



Sediment trap illustrates taxon-specific seasonal signals in Southern Ocean zooplankton

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Abstract

Southern Ocean zooplankton provide globally significant ecosystem services through their role in carbon sequestration, nutrient cycling and food webs. However, the remote and extreme nature of the Southern Ocean creates significant logistical difficulties for studying zooplankton all year round. Here, for the first time in the Southern Ocean, we present the seasonal occurrence of the zooplankton assemblage in the Northeast Scotia Sea using a sediment trap deployed throughout 2018 (P3 observation site, 52.80° S, 40.14° W). Results show that copepods and pteropods dominated trap abundance, representing 25.0–68.3% and 13.4–72.5% respectively, followed by amphipods (1.0–7.2%) and hydrozoa (0.2–15.6%). The dominant signal in copepods was consistent with previous observations using traditional (net) sampling methods while the relative contribution of pteropods, amphipods and hydrozoa was increased in our trap. Further, zooplankton showed taxon-specific seasonal signals, with a relatively high number of individuals throughout winter, including an increase in hydrozoa occurrences. This observation highlights the importance of zooplankton as source of nutrition for the benthic community in the winter. Our data reiterate the utility of sediment traps for observing zooplankton in remote locations and sampling specific taxa that might be otherwise understudied.

Keywords Zooplankton · Copepods · Pteropods · Gelatinous · Amphipods · Sediment trap · Southern Ocean · Winter

Introduction

The zooplankton present in the Southern Ocean support a vast and unique food web, whilst also driving biologically mediated carbon sequestration and nutrient cycling (Pinkerton et al. 2020; Johnston et al. 2022). These processes are heavily influenced by the type of zooplankton present (Richardson 2008; Benedetti et al. 2021). However, the Southern Ocean is an extensive, heterogeneous ecosystem, with the zooplankton assemblage varying with temperature, sea ice conditions, and nutrient content (Pinkerton et al. 2020). The Scotia Sea, located in the Atlantic sector of the Southern Ocean, is one of the most productive regions in Antarctic

waters with up to $\sim 10 \text{ mg m}^{-3}$ chlorophyll-*a* (Holm-Hansen et al. 2004). In the Northeast Scotia Sea, downstream of South Georgia, this productivity is translated into a highly effective carbon sink (Manno et al. 2022), although the presence and intensity of phytoplankton blooms can be highly patchy (Korb et al. 2005). Variability in phytoplankton composition influences the zooplankton community (Ward et al. 2012), with the zooplankton community composition also influencing the strength of the carbon sequestration (Liszka et al. 2019).

When compared to other areas of the Southern Ocean, the Scotia Sea has been subject to relatively extensive ecological study, with zooplankton surveys dating back to the 1920s (Kemp et al. 1929; Ward et al. 2008). Most famously, the Southern Ocean zooplankton community, including the Scotia Sea, was initially characterised by the Discovery Investigations (1924–1951) (e.g. Barnard 1932; Stiansy and Leiden 1934; Hardy and Gunther 1935). These expeditions included an effort to characterize zooplankton seasonality, and included winter sampling. These expeditions provided vital insight into zooplankton distribution and life cycles, which still provide important results when reanalysed (e.g.

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Atkinson and Sinclair 2000; Ward et al. 2014). However, sampling the Southern Ocean throughout the year remains a considerable logistical and financial endeavour. Consequently, the majority of contemporary zooplankton surveys consist of net sampling in the spring and summer (broadly focussing on the top 200 m) (e.g., Ward et al. 2004; Pakhomov et al. 2020; Cook et al. 2023). Some studies have aimed to address this seasonal bias (e.g., Atkinson et al. 1990; Ward et al. 2012), though consistent winter monitoring has not been achievable. Limited long-term data, as well as a lack of winter data, are hindering our ability fully understand zooplankton distribution and behaviour. A comprehensive understanding of modern zooplankton communities is crucial for determining the resilience of this community as well as predicting the state of the Southern Ocean system under rapid climate change (Johnston et al. 2022).

Sediment traps were developed to quantify sinking particulate matter, which also includes sinking of zooplankton carcasses. Yet, zooplankton can actively swim into the trap. These specimens (swimmers) are not part of the particulate flux and consequently, biogeochemists have had to incorporate extra processing steps to remove swimmers prior to analysis. Recently, however, swimmers in sediment traps have become the focus of ecological studies themselves. Amphipods (Kraft et al. 2012, 2013; Ramondenc et al. 2022) and pteropods (Gardner et al. 2023) collected from sediment trap samples have been investigated in the Fram Strait and Scotia Sea respectively, providing new insight in their life history and ecology. Studies looking to assess the entire zooplankton assemblage have focused on various locations such as Beaufort Sea (Makabe et al. 2010), Franklin Bay (Makabe et al. 2016), Western North Pacific (Yokoi et al. 2018) and the Mediterranean Sea (Danovaro et al. 2017).

