



# Variability in Benthic Ecosystem Functioning in Arctic Shelf and Deep-Sea Sediments: Assessments by Benthic Oxygen Uptake Rates and Environmental Drivers

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Remineralization of organic matter at the seafloor is an important ecosystem function, as it drives carbon and nutrient cycling, supplying nutrients for photosynthetic production, but also controls carbon burial within the sediment. In the Arctic Ocean, changes in primary production due to rapid sea-ice decline and thinning affect the export of organic matter to the seafloor and thus, benthic ecosystem functioning. Due to the remoteness and difficult accessibility of the Arctic Ocean, we still lack baseline knowledge about patterns of benthic remineralization rates and their drivers in both shelf and deep-sea sediments. Particularly comparative studies across regions are scarce. Here, we address this knowledge gap by contrasting benthic diffusive and total oxygen uptake rates (DOU and TOU), both established proxies of the benthic remineralization function, between shelf and deep-sea habitats of the Barents Sea and the central Arctic Ocean, sampled during a RV Polarstern expedition in 2015. DOU and TOU were measured using *ex situ* porewater oxygen microprofiles and sediment core incubations, respectively. In addition, contextual parameters including organic matter availability and microbial cell numbers were determined as environmental predictors. Pan-Arctic regional comparisons were obtained by extending our analyses to previously published data from the Laptev and Beaufort Seas. Our results show that (1) benthic oxygen uptake rates and most environmental predictors varied significantly between shelf and deep-sea habitats; (2) the availability of detrital organic matter is the main driver for patterns in total as well as diffusive respiration, while bacterial abundances were highly variable and only a weak predictor of differences in TOU and DOU; (3) regional differences in oxygen uptake across shelf and deep-sea sediments were mainly related to organic matter availability and may reflect varying primary production regimes and distances to the nearest shelf. Our findings suggest that the expected decline in sea-ice cover and the subsequent increase in export of organic matter to the seafloor may particularly enhance remineralization in the deep seas of the Arctic Ocean, altering benthic ecosystem functioning in future climate scenarios.

**Keywords:** sediment oxygen uptake, organic matter, central Arctic Ocean, shelf, deep-sea, pan-Arctic, Laptev Sea, Beaufort Sea

## INTRODUCTION

A major function of benthic ecosystems is the turnover of organic matter, mainly driven by microorganisms (Glud et al., 1998), which we refer to as the “benthic remineralization” function (Link et al., 2013b). This remineralization is crucial for the replenishment of nutrients to the water column (Canfield, 1993) and determines the amount of buried carbon in the seafloor (Archer and Maier-Reimer, 1994). It is dependent on exported organic matter from the upper water column to the seafloor, which constitutes a crucial food source for benthic communities. This is especially valid for 95% of the seabed (67% of the Earth’s surface), where the absence of light impedes primary production (Jørgensen and Boetius, 2007). It is therefore not surprising that benthic remineralization rates are dependent on water depth (Wenzhöfer and Glud, 2002). On a global scale, 15–50% (Glud, 2008) of the pelagic primary production finally reach the seafloor on the shelf, while the deep sea only receives about 1 – 5% of the exported organic matter (Klages et al., 2004; Smith et al., 2008). From these 1 – 5%, only 1 – 2% are remineralized within a few days, while the remaining proportion is turned over very slowly and gets finally buried in the seabed (Turley and Lochte, 1990; Jørgensen and Boetius, 2007).

Shelf seas in the Arctic Ocean are generally known to have higher turnover rates than deeper areas of the central Arctic (Clough et al., 2005; Grebmeier et al., 2006; Link et al., 2013b). In the latter, the perennial sea-ice cover further hampers primary production and thus, the export of organic matter to the seafloor (Bleil and Thiede, 1990; Grebmeier, 2012; Fernández-Méndez et al., 2015). Sea-ice cover in September is currently estimated to decline by 43 to 94% by 2100 (IPCC, 2013) and production regimes are predicted to change with sea-ice decline (Arrigo et al., 2008). This will ultimately affect benthic ecosystem functioning, as the quantity and quality of organic matter exported to the seafloor changes, enhancing benthic remineralization and carbon burial (Arrigo et al., 2008; Bauerfeind et al., 2009; Lalande et al., 2014; Sørensen et al., 2015; Hoffmann et al., 2017). This has previously been stressed by Boetius et al. (2013), who reported that sea-ice thinning may result in an increased export of ice algae to the deep-sea floor, triggering an increase in benthic turnover rates at latitudes >87°N. Arctic deep seas are still largely covered by sea ice on a perennial basis, whereas the presence of sea-ice on the shelves is highly seasonal (Bleil and Thiede, 1990). Thus, it is unclear if changes in benthic remineralization in the Arctic will develop differently on the continental shelves compared to the deep basins.

Benthic remineralization can be studied by measuring sedimentary oxygen uptake (Wenzhöfer and Glud, 2002; Glud, 2008; Link et al., 2013b). The latter can be assessed by measuring either total sedimentary oxygen uptake rates (TOU<sub>sed</sub>) or diffusive oxygen uptake (DOU) rates and reflects heterotrophic activity (and thus remineralization) in the absence of primary producers. TOU<sub>sed</sub> is an indicator of the total benthic carbon mineralization, including oxygen consumption induced by macrofauna (Rasmussen and Jørgensen, 1992; Glud, 2008). In contrast, DOU is calculated from oxygen microprofiles profiles in the sediment and mainly assesses microbial respiration

(Glud et al., 1994; Wenzhöfer and Glud, 2002). Since macrofauna is dominant in shelf sediments, whereas bacteria and meiofauna dominate at greater depths (Rowe et al., 1991) the differences between TOU<sub>sed</sub> and DOU should decrease with increasing water depth (Glud et al., 2000; Glud, 2008; Sørensen et al., 2015).

Besides differences in TOU<sub>sed</sub> and DOU, benthic remineralization rates between shelf and deep-sea habitats may also vary depending on the Arctic region, hampering pan-Arctic predictions based on local studies. For example, benthic remineralization rates are ultimately dependent on a combination of factors, of which water depth and chlorophyll pigments in the sediment (as an indicator of phytodetritus) were shown to be the most important ones (Boetius and Damm, 1998; Bourgeois et al., 2017). However, the availability of phytodetritus is dependent on regional factors, such as nutrient availability and sea-ice conditions (Grebmeier et al., 2006; Arrigo et al., 2008; Hoffmann et al., 2018).

A few studies have recently improved our understanding of benthic oxygen uptake and the respective influence of environmental predictors in the Arctic Ocean (Cathalot et al., 2015; Bourgeois et al., 2017; Hoffmann et al., 2017, 2018). Still, the prevailing lack of measurements in the central Arctic Ocean (as well as for the Russians Seas and main Arctic rivers) stresses the need for further investigations in these areas to provide a benchmark and to confirm and sharpen models of pan-Arctic sedimentary oxygen demand and food supply.

To estimate the impact of environmental changes on benthic remineralization as an important ecosystem function, we need to set a baseline for sediment oxygen consumption rates in shelf and deep-sea habitats and identify drivers for regional differences across the Arctic. Here, we address this knowledge gap by contrasting benthic oxygen uptake (TOU<sub>sed</sub> and DOU) and selected environmental parameters between the Barents Sea Shelf and the deep central Arctic Ocean, and comparing those to previously published measurements from the Beaufort and Laptev Sea. We specifically address the following three questions: (1) How large are variations in TOU<sub>sed</sub>, DOU and environmental parameters among the Barents Sea shelf and the central Arctic deep sea? (2) How much of the variability in TOU<sub>sed</sub> and DOU can be explained by environmental proxies and microbial abundance? (3) How do variations in benthic activity and environmental parameters among shelf and deep seas compare across different regions in the Arctic Ocean?

## MATERIALS AND METHODS

### Study Area

The Arctic seas are characterized by low water temperatures, seasonal ice cover among most shelf seas and long lasting ice cover above the basins. Furthermore, seasonal fluctuations in solar irradiation determine patterns of primary production (Piepenburg, 2005). Differences in primary production found in the literature illustrate a latitudinal gradient, representing the distinctness between Arctic shelf and deep seas (Codispoti et al., 2013). Primary production rates vary from highest values in the Barents Sea, with 110 g C m<sup>-2</sup> a<sup>-1</sup> (Sakshaug, 1997),

to lowest values found in the central Arctic, where for the Lomonosov Ridge values of  $18 \text{ g C m}^{-2} \text{ a}^{-1}$  have been estimated (Harada, 2016).

Stations in the Barents Sea and central Arctic Ocean were investigated during RV Polarstern expedition PS 94 between August and October 2015, hereafter referred to as “this study.” During the cruise, a total of 12 stations were sampled, five of which located on the Barents Sea shelf and seven in the central Arctic deep-sea basin (Table 1 and Figure 1). Shelf stations are hereafter also referred to as Barents Sea and deep-sea stations as the central Arctic Ocean. In Tables 1, 2, station names are reported following the regulations of the PANGAEA data repository; throughout the text, we only report the station numbers (e.g., 20 instead of PS94/020-2).

Some stations in the central Arctic deep sea are particularly noteworthy. One of them constitutes station 32, which was measured at 3167 m water depth, situated at the foot of the Barents Sea slope. The Barents Sea is considered a “flow through shelf”, a major passage for waters from the North Atlantic which enter the central Arctic Ocean. It comprises 49% of the total pan-Arctic shelf primary production (Sakshaug, 2004; Wassmann et al., 2006). Another exceptional deep-sea station (66) was located on the edge of the Gakkel Ridge, on top of the Karasik Mountain. This site is comparatively shallow with 656 m, but also unique in its setting on top of a lapsed volcano. Stations 105 and 130 are situated on the Lomonosov Ridge. At the time of sampling, all shelf stations (except station 21) had no ice cover, while deep-sea stations were ice-covered (Table 1).

In order to investigate regional differences in DOU,  $\text{TOU}_{\text{sed}}$  and environmental parameters, we further analyzed comparable measurements from the Beaufort (measured 2008/9) (Link et al., 2019) and the Laptev Sea (measured in 2012) (Bienhold and Boetius, 2016, 2018a,b; Wenzhöfer et al., 2018). For information on the methods used by both studies to measure

the parameters presented in this article, we refer to the respective publications.

