

PRIMARY RESEARCH ARTICLE

Quantification of blue carbon pathways contributing to negative feedback on climate change following glacier retreat in West Antarctic fjords

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Abstract

Global warming is causing significant losses of marine ice around the polar regions. In Antarctica, the retreat of tidewater glaciers is opening up novel, low-energy habitats (fjords) that have the potential to provide a negative feedback loop to climate change. These fjords are being colonized by organisms on and within the sediment and act as a sink for particulate matter. So far, blue carbon potential in Antarctic habitats has mainly been estimated using epifaunal megazoobenthos (although some studies have also considered macrozoobenthos). We investigated two further pathways of carbon storage and potential sequestration by measuring the concentration of carbon of infaunal macrozoobenthos and total organic carbon (TOC) deposited in the sediment. We took samples along a temporal gradient since time of last glacier ice cover (1–1000 years) at three fjords along the West Antarctic Peninsula. We tested the hypothesis that seabed carbon standing stock would be mainly driven by time since last glacier covered. However, results showed this to be much more complex. Infauna were highly variable over this temporal gradient and showed similar total mass of carbon standing stock per m² as literature estimates of Antarctic epifauna. TOC mass in the sediment, however, was an order of magnitude greater than stocks of infaunal and epifaunal carbon and increased with time since last ice cover. Thus, blue carbon stocks and recent gains around Antarctica are likely much higher than previously estimated as is their negative feedback on climate change.

KEYWORDS

Benthic–Pelagic coupling, Benthos, carbon standing stock, carbon storage, fjords, global warming, polar, sequestration

See also Commentary on this article by Pineda-Metz, 28, 8–20.

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1 | INTRODUCTION

The Antarctic Peninsula is a global hotspot for the loss of sea ice, glacier ice and ice shelves (Rogers et al., 2020) with implications for the physical, biogeochemical and biological processes operating in these systems. Accelerating retreat of glaciers, break-up of ice shelves and reduction in sea ice extent (e.g. fast ice) is driving a shift from a white to a blue sea, reducing albedo and leading to an increase in sea surface temperatures (Barnes, 2015; Cook et al., 2016; Massom et al., 2018; Meehl et al., 2019; Peck et al., 2010). The causes of glacier retreat along the Antarctic Peninsula are complex and variable, but Cook et al. (2016) considered rising air temperatures a key factor in the north while mass incursions by upper Circumpolar Deep Water were important further south. Further consequences are an increase in the duration of phytoplankton blooms and the generation of new low-energy coastal environments (fjord systems; Arrigo et al., 2008; Cook et al., 2016). These novel environments are rapidly colonized by a multiplicity of benthic species, benefiting from longer phytoplankton blooms and warmer temperatures (Barnes et al., 2020; Grange & Smith, 2013). Thereby they are contributing to new and stronger blue carbon capture, storage and sequestration (Barnes et al., 2018; Pineda-Metz et al., 2020).

Natural carbon sequestration can be visualized in three stages (Figure 1). Autotrophs begin the process with carbon capture (photosynthesis). In terrestrial systems, CO₂ is removed from the atmosphere and net O₂ released primarily by multicellular plants, such as trees. In the ocean, this is mainly achieved by single-celled algae—phytoplankton (Guidi et al., 2016; Peck et al., 2010), but macro-algae, seagrass, salt marsh and mangroves can be important along coasts (Campana et al., 2009; Mcleod et al., 2011; O'Connor et al., 2020). On land and in temperate and tropical coastal areas, long-lived plants also fulfil the role of carbon storage (O'Connor et al., 2020).

Phytoplankton, however, are short-lived and disintegrate quickly. Yet, a small percentage sinks to the seabed, evades microbial breakdown and is consequently buried in the sediment (for amounts, see Henley et al., 2020). Carbon captured by phytoplankton can also be stored when eaten by pelagic and benthic consumers. This can happen in the water column, for example, by copepods, krill and salps, or near the water–sediment interface by benthic suspension and deposit feeders (Arntz et al., 1994; Belcher et al., 2019; Vinogradov, 1999). All these sources contribute to the overall carbon standing stock (Henley et al., 2020; Peck et al., 2010). To prevent carbon from cycling back into the ocean or atmosphere, that is, for it to be sequestered, it needs to be buried below the activity of the microbial loop (Barnes, 2015; Henley et al., 2020; Nelleman et al., 2009). Whether deposited in the sediment as phytoplankton, or in the form of faeces and pseudofaeces from epi and infauna, carbon can be cycled deeper by the activity of organisms living within the sediment (Ehrnsten et al., 2019). Additionally, sequestration can be achieved by burial of carbon standing stock of accumulated dead phytoplankton and animals living in sediment. Areas close to a glacier terminus generally experience high rates of sedimentation which aids burial of benthic taxa and promotes carbon sequestration (Sahade et al., 2015; Włodarska-Kowalczyk et al., 2019).

Figure 1: The three different pathways of carbon storage which may lead to eventual sequestration of carbon in Antarctica represented in grey. These are (1) direct deposition and burial of primary production, (2) carbon storage in above-seabed animals (e.g. pelagic and epibenthic) and burial upon their death and (3) carbon storage and burial of infauna within the sediment. However, the majority of stored carbon will be recycled back into the system. Physical processes within the fjord which contribute to carbon sequestration are represented in green. The process of carbon storage is symbolized in the white arrow.

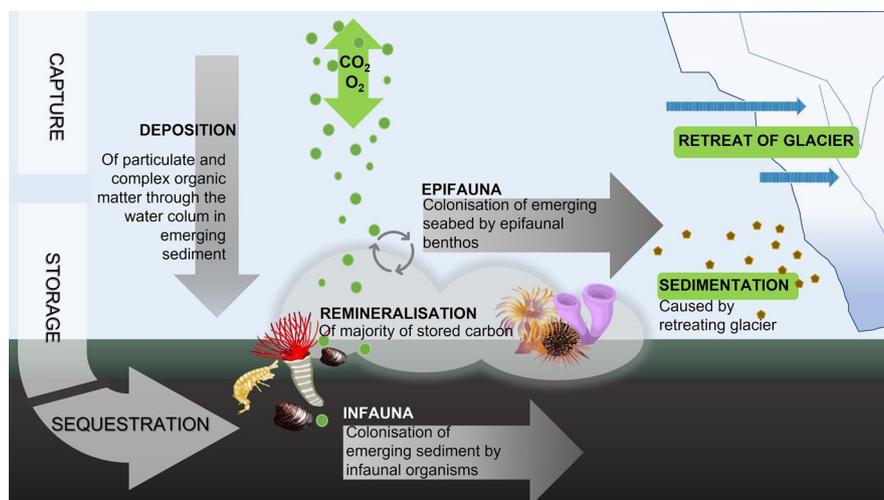


FIGURE 1 The three different pathways of carbon storage which may lead to eventual sequestration of carbon in Antarctica represented in grey. These are (1) direct deposition of primary production, (2) storage in above-seabed animals (e.g. pelagic and epibenthic) then deposition on their death and (3) infauna within the sediment. However, the majority of stored carbon will be recycled back into the system. Physical processes within the fjord which contribute to carbon sequestration are represented in green. The process of carbon storage is symbolized in the white arrow

