



# Structure and dynamics of cephalopod assemblages in the water column on shelf-break and slope grounds of the western Mediterranean



A. Quetglas<sup>a,\*</sup>, M. Valls<sup>a</sup>, F. Ordines<sup>a</sup>, A. de Mesa<sup>a</sup>, M.P. Olivar<sup>b</sup>, S. Keller<sup>a</sup>, E. Massutí<sup>a</sup>

<sup>a</sup> Instituto Español de Oceanografía, Centre Oceanogràfic de les Balears, Moll de Ponent s/n, Apdo. 291, 07015 Palma, Spain

<sup>b</sup> Institut de Ciències del Mar (CSIC), Passeig Marítim, 37-49, 08003 Barcelona, Spain

## ARTICLE INFO

### Article history:

Received 21 February 2013

Received in revised form 15 November 2013

Accepted 17 November 2013

Available online 22 November 2013

### Keywords:

Cephalopod fisheries  
Population density  
Pelagic environment  
Nycthemeral rhythms  
Mediterranean Sea

## ABSTRACT

The structure and dynamics of cephalopod assemblages in different bathymetric strata from the surface to bottom grounds, down to a depth of 900 m, in the western Mediterranean, were analysed. Data were collected both on the shelf-break and slope during the summer and early autumn surveys, using a midwater trawl and a bottom trawl gear, to catch pelagic and nekto-benthic species, respectively. The pelagic tows were not random, but targeted at the strongest and widest acoustic sound layers. A total of 26 cephalopod species belonging to 12 families were collected. With regard to the abundance, biomass and frequency of occurrence, we did not find a common seasonal trend for all the species, suggesting that their population dynamics are not governed by major environmental drivers. Most assemblage metrics (e.g., diversity, species richness, abundance and biomass) showed similar, low values in the pelagic layers compared to the bottom grounds. In general, assemblage metrics were lower in summer than in autumn on the shelf-break, while showing an inverse seasonal trend on the slope. There was a clear general increase in all metrics during the night compared to the day. Cluster results revealed differences in diel migratory strategies by stratum, vertical movements being scarce in the shelf-break species, but intense in the slope species.

© 2013 Elsevier B.V. All rights reserved.

## 1. Introduction

There is currently a general agreement on the key role played by cephalopods in the structure and dynamics of marine food webs, either as voracious predators or important prey of a large set of predators, including fishes, other cephalopods, marine mammals and seabirds (e.g., Cherel et al., 2009; Clarke, 1996b; Piatkowski et al., 2001). Despite such significance, there is a major lack of information on most aspects of the biology and ecology of pelagic and deep-sea species, especially when compared to their shelf-living relatives. However, the shelf species only represent a small percentage (15%) of all the cephalopod genera (Clarke, 1996b).

According to most specialists, the dearth of information on the oceanic species reflects the inability of the present day sampling equipment to catch them, as the stomach content analyses of their predators suggest that cephalopods are abundant in the water column (Bello, 2000; Cherel and Hobson, 2005; Clarke, 1996a; Lansdell and Young, 2007). Indeed, the number of beaks in the stomach contents of some large predators such as whales can be counted in thousands (e.g., Clarke and Kristensen, 1980; Clarke and Roper, 1998; Fernandez et al., 2009). Owing to the difficulties in catching pelagic cephalopods, the number of studies analysing the species and assemblages present

along the water column are very scarce worldwide. Most currently available studies are based on three different sources: the stomach contents of teuthophagous predators, such as, marine mammals or large pelagic fishes, the analysis of the paralarvae or cephalopod early life stages and, to a lesser extent, the use of traditional midwater trawl gears. To overcome the inefficiency of the fishing gear, three large pelagic fish species were used as samplers to analyse the composition of the species and the horizontal and vertical distribution of pelagic cephalopods from eastern Australia (Lansdell and Young, 2007). Planktonic gear, collecting paralarvae and small juveniles, was used to investigate the distribution of pelagic cephalopods from the surface down to a 1000 m depth in the Arabian Sea (Piatkowski and Welsch, 1991), as also the distribution in the waters of the upper 200 m of the Southern Ocean (Van de Putte et al., 2010). Examples of pelagic sampling using midwater trawls to collect adult and juvenile individuals are currently very scarce, for example, the analysis of cephalopods over depths of 169–4800 m in the western North Atlantic (Vecchione and Pohle, 2002). In other cases, a combination of different gear types collecting different cephalopod life stages was used (Chesalin and Zuyev, 2002; Vecchione et al., 2010).

Although the benthopelagic cephalopod assemblages from the Mediterranean are well known (e.g., Fanelli et al., 2012; González and Sánchez, 2002; Quetglas et al., 2000), the pelagic forms have received very little attention and have been restricted to the analysis of early life stages and inferences from predators. In the first case, Roper

\* Corresponding author. Tel.: +34 971401561; fax: +34 971404945.  
E-mail address: [toni.quetglas@ba.iao.es](mailto:toni.quetglas@ba.iao.es) (A. Quetglas).

(1974), analysed the vertical and seasonal distribution of larval and small juvenile pelagic cephalopods with discrete-depth tows, both in the day and night, from the surface down to a depth of 1000 m. In the second case, Romeo et al. (2012), studied the pelagic cephalopods of the central Mediterranean by analysing the stomach content of large fish predators. To our knowledge, at present, there is not a single study dealing with the species composition and distribution of adult pelagic cephalopods in the water column, using midwater trawl gear, in the Mediterranean. In this article, we have analysed the structure and dynamics of cephalopod assemblages at different bathymetric strata, from the surface to the bottom grounds, down to a depth of 900 m. The data used in this study were collected during the IDEADOS surveys ([www.ba.ieu.es/ideados](http://www.ba.ieu.es/ideados)), primarily addressed to investigate the spatiotemporal differences in the composition and structure of nektobenthic communities in the western Mediterranean (Massutí et al., 2014—in this issue). The availability of day and night sampling allowed comparisons of day–night cephalopod abundances and nycthemeral movements in the water column. Such comparisons are of prime importance to investigate midwater cephalopod assemblages, because many species undergo substantial diel vertical migrations, rising towards the surface each night (Boyle and Rodhouse, 2005).

## 2. Materials and methods

Sampling was conducted in late autumn (December 2009) and early summer (July 2010), off Mallorca (Balearic Islands, western Mediterranean). Samples were collected from the shelf-break (200 m depth) and slope (600–900 m) off the northwest and southeast of Mallorca (Sóller and Cabrera zones, respectively). In both the zones, a relatively small area was repeatedly sampled throughout the day using the following gear: (1) a commercial “huelvano”-type bottom trawl, with a 20 mm diamond-mesh cod-end and mean horizontal and vertical net openings of 25 m and 1.8–2.1 m, respectively; and (2) a double-warp modified commercial midwater trawl, with standard pelagic trawl doors (otter boards), graded-mesh netting to the cod-end (10 mm) and an estimated mouth opening of 280 and 112 m<sup>2</sup>, during the autumn and summer surveys, respectively. Although the bottom trawl sampling was only done during the daytime hours, midwater trawl samples were taken both during the day and night, which allowed comparisons of day–night cephalopod abundances and nycthemeral movements in the water column. The mean towing speeds of the bottom trawl and midwater trawl were 2.5 and 4.0 knots, respectively. Pelagic sampling was not performed randomly, but was done by using directed sampling, which meant that the hauls were targeted at the strongest and widest acoustic sound layers. The acoustic layers were detected with a Simrad EK60 echo sounder at different frequencies (18, 38, 70, 120 and 200 kHz). More details on the location of the study area, the vertical structure of the water column and the characteristics of the acoustic layers can be found elsewhere (Massutí et al., 2014—in this issue; Olivar et al., 2012).

In the shelf-break bathymetric stratum, sampling was carried out at: (1) the near surface (SUR1), from 0–60 m; (2) in the benthic boundary layer (BBL1), less than 50 m above the bottom; and (3) at the bottom (BOT1). In the slope bathymetric stratum, sampling was performed at: (1) the near surface (SUR2) from 0–80 m depth; (2) in the 400–600 m deep scattering layer (DSL); and (3) at the bottom (BOT2). For comparative purposes, a few hauls were also performed near the bottom in this slope bathymetric stratum (BBL2). In all cases, the SUR, BBL and DSL sampling were performed using the midwater trawl, while the BOT sampling was performed by using the bottom trawl. For each haul, the total abundance and biomass, by species, were taken. The size (mantle length, ML) and total weight (TW) were also taken for each specimen, except in a few cases, where random samples were analysed owing to the large amount of available material. All analyses were performed on fresh specimens, in the laboratory.

