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## RESEARCH ARTICLE

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## Key Points:

- Organic carbon content and burial are higher in temperate North Atlantic than in high-latitude subarctic and Arctic fjords sediments
- Glacial fjords are hot spots of carbon sequestration in the Arctic
- Faunal carbon mineralization does not impact organic carbon burial levels across regional scales

## Supporting Information:

- Supporting Information S1

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## Organic Carbon Origin, Benthic Faunal Consumption, and Burial in Sediments of Northern Atlantic and Arctic Fjords (60–81°N)

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**Abstract** Fjords have been recently recognized as hot spots of organic carbon ( $C_{\text{org}}$ ) sequestration in marine sediments. This study aims to identify regional and local drivers of variability of  $C_{\text{org}}$  burial in north Atlantic and Arctic fjords. We provide a comparative quantification of  $C_{\text{org}}$ ,  $\delta^{13}\text{C}$ , photosynthetic pigments content, benthic biomass, consumption,  $C_{\text{org}}$  accumulation, and burial rates in sediments in six fjords (60–81°N). Higher sediment  $C_{\text{org}}$  content in southern Norway reflected longer phytoplankton growth season and higher productivity. Higher contributions of terrestrial  $C_{\text{org}}$  were noted in temperate/southern Norway (dense land vegetation and high precipitation) and Arctic/Svalbard (glacial erosion) than in subarctic/northern Norway locations. Benthic biomass and carbon consumption were best correlated to  $\delta^{13}\text{C}$  and photosynthetic pigments content indicating control by quality rather than quantity of available food. Benthic faunal consumption did not seem to affect the variability in  $C_{\text{org}}$  burial. Regional environmental factors (water temperature and latitude) combined with local factors ( $C_{\text{org}}$ , grain size, and pigment concentration) explained 94% of  $C_{\text{org}}$  burial variability. Based on the present study and literature data on  $C_{\text{org}}$  content, origin, and burial rates, the fjords were classified into four categories: temperate, subarctic, Arctic with glaciers, and Arctic without glaciers. The variability in marine productivity, terrestrial inflows, and carbon sequestration in fjords must be considered for global estimates of their role in blue carbon storage and for building scenarios of future changes in the course of climate warming.

### 1. Introduction

Ocean capacity to absorb and sequester  $\text{CO}_2$  is crucial for mitigating effects of rising greenhouse gas emissions. However, it gained less attention in terms of scientific assessments and management mechanisms compared to terrestrial (e.g., forests) sequestration (Nellemann et al., 2010). Duarte et al. (2005) compiled organic carbon ( $C_{\text{org}}$ ) stocks and burial rates in seabed environments and highlighted that shallow vegetated zones and coastal depositional areas account for 52% and 46% (respectively) of the total  $C_{\text{org}}$  burial in oceanic sediments. Marine  $C_{\text{org}}$  is predominantly produced in the euphotic zone by pelagic primary producers. In subtidal regions, the pelagic production is partly consumed and mineralized through pelagic food webs before it sinks to the seafloor. The fate of  $C_{\text{org}}$  deposited on the seafloor can go through one of three routes: (1) it can be remineralized by benthos into  $\text{CO}_2$ , dissolved organic carbon and nutrients, and remixed with the water (returned to the hydrosphere); (2) stored in the benthic biomass; or (3) buried in the deeper sediments and isolated from the atmosphere for hundreds of years (Klages et al., 2004). The proportions of the carbon pool that go into each of these three routes determine whether a given sedimentary system acts as a sink or a source of  $\text{CO}_2$ .

Fjords have been recently recognized as hot spots of coastal  $C_{\text{org}}$  sequestration, with burial rates a hundred times higher than the global ocean average and 11% share in global marine carbon burial (though constituting only 0.1% of ocean area; Smith et al., 2015). Fjords may be more effective in the capture and long-term storage of  $C_{\text{org}}$  due to their restrictive nature compared to more open coastal environments, which experience greater flushing and turnover (Smeaton et al., 2016). Growing literature on deposition, mineralization, and preservation of  $C_{\text{org}}$  in fjordic sediments supports the great potential of these systems for long-term carbon preservation but also points to the large (more than tenfold) variability in carbon burial rates among fjords distributed across temperate and polar regions (from 40° to 80° latitude). Carbon sequestration in a

particular fjord depends on local climatic constraints, land-ocean processes, and terrestrial material inputs, as well as phenology and magnitude of local marine and terrestrial productivity, benthic faunal and microbial activity (bioturbation), and carbon consumption (Cui et al., 2016; Kuliński et al., 2014; Smith et al., 2015; Zaborska et al., 2018). The depositional and burial processes also vary spatially within fjords, with higher accumulation rates and burial potential close to terrestrial inflow sources (Hinojosa et al., 2014) and sediment accumulation focused toward the deepest areas due to steep fjord bank slopes (Norði et al., 2018).

