



The Role of Zooplankton in Establishing Carbon Export Regimes in the Southern Ocean – A Comparison of Two Representative Case Studies in the Subantarctic Region

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Marine ecosystems regulate atmospheric carbon dioxide levels by transporting and storing photosynthetically fixed carbon in the ocean's interior. In particular, the subantarctic and polar frontal zone of the Southern Ocean is a significant region for physically driven carbon uptake due to mode water formation, although it is under-studied concerning biologically mediated uptake. Regional differences in iron concentrations lead to variable carbon export from the base of the euphotic zone. Contrary to our understanding of export globally, where high productivity results in high export, naturally iron-fertilized regions exhibit low carbon export relative to their surface productivity, while HNLC (High Nutrient, Low Chlorophyll) waters emerge as a significant area for carbon export. Zooplankton, an integral part of the oceanic food web, play an important role in establishing these main carbon export regimes. In this mini review, we explore this role further by focusing on the impact of grazing and the production of fecal pellets on the carbon flux. The data coverage in the subantarctic region will be assessed by comparing two case studies - the iron-replete Kerguelen Plateau and the HNLC region south of Australia. We then discuss challenges in evaluating the contributions of zooplankton to carbon flux, namely gaps in seasonal coverage of sampling campaigns, the use of non-standardized and biased methods and under-sampling of the mesopelagic zone, an important area of carbon remineralization. More integrated approaches are necessary to improve present estimates of zooplankton-mediated carbon export in the Southern Ocean.

Keywords: biological carbon pump, zooplankton, southern ocean, subpolar, carbon cycle

INTRODUCTION

The fixation of inorganic carbon through photosynthesis by phytoplankton, and subsequent export and sequestration to deeper waters, is termed the Biological Carbon Pump (BCP). Without this process, atmospheric CO₂ levels would be 200 ppm higher than they are today (Parekh et al., 2006; Henson et al., 2019), thus the BCP is a critical component of climate regulation. Zooplankton

are part of the BCP, via ingestion of lower trophic levels, fecal pellet and carcass production and respiration of CO₂ (Schnack-Schiel and Isla, 2005; Turner, 2015; Steinberg and Landry, 2017). Furthermore, they actively transport carbon below the thermocline during daily migration and seasonal descent to overwinter at depth (Jónasdóttir et al., 2015; Klevjer et al., 2016; Steinberg and Landry, 2017; Record et al., 2018; Boyd et al., 2019). The role of zooplankton in the BCP is well-studied in some parts of the global ocean, e.g., the North Atlantic and the oxygen minimum zones in the Pacific (Jónasdóttir et al., 2015; Cavan et al., 2017), however, is less understood in the Southern Ocean.

The Southern Ocean plays a significant role in the functioning of the Earth system (Lumpkin and Speer, 2007; Mayewski et al., 2009), and provides important ecosystem services, such as climate regulation and nutrient recycling (Millennium Ecosystem Assessment, 2005). The region between the Subtropical Front and the Polar Front encompasses a large area of the Southern Ocean (hereafter called the “subantarctic region”) and represents an important carbon sink, as the formation of intermediate and mode waters in this region contributes notably to the sequestration of atmospheric CO₂ (Orsi et al., 1995; Sabine et al., 2004; Eriksen et al., 2018). Large parts of the subantarctic region are characterized by HNLC (High Nutrient, Low Chlorophyll) conditions: low iron concentrations in surface waters limit the uptake of macronutrients, such as phosphate and nitrate, and hence, restrict phytoplankton growth (Bucciarelli et al., 2001; Trull et al., 2001). In contrast, naturally iron-fertilized regions such as downstream of the Kerguelen Plateau, in the Indian sector of the Southern Ocean, are characterized by high primary production (Mosseri et al., 2008; Cavagna et al., 2015). However, high production does not always equal high carbon export as estimated from global models (e.g., Dunne et al., 2005; Laws et al., 2011) or sediment trap data (e.g., Marsay et al., 2015). Many reported an inverse relationship between primary production and export efficiency for the Southern Ocean (e.g., Maiti et al., 2013; Cavan et al., 2015; Laurenceau-Cornec et al., 2015; Le Moigne et al., 2016), which can be found at our study sites as well. While the Kerguelen Plateau is characterized as a HBLE (High Biomass, Low Export) region, the HNLC waters exhibit a relatively high carbon export below the mixed layer (Trull et al., 2001; Lam and Bishop, 2007; Ebersbach et al., 2011; Rembauville et al., 2015b). This mini review aims to understand the role that zooplankton play in establishing the characteristic carbon export regimes in the Southern Ocean by grazing on lower trophic levels and forming and repackaging sinking particles (Lam and Bishop, 2007). After a summary of the current state of knowledge, we also list contemporary knowledge gaps and propose future research priorities.

