



A 50-year (1971–2021) mesozooplankton biomass data collection in the Canary Current System: Base line, gaps, trends, and future prospect

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ABSTRACT

Mesozooplankton have been widely used as a bioindicator of marine ecosystems due to their key position in ocean food webs, rapid response to environmental changes, and ubiquity. Here, we show mesozooplankton biomass values in the Canary Current System from 1971 to 2021 in three different areas in relation to mesoscale activity: (1) scarcely affected by mesoscales structures (North of the Canary Islands), (2) affected by mesoscale activity and the presence of the islands (South and around the islands), and (3) close to the Northwest African coastal upwelling system (Upwelling influenced). A Generalized Additive Mixed Model (GAMM) was used to analyze the general mesozooplankton biomass trend throughout the studied period discriminating differences in biomass between the areas, annual cycle, and day-nighttime periods. The GAMM showed a significant negative biomass tendency North of the Canary Islands over the 50-year time-series compared to the South and around the islands, and significant differences between day and nighttime periods ($p < 0.001$) and the annual cycle ($p < 0.0001$). Linear regression analyses showed different tendencies depending on the area, season, and period. When comparing biomass data of the most oligotrophic zone (north of the islands) with other tropical-subtropical time-series stations in Hawaii (HOTS) and Bermuda (BATS), we obtained increasing biomass tendencies for both fixed time stations but decreasing tendency for our time-series.

1. Introduction

Zooplankton are the suitable sentinel through long-term monitoring due to their key role in almost all the marine food-web. They are responsible for multiple ecosystem services: from regulating fish recruitment via grazing on primary producers or feeding upon microzooplankton (Lomartire et al., 2021) to the transport of carbon downwards into the deep-sea (Hernández-León et al., 2020). Zooplankton mediate the export and sequestration of carbon through (1) consumption of large suspended particles decreasing their sinking rates (Svensen and Nejstgaard, 2003; Mayor et al., 2020), and through (2) diel vertical migrations (DVMs) enhancing active carbon transport efficiency. The outcome of these DVMs influence fish migration, food availability (Perissinotto and McQuaid, 1992), marine food webs trophic interactions (Sommer and Stibor, 2002; Trebilco et al., 2020), population dynamics, flux of energy (Winemiller and Polis, 1996), and recycling processes in the upper ocean (Legendre and Rivkin, 2005; Serrano et al., 2016).

Long-term series become the approach for understanding the natural variability of marine systems and detecting anthropogenic environmental changes (see Parr et al., 2003). Especially nowadays that climate change is a global threat for marine ecosystems, time-series are a valuable tool for tracing those changes. Although effects of climate change on ocean ecosystems are not fully understood, it is known that external variations of temperature or salinity might result in a cascade of indirect interactions and feedbacks through the food web with unpredictable consequences (Johnson et al., 2011; Marshall and Alvarez-Noriega, 2020). During the last decades, anthropogenic pressure over marine ecosystems led into a general tendency for developing plankton indicators to report on ecosystems status and trends (Serrano et al., 2016; Bedford et al., 2020), as plankton community changes are more likely to happen at a shorter time span compared to higher trophic levels (Hays et al., 2005; Serrano et al., 2016). Thus, under the currently climate change scenario, long-term monitoring has become a major concern in biological oceanography providing crucial information of the habitat conditions, dynamics, and species status, as well as giving integral

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science support for ecosystem-based management of resources, activities, and services (Harvey et al., 2020). This not only enables the assessment of ecosystem services and the impacts of human activities, but also helps to forecast future trends (Kaufman et al., 2009; Bedford et al., 2020).

The Canary Current System (CCS) is located within the eastern boundary gyre of the North Atlantic Ocean, comprising oceanic oligotrophic waters and the upwelling system off Northwest Africa, showing high variability in physical, chemical, and biological properties (Barton et al., 1998). The CCS holds one of the most important Eastern Boundary Upwelling Systems (EBUS) largely characterized by their high productivity supporting industrial fishing activities (Barton et al., 1998; Schmidt et al., 2020; Fischer et al., 2020; Harvey et al., 2020). However, this area is distinct from other EBUS, such as California, Humboldt, and Benguela, because of the presence of the Canary Islands. The archipelago extends westward from near the African coast to the open ocean, acting as a barrier to the path of the Canary Current inducing an intense mesoscale activity (Barton et al., 2004; Hernández-León et al., 2007). Waters north of the islands are characterized by a sharp oligotrophy due to water column stratification during most of the year, with a sharp deep chlorophyll maximum (Hernández-León et al., 2007). During the winter season, the thermocline and the nutricline (80–100 m depth) are eroded due to surface cooling and convective water mixing (De León and Braun, 1973; Hernández-León et al., 2007; Cianca et al., 2007; Neuer et al., 2007). Then, nutrients are able to reach the euphotic zone, increasing primary production and chlorophyll values (De León and Braun, 1973; Braun, 1979; Aristegui et al., 2001), allowing organisms to burst (Armengol et al., 2019), and promoting the so-called Late Winter Bloom (LWB; Menzel and Ryther, 1960). In spring, the seasonal thermocline is reestablished, restricting the injection of nutrients into the euphotic zone and limiting primary production (Schmoker et al., 2012). The southern area of the archipelago also follows this annual cycle but it holds cyclonic and anticyclonic eddies shed by the islands and occasional upwelling filaments, enhancing zooplankton biomass (Doty and Oguri, 1956; Hernández-León et al., 2001, 2007).

Zooplankton time-series in different areas of the world showed plankton changes in composition, structure, abundance, biomass, species distribution, and phenology (Hoffmeyer, 2004; Fernández de Puelles et al., 2007; Chiba et al., 2009; Escribano et al., 2012; Steinberg et al., 2012; Bedford et al., 2020). Trends of zooplankton variations are directly related to sea surface temperature (Bedford et al., 2020), water column stratification, primary production (Steinberg et al., 2012), and bottom-up or top-down cascading trophic interactions (Escribano et al., 2012). Knowledge of all variables affecting zooplankton trends is an arduous task, involving the parameterization of both abiotic and biotic factors, interactions between the components of the food web, and the increasingly growing anthropogenic footprint on the oceans. A tentative mesozooplankton time-series in the CCS started in 2012 with the project called “Radial Profunda de Canarias” (*RaProCan*, Canary Islands Deep Transect, Vélez-Belchí et al., 2015), sampling during the productive season (known as Late Winter Bloom, LWB, from January to April) and the stratified season (SS, from May to December). However, there are no long-term mesozooplankton studies in the CCS. Hence, our aim is to provide the existing data of mesozooplankton biomass in order to establish the mesozooplankton community baseline of the last five decades (1971–2021) in three distinct areas of the CCS during the LWB and the SS, and day-nighttime periods. Spatial, temporal, and diel patterns of mesozooplankton time-series were analyzed using Generalized Additive Mixed Model (GAMM) and linear-regression analysis. Moreover, we compared our time-series to other long-term studies in the Pacific and Atlantic Oceans, such as the time-series stations off Hawaii (HOTS) and Bermuda (BATS). Finally, we explored different time periods in our database to see how biomass tendencies change according to the studied years.

