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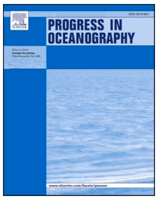

Spatio-temporal changes in the macrozooplankton community in the eastern Indian sector of the Southern Ocean during austral summers: A comparison between 1996 and 2018–2019☆

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ABSTRACT

Several large-scale studies have examined the spatial and temporal (seasonal and interannual) variability in macrozooplankton communities in the eastern Indian sector of the Southern Ocean. In this study, variability in these communities was analyzed using samples collected by the RMT8 during the KY1804 survey, conducted between 80° and 150° E during the austral summer of 2018–2019. Furthermore, these findings were compared with those of the BROKE survey conducted in 1996. Using cluster analysis, the macrozooplankton community was divided into six groups. In both surveys, the zooplankton communities varied between the southern and northern stations of the sampling areas, though their distribution patterns differed between the two years. During the KY1804 survey, *Thysanoessa macrura* was more prevalent in the western region, while *Themisto gaudichaudii* and chaetognaths were more abundant in the eastern region; *Salpa thompsoni* dominated in the eastern region during the BROKE survey. Water temperature had the strongest influence on the macrozooplankton community during the KY1804 survey, whereas salinity was the primary influencing factor during the BROKE survey. This difference may largely reflect differences in sampling timing and latitudinal coverage, though a southward shift in the southern boundary of the Antarctic Circumpolar Current between the surveys may also have contributed. Hydrographic changes over the two decades between 1996 and 2019 likely affected the macrozooplankton community in this region, though differences in spatial and temporal survey coverage complicate interpretation of the results.

1. Introduction

The Southern Ocean is highly sensitive to environmental changes, particularly global warming. For example, water temperatures in the Antarctic Circumpolar Current (ACC) region have increased (Gille, 2008), while sea ice extent has declined since spring 2016 (Purich and Doddridge, 2023). Additionally, poleward shifts in oceanic fronts have been reported, raising concerns about potential impacts on the Southern Ocean ecosystem (Constable et al., 2014; Turner et al., 2014). Zooplankton plays a critical role in marine ecosystems by transferring energy from primary producers to higher trophic levels, including marine mammals, seabirds, and fish. Among zooplankton,

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macrozooplankton communities respond more rapidly to environmental changes than organisms at higher trophic levels (Takahashi et al., 2011). According to Constable et al. (2014), the poleward shift in ocean fronts and increasing water temperatures may drive a southward shift in zooplankton distributions. Such shifts could have broader implications for the entire Southern Ocean ecosystem (Tanimura et al., 1999; Nicol et al., 2000; Chiba et al., 2001).

Antarctic krill (*Euphausia superba*) is a pivotal zooplankton species in the Southern Ocean food web. With its substantial biomass, high nutritional value, and role as a primary prey for higher trophic levels, *E. superba* is regarded as a keystone species in the Antarctic marine ecosystem (Atkinson et al., 2004; Hill et al., 2013). Recent biomass estimates (2018–2019) for *E. superba* in the eastern Indian sector (Abe et al., 2023) were comparable to those in 1996 (Pauly et al., 2000), suggesting no evidence of a long-term decline in this region, although methodological differences between surveys limit direct comparisons. Similarly, studies in the Atlantic sector show no significant change in *E. superba* biomass from 1976 to 2016 (Cox et al., 2018), and the biomass estimate in the Southwest Atlantic sector in 2018–2019 was similar to levels in 2000 (Krafft et al., 2021). However, other studies suggest that regions like the Ross and Lazarev Seas may become increasingly important habitats for *E. superba* in response to environmental changes (McCormack et al., 2020; Yang et al., 2021).

Most research on macrozooplankton in the Southern Ocean has focused on *E. superba*, with limited studies on other macrozooplankton species, including other krill species (Johnston et al., 2022). Hosie et al. (2000) investigated the spatio-temporal variability of the macrozooplankton community in the eastern Indian sector (80–150° E) during the austral summer of 1996, based on data from the Baseline Research on Oceanography, Krill, and the Environment (BROKE) survey, which primarily aimed to estimate *E. superba* biomass using echosounder data. In their study, *Thysanoessa macrura*, chaetognaths, and *Salpa thompsoni* were dominant in the offshore zone (north of the shelf break), while *Euphausia crystallorophias* was abundant in the inshore zone (south of the shelf break). Additionally, *Themisto gaudichaudii* was common in the northern offshore zone (Hosie et al., 2000). High abundances of *S. thompsoni*, particularly east of 110° E, were notable, and the species' distribution had expanded compared to previous years (Hosie et al., 2000).

T. macrura, an omnivorous species feeding on small copepods and euphausiid larvae, is a cosmopolitan species found in substantial numbers in the Southern Ocean (Pinkerton et al., 2020). It is the most numerically abundant euphausiid species in the Southern Ocean that does not form local dense aggregations, yet its circumpolar distribution remains poorly described (Nordhausen, 1992; Pinkerton et al., 2020). Populations of *T. macrura* are expected to increase in warmer waters due to the species' broad thermal tolerance and rapid growth rate (Pinkerton et al., 2020). Additionally, elevated primary production in the region north of the Antarctic Polar Front is expected to enhance habitat availability for *T. macrura* (Pinkerton et al., 2020).

T. gaudichaudii, a typical cruising carnivore (Kruse et al., 2015), is the most abundant hyperid amphipod in the Southern Ocean, widely distributed from the subtropical regions to the southern boundary (Pakhomov and McQuaid, 1996; Hosie et al., 2000; Mackey et al., 2012). This species performs diel vertical migration, moving from 200 m to the surface 50 m (Williams and Robins, 1981). However, studies on the circumpolar distribution and responses to environmental drivers for *T. gaudichaudii* remain limited. This species is an important prey for higher trophic levels (Murphy et al., 2007; Mackey et al., 2012).

S. thompsoni, a filter feeder, exhibits the highest abundance in the warmer waters of the Southern Ocean within the Antarctic Polar Frontal Zone (APFZ; Pakhomov et al., 2002). It primarily grazes on micro-sized phytoplankton at relatively low densities (Chiba et al., 1999; Pakhomov et al., 2006; Sutherland et al., 2010). High food concentrations can clog its filter, significantly reducing feeding efficiency and leading to population declines (Perissinotto and Pakhomov, 1998). This species is considered a low-quality food source for higher trophic levels due to its high water content and low lipid levels (Phleger et al., 1998; Kiørboe, 2013), though it contributes notably to the biological pump through diel vertical migration, high grazing rates, and high fecal pellet production (Henschke et al., 2021).

The BROKE expedition was the last large-scale study on macrozooplankton distribution in the eastern Indian sector of the Southern Ocean between 80° and 150° E (Hosie et al., 2000; Nicol et al., 2000). The KY1804 survey, conducted in the Japanese fiscal year of 2018, was designed as a follow-up to BROKE. This study aims to investigate the macrozooplankton community structure in the eastern Indian sector during the austral summer of 2018–2019 and to compare findings with those of BROKE. Additionally, the effects of environmental parameters on community structure during both surveys were investigated.

The hydrography of the eastern Indian sector is defined by three oceanic fronts: from north to south, the Southern Antarctic Circumpolar Current Front (SACCF), the southern boundary of the ACC (SB), and the Antarctic Slope Front (ASF) (Yamazaki et al., 2024). These fronts divide the sector into three zones: the southern zone between the SACCF and SB, the subpolar zone between the SB and ASF, and the continental zone south of the ASF. The offshore and inshore regions generally correspond to the southern and subpolar zones, and the continental zone, respectively. Between 1996 and 2018–2019, the position of the SB in the eastern Indian sector shifted southward by 50–120 km, resulting in full-depth warming (Yamazaki et al., 2021). Additionally, the Antarctic Slope Current (ASC) front shifted over 20 km offshore between 112° and 140° E, reducing the subpolar zone in 2018–2019 compared to 1996 (Yamazaki et al., 2024). Consequently, this study further investigates whether these shifts in front positions and currents have affected macrozooplankton community structure.

