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ORIGINAL PAPER

Species diversity and spatial distribution of pelagic amphipods in Terra Nova Bay (Ross Sea, Southern Ocean)

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Abstract

A greater understanding of biodiversity and the roles of various species involved in Southern Ocean pelagic food webs is needed to predict and hypothesize about responses to future scenarios in relation to climate changes. The aim of this paper was to describe for the first time the composition, relative abundance, spatial distribution and relation with water masses of pelagic amphipods in Terra Nova Bay, Ross Sea, based on stratified sampling. Zooplankton was collected by BIONESS (Bedford Institute of Oceanography Net Environmental Sampling System), during the 1987–1988 Italian Antarctic *R/V Polar Queen* Expedition. A total of 1331 specimens of pelagic amphipods was counted and 17 species belonging to nine families were identified. Significantly relative higher abundances were related to Modified Circumpolar Deep Water (MCDW) in the upper layer than modified Ross Sea Shelf Water (RSSW) and High Salinity Shelf Water (HSSW). *Hyperiella dilatata* was the most abundant species (48% of relative abundance), followed by *Pseudorchomene plebs* (14%), *Hyperia macrocephala* (8%) and *Hyperiella macronyx* (6%). *Hyperiella dilatata* was distributed widely across the study area and showed a link with Antarctic Surface Waters (AASW) and MCDW. *Hyperiella macronyx* and *Pseudorchomene rossi* were also distributed widely though were much lower in abundance. *Hyperia macrocephala* were high in abundance though had a narrow distribution that was linked with AASW. The vertical distributions showed variable patterns for adult and juvenile specimens. This study represents a knowledge base against which to compare more recent studies to highlight any structural changes attributable to ongoing climate change in the Terra Nova Bay and Ross Sea ecosystems.

Keywords Indicator values · Sea ice · Community structure · Horizontal and vertical distribution · *Hyperiella dilatata*

Introduction

The Southern Ocean is characterized by low water temperatures year-round and seasonal formation of pack-ice on the surface. Sea ice surrounding the Antarctic continent varies in extent from 3.1×10^6 km^2 in February to a maximum of 18.5×10^6 km^2 in September, making it one of the largest and most dynamic ecosystems on Earth (Arrigo et al. 1997; Eayrs et al. 2019; Parkinson 2019). The processes of ice formation and melting help determine the makeup of planktonic communities (Garrison and Buck 1991; Dieckmann et al. 1998; Gleitz et al. 1998; Granata et al. 2022), particularly those processes that regulate the availability of suspended particles for planktonic and benthic suspension feeders, especially during summer (Guglielmo et al. 2000; Cau et al. 2021).

Terra Nova Bay is characterized by an extended polynya, which is formed by katabatic winds that blow downslope from the Trans-Antarctic Mountains, resulting in open water that extends through the winter (Kurtz and Bromwich 1985). In this region the polynya is a major driver of ice growth and decay processes, which, in turn, control the growth of coastal sea ice microalgae and the availability of suspended particles

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in the upper coastal waters of Terra Nova Bay (Guglielmo et al. 2000; Misic et al. 2002; Pane et al. 2004). The waters of the bay show peculiar physical–chemical features within the Ross Sea system, as summer heating that can cause temperature increases of the surface layers. In Terra Nova Bay, the summer meso- and macrozooplankton is mostly composed of copepods (Carli et al. 2000; Zunini Sertorio et al. 2000; Pane et al. 2004), ichthyoplankton (Granata et al. 2002), with key species including the ice krill *Euphausia crystallorophias* (Guglielmo et al. 2009), the notothenioid fish *Pleuragramma antarcticum* (Guglielmo et al 1998; Granata et al. 2009), the mysid *Antarctomysis ohlini* (Crescenti et al. 2000) and the pteropod *Limacina helicina antarctica* (Manno et al. 2010). These species represent a fundamental link for predictive distributions (Grillo et al. 2022), food web structure and modelling (Pinkerton and Bradford-Grieve 2014; Signa et al. 2019).

Amphipods are well represented in all three macrohabitats of Terra Nova Bay: the sea floor with Gammaridea and Corophiidea, the water column with Hyperiidea and pelagic and bentho-pelagic Gammaridea, and the sea ice with epontic Gammaridea (De Broyer and Jażdżewska 2014). Amphipods of the benthic realm have been investigated, although many areas of the continental shelf remain unexplored and the deep sea has been sampled rarely (Zeidler and De Broyer 2009; De Broyer and Jażdżewska 2014; Jażdżewska and Siciński 2017). Amphipods exhibit diverse lifestyles, trophic habits, habitat and size spectra, and they constitute a significant trophic resource for Southern Ocean fishes, invertebrates, seabirds and mammals (Zeidler and De Broyer 2009). Considering the key role of this oceanic sector in the Earth system and the growing impact of global environmental change, it is fundamental to collect information on the status of Antarctic marine biodiversity. It is well-known that the majority of amphipods inhabit the benthic environment, and comparatively few species belonging to a very few families have evolved to colonize the pelagic realm (Zeidler and De Broyer 2009). Very little is known about oceanic species, in particular their vertical distribution as they have rarely been sampled with a stratified multi-net system (Zeidler and De Broyer 2009).

The aim of this paper was to describe for the first time the composition, relative abundance and spatial distribution of pelagic amphipod species in Terra Nova Bay, based on stratified sampling. An additional goal was to describe the main water masses influencing the region and, where possible, relate the species assemblages to these water masses and latitude–longitude gradient in Terra Nova Bay.

Materials and methods

Sampling procedure

During the 1987–1988 Italian Antarctic Expedition of the *R/V Polar Queen*, between 5 January and 21 February 1988, zooplankton samples were collected in Terra Nova Bay, Ross Sea (Fig. 1). A total of 31 stations were investigated, where samples were collected in several depth-layers from the surface to near the seabed. All the sampling details are shown in Table 1. The study area extended from Cape Washington (74°39′00’’S) to Drygalski Ice Tongue (75°29′00’’S), along a longitude from 163°49′00’’E to 168°04′00’’E. The sampling stations were located on the continental shelf of the Ross Sea, except for two stations (1SK located offshore from the coast and ANZ near Cape Adare, see Table 1). Samples were collected with an electronic multinet BIONESS (Bedford Institute of Oceanography Net Environmental Sampling System) (Sameoto et al. 1980), which had a mouth area of 0.25 m^2 and was equipped with 10 nets (mesh size 230-µm or 500-µm). The BIONESS continuously measured temperature, salinity and depth during tows with an Applied Microsystems digital CTD. Filtered volume was monitored using external and internal TSK flowmeters. 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. The number and the thickness of the sampled strata depended on the bottom depth (Table 1). Fishing upward, the nets were opened and closed on command, at 100- to 20-m intervals in the hauls programmed in the upper 200 m according to different water masses, and between 30- and 100-m intervals below this zone to the maximum depth sampled. Due to technical reasons, it was not always possible to collect the same number of samples at all stations, whereas the lack of surface samples at some stations was our choice for 50-m intervals in the deep hauls. A total of 266 samples (for a total of 9780 m^3 of filtered water) was collected from the 31 sampling stations. The zooplankton samples collected at each station from the surface to the maximum sampled depth (800 m), during the downward deployment of the BIONESS, were useful in lab for rare species potential detection, but not used for this work. On board, all the zooplankton samples were preserved in a 4% buffered formaldehyde-seawater solution (Table 2).

