

#### Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem

Marz, Christian; Freitas, Felipe; Faust, Johan; Godbold, Jasmin; Henley, Sian; Tessin, Allyson; Arndt, Sandra; Barnes, David; Grange, Laura; Gray, Neil; Head, lan; Hendry, Katharine; Hilton, Robert; Reed, Adam; Rhul, Saskia; Solan, Martin; Souster, Terri; Stevenson, Mark; Tait, Karen; Widdicombe, Stephen **AMBIO** 

DOI:

https://doi.org/10.1007/s13280-021-01638-3

Published: 01/02/2022

Peer reviewed version

Cyswllt i'r cyhoeddiad / Link to publication

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA): Marz, C., Freitas, F., Faust, J., Godbold, J., Henley, S., Tessin, A., Arndt, S., Barnes, D., Grange, L., Gray, N., Head, I., Hendry, K., Hilton, R., Reed, A., Rhul, S., Solan, M., Souster, T., Stevenson, M., Tait, K., & Widdicombe, S. (2022). Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem. *AMBIO*, *51*(2), 370–382. https://doi.org/10.1007/s13280-021-01638-3

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### **Ambio**

# Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem --Manuscript Draft--

Manuscript Number:	AMBI-D-21-00214R2
Full Title:	Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem
Article Type:	Research Article
Keywords:	Arctic Ocean; biogeochemistry; Ecology; carbon; nutrients; trawling
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Funding Information:	Natural Environment Research Council (NE/P006493/1)	Dr Christian März
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	Natural Environment Research Council (NE/P006434/1)	Prof Steven Widdicombe
	Natural Environment Research Council (NE/P00637X/1)	Dr Geoffrey Abbott
Abstract:	climate change, but academic, public and focussed on the most visible and direct as permafrost thaw, the fate of charismatic n Such narratives disregard the importance particular, miss the substantive contribution and sequestering carbon. Here, we summe	negafauna, and the expansion of fisheries. of less visible and indirect processes and, in on of the shelf seafloor in regulating nutrients narise the biogeochemical functioning of the ow climate change and regional adjustments ression and dynamics. We highlight the moderating climate and anthropogenic idence from the Barents Sea region, offer

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Cover letter – Submission of revised version of "Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem" to AMBIO

To whom it may concern,

It is our pleasure to submit our revised Article "Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem" for consideration for publication with AMBIO. We believe that our contribution adds important knowledge and perspectives to a critically important, yet underappreciated part of the Arctic Ocean system that is facing a multitude of challenges from climate change and increased human exploitation of the Arctic. We are also confident that we have taken all comments by editor and reviewers into account in this revised version.

With kind regards, for all authors,

Dr Christian März

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#### Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem

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#### Acknowledgements

We thank the crew and participants of cruises JR16006, JR17007 and JR18006, RRS *James Clark Ross*, administrative and technical personnel that conducted analyses, and National Marine Facilities, Southampton and the British Antarctic Survey, Cambridge for logistical support. We are grateful to members and facilitators of the Changing Arctic Ocean programme and the Nansen LEGACY project for sharing findings and experiences. Supported by 'The Changing Arctic Ocean Seafloor (ChAOS)' project (NE/N015894/1, 2017–2021), jointly funded by the Natural Environment Research Council (NERC) in the UK and the German Federal Ministry of Education and Research (BMBF). We also thank two anonymous reviewers and Guest Editor David Thomas for their comments which significantly improved the manuscript.

#### Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem

Abstract

Unprecedented and dramatic transformations are occurring in the Arctic in response to climate change, but academic, public and political discourse has disproportionately focussed on the most visible and direct aspects of change, including sea ice melt, permafrost thaw, the fate of charismatic megafauna, and the expansion of fisheries. Such narratives disregard the importance of less visible and indirect processes and, in particular, miss the substantive contribution of the shelf seafloor in regulating nutrients and sequestering carbon. Here, we summarise the biogeochemical functioning of the Arctic shelf seafloor before considering how climate change and regional adjustments to human activities may alter its biogeochemical and ecological dynamics, including ecosystem function, carbon burial, or nutrient recycling. We highlight the importance of the Arctic benthic system in mitigating climatic and anthropogenic change and, with a focus on the Barents Sea, offer some observations and our perspectives on future management and policy.

#### 1. Introduction

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The Arctic Ocean seafloor hosts a diverse and productive benthic ecosystem that is a crucial component of an intimately coupled benthic-pelagic system (Fig. 1; Piepenburg 2005). Benthic organisms modulate sequestration, transformation and storage of bio-essential nutrients and carbon across the Arctic shelf seas (Morata et al. 2020). A significant proportion of organic matter (OM) from marine, terrestrial, or sea ice sources is further recycled via microbially mediated processes that are coupled to the activities of benthic meio-, macro- and mega-fauna (e.g., via bioturbation, bioirrigation; Piepenburg et al. 1995; Renaud et al. 2008). These biological and biogeochemical processes partition the carbon and nutrient pools into a fraction that is recycled to drive a benthicpelagic feedback loop, and a fraction that is buried in the sediment. On the shallow Arctic shelf, the feedback with water column processes (via physical mixing and primary productivity) is more pronounced than in the deep ocean and plays a crucial role for benthic-pelagic coupling and ecosystem productivity; the latter could then contribute to the long-term removal of carbon from the ocean-atmosphere system. Key uncertainties exist, however, in how changing sea ice dynamics (e.g., thickness, extent, inter-annual variability) will alter existing biological community composition and structure, biogeochemical processes, and associated ecosystem functioning. Understanding how these responses are manifest in the benthic environment, both directly and indirectly, is crucial to understanding the Arctic ecosystem as a whole and its importance at the larger scale (Macdonald et al. 2015). One frequently debated proposition on Arctic change is that longer and more extensive open water conditions, especially across Arctic shelves, could lead to prolonged growing seasons and enhanced CO<sub>2</sub> uptake by biomass (Arrigo and Van Dijken 2015; Slagstad et al. 2015). Eventually, this could result in a negative feedback on the CO<sub>2</sub>-induced greenhouse effect in the Arctic as more carbon is sequestered into the sediment. However, modelling the response of the Arctic Ocean carbon and nutrient cycles to reduced sea ice and its associated, and partly counteracting, effects (deeper light

penetration, longer growth seasons, increased water column stratification, ocean acidification, warming), is difficult – partly due to an incomplete mechanistic understanding of the changing Arctic Ocean seafloor. It is currently unclear which fraction of carbon and nutrients will be metabolised and transformed at the seafloor, which interactions between microbial and macro-benthic activity dominate these transformations, and what the effects are on ecosystem structure and functioning. Seafloor recycling likely plays a significant role for the whole Arctic Ocean, with associated societal feedbacks on fisheries and other marine resources, highlighting the critical importance of understanding and quantifying biogeochemical processes at the Arctic seafloor. The carbon storage potential of marine sediments in particular has only recently been recognised and evaluated (Luisetti et al. 2020). Aspects to consider here are the reliable knowledge of carbon contents, the vulnerability of this carbon store, and its assignment to specific nations. These questions will be relevant for designing governance frameworks on sediment carbon storage, but there is little empirical support to the assumed carbon inventory. Although sophisticated, multi-component diagenetic models now exist, most regional to global scale biogeochemical and Earth system models do not resolve the complexity of the seafloor environment. Moreover, models tend to neglect or simplify biogeochemical processes by using a limited number of parameters in the sediment and, in so doing, misrepresent organism-sediment interactions and benthic-pelagic coupling (Lessin et al. 2018; LaRowe et al. 2020). With the recognition that the Arctic is undergoing transformative, and possibly irreversible, changes comes a need to re-evaluate how external forcing could change the fundamentals of the system. For context, we describe the role of the Arctic Ocean seafloor in carbon and nutrient cycling, OM burial and ecological function, provide context of how this role might change in the future, use a reactiontransport model to estimate possible changes to carbon and nutrient cycling in the Barents Sea, and give perspectives on human activities and management.

