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Chronic bottom trawling impacts on different size fractions of benthic communities and sediment properties: A case study from the Kattegat (North Sea)

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ABSTRACT

Bottom trawling is one of the most destructive fishing methods currently in use, with acute impacts on benthic ecosystems and chronic impacts on macrofauna communities. However, the long-term effects of chronic bottom trawling on smaller components of benthic communities and on sediment biogeochemistry are less well understood. To address this knowledge gap, we examined the effects of bottom trawling and environmental variables (bottom water and sediment properties) on alpha diversity and community structure of prokaryotes, meiofauna (including metazoans and foraminifera), and macrofauna over a spatial gradient of commercial bottom trawling, including a marine protected area which has been unfished for 12 years after >100 years of chronic trawling. Our results showed that chronic trawling affected the four organism groups in different ways. Prokaryote and foraminifera diversities were slightly higher at sites with higher trawling intensities, due to a greater number of rare species. Community composition was affected by trawling in all groups except meiofaunal metazoans. Sedimentary carbon played a significant role in shaping all four communities, as well as carbon degradation rates, but was not itself affected by trawling. Our results highlight that the complex interactions between environmental variables and disturbances from bottom trawling affect different components of the benthic fauna in different ways. Differences in organism size, population turnover rates, metabolic and ecological plasticity, feeding traits, and sensitivity to physical disturbance probably explain these differences.

1. Introduction

Bottom trawling (such as beam trawling, otter trawling and dredging) is a fishing method where the gear has contact with the seabed and is one of the most productive and least sustainable fishing practices currently in use (Eigaard et al., 2017). In particular, bottom trawling accounts for 26% of global marine fisheries catches (Hilborn et al., 2023) and has impacted nearly all European seas, resulting in 28 to 85% of the shallow (0–200 m) European sea areas being annually trawled with a mean trawling intensity ranging from 0.5 to 8.5 times a year (Eigaard et al., 2017). Therefore, a better understanding and predictions of trawling impacts are essential for understanding environmental impacts on all marine ecosystem components and providing knowledge to help implement sustainable marine management.

Bottom trawling involves dragging a weighted net or rigid structure across the seafloor, thereby resulting in displacement and resuspension of several tons of sediment per km (Durrieu de Madron et al., 2005; Linders et al., 2018; Bradshaw et al., 2021). Trawling effects are well documented for larger (> 1 mm) components of the invertebrate benthos. Bottom trawling can cause a decline in biomass, biodiversity

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and production of benthic communities (Queirós et al., 2006). For example, on average, a single gear pass can lead to a 26% decrease in abundance and 19% decrease in species richness of benthic invertebrates (Sciberras et al., 2018). The percentage of removed macrofaunal biomass depends on the type of trawling gear used, particularly how deeply it penetrates the seabed, and can range from 6 to 41% per trawl pass (Hiddink et al., 2017). The traits of different macrofaunal species, such as fragility, mobility, size, life span, feeding mode, position in the sediment and recovery ability, determine their sensitivity to trawling disturbance (Hiddink et al., 2017; Sciberras et al., 2018; Beauchard et al., 2023) and relative impacts on different species lead to indirect effects through altered species interactions. Furthermore, trawling has been shown to have top-down effects on benthic communities. For example, trawling reduced populations of predatory fish that feed on brittle stars, resulting in increased brittle star abundance and subsequent decreased macrofauna diversity and promotion of species resistant to trawling disturbances (Sköld et al., 2018; Sköld et al., 2025). Overall, soft-bottom macrofauna suffer substantial mortality and prolonged recovery times, spanning years, due to the severe impacts of bottom trawling (Kaiser et al., 2006; Hiddink et al., 2017). Altered macrofaunal communities have the potential to impact sediment biogeochemistry, in particular through changes in bioturbation and bioirrigation activity (Beauchard et al., 2023).

Less well understood are trawling effects on meiofauna (invertebrates <1 mm in size, including foraminifera), the most abundant and diverse yet microscopic component of benthic communities. This is a significant knowledge gap given that meiofauna have been shown to mediate sediment biogeochemistry and ecosystem processes and have been considered as ecosystem engineers, especially in the absence of macrofauna (Schratzberger and Ingels, 2018; Bonaglia and Nascimento, 2023). Due to their relatively small size, meiofauna can be displaced or suspended and redeposited when exposed to contact with trawling gear rather than being killed or damaged like many macrofauna species (Giere and Schratzberger, 2023). Despite this, sediment suspension, displacement and modification are likely to affect meiofauna, at least in the short term. Contrasting effects have been reported for meiofauna, showing an increase, decrease, or no significant change in abundances in fishing grounds (Schratzberger and Somerfield, 2020; Bradshaw et al., 2024). These different results probably depend partly on the timescales of the studies, especially the time since disturbance. In addition, meiofauna may be affected by alterations to physical and chemical sediment structure. Together with removal of bioturbating macrofauna, this can lead to altered release of nutrients and metals from the sediment into the water column (Olsgard et al., 2008; Bradshaw et al., 2021). Overall, bottom trawling impacts on both biogeochemical processes and meiofauna may significantly vary from one area to another, due to differences in sediment type, redox conditions, trawling intensity, etc. (Epstein et al., 2022; Giere and Schratzberger, 2023).

The knowledge gap regarding the effects of bottom trawling extends beyond meiofauna to include even smaller microorganisms, such as prokaryotes. These prokaryotic communities are shaped by a multitude of factors, including both natural environmental factors and anthropogenic disturbances and, apart from some field and laboratory studies on bacterial abundance and activity (Polymenakou et al., 2005b; Pusceddu et al., 2005), the effects of bottom trawling on prokaryotes have only rarely been assessed. The existing literature indicates that environmental factors, such as sediment properties, temperature, organic matter and shear bed stress are more effective in shaping microbial communities than trawling (e.g. Bonthond et al., 2023; Bradshaw et al., 2024) and also demonstrate that bottom trawling may induce prokaryotic diversity loss, and a shift of the community towards more aerobic heterotrophic metabolism. Furthermore, both changes in diversity and activity (e.g., denitrification) of microorganisms, ultimately altering biogeochemical cycling, have been ascribed to bottom trawling (Polymenakou et al., 2005a; Ramalho et al., 2020).

The Kattegat is located in the northern part of Europe between the Danish Jutland peninsula and the western coast of Sweden and is one of Europe's most intensively fished areas (Eigaard et al., 2017). Fishing activities in the Kattegat have been documented since the early 1900s (Bartolino et al., 2012), leading to varying trawling intensities over time and across different areas. In 2009, a 653 km^2 no-take zone was established in the south-eastern Kattegat to protect the collapsed cod stock (Sköld et al., 2018; Sköld et al., 2022). The combination of a strong gradient in trawling intensities and the creation of this no-take zone creates a unique large-scale field experimental setup to study the chronic effects of bottom trawling on marine benthic ecosystems. Previous studies in the area have primarily focused on trawling effects on macrofauna (Sköld et al., 2018; Sköld et al., 2025), but in this study we report for the first time on trawling effects on different size fractions of the benthic community.

The aim of this study was to investigate the potential effects of bottom trawling on organisms in sediments (macrofauna, meiofauna, and prokaryotes). Sediments were investigated along a gradient of different trawling intensities, including a no-take zone that had not been trawled for the last 12 years. Furthermore, the study examined the relative importance of trawling and environmental variables for each organism group in order to understand the complex relationships between natural variation and anthropogenic disturbance.

2. Methods

2.1. Study area and sampling strategy

The Kattegat is characterized by an estuarine circulation pattern with saline bottom water inflows from the North Sea and brackish surface water outflows from the Baltic Sea. Since there is a strong vertical stratification, with a halocline at 15–20 m, bottom water conditions are fairly stable (Andersson and Rydberg, 1988) although there is some seasonal variation in oxygenation (Granéli, 1992).

Historically, the Kattegat has been an important fishing area for cod and other demersal fish species. However, after a significant decline in cod populations, trawl fisheries now primarily target Norway lobster, *Nephrops norvegicus,* and demersal fish using otter trawling in a mixed fishery (Hornborg et al., 2016). A marine protected area in the southeast Kattegat was established in 2009 to protect spawning grounds for cod (Sköld et al., 2018) and had therefore been closed to all fishing activities for 12 years at the time of this study.

Benthic sampling was conducted at 26 stations between 25th and 29th October 2021, on board R/V Svea. In the Kattegat, 95% of all bottom trawling occurs below 22 m water depth, i.e. on muddy sediment below the halocline (Pommer et al., 2016). We selected 26 sampling stations from an existing monitoring programme (Sköld et al., 2018) along a gradient of trawling intensities but within a narrow depth range (41 ± 7 m) in order to minimise potential depth-related effects.

2.2. Calculating bottom trawling intensity

Trawling intensity was defined using a yearly swept area ratio (SAR) which, for a given area of seabed, is the ratio between the total area contacted by trawling gear during one year divided by the seabed area (Eigaard et al., 2015; Eigaard et al., 2017). Thus, a SAR of 1 y^{-1} means that the entire area was disturbed once during the year, though this may not have been evenly distributed across the area. We used high resolution SAR data available for the period 2012–2014 (Sköld et al., 2018). This pattern was verified against spatial patterns at coarser resolution in more recent years (ICES, 2022) indicating that trawling intensity and spatial distribution have remained similar between 2012 and 2014 and at the time of this study (2021). Accordingly, trawling intensity was calculated from the summed area trawled over 32 months within a 250 m radius around each sampling station, standardised to yearly SAR, and includes data from both the Danish and Swedish fishing fleets (see Sköld et al. (2018) for details). A SAR value of zero was assigned for stations within the MPA. For some of our data analyses we defined three trawling intensity groups, based on the lower, middle two and upper quartiles of the data distribution (see Sköld et al., 2018): SAR <0.4 yr^{-1} (in practice, this is the MPA sites, i.e., no trawling), low intensity (SAR 0.4–4.6 yr^{-1}), and high intensity (SAR > 4.6 yr^{-1}).

