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Spatio-temporal variability of the zooplankton community in the SW Mediterranean 1992–2020: Linkages with environmental drivers

Lidia Yebra [*], Marta Puerto, Nerea Valcárcel-Pérez, Sébastien Putzeys, Francisco Gómez-Jakobsen, Candela García-Gómez, Jesús M. Mercado

Centro Oceanográfico de Málaga (IEO, CSIC), Puerto Pesquero s/n, 29640 Fuengirola, Spain

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A B S T R A C T

Variability in the spatial and temporal distribution of the mesozooplankton abundance in the N Alboran Sea (SW Mediterranean) was assessed intermittently from 2010 to 2020, and compared with 1992–2000 historical time series data. Total abundance of mesozooplankton was significantly higher in the coast than in the shelf and slope waters. There were significant differences in mesozooplankton abundance between 1992–2000 and 2010–2020 at the three zones. Copepods dominated the mesozooplankton during winter and spring, but cladocerans and doliolids also became important components of the community in summer and autumn. We found significant increases between the first and the second decadal periods in the abundance of copepods, appendicularians, holoplanktonic gastropods and siphonophores in the shelf. However, in the coast, copepod nauplii, doliolids, gastropods and siphonophores increased, while euphausiids abundance decreased significantly. These trends contrast with the ongoing decline of the sardine stocks in European waters. Increasing temperature and decreasing predation pressure are suggested to be the main drivers of mesozooplankton variability.

1. Introduction

One of the most productive regions of the Mediterranean Sea is the N Alboran Sea, the westernmost basin (Mercado et al., 2012; Yebra et al., 2017, 2018). The Alboran Sea is characterized by a high mesoscale hydrodynamics (Prieur and Sournia, 1994; Rodríguez et al., 1998) fuelled by the jet of Atlantic water incoming through the Strait of Gibraltar. Further, westerly winds trigger recurrent upwelling events throughout the year (Prieur and Sournia, 1994; Sarhan et al., 2000), which promote nutrient enrichment and growth of plankton, especially in the Bay of Malaga, where the biomass of both phytoplankton and zooplankton is often high (Sampaio de Souza et al., 2005; Mercado et al., 2007; Yebra et al., 2017). These characteristic hydrographic conditions lead to a zooplankton annual cycle differentiated from nearby areas (Rodríguez, 1983), with communities typical of upwelling zones and warm waters and predominance of neritic forms (Rodríguez et al., 1982; Sampaio de Souza et al., 2005).

Zooplankton play a key role in the marine ecosystem dynamics, being predators of primary producers (Calbet and Landry, 2004; Yebra et al., 2017), preys for higher trophic levels (Yebra et al., 2019), and link between the classical food web and the microbial loop by releasing organic matter and nutrients (León Díaz, 2010; Steinberg and Landry, 2017). Furthermore, diel vertical migrant zooplankton play an important role on the biogeochemical fluxes in the region (Yebra et al., 2018). Besides, the Bay of Malaga is the main nursery site for *Sardina pilchardus* in the Mediterranean Sea (García et al., 1988; García, 2010). Currently, there is a growing concern on the decline of the artisanal coastal fisheries due to the decrease of the populations of small pelagic fishes observed in the W Mediterranean in the past decade (Brosset et al., 2017). The study area is particularly suitable to understand the impact of changes in the zooplankton community structure on the recruitment of small pelagic fishes, with notable importance for the local economy.

Despite the strong link observed between zooplankton and small pelagic fish populations (Quintanilla et al., 2020; Yebra et al., 2020), there are few studies on the spatio-temporal variability in the abundance and composition of the zooplankton communities in this region (Mercado et al., 2007; Yebra et al., 2017).

Climate change, and other stress factors, modify the abundance and composition of the planktonic communities (Beaugrand et al., 2002; Richardson, 2008; Mackas et al., 2012). Zooplankters usually have short life cycles, which favors rapid responses to changes in their environment (Taylor et al., 2002; Fernández de Puelles and Molinero, 2008). Some of

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[*] Corresponding author.
E-mail address: lidia.yebra@ieo.csic.es (L. Yebra).

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the observed effects of climate change over plankton include shifts in their spatial distribution and abundance seasonal cycle, producing important reorganizations in the plankton and fish communities (Beaugrand et al., 2003; Hays et al., 2005). Considering the central role of zooplankton in the food web, changes in this community may spread to the entire pelagic ecosystem (Fernández de Puelles and Molinero, 2008). Thus, studying zooplankton communities' variability over time, e.g. through keeping time series, is vital to understand ongoing changes and predict future shifts in the marine environment.

To research the driving processes behind the spatial and temporal variability of the mesozooplankton total abundance and community structure in the N Alboran Sea, we first assessed shifts in their distribution and taxonomic composition at group level from 1992–2000 to 2010–2020. Then we studied the potential linkages with environmental drivers, such as temperature, food and predator abundances.

2. Materials and methods

Oceanographic cruises were conducted intermittently from 2010 to 2020 (Suppl. Table 1), in a transect perpendicular to the coast within the Bay of Malaga (MA). Each sampling included 3 to 7 stations, located between 0.5 and 15 Km from the coast, with bottom depths ranging from 10 to 500 m (Fig. 1, Suppl. Table 2). Note that stations MA2, MA4 and MA5 correspond to stations M1, M2 and M3, respectively, in the time series ECOMALAGA (1992–2000), analyzed in Mercado et al. (2007).

2.1. Zooplankton

From 2010 to 2020, mesozooplankton was collected by means of vertical hauls performed with a double WP2 net (200 μm mesh) from the bottom depth (minus 3 m net length) to the surface (Suppl. Table 2). When bottom depth was deeper than 100 m, hauls were made from 100 m depth to the surface. A total of 52 samples were preserved in borax-buffered formalin (f.c. 4%) until analyzed in the laboratory. Zooplankton abundance and composition of major taxa until 2015 were determined following the same protocol as during the 1992–2000 period, using a stereomicroscope (Leica M165C). Identification was made according to Rose (1933), Trégouboff and Rose (1957) and Razouls et al. (2005–2021). Samples collected in the 2019–2020 period were scanned with an EPSON Perfection V700 photo scanner at 3200 dpi, and processed using Zooimage and Ecotaxa. The automatic prediction in Ecotaxa was made with a set of samples developed for the

