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Diversity and spatial distribution of pelagic amphipods in the Western Ross Sea and the Pacific sector of the Southern Ocean

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Amphipods play an important role in Southern Ocean trophic chains. Considering the key role of Pacific Ocean and sea ice ecosystems in the Earth system and the growing impact of global environmental change, it is important to collect information on the status of marine amphipod biodiversity. A total of 410 zooplankton samples were collected by BIONESS (Bedford Institute of Oceanography Net Environmental Sampling System) from 27 stations during the Vth ItaliaAntartide Expedition, between 25 November 1989 and 12 January 1990, in the Pacific sector of the Southern Ocean, from New Zealand to the Western Ross Sea. The aim of this study was to describe the composition, relative abundance, spatial distribution and latitudinal boundaries of pelagic amphipods. An additional goal was to describe the main water masses and the pack ice extent and its temporal evolution during the cruise and relate species assemblages to the physical structure of the region. A total of 2058 specimens of pelagic amphipods was counted, and 43 taxa belonging to 18 families were identified. *Hyperiella dilatata* was the most abundant species (45% of relative abundance) followed by *Primno macropa* (12%), *Pseudorchomene plebs* (12%) and *Hyperiella macronyx* (8%). The composition of amphipod species differed significantly between stations. Three different clusters were identified through the k-means algorithm based on species abundance and confirmed by an NMDS plot. Cluster 1 was mainly composed of the southernmost stations, Cluster 2 included the northernmost stations, while the stations in the central part were grouped in

Cluster 3. A correlation between species composition and the sampled layers at the different stations was highlighted. Knowledge of amphipod biodiversity by means of this study can represent a baseline for future studies, to provide evidence of potential changes as signal of alterations in the environment.

KEYWORDS

amphipods, sea ice, community structure, spatial and temporal scales, latitudinal boundaries, *Hyperiella dilatata*

1 Introduction

Amphipods occupy many different habitats in both the pelagic and benthic realms (De Broyer et al., 2007; De Broyer and Danis, 2011; De Broyer and Jażdżewska, 2014; Jażdżewska and Siciński, 2017). They also span the spectrum of trophic behaviors, from herbivory, carnivory and omnivory through to scavenging (Dauby et al., 2001a, b). Amphipod crustaceans exist across marine habitats from the polar regions to the tropics, providing a critical biological link between benthic/pelagic processes and marine/atmospheric ecosystems (Ritter and Bourne, 2024). Amphipods play important roles in Southern Ocean ecosystems, acting as a food source for both invertebrates (mainly polychaetes, echinoderms and squid), and higher trophic levels such as fish, seabirds and marine mammals (Duarte and Moreno, 1981; Jażdżewski, 1981; Jażdżewski and Konopacka, 1999; Dauby et al., 2003). According to the World Amphipoda Database (Horton et al., 2023), the order Amphipoda is divided into six marine accepted suborders: Amphilochidea, Colomastigidea, Hyperiidea, Hyperiopsidea, Pseudingolfiellidea and Senticaudata. Among these, the suborder Senticaudata is the most represented, followed by Amphilochidea and Hyperiidea.

Pelagic amphipods encompass only few species from the suborders Amphilochidea and Senticaudata, and instead many species from Hyperiidea (Sanvicente-Añorve et al., 2023). All these species are found worldwide (Sanvicente-Añorve et al., 2023). Amphipods of the suborder Amphilochidea inhabit both benthic and pelagic marine habitats, and were found in various environments, such as sands and muds, coral reefs and open oceans, playing important ecological roles as detritivores and predators. Autochthonous sympagic amphipods (i.e., those produced within the sea ice) have only been recorded from the Arctic (Hop et al., 2021), feeding on ice algae and pelagic fauna as well as detritus (Werner, 1997; Poltermann, 2001), while allochthonous sympagic organisms (i.e., those arising from outside of the sea ice habitat *sensu stricto*) have been recorded from both the Antarctic and the Arctic (Gullisen and Lonne, 1991). Seasonally, ice covers large areas, mainly over deep water, and pelago-sympagic organisms play a key role in utilizing the primary production from sea ice algae; e.g., it has been shown that the amphilochidean sympagic amphipod *Eusirus laticarpus* consumed from 54% - 67% of ice algal carbon (Kohlbach et al., 2018). In recent decades, a decrease in the abundance of these crustaceans has been detected in the Arctic (Hop et al., 2021), while in the Antarctic, research on diversity and abundance is still in its infancy. Therefore, despite important steps being taken in marine amphipod research, the roles of sympagic assemblages in polar marine ecosystems remain largely unknown (Arndt and Swadling, 2006). To understand how sea ice ecosystems will be influenced by climate change, obtaining baseline knowledge on the biodiversity of species is critical (IPCC, 2021).Differently from Amphilochidea, the suborder Hyperiidea is a primarily pelagic marine group, distributed from the upper ocean surface to the abyssopelagic depths. Their habitat is therefore, meso- and macrozooplankton biota, where many species live as parasites or predators of other gelatinous organisms such as salps and jellyfish, while other species are more free-living predators of small mesozooplanktonic animals, like copepods. Of these suborders, Hyperiidea is the most abundant, with 282 species described in the world (Horton et al., 2023). They exhibit high diversity in the oceanic zone (Bowman and Gruner, 1973; Lorz and Peracy, 1975; Violante-Huerta, 2019), while in neritic zones their diversity is lower, but abundance is higher (Gasca, 2004; Velázquez-Ramírez, 2021). Vertically in the ocean, order Amphipoda occur from surface to abyssal depths, as far down as the hadal zone (Vinogradov et al., 1996; Vinogradov, 1999). Hyperiideans are mainly carnivores and feed on other zooplankton organisms, such as Polychaeta, Chaetognatha, Copepoda, small crustaceans and other amphipods (Bowman, 1978; Williams and Robins, 1981; Zeidler, 1984; Sanvicente-Añorve et al., 2023). As hyperiid amphipods are known to occur in the vicinity of krill swarms (Pakhomov and Perissinotto, 1996; Dauby et al., 2003), they are likely to also contribute to the diets of plankton-feeding cetaceans.

It is well known that sea-ice variability affects biological processes and polar food webs (Massom and Stammerjohn, 2010; Castellani et al., 2020; Granata et al., 2022; Fraser et al., 2023; Swadling et al., 2023). The Southern Ocean is characterized by latitudinal variations in sea-ice concentration and extent at both local and regional scales (Ferola et al., 2023; Fraser et al., 2023). Recent observations in the Atlantic and Pacific sectors show a strong decrease in sea ice extent during the last four decades (Parkinson and Cavalieri, 2012; Stammerjohn et al., 2012; Yang et al., 2021; Wachter et al., 2021; Fraser et al., 2023), whereas in the Ross Sea a slight increase has been detected (Ferola et al., 2023). We

now know that many key species, particularly copepods and amphipods, are abundant in the sea ice zone at both poles, either living within the brine channel system of the ice-crystal matrix or inhabiting the ice-water interface (Arndt and Swadling, 2006).

Considering the key role of the Pacific Ocean in the Earth system and the growing impact of global environmental change, it is important to collect information on the status of marine amphipod biodiversity as integral members of global ocean ecosystems (Ritter and Bourne, 2024). Amphipod families are common in the region under study; namely, the Pacific sector of the Southern Ocean, the Ross Sea and Terra Nova Bay. The suborders Amphilochoidea and Senticaudata are found on or near the seafloor, Hyperiidea and bentho-pelagic Amphilochoidea and Senticaudata are present in the water column, while the sea ice is habitat for epontic species (De Broyer and Jażdżewska, 2014; Minutoli et al., 2023). While there are several studies on Antarctic benthic amphipods, many areas of the continental shelf and the deep sea remain unexplored (Zeidler and De Broyer, 2009; De Broyer and Jażdżewska, 2014; Jażdżewska and Siciński, 2017; Minutoli et al., 2023). Notably, few studies have been carried out on pelagic species, and little is known about their vertical distribution or their biogeographical boundaries (Zeidler and De Broyer, 2009; Minutoli et al., 2023).

The amphipods analyzed in the present study were collected in oceanic waters characterized as permanently open ocean (POOZ), seasonal pack-ice (SIZ), or the pack ice zone (PIZ). The aim of this paper was to describe the composition, relative abundance, spatial distribution and latitudinal boundaries of pelagic amphipod species in the Pacific sector of the Southern Ocean, in the Ross Sea and within Terra Nova Bay, based on thinly stratified vertical sampling. An additional goal was to describe the main water masses and the pack ice extent and its temporal evolution during the cruise and relate species assemblages to the physical structure of the region.

2 Materials and methods

2.1 Sea ice conditions and sampling strategy

The Southern Ross Sea is characterized by the presence of a polynya, large area of open water surrounded by sea ice, that is generated by strong katabatic winds (a downslope wind caused by the flow of an elevated, high-density air mass into a lower-density air mass below under the force of gravity), that transport and control the dynamics and temporal coverage of sea ice (Zwally et al., 1983; Jacobs and Comiso, 1989). This physical phenomenon plays a major role in driving variability in the functioning of the ecosystem on a short time scale (Hecq et al., 1993). Typically, during late winter and early spring in the western Ross Sea, the ice-free surface spreads from south to north starting from the Ross Ice Shelf Polynya (RISP), causing the ice to retreat and melt and expose the water column to sunlight earlier than in other areas (Hecq et al., 1992). This characteristic extension of the marginal ice edge seems to be responsible for higher productivity, and an increase in the production season due to the shift in the length of the ice edge from south to north (Saggiomo et al., 1998; Lazzara et al., 2000).

To characterize sea-ice variability within the study area during the cruise period, monthly percent sea-ice concentration maps, derived from satellite observations (www.nsidc.org), were examined for the two months prior to the winter surveys, then during and up to one month after completion of the survey (Figure 1). Due to the very bad meteo-oceanographic conditions that were encountered between stations 1 and 2, and the very extensive ice cover between latitudes 65°S and 70°S, the sheduled distribution of the stations was changed to accommodate the conditions. The zone near the Sub-Antarctic Front (SAF), south of New Zealand, included only station 1, located at 50.9222°S and 172.0011°E (Figure 2), while stations 2–4 were located in the Polar Front (PF) free ice area, north (station 2) and south (stations 3 and 4) of the Antarctic Convergence (AC). South of the AC, stations 5 and 6 were located near the Balleny Islands in an area nearly continuously covered by pack-ice and the presence of icebergs, (e.g. station 7, which was NE of Cape Adare). The oceanic zone, which was covered with drifting ice between 66°S and 70°S, included stations 8 and 9. The pack-ice-free zone between 71° and 73°S included the northern stations 10–12 and the southern transects (stations 13-16), which cut transversely through the Scott Canyon that separates the Mawson Bank from the Iselin Bank, and connects the Ross Sea with the ocean. Stations 17–19 represented a north-south transect, from the Campbell Plateau to the Ross Sea shelf, thus including the area before the Convergence, the Antarctic Convergence and Divergence and the Continental Slope. Stations 19–25 represented a transverse transect that cut the Ross Sea from east to west, along the latitude of 75°S.