TWO CONTRASTING EXPORT REGIONS

The Kerguelen Plateau, located on the 70°E meridian, forms a naturally iron-fertilized region in the Polar Frontal Zone (PFZ) at the border of the Antarctic zone, with iron concentrations ranging from 0.45 to 0.7 nM in spring, decreasing to 0.09 nM in late summer due to phytoplankton growth (Table 1;

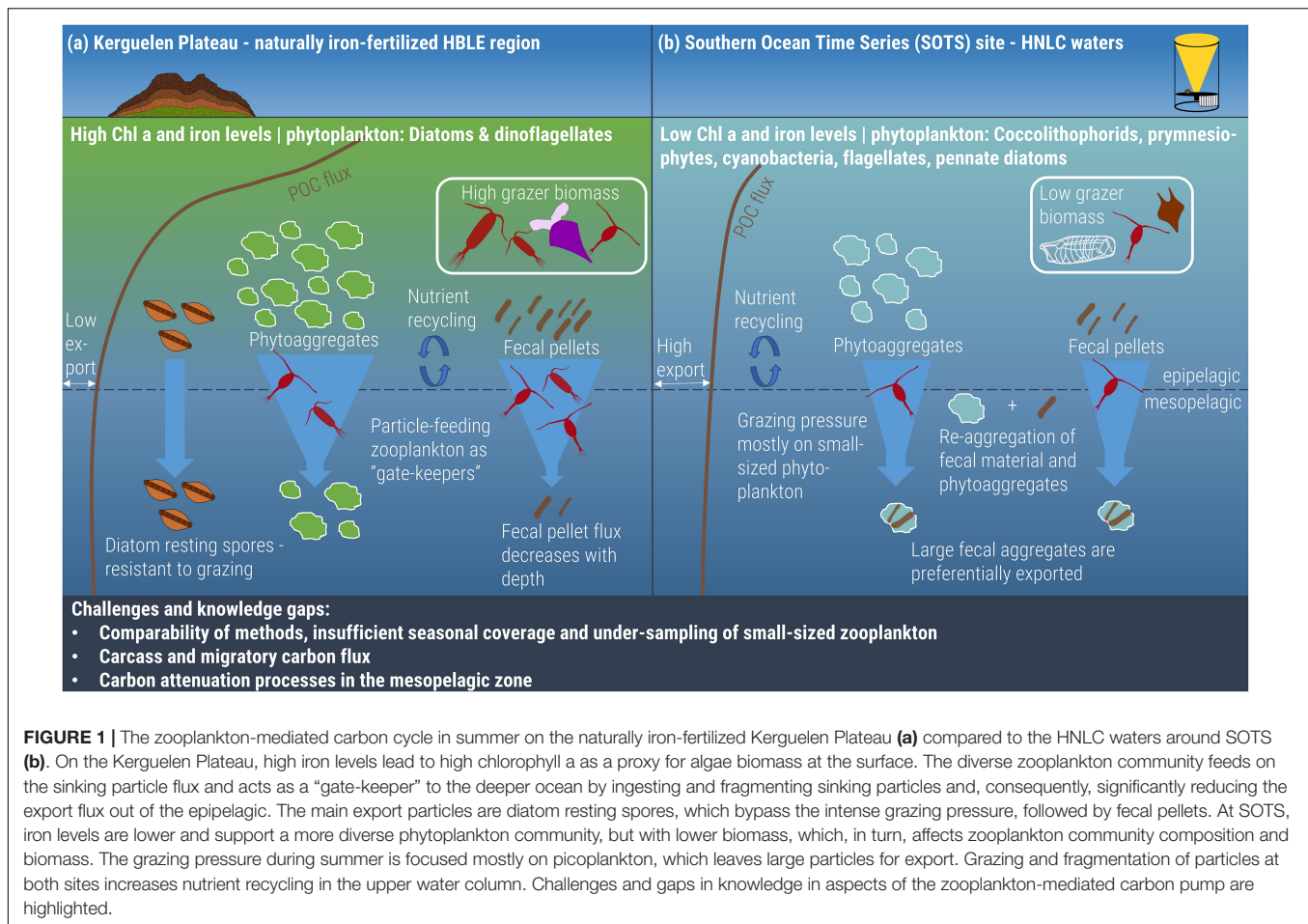
TABLE 1 | Comparison of environmental parameters and plankton groups between the HBLE Kerguelen Plateau and the HNLC waters south of Australia.

