

Article

Decadal Trends in the Zooplankton Community of the Western Mediterranean

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Abstract: Decadal trends in the zooplankton community were seasonally investigated in multiple monitoring transects of the western Mediterranean Sea during a period of increasing and record-high water temperatures. The transition area around the Balearic archipelago can be separated into two regions: the Alborán Sea and the Balearic Sea. Differences were found in the abundance and structure of the dominant zooplankton groups: the cladocerans and copepods. The highest zooplankton abundances were found during the stratified summer season, when cladoceran numbers peaked. However, copepods were more abundant during the winter. A marked seasonality was found in all groups and the dominant taxa: 114 species of copepods and 5 species of cladocerans were identified, but less than 8 species of copepods and 2 species of cladocerans dominated the populations. During the 2007–2017 study, warm and salty waters were observed in the Balearic Sea. In the Alborán Sea, cool and fresh waters were observed, along with a decline in chlorophyll. Irregular group and species trends were observed in both regions, exhibiting both increases and decreases depending on region and season. Trends differed, often oppositely, for the Alborán versus the Balearic Sea, with the transition region between them mirroring one or the other, switching with the seasons. The most dominant species, including *Penilia avirostris* and *Clausocalanus arcuicornis*, but also *Evadne spinifera*, *C. lividus*, *C. furcatus*, *Paracalanus parvus*, *Acartia clausi*, *Centropages typicus*, *Subeucalanus monachus*, and *Calanus helgolandicus*, are proposed as biological tracers to be used in further studies on climate and zooplankton community changes in the western Mediterranean Sea.



Citation: Fernandez de Puelles, M.L.; Gazá, M.; Cabanellas-Reboredo, M.; O'Brien, T.D. Decadal Trends in the Zooplankton Community of the Western Mediterranean. *Water* **2023**, *15*, 4267. <https://doi.org/10.3390/w15244267>

Academic Editor: Ryszard Gołdyn

Received: 29 September 2023

Revised: 25 November 2023

Accepted: 27 November 2023

Published: 13 December 2023



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Keywords: spatio-temporal zooplankton variability; decadal zooplankton changes; copepods; cladocerans; western Mediterranean Sea; climate change tracers

1. Introduction

The Mediterranean Sea (MS) is the largest semi-enclosed sea, composed of both western and eastern basins, each with different characteristics, and when combined, it represents 1% of the total surface area of the global oceans [1]. Over most of the MS, annual evaporation exceeds rainfall and river run-off, leading to high salinity [2]. The complex coastline and bathymetry lead to a high environmental diversity at regional and local scales. Hence, the MS is considered one of the most complex marine environments and is influenced and impacted by the pressures of tourism, agriculture, and industrial sectors from the surrounding continents. The MS is characterized by a strong eastward declining gradient in nutrients and primary production, while any trends and gradients in zooplankton abundance and distribution that may be present are still unclear and are often heavily regionalized [3–5].

Located at a boundary area between the temperate and subtropical zones of the northern hemisphere (30–45° N), the MS is highly vulnerable and exposed to all of the major processes acting upon the global climate system, which makes it a hot spot for analyzing the impacts of climate change. The western basin (western Mediterranean Sea; WMS)

has experienced significant change over time [6], displaying deep water mass formation and a high stratification trend that can greatly affect the zooplankton community [7]. In the eastern basin, the increased evaporation rate and the surface production are linked to the lower amount of stratification, and no great changes have been seen regarding zooplankton [8]. The WMS is also a direct and continuous source of warm and salty waters into the North Atlantic area, playing a substantial role in the heat content and water formation processes that drive the circulation of the world's oceans. For these reasons, understanding WMS temporal variability itself [9], and especially how it affects planktonic communities, the sentinels of the pelagic marine ecosystem [10], is of local and global importance.

While the WMS is generally considered oligotrophic, there are several exceptions of high productivity in coastal areas, mainly due to the influence of river discharges. High productivity is also located in deep zones, such as the Gulf of Leon and the Alborán Sea, where deep convection processes and strong mesoscale structures favor upwelling events. All these events inject nutrients into the upper waters, which help sustain large fisheries and marine mammal communities [11,12].

Surface circulation in the WMS is highly complex and usually follows a cyclonic pattern that involves both cool and salty waters from the northeastern Balearic Sea region and warmer and less saline waters from the southwestern Alborán Sea region [13,14]. In this latter area, the surface circulation is mainly driven by an inflow of Atlantic water through the Strait of Gibraltar and the subsequent thermohaline circulation, with the temperature and salinity signature of these waters changing as they travel eastward [15]. Current flow along the African coast can also reach the Balearic Islands via eddies detaching from the main current. These currents, fronts, and eddies can affect the nutrient supply to the photic layer, producing a remarkable spatial and temporal heterogeneity in an otherwise highly oligotrophic sea [10]. Strong winds can also enable deep water convection, the mixing of the water column, and the injection of nutrients into the photic layer [16]. In the Balearic Sea region, productivity is mainly dominated by a winter–spring bloom [17], while in the Alborán Sea region, production is more associated with upwelling events that are much weaker and often localized to specific regions. Productivity in the Alborán Sea is also influenced by the inflow of Atlantic waters throughout Gibraltar [17,18].

In the transition area between the Alborán and Balearic seas, complex interactions occur around the channels of the Balearic Islands, controlling meridional mass transport, fluxes, and seasonal exchange between the two seas [14] and affecting the distribution of species between their respective zooplankton populations [19]. The exchange and dominance of water currents in the region vary interannually and seasonally [20,21]. Severe winters are associated with an increasing inflow of Balearic Sea waters, whereas milder winters result in a higher northward flow of Alborán and Atlantic waters [22,23].

Long-term climate change plays a key role in the dynamics of marine ecosystems by directly and indirectly affecting ecosystem functioning over a wide range of temporal and spatial scales. How warming and marine heat waves affect productivity in marine ecosystems is a pressing concern and a central question of ongoing research in marine sciences. Growing evidence shows that changes in marine ecosystems can be tracked according to the variability of zooplankton organisms, whose pivotal roles in food webs and non-linear responses make them valuable sentinels of climate-driven ecosystem changes [24–28]. Including zooplankton in oceanographic monitoring is a priority in many international scientific programs [29–31], where comparative studies of zooplankton changes over time have been widely recommended [32–35]. Due to the expertise and time needed for taxonomic identification, however, very few long-term series with a detailed zooplankton community composition exist. While several longer-running, single-location (fixed) monitoring stations exist [5,36,37], they do not cover extensive area of the WMS or cross biogeographic sub-areas [38].

The goal of this study was to analyze variability in the biomass, abundance, and composition of the zooplankton community, examining dominant species and major groups, across an extensive area of the WMS. These changes would be further correlated with

changes observed in the environmental sea (i.e., temperature, salinity, wind, and chlorophyll), looking for significant community changes linked to climate variables and searching for zooplankton species or groups that can act as tracers or indicators for future monitoring.

2. Materials and Methods

2.1. Recording Data: Zooplankton Sampling Procedure and Environmental Data

From 2007 to 2017, zooplankton samples were collected seasonally during 36 oceanographic cruises at 23 sampling stations along 11 transects across the WMS (Table 1, Figure 1). In the western-most Alborán Sea sub-area, five transects were sampled (Pino Cape, Málaga, Vélez, Sacratif, and Gata Cape). In the northeastern Balearic Sea sub-area, three transects were sampled (Tarragona, Barcelona, and Menorca). And in the transition between these sub-areas, three additional transects were included (Palos Cape, Ibiza Channel, and Balears). Due to ocean currents and geography, the transition transects vary with different seasons and different parameters, sometimes synchronizing with the Alborán Sea transects and sometimes with the Balears Sea transects. The classification of inshore/offshore was assigned to each station, based on bottom depths of <200 m or >200 m at each location.

Table 1. Summary of the different transect stations, assigned sub-regions, geographic coordinates, and bottom depths. Transect ordering is from southwest (Alborán Sea) to northeast (Balearic Sea).

Sub-Region	Transect	Station	Latitude	Longitude	Depth (m)	Shore
Alborán Sea	Pino Cape	P2	4°44'50'' W	36°25'43'' N	130	inshore
		P4	4°44'50'' W	36°15'00'' N	870	offshore
	Málaga	M2	4°21'22'' W	36°38'32'' N	75	inshore
		M4	4°15'83'' W	36°32'54'' N	350	offshore
	Vélez	V2	4°03'85'' W	36°41'25'' N	75	inshore
		V4	4°03'90'' W	36°34'20'' N	490	offshore
	Sacratif	S2	3°28'09'' W	36°39'35'' N	300	offshore
		S4	3°28'09'' W	36°34'61'' N	650	offshore
	Gata Cape	CG2	2°09'91'' W	36°40'65'' N	75	inshore
		CG4	2°09'91'' W	36°29'83'' N	700	offshore
Transition	Palos Cape	CP2	0°45'45'' W	37°29'79'' N	75	inshore
		CP4	0°45'45'' W	37°22'37'' N	2100	offshore
	Ibiza Channel	20	0°14'60'' E	38°52'20'' N	95	inshore
		18	0°27'00'' E	38°52'20'' N	300	offshore
	Balears	B1	2°25'60'' E	39°28'60'' N	75	inshore
		B2	2°25'60'' E	39°24'10'' N	100	inshore
Balearic Sea	Menorca	MH2	4°25'00'' E	39°57'00'' N	180	inshore
		MH4	4°34'96'' E	40°10'00'' N	2500	offshore
	Tarragona	T2	1°03'88'' E	40°28'77'' N	75	inshore
		T4	1°26'00'' E	40°25'90'' N	950	offshore
	Barcelona	BNA2	2°18'13'' E	41°15'00'' N	295	offshore
		BNA4	2°31'17'' E	41°05'00'' N	1320	offshore

Zooplankton samples were seasonally collected (11 in February/March, 9 in April/May, 7 in June/July, 9 in October/November), with a total of 653 zooplankton samples across the Iberian WMS. A Bongo plankton net fitted with 250 µm mesh, and a General Oceanic flowmeter, were used for oblique tows in the top 100 m water layer. Net hauls were consistently carried out during the day to minimize variability associated with diel vertical migration. Each sample was divided into two aliquots, one to determine the total sample biomass and the other to analyze the taxonomic composition of the zooplankton community. The net sample used for taxonomic studies was preserved in 4% formaldehyde. For the zooplankton biomass estimation, we used traditional dry mass measuring methods [39], drying the sample to 60 °C for 24–48 h, with values given in mg of dry mass (DM), and later to 500 °C to calculate the

ash-free dry mass (AFDM) per m^3 of water sampled. These methods are the same protocol used at the Balearic station with a 13-year monitoring started in 1994 [22,40].

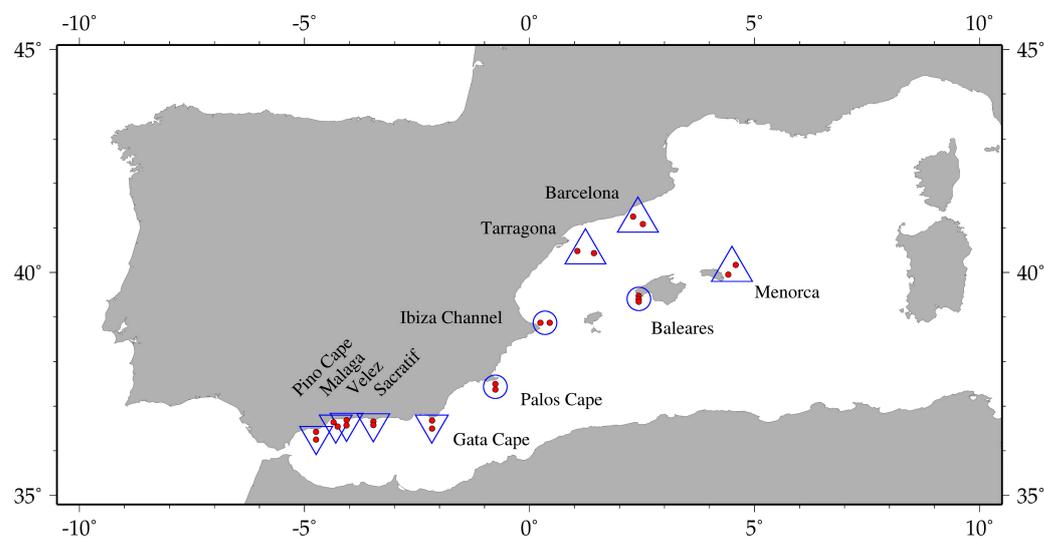


Figure 1. Map of the western Mediterranean Sea, showing locations and names of the eleven zooplankton transects (blue-outlined symbols) and locations of the within-transect sampling stations (red dots). Downward-pointing blue triangles identify transects in the Alborán Sea region, upward-pointing blue triangles identify transects in the Balearic Sea region, and blue circles identify transects in the transition region.