The largest carbon storage increases in Antarctic regions are considered to be a consequence of sea ice loss followed by loss of ice shelves (Barnes et al., 2018, 2021). Recent bluing of the productive Weddell Sea is expected to further increase blue carbon gains from sea ice losses (Fogwill et al., 2020; Pineda-Metz et al., 2020). It is important to bear in mind that true sequestration of carbon, defined as removal of carbon for more than 100 years (Erbach & Andreo Victoria, 2021), rather than storage (removal of carbon over the lifespan of taxa) has an important negative feedback on climate and hence is ultimately societally valuable (Bax et al., 2020). Nearly 90% of West Antarctic Peninsula (WAP) glaciers are now in retreat and retreat rates are accelerating (Cook et al., 2016). Thus, fjords must be amongst Antarctica's most rapidly increasing and novel habitats. Current predictions estimate that epibenthic megazoobenthos alone will generate up to 4536 t C/year and sequester more than 780 t C/year along emerging WAP fjordic habitats recently uncovered by glacial retreat (Barnes et al., 2020).

Of blue carbon responses to marine ice loss, we know little about fjords emerging from glaciers (Barnes et al., 2021). What we do know has focused on the distribution of epibenthic fauna and has neglected other pathways of carbon storage and sequestration (Barnes et al., 2020; but see Pineda-Metz et al., 2020; Włodarska-Kowalczyk et al., 2019). The Antarctic continent is lacking in multicellular plant; thus, benthic epifauna seems to be an obvious pathway for carbon captured by phytoplankton. However, it is unclear what proportion of benthos is represented by epifauna and how much of epifaunal carbon is actually sequestered, that is, buried. Infaunal species may have lower carbon standing stocks but, by their nature, are already buried within the sediments, and thus, we argue are more likely to become sequestered. Likewise, total organic carbon (TOC) deposited via sedimentation or benthic–pelagic coupling is more likely to be either taken up by infaunal species or cycled further into anoxic sediment (Middelburg, 2018). In this study, we aimed to gain a more holistic quantification of carbon gains driven by glacier retreat. To do this, we sampled along three fjords with a known history of glacier retreat to quantify the potential of infaunal carbon and TOC contributing to carbon storage and sequestration and compare it to that held by epifauna from previous predictions. We hypothesize that the distribution of these two carbon pathways follows a predictable pattern (i) increasing with time free of ice (i.e. age of seabed) and (ii) decreasing within depths of the sediment. This enables us to reduce uncertainty in numerical models incorporating this negative feedback loop into future climate predictions.

2 | MATERIALS AND METHODS

2.1 | Location

Three sites were selected along the WAP based on vessel accessibility, a strong record of previous glacial retreat through satellite imagery (Cook et al., 2016) and contrast in hydrographic context. Marian Cove (Maxwell Bay, King George Island, South Shetland

Islands) was the most northerly site, followed by William Glacier (Börge Bay, Anvers Island) and finally Sheldon Glacier (Sheldon Cove, Ryder Bay, Adelaide Island) as the most southerly site (Figure 2; Table S2). During December 2018, as part of the ICEBERGS II research cruise (JR18003) on the RRS James Clark Ross, five to six stations were sampled at each site along a gradient of glacial retreat from the fjord mouth (no glacier ice cover since records began) to the glacier terminus (recent ice cover). These sites, therefore, provide a gradient of ice coverage spanning from within last decade coverage to not covered for at least half a century (Cook et al., 2016).

2.2 | Experimental design

2.2.1 | Infaunal carbon

To estimate infaunal carbon an Oktopus 12-core multi-corer was deployed from the RRS James Clark Ross. Each core has an inner diameter of 95 mm and a length of 610 mm. At least five replicate cores over three different deployments were taken to capture within station variability at each station. Samples from Marian Cove and Börge Bay were processed one core at a time by sieving each core individually over a 1-mm sieve by gentle washing with seawater. All animals present in the sieve were then preserved together as an assemblage sample in 100% ethanol. At Sheldon Cove, each core was sectioned into 5 cm sections starting from the core top to the bottom. Each section of each core was individually sieved over a 1-mm sieve and all animals present were preserved in 100% ethanol. This was only done at Sheldon Cove as a pilot study because it was a time-intensive method in a very time-constrained project. The preserved animals were then sorted into closest identifiable taxonomic groups (e.g. class) and counted. For each core, dry mass and ash-free dry mass (AFDM) were estimated by drying all individuals within each taxonomic group to constant mass at 60°C for 24 h before burning them at 480°C for 6 h. AFDM was calculated by subtracting ash mass from dry mass. Approximate carbon content was calculated as ~50% of organic mass (AFDM) plus 13% of ash (skeleton) mass (see Salonen et al., 1976).

