*Mediterranean demersal resources and ecosystems: 25 years of MEDITS trawl surveys*
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# Long-term spatiotemporal dynamics of cephalopod assemblages in the Mediterranean Sea

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**Summary:** The Mediterranean Sea shows a trend of increasing temperature and decreasing productivity from the western to the eastern basin. In this work we investigate whether this trend is reflected in the cephalopod assemblages found throughout the Mediterranean. Data obtained with bottom trawl surveys carried out during the last 22 years by EU Mediterranean countries were used. In addition to analysing spatial differences in cephalopod assemblages, we also analysed putative temporal changes during the last two decades. For this purpose, the basin was spatially divided into bioregions, the trawling grounds were subdivided into depth strata, and the dataset was split into two time series of 11 years each. All analyses were done using PRIMER software. The species richness did not vary with the longitudinal gradient, though in most bioregions it showed a mild decrease with depth before plummeting in the deepest waters. Cluster analysis revealed four different bathymetric assemblages in all bioregions. Despite the contrasting conditions between basins and the claims of biodiversity loss, our study revealed that spatial and temporal differences during the last two decades were restricted to changes in the relative abundance of species from a common pool of species inhabiting the whole Mediterranean.

**Keywords:** monitoring; bottom trawling; biodiversity; biogeography; dominant species; continental shelf; continental slope.

**Dinámica espaciotemporal a largo plazo de comunidades de cefalópodos en el mar Mediterráneo**

**Resumen:** El mar Mediterráneo muestra un patrón de aumento de la temperatura y disminución de la productividad de la cuenca occidental a la oriental. En este trabajo se investiga si este patrón se refleja en las comunidades de cefalópodos que habitan el Mediterráneo. Se utilizaron datos obtenidos en campañas de arrastre de fondo realizadas durante los últimos 22 años por la mayoría de países mediterráneos de la UE. Junto con el análisis de las diferencias espaciales en las comunidades de cefalópodos, también se analizaron cambios temporales durante las dos últimas décadas. Para ello, la cuenca se dividió espacialmente en diferentes bioregiones, mientras que el conjunto de datos se dividió en dos series temporales de 11 años cada una. Todos los análisis se realizaron utilizando el software PRIMER. La riqueza específica no varió con el gradiente longitudinal, aunque en la mayoría de las bioregiones mostró una leve disminución con la profundidad antes de desplomarse en el estrato más profundo. El análisis cluster reveló cuatro comunidades batimétricas diferentes en todas las bioregiones. A pesar de las contrastadas condiciones ambientales entre las cuencas y las afirmaciones de pérdida de biodiversidad, nuestro estudio reveló que las diferencias espaciales y temporales durante las dos últimas décadas se limitaron a cambios en la abundancia relativa de las especies a partir de un conjunto faunístico común que habita todo el Mediterráneo.

**Palabras clave:** monitoreo; arrastre de fondo; biodiversidad; biogeografía; especies dominantes; plataforma continental; talud continental.

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## INTRODUCTION

The distribution of living species and communities is determined by a combination of large-scale biogeographic history, migration patterns and environmental conditions (Wiens and Donoghue 2004). The biodiversity of the Mediterranean Sea is therefore primarily shaped by its geographical position and the main connections with surrounding oceans, its geological history and the prevailing oceanographic conditions. The Mediterranean is the largest of the seas peripheral to the main oceans, being located between three continents and occupying an elongated basin of 4000 km length (Tyler 2003). It is naturally connected to the Atlantic Ocean through the Strait of Gibraltar (320 m depth) and to the Black Sea through the Dardanelles Strait (103 m depth). Since 1869, it has also been artificially connected to the Red Sea by the Suez Canal. Between six and five million years ago, the connection between the Atlantic and the Mediterranean Sea through the Strait of Gibraltar was closed, giving rise to the Messinian Salinity Crisis (Manzi et al. 2013, Vasiliev et al. 2017). This salinity crisis involved the complete disappearance of former deep benthic fauna, which means that the present deep Mediterranean organisms have originated from Atlantic migrations since 5.5 million years ago (Lugli et al. 2015).

The Mediterranean Sea is considered a biodiversity hotspot, with an estimate of about 17000 marine species (Coll et al. 2010). Most organisms presently living in the Mediterranean have an Atlantic origin, but tropical species have entered the basin for decades, either actively through the Suez Canal (Lessepsian migration) or the Strait of Gibraltar, or passively mainly through ship transport (Coll et al. 2010). During the last few decades, climate change has also affected the distribution and relative abundances of Mediterranean marine species (Bianchi and Morri 2004, Lejeusne et al. 2010, Lasram et al. 2010).

A gradient of species richness from the northwestern to the southeastern Mediterranean is driven by different oceanographic conditions between the two basins (Coll et al. 2010). The main differences are related to a decrease in productivity, as well as an increase in temperature and salinity, from the western to the eastern basin (Danovaro et al. 1999, Turley et al. 2000). As a result of such contrasting conditions, the western and eastern basins display biological similarities to the Atlantic ecosystem (higher number of cold-temperate species) and the Indo-Pacific ecosystem (higher number of subtropical species), respectively (Coll et al. 2010).

In this paper we investigate whether the different environmental conditions between the western and eastern basins are reflected in the cephalopod assemblages found throughout the Mediterranean. Cephalopods represent excellent case studies for analysing species-environment interactions owing to their high sensitivity to environmental conditions (Pierce et al. 2008, Rodhouse et al. 2014). They have short life spans (1.5–2 years at most) and a high population turn-over, so they show rapid responses to changes in external conditions. Although there are several studies on cephalopod assemblages relative to Mediterranean areas in both the western (e.g. Quetglas et al. 2000, González and Sánchez 2002, Fanelli et al. 2012) and eastern (e.g. Lefkaditou et al. 2003, Krstulović Šifner et al. 2005, 2011) basins, all of them are restricted to local scales and differences in sampling and data analysis prevent the comparison of results in most cases (Gaertner et al. 2013).

Like all other faunal components, the bulk of the current Mediterranean teuthofauna comes from the Atlantic Ocean (Bello 2003). Up to now, a total of 70 cephalopod species have been reported in the Mediterranean (Bello 2008, 2016) but only 53 of them are represented by well-established populations (Bello 2003). Ten cephalopods are endemic or quasi-endemic in the Mediterranean (Bello 2003, and pers. comm.), accounting for 14.3% of its teuthofauna.

In this work, data from standardized bottom trawl surveys carried out during the last 22 years by EU Mediterranean countries were used. The wide spatiotemporal scale of these scientific surveys and the data standardization used during the sampling and data processing allow a reliable comparative analysis of the cephalopod assemblages inhabiting the whole Mediterranean basin. In addition to investigating spatial differences in cephalopod assemblages, the available database will also be used to analyse temporal changes in species composition during the last two decades.

## MATERIALS AND METHODS

### Main oceanographic conditions of the Mediterranean

The Mediterranean is a semi-enclosed sea characterized by high salinities, temperatures and densities. The net evaporation exceeds the precipitation, driving an anti-estuarine circulation through the Strait of Gibraltar and contributing to very low nutrient concentrations (Tanhua et al. 2013). The Mediterranean has a basin-scale east-west gradient in the chlorophyll (Chl *a*) distribution, with an extremely oligotrophic eastern basin and a more productive western basin (D'Ortenzio and D'Alcala 2009). Two main types of dynamics coexist (Lavigne et al. 2015): i) a mid-latitude dynamics associated with bloom conditions in the northwestern basin, showing high occurrence of high surface Chl *a* profiles in March-April; and ii) a subtropical dynamics encompassing most of the remaining basin, characterized by an omnipresent deep Chl *a* maximum from spring to autumn and a large variety of Chl *a* vertical shapes during winter.

The mid-latitude behaviour is also observed for sea surface temperature (SST), with the lowest values found in February and the highest ones in summer, between July and August (Pastor et al. 2017). Although SST shows great spatial variability, and hence clustered areas do not always have the same size or shape or are centred on the same SST values, a set of common shapes are found for every season/month. The winter regime is characterized by a north-to-south increasing temperature gradient organized in latitudinal bands, while summer shows a highly complex structure with a set of distinct well-defined areas not following any simple gradient structure, although in general SST is higher in the southeastern Mediterranean basin. Both spring and autumn show transitional regimes between the two main modes.

A consistent warming trend has been found for Mediterranean SST in the 1982–2016 period (Pastor et al. 2017). This warming rate is not constant throughout the whole time series but shows differences, with a much steeper trend for the last two decades. Analysis of decadal trends has shown a clear increase of the warming trend from 1993 to the present. Three "almost decadal" periods were identified for the last 35 years, with the following mean values (expressed as $\times 10^{-4}$ °C $day^{-1}$): i) 1982-1992 (1.67±0.53); ii) 1993-2004 (2.82±0.47); and iii) 2005-2016 (3.08±0.47).

The salinity of the Mediterranean has also increased during the last 40 years (Borghini et al. 2014). Apart from the SST and salinity increases, other available information indicates that the Mediterranean is clearly not in a steady state. River run-off has been reduced as rivers are dammed and used for irrigation, and models suggest that evaporation is increasing due to the warming climate (Borghini et al. 2014).

### Data sampling and analysis

Data were obtained from the international Mediterranean bottom trawl surveys (MEDITS), which have been conducted annually between May and August since 1994, covering depths from 10 down to 866 m. The surveys are performed annually by all riparian EU countries plus Montenegro and Albania. The sampling methodology is standardized among all the countries (for details see Bertrand et al. 2002). A stratified random sampling design is used in the surveys, with the following bathymetric strata: 10-50, 51-100, 101-200, 201-500 and 501-800 m. The standardized gear used is a GOC 73 trawl with a cod-end mesh size of 20 mm and a vertical and horizontal opening of the net of about

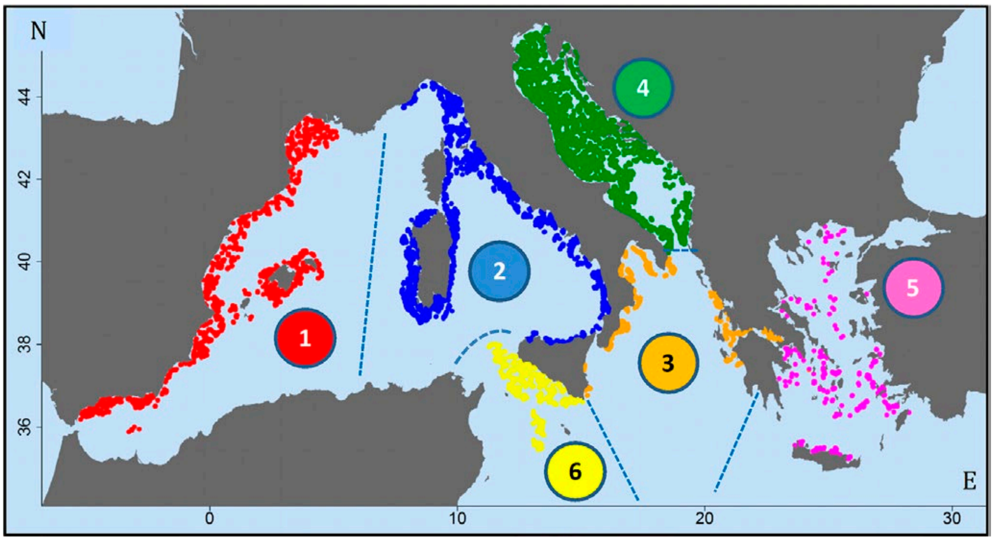


Fig. 1. – Map of the Mediterranean Sea showing the MEDITS stations sampled in 1994–2015. Colours correspond to the following bioregions: 1, Iberian-Lions; 2, Tyrrhenian Sea; 3, Ionian Sea; 4, Adriatic Sea; 5, Aegean Sea; and 6, Strait of Sicily. The separations between bioregions are marked with dotted lines.

2 and 18 m, respectively. The net opening is measured by an attached underwater Scanmar system to calculate the swept area. Trawling is conducted in daylight, with a towing speed of 2-3 knots and haul duration of 30 and 60 minutes over shelf and slope grounds, respectively.

To analyse spatiotemporal differences in cephalopod assemblages over the whole Mediterranean, the basin was divided into six biogeographical zones or bioregions (Fig. 1) in accordance with previous studies (Gaertner et al. 2007, 2013, Keller et al. 2016): Iberian-Lions (B1); Tyrrhenian (B2); Ionian (B3); Adriatic (B4); Aegean (B5); and Strait of Sicily (B6). A total of 23749 stations sampled during the last 22 years (1994-2015) were analysed (Table S1 in Supplementary material). Data used in the analyses included the standardized density of cephalopod species in number of individuals (N km$^{-2}$) taken at all individual sampling stations.