Zooplankton analysis

In laboratory, subsamples of different volumes, from 1/10 to 1/25 of the original sample, were observed under a Leica Wild M10 stereomicroscope. The whole sample

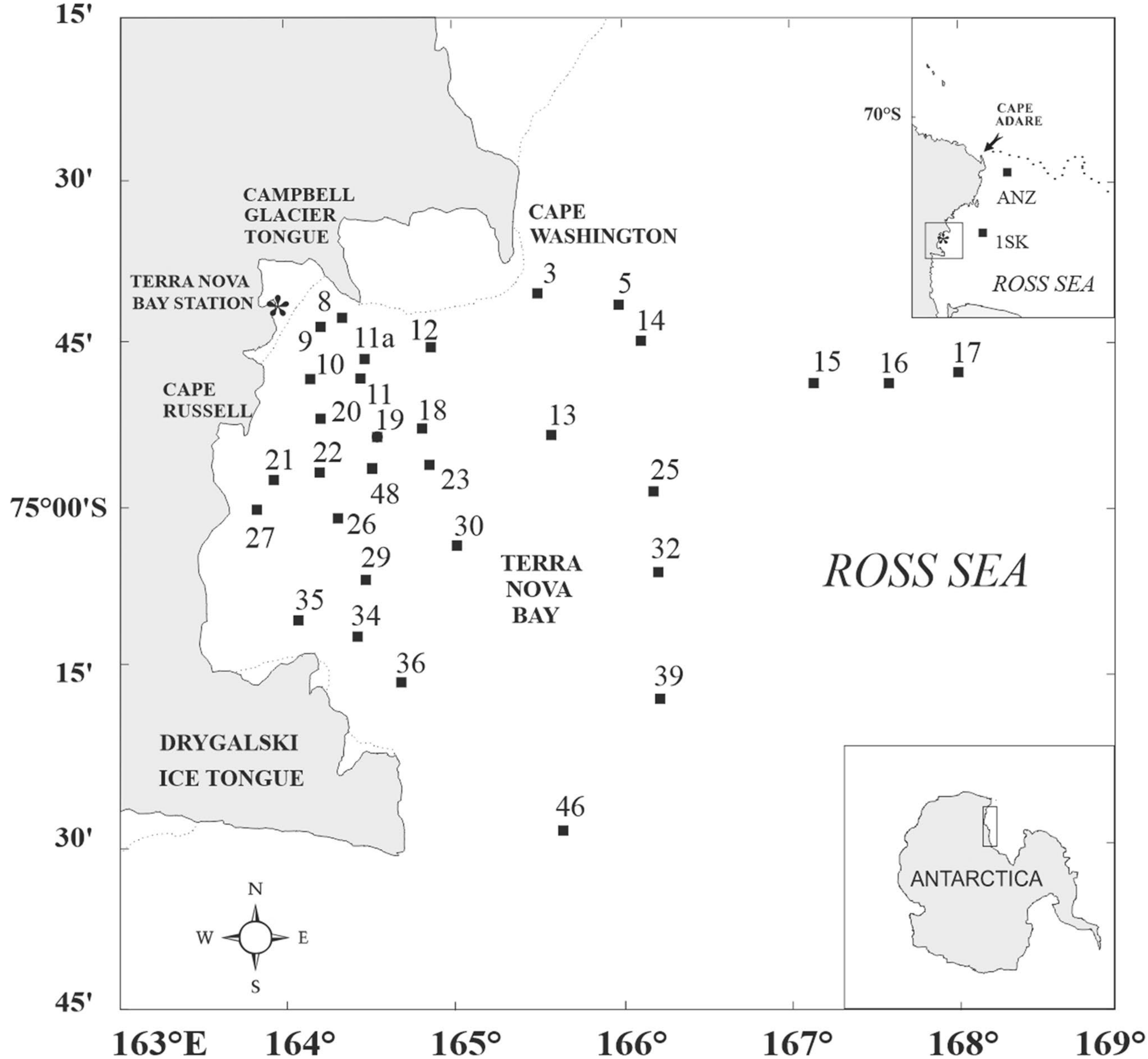

Fig. 1 Map showing the stations in Terra Nova Bay that were sampled from 5th January to 21th February 1988 during the *R/V Polar Queen* oceanographic cruise, 1987–1988 Italian Antarctic Expedition

was examined for the identification and enumeration of macrozooplankton and micronekton, as for amphipods. All the specimens of each taxon were counted and identified at higher taxonomic levels, while diagnosis at the species level was undertaken for the amphipods. The abundance of amphipods for each stratum was calculated by dividing the total number by the filtered water volume 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 amphipods counted dividing by the total volume of seawater filtered (m^3), multiplied by the water column thickness and expressed as individuals m^{-2}. The mean total abundance of a given species for the 31 sampled stations is represented by the geometric mean and expressed as individuals m^{-2}, to minimize the difference in water column depth.

Statistical analysis

Temperature and salinity data collected during the BIONESS samplings were processed with Ocean Data View (ODV version 5.5.2) software (Schlitzer 2001) to map the position of each of the 266 datapoints on the Θ-S diagram and assign them to a specific water mass. The 'elbow'

Table 1 Station data for EZ-NET BIONESS zooplankton samples taken during the Italian Oceanographic Antarctic Expedition (1987–88) in Terra Nova Bay

