Oceanologia, 67 (2)/2025, 67208
Polish Academy of Sciences
Institute of Oceanology
Open access article under the CC BY license
https://doi.org/10.5697/HOHD9156

Climate change threatens shallow Arctic macrofaunal blue carbon stocks

Marc J. Silberberger[1,2]

Abstract

This study examines mollusk communities in shallow (< 150 m) and deep (> 200 m) zones of Arctic, sub-Arctic, and temperate fjords to assess macrofaunal blue carbon storage under climate change. Biomass and trait-based analyses show that shallow Arctic habitats support long-lived, large suspension feeders with high carbon storage potential. In contrast, warmer regions host smaller, short-lived taxa, indicating reduced carbon storage and altered climate feedbacks. These findings underscore the vulnerability of existing zoobenthic carbon stocks and highlight the need to expand research to other taxa and full benthic communities across the European Arctic.

Keywords

Mollusca; Infauna; Biomass; Latitudinal gradient; Ecosystem functioning

[1] *Department of Fisheries Oceanography and Marine Ecology, National Marine Fisheries Research Institute, Hugo Kołłątaja 1, 81–332 Gdynia, Poland*

[2] *Institute of Oceanology Polish Academy of Sciences, Powstańców Warszawy 55, 81–712 Sopot, Poland*

Correspondence: msilberberger@mir.gdynia.pl

Received: 5 August 2024; **revised:** 5 May 2025; **accepted**: 19 May 2025

Benthic communities are an integral part of marine ecosystems and have an important role for their functioning (Campanyà-Llovet et al., 2017; Griffiths et al., 2017). Numerous ecosystem services, like food provision or organic matter processing, have long been recognized to be tightly linked to benthic communities (Costanza et al., 1997; Snelgrove, 1999). In addition, the biomass of benthic communities themselves was identified as important blue carbon stocks in recent years (Barnes, 2017; Barnes et al., 2019; Zwerschke et al., 2022). This faunal blue carbon has been identified as a negative climate feedback loop in high polar systems, where ongoing marine ice losses cause longer phytoplankton blooms and make new benthic habitats available for colonization (Barnes et al., 2021). However, how already existing zoobenthic blue carbon stocks in already ice-free areas will be affected by climate change through e.g. range extensions of species and altered organic matter recycling in the water column is not known.

Efforts to assess zoobenthic blue carbon storage in the European Arctic and sub-Arctic were so far limited to epibenthos in the Barents Sea, which is comparable with the highest levels in Antarctic shelf sediments (Souster et al., 2020, 2024). Whether the same is true for infaunal blue carbon is not known, but Souster et al. (2024) emphasized the potential importance of the infaunal blue carbon stocks. Gaining knowledge about the faunal blue carbon stocks in this region is important, since climate change is altering benthic community composition and functioning along the northern European continental shelf (Brattegard, 2011; Silberberger et al., 2024). Based on latitudinal patterns in resource partitioning among different feeding types in benthic communities, Silberberger et al. (2024) proposed that climate change will alter the carbon sequestration potential in high-latitude sedimentary habitats. Their observations were, however, based on non-quantitative sampling for stable isotopes and accordingly, it remains unknown whether the described functional changes are important for the quantitative composition of benthic community biomass and the blue carbon associated with it.

Here I studied the macrofaunal mollusk communities in two depth zones (shallow: < 150 m; deep: > 200 m) of four European fjords in three climate zones (Figure 1). The sampling was conducted in the summer of 2021 (between 3 August and 4 September) from r/v *Tanteyen* (Saltfjord) and r/v *Oceania* (all other fjords). All locations were placed in the outer basin of the studied fjords to reduce the influence of local confounding environmental drivers that are typically strongest within the inner parts of fjords (Włodarska-Kowalczuk et al., 2012; Jordà Molina et al., 2019). The studied fjords are located along a latitudinal gradient that has been previously used as a space-for-time substitution to study potential climate change impacts