2. Materials and methods

2.1. Survey area and timing

Macrozooplankton sampling took place during the austral summer of 2018–2019 as part of a multidisciplinary ecosystem survey (the fourth survey of the R/V Kaiyo-Maru in the Japanese fiscal year of 2018: KY1804) in the eastern Indian sector of the Southern Ocean, focusing on Antarctic krill. The survey spanned the longitudinal range (80–150°E) of Division 58.4.1 designated by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) south of 60°S (Fig. 1). Conducted by the R/V Kaiyo-Maru (2942 GT, Fisheries Agency of Japan), the survey included two legs: Leg 1 (80–120.32°E) from December 15, 2018, to January 7, 2019, moving eastward from 80°E, and Leg 2 (125.83–150°E) from January 26 to February 23, 2019, moving westward from 150°E.

The initial southern and northern boundaries for the survey area were intended to extend from approximately 63°S to the sea-ice edge or the 200 m isobath if sea-ice extended beyond the ice edge, similar to the BROKE survey. However, due to the more northern location of sea-ice at the beginning of the austral summer (mid-December), the northern boundary was extended to 60°S in the western part of the survey area. BROKE, conducted from January 30 to April 4, 1996, proceeded eastward from 80°E (Hosie et al., 2000). Notably, the KY1804 survey in both its western and eastern regions was conducted approximately 40 days earlier than BROKE.

2.2. Macrozooplankton sampling

For macrozooplankton sampling, a multiple opening and closing rectangular mid-water trawl with a mouth opening of 8 m^2 (RMT8) was used (Baker et al., 1973; Roe and Shale, 1979), equipped with a mesh size of 4.5 mm. Standard double oblique tows were conducted from near the surface (15–20 m) to a depth of 200 m at 43 pre-determined stations (Fig. 1; Supplementary Table 1). Expendable conductivity-temperature-

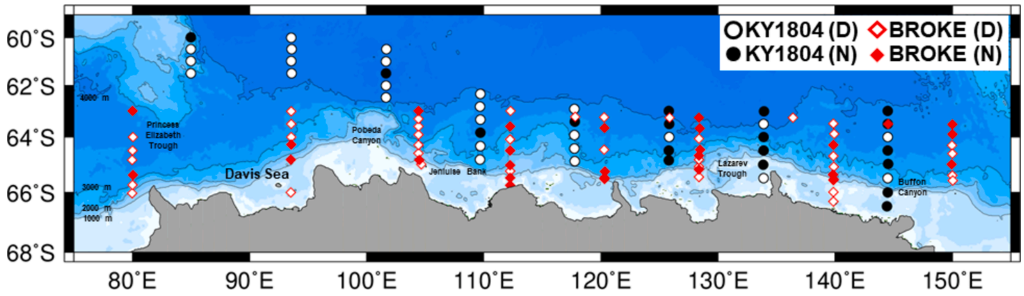

Fig. 1. Sampling stations in the eastern Indian sector of the Southern Ocean during KY1804 (black circles, this study) and BROKE (red diamonds, Hosie et al., 2000; Hoddell et al., 2016). Open and solid symbols represent daytime and nighttime sampling, respectively.

depth profilers (XCTD; MK-130, Tsurumi Seiki Co., Ltd., Japan) were deployed at each station (Fig. 1). The KY1804 sampling protocol followed CCAMLR guidelines (CCAMLR, 2000). Details on RMT8 sampling during BROKE are available in Hosie et al. (2000), and a summary of BROKE's 66 sampling stations is provided in Supplementary Table 2. Conductivity-temperature-depth (CTD) data for BROKE, reprocessed by Yamazaki et al. (2021), were also utilized in this study.

2.3. *Processing of macrozooplankton samples*

Macrozooplankton species were classified into four groups (*E. superba*, other krill, salps, and other zooplankton), and the total wet weight (WW) of each group was recorded on board the R/V Kaiyo-Maru. Samples were preserved in 10 % sodium tetraborate decahydrate-buffered formalin for further analysis in our laboratory. Other zooplankton samples were subsampled using a Motoda box splitter (Motoda, 1959) to obtain fractions ranging from 1/2 to 1/64 of the total sample. These subsamples were examined on a light table, and taxa—including krill other than *E. superba*, copepods, amphipods, pteropods, chaetognaths, polychaetes, and jellyfish—were sorted and counted. Amphipod and pteropod species were identified under a stereomicroscope (SMZ1000, C-BD115, Nikon Corporation, Japan) with reference to Vinogradov (1999) for Amphipoda and Spoel and Dadon (1999) for Pteropoda. WW of each taxon was measured to an accuracy of 0.01 g using an electronic balance (PL602-S, Mettler-Toledo Group). Macrozooplankton abundance and biomass (WW) were reported as individuals and grams per 1000 m^{-3}, respectively, following methods used in previous studies (Hosie et al., 2000; Chiba et al., 2001). Copepods were excluded from this study due to ineffective collection by the RMT8 large mesh size (Tanimura et al., 2008). Abundance and biomass of macrozooplankton species at BROKE station were sourced from the Australian Antarctic Data Center (https://data.aad.gov.au/; Hoddell et al., 2016), with copepod data from BROKE similarly excluded from analyses in this study.

2.4. *Environmental data*

The mean temperature from the surface to a depth of 200 m (MTEM-200) was calculated using XCTD data collected at each station. This index represents the temperature gradient and captures seasonal changes in the surface layer, used to correlate the spatial distribution of *E. superba* with environmental variations (Naganobu and Hirano, 1982, 1986). MTEM-200 has also been applied in various studies as a key variable for understanding the distribution of other Antarctic macrozooplankton species (Hosie et al., 2000; Murase et al., 2013; Schaafsma et al., 2024a). Following Murase et al. (2013), mean salinity from the surface to 200 m depth (MSAL-200) was similarly calculated. The survey area was divided into three latitudinal zones—southern, subpolar, and continental—based on the positions of the SACCF, SB, and ASF as outlined by Yamazaki et al. (2024).

The melt day and time since sea-ice melt (TSM) values were calculated at each sampling station using data from the Advanced Microwave Scanning Radiometer 2 and the Special Sensor Microwave Imager/Sounder, sourced from the Arctic Data Archive System (https://ads.nipr.ac.jp/; January 8, 2021). Melt day was determined as the interval between the final day when sea-ice concentration dropped below 15 % and the base date of December 1, while TSM was defined as the period from the last day with sea-ice concentration below 15 % to the sampling date. Melt day values were calculated for both BROKE and KY1804 at all stations.

To examine spatial and temporal variability of chlorophyll *a* (Chl. *a*) concentrations in the survey region, satellite data were obtained from the GlobColour project (https://hermes.acri.fr/index.php) covering December 2018 to February 2019. Using a weighted averaging method, the data were merged to achieve a spatial resolution of 4 km and a temporal resolution of 8 days. Surface Chl. *a* data for 1996 were accessed from the Australian Antarctic Data Centre (http://dx.https://doi.org/10.4225/15/57B-A97EA8A22D) (cf., Rintoul et al., 2008).

2.5. *Statistical analysis*

A Mann–Whitney *U* test was used to assess differences in taxon abundance (euphausiids, salps, amphipods, and pteropods at the lowest taxonomic level) between day and night hauls across both sampling years. Before cluster analysis, abundance data (X; ind. 1000 m^{-3}) for each taxon were fourth-root transformed to reduce the influence of highly abundant species (Quinn and Keough, 2002). A similarity matrix was then created using the Bray–Curtis index, and hierarchical agglomerative clustering was applied with a complete linkage method (unweighted pair-group method using arithmetic mean; Field et al., 1982).

Significance testing for differences in macrozooplankton abundance among cluster groups was performed using the indicator value function (Dufrêne and Legendre, 1997). To identify species comprising the top 50 % of abundance within each group, a similarity percentage (SIMPER) analysis was conducted. Effects of different water zones (southern, subpolar, and continental) on macrozooplankton community structure were tested with permutational multivariate analysis of variance (PERMANOVA) for each survey year. Additionally, the correlation between environmental variables and macrozooplankton community abundance was analyzed using BIOENV for each year. The environmental variables included sampling date, MTEM-200, MSAL-200, latitude, longitude, and TSM. Variables were normalized by subtracting the mean and dividing by the standard deviation across all samples for each variable before conducting BIOENV analysis.

All cluster analysis, SIMPER, PERMANOVA, and BIOENV calculations were performed using Primer v7 (PRIMER-E Ltd.), while the Mann–Whitney *U* test was conducted in StatView v5 (SAS Institute Inc.).

