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RESEARCH ARTICLE

Seasonally migrating zooplankton strongly enhance Southern Ocean carbon sequestration

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Abstract

High-latitude zooplankton can sequester millions of tons of carbon due to their seasonal migration from the surface ocean to depth, and their respiration and mortality during overwintering. This seasonal vertical migration pump (SVMP) efficiently removes carbon but not limiting nutrients such as iron from the surface layers. However, this process is not included in Earth System Models and whole Southern Ocean estimates are still lacking. Here, we compile large datasets of Southern Ocean zooplankton biomass and physiology to estimate that the SVMP transports 65 Mt carbon annually to sequestration-achieving depths of > 500 m. Mesozooplankton are the main agents (80%), followed by krill (14%), and salps (6%), with respiration and mortality at depth contributing a similar share. This SVMP adds greatly to existing modeled or measured estimates of Southern Ocean carbon sequestration, equating to 38–56% of particulate organic carbon flux at 500 m and 78–103% of the flux at 1000 m. Given their large biomass but projected change under polar warming, understanding how zooplankton transport carbon and nutrients will underpin improved model projections of ocean carbon storage in a warmer world.

Zooplankton provide a vital connection between primary producers and higher trophic levels within marine ecosystems and play a significant role in the Biological Carbon Pump (Steinberg and Landry 2017). Current research focuses predominantly on their role in passive sinking mechanisms, including fecal pellets, molts, and carcasses as drivers of carbon export through the mesopelagic layer (Steinberg and Landry 2017; Belcher et al. 2019; Manno et al. 2020). However, zooplankton can also affect the efficiency of the carbon pump through active processes, such as vertical migration and fragmentation of sinking particles, and these combined particle injection pumps may sequester as much carbon as the passive gravitational pump (Boyd et al. 2019; Briggs et al. 2020). These significant but hitherto understudied active processes remain major challenges for the reduction of uncertainties in forecasting trends in future carbon export flux (Henson et al. 2022; Nowicki et al. 2022; Siegel et al. 2023; Stukel et al. 2023). Better understanding of how vertically migrating zooplankton sequester carbon is urgently needed to facilitate their integration into Earth System Models (Boyd et al. 2019; Wang et al. 2023).

At high latitudes, copepods and other zooplankton species accumulate significant lipid reserves through feeding in summer and then vertically migrate to deeper waters to overwinter

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(Johnston et al. 2022). During this process, lipids stored in summer provide zooplankton with energy for respiration or can be a source of prey for midwater predators (Halfter et al. 2022; Tarling et al. 2022). The process by which zooplankton catabolize stored lipids at depth during winter efficiently releases carbon directly into the deep sea, and their combined respiration and mortality at depth has been termed the "lipid pump" (Jónasdóttir et al. 2015). Zooplankton typically have much higher carbon to iron ratios than phytoplankton (Schmidt et al. 2016; Le Mézo and Galbraith 2021), so the lipid pump efficiently injects carbon to sequestration depths with relatively little loss of limiting nutrients. Lipid pump studies have mainly focused on dominant copepod species (e.g., *Calanus finmarchicus* and *Calanus hyperboreus*) in the North Atlantic, North Pacific, and Arctic regions, and the results reveal that even a single species can contribute considerably to the total downward carbon flux in high-latitude northern seas (Jónasdóttir et al. 2015; Visser et al. 2017; Tarling et al. 2022).

The Southern Ocean plays a key role in global carbon sequestration and climate regulation (Long et al. 2021). Despite its massive zooplankton biomass (Atkinson et al. 2017; Yang et al. 2022) and well-documented, extensive, seasonal migrations of biomass-dominant zooplankton (Foxton 1956, 1966; Siegel 2005), the lipid pump in the Southern Ocean has been surprisingly neglected (Bradford-Grieve et al. 2001; Shreeve et al. 2005; Pinti et al. 2023). Lipid pump studies, whether in the north or south, have hitherto focused on respiration losses from lipid-rich copepods. However, in the Southern Ocean, a wide range of zooplankton taxa are known to vertically migrate to overwinter, including various copepod species, krill and salps (Mackintosh 1937; Foxton 1956, 1966; Atkinson and Sinclair 2000; Siegel and Watkins 2016). Through growth in surface waters in summer and respiration and mortality at depth in winter, they all contribute to carbon sequestration. Our approach differs from previous attempts because we have compiled literature data to estimate carbon export from respiration and mortality for the total seasonally migrating biomass, including mesozooplankton, krill and salps. Accordingly, we hereafter term this carbon sequestration process more broadly as the "seasonal vertical migration pump" (SVMP), rather than the lipid pump.

The objectives of this study are: (i) to quantify the SVMP of mesozooplankton, krill, and salps, (ii) to clarify the respective contributions of respiration and mortality to the SVMP, and (iii) to evaluate whether the SVMP is a substantial contributor to Southern Ocean carbon flux. We calculated that the seasonal migrant pump is at least half that of the particulate organic carbon (POC) export at an equivalent depth. Furthermore, we demonstrate that the SVMP is dominated by mesozooplankton, rather than by krill or salps, and that deep respiration and mortality contribute in roughly similar portions.

Data and methods

Four combining factors, namely the biomass, respiration, mortality, and length of overwintering period of migrating populations are important parameters which determine the strength of the SVMP (Jónasdóttir et al. 2015; Visser et al. 2017; Tarling et al. 2022). In this study, we aim to quantify the SVMP within three dominant zooplankton functional groups, namely mesozooplankton (mainly small metazoan zooplankton, dominated by copepods and excluding Antarctic krill and salps, Table S1), krill (Antarctic krill: *Euphausia superba*) and salps (aggregates and solitaries of all species, mainly *Salpa thompsoni* and *Ihlea racovitzai*).

Biomass

Mesozooplankton

The mesozooplankton biomass in the upper water column (0–250 m) was derived from our compiled dataset covering the years 1926–2020 (Yang et al. 2022). Given that most records in our dataset (74.8%) originated from the months November, December, January, February, and March, we consider these "summer" records to provide a more precise estimate of the total mesozooplankton biomass in the Southern Ocean. In this study, the Southern Ocean refers to the region covering the nine marine protected area planning domains defined by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) around Antarctica, with a total area of approximately 36 million km^2. The biomass of mesozooplankton in each planning domain was calculated by averaging values from all stations within the domain while accounting for its area. Our data show that the combined carbon biomass for mesozooplankton in 0–250 m of the Southern Ocean (summed across all planning domains) amounts to 67 Mt (Yang et al. 2022).

Based on a circumpolar study of mesozooplankton biomass across various months (Foxton 1956), there is relatively little seasonal variation in the median value of zooplankton biomass in the Southern Ocean (displacement volume ranging from 6.2 to 9.8 mL) throughout the entire year and across the water column (0–1000 m). We assume that the entire mesozooplankton population remains concentrated in the top 1000 m with consistent total biomass year-round in the Southern Ocean. Month-specific ratios of biomass in the 0–250 m and 500–1000 m strata to the total biomass in the 0–1000 m stratum (i.e., $B_{0\text{–}250\text{m}}/B_{0\text{–}1000\text{m}}$, $B_{500\text{–}1000\text{m}}/B_{0\text{–}1000\text{m}}$) were calculated (refer to Fig. 1b) based on previous studies (Foxton 1956; Hopkins 1971) and were utilized to estimate the biomass of seasonally migrating mesozooplankton. Using the median value (0.51) of $B_{0\text{–}250\text{m}}/B_{0\text{–}1000\text{m}}$ in summer (spanning November to March), the total mesozooplankton biomass in the top 1000 m of the Southern Ocean was calculated as 132 Mt C. Some individuals reside in deep waters permanently or for extended periods (Johnston et al. 2022) and this fraction should be removed from the SVMP calculation