In comparison to a ship-based (net) sampling campaigns, sediment traps are a far cheaper logistical and financial investment, facilitating vital year-round remote sampling, with discrete time windows. This is particularly advantageous in remote locations, such as the Southern Ocean, which are difficult to access outside of spring and summer. For the first time, this study examines all zooplankton caught in a sediment trap deployed northwest of South Georgia. It aims to evaluate the taxonomic diversity within the trap and, where present, identify seasonal signals in trap occurrence. By presenting this novel data, this study looks to contribute to the growing number of ecology-based sediment trap studies, highlighting their utility for zooplankton monitoring in remote locations.

Materials and methods

Sampling

The sediment trap (McLane PARFLUX, 0.5 m² capture area; McLane labs, Falmouth MA, USA) was located at the observation site P3 (Fig. 1a) in Northeast Scotia Sea (52.80° S, 40.14° W). The sampling location is a productive area of the Southern Ocean associated with consistent and strong phytoplankton blooms (Borrione and Schlitzer 2013). The sediment trap was deployed at 400 m and secured using a mooring line anchored to the seabed at 3748 m depth. The trap was deployed from 25/01/2018 until 31/12/2018 during research cruise JR17002, *RSS James Clark Ross* (recovered during research cruise DY098; *RRS Discovery*). The mooring line also contained a CTD (SBE-37) at 200 m depth, and a Seagard™ current meter at 350 m, which recorded throughout deployment. The P3 mooring is part of an ongoing observation programme (Scotia Open Ocean Observatory, SCOOBIES, <https://www.bas.ac.uk/project/scoobies/>).

The trap was fitted with 500 ml bottles filled with a formalin solution (filtered seawater containing 2% v/v formalin, mixed with sodium tetraborate (BORAX; 0.025% w/v), and 0.5% w/v sodium chloride) to preserve organic material and prevent mixing with the water column. The trap was fitted with a baffle to prevent larger organisms entering. The bottles are placed in a carousel pre-programmed to rotate under the funnel and collect material every month (28–31 days, Supplementary Table 1). Once recovered, samples were stored at 4 °C until analysis.

Sample processing and swimmer identification

In total, 14 collection bottles were analysed for swimmers. Specimens were identified and counted under an Olympus SZX16 fitted with a canon EOS 60D DSLR camera. For small individuals (< 1 mm) samples were analysed in sub-aliquots, with totals estimated from the aliquots, otherwise, bottles were analysed in their entirety.

We have classified swimmers as any intact animal. Animals with shells (e.g., pteropods) are prone to more damage during storage and handling, consequently they were still considered “intact” where there was minor (non-structural) damage to the shell and the somas was still present and whole. In this study we do not discriminate between swimmers and carcasses (i.e., zooplankton that have died shortly before sinking into the trap). However, Ivory et al. (2014), found the number of swimmers to be an order of magnitude higher than sinking carcasses, indicating they are a relatively minor component of the trap.

Swimmers were identified to class or order, where possible, with classification aiming to resolve to highlight

