

Demersal cephalopod communities in the Mediterranean: a large-scale analysis

Stefanie Keller^{1,*}, Manuel Hidalgo¹, Diego Álvarez-Berastegui², Isabella Bitetto³,
Loredana Casciaro³, Danila Cuccu⁴, Antonio Esteban⁵, Germana Garofalo⁶,
Maria Gonzalez⁷, Beatriz Guijarro¹, Marios Josephides⁸, Angelique Jadaud⁹,
Evgenia Lefkaditou¹⁰, Porzia Maiorano¹¹, Chiara Manfredi¹², Bojan Marceta¹³,
Reno Micallef¹⁴, Panagiota Peristeraki^{15,16}, Giulio Relini¹⁷, Paolo Sartor¹⁸,
Maria Teresa Spedicato³, George Tserpes¹⁵, Antoni Quetglas¹

¹Instituto Español de Oceanografía, Centro Oceanográfico de Baleares, 07015 Palma de Mallorca, Spain

²Balearic Islands Coastal Observing and Forecasting System (SOCIB), 07122 Palma de Mallorca, Spain

³COISPA-Tecnologia & Ricerca, Stazione Sperimentale per lo Studio delle Risorse del Mare, 70126 Bari, Italy

⁴Dipartimento di Scienze della Vita e dell'Ambiente, Università di Cagliari, 09124 Cagliari, Italy

⁵Centro Oceanográfico de Murcia, San Pedro del Pinatar, 30740 Murcia, Spain

⁶IAMC – Coastal Marine Environment Institute – CNR, 91026 Mazara del Vallo (TP), Italy

⁷IEO, Centro Oceanográfico de Málaga, Fuengirola, 29640 Málaga, Spain

⁸Dept of Fisheries and Marine Research, Ministry of Agriculture, Rural Development and Environment, 1416 Nicosia, Cyprus

⁹IFREMER, Laboratoire Halieutique Méditerranéenne, UMR MARBEC, 34203 Sète, France

¹⁰HCMR, Hellenic Centre of Marine Research, 16777 Athens, Greece

¹¹University of Bari Aldo Moro - Department of Biology, 70125 Bari, Italy

¹²Laboratorio Biologia Marina e Pesca, Università di Bologna, 61032 Fano (PS), Italy

¹³Fishery Research Institute of Slovenia, 1211 Ljubljana-Smartno, Slovenia

¹⁴Ministry for Sustainable Development, Department of Fisheries and Aquaculture, MRS 3303 Marsa, Malta

¹⁵HCMR, Hellenic Centre of Marine Research, 71003 Heraklion, Crete, Greece

¹⁶University of Crete, Biology Department, 71409 Heraklion, Crete, Greece

¹⁷SIBM, Società Italiana di Biologia Marina, Genova and DISTAV, Università di Genova, 16132 Genova, Italy

¹⁸CIBM – Centro Interuniversitario di Biologia Marina ed Ecologia Applicata, 57128 Livorno, Italy

ABSTRACT: Cephalopod assemblages at the scale of the entire Mediterranean Sea were analysed using information from 2 decades of standardized scientific bottom trawl surveys. Western and eastern assemblages (6 yr of data) were compared using a combined approach of multivariate ordination techniques and non-linear regressions. These methods enabled us to distinguish assemblages and simultaneously analyse the influence of geographic, bathymetric and environmental (sea surface temperature and chlorophyll a concentration) gradients on observed community patterns. Despite few differences in species composition between sub-basins, the relative contribution of species differed. Bathymetry was the primary structural driver for the cephalopod communities of both basins, and contributed to 3 assemblages (shallow water, upper slope and middle slope). Winter temperature influenced community assemblages more strongly in the western than in the eastern basin, in contrast to a small but consistent winter productivity influence on community assemblages in both basins. Thus, the environmental parameters analysed did not cause an immediate change in cephalopod assemblages, but rather an effect lagged by several months. Differences in the relative importance of environmental drivers show that different processes operate in the 2 basins. These results demonstrate similarities and differences between Mediterranean basins regarding important cephalopod functional groups. This information should help integrative ecosystem management approaches currently used in fisheries and conservation management.

KEY WORDS: Cephalopods · Mediterranean · Environmental gradients · Community analysis · Bottom trawl surveys · MEDITS

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INTRODUCTION

The Mediterranean Sea is characterized by strong regional differences. The influences of river inflows, Atlantic waters and the Suez Canal, amongst other features, cause differences in sedimentation and hydrography (Millot 2005, Rossi et al. 2014) as well as environmental gradients in temperature, salinity and productivity (D'Ortenzio & Ribera d'Alcalà 2009). Anthropogenic influences also vary among regions (Coll et al. 2012), and the influence of Lessepsian migrants declines from east to west (Golani 1998). Given these contrasting local conditions and the reduced water exchange between basins through the shallower Strait of Sicily, many researchers consider the western and the eastern Mediterranean basins as different ecosystems (Piroddi et al. 2015). Given the different tolerances and habitat preferences of marine species, these contrasting conditions are expected to produce differences in faunal communities.

Community analyses at the scale of the whole Mediterranean have only focussed on fishes so far, with most analyses emphasizing species diversity and marine protected areas (Gaertner et al. 2007, Mouillot et al. 2011, Granger et al. 2015). Recent research shows regional differences in the diversity of Mediterranean cephalopods (Keller et al. 2016), a species group of key importance for ecosystem functioning (André et al. 2010, Hunsicker et al. 2010) and high socio-economic importance in Mediterranean countries. A species-level study revealed different population dynamics in the eastern and western Mediterranean basin for *Octopus vulgaris* and *Illex coindetii* (Keller et al. 2017), with the population dynamics of each species being more uniform in the eastern than in the western basin. However, no large-scale study has compared Mediterranean cephalopod community structure in areas with contrasting environmental conditions. This is remarkable, as at the species level, cephalopods are very sensitive to environmental influences, a fact that has already been highlighted in various studies (Lloret et al. 2001, Pierce et al. 2008, Keller et al. 2014, Puerta et al. 2014).