In the laboratory, a Folsom plankton splitter was used to divide the sample for microscope-based taxonomic identification and enumeration. Usually, two aliquots were counted, representing the organism abundance. In each sample, at least 500 ind. m^{-3} was counted. All zooplankton groups were identified and standardized to ind. m^{-3} . Adults of copepods and cladocerans were further identified to the species level, while juveniles were identified to the genus, following the most common taxonomic bibliography [41–45]. During the initial years, 2007–2008, identification was only performed on major zooplankton groups (not to species or genera).

Across the 11 transects, co-sampled *in situ* water temperature, salinity, and chlorophyll data were not always available. To provide uniform and consistently sampled environmental data for each transect, corresponding data were extracted from satellite and global datasets as per the methods of [46–48]. Data of monthly averages by year were extracted for the 2007–2017 period, matching the zooplankton samples' month, year, and locations. Sea surface temperature (SST) was extracted from the NOAA OI-SST [49] and the Hadley HadISST [50] datasets [50], chlorophyll was extracted from the ESA OC-CCI v5.0 ocean color dataset [51], sub-surface salinity was extracted from the Hadley EN4 dataset [52], and scalar wind speed was extracted from the ICOADS wind dataset [53].

These environmental datasets were also used to investigate trends and conditions before the 2007–2017 study period. For example, the satellite chlorophyll data go back to 1998, the wind and salinity data go back to 1960s, and the HadISST temperature data go back to the 1900s. These data were used to generate long-term environmental state and trend figures across the WMS study areas.

2.2. Statistical Analyses

The monthly zooplankton data were paired according to their targeted sampling season: February/March data were averaged into a single winter time period, April/May were averaged into a spring time period, June/July data were averaged into a summer time period, and October/November data were averaged into autumn time period. Based on the knowledge of local currents/geography, three sub-regions were distinguished: Alborán Sea, transition region, and Balearic Sea, with the stations mentioned above. The data from

the eleven individual-transect time series were also spatially averaged into three regional time series (see Table 1 and Figure 1).

For each abundance time series, an additional relative abundance index was also calculated. This index represents a taxa group's relative contribution to the total zooplankton population, which can highlight subtle changes in the zooplankton community structure. For example, if total copepods and total zooplankton were both decreasing over time, but the total zooplankton were decreasing at a faster rate, the total copepod percentage of total zooplankton would actually be increasing over time. This increase in relative contribution would not be readily obvious if only looking at the two decreasing abundances.

The transects, sub-areas, or regions were analyzed using seasonal and annual difference anomalies, using the methods of [54]. Similar to the method of [24], each year's annual anomaly was calculated from the average of all that year's monthly anomalies. This method removes the seasonal bias and is fairly robust to missing data. The O'Brien and Oakes method does not log-transform the data, preserving the original units but requiring nonparametric statistics [54].

The hundreds of results from the eleven transects, three main regions, four seasons (plus the annual average), and thirty zooplankton variables were visualized using standardized figure sets that included seasonal cycle plots, colored-coded heat tables, and box-n-whisker plots (Figure 2). The Supplemental Data contains the full collection of all figures, tables, and variables (SA, SB, SC, SD, and SE). While portions of these figures may overlap with each other in their displayed content, each set also uniquely presents information on statistical trends, spatio-temporal distribution, and average values. Within the body of this paper, only select variables and figures are included.

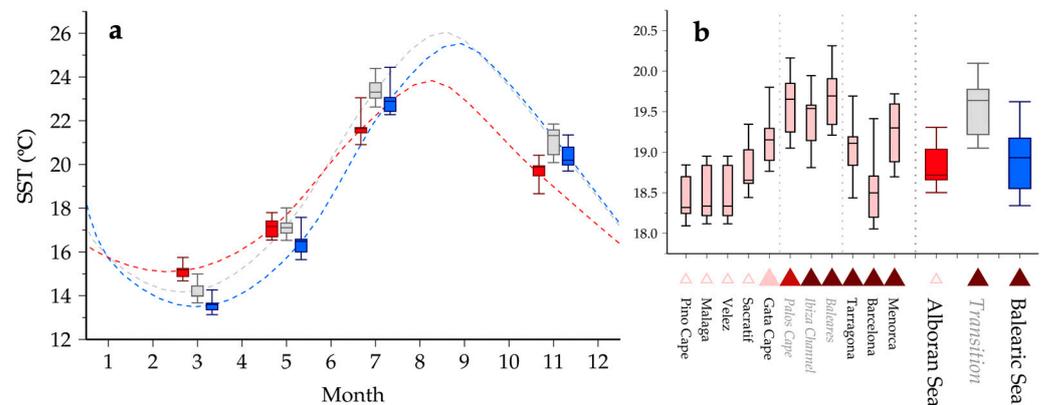


Figure 2. Sea surface temperature (°C) averages and trends across the western Mediterranean Sea transects and regions (red color, Alborán Sea; blue color, Balearic Sea; and in grey, transition region) including (a) average seasonal cycles of temperature in each region and (b) annual averages and trends of temperature in each transect and region. Upward-pointing triangles (b) indicate increasing temperatures in that transect or region, with the size and shading of the triangle indicating the statistical significance of the trend (e.g., darkest shading indicates $p < 0.01$, lightest shading indicate marginally or non-significant trends). A comprehensive overview of all temperature trends and patterns is available in Supplemental file A Table S01.

The significance level of a statistical trend test is influenced by the length of the time series (n), the magnitude of the trend, and the magnitude of variance in the measured variable [54,55]. A weak trend is more likely to be detected (e.g., have $p < 0.05$) in low-variance physical data (e.g., temperature or salinity) than in higher-variance biological data (e.g., zooplankton counts or biomass), especially in relatively short time series. Trends in the higher-variance biological variables often need to have a stronger trend or a longer length of time series for statistical significance. While not finding a significant trend ($p < 0.05$) can mean there is indeed no trend present, it can also mean that insufficient data were available to illuminate an existing trend [56,57]. While this was an 11-year study, occasional gaps (e.g., missed months of

sampling in some years) reduced some seasons and transects, leaving us with as few as only seven years present. To address the challenge of analyzing these shorter time series of higher-variable biological data, we are also reporting marginally significant trends ($p < 0.10$) in the summary tables and figures. This additional information is intended to highlight spatio-temporal cohesion within and across transects and variables, even when the trends are not traditionally ($p < 0.05$) significant.

For each variable, a seasonal cycle plot (e.g., Supplementary file A Table S01a) shows the averaged value ranges for each region and season. Since the environmental variables (e.g., temperatures, salinity, wind, chlorophyll) all have 12-month sampling resolution, their seasonal cycle plots also include dashed lines that represent the median monthly values that fall outside of the four zooplankton sampling seasons.

The 2007–2017 trends for each transect and seasons are visualized in a colored heat table format, where the strength and direction of the trend are indicated with both text and background cell coloration (e.g., supplementary file A Table S01b). Eleven-year trends at each transect and region are also shown (supplementary file A Table S01c,d). Different environmental variables and zooplankton groups are presented in supplementary file A Tables S01–S26. To test for interannual increases or decreases in variables at a given transect or region, the nonparametric Mann–Kendall test was run to test for monotonic trends [58–60]. To assess relationships between the environmental and zooplankton variables, Spearman's rank correlation was used [57]. This non-parametric correlation coefficient test was used for monotonic relationships in which two variables may move in the same (or opposite) direction but not necessarily at a constant (linear) rate.

Redundancy analysis (RDA; [61]) was used to test for potential effects of sampling station peculiarities (inshore/offshore and seasons; all as categorical variables) on the main zooplankton groups and dominant copepod ($n = 23$) and cladoceran ($n = 2$) species (contributing $\geq 2\%$ of the total abundance). The potential variance conferred by each sampling station was controlled including stations as condition factors. The significant effect of each co-variable was assessed using the permutation procedure implemented in the ANOVA function. With the same statistical procedure and in order to test spatial differences among this plankton community, a second RDA was performed including season (as the only significant co-variable; see below Results section) and the three regions as categorical variables. In that case, in order to avoid collinearity with co-variables, it was not possible to include "stations" as a condition factor. RDAs were completed using the RDA function of the R software package version 2.2.1 [62].

3. Results

3.1. Sea Surface Temperature

Sea surface temperature (SST) across the three WMS survey regions (Balearic Sea, Alborán Sea, and transition) ranged from 13 to 26 °C (Figure 2a) with the maximum in late summer and the minimum in winter. Seasonally, two main modes were observed, the warmer and stratified waters in summer and autumn and then colder mixed waters in winter and spring. The largest minimum-to-maximum seasonal water temperature ranges were found in the Balearic Sea and transition regions, while the Alborán Sea had a smaller seasonal range, with temperatures ~ 2 °C warmer in the winter (and ~ 2 °C cooler in the summer).

During the eleven-year study-period, there were significant warming trends ($p < 0.01$) in the annual average SST in all of the transition and Balearic Sea transects (Figure 2b, see also supplementary file A Table S01). Seasonally, this warming was most evident in the Balearic Sea in summer and in both the Balearic Sea and transition areas in autumn. While significant annual trends were not present in the Alborán Sea, marginally significant warming trends were present throughout all of the Alborán Sea during the spring transects, as well as in many of the summer transects (see supplementary file A Table S01).

The long-term environmental plot for SST across the combined WMS areas (Figure 3a) shows the 2007–2017 warming trends are part of a 50+-year warming trend that started in the early 1970s. During the 11-year survey period (light blue box outlined in Figure 3a),

many of the annual average temperatures were at or above the highest temperature values seen in the previous century (e.g., 1900–1999), with annual values that were 0.3–1.1 °C above the 1900–2020 long-term average.

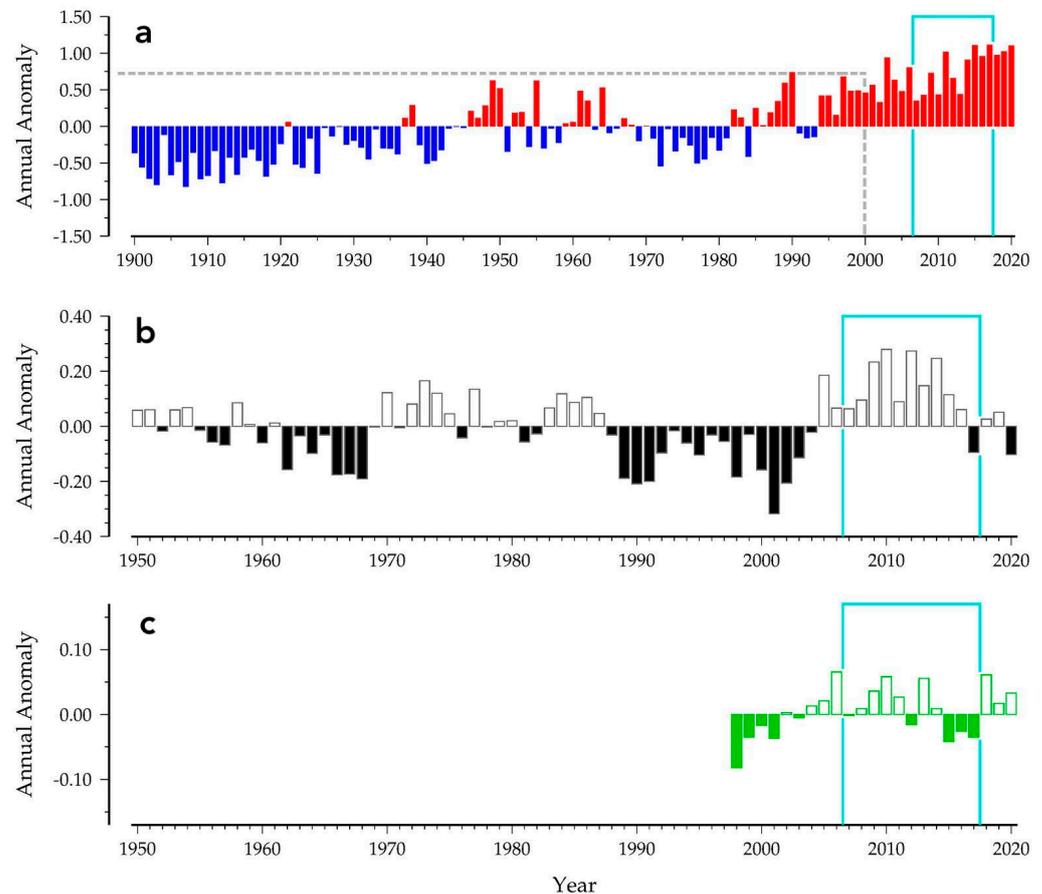


Figure 3. Long-term anomaly plots of (a) sea surface temperature (SST, °C, 1900–2020), (b) surface salinity (SSS, PSU, 1950–2020), and (c) satellite chlorophyll (CHL, mg/m³, 1998–2020), from the western Mediterranean Sea study area. In each subfigure, the 2007–2017 zooplankton survey period is indicated with a light blue box. The anomaly columns represent differences above or below the long-term average for each variable. Bar columns in red and blue show positive and negative temperature anomalies; white and black are positive and negative salinity anomalies; and white and green are positive and negative chlorophyll anomalies. The gray dashed line in the SST subfigure (a) indicates the highest temperature observed in the 100-year (1900–1999) period prior to 2000. Comprehensive overviews of all SST, SSS, and CHL trends and patterns are available in supplementary file A Tables S01, S02 and S04.