Station	Date	Start		End	End	Local time		Depth (m)		Nets	
		Lat (° S)	Long (° E)	Lat (° S)	Long (° E)	Start	End	Bottom	Bioness haul	mm	Samples
8	05/01/1988	74.7100	164.4310	74.7130	164.5310	16.15	16.51	570	500	500	8
11	05/01/1988	74.8110	164.4850	74.8580	164.4160	22.48	00.03	640	600	500	7
9	06/01/1988	74.7140	164.2550	74.7380	164.2080	12.08	12.51	560	300	500	9
10	06/01/1988	74.8030	164.1570	74.8100	164.1600	17.45	18.02	325	300	500	9
11A	07/01/1988	74.7840	164.5120	74.7550	164.4690	12.25	13.09	530	100	500	8
20	09/01/1988	74.8665	164.2360	74.8861	164.1670	16.38	17.12	257	200	500	9
19	10/01/1988	74.8850	164.5562	74.9154	164.6327	18.58	19.57	660	500	500	9
21	12/01/1988	74.9544	163.9320	74.9610	164.2041	08.34	09.19	565	400	500	7
22	12/01/1988	74.9390	164.1857	74.9850	164.2500	14.58	16.01	645	600	500	9
26	13/01/1988	75.5400	164.2850	75.3700	164.1120	08.25	09.43	930	800	500	8
27	13/01/1988	75.1800	163.8650	75.5510	163.8130	21.48	22.19	815	600	500	9
29	14/01/1988	75.1300	164.4000	75.1300	164.1600	11.24	12.17	1010	500	500	9
35	14/01/1988	75.1850	163.9800	75.1810	164.2820	22.21	23.24	1040	100	500	7
34	15/01/1988	75.2030	164.2670	75.2010	164.4080	10.27	11.47	1100	600	500	9
36	15/01/1988	75.2550	164.6300	75.3030	164.6150	16.01	16.44	945	150	500	9
12	24/01/1988	74.7500	164.8300	74.6800	164.8300	23.09	00.14	560	450	250	9
3	25/01/1988	74.6500	165.4500	74.6800	165.5000	12.31	13.08	187	150	250	9
13	25/01/1988	74.8550	165.5330	74.8850	165.5550	19.21	20.26	810	700	250	9
5	26/01/1988	74.6520	165.9530	74.6850	166.6000	07.25	08.31	700	500	250	9
14	26/01/1988	74.7500	166.8000	74.7890	166.1350	11.38	12.51	875	600	250	7
17	27/01/1988	74.7800	168.6000	74.7500	167.9800	07.47	08.41	550	350	250	9
16	27/01/1988	74.8000	167.5600	74.8000	167.3600	14.09	16.08	650	500	250	9
18	28/01/1988	74.8628	164.7610	74.8859	164.9524	17.03	18.17	655	500	250	9
23	28/01/1988	74.9160	164.8300	74.9670	164.8500	21.51	23.03	1000	600	250	9
48	29/01/1988	74.9170	164.5000	74.9650	164.5000	06.58	08.04	700	450	250	9
46	02/02/1988	75.4800	165.6580	75.4020	165.5154	07.48	09.15	810	500	250	9
39	02/02/1988	75.2850	166.1380	75.2330	166.1160	13.24	14.32	840	550	250	9
32	02/02/1988	75.1080	166.1130	75.5000	166.3300	17.34	19.04	895	650	250	9
15	02/02/1988	74.8000	167.1300	74.7670	166.7600	23.41	00.57	700	600	250	9
1SK	04/02/1988	74.8354	172.5849	74.8358	172.7643	17.16	18.17	520	350	250	9
ANZ	21/02/1988	72.3100	172.0000	72.2600	172.1000	15.39	16.27	400	300	250	7

method on the inertia curve (k-means algorithm in the R package *factoextra*) guided the choice of the best number of clusters ($k=4$). These four clusters were named according to the dominant water masses in the area (Orsi et al. 2009): Antarctic Surface Waters (AASW); Modified Circumpolar Deep Water (MCDW); modified Ross Sea Shelf Water (RSSW) and High Salinity Shelf Water (HSSW). Completeness of the samples was evaluated according to the standardization approach proposed by Chao and Jost (2012). To correctly compare informative though uneven subsample aggregations, rarefaction/extrapolation curves based on the reference samples were used (Colwell et al. 2012; Chao et al. 2014). Expected species richness was calculated through the Chao1 estimator (classic formula) and first order jackknife analysis. Asymptotic species richness in subsample aggregations were obtained with the R package *iNEXT* (Hsieh et al. 2016). Taking into account the sampling strategy, amphipod density and diversity across relevant factors (six levels for the factor "depth range", four levels for the factor "water masses", see Table 3) were examined using R version 4.0.3 to test for significant differences between and within groups of data (ANOVA and Kruskal–Wallis non-parametric tests on medians in case of non-homogeneity of variances, coupled with *post-hoc* Dunn test). Indicator species analysis (IndVal) has been used to identify species that were representative of different sample aggregations (layers, water masses) and inform about their "specificity" (i.e., degree of exclusivity) and "fidelity" (i.e., probability of occurrence) as indicators of groups of samples throughout the

Table 2 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 occurence in the sampling stations

Species	Abundance (ind m^{-2})	Percent (%)	*N*	Frequency (%)
Acanthonotozomatidae Stebbing, 1906	0.05	0.1	1	3.2
Epimeriidae Boeck, 1871				
Epimeria sp. Costa in Hope, 1851	1.59	3.9	43	51.6
Eusiridae Stebbing 1888				
Eusirus antarcticus Thomson, 1880	0.78	1.9	17	35.5
Eusirus perdentatus Chevreux, 1912	0.05	0.1	1	3.2
Hyperiidae Dana, 1852				
Hyperia macrocephala (Dana, 1853)	3.33	8.1	104	9.7
Hyperiella dilatata Stebbing 1888	19.93	48.3	771	100
Hyperiella macronyx (Walker, 1906)	2.43	5.9	82	64.5
Hyperiopsidae Bovallius, 1886				
Hyperiopsis australis Walker, 1906	0.07	0.2	2	6.5
Pardaliscidae Boeck, 1871				
Halice tenella Birstein & Vinogradov, 1962	0.12	0.3	1	3.2
Phrosinidae Dana, 1852				
Primno macropa Guérin-Méneville, 1836	0.12	0.3	5	6.5
Tryphosidae Lowry & Stoddart, 1997				
Cheirimedon femoratus (Pfeffer, 1888)	0.02	0.04	1	3.2
Orchomenella franklini Walker, 1903	0.06	0.2	2	3.2
Orchomenyx macronyx (Chevreux, 1905)	1.07	2.6	27	41.9
Pseudorchomene plebs (Hurley, 1965)	5.91	14.3	149	80.6
Pseudorchomene rossi (Walker, 1903)	1.74	4.2	35	61.3
Pseudorchomene sp. Schellenberg, 1926	3.8	9.2	84	87.1
Tryphosella adarei (Walker, 1903)	0.07	0.2	3	9.7
Uristidae Hurley, 1963				
Abyssorchomene abyssorum (Stebbing 1888)	0.02	0.1	1	3.2
Debroyerella fougneri (Walker, 1903)	0.02	0.04	1	3.2
Debroyerella solidus (Andres, 1986)	0.05	0.1	1	3.2

Table 3 Observed richness in amphipod community

Sample groups	# of Specimens	# of Species	Coverage (%)
By depth range 0–50 (*n* = 32)	683	11	99
50–100 (*n* = 31)	180	10	98
100–200 (*n* = 39)	156	9	100
200–400 (*n* = 68)	251	11	98
400–600 (*n* = 27)	56	12	89
> 600 (*n* = 3)	5	3	73
By water mass ASSW (*n* = 4)	117	3	100
MCDW (*n* = 15)	403	11	99
RSSW (*n* = 130)	661	18	99
HSSW (*n* = 51)	150	9	99
Total (*n* = 200)	1331	20	99

Samples are grouped by depth range and by water mass. The coverage (in %) estimates are based on the rarefaction/extrapolation curves and can be used to have indications on the completeness of each group of samples in terms of the caught species richness

water column (Dufrene and Legendre 1997; Podani and Csanyi 2010). The function 'multipatt' of the R package *indicspecies* has been used.

