

Biodiversity and functioning of mesozooplankton in a changing Ross Sea

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ABSTRACT

Literature on Ross Sea zooplankton is limited, although it is the most productive system and has the highest biomass of phytoplankton in the Southern Ocean. Energy transfer within the food web and response of continental shelf food web to climate change depend on the knowledge of the density and distribution of zooplankton. We evaluated its density, composition, spatial distribution and their potential relations with environmental factors and specific water mass presence. Particular attention was given to copepods. Mesozooplankton samples were collected between 14 January and February 11, 2017 from 14 stations in the western Ross Sea and Terra Nova Bay, while other micronekton samplings were completed at 6 stations. Results highlighted three pools of stations: one inside Terra Nova Bay with the highest densities, one on the platform with lower mean density, and the third represented by a N-S transept at 175°E with the lowest mean density. This partitioning of the region fit with the grouping of stations according to a ternary plot based on the different percentages of water masses in each station and reflected the similarity of zooplankton. The presence of specific water masses and their contribution in the upper 200 m influences zooplankton biodiversity and density. A phylogenetic tree of the zooplankton was constructed to analyse the distance among the observed taxa. The area located near the coast exhibited the highest degree of phylogenetic overdispersion. In coastal waters, typical copepod species constituted the main part of the neritic zooplankton of Terra Nova Bay and Ross Sea. *Oithona similis* was the most abundant species both in coastal and offshore sectors, followed by pteropods, polychaetes and euphausiids.

1. Introduction

Zooplankton are a fundamental link in Southern Ocean food webs (Schaafsma et al., 2018), connecting primary producers with higher trophic levels and modulating the fate of biogenic carbon (Mayzaud and Pakhomov, 2014). There are three major food web pathways through zooplankton (Atkinson et al., 2012): (i) the Antarctic krill (*Euphausia superba* Dana) pathway from large diatoms to large predators such as fish, squids, penguins, seals and whales, often regarded as the classical

Southern Ocean food web, (ii) the fish-copepod pathway linking the complex microbial food web with higher trophic levels, and (iii) the salp pathway linking the small phytoplankton with top predators. Among them, the krill pathway is the best known, providing a highly nutritious food source for top predators (Hecq and Guglielmo, 1992; Atkinson et al., 2002, 2012; Farber-Lorda et al., 2009; Meyer et al., 2010; Farber-Lorda and Ceccaldi, 2020). In the Southern Ocean pelagic (*E. superba*) and coastal (*Euphausia crystallorophias* Holt & Tattersall) krill play an important role in mediating the vertical flux of carbon

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(Guglielmo et al., 2009; Cavan et al., 2019; Yang et al., 2021). The second pathway (copepods-fish) contains more trophic linkages, thus being potentially less energy efficient (Granata et al., 2009; Swadling et al., 2023). The salp pathway is poorly understood, although salps are present in the diets of over 200 predators (Henschke et al., 2016).

Several mesozooplankton taxa, as well as copepods, may play critical role within food webs of the continental shelf (Pinkerton and Bradford-Grieve, 2014). In the Ross Sea, pteropods are likely to represent a fourth energy pathway integrating both sea-ice and pelagic habitats (Granata et al., 2009; Bednarsek et al., 2012; Minutoli et al., 2016; Cau et al., 2021). Feeding activity under and near sea ice with the subsequent release of faecal material affects the rate of particulate carbon export from the surface to the deep ocean (Liszka et al., 2019). The vertical migration and swarming behaviour of krill can give rise to space-time heterogeneity in particle fluxes. It is reasonable to hypothesize that similar phenomena may occur in other zooplankton. The potential decline in Southern Ocean pteropods raises many uncertainties, including whether *Salpa thompsoni* Foxton will occupy the Antarctic krill trophic niche and how this will alter the flow of energy within pelagic waters (Constable et al., 2014; Steinberg et al., 2015; Cavan et al., 2019). In the West Antarctic Peninsula, there is evidence that sea ice influences the relative importance of *S. thompsoni* and *E. superba* (Loeb et al., 1997; Atkinson et al., 2004). Recent studies have also presented evidence for co-dominance of salps and Antarctic krill; however, temperature, primary productivity and large-scale climatic events have also been identified as environmental controls (Lee et al., 2010; Steinberg et al., 2015; Fraser et al., 2023).

In comparison with West Antarctica, information on many regions, including the Ross Sea, are more limited. On an annual basis, the Ross Sea is the most productive ecosystem and with the highest biomass of phytoplankton in the Southern Ocean (Smith et al., 2014). It also has substantial standing stocks of higher trophic levels (e.g., 38% of the world Adelie penguins, 25% of the world Emperor penguins and 42% of the global petrel stocks; Ballard et al., 2011). However, there are few studies on density and distribution of mesozooplankton in this area, despite that the suggestion that zooplankton is the most important factor in regulating food web dynamics and ecological interactions in the Ross Sea (Ainley et al., 2010, 2015). Energy transfer within the food web and response of continental shelf food web to climate change depend on knowledge of the density and distribution of meso- and macrozooplankton. Studies on Ross Sea mesozooplankton have mainly been conducted near international stations, such as McMurdo Sound (e.g. Elliot et al., 2009; Stevens et al., 2015; Smith et al., 2017) and Terra Nova Bay (e.g. Guglielmo et al., 2015a; Granata et al., 2022; Grillo et al., 2022; Minutoli et al., 2023).

The main aims of this study were to evaluate the density, composition and distribution of mesozooplankton, and their relationships with environmental factors and water masses. Particular attention was given to copepods in terms of density, species composition and spatial distribution. The quantification of mesozooplankton stocks and their distribution allow the available resources for fish, birds and marine mammal populations.

2. Material and methods

2.1. Sampling procedure

Sampling was conducted as part of the 2016–2017 Italian Antarctic Expedition on the *R/V Italica*, as part of P-ROSE project (Plankton biodiversity and functioning of the ROSS Sea Ecosystems in a changing Southern Ocean) between 14 January and February 11, 2017. Mesozooplankton were collected from 14 stations in Terra Nova Bay and Ross Sea (Fig. 1).

Vertical mesozooplankton samples were obtained from 0 to 200 m by a WP2 standard net (57 cm mouth diameter, 200 μ m mesh size) equipped with a General Oceanics flowmeter. Repeated samplings were

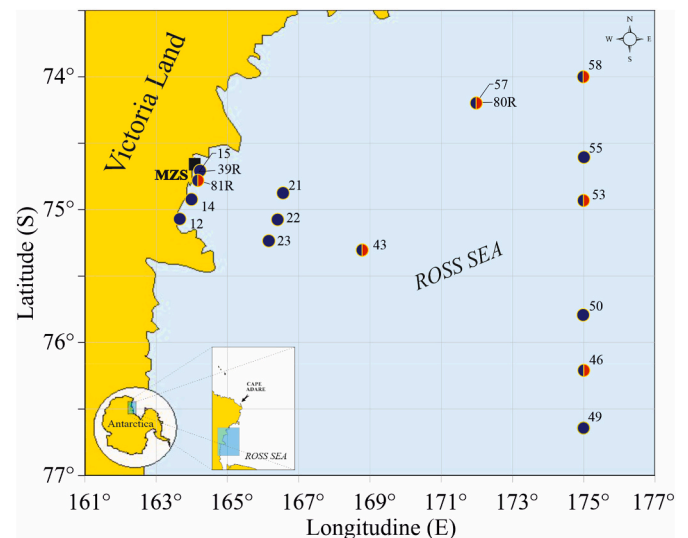


Fig. 1. Map showing where mesozooplankton were sampled during 2016–2017 in the western Ross Sea (at the stations coloured in red, micronekton samples were also collected).

performed at St. 15 (St. 39R and 81R) and 57 (St. 80R) for a total of 17 samples and 878.4 m³ of total filtered water. On board, all the zooplankton samples were preserved in a 4% buffered formaldehyde-seawater solution (Table 1).

In addition, samples were collected at 6 stations (St. 43, 46, 53, 57, 58, 81R) for micronekton (Fig. 1). Sampling in St. 57 was duplicated (St. 80R). Oblique catches using a Bongo 90 (1 mm mesh size) equipped with a General Oceanics flowmeter for each mouth were completed.

Table 1
Station data for WP2 zooplankton samples.

Station	Date	Local Time	Latitude (S)	Longitude (E)	Bottom depth (m)
12	January 14, 2017	00:13	75°04.2018'	163°39.7584'	867
14	January 14, 2017	03:07	74°55.3590'	163°59.6436'	342
15	January 14, 2017	07:20	75°43.0206'	164°12.2358'	498
21	January 15, 2017	14:14	74°52.4934'	166°33.6870'	886
22	January 15, 2017	18:18	75°04.4826'	166°24.5370'	855
23	January 15, 2017	23:45	75°14.0796'	166°09.7890'	852
39R	January 23, 2017	11:48	74°42.7698'	164°12.8010'	497
43	January 26, 2017	02:35	75°18.9300'	168°54.1488'	351
46	January 26, 2017	16:27	76°11.9046'	174°59.3142'	568
49	January 27, 2017	04:47	76°38.5707'	174°59.6586'	425
50	January 27, 2017	13:04	75°47.5608'	174°59.0334'	403
53	January 29, 2017	13:41	74°56.5296'	174°59.9520'	326
55	January 30, 2017	02:05	74°36.2902'	175°00.3588'	439
57	January 30, 2017	09:41	74°11.8282'	171°59.5350'	410
58	January 30, 2017	20:15	73°59.9913'	175°01.1472'	472
80R	February 10, 2017	21:43	74°11.9616'	172°00.4314'	406
81R	February 11, 2017	14:25	74°42.6334'	164°13.2498'	490

Maximum sampling depth was between 12 and 80 m, with a filtration time between 10 and 16 min and a towing speed of about 1.5 kts. The filtered water volume ranged between 345 and 1062 m³. 14 samples were taken from the two Bongo mouths, of which 7 were immediately frozen at -20 °C. The other 7 were preserved in a 5% buffered formaldehyde-seawater solution.

Along with the zooplankton sampling, environmental parameters were recorded by a SBE911 CTD, equipped with sensors for: conductivity (mS), temperature (°C), depth (m), fluorescence (V), and dissolved oxygen (ml/l).

2.2. Laboratory analysis

Taxonomic identification and counts of WP2 mesozooplankton were performed using a Wild M10 dissecting microscope and a Leitz M20 light microscope. After macrozooplankton sorting, three sub-samples (depending on the total density) were made by a Folsom splitter (Motoda, 1959) and, if necessary, by Stempel pipettes. All the specimens of each taxon were counted and identified at higher taxonomic levels, while diagnosis at the species level was undertaken for copepods (at least on 300–400 specimens), euphausiids, fish larvae, gastropod and peropod molluscs, ostracods, and polychaetes. Mesozooplankton density was calculated by dividing the total abundance by the filtered water volume and expressed both as individuals m⁻³ or individuals m⁻².

From each Bongo micronekton sample, large animals between 1 and 10 cm were removed and counted. All specimens were identified at higher taxonomic levels using a Leitz M20 light microscope, while diagnosis at the species level for amphipods, euphausiids, fish larvae, and peropod molluscs was undertaken according to Mauchline and Fisher (1969), Rampal (1975), Guglielmo et al. (1997, 2015b), Zeidler and De Broyer (2009). Micronekton density was expressed as individuals m⁻³.

2.3. Statistical analysis

Temperature and salinity data were processed with Ocean Data View (ODV version 5.5.2) software (Schlitzer, 2001) to map datapoints on the θ -S diagram and assign them to a specific water mass. Since the plankton samples were integrated from 0 to 200 m, to correctly intertwine the information on vertical structure of water column and plankton we estimated which water masses were sampled at each station. For this, vertical profiles (T, S, and the derived neutral density γ^n) were examined to identify the depth of the "floor" ($\gamma^n = 28$) and the "roof" ($\gamma^n = 28.24$) of the modified Circumpolar Deep Water (mCDW) and obtain the relative percentage of the three water masses (i.e., the thickness compared to 200 m of the Antarctic Surface Water (AASW), mCDW, Ross Sea Surface Water (RSSW), respectively). Each station was mapped onto the ternary diagram based on the estimated water mass content, so that stations with similar structure from 0 to 200 m are close to each other.

