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

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ABSTRACT

The structure and dynamics of cephalopod assemblages at different bathymetric strata from the surface to bottom grounds down to 900 m depth in the western Mediterranean were analysed. Data were collected both on the shelf-break and slope during summer and early autumn surveys using a mid-water trawl and a bottom trawl gear to catch pelagic and nektobenthic species, respectively. 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 was taken. Concerning abundance, biomass and frequency of occurrence, we did not found a common seasonal trend for all species, suggesting that population dynamics are not governed by major environmental drivers. Most assemblage metrics (e.g. diversity, species richness, abundance and biomass) showed similar, low values on pelagic layers compared to bottom grounds. In general, assemblage metrics were lower in summer than in autumn on the shelf-break, while showing the inverse seasonal trend on the slope. There was a clear general increase in all metrics during the night compared to daylight. Cluster results revealed differences in diel migratory strategies by stratum, vertical movements being scarce on shelf-break species but intense on slope species.

Keywords: Cephalopod fisheries; Population density; Pelagic environment; Nycthemeral rhythms; Mediterranean Sea

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 importance, 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, shelf species only represent a small percentage (15%) of all cephalopod genera (Clarke, 1996b).

According to most specialists, the dearth of information on oceanic species reflects the inability of present day sampling equipments to catch them, since stomach content analyses of their predators suggest that cephalopods are very abundant along the water column (Bello, 2000; Cherel and Hobson, 2005; Clarke, 1996a; Lansdell and Young, 2007). Indeed, the number of beaks in stomach contents of some large predators such as whales can be counted by thousands (e.g. Clarke and Roper, 1998; Clarke and Kristensen, 1980; 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 paralarvae or cephalopod early life stages and, to a lesser extent, the use of traditional mid-water trawl gears. To overcome the inefficiency of fishing gears, three large pelagic fish species were used as samplers to analyse the species composition and horizontal and vertical distribution of pelagic cephalopods from the eastern Australia (Lansdell and Young, 2007). Planktonic gears collecting paralarvae and small juveniles were used to investigate the distribution of pelagic cephalopods from the surface down to 1000 m depth in the Arabian Sea (Piatkowski and Welsch, 1991) and the distribution in the upper 200 m from Southern Ocean waters (Van de Putte et al., 2010). Examples of pelagic samplings using mid-water trawls to collect adult and juvenile individuals are currently very scarce, such as 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 know (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 (1974) analysed the vertical and seasonal distribution of larval and small juvenile pelagic cephalopods with discrete-depth tows both day and night from the surface down to 1000 m depth. In the second case, Romeo et al. (2012) studied the pelagic cephalopods of the central Mediterranean analyzing the stomach content of large fish predators. To our knowledge, there is not currently a single work dealing with the species composition and distribution of adult pelagic cephalopods along the water column using mid-water trawl gears in the Mediterranean. In this paper, we analysed the structure and dynamics of cephalopod assemblages at different bathymetric strata from the surface to bottom grounds down to 900 m depth. The data used in this study were collected during the IDEADOS surveys (www.ba.ieo.es/ideados), primarily addressed to investigate spatio-temporal differences in the composition and structure of nektobenthic communities in the western Mediterranean (Massutí et al., 2013). The availability of day and night samplings allowed comparisons of day-night cephalopod abundances and nycthemeral movements along the water column. Such comparisons are of prime importance to investigate mid-water 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 on 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 zones, a relatively small area was repeatedly sampled throughout the day using the following gears: 1) commercial “huelvano”-type bottom trawl with 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) double-warp modified commercial mid-water trawl, with standard pelagic trawl doors (otter boards), graded-mesh netting to the cod-end (10 mm) and estimated mouth opening of 280 and 112 m^2 during the autumn and summer surveys, respectively. Whereas bottom trawl samplings were only done during daytime hours, mid-water trawl samples were taken both during the day and night, which allowed comparisons of day-night cephalopod abundances and nycthemeral movements along the water column. The mean towing speeds of the bottom trawl and mid-water trawl were 2.5 and 4.0 knots, respectively. Pelagic samplings were not performed randomly, but using directed sampling, which means that the hauls were targeted at the strongest and widest acoustic sound layers. The acoustic layers were detected with a Simrad EK60 echosounder 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., 2013; Olivar et al., 2012).

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

For analysis, abundance and biomass were standardized to the number of individuals and weight in kilograms, respectively, per Hm^3 ($ind \cdot Hm^{-3}$ and $kg \cdot Hm^{-3}$). The volumes were calculated using the mouth area of the nets and the distance traveled by each haul. Together with 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

Cephalopod assemblage structure was analyzed through hierarchical agglomerative and unweighted arithmetic average clustering (CLUSTER procedure; Clarke and Gorley, 2006) by calculating Bray-Curtis similarity resemblance matrices of 4th root-transformed abundance data. The SIMPER procedure was applied to identify the species that characterize each group and 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 bathymetric stratum (shelf-break, slope), season (summer, autumn) and light (day, night; except BOT samples): 1) Shannon diversity index (*H’*); 2) Pielou’s evenness index (*J’*); 3) mean species richness (*meanS*); and 4) total species richness (*S*). Abundance, biomass and those four ecological indices are thereafter 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 samples allowed analyzing the effects of season, location and layer; in the second case, differences related to light and layer were tested using SUR2 and DSL samplings. In both cases, differences were tested by means of a factorial ANOVA using STATISTICA version 7 (StatSoft Inc., 2004).