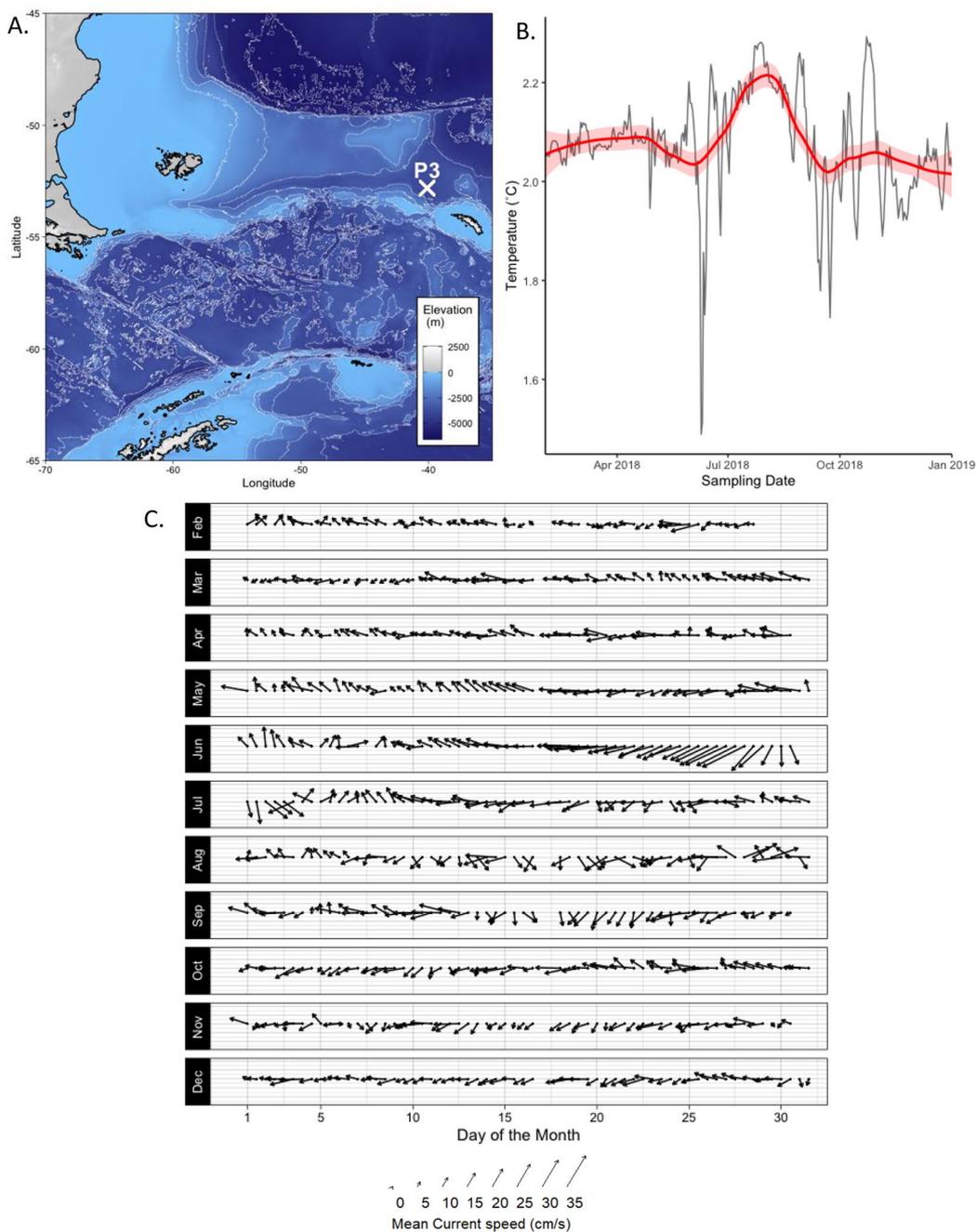


Fig. 1 (A) Location of the sediment trap mooring in the Northeast Scotia Sea; P3 (52.80° S, 40.14° W) deployed between 25/01/2018–01/12/2018. (B) Temperature at the P3 mooring at 200 m during deployment of the sediment trap. Daily mean temperature is represented in grey. Smoothed temperature (using loess method) with a 95% confidence interval is represented in red. (C) Current vector

stick plots of filtered (de-tided with 33-hour half amplitude period) current data collected from 350 m during sediment trap deployment. Smoothed data are shown every 12 h. Arrow length relates to current speed (cm/s), as indicated by the scale bar, and arrow angle indicates current direction (degrees). Adapted from Belcher et al. (2023)

ecologically important zooplankton groups. For example, salps (order salpida) and appendicularia are within the subphylum tunicate yet salps and appendicularians were highlighted due to their high abundance and contribution to zooplankton dynamics in the Southern Ocean ecosystem

(Atkinson et al. 2012). The number of swimmers within each taxonomic group per month are defined as the occurrence (in the trap). Swimmer size was measured using callipers accurate to 0.5 mm. In addition to occurrence, we were able to collect alternative observations such as the presence

of other animal products (e.g., exuviae and eggs). Exuviae were often fragmented in the trap, as such each fragment was counted once, regardless of size. Eggs were noted but not counted (Supplementary Table 1).

To assess taxonomic diversity and richness, swimmer identities were reclassified to class level, where possible. The swimmer IDs: Ctenophores, Fish Larvae, Tunicates and Unidentified, could not be assigned to class and were excluded from the analysis, resulting in 11 classes (Supplementary Table 2). The number of classes present in the sample for each month were totalled.