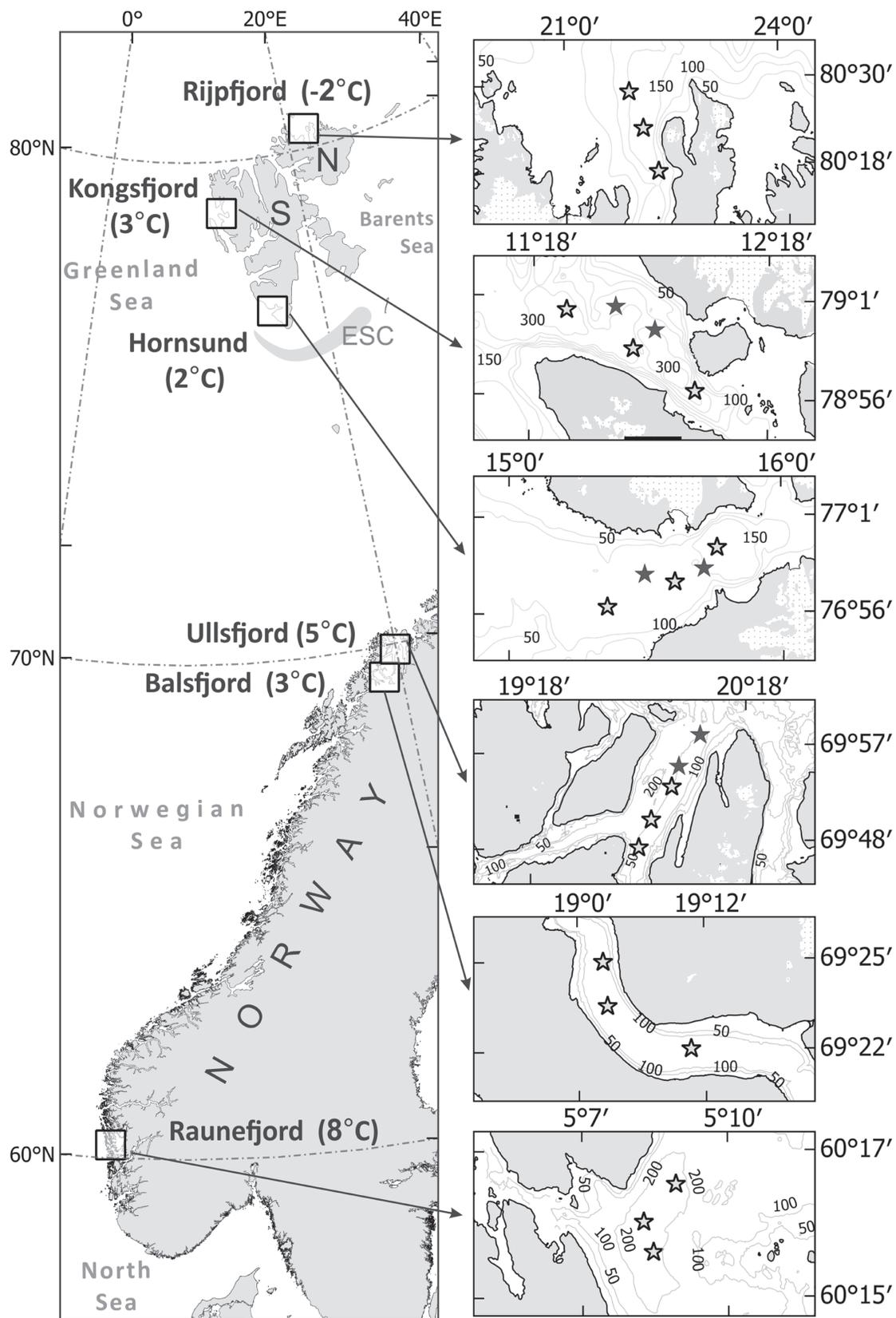
Burial in deeper sediment layers depends both on the magnitude of carbon deposition on the sea bottom and on the rate of benthic remineralization within the upper sediment layers. Benthic remineralization is realized through various degradation pathways by two main players: bacteria employing low-intensity hydrolysis based on extracellular enzymes and fauna that digests and subsequently mineralizes organic matter in organisms' digestive systems (Koho et al., 2013) but can also enhance organic matter degradation indirectly. During feeding and burrowing activities, macrofaunal organisms extensively rework the upper sediments and thus deepen vertical extent of aerobic microbial respiration (Ståhl et al., 2004) and transport labile organic matter to deeper sediment layers and stimulate microbial degradation of more refractory material through priming effect (Arndt et al., 2013). Benthic remineralization is most often estimated using sediment community oxygen consumption (SCOC), a bulk proxy that integrates chemical oxygen uptake and microbial and faunal aerobic respiration. The partitioning of SCOC among the main components can be obtained by using weight-specific estimates of respiration for different faunal groups (Piepenburg et al., 1995). Published estimates vary in claiming microbial or faunal dominance in the total sedimentary respiration (Woulds et al., 2016). Macrofauna was estimated to make 25% (Piepenburg et al., 1995) or 50% (Grant et al., 1991) of the total benthic oxygen consumption in Arctic shelf sediments. Heip et al. (2001) postulated that metazoan respiration dominated in shelf and upper slope, while microbiota predominated in lower slope and abyssal sediments. Regardless of the actual proportions, faunal community characteristics are usually indicative of the total organic matter degradation processes. Oxygen fluxes in sediment were significantly correlated to macrofaunal biomass (south Atlantic Namibian continental slope; Glud et al., 1994) or density (Mediterranean slope; Tahey et al., 1994). Changes in macrofaunal biomass mirrored the long-term temporal variability in SCOC during the warming-induced regime shift in the northern Bering Sea (Grebmeier et al., 2006) and explained 74% of the spatial variability of SCOC in western Arctic Ocean (Clough et al., 2005).

The organic carbon production and processing in coastal waters and sediments are controlled by environmental settings that are likely to be reshaped in the course of global warming. The fastest and strongest changes are expected to occur in polar regions (IPCC, 2014). While the literature on fjordic carbon burial processes is growing, most studies are geographically restricted. Larger-scale studies or compilations of the literature data are focused toward the Pacific regions (mostly New Zealand, west Canada, and Alaska; Cui, Bianchi, Jaeger, & Smith, 2016; Cui et al., 2016; Walinsky et al., 2009). Our study will provide a comparative quantification of organic carbon content, origin, faunal consumption, and burial in North Atlantic and Arctic fjords across a wide latitudinal range (60–81°N). In this study, we visited six fjords not subject to anthropogenic impacts and sampled at stations located in central and outer basins, at a distance from local terrestrial inflows, allowing for an assessment of  $C_{\text{org}}$  delivery without sediment dilution from strong glacial or fluvial material sedimentation. By exploring these results and information from other Atlantic and Arctic fjords, we aimed to learn the following: (1) How fjordic  $C_{\text{org}}$  content and characteristics are shaped by local and regional constraints? (2) Are there regional differences in magnitude of carbon burial across North Atlantic and Arctic fjords? (3) What drives the variability of metazoan community carbon consumption? Does metazoan carbon mineralization affect the carbon sequestration? The comparison of burial processes in present-day Arctic and temperate fjords may also provide the baseline for predicting the climate warming consequences on carbon cycling in the Arctic coastal sediments.

## 2. Material and Methods

### 2.1. Study Area and Sampling

Samples were collected in fjords located in southern Norway (Raunefjord, RAU), northern Norway (Balsfjord, BSF; Ullsfjord, ULS), west Spitsbergen (Hornsund, HSD; Kongsfjord, KGF), and Nordauslandet (Rijpfjord, RIJP). In each fjord, materials were collected at three or five stations (Figure 1). The stations



**Figure 1.** Location of sampling sites and stations (indicated by asterisks in the right row of maps, black symbols indicate stations with only sediments sampled). Mean bottom water temperature (this study's measurements) at each site is indicated. S = Spitsbergen; N = Nordauslandet; ESC = East Spitsbergen Current.

**Table 1**  
Basic Characteristics of the Six Studied Fjords

Fjord	Station depths (m)	C <sub>org</sub> (mg/g)	terC <sub>org</sub> (%)	LAR (cm/year)	MAR (g·m <sup>-2</sup> ·year <sup>-1</sup> )	C <sub>org</sub> BR (gC·m <sup>-2</sup> ·year <sup>-1</sup> )	marC <sub>org</sub> BR (gC·m <sup>-2</sup> ·year <sup>-1</sup> )	marC <sub>org</sub> BR/PP (%)	CD/PP (%)
Raunefjord	220–230	33.2 ± 7.4	37 ± 12	0.28 ± 0.04	2,620 ± 475	71 ± 26	43 ± 11	19 ± 5	17 ± 4
Balsfjord	167–182	17.4 ± 4.6	20 ± 4	0.13 ± 0.04	985 ± 493	14 ± 9	12 ± 7	12 ± 7	29 ± 13
Ullsfjord	180–230	17.8 ± 4.2	17 ± 5	0.11 ± 0.01	855 ± 61	10 ± 4	9 ± 3	9 ± 3	20 ± 0
Hornsund	154–180	16.6 ± 1.8	56 ± 4	0.20 ± 0.03	1,811 ± 234	28 ± 1	12 ± 1	8 ± 1	61 ± 23
Kongsfjord	250–330	13.2 ± 3.6	33 ± 6	0.22 ± 0.03	2,139 ± 293	28 ± 6	20 ± 5	13 ± 3	36 ± 11
Rijpfjord	213–277	15.7 ± 2.0	32 ± 4	0.12 ± 0.01	642 ± 88	8 ± 2	6 ± 2	13 ± 4	63 ± 11