To detect nycthemeral movements at species level, day and night abundance values of the most abundant species throughout the water column (SUR, DSL, BBL; only day for BOT) both on the shelf-break and slope, were analyzed. Moreover, the individual sizes of these species were also analyzed by water level and light based on the reasoning that similar size ranges might indicate movements among different levels. 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 were caught (Table 1). The most frequent species was *T. sagittatus* (F=47%) followed by *A. veranyi* (F=41%), *I. coindetii* (F=40%) and *H. reversa* (F=31%); four species (*A. lesueurii, O. vulgaris, O. banksii* and *G. armata*) only appeared once (F=1.4%). In terms of abundance, *I. coindetii* was by far the most abundant species (50.0 ind·Hm^{-3}) followed by *S. oweniana* (28.9 ind·Hm^{-3}) and *A. media* (8.4 ind·Hm^{-3}); the total abundance of all other species was <3 ind·Hm^{-3}. The dominance of *I. coindetii* was even more pronounced in terms of biomass (68.8 kg·Hm^{-3}), since the second and third most important species only accounted for 12.6 (*L. forbesii*) and 7.4 (*T. sagittatus*) kg·Hm^{-3}; with the only exception of *E. cirrhosa* (3.2 kg·Hm^{-3}) and *S. oweniana* (2.2 kg·Hm^{-3}), all other species had biomass values ≤1 kg·Hm^{-3}.

Concerning abundance, biomass and frequency of occurrence, there was not a 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. coindetii, O. salutii, R. minor*), whereas others showed the inverse pattern (*H. dispar, H. reversa, P. tetracirrhus* and *S. orbignyana*). For some species, the frequency of occurrence did not show significant differences between seasons (*B. sponsalis, L. forbesii, N. caroli, O. calypso, R. macrosoma, T. sagittatus*). Finally, some species (excluding those appearing only once) were exclusively taken during one sampling season (*A. media, A. lichtensteinii, C. veranyi, S. unicirrhus, T. 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 autumn samplings with a mean abundance of 13.2 ind·Hm^{-3}. The abundance and biomass of *I. coindetii* increased from 10.3 ind·Hm^{-3} and 39.3 kg·Hm^{-3} in summer to 72.8 ind·Hm^{-3} and 82.0 kg·Hm^{-3} in autumn. In other species, abundance or biomass values were clearly higher in summer than in autumn (*L. forbesii*, 23.7 vs 7.5 kg·Hm^{-3}; *S. oweniana*, 66.8 vs 7.1 ind·Hm^{-3}; *T. sagittatus*, 14.7 vs 4.1 kg·Hm^{-3}).

The cluster analysis revealed three main groups at a similarity cut-off value near 20 (Fig. 1). Group A was mainly characterized by bottom trawl samplings carried out on continental shelf-break grounds, independently of season and zone, together with a set of three summer samplings on slope depths of Cabrera. Group B was exclusively composed by pelagic samplings, primarily from the shelf-break (SUR1, BBL1), but also by a set of autumn slope samplings (with the only exception of a summer SUR2 sampling). Finally, group C contained bottom trawl samplings and summer pelagic samplings (SUR2, DSL, BBL2) from the slope. Similarity percentage analysis (Table 2) showed that group A was mainly characterized 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 *B. sponsalis* (15%). Average dissimilarities among these three groups were higher than 80%: A vs B (87.8), A vs C (85.9%) and B vs C (80.3%).

3.2. Assemblage metrics

For each level of the water column, all assemblage metrics were analyzed by bathymetric stratum (shelf-break, slope), season (summer, autumn) and light (day, night). Diversity was higher in summer than in autumn in all water levels except BBL1 (Fig. 2). The highest diversity was found on BOT1 and, with the only exception of summer BBL1 samplings, there was an increasing trend with depth both on the shelf-break and 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, evenness showed a marked increase with depth on the slope from DSL (0.3) to BOT2 (0.9). On the shelf-break, total species richness was higher in autumn than in summer, but this pattern inverted on the slope. Total species richness ranged from 11 to 15 at BOT grounds, but from 3 to 6 in all other water levels. Mean species richness was higher in summer than in autumn in 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, abundance and biomass values were higher in summer than in autumn. However, this did not apply to 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 on all water levels but 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 daylight in all water levels but BBL2 (Fig. 3). Diversity at night was similar at all water levels, except SUR2 (0.50), ranging from 0.73 to 0.84. Except BBL2 (0.85), diversity during the day ranged from 0.14 to 0.45 at DSL and SUR1, respectively; no species was taken during daytime at SUR2. Evenness at night showed similar values in 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, night total species richness values were twofold higher than those found during daylight, with the exception of BBL2 (4 and 3 species at daylight and night, respectively). Mean species richness followed the same trend as total species richness, with markedly higher values at night than during daylight in all cases except BBL2, which in fact had the highest value (4 species during daytime). Abundance and biomass were also clearly higher at night in all levels, except abundance at BBL2 (21 and 7 ind·Hm^{-3} at day and night respectively).

The first ANOVA, testing the effects of season, zone and level of the water column on BOT samplings, showed significant differences due to level for the metrics 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 samplings, 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 along the different water levels both on the shelf-break and slope were computed to analyze nycthemeral movements (Fig. 4). On those water levels with samplings at the two time periods (all but BOT), abundances were in general markedly higher at night than during daytime both on the shelf-break and slope. Considering the shelf-break, the highest abundances corresponded to *I. coindetii*, *S. oweniana* and *A. veranyi* taken on bottom daylight samplings (1105, 670 and 25 ind·Hm^{-3} respectively). The two former species, *I. coindetii* and *S. oweniana,* did not occur at daylight samplings in any other water level, appearing exclusively in night samplings at SUR1 and BBL1 with abundances lower than 2.5 ind·Hm^{-3}. By contrast, *A. veranyi* was taken in all other water levels both at daylight and night and, whereas abundances on SUR1 were similar (8 and 10 ind·Hm^{-3}), night abundances on BBL1 were clearly higher at night than during daytime (10 vs 0.5 ind·Hm^{-3}). Finally, the squid *T. sagittatus* was taken on BOT1 daytime samplings, BBL1 night samplings and both daylight and night SUR1 samplings, in all cases with abundances lower than 3.5 ind·Hm^{-3}.