3. Results

3.1. Hydrography and sea-ice distribution

At the KY1804 sampling stations, mean temperature from the surface to 200 m (MTEM-200) ranged from −1.45 to 1.51 °C, and mean salinity from the surface to 200 m (MSAL-200) ranged from 34.0 to 34.5 (Fig. 2a, 2b). During BROKE, these values were slightly broader, with MTEM-200 ranging from −1.83 to 1.35 °C and MSAL-200 from 33.8 to 34.5 (Fig. 3a, 3b). Warm-water zones, primarily identified as the southern zone, were mostly located north of 64° S in both KY1804 and BROKE, particularly in the eastern regions. In contrast, colder, continental water zones were consistently found in the southern parts of the study area.

In KY1804, cold-water masses with temperatures below 1.0 °C were mainly observed between 20 and 80 m depth in the northern regions, while in BROKE, such cold-water masses were noted deeper, at depths over 40 m, in the southern area (Fig. 2f, 3f). The Southern Antarctic Circumpolar Current Front (SACCF), Southern Boundary (SB), and Antarctic Slope Front (ASF) locations revealed hydrographic differences between KY1804 and BROKE. Notably, the ASF was recorded solely in the eastern survey area during KY1804, reflecting the survey's more limited geographical coverage. The SB appeared to have shifted southward in KY1804, while the SACCF, which was limited to the eastern portion during BROKE, extended throughout the longitudinal range in KY1804, covering a more northern portion of the survey area.

Sea-ice melt day and time since melt (TSM; Fig. 2c, 2d) generally reflected the seasonality of each survey, with the eastern portion surveyed earlier than the western portion as sea-ice melted throughout the summer season. However, sea ice in the eastern portion of KY1804 appeared to have melted faster than during BROKE, even though BROKE took place about 40 days later. Chlorophyll *a* (Chl. *a*) concentrations were generally low across the entire region during KY1804, with slightly higher concentrations in the eastern part, peaking at approximately 0.9 mg m^{-3} (Fig. 2e). In contrast, Chl. *a* exhibited notable spatial variation between KY1804 and BROKE, with high concentrations of about 3.0 mg m^{-3} recorded in the western portion during BROKE, while in KY1804, the eastern portion had relatively elevated Chl. *a* concentrations of around 1.0 mg m^{-3} (Fig. 2e, 3e).

3.2. Abundance and biomass of macrozooplankton

The macrozooplankton species observed during the KY1804 survey were consistent with those detected in BROKE (Hosie et al., 2000). Dominant species during KY1804 included *Themisto gaudichaudii* (32.70 ind. 1000 m^{-3}), *Thysanoessa macrura* (16.24 ind. 1000 m^{-3}), and *Limacina helicina rangii* (4.80 ind. 1000 m^{-3}) (Supplementary Table 3). Day-night comparisons showed significant differences in species abundance: *Clio pyramidata* and *Clione limacina antarctica* were more abundant during the day, while *T. gaudichaudii* was more abundant at night (Table 1). Species such as *Salpa thompsoni* (140.86 ind. 1000 m^{-3}) and *Euphausia crystallorophias* (8.77 ind. 1000 m^{-3}) were more abundant during BROKE than KY1804, whereas *T. gaudichaudii* was less abundant in BROKE (10.28 ind. 1000 m^{-3}) than in KY1804. In BROKE, day-night comparisons revealed higher abundances of chaetognaths during the day and of *Euphausia frigida* and *E. triacantha* at night (Table 1).

Overall, KY1804 exhibited higher abundances of *T. macrura*, *T. gaudichaudii*, and *L. helicina rangii*, while BROKE had greater abundances of *E. superba*, *E. crystallorophias*, and *S. thompsoni* (Table 1). Horizontally, euphausiids were uniformly distributed in both surveys (Fig. 4). In both KY1804 and BROKE, *T. macrura* was predominant on the western side, while *E. frigida*, *E. triacantha*, and *E. superba* (the latter only in 1996) co-dominated the eastern side. Amphipods were abundant east of 110° E, where *T. gaudichaudii* was the dominant species in both surveys. Pteropods showed relatively high abundances between 90 and 120° E in KY1804 (6.04 ind. 1000 m^{-3}) but were sparse throughout BROKE (1.35 ind. 1000 m^{-3}). Salps were infrequently sampled during KY1804, except at 90° E (4.89 ind. 1000 m^{-3}), whereas they were more prevalent in BROKE, particularly east of 120° E (140.93 ind. 1000 m^{-3}). Chaetognaths were widely dispersed across the survey area and particularly abundant north of 65° S in KY1804. Polychaetes were evenly distributed, though in low abundance, in both surveys. Jellyfish exhibited low abundance in BROKE but were more concentrated between 90 and 120° E in KY1804 (Fig. 4). The biomass distribution largely followed abundance trends, with especially high salp and jellyfish biomass noted in BROKE's eastern region (Fig. 4; Supplementary Table 4).

3.3. Zooplankton community

Cluster analysis revealed that the macrozooplankton community was divided into six groups with 44.4 and 55.8 % similarity when using both data from KY1804 and BROKE. The identified groups included A (34 stations), B (34 stations), C (13 stations), D (11 stations), E (4 stations), and F (5 stations). Small or geographically isolated groups were designated as outliers (Fig. 5a). Group distributions for both years are mapped in Fig. 5b. During KY1804, longitudinal separation was observed: Group A stations dominated the western and central regions, Group B occupied primarily the eastern area, and Groups E and F were situated near the Antarctic coast. Groups C and D were absent in KY1804. In BROKE, Group A stations were found in the western region, Group B in the central, Group C in the northeast, Group D in the southeast, and Group F in coastal regions (Fig. 5b).

Each group had characteristic species: Group A stations were marked by high abundances of *T. macrura*, *C. limacina antarctica*, *L. helicina rangii*, chaetognaths, and jellyfish (Table 2). Group B stations were characterized by *T. gaudichaudii* and chaetognaths. Group C was defined by the presence of *S. thompsoni*, *E. triacantha*, *Hyperiella dilatata*, *Vibilia antarctica*, *Clio pyramidata*, and *Spongiobranchaea australis*. Group D was notable for *Cyllopus lucasii*, *T. gaudichaudii*, and a high abundance of *S. thompsoni*. Group E contained *T. gaudichaudii* and *Eusirus propeperdentatus*, while Group F was characterized by *Hyperiella macronyx*, *Pseudorchomene* species, and *E. crystallorophias*.

The PERMANOVA analysis indicated that water zones significantly influenced the zooplankton community composition in both KY1804 and BROKE surveys (Table 3). The analysis showed that the water zones, as identified by Yamazaki et al. (2024), had a stronger impact on community composition in BROKE than in KY1804. The BIOENV analysis revealed that the sampling date was the most correlated variable with variations in species abundance in both surveys. For BROKE, salinity was the second most influential factor, whereas, in KY1804, the temperature had the most significant effect on community composition after the sampling date (Table 4).

4. Discussion

4.1. Spatio-temporal variability in continental zone

In the area south of the Antarctic Slope Front (ASF), Groups E and F were identified, dominated by *Themisto gaudichaudii* and *Euphausia crystallorophias*, respectively. Some stations in this zone had distinct macrozooplankton community composition classified as outliers, displaying low overall abundance and a limited number of species. In KY1804, Group F stations had water-column temperatures below −1.0 °C. Previous studies suggest that *E. crystallorophias* is commonly found in coastal areas with temperatures below 0 °C, where its distribution aligns with temperature and salinity levels (Nordhausen, 1994; Petersen et al., 1999; Hunt et al., 2007; Tanimura et al., 2008).