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#### 2. Biogeochemical functioning of the Arctic shelf seafloor – Recycling versus storage

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Fundamentally, benthic recycling of carbon and nutrients is driven by the supply of biogenic material to the seafloor, and its subsequent degradation and dissolution (Fig. 1; e.g., Middelburg 2019). Rates of seafloor recycling are enhanced by intense activity of macro- and microorganisms, such as faunal feeding, sediment mixing, microbial degradation. Recycling-induced fluxes across the sedimentwater interface influence nutrient budgets in the overlying waters (e.g., Bourgeois et al. 2017), which, in turn, can impact primary production in the surface ocean. Any carbon that escapes benthic recycling gets preserved below the seafloor, and this carbon burial is crucial for transferring atmospheric CO2 to a long-term sediment store. It is this balance between benthic recycling and storage of carbon and nutrients that is likely to change in the future Arctic shelf seas. In terms of carbon and nutrient cycling, Arctic shelf seas (e.g., the Barents Sea) are special because (i) they are often highly productive, with significant atmospheric CO₂ uptake (Arrigo and van Dijken 2015); (ii) their shallow waters allow for a fast transfer of OM to the seafloor; and (iii) strong seasonality and cold temperatures allow for efficient, pulsed carbon transfer to the seafloor (Wassmann et al. 2006a; DeVries and Weber 2017). Once at the seafloor, the fate of carbon and nutrients depends on the quality and quantity of exported OM (Morata and Renaud, 2008; Stevenson et al. 2020), the stability of sedimentary OM and nutrients linked to reactive iron phases in the upper sediments (Faust et al. 2020, 2021), and the composition and process rates of benthic biota (McTigue et al. 2016; Solan et al. 2020). For the Barents Sea, recent models (Freitas et al. 2020) suggest that benthic recycling of nutrients from sediments to overlying waters is mainly controlled by OM reactivity, and therefore its source, age, and total amount (Fig. 2). Additionally, this study shows the magnitude of nutrient fluxes to be somewhat independent from sea-ice extent and, instead, to be mostly impacted by the (physico-chemical) structure of the overlying waters (Freitas et al. 2020). With the pronounced changes in Arctic Ocean ecosystems (e.g., changes in sea ice, water masses, phytoplankton species) that are projected to intensify in the coming decades (e.g.,

Arthun et al. 2012; Smedsrud et al. 2013; Oziel et al. 2017, 2020; Lewis et al, 2020), the trajectory of carbon and nutrient recycling at the seafloor is uncertain.

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#### 3. Altered system expressions and dynamics

Available evidence suggests that conditions across the Barents Sea, and other Arctic inflow shelves, will become more akin to those of sub-Arctic seas. Warming is predicted to promote Barents Sea 'Atlantification' and Chukchi Sea 'Pacification' whereby warmer, saltier and nutrient-richer waters routinely expand further north, often leading to higher primary productivity (Lind et al. 2018; Barton et al. 2018). If sea ice reduction is paralleled by enhanced vertical mixing (Lind et al. 2018; Randelhoff et al. 2020), phytoplankton growing seasons are extended. Enhanced mixing and bloom duration could shift nutrient demands (Downes et al. 2021), with knock-on effects on carbon export. It should be noted, however, that due to the environmental complexities there is significant uncertainty in any prediction of Arctic Ocean primary productivity (Vancoppenolle et al. 2013). In addition, thawing permafrost is now prevalent around the Arctic Ocean (in particular in Siberia) which, combined with higher river runoff, will deliver more carbon and nutrients to the Arctic shelves (e.g., Bröder et al. 2018; Terhaar et al. 2021). These changes in the status quo will likely alter pathways of carbon delivery to the seafloor and, in turn, the amount of carbon preserved within sediments. Further, changes in the composition and behaviour of the benthic community will affect the fate of both organic and inorganic carbon accumulation at the seafloor. While there is a basic understanding of current factors affecting Arctic seafloor biogeochemistry, some controls on OM burial play out over thousands of years (e.g., Faust et al. 2021). It is unknown if ongoing/future climate change may perturb these processes, either by modifying carbon inputs and/or the microbial communities and degradation pathways below the seafloor (Brüchert et al. 2018). In addition, while the burial of zoobenthic carbon may be more strongly affected by ecosystem change (i.e., the dominant benthic fauna), no clear link between this carbon pool and the position of the sea ice

margin was found in the Barents Sea (Souster et al. 2020). This may be partly due to the limited number of habitats studied, or the numerous and complex interactions along the process chain from sea ice cover and carbon export to dynamic ecosystem responses. At similar water depths around Antarctica, across-habitat studies have suggested maximum burial may occur in habitat interface zones, e.g., where basins meet glacial moraines (Barnes and Sands 2017). Intimately linked to OM deposition at the seafloor is the cycling of nutrients. Benthic nutrient recycling rates and fluxes are highly sensitive to the impacts of primary production and OM export changes (e.g., Freitas et al. 2021). Extension of the phytoplankton growing season in the Barents Sea carries with it the potential to increase total primary production if sufficient nutrients are available (e.g., Lewis et al. 2020; Henley et al. 2020). Should this occur, and translate into greater export of 'fresh' OM, it could lead to higher benthic nutrient fluxes, although any effect is unlikely to be universally expressed due to strong regional differences (e.g., Oziel et al. 2020; Downes et al. 2020). Indeed, the highly seasonal, often short-term, and highly regional benthic-pelagic dynamics on Arctic shelves go some way in explaining why an often assumed link between sea ice cover and benthic nutrient fluxes is not always found (Freitas et al. 2020). This contrasts with sediment carbon dynamics, with seasonally ice-covered parts of the Barents Sea exhibiting lower organic carbon contents, but higher organic carbon burial rates (Faust et al. 2020) and higher abundances of benthic fauna (Souster et al. 2020). On Arctic shelves and margins currently more permanently ice-covered (e.g., Yermak Plateau), changes in primary production and OM delivery to the seafloor can lead to comparatively greater changes in benthic nutrient fluxes as compared to the low background values (Tessin et al. 2020). While no systematic relationship between benthic nutrient fluxes and sea ice cover was found in the Barents Sea, there is a significant link with water mass distributions and 'Atlantification'. Benthic nutrient fluxes in summer 2017 were higher at stations dominated by Atlantic water (B13, B14, B17; Fig. 2) than at those dominated by Arctic water (B15, B16; Fig. 2) (Freitas et al 2020). If

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'Atlantification' continues, benthic nutrient fluxes are likely to increase across the region, irrespective of superimposed seasonal and spatial variability. However, patterns of response will depend on the relative importance of, and interactions between, increased bottom water temperatures, changes in primary production and phytoplankton communities, and OM delivery to the seafloor. And since the benthic efflux depends on fixation of nutrients in deposited organic biomass, a net addition to benthic nutrient effluxes will only occur if the Barents Sea system as a whole receives increased external nutrients, for example, through Atlantic water (Oziel et al. 2017) or by increased input (and degradation) of terrestrial OM (Terhaar et al. 2019, 2021).

### 4. Estimating future organic carbon burial and benthic nutrient cycling using a reactiontransport model

Working from the realistic assumption (for reasons stated above) that reduced sea ice in the Barents Sea may lead to increased OM export to the seafloor, we estimate the impact of this on carbon burial and degradation rates by performing a simple model sensitivity analysis (Fig. 3). We use our baseline model for the Barents Sea shelf (Freitas et al. 2020) that is confounded in biogeochemical data from five key stations across the Polar Front in the summers of 2017-2019 (Fig. 2). Here we test how relative fluctuations in OM input (1-3 times the baseline values; expressed as total organic carbon, TOC) to the seafloor translate into absolute and relative changes in burial and degradation rates. Whilst an increase in OM export to the seafloor from primary productivity will impact OM degradation pathways, the impact on long-term sediment carbon burial will be minor, as phytoplankton OM is quickly degraded at the seafloor (Fig. 3). However, we also observe that the fraction of carbon preserved at depth is highest at stations B15 and B16 (just north of the Polar Front), for poorly known reasons but presumably related to the dominance of Arctic water and/or seasonal sea ice at those stations. How much of the carbon delivered into shelf seas by permafrost thaw, coastal erosion and major river systems is degraded before burial is debated (e.g., Tank et al.

