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Zooplankton Abundance and Diversity in the Tropical and Subtropical Ocean

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Abstract: The abundance and composition of zooplankton down to 3000 m depth was studied in the subtropical and tropical latitudes across the Atlantic, Pacific and Indian Oceans (35 °N–40 °S). Samples were collected from December 2010 to June 2011 during the Malaspina Circumnavigation Expedition. Usually, low abundances were observed with the highest values found in the North Pacific Ocean, Benguela, and off Mauritania, and the lowest in the South Pacific Ocean. No significant differences in abundance and zooplankton composition were found among oceans, with depth being consistently the most important factor affecting their distribution. Each depth strata were inhabited by distinct copepod assemblages, which significantly differed among the strata. The contribution of copepods to the zooplankton community increased with the depth although, as expected, their abundance strongly decreased. Among the copepods, 265 species were identified but 85% were rare and contributed less than 1% in abundance. *Clausocalanus furcatus* and *Nannocalanus minor* dominated the epipelagic strata. *Pleuromamma abdominalis* and *Lucicutia clausi* were of importance in the mesopelagic layer, and *Pareucalanus*, *Triconia*, *Conaea* and *Metridia brevicauda* in the bathypelagic layer. Our results provide a global-scale assessment of copepod biodiversity and distribution, providing a contemporary benchmark to follow future ocean changes at low latitudes.

Keywords: copepods; vertical distribution; biodiversity; community composition; abundance; deep ocean

1. Introduction

The deep-sea is the largest habitat on earth and also the least known [1]. About 88% of the ocean surface is deeper than 1 km, the boundary between the mesopelagic (200–1000 m depth) and bathypelagic (below 1000 m depth) layers and almost 80% is between 3–6 km depth [2]. Yet, the exploration of the dark ocean (>200 m) lags well behind that of the epipelagic (0–200 m depth) layer. Deep-sea zooplankton communities generally have low abundances and thus, large sampling systems are needed to filter sufficient amounts of water. Due to the high cost of gear, ship-time, and large

research vessels, sampling efforts of the deep-sea zooplankton are often too expensive. In addition, the zooplankton community in the subtropical-tropical regions is poorly studied, particularly in the southern hemisphere, which contains almost 80% of the ocean surface. These areas are widely unexplored in comparison to coastal areas, and most studies so far are carried out in northern neritic waters [3].

Overall, the deep-sea zooplankton community is characterized by strong latitudinal and bathymetric gradients and its diversity mainly regulated by complex interactions among environment and the species-specific performances. However, the major driving mechanisms generating the structure of the pelagic deep sea still poorly understood [4,5]. In this vast environment, zooplankton supports life and represents a key component in the functioning of the ocean food web. Therefore, understanding the response of this community to hydrographical and meteorological forcing is crucial in the present context of anthropogenic global change [3,6]. The current interest on whole ocean ecosystem models makes it necessary to ascertain whether it is possible to identify different zooplankton assemblages and if so, how they are distributed at the relevant spatial and depth scales. Although the first goal of the expedition was to explore the open ocean areas, we sailed through different domains and biogeographical provinces [7] of different biological productivities such as the warm ocean and upwelling systems [8], promoting contrasting ocean scenarios. Moreover, environmental factors affect the spatial and vertical distribution of the zooplankton including mainly temperature, oxygen minimum zones [9], and food availability [8,10–12].

The sparse data on the distribution of the main zooplankton groups in particular copepods, in subtropical and tropical result, from a series of expeditions mostly in the Atlantic Ocean [13–17] and fewer data in the Indian [18–21] and in the Pacific oceans [22–24]. Nevertheless, these studies were regional in scope and used different methodologies, which hinders comparisons of the results obtained. According to them, the tropical and subtropical zooplankton community is mainly characterized by high species diversity, complex trophic networks and small changes of biomass throughout the year. Due to the absence of physical barriers allowing co-occurrence and wide latitudinal ranges of many oceanic species the horizontal distribution in these low latitudes is almost unrestricted. In contrast, a vertical structure could appear due to the physiological performances of the different species [17,25,26].

However, available data show that zooplankton abundance in the deep-sea decreases with depth [27], the rate of this decrease varies in different geographical areas [5,28–30], and changes in diversity and community structure still are poorly resolved. The feeding mode of zooplankton also varies with depth, with herbivorous and omnivorous species occurring in the epipelagic, and carnivores and detritivores copepods increasing toward the bathypelagic zone [31]. In the latter zone, species tend to be geographically widespread. However, community structure data tends to be relatively coarse as it requires quantitative taxonomic assessments across multiple taxa, where taxonomic expertise is increasingly harder to find and largely dependent on time consuming microscopical observations.

The remarkable paucity well into the 21st Century of data on deep-sea zooplankton in the subtropical and tropical oceans is a major gap in our understanding of the ocean, provided the key role of zooplankton in the functioning of the marine food webs and associated biogeochemical cycles [4]. Copepods, are the dominant zooplankton group throughout the water column [10,27], major prey of the meso- and bathypelagic fauna [32,33] and a relevant component of the biological pump transporting organic matter to the deep ocean throughout their diel or seasonal vertical migration [27,34,35].

Hence, there is a impending need to sample the subtropical-tropical ocean using consistent methods down to the ocean interior to produce a global reference baseline of zooplankton community structure [6,36,37]. Accordingly, the main goal of this work was to describe and study the structure of the marine zooplankton community from the epipelagic to bathypelagic layers across the subtropical and tropical ocean, with a particular focus on copepods collected during the Malaspina Circumnavigation Expedition, which sailed the three main oceans (Atlantic, Indian and Pacific Oceans) between December 2010 and June 2011 to explore the ecology of the deep sea [38]. The cruise track was planned to

sample open-ocean regions, including poorly studied domains of the subtropical and tropical ocean, using consistent and standardized procedures. The data acquired provides a global contemporary benchmark to resolve responses of zooplankton communities to future ocean changes.

2. Materials and Methods

The Malaspina Expedition was carried out between December 2010 and July 2011 across the Atlantic, Indian and Pacific Oceans (35 °N–40 °S, Figure 1). Zooplankton sampling covered 15 biogeographical provinces [7] including regions of the Indian and southwest Pacific oceans (EAFC; ISSG; SPSG; Table 1), the highly productive region of the North Pacific Tropical Gyre (NPTG), and the North Pacific Equatorial countercurrent (NPEC), among others [8].

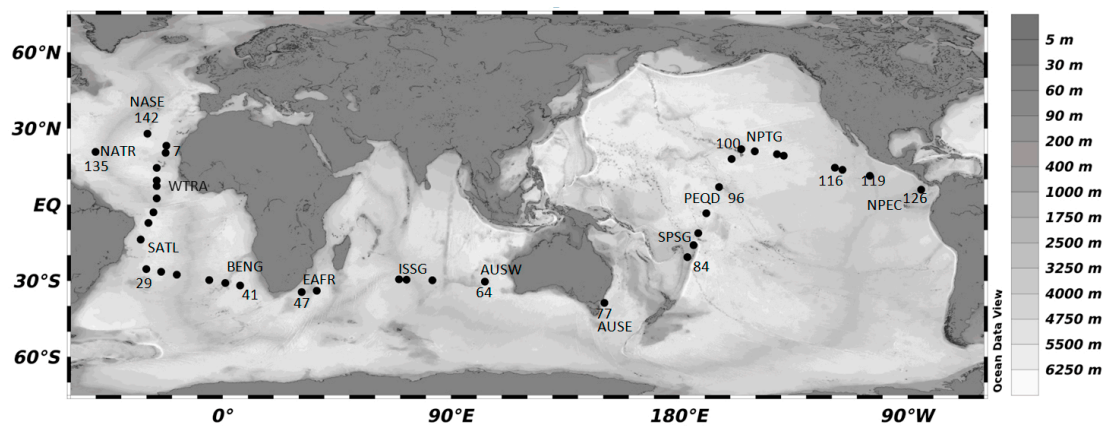


Figure 1. Stations sampled for zooplankton community analyses along the Malaspina 2010 Circumnavigation Expedition and the outline of the Longhurst provinces visited along the cruise track according to Table 1 [7]. The numbers indicate the first and last zooplankton stations samples at each leg.

Table 1. Different legs, stations, and Longhurst provinces visited during the Malaspina 2010 expedition.

Leg	Starting (City, Date)	End (City, Date)	Provinces	Abbrev. (Stations)
1	Cadiz (14/12/2011)	Rio de Janeiro (13/01/2011)	North Atlantic Tropical Gyre Western Tropical Atlantic South Atlantic Gyre	NATR (5–10) WTRA (11–18) SATL (19–26)
2	Rio de Janeiro (17/01/2011)	Cape Town (06/02/2011)	South Atlantic Gyre Benguela Current Coastal	SATL (27–40) BENG (41–44)
3	Cape Town (11/02/2011)	Perth (11/02/2011)	East Africa Coastal Indian South Tropical Gyre West Australian Current	EAFC (45–47) ISSG (48–63) AUSW (64–65)
4	Perth (17/03/2011)	Sydney (30/03/2011)	East Australian Current	AUSE (77)
5	Auckland (16/03/2011)	Honolulu (8/05/2011)	South Pacific Subtropical Gyre Pacific Equatorial Divergence North Pacific Tropical Gyre	SPSG (80–89) PEQD (90–97) NPTG (98–100)
6	Honolulu (10/05/2011)	Cartagena de Indias (10/06/2011)	North Pacific Tropical Gyre North Pacific Equatorial Countercurrent	NPTG (101–115) NPEC (116–126)
7	Cartagena de Indias (19/06/2011)	Cadiz (14/07/2011)	North Atlantic Tropical Gyre North Atlantic Subtropical Gyre	NATR (131–139) NASE (142–147)

Samples were collected from the surface layer down to 3000 m depth with an opening-closing 0.5 m² Hydrobios Multinet equipped with 5 nets of 300 µm mesh and a flowmeter to measure the volume of water filtered. Stratified vertical tows were performed during day hours (10:00 to 14:00 am

local time) in 5 strata (0–200, 200–500, 500–1000, 1000–2000 and 2000–3000 m depth). Seven legs were conducted and 145 hydrographic stations sampled, starting in Cadiz (Spain, Figure 1) to Rio de Janeiro and Cape Town, through the Indian Ocean to Perth and Sydney (Australia), Auckland to Hawaii and Cartagena de Indias in the Pacific Ocean. The last leg started in Cartagena de Indias and ended in Cadiz (Spain). The zooplankton stations visited were assigned to the different biogeographical provinces ([7]; Figure 1).

