Diversity and mesoscale spatial changes in the planktonic cnidarian community under extreme warm summer conditions

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Knowing the variations of planktonic cnidarians under climate change conditions is of importance due to the key role of carnivorous gelatinous zooplankton in the pelagic ecosystem. We investigated the abundance, spatial distribution, species richness and community structure of planktonic cnidarians in a temperate area, the NW Mediterranean, during the extremely warm summer of 2003 and the average summer of 2004. The surveys covered a broad and heterogeneous area. During the warm summer, the cnidarian community was half as abundant as during 2004, whereas its diversity was higher. The mesoscale spatial distribution of several species varied between the years. The structure of the community had a coastal-offshore ordination in the typical summer, but a north–south one in the warm summer when the temperature gradient prevailed instead of the bathymetry. Only hydromedusae were more abundant during the warm summer. The dominant siphonophore, *Muggiaea atlantica*, exhibited one of the greatest abundance decreases in 2003. Our results emphasize that exceptionally warm summer conditions could reduce gelatinous zooplankton abundance and change their latitudinal distribution and community composition. We stress the importance of mesoscale plankton surveys, including detailed taxonomic identification, as a critical tool for better understanding marine ecosystem responses to climatic variability.

KEYWORDS: species richness; extreme climatic events; summer 2003 heat wave; NW Mediterranean; Shannon diversity index.

INTRODUCTION

Gelatinous zooplankters are common components of the pelagic fauna with important roles within the trophic web (Pagès *et al.*, 2001; Robison, 2004). They are ubiquitous, diverse and among the most abundant components of the oceanic community (Pugh, 1989; Haddock, 2004; McClatchie *et al.*, 2012). In temperate seas, such as the Mediterranean, gelatinous zooplankton

are an important fraction of all zooplankton in terms of both abundance and species richness (Estrada *et al.*, 1985; Mills *et al.*, 1996; Saiz *et al.*, 2014). Their patterns of distribution, abundance and species richness are tightly linked to oceanographic dynamics and water mass structures, as well as to climate patterns (Graham *et al.*, 2001; García-Comas *et al.*, 2011; Brotz *et al.*, 2012; Licandro *et al.*, 2012). Thus, both mesoscale physical processes, such as currents, fronts and eddies, and climate variability, can shape and determine their distributions (Pagès and Gili, 1991; Graham *et al.*, 2001; Boero *et al.*, 2016; Guerrero *et al.*, 2016).

Changes in environmental and climatic conditions affect the composition, abundance and distribution of several groups of zooplankton (Hays *et al.*, 2005; Piontkovski *et al.*, 2011; Saiz *et al.*, 2014), including gelatinous forms (Lynam *et al.*, 2010; Licandro *et al.*, 2012). Climate change has been suggested to be among the global phenomena driving increased jellyfish abundance and blooms (Brotz and Pauly, 2012; Boero *et al.*, 2016), as well as changes in their species richness (Batistić *et al.*, 2014; Boero *et al.*, 2016). In temperate regions, gelatinous zooplankters appear to be expanding their distributions and broadening their reproductive periods, which results in larger populations with significantly negative socio-economic impacts on maritime tourism in some areas (Boero *et al.*, 2016).

The Mediterranean is a strongly seasonal sea (Estrada *et al.*, 1985; Bosc *et al.*, 2004), where the distributions and abundances of gelatinous zooplankters are regulated by the annual temperature cycle (Gili *et al.*, 1987b; Batistić *et al.*, 2007; Licandro *et al.*, 2012). The highest abundance and diversity occur in spring and summer (Gili *et al.*, 1987b; Batistić *et al.*, 2007; Licandro *et al.*, 2012; Saiz *et al.*, 2014). Interannual variability in temperature has been pointed out as a determining factor in jellyfish abundance changes (Molinero *et al.*, 2008; Brotz and Pauly, 2012). It is known that higher temperatures promote faster life cycles and greater reproductive rates in many jellyfish species (Purcell, 2005; Boero *et al.*, 2016). In addition, high temperatures may favour earlier sexual and asexual reproduction of cnidarians, advancing the timing of their seasonal abundance peaks (Boero *et al.*, 2016). In recent years, rising ocean temperatures, due to climate change, have been well documented at global and local scales, including the Mediterranean Sea (Levitus *et al.*, 2005; IPCC, 2014; Boero *et al.*, 2016), as well as an increase in the occurrence of extreme climatic events (Schär *et al.*, 2004). The summer of 2003 was exceptionally warm in Europe, where a heat wave from early June to mid-August produced record air temperatures, from 3 to 6°C above the seasonal averages (Schär *et al.*, 2004). This heat wave raised the sea surface temperature by 2–3°C over the whole Mediterranean (Grazzini and Viterbo, 2003; Sparnocchia *et al.*, 2006),

an increase in line with the values foreseen in the future from the climatic trends in the region (Schär *et al.*, 2004; Maynou *et al.*, 2014). During that same period, extensive mass mortality of rocky benthic macroinvertebrates (mainly gorgonians and sponges) was documented along the entire northwestern Mediterranean coast (Garrabou *et al.*, 2009), and Piontkovski *et al.* (2011) reported an increase of warm-water planktonic species in the Adriatic Sea. Along the Catalan coast, Atienza *et al.* (2016) and Maynou *et al.* (2014) observed reduced abundances of both zooplankton and ichthyoplankton. However, the consequences of such a warm anomaly for gelatinous and other planktonic communities are still poorly understood (Piontkovski *et al.*, 2011; Atienza *et al.*, 2016; Oliver *et al.*, 2017).

Studies of zooplankton time-series conducted in different areas of the Mediterranean Sea have shown long-term changes in gelatinous and non-gelatinous zooplankton in relation to climate variability (Benović *et al.*, 2000; Molinero *et al.*, 2005, 2008; García-Comas *et al.*, 2011; Berline *et al.*, 2012; Licandro *et al.*, 2012; Batistić *et al.*, 2014). Nevertheless, the observed effects show no strongly coherent responses among sampling sites (Berline *et al.*, 2012; Saiz *et al.*, 2014). Most of those studies were conducted at only a few stations, over limited geographical areas, and identified either some species or broad taxonomic groups. However, latitudinal changes in species distributions do reflect the responses of ecosystems to rising temperatures (Hughes, 2000; Beaugrand *et al.*, 2002).

In the present work, we aim to add a spatial dimension to the study of changes in marine zooplankton communities under extremely warm summer conditions, while also dealing with taxonomic identification at species level of the whole planktonic cnidarian community (siphonophores, hydromedusae and scyphomedusae). We compared two summers with contrasting temperatures: the exceptionally warm summer of 2003 and the summer of 2004 with temperatures near the climatic average for the period 2000–2012 (Sparnocchia *et al.*, 2006; Maynou *et al.*, 2014). The study covered a broad and heterogeneous area of the Mediterranean, the Catalan coast. It provides different environmental gradients for study: those in bathymetry, temperature, salinity and primary production. The comparative study of those two summers can shed light on the potential effects of extremely high temperatures upon gelatinous zooplankton, and their responses to strong and sudden temperature variations.

The initial hypothesis in this study was that the exceptionally warm summer conditions of 2003 would cause considerable changes in the abundance, spatial distribution, species richness and community structure of the

planktonic cnidarians in the temperate area studied. The response of the cnidarian community to this extreme event provides new insights about the likely impacts of climate change on marine ecosystems during future warming conditions.

METHOD

The study area was along the Catalan coast in the NW Mediterranean (Fig. 1). Oceanographic cruises were conducted during the summer of two consecutive years: 18–25 July 2003 and 21–29 July 2004. During each survey, 66 stations were sampled on transects perpendicular to the shoreline, over the continental shelf and slope. Stations on each transect were 14 km apart, while the distance between transects was 18.5 km. Vertical profiles of basic hydrographic variables (temperature, salinity and fluorescence) were obtained with a Neil Brown Mark III-CTD (WOCE standard) equipped with a Sea Tech fluorometer. The vertical profiles were averaged over 1 m depth intervals. Water for chlorophyll *a* determinations was collected with a rosette sampler from three depths down to 70 m at each station during both day and night occupations, in order to calibrate the *in situ* fluorometer (see Sabatés *et al.*, 2009 for a methodological description). Circulation in the area was estimated from geostrophic fields obtained from dynamic heights at the stations. The reference level was 600 m and, where the depth of a station was less, the dynamic height was extrapolated using a continuity equation applied to the deepest levels of three-station clusters (Hidaka, 1940). Along- and across-shore

Fig. 1. Geographical location of the study area off the Catalan coast, NW Mediterranean. Black dots represent the grid of sampled stations (*n* = 66). Grey lines indicate bathymetry (every 100 m).

geostrophic velocity components at the stations were derived from a stream function obtained by interpolating dynamic heights over the whole area (Stewart, 2008). Given the general NE–SW orientation of the Catalan coast, the velocity components were rotated 45°, such that U45 is the across-shore component of the current velocity, with positive values directed offshore, and V45 is the alongshore component, with positive values toward the SW. Vorticity or curl of the current velocity at each station was obtained from the spatial derivative of the stream function (Stewart, 2008).

Zooplankton was sampled with a Bongo net with 60 cm mouth diameters and 300 μm mesh size. Hauls were oblique from a maximum depth of 200 m to the surface (or from 5 m above the bottom to the surface at stations shallower than 200 m). The volume of water filtered was estimated using a flowmeter suspended in the centre of the net mouth. Zooplankton samples were fixed immediately after collection in 5% formaldehyde buffered with sodium tetraborate. In the laboratory, the whole planktonic cnidarian community (hydromedusae, siphonophores and scyphomedusae) was analysed to the species level using a stereomicroscope. Aliquots were taken only to quantify the most abundant species (e.g. *Muggiaea atlantica* and *Aglaura hemistoma*), and minima of 100 individuals per species were counted to estimate the actual number in the sample (Postel *et al.*, 2000). Calycophoran polygastric stages were counted as the number of complete colonies, plus the highest number of either anterior or posterior nectophores. The distinctly eudoxid sexual stages of *Abylopsis tetragona*, *Chelophyes appendiculata* and *Eudoxoides spiralis* were identified and counted based on the number of detached bracts and intact eudoxids; that is a relevant piece of information, since they represent the reproduction and continuity of the species in an area. Quantitative study of them is indispensable for estimating the importance of these species in marine food webs (Gamulin and Kršinić, 1993; Grossmann *et al.*, 2014). Nectophores of physonect siphonophores and the calycophoran *Hippopodius hippopus* were counted and divided by 10, following Pugh (1984), to estimate the number of colonies sampled. The numbers of individual medusae, siphonophore colonies and eudoxid stages were standardized to the number of individuals per 1000 m³ of filtered seawater.

Data analysis

For each species and survey, the mean abundance values, frequencies of occurrence (FO, percentage of stations where a taxon occurred) and the relative abundances (RA, percentage contribution of a taxon to the
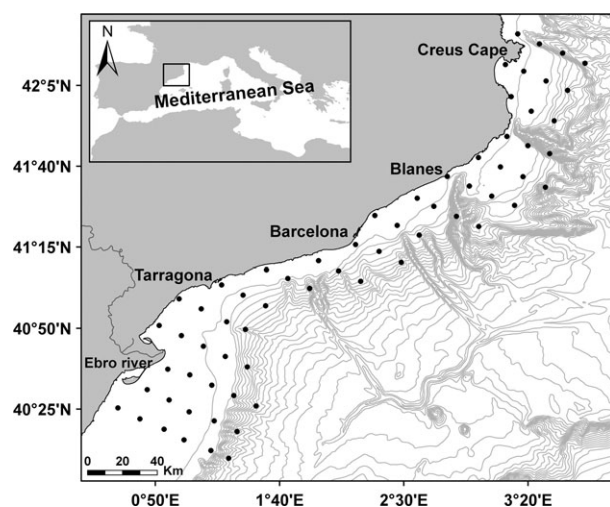
total mean abundance of individuals) were calculated. For each station and cruise, the species richness (S) of the cnidarian community was estimated as the total number of species, and the diversity was calculated as the Shannon diversity index (H'), using natural logarithms.

