Feeding ecology of two squid species from the western Mediterranean

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ABSTRACT: The squid *Loligo vulgaris* (LV) and *L. forbesii* (LF) are 2 cephalopod species occurring in the Atlantic Ocean and the Mediterranean Sea. Bathymetric segregation allows the co-existence of both species, with LV preferentially inhabiting the shallow shelf and LF living on the shelf-break and upper slope grounds. In this paper, the feeding habits of LV and LF were studied for the first time in the Mediterranean, by means of stomach content analysis (1452 and 900 individuals of LV and LF, respectively). The main objective was to determine the diet of both species, analysing temporal and ontogenetic diet changes and inferring predator–prey interactions. Fish were by far the most important prey in both squid, followed by crustaceans and cephalopods. Prey composition revealed the bathymetric segregation of both species in the Mediterranean. Whereas LV preferentially consumed typical coastal species of sparids and gobiids, LF preyed on slope inhabitants such as myctophids and euphausiids. Ontogenetic shifts of diet occurred in both squid, but took place at contrasting sizes, suggesting that the factors triggering them might be species-specific. The diet of small-sized LV individuals was more dependent on bottom-living organisms than in large individuals, which preyed mainly on benthopelagic fish. During the main reproductive period in spring, LV increased the consumption of highly nutritive prey such as polychaetes (nereidids). Size-related differences in LF diet during the second half of the year indicated a deeper distribution of large individuals, preferentially preying on mesopelagic species and being thus involved in benthic–pelagic coupling.

KEY WORDS: Diet analysis · Stomach contents · *Loligo* spp. · Ontogenesis · Seasonal variation · Predator–prey interactions · Bathymetric segregation

INTRODUCTION

The squid *Loligo vulgaris* Lamarck (1798) and *L. forbesii* Steenstrup (1857) are 2 cephalopod species with few external morphological differences and which inhabit the eastern Atlantic Ocean and Mediterranean Sea (Jereb & Roper 2010). They are important prey for a number of marine predators such as pelagic and demersal fish and marine mammals (e.g. Morte et al. 1997, Peristeraki et al. 2005, Bearzi et al. 2011). In turn, they prey on a broad spectrum of species, especially fish, but also crustaceans, cephalopods and polychaetes (Roper et al. 1984, Collins et al. 1994,

Guerra & Rocha 1994, Pierce et al. 1994, Coelho et al. 1997, Wangvoralak et al. 2011). It is accepted that squid have a large trophic impact on other species in the food web and top-down control from squid to their prey can be high (Coll et al. 2013, Young et al. 2013). They are also important fishery resources. Both species are taken as by-catch of the Mediterranean bottom trawl fishery (Guerra & Rocha 1994, Relini et al. 1999, Sifner & Vrgoc 2004, Massutí & Reñones 2005), while *L. vulgaris* also supports important artisanal and recreational fisheries (Guerra & Rocha 1994, Morales-Nin et al. 2005, Cabanellas-Reboredo et al. 2014a). Thus, the role of these squid, as predator and

prey, and the interactions they have with other species, are key factors in the trophodynamics of marine ecosystems (Rocha et al. 1994, Navarro et al. 2013), and adequate knowledge about their role and interactions is important to allow appropriate resource management (Moreno et al. 2013).

Diet composition and feeding ecology of these loliginids are well documented in Atlantic waters. They mainly feed on fish, with little frequency variation but different species composition depending on the region (Roper et al. 1984, Collins et al. 1994, Guerra & Rocha 1994, Pierce et al. 1994, Coelho et al. 1997, Wangvoralak et al. 2011). Seasonal and daily spatial migrations, related to reproduction and feeding, are known to occur in both species (Rocha & Guerra 1999, Cabanellas-Reboredo et al. 2012, 2014b). However, to date nothing is known about the diet of *L. vulgaris* and *L. forbesii* in the Mediterranean, although different aspects of their life cycle (e.g. growth and reproduction) are relatively well studied both in the western (Mangold-Wirz 1963, Worms 1979, Wurtz & Giuffra 1989, Sánchez & Demestre 2010) and central (Ragonese & Jereb 1986, Sifner & Vrgoc 2004) regions. In the Mediterranean Sea, both species show a clear bathymetric segregation, as *L. vulgaris* preferentially inhabits waters shallower than 200 m and *L. forbesii* is found at depths between 100 and 600 m, slightly overlapping on the deep continental shelf (Quetglas et al. 2000).

All available information on squid diet is based on stomach content analysis. In general, gut content analysis fails to provide information on long-term feeding habits (Jackson et al. 2007) and neglects some dietary materials. These analyses are further biased in cephalopods, which reduce the food to hardly recognizable pieces (Hyslop 1980, Boyle & Rodhouse 2005). Despite these shortcomings, stomach content analysis remains the main source of data for prey items and provides useful information on predator feeding habits and ecology (Clarke & Kristensen 1980, Laptikhovsky et al. 2010, Miller et al. 2013). Although isotopic analysis performs better than dietary analysis in revealing assimilated food, it does not provide information on predator–prey interactions at the species level (Winemiller et al. 2007, Young et al. 2015).

We investigated the feeding habits of *L. vulgaris* and *L. forbesii* for the first time in the Mediterranean Sea by means of stomach content analysis. The diets were expected to reflect the bathymetric segregation of the 2 species in the area, yet some competition should exist at depths where the squid overlap. The main objective was to analyse the feeding habits of these 2 squid, to determine differences and similarities in their feeding ecology. We also investigated whether these species display differences in diet related to sex, season or ontogenetic growth. Diet composition studies constitute a crucial first step in order to better understand trophic interactions, which in return allow building robust, meaningful marine food web models (Christensen & Walters 2004, Coll et al. 2006, 2008, Moreno et al. 2013).