To describe the environmental scenario and relate later with the zooplankton distribution, temperature, salinity, oxygen, and fluorescence data (as a proxy for phytoplankton biomass) were obtained through the water column using a Conductivity-Temperature-Depth (CTD) Seabird/911-plus equipped with dual conductivity and temperature sensors calibrated at Seabird laboratory before the cruise. A rosette of 24 Niskin bottles (12 l) was used for water samples for the different biological analysis. At each hydrographic station the different variables were averaged for each stratum.

For the zooplankton collection, a total of 190 samples (collected at 38 stations along the cruise track; Figure 1) were analyzed and 42,716 organisms counted within the epipelagic (Ep: 0–200 m), mesopelagic (Me1: 200–500 m and Me2: 500–1000 m), and bathypelagic zones (Ba1: 1000–2000 m and Ba2: 2000–3000 m). A Folsom plankton splitter was used to analyze at least two aliquots representing the total organism abundance. All zooplankton groups were identified and standardized to number of individuals per m^3 . Copepods were identified, whenever possible, to species level following the literature for different regions of the world [18,19,39–45].

Cluster and non-metric multi-dimensional scaling (NMDS) analysis were used to examine patterns in community structure. The analyses were based on the log-transformed abundance of zooplankton ($ind \cdot m^{-3}$). Those taxa which appeared in less than 2 stations or whose abundance was less than 0.1% were excluded from the Cluster and the NMDS analysis to avoid rare, poorly resolved taxa to dominate the analysis. The Bray-Curtis similarity index was applied coupled with group-average linkage. The same methodology was applied on the copepod species composition data in order to define copepod species assemblages. The similarity percentage (SIMPER) routine was then applied to identify the copepod species with higher contributions to the significant groups of samples. Significant differences in community structure between oceans and species were tested by ANOSIM. All procedures were performed using Primer-6 software package for the above analyses [46].

Principal Component Analysis was conducted in order to reveal correlation patterns and to avoid co-linearity with the environmental variables considered (temperature, salinity, fluorescence and dissolved oxygen data, averaging over each stratum). Redundancy Analysis (RDA; [47,48]). The most dominant copepods of each strata (>20% occurrence) were related to the environmental variables selected. The potential variance conferred by oceans, longitude and latitude, were controlled including these co-variables as condition factors. The significant effect of each environmental variable was assessed using the permutation procedure implemented in the ANOVA function. The goodness of RDA fitted was ensured after testing the linear dependencies among explicative variables by means of variance inflation factors (VIF) obtaining values >3 [47].

In addition, generalized linear mixed models (GLMMs, fitted using *R lme4* library; [49]) were used to test for potential differences in species abundance, number of species, and diversity (H' ; Shannon index) among layers and oceans. In this sense, response variables were individually tested in function of layer, ocean, and the interaction between them (*Layer*Ocean*). Considering the potential variability within sampling stations, the three GLMMs incorporated the *Station* as a random factor.

3. Results

3.1. Environmental Data

Temperature in the epipelagic layer ranged from 17 °C in BENG, NATR and NPEC to 24.2 °C in the South Atlantic (St 22; SATL), and almost 27 °C in the South Pacific (St. 88; SPSG, Figure 2).

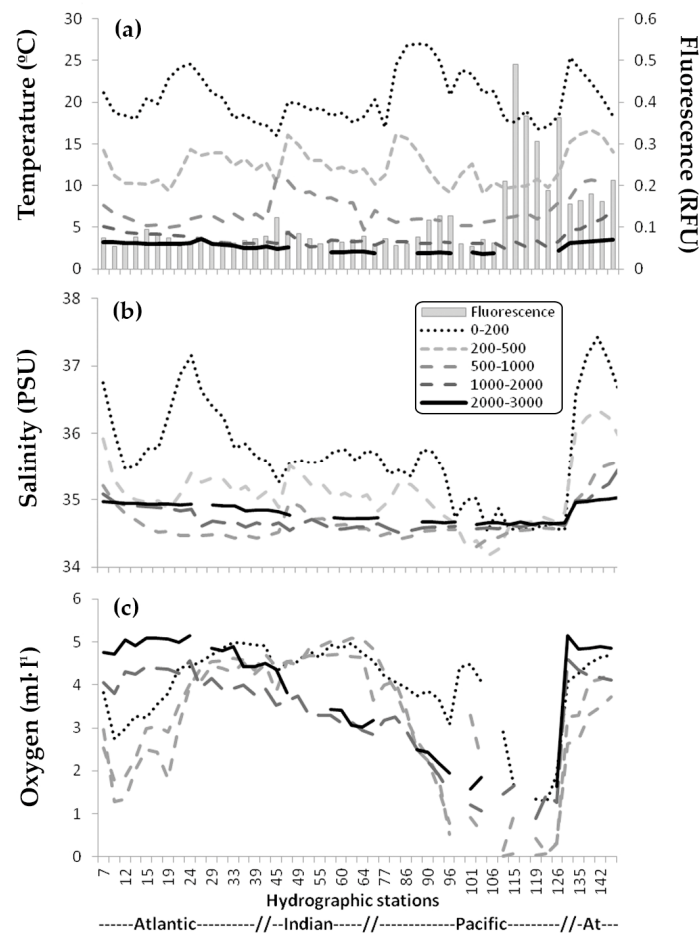


Figure 2. (a) Temperature ($^{\circ}\text{C}$) and in situ fluorescence (RFU: Relative Fluorescence Units), (b) salinity (PSU: Practical Salinity Units), (c) dissolved oxygen concentration ($\text{mL}\cdot\text{L}^{-1}$) determined at each hydrographic station and depth strata (data averaged within depth layers).

More uniform temperatures were observed in the Indian Ocean, ranging from 18 to 21 $^{\circ}\text{C}$. In the meso- and bathypelagic zones, temperature followed similar oscillations in the three oceans. Values in the upper mesopelagic zone (200–500 m depth) ranged from 16.0 $^{\circ}\text{C}$ in the North Atlantic to 9 $^{\circ}\text{C}$ in the North Pacific. In the lower mesopelagic zone (500–1000 m depth), these values were also similar among oceans ranging from 10.7 $^{\circ}\text{C}$ to 4.7 $^{\circ}\text{C}$. Finally, in the bathypelagic strata the temperature varied from 3.4 $^{\circ}\text{C}$ to 6 $^{\circ}\text{C}$ in 1000–2000 m depth and was rather uniform at about 1.9 $^{\circ}\text{C}$ below 2000 m depth (Figure 2a). Higher salinity values (37.4) were registered in the surface areas of SATL and in NATR and NASE, while the lowest values (<35) were observed in the NPTG and NPEC (from St. 107 to 126; Figure 2b). In the deepest layer (2000–3000 m depth), uniform values (around 35) were observed all along the sampled oceans. Dissolved oxygen concentration (Figure 2c) varied from highest values in Atlantic Ocean (WTRA and SATL, >5 mL/L) to almost zero in the oxygen minimum zone (OMZ) of the North Pacific. These low oxygen concentrations were observed from the PEQD (St 96) through the NPTG and NPEC (St. 115, 116, 119 and 126). In the Atlantic Ocean, low oxygen concentrations were also observed off the Mauritanian upwelling zone to the Equator (St 12 to 19; NATR and WTRA).

Quite low values of fluorescence (mean integrated values over the 0–100 m layer) were observed in most of the sampled stations (Figure 2a), with rather high values corresponding to the North Pacific area (NPTG and NPEC; from St 106 to 126), contrasting with the low values of other marine regions. Nevertheless, slightly high peaks were recorded in areas of WTRA (St. 10), BENG (St. 41), and in PEQD (St.92).

3.2. Zooplankton Abundance and Main Groups

The abundance of zooplankton was generally low throughout the subtropical and tropical oceans (Figure 3a), reflecting the prevailing oligotrophic nature of the waters sampled. However, higher values off upwelling divergence areas such as WTRA, SATL, BENG, and NPTG-PNEC (Figure 3a) were observed.

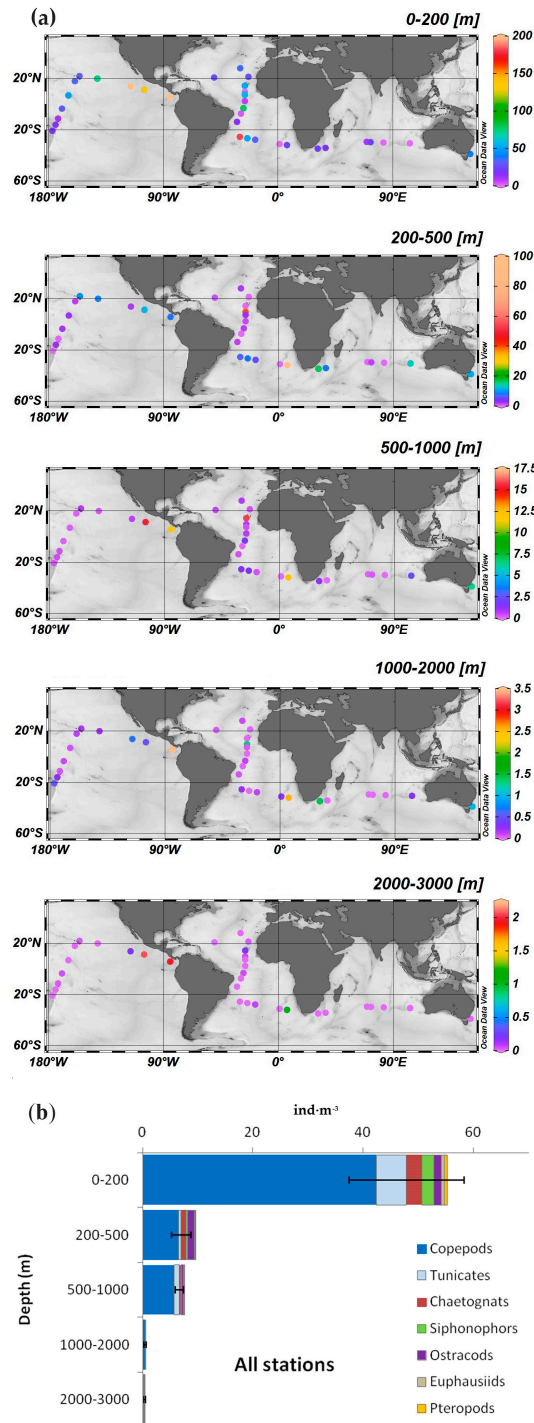


Figure 3. (a) Zooplankton abundance at each sampled station and depth layer (scale color bars indicate ind·m⁻³) and (b) depth distribution of the average abundance of the main zooplankton groups (averaged data at each stratum as ind·m⁻³).

