Polar Biology (2026) 49:9
https://doi.org/10.1007/s00300-026-03448-3

RESEARCH

Seasonal variation in zooplankton assemblages in Ryder Bay, Adelaide Island, Antarctic Peninsula

Alice Clement[1] · **Simon A. Morley**[1] · **Lloyd S. Peck**[1]

Received: 23 July 2025 / Revised: 30 December 2025 / Accepted: 5 January 2026

Abstract

Seasonal and inter-annual variations in zooplankton play a vital role in marine ecosystems. In Antarctica, because of the extreme seasonality and ice extent, zooplankton studies are predominantly conducted in summer and are based offshore. Therefore the drivers of variability are poorly understood. Here, we present one of the few year-round studies of seasonality of zooplankton communities at a coastal site in Ryder Bay, Western Antarctic Peninsula (WAP), encompassing both holoplankton and meroplankton. While there were consistent species components to the assemblage, there was also substantial intra- and inter-annual variation throughout the study, suggesting short-term and single-season evaluations are insufficient to provide a comprehensive understanding of zooplanktonic assemblage dynamics and controlling factors. Small copepods and nemertean pilidium (32% and 28% of all individuals seen, respectively) were present throughout all seasons, and both organisms were present in all but one event, peaking at 89% and 90% of individuals sampled, respectively. However, some organisms, such as some species of pteropoda, cnidaria, and echinodermata, were only present once in the 3-year period, suggesting greater overall diversity than this study found and possibly indicating unusual spatial patchiness or multi-year phenologies. Planktonic larvae of benthic species were more abundant in deeper water samples, closer to the seabed, and assemblage composition and abundance were affected by chlorophyll levels. Larvae and zooplankton of pelagic species assemblages were significantly correlated with temperature, salinity, and pigment levels, strongly suggesting links between specific species and environmental conditions, relationships that are likely to be affected by climate change.

Keywords Seasonality · Marine · Zooplankton · Copepod · Nemertean · Larva

Introduction

Zooplankton communities play a vital role in all of the Earth's marine ecosystems. They are essential food web elements linking primary production to higher trophic levels. Meroplanktonic larval stages play an important role in the recruitment of benthic communities by dispersal, resulting in plankton fluctuations impacting both benthic and pelagic populations (Arntz et al. 1992).

Antarctic zooplankton communities consist of holoplankton and meroplanktonic larvae. Dominant holoplanktonic groups found in the Western Antarctic Peninsula (WAP) are copepods and euphausiids, which are consumed by many higher trophic levels and have a key grazing effect on phytoplankton (Marrari et al. 2011; Conroy et al. 2020). Many zooplankton undertake diel vertical migration to feed at the surface at night and to dive to evade predation during daylight. Diel vertical migration occurs year-round in some zooplankton, but to a lesser extent in 24-h daylight months in polar regions (Conroy et al. 2020).

Copepod and euphausiid populations are reported to be positively correlated with chlorophyll concentration in the WAP (Devrekera et al. 2005; Marrari et al. 2011). The community composition of other zooplankton species such as ostracods, pteropods, chaetognaths, medusa, amphipods and mysids is not as closely linked to environmental conditions, but they remain key components of zooplankton communities by acting as predators on other plankton and providing a food source for larger predators (Marrari et al. 2011; Barnes and Tarling 2017).

The Antarctic Peninsula shows strong seasonality and inter-annual variability in oceanographic parameters such

---

✉ Alice Clement
alent@bas.ac.uk

[1] British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK

as salinity, temperature, freshening, stratification and light levels. These factors affect phytoplankton community structure, productivity and chlorophyll levels (Marrari et al. 2011; Venables et al. 2013; Rozema et al. 2016; Venables et al. 2023). The variation in phytoplankton results in strong seasonality in heterotrophic zooplankton (Annett et al. 2010). Over the summer, nearshore chlorophyll levels can exceed 25 mg m^{-3} with diatoms dominating the composition of early blooms and smaller fractions later (Clarke et al. 2008).

Various studies have focussed on phytoplankton variation and impacts during the Antarctic summer (Clarke et al. 2008; Annett et al. 2010). In contrast, year-round seasonality in zooplankton on the WAP has received little attention to date (Sewell 2005; Bowden et al. 2009), probably because of the technical and logistic difficulties of sampling across seasons and years in extreme polar environments. Further studies on seasonal and inter-annual variability of Antarctic zooplankton are needed to increase our comprehension of their role in the Antarctic ecosystem, impacts on blue carbon pathways and prospects under future change scenarios (Pearce et al. 2008; Zwerschke et al. 2021).

Polar zooplankton assemblages contain both wholly pelagic species and larvae of benthic species, which have meroplanktonic early life histories (Bowden et al. 2009; Thorson 1936). In the early stages of research on reproduction of marine invertebrates, it was thought that the lack of nutrients, sunlight and cold temperatures over winter would reduce the number of species with a meroplanktonic larva, called Thorson's rule (Thorson 1936; Mileykovsky 1971). Later research showed that similar proportions of species with meroplanktonic larvae occurred in South America and Antarctica (Hain and Arnaud 1992; Pearse et al. 1991), and it is now known that planktonic phases are important for dispersal in many Antarctic benthic species (Stanwell-Smith et al. 1999).

Spawning seasonality of Antarctic macrobenthos varies amongst species (Bowden et al. 2009). Many species spawn so that embryonic and larval development occurs to align feeding stages with key food resources (Peck et al. 2024; Todd and Doyle 1981). Studying zooplankton communities year-round allows assessment of seasonality and spawning periods of benthos, which in turn are linked to sea-ice cover, oceanographic conditions or chlorophyll levels. Not all benthic larvae feed whilst in a meroplanktonic stage. Some macrobenthos disperse via lecithotrophic larvae (Pearse 1994; Stanwell-Smith et al. 1999).

Zooplankton are a key part of the biological carbon pump, especially in polar regions, and in Antarctica, they play important roles in carbon pathways by grazing and the production of faecal pellets (Barnes and Tarling 2017; Mayzaud and Pakhomov 2014; Sands et al. 2023; Zwerschke et al. 2021). Research on the impact of zooplankton on carbon fluxes is often under-represented compared to phytoplankton and higher trophic levels (Cavan et al. 2024). However, zooplankton are key in recycling carbon captured through primary production in the Southern Ocean (Mayzaud 2014), and understanding their seasonality, and how this will be impacted by climate change, is key to understanding carbon pathways.

Aims and objectives

This study sampled zooplankton from a nearshore, fjordic site on the Antarctic Peninsula at three depths, with the aim of describing seasonal variation in zooplankton assemblages and suggesting potential environmental and oceanographic factors affecting zooplankton community structure. We further aimed to evaluate the larval stages of benthic species to identify the drivers of their seasonality. These drivers of zooplankton assemblages are then discussed in terms of how projected effects of climate change could influence zooplankton dynamics.

Materials and methods

Site and sampling

The study area was at South Cove, Ryder Bay, Rothera Point, Adelaide Island, − 67.5722, − 68.1328, the same site used by Venables et al. (2023).

Plankton were collected with a vertical trawl using a hand winch. The trawl net was 1.80 m long and consisted of an 860-mm-diameter stainless-steel circular frame with 1 mm mesh, attached to a winch by three strops. The net end was 100 mm in diameter, with a screw-fit plastic cod-end to collect the samples. The cod-end containers had 10 circular holes, each 20 mm in diameter, covered with 100 µm mesh (following Bowden et al. 2009). Two 3-kg weights attached to the cod-end allowed the net to sink and maintain an optimum position in the water column during hauls.

For each event, samples were taken from starting depths of 100 m, 40 m and 15 m and hauled vertically to the surface: three times from each depth. These depths matched the sampling regime of the ongoing 27-year Rothera Oceanographic and Biological Time Series (RaTS) CTD (conductivity, temperature and depth) sampling at the winter-accessible site (Venables et al. 2023). 100 m was close to the maximum depth of the site studied, but care was taken to ensure the net remained clear of the seabed, while sampling below the deepest extent of the bloom. 15 m was chosen as the minimum sampling depth as this is the typical depth for the chlorophyll maximum at this site (Venables et al. 2023). 40 m was chosen as an additional intermediate depth for samples.

The net was hauled at a rate of 5 m min^{-1}. After each trawl, samples were decanted into a plastic container, kept in a cool box and returned to the laboratory for immediate processing. To ensure the net was clean, the cod-end was rinsed three times, and the net was rinsed between samples by the descent of the next trawl.