For analysis, the abundance and biomass were standardised to the number of individuals and weight in kilogrammes, respectively, per Hm<sup>3</sup> (ind·Hm<sup>-3</sup> and kg·Hm<sup>-3</sup>). The volumes were calculated using the mouth area of the nets and the distance travelled by each haul. Together with the abundance and biomass, the frequency of occurrence (F) of each species was computed by season and for the total. As diel migrations are associated with the mixing of layers, dawn or sunset samples were discarded for most analyses and were considered only for comparative purposes. Day was considered to span from one hour after sunrise to one hour before sunset, while night spanned from one hour after sunset to one hour before sunrise.

The cephalopod assemblage structure was analysed via the hierarchical agglomerative and unweighted arithmetic average clustering (CLUSTER procedure; Clarke and Gorley, 2006) procedure, by calculating the Bray–Curtis similarity resemblance matrices of the fourth root-transformed abundance data. The SIMPER procedure was applied to identify the species that characterised each group and to those accounting for the differences between groups. For each level of the water column (SUR, DSL, BBL, BOT), the abundance, biomass and the following four ecological indices were computed by the bathymetric stratum (shelf-break, slope), season (summer, autumn) and light (day, night; except the BOT samples): (1) the Shannon diversity index ( $H'$ ); (2) Pielou's evenness index ( $J'$ ); (3) mean species richness ( $meanS$ ) and (4) total species richness ( $S$ ). The abundance, biomass and these four ecological indices are hereafter referred to as assemblage metrics. With the only exception of two specific cases, the low number of replicates in most sampling settings precluded the statistical comparison of these metrics. In the first case, BOT sampling allowed analysing the effects of seasons (autumn, summer), location (Sóller, Cabrera) and layer (BOT1, BOT2); in the second case, SUR2 and DSL sampling allowed testing the differences related to light (day, night) and layer (SUR2, DSL). In both cases, the differences were tested by means of a factorial one-way analysis of variance (ANOVA), with all factors crossed with each other, using STATISTICA version 7 (StatSoft, Inc., 2004).

On the basis of the reasoning that either differences in species abundance or differences in individual sizes at the species level in the water column might indicate movements among layers, day and night abundance values and individual sizes of the most abundant species in each water layer (SUR, DSL, BBL; only day for BOT), both in the shelf-break and slope, were analysed, to infer nycthemeral movements. Size differences were not statistically tested owing to small sample sizes in some water level–light settings.

## 3. Results

### 3.1. Species assemblages

A total of 26 cephalopod species belonging to 12 families was caught (Table 1). The most frequent species was *Todarodes sagittatus* (F = 47%) followed by *Abralia veranyi* (F = 41%), *Illex coindetii* (F = 40%) and *Histioteuthis reversa* (F = 31%); four species (*Ancistrocheirus lesueurii*, *Octopus vulgaris*, *Onychoteuthis banksii* and *Galiteuthis armata*) only appeared once (F = 1.4%). In terms of abundance, *I. coindetii* was by far the most abundant species (50.0 ind·Hm<sup>-3</sup>) followed by *Sepietta oweniana* (28.9 ind·Hm<sup>-3</sup>) and *Alloteuthis media* (8.4 ind·Hm<sup>-3</sup>); the total abundance of all other species was <3 ind·Hm<sup>-3</sup>. The dominance of *I. coindetii* was even more pronounced in terms of biomass (68.8 kg·Hm<sup>-3</sup>), as the second and third most important species only accounted for 12.6 (*Loligo forbesii*) and 7.4 (*T. sagittatus*) kg·Hm<sup>-3</sup>. With the exception of *Eledone cirrhosa* (3.2 kg·Hm<sup>-3</sup>) and *S. oweniana* (2.2 kg·Hm<sup>-3</sup>), all other species had biomass values ≤ 1 kg·Hm<sup>-3</sup>.

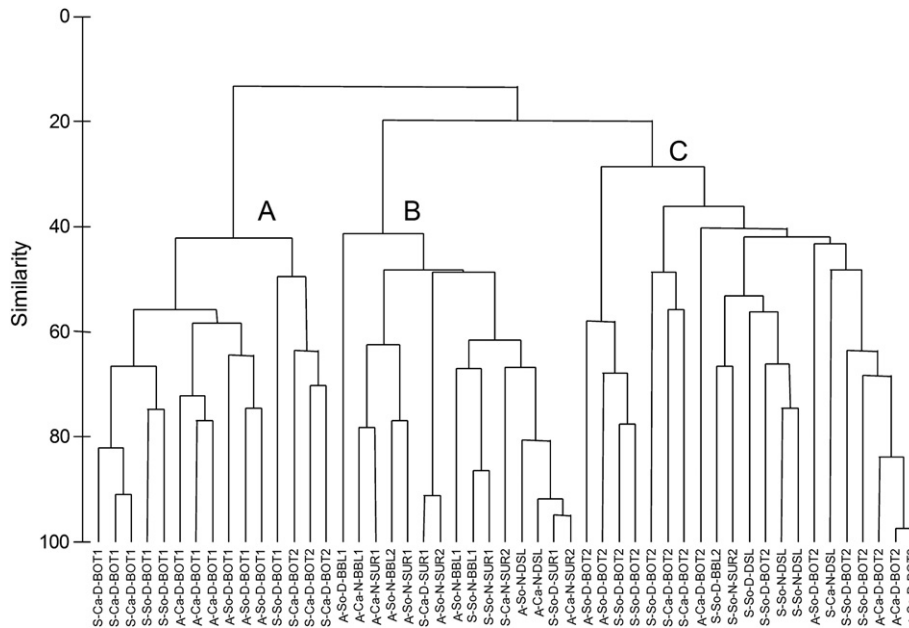
With regard to the abundance, biomass and frequency of occurrence, there was not a single common seasonal trend for all species (Table 1). From the set of species appearing in both seasons, some of them were more frequent in autumn than in summer (*A. veranyi*, *I.*

**Table 1**  
Total and seasonal (summer, autumn) abundance (Ab; ind·Hm<sup>-3</sup>), biomass (Bm; kg·Hm<sup>-3</sup>) and frequency of occurrence (F; %) of all cephalopod species taken in sampling, developed along the water column in the Balearic Sea (western Mediterranean).

Species	Family	Summer			Autumn			Total		
		Ab	Bm	F	Ab	Bm	F	Ab	Bm	F
<i>Abralia veranyi</i>	Enoploteuthidae	4.00	0.94	33.33	1.42	0.03	51.61	2.36	0.32	41.43
<i>Alloteuthis media</i>	Loliginidae	–	–	–	13.19	1.09	19.35	8.37	0.75	8.57
<i>Ancistrocheirus lesueurii</i>	Ancistrocheiridae	0.01	0.12	2.56	–	–	–	<0.01	0.04	1.43
<i>Ancistroteuthis lichtensteini</i>	Onychoteuthidae	0.14	0.22	10.26	–	–	–	0.05	0.07	5.71
<i>Bathypolypus sponsalis</i>	Octopodidae	0.79	1.71	17.95	0.36	0.69	16.13	0.51	1.01	17.14
<i>Chiroteuthis veranyi</i>	Chiroteuthidae	0.06	0.05	5.13	–	–	–	0.02	0.02	2.86
<i>Eledone cirrhosa</i>	Octopodidae	3.57	6.91	23.08	1.16	1.52	25.81	2.04	3.19	24.29
<i>Heteroteuthis dispar</i>	Sepioliidae	0.74	0.07	25.64	0.01	<0.01	3.23	0.27	0.02	15.71
<i>Histioteuthis bonnellii</i>	Histioteuthidae	0.02	0.02	5.13	–	–	–	0.01	0.01	2.86
<i>Histioteuthis reversa</i>	Histioteuthidae	1.77	1.50	38.46	0.21	0.43	22.58	0.78	0.76	31.43
<i>Illex coindetii</i>	Ommastrephidae	10.36	39.31	33.33	72.82	82.05	48.39	50.01	68.76	40.00
<i>Loligo forbesii</i>	Loliginidae	4.44	23.71	20.51	1.08	7.52	19.35	2.31	12.56	20.00
<i>Neorossia caroli</i>	Sepioliidae	0.07	0.05	2.56	0.55	0.01	3.23	0.38	0.02	2.86
<i>Octopus salutii</i>	Octopodidae	0.16	0.84	5.13	0.32	1.00	16.13	0.26	0.95	10.00
<i>Octopus vulgaris</i>	Octopodidae	0.01	0.08	2.56	–	–	–	<0.01	0.02	1.43
<i>Onychoteuthis banksii</i>	Onychoteuthidae	–	–	–	0.02	0.21	3.23	0.01	0.14	1.43
<i>Opisthoteuthis calypso</i>	Opisthoteuthidae	0.06	0.07	2.56	0.05	0.10	3.23	0.06	0.09	2.86
<i>Pteroctopus tetracirrhus</i>	Octopodidae	0.24	2.42	15.38	0.03	0.02	3.23	0.11	0.77	10.00
<i>Rossia macrosoma</i>	Sepioliidae	1.92	0.62	15.38	0.82	0.33	16.13	1.22	0.42	15.71
<i>Rondeletiola minor</i>	Sepioliidae	3.04	0.08	10.26	0.50	0.15	19.35	1.43	0.13	14.29
<i>Scaergus unicolor</i>	Octopodidae	0.11	0.01	7.69	–	–	–	0.04	<0.01	4.29
<i>Sepia orbignyana</i>	Sepiidae	0.74	0.82	15.38	0.02	0.02	3.23	0.28	0.27	10.00
<i>Sepietta oweniana</i>	Sepioliidae	66.78	5.75	20.51	7.10	0.66	25.81	28.90	2.24	22.86
<i>Galiteuthis armata</i>	Cranchiidae	0.03	<0.01	2.56	–	–	–	0.01	<0.01	1.43
<i>Todaropsis eblanae</i>	Ommastrephidae	–	–	–	0.05	0.02	6.45	0.03	0.01	2.86
<i>Todarodes sagittatus</i>	Ommastrephidae	0.93	14.69	48.72	0.32	4.15	45.16	0.54	7.43	47.14

