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Benthic diatom communities in deeper areas of the German Baltic Sea

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Abstract

The Baltic Sea is a shallow, semi-enclosed brackish ecosystem in northern Europe, which is strongly affected by climate change and other anthropogenic disturbances such as mobile bottom trawling. The resulting drag forces exerted by such fishing practice physically disturb the sea bed and impact all benthic organisms such as microphytobenthic communities, which represent key primary producers in marine soft-bottom ecosystems. Despite their ecological importance, little is known about the composition and productivity of these benthic communities in deeper areas of the German Baltic Sea. Therefore, this study investigates the occurrence and diversity of benthic diatoms in such unstudied areas, focusing on the Baltic Sea regions Fehmarnbelt, Rönnebank, and Oderbank. Sediment cores were collected from depths down to 36 meters, processed ex-situ and the biodiversity of benthic diatoms evaluated using morphological traits via light microscopy and high-throughput sequencing. The data provide novel insights on the occurrence of benthic diatom communities in deeper areas of the Baltic Sea and these microalgae seem to be suitable bioindicators to document any sediment disturbance by natural or anthropogenic forces.

Keywords

Microphytobenthos; Diatoms; Baltic Sea

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1. Introduction

The Baltic Sea is a shallow semi-enclosed, brackish ecosystem located in northern Europe, extending from the south in Germany and Poland to the Bothnian Sea in the north, just underneath the Arctic Circle. Water exchange with the Atlantic Ocean is limited due to geomorphological barriers, and water circulation is mainly driven by temperature and salinity gradients as well as wind force. The salinity varies from about 30 near the opening to the North Sea to close to 0 in the northernmost part next to Finland, thereby showing a strong horizontal gradient. Because of its rather young geological history with still ongoing dynamic geomorphological and subsidence processes along the coasts, cliff material is steadily eroding, transported by coastal parallel currents and deposited as sediment at other locations. Consequently, the surface sediment distribution and the upper part of the subsurface are very patchy in many parts of the Baltic Sea (Tauber and Lemke, 1995; Tauber et al., 1999). Fine sand, silt and clay typically accumulate in deeper basins while coarse material accumulates in shallow areas next to the shore.

The off-shore region of the German southwestern Baltic Sea is characterized by deep glacial meltwater channels (<35 m), deep basins (<45 m) and sandbanks (e.g. Oderbank) (Figure 1). In these areas movement of sediment particles is mainly caused by wind- and wave-driven hydrodynamic forces, but with increasing intensity and frequency, the anthropogenic influence also leads to significant disturbances of sediments. One of the main anthropogenic

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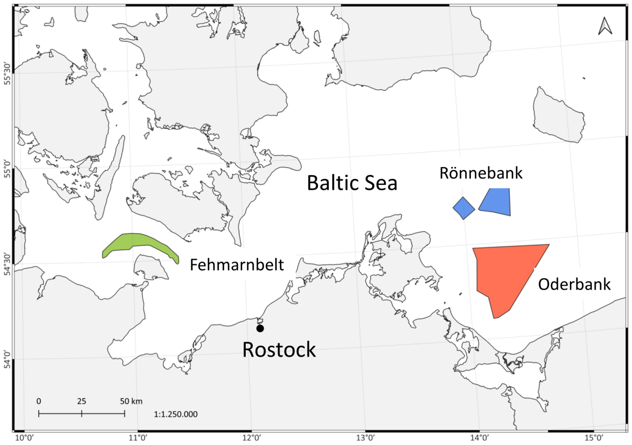

Figure 1. Map of the German Baltic Sea with the study sites Oderbank (red), Rönnebank (blue) and Fehmarnbelt (green). Samples were taken from board of a research vessel in a smaller area within each site. The map was generated with QGIS.

stressors for the Baltic Sea shelves is bottom-trawling. Fishing vessels using bottom trawls physically disturb the seabed by towing a gear (e.g. trawls) over the seafloor that damages or even kills many benthic organisms, reducing species biomass, abundance, and richness (de Groot, 1984; Collie et al., 2000; Sciberras et al., 2018). The drag force exerted by trawling gears can scrape off, re-suspend, and mix sediment particles (Palanques et al., 2001; O'Neill and Summerbell, 2016; Oberle et al., 2016), resulting in a strong disturbance of vertical physico-chemical gradients and for the inhabiting organisms. But the physiological, biogeochemical and finally ecological consequences are still unclear.

Shallow water sediments are typically occupied by microphytobenthic communities consisting of various phototrophic algal groups, such as Bacillariophyceae, Chlorophyceae, Dinophyceae, and Cyanobacteria, but in most cases are dominated by benthic diatoms. Such diatoms live either in the interspaces and porewater between soft bottom particles (=epipelic) or directly attached to soft bottom particles (=epipsammic) in the upper cm of the sediment (Karsten et al., 2021). The regular resuspension of sediments by hydrodynamic forces next to the shore and by bottom-trawling in off-shore areas can potentially lead to strong disturbances of benthic diatom communities as reflected by transient increases in shading effects due to higher turbidity or even the burial of cells. Both processes are expected to affect benthic diatom biomass and productivity, with unknown consequences for the benthic food web, as microphytobenthos plays a key role as a primary producer in many aquatic ecosystems (Cahoon, 1999). They also serve as a food source for higher trophic levels (Brown et al., 1969; Ragueneau et al., 2006; Christianen et al., 2017) and regulate vertical nutrient fluxes at the sediment-water interface (reviewed in Ragueneau et al. (2006), with references therein). Furthermore, microphytobenthic communities play a crucial role in the ecological dynamics of coastal environments, significantly contributing to oxygen production (Hope et al., 2019). Additionally, sediment-associated diatoms are able to enhance sediment stability through the secretion of adhesive extracellular polymeric compounds (EPS; Paterson, 1989; Miller et al., 1996; Lundkvist et al., 2007). Pelagic and benthic diatoms provide approximately 40–50 % of the global marine primary production (Nelson et al., 1995). The productivity and composition of microphytobenthic communities on tidal flats have been extensively investigated for over 40 years (for reviews see Underwood and Kromkamp, 1999; Glud et al., 2009; Serôdio and Paterson, 2022), whereas far fewer studies exist for the Baltic Sea. Nevertheless, the few data available clearly indicate that, for example, in the Gulf of Gdańsk 23% of the total primary production originated from microphytobenthic communities (Urban-Malinga and Wiktor, 2003), recalculated by Kuriyama et al. (2021). In addition, Ask et al. (2016) reported similar values for the Bothnian Bay with a share of 31% of the total annual primary production.