To evaluate the similarity of plankton among stations, cluster analysis (method: Ward) has been applied to the Kulczynski distance matrix between sites. Density data were transformed in fourth root and normalized. The distances were calculated by summing species density minima in each of the two stations and dividing this value by each site's total density. One minus the average of these two values was the distance between the two sites. The Kulczynski measure has been selected due to its robust monotonic relationship with ecological distance and is often used to detect underlying gradients (Faith et al., 1987). R packages 'vegan' (Oksanen et al., 2020) and 'dendextend' (Galili, 2015) were used.

Three habitat indicators (temperature at 10 m, chlorophyll at the Deep Chlorophyll Maximum DCM, depth of DCM) were selected to characterize each site and to test their ability in explaining the density and diversity differences of the plankton. Significant differences between and within groups were examined using R version 4.0.3 (ANOVA

and Kruskal-Wallis non-parametric tests on medians in case of non-homogeneity of variances, coupled with *post-hoc* Dunn test).

The NCBI Taxonomy Browser (<http://www.ncbi.nlm.nih.gov>, accessed on December 2023) has been used to build the species tree, by adopting some necessary refinement on the nomenclature. The tree has been converted to Newick format and imported in R for processing. Pairwise distances between the pairs of tips were calculated using the branch lengths of the tree and the mean nearest taxon distance (MNTD) for taxa was extracted. Following the approach of Webb et al. (2008) and Kembel (2009), NTI (nearest taxon index) was then calculated. It quantifies the number of standard deviations that the observed MNTD is from the mean of the null distribution (999 randomizations by shuffling the species names on the tree). For a single community, NTI greater than +2 indicates coexisting taxa are more closely related than expected by chance (phylogenetic clustering). NTI less than -2 indicates coexisting taxa are more distantly related than expected by chance (phylogenetic overdispersion). R packages 'ape', 'picante' and 'iCAMP' were used.

3. Results

3.1. Oceanographic conditions

The large scatter in the TS diagram related to neutral density anomaly less than 28 kg m⁻³, shows how varied the surface and sub-surface interactions were, which is related to cooling (winds and thermal flows) or freshening due to the melting of sea ice. The formation of new sea ice leads to an increase in salinity in the subsurface water. Conversely, neutral density anomaly greater than 28.27 characterize deeper and subsurface shelf waters which are formed or modified within the Ross Sea (Fig. 2).

The region between these two limits that identify Circumpolar Deep Water (CDW, 28 < γ^n < 28.27) constitutes the bulk of the Ross Sea waters. When CDW intrudes on the continental shelf, it interacts with the shelf water and is modified. The isopycnal mixing gradually forms modified Circumpolar Deep Water (mCDW) which is characterized by a local maximum of temperature. This maximum, which is found at ca. 300 m at the shelf break, can rise to 50–70 m in the Ross Sea.

In the TS diagram corresponding to $\gamma^n > 28.27$, at least two end

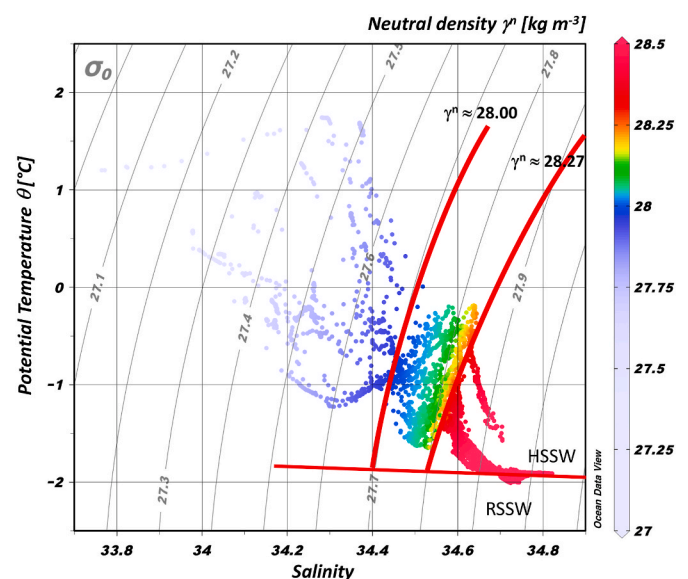


Fig. 2. T-S diagram, with the simultaneous indication of potential temperature, salinity and neutral density. The red curves mark the neutral density anomalies of 28 kg m⁻³ and 28.27 kg m⁻³ that characterize the "roof" and the "floor" of the Circumpolar Deep Water (CDW) and modified CDW (MCDW). High Salinity Shelf Water (HSSW) exhibits an absolute salinity maxima.

points can be distinguished: RSBW (Ross Sea Bottom Water, minimum temperature, winter water formed inside the Ross Sea) and HSSW (High Salinity Shelf Water, maximum salinity). These end points identify two important processes occurring that trigger the formation of “new” bottom water leaving the Ross Sea which is responsible for maintaining the conveyor belt and the characteristics of the abyssal waters in the Pacific Ocean.

Ice-Shelf Water (ISW) didn't exhibit its typical characteristics (temperature below the surface freezing point). ISW is generated under the Ross Ice Shelf and follows pathways that were not sampled by the P-ROSE cruise. However, temperatures slightly below the freezing point can be defined as Ross Sea Shelf Water or RSSW (Fig. 2), a water mass formed mainly in winter.

The movement from the local temperature maximum (of CDW) and towards the RSSW shows the processes that occur during the formation of new AABW (e.g. below 300 m at St. 57 and 80R). The HSSW is characterized by a maximum salinity and temperature (near the surface freezing point) and reflects the process of sea ice formation with consequent brine rejection, indicating that the most important mixing occurs along or very near the isopycnal surfaces. Conversely, a sharp departure from this path forming crossing the isopycnal contours identifies strong diapycnal mixing as the formation of new AABW when the shelf water reaches the continental shelf break.

3.2. Zooplankton density, composition and spatial distribution

Zooplankton density varied greatly over the continental shelf (Table 2).

The total mean density was 291,0 ind. m^{-3} (S.D. \pm 205.0). Density varied greatly, going from 80.8 (at St. 53) to 799.4 ind. m^{-3} (at St. 81R). The spatial distribution of total zooplankton (ind. m^{-2}) varied widely as well (Fig. 3). St. 57 was unusual in that had a very low total density (4.72 ind. m^{-3}).

Copepods were the dominant group, with a mean density of 207.0 ind. m^{-3} (S.D. \pm 153.9) and a mean incidence of 71.1% (46.9%–88.1% at St. 15 and St. 57). The highest copepod density was found at St. 81R and the lowest at St. 53 (Fig. 4).

Pelagic molluscs were represented by the gastropod *Cryocapulus subcompressus* (Pelseneer, 1903) and by the pteropods *Clione limacina* (Phipps, 1774) and *Limacina rangii* (A. d'Orbigny, 1835), in addition to veligers of the latter species. *C. subcompressus* was collected only at three stations, with density and incidence in each station less than 1 ind. m^{-3} and 1%. Pteropods (adults plus larvae) were the second most dense taxa after copepods. They were collected at all stations, except St. 53, and represented about 9% of the zooplankton, with a mean density of 26.3 ind. m^{-3} (S.D. \pm 29.5), ranging from 0.8% to 28.5% at St. 12 and St.50, respectively. The spatial distribution for the two pteropod species plus *L. rangii* veligers was also variable (Fig. 5) with the greatest abundance found at St. 15 and the lowest at St. 12.

Ovigerous sacs of the pteropod *L. rangii* were the third most commonly found group, being collected at 64.7% of the stations, representing 7% of the zooplankton, with a mean density of 20.1 ind. m^{-3} (S.D. \pm 32.9). Their incidence ranged between 0.9 at St. 46 to 25.7% at St. 22. *C. limacina*, *L. rangii*, *L. rangii* veligers and *L. rangii* ovigerous sacs varied substantially (Fig. 6). *C. limacina* was most abundant at St. 23, *L. rangii* at St. 50, *L. rangii* veligers at St. 15 and *L. rangii* ovigerous sacs at St. 22.

Polychaetes, represented by the species *Pelagobia longicirrata* Greeff, were collected at all stations except St. 57, with a mean abundance (adults plus larvae) of 19.9 ind. m^{-3} (S.D. \pm 20.6). They represented 6.8% of mesozooplankton with incidence ranging from 1.1 to 11% at St. 50 and St. 53, respectively. The distribution of *P. longicirrata* (adults plus trochophores) was greatest near shore (Fig. 7). The largest abundance occurred at St. 81R and the lowest at St. 50.

Euphausiids represented on average 2.8% of zooplankton (from 0.64 to 10.9% at St. 53 and St. 49), with a mean abundance of 8.13 ind. m^{-3}

(S.D. \pm 6.79). *Euphausia crystallorophias* was found at all stations except St. 57 (adults plus furcilia and calyptopis stages; Fig. 8).

All other taxa had an incidence of less than 1% each and overall less than 3.3%; they were ostracods (represented only by the species *Alacia hettacra* (Müller, 1906), chaetognaths, siphonophores, echinoderm larvae, appendicularians, amphipods, medusozoans, cirriped larvae, fish larvae (mainly the species *Pleuragramma antarcticum* Boulenger, 1902), and gastropods.

3.3. Copepod abundance, composition and spatial distribution

Copepods included 14 species, including 4 unidentified species of previously known genera and 5 unidentified species of other genera (Table 3). It was largely composed of Oithonidae (34.9%), Clausocalanidae (20.4%), Metridinidae (15.6%), Oncaeiidae (14%), Calanidae (10.8%) and Aetideidae (2.9%), which represented 98.6% of the total. Other identified families, accounting for the remaining 1.4%, were Acartidae, Spinocalanidae, Stephidae, Euchaetidae, Lucicutiidae and Lubbockiidae.

Oithona similis was the most abundant species (mean 71.3 ind. m^{-3} , S.D. \pm 6.79, corresponding to 34.7% of the copepod community), followed by *Ctenocalanus citer* (36.44 ind. m^{-3} , S.D. \pm 27.96, 17.7%), *Oncaea curvata* (28.65 ind. m^{-3} , S.D. \pm 35.29, 14%), *Metridia gerlachei* (21.88 ind. m^{-3} , S.D. \pm 28.77, 10.7%), *Calanoides acutus* (20.75 ind. m^{-3} , S.D. \pm 21.94, 10.1%), *Ctenocalanus vanus* (4.45 ind. m^{-3} , S.D. \pm 4.5, 2.2%). All other species had an incidence of less than 1% each and overall accounted for about 1.8%. The unidentified *Metridia* sp. showed the highest mean abundance (10.1 ind. m^{-3} , S.D. \pm 13.1, 4.9%), followed by *Pseudochirella* sp. (5.86 ind. m^{-3} , S.D. \pm 8.23, 2.9%). The other unidentified species represented each one less than 1%. Some species were noted as different developmental stages, mainly *C. acutus*, *Metridia* sp., *Microcalanus pygmaeus* and *Pseudochirella* sp. The spatial distribution of the most abundant copepod species varied widely (Fig. 9).