Parameter	Kerguelen Plateau (HBLE)	HNLC waters
Iron levels	0.45–0.7 nM (spring), 0.09 nM (summer) ⁽¹⁾⁽²⁾	0.05–0.11 nM (summer/autumn) ⁽³⁾
Phytoplankton biomass	High (>2.5 mg Chl a m ⁻³) ⁽⁴⁾	Low (<0.6 mg Chl a m ⁻³) ⁽⁵⁾
Dominant phytoplankton	Diatoms and dinoflagellates ⁽⁶⁾⁽⁷⁾⁽⁸⁾⁽⁹⁾	Coccolithophorids and other prymnesiophytes, cyanobacteria, autotrophic flagellates and pennate diatoms ⁽¹⁰⁾⁽¹¹⁾⁽¹²⁾⁽¹³⁾⁽¹⁴⁾
Dominant zooplankton	Large and medium-sized calanoid copepods, Oithonidae, pteropods ⁽¹⁵⁾	<i>Oithona similis</i> , foraminiferans, appendicularians, calanoid copepods, pteropods and salps ⁽¹⁶⁾
POC fluxes	66 mg C m ⁻² d ⁻¹ ^{(17)(a)}	127.2 mg C m ⁻² d ⁻¹ ⁽¹⁸⁾
e-ratio	0.03 ^{(17)(a)}	0.16 ^{(18)(b)}

(1) Blain et al., 2001, (2) Blain et al., 2008, (3) Cassar et al., 2011, (4) Blain et al., 2007, (5) Trull et al., 2019, (6) Armand et al., 2008, (7) Christaki et al., 2008, (8) Christaki et al., 2015 (9) Lasbleiz et al., 2016, (10) Trull et al., 2001, (11) Kopczynska et al., 2001, (12) Odate and Fukuchi, 1995, (13) Eriksen et al., 2018, (14) de Salas et al., 2011 (15) Carlotti et al., 2015, (16) Hunt and Hosie, 2006, (17) Laurenceau-Cornec et al., 2015, (18) Ebersbach et al., 2011. (a) High phytoplankton biomass site (A3-2). (b) SOTS site. Examples of carbon flux and e-ratios in the two regions are also given. The POC fluxes are estimated from polyacrylamide gel traps at 200 ± 10 m and 240 m depth on the Kerguelen Plateau and in the HNLC region, respectively. The e-ratio is an indicator for export efficiency and is calculated as the ratio between POC flux and primary productivity. Note that Laurenceau-Cornec et al. (2015) use net primary productivity (NPP) in the euphotic zone to calculate the e-ratio, while Ebersbach et al. (2011) use gross primary productivity (GPP).

Blain et al., 2001, 2008). This review focuses on the northern Kerguelen Plateau, which is separated from the southern part by the Fawn Trough at around 56°S (Park et al., 2014; Koubbi et al., 2016). The topography forces the Antarctic Polar Front to pass above the plateau south of the Kerguelen Islands, which introduces iron from the sediments (Blain et al., 2001), and leads to intensive seasonal phytoplankton blooms downstream of the plateau, with peaks of more than 2.5 mg Chl a m⁻³ (Blain et al., 2007, 2013; Rembauville et al., 2015b; Schallenberg et al., 2018). Blooms over the shallow plateau last the whole summer, while the bloom period over deep waters is only observed in spring for ~1 month (Schallenberg et al., 2018). The dominating phytoplankton are diatoms and dinoflagellates (Armand et al., 2008; Christaki et al., 2008, 2015; Lasbleiz et al., 2016). The zooplankton community consists of large and medium-sized calanoid copepods and small copepods in the family Oithonidae (Figure 1; Carlotti et al., 2015). Non-copepod taxa account for 4–8% of the total zooplankton community, though pteropods can be abundant over the shelf (7–12% of total abundance, Carlotti et al., 2008). Although the biomass in the pelagic ecosystem is high, the export flux is generally low (<0.5 mmol POC m⁻² d⁻¹, 289 m depth), except for short-lived (<14 days) export pulses in summer (up to 1.6 mmol m⁻² d⁻¹) (Rembauville et al., 2014). Hence, the Kerguelen Plateau is considered to be an HBLE environment (Lam and Bishop, 2007; Rembauville et al., 2014).