Significant differences in abundance between the two summers were tested for the total cnidarians and for the taxa Siphonophorae, Hydromedusae and Scyphomedusae by means of an analysis of variance using generalized linear models (GLM). The counts of total cnidarians and Siphonophorae, which followed a Poisson distribution, were analysed with the function "glm" from the "stats" library in R (R Core Team). For Hydromedusae and Scyphomedusae, which followed a negative binomial distribution, the "glm.nb" package (Venables and Ripley, 2002) was used with a log link function (Zuur *et al.*, 2009). The log of seawater filtered by the net was included as an offset inside all models to eliminate biases due to variable sample sizes (Penston *et al.*, 2008; Zuur *et al.*, 2009; Guerrero *et al.*, 2013).

To assess the existence of groups of stations similar on the basis of species composition and species abundance, a cluster analysis was performed using the "vegan" package (Oksanen *et al.*, 2015). Species with five or fewer presences and/or FO < 3% in each survey were not included in the analyses. The abundances of species were log-transformed (ln $(x + 1)$) and clustering of stations was carried out using Bray–Curtis distances and Ward's hierarchical agglomeration method. The graphical display of the ordered community table was carried out with the R routine "coldiss" from Borcard *et al.* (2011). Afterward, a canonical correlation analysis (CCA) was performed for each survey with the "vegan" package (Oksanen *et al.*, 2015), in order to explore the multivariate relationships between the station matrixes of species abundances and the environmental variables. Collinearity between pairs of variables was evaluated with scatterplots, Pearson's correlation coefficients (cut-off value |0.6|) and corroborated by the variance inflation factor (Zuur *et al.*, 2009). The variables chlorophyll *a* (at 5 m depth) and salinity (at 5 m depth) were collinear and salinity was kept for the analyses, since this parameter has been recognized previously as an important factor in the distributions of gelatinous zooplankton in the area (Gili *et al.*, 1988; Guerrero *et al.*, 2016). Initially, variables from near-surface (5 m) and intermediate layers (60 m) were included in the analyses. However, since surface variables were by far the most determinant, and inclusion of those from 60 m eliminated ~38% of the stations, i.e. those with depths shallower than 60 m, the deeper variables were not included in the final analyses. Thus, the environmental matrix used was composed of eight

explanatory variables: bathymetry (m, depth), time of sampling (day or night), surface (5m) temperature (°C) and salinity, integrated chlorophyll *a* concentration (µg l^{-1}) (from a maximum depth of 100 m to the surface), across-shore velocity (cm s^{-1}, U45), alongshore velocity (cm s^{-1}, V45) and vorticity (10^{-6} s^{-1}). Depth was log-transformed (ln(z)). All statistical analyses were done using the free statistical software R, version 3.0.2 (R Development Core Team, 2013). Maps of the horizontal distribution of the environmental parameters, by means of spline interpolation, and species abundance were generated by ArcGIS 10.2 software. The Catalano-Balearic Sea Bathymetric Chart (2005) was used to represent the bathymetry at 100 m intervals.

RESULTS

Hydrographic conditions

The summer of 2003 was warmer than that of 2004, with sea surface temperatures 2–3°C higher in July 2003 than in July 2004. In both years, a substantial difference in temperature was detected between the northern and southern parts of the region, and a marked thermal front perpendicular to the coastline of nearly 2°C was located around 41°30′N (Fig. 2). It separated colder waters in the north, with minimum values of 23.13°C in 2003 and 20.15°C in 2004, from warmer waters in the south, with maximum values of 27.62°C in 2003 and 25.98°C in 2004 (Table I and Fig. 2).

The surface salinity distribution showed similar average values in both years and was characterized by the presence of low-salinity patches on the continental shelf off the Ebro River mouth in the southern part of the area (Table I and Fig. 2). In both years, two low-salinity patches were detected: one close to the coast north of the Ebro delta and the other near the shelf edge at the southern limit of the sampled area. In July 2004, a water mass of high salinity (38.28) was located offshore in the southern half of the area.

Surface chlorophyll *a* was very low almost everywhere. There were, however, some patches of relatively high concentration near the Ebro delta (0.79 mg m^{-3} in 2003 and 1.14 mg m^{-3} in 2004; Table I and Fig. 2), in the same positions as the surface patches of low salinity described above. Small patches were also observed close to the coast in the vicinity of Barcelona, a highly populated zone, and at secondary river mouths (Fig. 2). Integrated (0–100 m) chlorophyll *a* was higher in July 2003 than in 2004 (Table I), with the lowest values close to the coast, then increasing over the shelf and slope. In July 2004, the lowest values were also found offshore (Fig. 2).
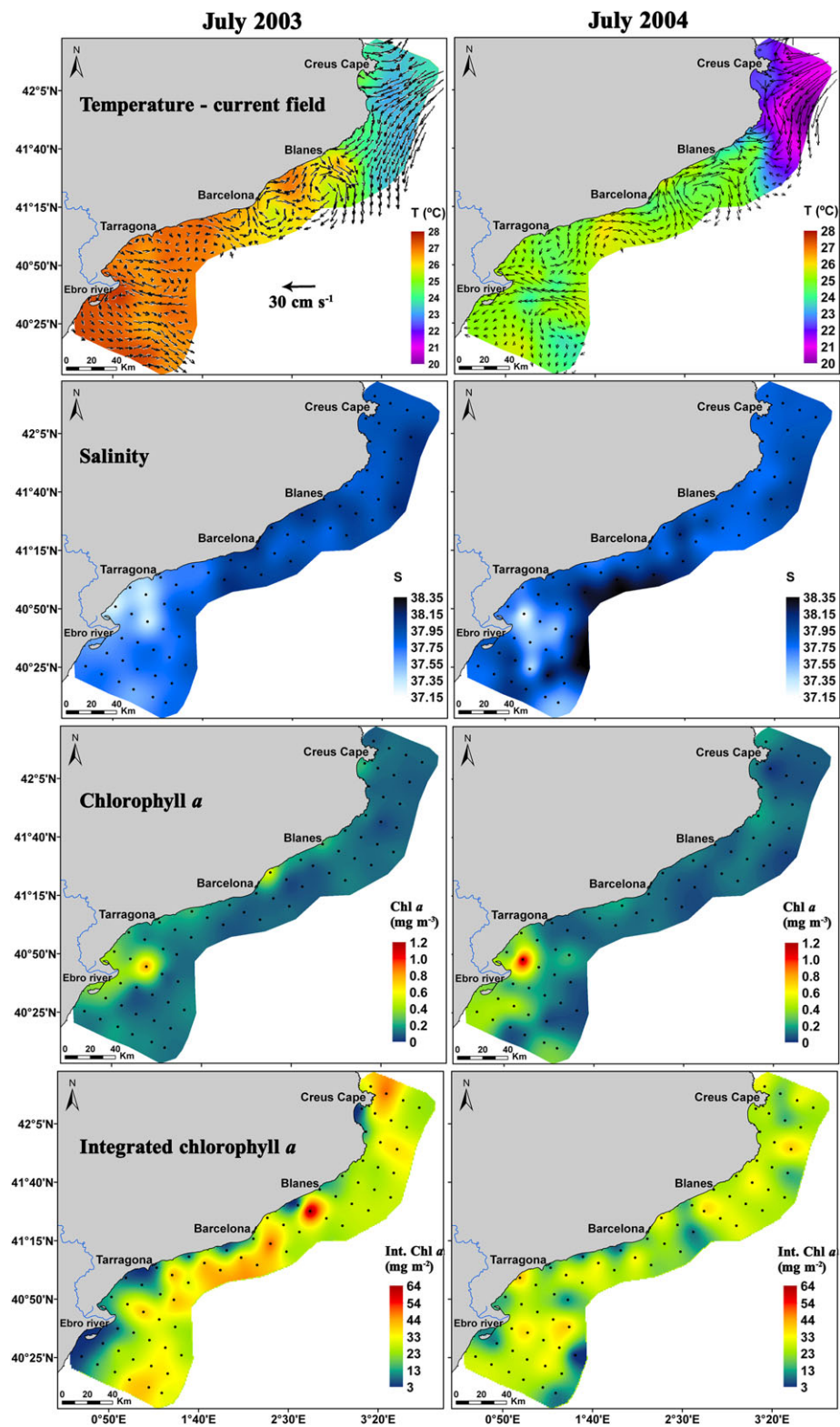
Fig. 2. From top to bottom, geostrophic current fields at 21 m depth, relative to 600 m, overlaid on surface (5 m) temperature, salinity, chlorophyll *a* concentration and integrated (0–100 m) chlorophyll *a* concentration in July 2003 and 2004, off the Catalan coast, NW Mediterranean.

Table I. *Values of the environmental parameters off the Catalan coast during July 2003 and July 2004*

	July 2003			July 2004		
	Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.
Depth (m)	289.53 ± 331.64	24.00	1331.00	291.45 ± 326.21	28.00	1322.00
T (°C)	25.82 ± 1.47	23.13	27.62	24.05 ± 1.56	20.15	25.98
S	37.82 ± 0.19	37.26	38.09	37.86 ± 0.20	37.16	38.28
Chl a (mg m^{-3})	0.16 ± 0.12	0.05	0.79	0.17 ± 0.16	0.02	1.14
Int. Chl a (mg m^{-2})	27.16 ± 11.82	4.39	63.54	25.42 ± 8.18	3.86	41.24
U45 (cm s^{-1})	−2.01 ± 19.74	−74.19	32.7	−2.26 ± 20.9	−58.18	67.78
V45 (cm s^{-1})	−3.65 ± 10.63	−30.66	18.91	0.31 ± 13.44	−27.28	39.62
Vorticity (10^{-6} s^{-1})	−0.12 ± 0.89	−3.65	2.20	0.00 ± 0.93	−2.19	2.76

Depth, bottom depth; T, temperature; S, salinity; Chl a, chlorophyll a; Int. Chl a, 0–100 m integrated chlorophyll a; U45, across-shore component of the current velocity; V45, alongshore component of the current velocity; SD, standard deviation; Min., minimum value; Max., maximum value.

In both surveys, the southwest flowing Northern Current was very apparent in the NE of the study area, (>41°-30′N), being more intense in July 2003 (Fig. 2). Two anticyclonic eddies were located in the central part of the area in 2003, whereas a large anticyclonic eddy was found to the east of Barcelona in 2004. In both years, complex current patterns were detected over the continental shelf in the vicinity of the Ebro delta, dominated by negative (anticyclonic) vorticity in well-defined eddies, particularly in 2003.

Abundance and species composition

A total of 56 species of planktonic cnidarians were found in the two summers, comprised of 17 siphonophorae, 36 hydromedusae and 3 scyphomedusae. The numbers of cnidarian species were quite similar, 46 (range: 3–22) in July 2003 and 44 (range: 1–17) in July 2004 (Table II). Nevertheless, the total abundance of cnidarians was over twice as great in the average summer (z-value = 102.8, P-value <0.001). Siphonophorae (z-value = 108.0, P-value <0.001) and scyphomedusae (z-value = 4.6, P-value <0.001) were both significantly more abundant in the average summer, while the abundance of hydromedusae (z-value = −3.2, P-value <0.01) was greater in the warm summer (Table II and Fig. 3). The Shannon index (H') indicated more diversity in the warm summer (1.38 ± 0.36; range: 0.52–2.19) than in the average summer (0.98 ± 0.57; range: 0.00–1.95).