2012; Brüchert et al. 2018; Bröder et al. 2018, 2019), and further complicated by lateral OM transport along the shelf (Stevenson et al. 2020). Nevertheless, terrestrial processes will likely exert a major control on OM quality/quantity by delivering less degradable OM to Barents Sea sediments (Freitas et al. 2020). Impacts of higher OM fluxes on zoobenthic carbon standing stocks are poorly studied in the Arctic but, in West Antarctic shelf seas, extended phytoplankton blooms promoted by sea ice loss have led to a doubling of zoobenthic carbon standing stock (Barnes 2015, 2017). It is tempting, therefore, to suggest that a similar development might occur on Arctic shelves. In a second step, to estimate the impacts of OM export changes on benthic nutrient fluxes (ignoring ecological drivers), we expand a simple model sensitivity analysis used for TOC degradation and burial rates (after Freitas et al. 2020) to calculate benthic nutrient fluxes (nitrate, ammonium, phosphate; Fig. 4). We change the OM content to 0.1-6 times relative to baseline values, keeping all other model parameters unchanged. Our simulation shows that any fluctuation in OM input to the seafloor will result in a concomitant adjustment in nutrient fluxes (Fig. 4), even though the responses are not strictly linear, vary between sites, and are nutrient-specific. Our results also suggest that absolute changes in nutrient fluxes are likely to be more pronounced at sites influenced by Atlantic Water, and that relative increases in OM input will trigger large changes in the way OM is being degraded at and below the seafloor. The relative contribution of aerobic OM degradation will decrease considerably as oxygen will become quickly depleted (Fig. 4), while anaerobic conditions will prevail in the upper end of OM addition scenarios. It should be noted that changes to ecological factors were ignored in the modelling exercise above, but there is no doubt that environmental and anthropogenic change will also affect the benthic ecosystem. A faunal separation occurs between northern (Arctic) and southern (Atlantic) assemblages at the operational Polar Front (e.g., Jørgensen et al. 2015). The distribution of functionally important species has received some attention (Degen and Faulwetter 2019), but there are few direct measurements of faunal activity or physiological state, and no regional-scale

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assessments of the faunal mediation of biogeochemistry (Solan et al. 2019). Nevertheless, recent observations in the Barents Sea indicate that spatial and temporal variability in environmental setting will be important in explaining biodiversity and ecological functions at larger scales, more so than localized sea ice changes (Solan et al. 2020, Souster et al. 2020, Oleszczuk et al. 2021). Changes in the quality and quantity of OM reaching the seabed can have significant implications for faunal physiology, behaviour, growth (Reed et al. 2021a) and reproduction (Reed et al. 2021b) and, in turn, biogeochemical cycling (Solan et al. 2020). Overall, however, there is a clear south-north increase in species richness, biomass and functional diversity of mega -and macro-zoobenthos, but the mixed depth of sediment and bioturbating activity of the community both decline with increasing latitude (Souster et al. 2020, Solan et al. 2020).

#### 5. Climate- and human-induced changes

The preservation of carbon within shelf sediments and benthic marine communities is likely to be altered by the expansion of human activities as sea ice retreats, including fishing, shipping, and petroleum exploration. With less challenging sea ice conditions and the northward migration of economically valuable fish stocks (e.g. Atlantic cod *Gadus Morhua*, Greenland halibut *Reinhardtuis hippoglossoides*, shrimp *Pandalus borealis*), commercial fisheries follow and start trawling some of the last unfished areas of the global shelf seafloor. Bottom trawling causes re-working and resuspension of seafloor sediment (Puig et al. 2012; O'Neill and Ivanovic 2016), which can lead to erosion and perturbations to benthic biogeochemistry, in particular a loss of sedimentary organic carbon (Paradis et al. 2021). However, in the Barents Sea, reactive OM is quickly degraded and recycled to CO<sub>2</sub> within the surface sediments (Freitas et al. 2020; Stevenson et al. 2020), even without human intervention. The question then arises as to whether trawling will impact the more stable, deeper, pre-degraded carbon stocks that remain in the sediments. This will depend on various factors, including the depth of trawl penetration (typically 10s of cm) and the overall

sediment accumulation rates (~4-200 cm/1000 years; Faust et al 2020): Under high sedimentation rates, reactive OM is buried relatively quickly, and re-exposure by trawling would negatively affecting overall carbon burial efficiency. In low sedimentation rate areas, trawling might have less of an effect on long-term carbon storage. Similar considerations can be made for nutrient recycling to the water column by the mechanical disturbance of sediments (Duplisea et al. 2001): If the disturbance reaches anaerobic layers where nutrient concentrations are significantly higher than in the overlying waters, the resulting enhanced nutrient fluxes can fuel additional pelagic primary production (Dounas et al. 2007; van der Velde et al. 2018; Tiano et al., 2021). Finally, the persistence of any trawling-induced disturbance in the Barents Sea would depend on type and frequency of trawling as well as primary productivity and sedimentation rates, but literature-based estimates range from several year to several decades (Buhl-Mortensen et al. 2016; Paradis et al. 2021). Besides the sediment, polar benthic marine communities also store considerable carbon in the form of biota. Zoobenthic carbon in the Barents Sea is comparable to the highest levels in Antarctic shelf sediments (Souster et al. 2020). Changes in the density, diversity, and composition of mega-benthic communities associated with bottom fishing activity in the Barents Sea have been observed (Buhl-Mortensen et al. 2016) and can significantly affect the biomass and stored carbon of all species (Jorgensen et al. 2016).

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#### 6. Implications for management and policy

Warming, in combination with increased disturbance of the Arctic shelf seafloor, is already imposing significant changes to carbon and nutrient cycles, as well as ecosystems. Following scientific recommendation, areas with fishing restrictions or closure in the Barents Sea, particularly around Svalbard, were recently expanded by the Norwegian government (Jørgensen et al. 2020). The ecosystem protection afforded by MPA or similar protection status increased the likelihood of safeguarding carbon stocks and the processes that control seafloor carbon sequestration (Atwood et

al. 2020; Sala et al. 2021). For example, modifying fishing gears, limiting or preventing seafloor trawling would reduce the physical disturbance that alters community composition and diversity, biogeochemical cycling, and the amount of carbon released back into the water (Duplisea et al. 2001; Dounas et al. 2007; De Borger et al. 2021). However, expansion of fishery exclusion zones in the Barents Sea is based largely on ecological/biodiversity criteria, rather than on the need for protecting carbon stocks (Jørgensen et al. 2020). Recognition of the carbon burial aspect of marine ecosystem services is currently missing in Arctic seas, but is increasingly recognised elsewhere (Luisetti et al. 2020; Atwood et al. 2020; Sala et al. 2021). Biologically rich, vulnerable marine environment hotspots can also be effective carbon sinks, as in the case of the first high seas MPA around the South Orkney Islands, Antarctic Peninsula (Trathan et al. 2014; Barnes et al 2016). Consideration of both nature and its functionality (ecosystem services or nature-based solutions, Solan et al. 2020) provides a stronger and more comprehensive approach compared to a focus on biodiversity alone (e.g., Sala et al. 2021). Societal and scientific pressure has recently resulted in creation of some Very Large Marine Protected Areas (VLMPAs) but, as Sala et al. (2021) note, this includes few areas within the polar regions. The polar regions have more governance complexity than most Exclusive Economic Zones (EEZs), but they lag behind global MPA creation, even though they could present new opportunities for carbon store protection. For example, 99% of most of Ascension Island's VLMPA is deeper than 1000 m, but the main carbon pathway to sequestration may occur in the shallowest 1000 m (Barnes et al. 2019). Protection of this shallow seabed safeguards £1-2 million of carbon capture to sequestration at UN shadow price of carbon estimates. There are opportunities in the Arctic to target such shallow carbon burial grounds. It is crucial to learn lessons from rushed MPA designations, since those are often agreed on economically unattractive areas, or implemented with clauses that allow resource exploitation to continue. Society has to decide the type, rate and level of human activity that is acceptable in Arctic regions, whilst balancing competing demands and world views, and to agree on equitable ways to resolve conflict and maximise win-win strategies. However, the data needed to support effective marine