2.2.2 | Organic matter

To capture standing stock of particulate organic carbon, one single core at each station was dedicated to quantifying organic matter within the sediment. It is likely that deposition in organic carbon in Antarctic fjords is patchy; thus, the low replication in this study could cause an over- or underestimation of total TOC. On recovery, these cores were sliced into 1 cm sections which were individually wrapped and immediately frozen at –80°C. To estimate organic matter content each, sample was dried to constant mass at 70°C for 48 h and subsequently burned at 480°C for 12 h. Because our sampling approach did not allow us to differentiate between inorganic and organic carbon, we estimate that a maximum of 20% of the organic

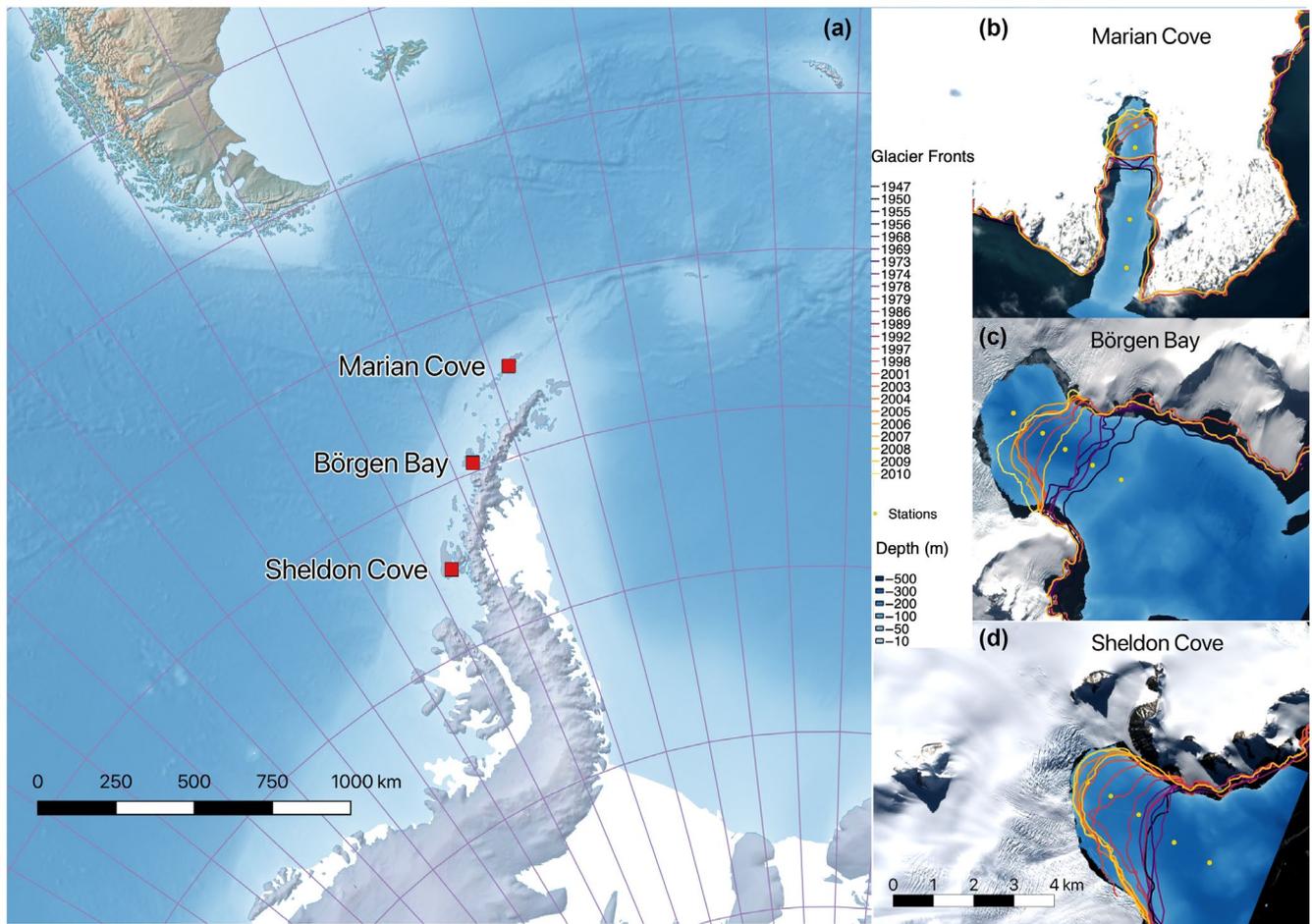


FIGURE 2 Position of the three sampled fjords along the West Antarctic Peninsula (WAP; a) and bathymetry (Retallick et al., 2021) as well as estimated glacial retreat lines for Marian Cove (b), William Glacier in Børgen Bay (c) and Sheldon Glacier in Sheldon Cove (d) (Cook et al., 2016). Yellow dots represent the different sampling station at each glacier. The large-scale map and satellite images for the individual glaciers were retrieved from Natural Earth (Natural Earth, 2021) and the Mapping and GIS team (MAGIC) of the British Antarctic Service respectively

matter contains organic carbon (Burdige, 2007). Thus, the AFDM, standardized to AFDM m^{-2} , was divided by five as a proxy for the amount of TOC in the sediment (Burdige, 2007).

2.2.3 | Environmental variables

Water depth was measured using the ship's multibeam EM122 for each sampling event. The distance of station to the glacier terminus was calculated using a 90° angled transect from each station GPS point to the glacier terminus at the head of the fjord in QGIS (throughout we consider that for each station: time since last ice cover = time since ice free). The approximate time each station has been free of ice was estimated using glacier retreat lines (see Cook et al., 2016; Figure 2). Stations that are presumed to never have been covered by the glacier were included as >1000 years in the analysis to be able to enable an analysis along a time gradient (Table S2). One additional sediment core was taken at each station to determine sediment composition (particle size of sediment) for each station.

These cores were sliced into 1 cm sections, which were immediately frozen at -80°C . Sections were dried to constant mass at 70°C for 48 h, after which they were disaggregated gently using pestle and mortar. Each section was subsequently filtered through a sieve stack (mesh sizes: 1 mm > 0.5 mm > 0.25 mm > 0.125 mm > 0.063 mm > 0.053 mm). Sediment composition was classified into five size fractions according to Blott and Pye (2012) (Table S1).

2.3 | Statistical analysis

Data for infaunal carbon and organic matter were standardized to m^2 and subsequently tested for normality, heterogeneity of variances, outliers and collinearity of predictor variables (Zuur et al., 2010). Two outliers exceeding $1.5\times$ interquartile range of box plots were removed (Cottenie, 2005; Hodge & Austin, 2004). Two samples, one in Marian Cove and one in Sheldon Cove, contained anomalous high mass of infaunal carbon because of the remainder of a silicate sponge in the sediment (94.99 , 97.63 $g\ m^{-2}$ respectively).