*coindetii*, *Octopus salutii*, *Rondeletiola minor*), whereas, others showed the inverse pattern (*Heteroteuthis dispar*, *Histioteuthis reversa*, *Pteroctopus tetracirrhus* and *Sepia orbignyana*). For some species, the frequency of occurrence did not show a significant difference between seasons (*Bathypolypus sponsalis*, *Loligo forbesii*, *Neorossia caroli*, *Opisthoteuthis calypso*, *Rossia macrosoma*, and *T. sagittatus*). Finally, some species (excluding those appearing only once) were exclusively taken during one sampling season (*A. media*, *Ancistroteuthis lichtensteini*, *Chiroteuthis veranyi*, *Scaergus unicolor*, and *Todaropsis eblanae*). A reduced number

of species displayed striking seasonal differences in terms of abundance and biomass. For instance, *A. media*, which did not occur in summer, appeared in 20% of the autumn sampling with a mean abundance of 13.2 ind·Hm<sup>-3</sup>. The abundance and biomass of *I. coindetii* increased from 10.3 ind·Hm<sup>-3</sup> and 39.3 kg·Hm<sup>-3</sup> in summer to 72.8 ind·Hm<sup>-3</sup> and 82.0 kg·Hm<sup>-3</sup> in autumn. In the other species, the abundance and biomass values were clearly higher in summer than in autumn (*L. forbesii*, 23.7 vs 7.5 kg·Hm<sup>-3</sup>; *S. oweniana*, 66.8 vs 7.1 ind·Hm<sup>-3</sup>; and *T. sagittatus*, 14.7 vs 4.1 kg·Hm<sup>-3</sup>).



**Fig. 1.** Cluster analysis of samples (N = 52) using the Bray–Curtis similarity matrix after four root transformations of cephalopod abundances. For each sample, the four letters stand for station (summer-S, autumn-A), location (Sóller–So, Cabrera–Ca), light (day–d, night–n) and water layer from both the shelf-break (SUR1, BBL1, BOT1) and slope (SUR2, DSL, BBL2, BOT2).

The cluster analysis revealed three main groups at a similarity cut-off value close to 20 (Fig. 1). Group A was mainly characterised by bottom trawl sampling carried out on continental shelf-break grounds, independently of season and zone, together with a set of three summer samplings on the slope depths of Cabrera. Group B was exclusively composed of pelagic sampling, primarily from the shelf-break (SUR1, BBL1), and also by a set of autumn slope sampling (with the only exception of a summer SUR2 sampling). Finally, group C consisted of bottom trawl sampling and summer pelagic sampling (SUR2, DSL, BBL2) from the slope. Similarity percentage analysis (Table 2) showed that group A was mainly characterised by *I. coindetii* (32%), *E. cirrhosa* (18%), *S. oweniana* (13%), *L. forbesii* (10%) and a set of eleven species with contribution percentages < 10%. Group B contained eight species and the pooled contribution of two of them was higher than 90% (*A. veranyi*, 77%; *T. sagittatus*, 16%). Group C consisted of eleven species and the most important ones were *H. reversa* (44%), *T. sagittatus* (23%) and *Bathypolypus sponsalis* (15%). The average dissimilarities among these three groups were higher than 80%: A versus B (87.8), A versus C (85.9%) and B versus C (80.3%).

### 3.2. Assemblage metrics

For each level of the water column, all the assemblage metrics were analysed by the bathymetric stratum (shelf-break, slope), season (summer, autumn) and light (day, night). The diversity was higher in summer than in autumn in all water levels except BBL1 (Fig. 2). The highest diversity was found on BOT1, with the only exception of the summer BBL1 sampling, where there was an increasing trend with depth, both on the shelf-break and the slope. Evenness did not show a homogeneous seasonal trend, and the lowest and highest values were found at DSL in autumn and summer, respectively. In autumn, the evenness showed a marked increase with depth, on the slope, from DSL (0.3) to BOT2 (0.9). On the shelf-break, the total species richness was higher in autumn than in summer, but this pattern was inverted on the slope. Total species richness ranged from 11 to 15 at the BOT grounds, but from 3 to 6 at all other water levels. The mean species richness was higher in summer than in autumn at all water levels except SUR1 and

BBL1; the BOT1 level had the highest values both in autumn (7.7) and summer (9.2). In general, the abundance and biomass values were higher in summer than in autumn. However, this did not apply to the abundance and biomass at BOT1 and biomass at BBL2. By far the highest abundance and biomass values were found at BOT1 in autumn. Biomass was always higher on the slope than on the shelf-break at all water levels, except BOT1 in autumn.

With the only exception of evenness, all other metrics (diversity, total and mean species richness, abundance and biomass) were clearly higher at night than during the day at all water levels, but BBL2 (Fig. 3). Diversity at night was similar at all water levels, except at SUR2 (0.50), ranging from 0.73 to 0.84. Except at BBL2 (0.85), the diversity during the day ranged from 0.14 to 0.45 at DSL and SUR1, respectively; no species was taken during the daytime at SUR2. Evenness at night showed similar values at all water levels (0.61–0.69), whereas, during daytime it ranged from 0.62 to 1.00 at BBL2 and DSL, respectively. In general, the total species richness values at night were twofold higher than those found during the day, with the exception of BBL2 (four and three species in the day and night, respectively). The mean species richness followed the same trend as that of the total species richness, with markedly higher values at night than during the day in all cases except BBL2, which in fact had the highest value (four species during the day). Abundance and biomass were also clearly higher at night in all levels, except the abundance of BBL2 (21 and 7 ind·Hm<sup>-3</sup> at day and night, respectively).

The first ANOVA, testing the effects of season, zone and level of the water column on BOT sampling, showed significant differences due to the level of the metrics of abundance, biomass, total species richness and evenness; additionally, the biomass also showed seasonal differences (Table 3). The second ANOVA, testing the effects of light and level on SUR2 and DSL sampling, revealed differences related to light for biomass, mean species richness and diversity.

### 3.3. Species nycthemeral migration

Day and night abundances of the most abundant species at different water levels, both on the shelf-break and slope, were computed, to analyse nycthemeral movements (Fig. 4). On those water levels with sampling during the two time periods (all but BOT), the abundances were in general markedly higher at night than during the day, both on the shelf-break and slope. With regard to the shelf-break, the highest abundances corresponded to *I. coindetii*, *S. oweniana* and *A. veranyi*, taken at the bottom, during day sampling (1105, 670 and 25 ind·Hm<sup>-3</sup>, respectively). The two former species, *I. coindetii* and *S. oweniana*, did not occur in the day sampling at any other water level, appearing exclusively in the night sampling, at SUR1 and BBL1, with abundances lower than 2.5 ind·Hm<sup>-3</sup>. By contrast, *A. veranyi* occurred at all other water levels both in the day and night, and although abundances on SUR1 were similar (8 and 10 ind·Hm<sup>-3</sup>), the night abundances on BBL1 were clearly higher at night than during the day (10 vs 0.5 ind·Hm<sup>-3</sup>). Finally, the squid *T. sagittatus* was taken on BOT1 daytime sampling, BBL1 night sampling and both day-light and night SUR1 sampling; in all cases, with abundances lower than 3.5 ind·Hm<sup>-3</sup>.