While at least some data exist on microphytobenthic communities of the shallow water coastal zone of the Baltic Sea, the deeper areas are almost unstudied. Therefore, we focused on the following research question: which diatom species occur in deeper areas of the Baltic Sea? This study was carried out within the framework of a German research project (https://www.io-warnemuende.de/dam-mgf-baltic-sea-home.html) on the effects of mobile bottom-contact fishing on marine benthic communities in the Baltic Sea from bacteria to macrozoobenthos. Because benthic diatom communities in deeper areas are so poorly investigated, we evaluated their structure for the first time using numerous intact sediment cores from Fehmarnbelt, Rönnebank, and Oderbank, in order to provide an initial baseline for biodiversity at these sites. Such data are essential to document any sediment disturbance and potential community changes by natural or anthropogenic forces.

2. Material and methods

2.1 Site description

We participated in cruises organized by GEOMAR Helmholtz Centre for Ocean Research Kiel, which provided the research vessel *Alkor*, and by the Leibniz Institute for Baltic Sea Research Warnemünde, which provided the research vessel *Elisabeth Mann Borgese* (EMB). Rönnebank was sampled in March 2022 during *Alkor* cruise (AL570; https://oceanrep.geomar.de/view/platform/Alkor/monograph=5Fcruise.html), whereas Fehmarnbelt (May/June 2020) and Oderbank (June 2021) were sampled during EMB cruises (EMB238 and EMB267; https://www.io-warnemuende.de/cruise-reports.html).

Table 1. List of sampling sites. FB: Fehmarnbelt, OB: Oderbank, RB: Rönnebank.

Station	Number of samples	Sediment characteristics	Salinity (S_A)	Water temperature [°C]	Depth [m]	Date of sampling
FB	8	muddy sediments with fine sand components	20	9.6–10.3	22	May/June 2020
OB	7	well-sorted fine sand with shell-gravel	8	11.8–14.6	14	June2021
RB	6	fine sand and gravel	12	4.5–5	38	Mar/April 2022

All sampling for this study took place in three different locations within the German sector of the Baltic Sea (Figure 1, Table 1). Fehmarnbelt is located between Kiel Bay and Mecklenburg Bay. It is a deep glacial meltwater channel with a maximum depth of 35 m. The salinity is around 20 S_A (absolute salinity) due to the near opening to the North Sea. The sediment of Fehmarnbelt is fine silt with a fluffy layer on top. The near-bottom water temperature ranged between 9.6 and 10.3°C (Table 1). Oderbank is located in the east of the German sector and is a shallow sandy bottom shoal within Adlergrund. The samples were taken here at 15 m depth with a salinity of 12 S_A and a temperature of 11.8 to 14.6°C (Table 1). Rönnebank is the deepest sampling site with 38 m located to the east within Arkona Bay. The near bottom temperature at the sampling site was between 4.5 and 5°C. The sediment here is composed of mainly fine sand and gravel (Table 1). All three locations are part of the Natura 2000 area in the Baltic Sea.

2.2 Field sampling and diatom analysis

Samples were taken in different locations within the areas of Fehmarnbelt, Oderbank and Rönnebank between 2020 and 2022. In total 8 samples were collected in Fehmarnbelt, 6 in Rönnebank and 7 in Oderbank. Samples were taken as a subsample from sediment cores collected by a multicorer (MUC) with Plexiglas-tubes of 10 cm Ø and with smaller tubes of 5 cm Ø. In addition, standard physicochemical parameters were recorded from the research vessel's CTD rosette including PAR (photosynthetically active radiation, 400–700 nm) values during the EMB cruises (for details see the respective cruise reports mentioned above). For both EMB cruises the diffusive attenuation coefficient of downwelling PAR (K_d (PAR) m^{-1}) was calculated according to Kirk (1994).

The sediment cores were first used for oxygen measurements on the intact core. For diatom community analyses, always the top surface layer of each sediment core (0–1 cm) was carefully removed using a spatula, right after the oxygen measurements. Each of the samples was either conserved with Lugol's solution and afterwards stored in the fridge or samples were frozen directly after sampling, until further preparations in the lab. After a thorough washing, organic matter was removed by boiling with hydrogen peroxide (35%), following the protocol of Kuriyama et al. (2023). The cleaned diatom frustules were then mounted on microscopy slides using Naphrax®(Brunel Microscopes Ltd, Wiltshire, UK). For identification of diatoms, a light microscope with 1,000× magnification was used (Olympus BX 52, Olympus Hamburg, Germany). For each sample a minimum of 200 intact frustules per sample were counted, but in most cases >350 valves were available for this approach. The identification of each diatom species is based on morphological traits and was carried out with the help of several monographies on diatom taxonomy and more specific publications (e.g Witkowski (2000) and taxonomic literature given by Woelfel et al. (2014)). After species identification, taxa counts were transformed into relative abundances and taxonomic names were verified according to (Guiry and Guiry, 2025).

2.3 Molecular sampling and DNA extraction

Sediment samples for the DNA extraction were taken out of a Multicorer core (10 Ø) from the upper 1 cm layer, and immediately frozen. DNA samples were stored at −20°C until further use. The extraction of the DNA was conducted with a commercial kit (DNeasy Power Score Pro, Qiagen, Hilden, Germany) following the manufacturer's instructions. PCR was conducted for the V4 region of 18S rRNA gene using TAReuk454FWD1 and TAReukREV3 primers following the protocol of Bradley et al. (2016). DNA concentrations were checked using gel electrophoresis (1.2% agarose gel) and Nanodrop® (PeqLab Biotechnology LLC; Erlangen, Germany). The PCR products were sent to Microsynth (SEQlab Göttingen, Germany) for library sequencing. Genetic differences among diatom species found in Oderbank and Fehmarnbelt were investigated based on the 18S V4, which is thelargest and most complex of the highly variable regions on the 18S locus (Zimmermann et al., 2011).

2.4 Bioinformatics

18S Illumina sequencing amplicons were denoised with DADA (version 1.18.0; Callahan et al., 2016), and operational taxonomic units (OTUs) were assigned to the denoised fragments using the sklearn classifier (version 0.23.1; Pedregosa et al., 2011) against rRNAs clustered to 99% identity from the SILVA database version 138 (Quast et al., 2013). Both procedures of denoising and assignment were carried out with the QIIME2 pipeline version 2020.11 (Bolyen et al., 2019). The obtained OTU table was then processed with the phyloseq (version 1.22.3; McMurdie and Holmes, 2013) and microbiome R package (version 1.9.96; Salonen et al., 2012; Shetty et al., 2017) and Bioconductor R packages.

