

Cephalopod assemblages, abundance and species distribution in the Gulf of Cadiz (SW Spain)

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Abstract – Spatial distribution and species diversity of Cephalopoda caught in ARSA bottom trawl surveys were studied out during two different seasons (autumn and spring) in the Gulf of Cadiz (Spain) from 2000 to 2007. Species composition of cephalopod assemblages was analysed, using both clustering analyses and non-metric multidimensional scaling analysis (nMDS). Spatial distribution of the assemblages identified and abundance of the main species were mapped with Surfer 8.0 software, using kriging as the geostatistical gridding method. A total of 35 cephalopod species belonging to 6 families were found at depths between 20 and 700 m. In each season, Sepiidae was the most abundant family in terms of number of species, followed by Octopodidae. The species richness increased up to 100–120 m depth, where it reached the maximum value. From 120 m, the species richness decreased progressively with depth. In spring, the species with the highest occurrence was *Eledone moschata* (34%) and in autumn it was *Alloteuthis media* (70%). In both seasons, the most abundant species in terms of weight was *Octopus vulgaris*, while *Alloteuthis media* showed the highest yields in terms of numbers. Most species showed wide bathymetric ranges, especially in autumn. Three different assemblages were found in both seasons during the time period analysed (although 2003 and 2006 were not included in the cluster analysis): shelf assemblage (20–160 m), deep shelf/upper slope assemblage (100–350 m) and middle slope assemblage (320–700 m). The specific composition of these three assemblages was similar between spring and autumn and an overlap could be observed between them, mainly in the two continental shelf groups: shelf and deep shelf/upper slope assemblages. *Alloteuthis media* and *Alloteuthis subulata* were the most abundant species in the shelf assemblage as well as in the deep shelf/upper slope assemblage. In the middle slope assemblage, *Illex coindetii* was the most abundant species. The assemblages and their spatial distributions could be largely related to a combination of physical and biological factors and their interactions.

Key words: Cephalopod assemblages / Bottom trawl Survey / Species diversity / Octopoda / Sepioidea / Teuthoidea / Atlantic Ocean / Gulf of Cadiz

1 Introduction

The Gulf of Cadiz is located to the southwest of the Iberian Peninsula. This geographical location in the Atlantic Ocean, close to the Mediterranean Sea, has specific oceanographic conditions for the exchange of water masses and these affect the different communities inhabiting this area to a greater or lesser extent (Ruiz and García-Lafuente 2006). The demersal fisheries operating in the Gulf of Cadiz are markedly multi-gear and multi-species in nature (Sobrino et al. 1994; Jiménez et al. 2002; Silva et al. 2002a), with an average landing of 9000 tonnes per annum in the last ten years. Molluscs accounted for 26% of the total landings; 95% of these were cephalopod species, including 12 commercial species. Most of the cephalopod species are caught by the demersal fishery, which is composed of demersal trawlers and artisanal vessels that use different gear types (trap, clay pot, hand-jig, among others) (Silva et al. 2002a).

The first reference on Gulf of Cádiz cephalopod fauna was published by Guerra (1982), based on biological material collected during a bottom-trawl research survey. In the last ten years, a series of studies carried out in waters of the Gulf of Cadiz has improved knowledge of some biological and fisheries aspects of the cephalopod species (Silva et al. 2002a,b, 2004). Recently, the role of the cephalopod species in the trophic webs of the Gulf of Cadiz has been studied (Torres, unpublished data) here as had previously been done in the North of the Iberian Peninsula (Velasco et al. 2001). However, in this study area, no cephalopod assemblage studies had been made, although other taxonomic groups such as deep sea fishes (Torres et al. 2007), sparids (Baro and Serna 2000; Silva et al. 2007), flatfishes (Vila et al. 2008) and coastal demersal assemblages (Catalán et al. 2006) had been studied.

Nowadays, species assemblage analyses are of great interest since fisheries research is now focusing on the ecosystem approach. The present study, with relevance to this approach, examines the distribution, abundance and assemblages of the

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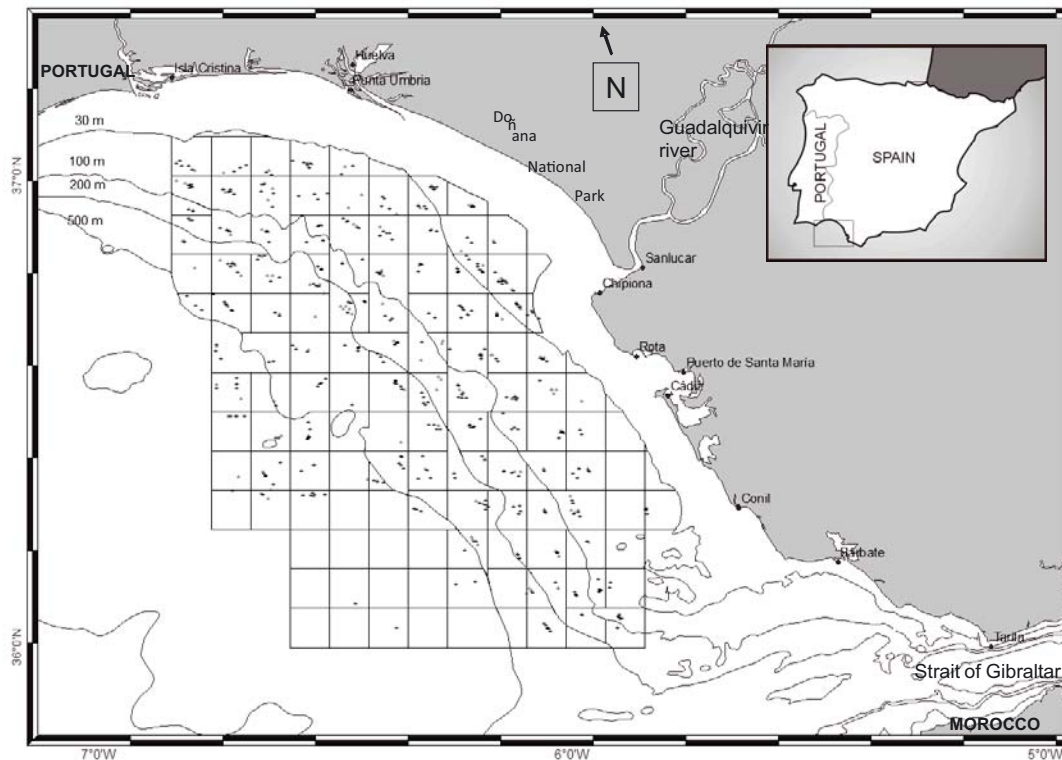


Fig. 1. Study area showing the surveyed area and haul positions.

cephalopod species in the Gulf of Cadiz, obtained using the historical series of bottom trawl survey data in spring and autumn.

2 Material and methods

The Spanish Institute of Oceanography has carried out bottom trawl surveys (ARSA series) in spring and autumn since 1993 in order to assess the most important demersal resources of the Gulf of Cadiz (Fig. 1). A total of 15 surveys, 7 in March and 8 in November, were analysed in the present study (2000–2007 period). Sampling design followed a random stratified scheme with 5 depth strata (15–30 m, 31–100 m, 101–200 m, 201–500 m and 501–800 m). The number of hauls in each depth stratum was proportional to the trawlable surface adjusted to the ship time available at sea and the haul duration was 60 min. All hauls were carried out during daylight hours using Baka 40/60 trawl gear with a 43.6 m footrope and a 60.1 m headline. An inner 20 mm mesh codend liner was used to prevent the escape of small individuals. In each haul, all the species were identified to the lowest taxon possible, weighed, counted and measured. The R/V “*Cornide de Saavedra*” was used in all surveys.