2.2 Macrozooplankton sampling and processing

An interdisciplinary study of the Ross Sea ecosystem was undertaken during the Vth ItaliaAntartide Expedition on board the *R/V Cariboo* (Guglielmo et al., 1992). Between 25 November 1989 and 12 January 1990, 27 stations were sampled in the Pacific sector of the Southern Ocean, from New Zealand to the Western Ross Sea, across the Antarctic Convergence (Figure 2). Zooplankton was collected over several depth-layers, from the surface to near the seabed (Table 1), by BIONESS (Bedford Institute of Oceanography Net Environmental Sampling System), equipped with ten black nets of 500 µm mesh size (0.25 m^2 mouth area; Sameoto et al., 1980). An altimeter PSA-900 (Benthos Inc.) provided information on the real-time distance to the bottom. At each sampling station, a multiparametric probe SBE 911plus (Sea-Bird Scientific, Bellevue, WA USA), which was mounted on the BIONESS frame, recorded vertical profiles of temperature (°C), salinity, and fluorescence (µg L^{-1} Chl *a*). The BIONESS was deployed at low speed along an oblique path to the maximum selected depth to be investigated, then towed at a speed of 1.5–2 m s^{-1} until closing, with the simultaneous opening of a new net. At almost all stations, two vertical profiles were undertaken, one from the maximum depth up to 100–200 m

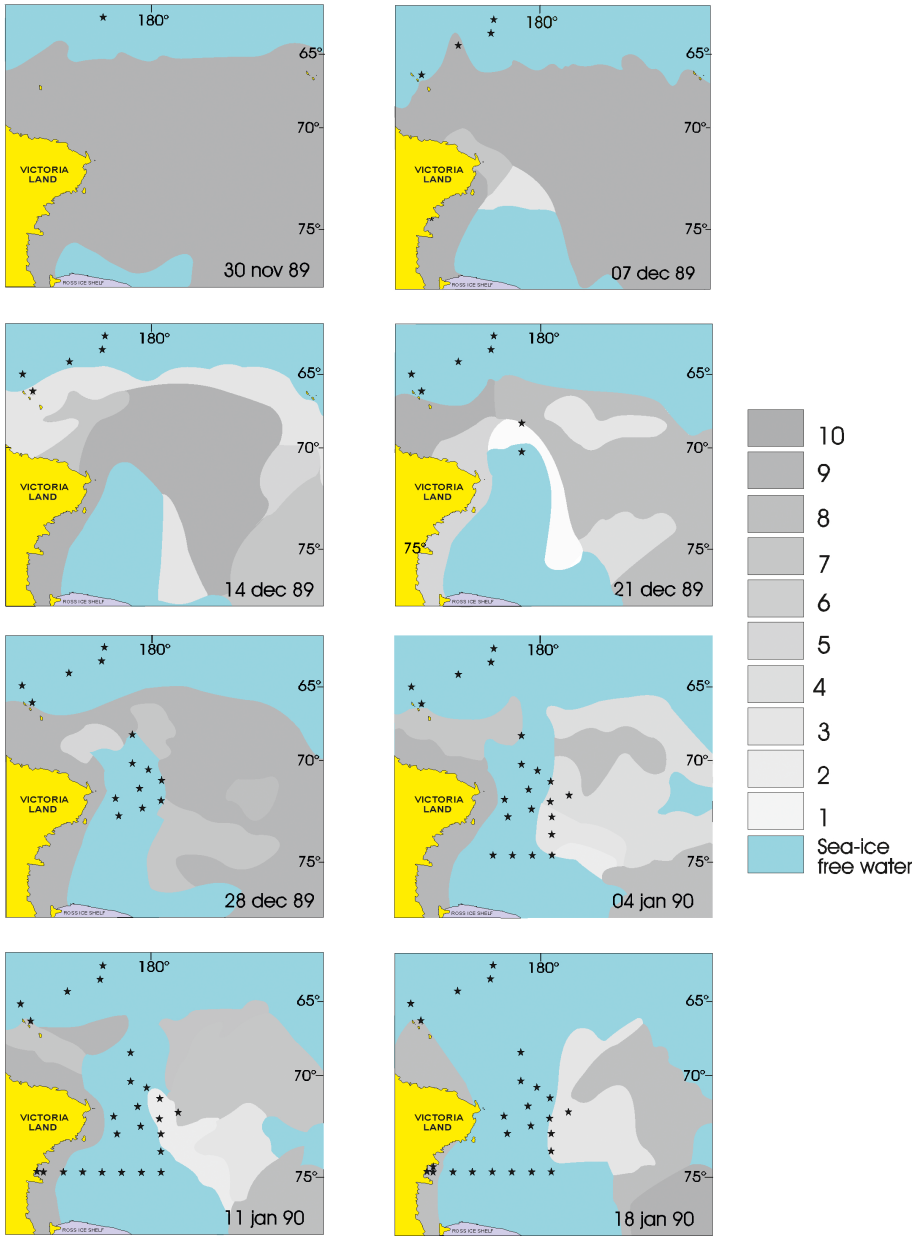

FIGURE 1
Temporal evolution of ice cover in the southern part of the studied area during the cruise period (from Hecq et al., 2000, modified). The shade of gray represents sea surface ice cover in tenths. Data are taken from satellite images published weekly by NAVY-NOAA Joint ICE Center. Stars represent the location of the BIONESS stations until the date of the image.

and the other over the depth of the euphotic layer. Depths for the euphotic layer samples were chosen according to the thermohaline structure and the fluorescence profiles. The depths of the sampled strata depended on the bottom depth (Table 1). Fishing upward, the nets were opened and closed on command, between 10–20 and 200 m intervals. Due to differences in depth at the sampling sites it was not always possible to collect the same number of samples. The volume of water filtered for each layer varied between 43 and 372 m^3, according to the thickness of the sampled layer. A total of 410 samples was collected, with a total volume of 32684 m^3 of water filtered. The zooplankton samples collected at each station from the surface to the maximum sampled depth, during the downward deployment of the BIONESS, were not used for this work but observed in the laboratory for the detection of rare species. On board, all the zooplankton samples were preserved in a 4% buffered formaldehyde-seawater solution.

In the laboratory all amphipods were counted and removed, fixed in 70% ethyl alcohol and identified to species level based on the taxonomic keys provided by Bowman (1973, 1978), Bowman and Gruner (1973); Shih (1991); Vinogradov et al. (1996), and

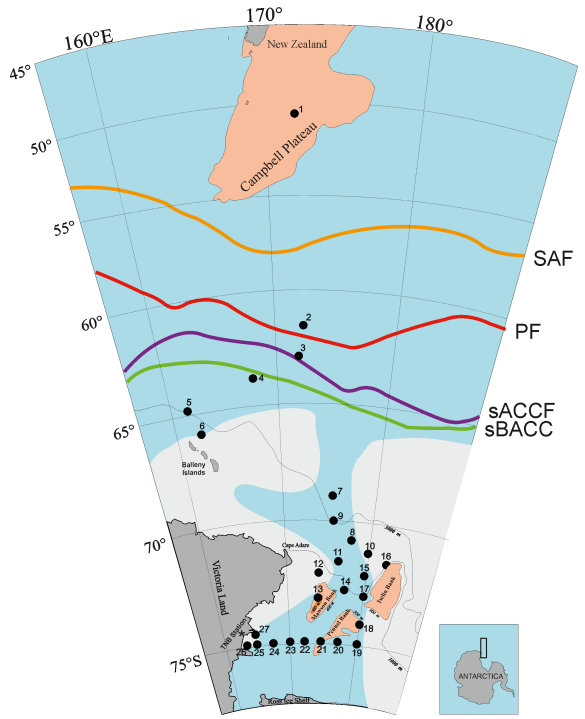

FIGURE 2
Map of study area in the Southern Pacific Ocean with ice edge extension during the cruise (from Hecq et al., 1993, modified). Location of sampling stations during the Vth ItaliAntartide Expedition (1989-1990) and fronts (SAF, Sub-Antarctic Front); PF, Polar Front; sACCF, southern Antarctic Circumpolar Current Front; sBACC, southern Boundary Antarctic Circumpolar Current (from Tesi et al., 2012 and Chapman, et al., 2020, modified).

Zeidler (1999, 2003, 2004a, 2004b, 2009, 2012a, 2012b, 2015, 2016) and classified in accordance with Lowry and Myers (2017). Taxonomic names were verified against the World Register of Marine Species (WoRMS) (Horton et al., 2019). All occurrence records at the subspecies level, synonyms, and misspellings were corrected to the valid species name and included.

Subsamples (1 to 10 mL) were extracted by Stempel pipette and observed under a Leica Wild M10 stereomicroscope for the determination of mesozooplankton abundance. The abundance of amphipods in each stratum was calculated by dividing the total number (N) by the volume of filtered water and expressed as individuals 100 m^{-3}. For the entire water column, the total abundance of amphipods at each station was expressed as a weighted mean, summing all counted amphipods and dividing by the total of seawater filtered volume (m^3), then multiplied by the water column thickness and expressed as individuals m^{-2}. The mean total abundance of a given species is represented by the geometric mean and expressed as individuals m^{-2}, to minimize the difference in water column depth.

Using the Seabird CTD profiles potential temperature (θ, °C) and potential density anomaly (σ_0, kg m^{-3}) were calculated and plotted with Ocean Data View software (Schlitzer, 2023). Flow velocity and filtration efficiency were monitored by internal and external TSK flowmeters.

2.3 Diversity and species assemblages

Species richness R and genus richness D for amphipods were calculated for each station and used to summarize their diversity over the sampling region (Burridge et al., 2017).

To gain insight into the underlying causes of the latitudinal trends in species richness, a partitioning clustering method named k-means algorithm (Jain and Dubes, 1988) was used to classify observations and distinguish the spatial distribution of different groups or clusters. It classifies objects into multiple groups, so that objects within the same cluster are as similar as possible. Since the number of clusters (k) was not known *a priori*, a preliminary analysis was performed to evaluate the partitioning of the observations between the different clusters, considering a number of clusters between 2 and 10. For each k value, 10 iterations were performed, starting from random initial positions for the k centers and taking into account the relative average values obtained. To further evaluate how many clusters to consider when determining an optimal solution, internal validity indexes were applied. In particular, the indices used by Giacalone et al. (2022) were considered (Table 2), using the NBClust package (Charrad et al., 2014) in the R statistical environment (R Core Team, 2020).

The factoextra package in R was used for carrying out the cluster analysis through k-means. Once the number of clusters was identified, the main species that were more abundant in the study area were analyzed and boxplots were generated to illustrate their abundance and distribution within the identified clusters.