This taxon has increased in importance in many areas worldwide for several reasons. On the one hand, reports of increasing abundances for many years likely link to ecosystem changes (Balguerías 2000, Vecchione et al. 2009, Doubleday et al. 2016, Keller et al. 2017). On the other hand, cephalopods have become increasingly important fishery resources, in large part because of depletion of many commercial fish stocks (FAO 2016). Therefore, many

studies have focussed on Mediterranean cephalopod communities (e.g. Relini & Orsi-Relini, 1984, Quetglas et al. 2000, 2014; see Krstulovic Sifner et al. 2005 for a summary of works in the eastern basin), but only at local scale. Given that community structure depends on bathymetric, hydrographic and biological features (e.g. depth, temperature, salinity, productivity), contrasting external regimes are likely to influence cephalopods at the community level. Numerous studies link local cephalopod community structure to depth (Sanchez et al. 1998, Quetglas et al. 2000, Krstulovic Sifner et al. 2005); however, few studies include other physical factors such as temperature and chlorophyll *a* (chl *a*) content (González & Sánchez 2002). Many studies identify these factors as important drivers of diversity distribution patterns (Moutin & Raimbault 2002, Rosa et al. 2008a,b, Siddon et al. 2011), and thus presumably community structure for different marine communities (Siddon et al. 2011, Hidalgo et al. 2014).

Here we analysed cephalopod communities at the whole Mediterranean scale using fishery-independent data from annual standardized scientific trawl surveys. Our objective was to determine differences in cephalopod communities between basins and to identify possible drivers of these differences. To this end, we compared cephalopod communities in the western and eastern Mediterranean basins by applying a combination of community analyses and non-linear regression techniques. Our specific objectives were to: (1) differentiate species assemblages, (2) identify the most characteristic species of each assemblage and (3) investigate possible drivers of assemblage structure. These results may serve as a baseline for ongoing changes in marine ecosystems at the whole Mediterranean scale, because overfishing and climate change will certainly affect species distribution ranges and therefore community composition in the future.

MATERIALS AND METHODS

Biological sampling

Biological data were obtained from the international Mediterranean bottom trawl surveys (MEDITS; www.sibm.it/SITO%20MEDITS/), which have been conducted every year between May and August since 1994, spanning depths from 10 to 800 m. The surveys are performed annually by all coastal EU countries, in addition to Montenegro and Albania, and currently comprise the most valuable

data source on demersal ecosystems in the Mediterranean Sea. The MEDITS area is divided into geographical sub-areas (GSAs; Fig. 1) established by the General Fisheries Commission for the Mediterranean (GFCM, www.fao.org/gfcm/en/), and all countries use a standardized sampling methodology (for details see Bertrand et al. 2002, MEDITS 2016).

This survey uses a stratified random sampling design, with bathymetric strata comprising 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 2 and 18 m, respectively (Bertrand et al. 2002). An attached underwater gear-opening monitor system measures the net opening, which allows calculation of the swept area. Trawling occurs during daylight, with a towing speed of 3 knots and haul durations of 30 and 60 min over shelf and slope grounds, respectively. Abundance data for each species are standardized to number of ind. km⁻² using the swept area method (Saville 1977, Souplet 1996).

For the compilation of the species list, we used all data from 1994–2012, while basing the community analysis on data from 2003–2008. Data from the selected years represent the best compromise between continuous sampling, wide geographical range, rea-

sonable temporal scale and available satellite data. Some areas sampled only in recent years were excluded from the analysis, and no survey was conducted in Greek waters in 2007. To account for possible variability in taxonomic expertise among the various national surveys, possibly doubtful species were joined at the genus level (e.g. *Alloteuthis media* and *A. subulata* were joined as *Alloteuthis* spp.). The final dataset for the community analysis included 6258 sampling stations with cephalopod records, whereas the species list was compiled using 18 214 stations.

Satellite data

Satellite data for sea surface temperature (SST) and chl *a* were obtained from MODIS-Aqua and NPP-VIIRS sensor measurements already processed with regional ocean colour algorithms (resolution 1 km, daily data), and downloaded from the MyOcean database provided by COPERNICUS Marine service (<http://marine.copernicus.eu/web/69-interactive-catalogue.php>). The chl *a* data resulted from means of the MedOC4 algorithm (Volpe et al. 2007) from the merging of SeaWiFS, MODIS-Aqua and MERIS sensors.

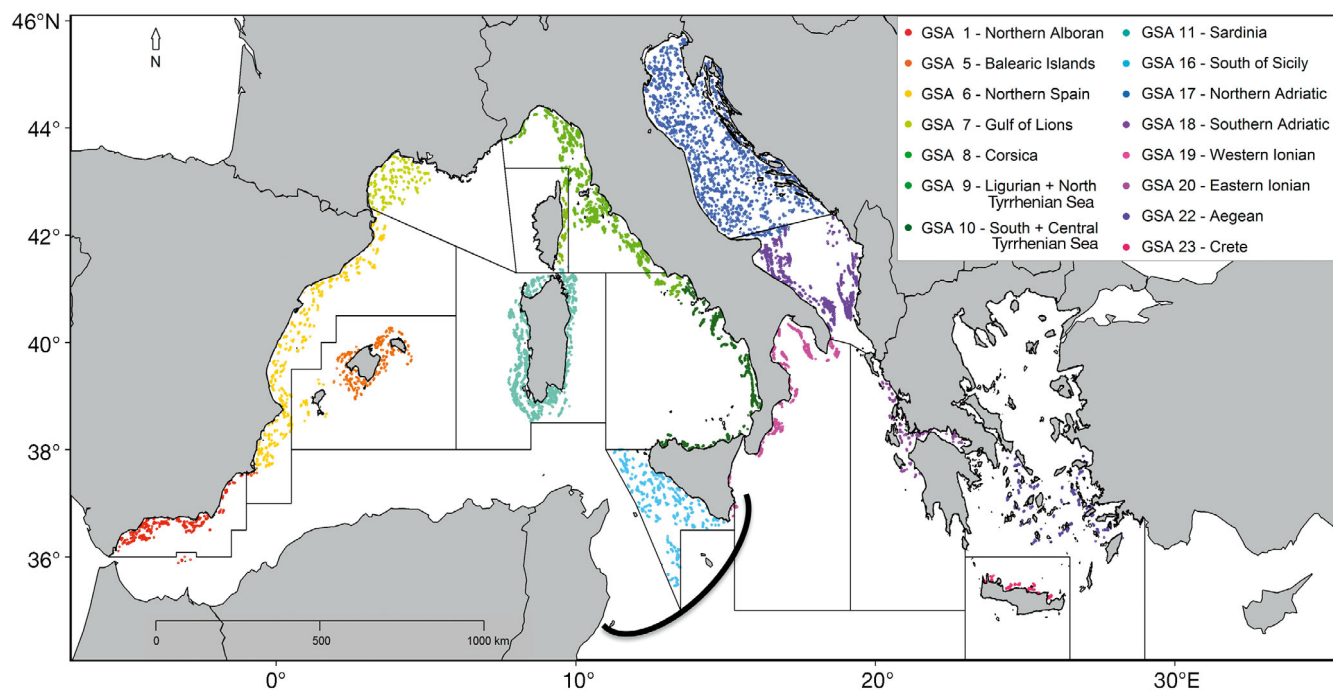


Fig. 1. Mediterranean Sea, showing the MEDITS sampling stations included in the analysis (2003–2008). The thick black line shows the division into western and eastern basin used in this study, while thin black lines represent the geographical sub-areas (GSAs) established by the General Fisheries Commission for the Mediterranean and used as spatial units in the survey