These samples reduced model fit and thus were removed. To test for any potential effect of these samples, analysis was carried out with and without the removal of outliers (Table S3 and S4). Where data were not normally distributed nor homogenous, but residuals of the chosen model fitted the assumptions, we still accepted the model outcome. The best model fit was chosen by using the model with the lowest Akaike information criterion (AIC; Zuur et al., 2009).

To determine how infaunal carbon and TOC contribute to carbon standing stock with time since last ice cover (Time), linear mixed effects models (LME) were carried out using the nlme package in R (Pinheiro et al., 2021). Best model fit was achieved by including time since last ice cover (time—continuous), site (three levels: Marian Cove, Børgen Bay, Sheldon Cove—categorical) and sediment composition (sediment; five levels: mS, (m)S, (g)(m)S, (vg)(m)S, (vg)mS—categorical) as fixed factors. Sampling stations (five or six levels) were included as random factor to account for dependencies of samples from the same station.

To estimate how carbon standing stock changes with depth in the sediment along a gradient of a retreating glacier, a second set of analyses using LMEs was carried out using infaunal carbon in Sheldon Cove and TOC collected in Marian Cove, Børgen Bay and Sheldon Cove as response variable. Factors included site (three levels; categorical: only for analysis of TOC), depth of sediment (0–5, 5–10, 10–15, 15–20, >20 cm—continuous) and sediment composition (five levels, categorical). Samples were analysed along a distance from glacier gradient (continuous) rather than time as the AIC showed a better model fit for this option. Ultimately, time since last ice cover and distance from glacier are collinear and thus are interchangeable. Distance from glacier represents a greater resolution for samples, because for the gradient of time, stations furthest away from the glacier were clustered into the same grouping (>1000 years). Sampling station was, again, included as random factor.

Least square post hoc tests were carried out to distinguish between groups of significant results where possible. However, most of our explanatory variables were continuous, not categorical, making comparisons between interactions difficult to interpret.

To test whether infaunal assemblages differed between sites and showed signs of successional stages with glacier retreat, a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001; McArdle & Anderson, 2001; Oksanen et al., 2020) was carried out using the vegan package. Analysis was carried out

on untransformed and fourth-root transformed data to distinguish between the impact of rare and dominant taxa (Clarke & Warwick, 2001). To determine differences in community response, abundance as well as biomass data were tested against site and distance as fixed factors and stations as random factor. The reduced model was carried out with 9999 permutations of the residuals. Pairwise PERMANOVA was used to distinguish between significantly different levels of factors. Taxa driving assemblage differences between factor levels were identified using similarity of percentage analysis on untransformed data. A 50% cut-off was used for the cumulative dissimilarity between groups, because, thereafter, remaining taxa individually contributed to <2% of overall differences in assemblage structure. All analyses were carried out with the free software package R, version 4.0.0 (R Core Team, 2020).

3 | RESULTS

Fjord bed carbon storage varied across the three study fjord samples showing some strong but complex responses to potential influencing variables. Infaunal carbon mass was similar between sites and was not affected by time since last glacier cover (Table 1; Table S3; Figure 3a) nor was it affected by differences in sediment type (grain size; Figure S2).

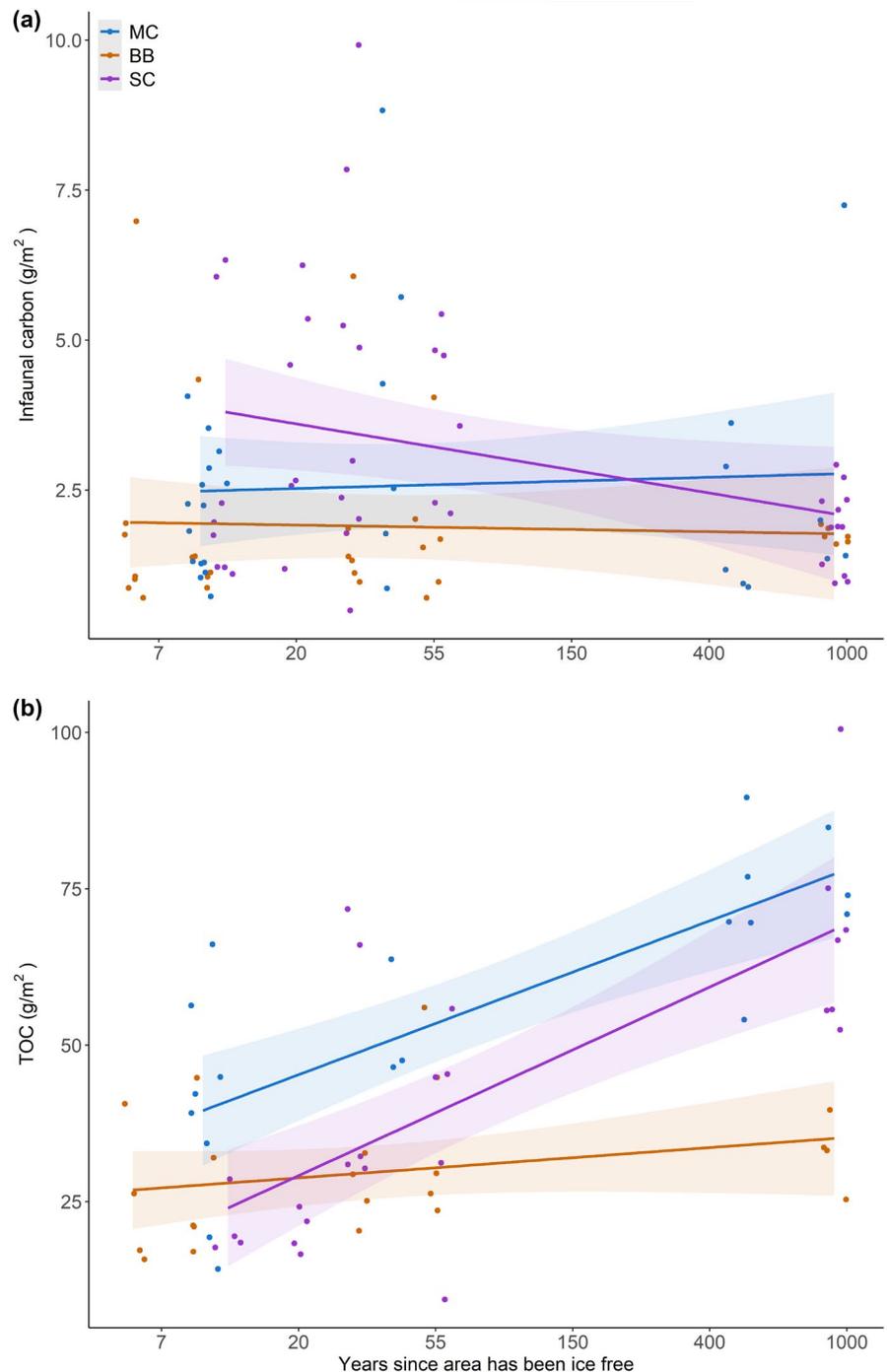
Content of TOC in the sediment significantly increased over time since fjord has been glacier ice free across all fjords. Overall content of TOC was greatest at Marian Cove and lowest at Børgen Bay (Table 1; Table S3; Figure 3b). Interestingly, no significant interaction between time and site was found despite both Marian Cove and Sheldon Cove showing a much greater accumulation of TOC towards stations that had been ice free longer than Børgen Bay (Table 1; Figure 3b). Again, sediment composition did not seem to affect the accumulation of TOC (Table 1; Table S3). Despite the low replication, our results for TOC were the most consistent across all three fjords.

