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Temporal variability in the biomass size spectra, secondary production, and carbon demand of deep-sea benthos in a warming Arctic ocean (79°N, Fram strait)

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ABSTRACT

Body size is one of the most significant functional trait of an organism, while the size spectrum defines the functioning of a multispecies community. Body size affects energetics, which is why changes in body size have implications for resilience to climate change at both individual and community scales. To investigate the influence of changing environmental conditions on body size, secondary production, and carbon demand of deep-sea benthos in the Fram Strait, the passage between NE Greenland and the Svalbard archipelago, we analyzed meiofauna and macrofauna samples collected in 2000, 2010, and 2017 at station depths ranging from 973 m to 5561 m. Surface sediments were collected using a box corer to assess the influence of environmental changes on the structure (biomass size spectra) and functioning (secondary production and carbon demand) of benthic communities. At depths between 900 and 1500 m (RIDGE), macrofauna individual biomass decreased from 2000 to 2017. However, at depths below 2000 m, it remained at a similar level across the studied years. In all bathymetric zones, macrofauna secondary production and carbon demand remained stable across the three years. In contrast, nematodes individual biomass, total biomass and secondary production decreased from 2000 to 2017. Results of DISTLM model confirmed that nematodes did not rely on the bacterial activity (indicated by FDA). Responses of benthic biomass size spectra to the environmental changes varied among bathymetric zones. The decreasing nematodes standing stocks and magnitude of its functioning may be due to an increasing interference competition with macrofauna.

1. Introduction

The Arctic is a region of rapid environmental change, with air temperatures increasing twice as fast as the global average (e.g., Pörtner et al., 2022; Shu et al., 2022). The strong temperature increase is accompanied by a rapid decline in sea ice thickness and extent (Onarheim et al., 2018; Pörtner et al., 2022) in all parts of the region and all seasons. The dramatic transformations in terrestrial, coastal and offshore environments have immediate and long-term consequences on ecosystems functioning such as magnitude and timing of primary production, pelagic-benthic coupling, and carbon cycling (Solan et al., 2020). Significant changes in the type, thickness and extent of ice, the input of meltwaters, and dynamics of water masses, coupled with warming and acidification have already impacted ecosystem processes and organisms that inhabit a variety of Arctic habitats (Haine et al., 2015; Solan et al., 2020; Terhaar et al., 2020). This makes the Arctic a key area for studying the effects of climate change. Sea ice loss influences Arctic marine life by changing underwater light regimes, habitat availability and hydrography (Grebmeier et al., 2018; Macias-Fauria and Post, 2018). Changes in the physical environment have cascading effects for biogeochemistry and ecology of the Arctic pelagic system (Bluhm et al., 2011; Wassmann, 2011), and thereafter for the export of organic matter from the productive surface layer to the seafloor (Bauerfeind et al., 2009). Wiedmann et al. (2020) in their review article about carbon budget in the deep Arctic Ocean emphasize that studies on metabolic rates of benthic organisms are crucial to get a better understanding for Arctic Ocean deep-sea ecosystem functioning.

The deep ocean absorbs huge amounts of heat and carbon dioxide, acting as a buffer against climate change induced transformations. However, these changes expose deep-sea ecosystems to the combined stress of warming, ocean acidification, deoxygenation, and varying food input (Levin and Le Bris, 2015). The climate change driven shifts in pelagic productivity may impact the functioning of benthic deep-sea communities as they are highly dependent on particle flux from surface waters. Knowledge of the functional interactions in deep-sea food webs is necessary to understand and predict the response of deep-sea ecosystem to global changes (Soetaert and van Oevelen, 2009).

Body size is a key trait that is closely linked to ecological properties and processes at individual, population, and community levels. Body size can be used as a unifying tool in the description of the structure of

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food webs in aquatic ecosystems due to relation of size and physiological rates, regardless of taxonomic affiliation (Bett, 2013). Body size influences, among other things, metabolic rate, tolerance to chemical stress and disturbance, dispersal and mobility capacity, as well as susceptibility to predation (Peters, 1983), all of which are critical attributes linked to population fitness. A size-based, taxonomy-free approach can serve as an alternative way to describe community structure in ecological research, especially in deep-sea environments where accurate species identification require extensive taxonomic expertise. Measurements of individual biomass make it possible to estimate both secondary production and respiration at the level of single organisms as well as entire communities (Bourassa and Morin, 1995), which subsequently enables calculations of benthic carbon demand. The mineralization of organic carbon within marine sediments represents a significant pathway in the global carbon cycle, connecting surface carbon reservoirs to long-term sequestration in sediments (Woulds et al., 2016). Several environmental factors (e.g., temperature, food availability, disturbance) can influence the partitioning of benthic biomass and production among size components, which has implications for carbon cycling (Schwinghamer, 1981).

It is predicted that a reduction in body size together with shifts in species distribution and phenology will be a universal response to global warming (Gardner et al., 2011). Moreover, changing physicochemical properties of the ocean influence food quality and quantity, and thus, organism body size. The predicted decrease in organic matter input to benthic communities, as suggested by most ocean biogeochemistry models (Steinacher et al., 2010), may lead to shifts toward smaller body sizes. However, both basic patterns and factors affecting the temporal variability of biomass and production partitioning in benthic communities among size classes remains undescribed, especially in the deep sea. This fundamental knowledge is highly important if we are to predict changes in organisms functioning in response to climate-induced changes. It is urgently needed to describe the scale of the temporal variability of body size distribution in Arctic Ocean benthic communities, where severe climate changes have already been observed.

Data presented in this study add to a rare collection of published meiofauna and macrofauna size spectra in deep-sea benthic communities. What is more, our study is the first to explore temporal changes in benthic biomass size spectra along a bathymetric transect from Vestnesa Ridge to abyssal depths in the eastern Fram Strait (79°N). In this area, significant episodic increases in temperature of surface waters, defined as Warm Water Anomalies (WWA) were observed between late 2004 and 2008, and between 2015 and 2016 (Beszczynska-Möller et al., 2012, McPherson et al., in prep). A previous study from this area identified that macrofauna species composition significantly changed and species diversity increased after the WWA period (Górska et al., 2022). This study is focused on biomass-based community functioning descriptors and aims to explore whether WWA-related changes in food availability have an influence on nematodes and macrofauna biomass size spectra, secondary production and carbon demand across the depth range from continental margins to abyssal plains. We hypothesize that the increased rates of organic matter sedimentation, observed during the WWAs resulted in increasing macrofauna and nematodes biomass, secondary production and carbon demand across the bathymetric range in eastern parts of the Fram Strait.

2. Materials and methods

2.1. Study area

The area of investigation was located in the Fram Strait, the deep passage (with a maximum depth 5560 m) between Greenland and the Svalbard Archipelago, which is a key area in terms of water masses and heat exchange between the North Atlantic and the central Arctic Ocean. The sampling stations were aligned along the bathymetric gradient at approx. 79°N, from the Vestnesa Ridge (1200 m) to the Molloy Deep (maximum depth of 5569 m) in the Fram Strait. Some of the stations (named "HG"; Table A1) are permanent sampling sites of the Long-Term Ecological Research (LTER) Observatory HAUSGARTEN, established in 1999 by the Alfred-Wegenr-Institut Helmholtz-Zentrum für Polar-und Meeresforschung (Bremenhaven, Germany). Within HAUSGARTEN observatory multidisciplinary research on impacts of climate changes on Arctic marine ecosystem are conducted (Soltwedel et al., 2005). Almost all aspects of Arctic marine ecosystem from the sea surface to the bottom are explored (Soltwedel et al., 2005).

Based on measurements from an array of oceanographic moorings at 78°50' N from 1997 to 2022, Beszczynska-Möller et al. (2012) and McPherson et al. (in prep) calculated a positive linear trend (0.31 °C per decade) for the mean temperature of Atlantic Water transported by the West Spitsbergen Current in the eastern part of the strait. In addition to this positive trend, between the end of 2004 and 2008 Beszczynska-Möller et al. (2012) and between 2015 and 2016, McPherson et al. (in prep) identified temperature anomalies at the central HAUSGARTEN station (HG IV, at 2500 m water depth) exceeding 0.4 °C (Warm Water Anomalies, WWA).