Bloom analysis

Pigment levels (determined by in situ fluorescence measurements using a Sea-Bird Eco Flnturt Chl *a* fluorometer), salinity and temperature were sampled simultaneously using a CTD. The CTD was taken as close to the trawling event as possible.

The bloom period was defined using the Threshold Method (Brody et al. 2013; Siegel et al. 2002) as 5% above the median of the time series for the study period. This was possible because of the weekly CTD events taken as part of the ongoing RaTS programme. Over this study, this was calculated as 0.57 mg m^{-3}, using 118 CTD events.

Zooplankton analysis

Samples were kept at ambient seawater temperature in a container suspended within a flow-through aquarium until processing to maintain ambient temperatures. Processing occurred immediately for 17 events, and within 24 h of sampling for the other 2. Large zooplankton were immediately recorded and removed to minimise post-sampling predation. All individuals were removed by pipette from each sample and identified to the lowest taxonomic grouping possible by microscopy and identification guides (Stanwell-Smith et al. 1997). Individual numbers in each Operational Taxonomic Units (OTUs) were recorded. All individuals were enumerated. A digital reference collection was compiled to allow consistent identification. New zooplankton morphotypes were photographed to ensure consistent identification between events. A physical reference collection of each organism or OTU type was preserved in ethanol. Copepods below 5 mm long were classed as small.

Identifying individuals into OTUs has been widely used in meroplankton studies evaluating community structure (e.g. Sewell 2005; Stanwell-Smith et al. 1999). Commonly, individuals are grouped by similar morphology, which can lead to under- or overestimation of true species diversity. However, OTUs have the advantage when identification of organisms to the species level is not possible, and this is a common approach (e.g. Bowden et al. 2009; Stanwell-Smith et al. 1999). OTUs were categorised as larvae and zooplankton of pelagic species (Holoplankton, HP) and as benthic invertebrate larvae (BL).

Taxa were analysed as individual counts per trawl and as individuals m^{-3}. Trawls took place opportunistically (Table 1). Trawl samples were assessed per individual haul, by totalling the three repetitions at the same depth into one, and by totalling all 9 hauls of one sampling event to allow for a broad overview of temporal fluctuations in species and to allow for depth differentiation.

Statistical analysis

A regression was calculated to show the correlation of temperature and salinity of events. Data were non-normally distributed, and so a Siegel median regression was calculated (Siegel 1982). The Shannon–Wiener index (Ortiz-Burgos 2016) was calculated for each event to assess the diversity of assemblages against the total number of organisms identified per event.

Multi-dimensional analyses of the factors affecting zooplankton assemblage over depth and time were conducted in Primer 7 (Clarke and Gorley 2015). To reduce the influence of the most abundant species, data were transformed by fourth route (assessed using shade plots) before Bray–Curtis similarity matrices were calculated for assemblage analyses, while Euclidean distance matrices were calculated to compare environmental drivers (BEST biota-environment—BIOENV). PERMANOVA was conducted (using 999 permutations, Bray–Curtis similarity) to assess the

Table 1 Dates of haul events, bloom status and season.

Event	Month	Bloom	Season
1	Aug-22	n	Winter
2	Oct-22	n	Winter
3	Oct-22	n	Winter
4	Dec-22	y	Summer
5	Jan-23	y	Summer
6	Dec-23	n	Summer
7	Dec-23	y	Summer
8	Dec-23	y	Summer
9	Feb-24	y	Summer
10	Mar-24	y	Summer
11	Apr-24	n	Winter
12	Jul-24	n	Winter
13	Aug-24	n	Winter
14	Sep-24	n	Winter
15	Oct-24	n	Winter
16	Oct-24	n	Winter
17	Nov-24	n	Summer
18	Nov-24	n	Summer
19	Dec-24	n	Summer

Bloom status was calculated by Threshold Method effect of depth on abundance for each OTU (m^{-3}). After studying the PERMANOVA results, additional pairwise PERMANOVA was performed on significant results to assess differences between depths.

Principal Coordinates Analysis (PCO; Bray–Curtis similarity) was used to highlight the species driving the relationships in assemblages amongst sampling events. BEST analysis was used to identify which environmental factors, normalised depth, salinity, pigment and temperature, had the greatest effect on the plankton assemblage structure (using 99 Euclidean distance permutations and Spearman's Rank correlations). BEST analysis calculates the combination of variables that has the highest correlation with the assemblages. For each of the most correlated environmental variables identified by the BEST analysis, a SIMPER (Similarity percentages) analysis was then conducted to identify the key species contributing to the differences between assemblages. SIMPER calculates the percentage of the similarities and dissimilarities between assemblages attributed to each species. Vectors, showing the direction of the effects of each of these species, were plotted onto the PCO figures.

Results

A total of 171 trawls were analysed over 29 months (Table 1). The volume of water (net mouth area × depth) sampled by each individual trawl was 254.5 m^3 for 100 m, 101.8 m^3 for 40 m and 38 m^3 for 15 m trawls. Each event had three replicates at each depth, and a total of 22,485 m^3 of water was therefore sampled.

Environmental variables

Pigment levels on our sampling dates at 15 m ranged from 0.05 to 10.19 mg m^{-3} salinity ranged between 33.21 and 34.01 psu, and temperature ranged from − 1.76 to 0.51 °C. The coldest temperatures were recorded in October 2022 and September 2024. Temperature was negatively correlated with salinity (Siegel's median linear regression, Intercept, V value = 1653, $P < 0.001$; slope, V value = 24.1, $P < 0.001$, Fig. 1).

The phytoplankton bloom

Of the 19 sampling events, 13 had chlorophyll concentrations below the threshold for a phytoplankton bloom (0.57 mg m^{-3}) and six were above the threshold (Fig. 2). From RaTS data, the 2023 bloom was from late November 2022 to late April 2023. The 2024 bloom was from late December 2023 to late March 2024, and the 2025 bloom began in early January (after this study had finished).

Diversity

A total of 41 morphotypes (OTUs) were identified, representing 9 phyla and at least 16 different classes (Table 2). Of these, 20 were HP, 19 BL 1 was Unknown, and 1 was an unknown egg. Unknown OTUs were not included in HP or BL analysis. A total of 10,713 individuals were counted and sorted into OTUs. The number of different OTUs per sampling event ranged from 5 to 19 and averaged 11. The highest number of any one OTU during an event was 1,447 small copepods, representing 89% of all individuals sampled during

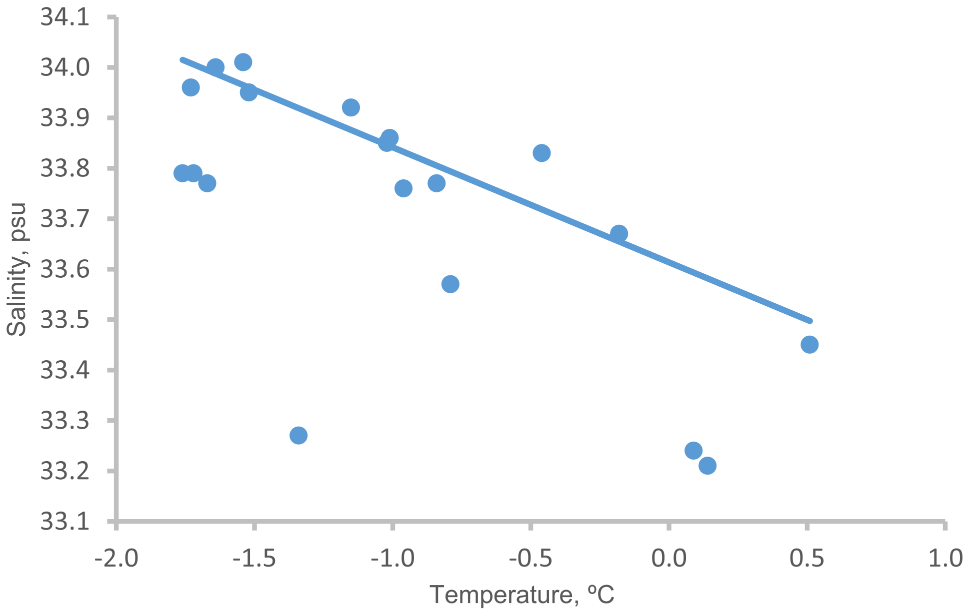

Fig. 1 Temperature and salinity at 15 m depth for each event (from CTD data). Graph shows the negative correlation between temperature and salinity (salinity = 33.61 − 0.228 × temperature) with Siegel's median linear regression fit (Siegel 1982)