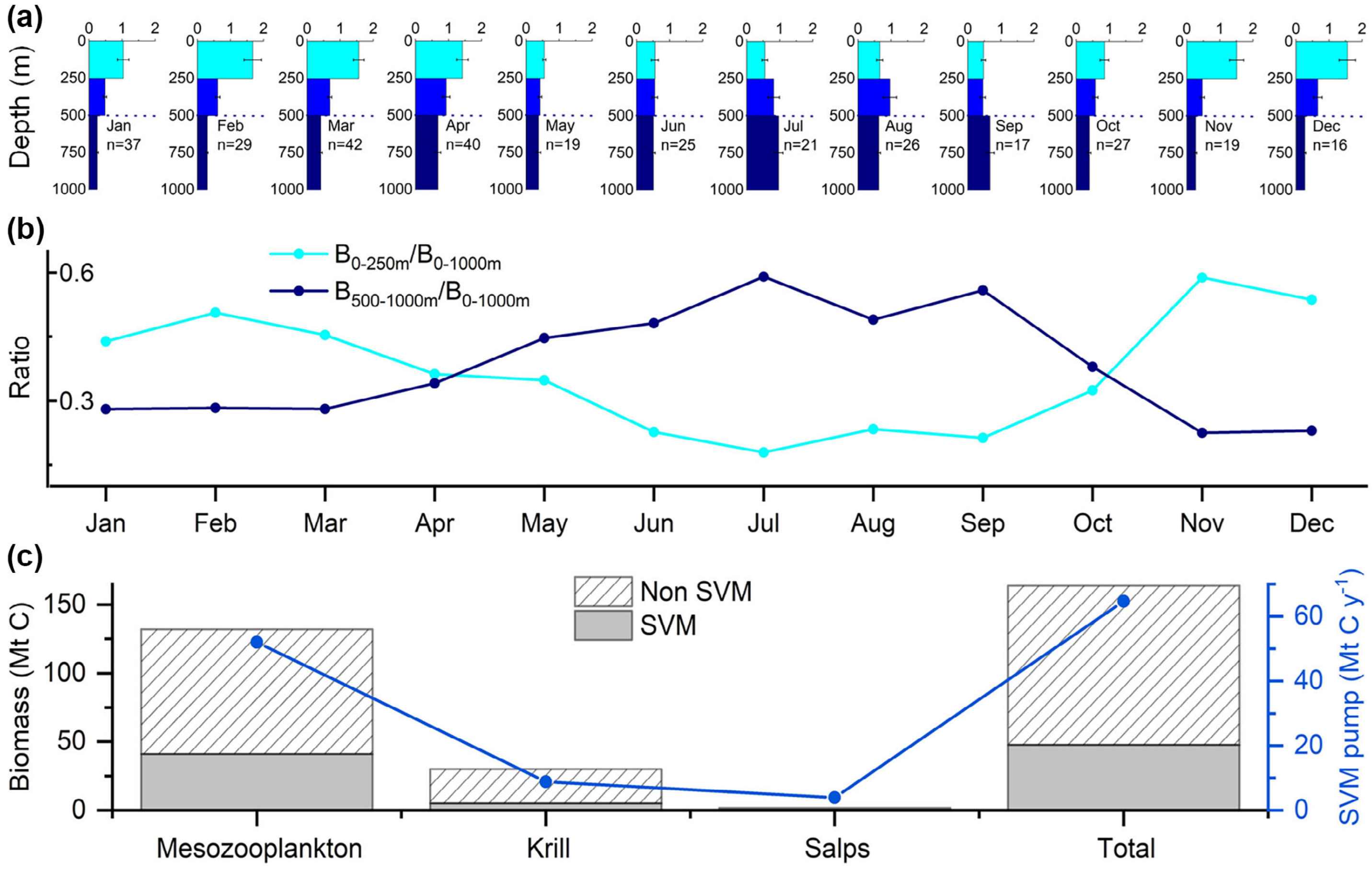

Fig. 1. Source biomass and seasonal vertical migration pump (SVMP) of mesozooplankton, krill, and salps. (**a**) Month-specific biomass (carbon biomass, mg C m^{-3}) of mesozooplankton in the three key depth strata (0–250 m, 250–500 m, 500–1000 m) based on data from Foxton 1956 and Hopkins 1971. Displacement volume data (mL m^{-3}) from Foxton 1956 and dry mass data (mg m^{-3}) from Hopkins (Hopkins 1971) were converted to carbon biomass according to equations from Yang (Yang et al. 2022). Mean, standard error, and number of records in each summer month (November to March) and winter month (April to October) are shown. The dotted lines at 500 m of each plot indicate the threshold depth below which we assume the seasonally migrating mesozooplankton dwell over winter. (**b**) Median month-specific ratios of mesozooplankton biomass in the 0–250 m ($B_{0\text{–}250\text{m}}$) and 500–1000 m ($B_{500\text{–}1000\text{m}}$) strata, compared to the total biomass in the 0–1000 m stratum ($B_{0\text{–}1000\text{m}}$) based on data from Foxton 1956 and Hopkins 1971. (**c**) Biomass (Mt C) of seasonally vertical migrating (SVM) and non-migrating (non-SVM) mesozooplankton, krill, salps, and total zooplankton in the Southern Ocean, as well as their contribution to the SVMP (Mt C m^{-2} yr^{-1}).

(Darnis and Fortier 2012). The median value of $B_{500\text{–}1000\text{m}}/B_{0\text{–}1000\text{m}}$ (0.28) across the five summer months (November to March, Fig. 1b) indicates that the deep-dwelling portion can contribute 28% of the total mesozooplankton biomass. By subtracting this value from the month-specific ratios of $B_{500\text{–}1000\text{m}}/B_{0\text{–}1000\text{m}}$ during winter (April to October), the biomass of seasonally migrating mesozooplankton in each winter month was computed.

Krill and salps

The carbon biomass data for krill and salps in the Southern Ocean were converted from abundance data (ind m^{-2}) sourced from the openly accessible database KRILLBASE (Atkinson et al. 2017) using a fixed conversion factor between abundance and biomass. The total carbon biomass of krill and salps (summed across all nine CCAMLR planning domains) referenced in our prior studies (Yang et al. 2022) was used in this study, with krill and salps accounting for 30 and 1.7 Mt C, respectively.

For krill, 87% of the population was found to be distributed in the open ocean, with the remaining 13% on and around continental shelves as reported in a circumpolar review (Atkinson et al. 2008). An extensive meta-analysis of over 30 studies (Schmidt et al. 2011) indicated that approximately 19% of krill in the open ocean and 2% of krill in shelf waters inhabit depths below 400 m. Despite previous research largely focusing on summer seasons, here we assume that these krill (totaling 5.04 Mt C) are contributing to the SVMP, acknowledging this estimate to be conservative (Schmidt et al. 2011).

For salps, the initial aggregate-to-solitary abundance ratio in the beginning of winter (ie. March) is reported as 10 : 1

(Foxton 1966). From comprehensive length-frequency data of salps ($N \approx 5000$) (Henschke and Pakhomov 2019), the median oral to atrial opening (OAL) length for aggregates is 16 mm, compared to 40 mm for solitary salps. The aggregate-to-solitary carbon mass ratio in March can be determined using the formula: (10 × mass of 16 mm aggregate)/(1 × mass of 40 mm solitary). Carbon mass (CM, mg C) of individual salps can be derived from the relationship between CM and body length (OAL, mm), as expressed by $\mathrm{CM} = 0.002 \times \mathrm{OAL}^{2.148}$ (Dubischar et al. 2021). Based on the total carbon biomass of salps in the Southern Ocean (1.7 Mt, Yang et al. 2022) and the aforementioned carbon mass ratio, it is calculated that the carbon biomass of aggregate and solitary forms of salps at the onset of winter stands at 1.0 and 0.7 Mt, respectively. Due to the knowledge gaps in the depth distribution of salps throughout the year in the Southern Ocean, we assume the entire salp population (1.0 Mt for aggregate forms and 0.7 Mt for solitary forms) undergoes seasonal vertical carbon transport in this study.

Respiration rate

The respiration rates of various polar zooplankton species during winter were compiled (Table S2). These raw respiration values, reported in different units (e.g., μgC mgDM^{-1} d^{-1}, μlO$_2$ ind^{-1} d^{-1}, μlO$_2$ mgDM^{-1} d^{-1}) were converted to carbon weight-specific respiration rate.

O_2 consumption rates were converted to respiratory carbon losses as follows:

$$\mu\mathrm{gC\,d^{-1}} = \mu\mathrm{L\,O_2\,d^{-1}} \times 12/22.4 \times \mathrm{RQ}$$

where 12/22.4 is the carbon weight in 1 mol (22.4 L) of CO_2, and the respiratory quotient (RQ) was assumed as 0.97 (Ikeda and Bruce 1986; Steinberg and Landry 2017).

The weight-specific respiration rates were finally standardized to carbon weight-specific respiration rates (gC gC CM^{-1} d^{-1}) using species-specific inter-conversion factors between dry mass and carbon mass, as outlined by Atkinson et al. 2012.

The median values of our compiled winter respiration rate of zooplankton (Table S2) in deep waters of the Southern Ocean were used in our SVMP estimation (mesozooplankton: 0.00585 gC gC CM^{-1} d^{-1}, krill: 0.00805 gC gC CM^{-1} d^{-1}, salps: 0.01926 gC gC CM^{-1} d^{-1}). The only available measurements of salp respiration rate were recorded in surface waters of the Southern Ocean (0–15 m, Table S2). We used the median value of these surface records to represent the metabolic rate of overwintering salps.

Mortality rate

The mortality rate of zooplankton during the overwintering period has been seldom reported (refer to Table S3). Prior modeling studies have typically utilized a conservative value of 0.001 d^{-1} to estimate the SVMP by high-latitude copepods (Visser et al. 2017; Pinti et al. 2023). In our analysis, we utilized the median value of our compiled mortality rates to estimate the SVMP, resulting in a value of 0.0056 d^{-1} for mesozooplankton (Table 1).

Few mortality rates of overwintering salps have been reported (Henschke et al. 2018). The monthly mortality rates of krill in surface waters of the Southern Ocean during winter were only reported by McClatchie et al. 1991 (Table S3). However, based on these values we project that almost no krill would survive the 7 winter months given these exceptionally high values. To make a more conservative and realistic estimate, we used the relatively lower mortality rates of krill from Reiss 2016 of 0.00252 d^{-1}.

Length of overwintering period

The overwintering period of copepods in previous SVMP studies (mostly from the Arctic Ocean) spans from 100 d to more than 300 d (Jónasdóttir et al. 2015; Visser et al. 2017; Tarling et al. 2022). This different duration within the Arctic Ocean was calculated using models based on length-dependent lipid reserves and temperature-dependent respiration (Pierson et al. 2013; Visser et al. 2017). Additionally, the overwintering duration can vary with regions in response to light intensity and the timing of spring primary production in the Southern Ocean (Atkinson et al. 1997; La et al. 2019; Flores et al. 2023). In our calculation, we assume the overwintering durations for mesozooplankton, krill, and salps to be 214 d (time period spanning from 1st April to 31st October) based on the seasonal patterns in vertical distribution of the zooplankton biomass in the Southern Ocean (Fig. 1).

Seasonal vertical migration pump calculation throughout the Southern Ocean

Mesozooplankton

The SVMP calculation from the mortality of mesozooplankton on the first day of each winter month ($S_{\mathrm{m},1}$) was conducted as follows:

$$S_{\mathrm{m},1} = B_0 \times m$$

where B_0 represents the initial biomass of mesozooplankton at the beginning of each winter month, and m signifies the mortality rate of mesozooplankton; the SVMP from respiration of mesozooplankton on the first day of each winter month ($S_{\mathrm{r},1}$) was determined by the formula:

$$S_{\mathrm{r},1} = (B_0 - S_{\mathrm{m},1}) \times r$$

where r represents the respiration rate of mesozooplankton during the overwintering period.

Then the SVMP by mortality ($S_{\mathrm{m,n}}$) and respiration ($S_{\mathrm{r,n}}$) of the remaining mesozooplankton biomass (B_{n}) in each day (n) was calculated as:

Table 1. Components of the seasonal vertical migration pump for mesozooplankton, krill, and salps.

