,502.0	114.6	348.0
Decapodiformes														
Oegopsida	Brachioteuthidae	*Brachioteuthis riisei*	6	2.4	0.4	38.8	6.5	2.7	0			0		
	Chiroteuthidae	*Chiroteuthis veranyi*	19	2.3	0.8	177.8	9.4	9.2	1	–	–	82.3	–	–
	Cranchiidae	*Galiteuthis armata*	16	2.6	0.9	178.1	11.1	17.4	0			0		
	Ancistrocheiridae	*Ancistrocheirus lesueurii*	3	2.6	3.0	515.7	171.9	296.8	1	–	–	1.0	–	–
	Enoploteuthidae	*Abralia veranyi*	4	1.5	0.4	8.7	2.2	1.2	0			0		
	Histioteuthidae	*Histioteuthis bonnellii*	13	2.1	0.6	393.9	30.3	21.3	1	–	–	247.4	–	–
		Histioteuthis reversa	19	2.9	0.6	1,041.7	54.8	24.6	3	2.6	0.9	126.4	42.1	35.5
	Octopoteuthidae	*Octopoteuthis cfr sicula*	1	–	–	935.3	–	–	0			0		
	Ommastrephidae	*Illex coindetii*	103	3.7	1.2	9,916.1	96.3	62.4	4	2.9	1.4	243.3	60.8	55.6
		Ommastrephes bartrami	35	4.1	2.5	5,635.0	161.0	253.0	4	5.1	3.3	976.4	244.1	319,3
		Todarodes sagittatus	315	3.8	1.6	43,923.1	139.4	138.0	26	2.3	1.1	988.5	38.0	50.9
		Todaropsis eblanae	0			0			2	3.7	–	273.8	136.9	–
	Onychoteuthidae	*Ancistroteuthis lichtensteinii*	202	2.9	1.1	10,397.5	51.5	57.7	9	2.7	1.4	434.6	48.3	59.4
		Onychoteuthis banksii	71	1.4	0.6	885.7	12.5	27.0	17	1.5	0.9	468.0	27.5	45.3
	Thysanoteuthidae	*Thysanoteuthis rhombus*	5	5.4	4.1	40,100.8	8,020.2	12,521.8	1	–	–	5,091.2	–	–
Myopsida	Loliginidae	*Alloteuthis subulata*	0			0			0			0		
Sepioidea	Sepiolidae	*Heteroteuthis dispar*	172	1.0	0.3	224.9	1.3	3.3	10	0.8	0.2	9.3	0.5	0.4
	Total cephalopods per predator		1,032			119,580.8			131			14,531.2		