During KY1804, stations south of the ASF had water temperatures between −1.5 to −1.1 °C, with dominant species varying by station. Despite the cold conditions, euphausiids remained highly abundant, indicating their importance as a food source for higher trophic levels (La Mesa et al., 2004; Tamura and Konishi, 2009). Due to the

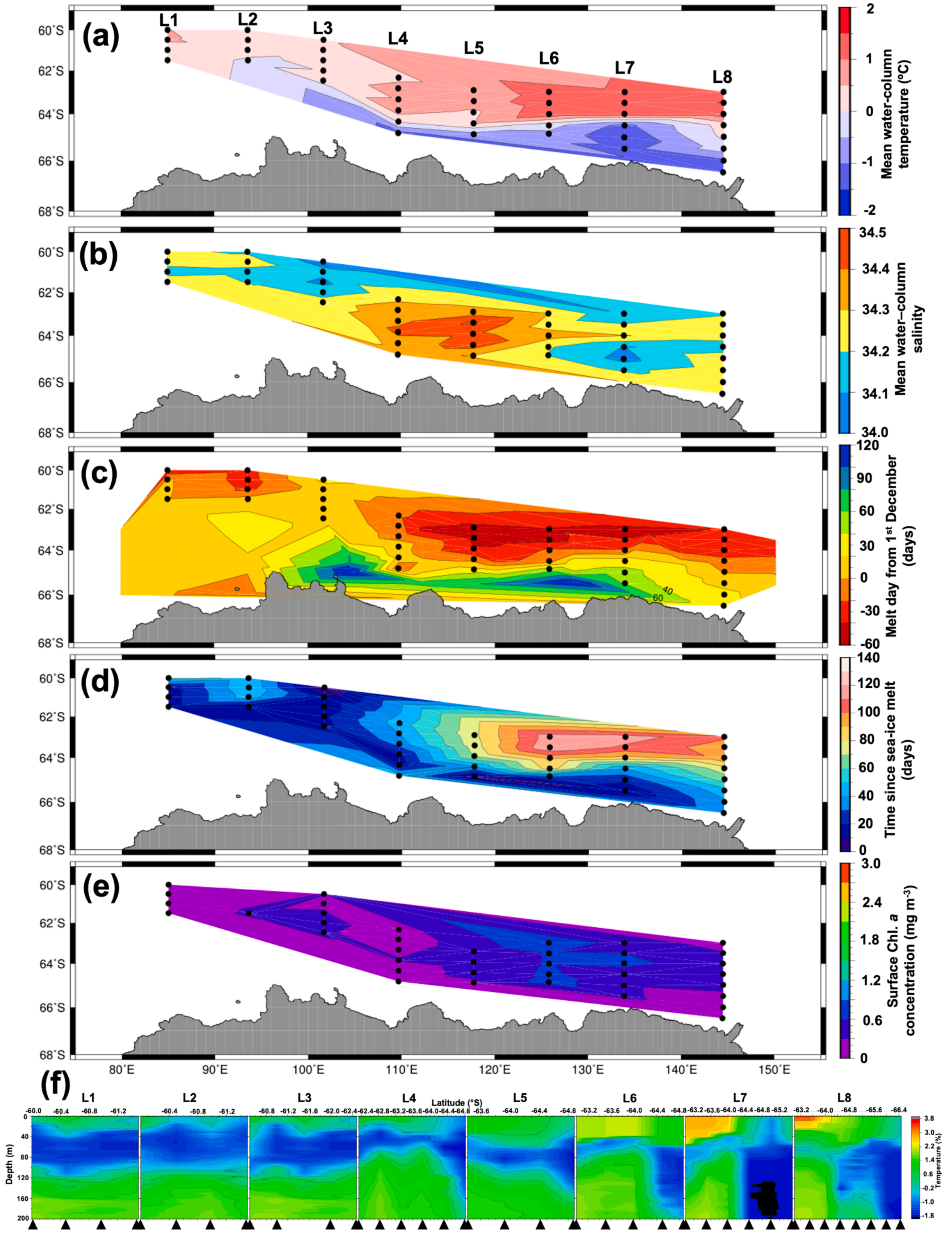

Fig. 2. Horizontal distribution of (a) mean water-column temperature from the sea surface to 200 m depth (MTEM-200), (b) mean water-column salinity from the sea surface to 200 m depth (MSAL-200), (c) melt day from 1 December, (d) time since sea-ice melt, (e) surface chlorophyll *a*, and (f) cross-sectional distribution of temperature in the eastern Indian sector of the Southern Ocean during KY1804. L1–L8 indicate transect lines. Solid triangles denote sampling stations at each transect.

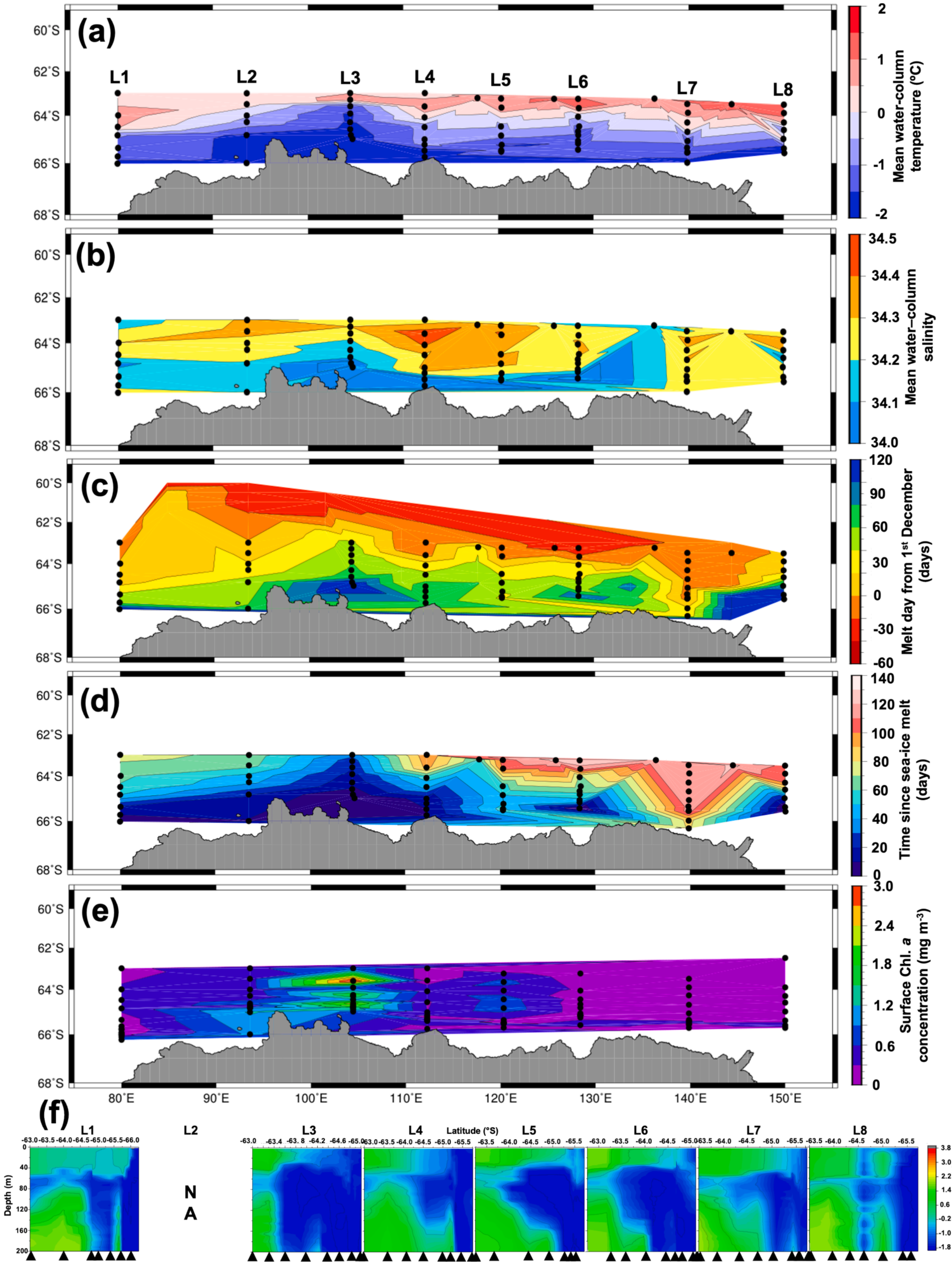

Fig. 3. Horizontal distribution of (a) mean water-column temperature from the sea surface to 200 m depth (MTEM-200), (b) mean water-column salinity from the sea surface to 200 m depth (MSAL-200), (c) melt day from 1 December, (d) time since sea-ice melt, (e) surface chlorophyll *a*, and (f) cross-sectional distribution of temperature in the eastern Indian sector of the Southern Ocean during BROKE (Hosie et al., 2000; Hoddell et al., 2016). L1–L8 indicate transect lines. Solid triangles denote sampling stations at each transect. NA: not available.