## General Sampling

Undisturbed sediment samples were collected by deploying both a multiple corer (MUC) (Barnett et al., 1984) and a giant box corer (GBC) (Table 1). The MUC was equipped with eight core liners, each with an inner diameter of 9.4 cm and 50 cm length. After MUC retrieval, replicate sediment cores with a visibly intact sediment surface were chosen for further laboratory analysis. The GBC retrieves an undisturbed and coherent patch of seafloor sediments ( $50 \times 50 \times 30 \text{ cm}$ ) with bottom water on top. Replicate cores were taken from the GBC on board by using the same core liners as for the MUC. Overall, six replicate cores were taken from the MUC and the GBC, respectively, three of which were used for measuring diffusive oxygen uptake rates and selected environmental parameters (see sections “Chlorophyll Pigment Analyses,” “Total Organic Carbon,” and “Microbial Cell Numbers”) and three to derive total oxygen uptake rates. The selected cores were closed with a bottom lid and carefully pushed up with an extruder, so that the overlying water phase had a height of about 15 cm. Afterward cores were brought to the laboratory for further analysis of diffusive and total oxygen uptake rates, as well as for taking sediment samples for the subsequent analysis of environmental parameters. Bottom water temperature and salinity were derived from CTD (conductivity, temperature and depth) measurements, which were taken at the same location as MUC or GBC samples. CTD data (Rabe et al., 2016) and all further data from this study are available from PANGAEA (Kiesel et al., 2019).

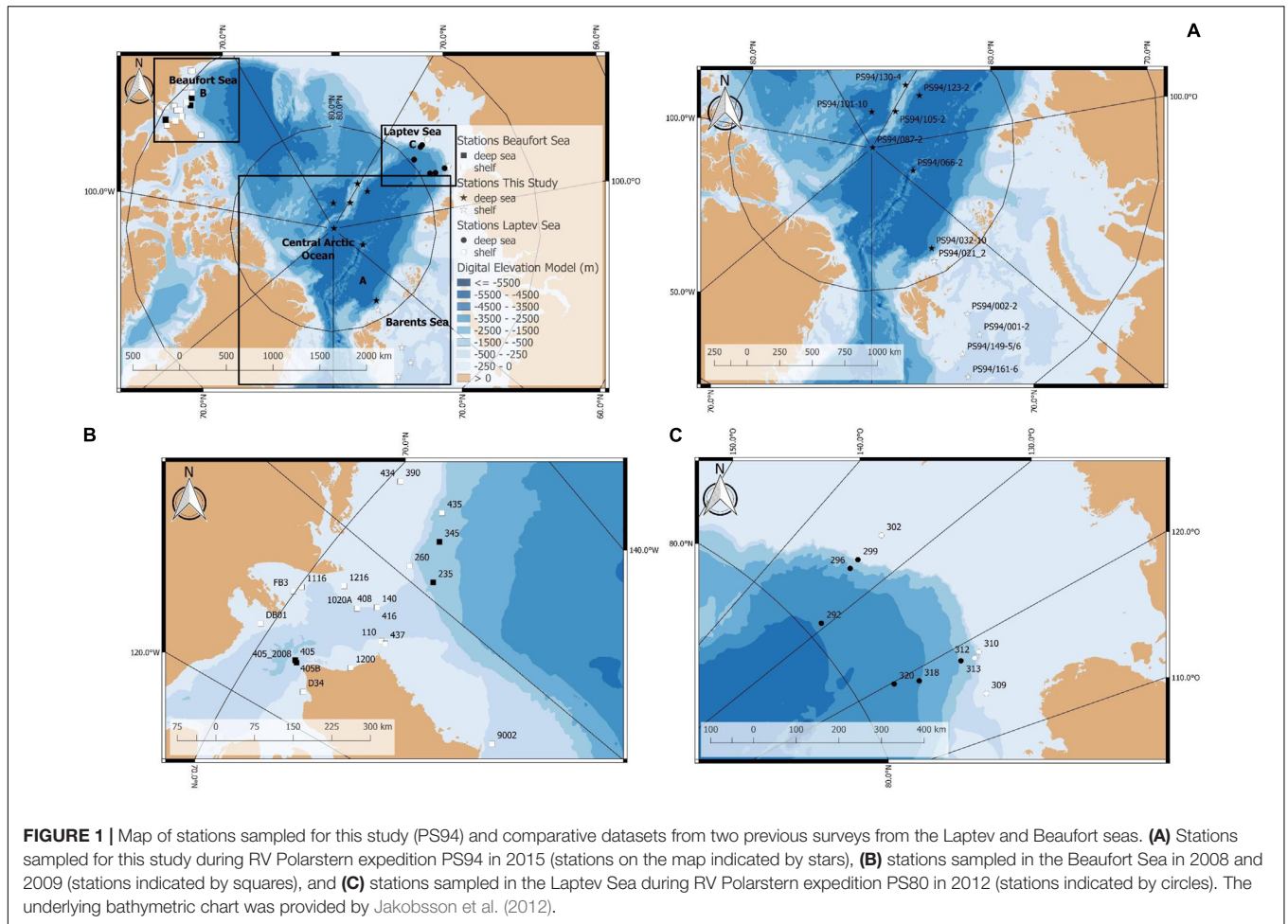
## Diffusive Oxygen Uptake

We assessed diffusive oxygen uptake rates by measuring *ex situ* porewater oxygen microprofiles in retrieved sediment cores. After retrieval and preparation on deck, three cores were

**TABLE 1** | List of stations and metadata of PS94.

Station	Sampling Device	Date	Latitude	Longitude	Sea-ice Cover (%)	Depth (m)	Habitat	Bottom Temp. (°C)	Bottom sal. (Psu)
PS94/001-2	MUC	18.08.2015	75°0.055'N	30°0.333'E	0	373	Shelf	1.64	35.06
PS94/002-2	MUC	19.08.2015	76°40.579'N	30°0.213'E	0	265	Shelf	1.69	35.05
PS94/021-2	MUC	21.08.2015	80°59.762'N	28°58.324'E	60	390	Shelf	0.72	34.88
PS94/032-10	MUC	22.08.2015	81°51.409'N	30°54.656'E	99	3167	Deep sea	-0.74	34.95
PS94/066-2	GBC	01.09.2015	86°42.756'N	61°21.732'E	100	656	Deep sea	0.22	34.88
PS94/087-2	MUC	08.09.2015	89°55.482'N	120°33.864'E	100	4262	Deep sea	-0.93	34.94
PS94/101-10	MUC	14.09.2015	87°29.807'N	179°54.151'E	90	3995	Deep sea	-0.25	34.95
PS94/105-2	GBC	16.09.2015	86°58.665'N	146°50.676'E	90	1001	Deep sea	-0.25	34.89
PS94/123-2	MUC	22.09.2015	85°03.575'N	137°36.566'E	95	4113	Deep sea	-0.93	34.93
PS94/130-4	MUC	24.09.2015	85°0.926'N	151°45.503'E	100	867	Deep sea	-0.07	34.89
PS94/149-5/6	MUC	07.10.2015	74°19.132'N	23°48.340'E	0	301	Shelf	2.05	35.05
PS94/161-6	MUC	08.10.2015	72°44.062'N	22°49.248'E	0	395	Shelf	4.8	35.11

Bottom water temperature and salinity were obtained from the conductivity, temperature and salinity (CTD) probe. This data is available from PANGAEA (see Rabe et al., 2016). Habitat type was classified in order to conduct the comparative analyses between shelf and deep-sea environments and is based on topography. MUC, multicorer; GBC, giant box corer.



**TABLE 2** | Range of all parameters assessed during PS94 (min/max).

Station	Depth (m)	Category	DOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	TOU <sub>sed</sub> (mmol m <sup>-2</sup> d <sup>-1</sup> )	FOU (mmol m <sup>-2</sup> d <sup>-1</sup> )	Chl a (μg ml <sup>-1</sup> )	Phaeo (μg ml <sup>-1</sup> )	CPE (μg ml <sup>-1</sup> )	% Chl a	TOC (μg mg <sup>-1</sup> )	Microbial cell numbers (10 <sup>9</sup> ml <sup>-1</sup> )
PS94/001-2	373	Shelf	0.36–0.47	1.68–2.4	1.72	1.29–3.25	3.25–6.3	4.54–9.55	28–34	25.12–25.54	1.86
PS94/002-2	265	Shelf	0.16–0.57	1.47–5.7	2.56	2.53–3.13	3.35–6.04	6.20–9.17	34–46	24.76–26.51	3.84
PS94/21-2	390	Shelf	0.16–1.13	NA	NA	2.44–4.12	4.16–5.08	7.31–9.20	33–48	18.52–21.28	2.91
PS94/032-10	3167	Deep sea	0.29–0.45	0.88	0.51	0.28–0.506	0.7–1.58	0.98–2.09	24–28	20.66–23.53	2.21
PS94/066-2	656	Deep sea	NA	0.13–2.52	NA	0.27–2.1	0.07–0.61	0.34–0.95	36–80	5.29–13.25	0.44
PS94/087-2	4262	Deep sea	0.14–0.19	0.29–0.59	0.28	0.121–0.14	0.06–0.2	0.18–0.34	40–67	4.93–12.62	0.71
PS94/101-10	3995	Deep sea	0.12–0.22	NA	NA	0.003–0.01	0.03–0.07	0.03–0.1	9–29	4.76–6.05	0.46
PS94/105-2	1001	Deep sea	0.27–0.29	1.00–1.2	0.82	0.07–0.09	0.11–0.13	0.20	35–44	5.86–11.09	0.81
PS94/123-2	4113	Deep sea	0.18–0.21	NA	NA	0.119–0.24	0.33–0.38	0.45–0.62	27–39	10.76–11.17	0.73
PS94/130-4	867	Deep sea	0.2–0.27	0.2–0.61	0.24	0.059–0.38	0.13–0.58	0.25–0.96	24–66	6.15–14.37	1.23
PS94/149-5/6	301	Shelf	0.56–1.11	2.21–3.15	1.66	1.57–2.10	1.19–6.09	2.76–8.19	26–57	12.15–15.03	2.17
PS94/161-6	395	Shelf	0.23–0.87	NA	NA	0.86–1.01	2.39–3.57	3.25–4.44	20–30	9.27–9.45	1.78

Besides microbial cell numbers (only one replicate), three replicates were measured for every parameter (dataset published in PANGAEA; Kiesel et al., 2019). TOU<sub>sed</sub>, total oxygen uptake; DOU, diffusive oxygen uptake; CPE, chloroplastic pigment equivalent; TOC, sediment total organic carbon content; Chl a, sediment chlorophyll a concentration; Phaeo, sediment phaeopigment concentration; FOU, Fauna mediated oxygen uptake; NA, not assessed.

immediately taken to a temperature-controlled water bath and kept at a constant temperature of 2°C. After placing the cores in the water bath, a magnetic stirring device was implemented

in each core to homogenize the overlying water column and to create a diffusive boundary layer (DBL) that was similar to *in situ* conditions (Wenzhöfer et al., 2001).