Both temperature and chl *a* concentration (proxy for food availability) might influence ecological and metabolic processes differently at different stages of an animal's life history, with an expected time-lagged response for chl *a* given the time required for energy transfer between trophic levels. Both parameters were therefore modelled using different seasonal means: (1) the spring (March–May) concurrent with the survey and (2) the preceding winter (December–February). These months were chosen because they represent good descriptors of the key oceanographic processes determining spring productivity in the Mediterranean (Lloret et al. 2001, Quetglas et al. 2011, Puerta et al. 2016). Means were calculated for each of the geographical sub-divisions within the MEDITS programme (GSAs), and each sampling station was assigned to its respective GSA in the model. This approach represented the best compromise between the higher environmental variability of single stations and the regional spatial scale of the modelled response (regional community composition).

Community analysis

Noting pronounced differences in environmental conditions (temperature, productivity regimes), oceanographic properties and hydrography between the western and eastern Mediterranean basins (Danovaro et al. 1999, Lascaratos et al. 1999, Turley et al. 2000), we analysed the data separately for both basins (Fig. 1). To describe gradients in species composition relative to environmental drivers, we used a combination of community analyses (nonmetric multidimensional scaling, NMDS) and non-linear regressions (general additive modelling, GAM). Past studies have used this combined methodology to reveal spatial and/or temporal differences in community structure as functions of relevant covariates (Siddon et al. 2011, Muenchow et al. 2013, Hidalgo et al. 2014). This way, while communities are not defined as separate units, recurrent combinations of species are associated with environmental or geographic characteristics. First, NMDS was applied to the community dataset to reduce the community composition information of each station to 3 major modes of variability (NMDS axes). NMDS is an ordination technique that arranges samples (in our case stations) to best match observed similarities among communities. NMDS separates communities along multiple dimensions, with the first axis accounting for the greatest portion of the variance. Standardized CPUE

data (see 'Biological sampling' above) were fourth root transformed to reduce the influence of highly abundant species. Transformation was followed by data standardization to species maxima to allow better comparison among species occurring at very different abundance levels (Field et al. 1982). We then computed Bray-Curtis similarity matrices among all different stations and analysed by NMDS ordination using 50 runs to find the best global model solution (R-library 'vegan'). This number of runs makes us confident that NMDS was not trapped in a local optimum. The resulting 3 ordination axes of the NMDS plot gave 3 dimensionless scores (1 for each axis) per station, which we then used as response variables in the non-linear GAMs (R-library 'mgcv').

We included sampling location, depth, SST and chl *a* as covariates to explain differences in cephalopod assemblages because these parameters represent important geographic, bathymetric and environmental gradients. Although interannual variability may be interesting, year was not included as a covariate, as results would be difficult to interpret in an analysis of this large a scale. Different regions have different temporal variations, and their classification was not our objective in this study. Several years were only included in order to avoid choosing an exceptional year. We used 1-dimensional smoothers to describe bathymetric and environmental influences, and a 2-dimensional smoother that combined latitude and longitude to represent a potential geographic gradient underlying the environmental and bathymetric influences. To ensure an ecological interpretation of non-linear effects and to avoid overfitting to the data, we restricted the number of knots for the smoothers of depth and the environmental variables to 3 and 4, respectively (cubic splines with up to a maximum of 2 and 3 degrees of freedom). The general model structure for each axis was as follows:

$$\text{Axis NMDS 1, 2, 3} \sim s(\text{Lat, Long}) + s(\text{depth}) + s(\text{Chla}_{\text{Winter}}) + s(\text{SST}_{\text{Winter}}) + s(\text{Chla}_{\text{Spring}}) + s(\text{SST}_{\text{Spring}})$$

We adopted a step-wise procedure for model selection, removing 1 non-significant covariate ($p > 0.05$) at a time from the full model. In addition, our best model excluded covariates displaying non-significant effects (i.e. 95% intervals containing 0 value in the partial effects plots) in most of the range of variation of the covariate. Best model selection was then based on the minimization of both the generalized cross-validation and Akaike's information criterion (AIC). For all GAMs, residual plots were checked and confirmed the assumptions of variance homogeneity and normal distribution. Finally, to identify

the species most strongly correlated with the respective axis and therefore most characteristic for the observed community composition, we used Spearman rank correlations, correcting significance levels *a posteriori* using the Bonferroni method.

RESULTS

In total, our analysis of the western and eastern basin included 40 and 41 species or genus complexes (e.g. *Alloteuthis* spp.) respectively, representing 17

different families. During the MEDITS surveys of 1994–2012, species caught only in the western basin were *Stoloteuthis leucoptera*, *Ommastrephes bartramii* (only in the Strait of Sicily), *Ocythoe tuberculata* and *Opisthoteuthis calypso* (only in the Iberian Sea) (Table 1). *Ancistrocheirus lesueurii*, *Pyroteuthis margaritifera* and *Abrialopsis morisii* were recorded only in the eastern basin (Ionian Sea), and *Octopoteuthis sicula* was collected only in the Ionian and Aegean Seas. *Ctenopteryx sicula* and *Chiroteuthis veranyi* were collected in both basins, but only in Italian waters (Tyrrhenian and Ionian Seas). To date,

Table 1. All cephalopod species found in the western and eastern basins of the Mediterranean Sea during the MEDITS surveys, by basin. Numbers denote frequency of occurrence (%) averaged from 1994–2012. Species only sampled in the western or eastern basin are marked by **boldface** type and respective superscript W or E