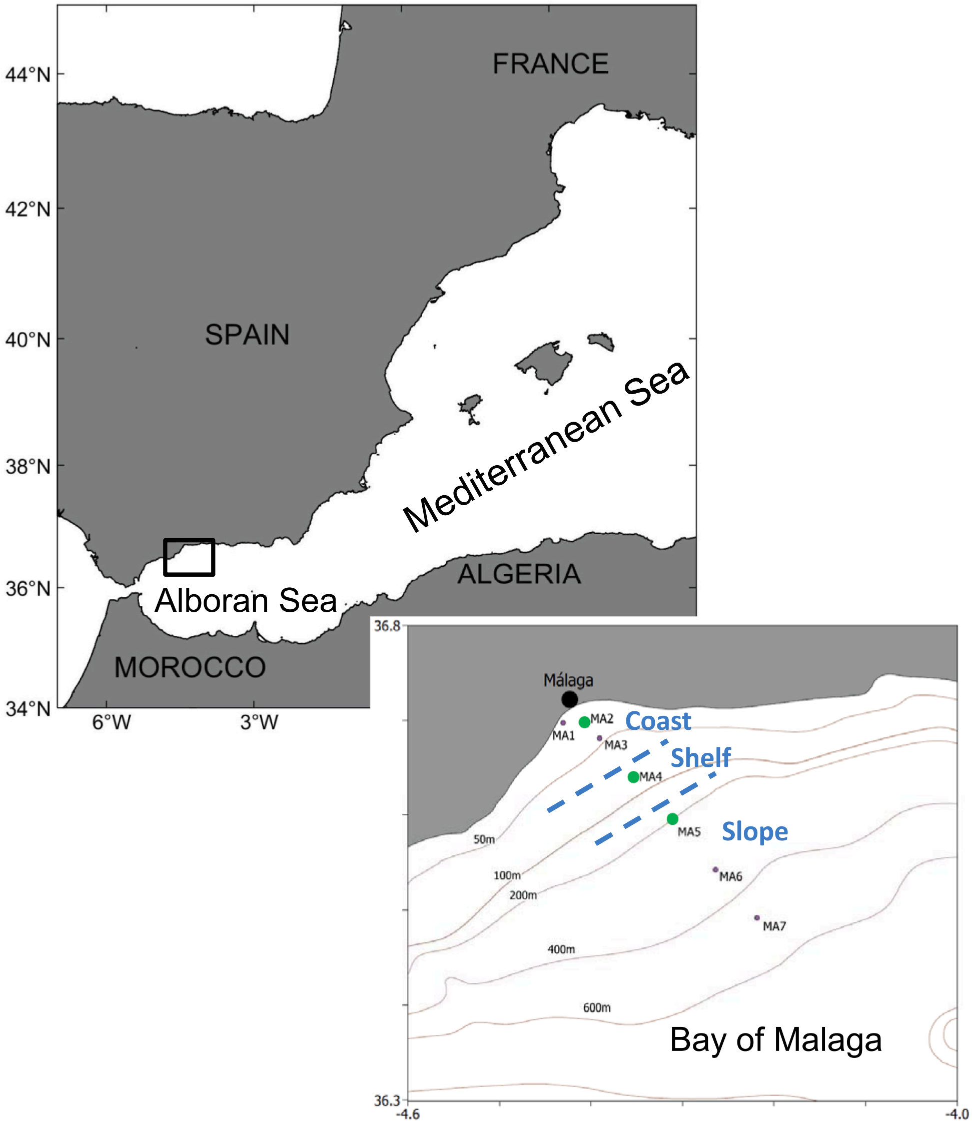

Fig. 1. Sampling stations location map in the Bay of Malaga, indicating bathymetry and zones along the MA transect. Green dots indicate stations also sampled during the 1992–2000 time series. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

study area, which identified the main taxonomic groups with an accuracy of 66–91% (Valcárcel-Pérez et al., 2019). After the prediction, all the images (192,531 in total) were manually validated before extracting the data.

Collection and analyses of samples from the 1992–2000 period were described in Mercado et al. (2007). In brief, 95 zooplankton samples were collected quarterly with Bongo net (40 cm diameter, 200 µm mesh) oblique tows down to 100 m depth, and fixed with 40% formaldehyde solution. Samples were analyzed on a stereoscopic microscope Leica MZ8.

2.2. Environmental variables

Environmental variables were collected following the same procedures during the 1992–2000 and 2010–2020 periods. Vertical profiles of temperature and salinity were obtained at each station with a CTD Seabird 25. Seawater samples were collected with Niskin bottles at different fixed depths (surface, 10, 20, 30, 50, 75 and 100 m). For the determination of chlorophyll *a* (hereafter Chl *a*), 1 to 3 L of seawater were filtered through Whatman GF/F filters which were subsequently frozen at −20 °C until their analysis in the laboratory. The analysis of Chl *a* was conducted by spectrophotometry, after extraction in 90% acetone overnight at 4 °C. Means of temperature and Chl *a* concentration 0–20 m were calculated for each station to represent the zooplankton field conditions.

2.3. Statistical analyses

Kruskal-Wallis (K-W) ANOVA were performed to assess seasonal and zonal differences of total mesozooplankton abundances; and Mann-Whitney (M-W) U tests were used to determine differences between periods. Independent samples Student t-tests were performed to determine significant differences on square-root transformed abundances of main taxa among zones (coast, mid shelf and slope) and time periods.

Notwithstanding the data gap between both decades, we explored potential long-term trends from 1992 to 2020 by analyzing the seasonally adjusted abundance time series at two stations regularly sampled during both the 1992–2000 and 2010–2020 periods: MA2 (former M1 in Mercado et al., 2007) in the coast, and MA4 (former M2) in the mid shelf waters. No analysis was attempted for the slope zone due to the reduced number of samples available from MA5 (former M3) for the 2010–2020 period (Suppl. Table 1). Interannual time trends in zooplankton abundance and environmental variables for the whole analyzed period were assessed on the seasonally adjusted time series. We calculated these deseasonalized time series by subtracting the seasonal mean calculated for 1992–2020 from the raw time series. Interannual trends in abundance for each seasonal period (season-based trends) were calculated by analyzing separately the deseasonalized time series of each season: winter (December, January, February), spring (March, April, May), summer (June, July, August) and autumn (September, October, November). The significance of the interannual trends was assessed through Pearson's correlations. Interannual trends in abundance and their statistical significance were visually compiled in a heat map. The software package Statistica 7 was used for these statistical analyses. Cluster and MDS analyses based on the Bray Curtis similarity matrix of square-root transformed data of main taxa abundances were carried out with Primer 6β.