Note. Mean (±SD) values of organic carbon content (C<sub>org</sub>), terrestrial C<sub>org</sub> contribution (terC<sub>org</sub>), linear and mass sediment accumulation rates (LAR and MAR), and C<sub>org</sub> burial rates (C<sub>org</sub>BR) in sediments, as well as ratios of marine C<sub>org</sub> burial rates and benthic carbon demand to pelagic primary production (marC<sub>org</sub> BR/PP and CD/PP) in fjords are presented. PP levels in fjords according to literature as described in section 4.

were located in central parts of outer fjordic basins (depths 150–330 m; Table 1), to minimize the effects of gravity flows likely to occur on the slopes. CTD measurements were performed with the use of a CT-set mounted at Hydro Bios MultiNet. Standard sampling methods were used for sampling benthos and sediments (e.g., Włodarska-Kowalczyk et al., 2016; Zaborska et al., 2018). Benthic samples (one replicate per station) were collected using van Veen grab (macrofauna) and a syringe (5-cm diameter) inserted 10 cm into the sediments collected using box corer (meiofauna). Macrofaunal samples were sieved on 500 μm on board, and all samples were fixed with 4% formaldehyde. Nemisto gravity corer was used to collect sediments: one replicate core for <sup>210</sup>Pb dating; one for C<sub>org</sub>, δ<sup>13</sup>C, and grain size; and three for photosynthetic pigment content. Each core was sliced into 1-cm (0–10 cm) and 2-cm (below 10 cm) layers and kept frozen.

## 2.2. Laboratory Analyses

The grain-size composition was determined using a Malvern Mastersizer 2000 particle size analyzer and computed using GradiStat 4.0. software. C<sub>org</sub> and δ<sup>13</sup>C were analyzed via continuous flow-elemental analysis-isotope ratio mass spectrometry (CF-EA\_IRMS) at University of Liège, using a vario MICRO cube elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) coupled to an IsoPrime100 (Isoprime, Cheadle, UK) mass spectrometer. Prior to analysis, sediment samples were freeze dried, grounded, and acidified with direct addition of HCl to eliminate carbonates. Standard deviation on repeated measurements of sediment samples was 0.2‰ for δ<sup>13</sup>C and 0.05% for C<sub>org</sub>. Concentrations of chlorophyll *a* (Chl *a*) and pheopigments (in total with Chl *a* referred to as chloroplastic pigments equivalent, CPE) were measured using fluorometric method at PerkinElmer LS55 Fluorescence Spectrometer. Pigments were extracted from freeze-dried sediments using 90% acetone for 24 hr at 4 °C. Measurements of emissions at 671 nm and excitations at 431 nm were performed before and after acidification of samples with 1 M HCl.

Linear and mass accumulation rates were determined using <sup>210</sup>Pb sediment dating method. The <sup>210</sup>Pb activity concentration measurements were performed using alpha spectrometry (measurement of the <sup>210</sup>Pb daughter radionuclide—<sup>210</sup>Po). Sediment samples were stored frozen for a year to reach secular equilibrium between <sup>210</sup>Pb and <sup>210</sup>Po. The efficiency of chemical separation and alpha detection was calculated for every sample using an internal standard (<sup>209</sup>Po). Sediment porosity was measured to make a correction for compaction of sediments. The detailed analytical procedure is described in Zaborska et al. (2007). The <sup>226</sup>Ra (supported <sup>210</sup>Pb) was measured for each sediment layer as a mean activity concentration of <sup>214</sup>Pb and <sup>214</sup>Bi measured in a high-purity, germanium detector (Canberra) with 20% relative efficiency. Gamma detector efficiencies were calibrated using several sources (e.g., standardized mixture of radionuclides; Braunschweig, Germany). IAEA standard materials (IAEA-300, IAEA-315, and IAEA-326) were measured as procedure controls.

Meiofauna was washed on two sieves with a mesh diameter of 500 μm (to retain macrofaunal nematodes) and 32 μm (to retain meiofauna). The washed sample of meiofaunal fraction was centrifuged three times in a solution of colloidal silica (Ludox TM-50) and stained with Rose Bengal. Organisms in meiofaunal and macrofaunal samples were identified taxonomically, enumerated, and photographed with Leica

DFC450 digital camera connected to Leica M205C stereomicroscope (maximum magnification 320X). Body dimensions were measured using the Leica Application Suite software v.4.2. Five hundred randomly selected meiofaunal nematode individuals per sample were measured using semi-automated image analysis method (Mazurkiewicz et al., 2016). Morphometric relationships were used to assess body length in damaged polychaetes (Górska et al., 2019). For macrofauna taxa with over 250 specimens per sample, a subsample of 200 randomly picked individuals was measured.