In each of the three sediment cores one oxygen microprofile was measured within the first 2 to 3 h after core recovery ( $n = 3$  per station), except stations 32, 87, 105, and 123, where only two profiles could be obtained. Two types of fiber-optical needle sensors, OXR50 (tip diameter 50  $\mu\text{m}$ , response time ( $t_{90}$ ) < 2 s) and OXR230 (tip diameter 230  $\mu\text{m}$ , response time ( $t_{90}$ ) < 2 s; both from Pyroscience, Germany) were used. All sensors were two-point calibrated (zero and 100% air saturation) at 2°C with bottom water taken from the rosette. Afterward, the sensors were connected to a *Firesting O2* oxygen meter (Pyroscience, Germany). Oxygen microprofiles were measured with a vertical resolution of 100  $\mu\text{m}$  controlled by a motor-driven micromanipulator, with resting time per data point of 5 s. Total profile length was programmed to be 6.5 cm. Examples of four microprofiles are shown in the Supplementary Material (Supplementary Figure S1).

The diffusive oxygen uptake (DOU in  $\text{mmol m}^{-2} \text{d}^{-1}$ ) was calculated from the obtained microprofiles using the linear  $\text{O}_2$  concentration gradient in the DBL applying Fick's first law of diffusion (Jørgensen and Revsbech, 1985; Glud et al., 1994; Boetius and Damm, 1998; Wenzhöfer and Glud, 2002; Jørgensen et al., 2005):

$$\text{DOU} = D_0 * dC/dz,$$

where  $D_0$  ( $\text{cm}^{-2} \text{s}^{-1}$ ) is the molecular diffusion coefficient, recalculated to the temperature of the water bath and its salinity, taken from Schulz and Zabel (2006).  $C$  ( $\mu\text{M}$ ) is the solute  $\text{O}_2$  concentration at depth  $z$  (cm) within the DBL.

## Total Sedimentary Oxygen Uptake ( $\text{TOU}_{\text{sed}}$ )

Total Sedimentary Oxygen Uptake rates were assessed by conducting sediment core incubations. After MUC retrieval and sediment core preparation on deck, three cores were taken to a dark, temperature-controlled laboratory that was refrigerated to 2–4°C. Incubation procedure generally followed the approach described by Link et al. (2013a,b). At the onset of each incubation, sediment cores were carefully topped with bottom water from the same station, taken from the rosette. Additionally, three control cores, which were exclusively filled with bottom water, were established. Cores were acclimatized for 6 to 8 h, while being saturated with air to avoid suboxic conditions during incubation (Link et al., 2013b). After acclimatization, cores were hermetically closed and a magnetic stirring device was implemented in each core. The magnetic stirring device was used to homogenize the water column without resuspending the sediment as turbulence or currents are known to affect benthic oxygen uptake rates (Hall et al., 1989; Link et al., 2013b). Oxygen was periodically measured a few centimeters above the sediment surface, with an optical sensor spot attached to the inner liner wall and measured with a non-invasive optical probe (Fibox 3 LCD, PreSens, Regensburg, Germany). Measurements were repeated every 5 to 6 h for overall 2 to 4 days. Only those measurements were considered, where oxygen concentration had not fallen below 70%, in order to avoid the influence of suboxic conditions on the oxygen uptake rates.  $\text{TOU}$  ( $\text{mmol m}^{-2} \text{d}^{-1}$ ) from the retrieved sediment core and overlying bottom water was calculated from the slope of the linear

regression of the oxygen concentration change ( $dC$ ) over the incubation time ( $dt$ ), taking the area enclosed by the microcosm ( $Ach$ ) as well as the bottom water volume  $V_{bw}$  into consideration (Link et al., 2011, 2013a,b).

$$\text{TOU} = (V_{bw}/Ach) * (dC/dt)$$

To estimate the total sedimentary oxygen uptake ( $\text{TOU}_{\text{sed}}$ ),  $\text{TOU}$  was corrected for the bottom water oxygen uptake ( $\text{BWU}$ ).

$$\text{TOU}_{\text{sed}} = \text{TOU} - \text{BWU}$$

An example of a time series core incubation showing the linear regression of oxygen consumption over time is shown in the Supplementary Material (Supplementary Figure S2).

## Fauna Mediated Oxygen Uptake (FOU)

Since DOU mostly assesses microbial respiration (Glud et al., 1994; Wenzhöfer and Glud, 2002) and  $\text{TOU}_{\text{sed}}$  additionally involves oxygen consumption by meio- and macrofauna, we used the difference between both ( $\text{TOU}_{\text{sed}} - \text{DOU}$ ) as a proxy for fauna-mediated oxygen uptake (FOU, Wenzhöfer and Glud, 2002). Since different sediment cores were used for the calculation of DOU and  $\text{TOU}_{\text{sed}}$ , we subtracted mean DOU of each station from mean  $\text{TOU}_{\text{sed}}$  of the same station, which is why only one replicate per station exists. Using the difference between  $\text{TOU}_{\text{sed}}$  and DOU as a proxy for FOU has been suggested previously by many studies, which have shown that FOU correlates with the biomass of benthic fauna (Archer and Devol, 1992; Glud et al., 1994, 1998; Wenzhöfer and Glud, 2002).

## Chlorophyll Pigment Analyses

Three subsamples from three different cores were obtained per station, taking the top first cm of sediment using cut-off 5 ml plastic syringes. Samples for chlorophyll pigment analyses were stored dark and frozen at  $-20^\circ\text{C}$  until further analyses in the home laboratory. Chlorophyll pigments were extracted from 1 ml sediment in 90% acetone, after addition of glass beads and grinding in a cell mill (Vibrogenzelmühle VI 6, Edmund Bühler GmbH). Extraction was repeated three times. After each extraction, samples were centrifuged and after each of the three extraction steps, 2 ml of supernatant were collected and combined for the subsequent measurement. Concentrations of chlorophyll *a* and phaeopigments (after acidification with 20% hydrochloric acid) were determined with a Turner Trilogy fluorometer (Turner Designs), equipped with a "Chlorophyll *a* – Acidification fluorescent module" (excitation at 485 nm, emission at 685 nm). The sum of chlorophyll *a* and phaeopigments (Phaeo) is expressed as chloroplast pigment equivalents (CPE). The proportion of chlorophyll *a* from CPE (% Chl *a*) is an indicator of the freshness of phytodetritus (Pastor et al., 2011). Pigment concentrations are provided in  $\mu\text{g ml}^{-1}$  sediment.

## Total Organic Carbon

Three subsamples from three different cores were also obtained per station, taking the top first cm of sediment using cut-off 20 ml plastic syringes. Samples were stored frozen at  $-20^\circ\text{C}$  until further analyses in the home laboratory. Samples of at least 1 g

were lyophilized and homogenized using a mortar and pestle. The total carbon content of sediment samples was determined in about 20 mg of dried sample material by combustion and gas chromatography with a Carlo Erba NA-1500 CNS elemental analyzer. An aliquot of the freeze-dried sample material was acidified with hydrochloric acid ( $6\text{--}10\text{ mol l}^{-1}$ ) to remove the fraction of inorganic carbon and to determine the total amount of organic carbon (TOC).

## Microbial Cell Numbers

For the determination of prokaryotic cell numbers, 1 ml sediment was fixed with sterile filtered formalin/seawater at a final concentration of 2% and stored at  $4^{\circ}\text{C}$  until further analyses in the home laboratory. Samples were 4,000-fold diluted and filtered on  $0.2\text{ }\mu\text{m}$  polycarbonate filters, stained with acridine orange (Meyer-Reil, 1983), and counted using an epifluorescence microscope (Axiophot II Imaging, Zeiss, Jena, Germany). For each sample, 30 random grids from two replicate filters were counted and averaged.

## Statistical Analyses

All stations were categorized by region, i.e., separating samples from this study (central Arctic and Barents Sea), the Beaufort Sea (Link et al., 2013a, 2019) and the Laptev Sea (Bienhold and Boetius, 2016, 2018a,b; Wenzhöfer et al., 2018), and further divided into shelf (ranging from 45 m – 520 m) or deep-sea (5200 m – 546 m) sites, which in the following we refer to as habitats. Stations of this study varied from 265 to 395 m on the shelf and from 656 to 4262 m in the central Arctic deep sea. In the Beaufort Sea, 19 stations on the shelf varied from 45 to 400 m and from 546 to 596 m in the deep sea (five stations). Stations in the Laptev Sea varied from 57 to 520 m on the shelf (four stations) and between 774 and 3437 m in the deep sea (six stations). For a summary of the stations and parameters sampled in each region see **Supplementary Table S1** in the Supplementary Material. The differentiation between shelf and deep-sea sites of all three regions was based on water depth and topography.

We tested for significant differences in benthic oxygen uptake (DOU and  $\text{TOU}_{\text{sed}}$ ) and environmental parameters (Chl *a*, CPE, % Chl *a*, TOC, and microbial cell numbers) between shelf and deep-sea habitats (Question 1). The same approach was used in order to test for differences between the three regions (Question 3). None of the parameters were normally distributed or homoscedastic. We thus used a non-parametric Kruskal–Wallis test to test for differences between the three regions and a Wilcoxon rank sum test to test for differences between the two habitat types, i.e., shelf and deep sea.

Additionally, a partitioning of the variation in DOU ( $n = 11$ ) and  $\text{TOU}_{\text{sed}}$  ( $n = 8$ ) measurements between different environmental parameters was performed across all stations from this study (including both shelf and deep-sea stations). We tested different variation partitioning models using the following combinations of environmental parameters to explain variations in DOU and  $\text{TOU}_{\text{sed}}$ . Models 1–3 included CPE or Chl *a* or % Chl *a*, TOC, microbial cell numbers and bottom water temperature. Models 4–6 included CPE or Chl *a* or % Chl *a*, TOC and microbial cell numbers. Chl *a*, Phaeopigments and

CPE were inherently all highly correlated (Pearson correlation  $>0.9$ ,  $p < 0.01$  for all pairwise comparisons), while % Chl *a* was not correlated to any of the other pigment parameters. Variation partitioning models were thus tested using CPE as an estimate of total pigments and Chl *a* as well as % Chl *a* as an indicator for fresh phytodetrital material. CPE and Chl *a* were  $\log_{10}$ -transformed to normalize their distribution prior to subsequent analyses. In this paper, we only refer to those models, which were overall statistically significant (models 1 and 2), while the results of other models are provided as Supplementary Material (**Supplementary Table S2**). We did not include water depth in the models, since our data shows the bimodal distribution between shelf and deep sea. For discussion purpose only, we did, however, test the simple correlations between water depth and DOU, TOU as well as the environmental parameters (see **Supplementary Figure S3**). For additional information about covarying parameters we also tested for simple correlations between microbial cell numbers and DOU, CPE, phaeopigments and Chl *a*. Variation partitioning was conducted according to Legendre (2008). Analyses were performed in RStudio version 1.1.447, using the package *vegan* (Oksanen et al., 2019) and custom R scripts.