Siphonophores were the most abundant cnidarians in both summers, with polygastric stages of *M. atlantica* and *Lensia subtilis* representing the most numerous and widespread species (Table II). Siphonophore species composition was virtually the same in the two years, although *Agalma elegans* was only found in 2004 and a free-swimming siphosome fragment of *Apolemia* sp. was collected once in 2003 (Table II). The dominant *M. atlantica*, was one of the most reduced species in the warm summer, while *Muggiaea*

kochii was more abundant in that summer (Table II). The quantified eudoxid stages constituted a relatively high percentage of the total cnidarian community (~10%) and were more abundant in the average year. Eudoxid stages of *C. appendiculata* were the most abundant and widespread in the two summers (Table II).

Hydromedusae were the only cnidarian taxon that had higher abundances in the warm summer, with *A. hemistoma* and *Rhopalonema velatum* the most common and widespread species. This taxon showed the most important changes in species composition between summers due to the more diverse orders Anthoathecata and Leptothecata, while the less diverse Narcomedusae and Trachymedusae conserved the same species compositions (Table II). In both summers, holoplanktonic hydromedusae (Narcomedusae, Trachymedusae and the neustonic colonies *Porpita porpita* and *Velella velella*) were more abundant than the meroplanktonic (Anthomedusae and Leptomedusae). The holoplanktonic species were more abundant in the warm summer than the normal one (375 ± 371 compared with 201 ± 318 ind. 1000 m^{-3}), while meroplankton were more abundant in the average summer (increasing from 14 ± 18 to 21 ± 98 ind. 1000 m^{-3}).

Scyphomedusae were the second most abundant taxon in the average summer due to the high abundance of *Pelagia noctiluca* ephyrae and juveniles. The abundance of that species was markedly lower in the warm summer (Table II). With regard to occurrences of species, the only difference between the years was one specimen of *Nausithoe punctata* taken in 2003.

Spatial distribution and relationships with environmental variables

In the warm summer, stations discriminated by the cluster analysis were strongly separated into north and south sets of groups (Fig. 4). Two groups (C and E) were located in the northern part of the area and two groups

Table II. *Mean (±SD) abundance values (Ind·1000 m⁻³), relative abundance (RA), frequency of occurrence (FO) and abundance range values for all species found during July 2003 and 2004 off the Catalan coast*

	July 2003				July 2004			
	Mean ± SD	RA	FO	Range	Mean ± SD	RA	FO	Range
Total Cnidaria	**1759.03 ± 1351.17**	**100**	**100**	**0–4155.9**	**3754.84 ± 3661.98**	**100**	**100**	**0–19 013.5**
Siphonophorae	**1366.39 ± 1163.49**	**77.68**	**100**	**0–4155.9**	**3201.81 ± 2736.17**	**85.27**	**100**	**0–9513.6**
Abylopsis tetragona P	11.95 ± 20.67	0.68	60.6	0–94.1	25.37 ± 42.01	0.68	66.7	0–194.4
Abylopsis tetragona E	12.80 ± 15.66	0.73	68.2	0–73.6	15.44 ± 16.60	0.41	52.0	0–71.2
Chelophyes appendiculata P	53.17 ± 65.03	3.02	81.8	0–348.2	42.44 ± 30.65	1.13	97.0	0–155.0
Chelophyes appendiculata E	175.00 ± 266.28	9.95	83.3	0–1394.4	316.15 ± 361.36	8.42	98.5	0–1973.9
Eudoxoides spiralis P	0.83 ± 2.57	0.05	13.6	0–13.6	0.05 ± 0.39[a]	0.001	1.5	0–3.2
Eudoxoides spiralis E	2.46 ± 8.51	0.14	15.2	0–42.5				
Lensia conoidea	5.85 ± 8.68	0.33	54.5	0–42.3	6.70 ± 10.85	0.18	50.0	0–48.6
Lensia fowleri	0.12 ± 0.58	0.01	4.5	0–3.4	0.10 ± 0.56	0.003	3.0	0–3.3
Lensia meteori	3.87 ± 15.03	0.22	31.8	0–118.9	25.06 ± 64.15	0.67	39.4	0–307.3
Lensia subtilis	136.74 ± 135.98	7.77	95.4	0–611.3	122.05 ± 118.54	3.25	92.4	0–604.6
Lensia subtiloides	0.34 ± 2.74	0.02	1.5	0–22.2	0.21 ± 1.29	0.01	3.0	0–9.7
Muggiaea atlantica	865.51 ± 1002.11	49.20	95.5	0–4155.9	2610.93 ± 2709.88	69.54	100	4.7–9513.6
Muggiaea kochii	92.78 ± 209.30	5.27	89.4	0–1241.3	28.53 ± 30.98	0.76	84.8	0–138.4
Sulculeolaria chuni	0.08 ± 0.69[a]	0.005	1.5	0–5.6	0.04 ± 0.29[a]	0.001	1.5	0–2.4
Hippopodius hippopus	0.67 ± 2.12	0.04	12.1	0–10.5	0.05 ± 0.38[a]	0.001	1.5	0–3.1
Agalma elegans					0.21 ± 0.83	0.01	6.1	0–4.2
Halistemma rubrum	1.50 ± 2.47	0.09	34.9	0–10.3	2.84 ± 5.14	0.08	42.4	0–30.0
Nanomia bijuga	1.84 ± 1.89	0.10	56.1	0–7.4	5.67 ± 12.75	0.15	60.6	0–93.2
Apolemia sp.	0.04 ± 0.33[a]	0.002	1.5	0–2.6				
Physophora hydrostatica	0.85 ± 1.87	0.05	24.2	0–9.8	0.14 ± 0.62	0.004	4.5	0–3.0
Hydromedusae	**388.22 ± 378.00**	**22.07**	**98.5**	**0–1786.7**	**221.98 ± 329.96**	**5.91**	**98.5**	**0–2173.8**
Order Anthoathecata	**7.47 ± 22.15**	**1.92**[b]	**59.1**	**0–169.1**	**15.70 ± 26.04**	**7.07**[b]	**83.3**	**0–166.5**
Thamnostoma dibalium	0.04 ± 0.32[a]	0.002	1.5	0–2.6	0.09 ± 0.38	0.002	6.1	0–2.0
Cystaeis sp.	0.03 ± 0.28[a]	0.002	1.5	0–2.3				
Amphinema rubrum	0.17 ± 0.73	0.01	6.1	0–4.7	0.19 ± 1.19	0.01	3.0	0–9.1
Merga tergestina					0.39 ± 1.42	0.01	9.1	0–9.1
Merga tregoubovii	0.04 ± 0.29[a]	0.002	1.5	0–2.4				
Leuckartiara octona	0.64 ± 1.61	0.04	19.7	0–9.0	0.86 ± 2.12	0.02	16.7	0–9.4
Neoturris pileata					0.05 ± 0.38[a]	0.001	1.5	0–3.2
Rhabdoon singulare					0.43 ± 1.73	0.01	9.1	0–12.5
Porpita porpita (col.)					0.28 ± 0.99	0.01	7.6	0–4.7
Velella velella (col.)	6.06 ± 21.79	0.34	42.4	0–169.1	12.40 ± 25.89	0.33	69.7	0–166.5
Zanclea sp.					0.10 ± 0.78	0.003	1.5	0–6.3
Zanclea sessilis					0.19 ± 1.20	0.01	3.0	0–9.2
Codonium proliferum					0.06 ± 0.50[a]	0.002	1.5	0–4.1
Corymorpha bigelowi	0.09 ± 0.75	0.01	1.5	0–6.1				
Euphysa flammea	0.19 ± 1.24	0.01	3.0	0–9.8				
Euphysa aurata	0.20 ± 0.96	0.01	6.1	0–6.9	0.11 ± 0.64	0.003	3.0	0–4.2
Order Leptothecata	**12.26 ± 17.49**	**3.16**[b]	**66.7**	**0–101.3**	**17.64 ± 95.60**	**7.95**[b]	**51.5**	**0–377.2**
Aequorea forskalea	0.06 ± 0.51[a]	0.004	1.5	0–4.2				
Eirene viridula	0.03 ± 0.28[a]	0.002	1.5	0–2.3				
Eutima gegenbauri	0.46 ± 2.70	0.03	4.5	0–20.8	0.25 ± 1.62	0.01	3.0	0–12.6

Species	mean ± SD	RA	F%	Range	mean ± SD	RA	F%	Range
Eutima gracilis					5.76 ± 46.43	0.15	3.0	0–377.2
Eutonina scintillans					0.19 ± 1.55[a]	0.01	1.5	0–12.6
Helgicirrha schulzii	5.89 ± 7.81	0.34	56.1	0–29.2	4.68 ± 7.75	0.12	42.4	0–35.6
Laodicea undulata	0.12 ± 0.74	0.01	3.0	0–5.6				
Staurostoma mertensii	0.04 ± 0.32[a]	0.002	1.5	0–2.6				
Earleria araiae	0.07 ± 0.39	0.004	3.0	0–2.3				
Clytia spp.	0.04 ± 0.32[a]	0.002	1.5	0–2.6	0.14 ± 1.17	0.004	1.5	0–9.5
Gastroblasta raffaelei	1.28 ± 4.56	0.07	10.6	0–23.4				
Obelia spp.	4.27 ± 14.23	0.24	28.8	0–101.3	6.62 ± 46.42	0.18	13.6	0–377.2
Order Narcomedusae	**5.02 ± 10.88**	**1.29**[b]	**48.5**	**0–41.2**	**2.90 ± 5.83**	**1.31**[b]	**33.3**	**0–27.4**
Cunina octonaria	0.04 ± 0.31[a]	0.002	1.5	0–2.5	0.08 ± 0.68[a]	0.002	1.5	0–5.5
Solmissus albescens	1.17 ± 4.91	0.07	9.1	0–32.4	0.56 ± 2.35	0.01	6.1	0–12.8
Solmundella bitentaculata	3.81 ± 7.42	0.22	43.9	0–41.2	2.26 ± 5.11	0.06	27.3	0–27.4
Order Trachymedusae	**363.46 ± 369.00**	**93.62**[b]	**98.5**	**0–1786.7**	**185.74 ± 317.93**	**83.7**[b]	**97.0**	**0–2173.8**
Liriope tetraphylla	6.05 ± 8.36	0.34	63.6	0–33.4	0.81 ± 2.26	0.02	15.1	0–12.0
Aglaura hemistoma	234.37 ± 304.59	13.33	97.0	0–1786.7	117.55 ± 307.96	3.13	86.4	0–2173.8
Persa incolorata	25.14 ± 57.17	1.43	57.6	0–303.5	3.86 ± 26.15	0.10	12.1	0–212.1
Rhopalonema funerarium	0.09 ± 0.75	0.01	1.5	0–6.1	0.27 ± 1.68	0.01	3.0	0–12.6
Rhopalonema velatum	97.81 ± 104.15	5.56	89.4	0–413.7	63.24 ± 68.94	1.68	90.9	0–283.9
Scyphomedusae	**4.42 ± 7.36**	**0.25**	**47.0**	**0–33.3**	**331.06 ± 2340.13**	**8.82**	**72.7**	**0–19 013.5**
Atolla sp.	3.06 ± 5.93	0.17	40.9	0–33.3	6.28 ± 10.52	0.17	53.0	0–63.4
Nausithoe punctata	0.02 ± 0.20[a]	0.001	1.5	0–1.6				
Pelagia noctiluca	1.34 ± 4.60	0.08	16.7	0–31.2	324.77 ± 2340.99	8.65	27.3	0–19 013.5

Text and values in bold make reference to phylum, class and orders.