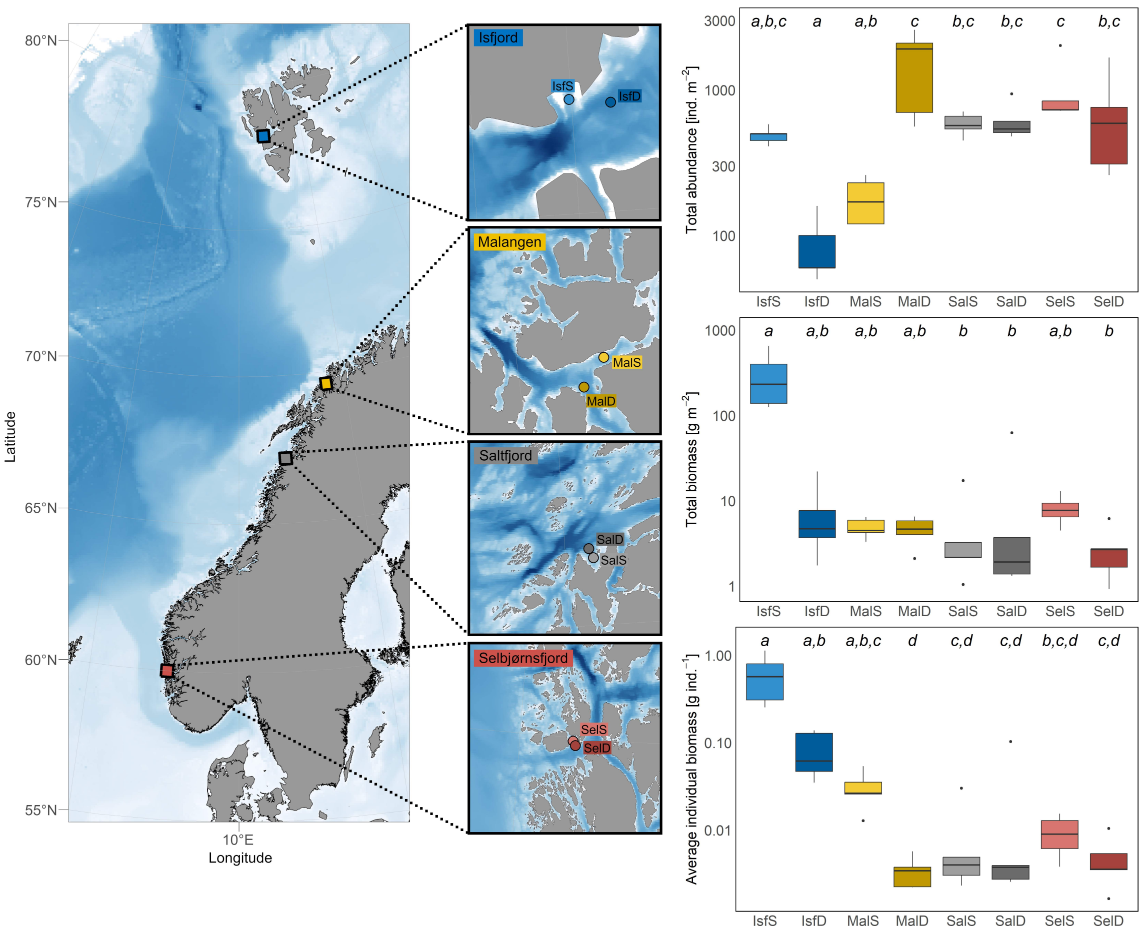

Figure 1. Representation of the studied latitudinal and depth gradient and univariate community measures. The map on the left shows the study region and the locations of the studied fjords in the Arctic (Isfjord), sub-Arctic (Malangen and Saltfjord), and temperate climate zone (Selbjørnfjord). Detailed maps of the studied fjords show the shallow (< 150 m depth) and deep (> 200 m depth) sampling locations. Station abbreviations use the first 3 letters of the fjord name together with S (shallow) or D (deep). Boxplots depict total abundance, total biomass, and average individual biomass across all sampling locations. Letters indicate significant differences according to Dunn's test ($\alpha = 0.05$). Sampling locations that have the same letter are not significantly different. Results of statistical tests can be found in the Supplementary Information.