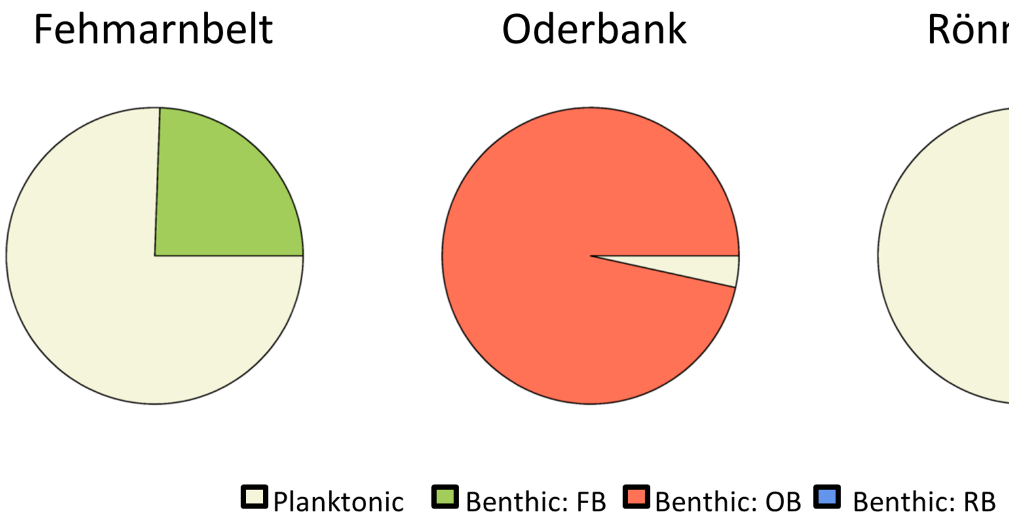

Figure 2. Relative abundance of benthic diatom valves compared to planktonic valves for each study site (Fehmarnbelt (n = 8), Oderbank (n = 7), Rönnebank(n = 6)). The data are based on microscopical counts of a minimum of 200 valves for each sample.

2.5 Statistics

Individual sediment core communities were counted under the light microscope and the relative abundance for each species was expressed as percentage of the total community. For all taxa >5% relative abundance mean value ± standard deviation was calculated. All calculations were undertaken using Microsoft Office Excel (2021). The statistical analyses and graphical illustrations were carried out with R (R Core Team, 2019) and R Studio (Boston, MA, USA). Cluster analyses and analysis of similarity (AnoSim) were calculated using Bray-Curtis distance and 1000 permutations in the vegan package (Barry and Hartigan, 1999), $p < 0.05$ was considered as significant. Figures were illustrated, using ggplot2 (Wickham, 2016).

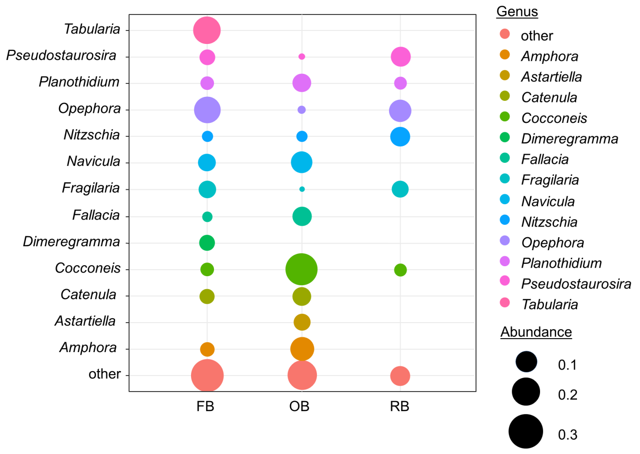

Figure 3. Proportions of the most abundant benthic diatom genera grouped by the sampling sites Fehmarnbelt (FB, n = 8), Oderbank (OB, n = 7) and Rönnebank (RB, n = 6) based on counts of a minimum of 200 valves per sample, visualized as a bubble plot.

3. Results

The samples were taken in three different locations. The sediment varied from muddy sediment with fine sand components in Fehmarnbelt to fine sand with shell gravel in Oderbank and Rönnebank. Salinity differed also among locations. The highest salinity was measured in Fehmarnbelt with 20 S_A and the lowest in Oderbank with 8 S_A. Rönnebank was in between those values with 12 S_A. The diffusive attenuation coefficient K_d(PAR) m^{-1} at Fehmarnbelt slightly varied between 0.31 and 0.34, while it was almost stable at Oderbank with 0.38.

In total 102 benthic diatom taxa were identified in Fehmarnbelt, 71 in Oderbank and 13 taxa in Rönnebank (Figure 2). For the area of Oderbank a total of 97% of all valves counted were assigned to benthic diatoms and only 3% were members of planktonic genera (Figure 2). In Fehmarnbelt 24% of all counted valves belonged to benthic diatoms and 76% were planktonic species. In Rönnebank the least amount of benthic diatoms was counted with a share of only 3% benthic diatom species compared to 97% share of planktonic diatoms (Figure 2).

The main genera of benthic diatoms found in Fehmarnbelt with an abundance > 5% were *Tabularia* spp. (17.3 ± 8.4%), *Opephora* spp. (16.8 ± 11.1%), *Fragilaria* spp. (6.1 ± 4.1%), *Navicula* spp. (8.2 ± 5.6%), *Pseudostaurosira* spp. (5.4 ± 3.8%) and *Dimeregramma* spp. (5.4 ± 3.7%) (Figures 3 and 5). In the area of Oderbank members of *Cocconeis* spp. (24.2 ± 7.6%), *Amphora* spp. (12.8 ± 3.5%), *Navicula* spp. (9.8 ± 2.9%), *Fallacia* spp. (7.1 ± 1.6%),