Data analysis

All data wrangling and figure generation was carried out in R (Version 4.2.3, R Core Team 2023). Daily mean temperatures were calculated, encompassing the sampling period from 01/02/2018 to 01/01/2019. Overall, trends in temperature were highlighted by locally estimated scatter plot smoothing (LOESS), with a span of 0.4. Because zooplankton actively enter the trap, we cannot assume random sampling. Therefore, Brillouin's Diversity Index (calculated using class) was used to assess diversity within each month using Eq. (1).

$$B = \frac{\ln N! - \sum \ln n_i!}{N} \quad (1)$$

Where B is Brillouin's Diversity Index, N is the total number of zooplankton and n_i is the total number of zooplankton within a specified class (i).

Table 1 Taxonomic richness and diversity of zooplankton swimmers occurring in the P3 sediment trap (Northeast Scotia Sea, 52.80° S, 40.14° W). Swimmers were reclassified to class level for richness and diversity metrics. Swimmers that could not be classified to class level were excluded from that analysis (Supplementary Table 2)

Month	No. of Classes (richness)	Brillouin diversity index
February	7	0.92
March	7	0.70
April	7	0.84
May	7	1.12
June	6	1.31
July	7	0.98
August	6	0.99
September	6	0.98
October	7	0.91
November	8	0.85
December	9	1.09

Results

The temperature at the P3 mooring site (200 m depth) varied between 1.47 and 2.29 °C (Fig. 1b). Temperatures were relatively stable in up until April/May 2018, where daily fluctuations in temperature started to increase, with a maximum change of 0.43 °C from 09/06/2018 to 10/06/2018. Smoothed temperature data indicate a small increase in temperature during winter of ~0.2 °C. Current velocity data indicate the peak in flow rate and directional variability occurred in June and July with minima in February and March (Fig. 1c).

A broad range of taxa (including 11 different taxonomic classes) were observed throughout the year with the peak in taxonomic diversity occurring in June, with a Brillouin diversity index of 1.31) with minima in March of 0.70 (Table 1). These results differ from the number of classes present which are relatively stable throughout, peaking in December with 9 classes present. There was a strong seasonal signal in the total number of zooplankton occurrences in the trap (ranging between 5480 and 184), with peaks in spring/summer (February) and minima in winter (July, August and September) (Fig. 2a). The dominant zooplankton groups in the sediment trap were copepods and pteropods. Smaller copepods and pteropods (<1 mm) contributed between 21.9 and 63.4% and 9.8–72.4% of monthly zooplankton occurrence respectively, while larger individuals (copepods <9 mm and pteropods <24 mm) were consistently present in lower abundances (<35% of monthly occurrence) (Fig. 2b). Amphipods (1–32 mm), and hydrozoa (3–21 mm) were also present throughout the year reaching up 7.2% and 15.6% of the total zooplankton abundance respectively (Fig. 2c).

Given the high occurrence of small individuals, the pattern in copepod and pteropod occurrence follows a similar trend of the total zooplankton assemblage, with a strong peak in February followed by minima in June and July (Fig. 3a, b). Amphipods also had a distinct seasonal signal, peaking in February, with a minimum in July and August (Fig. 3c). The peak in amphipod occurrence in February peak included 264 juveniles (<1 mm), clear outlier relative to other months which contained only larger amphipods (>1 mm). In contrast to amphipods, pteropods and copepods, the occurrence of medusozoa increased in winter (peaking in May) and decreased in spring/summer (minimum in November) (Fig. 3d).

Eggs and exuviae were observed throughout the sampling period (Supplementary Table 1). The overwhelming majority of exuviae were from Euphausiids. There were also a number of different eggs caught in the trap including fish eggs, pteropod eggs and amphipod eggs. These eggs were in various stages of development, including some partially