2.3. Bottom water variables in the study area

Bottom water salinity, oxygen concentration, temperature, and current speed were obtained from the Copernicus Marine Environment Monitoring Service (https://marine.copernicus.eu/); salinity, temperature and currents were extracted from the model Nemo (Nucleus for European Modelling of the Ocean, https://nemo-ocean.eu) and oxygen from the model ERGOM (Ecological Regional Ocean Model, https://ergom.net/). In the model, current velocities are given as N and E vectors; we converted these to current velocity ($m\ s^{-1}$) independent of direction. The model resolution is 1 × 1 nautical miles (i.e., 1.85 × 1.85 km) with 56 different depth levels. We selected the grid cell that was closest to each of our sampling stations and had as similar depth as possible. If several grid cells met these criteria median values were taken. For each variable, we extracted monthly values for the period 2014–2021 and from these calculated the minimum, maximum, 5th, 50th and 95th percentiles and the coefficient of variation and range (Table S1). Since medians, percentiles and variation are often highly correlated for each environmental variable, we used expert judgement to choose which one to use in the data analyses. For example, we considered minimum oxygen concentrations to be more important for benthic communities than median oxygen concentrations. Different organisms react on different timescales according to their life-history traits, as well as the timing and frequency of environmental changes. High resolution time series of communities and environmental variables would be needed to tease apart this range of responses, and these do not exist. We therefore used these longer-term averages as explanatory variables in order to focus on how general environmental conditions, in combination with chronic trawling pressure, might have shaped the benthic communities seen in the study area in 2021.

2.4. Sediment properties and carbon degradation rates

At each of the 26 stations, one Gemini core (50 cm^2) was sliced at 1 cm intervals from the top to the base. Each slice was stored in a ziplock bag and frozen at −18 °C for later analysis of sediment properties such as porosity, dry bulk density, total organic matter content (loss on ignition, LOI) and chlorophyll concentration. At each station, a second Gemini core was sliced at 1 cm intervals down to 5 cm depth and frozen at −18 °C for later analysis of sedimentary carbon biochemistry.

Porosity (water %, by volume) and organic matter (%, by weight) were calculated based on change of sediment weight after drying and combustion, respectively. This was done by taking a 5 cm^3 subsample using a cut-off syringe and initially weighed in its wet state. It was then dried at 60 °C for ~24 h and weighed again to determine dry weight; water lost was converted to volume to calculate porosity. Finally, the sample was combusted at 400 °C for 4 h to remove organic matter and was weighed once more; loss on ignition (LOI) was used to calculate % OM. Grain size distributions, analysed using a Malvern Mastersizer 3000, were only determined at eleven of the stations and could not therefore be used in the data analyses. However, for those stations, median grain size had a strong negative correlation with % OM ($R^2 = 0.8$) and porosity ($R^2 = 0.9$), so is thus implicitly included in the analyses by including those two sedimentary variables.

For chlorophyll measurements, an additional three subsamples of 1 mL were taken per sediment slice. The subsamples were extracted overnight in the dark in a fridge using 9 mL of 96% Ethanol. Following the extraction period, the samples were thoroughly shaken and then centrifuged at 4000 rpm for 5 min. After centrifugation, 4 mL of supernatant was filtered through a GF/F filter into a cuvette and chlorophyll was quantified using a Shimadzu spectrophotometer at 663 nm and 750 nm and final concentrations calculated as $\mu g/cm^3$, averaged for the three subsamples (Helcom, 1988).

In order to determine quality of organic matter, sediment protein (PRT) and carbohydrate (CHO) were analysed spectrophotometrically according to Danovaro (2009) and their concentrations (mg gdw sediment^{-1}) were calculated using standard solutions of bovine albumin and D+ glucose, respectively.

Carbon degradation rates were calculated from extracellular enzyme activities. Extracellular aminopeptidase and β-glucosidase activities, here used as proxies of protein and carbohydrate degradation rates, respectively, were estimated by the cleavage of fluorogenic substrates (L-leucine-4-methylcoumarinyl-7-amide and 4-MUF-D-glucopyranoside, respectively; all from Merck) at saturating concentrations (Danovaro, 2009). Aminopeptidase and β-glucosidase activities (μmol of substrate $g^{-1}\ h^{-1}$) were converted into C equivalents using 72 as a conversion factor, and their sum reported as the C degradation rate (μgC $g^{-1}\ h^{-1}$) (Pusceddu et al., 2014). In the data analyses, the average of the top 2 cm (0–1 cm and 1–2 cm) of each sediment variable was used, since this is the depth at which most faunal activity occurs. Due to human error, no PRT, CHO or C degradation rates are available for site N10.

2.5. Macrofauna sampling

One Smith-McIntyre grab (0.1 m^2 surface area) was taken at each station. All macrofauna were sieved out of each sample on a 1 mm mesh sieve, preserved in 95% ethanol diluted with 10% glycerol and later identified to the lowest possible taxonomic level. For each taxon, the number of individuals and wet weight were recorded. These data, together with information on taxon traits (own database (Nyström Sandman et al., 2024)), were also used to calculate two indices for each sample. Community bioturbation potential (BP_c), was calculated using the method of Queirós et al. (2013), slightly modified by using fuzzy coding to weight the trait modality scores to account for plasticity or certainty of a given trait. Thus, taxa were assigned one or multiple trait modalities based on their affinity to these, according to a 0–3 scoring system, where 0 means no affinity and 3 is a high affinity to a modality (Chevenet et al., 1994). The Benthic Quality Index (BQI) was calculated according to Leonardsson et al. (2009); it is a metric that reflects structural changes in communities due to disturbance (Josefson et al., 2009), including bottom trawling (Sköld et al., 2018; McLaverty et al., 2023). The indices BP_c and BQI were then used as explanatory variables in some of the data analyses.

2.6. DNA extraction and sequencing

To estimate the diversity of meiofaunal metazoan and bacterial communities at each of the 26 stations, we subsampled a few grams from the top slice (0–1 cm) of the sediment core that was initially frozen for sediment properties analysis. Some macrofaunal sequences can also be detected in 18S rRNA metabarcoding data, but due to the small sediment sample size, the method mainly reflects meiofaunal communities and does not accurately represent macrofaunal diversity (Mazurkiewicz et al., 2024). We refer to these data as meiofaunal metazoan communities in this paper. All samples were homogenised and a total of 250 mg of sediment was used for the extraction using DNeasy PowerSoil Pro Kit following manufacturer's guidelines. The concentration of extracted DNA was measured using a Qubit 2.0 fluorometer, while the quality was measured using a NanoDrop 2000 spectrophotometer. DNA concentrations were then standardised for the samples designated for 16S rRNA gene amplicon sequencing and sent to Science for Life Laboratory (SciLifeLab; Stockholm, Sweden) for library preparation and sequencing. For the 18S rRNA gene amplicon sequencing, the target region was amplified using forward CCAGCASCYGCGGTAATTCC and reverse ACTTTCGTTCTTGATYRA primers (Stoeck et al., 2010). The resulting concentrations of amplicons were standardised and sent to the same laboratory for sequencing.

SciLifeLab prepared the 16S rRNA library according to their standard methods and it was sequenced together with 18S rRNA library on the same run on the Illumina MiSeq (2 × 301 bp) setup using the "Version3" chemistry. The resulting fastQ files were delivered after internal quality checks and further processed (see Bioinformatics).

2.7. Bioinformatics

The raw 16S rRNA gene amplicon sequencing data were run through the standardised nf-core-pipeline for amplicon sequencing "ampliseq" (v2.8.0) within Nextflow (v.23.10.1) using the default settings (Straub et al., 2020). In summary, cutadapt (v. 3.4, (Martin, 2011)) trimmed primers and untrimmed sequences were discarded which resulted in less than 1.6% of sequences per sample being discarded and 98.7% being kept. The sequences were then forwarded into the incorporated DADA2 (v. 1.28.0) pipeline where the forward sequences were trimmed at 269 bp, and the reverse were trimmed at 209 bp. Sequences were then denoised, quality controlled (correct errors) and amplicon sequence variants (ASVs) were generated (Table S1). A total of 53,069 ASVs were obtained (average 75% reads and 111,263 counts per sample). At the last step, the taxonomic classification was done using the SBDI-GTDB (sativa curated 16S GTDB, Release R07-RS207–1) database (FigShare. doi:10.17044/scilifelab.14869077.v3); Eddy, 2011; Callahan et al., 2016; Kozlov et al., 2016; Parks et al., 2018).

A similar approach was used for the 18S rRNA amplicon sequencing data. Differences between the 16S rRNA and 18S rRNA standardised ampliseq pipeline were in the selection of the database for the taxonomic annotation (SILVA v132 (Quast et al., 2012)) of the sequences as well the version of the pipeline (Nextflow v24.04.2, ampliseq v2.9.0). In summary, less than 7.2% of sequences were discarded after primer trimming and an average of 97.4% sequences per sample were kept. 14,511 ASVs were obtained across all samples with an average of 85.9% per sample (average of 173,653 counts per sample) (Table S1). Only ASVs classified as typical metazoan meiofauna at phylum level were kept in the data set and classified to order level for further interpretation (749 unique ASVs in total). That said, with this filtering option, a limited number of macrofauna taxa will also have been included in the final ASV list. However, we refer to this dataset as 'meiofauna' in the paper.

Taxonomic assignments were conservatively limited to the order level because, under our strict sequence quality filtering and classifier confidence thresholds, many prokaryotic and meiofaunal ASVs could not be reliably classified at family or genus level. Attempting finer resolution substantially increased ambiguous or conflicting assignments; order was the lowest taxonomic rank that was robust across samples.

The downstream analysis of all data was conducted using R (v. 4.4.0) in Rstudio (v 2024.04.0) (R Studio Team, 2020). Rarefaction curves were constructed using the 'vegan' (v.2.6–6.1) package (Oksanen, 2010) and showed that most diversity was covered in the samples of the 16S and 18S rRNA gene amplicon sequencing (Fig. S1).

2.8. Benthic foraminifera counting and identification

The top 0–3 cm sediment layer was subsampled and prepared for benthic foraminifera. In total, 17 samples (12 trawled and 5 within MPA) were stained with rose Bengal-ethanol solution to distinguish individuals living at the time of sampling (Schönfeld et al., 2012) and sieved over 1 mm and 63 μm sieves. The sieve residues were transferred respectively to filter paper and dried overnight in an oven at 50 °C. The fraction greater than 63 μm was split into manageable aliquots, from which at least 300 living (stained) benthic foraminifera were picked and identified to the species level whenever possible, using previous foraminifera studies in the region (Höglund, 1947; Feyling-Hanssen, 1964; Qvale and Nigam, 1985; Nordberg et al., 2017; Polovodova Asteman et al., 2021; Cage et al., 2021). Absolute abundances for each species were calculated as individuals per 10 mL of sediment.