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management within the Arctic are sparse, incomplete or poorly quantified, making planning and more informed decision-making challenging. Even in the better investigated regions such as the Barents Sea, only parts of the carbon pathway (from capture to sequestration) is quantified and even then - only for some habitats (e.g., muddy glacial troughs; Faust et al. 2020; Freitas et al. 2020; Stevenson et al. 2020; Souster et al. 2020; Solan et al. 2020). Where appropriate socio-ecological data do exist, the focus is spatially constrained and in a limited number of areas (Falardeau and Bennett 2020). However, we understand enough to know that vulnerable marine ecosystems on Arctic continental shelves are not necessarily co-located with the main carbon burial environments. The most productive and most heavily fished ecosystems are situated on shoals, around the coasts and above rocky ground, while most organic carbon is likely sequestered in muddy sediments of glacial troughs. We also know that high productivity and throughput of carbon does not necessarily mean high carbon sequestration. The prevailing systems controlling the cycling and storage of carbon in the Arctic seafloor are complex and there is a general paucity of fully comprehensive data sets. Despite the challenges, it is possible to make considerable progress in identifying the most significant unprotected carbon burial hotspots, allowing for an effective assessment of the landscape of potential threats and the risks and rewards surrounding seafloor protection. Most ecosystems affected by human disturbance can recover when conditions improve, for example, if appropriate conservation measures are enacted and human pressure is managed (Jones and Schmitz 2009). To continue to benefit from seafloor carbon sinks and buy more time against climate change, we contend that MPAs (no bottom fishing) for newly exposed ice-free regions in the Arctic will be beneficial.

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## 299 References

- 300 Arrigo, K. R., and G. L van Dijken. 2015. Continued increases in Arctic Ocean primary productivity.
- 301 *Progress in Oceanography* 136: 60-70. doi:10.1016/j.pocean.2015.05.002.
- 302 Årthun M., T. Eldevik, L.H. Smedsrud, Ø. Skagseth, R.B. Ingvaldsen. 2012. Quantifying the Influence
- of Atlantic Heat on Barents Sea Ice Variability and Retreat. *Journal of Climate*, 25(13): 4736-4743.
- 304 doi.org/10.1175/JCLI-D-11-00466.1
- 305 Atwood T.B., A. Witt, J. Mayorga, E. Hammill, E. Sala. 2020. Global Patterns in Marine Sediment.
- 306 Frontiers in Marine Science 7: 165. doi: 10.3389/fmars.2020.00165.
- 307 Barnes, D. K. A. 2015. Antarctic sea ice losses drive gains in benthic carbon drawdown. *Current*
- 308 *Biology* 25: R789–R790. doi:10.1016/j.cub.2015.07.042.
- 309 Barnes, D. K. A. 2017. Polar zoobenthos blue carbon storage increases with sea ice losses, because
- across-shelf growth gains from longer algal blooms outweigh ice scour mortality in the shallows.
- 311 *Global Change Biology* 23: 5083–5091. doi:10.1111/gcb.13772.
- Barnes, D. K. A., and C. J. Sands. 2017. Functional group diversity is key to Southern Ocean benthic
- carbon pathways. Edited by Carlo Nike Bianchi. *PLOS ONE* 12: e0179735.
- 314 doi:10.1371/journal.pone.0179735.
- Barnes, D. K. A., L. Ireland, O. T. Hogg, S. Morley, P. Enderlein, and C. J. Sands. 2016. Why is the
- 316 South Orkney Island shelf (the world's first high seas marine protected area) a carbon
- immobilization hotspot? *Global Change Biology* 22: 1110-1120. doi:10.1111/gcb.13157.
- Barnes, D. K. A., C. J. Sands, A. Richardson, and N. Smith. 2019. Extremes in benthic ecosystem
- 319 services; blue carbon natural capital shallower than 1000 m in isolated, small, and young
- 320 Ascension Island's EEZ. Frontiers in Marine Science. doi:doi.org/10.3389/fmars.2019.00663.

321 Barton, B. I., Y.-D. Lenn, and C. Lique. 2018. Observed Atlantification of the Barents Sea Causes the 322 Polar Front to Limit the Expansion of Winter Sea Ice. Journal of Physical Oceanography 48: 1849-1866. doi:10.1175/JPO-D-18-0003.1. 323 324 Bourgeois S., P. Archambault, U. Witte. 2017. Organic matter remineralization in marine sediments: A Pan-Arctic synthesis. Global Biogeochemical Cycles, 31(1): 190-213. 325 326 doi.org/10.1002/2016GB005378. 327 Bröder, L., T. Tesi, A. Andersson, I. Semiletov, and Ö. Gustafsson. 2018. Bounding cross-shelf transport time 328 and degradation in Siberian-Arctic land-ocean carbon transfer. Nature Communications 9: 806. doi:10.1038/s41467-018-03192-1. 329 330 Bröder, L., A. Andersson, T. Tesi, I. Semiletov, and Ö. Gustafsson. 2019. Quantitative degradation loss of 331 terrigenous organic carbon in surface sediments across the Laptev and East Siberian Sea. Global 332 Biogeochemical Cycles 33: 85-99. doi:10.1029/2018GB005967. 333 Brüchert, V., L. Bröder, J. E. Sawicka, T. Tesi, S. P. Joye, X. Sun, I. Semiletov, and V. A. Samarkin. 2018. 334 Carbon mineralization in Laptev and East Siberian sea shelf and slope sediments. Biogeosciences 15: 471-490. doi:10.5194/bg-471-2018. 335 336 Buhl-Mortensen, L., K. E. Ellingsen, P. Buhl-Mortensen, K. L. Skaar, and G. Gonzalez-Mirelis. 2016. 337 Trawling disturbance on megabenthos and sediment in the Barents Sea: chronic effects on 338 density, diversity, and composition. ICES Journal of Marine Science 73: i98-i114. doi:10.1093/icesjms/fsv200. 339 340 Degen R., and S. Faulwetter. 2019. The Arctic Traits Database – a repository of Arctic benthic 341 invertebrate traits. Earth System Science Data 11: 301–322. doi:10.5194/essd-11-301-2019. 342 DeVries, T., and T. Weber. 2017. The export and fate of organic matter in the ocean: New constraints 343 from combining satellite and oceanographic tracer observations. Global Biogeochemical Cycles 31: 535-555. doi:10.1002/2016GB005551. 344