O. similis was found at all stations, showing the lowest abundance at St. 57 (1.04 ind. m^{-3}) and the greatest at St. 22 (228.2 ind. m^{-3}). *C. citer* was collected at all stations except St. 57, with abundances ranging from 3.65 to 90 ind. m^{-3} at St. 21 and 39R. *O. curvata* was present at all stations except for 80R and ranged from 0.93 to 141.0 ind. m^{-3} at St. 43 and 81R. *M. gerlachei* and *C. acutus* were found at all stations except St. 57. The former's abundance ranged from 0.52 to 109.5 ind. m^{-3} (at St. 21 and 14), while the latter's abundance varied from 2.61 to 85.9 ind. m^{-3} (at St. 21 and 80R). *C. vanus* was collected at 11 stations, with its abundance ranging from 0.98 to 15 ind. m^{-3} at St. 80R and 39R.

3.4. Linking oceanographic processes and mesozooplankton

Three groups of stations were found during our study (Fig. 10). The first group (Type A) includes the stations in which RSSW is weakly present or absent (RSSW < 20%) while both AASW and mCDW are present. These are the offshore stations (except St. 46) in the N–S transect and stations 57 and 80R. A second group (Type C) includes the stations dominated by RSSW (> 60%), which lie near the coast or in the Drygalski basin where RSSW is forming and will then occur in the deep part of the water column or exit towards the north. The third group (Type B) includes the stations where all three water masses are present with non-zero percentages, located in a geographically intermediate position between the Type A and C stations.

The stations have been further grouped according to the type of local processes to which the surface water (AASW) is or has just been subjected by distinguishing the “melting ice” (circle markers) from the “warming” (triangle markers), creating two different habitats. St. 21, 22 and 23 appear to be subject to ice melting (T at 10 m \leq 0 °C) while at St. 12, 15, 39R and 81R seasonal warming had progressed (T at 10 m > 0).

The membership of each site, based on zooplankton similarity (Fig. 11), agrees with the partitioning found with the ternary plot, except St. 57 which is mapped separately. Compositional similarity is

Table 2
Density, as individuals m⁻³, of taxa.

Taxa	Sampling stations																
	12	14	15	21	22	23	039R	43	46	49	50	53	55	57	58	80R	081R
Amphipods	0.00	3.80	1.67	2.08	0.91	0.36	1.00	1.87	0.00	1.00	0.95	2.54	1.80	0.00	1.20	0.00	0.00
Appendicularians	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.47	0.00	2.00	0.95	0.00	0.00	0.00	0.00	11.71	3.81
Chaetognaths	0.08	0.50	0.00	0.00	0.00	1.54	0.00	18.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.40	2.40
Cirriped larvae	0.00	0.00	0.83	0.52	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	1.95	0.00
Copepods	85.16	382.79	176.00	100.63	319.11	342.97	302.00	194.45	259.02	147.00	134.26	67.56	74.27	4.16	97.00	179.50	625.71
Copepod nauplii	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.00	10.80	0.00	8.40	0.00	0.00	0.00	0.00	4.80	3.00
Echinoderm larvae	0.00	5.60	0.00	0.00	0.02	0.00	3.00	0.00	0.00	0.00	0.00	0.00	1.90	0.00	0.00	1.95	8.57
Euphausiids																	
<i>Euphausia crystallorophias</i> Holt and Tattersall, 1906	1.80	10.30	4.29	9.39	10.91	2.66	14.00	3.72	20.95	20.80	10.83	1.78	1.90	0.00	2.00	4.88	14.29
Calyptopis stage	0.01	0.00	0.00	0.00	0.00	0.42	0.00	0.00	0.00	1.20	0.60	0.00	0.00	0.00	0.00	0.00	0.00
Furcilia stage	0.00	0.00	1.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fish larvae																	
<i>Pleuragramma antarcticum</i> Boulenger, 1902	0.01	0.90	0.83	0.52	0.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Others	0.00	0.67	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Hydrozoans	0.00	1.90	0.42	0.00	0.02	1.54	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.93	3.81
Mollusc gastropods																	
<i>Cryocapulus subcompressus</i> (Pelseneer, 1903)	0.00	0.00	0.42	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95
Mollusc pteropods																	
<i>Clione limacina</i> (Phipps, 1774)	0.13	0.00	6.24	0.00	1.82	7.69	0.00	0.93	0.00	3.00	1.90	0.00	0.00	0.00	0.00	0.00	1.90
<i>Limacina rangii</i> (d'Orbigny, 1835)	0.00	5.39	0.00	3.65	0.91	6.92	0.00	1.86	5.71	4.70	46.20	0.00	1.80	0.48	1.80	0.00	0.95
Veligers (<i>L. rangii</i>)	0.60	45.08	96.28	17.93	8.33	4.67	18.00	16.21	2.81	12.50	15.08	0.00	0.95	0.08	7.00	76.10	21.24
Ovigerous sacs (<i>L. rangii</i>)	2.50	25.30	56.17	19.82	122.73	61.54	10.00	6.05	2.86	3.00	0.00	0.00	0.00	0.00	0.00	0.00	32.38
Ostracods																	
<i>Alacia hettacra</i> (Müller, 1906)	0.60	13.10	0.49	0.00	0.91	2.31	0.00	0.93	0.60	0.00	0.00	0.00	0.95	0.00	1.80	0.00	6.67
Polychaetes																	
<i>Pelagobia longicirrata</i> Greeff, 1879	6.13	48.68	27.26	6.28	4.31	22.62	22.50	12.03	1.08	3.10	1.55	8.89	5.68	0.00	10.80	17.40	61.36
Trochophores	0.00	2.80	2.08	1.04	6.36	25.38	6.00	3.26	5.71	4.00	0.95	0.00	0.00	0.00	1.00	7.80	12.38
Siphonophores	0.19	0.00	0.00	0.66	0.20	1.21	0.00	18.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.93	0.00

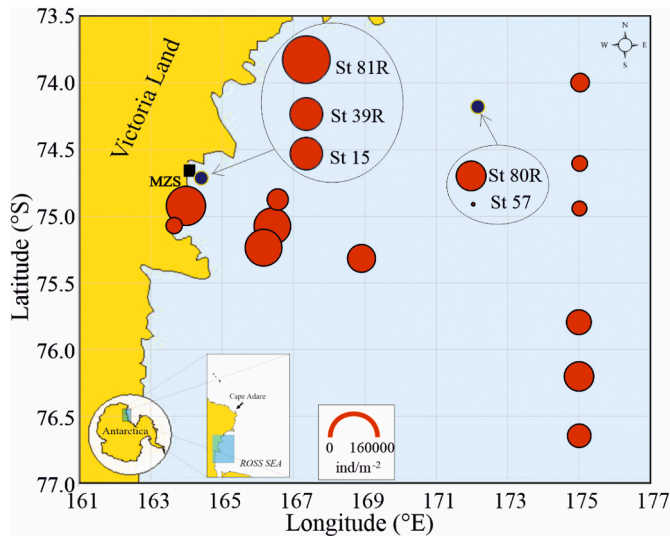


Fig. 3. Distribution of integrated zooplankton.

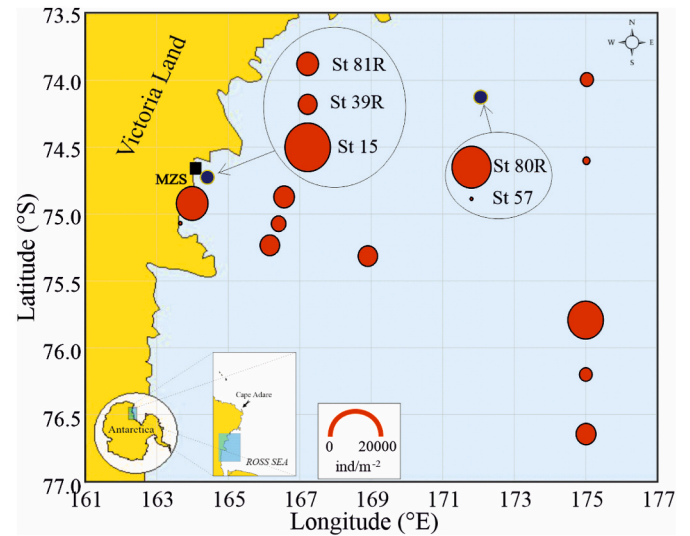


Fig. 5. Distribution of pteropod molluscs (*C. limacina* plus *L. rangii* adults and veligers).

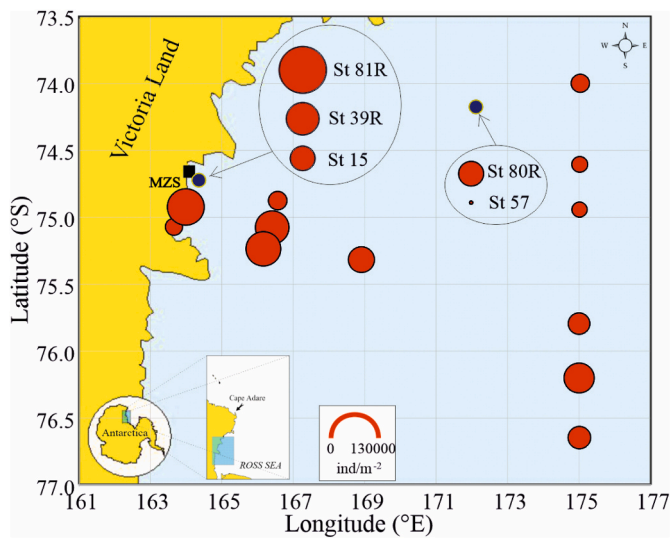


Fig. 4. Distribution of copepods.

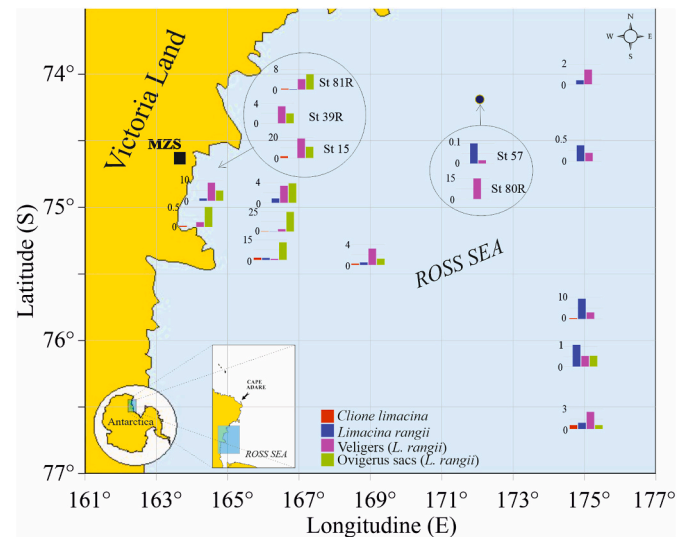


Fig. 6. Abundance of pteropod molluscs *C. limacina*, *L. rangii*, *L. rangii* veligers, and *L. rangii* ovigerous sacs in thousands of ind. m⁻².

greater between intermediate (Type B) and coastal (Type C) sites than between intermediate and offshore (Type A) sites. Overall, *O. similis* is the most abundant taxon with a 100% occurrence and a dominance ranging from 20% to 31% in Type A and Type C sites respectively. The partitioning based on the dispersion index identifies the "core" species. Among the copepods, *O. similis*, *M. gerlachei* and *O. curvata* play this role throughout the whole region, while *C. citer* is a core species only in Type C sites. The polychaete *P. longicirrata* and the pteropod *L. rangii* are core species of Type C and Type A sites respectively. Unexpectedly, sites 57 and 80R, geographically coinciding, with the same vertical structure (see ternary plot) but sampled approximately 10 days apart, were assigned to different clusters. In particular, St. 57, that is very "poor" in abundance (4.6 ind. m⁻³) and number of taxa (4), is separated from the others while 80R (221 ind. m⁻³, 12 taxa) belongs to Type B sites.

3.5. Exploring underlying relations with environmental data

The depth of DCM did not significantly vary depending on "melting"/"warming" character of the site, whereas it was significantly different according to the group of stations, being minimal (20 m) in Type C sites (close to the coast). Conversely, temperature at 10 m depth

did not differ across the group of sites, while it was significantly lower in melting than in warming habitats (K–W, Dunn test, $p_{adj} = 0.001$).