To identify the main cephalopod assemblages of each bioregion, cluster analyses were applied to the mean cephalopod abundances obtained from the whole time series (1994-2015). Owing to the low frequency of occurrence of most species, samples were pooled within 25-m depth intervals. The resemblance matrix was calculated on the basis of Bray-Curtis similarities between hauls, with a fourth-root transformation of the densities in order to down-weight the effect of the most abundant species (Clarke and Warwick 2001). The cluster analysis was carried out with the similarity profile (SIMPROF) routine, which defines statistically significant groups among samples (Clarke and Gorley 2006). Subsequently, the similarity percentage analysis (SIMPER) was used to determine the species characterizing the bathymetric assemblages obtained.

To analyse temporal differences in assemblages, the available dataset was split into two time series of 11 years each (1994-2004 and 2005-2015), corresponding to the last two periods of the aforementioned three warming decadal trends identified in the Mediterranean (Pastor et al. 2017). These two time periods are hereafter referred to as the old and the recent time series. Spatial (6 bioregions) and temporal (old vs. recent time series) differences in cephalopod assemblages were tested using the permutational multivariate analysis of variance (PERMANOVA), based on Bray-Curtis similarity matrices after square root transformation (Anderson et al. 2008). Spatial and temporal comparisons were exclusively done for equivalent bathymetric assemblages coming from the cluster analysis. The analyses were obtained after 9999 permutations of raw data. When the number of unique permutations was lower than 100, the Monte Carlo p-value was used instead of the permutation p-value (Anderson et al. 2008). Prior to the PERMANOVA, the homogeneity of multivariate dispersions was tested for all factors using the permutational analysis of multivariate dispersions (PERMDISP). When the PERMANOVA revealed spatial differences in assemblages, pairwise comparisons were carried out to determine which pairs of bioregions differed. The species composition of these differing pairs of assemblages was then used to explain the spatial differences found. Finally, when temporal differences in assemblages were detected, SIMPER analyses comparing the dissimilarity between the old and the recent time series were used to determine the species contributing to those differences.

## RESULTS

### Cephalopod assemblages

Altogether, 47 cephalopod species were taken during the sampling (although shells of *Argonauta argo* females were noticed in most bioregions, the species was not considered because no live individuals were captured). The highest species richness (S) was found in bioregions B1 (S=42) and B2 and B3 (both with S=41), whereas bioregions B4, B5 and B6 had 35, 36 and 34 species, respectively (Table S2 in Supplementary material). Considering the three main Mediterranean biogeographical provinces that have traditionally been used (Lejeusne et al. 2010), the western (including B1 and B2) and eastern (including B3, B5 and B6) basins had the same number of species (S=43) and the Adriatic (B4) had 35 species.

Cluster analysis revealed four different bathymetric assemblages in all bioregions (Fig. 2). Although the depth ranges of these assemblages varied with the bioregions, they are hereafter referred to as: i) continental shelf (<200 m); ii) upper slope (200-400 m); iii) middle slope (400-650 m); and iv) lower slope (>650 m). In all cases (except between groups A and B from B6), the average similarity between assemblages obtained with the SIMPER analysis decreased with increasing depth (Table S3 in Supplementary material). In most bioregions (B1-B4) the species richness decreased slightly with depth from the shelf to the middle slope and then dropped to the lowest values on the lower slope (Fig. 3). This was not the case, however, for bioregions B5 and B6, which did not show such a decreasing trend and had richness values much higher than the other bioregions in the deepest stratum.

Except on the lower slope of B2 and B4, there were no clear dominant species in any stratum, but a rather homogeneous blend of different species. The lower slopes of B2 and B4, by contrast, were characterized by two dominant species contributing 66% (*Histioteuthis reversa* and *Todarodes sagittatus*) and 75% (*Todaropsis eblanae* and *H. reversa*), respectively, to the cephalopod assemblage. In all bioregions, a number of generalist species appear in most strata (e.g. *Abralia veranyi, Sepietta oweniana, Illex coindetii*) and some specialized species characterizing specific strata appear in shallow (e.g. *Eledone moschata, Sepia officinalis*) and deep (e.g. *Bathypolypus sponsalis*, *Histioteuthis* spp.) waters.

### Spatial differences

The PERMDISP test revealed homogeneous within-group multivariate dispersions for all four bathymetric assemblages (shelf, p=0.318; upper slope, p=0.287; middle slope, p=0.582; lower slope, p=0.046). The PERMANOVA showed significant spatial differences on the continental shelf (pseudo-F=33.19; p<0.0001),

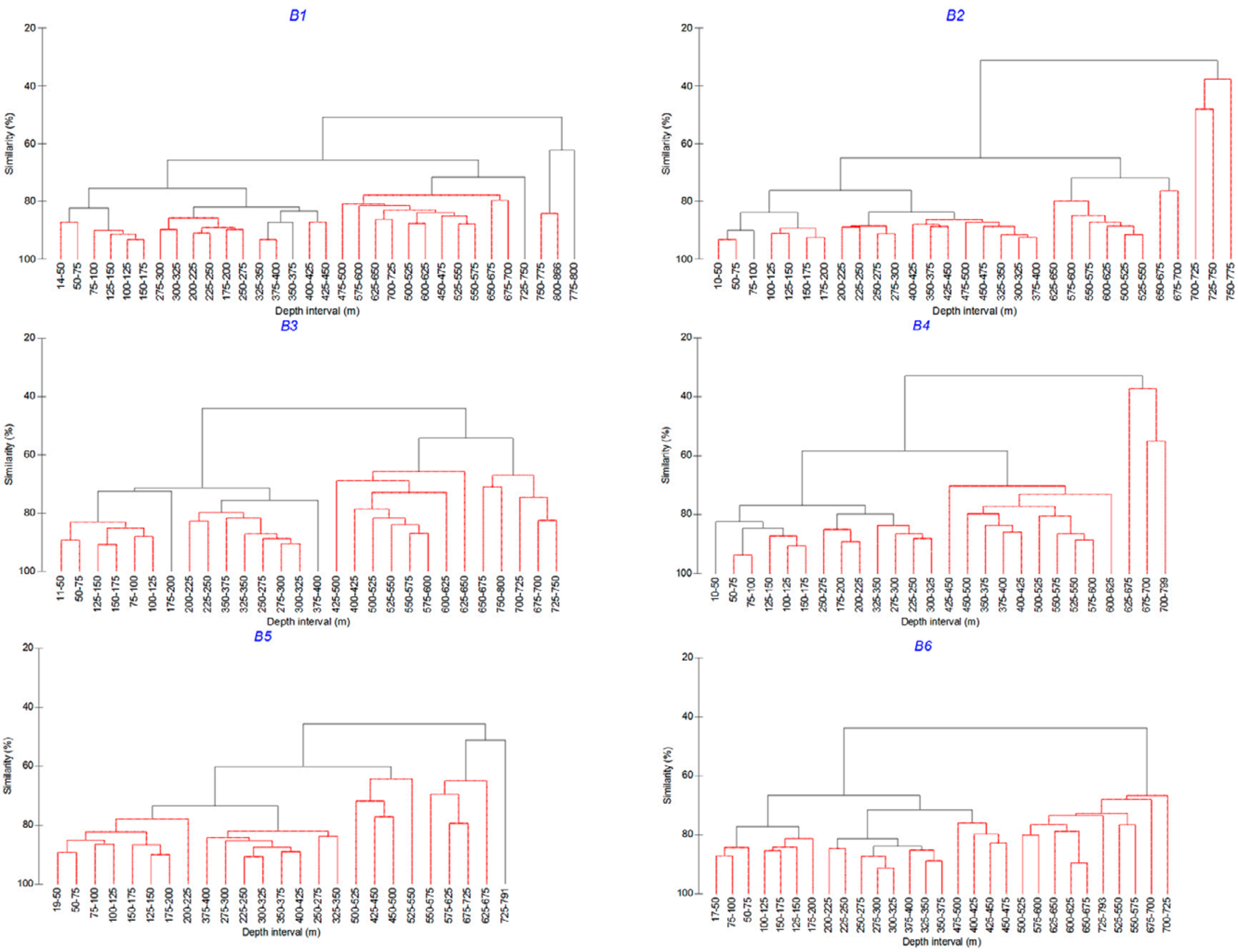


Fig. 2. – Cluster analysis of cephalopod abundances from the following Mediterranean bioregions: Iberian-Lions (B1); Tyrrhenian (B2); Ionian (B3); Adriatic (B4); Aegean (B5); and Strait of Sicily (B6).

upper slope (pseudo-F=79.86; p<0.0001), middle slope (pseudo-F=54.39; p<0.0001) and lower slope (pseudo-F=3.83; p<0.0001). Pairwise comparisons between bioregions showed significant differences in all cases for the upper slope and middle slope (Table 1). Regarding the continental shelf, significant differences were found for all pairs except for B1-B2 and B3-B6. The lower slope was the most homogeneous stratum since it had the highest number of non-significant pairwise comparisons: B1-B2, B1-B3, B1-B4, B2-B3, B2-B4 and B2-B6.

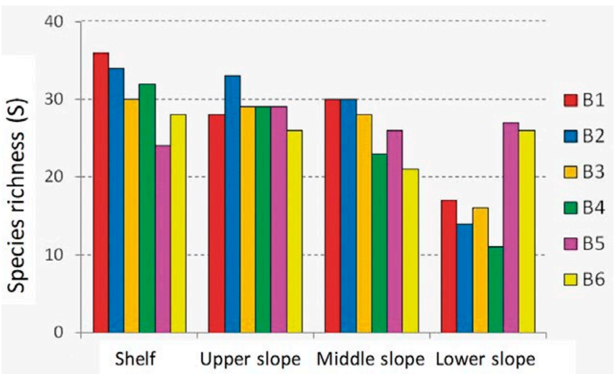


Fig. 3. – Species richness (S) of the different Mediterranean cephalopod assemblages by bioregion (B1 to B6). B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; and B6, Strait of Sicily.

The SIMPER (Table S3 in Supplementary material) showed that there are no significant changes in the spe-

Table 1. – PERMANOVA results (permutation p-values) of pairwise comparisons of cephalopod assemblages between bioregions (B1-B6) for each of the four bathymetric strata obtained from cluster analysis. When the number of unique permutations was lower than 100, the Monte Carlo p-value was used (italics). Statistically significant values are highlighted in bold. B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; B6, Strait of Sicily.

| Groups | Continental shelf | Upper slope | Middle slope | Lower slope |
|---|---|---|---|---|
| B1, B2 | 0.053 | **0.017** | **0.008** | *0.098* |
| B1, B3 | **0.005** | **0.000** | **0.000** | *0.057* |
| B1, B4 | **0.002** | **0.000** | **0.000** | *0.102* |
| B1, B5 | **0.011** | **0.000** | **0.002** | **0.007** |
| B1, B6 | **0.004** | **0.000** | **0.001** | ***0.011*** |
| B2, B3 | **0.005** | **0.000** | **0.002** | *0.240* |
| B2, B4 | **0.009** | **0.000** | **0.001** | *0.203* |
| B2, B5 | **0.003** | **0.000** | **0.005** | **0.016** |
| B2, B6 | **0.002** | **0.000** | **0.001** | *0.059* |
| B3, B4 | **0.039** | **0.003** | **0.006** | ***0.019*** |
| B3, B5 | **0.006** | **0.000** | **0.007** | **0.002** |
| B3, B6 | 0.103 | **0.000** | **0.002** | **0.009** |
| B4, B5 | **0.008** | **0.000** | **0.004** | **0.008** |
| B4, B6 | **0.040** | **0.000** | **0.001** | ***0.013*** |
| B5, B6 | **0.004** | **0.000** | ***0.021*** | **0.021** |

cies composition when the same bathymetric stratum is compared among bioregions, but only a change in the contribution of the relative abundance of the different species to the cephalopod assemblages.

The species reported in the following paragraphs refer to those included in the SIMPER results when considering the 80% cut-off value, not the whole list of species found in each bioregion. A number of species appearing in all bioregions characterize the continental shelf, such as *Alloteuthis* spp., *Illex coindetii, Loligo vulgaris* and *Sepia elegans*. Some species were absent in various bioregions (e.g. *Loligo forbesii* in B3, B4, B6; *Octopus vulgaris* in B2, B3, B6; *Eledone moschata* in B2, B3), whereas some species only appeared in a single bioregion (e.g. *Octopus salutii* in B4; *Sepia officinalis* in B2).

