







How is copepod functional diversity shaped by 2015-2016 El Niño and seasonal water masses in a coastal ecosystem of Southwest Atlantic?

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ABSTRACT

Functional traits, short life cycles, and the pivotal role in the ocean make copepod diversity a solid foundation for assessing the effect of global changes in marine food webs and ecosystem functioning. Climate change and extreme events, particularly El Niño, can affect coastal ecosystems. The Arvoredo Marine Biological Reserve (MPA), located in highly productive coastal waters of the Southern Brazilian Bight, presents complex climate and oceanographic conditions. This study investigates the influence of oceanographic processes and El Niño 2015-2016 on the copepod functional diversity from 2014 to 2016 in the Arvoredo MPA. Horizontal tows were performed using a WP2 net with a mesh size of 200 µm. The 41 species accounted for 19 functional entities and four functional groups. Our findings reveal that the seasonal intrusion of water masses influenced copepod functional diversity. During summer, the upwelling of South Atlantic Central Water increased nutrient availability and favored large herbivore-omnivores and carnivores. The Plata Plume Water enrichment during winter coincided with a decline in functional richness and abundance, leading to the predominance of the *Oithona nana*, a small-sized omnivore. Compensatory mechanisms were observed as functional equivalence and species composition shifts. *Acartia lilljeborgii* and *Temora turbinata* exhibited functional equivalence and compensated for each other in response to salinity changes associated with upwelling and El Niño. The copepod assemblage demonstrated the ability to maintain functional diversity despite changes in copepod abundance. However, the decline in functional diversity and abundance during the intense winter indicated potential disruption in trophic dynamics and ecosystem functioning. Maintaining balance and compensating for disturbances such as El Niño is crucial for marine food web resilience. The functional trait approach provided a comprehensive understanding of the copepod assemblage in Arvoredo MPA, contributing to a broader knowledge of the impact of oceanographic processes intensification. Monitoring functional diversity and abundance is crucial for evaluating the effects of copepod assemblage changes in ecosystem functionings.

Keywords: Zooplankton, Copepod traits, Marine Protected Area, ENSO, Brazilian Continental Shelf

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INTRODUCTION

Copepods are the most well-studied group concerning functional traits among zooplankton (e.g., Kjørboe, 2011; Kjørboe et al., 2015; Benedetti

et al., 2016; Brun et al., 2017). Their major traits are associated with behavior and life-history characteristics, such as trophic regime, feeding, spawning strategy, and body size, which is considered a “meta-trait” since it transcends several ecological functions and influences many other functional traits (Litchman et al., 2013; Brun et al., 2017). The functional traits distribution along space and time impacts ecological processes, linking the community structure and ecosystem functioning (Litchman et al., 2013). Therefore, classifying copepods into functional groups can improve knowledge of their ecological role in coastal ecosystems (Neumann-Leitão et al., 2018). Consequently, studies examining the variability and functional structure of the plankton community and their covariation with climate are needed to understand how Marine Protected Areas (MPA) may benefit from ecosystem-based approaches to achieve their conservation targets (Benedetti et al., 2019).

Seasonal oceanographic processes can modify the environment, briefly changing the predominant plankton functional groups; therefore, the trophic state can shape the feeding traits. For example, in oligotrophic settings, detritivore and carnivore copepods prevail, while in eutrophic conditions, the presence of herbivores and current feeding species is more frequent (Azam et al., 1983; Sherr and Sherr, 1988). The environment also selects species according to a mix of feeding or spawning strategies. Copepods with active feeding mode and broadcast spawning demand more energy and benefit when more food is available, as in eutrophic systems with abundant phytoplankton (Kjørboe et al., 2015).

The no-take Arvoredo Marine Biological Reserve (Arvoredo MPA) is located in the highly productive waters of the Southern Brazilian Bight (SBB - 22°-28°S). Being only 11 Km from the coast, this MPA is threatened by nutrients and pollutants input from the mainland, port and aquaculture activities, artisanal and industrial fishing, nautical tourism, and diving activities (Misturini and Segal, 2017). The high productivity and biodiversity in the Arvoredo MPA are attached to the seasonal presence of upwelling

waters and the influence of the Plata Plume Water (Acha et al., 2004; Brandini et al., 2018).

There is increasing scientific evidence that links El Niño and global climate change. The species adaptation strategies against climate change can be ineffective if an extreme El Niño threatens the ecological functioning and biodiversity of the coastal and marine ecosystems (Rossi and Soares, 2017). These alterations depict responses of the zooplankton community towards the El Niño-affected ecosystems worldwide. The 2010–2011 El Niño to La Niña transition in the central Mexican Pacific was defined by seasonal modifications of the mesoscale processes. These modifications seemed to disrupt the coastal-ocean gradient, importing the offshore carnivorous species to the inshore, which caused marked reductions in copepod abundance and increasing dominance of small-sized species (Kozak et al., 2018). The recent 2015–2016 El Niño, one of the strongest since the first recorded El Niño event ([Figure S1a, Supplementary Material](#)), benefited the abundances of calanoids and poecilostomatoids during the peak period, as well as the harpacticoid abundance during the waning phase of the El Niño in the Indian Ocean (Vineetha et al., 2018).

Seasonal oceanographic processes in Arvoredo MPA surroundings have been intensified by the increase in temperature anomalies over the years and by the severe 2015-2016 El Niño Southern Oscillation event (CPTEC/INPE, 2016). The consequences of El Niño in southern Brazil are intense rainfall, mainly from May to July, and an increase in the average annual temperature (CPTEC/INPE, 2016), but its influence in the South Atlantic is still not fully understood. However, Freire et al. (2017) suggest that the 2015-2016 El Niño influenced the precipitation, winds, current circulation, and seawater temperature in Arvoredo MPA surroundings. Increased rainfall may enhance river discharge, which contributes to low salinity conditions. Coincidentally, the PPW reached the Arvoredo MPA during the intense El Niño period, when the influence of its plume during winter 2016 on the southern coast of South America was more intense. In this context, we expect that copepod functional groups respond to the interannual

variability of contrasting seasons induced by climatic variability in the Southern Brazilian Bight. Therefore, functional groups should be associated with similar oceanographic conditions, and the intense meteo-oceanographic events could disrupt the natural ecosystem functioning. Thus, this study aims to evaluate the seasonal and interannual variability of copepod assemblage composition and functional diversity during three consecutive summers and winters (2014-2016) in the surrounding waters of the Arvoredo MPA.

METHODS

STUDY AREA

Oceanographic cruises were carried out around the Arvoredo Marine Biological Reserve (REBIO Arvoredo - 27°11'-27°16'S and 48°19'-48°24'W), a Marine Protected Area (MPA) covering 160 km² of the Southern Brazilian Bight (SBB - Figure 1a), managed by the Chico Mendes Institute for Biodiversity Conservation (ICMbio). Created in March 1990, the goal of the MPA is the integral conservation of the natural heritage of the coastal region to the north of Santa Catarina Island, its islands, islets, and continental shelf (Brazilian Decree No. 99.142). It covers an area of 98% underwater, in which 2% corresponds to the land area of Arvoredo, Deserta, Galé, and Calhau de São Pedro islands. This area is considered a transitional system and a boundary between tropical and temperate marine fauna (Floeter et al., 2008). More than 1,600 marine and terrestrial species have already been recorded, including 26 endangered species. (Misturini and Segal, 2017). The SBB is an oligotrophic environment due to the predominance of Tropical Water (TW) in the upper layers. Nevertheless, during summer, the interaction of northeast winds and bottom topography promotes the availability of nutrients in the euphotic zone by the upwelling of the cold and nutrient-rich South Atlantic Central Water (SACW) to the shallow area (Möller et al., 2008). During winter, the cold fronts and southern winds allow Plata Plume Water (PPW) to reach the Arvoredo MPA, which also brings nutrients to the area (Bordin et al., 2019).

Besides, the freshwater discharge of the Tijucas River creates a plume that enhances the nutrient availability throughout the area (Freire et al., 2017).