The determination of patterns of carbon distribution with sediment depth showed clear patterns. Infaunal carbon mass divided by depth zones in the sediment was only measured at Sheldon Cove because of time constraints and showed a general decrease with increasing sediment depth (Table 2; Table S4). Infaunal carbon mass over 5 g/m² was only found to a maximum of 10 cm depth and was

| | Infaunal carbon | | | Total organic carbon (TOC) | | |
|----------------|-----------------|---------|---------|----------------------------|---------|--------------|
| | Df | F-value | p-value | Df | F-value | p-value |
| Intercept | 1 | 200.52 | <0.001 | 1 | 268.69 | <0.001 |
| Site = S | 2 | 3.83 | 0.098 | 2 | 8.19 | 0.026 |
| Time (log) = T | 1 | 4.02 | 0.101 | 1 | 18.90 | 0.007 |
| Sediment = Sed | 5 | 1.42 | 0.354 | 5 | 0.96 | 0.515 |
| S*T | 2 | 0.53 | 0.620 | 2 | 2.56 | 0.172 |
| Residuals | 91 | | | 55 | | |

TABLE 1 Linear mixed effect model (LME) excluding outliers to test if mass of carbon storage in the two different pathways: (a) infaunal carbon and (b) total organic carbon differed between sites, with time that sample station had been ice free or sediment characterization at each sampling station. Station was included as a random factor in the analysis to eliminate effects of pseudoreplication. Results in bold and italic denote significant factors

FIGURE 3 Infaunal carbon (a) and total organic carbon (TOC; b) deposited in the sediment along time gradient since sampled areas had been glacier ice free (years) at Börger Bay (BB—orange), Marian Cove (MC—blue) and Sheldon Cove (SC—purple). Lines visualize outcome of the linear model, shaded areas represent the 95% confidence interval



negligible below 20 cm (Figure 4a). Examinations of patterns with distance to the glacier showed increasing variation in infaunal carbon mass in the upper layers of the sediment closer to the glacier terminus which also seemed to cause a decrease in infaunal carbon in deeper sediment layers (Table 2; Table S4, Figure 4b).

Mass of TOC also showed a decrease with sediment depth (Table 2; Table S4; Figure 5). Crucially, however, the relationship of TOC and sediment depth did not differ between sites (Table 2; Table S4; Figure 5a). In stations further away from the glacier, TOC typically decreased with sediment depth (Figure 5b). At Marian Cove and Börger Bay, this was also the case at stations closer to the glacier terminus whilst in Sheldon Cove, TOC did not follow the same

pattern (Figure 5b). Mass of TOC also seemed to be affected by a change in sediment type at different depths in the sediment column (Figures S2 and S3).

Assemblages dependent on abundance differed significantly between sites (transformed: $F_{2,104} = 2.17$, $p = 0.022$, untransformed: $F_{2,104} = 2.18$, $p = 0.01$) and with distance to glacier (transformed: $F_{1,104} = 8.44$, $p < 0.001$, untransformed: $F_{1,104} = 12.69$, $p < 0.001$) but showed no interactions between sites and distance (transformed: $F_{2,104} = 0.56$, $p = 0.853$, untransformed: $F_{2,104} = 0.99$, $p = 0.451$; Figure S3). Pairwise PERMANOVA showed that assemblages in Börger Bay differed from Marian Cove but that they were both similar to Sheldon Cove. Community assemblages dependent on

| | Infaunal carbon | | | Total organic carbon (TOC) | | |
|----------------------------|-----------------|-------|------------------|----------------------------|--------|------------------|
| | Df | Mean | Sq | Df | Mean | Sq |
| Intercept | 1 | 14.53 | <0.001 | 1 | 453.95 | <0.001 |
| Site = S | | | | 2 | 12.70 | 0.001 |
| Distance from glacier = DG | 1 | 2.95 | 0.161 | 1 | 34.62 | <0.001 |
| Depth of sediment = Ds | 1 | 18.61 | <0.001 | 1 | 144.49 | <0.001 |
| Sediment = Sed | 4 | 0.73 | 0.573 | 6 | 2.98 | 0.008 |
| S*D _s | | | | 2 | 0.51 | 0.602 |
| S*DG | | | | 2 | 4.64 | 0.010 |
| DG*D _s | 1 | 8.79 | 0.004 | 1 | 1.22 | 0.270 |
| S*D _s *DG | | | | 2 | 2.50 | 0.084 |
| Residuals | 135 | | | 291 | | |

TABLE 2 Linear mixed effect model (LME) excluding outliers to test if mass of carbon storage for (a) infaunal carbon and (b) total organic carbon (TOC) changes with depth in sediment along the gradient between glacier terminus and fjord mouth (Distance from glacier) as well as with sediment type. Significant results are printed in bold and italic