2. Material and methods

2.1. Mesozooplankton database sources and analysis

All the biomass data used in this study is related to mesozooplankton (>200 μm) in the epipelagic layer (0–200 m). First, we compiled all biomass values from existing data published in scientific literature or provided by authors (see Suppl. Table 1). Then, we divided the studied area in three different zones according to their mesoscale activity: (1) “North” of the islands, (2) “South and around” the islands, and (3) “Upwelling influenced” area. The division was done according to the mesoscale activity of the area: North grouped those stations sampled north of the Canary Islands, thus oceanic waters not affected by the presence of the islands. South and around (therefore just South) comprised those stations affected by the presence of the islands, thus including those stations close to the islands as they are also influenced due to their proximity. Finally, the third group of stations was characterized because of the influence of the upwelling system (see Fig. 1). The limits between the South and the Upwelling area was selected following the results of Hernández-León et al. (2002) observing a decrease in chlorophyll, primary production, and zooplankton biomass at 60–80 Km from the African coast.

A total of 1967 biomass measurements performed in the three areas between 1971 and 2021 were compiled (Fig. 1, Suppl. Table 2). Biomass values obtained as protein content (Lowry et al., 1951) were transformed to dry weight using a ratio of 2.49 given by Hernández-León et al. (2019) for tropical and subtropical waters, and converted to carbon units assuming a carbon content of 40% of dry weight (Dam and Peterson, 1993).

We obtained a relationship between biomass values from 0 to 100 m depth and biomass values from 0 to 200 m depth using data from the project COCA (see Hernández-León et al., 2019) and 5 data points located south of the Canary Islands. The relationship was obtained by comparing data from 0 to 200 m depth with 0–100 m depth in the same station sampled every 20–40 m depth intervals using a Longhurst-Hardy Plankton Recorder (LHPR) net (see Suppl. Fig. 1). For this comparison, we used day ($n = 21$) and night ($n = 21$) samples obtaining the following relationship:

$$\ln(\text{biomass}_{0-200\text{m depth}}) = 0.684 + 0.945\ln(\text{biomass}_{0-100\text{m depth}}) \quad (R^2 = 0.894, p < 0.001, n = 42).$$

Then, the biomass values from 100 m depth to the surface of our database were converted to 0–200 m biomass values and added to our database using the obtained regression (Suppl. Fig. 1).

Mesozooplankton biomass distribution over the 50-years period was studied by averaging annual values in the different areas, distinguishing between day-nighttime periods, to account for changes due to DVM, and between the sampled seasons (i.e. LWB or SS) due to seasonality. Afterwards, least-square linear regressions were fitted for each period and

Table 1

Spearman correlation coefficients and p-values between the environmental variables and zooplankton biomass North, South (and around), and in the Upwelling influenced area. “n” stands for the number of samples in each area, “SST” for Sea Surface Temperature, “Chl a” for chlorophyll a concentration, and “PP” for primary production.

Area	n	Environmental variable	Spearman correlation coefficient	p-value
North	278	SST	−0.31	<0.001
		Chl a	−0.23	0.001
		PP	−0.01	0.8
South and around	1516	SST	−0.29	<0.001
		Chl a	0.32	<0.001
		PP	0.33	<0.001
Upwelling influenced	173	SST	−0.09	0.3
		Chl a	−0.53	<0.001
		PP	−0.53	<0.001

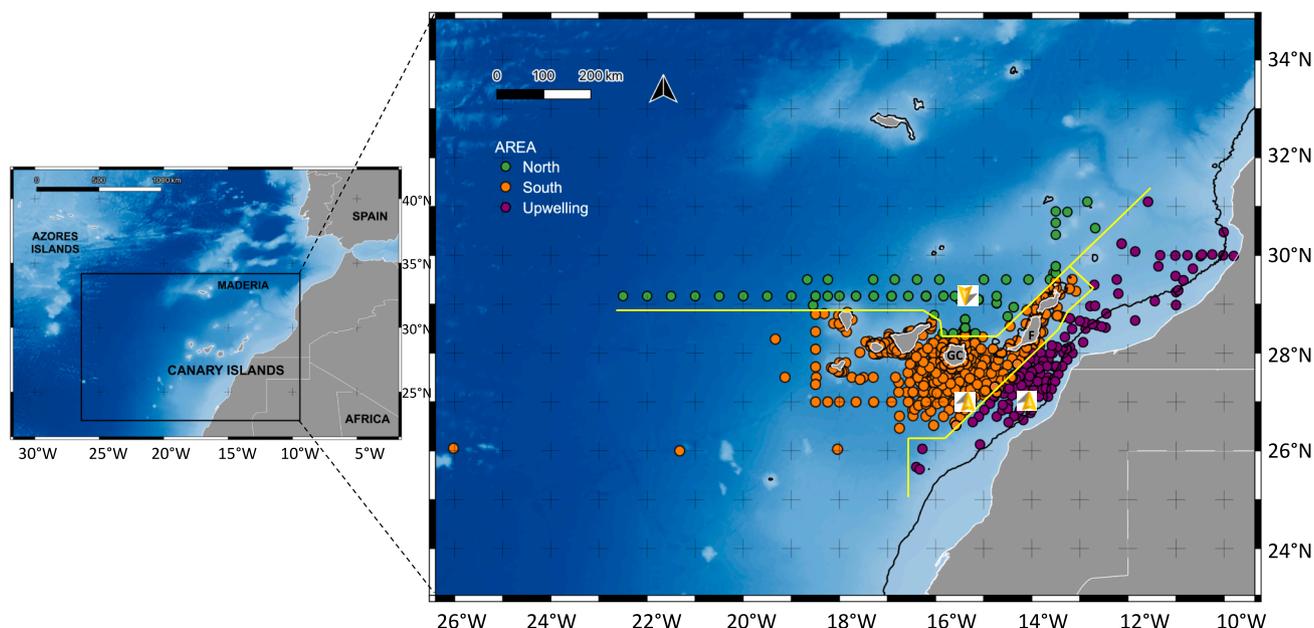


Fig. 1. Location of the sampled oceanographic stations from 1971 to 2021. Green dots stand for samples obtained North of the Canary Islands, orange dots for samples obtained South and around the islands, and purple dots for those samples in the Upwelling influenced area. Yellow arrow stands for reference points of each delimited area (see text), yellow line indicates the separation between areas according to proximity to the coast and position in relation to the islands, and black line stands for 200 m depth bathymetry. GC stands for Gran Canaria, and F for Fuerteventura.

Table 2

Average mesozooplankton biomass ($\text{mgC}\cdot\text{m}^{-2}$) and standard deviation ($\pm\text{SD}$) in all the area studied, North, South (and around the islands), and in the Upwelling influenced area sampled during the Late Winter Bloom (LWB) and the Stratified Season (SS), during day time. “n” stands for the number of samples in each area/season/period.

Area	Season	Mesozooplankton biomass	n
All area	LWB	445.4 ± 353.8	709
	SS	343.0 ± 274.6	896
North	LWB	320.3 ± 200.4	115
	SS	239.9 ± 178.0	70
South and around	LWB	486.5 ± 377.5	543
	SS	352.3 ± 283.6	773
Upwelling influenced	LWB	289.8 ± 218.3	51
	SS	343.3 ± 193.0	53

season in the different areas. Annual cycles of mesozooplankton biomass were studied by obtaining the monthly average value in the different areas. Finally, longitudinal zooplankton biomass distribution from the open ocean to the African coast was studied.