Species	Western	Eastern	Species	Western	Eastern
Order Sepiida			<i>Histioteuthis</i> spp.	0.15	0.03
Family Sepiidae			Family Onychoteuthidae		
<i>Sepia elegans</i> Blainville, 1827	25.48	31.88	<i>Ancistroteuthis lichtensteinii</i> Orbigny, 1839	1.92	1.01
<i>Sepia officinalis</i> Linneus, 1758	6.98	8.38	<i>Onychoteuthis banksii</i> (Leach, 1817)	0.27	0.23
<i>Sepia orbignyana</i> Férussac, 1826	24.76	16.98	Family Enoploteuthidae		
<i>Sepia</i> spp.	0.64	0.25	<i>Abrialia veranyi</i> (Rüppell, 1844)	10.88	7.06
Family Sepiolidae			<i>Abrialopsis morisii</i> (Vérany, 1839)^E	0.00	0.02
<i>Sepioida affinis</i> Naef, 1912	0.11	0.33	Unidentified Enoploteuthidae	0.00	0.05
<i>Sepioida intermedia</i> Naef, 1912	0.78	1.80	Family Ctenopterygidae		
<i>Sepioida ligulata</i> Naef, 1912	0.23	0.82	<i>Ctenopteryx sicula</i> (Veranyi, 1851)	0.02	0.02
<i>Sepioida robusta</i> Naef, 1912	0.22	2.20	Family Octopoteuthidae		
<i>Sepioida rondeleti</i> Leach, 1817	0.45	0.34	<i>Octopoteuthis sicula</i> Rüppell, 1844^E	0.00	0.11
<i>Sepioida</i> spp.	12.58	14.23	Family Chiroteuthidae		
<i>Rondeletiola minor</i> Naef, 1912	9.75	10.47	<i>Chiroteuthis veranii</i> (Férussac, 1835)	0.01	0.15
<i>Sepietta obscura</i> Naef, 1916	0.33	0.39	Family Ancistrocheiridae		
<i>Sepietta neglecta</i> Naef, 1916	0.27	0.88	<i>Ancistrocheirus lesueurii</i> (Orbigny, 1842)^E	0.00	0.06
<i>Sepietta oweniana</i> (D'Orbigny in Férussac & d'Orbigny)	24.97	11.79	Family Brachioteuthidae		
<i>Sepietta</i> spp.	2.22	5.47	<i>Brachioteuthis riisei</i> (Steenstrup, 1882)	0.27	0.12
Unidentified Sepiolinae	0.52	1.13	Family Pyroteuthidae		
<i>Rossia macrosoma</i> (Delle Chiaje, 1830)	12.68	7.36	<i>Pyroteuthis margaritifera</i> (Rüppell, 1844)^E	0.00	0.05
<i>Neorossia caroli</i> (Joubin, 1902)	5.81	2.52	Order Octopoda		
<i>Heteroteuthis dispar</i> (Ruppell, 1844)	2.31	1.52	Family Octopodidae		
<i>Stoloteuthis leucoptera</i> (Verrill, 1878)^W	0.34	0.00	<i>Octopus vulgaris</i> Cuvier, 1798	25.48	12.21
Order Myopsida			<i>Callistoctopus macropus</i> Risso, 1826	0.35	0.40
Family Loliginidae			<i>Octopus salutii</i> (Veranyi, 1839)	11.46	5.98
<i>Alloteuthis media</i> (Linnaeus, 1758) ^a	34.16	55.05	<i>Macrotritopus defilippi</i> (Vérany, 1851)	1.30	0.29
<i>Alloteuthis subulata</i> Lamarck, 1798 ^a	12.89	6.16	<i>Octopus</i> spp.	0.12	0.09
<i>Alloteuthis</i> spp. ^a	7.20	1.72	<i>Pteroctopus tetracirrhus</i> (Delle Chiaje, 1830)	12.02	2.00
<i>Loligo forbesii</i> Steenstrup, 1856	10.23	3.36	<i>Scaevargus unicolor</i> (Orbigny, 1840)	18.51	8.94
<i>Loligo vulgaris</i> Lamarck, 1798	15.51	31.34	<i>Bathypolypus sponsalis</i> (P. & H. Fischer, 1892)	5.37	0.03
<i>Loligo</i> spp.	0.91	0.09	<i>Eledone cirrhosa</i> (Lamarck, 1798)	59.26	33.67
Order Oegopsida			<i>Eledone moschata</i> (Lamarck, 1798)	16.91	28.93
Family Ommastrephidae			Family Ocythoidae		
<i>Ommastrephes bartramii</i> (LeSueur, 1821)^W	0.01	0.00	<i>Ocythoe tuberculata</i> Rafinesque, 1814^W	0.01	0.00
<i>Illex coindetii</i> (Veranyi, 1839)	46.49	62.59	Family Argonautidae		
<i>Todarodes sagittatus</i> (Lamarck 1798)	18.41	7.19	<i>Argonauta argo</i> Linnaeus, 1758	0.03	0.03
<i>Todaropsis eblanae</i> (Ball, 1841)	28.40	21.10	Family Opisthoteuthidae		
Family Histioteuthidae			<i>Opisthoteuthis calypso</i> Villanueva et al. 2002^W	0.03	0.00
<i>Histioteuthis bonnellii</i> (Férussac, 1835)	5.46	2.52	<i>Opisthoteuthis</i> spp.	0.01	0.00
<i>Histioteuthis reversa</i> (Verrill, 1880)	5.25	4.86			

^aSpecies joined for analysis

Bathypolypus sponsalis has not been caught in the easternmost parts of the Mediterranean (Adriatic and Aegean Seas).

Although species composition did not differ between the western and eastern basins, the relative contribution of the different species (in terms of frequency of occurrence) changed between basins: *Eledone cirrhosa* (59%), *Alloteuthis* spp. (54%) and *Illex coindetii* (46%) dominated the western basin, in contrast to *I. coindetii* (62%), *Alloteuthis* spp. (62%) and *E. cirrhosa* (33%) in the eastern basin.

Following analysis of the community data for each basin with NMDS, we applied GAMs to model the 3 most important axes. The 3 best models for each axis and basin are shown in Table 2.

In the western basin, the first axis of the NMDS mainly described the depth gradient of the cephalopod community, as seen by the linear depth effect in our GAM (Fig. 2a). Deep-sea assemblages correlated positively with the first axis values and included *Todarodes sagittatus*, *Histioteuthis bonnellii*, *H. reversa* and *Bathypolypus sponsalis* (Table 3). More coastal communities correlated negatively with the first axis and were characterized mainly by demersal species such as *Octopus vulgaris*, *Alloteuthis* spp., *Eledone moschata* and *Loligo vulgaris* (Table 3). In addition to depth, winter SST influenced community composition, and the best model included low temperature values related to positive axis 1 scores. The remaining spatially structured variance captured by the geographic pattern reveals that north-westernmost waters (i.e. Gulf of Lions and Catalan coast) and south-westernmost waters off the Italian mainland and Sicily related to more positive values of axis 1.