(Mazurkiewicz et al., 2020; Silberberger et al., 2024). The depth zones follow Silberberger et al. (2024), who identified distinct trophic niches of macrobenthos between the two zones, particularly in the sub-Arctic. The latitudinal gradient represents variation in benthic community composition, and patterns of primary production, organic matter transformation and export that are expected to gradually move northward with the progressing climate change (Silberberger et al., 2024). Accordingly, the communities at southern locations were used as predictors for the future of the more northern locations. I hypothesize that a future loss of suspension-feeding bivalves at high latitudes (Silberberger et al., 2024) will be accompanied by a simultaneous large reduction of the macrofaunal blue carbon stock. This will be visible along the studied latitudinal gradient through a reduced overall biomass, smaller individuals, and more short-lived individuals when moving from North to South.

The focus on Mollusca was chosen due to the typically high relative contribution of this phylum to macrofaunal abundance and biomass, as well as the extreme taxonomic and functional diversity within Mollusca (Wanninger and Wollesen, 2019). Furthermore, most mollusk species in the study region have a southern or northern distribution limit within the study region and a large proportion of the mollusk species with a northern distribution limit within the study region have been shown to expand their distribution to the North (Brattegard, 2011).

Macrofauna samples were collected with a van Veen grab (sampling area: 0.1 m^2). Five replicate grab samples were collected from each study location. The entire samples were washed over a 0.5-mm sieve prior to fixation in 4% formaldehyde (borax-buffered). In the laboratory, all mollusks were collected from the samples and identified to the lowest possible taxonomic level, counted (abundance) and the blotted wet-weight (biomass) was determined. In total, 2627 individuals were assigned to 74 taxa, comprising 57 species, 9 genera, 4 families, and 4 classes (see Supplementary Information for taxon list). Abundance and biomass were standardized to 1 m^2 sediment surface area. Average individual biomass was estimated for each Van Veen grab sample by dividing the total macrofaunal community biomass by the total macrofaunal community abundance. To identify significant differences in univariate community measures (i.e., total abundance, total biomass, average individual biomass) the non-parametric Kruskal-Wallis test (Kruskal and Wallis, 1952) was used. Dunn's test (Dunn, 1964) with p-value correction according to the Benjamini–Hochberg method (Benjamini and Hochberg, 1995) was used for post-hoc pairwise comparisons. The univariate community measures revealed gradual variation across stations, with no clearly defined station groupings emerging from the statistical analysis (Figure 1). Although not significant for all pairwise comparisons among stations, strong patterns were observed within the data. Total biomass was more than one order of magnitude higher for the shallow Arctic location (IsfS) than for any other station. Furthermore, total biomass was considerably elevated at shallow locations in Arctic and temperate fjords in comparison to deep locations in the same fjords, a pattern that was not observed for sub-Arctic fjords. Across all fjords, the average individual biomass was higher in the shallow habitats. The magnitude of this difference between the depth zones differed strongly between the fjords and was particularly high in the Arctic and the more northern sub-Arctic fjord (Figure 1). The average individual biomass was highest in the Arctic fjord and particularly high for the shallow location. Given that maximum shell size is generally correlated with longevity in bivalves (Ridgway et al., 2011), it is likely that the relatively large individuals collected from the shallow Arctic fjord are also relatively old. Taken together, these biomass and individual biomass patterns indicate the shallow Arctic community as the community with outstanding high faunal blue carbon storage (high biomass) that has been stored for a long time (large-sized individuals that are most likely old).