3. Results

3.1. Mesozooplankton spatial variability

Total mesozooplankton abundance from 2010 to 2020 ranged from 243 to 24,676 ind·m^{-3}. Stations were grouped according to their location in three zones; coast: MA1-3, mid shelf: MA4, and slope: MA5-7, as we found no significant differences in mesozooplankton total abundances within zones (K-W, H = 0.40–1.61, p > 0.5). We found significant differences in abundances between these zones (K-W, H = 8.67, p < 0.01; Fig. 2, Suppl. Table 2); with higher mean values in the coast (stations MA1-MA3, 6,244 ± 5,645SD ind·m^{-3}) than in the mid shelf (st. MA4, 2,452 ± 2,544 ind·m^{-3}, z'=2.14, p = 0.097) and slope (sts. MA5-7, 1980 ± 2083 ind·m^{-3}, z'=2.47, p < 0.04). Likewise, mesozooplankton abundance was higher at the shelf than at the slope, but no significantly (z'=0.41, p = 1.0). A similar decreasing pattern was found for the 1992–2000 period (K-W, H = 27.03, p < 0.0001), with significant differences between the coast and the two other zones (shelf: z'=3.28, p < 0.003; slope: z'=5.14, p < 0.0001) but without differences between shelf and slope (z'=1.87, p = 0.18).

From 2010 to 2020, the mesozooplankton community structure was dominated by copepods, followed by cladocerans and appendicularians (Table 1). Other groups identified in variable concentrations were doliolids, siphonophores, chaetognaths, copepod nauplii, holoplanktonic gastropods, and euphausiids. Mesozooplankton taxa representing <1% of the total abundance included amphipods, ctenophores, fish eggs and larvae, isopods, medusa, mysids, polychaetes, salps, ostracods, and meroplanktonic larvae.

Most taxa presented higher abundances in the coast compared to the shelf or slope. However, euphausiids abundance increased towards the slope, and gastropods presented similar values in the coast and the slope being double their abundance than in the shelf. We only found significant differences between zones for the copepods (F = 5.55, p = 0.007), presenting significantly higher abundances in the coast than in the mid shelf (t = 2.32, p = 0.023) and the slope (t = 2.49, p = 0.017). Concerning the relative contribution of each taxon, there were no differences between zones for the most abundant groups (Table 1). However, the contribution of chaetognaths was significantly higher in the shelf than in the coast (t = -2.42, p = 0.020), and the relative abundance of gastropods was significantly higher in the slope than in the shelf (t = -3.04, p = 0.004) and the coast (t = -3.08, p = 0.006).

3.2. Mesozooplankton seasonal variability

Total zooplankton abundances presented a marked seasonality (Fig. 3, Suppl. Table 3), with maxima in summer and autumn and minima in winter. We found significant differences between seasons during the 1992–2000 and 2010–2020 periods (K-W, H = 28.85, p < 0.0000), driven by the significant differences between summer and winter (z'=3.92, p < 0.001) and spring (z'=4.90, p < 0.00001). Mesozooplankton abundance decreased from the coast to the open sea, except in winter of the 2010–2020 period, when coast and slope abundances were similar. We found significantly higher median values in 2010–2020 compared to 1992–2000 for summer in the shelf (M-W, Z = -2.04, p < 0.04).

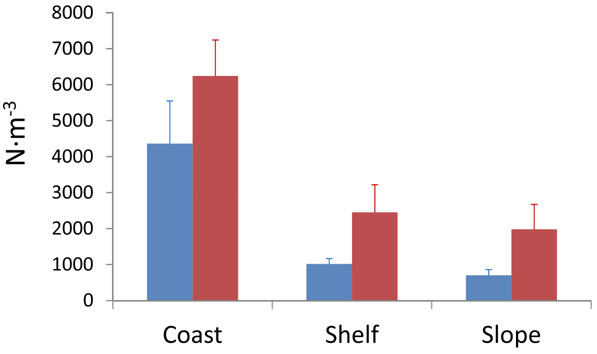

Fig. 2. Mean mesozooplankton abundance (N·m^{-3} ± SE) in the different zones (coast, shelf, slope) during the 1992–2000 (blue) and 2010–2020 (brown) periods. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Mean abundances (N·m^{-3} ± SD) and relative abundances (%±SD) of the main mesozooplankton taxa in each zone for the 2010–2020 period. n = number of observations.

	Coast (n = 31)		Shelf (n = 11)		Slope (n = 9)	
Taxa	N m^{-3}	%	N m^{-3}	%	N m^{-3}	%
Appendicularia	350.0 ± 452.8	5.0 ± 3.8	227.6 ± 324.6	7.5 ± 6.8	146.6 ± 140.9	8.7 ± 5.6
Chaetognatha	28.0 ± 30.5	0.5 ± 0.6	28.4 ± 24.5	1.9 ± 3.1	10.8 ± 6.5	0.8 ± 0.4
Cladocera	1703.0 ± 2016.8	24.1 ± 21.1	361.3 ± 420.7	12.6 ± 14.7	431.9 ± 450.1	23.3 ± 19.9
Copepoda	2956.2 ± 2061.1	51.5 ± 16.7	1105.6 ± 940.1	50.2 ± 18.4	1105.6 ± 1142.6	47.4 ± 13.6
Copepoda nauplii	143.6 ± 357.6	2.0 ± 3.4	73.6 ± 88.6	4.0 ± 3.9	73.6 ± 61.9	2.0 ± 1.7
Doliolida	519.5 ± 1335.2	4.4 ± 7.8	357.2 ± 928.8	5.7 ± 10.0	95.6 ± 122.4	4.4 ± 2.4
Euphausiacea	3.9 ± 4.6	0.2 ± 0.3	6.6 ± 9.3	0.5 ± 0.5	10.9 ± 13.5	0.6 ± 0.6
Gastropoda	69.7 ± 61.7	1.4 ± 1.0	35.6 ± 63.3	1.6 ± 1.8	72.2 ± 101.7	3.3 ± 2.1
Siphonophora	187.6 ± 493.96	2.16 ± 4.61	59.9 ± 87.4	3.6 ± 4.4	24.9 ± 29.2	2.5 ± 3.5
Others	512.1 ± 456.7	8.9 ± 6.5	196.3 ± 152.3	12.5 ± 11.9	98.0 ± 54.0	7.2 ± 4.6