2.2. Environmental parameters

For a better understanding of biomass fluctuations over the study period in the different areas, we studied the annual cycles and time-series of sea surface temperature (SST), chlorophyll *a* (Chl *a*), and primary production (PP) in three fixed points in each area. Environmental data was obtained for the following coordinates (see Fig. 1, yellow arrows): (1) North: $29^\circ\text{N } 15^\circ 30'\text{W}$ – coordinates of the European Station for Time-series in the Ocean of the Canary Islands (ESTOC); (2) South: $27^\circ\text{N } 15^\circ 30'\text{W}$, and (3) Upwelling influenced: $27^\circ\text{N } 14^\circ\text{W}$. Fixed coordinates were selected for the environmental parameters in order to reduce spatial biases in the analysis. Monthly average SST values were directly downloaded from the NOAA website (<https://psl.noaa.gov/data/timeseries/>) since 1971, using the NCEP/NCAR reanalysis monthly means dataset. Monthly Chl *a* average data was obtained from the Ocean Color web site (<https://oceancolor.gsfc.nasa.gov/>) using OCI algorithm and Aqua MODIS information (available period from 2002 to

2021). Monthly average PP since 2002 was downloaded from the Ocean Productivity website (<https://sites.science.oregonstate.edu/ocean.productivity/>) using the Vertical Generalized Production Model (VGPM) as the standard algorithm.

Annual cycles of SST, Chl *a*, and PP were studied by monthly averaging values since 1971 for SST, and since 2002 for PP and Chl *a*. For the time-series tendencies, each environmental data set was detrended to remove the seasonal effects from the time-series, setting a moving average of 12 months, and using an additive model since random fluctuations in the data were roughly constant in size over time (annual cycle). Least-square linear regression analyses to describe tendencies were then performed. Finally, we performed Spearman correlation analyses between monthly values of environmental variables and zooplankton biomass at each location. Normality was tested based on histogram analysis and the Lilliefors (Kolmogorov-Smirnov) test (Lilliefors, 1967). Homogeneity of variance across groups was tested using Levene’s test (Levene, 1960).

2.3. Modeling mesozooplankton biomass

Due to year-gaps biases of our database, we studied mesozooplankton biomass shifts through the 50-years period by using a Generalized Additive Mixed Model (GAMM). First, we transformed biomass (BM) using a Box-Cox transformation to adjust model residual normality:

$$TBM = \frac{BM^\lambda - 1}{\lambda}$$

being $\lambda = 0.25$.

For the GAMM we selected the southern area as a reference to test biomass variations, as it was the area with more information:

$$TBM = \beta_0 + \beta_{0,\text{North}} I_{\text{North}} + \beta_{0,\text{Upwelling}} I_{\text{Upwelling}} + \beta_{0,\text{Night}} I_{\text{Night}} + \beta_1 t + s(\text{day}) + b(\text{cruise}) + \epsilon.$$

where TBM stands for the biomass transformed by Box-Cox transformation.

The model evaluates biomass differences (β_0) and biomass tendencies over the period studied (β_1), considering the random effect *b* (cruise) due to the measurements being made over time by different

ships (cruises). “ β_0 ” stands for biomass global mean value in the South. That means that each β_0 compare biomass differences between the area and the South. “ $\beta_{0,North}$ ” represents biomass mean difference between the North and the South, and “ $\beta_{0,Upwelling}$ ” biomass mean difference between the Upwelling influenced area to the South, while the other variables were kept constant. The term “ $\beta_{0,Night}$ ” stands for biomass differences between day and nighttime periods, while keeping the other variables constant. “ β_1 ” evaluates tendencies over the 50-years, keeping the South as the reference area, rather than biomass differences over the time (t). “ $s(day)$ ” is a spline modeling the biomass seasonal pattern. The term $b(cruise)$ is a random variable modeling the random variation existing from one cruise to another.

Data for each cruise were measured over several successive days, introducing autocorrelation between measurements. Also, data from the different cruises were unevenly spaced in time. Thus, it was not possible to use a global autoregressive structure, and so the model included a continuous time autoregressive temporal correlation structure of data in each cruise. This structure assumed that values quite close in time were highly correlated with each other, and this correlation dampened rapidly as time passes. Finally, as time course measurements were sensitive to autocorrelation problems, so we reduced it by implementing an autocorrelative parameter (“ $b(cruise)$ ”) in the model. We compared the Bayesian information criterion (BIC) considering or not autocorrelation, obtaining lower values for the model with autocorrelation.

2.4. Databases comparison

In order to compare with other published time-series, we extracted mesozooplankton biomass values from the North time-series, as the ESTOC is located in that area. For BATS, we downloaded the available database of zooplankton from April 1994 to February 2020 (<https://bats.bios.edu/bats-data/>). For the analysis of tendencies in each productive period, we distinguished an annual cycle as for the CCS (i.e the LWB from January to April, and the SS from May to December) (Madin et al., 2001). For HOTS, we downloaded the available data from January 1994 to July 2021 (<https://hahana.soest.hawaii.edu/hot/hot-dogs/mextract.html>). Unfortunately, data was not available to download for the years 2002, 2003 and 2004. To analyze seasonal patterns, first we distinguished between summer, as the period of higher total mesozooplankton standing stocks, and winter, according to Landry et al. (2001). Then, we estimated the average values and standard deviation for the different seasons and performed linear regressions to obtain tendencies for each season.

3. Results

3.1. Time-series biases

We reviewed, gather, and curate the available mesozooplankton biomass data between 1971 and 2021 with the objective to obtain the baseline for future studies in the area. However, our database had evident biases: (1) mesozooplankton measurements were not performed in a fixed station throughout the years, seasons, and periods, (2) the important gaps for some years, mainly in the North and Upwelling influenced area, (3) the unbalanced number of samples collected during the main seasons (LWB and SS) and periods (day and nighttime), and (4) the absence of taxonomic composition data.

The first bias was addressed by separating the data geographically in three different areas according to their mesoscale activity and analyzing environmental parameters separately in those areas. The second and third bias cannot be directly addressed but were considered in the GAMM by adding the smoother for biomass variations throughout the years, seasons, and periods. Finally, absence of taxonomic data prevents community composition analysis, hampering to explain shifts in biomass due to abundance changes over the annual cycle and through the years.

3.2. Environmental parameters

Linear regression analysis of the environmental time-series (Fig. 2) showed an increase of all the studied parameters in the three areas. SST (Fig. 2a) exhibited an increase of about 0.5 °C since 1971 in all the areas, the North area showing the highest increase. The lowest temperatures were found in the Upwelling influenced area and the highest in the South, as expected. Chl *a* (Fig. 2b) and PP (Fig. 2c) showed the highest values in the Upwelling influenced area, as also observed during the annual cycles. Chl *a* tendency was slightly higher in the Upwelling influenced, while the highest PP tendency occurred in the South. Time-series of environmental data also showed an important interannual variability.