FIELDWORK AND LABORATORY PROCEDURES

The surveys were performed by the project “Monitoring Program of the Arvoredo Marine Biological Reserve” (MAArE) during austral summers and winters of 2014, 2015, and 2016. The cruises were conducted once per season, and each cruise lasted for three days. Sampling stations were limited in the north-south axis from the Porto Belo peninsula to the output of the Northern Channel of the Santa Catarina Island, and east-west by the 50 m isobath and 5 m isobath next to the Tijucas River mouth.

Salinity, temperature, depth, and dissolved oxygen were obtained in all 22 stations using a Sea-Bird Electronics (SBE) 19 plus CTD with fluorescence and oxygen sensors (Figure 1b). The Secchi disc measurements were used to calculate the depth of the euphotic zone. Plankton and seawater properties were simultaneously sampled in 12 of the 22 sampling stations (white dots; Figure 1b). Seawater was sampled with Van Dorn bottles at 0.5-meter depth, in the mid layer, and close to the bottom to analyze suspended matter, dissolved nutrients, particulate and dissolved carbon and nitrogen, and chlorophyll-*a* concentration (Grasshoff et al., 1983; SCOR/UNESCO, 1966). The chlorophyll-*a* data was provided by the MAArE project. Biochemical data were detailed in Bordin et al. (2019). Zooplankton was sampled using a WP2 net with a 0.5 m diameter mouth and 200 µm mesh size, coupled with a General Oceanics flowmeter. Horizontal tows were performed in the subsurface of the water column for 3 minutes in inner waters and for 5 minutes in 50 m isobath stations. The samples were preserved in a 4% buffered seawater-formaldehyde solution.

Zooplankton samples were subsampled using a Folsom splitter (McEwen et al., 1954) in 1/2 to 1/64 fractions according to the sample concentration. The fraction was diluted to 1,000 mL, homogenized, and a maximum of three aliquots of 10 mL were obtained to sort at least

100 copepods from each sample (Frontier, 1981). Copepods were identified to the species level under a Nikon SMZ800 stereoscopic and Olympus CX21 optical microscopes according to Björnberg (1981), Bradford-Grieve et al. (1999),

Razouls et al. (2005), and Walter and Boxshall (2018). Copepod abundance was standardized in individuals per m^3 (ind. m^{-3}). The mean and standard deviation (\pm SD) volume of water filtered by the net was $45.9 \pm 15.4 m^3$.

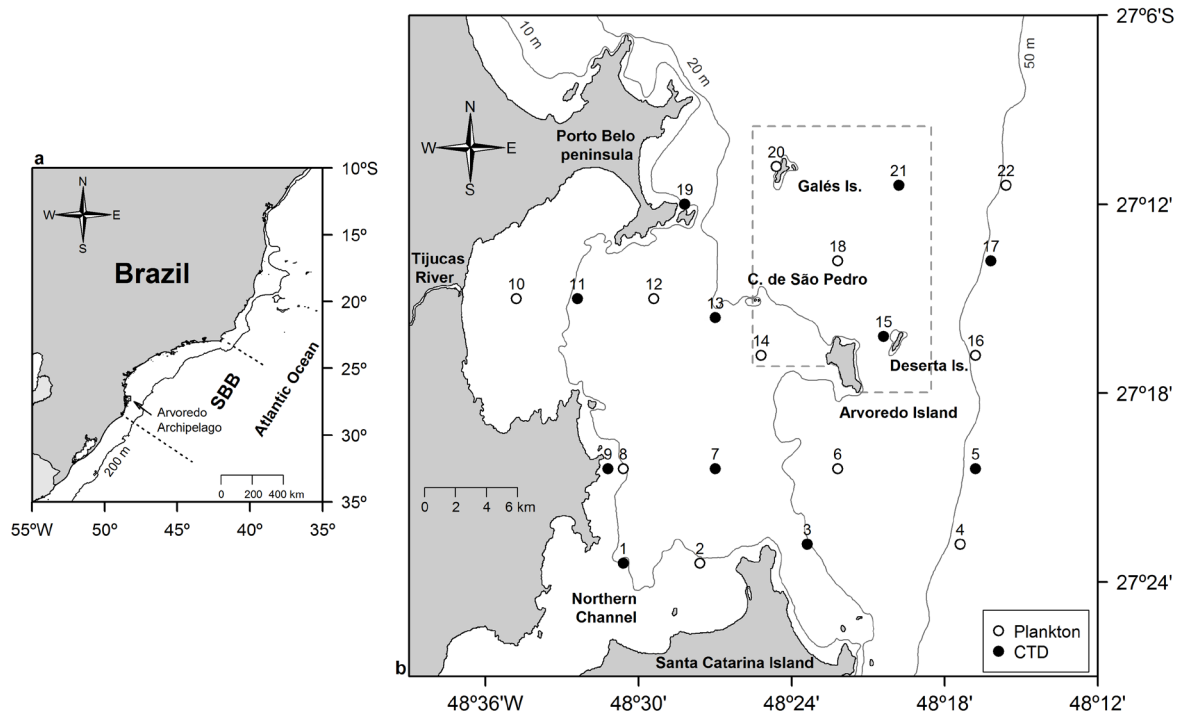


Figure 1. (a) Location of the Southern Brazilian Bight (SBB), and (b) the sampling stations distributed across the Arvoredo MPA surroundings (dashed polygon). Plankton stations (white dots): suspended matter, nutrients, chlorophyll-a, and zooplankton sampling and CTD profiles. Black dots: only CTD profiles. Isobaths: 10 m, 20 m and 50 m.

COPEPOD TRAIT DATA

The copepod functional traits were selected according to the most important traits of the life story: trophic regime, feeding and spawning strategy, and body size (Litchman et al., 2013, Benedetti et al., 2016). The body size was determined by the mean of the minimum and maximum total body length described for each species in the current literature, along with other traits (Björnberg, 1981, Bradford-Grieve, 1999, Benedetti et al., 2016, Kiørboe, 2011, Razouls, 2005). The body size was classified into three classes: Small - ≤ 1.00 mm; Medium - $1.01-2.00$ mm; Large - > 2.00 mm. The spawning strategy is determined as either broadcaster or sac-spawner. The feeding strategy

included current feeding (CF), cruise (Cru), and ambush (Amb). Species having a mix of two or more feeding strategies were assigned the corresponding levels. The trophic regime was determined as herbivore, carnivore, omnivore, detritivore, or a combination of them. The qualitative species, those without valid information about traits, and taxa that do not represent one single species were removed from the statistical analysis (Table S1).

DATA ANALYSES

Water masses were characterized using thermohaline indices provided by Piola et al. (2008) and Möller Jr. et al. (2008). The temperature-salinity diagram and horizontal distribution of surface water

temperature were constructed using the Ocean Data View (ODV) software (Schlitzer, 2016) and the 'fields' Package in R (R Core Team, 2022; Nychka et al., 2021), respectively.

To address the intensity of the El Niño-Southern Oscillation (ENSO) cycle over the sampling period, ENSO data was accessed in R (Albers, 2020). The Oceanic Niño Index (ONI) tracks the 3-month average and serves as NOAA's primary indicator for monitoring the oceanic part of the seasonal climate pattern of ENSO. Additionally, to assess how the in situ temperature measurements from 2014-2016 differed in relation to long-term temporal variability (1982-2021), satellite-based Sea Surface Temperature (SST) data were obtained from the COPEPOD database (www.st.nmfs.noaa.gov/copepod/time-series/) at Longitude: -48.58; -48.18; Latitude: -27.16; -27.41. For spatio-temporal analysis, temperature data from the NOAA Optimum Interpolation Sea Surface Temperature dataset (OISST version 2.1, www.ncdc.noaa.gov/oisst) were used. The datasets were acquired in a prepared-product form, and monthly mean values by year were downloaded as a regular global grid. ICES-WGZE standardized pixel plots were performed within the specified coordinates, and the resulting time series were plotted to visualize the seasonal cycle of satellite-based SST and matrices of monthly means.