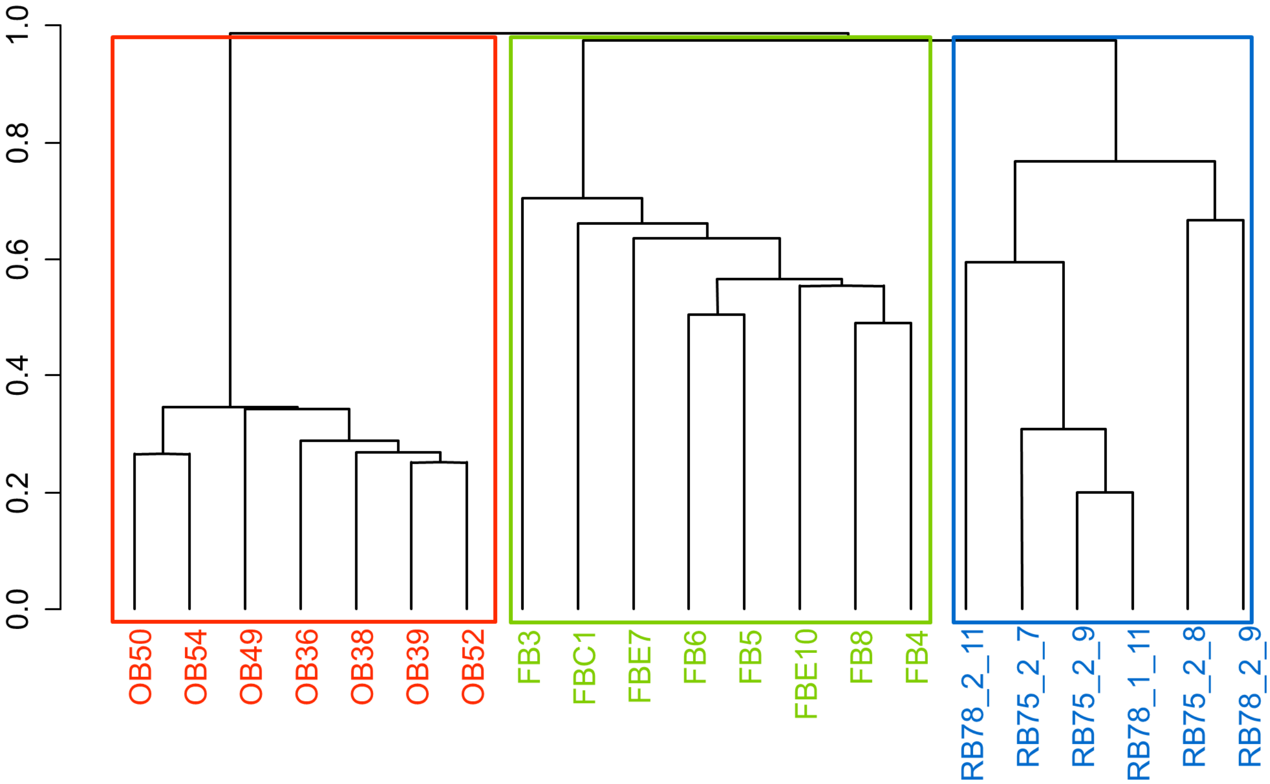

Figure 4. Cluster analysis of benthic diatom species composition across the three sites based on Bray-Curtis dissimilarity. The dendrogram illustrates the similarity of community structure, with branch colors indicating site-specific groups. FB – Fehrmanbelt (green), OB – Oderbank (red), RB – Rönnebank (blue).

Planothidium spp. (6.8 ± 3.1%), *Catenula* spp. (6.9 ± 3.9%) and *Astartiella* spp. (5.7 ± 2.7%) dominated (Figures 3 and 5). In Rönnebank much fewer species were observed in general, and the genera counted with an abundance >5 % were *Navicula* spp. (52.8 ± 19.2%), *Opephora* spp. (11.1 ± 5.1%), *Nitzschia* spp. (8.3 ± 3.1%), *Pseudostaurosira* spp. (8.3 ± 4.7%) and *Fragilaria* spp. (5.6 ± 3.0%) (Figures 3 and 5).

In the sediment samples from Oderbank, the total number of epipelic taxa was higher than that of epipsammic species, but the latter were more abundant: the epipsammic diatom group attached to sand grains made up 39.5% of the benthic diatoms, while the group of epipelic diatoms accounted for 21.5%. However, species that are documented to have different life-forms including epipelic and epipsammic ones reached with 39.1% of all valves a relatively large portion of total benthic diatom valves.

For Fehmarnbelt the total number of epipsammic taxa was higher than any other group with 44 different species and a total benthic abundance of 50.5%. Epipelic species made up 13.8% of the total benthic valve counts. Species with a mixed life-form of epipsammic, epipelic, epiphytic etc. made up 11.7%. Six additional valve types could not be assigned to any described taxa.

The most abundant benthic diatom group at Rönnebank is epipelic with 66.7% of the total benthic valve count. This large portion is mostly due to one species that occurred in all samples of Rönnebank with an abundance of 52.8% of all counted valves, namely *Navicula* cf. *flagellifera* Hustedt.

Cyclotella choctawhatcheeana A.K.S. Prasad, classified by Snoeijs (1993) as pelagic and sometimes epilithic taxa, was also identified in samples from Oderbank and Fehmarnbelt. Although it can also occur attached to sand grains (Kuriyama et al., 2023), in our samples it was counted mainly as pelagic. Purely planktonic taxa were observed in all sampling sites, with the least percentage in Oderbank (3% plankton). The most abundant planktonic genera observed were *Thalassiosira* spp., *Skeletonema* spp. and *Chaetoceros* spp. in a permanent stage.

The benthic diatom community composition differed significantly between the three sites, each site forming a separate cluster (AnoSim: $R = 0.9996$, $p = 0.001$; Figure 4).

Comparing the counted genera from Fehmarnbelt and Oderbank (Figure 6), Fehmarnbelt has a larger set of exclusive species (16) compared to Oderbank (8), but there is still a significant overlap, with 18 species shared between the two sites.