The warming of the Atlantic Water core in the eastern Fram Strait significantly affected primary production in the study area. During the productive seasons (April – August) monthly mean values of chlorophyll *a* concentrations in surface waters increased from 1.0 to 1.5 mg m^{-3} in years 1998-2003 to 1.5-2.0 mg m^{-3} in years 2009-2012 (Nöthig et al., 2015). The annual downward flux of particulate organic matter also increased after 2008. Based on measurements from sediment traps deployed at the central HAUSGARTEN station HG-IV, downward flux of particulate organic matter at depths between 179 and 208 m increased form 8.6-10.0 g m^{-2} y^{-1} in 2000-2008 to 11.0-15.6 g m^{-2} y^{-1} in 2009-2012 (Lalande et al., 2013; Soltwedel et al., 2016). The changes in surface waters were mirrored in concentrations of chloroplastic pigments (Chloroplastic Pigment Equivalents, CPE) in the sediments, an indicator of the amount of settled phytodetritus available to benthic organisms. At nine HAUSGARTEN stations investigated in this study, CPE increased from 3.2 to 12.2 μg cm^{-3} in 2000 to 12.6–30.0 μg cm^{-3} in 2017 (Górska et al., 2022; Fig. A1). This increase of CPE concentrations in sediments was accompanied with an increase in total biomass of 'living' and 'dead' organic matter (indicated by particulate proteins in the sediments). While the availability of phytodetritus at the seafloor increased after 2006, the total organic matter in sediments indicated by ash-free dry weights of the sediment generally decreased (0.12-0.15 mg cm^{-3} in 2000 and 0.08-0.13 mg cm^{-3} in 2017; Górska et al., 2022; Fig. A1).

2.2. Sampling and samples processing

Sediment samples were collected during summer cruises in July/August 2000, July 2010 and July/August 2017 from board *r/v Polarstern* using a large USNEL box corer (sampling area of 0.25 m^2; Fig. 1, Table A1). At each station one box was collected, from each box two subsamples of upper 20 cm of sediments (sampling area of each subsample: 0.1 m^2) were collected for macrofauna. From remaining 0.05 m^2 of the box corer sample, three subsamples of upper 5 cm of sediment (using plastic syringes) were collected for meiofauna (sampling area of each subsample: 10 cm^2). In 2000, meiofauna were collected using multiple corer only at seven HAUSGARTEN stations (00HGI, 00HGII, 00HGIII, 00HGV, 00HGVI, 00HGVII, 00HGVIII; Table A1). Three samples (pseudo-replicates) from different cores of the same multiple corer (located within ca. 20 cm of each other) were taken using plastic syringes with cut-off anterior ends (sampling area of each pseudo-replicate: 3 cm^2) at each station for meiofauna analyses. Macrofauna samples were sieved through a 0.5 mm sieve. All faunal samples were immediately fixed with a 4% formaldehyde solution buffered with sea water.

In the laboratory, all macrofauna specimens were counted, identified to the lowest possible taxonomic level (mostly to the species level) and

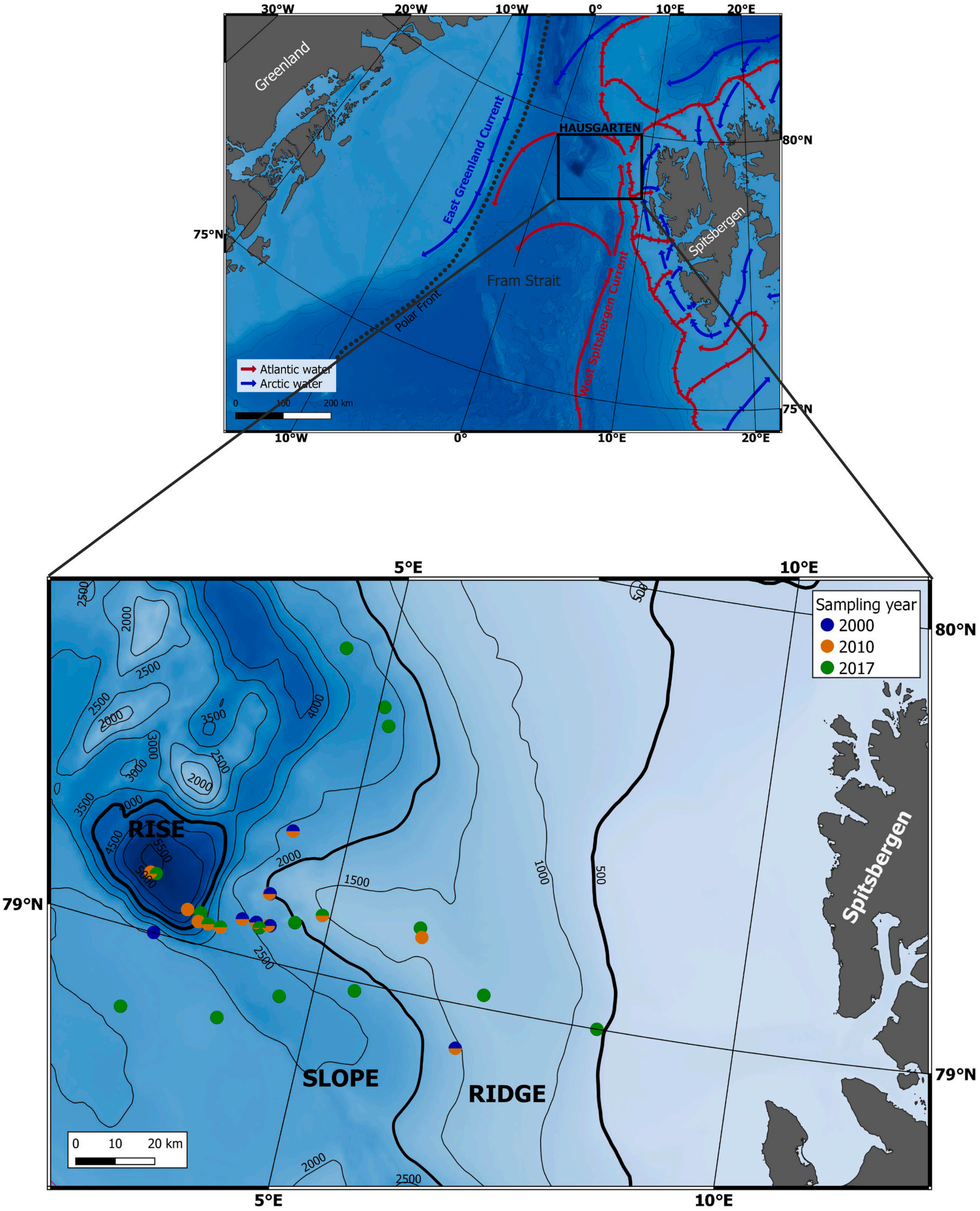

Fig. 1. Schematic water circulation (upper plot; currents arrows after Vihtakari et al., 2019) in the Fram Strait with sampling area indicated by a frame. Sampling stations with colors indicating sampling year and bathymetric delineation of grouping into RIDGE, SLOPE, and RISE (lower plot). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

photographed with a camera connected with stereomicroscope. For each specimen, the maximum length and width (and thickness for bivalves) were measured using the digital image analysis of Leica Application Suite v. 4.2. Macrofaunal body dimensions were used to calculate biovolume (V [μm^3]). Wet weight [µg] was calculated using the available published equations (crustaceans after Berestovski et al. (1989), echinoderms after Lebrato et al. (2010)) or from a volume of the nearest geometric shapes (e.g., polychaetes, gastropods – cone; bivalves – ellipse; sipunculans – cylinder) and a density of 1.13 g cm^{-3}. For fragmented polychaete specimens, the total length was calculated using its morphometric relationship with the width of a selected chaetiger: $L = a \cdot chet + b$, where L – total length, $chet$ – best-fitted chaetiger width for each family, a and b – coefficients specific for polychaetes family according to Górska et al. (2019). Wet weight was converted to dry weight [µg] using published conversion factors (Brey, 2001; Brey et al., 2010). For shelled taxa dry weight was estimated without shell.

The meiofauna samples were initially sieved through a 500-µm sieve to separate the macrofauna fraction from the meiofauna fraction. All the material retained on a 32-μm sieve was centrifuged three times in colloidal silica (Ludox-TM 50) with a density of 1.18 g cm^{-3} and stained in a 4% formaldehyde solution with Rose Bengal for at least 24 h (Heip et al., 1985). For meiofauna samples collected in 2000, all metazoan organisms were counted and identified to the higher taxa. All nematodes were removed and mounted on slides for measurements (Hoste et al., 2007). The maximum length and width were measured using the Image J program. For samples from 2010 to 2017, all metazoan organisms in the meiofauna samples were counted, identified to the higher taxa and photographed with a camera connected with stereomicroscope. For each specimen, the maximum lengths and widths were measured using the digital image analysis of Leica Application Suite v. 4.2. For nematodes, a subsample of at least 200 randomly selected specimens was taken. Nematode lengths and widths were measured using a semi-automated image analysis method (Mazurkiewicz et al., 2016). Since only nematodes were measured in the meiofauna samples from 2000 and they constituted from 90 to 94% of meiofauna abundance (both in 2000 and in other studied years, Hoste et al., 2007), we used measurements of nematodes exclusively for all years in the subsequent analysis. Nematode biovolume (V [μm^3]) was calculated by using an equation for the volume of a cylinder: $V = r^2L/10^6$, where r [μm] is the radius (width/2) and L [μm] is the nematode length (Mazurkiewicz et al., 2016). The wet weight (*WW*), dry weight (*DW*) and *individual biomass* [gC] were calculated using the following equations: $WW = 1.13\ V$; $DW = WW \bullet 0.25$ (Feller and Warwick, 1988); and *individual biomass* = $DW \bullet 0.463$ (Brey, 2001), respectively.