Similarly, the upper slope was characterized by sepiolids (*Sepietta oweniana,* Sepiolidae*, Rondeletiola minor*), *Alloteuthis* spp., *Illex coindetii* and *Sepia orbignyana*. Some species were also absent in various bioregions (e.g. *Octopus salutii* in B2, B5, B6; *Loligo vulgaris* in B1, B3, B5, B6; *Neorosia caroli* in B1, B3, B4, B6) and some species were only present in one bioregion (e.g. *Bathypolypus sponsalis* and *Pteroctopus tetracirrhus* in B1).

On the middle slope, the list of cephalopods appearing in all bioregions included species such as *Abralia veranyi, Illex coindetii, Rossia macrosoma* and *Todaropsis eblanae*. A single taxon appeared in only one bioregion (*Alloteuthis* spp. in B5), whereas the number of species absent in different bioregions was larger than that in the rest of the assemblages (a total of 12 cephalopods, including *Todarodes sagittatus, Sepietta oweniana* and *Eledone cirrhosa*).

Finally, the SIMPER results from the lower slope differed from the results obtained in the remaining assemblages because there was no common list of species characterizing this assemblage; in fact, only a single species was present in all bioregions (*Histioteuthis reversa*). Two cephalopods were found only in one bioregion (*B. sponsalis* and *R. minor*), whereas the rest of species appeared in various bioregions (e.g. *A. veranyi, T. sagittatus, A. lichtensteinii, T. eblanae*).

### Temporal differences

The PERMDISP test showed homogeneous within-group multivariate dispersions in all cases (Table 2). The PERMANOVA only revealed temporal differences between the old (1994-2004) and the recent (2005-2015) time series for three bioregions (B1, B3 and B6). The Strait of Sicily (B6) was the only bioregion showing significant differences in all four bathymetric assemblages. The Iberian-Lions bioregion (B1) showed differences in all assemblages except on the lower slope, whereas the Ionian bioregion (B3) only displayed differences in two assemblages (upper and lower slope).

As in the case of the spatial analysis, the SIMPER (Table S4 in Supplementary material) showed that there were no significant changes in the species composition within equivalent bathymetric strata when the two time periods are compared, but only changes in the relative species abundances.

Table 2. – Results of PERMDISP testing for homogeneity within-group multivariate dispersions, and posterior PERMANOVA comparing the cephalopod assemblages between the old (1994-2004) and recent (2005-2015) time series for each bathymetric stratum of all bioregions. Statistically significant values are highlighted in bold. For all significant cases, a SIMPER was performed (see Table S4 in Supplementary material) to determine the species contributing to the dissimilarity between periods (the average dissimilarity percentages are shown here in brackets behind the p-value). B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; B6, Strait of Sicily.

| Stratum | Bioregion | PERMDISP | PERMANOVA |
|---|---|---|---|
| Continental shelf | B1 | p=0.850 | **p<0.05** (28.97%) |
| | B2 | p=4.820 | p=0.306 |
| | B3 | P=0.668 | p=0.812 |
| | B4 | p=0.391 | p=0.325 |
| | B5 | p=0.677 | p=0.113 |
| | B6 | p=0.403 | **p<0.05** (41.18%) |
| Upper slope | B1 | p=0.568 | **p<0.001** (35.97%) |
| | B2 | p=0.863 | p=0.512 |
| | B3 | p=0.657 | **p<0.05** (39.80%) |
| | B4 | p=0.691 | p=0.635 |
| | B5 | p=0.503 | p=0.062 |
| | B6 | p=0.588 | **p<0.001** (50.37%) |
| Middle slope | B1 | p=0.896 | **p<0.05** (35.95%) |
| | B2 | p=0.746 | p=0.974 |
| | B3 | p=0.538 | p=0.403 |
| | B4 | p=0.840 | p=0.098 |
| | B5 | p=0.378 | p=0.349 |
| | B6 | p=0.699 | **p<0.01** (39.63%) |
| Lower slope | B1 | p=0.453 | p=0.878 |
| | B2 | NA | NA |
| | B3 | p=0.420 | **p<0.05** (63.68%) |
| | B4 | NA | NA |
| | B5 | p=0.316 | p=0.313 |
| | B6 | p=0.496 | **p<0.01** (50.39%) |

## DISCUSSION

A total of 47 different cephalopod species have been taken from the Mediterranean Sea during the last 22 years, accounting for 67.1% of the cephalopods recorded in the basin up to now. This percentage highlights the high number of cephalopods that have not been captured by bottom trawl gears during the study period—one third of recorded species—despite the large spatiotemporal sampling (23749 sampling stations). Although the westernmost bioregion (Iberian-Lions; B1) held a higher number of cephalopod species (S=42 vs 36) than the easternmost bioregion (Aegean Sea; B5), there was no clear trend in species richness throughout the Mediterranean, as has already been reported in a recent study (Keller et al. 2016). Whereas Mangold and Boletzky (1988) suggested a general decrease in the species richness from west to east, Bello (2003) noted that this theory should be revised according to available updated information. Even for the three main biogeographical provinces traditionally used to divide the Mediterranean (the western and eastern basins and the Adriatic Sea; Mangold and Boletzky 1988, Lejeusne et al. 2010), the species richness obtained with our data was the same in both the western and eastern basins (S=43), but was lower in the Adriatic (S=35). As already reported for fish (Gaertner et al. 2007, Granger et al. 2015), the absence of a west-east decreasing trend suggests that primary production (i.e. food availability) is possibly not the major factor explaining large-scale patterns of species richness of demersal cephalopods. At a global scale it was found that although net primary productivity at the ocean surface seems to drive diversity patterns of pelagic cephalopods, coastal species diversity can be predicted by climate (SST) and non-climate (spatial area) variables (Rosa et al. 2008).

Given that cephalopods are highly sensitive to changing environmental conditions (Pierce et al. 2008, Rodhouse et al. 2014), it was expected to find spatial differences in the species composition over the Mediterranean. However, our results revealed no differences in species composition among bioregions, but only changes in the species' relative abundances, which led to significant differences between all pairs of bioregions in intermediate waters (upper and middle slope assemblages). Assemblages from the upper and middle slope, for instance, are dominated by the squid *lllex coindetii* in the easternmost bioregions (B3, B4, B5), whereas sepiolids predominate in the remaining bioregions. Assemblages from the shelf were also significantly different between all pairs of bioregions except in two cases, the Iberian-Lions (B1) vs Tyrrhenian Sea (B2) and the Ionian Sea (B3) vs Strait of Sicily (B6). The homogeneity of shelf assemblages in the B1-B2 bioregions might be related to the counter-clockwise circulation of Atlantic waters in the western basin, which produces a basin-wide cyclonic gyre through the Tyrrhenian vein (Millot and Taupier-Letage 2005) that might hinder exchanges of low-moving life stages such as cephalopod paralarvae. The strategic situation of the Strait of Sicily might explain the differences found between the B1-B2 and the B3-B6 assemblages: the surface isotherm of 15°C for February (the coldest month in the year) follows quite closely the biogeographic boundaries of the Strait of Sicily, and biotic differences between the two basins are probably due to differences in temperature regime, i.e. a physiological barrier separating the western and eastern Mediterranean (Bianchi 2007). In addition, the Strait of Sicily is also characterized by high mesoscale activity (Nieblas et al. 2014) and high fishing rates (Colloca et al. 2017). The lower slope was the most homogeneous stratum since it had the highest number of non-significant pairwise comparisons. This faunal homogeneity is a general feature of deep-sea waters (McClain and Hardy 2010, Rex and Etter 2010) and is proably related to the homogeneous conditions and the circulation pattern at such great depths (Millot and Taupier-Letage 2005). Results also revealed that the Aegean bioregion (B5) was significantly different from all other bioregions, a finding which might be related to its high spatial bathymetric variability (Millot and Taupier-Letage 2005, Nieblas et al. 2014) and low fishing exploitation rate (Colloca et al. 2017). Compared with the rest of bioregions, for instance, the broader upper slope of the Aegean Sea was characterized by higher abundances of the cuttlefishes *Sepia elegans* and *S. orbignyana,* which is in accordance with the sustainable exploitation exerted in the area with a high prevalence of small-scale fisheries (Colloca et al. 2017).

In most bioregions (Iberian-Lions, Tyrrhenian, Ionian and Adriatic) the species richness showed a slight decrease with depth from the shelf to the middle slope before plummeting to the lowest values on the lower slope. The Aegean Sea and the Strait of Sicily, however, did not show that decreasing trend and their richness values at the deepest stratum were much higher than those of the remaining bioregions. Such high values might be due to the fact that the lower slope stratum obtained from our cluster analysis for these two bioregions encompassed a much wider depth range than the rest of the bioregions. Our results did not show the hump-shaped trend of species richness with depth reported in previous cephalopod studies carried out in the Mediterranean (González and Sánchez 2002, KrstulovićŠifner et al. 2011, Keller et al. 2016).

Except in the deepest stratum of the Adriatic Sea (B4), there were no clear dominant species in any cephalopod assemblage, but a rather homogeneous mix of different species. This indicates a continuous substitution of species with depth rather than discrete assemblages separated by distinct boundaries. In all bioregions, a number of eurytopic (generalist) species appeared in most strata (e.g. *A. veranyi, S. oweniana, I. coindetii*) and some specialized species characterizing specific strata appeared in shallow (e.g. *E. moschata, S. officinalis*) and deep (e.g. *B. sponsalis*, *Histioteuthis* spp.) waters. On the lower slope of the Adriatic Sea, two deep-sea squid species (*T. eblanae* and *H. reversa*) accounted for up to 75% of the cephalopod assemblage. This finding agrees with the well-known comparatively poor deep-sea teuthofauna of the Adriatic, despite the fact that it reaches 1200 m depth in the southern basin and has a relatively wide connection with the Ionian Sea (Mangold and Boletzky 1988, Bello 2003, Keller et al. 2016).

As stated above, the bulk of the current Mediterranean teuthofauna comes from the Atlantic Ocean (Bello 2003). However, a comparison of the cephalopod assemblages from the westernmost bioregion (Iberian-Lions; B1) with those from the Gulf of Cadiz (Silva et al. 2011), an Atlantic area adjacent to the Strait of Gibraltar, revealed great differences in species contribution. Such differences in species relative abundance might be related to the contrasting oceanographic conditions in these two areas (Millot and Taupier-Letage 2005, Tanhua et al. 2013).

Despite claims of biodiversity loss as a result of high anthropogenic impacts in the Mediterranean (Danovaro 2003, Calvo et al. 2011, Vasilakopoulos et al. 2014), the species composition of the cephalopod assemblages has not changed during the last 22 years. As in the case of the spatial analysis, temporal differences were only found in the species' relative abundance of three bioregions: Iberian-Lions, Ionian and Strait of Sicily. The Strait of Sicily was the only bioregion showing significant differences in all four bathymetric assemblages, whereas the Iberian-Lions and the Ionian bioregions displayed differences in three and two assemblages, respectively. As stated above, both natural factors (15°C isotherm boundary, complex topography, high mesoscale variability) and anthropogenic factors (high exploitation rates) might explain the existence of differences at all depths in the Strait of Sicily. The remaining bioregions (Tyrrhenian, Adriatic and Aegean Seas) showed no long-term temporal differences in species' relative abundance, a finding which might be related, at least in the Tyrrhenian and Aegean Seas, to reduced interchanges of water masses owing to the main topographic characteristics (Millot and Taupier-Letage 2005).

Previous studies of cephalopod assemblages in the Mediterranean confirm our results. A long-term study carried out in the western basin (Fanelli et al. 2012) found no significant differences in the bathyal cephalopod assemblages or in the species abundances between the two time periods analysed (1985-92 vs. 2007-10). In a shorter-term study (2000-2007) from the Gulf of Cadiz, the species composition also remained unchanged and only the relative abundance of different groups varied (Silva et al. 2011). The lack of changes in species composition during the last two decades also applies to fish (Granger et al. 2015), which might indicate that the demersal ecosystem was already altered before the beginning of our time series or that noticeable changes will only be revealed at longer temporal scales (Granger et al. 2015, Keller et al. 2016).