Table 1

Day-night comparison of species abundance (ind. 1000 m^{-3}) in the eastern Indian sector of the Southern Ocean (80–150°E) during KY1804 (this study) and BROKE (Hosie et al., 2000; Hoddell et al., 2016). The Mann–Whitney *U* test was used to assess differences in the abundance between day and night. Underlined values in the *U* test column indicate significant day-night differences.

Species	KY1804										BROKE									
	Total (43)			Day (25)			Night (18)			*U* test	Total (66)			Day (40)			Night (26)			*U* test
	Mean	±	SD	Mean	±	SD	Mean	±	SD		Mean	±	SD	Mean	±	SD	Mean	±	SD	
Euphausiacea																				
Euphausia crystallorophias	1.59	±	10.14	2.69	±	13.18	0.06	±	0.18	0.41	8.77	±	57.4	13.47	±	73.15	1.55	±	6.81	0.418
Euphausia frigida	3.62	±	14.29	0.6	±	1.03	7.82	±	21.35	0.11	2.01	±	4.2	0.44	±	1.41	4.43	±	5.67	0.006
Euphausia superba	0.27	±	0.63	0.19	±	0.39	0.38	±	0.85	0.34	3.15	±	10.95	1.32	±	3.84	5.97	±	16.38	0.095
Euphausia triacantha	1.41	±	4.94	1.77	±	6.38	0.92	±	1.13	0.59	1.52	±	5.07	0.08	±	0.29	3.72	±	7.55	0.012
Euphausiid indet	NA			NA			NA				0.1	±	0.48	0.04	±	0.23	0.18	±	0.71	0.577
Thysanoessa macrura	16.24	±	23.76	21.52	±	27.37	8.91	±	14.67	0.09	4.1	±	9.39	4.61	±	11.3	3.31	±	5.14	0.274
Amphipoda																				
Amphipod indet	0.05	±	0.26	0.08	±	0.34	NA			0.35	0.02	±	0.06	0.02	±	0.05	0.03	±	0.08	0.614
Cyllopus lucasii	0.45	±	0.76	0.56	±	0.83	0.29	±	0.61	0.26	2.32	±	14.46	3.39	±	18.48	0.67	±	1	0.481
Eusirus antarcticus	0	±	0.01	0	±	0.01	NA			0.40	NA			NA			NA			
Eusirus microps	0.02	±	0.1	0.04	±	0.13	0.01	±	0.04	0.40	NA			NA			NA			
Eusirus propeperdentatus	0.03	±	0.13	NA			0.06	±	0.19	0.14	NA			NA			NA			
Eusirus spp.	0	±	0.01	0	±	0.02	NA			0.40	0.01	±	0.02	0.01	±	0.02	0.01	±	0.02	0.816
Gammaridae	NA			NA			NA				0.01	±	0.06	0.01	±	0.07	0.02	±	0.05	0.954
Hyperia macrocephala	0.04	±	0.27	NA			0.1	±	0.4	0.24	0	±	0.01	0	±	0.01	NA			0.424
Hyperiella antarctica	NA			NA			NA				0	±	0.01	0	±	0.01	NA			0.424
Hyperiella dilatata	0.09	±	0.24	0.11	±	0.24	0.06	±	0.23	0.52	0.3	±	1.93	0.45	±	2.46	0.07	±	0.1	0.431
Hyperiella macronyx	0.01	±	0.05	0.01	±	0.06	NA			0.40	NA			NA			NA			
Hyperoche medusarum	NA			NA			NA				0	±	0.01	NA			0	±	0.01	0.218
Lysianassidae	NA			NA			NA				0	±	0.01	0	±	0.01	NA			0.424
Primno macropa	0.48	±	0.72	0.44	±	0.65	0.53	±	0.8	0.69	0.13	±	0.15	0.16	±	0.16	0.09	±	0.13	0.073
Pseudorchomene spp.	0.01	±	0.05	0.01	±	0.06	0.01	±	0.04	0.82	NA			NA			NA			
Scina spp.	0.02	±	0.14	0.04	±	0.18	0.01	±	0.04	0.53	NA			NA			NA			
Stegocephalidae	NA			NA			NA				0	±	0.01	NA			0	±	0.02	0.218
Themisto gaudichaudii	32.7	±	57.77	10.3	±	20.78	63.8	±	75.56	0.002	10.28	±	15.76	11.19	±	19.05	8.89	±	8.28	0.441
Vibilia antarctica	0.01	±	0.04	0.01	±	0.06	NA			0.40	0.23	±	0.57	0.15	±	0.6	0.34	±	0.5	0.568
Pteropoda																				
Clio pyramidata	0.55	±	1.43	0.93	±	1.78	0.02	±	0.07	0.04	1.01	±	2.75	1.16	±	3.04	0.78	±	2.21	0.238
Clio sp.	NA			NA			NA				0	±	0.02	0	±	0.02	0	±	0.02	0.901
Clione limacina antarctica	0.53	±	0.78	0.77	±	0.87	0.2	±	0.46	0.02	0.06	±	0.14	0.06	±	0.15	0.06	±	0.13	0.585
Creseis spp.	0.03	±	0.16	0	±	0	0.06	±	0.25	0.24	NA			NA			NA			
Limacina helicina rangii	4.8	±	6.55	6.15	±	6.23	2.93	±	6.53	0.12	0	±	0.03	0.01	±	0.04	NA			0.424
Limacina retroversa australis	0.06	±	0.29	0.1	±	0.38	0	±	0	0.29	0.03	±	0.21	0.05	±	0.27	NA			0.362
Spongiobranchaea australis	0.07	±	0.2	0.07	±	0.2	0.08	±	0.21	0.89	0.23	±	0.97	0.29	±	1.23	0.15	±	0.25	0.436
Thaliacea																				
Doliolina intermedia	NA			NA			NA				0	±	0.01	0	±	0.02	NA			0.424
Ihlea racovitzai	0.16	±	0.55	0.25	±	0.7	0.03	±	0.13	0.20	0.06	±	0.26	0.07	±	0.32	0.05		0.14	0.742
Salpa thompsoni	4.73	±	12.72	6.49	±	15.15	2.28	±	7.59	0.30	140.86	±	572.63	150.75	±	710.89	125.63	±	233.48	0.585
Chaetognatha	60.21	±	62.95	45.93	±	47.79	80.04	±	74.95	0.08	10.44	±	12.16	13.53	±	13.72	5.69	±	6.95	0.011
Polychaeta	1.45	±	1.81	1.54	±	1.78	1.31	±	1.84	0.69	0.5	±	0.78	0.59	±	0.96	0.36	±	0.32	0.548
Jellyfish	15.34	±	21.31	18.26	±	26.49	11.27	±	9.04	0.30	4.4	±	20.27	6.29	±	25.84	1.49	±	1.47	0.338