High variability of zooplankton abundance was found in the studied area among strata (Figure 3a). In the epipelagic layer, the zooplankton abundance was usually $>200 \text{ ind}\cdot\text{m}^{-3}$. The highest abundance was found in the SATL area (St. 29) at the epipelagic layer but also in WTRA and BENG, which also exhibited high abundances in the mesopelagic layer (200 to 500 m depth, $100 \text{ ind}\cdot\text{m}^{-3}$). In the bathypelagic zone, very low abundances were generally observed ($<3 \text{ ind}\cdot\text{m}^{-3}$) with the highest abundance in upwelling zones ($<6 \text{ ind}\cdot\text{m}^{-3}$). Zooplankton abundance declined sharply with depth, comprising, on average, 82% of the depth-integrated abundance in the epipelagic layer (Figure 3b). Mesopelagic zooplankton contributed 4 to 12% of water column abundance, while the bathypelagic layer comprised $<1\%$ of the abundance. Seventeen different zooplankton groups were identified of which seven displayed abundances $<1\%$. Overall, copepods were the dominant group in all samples (80%), followed by chaetognaths (5%), ostracods (3%), and siphonophores (3%). Other groups such as appendicularians (2%), euphausiids (1%), and amphipods (1%) were rarely observed (Figure 3 and Figure 4).

The vertical distribution of zooplankton abundance was consistent across the three oceans sampled and significant differences were found in the abundance and structure of main zooplankton groups (ANOSIM R: 0.049; significance level of 10.3%). Nevertheless, we found significant differences among the five sampled layers (ANOSIM R: 0.559; significance level of 0.1%). Simper analysis indicated the contribution of main zooplankton groups at each layer, from the surface down to greater depths where copepods exhibited always the highest dominance (Table 2). Copepod abundance was always $>78\%$, chaetognaths and siphonophores were found across the different layers of the water column, while euphausiids were mainly found at mesopelagic layers, and ostracods in bathypelagic depths down to 2000 m depth (Figure 4; Table 2).

Table 2. Contribution of main zooplankton groups at the different strata (Simper analysis). Av. Abund. stands for Average Abundance ($\text{ind}\cdot\text{m}^{-3}$).

	Groups	Av. Abund.	%	Cum. %
Epipelagic (0–200 m) Average similarity: 63%	Copepods	3.4	54.2	54
	Chaetognaths	1.2	14.5	69
	Siphonophores	0.9	11.3	80
	Ostracods	0.7	7.2	87
	Euphausiids	0.5	4.7	92
Upper mesopelagic (200–500 m) Average similarity: 45%	Copepods	1.5	62.5	62
	Ostracods	0.5	12.5	75
	Chaetognaths	0.4	8.8	84
	Siphonophores	0.2	7.9	92
Lower mesopelagic (500–1000 m) Average similarity: 42%	Copepods	0.8	79.2	79
	Chaetognaths	0.1	8.1	87
	Siphonophores	0.1	6.2	93
Upper bathypelagic (1000–2000 m) Average similarity: 41%	Copepods	0.3	87	87
	Chaetognaths	0.03	5.6	93
Lower bathypelagic (2000–3000 m) Average similarity: 50%	Copepods	0.14	91.7	92

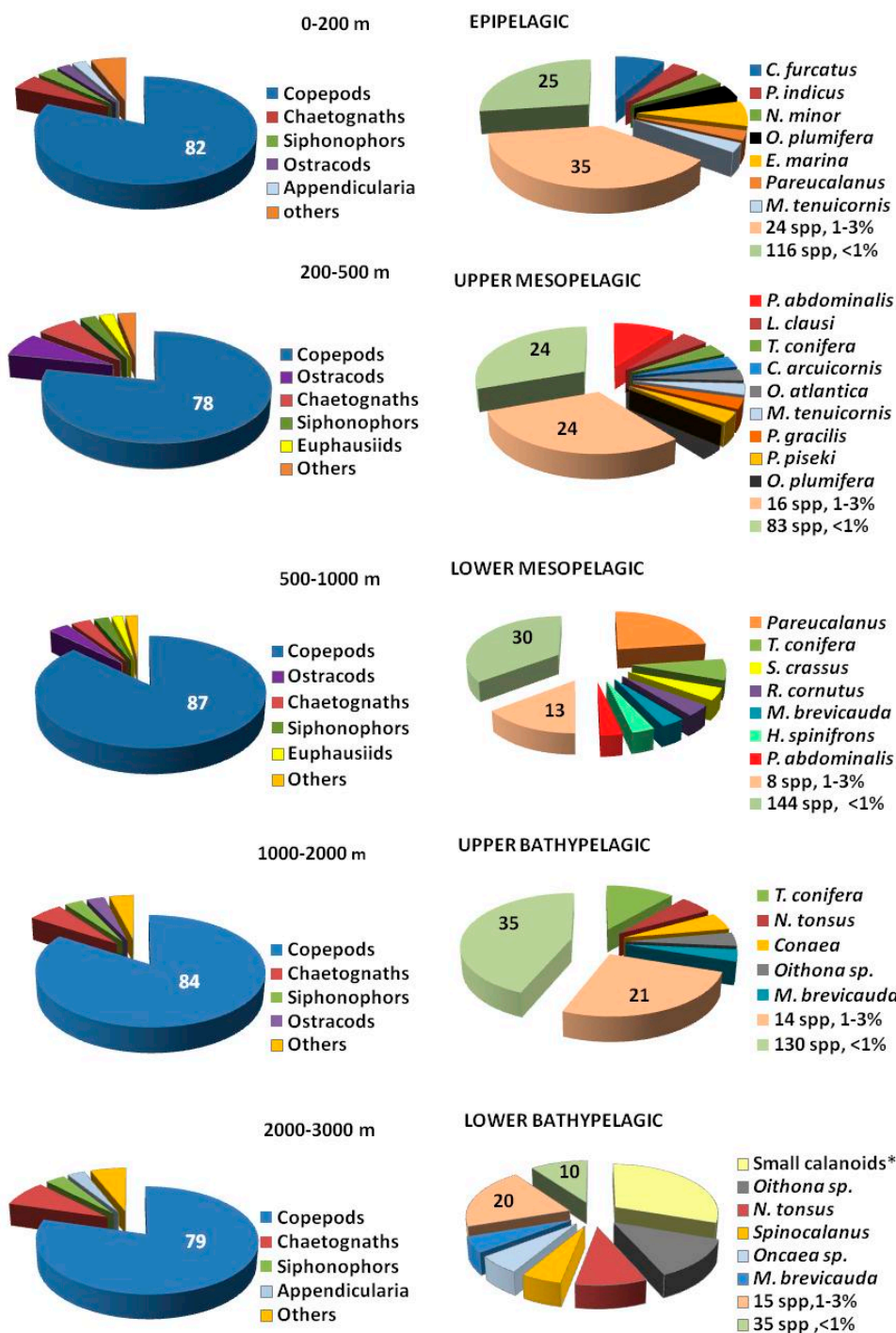


Figure 4. Relative abundance of main zooplankton groups (%), and dominant copepods (*Clausocalanus furcatus*, *C. arcuicornis*, *Paracalanus indicus*, *Nannocalanus minor*, *Neocalanus tonsus*, *Euchaeta marina*, *Mesocalanus tenuicornis*, *Subeucalanus crassus*, *Metridia brevicauda*, *Heterorardhus spinifrons*, *Rhincalanus cornutus*, *Oithona plumifera*, *O. atlantica*, *Pleuromamma abdominalis*, *P. gracilis*, *P. piseki*, *Lucicutia clausi*, *Triconia conifera* and small calanoids* as possible contaminants) found at each depth layer (averaged across all stations sampled).

Multidimensional analysis of main zooplankton groups and copepod species revealed the highest similarity among epipelagic stations (40%) followed by the mesopelagic ones (30%). Below 500 m depth, zooplankton abundance was more irregular among the stations and less similarity was observed

going to the deep strata (Figure 5a). When all stations were averaged at each stratum, it was observed clear ordination among the strata but in particular from 500 m depth to deeper waters (Figure 5b). Interesting to mention that besides the highest abundances found in the Ep strata, high abundances of zooplankton were also found at the Me1 stratum in WTRA, BENG, NPEC, and NPTG areas.

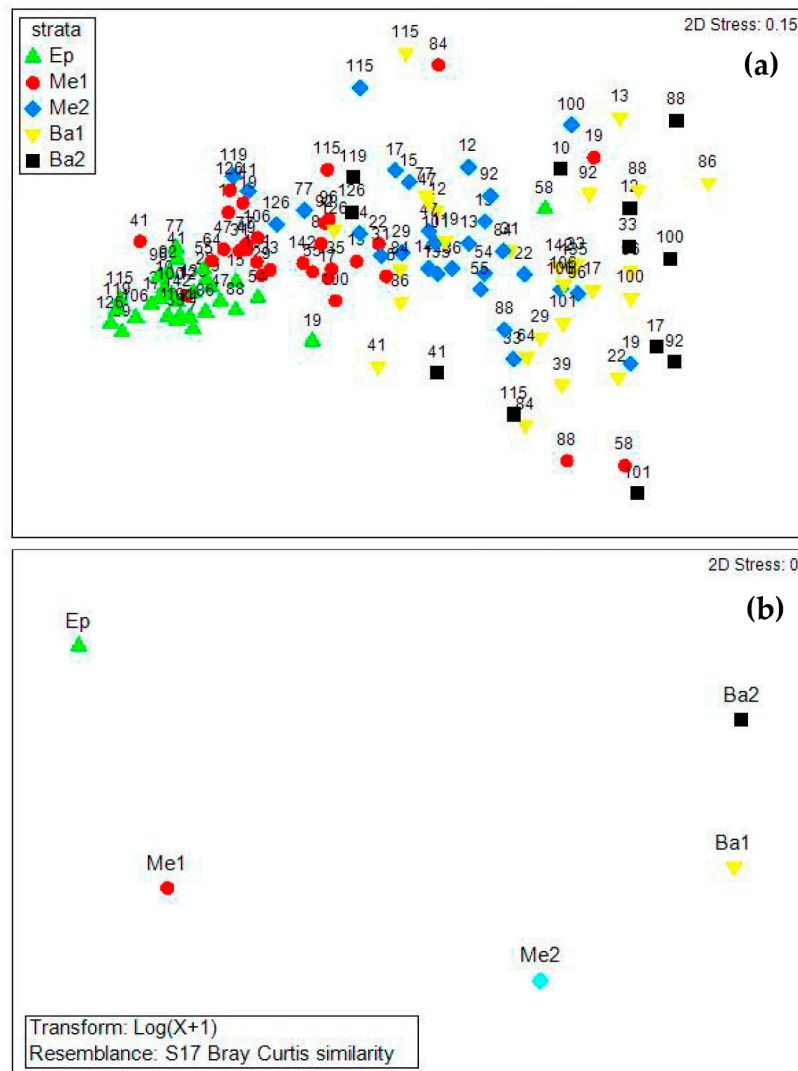


Figure 5. NMDS Ordination analysis of zooplankton community found at the stations and depth layers (Epipelagic: Ep; Upper and lower Mesopelagic: Me1 and Me2; Upper and Lower Bathypelagic: Ba1 and Ba2) regarding (a) the abundance of copepods (ind.m^{-3}) at each sampled stations, and (b) average abundance of copepods at each depth layer.