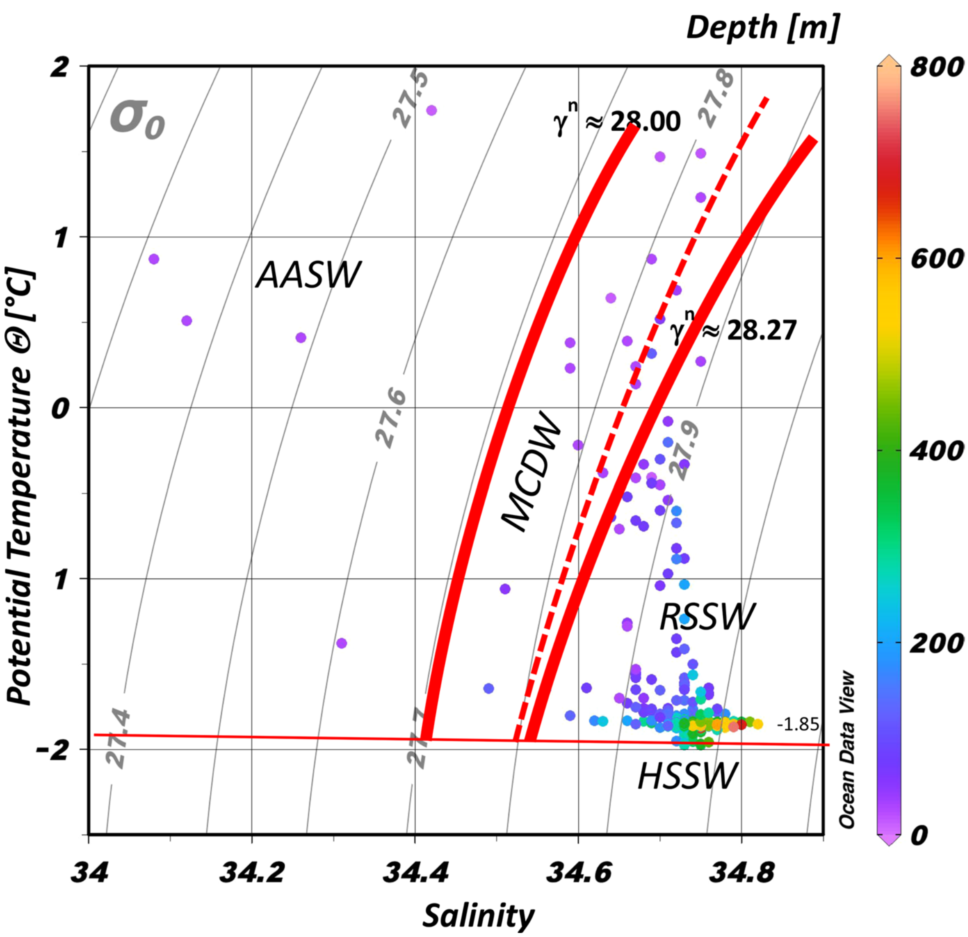

Fig. 2 Θ-S scatter plot of the BIONESS samples. Water masses present in the area are indicated: Antarctic Surface Waters (AASW); Modified Circumpolar Deep Water (MCDW); modified Ross Sea Shelf Water (RSSW); High Salinity Shelf Water (HSSW). Cluster Center of Mass based on Depth, Temperature and Salinity are: ASSW (20-m, 0.35 °C, 34.14); MCDW (40 m, 0.35 °C, 34.65); RSSW (210 m, − 1.55 °C, 34.72); HSSW (340 m, − 1.87 °C, 34.74)

Results

Environmental parameters

The Θ-S scatter plot revealed four water masses present on the Ross Sea Shelf at depth < 700 m (Fig. 2). These were: (1) AASW with lower salinity, temperature often exceeding 0 °C and density anomaly $\sigma 0 < 27.75$ ($\gamma^n \approx 28$ kg m^{-3}); (2) the MCDW that includes a relatively warmer and more saline core delimited by the 28.27 kg m^{-3} neutral density γ^n surface and, below it, (3) the RSSW modified by the interaction with coastal processes (such as e.g. upwelling due to katabatic winds) and glacier presence. In this region of the Θ-S plane, a more saline ($S > 34.75$) water mass with a temperature close to the freezing temperature at the surface ($\Theta \approx -1.85$ °C) was found. The signature of a (4) slightly colder HSSW ($\Theta \approx -1.95$ °C, $S > 34.62$, depth 400 m) was also noted, which was formed by the deep melting of the Drygalski Ice Tongue and is a precursor of the Deep Ice Shelf Water (DISW).

Zooplankton community

Mean total zooplankton abundance across the 31 sampled stations was 15,176 ± 20,199 ind. 100 m^{-3}. Copepods were the most abundant taxa comprising 49% of total zooplankton (total weighted mean abundance 7319 ind. 100 m^{-3}), followed by euphausiids (total weighted mean abundance 3296 ind. 100 m^{-3}, 22%) and pteropod molluscs (total weighted mean abundance 2916 ind. 100 m^{-3}, 20%). Other taxa that together accounted for less than 9%, were, in decreasing order, polychaete larvae, ostracods, fish larvae, siphonophores, chaetognaths, gastropod mollusc larvae, mysids, salps and decapod larvae.

Pelagic amphipod composition and abundance

Overall, about 25% samples (66 out of 266) were empty (they did not contain amphipod specimens) regardless of the filtered water volume. A total of 1331 pelagic amphipods were counted in the whole study area, representing 0.09% of the total zooplanktonic community abundance, ranging from 0.01% (St.3) to 0.6% (St.35).

A total of 20 taxa were recovered in Terra Nova Bay (Table 2). We identified 17 species belonging to nine families, two groups identified to genus (*Epimeria* sp. and *Pseudorchomene* sp.) and one taxon at family level (Acanthonotozomatidae).

Observed richness, grouping samples by depth range and by water mass, is shown in Table 3. The sampling effort was suitable to describe in detail the amphipod community in the different water masses (coverage > 99%) with only a minor reduction below 400 m depth. The reference overall sample ($n = 1331$ identified specimens, including 7 singleton species) exhibited a strong degree of completeness (99%) efficiently representing the amphipod community in Terra Nova Bay in summer. However, the overall species accumulation curve did not reach an asymptote within the size of the reference sample nor in the extrapolation to a 2-time size, suggesting a remarkably greater species richness for amphipods in the whole area, on the order of at least 50 species (32 ± 13 s.e. species, Chao1 estimator, classic formula). The RSSW showed the greatest richness, higher than MCDW with which there is overlap between the 95% confidence intervals (Fig. 3). The lowest diversity can be assigned to AASW, which is possibly dependent on the extremely uneven sampling in these deep waters. HSSW contained about 50% of the overall richness, with nine species (*Hyperiella dilatata, Hyperiella macronyx, Pseudorchomene rossi, Pseudorchomene plebs, Pseudorchomene sp., Orchomenyx macronyx, Epimeria sp., Eusirus antarcticus, Halice tenella*) recorded out of 20, none of them exclusive to this water mass, except the single observation of *H. tenella*. Moreover, while the extrapolated trends in richness for RSSW and MCDW did not plateau at a size near the reference sample and far beyond, HSSW appeared to have reached its asymptotic richness.