	Biomass			Overwintering variables			Seasonal vertical migration pump ($\mathrm{Mt\ C\ yr^{-1}}$)		
Taxon	$\mathrm{Total_{0–250m}}$ ($\mathrm{g\ C\ m^{-2}}$)	$\mathrm{Total_{0–1000m}}$ (Mt C)	Overwintering (Mt C)	Respiration ($\mathrm{gC\ gC\ CM^{-1}\ d^{-1}}$)	Mortality ($\mathrm{d^{-1}}$)	Length of overwintering (d)	By respiration	By mortality	Total
Mesozooplankton	1.9	132	41	0.00585	0.0056	214	26.5	25.5	52.1
Krill	1.8	30	5	0.00805	0.00252	214	6.7	2.1	8.8
Salps	0.04	1.7	0.7	0.01907		214	2.9	1.0	3.9
Total		**164**	**48**			214	**36**	**29**	**65**

Biomass information includes concentrations of zooplankton groups in the top 250 m ($\mathrm{Total_{0–250m}}$, $\mathrm{gC\ m^{-2}}$), total carbon biomass in the top 1000 m ($\mathrm{Total_{0–1000m}}$, Mt C), and biomass of the overwintering population (Mt C).

$$S_{\mathrm{m,n}} = B_0 \times (1-m)^{n-1} \times (1-r)^{n-1} \times m$$

$$S_{\mathrm{r,n}} = B_0 \times (1-m)^{n} \times (1-r)^{n-1} \times r$$

$$B_{\mathrm{n}} = B_0 \times (1-m)^{n} \times (1-r)^{n}$$

The SVMP by mortality and respiration of mesozooplankton in each winter month can be estimated based on the sum of $S_{\mathrm{m,n}}$ and $S_{\mathrm{r,n}}$ over 30–31 d (detailed calculations in Table S4).

As part of a sensitivity analysis, an alternative approach (Method 2) in which different assumptions on mortality and respiration rate were used to estimate the SVMP derived from mesozooplankton are detailed fully in Supporting Information Table S5.

Krill

Unlike diapausing copepods that cease feeding during the overwintering period, krill have been observed to adopt various overwintering strategies, such as “business as usual,” “quiescence,” and “flexibility,” depending on the habitat (Schmidt et al. 2014). Studies on the energy budget of krill suggest that they continue to feed, albeit at greatly reduced rates, to supplement diminished metabolism and lipid utilization, thereby preventing an energy deficit upon entering the following spring (Meyer 2012). In this study, we assume the body weight of krill remains unchanged during winter.

The SVMP by mortality ($S_{\mathrm{m,n}}$) and respiration ($S_{\mathrm{r,n}}$) of krill in each day (n) was calculated as:

$$S_{\mathrm{m,n}} = B_0 \times (1-m)^{n-1} \times m$$

$$S_{\mathrm{r,n}} = B_0 \times (1-\mathrm{m})^{n} \times r$$

Detailed calculations based on the median value of respiration rate and mortality rate of krill based on our meta-analysis (Tables S2, S3) are shown in the Table S6.

The respiration rate of overwintering krill may vary across different months (Meyer 2012). In an alternative approach (Method 2), by employing the month-specific respiration rates derived from our meta-analysis (including 9 deep records and 21 surface records, refer to Table S2: April and May: 0.0108 $\mathrm{gC\ gC\ CM^{-1}\ d^{-1}}$; June to September: 0.0101 $\mathrm{gC\ gC\ CM^{-1}\ d^{-1}}$; October: 0.0129 $\mathrm{gC\ gC\ CM^{-1}\ d^{-1}}$), we calculated the SVMP by krill (refer to Table S7).

Salps

The mortality rate of salps has only been reported in a modeling based study (Henschke et al. 2018) and no data can be found for the overwintering population. A circumpolar study of salps showed that the abundance of the aggregate forms decreases abruptly in March and falls to a low level during winter (fig. 6 in Foxton 1966). We assume that the entire aggregate population die off at the winter onset and the solitary population overwinter (Henschke et al. 2018). The seasonal vertical carbon transport by salps was then calculated based on the death of aggregates and the respiration of solitaries during winter. It is assumed that the body weight of solitary forms of salps remains constant during winter and the calculation of the contribution from respiration of solitaries to the total seasonal vertical carbon transport (S_r) is as follows:

$$S_r = B_s \times r \times L$$

where B_s is the carbon mass of solitary forms of salps (0.7 Mt), r is the median value of our compiled respiration rate for salps during winter (0.01907 gC gC CM^{-1} d^{-1}), and L is the length of the overwintering period (214 d).

Lastly, for the mapping of SVMP fluxes, seasonal vertical carbon transport from the three zooplankton functional groups at each sampling station in the Southern Ocean (gC m^{-2} yr^{-1}) were also calculated using our compiled biomass dataset (gC m^{-2}) and the species-specific assumptions and equations mentioned above.

Particulate organic carbon flux in the Southern Ocean

The modeled POC fluxes at 500 m and 1000 m of the Southern Ocean (South of 30° S) with resolution of 1° latitude by 1° longitude were extracted from various Coupled Model Intercomparison Project Phase 6 (CMIP6) models including Community Earth System Model version 2 (CESM2), CESM2-finite volume (CESM2-FV2), CESM2 Whole Atmosphere Community Climate Model version 6 (CESM2-WACCM), CESM2-WACCM-finite volume (CESM2-WACCM-FV2) and Geophysical Fluid Dynamics Laboratory's Earth System Model (GFDL-ESM4). The averages of annual mean POC flux values from these models are utilized in this study. These independent model data facilitate comparison of our SVMP estimate with the POC flux. All these POC flux outputs from CMIP6 model used in this study are freely available from http://esgf-data.dkrz.de/projects/cmip6-dkrz/.

Furthermore, we compiled a dataset of POC fluxes based on sediment traps deployed in the Southern Ocean to complement the model data (Table S8). This dataset encompasses a total of 107 sediment trap records from regions including Ross Sea, Amundsen Sea, Scotia Sea, Kerguelen Islkands, Prydz Bay, and other areas of the Southern Ocean were compiled (Table S8). The traps were deployed between 1983 and 2023 at depth ranging from 100 to 4556 m (Table S8). The measured annual POC flux at 500 and 1000 m was calculated as the mean value based on traps deployed between 300 and 700 m ($n = 28$; Table S8) and those deployed between 700 and 1300 m ($n = 21$; Table S8), respectively.

Results

Biomass of seasonally vertically migrating mesozooplankton, krill, and salps and the length of the overwintering period

For this study we defined the Southern Ocean as the 36 M km^2 area encompassing the nine Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Marine Protected Area planning domains which extend out to Subantarctic waters (with the northernmost region reaching 45° S, Yang et al. 2022). Most net sampling in this area is within the top 250 m layer and in summer months, so we used these as a basis for estimating total epipelagic summer biomasses of the three major zooplankton groups. For the group termed hereafter "mesozooplankton" we estimated that copepods accounted for about 70% of their total biomass, with euphausiid species, salps, ostracods, chaetognaths, and amphipods making up the remainder (Table S1). Based on large, multi-year compilations of summer data (i.e., 1770, 9700, and 5432 stations for mesozooplankton, krill, and salps, respectively), we estimated respective total carbon biomasses of 67, 30, and 1.7 Mt C for the upper 250 m water column, as detailed in Yang et al. 2022.

For the mesozooplankton, we compiled monthly, vertically resolved net sample data of biomass distribution around Antarctica, mainly from Foxton 1956 and Hopkins 1971, and re-plotted them as mean values in each of three depth strata, namely 0–250, 250–500, and 500–1000 m (Fig. 1a). Based on seasonal variations in vertical distribution of mesozooplankton biomass (Foxton 1956), we assume mesozooplankton remain in deep water and undergo overwintering from April to October. In the remaining "summer" months (November to March) a median of 51% of the total (0–1000 m) water column biomass is in the top 250 m (Fig. 1b). Applying this to our 0–250 m estimate of 67 Mt C yields a total (0–1000 m) mesozooplankton biomass of 132 Mt C. The detailed seasonal comparison of Foxton 1956 shows little seasonal change in full depth integrated biomass, so we use this 132 Mt C value as an annual average. To estimate the portion of this biomass participating in the SVMP, we chose the threshold depth of 500 m since this is a consistently used net sampling depth and exceeds the mean Southern Ocean depth needed for 100-yr carbon storage (i.e., 381 m, Cavan et al. 2024). We thus calculated that 41 Mt C of mesozooplankton participate in this pump (Fig. 1c), based on the fraction of the total 132 Mt C that is below 500 m in each overwintering month from April to October (Fig. 1b), minus the 28% of total biomass that we calculate to reside year round in this deep stratum based on the median value for the five summer months. As described in the Methods, the biomass of seasonally migrating krill and salps was calculated from KRILLBASE (Atkinson et al. 2017) and estimated to be 5 and 1.7 Mt C, respectively (Fig. 1c).

Respiration rates and mortality of overwintering mesozooplankton, krill, and salps

We compiled 305 records of respiration data for high-latitude zooplankton, including 178 from the surface (< 200 m), 106 from greater depths (mainly > 200 m), and a further 21 records where the sampling depth could not be determined (Table S2). Trends in respiration rates at the surface aligned with the Metabolic Theory of Ecology (Brown et al. 2004) during summer, in that smaller zooplankton like mesozooplankton (only data from copepods were used) had higher mass-specific respiration rates compared to larger zooplankton like krill and salps (Fig. 2a). In winter, krill had higher respiration rates than mesozooplankton (Fig. 2a), indicating species-specific overwintering strategies. Respiration rates during winter were generally lower than in summer. Similarly, respiration rates at depth ranged from 0.003 to 0.02 gC gC CM^{-1} d^{-1}, and were significantly lower than rates observed near the surface ($p < 0.01$; Fig. 2a; Table S2). Based on our compilation of available literature on mortality rates of overwintering polar species (Table S3; Fig. 2b), mesozooplankton (with all records from copepods) generally exhibit rates below 0.02 d^{-1}, while krill have lower mortality rates (below 0.005 d^{-1}; Table S3) and salps, higher mortality rates (0.03 d^{-1}; Fig. 2b). We selected the median values of respiration and mortality rates from samples collected in deep water during winter for our estimation of the SVMP (Table 1).