3.2. Sea Surface Salinity

Sea surface salinity (SSS) in the three regions during the 11 years was slightly higher in winter and often lowest in summer or autumn (Figure 4a). The SSS ranged from 36.82 in the stations closer to the Gibraltar Strait to 38.00 offshore of Barcelona. During the 2007–2017 study period, annual average salinity was significantly decreasing ($p < 0.05$) in most of the Alborán Sea transects (Figure 4b, see also supplementary file A Table S02). The summer and autumn decreases were also evident in some of the western-most transition transects, but no salinity trends were found in any of the Balearic Sea transects. A long-term SSS anomaly (Figure 3b) suggests these decreases are a reversal from generally higher salinities that occurred from 2005 to 2015. Salinities during the 2007–2017 survey periods were ~0.2 higher than the 1950–2020 long-term average, and they were frequently higher than salinities seen in the previous 1950–2000 period.

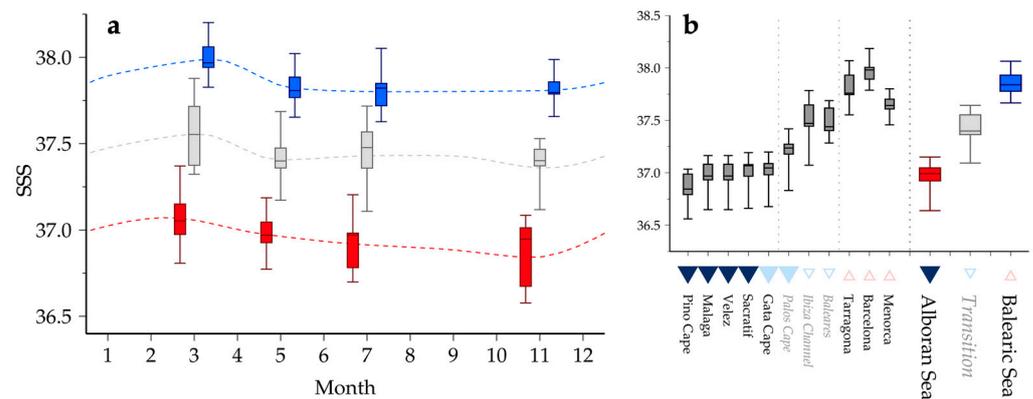


Figure 4. Sea surface salinity (unitless) averages and trends across the western Mediterranean Sea transects and regions (red color, Alborán Sea; blue color, Balearic Sea; and in grey, transition region), including (a) average seasonal cycles of salinity in each region and (b) annual averages and trends of salinity in each transect and region. Downward-pointing triangles (b) indicate decreasing salinities in that transect or region, with the size and shading of the triangle indicating statistical significance of the trend (e.g., darkest shading indicates $p < 0.01$, lightest shading indicate marginally or non-significant trends). On the contrary, upward-pointing triangles indicate increasing salinities in each transect and region. A comprehensive overview of all salinity trends and patterns is available in supplementary file A Table S02.

3.3. Scalar Surface Winds

Scalar surface winds (SSW, $m s^{-1}$) across the WMS survey areas ranged from 5 to $9.5 m s^{-1}$ (Figure 5a), with winds in the Alborán Sea consistently stronger than those in the transition and Balearic Sea for all seasons except autumn. Seasonally, the highest winds were present in winter and the lowest winds were found in summer.

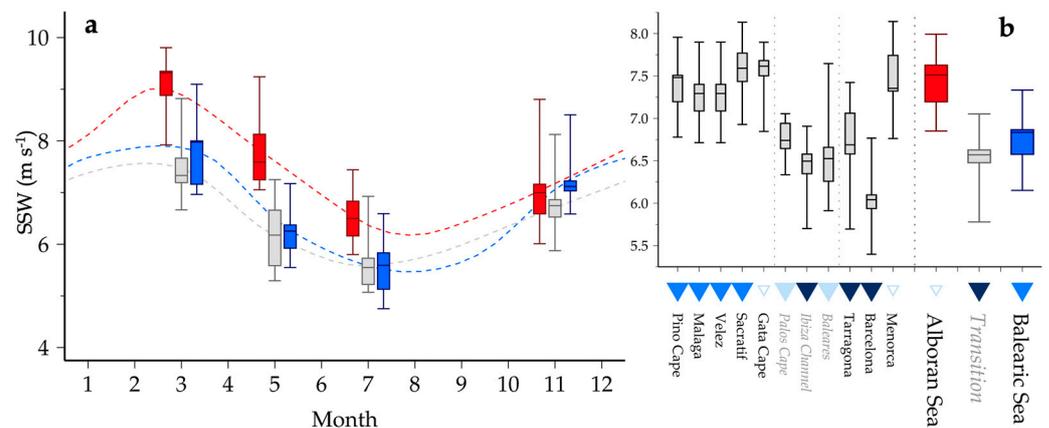


Figure 5. Scalar surface wind ($m s^{-1}$) averages and trends across the western Mediterranean Sea transects and regions (red color, Alborán Sea; blue color, Balearic Sea; and in grey, transition region), including (a) average seasonal cycles of wind in each region and (b) annual averages and trends of wind in each transect and region. Downward-pointing triangles (b) indicate decreasing winds in that transect or region, with the size and shading of the triangle indicating statistical significance of the trend (e.g., darkest shading indicates $p < 0.01$, lightest shading indicate marginally or non-significant trends). A comprehensive overview of all wind trends and patterns is available in supplementary file A Table S03.

During the 2007–2017 study period, annual average SSW was significantly decreasing across most transects and areas (Figure 5b, see also supplementary file A Table S03). Seasonally, the strongest wind changes in the Alborán Sea occurred in spring and summer, while in the

Balearic Sea, changes were mainly found in spring and autumn. In the transition area, however, changes were only present in autumn (supplementary file A Table S03).

Long-term correlations between wind and SST showed a significant negative correlation in all five transects of the Alborán Sea during the autumn season (see supplementary file B Table S01), but not in any of the other regions. These Alborán Sea transects were the only WMS transects not experiencing significant warming in any season (Section 2.1).

3.4. Satellite Chlorophyll

Satellite-estimated chlorophyll concentration (CHL, mg m^{-3}), as a proxy for primary producers, was relatively low in the WMS, with the highest values found in the Alborán Sea (Figure 6a), especially due to the values recorded in the Malaga and Velez transects (Figure 6b). Seasonally, chlorophyll concentrations were highest in the winter and lowest in the summer (Figure 6a). Across all seasons, Alborán Sea chlorophyll concentrations were 50–100% higher than those in the other sub-regions, with the lowest values found in the Balearic Sea transects.

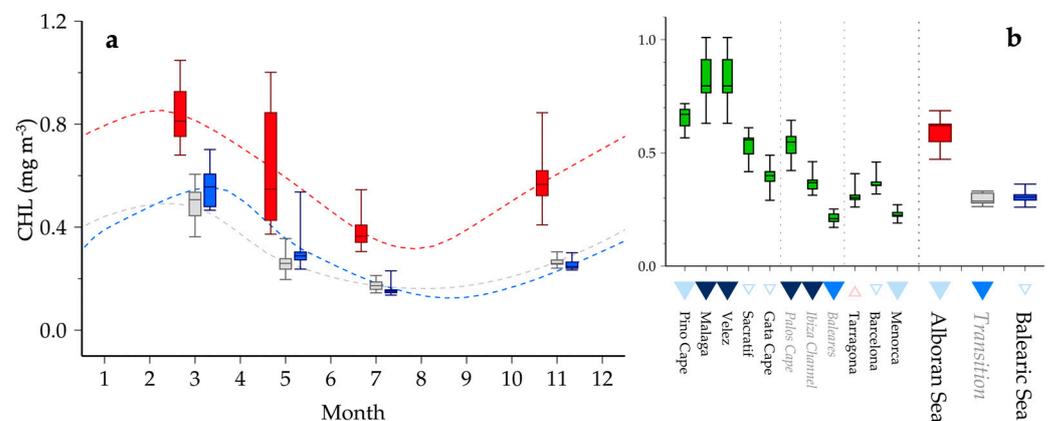


Figure 6. Satellite chlorophyll (mg m^{-3}) averages and trends across the western Mediterranean Sea transects and regions (red color, Alborán Sea; blue color, Balearic Sea; and in grey, transition region), including (a) average seasonal cycles of chlorophyll in each region and (b) annual averages and trends of chlorophyll in each transect and region. Downward-pointing triangles (b) indicate decreasing chlorophyll in that transect or region, with the size and shading of the triangle indicating statistical significance of the trend (e.g., darkest shading indicates $p < 0.01$, lightest shading indicate marginally or non-significant trends). On the contrary, upward-pointing triangles indicate increasing chlorophyll in each transect and region. A comprehensive overview of all chlorophyll trends and patterns is available in supplementary file A Table S04.

Many transects and regions experienced a decrease in chlorophyll during the 2007–2017 period (Figures 3b and 6b, see also supplementary file A Table S04). The strongest decreases ($p < 0.01$) were observed at Malaga, Velez, and across the transition region (Figure 6b). The available long-term satellite data were the shortest (1998–2020) of all the environmental variables used in this study (Figure 3c). The shape of the available chlorophyll data suggested a possible cyclical pattern, during which 2007–2017 fell within a decreasing phase.

Long-term correlations between chlorophyll and the other environmental variables showed mixed results. Multiple strong negative correlations existed between chlorophyll and SST, in almost every transect and region, but they varied by season and location (see Supplemental Materials supplementary file B Table S02). In the Alborán Sea, significant correlations were found in almost every transect, but only present in the spring ($p < 0.01$) and autumn ($p < 0.05$), and strong enough to influence the annual average relationships. In contrast, the transition transects had significant correlations in the winter, spring, and summer, but not in autumn. In the Balearic Sea, the summer had the more significant correlations.

Correlations between chlorophyll and wind had a few strong relationships in the transects in/near the transition region, but only during autumn (See supplementary file B Table S03).

There were no significant correlations between chlorophyll and salinity in any season or transect.

3.5. Zooplankton Biomass and Abundance

Zooplankton biomass ranged from 2 to 17 mg m⁻³ dry mass (DM, Figure 7a) and from 1.4 to 10 mg m⁻³ ash-free dry mass (AFDM, supplementary file A Table S05). Considerable spatial and temporal variability was seen among the transects, most often due to high biomass values from abundant salps, particularly in late winter, while the lowest values were observed in summer and autumn. Zooplankton biomass was generally decreasing from west to east, with higher values (> 10 mg/m³ DM) in the western Alborán Sea and lower values (< 5 mg/m³ DM) in the eastern Balearic Sea (Figure 7b; supplementary file A Table S06).