Hyperiella dilatata (Hyperiidae) was the most abundant species, representing about 48% (771 total counted specimens, 19.93 ind. m^{-2}) of the total amphipods collected in the entire study area, followed by *P. plebs,* which represented about 14% (149 total counted specimens, 5.91 ind. m^{-2}). In decreasing order, *Pseudorchomene* sp. represented ~ 9% (84 total counted specimens, 3.8 ind. m^{-2}) followed by *Hyperia macrocephala* at 8% (104 total counted specimens, 3.33 ind.

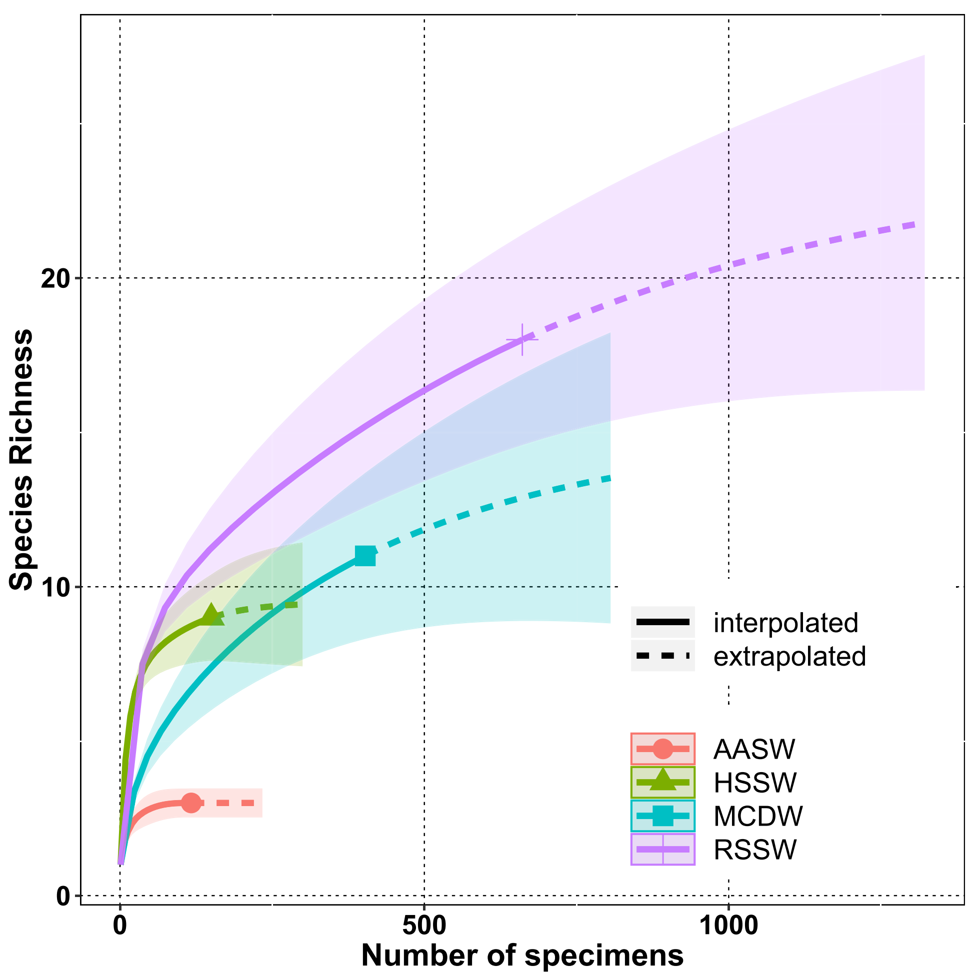

Fig. 3 Species accumulation curves for the samples aggregated by water mass. Estimates of species richness are extrapolated to a double sample size

m^{-2}), *H. macronyx* 6% (82 total counted specimens, 2.43 ind. m^{-2}), *P. rossi* 4% (35 total counted specimens, 1.74 ind. m^{-2}), *Epimeria* sp. 4% (43 total counted specimens, 1.59 ind. m^{-2}), *O. macronyx* 2.6% (27 total counted specimens, 1.07 ind. m^{-2}) and *E. antarcticus* 2% (17 total counted specimens, 0.78 ind. m^{-2}). All the other species occurred with very few individuals, with percentage contribution to total amphipod abundance less than 1%.

The total abundance was generally low (average of 21 ind. 100 m^{-3}). The highest value (525 ind. 100 m^{-3}) was observed at St. 17 (0–30 m layer), due to the dominant (90%) monospecific presence of *H. macrocephala* in this off-shore AASW sample. Densities on the order of 100 ind. 100 m^{-3} were found at the surface, in stations 35 and 36, close to the Drygalsky ice tongue (Fig. 4a).

Pelagic amphipod spatial distribution

Hyperiella dilatata had the widest distribution among all the recorded species, with a percentage frequency of occurrence of 100%; i.e., it was observed at all 31 sampling stations (Table 2). Some species, including *H. macronyx* and *P. rossi*, were present in low abundance although showed a wide horizontal distribution, while others, including *H. macrocephala* had high abundance but were narrowly distributed (St. 17, 35, ANZ only).

Comparison of species richness between the stations, showed that St. 34 had the highest richness, seven species, further to the presence of specimens belonging to the genus *Epimeria* and to the family Acanthonotozomatidae. St. 11 showed the lowest richness, with only *H. dilatata* and one specimen of *Pseudorchomene* sp. recorded.

Density showed a general decreasing trend with depth (Fig. 4b). Median densities were significantly different throughout the water column (Kruskal–Wallis test: $H_5 = 78.12$, $p < < 0.001$). Significantly higher abundances were related to MCDW in the upper layer than RSSW and HSSW (Dunn test, adjusted $p < 000.1$) (Fig. 5a). Diversity, based on the Margalef index, varied across the water masses (Kruskal–Wallis test: $H_3 = 10.73$, $p = 0.013$), and was slightly higher in HSSW (Fig. 5b).

Different patterns of vertical distribution were shown for the four most abundant species, and between adult and juvenile specimens (Fig. 6). The main distribution (74%) of *H. dilatata* adults occurred in the upper 50-m, with very few specimens until 700 m in depth. In contrast, *H. dilatata* juveniles has their centre of distribution lower in the water column, where 85% of the population occupied the 200–500 m layer, (range 50–600 m). For *P. plebs*, similar patterns of vertical distribution were shown by the adults and juveniles. The main part of the population (79% of adults and 93% of juveniles) occupied the same layers from the surface to 250 m. Few *P. plebs* adults were recorded between 300 and 600 m, while all juveniles were shallower than 350 m. The third most abundant species, *H. macrocephala*, was recorded above 30 m depth, except for 1 specimen occupying the 220–260 m layer m at St. ANZ. *H. macronyx* adults and juveniles showed different patterns in their vertical distributions: 74% of the adults occupied the 0–150 m layer, with a total range from 0 to 450 m, while all the juveniles were concentrated between 100 and 350 m.