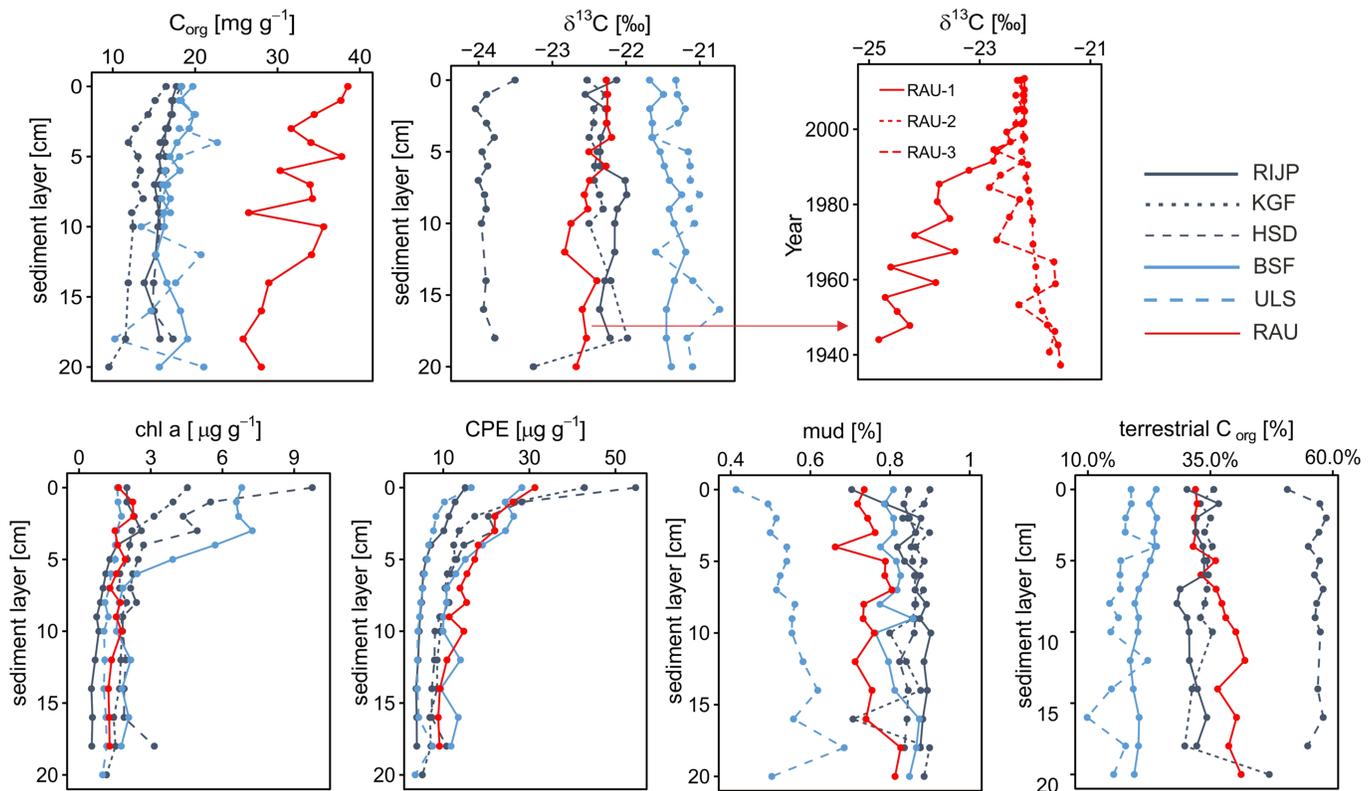
### 2.3. Data Analyses

Sediment accumulation rates were calculated using CF:CS (Constant Flux:Constant Sedimentation) and CRS (Constant Rate of Supply) models. Linear accumulation rate (LAR) and mass accumulation rate (MAR) were calculated assuming an exponential decay in  $^{210}\text{Pb}_{\text{ex}}$  ( $^{210}\text{Pb}_{\text{total}} - ^{210}\text{Pb}_{\text{supported}}$ ) with sediment depth. When surface mixing was found based on  $^{210}\text{Pb}_{\text{ex}}$  profiles, only the  $^{210}\text{Pb}_{\text{ex}}$  values below mixed zone were taken into account. Surface  $C_{\text{org}}$  accumulation rate was estimated based on the  $C_{\text{org}}$  concentration in the surface-most sediment layer multiplied by the MAR. The  $C_{\text{org}}$  burial rate ( $C_{\text{org}}\text{BR}$ ) was calculated by multiplying the MAR by the deepest measured  $C_{\text{org}}$  concentrations (mean for layers deposited below 20-cm depth), to refer to the carbon pool that will not be subjected to benthic mineralization. While the  $C_{\text{org}}$  vertical variability within the sediment core can be both due to benthic mineralization and the temporal changes in organic matter production and supply to sea bottom, these two effects cannot be easily differentiated.

The contributions of marine and terrestrial sources to sedimentary  $C_{\text{org}}$  were estimated using simple two end-member mixing model applying  $\delta^{13}\text{C}$ . The terrestrial  $\delta^{13}\text{C}_{\text{org}}$  end-member in the Arctic varies depending on the vegetation structure from  $-29.3\text{‰}$  to  $-25.5\text{‰}$  with an average of  $-26.8\text{‰}$  (Koziorowska et al., 2016; Kuliński et al., 2014; Winkelmann & Knies, 2005). Similar  $\delta^{13}\text{C}_{\text{org}}$  end-member value ( $-27\text{‰}$ ) has been applied in Norwegian fjords (Huguet et al., 2007). The marine  $\delta^{13}\text{C}_{\text{org}}$  end-member is more difficult to determine since it may change seasonally along with changes in marine organic compositions, but usually, the value of  $-20.6\text{‰}$  is applied (Koziorowska et al., 2016; Kuliński et al., 2014). In this study, values of  $-26.8\text{‰}$  and  $-20.6\text{‰}$  were used for terrestrial and marine  $\delta^{13}\text{C}_{\text{org}}$  end-members, respectively.

Faunal body dimensions were used to calculate biovolume and biomass according to procedures described by Mazurkiewicz et al. (2016) for nematodes and Górska and Włodarska-Kowalczyk (2017) for other taxa. For nematodes and other meiofaunal taxa annual secondary production and respiration were estimated using equations in Schwinghamer et al. (1986). For macrofauna production/biomass ratio, annual secondary production, mass specific respiration rate, and respiration were estimated using the Artificial Neural Network models (Brey, 2010, 2012) that consider animal individual biomass, taxonomic affinity, mode of life and feeding type, depth, and water temperature at a sampling site. Carbon demand (CD), an indicator of carbon consumption, was calculated assuming a ratio of 0.608 of an assimilation (respiration plus production) to CD after Klages et al. (2004). Biomass (B) was expressed in  $C_{\text{org}}$  content units ( $\text{gC}/\text{m}^2$ ).

Differences in mud content,  $C_{\text{org}}$ ,  $\delta^{13}\text{C}$ , Chl *a*, CPE, and total benthic B and CD among fjords were tested using one-way PERMANOVA model based on a similarity matrix created from the Euclidean distances among stations. Relationships between environmental variables and benthic B and CD were investigated using the Distance-based Linear Models (DistLM) procedure in PERMANOVA+ (Anderson et al., 2008). The data set used for the analyses included variables describing bottom water and sediment characteristics: latitude, temperature, and salinity in surface (0–5 m) and bottom (the deepest 5 m of vertical profile) waters and average values of  $C_{\text{org}}$ ,  $\delta^{13}\text{C}$ , Chl *a*, CPE, and mud content in sediment profiles as well as Chl *a* and CPE in surface sediment layer (Chl  $a_{1\text{cm}}$  and CPE $_{1\text{cm}}$ ). Surface temperature and latitude were strongly correlated to bottom temperature (Pearson's correlation  $r > 0.9$ ) and thus excluded from the analysis. Marginal tests investigated a relationship of each environmental variable to B or CD ignoring all the other variables, sequential test explored the effects of a given variable after fitting one or more variables. Forward selection procedure based on adjusted  $R^2$  as a selection criterion was used to determine the best combination of predictor variables (Anderson et al., 2008). Similar procedure was applied to seek the predictor variables best explaining the variability in  $C_{\text{org}}\text{BR}$  among stations, using the data set including environmental variables, B and CD as tested variables.



**Figure 2.** Sediment characteristics in studied fjords (average values): organic carbon ( $C_{org}$ ) content, carbon stable isotopes composition ( $\delta^{13}C$ ), mud, chlorophyll *a* (Chl *a*), photosynthetic pigments (CPE) content, and percentage of terrestrial  $C_{org}$  in sediment cores. The last plot in upper panel presents  $\delta^{13}C$  in sediments at three Raunefjord stations with sediment layer deposition year based on  $^{210}Pb$  dates on vertical scale.

