Progress in Oceanography 226 (2024) 103303

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

# Zooplankton communities at the sea surface of the eastern Indian sector of the Southern Ocean during the austral summer of 2018/2019

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## ARTICLE INFO

*Keywords:*
Zooplankton
Community structure
Surface waters
East Antarctica
Antarctic krill

## ABSTRACT

Knowledge on the distribution of zooplankton in the many unique habitats of the Southern Ocean is essential for understanding food web dynamics, assessing the impacts of environmental change and for managing the exploitation of marine living resources. Variation in the distribution of zooplankton may occur in the horizontal as well as the vertical plane, and the latter may show a diel cycle (diel vertical migration or DVM). Conventional sampling methods, including several types of nets and acoustics, often undersample or ignore the top 10 m of the water column. The surface waters may, however, host a specific zooplankton community and therefore be an important foraging ground for higher trophic level predators. In order to investigate the importance of the surface waters for understanding the distribution of species and potentially improving abundance estimates, the upper two meters of the water column were sampled in the eastern Indian sector of the Southern Ocean using a Surface and Under Ice Trawl (SUIT). Findings were compared to the zooplankton community structure in the epipelagic (15–200 m). Results showed that the surface zooplankton community could largely be divided into two regions. The surface community of the western side of the sampling area hosted large numbers of Antarctic krill, *Euphausia superba*, which were only present in low densities in the epipelagic depth layer. Densities of *Limacina helicina* were also relatively high in the west. The copepod *Calanus propinquus* and the amphipod *Themisto gaudichaudii* were present in relatively large numbers throughout the sampling area. *T. gaudichaudii* was the dominant species of the surface in the eastern side of the sampling area in the absence of Antarctic krill. Apart from cirripedia nauplii, no species were uniquely found in the surface water compared to the 15–200 m depth layer. Surface water sampling revealed patterns in vertical distribution and DVM, and showed that these patterns changed between the first and second half of the expedition. This could partially be explained by environmental variables but was likely also a result of sampling time and location, and associated variation in the size and ontogeny of species. Results revealed the impact of undersampling the surface layer regarding knowledge on distribution and vertical migration patterns of zooplankton species.

## 1. Introduction

The Southern Ocean ecosystem comprises many unique habitats that differ in physical, chemical and geographical parameters, and that may host different species and communities (Grant et al., 2006; Post et al., 2014). Distribution of zooplankton and micronekton species are key

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https://doi.org/10.1016/j.pocean.2024.103303

parameters for investigating e.g. pathways of carbon transfer, relationships between primary and secondary producers, or foraging strategies and energetics of higher trophic level predators (Pakhomov & Froneman, 2004; Ward et al., 2005; Lea et al., 2006). The zooplankton community structure varies with environmental variables, and may be used as an indicator of changes resulting from e.g. climate warming (Quetin et al., 1996; Tanimura et al., 1999; Hosie et al., 2000). Zooplankton distribution is locally influenced by life cycle strategies, trophic interactions and primary production cycles (Swadling et al., 2010).

Apart from changes in distribution on the horizontal plane, changes may occur vertically depending on e.g. region or season (Hosie et al., 2000). The vertical distribution of species is often assumed to be a result from a trade-off between food availability and predation pressure, and species may change the depth layer they occupy over a daily cycle (Diel Vertical Migration or DVM). Although the mechanisms and cues of DVM remain unclear and different patterns exist, a common form of DVM is that animals come up to the surface at night to feed and move to deeper layers during the day to avoid predators (Lampert, 1989).

The variation in the zooplankton community has been studied using several vertically and obliquely towed nets, targeting a range of zooplankton sizes and depth layers depending on type of net and mesh size used. Acoustic methods are also used to survey zooplankton distribution in the water column. Both methods do not provide any information about the upper 10–15 m of the water column, as this layer is not visible using acoustics and nets often do not sample this depth stratum properly (Atkinson et al., 2012). Many nets sample the upper 10 to 15 m in the wake of the ship, including the Rectangular Midwater Trawl (RMT), which is used to sample meso- and macrozooplankton communities in many large-scale studies (Swadling et al. 2010). In the ship's wake, the surface water is displaced by the moving vessel and the ship's propellers (Everson & Bone, 1986; Methot, 1986; Flores et al., 2012a; Flores et al., 2014). Previous studies have observed species such as Antarctic krill (*Euphausia superba*) being moved or carried away from the ship's stern (Marr, 1962). In addition, studies revealed that abundances of juvenile krill are often underestimated, possibly due to the undersampling of the surface layer (references in Atkinson et al. 2012).

High chlorophyll *a* concentrations have been found in the upper 15 m to 20 m of the water column in certain regions, such as waters close to the ice edge, the sea-ice zone of the Atlantic sector of the Southern Ocean and the northern Polar Frontal Zone (Bracher et al., 1999; Tremblay et al., 2002). Diatoms were found to thrive in waters which were highly stratified and had shallow mixed layers (5–20 m) in the Ross Sea in summer (Arrigo et al., 1999). Thus the upper surface layer may host a high phytoplankton and zooplankton biomass, and may be an important foraging ground for higher trophic level predator species that forage at shallow depths. However, due to the undersampling by most conventional survey methods, the zooplankton community in the upper surface layer is likely underrepresented in scientific studies (Flores et al., 2014).

Previous investigations using a Continuous Plankton Recorder provide evidence for elevated abundances and particular use of the upper surface layer (0——6 m) by micro- and mesozooplankton, and indicated the importance of this layer as a habitat (Hays & Warner, 1993; Hunt & Hosie, 2003). The Surface and Under Ice Trawl (SUIT; Van Franeker et al., 2009) provided information on the meso- and macrozooplankton community of the upper two meters of the water column (0–2 m), showing that this surface layer can host species that are exclusively found there while other species seem to avoid the surface altogether or occupy multiple depth layers (Flores et al. 2014).

SUIT sampling showed that the distribution of species in various depth layers varies with season (Flores et al., 2014). The zooplankton community in the summer surface layer of the Lazarev Sea was found to differ between ice-covered and open waters (Flores et al., 2011; 2014), while the zooplankton community in the epipelagic was more uniform. Bottom depth had an influence on community composition in both the surface and the epipelagic layers (Flores et al., 2014). In addition, DVM has been suggested to cease during austral summer, but Flores et al. (2014) showed that DVM actually still occurred with a decreased amplitude at depths shallower than 50 m, for example for the krill species *Thysanoessa macrura*. This indicates that certain DVM patterns are overlooked when using conventional sampling methods because the rise to surface goes unnoticed.

For this study, samples were collected in the eastern Indian sector of the Southern Ocean. The study aims to describe the zooplankton community structure in the top two meters of the water column in this area, and the horizontal distribution of zooplankton species in this undersampled depth layer. Effects of environmental parameters on the surface community composition are investigated. We further aim to gain knowledge on possible vertical distribution and DVM strategies of certain species. Therefore, the surface community structure is compared to the meso- and macrozooplankton community structures of the epipelagic layer as studied by Matsuno et al. (2018) and Urabe et al. (this issue), respectively. One of the main objectives of the survey was to provide an Antarctic krill biomass estimate for CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) statistical division 58.4.1. Therefore, this study also aims to increase knowledge regarding the distribution and biology of Antarctic krill, and relationships with the distribution of other species, which can be used for ecosystem-based management of potential krill fisheries in the area by CCAMLR.

## 2. Materials and methods

### 2.1. Sampling and sample analysis

Sampling was conducted on board RV *Kaiyo-maru* (2942 GT, Fisheries Agency of Japan) in the eastern Indian sector of the Southern Ocean between 80 and 150°E (west and east borders of CCAMLR Statistical Division 58.4.1), and 60 and 66°S (Fig. 1). The southern boundary was set at either the sea-ice edge or the 2000 m isobath if it had extended beyond the ice edge. The northern boundary was set approximately 150 nautical miles (278 km) to the north of the sea-ice edge. This research was performed as a part of the multidisciplinary ecosystem survey in the eastern Indian sector of the Southern Ocean (KY1804 survey, acronym for the fourth survey of the vessel in Japanese fiscal year 2018) (Murase et al., this issue). The survey was conducted during two periods. During Leg 1, which was conducted from 15 December 2018 to 7 January 2019, net sampling was performed on 5 transects from west to east (80 to 120°E). During Leg 2, conducted from 26 January to 23 February 2019, net sampling was performed from east to west on 3 transects (150 to 125°E).

Standard double oblique tows were conducted at 43 predetermined stations on 8 transects using a multiple opening and closing RMT 1 + 8 (Baker et al. 1973; Roe and Shale 1979), from the near surface (15–20 m depth) to 200 m depth (Fig. 1). Although the RMT net is hauled up to the surface, it is presumed to undersample the upper 10–15 m. The RMT 1 and RMT 8 have mouth openings of 1 $m^2$ and 8 $m^2$, and mesh sizes of 0.33 mm and 4.5 mm, respectively. At 27 RMT 1 + 8 stations conducted (Matsuno et al. 2018; Urabe et al. this issue), surface water community sampling (0 to 2 m depth) was also performed using a SUIT (Fig. 1; Sup. Table S1). Of the 16 stations sampled during Leg 1, 11 were conducted during day-time (between sun rise and sun set) and five were conducted during night-time (between sun set and sun rise). During Leg 2, nine out of the 11 stations sampled were conducted during the day, and two during the night. The SUIT consisted of a 2 x 2 m steel frame with two nets attached. The first net was a 7 mm half-mesh commercial shrimp net attached over 1.5 m width. The rear 3 m of this shrimp net was lined with 0.3 mm plankton gauge. The second net was a 0.3 mm mesh plankton net, attached over 0.5 m width of the frame. The net was towed with 200 m wire at a constant speed of 2.5 to 3 kn. Due to an asymmetric bridle, the net was forced to tow off at an angle allowing it to sample outside the ship's wake. Filtered water volume was measured during trawling using an Acoustic Doppler Current Profiler (ADCP, Nortek,

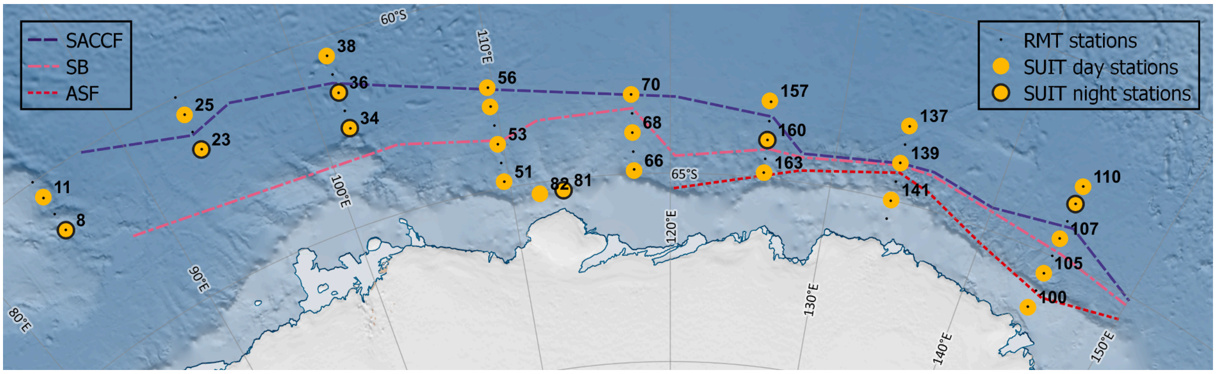

**Fig. 1.** Map of the sites in the eastern Indian sector of the Southern Ocean in 2018/19 where summer sampling was conducted during expedition KY1804, using a Surface and Under Ice Trawl (SUIT) and a Rectangular Midwater Trawl (RMT). For the SUIT, stations conducted during day-time and stations conducted during the night-time are indicated. SACCF = Southern Antarctic Circumpolar Current Front, SB = the Southern Boundary of the Antarctic Circumpolar Current and ASF = Antarctic Slope Front.