Seasonal vertical carbon transport by mesozooplankton, krill, and salps

Based on our best estimates of the biomass of seasonal migrants, the length of their overwintering periods and their respiration rates and mortality during this time (*see* Methods and Tables S2, S3), mesozooplankton, krill and salps collectively transport 65 Mt carbon to depths of at least 500 m (Table 1). In this process, mesozooplankton account for 80% of the total SVMP, while krill and salps contribute 14% and 6%, respectively (Table 1). Specifically, the SVMP attributed to mesozooplankton was calculated to be 52 Mt C yr^{-1} in the Southern Ocean, with 26.5 Mt C resulting from respiration and 25.5 Mt C from mortality (Tables 1, S4; Fig. 3a). These values were approximately five times higher than the estimates for krill (8.8 Mt C yr^{-1}, with 6.7 Mt C from respiration and 2.1 Mt C from mortality, Tables 1, S6; Fig. 3b) and one order of magnitude greater than for salps (3.9 Mt C yr^{-1}, with 2.9 Mt C from respiration and 1.0 Mt C from mortality; Table 1; Fig. 3c).

Mean values of the SVMP by these three zooplankton functional groups across the study area are presented in Fig. 3. The strength of SVMP by each group ranges from 0 to 12 gC m^{-2} yr^{-1} in each cell (Fig. 3). The mesozooplankton SVMP hotspots were notably clustered near islands such as Kerguelen, South Georgia, and South Shetland Islands (Fig. 3a), while the krill SVMP hotspots were predominantly distributed in the Atlantic sector, particularly in the Scotia Sea region (Fig. 3b). Hotspots of salps' SVMP were primarily concentrated in lower latitude areas (Fig. 3c).

Comparison of seasonal vertical migration pump with particulate organic carbon fluxes from Coupled Model Intercomparison Project models and sediment traps

Based on five Earth System Models from the Coupled Model Intercomparison Project (CMIP6), the ensemble average POC flux for our 38 M km^2 study area is 4.8 g C m^{-2} yr^{-1} at 500 m and 1.8 gC m^{-2} yr^{-1} at 1000 m depth (Fig. 4). In the highly productive neritic waters surrounding the continent the POC flux at 500 m exhibited a comparatively higher range, spanning 1.5–41.9 gC m^{-2} yr^{-1} (Fig. 4). Particulate organic carbon flux in mesopelagic regions of the Southern Ocean, measured by sediment traps, was similar, averaging 3.2 g C m^{-2} yr^{-1}at 500 m (traps deployed between 300 and 700 m) and 2.1 gC m^{-2} yr^{-1} at 1000 m (traps deployed between 700 and 1300 m) (Table S8).

How do our estimates for the SVMP compare with these POC fluxes? In terms of measured estimates, the SVMP equates to 56% and 88% of this flux at 500 and 1000 m, respectively, and for modeled estimates it is 38% at 500 m and 103% at 1000 m (Fig. 4). The contributions of respiration

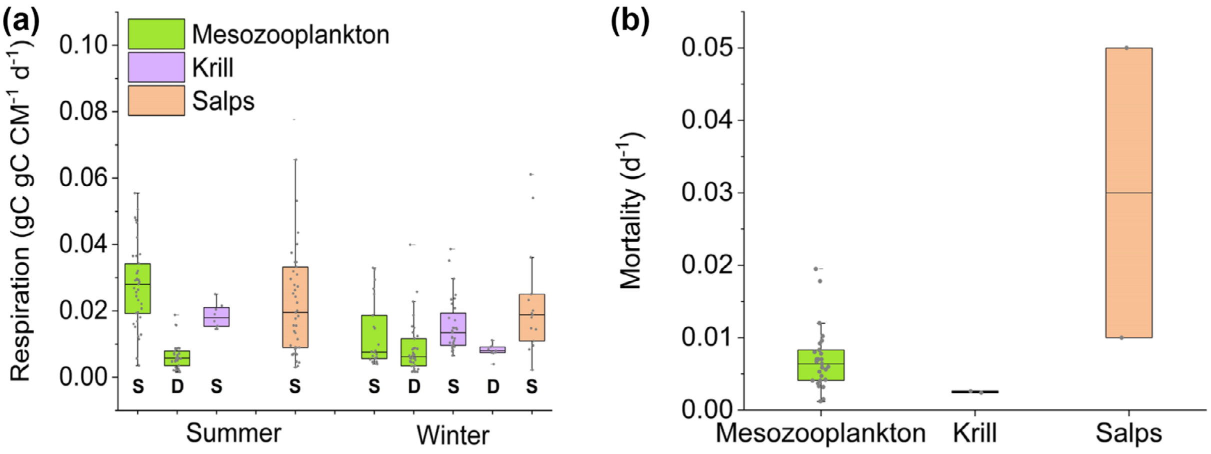

Fig. 2. Respiration and mortality of the three Southern Ocean zooplankton groups. (**a**) carbon mass (CM) related respiration rate (gC gC CM^{-1} d^{-1}) in surface water (S) and deep water (D) and (**b**) estimated overwintering mortality rate (d^{-1}). Box and whisker plots show the minimum, first quartile, median, third quartile, and maximum values of individual observations (dots) for each zooplankton group. Only data from copepods (major contributors of the mesozooplankton group) were used to calculate mesozooplankton rates.

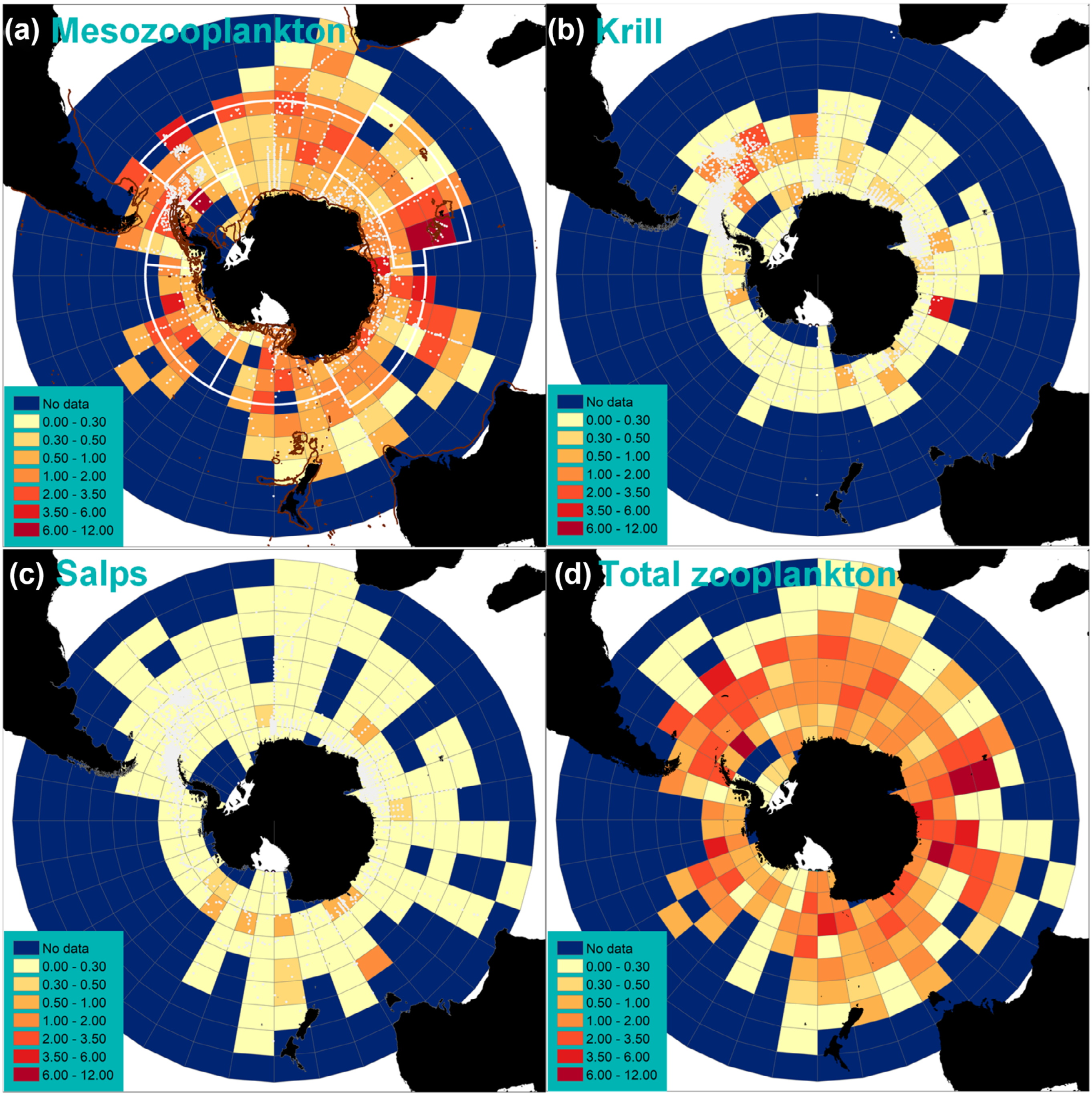

Fig. 3. The seasonal vertical migration pump (SVMP, g C m^{-2} yr^{-1}) of key Southern Ocean zooplankton groups. (**a**) mesozooplankton, (**b**) krill, (**c**) salps, and (**d**) total zooplankton within 5° latitude by 10° longitude grid cells. Cell values in a–c represent the mean SVMP value averaged across each of the sampling stations within the cell. Cell values in d represent the sum of cell values from a–c. The area of the Southern Ocean (defined as regions within the 9 CCAMLR planning domains) and the 500 m isobath is marked with white line and brown lines, respectively, in a. Sampling stations for mesozooplankton, krill, and salps are shown by white dots in panels a–c.

and mortality of seasonally migrating mesozooplankton to the carbon flux were nearly equal, whereas the respiratory contribution from overwintering krill and salps at depth exceeded that from mortality by a factor of three (Table 1).