MATERIALS AND METHODS

Species sampling

Individuals from both species were sampled monthly from commercial fishing boats off the Balearic Islands (western Mediterranean) between January 2009 and January 2010 (N = 984 *Loligo vulgaris* and 693 *L. forbesii*). Squid were obtained from bottom trawlers operating between 50 and 750 m and small-scale boats generally fishing down to 100 m. Species were identified on the basis of macroscopic external characters (e.g. tentacular club) after Roper et al. (1984). Whereas *L. vulgaris* were collected from trawl (76%) and artisanal fishery (24%), *L. forbesii* were all obtained from the trawl fishery. Additional samples were taken from the fishery-independent MEDITS bottom-trawl surveys (Bertrand et al. 2002) conducted in the study area during early summer from 2007 to 2010 (N = 468 *L. vulgaris* and 207 *L. forbesii*). For each individual, the following measurements were taken: dorsal mantle length (ML, to the nearest mm), total weight (TW, to the nearest 0.1 g) and sex (male, female, undetermined).

Stomach sampling and diet indices

Prey items from gut contents were analysed under a binocular microscope and identified to the lowest possible taxon considering key morphological features (i.e. otoliths or claws) using published guides (Zariquiey 1968, Lombarte et al. 2006) and our own reference collections. The number of examples of prey within a prey category was recorded and the following indices calculated to analyse the diet and feeding intensity (Hyslop 1980): (1) relative abundance (%N), calculated as the percentage of each prey item compared to the total number of prey items; (2) frequency of occurrence (%O), calculated as the percentage of stomachs containing each prey item compared to the total number of stomachs containing food; and (3) vacuity index (%v), or the percentage of empty stomachs.

To determine the feeding strategy, niche breadth was calculated using Levins' standardized index B_i:

$$B_i = \frac{1}{n-1}\left(\frac{1}{\sum_j p_{ij}^2} - 1\right) \quad (1)$$

where p_{ij} is the proportion of diet of predator i that is made up of prey j, and n is the number of prey categories (Krebs 1999). The values of p_{ij} are determined from a matrix (e.g. Table S1 in the Supplement at www.int-res.com/articles/suppl/m531p207_supp.pdf) as described by Colwell & Futuyma (1971). This index ranges from 0 to 1, with low and high values indicating specialist and generalist diets, respectively.

Data analysis

The cumulative number of prey items was plotted against the cumulative number of non-empty stomachs in order to determine sample size sufficiency (Ferry & Cailliet 1996). The PRIMER software was used to compute a prey species accumulation plot as an average of 999 curves based on different random orders of the stomachs. A curve approaching an asymptote with low variability indicates that the number of stomachs examined is sufficient to characterize the diet.

Different statistical analyses were performed to address the following goals: (1) a cluster analysis to detect ontogenetic shifts in diet; (2) a permutational multivariate analysis of variance (PERMANOVA) to test biological (sex and size) and environmental (season) factors affecting diet; and (3) a similarity percentage (SIMPER) analysis to identify the prey item contribution to diet dissimilarities.

Ontogenetic variation

Major prey categories were established from prey items (with N > 5) to eliminate biases associated with comparisons based on variable levels of prey identification (Cortés 1997). Fish prey were grouped to the family level (11 groups), and invertebrates were divided into 14 categories (see Table 1). The unidentifiable remains were excluded from these analyses.

For each species, individuals were grouped into 10 mm size classes. The first (<100 mm) and last (>250 mm) size group were based on the availability of a sufficient sample for the analyses. Specimens were then divided into small and large categories through hierarchical agglomerative and unweighted

arithmetic average clustering (Clarke & Gorley 2006) by calculating Bray-Curtis similarity resemblance matrices. Analyses were done using abundance data. In order to reduce the weight of numerically dominant species, a prior square root transformation of the data was performed. The significant groups were determined using the SIMPROF test (p < 0.01) (Clarke & Gorley 2006).

Effects of sex, size and season

Data on diet based on major groups (mean abundance/sampling and size class) were analysed using multivariate analyses on all individuals with gut contents. First, the factors season (winter, W: January–March; spring, SP: April–June; summer, S: July–September; and autumn, A: October–December), size (small and large) and sex (males and females) were tested. Standardized prey group abundances were square-root transformed and used to develop a Bray-Curtis similarity matrix. PERMANOVA examined the effects of season, sex and size and their crossed effects (9999 permutations under a reduced model) on the variation of the squid diet composition. Significant factors (p < 0.05) were further analysed using a PERMANOVA pairwise comparison. Finally, SIMPER analysis was employed to evaluate the contribution of prey categories to variations among and/or within factors (Clarke 1993). Homogeneity of multivariate variance was confirmed for all factors using PERMIDISP. All of these analyses were performed using the statistical software PRIMER6 & PERMANOVA (Clarke & Warwick 2001, Anderson et al. 2008).

RESULTS

Diet composition

The diet composition of each squid species is summarized taking into account the lowest identified taxonomic levels (Table S1 in the Supplement at www.int-res.com/articles/suppl/m531p207_supp.pdf).

Loligo vulgaris

Of the 1452 stomachs analysed, 49.8% were from females (55–357 mm ML), 45.1% were from males (52–417 mm ML), and 5.1% could not be sexed (23–288 mm ML); the percentage of empty stomachs was 45%. Overall, 80 different prey items belonging

to 12 taxa were identified (59 categories identified to genus/species level). The feeding spectrum included teleosts, cephalopods, stomatopods, polychaetes, cumaceans, decapod crustaceans, isopods, mysids, euphausiids, amphipods, salps and algae. The most important prey were fish (%O = 79.7, %N = 57.8), followed by crustaceans (%O = 21.6, %N = 19.8), cephalopods (%O = 19.5, %N = 6.8) and polychaetes (%O = 8.7, %N = 12.8). Among fish, 13 families and 26 species were identified, of which the sparids *Spicara* spp. (%O = 5.8, %N = 2.5) and benthic gobies *Lesueurigobius* spp. (%O = 3.9, %N = 3.4) were the most frequent and abundant prey.