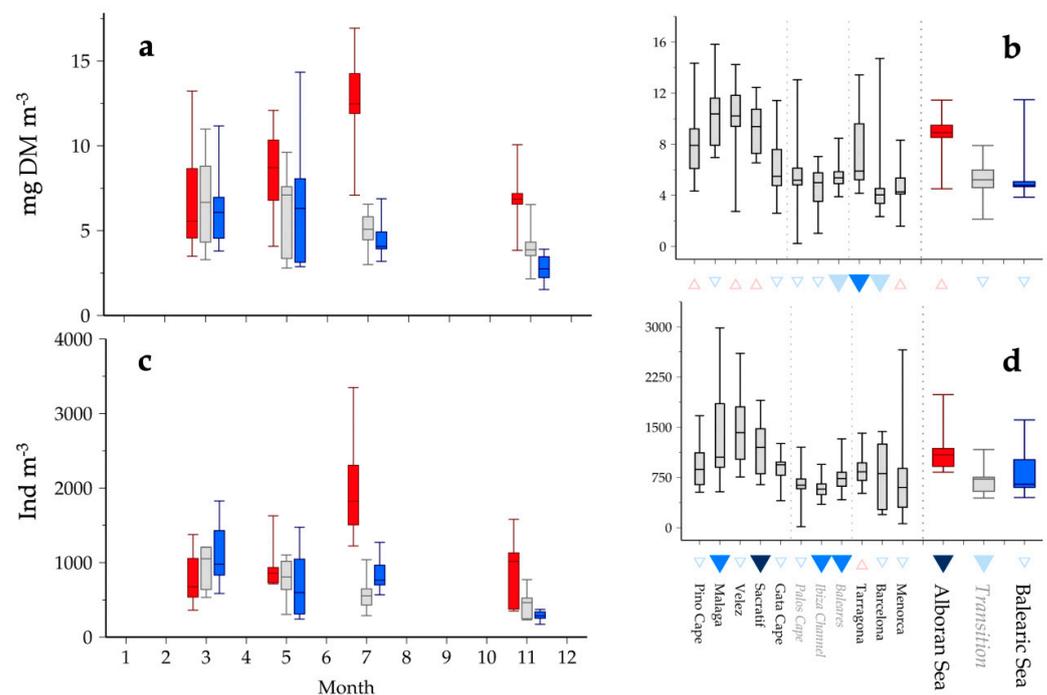


Figure 7. Zooplankton biomass (dry mass, mg m⁻³) and abundance (individuals m⁻³) averages and trends across the western Mediterranean Sea transects and regions (red box color, Alborán Sea; blue color, Balearic Sea; and in grey, transition region), including (a,c) average seasonal cycles in each region and (b,d) annual averages and trends in each transect and region. Downward-pointing triangles (b,d) indicate decreasing biomass or abundance in that transect or region, with the size and shading of the triangle indicating statistical significance of the trend (e.g., darkest shading indicates $p < 0.01$, lightest shading indicate marginally or non-significant trends). On the contrary, upward-pointing triangles indicate increasing chlorophyll in each transect and region. A comprehensive overview of zooplankton abundance and biomass trends and patterns is available in supplementary file A Tables S05–S08 and includes additional variables not shown here (e.g., ash-free dry mass).

During the 2007–2017 period, there were no clear trends in either the DM or AFDM (Figure 7b, supplementary file A Tables S05 and S06). Curiously, from 2007 to 2017, the ratio of AFDM to DM was significantly decreasing over time ($p < 0.05$) in many of the Alborán Sea and transition transects (supplementary file A Table S07). A decreasing AFDM-to-DM ratio could indicate a decrease in crustacean biomass relative to other lower-ash organisms such as gelatinous zooplankton, phytoplankton, or mucilage.

Zooplankton abundance had a similar seasonal cycle to that of the biomass (Figure 7c), and it was also generally decreasing from west to east (Figure 7d), with higher values in the Alborán Sea and lower values in the Balearic Sea. During the 2007–2017 study

period, decreasing abundance trends were present in many areas of the Alborán Sea and the transition region, both annually and also during spring, summer, and autumn seasons (Figure 7d and supplementary file A Table S08), while no significant trends were present in the Balearic Sea transects.

3.6. Dominant Zooplankton Groups

While 24 major zooplankton groups were identified and counted in the studied zooplankton samples (14 holoplankton and 10 meroplankton), only 12 of these groups regularly represented more than 2% of the total zooplankton abundance (Figure 8 and Table 2). Eleven holoplankton groups and one meroplankton larvae group were included in the analysis, with the remaining group counts summed into the “other meroplankton” or “other zooplankton” category (Table 2, Figure 8).

Copepods were easily the dominant zooplankton group in all transects and seasons (Table 2, first row), with an annual average contribution of 50–65% of the total zooplankton, and seasonal peaks reaching over 80% in winter. Cladocerans were the frequently the second most dominant group, especially in summer, reaching 22–27% of the total zooplankton (Table 2, second row). In the non-summer seasons, appendicularians frequently outnumbered the cladocerans (Table 2, fifth row). The remaining holo- and mero-plankton groups generally contributed less than 6% each to the total zooplankton, although summer/autumn peaks could reach slightly higher values (e.g., summer doliolids of 14% in the Alborán Sea, Table 2).

The following section presents the trends and patterns of the dominant zooplankton groups (copepods, cladocerans, appendicularians, doliolids, siphonophores, chaetognaths, ostracods, and pteropods). A full summary of all groups and seasonal patterns is available in supplementary file A Tables S11–S26).

Annual-average Relative Abundance

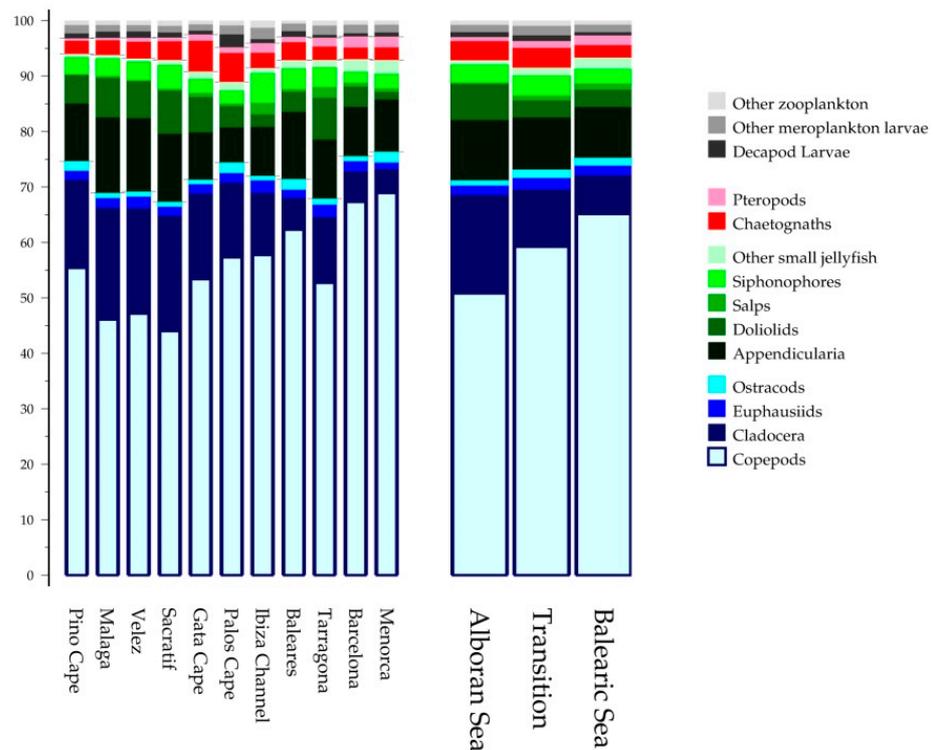


Figure 8. Annual average relative contributions (%) of major zooplankton groups to total abundance at each transect (11 left columns) and in the three regions (right columns). Seasonal contributions are shown in Table 2.

Table 2. Annual and seasonal percentages of total zooplankton abundances for the major taxonomic groups in the three WMS regions (AS = Alborán Sea, Tr = transition, BS = Balearic Sea) during the 2007–2017 period. Red text indicates the most numerically dominant group in each region and season. Blue text indicates the second most dominant group. Seasonal maximums are listed in the far-right column.

	Annual Average			Winter Average			Spring Average			Summer Average			Autumn Average			Seasonal Maximum		
	AS	Tr	BS	AS	Tr	BS												
Copepods	50.8	59.2	65.1	65.7	75.7	83.0	54.5	59.0	68.3	27.4	40.7	41.9	47.0	58.1	66.2	65.7	75.7	83.0
Cladocerans	17.7	10.3	7.0	5.1	1.1	0.3	4.8	5.3	3.1	35.8	24.0	21.9	26.7	9.3	3.1	35.8	24.0	21.9
Euphausiids	1.7	2.1	1.7	3.1	1.9	2.8	2.4	2.8	1.8	0.5	1.9	1.1	1.3	0.9	0.6	3.1	2.8	2.8
Ostracods	0.9	1.5	1.4	1.3	1.8	0.7	0.8	0.8	1.1	0.4	0.8	0.8	1.5	3.0	3.2	1.5	3.0	3.2
Appendicularians	10.9	9.4	9.2	11.6	8.4	7.9	15.8	12.3	10.8	11.5	10.0	9.8	7.5	9.4	9.2	15.8	12.3	10.8
Doliolids	6.5	3.1	3.1	3.1	1.9	0.2	7.3	2.4	0.5	14.3	4.2	9.7	2.1	3.8	2.9	14.3	4.2	9.7
Salps	0.3	0.9	1.1	0.8	2.2	1.4	0.4	1.7	1.3	0.2	0.1	0.1	0.1	0.3	0.4	0.8	2.2	1.4
Siphonophores	3.2	3.7	2.7	2.9	2.5	1.3	6.2	7.0	3.7	2.3	3.8	3.9	2.2	2.3	2.0	6.2	7.0	3.9
Small jellyfish	0.8	1.4	2.0	0.4	0.5	0.3	1.3	3.0	4.0	0.6	1.5	3.2	0.6	0.7	0.6	1.3	3.0	4.0
Chaetognaths	3.5	3.6	2.3	2.5	1.3	0.3	2.2	1.4	0.7	4.1	6.3	2.4	6.3	5.7	5.9	6.3	6.3	5.9
Pteropods	0.7	1.2	1.7	0.4	0.6	0.4	0.9	0.5	1.5	0.7	1.7	1.8	0.9	2.0	2.8	0.9	2.0	2.8
Decapod larvae	0.9	1.1	0.6	1.1	0.7	0.6	1.1	0.7	0.7	0.7	2.1	0.6	1.0	0.8	0.7	1.1	2.1	0.7
Other Meroplankton	1.3	1.7	1.3	1.3	0.5	0.4	1.5	2.2	1.4	1.1	1.8	2.5	1.7	2.7	1.5	1.7	2.7	2.5
Other Zooplankton	0.7	0.8	0.7	0.7	0.5	0.3	0.8	1.0	1.1	0.3	0.7	0.3	1.1	0.8	0.9	1.1	1.0	1.1

3.6.1. Copepods

During the 2007–2017 study period, total copepod abundance ranged from 200 to 1500 ind. m^{-3} , with highest abundances observed in the winter and spring seasons and the lowest abundances observed in the summer (Figure 9a). There were no significant annual average copepod abundance trends, although marginally significant and non-significant trends of decreasing abundance were present in almost all the transects (Figure 9b). In autumn, many of these decreasing abundance trends did become significant ($p < 0.05$, see supplementary file A Table S11), likely corresponding to the autumn period of the warmest water temperatures (Figure 2a). More than 114 species of copepods were identified across the WMS survey area, with the greatest number of different species found in the Alborán Sea. Less than 10 of these 114 copepod species had a relative abundance greater than 2% of the total zooplankton (these species will be reported in Section 3.8).

3.6.2. Cladocerans

The abundance of the cladocerans in the WMS ranged from 1000 ind. m^{-3} to near zero in several transects (Figure 9d). The highest abundances were found in the summer, while the lowest were found in the winter and spring (Figure 9c, see also supplementary file A Table S12). The highest cladoceran abundances were found in the Alborán Sea across all seasons, with summer and autumn abundances being considerably higher than in any of the other regions. During the 2007–2017 study period, there were significant decreasing trends in total cladoceran abundances at the annual and seasonal levels across many of the Alborán Sea and some transition transects (Figure 9d and supplementary file A Table S12). Among the cladocerans, five species were identified during the study, of which only *Penilia avirostris* had a relative abundance greater than 2% of the total zooplankton (this species will be reported in Section 3.8).