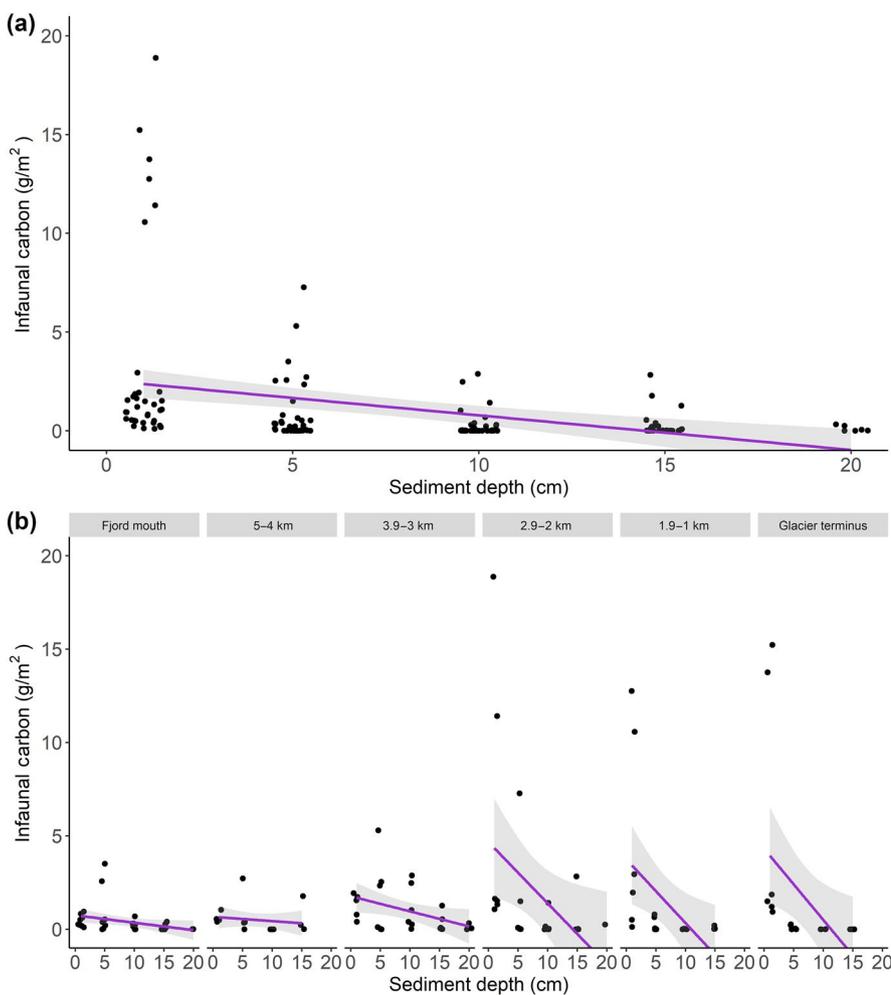
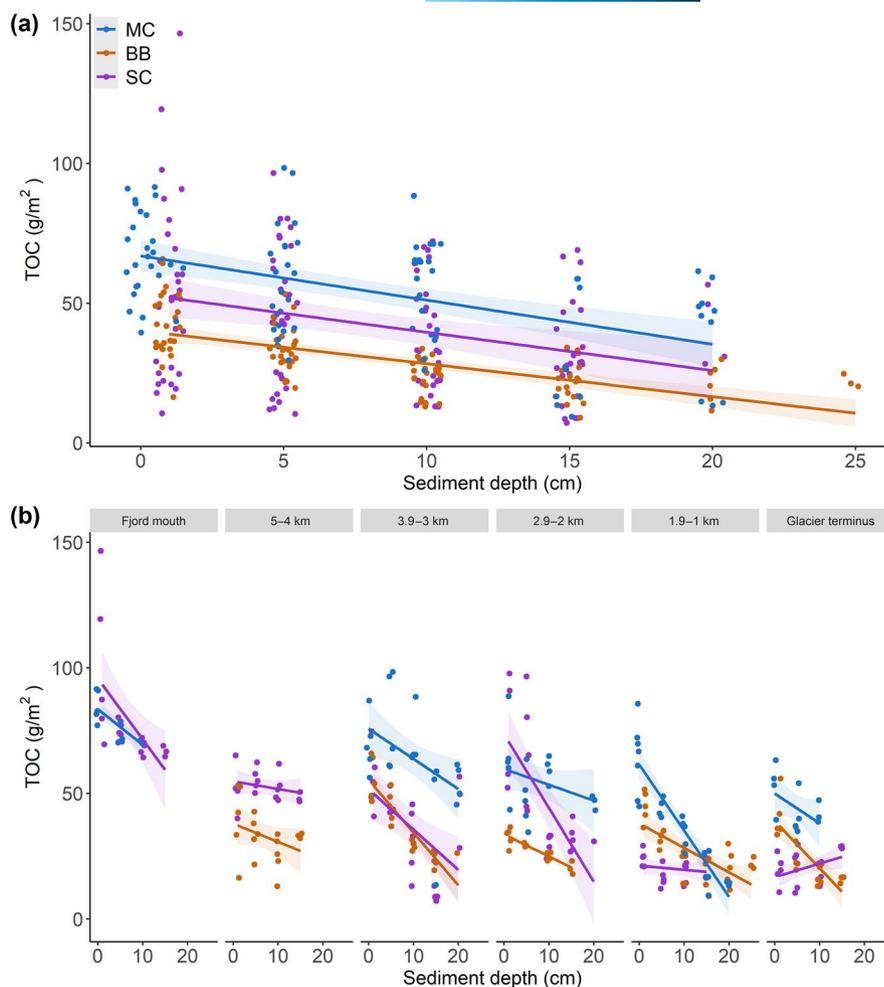


FIGURE 4 Infaunal carbon mass with sediment depth in Sheldon Cove. This is shown for (a) all sampled stations, and with (b) distance to glacier in Sheldon Cove. The purple line indicates the outcome of the linear model and the grey shading shows the 95% confidence interval

biomass showed similar results; however, slight differences between transformed and untransformed data show that less dominant species are responsible for differences between sites (transformed: $F_{2,104} = 5.16$, $p = 0.051$, untransformed: $F_{2,104} = 1.54$, $p = 0.063$). Pairwise PERMANOVA on transformed biomass data was inconclusive but indicated that assemblages differed between Børgen Bay and Sheldon Cove, but both were similar to Marian Cove. Community analysis based on biomass still differed with distance to glacier