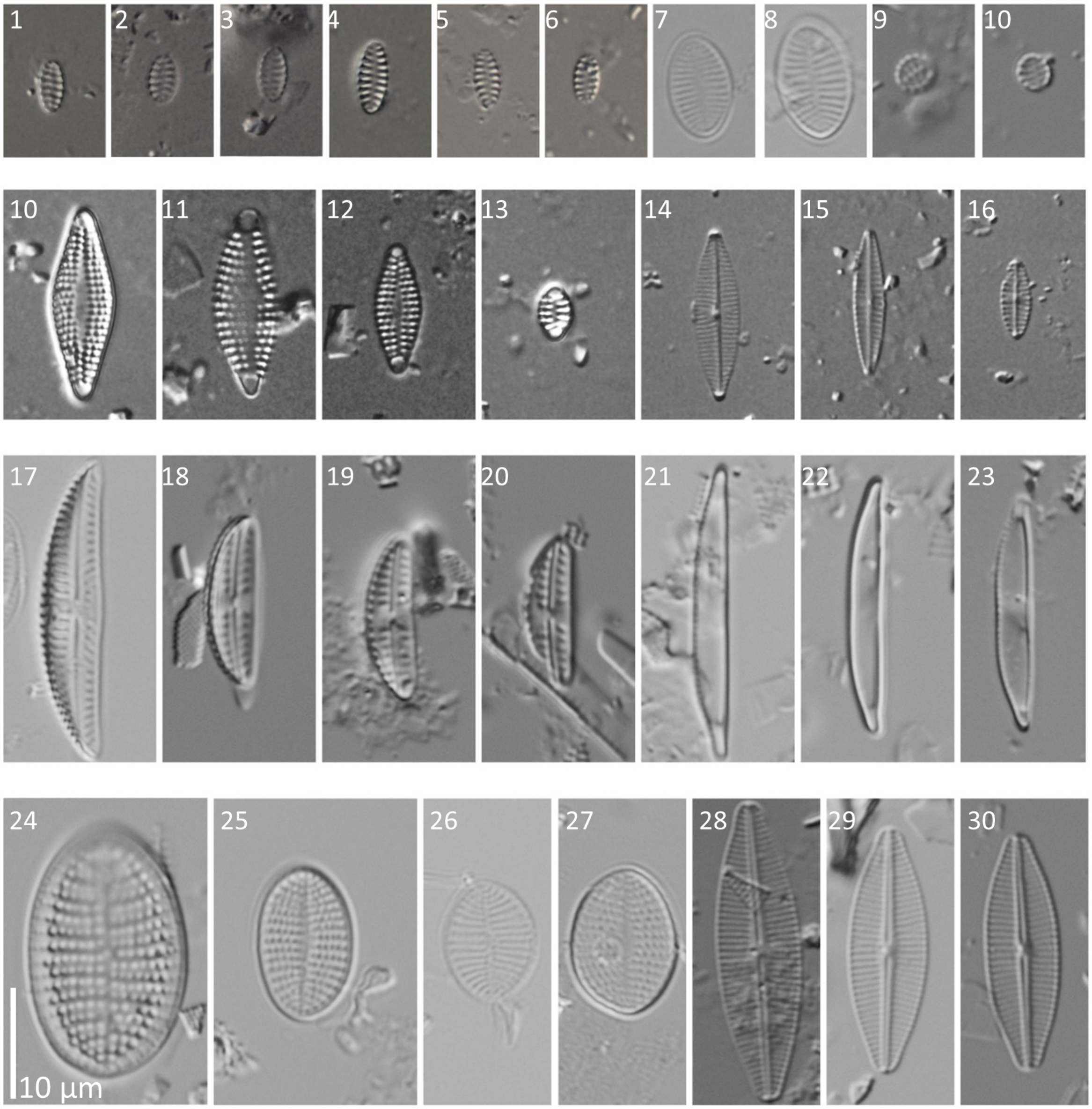

Figure 5. Representative light microscopic images of valves of the most abundant benthic diatom species found at the different sampling sites. No. 10–6: *Opephora guenter grassii*, no. 7–8: *Cocconeis nugalas*, no. 9–10: *Nanofrustulum krumbeinii*, no. 11–13: *Dimeregramma menor*, no. 14–16: *Navicula perminuta*, no. 17–20: *Amphora inariensis*, no. 21–23: *Catenula adherens*, no. 24–27: *Cocconeis disculoides*, no. 28–30: *Astartiella bahusiens*. Scale bar (no. 24) = 10 μm.

Samples for the molecular biological community analysis were sampled only at Oderbank and Fehmarnbelt (Figure 7). While in the samples of Fehmarnbelt only planktonic species could be identified using the molecular marker V4 region of the 18S rRNA gene, samples from the Oderbank showed signals also from benthic species. As a result, the diatom composition between those sites differed significantly (AnoSim: $R = 0.3906$, $p = 0.001$). Most Fehmarnbelt samples form a unique cluster (Figure 4 – green block). In comparison, the diatom communities from Oderbank were more heterogeneous, resulting in three distinct clusters (Figure 4 – red block).

Detected species with the highest abundances were *Skeletonema* spp., *Thalassiosira* spp. and *Chaetoceros* spp. These molecular data are similar to those derived from the morphological light microscopy approach (Figure 8) in terms of planktonic species. The genus *Pinnularia* was detected only by using the molecular approach but not with the morphological method. However, closely related species of *Chamaepinnularia* were observed several times in the Oderbank sediment samples.

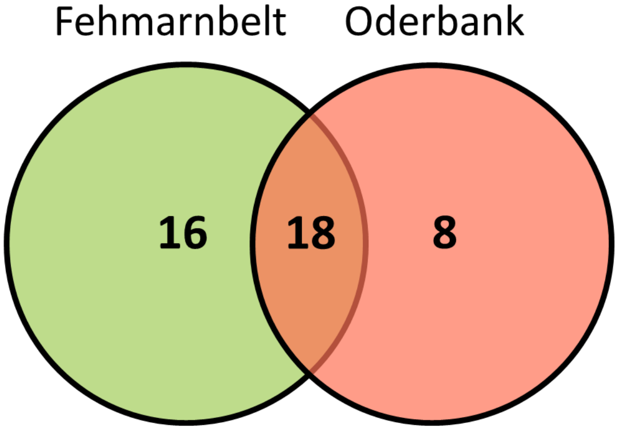

Figure 6. Comparison of counted genera found in Fehmarnbelt (n = 8) and Oderbank (n = 7). Based on counts of a minimum of 200 valves per sample.

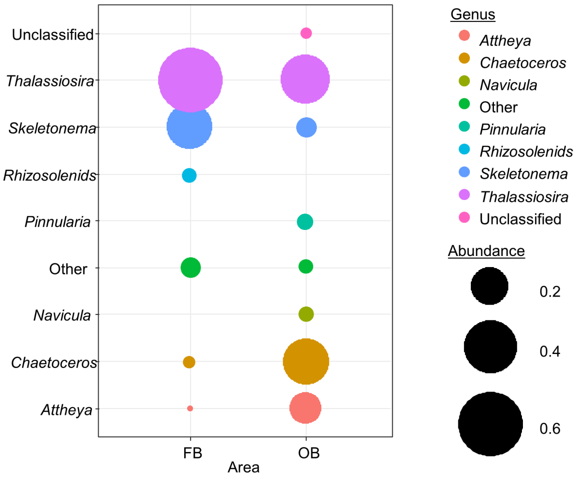

Figure 7. Comparison of diatom genera (plankton and benthic) detected with NGS in Oderbank (n = 46) and Fehmarnbelt (n = 44), visualized as a bubble plot. Depicted in the diagram are the most common genera for both areas. NGS analysis based on V4 region of the 18S rRNA subunit. OTUs used over following threshold: Detection 0.1%, Prevalence 5%.