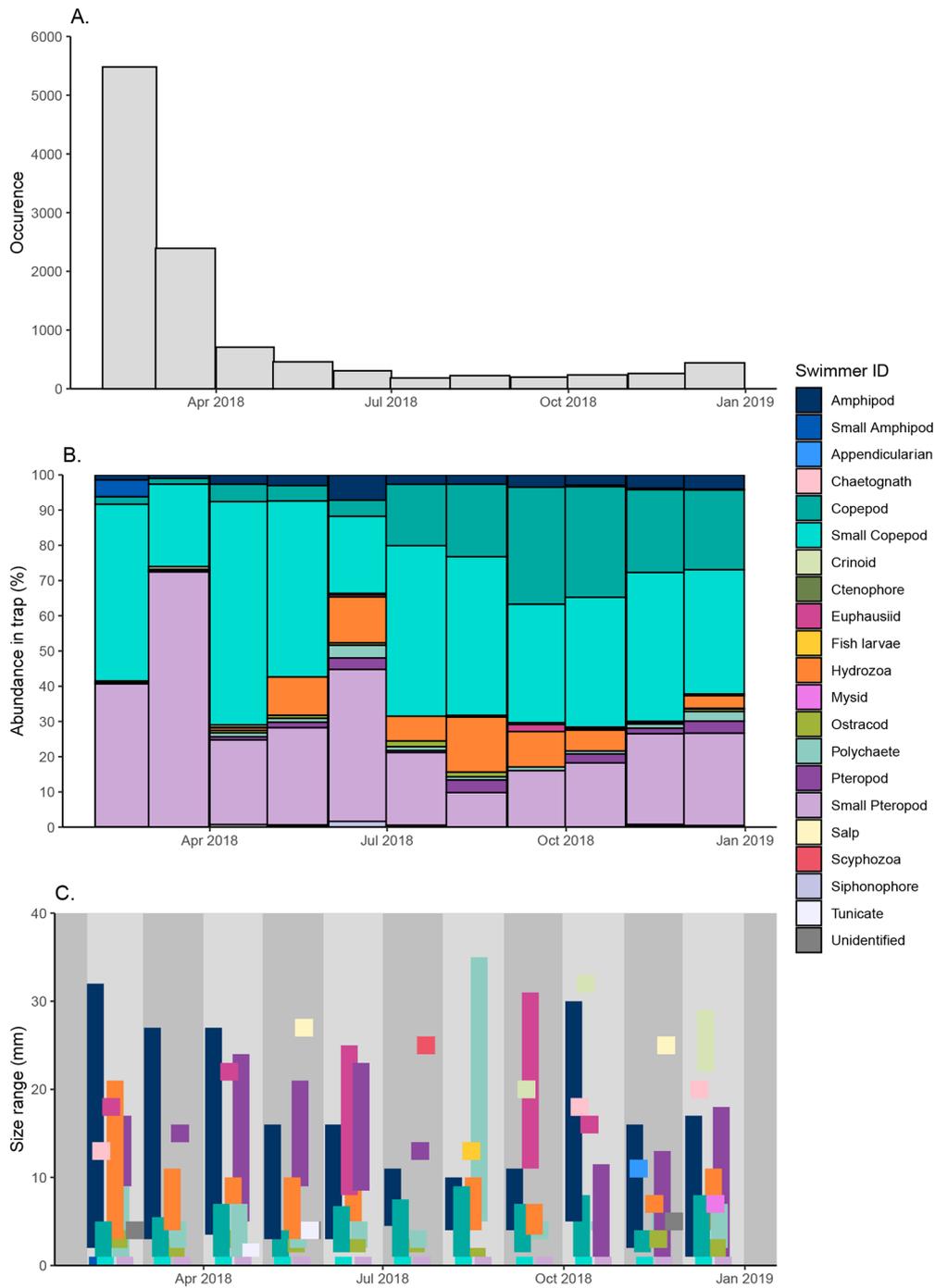


Fig. 2 Occurrence (A) and abundance (%) (B) of swimmers in the P3 sediment trap per month with the size (mm) range (C) of swimmers within their taxonomic group. The trap was deployed at 400 m depth

and was located off the coast of South Georgia in the Northeast Scotia Sea (52.80° S, 40.14° W). Collection bottles sampled for a calendar month