## RESULTS

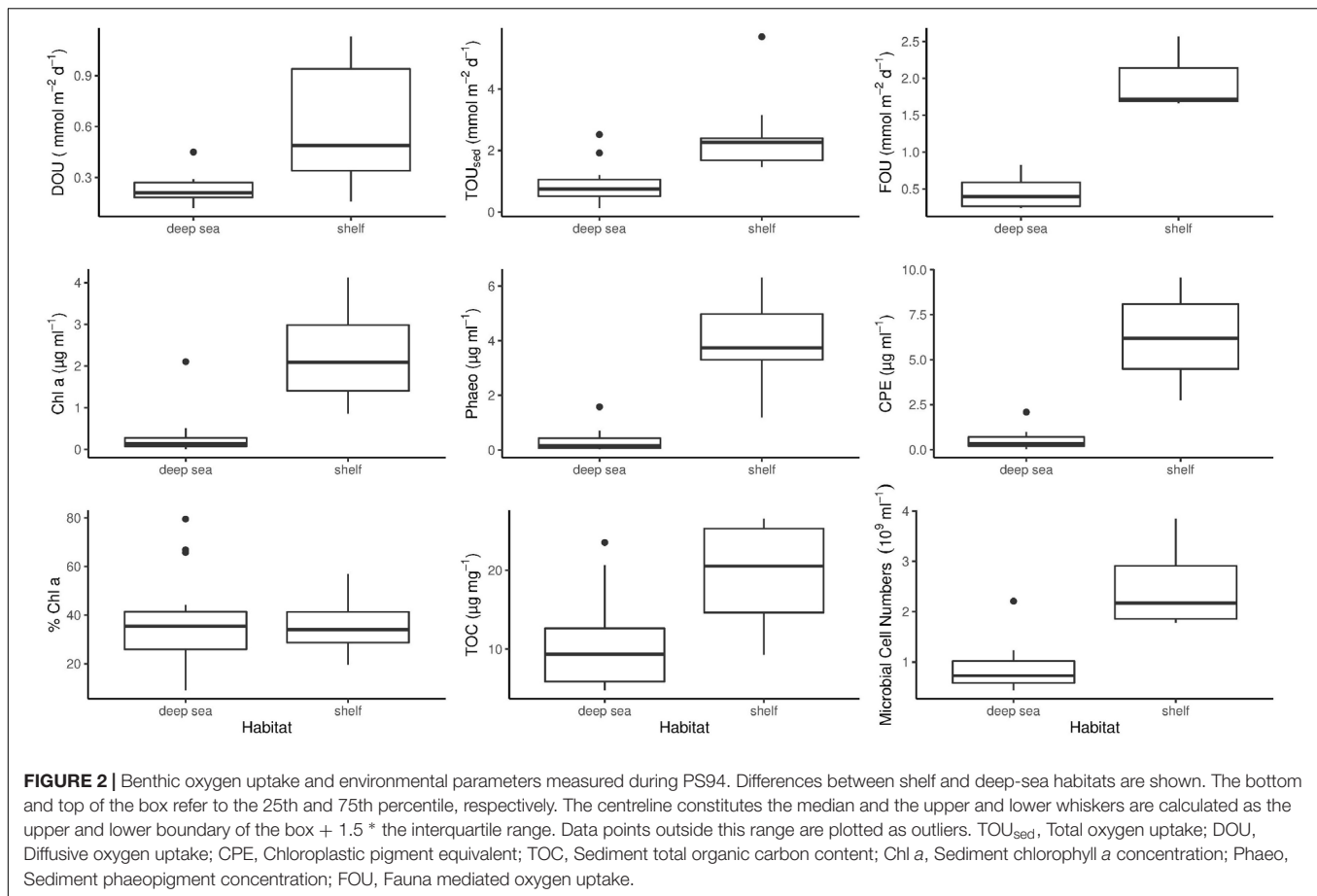
### How Large Are Variations in $\text{TOU}_{\text{sed}}$ , DOU and Environmental Parameters Between the Barents Sea Shelf and the Central Arctic Deep Sea?

#### Benthic Activity (DOU, $\text{TOU}_{\text{sed}}$ , and FOU)

During this study, highest DOU rates were measured on the Barents Sea shelf. Here, DOU ranged from  $0.16\text{ mmol m}^{-2}\text{ d}^{-1}$  at stations 2 and 21 (265 and 390 m) to  $1.13\text{ mmol m}^{-2}\text{ d}^{-1}$  at station 21 (390 m), with a mean value of  $0.59\text{ mmol m}^{-2}\text{ d}^{-1}$ . At deep-sea stations in the central Arctic, values varied from  $0.12\text{ mmol m}^{-2}\text{ d}^{-1}$  at station 101 (3995 m) to  $0.45\text{ mmol m}^{-2}\text{ d}^{-1}$  at station 32 (3164 m), which is situated at the foot of the Barents Sea slope (**Table 2**). Mean DOU in the deep sea was  $0.23\text{ mmol m}^{-2}\text{ d}^{-1}$ . The Wilcoxon rank sum test revealed that DOU on the shelf was significantly different from the deep sea ( $p = 0.0015$ ) (**Figure 2**).

On the shelf, benthic activity measured by means of  $\text{TOU}_{\text{sed}}$  was higher compared to DOU. In the Barents Sea,  $\text{TOU}_{\text{sed}}$  rates ranged from 1.47 to  $5.7\text{ mmol m}^{-2}\text{ d}^{-1}$ , both measured at station 2. Mean  $\text{TOU}_{\text{sed}}$  across shelf stations was  $2.53\text{ mmol m}^{-2}\text{ d}^{-1}$  (**Table 2**). In the deep sea, TOU ranged from 0.13 to  $2.52\text{ mmol m}^{-2}\text{ d}^{-1}$ , with a mean of  $0.9\text{ mmol m}^{-2}\text{ d}^{-1}$ . The result of a Wilcoxon rank sum test clarified that the difference between shelf and deep-sea stations was statistically significant ( $p = 0.0019$ ) (**Figure 2**).

The importance of macrofauna on sedimentary oxygen uptake, as expressed in FOU, was not significantly different between the Barents Sea shelf and the central Arctic Ocean (Wilcoxon rank sum test  $p = 0.057$ ) (**Figure 2**). Highest FOU was measured at station 2 ( $2.56\text{ mmol m}^{-2}\text{ d}^{-1}$ ), while lowest



FOU was assessed at station 130 on the Lomonosov Ridge ( $0.24 \text{ mmol m}^{-2} \text{ d}^{-1}$ ). Second lowest FOU was found at station 87 ( $0.28 \text{ mmol m}^{-2} \text{ d}^{-1}$ ), located at the North Pole. Two deep-sea stations exhibited above average FOU rates. These were station 32 ( $0.51 \text{ mmol m}^{-2} \text{ d}^{-1}$ ), situated at the foot of the Barents Sea slope and station 105 on the Lomonosov Ridge ( $0.82 \text{ mmol m}^{-2} \text{ d}^{-1}$ ) (Table 2).

## Environmental Parameters

### Phytodetritus (chlorophyll pigments)

As for DOU and TOU<sub>sed</sub>, Chl *a* concentrations on the shelf were significantly different from concentrations in the deep sea (Wilcoxon rank sum test  $p < 0.0005$ ) (Figure 2). On the shelf, the lowest concentration was measured at station 161 (395 m) exhibiting  $0.86 \mu\text{g ml}^{-1}$ , while the highest concentration was  $4.12 \mu\text{g ml}^{-1}$ , measured at station 21 (390 m) (Table 2). Mean Chl *a* concentration on the shelf was  $2.22 \mu\text{g ml}^{-1}$ . In the deep sea concentrations were considerably lower. Here, values ranged from 0 ( $0.003$ ) to  $2.1 \mu\text{g ml}^{-1}$  at stations 101 and 66, respectively, and mean concentration was  $0.29 \mu\text{g ml}^{-1}$ .

Phaeopigment concentrations were higher compared to Chl *a* concentrations, exhibiting mean values of  $4 \mu\text{g ml}^{-1}$  on the Barents Sea shelf and  $0.33 \mu\text{g ml}^{-1}$  in the central Arctic deep sea. This difference was statistically significant ( $p < 0.0005$ ) (Figure 2). On the shelf, phaeopigment concentrations ranged

from  $1.19 \mu\text{g ml}^{-1}$  to  $6.3 \mu\text{g ml}^{-1}$  and in the deep sea they varied between  $0.03 \mu\text{g ml}^{-1}$  at station 101 and  $1.58 \mu\text{g ml}^{-1}$  at station 32 (Table 2).

Chloroplast pigment equivalents on the shelf ranged from  $2.76 \mu\text{g ml}^{-1}$  at station 149 to  $9.55 \mu\text{g ml}^{-1}$  at station 1, with a mean concentration of  $6.22 \mu\text{g ml}^{-1}$ . Similar to phaeopigments, minimum concentration in the deep sea was measured at station 101, exhibiting  $0.03 \mu\text{g ml}^{-1}$ , while maximum concentrations were found at station 32, with  $2.09 \mu\text{g ml}^{-1}$  (Table 2). Mean concentration in the deep sea was  $0.51 \mu\text{g ml}^{-1}$ . The difference between CPE concentrations on the shelf and in the deep sea was significant (Wilcoxon rank sum test  $p < 0.0005$ ) (Figure 2).

In contrast to any other parameter analyzed in this study, the difference in % Chl *a* between shelf and deep-sea habitats was not statistically significant (Wilcoxon rank sum test  $p = 0.98$ ) (Figure 2). % Chl *a* ranged between 20% (station 161) and 57% (station 149) on the shelf. Mean % Chl *a* on the shelf was 35%. In the deep sea, values scattered from 9% at station 101 to 80% at station 66, which was measured at the top of the Karasik Mountain at 656 m water depth (Table 2). Mean % Chl *a* in the central Arctic deep sea was 38%.