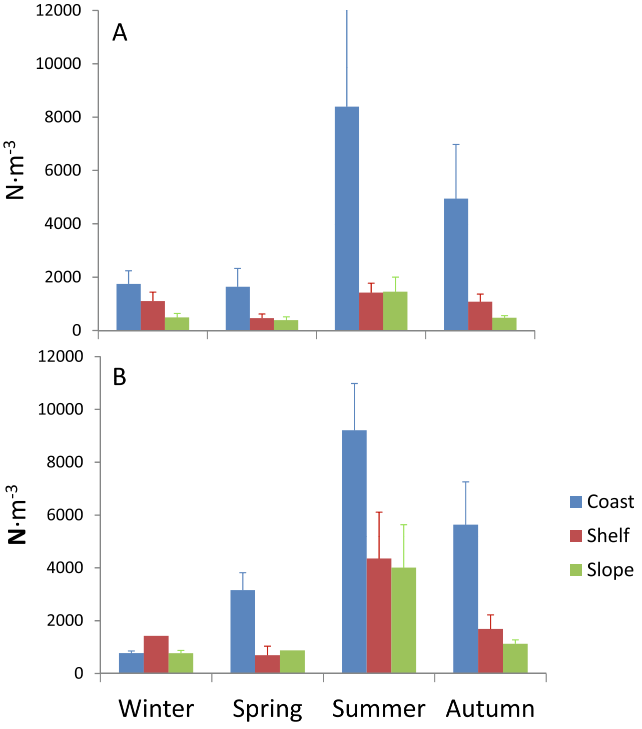

Fig. 3. Seasonal variability in the mean mesozooplankton abundance (N·m^{-3} ± SE) in the different zones (coast, shelf, slope) during A) 1992–2000 and B) 2010–2020.

The mesozooplankton community composition also varied seasonally (Fig. 4). During 2010–2020, copepods dominated in spring and winter (65–87% of the community), followed by appendicularians (2–13%). However, in summer copepods contribution reduced to a 32–43% of the total abundance, and cladocerans increased up to a 38%. Also, doliolids increased their contribution in summer, reaching 22% in the mid shelf. In autumn, copepods mean contribution increased (45–53%) but cladocerans remained the second most abundant group (17–32%). This seasonality was reflected in the MDS analysis of root transformed abundance data for the entire 146 samples collected in the 1992–2000 and 2010–2020 periods (Fig. 5). Cluster analysis based on a Bray Curtis similarity matrix showed that stations grouped by seasons, rather than by zones or years (Suppl. Fig. 1).

3.3. *Mesozooplankton interannual variability*

Total mesozooplankton abundance presented high interannual variability, with the highest peaks observed in the coast during the summer and/or autumn of 1993, 1999, 2000 and in the 2010–2012 period (Fig. 6). In the shelf, the highest abundance was found in summer 2010, followed by 2020, 1993 and 1999. The mesozooplankton abundance in the slope area presented its maximum value in 2020, followed by 1993 and 1999. Also, in those three years the total abundance was higher in the slope than in the shelf.

Median mesozooplankton abundances were significantly higher in 2010–2020 than in 1992–2000 at the three zones (Fig. 2, M-W, coast: $Z = -2.28$, $p < 0.02$; shelf: $Z = -2.20$, $p < 0.03$; slope: $Z = -2.58$, $p < 0.01$). We also observed significant differences in the community structure between 1992 and 2000 and 2010–2020 (Table 2, Suppl. Table 4). In the coast, the annual mean abundances of copepod nauplii, gastropods and siphonophores were significantly higher in 2010–2020; whereas euphausiid abundance decreased significantly in that period. Also, doliolids increased in 2010–2020, as well as the total gelatinous organisms' abundance, although not significantly ($p < 0.1$, Table 2). However, these differences were not reflected as significant changes in their relative abundances, except for the siphonophores (Suppl. Table 4). In the mid shelf, we observed a significant increase for 2010–2020 in the abundances of appendicularians, copepods, gastropods and siphonophores, as well as on the averaged abundances of crustaceans and gelatinous organisms (Table 2). However, the ratio crustaceans/gelatinous remained similar in both decades. Accordingly, only the relative abundance of euphausiids, gastropods and siphonohores varied significantly in 2010–2020 with respect to 1992–2020 (Suppl. Table 4).

The observed differences had a seasonal component, and most of them were only significant during a given season of the annual cycle (Suppl. Table 5). In spring, we found significant differences between periods for copepod nauplii and siphonophores; whereas in summer, the differences were significant for appendicularians and copepods in the shelf, and for siphonophores in the coast. In autumn, only coastal siphonophores presented significant differences between decades; and gastropods were the only taxon presenting significant differences in winter in the shelf, although this result must be taken cautiously since only one winter cruise was carried out in the 2010–2020 period.

In the shelf area, we found a positive and significant trend in total mesozooplankton abundance when the whole deseasonalized time series (1992 to 2020) was analyzed (Suppl. Fig. 2); however, trends calculated for each season separately were not significant (Fig. 7, Suppl. Table 6). Opposite to this, in the coast we found negative but not significant interannual trends for the annual period and for all seasons, except spring. Regarding the different mesozooplankton taxa, we observed different tendencies in the coast and the shelf zones (Suppl. Fig. 2). In the coast only gastropods presented a positive significant annual trend, driven by the summer and autumn significant trends (Fig. 7, Suppl. Fig. 2, Suppl. Table 6). The siphonophores also presented a significant positive trend but only in spring. Also, in spring, copepod nauplii, doliolids and gastropods showed slightly significant positive trends ($p < 0.1$). On the contrary, euphausiids presented negative trends. In the shelf, significant positive interannual trends for appendicularians and copepods were found, the latter driven by a significant positive trend in the summer season (Suppl. Fig. 2, Suppl. Table 6). Copepod nauplii also presented significant positive trends during spring and summer, but not