Table 3 continued

Superorder and order	Family	Cephalopod species	ALB						MSP					
			N	LRL/LHL (mm)		*eW* (g)			*N*	LRL/LHL (mm)		*eW* (g)		
				Mean	SD	Tot	Mean	SD		Mean	SD	Tot	Mean	SD
Octopodiformes														
Octopoda	Octopodidae	*Eledone cirrhosa*	1	–	–	2.7	–	–	0			0		
		Pteroctopus tetracirrhus	64	0.6	0.2	99.1	1.6	0.1	0			0		
		Scaeurgus unicirrhus	30	0.6	0.1	45.1	1.5	0.1	0			0		
	Argonautidae	*Argonauta argo*	18	0.6	0.2	51.7	0.1	0.1	11	2.1	0.9	193.4	17.6	13.0
	Ocythoidae	*Ocythoe tuberculata*	7	0.9	0.5	10.3	0.5	0.7	0			0		
	Tremoctopodidae	*Tremoctopus violaceus*	0			0			14	2.0	1.0	710.8	50.8	71.9
Decapodiformes														
Oegopsida	Brachioteuthidae	*Brachioteuthis riisei*	0			0			0			0		
	Chiroteuthidae	*Chiroteuthis veranyi*	0			0			0			0		
	Cranchiidae	*Galiteuthis armata*	0			0			0			0		
	Ancistrocheiridae	*Ancistrocheirus lesueurii*	8	0.7	0.3	9.4	0.4	0.6	4	4.4	1.8	967.5	241.9	243.6
	Enoploteuthidae	*Abralia veranyi*	0			0			0			0		
	Histioteuthidae	*Histioteuthis bonnellii*	0			0			7	1.7	0.8	156.1	22.3	21.9
		Histioteuthis reversa	1	–	–	142.6	–	–	4	2.8	0.6	192.6	48.1	21.3
	Octopoteuthidae	*Octopoteuthis cfr sicula*	0			0			0			0		
	Ommastrephidae	*Illex coindetii*	32	1.1	0.8	364.5	11.4	24.1	13	2.7	1.6	735.8	56.6	55.0
		Ommastrephes bartrami	0			0			0			0		
		Todarodes sagittatus	221	1.2	0.5	1,086.4	4.9	6.9	3	2.3	1.2	100.2	33.4	27.7
		Todaropsis eblanae	0			0			0			0		
	Onychoteuthidae	*Ancistroteuthis lichtensteini*	91	1.2	0.6	502.9	5.5	18.5	0			0		
		Onychoteuthis banksii	181	1.1	0.5	1,101.3	6.1	12.8	1	–	–	132.1	–	–
	Thysanoteuthidae	*Thysanoteuthis rhombus*	0			0			0			0		
Myopsida	Loliginidae	*Alloteuthis subulata*	2	0.8	–	7.7	3.9	–	0			0		
Sepioidea	Sepiolidae	*Heteroteuthis dispar*	1,220	0.9	0.2	1,083.6	0.7	0.5	0			0		
	Total cephalopods per predator		1,876			4,507.3			57			3,188.4		

Table 4 Abundance percentage (*%N*), estimated weight percentage (*%eW*) and frequency of occurrence (*%F*) of cephalopod prey (species and family) identified from the stomach contents of large pelagic predators caught in the central Mediterranean (SWO = Swordfish; BFT = Blue-fin tuna; ALB = Albacore; MSP = Mediterranean spearfish)