The functional trait data were transformed into a binary matrix to address the issue of multiple levels within each functional category, such as species with two trophic regimes or combined feeding strategies. The matrix structure consisted of copepod species in each row and functional traits in the columns. For example, if a species is omnivore-herbivore, a value of 1 was assigned in the columns corresponding to omnivore and herbivore, and a value of 0 was assigned in the columns related to the other trophic regimes.

To ordinate the species based on their functional traits and create a hierarchical clustering, the Unweighted Pair Group Method with Arithmetic Averages (UPGMA) based on the Bray Curtis dissimilarity was performed. The resulting groups from the similarity profile routine (SIMPROF; Clarke et al., 2008) were then regrouped based on the major similar traits among species. The hierarchical

clustering and SIMPROF analyses were performed using 'vegan' and 'clustsig' Packages (Oksanen et al., 2019; Whitaker and Christman, 2014).

Pairwise functional distances between functional entities were computed using the Gower distance, which allows for the combination of different types of variables (Gower, 1971). These distances were used to generate combinations of trait values called Functional Entities (FE) for each of the four functional categories (Mouillot et al., 2013). The FE coordinates on the first four axes (PC) of the Principal Coordinate Analysis (PCoA) were retained to build a multidimensional functional space (Villéger et al., 2008; Mouillot et al., 2013) across years (2014, 2015, and 2016) and seasons (summer and winter).

Procrustes Rotation analysis was conducted to assess changes in functional space between years (interannual variability) and seasons (summer and winter) (Legendre and Legendre, 2012). This analysis compared pairs of summer surveys (e.g. summer 2014 vs. summer 2015, summer 2014 vs. summer 2016, summer 2015 vs. summer 2016) and pairs of winter surveys. In addition, pairs of summer and winter for each year were compared to test within-year variability. All four PCoA axes were considered to account for the multidimensionality of functional spaces. The significance of fits was tested using the PROTEST routine and was adjusted using Bonferroni correction.

Different indexes of Functional Diversity (FD) were calculated, ranging from 0 to 1. Functional Richness (FRic) represents the extent of the functional space filled by the FEs in a community. Functional Evenness (FEve) measures the evenness of species abundance distribution along the minimum spanning tree in the multidimensional functional space. Functional Dispersion (FDis) is the mean distance of individual species to the centroid of all species in the multidimensional trait space. Functional Divergence (FDiv) represents the proportion of total abundance supported by species with extreme functional traits, i.e., the entities at the limits of the functional space (Mouillot et al., 2013). The FD indices were calculated using the FD and vegan packages (Laliberté et al., 2015; Oksanen et al., 2019).

Redundancy Analysis (RDA) was performed to investigate relationships between trait abundances and physicochemical variables (Legendre and Legendre 2012). Abundances were Hellinger-transformed to reduce differences in magnitude. Collinearity among physicochemical variables was diagnosed using the Variance Inflation Factor (VIF), and variables with $VIF > 10$ were removed from the analysis. A permutation test based on Monte Carlo simulations was applied to test the null hypothesis of independence between the response and explanatory matrices, as well as the significance of each canonical axis and physicochemical variable (Borcard et al., 2018). Biplots were generated using scaling = 2, and only significant explanatory variables were included. Sites were plotted using linear combinations of constraining variables (fitted site scores). Redundancy Analysis and additional tests were performed using the *vegan* (Oksanen et al., 2019) and *HH* (Heiberger, 2013) packages.

All graphics and analyses, except for the T-S diagram, were performed in R (R Core Team, 2022). Most graphics were produced using the *ggplot2* package (Wickham, 2016).

RESULTS

OCEANOGRAPHIC CONDITIONS

The following water masses were identified in the study area: Subtropical Shelf Water (STSW), Tropical Water (TW), South Atlantic Central Water (SACW), and Plata Plume Water (PPW) (Figure 2). The STSW was predominant from the surface to the depth of 25 m during summers and 50 m during winters. The TW occurred only during summers in depths of 10 m to 25 m. The SACW was also observed exclusively during summers, mostly below 30 m depth. In addition to the STSW, the PPW was predominantly detected on the surface during winters (Figure 2). Moreover, the continental runoff from the Tijucas River (TRp) and the Northern channel of Santa Catarina Island (NC) created a plume of low salinity (<33.5) in the shallow area. This plume had a lower salinity than STSW during summers, and lower than PPW during winters (Figure 2).

The year-to-year in situ temperature showed that the warmest summer and the coldest winter

occurred in 2016 (Figures 3 and 4), coinciding with the strongest El Niño recorded thus far (Figure S1a). The monthly mean satellite Sea Surface Temperature (SST) indicated longer periods of high and low temperatures, resembling summer and winter, respectively, in 2016 compared to 2014 and 2015 (Figure S1b). In situ sea surface temperature exhibited a relatively uniform distribution during summer but increased over the three years (Figure 3). A clear trend of SACW intrusion at the bottom was observed. The SACW intrusion ($T: 18.5^{\circ}\text{C}$) reached the 50 m isobath in 2014, moved closer to the coast in 2015, and resulted in an upwelling reaching the euphotic zone in the inner waters in 2016. No apparent water temperature vertical stratification occurred during winter (Figure 4), and due to the high continental runoff and water mixture, the mean euphotic zone was usually shallower in winter (45%) than in summer (76%). The year of 2016 stands out with extended periods of cold monthly means from June to September (Figure S1a). In addition, the PPW was detected with the highest intensity during winter 2016, corroborating the low temperatures (Figure 4).

COPEPOD FUNCTIONAL GROUPS AND DIVERSITY

Out of the 48 identified species, six were identified only qualitatively (Table S2) and 11 and five were exclusively found during winter and summer, respectively. Copepod average abundances were the highest in 2014 and the lowest in 2016 in both seasons. The sharpest decreases occurred during summer. It decreased almost by half from the summer of 2014 to 2015 (12,044 ind. m^{-3} and 7,039 ind. m^{-3} , respectively), and nearly three times from 2015 to 2016 (2,525 ind. m^{-3}). The peak in summer 2014 was due to the massive abundance of *Acartia lilljeborgi* in the shallow area near the Tijucas River mouth, which represented 94% of copepods in this area. Copepods were less abundant in winter than summer (3,883 ind. m^{-3} , 1,472 ind. m^{-3} , and 951 ind. m^{-3} , respectively), and decreased over the years. The copepod assemblage shifted completely in composition during winter 2016, depicting the dominance of *Oithona nana* that is related to the stronger influence of PPW (Figure 2; Table S2).

The cluster analysis (Figure 5) showed four functional groups (FG) that were primarily distinct in sac-spawner species (Groups 1 and 2) and egg broadcasters (Groups 3 and part of 4). The trophic regime was also a trait that defined the FG. Groups 1 and 4 were both carnivore copepods, distinguished into small and large sizes, respectively. Although *Euchaeta marina* is a sac-spawner species, it was separated from the others due to its large size (Figure 5). Most species

were from Groups 2 and 3, represented mainly by omnivore copepods. The exception was the carnivore *Corycaeus speciosus*, present in Group 2 with omnivore species (Figure 5). The Group 2, dominated by ambush and cruise-feeders of small- and medium-size, was formed by Cyclopoida and Harpacticoida species. Group 3 contained Calanoida exclusively, with 24 species (Figure 5), most of them are medium- and large-size, current-feeders, and omnivores and herbivores.