The IndVal analysis performed on the amphipod assemblages, identified the most characteristic species of the different water masses (Table 4). In the very surface layer the clearest indicator species was *H. dilatata*, by far the dominant species in the area, with an occurrence of 100% in the AASW + MCDW water mass (fidelity = 1). Representative of the AASW, with a high specificity but quite low occurrence, was *H. macronyx* that could prefer a deeper habitat linked with AASW. In the subsurface photic layer the strongest indicator was *Pseudorchomene* sp. Interestingly, no species emerged as a significant indicator of either HSSW or RSSW.

Discussion

Pelagic amphipods are often not dominant in terms of abundance in zooplankton samples, but they do have a substantial role within the Antarctic food web (Pinkerton et al. 2010; Havermans et al. 2019). They are important in recycling of organic matter and are a prey item for many fish species, higher marine predators and migratory seabirds (DeWitt and Hopkins 1977; Eastman 1985a, b; Stowasser et al. 2012; Xavier et al. 2018; Waluda et al. 2012). *Trematomus bernacchii, T. newnesi* and *T. pennelli* show a wide trophic spectrum, consisting mainly of amphipods, like *Pseudorchomene plebs*, *Debroyerella fougneri*, specimens of Eusiridae, Hyperiidae and Acanthonotozomatidae families, along with gastropods and polychaetes (Richardson 1975; Vacchi et al. 1994; Vacchi and La Mesa 1995; La Mesa et al. 2004).

Recent importance was also given to amphipods in Southern Ocean for microplastic uptake phenomenon by lower trophic organisms that has been hypothesised as a conduit for microplastics up the food-chain. Evidence for this has been founded on positive identification of microplastics/fibres in the scats of zooplanktivore higher predators (Jones-Williams et al. 2020).

In Terra Nova Bay polynya, the omnivorous ostracods and amphipods were restricted below the pycnocline and the plankton ecosystem is dominated overall by macrozooplankton food-chain (diatoms, molluscs, amphipods), and larval stages of *Pleuragramma antarcticum* representing the carnivorous level (Hecq et al. 2000). In the southern area of Terra Nova Bay, *P. antarcticum* old postlarvae and juveniles were more abundant than in the norther one and the seem to

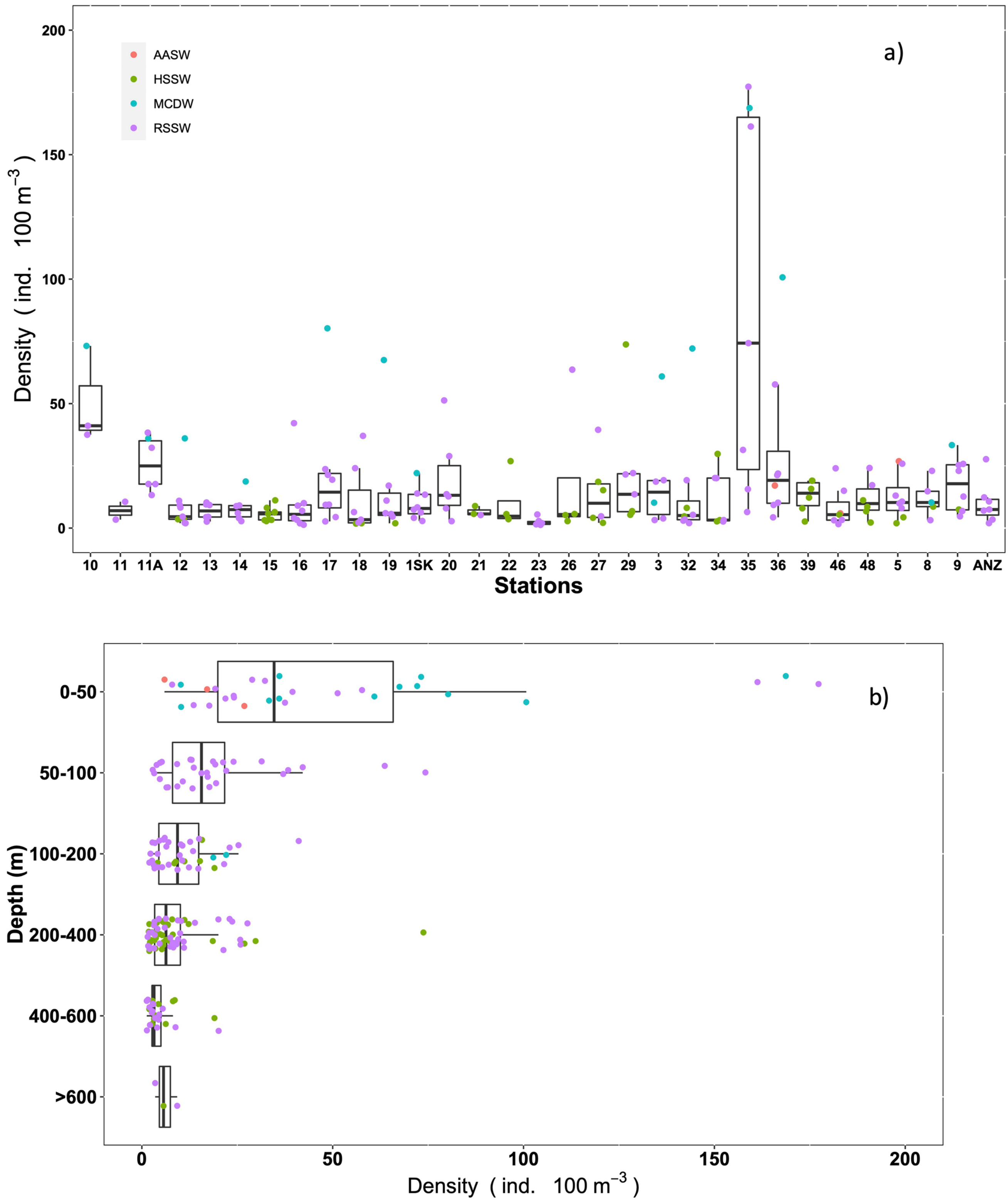

Fig. 4 Observed amphipod abundance (ind. 100 m^{-3}) at the different stations (**a**) and throughout the water column, from the surface layer to the deepmost one (**b**)