Superorder and order	Prey types	SWO			BFT			ALB			MSP		
		%N	*%eW*	*%F*	*%N*	*%eW*	*%F*	*%N*	*%eW*	*%F*	*%N*	*%eW*	*%F*
Octopodiformes													
Octopoda	Octopodidae	0.4	<0.1	2.4	–	–	–	5.1	3.3	24.0	–	–	–
	E. cirrhosa	0.1	<0.1	0.8	–	–	–	0.1	0.1	1.0	–	–	–
	P. tetracirrhus	0.3	<0.1	1.6	–	–	–	3.4	2.2	24.0	–	–	–
	S. unicirrhus	–	–	–	–	–	–	1.6	1.0	5.0	–	–	–
	Argonautidae (*A. argo*)	1.4	0.1	7.3	3.1	0.6	18.2	1.0	1.1	10.0	19.3	6.1	2.0
	Ocythoidae (*O. tuberculata*)	1.1	0.1	5.6	–	–	–	0.4	0.2	4.0	–	–	–
	Tremoctopodidae (*T. violaceus*)	1.8	4.2	4.8	36.6	37.9	36.4	–	–	–	24.6	22.3	1.8
Decapodiformes													
Oegopsida	Brachioteuthidae (*B. riisei*)	0.6	<0.1	3.2	–	–	–	–	–	–	–	–	–
	Chiroteuthidae (*C. veranyi*)	1.8	0.1	5.6	0.8	0.6	4.5	–	–	–	–	–	–
	Cranchiidae (*G. armata*)	1.6	0.1	6.5	–	–	–	–	–	–	–	–	–
	Ancistrocheiridae (*A. lesueurii*)	0.3	0.4	2.4	0.8	<0.1	4.5	0.4	0.2	7.0	7.0	30.3	0.8
	Enoploteuthidae (*A. veranyi*)	0.4	<0.1	2.4	–	–	–	–	–	–	–	–	–
	Histioteuthidae	3.1	1.2	15.3	3.1	2.6	13.6	0.1	3.2	1.0	19.3	10.9	1.5
	H. bonnellii	1.3	0.3	7.3	0.8	1.7	4.5	–	–	–	12.3	4.9	0.8
	H. reversa	1.8	0.9	8.9	2.3	0.9	9.1	0.1	3.2	1.0	7.0	6.0	1.0
	Octopoteuthidae (*O. cfr sicula*)	0.1	0.8	0.8	–	–	–	–	–	–	–	–	–
	Ocythoidae (*O. tuberculata*)	1.1	0.1	5.6	–	–	–	0.4	0.2	4.0	–	–	–
	Ommastrephidae	43.9	49.7	79.8	27.5	17.1	63.6	13.5	32.2	48.0	28.1	26.2	2.0
	I. coindetii	10.0	8.3	37.9	3.1	1.7	13.6	1.7	8.1	18.0	22.8	23.1	1.5
	O. bartrami	3.4	4.7	18.5	3.1	6.7	13.6	–	–	–	–	–	–
	T. sagittatus	30.5	36.7	62.9	19.8	6.8	59.1	11.8	24.1	46.0	5.3	3.1	0.5
	T. eblanae	–	–	–	1.5	1.9	9.1	–	–	–	–	–	–
	Onychoteuthidae	26.5	9.4	58.9	19.8	6.2	54.6	14.5	35.6	58.0	1.8	4.1	0.3
	A. lichtensteini	19.6	8.7	48.4	6.9	3.0	31.8	4.9	11.2	33.0	–	–	–
	O. banksii	6.9	0.7	21.8	13.0	3.2	31.8	9.6	24.4	57.0	1.8	4.1	0.3
	Thysanoteuthidae (*T. rhombus*)	0.5	33.5	2.4	0.8	35.0	4.5	–	–	–	–	–	–
Myopsida	Loliginidae (*A. subulata*)	–	–	–	–	–	–	0.1	0.2	1.0	–	–	–
Sepioidea	Sepiolidae (*H. dispar*)	16.7	0.2	33.9	7.6	0.1	13.6	65.0	24.0	66.0	–	–	–

predators is a significant source of data to describe this component of the marine fauna (Tsuchiya et al. 1998; Lansdell and Young 2007). Limitations of this method could be related to the retention of larger beaks in the stomachs of predators for several days (Santos et al. 2001) and to the migratory behavior of large pelagic predators. To minimize potential biases, four "cephalopod-samplers" were considered which differed in size, feeding habits, and preferential habitats were. In fact, the presence of cephalopods in the diet of large pelagics is strictly related to the water layer where the predator usually feeds and to its capability to carry out vertical movements.

Much information on horizontal and vertical migration was recently acquired by tagging experiments with swordfish (Carey and Robinson 1981; Takahashi et al. 2003; Canese et al. 2004, 2008), blue-fin tuna (Lutcavage et al. 2000; Block et al. 2001, 2005), and albacore (Arrizabalaga et al. 2002; Cosgrove et al. 2006). Swordfish perform vertical excursions, reaching depths up to 800 m during daylight and remaining near the surface at night (Carey and Robinson 1981; Carey 1990; Takahashi et al. 2003). Their diel vertical excursions are usually discontinoous and frequently interrupted by vertical rises (Canese et al. 2008).

Blue-fin tuna follows a similar behavioral path, diving to depth >600 m (Block et al. 2001), whereas the albacore depth range varies from the surface layers to 450 m (Bard 2001). While these three species are usually able to explore a large part of the water column, the Mediterranean spearfish does not seem to dive deeper than the thermocline (Nakamura 1985), as reported in studies on its feeding