4. Discussion

This is the first field study on benthic diatom communities from deeper off-shore areas of the Baltic Sea, with a focus on three different sites within the German sector of this brackish ecosystem. The diatom community was mostly composed of benthic diatom genera. 97% of all valves counted were in fact benthic and only 3% of the valves belonged to planktonic genera. Consequently, the off-shore Oderbank community resembled a typical microphytobenthic community as described from the shallow coastal zone of different Baltic Sea locations (Witkowski, 1994; Vilbaste et al., 2000; Virta and Soininen 2017; Kuriyama et al., 2023). Fehmarnbelt is located in the western Baltic Sea, and is characterized by a deep glacial meltwater channel, 22 m depth, fine silt sediment with a fluffy layer on top, and a salinity of around 20 S_A. Here the composition of the diatom genera conspicuously differed from Oderbank as planktonic species (76%) dominated over benthic taxa (24%). At the Fehmarnbelt station the microphytobenthic community was partly composed of typical benthic species, but the most abundant group was represented by planktonic diatom specimens that most probably sedimented from the water column along with tychoplanktonic taxa. Tychoplankton refers to diatoms that are typically found attached or associated to sediments or solid substrates and that enter the water column when physical forces (waves, currents etc.) suspend them or tear them loose from the substrate (Hendey, 1965). Rönnebank is the deepest sampling area of those three investigated in the present study with depth of 38 m and characterized by fine silt and gravel sediment and a salinity of 12 S_A. Considering the depth of this sampling site the composition of the diatom community is not surprising with 97% planktonic genera over only 3% benthic species. Although the number of benthic diatom species strongly declined at Rönnebank, some taxa, such as *Navicula* cf. *flagellifera*, were highly abundant, pointing to numerous vital and physiologically active cells. Nevertheless, the diversity of microphytobenthic communities declined with increasing water depth across the three sampling stations which might be explained by the underwater light conditions. Optical measurements in the Gulf of Finland indicated a 1% euphotic depth of 18 m during summer, i.e. at this water depth 1% of the incident solar PAR (photosynthetically active radiation) could be detected (~16 µmol photons m^{-2} s^{-1}) (Luhtala et al., 2013). Other studies in this region reported even depths between 25 and 35 m in summer with sufficient light for marine phototrophic organisms (Lindström, 2000). However, the underwater light conditions in the Baltic Sea and adjacent inner coastal waters are extremely variable due to regular meteorological and hydrodynamic changes along with seasonal phytoplankton blooms, suspended particles and colored dissolved organic matter (cDOM) (Schubert et al., 2001). If we consider the data of Luhtala et al. (2013) for calculation of the underwater conditions at 15 m depth at the Oderbank and 22 m depth at Fehmarnbelt, ~20–30 µmol photons PAR m^{-2} s^{-1} and ~10–15 µmol photons PAR m^{-2} s^{-1}, respectively, can be estimated for a typical summer day. For Rönnebank we expect <5 µmol photons PAR m^2 s^{-1} at 38 m depth. These considerations are supported by the calculated diffusive attenuation coefficients K_d(PAR) m^{-1} of 0.31–0.34 at Fehmarnbelt and 0.38 at Oderbank, both for June. During a sunny late spring day around 5 and 7