Given that temperature is a key driver of the biogeographic distribution (Puerta et al. 2014) and habitat selection (Lauria et al. 2016) of cephalopods, it is expected that climate change will have significant effects on many temperate species (Hastie et al. 2009). Climate change projections for the Mediterranean indicate that it might be an especially vulnerable region (Giorgi and Lionello 2008, Albouy et al. 2013). In fact, a consistent warming trend has already been reported in the 1982-2016 period (Pastor et al. 2017). As a whole, 25% of the Mediterranean Sea continental shelf was predicted to experience a total modification of endemic species assemblages by the end of the 21st century (Lasram et al. 2010). Some cephalopod populations from the Mediterranean show an increasing trend in abundance that might be related to the global change (Doubleday et al. 2016, Keller et al. 2017). Currently, however, none of the Lessepsian species (*Octopus aegina, O. cyanea, Sepioteuthis lessoniana* and *Tremoctopus gracilis*) reported in the Mediterranean up to now (Bello 2016) were found in our samples. As most Lessepsian species inhabit depths shallower than those prospected during the MEDITS and/or non-trawlable grounds, they in principle are not prone to being captured by trawling gears. A few Lessepsian fish species have been recorded in the MEDITS surveys in the south Aegean and Cretan Seas (Peristeraki et al. 2017), but no Lessepsian cephalopod species have been recorded so far, although some of them have well-established populations in the eastern Mediterranean (Zenetos et al. 2011; Lefkaditou, unpublished data). It is therefore expected that these Lessepsian migrants will spread westwards, as some fish species have already done (Bianchi 2007, Calvo et al. 2011), probably leading to spatiotemporal differences in cephalopod assemblages through the Mediterranean, at least during the westward spreading phase. Our study has shown, however, that spatiotemporal differences during the last two decades only affected some specific bioregions and were restricted to variations in the relative species abundance from a common pool of species inhabiting the whole Mediterranean.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available through the on-line version of this article and at the following link:
http://scimar.icm.csic.es/scimar/supplm/sm04841esm.pdf

Table S1. – Number of sampling stations by bioregion (Bioreg) sampled during the Mediterranean trawl surveys (MEDITS) carried out in the region between 1994 and 2015. B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; B6, Strait of Sicily.

Table S2. – Total number of taxa caught in the different bioregions and for the whole Mediterranean (all bioregions combined). Taxa are ordered according to their decreasing values of mean abundance (N $km^{-2}$). Tick marks show the taxa not taken into account when calculating the species richness. B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; B6, Strait of Sicily. (Next pages).

Table S3. – Results of similarity percentage analysis (SIMPER) for the bathymetric cephalopod assemblages obtained by the cluster analysis shown in Figure 2 for the six Mediterranean bioregions analysed (B1-B6). Abu (average abundance); AvSim (average similarity); Con (percentage contribution); Cum (cumulative percentages).

Table S4. – SIMPER analyses of the dissimilarity between the old (1994-2004) and recent (2005-2015) time series by bathymetric strata and bio-region for those stratum-bioregion settings showing significant differences from a previous PERMANOVA (see Table 2). Av.Abu (average abundance); Contrib% (percentage contribution); Cum% (cumulative percentages).

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# Long-term spatiotemporal dynamics of cephalopod assemblages in the Mediterranean Sea

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Supplementary material

Table S1. – Number of sampling stations by bioregion (Bioreg) sampled during the Mediterranean trawl surveys (MEDITS) carried out in the region between 1994 and 2015. B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; B6, Strait of Sicily.

| Bioreg | 1994 | 1995 | 1996 | 1997 | 1998 | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 | 2011 | 2012 | 2013 | 2014 | 2015 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| B1 | 147 | 174 | 170 | 173 | 163 | 180 | 177 | 233 | 255 | 262 | 267 | 249 | 275 | 231 | 224 | 231 | 186 | 232 | 244 | 260 | 280 | 290 | 4903 |
| B2 | 370 | 367 | 385 | 376 | 386 | 383 | 383 | 382 | 289 | 312 | 307 | 310 | 311 | 310 | 310 | 309 | 311 | 314 | 314 | 314 | 316 | 312 | 7371 |
| B3 | 11 | 88 | 96 | 92 | 106 | 105 | 106 | 104 | 70 | 103 | 101 | 101 | 100 | 70 | 102 | 70 | 70 | 70 | 69 | 70 | 106 | 70 | 1880 |
| B4 | 158 | 160 | 250 | 251 | 252 | 198 | 249 | 250 | 270 | 273 | 271 | 271 | 269 | 272 | 272 | 273 | 272 | 272 | 271 | 218 | 270 | 270 | 5512 |
| B5 | 92 | 103 | 130 | 145 | 147 | 143 | 141 | 139 | | 142 | 146 | 148 | 147 | | 148 | | | | | | 149 | | 1920 |
| B6 | 36 | 41 | 41 | 41 | 42 | 42 | 42 | 42 | 66 | 66 | 65 | 153 | 159 | 165 | 165 | 165 | 165 | 164 | 164 | 164 | 55 | 120 | 2163 |
| Total | 814 | 933 | 1072 | 1078 | 1096 | 1051 | 1098 | 1150 | 950 | 1158 | 1157 | 1232 | 1261 | 1048 | 1221 | 1048 | 1004 | 1052 | 1062 | 1026 | 1176 | 1062 | 23749 |

Table S2. – Total number of taxa caught in the different bioregions and for the whole Mediterranean (all bioregions combined). Taxa are ordered according to their decreasing values of mean abundance (N km$^{-2}$). Asterisks show the taxa not taken into account when calculating the species richness. B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; B6, Strait of Sicily.

| | Iberian-Lions (B1) | | | Tyrrhenian Sea (B2) | |
|---|---|---|---|---|---|
| | Taxon | Mean Ab. | | Taxon | Mean Ab. |
| 1 | *Alloteuthis media* | 747.9 | 1 | *Alloteuthis* spp. * | 788.4 |
| 2 | *Alloteuthis* spp. * | 556.5 | 2 | *Alloteuthis media* | 371.4 |
| 3 | *Alloteuthis subulata* | 259.6 | 3 | *Sepietta oweniana* | 318.4 |
| 4 | *Sepiola* spp. * | 231.4 | 4 | *Loligo forbesii* | 308.9 |
| 5 | *Sepietta oweniana* | 226.8 | 5 | *Loligo vulgaris* | 303.6 |
| 6 | *Sepiola affinis* | 215.2 | 6 | *Sepiola* spp. * | 297.4 |
| 7 | *Brachioteuthis riisei* | 196.1 | 7 | *Illex coindetii* | 187.1 |
| 8 | *Loligo forbesii* | 189.9 | 8 | *Rondeletiola minor* | 183.8 |
| 9 | *Abralia veranyi* | 175.8 | 9 | *Sepiola affinis* | 182.3 |
| 10 | *Illex coindetii* | 167.6 | 10 | *Alloteuthis subulata* | 169.3 |
| 11 | *Sepiola rondeletii* | 156.5 | 11 | *Sepia orbignyana* | 133.3 |
| 12 | *Loligo vulgaris* | 154.2 | 12 | *Sepiola rondeletii* | 105.8 |
| 13 | *Sepia orbignyana* | 124.7 | 13 | *Sepietta obscura* | 101.6 |
| 14 | *Eledone cirrhosa* | 123.9 | 14 | *Sepia officinalis* | 92.2 |
| 15 | *Rondeletiola minor* | 112.7 | 15 | *Sepiola ligulata* | 90.0 |
| 16 | *Octopus vulgaris* | 91.2 | 16 | *Sepia elegans* | 85.4 |
| 17 | *Sepiola intermedia* | 81.5 | 17 | *Eledone cirrhosa* | 83.5 |
| 18 | *Sepia officinalis* | 76.1 | 18 | *Todaropsis eblanae* | 77.1 |
| 19 | *Sepia elegans* | 76.1 | 19 | *Octopus vulgaris* | 71.3 |
| 20 | *Bathypolypus sponsalis* | 69.2 | 20 | *Sepietta neglecta* | 60.7 |
| 21 | *Sepietta neglecta* | 63.2 | 21 | *Sepiola robusta* | 59.2 |
| 22 | *Sepiola robusta* | 62.9 | 22 | *Sepietta* spp. * | 53.6 |
| 23 | *Sepiola ligulata* | 57.4 | 23 | *Bathypolypus sponsalis* | 53.0 |
| 24 | *Eledone moschata* | 52.4 | 24 | *Ancistroteuthis lichtensteinii* | 51.9 |
| 25 | *Todarodes sagittatus* | 48.6 | 25 | *Abralia veranyi* | 50.3 |
| 26 | *Todaropsis eblanae* | 45.7 | 26 | *Eledone moschata* | 43.9 |
| 27 | *Rossia macrosoma* | 40.9 | 27 | *Sepiola intermedia* | 41.3 |
| 28 | *Scaeurgus unicirrhus* | 35.2 | 28 | *Rossia macrosoma* | 38.8 |
| 29 | *Sepietta* spp. * | 34.3 | 29 | *Todarodes sagittatus* | 36.3 |
| 30 | *Callistoctopus macropus* | 33.5 | 30 | *Scaeurgus unicirrhus* | 34.3 |
| 31 | *Ancistroteuthis lichtensteinii* | 33.3 | 31 | *Chiroteuthis veranii* | 33.4 |
| 32 | *Octopus salutii* | 32.1 | 32 | *Opisthoteuthis calypso* | 27.4 |
| 33 | *Neorossia caroli* | 30.9 | 33 | *Neorossia caroli* | 26.6 |
| 34 | *Chiroteuthis veranii* | 29.8 | 34 | *Heteroteuthis dispar* | 25.4 |
| 35 | *Macrotritopus defilippi* | 27.9 | 35 | *Callistoctopus macropus* | 25.4 |
| 36 | *Pteroctopus tetracirrhus* | 25.2 | 36 | *Octopus salutii* | 23.8 |
| 37 | *Histioteuthis reversa* | 23.7 | 37 | *Histioteuthis reversa* | 22.2 |
| 38 | *Sepietta obscura* | 23.3 | 38 | *Macrotritopus defilippi* | 22.1 |
| 39 | *Ocythoe tuberculata* | 19.8 | 39 | *Pteroctopus tetracirrhus* | 21.3 |
| 40 | *Histioteuthis* spp. * | 18.5 | 40 | *Onychoteuthis banksii* | 21.2 |
| 41 | *Heteroteuthis dispar* | 18.5 | 41 | *Chtenopteryx sicula* | 19.4 |
| 42 | *Histioteuthis bonnellii* | 18.0 | 42 | *Histioteuthis bonnellii* | 16.5 |
| 43 | *Onychoteuthis banksii* | 15.8 | 43 | *Stoloteuthis leucoptera* | 12.1 |
| 44 | *Opisthoteuthis calypso* | 15.1 | 44 | *Octopoteuthis sicula* | 10.1 |
| 45 | *Stoloteuthis leucoptera* | 13.8 | 45 | *Histioteuthis* spp. * | 8.2 |
| 46 | *Chtenopteryx sicula* | 9.7 | | | |
| | Ionian Sea (B3) | | | Adriatic Sea (B4) | |
| | Taxon | Mean Ab. | | Taxon | Mean Ab. |
| 1 | *Alloteuthis media* | 687.6 | 1 | *Alloteuthis media* | 754.3 |
| 2 | *Loligo vulgaris* | 527.1 | 2 | *Illex coindetii* | 384.8 |
| 3 | *Todarodes sagittatus* | 465.1 | 3 | *Loligo vulgaris* | 313.2 |
| | | | 4 | *Sepia elegans* | 173.5 |
| 4 | *Illex coindetii* | 271.0 | 5 | *Alloteuthis subulata* | 187.1 |
| 5 | *Sepiola* spp. * | 208.8 | 6 | *Eledone moschata* | 161.7 |
| 6 | *Loligo forbesii* | 198.9 | 7 | *Sepiola affinis* | 161.0 |
| 7 | *Rondeletiola minor* | 135.7 | 8 | *Sepia officinalis* | 157.7 |

Table S2 (Cont.). – Total number of taxa caught in the different bioregions and for the whole Mediterranean (all bioregions combined). Taxa are ordered according to their decreasing values of mean abundance (N km$^{-2}$). Asterisks show the taxa not taken into account when calculating the species richness. B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; B6, Strait of Sicily.

