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

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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 nektobenthic 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.

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 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

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(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.ieo.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^2, 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^3 ($ind \cdot Hm^{-3}$ and $kg \cdot Hm^{-3}$). 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 $ind \cdot Hm^{-3}$) followed by *Sepietta oweniana* (28.9 $ind \cdot Hm^{-3}$) and *Alloteuthis media* (8.4 $ind \cdot Hm^{-3}$); the total abundance of all other species was <3 $ind \cdot Hm^{-3}$. The dominance of *I. coindetii* was even more pronounced in terms of biomass (68.8 $kg \cdot Hm^{-3}$), as the second and third most important species only accounted for 12.6 (*Loligo forbesii*) and 7.4 (*T. sagittatus*) $kg \cdot Hm^{-3}$. With the exception of *Eledone cirrhosa* (3.2 $kg \cdot Hm^{-3}$) and *S. oweniana* (2.2 $kg \cdot Hm^{-3}$), all other species had biomass values ≤ 1 $kg \cdot Hm^{-3}$.

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.*