L. forbesii

Of the 900 stomachs analysed, 43.9% were from females (38–286 mm ML), 48.3% were from males (40–451 mm ML), and 7.8% could not be sexed (36–152 mm ML); the vacuity index was 45.2%. Overall, 65 different prey items belonging to 7 taxa were identified (50 categories to genus/species). The feeding spectrum included teleosts, elasmobranchs, molluscs, crustacean decapods, isopods, mysids and euphausiids. The main prey were fish (%O = 73.4, %N = 56.5), followed by crustaceans (%O = 39.0, %N = 41.5). Among fish, 12 families and 35 species were identified; the transparent goby *Aphia minuta* was by far the most important identified species (%N = 26.5, %O = 9.7), followed by the mesopelagic fish *Maurolicus muelleri* (%N = 3.1, %O = 6.5). Among crustaceans, euphausiids were the most common group (%N = 26.8, %O = 25).

Ontogenetic and seasonal effects

Cumulative prey curves (not shown) revealed that our data provide a good description of the diet of *L. vulgaris* and *L. forbesii* by size group.

L. vulgaris

Four main prey groups were found in the diet: fish, crustaceans, molluscs and polychaetes. Clustering classification revealed diet differences between size classes. This allowed the identification of 2 size groups (Fig. 1): small (<210 mm ML) and large (≥210 mm ML); this grouping was validated by the SIMPROF test. Clupeids, myctophids, brachyurans, mysids, euphausiids, amphipods and cumaceans were only found in stomachs of small squid. The rest of prey was present in both size categories (Table 1). Fish were always the most frequent prey across all sizes
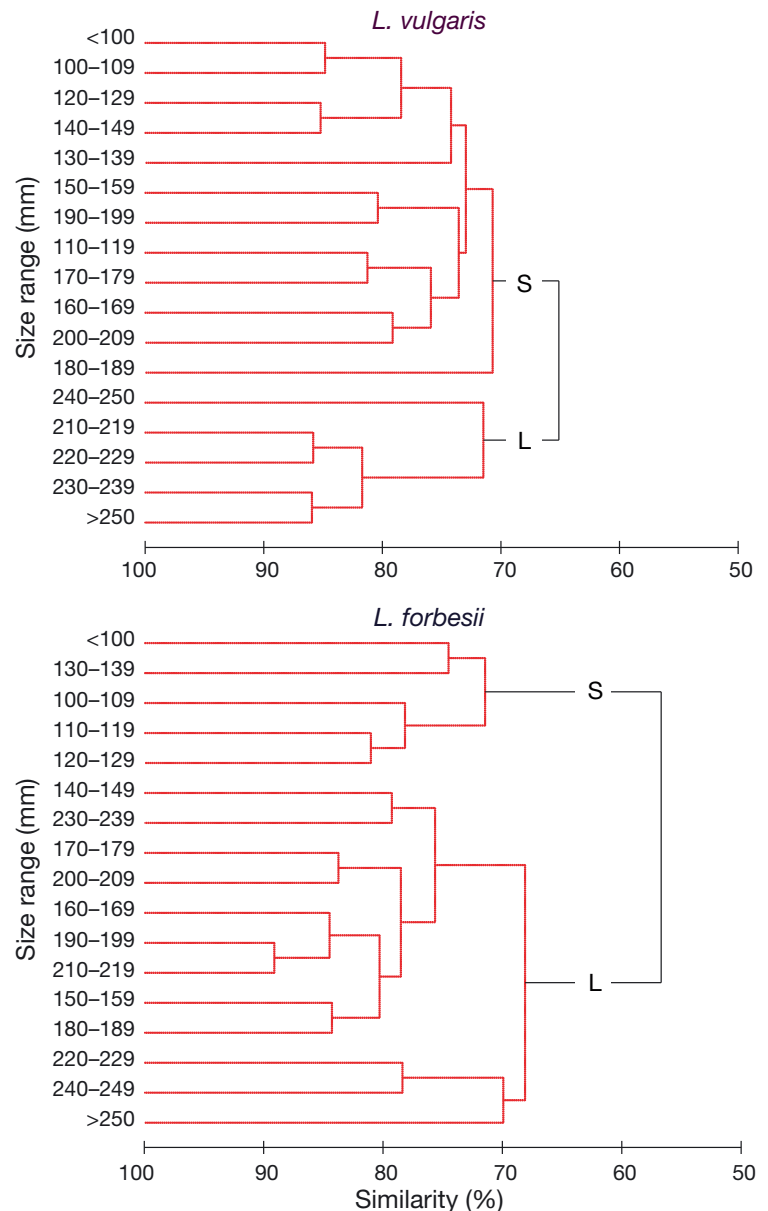

Fig. 1. Cluster analysis applied on the Bray-Curtis similarity matrix for *Loligo vulgaris* and *L. forbesii* (based on prey occurrence). Red lines indicate size groups not separated (at p < 0.01), black lines separate significantly different groups (S: small; L: large)

Table 1. Frequency of occurrence (%O) of the main prey groups found in stomach contents of *Loligo vulgaris* and *L. forbesii* by season (W: winter; SP: spring; S: summer; A: autumn) and size-class (small, large). The number of stomachs analysed (N), percentage of empty stomachs (%v) and Levin's standardized index (B_i) are also shown. Cut-off values defining small and large individuals are 210 and 140 mm dorsal mantle length for *L. vulgaris* and *L. forbesii*, respectively; unid.: unidentified