| | | | | | |
|---|---|---|---|---|---|
| 8 | *Sepia elegans* | 106.8 | 9 | *Alloteuthis* spp. * | 140.1 |
| 9 | *Alloteuthis subulata* | 91.4 | 10 | *Sepietta oweniana* | 100.9 |
| 10 | *Sepietta oweniana* | 89.3 | 11 | *Todaropsis eblanae* | 98.3 |
| 11 | *Abralia veranyi* | 77.8 | 12 | *Rondeletiola minor* | 87.2 |
| 12 | *Sepia orbignyana* | 77.7 | 13 | *Sepiola rondeletii* | 82.6 |
| 13 | *Sepiola rondeletii* | 62.5 | 14 | *Abralia veranyi* | 78.8 |
| 14 | *Todaropsis eblanae* | 61.7 | 15 | *Sepiola* spp. * | 78.2 |
| 15 | *Sepiola intermedia* | 56.0 | 16 | *Eledone cirrhosa* | 69.2 |
| 16 | *Eledone cirrhosa* | 55.8 | 17 | *Todarodes sagittatus* | 66.2 |
| 17 | *Sepia officinalis* | 47.8 | 18 | *Callistoctopus macropus* | 64.7 |
| 19 | *Eledone moschata* | 44.7 | 19 | *Sepiola intermedia* | 55.4 |
| 20 | *Scaeurgus unicirrhus* | 43.6 | 20 | *Sepietta neglecta* | 43.3 |
| 21 | *Rossia macrosoma* | 42.8 | 21 | *Sepiola robusta* | 42.5 |
| 22 | *Octopus vulgaris* | 35.9 | 22 | *Loligo forbesii* | 36.8 |
| 23 | *Sepietta neglecta* | 33.0 | 23 | *Scaeurgus unicirrhus* | 34.6 |
| 24 | *Callistoctopus macropus* | 32.0 | 24 | *Sepietta obscura* | 34.5 |
| 25 | *Ancistroteuthis lichtensteinii* | 25.6 | 25 | *Onychoteuthis banksii* | 33.8 |
| 26 | *Histioteuthis reversa* | 24.9 | 26 | *Sepia orbignyana* | 33.6 |
| 27 | *Macrotritopus defilippi* | 24.0 | 27 | *Sepiola ligulata* | 31.2 |
| 28 | *Sepietta* spp. * | 23.5 | 28 | *Sepietta* spp. * | 31.2 |
| 29 | *Sepiola robusta* | 22.1 | 29 | *Octopus vulgaris* | 30.7 |
| 30 | *Octopus salutii* | 22.0 | 30 | *Macrotritopus defilippi* | 30.6 |
| 31 | *Sepiola affinis* | 21.7 | 31 | *Ancistroteuthis lichtensteinii* | 30.5 |
| 32 | *Heteroteuthis dispar* | 20.7 | 32 | *Octopus salutii* | 27.4 |
| 33 | *Neorossia caroli* | 19.7 | 33 | *Rossia macrosoma* | 26.1 |
| 34 | *Onychoteuthis banksii* | 17.6 | 34 | *Neorossia caroli* | 25.2 |
| 35 | *Histioteuthis bonnellii* | 17.2 | 35 | *Pteroctopus tetracirrhus* | 22.7 |
| 36 | *Pteroctopus tetracirrhus* | 16.3 | 36 | *Histioteuthis bonnellii* | 21.1 |
| 37 | *Bathypolypus sponsalis* | 12.6 | 37 | *Heteroteuthis dispar* | 20.7 |
| 38 | *Chtenopteryx sicula* | 12.4 | 38 | *Histioteuthis reversa* | 17.8 |
| 39 | *Brachioteuthis riisei* | 12.1 | 39 | *Histioteuthis* spp. * | 10.7 |
| 40 | *Octopoteuthis sicula* | 12.0 | | | |
| 41 | *Ancistrocheirus lesueurii* | 11.5 | | | |
| 42 | *Abraliopsis morisii* | 11.5 | | | |
| 43 | *Histioteuthis* spp. * | 11.1 | | | |
| 44 | *Chiroteuthis veranii* | 11.1 | | | |

| | Aegean Sea (B5) | | | Strait of Sicily (B6) | |
|---|---|---|---|---|---|
| | Taxon | Mean Ab. | | Taxon | Mean Ab. |
| 1 | *Loligo* spp. * | 995.7 | 1 | *Alloteuthis media* | 1497.8 |
| 2 | *Illex coindetii* | 753.9 | 2 | *Alloteuthis* spp. * | 1298.1 |
| 3 | *Alloteuthis* spp. * | 706.6 | 3 | *Alloteuthis subulata* | 866.1 |
| 4 | Sepiolidae* | 495.0 | 4 | *Sepiola* spp. * | 270.4 |
| 5 | *Alloteuthis subulata* | 388.5 | 5 | *Illex coindetii* | 211.8 |
| 6 | *Alloteuthis media* | 376.2 | 6 | *Sepietta oweniana* | 177.0 |
| 7 | *Loligo forbesii* | 338.6 | 7 | *Rondeletiola minor* | 158.4 |
| 8 | *Sepia orbignyana* | 271.5 | 8 | *Abralia veranyi* | 144.1 |
| 9 | *Sepia elegans* | 258.3 | 9 | *Todaropsis eblanae* | 134.4 |
| 10 | *Loligo vulgaris* | 225.7 | 10 | *Loligo vulgaris* | 113.2 |
| 11 | *Abralia veranyi* | 202.4 | 11 | *Sepia officinalis* | 89.5 |
| 12 | *Sepia officinalis* | 190.6 | 12 | *Macrotritopus defilippi* | 69.9 |
| 13 | *Onychoteuthis banksii* | 176.2 | 13 | *Sepiola affinis* | 65.7 |
| 14 | *Rondeletiola minor* | 138.0 | 14 | *Sepia elegans* | 64.5 |
| 15 | *Brachioteuthis riisei* | 120.0 | 15 | *Sepietta* spp. * | 59.1 |
| 16 | *Todarodes sagittatus* | 119.8 | 16 | *Neorossia caroli* | 56.5 |
| 17 | *Sepiola rondeletii* | 112.0 | 17 | *Eledone moschata* | 56.2 |
| 18 | *Eledone cirrhosa* | 104.0 | 18 | *Sepia orbignyana* | 54.0 |
| 19 | *Sepiola* spp. * | 103.1 | 19 | *Sepiola intermedia* | 51.0 |
| 20 | *Sepietta oweniana* | 81.6 | 20 | *Octopus vulgaris* | 48.7 |
| 21 | *Eledone moschata* | 80.2 | 21 | *Rossia macrosoma* | 47.3 |
| 22 | *Sepietta* spp. * | 76.1 | 22 | *Sepiola rondeletii* | 43.6 |
| 23 | *Scaeurgus unicirrhus* | 71.0 | 23 | *Heteroteuthis dispar* | 42.4 |
| 24 | *Todaropsis eblanae* | 58.9 | 24 | *Eledone cirrhosa* | 41.4 |
| 25 | *Neorossia caroli* | 57.1 | 25 | *Todarodes sagittatus* | 37.1 |
| 26 | *Octopus vulgaris* | 54.1 | 26 | *Scaeurgus unicirrhus* | 36.4 |
| 27 | *Sepiola affinis* | 52.6 | 27 | *Loligo forbesii* | 35.9 |
| 28 | *Rossia macrosoma* | 44.3 | 28 | *Octopus salutii* | 24.4 |
| 29 | *Sepiola intermedia* | 38.8 | 29 | *Callistoctopus macropus* | 23.4 |
| 30 | *Chtenopteryx sicula* | 32.9 | 30 | *Histioteuthis* spp. * | 20.1 |
| 31 | *Histioteuthis bonnellii* | 32.8 | 31 | *Pteroctopus tetracirrhus* | 18.8 |
| 32 | *Sepiola ligulata* | 24.8 | 32 | *Histioteuthis reversa* | 15.0 |
| 33 | *Octopus salutii* | 23.1 | 33 | *Bathypolypus sponsalis* | 14.6 |
| 34 | *Ancistroteuthis lichtensteinii* | 22.6 | 34 | *Histioteuthis bonnellii* | 12.9 |
| 35 | *Bathypolypus sponsalis* | 20.3 | 35 | *Ancistroteuthis lichtensteinii* | 10.1 |
| 36 | *Pteroctopus tetracirrhus* | 18.5 | 36 | *Ommastrephes bartramii* | 10.0 |
| 37 | Octopodidae* | 17.2 | 37 | *Ancistrocheirus lesueurii* | 9.9 |
| 38 | *Heteroteuthis dispar* | 16.3 | 38 | *Onychoteuthis banksii* | 9.7 |
| 39 | *Octopoteuthis sicula* | 14.2 | | | |
| 40 | *Pyroteuthis margaritifera* | 13.9 | | | |
| 41 | *Histioteuthis reversa* | 13.5 | | | |
| 42 | *Chiroteuthis veranii* | 11.5 | | | |

Table S2 (Cont.). – Total number of taxa caught in the different bioregions and for the whole Mediterranean (all bioregions combined). Taxa are ordered according to their decreasing values of mean abundance (N km$^{-2}$). Asterisks show the taxa not taken into account when calculating the species richness. B1, Iberian-Lions; B2, Tyrrhenian; B3, Ionian; B4, Adriatic; B5, Aegean; B6, Strait of Sicily.

| | Mediterranean Sea (B1-B6) | | | | |
|---|---|---|---|---|---|
| | Taxon | Mean Ab. | | Taxon | Mean Ab. |
| 1 | *Loligo* spp. * | 995.7 | 45 | *Chtenopteryx sicula* | 18.8 |
| 2 | *Alloteuthis* spp. * | 734.1 | 46 | *Chiroteuthis veranii* | 18.0 |
| 3 | *Alloteuthis media* | 709.0 | 47 | Octopodidae* | 17.2 |
| 4 | Sepiolidae* | 495.0 | 48 | *Histioteuthis* spp. * | 15.1 |
| 5 | *Illex coindetii* | 329.4 | 49 | *Pyroteuthis margaritifera* | 13.9 |
| 6 | *Alloteuthis subulata* | 296.5 | 50 | *Stoloteuthis leucoptera* | 12.9 |
| 7 | *Loligo vulgaris* | 264.4 | 51 | *Octopoteuthis sicula* | 12.6 |
| 8 | *Sepiola* spp. * | 193.2 | 52 | *Abraliopsis morisii* | 11.5 |
| 9 | *Loligo forbesii* | 185.3 | 53 | *Ancistrocheirus lesueurii* | 10.7 |
| 10 | *Sepietta oweniana* | 161.7 | 54 | *Ommastrephes bartramii* | 10.0 |
| 11 | *Rondeletiola minor* | 134.8 | | | |
| 12 | *Todarodes sagittatus* | 131.6 | | | |
| 13 | *Abralia veranyi* | 121.5 | | | |
| 14 | *Sepia orbignyana* | 120.5 | | | |
| 15 | *Sepia elegans* | 115.1 | | | |
| 16 | *Sepiola affinis* | 109.1 | | | |
| 17 | *Sepia officinalis* | 109.0 | | | |
| 18 | *Brachioteuthis riisei* | 108.1 | | | |
| 19 | *Sepiola rondeletii* | 97.6 | | | |
| 20 | *Todaropsis eblanae* | 79.4 | | | |
| 21 | *Eledone cirrhosa* | 79.1 | | | |
| 22 | *Eledone moschata* | 70.1 | | | |
| 23 | *Sepietta obscura* | 59.1 | | | |
| 24 | *Sepietta spp. ** | 56.3 | | | |
| 25 | *Octopus vulgaris* | 56.1 | | | |
| 26 | *Sepiola ligulata* | 52.3 | | | |
| 27 | *Sepiola intermedia* | 51.0 | | | |
| 28 | *Onychoteuthis banksii* | 49.9 | | | |
| 29 | *Sepietta neglecta* | 49.6 | | | |
| 30 | *Scaeurgus unicirrhus* | 43.2 | | | |
| 31 | *Callistoctopus macropus* | 42.2 | | | |
| 32 | *Rossia macrosoma* | 40.0 | | | |
| 33 | *Bathypolypus sponsalis* | 39.9 | | | |
| 34 | *Sepiola robusta* | 39.0 | | | |
| 35 | *Neorossia caroli* | 36.0 | | | |
| 36 | *Macrotritopus defilippi* | 34.9 | | | |
| 37 | *Ancistroteuthis lichtensteinii* | 32.3 | | | |
| 38 | *Octopus salutii* | 25.6 | | | |
| 39 | *Heteroteuthis dispar* | 24.7 | | | |
| 40 | *Pteroctopus tetracirrhus* | 20.1 | | | |
| 41 | *Ocythoe tuberculata* | 19.8 | | | |
| 42 | *Histioteuthis reversa* | 19.7 | | | |
| 43 | *Histioteuthis bonnellii* | 19.4 | | | |
| 44 | *Opisthoteuthis calypso* | 19.2 | | | |

Table S3. – Results of similarity percentage analysis (SIMPER) for the bathymetric cephalopod assemblages obtained by the cluster analysis shown in Figure 2 for the six Mediterranean bioregions analysed (B1-B6). Abu (average abundance); AvSim (average similarity); Con (percentage contribution); Cum (cumulative percentages).