Copepod abundance decreased with the increase of DCM depth (Spearman rank correlation, $R^2 = 0.30$, $p = 0.02$, $n = 17$) while it is not significantly correlated with the concentration of DCM Chlorophyll *a*. Likewise, copepod abundance increased with the increase of T at 10 m (Spearman rank correlation, $R^2 = 0.51$, $p = 0.03$, $n = 17$). No significant correlations were found between richness (number of copepod species, number of zooplankton taxa) and habitat descriptors, whereas the Margalef diversity index was significantly different among the sites (K–W test, $p = 0.05$) and higher, though not significantly, in melted than in warming sites (Fig. 12).

Common constrained ordination methods (CCA, dbRDA) have not identified the underlying factors explaining the variability of composition. To develop a more robust interpretation of the habitat gradients linked to preference and fitness of the different taxa, we compared the phylogenetic trees realized in each site (Fig. 13).

The Nearest Taxon Index (NTI) in each site is based on the mean phylogenetic distance among the nearest taxa. The mean NTI taken

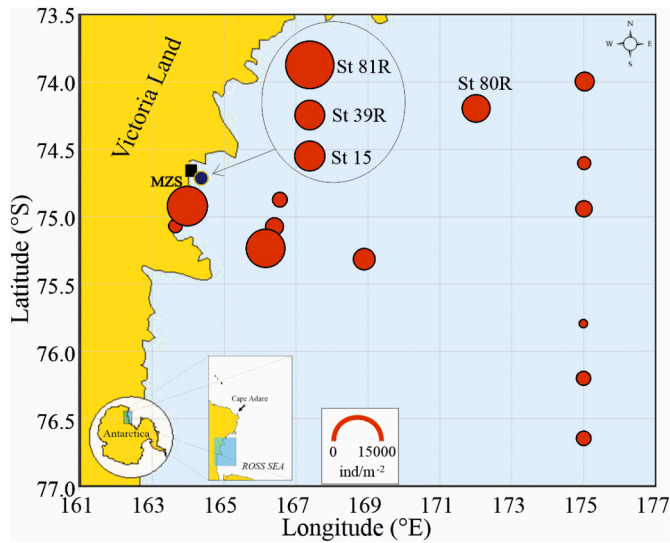


Fig. 7. Abundance of the polychaete *P. longicirrata* (adults plus trochophores).

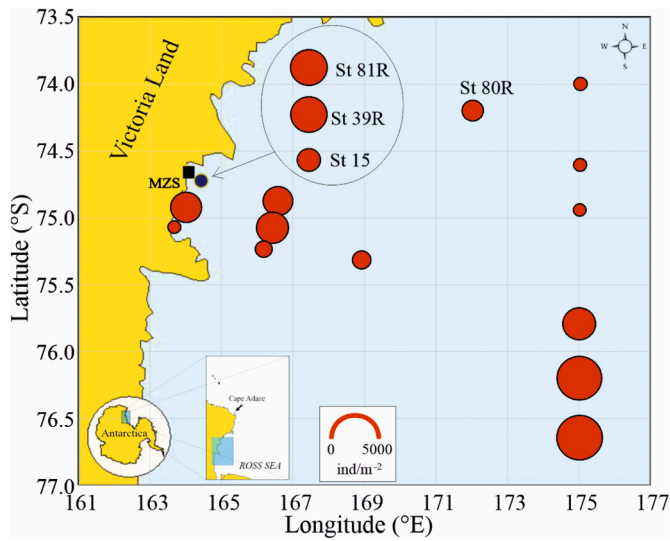


Fig. 8. Abundance of *E. crystallorophias* (adults plus calyptopis and furcilia stages).

across all communities (-1.34) is negative, although not significantly different from zero, meaning that in the region there is an overall weak overdispersion. Looking at the sites (Fig. 14), the nearest taxon distance is in the range ± 1 (e.g., between one standard deviation on 999 permutations made on the phylogenetic tree); nevertheless, the Type C sites close to the coast where a shallow DCM is established exhibit more overdispersion ($NTI < -2$).

3.6. Micronekton

Micronekton abundance were similar throughout the area (Table 4). St. 53, however, showed a very low total density of $0.0016 \text{ ind. m}^{-3}$, as only one amphipod was collected. The overall abundance was $102.0 \text{ ind. m}^{-3}$ (S.D. ± 2.68).

Amphipods dominated the micronekton. They occurred at all stations and represented 35% of the total, with a mean abundance of 35.8 ind. m^{-3} (S.D. ± 28.6), ranging from 4.8% in St. 43–73.1% in St. 80R. Fish larvae were the second most abundant taxa, with a mean abundance of 29.4 ind. m^{-3} (S.D. ± 29.3) and a mean incidence of 28.8%, from 0.8% to 79.5% in St. 58 and St. 43. *Pleuragramma antarcticum* was

Table 3
Copepod abundance as individuals m^{-3} .

Copepod species	Sampling stations																	
	12	14	15	21	22	23	39R	43	46	49	50	53	55	57	58	80R	81R	
<i>Acartia</i> sp.	0.00	0.00	0.00	0.52	1.82	0.00	1.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95
<i>Calanoides acutus</i>	30.63	43.05	11.65	2.61	15.46	39.24	14.00	11.63	13.33	11.00	15.23	3.56	3.8	0.00	7.00	85.85	44.76	0.00
<i>Calanoides</i> sp.	0.00	2.81	0.00	1.56	0.91	6.15	0.00	0.47	3.81	0.00	0.00	0.00	0.00	0.00	0.00	1.95	0.00	0.00
<i>Calanus propinquus</i>	0.00	0.00	0.00	0.00	0.91	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Calanus</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.00
<i>Clausocalanus brevipes</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00
<i>Ctenocalanus citer</i>	10.42	87.98	34.53	3.65	27.27	46.15	90.00	33.95	41.9	52.00	24.76	13.33	8.57	0.00	27.00	38.05	80.00	0.00
<i>Ctenocalanus vanus</i>	0.00	0.00	5.41	0.00	0.00	3.08	15.00	6.05	4.76	9.00	9.52	7.11	5.71	0.00	9.00	0.98	0.00	0.00
<i>Lubbockia</i> sp.	0.00	0.00	0.00	0.00	0.00	0.77	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lucicutia</i> sp.	0.00	0.00	0.00	0.00	0.91	0.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Metridia gerlachei</i>	6.74	109.5	52.42	0.52	10.00	30.77	13.00	7.44	2.86	47.00	1.9	10.67	2.86	0.00	20.00	5.85	50.48	0.00
<i>Metridia</i> sp.	1.23	4.68	12.48	3.13	4.55	29.22	2.00	10.24	3.81	8.00	3.8	5.33	2.86	0.00	10.00	18.53	52.38	0.00
<i>Microcalanus pygmaeus</i>	0.00	3.74	0.00	0.00	0.00	5.39	0.00	0.00	0.00	0.00	3.81	0.00	1.9	0.00	1.00	0.00	0.00	0.00
<i>Microcalanus</i> sp.	0.00	0.94	0.00	0.00	0.00	0.00	0.00	0.47	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Oithona frigida</i>	0.00	0.00	0.00	1.04	0.00	3.85	0.00	0.00	0.95	1.00	0.00	0.00	0.95	0.00	0.00	0.00	0.00	0.00
<i>Oithona similis</i>	4.9	84.23	53.26	70.92	228.18	83.85	122.00	120.93	111.42	11.00	56.19	7.11	7.62	1.04	5.00	23.41	220.96	0.00
<i>Oncaea curvata</i>	30.63	22.46	2.5	11.47	16.36	66.92	35.00	0.93	65.71	5.00	18.1	16.89	1.9	2.96	16.00	0.00	140.95	0.00
<i>Paraeuchaeta exigua</i>	0.61	1.87	0.00	0.00	0.91	0.77	0.00	0.00	0.00	1.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00
<i>Paralibidocera antarctica</i>	0.00	6.55	0.00	4.17	4.55	1.10	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.86	0.00
<i>Pseudochirella</i> sp.	0.00	12.17	3.33	1.04	7.28	23.84	9.00	1.87	0.00	1.00	0.95	1.78	3.81	0.00	2.00	3.9	27.61	0.00
<i>Spinocalanus</i> sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.52	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.00
<i>Stephos longipes</i>	0.00	0.00	0.42	0.00	0.00	1.10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.76	0.00
<i>Triconia conifera</i>	0.00	0.00	0.00	0.00	0.00	0.77	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.00	0.00	0.00	0.00	0.00

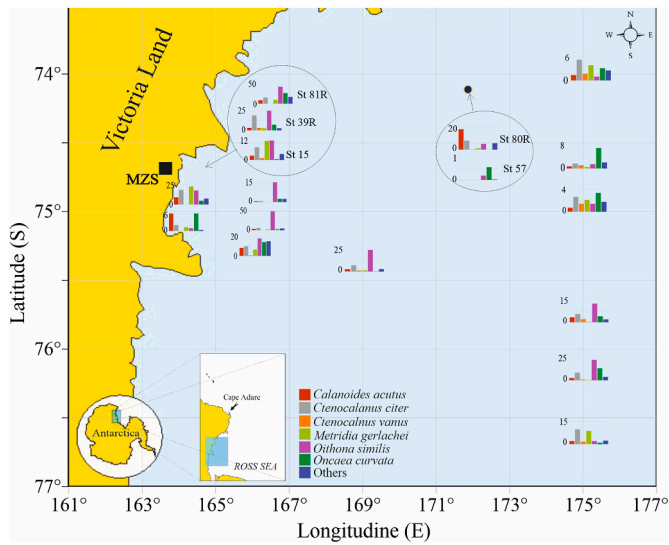


Fig. 9. Abundance of the six most abundant copepod species (*C. acutus*, *C. citer*, *C. vanus*, *M. gerlachei*, *O. similis*, *O. curvata*) as thousands ind. m⁻².

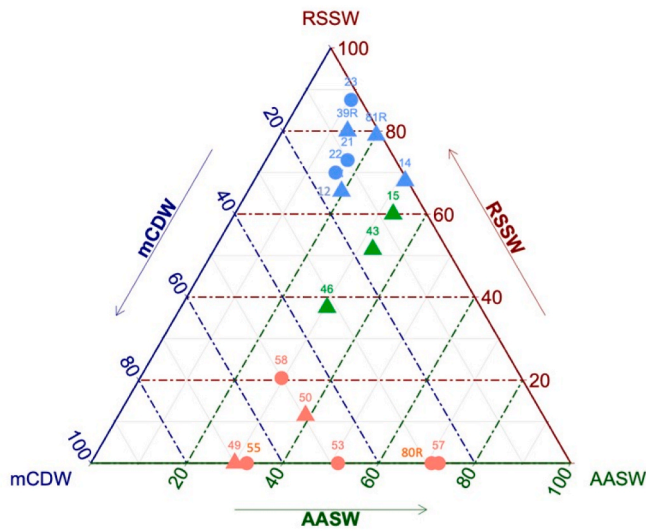


Fig. 10. Ternary plot of water masses. Each station is mapped according to the relative percentage of the surface layer occupied by each of the three water masses (AASW, mCDW, RSSW). Sites can be partitioned in three groups: Type A (red symbols), Type B (green symbols) and Type C (light blue symbols). Shape of the symbols identifies the local surface processes of “melting ice” (circles) and “warming” (triangles).

collected at all stations except St. 53 and represented the 99.3% of the total fish larvae. Pteropod molluscs, collected at 5 stations, represented the third most abundant group within the micronekton (13.6%), with a mean abundance of 13.9 ind. m⁻³ (S.D. ± 14.3). They were represented by two species: *Clione limacina*, found at five stations (ranging from 0.4% in St. 43 to 15.9% at St. 46), and *Limacina rangii*, found at four stations (ranging from 1.7% in St. 58 to 26.9% at St. 81R). Also sampled were euphausiids (9.7%) represented by *E. crystallorophias* and *Thysanoessa macrura*, collected at four stations, with a mean value of 9.92 ind. m⁻³ (S.D. ± 19.16); chaetognaths (8.8%), collected at three stations, that showed a mean abundance of 9 ind. m⁻³ (S.D. ± 4.28); siphonophores (2.9%), collected only at St. 57, with an abundance of 2.91 ind. m⁻³. Appendicularians and decapod larvae were also found in 1.1% of the study area.