Norway) mounted in the SUIT-net frame. All the sampling stations were located in open water.

After trawling the catches were immediately preserved on 10 % sodium tetraborate decahydrate-buffered formalin before or after sorting, depending on available time. All zooplankton samples were sorted to the lowest taxonomic level possible. Mesozooplankton was counted in the smaller mesh plankton net and the RMT 1, while macrozooplankton was counted from the larger mesh shrimp net and the RMT 8. When necessary, species present in high numbers were enumerated in a fraction of the sample which was subsampled using a Motodo plankton splitter. Details of RMT sample analysis can be found in Matsuno et al. (2018) and Urabe et al. (this issue). Rare species in the SUIT were enumerated in the entire sample from both the plankton and shrimp nets. Volumetric density (individuals m$^{-3}$) was then calculated by dividing the counted number per species by the trawled distances, as calculated using the ADCP data, multiplied by depth (2 m) and the width of the respective nets. Certain species have a wide size range or have several developmental stages represented in the zooplankton catch, indicating that using data from one net or the other would underestimate numbers of a certain size and thus their contribution in the zooplankton community. Therefore, for krill species volumetric densities are calculated from the catch of the plankton net for krill $<$ 20 mm, and from the catch of the shrimp net for krill $\geq$ 20 mm (Siegel, 1986; Flores et al., 2012a; Schaafsma et al., 2016). For species in very low numbers, where often single or few specimens were found in either one of the nets regardless of size, volumetric densities were calculated by using the total number in both nets and dividing by the trawled distance times the depth and total width of both nets together. A small number of fish (larvae) and squid were caught in the SUIT net which were included in further data analysis to keep the overview of the catch in the surface waters complete. In addition, it has been under debate if large krill should still be regarded as plankton. The community including fish, squid and krill is, however, further referred to as the "zooplankton community" throughout this study. Densities of copepods identified to species level include both adult individuals and copepodites, although the number of identifiable copepodites for species other than *Calanus propinquus* and *Calanus simillimus* was generally very low. For unidentifiable species, the densities of adults individuals and copepodites are presented separately.

### 2.2. Data analysis

The community structure of zooplankton was investigated with a hierarchical agglomerative cluster analysis based on a Bray-Curtis similarity matrix and group-average linkage (Clarke & Warwick, 2001). For the cluster analysis, data was square root transformed, which downweighs the effect of highly abundant species, but takes rare species less into account compared to e.g. a 4th root or log transformation (Clarke & Warwick, 2001). The association of the community structure with a set of environmental variables was assessed using a BioEnv analysis (Clarke & Ainsworth, 1993). Before analysis, a draftsman plot of the environmental data was used to assess skewness of the data and correlation of variables. Environmental variables used (Sup. Table S2) were mean water temperature over 0–200 m depth (MTEM-200), the surface water temperature at 1 m depth (TEM1), mean salinity over 0–200 m depth (MSAL-200), the surface water salinity at 1 m depth (SAL1), bottom depth (DPT), sea-surface chlorophyll *a* (CHL; mg m$^{-3}$) and time since sea-ice melt (TSM). MTEM-200 was previously used to related spatial distribution patterns of *E. superba* (Naganobu & Hirano, 1982; 1986). Temperatures and salinities were obtained using an XCTD (Tsurumi Seiki Co., Ltd., Japan, MK-130) conducted at each RMT station. TSM represents the period between the day after which the sea-ice concentration dropped below 15 % and the day of sampling (in number of days), which was obtained using AMSR2 (Advanced Microwave Scanning Radiometer 2) and SSMIS (Special Sensor Microwave Imager/Sounder) satellite data from the Arctic Data archive System (ADS, https://ads.nipr.ac.jp/). Merged satellite data downloaded from the GlobColour project (https://hermes.acri.fr/index.php) were used to obtain CHL at a spatial resolution of 4 km and a temporal resolution of 8 d using a weighted averaging merging (AVW) method. The TEM1 was removed from the dataset because it was correlated with MTEM-200 (Pearson correlation = 0.7). MTEM-200 was retained because environmental conditions below the sampling depth have been shown to influence surface abundance of certain species (Hosie et al., 2000; Takahashi et al., 2011; Murase et al., 2013), but either one of the temperature variables could have been used. The environmental data was not transformed except for CHL which was log(x) transformed because of skewness of the data. All environmental data was then normalised by subtracting the mean value and dividing by the standard deviation over all samples of that variable to obtain a consistent scale for each and to ensure equal variance (Clarke & Warwick, 2001). Stations 25 and 157 were removed from the analysis due to missing environmental data. For the BioEnv analysis the abundance data was 4th root transformed, further decreasing the effect of abundant species and increasing the importance of rarer species. A Mantel test was used to test the significance of the association of the environmental variables selected with BioEnv with the community data using Spearman's correlation. The significance of Mantel test correlations was assessed with a bootstrapping procedure using 999 iterations. For all multivariate analyses, species that were only present at a single station were removed from the dataset, because the occurrence of very rare species in a sample is likely random, which may confuse any patterns in the community structure, and such species do not provide any information on spatial effects (Clarke & Warwick, 2001). In addition, the species *Clione limacina* and *Spongiobranchaea australis* were pooled together with unidentified Gymnosomata as these unidentified individuals were likely one of these two aforementioned species, and thus keeping them apart would give an unrealistic image of their distribution over the sampling area. In addition, the number of Gymnosomata that could be identified to species level was very low. For the same reason, *Salpa thompsoni* was pooled together with unidentified salps and all fish were pooled together with the unidentified ones as "fish spp.".

For the groups identified using cluster analysis, indicator species were determined using the IndVal method (Dufrêne & Legendre, 1997). The indicator value is calculated as:

$$IndVal = A_{ij} * B_{ij} * 100 \tag{1}$$

where $A_{ij}$ is the group specificity and $B_{ij}$ is the group fidelity. Group specificity and fidelity are calculated as:

$$A_{ij} = Nindividuals_{ij} / Nindividuals_{i} \tag{2}$$

where $Nindividuals_{ij}$ represents the mean number of individuals of species *i* in cluster *j*, and $Nindividuals_{i}$ is the sum of the mean numbers of individuals of a species *i* over all clusters, and:

$$B_{ij} = Nsamples_{ij} / Nsamples_{j} \tag{3}$$

where $Nsamples_{ij}$ is the number of samples in cluster *j* where species *i* is present, and $Nsamples_{j}$ is the number of samples in cluster *j*. Species with an IndVal $\geq$ 25 % were considered indicator species. An IndVal of over 25 % indicated that a species is present in more than 50 % of the samples in that cluster and that its abundance in that cluster was more than 50 % of the summed abundance over all clusters (Dufrêne & Legendre, 1997).

Differences in total species densities, in numbers 1000 $m^{-3}$, between legs, gears or day/night hauls were analysed using the non-parametric Wilcoxon rank-sum test. The volumetric densities between depth layers were compared for the species that dominated the 0–2 m depth layer, the 15–200 m depth layer (Matsuno et al., 2018; Urabe et al., this issue). Statistical significance was set at $\alpha = 0.05$. All statistical tests were performed with the R software, version 4.2.1 (R Core Team, 2022), and packages "vegan" (Oksanen et al. 2020), "ecodist" (Goslee & Urban, 2007), and "mclust" (Scrucca et al. 2016). Maps were generated using Quantarctica (Matsuoka et al., 2021).

## 3. Results

### 3.1. Surface zooplankton

In the surface waters, highest average densities were found for the krill *E. superba*, followed by the amphipod *Themisto gaudichaudii*, the copepods *C. propinquus* and *Oithona similis,* and then by the krill *Thysanoessa macrura* (post-larval) and the gastropod *Limacina helicina* (Table 1; Fig. 2). Some species were only encountered at a single station, including the copepods *Calanoides acutus* and *Pleuromamma robusta*, the amphipods *Hyperia medusarum* and *Vibilia antarctica*, siphonophores and a single comb jelly fish.

Generally, the total mean abundance of copepods was higher during Leg 1 compared to Leg 2 (Table 1; Fig. 2). *Metridia lucens* was only present at two stations (157 and 160) during Leg 2, with a relatively high number at station 157 (182.9 ind. 1000 $m^{-3}$) conducted at night. For *C. propinquus* (range 1.23 to 6412.38 ind. 1000 $m^{-3}$), *C. simillimus* (range 1.89 to 58.21 ind. 1000 $m^{-3}$), *O. similis* (range 0.73 to 2269.24 ind. 1000 $m^{-3}$) and *Rhincalanus gigas* (range 1.16 to 50.93 ind. 1000 $m^{-3}$), densities did not significantly differ between legs or between day/night stations. Further unidentified copepods (range 1.16 to 339.49 ind. 1000 $m^{-3}$), which generally represent copepods smaller than 1 mm, and unidentified copepodites (range 1.38 to 159.92 ind. 1000 $m^{-3}$) were found throughout the sampling area, sometimes in relatively high numbers. The majority of *C. propinquus* found in the surface were adult females (average 72.9 % of the total number of *C. propinquus* per station) followed by CV copepodites (17.5 %; Sup. Table S3). CIV and CIII copepodites occurred occasionally. Findings were similar for *C. simillimus*, with the population of this species consisting of, on average, 41.1 % adult females and 43.8 % CV copepodites per station (Sup. Table S4). CIII copepodites of *C. simillimus* were not present in the sampling area.