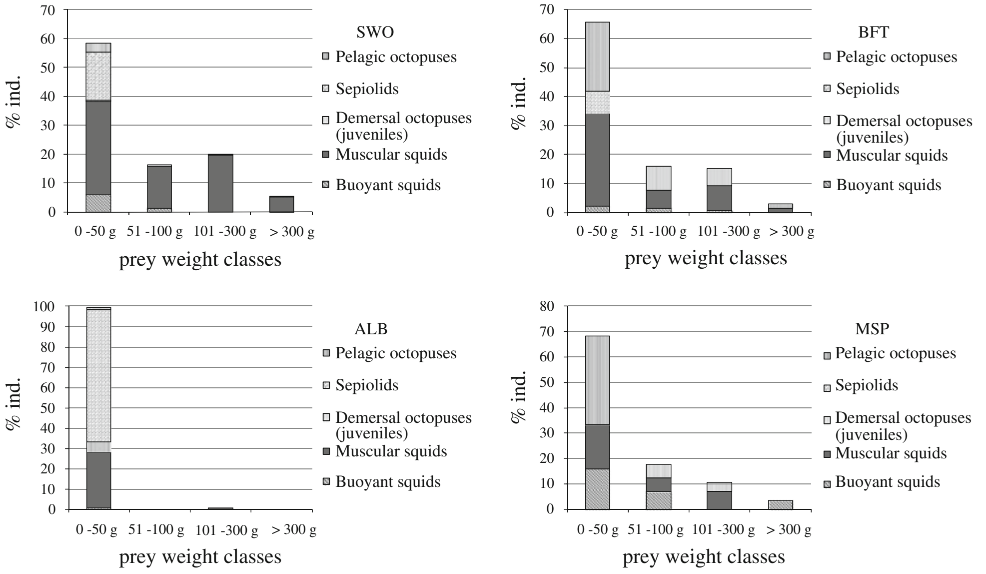

Fig. 2 Prey species composition (%) within the four weight ranges (0–50; 51–100; 101–300; >300 g) in the stomach content of predator species (*SWO* swordfish, *BFT* bluefin tuna, *ALB* albacore, *MSP* Mediterranean spearfish)

behavior in the Mediterranean Sea (Castriota et al. 2008; Romeo et al. 2009).

The analysis of cephalopod prey from a large number of stomachs of *X. gladius*, *T. thynnus*, *T. alalunga,* and *T. belone* provides a clearer picture of the pelagic cephalopod fauna in a macro-area of the central Mediterranean Sea (southern Tyrrhenian Sea and Strait of Messina). Cephalopods in the study area are mainly dominated by Sepiolidae, Ommastrephidae, and Onychoteuthidae. The pelagic Sepiolidae are only represented by *H. dispar*. The high number of specimens ($n = 1{,}402$) found in the present study as well as the huge biomass of this species recorded in other areas (Bello 1999; Salman and Karakulak 2009) suggest this squid being a key-species in the Mediterranean pelagic food web. In particular, *H. dispar* is an important food item for *T. alalunga* since this fish usually hunts small prey aggregated in schools (Bello 1999; Consoli et al. 2008). In fact, *H. dispar* is a small-sized sepiolid that usually lives in groups in lower epipelagic and in mesopelagic zones, most commonly in depths between 200 and 300 m (Jereb and Roper 2005).

The greatest overall prey biomass was represented by Ommastrephidae (especially *T. sagittatus*, *O. bartramii*, and *I. coindetii*) and Onychoteuthidae (*O. banksii* and *A. lichtensteinii*), highlighting the importance of these widely distributed families in the pelagic ecosystem of the area. Moreover, it is well known that these muscular fast-swimming squids are high-speed growing active predators, which efficiently convert their prey into own biomass (Clarke 1996b), thus representing a primary source of energy for large marine fishes. The importance of the Ommastrephidae in the study area, especially in the area around the Aeolian Islands, is also confirmed by the presence of a specific professional fishing activity by squid hand-jig lines targeting *T. sagittatus* (Battaglia et al. 2010).