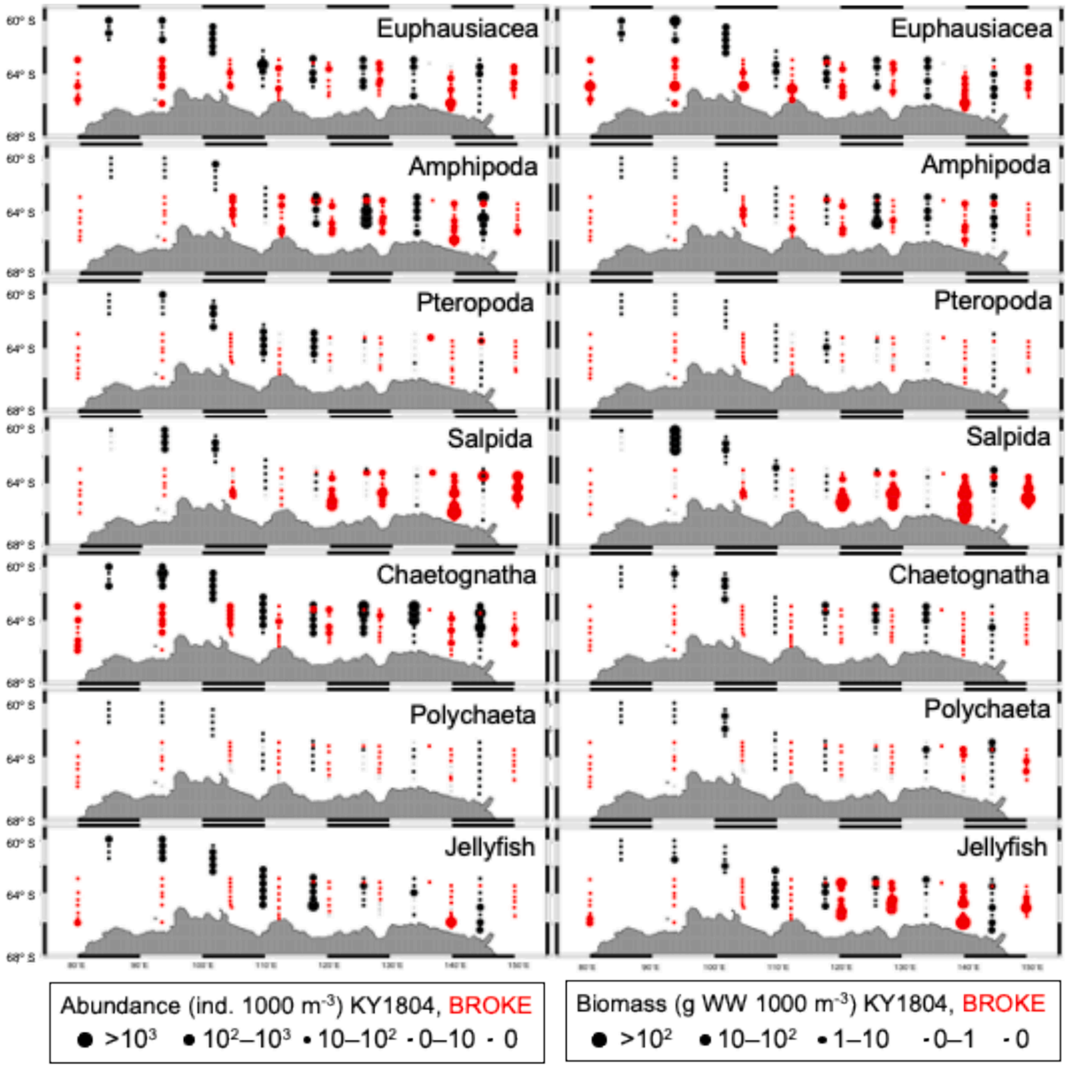

Fig. 4. Horizontal distribution of the zooplankton abundance and biomass (WW) collected by RMT8 in the eastern Indian sector of the Southern Ocean during KY1804 and BROKE (Hosie et al., 2000; Hoddell et al., 2016). Black and red circles denote abundance and biomass during KY1804 and BROKE, respectively.

December–January timing of KY1804, sampling south of 65° S was limited in the western area, while BROKE covered the full longitudinal range in the continental zone. Community structures were similar across both surveys, except east of 110° E in BROKE, where Group D stations, characterized by high abundances of *S. thompsoni*, were noted. The KY1804 sampling area did not encompass the main coastal habitat of *E. crystallorophias*, potentially leading to lower observed abundances. These structural differences in communities may reflect seasonal and geographical variations.

4.2. Spatio-temporal variability in Southern and subpolar zones

Compared to community composition in the continental zone, temporal variation in the offshore community was more pronounced. *Themisto macrura* and chaetognaths were characteristic of Group A stations, located in the western part of the KY1804 survey area (west of 120° E), but were restricted to areas west of 100° E during BROKE. The Group A stations in KY1804 were all situated in relatively warm waters (>0°C). Prior research has indicated a correlation between *T. macrura* and elevated water temperatures (Driscoll et al., 2015). However, the BROKE stations where Group A appeared exhibited a wide range of water temperature values and lacked discernible salinity patterns.

Group B, comprising *T. gaudichaudii* and chaetognaths, was distributed in the eastern part of the KY1804 survey area and the central region during BROKE. Most Group B stations in KY1804 were found in high-temperature waters (>1 °C). Previous studies have suggested an association between water temperature and the abundance and reproduction of *T. gaudichaudii* (Labat et al., 2005; Watts and Tarling, 2012). Thus, the outcomes of the BIOENV analysis for KY1804 indicate a link between community composition, sampling date, and water temperature. In contrast, no such association with water temperature was found during BROKE, where the BIOENV analysis revealed that Group B's distribution was relatively high in salinity, aside from date, latitude, and longitude. Consequently, the results for Groups A and B suggest that different environmental factors (salinity during BROKE and temperature during KY1804) influenced macrozooplankton communities in these surveys.

Previous studies in the eastern Southern Ocean have consistently indicated that water temperature significantly influences meso- and macrozooplankton community variability, with salinity showing lesser correlations in most cases (Hosie and Cochran, 1994; Hunt et al., 2007; Mackey et al., 2012; Matsuno et al., 2020). Hosie et al. (2000) similarly linked the community composition of BROKE to water temperature. Notably, the BROKE community study included copepods (excluded from this study), with several species categorized as taxonomic assemblages (Hosie et al., 2000). In this study, data from KY1804 and BROKE

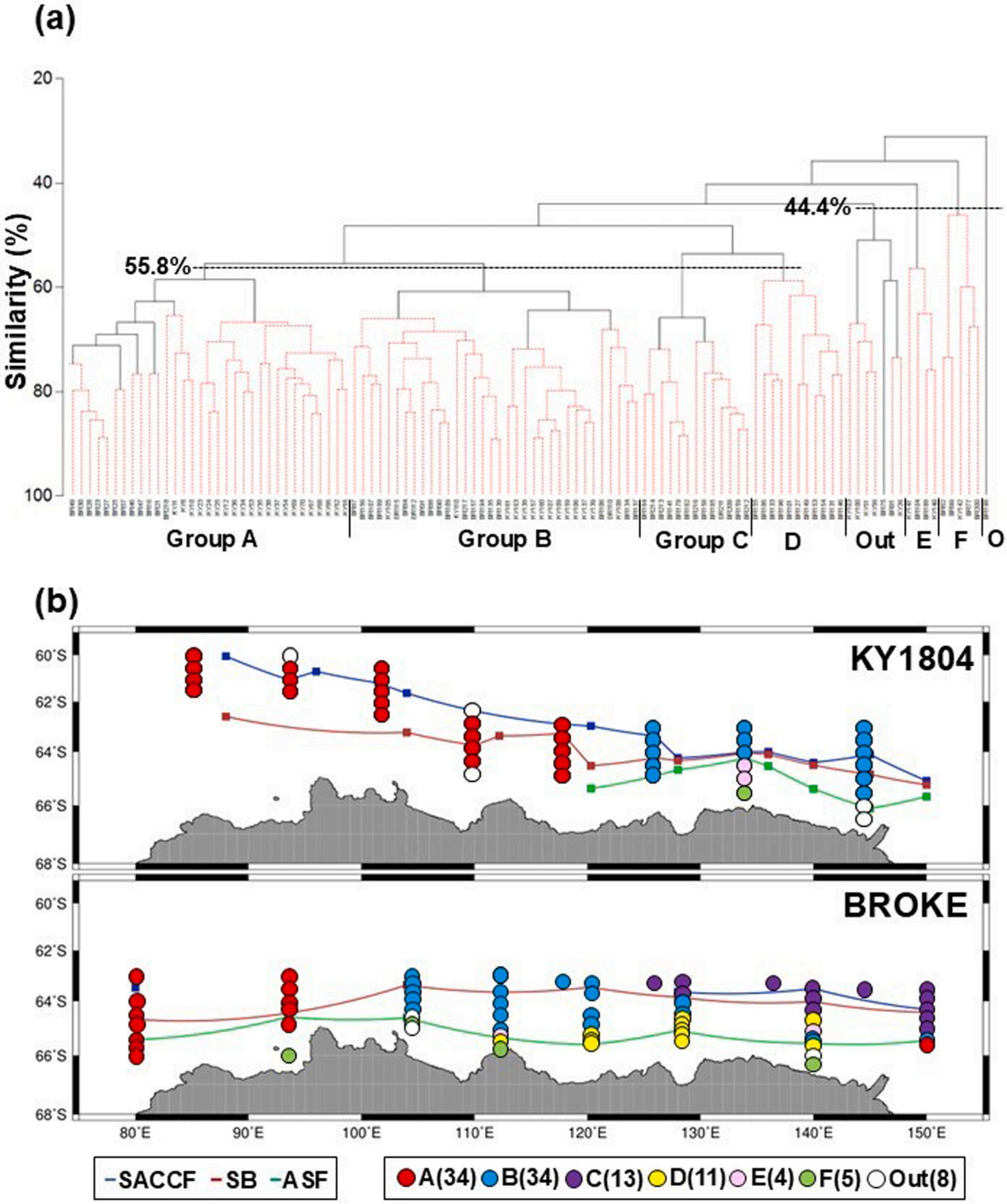

Fig. 5. Results of the cluster analysis based on zooplankton abundance using Bray–Curtis similarity linked to the unweighted pair group method with arithmetic mean. (a) Six groups (A–F) were identified with similarities between 44.6% and 51.5% (dashed lines). Horizontal distribution of the six groups in the eastern Indian sector of the Southern Ocean during KY1804 and BROKE. (b) Groups are color-coded, and the numbers in parentheses represent the number of stations. The locations of the fronts were determined by Yamazaki et al. (2024). SACCF: Southern Antarctic Circumpolar Current Front, SB: Southern Boundary of Antarctic Circumpolar Current, and ASF: Antarctic Slope Front.