The information obtained from the 2000–2007 survey historical series was used to analyse the abundance and distribution of the main cephalopod species caught. Data were analysed from surveys performed in the years 2000, 2001, 2002, 2004, 2005 and 2007, in spring and autumn, with a total of 274 and 305 hauls, respectively. Firstly, species

composition of cephalopod assemblages was analysed, using both clustering analyses and non-metric multidimensional scaling analysis (nMDS). The similarity matrix was calculated by Bray-Curtis’s similarity index between hauls after quarter root transformation of the initial data. Based on this similarity matrix, nMDS and the clustering algorithm of the unweighted pair group method with arithmetic mean (UP-GMA) were computed to group samples (hauls) with similar species compositions and abundance. PRIMER 6 software (Clarke and Warwick 1994) was used to perform these analyses. Secondly, spatial distribution of the assemblages identified and abundance of the main species were mapped with Surfer 8.0 software, using kriging as the geostatistical gridding method. Finally, species diversity was assessed by species richness, Shannon-Wiener heterogeneous index (Shannon and Weaver 1949), and Pielou’s evenness index (Pielou 1966), as well as by taxonomic indices such as taxonomic diversity (Δ), for abundance data, and average taxonomic distinctness (Δ^+), for presence/absence data. Differences in the diversity indices between the assemblages obtained in each season were tested with the Kruskal-Wallis test, followed by the Mann-Whitney test in order to find out which assemblages presented significant inter-seasonal differences. In addition, for each season, species richness and Pielou’s evenness index by haul were plotted according to depth, and the trends were analysed by means of a piecewise regression.

K -dominance curves were used to graphically display the cumulative proportion abundance as a function of species rank of the different assemblages (Lambhead et al. 1983). Data analyses were performed on spring and autumn data in order to detect possible differences between these two periods.

Table 1a. Cephalopod species occurring in spring ARSA surveys (2000–2007). Mean yield (g/haul), mean yield (n: number of individuals/haul), frequency of occurrence in the whole hauls (%) and depth range (m).

	SPRING				
	Freq-occur (%)	Yield (g/haul)	Yield (n/haul)	Depth range (m)	Mean depth (m)
Octopoda					
Octopodidae					
<i>Bathypolipus arcticus</i>	–	–	–	–	–
<i>Bathypolipus sponsalis</i>	1	0.6	0	475–521	496
<i>Benthoctopus ergasticus</i>	1.3	0.5	0	95–630	492
<i>Eledone cirrhosa</i>	53	716.2	4.6	45–701	275
<i>Eledone moschata</i>	63.8	1725.1	10.3	20–447	96
<i>Octopus defilippi</i>	1	3.3	0	474–495	487
<i>Octopus salutii</i>	3.5	25.1	0.1	146–555	405
<i>Octopus vulgaris</i>	52.1	3635.9	5.2	20–347	92
<i>Pteroctopus tetracirrhus</i>	–	–	–	–	–
<i>Scaergus unicolorrhus</i>	3.5	3.3	0.1	109–482	234
Sepioidea					
Sepiidae					
<i>Sepia elegans</i>	45.4	50.5	5.7	27–447	114
<i>Sepia officinalis</i>	49.2	943.7	2.1	20–242	72
<i>Sepia orbignyana</i>	14.9	36.5	1.1	24–447	187
Sepiolidae					
<i>Heteroteuthis dispar</i>	0.3	0.1	0	431–431	431
<i>Neorossia caroli</i>	13	16.4	0.3	345–665	509
<i>Rondeletiola minor</i>	33.7	7.8	4.8	22–563	216
<i>Rossia macrosoma</i>	4.4	6.1	0.1	291–493	396
<i>Sepietta neglecta</i>	2.9	0.8	0.2	77–533	281
<i>Sepietta obscura</i>	1	0.7	0.3	83–301	158
<i>Sepietta oweniana</i>	21	18.2	5.9	42–619	347
<i>Sepiola affinis</i>	0.3	0.2	0.1	77–77	77
<i>Sepiola atlantica</i>	9.2	1.4	0.4	22–138	75
<i>Sepiola aurantiaca</i>	0.3	6.4	3.6	353–353	353
<i>Sepiola ligulata</i>	0.3	0	0	138–138	138
<i>Sepiola robusta</i>	3.8	2.7	0.9	73–110	91
<i>Sepiola rondeleti</i>	0.6	0.5	0.1	68–423	245
<i>Sepiola</i> sp.	37.8	1.6	0.5	26–674	122
Teuthoidea					
Enoploteuthidae					
<i>Abralia veranyi</i>	6.3	0.5	0.1	95–620	363
Loliginidae					
<i>Alloteuthis africana</i>	3.5	4.6	0.6	47–674	172
<i>Alloteuthis media</i>	54	227.9	87.5	20–674	97
<i>Alloteuthis subulata</i>	48.3	297.6	68.8	20–301	77
<i>Loligo forbesi</i>	9.8	83.3	0.7	68–431	192
<i>Loligo vulgaris</i>	33.3	303.4	3.1	20–141	56
Ommastrephidae					
<i>Illex coindetii</i>	47.6	1991	28.7	51–650	263
<i>Todarodes sagittatus</i>	–	–	–	–	–
<i>Todaropsis eblanae</i>	41.6	316.2	5.7	42–686	285

3 Results

3.1 Collected species

A total of 35 species belonging to 19 genera and 6 families were identified in the two seasonal series of surveys (Table 1a,b). *Bathypolypus arcticus*, *Pteroctopus tetracirrhus* and *Todarodes sagittatus* were not present in spring, and *Sepiola affinis*, *Sepiola aurantiaca* and *Sepiola ligulata* were not caught in autumn. The rest of the species were present in both seasons. Sepiolidae was the most abundant family in terms of

number of species, accounting for 42% in spring and 33% in autumn, followed by the Octopodidae, accounting for 24% of the total species in spring and 30% in autumn (Fig. 2). The Enoploteuthidae family was represented by only one species (*Abralia veranyi*) in both seasons.

3.2 Abundance and distribution

The occurrence frequency in whole hauls showed different values depending on the species and the season. In spring, it

Table 1b. Cephalopod species occurring in autumn ARSA surveys (2000–2007). Mean yield (g/haul), mean yield (n/haul), frequency of occurrence in the whole hauls (%) and depth range (m).