Referring to the slope, no species was taken during the daytime SUR2 sampling. The highest abundance corresponded again to *I. coindetii* on daytime bottom sampling (~30 ind·Hm<sup>-3</sup>); this squid did not appear on daytime sampling at any other water level, being exclusively taken at night at the DSL and BBL2 levels, with abundances lower than 1.5 ind·Hm<sup>-3</sup>. The daytime abundance of *H. reversa* was highest at BBL2 sampling (15 ind·Hm<sup>-3</sup>), decreased at the adjacent upper (DSL: 0.5 ind·Hm<sup>-3</sup>) and lower (BOT2: 4.4 ind·Hm<sup>-3</sup>) water levels and did not appear on SUR2. At night, *H. reversa* only occurred at the DSL and SUR2 levels, its abundance being highest in the DSL sampling (10 ind·Hm<sup>-3</sup>). Interestingly, the sepiolid *H. dispar* followed the same pattern as *H. reversa*. The enoploteuthid *A. veranyi* was taken as

**Table 2**

Similarity percentages (species contributions) within groups determined from the cluster analysis of the cephalopod assemblages identified in the Balearic Sea (western Mediterranean). The different groups (A, B, C) correspond to the clusters displayed in Fig. 1. Values between brackets below the groups are the average similarities within the group. For each group, the three most important species are shown in bold.

Group	A	B	C
Species	(52.82)	(54.31)	(39.85)
<i>Abralia veranyi</i>	0.44	<b>77.09</b>	1.41
<i>Alloteuthis media</i>	1.25	0.30	
<i>Ancistroteuthis lichtensteini</i>			0.72
<i>Bathypolypus sponsalis</i>			<b>14.69</b>
<i>Chiroteuthis veranyi</i>			0.18
<i>Eledone cirrhosa</i>	<b>18.45</b>		0.23
<i>Heteroteuthis dispar</i>		0.61	6.20
<i>Histioteuthis bonnellii</i>			0.20
<i>Histioteuthis reversa</i>		0.33	<b>43.77</b>
<i>Illex coindetii</i>	<b>32.28</b>	<b>2.71</b>	9.70
<i>Loligo forbesii</i>	10.41		
<i>Neorossia caroli</i>	0.2		
<i>Octopus salutii</i>	1.75		
<i>Opisthoteuthis calypso</i>			0.35
<i>Pteroctopus tetracirrhus</i>	2.99		
<i>Rondeletiola minor</i>	3.35	1.18	
<i>Rossia macrosoma</i>	8.11		
<i>Scaevargus unicolor</i>	0.08		
<i>Sepia orbignyana</i>	2.18		
<i>Sepietta oweniana</i>	<b>13.21</b>	1.97	
<i>Todarodes sagittatus</i>	5.2	<b>15.82</b>	<b>22.56</b>
<i>Todaropsis eblanae</i>	0.11		



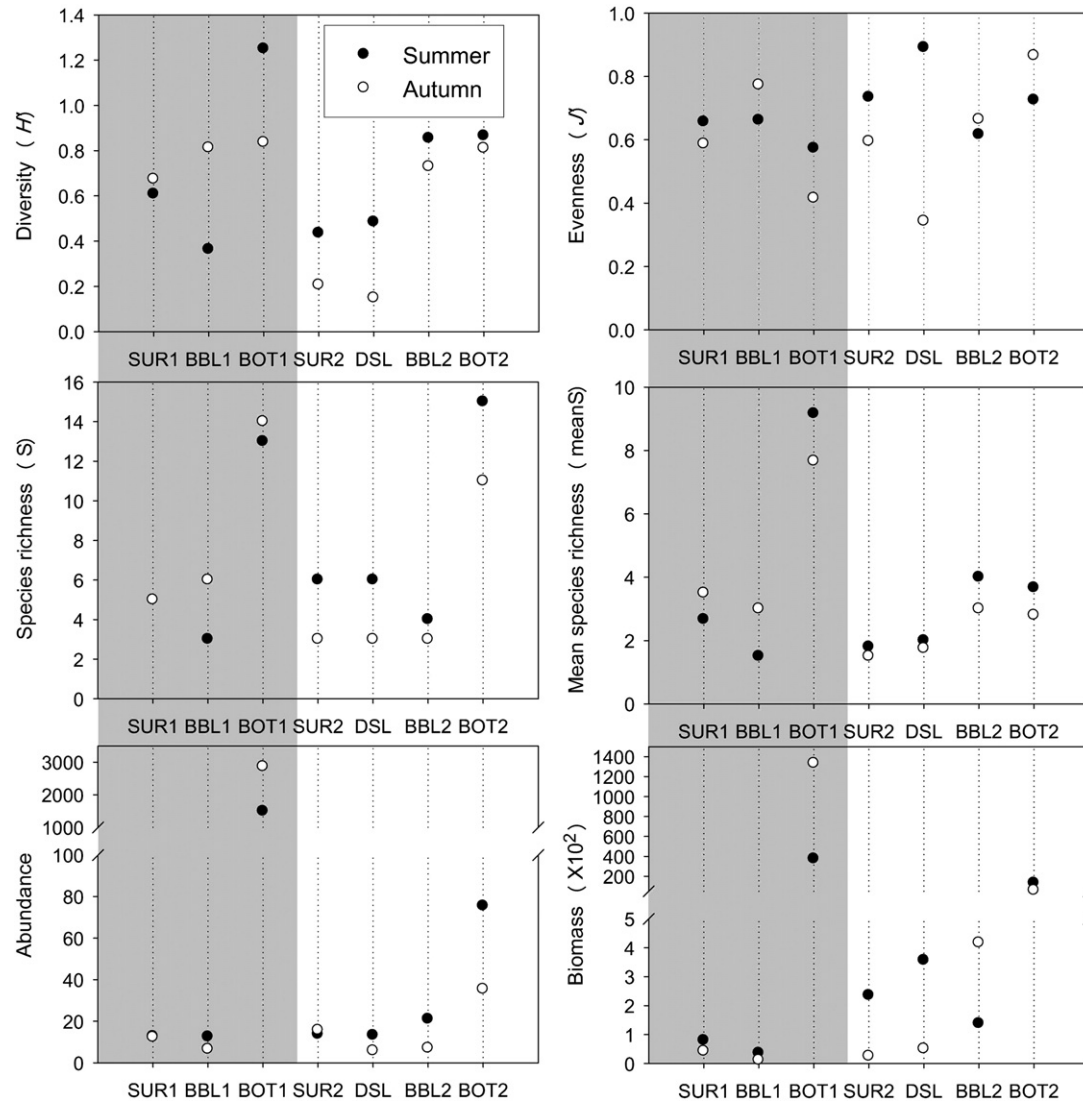


Fig. 2. Summer and autumn values of different assemblage metrics (diversity, evenness, species richness, mean species richness, abundance and biomass) from western Mediterranean cephalopod assemblages at different water layers from both the shelf-break (SUR1, BBL1, BOT1; in grey background) and slope (SUR2, DSL, BBL2, BOT2; in white background).

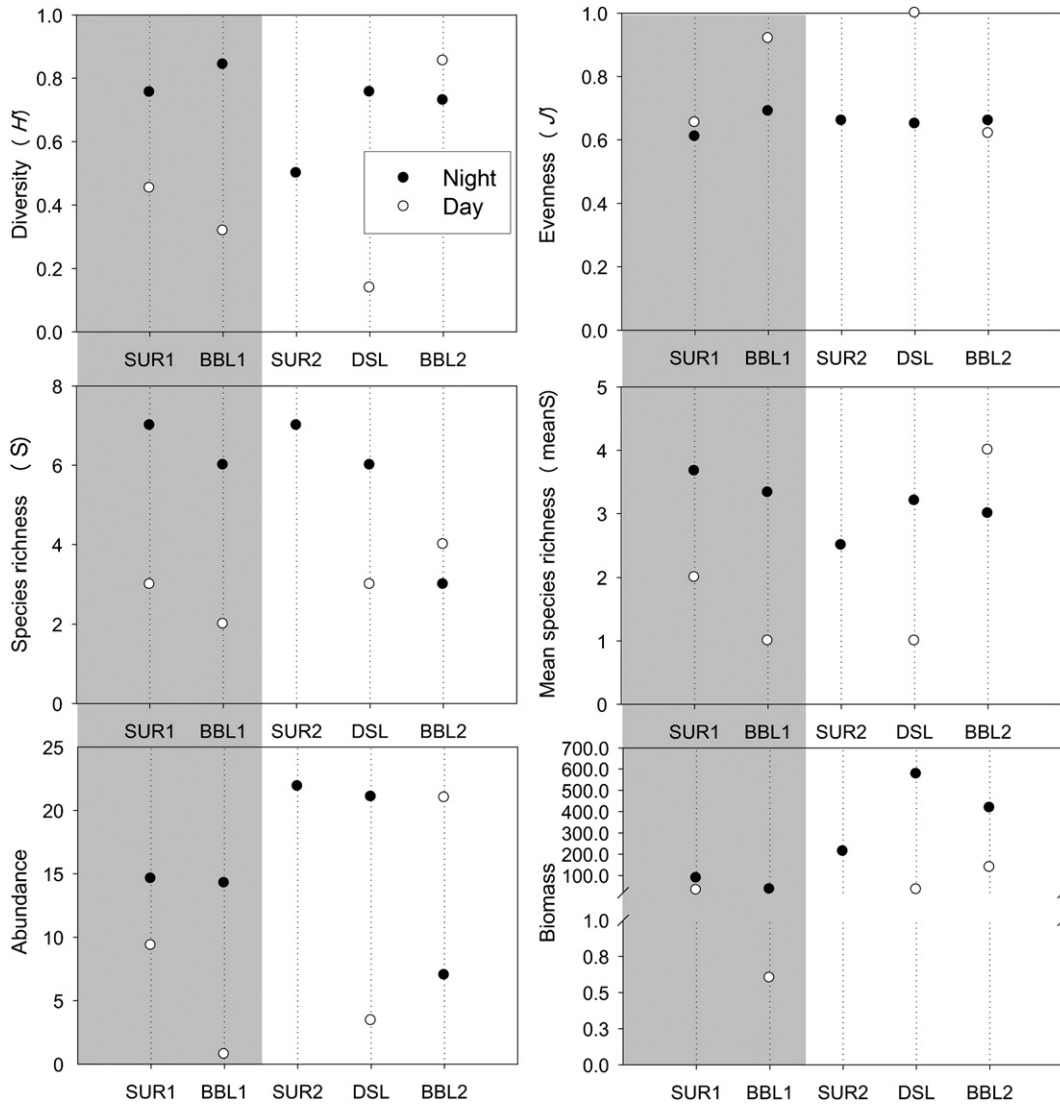
a catch both during the day and night, exclusively in the DSL and BBL sampling, with abundances markedly higher at night, in both cases; however, the abundance was highest at night on SUR2 ( $14 \text{ ind} \cdot \text{Hm}^{-3}$ ). Night abundances of *T. sagittatus* were higher on SUR2 and DSL ( $\sim 2 \text{ ind} \cdot \text{Hm}^{-3}$  in both cases) than on BBL2 ( $0.5 \text{ ind} \cdot \text{Hm}^{-3}$ ); during the day, it only appeared on BOT2 and DSL sampling ( $4$  and  $0.4 \text{ ind} \cdot \text{Hm}^{-3}$ , respectively).