*E. superba* was found in the surface waters at all stations conducted during Leg 1, with abundances ranging from 2.51 to 44144.14 ind. 1000 $m^{-3}$ (Table 1; Fig. 2). A low number of individuals was only found at one station during Leg 2, resulting in a statistically significant difference in abundance between legs ($W = 176$, $p < 0.0001$). Densities were significantly higher during the night compared to the day ($W = 33.5$, $p = 0.04$), also when analysed within Leg 1 only ($W = 7$, $p = 0.02$). Similar patterns were found for post-larval *T. macrura* (range 2.05 to 609.29 ind. 1000 $m^{-3}$), which were also absent during Leg 2, and also more abundant during the night than during the day in Leg 1 ($W = 6$, $p = 0.01$). *Euphausia frigida* was only present at two stations (160 and 163) sampled during Leg 2 (5.79 and 0.18 ind. 1000 $m^{-3}$, respectively). Krill larvae were found throughout the sampling area with no statistical difference in numbers between either legs or day/night stations. The majority of krill larvae were damaged and could not be identified, but *T. macrura* larvae were at least present at stations 70, 107 and 109, and included larval stages furcilia I and furcilia VI (FI and FVI).

Many amphipod species were present in the surface waters of the sampling area at low abundances, and nine out of 14 species encountered were only present during Leg 1 (Table 1; Fig. 2). The amphipod *Cyllopus lucasii* (range 0.63 to 11.36 ind. 1000 $m^{-3}$) was one of the species only occurring at the surface during Leg 1. Within this Leg, densities were significantly higher during the night compared to the day ($W = 6$, $p = 0.004$). Both *Hyperiella dilatata* (range 0.29 to 2.39 ind. 1000 $m^{-3}$) and *Hyperoche medusarum* (range 0.62 to 1.77 ind. 1000 $m^{-3}$) also only occurred in the surface during Leg 1, but densities did not significantly differ between day and night. The amphipod *Primno macropa* was found throughout the survey area, and abundances did not significantly differ between legs or between day and night stations. *T. gaudichaudii* was also found throughout the sampling area at almost all stations (Fig. 2), with very variable densities per station (ranging from 0.14 to 4495.62 ind. 1000 $m^{-3}$). Although very high abundances of *T. gaudichaudii* were encountered a couple of times during Leg 2 (e.g. 1549.90 and 4495.62 ind. 1000 $m^{-3}$ at stations 107 and 109), numbers were, on average, not significantly different between legs nor day/night (Table 1). Because *E. superba* was only found occasionally during Leg 2, *T. gaudichaudii* became, on average, the dominant species in the zooplankton community of this Leg. Low numbers of *Eusirus* spp., including *Eusirus laticarpus* and *Eusirus tridentatus*, were found at 3 stations during Leg 1. A high number of juvenile hyperiid amphipods were found at one station (station 70, 459.82 ind. 1000 $m^{-3}$) during Leg 1, and occurred at two more stations (23 and 137) in lower numbers.

Gastropods occurred only during Leg 1 (Table 1; Fig. 2), resulting in a statistically significant difference in densities between legs for *L. helicina* ($W = 165$, $p < 0.0001$) and for Gymnosomata, including *Clione limacina* and *Spongiobranchaea australis* ($W = 159.5$, $p < 0.001$). *L. helicina* was by far the most abundant species found (ranging from 4.38 to 188.45 ind. 1000 $m^{-3}$). Within Leg 1, densities did not differ between day and night for any of the gastropods.

Salps occurred at five stations of which four were conducted during Leg 1 and four were conducted during the night (Fig. 2). At these stations, densities ranged from 0.91 to 41.17 ind. 1000 $m^{-3}$ (Table 1). The majority of the salps could not be identified to species level because they were damaged. There was no significant difference in densities between legs, but densities were significantly higher during the night ($W = 31.5$, $p = 0.002$). Average densities of chaetognaths (range 0.33 to 347.58 ind. 1000 $m^{-3}$) were significantly higher during Leg 1, compared to Leg 2 ($W = 21.5$, $p = 0.005$) where they occurred at only two stations. Numbers were significantly higher at night-time stations compared to day-time stations ($W = 6$, $p = 0.02$). Polychaetes of the genus *Tomopteris* were

**Table 1**
Summary of the zooplankton community of the surface water (0–2 m) of the eastern Indian sector of the Southern Ocean in 2018/19 including average densities and frequency of occurrence (%FO), which indicates the percentage of the total 27 stations at which the species was present. Average densities are also given per leg and separated for stations conducted at day-time or night-time.

| | Totals sampling area | | Average 1000 m$^{-3}$ Leg 1 | | Average 1000 m$^{-3}$ Leg 2 | |
|---|---|---|---|---|---|---|
| ***n*** | 27 | 27 | 11 | 5 | 9 | 2 |
| | Average 1000 m$^{-3}$ ± sd | %FO | Day stations | Night stations | Day stations | Night stations |
| **Copepods** | | | | | | |
| *Calanoides acutus* | 0.06 ± 0.30 | 3.7 | 0.14 ± 0.48 | 0 | 0 | 0 |
| *Calanus propinquus* | 291.93 ± 1231.96 | 55.6 | 637.08 ± 1921.57 | 144.12 ± 251.24 | 1.99 ± 4.08 | 67.92 ± 87.27 |
| *Calanus simillimus* | 3.61 ± 11.33 | 25.9 | 1.20 ± 2.76 | 11.64 ± 26.03 | 2.20 ± 4.01 | 3.10 ± 4.39 |
| *Metridia lucens* | 6.87 ± 35.18 | 7.4 | 0 | 0 | 0.28 ± 0.83 | 91.44 ± 129.31 |
| *Oithona similis* | 91.68 ± 435.61 | 48.1 | 216.12 ± 681.55 | 0.99 ± 2.22 | 6.14 ± 7.69 | 18.99 ± 17.04 |
| *Pleuromamma robusta* | 0.17 ± 0.89 | 3.7 | 0 | 0 | 0 | 2.31 ± 3.27 |
| *Rhincalanus gigas* | 2.31 ± 9.81 | 14.8 | 0 | 1.14 ± 2.54 | 0.63 ± 1.52 | 25.46 ± 36.01 |
| Unidentified copepodites | 9.29 ± 32.72 | 22.2 | 21.59 ± 49.97 | 1.50 ± 3.34 | 0.66 ± 1.53 | 0 |
| Unidentified copepods | 29.89 ± 73.42 | 63.0 | 47.30 ± 105.98 | 1.58 ± 2.23 | 16.65 ± 34.88 | 64.45 ± 82.36 |
| *Total copepods* | *435.81 ± 1299.05* | *92.6* | *923.43 ± 1974.55* | *160.96 ± 243.46* | *28.54 ± 36.95* | *273.67 ± 316.80* |
| **Euphausiids** | | | | | | |
| *Euphausia frigida* | 0.22 ± 1.11 | 7.4 | 0 | 0 | 0.02 ± 0.06 | 2.89 ± 4.09 |
| *Euphausia superba* | 2457.02 ± 9031.34 | 63.0 | 1645.13 ± 5390.79 | 9648.47 ± 19351.04 | 0 | 0.37 ± 0.52 |
| *Thysanoessa macrura* | 31.92 ± 117.910 | 29.6 | 10.36 ± 27.10 | 149.57 ± 259.09 | 0 | 0 |
| Unidentified krill | 1.70 ± 5.88 | 29.6 | 2.87 ± 9.02 | 1.34 ± 1.60 | 0.85 ± 2.46 | 0 |
| *Total euphausiids* | *2490.86* ± 9030.30 | *74.1* | *1658.36* ± 5396.45 | *9799.37* ± 19275.07 | *0.87 ± 2.46* | *3.26* ± 4.61 |
| *T. macrura* larvae | 2.11 ± 9.80 | 11.1 | 0.46 ± 1.52 | 0 | 0.13 ± 0.39 | 25.45 ± 35.99 |
| Unidentified krill larvae | 1.70 ± 5.88 | 29.6 | 2.87 ± 9.02 | 1.34 ± 1.6 | 0.85 ± 2.46 | 0 |
| *Total euphausiid larvae* | *3.82 ± 11.10* | *40.7* | *3.33 ± 8.99* | *1.34 ± 1.6* | *0.98 ± 2.44* | *25.45 ± 35.99* |
| **Amphipods** | | | | | | |
| *Cyllopus lucasii* | 0.91 ± 2.56 | 18.5 | 0.06 ± 0.19 | 4.79 ± 4.42 | 0 | 0 |
| *Cyllopus magellanicus* | 0.03 ± 0.14 | 3.7 | 0 | 0.14 ± 0.32 | 0 | 0 |
| *Eusirus laticarpus* | 0.05 ± 0.18 | 7.4 | 0 | 0.27 ± 0.37 | 0 | 0 |
| *Eusirus tridentatus* | 0.05 ± 0.19 | 7.4 | 0 | 0.26 ± 0.41 | 0 | 0 |
| *Eusirus* sp. | 0.01 ± 0.03 | 3.7 | 0.02 ± 0.05 | 0 | 0 | 0 |
| *Hyperia medusarum* | 0.05 ± 0.27 | 3.7 | 0.13 ± 0.42 | 0 | 0 | 0 |
| *Hyperiella dilatata* | 0.18 ± 0.54 | 18.5 | 0.24 ± 0.72 | 0.45 ± 0.67 | 0 | 0 |
| *Hyperiella* sp. | 0.02 ± 0.09 | 7.4 | 0.03 ± 0.08 | 0.07 ± 0.16 | 0 | 0 |
| *Hyperoche medusarum* | 0.11 ± 0.38 | 11.1 | 0.06 ± 0.21 | 0.48 ± 0.77 | 0 | 0 |
| *Primno macropa* | 1.14 ± 2.47 | 51.9 | 0.70 ± 1.06 | 1.10 ± 1.14 | 0.54 ± 1.02 | 6.28 ± 8.68 |
| *Themisto gaudichaudii* | 299.98 ± 895.17 | 96.3 | 81.47 ± 136.09 | 154.54 ± 235.93 | 211.45 ± 506.21 | 2263.80 ± 3156.28 |
| *Vibilia antarctica* | 0.17 ± 0.89 | 3.7 | 0 | 0.92 ± 2.06 | 0 | 0 |
| Juvenile hyperiids | 17.29 ± 88.45 | 11.1 | 41.80 ± 138.64 | 1.28 ± 2.87 | 0.07 ± 0.21 | 0 |
| Unidentified amphipods | 1.39 ± 3.08 | 40.7 | 2.03 ± 3.81 | 2.92 ± 4.04 | 0.02 ± 0.05 | 0.16 ± 0.22 |
| *Total amphipods* | *321.38 ± 899.47* | *100.0* | *126.53 ± 277.04* | *167.23 ± 230.52* | *212.08 ± 506.06* | *2270.23 ± 3165.17* |
| **Salps** | | | | | | |
| *Salpa thompsoni* | 0.06 ± 0.32 | 3.7 | 0 | 0.33 ± 0.74 | 0 | 0 |
| Unidentified salps | 2.60 ± 9.18 | 14.8 | 0.08 ± 0.27 | 13.42 ± 19.15 | 0 | 1.16 ± 1.64 |
| *Total salps* | *2.67 ± 9.17* | *18.5* | *0.08 ± 0.27* | *13.75 ± 18.87* | *0* | *1.16 ± 1.64* |
| **Gastropods** | | | | | | |
| *Clione limacina* | 0.13 ± 0.33 | 14.8 | 0.31 ± 0.46 | 0 | 0 | 0 |
| *Clio pyramidata* | 0.65 ± 3.32 | 7.4 | 0 | 3.50 ± 7.71 | 0 | 0 |
| *Limacina helicina* | 30.43 ± 52.13 | 51.9 | 52.50 ± 66.61 | 48.80 ± 47.60 | 0 | 0 |
| *Spongiobranchaea australis* | 0.01 ± 0.05 | 3.7 | 0.02 ± 0.08 | 0 | 0 | 0 |
| Unidentified Gymnosomata | 1.16 ± 2.47 | 37.0 | 0.74 ± 1.36 | 4.64 ± 3.96 | 0 | 0 |
| *Total gastropods* | *32.37 ± 53.36* | *51.9* | *53.57 ± 66.97* | *56.93 ± 49.22* | *0* | *0* |
| **Fish** | | | | | | |
| *Cryodraco antarcticus* | 0.01 ± 0.04 | 3.7 | 0.02 ± 0.06 | 0 | 0 | 0 |
| Ice fish | 0.01 ± 0.07 | 3.7 | 0 | 0 | 0.04 ± 0.12 | 0 |
| *Notolepis coatsi* | 0.04 ± 0.17 | 7.4 | 0 | 0.23 ± 0.36 | 0 | 0 |
| Unidentified fish | 0.67 ± 1.97 | 18.5 | 0 | 3.62 ± 3.47 | 0 | 0 |
| *Total fish* | *0.73 ± 2.04* | *25.9* | *0.02 ± 0.06* | *3.84 ± 3.48* | *0.04 ± 0.12* | *0* |
| **Polychaetes** | | | | | | |
| *Tomopteris* sp. | 1.41 ± 3.59 | 22.2 | 0.10 ± 0.34 | 7.38 ± 5.36 | 0 | 0 |
| Unidentified polychaetes | 1.07 ± 3.90 | 18.5 | 0.11 ± 0.36 | 4.05 ± 8.59 | 0.76 ± 2.27 | 0.29 ± 0.41 |
| *Total polychaetes* | *2.48 ± 6.90* | *29.6* | *0.21 ± 0.70* | *11.43 ± 13.20* | *0.76 ± 2.27* | *0.29 ± 0.41* |
| **Chaetognaths** | 19.26 ± 67.55 | 55.6 | 2.37 ± 3.32 | 94.19 ± 144.61 | 0.14 ± 0.41 | 10.90 ± 15.41 |
| **Other** | | | | | | |
| Siphonophora | 0.01 ± 0.04 | 3.7 | 0 | 0 | 0.02 ± 0.07 | 0 |
| Squid | 0.05 ± 0.17 | 11.1 | 0.03 ± 0.10 | 0.17 ± 0.37 | 0 | 0.10 ± 0.14 |
| Comb jelly | 0.01 ± 0.03 | 3.7 | 0 | 0.03 ± 0.07 | 0 | 0 |
| Ostracods | 0.08 ± 0.30 | 7.4 | 0 | 0 | 0.25 ± 0.51 | 0 |
| Cirripedia nauplii | 2.67 ± 10.39 | 22.2 | 4.87 ± 16.16 | 0.21 ± 0.48 | 1.94 ± 3.42 | 0 |
| *Total other* | *2.82 ± 10.40* | *40.7* | *4.90 ± 16.15* | *0.41 ± 0.50* | *2.21 ± 3.62* | *0.10 ± 0.14* |