345 Dounas C., I. Davies, G. Triantafyllou, P. Koulouri, G. Petihakis, C. Arvanitidis, G. Sourlatzis and A. 346 Eleftheriou. 2007. Large-scale impacts of bottom trawling on shelf primary productivity. Continental Shelf Research, 27(17): 2198-2210. 347 348 Downes, P. P., S. J. Goult, E. M. S. Woodward, C. E. Widdicombe, K. Tait, and J. L. Dixon. 2020. 349 Phosphorus dynamics in the Barents Sea. Limnology and Oceanography 66. 350 doi:10.1002/lno.11602. 351 Duplisea, D.E., S. Jennings, S.J. Malcolm, R. Parker and D.B. Sivyer. 2001. Modelling potential impacts 352 of bottom trawl fisheries on soft sediment biogeochemistry in the North Sea. Geochemical *Transactions*, 2(1): 1-6. 353 354 Falardeau, M. & E.M. Bennett. 2020. Towards integrated knowledge of climate change in Arctic 355 marine systems: a systematic literature review of multidisciplinary research. Arctic Science 6: 1-356 23. doi:10.1139/as-2019-0006. 357 Faust, J. C., M. A. Stevenson, G. D. Abbott, J. Knies, A. Tessin, I. Mannion, A. Ford, R. Hilton, et al. 358 2020. Does Arctic warming reduce preservation of organic matter in Barents Sea sediments? 359 Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 378: 20190364. doi:10.1098/rsta.2019.0364. 360 361 Faust, J. C., A. Tessin, B. J. Fisher, M. Zindorf, S. Papadaki, K. R. Hendry, K. A. Doyle, and C. März. 362 2021. Millennial scale persistence of organic carbon bound to iron in Arctic marine sediments. Nature Communications 12: 275. doi:10.1038/s41467-020-20550-0. 363 364 Freitas, F. S., K. R. Hendry, S. F. Henley, J. C. Faust, A. C. Tessin, M. A. Stevenson, G. D. Abbott, C. März, and S. Arndt. 2020. Benthic-pelagic coupling in the Barents Sea: an integrated data-model 365

framework. Philosophical Transactions of the Royal Society A: Mathematical, Physical and

Engineering Sciences 378: 20199359. doi:10.1098/rsta.2019.0359.

366

- Freitas, F. S., Pika, P. A., Kasten, S., Jørgensen, B. B., Rassmann, J., Rabouille, C., Thomas, S., Sass, H.,
- Pancost, R. D., and Arndt, S. 2021. New insights into large-scale trends of apparent organic
- 370 matter reactivity in marine sediments and patterns of benthic carbon transformation.
- 371 *Biogeosciences* 18: 4651–4679. doi.org/10.5194/bg-18-4651-2021.
- Hemingway, J. D., D. H. Rothman, K. E. Grant, S. Z. Rosengard, T. I. Eglinton, L. A. Derry, and V. V.
- Galy. 2019. Mineral protection regulates long-term global preservation of natural organic
- 374 carbon. *Nature* 570: 228-231. doi:10.1038/s41586-019-1280-6.
- Henley, S. F., E. L. Cavan, S. E. Fawcett, R. Kerr, T. Monteiro, R. M. Sherrell, A. R. Bowie, P. W. Boyd,
- et al. 2020. Changing Biogeochemistry of the Southern Ocean and Its Ecosystem Implications.
- *Frontiers in Marine Science* 7. doi:10.3389/fmars.2020.00581.
- 378 Jones, H. P., and O. J. Schmitz. 2009. Rapid Recovery of Damaged Ecosystems. Edited by Geoffrey
- 379 Clayton Trussell. *PLoS ONE* 4: e5653. doi:10.1371/journal.pone.0005653.
- Jørgensen, L. L., P. Ljubin, H. R. Skjoldal, R. B. Ingvaldsen, and N. Anisimova, I. M. 2015. Distribution
- of benthic megafauna in the Barents Sea: baseline for an ecosystem approach to management.
- 382 *ICES Journal of Marine Science* 72: 595–613.
- Jørgensen, L. L., B. Planque, T. H. Thangstad, and G. Certain. 2016. Vulnerability of megabenthic
- species to trawling in the Barents Sea. *ICES Journal of Marine Science* 73: i84–i97.
- 385 doi:10.1093/icesjms/fsv107.
- Jørgensen, L. L., G. Bakke, and A. H. Hoelb. 2020. Responding to global warming: New fisheries
- management measures in the Arctic. *Progress in Oceanography* 188: 102423.
- 388 doi.org/10.1016/j.pocean.2020.102423.
- LaRowe, D. E., S. Arndt, J. A. Bradley, E. R. Estes, A. Hoarfrost, S. Q. Lang, K. G. Lloyd, N. Mahmoudi,
- 390 et al. 2020. The fate of organic carbon in marine sediments New insights from recent data and
- analysis. *Earth-Science Reviews* 204: 103146. doi:10.1016/j.earscirev.2020.103146.

392 Lessin G., Y. Artioli, E. Almroth-Rosell, J. C. Blackford, A. W. Dale, R. N. Glud, J. J. Middelburg, R. 393 Pastres, et al. 2018. Modelling Marine Sediment Biogeochemistry: Current Knowledge Gaps, 394 Challenges, and Some Methodological Advice for Advancement. Frontiers in Marine Science 5:19. 395 doi: 10.3389/fmars.2018.00019. 396 Lewis K.M., G.L. van Dijken, K.R. Arrigo. 2020. Changes in phytoplankton concentration now drive 397 increased Arctic Ocean primary production. Science, 369(6500): 198-202. 398 doi.org/10.1126/science.aay8380 399 Lind S., R. B. Ingvaldsen, and T. Furevik. 2018. Arctic warming hotspot in the northern Barents Sea 400 linked to declining sea-ice import. Nature Climate Change 8: 634-639. doi:10.1038/s41558-018-401 0205-y. 402 Luisetti T., S. Ferrini, G. Grilli, T. D. Jickells, H. Kennedy, S. Kröger, I. Lorenzoni, B. Milligan, et al. 2020. 403 Climate action requires new accounting guidance and governance frameworks to manage 404 carbon in shelf seas. Nature Communications 11: 4599. doi:10.1038/s41467-020-18242-w. 405 Macdonald R.W., Z. Z. Kuzyk, and S. C. Johannesson. 2015. The vulnerability of Arctic shelf sediments 406 to climate change. Environmental Reviews 4: https://doi.org/10.1139/er-2015-0040. 407 McTigue N.D., W. S. Gardner, K.H. Dunton, A.K. Hardison. 2016. Biotic and abiotic controls on co-408 occurring nitrogen cycling processes in shallow Arctic shelf sediments. Nature Communications 409 7: 13145. doi:10.1038/ncomms13145. 410 Middelburg, J.J. 2019. Marine Carbon Biogeochemistry - A Primer for Earth System Scientists. 411 Springer Briefs in Earth System Sciences. Springer International Publishing. (Book) doi.org/10.1007/978-3-030-10822-9 412 413 Morata N., P.E. Renaud. 2008. Sedimentary pigments in the western Barents Sea: A reflection of 414 pelagic-benthic coupling? Studies in Oceanography, 55(20-21): 2381-2389. 415 doi.org/10.1016/j.dsr2.2008.05.004

416 Morata N., E. Michaud, M.-A. Poullaouec, J. Devesa, M. Le Goff, R. Corvaisier, and P. E. Renaud. 417 2020. Climate change and diminishing seasonality in Arctic benthic processes. Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 378: 418 419 https://doi.org/10.1098/rsta.2019.0369. 420 O'Neill, F. G., and A. Ivanović. 2016. The physical impact of towed demersal fishing gears on soft 421 sediments. ICES Journal of Marine Science 73: i5–i14. doi:10.1093/icesjms/fsv125. 422 Oleszczuk, B., K. Grzelak, M. Kędra. 2021. Community structure and productivity of Arctic benthic 423 fauna across depth gradients during springtime. Deep Sea Research I, 170, 103457. doi: 10.1016/j.dsr.2020.103457 424 425 Oziel L., G. Neukermans, M. Ardyna, C. Lancelot, J.-L. Tison, P. Wassmann, J. Sirven, D. Ruiz-Pino, J.-C. 426 Gascard. 2017. Role for Atlantic inflows and sea ice loss on shifting phytoplankton blooms in the 427 Barents Sea. *Journal of Geophysical Research – Oceans*, 122(6): 5121-5139. doi.org/10.1002/2016JC012582 428 429 Oziel L., A. Baudena, M. Ardyna, P. Massicotte, A. Randelhoff, J.-B. Sallée, R. B. Ingvaldsen, E. Devred 430 and M. Babin. 2020. Faster Atlantic currents drive poleward expansion of temperate 431 phytoplankton in the Arctic Ocean. Nature Communications, 11: 1705. doi.org/10.1038/s41467-020-15485-5 432 433 Paradis S., M. Goñi, P. Masqué, R. Durán, M. Arjona-Camas, A. Palanques, and P. Puig. 2021. Persistence of Biogeochemical Alterations of Deep-Sea Sediments by Bottom Trawling. 434 Geophysical Research Letters 48. doi:10.1029/2020GL091279. 435 436 Piepenburg D., T. H. Blackburn, C. F. von Dorrien, J. Gutt, P. O. J. Hall, S. Hulth, M. A. Kendall, K. W. 437 Opalinski, E. Rachor, and M. K. Schmid. 1995. Partitioning of benthic community respiration in

the Arctic (northwestern Barents Sea). Marine Ecology Progress Series 118: 199-213.