With the exceptions of *A. veranyi* and *S. oweniana*, all other species displayed a general trend, whereby the bottom trawl samples had larger sizes than the pelagic samples (Fig. 5). Individuals of *A. veranyi* with size ranges between 3.0 and 4.5 cm ML were present at all water levels from the shelf-break; however, individuals with sizes smaller than 3.0 cm ML were almost exclusively taken on SUR1 and BBL1, during night sampling. The BBL2 and BOT2 individuals of this squid ranged from 1.5–3.0 cm ML, whereas, those caught on SUR2 and DSL ranged from 1.5–4.0 cm ML; on slope surface waters, the species only occurred at night. The sepiolid *H. dispar* and the squid *H. reversa* showed a similar trend, as they were exclusively taken from slope water levels, appearing both at night and day sampling on DSL, but only in the day on BBL and at night on SUR. With some exceptions, the pattern followed by the ommastrephids *I. coindetii* and *T. sagittatus*, and the sepiolid *S. oweniana*, was also similar. Although *S. oweniana* appeared exclusively in the

shelf-break waters, all three species were only caught at daytime hours on bottom trawl sampling and at night in the pelagic waters (SUR, BBL and DSL). In the two ommastrephid squids, individuals from BOT sampling had larger sizes than those caught in pelagic waters.

#### 4. Discussion

The intensive sampling programme undertaken during the IDEADOS surveys using both bottom and pelagic trawl gears yielded a total of 26 cephalopod species, belonging to 12 families, which accounted for about 40% of the 66 species currently reported in the Mediterranean Sea (Bello, 2008). The species number collected in those two surveys is in agreement with the 27 cephalopods taken between a 200 and 800 m depth during a sampling period of 14 months ( $N = 79$  hauls) in the same study area, using exclusively bottom trawl gears (Quetglas et al., 2000). Although the depth ranges are not the same, both estimates are markedly higher than the 15 species caught at the 450–2200 m depth during different samplings ( $N = 111$  hauls) conducted in the adjacent Catalan Sea between 1985 and 2010 (Fanelli et al., 2012). Other studies carried out in the Catalan Sea reported nine species (number of hauls not specified) between 200 and 550 m (Sánchez et al., 1998) and 13 species ( $N = 105$  hauls) between 200 and 832 m (Sánchez, 1986).



**Fig. 3.** Day and night values of different assemblage metrics (diversity, evenness, species richness, mean species richness, abundance and biomass) from western Mediterranean cephalopod assemblages at different water layers from both the shelf-break (SUR1, BBL1; in grey background) and slope (SUR2, DSL, BBL2; in white background).

These results would indicate that cephalopod diversity is higher in waters around the Balearic Archipelago than in the adjacent Catalan Sea. Notwithstanding the putative effects of the differences in the gears used in all those studies, such results may be related to differences in

biogeographic factors or to the lower fishing intensity in the archipelago than along the coast of the Iberian peninsula (Quetglas et al., 2012).

In accordance with the previous studies, in the Mediterranean (Fanelli et al., 2012), we found seasonal differences at species level in

**Table 3**

Results of factorial ANOVAs used to test the effects of several factors on different ecological indices (abundance, biomass, mean species richness, diversity and evenness) on the cephalopod assemblages identified in the Balearic Sea (western Mediterranean). Model 1 tested the effects of the factors, season, zone and water level for the levels BOT1 and BOT2. Model 2 tested the effects of light and water level for the levels SUR2 and DSL. The significant results are shown in bold.

Effect	Abundance		Biomass		Mean species richness		Diversity		Evenness		
	F	p	F	p	F	p	F	p	F	p	
Model 1											
Intercept	<b>25.32</b>	<b>&lt;10<sup>-3</sup></b>	<b>67.15</b>	<b>&lt;10<sup>-3</sup></b>	<b>404.53</b>	<b>&lt;10<sup>-3</sup></b>	<b>110.41</b>	<b>&lt;10<sup>-3</sup></b>	<b>215.77</b>	<b>&lt;10<sup>-3</sup></b>	
Season	2.24	0.15	<b>14.61</b>	<b>&lt;10<sup>-2</sup></b>	4.17	0.05	1.71	0.20	<10 <sup>-2</sup>	0.97	
Zone	1.76	0.20	<0.01	0.95	1.75	0.20	0.57	0.46	0.43	0.52	
Level	<b>22.87</b>	<b>&lt;10<sup>-3</sup></b>	<b>42.83</b>	<b>&lt;10<sup>-3</sup></b>	<b>80.08</b>	<b>&lt;10<sup>-3</sup></b>	1.31	0.26	<b>11.42</b>	<b>&lt;10<sup>-2</sup></b>	
Season-zone	2.60	0.12	1.67	0.21	0.96	0.34	0.01	0.92	0.10	0.76	
Season-level	2.52	0.12	<b>19.88</b>	<b>&lt;10<sup>-3</sup></b>	0.30	0.59	1.00	0.33	3.13	0.09	
Zone-level	1.47	0.23	0.31	0.58	0.48	0.50	1.17	0.29	1.93	0.18	
Season-zone-level	2.85	0.10	0.06	0.81	1.07	0.31	0.59	0.45	1.23	0.28	
Model 2											
Intercept	<b>14.91</b>	<b>&lt;10<sup>-2</sup></b>	<b>6.71</b>	<b>0.02</b>	<b>57.19</b>	<b>&lt;10<sup>-3</sup></b>	<b>23.38</b>	<b>&lt;10<sup>-3</sup></b>	<b>61.96</b>	<b>&lt;10<sup>-3</sup></b>	
Light	4.16	0.05	<b>4.93</b>	<b>0.04</b>	<b>18.31</b>	<b>&lt;10<sup>-3</sup></b>	<b>10.05</b>	<b>&lt;10<sup>-2</sup></b>	0.20	0.66	
Level	0.09	0.77	1.41	0.25	1.11	0.30	0.16	0.69	1.28	0.29	
Light-level	0.31	0.58	1.56	0.23	0.05	0.82	0.73	0.40	0.40	0.54	