2.9. Statistics

Two overall approaches were used: a gradient design, where the effect of fishing intensity (SAR) as a continuous explanatory variable was used to explain trends in continuous variables of (e.g.) species diversity or sediment properties using linear modelling; and an ANOVA-type design (PERMANOVA), where sampling stations were grouped into three categories according to fishing intensity. In both cases, environmental variables were also included as explanatory variables.

To test whether trawling intensity affected sediment properties, a mixed linear model was constructed using the 'lme' function within the 'nlme' package (v.3.1–164) (Pinheiro, 2011). Trawling intensity (SAR) was used as a fixed continuous variable, while the variable 'site' was used as a random effect (default settings) and as a proxy for environmental variability. The sediment properties analysed were organic matter content (% OM), chlorophyll concentration, porosity and the PRT:CHO ratio, averaged for the top 2 cm of sediment. Since no relationships between sediment properties and SAR were found, these were used as independent explanatory variables in subsequent data analyses.

2.9.1. Shannon's H diversity indices of microbial, meiofaunal metazoan, foraminifera and macrofauna communities

For the prokaryotic and meiofaunal metazoan data, relative abundances were calculated using sequence based ASVs, while absolute abundances (from raw count data) were used for foraminifera and macrofauna. Alpha diversity (Shannon's H diversity index) was calculated for each group using the normalisation method scaling with ranked subsampling (SRS package, default settings, v.0.2.3) (Beule and Karlovsky, 2020). Shannon's Index was then calculated using the diversity function in vegan package in R using default settings.

2.9.2. Factors affecting alpha diversity and sediment biogeochemistry

Stepwise multiple linear regressions were performed to evaluate the relative contribution of trawling intensity (SAR), environmental and sedimentary variables and macrofauna bioturbation potential (BPc) on a) Shannon (alpha) diversity of prokaryotic, meiofauna, foraminifera and macrofauna communities and b) C degradation rates in the top 2 cm. SAR was always included in the model, since it was our main variable of interest. However, we also ran the stepwise selection starting from the null model in order to check if SAR was actively selected as a variable. The other explanatory variables were chosen to reflect environmental conditions (salinity$_{range}$, oxygen$_{min}$ and current$_{median}$), sedimentary organic matter quantity (% OM) and 'quality' (chlorophyll concentration and PRT:CHO ratio)(averages of top 2 cm) and macrofaunal bioturbation activity (BP$_c$), since this is known to affect sediment characteristics, biogeochemical cycling and meio- and microbial communities (Mermillod-Blondin and Rosenberg, 2006; Mermillod-Blondin, 2011; Aller and Cochran, 2019). BP$_c$ was excluded as an explanatory variable in the macrofauna diversity analyses, since it is derived from those same data. If any explanatory variables had a Variance Inflation Factor (VIF) >5 they were sequentially excluded until all VIFs were below five. Multiple linear regressions were performed in R with the *lm*() function in the 'AED' package, and model assumptions were confirmed through inspection of diagnostic plots. No data transformation was required. Stepwise (forward and backward) selection (R: *step*()) was used to identify the best model. The proportion of the dependent variable's total variance that was explained by each significant variable was calculated using the LMG method (R: *relaimpo*) (Grömping, 2015).

2.9.3. Multivariate analyses of community structure

Environmental variables were first pre-selected using a correlation matrix (Fig. S2) of all potential explanatory variables to check for collinearity. If variables had critical r value, i.e. >|0.7| (Dormann et al., 2013) they were removed unless they were judged to be most representative and ecologically relevant. For sedimentary data, values from the top 2 cm were used for this pre-selection. Transformation was done if variables had a skewed distribution. The resulting first selection of variables was: water depth, % OM, sediment chlorophyll, oxygen$_{min}$, $\log_{10}$(current$_{range}$), $\log_{10}$(PRT:CHO), sqrt(SAR) and BQI and sqrt(BP$_c$), for all except macrofauna analyses since these indices are also calculated from macrofauna data.

Multivariate analysis was conducted on each of the four organism groups (prokaryotes, meiofaunal metazoans, foraminifera, and macrofauna) and were analysed in a stepwise procedure. A Permanova analysis was performed to assess if trawling intensity was a contributing factor to explain the community composition. Sampling stations were assigned to three fixed categories of trawling intensity (<0.4, 0.4–4.6, >4.6 SAR (y^{-1}))(see 2.2). Resemblance matrices were constructed using Bray-Curtis similarity. All data were evaluated with a distance-based test for homogeneity of multivariate dispersions using the function PERMDISP (Table S3). To avoid heterogenous dispersions, input data were log ($x + 1$) transformed for prokaryotes and meiofaunal metazoans, and square root transformed for foraminifera and macrofauna. If the Permanova analysis was significant, results were visualised using canonical analysis of principal coordinates (CAP), including overlaying the taxa that contributed most to the CAP axis that best separated the categories of trawling intensity. Furthermore, if the Permanova analysis was significant, a dbRDA + distLM analysis was performed to assess the relative contribution of SAR (here used as a continuous variable) and environmental variables to community structure. The pre-selected explanatory variables (see above) were extracted for the 0–1 cm layer for prokaryote and meiofaunal metazoans and averaged for 0–3 cm and 0–5 cm for foraminifera and macrofauna, respectively, reflecting the sediment depths at which these were sampled/found in the field. Each dbRDA+distLM analysis further reduced this list using a stepwise procedure to identify the most important variables. The CAP axis and the dbRDA axis that best correlated with trawling intensity were identified from the plots and the taxa that correlated best ($r > |0.3|$) with both of these were identified. Likewise, we identified the taxa that correlated best with the dbRDA axes representing significant environmental variables.

All multivariate analyses were performed using the statistical package PERMANOVA+ for PRIMER (Anderson et al., 2008).

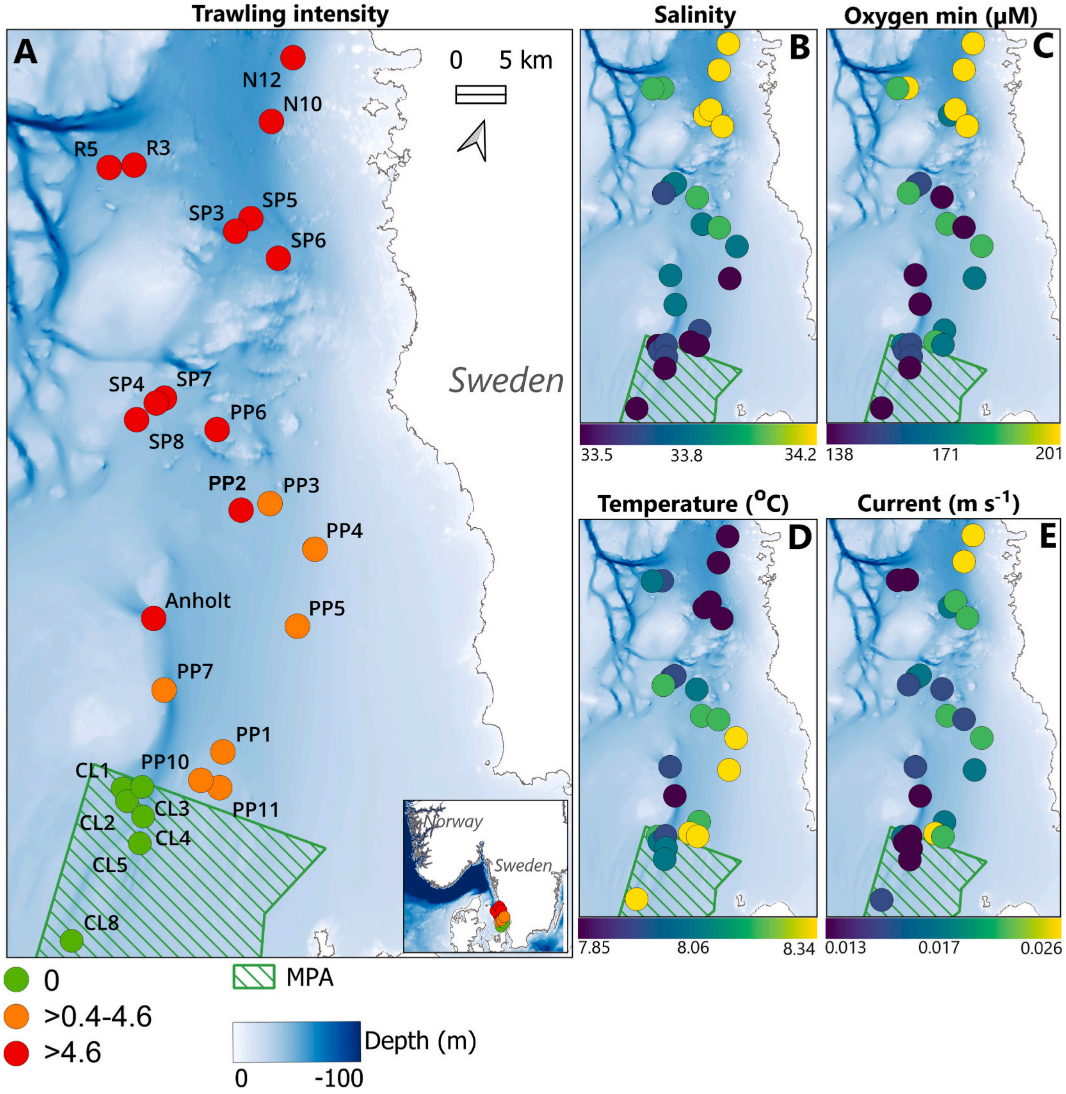

Fig. 1. Map of sampling sites with details of trawling intensity (a), median bottom water salinity (b), minimum bottom water oxygen concentration (oxygen$_{min}$) (c), median bottom water temperature (d), median bottom water current speed (e). Environmental variables are extracted from the Copernicus Marine Environment Monitoring Service database for the period 2014–2021. In a), trawling intensity is the yearly swept area ratio (SAR, year^{-1}) For some of the analyses in this study, trawling intensity groups are defined as: zero (MPA; green), medium (SAR >0.4–4.6 year^{-1}; orange) and high (SAR >4.6 year^{-1}; red). Green polygon indicates marine protected area (MPA) established in 2009, and since then closed for all fisheries, including recreational activities. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Bottom water conditions

Median bottom water salinity, although similar across stations (33.5–34.3), showed a slight increase from south to north (Fig. 1B). Higher minimum bottom water oxygen concentration was also observed at the seven northernmost stations (>180 μM) and minimum oxygen concentrations across the study area were not at a level generally considered detrimental to marine life (i.e., all were well above the hypoxia threshold of 62.5 μM) (Fig. 1C). Median bottom water temperature was lowest in the north (Fig. 1C) but varied by only 0.5 °C across sites (7.85–8.34 °C). Median current speed varied from 0.013 to 0.026 m s^{-1} (Fig. 1D) and the range in current speed at any one station varied from 0.038 to 0.097 m s^{-1}.