The characterization of the sedimentary environment was carried out using data collected within the scope of the Alfred-Wegener-Institute's monitoring program performed at the LTER observatory HAUSGARTEN (Górska et al., 2022). Only part of the stations sampled in this study were the same as LTER HAUSGARTEN stations (marked as "HG"; Table A1). For the other, non-LTER stations listed in Table A1, environmental data were not available. A detailed description of sampling and processing of samples for environmental parameters (oxygen concentration at the seafloor (O_2), sediment water content (H_2O), ash-free dry weights of the sediment (AFDW), potential bacterial activity (fluorescein-di-acetate turn-over (FDA), sediment-bound phospholipids (LIPIDS), particulate proteins (PROT), chloroplastic pigment equivalents (CPE)) can be found in Górska et al. (2022).

2.3. Data analysis

Macrofauna secondary production (P [g C m^{-2} y^{-1}]) and respiration were estimated based on *individual biomass* [g C] using the Artificial Neural Network (ANN) model developed by Brey (2012). This model was trained on a large empirical dataset of marine invertebrates and uses a neural network approach to approximate non-linear relationships between body mass, environmental conditions, and organismal traits. The ANN predicts annual production and respiration from individual biomass (expressed in kJ) together with environmental and biological predictors such as bottom water temperature, water depth, taxonomic affiliation (5 categories: Mollusca, Annelida, Crustacea, Echinodermata), mobility (4 categories: infauna, sessile, crawler, facultative swimmer), feeding type (3 categories: herbivore, omnivore, carnivore) and the habitat (4 categories: lake, river, marine, subtidal) defined for each individual. All categorical variables were binary (0 or 1). Individual body mass (in dry weight) was converted into energy content [kJ] using conversion factors (Brey, 2001, 2010). Bottom water temperature was measured by the CTD rosette and the data were taken from the PANGEA open data base (Beszczynska-Möller and Wysotzki, 2010; Schauer, 2010; von Appen and Rothardt, 2018). Nematoda secondary production and respiration were estimated using equations published by Schwinghamer et al. (1986). Carbon demand (CD [g C m^{-2} y^{1-}]) for both Nematoda and macrofauna was estimated using the equation $CD = 0.608\ A$, where A is the assimilation rate (respiration plus production; Klages et al., 2004).

Based on the previous macrofaunal studies conducted in the Fram Strait (Górska et al., 2020, 2022; Włodarska-Kowalczuk et al., 2004), for statistical analyses stations were grouped *a priori* into four groups representing bathymetric zones: RIDGE (from 900 to 1572 m), SLOPE (from 1910 to 3382 m), RISE (from 4000 to 5000 m), and RISE Molloy (5561 m in the Molloy Deep, with an exceptionally high organic carbon (C_{org}) content compared to other RISE stations).

Benthic biomass size spectra (BBSS) were constructed by plotting biomass [μg] in each size class against the log_2-transformed size of a class. Each individual was classified into a log_2 size class based on its dry weight [μg] (from $> 2^x$ to 2^{x+1}). For example, class 0 includes all organisms for which *dry weight* ≥ 1 and < 2 μg (i.e., $\geq 2^\circ$ and $< 2^1$ μg). Normalized biomass size spectra (NBSS) were constructed by regressing log_2 [(*dry weight* in each class)/(Δ of size class)] with log_2 of the upper limit of each class (Sprules and Munawar, 1986). As recommended by Sprules and Barth (2015), regression models were inspected using Cook's distance with a threshold of 4/n to eliminate observations based on small number of samples, especially extreme size classes. Underestimation of biomass in the smallest and the largest size classes may distort the outcome of linear regression model and produce incorrect results. The multiple linear regression was used to assess the parameters (slope and intercept) of the obtained NBSS. To test for differences in the NBSS among years in group of stations, analysis of covariance (ANCOVA) was performed for each group of stations separately with the size class as a continuous covariate and the year as a categorical covariate. Pairwise *post hoc* comparisons were performed with a Tukey's adjustment of p-values. Statistical analyses of normalized biomass were performed in R v. 4.4.1 (R-Core-Team, 2025); the ANCOVA *post hoc* tests were performed using the *lsmeans* function from the *emmeans* package (Lenth, 2018).

Differences among years and group of stations in univariate fauna characteristics (average individual biomass *(AvIB)*, total biomass *(B)*, *P*, *CD*, and CD_{nem}:CD_{macro}) were tested using non-parametric Kruskal-Wallis test with U Mann Whitney post hoc tests with Bonferroni correction (Siegel and Castellan, 1988). Macrofauna characteristics at RISE and RISE Molly and nematodes characteristics at RISE Molloy were not tested due to low number of replicates.

The relationships between environmental parameters (O2, H_2O, AFDW, FDA, LIPIDS, PROT, CPE) and benthic characteristics (*B, P, CD,* size structure – biomass distribution among size classes) were analyzed only for the 'HG' stations (for which both data sets were available) using the Distance-based Linear Model routine (DistLM) in PRIMER PERMANOVA + software v 7.0.24 (Anderson et al., 2008). Each predictor was analyzed separately (marginal test). Next, the forward selection procedure was based on adjusted R^2 to determine the best combination of predictor variables to explain variation in the biotic community (Anderson et al., 2008). Distance-based redundancy analysis (dbRDA) plot was performed using a DistLM to visualize the relationships between environmental parameters and biomass distribution among size classes. Additionally, to detect effect (positive or negative) of environmental variables on benthic univariate characteristics (log transformed *B, P,* and *CD*), set of linear regression models were performed.

3. Results

3.1. Total benthic biomass and average individual biomass

The highest total macrofauna biomass (B_{macro}) was observed at RIDGE in 2010 and the lowest at RISE in 2017 (Fig. 2; Table 1). At RIDGE macrofauna biomass differ significantly among years ($p < 0.05$; Table A2), where it was significantly higher in 2010 than in 2017 ($H = 6.68$, $p < 0.05$). At SLOPE stations macrofauna biomass did not differ significantly among years ($p > 0.05$; Table A2). At RISE macrofauna biomass was three times higher in 2010 than in 2017 (Table 2), contrary to RISE Molloy station where it was three times higher in 2017. In the DistLM model, FDA explained over 51% of variation in B_{macro}. From

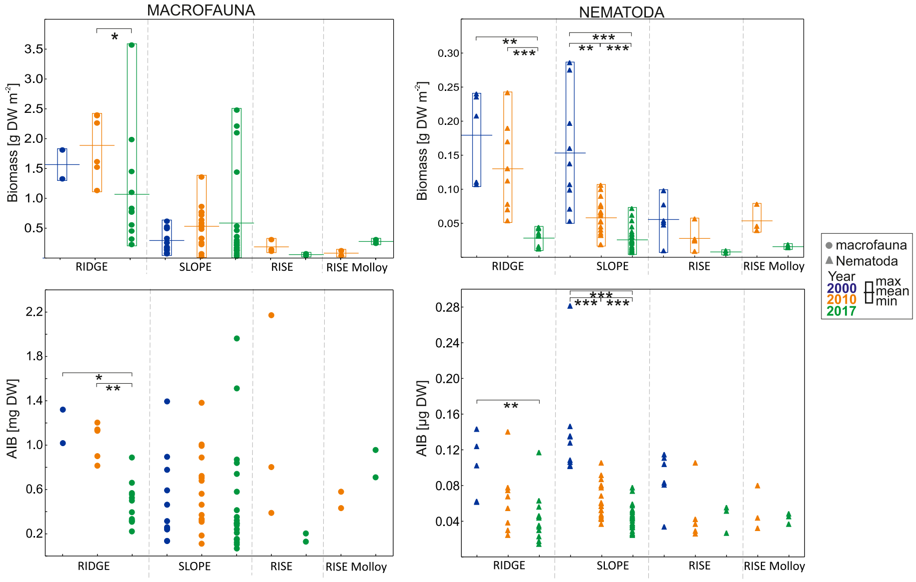

Fig. 2. Biomass (B [g DWT*m^{-2}]; upper panels) and average individual biomass (*AvIB* [mg DWT]; lower panels) for macrofauna (left panels) and Nematoda (right panels) in groups of stations localized in the Fram Strait in three sampling years. Significant p-values for Kruskal-Wallis multiple comparison post hoc test (*$p < 0.05$, **$p < 0.001$).