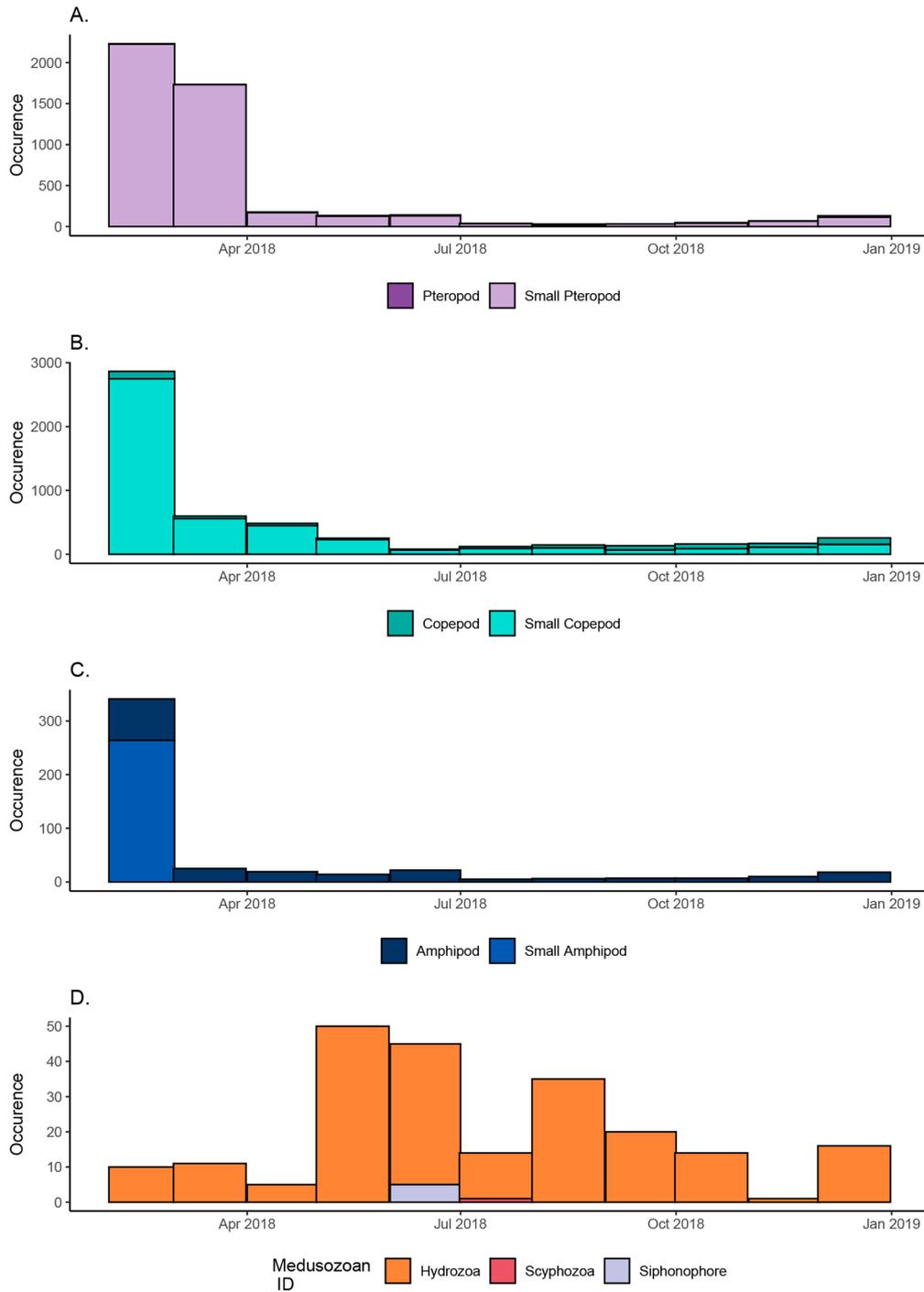


Fig. 3 The occurrence of pteropods (A) copepods (B), amphipods (C) and medusozoans (D) in the P3 sediment trap in the Northeast Scotia Sea (400 m, 52.80° S, 40.14° W). The collection bottles sampled for a calendar month

hatched. In addition, multiple ephemeral breeding events were captured. In February, April, June and November, amphipods were preserved whilst still holding their clutch (Supplementary Table 1; Supplementary Fig. 1). Multiple photographs of the zooplankton and the biological material captured are available in the supplementary materials (Supplementary Fig. 1).

Discussion

The observed broad range of taxa in the trap, were generally consistent with previous zooplankton studies around South Georgia using traditional sampling techniques (i.e., net). These studies highlight important taxa such as copepods, euphausiids, pteropods and chaetognaths (Ward et al. 1995; Atkinson et al. 1996; Pakhomov et al. 1997; Shreeve et al. 2002) as well as the presence of amphipods, appendicularia, ostracods, polychaetes, salps and siphonophores (Atkinson et al. 1990; Liszka et al. 2019, 2022). All the studies mentioned above are focused on the spring/summer seasons. Here we show that the zooplankton presence and composition in this region is also relatively dynamic during the winter period. We found that copepods and pteropods dominate the zooplankton assemblage in the trap. Our observations of copepods (25.0–68.3% trap abundance) agree with previous zooplankton net studies in this region where, though sampling techniques and depth vary, copepods represent 30–100% of the total zooplankton assemblage in this region (Ward et al. 2005, 2012; Liszka et al. 2019, 2022; Cook et al. 2023). However, maximum contribution of copepods in our samples is comparatively lower, highlighting the relative importance of other taxa, such as pteropods. Indeed, pteropod contribution to the total zooplankton assemblage from net samples is usually much lower (0.1–13.1% of the total zooplankton assemblage) than the observed contribution in our study (13.4–72.5%) (Atkinson and Peck 1988; Ward et al. 2005). We observed a strong seasonal signal in copepod abundance, despite the multiple genera within this broad taxonomic group (Fig. 3b). Studies surveying zooplankton in the Scotia Sea in winter are scarce and tend to be more focused on the coast of South Georgia for logistical reasons. However, a study assessing zooplankton compositions around South Georgia in summer 1981 and winter 1983 (Atkinson and Peck 1988) found an overall drop in winter zooplankton biomass and abundance in the top 1000 m. The decrease in zooplankton biomass was mainly attributed to a drop in the abundance of copepods. This is consistent with our data if we compare February and April (months with the highest copepod occurrences) to June and July, where the occurrence of copepods substantially decreased. Though copepods and pteropods were dominant throughout the year,