It is important to highlight the maximum values of the SVMP compared to POC fluxes at smaller spatial scales. Within the scale of 10° longitude × 5° latitude grid, the SVMP from mesozooplankton, krill, and salps can respectively reach

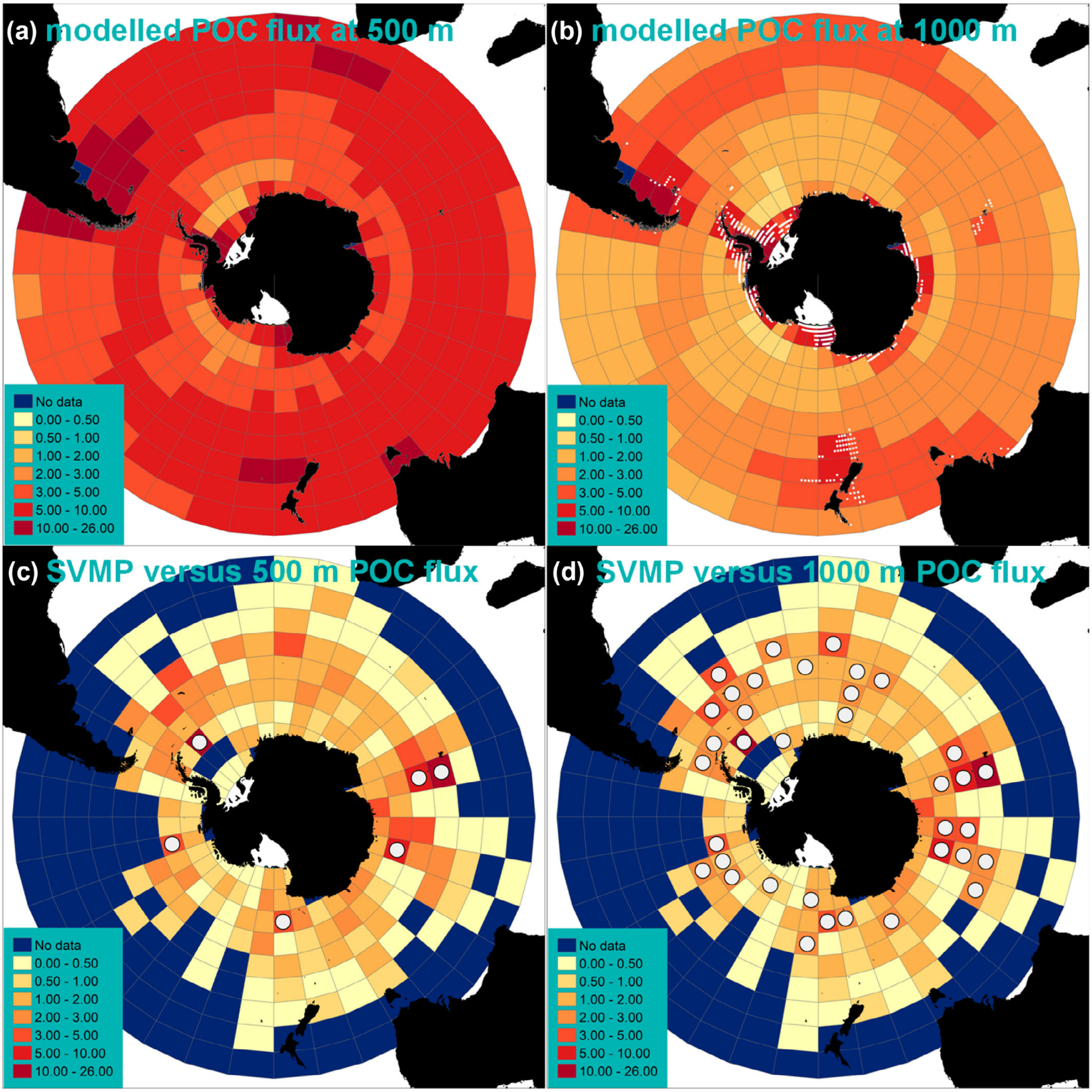

Fig. 4. Comparison between gravitational flux and the seasonal vertical migration pump. (**a**) POC flux (g C m^{-2} yr^{-1}) at 500 m and (**b**) 1000 m using IPCC CMIP6 climate model outputs and (**c**) the seasonal vertical migration pump flux, with 5° by10° grid cells marked with a white dot where the seasonal vertical migration pump exceeds the modeled POC flux at 500 m. (**d**) same as panel c but white dots are cells where seasonal vertical migration pump flux exceeds modeled POC export at 1000 m. In regions where the depth is less than 1000 m (indicated by white dots) on plot b, the POC flux at 500 m was utilized.

up to 230%, 116%, and 33% of the modeled POC flux at 500 m (Fig. 3). This reflects regionally high biomass values covered by this scale of analysis, but of course, more localized deep aggregations or swarms of zooplankton will lead to even more intense hotspots of sequestration.

Sensitivity analysis

Our SVMP estimates are the product of various components listed in Table 1 (*see* equations in Methods). We tested a series of alternative approaches for the calculation of these values (detailed fully in the Supporting Information). First, we tested an alternative method of estimating the migrating biomass of mesozooplankton. Specifically, we assume that both the biomass residing in deep water (> 500 m) during summer as well as the portion staying in surface water (< 250 m) during winter do not contribute to seasonal vertical migration (*see* Fig. 1b). With these assumptions, the remaining mesozooplankton biomass (65 Mt) would drive a SVMP of 59.3 Mt C yr^{-1}. This value is higher than our "best estimate" and comprises 30.2 Mt C from respiration (range 13.9–46.4 Mt C) and 29.1 Mt C from mortality (range 12.9–45.2 Mt C), with ranges derived from varying the date of mortality (*see* Tables S5, S9).

We also conducted a series of calculations of the SVMP of mesozooplankton based on the upper and lower plausible values of key parameters (migrating biomass, respiration rate, mortality rate and overwintering period). The lower estimated migrating biomass of mesozooplankton was based on the assumption that only large copepods undergo seasonal vertical migration, while the upper estimate was derived from the assumption that a proportion overwinter below 1000 m. The upper and lower bounds of respiration and mortality parameters were the 25th and 75th percentiles from our meta-analysis. These analyses identify that migrating biomass has the greatest influence on the mesozooplankton SVMP estimate, resulting in a range of values from 38% to 150% of the best estimate of mesozooplankton SVMP (Fig. S1). This strong relationship between abundance/biomass and SVMP magnitude is consistent with previous models (Pinti et al. 2023; Tarling et al. 2022). Migrating biomass of mesozooplankton was the most sensitive and least certain parameter, warranting further study.

Discussion

The seasonal vertical migration pump in relation to particulate organic carbon flux

Growing evidence points to the significant contribution of overwintering zooplankton, primarily copepods, to carbon export in the ocean (Jónasdóttir et al. 2015; Tarling et al. 2022; Pinti et al. 2023). Using available data on respiration and mortality and our compiled dataset of mesozooplankton, krill, and salp biomass (Yang et al. 2022), we have obtained estimates of the SVMP by these three zooplankton functional groups in the Southern Ocean (Fig. 5). Our estimates suggest that approximately 65 Mt of carbon are released annually in deep waters by seasonally migrating zooplankton, forming 56% of the measured and 38% of the modeled POC flux at a depth of 500 m, and respectively 88% and 103% of the measured and modeled POC flux at 1000 m. Regionally, the strength of the SVMP may surpass the POC flux by orders of magnitude (Fig. 4). Previous studies suggesting migrating zooplankton account for 10% of total global carbon export via biological pump[7] might underestimate the contribution of the SVMP.

Vertical migrations of zooplankton can reach up to 1000 m or deeper (Jónasdóttir et al. 2015; Visser et al. 2017), while the mean carbon sequestration depth (defined as the depth where the carbon remains sequestered for more than 100 yr) in the Southern Ocean is only 381 m (ranging from 137 to 758 m; Cavan et al. 2024). Hence, the direct injection of carbon into the ocean interior through the SVMP could lead to slower attenuation and serve as an effective contributor to carbon sequestration in the region. These various aspects of the SVMP challenge the conventional view that gravitational flux is the dominant particle downward pathway to the deep ocean (Boyd et al. 2019; Ricour et al. 2023).

Comparison with seasonal vertical migration pump estimations from other ocean regions

Previous assessments of the SVMP in the North Atlantic and Arctic have provided estimates solely for individual copepod species, and these range from 0.08 to 11.5 g C m^{-2} yr^{-1} (median 1.60 g C m^{-2} yr^{-1}; Table S10), and suggest they are capable of sequestering a comparable amount of carbon as the traditional gravitational biological carbon pump in these regions (Jónasdóttir et al. 2015; Visser et al. 2017). The total SVMP estimates for the Southern Ocean (i.e., 1.8 g C m^{-2} yr^{-1} equating to 65 Mt C in an area of approximately 36 million km^2) thus are very close to the median value for individual copepod species in other oceanic regions. This is surprising, given that our estimates are derived from the entire zooplankton community, while most of those previous studies have focused only on individual copepod species (Table S10). One explanation may be that the copepod species in previous SVMP estimates comprised a sizable portion, 50–80%, of the total zooplankton biomass (Søreide et al. 2008). Moreover, it is important to consider area coverage when assessing the concentration or density of the SVMP. Our estimate is based on the entire Southern Ocean (approximately 36 million km^2), which is much larger than the regions examined in prior studies (e.g., table 7 in Tarling et al. 2022). Higher estimates of SVMP can be observed when focusing on smaller areas (e.g., 11.1 g C m^{-2} yr^{-1} in the grid cell east of the Kerguelen islands, Fig. 3). These hotspots of the SVMP by zooplankton are expected to shift in accordance with changes in their core distribution range and biomass (Freer et al. 2022; Johnston et al. 2022). This mechanistic understanding can improve predictions of carbon sequestration in the Southern Ocean and other global ocean regions under climate change.