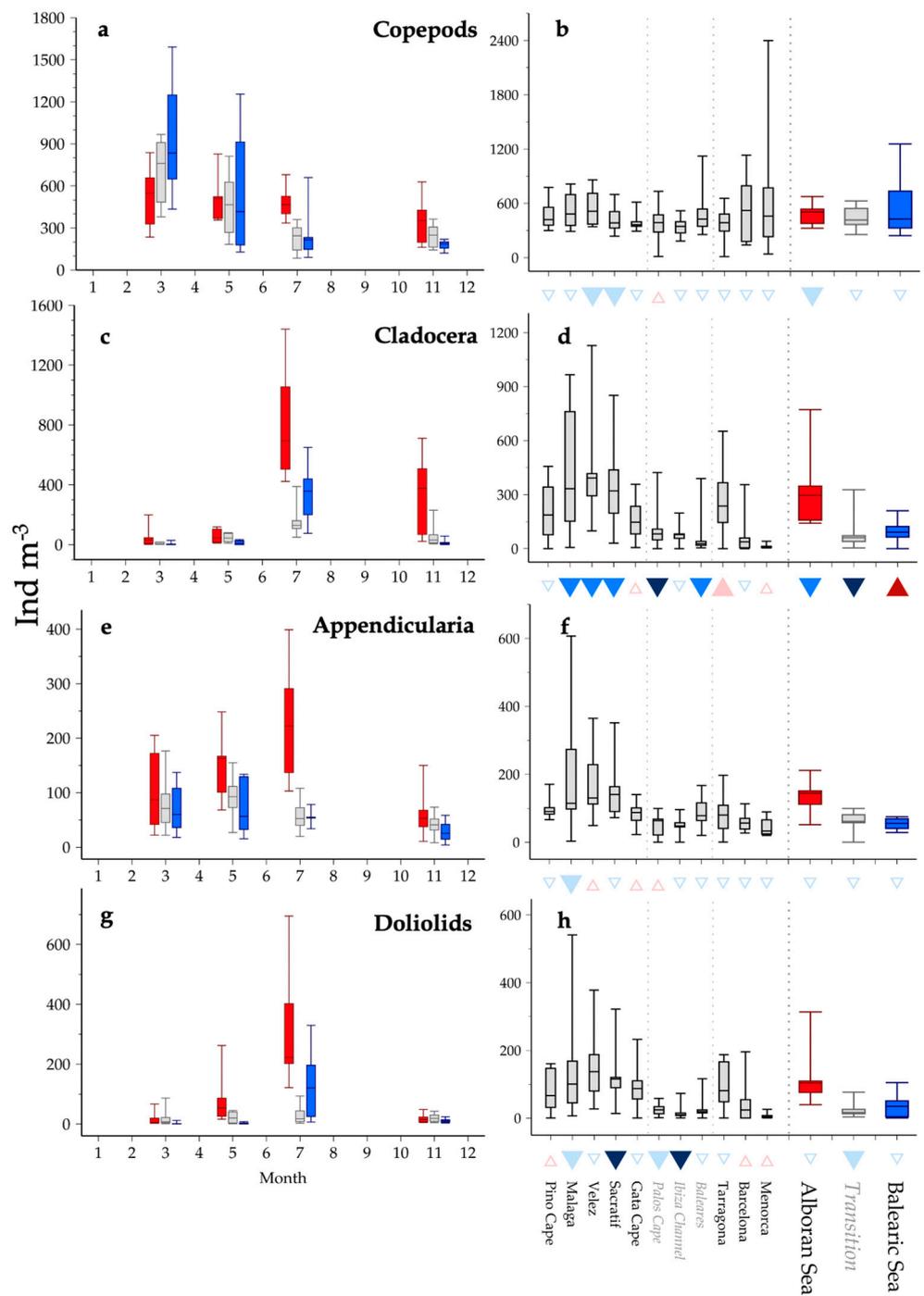


Figure 9. Cont.

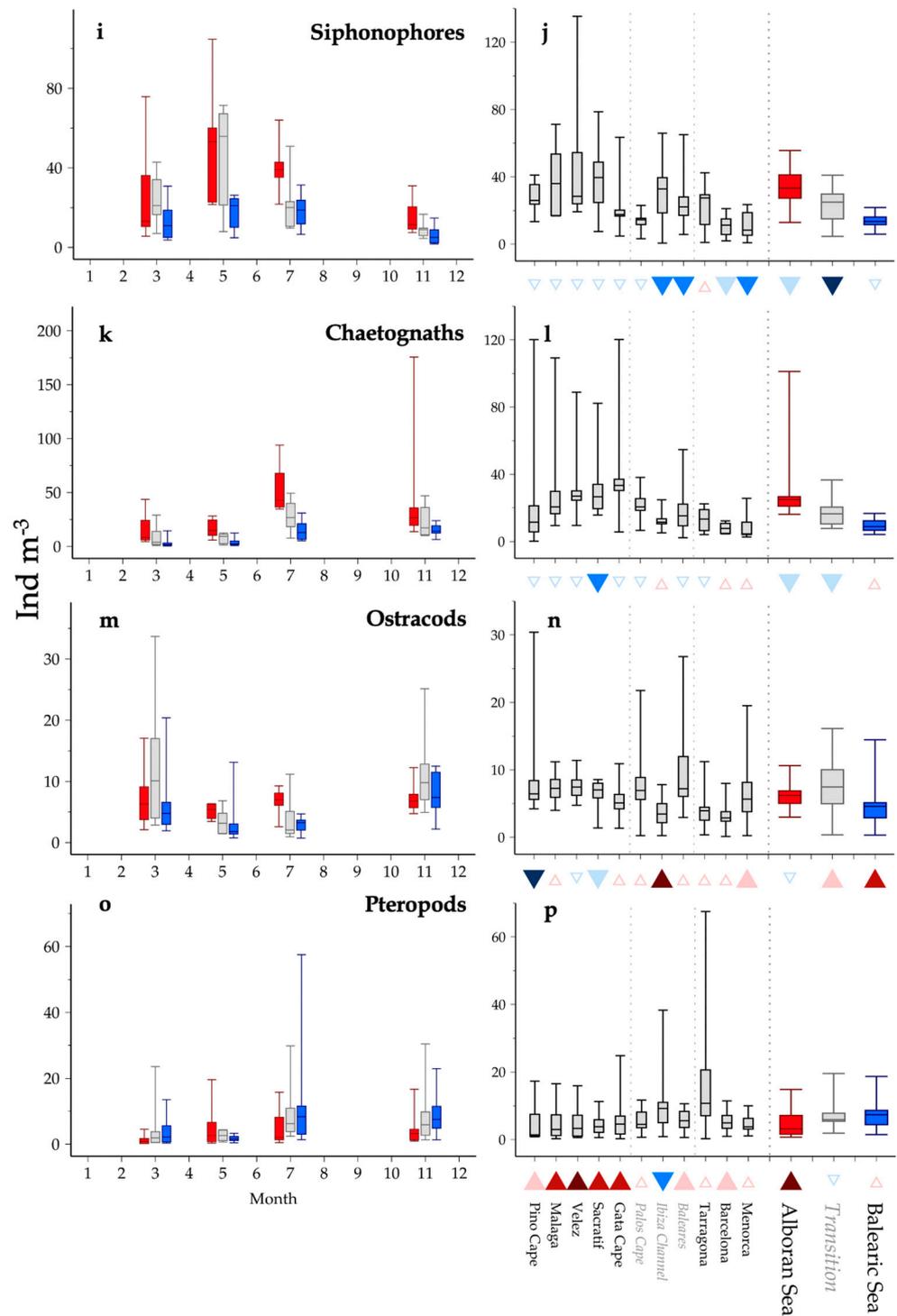


Figure 9. Box-n-whisker plots of the dominant zooplankton groups across the three WMS regions, showing seasonal averages (left column of figures) and the 11-year trends (right column of figures). Red box color, Alboran Sea; blue color, Balearic Sea; and in grey, transition region. All figures are total abundances (ind. m^{-3}) of (a,b) copepods, (c,d) cladocerans, (e,f) appendicularians, (g,h) doliolids, (i,j) siphonophores, (k,l) chaetognaths, (m,n) ostracods, and (o,p) pteropods. Additional information for these groups and the other minor zooplankton groups is available in supplementary file A Tables S11–S26. Downward triangles indicate decreasing abundance in that transect or region, with the size and shading of the triangle indicating statistical significance of the trend (e.g., darkest shading indicates $p < 0.01$, lightest shading indicate marginally or non-significant trends). On the contrary, upward-pointing triangles indicate increasing abundance in each transect and region.

3.6.3. Appendicularians

Appendicularian abundances ranged from 30 to over 300 ind. m^{-3} (Figure 9e) with the highest abundances found in the Alborán Sea region (Figure 9f). In the Alborán Sea, a clear summer peak was found, yet it was absent in the transition and Balearic Sea summer abundances (Figure 9f and supplementary file A Table S22). During the study period, there were not clear or significant trends in appendicularian abundances (Figure 9f).

3.6.4. Doliolids

The abundance of the doliolids ranged from over 600 ind. m^{-3} to near zero (Figure 9g), with the highest values usually found in the Alborán Sea region (Figure 9h). In the Alborán Sea and Balearic Sea, a summer peak was present, but this peak was absent in the transition region (Figure 9g and supplementary file A Table S23). During the 2007–2017 study period, significant decreases in total abundance were present in some of the Alborán Sea and transition transects (Figure 9h), seasonally strongest in the winter and summer (supplementary file A Table S23).

3.6.5. Siphonophores

The abundances of Siphonophores ranged from 5 to over 50 ind. m^{-3} (Figure 9i), with the highest abundances usually found in the spring Alborán Sea and transition transects and the lowest values found in the winter across all transects (Figure 9j). During the study period, significant decreases in total abundance were present in many of the transition and Balearic Sea transects (Figure 9j and supplementary file A Table S25).

3.6.6. Chaetognaths

Chaetognath abundances ranged from 1 to 79 ind. m^{-3} (Figure 9k), with the highest values usually found in summer in all regions but particularly in the Alborán Sea and Gata Cape (Figure 9l; Supplemental Material in supplementary file A Table S18). During the 2007–2017 study period, the only significant annual average decrease was found in the Sacratif transect of the Alborán Sea (Figure 9l). Seasonally, however, multiple transects from the Alborán Sea and transition region exhibited significant decreasing trends (supplementary file A Table S18).

3.6.7. Ostracods and Pteropods

Although minor groups, ostracods (Figure 9m,n) and pteropods (Figure 9o,p) were included since both showed significant trends at some transects. Ostracods were frequently decreasing in the Alborán Sea, yet increasing in many of the transition and Balearic Sea transects (Figure 9n and supplementary file A Table S13). In contrast, pteropods were significantly increasing in all but the westernmost Alborán Sea transects (Figure 9p and supplementary file A Table S19). The remaining zooplankton groups shown in Figure 8 (e.g., amphipods, isopods, polychaetes, etc.) are reported in supplementary file A Tables S14–S26.

3.7. Structure and Distribution of the Dominant Copepods and Cladoceran Taxa

With rare exceptions, the zooplankton community was numerically dominated by the copepods, as a total group sum, across all of the WMS transects and across all seasons (Table 2, Figure 8, Section 3.6). The second dominating group was most often the cladocerans. When looking at individual species, not group totals, the zooplankton community in the WMS was frequently dominated by just one of two species (Table 3). When averaging across all seasons, the Alborán Sea transects were dominated by the cladoceran *P. avirostris*, while the transition and Balearic Sea were dominated by the copepod *Clausocalanus arcuicornis* (Table 3, top row). When looking within individual seasons, there were clear differences between the winter/spring and the summer/autumn dominant species, with copepods and cladocerans both gaining and then losing their dominance (Table 3, middle and lower rows).

Table 3. Dominant (numerically most abundant) copepod or cladoceran species in each transect, annually and by season. Cells with different yellow background shadings indicate the dominant species was a cladoceran, with the brightest yellow assigned to *Penilia avirostris*, the most frequently dominant species of cladoceran. In white, *Evadne spinifera* is shown with a lower abundance. Cells with different green background shadings indicate the dominant species was a copepod, with the brightest green assigned to *Clausocalanus arcuicornis*, the most frequently dominant species copepod.