Table 1
Mean (±SD) values of average individual biomass (AIB [µg]), biomass [g m^{-2}], secondary production (P [g C y^{-1} m^{-2}]), and carbon demand (CD [g C y^{-1} m^{-2}]) for Nematoda and macrofauna in groups of stations for three sampling years.

		Nematoda							
Group	Year	AIB [µg]		biomass [g m^{-2}]		P [g C y^{-1} m^{-2}]		CD [g C y^{-1} m^{-2}]	
RIDGE	2000	0.10	±0.04	0.18	±0.07	0.77	±0.18	6.10	±1.36
RIDGE	2010	0.06	±0.04	0.13	±0.07	0.62	±0.18	4.98	±1.38
RIDGE	2017	0.04	±0.03	0.03	±0.01	0.17	±0.08	1.38	±0.69
SLOPE	2000	0.14	±0.06	0.15	±0.08	0.60	±0.35	4.72	±2.76
SLOPE	2010	0.06	±0.02	0.06	±0.02	0.27	±0.09	2.19	±0.73
SLOPE	2017	0.04	±0.01	0.03	±0.02	0.14	±0.08	1.13	±0.65
RISE	2000	0.09	±0.03	0.06	±0.03	0.25	±0.14	1.98	±1.09
RISE	2010	0.05	±0.03	0.03	±0.02	0.12	±0.04	0.96	±0.29
RISE	2017	0.04	±0.01	0.02	±0.002	0.08	±0.01	0.65	±0.05
RISE Molloy	2010	0.05	±0.02	0.05	±0.02	0.26	±0.03	2.10	±0.25
RISE Molloy	2017	0.04	±0.02	0.01	±0.002	0.08	±0.01	0.32	±0.04
macrofauna									
Group	Year	AIB [µg]		biomass [g m^{-2}]		P [g C y^{-1} m^{-2}]		CD [g C y^{-1} m^{-2}]	
RIDGE	2000	1169	±212	1.57	±0.34	0.34	±0.1	2.33	±0.48
RIDGE	2010	1056	±157	1.89	±0.53	0.49	±0.1	3.14	±0.7
RIDGE	2017	466	±187	1.07	±0.93	0.40	±0.34	2.48	±2.19
SLOPE	2000	475	±380	0.29	±0.19	0.12	±0.06	0.71	±0.35
SLOPE	2010	586	±349	0.53	±0.33	0.18	±0.11	1.17	±0.68
SLOPE	2017	490	±493	0.59	±0.79	0.19	±0.26	1.22	±1.5
RISE	2010	1121	±935	0.19	±0.10	0.06	±0.01	0.47	±0.16
RISE	2017	168	±49	0.06	±0.02	0.03	±0.01	0.17	±0.07
RISE M	2010	504	±105	0.08	±0.06	0.03	±0.01	0.16	±0.08
RISE M	2017	834	±174	0.28	±0.04	0.10	±0.01	0.60	±0.04

seven environmental characteristics included in the DistLM best fitting model (together explaining 82% of biomass variability), only FDA was statistically significant ($p < 0.01$; Table 2).

At RIDGE stations, significantly lower $AvIB_{macro}$ was noted in 2017 (Fig. 2; Table 1) than in 2000 and 2010 ($H = 13.25$, $p < 0.01$; Table 1; Table A2). At SLOPE stations, $AvIB_{macro}$ did not differ significantly among years ($p > 0.05$; Table A2). At RISE stations $AvIB_{macro}$ was higher in 2010 than in 2017, while at RISE Molloy station $AvIB_{macro}$ was higher in 2017 (Table 1).

Total Nematoda biomass (B_{nem}) differed significantly among years in the different groups of stations ($p < 0.05$; Table A3). In all groups of stations, the lowest B_{nem} was noted in 2017. At RIDGE stations, significantly higher B_{nem} was observed in 2000 and 2010 compared to 2017 (Table 1; $p < 0.01$; Table A3). At SLOPE stations, the highest B_{nem} was observed in 2000 and the lowest in 2017 ($p < 0.01$). At RISE stations, B_{nem} decreased from 2000 to 2017 (Table 1), but differences were not statistically significant ($p > 0.05$; Table A3). At the deepest station (Molloy Deep), more than two times lower B_{nem} was noted in 2017 than

Table 2

Results of DistLM procedure for fitting environmental characteristics measured at the nine HAUSGARTEN stations (oxygen concentration (O_2), water content (H_2O), ash free dry weight of sediment (AFDW), sediment-bound phospholipids (LIPIDS), fluorescein-di-acetate (FDA), chloroplastic pigments equivalent (CPE), and particulate proteins (PROT)) to Nematoda (nem) and macrofauna (macro) univariate measures (biomass (*B*), secondary production (*P*) and carbon demand *(CD)*), and benthic size classes composition (Comp – biomass of Nematoda and macrofauna in size classes) for samples collected at "HG" stations (Table A1). Sets of best fitted descriptor variables selected in sequential test are presented. Var – variable, adj R^2 – adjusted R^2, PsF – Pseudo F, var% – percentage of explained variance, cum% - cumulative percentage explained by the added variable, β – linear regression coefficient. Significant effects: *$p < 0.05$, **$p < 0.01$.

Var	adj R^2	PsF	var%	cum %	β	Var	adj R^2	PsF	var%	cum %	β
B_{macro}						P_{macro}					
FDA	0.49	20.0**	51.3	51.3	0.75**	FDA	0.48	19.7**	50.9	50.9	0.71**
CPE	0.50	1.4	3.6	54.9	0.61**	CPE	0.53	3.1	7.1	58.1	0.61**
Temp	0.56	3.7	8.1	63.0	−0.61**	Temp	0.61	4.4*	8.6	66.7	−0.57**
O2	0.63	4.1	7.6	70.6	−0.13	O2	0.68	5.0*	7.9	74.6	−0.06
H2O	0.69	4.0	6.2	76.8	0.62**	H2O	0.70	1.9	2.9	77.5	0.57**
PROT	0.73	3.0	4.1	80.9	0.01	LIPIDS	0.72	1.9	2.7	80.1	−0.11
LIPIDS	0.73	1.0	1.4	82.3	−0.07	AFDW	0.75	2.6	3.3	83.5	0.28
CD_{macro}											
FDA	0.55	25.6**	57.4	57.4	0.79**						
CPE	0.58	2.2	4.6	62.0	0.62**						
Temp	0.65	4.7*	8.2	70.2	−0.66**						
O2	0.73	5.7*	7.8	78.0	−0.13						
H2O	0.75	2.6	3.3	81.3	0.58**						
LIPIDS	0.77	2.6	3.0	84.2	−0.08						
AFDW	0.78	1.6	1.7	86.0	0.31						
B_{nem}						P_{nem}					
Temp	0.41	16.9**	43.4	43.4	−0.72**	Temp	0.47	21.8**	49.7	49.7	−0.74**
PROT	0.47	3.4	7.9	51.4	−0.48*	PROT	0.50	2.0	4.3	54.1	−0.41*
H20	0.57	6.1*	11.3	62.7	0.37	H20	0.63	8.4*	13.6	67.6	0.46*
CPE	0.63	3.9	6.4	69.1	−0.14	FDA	0.65	2.0	3.1	70.8	0.37
						LIPIDS	0.65	1.1	1.6	72.4	0.34
CD_{nem}											
Temp	0.48	22.3**	50.4	50.4	−0.74**						
PROT	0.50	1.8	3.9	54.2	−0.40						
H2O	0.63	8.6**	13.7	68.0	0.46*						
FDA	0.65	1.9	2.9	70.9	0.38						
LIPIDS	0.65	1.0	1.6	72.5	0.34						
Comp											
FDA	0.27	8.1**	31.2	31.2							
Temp	0.28	1.1	4.1	35.2							
CPE	0.29	1.2	4.6	39.8							

in 2010 (Table 1). In the DistLM model, temperature explained 43% of variation in nematode biomass. From four environmental characteristics included in the DistLM best fitting model (together explaining 69% of composition variability), two (i.e., Temp and H_2O) were statistically significant ($p < 0.05$; Table 2).