To further assess the blue carbon potential of the studied mollusk communities, modalities for three biological traits related to resource utilization (feeding mode) and carbon storage potential (maximum size, life span) were assigned to all individuals except for juvenile bivalves and gastropods (see Supplementary Information for trait descriptions). In the context of my study, resource utilization serves as a response trait (Lavorel and Garnier, 2002) (i.e., linking the observed community composition to the habitat-specific food availability) and carbon storage potential as an effect trait (Lavorel and Garnier, 2002) (i.e., how much biomass can be stored for how long in response to the experienced environmental conditions). Fuzzy coding was used to assign modalities to indicate the degree to which a taxon expresses a trait modality. The modalities were assigned on the genus level (or higher for individuals classified on a higher taxonomic level) using the Cefas benthic trait database (Clare et al., 2022) and the Arctic trait database (Degen and Faulwetter, 2019), supplemented with information from other scientific literature and own expert opinion, if necessary. Traits were assigned at the genus level, as species-level trait information was not available for all taxa. While this lower taxonomic resolution introduces some uncertainty into the trait data, it does not pose a major issue for the interpretation of the results. On the contrary, any patterns detected in the trait-based analysis are likely robust, as they emerge despite the coarser taxonomic resolution. Juvenile bivalves and gastropods that were identified only to the class level were not assigned any traits and were excluded from the trait-based analysis. The assignment of traits on a class level to bivalves and gastropods would be non-informative, since all modalities for the three studied traits are represented in the two classes. The exclusion of juvenile bivalves and gastropods is unlikely to have significantly affected the results, as these individuals are likely to belong to taxa that were already recorded among the adult specimens at the same locations. Therefore, their inclusion would not have substantially enhanced trait representation. Additionally, the juveniles were all very small, meaning their exclusion could only meaningfully influence abundance-based analyses. Biomass-based analyses, however, are not notably affected, given the extremely low biomass of such small individuals. Two RLQ analyses (Dray et al., 2014) were conducted with two different community data sets (abundance; biomass) to explore how functional differences in the communities are related to the different habitat characteristics (climate and depth zone). RLQ analysis produces a simultaneous ordination of three data matrices (R – habitat characteristics per sample; L – taxon abundances per sample; Q – biological traits per taxon). First, individual ordinations for each matrix were computed: correspondence analysis for L; multiple correspondence analysis for R; principal component analysis for Q. The ordinations of R and Q were weighed by species and sites weights, respectively, derived from the correspondence analysis of L. Then, the final RLQ analysis maximizes the covariance between R and Q. All data matrices and a code for the RLQ analysis are available from Zenodo (Silberberger, 2024).

The biomass-based RLQ analysis, linked the high contribution of long-lived (> 10 y), large (> 100 mm), and suspension-feeding taxa to shallow (< 150 m) and Arctic habitats (habitat and trait scores in Figure 2). This result is in line with the above-identified blue carbon potential of this habitat and the previously described latitudinal and