(transformed: $F_{1,104} = 5.16$, $p < 0.001$, untransformed: $F_{1,104} = 5.5$, $p < 0.001$) and showed no interaction between sites and distance (transformed: $F_{2,104} = 0.41$, $p = 0.962$, untransformed: $F_{2,104} = 0.58$, $p = 0.938$; Figure S4). Differences in abundance between Børgen Bay and Marian Cove were primarily caused by a greater abundance of suspension feeding and errant polychaetes at Marian Cove. Børgen Bay had a greater abundance of deposit-feeding polychaetes (Table S5). Although abundance of individuals was lower at Børgen

FIGURE 5 Total organic carbon mass (TOC) with sediment depth in Antarctic fjords. This is shown for (a) all sampled stations and with (b) distance to glacier terminus. Lines indicate the outcome of the linear model for Marian Cove (blue), Børgen Bay (orange) and Sheldon Cove (purple). The shading shows the 95% confidence interval



Bay, biomass was generally greater than at Marian Cove (Table S5). Differences between Børgen Bay and Sheldon Cove were based on a greater abundance of suspension-feeding and errant polychaetes in Sheldon Cove and more bivalves in Børgen Bay. However, biomass of bivalves and ophiuroids was greater at Sheldon Cove while biomass of deposit-feeding polychaetes and holothuroids was greater at Børgen Bay (Table S5). Stations closest to glacier termini had significantly different assemblages to any other station, dominated by deposit-feeding polychaetes. This was true for both abundance and biomass (Table S6). Interestingly, also stations 2–3 km away from the glacier terminus were uniquely different to any other station, which seemed to be generally driven by paucity of fauna. Stations closest to the fjord mouth showed most assemblage similarity and consisted of increasing numbers and biomass of suspension-feeding bivalves and sedentary polychaetes as well as scavengers including ophiuroids, nemertean and errant polychaetes (Table S6).

4 | DISCUSSION

High-latitude polar environments are deprived of the most common and effective blue carbon storage pathways found in coastal temperate and tropical latitudes including mangrove swamps, seagrass

meadows, salt marshes and kelp forests amongst the most high profile and studied (Henley et al., 2020; McLeod et al., 2011; O'Connor et al., 2020). However, there has been an increasing recognition that offshore soft sediment habitats, which are not dominated by vegetation, could also contribute significantly to blue carbon sequestration (Bax et al., 2020; Hughes et al., 2020; Queirós et al., 2019). Here, we show that even in habitats lacking the more intuitive pathways of blue carbon storage such as polar fjords emerging from glacier retreat, several pathways of carbon storage exist. More importantly, most of these rarely quantified pathways have the potential to contribute to eventual carbon sequestration and might already do so. We found that fjord bed carbon storage varies across fjords, storage pathways and sediment depths. Most striking for carbon budgets, we show that TOC within sediment tends to be ~10 times greater than carbon standing stock of infaunal carbon and previously quantified epibenthic carbon (Barnes et al., 2020; Emerson, 1985; Tromp et al., 1995). At all fjords, stocks of TOC increase with time since last ice cover as expected (Włodarska-Kowalczyk et al., 2019), but showed a primarily uniform distribution of infaunal carbon standing stock. This was surprising given previously observed colonization rates along retreating glaciers (Moon et al., 2015), yet different taxonomic groups contributed to biomass between glacier termini and fjord mouth. Crucially, TOC followed a similar pattern within the

sediment at all three sites but varied in amount of TOC stored across all three sites. Our most northerly study fjord, Marian Cove, showed greatest amount of TOC in the sediment, followed by Sheldon Cove which was the most southerly. Generally, Børgen Bay had the lowest carbon standing stock in both infaunal and TOC pathways, and this was unrelated to the time since being glacier ice free.

To date, most of the blue carbon in Antarctica is measured as standing stock of benthic epifauna (Barnes, 2017; Barnes et al., 2018, 2020). A recent Weddell Sea study, however, has used sediment cores to assess wider biota including infauna (Pineda-Metz et al., 2020). So far, it is unclear how much of this epibenthic carbon has the potential to become sequestered, which effectively means being buried below the oxygenated layer and microbial carbon loop. It is likely that the majority of epibenthic megafauna species store much carbon over their lifespan which can be up to several hundred years (Clarke, 1979). It is also likely that carbon stored in epibenthic megafauna is immobilized in complex skeletons which hinder microbial access to soft tissue decomposition and will disintegrate more slowly than soft organic matter (Barnes, 2017; Barnes & Sands, 2017). Sediment accumulation rates along the Antarctic Peninsula are generally highest close to glacier termini (Eidam et al., 2019; Syvitski, 1989) but remain low within a range of 0.25–3.11 mm year⁻¹. In comparison, subantarctic fjord systems show greater accumulation rates between 11.4 and 23.6 mm year⁻¹, and sedimentation rates in the Arctic which average 37 mm year⁻¹ (Boldt et al., 2013; Eidam et al., 2019; Isla et al., 2004; Koppes & Hallet, 2002). The distribution of epifaunal carbon within fjord systems is patchy and greatest in areas with hard substratum such as dropstones and moraines which do not promote burial (Barnes & Sands, 2017; Lacharité & Metaxas, 2017; Ziegler et al., 2017). It, therefore, seems unlikely that the majority of carbon in epibenthic megafauna is ultimately sequestered and probable that it is recycled as food source or remineralized (Henley et al., 2020). We suggest that epifaunal carbon might play an important role in carbon storage, but that other hitherto neglected pathways including infaunal carbon mass and TOC in sediment might be more important to overall carbon sequestration.

Comparisons with literature data show that, typically, epifaunal carbon (mean \pm SD: 2.54 \pm 1.2 g/m² extracted from Barnes et al., 2020) is of similar magnitude to infaunal carbon measured by the current study (mean \pm SD: 2.58 \pm 1.93 g/m²) in each fjord. Thus, previous estimations of Antarctic zoobenthic carbon storage may be underestimated by 50%. Interestingly, the distribution of infauna does not follow the anticipated pattern of greater carbon standing stock in areas which have been ice free for longer and decreasing towards areas from which the glaciers have recently retreated. Although, similar to epifaunal megafauna in Marian Cove, infaunal communities in all three fjord systems have shown signs of succession along a distance gradient to the glacier with a clear distinction between sites closest to the glacier termini and more mature communities towards the fjord mouth (Moon et al., 2015). This shows that the great variation in infaunal carbon mass closer to the glacial termini might not be necessarily related to the maturity of the community but could be explained by changes in habitat characteristics

towards the glacier terminus. Sedimentation and differences in sediment characteristics are known to affect the distribution of infauna (Anderson et al., 2004; Bergen et al., 2001). Thus, it can be expected that sedimentation caused by glacial retreat not only affects composition but also abundance and therefore biomass. This would suggest that sedimentation affects infauna in a similar manner as it affects distribution and population structure of epibenthic megafauna (Pasotti et al., 2015). This is also reflected in the composition of infaunal assemblages which was dominated by deposit-feeding organisms closer to the glacier and with distance to the glacier increasingly by suspension-feeding organisms. It is also likely that colonization of bare substratum is patchy and can occur at a much faster rate than previously expected for Antarctic systems (e.g. Zworschke et al., 2021).