Relationships between the amphipod communities and environmental variables at the sampling stations were explored using a combination of non-metric multidimensional scaling (NMDS), an ordination method that can summarize relationships into 2-dimensional space and an Envfit function that fits environmental vectors or factors onto an ordination. For this a R's Vegan package was used (Oksanen et al., 2017). To perform the NMDS analysis, the environmental data and species abundances were grouped in three sub-layers, that were chosen based on the physical features of the stations. The distance matrix used in the NMDS was the Bray-Curtis similarity index. The dataset was square-root transformed and standardized by means of the Wisconsin method before computing the distance matrix. The square-root transformation was used to downweight the importance of very abundant species, while the Wisconsin standardization (performing a double standardization in terms of species maxima and layer abundance) enabled the highlighting of the differences between layers. The performance of the ordination was evaluated by looking at the stress coefficient, where stress values higher than 0.2 highlight poor NMDS performance (Clarke, 1993) and results should be interpreted with caution.

TABLE 1 Station data for BIONESS zooplankton samples taken during the Vth ItaliAntartide Expedition (1989-1990) in the Pacific sector of Southern Ocean.

Station	Date	Start			End			Local time		Depth (m)		Samples
		Lat (° S)	Long (° E)		Lat (° S)	Long (° E)		Start	End	Bottom	Bioness haul	
1	25-Nov-89	50.9222	172.0011		50.9717	171.9278		15.48	16.41	517	400	9
2	29-Nov-89	61.9956	172.1753		61.9564	172.2892		9.27	10.58	4230	1000	9
3	1-Dec-89	63.0764	171.9894		63.1253	171.9217		8.47	9.55	2150	800	16
4	3-Dec-89	63.9489	168.1203		63.9494	168.0375		21.21	22.40	3125	1000	9
5	5-Dec-89	64.8675	161.8367		64.8944	161.9778		10.38	12.10	3130	1000	9
6	6-Dec-89	66.0872	163.6733		66.0986	163.5508		16.37	17.25	2700	1000	9
7	17-Dec-89	69.5917	176.4111		68.6056	176.4389		17.48	18.17	3505	200	13
9	21-Dec-89	70.2083	176.4528		70.1667	176.3556		13.13	14.37	3285	1000	16
8	22-Dec-89	70.7000	178.1083		70.6750	178.1583		8.06	8.45	3350	200	16
10	23-Dec-89	71.2194	179.6806	W	71.1917	179.7472	W	15.02	15.47	1325	200	16
11	24-Dec-89	71.6139	176.8917		71.6361	176.9222		16.40	17.18	940	200	15
12	25-Dec-89	72.1667	173.9611		72.1667	173.9750		14.34	15.08	685	200	14
13	26-Dec-89	73.1444	174.4028		73.1750	174.3972		8.22	9.09	315	280	18
14	27-Dec-89	72.7333	177.5167		72.7500	177.4361		8.18	8.59	1575	200	16
15	28-Dec-89	72.3333	179.9111		72.3500	179.8889		8.21	8.55	2120	200	16
16	29-Dec-89	71.9500	177.7472	W	71.9556	177.7944	W	8.17	8.53	760	200	16
17	30-Dec-89	73.1694	179.9722	W	73.1694	179.9583	W	9.02	9.47	535	450	18
18	31-Dec-89	73.9778	179.9333		73.9917	179.9722		8.25	8.54	280	250	18
19	1-Jan-90	75.0056	179.9778		75.0361	179.8917	W	10.35	11.33	460	400	18
20	2-Jan-90	74.9889	177.4917		75.0056	177.5389		8.15	8.47	390	350	18
21	3-Jan-90	74.9861	175.0000		75.0028	175.0306		8.22	8.58	300	250	18
22	4-Jan-90	74.9833	172.4722		75.0361	172.5333		8.11	9.19	545	500	16
23	5-Jan-90	75.0028	169.9556		74.9750	170.0778		8.24	9.09	345	300	18
24	6-Jan-90	74.9972	167.5500		74.9833	167.3833		8.28	9.27	520	450	18
25	7-Jan-90	74.9389	165.4000		74.9889	165.3111		12.20	13.51	885	800	15
26	8-Jan-90	74.9528	164.1444		74.9528	164.3139		14.59	15.57	635	450	18
27	12-Jan-90	74.7667	164.9861		74.7889	164.8250		11.01	12.10	735	600	18

3 Results

3.1 Environmental parameters

The analysis of the hydrological characteristics of the 27 CTD stations provided evidence for the presence of several water masses. The potential temperature (θ in °C) and salinity (S) measurements obtained from CTD casts were used to construct the θ/S diagrams (Figures 3A, B), where the dashed line indicates the surface freezing point (Tf, Figure 3A). All waters with σ_0 less than 27.55 kg m^{-3} can be generically encompassed under the definition of Antarctic Surface Water (AASW), in agreement with Bergamasco et al. (2002). This water mass occupies the upper ocean and is significantly affected by surface processes such as cooling/heating, air temperature, wind and precipitation (Wang et al., 2023).

Temperatures higher than 1.0 °C are typical of the stations dominated by Circumpolar Deep Water (CDW; Bergamasco et al., 2002). The CDW signal was identified at some CTD stations (4, 5, 8, 9, 10, 11, 14 and 15 in Figure 1) by the typical bell shape with temperatures higher than 1.0 °C between 200 m and 850 m (Figures 4 and 5). According to Orsi and Wiederwohl (2009), some CDW continues poleward and enters the cyclonic circulation of the Ross Gyre, entrenched between the colder AASW above and the Antarctic Bottom Water below (Orsi et al., 1999). During the survey this structure in the water masses was observed in the stations 8, 9, 10 and 11. The Modified Circumpolar

TABLE 2 Indexes used to evaluate the clusters number (Charrad et al., 2014), with the number of cluster obtained.

Index name	Cluster
"kl" (Krzanowski and Lai, 1988)	9
"ch" (Calinski and Harabasz, 1974)	9
"hartigan" (Hartigan, 1975)	10
"cindex" (Hubert and Levin, 1976)	3
"db" (Davies and Bouldin, 1979)	8
"silhouette" (Rousseeuw, 1987)	2
"duda" (Duda and Hart, 1973)	3
"beale" (Beale, 1969)	3
"ratkowsky" (Ratkowsky and Lance, 1978)	7
"ball" (Ball and Hall, 1965)	3
"gap" (Tibshirani et al., 2001)	2
"mcclain" (McClain and Rao, 1975)	2
"sindex" (Halkidi et al., 2000)	6
"sdbw" (Halkidi et al., 2001)	6
"ptbiserial" (Milligan, 1980, 1981)	8

Deep Water (MCDW) originates from CDW and is modified by cooling and mixing with shelf waters (Wang et al., 2023). It is defined by temperatures up to -1.0 °C at the shelf-break (Jacobs et al., 1985) and was observed at CTD stations 12, 13, 17, 19, 20 and 21. The waters with temperatures below the sea surface freezing point (Tf) define the Ice Shelf Water (ISW; Jacobs et al., 1985). ISW found on the continental shelf (stations 25, 26 and 27) had salinities around 34.7 and minimum temperatures reaching down to -2.08 °C, values which agree well with previous observations (Gouretskvi, 1999).

Fluorescence profiles show the presence of DCM (Deep Chlorophyll Maxima) at depths between 10 m and 28 m. The comparison of chlorophyll values (as a proxy of primary production), recorded in the S-N (Figure 4) and W-E (Figure 5) sections, shows that the innermost area of the Ross Sea is characterized by higher productivity.

3.2 Zooplankton community

Mean total zooplankton abundance across the 27 sampled stations was in the range 1392.27 ± 2457.23 ind. 100 m^{-3}. Copepoda was the most abundant taxon, representing 79.3% of total zooplankton (total weighted mean abundance 1103.76 ± 1943.43 ind. 100 m^{-3}), followed by Chetognatha (65.49 ± 85.27 ind. 100 m^{-3}, 4.7%), Euphausiacea (44 ± 152.46 ind. 100 m^{-3}, 3.2%), Pteropoda (32.93 ± 49.83 ind. 100 m^{-3}, 2.4%), Ostracoda (32.98 ± 36.34 ind. 100 m^{-3}, 2.4%), Polychaeta (34.46 ± 185.74 ind. 100 m^{-3}, 2.5%), Salpida (20.69 ± 120.17 ind. 100 m^{-3}, 1.5%) and fish larvae (13.96 ± 67.2 ind. 100 m^{-3}, 1%). All the other taxa represented less than 1% each and together accounted for 5.4%.

3.3 Amphipod diversity and abundance

A total of 2058 pelagic amphipods were observed for the study region, representing 0.4% of the total zooplanktonic community abundance. Overall, 24.8% samples (106 out of 410) did not contain amphipod specimens, regardless of the filtered water volume. The

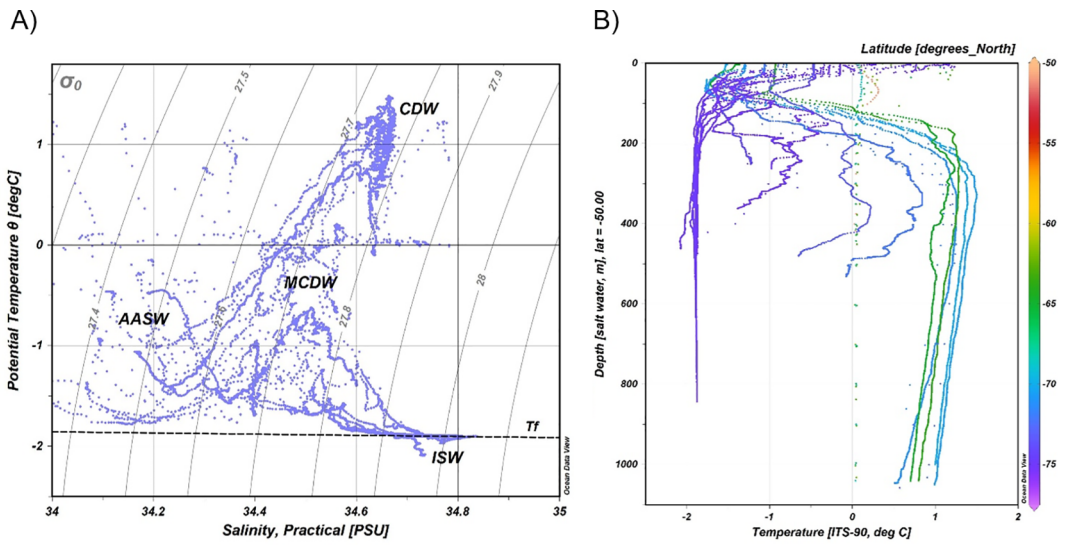

FIGURE 3
(A) θ/S characteristics from the 27 hydrological stations. The diagram is supplemented by isopycnals (σ_0) and freezing temperature (T_f) relative to sea surface pressure. The dashed line indicates the surface freezing point (Tf). The main water masses are labelled with ISW (Ice Shelf Water), MCDW (Modified Circumpolar Deep Water), AASW (Antarctic surface water) and CDW (Circumpolar Deep Water). **(B)** Temperature profiles of the 27 hydrological stations; the color of each profile is linked to the latitude of each station.