| | *L. vulgaris* (%O) | | | | | | | | *L. forbesii* (%O) | | | | | | | |
| | W | | SP | | S | | A | | W | | SP | | S | | A | |
	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large	Small	Large
Pisces	73.5	78.9	85.1	87.8	79.8	87.2	79.4	76.2	33.8	76.2	88.7	83.2	62.5	74.3	78.6	79.8
Argentinidae									1.4		2.1	9.9				13.8
Blenniidae	1.0	2.6	0.3				2.8	2.4								
Callionymidae									1.4			3.0		1.4	7.1	1.1
Carangidae		5.3	1.7	2.0	6.7	2.6	0.9	4.8								
Clupeidae			3.1		5.9		0.9									
Sparidae	4.1	10.5	1.7	14.3	6.7	28.2	11.2	14.3								
Gadiformes		2.6	2.1								6.2	8.9	12.5	12.9		7.4
Gobiidae	10.2	2.6	29.4	6.1	25.2	2.6	18.7	2.4	4.2		46.4	17.8	31.3	5.7	7.1	3.2
Myctophydae			0.3				0.9					5.0		22.9		22.3
Pleuronectiformes									4.8		2.0				2.1	
Sternoptychidae									1.4	4.8	4.1	17.8		1.4		10.6
Pisces unid.	60.2	55.3	52.6	67.3	41.2	61.5	53.3	57.1	26.8	66.7	34.0	32.7	18.8	41.4	64.3	41.5
Mollusca																
Cephalopoda	32.7	21.1	17.0	6.1	20.2	20.5	21.5	26.2		14.3	1.0	6.9	6.3	10.0	7.1	9.6
Bivalvia									1.4			1.0		1.4		
Crustacea	23.5	28.9	21.1	16.3	30.3	15.4	22.4	21.4	67.6	28.6	49.5	25.7	37.5	32.9	21.4	34.0
Brachyura	1.0		2.1		7.6		4.7									
Decapoda unid.			1.7				1.9									
Natantia		2.6	2.8	2.0	5.9		3.7	4.8			3.1	8.9		12.9	21.4	19.1
Cumacea			0.3		1.7		0.9									
Isopoda	14.3	26.3	7.3	6.1	8.4	15.4	4.7	7.1				1.0		1.4		2.1
Mysidacea	10.2		4.8		5.9		5.6				15.5		37.5		14.3	
Euphausiacea	2.0		1.7		1.7				63.4	28.6	33.0	13.9		15.7		16.0
Amphipoda	2.0		0.3				1.9									
Stomatopoda			0.3		2.5		2.8	7.1								
Crustacea unid.	1.0		4.2	8.2	1.7		5.6	4.8	4.2		5.2	2.0		2.9		3.2
Polychaeta	2.0	2.6	18.7	12.2	2.5	2.6	3.7									
Algae	8.2		1.0		8.4	15.4	9.3	26.2								
N	191	63	601	88	189	60	191	69	102	42	193	204	59	131	35	134
% v	46.6	36.5	49.6	42.0	35.4	31.7	41.9	39.1	49.2	50	49.2	48.5	72.9	45	57.1	29.1
B_i	0.13	0.12	0.17	0.08	0.25	0.12	0.20	0.16	0.05	0.06	0.15	0.27	0.11	0.19	0.08	0.24

(Fig. 2). Diet composition differed among seasons and size group (Table 2); spring diet differed from all other seasons (Table 3). A greater abundance of unidentified fish, gobiids and polychaetes, and lower abundance of isopods, sparids and cephalopods contributed to these differences (Table 4). Two fish families (Sparidae and Gobiidae), cephalopods and isopods were present in the diet of both size groups in every season. No differences were detected between sexes.

A narrow niche breadth ranging from 0.08 to 0.25 was observed across seasons and group size, indicating a specialized foraging strategy. Large individuals displayed a narrower niche breadth during spring, while the highest value was found in small individuals during summer (Table 1).

L. forbesii

Three main prey groups were found in the diet of *L. forbesii*: fish, crustaceans and molluscs. Clustering classification and SIMPROF test also differentiated 2 size groups (Fig. 1): small (<140 mm ML) and large (≥140 mm ML). Myctophids, pleuronectiformes and isopods were only found in stomachs of large squid, while mysids were only present in small individuals. Fish were always the most frequent prey across all sizes (Fig. 2).

The interaction between size and season was found to significantly influence the diet of *L. forbesii* (Table 2). As in *L. vulgaris*, diet did not vary between sexes. Within small *L. forbesii*, winter diet differed from that in spring (Table 3), with the
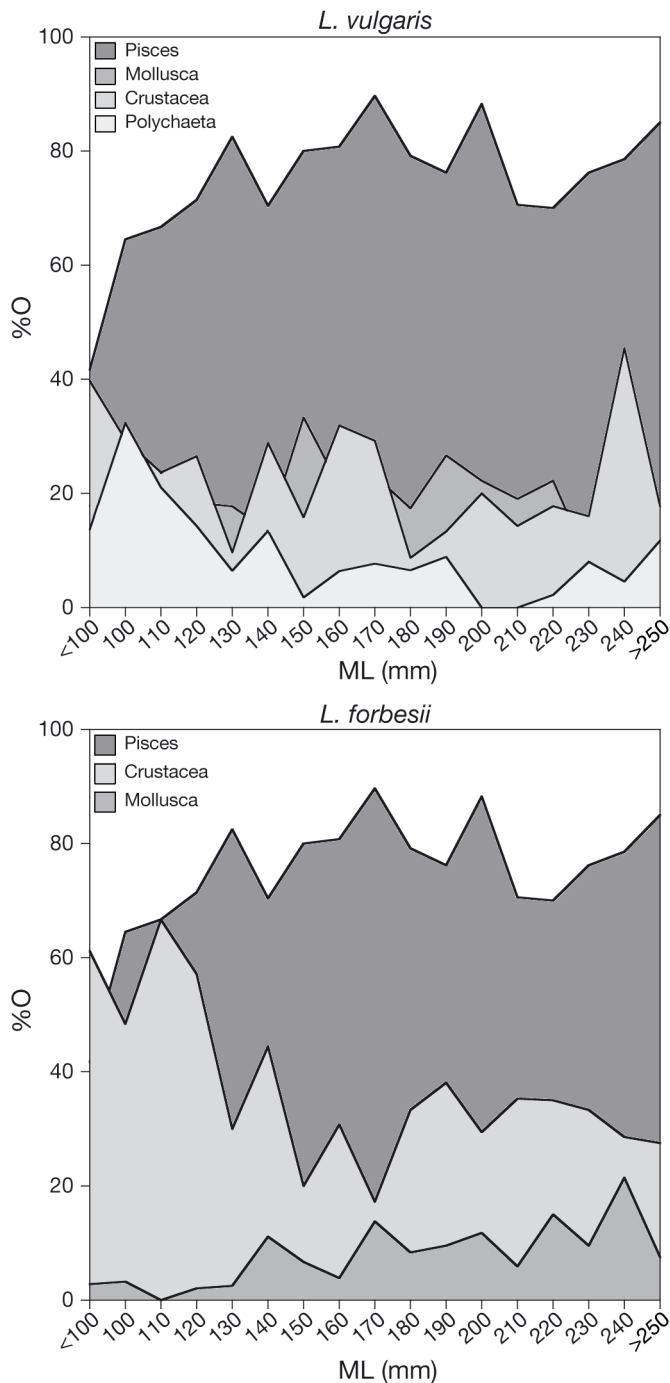
Fig. 2. Variation with growth of the frequency of occurrence (%O) of the main prey groups (Pisces, Crustacea, Mollusca, Polychaeta) in the diet of *Loligo vulgaris* and *L. forbesii*. ML: dorsal mantle length