	AUTUMN				
	Freq-occur (%)	Yield (g/haul)	Yield (n/haul)	Depth Range (m)	Mean Depth (m)
Octopoda					
Octopodidae					
<i>Bathypolipus arcticus</i>	0.6	0.4	0	433–562	497
<i>Bathypolipus sponsalis</i>	0.6	0.4	0	517–580	548
<i>Benthoctopus ergasticus</i>	0.9	1.7	0.1	513–559	543
<i>Eledone cirrhosa</i>	41.6	362.3	4.7	44–618	228
<i>Eledone moschata</i>	59.2	1009.6	9	21–245	80
<i>Octopus defilippi</i>	4.6	20.7	0.2	28–618	316
<i>Octopus salutii</i>	4.6	22.9	0.2	70–513	367
<i>Octopus vulgaris</i>	46.8	2328	5.3	20–264	79
<i>Pteroctopus tetracirrhus</i>	0.3	9	0.1	331–331	331
<i>Scaergus unicolorrhus</i>	3.2	3.7	0.1	122–441	261
Sepioidea					
Sepiidae					
<i>Sepia elegans</i>	54	144.7	13.6	40–433	122
<i>Sepia officinalis</i>	39	1422	3.4	20–262	59
<i>Sepia orbignyana</i>	12.7	44.2	1.8	21–580	168
Sepiolidae					
<i>Heteroteuthis dispar</i>	0.3	0.1	0	496–496	496
<i>Neorossia caroli</i>	10.7	14.2	0.3	262–633	509
<i>Rondeletiola minor</i>	41.6	7.8	5.4	28–553	195
<i>Rossia macrosoma</i>	9	5.3	0.2	195–618	415
<i>Sepietta neglecta</i>	1.4	0.1	0.1	94–561	411
<i>Sepietta obscura</i>	3.2	3.6	1.4	22–92	55
<i>Sepietta oweniana</i>	15.3	62.9	19	117–701	438
<i>Sepiolo affinis</i>	–	–	–	–	–
<i>Sepiolo atlantica</i>	2.9	2.6	1.8	47–242	91
<i>Sepiolo aurantiaca</i>	–	–	–	–	–
<i>Sepiolo ligulata</i>	–	–	–	–	–
<i>Sepiolo robusta</i>	4.6	4	1.1	37–331	103
<i>Sepiolo rondeleti</i>	0.6	0.1	0.1	67–442	254
<i>Sepiolo sp.</i>	44.2	2.5	1	25–538	98
Teuthoidea					
Enoploteuthidae					
<i>Abralia veranyi</i>	6.9	1	0.2	115–687	406
Loliginidae					
<i>Alloteuthis africana</i>	8.4	36.4	7	67–315	136
<i>Alloteuthis media</i>	69.7	776.6	304.1	20–492	107
<i>Alloteuthis subulata</i>	58.7	344.9	57.7	20–492	105
<i>Loligo forbesi</i>	14.5	481.1	3.6	27–608	242
<i>Loligo vulgaris</i>	43.6	1200.3	8.2	20–359	61
Ommastrephidae					
<i>Illex coindetii</i>	39.6	1232.3	11.9	63–608	272
<i>Todarodes sagittatus</i>	4.9	155.2	0.1	369–701	500
<i>Todaropsis eblanae</i>	40.8	453.4	6.5	44–618	290

ranged between 63.8% for *E. moschata* and 0.3% for *S. affinis*, *S. aurantiaca* and *S. ligulata*. In autumn, *A. media* presented the highest values and *Bathypolypus* sp. and *Sepiolo rondeleti* showed the lowest values with 69.7 and 0.6%, respectively (Table 1a,b).

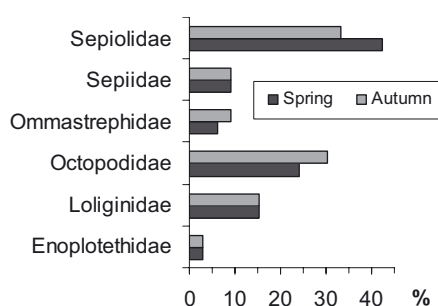
The yield in terms of weight showed the highest values for *Octopus vulgaris*, with 3636 and 2328 g/haul in spring and autumn, respectively. In spring, this species was followed in order of importance by *Illex coindetii* (1991 g/haul), *E. moschata* (1725 g/haul) and *Sepia officinalis* (943 g/haul). In

autumn, *S. officinalis* was the second most important species with 1422 g/haul, followed by *I. coindetii* and *Loligo vulgaris* with 1200 g/haul each. *E. moschata* showed a value slightly higher than 1000 g/haul (Table 1a,b).

The highest values of yield in number of individuals corresponded to the *Alloteuthis* species in both seasons. *A. media* presented yield values higher than *A. subulata*, with 87.5 and 68.8 n/haul, and 304.1 and 57.7 n/haul, in spring and autumn, respectively. The difference between the yields of these species was, therefore, higher in autumn. *I. coindetii* and *E. moschata*,

Table 2. Relative importance of cephalopod species (mean yield, in number of individuals by haul, expressed as percentages) in the three assemblages obtained in spring and autumn ARSA surveys (2000–2007).

Species (%)	Assemblages					
	Shelf		Deep shelf / upper slope		Middle slope	
	Spring	Autumn	Spring	Autumn	Spring	Autumn
<i>Alloteuthis media</i>	51.48	76.09	20.45	53.90	0.14	0.51
<i>Alloteuthis subulata</i>	35.84	13.12	13.61	10.57	0.00	0.14
<i>Eledone cirrhosa</i>	0.44	0.51	4.72	1.91	4.69	1.91
<i>Eledone moschata</i>	4.26	1.79	4.37	1.18	0.19	0.00
<i>Illex coindetii</i>	0.39	0.07	21.86	10.97	72.12	11.74
<i>Loligo forbesii</i>	0.06	0.02	1.11	3.39	0.17	0.96
<i>Loligo vulgaris</i>	2.25	2.07	0.04	0.02	0.00	0.24
<i>Neorossia caroli</i>	0.00	0.00	0.04	0.02	0.96	0.96
<i>Octopus vulgaris</i>	1.25	1.63	3.00	0.27	0.00	0.00
<i>Rondeletiola minor</i>	0.24	0.33	7.95	2.75	1.78	8.49
<i>Sepia elegans</i>	1.76	1.86	4.44	5.50	0.01	0.06
<i>Sepia officinalis</i>	0.92	0.71	0.31	0.09	0.00	0.00
<i>Sepia orbignyana</i>	0.03	0.02	2.04	0.32	0.59	2.85
<i>Sepietta oweniana</i>	0.02	0.00	4.02	1.70	10.41	33.89
<i>Sepioida</i> sp.	0.41	0.21	1.80	2.56	2.09	23.02
<i>Todaropsis eblanae</i>	0.19	0.07	8.31	3.95	5.90	13.25
Others	0.47	1.49	1.94	0.90	0.94	1.96

**Fig. 2.** Relative importance of cephalopod families (in percentages of species number) in spring and autumn ARSA survey series (2000–2007).

with 28.7 and 10.3 n/haul, were the third and fourth most frequent species, in spring. However, in autumn, the *Alloteuthis* species were followed by *Sepietta oweniana* and *Sepia elegans* with 19 and 13.6 n/haul, respectively (Table 1a,b).

Most of the cephalopod species showed wide bathymetric ranges, with 48% of the total number of species exhibiting ranges greater than 400 m (Table 1a,b). In spring, the widest ranges belonged to *Eledone cirrhosa* (45–701 m), *Todaropsis eblanae* (42–686 m) and *Illex coindetii* (51–650 m). In autumn, the widest ranges were again shown by the same species with similar distribution ranges, joined by *Loligo forbesii* (27–608 m). Only a few species were restricted to shelf areas, including *O. vulgaris*, *S. officinalis*, *Sepioida atlantica*, *L. vulgaris* and *E. moschata*, which were caught below 300 m depth. In autumn, *E. moschata* was caught at depths up to 440 m, although the mean depth was less than 100 m in both seasons. Other species only occurred in the middle-slope area, including the species of genera *Bathypolypus* and *Benthoctopus*, which were caught between 500 and 700 m depth.

Spatial distributions of these species with the highest yields in terms of numbers are represented (Fig. 3). In general,

these spatial distributions were similar in the two seasons, although a greater number of patches with high abundance can be observed in autumn than in spring. The ommastrephid species *T. eblanae* and *I. coindetii* were caught in the deepest surveyed areas, located close to the Strait of Gibraltar. Both *Alloteuthis* species were caught along the study area, although the highest abundances were found in the central area of the Gulf of Cadiz shelf. However, *O. vulgaris* presented the highest yields in the shallowest shelves in the West and East of the study area, showing the lowest values in the middle area close to the mouth of the Guadalquivir River. *S. elegans* was mainly caught in the depth range 100–200 m, in the whole surveyed area, while *S. oweniana* was caught in the western extremity of the deep strata.