3.2. Surface sediment properties

Sediment properties in the upper (0–2 cm) sediment across the 26 stations were (mean ± sd): % organic matter (7% ± 4%), porosity (0.73 ± 0.16), chlorophyll (2.87 ± 0.68 μg cm^{-3}), and PRT/CHO (1.37 ± 0.32) (Table S1). None of these surface sediment properties showed a significant relation to trawling intensity; organic matter content (mixed linear model, ANOVA, $F_{1,24} = 0.01$, $p = 0.90$), porosity ($F_{1,24} = 0.2$, $p = 0.6$), chlorophyll ($F_{1,24} = 0.01$, $p = 0.8$), and the PRT/CHO ratio ($F_{1,24} = 1.7$, $p = 0.1$) (Fig. 2). The lack of relationship between sediment properties and SAR justified their use as independent explanatory variables in analyses of sediment fauna and biogeochemistry.

3.3. Sediment carbon degradation rates

Carbon degradation rates in the top 0–2 cm of the sediment were on average 2.80 ± 1.75 μgC g^{-1} h^{-1}, $n = 25$. The carbon degradation rates in the surface 0–2 cm sediment were best explained by a combination of organic matter content (% OM), oxygen$_{min}$ concentration and SAR (multiple linear regression; $F_{3,\ 21} = 11.87$, Adj-$R^2 = 0.58$, $p < 0.0001$). The organic matter content (% OM, $t = 4.528$, $p < 0.001$) and oxygen$_{min}$ ($t = -3.295$, $p = 0.003$) were significant explanatory variables and explained 33% and 21% of the variance, respectively. SAR contributed to the best model but was not significant ($t = -1.297$, $p = 0.209$), explaining only 8% of the variance (Table S2).

3.4. Sediment prokaryote community diversity across the trawling gradient

We recovered 32,005 unique ASVs corresponding to 105 phyla, and 612 orders from the 26 sampling stations. Prokaryotic communities showed an average Shannon's H diversity index of 7.21 ± 0.16. Prokaryotic alpha diversity increased with higher trawling intensities (Fig. 3A) and was best explained by SAR alone, although the model was only significant at the $\alpha = 0.1$ level (multiple linear regression; $F_{1,\ 24} = 3.901$, Adj-$R^2 = 0.104$, $p = 0.0599$). None of the environmental variables contributed to the best model (Table S2). The same result was obtained when starting the stepwise regression with the null model.

Trawling intensity significantly affected microbial community composition (Permanova: pseudo-$F_{2,\ 24} = 1.3097$, $p = 0.018$) (Fig. 3B). Distanced-based redundancy analysis (db-RDA, Fig. 3C) did not identify any variables as significantly affecting community composition, though sediment chlorophyll concentration was significant at the $\alpha = 0.1$ level

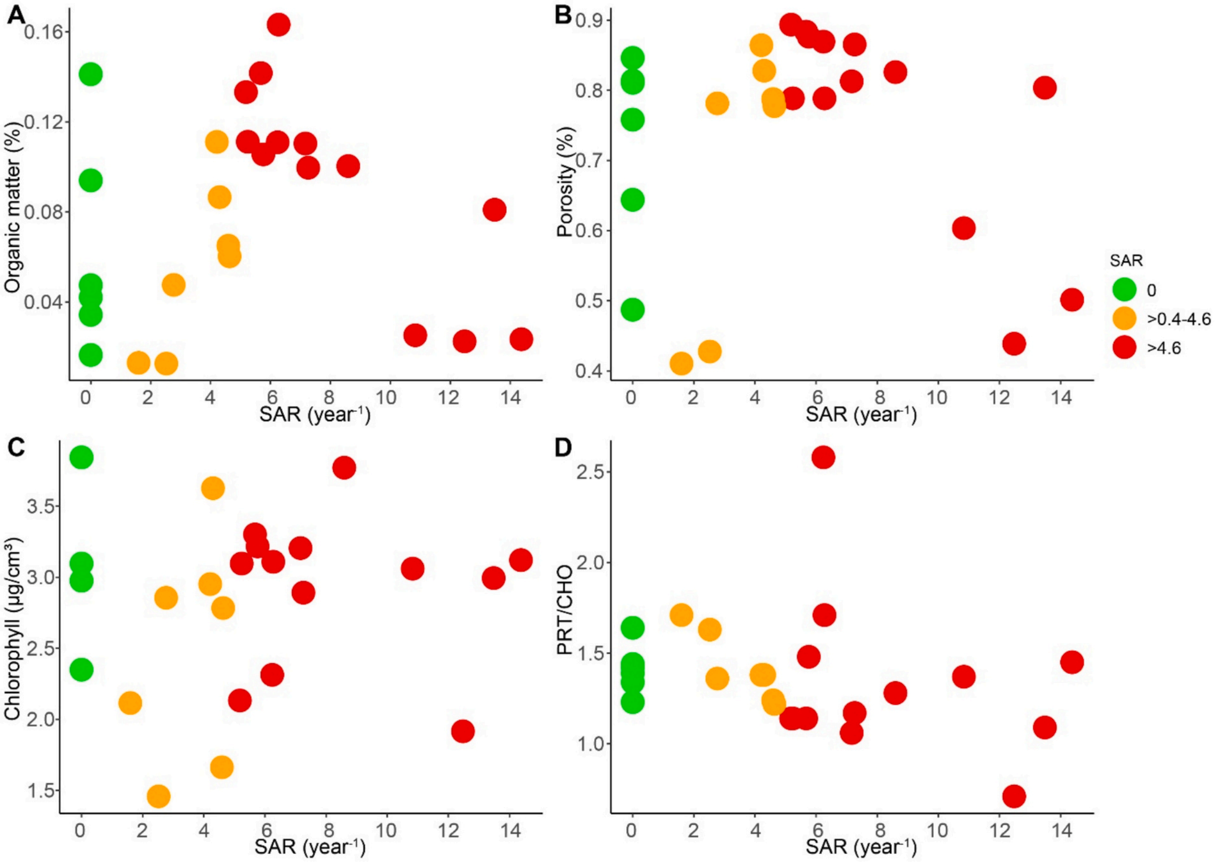

Fig. 2. Surface (0–2 cm) sediment properties in relation to the trawling intensity gradient (SAR ($year^{-1}$)), shown on the x axis. A) organic matter content, B) porosity, C) chlorophyll concentration, and D) protein to carbohydrate ratio. Different colours denote the three trawling intensity groups. Each datapoint represents an individual sampling station. SAR did not affect any of the four variables.