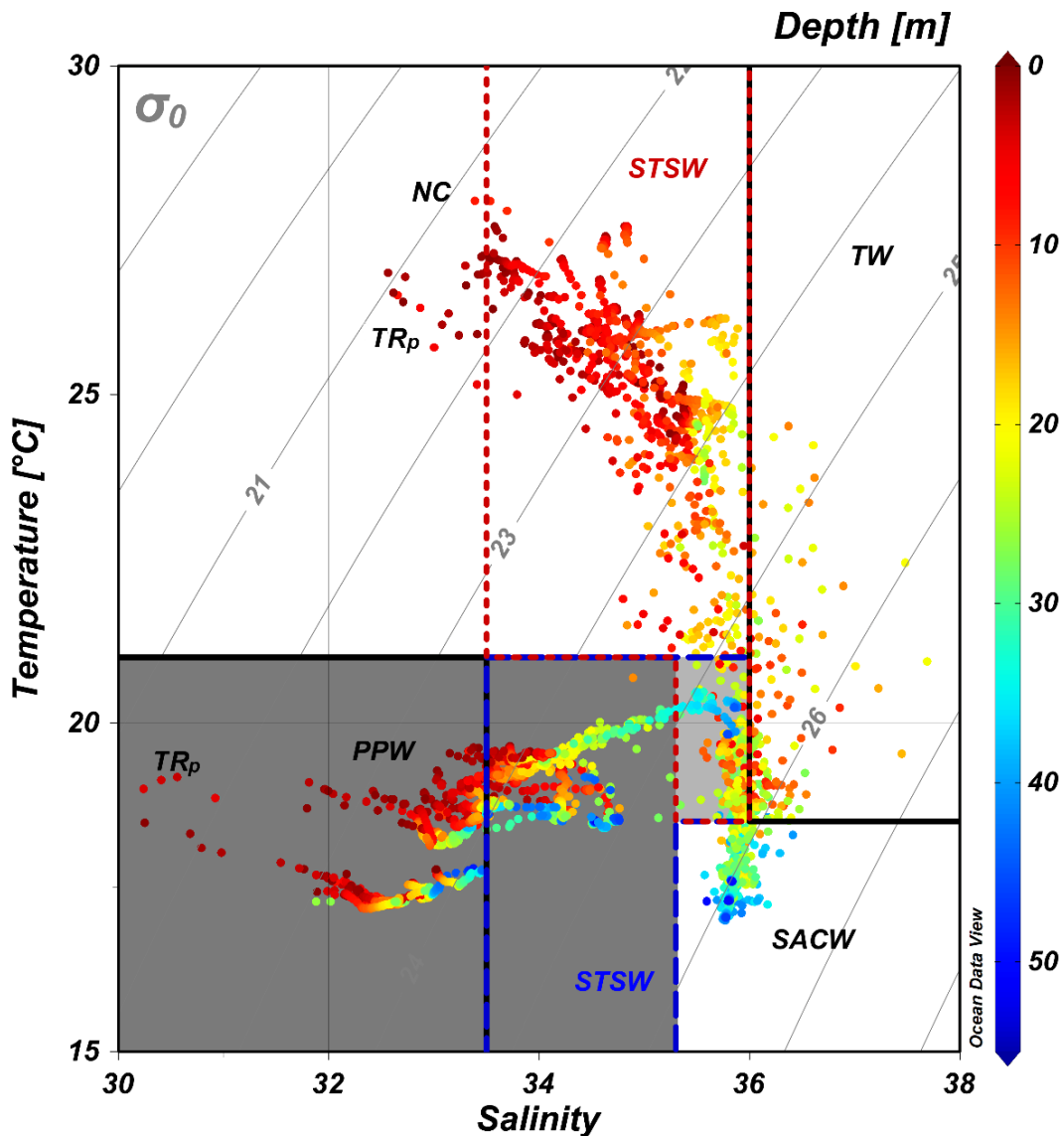


Figure 2. Temperature-salinity diagram of the Arvoredo MPA surroundings during summer (white background), winter (dark gray), and in both seasons (light gray) over the years (2014-2016). NC: Northern Channel of Santa Catarina Island; TRp: Tijucas River plume; SACW: South Atlantic Central Water; STSW: Subtropical Shelf Water; TW: Tropical Water; PPW: Plata Plume Water. Dot colors are the depth shown in the vertical scale.

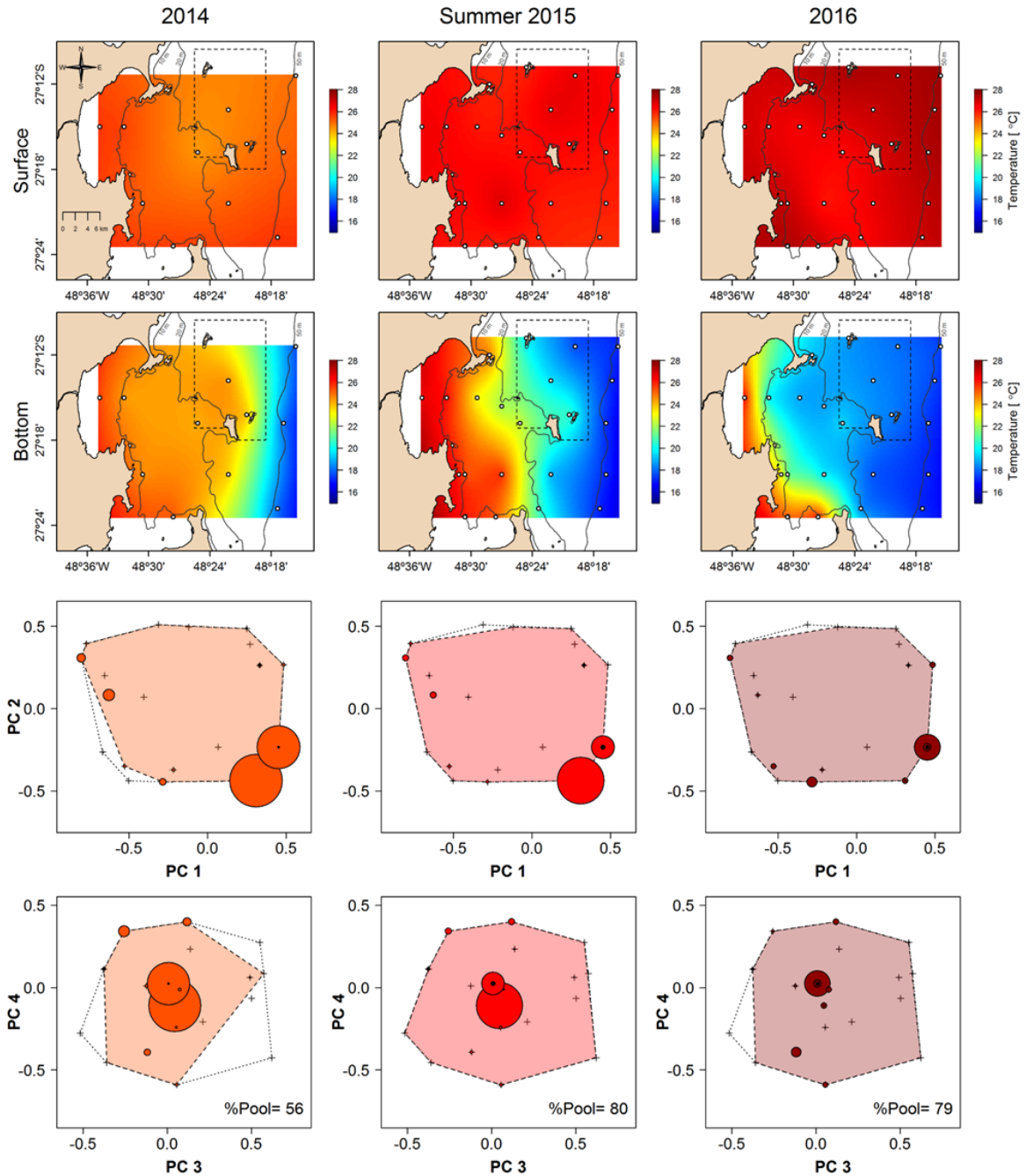


Figure 3. Temperature variability on the surface and bottom during summer in the Arvoredo MPA surroundings (2014-2016). The PC1–PC2 and PC3–PC4 axes from the PCoA represent the functional entities (FE) distribution in the functional spaces. The gray dashed line shows the global pool of the assemblage, including the 41 species. Color-filled areas show the functional volume by each season/year, and the colors demonstrate the interannual temperature variability of summers. The point size represents the FE relative abundance in relation to the total abundance of both summers and winters. Gray crosses are FE absent in the assemblage. Functional richness is expressed as a percentage of the global pool (%Pool).