3.3. Copepod Composition, Dominant Species, and Diversity

Copepods dominated the zooplankton community across the subtropical and tropical oceans. Particularly higher values were observed in areas fertilized by upwelling-divergence areas, such as SATL (St. 29), NPEC (St. 115 St. 119 and St. 126), BENG (St. 41), and WTRA (St. 7 and St. 10). Rather low values were found in all the other stations (Figure 6). We identified a total of 36 families, and 265 species of copepods (Table 3), but almost 80% of copepod species were consistently rare (each less than 1% of the community). The highest number of copepod species with a contribution higher than 1% was found in the epipelagic layer (21% of the total species number, Figure 4), but considering the total number of the species found, the highest copepod species number was found between 500 and 1000 m ($n = 158$ species) where almost 92% of the total species were less than 1% in abundance. The abundance

of copepods, species number, and H' clearly declined from the epipelagic to the bathypelagic layer ($p < 0.001$; Figure 6). Such a decrease was similar across the three sampled oceans ($p > 0.05$, Figure 6).

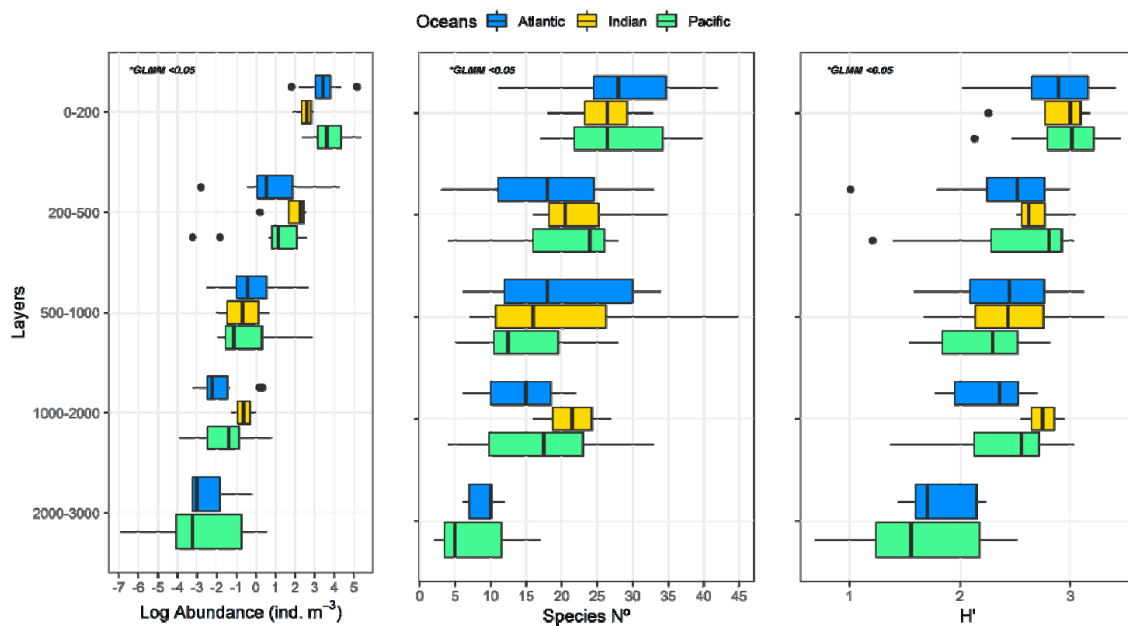


Figure 6. Box plots showing the distribution of copepod abundance (log-transformed) as $\text{ind}\cdot\text{m}^{-3}$, number of species and diversity (H' as Shannon index) at the five depth layers (m) sampled in the Atlantic, Pacific, and Indian Oceans (averaged stations). The central line in the boxes represents the median, the boxes extend from the 25% to 75% percentiles, and the whiskers encompass 95% of the data. Values beyond these limits are shown as closed circles.

Nevertheless, the decrease was not linear because of the increased values in the mesopelagic zones. The highest diversity was usually observed in the epipelagic layer but it was only slightly above that observed in mesopelagic layers, with the strongest decrease observed below 2000 m depth. It was interesting to see that meanwhile the highest diversity in the mesopelagic zone was found in the Pacific Ocean at Me1, in the Atlantic Ocean was found deeper (in Me2). The Indian Ocean showed the highest diversity in the bathypelagic layer (Figure 6).

Among the 78 genera of copepods found in our study, *Clausocalanus*, *Oithona*, *Oncaea*, *Corycaeus*, *Acartia*, *Euchaeta*, and the Calanids dominated the Ep layer. *Pleuromamma*, *Lucicutia*, *Heterorhabdus*, Auggaptilids, *Aetideus* dominated in the Me1, while *Metridia*, *Gaetanus*, *Euchirella*, *Lophothrix* and *Chiridius* in the Me2. In the bathypelagic layers, *Amallothrix*, *Undeuchaeta*, *Chirundina*, *Scottocalanus*, and *Tortanus* dominated. *Conaea* and *Oncaea* were also important below 1000 m depth. Here, we mention that, although not very abundant, in the bathypelagic layers of productive areas, we identified some small calanoids (*Paracalanus*, *Clausocalanus*, *Calocalanus*, *Acrocalanus*) and non-calanoids such as *Oithona*.

Only 12 species of copepods were found having abundances $>3\%$ (*Clausocalanus furcatus*, *Nannocalanus minor*, *Euchaeta marina*, *Pareucalanus attenuatus*, *Mesocalanus tenuicornis*, *Calocalanus pavo*, *Acartia danae*, and *Scolecithrix danae* among calanoids, and *Oithona plumifera*, *Triconia conifera*, *Oncaea venusta*, and *O. mediterranea* among the non-calanoids. Accordingly, the small cosmopolitan copepods were prevalent in the three oceans. *C. furcatus* (8%) was the most abundant species with a sharp presence in the upper layer of the Atlantic Ocean. *N. minor* was more abundant in the Pacific Ocean (Table 4), and *P. indicus* (9%), *P. attenuatus* (6%), and *E. marina* (5%) in the North Pacific Ocean. *A. negligens* was found dominant in the Indian Ocean. Among the non-calanoids, *O. plumifera* was present similarly in all the three oceans.

Table 3. List of families and species of copepods identified in this study. No-calanoids families and species are highlighted in grey. *Calanoides from the eastern Atlantic recently re-described [50].