### 3. Results

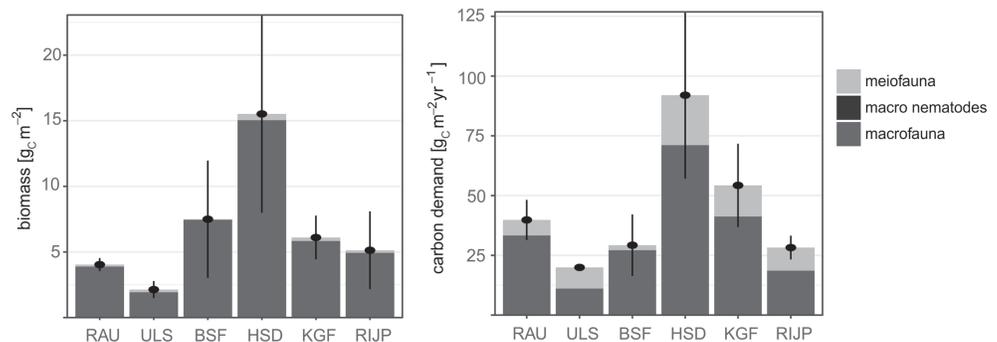
#### 3.1. Environmental Settings and Characteristics of Organic Matter in Sediments

Significant differences among fjords (PERMANOVA main tests,  $p = 0.0001$ ) were documented for all analyzed sediment characteristics (Table S1 in the supporting information). Mean  $C_{org}$  was higher in RAU (33.2 mg/g) than in other localities (Figure 2). The lowest  $C_{org}$  values were recorded in KGF (13.2 mg/g). Average  $\delta^{13}C$  was significantly lower in HSD ( $-23.9\text{‰}$ ) compared to other localities. Intermediate values were noted in RIJP, KGF, and RAU (from  $-22.2\text{‰}$  to  $-22.5\text{‰}$ ). Higher values were noted in ULS ( $-21.2\text{‰}$ ) and BSF ( $-21.4\text{‰}$ ). High mud content was noted in Svalbard fjords (85.4–85.7%), lower values in BSF (81.7%) and RAU (75.3%), and the lowest in ULS (53.8%). Chl *a* was higher in HSD and BSF (3.37 and 3.67  $\mu\text{g/g}$ ) than in other fjords: KGF, RAU, ULS, and RIJP (1.28–2.24  $\mu\text{g/g}$ ). The highest CPE was noted in RAU (18.3  $\mu\text{g/g}$ ). Lower values were noted in HSD, BSF, and KGF (14.1–16.6  $\mu\text{g/g}$ ). The lowest values were noted in RIJP and ULS (7.0 and 6.7  $\mu\text{g/g}$ ).

The lowest mean contribution of terrestrially derived organic matter was estimated for ULS and BSF sediments ( $17 \pm 5\%$  and  $20 \pm 4\%$ ; Table 1). The largest mean proportion of land-derived  $C_{org}$  was found in HSD ( $56 \pm 4\%$ ). In the remaining three fjords the mean terrestrial  $C_{org}$  constituted 32–37% of total  $C_{org}$  (except for 48% at station RAU-1 in Raunefjord). The enhanced contribution of terrestrial  $C_{org}$  (lower  $\delta^{13}C$ ) at station RAU-1 was documented only in sediment layers deeper than 10 cm—accumulated before late 1980s (Figure 2).

#### 3.2. Sediment Accumulation Rates and $C_{org}$ Accumulation/Burial Rates

Most of  $^{210}Pb_{ex}$  activity concentration profiles decreased exponentially downcore, indicating no mixing. Only in some cores, surface sediment mixing was visible (Figure S1). Mean LAR ranged from 0.11 in ULS to 0.28 cm/year in RAU (Table 1). The lowest mean MAR ( $642 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) was measured in RIJP while



**Figure 3.** Benthic biomass and carbon demand in fjords. Mean  $\pm$  SD values and contributions of three main groups (meiofauna, macrofaunal nematodes, and macrofauna) are presented.

the highest ( $2,620 \text{ g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) in RAU (Table 1). Surface  $C_{\text{org}}$  accumulation rates were the highest in RAU (from  $79$  to  $133 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) and the lowest in RIJP where it ranged from  $8$  to  $14 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (Figure S2). The  $C_{\text{orgBR}}$  (burial rate) was the highest in RAU ( $43$ – $94 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) and much lower in RIJP ( $7$ – $11 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ), four stations of ULS ( $7$ – $18 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ), and two stations of BSF ( $7$ – $11 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ; Tables 1 and S3). In HSD and KGF  $C_{\text{orgBR}}$  was very similar and ranged from  $27$  to  $29$  and  $22$  to  $36 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ , respectively (Tables 1 and S3).

Marginal DistLM tests for  $C_{\text{orgBR}}$  identified bottom temperature,  $C_{\text{org}}$ , and CPE as significant factors ( $p < 0.05$ ) independently explaining, respectively,  $36\%$ ,  $60\%$ , and  $31\%$  variability in  $C_{\text{org}}$  burial in sediments. In sequential test  $C_{\text{org}}$ ,  $\delta^{13}\text{C}$ , bottom temperature, mud, Chl  $a$ , and Chl  $a_{1\text{cm}}$  were identified as the best solution explaining  $94\%$  of variability in  $C_{\text{orgBR}}$ .

### 3.3. Benthic Biomass (B) and Carbon Consumption (CD)

Benthic biomass (B) in fjords varied from  $2.1$  (ULS) to  $15.5$  (HSD)  $\text{gC}\cdot\text{m}^{-2}$  on average (Figure 3 and Tables 1 and S3). PERMANOVA main test identified significant differences in B among fjords ( $\text{psF} = 4.4$ ,  $p = 0.019$ ), with B being significantly lower in ULS than in KGF, HSD, and RAU ( $p_{\text{MC}} < 0.05$ , post hoc tests). Mean CD in fjords varied from  $19.9$  (ULS) to  $92.0 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (HSD). CD varied significantly among fjords (PERMANOVA main test,  $\text{psF} = 7.1$ ,  $p = 0.009$ ). It was significantly higher in HSD, KGF, and RAU than in three other fjords (post hoc tests,  $p_{\text{MC}} < 0.05$ ); the lowest values were noted in ULS (Figure 3). Meiofauna contributions to B varied from  $0.54$  (BSF) to  $9.32\%$  (ULS), while its contributions to CD varied from  $7.1\%$  (BSF) to  $44.0\%$  (ULS). Macrofaunal B and CD were dominated by Polychaeta ( $46\%$  to  $92\%$ ), with considerable contributions of another group only in BSF (Asteroidea,  $50\%$  of B). Meiofaunal B and CD were dominated by Nematoda ( $46\%$  to  $84\%$ ).

Marginal DistLM tests for B identified  $\delta^{13}\text{C}$ , Chl  $a_{1\text{cm}}$ ,  $\text{CPE}_{1\text{cm}}$ , and Chl  $a$  as significant factors ( $p < 0.05$ ) independently explaining  $38\%$ ,  $45\%$ ,  $23\%$ , and  $32\%$  in B, in sequential test Chl  $a_{1\text{cm}}$ ,  $\delta^{13}\text{C}$ ,  $C_{\text{org}}$ , and bottom salinity were identified as the best solution explaining  $68\%$  of variability in B. For CD  $\delta^{13}\text{C}$ , Chl  $a_{1\text{cm}}$ , and  $\text{CPE}_{1\text{cm}}$  were significant in marginal tests ( $R^2 = 0.66$ ,  $0.35$ , and  $0.41$ , respectively), while  $\delta^{13}\text{C}$ , CPE,  $C_{\text{org}}$ , and bottom temperature were identified by sequential test as the best solution explaining  $80\%$  of variability in CD.