Time Period	Alboran Sea						Transition Ibiza Ch	Balears	Tarragona	Balearic Sea	
	Pino Cape	Malaga	Velez	Sacratif	Gata Cape	Palos Cape				Barcelona	Mahon
Annual Average	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>	<i>Penilia avirostris</i>	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>
Winter (Feb/Mar)	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>	<i>Subeucalanus monachus</i>	<i>Evadne spinifera</i>	<i>Evadne spinifera</i>	<i>Clausocalanus arcuicornis</i>					
Spring (Apr/May)	<i>Clausocalanus arcuicornis</i>	<i>Acartia clausi</i>	<i>Clausocalanus arcuicornis</i>	<i>Evadne spinifera</i>	<i>Clausocalanus arcuicornis</i>	<i>Evadne spinifera</i>	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>	<i>Centropages typicus</i>
Summer (Jun/Jul)	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Evadne spinifera</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Clausocalanus arcuicornis</i>
Autumn (Oct/Nov)	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Penilia avirostris</i>	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>	<i>Clausocalanus arcuicornis</i>

When averaged across space and time, *P. avirostris* and *C. arcuicornis* were the most prominent species across the entire WMS region. In the cladocera, 76% of the annual average total cladoceran abundance was from *P. avirostris*, followed by *Evadne tergestina* (20%), while the remaining members contributed less than 5% combined. In the copepods, almost 29% of the annual average total copepod abundance was from *C. arcuicornis*, followed by *Clausocalanus lividus* (9%), *Clausocalanus furcatus* (8%), *Centropages typicus* (7%), and *Paracalanus parvus* (7%). The remaining species contributed no more than 5% each and less than 2% each. Seasonally and regionally, these relative contributions of each species would change, with other members temporarily becoming dominant for a short period. For example, *Evadne spinifera* became dominant briefly in the winter/spring in the Sacratif transect, returning to *P. avirostris* dominance again in the summer/autumn. RDAs indicated that the season was clearly a co-variable with significant influence on the structure of the dominant copepods and cladocerans ($p < 0.001$; Figure 10a). Furthermore, such communities presented spatial differences in their assemblages when the different regions were considered with the seasons ($p < 0.001$; Figure 10b).

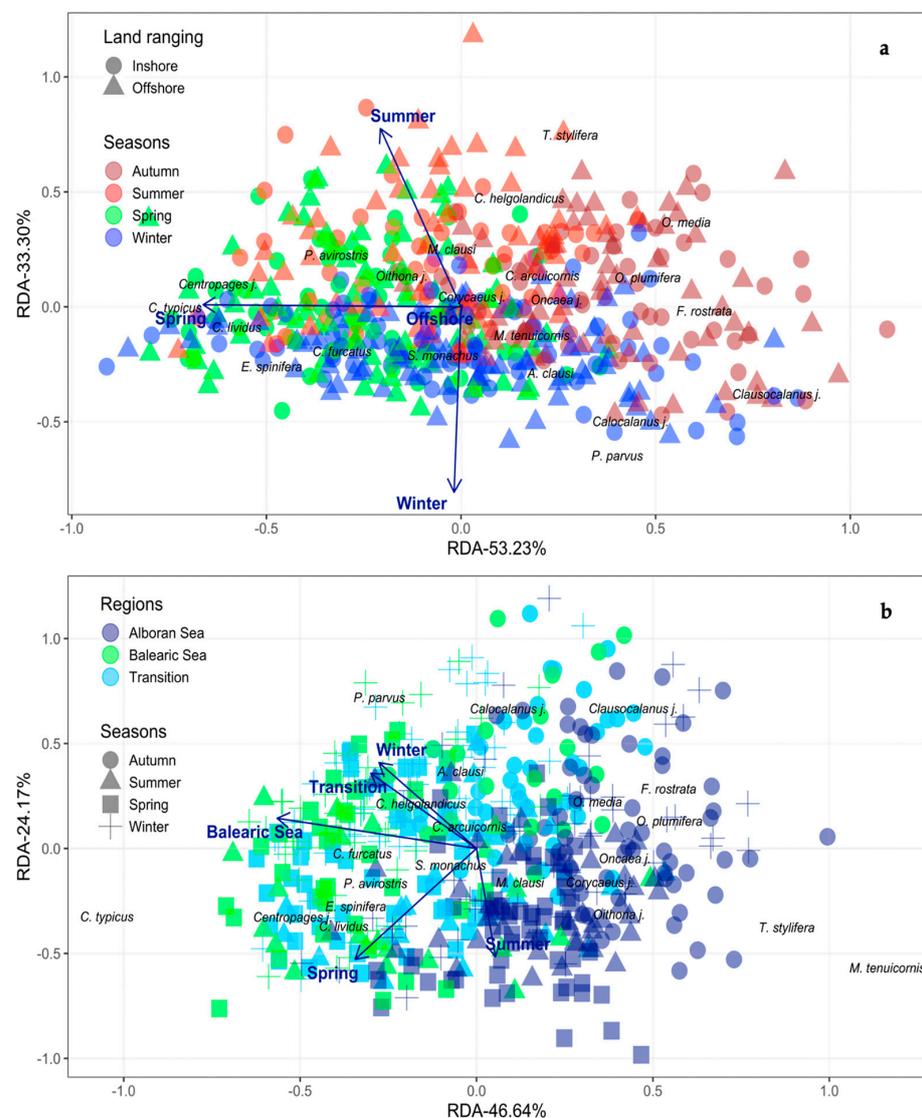


Figure 10. RDA of the most dominant species (>2%) in relation to their presence in the different (a) seasons and land ranging (inshore/offshore) and (b) regions and seasons in the whole study area during the 11 years. The first RDA accounted for 86.53% of the variance explained in the first two canonical axes (a). The spatio-temporal difference among regions and seasons accounted 71.35% of the variance explained in the first two canonical axes' account.

3.7.1. *Penilia avirostris*

The abundance of this cladoceran was higher in summer (Figure 11 and supplementary file D Table S01c), reaching over 1000 ind. m^{-3} . This species was frequently numerically dominant in the Alborán Sea (Table 3). In autumn, this dominance receded to only include the Alborán Sea and some transition transects. In the winter and spring, this species was frequently absent from the Balearic Sea (supplementary file D Table S01a,b). During the 2007–2017 study period, annual average trends (Figure 12) did not capture the multiple significant decreasing trends present in many of the Alborán Sea and transition transects (supplementary file D Table S01a,b).

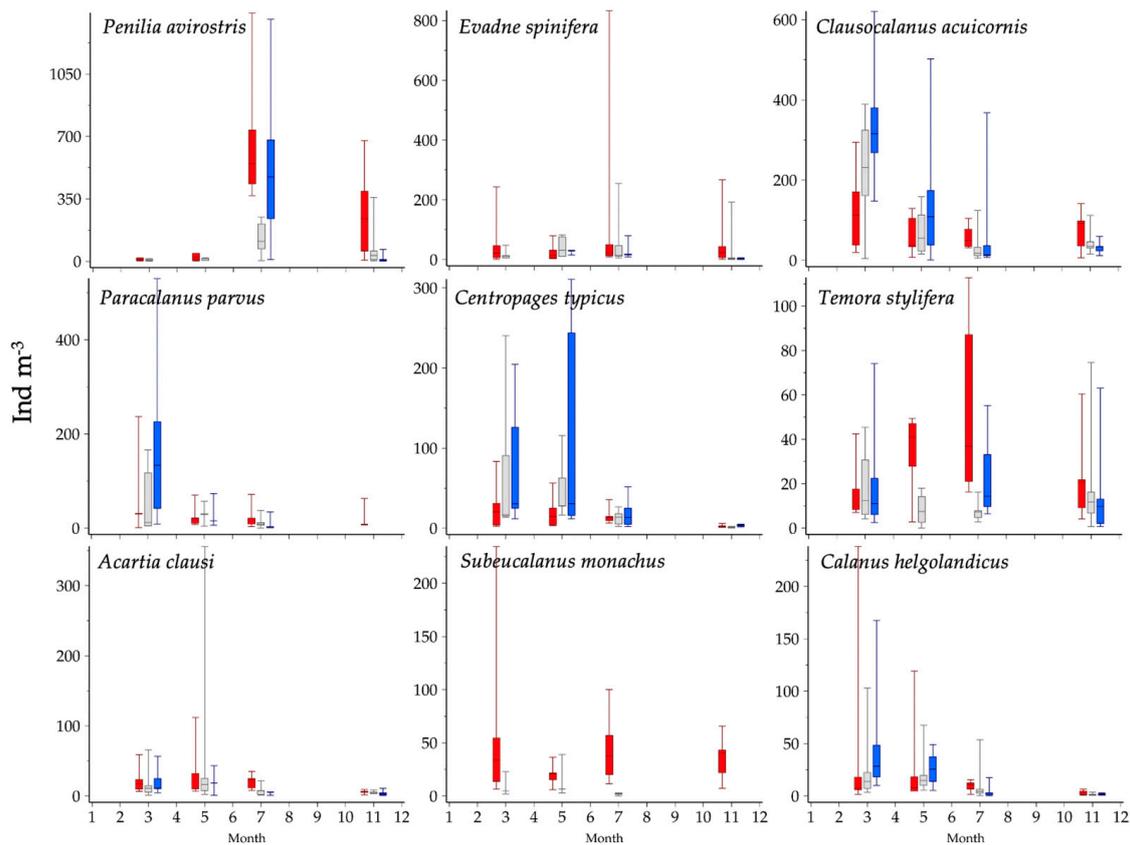


Figure 11. Seasonal trends of the dominant species of cladocera and copepods during the studied period 2007–2017 in the Iberian western Mediterranean Sea (*P. avirostris*, *E. spinifera*, *C. arcuicornis*, *P. parvus*, *C. typicus*, *T. stylifera*, *A. clausi*, *S. monachus*, and *C. helgolandicus*). Red box color, Alborán Sea; blue color, Balearic Sea; and in grey, transition region.

3.7.2. *Evadne spinifera*

This cladoceran had a relatively flat seasonal cycle, with near-zero median abundances but occasional summer blooms of over 800 ind. m^{-3} (Figure 11 and supplementary file D Table S02c). In spite of these low numbers, it still managed to be the dominant winter species in the Sacratif and Gata Cape transects of the Alborán Sea (Table 3). Like *P. avirostris*, it also became absent from the Balearic Sea in the winter. There were multiple significant decreasing abundance trends in the Alborán Sea and transition areas (Figure 12), and these decreasing trends were also found across many seasons (supplementary file D Table S02a,b).

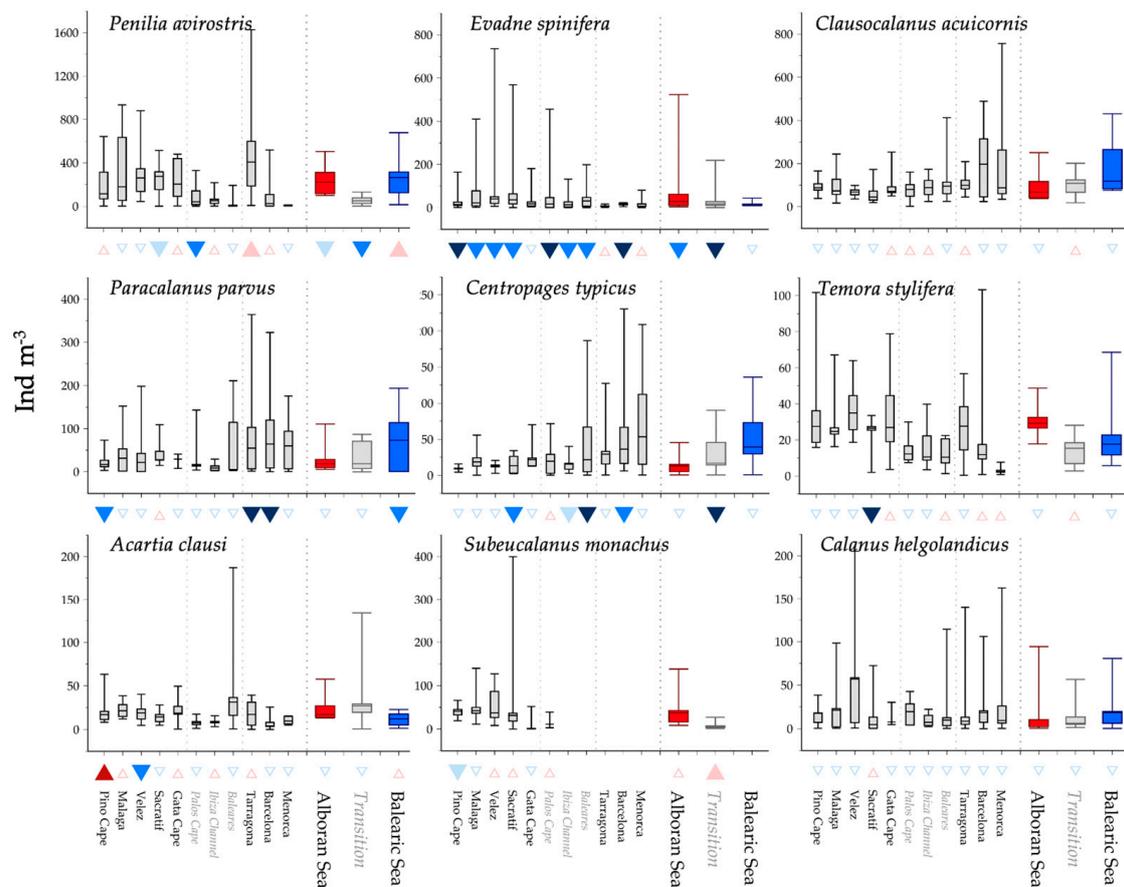


Figure 12. Box plots of the dominant species trend (annual average) at each transect during the whole studied period (*P. avirostris*, *E. spinifera*, *C. arcuicornis*, *P. parvus*, *C. typicus*, *T. stylifera*, *A. clausi*, *S. monachus*, and *C. helgolandicus*). Red box color, Alborán Sea; blue color, Balearic Sea; and in grey, transition region. Downward triangles indicate decreasing abundance in that transect or region, with the size and shading of the triangle indicating statistical significance of the trend (e.g., darkest shading indicates $p < 0.01$, lightest shading indicate marginally or non-significant trends). On the contrary, upward-pointing triangles indicate increasing abundance in each transect and region.