Acartiidae	Arietellidae	Candaciidae (Continuation)	Euchaetidae (Continuation)
<i>Acartia danae</i> Giesbrecht, 1889	<i>Arietellus aculeatus</i> (T. Scott, 1894)	<i>Candacia ethiopica</i> Dana, 1849	<i>Euchaeta media</i> Giesbrecht, 1888
<i>Acartia enzoii</i> (Crisafi, 1974)	<i>Arietellus giesbrechti</i> Sars G.O., 1905	<i>Candacia katchumi</i> Grice, 1961	<i>Euchaeta spinosa</i> Giesbrecht, 1892
<i>Acartia longiremis</i> (Lilljeborg, 1853)	<i>Arietellus pavoninus</i> Sars G.O., 1905	<i>Candacia longimana</i> Claus, 1863	<i>Paraeuchaeta exigua</i> (Wolfenden, 1911)
<i>Acartia negligens</i> Dana, 1849		<i>Candacia pachydactyla</i> Dana, 1849	<i>Paraeuchaeta tonsa</i> (Giesbrecht, 1895)
	Augaptilidae	<i>Candacia tenuimana</i> Giesbrecht, 1889	
Aetideidae	<i>Augaptilus longicaudatus</i> (Claus, 1863)	<i>Candacia truncata</i> (Dana, 1849)	Fosshageniidae
<i>Aetideus acutus</i> (Farran, 1929)	<i>Centraugaptilus rattrayi</i> (T. Scott, 1894)	<i>Candacia simplex</i> Giesbrecht, 1889	<i>Temoropia</i> spp. T. Scott, 1894
<i>Aetideus australis</i> (Vervoort, 1957)	<i>Euaugaptilus hecticus</i> (Giesbrecht, 1889)	<i>Candacia varicans</i> Giesbrecht, 1893	<i>Temoropia mayumbaensis</i> T. Scott, 1894
<i>Aetideus armatus</i> (Boeck, 1872)	<i>Euaugaptilus magnus</i> (Wolfenden, 1904)	Centropagidae	Heterorhabdidae
<i>Aetideus giesbrechti</i> Cleve, 1904	<i>Euaugaptilus marginatus</i> (Tanaka, 1964)	<i>Centropages</i> sp. Kröyer, 1849	<i>Disseta magna</i> Bradford, 1971
<i>Aetideus pseudoarmatus</i> (Bradford, 1971)	<i>Euaugaptilus palumboi</i> Giesbrecht, 1889	<i>Centropages calaninus</i> (Dana, 1849)	<i>Disseta palumboi</i> Giesbrecht, 1889
<i>Bradyidius armatus</i> (Giesbrecht, 1897)	<i>Haloptilus aculeatus</i> (Brady, 1883)	<i>Centropages elongatus</i> (Giesbrecht, 1896)	<i>Heterorhabdus clausi</i> (Giesbrecht, 1889)
<i>Chiridiidus gracilis</i> (Farran, 1908)	<i>Haloptilus fons</i> Farran, 1908	<i>Centropages furcatus</i> (Dana, 1849)	<i>Heterorhabdus papilliger</i> (Claus, 1863)
<i>Chiridiidus poppei</i> Giesbrecht, 1892	<i>Haloptilus longicornis</i> Claus, 1863	<i>Centropages longicornis</i> Mori, 1932	<i>Heterorhabdus spinifer</i> Park, 1970
<i>Chirundina streetsii</i> Giesbrecht, 1895	<i>Haloptilus ornatus</i> (Giesbrecht, 1893)		<i>Heterorhabdus spinifrons</i> (Claus, 1863)
<i>Euchirella amoena</i> Giesbrecht, 1888	<i>Haloptilus oxycephalus</i> (Giesbrecht, 1889)	Clausocalanidae	<i>Heterostylites longicornis</i> (Giesbrecht, 1889)
<i>Euchirella curticauda</i> Giesbrecht, 1888	<i>Haloptilus spiniceps</i> (Giesbrecht, 1893)	<i>Clausocalanus arcuicornis</i> (Dana, 1849)	<i>Heterostylites major</i> (F. Dahl, 1894)
<i>Euchirella maxima</i> Wolfenden, 1905	<i>Pachyptilus eurygnathus</i> G.O. Sars, 1920	<i>Clausocalanus farrani</i> (Sewell, 1929)	<i>Paraheterorhabdus compactus</i> (G.O. Sars, 1900)
<i>Euchirella messiniensis</i> (Claus, 1863)	<i>Pachyptilus</i> sp. G.O. Sars, 1920	<i>Clausocalanus furcatus</i> (Brady, 1883)	Lucicutiidae
<i>Euchirella pulchra</i> (Lubbock, 1856)		<i>Clausocalanus ingens</i> Frost & Fleminger, 1968	<i>Lucicutia bicornuta</i> Wolfenden, 1905
<i>Euchirella rostrata</i> (Claus, 1866)	Bathypontiidae	<i>Clausocalanus jobei</i> Frost & Fleminger, 1968	<i>Lucicutia clausi</i> (Giesbrecht, 1889)
<i>Euchirella splendens</i> (Vervoort, 1963)	<i>Temorites</i> spp. G.O. Sars, 1900	<i>Clausocalanus lividus</i> Frost & Fleminger, 1968	<i>Lucicutia curta</i> Farran, 1905
<i>Euchirella truncata</i> Esterly, 1911	<i>Temorites brevis</i> G.O. Sars, 1900	<i>Clausocalanus mastigophorus</i> (Claus, 1863)	<i>Lucicutia flavicornis</i> (Claus, 1863)
<i>Gaetanus</i> spp. Giesbrecht, 1888	Calanidae	<i>Clausocalanus minor</i> (Sewell, 1929)	<i>Lucicutia gaussae</i> Grice, 1963
<i>Gaetanus armiger</i> Giesbrecht, 1888	<i>Canthocalanus pauper</i> (Giesbrecht, 1888)	<i>Clausocalanus parapergens</i> Frost & Fleminger, 1968	<i>Lucicutia gemina</i> Farran, 1926
<i>Gaetanus brevicaudatus</i> G.O. Sars, 1907	<i>Calanoides cf. carinatus</i> (Krøyer, 1848)*	<i>Clausocalanus paululus</i> Farran, 1926	<i>Lucicutia grandis</i> (Giesbrecht, 1895)
<i>Gaetanus brevicornis</i> Esterly, 1906	<i>Calanoides macrocarinatus</i> (Brodsky, 1967)*	<i>Clausocalanus pergens</i> Farran, 1926	<i>Lucicutia intermedia</i> G.O. Sars, 1905
<i>Gaetanus kruppianus</i> Giesbrecht, 1903	<i>Cosmocalanus darwini</i> (Lubbock, 1860)	<i>Ctenocalanus vanus</i> Giesbrecht, 1888	<i>Lucicutia longicornis</i> (Giesbrecht, 1889)
<i>Gaetanus latifrons</i> G.O. Sars, 1905	<i>Mesocalanus tenuicornis</i> (Dana, 1849)		<i>Lucicutia longiserrata</i> (Giesbrecht, 1889)
<i>Gaetanus miles</i> Giesbrecht, 1888	<i>Nannocalanus minor</i> (Claus, 1863)	Eucalanidae	<i>Lucicutia magna</i> Wolfenden, 1903
<i>Gaetanus minor</i> Farran, 1905	<i>Neocalanus gracilis</i> (Dana, 1849)	<i>Eucalanus hyalinus</i> (Claus, 1866)	<i>Lucicutia maxima</i> Steuer, 1904
<i>Gaetanus pileatus</i> Farran, 1903	<i>Neocalanus robustior</i> (Giesbrecht, 1888)	<i>Pareucalanus sewelli</i> (Fleminger, 1973)	<i>Lucicutia ovalis</i> (Giesbrecht, 1889)
<i>Gaetanus pungens</i> Giesbrecht, 1895	<i>Neocalanus tonsus</i> (Brady, 1883)	<i>Subeucalanus crassus</i> (Giesbrecht, 1888)	<i>Lucicutia wolfendini</i> (Sewell, 1932)
<i>Gaetanus brevispinus</i> G.O. Sars, 1900	<i>Undinula vulgaris</i> (Dana, 1849)	<i>Subeucalanus monachus</i> (Giesbrecht, 1888)	
<i>Gaetanus tenuispinus</i> G.O. Sars, 1900	Candaciidae	<i>Subeucalanus subtenuus</i> (Giesbrecht, 1888)	Megacalanidae
<i>Pseudochirella</i> sp. G.O. Sars, 1920	<i>Candacia bipinnata</i> Giesbrecht, 1889	<i>Subeucalanus longiceps</i> (Matthews, 1925)	<i>Bradycalanus sarsi</i> (Farran, 1939)
<i>Pseudochirella spinosa</i> (Wolfenden, 1905)	<i>Candacia bispinosa</i> Claus, 1863		<i>Megacalanus princeps</i> Wolfenden, 1904
<i>Pseudochirella major</i> (Sars, 1907)	<i>Candacia catula</i> (Giesbrecht, 1889)	Euchaetidae	Metridiidae
<i>Undeuchaeta major</i> Giesbrecht, 1888	<i>Candacia cheirura</i> Cleve, 1904	<i>Euchaeta acuta</i> Giesbrecht, 1893	<i>Metridia</i> sp. Boeck, 1865
<i>Undeuchaeta plumosa</i> (Lubbock, 1856)	<i>Candacia elongata</i> Boeck, 1872	<i>Euchaeta concinna</i> Dana, 1849	<i>Metridia brevicauda</i> Giesbrecht, 1889
		<i>Euchaeta marina</i> (Prestandrea, 1833)	

Table 3. Cont.