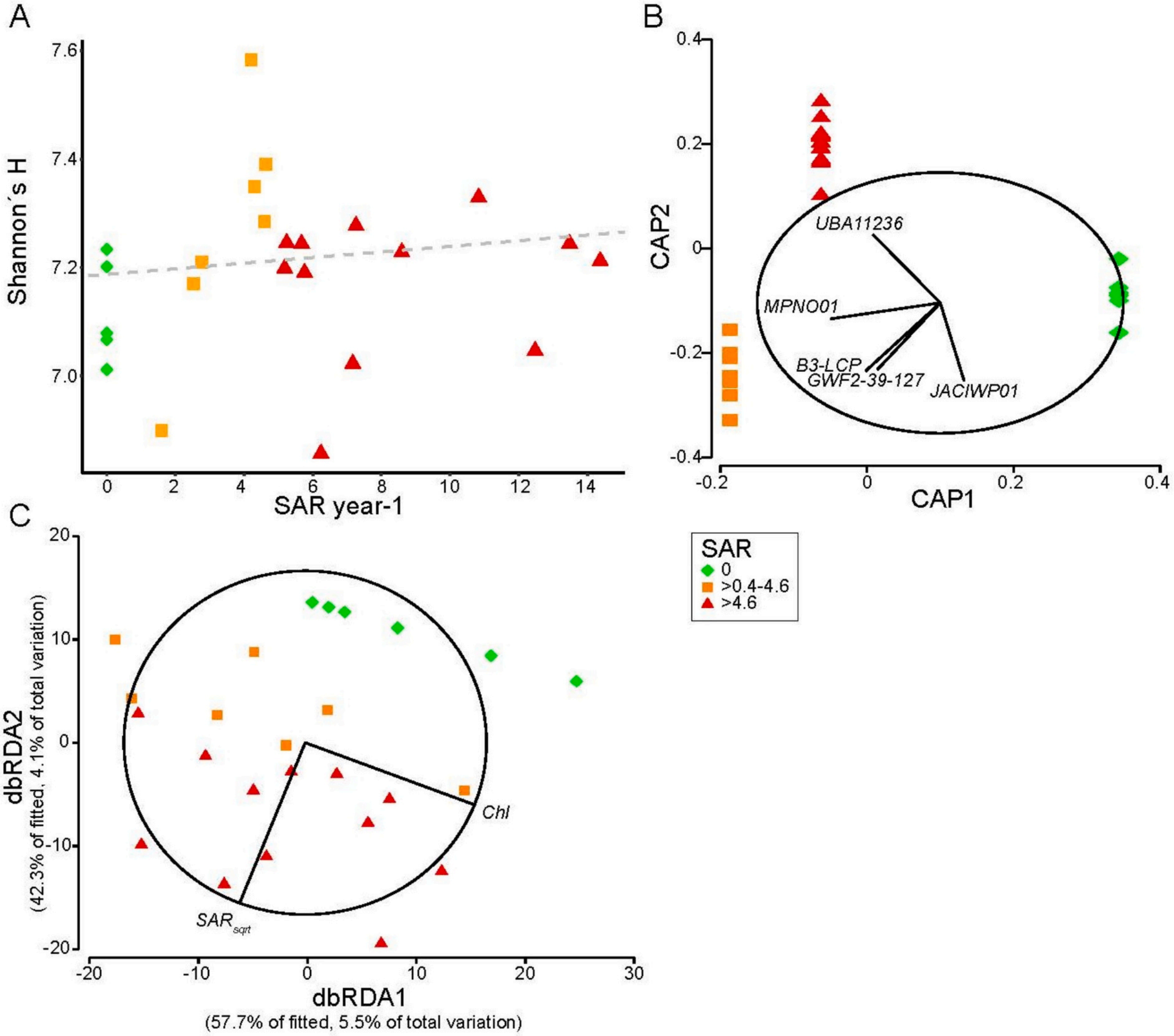

Fig. 3. Microbial community alpha diversity and community composition based on 16S rRNA amplicon sequencing. A) Shannon's H diversity index shows a weak increase with increasing trawling intensity (SAR)(Adj-R2 = 0.104, $p = 0.0599$). B) CAP plot with the taxa correlating most strongly to either axis shown. B) Ordination via distance-based redundancy analysis (db-RDA) bi-plot with SAR and the most important explanatory variable (sediment chlorophyll (chl), $p = 0.066$) shown as arrows. Coloured shapes represent the three trawling intensity groups (see legend).

(Marginal test: pseudo-F = 1.2919, $p = 0.066$), correlating mainly with dbRDA axis 1 that explained 5.5% of the total variation. Trawling intensity was not significant but contributed best to dbRDA axis 2 that explained 4.2% of the total variation (Fig. 3C).

Prokaryotic taxa commonly associated with higher trawling intensities included, but were not limited to, *SRT547* (Planctomycetes), *REDH01* (Bradymonadia), Micavibrionales, *SM23–33* (Phycisphaerae), *Ga0077536* (Gammaproteobacteria), and Saccharimonadales (Table S4). Sediment chlorophyll concentrations also appeared to affect prokaryotic community composition; prokaryotic taxa which increased along the dbRDA1 axis (which correlated with increased sediment chlorophyll concentrations, p = 0.066) included *PUPC01* (Planctomycetota), *UBA7937* (Chloroflexota), Tenderiales, Myxococcales, Chitinophagales, and *UTPRO1* (Table S4). Furthermore, Cyanobacteria relative abundances were 36% higher in the MPA (0.068% relative abundance) compared to the high trawled area (0.050%), and 21% higher than the low trawled area (0.056%) (Fig. S3). Apart from two taxa, all Cyanobacteria abundances were positively correlated with sediment chlorophyll concentrations, although these relationships were not strong (r = 0.06–0.28).

3.5. *Meiofaunal metazoan diversity along the trawling gradient*

After filtering for typical meiofaunal metazoan phyla we recovered 700 unique ASVs with 16 phyla, 39 orders. Meiofaunal metazoan alpha diversity (Shannon's H index) was 2.74 ± 0.63 and showed no relationship with trawling intensity (Fig. 4A) or any of the other explanatory variables (multiple linear regression: $F_{2,\,23} = 1.895$, Adj-$R^2 = 0.067$, $p = 0.173$) (Table S2). The same result was obtained when starting the stepwise regression with the null model. Trawling intensity did not affect community composition (Permanova: pseudo-$F_{2,\,24} = 0.690$, $p = 0.795$). Distanced-based redundancy analysis (db-RDA, Fig. 4B) did not identify any variables as significantly affecting community composition, although % OM was significant at $\alpha = 0.1$ (Marginal test: pseudo-F = 2.047, $p = 0.052$), correlating mainly with dbRDA axis 1 that explained 8.5% of the total variation. Trawling intensity was not significant but contributed best to dbRDA axis 2, though this axis only explained 2.6% of the total variation (Fig. 4B). Taxa which correlated most with dbRDA1 (i.e., higher sedimentary % OM) were, for example, Harpacticoida, Enterogona, and Cyclopoida, while nematode taxa such as Araeolaimida, Monhysterida and Desmodorida correlated mostly with lower % OM (Table S5).

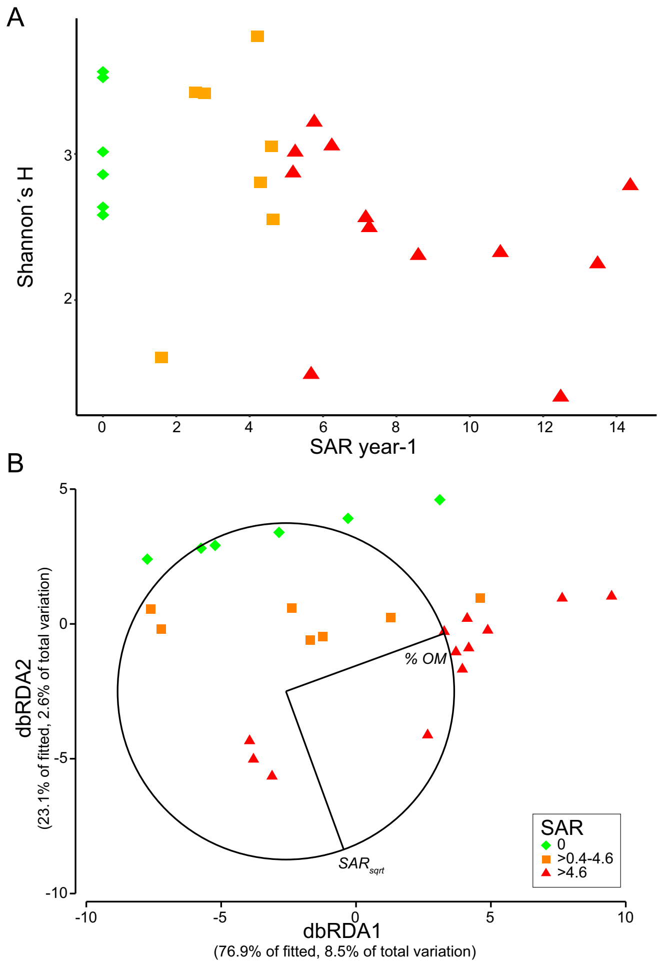

Fig. 4. Meiofaunal metazoan alpha diversity and community composition. A) Shannon's H alpha diversity shows no relationship with trawling intensity (SAR). B) Ordination via distance-based redundancy analysis (db-RDA) bi-plot with SAR and the most important explanatory variable, % organic matter in the sediment (% OM)($p = 0.052$), represented as biplot arrows. Coloured shapes represent the three trawling intensity groups (see legend). As the Permanova was not significant, the CAP plot is not shown.

3.6. Foraminifera diversity along the trawling gradient

A total of 63 taxa from 16 sediment samples (0–3 cm depth layer) identified. The foraminiferal Shannon's H alpha diversity (mean ± sd, 2.48 ± 0.14) increased with increasing SAR (Fig. 5A) and was best explained by SAR alone (multiple linear regression; $F_{1,15} = 6.33$, Adj-R2 = 0.250, $p = 0.024$), while none of the environmental variables contributed to the best model (Table S2). The same result was obtained when starting the stepwise regression with the null model.

Trawling intensity significantly affected community composition (Permanova: pseudo-$F_{2,\ 16} = 1.5477$, $p = 0.049$) (Fig. 5B). The dbRDA identified sediment chlorophyll and oxygen$_{min}$ as significantly contributing to the observed differences (pseudo-F = 1.7858, $p = 0.042$ and pseudo-F = 2.2885, $p = 0.009$, respectively) (Fig. 5C), though several other variables were significant at the $\alpha = 0.1$ level (% OM, BQI and sqrt_BPc).

Taxa which most correlated with higher trawling were, for example, *Hyalinea balthica*, *Textularia earlandi*, and *Epistominella vitrea*, while *Stainforthia fusiformis* and some Nonionelliids (such as *Nonionella* sp. T1, *N. turgida* and *Nonionellina labradorica*) were associated with lower trawling intensities (Table S6). The taxa which mostly correlated with lower oxygen$_{min}$, i.e. that are presumably less sensitive to lower oxygen, were for example *Hyalinea balthica*, *Textularia earlandi*, *T. truncata*, *Bolivina pseudopunctata* and *B. spathulata*. On the other hand, taxa sensitive to lower oxygen were mostly Nonionelliids (e.g., *Nonionella* sp. T1, *N. turgida* and *N. labradorica*) and *S. fusiformis* (Table S4). Finally, taxa such as *H. balthica* and *Ammoscalaria pseudospiralis* were more abundant at sites with higher chlorophyll (Table S6).

3.7. Sediment macrofauna communities across trawling gradient

A total of 95 macrofauna taxa were identified across the 26 stations, although across stations species richness ranged from 11 to 37. Alpha diversity (Shannon's H index) was 2.1 ± 0.43 and showed no clear trend with trawling intensity (Fig. 6A) but decreased significantly with increased sediment organic matter content (multiple linear regression; $F_{2,\ 23} = 11.37$, Adj-$R^2 = 0.4534$, $p \leq 0.001$). SAR was not significant ($t = -0.807$, $p = 0.428$), accounting for only 1.6% of the variation, while organic matter content was significant ($t = -4.680$, $p < 0.001$) and explained 48% of the variance (Table S2). The same result was obtained when starting the stepwise regression with the null model.

Trawling intensity significantly affected community composition (Permanova: pseudo-$F_{2,\ 25} = 1.6549$, $p = 0.039$) (Fig. 6B). The db-RDA identified water depth, % OM and chlorophyll as significant explanatory variables of macrofauna community composition and trawling intensity (SAR) as significant at $\alpha = 0.1$ ($p = 0.06$) (Fig. 6C). Of these, % OM and water depth correlated best with dbRDA1 which contributed 21% to the total variation, and trawling intensity and chlorophyll best to the dbRDA2 which contributed 7% to the total variation.