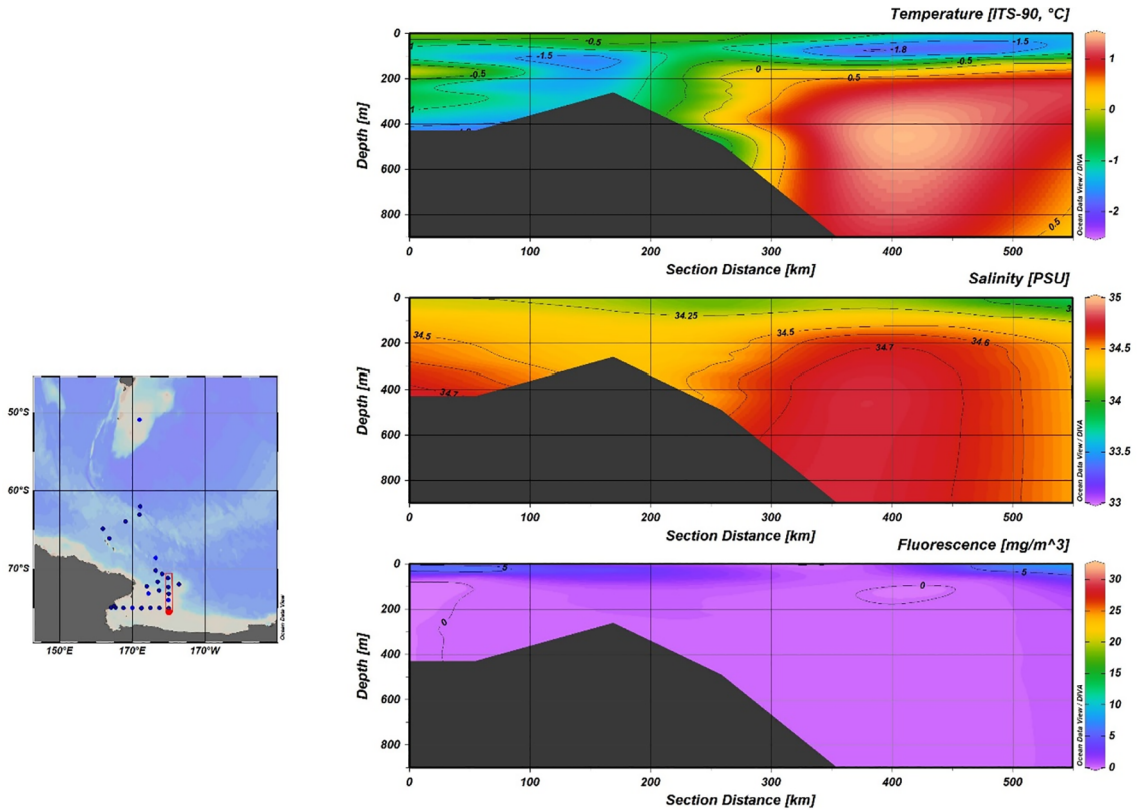

FIGURE 4
Temperature, salinity and fluorescence distribution along the S-N section including CTD Stations 10, 15, 17, 18, 19.

total amphipod abundance was 925.6 ind. m^{-2} and the mean abundance among the 27 sampling stations was 34.3 ind. m^{-2} (± 33.6 ind. m^{-2}). Forty-three taxa were recovered in the investigated area (Table 3), that belonged to 18 families of amphipods and to 2 suborders. Twenty-seven species (belonging to 15 families), twelve genera (belonging to 8 families) and one taxon at family level (Phoxocephalidae) were identified.

Hyperiella dilatata (Hyperiidae) was the most abundant species, representing 44.9% (1033 total counted specimens, 15.4 ind. m^{-2}) of the total collected amphipods. *Primno macropa* and *Pseudorchomene plebs* represented 12% (169 total counted specimens, 4.11 ind. m^{-2}) and 11.8% (289 total counted specimens, 4.05 ind. m^{-2}), respectively. In decreasing order the amphipod community included *Hyperiella macronyx* 8.1% (191 total counted specimens, 2.77 ind. m^{-2}), *Scina* sp. 3.4% (44 total counted specimens, 1.16 ind. m^{-2}), *Vibilia armata* 3.3% (61 total counted specimens, 1.12 ind. m^{-2}), *Themisto* sp. 3% (59 total counted specimens, 1.02 ind. m^{-2}), *Themisto gaudichaudii* 2.6% (36 total counted specimens, 0.9 ind. m^{-2}), *Epimeria (Epimeriella) macronyx* 2.5% (47 total counted specimens, 0.84 ind. m^{-2}) and *Pseudorchomene rossi* 1.2% (32 total counted specimens, 0.42 ind. m^{-2}). The remaining 33 identified taxa contributed less than 1% to the total amphipod abundance, although many contributed to high biodiversity. Together these rarer taxa represented 7% of the amphipod community.

3.4 Distribution patterns: horizontal distribution

Amphipods were observed at all sampling stations, though not in every sample from each station. The horizontal distribution of total amphipod abundance across the 27 stations is shown in Figure 6. Highest abundance (119.4 ind. m^{-2}) was observed at station 25 within Terra Nova Bay and the lowest (6.73 ind. m^{-2}) at station 14. A high abundance was also observed at station 1 at the Sub-Antarctic sampling site south of New Zealand. Amphipods were particularly abundant in the Polar Frontal Zone, both at station 2, north of the Antarctic Convergence (six identified species and four genera of unidentified species) and at the southern station 3 (seven identified species and three genera of unidentified species). The lowest amphipod richness (three species) was found at stations 12 and 18 (Figure 7).

Hyperiella dilatata and *P. macropa* were distributed widely (20 out of 27 sampling stations), with a percentage frequency of occurrence (PFO) of 74% (Table 3). *Hyperiella macronyx* (PFO =

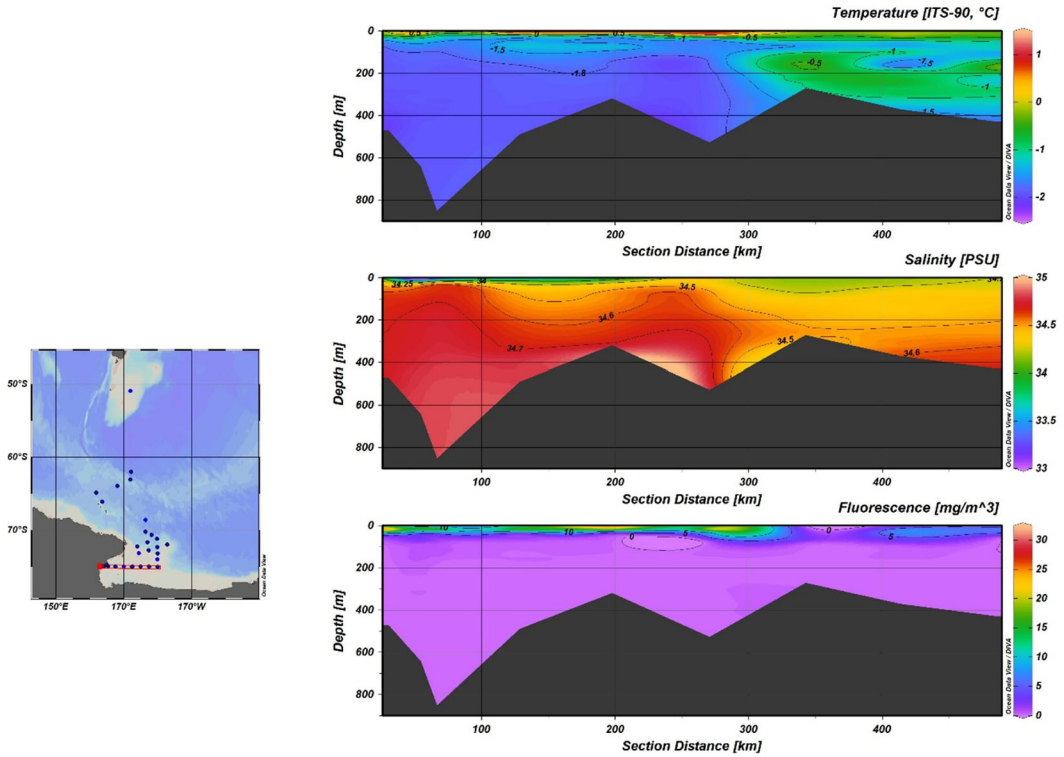

FIGURE 5
Temperature, salinity and fluorescence distribution along the W-E section including CTD Stations 19, 20, 21, 22, 23, 24, 25, 26.

67%) was detected at 18 sampling stations. *Pseudorchomene plebs* was present at 48% of the stations, followed by *P. rossi* (37%, 10 stations), *E.* (*Epimeriella*) *macronyx* and *Scina* sp. (7 stations), *Scina antarctica* (5 stations) and *V. armata* (4 stations). All the other identified 25 species or taxa were detected occasionally, being present at one to three stations.

The horizontal distribution of the four most abundant species is shown in Figure 8. *Hyperiella dilatata* had the highest abundances in the Ross Sea, particularly inside Terra Nova Bay near the coast at station 26 (90.3 ind. m^{-2}). *Primno macropa* had a more pelagic distribution, starting from the eastern part of Cape Adare and the southern Pacific sector north of the Balleny Islands, with the highest abundance observed at station 7 (18.56 ind. m^{-2}). *Pseudorchomene plebs* was not detected off Cape Adare going north towards New Zealand. The highest abundance was at station 20 (23.3 ind. m^{-2}), where the juveniles (17.8 ind. m^{-2}) were more abundant than the adults. *Hyperiella macronyx* showed a similar horizontal distribution to *P. plebs*, but with the highest abundance inside Terra Nova Bay, especially at station 27 (14.6 ind. m^{-2}). The other six species that followed in decreasing order of abundance (see Table 3), present each one with a percent contribution between 3.4% and 1.2%, showed distinct narrow horizontal distributions. *Scina* sp. was absent in the Ross Sea and present only off Cape Adare going northwards; *V. armata* was detected at stations 1 to 5; *Themisto* sp. was collected at station 1, the sampling site closest to New Zealand; *T. gaudichaudii* was present at stations 1 to 3; *E. (Epimeriella) macronyx* and *P. rossi* were detected only in the Ross Sea and inside Terra Nova Bay.

3.5 Vertical distribution

Over the vertical plane the amphipod community mainly (75%) occupied the 20–100 m layer. The 7.3% of the community was collected in the surface layer, while 15.9% occurred between 100 and 500 m. Only 1.6% were detected in the deepest layers between 500 and 1000 m. The patterns of vertical distribution for the four most abundant species are shown in Figure 9. For *H. dilatata*, *P. macropa* and *H. macronyx* the abundance includes both adults and a very few juvenile specimens, while for *P. plebs* the two developmental stages are shown separately.

Hyperiella dilatata occupied the depth from 800 m to the surface, although the bulk of the population (88%) was found in the 0–100 m layer.

Primno macropa showed a more uniform distribution through the water column than *H. dilatata* and was collected from the surface to 700 m. The main part of the population (80%) showed a wide distribution, occupying the 40-300m depth layer. No individuals were found in the 400-500 m layer. Only six *P.*

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TABLE 3 Amphipod species identified in the study area: total mean weighted abundance overall all stations, per cent contribution of each species, number of counted specimens (N), per cent frequency of occurrence in the sampling stations.