P, polygastric stage (asexual); E, eudoxid stage (sexual).

[a]Only one individual found.
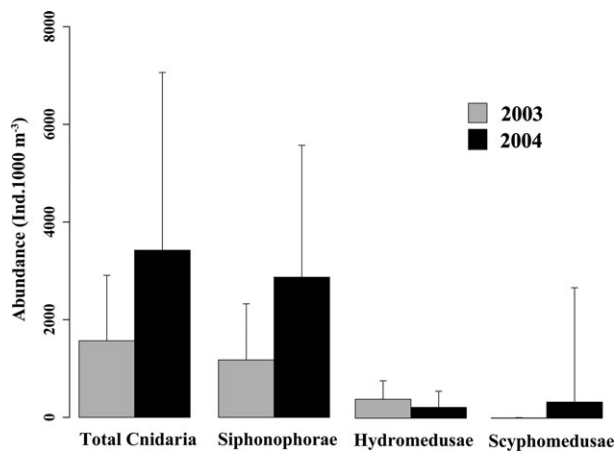
[b]RA relative to the total Hydromedusae abundance.

Fig. 3. Mean abundance (±SD) differences between July 2003 and 2004 for the total cnidarian abundance, and the Siphonophorae, Hydromedusae and Scyphomedusae taxa.

were in the south (B and D). There was a mixing zone located south of the thermal front between Blanes and Barcelona (Figs 2 and 4). The two groups in the northern area were characterized by high abundances of *Persa incolorata* and *C. appendiculata* (polygastric and eudoxid stages). Group C was located over the shelf and had both the highest abundance of *M. kochii* and the exclusive occurrences of *Euphysa aurata* and *Eutima gegenbauri* (Fig. 4), while group E was located over the continental slope and presented the lowest abundances of *M. atlantica*, *A. hemistoma* and *R. velatum*. In the southern area, group D was located close to the coast and presented both the highest abundances of *Obelia* spp. and a low frequency of *C. appendiculata* (polygastric and eudoxid stages). Over the continental shelf and slope, group B had both the highest abundances of *A. tetragona* (polygastric stage) and *P. noctiluca* and the exclusive occurrences of *E. spiralis* and *Gastroblasta raffaelei* (except for one station in group D). South of the Ebro delta, one station group (A) had the fewest species (Fig. 4).

In the average summer, however, a strong coastal-offshore separation was evident (Fig. 4). Groups F and I extended all along the region, the first close to the coast and the second over the slope region. Two other groups were near the coast, but extending over the shelf: group J in the north and group G in the south (Fig. 4). The coastal groups (F and J) were characterized by the highest abundances of *Obelia* spp. and *M. kochii*, while the large group over the slope (I) was defined by the highest abundance and occurrence of *Lensia conoidea*, *Lensia meteori* (except one station in group J) and *Solmissus albescens* (Fig. 4). Group G, over the southern continental shelf, was characterized by the greatest abundance and frequency of *A. tetragona* and *P. noctiluca*. As in the warm

summer, a small group of stations (H) with the lowest number of species was located south of the Ebro delta.

Relationships among planktonic cnidarian abundance and environmental variables shown by the CCA analyses explained 82 and 78% of the total variance in the warm and the average summers, respectively. In the warm summer, the first ordination axis accounted for 37% of the constrained variance. It was negatively correlated with temperature (−0.85) and positively correlated with salinity (0.76) (Table III and Fig. 5). Species associated with this axis were *A. tetragona* (polygastric stage), *P. notiluca*, *E. spiralis* (polygastric and eudoxid stages) and *G. raffaelei* located on the left side of the dispersion diagram, associated with increasing temperature and decreasing salinity (Fig. 5). They were particularly abundant in the southern part of the study area, characterized by high temperature and low salinity, and very scarce north of the thermal front (Fig. 6; *A. tetragona*, as example). On the other side of the axis, *P. incolorata*, *C. appendiculata* (polygastric and eudoxid stages), *M. kochii*, *E. aurata* and *E. gegenbauri* were related to decreasing temperature and increasing salinity (Fig. 5). These species were mainly distributed north of the thermal front (Fig. 6; *P. incolorata*, as example). The second axis explained 28% of the constrained variance and was positively correlated with depth (0.72) and integrated chlorophyll *a* (0.56). The species associated with these environmental conditions were *L. conoidea*, *L. meteori* and *S. albescens*, located in the upper-right side of the diagram, and associated with increasing depth and integrated chlorophyll *a* (Fig. 5). The distributions of these species were limited to the most offshore stations with the highest and intermediate values of integrated chlorophyll (Fig. 6; *L. conoidea*, as example). On the opposite side of the axis, the coastal hydromedusan *Obelia* spp. was related to shallower depths and decreasing integrated chlorophyll *a*, mainly in the central coastal area (Fig. 6).

In the average summer, the first ordination axis explained 46% of the constrained variance and was positively correlated with depth (0.86) (Table III and Fig. 5). As observed in the warm summer, the species associated with increasing depth were *L. conoidea*, *L. meteori* and *S. albescens*, while *Obelia* spp. and *M. kochii* were associated with shallower depths (Fig. 6; *L. conoidea* and *Obelia* spp., as examples). The second axis explained 19% of the constrained variance and was negatively correlated with temperature (−0.68). The species related to warmer waters were *A. tetragona* (polygastric stages), *P. noctiluca* and *L. tetraphylla* and, as observed in the previous summer, these were mainly collected in the warm southern part of the area (Fig. 6; *A. tetragona*, as example). On the other side of the axis, species such as *P. incolorata* and *Rhabdon singulare* were associated with colder waters north of the thermal front (Fig. 6; *P. incolorata*, as example).
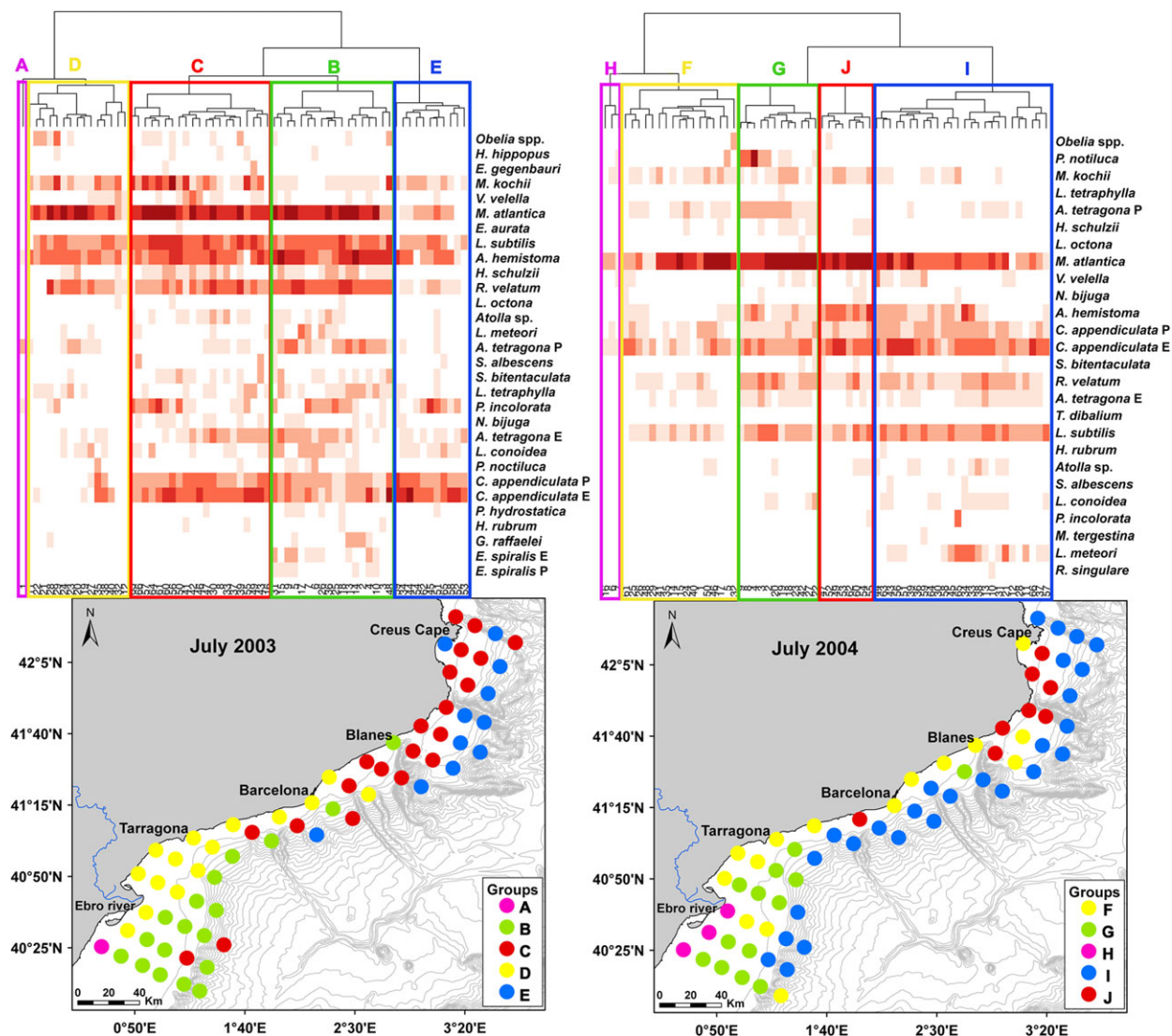
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Fig. 4. Upper: hierarchical clustering of stations in July 2003 (left panel) and July 2004 (right panel) and heatmap representing the abundance of the species (colour gradation from white to dark red represents from absence to the highest abundance), the five species-groups are indicated within different boxes labeled with letters. P, polygastric stage (asexual); E, eudoxid stage (sexual). Lower: spatial distribution of the five species-groups in the study area. Note that the same colour/symbol group indicates only a similar spatial distribution in both years but not the same species composition.

Species with a weaker relationship with environmental parameters were located close to the axis origins in CCA plots (Fig. 5), including *M. atlantica*, *A. hemistoma*, *L. subtilis*, *C. appendiculata* and *R. velatum*. They had wide distributions over the survey area (Fig. 7; showing *M. atlantica* and *A. hemistoma* as examples).

DISCUSSION

Climatic conditions, especially temperature variations, have a decisive influence on gelatinous zooplankton

distributions and abundance (Brodeur *et al.*, 1999; Lynam *et al.*, 2010; Brotz *et al.*, 2012). In recent years, studies conducted in different regions show that warmer conditions are frequently accompanied by increased abundance of gelatinous species (e.g. Purcell, 2005; Brodeur *et al.*, 2002). However, the present study shows that the community of planktonic cnidarians was significantly less abundant in the exceptionally warm summer of 2003.

In both summers, siphonophores were the dominant taxon, as observed in previous studies in the NW Mediterranean (Gili *et al.*, 1988; Andersen *et al.*, 2001;

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Table III. Summary of the results of the CCA performed with the planktonic cnidarians and the explanatory variables

	July 2003		July 2004	
Total deviance explained (total inertia)	82%		78%	
Constrained variance explained by axis 1	37%		46%	
Constrained variance explained by axis 2	28%		18%	
Axis	1	2	1	2
Constrained eigenvalues	0.08	0.06	0.08	0.03
Correlation of environmental variables				
Depth	0.50	**0.71**	**0.86**	−0.36
Temperature (5 m)	**−0.85**	0.38	−0.54	**−0.68**
Salinity (5 m)	**0.76**	0.04	0.50	−0.14
Int. Chl *a*	0.18	**0.56**	0.02	−0.09
Day–night	0.10	−0.25	−0.07	0.39
U45	−0.44	0.07	−0.21	−0.50
V45	−0.12	−0.14	0.01	0.09
Vorticity	−0.25	−0.23	−0.06	0.32

In **bold**, the most significant relationships for each year (>0.55). Depth, bottom depth; Int. Chl *a*, 0–100 m integrated chlorophyll *a*; U45, across-shore component of the current velocity; V45, alongshore component of the current velocity.