The species that were more abundant in areas with lower trawling intensities included bivalves (*Abra nitida* and *Ennucula tenuis*), small crustaceans (*Harpinia antennaria*, *Eudorella emarginata* and *Leucon nasica*) and the polychaete *Spiophanes kroyeri*. Species more commonly found at stations with high trawling intensity included the bivalve *Varicorbula gibba*, the gastropod *Hermania scabra* and several polychaete species (Table S7). The brittle star *Amphiura chiajei* was the dominant species in areas with higher % OM. A range of species were more abundant in areas with lower % OM (Table S7).

4. Discussion

The Kattegat has been intensively trawled for 121 years, and although effects on macrofauna have previously been reported (Sköld et al., 2018; Sköld et al., 2025), this is the first study in the area simultaneously examining chronic bottom trawling effects on macrofauna, meiofaunal metazoans, foraminifera, prokaryotes and sediment properties. We showed that Shannon's H diversity of prokaryotes and benthic foraminifera increased slightly with higher trawling intensity, and for those groups, trawling intensity was the only factor explaining the differences in diversity across sites. Community composition of macrofauna, foraminifera and prokaryotes were influenced by a combination of natural environmental factors, such as bottom water oxygen, sedimentary chlorophyll and organic matter, together with trawling intensity. Only meiofaunal metazoan community composition was not affected by fishing. Trawling did not affect sediment properties. However, in surface sediments, carbon degradation rates were best explained by a combination of trawling intensity, sedimentary organic matter, and bottom water oxygen concentrations. A summary of the main results is presented in Fig. 7 and discussed in more detail in the rest of this section.

4.1. Carbon degradation rates are influenced most by environmental factors

The effect of trawling on sedimentary carbon has been receiving increasing attention during the last few years; reported effects range from positive to negative and are highly context dependent (Epstein et al., 2022; Tiano et al., 2024). One hypothesis is that carbon degradation rates are higher with increasing trawling intensity because sedimentary organic matter is repeatedly exposed to oxygenated water,

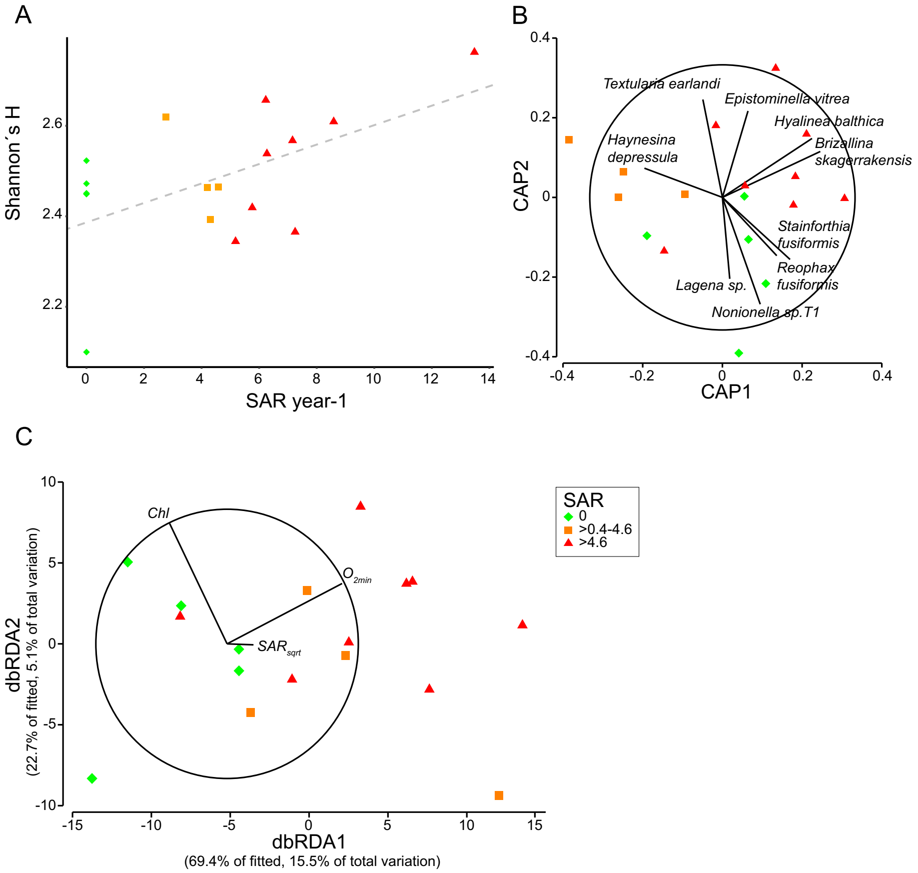

Fig. 5. Foraminiferal alpha diversity and community composition. A) Shannon's H diversity index increases with increased trawling intensity (SAR)(Adj-R2 = 0.250, $p = 0.024$). B) CAP plot with the taxa correlating most strongly to either axis shown. C) Ordination via distance-based redundancy analysis (db-RDA) bi-plot with SAR and significant explanatory variables (bottom water oxygen$_{min}$ (O_{2min}), sediment chlorophyll (chl)) represented as biplot arrows. Coloured shapes represent the three trawling intensity groups (see legend).

potentially enhancing microbial activity (Epstein et al., 2022), at least over short time scales. After decades of chronic trawling this could result in seafloor carbon becoming highly refractory, especially if suspended organic matter is also exported from the trawled area (Pusceddu et al., 2014; Pusceddu et al., 2015) and as a result, continued disturbance may have little effect on the remaining refractory carbon (Epstein et al., 2022). However, this is unlikely to be an explanation for the weak trawling effect on carbon degradation and sedimentary variables measured in this study area, since bottom currents are quite weak (<0.1 m s $^{-1}$), and the surface sediments are rich in organic matter (e.g., up to 16% OM and 2.7% TOC) and labile carbon (e.g., chlorophyll content up to 3.8 μg cm^{-3} and total biopolymeric carbon up to c. 10 mgC g $^{-1}$). Continuous carbon inputs to the seafloor from terrestrial sources and from pelagic primary production in this eutrophic sea may compensate for increased carbon degradation caused by trawling. It is therefore not surprising that % OM was the main factor affecting carbon degradation rates in this study, though perhaps the carbon quality (here measured as chlorophyll concentration and PRT:CHO ratio) would also have been expected to play a role (Tiano et al., 2024).

4.2. *Molecular methods for taxonomy*

Molecular metabarcoding approaches such as 16S and 18S rRNA amplicon sequencing provide high-throughput recovery of sequence variants (ASVs) from environmental samples, but they do not represent a one-to-one match with morphologically defined species. ASVs are unique sequence variants that may derive from multiple biological sources (e.g. intra-specific variation, multiple rRNA copies) and do not necessarily equate to formally described taxa (Callahan et al., 2016). Moreover, the completeness and taxonomic coverage of reference databases constrains the ability to assign ASVs to fine taxonomic ranks, often resulting in many sequences only classifiable at higher ranks such as Order or Family. We therefore took a conservative approach when using taxonomic databases (SBDI-GTDB database for 16S, SILVA v132 for 18S) to identify which taxa are represented by the ASV data, choosing Order as the lowest level that was robust across samples, even though this meant a lack of taxonomic resolution in some cases; this is discussed further in 4.3 and 4.4. Comparative studies have shown that metabarcoding and morphological inventories often yield overlapping but non-identical assessments of community composition and richness. For example, sediment DNA metabarcoding detected more meiofaunal groups but differed in taxonomic representation compared with morphological approaches in Arctic (Mazurkiewicz et al., 2024), Mediterranean (Good et al., 2022) and freshwater nematode (Schenk et al., 2020) communities. These discrepancies arise both from methodological biases (primer choice, amplification efficiency) and from fundamental differences between sequence-based diversity estimates and morphology-based species inventories. Accordingly, our analyses and results of prokaryote and meiofaunal diversity and community structure focus on ASV-level patterns and we acknowledge that metabarcoding may under- or over-represent some taxonomic groups relative to morphological surveys.

4.3. *Prokaryotic diversity increases slightly with trawling, while community structure also depends on sediment properties*

Aquatic prokaryotes play crucial roles in the regulation of biogeochemical cycling and in the decomposition of organic matter and

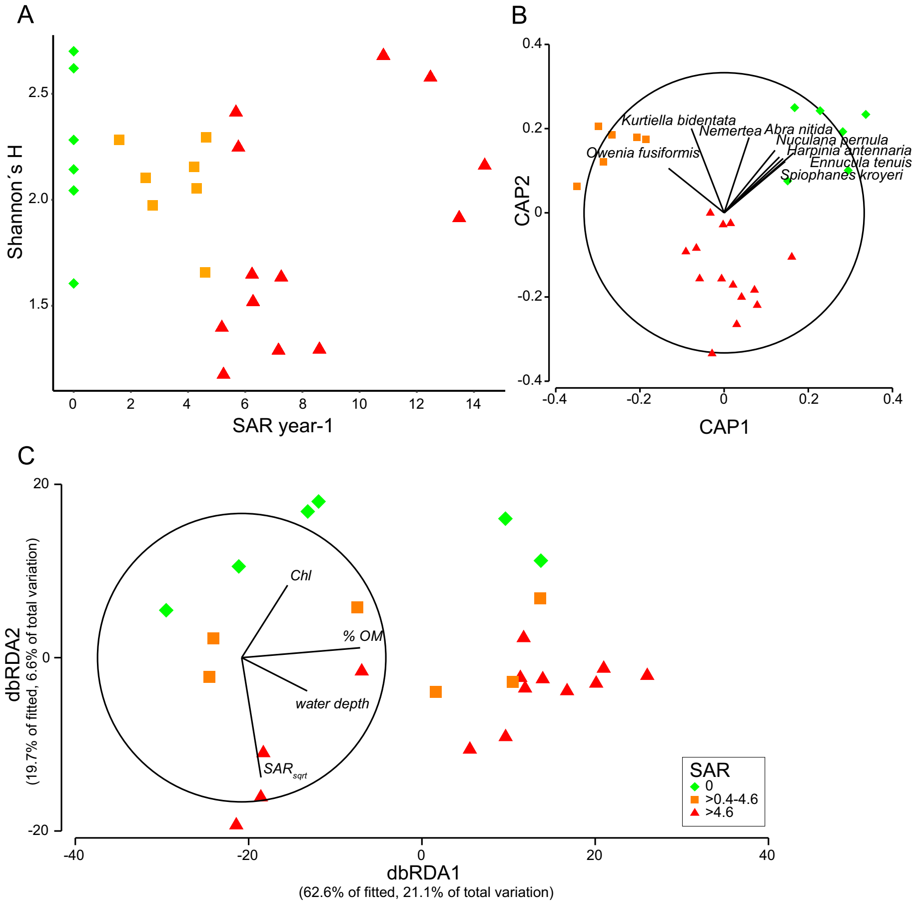

Fig. 6. Macrofaunal alpha diversity and community composition. A) Shannon's H alpha diversity shows no relationship with trawling intensity (SAR). B) CAP plot with the taxa correlating most strongly to either axis shown. C) Ordination via distance-based redundancy analysis (db-RDA) bi-plot with SAR and significant explanatory variables (sediment chlorophyll (chl), % organic matter in the sediment (%OM), water depth) shown as biplot arrows. Coloured shapes represent the three trawling intensity groups (see legend).

nutrient dynamics in the food web (Arrigo, 2005; Logue et al., 2015). Benthic prokaryotes, especially at the sediment-water interface, have been studied across various parts of the marine environment (Bale et al., 2014; Perliński et al., 2019; Seidel et al., 2022; Fu et al., 2024). While prokaryotic communities are commonly shaped by their environment (Moreno-Gámez, 2022), little is known about potential trawling effects on their community structure.