3.3 Species composition

The dendrograms obtained from clustering the Bray-Curtis matrix between the spring and autumn ARSA hauls carried out in 2000, 2001, 2002, 2004, 2005 and 2007 are shown (Fig. 4a,b), respectively. Three cephalopod assemblages were obtained: shelf assemblage, in depths between 20 and 160 m (continuous line); deep shelf/upper slope assemblage, between 100 and 350 m (fine dotted line) and middle slope assemblage, between 320 and 700 m (thick dotted line). The cephalopod assemblage distribution was supported by the nMDS analyses. All Kruskal stress coefficient values were below 0.15, indicating that the original inter-sample relationships stated in the Bray-Curtis similarity matrix were relatively well preserved by the two dimensional space ordination of the nMDS (Fig. 4). Similar assemblages were obtained in spring and autumn, although only two groups were obtained in spring 2007 because the deepest hauls were not carried out at this time.

The species composition of the three groups, and the relative importance expressed in terms of average yields (n/haul)

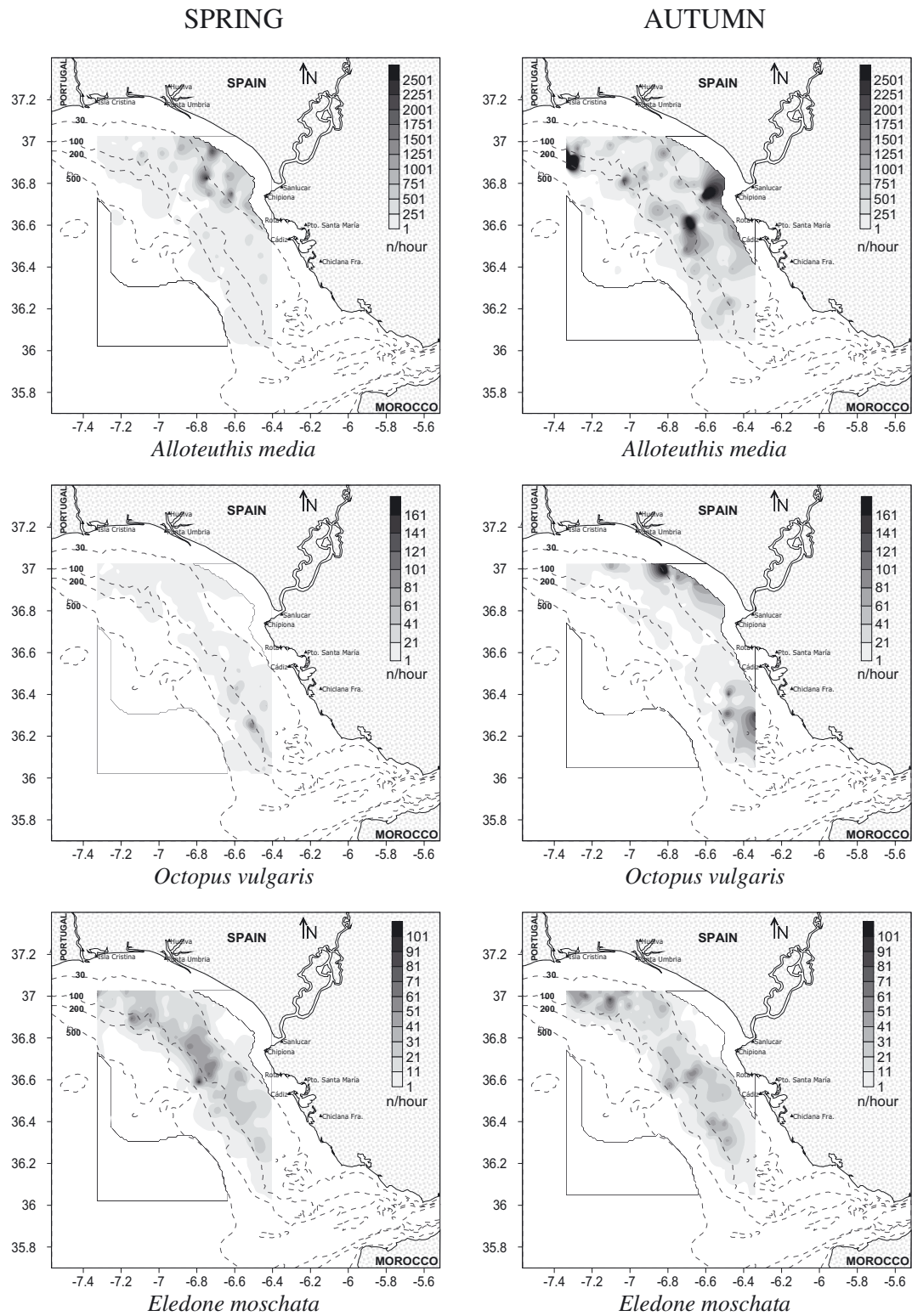


Fig. 3. Spatial distribution of the most abundant species (in numbers of individuals) in spring and autumn ARSA survey series (2000–2007): *Alloteuthis media*, *Octopus vulgaris*, *Eledone moschata*, *Sepia elegans*, *Sepietta oweniana* and *Illex coindetii*.

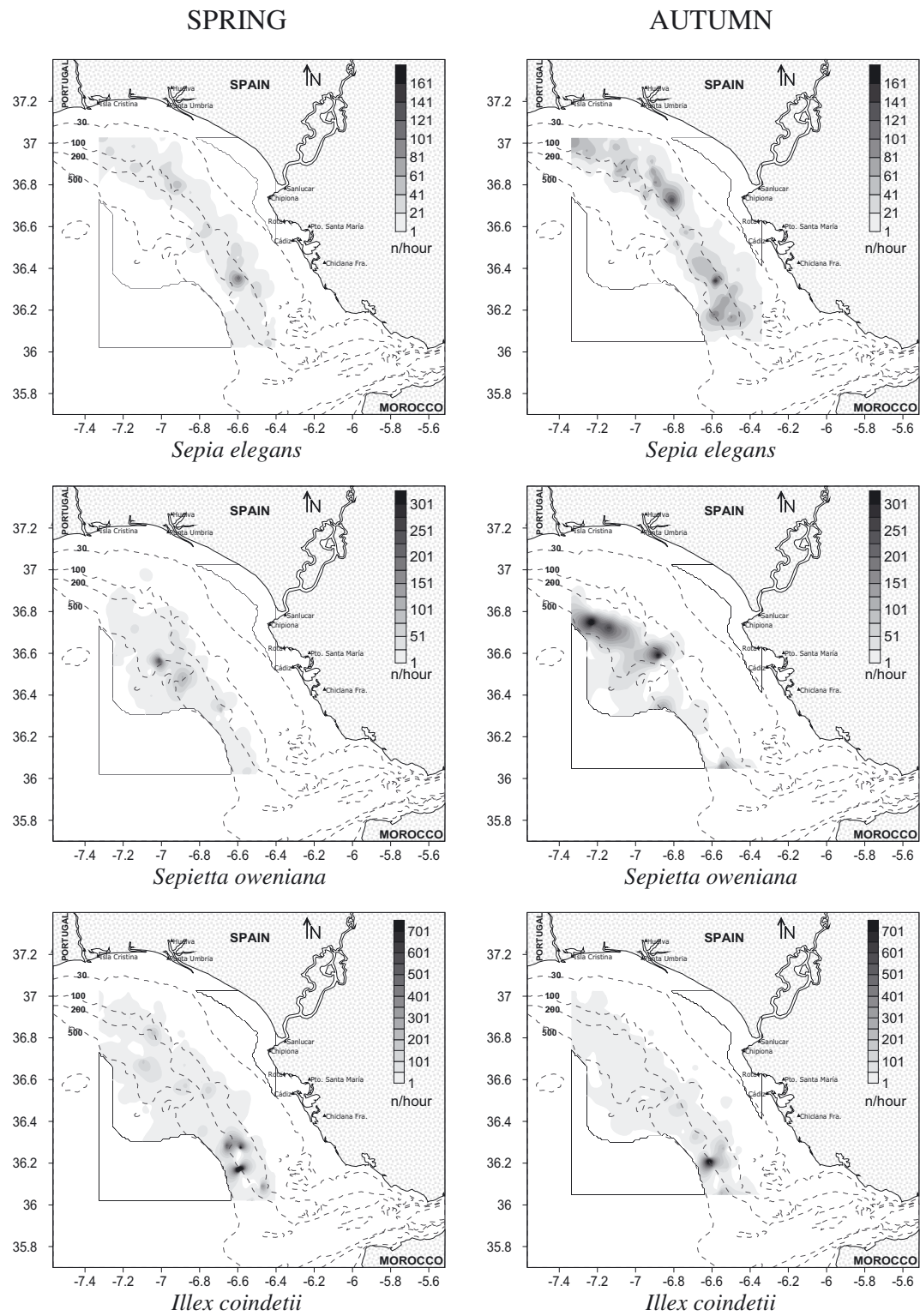


Fig. 3. Continued.