were combined to analyze community structure. Salinity emerged as a significant variable explaining zooplankton community structure during BROKE, potentially reflecting seasonal and geographical differences between the two surveys. Additionally, the observed southward shift of the Subantarctic Front (SB) and changes in water temperature between the two surveys may also relate to these factors (Fig. 3a, Fig. 5b).

The effects of water temperature on key macrozooplankton species have been documented in other studies. For instance, while the abundance of *Euphausia superba* is thought to decrease as water temperature rises, *T. macrura* abundance is expected to increase (Pinkerton et al., 2020) due to its wide distribution, high thermal tolerance, and rapid growth rate in warmer conditions (Driscoll et al., 2015). The same applies to *T. gaudichaudii*, whose abundance is also anticipated to rise due to increased growth rates at higher temperatures (Labat et al., 2005; Watts and Tarling, 2012). Therefore, if the trends observed in this study persist, it is likely that communities characterized by *T. macrura*, *T. gaudichaudii*, and chaetognaths will thrive to a greater extent in the southern and subpolar zones of the eastern Indian sector of the Southern Ocean.

The species investigated in this study (*T. macrura*, *T. gaudichaudii*, and chaetognaths) are major components of the Antarctic krill-independent pathway within the Southern Ocean food web (Murphy

Table 2
Comparison of zooplankton abundance (ind. 1000 m^{-3}) in the groups identified by cluster analysis (cf. Fig. 5) in the eastern Indian sector of the Southern Ocean (80–150°E) during KY1804 and BROKE (Hosie et al., 2000). Bold values indicate an indicator value greater than 25 % for that group. An asterisk (*) represents species that contributed to the top 50 % of the abundances in each group based on SIMPER analysis. Values represent mean abundances. The numbers in parentheses represent the number of stations where each group was found.

Species	Groups					
	A (34)	B (34)	C (13)	D (11)	E (4)	F (5)
Euphausiacea						
Euphausia superba	2.07	2.74	0.01	2.21	2.85	3.98
Euphausia crystallorophias	0	0	0	0.04	0.19	**35.79***
Euphausia triacantha	0.53	1.84	**6.16**	0.02	0	0
Euphausia frigida	0.84	5.18	**5.30**	1.37	0	0
Euphausiid indet	0.16	0.03	0	0	0	0
Thysanoessa macrura	**20.48***	3.85	2.96	0.25	1.88	0.60
Amphipoda						
Amphipod indet	0.04	0.05	0.05	0	0	0
Cyllopus lucasii	0.66	0.13	0.72	**1.42**	0.03	0.13
Eusirus spp.	0.01	0.01	0	0.01	0	0.02
Eusirus antarcticus	0.00	0	0	0	0	0
Eusirus microps	0.02	0	0	0	0	0.06
Eusirus propeperdentatus	0	0	0	0	**0.27**	0
Gammaridae	0	0	0	0.01	0	**0.08**
Hyperia macrocephala	0.05	0	0	0	0	0
Hyperiella antarctica	0	0	0.01	0	0	0
Hyperiella dilatata	0.11	0.03	**0.21**	0.01	0	0
Hyperiella macronyx	0	0	0	0	0	0.06
Hyperoche medusarum	0	0	0.01	0	0	0
Lysianassidae	0	0.01	0	0	0	0
Primno macropa	0.34	**0.44**	0.14	0.01	0.13	0.03
Pseudorchomene spp.	0	0	0	0	0	0.06
Scina spp.	0.03	0	0	0	0	0
Stegocephalidae	0	0	0.01	0	0	0
Themisto gaudichaudii	3.32	**47.68***	6.96	13.29	23.91*	2.09
Vibilia antarctica	0.01	0	**0.94**	0.23	0	0.05
Pteropoda						
Clio pyramidata	1.20	0.09	**3.31**	0.18	0	0.07
Clio sp.	0	0.01	0	0	0	0
Clione limacina antarctica	**0.57**	0.06	0.04	0	0	0.06
Creseis spp.	0	0.03	0	0	0	0
Limacina helicina rangii	**5.79**	0.04	0	0	0	0
Limacina retroversa australis	0.07	0	0.15	0	0	0
Spongiobranchaea australis	0.12	0.05	**0.33**	0.03	0.02	0
Thaliacea						
Doliolina intermedia	0.01	0	0	0	0	0
Ihlea racovitzai	0.12	0.01	0	0.32	0	0.25
Salpa thompsoni	3.79	5.45	**138.17***	**241.42***	0.09	24.93*
Chaetognatha	**30.36***	**60.15***	8.36	2.54	0.85	3.90
Polychaeta	**1.62**	0.53	**1.50**	0.04	0.02	0
Jellyfish	**16.40**	3.35	1.70	0.24	0	2.15
Total	88.70	131.74	177.02	263.63	30.23	74.33

Table 3
Results of PERMANOVA analysis on zooplankton abundance with cruise and water zone in the eastern Indian sector of the Southern Ocean (80–150°E) during KY1804 and BROKE. The water zones were identified according to Yamazaki et al. (2024).

Survey	**Source**	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**
KY1804	Water zone	3	9423.6	3141.2	3.5703	0.001
	Residuals	39	34,313	879.81		
BROKE	Water zone	3	16,295	5431.5	5.5269	0.001
	Residuals	62	60,930	982.74		

et al., 2007; Moteki et al., 2018). *T. macrura* is widely distributed in mid- to high-latitudes of the Southern Ocean, with standing stocks comparable to those of *E. superba* in specific regions such as the Gerlache Strait, Crystal Sound, and Kerguelen Plateau (Nordhausen, 1992; Färber-Lorda, 1994; Wallis et al., 2020). Significant ecological differences exist between the two species. Although both are omnivorous, the diet of *E. superba* in the early stages comprises a larger proportion of phytoplankton, such as diatoms and ice algae, whereas *T. macrura* consumes more zooplankton, including small copepods and euphausiid larvae. This dietary preference contributes to *T. macrura*'s lack of a sea-ice-dependent life history compared to *E. superba* (Hopkins, 1985; Färber-Lorda, 1994; Petersen et al., 1999; Färber-Lorda and Mayzaud, 2010). As a prey species, *T. macrura* has been identified in the stomach contents of various predators, including birds, fish, and baleen whales, and possesses a lipid content comparable to that of *E. superba* (Bocher et al., 2000; Niemandt et al., 2016; Schaafsma et al., 2018; Wallis et al., 2020). In contrast, *T. gaudichaudii* is a highly carnivorous species that preys on a variety of zooplankton, including copepods, krill, and chaetognaths (Kruse et al., 2015). This species is widespread in the Southern Ocean and plays a crucial trophic role in many areas as prey for various seabird species and fish (Bocher et al., 2001; Padovani et al., 2012).

Table 4
Results of the BIOENV analysis for zooplankton communities with environmental parameters in the eastern Indian sector of the Southern Ocean (80–150°E) during KY1804 and BROKE. Date: sampling day, Lat: latitude, Long: longitude, Tem: mean water-column temperature from sea surface to 200 m (MTEM-200), Sal: mean water-column salinity from sea surface to 200 m (MSAL-200), TSM: time since sea-ice melt. Spearman Rank Correlation Coefficients are shown in parentheses.