- Piepenburg D. 2005. Recent research on Arctic benthos: common notions need to be revised. *Polar*
- 440 *Biology*, 28: 733-755.
- 441 Polyakov, I. V., A. V. Pnyushkov, M. B. Alkire, I. M. Ashik, T. M. Baumann, E. C. Carmack, I. Goszczko,
- J. Guthrie, et al. 2017. Greater role for Atlantic inflows on sea-ice loss in the Eurasian Basin of the
- 443 Arctic Ocean. *Science* 356: 285–291. doi:10.1126/science.aai8204.
- Puig P., M. Canals, J.B. Company, J. Martín, D. Amblas, G. Lastras, A. Palanques, and A.M. Calafat
- 2012. Ploughing the deep sea floor. *Nature*, 489(7415): 286-289.
- Randelhoff A., J. Holding, M. Janout, M. K. Sejr, M. Babin, J.-É. Tremblay, and M. B. Alkire. 2020. Pan-
- 447 Arctic Ocean Primary Production Constrained by Turbulent Nitrate Fluxes. Frontiers in Marine
- 448 Science 150. doi: 10.3389/fmars.2020.00150.Reed A.J., J.A. Godbold, L.J. Grange, and M. Solan
- 2021a. Growth of marine ectotherms is regionally constrained and asymmetric with latitude.
- 450 Global Ecology and Biogeography, 30, 578–589. doi: 10.1111/geb.13245.
- 451 Reed A.J., J.A. Godbold, M. Solan, and L.J. Grange (2021b) Reproductive traits and population
- 452 dynamics of benthic invertebrates indicate episodic recruitment patterns across an Arctic polar
- 453 front. Ecology and Evolution. doi: 10.1002/ece3.7539
- 454 Renaud P. E., N. Morata, M. Carroll, S. G. Denisenko, and M. Reigstad. 2008. Pelagic-benthic
- coupling in the western Barents Sea: Processes and time scales. Deep-Sea Research II, 55: 2372-
- 456 2380.
- 457 Sala E., J. Mayorga, D. Bradley, R. B. Cabral, T. B. Atwood, A. Auber, W. Cheung, C. Costello et al.
- 458 2021. Protecting the global ocean for biodiversity, food and climate. *Nature* 592: 397–402.
- 459 doi.org/10.1038/s41586-021-03371-z.
- Slagstad D., P. F. J. Wassmann, and I. Ellingsen 2015. Physical constrains and productivity in the
- future Arctic Ocean. Frontiers in Marine Science, 2, 85.

462 Smedsrud L.H., I. Esau, R.B. Ingvaldsen, T. Eldevik, P.M. Haugan, C. Li, V.S. Lien, A. Olsen et al. 2013. 463 The role of the Barents Sea in the Arctic climate system. Reviews of Geophysics, 51(3): 415-449. 464 Solan M., E. M. Bennett, P. J. Mumby, J. Leyland, and J. A. Godbold 2020. Benthic-based 465 contributions to climate change mitigation and adaptation. Philosophical Transactions of the 466 Royal Society B: Biological Sciences, 375: 20190107. doi: 10.1098/rstb.2019.0107 467 Solan, M., E.R. Ward, E.L. White, E. E. Hibberd, C. Cassidy, J. M. Schuster, R. Hale, J.A. and 468 Godbold 2019. Worldwide measurements of bioturbation intensity, ventilation rate, and the 469 mixing depth of marine sediments. Scientific Data 6, 58. doi: 10.1038/s41597-019-0069-7 470 Solan, M., E. R., Ward, C. L. Wood, A. J. Reed, L. J. Grange, and J. A. Godbold. 2020. Climate-driven 471 benthic invertebrate activity and biogeochemical functioning across the Barents Sea polar front. 472 Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering 473 Sciences 378: 20190365. doi:10.1098/rsta.2019.0365. 474 Souster, T. A., D. K. A. Barnes, and J. Hopkins. 2020. Variation in zoobenthic blue carbon in the Arctic's Barents Sea shelf sediments. Philosophical Transactions of the Royal Society A: 475 476 Mathematical, Physical and Engineering Sciences 378: 20190362. doi:10.1098/rsta.2019.0362. 477 Stevenson, M. A., and G. D. Abbott. 2019. Exploring the composition of macromolecular organic 478 matter in Arctic Ocean sediments under a changing sea ice gradient. Journal of Analytical and 479 Applied Pyrolysis 140: 102-111. doi:10.1016/j.jaap.2019.02.006. 480 Stevenson, M. A., J. C. Faust, L. L. Andrade, F. S. Freitas, N. D. Gray, K. Tait, K. R. Hendry, R. G. Hilton, 481 et al. 2020. Transformation of organic matter in a Barents Sea sediment profile: coupled 482 geochemical and microbiological processes. Philosophical Transactions of the Royal Society A: 483 Mathematical, Physical and Engineering Sciences 378: 20200223. doi:10.1098/rsta.2020.0223.

484 Tank, S. E., P. A. Raymond, R. G. Striegl, J. W. McClelland, R. M. Holmes, G. J. Fiske, and B. J. Peterson. 2012. 485 A land-to-ocean perspective on the magnitude, source and implication of DIC flux from major Arctic 486 rivers to the Arctic Ocean. Global Biogeochemical Cycles 26: n/a-n/a. doi:10.1029/2011GB004192. 487 Terhaar, J., J. C. Orr, C. Ethé, P. Regnier, and L. Bopp. 2019. Simulated Arctic Ocean Response to Doubling 488 of Riverine Carbon and Nutrient Delivery. Global Biogeochemical Cycles 33: 1048–1070. 489 doi:10.1029/2019GB006200. 490 Terhaar, J., R. Lauerwald, P. Regnier, N. Gruber, and L. Bopp. 2021. Around one third of current Arctic 491 Ocean primary production sustained by rivers and coastal erosion. *Nature Communications* 12: 169. 492 doi:10.1038/s41467-020-20470-z. 493 Tessin, A., C. März, M. Kedra, J. Matthiessen, N. Morata, M. Nairn, M. O'Regan, and I. Peeken. 2020. 494 Benthic phosphorus cycling within the Eurasian marginal sea ice zone. Philosophical Transactions of 495 the Royal Society A: Mathematical, Physical and Engineering Sciences 378: 20190358. 496 doi:10.1098/rsta.2019.0358. 497 Tiano J. C., R. Witbaard, M. J. N. Bergman, P. van Rijswijk, A. Tramper, D. van Oevelen, and K. Soetaert. 498 2019. Acute impacts of bottom trawl gears on benthic metabolism and nutrient cycling. ICES Journal of 499 Marine Science, 76(6): 1917-1930. doi.org/10.1093/icesjms/fsz060. 500 Tiano J. C., E. de Borger, S. O'Flynn, C. H. Cheng, D. van Oevelen, and K. Soetaert. 2021. Physical and 501 electrical disturbance experiments uncover potential bottom fishing impacts on benthic ecosystem 502 functioning. *Journal of Experimental Marine Biology and Ecology*, 545: 151628. 503 Trathan, P. N., M. A. Collins, S. M. Grant, M. Belchier, D. K. A. Barnes, J. Brown, and I. J. Staniland. 504 2014. Chapter Two – The South Georgia and the South Sandwich Islands MPA: Protecting a 505 biodiverse oceanic island chain situated in the flow of the Antarctic Circumpolar Current. 506 Advances in Marine Biology 69: 15-28. doi:10.1016/B978-0-12-800214-8.00002-5.