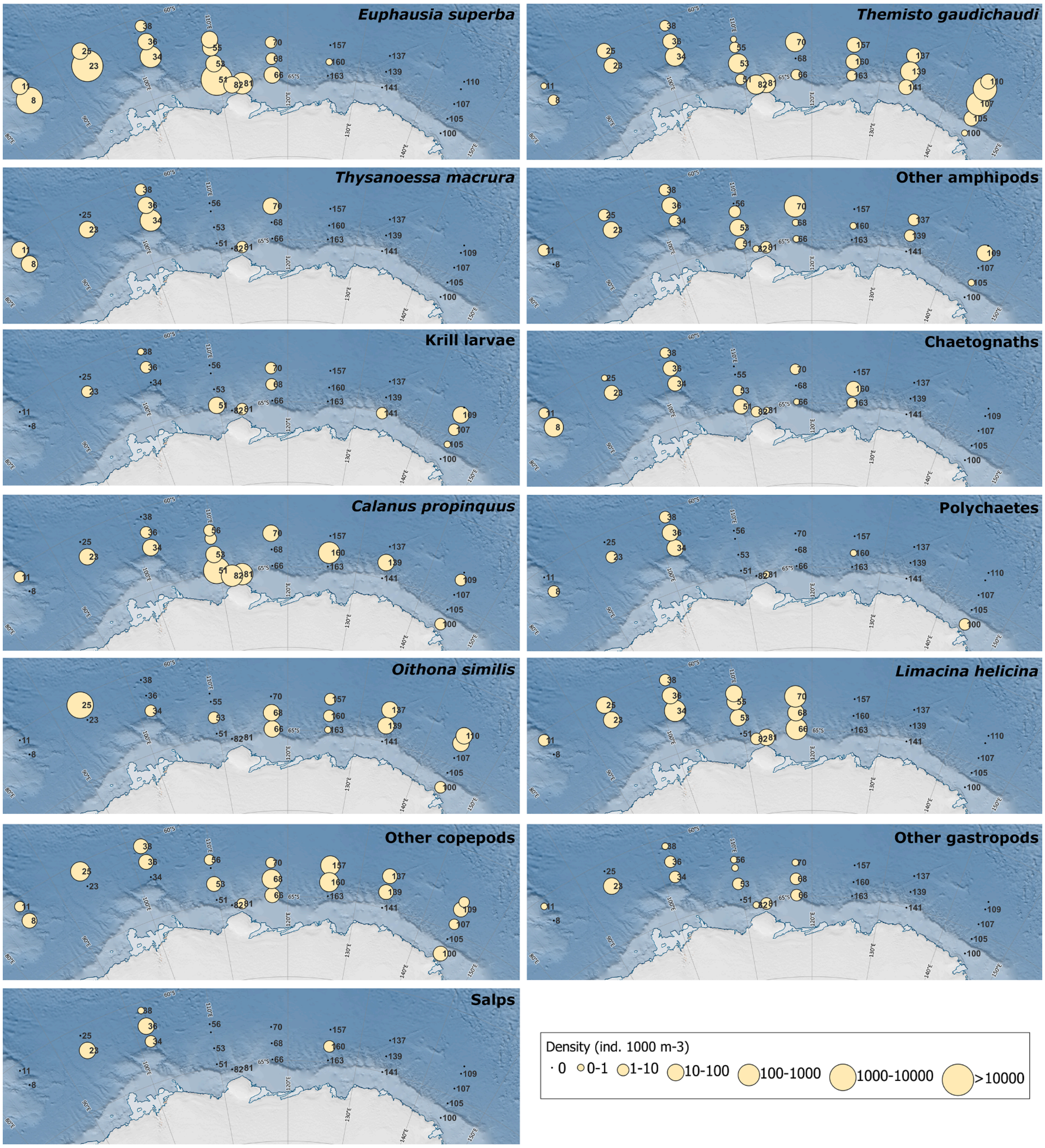

**Fig. 2.** Distribution of zooplankton in the upper two meters of the water column collected using a Surface and Under Ice Trawl (SUIT) in the eastern Indian sector of the Southern Ocean in 2018/19. The size of the points indicate the density (ind. 1000 $m^{-3}$). Black dots indicate sites were sampling was conducted but where the taxon was not present. “Other copepods”, “Other amphipods” and “Other gastropods” refer to all species (including unidentified species) other than those species presented individually in this figure.

only present in Leg 1 (range 0.20 to 14.67 ind. 1000 $m^{-3}$), during which they were almost exclusively found during night-time stations, resulting in statistically significant differences in densities between legs ($W = 121$, $p = 0.03$) and day/night stations ($W = 22$, $p < 0.001$).

Fish and squid were found occasionally throughout the sampling area, similar to cirripedia nauplii, although the latter sometimes occurred in relatively high numbers (range 1.06 to 53.60 ind. 1000 $m^{-3}$; Table 1). There was no significant difference between the number of fish encountered during Legs 1 and 2, but densities were higher during the night-time stations, compared to the day-time stations ($W = 23$, $p < 0.001$). No significant differences between legs or day/night stations were found for either squid or cirripedia nauplii. Ostracods occurred in low numbers at two stations sampled during Leg 2 (stations 139 and 157). All densities per stations can be found in Sup. Table S5.