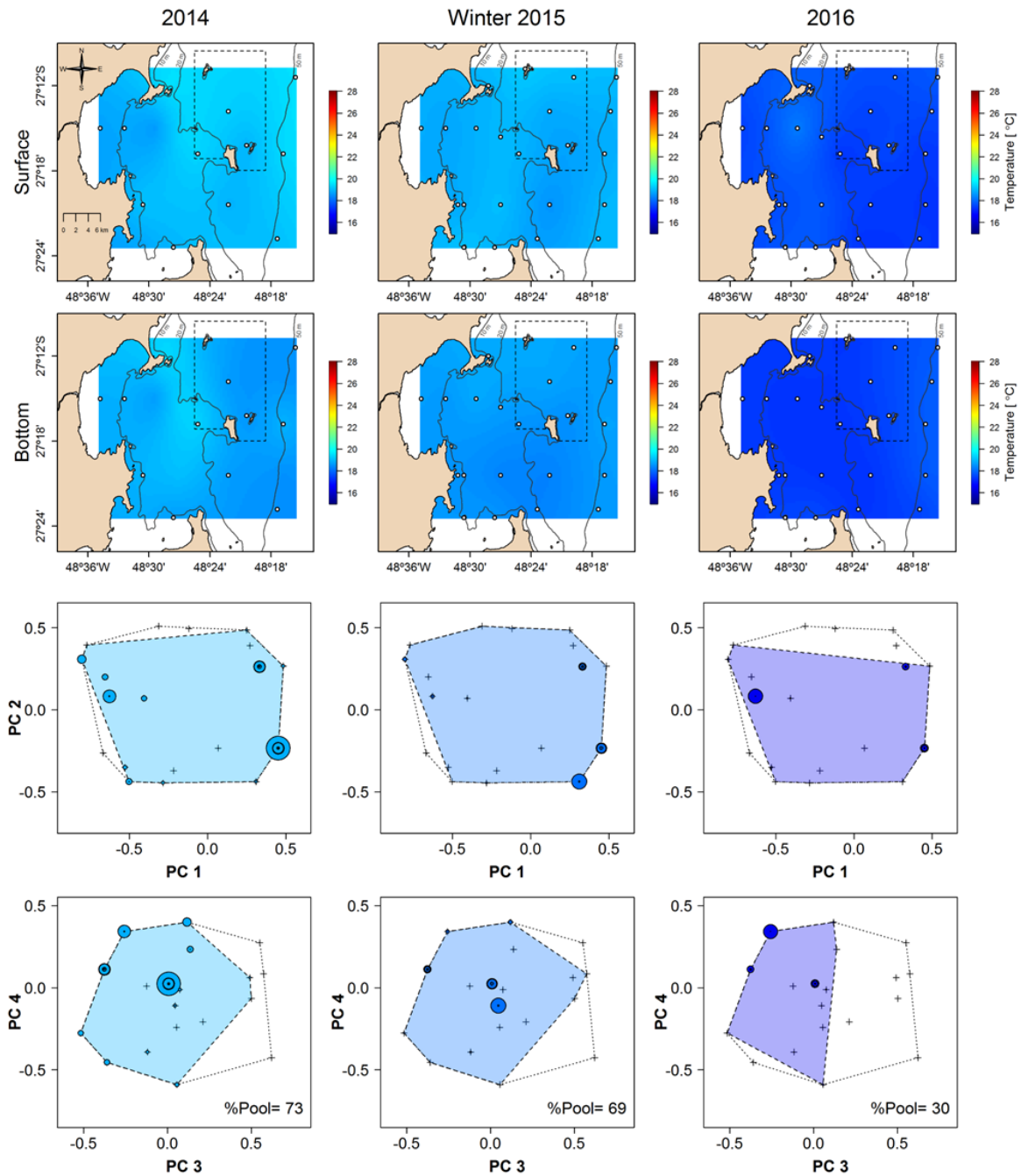


Figure 4. Temperature variability on the surface and bottom during winter in the Arvoredo MPA surroundings (2014-2016). The PC1–PC2 and PC3–PC4 axes from the PCoA represent the functional entities (FE) distribution in the functional spaces. The gray dashed line shows the global pool of the assemblage, including the 41 species. Color-filled areas show the functional volume by each season/year, and the color demonstrate the interannual temperature variability of winters. The point size represents the FE relative abundance in relation to the total abundance of both summers and winters. Gray crosses are FE absent in the assemblage. Functional richness is expressed as a percentage of the global pool (%Pool).

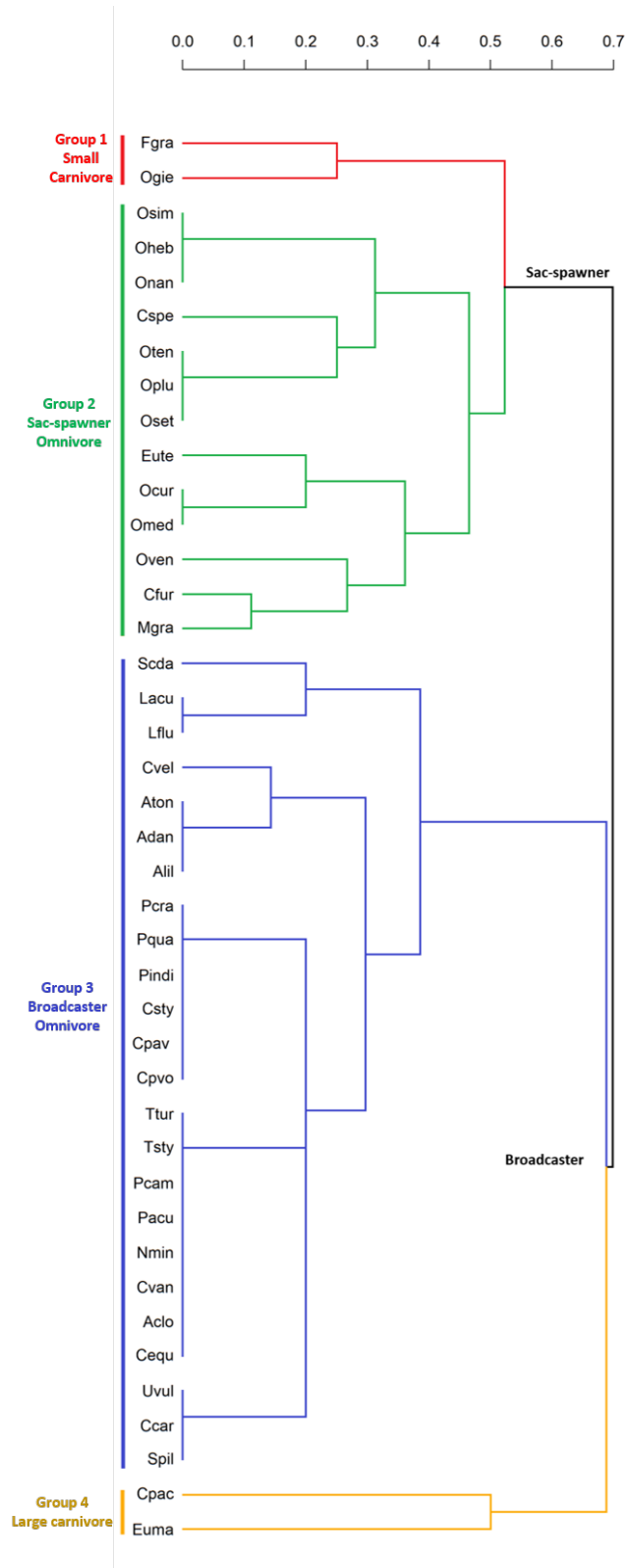


Figure 5. UPGMA cluster based on the Bray Curtis index showing the ordination of the 41 copepod species according to functional traits. [Table S1](#) shows the species codes.