Sabatés *et al.*, 2010). *Muggiaea atlantica* was the most abundant species in both summers, but markedly decreased during 2003 (Table II and Fig. 7). *Muggiaea atlantica* has been the dominant species in the NW Mediterranean since it replaced the formerly dominant, congeneric species *M. kochii* in the 1980s (Cervigón, 1958; Riera *et al.*, 1986; Gili *et al.*, 1988; Licandro *et al.*, 2012). *Muggiaea atlantica* is a cold-temperate species, with reduced abundance at temperatures higher than 24°C (Marques *et al.*, 2008; Batistić *et al.*, 2013). *Muggiaea kochii* is a warm-temperate species with a seasonal peak of abundance in summer (Riera *et al.*, 1986; Gili *et al.*, 1988; Licandro *et al.*, 2012). The alternation of the two species is well known from the English Channel and in other regions (Russell, 1934; Mackie *et al.*, 1987; Blackett *et al.*, 2014). In the present study, this alternation seemed to take place in relation to water temperature changes. Probably, the high temperatures recorded in summer 2003 negatively affected the *M. atlantica* population, allowing other species to increase in abundance by taking advantage of its under-used trophic niche.

Among siphonophores, the eudoxid stages of several species were very well represented in both summers. Studies on the distributions of calycophoran eudoxid stages in the Western Mediterranean are very few (Cervigón, 1958; Dallot *et al.*, 1988; Sabatés *et al.*, 2010). In the present study, *C. appendiculata* and *A. tetragona* were the most abundant, in agreement with the observations of Cervigón (1958) and Dallot *et al.* (1988). In the warm summer, both eudoxid species showed lower abundance compared with the average one, and they were absent

in the warmer southern area with their distributions displaced northward and seaward. This could be a sign that the highest temperatures of 2003 were unfavourable for the sexual reproduction of these species, although there are not enough studies that confirm the relation between high temperatures and siphonophores reproduction (Mackie *et al.*, 1987; Mapstone, 2009). In addition, zooplankton had reduced abundance in the southern area in 2003 (Maynou *et al.*, 2014; Atienza *et al.*, 2016), and according to Purcell (1982), the production of eudoxids decreases when food is scarce. Consistent with our observations, Dallot *et al.* (1988) found significantly higher abundance of eudoxids in areas of greater food availability.

Contrary to the findings for siphonophores, hydromedusae were more abundant in the warm summer. There were high densities of holoplanktonic species such as the trachymedusae *A. hemistoma* and *R. velatum*. These are warm-water species, which are often very abundant in the western Mediterranean (Gili *et al.*, 1988; Licandro and Ibañez, 2000; Batistić *et al.*, 2007) and Atlantic Ocean (Pagès and Gili, 1991; Hosia *et al.*, 2008; Nogueira Júnior *et al.*, 2014), particularly in the summer months. The increased abundance of both species in the warm summer seems a natural consequence of high temperatures favouring these warm-water species. Moreover, holoplanktonic species could take advantage more efficiently than the meroplanktonic species of the under-used trophic niche left by *M. atlantica* during the warm summer. The dominance of holoplanktonic hydromedusae compared with meroplanktonic species relates to their different life cycles. Holoplanktonic hydromedusae are always present in the water column, whereas meroplanktonic hydromedusae have a temporary presence in the plankton. When environmental conditions are optimal for their benthic phase (polyp), it releases the free-swimming medusae for sexual reproduction (Boero and Bouillon, 1993; Gili *et al.*, 1998). Thus, holoplanktonic species tolerate wider ranges of temperature. On the other hand, the lower abundance of meroplanktonic species in the warm summer could have been due to earlier than usual release of medusae from the polyps (Boero *et al.*, 2016). It is known that higher temperatures promote faster life cycles and greater reproductive rates in many jellyfish species (Purcell, 2005; Boero *et al.*, 2016). On the other hand, the low abundance of zooplankton prey for the polyps during the warm summer (Maynou *et al.*, 2014; Atienza *et al.*, 2016) could have had a negative effect on the release of medusae (Gili *et al.*, 1998). Extremely warm conditions would especially and negatively affect the meroplanktonic species with short-lived medusa stages since their survival depends on narrower temperature ranges and sufficient food availability (Matsakis, 1993; Edwards and Richardson, 2004).
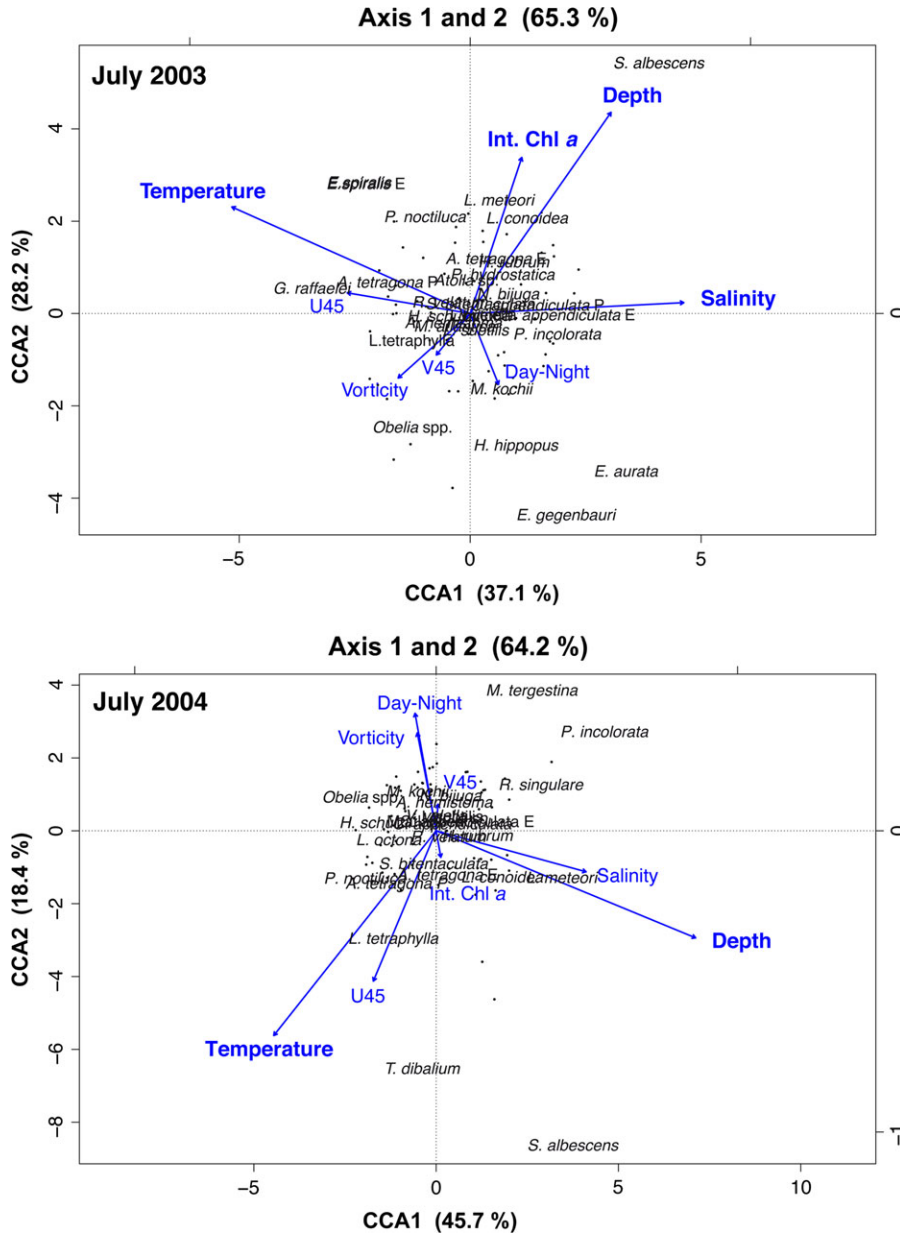
Fig. 5. Ordination plots of the CCA showing the relationships between the species (text in black) and the environmental variables (arrows) for July 2003 and 2004. Environmental variables in bold represent the most significant relationships in each year (see Table III). Black dots represent the location of the sampling stations. Depth, bottom depth; Int. Chl *a*, integrated (0–100 m) chlorophyll *a*, U45, across-shore component of the current velocity, V45, alongshore component of the current velocity.

Ephyrae of the scyphomedusan *P. noctiluca* are one of the most abundant planktonic cnidarians off the Catalan coast during the early summer months (Gili *et al.*, 1988; Sabatés *et al.*, 2010; Tilves *et al.*, 2016). Their abundance was remarkably low during the warm summer. As the sexual reproduction in this species takes place in late spring and early summer (Canepa *et al.*, 2014), the higher temperatures experienced during the 2003 summer could have triggered earlier sexual reproduction and, thus, low

abundance of ephyrae during our sampling. On the other hand, the lower abundance of siphonophores during the warm summer could reduce the abundance of ephyrae, since it has been reported recently that siphonophores are the most abundant and frequent prey of ephyrae in the area (Tilves *et al.*, 2016).