Bioregion B1: Iberian-Lions

| Group A (14-175 m) | AvSim: 86.08 | | | Group B (175-450 m) | AvSim: 84.11 | | | Group C (450-750 m) | AvSim: 79.51 | | | Group D (750-866 m) | AvSim: 69.57 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum |
| *Alloteuthis* spp. | 5.89 | 8.36 | 8.36 | *S. oweniana* | 4.89 | 7.48 | 7.48 | *A. veranyi* | 3.00 | 6.93 | 6.93 | *B. sponsalis* | 2.45 | 12.90 | 12.90 |
| *L. forbesii* | 4.68 | 6.53 | 14.89 | Sepiolidae | 4.73 | 6.94 | 14.41 | Sepiolidae | 3.08 | 6.10 | 13.03 | *A. veranyi* | 2.79 | 12.86 | 25.76 |
| *I. coindetii* | 4.33 | 6.02 | 20.91 | *Alloteuthis* spp. | 3.76 | 5.65 | 20.07 | *T. sagittatus* | 2.52 | 5.88 | 18.91 | *T. sagittatus* | 2.30 | 12.03 | 37.79 |
| *L. vulgaris* | 4.06 | 5.61 | 26.52 | *A. veranyi* | 3.78 | 5.60 | 25.67 | *B. sponsalis* | 2.39 | 5.72 | 24.63 | *A. lichtensteinii* | 1.99 | 10.06 | 47.85 |
| *E. cirrhosa* | 3.85 | 5.50 | 32.02 | *I. coindetii* | 3.56 | 5.40 | 31.06 | *I. coindetii* | 2.56 | 5.56 | 30.19 | *N. caroli* | 1.79 | 9.64 | 57.50 |
| *S. elegans* | 3.45 | 4.90 | 36.92 | *R. minor* | 3.42 | 5.11 | 36.18 | *H. reversa* | 2.24 | 5.33 | 35.52 | *T. eblanae* | 1.82 | 9.50 | 67.00 |
| *A. veranyi* | 3.60 | 4.90 | 41.82 | *E. cirrhosa* | 3.04 | 4.80 | 40.98 | *R. macrosoma* | 2.27 | 5.27 | 40.79 | Sepiolidae | 1.87 | 9.26 | 76.26 |
| *Sepiolidae* | 3.21 | 4.68 | 46.50 | *S. orbignyana* | 3.25 | 4.66 | 45.64 | *T. eblanae* | 2.18 | 5.19 | 45.99 | *H. reversa* | 1.95 | 9.25 | 85.51 |
| *O. vulgaris* | 3.44 | 4.63 | 51.13 | *L. forbesii* | 3.05 | 4.24 | 49.88 | *H. bonnellii* | 2.14 | 5.13 | 51.12 | | | | |
| *S. oweniana* | 3.24 | 4.53 | 55.66 | *O. salutii* | 2.63 | 4.23 | 54.11 | *H. dispar* | 2.07 | 4.94 | 56.05 | | | | |
| *S. orbignyana* | 3.41 | 4.50 | 60.16 | *R. macrosoma* | 2.67 | 4.22 | 58.33 | *N. caroli* | 2.08 | 4.84 | 60.90 | | | | |
| *R. minor* | 3.17 | 4.26 | 64.42 | *T. eblanae* | 2.64 | 4.15 | 62.48 | *A. lichtensteinii* | 1.96 | 4.84 | 65.73 | | | | |
| *T. eblanae* | 2.99 | 4.17 | 68.60 | *T. sagittatus* | 2.62 | 4.15 | 66.63 | *S. oweniana* | 2.50 | 4.81 | 70.55 | | | | |
| *E. moschata* | 2.95 | 4.10 | 72.69 | *S. elegans* | 2.57 | 3.66 | 70.29 | *P. tetracirrhus* | 1.98 | 4.74 | 75.29 | | | | |
| *R. macrosoma* | 2.69 | 3.86 | 76.56 | *P. tetracirrhus* | 2.23 | 3.58 | 73.87 | *E. cirrhosa* | 2.24 | 4.64 | 79.93 | | | | |
| *S. unicirrhus* | 2.64 | 3.78 | 80.34 | *B. sponsalis* | 2.30 | 3.54 | 77.41 | *O. salutii* | 2.23 | 4.52 | 84.45 | | | | |
| | | | | *S. unicirrhus* | 2.28 | 3.36 | 80.77 | | | | | | | | |

Bioregion B2: Tyrrhenian

| Group A (10-200 m) | AvSim: 86.64 | | | Group B (200-500 m) | AvSim: 85.76 | | | Group C (500-700 m) | AvSim: 78.84 | | | Group D (700-775 m) | AvSim: 41.07 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum |
| *Alloteuthis* spp. | 5.45 | 8.26 | 8.26 | *S. oweniana* | 4.92 | 7.81 | 7.81 | *S. oweniana* | 2.95 | 6.61 | 6.61 | *H. reversa* | 2.16 | 35.62 | 35.62 |
| *L. vulgaris* | 5.10 | 7.61 | 15.87 | Sepiolidae | 4.86 | 7.54 | 15.34 | *A. veranyi* | 2.32 | 5.78 | 12.39 | *T. sagittatus* | 1.92 | 30.76 | 66.38 |
| *L. forbesii* | 4.75 | 6.87 | 22.74 | *R. minor* | 3.79 | 5.69 | 21.04 | *I. coindetii* | 2.43 | 5.74 | 18.13 | *I. coindetii* | 1.41 | 13.51 | 79.88 |
| *I. coindetii* | 4.39 | 6.00 | 28.74 | *I. coindetii* | 3.44 | 5.24 | 26.28 | *R. macrosoma* | 2.30 | 5.71 | 23.84 | *P. tetracirrhus* | 1.24 | 10.29 | 90.17 |
| *E. cirrhosa* | 3.66 | 5.64 | 34.38 | *Alloteuthis* spp. | 3.50 | 5.16 | 31.44 | *T. sagittatus* | 2.20 | 5.69 | 29.53 | | | | |
| Sepiolidae | 3.35 | 5.01 | 39.39 | *S. orbignyana* | 3.09 | 5.09 | 36.53 | *H. bonnellii* | 2.11 | 5.63 | 35.16 | | | | |
| *S. elegans* | 3.23 | 4.94 | 44.33 | *T. eblanae* | 3.22 | 5.08 | 41.61 | *E. cirrhosa* | 2.27 | 5.56 | 40.71 | | | | |
| *S. orbignyana* | 3.28 | 4.86 | 49.19 | *E. cirrhosa* | 3.12 | 5.06 | 46.67 | *H. reversa* | 2.07 | 5.53 | 46.24 | | | | |
| *S. oweniana* | 3.13 | 4.79 | 53.98 | *L. forbesii* | 3.27 | 5.04 | 51.72 | *N. caroli* | 2.14 | 5.49 | 51.73 | | | | |
| *R. minor* | 3.28 | 4.60 | 58.58 | *A. veranyi* | 2.94 | 4.67 | 56.39 | *T. eblanae* | 2.16 | 5.41 | 57.14 | | | | |
| *T. eblanae* | 3.04 | 4.50 | 63.08 | *L. vulgaris* | 3.37 | 4.37 | 60.76 | *B. sponsalis* | 2.18 | 5.41 | 62.55 | | | | |
| *S. unicirrhus* | 2.92 | 4.45 | 67.53 | *T. sagittatus* | 2.48 | 4.03 | 64.79 | *P. tetracirrhus* | 2.02 | 5.27 | 67.81 | | | | |
| *S. officinalis* | 2.90 | 4.45 | 71.98 | *R. macrosoma* | 2.43 | 4.03 | 68.82 | *H. dispar* | 1.93 | 4.97 | 72.78 | | | | |
| *T. sagittatus* | 2.87 | 4.18 | 76.16 | *S. elegans* | 2.64 | 4.02 | 72.84 | *A. lichtensteinii* | 1.90 | 4.90 | 77.68 | | | | |
| *A. veranyi* | 2.62 | 4.07 | 80.23 | | | | | Sepiolidae | 2.40 | 4.82 | 82.50 | | | | |

Table S3 (Cont.). – Results of similarity percentage analysis (SIMPER) for the bathymetric cephalopod assemblages obtained by the cluster analysis shown in Figure 2 for the six Mediterranean bioregions analysed (B1-B6). Abu (average abundance); AvSim (average similarity); Con (percentage contribution); Cum (cumulative percentages).

| Bioregion B3: Ionian | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Group A (11-200 m) | AvSim: 81.26 | | | Group B (200-400 m) | AvSim: 80.88 | | | Group C (400-650 m) | AvSim: 73.23 | | | Group D (650-800 m) | AvSim: 70.41 | | |
| Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum |
| *Alloteuthis* spp. | 6.30 | 12.55 | 12.55 | *I. coindetii* | 4.35 | 8.45 | 8.45 | *A. veranyi* | 2.50 | 8.17 | 8.17 | *H. reversa* | 2.35 | 15.06 | 15.06 |
| *I. coindetii* | 4.67 | 8.88 | 21.42 | *S. oweniana* | 3.62 | 6.95 | 15.40 | *I. coindetii* | 2.56 | 7.91 | 16.09 | *I. coindetii* | 2.56 | 14.45 | 29.51 |
| *S. elegans* | 3.69 | 7.25 | 28.67 | *R. minor* | 3.61 | 6.89 | 22.29 | *H. reversa* | 2.24 | 7.32 | 23.41 | *A. veranyi* | 2.39 | 13.74 | 43.25 |
| *S. orbignyana* | 3.43 | 6.65 | 35.32 | *A. veranyi* | 3.10 | 5.99 | 28.29 | *T. sagittatus* | 2.16 | 7.05 | 30.46 | *A. lichtensteinii* | 2.07 | 13.07 | 56.32 |
| *L. vulgaris* | 4.39 | 6.01 | 41.33 | *T. eblanae* | 2.96 | 5.83 | 34.11 | *T. eblanae* | 2.30 | 7.01 | 37.46 | *H. bonnellii* | 1.98 | 12.49 | 68.81 |
| *T. eblanae* | 3.18 | 5.98 | 47.30 | *E. cirrhosa* | 2.55 | 5.21 | 39.32 | *H. bonnellii* | 1.99 | 6.59 | 44.06 | *T. sagittatus* | 1.57 | 7.61 | 76.42 |
| *R. minor* | 3.10 | 5.94 | 53.24 | *S. elegans* | 2.65 | 5.05 | 44.37 | *N. caroli* | 1.94 | 6.42 | 50.48 | *O. banksii* | 1.49 | 7.52 | 83.94 |
| *S. unicirrhus* | 3.01 | 5.84 | 59.09 | *S. unicirrhus* | 2.33 | 4.92 | 49.29 | *S. oweniana* | 2.08 | 5.23 | 55.71 | | | | |
| *E. cirrhosa* | 3.00 | 5.70 | 64.79 | *R. macrosoma* | 2.41 | 4.77 | 54.06 | *H. dispar* | 1.84 | 5.16 | 60.87 | | | | |
| *S. oweniana* | 2.84 | 5.61 | 70.40 | *Alloteuthis* spp. | 3.12 | 4.56 | 58.62 | *S. unicirrhus* | 1.68 | 4.81 | 65.68 | | | | |
| *A. veranyi* | 2.79 | 5.35 | 75.75 | *S. orbignyana* | 2.26 | 4.55 | 63.17 | *O. salutii* | 1.76 | 4.65 | 70.33 | | | | |
| *R. macrosoma* | 2.77 | 5.07 | 80.82 | *T. sagittatus* | 2.09 | 4.31 | 67.48 | *P. tetracirrhus* | 1.77 | 4.63 | 74.96 | | | | |
| | | | | *L. forbesii* | 2.73 | 4.31 | 71.79 | *L. forbesii* | 2.11 | 3.72 | 78.68 | | | | |
| | | | | Sepiolidae | 3.07 | 4.23 | 76.01 | *R. macrosoma* | 1.70 | 3.69 | 82.37 | | | | |
| | | | | *O. salutii* | 2.09 | 4.22 | 80.24 | | | | | | | | |
| Bioregion B4: Adriatic | | | | | | | | | | | | | | | |
| *Group A (10-175 m)* | AvSim: 85.21 | | | *Group B (175-350 m)* | AvSim: 82.28 | | | *Group C (350-625 m)* | AvSim: 76.57 | | | *Group D* (625-799 m) | AvSim: 43.13 | | |
| Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum |
| *Alloteuthis* spp. | 5.89 | 10.16 | 10.16 | *I. coindetii* | 5.01 | 10.62 | 10.62 | *I. coindetii* | 2.78 | 9.24 | 9.24 | *T. eblanae* | 3.19 | 46.40 | 46.40 |
| *I. coindetii* | 5.02 | 8.16 | 18.32 | *T. eblanae* | 3.56 | 7.78 | 18.40 | *A. veranyi* | 2.50 | 8.42 | 17.66 | *H. reversa* | 1.86 | 28.77 | 75.17 |
| *L. vulgaris* | 4.78 | 7.68 | 25.99 | *R. minor* | 3.43 | 7.17 | 25.57 | *T. eblanae* | 2.48 | 8.30 | 25.96 | *R. macrosoma* | 1.20 | 8.75 | 83.92 |
| *S. oweniana* | 3.17 | 5.49 | 31.48 | Sepiolidae | 3.43 | 6.87 | 32.44 | *R. macrosoma* | 2.13 | 7.20 | 33.16 | | | | |
| *E. moschata* | 3.37 | 5.37 | 36.85 | *Alloteuthis* spp. | 3.68 | 6.74 | 39.18 | *H. reversa* | 2.07 | 7.11 | 40.27 | | | | |
| *E. cirrhosa* | 3.07 | 5.32 | 42.17 | *S. oweniana* | 3.18 | 6.46 | 45.64 | *T. sagittatus* | 2.07 | 7.08 | 47.35 | | | | |
| *S. elegans* | 3.25 | 5.29 | 47.46 | *E. cirrhosa* | 2.84 | 6.15 | 51.79 | *N. caroli* | 2.16 | 6.89 | 54.24 | | | | |
| Sepiolidae | 2.91 | 5.13 | 52.59 | *L. vulgaris* | 3.07 | 5.84 | 57.63 | Sepiolidae | 2.13 | 6.12 | 60.36 | | | | |
| *R. minor* | 2.99 | 4.96 | 57.54 | *T. sagittatus* | 2.68 | 5.38 | 63.01 | *H. bonnellii* | 1.88 | 5.72 | 66.08 | | | | |
| *T. eblanae* | 2.87 | 4.95 | 62.49 | *O. salutii* | 2.38 | 5.25 | 68.26 | *E. cirrhosa* | 1.84 | 5.45 | 71.53 | | | | |
| *S. orbignyana* | 2.92 | 4.92 | 67.41 | *R. macrosoma* | 2.24 | 4.89 | 73.14 | *O. salutii* | 1.77 | 5.28 | 76.81 | | | | |
| *T. sagittatus* | 2.94 | 4.77 | 72.18 | *S. unicirrhus* | 2.06 | 4.56 | 77.70 | *H. dispar* | 1.68 | 5.14 | 81.96 | | | | |
| *O. vulgaris* | 2.63 | 4.47 | 76.66 | *S. orbignyana* | 1.98 | 4.23 | 81.94 | | | | | | | | |
| *O. salutii* | 2.48 | 4.42 | 81.07 | | | | | | | | | | | | |