### *3.2. Surface community structure and the relation with the environment*

The cluster analysis divided the stations into six groups (Fig. 3). Group A consisted of three stations close to the sea-ice edge, sampled during Leg 1. Stations in this group had high numbers of *E. superba*, which also had a maximum IndVal value (IndVal = 100). In addition, chaetognaths had a high IndVal value (IndVal = 88), followed by *C. propinquus* (IndVal = 62), fish (IndVal = 62), unidentified krill larvae (IndVal = 50) and the gastropod *Clio pyramidata* (IndVal = 33)(Table 2). Group B stations were also located at the southern side of the sampling area, but were conducted during Leg 2. Ice fish were the only indicator species for this group (IndVal = 33), in which stations were further characterized by low numbers of animals in general (Table 2). Three Leg 1 stations with no obvious distributional pattern grouped together (C), characterized by high IndVals for *O. similis* (IndVal = 97) and small,

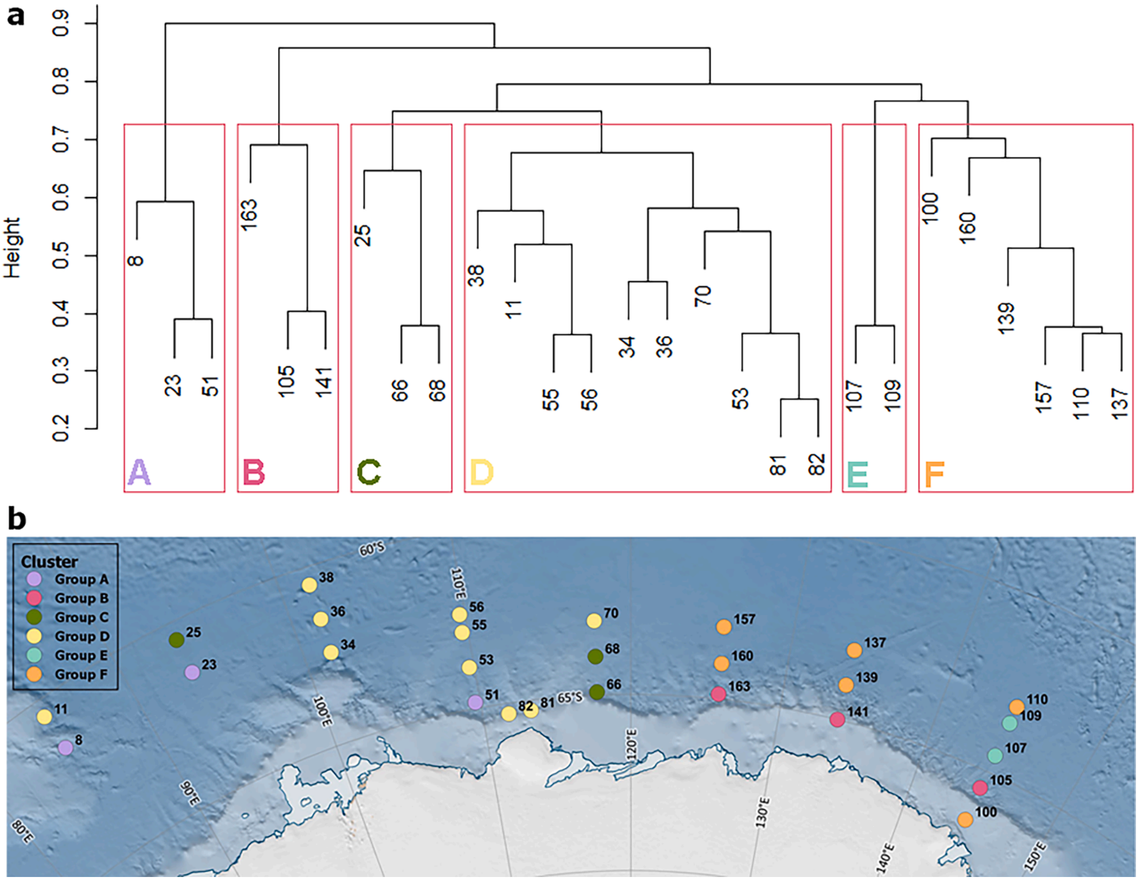

**Fig. 3.** Results of a cluster analysis performed on the zooplankton community of the surface water (0–2 m depth) collected in the eastern Indian sector of the Southern Ocean in 2018/19 (a). Numbers indicate station numbers. Six groups were identified which are indicated with red rectangles and which are named A to F from left to right. The geographic distribution of these six groups is indicated with different colours on the map (b).

<1mm, copepods (IndVal = 76), followed by copepodites (IndVal = 63), *L. helicina* (IndVal = 55), Gymnosomata (IndVal = 33) and cirripedia nauplii (IndVal = 28), which were all present in relatively high numbers compared to the other groups (Table 2). The majority of the stations formed two clusters consisting of stations sampled during Leg 1 (group D) and Leg 2 (Group F). *T. macrura* (IndVal = 41), *L. helicina* (IndVal = 40), *H. medusarum* (IndVal = 30) and Gymnosomata (IndVal = 30) were indicator species of the 10 stations in group D. The six Group F stations were indicated by *M. lucens* (IndVal = 33), ostracods (IndVal = 33) and *R. gigas* (IndVal = 30). Two stations at the easternmost side of the sampling area formed a separate cluster (group E), which had very high numbers of *T. gaudichaudii*, and generally a low number of other species. *T. macrura* larvae (IndVal = 98) and *P. macropa* (IndVal = 33) were other indicator species for this group (Table 2).

### 3.3. Comparison with the 15–200 m depth layer

Volumetric densities between depth layer were compared for post-larval *E. superba*, *T. gaudichaudii*, chaetognaths, *C. propinquus*, *Oithona sp*, post-larval *T. macrura*, *L. helicina* and salps (Fig. 4). Volumetric densities of *E. superba* were significantly higher in the upper surface compared to the 15–200 m depth layer ($W = 822$, $p = 0.003$). This was also the case for *T. gaudichaudii* ($W = 380$, $p = 0.02$). Volumetric densities of *T. macrura* ($W = 894$, $p < 0.001$), chaetognaths ($W = 152$, $p < 0.001$), *C. propinquus* ($W = 112$, $p < 0.001$), *Oithona* sp. ($W = 49$, $p < 0.001$) and salps ($W = 801$, $p = 0.004$) were significantly higher in the 15–200 m depth layer compared to the upper surface. There was no significant difference in volumetric densities between depth layers for *L. helicina*.

### 3.4. Relation surface community with environmental variables

TSM had the highest correlation between any single environmental variable and the variability of species composition (Table 3). The highest correlation between any set of environmental variables and species composition was reached with a combination of MTEM-200, CHL and TSM (Spearman correlation coefficient $r = 0.25$, Mantel test $p = 0.006$). Adding DPT, MSAL-200 or SAL1 to the set of environmental variables did not improve the correlation with species composition (Table 3).

## 4. Discussion

### 4.1. Surface water community structure

The macrozooplankton community of the surface waters could largely be divided in the two legs according to the cluster analysis, separating zooplankton communities between 80 and 120E and 120-150E. The majority of the southernmost stations belong to different groups in both legs. The analysis also indicated that dissimilarity between the southernmost stations and northern stations was often greater than the dissimilarity between legs. Particularly during Leg 2, this may be attributed to the variability in temperature as a steep north–south temperature gradient with the highest and lowest temperatures of the sampling area were found here (Urabe et al., this issue). These results largely correspond with the macrozooplankton community structure of the epipelagic (15–200 m depth) layer, that also showed that the area could largely be divided in the two legs, with three stations located south of the Antarctic Slope Front belonging to different groups in Leg 2

**Table 2**
Average densities of zooplankton per groups identified in Fig. 3. The Leg during which the stations in the group were conducted is indicated in brackets in the top row. Bold numbers, further indicated with (I), represent indicator species for that group.