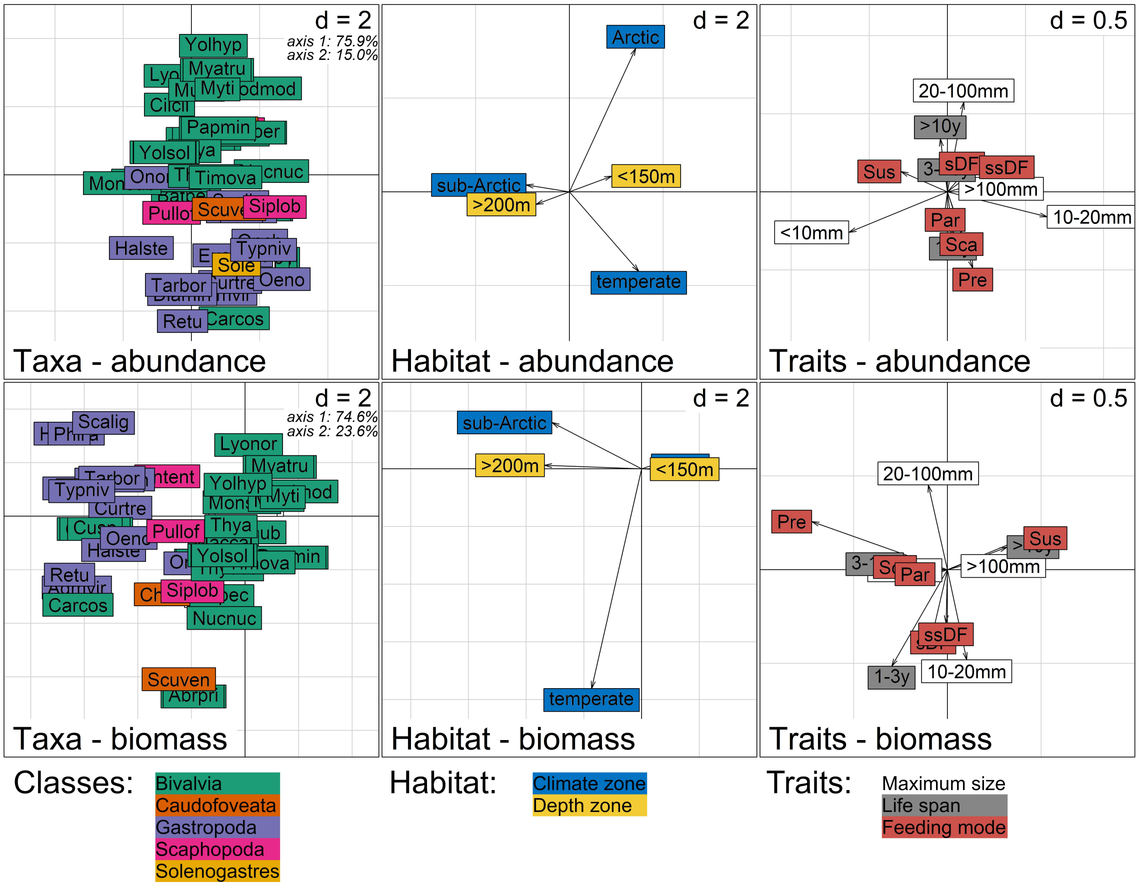

Figure 2. Results of the first two axes of the RLQ analyses using abundance (top) and biomass community data (bottom). Scores of taxa (left), habitat (middle), and traits (right) are shown. Colors indicate class membership, habitat classification categories, and traits. The values of d give the grid size. The percentages of the total inertia projected on each axis are given in the taxa plot. Exact scores and abbreviations are available in the Supplementary Information. For clarification regarding any label ambiguities caused by overlaps, please consult Supplementary Figure S3.

depth patterns in suspension feeding (Silberberger et al., 2024). Therefore, the results demonstrate that the potential loss of the long-lived suspension-feeding bivalves from shallow Arctic communities (Figure 2) will likely reduce the macrofaunal biomass by up to one order of magnitude (Figure 1). My results appear to contrast with an earlier study (Mazurkiewicz et al., 2020) that concluded that the macrofaunal size structure may be resilient to major climatic changes, based on a high consistency in biomass size spectra in different fjords along the same latitudinal gradient. All samples in Mazurkiewicz et al. (2020), however, were collected deeper than 150 m and even below 200 m for Svalbard fjords. Accordingly, the patterns in communities shallower than 150 m could not have been discovered by them and the reported latitudinal consistency in biomass size spectra (Mazurkiewicz et al., 2020) must be limited to deep habitats, where much of the biomass is already associated with deposit feeders and predators (Figure 2; Silberberger et al., 2024).