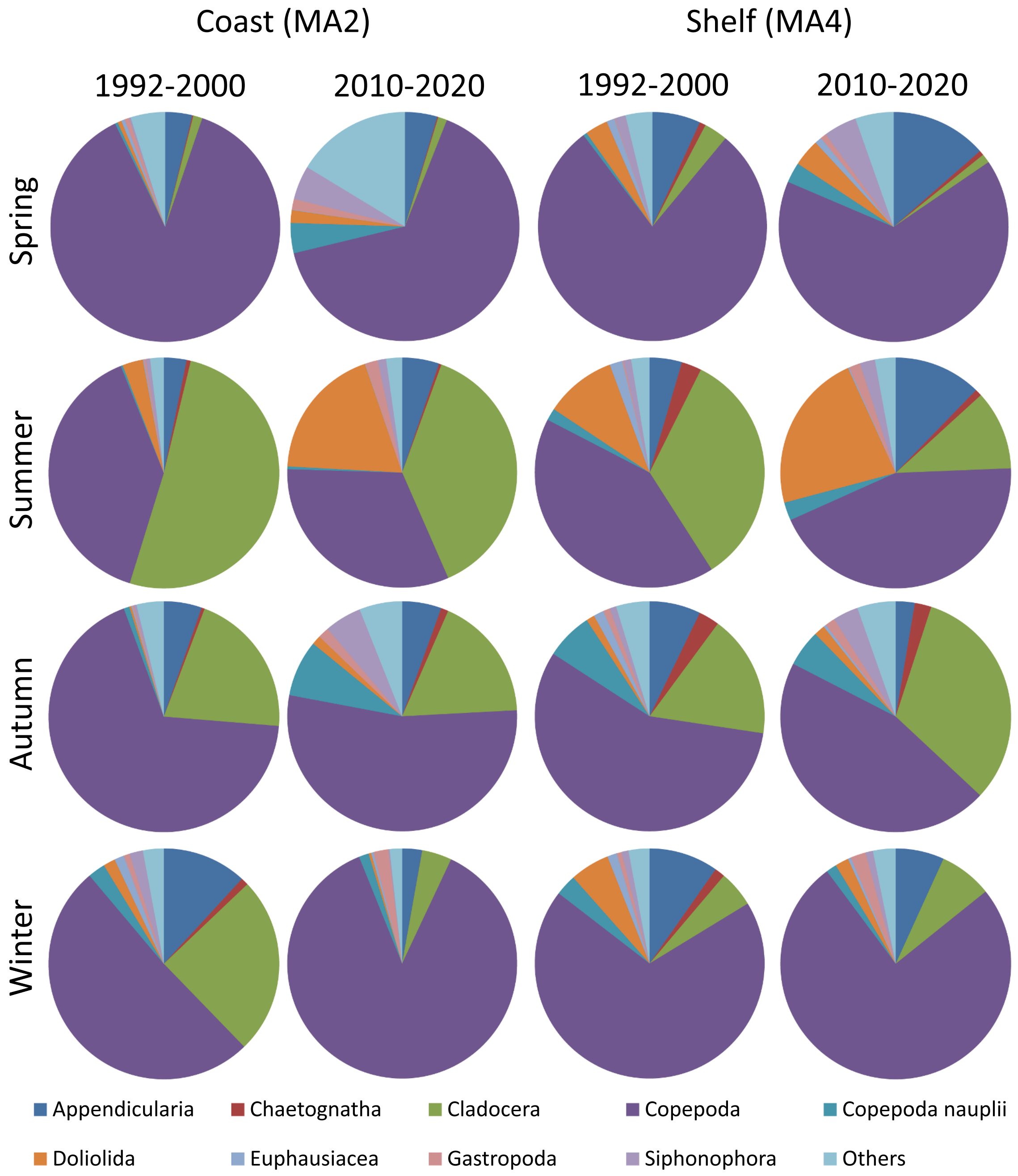

Fig. 4. Mean season relative abundances (%) of mesozooplankton taxa in the coast (MA2) and shelf (MA4) in the 1992–2000 and 2010–2020 periods.

on an annual basis. Gastropods presented a positive significant annual trend, as in the coast, but driven by spring and winter trends. Siphonophores presented slightly significant positive trends during spring and autumn, and appendicularians in summer.

3.4. Environmental variables

We found no significant differences ($p > 0.05$) in temperature, salinity or Chl *a* between 1992 and 2000 and 2010–2020 in the coast (Suppl. Table 7). In the shelf, only temperature was slightly higher in 2010–2020 compared with 1992–2000 (17.90 ± 2.75 *vs* 16.51 ± 2.08, t = -1.94, p = 0.058). Surface mean temperature (0–20 m depth) presented positive but not significant trends during the 1992–2020 period in the coast and shelf zones ($p > 0.05$, Suppl. Fig. 3); whilst salinity and chlorophyll *a* showed negative trends, also not significant.

We found positive and significant correlations between temperature and total mesozooplankton abundances in the coast and the shelf (Suppl. Table 8); while salinity was not significantly correlated in any of the zones. Chl *a* was negative and significantly correlated with mesozooplankton abundance in the shelf but not in the coast. Temperature showed significant positive correlations in both zones with chaetognaths, cladocerans and doliolids; while with appendicularians and gastropods only in the coast. Salinity presented significant negative correlations with gastropods in both zones, and with chaetognaths in the shelf. Chl *a* was only negative and significantly correlated with chaetognaths and cladocerans in the shelf (Suppl. Table 8).

4. Discussion

The SW Mediterranean Sea is characterized by an intense hydrodynamics that promotes high plankton productivity (Mercado et al., 2007; Yebra et al., 2017, 2018). Mesozooplankton abundance is driven by a

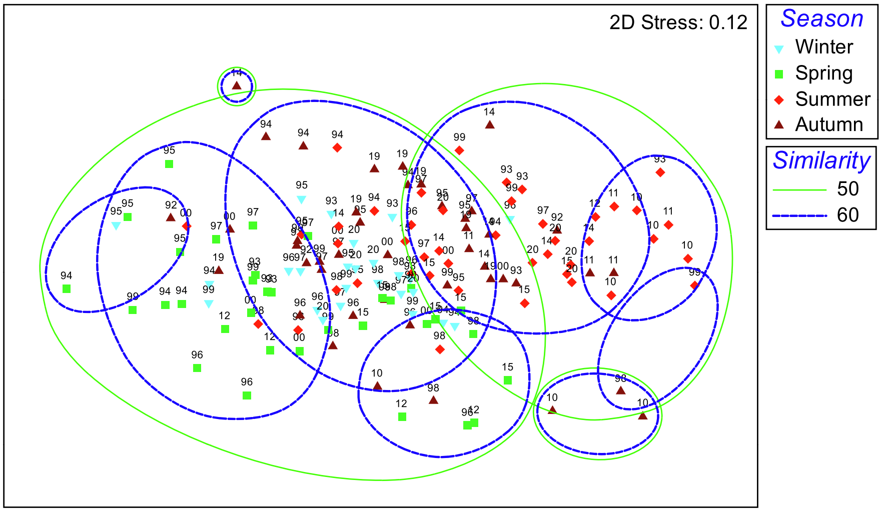

Fig. 5. MDS plot based on Bray Curtis similarity matrix of square root transformed mesozooplankton taxa abundances recorded in the 1992–2000 and 2010–2020 periods. Colors indicate season: 1, winter; 2, spring; 3, summer; 4, autumn. Numbers indicate the year of sampling.