3.7.3. *Clausocalanus arcuicornis*

Abundances for this copepod peaked in winter, especially in the Balearic Sea and transition transects (Figure 11). With an abundance up to 600 ind. m^{-3} , this species competed with *P. avirostris* for dominance, becoming the dominant species in many of the Alborán Sea areas in winter and spring. It dominated in almost all seasons and transects in the Balearic Sea and transition areas (Table 3). During the 2007–2017 study period, there were no significant trends in the annual average abundances (Figure 12). Seasonally, multiple transects in the Alborán and Balearic seas had positive increases in winter or spring, followed by decreases during the autumn (supplementary file D Table S03a,b).

3.7.4. *Paracalanus parvus* Group

Peak abundance of these copepods occurred in spring, with the highest abundance (up to 400 ind m^{-3}) found in the Balearic Sea (Figure 11). In summer and autumn, this species decreased to near-zero or was absent in many of the transition and Balearic Sea transects (Figure 11 and supplementary file D Table S06a,c). Annual abundance trends (Figure 12) partially captured the multiple significant decreasing trends present in the western Alborán Sea transects (all seasons) and the winter decreasing trends in two of the Balearic Sea transects (supplementary file D Table S06a,b).

3.7.5. *Centropages typicus*

Abundances for this copepod were highest in the Balearic Sea (up to 300 ind. m^{-3}), peaking in summer after high spring abundances (Figure 11). This species had multiple significant decreasing trends, from all three regions (Figure 12) and found in all seasons (supplemental File D Table S07a,b).

3.7.6. *Temora stylifera*

This copepod was more abundant in the Alborán Sea than the other transects (up to 100 ind. m^{-3}), with a peak in summer and moderately high presence in spring (Figure 11). In spring, this species became near-zero or was absent in many of the transition and Balearic Sea transects. The only significant annual average trend for this species was a decreasing trend in the Sacratif transect of the Alborán Sea (Figure 12). During the winter, there were significant increasing trends in two of the transition areas (supplementary file D Table S08a,b).

3.7.7. *Acartia clausi*

This copepod had relatively low (<30 ind. m^{-3}) average abundances across all seasons (Figure 11), with occasional summer blooms that were magnitudes higher than those. Aside from a positive spring trend in the Pino Cape transect, all other significant trends for this species were negative and occurred in the summer or winter (Figure 12 and supplementary file D Table S11).

3.7.8. *Subeucalanus monachus*

This copepod was only found in the Alborán Sea transects, and it had a relatively flat seasonal cycle (Figure 11). While there were no significant annual average trends (Figure 12), autumn had multiple significant decreasing trends in the west of the Alborán Sea (supplementary file D Table S10a,b).

3.7.9. *Calanus helgolandicus*

This copepod was found in all regions, with the highest average abundances in winter and spring in the Alborán Sea and Balearic Sea transects (Figure 11). While there were no significant annual average trends (Figure 12), this species was decreasing significantly in many of the Alborán Sea transects and in all seasons (supplementary file D Table S09a,b). Decreasing trends were also found in the Balearic Sea transects in summer.

3.8. Correlations between Zooplankton and Environmental Variables

In a time series analysis, the detection and significance level of a trend or correlation are influenced by the number of years of data, the strength of any relationship, and the magnitude of variance within the tested variables (see Section 2.2, Statistical Analysis). In our correlation test, there were now two variables with variance added to this equation, and these were further compounded by the fact that most of the WMS variables also had strong seasonal patterns. Without adding an additional 10 or 20 years of data, it is likely that only the strongest relationships (correlations) will be detected or found significant.

Correlations between the major zooplankton groups (e.g., copepods, pteropods, etc.) and environmental variables (e.g., temperature, salinity, chlorophyll) were heterogenous and varied by group, transect/region, and variable. Result tables for the correlations are included in Supplemental File C, with notable results reported below. Only correlations between annual average values are reported. Seasonal correlation results are not included as they were almost exclusively populated with non-significant results. Even as annual averages, many of the correlations were non-significant.

Correlations with SST generally did not show any large, cohesive patterns within zooplankton groups or regions (supplementary file C Table S01). Two exceptions were the significant positive correlation of pteropods in most of the Alborán Sea transects, and the significant negative correlations of total zooplankton in the transition transects.

Correlations with salinity (SSS) also did not show any cohesive patterns within groups or regions (supplementary file C Table S02), with the exception of multiple strong ($p < 0.01$) positive correlations within the Barcelona transect.

Correlations with wind (supplementary file C Table S03) had multiple strong positive correlations ($p < 0.01$) between total zooplankton and also with many gelatinous species, primarily in the transects in and around the transition region.

Correlations with satellite chlorophyll (supplementary file C Table S04) did not have any clear cohesive patterns within the crustacean zooplankton organisms (e.g., copepods, decapods, cladocera, etc.), but there were multiple strong positive correlations ($p < 0.01$) in the gelatinous zooplankton groups, especially in the transects in and around the transition region.

Correlations between the dominant copepod/cladoceran species and environmental variables (supplementary file E) generally did not show cohesive patterns within groups or regions. One interesting exception was a cluster of positive (significant and marginally significant) correlations with salinity across many of the species in the Balearic Sea Barcelona and Menorca transects (supplementary file E Table S02). Correlations with SST were rare (supplementary file E Table S01), but almost exclusively negative (e.g., decreasing species abundances corresponded with warming waters). Correlations with chlorophyll (supplementary file E Table S03) were extremely rare, only marginally significant, and only found in the Alborán Sea transects.

4. Discussion

Using historical in situ and satellite data, it was possible to extend the environmental variables beyond the 2007–2017 study period. After almost 120 years of general warming, the water temperatures the zooplankton experienced during this study were frequently higher than any seen in the last 100 years by $0.5\text{ }^{\circ}\text{C}$, and almost $2\text{ }^{\circ}\text{C}$ warmer than the water temperatures of the early 1900s (Figure 3a). This prolonged increase in temperature has been reported in other studies [7,63], especially in the deep waters [64].

Warming of the surface water layers often leads to an increase in thermal stratification, reducing the efficiency of the deep convection processes to replenish nutrients, and reducing the productivity of the marine ecosystems [64,65]. Over the last 30 years, increasing salinity was also seen in the open waters of the WMS, where deep Tyrrhenian high-salinity waters contribute to the flow of Mediterranean waters passing through the Gibraltar Strait [9]. Nevertheless, the decrease in salinities (freshening) observed in the Alborán Sea transects in this study suggests an increasing influx of lower-salinity Atlantic waters into the region.

Moreover, a decreasing period of chlorophyll was observed in the study area, which could be associated with a declining wind, and also a decreasing of zooplankton abundance in some transects. The zooplankton decreases appear minor, according to the average values observed of the zooplankton abundance ($\sim 1500\text{ ind. m}^{-3}$) and biomass ($\sim 10\text{ mean mg m}^{-3}$), but still within the ranges cited by other studies in the MS [4,65]. However, as biomass and total zooplankton are mass measurements of the entire community, they can mask or miss compositional changes in the individual groups or species (e.g., decreases in cladoceran and copepod species, or seasonal gelatinous increases). For this reason, it is equally important looking for changes in the major taxonomic groups and species.

4.1. Zooplankton Seasonal Patterns

Although still known as an oligotrophic sea, the WMS is generally more productive than the eastern Mediterranean Sea [4,17]. In the WMS, strong deep convection processes in the northern basin and different mesoscale processes in the south can enhance its productivity [4,66]. As was expected, we observed the highest abundance of zooplankton, especially copepods, in late winter after the presence of the intense phytoplankton bloom when strong north winds inject nutrients into the photic layer [67]. Later, in summer, cladocerans can surpass copepods [65,68]. In autumn, when the thermocline disappears, a second seasonal peak of copepods usually occurs [10].

The high increase in cladocerans is common in the Alborán Sea [65,68] (as well as in the Ebro river estuary (close to the Tarragona transect), where during the stratified season, cladocerans can be quite abundant [65,68]. Copepods frequently had a higher abundance in the Balearic Sea, while cladocerans, appendicularians, and doliolids had higher abundances in the southern region. Doliolids always dominate in summer during periods when copepods are scarce and cladocerans very abundant [65,69]. Siphonophores, however, dominate in spring, and they were also relevant in our study in the transition area as well as in the Alborán Sea. Other groups like meroplankton larvae were also periodically relevant, which can be linked to the reproductive cycle of their benthic stages [69]. Overall, the observed seasonal patterns of the dominant zooplankton groups were quite similar to those found in other areas and studies within the Mediterranean Sea [5,22,36,37].

In the Balearic Sea (Barcelona and Menorca transects), nutrient influxes early in the year produce the highest values of plankton [14,65,67]. In addition to seasonal currents, interannual currents flowing through the Balearic archipelago could also affect its productivity [14]. Among the three regions of this study, the lowest zooplankton abundances were found in the transition region (Ibiza, Mallorca, and Palos Cape), which is often considered one of the most oligotrophic areas of the WMS [19,70].

In the Alborán Sea, the zooplankton abundances are generally higher, due to physical processes that allow the necessary nutrients to persist across seasons [65,68]. For example, in this region, strong physical forcing and cyclonic structures usually produce high values of primary productivity [18,71].

Usually, in the Mediterranean, the copepods appear in high density in winter and spring, decreasing during the year, and the cladocera in summer, exhibiting a clear seasonality [72]. This seasonality is a key factor, favoring the coexistence of many species and the richness of the Mediterranean Sea, maintaining the high actual biodiversity [4]. The opportunity to carry out cruises in an extensive area of the WMS allowed us to see a possible Alboran Sea vs. Balearic Sea gradient of decline in copepod abundances, opposite to the cladocera gradient. These gradients were apparently opposite to the typical zooplankton gradient of the WMS [65], where a regionalization was also indicated [5]. Changes in composition, phenology, and distribution of zooplankton were expected to be found, but the lack of synoptic cruises did not allow us to draw comparisons with any previous expected gradient in the zooplankton community [38].

4.2. Decadal Zooplankton Trends

Over the last century, an increase in water temperatures has been observed in the WMS, causing an enhancement in the thermal stratification, which is leading to higher oligotrophy in the region [4,9,63]. We have seen changes in many of the dominant zooplankton groups and species distribution, but due to the high variability of the environmental variables, they have not always been cohesive, showing changes in select seasons and in small areas. Declines were present in many regions, usually with a strong seasonal component, which could be a signal of increasing oligotrophy if the sea warming continues [7]. It does not seem that all regions will suffer, however. In the Alborán Sea, strong tidal mixing inflow from the Atlantic Ocean and the quasi-permanent frontal structures can lead to periods and areas of high productivity. In relation to that, warming waters and stratification often lead to a predominance of smaller phytoplankton cells, which have a lower nutrient requirement [73]. This environment can favor smaller zooplankton and gelatinous groups that can more easily catch the smaller phytoplankton and prey [65,69].

In these conditions, diatoms can dominate in winter/spring and small flagellates in summer/autumn [74]. During these stratified seasons, it has been also observed up to the Balearic archipelago that the phytoplankton structure changes with the predominance of small flagellates [11,16,75]. This trend seems to continue going northward with the exception of the winter season, when large diatoms are prevalent [76].