Suborder	Family/Species	Abundance	Percent	N	Frequency
		ind m^{-2}	%		%
Amphilochidea	Cyphocarididae Lowry & Stoddart, 1997				
	Cyphocaris richardi Chevreux, 1905	0.06	0.2	2	11.1
	Epimeriidae Boeck 1871				
	Epimeria (*Epimeriella*) *macronyx* (Walker, 1906)	0.84	2.5	47	25.9
	Eusiridae Stebbing, 1888				
	Cleonardo longipes Stebbing, 1888	0.02	0.1	1	3.7
	Eusirus microps Walker, 1906	0.08	0.2	5	11.1
	Pardaliscidae Boeck, 1871				
	Halice tenella Birstein & Vinogradov, 1962	0.01	0.04	1	3.7
	Phoxocephalidae	0.02	0.1	1	3.7
	Scopelocheiridae Lowry & Stoddart, 1997				
	Scopelocheiropsis abyssalis Schellenberg, 1926	0.10	0.3	1	3.7
	Stegocephalidae Dana, 1852				
	Parandania boecki (Stebbing, 1888)	0.09	0.3	3	3.7
	Parandania sp. Stebbing, 1899	0.03	0.1	1	3.7
	Tryphosidae Lowry & Stoddart, 1997				
	Pseudorchomene plebs Hurley, 1965	4.05	11.8	289	48.1
	Pseudorchomene rossi Walker, 1903	0.42	1.2	32	37.0
	Uristidae Hurley, 1963				
	Abyssorchomene scotianensis (Andres, 1983)	0.01	0.04	1	3.7
Hyperiidea	Archaeoscinidae K.H. Barnard, 1930	0.03	0.1	1	3.7
	Archaeoscina sp. Stebbing, 1904	0.03	0.1	1	3.7
	Cyllopodidae Bovallius, 1887				
	Cyllopus lucasii Spence Bate, 1863	0.02	0.1	1	3.7
	Cyllopus magellanicus Dana, 1853	0.21	0.6	9	7.4
	Cyllopus sp. Dana, 1852	0.08	0.2	3	7.4
	Hyperiidae Dana, 1852	0.05	0.2	2	3.7
	Hyperiella antarctica Bovallius, 1887	0.03	0.1	1	7.4
	Hyperiella dilatata Stebbing, 1888	15.39	44.9	1033	74.1
	Hyperiella macronyx Walker, 1906	2.77	8.1	191	66.7
	Hyperoche capucinus Barnard, 1930	0.05	0.1	2	7.4
	Hyperoche sp. Bovallius, 1887	0.03	0.1	1	3.7
	Themisto abyssorum (Boeck, 1871)	0.01	0.02	1	3.7
	Themisto compressa Goës, 1866	0.22	0.7	13	3.7
	Themisto gaudichaudii Guérin, 1825	0.90	2.6	36	11.1
	Themisto sp. Guérin, 1826	1.02	3.0	59	3.7

(Continued)

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TABLE 3 Continued

Suborder	Family/Species	Abundance	Percent	N	Frequency
		ind m^{-2}	%		%
	Lanceolidae Bovallius, 1887	0.03	0.1	1	3.7
	Lanceola clausii pirloti Shoemaker, 1945	0.02	0.1	1	3.7
	Lanceola sp. Say, 1818	0.03	0.1	1	3.7
	Scypholanceola sp. Woltereck, 1905	0.08	0.2	3	11.1
	Mimoscinidae Zeidler, 2012				
	Mimoscina sp. Pirlot, 1933	0.17	0.5	4	11.1
	Phronimidae Rafinesque, 1815				
	Phronima atlantica Guérin-Méneville, 1836	0.02	0.05	1	3.7
	Phrosinidae Dana, 1852				
	Primno macropa Guérin-Méneville, 1836	4.11	12.0	169	74.1
	Scinidae Stebbing, 1888				
	Acanthoscina sp. Vosseler, 1900	0.13	0.4	2	7.4
	Ctenoscina brevicaudata Wagler, 1926	0.05	0.1	2	7.4
	Ctenoscina sp. Wagler, 1926	0.03	0.1	1	3.7
	Scina antarctica Wagler, 1926	0.31	0.9	14	18.5
	Scina borealis (G.O. Sars, 1883)	0.23	0.7	10	11.1
	Scina pusilla Chevreux, 1919	0.12	0.4	2	7.4
	Scina sp. Prestandrea, 1833	1.16	3.4	44	25.9
	Vibiliidae Dana, 1852				
	Vibilia armata Bovallius, 1887	1.12	3.3	61	14.8
	Vibilia sp. H. Milne Edwards, 1830	0.11	0.3	4	7.4

macropa juvenile specimens were collected, in the 300-400 m and 100-200 m layers.

Adult *Pseudorchomene plebs* occurred between 500 m and the surface. The main part of the adult population (87%) occupied the 20–100 m layer, while only 2% were present in the most superficial layer (0–20 m). Juvenile *P. plebs* were almost as abundant as adults and showed similar vertical distribution.

Hyperiella macronyx were distributed from 400 m to the surface. Approximately 80% occupied the 20–100 m layer, with ~4% in the more superficial layer and the 16% below 100 m depth. Only two juveniles were collected in the 200–300 m layer.

3.6 Latitudinal boundaries

The spatial distribution boundaries of the amphipod taxa collected during this study, are shown in Table 4. Only two species (*Phronima atlantica* and *Themisto compressa*) and one genus (*Themisto* sp.) were found exclusively in the Sub-Antarctic zone (station 1) at latitude 50.9222°S, while three species (*Halice tenella, Hyperiella antarctica* and *Parandania boecki*) and one family (Lanceolidae) were found only in the area north of the Polar Front (station 2, 61.9956°S). *Cyllopus magellanus* and *T. gaudichaudii* were recovered only between the Sub-Antarctic zone and Polar Front (stations 1 and 3), while *Cyphocaris richardi* and two genera (*Cyllopus* sp. and *Vibilia* sp.) were present only in the Polar Front (stations 2 and 3), between 61.9956 and 63.0764°S. Four genera (*Archaeoscina* sp., *Ctenoscina* sp., *Lanceola* sp. and *Parandania* sp.) were found in the area south of the Polar Front (station 4, 63.9489°S). One species (*Scopelocheiropsis abyssalis*), one genus (*Acantoscina* sp.) and one family (Archaeoscinidae) were found in the ice-covered stations 6 and/or 7. *Hyperiella dilatata* and *H. macronyx* were present throughout all the study area, including Terra Nova Bay, with a small difference in the northern limit of their detection: the Polar Front (61.9956°S) and the Balleny Islands (64.8675°S), respectively. *Primno macropa* was collected over a large area, from the Sub-

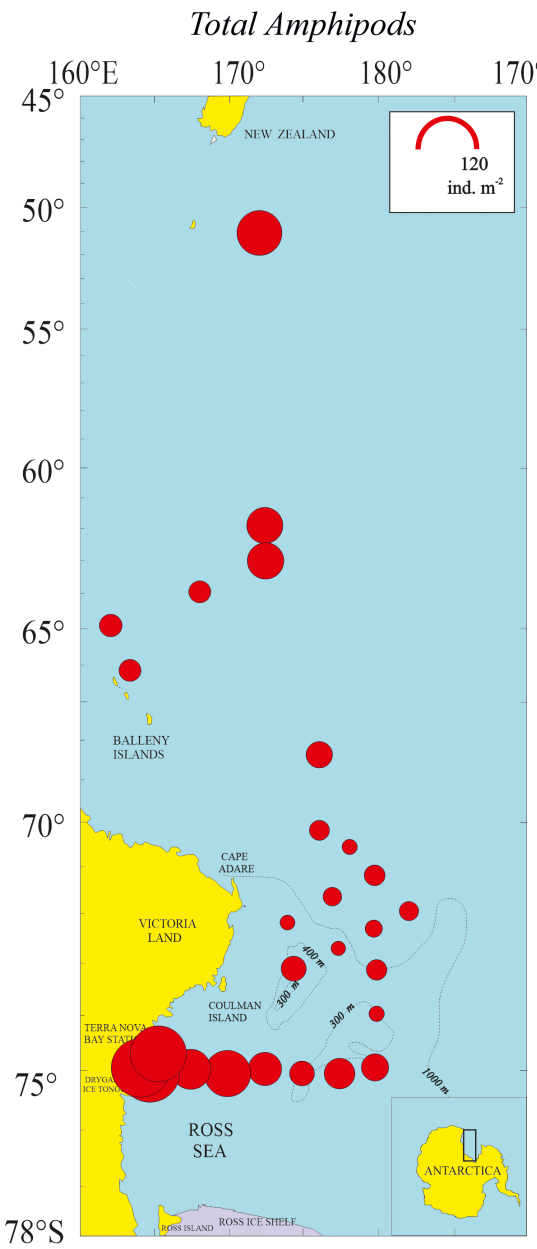

FIGURE 6
Density representation (ind m^{-2}) of total amphipod community in the 27 sampled stations.

Antarctic Front to the mid Ross Sea Region (at station 21). Some species were found only along the two transects at the northern entrance of the Ross Sea: *Cleonardo longipes, Lanceola clausii pirloti* and the family Phoxocephalidae were found exclusively in station 10 (71.2194°S), while *Ctenoscina brevicaudata, Cyllopus lucasii* and *Temisto abyssorum* were recorded at stations 13,14,15. *Eusirus microps* and *Abyssorchomene scotianensis* are exclusive species of Terra Nova Bay (about 75°S).

3.7 Species assemblages

The k-means algorithm, applied to species abundances estimated for the 27 stations, enabled the evaluation of the spatial distribution of different groups. To evaluate the optimal number of clusters, 15 indices were estimated (Table 2). The results of this approach revealed the presence of three clusters (Figure 10). Cluster 1 was mainly composed of the southernmost stations, Cluster 2 included the three northernmost stations, while the stations in the central part of the study area were grouped in Cluster 3 (Figure 10). The boxplots of the main species in the three clusters are shown in Figure 11.

CTD profiles belonging to Cluster 1 showed the presence of a strong chlorophyll signal, with the DCM located at around 28 m depth. Profiles belonging to cluster 2 were characterized by an almost homogeneous upper layer (0–200 m) in terms of temperature, salinity and fluorescence; for this cluster no clear DCM signal was evident. Most of the stations belonging to cluster 3 were influenced by the presence of CDW and MCDW. At these stations the presence of a DCM was less evident than in stations of cluster 1 and was located around 50 m depth.