## 4. Discussion

### 4.1. Organic Carbon Content and Characteristics

The interplay of regional settings and local processes shapes the differences in organic matter content and characteristics in fjordic sediments. More than twice higher sediment  $C_{\text{org}}$  in the southernmost Raunefjord than in other studied fjords match the regional contrasts in marine pelagic primary productivity between southern Norway and northern locations. Annual pelagic primary production (PP) was reported to be  $230 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  in Raunefjord (Wassmann & Aadnesen, 1984) compared to  $100$  and  $150 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  in northern Norway and west Spitsbergen, respectively (Eilertsen et al., 1981;

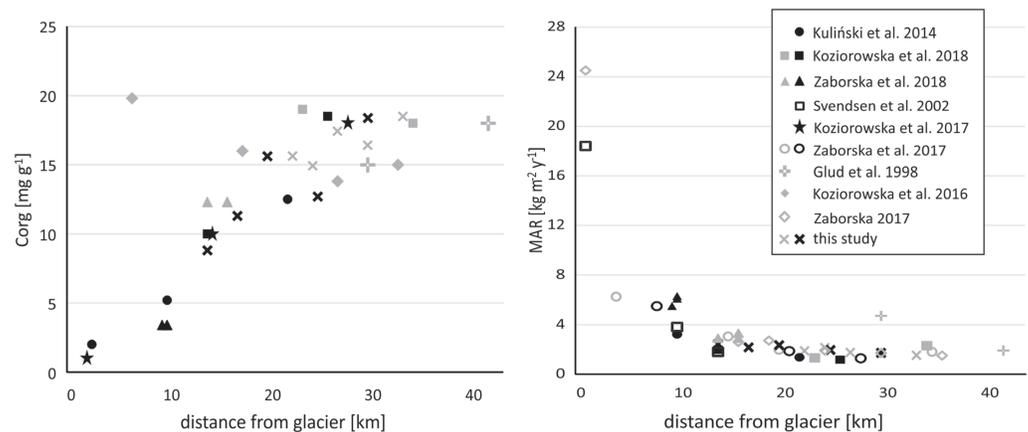
Eilertsen et al., 1989). PP is related to the duration of phytoplankton growth season: 6–7 months at the Arctic Circle latitudes and north of it compared to 9–12 months in southern coastal Norway (Eilertsen & Degerlund, 2010). In seasonally ice-covered high Arctic waters, PP linearly decreases with decreasing productive open water period (Rysgaard et al., 1999). PP in the northernmost Rjippfjord (ice-covered during 8 months) has not been documented, but it may be close to present rates reported from Young Sound (Greenland fjord with 2 months of open-water period), that is,  $10 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (Rysgaard et al., 1999), or to the  $30 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  projected for this fjord for the end of twenty-first century, when the sea-ice free window is expected to extend to four months (Rysgaard & Glud, 2007). In Rjippfjord, specialized sea-ice algae blooming underneath and within the ice in spring can produce  $10\text{--}15 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$  (Leu et al., 2011), so a rough estimate of a total pelagic and sea-ice algae production would be  $45 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ . Meire et al. (2017) compared PP in Young Sound system to that in Gothabsgfjord (off south west Greenland,  $120 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) and stated that besides the differences in sea-ice cover duration, the presence of active marine-terminating glaciers in the later locality supported higher PP due to nutrient enrichment by glacial meltwaters upwelling in summer. Similar contrasts in PP may be expected to occur between Rjippfjord (seasonally ice-covered, no major active glacier) and the other two Spitsbergen fjords (limited ice cover, active glaciers in inner basins) visited in the present study.

Besides the high phytoplankton productivity, sediments of southern Norway fjords can be substantially enriched by nonpoint sources of terrestrial organic matter originating from fjord watersheds, as indicated by high shares of terrestrial  $C_{\text{org}}$  estimated for Raunefjord. Additionally, in fjords in this region, massive blooms of mesopelagic medusa *Periphylla periphylla* can form fluxes of gelatinous  $C_{\text{org}}$  that equal or even exceed fluxes of phytodetritus  $C_{\text{org}}$  (Sweetman & Chapman, 2015). Anthropogenic pressure is obviously higher in southern Norway than in northern Norway and Arctic fjords. However, Raunefjord was selected for this study because it was reported as not subjected to eutrophication or direct anthropogenic organic pollution (Molvær et al., 2007). An interesting shift in  $\delta^{13}\text{C}$  occurred in sediments deposited at station RAU-1, probably indicating local point sources of anthropogenic organic pollution operating close to this station or an event like bank erosion occurring in the past.  $\delta^{13}\text{C}$  in first 5 cm of sediment at this station was similar to values at other stations, but in deeper layers, it decreased until  $-24.8\text{‰}$  (in sediments deposited between 1940s and early 1980s), suggesting lower importance of marine  $C_{\text{org}}$  in the past (Figure 2). Similar change in  $\delta^{13}\text{C}$  values was also observed in nearby Nordåsvannet where the discharge of sewage outlets was substantially reduced in 1988 (Paetzel & Schrader, 1995).

Shares of terrestrial  $C_{\text{org}}$  in all Svalbard fjords remain high (32–56%), comparable to those estimated for high-latitude Canadian and Greenland fjords (40–70%; Cui, Bianchi, Savage, & Smith, 2016). The lowest  $\delta^{13}\text{C}$  values and highest contributions of terrestrially derived  $C_{\text{org}}$  (over 50%) were noted in Hornsund (west Spitsbergen). Similar contribution (up to 75%) of land-derived  $C_{\text{org}}$  in Hornsund was also reported by Winkelmann and Knies (2005) and Koziorowska et al. (2017). A few mechanisms have been postulated to explain the high (compared even to other Svalbard fjords) contribution of land-originated  $C_{\text{org}}$  in Hornsund, including supplies from ornithogenic tundra enriched by large seabirds colonies dwelling in this fjord (Węśławski et al., 2017) or contribution of ancient organic matter originating from melting glaciers (Szczuciński, unpublished data of  $^{14}\text{C}$  dating of  $C_{\text{org}}$  in Brepollen, Hornsund glacial bay) in inner basin. However, similarly low  $\delta^{13}\text{C}$  (around  $-24\text{‰}$ ) were also found in sediments on the shelf break off Hornsund and was interpreted as reflecting input of terrestrial matter transported by drift ice from the Barents Sea with East Spitsbergen Current (Sanchez-Vidal et al., 2015).

Highest  $\delta^{13}\text{C}$  and highest contributions of marine origin organic matter ( $\sim 80\%$ ) were found in two northern Norway fjords. Similar range of  $\delta^{13}\text{C}$  in Ullsfjord were also reported by Sauer et al. (2016) and interpreted as indicators of organic matter originating predominantly from marine phytoplankton. Relatively high photosynthetic pigments concentrations in Balsfjord sediments support the findings of Reigstad et al. (2000), who showed that both in Balsfjord and Ullsfjord phytoplankton cells may dominate the vertical fluxes during bloom periods (as opposed to earlier suggestions of very strong zooplankton grazing and low sedimentation of fresh pelagic material to the sea bottom in northern Norwegian fjords).