Axis 2 mainly distinguished upper slope communities as evidenced by the dome-shaped form of the bathymetric effect (Fig. 2b). The species positively related to this axis were *Todaropsis eblanae*, *Sepietta oweniana*, *Octopus salutii*, *Abralia veranyi*, *Rossia macrosoma* and *Scaevargus unicolor* (Table 3). Winter SST also was a significant driver, affecting spatial variability of this axis (Fig. 2b). Warmer waters at the surface favoured upper slope communities, in that

Table 2. Best model selection based on explained deviance (%DEV) and Akaike's information criterion (AIC). The 3 best general additive models for each axis and Mediterranean Sea basin are shown (best models in **bold**). Significant covariates ($p < 0.05$) entering in the models are marked by +. Chl *a* Spring (Winter): mean chl *a* concentration during spring (winter). SST Spring (Winter): mean sea surface temperature during spring (winter)

	Location	Depth	SST Winter	SST Spring	Chl <i>a</i> Winter	Chl <i>a</i> Spring	%DEV	AIC
Western basin								
Axis 1	+	+	+				76.2	3809.8
	+	+					76.1	3824.6
		+					74.1	4079.9
Axis 2	+	+	+				25.6	2304.9
	+	+					25.1	2326.9
		+					15.1	2754.5
Axis 3	+	+			+		12.8	2654.9
	+	+					12.3	2672.3
	+						10.8	2731.7
Eastern basin								
Axis 1	+	+					68.1	3848.9
		+					62.4	4190.0
	+						44.0	5198.9
Axis 2	+	+					45.4	951.0
	+						41.7	1102.0
		+					3.20	2263.6
Axis 3	+	+	+	+	+		20.5	1431.8
	+	+		+	+		19.1	1461.3
	+	+			+		18.6	1473.7

positive values of axis 2 correlated positively with higher temperatures. *Todarodes sagittatus* and *Alloteuthis* spp., in contrast, may benefit from colder waters (Table 3). The remaining variance captured by the spatial effect reveals a gradient from the west to the east of the basin, with positively correlated species favoured in eastern areas.

Species positively related to Axis 3 were primarily influenced by greater depth, whereas those negatively linked with the axis were associated with relatively high values of winter concentration of chl *a* (Fig. 2c). Those species linked with more productive areas were *Sepia orbignyana*, *Illex coindetii*, *Scaevargus unicolor*, *Todaropsis eblanae* and *Sepia elegans* (Table 3). The most favourable conditions for these communities (i.e. negative correlation with axis 3) occur in the strait of Sicily (Fig. 2c).

Results for the eastern basin paralleled those in the western basin in terms of bathymetry largely delineating the communities associated with each axis. The first axis described a bathymetric gradient in the communities (Fig. 3a). Despite similarities in the composition of the shallow-water community to the western basin, the most characteristic species differed, with *Eledone moschata* in the eastern basin

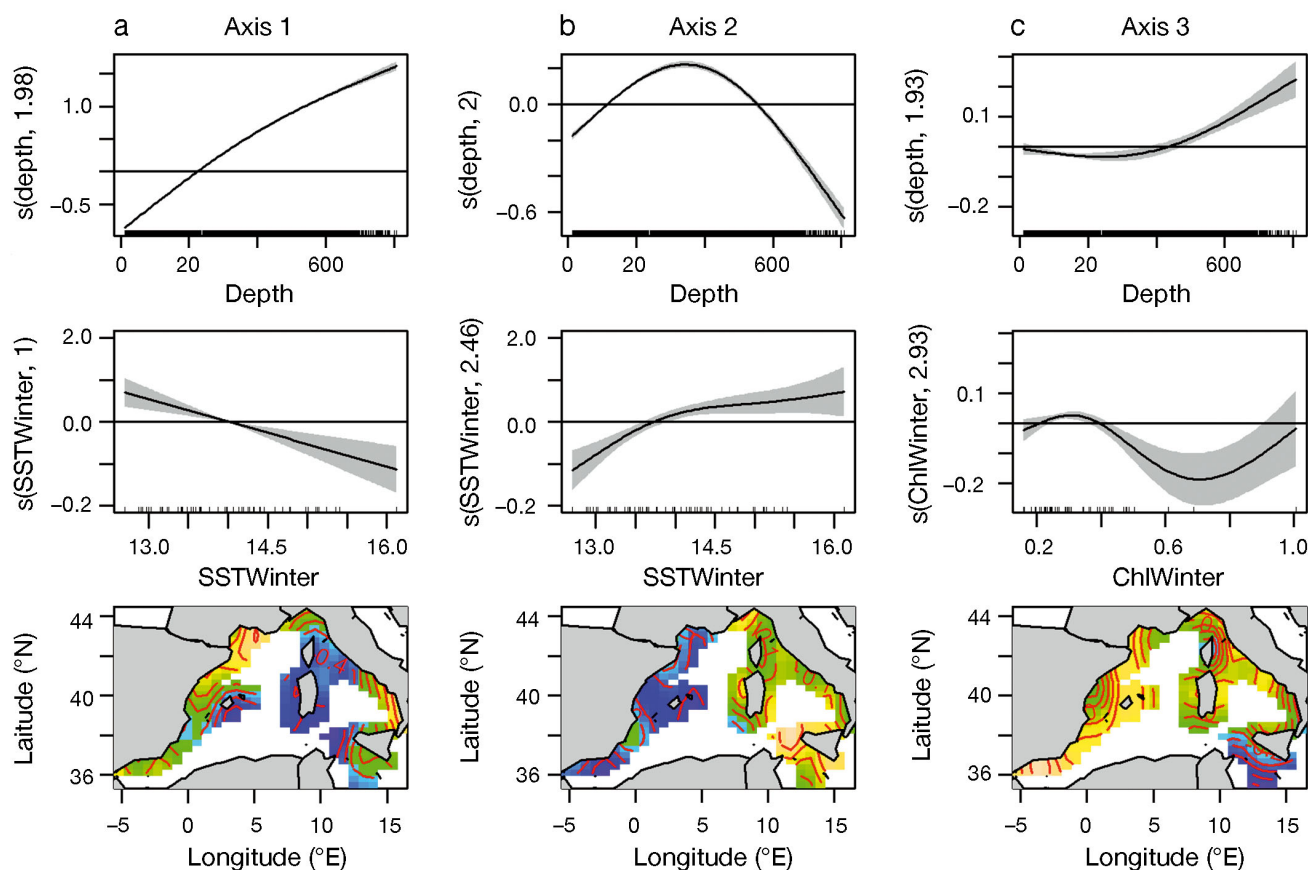


Fig. 2. Results of the general additive modelling (GAM) analysis performed on (a) axis 1, (b) axis 2 and (c) axis 3 of the non-metric multidimensional scaling (NMDS) results for the western basin. Plotted are the significant partial effects of each model (fitted line) together with 95 % confidence intervals (grey shading). Vertical axes of the effect graphs for depth and environmental variables show the smoother function for each variable resulting from the GAM analysis. The maps show the geographical effects of the sampling locations. The colour gradient of the geographical effect codes from low values (darker colours) to high values (lighter colours)

and *Octopus vulgaris* in the west (Table 3). The slope community included a species mix dominated by *Todarodes sagittatus*, *Todaropsis eblanae*, *Eledone cirrhosa* and *Illex coindetii*. A regional effect was evident near the Gulf of Taranto, a region with stronger affinities to the above communities than the rest of the eastern basin.