Previous studies, most of which rely on modeling methods, have indicated that the carbon flux transported via the seasonal vertical migration of copepods is predominantly influenced by respiration, often exceeding mortality rates by an order of magnitude (Visser et al. 2017; Tarling et al. 2022; Pinti et al. 2023). However, our study presents a contrasting perspective, revealing that mortality also plays a significant role in the SVMP process and can make an equivalent contribution to seasonal carbon flux when compared to respiration (Table 1). The relative significance of mortality and respiration in driving the SVMP dynamics depends on the respective rates of respiration and mortality in

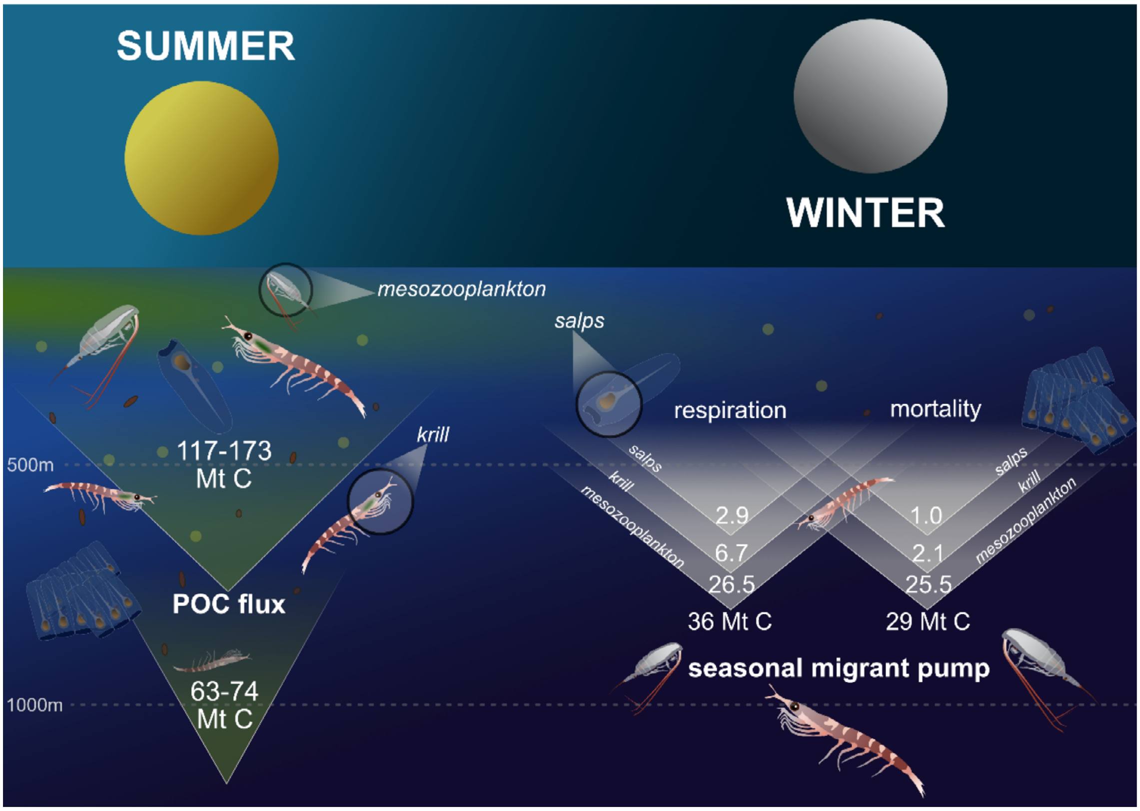

Fig. 5. A schematic representation of our calculations of the seasonal vertical carbon transport by mesozooplankton, krill, and salps during winter of the Southern Ocean. The values for SVMP flux are totals for mesozooplankton, krill, and salps and the upper and lower ranges for POC flux refer to annual estimates based on sediment traps and earth system models.

migrating zooplankton. Previous models based on metabolic theory and isomorphism commonly adopted a conservative (i.e., low) mortality rate of 0.001 d^{-1} (Visser et al. 2017; Tarling et al. 2022). Thereby, it is plausible that the SVMP estimates derived from mortality in prior studies may be biased. Moreover, a portion of the carcasses of overwintering zooplankton with intact bodies can be collected by deep sediment traps but, due to the difficulty in separating carcasses from swimmers, may be discarded from POC flux estimates to avoid overestimating the gravitational flux (Halfter et al. 2022), further underestimating the contribution of carcasses to the SVMP. Dead overwintering zooplankton could serve as a crucial additional food source to sustain midwater species, as gravitational flux alone is usually insufficient to meet the carbon demands of mid-water organisms (Boyd et al. 2019). Given the significant role of mortality in the SVMP, further exploration is warranted, especially considering the limited data available on overwintering zooplankton in the Southern Ocean.

Uncertainties in our estimate

Our estimates are based solely on seasonally migrating biomass. However, it is important to note that not all of this biomass feeds at the surface, as is commonly assumed in SVMP calculations. Some migrating species such as chaetognaths and krill could feed at depth (Schmidt et al. 2011). A proportion of carbon from overwintering organisms may be respired at the surface via midwater predators who return to the surface and are themselves preyed upon by higher trophic level species (Saunders et al. 2019). All of these processes can lead to an overestimation of our findings. On the other hand, certain overwintering copepods (such as *Calanoides acutus*) may inhabit depths greater than 1000 m (Andrews 1966), potentially resulting in their exclusion from our SVMP estimate and an underestimation of the results. In this study, we define 500 m as the threshold for carbon sequestration. Given that many overwintering copepods can reside much deeper than 500 m, our comparison of the magnitude of the SVMP with the POC flux at both 500 and 1000 m remains valid.

Our estimation is also subject to uncertainties stemming from the limited observations and data availability regarding seasonally migrating zooplankton in the Southern Ocean (Tables S2, S3). While our estimate employed uniform values for respiration, mortality, and length of the overwintering period across the entirety of the Southern Ocean, variations in these parameters could exist among different sectors within the region due to location-specific differences in oceanographic conditions and food dynamics (Morley et al. 2020).

Salps appeared to be the least understood group during our analysis, and further studies on their biomass, respiration, and mortality are warranted. Enhanced access to field data from diverse regions within the Southern Ocean, facilitated by large-scale observational studies and autonomous platforms, would be valuable to improve the accuracy of estimates of this flux in forthcoming studies (Boyd et al. 2024). Notwithstanding these issues, even our most pessimistic sensitivity analysis suggested a SVMP flux that was 38% of our best estimate, emphasizing that this sequestration pathway should be better quantified rather than ignored.

Ecological and biogeochemical implications

The biological carbon pump in the Southern Ocean is suggested to make a disproportionate contribution to carbon flux in the global ocean (Boyd et al. 2024). In addition to the recognized impact of passively sinking particles such as fecal pellets, carcasses, and molts as evidenced in prior studies (Belcher et al. 2019; Cavan et al. 2019; Manno et al. 2020; Décima et al. 2023), our study emphasizes the significant role that zooplankton, through active processes like seasonal vertical migration, can play in enhancing the carbon flux to the deep Southern Ocean. Including these key processes into Earth System Models and carbon budgets would result in a better appreciation of carbon export and sequestration and increased confidence when projecting how the biological carbon pump will respond to climate change (Henson et al. 2022).

Evidence from the Southern Ocean would suggest that carbon sequestration via sinking fecal pellets is likely to be more important for large, swarming species like krill and salps than for mesozooplankton (Belcher et al. 2019; Manno et al. 2020). While krill fecal pellets are suggested to be more robust and better at exporting carbon than those of salps, this is currently under debate (Pauli et al. 2021; Décima et al. 2023). Notwithstanding these uncertainties, metazoan grazers tend to have higher carbon to iron ratios than their phytoplankton food, thereby leading to relatively iron-rich pellets due to the lack of a need to assimilate iron efficiently from their food (Schmidt et al. 2016; Le Mézo and Galbraith 2021). This is important, since sinking pellets would export iron in the “fecal iron pump” alongside carbon, thereby removing limiting nutrients (Le Mézo and Galbraith 2021). However, there is no such issue with the SVMP (Jónasdóttir et al. 2015), since respiration at depth injects DIC directly to depth and mortality of carbon-rich zooplankton at depth transports small quantities of iron relative to carbon. Given the southwards range shifts of krill and salps (Pakhomov et al. 2002; Atkinson et al. 2004; Atkinson et al. 2022), coupled with increases in large copepods (Ward et al. 2018), we may expect a shift in their relative roles in the gravitational flux of pellets and mesopelagic migrant flux, with implications for the export of limiting nutrients as well as carbon.

Climate change impacts the phenology of zooplankton as well as their abundance and distributional range (Atkinson et al. 2019; Ratnarajah et al. 2023), which can alter zooplankton-related carbon export (Brun et al. 2019; Trinh et al. 2023). For instance, the length of overwintering periods for zooplankton in the Amundsen Sea polynya is shorter during positive phases of the Southern Annular Mode (SAM) and La Nina events than during negative SAM and El Nino years (La et al. 2019). In the North Atlantic, a > 30% reduction in overwintering duration of *C. finmarchicus* is projected, which could diminish the efficiency of the SVMP (Wilson et al. 2016). The decline in Arctic sea ice has been suggested to keep zooplankton deeper for longer (Flores et al. 2023), but this may be counteracted by reduced feeding opportunities in surface waters (Søreide et al. 2010). These complexities underline a need for a more holistic understanding of climate change impacts on high-latitude zooplankton, including a better appreciation of how their contribution to the biological carbon pump will be affected. Achieving this will require a wider consideration of the seasonal vertical migration pump.