Metridinidae	Rhincalanidae	Tortanidae	Mormonillidae
<i>Metridia curticauda</i> Giesbrecht, 1889	<i>Rhincalanus cornutus</i> (Dana, 1849)	<i>Tortanus</i> spp. (Giesbrecht, 1898)	<i>Mormonilla</i> spp. Giesbrecht, 1891
<i>Metridia longa</i> (Lubbock, 1854)	<i>Rhincalanus gigas</i> Brady, 1883	Phaennidae	Oithonidae
<i>Metridia lucens</i> Boeck, 1864	<i>Rhincalanus nasutus</i> Giesbrecht, 1888	<i>Onchocalanus</i> spp.(G.O. Sars, 1905)	<i>Oithona atlantica</i> Farran, 1908
<i>Metridia princeps</i> Giesbrecht, 1889	Scolecitrichidae	<i>Phaenna spinifera</i> (Claus, 1863)	<i>Oithona brevicornis</i> Giesbrecht, 1891
<i>Metridia venusta</i> Giesbrecht, 1889	<i>Amalothrix farrani</i> Rose, 1942	<i>Xanthocalanus</i> spp. Giesbrecht, 1893	<i>Oithona nana</i> Giesbrecht, 1892
<i>Pleuromamma abdominalis</i> (Lubbock, 1856)	<i>Amalothrix</i> spp. G.O. Sars, 1925	<i>Xanthocalanus agilis</i> Giesbrecht, 1893	<i>Oithona plumifera</i> Baird, 1843
<i>Pleuromamma borealis</i> (F. Dahl, 1893)	<i>Landrumius gigas</i> (A. Scott, 1909)	Aegisthidae	<i>Oithona robusta</i> Giesbrecht, 1891
<i>Pleuromamma gracilis</i> (Claus, 1863)	<i>Lophothrix frontalis</i> Giesbrecht, 1895	<i>Aegisthus</i> spp. Giesbrecht, 1891	<i>Oithona setigera</i> (Dana, 1849)
<i>Pleuromamma piseki</i> Farran, 1929	<i>Lophothrix humilifrons</i> G.O. Sars, 1905	<i>Aegisthus aculeatus</i> Giesbrecht, 1891	<i>Oithona tenuis</i> Rosendorn, 1917
<i>Pleuromamma quadrangulata</i> (F. Dahl, 1893)	<i>Lophothrix latipes</i> (T. Scott, 1894)	<i>Aegisthus mucronatus</i> Giesbrecht, 1891	<i>Oithona</i> spp. Baird, 1843
<i>Pleuromamma robusta</i> (F. Dahl, 1893)	<i>Lophothrix quadrispinosa</i> Wolfenden, 1911	Corycaeidae	Oncaeidae
<i>Pleuromamma xiphias</i> (Giesbrecht, 1889)	<i>Pseudoamallothrix emarginata</i> (Farran, 1905)	<i>Agetus flaccus</i> (Giesbrecht, 1891)	<i>Oncaea</i> spp. Philippi, 1843
Nullosetigeridae	<i>Pseudoamallothrix obtusifrons</i> (G.O. Sars, 1905)	<i>Agetus limbatus</i> (Brady, 1883)	<i>Oncaea media</i> Giesbrecht, 1891
<i>Nullosetigera aequalis</i> (G.O. Sars, 1920)	<i>Scaphocalanus</i> sp. G.O. Sars, 1900	<i>Agetus typicus</i> Krøyer, 1849	<i>Oncaea mediterranea</i> (Claus, 1863)
<i>Nullosetigera bidentata</i> (Brady, 1883)	<i>Scaphocalanus affinis</i> (G.O. Sars, 1905)	<i>Corycaeus clausi</i> F. Dahl, 1894	<i>Oncaea mediterranea flava</i> Giesbrecht, 1892
<i>Nullosetigera helgae</i> (Farran, 1908)	<i>Scaphocalanus brevicornis</i> (G.O. Sars, 1900)	<i>Corycaeus crassiusculus</i> Dana, 1849	<i>Oncaea venusta</i> Philippi, 1843
<i>Nullosetigera impar</i> (Farran, 1908)	<i>Scaphocalanus brevisrostris</i> Park, 1970	<i>Corycaeus speciosus</i> Dana, 1849	<i>Triconia conifera</i> (Giesbrecht, 1891)
<i>Nullosetigera mutica</i> (G.O. Sars, 1907)	<i>Scaphocalanus emine</i> Uysal & Shmeleva, 2002	<i>Ditrichocorycaeus amazonicus</i> (F. Dahl, 1894)	<i>Triconia dentipes</i> (Giesbrecht, 1891)
Paracalanidae	<i>Scaphocalanus insignis</i> Brodsky, 1950	<i>Farranula carinata</i> (Giesbrecht, 1891)	<i>Conaea</i> spp. Giesbrecht, 1891
<i>Acrocalanus andersoni</i> Bowman, 1958	<i>Scaphocalanus magnus</i> (T. Scott, 1894)	<i>Farranula gracilis</i> (Dana, 1849)	<i>Pachos punctatum</i> (Claus, 1863)
<i>Acrocalanus gibber</i> Giesbrecht, 1888	<i>Scolecithricella abyssalis</i> (Giesbrecht, 1888)	<i>Farranula rostrata</i> (Claus, 1863)	<i>Pachos tuberosum</i> (Giesbrecht, 1891)
<i>Acrocalanus gracilis</i> Giesbrecht, 1888	<i>Scolecithricella profunda</i> (Giesbrecht, 1892)	<i>Onychocorycaeus agilis</i> (Dana, 1849)	Sapphirinidae
<i>Acrocalanus longicornis</i> Giesbrecht, 1888	<i>Scolecithricella dentata</i> (Giesbrecht, 1892)	<i>Onychocorycaeus giesbrechti</i> (F. Dahl, 1894)	<i>Sapphirina</i> spp. J. V. Thompson, 1830
<i>Acrocalanus monachus</i> Giesbrecht, 1888	<i>Scolecithricella minor</i> (Brady, 1883)	<i>Urocorycaeus furcifer</i> (Claus, 1863)	<i>Copilia quadrata</i> Dana, 1849
<i>Calocalanus contractus</i> Farran, 1926	<i>Scolecithricella tenuiserrata</i> (Giesbrecht, 1893)	<i>Urocorycaeus longistylis</i> (Dana, 1849)	<i>Copilia hendorffi</i> (Dahl, 1892)
<i>Calocalanus elegans</i> Shmeleva, 1965	<i>Scolecithricella vittata</i> (Giesbrecht, 1893)	Clytemnestridae	<i>Copilia mirabilis</i> Dana, 1849
<i>Calocalanus indicus</i> Shmeleva, 1974	<i>Scolecithrix bradyi</i> Giesbrecht, 1888	<i>Clytemnestra</i> spp. Dana, 1847	
<i>Calocalanus pavo</i> (Dana, 1849)	<i>Scolecithrix danae</i> (Lubbock, 1856)	Ectinosomatidae	
<i>Calocalanus pavoninus</i> Farran, 1936	<i>Scottocalanus securifrons</i> (T. Scott, 1894)	<i>Microsetella norvegica</i> (Boeck, 1864)	
<i>Calocalanus plumulosus</i> (Claus, 1863)	Spinocalanidae	<i>Microsetella rosea</i> (Dana, 1848)	
<i>Calocalanus styliremis</i> Giesbrecht, 1888	<i>Spinocalanus</i> spp.(Giesbrecht, 1888)	Lubbockiidae	
<i>Calocalanus tenuis</i> Farran, 1926	<i>Spinocalanus longicornis</i> G.O. Sars,1900	<i>Lubbockia aculeata</i> Giesbrecht, 1891)	
<i>Paracalanus indicus</i> Wolfenden, 1905	<i>Monacilla</i> sp. G.O. Sars, 1905	<i>Lubbockia squillimana</i> Claus, 1863	
<i>Paracalanus nanus</i> G.O. Sars, 1907)	<i>Monacilla typica</i> G.O. Sars, 1905	Miraciidae	
<i>Paracalanus parvus</i> (Claus, 1863)	Temoridae	<i>Miracia efferata</i> Dana, 1849	
<i>Mecynocera clausi</i> I.C.Thompson, 1888	<i>Temora discaudata</i> Giesbrecht, 1889	<i>Macrosetella gracilis</i> (Dana, 1847)	
Pontellidae	<i>Temora stylifera</i> Dana, 1849		
<i>Calanopia elliptica</i> (Dana, 1849)			
<i>Calanopia minor</i> A. Scott, 1902			
<i>Labidocera acutifrons</i> (Dana, 1849)			
<i>Pontellina plumata</i> (Dana, 1849)			

Table 4. Contribution of main copepod taxa (%) to the strata in the three Oceans: Atlantic, Indian, and Pacific. Calanoid juveniles (as Copepodites). Small calanoids* (*Paracalanus*, *Clausocalanus*, *Calocalanus*, and *Acartia*) as possible contaminants. AvS stands for Average Similarity.

	Atlantic		Indian		Pacific	
	Species	%	Species	%	Species	%
Epipelagic	<i>C. furcatus</i>	11.3	<i>A. negligens</i>	7	<i>N. minor</i>	10
	<i>O. plumifera</i>	8.4	<i>L. flavicornis</i>	6.1	<i>Acrocalanus</i>	6.2
	<i>N. minor</i>	8.1	<i>U. furcifer</i>	5.4	<i>A. danae</i>	4.6
	<i>M. tenuicornis</i>	5.9	<i>C. pavo</i>	5.2	<i>E. marina</i>	4.5
	<i>E. marina</i>	5.4	<i>M. tenuicornis</i>	5.1	<i>C. furcatus</i>	4.5
	<i>A. danae</i>	4.9	<i>O. plumifera</i>	4.9	<i>F. gracilis</i>	4.3
	<i>C. pavo</i>	4.8	<i>Pleuromamma</i> juv.	4.9	<i>O. plumifera</i>	4.1
			<i>C. arcuicornis</i>	4.2	<i>M. tenuicornis</i>	4.1
		<i>H. spinifrons</i>	3.9	<i>N. gracilis</i>	3.3	
				<i>P. indicus</i>	3	
	AvS: 22%		AvS: 14%		AvS: 24%	
Upper Mesopelagic	<i>P. gracilis</i>	16	<i>Pleuromamma</i> juv.	25	<i>T. conifera</i>	14
	<i>P. abdominalis</i>	15.2	<i>T. conifera</i>	10.7	<i>P. abdominalis</i>	8.7
	<i>P. piseki</i>	10.5	<i>M. tenuicornis</i>	11	<i>L. clausi</i>	6.8
	<i>O. mediter. flava</i>	6.1	<i>C. jobei</i>	10.2	<i>P. xiphias</i>	6.8
	<i>U. furcifer</i>	4.8	<i>P. gracilis</i>	7.7	<i>P. piseki</i>	6.1
	<i>T. conifera</i>	2.7			<i>P. robusta</i>	6
	AvS: 14%		AvS: 17%		AvS: 13%	
Lower Mesopelagic	<i>M. brevicauda</i>	22	<i>P. abdominalis</i>	58	<i>Conaea</i>	27
	<i>Conaea</i>	10.4	<i>T. conifera</i>	28	<i>M. brevicauda</i>	13.5
	<i>P. xiphias</i>	9.1	<i>Heterostylites</i>	13.5	<i>P. abdominalis</i>	7.1
	<i>N. helgae</i>	8.2			<i>T. conifera</i>	5.2
	<i>R. cornutus</i>	8.2			<i>P. attenuatus</i>	4.2
	AvS: 12%		AvS: 6%		AvS: 8%	
Upper Bathypelagic	<i>Conaea</i>	31	<i>M. brevicauda</i>	66.6	<i>M. brevicauda</i>	17
	Copepodites	10	<i>L. gaussae</i>	33.4	<i>T. conifera</i>	14.6
	<i>M. brevicauda</i>	7.7			Copepodites	10.7
	<i>T. conifera</i>	7.1			Small calanoids*	12.9
	AvS: 10%		AvS: 4%		AvS: 7%	
Lower Bathypelagic	Copepodites	63.2			Small calanoids*	60.6
	<i>T. conifera</i>	12.8			Copepodites	12
	<i>Conaea</i>	8.5			<i>M. brevicauda</i>	10
					<i>Conaea</i>	8
	AvS: 7%				AvS: 4%	

Pleuromamma abdominalis and *Lucicutia clausi* were the dominant copepods in Me1. Among the non-calanoids, *T. conifer*, and *O. plumifera* also dominated from 200 to 500 m. In the Me2, *P. attenuatus* was particularly abundant in the East-North Pacific, but *Rhincalanus cornutus*, *Metridia brevicauda*, *Conaea*, and *Subeucalanus crassus* dominated in the three oceans. In the bathypelagic layers, *M. brevicauda* was also abundant as well as *Conaea* and *T. conifera*. Copepodites of *Neocalanus tonsus* and *Calanoides* cf. *carinatus* were also collected in the deep layers of the upwelling areas off BENG and WTRA, respectively. The whole contribution (%) of the dominant copepods to each stratum is detailed in Table 5. *C. furcatus* and *P. indicus* were also found below 1,000 m depth in the productive areas of the Atlantic and Pacific Oceans.

Table 5. Copepod contribution taxa to the different strata (%). AvS stands for Average Similarity, Copepodites for juvenile Calanoids, and BC for organisms in bad conditions. Small calanoids * (*Paracalanus*, *Clausocalanus*, *Calocalanus*, *Acartia*) were possible contaminants.