Referring to the slope, no species was taken during daytime SUR2 samplings. The highest abundance corresponded again to *I. coindetii* on daytime bottom samplings (~30 ind·Hm^{-3}); this squid did not appear on daytime samplings at any other water level, being exclusively taken at night on DSL and BBL2 levels with abundances lower than 1.5 ind·Hm^{-3}. Daytime abundance of *H. reversa* was highest on BBL2 samplings (15 ind·Hm^{-3}), decreased on adjacent upper (DSL: 0.5 ind·Hm^{-3}) and lower (BOT2: 4.4 ind·Hm^{-3}) water levels, and did not appear on SUR2. At night, *H. reversa* only occurred on DSL and SUR2 levels, its abundance being highest in DSL samplings (10 ind·Hm^{-3}). Interestingly, the sepiolid *H. dispar* followed the same pattern as *H. reversa*. The enoploteuthid *A. veranyi* was taken during both daylight and night exclusively in DSL and BBL samplings, with abundances markedly higher at night in both cases; however, the abundance was highest at night on SUR2 (14 ind·Hm^{-3}). Night abundances of *T. sagittatus* were higher on SUR2 and DSL (~2 ind·Hm^{-3} in both cases) than on BBL2 (0.5 ind·Hm^{-3}); during daytime, it only appeared on BOT2 and DSL samplings (4 and 0.4 ind·Hm^{-3} respectively).

With the only exceptions of *A. veranyi* and *S. oweniana*, all other species displayed a general trend whereby bottom trawl samples had larger sizes than pelagic samples (Fig. 5). Individuals of *A. veranyi* with size ranges between 3.0 and 4.5 cm ML were present in 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 samplings. BBL2 and BOT2 individuals of this squid ranged 1.5-3.0 cm ML, whereas those caught on SUR2 and DSL ranged 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, since they were exclusively taken on slope water levels, appearing both at night and daylight samplings on DSL, but only at daylight on BBL and at night on SUR. With some exception, the pattern followed by the ommastrephids *I. coindetii* and *T. sagittatus*, and the sepiolid *S. oweniana*, was also similar. Although *S. oweniana* appeared exclusively on shelf-break waters, all three species were only caught at daytime hours on bottom trawl samplings and at night on pelagic waters (SUR, BBL and DSL). In the two ommastrephid squids, individuals from BOT samplings had larger sizes than those caught on pelagic waters.

4. Discussion

The intensive sampling program undertaken during the IDEADOS surveys using both bottom and pelagic trawl gears yielded a total of 26 cephalopod species belonging to 12 families, which account 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 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). Despite the depth ranges are not fully comparable, both estimates are markedly higher than the 15 species caught at 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 9 species (number of hauls not specified) between 200-550 m (Sánchez et al., 1998) and 13 species (N=105 hauls) between 200 and 832 m (Sánchez, 1986). 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 differences in the gears used in all those studies, such results could be related to differences in biogeographic factors or to the lower fishing intensity in the archipelago than along the peninsular coast (Quetglas et al., 2012).

In accordance with previous studies in the Mediterranean (Fanelli et al., 2012), we found seasonal differences at species level in terms of abundance and biomass. Nevertheless, the lack of a common seasonal trend for all species suggests that populations are driven by specific life-history characteristics (mainly reproduction) rather than by major environmental forces affecting most species equally. However, assemblage metrics of all species combined showed some general trends for all water levels analyzed, in spite that such trends differed between shelf-break and slope grounds. Whereas 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 spring and autumn productivity peaks characteristics 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 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 chlorophyll-a concentration recorded one month before and simultaneously to sampling and to river discharge recorded simultaneously. According to these authors, simultaneous responses corresponded to diel vertical migrators (e.g. ommastrephids, onychoteuthids, histioteuthids), whereas delayed responses corresponded to species preying on benthic organisms (e.g. *Bathypolypus sponsalis, Neorossia 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 *Eledone cirrhosa,* which also feeds on benthic preys, have also been reported (Lloret et al., 2001).

Comparisons between shelf-break and slope strata showed that most assemblage metrics had similar, low values at pelagic layers (SUR, DSL, BBL) but increased abruptly on bottom grounds. The highest diversity, mean species richness, abundance and biomass values were found on bottom shelf-break grounds. However, biomass from pelagic layers (SUR, BBL) were 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 along the water column contrasts with the decreasing trend observed on 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; Tselepides et al., 2000). However, exceptions to such trend have also been reported (Fanelli et al. 2012), which suggests that it might vary depending on the faunal group (Stefanescu et al., 1993; Cartes and Sarda, 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 migratory strategies. The first group exclusively consisted of bottom samplings, most of them from the shelf-break, suggesting scarce movements along the water column on this stratum. This group was mainly characterized by the benthic octopus *Eledone cirrhosa* and the squid *Illex coindetii*. The huge differences found in the abundances of this squid between bottom and pelagic layers from the shelf-break, together with the differences in size composition between bottom and pelagic samplings, agree with the idea of scarce vertical movements on the shelf-break. The second cluster group only contained pelagic samplings both from the shelf-break and slope, indicating interchanges among pelagic waters exclusively. This group was mostly characterized by the enoploteuthid *Abralia veranyi* and the lack of size differences among populations 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 *Histioteuthis reversa* and *Todarodes sagittatus* were the most characteristic species of this group and both seem to display diel vertical movements. The first species were found both at the bottom and the BBL during the day, but in adjacent upper pelagic layers (DSL, SUR) during the night. Similarly, the ommastrephid squid *T. sagittatus* occurred in 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.

There was a consistent, general increase in all assemblage metrics during the night compared to daylight for all water layers analyzed. Such a general increase during night hours must be at the expense of a decrease in other layers, most likely at bottom grounds. Although we did not carry out night bottom samplings to confirm this decrease, diel migrations from bottom grounds to epipelagic layers during 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 daytime hours those remaining cephalopods were scattered across other pelagic layers we neither sampled.