The pattern observed in this study (higher contributions of marine organic matter in northern Norway than in Svalbard and southern Norway fjords) agrees with the latitudinal pattern postulated by Cui, Bianchi, Savage, and Smith (2016). They reported the stronger inputs of marine productivity to sedimentary



**Figure 4.** Organic carbon content ( $C_{org}$ ) and mass accumulation rates (MAR) in sediments of Kongsfjord (black symbols) and Hornsund (gray symbols) in relation to the distance from major active glacier fronts. Based on this study and literature data.

organic pools in west Canada and Chile compared to Alaska or New Zealand, where stronger terrestrial inputs are mediated by glacier erosion or by the strong precipitation coupled with dense land vegetation, respectively.

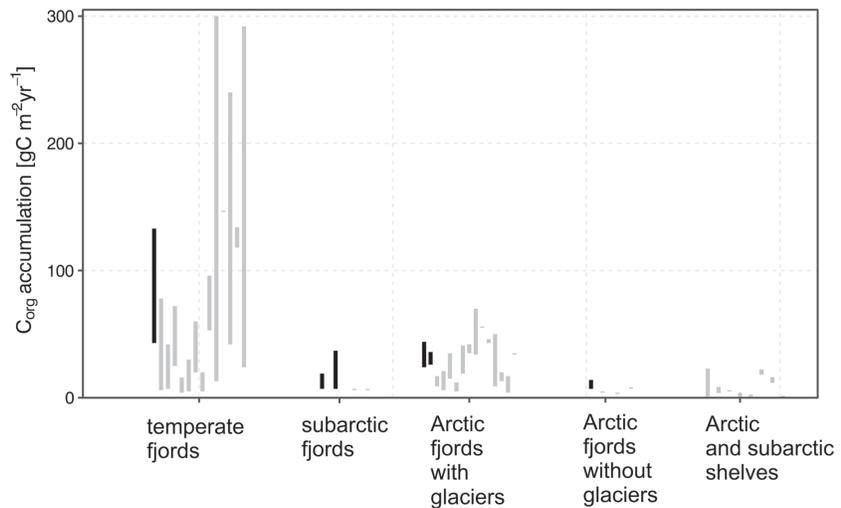
#### 4.2. Organic Carbon Accumulation and Burial

Organic carbon accumulation and burial in marine sediments can be controlled by several factors such as marine and terrestrial primary productivity, other organic matter sources, sediment accumulation rate, bottom water oxygenation, and benthic community composition (Hedges & Keil, 1995). In the DistLM model both the regional (temperature and latitude) and local ( $C_{org}$ , grain size, and pigment concentrations) variables were included and explained as much as 94% of the total variability in  $C_{org}$  burial values across the studied localities.

The highest  $C_{org}BR$  documented in Raunefjord was linked to high  $C_{org}$  coupled with high sediment accumulation rates. In temperate fjords, where organically rich soils in vegetated watersheds form nonpoint sources that deliver both mineral and organic particles, high  $C_{org}$  content often co-occur with high sediment accumulation rates, and this contrasts with polar glaciated fjords, where high sedimentation rates result from delivery of mineral glacial material (Cui, Bianchi, Savage, & Smith, 2016; Walinsky et al., 2009). Similarly high  $C_{org}$  content and  $C_{org}BR$  were linked to high primary production ( $335 \text{ gC}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$ ) in temperate fjord Kaldbaksfjordur in Faroe Islands (Norði et al., 2018). High rates of  $C_{org}$  burial were also documented in other southern Norwegian fjords (Barsnesfjord (Paetzel & Schrader, 1992), Drammensfjord (Huguet et al., 2007), and Lurefjord (Torper, 2017); Table S4). The subarctic fjords located in northern Norway (Balsfjord and Ullsfjord) were characterized by much lower  $C_{org}$  accumulation (and burial) rates, probably due to lower marine primary production and poorer terrestrial vegetation in this region. The low  $C_{org}$  accumulation was also reported for Ullsfjord and adjacent Malagenfjord (Glud et al., 1998; Sauer et al., 2016).

Compared to northern Norway,  $C_{org}BR$  was higher in west Spitsbergen fjords, probably due to high sediment accumulation rates connected to discharge from intensively melting glaciers. In Kongsfjord  $C_{org}BR$  calculated for stations visited in this study were higher than those reported from stations located closer to the fjord head (Koziarowska et al., 2018; Kuliński et al., 2014; Zaborska et al., 2018). As one gets closer to a glacier, sediment accumulation rates increase, but  $C_{org}$  contents in sediments decline due to lower primary production in turbid waters and dilution of organic material in large mass of mineral particles transported by glacial meltwaters (Figure 4).

The northernmost Rijpfjord was characterized by low sediment accumulation rates and  $C_{org}$  content in sediments, reflecting low productivity in seasonally ice-covered high Arctic fjord. As a consequence,  $C_{org}BR$  was also lower than in glacially impacted west Spitsbergen fjords. Similarly low sequestration was reported for Rijpfjord by Turner (2014), Storfjord, the fjordlike area between Spitsbergen and other Svalbard islands



**Figure 5.** Organic carbon accumulation rates in North Atlantic and Arctic fjords visited in this study (black) and fjords and shelf locations reported in the literature (gray, based on information summarized in Table S4), divided into five categories: temperate, subarctic, Arctic fjords (with and without glacial inflows), Arctic shelves and subarctic shelves. Range (minimum to maximum) of documented values is presented for each site.

(Glud et al., 1998) and Young Sound, high Arctic Greenland fjord with short marine vegetation period and no active glacier impact (Rysgaard & Nielsen, 2006). Also, Cui, Bianchi, Jaeger, and Smith (2016) reported lower  $C_{org}$  BR in nonglaciated compared to glaciated fjords in Alaska.

The  $C_{org}$  burial and accumulation rates documented in the studied locations did not deviate from values reported from other Arctic or North Atlantic fjords (Figure 5 and Table S4). Based on the present study and literature results, the fjords can be classified into four categories (Figure 5). Temperate fjords (represented by Raunefjord in this study) are characterized by high marine primary production, organically rich soils in vegetated watersheds, relatively high proportion of terrestrial  $C_{org}$ , and high carbon burial rates in sediments. In subarctic fjords (Ullsfjord and Balsfjord) shorter phytoplankton growth season is coupled with less-developed terrestrial vegetation, and both the proportion of terrestrial  $C_{org}$  and carbon burial rates are lower. Among the Arctic fjords,  $C_{org}$  accumulation and burial, as well as the terrestrial inputs, are higher in fjords where temperature-driven glacial meltwater influence dominates the system (Hornsund, Kongsfjord) than in fjords with short open-water marine vegetation period and low glacier melting (Rijpfjord). The grouping of the fjords into temperate, subarctic, and Arctic with glacial impact corresponds to that proposed by Cui, Bianchi, Savage, and Smith (2016). They compiled data on proportions of terrestrial and marine sources in sedimentary carbon pools in (mostly Pacific) fjords and proposed three dominant types of fjords, grouped by regions as (1) SE Alaska, Greenland, and Antarctica (moderate fractions of terrestrial  $C_{org}$  and marine primary production stimulated by nutrients supplied from seawater intrusion and glacier meltwaters); (2) West Canada and Chile (with  $C_{org}$  dominated by marine sources with minimal contributions from glacier erosion and terrestrial plant derived materials); and (3) New Zealand and North West Europe (with coasts covered by extensive plant vegetation, which they regarded as dominant source of  $C_{org}$ ). Evidently within the Arctic region, fjords have higher  $C_{org}$  storage capacity than open shelf sediments (Figure 5 and Table S4), supporting the recognition of fjordic environments as carbon sink hot spots. For example, almost 10 times lower  $C_{org}$ BR were documented for the Barents Sea sediments (Carroll et al., 2008) than for Spitsbergen fjords visited in the present study. Similarly, for temperate locations Hinojosa et al. (2014) showed higher  $C_{org}$  burial rates in fjords compared to nonfjordic continental margin sedimentary environments.