### Total organic carbon

On the shelf, total organic carbon ranged from  $9.27 \mu\text{g mg}^{-1}$  at station 161 to  $26.51 \mu\text{g mg}^{-1}$  at station 2. Average TOC

concentration on the shelf was  $19.48 \mu\text{g mg}^{-1}$ . In the deep sea, values scattered from  $4.76 \mu\text{g mg}^{-1}$  to  $23.53 \mu\text{g mg}^{-1}$  at stations 101 and 32, respectively (Table 2). Here, mean TOC concentration was  $10.1 \mu\text{g mg}^{-1}$ . The difference between shelf and deep sea was found to be significant (Wilcoxon rank sum test  $p < 0.0005$ ) (Figure 2).

### Microbial cell numbers

On the Barents Sea shelf, microbial cell numbers varied from  $1.78 \times 10^9$  cells  $\text{ml}^{-1}$  sediment at station 161 to  $3.84 \times 10^9$  cells  $\text{ml}^{-1}$  sediment at station 2 with an average of  $2.51 \times 10^9$  cells  $\text{ml}^{-1}$  sediment. In the deep sea, cell numbers were lower and ranged from  $0.44 \times 10^9$  to  $2.21 \times 10^9$  cells  $\text{ml}^{-1}$  sediment at stations 66 and 32, respectively (Table 2). Mean microbial cell number in the deep sea was  $0.9 \times 10^9$  cells  $\text{ml}^{-1}$  sediment. The difference in microbial cell numbers was significantly different between shelf and deep-sea stations (Wilcoxon rank sum test  $p = 0.018$ ) (Figure 2).

Overall, highest mean values in Chl *a* and CPE were measured at station 21, whereas highest values for  $\text{TOU}_{\text{sed}}$ , TOC and bacterial cell numbers were found at station 2 (note that  $\text{TOU}_{\text{sed}}$  was not measured at station 21). Station 2 and station 21 were 480 km apart and located at 265 m and 390 m water depth, respectively. Most of the parameters in the deep sea peaked at station 66, situated on top of the Karasik Mountain ( $\text{TOU}_{\text{sed}}$ , Chl *a*, % Chl *a*) and station 32 (DOU, CPE, Phaeo, TOC, microbial cell abundance), the latter situated at the foot of the Barents Sea slope.

## How Much of the Variation in $\text{TOU}_{\text{sed}}$ and DOU Can Be Explained by Environmental Proxies and Microbial Abundance?

Variation partitioning models were tested using different combinations of environmental parameters (Table 3). The model explaining most of the variation in DOU across shelf and deep-sea habitats included CPE, TOC, and microbial cell numbers. The overall model explained 64 % of the total variation in DOU ( $p = 0.035$ ), with CPE explaining 33% ( $p = 0.03$ ) and co-variation between all fractions summing up to 31%.

**TABLE 3** | Results of partitioning the variation in DOU and  $\text{TOU}_{\text{sed}}$  across shelf and deep-sea stations sampled during Polarstern expedition PS94 (only significant models are shown; for other models tested, see Supplementary Table S2).

		DOU	$\text{TOU}_{\text{sed}}$
Model 1	Overall model	*	n.s.
	CPE	33%*	n.s.
	TOC	n.s.	n.s.
	Microbial cell numbers	n.s.	n.s.
	Total covariation	31%	–
Model 2	Overall model	*	**
	Chl <i>a</i>	29%*	56%
	TOC	n.s.	n.s.
	Microbial cell numbers	n.s.	n.s.
	Total covariation	31%	44%

Entries indicate % of variation explained by environmental parameters in the different models. \*\* $p < 0.01$ , \* $p < 0.05$ , n.s. –  $p > 0.05$  not significant.

For  $\text{TOU}_{\text{sed}}$  the best model included Chl *a*, TOC, and microbial cell numbers. The overall model was significant ( $p = 0.008$ ), with Chl *a* explaining a significant fraction of the variation in  $\text{TOU}_{\text{sed}}$  (56%,  $p = 0.007$ ). Total co-variation between parameters was 44%. TOC and microbial cell numbers alone did not have significant explanatory power, neither in the models for DOU nor for  $\text{TOU}_{\text{sed}}$ . Bottom water temperature did not explain additional variation in the models we evaluated. Of the environmental parameters tested, chlorophyll pigments (CPE and Chl *a*) were thus the only parameter with explanatory power. It needs to be noted that the overall number of samples was relatively low ( $n = 11$  for DOU,  $n = 8$  for  $\text{TOU}_{\text{sed}}$ ), and results thus need to be treated with caution.

Microbial cell numbers were significantly correlated with Chl *a*, Phaeo and CPE, respectively (Figure 3), and had a weak but significant relation with DOU (Figure 4).

## How Do Variations in Benthic Activity and Environmental Parameters Among Shelf and Deep Seas Compare Across Different Regions in the Arctic Ocean? Benthic Activity (DOU and $\text{TOU}_{\text{sed}}$ )

Diffusive oxygen uptake measurements were available for stations from this study and from the Laptev Sea (Table 4 and Figure 5). In contrast to this study, the Wilcoxon rank sum test revealed that the difference between shelf and deep-sea stations was not statistically significant in the Laptev Sea ( $p = 0.1$ ). We note, however, that only six values (three per category) were available for this region, which may have compromised the power of the test. The regional comparison revealed similar DOU rates on both shelf habitats (Wilcoxon rank sum test  $p = 0.43$ ) and significant differences between both deep-sea habitats ( $p = 0.049$ ). Higher DOU rates in the deep Laptev Sea coincided with higher concentrations of Chl *a* and CPE (Table 4 and Figure 5). Mean water depth of deep-sea stations measured during this study was 2413 m compared to 2213 m in the deep Laptev Sea.

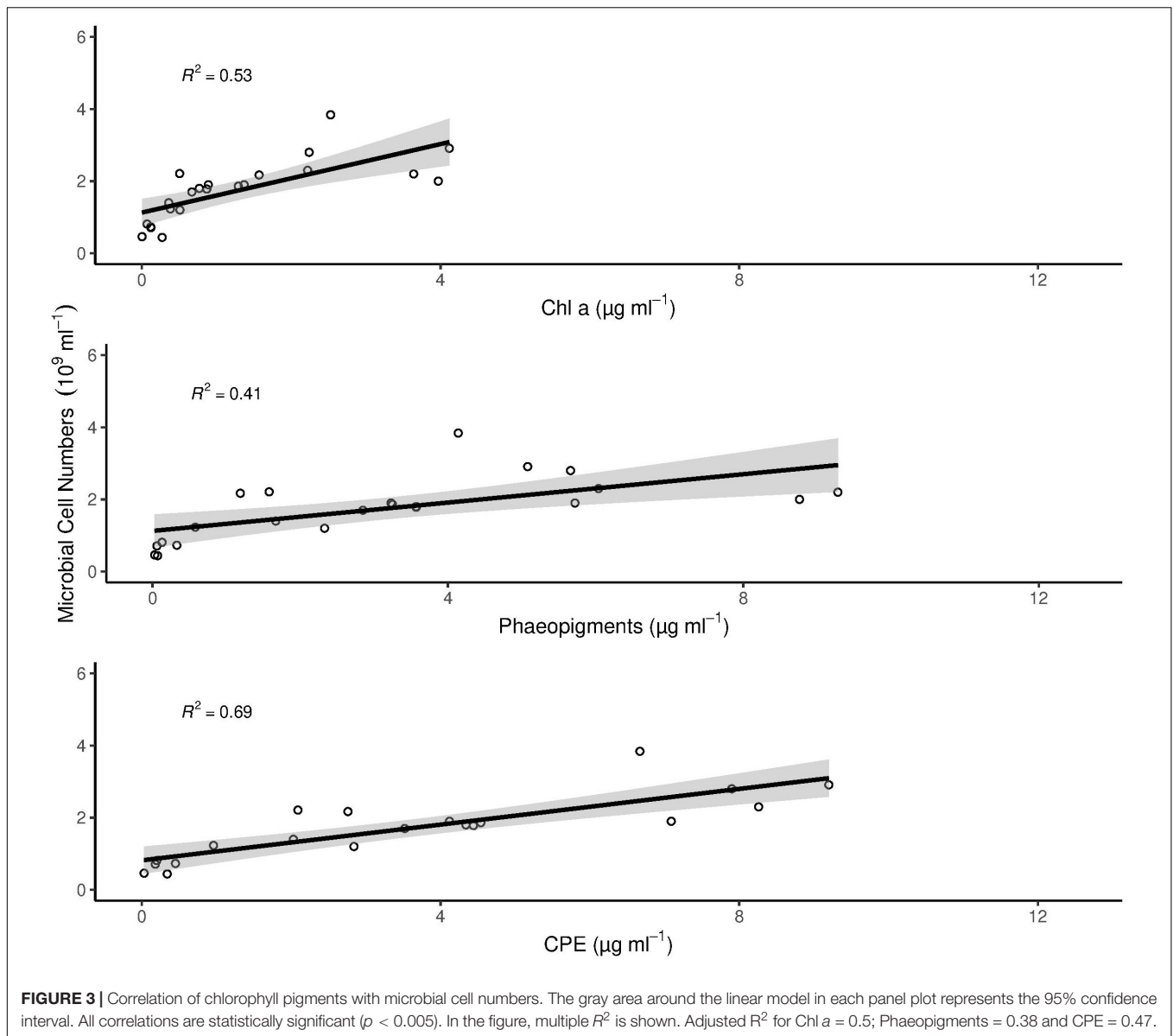
Total sedimentary oxygen uptake rates were available for stations from this study and the Beaufort Sea (Link et al., 2013a, 2019). As for this study,  $\text{TOU}_{\text{sed}}$  in the Beaufort Sea was significantly different between shelf and deep-sea habitats (Wilcoxon rank sum test  $p < 0.0005$ ). However, similar to DOU, differences between both shelf seas were not statistically significant (Wilcoxon rank sum test  $p = 0.14$ ). In contrast to DOU,  $\text{TOU}_{\text{sed}}$  rates among both deep seas ranged in the same order of magnitude ( $p = 0.54$ ). Despite similar  $\text{TOU}_{\text{sed}}$  rates, mean water depth and distance to the shelf were considerably higher in the central Arctic compared to the deep Beaufort Sea.