Furthermore, RLQ analyses of abundance and biomass associated intermediate life spans (3–10 y) with sub-Arctic fjords and short life spans (1–3 y) with temperate fjords (Figure 2). This suggests that biomass and zoobenthic blue carbon turnover will accelerate with progressing climate change. Accordingly, the potential of benthic macrofauna in fjords to act as a blue carbon reservoir appears to be limited to newly emerging habitats due to sea-ice loss, as known for Antarctic fjords (Zwerschke et al., 2022). For all other habitats that already contain a macrofaunal community, a future warmer climate will likely cause a reduction of the blue carbon storage and the associated climate feedback loop is expected to reinforce human-made climate change. Although the present study does not permit an overall assessment of the macrofaunal blue carbon stock in the studied sedimentary habitats due to the focus on Mollusca only, the results emphasize that increased efforts to study macrofaunal blue carbon stocks of other phyla and entire communities in the Arctic are urgently needed, due to the potential negative impact that the progressing climate change will have on these blue carbon stocks.

Acknowledgements

I want to thank the captains and crews of s/y *Oceania* and r/v *Tanteyen*. Thanks to all co-workers and students for their help during sampling. Furthermore, I want to thank Katarzyna Gomuła for the pre-sorting of macrofauna samples.

Funding statement

This study was funded by the National Science Centre, Poland, grant no. 2019/35/D/NZ8/01282.

Author contribution

M.J.S. conceived the ideas, designed the methodology, collected the samples, conducted taxonomic identification, analyzed and interpreted the data, received funding, and wrote the manuscript.

Data and code availability

All data and code for RLQ analysis are available at https://zenodo.org/doi/10.5281/zenodo.11261015

Supplementary materials

Please follow this link to see the supplementary material associated with this article.

Conflict of interest

None declared.

References

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*. Glob. Change Biol. 23, 5083–5091. https://doi.org/10.1111/gcb.13772

Barnes, D.K.A., Sands, C.J., Paulsen, M.L., Moreno, B., Moreau, C., Held, C., Downey, R., Bax, N., Stark, J.S., Zwerschke, N., 2021. *Societal importance of Antarctic negative feedbacks on climate change: blue carbon gains from sea ice, ice shelf and glacier losses*. Sci. Nat. 108, 43. https://doi.org/10.1007/s00114-021-01748-8

Barnes, D.K.A., Sands, C.J., Richardson, A., Smith, N., 2019. *Extremes in Benthic Ecosystem Services; Blue Carbon Natural Capital Shallower Than 1000 m in Isolated, Small, and Young Ascension Island's EEZ*. Front Mar Sci 6. https://doi.org/10.3389/fmars.2019.00663

Benjamini, Y., Hochberg, Y., 1995. *Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing*. J. Roy. Stat. Soc. B Met. 57, 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Brattegard, T., 2011. *Endringer i norsk marin bunnfauna 1997–2010*. DN-utredning.

Campanyà-Llovet, N., Snelgrove, P.V.R., Parrish, C.C., 2017. *Rethinking the importance of food quality in marine benthic food webs*. Prog. Oceanogr. 156, 240–251. https://doi.org/10.1016/j.pocean.2017.07.006

Clare, D.S., Bolam, S.G., McIlwaine, P.S.O., Garcia, C., Murray, J.M., Eggleton, J.D., 2022. *Biological traits of marine benthic invertebrates in Northwest Europe*. Sci Data 9, 339. https://doi.org/10.1038/s41597-022-01442-y

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. *The value of the world's ecosystem services and natural capital*. Nature 387, 253–260. https://doi.org/10.1038/387253a0

Degen, R., Faulwetter, S., 2019. *The Arctic Traits Database – A repository of Arctic benthic invertebrate traits*. Earth Syst. Sci. Data 11, 301–322. https://doi.org/10.5194/essd-11-301-2019

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S., ter Braak, C.J.F., 2014. *Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation*. Ecology 95, 14–21. https://doi.org/10.1890/13-0196.1