Spearman correlation analysis showed a negative relationship between zooplankton biomass and SST in all areas, only not significant in the Upwelling area (Table 1). In that area and in the North, we obtained negative correlations between zooplankton biomass and Chl *a* and PP values, while in the South the correlations were significantly positives.

3.3. Mesozooplankton time-series results

Time-series linear regression analyses showed a significant general nighttime decreasing tendency of zooplankton biomass (Fig. 3a) but no significant tendency for the daytime period. However, different scenarios were observed according to the area. The North (Fig. 3b) showed a significant decreasing tendency during daytime, being not significant for the nighttime data over the 50-year time-series. The South (Fig. 3c) showed significant tendencies, increasing during daytime but decreasing during nighttime. In the Upwelling influenced area (Fig. 3c) we obtained decreasing tendencies over the years, independently of the period, but just significant during nighttime.

When comparing biomass tendencies during different seasons over the 50-year period, we obtained significant biomass decreasing tendencies in all areas for both seasons (Fig. 4a). We also obtained a significant biomass decreasing tendency during the LWB in the North zone (Fig. 3b). No significant tendencies were observed in the South (Fig. 4c). For the Upwelling influenced area (Fig. 4d), both seasons also showed a significant biomass decreasing tendency.

Zooplankton showed a tendency of biomass increase towards the African coast (Fig. 5). Moreover, our results showed a biomass accumulation and increase south and around the islands, especially in Gran Canaria and Fuerteventura Islands (between 16.5° and 14°W, location of the islands shown in Fig. 1).

3.4. Annual cycle of environmental parameters and mesozooplankton biomass

SST (Fig. 6a) displayed low temperatures during the LWB as expected, with the lowest values during March, and increasing during the SS. The lowest temperature for the different zones were found in the Upwelling influenced area throughout the annual cycle. In the latter area, Chl *a* (Fig. 6b) and PP (Fig. 6c) monthly average values were higher compared to the other areas, displaying a strong peak during August. For the North and South, the Chl *a* and PP maxima were found during February, right before the zooplankton biomass increase during March (see below).

Mesozooplankton biomass annual cycle (Fig. 6d) in the North and South displayed similar pattern throughout the year: a biomass increase during the LWB, then decreasing through the SS, and exhibiting a maximum during March. In the North, biomass showed higher values during March and June. On the other hand, in the Upwelling influenced area we found higher values during February, April, and August.

Zooplankton biomass values during the LWB and SS season are given in Table 2 jointly with the average values for all data, during daytime. As observed, average values during the LWB were about a 26% higher in the northern and southern areas compared to the stratified season.

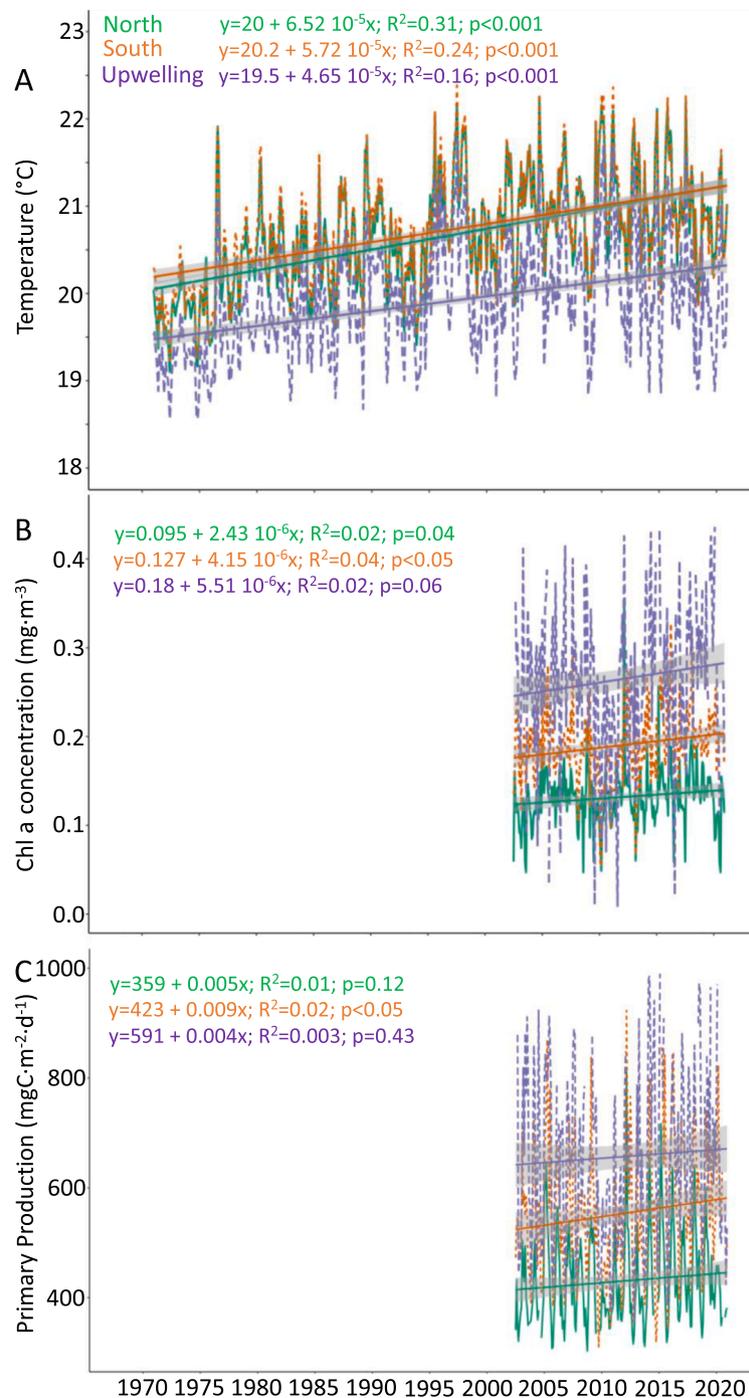


Fig. 2. Time-series of (A) monthly average sea surface temperature ($^{\circ}\text{C}$) North (29°N , $15^{\circ}30'\text{W}$), South (27°N , $15^{\circ}30'\text{W}$) and in the Upwelling influenced area (27°N , 14°W) since 1971 obtained from remote sensing. (B) Satellite data of chlorophyll a concentration ($\text{mg} \cdot \text{m}^{-3}$) and (C) primary production ($\text{mgC} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) from 2002 to 2020, also using remote sensing data (see text for coordinates explanation).

3.5. Modeling mesozooplankton biomass

Due to our time-series biases mentioned above, we opted to use a GAMM that considered the information-gaps and could provide a more accurate statistic point of view for biomass differences between areas compared to the South (β_0) and tendencies (β_1) in the different areas through the 50-year study, seasons, and periods. Results from the model (Table 3) showed no significant biomass tendency in the South (β_1 , p-value = 0.8) over the 50-year time-series. However, significant differences were found in the tendencies between the North and the South (β_1 , North, p-value = 0.02), thus the North is undergoing a decrease of

biomass ($\beta_{1,\text{North}}$ transformed biomass value tendency = -0.000081). No significant differences were found between the South and the Upwelling influenced tendencies ($\beta_{1,\text{Upwelling}}$, p-value = 0.61). The model found significant day/night differences ($\beta_{0,\text{Night}}$, p-value < 0.0001), and biomass differences in the South through the 50-year studied ($\beta_{0,\text{South}}$, p-value < 0.0001).