507	Vancoppenolle M., L. Bopp, G. Madec, J. Dunne, T. Ilyina, P. R. Halloran, and N. Steiner. 2013. Future
508	Arctic Ocean primary productivity from CMIP5 simulations: Uncertain outcome, but consistent
509	mechanisms. Global Biogeochemical Cycles 27: 605–619.
510	Van de Velde, S., V. Van Lancker, S. Hidalgo-Martinez, W.M. Berelson and F.J. Meysman. 2018.
511	Anthropogenic disturbance keeps the coastal seafloor biogeochemistry in a transient state.
512	Scientific Reports, 8(1): 1-10.
513	Wassmann P., D. Slagstad, C. Wexels Riser, and M. Reigstad. 2006a. Modelling the ecosystem
514	dynamics of the Barents Sea including the marginal ice zone: II. Carbon flux and interannual
515	variability. <i>Journal of Marine Systems</i> , 59(1-2): 1-24. doi.org/10.1016/j.jmarsys.2005.05.006
516	Wassmann P., M. Reigstad, T. Haug, B. Rudels, M.L. Carroll, H. Hop, G.W. Gabrielsen, S. Falk-
517	Petersen, et al. 2006b. Food webs and carbon flux in the Barents Sea. Progress in Oceanography,
518	71(2-4): 232-287. doi.org/10.1016/j.pocean.2006.10.003.
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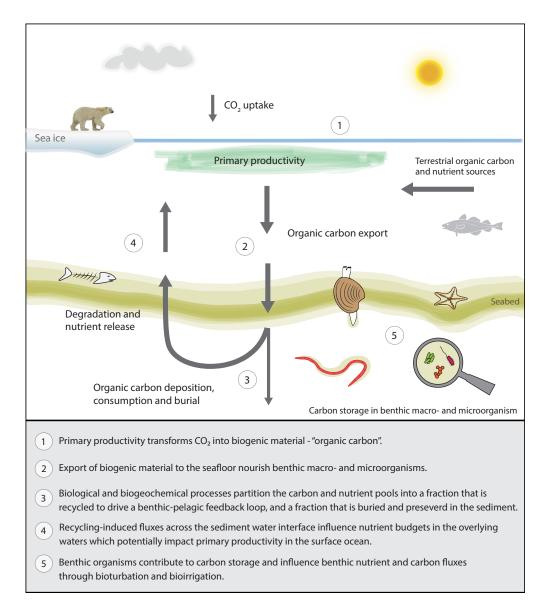
#### **Figures**

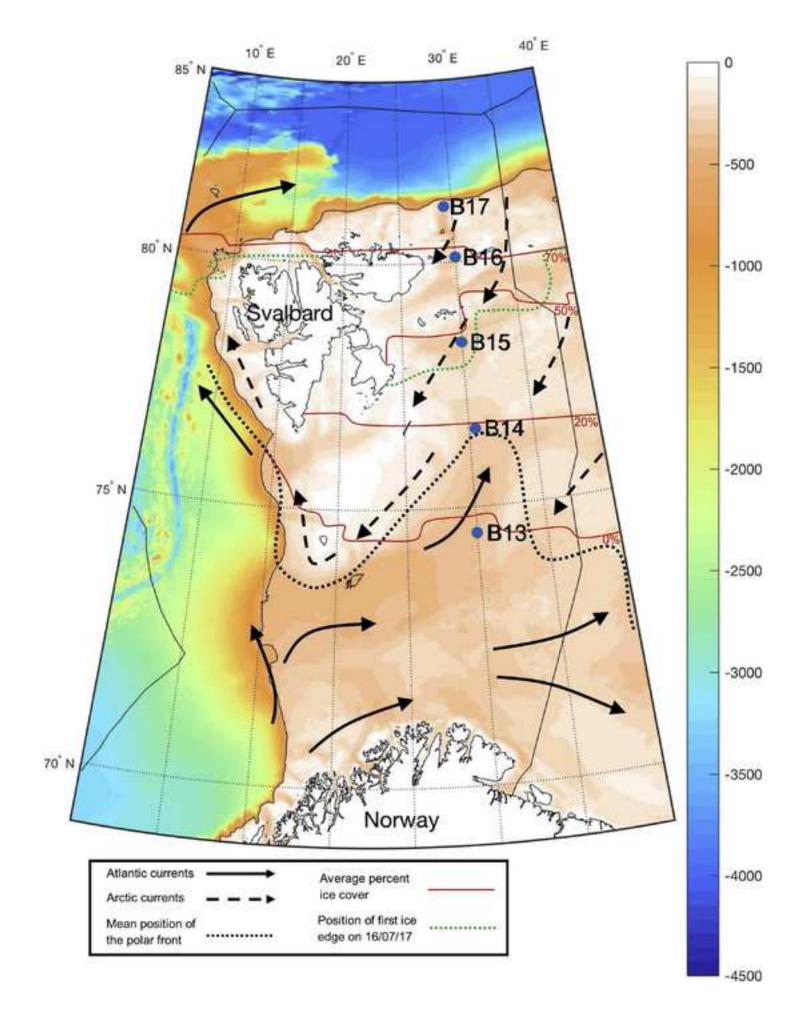
Figure 1: Schematic illustration of ecological and biogeochemical parameters in Arctic Ocean shelf seas, with a focus on processes at the seafloor.