highest consumption of euphausiids in the winter, whereas unidentified fish and pelagic gobiids (mainly *A. minuta*) dominated the diet in the spring. Gobiids and mysids were most frequently found in summer compared to autumn (Table 5). For large

individuals, the spring diet differed from that of summer and autumn. Unidentified fish, gobiids, natantian decapods, euphausiids and gadiforms (in descending order of abundance) were the main food categories in spring, in contrast to the greater abundance of unidentified fish, natantian decapods, gadiforms, cephalopods and myctophids in summer (Table 5). Diet variation between autumn and spring was due to the greater consumption of un-identified fish, euphausiids, natantian decapods, myctophids and cephalopods in autumn.

L. forbesii diet also varied seasonally between size classes in summer and autumn (Table 3). In summer, gobiids and mysids were the main contributors to the diets of small individuals, while unidentified fish, natantian decapods, cephalopods and gadiforms were the main prey for large individuals. During autumn, euphausiids and myctophids were absent from the diet of small individuals (Table 6).

Niche breadth values were overall low (0.05 to 0.27) regardless of size or season, which indicates high specialization (Table 1). The lowest B_i values were found in winter for both size groups, whereas a wider niche breadth was observed for large individuals during spring and autumn.

DISCUSSION

Although squid have been identified as a keystone group in Mediterranean ecosystems (Coll et al. 2006, Tsagarakis et al. 2010, Bănaru et al. 2013), further studies are needed to better understand their importance in the functioning of marine trophic webs in this area (Tsagarakis et al. 2010, Navarro et al. 2013), where the currently available information is very scarce (Table S2 in the Supplement at www.int-res.com/articles/suppl/m531p207_supp.pdf). In this study, we present for the first time a description of the diet of *Loligo vulgaris* and *L. forbesii* in the Mediterranean and analyse the trophic ecology of these loliginids.

Diet composition and spatial segregation

In agreement with previous work carried out in Atlantic waters, our study revealed that in the Mediterranean, both squid species display a mixed diet including pelagic, benthopelagic and benthic organisms with a clear preference for fish (e.g. Collins et al. 1994, Boyle & Pierce 1994, Pierce et al. 1994, Coelho et al. 1997, Wangvoralak et al.

Table 2. Results of PERMANOVA testing the effect of sex, size (small, large) and season (winter, spring, summer, autumn) in diet composition of *Loligo vulgaris* and *L. forbesii*. Significant effects are shown in **bold**; res: residuals; perm: permutation

Source	df	SS	MS	Pseudo-*F*	p(perm)	Unique perms
L. vulgaris						
Sex	1	1448.1	1448.1	0.6804	0.6628	9949
Size	1	17983	17983	8.4501	**0.0001**	9945
Season	3	17531	5843.7	2.7460	**0.0004**	9924
Sex×Size	1	2566.2	2566.2	1.2059	0.2896	9943
Sex×Season	3	3031.6	1010.5	0.4748	0.9615	9900
Season×Size	3	8403.9	2801.3	1.3163	0.1697	9920
Sex×Season×Size	3	4395.1	1465	0.6884	0.8125	9920
Res	137	2.9155×10^5	2128.1			
Total	152	3.5236×10^5				
L. forbesii						
Sex	1	1189.8	1189.8	0.4179	0.8440	9959
Size	1	10144	10144	3.5636	**0.0042**	9951
Season	3	22020	7340	2.5785	**0.0013**	9885
Sex×Size	1	2975.3	2975.3	1.0452	0.3855	9948
Sex×Season	3	4235.2	1411.7	0.4959	0.9446	9925
Season×Size	3	15684	5228.1	1.8366	**0.0299**	9922
Sex×Season×Size	3	3541.1	1180.4	0.4146	0.9739	9922
Res	78	2.2204×10^5	2846.7			
Total	93	2.8562×10^5				

Table 3. Pairwise tests for significant factors found in PERMANOVA (see Table 1 for abbreviations). Significant effects are shown in **bold**