The cnidarian species composition and richness found in the two summers studied were similar to those observed previously in the area (Gili *et al.*, 1987b, 1988; Sabatés
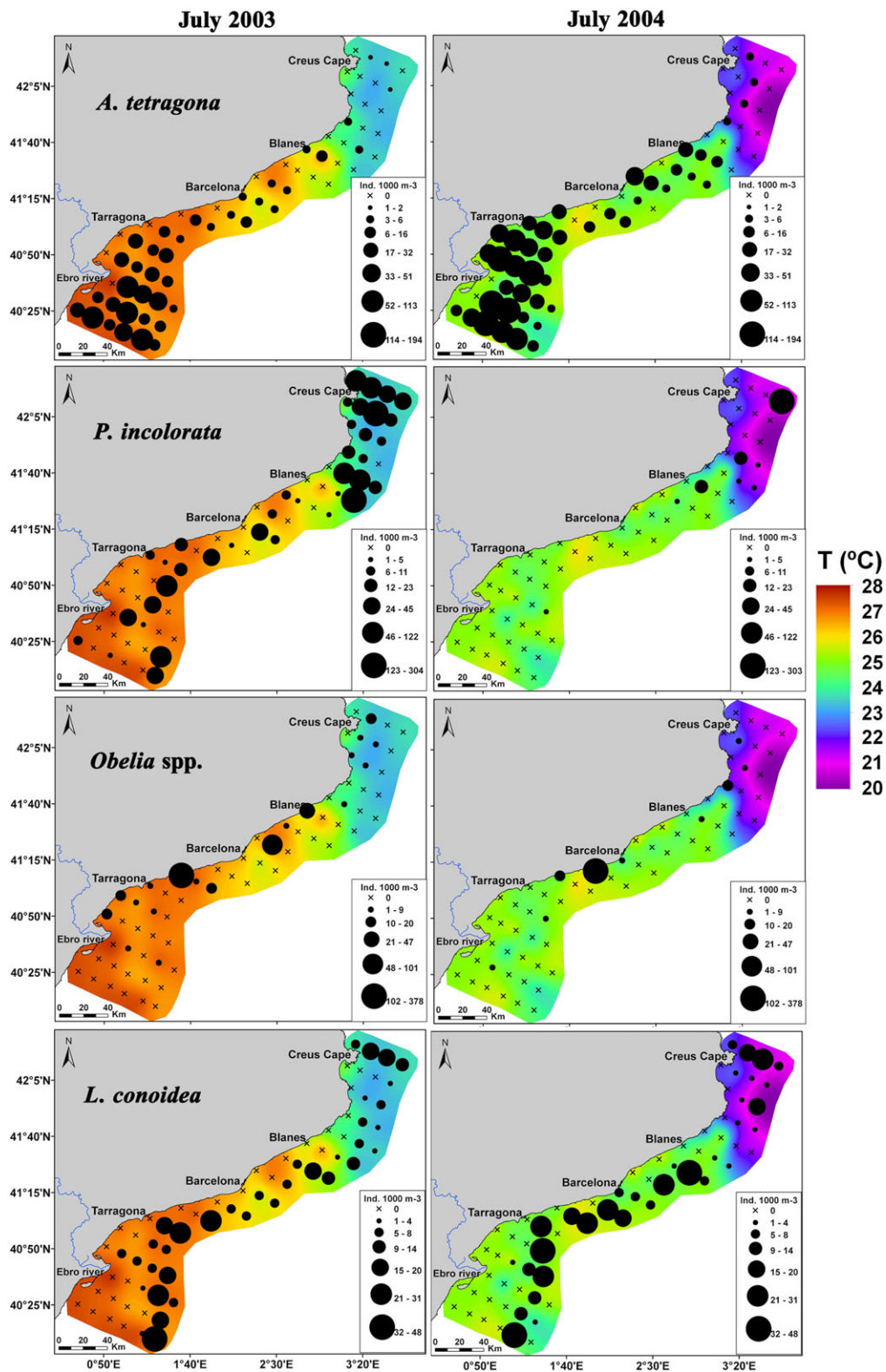
Fig. 6. Spatial abundance distributions of the species *Abylopsis tetragona*, *Persa incolorata*, *Obelia* spp. and *Lensia conoidea* overlaid on surface (5 m) temperature in July 2003 and July 2004.
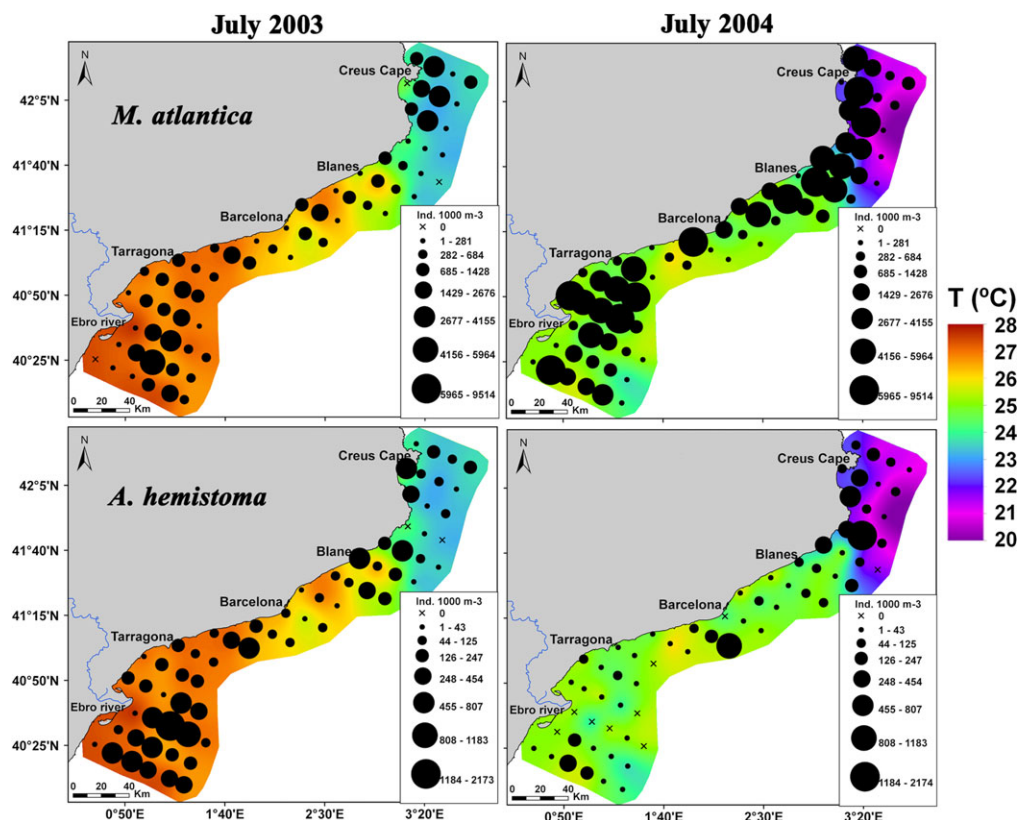
Fig. 7. Spatial abundance distributions of the widespread species *Muggiaea atlantica* and *Aglaura hemistoma* overlaid on surface (5 m) temperature in July 2003 and July 2004.

et al., 2010). The higher diversity (H') of the warm summer was mainly due to the lower abundances of the dominant cnidarian species, *M. atlantica* and *P. noctiluca*. The holoplanktonic cnidarian community species composition was practically the same in both years; those species are widely distributed, more generally tolerant than the meroplanktonic species and thus they can maintain viable populations in strongly variable environments (Gibbons *et al.*, 2010). The meroplanktonic cnidarian community composition differed considerably between the two summers, as expected from their life cycles (Arai, 1992; Boero and Bouillon, 1993; Gibbons *et al.*, 2010). There is little information regarding diversity indices of planktonic cnidarian communities in similarly extensive areas. Compared with other regions, our diversity values for both summers are lower than those found in the channels of southern Chile (Palma *et al.*, 2007a, 2007b) but similar to those reported off Redang Island, Malaysia (Nakajima *et al.*, 2013) and in the upwelling zone off central Chile (Pavez *et al.*, 2010). The species richness (number of species) found along the Catalan coast was quite high compared with those cited areas; however, the high abundance of *M.*

atlantica (up to 70%) in the Mediterranean decreased our diversity indices.

The coastal-offshore ordination of the community in the average summer is consistent with previous studies in the area (Gili *et al.*, 1988; Sabatés *et al.*, 2010). A coastal-to-open sea gradient in the community composition has also been described in other geographic regions (e.g. Palma *et al.*, 2007b; Nagata *et al.*, 2014). However, the conditions of the warm summer shifted the weight of the environmental factors, with the latitudinal temperature gradient being the key factor structuring the community and bathymetry taking a secondary role.

During both summers, the species characterizing the coastal and offshore communities remained the same. The coastal community was defined by *Obelia* spp. and *M. kochii*, both very common species in coastal areas (Gili *et al.*, 1988; Batistić *et al.*, 2013; Nagata *et al.*, 2014). *Obelia* spp. are filter-feeders able to feed even on bacteria (Boero *et al.*, 2007), and they are able to take advantage of highly productive areas and seasons to increase their populations rapidly (Orejas *et al.*, 2000;

Guerrero *et al.*, 2013). *Muggiaea kochii* is one of the few siphonophores inhabiting coastal and estuarine waters (Nagata *et al.*, 2014; D'Ambrosio *et al.*, 2016). The offshore community, distributed all along the shelf-slope, was well defined by *L. conoidea*, *L. meteori* and *S. albescens*. These are mesopelagic species performing extensive diel vertical migrations (Pugh, 1974; Kirkpatrick and Pugh, 1984; Mills and Goy, 1988), and they have been recorded previously over the Catalan continental slope (Sabatés *et al.*, 2010).

The northern and southern communities showed the most important changes in species composition between the two summers, though some species characteristic of the two areas remained in both years. The northern community, related with the colder and more saline waters, was defined by the presence of *R. singulare* in the average summer and *E. aurata* in the warm summer, whereas in both years, there were high abundances of *P. incolorata*. These three hydromedusae are mesopelagic and have been previously observed in colder and saline waters in the NW Mediterranean (Berhaut, 1969; Gili *et al.*, 1988; Goy, 1991; Buecher and Gibbons, 1999). The siphonophores *C. appendiculata* (polygastric and eudoxid stages) and *M. kochii*, both warm-temperate species (Alvariño, 1971; Bouillon *et al.*, 2004), were mainly located in the north during the warm summer, probably because the higher temperatures recorded in the southern area negatively affected their abundance, either directly or indirectly due to the low prey resources (Purcell, 1982; Dallot *et al.*, 1988). The southern community, related with the warmer and less saline waters, was defined by *A. tetragona* and *P. noctiluca* in both years and by the appearance in only 2003 of both *E. spiralis* (polygastric and eudoxids stages) and *G. raffaelei*. The two first species are common and abundant in the area, previously correlated with warm temperatures (Gili *et al.*, 1987a, 1988). The epipelagic siphonophore *E. spiralis* is associated with high temperatures in both the Mediterranean and the Atlantic Ocean (Gamulin and Kršinić, 1993; Nogueira Júnior *et al.*, 2014). The hydromedusa *G. raffaelei* is endemic in the Mediterranean Sea, found so far only in the Adriatic, Tyrrhenian and Ligurian Seas (Gravili *et al.*, 2007). This is the first report of it in the Catalan Sea.

During only the warm summer, the gradient of the integrated chlorophyll *a* was correlated to some extent to the coastal-offshore ordination axis; however, since its distribution was correlated with the bathymetry (see Fig. 2), and non-significantly so in 2004, we believe that variable had no direct effect on the spatial distribution of cnidarians. Instead we conclude that bathymetry is the effective variable. Although hydrographic features such as currents and vorticity have been reported to influence the spatial

distribution of other zooplankters in the area, including fish larvae (Sabatés *et al.*, 2013), their effects on the planktonic cnidarian distributions in our study could be masked by depth and temperature gradients.

Long-term studies carried out in the NW Mediterranean have reported increased abundances of jellyfish (Molinero *et al.*, 2005, 2008), while others showed no increasing trend (García-Comas *et al.*, 2011; Berline *et al.*, 2012; Licandro *et al.*, 2012). Nevertheless, major changes in community composition have been observed (Licandro *et al.*, 2012). Our observations did not match a trend toward generally increasing planktonic cnidarian abundance, given the substantial decrease observed during the anomalously warm summer in 2003. The effects of temperature changes on marine systems are far from simple and depend on the temporal scale of variability, from sudden changes to trends over time. They also depend on the responsive capacities of the organisms. The summer heat conditions of 2003 constituted an extreme event (Schär *et al.*, 2004), involving strong and sudden temperature changes. Thus, their effects on the planktonic community may not be comparable with those caused by long-term warming. In addition, high temperatures may favour earlier sexual and asexual reproduction of cnidarians and other species (Hays *et al.*, 2005; Boero *et al.*, 2016), advancing the timing of their seasonal abundance peaks. That is particularly likely for meroplanktonic and cool-temperate species. Finally, we must take into account the reduction of food availability, due to a general decrease in zooplankton during the extreme event of 2003 (Piontkovski *et al.*, 2011; Maynou *et al.*, 2014; Atienza *et al.*, 2016), which could also have negatively affected the planktonic cnidarians. We wish to stress the importance of spatial mesoscale plankton surveys with detailed taxonomic identification (including distinctly different life stages), as a critical tool for tracking changes in the community structure of high diversity regions, such as the Mediterranean, and for better understanding of marine ecosystem responses to climatic variability.