NMDS was used to investigate the relationships between amphipod taxa and the sampling stations. The NMDS stress value was 0.11, indicating acceptable fit. The NMDS plot (Figure 12) showed a clear separation between northern and southern stations along the first NMDS axis (NMDS1). In particular, the upper layers (0–50 m and 50–200 m) of the southern stations, belonging to Cluster 1 and affected by higher fluorescence and lower temperatures, were characterized by higher proportions of *H. dilatata*, *H. macronyx* and *P. plebs*, while the species *Epimeria (Epimeriella) macronyx* was more common in the middle layer (50–200 m) in the south-western side of the Ross Sea. The deepest layer (>200 m) in these stations was characterized by a species assemblage composed of *Hyperiella dilatata, H. macronyx, Pseudorchomene plebs* and *P. rossi*. The NMDS plot also showed that the upper layers (0–50 m and 50–200 m) of the stations belonging to Cluster 3, influenced by relatively higher temperature and lower fluorescence values, were mainly characterized by higher proportions of *P. macropa*. Lower proportions of *H. dilatata*, *H. macronyx* and *Scina* sp. were also observed at a few stations in this cluster. The deepest layer (>200 m), where higher salinity was observed, was mainly characterized by the presence of *P. macropa* and *Scina* sp. Higher proportions of *T. gaudichaudii*, *V. armata*, and *Vibilia* sp. characterized the three northernmost stations belonging to Cluster 2. Finally, juvenile specimens of *Themisto* sp. were found in the upper and saltier layers of station 1.

4 Discussion

A review of marine biodiversity in the Southern Ocean highlighted the relative importance of some zoological groups like

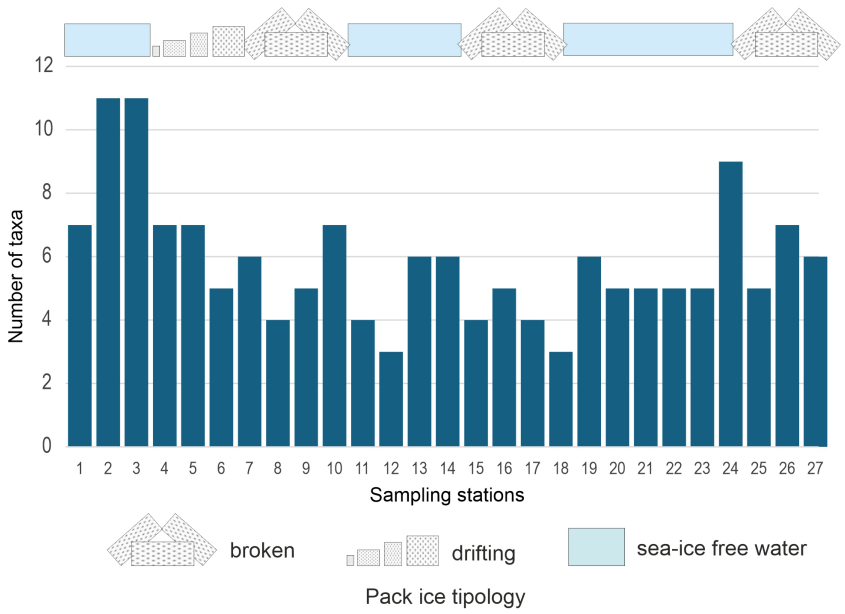

FIGURE 7
Amphipod species richness and representation of pack-ice tipology in the sampled stations.

molluscs and polychaetes, and the predominance of crustaceans (Dauby et al., 2003). Among the latter, amphipods represent the richest group, with more than 820 species recorded in the Antarctic and Sub-Antarctic regions (De Broyer and Jażdżewski, 1993, 1996). These crustaceans have colonized a wide variety of ecological niches, including benthic, pelagic and ice-habitats (De Broyer et al., 2001), and have developed a wide range of feeding strategies (Dauby et al., 2001a; Nyssen et al., 2002; Dauby et al., 2003). The faunal diversity of amphipods indicates the importance of these crustaceans to total pelagic biomass, and thus their major role in the trophodynamics of Antarctic ecosystems, both as consumers and prey. Information about the biodiversity and biogeography of Atlantic and Pacific Sectors of Southern Ocean pelagic amphipods is lacking and only available for some restricted areas including the eastern Weddell Sea and Terra Nova Bay (e.g. Gerdes et al., 1992; Minutoli et al., 2023).

In the present study high biodiversity of pelagic amphipods was observed for the Pacific sector of the Southern Ocean. A total of 43 taxa was recovered, which was more than double the 20 identified in a previous study in a more restricted area, the Ross Sea and Terra Nova Bay, during the 1987–1988 Vth ItaliaAntartide R/V Polar Queen Expedition (Minutoli et al., 2023). Only five species (*Hyperiella dilatata*, *H. macronyx*, *Primno macropa*, *Pseudorchomene plebs*, *P. rossi*) were common to both oceanographic campaigns. This can be linked to the wider geographic coverage of the investigated area in the present study, which covered a greater range in bathymetry and oceanography. Hyperiidea was the most represented suborder (83.3% of the collected specimens), instead the other 16.7% were Amphilochidea. Hyperiidae was the most abundant family (60%), confirming that, in the Southern Ocean, hyperiidean amphipods are particularly abundant, with distributions ranging from the Polar Frontal Zone to Antarctic shelf waters (Havermans et al., 2019). This family was represented in the present study by seven species and two genera of unidentified species, with a dominance of *H. dilatata* (Minutoli et al., 2023). Given its wide spatial distribution in the studied area, *H. dilatata* has been described as cosmopolitan in the Southern Ocean. It is common in the Pacific sector and represents the most abundant and key amphipod species in the Ross Sea food chain (Barnard, 1930; Foster, 1987; Stebbing, 1888; Weigmann-Haass, 1989; Hubold, 1992; Jażdżewski et al., 1992; Dinofrio, 1997; Guglielmo et al., 1998; Vinogradov, 1999; La Mesa et al., 2004; Guglielmo et al., 2011; Minutoli et al., 2023).

The family Tryphosidae was the second most abundant family (13%), represented by two species, of the most common which was *P. plebs*. Literature reports show that this species as widely distributed in the Southern Ocean and in the Ross Sea (d'Udekem d'Acoz and Havermans, 2012; De Broyer et al., 2007), confirming the observations made during the 1987–1988 study. *Pseudorchomene plebs* has a bentho-pelagic way of life and a diversified feeding habit. Crustacean parts have been observed frequently in their gut contents, along with remains of carrion (muscles) and diatoms (d'Udekem d'Acoz and Havermans, 2012). Swarms of *P. plebs* have been recorded to devour fish carcasses in

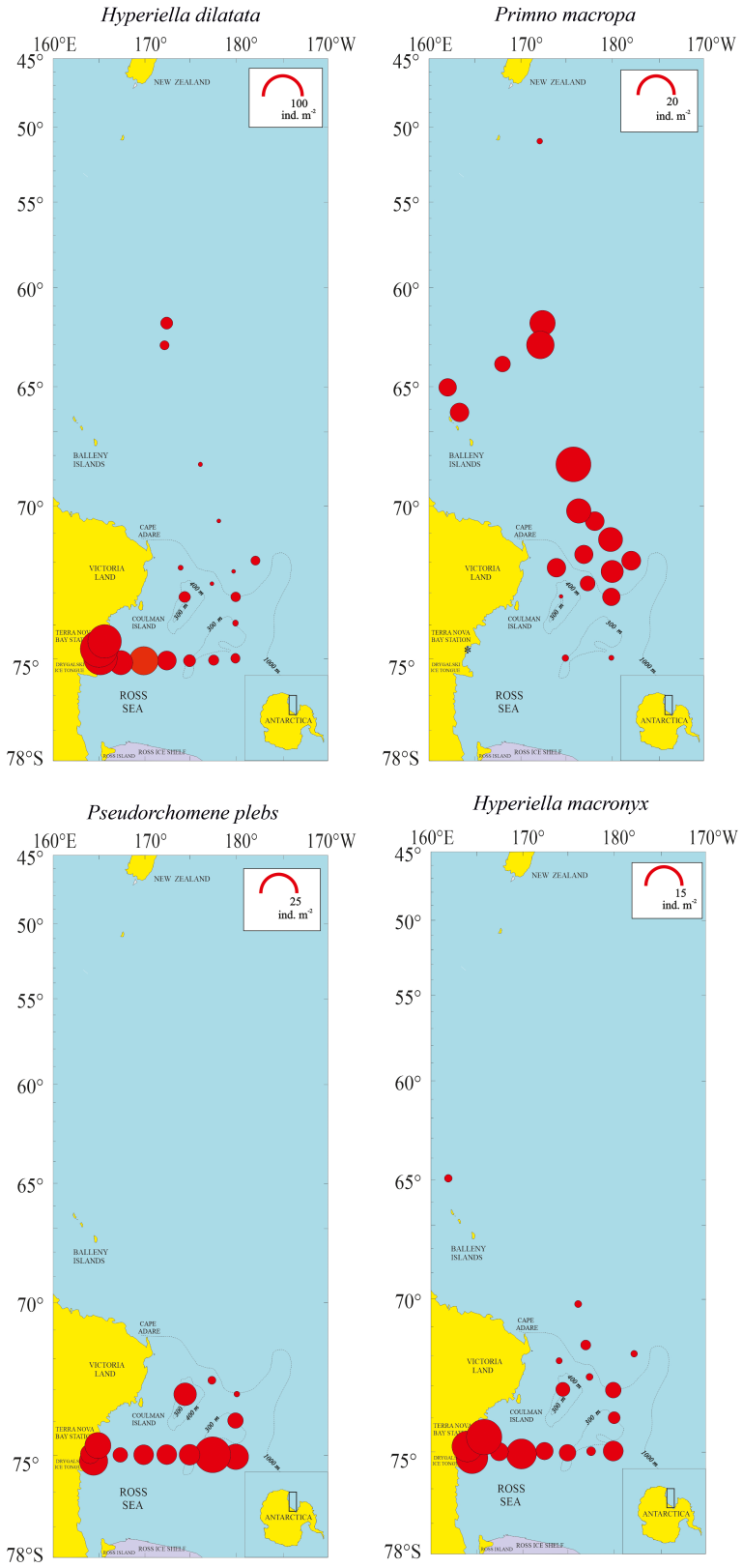

FIGURE 8
Density representation (ind m^{-2}) of the four most abundant amphipod species (*Hyperiella dilatata*, *Primno macropa*, *Pseudorchomene plebs*, *Hyperiella macronyx*) in the 27 sampled stations.