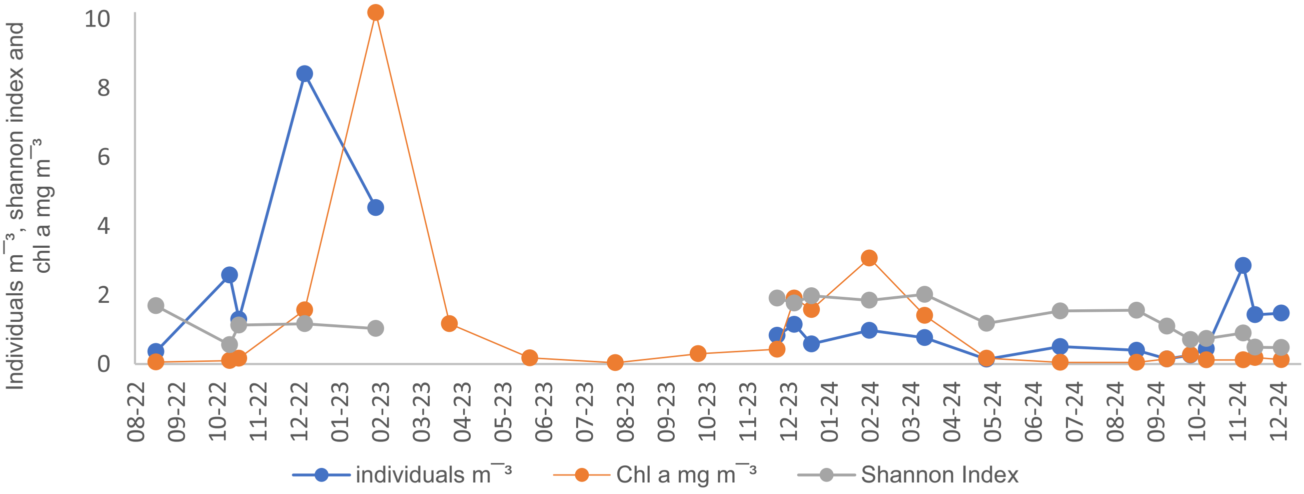

Fig. 2 Abundance (total individuals m^{-3}), CTD pigment (Chl *a* mg m^{-3}) and Diversity (Shannon–Wiener H) of assemblages plotted against the date of each sampling event. There is a suggestion of a rise in larval abundance before chlorophyll levels increased at the start of the summer. Although no significant correlation was detected between overall abundance and Chl *a*, in December 2022 and 2024, larval levels increased before the phytoplankton increased

Table 2 A breakdown of the taxa sampled showing number of OTU types per taxonomic group

Phylum	Class	Life stage	OTU
Arthropoda	Copepoda	Holoplankton	3
	Malacostraca	Holoplankton	5
	Malacostraca	Calyptopis	1
	Ostracoda	Holoplankton	1
	Pycnogonida	Meroplankton	1
Chaetognatha	Sagittoidea	Holoplankton	1
Cnidaria	Hydrozoa	Planulae	2
	Medusozoa	Medusa	1
	Medusozoa	Holoplankton	1
Ctenophora	Ctenophora	Holoplankton	1
Mollusca	Gastropoda	Holoplankton	2
	Gastropoda	Egg	2
	Gastropoda	Veliger	1
	Bivalvia	Veliger	1
		Trochophore	1
Nemertea		Pilidium	2
Annelida	Polychaeta	Meroplankton	2
		Metatrochophore	1
		Nectochaete	1
		Meroplankton	1
		Trochophore	1
Echinodermata	Asteroidea	Gastrula	2
	Holothuroidea	Pentacula	2
		Echinopluteus	1
		Bipinnaria	1
Chordata	Actinopterygii	Meroplankton	1
Unknown			1
Unknown egg			1

that event. Nemertean pilidia were the dominant OTU in 9 events, and small copepods were dominant in 7. Ctenophores, leptothecata hydrozoa and siphonophores each dominated one event. Throughout events, the dominant OTU ranged from 27 to 91% of the total sample, averaging 59%. Some OTUs showed extreme seasonality, only appearing in high numbers during one event. For example, 453 pteropod eggs and 36 pteropods were sampled in event 4, comprising 21 and 1.6%, respectively, of individuals sampled during that event. However, this was the only event during which pteropods were present. 10 OTU types were only seen during one event, and 6 of these were single individuals.

Small copepods made up 32% of all individuals counted and were present in all but one event (October 2024 during winter), before the bloom. Nemertean pilidia made up 28% of all individuals and were present in all but one event in May 2024, during winter. Ctenophores made up 13% of all individuals; however, they were only present during four events. The highest ctenophore numbers occurred during two events, and ctenophores were the dominant taxon in one event, comprising 62% of individuals in that haul, which was also the event with the most individuals counted (2125). Only 9 individual ctenophores were sampled outside of these two events.

Diversity did not increase with abundance. A plot of the Shannon–Wiener index and abundance for each sampling event demonstrates how some events with the highest abundances of individuals also had low diversities, indicating dominance of a few taxa in these events (Fig. 2). Indeed, the samples with the six highest abundances had the three lowest Shannon–Wiener indices and all were amongst the lowest 10 of the 19 samples taken.

The composition of the assemblage varied substantially between years. Sampling events were taken in December in three separate years in this study: one sample was taken in each of December 2022 and 2024, but three sampling events were made in December 2023. In 2023, there were differences across the month, but the overall composition was similar between events, with leptothecata hydrozoans, gastropod veligers, small copepods, and nemertean pilidia all being well represented (Fig. 3). This contrasts with 64% of the December 2022 sample being ctenophores and a further 22% being pteropod eggs. The 2024 sample was different again, with 92% being accounted for by nemertean pilidia (Fig. 3).

There were large variations in the abundances of individual taxa between sampling events. Several of these demonstrated extremely high numbers in a single or a small number of samples (Fig. 4). Data for the highest abundances of each of the three most abundant taxa in the study, copepods, nemertean pilidia and ctenophores, showed values up to an order of magnitude higher than in other events. This was especially so for ctenophores, which showed more than an order of magnitude difference in average density: 1.68 and 0.068 individuals m^{-3} in the densest samples when combining all events' hauls, whereas no other samples had densities above 0.004 individuals m^{-3} (Fig. 4).

Vertical distribution and environmental correlates

Benthic invertebrate larvae

PERMANOVA analysis showed a significant effect of depth on abundance for planktonic larvae of benthic taxa (BL Individuals m^{-3}) (PERMANOVA, pseudo-$F_{(2,54)} = 5394.3$, $P = 0.002$). A post hoc test demonstrated a significant difference in abundance between 15 and 100 m depth ($t = 2.589$, $df = 2$, $P = 0.001$). There was no significant difference between the abundance in 100 and 40 m samples ($t = 1.32$, $df = 2$, $P = 0.13$) or 15 and 40 m samples ($t = 1.26$, $df = 2$, $P = 0.182$). At 15 m, there was a 52% similarity across samples, with 43% at 40 m and 50% at 100 m (SIMPER; individuals m^{-3}). Nemertean pilidia had the highest effect on similarity in group assemblages within depths, to the highest extent, accounting for 96% of the similarity at 15 m. They accounted for 84% at 40 m and 55% at 100 m. After nemertean pilidia, the next OTU of importance was gastropod veligers in 100 m samples, which accounted for 20% of the similarity in assemblage composition. Nemertean pilidia were the most common contribution to differences in assemblage composition, whether depths, salinities or pigment were compared.