Significant differences in nematode average individual biomass (*$AvIB_{nem}$*) among the studied years were noted at RIDGE and SLOPE stations ($p < 0.001$; Table A3). At RIDGE stations, *$AvIB_{nem}$* was

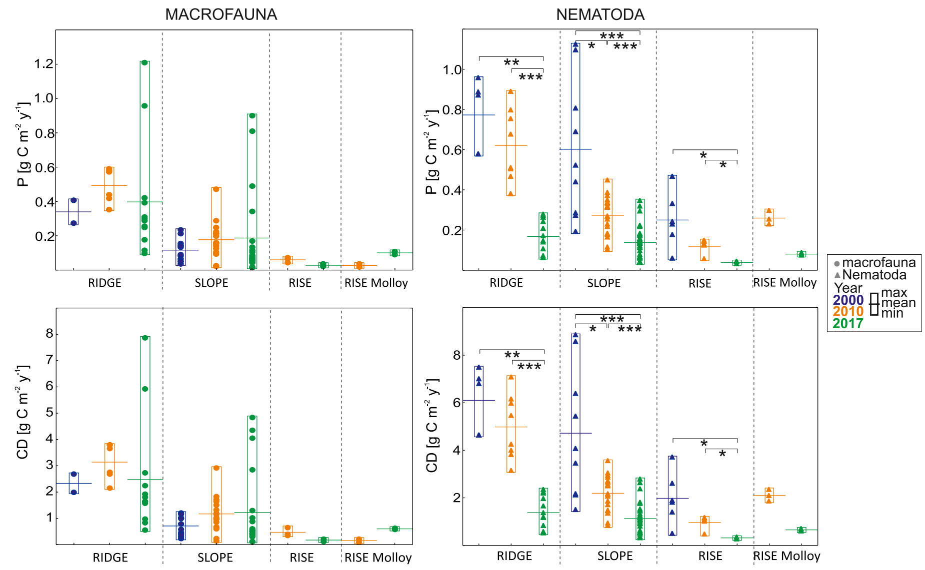

Fig. 3. Secondary production (P [g C m^{-2} y^{-1}]; upper panels) and carbon demand (CD [g C m^{-2} y^{-1}]; lower panels) for macrofauna (left panels) and Nematoda (right panels) in groups of stations localized in the Fram Strait in three sampling years. Significant p-values for Kruskal-Wallis multiple comparison post hoc test (*p < 0.05, **p < 0.001).

significantly higher in 2000 than in 2017 (Table 1). At SLOPE stations, the highest $AvIB_{nem}$ was noted in 2000 and the lowest in 2017 (Table 1).

3.2. Benthic secondary production and carbon demand

Macrofauna secondary production (P_{macro}) did not differ significantly among years in all groups of stations (Fig. 3). At RIDGE stations, mean P_{macro} varied between 0.33 g C m^{-2} y^{-1} in 2000 and 0.49 g C m^{-2} y^{-1} in 2010. At SLOPE stations, mean P_{macro} varied between 0.12 g C m^{-2} y^{-1} in 2000 and 0.18 g C m^{-2} y^{-1} in 2017. At RISE stations, P_{macro} was higher in 2010 than in 2017, while at RISE Molloy station P_{macro} was higher in 2017 (Table 1). DistLM analysis showed that FDA explained over 50% of P_{macro} variation. In the best-fitting model, DistLM included seven variables (together explaining 83% of variation), and three of them (i.e., FDA, CPE, O_2) were statistically significant ($p < 0.05$; Table 2).

Nematoda secondary production (P_{nem}) differed significantly among years in the different groups of stations ($p < 0.05$; Table A3; Fig. 3). At RIDGE stations, significantly lower P_{nem} was noted in 2017 compared to 2000 ($p < 0.001$) and 2010 ($p < 0.001$; Table 1). At SLOPE stations, the lowest P_{nem} was noted in 2017 ($p < 0.001$) and the highest in 2000 ($p < 0.001$; Table 1). At RISE stations, significantly lower P_{nem} was observed in 2017 than in 2000 ($p < 0.001$) and 2010 ($p < 0.001$; Table 1). At the deepest station (Molloy Deep) P_{nem} in 2010 was three times higher (mean 0.26 C m^{-2} y^{-1}) than in 2017 (mean 0.08 g C m^{-2} y^{-1}). In the DistLM model, Temp explained almost 50% of variation in P_{nem}. From five environmental characteristics included in the DistLM best fitting model (together explaining 72% of composition variability), two characteristics (i.e., Temp and H_2O) were statistically significant ($p < 0.05$; Table 2).

Macrofauna carbon demand (CD_{macro}) at RIDGE and SLOPE did not differed significantly among years (Table A2; Fig. 3). Mean CD_{macro} at RIDGE stations varied between 2.33 g C m^{-2} y^{-1} in 2000 and 3.14 g C m^{-2} y^{-1} in 2010. At SLOPE stations, CD_{macro} varied between 1.22 g C m^{-2} y^{-1} in 2017 and 0.71 g C m^{-2} y^{-1} in 2000. At RISE stations, CD_{macro} was higher in 2010 than in 2017, while at RISE Molloy station it was higher in 2017 (Table 1). DistLM procedure showed that FDA was the most important factor which explained 57% of CD_{macro} variability. Among seven variables included in the best fitted model (together explained 86% of variability), three of them (i.e., FDA, Temp, and O_2) were statistically significant ($p < 0.05$; Table 2).

Nematoda carbon demand (CD_{nem}) differed significantly among years in different groups of stations ($p < 0.05$; Table A3; Fig. 3). At RIDGE stations, significantly lower CD_{nem} was noted in 2017 compared to 2000 and 2010 ($p < 0.001$; Table 1). At SLOPE stations, the highest CD_{nem} was observed in 2000 ($p < 0.05$) and the lowest in 2017 ($p < 0.05$; Table 1). At RISE stations, CD_{nem} was lower in 2017 than in 2000 ($p < 0.001$) and 2010 ($p < 0.05$; Table 1). At deepest station CD_{nem} varied between 0.32 g C m^{-2} y^{-1} in 2017 and 2.10 g C m^{-2} y^{-1} in 2010. The DistLM showed that Temp explained 50% of the CD_{nem} variation. The best-fitting model included Temp, PROT, H2O, FDA and LIPIDS, but only two variables were statistically significant (i.e., Temp and H_2O, $p < 0.05$; Table 2).

The CD_{nem}:CD_{macro} ratio in all groups of stations was generally higher than 1. Only at RIDGE in 2017, mean ratio was 0.98 (Fig. A2). At RIDGE stations, CD_{nem}:CD_{macro} in 2017 was significantly lower (0.98) than in other years (2.3 in 2000 and 1.7 in 2010; PERMANOVA, $p < 0.05$; Fig. A2). At SLOPE stations, CD_{nem}:CD_{macro} was significantly higher in 2000 (18.5) than in 2010 and 2017 (2.1 and 1.8, respectively; PERMANOVA, $p < 0.05$). We did not perform PERMNOVA tests for RISE and RISE Molloy stations due to low number of replicates. At RISE and RISE Molloy stations, CD_{nem}: CD_{macro} was higher in 2010 (2.1 and 13.3, respectively) than in 2017 (1.8 and 1.1, respectively).

3.3. Biomass size spectra

The individual biomass in the studied materials spanned 31 size classes (from −15 to 15), ranging from $2.64 \cdot 10^{-5}$ to $4.8 \cdot 10^{4}$ μg (Fig. 4). At RIDGE stations, the range and number of size classes were similar in all years (26-27 size classes). The trough between nematodes and macrofauna was observed between size classes 2 and 3. At RIDGE stations, the peaks of biomass were at similar levels in all three years (Fig. 4). In 2017, biomass in size classes from −7 to −1 were lower than in two other years. At SLOPE stations, the range of size classes was the smaller in 2000 (from −13 to 11) compared to 2010 (from −12 to 15) and 2017 (from −12 to 14). In 2000, biomass in the small size classes (size classes <3) was higher than in other years, but in the bigger size classes, biomass was lower than in 2010 and 2017. In 2000, the trough between nematodes and macrofauna (located in size class 3) was shifted towards higher size classes compared to 2010 and 2017 (trough located in size class 2). At RISE stations, the range and number of size classes were higher in 2010 (28 size classes, from −14 to 13) than in 2017 (22 size classes, from −12 to 9). In meiofauna size classes (<2), biomass was lower in 2017. In macrofauna size classes, biomass was similar in both years, but in 2017, organisms belonging to size classes higher than 9 were not observed. At the deepest stations (Molloy Deep), the range and number of size classes was similar in both sampling years. In 2010, biomass was higher in meiofauna size classes, but in macrofauna size classes higher biomass was observed in 2017. Biomass size spectra at RISE-Molloy station was not continuous; organisms belonging to size class 2 (in 2017 size classes 1 and 2) were not observed.