Epipelagic AvS: 23%		Upper Mesopelagic AvS: 11%		Lower Mesopelagic AvS: 9%		Upper Bathypelagic AvS: 7%		Lower Bathypelagic AvS: 5%	
Species	%	Species	%	Species	%	Species	%	Species	%
<i>C. furcatus</i>	8.9	<i>P.abdominalis</i>	12.9	<i>M. brevicauda</i>	18.3	<i>Conaea</i>	17.4	Calanoids BC	31.6
<i>N. minor</i>	8.6	<i>P. gracilis</i>	10	<i>Conaea</i>	16.7	<i>M. brevicauda</i>	10.4	Small calanoids*	31.5
<i>O. plumifera</i>	5.6	<i>T. conifera</i>	8.4	<i>P. xiphias</i>	9	Calanoids BC	7.1	<i>T. conifera</i>	6.1
<i>E.marina</i>	5.4	<i>P. piseki</i>	7.6	<i>P. abdominalis</i>	6.3	Small calanoids*	6.9	Copepodites	4.9
<i>M. tenuicornis</i>	4.8	<i>O. mediter. flava</i>	4.7	<i>R. cornutus</i>	5.4	<i>T. conifera</i>	6.4	<i>Oithona spp.</i>	4.7
<i>C. pavo</i>	3.9	<i>Pleuromamma juv.</i>	4.4	<i>T. conifera</i>	5.3	<i>N. helgae</i>	3.5	<i>Oncaea spp.</i>	4.6
<i>A. danae</i>	3.5	Copepodites	3.9	<i>N. helgae</i>	5.3	<i>H. spinifrons</i>	3.5	<i>Conaea</i>	4.1
<i>A. negligens</i>	3.3	<i>M. brevicauda</i>	3.7	Copepodites	3.5	<i>O. plumifera</i>	3.5	<i>M. brevicauda</i>	3.7
<i>Acrocalanus spp.</i>	3.3	<i>L. gemina</i>	3.4	<i>O. plumifera</i>	3.3	<i>Aegisthus</i>	3.4		
<i>F. gracilis</i>	2.6	<i>U. furcifer</i>	3.2	<i>H. spinifrons</i>	2.8	<i>P. abdominalis</i>	2.4		
<i>S. danae</i>	2.4	<i>L. clausi</i>	2.7	<i>Heterostylites</i>	2	<i>M. princeps</i>	2.4		
<i>Euchaeta juv.</i>	2.1	<i>P. xiphias</i>	2.3	<i>Pareucalanus</i>	1.9				
<i>C. jobei</i>	2.0	<i>P. robusta</i>	2.3	<i>C. furcatus</i>	1.8				
<i>N. gracilis</i>	1.9	<i>O. plumifera</i>	1.9						
<i>N. robustior</i>	1.7	<i>H. spinifrons</i>	1.9						
<i>O. atlantica</i>	1.6								
<i>H. longicornis</i>	1.6								
<i>L. gemina</i>	1.5								
<i>O. agilis</i>	1.5								
<i>O. setigera</i>	1.5								
<i>O. venusta</i>	1.5								
Copepodites	1.3								
<i>Pareucalanus</i>	1.2								
<i>C. farrani</i>	1.1								
<i>M. clausi</i>	1.1								
Total	78.4		73.3		81.6		66.9		91.2

Cluster analysis revealed several assemblages, grouping those species dominating the epipelagic layer with 68% similarity level (Figure 7, *C. furcatus* and *N. minor* among others, Group a). The more abundant species in mid-layers were grouped at 50% similarity level (Groups b and c). *P. abdominalis* and *L. clausi* as well as *Aetideus* and *Heterorhabdus* predominated in the whole mesopelagic. *M. breviceauda*, *P. xiphias*, *P. robusta*, *N. tonsus* and *Gaetanus* showed, however, other assemblage with high similarity (62%, group d), dominant in the low mesopelagic layer. Among others, *Undeuchaeta*, *Chirundina*, *Scottocalanus*, *Rhincalanus*, *C. cf. carinatus*, and *E. hyalinus* (Group e) showed preference for the deepest layers.

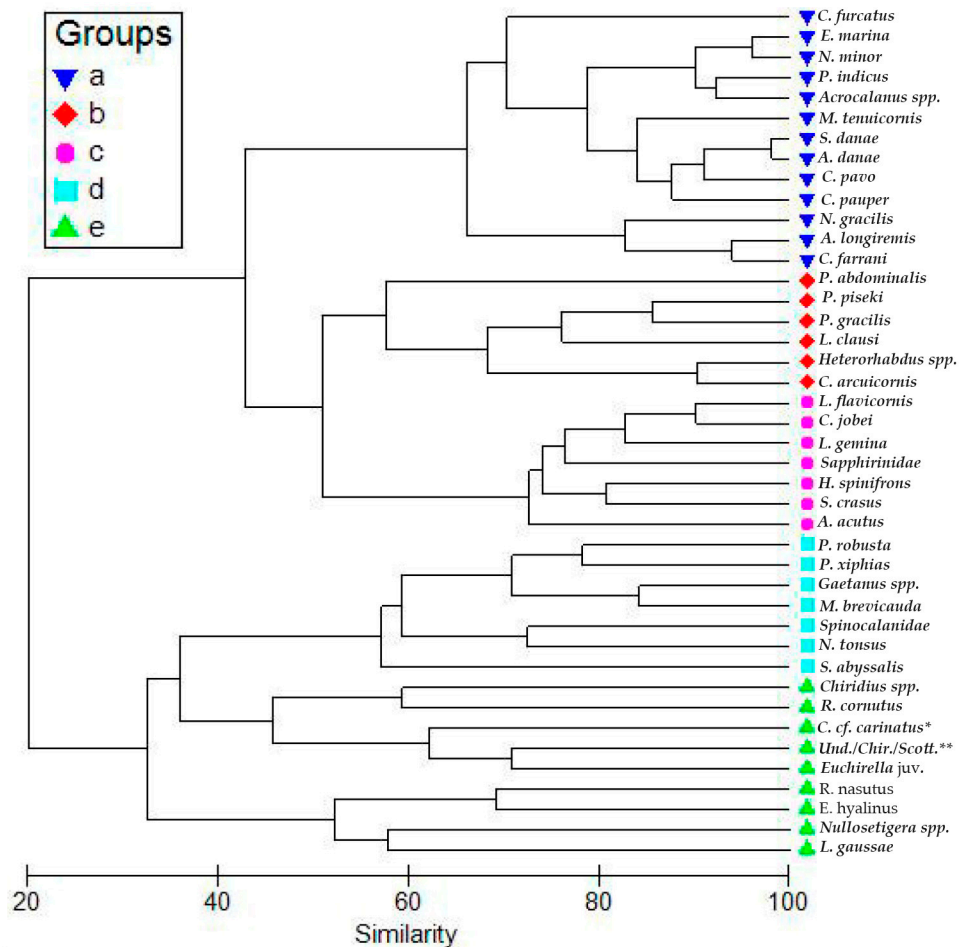


Figure 7. Cluster analysis of main copepod species found ($\log x + 1$) in the zooplankton stations using Bray-Curtis similarity. * *C. cf. carinatus* from the eastern Atlantic recently re-described [50]. ** *Undeuchaeta* (Und), *Chirundina* (Chi) and *Scottocalanus* (Scott) were joined as a group due to the high similarity.

In summary, regarding the contribution (%) of the dominant copepods found at each layer, 12 species (41%) predominated in the epipelagic layer with *C. furcatus*, *P. indicus*, *N. minor* and *E. marina* (25%), and *O. plumifera* and *O. venusta* among the non-calanooids. In Me1, 15 species dominated (48%) with *P. abdominalis* and *L. clausi* (12%) as the most abundant. Ten species were found dominant in Me2 (26%) with *Pareucalanus* and *T. conifera* (23%) as the best represented. Below 1000 m depth, 9 and 11 species dominated in the upper and lower stratum respectively, being *M. breviceauda*, *T. conifera*, and *Conaea* the most abundant.

Temperature, salinity, fluorescence, and dissolved oxygen as main environmental variables shaped the structure of the copepod community in the tropical and subtropical domains (RDA; Figure 8).

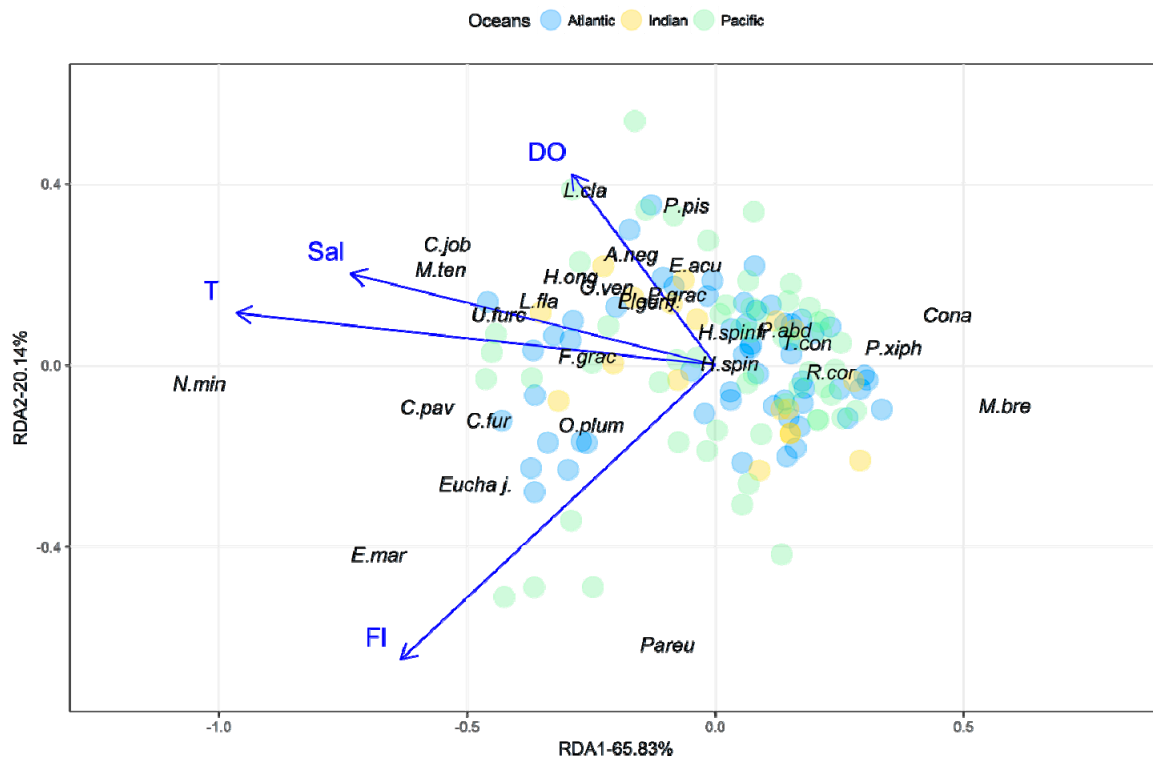


Figure 8. RDA of most dominant copepods and their environmental variables (Temperature-T, Fluorescence-FI, Salinity-Sal, and Dissolved Oxygen-DO) in the whole study area. The first two canonical axes account with 85.97% of the variance explained. Dots indicate sampling stations at the different oceans, and they are ordered based on their environmental conditions. *Nannocalanus minor* (*N.min*), *Euchaeta marina* (*E.mar*), *E. acuta* (*E.acu*), *Euchaeta juveniles* (*Eucha.j.*), *Calocalanus pavo* (*C.pav*), *Clausocalanus jobei* (*C.job*), *C. furcatus* (*C.fur*), *Mesocalanus tenuicornis* (*M.ten*), *Urocycaeus furcifer* (*U.furc*), *Lucicutia flavicornis* (*L.fla*), *L. clausi* (*L.cla*), *Farranula gracilis* (*F.gra*), *Oithona plumifera* (*O.plum*), *Oncaea venusta* (*O.ven*), *Triconia conifera* (*T.conif*), *Haloptilus ornatus* (*H.orn*), *H. longicornis* (*H.long*), *Acartia negligens* (*A.neg*), *Pleuromamma abdominalis* (*P.abd*), *P. gracilis* (*P.grac*), *P. xiphias* (*P.xiph*), *P. piseki* (*P.pis*), *Pleuromamma juveniles* (*Pleuro.j.*), *Heterorhabdus spinifer* (*H.spin*), *H. spinifrons* (*H.spinf*), *Rhincalanus cornutus* (*R.cor*), *Pareucalanus* (*Pareu*), *Conaea* (*Cona*), and *Metridia brevicauda* (*M.bre*).