In comparison to the Kerguelen Plateau, the HNLC waters south of Australia exhibit lower iron concentrations and phytoplankton biomass, but relatively higher POC export flux



(Table 1). We focus on the region around the Southern Ocean Time Series (SOTS) site at 142°E and 47°S, which is representative of a broad HNLC region of the SAZ between 90°E and 140°E (Sedwick et al., 1999; Shadwick et al., 2015). Phytoplankton growth is limited by low iron (0.05–0.11 nM in summer/autumn and insufficient light conditions due to high cloud cover (Sedwick et al., 1999; Cassar et al., 2011)). The phytoplankton community is dominated by nanoplankton and picoplankton, coccolithophorids and other prymnesiophytes (such as *Phaeocystis antarctica*), cyanobacteria and autotrophic flagellates (Odate and Fukuchi, 1995; Kopczynska et al., 2001; Trull et al., 2001; Eriksen et al., 2018). Diatoms are mostly lightly silicified pennate diatoms rather than centric forms (de Salas et al., 2011). Phytoplankton biomass is low throughout the year, with chlorophyll a values generally below 0.6 mg m^{-3} (Trull et al., 2019). This has implications for zooplankton, which is dominated by the copepod *Oithona similis*, foraminiferans, and appendicularians (Hunt and Hosie, 2006), rather than a community of calanoid copepods that are not able to accumulate enough resources to complete their life cycles. During summer, a small number of species of calanoid copepods, along with the pteropods *Limacina* spp. and regionally large blooms of the salp *Salpa thompsoni*, are also observed (Figure 1; Hunt and Hosie, 2006). Though primary production is low in

surface waters, the total flux of POC is relatively high, e.g., $3.3 \pm 1.8 \text{ mmol POC m}^{-2} \text{ d}^{-1}$ at 150 m water depth, measured with free-drifting PPS 3/3 sediment traps (Ebersbach et al., 2011).

CONTRIBUTIONS OF ZOOPLANKTON TO CARBON FLUX IN THE SUBANTARCTIC REGION

The Northern Kerguelen Plateau

On the Kerguelen Plateau, zooplankton biomass increases four-fold from winter (July–August) to mid-summer (February) (Semelkina, 1993; Razouls et al., 1996; Carlotti et al., 2015). This is caused by (1) seasonal ontogenetic migrations by large calanoid copepods, such as *Rhincalanus gigas* and *Calanoides acutus*, which spend winter in diapause in deeper waters and ascend to surface in spring and (2) an increase in other species, e.g., *Calanus simillimus* and the smaller *Oithona* spp., that resume their population development from survivors of previous years to start reproduction in spring following the phytoplankton bloom (Atkinson, 1998; Schnack-Schiel, 2001; Carlotti et al., 2015). Remarkably, mesozooplankton (200 μm –20 mm) consume only a small fraction of the phytoplankton biomass directly; e.g.,

Sarthou et al. (2008) measured a low ingestion of 1–10% of total Chl a d^{-1} by copepods in summer. In contrast, they are known to control protist growth by grazing (Carlotti et al., 2008). Heterotrophic protists, such as ciliates and some dinoflagellates in turn reduce the standing stock of pico- and nanophytoplankton and diatoms through grazing (Calbet and Landry, 2004; Calbet, 2008; Peloquin et al., 2011; Quéguiner, 2013). The grazing pressure by mesozooplankton on protozooplankton releases the top-down control on diatoms and favors phytoplankton blooms dominated by large diatoms (Henjes et al., 2007; Carlotti et al., 2015).