Author Contributions

Guang Yang, Angus Atkinson, and Geraint A. Tarling designed the study. Guang Yang, Angus Atkinson, and Evgeny A. Pakhomov compiled the respiration and mortality data and performed data analysis. Katrin Schmidt, Jennifer J. Freer, and Geraint A. Tarling provided suggestions on the calculation of seasonal vertical migration carbon pump by zooplankton. Weilei Wang provided and analyzed the modeled particulate organic carbon flux data. Guang Yang, Angus Atkinson, and Evgeny A. Pakhomov completed the draft and all authors contributed to the development and writing of the manuscript.

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Conflicts of Interest

None declared.

References

Andrews, K. J. H. 1966. "The Distribution and Life-History of *Calanoides acutus* (Giesbrecht)." *Discovery Reports* 34: 117–162.

Atkinson, A., S. L. Hill, E. A. Pakhomov, et al. 2017. "KRILLBASE: A Circumpolar Database of Antarctic Krill and Salp Numerical Densities, 1926–2016." *Earth System Science Data* 9: 193–210. https://doi.org/10.5194/essd-9-193-2017.

Atkinson, A., S. L. Hill, E. A. Pakhomov, et al. 2019. "Krill (*Euphausia superba*) Distribution Contracts Southward During Rapid Regional Warming." *Nature Climate Change* 9: 142–147. https://doi.org/10.1038/s41558-018-0370-z.

Atkinson, A., S. B. Schnack-Schiel, P. Ward, and V. Marin. 1997. "Regional Differences in the Life Cycle of *Calanoides acutus* (Copepoda: Calanoida) Within the Atlantic Sector of the Southern Ocean." *Marine Ecology Progress Series* 150: 99–111. https://doi.org/10.3354/meps150099.

Atkinson, A., V. Siegel, E. A. Pakhomov, and P. Rothery. 2004. "Long-Term Decline in Krill Stock and Increase in Salps Within the Southern Ocean." *Nature* 432: 100–103. https://doi.org/10.1038/nature02996.

Atkinson, A., V. Siegel, E. A. Pakhomov, et al. 2008. "Oceanic Circumpolar Habitats of Antarctic Krill." *Marine Ecology Progress Series* 362: 1–23. https://doi.org/10.3354/meps07498.

Atkinson, A., and J. D. Sinclair. 2000. "Zonal Distribution and Seasonal Vertical Migration of Copepod Assemblages in the Scotia Sea." *Polar Biology* 23: 46–58. https://doi.org/10.1007/s003000050007.

Atkinson, A., P. Ward, B. P. V. Hunt, E. A. Pakhomov, and G. W. Hosie. 2012. "An Overview of Southern Ocean Zooplankton Data: Abundance, Biomass, Feeding and Functional Relationships." *CCAMLR Science* 19: 171–218.

Atkinson, A., S. L. Hill, C. S. Reiss, et al. 2022. "Stepping Stones Towards Antarctica: Switch to Southern Spawning Grounds Explains an Abrupt Range Shift in Krill." *Global Change Biology* 28: 1359–1375. https://doi.org/10.1111/gcb.16009.

Belcher, A., S. A. Henson, C. Manno, et al. 2019. "Krill Faecal Pellets Drive Hidden Pulses of Particulate Organic Carbon in the Marginal Ice Zone." *Nature Communications* 10: 889. http://doi.org/10.1038/s41467-019-08847-1.

Boyd, P. W., K. R. Arrigo, M. Ardyna, et al. 2024. "The Role of Biota in the Southern Ocean Carbon Cycle." *Nature Reviews Earth and Environment* 5: 390–408. https://doi.org/10.1038/s43017-024-00531-3.

Boyd, P. W., H. Claustre, M. Levy, D. A. Siegel, and T. Weber. 2019. "Multifaceted Particle Pumps Drive Carbon Sequestration in the Ocean." *Nature* 568: 327–335. https://doi.org/10.1038/s41586-019-1098-2.

Bradford-Grieve, J. M., S. D. Nodder, J. B. Jillett, K. Currie, and K. R. Lassey. 2001. "Potential Contribution that the Copepod *Neocalanus tonus* Makes to Downward Carbon Flux in the Southern Ocean." *Journal of Plankton Research* 9: 963–975. http://doi.org/10.1093/plankt/23.9.963.

Briggs, N., G. Dall'Olmo, and H. Claustre. 2020. "Major Role of Particle Fragmentation in Regulating Biological Sequestration of CO_2 by the Oceans." *Science* 367: 791–793. https://doi.org/10.1126/science.aay1790.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. "Toward a Metabolic Theory of Ecology." *Ecology* 85: 1771–1789. https://doi.org/10.1890/03-9000.

Brun, P., K. Stamieszkin, A. W. Visser, P. Licandro, M. R. Payne, and T. Kiørboe. 2019. "Climate Change Has Altered Zooplankton-Fuelled Carbon Export in the North Atlantic." *Nature Ecology & Evolution* 3: 416–423. https://doi.org/10.1038/s41559-018-0780-3.

Cavan, E. L., A. Belcher, A. Atkinson, et al. 2019. "The Importance of Antarctic Krill in Biogeochemical Cycles." *Nature Communications* 10: 4742. https://doi.org/10.1038/s41467-019-13390-0.

Cavan, E. L., N. Mackay, S. Hiss, A. Atkinson, A. Belcher, and A. Visser. 2024. "Antarctic Krill Sequester Similar Amounts of Carbon to Key Coastal Blue Carbon Habitats." *Nature Communications* 15: 7842. http://doi.org/10.1038/s41467-024-52135-6.

Darnis, G., and L. Fortier. 2012. "Zooplankton Respiration and the Export of Carbon at Depth in the Amundsen Gulf (Arctic Ocean)." *Journal of Geophysical Research: Oceans* 117: C04013. http://doi.org/10.1029/2011JC007374.

Décima, M., M. R. Stukel, S. D. Nodder, et al. 2023. "Salp Blooms Drive Strong Increases in Passive Carbon Export in the Southern Ocean." *Nature Communications* 14: 425. https://doi.org/10.1038/s41467-022-35204-6.

Dubischar, C. D., E. A. Pakhomov, L. von Harbou, B. P. V. Hunt, and U. V. Bathmann. 2021. "Salps in the Lazarev Sea, Southern Ocean: II. Biological Composition and Potential Prey Value." *Marine Biology* 159: 15–24. http://doi.org/10.1007/s00227-011-1785-5.

Flores, H., G. Veyssière, G. Castellani, et al. 2023. "Sea-Ice Decline Could Keep Zooplankton Deeper for Longer." *Nature Climate Change* 13: 1122–1130. https://doi.org/10.1038/s41558-023-01779-1.

Foxton, P. 1956. "The Distribution of the Standing Crop of Zooplankton in the Southern Ocean." *Discovery Reports* 28: 191–236.

Foxton, P. 1966. "The Distribution and Life History of *Salpa thompsoni* Foxton, With Observations on a Related Species, *Salpa gerlachei* Foxton." *Discovery Reports* 34: 1–116.

Freer, J. J., M. Daase, and G. A. Tarling. 2022. "Modelling the Biogeographic Boundary Shift of *Calanus finmarchicus* Reveals Drivers of Arctic Atlantification by Subarctic Zooplankton." *Global Change Biology* 28: 429–440. https://doi.org/10.1111/gcb.15937.

Halfter, S., E. L. Cavan, P. Butterworth, K. M. Swadling, and P. W. Boyd. 2022. "'Sinking Dead'-How Zooplankton Carcasses Contribute to Particulate Organic Carbon Flux in the Subantarctic Southern Ocean." *Limnology and Oceanography* 67: 13–25. https://doi.org/10.1002/lno.11971.

Henschke, N., and E. A. Pakhomov. 2019. "Latitudinal Variations in *Salpa thompsoni* Reproductive Fitness." *Limnology and Oceanography* 64: 575–584. https://doi.org/10.1002/lno.11061.

Henschke, N., E. A. Pakhomov, J. Groeneveld, and B. Meyer. 2018. "Modelling the Life Cycle of *Salpa thompsoni*." *Ecological Modelling* 387: 17–26. https://doi.org/10.1016/j.ecolmodel.2018.08.017.

Henson, S. A., C. Laufkötter, S. Leung, S. L. C. Giering, H. I. Palevsky, and E. L. Cavan. 2022. "Uncertain Response of Ocean Biological Carbon Export in a Changing World." *Nature Geoscience* 15: 248–254. https://doi.org/10.1038/s41561-022-00927-0.

Hopkins, T. L. 1971. "Zooplankton Standing Crop in the Pacific Sector of the Antarctic." *Antarctic Research* 17: 347–362.

Ikeda, T., and B. Bruce. 1986. "Metabolic Activity and Elemental Composition of Krill and Other Zooplankton From Prydz Bay, Antarctica, During Early Summer (November–December)." *Marine Biology* 92: 545–555. https://doi.org/10.1007/BF00392514.

Johnston, N. M., E. J. Murphy, A. Atkinson, et al. 2022. "Status, Change, and Futures of Zooplankton in the Southern Ocean." *Frontiers in Ecology and Evolution* 9: 624692. https://doi.org/10.3389/fevo.2021.624692.

Jónasdóttir, S. H., A. W. Visser, K. Richardson, and M. R. Heath. 2015. "Seasonal Copepod Lipid Pump Promotes Carbon Sequestration in the Deep North Atlantic." *Proceedings of the National Academy of Sciences of the United States of America* 112: 12122–12126. https://doi.org/10.1073/pnas.1512110112.

La, H. S., K. Park, A. Wåhlin, et al. 2019. "Zooplankton and Micronekton Respond to Climate Fluctuations in the Amundsen Sea Polynya, Antarctica." *Scientific Reports* 9: 10087. http://doi.org/10.1038/s41598-019-46423-1.