The DistLM showed that FDA explained 30% of benthic size composition variation, and this characteristic was statistically significant ($p < 0.05$; Table 2). Three environmental characteristics included in the DistLM best fitting model together explaining 40% of benthic size composition variability (Table 2; Fig. A3).

3.4. Normalized biomass size spectra

In all groups of stations there was a statistically significant relationship between normalized biomass and the size classes (linear regression $p < 0.05$; Fig. 5, Table 3). Slopes varied between −0.74 and −0.51 and did not differ statistically among years in groups of stations ($p > 0.05$, Table A4). When slopes did not differ significantly, we tested for differences in the intercepts. There were no statistically significant differences in the intercepts among years in groups of stations ($p > 0.05$, Table A4).

4. Discussion

4.1. Macrofauna biomass and secondary production

Temporal variability of macrobenthic biomass was distinct in different depth zones. At water depths between 900 and 2000 m macrobenthic biomass increased from 2000 to 2010, but then it dropped in 2017. In the same years and at the same stations, Górska et al. (2022) noted an increase of macrofauna abundance from 2000 to 2017. Higher abundance and lower biomass suggest lower individual biomass of macrofauna individuals. In fact, macrofauna average individual biomass was the lowest in 2017. A shift towards smaller body sizes in macrofaunal individuals could have resulted from higher recruitment of juveniles after the second WWA, driven by favorable conditions associated with increased phytodetritus availability for benthic organisms (increased CPE concentration in sediments after WWA; Górska et al., 2022). However, the decrease in average individual biomass of macrofauna in 2017 may also reflect a shift in community composition towards a higher proportion of smaller taxa carried by warm Atlantic waters. This pattern is consistent with observations by Górska et al. (2022), who reported that species composition at RIDGE stations changed significantly after WWAs, and that the size mode in functional

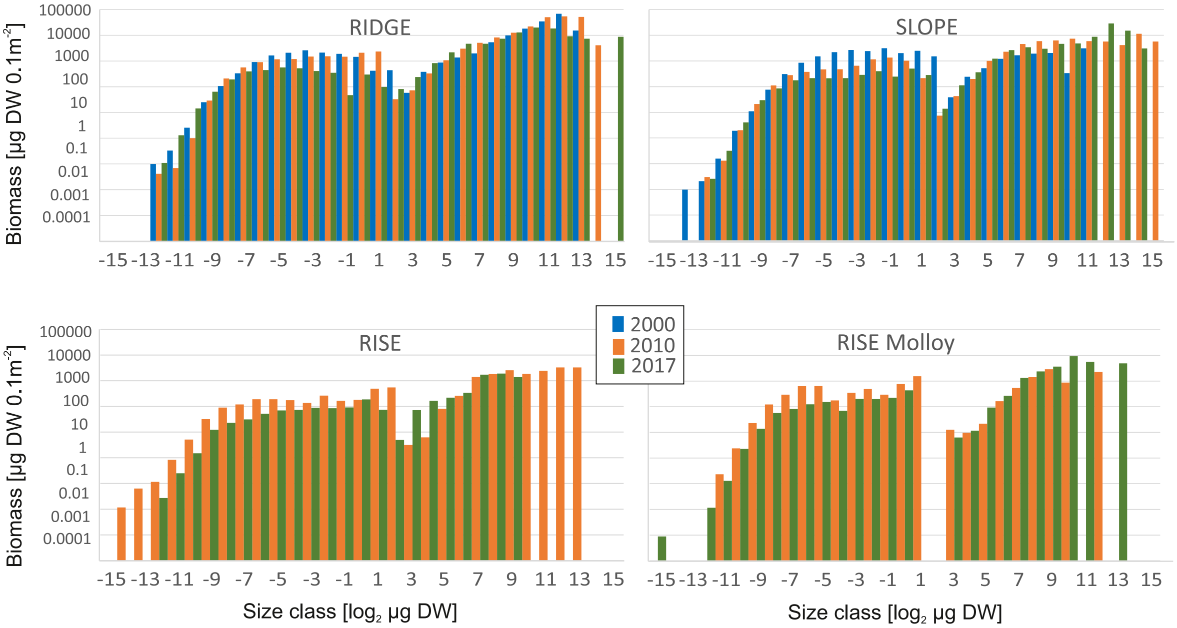

Fig. 4. Benthic biomass size spectra in groups of stations localized in the Fram Strait in three sampling years.

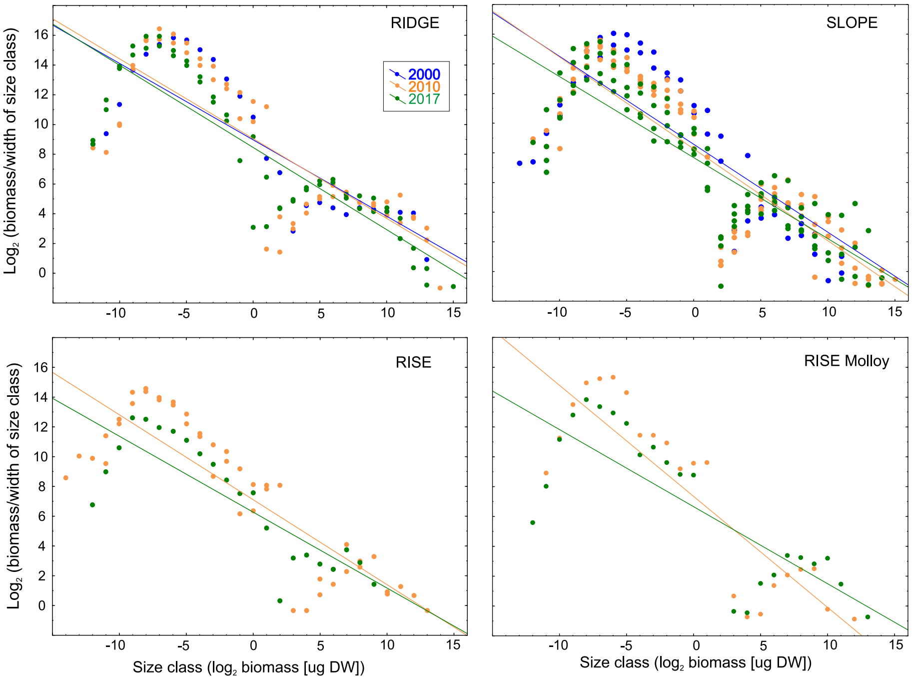

Fig. 5. Normalized biomass size spectra in groups of stations in three sampling years. The lines represent the regression lines.

trait analysis also changed across years at those stations. Large numbers of small individuals (in size classes 4-6) in 2017 was also visible in macrofauna abundance size spectra (Fig. A4). Those size classes in 2017 were dominated by small species (functional trait size modes small and small-medium; Górska et al., 2022), e.g., *Paradoneis sp.*, *Chaetozone jubata* and *Aricidea (Strelzovia) abranchata*.

At SLOPE stations (2000-4000 m), macrobenthic biomass and individual biomass remained at similar levels among studied years. Different response of macrobenthic communities to changing environmental conditions may resulted from different functional traits compositions of species occupying different depth zones. At SLOPE stations higher proportion of sessile filter feeders was observed compared to other studied depth zones (Górska et al., 2022). Suspension feeding organisms could supplement their diet with remineralized and resuspended matter available in the system (Lalande et al., 2016), and thus may be less dependent on changes in food supply from surface waters. The DISTLM model showed that temperature was the third most important factor (after FDA and CPE) affecting macrofauna biomass variability. Similarly to Dannheim et al. (submitted), at SLOPE stations, bottom water temperatures showed less variability among years than at RIDGE stations (Fig. A5), what suggest more stable conditions than at shallower depths and reflected in no significant changes in macrofaunal biomass.

At water depths between 4000 and 5000 m macrobenthic biomass was lower in 2017, compared to 2010. Also average individual biomass of macrofauna dropped substantially in 2017. At those stations in 2010 average individual biomass varied between 387 and 2173 µg, and total

Table 3

Linear regression parameters of the normalized biomass size spectra calculated for group of 'HG' stations for three sampling years. The normalized biomass (NB) was modeled as a function of size class: $NBi = \beta_1 + \beta_2 \times \text{SizeClass}$, where β_1 is the intercept, β_2 is the slope.