For the copepods, although a decline was seen particularly during autumn no clear trends were annually observed. Moreover, it was interesting to see the increasing contri-

bution of the copepods throughout this study (%). Nevertheless, the cladocerans (second dominant group) declined in several transects as well as the doliolids. It was particularly remarkable that *E. spinifera* declined all through the studied period. The other groups that predominated in spring or in other seasons did not show any trend. A particular mention has to be given to the siphonophores (eminently oceanic and carnivores), which declined in the northern regions. They exhibited negative correlations with SST. The increase of SST in the northern area could have been the cause of their decrease. We did not find correlations with the salinity despite the fact they can be highly sensitive to salinity changes [77]. Particularly interesting were the pteropods and the ostracods, open-ocean organisms that both increased during the studied period. However, pteropods increased, particularly in the Alborán Sea, and the ostracods in the northern regions, suggesting both groups were quite sensitive to the temperature and salinity changes observed in the WMS. Usually, species and groups common in the epipelagic layers are more influenced by climate changes. In this sense, longer studies are needed, stressing environment relationships with other minor zooplankton groups [78,79]. In addition, we did not find a significant trend with small jellies despite the clear increase with the warming [80]. However, this group as well as the salps (supplementary file A Tables S24 and S26) should be considered with a lot of caution because the collection methods used for the zooplankton community are not always adequate for their counting [41]. In the present study, no clear correlation appeared with any of the environmental variables, especially in the Alborán Sea, probably due to the continuous entrance of less saline waters from the Atlantic Ocean and the freshening observed during our study.

4.3. Dominant Copepods and Cladocera Taxa

Clausocalanus is one of the most abundant genera in all oceans, as it was in the present work, showing a temporal succession of species, and suggesting ecological differentiation among the congener species [81]. *C. arcuicornis* dominated in winter, *C. lividus* in spring, and *C. furcatus* in late summer. With regard to the dominant copepods, *C. arcuicornis* increased particularly in the Balearic Sea. Nevertheless, the group of *P. parvus*, which was cited in the literature as a cold water taxon [82], showed a decline in the same area. *C. typicus*, cited as a sensitive species to the warming [38,83], had a similar decrease and, it was negatively correlated with SST. *A. clausi* and *T. stylifera* did not show any clear trend or correlations with the environmental variables. Both species peak usually in summer and autumn [84], but, in our study, were even observed in winter. According to the previous works, not only warming but also high salinity may favor the increase of some thermophilic species and the decrease of others. Thus, if warming and a high salinity continue in the north basin, some species can be expected to increase in their density (e.g., *Clausocalanus*); others, however (e.g., *P. parvus* group and *C. typicus*), will disappear firstly in the northern area. Nevertheless, the overall seasonal distribution observed in the bulk of the copepods seems to be persistent year through year in the WMS [5,81]. The same authors as those just cited indicated that the dominant copepods display a common succession pattern in the MS, where the presence of congeneric species means they can maintain their total abundance, although some variations in timing can be observed [37]. The timing peaks of the dominant species can extend their presence or change their peaking season in relation to warming and other environmental changes. The most common phenological response of the dominant copepods to temperature observed in the North Atlantic is “earlier when and where warmer”, but in the Mediterranean, those species with maxima in late summer or autumn usually have a “later when warmer response” [37]. Other species such as *S. monachus* and *C. helgolandicus* showed a different presence in the upper waters because they usually were sub-superficial species, appearing at the surface only with the upwelled water or during cold seasons. In this respect, *S. monachus* was only found in the Alborán Sea at any given time [65,85], and *C. helgolandicus* was found during the cold winter mixing layer in the proximity of the Gulf of Leon [86]. In addition, it is remarkable that the non-calanoids (e.g., *Oithona*, *Farranula*, and *Microsetella*) were less abundant in our samples

than in other zooplankton studies in the WMS [4,65], probably due to the large mesh used (250 μm in the present study). A smaller mesh size could collect all of these genera with a higher abundance [40,69].

The cladocerans are a relevant component of zooplankton in the MS [87,88]. They have parthenogenetic reproduction and production of resting eggs, and they are characterized by high bursts of population during the stratified season [78], and blooms of *P. avirostris* are usually seen in high numbers. This cosmopolitan filter feeder can graze efficiently on small flagellates when they are present during the warmer periods and is, therefore, well adapted to oligotrophic conditions [72]. Similar to the copepods, the dominant cladocerans can also show variations in timing throughout the Mediterranean [37]. Nevertheless, the lack of correlations among many zooplankton groups and species with the salinity, particularly in the Alborán Sea, could be due to the proximity of the Atlantic and the continuous entrance of less saline waters, preventing the increasing of salinity in the WM [7]. It is important to remember that changes in the hydrological and meteorological conditions with warming waters, less rainfall, lower winds, and progressive acidification have been previously reported in the whole Mediterranean [64]. With a focus on the zooplankton community, these changes could be also related to atmospheric patterns in the close North Atlantic [22]. Long-term temperature increase has been observed to affect the boundaries of biogeographical regions with thermophilic species, extending their ranges and enabling them to colonize new areas where they were previously absent [89]. The northward migration of small pelagic fish with an affinity for warmer waters has been reported in the Balearic Sea [90]. The increase in thermophilic biota in the MS would involve changes in the spatial distributions of many indigenous species [91]. In the North Atlantic Ocean, strong biogeographical shifts in the spatial distribution of the copepods were observed in relation to changes in sea water temperature involving a northward extension of warm-water species and a decrease in the number of cold-water species [27,92]. Very little information on this exists in the MS, with authors reporting that only some rare species have changed drastically in presence in some regions, with the mechanisms behind these changes unfortunately difficult to understand [84]. During the 11 years under study, *P. parvus* and *C. typicus* seemed to decrease northward, as well as *E. spinifera*, and declined in the Alborán Sea. Although these observations have to be clearly elucidated with further studies, the small dimensions of the WMS and the reduced umbral of the Gibraltar Strait (320 m depth), limiting the entrance of deep oceanic species, can produce great homogeneity in the species diversity [93]. In addition, another relevant change that should not be neglected is the invasion of non-indigenous species through Gibraltar and the Suez Canal (in the eastern MS), as well as, nowadays, exotic species coming by ship transports. The location of the MS between tropical and temperate latitudes makes for a perfect sea and proper conditions for biological invasions [91]. All of that has to be considered, particularly when the temperature increases and we speak about the proliferation of gelatinous species (e.g., jellyfish, ctenophores, and/or siphonophores). It is evident that the MS is always changing as a worldwide ecosystem; moreover, the semi-enclosed sea under the pressure of three crowded continents has to be monitored since it is highly impacted by human-mediated threats [65].

With all these considerations, it is important to take into account that in 11 years of seasonal sampling in the WM, detailed patterns or clear changes of zooplankton communities cannot be easily observed. Furthermore, it was shown that when the time series are shorter than 10, 15, or even 20 years, the trends will not always be the same since complex mechanisms drive the overall zooplankton community, particularly in areas with high environmental variability such as in the MS [94]. Nevertheless, the drastic warming and changes in salinity observed in this study to be affecting the zooplankton community have to be taken in consideration for future studies, and it is necessary for research to continue so we can gain a better understanding of the distribution of the dominant species and their presence or absence in the WM. In this sense, taxonomic studies in detail provide the best information since changes due to climate variation are first detected at the species

level rather than with groups [84]. This is consistent with the fact that when species are identified, the ranges of variability can be described in a timely manner. Accordingly, the need for longer time series is stressed. Despite the high variability evidenced in the study area over more than a decade, robust and persistent patterns can be distinguished among the dominant species and within the long-term environmental trends. In the present work, a north–south spatial variability among the two sub-basins as well as different trends were found in the zooplankton groups and dominant taxa during the 11-year time series (e.g., copepods, cladocera, doliolids, and siphonophores). Great variability appeared in the distributions of the dominant species during the 11 years of the study, but we suggest they can be used as target species, providing a good baseline for further research into climate change in the WMS.

5. Conclusions

This 11-year study of zooplankton communities in the WMS took place in an ecosystem experiencing water temperatures near to and greater than those observed in the previous 100 years (Section 3.1, Figure 3a), in salinities considerably above a 70-year average (Section 3.2, Figure 3b), and during a decline in chlorophyll concentrations (Figure 3c). Covering an extensive area of the WMS between two different regions, and the transitional region between them, the results of this study highlighted that even with the noise of localized forcing and natural variability, cohesive changes can still be found among the major taxonomic groups and species, and that they vary by season and location. However, the results also stressed the importance of continued sampling and the need for additional years of data to allow for future analyses to expand and tease out more of the temporal and spatial patterns in this highly dynamic region.

While some changes and trends were detected using the “total” measurements (e.g., total biomass, total zooplankton abundance, and abundance of the copepods), they did not capture the large interannual and seasonal change and variability seen in many of the dominant species. These species-level identifications require the expertise and time of trained taxonomists, especially for the smaller crustacean species, and would not have been possible using only the currently available automated, image-based identification technologies. As these expert taxonomists retire, some monitoring programs may be tempted to switch to image-based sampling. Without caution and consideration of the limits of these systems (e.g., inability to identify all copepod species), this could greatly reduce the ability of their monitoring to detect and evaluate future changes in their oceans and regions.

Sadly, the warming water and ecosystem changes in the WMS appear to only be the beginning. Record-breaking water temperatures in this region continue to happen [95,96], surpassing the highest values observed during this study or found in Figure 3a. Understanding the past, present, and future impacts of these extreme and worsening conditions can only be accomplished through funding and continued sampling by the long-running time-series programs operating across this region.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/w15244267/s1>. Five groups of supplementary files are indicated with figures and tables in A: Environmental variable trends (SST, SSS, Wind, Chl, DM, AFDM, Ratio DM/AFDM, zooplankton abundance): a) 11-year averages in the different areas or regions. b) 11-year trends (annually and seasonally). c) Plots of average trends (annually and seasonally). d) Regional average plots. Supplementary File B: Correlations of annual averages among the analyzed environmental variables (SST, SSS, wind, and Chl). Supplementary File C: Correlations with annual averages between each zooplankton group and environment variables. Supplementary File D: Trends of the dominant species identified during the period of 2007–2017. Supplementary File E: Dominant species’ correlations with the environmental variables (SST, SSS, wind, and Chl).

Author Contributions: Conceptualization, M.L.F.d.P.; methodology, M.L.F.d.P. and T.D.O.; validation, M.L.F.d.P., M.G., T.D.O. and M.C.-R.; formal analysis, M.L.F.d.P., T.D.O., M.G. and M.C.-R.; investigation, M.L.F.d.P.; resources, M.L.F.d.P.; data curation, M.L.F.d.P., T.D.O. and M.C.-R.; writing—original draft preparation, M.L.F.d.P., T.D.O. and M.C.-R.; writing—review and editing, M.L.F.d.P. and M.C.-R.;

visualization, M.L.F.d.P., T.D.O. and M.C.-R.; supervision, M.L.F.d.P. and T.D.O.; project administration, M.L.F.d.P.; funding acquisition, M.L.F.d.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Radiales in the Mediterranean (RADMED Institutional monitoring Project) from the Spanish Institute of Oceanography (IEO/CSIC). The research activity of Miguel Cabanellas-Reboredo was funded by the Juan de la Cierva Program of the Spanish Ministry of Science and Innovation MCIN/AEI/10.13039/501100011033. We also thank the collaboration of the project “Disentangling Seasonality and Active Flux In the Ocean” (DESAFÍO, PID2020-118118RB-I00) from the Spanish Ministry of Science and Innovation, the European Union (Horizon 2020 Research and Innovation Programme) for support through the project SUMMER (Grant Agreement 817806), and the ICES and the ICES Working Group on Zooplankton Ecology (WGZE) from its continuing help. We are also very grateful to the three anonymous reviewers for their accurate and constructive criticisms and suggestions, which helped to improve the manuscript.

Data Availability Statement: This study was conducted using confidential data. Access to or information about the confidential zooplankton data used for this study can be requested from the Instituto Español de Oceanografía (IEO/CSIC) of the Balearic Islands via email to mluz.fernandez@ieo.csic.es. Information or access to environmental data can be requested via email to todd.obrien@noaa.com from the NOAA Fisheries Office of Science & Technology.

Acknowledgments: We thank all the crew of the O/V Francisco de Paula Navarro and, in particular, the people collecting zooplankton samples. We would like to thank Lucas Lopez-Lax for his graphical support and ideas related to data treatment. In the same sense, our thanks go to the WGZE group for their continual help with the manuscript.

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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