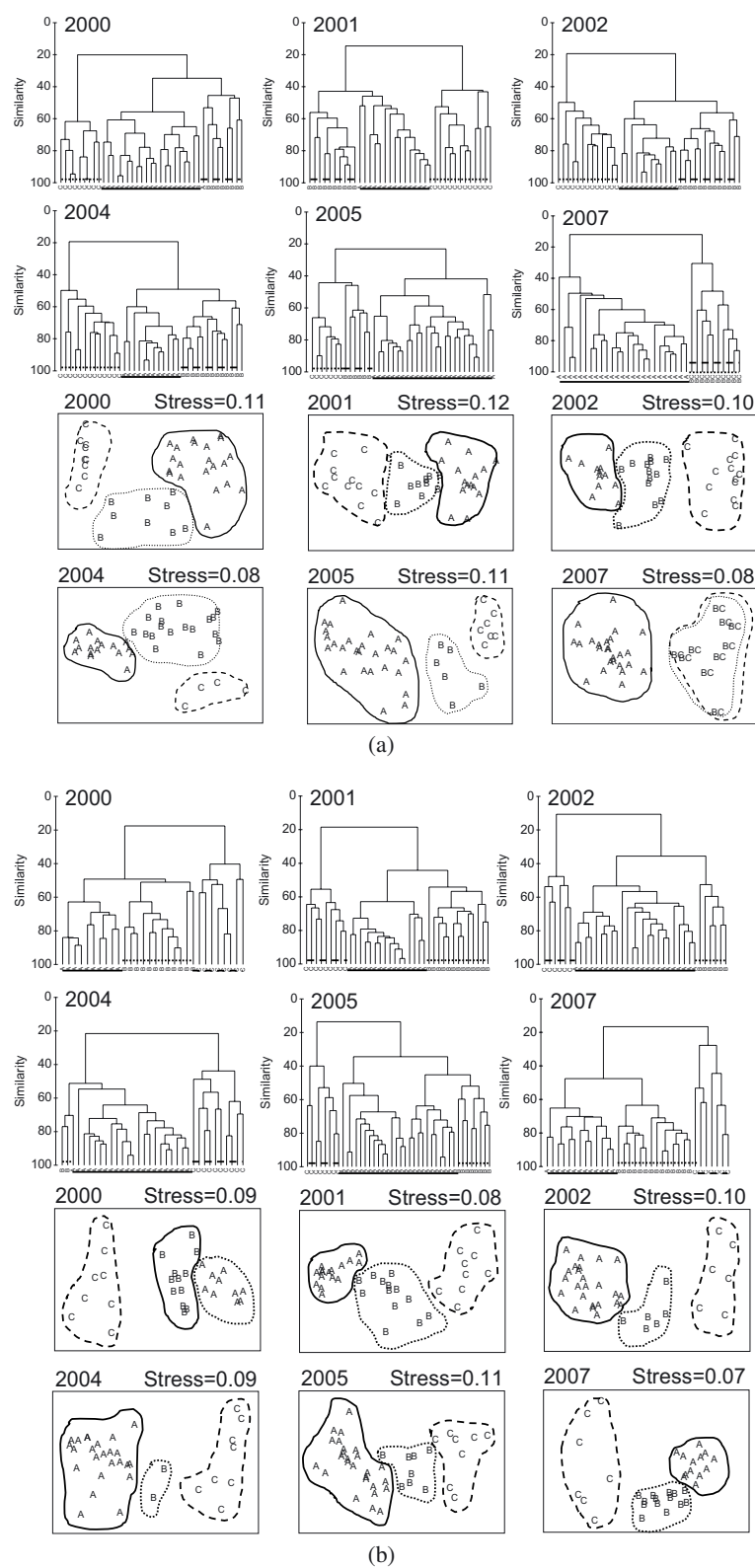


Fig. 4. UPGMA (unweighted pair group method with arithmetic mean) and nMDS (non-metric multidimensional scaling analysis) computed on Bray-Curtis similarity matrix: the assemblages obtained from the SPRING (a) and AUTUMN (b) ARSA surveys (years 2000, 2001, 2002, 2004, 2005 and 2007). Shelf assemblage (“A” continuous line), deep shelf/upper slope assemblage (“B” fine dotted line) and middle slope assemblage (“C” thick dotted line). The Kruskal stress coefficient obtained is shown in each nMDS plot.

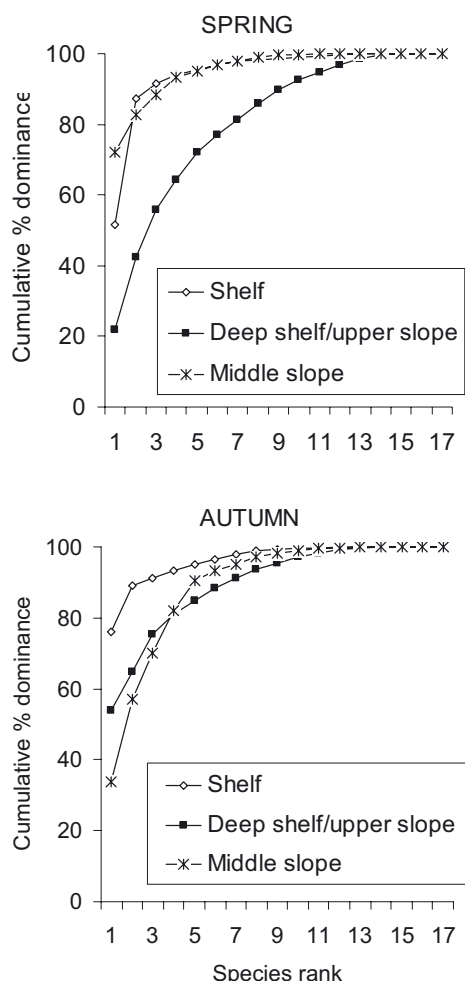


Fig. 5. Abundance k -dominance curves of the principal clusters obtained for each season.

are shown in Table 2. The species composition of the different assemblages were similar in spring and autumn, but with different relative species importance.

Figure 5 shows the abundance k -dominance curves of the principal clusters obtained. Two species contributed to almost 90% of the total abundance in the shelf assemblages in both seasons. *Illex coindetii* was the dominant species in middle slope assemblages, representing 72% and 34% in spring and autumn, respectively (Fig. 5). *A. media* and *A. subulata* were the most abundant species found in the shelf assemblages in both seasons, *A. media* being the species with the highest percentage in both seasons (Table 2). In spring, the *Alloteuthis* species were followed by *E. moschata* (4.3%), *L. vulgaris* (2.2%), *S. elegans* (1.8%) and *O. vulgaris* (1.2%). In autumn, these species presented similar values, except *E. moschata*, which decreased to 1.8%.