Our results showed that microbial Shannon's H diversity showed a weak positive relationship with trawling intensity that could be explained by an increase in rare taxa. Trawling events, where deeper sediment layers are mixed with surface ones, may combine bacterial species of different layers, thus increasing diversity in the surface sediment. Similar responses have been observed in sediment disturbance experiments, where an increase of diversity was connected to promotion of cohabitation of ecologically different microorganisms (Galand et al., 2016), and sediment dredging, where an increase of Shannon's H prokaryotic diversity occurred, which was mostly explained by higher prokaryotic abundance, wider distribution, and environmental factors (Zhang et al., 2017).

Despite this weak effect on the rare taxa and alpha diversity, more abundant (>0.5% relative abundance) taxa did not show any direct effects of trawling. Prokaryotes' small size, fast turnover rates, and metabolic plasticity could decrease the direct influence of trawling (see also Bradshaw et al., 2024). These authors proposed that a shift in function rather than community composition might occur. In the Kattegat, community composition was related to a combination of SAR and sediment properties, in particular chlorophyll. This agrees with previous studies in trawled areas, which showed that prokaryotic communities are largely shaped by their environment. Bonthond et al. (2023), found that microbial composition and diversity were most strongly determined by sediment particle size, permeability, organic matter content and shear stress, and less so by bottom trawling in the south-eastern North Sea. Likewise, Bradshaw et al. (2024) found a group of ‘physical’ properties, including sediment OM and porosity and bottom water oxygen and salinity, to be most important for prokaryotic communities in the southern Baltic Sea.

Looking into the taxa most responsible for community differences in our results indicated that prokaryotes with a predatory life-style (i.e. those that consume other prokaryotes) were more likely to be found at sites with low trawling and higher chlorophyll. For example, *C. uabimicrobium amorphum* (SRT547) (Shiratori et al., 2019) belonging to the Phylum Planctomycetes, *REDH01* belonging to Bradymonadia (Mu et al., 2020), or *Micavibrionales* (Davidov et al., 2006) all prey on other prokaryotes, such as pathogens (e.g., *E. coli*, *Pseudomonas*, and *Vibro*). However, the taxa found herein are not related to typical bacteria predating on cyanobacteria, such as *Bdellovibrio bacteriovorus* or *Myxococcus xanthus* (Bauer and Forchhammer, 2021), and therefore cannot be directly linked to the higher cyanobacteria concentrations found in the MPA. The slightly higher abundances of cyanobacteria (e.g., *Cyanobium*, *Planktothrix*, and *Synechococcus*) observed in the MPA (0.068% relative abundance) compared to the low (0.056%) and high (0.050%) trawled sites did not show typical species of cyanobacteria that can be found in this area (e.g., *Nodularia spumigena* or *Anabaena*). This could be due to the fact that the Genome Taxonomy Database (Parks et al., 2018) used does not provide a sufficient resolution of cyanobacteria on lower taxonomical levels, therefore resulting in increased unknown species.

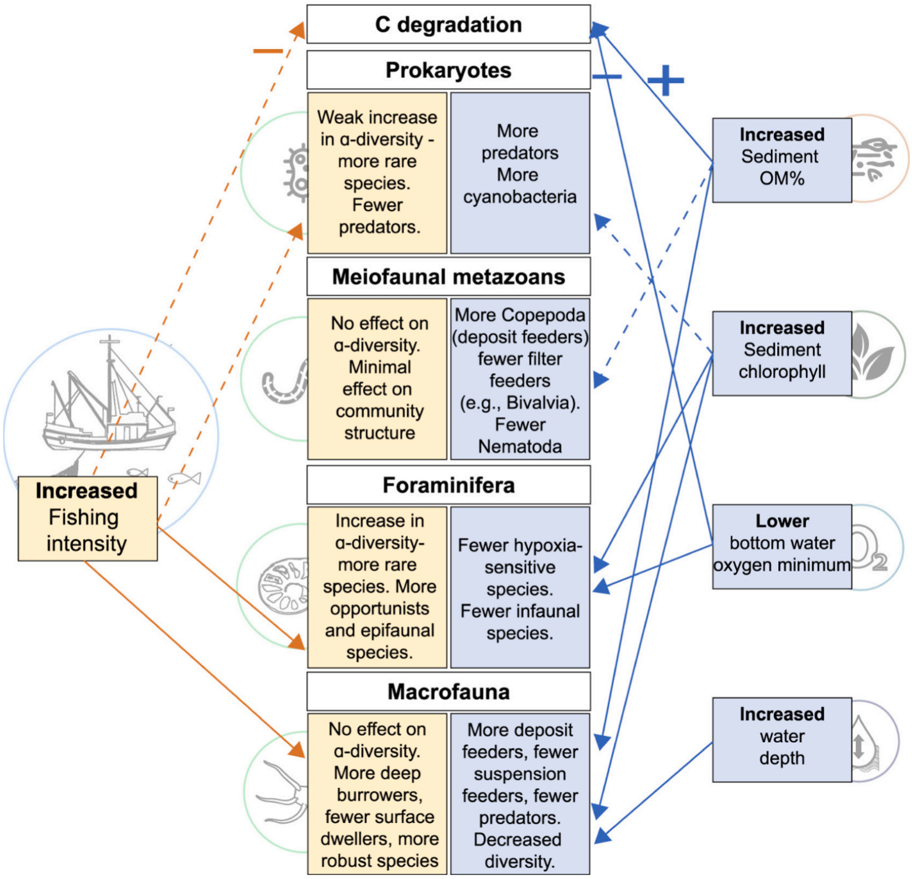

Fig. 7. Summary of the main results. Solid lines indicate significant and/or strong effects, dotted lines are relationships that are weak or significant at α = 0.1. Left side of the figure (orange) shows effects of trawling, right side (blue) shows effects of other variables. For carbon degradation, + indicates a positive effect and – a negative effect. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

However, the higher concentration of chlorophyll found in the MPA could be to some degree due to higher abundances of cyanobacteria or their resting stages (Wood et al., 2021) in surface sediments.

4.4. Meiofaunal metazoans show resilience to chronic bottom trawling; community structure is mainly affected by sediment organic matter

The results of this study are based on unsieved sediment 18S eDNA sequencing focusing on metazoan taxa. Although the data were filtered to retain only typical meiofaunal taxa, some metazoan taxa remaining in the dataset may belong to macrofauna rather than meiofauna. Nevertheless, we focus on the overall effect on 18S rRNA metazoans. Our results suggest that there was very little impact of trawling on metazoan diversity or community structure. Similar results have been found in coastal waters of the southern Baltic Sea (Bradshaw et al., 2024) and Aegean Sea (Lampadariou et al., 2005). These studies suggested that due to their small size meiofauna are rather displaced than damaged by the trawl. Many meiofauna are also highly mobile, allowing them to move back to their original sediment depth after burial or displacement by trawling (Schratzberger et al., 2000).

Organic matter seemed to be the most important driver of community composition in our study, though this relationship was weak. Meiofaunal orders that were positively associated with higher organic matter concentrations were the copepods Harpacticoida and Cyclopoida, both of which include many benthic deposit feeders. Their abundance is usually determined by sediment conditions, with factors such as organic matter being a limiting factor for population dynamics (Bodiou et al., 1990). Lower sedimentary organic matter favoured some orders of the biggest group of metazoans, Nematoda, such as Araeolaimida, Monhysterida, and Desmodorida. This is perhaps surprising given that Nematoda are often associated with high OM habitats (Moens et al., 2014), but the relationship between nematode abundance and diversity and sediments is probably more complex, also being driven by grain size and permeability-related biogeochemical characteristics (Vanaverbeke et al., 2011) and varying widely among species in any given order. The low taxonomic resolution at which we classified the meiofauna in our dataset precludes detailed interpretation; there are hundreds of species within these nematode orders (Schmidt-Rhaesa, 2014) and exactly which were favoured by lower % OM cannot be determined. Also more frequent at lower % OM were two bivalve orders (Myida, Venerida) and one polychaete order (Terebellida). All these orders are also well-represented as macrofauna in our data, so we cannot be sure whether their presence in the 18S dataset reflects DNA from larger individuals, temporary meiofauna in the form of juvenile life stages of these macrofauna, or true meiofaunal taxa. However, many of the adult (macrofaunal) bivalve species in the orders Myida (e.g., *Varicorbula gibba*) and Venerida (e.g., *Arctica islandica*, *Kurtiella bidentata* and *Mysia undata*) are obligate or facultative filter feeders, a functional group that is often associated with lower sedimentary OM. Other authors have suggested that indirect effects of trawling on meiofauna occur through trawl-induced changes in % OM (Pusceddu et al., 2014), however, our between-site differences in % OM did not seem to be related to trawling.