A total of 19 functional entities (FE) were identified based on unique combinations of categorical morphological, physiological, and life history traits of the 41 copepod species (Figure 6, Table S1 and S2). In general, FRic presented a trend to increase in summers from 2014 to 2015 (Figure 7). The summers of 2015 and 2016 showed similarly higher FRic (0.8 and 0.79) and FEve (0.29 and 0.26) than summer 2014 (0.55 and 0.14, respectively). The increasing FRic during summers was associated with the appearance of carnivores *Corycaeus speciosus* (medium-size) and *Candacia pachydactyla* (large-size) in 2015 and 2016. Moreover, this increase in FRic was also associated with the abundance increasing in 2016 of detritivore-omnivore *Oncaea venusta* and the herbivore-omnivore *Undinula vulgaris*, medium and large-size respectively (Figures 3 and 6). Nevertheless, the large carnivore *Euchaeta marina* disappeared in 2015 and 2016. It is noteworthy that the large abundance of *Acartia lilljeborgi* decreased during the warming summers, whereas the most redundant functional entity with eight species, represented in the summers by *Temora turbinata*

and *T. stylifera*, increased in abundance, all these species belong to the same functional group 3 (Figures 3, 5, and 6). The most important functional entities in summer have a similar combination of traits of medium body size, herbivore-omnivore, and broadcaster, which are the traits with the highest abundance in all three summers (Figures 3 and 6). The only difference between them is that *A. lilljeborgi* performs a mixed foraging behavior (current feeding - CF - and ambush) and the other one is exclusive CF.

The winters of 2014 and 2015 were similar in terms of functional entities (FE: 16), FRic (0.73 and 0.69), and FDiv (0.91 and 0.98, respectively), with a higher value than 2016 winter (Figure 7). Despite hosting a smaller proportion of copepod assemblage (30% of the total pool) and the lowest FDiv (0.79), the 2016 winter showed the highest FEve (0.40) and FDis (0.26) (Figure 7). *Oithona nana*, a small sac-spawner, prevailed in the severe winter of 2016, rather than the medium broadcaster copepods that were abundant during 2014 and 2015 (Paracalanidae and Temoridae; Figures 4 and 6).

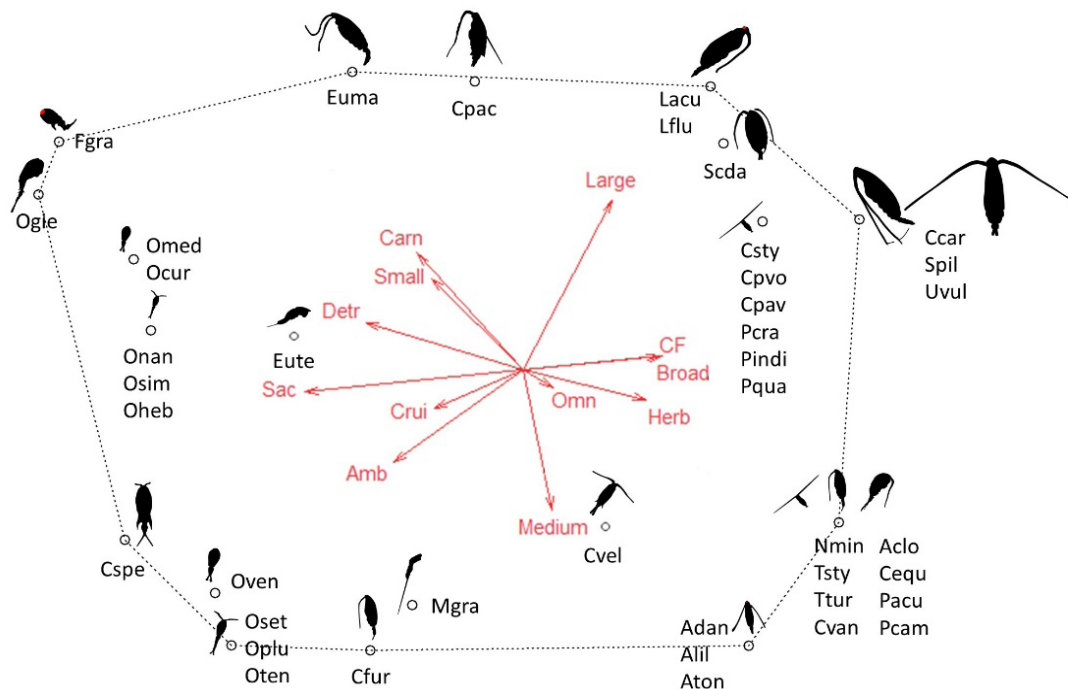


Figure 6. Copepod functional entities silhouettes positioned in the 2-dimensions functional space built based on four copepod traits. In the center, the copepod trait vector is depicted. Carn: carnivore. Detr: detritivore. Omn: omnivore. Herb: herbivore. Amb: ambush. Cru: cruise. CF: current feeding. Broad: broadcaster. Sac: sac-spawner. Table S1 shows species codes.

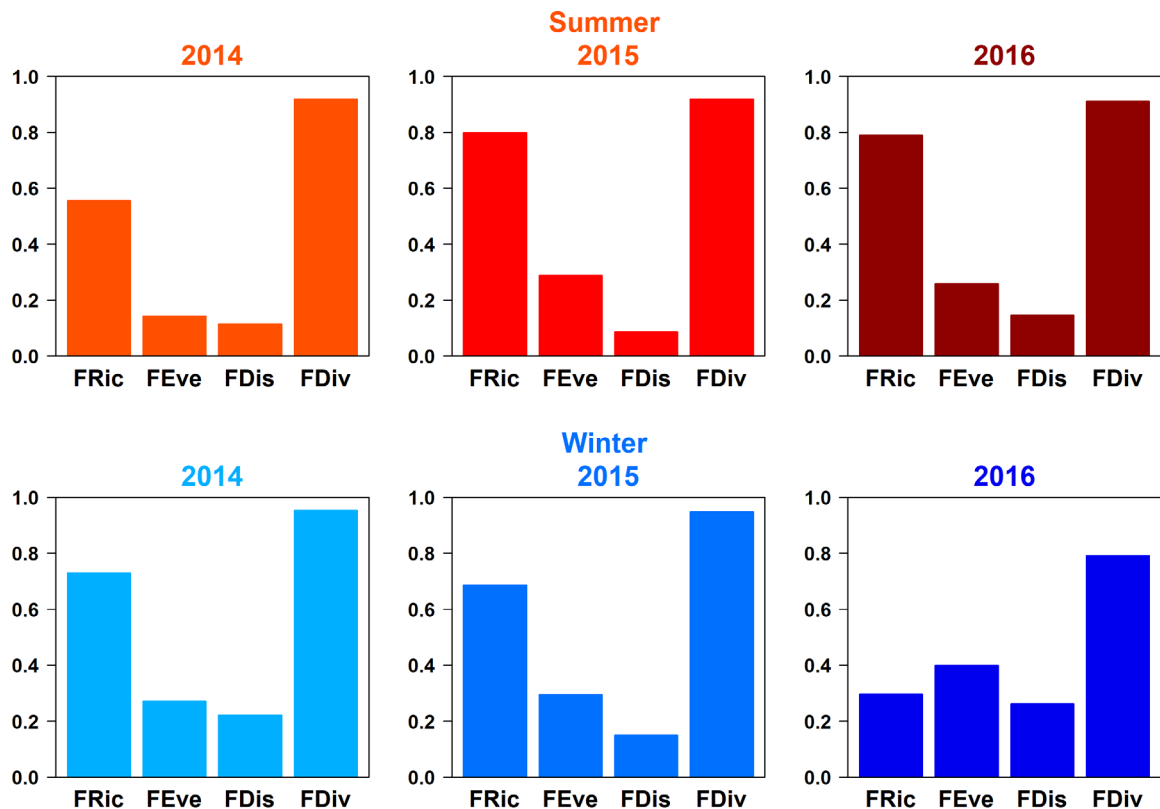


Figure 7. Interannual and seasonal changes in the copepod functional diversity in the Arvoredo MPA surroundings. Barplots show the functional diversity indices. FRic: Functional Richness, FEve: Functional Evenness, FDiv: Functional Divergence, FDis: Functional Dispersion.