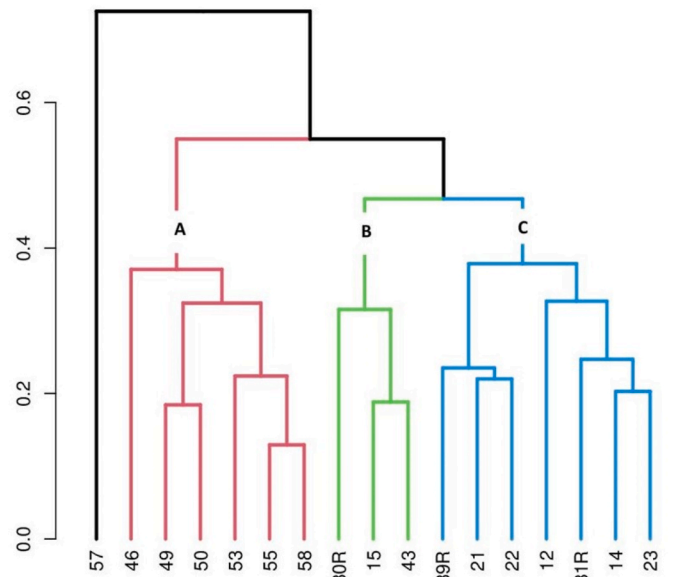


Fig. 11. Compositional similarity of zooplankton (Type A in red; Type B in green; Type C in light blue).

4. Discussion

Zooplankton are an essential component of food webs and biogeochemical cycles, processing particulate matter generated by phytoplankton into energy available to higher trophic levels. Zooplankton metabolize and transfer organic carbon within the water column, playing an important role in the biological pump (Turner, 2015; Minutoli et al., 2016, 2017; Steinberg and Landry, 2017). The Ross Sea is the most productive region with the greatest phytoplankton biomass (Mangoni et al., 2017; Bolinesi et al., 2020); data on mesozooplankton density and distribution in this sector are still scarce. The density varies by two orders of magnitude with respect to the Victoria Land coast (Smith et al., 2006, 2014). Selected sub-regions show similar variability, suggesting that other processes, either oceanographic or biological, influence zooplankton on smaller scales (Smith et al., 2017).

The mean mesozooplankton abundance at Terra Nova Bay and the Ross Sea Shelf is comparable to other areas in the Southern Ocean. It is lower than that found by Pane et al. (2004) that used similar methods at a single station in Terra Nova Bay, and about 12 times higher than Smith et al. (2017). Stevens et al. (2015) found that mesozooplankton abundance at two stations on the shelf were similar to those found in other Antarctic coastal areas. Data on mesozooplankton abundance and distribution are still too scarce and methodologically and seasonally inconsistent.

Our results on zooplankton abundance distribution in the upper 200 m of the water column highlighted a coastal-offshore gradient with three different areas: (a) inside Terra Nova Bay with the highest abundance (mean of 439.6 ind. m⁻³) and with higher abundances in the north, (b) a shelf area with lower mean abundances (mean abundance of 350.2 ind. m⁻³), and (c) an area characterized by a N–S transect at 175°E with the lowest mean abundance (171.5 ind. m⁻³) that decreased in the north.

The three pools of stations grouped by zooplankton abundance were correlated with water mass composition (Ternary plot) which in turn overlaps with the clustering based on compositional similarity of zooplankton. Hence, the presence of specific water masses and their percentage contribution into the surface layer influence the mesozooplankton diversity and density (Smith et al., 2017). The compositional similarity of stations in the shelf area is greater than the coastal ones, with respect to the offshore ones. St. 57, where the sampling was replicated ten days later (St. 80R), was anomalous. The stations geographically coincide and showed the same oceanographic structure

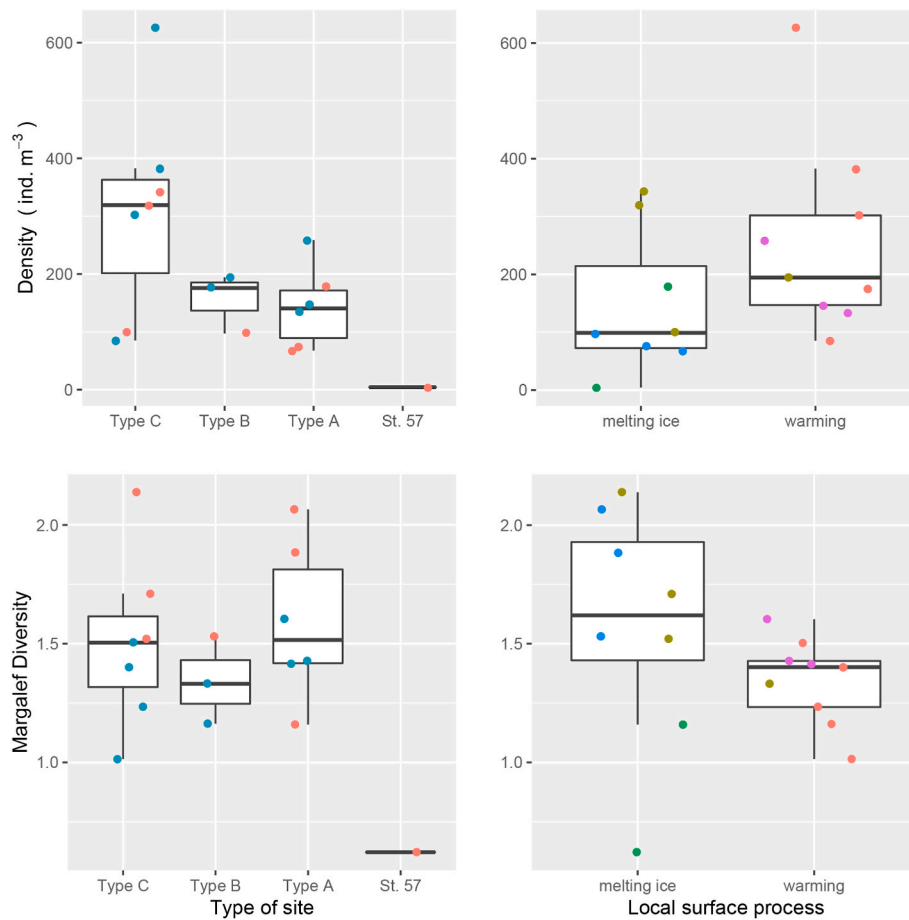


Fig. 12. Variability of copepod abundance (upper panels) and Margalef diversity index (lower panels) across the identified types of sites (left) and according to the local surface processes (right).

(same colour in the Ternary plot), but St. 57 was clustered, as compositional similarity of zooplankton, separately from all the other stations because of the very low density and biodiversity value. St. 80R belongs to Type B intermediate site cluster. This is because the intermediate stations are in a relatively shallower transition region, and subject to transient mixing processes (between the intruding mCDW and the exiting RSSW) induced by the ongoing melting and warming.

The identified copepod species are known to be representative and abundant in Antarctic waters (Bradford, 1971) and are typical of Antarctic coastal waters (Schnackiel et al., 2004; Bonello et al., 2020; Grillo et al., 2022). A similar composition was found during summer under sea-ice at Terra Nova Bay and McMurdo (Guglielmo et al., 2007; Elliot et al., 2009). Our study shows that copepods near Terra Nova Bay consist of few small-sized species dominating the zooplankton, such as *Oithona similis*, *Oncaea curvata* and *Ctenocalanus vanus*, whose presence suggests their high degree of adaptability to the environment and trophic conditions (Mangoni et al., 2017; Bolinesi et al., 2020), even if their role in the zooplankton may be underestimated (Chahsavari-Archad and Razouls, 1982). *Metridia gerlachei* and *Calanoides acutus* were also well represented. They are known to be abundant in Terra Nova Bay and in neighbouring areas (Carli et al., 1990, 2000, 2002; Smith et al., 2017).

The patchy spatial distribution of the pteropods *Limacina rangii* and *Clione limacina* is in agreement with other observations that have detected spatial changes in pteropods during summer within coastal and shelf waters (Ross et al., 2008; Bednarek et al., 2012). Pteropods account for up to 93% of the total macrozooplankton in many Antarctic systems and their distribution is closely related to oceanographic frontal zones (Hosie et al., 2000). At Terra Nova Bay, inter-annual summer peaks of abundance and biomass have shown that zooplankton in

shallow waters (<50 m) are dominated by *L. rangii* (Hopkins, 1987; Pane et al., 2004; Guglielmo et al., 1998, 2007) and Minutoli et al. (2017) identified a trend of increasing pteropod abundances from pelagic to coastal stations and from north to south in the same region. *Limacina rangii* and *Clione limacina* are key species in the carbon cycle of polar seas (Cau et al., 2021).

The abundant presence of veligers and ovigerous sacs of *L. rangii* found at many of the stations indicates that Terra Nova Bay provides a suitable environment for reproduction. *L. rangii* can reproduce rapidly under optimal conditions in the Ross Sea through its efficient filtering system, and this species, as many other zooplanktonic herbivores, can take advantage of the large phytoplankton biomass inside Terra Nova Bay and the neighbouring continental shelf areas (Mangoni et al., 2017; Bolinesi et al., 2020).

Despite their low abundance, holoplanktonic polychaetes may play an important role in the pelagic food web and organic matter remineralization (Hopkins, 1985; Fernández-Álamo and Añorve, 2005; Uttal and Buck, 1996). *Pelagobia loncirrata*, the only species present, represents a basic food item, rich in calories, for several fishes and large predatory copepods (Fernández-Álamo and Thuesen, 1999; Guglielmo et al., 2011).