The neutrally buoyant and slowly swimming ammoniacal squids belonging to the Histioteuthidae, *Histioteuthis bonnellii* (Férussac 1835) and *H. reversa*, and to the Chiroteuthidae, *Chiroteuthis veranyi* (Férussac 1835) seem to characterize the deeper water layers in the study area. This is confirmed by their morphological features (e.g., the presence of light organs) as well as by their occurrence mainly in swordfish stomachs (i.e., in that predator which carries out feeding excursions to deep water layers). The abundance of Histioteuthidae in deeper waters was also recorded in other Mediterrranean areas, such as Spanish waters (Quetglas et al. 2010), where *H. bonnellii* and *H. reversa* show a spatial segregation with peaks of occurrence at 500–600 m and 600–700 m depth, respectively. Moreover, Quetglas et al. (2010) reported an increase in mean size of *H. reversa* with depth, indicating an ontogenetic migration to deeper waters. Therefore, the species' abundance might be even higher than reported in the present paper, because of the limited bathymetric range in which predators are usually hunting.

The occurrence of some specimens of neutrally buoyant squids in the diet of the surface-feeding predator *T. belone* may be due to the upwelling currents in the Strait of Messina that concentrates deep fauna in the area, and to the species' diel vertical migrations to shallow depths at night (Quetglas et al. 2010).

Pelagic octopuses (*T. violaceus*, *A. argo,* and *Ocythoe tuberculata* Rafinesque 1814), belonging to the Argonauthoidea, inhabit epipelagic waters of the study area and, according to our results, seem to be more common than previously thought. These cephalopods occur in near-surface waters and rarely descend below the thermocline

(Voss 1953; Thomas 1977; Bello 1993). For this reason, *T. violaceus* and *A. argo* represented a consistent part of the cephalopods collected by the surface-feeding *T. belone*. A clear preference for *T. violaceus* was showed for the predator *T. thynnus*, as it was also reported also by Karakulak et al. (2009) for the eastern Mediterranean Sea.

The occurrence of small specimens of the demersal species *Eledone cirrhosa* (Lamarck 1798), *Pteroctopus tetracirrhus* (Delle Chiaje 1830), and *S. unicirrhus* is likely to be due to the local presence of schools of juveniles (Giordano et al. 2010). Pelagic predators can take advantage of demersal octopuses as long as their young stages have not yet settled on the bottom.

On the other hand, records of both adult and juvenile individuals of a prey species in the stomachs of several cephalopods (*A. lichtensteinii, H. dispar, I. coindetii, O. banksii, T. rhombus, and T. sagittatus*) indicate that these species are likely to complete their entire life cycle in this area.

The present study also provided the opportunity to improve our knowledge on the distribution of some scarcely known and rare cephalopod species. A large beak (LRL = 14.1 mm) probably belonging to a specimen of the octopoteuthid *Octopoteuthis sicula* (Rüppell 1844) was found in a swordfish stomach. Large individuals of this species have never been recorded before, and among the few specimens caught until now, most records remained uncertain (Villari and Ammendolia 2009). This new data suggest that *O. sicula* can reach a larger size and that the growth of this species should be revaluated. Other rare cephalopods recorded in the study area were *A. veranyi* and *G. armata*.

The highest number of different prey species (20) was recorded in swordfish stomachs. This indicates that *X. gladius* can be considered the most efficient "cephalopod collector" that probably relates to the species' hunting behavior during large vertical migrations (Canese et al. 2008). Both epipelagic (*T. violaceus, A. argo,* etc.) and deep-water cephalopods (*C. veranyi*, *H. bonnellii*, *H. reversa*, *O.* cfr *sicula*, and *A. veranyi*) were recorded in its diet. The intake of cephalopod prey species that follow a dial vertical migration pattern seems to be important for all predators except for *T. belone*. This species usually hunts above the thermocline and mainly during daylight, therefore not exploiting the vertical migrations of several cephalopods at night time (Castriota et al. 2008; Romeo et al. 2009).

In the light of the results achieved so far, analyses of the diet of pelagic predators are still the best tool to investigate the cephalopod community in pelagic areas (Cherel et al. 2004). In this context, the collection of cephalopod beaks in the stomachs of predators is a fundamental part in assessing the importance of cephalopods in the marine food web and in understanding the cephalopod diversiy in pelagic waters. Therefore, as far as the Mediterranean Sea is concerned, diagnostic tools for cephalopod beak identification (Clarke 1977) should be improved.

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