CONCLUSIONS

Our study confirms that bathymetry (the coastal-offshore gradient) is the main factor determining the spatial distribution pattern of the planktonic cnidarian community under average summer conditions. The anomalously high temperatures of summer 2003 strengthened the latitudinal (N–S) community ordination, with the appearance of some species characteristic of warmer waters (*E. spiralis* and *G. raffaelei*), and the northward displacement of certain other species (*M. kochii* and *C. appendiculata*) and of the sexual stages of some siphonophores (*C. appendiculata* and *A. tetragona*). These distributional changes were associated

with strong reductions in the abundance of the dominant species (*M. atlantica* and *P. noctiluca*) and of the sexual stages of siphonophores (*C. appendiculata* and *A. tetragona*). Our results agree with the few other studies of the footprints of the 2003 Mediterranean heat anomaly on marine plankton communities (Piontkovski *et al.*, 2011; Atienza *et al.*, 2016) and the general effects of the ocean warming on jellyfish (Boero *et al.*, 2016). Under possible future extreme climate change scenarios, planktonic cnidarian communities in temperate regions would change their structure, by varying their abundance, species composition, spatial distribution and phenology, with implications in the marine trophic webs and the populations of apex predators like fish.

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REFERENCES

Alvariño, A. (1971) Siphonophores of the Pacific with a review of the world distribution. *Bull. Scripps Inst. Oceanogr.*, **16**, 1–432.

Andersen, V., Nival, P., Caparroy, P. and Gubanova, A. (2001) Zooplankton community during the transition from spring bloom to oligotrophy in the open NW Mediterranean and effects of wind events. 1. Abundance and specific composition. *J. Plankton Res.*, **23**, 227–242.

Arai, M. N. (1992) Active and passive factors affecting aggregations of hydromedusae: a review. *Sci. Mar.*, **56**, 99–108.

Atienza, D., Sabatés, A., Isari, S., Saiz, E. and Calbet, A. (2016) Environmental boundaries of marine cladoceran distributions in the NW Mediterranean: implications for their expansion under global warming. *J. Mar. Syst.*, **164**, 30–41.

Batistić, M., Garić, R. and Molinero, J. C. (2014) Interannual variations in Adriatic Sea zooplankton mirror shifts in circulation regimes in the Ionian Sea. *Clim. Res.*, **61**, 231–240.

Batistić, M., Jasprica, N., Caric, M. and Lučić, D. (2007) Annual cycle of the gelatinous invertebrate zooplankton of the eastern South Adriatic coast (NE Mediterranean). *J. Plankton Res.*, **29**, 671–686.

Batistić, M., Lučić, D., Carić, M., Garić, R., Licandro, P. and Jasprica, N. (2013) Did the alien calycophoran *Muggiaea atlantica* outcompete its native congeneric *M. kochi* in the marine lakes of Mljet Island (Croatia)? *Mar. Ecol.*, **34**, 3–13.

Beaugrand, G., Reid, P. C., Ibañez, F., Lindley, J. A. and Edwards, M. (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science*, **296**, 1692–1694.

Benović, A., Lučić, D. and Onofri, V. (2000) Does change in an Adriatic hydromedusan fauna indicate an early phase of marine ecosystem destruction? *Mar. Ecol.*, **21**, 221–231.

Berhaut, J. (1969) Étude qualitative, quantitative et écologique des Hydroméduses du Golfe de Marseille. *Tethys*, **1**, 667–708.

Berline, L., Siokou-Frangou, I., Marasović, I., Vidjak, O., Fernández de Puelles, M. L., Mazzocchi, M. G., Assimakopoulou, G., Zervoudaki, S. *et al.* (2012) Intercomparison of six Mediterranean zooplankton time series. *Prog. Oceanogr.*, **97–100**, 76–91.

Blackett, M., Licandro, P., Coombs, S. H. and Lucas, C. H. (2014) Long-term variability of the siphonophores *Muggiaea atlantica* and *M. kochi* in the Western English Channel. *Prog. Oceanogr.*, **128**, 1–14.

Boero, F. and Bouillon, J. (1993) Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria). *Biol. J. Linnean Soc.*, **48**, 239–266.

Boero, F., Brotz, L., Gibbons, M. J., Piraino, S. and Zampardi, S. (2016) Impacts and effects of ocean warming on jellyfish. In Laffoley, D. and Baxter, J. M. (eds), *Explaining Ocean Warming: Causes, Scale, Effects and Consequences*. UICN, Gland, Switzerland, pp. 213–237.

Boero, F., Bucci, C., Colucci, A. M. R., Gravili, C. and Stabili, L. (2007) *Obelia* (Cnidaria, Hydrozoa, Campanulariidae): a microphagous, filter-feeding medusa. *Mar. Ecol.*, **28**, 178–183.

Borcard, D., Gillet, F. and Legendre, P. (2011) *Numerical Ecology with R*. Springer, New York, p. 306.

Bosc, E., Bricaud, E. and Antoine, D. (2004) Seasonal and interannual variability in algal biomass and primary production in the Mediterranean Sea, as derived from 4 years of SeaWiFS observations. *Glob. Biogeochem. Cycles*, **18**, 1–17.

Bouillon, J., Medel, M. D., Pagès, F., Gili, J. M., Boero, F. and Gravili, C. (2004) Fauna of the Mediterranean Hydrozoa. *Sci. Mar.*, **68**, 438.

Brodeur, R. D., Mills, C. E., Overland, J. E., Gary, E. W. and Schumacher, J. D. (1999) Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. *Fish. Oceanogr.*, **8**, 296–306.

Brodeur, R. D., Sugisaki, H. and Hunt, G. L. (2002) Increases in Jellyfish Biomass in the Bering Sea: Implications for the Ecosystem. *Mar Ecol Prog Ser.*, **233**, 89–103.

Brotz, L., Cheung, W. W. L., Kleisner, K., Pakhomov, E. and Pauly, D. (2012) Increasing jellyfish populations: trends in large marine ecosystems. *Hydrobiologia*, **690**, 3–20.

Brotz, L. and Pauly, D. (2012) Jellyfish populations in the Mediterranean Sea. *Acta Adriat.*, **53**, 211–230.

Buecher, E. and Gibbons, M. J. (1999) Temporal Persistence in the Vertical Structure of the Assemblage of Planktonic Medusae in the NW Mediterranean Sea. *Mar Ecol Prog Ser.*, **189**, 105–115.

Canepa, A., Fuentes, V., Sabatés, A., Piraino, S., Boero, F. and Gili, J. M. (2014) *Pelagia noctiluca* in the Mediterranean Sea. In Pitt, K. A. and Lucas, C. H. (eds), *Jellyfish Blooms*. Springer, Netherlands, Dordrecht, pp. 237–266.

Catalano-Balearic Sea – Bathymetric Chart (2005). www.icm.csic.es/geo/gma/MCB

Cervigón, F. (1958) Contribución al estudio de los sifonóforos de las costas de Castellón (Mediterráneo Occidental). *Inv. Pesq.*, **12**, 21–47.

Dallot, S., Goy, J. and Carré, C. (1988) Peuplements de carnivores planctoniques gélatineux et structures productives en Méditerranée occidentale. *Oceanol. Acta*, **9**, 193–209.

D'Ambrosio, M., Molinero, J. C., Azeiteiro, U. M., Pardal, M. A., Primo, A. L., Nyitrai, D. and Marques, S. C. (2016) Interannual abundance changes of gelatinous carnivore zooplankton unveil climate-driven hydrographic variations in the Iberian Peninsula, Portugal. *Mar. Environ. Res.*, **120**, 103–110.

Edwards, M. and Richardson, A. J. (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, **430**, 881–884.

Estrada, M., Vives, F. and Alcaraz, M. (1985) Life and the productivity of the open sea. In Margalef, R. (ed.), *Western Mediterranean*. Pergamon Press, Oxford, pp. 148–197.

Gamulin, T. and Kršinić, F. (1993) On the occurrence of Calycophorae (Siphonophora) in the southern Adriatic and Tyrrhenian Sea: a comparison of the annual cycles off Dubrovnik and Naples. *J. Plankton Res.*, **15**, 855–865.

García-Comas, C., Stemmann, L., Ibanez, F., Berline, L., Mazzocchi, M. G., Gasparini, S., Picheral, M. and Gorsky, G. (2011) Zooplankton long-term changes in the NW Mediterranean Sea: Decadal periodicity forced by winter hydrographic conditions related to large-scale atmospheric changes? *J. Mar. Syst.*, **87**, 216–226.

Garrabou, J., Coma, R., Bensoussan, N., Bally, M., Chevaldonné, P., Cigliano, M., Diaz, D., Harmelin, J. G. *et al.* (2009) Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. *Glob. Chang. Biol.*, **15**, 1090–1103.

Gibbons, M. J., Janson, L. A., Ismail, A. and Samaai, T. (2010) Life cycle strategy, species richness and distribution in marine Hydrozoa (Cnidaria: Medusozoa). *J. Biogeogr.*, **37**, 441–448.

Gili, J. M., Alvà, V., Coma, R., Orejas, C., Pagès, F., Ribes, M., Zabala, M., Arntz, W. E. *et al.* (1998) The impact of small benthic passive suspension feeders in shallow marine ecosystems: the hydroids as an example. *Zool. Verh. Leiden*, **323**, 99–105.

Gili, J. M., Pagès, F. and Riera, T. (1987a) Distribución de las especies más frecuentes de sifonóforos calicóforos en la zona norte del Mediterráneo occidental. *Inv. Pesq.*, **51**, 323–338.

Gili, J. M., Pagès, F., Sabatés, A. and Ros, J. D. (1988) Small-scale distribution of a cnidarian population in the western Mediterranean. *J. Plankton Res.*, **10**, 385–401.

Gili, J. M., Pagès, F. and Vives, F. (1987b) Distribution and ecology of a population of planktonic cnidarians in the western Mediterranean. In Bouillon, J., Boero, F., Cicogna, F. and Cornelius, P. F. S. (eds), *Modern Trends in the Systematics, Ecology, and Evolution of Hydroids and Hydromedusae*. Oxford University Press, Oxford, UK, pp. 157–170.

Goy, J. (1991) Hydromedusae of the Mediterranean Sea. *Hydrobiologia*, **216–217**, 351–354.

Graham, W. M., Pagès, F. and Hamner, W. M. (2001) A physical context for gelatinous zooplankton aggregations: a review. *Hydrobiologia*, **451**, 199–212.

Gravili, C., Bouillon, J., D'Elia, A. and Boero, F. (2007) The life cycle of *Gastroblasta raffaelei* (Cnidaria, Hydrozoa, Leptomedusae, Campanulariidae) and a review of the genus Gastroblasta. *Ital. J. Zool.*, **74**, 395–403.

Grazzini, F. and Viterbo, P. (2003) Record-breaking warm sea surface temperature of the Mediterranean Sea. *ECMWF Newsletter*, **98**, 30–31.

Grossmann, M. M., Collins, A. G. and Lindsay, D. J. (2014) Description of the eudoxid stages of *Lensia havock* and *Lensia leloupi* (Cnidaria: Siphonophora: Calycophorae), with a review of all known *Lensia* eudoxid bracts. *Syst. Biodivers.*, **12**, 163–180.

Guerrero, E., Gili, J. M., Rodriguez, C. S., Araujo, E. M., Canepa, A., Calbet, A., Genzano, G., Mianzan, H. W. *et al.* (2013) Biodiversity and distribution patterns of planktonic cnidarians in San Matías Gulf, Patagonia, Argentina. *Mar. Ecol.*, **34**, 71–82.

Guerrero, E., Marrodán, A., Sabatés, A., Orejas, C. and Gili, J. M. (2016) High spatial heterogeneity of two planktonic cnidarian species related to the variability of a shelf-slope front at short time scales. *Sci. Mar.*, **80**, 487–497.

Haddock, S. H. D. (2004) A golden age of gelata: past and future research on planktonic ctenophores and cnidarians. *Hydrobiologia*, **530–531**, 549–556.