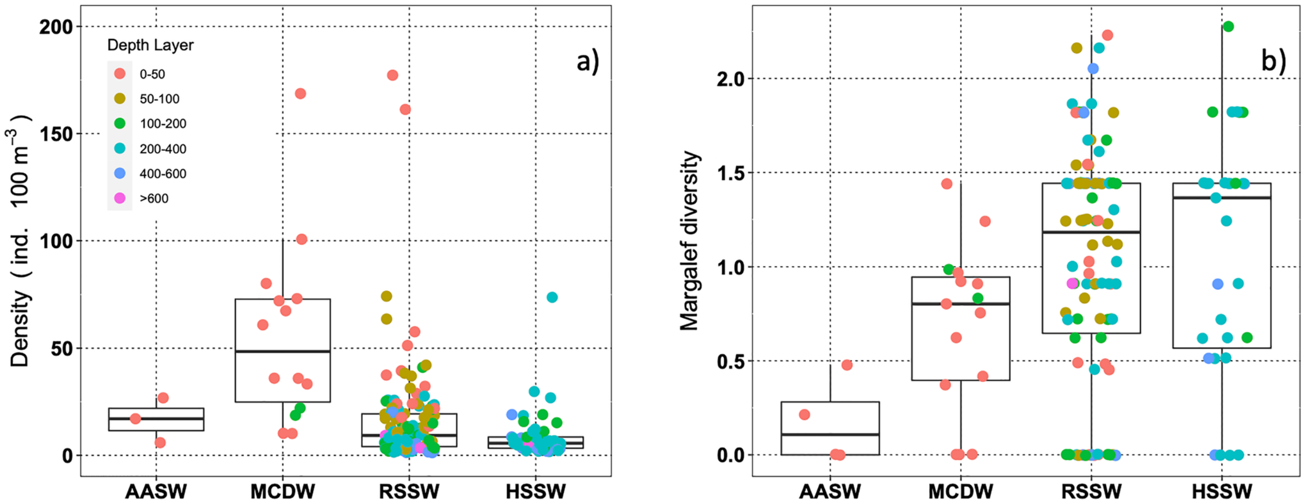

Fig. 5 Observed amphipod abundance (ind. 100 m^{-3}) within the different water masses (**a**) and the corresponding Margalef diversity index (**b**)

feed in the water column where *Calanoides acutus*, *Ctenocalanus vanus*, *Metridia gerlachei* copepodites, pelagic amphipods and young euphausiids were abundant inside zooplankton community (Guglielmo et al. 1998). In addition, two species of amphipods (*Hyperia macrocephala* and *Eusirus antarcticus*) and eggs with embryos of *P. antarcticum* were found in the platelet ice (Guglielmo et al. 2007).

In the present study a high biodiversity of pelagic amphipods off Terra Nova Bay, Ross Sea, was found. All the collected species were already cited as present in the pacific Sector of the Southern Ocean, particularly in the Ross Sea, except for *Cheirimedon femoratus*, *Orchomenyx macronyx* and *Debroyerella solidus*. All the species were also reported as found in the Atlantic sector, Weddell Sea, except *Hyperiopsis australis*, *Halice tenella*, *C. femoratus*, *O. macronyx*, *D. solidus* (De Broyer et al. 2007; Zeidler and De Broyer 2009).

Hyperiidae was the most abundant family (62% of relative abundance) with the dominant species being *Hyperiella dilatata*. Zeidler and De Broyer (2009) indicated this species to be cosmopolitan in the Southern Ocean, widely distributed in Atlantic, Indian and Pacific Sector (Stebbing 1888; Weigmann-Haass 1989; Jażdżewski et al. 1992; Dinofrio 1997; Vinogradov 1999). This species was reported in early years as the most abundant and frequent in Ross Sea and considered an important prey for many species of fish, as above mentioned (Barnard 1930; Foster et al. 1987; Hubold 1992; Guglielmo et al. 1998, 2011; La Mesa et al. 2004). The family Hyperiidae was represented by other two species in the present study, namely *Hyperia macrocephala* and *Hyperiella macronyx*. Both these two species show wide distribution in the Southern Ocean, having been found in the Atlantic, Indian and Pacific sectors, and their presence recorded in the Ross Sea over many decades (Barnard 1930; Hempel et al. 1983; Weigmann-Haass 1989; Jażdżewski et al. 1992; Browne et al. 2007).

The family Tryphosidae was the second most abundant family and was represented by six species, with *Pseudorchomene plebs* the most abundant. This species is also distributed widely in the Southern Ocean and has previously been recorded in Ross Sea (d'Udekem d'Acoz and Havermans 2012; De Broyer et al. 2007). The other five species in this family were encountered only occasionally, because they are not pelagic (De Broyer et al. 2007). *P. plebs* has been recorded in substantial numbers at the ice-water interface, where it probably feed on under-ice algae, unlike hyperiid species that live in free waters (Arndt and Swadling 2006). *P. plebs* is reported to be a facultative scavenger (Stockton 1982; Arndt and Swadling 2006), as some individuals taken from beneath the Ross Ice Shelf had copepod hard parts in the guts, while stomach contents of hatchlings indicated the presence of bacterial aggregations.

Comparing species richness in the different water masses suggests that the mixed waters on the Ross Sea Shelf (RSSW) encompass the main core of the community in Terra Nova Bay (18 of the 20 species observed), though there is important input from the offshore community that is associated with the MCDW. A probable role can be assigned to HSSW that could feed the deeper basin of Terra Nova Bay with adult or juvenile forms of ice-related species from the Drygalski area, so providing a deep path of remote connectivity, especially during melting.

Hyperiella dilatata was very abundant in the sampling region; some individuals in this species exhibit an interesting behaviour that guards against predation. In situ observations have shown specimens of *H. dilatata* carrying a gymnosome pteropod, *Clione limacina antarctica,* on their dorsal side, firmly holding it with their sixth and seventh