BEST analysis indicated depth to be one of the highest contributing factors to differences in species assemblages, along with pigment and salinity, with all three factors combined accounting for 51% of the variation in assemblage composition ($R^2 = 0.513$). PCO indicated some clusters of samples by depth, but with high variability

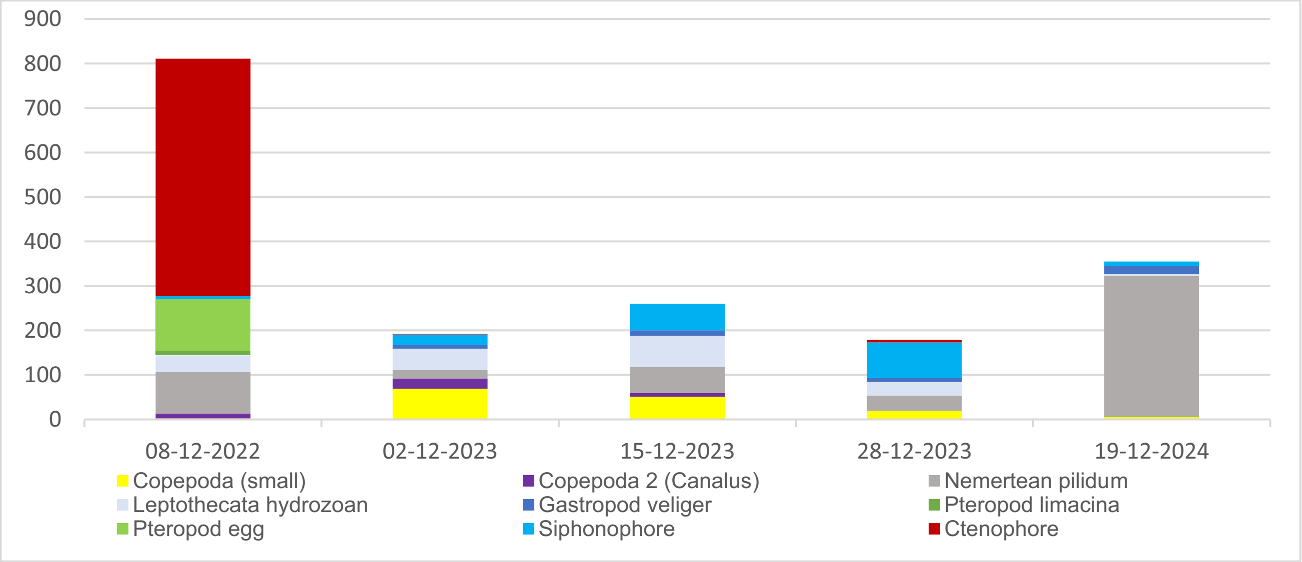

Fig. 3 A bar chart demonstrating the very large inter-annual variation of taxon composition within assemblages. Three years of December events are used for demonstration. Only 100-m trawls are displayed in this figure to address limitations of a depth-stratified approach. The output across all depths shows similar results (Supplementary Fig. 1)

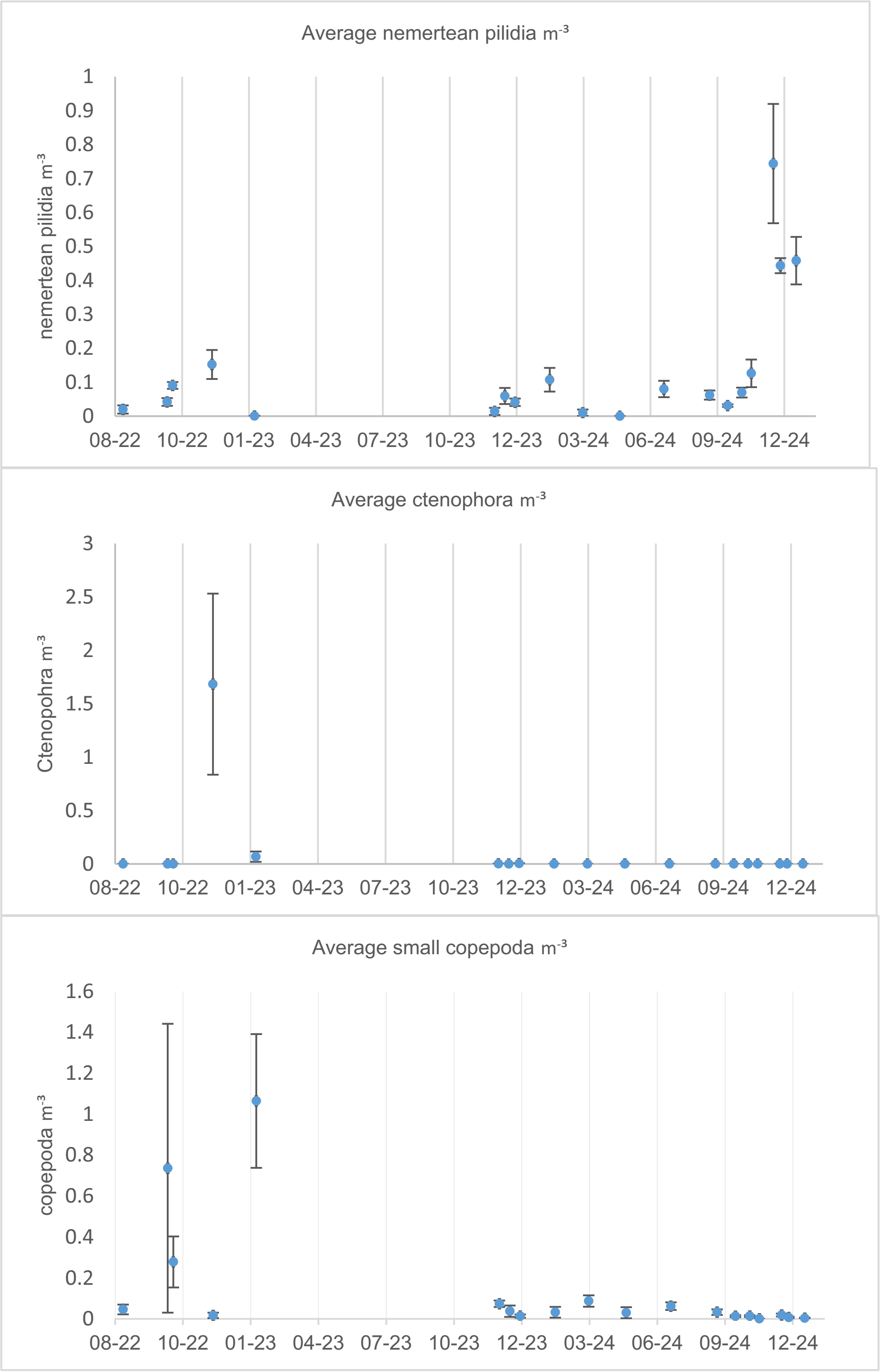

Fig. 4 Average density (individuals m^{-3}) of the three most numerous taxa in the study across the combined depths and trawls from all sampling events (month/year). Data shown are average values across the whole water column, and error bars (SD) represent variation between the three depths sampled

(Fig. 5). Salinity and pigment combined were the two best-correlated variables ($R^2 = 0.462$); however, neither of them showed any obvious salinity or pigment assemblage groups (Supplementary Figs. 2 and 3).

Larvae and zooplankton of pelagic species

There was no significant effect of depth on the number of OTUs m^{-3} for larvae and zooplankton of pelagic taxa (HP)

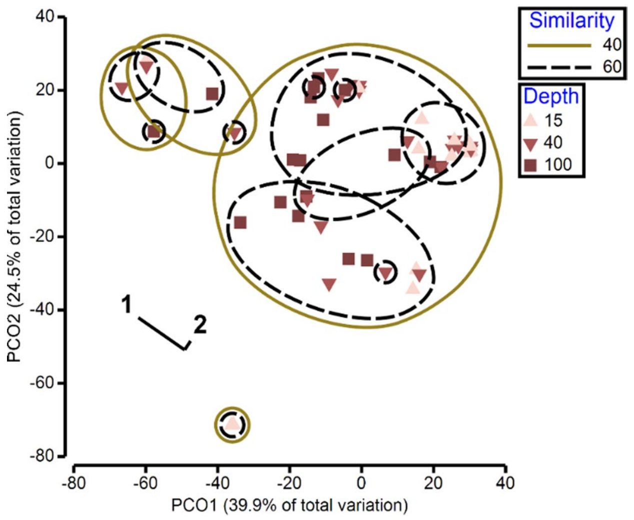

Fig. 5 PCO output for the assemblage of BL OTUs in relation to depth. Vectors are offset for clarity, but show the strength and direction of the two most important species driving the differences between assemblages in a SIMPER analysis. 1—Gastropod veliger; 2—Nemertean pilidia. PCO fitted on fourth-root-transformed data using Bray–Curtis similarity

(PERMANOVA, pseudo-$F_{(2,54)} = 2269.1$, $p = 0.51$). BEST analysis showed temperature and pigment to have the greatest correlated effect on assemblage ($R^2 = 0.343$). Temperature had the highest effect as a single variable ($R^2 = 0.337$), followed by pigment ($R^2 = 0.293$).