	Groups	*t*	p(perm)	Unique perms
L. vulgaris				
Season	W, SP	1.7896	**0.0121**	9948
	W, S	1.3588	0.0895	9944
	W, A	1.2361	0.1818	9952
	SP, S	2.1402	**0.0014**	9945
	SP, A	1.8316	**0.0102**	9948
	S, A	0.6497	0.8704	9955
L. forbesii				
Season				
Small (<140 mm)				
	W, SP	1.5921	**0.0370**	9956
	W, S	1.7291	0.0648	3314
	W, A	1.6690	0.0719	8281
	SP, S	1.5311	0.0613	9948
	SP, A	0.9196	0.4981	9948
	S, A	1.6534	**0.0493**	3466
Large (≥140 mm)				
	W, SP	1.2983	0.1346	9944
	W, S	1.4407	0.1055	9941
	W, A	1.4650	0.1062	9941
	SP, S	1.5652	**0.0330**	9943
	SP, A	1.6702	**0.0146**	9952
	S, A	1.2079	0.2080	9950
Size	W	0.7071	0.6251	8093
	SP	1.1094	0.2865	9957
	S	2.4063	**0.0005**	9894
	A	1.7135	**0.0398**	9947

2011). Although fish are known to be the most important prey for both squid, differences at the prey-specific level occur among regions probably due to their opportunistic behaviour (Jereb & Roper 2010, Wangvoralak et al. 2011). The families Ammodytidae, Gadidae, Carangidae or Gobiidae are among the most common prey along the geographic range of the squid (e.g. Collins et al. 1994, Rocha et al. 1994, Coelho et al. 1997). In the present study, benthic gobiids and sparids were of particular importance for *L. vulgaris*, while *L. forbesii* preferred pelagic gobiids and mesopelagic species. Unfortunately, data on prey availability are absent in the area and we cannot attribute the higher frequency of these prey to their abundance in the environment. The stomach content analysis also revealed the bathymetric segregation of both species in the Mediterranean. Typical coastal species such as the sparids *Centracanthus cirrus* and *Spicara smaris* and the gobiids *Lesueurigobius* spp. were frequent prey only present in the diet of *L. vulgaris*. By contrast, shelf-break and upper slope species such as myctophids (e.g. *Ceratoscopelus maderensis*, *Lampanyctus* spp.), the argentinid *Glossanodon leioglossus* or the euphausiid *Meganyctiphanes norvegica* were the main prey of *L. forbesii* with hardly any presence in *L. vulgaris* diet. The bathymetric segregation is further evidenced by the scarce overlap of the most frequent prey. These results indicate that these closely related squid segregate according to differences in horizontal habitat and food preferences. Further striking differences in the diet of both squid include cephalopods and isopods, which were more frequent in *L. vulgaris* than in *L. forbesii* (19.46% vs. 5.89% and 8.87% vs. 0.81%, respectively), euphausiids (24.95% in *L. forbesii* vs. 1.11% in *L. vulgaris*) and the importance of polychaetes (8.74%) in *L. vulgaris* that were absent in *L. forbesii* diet (see below). We also found noticeable quantities of algae in the stomach contents of small and large individuals of *L. vulgaris* that were completely absent from those of *L. forbesii*. In the Balearic Islands, the soft algae bottoms, characterized by a high abundance of free-living species and erect red algae, cover large areas of sea bottom at 40 to 90 m (Ballesteros 1994, Ordines

Table 4. SIMPER analysis identifying which prey contribute most (75% cut-off for low contributions) towards diet differences between size groups (Sm: small; L: large) and seasons (W: winter; SP: spring; S: summer; A: autumn) in *Loligo vulgaris*. Average abundance (Av.Ab.), average dissimilarity (Av.Diss.), standard deviation (SD), percentage contribution to the dissimilarity (Contrib%) and percentage contribution to the dissimilarity accumulated (Cum%) are shown; unid: unidentified

Prey items	Av.Ab.	Av.Ab.	Av.Diss	Diss/SD	Contrib%	Cum%
Size						
Sm & L (Av.Diss. = 65.09)	Group Sm	Group L				
Pisces unid.	5.33	6.65	13.58	1.14	20.87	20.87
Gobiidae	3.16	0.47	10.28	0.87	15.80	36.67
Cephalopoda	2.11	1.73	8.66	0.92	13.31	49.97
Isopoda	1.18	1.33	6.14	0.73	9.44	59.41
Sparidae	0.71	1.25	5.17	0.60	7.95	67.36
Polychaeta	0.90	0.53	4.07	0.48	6.25	73.61
Algae	0.60	0.55	3.13	0.45	4.81	78.43
Season						
SP & W (Av.Diss. = 61.48)	Group SP	Group W				
Pisces unid.	6.27	6.06	13.8	1.08	22.44	22.44
Cephalopoda	1.45	2.77	10.11	0.93	16.45	38.89
Gobiidae	2.58	1.09	9.77	0.78	15.89	54.78
Isopoda	0.7	1.99	7.17	0.73	11.67	66.44
Sparidae	0.3	1.05	4.22	0.47	6.87	73.31
Polychaeta	1.23	0.16	4.08	0.48	6.63	79.94
SP & S (Av.Diss. = 66.48)	Group SP	Group S				
Pisces unid	6.27	5.05	12.89	1.12	19.39	19.39
Gobiidae	2.58	2.12	9.91	0.91	14.91	34.31
Cephalopoda	1.45	1.96	7.35	0.91	11.06	45.37
Sparidae	0.3	1.81	5.81	0.7	8.74	54.1
Isopoda	0.7	1.7	5.49	0.87	8.25	62.36
Algae	0.09	1.41	4.74	0.52	7.13	69.49
Polychaeta	1.23	0.31	4.04	0.52	6.08	75.57
SP & A (Av.Diss. = 64.80)	Group SP	Group A				
Pisces unid.	6.27	5.49	12.31	1.11	19	19
Gobiidae	2.58	1.66	8.84	0.91	13.64	32.64
Cephalopoda	1.45	2.3	7.88	0.94	12.16	44.79
Sparidae	0.3	1.62	5.27	0.59	8.13	52.92
Polychaeta	1.23	0.67	5.04	0.53	7.78	60.71
Isopoda	0.7	1.25	4.95	0.56	7.64	68.35
Algae	0.09	1.38	4.06	0.6	6.26	74.61
Crustacea unid.	0.52	1.02	3.99	0.55	6.16	80.78

& Massutí 2009). In previous work, algae present in *L. vulgaris* stomachs were categorized as non-food items and considered misleading owing to the carnivorous habits of this species (Macy 1982, Guerra & Rocha 1994, Pierce et al. 1994). If algae were accidentally eaten when foraging benthic prey, its appearance in squid diet should be higher in spring; however, we recorded the lowest values in that season.