We found few larval stages (calyptopis and furcilia) and many adults of the euphausiid *Euphausia crystallorophias* that together with *Pleuromma antarcticum* fish larvae are known to be important components of western Ross Sea zooplankton and ichthyoplankton (Guglielmo et al., 1998, 2009; Granata et al., 2000, 2002, 2009; Sala et al., 2002; Vacchi et al., 2004). Antarctic krill requires deep water to complete its life cycle (Knox, 2006) and hence is absent from shallow continental shelf areas such as the Ross Sea (Smith et al., 2017). Bongo samples confirm the

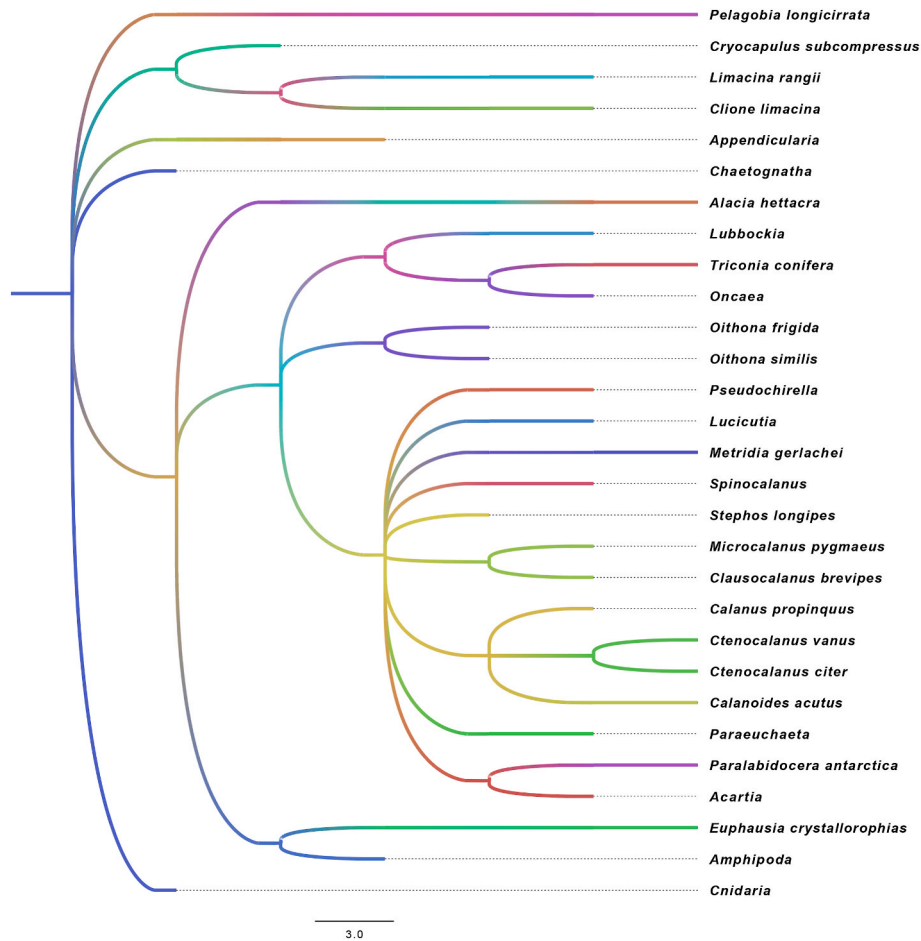


Fig. 13. Phylogenetic tree of the collected mesozooplankton.

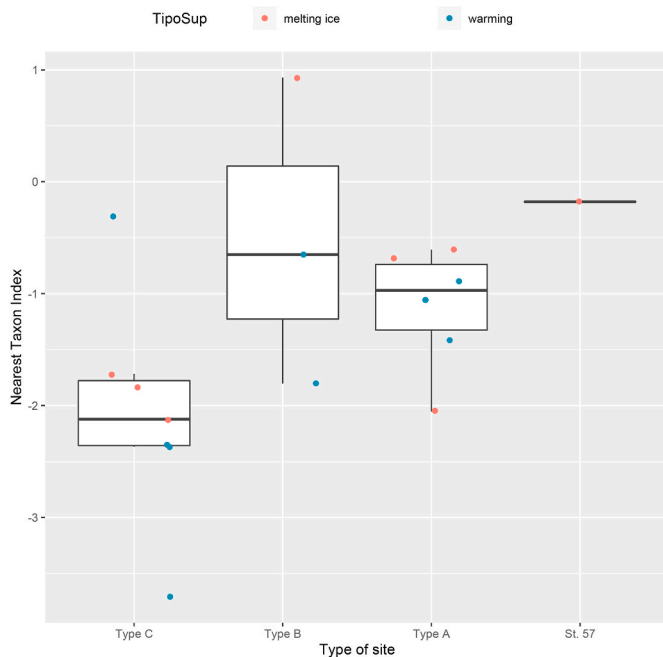


Fig. 14. Variability the nearest taxon index.

presence of *E. crystallorophias* and *P. antarcticum* larvae in coastal stations, with the largest abundance at St. 43 (Table 4), as well as amphipods, copepods and pteropods, likely distributed within the Sound Scattering Level (SSL). The echogram acquired at St. 81R (Fig. 15) shows the presence of *E. crystallorophias* and a reduction in the thickness of the surface SSL. At the same time, the collected biological samples at this station show a lower presence of *P. antarcticum* larvae and a greater abundance of *E. crystallorophias* adults (Tables 2 and 4). In particular, the area closest to the coast showed a strong SSL in the upper water column and a weaker one at ca. 100 m (Barra et al., 2023). The thickness of the superficial layer tends to decrease further from the coast (see echograms for St. 14 and 23; Fig. 15). The echograms show the presence of *E. crystallorophias* schools (Fontana et al., 2022; Barra et al., 2023).

St. 57 was characterized by lower backscattering values, whereas St. 80R had higher backscattering values.

No relationship between mesozooplankton abundance and sampling date was found, suggesting that the spatial differences were the result of smaller scale processes rather than temporal development, as argued by Smith et al. (2017). The sampling was completed under a wide range of hydrographic and biological conditions and since zooplankton show variable growth rates (smaller copepods grow faster than larger forms; Pinkerton and Bradford-Grieve, 2014), this could result in a substantial variability in space and time, similar to phytoplankton (Smith et al., 2006, 2011a, 2011b; Mangoni et al., 2017; Bolinesi et al., 2020). At the two replicated stations (St. 15 and 57), an increase in total zooplankton abundance was observed in time, which may be linked to the higher primary production, food availability and growth.

No relationship between mesozooplankton distribution and temperature was found. Temperature was similar at 10 m among the three

Table 4
Abundance as individuals m^{-3} of micronekton.

	Sampling stations						
	43	46	53	57	58	80R	081R
Maximum sampled depth (m)	50	60	12	78	55	38	121
Amphipods							
<i>Vibilia</i> spp.	0.00	6	0.00	0.00	0.00	0.00	0.00
Others	4.82	16	0.0016	18.12	69.74	73.07	26.75
Appendicularians	0.00	0.00	0.00	0.00	0.00	2.19	0.00
Chaetognaths	0.00	0.00	0.00	18.79	21.84	0.00	13.38
Decapod larvae	0.62	0.00	0.00	0.00	0.00	0.00	3.93
Euphausiids							
<i>Euphausia crystallorophias</i> Holt and Tattersall, 1906	12.43	27	0.00	0.00	0.00	0.00	0.00
<i>Thysanoessa macrura</i> G.O. Sars, 1883	0.62	15.5	0.00	0.00	0.84	0.00	3.15
Fish larvae							
<i>Pleurogramma antarcticum</i> (Boulenger, 1902)	80.12	6.5	0.00	45.63	0.84	19.23	22.83
Others	0.00	0.5	0.00	0.00	0.00	0.00	0.78
Mollusc pteropods							
<i>Clione limacina</i> (Phipps, 1774)	0.37	16.00	0.00	0.00	5.04	10.98	6.29
<i>Limacina rangii</i> (d'Orbigny, 1835)	1.76	13.00	0.00	0.00	1.68	0.00	28.34
Siphonophores	0.00	0.00	0.00	17.45	0.00	0.00	0.00

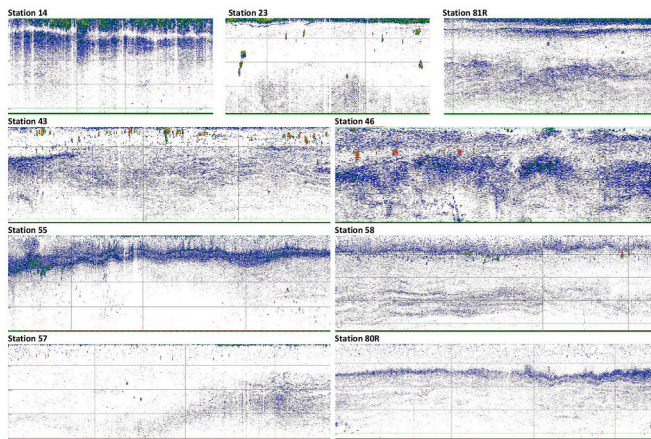


Fig. 15. Echograms of sound scattering layers in the Ross Sea.

groups of stations, although a difference in temperature was found between melting and warming stations. This may lead to the increase in copepod abundance with the increase of temperature at 10 m. No correlation occurred between copepod abundance and Chlorophyll *a* concentration at DCM. This may result from the omnivorous feeding of the main copepods (Castellani et al., 2005; Balazy et al., 2021), like the most abundant and distributed species (*O. similis*).

The phylogenetic tree provided a powerful tool for comparing the structure of zooplankton. In particular, zooplankton at stations near the coast (Type C) exhibited the highest degree of overdispersion (of phylogenetic distance). This is related to the higher richness in taxa and to the higher total abundance detected in coastal stations relative to offshore ones. In coastal area the variety of the observed taxa is greater than expected by chance. This means that underlying processes (e.g., oceanographic, seasonal climatic, edaphic) are structuring the local zooplankton. This could be related to phytoplankton providing a habitat to maintain a phylogenetically diverse zooplankton.

It is difficult to compare our study with others due to the spatial extent of our sampling being larger and different methodologies. Furthermore, our study only included summer conditions, while others included spring. However, the similarities and differences between the results of different field studies are worth noting. Several studies in the Ross Sea have shown that zooplankton faecal pellets can play an important role in carbon flux at depth at selected time points (Dunbar et al., 1998; Manno et al., 2010; Smith et al., 2011b) and their role does

not appear to be markedly different from other Antarctic systems (Ducklow et al., 2015; Manno et al., 2015). The coupling between phytoplankton and zooplankton in the Ross Sea and the seasonal role of faecal pellets remains to be fully resolved. Further observations and experiments are needed to better evaluate the role of mesozooplankton in food webs and biogeochemical cycles in the Ross Sea.

5. Conclusions

Climate change and ocean warming can have a marked impact on the structure and functioning of zooplankton (Fraser et al., 2023; Swadling et al., 2023). The complexity of the pelagic food web, from picoplankton to micronekton, has led the researchers to review field sampling strategies. Recently it has been recognized that there is a need for an integrated approach using different zooplankton technologies to better understand how matter and energy flow within the food web and to clarify the response of zooplankton to climate change (e.g. Everett et al., 2017; Ratnarajah et al., 2023). This study, conducted during austral summer in Terra Nova Bay and western Ross Sea, using different techniques and zooplankton nets, provides such an integrated approach.

CRedit authorship contribution statement

Roberta Minutoli: Writing – original draft, Formal analysis, Conceptualization. **Angelo Bonanno:** Writing – review & editing. **Letterio Guglielmo:** Writing – review & editing, Writing – original draft, Conceptualization. **Alessandro Bergamasco:** Writing – original draft, Methodology, Formal analysis, Conceptualization. **Marco Grillo:** Formal analysis. **Stefano Schiaparelli:** Writing – review & editing. **Marco Barra:** Formal analysis. **Andrea Bergamasco:** Methodology, Formal analysis. **Alessia Remirens:** Formal analysis. **Simona Genovese:** Writing – original draft, Formal analysis, Conceptualization. **Antonina Granata:** Writing – original draft, Formal analysis, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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References