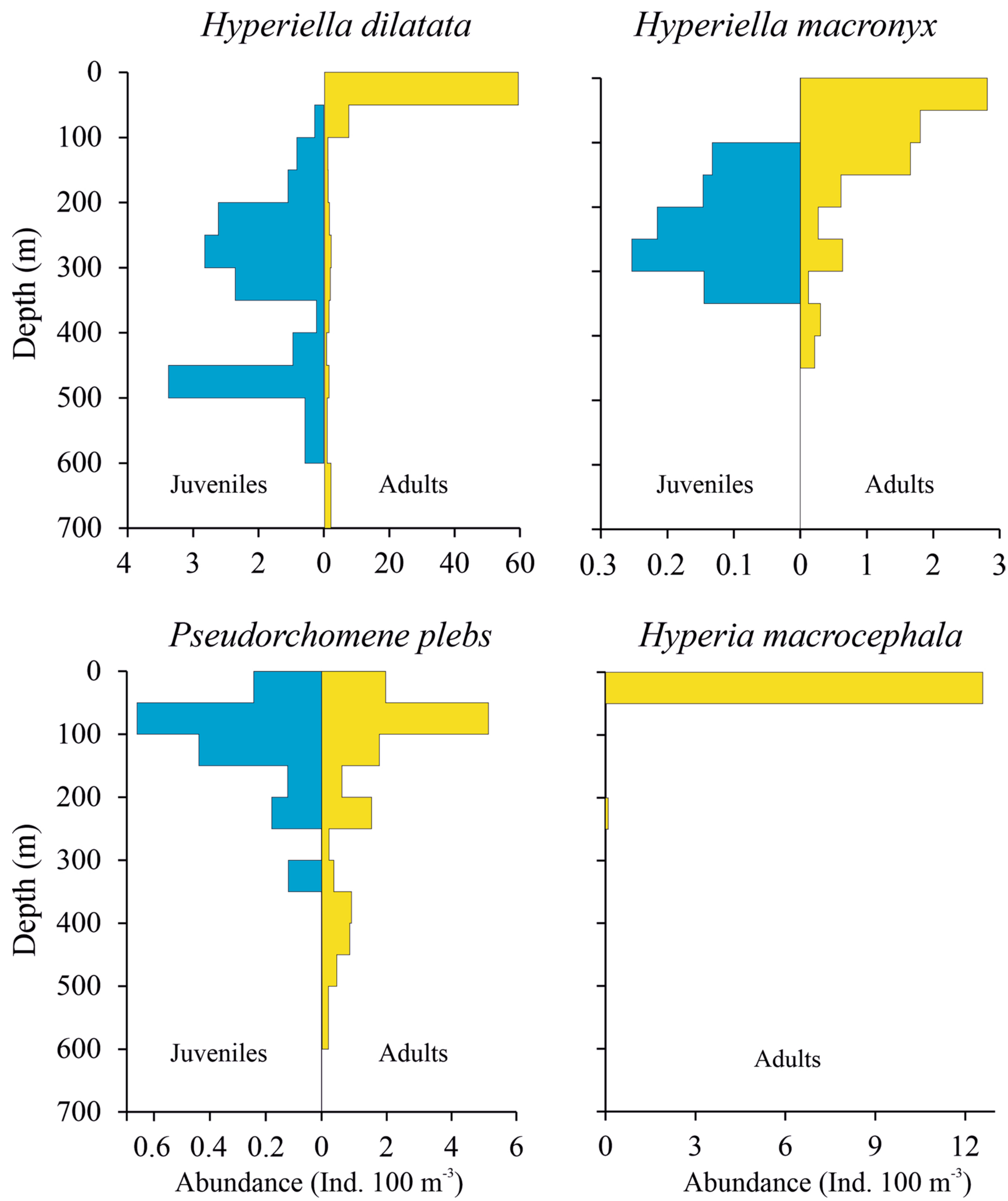

Fig. 6 Vertical profiles of **a** *Hyperiella dilatata*, **b** *Pseudorchomene plebs*, **c** *Hyperia macrocephala*, **d** *Hyperiella macronyx* mean weighed abundance (ind. 100 m^{-3}) in Terra Nova Bay. Profiles for adult and juvenile stages are shown. Note differences in scales on x-axis

pereopods (Havermans et al. 2018). In the under-ice environment around the Antarctic continent, *H. dilatata* is a regular component of zooplankton communities and is highly preyed upon by fish and seabirds (Foster 1987; Vacchi and La Mesa 1995; Pakhomov et al. 1999; Havermans et al. 2018). The amphipod incurs an energetic cost of carrying the pteropod but gains the benefit of chemical protection against predators (McClintock and Janssen 1990). *Clione limacina antarctica* produces an efficient predator-deterrent chemical called pteroenone, a β-hydroxy ketone that has been isolated, characterized and synthesized (Bryan et al. 1995; Asao et al. 2010). The defence mechanism is more suitable for female carrying eggs, because the effort of carrying a pteropod may result in protection for both the female and the offspring

Table 4 Multilevel pattern analysis: significant indicator species of the different groups of samples

	Species	IndVal	Specificity	Fidelity
Layer 0–100; > 600	*Hyperiella dilatata*	0.885 (*)	0.819	0.954
0–200	*Hyperiella macronyx*	0.554 (*)	0.868	0.353
50–200	*Pseudorchomene* sp.	0.610 (**)	0.765	0.486
> 600	*Halice tenella*	0.577 (*)	1.000	0.333
Water mass AASW	*Hyperiella macronyx*	0.499 (*)	0.997	0.250
AASW + MCDW	*Hyperiella dilatata*	0.930 (**)	0.865	1.000
	Hyperiella macronyx	0.665 (*)	0.840	0.526

(Layers throughout the water column and Water masses). Significance codes: (*)$p < 0.05$; (**)$p < 0.01$

(Havermans et al. 2018). In the present study many embryonated eggs, previously attached to female specimens were detected, especially in the 270–310 m layer at St. 17, along with ovigerous females, e.g. in the 400–500 m layer at St. 5. It has been reported that abducted pteropods could have been released by the amphipods during the sampling process (Havermans et al. 2018), in which could explain the absence of tandems in our samples.

The vertical distributions of the four dominant species in our study confirm patterns that have been observed previously for the Ross Sea (De Broyer et al. 2007; Zeidler and De Broyer 2009). H*yperiella dilatata* has been reported as occurring from 3700 m to the surface, although it seems to be most common in the shallower waters (0–300 m); for *P. plebs* the range is from the surface to 550 m; *H. macrocephala* is reported mainly in near-surface water; and *H. macronyx* from near the surface to 600 m depth. No evidence of diel vertical migration was detected with this study, and the sampling period was characterized by the constant presence of the sun. The centres of distribution for juvenile *H. dilatata* and *H. macronyx* were deeper than those observed for the adults. This might be a mechanism whereby food resources, in the form of particulate organic matter, are separated between adults and juveniles of similar species to reduce competition.

In conclusion, summer pelagic amphipods within Terra Nova Bay are represented by 17 species belonging to nine families. Only a few common species, among which just one (*H. dilatata*) is represented across the entire study area, particularly in surface waters and is related to AASW and MCDW water masses. Many studies conducted in recent years have confirmed that many areas of Antarctica are changing, even if ecosystems seem to respond differently to the stresses of climate change (Fraser et al. 2022; Swadling et al. 2023). A greater understanding of biodiversity and the roles of various species involved in Southern Ocean pelagic food webs is needed to predict and hypothesize about responses to future scenarios. Some important key species that are common to many Antarctic ecosystems and important in carbon cycling processes, have received very little attention, producing substantial gaps in our understanding of Antarctic ecosystem functioning. As Smith Jr et al. (2017) stated "Understanding the nature of the ecological changes that will occur in the Ross Sea in future years will be a major challenge for both oceanographers and polar ecologists".

Although our data refer to a study carried out 35 years ago we believe that, due to the scarcity of studies on pelagic amphipods, the data presented here highlight a need for further studies on the biodiversity and structure of the pelagic trophic web. These data also present a knowledge base against which to compare more recent studies to highlight any structural changes attributable to ongoing climate change in the Terra Nova Bay and Ross Sea ecosystems.

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Author contribution RM conceived experimental design, lab procedure, and wrote the ms; AB carried out statistical elaboration, water mass analysis, and wrote the ms; LG conceived the experimental design, wrote the ms; KS wrote the writing and done the language revision; AG and FV carried out the lab procedure; AG conceived the experimental design, supervised the lab procedure, wrote the ms. All authors read and approved the manuscript.

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Data availability The data presented in this study are available by Roberta Minutoli, rminutoli@unime.it.

Declarations

Conflict of interest There are not conflicts of interest.

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