The model also showed a significant biomass annual variation (s (day) p-value < 0.0001), increasing between January and March and decreasing through the rest of the year, as shown by the biomass annual cycles. The day/night variability found by the model in the linear regression tendencies, the seasonal changes in biomass obtained in the

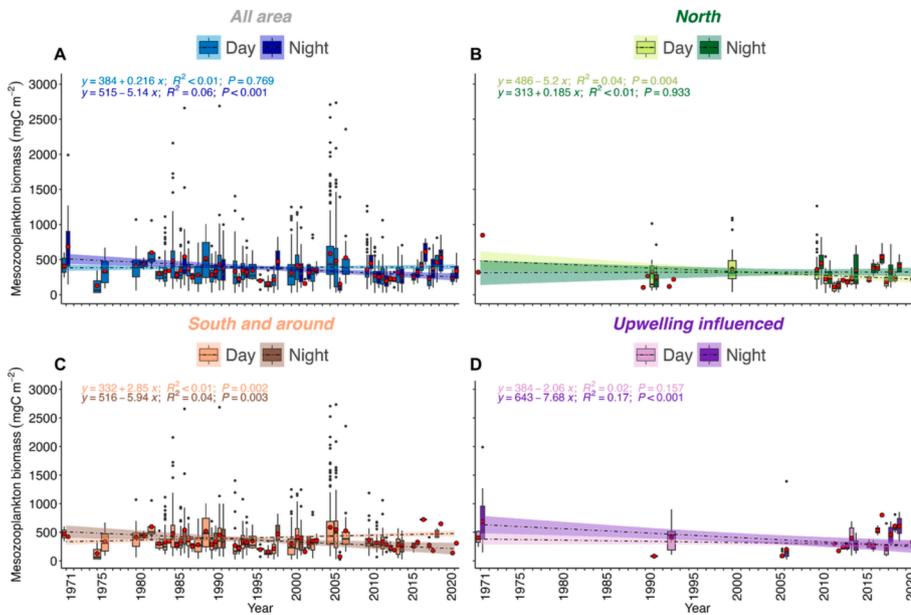


Fig. 3. Mesozooplankton biomass ($\text{mgC}\cdot\text{m}^{-2}$) in the upper 200 m depth during day and nighttime, from 1971 to 2021 in (A) all the area, (B) North, (C) South (and around) the islands, and (D) in the Upwelling influenced area. The size of the box is determined by the upper and lower quartiles, and median is indicated as a horizontal black line inside the box. Black dots represent the outliers and red dots inside the box stand for mean values. Regression line for each period (i.e. day or night) are presenting according to the period color.

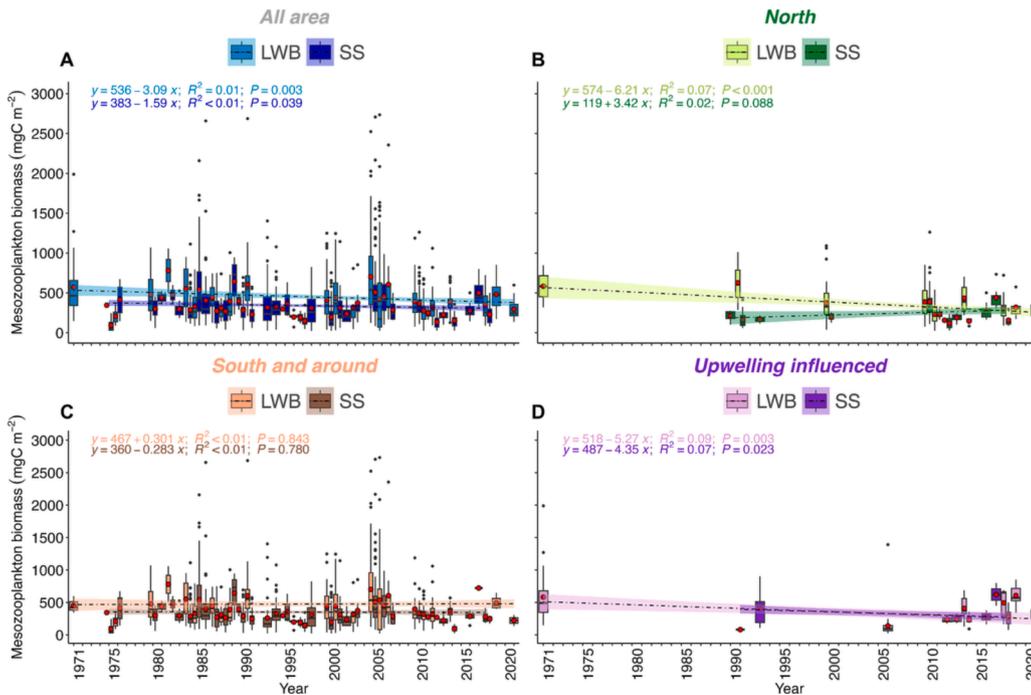


Fig. 4. Mesozooplankton biomass ($\text{mgC}\cdot\text{m}^{-2}$) in the upper 200 m depth during the Late Winter Bloom (LWB) and the Stratified Season (SS), from 1971 to 2021 in (A) all the area, (B) North, (C) South (and around) the islands, and (D) in the Upwelling influenced area, pooled day and nighttime values. The size of the box is determined by the upper and lower quartiles, and median is indicated as a horizontal black line inside the box. Black dots represent the outliers and red dots inside the box stand for mean values. Regression line for each season (i.e. LWB or SS) are presenting according to the period color.

regression, and annual cycle were also supported by the model. However, environmental parameters were not considered in the model as the different way of obtaining the biological and environmental data introduced a source of variability larger than the amount of variability they could explain. This could be solved by obtaining the environmental and biological data at the same time.

3.6. Databases comparison

When comparing the same time frame of our North time-series (Fig. 7a) with those data of HOTS (Fig. 7b) and BATS (Fig. 7c), linear regression analysis showed a biomass decreasing tendency during both seasons in the North CCS time-series, whereas in the other time-series showed biomass increasing tendencies over the period studied. Our

average values over the study period ($299.95 \pm 189.69 \text{ mgC}\cdot\text{m}^{-2}$) were similar to those obtained in HOTS ($325.77 \pm 161.45 \text{ mgC}\cdot\text{m}^{-2}$), but more than two-times lower than those recorded in BATS ($749.25 \pm 502.19 \text{ mgC}\cdot\text{m}^{-2}$).