- Ainley, D.G., Ballard, G., Blight, L.K., Ackley, S., Emslie, S.D., Lescroel, A., Olmastro, S., Townsend, S.E., Tynan, C.T., Wilson, P., Woehler, E., 2010. Impacts of cetaceans on the structure of Southern Ocean food webs. *Mar. Mamm. Sci.* 26, 482–489.
- Ainley, D.G., Ballard, G., Jones, R.M., Jongsomjit, D., Pierce, S.D., Smith, W.O. Jr, Veloz, S., 2015. Trophic cascades in the western Ross Sea, Antarctica: revisited. *Mar. Ecol. Prog. Ser.* 534, 1–16.
- Atkinson, A., Meyer, B., Bathman, U., Stubing, D., Hagen, W., Schmidt, K., 2002. Feeding and energy budget of Antarctic krill *Euphausia superba* at the onset of winter-II. Juveniles and adults. *Limnol. Oceanogr.* 47, 953–966.
- Atkinson, A., Siegel, V., Pakhomov, E., Rothery, P., 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103.
- Atkinson, A., Ward, P., Hunt, B.P.V., Pakhomov, E.A., Hsieh, G.W., 2012. An overview of Southern Ocean zooplankton data; Abundance, biomass, feeding and functional relationships. *CCAMLR Sci.* 19, 171–218.
- Balazy, K., Boehnke, R., Trudnowska, E., Soreide, J.E., Blachowiak-Samolyk, K., 2021. Phenology of *Oithona similis* demonstrates that ecological flexibility may be a winning trait in the warming Arctic. *Sci. Rep.* 11, 18599 <https://doi.org/10.1038/s41598-021-98068-8>.
- Ballard, G., Jongsomjit, D., Veloz, S.D., Ainley, D.G., 2011. Coexistence of mesopredators in an intact polar ocean ecosystem: the basis for defining a Ross Sea marine protected area. *Biol. Conserv.* <https://doi.org/10.1016/j.biocon.2011.11.017>.
- Barra, M., Guglielmo, L., Bonanno, A., Mangoni, O., Rivaro, P., Rumolo, P., Falco, P., Basilone, G., Fontana, I., Ferreri, R., Giacalone, G., Aronica, S., Minutoli, R., Memmola, F., Granata, A., Genovese, S., 2023. Vertical structure characterization of acoustically detected zooplankton aggregation: a case study from the Ross Sea. *Front. Mar. Sci.* 10, 1304493 <https://doi.org/10.3389/fmars.2023.1304493>.
- Bednarek, N., Mozina, J., Vogt, M., O'Brien, C., Tarling, G.A., 2012. The global distribution of pteropods and their contribution to carbonate and carbon biomass in the modern ocean. *Earth Syst. Sci. Data* 4, 167–186.
- Bolinesi, F., Saggiomo, M., Ardini, F., Castagno, P., Cordone, A., Fusco, G., Rivaro, P., Saggiomo, V., Mangoni, O., 2020. Spatial-related community structure and dynamics in phytoplankton of the Ross Sea, Antarctica. *Front. Mar. Sci.* 7, 574963 <https://doi.org/10.3389/fmars.2020.574963>.
- Bonello, G., Grillo, M., Cecchetto, M., Giallain, M., Granata, A., Guglielmo, L., Pane, L., Schiaparelli, S., 2020. Distributional records of Ross Sea (Antarctica) planktic copepoda from bibliographic data and samples curated at the Italian national antarctic museum (mna): checklist of species collected in the Ross Sea Sector from 1987 to 1995. *ZooKeys* 969, 1–22.
- Bradford, J.M., 1971. The fauna of the Ross Sea. Part 8. Pelagic copepoda. *N. Z. Oceanogr. Inst. Mem.* 59, 9–32.
- Carli, A., Mariottini, G.L., Pane, L., 1990. Contribution to the study of copepods collected in Terra Nova Bay (Ross Sea). In: National Scientific Commission for Antarctica (Ed) Oceanographic Campaign 1987–88, Data Report Part II. National Scientific Commission for Antarctica, Genova, pp. 129–167.
- Carli, A., Pane, L., Stocchino, C., 2000. Planktonic copepods in Terra Nova Bay (Ross Sea): distribution and relationship with environmental factors. In: Faranda, F.M., Guglielmo, L., Ianora, A. (Eds.), *Ross Sea Ecology*. Springer, Berlin, pp. 309–321.
- Carli, A., Feletti, M., Pane, L., 2002. Zooplankton biomass and copepod abundance of Terra Nova Bay, Ross Sea Antarctic Campaign 1994/1995. *Terra Antarct. Rep.* B1, 5–55.
- Castellani, C., Irigoien, X., Harris, R.P., Lampitt, R.S., 2005. Feeding and egg production of *Oithona similis* in the North Atlantic. *Mar. Ecol. Prog. Ser.* 288, 173–182.
- Cau, A., Ennas, C., Moccia, D., Mangoni, O., Bolinesi, F., Saggiomo, M., Granata, A., Guglielmo, L., Swadling, K.M., Pusceddu, A., 2021. Particulate organic matter release below melting sea ice (Terra Nova Bay, Ross Sea, Antarctica): possible relationships with zooplankton. *J. Mar. Syst.* <https://doi.org/10.1016/j.jmarsys.2021.103510>.
- Cavan, E.L., Belcher, A., Atkinson, A., Hill, S.L., Kawaguchi, S., McCormack, S., Meyer, B., Nicol, S., Ratnarajah, L., Schmidt, K., Steinberg, D.K., Tarling, G.A., Boyd, P.W., 2019. The importance of Antarctic krill in biogeochemical cycles. *Nat. Commun.* 10, 4742. <https://doi.org/10.1038/s41467-019-12668-7>.
- Chahsavari-Archad, V., Razouls, C., 1982. Les copepodes pélagiques au sud-Est des Iles du Cap Vert. II. Aspects quantitatifs. *Vie Milieu* 32, 89–99.
- Constable, A.J., Melbourne-Thomas, J., Corney, S.P., Arrigo, K., Barbraud, C., Barnes, D., Bindoff, N., Boyd, P., Brandt, A., Costa, D.P., Davidson, A., Ducklow, H., Emmerson, L., Fukuchi, M., Gutt, J., Hindell, M.A., Hofmann, E.E., Hsieh, G., Iida, T., Jacob, S., Johnston, N.M., Kawaguchi, S., Koubbi, P., Lea, M.-A., Makhado, A., Massom, R., Meiners, K., Meredith, M., Murphy, E., Nicol, S., Richardson, K., Riddle, M.J., Rintoul, S.R., Smith, Jr W., Southwell, C., Stark, J.S., Sumner, M., Swadling, K.M., Takahashi, K., Trathan, P., Welsford, D., Weimerskirch, H., Westwood, K., Wienecke, B., Wolf-Gladrow, D., Wright, S., Xavier, J.C., Ziegler, P., 2014. Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Global Change Biol.* 20, 3004–3025.
- Ducklow, H.W., Wilson, S.E., Post, A.F., Stammerjohn, S.E., Erickson, M., Lee, S., Lowry, K.E., Sherrell, R.M., Yager, P.L., 2015. Particle flux on the continental shelf in the Amundsen Sea Polynya and Western Antarctic Peninsula. *Elementa*. <https://doi.org/10.12952/elementa.000046>.
- Dunbar, R.B., Leventer, A.R., Mucciarone, D.A., 1998. Water column sediment fluxes in the Ross Sea, Antarctica: atmospheric and sea ice forcing. *J. Geophys. Res.* 103, 10741–10760.
- Elliot, D.T., Tang, K.W., Shields, A.R., 2009. Mesozooplankton beneath the summer sea ice in McMurdo Sound, Antarctica: abundance, species composition, and DMSP content. *Polar Biol.* 32, 113–123.
- Everett, J.D., Baird, M.E., Buchanan, P., Bulman, C., Davies, C., Downie, R., et al., 2017. Modeling what we sample and sampling what we model: challenges for zooplankton model assessment. *Front. Mar. Sci.* 4, 77. <https://doi.org/10.3389/fmars.2017.00077>.
- Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69, 57–68.
- Farber-Lorda, J., Ceccaldi, H.J., 2020. Relationships of morphometrics, total carotenoids, and total lipids with activity and sexual and spatial features in *Euphausia superba*. *Sci. Rep.* 10, 1317. <https://doi.org/10.1038/s41598-020-69780-8>.
- Farber-Lorda, J., Gaudy, R., Mayzaud, P., 2009. Elemental composition, biochemical composition and caloric value of Antarctic krill: implications in energetics and carbon balances. *J. Mar. Syst.* 78, 518–524.
- Fernández-Álamo, M.A., Añorve, Sanvicente, 2005. Holoplanktonic polychaetes from the gulf of Tehuantepec, Mexico. *Cah. Biol. Mar.* 46, 227–239.
- Fernández-Álamo, M.A., Thuesen, E.V., 1999. Polychaeta. In: Boltovskoy, D. (Ed.), *South Atlantic Zooplankton*, 1. Backhuys Publishers, Leiden, pp. 595–619.
- Fontana, I., Barra, M., Bonanno, A., Giacalone, G., Rizzo, R., Mangoni, O., Genovese, S., Basilone, G., Ferreri, S., Mazzola, S., Lo Bosco, G., Aronica, S., 2022. Automatic classification of acoustically detected krill aggregations: a case study from Southern Ocean. *Environ. Model. Software* 151, 105357. <https://doi.org/10.1016/j.envsoft.2022.105357>.
- Fraser, A.D., Wongpan, P., Langhorne, P.J., Klekociuk, A.R., Kusahara, K., Lannuzel, D., et al., 2023. Antarctic landfast sea ice: a review of its physics, biogeochemistry and ecology. *Rev. Geophys.* 61, e2022RG000770 <https://doi.org/10.1029/2022RG000770>.
- Granata, A., Guglielmo, L., Greco, S., Vacchi, M., Sidoti, O., Zagami, G., La Mesa, M., 2000. Spatial distribution and feeding habits of larval and juvenile *Pleuragramma antarcticum* in the Western Ross Sea (Antarctica). In: Faranda, F., Guglielmo, L., Ianora, A. (Eds.), *Ross Sea Ecology*. Springer, Berlin, pp. 369–393.
- Gallii, T., 2015. dendextend: an R package for visualizing, adjusting, and comparing trees of hierarchical clustering. *Bioinformatics*. <https://doi.org/10.1093/bioinformatics/btv428>.
- Granata, A., Cubeta, A., Guglielmo, L., Sidoti, O., Greco, S., Vacchi, M., La Mesa, M., 2002. Ichthyoplankton abundance and distribution in the Ross Sea during 1987–1996. *Polar Biol.* 25, 187–202.
- Granata, A., Zagami, G., Vacchi, M., Guglielmo, L., 2009. Summer and spring trophic niche of larval and juvenile *Pleuragramma antarcticum* in the Western Ross Sea, Antarctica. *Polar Biol.* 32, 369–382.
- Granata, A., Weldrick, C.K., Bergamasco, A., Saggiomo, M., Grillo, M., Bergamasco, A., Swadling, K.M., Guglielmo, L., 2022. Diversity in zooplankton and sympagic biota during a period of rapid sea ice change in Terra Nova Bay, Ross Sea, Antarctica. *Diversity* 14, 425. <https://doi.org/10.3390/d14060425>.
- Grillo, M., Huetmann, F., Guglielmo, L., Schiaparelli, S., 2022. Three-dimensional quantification of copepods predictive distributions in the Ross Sea: first data based on a machine learning model approach and open access (FAIR) data. *Diversity* 14, 355. <https://doi.org/10.3390/d14050355>.
- Guglielmo, L., Antezana, T., Crescentini, N., Granata, A., 1997. Euphausiids. In: Guglielmo, L., Ianora, A. (Eds.), *Atlas of Marine Zooplankton, Strait of Magellan*. Springer, Berlin, pp. 87–130.
- Guglielmo, L., Granata, A., Greco, S., 1998. Distribution and abundance of postlarval and juvenile *Pleuragramma antarcticum* (Pisces, Nototheniidae) off Terra Nova Bay (Ross Sea, Antarctica). *Polar Biol.* 19, 37–51.
- Guglielmo, L., Zagami, G., Saggiomo, V., Catalano, G., Granata, A., 2007. Copepods in spring annual sea ice at Terra Nova Bay (Ross Sea, Antarctica). *Polar Biol.* 30, 747–758.
- Guglielmo, L., Donato, P., Zagami, G., Granata, A., 2009. Spatio-temporal distribution and abundance of *Euphausia crystallophias* in Terra Nova Bay (Ross Sea, Antarctica) during austral summer. *Polar Biol.* 32, 347–367.
- Guglielmo, L., Minutoli, R., Bergamasco, A., Granata, A., Zagami, G., Antezana, T., 2011. Short-term changes in zooplankton community in Paso Ancho basin (Strait of Magellan): functional trophic structure and diel vertical migration. *Polar Biol.* 34, 1301–1317.
- Guglielmo, L., Arena, G., Brugnano, C., Guglielmo, R., Granata, A., Minutoli, R., Sitrán, R., Zagami, G., Bergamasco, A., 2015a. MicroNESS: an innovative opening-closing multinet for under pack-ice zooplankton sampling. *Polar Biol.* 38 <https://doi.org/10.1007/s00300-015-1763-3>.
- Guglielmo, L., Granata, A., Guglielmo, R., 2015b. Order Euphausiacea. *Revista IDE@ - SEA 86B*, 1–20. ISSN 2386-7183. <http://www.sea-entomologia.org/IDE@/revista/86B.pdf>.
- Heq, J.H., Guglielmo, L., 1992. Structure and functioning of the Ross Sea pelagic ecosystem: an interdisciplinary approach. In: Gallardo, V.A., Ferretti, O., Moyano, H. I. (Eds.), *Oceanografía en Antártide*. ENEA-PNRA-EULA, Concepción, Chile, pp. 227–233.
- Henschke, N., Everett, J.D., Richardson, A.J., Suthers, I.M., 2016. Rethinking the role of salps in the ocean. *Trends Ecol. Evol.* 31, 720–733.