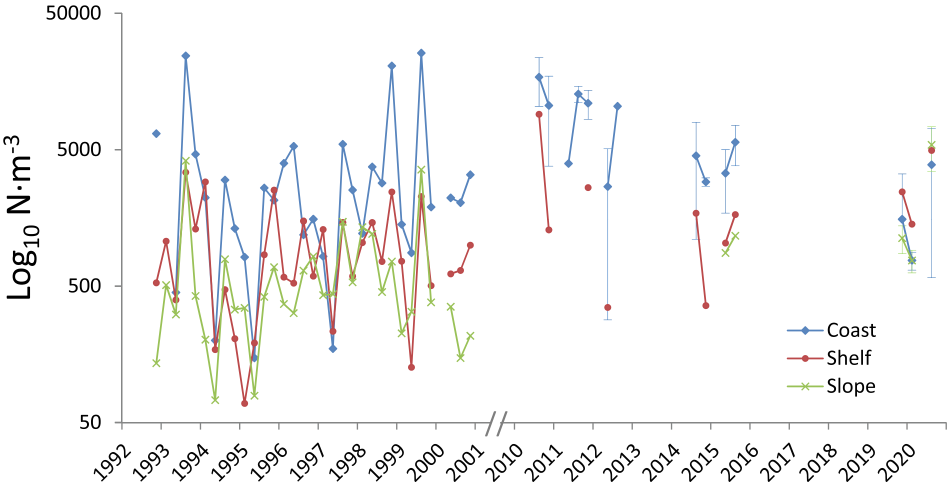

Fig. 6. Mean mesozooplankton abundance (N·m^{-3} ± SD) variability in the different zones (coast, shelf, slope) during the 1992–2000 and 2010–2020 periods.

Table 2
Mean abundances (N·m^{-3} ± SD) of the main mesozooplankton taxa in the coast (MA2) and shelf (MA4) for the 1992–2000 and 2010–2020 periods. Student *t*-test statistics (t, p) indicate significant differences between time periods. Bold: $p < 0.05$, italics: $0.05 < p < 0.1$. n = number of observations.

	Coast (MA2)				Shelf (MA4)			
Taxa	1992–2000 (n = 31)	2010–2020 (n = 12)	t	p	1992–2000 (n = 32)	2010–2020 (n = 11)	t	p
Appendicularia	200.0 ± 210.1	253.3 ± 288.3	−0.67	0.51	68.4 ± 64.9	227.6 ± 324.6	−2.68	**0.01**
Chaetognatha	23.4 ± 39.6	26.2 ± 35.2	−0.21	0.83	22.9 ± 27.9	28.4 ± 24.5	−0.58	0.56
Cladocera	1483.0 ± 3832.1	1387.5 ± 1926.8	0.08	0.94	184.2 ± 420.8	361.3 ± 420.7	−1.20	0.24
Copepoda	2357.1 ± 4089.7	2030.0 ± 1482.7	0.27	0.79	569.7 ± 505.2	1105.6 ± 940.1	−2.39	**0.02**
Copepoda nauplii	27.1 ± 48.5	143.5 ± 316.4	−2.03	**0.05**	33.5 ± 102.7	73.6 ± 88.6	−1.15	0.26
Doliolida	74.5 ± 215.0	585.7 ± 1668.2	−1.70	*0.096*	55.4 ± 148.7	357.2 ± 928.8	−1.81	*0.08*
Euphausiacea	12.3 ± 16.5	2.1 ± 4.2	2.30	**0.04**	15.0 ± 17.3	6.6 ± 9.3	1.53	0.13
Gastropoda	14.3 ± 12.9	81.9 ± 90.8	−4.12	**0.0002**	5.2 ± 9.5	35.6 ± 63.3	−2.69	**0.01**
Siphonophora	25.3 ± 33.0	129.6 ± 250.9	−2.31	**0.026**	10.6 ± 8.4	59.9 ± 87.4	−3.22	**0.003**
Crustaceans	3900.3 ± 6268.1	3586.9 ± 2843.3	0.17	0.87	810.6 ± 724.5	1577.4 ± 1278.4	−2.44	**0.019**
Gelatinous	309.4 ± 394.6	996.9 ± 1984.4	−1.86	*0.07*	137.7 ± 194.2	657.8 ± 1328.2	−2.20	**0.034**
Crust/gelat ratio	17.2 ± 21.4	12.3 ± 10.7	0.76	0.45	27.6 ± 96.1	11.5 ± 19.5	0.55	0.59

combination of factors such as the hydrology of the Alboran basin (Sampaio de Souza et al., 2005), food availability (Yebra et al., 2017) and predators abundance (Yebra et al., 2020). These factors may vary at different spatial and temporal scales, also shaping the interannual variability of mesozooplankton abundance distribution and their community structure in the region. This study provides the first analysis of

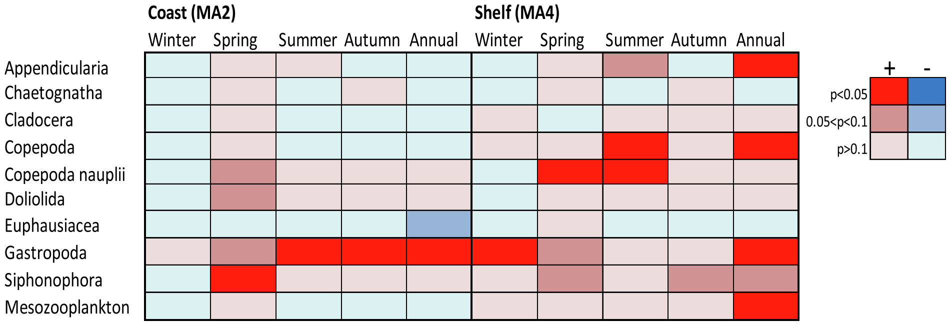

Fig. 7. Heat map showing interannual trends of seasonally adjusted abundances, and season-based interannual trends in abundance of main mesozooplankton taxa in the coast (MA2) and shelf (MA4) from 1992 to 2020. Red: positive, blue: negative.

interdecadal variations (1992–2000 and 2010–2020) in the mesozooplankton abundance and community composition in the SW Mediterranean in relation to environmental factors.

4.1. Spatial variability

Mesozooplankton total abundances decreased significantly from the coast towards open waters through the study, as previously reported by Sampaio de Souza et al. (2005) for 1992–2000. This horizontal gradient in mesozooplankton abundance was also reported by Fernández de Puelles et al. (2007) for 1994–1999 in a cross-shelf transect in the Balearic Sea. As in previous studies, most taxa presented higher abundances in the coast than in the shelf. However, the relative contribution of the dominant groups remained similar in both zones, and only less abundant groups like chaetognaths, doliolids and holoplanktonic gastropods presented an increased percentage contribution in offshore waters; similar to the observed by Fernández de Puelles et al. (2007). The coast-shelf gradient would be mainly related to nutrients input reaching the shelf area, that favor the phytoplankton growth in the coastal stations (Mercado et al. 2012); although upwelled waters rich in nutrients from Algeciras may also reach the slope waters of the study area by advection (Gómez-Jakobsen et al., 2019). The different hydrodynamic features present in each zone may also contribute to the observed differences. The Atlantic jet entering the Alboran Sea through the Strait of Gibraltar would mainly affect the slope (Sampaio de Souza et al., 2005), whereas enrichment episodes in the coast and shelf currents would be driven by wind (Cano and García-Lafuente, 1991).