Dunn, O.J., 1964. *Multiple Comparisons Using Rank Sums*. Technometrics 6, 241–252. https://doi.org/10.1080/00401706.1964.10490181

Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M.C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S., Winder, M., 2017. *The importance of benthic–pelagic coupling for marine ecosystem functioning in a changing world*. Global Change Biol. 23, 2179–2196. https://doi.org/10.1111/gcb.13642

Jordà Molina, È., Silberberger, M.J., Kokarev, V., Reiss, H., 2019. *Environmental drivers of benthic community structure in a deep sub-arctic fjord system*. Estuar. Coast. Shelf Sci. 225. https://doi.org/10.1016/j.ecss.2019.05.021

Kruskal, W.H., Wallis, W.A., 1952. *Use of Ranks in One-Criterion Variance Analysis*. J. Am. Stat. Assoc. 47, 583–621. https://doi.org/10.1080/01621459.1952.10483441

Lavorel, S., Garnier, E., 2002. *Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail*. Funct. Ecol. 16, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Mazurkiewicz, M., Górska, B., Renaud, P.E., Włodarska-Kowalczuk, M., 2020. *Latitudinal consistency of biomass size spectra – benthic resilience despite environmental, taxonomic and functional trait variability*. Sci. Rep. 10, 4164. https://doi.org/10.1038/s41598-020-60889-4

Ridgway, I.D., Richardson, C.A., Austad, S.N., 2011. *Maximum Shell Size, Growth Rate, and Maturation Age Correlate With Longevity in Bivalve Molluscs*. J. Gerontol. A-Biol. 66A, 183–190. https://doi.org/10.1093/gerona/glq172

Silberberger, M.J., 2024. *Infaunal mollusca in 4 fjord along a long latitudinal gradient (v1.0.0)* [Data set]. https://doi.org/10.5281/zenodo.11261016

Silberberger, M.J., Koziorowska-Makuch, K., Reiss, H., Kędra, M., 2024. *Trophic niches of macrobenthos: Latitudinal variation indicates climate change impact on ecosystem functioning*. Global Change Biol. 30, e17100. https://doi.org/https://doi.org/10.1111/gcb.17100

Snelgrove, P.V.R., 1999. *Getting to the Bottom of Marine Biodiversity: Sedimentary Habitats*. Bioscience 49, 129. https://doi.org/10.2307/1313538

Souster, T.A., Barnes, D.K.A., Hopkins, J., 2020. *Variation in zoobenthic blue carbon in the Arctic's Barents Sea shelf sediments*. Philos. T. R. Soc. A, 378, 20190362. https://doi.org/10.1098/rsta.2019.0362

Souster, T.A., Barnes, D.K.A., Primicerio, R., Jørgensen, L.L., 2024. *Quantifying zoobenthic blue carbon storage across habitats within the Arctic's Barents Sea*. Front. Mar. Sci. 10. https://doi.org/10.3389/fmars.2023.1260884

Wanninger, A., Wollesen, T., 2019. *The evolution of molluscs*. Biol. Rev. 94, 102–115. https://doi.org/10.1111/brv.12439

Włodarska-Kowalczuk, M., Renaud, P., Węsławski, J., Cochrane, S., Denisenko, S., 2012. *Species diversity, functional complexity and rarity in Arctic fjordic versus open shelf benthic systems*. Mar. Ecol. Prog. Ser. 463, 73–87. https://doi.org/10.3354/meps09858

Zwerschke, N., Sands, C.J., Roman-Gonzalez, A., Barnes, D.K.A., Guzzi, A., Jenkins, S., Muñoz-Ramírez, C., Scourse, J., 2022. *Quantification of blue carbon pathways contributing to negative feedback on climate change following glacier retreat in West Antarctic fjords*. Global Change Biol. 28, 8–20. https://doi.org/10.1111/gcb.15898