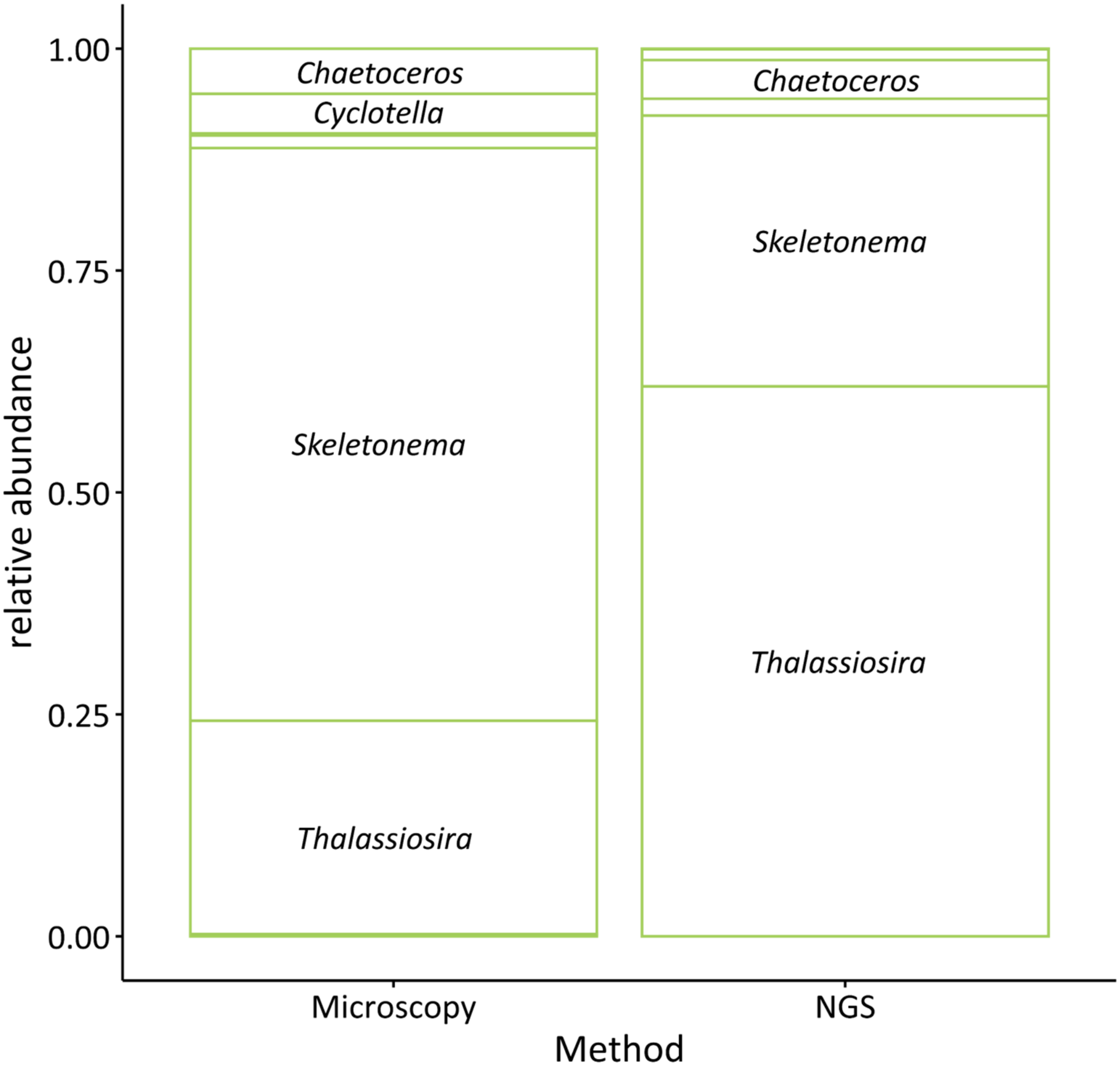

Figure 8. Comparison of diatom genera (plankton) detected with NGS and valves counted using microscopy for species found in Fehmarnbelt (n = 8) only. Graph includes only valves of planktonic diatoms.

μmol photons PAR m^{-2} s^{-1} would reach the sea floor of Fehmarnbelt and Oderbank, respectively. Such seemingly low photon fluence rates are more than sufficient to support photosynthetic growth, as theoretical considerations based on biochemical knowledge clearly indicate as the absolute lower light requirement for photosynthetic growth in microalgae light values of around 0.01 μmol photons PAR m^{-2} s^{-1} (Raven et al., 2000). In the water column, phytoplankton primary production has been documented at photon fluence rates as low as 0.3–5 μmol photons PAR m^{-2} s^{-1} (Robinson et al., 1995), and the depth-record for viable benthic diatoms stems from 67 to 191 m of the North Carolina continental margin with light levels >0.106 μmol photons PAR m^{-2} s−1 (McGee et al., 2008). A recent study by Hoppe et al. (2024) confirmed such low light values, as these authors reported photosynthetic growth and algal biomass buildup of under-ice associated Arctic diatoms at a daily average photon fluence rate $<0.04 \pm 0.02$ μmol photons PAR m^{-2} s^{-1}, which is >100-fold less compared to the calculated PAR values for the Baltic Sea stations. Nevertheless, continuous underwater light measurements over the course of the seasons are missing for deeper stations of the Baltic Sea.

Many benthic diatoms from the Baltic Sea exhibit very low light requirements for photosynthesis together with a pronounced photophysiological plasticity (Prelle et al., 2021; Prelle and Karsten, 2022), both of which might explain their abundance and obvious ecological success at greater depth in the off-shore region. Besides photosynthesis, also the presence of dissolved organic molecules such as cDOM can potentially support a heterotrophic or mixotrophic lifestyle in benthic diatoms. Both facultative and obligate heterotrophic metabolism has been documented in benthic diatoms (Villanova et al., 2017). Prelle and Karsten (2022) reported strong stimulation of growth in various benthic Baltic Sea diatoms in the dark by organic compounds derived from a coastal peatland, providing experimental evidence for heterotrophic metabolism.

The presence of microphytobenthic communities at greater depth in the off-shore region of the Baltic Sea is a significant finding, as these phototrophic biofilms play a generally crucial role as primary producers in aquatic ecosystems (Cahoon, 1999) and provide numerous other ecosystem services such as food sources for many invertebrates and a stabilization of sediment surfaces etc. (see Introduction). However, benthic diatoms have mainly been studied in the intertidal zone and the shallow water area of various coasts of the Baltic Sea (Ask et al., 2016; Christianen et al., 2017; Karsten et al., 2021), and hence the assumed function of these phototrophs, also in deeper off-shore regions, still has to be verified. Besides a lack of data concerning the ecological functions of microphytobenthic communities in deeper areas of the Baltic Sea and their contribution to the ecosystem, there is also very little known on the structure of such communities.

Overall, we found a surprisingly high number of benthic diatom species and a diverse community in our samples. We identified 102 different benthic diatom taxa in the Fehmarnbelt samples, 71 in the Oderbank samples and still 13 species in Rönnebank samples. Considering the depth of the sampling area the diversity can be described as high compared to other studies in purely shallow coastal areas, for which authors reported 103 taxa in a brackish lagoon of the southern Baltic coast (Kuriyama et al., 2023), 129 taxa in the littoral zone of the Gulf of Riga (Vilbaste et al., 2000), 230 taxa in the Gulf of Finland and Bothnian Bay (Virta and Soininen, 2017), or 245 taxa in a rewetted coastal peatland (Schultz et al., 2024). The analysis of benthic diatom assemblages from sediment samples collected at Oderbank, Fehmarnbelt, and Rönnebank revealed distinct differences in species diversity, abundance, and life-forms. These findings highlight the complexity of diatom communities in marine environments.

The diatom communities in Fehmarnbelt and Oderbank are made up of a mix of epipsammic, epipelic and partly epiphytic taxa. At Oderbank, the total number of epipelic taxa was higher than that of epipsammic taxa. However, the epipsammic diatom group, which attaches to sand grains, was more abundant, accounting for 39.5% of all benthic diatoms. In contrast, the epipelic diatoms made up only 21.5% of the benthic community. Interestingly, species capable of adopting multiple life-forms, including epipelic and epipsammic, represented a substantial 39.1% of all benthic diatom valves. In Fehmarnbelt, the benthic diatom assemblage was characterized by a higher total number of epipsammic taxa than any other group, with 44 identified species contributing 50.5% to the total benthic diatom abundance. Epipelic species, in comparison, accounted for 13.8% of the total benthic valve counts, while taxa with mixed life-forms (epipsammic, epipelic, epiphytic, etc.) contributed 11.7%. Rönnebank presented a contrasting pattern, where epipelic diatoms dominated the benthic community, comprising 66.7% of the total benthic valve count. However, the only abundant benthic species observed in Rönnebank is an unidentified species belonging to the genera *Navicula* spp. Notably, many species could not be identified further than to genus level, reflecting a significant gap in current taxonomic knowledge, especially in the southern areas of the Baltic Sea. The community structure found is common in many shallow water bodies of the Baltic Sea as described earlier (e.g., Vilbaste et al., 2000; Kuriyama et al., 2023). However, the striking differences in diatom community composition among the surveyed areas are noteworthy, especially given their geographic proximity. We found 16 genera that were only abundant in Fehmarnbelt (e.g. *Tabularia* spp. 17.3% and *Dimeregramma* sp. 5.3%) and 8 genera that only occurred in Oderbank (e.g. *Astartiella* spp. 5.8%). In addition, the benthic diatom communities described in the present study are similar, but not identical to those found at shallow coastal sites of the Baltic Sea (Vilbaste et al., 2000; Schultz et al., 2024, and references therein). On the other hand, abundant species such as *Cocconeis disculoides* from Oderbank or *Dimeregramma minus* from Fehmarnbelt are not known from shallow coast sediments. Consequently, the benthic diatom communities from different Baltic Sea habitats appear to consist of a mixture of widely distributed and highly specific taxa.