| | Group | | | | | |
|---|---|---|---|---|---|---|
| | A (1) | B (2) | C (1) | D (1) | E (2) | F (2) |
| **Copepods** | | | | | | |
| *Calanoides acutus* | 0 | 0 | **0.53 ± 0.91(I)** | 0 | 0 | 0 |
| *Calanus propinquus* | **2169.58** ± **3674.69 (I)** | 0 | 0 | 121.97 ± 228.16 | 3.10 ± 4.39 | 24.58 ± 51.67 |
| *Calanus simillimus* | 0 | 0 | 0 | 7.14 ± 18.17 | 3.10 ± 4.39 | 3.29 ± 4.63 |
| *Metridia lucens* | 0 | 0 | 0 | 0 | 0 | **30.89** ± **74.46 (I)** |
| *Oithona similis* | 0 | 0.24 ± 0.42 | **791.96 ± 1280.10 (I)** | 0.64 ± 1.58 | 15.52 ± 21.95 | 10.25 ± 6.78 |
| *Pleuromamma robusta* | 0 | 0 | 0 | 0 | 0 | 0.77 ± 1.89 |
| *Rhincalanus gigas* | 0 | 0 | 0 | 0.57 ± 1.80 | 0.58 ± 0.82 | **9.25** ± **20.50 (I)** |
| Unidentified copepodites | 2.49 ± 4.32 | 0 | **75.41** ± **80.35 (I)** | 1.13 ± 3.58 | 0 | 0.99 ± 1.83 |
| Unidentified copepods | 1.07 ± 1.85 | 0 | **168.**08 ± 161.37 **(I)** | 2.07 ± 2.49 | 3.68 ± 3.57 | 45.23 ± 54.78 |
| *Total copepods* | *2173.14* ± 3671.54 | *0.24* ± 0.42 | *1035.97* ± 1370.75 | *133.52* ± 223.91 | *25.99* ± 33.47 | *125.25* ± 185.37 |
| **Euphausiids** | | | | | | |
| *Euphausia frigida* | 0 | 0.06 ± 0.11 | 0 | 0 | 0 | 0.96 ± 2.36 |
| *Euphausia superba* | **21953.57** ± **20466.71(I)** | 0 | 19.30 ± 21.11 | 42.01 ± 48.82 | 0 | 0.12 ± 0.30 |
| *Thysanoessa macrura* | 36.15 ± 48.42 | 0 | 0 | 75.34 ± 189.60 | 0 | 0 |
| Unidentified krill | **10.55** ± **16.90 (I)** | 2.56 ± 4.22 | 0.40 | 0.54 | 0 | 0 |
| *Total euphausiids* | *22000.27* ± 20433.60 | *2.62* ± 4.16 | *19.70* ± 20.65 | *117.89* ± 230.78 | *0* | *1.09* ± 2.66 |
| *T. macrura* larvae | 0 | 0 | 0 | 0.50 ± 1.59 | **26.03** ± **35.17 (I)** | 0 |
| Unidentified krill larvae | **10.55** ± **16.90 (I)** | 2.56 ± 4.22 | 0.40 ± 0.69 | 0.54 ± 1.24 | 0 | 0 |
| *Total euphausiid larvae* | *10.55* ± 16.90 | *2.56* ± 4.22 | *0.40* ± 0.69 | *1.04* ± 1.86 | *26.03* ± 35.17 | *0* |
| **Amphipods** | | | | | | |
| *Cyllopus lucasii* | 2.16 ± 3.74 | 0 | 0 | 1.81 ± 3.63 | 0 | 0 |
| *Cyllopus magellanicus* | 0 | 0 | 0 | 0.07 ± 0.22 | 0 | 0 |
| *Eusirus laticarpus* | 0 | 0 | 0 | 0.13 ± 0.28 | 0 | 0 |
| *Eusirus tridentatus* | 0 | 0 | 0 | 0.13 ± 0.30 | 0 | 0 |
| *Eusirus* sp. | 0 | 0 | 0 | 0.02 ± 0.05 | 0 | 0 |
| *Hyperia medusarum* | 0 | 0 | 0 | 0.14 ± 0.44 | 0 | 0 |
| *Hyperiella dilatata* | 0.54 ± 0.93 | 0 | 0.09 ± 0.16 | 0.30 ± 0.74 | 0 | 0 |
| *Hyperiella* sp. | 0 | 0 | 0.09 ± 0.16 | 0.04 ± 0.11 | 0 | 0 |
| *Hyperoche medusarum* | 0 | 0 | 0 | **0.31** ± **0.58 (I)** | 0 | 0 |
| *Primno macropa* | 1.44 ± 1.36 | 0.08 ± 0.14 | 0 | 0.89 ± 1.06 | **6.21** ± **8.78 (I)** | 0.80 ± 1.19 |
| *Themisto gaudichaudii* | 13.31 ± 16.37 | 12.47 ± 7.83 | 3.69 ± 5.54 | 161.79 ± 193.71 | **3022.76** ± **2082.94 (I)** | 57.95 ± 78.03 |
| *Vibilia antarctica* | 0 | 0 | 0 | 0.46 ± 1.46 | 0 | 0 |
| Juvenile hyperiids | 2.14 ± 3.71 | 0 | 0 | 45.98 ± 145.41 | 0 | 0.11 ± 0.26 |
| Unidentified amphipods | 2.14 ± 3.71 | 0 | 0.85 ± 0.51 | 2.80 ± 4.42 | 0.16 ± 0.22 | 0.03 ± 0.06 |
| *Total amphipods* | *21.72* ± 28.67 | *12.55* ± 7.91 | *4.72* ± 6.35 | *214.87* ± 253.66 | *3029.13* ± 2091.94 | *58.88* ± 78.75 |
| **Salps** | | | | | | |
| *Salpa thompsoni* | 0 | 0 | 0 | 0.17 ± 0.52 | 0 | 0 |
| Unidentified salps | 8.64 ± 14.97 | 0 | 0 | 4.21 ± 13.00 | 0 | 0.39 ± 0.95 |
| *Total salps* | *8.64* ± 14.97 | *0* | *0* | *4.37* ± 12.94 | *0* | *0.39* ± 0.95 |
| **Gastropods** | | | | | | |
| *Clione limacina* | 0 | 0 | 0.42 ± 0.72 | 0.21 ± 0.36 | 0 | 0 |
| *Clio pyramidata* | **5.76** ± 9.98 **(I)** | 0 | 0 | 0.02 ± 0.06 | 0 | 0 |
| *Limacina helicina* | 7.00 ± 12.12 | 0 | **77.15** ± **79.23 (I)** | **56.91** ± **60.03 (I)** | 0 | 0 |
| *Spongiobranchaea australis* | 0 | 0 | **0.08** ± **0.14 (I)** | 0 | 0 | 0 |
| Unidentified Gymnosomata | 2.16 ± 3.74 | 0 | 0.83 ± 1.03 | **2.23** ± **3.31 (I)** | 0 | 0 |
| *Total gastropods* | *14.92* ± 25.84 | *0* | *78.48* ± 79.93 | *59.38* ± 61.28 | *0* | *0* |
| **Fish** | | | | | | |
| *Cryodraco antarcticus* | 0 | 0 | 0 | 0.02 ± 0.06 | 0 | 0 |
| Ice fish | 0 | **0.12** ± **0.20 (I)** | 0 | 0 | 0 | 0 |
| *Notolepis coatsi* | 0.10 ± 0.17 | 0 | 0 | 0.08 ± 0.26 | 0 | 0 |
| Unidentified fish | **4.78** ± **4.39 (I)** | 0 | 0 | 0.37 ± 0.74 | 0 | 0 |
| *Total fish* | *4.88* ± 4.53 | *0.12* ± 0.20 | *0* | *0.48* ± 0.92 | *0* | *0* |
| **Polychaetes** | | | | | | |
| *Tomopteris* sp. | 4.04 ± 3.52 | 0 | 0 | 2.59 ± 5.25 | 0 | 0 |
| Unidentified polychaetes | 0 | 0 | 0 | 2.14 ± 6.08 | 0 | 1.23 ± 2.75 |
| *Total polychaetes* | *4.04* ± 3.52 | *0* | *0* | *4.73* ± 10.84 | *0* | *1.23* ± 2.75 |
| **Chaetognaths** | **125.02** ± **192.77 (I)** | 0.41 ± 0.70 | 0.20 ± 0.18 | 12.14 ± 24.70 | 0 | 3.63 ± 8.83 |
| **Other** | | | | | | |
| Siphonophora | 0 | 0 | 0 | 0 | 0 | 0.04 ± 0.08 |
| Squid | 0 | 0 | 0 | 0.12 ± 0.27 | 0 | 0.03 ± 0.08 |
| Comb jelly | **0.05** ± **0.09 (I)** | 0 | 0 | 0 | 0 | 0 |
| Ostracods | 0 | 0 | 0 | 0 | 0 | **0.37** ± **0.60 (I)** |
| Cirripedia nauplii | 0.36 ± 0.62 | 0.35 ± 0.61 | **17.87** ± **30.95 (I)** | 0 | 0 | 2.74 ± 4.04 |
| *Total other* | *0.41* ± 0.58 | *0.35* ± 0.61 | *17.87* ± 30. 95 | *0.12* ± 0.27 | *0* | *3.17* ± 4.18 |

(Urabe et al., this issue). A similar longitudinal separation of the macrozooplankton community was found during the BROKE (Baseline Research on Oceanography, Krill and the Environment) expedition in 1996 (Hosie et al., 2000), where the western side of the sampling area showed high densities of chaetognaths, siphonophores and *T. macrura* (Hosie et al., 2000). In contrast to the findings of Hosie et al. (2000) and Urabe et al. (this issue) the cluster analysis of the surface waters showed a clear Antarctic krill dominated group, which was also characterized by high densities of *C. propinquus*.

The mesozooplankton community was much more uniform

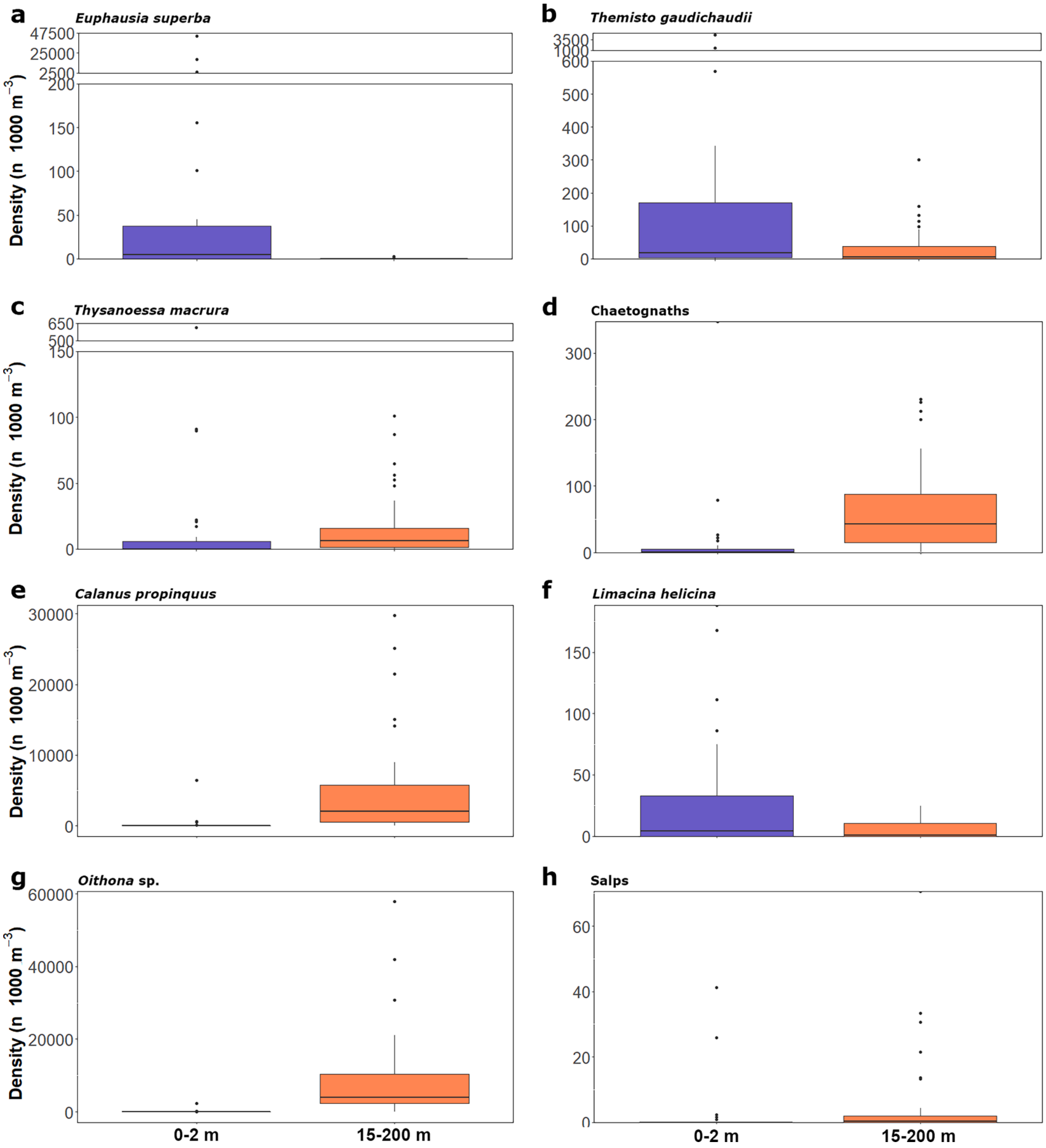

**Fig. 4.** Comparison of volumetric densities of selected zooplankton species between depth layers, which were sampled with the suit (0–2 m) and RMT (15–200 m) nets: a) *Euphausia superba*, b) *Themisto gaudichaudii*, c) *Thysanoessa macrura*, d) chaetognaths, e) *Calanus propinquus*, f) *Limacina helicina*, g) *Oithona* sp. and h) salps.