Copepods had the highest effect on differences in the composition of group assemblages across temperature and pigment, with up to 100% contribution to certain within-group similarities. Siphonophores, chaetognaths, hydroids, hyperiid amphipods, pteropods, krill and medusae also had an effect in a few events. PCO representation of temperature and different pigment levels did not show strong trends but some possible clusters highlighted important OTUs (Supplementary Figs. 4 and 5).

Discussion

This study was one of the few multi-year, year-round assessments of Antarctic plankton assemblages (Conroy et al. 2023). It recorded large inter- and intra-annual variation in the zooplankton communities in a WAP fjordic bay. A key finding was the heterogeneity of dominant species within assemblages, as also noted by Pinkerton et al. (2020). Annual sampling of the same month across 3 years highlighted the large inter-annual taxon variability, particularly gelatinous zooplankton, previously reported by Pages (1997). Although some species, such as copepods and nemertean pilidia, were common throughout, some taxa were only seen once over the three sampling years, a level of temporal variation rarely documented. Understanding the magnitude and timing of inter-annual and seasonal oceanographic drivers of assemblages is key, as they provide insights into how climate change might affect future biodiversity patterns.

Several drivers were highlighted as important correlates of community composition and these differed between the larvae and zooplankton of pelagic species (HP) and the larvae of benthic species (BL). Pigment was the only factor identified as influencing both pelagic and benthic species. HP were most closely correlated with temperature and pigment, whereas BL were most closely correlated with depth, pigment and salinity. Larval stages are often cited as the most sensitive to environmental change (Peck et al. 2016; Byrne et al. 2022), and varying larval survival rate has long been thought to be one of the determinants of variation in recruitment and therefore adult population size (Hjort 1914). Changes in abundance, or mismatches between the timing of feeding and the phytoplankton bloom (Cushing 1990), are expected to affect larval assemblages, and hence post-settlement recruitment.

Inter-annual variation

Although copepods were consistently recorded throughout the study (Fig. 4), the dominant taxa in December were different in all three years (Fig. 3). Meroplanktonic communities dominated by copepods have been reported in several studies along the WAP (e.g. Vázquez et al. 2007; Pinkerton et al. 2020; Criales-Hernández et al. 2022; Borup et al. 2024). The dominance of smaller copepods, rather than larger ones, agrees with findings from previous years in a similar location (Criales-Hernández et al. 2022).

The biggest signal of climate change on the WAP is the change in ice cover (Morley et al. 2020). Phytoplankton bloom timing is strongly linked to sea-ice extent (Venables et al. 2013) and is therefore a main driver linking future variability in zooplankton assemblages to environmental variability. Many organisms, including some of the copepods, amphipods and euphausiids seen in this study, depend on sea-ice for food or habitat (Brierley and Thomas 2002; Swadling et al. 2023). Sea-ice loss of up to 43% is predicted over the next 50 years (Rintoul et al. 2018), though it should be noted that the loss of Antarctic sea-ice has accelerated in recent years (Josey et al. 2024), which will have a direct impact on many of the key species found to drive differences in assemblages from this study.

Seasonal diversity

The development period of the plankton species studied varies greatly; however, long development periods are common for larvae in polar latitudes (Thorson 1936; Peck 2018; Borup et al. 2024; Peck 2024). This study found an increase in larval abundance prior to the bloom. Some meroplanktonic larval presence in the water column is timed to ensure that benthic settlement coincides with optimum benthic food availability, which is often linked to detritus from the bloom (Pearse et al. 1991; Bowden et al. 2009; Peck 2018).

These pre-bloom peaks are expected, as they allow zooplankton to reach their feeding stage in time for the bloom (Cushing 1990). In this study, nemertean pilidia were present year-round but peaked from October to February. This contrasts with Bowden et al. (2009) who found peaks in winter, out of phase with the bloom, which coincided with a peak in spawning detected by gonad development assessments (Grange et al. 2011). Nemertean larvae over a wide range of development types have been reported during a single 2-month sampling period in the Bellingshausen Sea (Shreeve and Peck 1995), and nemertean development in Antarctica is highly protracted (Peck 1993), so larvae would be expected to be in the water column throughout the year. Further study is required to determine if the differences between the studies are indicative of systemic changes in the plankton assemblage, and hence the result of a change in environment, or whether this can be explained by natural variability.

Cryptic speciation could explain some of the variability, as identifying nemertean pilidia as a single OTU could combine several species with different life histories. DNA analyses identified five distinct nemertean lineages amongst larval samples from the Antarctic Peninsula by Mahon et al. (2010). Bowden et al. (2009) suggested a major constraint on such studies is the limited availability of identification guides and the limited reliability of molecular identification due to a lack of research in this area. It is likely that many OTUs in studies like this one include multiple species. With nemerteans being a key taxon in this study, underestimation of diversity should be considered likely (Grange et al. 2011).

The episodic high densities of gelatinous species such as ctenophores and pteropods recorded in this study are commonplace in Antarctic waters (Pages 1997; Scolardi et al. 2006). Pelagic zooplankton distributions are extremely heterogeneous and highly influenced by oceanographic factors such as mixing, currents, wind and stratification (Abraham 1998; Loeb and Santora 2013; Pinkerton et al. 2020). While wind strengths are linked to yearly or decadal climate variability, such as ENSO and Southern Annular Mode (Morley et al. 2020), there are also seasonal changes in wind direction that affect surface water masses. Ctenophore growth rate is highly dependent on external food supply (Reeve et al. 1989) which results in extreme variability of populations both spatially and seasonally (Lancraft et al. 1991). Events with high ctenophore numbers in this study occurred during moderate to high blooms. Such blooms would support an abundance of micro- and meso-zooplankton, providing a food source for gelatinous macro-zooplankton. Ryder Bay is affected by variable local currents from changes in wind and ice, which could explain the stochastic occurrence of pteropods reported here (Beardsley et al. 2004; Loeb and Santora 2013). Pteropods and ctenophores are often reported as key components of Antarctic zooplankton; however, their appearance was rare in this study, highlighting their patchy spatial and temporal distributions. Pteropod distribution varies spatially and is affected by local topography, prey abundance, sea-ice and climate making a study, emphasising the need for extended inter- and intra- annual studies to assess population dynamics (Thibodeau et al. 2019; Johnston et al. 2022). Three of the factors included here were correlated with larval occurrence, and the implications are discussed below. However, it should be noted that these factors varied seasonally and are only part of many complex seasonal variables. Because of this, their effect may not directly map on to the consequences of a changing climate.

Environmental variable effects on assemblages

Depth

The BL assemblage was significantly different between depths, with a notable difference in the number of individuals between samples from 0 to 15 and 0 to 100 m deep, but no difference between other depth ranges. All hauls sampled from the target depth to surface, and so this method detects if there are larvae found in deeper water masses, that are missing from shallower samples. The method does have a limitation in that the 0–100 m samples contain samples from 0 to 40 m and 0 to 15 m, which reduces the ability to identify depth zonation of plankton. This method does, however, allow identification of taxa that are predominantly at depth as they would be absent from shallower hauls. Depth also auto-correlates with many key environmental parameters (e.g. pigment, salinity and temperature), which makes it difficult to determine whether depth or a correlated variable is influencing depth distribution.

Vázquez et al. (2007) found maximum abundance of benthic invertebrate larvae between 100 and 200 m deep. The deepest trawl here was close to the study site seabed; therefore, BL depth could be explained by seabed proximity, surface water avoidance, or a combination of both. When studying Ryder Bay Bowden et al. (2009) found no depth differentiation of larval numbers during horizontal divertowed trawls close to the seabed at 20 and 6 m, suggesting the difference in the current study between 100 and 15 m samples is an association with the seabed, rather than an avoidance of the surface. Predator evasion and feeding strategy would influence location of different species in the water column (Conroy et al. 2020). For example, zooplankton are not restricted to the euphotic zone as they can feed throughout the water column. BL feeding strategy ranges from lecithotrophic to planktotrophic (Hain and Arnaud 1992); however, lecithotrophy is common in Antarctica (Pearse et al. 1991; Peck 2018). No requirement for lecithotrophic larvae to externally feed removes the need to inhabit surface waters, where phytoplankton is most abundant, reducing the exposure to predatory zooplankton, and could also explain some depth distributions.

Increased glacial ice melt from climate warming will lead to reduced surface water salinities, which could force stenohaline larvae deeper and potentially out of the photosynthetic range for their food. Phytoplankton could also change in composition with increased freshening, affecting zooplankton communities' ability to assimilate energy (Saba et al. 2014; Dawson et al. 2023).