Diel vertical movements of large-sized cephalopods (e.g. *I. coindetii T. sagittatus, H. reversa*) might be basically performed by small-sized, juvenile individuals, given that adults were almost exclusively caught on 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 small-sized species (e.g. *A. veranyi, H. dispar, S. oweniana*); on the contrary, it seems that large-sized individuals of *A. veranyi* live in surface waters during the day, being joined by migratory small-sized individuals at night. The high abundances of *I. coindetii* on the bottom compared to pelagic waters, especially for large-sized individuals, points to marked nektobenthic habits and do not tally with the idea of mature squids being distributed over the whole depth range and undergoing daily vertical migrations (Jereb and Roper, 2010). Our hypothesis is further reinforced by isotopic analyses of a large set of Mediterranean cephalopods from our study area (Keller et al., 2012; Valls et al., 2013), which showed that *I. coindetii* was much closer to benthic species (e.g. *Bathypolypus sponsalis, Octopus salutii, Pteroctopus tetracirrhus*) than to pelagic species (e.g. *Histioteuthis* spp.*, Ancistrocheirus lesueurii, A. veranyi*).

As aforementioned, during the mid-water trawling we performed directed sampling, rather than random sampling, which means that the hauls were targeted at the strongest and widest acoustic sound layers. Despite this, total cephalopod densities were very low (<3 ind·Hm^{-3} or <1 kg·Hm^{-3}) in all but five species (Table 1). Taking into account the different water layers at both strata analyzed (shelf-break and slope), the densities of the most abundant species was lower than 30 ind·Hm^{-3} in all but two species on shelf-break bottom grounds (*Illex coindetii* and *Sepietta oweniana*). The abundances of these two species on shelf-break bottoms were exceedingly high compared to the rest of species (1105 and 670 ind·Hm^{-3} for *I. coindetii* and *S. oweniana*, respectively); however, these values are not the result of taking a large shoal by chance because high densities of these two species are usually recorded during the annual spring surveys we carry out in the study area from 2001 on. The low densities of all other species along the water column do not agree with the hypothesis of pelagic species being very abundant, as the stomach contents of teutophagous predators suggest (Bello, 2000; Cherel and Hobson, 2005; Clarke, 1996a; Lansdell and Young, 2007). Nevertheless, it should be taken into account that our samplings were restricted to the 900 m depth and the bathymetric distribution of some species may extend far deeper. The scarcity of pelagic cephalopods in catches has traditionally been explained by the inefficiency of mid-water trawl gears in fishing them compared to bottom trawl gears (Lansdell and Young, 2007; Piatkowski and Welsch, 1991; Vecchione et al., 2010). In our samplings, however, the abundances of species from the slope taken with the bottom trawl gear were not higher, but fully comparable, to those obtained using the mid-water trawl gear (Fig. 4). Although this does not exclude the idea of pelagic cephalopods being very abundant along the water column, as we might be taking only a small fraction of the actually present, it could alternatively indicate that both gears showed comparable efficiencies in catching cephalopods.

To summarize, our study has shed some light on the cephalopod assemblages present along the water column in the Mediterranean, which knowledge is currently very scarce. First, the lack of a common seasonal trend of abundance or biomass for all species suggests that population dynamics are governed by specific life-history characteristics rather than by major environmental drivers. Second, most assemblage metrics (e.g. abundance, biomass, diversity) show similar, low values on pelagic layers compared to bottom grounds. Third, there is a general increase in all those metrics during the night for all the water levels analyzed. Fourth, there seems to be differences in diel migratory strategies depending on the stratum, movements being scarce on the shelf-break but evident on the slope. Fifth, diel vertical movements might be mainly performed by small-sized, juvenile individuals. Finally, species densities along the water column are very low, giving little support to the idea that pelagic cephalopods are very abundant as the stomach contents of teuthophagous predators suggest.

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Table 1

Total and seasonal (summer, autumn) abundance (Ab; ind·Hm^{-3}), biomass (Bm; kg·Hm^{-3}) and frequency of occurrence (F; %) of all cephalopod species taken in samplings developed along the water column in the Balearic Sea (western Mediterranean).

		Summer			Autumn			Total		
Species	Family	Ab	Bm	F	Ab	Bm	F	Ab	Bm	F
Abralia veranyi	Enoploteuthidae	3.996	0.941	33.333	1.416	0.034	51.613	2.358	0.316	41.429
Alloteuthis media	Loliginidae	–	–	–	13.186	1.095	19.355	8.371	0.754	8.571
Ancistrocheirus lesueurii	Ancistrocheiridae	0.012	0.120	2.564	–	–	–	0.004	0.037	1.429
Ancistroteuthis lichtensteinii	Onychoteuthidae	0.143	0.225	10.256	–	–	–	0.052	0.070	5.714
Bathypolypus sponsalis	Octopodidae	0.791	1.706	17.949	0.356	0.693	16.129	0.515	1.008	17.143
Chiroteuthis veranii	Chiroteuthidae	0.062	0.050	5.128	–	–	–	0.023	0.016	2.857
Eledone cirrhosa	Octopodidae	3.570	6.907	23.077	1.159	1.517	25.806	2.039	3.193	24.286
Heteroteuthis dispar	Sepiolidae	0.742	0.068	25.641	0.006	<0.001	3.226	0.274	0.021	15.714
Histioteuthis bonnellii	Histioteuthidae	0.023	0.018	5.128	–	–	–	0.009	0.006	2.857
Histioteuthis reversa	Histioteuthidae	1.766	1.502	38.462	0.209	0.432	22.581	0.778	0.765	31.429
Illex coindetii	Ommastrephidae	10.356	39.310	33.333	72.816	82.050	48.387	50.006	68.758	40.000
Loligo forbesiii	Loliginidae	4.439	23.715	20.513	1.083	7.519	19.355	2.309	12.556	20.000
Neorossia caroli	Sepiolidae	0.070	0.049	2.564	0.552	0.012	3.226	0.376	0.024	2.857
Octopus salutii	Octopodidae	0.156	0.843	5.128	0.316	1.002	16.129	0.258	0.953	10.000