4. Discussion

Mesozooplankton biomass data over the last five decades (1971–2021) was compiled and examined in the CCS with the aim of providing a dataset for this subtropical region of the East Atlantic that lacks of a proper time-series station (Ratnarajah et al., 2023). GAMM model showed a significant decreasing tendency of mesozooplankton biomass over the 50-year period North of the islands, the most oligotrophic area. Tendencies were also obtained for a 30-year period in

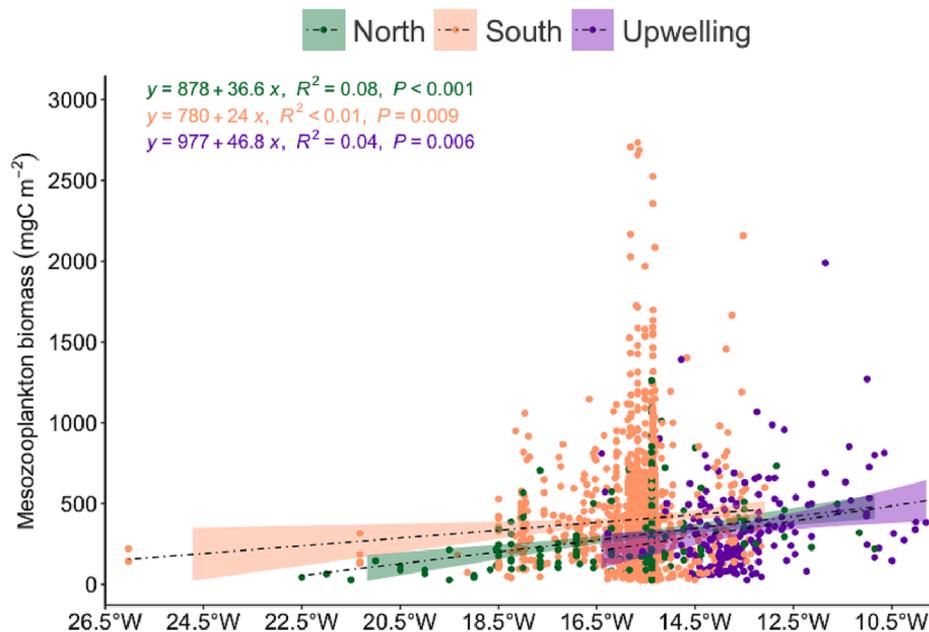


Fig. 5. Mesozooplankton biomass ($\text{mgC}\cdot\text{m}^{-2}$) longitudinal distribution in the upper 200 m depth from 1971 to 2021, during day and nighttime. Green dots stand for mesozooplankton biomass sampled in the North area, orange for the South (and around) the islands, and purple for the Upwelling influenced.

order to compare to other oceanic time-series in the ocean (HOT and BATS).

4.1. Time-series biases

Undeniably, the 50-year time-series showed some crucial biases complicating the interpretation of results, as mentioned above. Horizontal advection promotes a bias in sampling zooplankton communities, so hauls in the same geographical position also lacks sinopticity. Therefore, the division of the CCS in different areas makes our database somewhat feasible to become three time-series. Nevertheless, a fixed point could dismiss to a great extent the noise in the GAMM analysis, moreover in a highly variable area as the CCS. Further, the already well-known annual cycle of environmental parameters and zooplankton (Hernández-León et al., 2007), along with the lack of continuous data during the years and seasons, hampers the statistical analysis of the results. Also, a further major weakness of our database, which may account for much of the variation in zooplankton biomass is the lack of taxonomic information.

There is a growing recognition that knowledge of the community composition adds considerable interpretive value to any regional time-series (Mackas and Beaugrand, 2010). Standing zooplankton biomass production were used as a rough proxy for total annual productivity as it regulates material and energy flow through food webs, and therefore the amount of food for higher trophic levels (Mackas and Beaugrand, 2010; Hébert et al., 2017). High ratios of new production to total community production results in zooplankton being dominated by large copepods with short, efficient and nutritionally-rich food webs, thus supporting larger food-webs. However, this top-down control might have a strong negative effect on standing stocks resulting in a zooplankton biomass decrease. This could be assessed only by taxonomic information (Kodama et al., 2022). Moreover, when the phytoplankton community depend on recycled nitrogen, the zooplankton is dominated by gelatinous zooplankton (salps, doliolids, ctenophores) and small crustaceans, supporting a far smaller biomass of higher trophic levels (see Richardson, 2008). Thus, zooplankton production is directly affected by the taxonomic and functional community structure (St-Gelais et al., 2023). Knowledge of the taxonomic composition could help to understand the natural variability of zooplankton.

4.2. Mesozooplankton time-series

Zooplankton is being notably affected by climate change, responding in terms of long-term shifts in their biomass and abundance, composition, size, phenology, and spatial distribution (Richardson, 2008; Mackas et al., 2012; Brun et al., 2019; Conroy et al., 2023; Huggett et al., 2023; Kodama et al., 2022). The outcomes lead to a still poorly understood renewal of the biogeochemical cycles, changes in daily vertical migrations which strongly influence the carbon flux (Brun et al., 2019), and shifts in the food-web size structure and transfer efficiency (Ratnarajah et al., 2023). Results from our database showed a general temporal decrease of zooplankton biomass over the 50-year period, contrasting with reported tendencies in other time-series carried out in other subtropical oceanic sites (Madin et al., 2001; Steinberg et al., 2012). Analysis of the causes of zooplankton shifts over the 50-year period in a such different area is a tough task, thus we opted for the analysis of each area separately.

We found a zooplankton biomass decreasing tendency during the daytime and during the LWB, and a negative Spearman correlation with the environmental variables in the northern area. This decrease during the LWB might be related to the temperature increase as warmer and more stratified waters are usually associated with lower biomass (Steinberg et al., 2012). Atmospheric patterns from 1950 to 2008 showed a rather clear change in the CCS (Alonso-Pérez et al., 2011). While the Azores High during winter displayed an oceanic pattern transporting oceanic winds from the Northern Atlantic Ocean, during the 21st century the high pressure entered the African continent transporting winds from the Sahara Desert. This change in the wind pattern during winter could be enhancing ocean temperature in the CCS as observed for the area (Aristegui et al., 2009). Thus, a higher ocean stratification could be diminishing the erosion of the seasonal thermocline during winter as the effect of less convective mixing (Cianca et al., 2007). However, the available time-series of chlorophyll and primary production do not show this tendency. In any case, the latter time-series are still short (≈ 20 years) and interannual variability could mask the real tendency. In fact, the zooplankton biomass time-series during the last 10 years showed a positive tendency (not shown) due to the low biomass during 2010 and large biomass during years 2017 and 2019, something also observed in the chlorophyll and PP data.