As in the western basin, the second axis described the upper slope communities (Fig. 3b), with communities characterized by species with an intermediate depth spectrum like *Eledone cirrhosa*, *Todaropsis eblanae* and *Illex coindetii* (Table 3). Regional effects positively influenced this assemblage on the west coast of the northern Adriatic Sea.

The third axis was influenced not only by depth and geographic position, but also by environmental parameters such as the winter productivity regime (chl *a* - Winter) as well as by winter and spring tem-

peratures (Fig. 3c). Higher productivity during winter, intermediate to high winter SST, and low SST in spring favoured species positively correlated with the axes (*Loligo vulgaris*, *Octopus vulgaris*, *Todaropsis eblanae*, *Sepia officinalis* and others; Fig. 3c, Table 3). Regional effects fostering these communities occur in the Ionian Sea, whereas the northern Adriatic favours *Illex coindetii*, the only important species negatively correlated with the third axis (Table 3).

DISCUSSION

Despite the contrasting oceanographic conditions governing the western and the eastern Mediterranean basins, the communities differ very little in species composition, although they do vary in relative

Table 3. Spearman rank correlations of the 3 axes (dimensions) from the non-metric multidimensional scaling (NMDS) correlated with cephalopod taxa density in the western and eastern basins of the Mediterranean Sea. Only significant correlations ≥ 0.20 (for positive correlations, lower set per basin) and ≤ -0.2 (for negative correlations, upper set per basin) are shown. Numbers (n) and means of the significant correlations are shown for each group

WESTERN BASIN					
Axis 1		Axis 2		Axis 3	
n = 6; mean = -0.50		n = 2; mean = -0.253		n = 6; mean = -0.218	
<i>Octopus vulgaris</i>	-0.63	<i>Todarodes sagittatus</i>	-0.30	<i>Sepia orbignyana</i>	-0.53
<i>Alloteuthis</i> spp.	-0.60	<i>Alloteuthis</i> spp.	-0.21	<i>Illex coindetii</i>	-0.39
<i>Eledone moschata</i>	-0.52			<i>Scaevargus uncinatus</i>	-0.32
<i>Loligo vulgaris</i>	-0.49			<i>Todaropsis eblanae</i>	-0.24
<i>Sepia elegans</i>	-0.38			<i>Sepia elegans</i>	-0.23
<i>Sepia officinalis</i>	-0.38			<i>Alloteuthis</i> spp.	-0.22
n = 10; mean = 0.31		n = 9; mean = 0.308		n = 3; mean = 0.264	
<i>Todarodes sagittatus</i>	0.53	<i>Todaropsis eblanae</i>	0.57	<i>Octopus vulgaris</i>	0.35
<i>Histioteuthis bonnellii</i>	0.37	<i>Sepietta oweniana</i>	0.44	<i>Sepia officinalis</i>	0.24
<i>Bathypolypus sponsalis</i>	0.32	<i>Octopus salutii</i>	0.30	<i>Eledone moschata</i>	0.20
<i>Histioteuthis reversa</i>	0.31	<i>Abralia veranyi</i>	0.28		
<i>Abralia veranyi</i>	0.31	<i>Rossia macrosoma</i>	0.25		
<i>Octopus salutii</i>	0.27	<i>Scaevargus uncinatus</i>	0.24		
<i>Neorossia caroli</i>	0.27	<i>Rondeletiola minor</i>	0.24		
<i>Todaropsis eblanae</i>	0.27	<i>Pteroctopus tetracirrus</i>	0.23		
<i>Rossia macrosoma</i>	0.26	<i>Loligo forbesii</i>	0.21		
<i>Pteroctopus tetracirrus</i>	0.21				
EASTERN BASIN					
Axis 1		Axis 2		Axis 3	
n = 5; mean = -0.421		n = 6; mean = -0.347		n = 1; mean = -0.237	
<i>Eledone moschata</i>	-0.59	<i>Sepia elegans</i>	-0.55	<i>Illex coindetii</i>	-0.24
<i>Loligo vulgaris</i>	-0.54	<i>Eledone moschata</i>	-0.50		
<i>Alloteuthis</i> spp.	-0.41	<i>Octopus vulgaris</i>	-0.27		
<i>Sepia officinalis</i>	-0.36	<i>Scaevargus uncinatus</i>	-0.27		
<i>Sepia elegans</i>	-0.20	<i>Sepia orbignyana</i>	-0.26		
		<i>Loligo forbesii</i>	-0.23		
n = 12; mean = 0.299		n = 3; mean = 0.327		n = 6; mean = 0.308	
<i>Todarodes sagittatus</i>	0.45	<i>Eledone cirrhosa</i>	0.54	<i>Loligo vulgaris</i>	0.44
<i>Todaropsis eblanae</i>	0.44	<i>Todaropsis eblanae</i>	0.24	<i>Octopus vulgaris</i>	0.39
<i>Eledone cirrhosa</i>	0.35	<i>Illex coindetii</i>	0.20	<i>Todaropsis eblanae</i>	0.34
<i>Illex coindetii</i>	0.31			<i>Sepia officinalis</i>	0.27
<i>Abralia veranyi</i>	0.31			<i>Sepietta oweniana</i>	0.21
<i>Rossia macrosoma</i>	0.30			<i>Eledone moschata</i>	0.20
<i>Histioteuthis reversa</i>	0.30				
<i>Scaevargus uncinatus</i>	0.25				
<i>Rondeletiola minor</i>	0.24				
<i>Octopus salutii</i>	0.23				
<i>Neorossia caroli</i>	0.21				
<i>Sepia orbignyana</i>	0.20				

species contributions. Bathymetry was apparently a major structural driver for the cephalopod communities of both basins. Our analysis clearly distinguished 3 communities: the continental shelf communities, upper slope communities and middle slope communities, consistent with previous studies

at local scales (Sanchez et al. 1998, Quetglas et al. 2000, González & Sánchez 2002). SST, particularly in winter, influenced the western basin communities more strongly, with a weaker effect in the eastern basin. Productivity influenced community assemblages in both basins similarly and weakly. Our