## Environmental Parameters

### Phytodetritus (chlorophyll pigments)

As for stations in the Barents Sea and the central Arctic, we also found significant differences in Chl *a* between shelf and deep-sea habitats for the other two regions investigated ( $p = 0.01$  in the Laptev Sea and  $p < 0.0005$  in the Beaufort Sea). However,





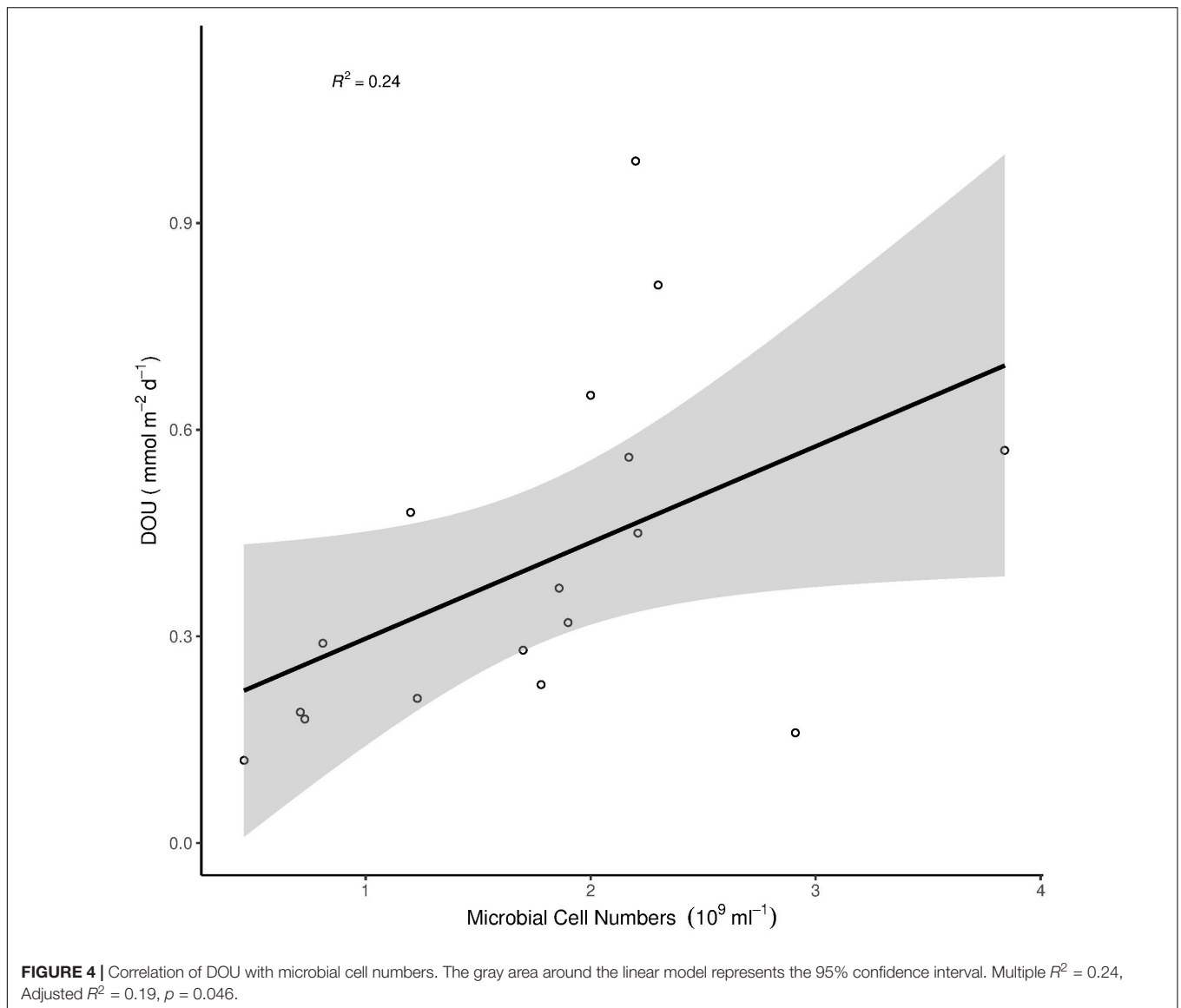
regional differences were identified for both shelf (Kruskal Wallis test  $p = 0.0007$ ) and deep-sea habitats (Kruskal Wallis test  $p = 0.002$ ). Highest concentrations for both habitats were detected in the Laptev Sea, while lowest Chl  $a$  values were found in the deep Beaufort Sea.

The comparison of phaeopigments between shelf and deep-sea habitats also revealed significant differences in the Laptev as well as Beaufort Sea (Wilcoxon rank sum test  $p = 0.02$  and  $< 0.0005$ , respectively). Moreover, regions differed significantly in phaeopigment concentration in both shelf and deep-sea habitats (Kruskal Wallis  $p$  of both  $< 0.0005$ ).

Differences in CPE concentrations between shelf and deep-sea habitats in the Laptev and Beaufort Sea were also statistically significant (Wilcoxon rank sum test  $p < 0.0005$  in both regions). In addition, CPE was also significantly different between the regions, which was valid for both, shelf and deep-sea habitats,

respectively (Kruskal Wallis test  $p < 0.0005$  for both habitats). Highest concentrations were detected in both habitats of the Beaufort Sea and lowest concentrations were detected for stations located in the central Arctic Ocean.

Differences in % Chl  $a$  between shelf and deep-sea habitats varied between regions. While we did not find significant differences between the Barents Sea shelf and the central Arctic Ocean in this study, % Chl  $a$  differed significantly between shelf and deep-sea habitats in the Laptev Sea (Wilcoxon rank sum test,  $p = 0.01$ ) and in the Beaufort Sea ( $p < 0.0005$ ). It is thus not surprising that differences between shelf and deep-sea habitats of the three regions were also significant (Kruskal Wallis test  $< 0.0005$  for both habitats). The highest % Chl  $a$  was measured on the Laptev Sea shelf, while lowest percentages were detected in the deep Beaufort Sea.



### Total organic carbon

Difference in TOC concentrations between shelf and deep-sea habitats were statistically significant for this study and the Beaufort Sea (Wilcoxon rank sum test  $p = 0.03$ ), but not for the Laptev Sea ( $p = 0.91$ ). The comparison between the three regions revealed significant differences among the shelf seas (Kruskal Wallis test  $p = 0.01$ ) and non-significant differences between the deep seas ( $p = 0.11$ ). On the Barents Sea shelf, TOC concentrations were more than two-fold higher compared to stations on the Laptev Sea shelf, whereas the Beaufort Sea ranged almost in the middle between the two (Table 4 and Figure 5).

### Microbial cell numbers

Microbial cell numbers were available for this study and the Laptev Sea (Table 4 and Figure 5). As for this study, the difference in microbial cell numbers between shelf and deep-sea habitats was found to be significant in the Laptev Sea (Wilcoxon rank

sum test  $p = 0.01$ ). While microbial cell numbers on the shelf stations ranged in the same order of magnitude between both regions (Wilcoxon rank sum test  $p = 0.81$ ), the deep Laptev Sea had significantly higher numbers compared to the central Arctic deep sea ( $p = 0.045$ ).

## DISCUSSION

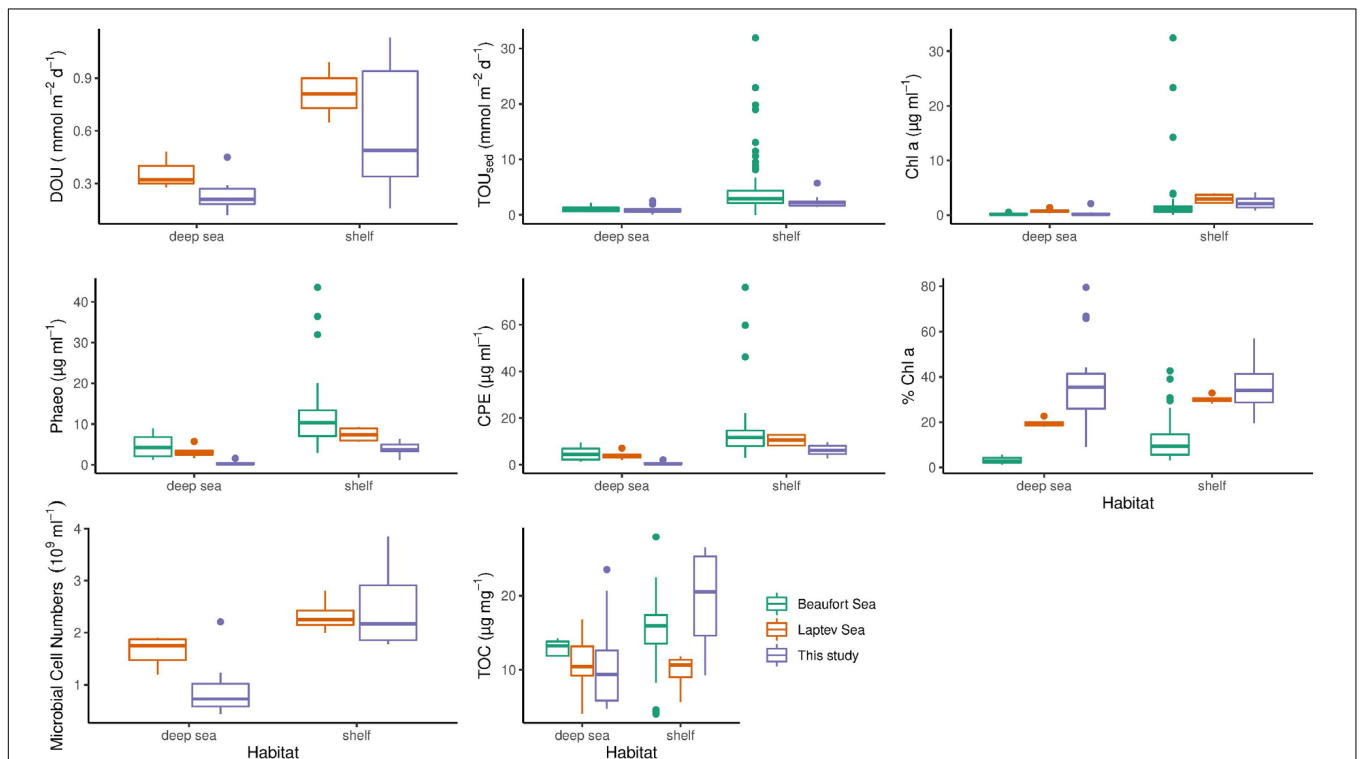
### Exceptions in Shelf-to-Deep-Sea Differences Are Related to Regional and Local Environmental Characteristics

Our findings support previous studies, which found water depth to be among the most important variables determining the distribution of available resources and thus, the performance of benthic remineralization (Boetius and Damm, 1998; Bourgeois et al., 2017; Hoffmann et al., 2018).