Table S3 (Cont.). – Results of similarity percentage analysis (SIMPER) for the bathymetric cephalopod assemblages obtained by the cluster analysis shown in Figure 2 for the six Mediterranean bioregions analysed (B1-B6). Abu (average abundance); AvSim (average similarity); Con (percentage contribution); Cum (cumulative percentages).

| Bioregion B5: Aegean | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Group A (19-225 m)* | AvSim: 83.40 | | | *Group B (225-425 m)* | AvSim: 85.03 | | | *Group C (425-550 m)* | AvSim: 71.17 | | | *Group D (550-791 m)* | AvSim: 61.71 | | |
| Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum |
| *Alloteuthis* spp. | 5.85 | 10.15 | 10.15 | *I. coindetii* | 6.04 | 9.02 | 9.02 | *I. coindetii* | 3.56 | 10.44 | 10.44 | *I. coindetii* | 3.15 | 14.48 | 14.48 |
| *I. coindetii* | 5.47 | 8.88 | 19.03 | *S. orbignyana* | 4.43 | 7.16 | 16.18 | *A. veranyi* | 3.20 | 8.61 | 19.05 | *T. sagittatus* | 2.66 | 11.32 | 25.80 |
| *S. elegans* | 4.30 | 7.40 | 26.43 | *S. elegans* | 4.23 | 6.74 | 22.92 | *T. sagittatus* | 2.93 | 8.47 | 27.51 | *R. macrosoma* | 2.45 | 10.11 | 35.91 |
| *L. vulgaris* | 4.71 | 7.31 | 33.74 | *Alloteuthis* spp. | 4.13 | 6.20 | 29.12 | *N. caroli* | 2.40 | 7.12 | 34.63 | *A. lichtensteinii* | 2.22 | 9.64 | 45.54 |
| *L. forbesii* | 4.73 | 6.97 | 40.71 | *L. forbesii* | 4.11 | 6.03 | 35.15 | *T. eblanae* | 2.40 | 7.11 | 41.74 | *H. reversa* | 2.03 | 9.52 | 55.06 |
| *E. cirrhosa* | 3.91 | 6.61 | 47.31 | Sepiolidae | 3.44 | 5.29 | 40.45 | *Alloteuthis* spp. | 2.63 | 6.96 | 48.70 | *A. veranyi* | 2.65 | 8.40 | 63.46 |
| *S. orbignyana* | 4.02 | 5.98 | 53.29 | *T. eblanae* | 3.08 | 4.92 | 45.36 | *E. cirrhosa* | 2.31 | 6.68 | 55.39 | *H. bonnellii* | 1.86 | 5.89 | 69.35 |
| *E. moschata* | 3.41 | 5.31 | 58.60 | *E. cirrhosa* | 3.03 | 4.85 | 50.21 | *H. bonnellii* | 2.38 | 6.40 | 61.78 | Sepiolidae | 1.78 | 5.78 | 75.13 |
| Sepiolidae | 3.09 | 5.07 | 63.67 | *T. sagittatus* | 3.10 | 4.84 | 55.06 | *B. sponsalis* | 2.07 | 6.13 | 67.91 | *R. minor* | 1.60 | 5.28 | 80.41 |
| *S. unicirrhus* | 3.16 | 4.94 | 68.61 | *A. veranyi* | 3.39 | 4.73 | 59.79 | *P. tetracirrhus* | 1.95 | 5.81 | 73.71 | | | | |
| *R. minor* | 3.28 | 4.81 | 73.42 | *R. minor* | 3.16 | 4.57 | 64.36 | *R. macrosoma* | 2.02 | 5.59 | 79.30 | | | | |
| *S. oweniana* | 3.01 | 4.68 | 78.10 | *S. oweniana* | 2.90 | 4.30 | 68.66 | Sepiolidae | 1.86 | 3.32 | 82.63 | | | | |
| *O. vulgaris* | 2.67 | 4.34 | 82.45 | *R. macrosoma* | 2.60 | 4.12 | 72.77 | | | | | | | | |
| | | | | *S. unicirrhus* | 2.78 | 4.11 | 76.88 | | | | | | | | |
| | | | | *N. caroli* | 2.83 | 3.58 | 80.47 | | | | | | | | |

| Bioregion B6: Strait of Sicily | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Group A (17-200 m)* | AvSim: 80.00 | | | *Group B (200-400 m)* | AvSim: 83.52 | | | *Group C (400-500 m)* | AvSim: 78.32 | | | *Group D (500-793 m)* | AvSim: 72.14 | | |
| Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum | Species | Abu | Con | Cum |
| *Alloteuthis* spp. | 7.14 | 13.34 | 13.34 | Sepiolidae | 5.57 | 10.09 | 10.09 | *A. veranyi* | 3.21 | 9.45 | 9.45 | *T. sagittatus* | 2.43 | 11.28 | 11.28 |
| *I. coindetii* | 4.46 | 8.37 | 21.71 | *S. oweniana* | 4.41 | 8.41 | 18.50 | *T. eblanae* | 2.89 | 8.68 | 18.13 | *T. eblanae* | 2.26 | 10.72 | 22.00 |
| *S. elegans* | 3.50 | 7.18 | 28.90 | *Alloteuthis* spp. | 5.15 | 8.27 | 26.77 | *R. macrosoma* | 2.62 | 8.09 | 26.22 | *N. caroli* | 2.19 | 9.58 | 31.58 |
| *T. eblanae* | 3.49 | 7.04 | 35.93 | *T. eblanae* | 4.02 | 7.84 | 34.61 | *I. coindetii* | 2.69 | 7.72 | 33.93 | *H. bonnellii* | 2.08 | 9.45 | 41.02 |
| *R. minor* | 3.71 | 6.93 | 42.87 | *A. veranyi* | 3.89 | 7.38 | 41.99 | *S. oweniana* | 2.82 | 7.69 | 41.63 | *H. reversa* | 2.02 | 9.16 | 50.18 |
| *S. oweniana* | 3.53 | 6.80 | 49.67 | *R. minor* | 3.90 | 6.65 | 48.65 | *L. forbesii* | 2.62 | 7.65 | 49.28 | *R. macrosoma* | 2.06 | 9.07 | 59.26 |
| *L. vulgaris* | 3.46 | 6.69 | 56.36 | *I. coindetii* | 3.46 | 6.23 | 54.88 | *N. caroli* | 2.71 | 7.64 | 56.91 | *P. tetracirrhus* | 1.85 | 8.80 | 68.06 |
| Sepiolidae | 3.28 | 6.18 | 62.54 | *E. cirrhosa* | 2.71 | 5.24 | 60.12 | *E. cirrhosa* | 2.19 | 6.60 | 63.51 | *A. veranyi* | 1.95 | 7.91 | 75.97 |
| *E. moschata* | 3.05 | 6.05 | 68.59 | *S. orbignyana* | 2.71 | 4.71 | 64.83 | *O. salutii* | 2.17 | 6.22 | 69.73 | *I. coindetii* | 2.34 | 7.91 | 83.88 |
| *S. unicirrhus* | 2.80 | 5.70 | 74.29 | *S. elegans* | 2.54 | 4.67 | 69.51 | *P. tetracirrhus* | 1.97 | 6.03 | 75.75 | | | | |
| *E. cirrhosa* | 2.78 | 5.55 | 79.84 | *L. forbesii* | 2.35 | 4.40 | 73.91 | *S. unicirrhus* | 2.03 | 6.02 | 81.77 | | | | |
| *S. orbignyana* | 2.81 | 5.38 | 85.21 | *S. unicirrhus* | 2.47 | 4.40 | 78.31 | | | | | | | | |
| | | | | *R. macrosoma* | 2.40 | 4.33 | 82.64 | | | | | | | | |

Table S4. – SIMPER analyses of the dissimilarity between the old (1994-2004) and recent (2005-2015) time series by bathymetric strata and bio-region for those stratum-bioregion settings showing significant differences from a previous PERMANOVA (see Table 2). Av.Abu (average abundance); Contrib% (percentage contribution); Cum% (cumulative percentages).