Octopus vulgaris	Octopodidae	0.006	0.080	2.564	–	–	–	0.002	0.025	1.429
Onychoteuthis banksii	Onychoteuthidae	–	–	–	0.020	0.206	3.226	0.013	0.142	1.429
Opisthoteuthis calypso	Opisthoteuthidae	0.064	0.068	2.564	0.054	0.097	3.226	0.058	0.088	2.857
Pteroctopus tetracirrhus	Octopodidae	0.241	2.420	15.385	0.027	0.021	3.226	0.105	0.767	10.000
Rossia macrosoma	Sepiolidae	1.922	0.619	15.385	0.820	0.328	16.129	1.222	0.419	15.714
Rondeletiola minor	Sepiolidae	3.041	0.084	10.256	0.503	0.151	19.355	1.430	0.130	14.286
Scaeurgus unicirrhus	Octopodidae	0.114	0.012	7.692	–	–	–	0.042	0.004	4.286
Sepia orbignyana	Sepiidae	0.740	0.818	15.385	0.017	0.016	3.226	0.281	0.265	10.000
Sepietta oweniana	Sepiolidae	66.784	5.751	20.513	7.098	0.657	25.806	28.895	2.241	22.857
Galiteuthis armata	Cranchiidae	0.027	0.003	2.564	–	–	–	0.010	0.001	1.429
Todaropsis eblanae	Ommastrephidae	–	–	–	0.046	0.020	6.452	0.029	0.013	2.857
Todarodes sagittatus	Ommastrephidae	0.935	14.691	48.718	0.315	4.149	45.161	0.541	7.428	47.143

Table 2

Similarity percentages (species contributions) within groups determined from 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 Figure 1. Values between brackets below the groups are the average similarity within group. For each group, the three most important species are shown in bold.

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

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) from 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. Significant results are shown in bold.

		Abundance		Biomass		Mean species richness		Diversity		Evenness	
	Effect	F	p	F	p	F	p	F	p	F	p
Model 1	Intercept	**25.316**	**0.000**	**67.146**	**0.000**	**404.535**	**0.000**	**110.409**	**0.000**	**215.772**	**0.000**
	Season	2.244	0.146	14.609	0.001	4.174	0.051	1.713	0.202	0.001	0.973
	Zone	1.762	0.196	0.004	0.951	1.752	0.197	0.571	0.457	0.426	0.521
	Level	**22.869**	**0.000**	**42.831**	**0.000**	**80.080**	**0.000**	1.312	0.263	**11.425**	**0.003**
	Season-zone	2.596	0.119	1.672	0.207	0.957	0.337	0.010	0.920	0.097	0.758
	Season-level	2.523	0.124	**19.880**	**0.000**	0.299	0.589	1.001	0.326	3.130	0.090
	Zone-level	1.475	0.235	0.310	0.582	0.477	0.496	1.170	0.289	1.934	0.178
	Season-zone-level	2.855	0.103	0.059	0.810	1.073	0.310	0.587	0.451	1.228	0.279
Model 2	Intercept	**14.908**	**0.001**	**6.712**	**0.017**	**57.186**	**0.000**	**23.383**	**0.000**	**61.958**	**0.000**
	Light	4.165	0.055	**4.930**	**0.038**	**18.313**	**0.000**	**10.055**	**0.005**	0.203	0.664
	Level	0.090	0.767	1.413	0.249	1.113	0.304	0.165	0.689	1.279	0.291
	Light-level	0.311	0.583	1.557	0.226	0.055	0.817	0.734	0.402	0.398	0.545

FIGURE CAPTIONS

Figure 1. Cluster analysis of samples (N=52) using Bray-Curtis similarity matrix after four root transformation 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).

Figure 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).

Figure 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).

Figure 4. Day (white bars) and night (dark bars) densities (ind·Hm^{-3}) 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.

Figure 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).