No HP depth differentiation suggests that species are evenly distributed throughout the water column. Many HP species are phytoplanktivores, restricting their feeding activity to the euphotic zone (Pinkerton et al. 2020). Criales-Hernández et al. (2022) found phytoplankton distribution in the Bransfield Strait during 2019–2020 to be homogeneous in the upper 40 m of water and decreasing at greater depths. A depth differentiation would therefore have been expected for HP here; however, it was not observed in this study.

Pigment

In this study, pigment was correlated with BL and HP assemblage structure. These assemblages are closely linked to the phytoplankton bloom (Borup et al. 2024), often with a lag between increases in zooplankton abundance and bloom peaks. The chlorophyll concentration measured closest to trawls in time may not explain population shifts if they were triggered weeks beforehand, with the length of the lag being another potential variable to consider (Conroy et al. 2020).

BL have been suggested to have little or no association with the bloom (Pearse et al. 1991; Grange et al. 2011). Nemertean pilidia were the most dominant BL, and these were present year-round. Their highest numbers often occurred in events with pigment lower than the bloom threshold; however, these were still in the austral summer. As nemertean pilidia feed on small planktonic unicells (Dassow et al. 2013), their numbers could be linked with the bloom of these smaller phytoplankton fractions and not with peak Chl *a*. Blooms of smaller phytoplankton species are usually present over substantially longer periods than the larger species (Clarke et al. 2008; Bowden et al. 2009).

Phytoplankton community composition, and therefore zooplankton food source, is affected by climate change (Schofield et al. 2017). Sea-ice extent and duration alter the community structure of phytoplankton in Antarctica between a diatom dominance and a dinoflagellate-dominated assemblage (Biggs et al. 2019; Deshmukh et al. 2024). This changes the food source and availability for many key primary consumers highlighted in this study, which would likely affect community structure (Schofield et al. 2017; Johnston et al. 2022). Leeuwe et al. (2020) acknowledge the highly variable nature of phytoplankton communities, affected by wind, sea-ice, El Nino and mixotrophy in cryptophytes, increasing the challenge of linking specific phytoplankton trends to zooplankton communities.

Sea-ice concentration is the main influence on bloom timing (Ferreira et al. 2024). A reduction in sea-ice increases light entering the water column, allowing an earlier bloom. This could allow many of the organisms sampled in this study a longer duration of access to higher concentrations of food in future. However, were the bloom to start earlier and nutrient availability limit the bloom duration, there could be a phenological mismatch in the timing of species feeding on phytoplankton, which could be detrimental if the bloom finished before organisms were competent to feed (Cushing 1990; Ferreira et al. 2024).

Salinity

Assessing responses to changes in salinity is a key component of predicting future climate change impacts (Antoni et al. 2020; Barrett et al. 2024, 2025). Increased melting from a warmer climate causes freshening in the surface layer in the polar regions (Swart et al. 2018). Salinity had a higher effect on BL assemblage composition than HP in this study; however, PCO did not suggest strong trends, just potential grouping of some individuals at low salinity. There is little research on in situ salinity effects on nemerteans, which were the key component of BL assemblages (Ingels et al. 2012). Research into salinity effects on marine zooplankton communities is very limited, and further research would provide a better predictive model for impacts on assemblages (Hall and Lewandowska 2022). In situ research on Antarctic phytoplankton responses to salinity changes reported alterations of phytoplankton communities with decreases in pennate diatoms and dominance of nano-diatoms and phytoflagellates (Antoni et al. 2020). Such a shift in food composition for many zooplankton would likely cause changes in abundances and assemblages, and hence food webs.

Temperature

Assessing temperature triggers in assemblage structural changes is essential to identifying zooplankton response to a changing climate (Conroy et al. 2020). Here, temperature was a key variable driving differences in HP. Temperature can impact phytoplankton community composition, causing variation in food type, and metabolic and developmental rates of zooplankton (Antoni et al. 2020; Criales-Hernández et al. 2022; Dawson et al. 2023).

There is variability in the findings of studies of temperature effects on zooplankton. Swadling et al. (2023) modelled an increase in temperature, showing a negative effect on copepods, krill and fish, with salp populations increasing. Whereas Tarling et al. (2018) found Antarctic zooplankton were resilient to the temperature increases seen since 1926, suggesting that other pressures determining community composition such as food availability are important. Temperature is suggested to be the primary influence on larval development rate and directly affects some of the species sampled in this study (Hoegh-Guldberg and Pearse 1995; Stanwell-Smith and Peck 1998; Peck 2018 Lamare et al. 2024). Studies on the Antarctic starfish *Odontaster validus* showed that a warming of 2 °C increased embryonic and larval development rates by around 50% (Peck and Prothero-Thomas 2002). This study demonstrates the challenges of correlating environmental conditions to zooplankton assemblage and shows the need for further research.

Wider impact

Understanding drivers of inter- and intra-annual variability of zooplankton assemblages will be key to predictions of how they will be affected by climate change and the impacts on carbon sequestration through carbon pathways. This oceanic biological carbon sink is one potential mitigation of the extent of effects of global warming (Barnes and Tarling 2017). Zooplankton is a key component of the biological carbon pump by consuming primary producers, producing faecal pellets, providing a food source to higher trophic levels and the zooplankton themselves sinking, or migrating, to the seabed (Cook et al. 2023; Cavan et al. 2024;). Understanding drivers in fluctuations of zooplankton would help predict the availability of food for planktivorous taxa and the potential grazing impact on phytoplankton. Correlating zooplankton, especially meroplankton, assemblages to environmental variables will improve predictions of likely larval recruitment in changing climates. This is particularly important in the Southern Ocean where reductions in sea-ice cover are increasing the open sea habitat available for planktonic community (Zwerschke et al. 2021).

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-026-03448-3.

Acknowledgements We thank the marine teams at Rothera Research Station for their never-ending enthusiasm and help in facilitating this project. Their contributions made this study possible. Particular thanks to L Day, N Frontier, H Rodger, R Mathews, K Brown, A Lines, A Giles, and J Stevenson for their support.

Author contributions AC conceived and designed research. AC and SM conducted experiments. SM analysed data. AC wrote manuscript with SM and LP comments. All authors read and approved the manuscript.

Funding This study was funded by the British Antarctic Survey through its Core funding program.

Data availability Data available upon request from corresponding author.

Declarations

Conflict of interest The authors declare no conflict of interest.

Compliance with ethical standards Permits were approved for this study's sampling. Work was conducted with unregulated invertebrate species.

References

Abraham ER (1998) The generation of plankton patchiness by turbulent stirring. Nature 391(6667):577–580

Annett AL, Carson DS, Crosta X, Clarke A, Ganeshram RS (2010) Seasonal progression of diatom assemblages in surface waters of Ryder Bay, Antarctica. Polar Biol 33:13–29. https://doi.org/10.1007/s00300-009-0681-7

Antoni JS, Almandoz GO, Ferrario ME, Hernando MP, Varela DE, Rozema PD et al (2020) Response of a natural Antarctic phytoplankton assemblage to changes in temperature and salinity. J Exp Mar Biol Ecol 532:151444

Arntz WE, Brey T, Gerdes D, Gorny M, Gutt J, Hain S, Klages M (1992) Patterns of life history and population dynamics of benthic invertebrates under the high Antarctic conditions of the Weddell Sea. In: Colombo G et al (eds) Proceedings of the 25th European Marine Biology symposium, Ferrara, Italy, Fredensborg. Olsen & Olsen, Denmark, pp 221–230

Barnes DKA, Tarling GA (2017) Polar oceans in a changing climate. Curr Biol 27(11):R454–R460. https://doi.org/10.1016/j.cub.2017.01.045

Barrett NJ, Harper EM, Peck LS (2024) The impact of acute low salinity stress on Antarctic echinoderms. Proc R Soc Lond B 291:20241038. https://doi.org/10.1098/rspb.2024.1038

Barrett NJ, Harper EM, Peck LS (2025) Evaluating the acclimation capacity of two keystone Antarctic echinoderms to coastal freshening. STOTEN 968:178895. https://doi.org/10.1016/j.scitotenv.2025.178895

Beardsley RC, Limeburner R, Brechner Owens W (2004) Drifter measurements of surface currents near Marguerite Bay on the Western Antarctic Peninsula shelf during austral summer and fall, 2001 and 2002. Deep Sea Res II 51(17–19):1947–1964. https://doi.org/10.1016/j.dsr2.2004.07.031