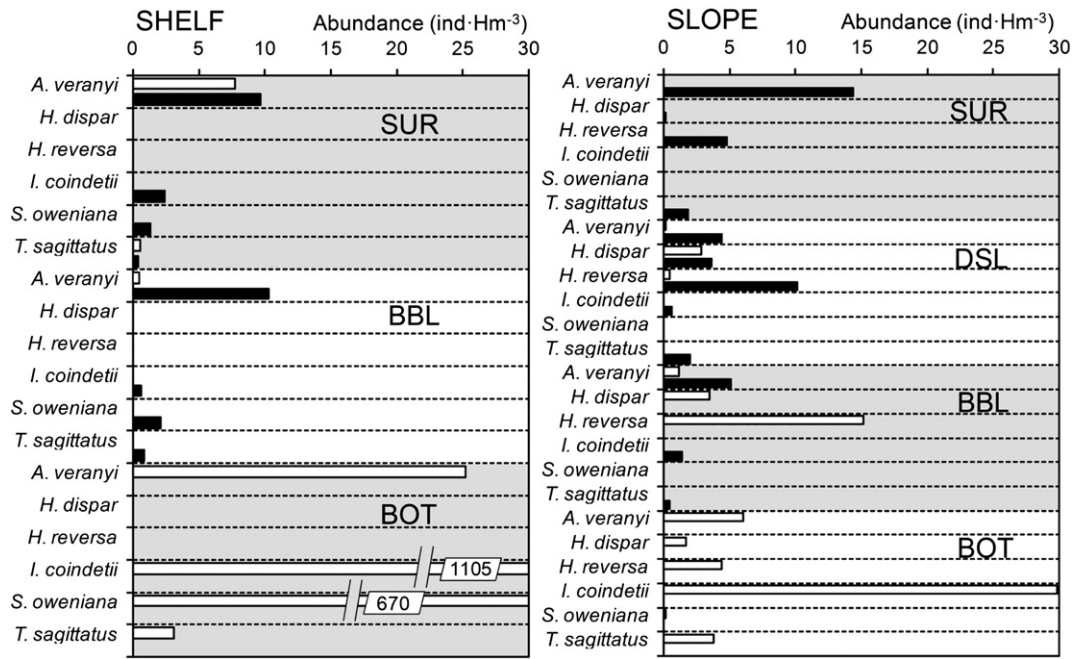


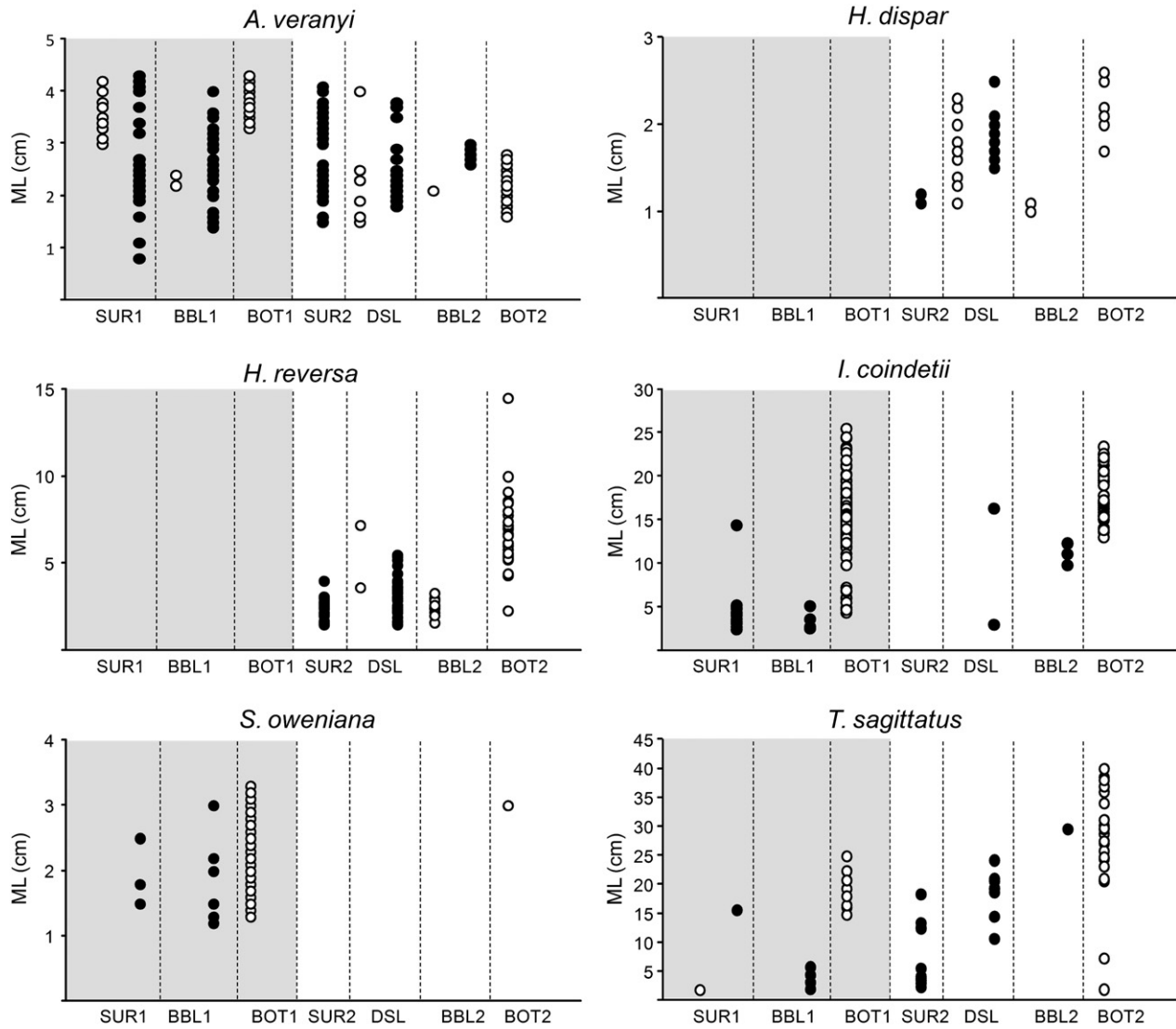
Fig. 4. Day (white bars) and night (dark bars) densities (ind·Hm<sup>-3</sup>) of the most abundant cephalopod species at different water layers from both the shelf-break and slope (SUR, DSL, BBL, BOT). BOT shelf values of *Illex coindetii* and *Sepietta oweniana* are shown in an inset because they are out of the axis range.

terms of abundance and biomass. Nevertheless, the lack of a common seasonal trend for all species suggested that populations were driven by specific life-history characteristics (mainly reproduction) rather than by major environmental forces, affecting most species equally. However, the assemblage metrics of all species combined, showed some general trends at all water levels analysed, in spite of the fact that such trends differed between shelf-break and slope grounds. Although diversity, species richness, abundance and biomass were higher in summer than in autumn on the slope, the inverse trend occurred on the shelf-break. This might be related to differences in the response of shelf and slope organisms to the peak characteristics of spring and autumn productivity of the Mediterranean (Estrada, 1996). Owing to the fast growth rates of cephalopods (Boyle and Rodhouse, 2005), populations from the shelf would benefit from the contemporary autumn peak. By contrast, enhanced slope populations, in summer, would reflect the lag time required to incorporate the spring peak into the deep slope ecosystems, since the main input of primary production into deep waters is the downward flux of material from the epipelagic zone (Miquel et al., 1994). Indeed, Fanelli et al. (2012) found that deep-sea cephalopod abundance from the Catalan Sea was mainly linked to the chlorophyll-*a* concentration recorded one month before, as also to the sampling and river discharge recorded simultaneously. According to these authors, these simultaneous responses corresponded to diel vertical migrators (e.g., ommastrephids, onychoteuthids and histioteuthids), whereas, delayed responses corresponded to species preying on the benthic organisms (e.g., *B. sponsalis* and *N. caroli*). Such contrasting responses were also observed for decapod crustaceans (Fanelli and Cartes, 2008). In the same study area, lag times of several months between the Ebro river discharges and the abundance of the octopus *E. cirrhosa*, which also feeds on benthic prey, have been reported (Lloret et al., 2001).

Comparisons between shelf-break and slope strata showed that most assemblage metrics had similar, low values at the pelagic layers (SUR, DSL, BBL), but they increased abruptly on bottom grounds. The highest diversity, mean species richness, abundance and biomass values were found on the bottom shelf-break grounds. However, biomass from the pelagic layers (SUR, BBL) was higher on the slope than on the shelf-break, which might be related to the low and high rate of vertical

movements, respectively, inferred for those strata from the cluster analysis (see below). The increase of diversity with depth in the water column contrasts with the decreasing trend observed on the Mediterranean bottom grounds for cephalopods (Quetglas et al., 2000), crustaceans (Cartes and Sarda, 1992), fishes (Moranta et al., 1998; Stefanescu et al., 1993) and whole communities (Fanelli et al., 2013; Tselepidis et al., 2000). However, exceptions to such a trend were also reported (Fanelli et al., 2012), which suggested that it might vary depending on the faunal group (Cartes and Sarda, 1993; Stefanescu et al., 1993) or other parameters, such as, season or local oceanographic conditions (Tecchio et al., 2011).