Lastly, meiofauna show strong temporal variation which may mask any potential trawling impacts. Lampadariou et al. (2005) and Schratzberger et al. (2002) attributed much of the observed meiofaunal community change to seasonal factors such as temperature and primary productivity, rather than trawling. Tinlin-Mackenzie et al. (2023)

showed that interannual variation in meiofauna alpha diversity and community structure was much higher than effects of trawling or sampling location, while species richness was positively or negatively correlated with SAR depending on the year.

4.5. Foraminifera are affected by both trawling disturbance and environmental factors

Higher trawling intensity significantly increased foraminiferal diversity, which was mainly due to higher numbers of rare species (i.e. species representing $<2\%$ of the total abundance). This response is similar to that found for the prokaryote community. Foraminifera are known to have bacteria as a part of their diet (Lee, 1980; Haynert et al., 2020; Schweizer et al., 2022), or as cytoplasmic endosymbionts and ectobionts (Bernhard et al., 2018) with different species being characterized by unique microbiomes (Salonen et al., 2021). Thus, the simultaneous increase in diversity of these groups may be due to increased ecological interactions between them.

Trawling disturbance may also create new habitats and dispersal opportunities for both microbes and foraminifera that could increase diversity and/or change community structure. Epifaunal and shallow-infaunal, opportunistic foraminifera have generally shown quick recovery following burial by sediment as compared to infaunal species (Ernst et al., 2002; Hess et al., 2013; Duros et al., 2017). Our study confirms this; with higher SAR we found higher abundances of the epifaunal to shallow-infaunal omnivore *Hyalinea balthica* (Klitgaard-Kristensen et al., 2002; Rosenthal et al., 2011) and the opportunistic *Textularia earlandi* and *Bulimina marginata* (Hess and Kuhnt, 1996; Hess et al., 2013). Among other species found at high SAR were *Epistominella vitrea, Elphidium clavatum* and *Bulimina marginata,* which all are associated with increased food supply and labile OM (Schönfeld and Numberger, 2007; Duffield et al., 2014; Yamashita et al., 2020)(Table S6). Other species that are usually considered to be opportunists and/or fast colonisers (e.g. *Stainforthia fusiformis* and non-indigenous *Nonionella* sp. T1) (Ernst et al., 2002; Duros et al., 2017; Morin et al., 2023), were in fact more common at low SAR. However, both these taxa were recorded at all sampling stations, which for *Nonionella* sp. T1 can be explained by its highly invasive behaviour and fast spreading rates, potentially facilitated by chronic trawling.

Several taxa that were more common at higher trawling intensities were also more common where oxygen conditions were less favourable, suggesting these taxa may be generally stress-tolerant. Many foraminifera can change their sediment microhabitats, for example by switching from deep infaunal to shallow infaunal microhabitat following changes of, e.g., oxygen or nitrate in the sediment (e.g., (Linke and Lutze, 1993; Choquel et al., 2021)). Conversely, several taxa, for example several Nonionelliids, were found where SAR was lower or oxygen conditions better, suggesting a lower tolerance to stress (Table S6). *Nonionellina labradorica*, a deep infaunal deposit-feeder (Wollenburg and Mackensen, 1998; Schmidt et al., 2022) has also been reported as sensitive to low oxygen conditions (Filipsson and Nordberg, 2004; Suokhrie et al., 2021; Tetard et al., 2024), which is consistent with our study (Table S6). Like *N. labradorica*, several other species at these sites (*N. turgida*, *Nonionella* sp. T1 and *S. fusiformis*), also showed an infaunal rather than epifaunal lifestyle.

Lastly, *H. balthica* and *Ammoscalaria pseudospiralis* were more abundant at higher chlorophyll sites (Table S6). In particular, *A. pseudospiralis* quickly migrates through the sediment column in response to fresh food (Gross, 2000), whilst *H. balthica* is a known omnivore, which in our case may display substantial ecological plasticity when it comes to food.

4.6. Macrofauna community structure is affected by trawling, sediment properties and water depth

Macrofauna alpha diversity was not affected by trawling, but was significantly impacted by % OM. Shannon's H may not be the best measure of alpha diversity for this community since it is dominated by the brittle stars *A. chiajei* and *A. filiformis*. In this study, brittle stars reached densities of >1000 individuals per m^2, representing 44% of all individual organisms and 59% of the biomass. These values are comparable to previous estimates in the area by (Sköld et al., 2018; Sköld et al., 2025) who have shown these species to be relatively insensitive to trawling, and even to benefit from reduced predation by flatfish in trawled areas.

In contrast, macrofauna community composition was significantly affected by trawling, as well as sedimentary organic matter, chlorophyll content, and water depth. Most of the species that were more common at less trawled sites were those that live and/or feed in the uppermost 2 cm of sediment (Nyström Sandman et al., 2024) and are thus more likely to be affected by trawling disturbance than deeper burrowers. In addition, the bivalves *Abra nitida* and *Ennucula tenuis* are thin-shelled (https://www.marlin.ac.uk) and the polychaete *Spiophanes kroyeri* is sessile and has fragile mucus-lined tubes (Lindroth, 1941; Hartmann-Schröder, 1996); these characteristics might be expected to make these species more vulnerable to benthic disturbance. In contrast, the species that are more common in heavily trawled areas are generally robust (e.g., the thick-shelled *Varicorbula gibba*), able to burrow to at least 10 cm (e.g., the polychaetes *Ophelina acuminata* and *Orbinia sertulata*) or are free-living predatory species (*Hermania scabra*, *Glycera unicornis*) (Nyström Sandman et al., 2024). Deep-burrowers have been shown to be more abundant in trawled areas across European seas (Beauchard et al., 2023), presumably since they can withdraw below the fishing gear penetration depth. The parts of otter trawls that penetrate deepest are the trawl doors which, depending on trawl size, towing speed and sediment type, can penetrate up to a maximum of 10–20 cm (Hiddink et al., 2017), but only represent a small fraction of the gear footprint. The ground gear and sweeps, which account for most of the footprint, only penetrate a few centimetres (Eigaard et al., 2015).

Deposit feeders dominated the sites where % OM and/or sedimentary chlorophyll was highest, particularly the brittle star *Amphiura chiajei*, the polychaete *Spiophanes kroyeri*, the bivalve *Ennucula tenuis* and the crustacean *Eudorella emarginata.* In contrast, at sites with lower % OM and/or chlorophyll, several obligate or facultative suspension feeders were present (e.g., *Phoronis muelleri, Turritellinella tricarinata, Kurtiella bidentata, Edwardsia* sp.), as were predatory species (*Sthenelais limicola*, *Nephtys hombergii, Edwardsia* sp.), as might be expected where the sediments themselves are not a good source of OM. Overall, the amount and type of sedimentary organic carbon is known to be a strong driver in structuring benthic macrofauna communities, often having a greater impact than trawling disturbance (Tinlin-Mackenzie et al., 2023; Bradshaw et al., 2024; McLaverty et al., 2024).

5. Summary and conclusions

Our findings support a growing body of literature indicating that chronic bottom trawling and environmental factors act together to shape benthic community structure at all sizes from microbes to macrofauna (e.g., Leduc et al., 2016; Bonthond et al., 2023; Nielsen et al., 2023; McLaverty et al., 2024). However, trawling effects differ depending on the size fraction of the fauna, probably due to differences in their population turnover rates and their response to physical disturbance. The smaller size fractions (meiofaunal metazoans and foraminifera (generally 40–1000 μm) and prokaryotes (a few μm at most) are probably suspended or displaced rather than damaged by trawling activity, and are thus often capable of re-establishing themselves after disturbance. This recovery may be quite rapid so that it may only be detectable for a few weeks or months after disturbance. In addition, many show a high degree of metabolic and ecological plasticity, and have short and opportunistic life cycles. Disturbance may even increase the diversity of microhabitats, or help to spread smaller organisms; we saw rarer prokaryote and foraminifera taxa and more surficial foraminifera in more highly trawled areas. In contrast, the larger macrofauna (>1 mm and often >1 cm) run a higher risk of being damaged or killed by trawling, and many taxa are long-lived (5–10 years) and only reproduce once a year; they are therefore slow to recover from disturbance. This may be the reason for the higher prevalence of deeper burrowers in more highly trawled areas, in this and other studies. A more detailed analysis of the sediment depth distributions of each of these four organism groups in the context of trawling disturbance would be revealing.

The main factor affecting community composition in all four organism groups was sedimentary organic matter (either in terms of % OM or chlorophyll concentrations). This is not surprising since aphotic benthic food webs are known to be highly dependent on the amount and type of organic matter that is available as food. Thus, we found more deposit-feeding and fewer filter-feeding meiofauna and macrofauna taxa at sites with more organic matter and/or chlorophyll. Trawling has been shown in many studies to affect the amount and type of organic matter in sediments (e.g., Epstein et al., 2022; Tiano et al., 2024). However, our study agrees with the 61% of studies reported by Epstein et al. (2022) that showed no effect of trawling on organic carbon content. In our study, sediment properties are driven more by natural phenomena than trawling, perhaps since this area has high inputs of organic matter from pelagic primary production and terrestrial sources.

Lastly, this study did not attempt to disentangle interactions between the four organism groups, although these groups are closely linked by diverse ecological interactions (e.g., predation, competition, facilitation). Effects of trawling and environmental factors on these taxa are most certainly mediated by these ecological interactions. However, without better taxonomic resolution of the meiofaunal metazoans and prokaryotes, and given the current lack of knowledge of the ecological role of many of these taxa, especially the prokaryotes, this is a challenge.

CRediT authorship contribution statement

Laura Seidel: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Adele Maciute:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Mattias Sköld:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Irina Polovodova Asteman:** Writing – review & editing, Supervision, Resources, Methodology, Formal analysis. **Nina Rumpfhuber:** Writing – review & editing, Investigation. **Stefano Bonaglia:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Antonio Pusceddu:** Writing – review & editing, Supervision, Resources, Methodology. **Claudia Ennas:** Writing – review & editing, Investigation. **Mats Blomqvist:** Writing – review & editing, Resources, Data curation. **Francisco J.A. Nascimento:** Writing – review & editing, Resources, Methodology, Formal analysis, Conceptualization. **Clare Bradshaw:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, 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.seares.2026.102684.

Data availability

All data is available either in Suppl. Info or on online databases (see paper for details)

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