Biggs TEG, Alvarez-Fernandez S, Evans C et al (2019) Antarctic phytoplankton community composition and size structure: importance of ice type and temperature as regulatory factors. Polar Biol 42:1997–2015. https://doi.org/10.1007/s00300-019-02576-3

Borup MD, Brokensha LN, Cataldo-Mendez C, Corney IHR, Gibson JAE, King SR et al (2024) Zooplankton biodiversity and life histories of common copepods in an Antarctic nearshore habitat. ICES J Mar Sci. https://doi.org/10.1093/icesjms/fsae176

Bowden D, Clarke A, Peck LS (2009) Seasonal variation in the diversity and abundance of pelagic larvae of Antarctic marine invertebrates. Mar Biol 156:2033–2047. https://doi.org/10.1007/s00227-009-1235-9

Brierley AS, Thomas DN (2002) Ecology of Southern Ocean pack ice. Adv Mar Biol 43:171–276. https://doi.org/10.1016/s0065-2881(02)43005-2

Brody SR, Lozier SM, Dunne JP (2013) A comparison of methods to determine phytoplankton bloom initiation. Geophys Res Oceans 118(5):2345–2357. https://doi.org/10.1002/jgrc.20167

Byrne M, Gall ML, Campbell H, Lamare MD, Holmes SP (2022) Staying in place and moving in space: contrasting larval thermal sensitivity explains distributional changes of sympatric sea urchin species to habitat warming. Glob Change Biol 28(9):3040–3053. https://doi.org/10.1111/gcb.16116

Cavan EL, Mackay N, Hill SL, Atkinson A, Belcher A, Visser A (2024) Antarctic krill sequester similar amounts of carbon to key coastal blue carbon habitats. Nat Commun 15:7842. https://doi.org/10.1038/s41467-024-52135-6

Clarke A, Meredith MP, Wallace MI, Brandon MA, Thomas DN (2008) Seasonal and interannual variability in temperature, chlorophyll and macronutrients in northern Marguerite Bay, Antarctica. Deep Sea Res Part II Top Stud Oceanogr 55(18–19):1988–2006. https://doi.org/10.1016/j.dsr2.2008.04.035

Clarke K, Gorley R (2015) PRIMER version 7: user manual/tutorial. PRIMER-E 192

Conroy JA, Steinberg DA, Thibodeau PS, Schofied O (2020) Zooplankton diel vertical migration during Antarctic summer. Deep Sea Res Part I Oceanogr Res Pap 162:103324. https://doi.org/10.1016/j.dsr.2020.103324

Conroy JA, Steinberg DK, Thomas MI, West LT (2023) Seasonal and interannual changes in a coastal Antarctic zooplankton community. Mar Ecol Prog Ser 706:17–32. https://doi.org/10.3354/meps14256

Cook KB, Belcher A, Bondyale Juez D, Stowasser G, Fielding S, Saunders RA et al (2023) Carbon budgets of Scotia Sea mesopelagic zooplankton and micronekton communities during austral spring. Deep Sea Res Part II Top Stud Oceanogr 210:105296. https://doi.org/10.1016/j.dsr2.2023.105296

Criales-Hernández MI, Jerez-Guerrer M, Latandret-Solanda SA, Gómez-Sánchez MD (2022) Spatial distribution of meso- and macro-zooplankton in the Bransfield Strait and around Elephant Island, Antarctic Peninsula, during the 2019–2020 austral summer. Polar Sci 32:100821. https://doi.org/10.1016/j.polar.2022.100821

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293. https://doi.org/10.1016/S0065-2881(08)60202-3

Dassow G, Emlet RB, Maslakova SA (2013) How the pilidium larva feeds. Front Zool 10(1):47. https://doi.org/10.1186/1742-9994-10-47

Dawson HM, Connors E, Erazo NG et al (2023) Microbial metabolomic responses to changes in temperature and salinity along the western Antarctic Peninsula. ISME J 17:2035–2046. https://doi.org/10.1038/s41396-023-01475-0

Deshmukh PD, George JV, Naik RK, Patil SM, Soares MA, Bhadran A, Anilkumar N (2024) Phytoplankton community structure during the melting phase of the land-fast ice in Prydz Bay, East Antarctica. Polar Sci 40:101046. https://doi.org/10.1016/j.polar.2024.101046

Devrekera D, Souissi S, Seuront L (2005) Effects of chlorophyll concentration and temperature variation on the reproduction and survival of *Temora longicornis* (Copepoda, Calanoida) in the Eastern English Channel. J Exp Mar Biol Ecol 318(2):145–162. https://doi.org/10.1016/j.jembe.2004.12.011

Ferreira A, Mendes CRB, Costa RR et al (2024) Climate change is associated with higher phytoplankton biomass and longer blooms in the West Antarctic Peninsula. Nat Commun 15:6536. https://doi.org/10.1038/s41467-024-50381-2

Grange LJ, Peck LS, Tyler PA (2011) Reproductive ecology of the circumpolar Antarctic nemertean *Parborlasia corrugatus*: no evidence for inter-annual variation. J Exp Mar Biol Ecol 404(1–2):98–107. https://doi.org/10.1016/j.jembe.2011.04.011

Hain S, Arnaud PM (1992) Notes on the reproduction of high-Antarctic mollusks from the Weddell Sea. Polar Biol 12:303–312. https://doi.org/10.1007/BF00238273

Hall CA, Lewandowska AM (2022) Zooplankton dominance shift in response to climate-driven salinity change: a esocosms study. Front Mar Sci. https://doi.org/10.3389/fmars.2022.861297

Hjort J (1914) Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp P V Reun 20:1–28

Hoegh-Guldberg OVE, Pearse JS (1995) Temperature, food availability, and the development of marine invertebrate larvae. Am Zool 35(4):415–425. https://doi.org/10.1093/icb/35.4.415

Ingels J, Vanreusel A, Brandt A, Catarino AI, David B, De Ridder C et al (2012) Possible effects of global environmental changes on Antarctic benthos: a synthesis across five major taxa. Ecol Evol 2(2):453–485. https://doi.org/10.1002/ece3.96

Johnston NM, Murphy EJ, Atkinson A, Constable AJ, Cotté C, Cox M et al (2022) Status, change, and futures of zooplankton in the southern ocean. Front Ecol Evol. https://doi.org/10.3389/fevo.2021.624692

Josey SA, Meijers AJS, Blaker AT et al (2024) Record-low Antarctic sea ice in 2023 increased ocean heat loss and storms. Nature 636:635–639. https://doi.org/10.1038/s41586-024-08368

Lamare M, Byrne M, Danis B, Deaker D, Di Luccio M, Dupont S, Foo SA et al (2024) Antarctic cushion star *Odontaster validus* larval performance is negatively impacted by long-term parental acclimation to elevated temperature. Sci Total Environ 956:177213. https://doi.org/10.1016/j.scitotenv.2024.177213

Lancraft TM, Hopkins TL, Torres JJ, Donnelly J (1991) Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). Polar Biol 11:157–167. https://doi.org/10.1007/BF00240204

Loeb VJ, Santora JA (2013) Pteropods and climate off the Antarctic Peninsula. Prog Oceanogr 116:31–48. https://doi.org/10.1016/j.pocean.2013.05.030

Mahon AR, Thornill DJ, Norenburg JL, Halanych KM (2010) DNA uncovers Antarctic nemertean biodiversity and exposes a decades-old cold case of asymmetric inventory. Polar Biol 33:193–202. https://doi.org/10.1007/s00300-009-0696-0

Marrari M, Daly KL, Timonin A, Semenova T (2011) The zooplankton of Marguerite Bay, Western Antarctic Peninsula-Part I: abundance, distribution, and population response to variability in environmental conditions. Deep Sea Res II 58(13–16):1599–1631. https://doi.org/10.1016/j.dsr2.2010.12.007

Mayzaud P, Pakhomov EA (2014) The role of zooplankton communities in carbon recycling in the Ocean: the case of the Southern Ocean. J Plankton Res 36(6):1543–1556. https://doi.org/10.1093/plankt/fbu076

Mileykovsky SA (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. Mar Biol 10:193–213. https://doi.org/10.1007/BF00352809

Morley SA, Abele D, Barnes DK, Cárdenas CA, Cotté C, Gutt J et al (2020) Global drivers on Southern Ocean ecosystems: changing physical environments and anthropogenic pressures in an earth system. Front Mar Sci 7:547188. https://doi.org/10.3389/fmars.2020.547188