Ontogenetic shift

The analysis of data at a high resolution level (e.g. family) evidenced ontogenetic changes in diet for both species that were not revealed when major groups were used, highlighting the importance of identifying prey at low taxonomic levels. Our work far outnumbered the list of prey reported in previous studies (e.g. Pierce et al. 1994, Rocha et al. 1994, Coelho et al. 1997, Wangvoralak et al. 2011), which allowed consistent statistical analysis of data by squid size. In contrast to our cluster analysis, ontogenetic changes were investigated separating individuals by maturity stages or pre-defined length classes in all previous studies (Collins et al. 1994, Pierce et al. 1994, Rocha et al. 1994, Coelho et al. 1997). From these studies, only *L. forbesii* specimens larger than 250–300 mm ML were found to vary from the small individuals (Rocha et al. 1994, Coelho et al. 1997). In studies using stable isotope analysis, *L. forbesii* did not show a clear ontogenetic pattern, whereas *L. vulgaris* showed an ontogenetic shift at 100 mm ML (Chouvelon et al. 2011).

Table 5. SIMPER analysis identifying which prey contribute most (75% cut-off for low contributions) towards diet differences between seasons (W: winter; SP: spring; S: summer; A: autumn) for small and large *Loligo forbesii*. Average abundance (Av.Ab.), average dissimilarity (Av.Diss.), standard deviation (SD), percentage contribution to the dissimilarity (Contrib%) and percentage contribution to the dissimilarity accumulated (Cum%) are shown; unid: unidentified

Prey items	Av.Ab.	Av.Ab.	Av.Diss	Diss/SD	Contrib%	Cum%
Small						
W & SP (Av.Diss. = 80.66%)	Group W	Group SP				
Euphausiacea	5.90	0.84	24.13	1.19	29.92	29.92
Pisces unid.	2.54	4.60	16.39	1.07	20.32	50.24
Gobiidae	1.73	3.20	13.97	0.87	17.32	67.56
Crustacea unid.	1.36	0.79	5.63	0.75	6.98	74.54
Sternoptychidae	0.81	0.81	5.23	0.48	6.48	81.03
S & A (Av.Diss. = 82.73%)	Group S	Group A				
Gobiidae	6.05	1.33	23.66	1.36	28.60	28.60
Pisces unid.	1.24	6.08	22.46	1.35	27.15	55.76
Mysidacea	4.75	1.15	18.27	1.03	22.09	77.84
Large						
SP & S (Av.Diss. = 71.80%)	Group SP	Group S				
Pisces unid.	3.61	5.45	13.00	1.14	18.11	18.11
Natantia	1.60	2.58	8.93	0.98	12.44	30.55
Gobiidae	2.58	0.27	8.27	0.73	11.52	42.06
Gadiformes	1.37	2.23	8.03	0.89	11.18	53.24
Euphausiacea	1.58	1.74	7.84	0.74	10.92	64.16
Cephalopoda	0.94	2.09	7.55	0.80	10.51	74.67
Myctophidae	0.69	1.46	4.91	0.79	6.84	81.52
SP & A (Av.Diss. = 71.31%)	Group SP	Group A				
Euphausiacea	1.58	3.83	10.10	1.18	14.16	14.16
Pisces unid.	3.61	4.16	9.75	1.14	13.68	27.84
Natantia	1.60	3.13	8.22	1.36	11.52	39.36
Gobiidae	2.58	1.13	7.56	0.82	10.61	49.97
Myctophidae	0.69	2.61	6.49	1.72	9.10	59.07
Cephalopoda	0.94	2.02	6.29	1.14	8.82	67.89
Sternoptychidae	0.96	1.34	4.80	0.71	6.73	74.62
Gadiformes	1.37	0.74	4.52	0.63	6.34	80.97

Table 6. SIMPER analysis identifying which prey contribute most (75% cut-off for low contributions) towards differences between small (Sm) and Large (L) *Loligo forbesii* during summer and autumn. Average abundance (Av.Ab.), average dissimilarity (Av.Diss.), standard deviation (SD), percentage contribution to the dissimilarity (Contrib%) and percentage contribution to the dissimilarity accumulated (Cum%) are shown; unid: unidentified

Prey items	Av.Ab.	Av.Ab.	Av.Diss	Diss/SD	Contrib%	Cum%
Summer						
Sm & L (Av.Diss. = 84.06%)	Group Sm	Group L				
Gobiidae	5.50	0.35	16.58	1.18	19.72	19.72
Mysidacea	4.89	0.00	14.55	0.94	17.31	37.03
Pisces unid.	1.74	5.79	13.18	1.52	15.68	52.71
Natantia	0.00	2.89	8.74	1.06	10.39	63.11
Cephalopoda unid.	0.37	2.81	7.92	1.46	9.42	72.53
Gadiformes	0.53	2.28	6.09	1.29	7.24	79.77
Autumn						
Sm & L (Av.Diss. = 69.51%)	Group Sm	Group L				
Natantia	4.36	3.51	10.78	1.29	15.50	15.50
Euphausiacea	0.00	3.81	10.16	1.10	14.61	30.11
Pisces unid.	4.65	4.63	8.90	1.48	12.81	42.93
Myctophidae	0.00	3.23	8.47	3.02	12.19	55.12
Cephalopoda unid.	1.92	1.49	6.46	1.54	9.30	64.41
Gobiidae	1.45	1.06	4.38	0.99	6.30	70.71