Temperature, dissolved oxygen, and fluorescence played a key role on the copepod community assemblages ($p < 0.01$), while for salinity such effect was not significant ($p > 0.05$). On the first axis, temperature and salinity were the main explanatory variables suggesting the important effect of layers on the community distribution. The second axis was mainly driven by fluorescence and dissolved oxygen, reflecting the importance of the upwelling on the copepod distribution. The bulk of copepods were found in the central area of the RDA (Figure 8), while main species along the first axis were related to temperature. *N. minor*, *E. marina*, *C. pavo*, and *C. furcatus* dominated the epipelagic strata and in those areas with a higher temperature, salinity, and fluorescence. By opposite, *M. brevicauda*, *Conaea*, and *P. xiphias* dominated the deepest layer characterized by low temperature and salinity values. Along the second axis, several copepods such as *M. tenuicornis*, *C. jobei*, and *L. clausi* at mid layers were found related to areas of higher dissolved oxygen concentrations. Similarly, *Pleuromamma* species such as *P. abdominalis*, *P. xiphias*, *P. gracilis*, and *P. piseki* were found also dominant in mid layers with high dissolved oxygen values. By opposite, *Pareucalanus* were found dominant at mid layers related to areas of low dissolved oxygen values.

4. Discussion

Our study provides a first coherent assessment of the zooplankton community in the three oceans at low latitudes (35 °N–40 °S) using the same technology, methods, and sampling strategy. At the same time our survey covered a broad depth range (0–3000 m depth) along 15 biogeographical provinces around the tropical and subtropical ocean [38,51].

According to our results, zooplankton abundance declined with depth across the three oceans, confirming the general view of zooplankton biomass vertical distribution [52], and consistent with results previously reported in similar latitudes [15,16,24]. Although some latitudinal differences are common (more biomass in high latitudes than in the tropical ones) the rate of biomass decrease when increasing depth was similar in all domains and climatic zones where the influence of the surface layer is known to extend over 4000 m depth [5,52,53]. For instance, in the North Pacific, 65% of the zooplankton biomass in the 0–4000 m depth occurs at in the upper 500 m depth, and this percentage is similar through all regions because the zooplankton food in the deep sea depends on particles sinking from upper layers [8,50–53]. On the other hand, differences in abundances through the different latitudes were not observed [1,53]. In the present work, one of the most remarkable characteristic of the vertical abundance changes across stations was observed between depth layers, as it was reported by several authors decades ago [5,54]. Moreover, it should be noted that usually the zooplankton abundance was low but higher abundance values were found close to upwelling areas (e.g., off Mauritania, off Brazil, Benguela, North Pacific), confirming the findings of studies performed in different surveys [10,15,16,53]. We also observed the impact of the upwelling on the enrichment of zooplankton abundance to affect the entire water column, even down to 3000 m. These observations highlight the significant role of the upwelling areas in the world oceans [10,52].

Within zooplankton, copepods always dominated the zooplankton community across oceans and depths (>70% of total zooplankton abundance), being more important in the open ocean environments [7,15,16,41,52,55–57]. The high dominance of copepods confirms their key role in the marine pelagic food web by transferring primary production and microzooplankton biomass to higher trophic levels [58], performing the overall abundance zooplankton pattern. The decrease of copepod abundance with increasing depth was similar in the three oceans, in accordance with the review of the zooplankton vertical distribution by Vinogradov [52]. Copepod abundances found in our study were usually low in comparison to other studies [16,59]. However, this comparison is subject to caveats due to differences in nets, vertical or oblique hauls, and mesh sizes used. In fact, the mesh size of our nets was relatively large (>300 µm) and may have underrepresented the tiny copepods, possibly accounting for the observed low abundances.

The number of copepod species was always higher than 100 within the upper 2,000 m. However, the majority of them were less abundant than 1% of the whole community. The high species diversity found is a common feature of the tropical and subtropical domains [15,16,25]. Although peaking in mid-waters, the decline of species richness with depth observed across the subtropical and tropical oceans demonstrates the global nature of such patterns reported in earlier regional assessments [27,60]. The vertical change in species diversity peaking in the mesopelagic layers was also observed in other areas and latitudes [53,61], suggesting this is a common pattern in the ocean worldwide. The different species are reported to strongly influence their feeding habits, reflecting diverse feeding modes. Large sinking particles such as marine snow or larvacean houses are present in the deep strata playing an important role in the organic matter transport to the deep ocean [62]. Accordingly, food is originated at the surface layers, more patent in the rich productive areas, but sinking and fueling the deep sea and maintaining the copepod community in the deep ocean [53].

Another characteristic of our study was the overall zooplankton community dominated by small sized copepod species. Smaller copepods were usually abundant at the upper strata while large copepods were mainly found deeper [10,55,56,61,63]. In oligotrophic areas, copepods are usually small sized [64,65] and their feeding modes and life strategies are adapted to the low productivity of the subtropical and tropical ocean, minimizing their energy losses and thus being more efficient in energy

transfer to higher trophic levels [66]. In fact, *Clausocalanus* species were found dominant in epipelagic waters along the tropical oceans [67]. These small copepods were almost restricted to the epipelagic layer with a quite limited vertical distribution, as it was noted long ago [68]. However, it is important to mention the presence of these copepods during our expedition in several upwelling divergent zones even in deep layers. They could be contaminants from shallower depths as observed in several reports in the literature [18,42,69–71]. However, it is interesting to note that in those upwelling areas the mixed layer was deeper (>160 m depth) than in open areas where normal stratified waters were about 30 m depth [51]. In any case, the presence of these small copepods in deep waters should deserve further research in order to discern between contaminants or the presence of some other mechanism explaining their deeper distribution.

We also observed the decline of copepod abundance accompanied by consistent changes in community structure from the epipelagic to bathypelagic layers. Zooplankton communities were structured by depth, with different species assemblages and the distribution of main groups clearly separated from the surface to deep waters, where temperature could reach uniform values below 2000 m depth.

The epipelagic zone was dominated by cosmopolitan species of small size [41], such as *C. furcatus*, *N. minor*, *E. marina*, *C. pavo*, *A. danae* and *S. danae*. However, *P. abdominalis*, *P. piseki*, *P. gracilis*, *P. xiphias* and *L. clausi* were mainly found in the mesopelagic zone; these species are mentioned as daytime inhabitants of the deep layers, and strong vertical migrants [14,41,57,72]. The non-calanoids *T. conifera*, *O. venusta*, and *O. plumifera* were present in epi- and bathypelagic waters, and they were also present in the mesopelagic zone, in accordance with their general distribution pattern [41], and their occurrence in the tropical zone off Brazil [57]. *M. brevicauda*, *Conaea*, *Monacilla*, *R. cornutus*, *N. tonsus* and *C. cf. carinatus* were found in the lower mesopelagic and bathypelagic zones, in accordance with their presence in other areas of the Atlantic Ocean [12,14,26] and their cosmopolitan distribution. In relation to the ontogenic vertical distribution, *N. tonsus* and *C. cf. carinatus* copepodites were observed in several stations at deep strata. They were only found in the meso- and bathypelagic layers of upwelling systems, as previously reported [11,12,14]. The cosmopolitan species occur widely throughout the uniform environmental conditions of low latitudes, in particular in the oligotrophic regions, and most native species seems to be important in the upwelling and productive areas [1]. The low temperature of the deep ocean could indicate that there was not barrier to the distribution of the deep sea cosmopolitan species as observed in our work.

The depth segregation of zooplankton assemblages was found to be consistent among oceans. Depth, rather than oceans or biogeographical provinces, seem to be the primary factor structuring the habitat and communities of zooplankton, as it has been already mentioned [10,73]. According to RDA analysis, the richer areas with high phytoplankton (as fluorescence) but in particular temperature and dissolved oxygen concentration were relevant variables and related to the copepod distribution. As expected, depth was correlated with temperature and it could explain better the copepod distribution. Accordingly, we observed *N. minor* and *M. brevicauda* segregated in relation to temperature, *L. clausi* and *Pareucalanus* also segregated in relation to the concentration of dissolved oxygen, or *Euchaeta marina* and *Conaea* in relation to the fluorescence. It was particularly interesting to observe that *Pareucalanus* organisms showed their highest abundance in the Eastern North Pacific, closer to the oxygen minimum zone. These copepods, together with *Eucalanids*, normally show a wide range of ecological strategies but are also known to tolerate low oxygen conditions [74]. To properly understand all this, further research has to be done but the relationship observed between copepod assemblages and temperature as well as oxygen could suggest that ocean warming and expanding OMZs, may lead to changes in some zooplankton assemblages. The data reported here provide a, hitherto unavailable, guideline to assess changes in future.

5. Conclusions

This study provides a useful global assessment of subtropical and tropical zooplankton communities along the Atlantic, Indian and Pacific Oceans, focusing on copepods and their main species dominating the communities. Whereas abundance declined with depth, species number and diversity remained high throughout the water column, peaking in the mesopelagic layer. Overall, vertical profiles of copepod abundance and diversity for the three oceans were similar, and differences were mainly due to some species and their proportion rather than total abundances. Moreover, the tropical-subtropical oceanic waters were characterized by cosmopolitan copepods and by the dominance of small-sized species, which are well adapted to the oligotrophic conditions of the tropical and subtropical oceans. As it was expected, several upwelling divergent areas showed higher zooplankton abundances down to bathypelagic depths highlighting the relevance of these areas for the whole tropical and subtropical ocean. Moreover, the relationship observed between dominant copepod species and main environmental variables such as temperature and oxygen suggest that ocean warming and the expansion of OMZs, could lead to changes in the zooplankton community. The data reported here provide a, hitherto unavailable, guideline to assess changes in the future.

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