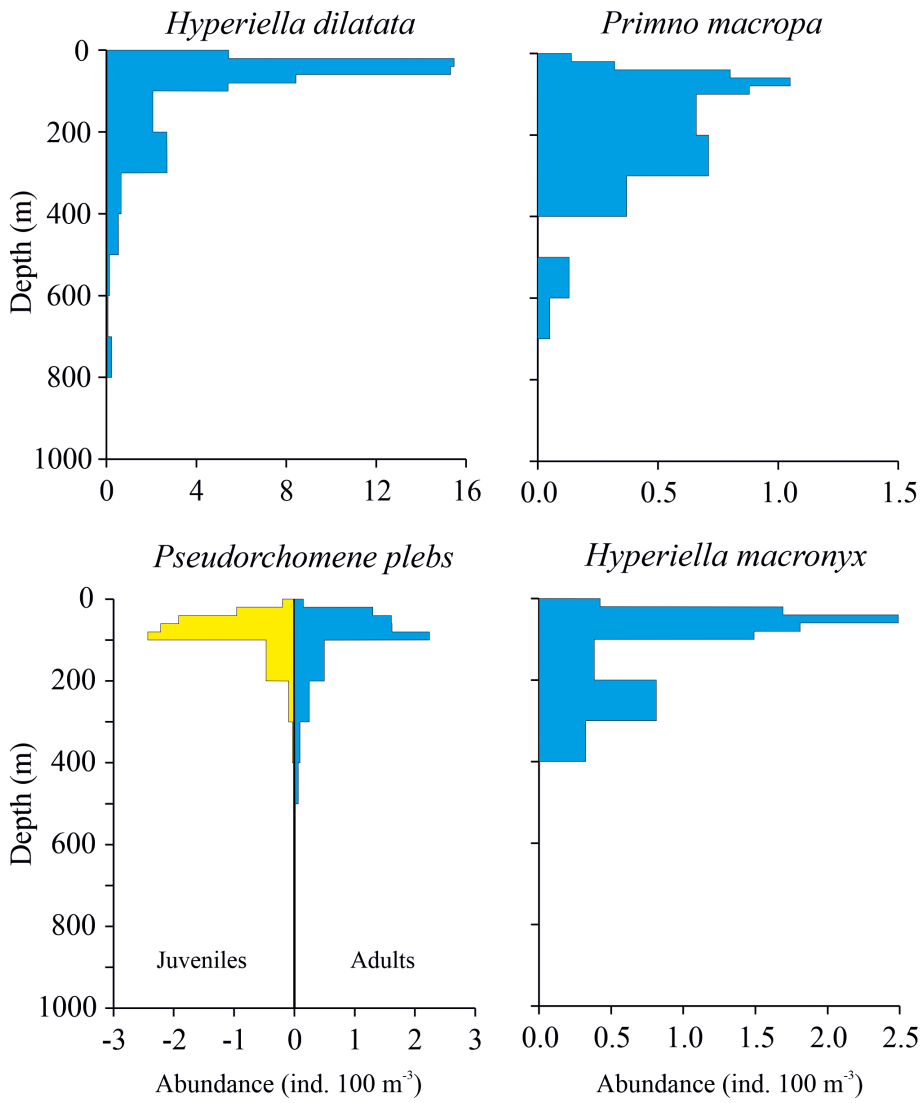

FIGURE 9
Vertical profiles of mean weighed abundance (ind. 100 m^{-3}) for the four most abundant amphipod species (*Hyperiella dilatata*, *Primno macropa*, *Pseudorchomene plebs*, *Hyperiella macronyx*). Profiles for adults are shown. Only for *P. plebs*, profiles also for juvenile stages are shown. Note differences in scales on x-axis.

TABLE 4 Spatial distribution boundaries of identified amphipod species inside the investigated area with this study.

Amphipod species/genus/family	Area	Coordinates				Stations of detection
		(latitude °S)		(longitude °E)		
		from	to	from	to	
Abyssorchomene scotianensis	Terra Nova Bay (TNB)	74.9528		164.1444		26
Acanthoscina sp.	Balleny Islands (BI)/Southern Pacific (SP)	66.0872	69.5917	163.6733	176.4111	6,7
Archaeoscina sp.	South of the Antarctic Convergence (AC)	63.9489		168.1203		4
Archaeoscinidae	Southern Pacific	69.5917		176.4111		7
Cleonardo longipes	Eastern Ross Sea (ERS)	71.2194		179.6805 W		10

(Continued)

TABLE 4 Continued

Amphipod species/genus/ family	Area	Coordinates				Stations of detection
		(latitude °S)		(longitude °E)		
		from	to	from	to	
Ctenoscina brevicaudata	Western Ross Sea (WRS)	72.3333	72.7333		177.5167	14,15
Ctenoscina sp.	South of the AC	63.9489		168.1203		4
Cyllopus lucasii	Western Ross Sea	72.7333		179.9111		14
Cyllopus magellanicus	Subantarctic zone/ South of the AC	50.9222	63.0764	171.9894	172.0011	1,3
Cyllopus sp.	Polar Front	61.9956		172.1753		2,3
Cyphocaris richardi	Polar Front	61.9956	63.0764	171.9894	172.1753	2,3
Epimeria (Epimeriella) macronyx	ERS/WRS/TNB	71.9500	75.0028	164.1444	177.7472W	16,20,23/27
Eusirus microps	WRS/TNB	74.7667	74.9972	164.1444	167.5500	24,26,27
Halice tenella	North of the AC	61.9956		172.1753		2
Hyperiella antarctica	North of the AC	61.9956		172.1753		2
Hyperiella dilatata	Polar Front/SP/WRS/ERS/TNB	61.9956	75.0056	164.1444	177.7472W	2,3,7,8,12/27
Hyperiella macronyx	BI/SP/WRS/ERS/TNB	64.8675	75.0028	161.8367	177.7472W	5,9,11/14,16/27
Hyperiidae	South of the AC	63.0764		171.9894		3
Hyperoche capucinus	Southern Pacific	69.5917	70.2083	176.4111	176.4528	7,9
Hyperoche sp.	Southern Pacific	70.7000		178.1083		8
Lanceolidae	North of the AC	61.9956		172.1753		2
Lanceola clausii pirloti	Eastern Ross Sea	71.2194		179.6806W		10
Lanceola sp.	South of the AC	63.9489		168.1203		4
Mimoscina sp.	Balleny Islands/Eastern Ross Sea	64.8675	71.2194	161.8367	179.6806W	5,6,10
Parandania boecki	North of the AC	61.9956		172.1753		2
Parandania sp.	South of the AC	63.9489		168.1203		4
Phoxocephalidae	Eastern Ross Sea	71.2194		179.6806W		10
Phronima atlantica	Subantarctic zone	50.9222		172.0011		1
Primno macropa	Everywhere except TNB	50.9222	75.0056	161.8367	177.7472W	1/17,19,21
Pseudorchomene plebs	WRS/ERS/TNB	72.7333	75.0028	164.1444	179.9722W	13,14,17/27
Pseudorchomene rossi	WRS/TNB	73.1444	75.0056	164.1444	179.9778	13,19/27
Scina antarctica	Balleny Islands/WRS/ERS	64.8675	75.0056	161.8367	177.7472W	5,11,15,16,19
Scina borealis	South of the AC/WRS/ERS	63.0764	71.6139	171.9894	179.6805W	3,10,11
Scina pusilla	Balleny Islands/ERS	66.0872	71.2194	163.6733	179.6805W	6,10
Scina sp.	Polar Front/BI/Southern Pacific	61.9956	70.7000	161.8367	178.1083	2/9
Scopelocheiropsis abyssalis	Balleny Islands	66.0872		163.6733		6
Scypholanceola sp.	North of the AC/BI/Southern Pacific	61.9956	70.2083	161.8367	176.4528	2,5,9
Themisto abyssorum	Western Ross Sea	73.1444		174.4028		13
Themisto compressa	Subantarctic zone	50.9222		172.0011		1
Themisto gaudichaudii	Subantarctic zone/Polar Front	50.9222	63.0764	172.1753	172.0011	1/3
Themisto sp.	Subantarctic zone	50.9222		172.0011		1

(Continued)

10.3389/fmars.2025.1633246

TABLE 4 Continued

Amphipod species/genus/family	Area	Coordinates				Stations of detection
		(latitude °S)		(longitude °E)		
		from	to	from	to	
Vibilia armata	Subantarctic zone/South of the AC/BI	50.9222	64.8675	161.8367	172.0011	1,3/5
Vibilia sp.	Polar Front	61.9956	63.0764	171.9894	172.1753	2,3

Boundaries of distribution as latitude °S and longitude °E are shown.

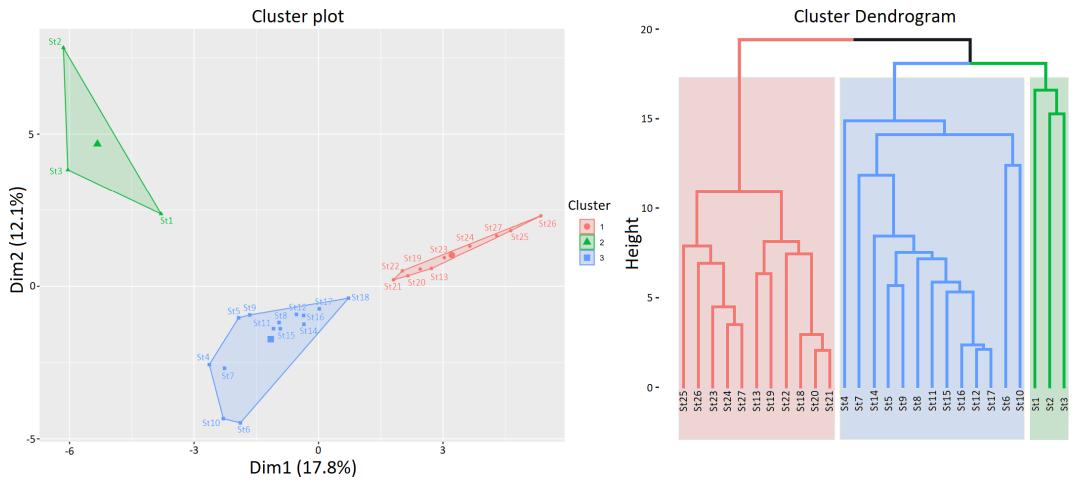

FIGURE 10
Results of the cluster analysis on amphipod species collected in the 27 stations.

three days, leaving perfectly clean skeletons (d'Udekem d'Acoz and Havermans, 2012). The family Phrosinidae was the third most abundant family (11%), represented by *P. macropa* only. In this study, *P. macropa* was present in front of Cape Adare and in the Pacific Ocean moving northwards to New Zealand. It was absent in the Ross Sea and inside Terra Nova Bay (Minutoli et al., 2023).

The combined information from the oceanographic profiles and the vertical distributions of the biological samples suggested that the water column was stratified in three main layers: the first layer (0–50 m) was mainly influenced by the possible presence of a DCM and of AASW; the second layer, covering 50–200 m, was characterized by the presence of temperature minima and by a wide range of temperature (between -1.92 °C and 1.23 °C); the third layer from 200 m to the bottom was influenced by CDW or MCDW and, at a few stations, by ISW.