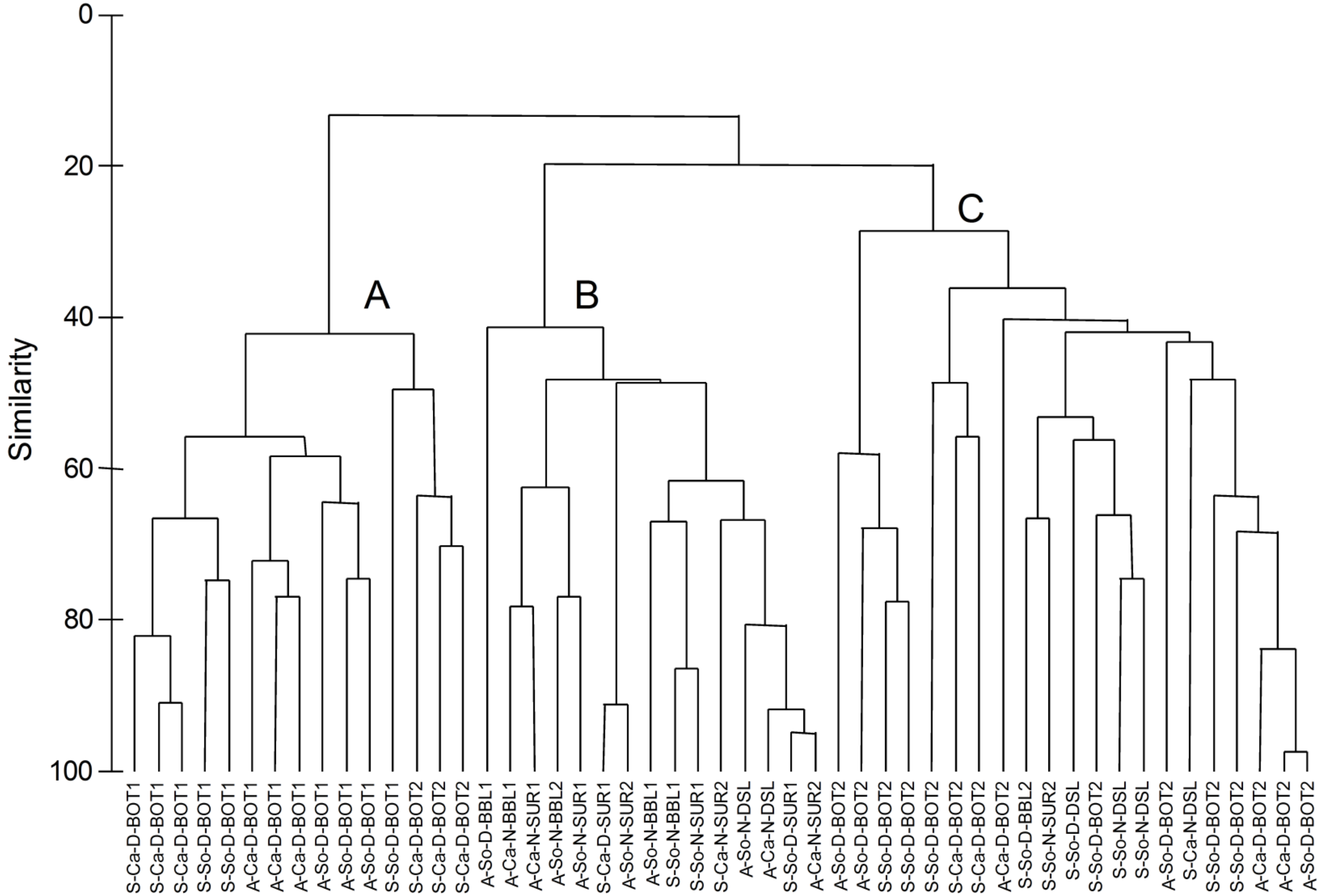
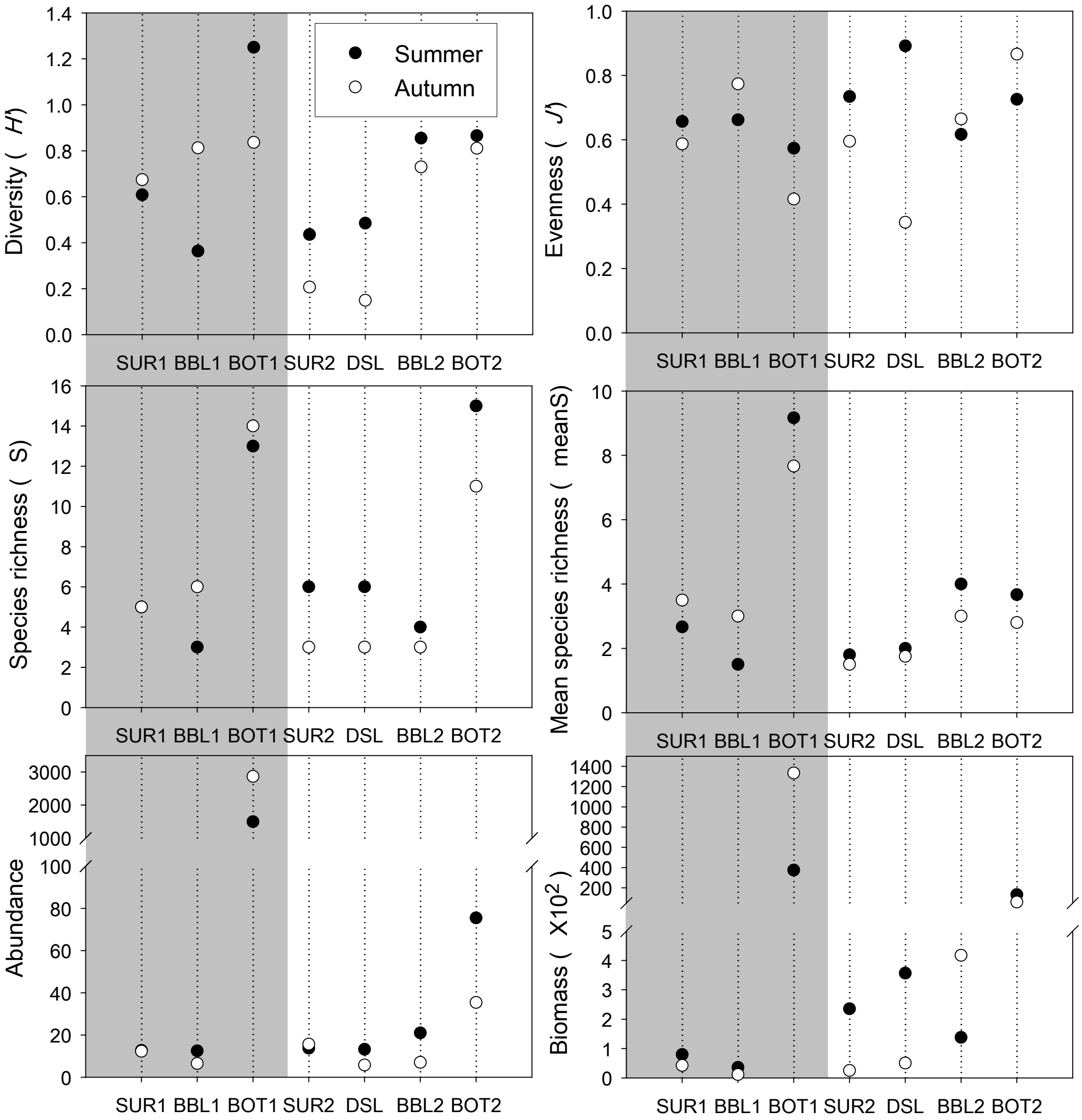


Fig. 1. Quetglas et al.