In the deep shelf-upper slope assemblage, a stronger dominance pattern was observed in autumn than in spring regarding to the two other assemblages (see the trend of curves in Fig. 5). The presence of *Alloteuthis* spp. was lower than in the shelf community in both seasons, although *A. media* showed a high value in autumn with 53.9%, as it was the main species

caught in this season. In spring, this species showed a lower value (20.45%) than in autumn, slightly lower than the *I. coindetii* value (21.8%). This ommastrephid species was the main species caught in this season within this assemblage. Other relevant species were *A. subulata* (13.6%), *T. eblanae* (8.3%), *Rondeletiola minor* (7.9%) and *E. moschata* (4.4%). In autumn, an increase in the percentage of these species regarding to shelf assemblage was also detected, but the difference was lower than that shown in spring. *Illex coindetii* was the second most important species, accounting for 11% (Table 2).

In the deep assemblage (middle slope), a lower dominance pattern was observed in autumn than in spring regarding to the two other assemblages (see the trend of curves, Fig. 5). *I. coindetii* was the most abundant species (72%) followed by *S. oweniana* (10.4%) and *T. eblanae* (5.9%), in spring. However, *S. oweniana* was the most abundant species (34%) in the same group in autumn, followed by *Sepiolo* sp. (23%), *T. eblanae* (13%) and *I. coindetii* (11.7%) (Table 2). *E. cirrhosa* showed similar values in the two deepest groups in both seasonal periods, but represented a lower percentage in autumn (1.9%) than in spring (4.7%).

The spatial distributions of the three assemblages were mapped for each season (Fig. 6). In each map the same assemblage distributions were observed in both seasons. An overlap can be seen between assemblages in both spring and autumn, mainly in the two groups located over the continental shelf.

3.4 Diversity indices

For each assemblage, species richness, Shannon-Wiener heterogeneous index, Pielou's evenness index, average taxonomic diversity (Δ) and average taxonomic distinctness (Δ^+) were plotted by year for each season (Fig. 7). Moreover, the number of species and Pielou's evenness by depth for all hauls were plotted for each season (Fig. 8).

Kruskal Wallis tests showed significant differences between the assemblages ($p < 0.01$) for all indices analysed in spring and autumn. In general, the highest values of the species richness, Shannon-Wiener heterogeneous and Pielou's indices were found in the deep-shelf/upper slope assemblage, followed by the shelf assemblage, in both seasons. Pielou's evenness was the only index that did not show significant differences between these groups ($p > 0.05$, Mann-Whitney test). All diversity indices showed significantly low values in the middle slope assemblage ($p < 0.05$, Mann-Whitney test).

Species richness according to depth showed an unimodal trend, with the highest values reaching around 13 species at the 110–160 m depth range (Fig. 8). Piecewise regression indicated that at bottoms deeper than 115 and 160 m (breakpoints BPx), in spring and autumn, respectively, species richness decreased progressively with depth (spring: $r^2 = 0.46$, $x < \text{BPx}$ and $r^2 = 0.57$, $x > \text{BPx}$; autumn: $r^2 = 0.31$, $x < \text{BPx}$ and $r^2 = 0.51$, $x > \text{BPx}$). Only one or two species were caught per haul in depths around 700 m (Fig. 8). This unimodal trend also appears with the Pielou's index according to depth. Piecewise regression indicated that at bottoms deeper than 100 and 300 m (breakpoints BPx), in spring and autumn, respectively, evenness decreased progressively with depth (spring: $r^2 = 0.17$,

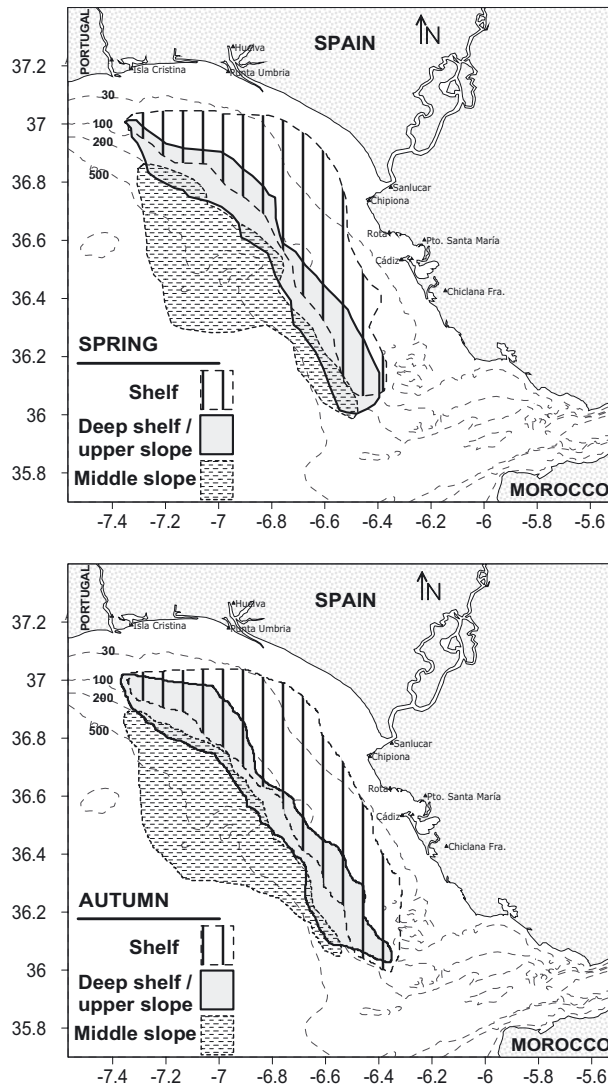


Fig. 6. Spatial distribution of shelf, deep shelf/upper slope and middle slope assemblages obtained in spring and autumn ARSA survey series. Shelf assemblage (continuous line), deep shelf/upper slope assemblage (fine dotted) and middle slope assemblage (thick dotted).

$x < \text{BPx}$ and $r^2 = 0.71$, $x > \text{BPx}$; autumn: $r^2 = 0.005$, $x < \text{BPx}$ and $r^2 = 0.54$, $x > \text{BPx}$) (Fig. 8).

The taxonomic indices, taxonomic diversity (Δ) and average taxonomic distinctness (Δ^+) are shown (Fig. 7). Taxonomic diversity did not show significant differences between deep-shelf/upper slope and middle slope assemblages, in either season ($p > 0.05$, Mann-Whitney test), although values were significantly higher than in the shelf assemblage ($p < 0.05$, Mann-Whitney test). However, average taxonomic distinctness did not present significant differences between the three assemblages ($p < 0.05$, Mann-Whitney test).

Overall, these results indicate that species diversity was greater on the continental shelf, i.e., in the shelf and deep-shelf/upper slope assemblages. However, from the taxonomic point of view, these results can be interpreted differently. Thus, the taxonomic diversity index indicates a similar diversity in the deep-shelf/upper slope and the middle slope assemblages

while the lowest diversity is observed in the shelf assemblage. This is because most of the abundance of this group is supported by two species of the same genus (*Alloteuthis media* and *A. subulata*). However, the average taxonomic distinctness, which uses only species presence/absence data showed similar taxonomic diversity in all assemblages.