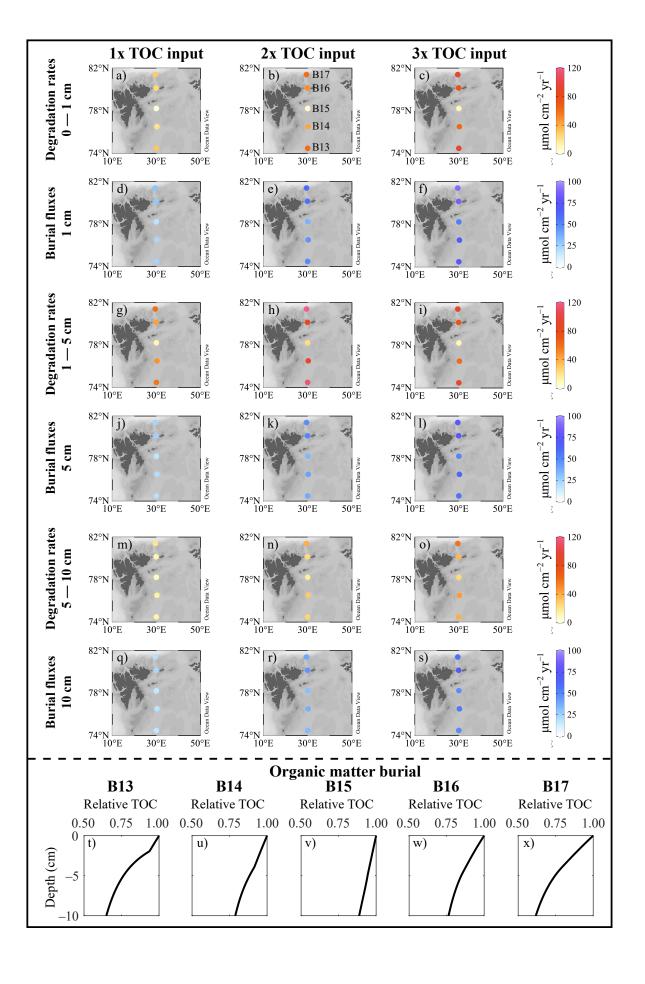
- Figure 2: Location of Barents Sea shelf stations B13–B17 sampled in July 2017. Bathymetric depth chart indicating meters below sea level (m.b.s.l). Depths of sampling were 359 m at B13 (74° 29.998 N; 30° 00.009 E), 293 m at B14 (76° 30.055 N; 30°30.241E), 317 m at B15 (78° 15.100 N; 30° 00.540 E), 283 m at B16 (80° 07.154 N; 30° 04.069 E) and 340 m at B17 (81° 16.765 N; 30° 19.496 E). From Stevenson and Abbott 2019.
- Figure 3: Changes in degradation and burial rates of total organic carbon (TOC) following increased OM export to the seafloor at the Barents Sea sites B13-B17. Model adopted from Freitas et al. (2020), with outputs based on data gathered in July 2017. Integrated TOC degradation rates (warm color bar) are shown for intervals (a—c) 0-1 cm, (g—i) 1-5 cm, and (m—o) 5-10 cm sediment depth. Corresponding TOC burial rates (cold color bar) are shown at (d—f) 1, (j—l) 5, and (q—s) 10 cm sediment depth. (t—x) Relative fraction of TOC burial with increasing burial depth (cm) in response to input at sediment surface.
- Figure 4: Changes in biogeochemical parameters following increases in OM export to the seafloor at the Barents Sea sites B13-B17. Model adopted from Freitas et al. (2020), with outputs based on data gathered in July 2017. Top row: Baseline nutrient fluxes of (a) nitrate, (b) ammonium and (c) phosphate. Note the different scales in the color bar and direction of fluxes: cold colors denote fluxes into sediments; warm colors denote fluxes out of the sediment. Middle row:

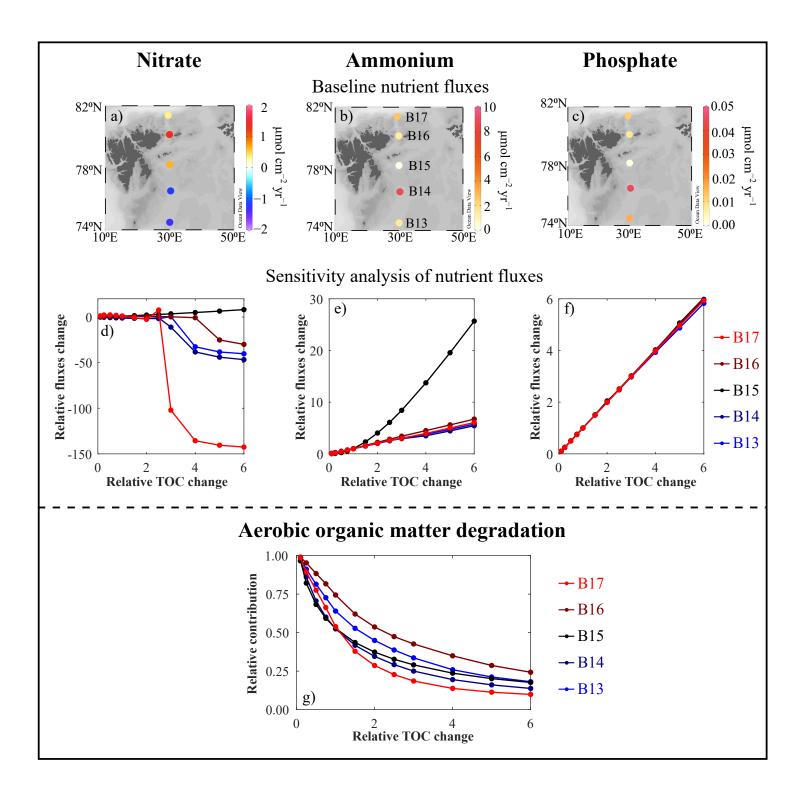
  Changes in nutrient fluxes of (d) nitrate, (e) ammonium and (f) phosphate relative to increased OM input. Note different scales in relative flux changes (y-axis) due to nutrient-specific response to OM input and transformation at the seafloor: (d) nitrate fluxes become negative (i.e., sediments acting as nitrate sink rather than source), while (e) ammonium and (f) phosphate fluxes increase. Line colors (d—g) denote reference sites in the Barents Sea. Bottom row: (g)

Changes in relative contribution of aerobic (presence of oxygen) OM degradation with gradual increase in OM input. Contribution of aerobic OM degradation decreases exponentially with higher OM input, which slows down overall degradation of OM.









## Rebuttal to AMBIO 2<sup>nd</sup> review "Biogeochemical consequences of a changing Arctic shelf seafloor ecosystem"

(author responses in italics)

This revision represents a big change c.f. the original submission and the authors have answered the original reviewer comments comprehensively and with obvious thought.

We thank the Editor for this acknowledgement of our revisions.

Figure 1 does not benefit from logical labeling and/or explanation in the legend. It is not clear what the various arrows are and why colored in different ways? Why have just phytoplankton, fish and a diversity of benthic organisms - surely the authors could be a bit more creative in depicting a more diverse pelagic foodweb supplying the benthos than just phytoplankton and fish? This manuscript will be used by none specialists and this rather depleted schematic is not really helping a non-specialist audience?

For example, presumably the U-bend structure on the left hand edge of the image is meant to be a burrowing animal, but I am not sure many others will, or even see it. The water disappearing behind the sediment on the left of the image is crude. The cloud & sun are just strange? There is no such change in relation to sea ice cover and again as it is, it is somewhat misleading. Conceptual figures like this are excellent and there is merit in having one here. However, this could do with considerable more thought as to how it could better serve the reader who is not necessarily a biologist. There are many biologists on the author list and it should be possible to create something more useful for a reader?

Thank you for these comments. We appreciate that figures like this one may be picked up by readers and can present a key piece of a publication. This is the very reason for trying to keep it simple, which obviously brings with it the omission of certain complexities of the natural system. However, we consider these simplifications as both justified (after all, the manuscript does focus on the benthic environment) and practical (too much visual information will distract the reader from the key points we are trying to make). The very fact that we have more "diversity" at the seafloor is intentional — this manuscript has a benthic focus, and while we appreciate a more "complete" atmosphere-ocean-sediment figure would be a great idea, this should probably be designed at the CAO program level.

Nevertheless, we have of course taken the Editor's comments to heart, and now present a strongly revised version of Figure 1. While a level of simplicity remains, we have tried to streamline the labelling of the figure in the sense of a true biogeochemical cycle. We have also decided to change the figure to a "status quo" version, removing any notion of parts or aspects of the system that may change as environmental conditions develop — the reason being that everything can (and probably will) change to an extent, making this overview figure too complex.

It is not clear in Figure 3 what the colors of the lines are associated with, especially in the middle row of figures...yes, on moving down to the lower figure on this plate it can be worked out, but again it is the reader having to do the work, rather than the figure helping them. Can something be added to the legend to help?

The differences in scales in the middle row of this plate really need to be highlighted in the legend and some explanation given? Some comment on the negative c.f with the two positive scales is surely needed in the legend?

The figure and caption has now been modified accordingly.

The different colors in the bottom row of Figure 4 are perplexing and need explanation? In the depth label on this row shouldn't it be -5 and -10

The figure and caption has now been modified accordingly.

At the end the authors reference to benthic disturbance and possible consequences. A good point, but this discussion could be made right up to date by considering works such as Tiano et al (2021) <a href="https://www.sciencedirect.com/science/article/pii/S0022098121001180?via%3Dihub">https://www.sciencedirect.com/science/article/pii/S0022098121001180?via%3Dihub</a> & their discussion?

A good point, and we have now included this reference.