Le Mézo, P. K., and E. D. Galbraith. 2021. "The Fecal Iron Pump: Global Impact of Animals on the Iron Stoichiometry of Marine Sinking Particles." *Limnology and Oceanography* 66: 201–213. https://doi.org/10.1002/lno.11597.

Long, M. C., B. B. Stephens, K. McKain, et al. 2021. "Strong Southern Ocean Carbon Uptake Evident in Air-Borne Observations." *Science* 374: 1275–1280. https://doi.org/10.1126/science.abi4355.

Mackintosh, N. A. 1937. "The Seasonal Circulation of the Antarctic Macroplankton." *Discovery Reports* 16: 365–412.

Manno, C., S. Fielding, G. Stowasser, E. J. Murphy, S. E. Thorpe, and G. A. Tarling. 2020. "Continuous Moulting by Antarctic Krill Drives Major Pulses of Carbon Export in the North Scotia Sea, Southern Ocean." *Nature Communications* 11: 6051. http://doi.org/10.1038/s41467-020-19956-7.

McClatchie, S., S. Rakusa-Suszczewski, and K. Filcek. 1991. "Seasonal Growth and Mortality of *Euphausia superba* in Admiralty Bay, South Shetland Islands, Antarctica." *ICES Journal of Marine Science* 48: 335–342. https://doi.org/10.1093/icesjms/48.3.335.

Meyer, B. 2012. "The Overwintering of Antarctic Krill, *Euphausia superba*, From an Ecophysiological Perspective." *Polar Biology* 35: 15–37. https://doi.org/10.1007/s00300-011-1120-0.

Morley, S. A., D. Abele, D. K. A. Barnes, et al. 2020. "Global Drivers on Southern Ocean Ecosystems: Changing Physical Environments and Anthropogenic Pressures in an Earth System." *Frontiers in Marine Science* 7: 547188. https://doi.org/10.3389/fmars.2020.547188.

Nowicki, M., T. DeVries, and D. A. Siegel. 2022. "Quantifying the Carbon Export and Sequestration Pathways of the Ocean's Biological Carbon Pump." *Global Biogeochemical Cycles* 36: e2021GB007083. https://doi.org/10.1029/2021GB007083.

Pakhomov, E. A., P. W. Froneman, and R. Perissinotto. 2002. "Salp/Krill Interactions in the Southern Ocean: Spatial Segregation and Implications for the Carbon Flux." *Deep Sea Research Part II: Topical Studies in Oceanography* 49: 1881–1907. https://doi.org/10.1016/S0967-0645(02)00017-6.

Pauli, N., N.-C. Pauli, C. M. Flintrop, et al. 2021. "Krill and Salp Faecal Pellets Contribute Equally to the Carbon Flux at the Antarctic Peninsula." *Nature Communications* 12: 7168. https://doi.org/10.1038/s41467-021-27436-9.

Pierson, J. J., H. Batchelder, W. Saumweber, A. Leising, and J. Runge. 2013. "The Impact of Increasing Temperatures on Dormancy Duration in *Calanus finmarchicus*." *Journal of Plankton Research* 35: 504–512. https://doi.org/10.1093/plankt/fbt022.

Pinti, J., S. H. Jonasdottir, N. R. Record, and A. W. Visser. 2023. "The Global Contribution of Seasonally Migrating Copepods to the Biological Carbon Pump." *Limnology and Oceanography* 68: 1147–1160. https://doi.org/10.1002/lno.12335.

Ratnarajah, L., R. Abu-Alhaija, A. Atkinson, et al. 2023. "Monitoring and Modelling Marine Zooplankton in a Changing Climate." *Nature Communications* 14: 564. http://doi.org/10.1038/s41467-023-36241-5.

Reiss, C. S. 2016. "Age, Growth, Mortality, and Recruitment of Antarctic Krill, *Euphausia superba*." In Biology and Ecology of Antarctic Krill. Advances in Polar Ecology, edited by V. Siegel, 101–104. Switzerland: Springer.

Ricour, F., L. Guidi, M. Gehlen, T. DeVries, and L. Legendre. 2023. "Centrury-Scale Carbon Sequestration Flux throughout the Ocean by the Biological Pump." *Nature Geoscience* 16: 1105–1113. https://doi.org/10.1038/s41561-023-01318-9.

Saunders, R. A., S. L. Hill, G. A. Tarling, and E. J. Murphy. 2019. "Myctophid Fish (Family Myctophidae) Are Central Consumers in the Food Web of the Scotia Sea (Southern Ocean)." *Frontiers in Marine Science* 6: 530. https://doi.org/10.3389/fmars.2019.00530.

Schmidt, K., A. Atkinson, D. W. Pond, and L. C. Ireland. 2014. "Feeding and Overwintering of Antarctic Krill Across Its Major Habitats: The Role of Sea Ice Cover, Water Depth, and Phytoplankton Abundance." *Limnology and Oceanography* 59: 17–36. https://doi.org/10.4319/lo.2014.59.1.0017.

Schmidt, K., A. Atkinson, S. Steigenberger, et al. 2011. "Seabed Foraging by Antarctic Krill: Implications for Stock Assessment, Bentho-Pelagic Coupling and the Vertical Transfer of Iron." *Limnology and Oceanography* 56: 1411–1428. https://doi.org/10.4319/lo.2011.56.4.1411.

Schmidt, K., C. Schlosser, A. Atkinson, et al. 2016. "Zooplankton Gut Passage Mobilizes Lithogenic Iron for Ocean Productivity." *Current Biology* 26: 2667–2673. https://doi.org/10.1016/j.cub.2016.07.058.

Shreeve, R. S., G. A. Tarling, A. Atkinson, P. Ward, C. Goss, and J. Watkins. 2005. "Relative Production of *Calanoides acutus* (Copepoda: Calanoida) and *Euphausia superba* (Antarctic Krill) at South Georgia, and its Implications at Wider Scales." *Marine Ecology Progress Series* 298: 229–239. https://doi.org/10.3354/meps298229.

Siegel, D. A., T. DeVries, I. Cetinic, and K. W. Bisson. 2023. "Quantifying the Ocean's Biological Pump and Its Carbon Cycle Impacts on Global Scales." *Annual Review of Marine Science* 15: 329–356. https://doi.org/10.1146/annurev-marine-040722-115226.

Siegel, V. 2005. "Distribution and Population Dynamics of *Euphausia superba*: Summary of Recent Findings." *Polar Biology* 29: 1–22. https://doi.org/10.1007/s00300-005-0058-5.

Siegel, V., and J. L. Watkins. 2016. "Distribution, Biomass and Demography of Antarctic Krill, *Euphausia superba*." In Biology and Ecology of Antarctic Krill, 21–100. Cham: Springer.

Søreide, J. E., S. Falk-Petersen, E. N. Hegseth, et al. 2008. "Seasonal Feeding Strategies of Calanus in the High-Arctic Svalbard Region." *Deep Sea Research Part II: Topical Studies in Oceanography* 55: 2225–2244. https://doi.org/10.1016/j.dsr2.2008.05.024.

Søreide, J. E., E. Leu, J. Berge, M. Graeve, and S. Falk-Petersen. 2010. "Timing of Blooms, Algal Food Quality and *Calanus glacialis* Reproduction and Growth in a Changing Arctic." *Global Change Biology* 16: 3154–3163. https://doi.org/10.1111/j.1365-2486.2010.02175.x.

Steinberg, D. K., and M. R. Landry. 2017. "Zooplankton and the Ocean Carbon Cycle." *Annual Review of Marine Science* 9: 413–444. https://doi.org/10.1146/annurev-marine-010814-015924.

Stukel, M. R., J. R. Irving, T. B. Kelly, M. D. Ohman, C. K. Fender, and N. Yingling. 2023. "Carbon Sequestration by Multiple Biological Pump Pathways in a Coastal Upwelling Biome." *Nature Communications* 14: 2024. http://doi.org/10.1038/s41467-023-37771-8.

Tarling, G. A., A. Belcher, M. Blackwell, et al. 2022. "Carbon and Lipid Contents of the Copepod *Calanus finmarchicus* Entering Diapause in the Fram Strait and their Contribution to the Boreal and Arctic Lipid Pump." *Frontiers in Marine Science* 9: 926462. https://doi.org/10.3389/fmars.2022.926462.

Trinh, R., H. W. Ducklow, D. K. Steinberg, and W. R. Fraser. 2023. "Krill Body Size Drives Particulate Organic Carbon Export in West Antarctica." *Nature* 618: 526–530. https://doi.org/10.1038/s41586-023-06041-4.

Visser, A. W., J. Grønning, and S. H. Jónasdóttir. 2017. "*Calanus hyperboreus* and the Lipid Pump." *Limnology and Oceanography* 62: 1155–1165. https://doi.org/10.1002/lno.10492.

Wang, W. W., W. Fu, F. A. C. Le Moigne, et al. 2023. "Biological Carbon Pump Estimate Based on Multidecadal Hydrographic Data." *Nature* 624: 579–585. https://doi.org/10.1038/s41586-023-06772-4.

Ward, P., G. A. Tarling, and S. E. Thorpe. 2018. "Temporal Changes in Abundances of Large Calanoide Copepods in the Scotia Sea: Comparing the 1930s With Contemporary Times." *Polar Biology* 41: 2297–2310. https://doi.org/10.1007/s00300-018-2369-3.

Wilson, R. J., N. S. Banas, M. R. Heath, and D. C. Speirs. 2016. "Projected Impacts of 21st Century Climate Change on Diapause in *Calanus finmarchicus*." *Global Change Biology* 22: 3332–3340. https://doi.org/10.1111/gcb.13282.

Yang, G., A. Atkinson, E. A. Pakhomov, S. L. Hill, and M. F. Racault. 2022. "Massive Circumpolar Biomass of Southern Ocean Zooplankton: Implications for Food Web Structure, Carbon Export, and Marine Spatial Planning." *Limnology and Oceanography* 67: 2516–2530. https://doi.org/10.1002/lno.12219.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

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