- Hopkins, T.L., 1985. Food web of an Antarctic midwater ecosystem. *Mar. Biol.* 89, 197–212.
- Hopkins, T.L., 1987. Midwater food web in McMurdo sound, Ross Sea, Antarctica. *Mar. Biol.* 96, 93–106.
- Hosie, G.W., Schultz, M.B., Kitchener, J.A., Cochran, T.G., Richards, K., 2000. Macrozooplankton community structure off East Antarctica (80–150°E) during the Austral summer of 1995/1996. *Deep Sea Res II* 47, 2437–2463.
- Kembel, S.W., 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure test. *Ecol. Lett.* 12, 949–960.
- Knox, G.A., 2006. *Biology of the Southern Ocean*. CRC Press, Boca Raton.
- Lee, C.I., Pakhomov, E., Atkinson, A., Siegel, V., 2010. Long-term relationships between the marine environment, krill and salps in the Southern Ocean. *J. Mar. Biol.* <https://doi.org/10.1155/2010/410129>.
- Liszka, C.M., Manno, C., Stowasser, G., Robinson, C., Tarlin, G.A., 2019. Mesozooplankton community composition controls fecal pellet flux and remineralization depth in the Southern Ocean. *Front. Mar. Sci.* 6, 230. <https://doi.org/10.3389/fmars.2019.00230>.
- Loeb, V., Siegel, V., Holm-Hansen, O., Hewitt, R., Fraser, W., Trivelpiece, W., Trivelpiece, S., 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. *Nature* 387, 897–900.
- Mangoni, O., Saggiomo, V., Bolinesi, F., Margiotta, F., Budillon, G., Cotroneo, Y., Mistic, C., Rivaro, P., Saggiomo, M., 2017. Phytoplankton blooms during austral summer in the Ross Sea, Antarctica: driving factors and trophic implications. *PLoS One* 12, e0176033. <https://doi.org/10.1371/journal.pone.0176033>.
- Manno, C., Tirelli, V., Accornero, A., Fonda, Umani S., 2010. Importance of the contribution of *Limacina helicina* faecal pellets to the carbon pump in Terra Nova Bay (Antarctica). *J. Plankton Res.* 32, 142–152.
- Manno, C., Stowasser, G., Enderlein, P., Fielding, S., Tarling, G.A., 2015. The contribution of zooplankton faecal pellets to deep-carbon transport in the Scotia Sea (Southern Ocean). *Biogeosciences* 12, 195–1965.
- Mauchline, J., Fisher, L.R., 1969. The biology of euphausiids. *Adv. Mar. Biol.* 7, 1–454.
- Mayzard, P., Pakhomov, E., 2014. The role of zooplankton communities in carbon recycling in the Ocean: the case of the Southern Ocean. *J. Plankton Res.* 36, 1543–1556.
- Meyer, B., Auerswald, L., Siegel, V., Spahic, S., Pape, C., Fach, B.A., Teschke, M., Lopata, A.L., Puentes, V., 2010. Seasonal variation in body composition, metabolic activity, feeding, and growth of adult krill *Euphausia superba* in the Lazarev Sea. *Mar. Ecol.: Prog. Ser.* 398, 1–18.
- Minutoli, R., Brugnano, C., Granata, A., Zagami, G., Guglielmo, L., 2016. Zooplankton electron transport system activity and biomass in the western Ross Sea (Antarctica) during austral summer 2014. *Polar Biol.* 40 <https://doi.org/10.1007/s00300-016-2043-6>.
- Minutoli, R., Zagami, G., Brugnano, C., Guglielmo, L., Pansera, M., Granata, A., 2017. Spring and autumn spatial distribution of zooplankton carbon requirement across the Mediterranean Sea. *Chem. Ecol.* 33, 1–22.
- Minutoli, R., Bergamasco, A., Guglielmo, L., Swadling, K.M., Bergamasco, A., Veneziano, F., Geraci, A., Granata, A., 2023. Species diversity and spatial distribution of pelagic amphipods in Terra Nova Bay (Ross Sea, Southern Ocean). *Polar Biol.* 46, 821–835.
- Motoda, S., 1959. Devices of simple plankton apparatus. *Mem. Fac. Fish. Hokkaido Univ.* 7, 73–94.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szocs, E., Wagner, H., 2020. Vegan: community ecology package. R package version 2, 5–7. <https://CRAN.R-project.org/package=vegan>.
- Pane, L., Feletti, M., Francomacaro, B., Mariottini, G.L., 2004. Summer coastal zooplankton biomass and copepod community structure near the Italian Terra Nova base (Terra Nova Bay, Ross Sea, Antarctica). *J. Plankton Res.* 26, 1479–1488.
- Pinkerton, M.H., Bradford-Grieve, J.M., 2014. Characterizing foodweb structure to identify potential ecosystem effects of fishing in the Ross Sea, Antarctica. *ICES J. Mar. Sci.* 71, 1542–1553.
- Rampal, J., 1975. Les Thécosomes (Mollusques pélagiques), Systématique et évolution - Ecologie et biogéographie méditerranéennes. Thèse de Doctorat Etat, Université Aix-Marseille I, 1–48.
- Ratnarajah, L., Abu-Alhaja, R., Atkinson, A., Batten, S., Bax, N.J., Bernard, K.S., et al., 2023. Monitoring and modelling marine zooplankton in a changing climate. *Nat. Commun.* 14, 564.
- Ross, R.M., Quetin, L.B., Martinson, D.G., Ianuzzi, R.A., Stammerjohn, S.E., Smith, R.C., 2008. Palmer LTER: patterns of distribution of five dominant zooplankton species in the epipelagic zone west of the Antarctic Peninsula, 1993–2004. *Deep Sea Res. II* 55, 2086–2105. <https://doi.org/10.1016/j.dsr2.2008.04.037>.
- Sala, A., Azzali, M., Russo, A., 2002. Krill of the Ross Sea: distribution, abundance and demography of *Euphausia superba* and *Euphausia crystallophias* during the Italian antarctic expedition (January–February 2000). *Sci. Mar.* 66, 123–133.
- Schaafsma, F.L., Cherel, Y., Flores, H., van Franeker, J.A., Lea, M.A., Raymond, B., van de Putte, A.P., 2018. Review: the energetic value of zooplankton and nekton species of the Southern Ocean. *Mar. Biol.* 165 <https://doi.org/10.1007/s00227-018-3386-z>.
- Schlitzer, R., 2001. Ocean data View. <https://odv.awi.de/software/download>. December 2023.
- Schnack-Schiel, S.B., Dieckmann, G.S., Kattner, G., Thomas, D.N., 2004. Copepods in summer platelet ice in the eastern Weddell Sea, Antarctica. *Polar Biol.* 27, 502–506.
- Smith, WO Jr, Shields, A.R., Peloquin, J.A., Catalano, G., Tozzi, S., Dinniman, M.S., Asper, V.L., 2006. Biogeochemical budgets in the Ross Sea: variations among years. *Deep Sea Res II* 53, 815–833.
- Smith, WO Jr, Asper, V., Tozzi, S., Liu, X., Stammerjohn, S.E., 2011a. Surface layer variability in the Ross Sea, Antarctica as assessed by in situ fluorescence measurements. *Prog. Oceanogr.* 88, 28–45.
- Smith, WO Jr, Shields, A.R., Dreyer, J.C., Peloquin, J.A., Asper, V.L., 2011b. Interannual variability in vertical export in the Ross Sea: magnitude, composition, and environmental correlates. *Deep-Sea Res. I* 58, 147–159.
- Smith, WO Jr, Ainley, D.G., Arrigo, K.R., Dinniman, M.S., 2014. The oceanography and ecology of the Ross Sea. *Ann. Rev. Mar. Sci.* 6, 469–487.
- Smith, W.O., Delizo, L.M., Herbolsheimer, C., Spencer, E., 2017. Distribution and abundance of mesozooplankton in the Ross Sea, Antarctica. *Polar Biol.* 40, 2351–2361.
- Steinberg, D.K., Landry, M.R., 2017. Zooplankton and the ocean carbon cycle. *Ann. Rev. Mar. Sci.* 9, 413–444.
- Steinberg, D.K., Ruck, K.E., Gleiber, M.R., Garzio, L.M., Cope, J.S., Bernard, K.S., Stammerjohn, S.E., Schofield, O.M.E., Quetin, L.B., Ross, R.M., 2015. Long-term (1993–2013) changes in macrozooplankton off the western antarctic Peninsula. *Deep-Sea Res.* 1101, 54–70.
- Stevens, C.J., Pakhomov, E.A., Robinson, K.V., Hall, J.A., 2015. Mesozooplankton biomass, abundance and community composition in the Ross Sea and the pacific sector of the Southern Ocean. *Polar Biol.* 38, 275–286.
- Swadling, K.M., Constable, A.J., Fraser, A.D., Massom, R.A., Borup, M.D., Ghigliotti, L., Granata, A., Guglielmo, L., Johnston, N.M., Kawaguchi, S., Kennedy, F., Kiko, R., Koubbi, P., Makabe, R., Martin, A., McMinn, A., Moteki, M., Pakhomov, E.A., Peeken, I., Reimer, J., Reid, P., Ryan, K.G., Vacchi, M., Virtue, P., Weldrick, C.K., Wongpan, P., Wotherspoon, S.J., 2023. Biological responses to change in Antarctic sea ice habitats. *Front. Ecol. Evol.* 10, 1073823 <https://doi.org/10.3389/fevo.2022.1073823>.
- Turner, J.T., 2015. Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. *Prog. Oceanogr.* 130, 205–248.
- Uttal, L., Buck, K.R., 1996. Dietary study of the midwater polychaete *Poeeobius meseres* in Monterey Bay, California. *Mar. Biol.* 125, 333–343.
- Vacchi, M., La Mesa, M., Dalù, M., Macdonald, J., 2004. Life stages in the life cycle of antarctic silverfish, *Pleuogramma antarcticum* in Terra Nova Bay, Ross Sea. *Antarct. Sci.* 16, 299–305.
- Webb, C.O., Ackerly, D.D., Kembel, S.W., 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinform.* 18, 2098–2100.
- Yang, G., Atkinson, A., Hill, S.L., Guglielmo, L., Granata, A., Li, C., 2021. Changing circumpolar distributions and isoscapes of Antarctic krill: Indo-Pacific habitat refuges counter long-term degradation of the Atlantic sector. *Limnol. Oceanogr.* 66, 272–287.
- Zeidler, W., De Broyer, C., 2009. Catalogue of the Hyperidean Amphipoda (Crustacea) of the Southern Ocean with distribution and ecological data. In: De Broyer, C. (Ed.), *Census of Antarctic Marine Life, Synopsis of the Amphipoda of the Southern Ocean*, 79. Bull. Inst. R. Sc. N. de Belgique, Biologie, pp. 1–103.