Additionally, zooplankton ingest and fragment particles, which enhances subsequent microbial respiration and increases the recycling of nutrients, e.g., iron (Sarthou et al., 2008) and ammonium (Mosseri et al., 2008). Grazing not only affects nutrient levels in surface waters but also the efficiency of carbon transfer (Dagg et al., 2014). The omnivorous and detritivorous zooplankton community acts as a “gate-keeper” in the mesopelagic zone (Figure 1): They ingest and fragment phytoplankton aggregates and fecal pellets that are quickly remineralized and retained in the surface layer (Iversen and Poulsen, 2007; Quéguiner, 2013; Dagg et al., 2014). Predominantly omnivorous and detritivorous copepod species in the genera *Oithona* and *Oncaea/Triconia* link the classical food web to the microbial loop (Atkinson, 1998; Pasternak et al., 2009). This efficient transfer of carbon to higher trophic levels or the microbial loop in surface waters leads to low export flux during most of the year and establishes the HBLE characteristics on the Kerguelen Plateau (Rembauville et al., 2014, 2015b). Despite the dominance of the carbon flux by fecal pellets in early spring ($56 \pm 19\%$ of total carbon flux, 200 m, Laurenceau-Cornec et al., 2015), the fecal pellet flux decreases rapidly with depth, while diatom resting spores (resistant to grazing; Davis et al., 1980; Smetacek, 1985; Salter et al., 2012) and detrital aggregates dominate the deeper flux at 289 m (Cavan et al., 2019). This indicates preferential reprocessing and remineralization of fecal material over other particles in the mixed layer and upper mesopelagic, which leads to a lower fecal pellet flux similar to other iron-fertilized regions, e.g., South Georgia (Cavan et al., 2015; Rembauville et al., 2015a).

HNLC Waters South of Australia

The dominance of protozooplankton, small copepods and patchy salp blooms in HNLC waters, rather than a diverse and abundant mesozooplankton community as on the northern Kerguelen Plateau, results in control of the low phytoplankton biomass by protist grazing, and efficient remineralization of carbon and nutrients in the upper water column (Figure 1; Landry et al., 2002; Mayzaud et al., 2002; Pakhomov et al., 2002; Atkinson et al., 2004). Considering the omnivorous and detritivorous diet of *Oithona similis* (Takahashi et al., 2010), it would be expected that the POC export out of the epipelagic zone would be low, as ingestion and fragmentation of sinking particles increase the particle flux attenuation. However, studies such as SAZ-Sense in January/February 2007 have shown a relatively high POC transfer efficiency out of the mixed layer in the HNLC waters around SOTS, in comparison to other sites in the SAZ with higher iron

levels or in the PFZ with a diatom-dominated phytoplankton community (Ebersbach et al., 2011). Even though the POC concentration was low at the surface (5.2 ± 0.9 mmol m^{-2} d^{-1}), the carbon export flux at SOTS was highest in both gel traps (8.1 mmol m^{-2} d^{-1} at 290 m water depth) and PPS 3/3 sediment traps (3.3 ± 1.8 mmol m^{-2} d^{-1} at 150 m water depth) (Ebersbach et al., 2011).

The two main differences from the Kerguelen Plateau that cause the higher relative and total export flux in HNLC waters are a different zooplankton community composition and size fraction distribution (Figure 1). The dominant microzooplankton (20–200 μm) and heterotrophic nanoflagellates at SOTS can consume 82% of the primary production per day in summer (Pearce et al., 2011). This is in line with Trull et al. (2019), who estimated a 10-fold higher grazing pressure in December compared to September as a function of zooplankton biomass. This grazing pressure focuses mostly on the picoplankton size fraction (0.2–2 μm), which leaves phytoplankton aggregates and other large particles for export below the mixed layer (Pearce et al., 2011). Omnivorous and detritivorous copepods are not as abundant as on the Kerguelen Plateau, which limits their abilities to efficiently reduce the sinking flux. Consequently, more particles (11–53% of the primary production; Jacquet et al., 2011) are exported from HNLC surface waters (Figure 1), predominantly as fecal aggregates (pellets and fecal material reaggregated with phytodetritus; Ebersbach and Trull, 2008; Laurenceau-Cornec et al., 2015).

Our findings indicate that species composition and size fraction distribution are important factors in modifying the downward carbon flux and establishing a regime of low biomass at the surface but with relatively high carbon transfer efficiency. Hence, zooplankton play a more important role in the export regimes in the subantarctic region than previously thought. However, common algorithms to estimate the carbon export efficiency in the Southern Ocean, such as by Arteaga et al. (2018) or Britten et al. (2017), only include temperature, net primary production or silicate concentration and do not contain a zooplankton term. In contrast, our findings show that zooplankton, while being influenced by their physical environment and food availability, also control lower trophic levels and carbon export efficiency. Future research efforts should therefore focus on including zooplankton in the algorithms, for example as size fractions or a proportion of trophic mode (e.g., ratio between herbivore to detritivore zooplankton), and improve our estimation of carbon uptake by the Southern Ocean.