Interannual variability among functional spaces was subtle since they were all correlated (Table 1). However, summer 2014 seems to be the most different, with the smallest pool filling the functional space (56% of the pool), compared to summer 2015 (80% pool, correlation = 0.769) and summer 2016 (79% pool, correlation = 0.804). In contrast, winter 2016 was less correlated between other years, with only 30% of the functional space pool filled (Figure 4). In the same way, correlations between summer and winter seasons showed a small variability in the maintenance of the functions performed by the functional entities within years (Table 1).

Redundancy Analysis ordination (RDA) revealed that environmental variables explained 47% of abundance traits distribution (Figure 8, $F = 3.863$, $p = 0.0001$). The RDA1, which explained

62.4% of the constrained variance ($F = 32.468$, $p = 0.0001$), represented a clear distinction between summer and winter. Over the years, there was an increase in temperature and a decrease in salinity during summer. POC exhibited higher levels in both seasons, with silicate peaking in winter, particularly in 2016. In terms of suspended matter, ISM gradually decreased during summer.

Small-sized omnivores, sac-spawner, and ambush feeder copepods were related to winter, while traits such as medium-sized, cruiser, and broadcaster copepods were associated with summer (Figure 8). Notably, winter 2016 was an outstanding period that showed the most severe winter conditions, featuring the lowest temperature and the highest silicate and POC (Figure 8). In these winter conditions, large carnivores were absent (Figures 4 and 6).

Table 1. Results of Procrustes Rotation analysis and PROTEST assessments on interannual and seasonal variability among functional spaces during summer and winter. Significances were adjusted by Bonferroni correction.

Procrustes/PROTEST	Sum of squares	Correlation	Significance (adjusted)
Summer/2014 vs Summer/2015	0.411	0.768	0.0009
Summer/2014 vs Summer/2016	0.353	0.804	0.0009
Summer/2015 vs Summer/2016	0.171	0.91	0.0009
Winter/2014 vs Winter/2015	0.341	0.812	0.0009
Winter/2014 vs Winter/2016	0.512	0.699	0.0009
Winter/2015 vs Winter/2016	0.454	0.739	0.0009
Summer/2014 vs Winter/2014	0.486	0.717	0.0009
Summer/2015 vs Winter/2015	0.420	0.762	0.0009
Summer/2016 vs Winter/2016	0.518	0.694	0.0009

DISCUSSION

Our findings demonstrate that the intensification of oceanographic processes (SACW, PPW, and TRp) influenced by the El Niño 2015-2016, together with the increase in SST in summer and decrease in winter, had a significant impact on the functional diversity of the copepod assemblage.

SACW intrusion is usually limited to the approximately 50 m isobath; however, in 2016, it raised up due to the intensified 2015-2016 El Niño. This upwelling of SACW normally occurs at Santa Marta Cape and Cabo Frio (Brandini et al., 2018). During summer, the SACW upwelling resulted in increased nutrient availability in the waters surrounding the Arvoredo MPA (Bordin et al., 2019), creating a more favorable environment for large herbivore-omnivores as *Undinula vulgaris*, as well as carnivores like *Corycaeus speciosus* and *Candacia pachydactyla*, and the medium-sized detritivore *Oncaea venusta*. During warmer summers, carnivore copepods are more abundant

in the oligotrophic conditions of the 50 m isobath. These findings are consistent with observations in subtropical environments, similar to what has been observed in the Mediterranean Sea (Benedetti et al., 2018), where carnivores tend to be more dominant in nutrient-poor conditions, while herbivores and omnivores tend to be dominant in productive environments.

During the winters, despite the declining SST over the years, the increase in PPW sprawling around Arvoredo MPA coincided with a decrease in functional richness and abundance, along with the absence of certain functional entities. For example, carnivores and detritivores from Group 2 and 3, such as *Scolecithrix danae* (winter 2015 and 2016), *Oncaea species*, *Centropages velificatus*, *Macrosetella gracilis*, *Labidocera acutifrons*, and *L. fluviatilis* (winter 2016), were not present, whereas there was an increase in the abundance of *Oithona nana*. The enrichment by PPW during winter likely favored the dominance of *O. nana*.

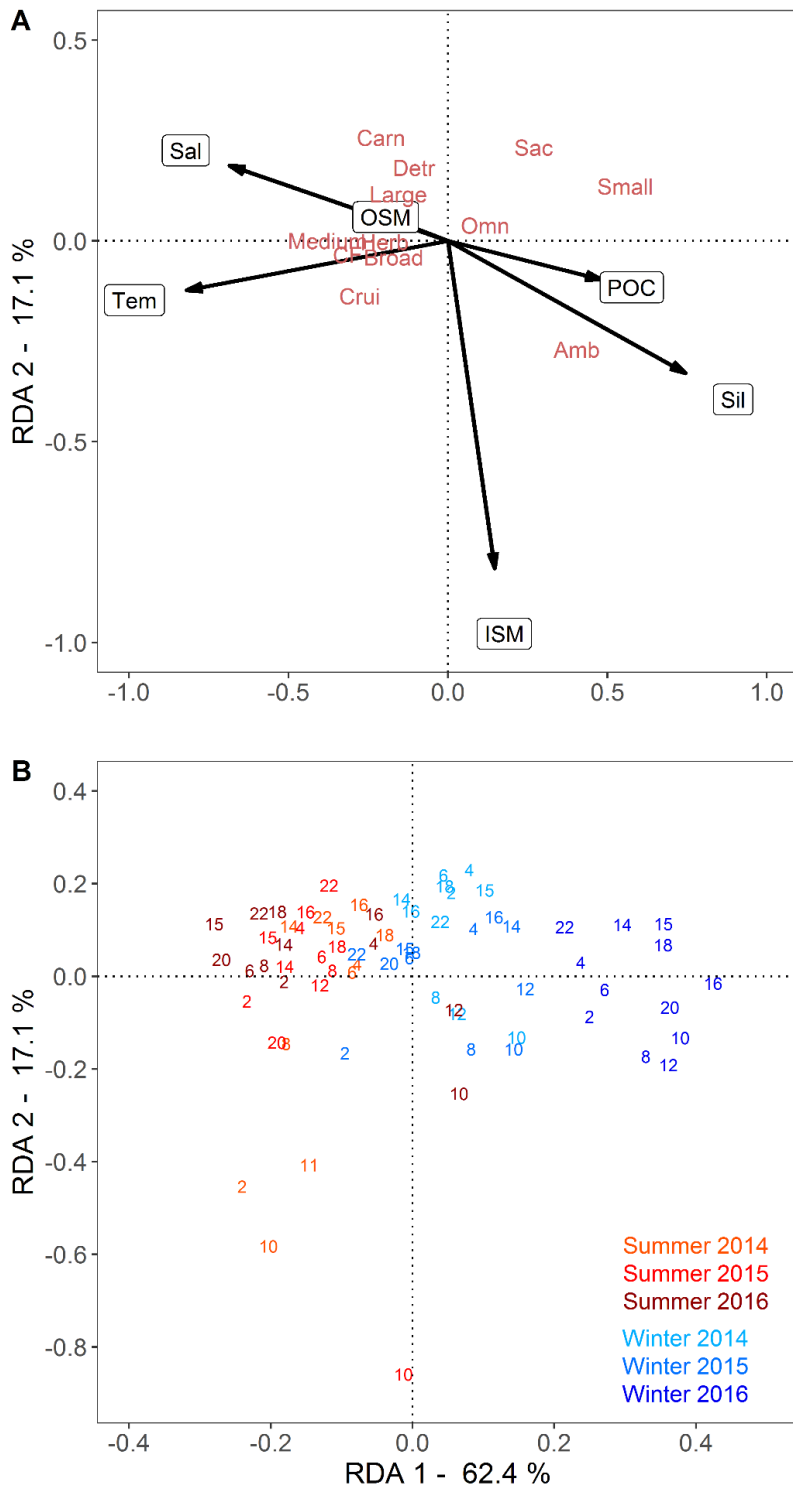


Figure 8. Biplot of the first and second axis of the redundancy analysis ordination (RDA) performed with environmental and abundance of traits (A), and the oceanographic stations distribution (B) in relation to the seasonal variability of the Arvoredo MPA surroundings over the years 2014-2016. Only the environmental vectors that were significantly correlated with the RDA axes were retrieved on the plot. ISM: inorganic suspended matter, OSM: organic suspended matter, POC: particulates organic carbon, Tem: temperature, Sal: salinity, Sili: silicate. Trait codes are shown in [Table S1](#).