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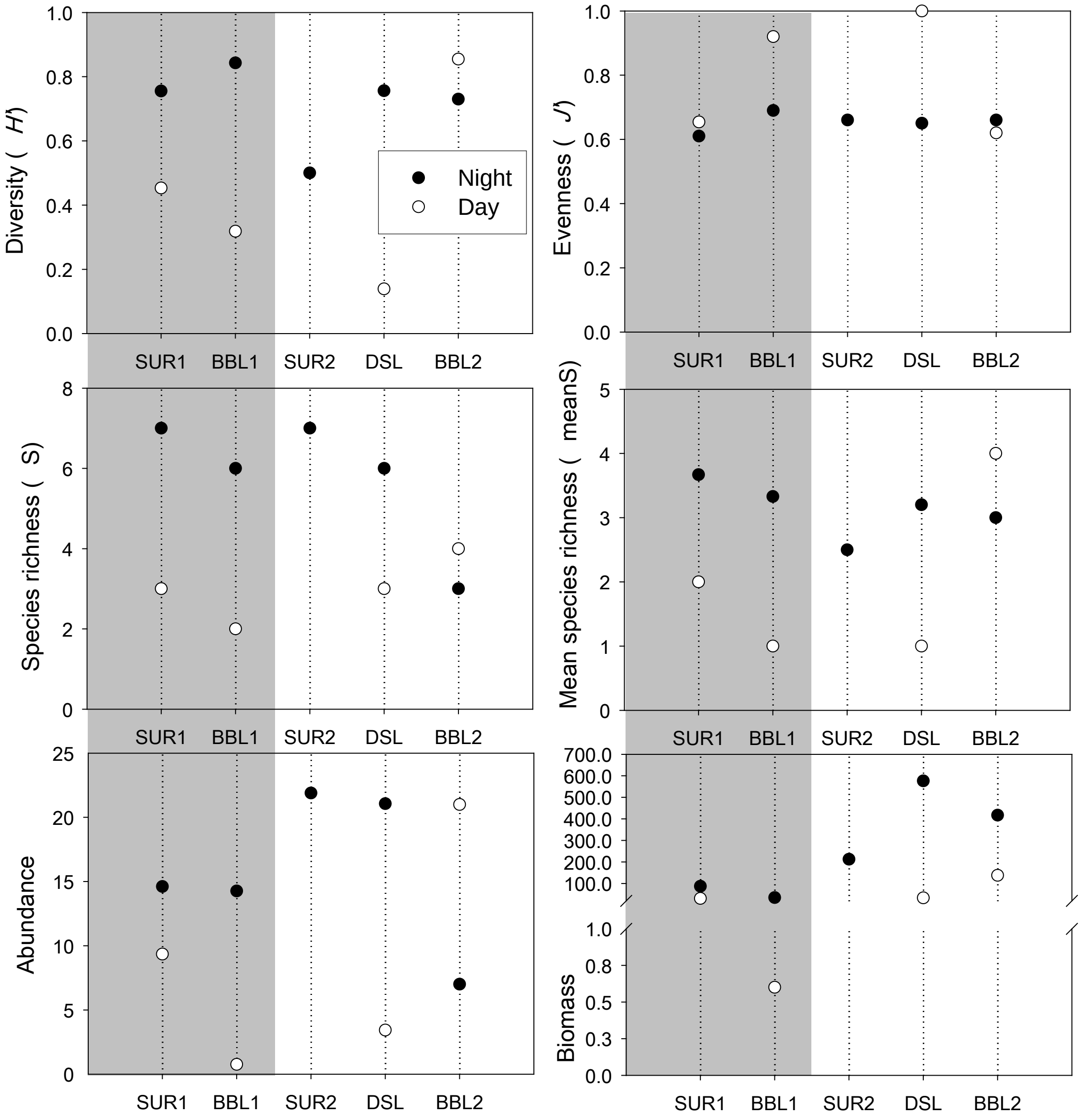

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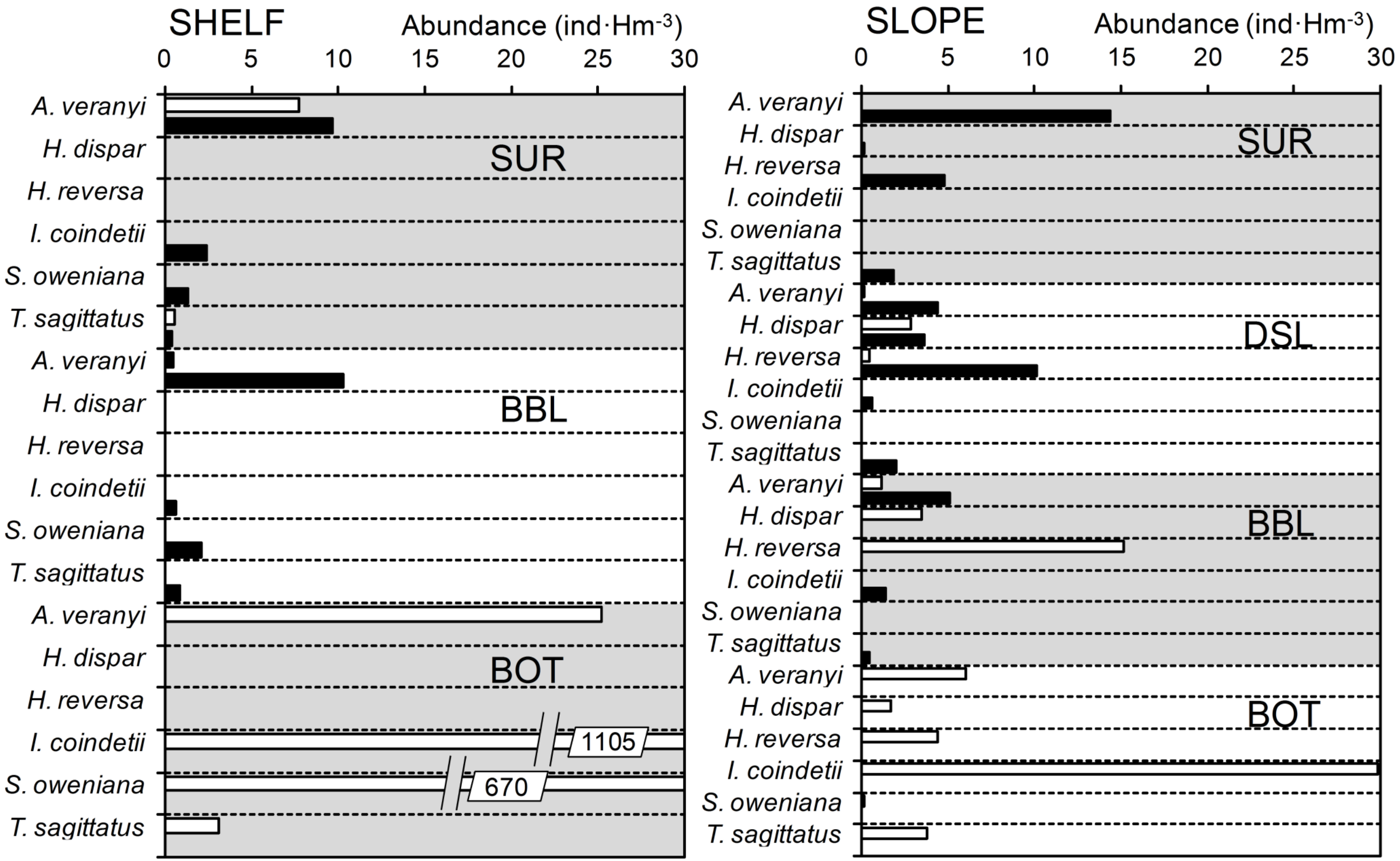