**Table 3**
Results of the BioEnv analysis conducted on the surface zooplankton community (0–2 m depth) and selected environmental variables of the Indian sector of the Southern Ocean. TSM = time since sea-ice melt, CHL = surface water chlorophyll *a*, MTEM-200 = the average water temperature over 0–200 m depth, MSAL-200 = is the average water salinity over 0–200 m depth and SAL1 = the water salinity at the surface (1 m depth).

| # variables | Variables | Correlation |
|---|---|---|
| 1 | TSM | 0.1681 |
| 2 | CHL TSM | 0.2077 |
| 3 | MTEM-200 CHL TSM | 0.2479 |
| 4 | DPT MTEM-200 CHL TSM | 0.2281 |
| 5 | DPT MTEM-200 MSAL-200 CHL TSM | 0.1871 |
| 6 | DPT MTEM-200 MSAL-200 CHL SAL1 TSM | 0.1248 |

throughout the study area in the 15–200 m depth layer (Matsuno et al., 2018). This also largely corresponds with our findings, as most copepods were distributed quite uniformly throughout the sampling area in the surface waters. The most abundant species (*C. propinquus* and *O. similis*), showed, on average, no difference in densities between legs, but the highest densities occurred during Leg 1 where they were both indicator species of a group that resulted from the cluster analysis. Small copepods also seem to have a quite uniform distribution throughout the sampling area, but these were not identified to species level, and previous studies indicate that changes in community structure may be observed in these small species (Chiba et al., 2001).

The number of studies conducted on zooplankton community structure in this part of the Indian Sector of the Southern Ocean is limited, and the surface waters are usually not studied in particular. However, some earlier studies of the mesozooplankton community structure of a depth layer relatively close to the surface (6–10 m depth) at the eastern side of the Indian sector may provide some comparison.

These studies showed a relatively high abundance of appendicularians (Hunt & Hosie, 2006; Takahashi et al., 2011). Appendicularians were absent in the surface layer during our study and occurred only occasionally in low numbers in the epipelagic layer (Matsuno et al., 2018). Dominant copepods in previous studies were small calanoid copepods, *O. similis* and *C. propinquus* or *C. simillimus*. Furthermore, high numbers of *Limacina* sp. were encountered (Hunt & Hosie 2006; Takahashi et al. 2011). A seasonal increase (from February to March) was indicated in the abundance of certain species such as *C. propinquus* (Hunt & Hosie, 2006), but was not observed in our study. Hunt & Hosie (2006) also found that an increase of salps, *E. superba* larvae and large copepods, such as *Metridia gerlachei* and *C. propinquus,* could be related to a corresponding decrease of small copepods, appendicularians and *Limacina* sp. Such patterns were also not confirmed by our results.

### 4.2. Influence of surface water sampling on knowledge of species distribution

All species found in the surface waters were also present in the 15–200 m depth layer, except for cirripedia nauplii and the amphipods *E. tridentatus* and *Cyllopus magellanicus*. The latter two species of amphipods were also only present in the surface waters incidentally. Several species or taxonomic groups present in the epipelagic layer were not encountered in the surface waters, including the krill species *Euphausia crystallorophias* and *Euphausia triancantha*, the amphipods *Eusirus microps*, *Eusirus properdentatus* and *Hyperia macrocephala*, Appendicularia, jelly fish (not taking into account the single comb jelly caught in the 0–2 m depth layer) and several copepods species such as *Paraeuchaeta* sp., *M. gerlachei* and other mesopelagic copepods such as *Gaetanus brevispinus* (Urabe et al., this issue; Matsuno et al., 2018). The aforementioned amphipod species also usually occurred only incidentally in the 15–200 m depth layer. Results indicate that regular surveys sampling standard depths may overlook the presence of some rare amphipod species and cirripedia nauplii. These latter animals seem to be the only ones with a distribution restricted to the surface waters. Knowledge on the presence of cirripedia nauplii in the surface waters may help to understand the relationship between the geographic distribution of adult barnacle and their larval dispersal (Scheltema et al., 2010).

The volumetric density of the amphipod *T. gaudichaudii* was higher in the surface waters compared to the 15–200 m depth layer, and this species dominated the surface zooplankton community structure during Leg 2. Although total numbers of *T. gaudichaudii* were higher when extrapolated over the water column, the average areal density ($m^{-2}$) in the 15–200 m depth layer was only four times higher than in the 0–2 m depth layer, despite the layer being two orders of magnitude larger.

*T. gaudichaudii* is an important prey item for myctophid fish species (Pakhomov et al., 1996). In addition, it has been shown to be an important prey item for various species of other fish, flying birds and penguins in the subantarctic zone where it was suggested to have a similar trophic role to that of *E. superba* further south (Kock et al., 1994; Bocher et al., 2001). Our findings suggest that also within Antarctic waters, *T. gaudichaudii* and *E. superba* may have a similar trophic role. High densities in the surface waters also indicate that regular surveys may underestimate the density of this species in the areas investigated. *T. gaudichaudii* is a non-specific opportunistic feeder, consuming the most abundant copepods, euphausiids and pteropods (Pakhomov & Perissinotto, 1996), and is an important link between the mesozooplankton community and higher trophic level predators (Pakhomov & Perissinotto 1996).

During Leg 1, large numbers of *E. superba* were found in the surface waters, while this species were largely absent in 15–200 m depth layer (average 0.27 ind. 1000 $m^{-3}$; Urabe et al., this issue). When taking into account the differences in size of the depth layers investigated, and comparing areal densities ($m^{-2}$) instead of volumetric densities, numbers in the surface waters would still exceed the total number in the entire water column (15–200 m) by two orders of magnitude (averages 0.05 ind. $m^{-2}$ for 15–200 m vs. 5 ind. $m^{-2}$ for 0–2 m depth).

Highest densities of Antarctic krill in the 0–2 m depth layer occurred mainly in the southernmost stations of the sampling area. Previous studies attributed this to being closer to the shelf break (Ichii 1990; Hosie, 1994). However, in contrast to e.g. the BROKE campaign (Nicol et al., 2000a), the high densities observed in the western part of our sampling area were located at lower latitudes covering the deep ocean water due to the presence of sea ice. Therefore, our results suggest that this distribution may be related to sea-ice retreat rather than bathymetry. In addition, earlier studies showed that on the eastern side of the study area (east of 110̊E), warmer waters intrude more southward while colder water occur at lower latitudes on the western side, which may be another explanation (Bindoff et al., 2000; Nicol et al., 2000b). It should be noted that Leg 1 of KY1804 was surveyed approximately 40 days earlier than BROKE.

High Antarctic krill abundances occurring particularly in the top layer of the water column indicate that previous surveys using trawls may have underestimated the number and biomass of Antarctic krill present in the area, although the number of surveys in this sector of the Southern Ocean is limited. Information from net sampling is often used to investigate population structure, recruitment and annual changes in biomass (e.g. Siegel, 1988; Siegel et al., 1998, De la Mare, 1994; Loeb et al., 1997; Nicol et al., 2000b). An estimation of the total Antarctic krill biomass in the different depth layers indicates that 672.43 g WM 1000 $m^{-2}$ occupied the surface layer, calculated using a length-weight regression established from measurements performed on krill collected during the KY1804 expedition, while 36.0 g WM 1000 $m^{-2}$ occupied the 15–200 m depth layer (Urabe et al., this issue).

For management purposes by CCAMLR, the biomass of *E. superba* has been estimated using echosounder data instead of net sampling data. The total Antarctic krill biomass in the entire survey area (0.909 million $km^{-2}$), established using acoustic data, was estimated at 4.325 million ton (Abe et al., 2023). Generally, conventional echosounders mounted on vessels cannot detect *E. superba* in surface blind zone (e.g., shallower than 10 m) because of various reasons such as the depth of the acoustic transducer on the hull of vessels (Abe et al., 2023; Krafft et al., 2021). The total krill biomass in the upper 0–2 m of the water column of the entire survey area was estimated at 0.611 million ton (wet mass). It seems likely that the 0–2 m densities will only gradually decrease to the densities as found below 10 m, estimated from acoustic data. Therefore, the actual surface stock between 0 and 10 m depth may be several times the stock size estimated by SUIT over the 0–2 m depth layer. Although this may give some idea on the part of the *E. superba* stock residing in, or moving to, the surface waters, it should be kept in mind that the krill distribution in the surface is not uniform throughout the survey area and that the different methods used are very different in nature, thus beyond proper compare.

The results from this study show that the surface water plays a significant role in the distribution of Antarctic krill biomass. This information increases the understanding of the biology of *E. superba*. It can further contribute to the understanding of the relationship of krill distribution with that of higher trophic level predators, the density and distribution of new recruits and recruitment success (necessary for population and ecosystem modelling). Finally, newly gained insights can aid successful ecosystem-based krill fisheries management by CCAMLR (Santora et al., 2010; Flores et al., 2012b; Meyer et al., 2020; Juares et al., 2021; Krafft et al., 2021). In addition, such knowledge could help to improve spatial planning and to predict potential implications of climate change on aforementioned factors, the inclusion of which has been regarded as necessary in future fisheries management (Flores et al., 2012b; Perry et al., 2019; Meyer et al., 2020). Further study of the surface waters is necessary to better understand when and where this stratum is occupied by *E. superba*, in order to be able to predict krill distribution in the upper water column in surveys during which no specific surface water sampling is performed. Alternative methods, such as Autonomous Underwater Vehicles (AUV) and ocean gliders could be used (Krafft et al. 2021; Reiss et al. 2021).

### 4.3. Vertical distribution patterns and DVM

The presence or absence of species in the surface waters can give insights in vertical distribution patterns and shallow DVM that may be overlooked in regular surveys using oblique hauls. It should, however, be kept in mind that there was no equal distribution of day and night hauls in space and time during our survey, particularly for the RMT net stations, which may hamper drawing conclusions on DVM.