4.2. Seasonal variability

Mesozooplankton abundance presented a marked seasonality, with significant differences between seasons. The annual cycle was characterized by highest abundances in summer-autumn and lowest in winter-spring, as previously described in the region (Rodríguez et al., 1982; Mercado et al., 2007), and in contrast with more oligotrophic areas of the Mediterranean showing maxima in spring and minima in summer (Siokou-Frangou, 1996; Fernández de Puelles et al., 2007; Fullgrabe et al., 2020; Feuilloley et al., 2021). Mesozooplankton abundance was correlated positively with temperature, and negatively with Chl *a* in the shelf, but not in the coast. Nevertheless, peaks of coastal abundance coincided in time with some of the highest Chl *a* concentrations or temperature values registered in the seasonally adjusted time series, such in 1993, 1999 and 2011, supporting previous works indicating that these factors may be modulating the variability of mesozooplankton abundance (Ramírez et al., 2005; Mercado et al., 2005, 2007; Yebra et al., 2017). The seasonal abundance pattern observed in the 2010–2020 decade coincides with the pattern of biomass previously described in the N Alboran Sea (García and Camiñas, 1985; Sampaio de Souza et al., 2005; Mercado et al., 2007). Specifically, Mercado et al. (2007) showed that the seasonal phytoplankton spring bloom and the permanent Chl *a* stock in the area were controlled by mesozooplankton predation. Further, Yebra et al. (2017) observed that the mean Chl *a* concentration during summer 2010 was lower than in previous years, coinciding with very high mesozooplankton biomass and abundance in the region. Also, they showed that the relationship between zooplankton biomass and Chl *a* was the main factor modulating zooplankton production spatial variability in these waters, instead of temperature.

The composition of the communities also varied seasonally, as it has been described in other coastal western Mediterranean areas (Calbet et al., 2001; Ribera d'Alcalà et al., 2004; Bernard et al., 2011; Fullgrabe et al., 2020; Feuilloley et al., 2021). Copepods dominated over the entire annual cycle, but their contribution varied with temperature. During the cold seasons (winter-spring) copepods comprised up to 87% of the community, followed by appendicularians that accounted for up to 13% (19% in summer 2014). However, during the warm seasons (summer-autumn), cladocerans mean contribution increased up to 38% (63% in summer 2012), and doliolids mean summer relative abundance was 22% (47% in summer 2010). This pattern coincides with previous studies in the Alboran Sea (Rodríguez 1979, 1983; Seguin et al., 1994; Sampaio de Souza et al., 2005) and other areas of the W Mediterranean Sea (Ribera d'Alcalà et al., 2004; Fernández de Puelles et al., 2007; Fullgrabe et al., 2020; Feuilloley et al., 2021). In the 1992–2000 period, Sampaio de Souza et al. (2005) observed a clear seasonality of mesozooplankton composition in the Bay of Malaga, with copepods dominating all year; except in summer, when cladocerans took the lead. Similarly, in this work, cladocerans surpassed copepods contribution in the summer of 2011, 2012 and 2020, but also in the autumn of 2014 and 2019 (44–77% of total abundance *vs* $< 36\%$ of copepods). Being cladocerans predominant in warm water conditions, the observed extension of their bloom into autumn might be indicator of sea warming conditions through 2010–2020, delaying the gradual increase in copepods towards the winter.

Mercado et al. (2007) showed that the increased total zooplankton abundance during summer, between 1992 and 2000, was due to the increase in cladocerans. Even though zooplankton was assumed to be controlling the permanent phytoplankton stock in these waters, they proposed that the seasonal pattern of zooplankton might be driven by the phytoplankton abundance. In fact, phytoplankton spring blooms in 1993 and 1999 were followed by high zooplankton abundances (Mercado et al., 2007). We observed that cladocerans abundance correlated with both temperature and Chl *a*; whereas copepods were not related to temperature or Chl *a*. Thus, suggesting that the copepods/cladocerans alternation would be driven by the ability of cladocerans to take better advantage of increased temperature and Chl *a* than copepods.

4.3. Interannual variability

There were significant differences between total mesozooplankton abundance during our study (2010–2020) and the previous time series (1992–2000) in the three zones considered. Further, we observed a significant positive trend from 1992 to 2020 in the total mesozooplankton abundance in the shelf area. This agrees with the previously reported increasing trends for the 1994–2000 period in zooplankton biomass and abundance in the region (Sampaio de Souza et al., 2005). However, in the coastal waters, total mesozooplankton abundance showed a slight, but not significant, decrease from 1992 to 2020. Similarly, in the NW Mediterranean no trends in abundance were observed for the 2004–2019 period, although low zooplankton abundance events in the last decade were suggested to be related to warmer winters (Fullgrabe et al., 2020; Feuilloley et al., 2021).

We are aware that differences between time periods might be due to the different sampling methods. Samplings until the year 2000 were made through oblique tows from the bottom (or max. 100 m) to the surface with a Bongo net (200 µm mesh, 0.40 m diameter); whereas since 2010, samples were collected by means of vertical tows from 3 m distance of the bottom (max. 100 m) to the surface with a double WP2 net (200 µm mesh, 0.58 m diameter). The Bongo net used in the first period presented a smaller sampling surface, although it was towed at a higher speed than the WP2 net of our study. Skjoldal et al. (2013) evaluated the differences between different gears to collect mesozooplankton, showing that the mesh size had a large influence on the biomass and taxonomic composition of the samples. They also found that different systems of vertical, oblique and multiple nets gave similar estimates when the meshes were comparable, and they reported no significant differences between values obtained with Bongo and WP2 nets of similar mesh size. In this sense, in our study we used the same mesh size as in the previous time series; thus we assumed that recorded abundances are comparable. If that is the case, then the observed increases in appendicularians, copepods, gastropods and siphonophores, and the decrease in euphausiids, would not be due to the different sampling protocol but to changes in the environment.