the extent of this dominance varied seasonally. In summer/early autumn, copepod and pteropod occurrence was nearly two orders of magnitude higher than other taxa, whereas for the rest of the year, their occurrence was more comparable with taxa such as amphipods and hydrozoa. This result was reflected in the Brillouin diversity index, which shows minimum values across February, March and April, when copepod and pteropod occurrence was highest. Amphipods and hydrozoa also represented a relatively significant proportion of trap abundance (1.0–7.2% and 0.2–15.6%, respectively), yet in previous studies in this region, amphipods and hydrozoa comprise such a small component of the zooplankton assemblage their abundance is rarely reported or enumerated specifically (e.g., Atkinson and Peck 1988; Ward et al. 2005, 2012; Liszka et al. 2019; Cook et al. 2023).

Differing proportions of taxa between net sampling and sediment traps have been reported before, where it was hypothesised entrapment rate in sediment traps may be taxon specific (Makabe et al. 2016). For example, vertical migration or feeding mode may facilitate the entrapment of some specific species or taxonomic groups. For pteropods, differences with previous studies may also reflect net-avoidance behaviour, or different mesh sizes excluding particular cohorts (Hunt et al. 2008; Bednaršek et al. 2012; Gardner et al. 2023). The sampling depth of the sediment trap (400 m) may also influence the proportion of zooplankton caught. The trap caught very few euphausiids (Fig. 2b, c), likely reflecting that euphausiids tend to gather at the surface (first 100–250 m) (Kalinowski and Witek 1980; Kane et al. 2018). However, evidence of their presence in the upper ocean is indicated in the trap as the vast majority of exuviae originated from euphausiids (Supplementary Table 1). In addition, Ward (1989) found the proportion of non-copepod zooplankton biomass increased with depth, with this change largely driven by both copepod biomass reducing and non-copepod biomass increasing. This may help explain the greater proportion of non-copepod biomass (e.g., pteropod, amphipod, hydrozoa) observed in the trap, relative to previous studies.

We identified two different suborders of amphipods, Amphilochidea and Hyperiidea, with the majority of amphipods present being hyperiids (when the outlying 264 juvenile *Parandania* sp. are excluded) (Supplementary Table 3). Though understudied in the Scotia Sea (Murphy et al. 2007), amphipods in the Ross Sea were found from 0 to 700 m, with adult abundance peaking in the surface, and juvenile amphipods often residing in deeper substrata (200–500 m) (Minutoli et al. 2023). We observed multiple amphipod breeding events, including *Primno* sp. with an egg clutch in November, *Scina* sp. with egg clutches in April and June as well as 264 small (< 1 mm), juvenile *Parandania* sp. in February and a *Parandania* sp. with its clutch in October (Fig. 2a,

b, Supplementary Fig. 1). In the Fram Strait, sediment trap time series studies have been used to identify seasonal occurrence, breeding strategy and cycle length in multiple amphipod species (Kraft et al. 2012, 2013; Ramondenc et al. 2022). Analysis of breeding strategy was achieved by observing the seasonal signal in juveniles as well as females with developing eggs. Amphipod species have highly plastic reproductive strategies which can become more seasonal with increasing latitude (Sainte-Marie 1991; Weslawski and Legeżyńska 2002; Watts and Tarling 2012). However, the ecology of Antarctic amphipods is still relatively poorly resolved (Nyssen et al. 2005; Murphy et al. 2007). To our knowledge, there are currently no studies investigating the reproductive strategy of any of the reproducing amphipods present in our trap. Our data indicate incorporating sediment trap occurrence at time series sites could improve our understanding of amphipod reproductive strategies in the Southern Ocean, where there is both high amphipod diversity and a high number of endemic species (Arfianti and Costello 2020).