Results indicate potential spatial segregation of certain related species. *C. propinquus* was very abundant in the 0–2 m depth layer, while *C. acutus* was almost absent. Both species did not show any signs of DVM based on density differences between day and night hauls of both the SUIT and the RMT (Matsuno et al., 2018). Although *M. lucens* was found only occasionally in the surface waters, the complete absence of *M. gerlachei* in this depth layer could indicate a similar spatial segregation. *M. gerlachei* was more abundant in 15–200 m depth layer during the night compared to the day (Matsuno et al., 2018), indicating that it comes up from deeper water layer during this time (Schnack-Schiel & Hagen, 1995).

Average surface density differences between day and night were also suggested for *E. superba* in this study. However, the second largest density of this krill species in the sampling area was found at a day station (station 51), indicating that high density swarms of Antarctic krill may not just be occurring at the surface at night. No obvious DVM patterns were revealed by the echosounder data, although differences in depth distribution between legs were observed indicating that krill occurred in shallower water in the night during Leg 1 compared to Leg 2 (Abe et al., 2023). More information on potential presence of DVM of Antarctic krill is necessary to fully understand the consequences of the undersampling of the surface layer, as surface krill may move into layers detectable by echosounders during certain times of the day.

Day and night density differences in the data from SUIT revealed patterns for *T. macrura*, *C. lucasii* and *Tomopteris* sp. In the 15–200 m depth layer, no significant different densities between day or night-time stations were seen, suggesting that these species perform a shallow DVM, coming up to the surface during the night. Similarly, densities of chaetognaths and salps were significantly different between day and night stations in the 0–2 m depth layer but not in the 15–200 m depth layer. For these taxonomic groups, density differences in day- and night-time samples observed during the BROKE expedition did suggest a DVM pattern. The lack of a differences in abundance between day and night stations performed in the epipelagic during the KY1804 expedition could be a results of the low density (for salps) or the uneven distribution of day- and night-time RMT trawls between both legs (Urabe et al, this issue). During BROKE higher abundances of chaetognaths were found in the epipelagic layer during the day, which may be a result of the chaetognaths accumulating in the surface at night. Their ascension to the surface waters at night may indicate a predator avoidance strategy. To the best of our knowledge, chaetognaths are not often recorded in the diets of birds from the Southern Ocean, apart from low numbers in the diet of Macaroni penguins (*Eudyptes chrysolophus*) at Heard Island (Deagle et al., 2007). They are, however, regularly found in the stomach contents of birds in the Arctic (Hartley & Fisher, 1936; Lønne & Gabrielsen, 1992), indicating that they may be a potential prey item for birds when present in sufficient numbers. Chaetognaths are, furthermore, known to follow the distribution of their prey (David et al., 2017). Copepods are important prey items for chaetognaths, but prey can also include krill larvae, jelly fish, ostracods and polychaetes (Froneman et al., 1998; Giesecke & González, 2012). For the majority of these prey species there were, however, no significant differences in day and night densities in either depth layer investigated.

The vertical distribution of chaetognaths seemed to change during Leg 2, during which they were almost absent in the surface, while their average distribution in the epipelagic layer remained similar in both legs. In contrast to the total densities, the distribution of different life stages of several copepod species and the krill *T. macrura* did differ between legs. These differences might be responsible for the subtle shift in vertical distribution of chaetognaths between legs found in SUIT samples. Chaetognaths have also been found to show ontogenetic migrations (Giesecke & González, 2012), so growth may also explain such a shift.

Similar to chaetognaths, *T. gaudichaudii* also seemed to accumulate closer to the surface during Leg 1, while during Leg 2, *T. gaudichaudii* seemed to be distributed more evenly throughout the water column, increasing their number in RMT catches. In contrast to the surface waters, *T. gaudichaudii* was significantly more abundant in the 15–200 m depth layer during Leg 2 compared to Leg 1 (Urabe et al., this issue). Leg 2 was dominated by stations conducted at night-time. Hosie et al. (2000) also found *T. gaudichaudii* throughout the sampling area, with no significant differences between densities of day- and night-time stations. Although, results do not clarify if and how this species performed DVM, they do indicate a difference in depth distribution between legs.

### 4.4. Shifts in patterns: Environmental variables or time?

In general, there were less animals in the surface waters during Leg 2. What attracted animals to the surface waters in both legs remains speculation. Food availability, as indicated by chlorophyll *a* values (Shiomoto et al., 2023) and copepod densities, were not particularly high in the surface compared to the epipelagic layer, and were also not markedly different between legs. The protist community structure did, however, show variation between the surface and deeper water layers, as well as between legs (Matsuno et al. 2023), indicating a variation in phytoplankton food availability related to cell shape and size. Predation from fish species dwelling in the mesopelagic or decreased competition with species that do not ‘dare’ to come up to the surface may be two other explanations. This might be related to the large time gap between sampling during Legs 1 and 2. With the progression of time, certain species’ size or development stage altered. Growth and development influences the trade-off between food availability, energy budget and predation risk, which is known to influence the vertical distribution of species (Lampert, 1989; Quetin et al., 1996). The absence of *E. superba* at the surface waters during Leg 2 may have led other species such as *T. gaudichaudii* or chaetognaths to become more vulnerable to predation from above, making it worthwhile to move to or remain in deeper water layers. It may also be that the decreased abundance of many zooplankton species in the epipelagic layer decreased competition for food in this layer, removing the need for species to come to the surface to avoid competition. Thus, behavioural changes from one or few key species may cascade through the food web as it alters predation risk and competition for food sources for many species (Beltran et al., 2021).

Hosie et al. (2000) suggested that the separation of the community structure between east and west is not a time-related alteration in composition or distribution, but a longitudinal separation between communities. Such separation between communities may be a result of oceanographic features. The latitudinal gradient in temperature was greater in Leg 2 (east) compared to Leg 1 (west), with warmer temperatures intruding more southward in the east along the path of the Antarctic Circumpolar Current (ACC) (Yamazaki et al., 2024; Urabe et al., this issue). Apart from the relatively large time gap between Legs 1 and 2, this temperature difference between both sides of the sampling area, as well as the wider sea-ice extend resulting from transportation of formed sea ice found in the west, may be attributed to a series of subgyres that can occur in the region between 80 and 130E̊, with several southward flowing warmer water currents and northward flowing colder waters from the Antarctic Slope Current (ASC)(Yamazaki et al., 2020; Hirano et al., 2021). The gyres are united with the ACC that travels towards the continental shelf further east (Yamazaki et al., 2020), which may explain the observation of fronts being closer together in this study (Yamazaki et al., 2024) and, concomitantly, the greater temperature gradient in this part of the sampling area (Yamazaki et al., 2024; Urabe et al., this issue).

Results from our study indicate that the TSM was the environmental variable that correlated best with the distribution of species communities. TSM was relatively short in the sampling area of Leg 1 in early summer and at the southernmost stations of Leg 2 in mid-summer compared to the northern stations of the latter (Urabe et al., this issue). The presence of sea ice influences the vertical distribution of certain zooplankton species (Flores et al., 2011; 2012a; 2014), and the observed changes in structure may partly be a result of a slow shift from a zooplankton community related to an ice-covered ocean to one related to open water. Previous studies of the surface waters, under ice and in open water, showed that certain zooplankton species are particularly associated with the sea ice, while others, such as *C. lucasii* were particularly observed in the upper meters of the open water (Flores et al., 2011). Differences in the distribution of surface water zooplankton between the southernmost and more northern stations may have various drivers between legs, e.g. sea-ice retreat (or TSM) during Leg 1 and the large temperature and small chlorophyll *a* differences between north and south during Leg 2 (Urabe et al., this issue). This may also explain the improved correlation with the species community when these latter variables were added in the BioEnv analysis even when there was no obvious east–west difference in values for these variables. However, the investigation of the influence of environmental patterns showed that these only partially explained patterns in the distribution. Therefore, our findings suggest that the distribution of zooplankton species is influenced by a combination of environmental variables, such as timing of sea-ice melt and (concomitant) temperature and chlorophyll *a* values, and time in the year. Future process studies on smaller areas and time scales may aid in disentangling environmental, seasonal and diurnal variation in community composition.

### *4.5. Conclusions*

Large-scale patterns in the structure of the meso- and macrozooplankton communities observed in the 15–200 m depth layer were also visible in the surface waters, indicating different macrozooplankton communities in the eastern and western side of the sampling area, and in the southernmost stations of both legs, while the mesozooplankton community showed a more uniform distribution throughout the sampling area. In contrast to the epipelagic, investigation of the surface waters revealed an Antarctic krill dominated community that was overlooked by conventional sampling methods. The information obtained regarding the density and distribution of Antarctic krill is important for conservation and fisheries management by CCAMLR. Surface water sampling revealed some patterns of DVM and of changes in the vertical distribution between legs for several species. This may be a result of size or ontogeny, food distribution, environmental variables or, likely, a combination of these. The accumulation of species like *E. superba* and *T. gaudichaudii* during certain times suggests that, by undersampling the surface waters, densities established by conventional trawls may be underestimated and distribution patterns may be different than previously assumed. Furthermore, the presence of (rare) species may be overlooked, although the vast majority of species occurring in the surface were also present in the sampled collected at deeper water layers.

## Declaration of competing interest

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

## Data availability.

The data underlying this article will be shared on reasonable request to the corresponding author, with permission from the funding institutes and agencies.

## Acknowledgements

We are very grateful to the officers, crew, and colleague researchers onboard RV *Kaiyo-Maru* for their indispensable assistance with the biological sampling. Special thanks to Giulia Castellani (Alfred Wegener Institute) for processing ADCP data, Oliver Bittner (Wageningen Marine Research) for help with SUIT sample analysis, Marinka van Puijenbroek (Wageningen Marine Research) for help making the maps and Michiel van Dorssen for technical support using SUIT. The KY1804 survey was supported by the Institute of Cetacean Research, the Japan Fisheries Research and Education Agency, and the Fisheries Agency of Japan. Antarctic research by Wageningen Marine Research is supported by the Netherlands Ministry of Agriculture, Nature and Food Quality (LNV) which funded this research under its Statutory Research Task Nature & Environment WOT-04-009-047.04. This work was partly supported by a Grant-in-Aid for Scientific Research JP21H02263 (B) from the Japanese Society for the Promotion of Science (JSPS).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2024.103303.

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