CHALLENGES AND KNOWLEDGE GAPS

Comparability of Methods, Under-Sampling of Small-Sized Zooplankton and Insufficient Seasonal Coverage

Different methodologies make it difficult to compare the zooplankton species composition and biomass between the

subantarctic regions. Ship-based net deployments are temporally and spatially limited, but provide higher vertical resolution in the water column, while the Continuous Plankton Recorder (CPR) covers a large geographical area but only provides surface data and under-samples the vertical migrating community during the day (Carlotti et al., 2008, 2015; Dippner and Krause, 2013). Acoustic data provides information on distribution and biomass of certain size fractions over the whole annual cycle, but cannot provide species composition data (Trull et al., 2019). It is also important to note that both the CPR (silk mesh size 270 μm) and standard zooplankton nets with a mesh size of $>200 \mu\text{m}$ are known to under-sample smaller-sized zooplankton, e.g., Oithonidae and copepodite stages (Gallienne and Robins, 2001) that dominate the community in HNLC waters. Finally, limited access to the subantarctic region due to logistical constraints results in a results in few winter datasets, as the sampling campaigns by research and supply vessels are mostly focused on the summer season.

Understudied Carbon Pathways – Zooplankton Carcass and Migratory Flux

As the literature on other high latitude systems suggests, zooplankton carcass flux can be a seasonally significant contribution to total carbon flux (Sampei et al., 2012; Daase et al., 2014; Tang and Elliott, 2014). However, data on drivers and rates of mortality and carcass flux from the Southern Ocean are currently not available. The lack of data could lead to an underestimation of carbon flux, especially in the HNLC waters, where fast-sinking salp blooms could significantly increase the downward carbon flux as “jelly falls,” e.g., by 330% in the Tasman Sea further north (Henschke et al., 2013). Similarly, active transport of carbon by zooplankton, both by diel and seasonal vertical migrators, is not well understood. Translating the seasonal changes in the distribution of acoustic scattering layers into transported carbon is not possible without information on species composition (Trull et al., 2019).

The “Black Box”: The Mesopelagic Zone

The transfer efficiency of organic matter through the mesopelagic ($\sim 200\text{--}1000 \text{ m}$) is driven by plankton species composition in the epi- and mesopelagic (Lam et al., 2011). Studies such as Liszka et al. (2019); Manno et al. (2015) and Marsay et al. (2015) suggest that vertical distribution of zooplankton, community composition, and feeding behavior, along with temperature in the mesopelagic, are important in shaping the downward carbon flux. However, mesopelagic processes, such as respiration and remineralization of organic material and food web interactions, are not well understood (Robinson et al., 2010). Sampling campaigns in both regions rarely include the mesopelagic: while zooplankton studies on the Kerguelen Plateau focus on the upper 300 m of the water column, zooplankton data in the HNLC waters around SOTS were either collected from surface waters or from deeper, moored sediment traps. To increase our understanding of interactions between mesopelagic zooplankton, protists and bacteria, and their influence on particle formation

and remineralization, future sampling campaigns need to focus on the mesopelagic.

CONCLUSION AND OUTLOOK

Zooplankton play an important role in the carbon flux of both subantarctic regions. On the Kerguelen Plateau, grazing by the mesozooplankton community limits protozooplankton growth, which releases the grazing pressure on phytoplankton. Zooplankton also fragment particles, leading to increased nutrient recycling, and contribute to the carbon flux by producing fecal pellets. High rates of omnivory and detritivory result in a low export flux and establish the HBLE conditions on the plateau. In contrast, the dominance of smaller-sized zooplankton and heterotrophic protists in HNLC waters leads to high grazing pressure on picoplankton, which leaves large aggregates and fecal pellets for export. The lower total abundance of detritus-feeders results in a larger export of fecal aggregates. Knowledge gaps, resulting from limited seasonal coverage, non-standardization and bias of methods between sampling campaigns, and under-sampling of the mesopelagic zone, impede our understanding of zooplankton-mediated carbon flux, especially of the carcass and migratory flux. To predict future changes in marine carbon storage efficiency, it is important to focus research efforts on the zooplankton-mediated carbon flux. The inclusion of, for example, zooplankton size fractions or trophic modes in algorithms can refine predictions of carbon export in the Southern Ocean. More integrated research approaches, e.g., using the network of biogeochemical Argo floats in combination with stationary moorings (e.g., Rembauville et al., 2017; Trull et al., 2019), are necessary to improve inter-seasonal and spatial data coverage of the Biological Carbon Pump in the Southern Ocean.

AUTHOR CONTRIBUTIONS

SH designed and wrote the review and produced the infographic, with edits from all co-authors.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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