The three groups revealed by clustering might indicate differences in the migratory strategies. The first group consisted exclusively of bottom sampling, most of them from the shelf-break, suggesting little movements in the water column on this stratum. This group was mainly characterised by the benthic octopus *E. cirrhosa* and the squid *I. coindetii*. The huge differences found in the abundances of this squid between the bottom and pelagic layers from the shelf-break, together with the differences in size composition between the bottom and pelagic sampling, concur with the idea of a little vertical movement on the shelf-break. The second cluster group only contained pelagic sampling, both from the shelf-break and slope, indicating only interchanges between the pelagic waters. This group was mostly characterised by the enoploteuthid *A. veranyi* and the lack of size differences among individuals inhabiting the different pelagic layers for this species would suggest movements among such layers. The third cluster group, which contained both bottom and pelagic samplings from the slope, would point to faunal interchanges between these slope domains. The squids *H. reversa* and *Todarodes sagittatus* were the most characteristic species of this group and both seemed to display diel vertical movements. The first species were found both at the bottom and the BBL during the day, but in the adjacent upper pelagic layers (DSL, SUR) during the night. Similarly, the ommastrephid squid *T. sagittatus* occurred in the daytime bottom samples, but was caught in pelagic waters only at night. The presence of nycthemeral migratory species in the diets of *H. reversa* (Quetglas et al., 2010) and *T. sagittatus* (Lordan et al., 2001; Quetglas et al., 1999) further supports the vertical movements of these two squids.



**Fig. 5.** Individual sizes (mantle length, ML) of the most abundant cephalopod species at different water layers from both the shelf-break (SUR1, BBL1, BOT1; in grey background) and slope (SUR2, DSL, BBL2, BOT2; in white background).

There was a consistent, general increase in all assemblage metrics during the night compared to the day, for all the water layers analysed. Such a general increase during the night hours must be at the expense of a decrease in other layers, most likely at the bottom grounds. Although we did not carry out bottom sampling at night to confirm this decrease, diel migrations from the bottom grounds to the epipelagic layers during the night hours are well-known in cephalopods (e.g., Chesalin and Zuyev, 2002; Katugin and Zuev, 2007) and other taxonomic groups such as fishes (e.g., Catul et al., 2011; Olivar et al., 2012) and crustaceans (e.g., Cartes et al., 1993). However, it is also possible that during the daytime hours those remaining cephalopods were scattered across other pelagic layers that we did not sample.

Diel vertical movements of large-sized cephalopods (e.g., *I. coindetii*, *T. sagittatus*, and *H. reversa*) might be basically performed by small-sized, juvenile individuals, given that adults were almost exclusively caught in the bottom waters. This pattern has already been reported for several mesopelagic fishes (Cartes and Stefanescu, 1992; Flynn and Kloser, 2012; Olivar et al., 2012). In our samples, however, such a pattern was not evident for the small-sized species (e.g., *A. veranyi*, *H. dispar*, *S. oweniana*); on the contrary, it seemed that large-sized individuals of *A. veranyi* lived in surface waters during the day, being joined by migratory small-sized individuals at night.

The high abundances of *I. coindetii* at the bottom compared to pelagic waters, especially for large-sized individuals, pointed to marked nektobenthic habits and did not tally with the idea of mature squids being distributed over the whole depth range, undergoing daily vertical migrations (Jereb and Roper, 2010). Our hypothesis was further reinforced by the isotopic analyses of a large set of Mediterranean cephalopods from our study area (Keller et al., 2012; Valls et al., 2014—in this issue), which showed that *I. coindetii* was much closer to the benthic species (e.g., *B. sponsalis*, *O. salutii*, and *Pteroctopus tetracirrhus*) than to the pelagic species (e.g., *Histioteuthis* spp., *A. lesueurii*, and *A. veranyi*).

As aforementioned, during midwater trawling we performed directed sampling, rather than random sampling, which meant that the hauls were targeted at the strongest and widest acoustic sound layers. Despite this, the total cephalopod densities were very low ( $<3 \text{ ind} \cdot \text{Hm}^{-3}$  or  $<1 \text{ kg} \cdot \text{Hm}^{-3}$ ) in all but five species (Table 1). Taking into account the different water layers in both the strata analysed (shelf-break and slope), the densities of the most abundant species were lower than  $30 \text{ ind} \cdot \text{Hm}^{-3}$  in all but two species on the shelf-break bottom grounds (*I. coindetii* and *S. oweniana*). The abundances of these two species on shelf-break bottoms was exceedingly high compared to the rest of the species ( $1105$  and  $670 \text{ ind} \cdot \text{Hm}^{-3}$  for *I. coindetii* and *S. oweniana*,



respectively); however, these values were not the result of taking a large shoal by chance, because the high densities of these two species were usually recorded during the annual spring surveys we carried out in the study area from 2001 on. The low densities of all other species in the water column did not agree with the hypothesis that pelagic species were very abundant, as the stomach contents of teutophagous predators suggested (Bello, 2000; Cherel and Hobson, 2005; Clarke, 1996a; Lansdell and Young, 2007). Nevertheless, it should be taken into account that our sampling was restricted to the 900 m depth and the bathymetric distribution of some species could extend far deeper. The scarcity of pelagic cephalopods in the catches has traditionally been explained by the inefficiency of midwater trawl gears in fishing them compared to bottom trawl gears (Lansdell and Young, 2007; Piatkowski and Welsch, 1991; Vecchione et al., 2010). In our sampling, however, the abundance of the species taken from the slope with the bottom trawl gear, were not higher, but fully comparable to those obtained using the midwater trawl gear (Fig. 4). Although this did not exclude the idea of pelagic cephalopods being very abundant in the water column, as we might be catching only a small fraction of them, it could alternatively indicate that both gears showed comparable efficiencies in catching cephalopods.

To summarise, our study has shed some light on the cephalopod assemblages present in the water column in the Mediterranean. This is of great importance, owing to the currently scarce knowledge on pelagic cephalopods worldwide. The lack of a common seasonal trend of abundance or biomass for all the species suggests that population dynamics are governed by contrasting responses, which may be related to specific life-history characteristics and to major environmental drivers. Nekto-benthic cephalopod assemblages are characterised by markedly higher abundances and diversities than mesopelagic assemblages. Similarly, abundance and diversity have shown a clear pattern of higher values during the night compared to the day, in all the water levels analysed. Our results have also revealed the existence of stratum-related differences in diel migratory strategies, as movements are scarce for the shelf-break cephalopods, but evident in the slope species. Furthermore, such, diel vertical movements may be mainly performed by small-sized, juvenile individuals. As a final major conclusion, species densities in the water column are very low, giving little support to the idea that pelagic cephalopods are very abundant, as the stomach contents of teutophagous predators suggest.