The findings are consistent with the results reported by Bordin et al. (2019), showing that an increase in nitrate-nitrite concentrations throughout summer was associated with SACW upwelling. Moreover increased silicate and nitrate-nitrite, chlorophyll-a, POC, and PON concentrations during winters was associated with PPW sprawling. Therefore, the intensity of the SACW and PPW, rather than just the changes in SST, played a key role in the occurrence of these species.

Even under atypical environmental conditions, the maintenance of functional diversity in copepod assemblages may be attributed to compensatory mechanisms. These mechanisms include changes in the size structure, increased functional redundancy, and shifts in species composition (Hooper et al., 2005). Our study further reveals two compensatory mechanisms that drive copepod functional diversity in the Arvoredo MPA. Firstly, *Acartia lilljeborgii* and *Temora turbinata*, belonging to the same functional group, demonstrate functional equivalence and can compensate for each other in response to environmental changes such as salinity increases associated with upwelling intensification and El Niño events. Secondly, the decrease in functional richness was followed by the dominance of *Oithona nana*, a small-size omnivore that is favored by high food availability and the advantage of its ambush behavior in the copepod community.

The broadcaster omnivore-herbivore copepods belonging to Group 3, such as *A. lilljeborgii*, *T. turbinata*, and *Paracalanus indicus*, are dominant when the river plumes (TRp and PPW) bring more nutrients to the shallow areas, increasing chlorophyll-a concentrations (Bordin et al., 2019). *A. lilljeborgii* and *T. turbinata* belong to the same functional group and are functionally equivalent, that is, they perform similar ecological roles in the ecosystem (Hubbell, 2005), even though they may differ in terms of seasonal abundance peaks and biological traits, such as foraging behavior as the Acartiidae are mixed. While *A. lilljeborgii* was very abundant in 2014 and 2015, disappearing in 2016, a year characterized by higher salinity associated with the presence of SACW, *T. turbinata* demonstrated greater tolerance to salinity variability and exhibited high abundance (Menezes

et al., 2019). The functional equivalence of these two species is important for compensating for each other in the face of environmental changes, such as salinity increases associated with upwelling intensification and El Niño events.

The increased nutrient levels and higher chlorophyll-a concentrations contributed to the abundance of sac-spawners with ambush-feeding behavior, especially during winter 2016. The abundance of *Oithona nana* was favored by the combination of its ambush feeding behavior and availability of food resources in winter. As a sac-spawner, it invested less energy in growth and feeding and more in developing egg sacs. Moreover, broadcasters spent more energy on survival and capturing food. The trade-off between feeding efficiency and available energy for growth and survival in low-food conditions is a common phenomenon among copepods (Litchman et al., 2013; Kiørboe, 2011). Besides, the dominance of small-size omnivores in the subtropical coastal areas with estuarine influences is a well-established pattern due to the high food availability and diversity in these ecosystems (Calbet, 2008; Neumann-Leitão et al., 2018).

These two compensatory mechanisms indicate that, despite the decrease in abundance over the years, the copepod assemblage can perform its role in the ecosystem and maintain its functional diversity. However, it is crucial to note that abundance changes can still significantly affect the ecosystem. A decrease in abundance can lead to changes in the trophic dynamics and interactions between species and can ultimately affect the overall functioning of the ecosystem (Hébert et al., 2017). During the most intense studied winter, the copepod assemblage experienced a decline in both functional diversity and abundance and had no replacement for lost functional entities. This reduction in functional diversity could indicate a potential disruption in the trophic dynamics, interactions between species, and significant impacts on the overall functioning of the ecosystem.

Maintaining balance and compensating for the impacts caused by disturbances, such as El Niño events, are of utmost importance for a marine protected area like Arvoredo MPA. The ability of planktonic populations to exhibit compensatory

responses contributes to the resilience and stability of the ecosystem in the face of environmental changes (Zhang et al., 2022). By compensating for shifts in copepod species composition and functional diversity, these mechanisms help to maintain essential ecological functions and processes within the ecosystem. This is particularly significant considering the transitional nature of the Arvoredo MPA, which acts as a boundary between tropical and temperate marine fauna (Floeter et al., 2008).

The functional approach in studies about plankton can lead to a broader understanding of local community ecology and how oceanographic variations affect it. Comprehending the copepods in the functional trait approach in the Arvoredo MPA surroundings provided an overview of the plankton community. The high variability of functional traits and the shift of copepod species showed the spatial and seasonal oceanographic complexity of the south boundary of the Southern Brazilian Shelf. Our findings can be used as a foundation to understand how the oceanographic events in these environments can shape the composition of the planktonic community concerning the functional groups, since copepods are the dominating planktonic organisms.

CONCLUSION

Our study provides valuable insights into the copepod functional diversity in the Arvoredo Marine Protected Area, highlighting the influence of seasonal and interannual changes in water masses, as well as the acute impact of the 2015-2016 El Niño event. The occurrence of distinct functional groups was driven by the intensity of oceanographic processes. Over the years, the changes observed in functional diversity and abundance within the copepod functional diversity indicate the presence of compensatory mechanisms.

Changes in copepod abundance can affect the ecosystem even if functional diversity is maintained. The presence or absence of certain species and the relative abundance of different functional groups can alter the trophic dynamics and species interactions distinctly over summers and winters. Our findings can be used as a starting point for further studies with time series data exploring the effects of numerous El Niño events

on the copepod functional diversity. Long-term monitoring is essential to capture the durability of compensatory responses that ecosystems undergo when faced with disturbances, and the resilience of the Arvoredo MPA in the face of environmental changes. Therefore, it is essential to monitor both functional diversity and abundance to gain an understanding of the impacts of changes in species composition on ecosystem function.

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While ASF experienced her first steps as an independent professional alongside motherhood, Paulo Lana guided her during the establishment of the regional "Marine Biology Centre," which later evolved into the large "Marine Studies Centre" in the early 1990s. With keen eyes and notable speaking skills, Paulo Lana encouraged creativity, precision, persistence, and focus among his colleagues. A good-humored, soft, and friendly professional partner has emerged from the powerful image built during the author's early career. It is certain that Paulo Lana would have been (he was) very happy and enthusiastic with all the knowledge shared in this volume in his honor. RIP, dear Paulo!

AUTHOR CONTRIBUTIONS

B.S.M.: Conceptualization; Investigation; Methodology; Writing – original draft; Writing – review & editing.

E.C.B.: Investigation; Methodology; Writing – original draft; Writing – review & editing.

F.B.A.: Investigation; Writing – original draft; Writing – review & editing.
 L.C.P.M.S.: Methodology; Writing – original draft; Writing – review & editing.
 C.O.D.: Writing – original draft; Writing – review & editing.
 A.S.F.: Supervision; Conceptualization; Investigation; Project Administration; Writing – original draft; Writing – review & editing.

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