Ortiz-Burgos S (2016) Shannon-weaver diversity index. In: Kennish MJ (ed) Encyclopedia of estuaries. Encyclopedia of earth sciences series. Springer, Dordrecht

Pages F (1997) The gelatinous zooplankton in the pelagic system of the Southern Ocean: a review. An Inst Oceanogr 73(2):139–158

Pearce I, Van Den Enden R, Davidson A, Wright S (2008) Seasonal changes in phytoplankton growth and microzooplankton grazing at an Antarctic coastal site. Aquat Microb Ecol 50(2):157–167. https://doi.org/10.3354/ame01149

Pearse JS (1994) Cold-water echinoderms break Thorson's rule. In: Young CM, Eckelbarger KJ (eds) Reproduction, larval biology and recruitment in deep-sea benthos. Columbia University, New York, pp 26–43

Pearse JS, McClintock JB, Bosch I (1991) Reproduction of Antarctic marine invertebrates: tempos, modes and timing. Am Zool 31(1):65–80. https://doi.org/10.1093/icb/31.1.65

Peck LS (1993) Larval development in the Antarctic nemertean *Parborlasia corrugatus* (Heteronemertea, Lineidae). Mar Biol 116:301–310. https://doi.org/10.1007/BF00350020

Peck LS (2018) Antarctic marine biodiversity: adaptations, environments and responses to change. Oceanogr Mar Biol Annu Rev 56:105–236. https://doi.org/10.1201/9780429454455-3

Peck LS, Prothero-Thomas E (2002) Temperature effects on the metabolism of larvae of the Antarctic starfish *Odontaster validus*, using a novel micro-respirometry method. Mar Biol 141:271–276. https://doi.org/10.1007/s00227-002-0834-5

Peck LS, Heiser S, Clark MS (2016) Very slow embryonic and larval development in the Antarctic limpet *Nacella Polaris*. Polar Biol 39:2273–2280. https://doi.org/10.1007/s00300-016-1894-1

Peck LS, Colman JG, Clarke A (2024) Development observed in the field of the Antarctic bivalve mollusc *Aequiyoldia eightsii* at Signy Island, South Orkney Islands. J Molluscan Stud 90(4):eyae036. https://doi.org/10.1093/mollus/eyae036

Pinkerton MH, Décima M, Kitchener JA, Takahashi KT, Robinson KV, Stewart R, Hosie GW (2020) Zooplankton in the Southern Ocean from the continuous plankton recorder: distributions and long-term change. Deep-Sea Res I 162:103303. https://doi.org/10.1016/j.dsr.2020.103303

Reeve MR, Syms MA, Kremer P (1989) Growth dynamics of a ctenophore (*Mnemiopsis*) in relation to variable food supply. II. Carbon budgets and growth model. J Plankton Res 11(3):535–552. https://doi.org/10.1093/plankt/11.3.535

Rintoul SR, Chown SL, DeConto RM et al (2018) Choosing the future of Antarctica. Nature 558:233–241. https://doi.org/10.1038/s41586-018-0173-4

Rozema P, Biggs T, Sprong P, Buma A, Venables H, Evans C, Meredith M, Bolhuis H (2016) Microbial community dynamics governed by mixed layer depth during an austral summer in Ryder Bay, Antarctica. Abstract from SCAR 2016, Kuala Lumpur, Malaysia, Ocean Ecosystems, p 212

Saba G, Fraser W, Saba V et al (2014) Winter and spring controls on the summer food web of the coastal West Antarctic Peninsula. Nat Commun 5:4318. https://doi.org/10.1038/ncomms5318

Sands CJ, Zwerschke N, Bax N, Barnes DKA et al (2023) Perspective: the growing potential of Antarctic Blue Carbon. Front Ocean Observing: Emerg Tech 36(1):16–17. https://doi.org/10.5670/oceanog.2023.s1.5

Schofield O, Saba G, Coleman K, Carvalho F, Couto N, Ducklow H et al (2017) Decadal variability in coastal phytoplankton community composition in a changing West Antarctic Peninsula. Deep Sea Res I 124:42–54. https://doi.org/10.1016/j.dsr.2017.04.014

Scolardi K, Daly K, Pakhomov E, Torres J (2006) Feeding ecology and metabolism of the Antarctic cydippid ctenophore *Callianira antarctica*. Mar Ecol Prog Ser 317:111–126. https://doi.org/10.3354/meps317111

Sewell M (2005) Examination of the meroplankton community in the south-western Ross Sea, Antarctica, using a collapsible plankton net. Polar Biol 28:119–131. https://doi.org/10.1007/s00300-004-0670-9

Shreeve R, Peck LS (1995) Distribution of pelagic larvae of benthic marine invertebrates in the Bellingshausen Sea. Polar Biol 15:369–374. https://doi.org/10.1007/BF00238488

Siegel AF (1982) Robust regression using repeated medians. Biometrika 69(1):242–244. https://doi.org/10.1093/biomet/69.1.242

Siegel DA, Doney SC, Yoder JA (2002) The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. Science 296(5568):730–733. https://doi.org/10.1126/science.1069174

Stanwell-Smith D, Peck LS (1998) Temperature and embryonic development in relation to spawning and field occurrence of larvae of three Antarctic echinoderms. Biol Bull 194(1):44–52. https://doi.org/10.2307/1542512

Stanwell-Smith D, Hood A, Peck LS (1997) A field guide to the pelagic invertebrate larvae of the maritime Antarctic. British Antarctic Survey, Cambridge

Stanwell-Smith D, Peck LS, Clarke A, Murray AW, Todd CD (1999) The distribution, abundance and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic. Philos Trans R Soc Lond 354:471–484

Swadling KM, Constable AJ, Fraser AD et al (2023) Biological responses to change in Antarctic Sea ice habitats. Front Ecol Evol 10:1073823. https://doi.org/10.3389/fevo.2022.1073823

Swart NC, Gille ST, Fyfe JC, Gillett NP (2018) Recent Southern Ocean warming and freshening driven by greenhouse gas emissions and ozone depletion. Nat Geosci 11:836–841. https://doi.org/10.1038/s41561-018-0226-1

Tarling GA, Ward P, Thorpe SA (2018) Spatial distributions of Southern Ocean mesozooplankton communities have been resilient to long-term surface warming. Glob Change Biol 24(1):132–142. https://doi.org/10.1111/gcb.13834

Thibodeau PS, Steinberg DK, Stammerjohn SE, Hauri C (2019) Environmental controls on pteropod biogeography along the Western Antarctic Peninsula. Limnol Oceanogr 64:S240–S256. https://doi.org/10.1002/lno.11041

Thorson G (1936) The larval development, growth and metabolism of Arctic marine bottom invertebrates compared with those of other seas. Medd Gronl 1:1–155

Todd CD, Doyle RW (1981) Reproductive strategies of marine benthic invertebrates: a settlement-timing hypothesis. Mar Ecol Prog Ser 4:75–83

Van Leeuwe MA, Webb AL, Venables HJ, Visser RJW, Meredith MP, Elzenga JTM, Stefels J (2020) Annual patterns in phytoplankton phenology in Antarctic coastal waters explained by environmental drivers. Limnol Oceanogr 65:1651–1668. https://doi.org/10.1002/lno.11477

Vázquez E, Ameneiro J, Putzeys S, Gordo C, Sangrà P (2007) Distribution of meroplankton communities in the Bransfield Strait, Antarctica. Mar Ecol Prog Ser 338:119–129. https://doi.org/10.3354/meps338119

Venables H, Clarke A, Meredith MP (2013) Wintertime controls on summer stratification and productivity at the western Antarctic Peninsula. Limnol Oceanogr 58(3):1035–1047. https://doi.org/10.4319/lo.2013.58.3.1035

Venables H, Meredith MP, Hendry KR et al (2023) Sustained year-round oceanographic measurements from Rothera Research Station, Antarctica 1997–2017. Sci Data 10:265. https://doi.org/10.1038/s41597-023-02172-5

Zwerschke N, Sands CJ, Roman-Gonzales A, Barnes DKA, Guzzi A, Jenkins S, Muñoz-Ramírez C, Scourse J (2021) Quantification of blue carbon pathways contributing to negative feedback on climate change following glacier retreat in West Antarctic fjords. Glob Change Biol 28:8–20. https://doi.org/10.1111/gcb.15898