Stratum: Continental shelf
Bio-region: Iberian-Lions
Time series old and recent
Average dissimilarity = 28.97

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| *L. forbesii* | 5.9 | 25.38 | 14.49 | 14.49 |
| *Alloteuthis* spp. | 39.51 | 32.22 | 8.29 | 22.78 |
| *L. vulgaris* | 10.24 | 19.28 | 7.9 | 30.68 |
| *I. coindetii* | 19.22 | 18.21 | 7.13 | 37.81 |
| *A. veranyi* | 7.19 | 13.21 | 6.12 | 43.93 |
| *B. sponsalis* | 2.7 | 7.57 | 4.74 | 48.67 |
| *O. vulgaris* | 9.61 | 13.54 | 4.7 | 53.37 |
| *S. orbignyana* | 9.12 | 11.56 | 4.56 | 57.92 |
| *R. minor* | 8.75 | 8.74 | 4.48 | 62.41 |
| *S. elegans* | 12.68 | 12.92 | 3.62 | 66.03 |
| *S. oweniana* | 9.1 | 11.23 | 3.23 | 69.26 |
| *T. eblanae* | 8.43 | 7.7 | 3.03 | 72.29 |
| *S. officinalis* | 5.55 | 6.05 | 3.02 | 75.31 |
| *E. moschata* | 9.47 | 9.55 | 2.97 | 78.28 |
| *R. macrosoma* | 4.93 | 7.59 | 2.59 | 80.87 |
| *E. cirrhosa* | 14.28 | 14.88 | 2.49 | 83.35 |
| *A. lichtensteinii* | 2.6 | 3.86 | 2.46 | 85.82 |
| Sepiolidae | 11.27 | 8.51 | 2.46 | 88.28 |
| *P. tetracirrhus* | 3.85 | 2.88 | 2.1 | 90.38 |

Bio-region: Strait of Sicily
Time series old and recent
Average dissimilarity = 41.18

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| *Alloteuthis* spp. | 43.88 | 49.07 | 20.98 | 20.98 |
| *R. minor* | 1.44 | 13.96 | 8.98 | 29.95 |
| *S. oweniana* | 0.59 | 12.62 | 8.56 | 38.51 |
| *I. coindetii* | 15.66 | 19.77 | 7.95 | 46.46 |
| *L. vulgaris* | 10.64 | 11.43 | 6.23 | 52.68 |
| Sepiolidae | 13 | 8.04 | 5.06 | 57.74 |
| *A. veranyi* | 3.87 | 7.58 | 4.82 | 62.56 |
| *S. elegans* | 12.69 | 10.05 | 4.81 | 67.37 |
| *E. moschata* | 6.44 | 7.95 | 4.04 | 71.41 |
| *S. officinalis* | 2.89 | 6.37 | 4.01 | 75.42 |
| *O. vulgaris* | 3.9 | 6.34 | 3.75 | 79.18 |
| *S. unicirrhus* | 8.42 | 7.83 | 3.58 | 82.76 |
| *S. orbignyana* | 7.42 | 6.52 | 3.5 | 86.26 |
| *T. eblanae* | 12.1 | 13 | 2.84 | 89.1 |
| *R. macrosoma* | 0 | 3.25 | 2.49 | 91.59 |

Stratum: Upper slope
Bio-region: Iberian-Lions
Time series old and recent
Average dissimilarity = 35.97

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| *S. oweniana* | 16.78 | 28.52 | 10.88 | 10.88 |
| Sepiolidae | 22.57 | 14.73 | 9.9 | 20.78 |
| *Alloteuthis* spp. | 15.11 | 5.95 | 7.87 | 28.65 |
| *L. forbesii* | 3.71 | 10.85 | 6.11 | 34.76 |
| *R. minor* | 12.47 | 8.25 | 5.5 | 40.26 |
| *A. veranyi* | 11.99 | 14.53 | 5.31 | 45.57 |
| *B. riisei* | 1.64 | 6.35 | 4.85 | 50.42 |
| *S. orbignyana* | 6.58 | 10.13 | 4.82 | 55.24 |
| *I. coindetii* | 9.39 | 14.46 | 4.71 | 59.96 |
| *L. vulgaris* | 4.61 | 3.65 | 4.1 | 64.06 |
| *S. elegans* | 5.34 | 4.85 | 4.01 | 68.07 |
| *N. caroli* | 5.71 | 4.13 | 3.46 | 71.53 |
| *A. lichtensteinii* | 4.07 | 2.77 | 2.85 | 74.38 |
| *O. vulgaris* | 4.2 | 3.72 | 2.3 | 76.68 |
| *T. eblanae* | 6.19 | 6.23 | 2.24 | 78.92 |
| *S. unicirrhus* | 4.99 | 4.45 | 2.23 | 81.15 |
| *R. macrosoma* | 7.21 | 6.79 | 2.12 | 83.27 |
| *E. moschata* | 3 | 2.4 | 2.06 | 85.34 |
| *H. reversa* | 2.2 | 2.54 | 2.04 | 87.38 |
| *B. sponsalis* | 4.3 | 5.05 | 1.94 | 89.32 |
| *H. bonnellii* | 1.24 | 1.94 | 1.62 | 90.94 |

Bio-region: Ionian
Time series old and recent
Average dissimilarity = 39.80

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| *I. coindetii* | 9.45 | 24.92 | 14.58 | 14.58 |
| *Alloteuthis* spp. | 14.41 | 6.04 | 10.25 | 24.83 |
| Sepiolidae | 12.15 | 5.16 | 10.15 | 34.97 |
| *L. forbesii* | 6.86 | 7.87 | 7 | 41.97 |
| *S. oweniana* | 12.57 | 12.45 | 6.93 | 48.9 |
| *R. minor* | 12.27 | 12.9 | 5.94 | 54.83 |
| *A. veranyi* | 12.29 | 7.32 | 5.05 | 59.89 |
| *S. elegans* | 6.78 | 6.54 | 4.07 | 63.95 |
| *L. vulgaris* | 3.82 | 1.89 | 3.32 | 67.28 |
| *T. eblanae* | 8.31 | 9.08 | 3.12 | 70.4 |
| *H. dispar* | 4.93 | 2.65 | 3.06 | 73.46 |
| *R. macrosoma* | 4.43 | 5.75 | 2.82 | 76.28 |
| *N. caroli* | 3.32 | 1.99 | 2.55 | 78.84 |
| *O. salutii* | 3.66 | 2.94 | 2.54 | 81.37 |
| *E. moschata* | 1.66 | 2.63 | 2.49 | 83.86 |
| *S. orbignyana* | 4.98 | 3.46 | 2.28 | 86.14 |
| *H. bonnellii* | 2.76 | 1.99 | 2.11 | 88.25 |
| *P. tetracirrhus* | 3.75 | 2.31 | 1.97 | 90.22 |

Bio-region: Strait of Sicily
Time series old and recent
Average dissimilarity = 50.37

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| *Alloteuthis* spp. | 21.5 | 36.1 | 19.83 | 19.83 |
| Sepiolidae | 27.63 | 2.53 | 16.48 | 36.31 |
| *S. oweniana* | 0 | 18.22 | 12.24 | 48.55 |
| *R. minor* | 0.4 | 11.98 | 7.77 | 56.32 |
| *A. veranyi* | 12.15 | 14.37 | 5.31 | 61.63 |
| *I. coindetii* | 7.46 | 14.18 | 4.91 | 66.54 |
| *N. caroli* | 3.25 | 2.62 | 3.66 | 70.19 |
| *S. orbignyana* | 5.77 | 8.21 | 3.25 | 73.45 |
| *S. elegans* | 2.97 | 6.86 | 3.22 | 76.66 |
| *T. eblanae* | 14.55 | 16.58 | 3.06 | 79.72 |
| *R. macrosoma* | 4.99 | 5.08 | 3.04 | 82.76 |
| *L. forbesii* | 1.75 | 5.29 | 2.65 | 85.41 |
| *L. vulgaris* | 0.7 | 4.49 | 2.64 | 88.05 |
| *S. unicirrhus* | 4.67 | 7.08 | 2.22 | 90.27 |

Table S4 (Cont.). – SIMPER analyses of the dissimilarity between the old (1994-2004) and recent (2005-2015) time series by bathymetric strata and bio-region for those stratum-bioregion settings showing significant differences from a previous PERMANOVA (see Table 2). Av.Abu (average abundance); Contrib% (percentage contribution); Cum% (cumulative percentages).

Stratum: Middle slope
Bio-region: Iberian-Lions
Time series old and recent
Average dissimilarity = 35.95

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| Sepiolidae | 8.81 | 6.51 | 11.53 | 11.53 |
| *S. oweniana* | 4.96 | 7.51 | 9.2 | 20.74 |
| *I. coindetii* | 4.29 | 8.27 | 7.1 | 27.84 |
| *Alloteuthis* spp. | 4.08 | 2.09 | 6.62 | 34.46 |
| *A. veranyi* | 8.83 | 7.98 | 5.67 | 40.13 |
| *L. forbesii* | 0 | 3.33 | 5.08 | 45.21 |
| *O. salutii* | 5.23 | 4.63 | 4.57 | 49.78 |
| *E. cirrhosa* | 5.53 | 5.04 | 4.33 | 54.11 |
| *R. macrosoma* | 4.44 | 3.62 | 4.27 | 58.38 |
| *S. orbignyana* | 1.6 | 1.84 | 3.59 | 61.97 |
| *H. dispar* | 3.26 | 3.51 | 3.35 | 65.31 |
| *R. minor* | 2.27 | 1.38 | 3.31 | 68.62 |
| *T. sagittatus* | 5.43 | 6.77 | 3.29 | 71.91 |
| *B. riisei* | 1.97 | 2.18 | 3.17 | 75.08 |
| *P. tetracirrhus* | 3.15 | 3.27 | 2.86 | 77.94 |
| *N. caroli* | 3.96 | 3.51 | 2.73 | 80.67 |
| *S. leucoptera* | 0.76 | 1.78 | 2.67 | 83.34 |
| *H. bonnellii* | 3.69 | 4.19 | 2.59 | 85.93 |
| *T. eblanae* | 4.92 | 4.51 | 2.57 | 88.5 |
| *O. vulgaris* | 1.75 | 0 | 2.47 | 90.97 |

Bio-region: Strait of Sicily
Time series old and recent
Average dissimilarity = 39.63

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| *S. oweniana* | 0 | 7.54 | 12.84 | 12.84 |
| Sepiolidae | 5.9 | 0 | 10.01 | 22.85 |
| *L. forbesii* | 2.26 | 7.48 | 9.17 | 32.01 |
| *A. veranyi* | 6.58 | 10.83 | 8.9 | 40.91 |
| *L. vulgaris* | 0 | 5.38 | 8.28 | 49.19 |
| *N. caroli* | 1.21 | 4.86 | 6.82 | 56.02 |
| *I. coindetii* | 7.2 | 6.12 | 5.01 | 61.03 |
| *T. sagittatus* | 1.82 | 4.16 | 4.71 | 65.74 |
| *T. eblanae* | 8.19 | 7.98 | 4.04 | 69.77 |
| *R. minor* | 0 | 2.34 | 3.78 | 73.55 |
| *R. macrosoma* | 8.27 | 6.67 | 3.77 | 77.32 |
| *S. orbignyana* | 0.79 | 2.52 | 3.77 | 81.09 |
| *Alloteuthis* spp. | 0.79 | 1.65 | 3.21 | 84.3 |
| *S. elegans* | 1.11 | 1.49 | 2.92 | 87.22 |
| *H. dispar* | 0 | 1.25 | 2.31 | 89.53 |
| *E. moschata* | 0 | 1.26 | 1.99 | 91.53 |

Stratum: Lower slope
Bio-region: Ionian
Time series old and recent
Average dissimilarity = 63.68

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| *I. coindetii* | 1.54 | 9.95 | 23.19 | 23.19 |
| *A. veranyi* | 2.84 | 3.14 | 10.73 | 33.91 |
| *H. reversa* | 4.63 | 4.85 | 9.82 | 43.73 |
| *N. caroli* | 1 | 2.8 | 7.5 | 51.23 |
| *A. lichtensteinii* | 3.46 | 1.51 | 7.22 | 58.45 |
| *T. eblanae* | 0.94 | 2.68 | 6.31 | 64.76 |
| *H. bonnellii* | 2.59 | 2.62 | 6.17 | 70.93 |
| *T. sagittatus* | 3.73 | 3.21 | 5.52 | 76.45 |
| *H. dispar* | 1.34 | 1.18 | 4.5 | 80.95 |
| *O. banksii* | 1.52 | 0.94 | 3.95 | 84.9 |
| *S. elegans* | 0 | 1.76 | 3.35 | 88.25 |
| *B. sponsalis* | 0 | 1.01 | 3.09 | 91.34 |

Bio-region: Strait of Sicily
Time series old and recent
Average dissimilarity = 50.39

| Species | Old Av.Abund | Recent Av.Abund | Contrib% | Cum.% |
|---|---|---|---|---|
| *I. coindetii* | 2.17 | 6.51 | 12.57 | 12.57 |
| *N. caroli* | 1.94 | 3.68 | 8.96 | 21.53 |
| *A. veranyi* | 3.84 | 3.27 | 7.98 | 29.51 |
| *H. reversa* | 1.53 | 3.96 | 7.64 | 37.15 |
| *T. eblanae* | 4.12 | 4.17 | 7.27 | 44.42 |
| *R. macrosoma* | 4.45 | 2.63 | 7 | 51.43 |
| *Histioteuthis* spp. | 2.28 | 0 | 5.24 | 56.67 |
| *H. bonnellii* | 4.51 | 3.91 | 4.58 | 61.25 |
| *S. oweniana* | 0 | 2.03 | 4.41 | 65.66 |
| *L. forbesii* | 0.35 | 2.05 | 4.34 | 70 |
| *B. sponsalis* | 1.57 | 1.08 | 4.33 | 74.33 |
| Sepiolidae | 1.79 | 0.28 | 4.27 | 78.6 |
| *O. salutii* | 1.8 | 1.15 | 3.98 | 82.58 |
| *P. tetracirrhus* | 2.86 | 3.1 | 3.62 | 86.2 |
| *T. sagittatus* | 4.95 | 6.09 | 3.56 | 89.75 |
| *S. unicirrhus* | 0.85 | 0.85 | 2.98 | 92.73 |