Group of stations	Year	Intercept (β_1) ± SE	Slope (β_2) ± SE	Adj. R^2	p
RIDGE	2000	8.97 ± 0.58	−0.51 ± 0.08	0.64	<0.0001
	2010	9.05 ± 0.44	−0.54 ± 0.06	0.63	<0.0001
	2017	8.46 ± 0.34	−0.55 ± 0.04	0.76	<0.0001
SLOPE	2000	8.58 ± 0.51	−0.59 ± 0.07	0.58	<0.0001
	2010	8.27 ± 0.27	−0.62 ± 0.04	0.75	<0.0001
	2017	7.68 ± 0.24	−0.55 ± 0.03	0.73	<0.0001
RISE	2010	7.11 ± 0.38	−0.57 ± 0.05	0.74	<0.0001
	2017	6.27 ± 0.50	−0.51 ± 0.08	0.67	<0.0001
RISE-Molloy	2010	7.35 ± 0.65	−0.74 ± 0.09	0.74	<0.0001
	2017	6.66 ± 0.64	−0.52 ± 0.08	0.62	<0.0001

biomass varied between 0.12 and 0.30 g m^{-2}. Such a huge differences in average individual biomasses are due to occurrence in one subsample two big crustaceans from genus *Lysianassidae,* which are highly motile and may be catch occasionally. Mean individual biomasses in 2010 in two other subsamples were similar to value in 2017.

At the deepest station, located in the Molloy Deep, macrofauna biomass and average individual biomass were higher in 2017 compared to 2010. In 2017, higher CPE (by 6 μg cm^{-3}), O_2 (by 15.1 mol dm^{-3}), and the potential microbial activity (indicated by FDA, higher by 0.35 μg cm^{-3}) was observed compared to 2010. Higher food availability at the bottom of the Molloy Deep together with better oxygenation of sediment-overlying waters created favorable conditions for microbial activity and thereafter may have led to an increase in macrofauna biomass.

The DistLM showed that phytodetritus concentration in sediments (indicated by increased CPE concentrations) together with bacterial activity (indicated by FDA) was the most important factors affecting macrofauna biomass variability. What is more, Dannheim et al. (submitted) showed that total bacterial numbers increased after 2016 in all bathymetric zones. This agrees with the findings of Gontikaki et al. (2011) who combined isotope tracer experiments data with modelling and showed that in subarctic bathyal benthic systems bacteria cover as much as 50% of the total macrofaunal carbon requirements and act as an important link between detritus and macrofauna. They contrasted this finding with those for nematodes that obtained 99% of their energy from refractory organic matter and did not rely on bacterial carbon (<1%). Similarly, Guilini et al. (2010) based on isotope tracer experiment performed at 1280 m in HAUSGARTEN area reported that nematodes do not rely on bacteria as food source to meet their metabolism needs. And accordingly, FDA was not a significant factor for nematode characteristics in DISTLM results. Microbial activity also plays an important role for deep-sea macrobenthic organisms as it increases the lability of the resources to deposit feeders (Lovvorn et al., 2005) in a way that more food can be extracted from the microbially modified particle than from unmodified one (Jumars et al., 1990).

Macrofauna secondary production remained stable in all studied bathymetric zones in three years, besides at the deepest station where secondary production increased in 2017 compared to 2010. At RIDGE stations, macrofauna secondary production in 2017 was higher than in 2000 and similar to values noted in 2010, besides significantly lower biomass at those stations in 2017. Lower biomass resulted from smaller sizes of individuals and due to inverse relationship between secondary production and biomass, smaller organisms had higher secondary production rates than bigger ones. Individual biomass of an organism has the strongest effect on estimation secondary production in Brey (2012) model, but the second strongest predictor is bottom water temperature. The higher temperature the higher P/B value. However, the relationship is positive but not strictly linear as artificial neural network is not a simple equation (Brey, 2012). At RIDGE stations increase of temperature from 2000 to 2017 was noted (Fig. A5). That may be why, despite of decreasing biomass in 2017, secondary production remained at similar level as in 2010.

4.2. Nematodes biomass and secondary production

Contrary to macrofauna, nematodes biomass and secondary production decreased from 2000 to 2017 in all bathymetric zones. One of possible mechanisms responsible for the decline of nematodes might be related to higher numbers of small macrofauna individuals (visible on macrofauna abundance size spectra; Fig. A4) that could increase competition between nematodes and macrofauna. Other factors that could have influenced nematode biomass and secondary production could be increasing bottom water temperature and decreasing sediment water content.

The increasing abundance of small macrofauna may intensify interactions between macrofauna and meiofauna. These interactions may include direct competition for food resources in sediments (Woodin and Jackson, 1979), increased predator pressure on meiofauna (Wołowicz et al., 2011), and indirect effects related to macrofauna bioturbation, which can reduce the available sediment volume for meiofauna (Nascimento, 2010).

Competition for organic matter may be particularly intense in environments where food arrives in pulses, such as during phytoplankton bloom deposition (Flach et al., 1999). In such situations, macrofaunal organisms may have a competitive advantage in accessing freshly settled phytodetritus due to higher food processing rates and faster responses to discrete food pulses (Nascimento et al., 2011). Stable isotope tracer experiments conducted in situ at the Porcupine Abyssal Plain showed that macrofauna incorporated phytodetritus within days, whereas nematode responses occurred weeks later (Witte et al., 2003), suggesting that macrofauna initially dominate the processing of fresh particulate organic matter. Similar patterns were reported from the Faroe–Shetland Channel (at 1080 m), where macrofauna responded more rapidly than nematodes to experimental phytodetritus additions (Gontikaki et al., 2011). These studies also indicate a degree of trophic differentiation between the two size groups. Linear inverse modelling applied to tracer experiments showed that macrofauna relied more strongly on labile detritus, whereas nematodes consumed primarily refractory detrital material (Gontikaki et al., 2011). Likewise, distinct stable isotope signatures reported by Nomaki et al. (2025) suggest that meiofauna often depend on more refractory carbon sources or bulk sediment organic matter. Thus, although macrofauna and meiofauna may exploit different fractions of sedimentary organic matter, rapid macrofaunal utilization of freshly deposited phytodetritus may reduce the availability of high-quality resources for meiofauna and indirectly intensify competitive interactions.

Additionally, Nascimento et al. (2011) reported negative correlations between meiofauna abundance and macrofaunal biodiversity. In the HAUSGARTEN area, an increase in macrofaunal species richness and Shannon–Wiener diversity index between 2000 and 2017 was documented by Górska et al. (2022), which may further enhance competitive or trophic interactions between these two benthic size groups.

DistLM showed that temperature and sediment water content were the most important factors shaping nematodes variability. Along the bathymetric transect bottom water temperature was higher in 2017 than in 2000 (maximum difference at RIDGE 0.31 °C and minimum difference at RISE MOLLOY 0.02 °C; Fig. A5). Meiofauna physiological performance and distribution depend on the maximum temperature experienced in their habitat (Giere, 2009). The increase of bottom water temperature may have negative effects not only on nematode abundance but also on species fitness and species interactions (Vafeiadou and Moens, 2021). Changes in the fitness of individual nematode species in response to elevated temperature could affect interactions between competing species and decrease nematode competiveness (De Meester et al., 2015; Vafeiadou et al., 2018; Vafeiadou and Moens, 2021). In presented study, nematodes biomass decreased in time with increasing bottom water temperature between 2000 and 2017. Sediment water content, which was the second significant factor in the DISTLM model, significantly influenced nematode spatial variability rather than temporal variability. Sediment water content did not significantly changed among years, but it changed along the bathymetric transect (Górska et al., 2022). Sediment water content decreased with increasing water depth from 65% at 1000 m to 37% at 4000 m, and it increase to 62% at 5560 m (Molloy Deep). The same pattern was observed for nematodes biomass which decreased with increasing water depth to 4000 m and it increased in Molloy Deep. High sediment water content supports high density of meiofauna as interstitial water transports e.g., nutrients, organic matter, microorganisms. Higher water content means greater movement of these resources (Giere, 2009).

Changes in physical environment (increasing bottom water temperature) together with increased competition with macrofauna led to decrease of nematodes biomass and secondary production in the studied years.

4.3. Benthic carbon demand

The valuation of the pelago-benthic coupling in the deep sea is very difficult due to problems with estimates of carbon flux to the benthos and estimates of benthic carbon demand. Studies on relative contributions of different size groups to deep-sea benthic metabolism are scarce. At the deep seafloor prokaryotes are responsible for over 93% of benthic respiration (van Oevelen et al., 2011). The higher water depth, the higher contribution of meiofauna to benthic eukaryotes carbon demand rising up to over 90% in the abyssal sites (Górska et al., 2020). In this study, the contribution of nematodes to the metazoan carbon demand decreased between 2000 and 2017. This decrease was higher at the deepest stations (from 93% in 2010 to 52% in 2017) compared to the RIDGE stations (from 70% in 2000 to 49% in 2017). The changing contributions to benthic carbon demand are due to decrease of nematodes carbon demand (macrofauna carbon demand in studied years remained at similar level).