We observed a “reverse” seasonal trend in medusozoa occurrence, with a peak May and June (winter) and a minimum in December (summer). The overwhelming majority of medusozoa in the trap were classified to the hydrozoa subgroup (3–21 mm) (Fig. 3d), including only the medusa stage (Supplementary Fig. 1). Previous studies have shown the distribution pattern of hydromedusa in the western South Atlantic to be seasonal and strongly linked with local water masses. However, these studies observed hydrozoa density peaks in summer (100 ind. m^{-3}) and autumn (> 40 ind. m^{-3}) (Vannucci 1957; Goy 1979; Zamponi and Genzano 1994). The latitudinal ranges of medusozoa of the Southern Ocean have been attributed to Antarctic endemics, originating from the continental shelf which can be upwelled around the Polar Front area, or cosmopolitan species, which can be transported out of their regular distribution range into Antarctic waters through horizontal advection (Lindsay et al. 2014). Consequently, the observed peak in hydrozoa occurrence may be linked to shifts in the Polar Front during winter, which cause stronger water mixing, and bring warmer sub-Antarctic and Deep Circumpolar water. Indeed, Atkinson and Peck (1988) observed Antarctic epipelagic species that naturally occur around South Georgia in the summer season are often replaced by sub-Antarctic or cosmopolitan species during the winter. In our study, smoothed temperatures at 200 m do show an increase of ~ 0.2 °C in winter, however, hydrozoa occurrence peaks in May, several months before the temperature maximum in August (Fig. 1b). The peak in hydrozoa occurrence does coincide with more variability in daily mean temperatures, suggesting that increased occurrence may be a result of changing hydrography, increased mixing and intrusion of warmer water masses. However,

current velocity data from 350 m on the P3 mooring show the peak in flow rate and directional variability occur in June and July, mirroring patterns in smoothed temperature as opposed to hydrozoa occurrence (Fig. 1c).

As consumers with low nutritional content themselves, gelatinous zooplankton (including hydrozoa) have previously been regarded as tropic ‘dead ends’, not contributing to economically important food webs (e.g., fish stocks) (Verity and Smetacek 1996). However, predation upon gelatinous zooplankton is far more widespread than previously thought and can confer additional nutritional benefits, with predators consuming gelatinous zooplankton also consuming the plankton caught in oral arms and stomachs (Thiebot et al. 2016; Hays et al. 2018). In addition, though less energetically dense than other animals (e.g., fish, copepods) gelatinous zooplankton may be digested at a far higher rate, counterbalancing the nutritional deficit (Arai et al. 2003). However, gelatinous zooplankton like the hydrozoa, are soft and extremely delicate bodied and as a such they do not fare well in net sampling, contributing to a lack of consistent, long-term data (Licandro et al. 2015). As a gentler method, sediment traps have the potential to play a significant role in improving our understanding of gelatinous zooplankton ecology as well as their role in Southern Ocean food webs.

Sediment traps have become valuable tools in studying ecology and life history strategy throughout the year, especially in remote locations. Though the trap occurrence of zooplankton cannot yet indicate absolute abundance, as with other more quantitative methods (e.g., net sampling), seasonal sediment trap sampling windows are comparable to each other, giving rare insight into zooplankton occurrence throughout the year. Our results indicate, taxon specific seasonal signals in occurrence whilst highlighting understudied taxa, including hydrozoa and amphipods, and re-emphasise the utility of sediment traps for assessing seasonal trends of zooplankton communities in isolated regions such as the Scotia Sea. Further, the observation of relatively high numbers of zooplankton during the winter supports their importance as a source of nutrition to fuel the benthos through this season. Future work in this region should look to increase the taxonomic and temporal resolution presented in this study, providing further insight into species-specific seasonal ecology. Studies should work towards coupling sediment trap zooplankton occurrences with traditional monitoring methods, providing a systemic view of ecosystem functioning.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-024-04487-2>.

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Declarations

Conflicts of interest The authors declare that they have no conflicts of interest. CM was supported by UK Research and Innovation Future Leaders Fellowships project CUPIDO (MR/T020962/1). Work was carried out as part of the Ecosystems programme at the British Antarctic Survey and the Scotia Sea Open Ocean Laboratories (SCOOBIES) sustained observation programme at the British Antarctic Survey in the frame of a Western Core Box-POETS survey cruise (<https://www.bas.ac.uk/project/scoobies/>). Data are available from the UK Polar Data Centre (<https://doi.org/10.5285/F803893C-7978-42CF-993A-E0886DC32A9A>). FA conducted the laboratory work, analysed the data and wrote the manuscript with input from CM and AS. CM conceived and planned the study, conducted fieldwork, supervised the project and contributed to the interpretation of results. AS contributed to interpretation and the manuscript.

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