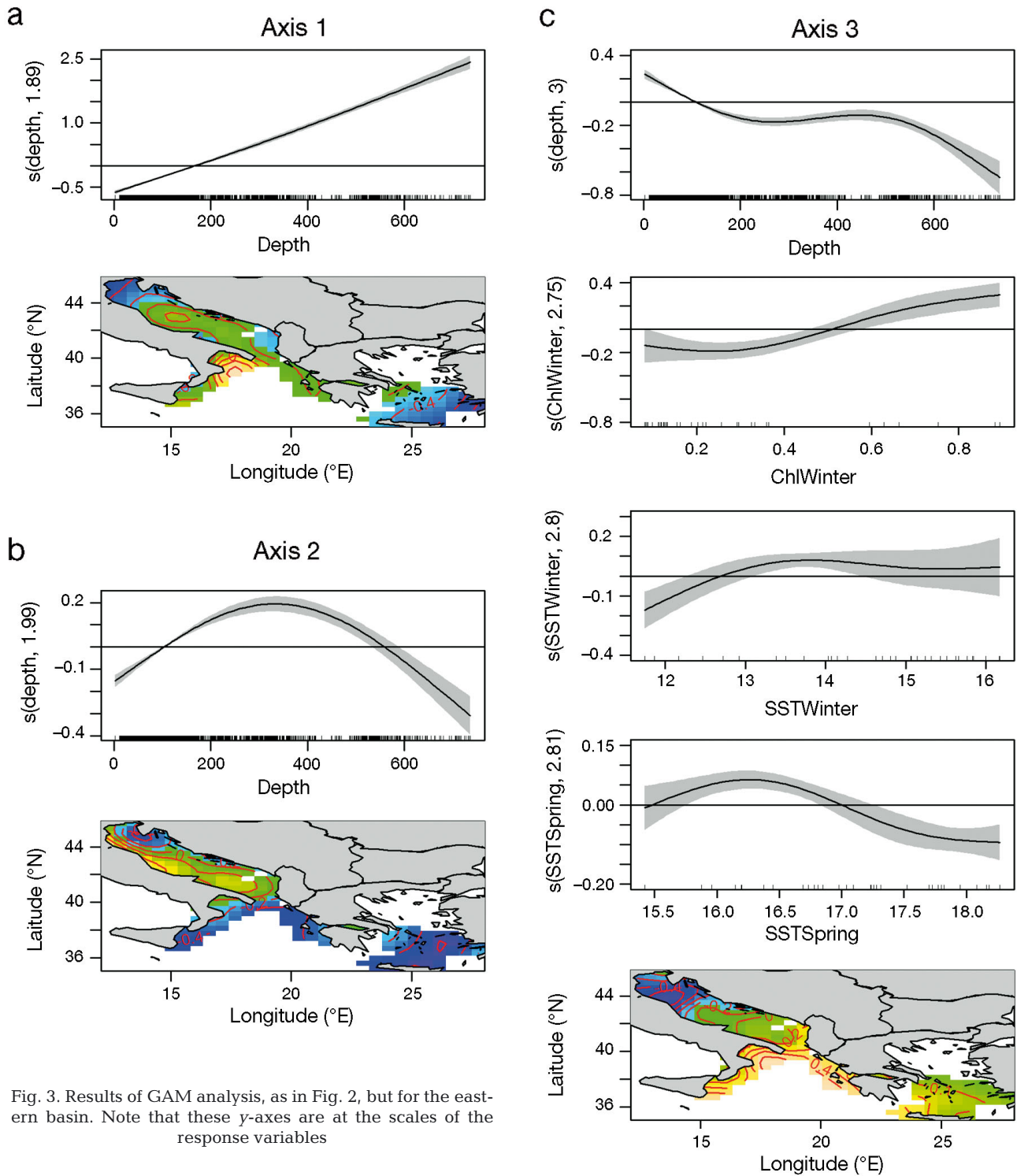


Fig. 3. Results of GAM analysis, as in Fig. 2, but for the eastern basin. Note that these y-axes are at the scales of the response variables

models detected geographic differentiation in the communities in both basins once the bathymetric and the environmental gradients were taken into account, suggesting that additional regional-scale drivers not included in our models affect cephalopod communities.

Community composition

The Strait of Sicily may represent a geographic barrier for deep-sea cephalopod species, as its relatively shallow bathymetry compared to the rest of the Mediterranean Sea may limit movement of organ-

isms and water circulation (Bianchi 2007). Nevertheless, the similar cephalopod faunal lists for both basins differ mostly in the abundances of individual species. Although warmer temperatures and lower productivity in the eastern basin may favour some cephalopod species, they do not fully preclude others. As noted earlier, differences in basin characteristics may influence the mechanisms that influence resident communities. The presence of the same species but varying species contribution within the 2 sub-basins may hint at different ecological processes, such as trophic pathways. Indeed, food web structures differ from region to region, with a lower proportion of small pelagic fish and other organisms of low trophic levels in the eastern basin (Tsagarakis et al. 2010, Halouani et al. 2015), and a higher relative total biomass of small pelagic fish km⁻² in the western basin and the Adriatic Sea (Piroddi et al. 2015). In addition, different exploitation patterns and food web structures result in different fishing impacts from basin to basin (Halouani et al. 2015). The 2 Mediterranean ecosystems also differ in flows of biomass and community energetic attributes, leading to structural differences in different regions (Hattab et al. 2013).

Our study identified *Eledone moschata* as the most characteristic shelf species in the eastern basin, followed by *Loligo vulgaris*, in contrast to *Octopus vulgaris* followed by *Alloteuthis* spp. in the west. In general, *O. vulgaris* has little importance in shallow waters in the eastern basin, an assertion consistent with its lower abundances in that basin (Belcari et al. 2002). Stronger fishing pressure on juvenile octopus in that area due to its high value as a fishery resource might explain this pattern, but species-specific preferences may also play a role. For example, Sobrino et al. (2002), Vargas-Yáñez et al. (2009) and Keller et al. (2017) supported the hypothesis that higher SST negatively affects *O. vulgaris* abundance, whereas Puerta et al. (2016) correlated *O. vulgaris* landings with chl *a* concentration. Thus higher temperatures and lower productivity in the eastern basin could explain the reduced importance of *O. vulgaris*. Alternatively, this species could inhabit shallower waters in the eastern zones, as reported for other cephalopod species (Tursi & D'Onghia 1992, Quetglas et al. 2000). If true, their underrepresentation in the eastern basin could reflect legal sampling restrictions in waters shallower than 50 m. In general, *Eledone* species and *Illex coindetii* characterize eastern basin communities more so than western basin communities, whereas *Alloteuthis* spp. predominate in the west. This pattern may reflect species-specific pref-

erences. For example, *I. coindetii* favours higher temperatures and more oligotrophic areas (Puerta et al. 2015, Lauria et al. 2016, Keller et al. 2017), a pattern consistent with our results.