At the central HAUSGARTEN station (2500 m) metazoan carbon demand varied between 6.5 g C m^{-2} y^{-1} in 2000, 3.1 g C m^{-2} y^{-1} in 2010, and 1.1 g C m^{-2} y^{-1} in 2017. However, in this study, estimations of meiofauna carbon demand was based on nematodes exclusively. Based on the entire dataset (including all other meiofauna taxa) we estimated that nematodes constituted about 77% in 2010 (Górska et al., 2020) and 78% in 2017 (Górska et al., in prep) of total meiofauna carbon demand. That is why our calculations probably are underestimated. However, percentage contribution of nematodes to total meiofauna were similar in studied years, so the temporal trend of decreasing carbon demand remain valid. The estimated mean POC flux (based on data from sediment traps at 2300 m) for studied period at this station was 2.7 g m^{-2} y^{-1} (Salter et al., 2023). Comparing those values, we must therefore recognize that in 2000 estimated POC flux supplied less than 42% of metazoan carbon demand (meiofauna and macrofauna). In contrast, in 2017, the POC flux is higher than the estimated metazoan carbon demand. However, if we look at these numbers, we did not consider prokaryotes and megafauna, which have substantial contribution into benthic carbon demand. To precise estimate the total benthic carbon demand and its temporal variability, studies which consider all benthic components (from bacteria to megafauna) are needed.

The mismatch between the estimated POC flux and benthic carbon demand suggested that there are other sources of carbon for deep-sea benthos. The main process for supplying particulate matter to deep waters in the eastern Fram Strait is lateral advection from the Svalbard shelf (Lalande et al., 2016). Another important source of organic matter for the benthic organisms could be remineralized and resuspended material (Lalande et al., 2016). Wiedmann et al. (2020) suggested that meaningful sources of carbon for deep-sea benthos could be also massive sedimentation events of microalgal aggregates and zooplankton carcasses, food falls of large crustaceans, fishes, and top predators. What is more, appendicularians, which are rarely taking into account in carbon cycling models, can considerably contribute to the carbon flux as they produce fast sinking fecal pellets and their houses contribute to the formation of marine snow (Wiedmann et al., 2020 and literature therein).

4.4. Benthic biomass size spectra

Responses of benthic biomass size spectra to the environmental changes varied among bathymetric zones. At RIDGE stations, benthic biomass size spectra changed little among years, only in meiofaunal size classes (from −7 to −1) biomass decreased in 2017. At SLOPE stations, a decrease of biomass in bigger meiofauna size classes (from −5 to 0) and an increase of biomass in macrofauna size classes (from 7 to 15 size class) was observed following the first and the second WWA. Moreover, in 2000 organisms belonging to the biggest size classes (>11) were not observed at all. Narrower size spectra in macrofauna size classes in 2000 was probably the effect of lower food availability than in following years. In low food conditions there is not enough energy to support a full range of macrofauna sizes (Górska et al., 2020). Organisms with different sizes can compete for the same food sources and in low food condition can competitively exclude the groups that are less efficient in food/energy acquisition (Campanyà-Llovet et al., 2017). A shift to lower macrofauna size classes as a response to decreasing food availability were also reported in shallow Arctic waters (Górska and Włodarska-Kowalczuk, 2017). Besides the observed shifts in biomass size classes, also the trough between nematodes and macrofauna shifted from 3 size class in 2000 to 2 size class in following years. There were less nematodes belonging to the biggest meiofauna size classes in years after WWAs and, in fact, peak of maximum abundance in Nematoda abundance size spectra (Fig. A6) after WWAs was strongly shifted towards smaller size classes.

At RISE stations, we observed a much wider range of size classes in 2010 than in 2017. In 2017, there were lack of organisms bigger than 9 size class and in the same time, in 3-6 size classes biomass were higher. It seems that in 2017 at RISE stations there was a decrease of bigger macrofauna individuals and an increase of small individual, which was also visible in the macrofauna abundance size spectra (Fig. A4). However, in 2010 the largest size classes (12–13) contained only a single individual each, which likely occurred sporadically. Therefore, the apparent decrease in larger macrofaunal individuals should be interpreted with caution. Also, bigger nematodes decreased in 2017 compared to 2010 (visible also in Nematoda abundance size spectra; Fig. A6). In this extremely food-limited, abyssal environment bigger nematodes seems to be more sensitive to ongoing changes as they are representing k-strategy (low growing rates and low metabolism).

At RISE MOLLOY station, the biomass size spectra were not continuous because we did not consider ‘other’ meiofauna taxa in those analyses. It seems that other taxa become more important in terms of biomass in deeper areas than in shallower waters. In −2 to 0 size classes ‘other’ taxa can constitute up to 35% of total meiofauna biomass, while in size classes from 1 to 3, other taxa can constitute even 100% of meiofauna biomass (Górska et al., in prep). That is why, to investigate temporal variability in the biomass size spectra at abyssal depths it is necessary to analyze the whole meiofauna assemblage, not only nematodes.

We did not observe significant changes in Normalized Biomass Size Spectra (NBSS) among years. In the studies on pelagic systems, slopes of NBSS are regarded as indicators of energy utilization within community (Sprules and Munawar, 1986). However, Blanchard et al. (2009) suggested that the slope of NBSS in benthic studies indicate the distribution of the biomass among the differently sized consumers sharing the same pool of food sources. In a previous study, Górska et al. (2020) observed that slope values did not change across bathymetric zones (from shelf to abyssal depths) in the Fram Strait despite a significant decrease of food availability with increasing water depth. Similarly, Mazurkiewicz et al. (2020) observed that organic matter content in sediments from three Spitsbergen fjords and three Norwegian fjords did not influence the NBSS slope. While, in response to physical disturbance (Górska et al., 2020), decreasing oxygen availability (Quiroga et al., 2005) or severe changes in salinity (Dolbeth et al., 2007), a significant steepening of NBSS slope was observed. The stability of NBSS slopes over the studied years in this study, and among bathymetric and latitudinal zones in previous works, suggests that the NBSS slope may be a sensitive parameter to disturbances but rather to coarse for changes in food availability.

The intercept of the NBSS is treated as an indicator of the total biomass in a benthic community (e.g., Quiroga et al., 2005) or the availability of food reserved in an ecosystem (Guiet et al., 2016). In our study, the intercept decreased with increasing water depth, but it changed only little among years, suggesting little change of total benthic biomass in system among years, besides some shifts in dominant size classes. It seems that small macrofauna individuals fill the niche occupied previously by bigger nematodes. However, to verify this hypothesis a detailed analysis of nematodes collected in 2000 (in terms of functional traits) would be needed.

Results of the present study, conducted in the HAUSGARTEN area (Fram Strait), revealed that: (1) macrofaunal responses to changing environmental conditions varied among depth zones. At 1000–2000 m, macrofaunal biomass and mean individual biomass decreased after the second WWA (in 2017); at depths between 2000 and 5000 m they remained at a similar level, whereas at the deepest station (5561 m) they increased. (2) Nematode biomass and secondary production decreased from 2000 to 2017 across all depth zones. (3) The variability of benthic biomass size spectra differed among depth zones. Based on these findings we need to reject of the hypothesis that increased rates of organic matter sedimentation observed during the WWAs resulted in higher macrofaunal and nematodes biomass, secondary production, and carbon demand across the bathymetric range in the eastern Fram Strait. Three factors could have potentially constrained our findings. First, we did not analyze the whole meiofauna assemblage, but we focused only on nematodes. This was dictated by lack of complete meiofauna data from 2000. However, in many meiofauna studies authors focused exclusively on nematodes as they constitute dominant component of meiofauna assemblages (usually over 90% of all individuals; Giere, 2009). Second, our study might be hampered by the limited data of environmental parameters, which were not available for all stations analyzed in this study. Finally, the size-based approach used here describes community structure independently of taxonomic identity and therefore cannot resolve potential species-level shifts that may underlie the observed biomass-size patterns. Future studies integrating taxonomic, functional, and environmental information would help to better understand the mechanisms underlying these patterns. All these possible constrains should be taken into account when future investigations into this subject are planned.

CRediT authorship contribution statement

Barbara Górska: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Thomas Soltwedel:** Writing – review & editing, Writing – original draft, Resources. **Maria Włodarska-Kowalczuk:** Writing – review & editing, Writing – original draft, Resources, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2026.104693.

Data availability

Data will be made available on request.

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