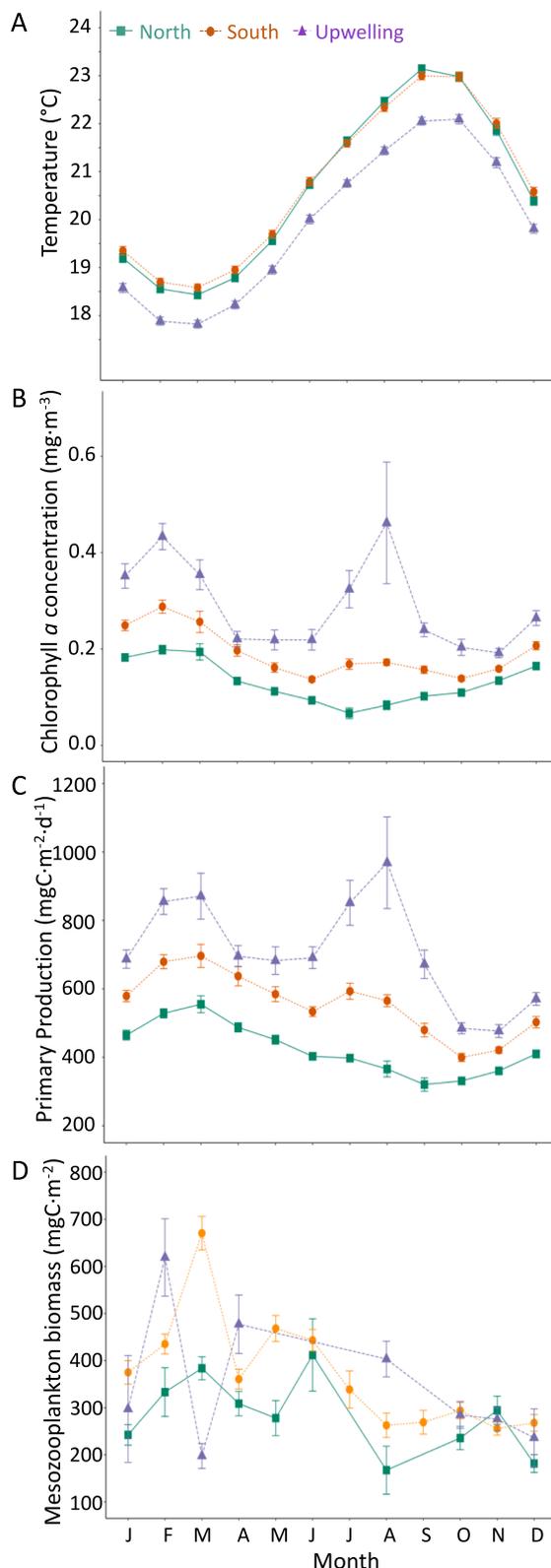


Fig. 6. Annual cycle of (A) temperature (°C) since 1971, (B) chlorophyll *a* concentration ($\text{mg}\cdot\text{m}^{-3}$), (C) primary production ($\text{mgC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) since 2002, and (D) mesozooplankton biomass ($\text{mgC}\cdot\text{m}^{-2}$), pooled day and nighttime values. Green squares represent the North, orange dots the South (and around), and purple triangles the Upwelling influenced area. Symbols stand for mean values and lines above and under the dots for standard error. Environmental variables were obtained by remote sensing (see text).

Table 3

Results obtained from the GAMM for the 50-year time-series. β_0 evaluates biomass differences in the South over the period. $\beta_{0,\text{North}}$ evaluates differences between the South (reference area) and the North, and $\beta_{0,\text{Upwelling}}$ differences between the South and the Upwelling influenced. $\beta_{0,\text{Night}}$ evaluates daily biomass differences. β_1 examine biomass tendencies over the time in the South. $\beta_{1,\text{North}}$ evaluates differences in tendencies between the South and the North, and $\beta_{1,\text{Upwelling}}$ differences in tendencies between the South and the Upwelling influenced. $s(\text{day})$ correspond to the smoother for annual variations.

Parameter	Transformed biomass values	$\pm\text{SD}$	p-value	edf
β_0	12.77	0.57	< 0.0001	
$\beta_{0,\text{North}}$	1.51	1.07	0.16	
$\beta_{0,\text{Upwelling}}$	0.79	0.93	0.39	
$\beta_{0,\text{Night}}$	0.90	0.23	<0.0001	
β_1	-0.000007	0	0.80	
$\beta_{1,\text{North}}$	-0.000081	0	0.02	
$\beta_{1,\text{Upwelling}}$	-0.000016	0	0.61	
$s(\text{day})$			< 0.0001	4.95

The upwelling affected area also showed a mesozooplankton biomass decreasing trend independently of the period or season. This decrease could be driven by atmospheric pattern described above but also wind forcing and other oceanic processes influencing the upwelling system. Global modeling studies projected consistent changes in the dominant subtropical atmospheric pressure systems that drive coastal upwelling in the EBUSs. In the CCS, climate models project a poleward displacement of the Azores High, resulting in stronger and weaker upwelling-favorable winds off the Iberian Peninsula and northwest Africa, respectively. Weakening upwelling intensity is especially prevalent during summer off northwest Africa, while the intensification in the northern CCS corresponds with more frequent high-intensity upwelling events and an extension of the upwelling season (see references in Bograd et al., 2023). Marrero-Betancort et al. (2020) showed a decreasing trend of wind intensity from the 1960 s to 2010 and increasing thereafter in CCS. This decreasing trend could explain, at least in part, the decrease in zooplankton biomass as the effect of the expected decrease in Ekman transport due to the decrease in wind intensity. However, how the EBUS will respond to anthropogenic climate change is still unknown and changes in the upwelling system is clearly outside of the scope of this study.

The spatial distribution of zooplankton biomass across the longitudinal gradient showed higher values near the African coast and south and around the islands. The island-mass effect was long ago described in the Canary Island waters (Hernández-León, 1988, 1991; Hernández-León et al., 2001). These studies explained the higher zooplankton biomass around the islands as the effect of accumulation due to the physical disturbance of the current due to the presence of the islands. Zooplankton biomass is also transported by upwelling filaments generated in the upwelling system (Hernández-León et al., 2002). This effect of mesoscale activity in the area promoted higher zooplankton biomass values near the African coast and around the islands, decreasing towards the central gyre waters (Fig. 5).

4.3. Annual cycle

The production cycle in the CCS is well documented (see Hernández-León et al., 2007): during most of the annual cycle the oceanic area is characterized by strong stratification but the thermocline is eroded during the LWB due to atmospheric cooling, promoting convective mixing, and allowing organisms to burst (Cianca et al., 2007; Neurer et al., 2007; Schmoker et al., 2012; Armengol et al., 2019). The enhanced PP allows zooplankton to grow increasing their biomass, and with a community characterized mainly by Copepoda, Hydrozoa, and Salpidae (Couret et al., 2023). After the LWB, the thermocline is re-established, and zooplankton biomass decreased after depleting the available food. During the rest of the annual cycle, the zooplankton is