Survey	Number of variables				
	1	2	3	4	5
KY1804	Date (0.519)	Date, Tem (0.684) Tem, Long (0.684)	Date, Tem, Lat (0.653) Date, Tem, Long (0.650) Date, Tem, TS (0.589)	Date, Tem, Lat, Long (0.624) Date, Tem, Lat, TSM (0.605) Date, Tem, Sal, Long (0.585) Date, Tem, Long, TSM (0.584)	Date, Tem, Lat, Long, Sal (0.586)
BROKE	Date (0.273)	Date, Sal (0.342)	Date, Sal, Lat (0.392) Sal, Lat, Long (0.389)	Date, Sal, Lat, Long (0.406) Sal, Lat, Long, TSM (0.371) Date, Sal, Lat, TSM (0.368) Date, Tem, Sal, Long (0.368)	Date, Sal, Lat, Long, TSM (0.387) Date, Tem, Sal, Lat, Long (0.384)

4.3. Note on changes in S. Thompsoni abundance

Group C, characterized by high abundances of *Salpa thompsoni* exceeding 100 individuals per 1000 m^3, was exclusively observed to the east of 110°E and north of the Antarctic Submarine Front (ASF) during the BROKE survey. This finding may be reflected in the BIOENV results, which indicate that sampling date significantly influenced community structures. Groups C and D of BROKE were observed only after March, a period during which no sampling occurred in KY1804. Notably, a relatively high abundance of *S. thompsoni* (>300 individuals per 1000 m^3) was reported in the region bounded by 58°S, the sea-ice edge, 60°E, and 100°E (Kerguelen Axis, K-Axis) between January and February 2016 (Kelly et al., 2020). Given these observations, the lower average abundance of this species (4.9 individuals per 1000 m^{-3}) in KY1804 may be attributed to factors beyond seasonal and geographical influences.

S. thompsoni is a filter feeder that primarily consumes microphytoplankton, with increased abundances typically associated with relatively low phytoplankton densities (Chiba et al., 1999; Pakhomov et al., 2006; Sutherland et al., 2010). Perissinotto and Pakhomov (1998) proposed that when chlorophyll *a* concentrations approach 1.0 mg m^{-3}, filter clogging can significantly reduce feeding efficiency, potentially leading to population collapses. Thus, the extremely low chlorophyll *a* concentrations in the eastern area (<0.3 mg m^{-3}) may have provided a favorable environment for this species during the BROKE survey. Conversely, diatom blooms (with a mean fluorescence of 3.21) recorded in the eastern area of KY1804 (Matsuno et al., 2023) could inhibit the ability of salps to flourish. Shiomoto et al. (2023) reported that large phytoplankton species (>10 μm) contributed significantly to primary production and chlorophyll *a* biomass at all stations north of the Subantarctic Front during KY1904. It is important to note that chlorophyll *a* concentrations during the K-axis survey in 2016 were relatively high (Matsuno et al., 2020).

An alternative explanation for the low abundance of *S. thompsoni* could involve a geographical migration of salps, which are considered a warm-water species, from northern regions not occurring prior to sampling. An individual-based model suggests that the migration of small populations during early spring is a prerequisite for salp blooms in summer (Groeneveld et al., 2020). Previous studies have indicated that a southward shift in the distribution range of *S. thompsoni* is linked to the southward movement of oceanic fronts and increased water temperatures (Pakhomov et al., 2002; Atkinson et al., 2004; Kruse et al., 2015). Although both environmental conditions—high water temperatures and shifts in the Subantarctic Front—were observed in KY1804, this species did not dominate any community. In conclusion, the differences in the occurrence of Groups C and D, dominated by *S. thompsoni*, may be attributed to variations in chlorophyll *a* concentration distribution.

Since the 1990 s, previous studies have documented an increase in the abundance and expansion of salp habitats (Loeb et al., 1997; Pakhomov et al., 2002; Atkinson et al., 2004). In the Atlantic sector, salp populations exhibited substantial interannual variations between 1975 and 1996, associated with krill distributional competition (Loeb et al., 1997). In the Indian sector of the Southern Ocean, high abundances (over 2500 individuals per 1000 m^3) of salp species have been observed locally in the past (Chiba et al., 1999; Hosie et al., 2000; Tanimura et al., 2008; Kelly et al., 2020). However, as previously mentioned, biomasses of *E. superba*, estimated using echosounders, were comparable between the KY1804 and BROKE surveys, suggesting that the findings of Loeb et al. (1997) may not accurately reflect the conditions at the basin scale of the eastern Indian Ocean sector.

4.4. Difference between day and night

The abundance of species exhibiting diel vertical migration may correlate with sampling times (i.e., day and night). Previous studies have documented that three krill species, including *E. superba*, were more frequently observed in shallow waters (less than 200 m) at night (Everson and Bone, 1986; Nordhausen, 1994; Hunt and Swadling, 2021), although no diurnal vertical migration was reported for *E. superba* during KY1804 (Abe et al., 2023). The total krill abundance in KY1804 was lower than that in BROKE. The Surface and Under Ice Trawl (SUIT) results indicated that *E. superba* was dominant at the sea surface (0–2 m) in the western part of the KY1804 survey area (Schaafsma et al., 2024a, Schaafsma et al., 2024b). This species may also have been underrepresented at predetermined daytime stations, considering its schooling behavior, which is known to decrease encounter rates (Mackintosh, 1973; Watkins, 2000; Nicol and Brierley, 2010).

Differences in the abundance of *T. gaudichaudii* and two pteropod species between the western (Leg 1) and eastern (Leg 2) regions of KY1804 may be attributed to the contrasting sampling times (day and night) in these areas. Most sampling in Leg 1 occurred during the day, dominated by Group A, while Leg 2 sampling was primarily conducted at night and dominated by Group B. *T. gaudichaudii* was sampled more frequently at night and emerged as the most prominent species in Group B. However, despite SUIT sampling revealing high abundances of this species in surface waters compared to the 0–200 m depth layer (Schaafsma et al., 2024a), its diel vertical migration could not be confirmed due to the uneven distribution of day and night stations. Nevertheless, the difference in abundance between the groups (Group A/Group B: 3.32/47.68) was greater than the disparity in sampling times (day/night: 10.3/63.8 in KY1804). Thus, the higher abundance of *T. gaudichaudii* in the eastern part of the sampling area likely resulted from factors related to location and date rather than sampling time alone (Tables 1 and 2), suggesting a shift in vertical distribution between the eastern and western regions (Schaafsma et al., 2024a).

5. Conclusions

This study highlights the spatial and temporal variability of the macrozooplankton community in the eastern Indian sector of the

Southern Ocean during the austral summers of 1996 (BROKE) and 2018–2019 (KY1804). Although decadal changes have not been monitored, clear alternations in the macrozooplankton community and its distribution are associated with hydrographical changes. Fronts were shown to separate the macrozooplankton community in both surveys, indicating that the front system is a critical factor in determining macrozooplankton distribution even amid alterations in circulation patterns.

Additionally, different environmental variables affected the macrozooplankton community during the two surveys: salinity was influential during BROKE, while the date and water temperature played a more significant role during KY1804. These differences can largely be attributed to the distinct seasonal and locational contexts of the surveys, though the southward shift of the Subantarctic Front (SB) may also have contributed. Consistent with previous findings, the spatial distribution of communities differed significantly between the north and south of the ASF, with *T. macrura*, *T. gaudichaudii*, *C. limacina antarctica*, *L. helicina rangii*, and chaetognaths dominating the northern region, while *E. crystallorophias* was abundant in the southern region.

In terms of temporal variation, the salp-dominant community observed during BROKE was diminished during KY1804, likely due to comparatively high phytoplankton concentrations observed in the latter. In contrast, *T. macrura* and *T. gaudichaudii* exhibited increased abundance in warmer conditions.

CRediT authorship contribution statement

Ippei Urabe: Formal analysis, Writing – original draft. **Kohei Matsuno:** Visualization, Writing – review & editing, Formal analysis, Writing – original draft. **Rikuto Sugioka:** Investigation. **Ryan Driscoll:** Investigation. **Sara Driscoll:** Investigation. **Fokje L. Schaafsma:** Investigation, Writing – review & editing. **Atsushi Yamaguchi:** Conceptualization, Methodology. **Ryuichi Matsukura:** Investigation. **Hiroko Sasaki:** Investigation. **Hiroto Murase:** Conceptualization, Methodology, Writing – review & editing.

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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.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pocean.2025.103414.

Data availability

Data will be made available on request.

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