Fig. 4. Quetglas et al.

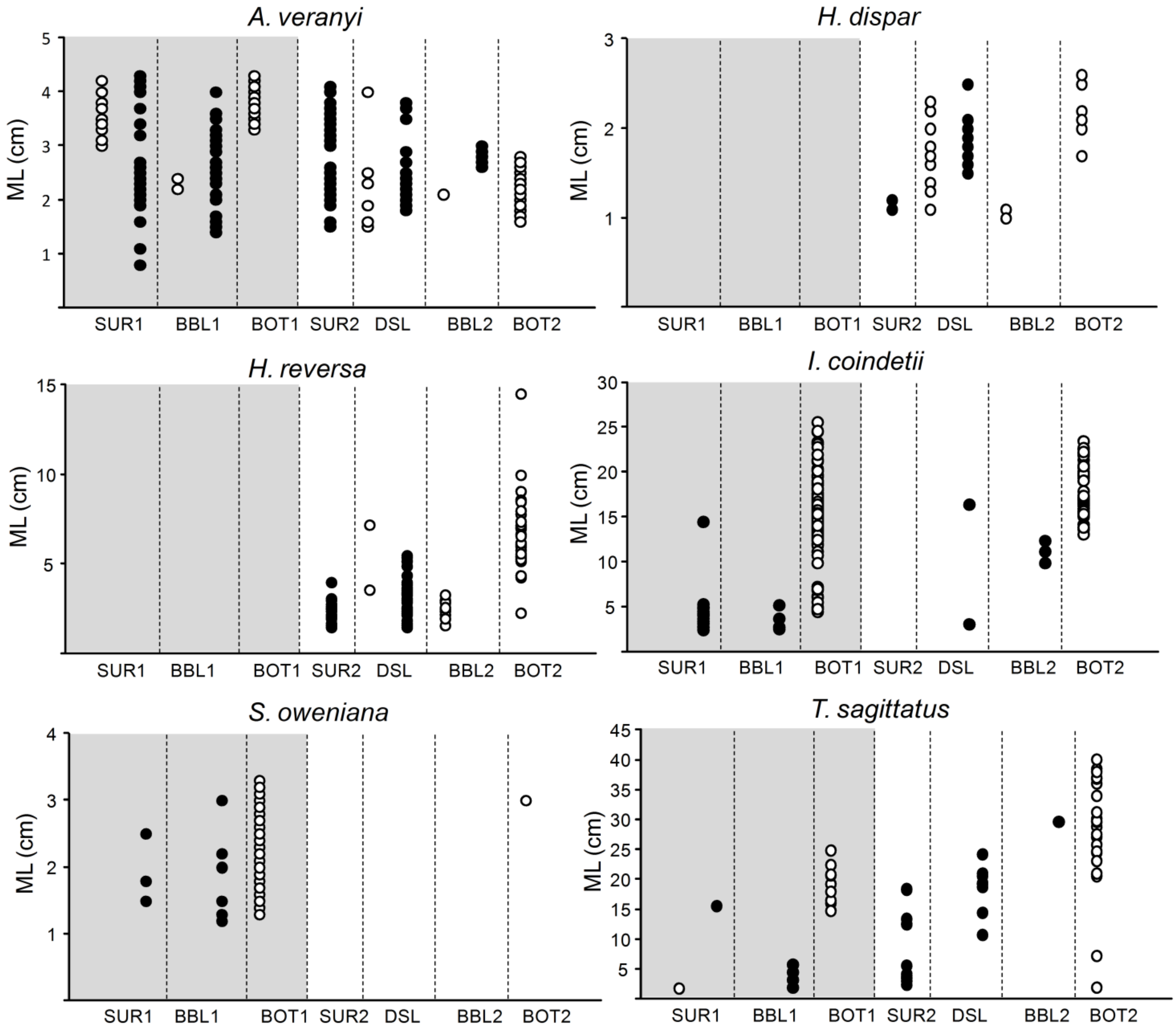

Fig. 5. Quetglas et al.