We observed mean sea surface temperature (SST, 0–20 m) increments of 1.1–1.4 °C from 1992 to 2000 to 2010–2020. Further, satellite data from 1982 to 2019 revealed a significant increasing trend in SST for the W Mediterranean Sea, with a warming rate of 0.035 $^{\circ}\mathrm{C}\cdot\mathrm{year}^{-1}$ (Pastor et al., 2020). Previous studies in the Bay of Biscay showed an increase in copepods in 1988–1990, related with increases in SST and sea surface salinity (SSS), attributed to climate change (Villate et al., 1997). Similarly, in the Bay of Malaga, in the 1994–2000 period, there was a significant correlation between the increase of copepods abundance and hydrological parameters (SST and SSS), as well as a positive correlation between cladocerans abundance and SST (Sampaio de Souza et al., 2005). In our study, copepods, appendicularians, and gastropods presented a significant interdecadal increase during the summer season. Also several other taxa presented higher abundances in recent years such as copepod nauplii, siphonophores and doliolids. However, euphausiids abundance was lower than in the 90 s.

Considering that the 2010–2020 decade included nine of the warmest years recorded to date, this could have directly affected the marine ecosystem producing their warming which, jointly with changes in its chemistry, would affect the mesozooplankton communities. In fact, the summer of 2010 was significantly warmer than usual in the region (Yebra et al., 2017). That year, besides high abundances of cladocerans and appendicularians, record numbers of doliolids (avg. 4,500 $\mathrm{ind}\cdot\mathrm{m}^{-3}$) and medusae (avg. 155 $\mathrm{ind}\cdot\mathrm{m}^{-3}$) were found, suggesting that increases of these groups were related to the high SST that year. Comparing the two decades studied, we found that doliolids and siphonophores mean abundances increased significantly. Appendicularians dominated the Chordata during the 1992–2000 period, but in recent years doliolids became the third most abundant group during the warm seasons, together with copepods and cladocerans. Increases in gelatinous plankton driven by overfishing and global warming have also been observed in other areas of the Mediterranean Sea (Bernard et al., 2011; Brotz and Pauly, 2012; Falkenhaug, 2014), having indirect effects on both tourism and trawl fishing (Bernard et al., 2011). In the Alboran Sea, beaching events of siphonophores (Guerrero et al., 2018) as well as extensive mass stranding of salps (El País, 2019) have also been reported in recent years. Further, the abundance of gelatinous organisms was 3-fold higher during the past decade than in the 90s, although the crustaceans/gelatinous ratio did not vary significantly. Opposite to this, we observed that euphausiid abundances decreased a 56–87% with respect to the 1992–2000 period. This might also be driven by the increase in SST, as a decrease of 50% in euphausiids abundance for the N Atlantic ocean has been recently related to warming waters (Edwards et al., 2021). However, the nets used in this study were not designed to efficiently capture macrozooplankton, and the trend observed might be also driven by the patchy distribution and low number of euphausiids collected with these nets. Nevertheless, we would expect that temperate water species inhabiting the N Alboran shelf (such as the copepod *Calanus helgolandicus* and the euphausiid *Nemastocelis megalops,* Vives et al., 1975) will not be able to move northwards in the basin, delimited by the Iberian Peninsula, and migrating to deep waters (below our sampling depths) might be the only option to survive in a warming environment.

Increments observed in mesozooplankton abundance, especially copepods and their nauplii, contrast with the declining trends observed in one of their major predators in the region, the European sardine (*Sardina pilchardus*). In the past two decades, small pelagic fish stocks have been decreasing in the Mediterranean Sea, coupled to their increased exploitation rate (Vasilakopoulos et al., 2014). Among them, sardine is the most abundant species in our study area, which harbours the main sardine nursery site in the Mediterranean Sea (García et al. 1988, García 2010). Nutritional condition and size at capture of adult sardines decline in the NW Mediterranean since 2004 (Brosset et al. 2017), although stock size and abundance ongoing decrease in Alboran started in 2009 (Torres et al., 2021). The larger resilience of the Alboran sardine, compared with other Mediterranean stocks, was suggested to be due to their connection with the Atlantic Ocean (Brosset et al. 2017). However, the Atlantic Iberian stocks are also in a state of low productivity since 2006, likely caused by a combination of fishing pressure and environmental changes (ICES, 2019). In this sense, a bottom-up control of the fish populations was proposed, in which changes in the environment would modify the plankton community, causing the sardine stock decline in the NW Mediterranean (Gulf of Lions; Brosset et al., 2016; Saraux et al., 2019; Feuilloley et al., 2020). Hence, in the Alboran Sea we would expect the decreasing trend observed in sardine stocks to be driven by a decline in their main prey (i.e., copepods and their nauplii; Costalago and Palomera, 2014; Yebra et al., 2019). However, opposite to the sardine decline, mesozooplankton abundance increased significantly from 1992 to 2020. Our data suggest that, instead of a bottom-up control of sardine by zooplankton, the steady decline of sardine would allow for the development of mesozooplankton populations in the shelf during the past decade. This is in agreement with recent works suggesting that sardine can exert a significant top-down control on the mesozooplankton in the W Mediterranean waters (Yebra et al., 2020). Further, Feuilloley et al. (2021) found no changes in the zooplankton community structure related to the small pelagic fish decline in the NW Mediterranean waters; hence, not supporting the hypothesis of a bottom-up control of zooplankton over fish stocks. Moreover, simultaneous declines of top predators and forage fish biomass and increasing trends in the abundance of lower trophic levels have been described for the NW Mediterranean and Adriatic Seas, driven by changes in primary productivity and excessive fishing pressure (Piroddi et al., 2017). In the Alboran Sea, we suggest the combination of both physical (increasing temperature) and trophic variables (predator pressure decline) as main drivers of the changes observed in the mesozooplankton populations.

5. Conclusions

This first assessment of interdecadal variations (1992–2000 and 2010–2020) in the abundance and composition of the mesozooplankton within the SW Mediterranean Sea revealed differentiated spatial, seasonal and interannual changes in the structure of their communities. Our work highlights that a combination of multiple drivers, hydrographic and trophic, could modulate the mesozooplankton variability in the region. Further, the high hydrodynamics in the Alboran basin, with recurrent upwellings of nutrient-rich cold Mediterranean waters, may act as a buffer of global environmental changes, like ocean warming. This might allow the species in the region to become resilient and/or adapt better than in other regions of the Mediterranean Sea. The lack of data for certain periods precluded the finding of strong significant temporal trends, highlighting the importance of continuity in zooplankton time series. The shifts and linkages depicted in our study need to be further monitored through concomitant time series surveys of plankton and small pelagic fishes in order to understand and predict the consequences that climate change and human activities may have on the long term for the pelagic ecosystem and the services it sustains in the region, such as artisanal fisheries and tourism.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2022.102782.

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