4 Discussion and conclusion

4.1 Species richness

The first descriptions of the tethofauna of the Gulf of Cádiz were carried out by Guerra (1982), reporting 23 cephalopod species belonging to 6 families. In terms of the number of hauls surveyed, the methodology was partly similar to that used in the present study. However, the sampling materials and the sampling time were different, as was the number of surveys sampled. Guerra only analysed the single survey carried out in the 1980s, while the present study analysed 15 surveys. Although the results are not comparable between the two studies, the information obtained provides complementary knowledge about the tethofauna in the study area. Guerra (1982) reported the presence of *Argonauta argo* (Argonautidae family), which was not present in the demersal fauna caught in the bottom trawl survey analysed in the present study. However, this pelagic species was caught in a pelagic haul of an acoustic survey carried out in June 2005 in the study area at 60 m depth (unpublished data). The pelagic habitat of this species may be the reason for the null catches in the bottom trawls, as trawl gears are not appropriate for catching pelagic species. For the same reason, deep cephalopod species such as the species belonging to the *Histiotheutis* genus were not caught during these surveys. However, analysis of stomach contents of *Pagellus bogaraveo* in waters of the Strait of Gibraltar reported the presence of the *Histiotheutis* genus in the Gulf of Cadiz (Polonio et al. 2008). With these two new species, *A. argo* and *Histiotheutis* sp, the number of species and families known in the Gulf of Cadiz is increased to 37 and 8, respectively. Finally, the Enoploteuthidae family was not reported by Guerra while it was caught in the ARSA survey series analysed here, represented by a single species (*Abralia veranyi*).

In nearby areas, such as the waters of the Mediterranean Sea, there have been many studies that provide information on species richness. However, species richness values cannot be directly compared due to differences in sampling effort, depth range and the catchability associated with the vessels used in the different studies. Information from these studies is given here as a short review of the main knowledge on species richness in this area. Gonzalez et al. (2002) identified 34 species in the Mediterranean coast of the Iberian Peninsula, in 480 hauls at depths between 25 and 786 m. Tursi and D'Onghì (1992) reported 24 species of cephalopods in the Ionian Sea in 252 hauls between 0 and 650 m. D'Onghia et al. (1996) caught 29 species in the North Aegean in 240 hauls between 32 and 490 m. Quetglas et al. (2000) found 30 species in the Balearic Sea, by analysing 79 hauls between 50 and 800 m. Finally, Sánchez et al. (1998) found 47 species in the Catalan Sea, although it should be taken into account that they used additional gear, such as plankton nets, and a long time series of 20 years.

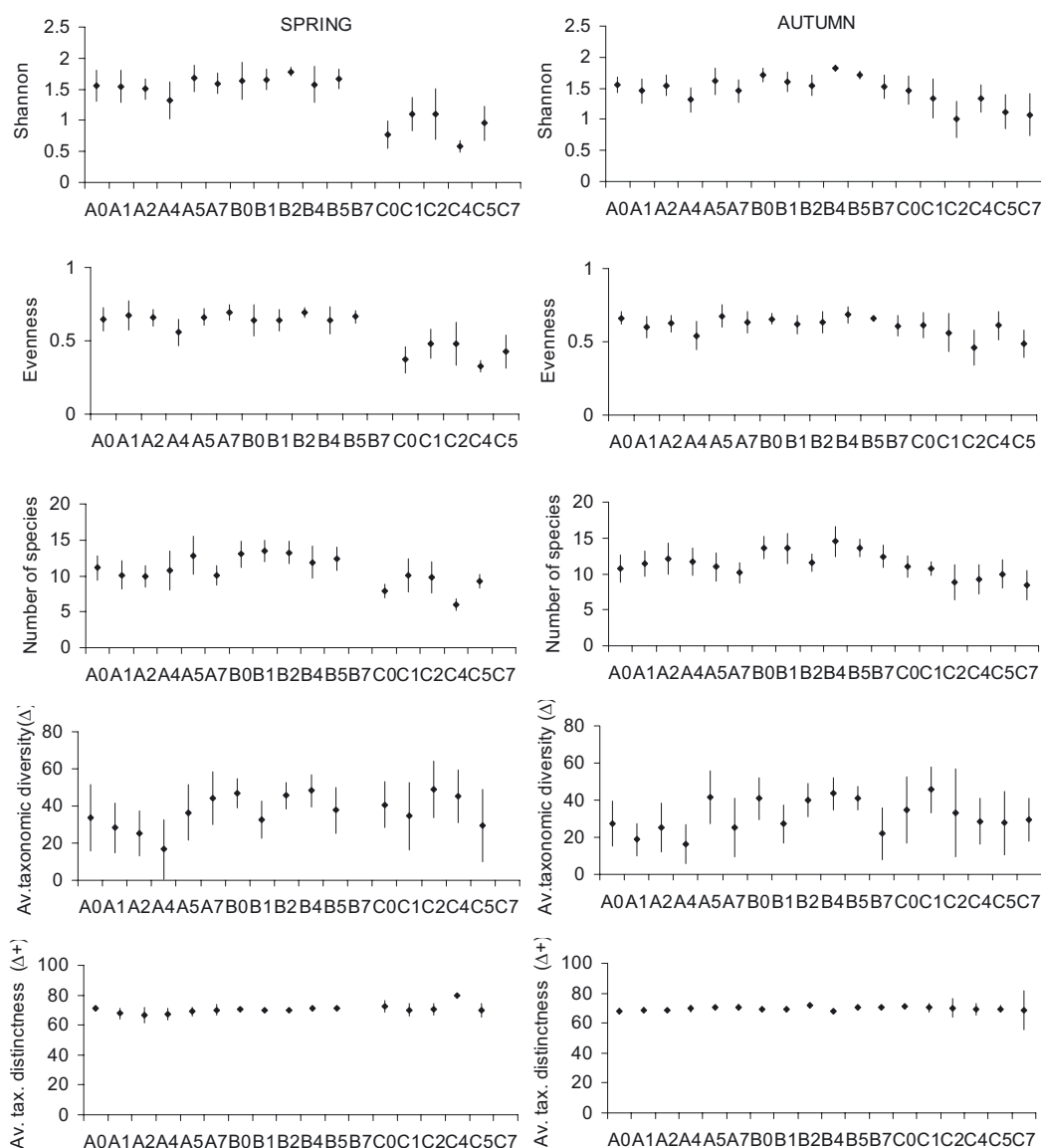


Fig. 7. Mean and 95% confidence intervals of species richness, Shannon-Wiener, Pielou's evenness, taxonomic diversity and average taxonomic distinctness indices for each assemblage (X-axes; A0 to A7: Shelf; B0 to B7: Deep shelf/upper slope; C0 to C7: Middle slope) and year (2000–2007), for each season.

A. veranyi, *Bathypolypus sponsalis*, *Scaevargus unicirrhus*, *O. defilippi*, *Pteroctopus tetracirrhus* and *Heteroteuthis dispar* are reported in the Gulf of Cadiz for the first time here, although this area is within their world area distribution. In the case of *Alloteuthis africana*, the distribution area is amplified from the Sahara coast (Nesis 1987; Guerra 1992) in the north of Africa to the Gulf of Cadiz. The bathymetric range of this species is quite wide, like the other two species of *Alloteuthis* genus present in the Gulf of Cadiz (40–600 m depth). Guerra (1982) confirmed the presence of this genus up to 500 m depth in the study area.

The Sepiolidae family was represented by 9 species, of which, *S. aurantiaca*, *S. ligulata* and *Sepiola robusta* are reported for the first time in the waters of the Gulf of Cadiz. The bathymetric ranges of *S. ligulata* and *S. robusta* are in

agreement with Guerra (1992), although the range is enlarged up to 300 m depth in the case of *S. robusta* in autumn. This species has been cited as an endemic species in the Mediterranean Sea (Guerra 1992).

Loligo forbesii is also reported for the first time in the Gulf of Cadiz, between 27 and 600 m depth, although the mean depth was around 200 m. *L. vulgaris* showed a depth range narrower than *L. forbesii*, with a maximum depth of 359 m in autumn. In addition, the mean depth was no higher than 100 m in the time series surveys.