## References

- Bello, G., 2000. How rare is *Histioteuthis bonnellii* (Cephalopoda: Histioteuthidae) in the eastern Mediterranean Sea? *J. Molluscan Stud.* 66, 575–577.
- Bello, G., 2008. Cephalopoda. *Biol. Mar. Mediterr.* 15, 318–322.
- Boyle, P.R., Rodhouse, P.G., 2005. Cephalopods: ecology and fisheries. Blackwell Science Ltd., Oxford.
- Cartes, J.E., Sarda, F., 1992. Abundance and diversity of decapod crustaceans in the deep-Catalan Sea (Western Mediterranean). *J. Nat. Hist.* 26, 1305–1323.
- Cartes, J.E., Sarda, F., 1993. Zonation of deep-sea decapod fauna in the Catalan Sea (Western Mediterranean). *Mar. Ecol. Prog. Ser.* 94, 27–34.
- Cartes, J.E., Stefanescu, C., 1992. Benthopelagic habits of adult specimens of *Lampanyctus crocodilus* (Risso, 1810) (Osteichthyes, Myctophidae) in the western Mediterranean deep slope. *Sci. Mar.* 56, 69–74.
- Cartes, J.E., Sarda, F., Company, J., Leonart, J., 1993. Day–night migrations by deep-sea decapod crustaceans in experimental sampling in the Western Mediterranean Sea. *J. Exp. Mar. Biol. Ecol.* 171, 63–73.
- Catul, V., Gauns, M., Karuppasamy, P.K., 2011. A review on mesopelagic fishes belonging to family Myctophidae. *Rev. Fish Biol. Fish.* 21, 339–354.
- Cherel, Y., Hobson, K.A., 2005. Stable isotopes, beaks and predators: a new tool to study the trophic ecology of cephalopods, including giant and colossal squids. *Proc. Roy. Soc. London B Biol.* 272, 1601–1607.
- Cherel, Y., Ridoux, V., Spitz, J., Richard, P., 2009. Stable isotopes document the trophic structure of a deep-sea cephalopod assemblage including giant octopus and giant squid. *Biol. Lett.* 5, 364–367.
- Chesalin, M.V., Zuyev, G.V., 2002. Pelagic cephalopods of the Arabian Sea with an emphasis on *Sthenoteuthis oualaniensis*. *Bull. Mar. Sci.* 71, 209–221.
- Clarke, M.R., 1996a. The role of cephalopods in the world's oceans: an introduction. *Philos. Trans. R. Soc. B* 351, 979–983.
- Clarke, M.R., 1996b. The role of cephalopods in the world's oceans: general conclusion and the future. *Philos. Trans. R. Soc. B* 351, 1105–1112.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
- Clarke, M.R., Kristensen, T.K., 1980. Cephalopod beaks from stomachs of two northern bottlenosed whales (*Hyperoodon ampullatus*). *J. Mar. Biol. Assoc. U. K.* 60, 151–156.
- Clarke, M.R., Roper, C.F.E., 1998. Cephalopods represented by beaks in the stomach of a sperm whale stranded at Paekakariki, North Island, New Zealand. *S. Afr. J. Mar. Sci.* 20, 129–133.
- Estrada, M., 1996. Primary production in the northwestern Mediterranean. *Sci. Mar.* 60, 55–64.
- Fanelli, E., Cartes, J.E., 2008. Spatio-temporal changes in gut contents and stable isotopes in two deep Mediterranean pandalids: influence on the reproductive cycle. *Mar. Ecol. Prog. Ser.* 355, 219–233.
- Fanelli, E., Cartes, J.E., Papiol, V., 2012. Assemblage structure and trophic ecology of deep-sea demersal cephalopods in the Balearic basin (NW Mediterranean). *Mar. Freshw. Res.* 63, 264–274.
- Fanelli, E., Cartes, J.E., Papiol, V., López-Pérez, C., 2013. Environmental drivers of megafaunal assemblage composition and biomass distribution over mainland and insular slopes of the Balearic Basin (Western Mediterranean). *Deep-Sea Res.* 1 78, 79–94.
- Fernandez, R., Santos, M., Carrillo, M., Tejedor, M., Pierce, G., 2009. Stomach contents of cetaceans stranded in the Canary Islands 1996–2006. *J. Mar. Biol. Assoc. U. K.* 89, 873–883.
- Flynn, A.J., Kloser, R.J., 2012. Cross-basin heterogeneity in lanternfish (family Myctophidae) assemblages and isotopic niches ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) in the southern Tasman Sea abyssal basin. *Deep-Sea Res.* 1 69, 113–127.
- González, M., Sánchez, P., 2002. Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. *Sci. Mar.* 66, 199–208.
- Jereb, P., Roper, C.F.E. (Eds.), 2010. Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Volume 2. Myopsid and Oegopsid Squids. *FAO Species Catalogue for Fishery Purposes*. No. 4, Vol. 2. FAO, Rome, p. 605. 10 colour plates.
- Katugin, O.N., Zuev, N.N., 2007. Distribution of cephalopods in the upper epipelagic north-western Bering Sea in autumn. *Rev. Fish Biol. Fish.* 17, 283–294.
- Keller, S., Quetglas, A., Valls, M., Ordines, F., de Mesa, A., Massuti, E., 2012. Trophic relationships among cephalopod species along the water column inferred from stomach contents and stable isotope analyses. *Cephalopod International Advisory Council Symposium 2012*, Florianópolis, Brazil.
- Lansdell, M., Young, J., 2007. Pelagic cephalopods from eastern Australia: species composition, horizontal and vertical distribution determined from the diets of pelagic fishes. *Rev. Fish Biol. Fish.* 17, 125–138.
- Lloret, J., Leonart, J., Sole, I., Fromentin, J.M., 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. *Fish. Oceanogr.* 10, 33–50.
- Lordan, C., Collins, M.A., Key, L.N., Browne, E.D., 2001. The biology of the ommastrephid squid, *Todarodes sagittatus*, in the north-east Atlantic. *J. Mar. Biol. Assoc. U. K.* 81, 299–306.
- Massuti, E., Olivar, M.P., Monserrat, S., Rueda, L., Oliver, P., 2014. Towards understanding the influence of environmental conditions on demersal resources and ecosystems in the western Mediterranean: Motivations, aims and methods of the IDEADOS project. *J. Mar. Syst.* 138, 3–19 (in this issue).
- Miquel, J.C., Fowler, S.W., Larosa, J., Buatmenard, P., 1994. Dynamics of the downward flux of particles and carbon in the open northwestern Mediterranean Sea. *Deep-Sea Res.* 1 41, 243–261.
- Moranta, J., Stefanescu, C., Massuti, E., Morales-Nin, B., Lloris, D., 1998. Fish community structure and depth-related trends on the continental slope of the Balearic Islands (Algerian basin, western Mediterranean). *Mar. Ecol. Prog. Ser.* 171, 247–259.
- Olivar, M., Bernal, A., Moli, B., Pena, M., Balbin, R., Castellon, A., Miquel, J., Massuti, E., 2012. Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. *Deep-Sea Res.* 1 62, 53–69.
- Piatkowski, U., Welsch, W., 1991. On the distribution of pelagic cephalopods in the Arabian Sea. *Bull. Mar. Sci.* 49, 186–198.
- Piatkowski, U., Pierce, G.J., da Cunha, M.M., 2001. Impact of cephalopods in the food chain and their interaction with the environment: preface. *Fish. Res.* 52, 1.
- Quetglas, A., Alemany, F., Carbonell, A., Merella, P., Sanchez, P., 1999. Diet of the European flying squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) in the Balearic Sea (western Mediterranean). *J. Mar. Biol. Assoc. U. K.* 79, 479–486.
- Quetglas, A., Carbonell, A., Sanchez, P., 2000. Demersal continental shelf and upper slope cephalopod assemblages from the Balearic Sea (north-western Mediterranean) Biological aspects of some deep-sea species. *Estuar. Coast. Shelf Sci.* 50, 739–749.
- Quetglas, A., de Mesa, A., Ordines, F., Grau, A., 2010. Life history of the deep-sea cephalopod family Histioteuthidae in the western Mediterranean. *Deep-Sea Res.* 1 57, 999–1008.
- Quetglas, A., Guijarro, B., Ordines, F., Massuti, E., 2012. Stock boundaries for fisheries assessment and management in the Mediterranean: the Balearic Islands as a case study. *Sci. Mar.* 76, 17–28.
- Romeo, T., Battaglia, P., Peda, C., Perzia, P., Consoli, P., Esposito, V., Andaloro, F., 2012. Pelagic cephalopods of the central Mediterranean Sea determined by the analysis of the stomach content of large fish predators. *Helgol. Mar. Res.* 66, 295–306.
- Roper, C.F.E., 1974. Vertical and seasonal distribution of pelagic cephalopods in the Mediterranean Sea: preliminary report. *Bull. Am. Malacol. Union* 27–30 (May 1974).
- Sánchez, P., 1986. Distribución batimétrica y abundancia de algunos cefalópodos del mar Catalán. *Investig. Pesq.* 50, 237–245.
- Sánchez, P., Belcari, P., Sartor, P., 1998. Composition and spatial distribution of cephalopods in two north-western Mediterranean areas. *S. Afr. J. Mar. Sci.* 20, 17–24.

- StatSoft, Inc., 2004. STATISTICA (data analysis software system), version 7. [www.statsoft.com](http://www.statsoft.com).
- Stefanescu, C., Lloris, D., Rucabado, J., 1993. Deep-sea fish assemblages in the Catalan Sea (Western Mediterranean) below a depth of 1000-m. *Deep-Sea Res.* 140, 695–707.
- Tecchio, S., Ramirez-Llodra, E., Sarda, F., Company, J.B., 2011. Biodiversity of deep-sea demersal megafauna in western and central Mediterranean basins. *Sci. Mar.* 75, 341–350.
- Tselepidis, A., Papadopoulou, K.N., Podaras, D., Plaiti, W., Koutsoubas, D., 2000. Macrobenthic community structure over the continental margin of Crete (South Aegean Sea, NE Mediterranean). *Prog. Oceanogr.* 46, 401–428.
- Valls, M., Sweeting, C.J., Olivar, M.P., Fernández de Puelles, M.L., Pasqual, C., Polunin, N.V.C., Quetglas, A., 2014. Structure and dynamics of food webs along the water column on shelf and slope grounds from the western Mediterranean. *J. Marine Syst.* 138, 171–181 (in this issue).
- Van de Putte, A.P., Jackson, G.D., Pakhomov, E., Flores, H., Volckaert, F.A., 2010. Distribution of squid and fish in the pelagic zone of the Cosmonaut Sea and Prydz Bay region during the BROKE-West campaign. *Deep-Sea Res. II* 57, 956–967.
- Vecchione, M., Pohle, G., 2002. Midwater cephalopods in the western North Atlantic Ocean off Nova Scotia. *Bull. Mar. Sci.* 71, 883–892.
- Vecchione, M., Young, R.E., Piatkowski, U., 2010. Cephalopods of the northern Mid-Atlantic Ridge. *Mar. Biol. Res.* 6, 25–52.