Most interesting is the fact that some abundant species of inner coastal waters of the southern Baltic Sea, such as, for example, *Epithemia gibba* and *Rhoicosphenia abbreviata*, which are known as indicators for eutrophic water conditions in the Darss Zingst lagoon (Kuriyama et al., 2023), were completely missing in our off-shore samples. The ecological preferences of dominant benthic diatom species in the Gulf of Gdańsk were studied by Stachura-Suchoples (2001), who considered *Pseudostaurosiropsis geocollegarum*, *Opephora guenter-grassii* and *Opephora mutabilis* as indicators for oligotrophic, and *Cyclotella choctawhatcheeana* and *Pseudostaurosira brevistriata* for eutrophic conditions. In our samples from Oderbank and Fehmarnbelt, both oligotrophic and eutrophic taxa occurred in parallel and in similar abundance, indicating that the bioindicator concept of Stachura-Suchoples (2001) is not plausible. An explanation might be related to physicochemical differences in near-shore (Gulf of Gdańsk) versus off-shore sites. However, the Baltic Sea with its diverse coastal zones and off-shore provinces is considered as a widely eutrophic marine ecosystem (Savchuk, 2018), and hence the occurrence of the oligotrophic species *P. geocollegarum*, *O. guenter-grassii* and *O. mutabilis* indicates that they can also tolerate a wide range of trophy levels. Despite the geographical proximity of the areas studied, they differ not only in depth, temperature, salinity and sediment characteristics, but most probably also in the availability of light, thereby explaining the site-specific differences in diatom communities. Nevertheless, Oderbank and Fehmarnbelt still share a significant overlap of 18 species that occur in both areas. The genus *Navicula* spp. is in all three sampling sites one of the most abundant genera.

For the genetic identification of the diatom genera, we utilized the widely applied V4 region of the 18S rRNA locus, known for its high variability (Zimmermann et al., 2011). This region is particularly effective for detecting genetic differences on the genus level, making it a popular choice in molecular ecology studies. Using Next-Generation Sequencing (NGS), we were able to predominantly identify planktonic diatom genera in our samples.

While the molecular data largely mirrored the LM observations in terms of planktonic diatom genera, they failed to detect most benthic taxa that were clearly identified through light microscopy – especially in samples from Oderbank, where LM revealed up to 97% benthic valves. This discrepancy highlights substantial limitations in current genetic reference libraries, which lack sufficient representation of benthic species. Many sequences remain unassigned, and the incomplete reference coverage restricts the accurate identification of benthic diatoms using genetic methods. As a result, it is currently impossible to reliably encode benthic diatoms through NGS alone. Given this limitation, LM currently remains the most reliable method for the identification of marine benthic diatoms. However, our findings also suggest that the V4 region may not be the optimal genetic marker for all benthic diatom taxa. Alternative loci, such as *rbc*L, which offers broader coverage and better reference support for benthic diatoms, might provide more accurate and comprehensive results in future studies on biodiversity.

In conclusion, while NGS using the V4 region is a powerful tool for detecting/identifying planktonic diatoms, its current application for benthic taxa is strongly limited. Further refinement of genetic libraries and the consideration of additional and/or alternative markers are necessary to improve the accuracy of molecular diatom identification particularly for benthic taxa.

This study provides a crucial baseline for future research on the structure of microphytobenthic communities and their key functions, such as primary production, in deeper off-shore regions of the Baltic Sea. Benthic diatoms in limnic systems have been used worldwide over decades as biological indicator organisms assessing the ecological status of water bodies. Their sensitivity to multiple abiotic factors, for example, eutrophication, pH and salinity, is well documented (Kwandrans et al., 1998; Kelly et al., 2009; Antonelli et al., 2017) and are nowadays systematically used in EU biomonitoring programs ("biological quality elements") legally required by the European Water Framework Directive. The goal is to assess the ecological status of aquatic habitats (= "ecosystem health") within all EU countries as a benchmark for both joint scientific and management purposes.

Currently, little to no data are available on benthic diatoms in deeper regions of the German Baltic Sea, and thus information on their diversity in the southern Baltic Sea is limited. This study helps to bridge this knowledge gap by documenting benthic diatom communities at offshore sites and provides a foundational dataset to support future research and monitoring programs. Given their well-established role as bioindicators in freshwater systems, understanding which diatom species are present in the Baltic Sea is essential for developing effective monitoring strategies. Such data can be particularly useful in assessing the impacts of sediment disturbances caused by anthropogenic activities such as bottom trawl fishing. By providing a clear picture of benthic diatom diversity, this study lays the groundwork for future investigations into environmental changes and human impacts on the Baltic Sea marine ecosystem, reinforcing the importance of microphytobenthic communities in sustaining primary production and overall ecosystem health.

5. Conclusion

This study provides the first experimental insights into benthic diatom communities in deeper off-shore areas of the Baltic Sea, establishing an essential baseline for future research. Our findings reveal distinct differences in diatom community composition among the three study sites, shaped by factors such as depth, salinity, and sediment characteristics. While the shallow Oderbank was dominated by benthic diatom species, Fehmarnbelt and Rönnebank exhibited a higher proportion of planktonic taxa, likely due to reduced light availability with increasing depth. Despite limitations in genetic identification, morphological analyses uncovered a surprisingly high diversity of benthic diatoms even at greater depths, underscoring their ecological significance. Future research should build on these findings by investigating seasonal variations in benthic diatom communities and their responses to environmental stressors such as sediment resuspension, eutrophication, and climate change. Additionally, integrating advanced molecular techniques with traditional microscopy could enhance species identification and improve our understanding of diatom diversity in these habitats. Finally, exploring the functional role of benthic diatoms in nutrient cycling and sediment stability could provide valuable insights into their broader ecological impact within the Baltic Sea ecosystem.

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Conflict of interest

None declared.

Supplementary material

Supplementary material associated with this article can be found here.

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