### 4.3. Benthic Biomass and Carbon Consumption

Benthic biomass and CD were best correlated to  $\delta^{13}C$  and photosynthetic pigment content, tracers of the organic matter origin and lability. The contrasts in carbon content between Raunefjord and other fjords were not accompanied by the parallel patterns in benthic carbon consumption. Apparently, benthic stocks and

activity were controlled by quality rather than quantity of available food. Zaborska et al. (2018) compared two localities in west Spitsbergen fjords and found lower macrofaunal CD at a site with organic matter occurring in higher quantity but being more refractory. Significant correlation to Chl *a* (but not to  $C_{\text{org}}$ ) was also documented for benthic fluxes in Skagerrak (Ståhl, Tengberg, et al., 2004) and for SCOC in Arctic seas reviewed by Bourgeois et al. (2017) and oligotrophic Aegean Sea (Ståhl et al., 2004). The fundamental role of the  $C_{\text{org}}$  origin for short-term benthic carbon processing was also indicated by stable isotope tracer experiments (Mäkelä et al., 2018) and bioturbation response after phytopigment addition (Morata et al., 2015). Grebmeier and McRoy (1989) demonstrated that the amount of labile organic material, rather than temperature, drove enhanced sediment oxygen uptake rates in Arctic sediments. However, temperature and grain size may play secondary roles in controlling levels of carbon consumption (Grant et al., 1991). Metabolic processes, including respiration and growth rate, are temperature dependent. Moodley et al. (2005) reported fivefold decrease in benthic respiration rates after experimental lowering of water temperature by 10 °C. The highest CD to biomass ratio (10 compared to 4–9 in other fjords) was observed in Raunefjord and Ullsfjord—the two warmest locations and bottom water temperature were included in the DistLM model best solution for CD. Also, sediment texture influences the benthic mineralization; fine sediments exhibited enhanced benthic activity levels and  $C_{\text{org}}$  consumption compared to coarse sediments in Eastern Canada shelves (Grant et al., 1991). Woulds et al. (2016) claimed that sandy sediments promoted the domination of microbial over the faunal mineralization of  $C_{\text{org}}$  (compared to muds). Indeed, the faunal  $C_{\text{org}}$  consumption was very low (compared to relatively high  $C_{\text{org}}$  and Chl *a*) in Ullsfjord sediments characterized by high sand content.

The community carbon consumption depends also on its size structure. Body size and temperature are primary determinants of an organism's metabolic rates, with metabolic rates per body mass unit inversely scaled with organism size (Gillooly et al., 2001). Gerlach (1971) assumed that meiofauna metabolism per mass unit is five times higher than that of macrofauna. In size spectra plotted for North Sea, meiofaunal size classes were much lower in biomass but similar in production compared to macrofaunal ones, leading Gerlach et al. (1985) to conclude that food resources are about equally utilized among all logarithmic size classes of benthic fauna. In the present study, meiofauna represented about 3% of the total faunal biomass in most fjords, except for Ullsfjord, where more heterogeneous grain size composition of sediments promoted higher meiofaunal standing stocks (7%) and Balsfjord where unusually low meiofaunal biomass (less than 1%) might result from intensive predation of epifaunal sea star *Ctenodiscus crispatus* (Sargent et al., 1983). The meiofaunal contributions to total faunal CD were much higher (from 7% to 44%) than those to total biomass, as a consequence of inverse relationships of metabolic rates and size.

Benthic consumption apparently did not affect the  $C_{\text{org}}$  sequestration across the studied locations, since neither B nor CD were included by the DistLM model as significantly correlated to  $C_{\text{org}}\text{BR}$ . Zaborska et al. (2018) visited two locations in Spitsbergen fjords and found inverse relationship between  $C_{\text{org}}$  faunal consumption and burial rates indicating that benthic community consumption levels may modify carbon burial variability at a local scale. Such effects may be of minor importance when variability at larger spatial scales is explored as in this study.

#### 4.4. How Much of Primary Production Is Buried?

Only rough literature estimates of pelagic primary productivity are available for the studied locations (see section 4.1). Comparing estimates of marine  $C_{\text{org}}\text{BR}$  to those primary productivity levels indicates that about 10% of PP is buried in sediments of northern Norway and Svalbard fjords, while almost 20% in the southern Norway fjord (Table 1). Thus, the high-latitude fjords seem to sequester higher portion of pelagic production compared to shelf systems as Barents sediments were reported to store 5–7% (Carroll et al., 2008), Canadian Beaufort Sea 3% (Goni et al., 2005), and Gulf of St Lawrence 4–5% (Silverberg et al., 2000) of pelagic production.

The highest efficiency of primary production sequestration in Raunefjord can be attributed to the high accumulation rates in this fjord, but it also coincides with the lowest efficiency of benthic faunal mineralization (only 16% of  $C_{\text{org}}$  produced annually in water column; Table 1). The larger fraction of pelagic primary productivity seems to be consumed by benthic communities in the Arctic (Svalbard) fjords than in lower-latitude locations visited in this study (Table 1). This agrees with a common notion of stronger pelago-

benthic coupling and higher portion of pelagic productivity fueled through the benthic mineralization pathways (Piepenburg, 2005; Schmid et al., 2006) in the Arctic than in temperate systems. However, it must be noted that our estimates do not take into account the lateral advection of carbon from shallow water benthic primary producers (kelp beds), which can also substantially support the diet of benthic fauna in Arctic fjord deeper basins (Renaud et al., 2015).

#### 4.5. Future Scenarios

The large variability of processes defining the particular fjord capacity of  $C_{org}$  storage implies that the future scenarios in the course of climate warming may largely differ among the studied locations. In fjords with strong glacial inflows like the present-day west Spitsbergen fjords, the long-term effect of ongoing glacier retreat will lead to shift from marine-terminating to land-terminating glaciers systems. Meire et al. (2017) predict that this will imply drastic reductions in primary productivity in fjords (via the change in hydrographic conditions and cessations of meltwater inflow mediated nutrient upwelling in summer). Decline in primary production coupled with reduced transport of mineral materials and lower sediment accumulation rates may result in declining  $C_{org}BR$  in glacial fjords. On the other hand, in the high Arctic fjords like Rijpfjord, shrinking ice-cover persistence and longer season of pelagic primary productivity will moderate increase in total primary production (Slagstad et al., 2015) and probably accelerate  $C_{org}BR$  in fjord seabed sediments. These different possible scenarios show that fjord variability must be considered both for the present-day global estimates of fjords' role as carbon sequestration hot spots and for predicting the future role they will play in blue carbon storage in the course of the ongoing climate warming.

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