Although mass of TOC differed substantially across the three fjords, the process in which it is stored and eventually sequestered in the sediment seems similar. This holds particularly true for stations furthest away from the glacier. Mass of TOC along the depth gradient in the sediment did vary at a greater rate closer to the glacier terminus between sites. These differences in TOC stock might be explained by the turbid layer of suspended sediment, caused by calving events close to the glacier terminus (Ashley & Smith, 2000). Simultaneously, different rates of terrigenous mud might be generated by glacier retreat at the three different sites, thus causing differences in TOC mass in these areas (Ashley & Smith, 2000). Nevertheless, this represents an important result as TOC signifies the greatest potential for blue carbon in Antarctica and although we cannot yet determine which factors are driving its mass, we know that the rates at which it is cycled through the sediment are likely to be similar across the WAP.

A high proportion of TOC and the majority of infaunal carbon occurred in the uppermost 5 cm of sediment, as found elsewhere around Antarctica and in other regions (Blake, 1994; Hines & Comtois, 1985; Isla, 2016). Unless close to a source of high sedimentation, it is likely that this portion of infaunal organic carbon and TOC will be remineralized into the water column (Silverberg et al., 2000). Remineralization occurs where sediment is oxygenated by micro- or macrofaunal activity (Silverberg et al., 2000). All of our sites showed oxygenation of at least the first 3 cm of the sediment (F. Sales de Freitas, personal observation). Based on mean carbon/m² estimates of this study, this suggests that at least ~68% of infaunal carbon and ~25% of TOC in sediment could be subject to remineralization into the carbon cycle. Previous evidence suggests that organic matter production is largely balanced by organic matter remineralization even in areas with low temperatures such as Antarctic fjord systems (Arnosti et al., 1998; Nedwell et al., 1993). This implies that only a minimal amount of TOC in the sediment will eventually be sequestered. Studies on the continental Canadian margin have shown that only about 9% of the annual primary production is deposited on the seafloor, of which two-thirds are remineralized and one-third is buried in the sediment (Silverberg et al., 2000). In Ryder Bay (Sheldon Cove), only ~1% of the primary production is exported to a depth of 200 m, and even less to greater depths (Weston et al.,

2013). Similar export rates have been found for other areas around the WAP (Isla et al., 2004). However, it seems little remineralization is taking place in these areas which would explain the small variation in the amount of TOC with sediment depth below the initial 5 cm (Weston et al., 2013).

It is unclear what drives the pronounced difference in fjord bed carbon storage between Børgen Bay and the other two fjord systems in this study. While it is comprehensible that carbon standing stock is dictated by environmental factors such as potential of terrestrial carbon input, presence of a marine-terminating glacier and seawater temperature (Henley et al., 2020), all fjord systems in this study are Antarctic fjords with marine-terminating glaciers. The low carbon standing stock in Børgen Bay is particularly interesting as research carried out between 1995 and 1996 suggests that the Gerlache Strait which feeds into the Neumayer Channel, where Børgen Bay is located, despite being colder is more productive and features higher carbon burial rates than the Bellingshausen Sea and the Bransfield Strait (Anadón & Estrada, 2002). More recent studies, however, have shown that because of climate-driven change, productivity in the Gerlache Strait has since decreased by as much as 97% during peak phytoplankton bloom seasons. In contrast, productivity in the coastal areas of the Bellingshausen Sea has dramatically increased (Montes-Hugo et al., 2009). This might also be a result of changes in hydrography in these regions (Cook et al., 2016) driven by freshwater input and modes of climate variability such as El Niño and the Southern Annual Mode which have been exacerbating the negative effect of climate change in recent years (Torres Parra et al., 2020).

Carbon storage pathways in Antarctic fjords that have not been included or differentiated for in this study involve immediately coastal terrestrial carbon input as part of the sedimentation process by glacial erosion, meltwater streams or aeolian transport (Rogers et al., 2020). However, terrestrial carbon input has not been found to be an important carbon source in marine Antarctic systems so far (Fabiano et al., 1996). In this study, we have identified and quantified two important, primarily marine, pathways that contribute to carbon storage which are likely to grow in response to sustained climate change. Current literature estimates of blue carbon storage actually represent only ~5.5% of the total carbon stored in Antarctic fjords (Barnes et al., 2020). Based on calculations from Barnes et al. (2020) and the outcome of our study, a more realistic average carbon storage arising from glacial retreat might be closer to $56,909 \pm 29,833$ t C/year (SD). These along with predicted macroalgal increases (Campana et al., 2009) need to be included into wider regional blue carbon calculations and projections. We also demonstrate that carbon storage is not a uniform function across all fjords of the Antarctic Peninsula and varies within different fjord system. Therefore, we suggest that the potential of a negative feedback loop created by the retreat of glaciers is actually much greater than previously thought, even when including the caveat that only a small (1%–2%) percentage of the stored carbon is eventually sequestered (Barnes et al., 2020; Henley et al., 2020). The field of blue carbon research in Antarctica is still relatively young and we recommend that

future research focuses on these four research questions to make predictions more precise:

1. Which factors are the most important drivers of differences in carbon storage across habitats (e.g. fjords)?
2. How much stored carbon is ultimately sequestered and what are the factors influencing this?
3. Is sedimentation associated with glacial retreat the most efficient and most likely pathway of carbon burial in Antarctica, or could other pathways such as burial by iceberg scouring be more important?
4. How does carbon storage in fjord habitats compare to other Antarctic habitats impacted by climate change (such as those underneath ice shelves)?

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CONFLICT OF INTEREST

The authors declare no competing interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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