4.2 Species assemblages

The cephalopod assemblages are strongly influenced by depth, as already observed by other authors in regions such as

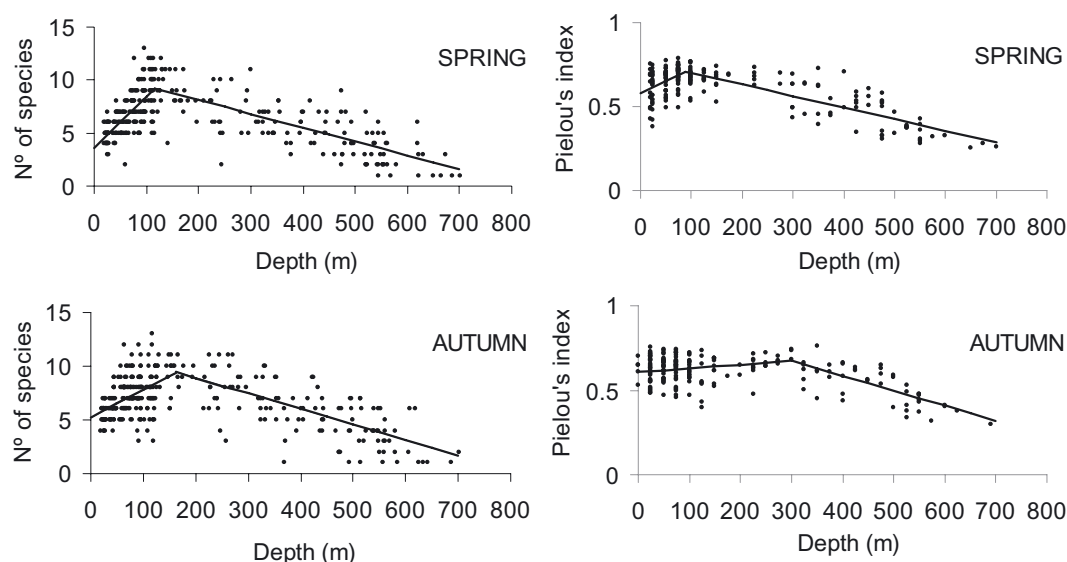


Fig. 8. Species richness and Pielou's evenness by haul according to depth, expressed in number, in spring and autumn ARSA survey series (2000–2007), including the piecewise regression.

the Mediterranean Sea, (González and Sanchez 2002; Quetlas et al. 2000) and Mozambican waters (Silva et al. 2009). Other authors included the sea temperature, oxygen concentration and types of bottom as possible variables that influenced in the demersal community composition (Smale et al. 1993; Demestre et al. 2000). In studies of demersal species assemblages (Sousa et al. 2005) and other specific taxonomic groups (Massuti et al. 1996: fish community; Smale et al. 1993: fish and cephalopods; Abelló et al. 1988: crustaceans), the distribution patterns were similar to those obtained in this study: shelf, deep shelf-upper slope and middle slope assemblages, with similar depth ranges.

4.3 Abiotic forcing factors

Throughout the analysed period, the species composition remained stable without any great changes. However, some quantitative variations in the species composition of different groups were observed and could possibly be related to different oceanographic variables. In the case of cephalopod species, annual recruitment seems to be responsible for the entire stock biomass and these species could, therefore, be especially susceptible to the environmental variability (Caddy 1983; Pierce 1995; Boyle and Rodhouse 2005; Pierce et al. 2008). It is widely accepted that temperature is one of the main factors affecting the cephalopod abundance and distribution. This fact is highlighted in a number of studies including Wang et al. (2003) on *S. officinalis* in the English Channel, Pierce (1995) on *L. forbesii* in the Scottish waters, Bazzino et al. (2005) on *Illex argentinus* in the Patagonian shelf, Vargas et al. (2009) on *Octopus vulgaris* in Mediterranean Sea, and Balguerías et al. (2002) on *O. vulgaris* on the Saharan bank. Generally, increases in abundance are associated with decreases in the average water temperature. These oscillations, in turn, are closely related to more complex processes such as upwelling intensity and, consequently, food availability, retention/dispersion processes,

or advection of water masses from distant areas (Vargas et al. 2009).

In the case of the Gulf of Cadiz, physiographic elements such as the mouths of large rivers (Guadalquivir and Guadiana) and the Strait of Gibraltar, with the exchanges of water masses between the Atlantic Ocean and the Mediterranean Sea, possibly affect the distribution of species, particularly cephalopods. In this regard, Sobrino et al. (2002) found that low temperatures in spring induced high *O. vulgaris* catches in the following fishing season. On the other hand, this author reported a negative and significant correlation with rainfall during the preceding rainy season. The fresh waters supplied by rivers could affect species in the shallowest depth layer. *O. vulgaris* is not caught in the waters adjacent to the mouth of the Guadalquivir River, but other species, like *Alloteuthis* sp., are favoured by this fresh water and their highest abundances are located by the mouth of the Guadalquivir River where the mixture of waters favours an increase in productivity.

The Strait of Gibraltar is characterized by strong currents and winds. The tidal currents and a submarine ridge that breaks the continental shelf of Cape Trafalgar cause upwelling of cold waters rich in nutrients that increase productivity in the area near the Strait of Gibraltar (Vargas et al. 2009). These aspects could be responsible for the distribution of the two main omastrephid species, *T. eblanae* and *I. coindetti*, in the deep shelf-upper slope and middle slope assemblages. The influence of these factors mentioned on the distribution, abundance and demersal assemblages, including cephalopod species, has been described by several authors (Sousa et al. 2005; Smale et al. 1993; Vargas et al. 2009; Pierce et al. 2008; Bazzino et al. 2005).

4.4 Biotic forcing factors

In the Gulf of Cadiz, some differences in the abundance in terms of numbers were observed seasonality, although the

specific composition showed no great changes. Besides the environmental and oceanographic factors, the life history of the species influences these differences. In spring surveys, before the beginning of its spawning period, *O. vulgaris* is caught along the shelf, whereas in autumn, after the spawning season, recruitment is found in shallow waters with bottoms rich in bivalves (Silva et al. 2002). *L. vulgaris* approach coastal areas during the autumn to spawn (Vila et al. 2010), whereas *E. moschata* increases its presence in the two shelf strata in spring in relation to the main spawning peak (Silva et al. 2004). Cases of reproductive and trophic migrations, related to the seasonal oscillations, have been widely studied in other areas by previous authors (Rocha et al. 2001).

The different assemblages are characterized by characteristic species. Those that inhabit the continental shelf form two shelf assemblages (shelf and deep shelf-upper slope), mainly due to their life history. In these cases, as described above, they undertake reproductive and trophic migrations along the shelf, which produces an overlap between the two shelf assemblages. Margalef (1974) described an increase of diversity indices in these boundaries or overlapping areas (ecotones). The results obtained in the present study are in agreement with this observation, since the species richness achieved maximum values at depths corresponding to the ecotone between the two shelf assemblages (110–160 m range) in both seasons. On the other hand, the deep shelf-upper slope appears as a transition area between the shelf and slope zones because the assemblage there shows the same composition and relative average abundance as the two other assemblages. In this study, it was similar in both seasons and ranged between 100 and 350 m depth. In the nearby areas of the Mediterranean Sea, this transition area corresponded to the end of continental shelf and the beginning of the slope was wider than in the present study and ranged between 150 and 480 m (González et al. 2002). Other authors, in studies carried out in the Atlantic areas off the Iberian Peninsula, noted the existence of this transition area, whose geographic boundaries may be associated with the bottom topography or other physical features in the area (Gomes et al. 2001; Sousa et al. 2005).

In conclusion, the observed abundance and spatial distribution of cephalopod species is closely related to both biological and physical factors as well as their combination. The distribution and abundance observed in the Gulf of Cadiz, as well as the assemblage composition and diversity, are possibly the result of the interaction of these factors. Further quantitative analysis should, therefore, be carried out, taking into account information on physical and biological factors, in order to confirm their influence on assemblage composition.

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