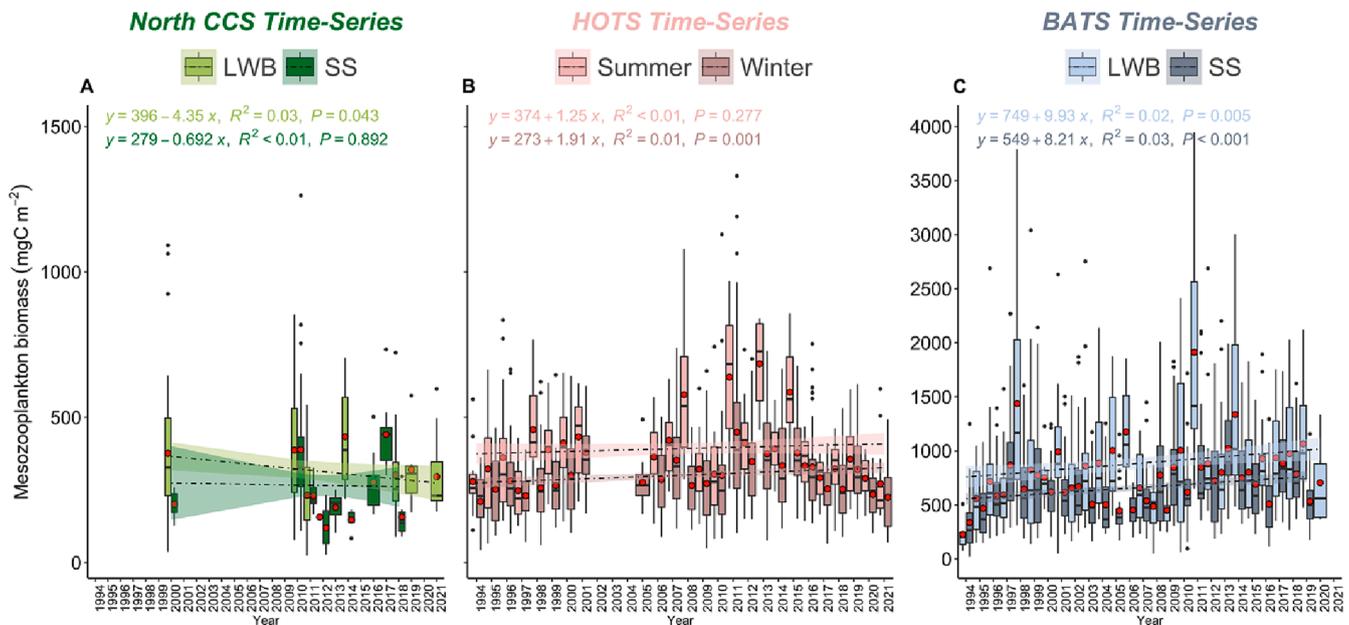


Fig. 7. Mesozooplankton biomass ($\text{mgC}\cdot\text{m}^{-2}$) in the upper 200 m depth during the Late Winter Bloom (LWB) and the Stratified Season (SS), from 1994 to 2021 in the (A) North of the Canary Current System (CSS), during day and nighttime, (B) Hawaii Ocean Time-series (HOTS), and (C) Bermuda Institute of Ocean Sciences Time-series (BATS), during day and nighttime. Data from HOTS was downloaded from <https://hahana.soest.hawaii.edu/hot/hot-dogs/mextraction.html>, and BATS data from <https://bats.bios.edu/bats-data/>. The size of the box is determined by the upper and lower quartiles, and median is indicated as a horizontal black line inside the box. Black dots represent the outliers and red dots inside the box stand for mean values. Regression line for each season (i.e. LWB or SS) are presenting according to the period color.

dominated by smaller size fractions (Couret et al., 2023). Results from the 50-year time-series, clearly show this annual cycle of environmental variables and zooplankton biomass, increasing during the LWB and decreasing through the SS. However, in the North we also observed a biomass increase during late spring (June). This maximum coincides with the maximum penetration of solar light in the area and it should be the subject of future research. In the upwelling area, zooplankton showed a higher biomass in August due to the higher intensity of the Trade Wind promoting Ekman transport and upwelling (Hernández-León et al., 2007). These areas are complex systems supporting a diversity of mid-trophic-level species key to the incorporation of primary productivity into ecosystem diversity (Bograd et al., 2023).

4.4. Modeling mesozooplankton biomass

GAMM results contribute statistically to the analysis of mesozooplankton biomass, becoming a powerful tool for data analysis since they incorporate non-parametric regressions, smoothing techniques, and generalized distributional modeling (Liu and Xiang, 2019). The model found a significant negative biomass tendency only in the North over the 50-year period, but no significant tendency was found in the Upwelling influenced area where the linear regression showed significant tendencies (except during daytime). This discrepancy should be related to the different approaches used. The GAMM incorporated more factors in the analysis such as the daily variance, differences between cruises or season to year gaps, which makes the analysis more robust than the linear regression analysis. The differences between the North and South tendencies could be directly related to the accumulation of zooplankton biomass south of the islands due to “island-mass effect” (Doty and Oguri, 1956). This term is related to the increase of plankton biomass associated with oceanic islands due to the disturbance of the oceanic flow, forming eddies downstream, thus affecting the distribution of nutrients, Chl α , PP and fish larvae (Hernández-León et al., 2001). The model also found significant day/night differences due to DVM, and between seasons (LWB and SS), because of the different productivities found around the annual cycle.

4.5. Databases comparison

The latest published time-series in Hawaii (station ALOHA) showed mesozooplankton biomass increasing over 20 years (1994–2013) related to bottom-up food-web dynamics (Valencia et al., 2016). In Bermuda (BATS), Steinberg et al. (2012) also found an increase of zooplankton biomass from 1994 to 2011, also suggesting to be promoted by bottom-up control. Extending the time-series analysis to 2021 in those time-series stations, we still obtained a positive tendency for both time-series stations (Fig. 7). By contrast, the North CSS time-series showed a biomass decreasing trend for that period.

Finally, time-series are crucial to understand the dynamics of pelagic ecosystems but most observational series were carried out only for a few decades long, limiting our understanding of long-term zooplankton dynamics (Jonkers et al., 2022). Mackas and Beaugrand (2010) suggested a century or more for the zooplankton time-series to be optimal. However, present-day time-series are to a great extent shorter and zooplankton interannual variability promote shifts in the total standing stock (Mackas and Beaugrand, 2010), community dominance and size structure (Conroy et al., 2023), spatial distribution (Huggett et al., 2023), or environmental-related variations (see Ratnarajah et al., 2023). Long time-series are needed to account for consistent biomass shift over time. Our study supports the notion that zooplankton in the North CCS time-series is decreasing as warming increases in the area. This could be the effect of the shift in the Atlantic Multidecadal Oscillation (AMO) as our time-series started during the colder period in the 70s and finished during the warmer phase during the present century (Alexander et al., 2014). Thus, the decreasing trend could be the effect of natural variability (AMO), or it is a symptom of the global warming in the area and the expected increase of oceanic deserts as the expansion of the subtropical gyre system (Siemer et al., 2021). A larger series is thus needed as suggested by Mackas and Beaugrand (2010).

5. Conclusions

Our database gathers all available mesozooplankton biomass data in

three different mesoscale activity areas of the CCS, showing biomass patterns over the 50-year period and the two characteristic productive seasons in these subtropical waters. The lack of time-series monitoring programs in the tropical-subtropical East Atlantic add value to our historical compilation of zooplankton biomass data, highlighting the need for long-term surveillance of mesozooplankton biomass. We suggest that the present database should be considered as a baseline before setting a future permanent time-series monitoring program in the CCS. For that, we encourage to set fixed time-series stations according to the mesoscale area with a monthly sampling strategy, or at least during the less and most productive season in each area (i.e. during the LWB in the North and South, and during August in the Upwelling influenced area). Light period must also be considered when sampling, ideally during both day- and nighttime to account for diel vertical migrants variability. Finally, we consider that in situ hydrographic parameters (e.g. temperature, salinity, chlorophyll *a*) measured jointly with zooplankton biomass would give a more accurate idea of the relationship between the abiotic and biotic components of the environment. In spite of the biases of this baseline data, the results showed a zooplankton biomass decreasing trend in the oligotrophic zone suggesting an effect of the increasing warming observed in the Canary Current. Whether this trend is natural variability as the effect of the AMO or global warming will remain.

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.

Data availability

Data will be available when published the article

Acknowledgments

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