Comparing the species lists of both basins revealed few major differences. Most of the species unique to some areas occur rarely in MEDITS surveys, so conclusions regarding their distributions should be drawn with care. For example, despite their absence in eastern basin samples, *Ommastrephes bartramii* and *Ocythoe tuberculata* have been recorded various times from the Aegean Sea and/or Levantine Sea (Salman 2009).

Drivers of cephalopod community patterns

In both basins, cephalopod communities subdivide into different sub-communities by depth, as suggested by previous studies on cephalopod communities of different regions at a smaller scale (Quetglas et al. 2000, González & Sánchez 2002, Krstulovic Sifner et al. 2005). Although our results are consistent with these studies in suggesting similar indicator species (Quetglas et al. 2000, González & Sánchez 2002, Soriano et al. 2003), the most relevant species and the relative contribution of species for the very same communities differ in each basin despite an identical functional relationship with depth (Figs. 2 & 3).

Apart from depth, environmental conditions likely influence community composition. In almost all models, winter values of significant variables proved important, indicating time-lagged rather than immediate environmental effects. Thus, environmental conditions months before the surveys exert the strongest influence on communities, suggesting particular importance of environmental conditions during the paralarval and early life stages of cephalopods. At that life stage, conditions will affect survival and abundance of different species differently, fostering a common spring-summer community of specific structure. Previous studies report such a time-lagged effect in cephalopods both in the Mediterranean (Lloret et al. 2001, Vargas-Yáñez et al. 2009, Quetglas et al. 2011, Puerta et al. 2015) and the Atlantic Ocean (Sobrino et al. 2002, Pierce et al. 2005).

In this respect, winter SST probably plays an important structuring role, influencing community composition more in the western than in the eastern basin. This observation is consistent with recent research (Puerta et al. 2015, Keller et al. 2017), which shows that, at a species level (e.g. *Octopus vulgaris*

and *Illex coindetii*), species in the western basin group at smaller scales according to spatial differences in environmental variability such as regional gradients of winter temperature. By contrast, in the eastern basin, species varied synchronously in the whole sub-basin, with no population sub-structuring (Keller et al. 2017).

Deep-sea communities apparently benefit from lower SSTs, presumably through the many surface-layer processes affected by temperature and later linked to the deeper layers via benthic-pelagic coupling. Such processes influence food and nutrient input, affecting growth and reproductive success, among others (Maynou 2008, Cartes et al. 2009, Fanelli et al. 2013, Tecchio et al. 2013). Detailed knowledge about the specific mechanisms affecting cephalopod communities will require further research. In contrast to deep-sea communities, higher SST during winter seems to favour shallow water and upper slope communities. Given that most cephalopods spend relatively little time at the surface, SST likely influences early life stages rather than adults, especially for deeper-water species (Pierce et al. 2008). In contrast, young animals often occur coastally (e.g. Sepiidae, Loliginidae) or planktonically (e.g. Ommastrephidae). Therefore we lagged temperature by several months, and winter temperature indeed proved more important than spring temperature. Milder winter temperatures likely enhanced the survival of young life stages and resulted in higher growth rates. For example, temperature positively influences ommastrephid paralarvae (Zaragoza et al. 2015). Few studies to date have assessed the importance of temperature for cephalopods at the community level (but see González & Sánchez 2002), but species-level studies show different preferences and physiological optima (see e.g. Robin & Denis 1999, Sobrino et al. 2002, Vargas-Yáñez et al. 2009, Lauria et al. 2016). Colder winter temperatures, on the other hand, cause stronger and deeper mixing of Mediterranean water masses through cascading events and convection via stronger winds or more frequent thunderstorms. Enhanced mixing leads to higher nutrient availability, with positive effects up the food chain. In the eastern basin, both spring and winter temperatures are of importance. This could result from the fact that the distribution of *I. coindetii*, the species which characterizes the community linked to negative axis values, is partly driven by spring temperatures (Keller et al. 2017).

Productivity showed the smallest, but consistent influence in our study. Shallow-water communities apparently benefit from higher chl *a* content, which

links with tighter benthic-pelagic coupling and faster transport of nutrients and organic matter to and from the bottom. Reaction time of shallow-water communities may therefore be quicker, increasing sensitivity of communities to changes in food availability. In contrast, low winter productivity positively affects abundances of *I. coindetii* at different spatial scales, as seen in previous studies (Puerta et al. 2015, Keller et al. 2017). These studies hypothesised that small pelagic fishes are effective competitors for food with early and juvenile stages of squid. As higher chl *a* typically enhances survival and growth of small pelagic fishes, juvenile squid may be favoured by areas of lower productivity.

Regional effects play a role in both basins, suggesting the influences of additional spatial drivers of community composition not included in our models. These effects differ for each of the communities, meaning that drivers affect different communities in different ways. Bottom type, for example, presumably influences relative distributions of demersal species. River inflows (lower salinity, more nutrients, higher turbidity, higher pollution) affect cephalopod species including *O. vulgaris* and *I. coindetii* (Lloret et al. 2001, Puerta et al. 2014, 2016). Various other influences add further complexity, such as Atlantic water inflow (less saline and colder water, larval supply), local wind regimes (increased mixing of water masses) or fishing pressure (selective pressure on certain species or their predators and food). The gradient in the western basin (Fig. 2b) could hint at an influence of Atlantic water masses or current patterns on the different sub-basins. These Atlantic water masses not only differ in their characteristics, but may also transport cephalopod paralarvae into (and within) the Mediterranean (Bouchet & Taviani 1992).

CONCLUSIONS AND FURTHER RESEARCH

Our study represents the first on cephalopod assemblages at the scale of the entire Mediterranean Sea. Assemblages in the 2 basins basically differ in relative importance of species within the communities, but very little in species composition. At this large scale, depth was the most important factor structuring cephalopod communities, but additional influences of environmental variability were evident in both basins.

These results will help in understanding responses of cephalopod communities to changing environmental conditions, especially in the framework of

global change and overexploitation of most Mediterranean stocks (Colloca et al. 2013, Vasilakopoulos et al. 2014). Given the observed temperature sensitivity of communities, we predict that ongoing climate warming will alter cephalopod community composition. Our models predict much stronger effects in the western basin, where the influence of temperature is higher.

Understanding influences on community composition may benefit fisheries and conservation management, which now utilize an integrated ecosystem approach that requires knowledge at the community level. In this context, a useful extension of our work would integrate other near-bottom environmental conditions such as salinity and bottom type, which play important roles in the distribution of demersal species (Demestre et al. 2000, González & Sánchez 2002).

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