Food preferences related to morphological and physiological changes as squid grow are expected. Accompanying these changes, species often undergo niche shifts involving diet, habitat use and interspecific interactions (Bergman & Greenberg 1994). Thus, ontogenetic variations in diet might be due to interactions between life-cycle traits (e.g. sex, maturity, size) and environmental conditions (e.g. season, climate, habitat). Given the impossibility of testing all putative drivers, 2 biotic (sex and size) and 1 abiotic (season) factors were tested in the current analysis. Remarkably, although both species are so similar in morphology and size, *L. forbesii* underwent the shift in diet much earlier than *L. vulgaris* (140 mm vs. 210 mm ML), suggesting that the factors triggering the ontogenetic shifts might be different. Whereas size and season statistically affected the diet of both squid, *L. forbesii* was also influenced by the interaction of those factors. This result indicates that neither of these factors on its own allows explanation for intraspecific differences in prey composition. The diet of small-sized individuals of *L. vulgaris* was more dependent on bottom-living organisms (e.g. suprabenthic/benthic species such as mysids and gobiids) than large individuals that mainly prey on benthopelagic fish (e.g. sparids). On the other hand, prey composition in *L. forbesii* diet was only size-dependent during summer and autumn, which is probably due to intraspecific differences in depth distribution (Guerra & Rocha 1994, Stowasser 2004, Smith et al. 2013). It is likely that changes in both biotic and abiotic factors contribute to the ontogenetic diet shifts observed. Regardless of the mechanism, it is clear that size shifts in diet occur in both species, and this has important implications for both trophodynamics and marine food models (Garrison & Link 2000).

Seasonal variation

The diet of *L. vulgaris* in spring differed significantly from all other seasons. An increase in benthic prey such as polychaetes and gobiids (e.g. *Lesueurigobius* spp.) together with a decrease in highly motile prey such as sparids and cephalopods was observed in that season. Additionally, the highest values of diet specialization in large-sized individuals also occurred in spring. A shift to benthic feeding coinciding with movement to the spawning grounds was also observed in *L. opalescens* (Karpov & Cailliet 1979). Moreover, a considerable increase in the consumption of polychaetes, mainly nereidids,

was observed in both small and large *L. vulgaris* individuals. Polychaetes, and specially nereidids, are known to improve the reproductive fitness of cultured animals due to their high content of omega-3 fatty acids (García-Alonso et al. 2008); thus consumption of these prey might improve the reproductive condition of squid. Spring diet differences might also reflect variations in spatial or temporal food resource availability (Macy 1982, Collins et al. 1994).

The diet of large-sized individuals of *L. forbesii* was characterized by a high proportion of mesopelagic prey during summer and autumn. Most prey were fish and crustacean species performing nycthemeral movements (e.g. *Hygophum* spp., *C. maderensis*, *Lampanyctus* spp., *Sergestes arachnipodus*, *Pasiphaaea sivado*) or were inhabitants of the deep scattering layer situated off-shore at 400–600 m depth (e.g. *A. hemigymnus*, *M. muelleri*) (Abelló et al. 2002, Olivar et al. 2012, Simao et al. 2014). This indicates that predator–prey interactions might occur during day–night vertical migrations of mesopelagic species or as a result of oblique offshore displacements displayed by large *L. forbesii*. Such oblique movements have been suggested for hake in our study area (Cartes et al. 2009) and the mesopelagic community around the Hawaiian Islands (Reid et al. 1991). Vertical movements into the water column at night chasing mesopelagic prey such as lanternfish, euphausiids and mysids have also been reported in *L. pealei* (Vinogradov & Noskov 1979, Vovk 1985). Although euphausiids have been reported as important prey for other loliginids (Karpov & Cailliet 1979, Macy 1982, Vovk 1985), they have not previously been reported in *L. forbesii* (Pierce et al. 1994, Rocha et al. 1994, Wangvoralak et al. 2011), except for the smallest sizes (<60 mm) in Irish waters (Collins et al. 1994). In our results, euphausiids were the most important crustacean prey both in small and large *L. forbesii* individuals. The most frequent species was *M. norvegica*, a near-surface migrant, which is abundant down to 150 m depth in winter moving to waters below 700 m in summer (Sardou et al. 1996). This euphausiid was consumed by large-sized squid year round, but only in winter and, to a lesser extent, in spring by small-sized squid. Such differences agree with the aforementioned migration of large squid to deeper waters. Competition for *M. norvegica* in winter is unlikely owing to its high abundance (Sardou et al. 1996).

The transparent goby *Aphia minuta* was also a major prey for small-sized *L. forbesii* individuals in spring and summer. This gobiid supports an important small-scale fishery in the western Mediterranean which takes place in shallow epipelagic waters

during winter (Iglesias et al. 1994). Driven by hydrographical conditions, the species migrates to deeper waters in spring (Iglesias & Morales-Nin 2001), where the squid would prey on them. The transparent goby was also an important resource for small *L. forbesii* in Irish waters (Collins et al. 1994).

To conclude, our study showed that, as expected, the diet composition of *L. vulgaris* and *L. forbesii* reflected the bathymetric segregation of these 2 squid species in the Mediterranean. Although both squid primarily preyed on fish, the most abundant were typical shallow shelf species in *L. vulgaris* and upper slope species in *L. forbesii*. In agreement with all previous studies, diet composition did not vary between males and females in either of the 2 squid species. Our results also revealed ontogenetic shifts of diet in both squid taking place at contrasting sizes (210 vs. 140 mm ML, respectively), suggesting that the factors triggering these shifts might be different. During the reproduction period, *L. vulgaris* prioritizes benthic prey over nektonic prey, in particular the highly nutritive polychaetes which are known to improve the individual condition of cultured animals. Size-related differences in *L. forbesii* diet during the second half of the year indicate a deeper distribution of large individuals, which preferentially prey on mesopelagic species and are thus involved in benthic–pelagic coupling.

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