Hays, G. C., Richardson, A. J. and Robinson, C. (2005) Climate change and marine plankton. *Trends Ecol. Evol.*, **20**, 337–344.

Hidaka, K. (1940) Absolute evaluation of oceanic currents in dynamic calculations. *Proc. Imp. Acad. (Tokyo)*, **16**, 391–393.

Hosia, A., Stemmann, L. and Youngbluth, M. J. (2008) Distribution of net-collected planktonic cnidarians along the northern Mid-Atlantic Ridge and their associations with the main water masses. *Deep-Sea Res. II*, **55**, 106–118.

Hughes, L. (2000) Biological consequences of global warming: is the signal already. *TREE*, **15**, 56–61.

IPCC (2014) *Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (Core Writing Team, Pachauri, R. K. and Meyer, L. A.)*. IPCC, Geneva, Switzerland.

Kirkpatrick, P. A. and Pugh, P. R. (1984) Siphonophores and velellids. In Kermack, D.M. and Barnes, R.S.K. (eds), *Synopses of the British Fauna (New Series)*. No. 29. E.J. Brill, Leiden, The Netherlands, p. 154.

Levitus, S., Antonov, J. and Boyer, T. (2005) Warming of the world ocean, 1955–2003. *Geophys. Res. Lett.*, **32**, L02604.

Licandro, P. and Ibañez, F. (2000) Changes of zooplankton communities in the Gulf of Tigullio (Ligurian Sea, Western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. *J. Plankton Res.*, **22**, 2225–2253.

Licandro, P., Souissi, S., Ibanez, F. and Carré, C. (2012) Long-term variability and environmental preferences of calycophoran siphonophores in the Bay of Villefranche (north-western Mediterranean). *Prog. Oceanogr.*, **97–100**, 152–163.

Lynam, C. P., Attrill, M. J. and Skogen, M. D. (2010) Climatic and oceanic influences on the abundance of gelatinous zooplankton in the North Sea. *J. Mar. Biol. Assoc. UK*, **90**, 1153–1159.

Mackie, G. O., Pugh, P. R. and Purcell, J. E. (1987) Siphonophore biology. *Adv. Mar. Biol.*, **24**, 97–262.

Mapstone, G. M. (2009) *Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific Waters. Mem. Mus. Comp. Zoöl. Harvard Coll*, **38**. NRC Research Press, Ottawa, Ontario, Canada, pp. 173–401 32 pls.

Marques, S. C., Azeiteiro, U. M., Leandro, S. M., Queiroga, H., Primo, A. L., Martinho, F., Viegas, I. and Pardal, M. Â. (2008) Predicting zooplankton response to environmental changes in a temperate estuarine ecosystem. *Mar. Biol.*, **155**, 531–541.

Matsakis, S. (1993) Growth of *Clytia* spp. hydromedusae (Cnidaria, Thecata): effects of temperature and food availability. *J. Exp. Mar. Bio. Ecol.*, **171**, 107–118.

Maynou, F., Sabatés, A. and Salat, J. (2014) Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. *Clim. Chang.*, **126**, 175–188.

McClatchie, S., Cowen, R., Nieto, K., Greer, A. T., Luo, J. Y., Guigand, C., Demer, D., Griffith, D. *et al.* (2012) Resolution of fine biological structure including small narcomedusae across a front in the Southern California Bight. *J. Geophys. Res.*, **117**, C04020.

Mills, C. E. and Goy, J. (1988) In situ observations of the behavior of mesopelagic *Solmissus* narcomedusae (Cnidaria, Hydrozoa). *Bull. Mar. Sci.*, **43**, 739–751.

Mills, C. E., Pugh, P. R., Harbison, G. R. and Haddock, S. H. D. (1996) Medusae, siphonophores and ctenophores of the Alboran Sea, south western Mediterranean. *Sci. Mar.*, **60**, 145–163.

Molinero, J. C., Casini, M. and Buecher, E. (2008) The influence of the Atlantic and regional climate variability on the long-term changes in gelatinous carnivore populations in the northwestern Mediterranean. *Limnol. Oceanogr.*, **53**, 1456–1467.

Molinero, J. C., Ibanez, F., Nival, P., Buecher, E. and Souissi, S. (2005) North Atlantic climate and northwestern Mediterranean plankton variability. *Limnol. Oceanogr.*, **50**, 1213–1220.

Nagata, R. M., Nogueira Júnior, M., Brandini, F. P. and Haddad, M. A. (2014) Spatial and temporal variation of planktonic cnidarian density in subtropical waters of the Southern Brazilian Bight. *J. Mar. Biol. Assoc. UK*, **94**, 1387–1400.

Nakajima, R., Lindsay, D. J., Yoshida, T., Othman, B. H. R. and Toda, T. (2013) Short-term temporal variation in gelatinous zooplankton populations over 48 hours in a coral reef at Redang Island, Malaysia. *Mar. Ecol.*, **35**, 254–260.

Nogueira Júnior, M., Brandini, F. P. and Codina, J. C. U. (2014) Distribution of planktonic cnidarians in response to South Atlantic Central Water intrusion in the South Brazilian Bight. *Cont. Shelf Res.*, **89**, 93–102.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P. *et al.* (2015) Vegan: community ecology package. R package version 2.3–0.

Oliver, E. C. J., Benthuysen, J. A., Bindoff, N. L., Hobday, A. J., Holbrook, N. J., Mundy, C. N. and Perkins-Kirkpatrick, S. E. (2017) The unprecedented 2015/16 Tasman Sea marine heatwave. *Nat. Commun.*, **8**, 1–12 doi:10.1038/ncomms16101.

Orejas, C., Gili, J. M., Alvà, V. and Arntz, W. (2000) Predatory impact of an epiphytic hydrozoan in an upwelling area in the Bay of Coliumo (Dichato, Chile). *J. Sea Res.*, **44**, 209–220.

Pagès, F. and Gili, J. M. (1991) Effects of large-scale advective processes on gelatinous zooplankton populations in the northern Benguela ecosystem. *Mar. Ecol. Progr. Ser.*, **75**, 205–215.

Pagès, F., González, H. E., Ramón, M., Sobarzo, M. and Gili, J. M. (2001) Gelatinous zooplankton assemblages associated with water masses in the Humboldt Current System, and potential predatory impact by *Bassia bassensis* (Siphonophora: Calycophorae). *Mar. Ecol. Progr. Ser.*, **210**, 13–24.

Palma, S., Apablaza, P. and Silva, N. (2007a) Hydromedusae (Cnidaria) of the Chilean southern channels (from the Corcovado Gulf to the Pulluche-Chacabuco Channels). *Sci. Mar.*, **71**, 65–74.

Palma, S., Apablaza, P. and Soto, D. (2007b) Diversity and aggregation areas of planktonic cnidarians of the southern channels of Chile (Boca del Guafo to Pulluche Channel). *Inv. Mar.*, **35**, 71–82.

Pavez, M. A., Landaeta, M. F., Castro, L. R. and Schneider, W. (2010) Distribution of carnivorous gelatinous zooplankton in the upwelling zone off central Chile (austral spring 2001). *J. Plankton Res.*, **32**, 1051–1065.

Penston, M. J., Millar, C. P., Zuur, A. F. and Davies, I. M. (2008) Spatial and temporal distribution of *Lepeophtheirus salmonis* (Krøyer) larvae in a sea loch containing Atlantic salmon, *Salmo salar* L., farms on the north-west coast of Scotland. *J. Fish Dis.*, **31**, 361–371.

Piontkovski, S. A., Fonda-Umani, S., Stefanova, K., Kamburska, L. and De Olazabal, A. (2011) An impact of atmospheric anomalies on zooplankton communities in the Northern Adriatic and Black Seas. *IJOO*, **5**, 53–71.

Postel, L., Fock, H. and Hagen, W. (2000) Biomass and abundance. In Harris, R. P., Wiebe, P. H., Lenz, J., Skjodal, H. R. and Huntley, M. (eds), *ICES Zooplankton Methodology Manual*. Academic Press, London, pp. 83–192.

Pugh, P. R. (1974) The vertical distribution of the siphonophores collected during the Sond Cruise, 1965. *J. Mar. Biol. Ass. UK*, **54**, 25–90.

Pugh, P. R. (1984) The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 7. Siphonophores. *Prog. Oceanogr.*, **13**, 461–489.

Pugh, P. R. (1989) Gelatinous zooplankton – the forgotten fauna. *Prog. Underwater. Sci.*, **14**, 67–78.

Purcell, J. E. (1982) Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham 1893). *J. Exp. Mar. Bio. Ecol.*, **62**, 39–54.

Purcell, J. E. (2005) Climate effects on formation of jellyfish and ctenophore blooms: a review. *J. Mar. Biol. Assoc. UK*, **85**, 461–476.

R Development Core Team (2013) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Riera, T., Gili, J. M. and Pagès, F. (1986) Estudio cuantitativo y estacional de dos poblaciones de cnidarios planctónicos frente a las costas de Barcelona (Mediterráneo occidental): ciclos entre 1966-67 y 1982-83. *Misc. Zool.*, **10**, 23–32.

Robison, B. H. (2004) Deep pelagic biology. *J. Exp. Mar. Biol. Ecol.*, **300**, 253–272.

Russell, F. S. (1934) On the occurrence of the siphonophores *Muggiaea atlantica* Cunningham and *Muggiaea kochi* (Will) in the English Channel. *J. Mar. Biol. Assoc. UK*, **19**, 555–559.

Sabatés, A., Pagès, F., Atienza, D., Fuentes, V., Purcell, J. E. and Gili, J. M. (2010) Planktonic cnidarian distribution and feeding of *Pelagia noctiluca* in the NW Mediterranean Sea. *Hydrobiologia*, **645**, 153–165.

Sabatés, A., Salat, J., Raya, V. and Emelianov, M. (2013) Role of mesoscale eddies in shaping the spatial distribution of the coexisting *Engraulis encrasicolus* and *Sardinella aurita* larvae in the northwestern Mediterranean. *J. Mar. Syst.*, **112**, 108–119.

Sabatés, A., Salat, J., Raya, V., Emelianov, M. and Segura-Noguera, M. (2009) Spawning environmental conditions of *Sardinella aurita* at the northern limit of its distribution range, the western Mediterranean. *Mar. Ecol. Progr. Ser.*, **385**, 227–236.

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Saiz, E., Sabatés, A. and Gili, J. M. (2014) The Zooplankton. In Goffredo, S. and Dubinsky, Z. (eds), *The Mediterranean Sea: Its History and Present Challenges*. Springer, Netherlands, Dordrecht, pp. 183–211.

Schär, C., Vidale, P. L., Lüthi, D., Frei, C., Häberli, C., Liniger, M. A. and Appenzeller, C. (2004) The role of increasing temperature variability in European summer heatwaves. *Nature*, **427**, 332–336.

Sparnocchia, S., Schiano, M. E., Picco, P., Bozzano, R. and Cappelletti, A. (2006) The anomalous warming of summer 2003 in the surface layer of the Central Ligurian Sea (Western Mediterranean). *Ann. Geophys.*, **24**, 443–452.

Stewart, T. H. (2008) Introduction to Physical Oceanography. http://oceanworld.tamu.edu/resources/ocng_textbook/contents.html

Tilves, U., Purcell, J. E., Fuentes, V. L., Torrents, A., Pascual, M., Raya, V., Gili, J. M. and Sabatés, A. (2016) Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs and larvae in the NW Mediterranean. *J. Plankton Res.*, **38**, 1243–1254.

Venables, W. N. and Ripley, B. D. (2002) *Modern Applied Statistics with S.* Springer, New York, p. 498.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. and Smith, G. M. (2009) *Mixed Effects Models and Extension in Ecology with R.* Springer, New York, p. 574.