**TABLE 4** | Comparison of benthic oxygen uptake and environmental parameters in shelf and deep-sea habitats across the regions of this study, the Laptev and Beaufort Sea.

		This study (PS94, 2015)	Laptev Sea (2012)	Beaufort Sea (2008/2009)
DOU ( $\text{mmol m}^{-2} \text{d}^{-1}$ )	Shelf	0.59	0.82	/
	<b>Deep Sea</b>	0.23	0.36	/
TOU <sub>sed</sub> ( $\text{mmol m}^{-2} \text{d}^{-1}$ )	Shelf	2.53*	/	4.41*
	Deep Sea	0.88	/	1.03
Chl a ( $\mu\text{g ml}^{-1}$ )	<b>Shelf</b>	2.22*	3.02*	2.3*
	<b>Deep Sea</b>	0.29	0.76	0.15
Phaeo ( $\mu\text{g ml}^{-1}$ )	<b>Shelf</b>	4*	7.44*	11.29*
	<b>Deep Sea</b>	0.33	3.23	4.59
CPE ( $\mu\text{g ml}^{-1}$ )	<b>Shelf</b>	6.22*	10.45	13.59*
	<b>Deep Sea</b>	0.51	3.99	4.74
(% Chl a)	<b>Shelf</b>	21.5	30.18*	11.79*
	<b>Deep Sea</b>	23.84	19.54	3.21
TOC ( $\mu\text{g mg}^{-1}$ )	<b>Shelf</b>	21.17*	9.77	15.3*
	Deep Sea	10.58	10.8	13
microbial cell numbers ( $10^9 \text{ ml}^{-1}$ )	Shelf	2.51*	2.33*	/
	<b>Deep Sea</b>	0.94	1.65	/

Mean values were calculated based on stations and per each subarea. Bold letters indicate that significant ( $p < 0.05$ ) differences between the regions were found, whereas an asterisk indicates significant differences between shelf and deep-sea habitats. TOU<sub>sed</sub>, total oxygen uptake; DOU, diffusive oxygen uptake; CPE, chloroplatic pigment equivalent; TOC, sediment total organic carbon content; Chl a, sediment chlorophyll a concentration; Phaeo, sediment phaeopigment concentration; FOU, Fauna mediated oxygen uptake.

**FIGURE 5** | Comparison of benthic oxygen uptake and environmental parameters across the regions of this study (purple boxes), the Laptev (orange boxes) and Beaufort Sea (green boxes). Differences between shelf and deep-sea habitats are shown. The bottom and top of the box refer to the 25th and 75th percentile, respectively. The centreline constitutes the median and the upper and lower whiskers are calculated as the upper and lower boundary of the box + 1.5 \* the interquartile range. Data points outside this range are plotted as outliers. TOU<sub>sed</sub>, Total oxygen uptake; DOU, Diffusive oxygen uptake; CPE, Chloroplatic pigment equivalent; TOC, Sediment total organic carbon content; Chl a, Sediment chlorophyll a concentration; Phaeo, Sediment phaeopigment concentration.

Most parameters analyzed during this and the comparative studies (besides % Chl *a* and FOU for this study and DOU and TOC in the Laptev Sea), were significantly different between Arctic shelf and deep-sea habitats (**Figure 5** and **Table 4**). Furthermore, despite of the bimodal distribution of water depths sampled in this study, most of the parameters were significantly correlated with water depth (**Supplementary Figure S3**; excluding DOU in the Laptev Sea, Chl *a* and % Chl *a* for this study, TOC in all three regions and microbial cell numbers for the Laptev Sea and this study).

Exceptions in the relationship between water depth and our measured parameters were identified in the Laptev Sea. Here, our results show that DOU and TOC did not differ between shelf and deep-sea habitats. While TOC was found to range in the same order of magnitude between both habitats, DOU was twice as high on the Laptev Shelf compared to the deep sea (**Figure 5** and **Table 4**). Due to the limited number of replicates, we assume that the Wilcoxon rank sum test was flawed, not rejecting a null hypothesis that was actually false (type II error).

Similar TOC concentrations between shelf and deep-sea habitats were observed before in many continental margin areas of the world's ocean (Walsh et al., 1985; Archer and Devol, 1992). Archer and Devol (1992) suggested three possible explanations for this phenomenon, including (1) higher rates of organic carbon remineralization on the shelf compared to the deep sea; (2) the shelf sweep hypothesis (much of potential carbon flux to shelf sediments may be swept away by energetic currents and deposited in areas of lower energy) and (3) the dilution of organic carbon on the shelf by loads of non-organic terrigenous material (Walsh et al., 1985; Archer and Devol, 1992). Our data support the idea that higher rates of organic carbon mineralization on the Laptev Sea shelf compared to the adjacent deep sea may have caused the comparatively low concentrations of TOC on the Laptev Sea shelf. However, we cannot exclude the possibility that explanations (2) and (3) have also contributed to similar TOC concentrations on the Laptev Sea shelf and its adjacent deep sea.

In contrast to DOU and TOC, we hypothesize that similar % Chl *a* values between shelf and deep-sea measurements of this study is a result of comparatively high shares of fresh algal material exported to the central Arctic at the time of sampling. This reasoning is supported as % Chl *a* in the central Arctic ranged in the same order of magnitude compared to measurements of the Laptev and Beaufort Sea shelf (**Table 4**). Furthermore, Hoffmann et al. (2018) measured mean % Chl *a* of 10% at average water depths of 1805 m, which is less than half of what we report for the central Arctic Ocean in this study. Studies found that in the deep sea, microbially mediated respiration dominates (Glud et al., 1994; Wenzhöfer and Glud, 2002; Donis et al., 2016), whereas on the shelf benthic infauna can elevate oxygen fluxes by a factor of three relative to molecular diffusion (Glud et al., 2000). Consequently, the relative importance of meio- and macrofauna (as expressed in FOU) on benthic oxygen uptake at the deep-sea stations 32 and 105, situated at the foot of the Barents Sea slope and the Lomonosov Ridge, respectively, may indicate recent (ice) algal deposits (Boetius et al., 2013; Hicks et al., 2017). At station 105 this hypothesis can be backed up by above average % Chl *a*,

which we use as an indicator for the freshness of the deposited organic material.

The comparison of benthic activity and environmental parameters in shelf and deep-sea habitats in this study revealed that seafloor topography and proximity to land may sometimes superimpose the effect of water depth, which has been suggested before for benthic carbon mineralization rates measured in hadal trenches (Luo et al., 2018). This is indicated by the comparison of oxygen uptake rates and the concentrations of environmental parameters between stations measured on the central Arctic Lomonosov Ridge (101, 105), and at the bottom of the Barents and Laptev Sea slopes. Even if stations at the bottom of the slope were at least an order of magnitude deeper compared to the Lomonosov Ridge, we found higher oxygen uptake rates as well as higher concentrations of chlorophyll pigments (excluding % Chl *a*), TOC and microbial cell numbers (**Table 2**). We ascribe this to the close proximity to the shelves of the Barents and Laptev Sea and lateral transport of organic matter nourishing higher benthic oxygen uptake rates (Walsh et al., 1985; Jahnke et al., 1990; Archer and Devol, 1992).

Another example for the importance of distance to the nearest shelf is provided by the analysis of microbial cell numbers. On the shelf, abundances were within the same range between the Barents and Laptev Sea ( $2.51 \times 10^9$  and  $2.33 \times 10^9$  cells ml<sup>-1</sup> sediment, respectively). In the deep sea, however, we found much higher abundances in the Laptev Sea ( $0.94 \times 10^9$  and  $1.65 \times 10^9$  cells ml<sup>-1</sup> sediment in the Barents and Laptev Sea, respectively). Since mean water depth of the Laptev deep-sea stations (2213 m) in fact compares to the deep-sea stations sampled during this study (2413 m), we argue that stations in the Laptev Sea are generally closer to the shelf (on average 92 km compared to 562 km in this study), which has likely affected the availability of organic matter and thus benthic activity (**Table 4**).

Seamounts, however, may be far away from continental shelves, but due to their hydrography and hydrodynamics, yet sustain rich benthic communities and are furthermore considered to be areas of elevated productivity, particularly in otherwise oligotrophic seas (Dower et al., 1992; Mouriño et al., 2001; White et al., 2007). The Karasik Mountain, for example, is far away from any continental shelf (station 66). This lapsed volcano rises from the middle of the Eurasian Basin and constitutes an oasis in terms of comparatively high concentrations of Chl *a* and TOC and of elevated benthic activity (TOU<sub>sed</sub>). Some replicates showed even higher TOU<sub>sed</sub> rates, Chl *a* and TOC concentrations than some stations on the shelf, which were only about half as deep (**Table 2**).

The shortage of available organic matter and concurrent lower benthic activity with increasing distance from the shelf may be particularly pronounced in the Arctic Ocean. The multiyear sea-ice cover above the deep-sea basins impedes primary production and thus exacerbates the already scarce availability of labile organic matter (Piepenburg, 2005; Grebmeier, 2012). In the central Arctic Ocean, ice algal production can contribute up to 60% to net primary production between August and September (Fernández-Méndez et al., 2015). It is not yet clear, whether ice-algal contribution to productivity is on the rise with thinning sea-ice, or whether it will decline due to overall sea-ice reduction



(Fernández-Méndez et al., 2015). However, the increase in ice-free areas during summer and the retreat of the sea-ice melting edge far beyond the continental shelf seas (Stroeve et al., 2007; Comiso et al., 2008), will affect pan-Arctic primary production (Kahru et al., 2016). An increased export flux of organic matter to the deep-sea floor may thus alter the magnitude of differences in ecosystem functioning between Arctic shelf and deep seas observed here. This idea is supported by the discovery of deposited ice algae at the central Arctic deep-sea floor and concurrent increases in benthic oxygen uptake (Boetius et al., 2013). We note, however, that limited nutrient availability in the vast central Arctic Ocean will likely remain a major factor that may limit the projected increase in primary production (Slagstad et al., 2015).