Amphipod species composition differed significantly between stations. The sampling strategy, spanning both a broad spatial (from 62°S to 74°S) and a broad temporal (approximately 50 days) scale, from late austral spring to early summer, allowed us to divide the study area into zones with different hydrological characteristics and ice coverage. The three different clusters identified through the k-means algorithm based on species abundance were confirmed by the NMDS plot. In particular, a correlation between species composition and the sampled layers at the different stations was highlighted. The species composition of southernmost stations in the first cluster characterized the area starting from the innermost stations in Terra Nova Bay (75°S) across east-west stations up to 180°, where higher fluorescence values, lower temperatures in the euphotic layer (0–50 m e 50–200 m) and a clear DCM at 28 m were detected. The three northernmost stations (St.1-3) were significantly different from all other stations. In this ice free zone between the Sub-Antarctic Front and Antarctic Convergence the greatest diversity of amphipod species was found in the upper and saltier layers, with high abundance of Hyperiidae like *Themisto gaudichaudii*. In this area, no DCM was found in an homogeneous upper layer as temperature, salinity and fluorescence. The stations in the central part of the study area were influenced by relatively higher temperature and by lower fluorescence values in the upper layers, and higher salinity in the deepest layers below 200 m, and also by the presence of CDW and MCDW water masses. Therefore, the oceanographic and environmental constrains of the water masses, together with the pack ice coverage, have determined the

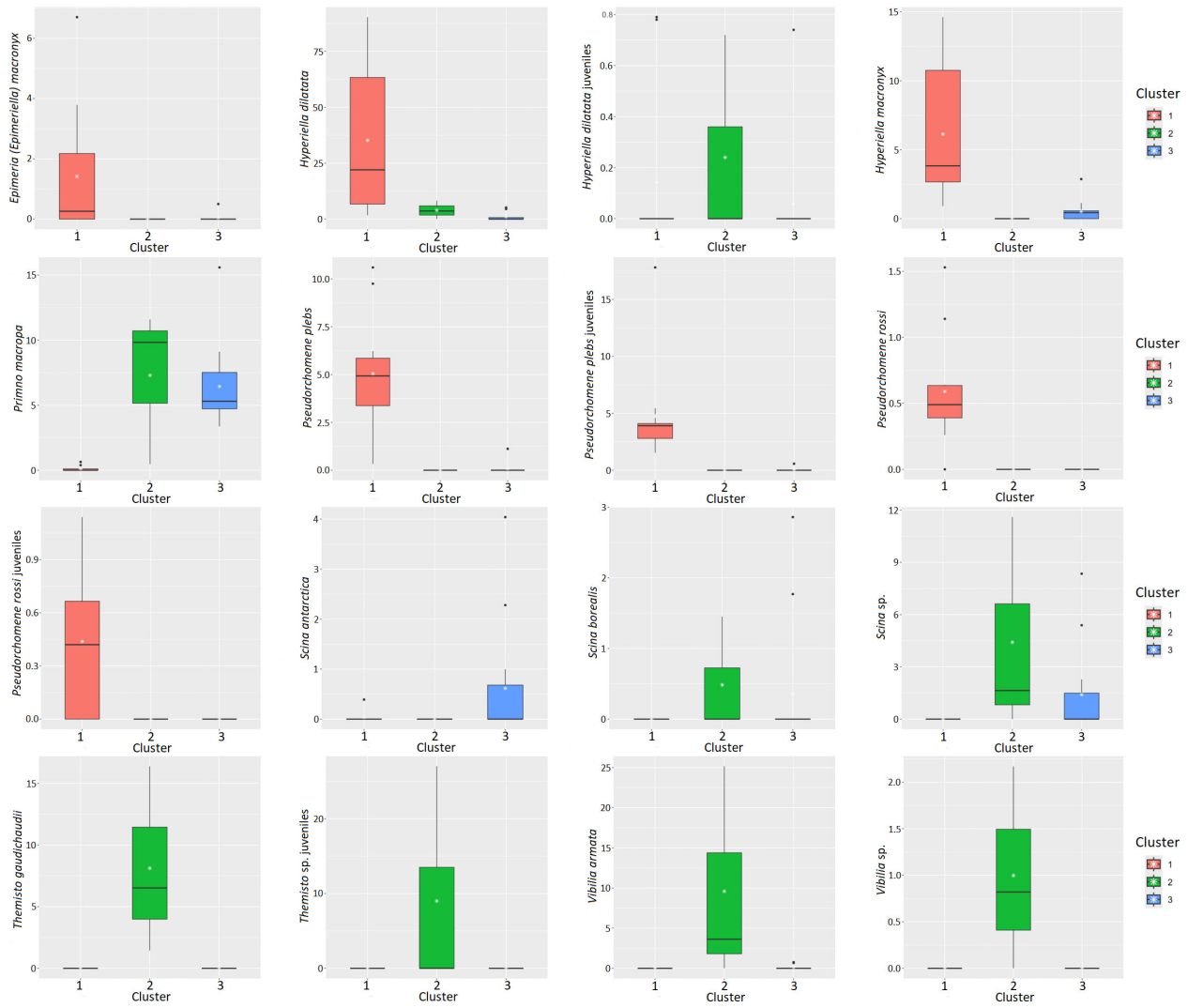

FIGURE 11
Boxplot of the main amphipod species in the three clusters.

different highlighted habitats suitable for pelagic amphipod species assemblages. These abiotic features of the study area should be so prioritized in future monitoring efforts in the Southern Ocean under changing climate conditions. On the other hand, it's well known that the sea ice plays a key role in structuring Antarctic ecosystem, and especially that the ice edge influences, with a cascade effect, the phytoplankton production and the zooplankton distribution and behavior and all the trophic food web (Carli et al., 2000; Hecq et al., 2000; Lazzara et al., 2000; Zunini Sertorio et al., 2000).

Knowledge of the relationship between pelagic amphipods and annual ice in the Southern Ocean is still very limited. The finding of some species, like *Eusirus antarcticus*, *E. perdentatus*, *E. microps* and *Cheirimedon femoratus* exclusively in the innermost stations of Terra Nova Bay (Minutoli et al., 2023; this study), where ice shelves along the coastline play an important role in the dynamics of Terra Nova Bay (Frezzotti, 1993), confirms the affinity of the above cited species for sea ice, as previously recorded during under-ice dives of the Weddell Sea and the Lazarev Sea (Krapp et al., 2008). Different for pelagic swimmer amphipods, as Hyperidae and Scinidae, that were routinely sampled in multinet hauls, isolated or few individuals of the above-mentioned species have been sampled (Minutoli et al., 2023; this study). According to Krapp et al. (2008), it would be advisable to use scuba or suitable tools for sampling zooplankton in the lower part of the pack-ice to obtain better estimates of biomass and improve our information on the habits of these species.

The finding of the three species of *Hyperiella* confirms that this genus is endemic to the Southern Ocean, found generally south of 55°S (Zeidler and De Broyer, 2009, 2014). In this study, *H.*

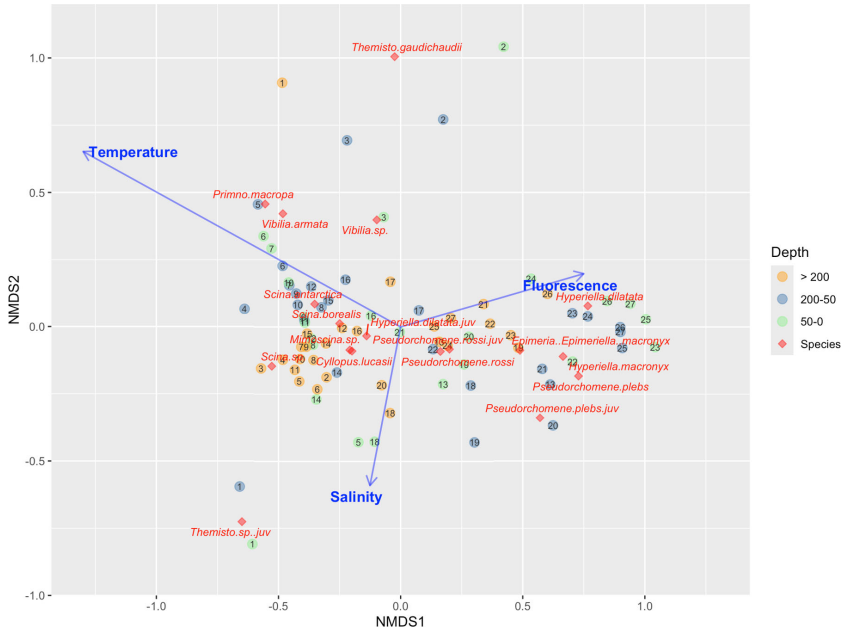

FIGURE 12
Non-metric multidimensional scaling (NMDS) ordination results, reporting the relationships among amphipods species, environmental factors (Temperature, Salinity and Fluorescence) and sampling stations. The number in each circle is the station number. Colors represent the considered layers: green for the layer 0–50 m, dark grey for the layer 50–200 m and yellow for the layer with depth > 200 m.

antarctica was collected between the Sub-Antarctic and the Antarctic Polar Front, confirming previous studies (Zeidler and De Broyer, 2009, 2014) and highlighting a lesser affinity to sea ice than its congeners (Flores et al., 2011). The highest abundances of *H. macronyx* and *H. dilatata* recorded in this study throughout the entire Ross Sea, and particularly inside Terra Nova Bay, may be explained by their affinity to colder waters and ice conditions. Weigmann-Haass (1989) recorded *H. dilatata* as relatively common around the tip of the Antarctic Peninsula and in the Weddell Sea.

5 Conclusions

The species composition, the abundance and the spatial distribution of amphipod crustaceans is of interest because they play a crucial role in ecosystems as a link between lower and higher trophic levels, and benthic-pelagic communities (Michel et al., 2016; Griffiths et al., 2017). Knowledge of the relationship between pelagic amphipods and annual ice in the Southern Ocean is still very limited. The large spatial scale investigated in this study gave us the opportunity to increase the state of knowledge on biodiversity and distribution of pelagic amphipods in the Pacific sector of the Southern Ocean. It has been proposed that pelagic species are more widespread than benthic species because of their mobility and relative homogeneity of their habitat (Costello et al., 2017). The much higher species richness found in the suborder Hyperidea (28) than in the suborder Amphilochidea (11) reflect the different investigated habitats, more ice-free pelagic waters than those covered by pack-ice. Despite only 3% of amphipod species are pelagic (Arfianti et al., 2018), this difference in biodiversity found between the two above cited suborders, could be justified by the behavior of these pelagic crustaceans that avoid predation in open pelagic waters by being relatively transparent, living within gelatinous zooplankton, having good eyesight, and being agile swimmers. Statistical analyses confirmed that sea-ice extension, water masses structure, physical and biological constraints, like water temperature, salinity and fluorescence (DCM) controlled the horizontal and vertical distribution of pelagic amphipod habitat and relative trophic behavior.

Amphipods are important in the Antarctic food chain, yet we have little knowledge of how alterations in environmental parameters linked to climate changes will influence plankton communities, particularly species distribution, life cycles and development (Beaugrand, 2009; Weydmann et al., 2018; Schröter et al., 2019). Knowledge of amphipod biodiversity by means of this study can represent a baseline for future studies. The comparison with newly collected samples may provide evidence of changes due to environmental alternations.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

RM: Conceptualization, Writing – original draft, Writing – review & editing. LG: Conceptualization, Writing – original draft, Writing – review & editing. AB: Formal Analysis, Writing – original draft. SG: Formal Analysis, Writing – original draft. RF: Formal Analysis, Writing – original draft. DD: Formal Analysis, Methodology, Writing – original draft. MG: Formal Analysis, Methodology, Writing – original draft. YG: Methodology, Writing – original draft. KS: Writing – review & editing. AG: Conceptualization, Supervision, Writing – original draft, Writing – review & editing. SA: Conceptualization, Supervision, Writing – original draft, Writing – review & editing.

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