### Variations in Benthic Activity Are Mostly Driven by the Availability of Phytodetritus

In this study, benthic oxygen uptake (DOU and  $\text{TOU}_{\text{sed}}$ ) across both habitats (shelf and deep sea) was mostly driven by concentrations of phytodetritus (CPE or Chl *a*) and TOC, as proxies for the availability of organic matter. This is in line with findings of previous studies from the Arctic (Clough et al., 2005; Bourgeois et al., 2017; Hoffmann et al., 2018). However, other studies have suggested that bottom water temperature and the quality of the phytodetritus (here assessed as % Chl *a*) instead of the overall presence of organic matter are the most important drivers of benthic oxygen uptake (Belley et al., 2016; Kotwicki et al., 2018). The similar quality of phytodetritus across both habitats (opposed to organic matter content) in this study indicates a secondary role of phytodetritus lability/freshness for explaining the variations in benthic oxygen uptake rates.

Bacterial cell numbers did not explain variations in benthic oxygen uptake (Table 3), although there were clear differences in microbial cell numbers between habitats (Figure 2), with a positive relationship between the abundance of bacteria and chlorophyll pigments (Figure 3). This is in line with previous studies that have indicated positive relationships between the presence of organic matter and bacterial abundances and related remineralization activity (Smith et al., 1997; Boetius and Damm, 1998; Turley and Dixon, 2002). The correlation between DOU and microbial cell numbers shows a marginally significant relationship between the two parameters (Figure 4). The weak correlation illustrates the strong variability of DOU on the shelf. The three strongest outliers at high DOU rates were all measured on the Laptev Sea shelf, while the strongest outlier in the lower range of DOU rates was measured at station 20, situated on the Barents Sea shelf. The lack of a clear relationship between bacterial abundances and oxygen uptake in our study may indicate that a higher availability of organic matter on the shelves increases cell-specific activities rather than total abundances, the latter of which are also controlled by viral lysis (Orcutt et al., 2011; Orsi, 2018). In addition, the presence of benthic fauna (especially meio- and macro-fauna) plays a role (Piot et al., 2014) and has been shown to co-vary with benthic activity in previous studies, while bacterial abundance did not (Hoffmann et al., 2018). Benthic fauna could, however, not be considered

in this study. In addition, the permeability of sediments may affect benthic oxygen uptake, with higher uptake rates in cohesive sediments (Fuchsman et al., 2015; Hicks et al., 2017). We did not determine sediment properties in this study, but based on visual inspection all samples were composed of fine-grained, muddy sediments.

In summary, our results support the claim that climate change driven alterations in organic matter input to the Arctic seafloor may most explicitly affect the deep-sea regions, as these are yet characterized by very limited resource availability due to comprehensive sea-ice cover. As a consequence of increased availability of organic matter at the deep-sea floor, we expect benthic activity (DOU,  $\text{TOU}_{\text{sed}}$ , and FOU) to be elevated, potentially diminishing differences (in benthic activity and environmental parameter: phytodetritus, TOC and microbial cell numbers) between Arctic shelf and deep seas during this century.

### Regional Differences in Benthic Activity and Environmental Parameters in Relation to Primary Production Regimes

In addition to the general differences in benthic parameters between shelf and deep-sea habitats, our study further confirmed regional variations. These include differences in DOU and microbial cell numbers between the central deep Arctic Ocean and the deep Laptev Sea, TOC on the shelves of all regions, as well as chlorophyll pigments across both habitats and all regions (Table 4). We have also shown that phytodetritus, most of all CPE, is a good predictor of benthic remineralization in shelf and deep-sea habitats, as it explained most of the variation within DOU (and  $\text{TOU}_{\text{sed}}$ ) (Table 3). The indicators for phytodetritus were indeed significantly different between both habitats and all three regions.

The varying concentrations in phytodetritus, however, do not necessarily reflect the patterns of primary production in the different regions. In general, primary production illustrates a latitudinal gradient across the Arctic Ocean and is highly dependent on several factors, such as season (light availability), the relatively large share of area covered by continental shelves (less sea ice, available nutrients, inflow of terrigenous organic material) (Jakobsson et al., 2003), sea-ice distribution and thickness (Arrigo et al., 2008; Comiso et al., 2008; Boetius et al., 2013), and nutrient availability (Macdonald et al., 1998; Maslowski et al., 2004; Sakshaug, 2004).

It was shown that highest overall primary production can be found in the Barents Sea, where rates of  $108 \text{ Tg C a}^{-1}$  (Pabi et al., 2008) and  $132 \text{ Tg C a}^{-1}$  (Arrigo and van Dijken, 2011) were measured. Also Codispoti et al. (2013) have described the Barents Sea as one of the most productive seas within the Arctic Ocean, only exceeded by the Bering and southern Chukchi Sea. However, measurements of net primary production per unit area suggest highest primary production rates in the Laptev Sea, being higher compared to both the Barents and Beaufort Seas ( $121 \text{ g C m}^{-2} \text{ a}^{-1}$ ,  $110 \text{ g C m}^{-2} \text{ a}^{-1}$ , and  $71.3 \text{ g C m}^{-2} \text{ a}^{-1}$ , respectively) (Arrigo and van Dijken, 2011). On the other hand, primary production rates are temporarily highly variable and highest variabilities were assessed in the Laptev and

Beaufort Sea (Pabi et al., 2008). This may help explaining why our measurements of phytodetritus do not necessarily reflect the estimated rates of primary production found in the literature. For example, we measured highest concentrations of CPE in the Beaufort Sea, even though studies have deemed primary production in the Beaufort Sea as comparatively low for an Arctic shelf (Hill et al., 2018). Differences in phytodetritus content between the deep-sea stations of the Beaufort, Laptev and the central Arctic Ocean in fact did reflect the patterns in primary production rates presented above, as primary production was found to be lowest in the central Arctic Ocean ( $<11 - 18 \text{ g C m}^{-2} \text{ a}^{-1}$ ) (Boetius and Damm, 1998; Sakshaug, 2004; Fernández-Méndez et al., 2015).

In summary, the varying concentrations in phytodetritus on the three analyzed shelves did not reflect integrated patterns of primary production found in the literature. This observation, however, is limited by the coarse scale of patterns compared: primary production patterns are not integrated across the same shelf area we used in our study, and have neither been reported from the same year. Moreover, the rates of vertical export of phytodetritus from the productive ocean layers to the seafloor may differ as well. For example, the low % Chl *a* values in the Beaufort sediments compared to the Laptev and central Arctic indicates highly degraded material and thus a higher loss of phytodetritus during vertical export. In the future, obtaining primary production and vertical export measures at the fitting scale of benthic uptake sampling could clarify this relationship across Arctic regions.

Other studies in hadal trenches have shown that benthic carbon remineralization (which we show is highly dependent on the availability of phytodetritus) follows patterns in primary production (Luo et al., 2018). However, the analyzed hadal trenches are not covered by sea-ice and the presented rates in primary production for the Arctic Ocean often do not take ice-algal production into account (Pabi et al., 2008; Hill et al., 2018). Watanabe et al. (2019) have estimated pan-Arctic ice-algal production between 1980 and 2009 in the Eurasian Basin, the Canada Basin and the Chukchi and Barents Sea. They found that ice-algal production was lowest in the otherwise highly productive Barents Sea and comparatively low in the central Arctic Ocean (Eurasian Basin). Higher rates were modeled instead for the Laptev Sea and the Canadian Polar shelf. The reason for the comparatively low ice-algal production in the Barents Sea may be that sea-ice does not extend over the entire Barents Sea region and low under ice production in the central Arctic can be explained by the presence of yet comprehensive and thick sea-ice during the studied period (Watanabe et al., 2019). This suggests that the correlation between primary production and benthic ecosystem functioning is more complex in the Arctic Ocean, where ice-algal production has to be considered. In perennially sea-ice covered regions, such as the central Arctic, this will become even more important in the future. Measurements from Fernández-Méndez et al. (2015) have shown that ice-algal production contributed up to 60% of net primary production in the central Arctic during the record sea-ice minimum of 2012. We therefore argue that benthic ecosystem functioning in regions with a currently high sea-ice cover (mostly deep-sea habitats

of higher latitudes) will be particularly prone to substantial alterations. These alterations are likely to occur well before the mid of the century, for which an ice free Arctic Ocean during summer has been projected (Notz and Stroeve, 2016). Due to the contribution of ice-algae, net primary production will already be boosted by sea-ice thinning and areal decline.

It is therefore reasonable to assume, that expected changes in ecosystem functioning will differ regionally, depending on primary production regimes (including ice-algal production), sea-ice cover and water depth, but may be particularly pronounced in the nutrient-starved central Arctic Ocean. This finding emphasizes the urgent need for baseline data from pan-Arctic regions, which will allow a better assessment of future changes and their consequences for the pan-Arctic marine ecosystem.

## CONCLUSION

Here we demonstrate that most of the measured benthic ecosystem parameters in the Arctic Ocean differ significantly between shelf and deep-sea habitats. The availability of organic matter, in form of phytodetritus, was the main driver for the patterns observed in benthic oxygen consumption, while bacterial abundance (as well as bottom water temperature) was not a good predictor, possibly indicating the influence of macro-organisms on remineralization in sediments. Indications for the latter were found at stations with high amounts of fresh phytodetritus, which were accompanied by high FOU rates, possibly indicating the exploitation of fresh algal material by benthic fauna.

Bacterial abundances were only weakly correlated with DOU rates. Instead, higher DOU rates may be the result of increased cell-specific activity, triggered by the availability of chlorophyll pigments.

Due to generally low organic matter concentrations compared to other regions of the Arctic Ocean, the projected sea-ice decline may particularly boost benthic remineralization in the central Arctic Ocean, diminishing the differences between benthic shelf and deep-sea habitats. This study indicates first shifts in the input of organic matter to benthic systems in this previously mostly ice-covered area. We speculate that benthic ecosystems in the Arctic Ocean will respond to an increase in organic matter with shifts in benthic ecosystem functioning.

## DATA AVAILABILITY STATEMENT

All data from this and the comparative studies are available from the data repository PANGAEA (<https://www.pangaea.de>). All datasets are cited in the text.

## AUTHOR CONTRIBUTIONS

HL, JK, CB, and FW conceived and designed this study. JK was responsible for sampling and work onboard

*RV Polarstern* expedition PS94. FW and HL helped in preparing the experiments on board and provided relevant equipment and know-how. JK and CB processed samples for TOC, Chl *a*, and microbial cell numbers. JK performed most data analyses with support from HL and CB and wrote the manuscript with strong support from all co-authors.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2020.00426/full#supplementary-material>

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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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