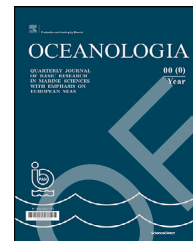


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ORIGINAL RESEARCH ARTICLE

Microphytobenthic primary production on exposed coastal sandy sediments of the Southern Baltic Sea using ex-situ sediment cores and oxygen optodes

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Abstract The shallow coastal water zone of the tide-less southern Baltic Sea is dominated by exposed sandy sediments which are typically inhabited by microphytobenthic communities, but their primary production is poorly studied, and hence four stations between 3.0 and 6.2 m depth were investigated. Sediment cores were carefully taken to keep the natural layering and exposed in a controlled self-constructed incubator. Respiratory oxygen consumption and photosynthetic oxygen production were recorded applying planar oxygen optode sensors. We hypothesized that with increasing water depths the effects of wind- and wave-induced erosion and mixing of the upper sediment layer are dampened and expected higher microphytobenthic biomass and primary production in the incubated cores.

Our data partly confirm this hypothesis, as cores sampled at the most exposed stations contained only 50% chlorophyll *a* m⁻² compared to the deeper stations. However, primary production was highly variable, probably due to fluctuating sediment-disturbing conditions before the cores were taken. Due to these physical forces sand grains were highly mobile and rounded, and small epipsamic benthic diatoms dominated, which preferentially occurred in some cracks

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and crevices as visualized by scanning electron microscopy. The data fill an important gap in reliable production data for sandy sediments of the southern Baltic Sea, and point to the ecological importance and relevant contribution of microphytobenthic communities to the total primary production of this marine ecosystem. Oxygen planar optode sensor spots proved to be a reliable, sensitive and fast detection system for ex-situ oxygen exchange measurements in the overlying water of intact sediment cores.

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1. Introduction

The Baltic Sea is a brackish young marginal sea in northern Europe. The German coastline of the Baltic Sea is roughly 2,000 km long (Jurasiński et al., 2018 and references therein), and the shoreline is characterized by a range of highly diversified coastal forms from rocky cliffs to sandy beaches. The southern Baltic Sea shoreline in particular exhibits a highly dynamic geomorphology. Rock particles are steadily eroding from cliff lines, transported by coastal parallel currents and deposited at other places, i.e. the processes of abrasion and sedimentation lead to a loss of upland relief and at the same time to the formation of spits, lagoon systems, shallow subtidal flats and wind flats (Karsten et al., 2012; Schwarzer, 1996). Besides these specific geomorphological processes, the Baltic Sea represents a non-tidal system. The tidal range is usually only 12–15 cm in the western Baltic Sea, and can be even lower in the eastern part (e.g. Polish coast 5 cm), but wind direction and wind speed in combination with atmospheric pressure might temporarily induce high waves and change sea water levels (Lass and Magaard, 1996). Consequently, meteorological and hydrodynamic conditions shape the southern Baltic Sea coastline resulting in many exposed shallow water sandy sites.

Coastal sediments are typically inhabited by microphytobenthic communities, which can make up about 30% of the global total coastal primary production (Ask et al., 2016; Cahoon, 1999; Gerbersdorf et al. 2005; Schreiber and Pennock, 1995). Benthic microalgal communities typically exhibit a high diversity of taxa consisting of representatives of euglenids, chlorophytes, cyanobacteria, dinoflagellates and diatoms (Cotijn and De Jonge, 1984; Launeau et al., 2018; Sundbäck and Miles 2002). But at most sites the dominant group are benthic diatoms (Cahoon, 1999), which fulfill important ecological functions in shallow marine inter- and subtidal environments as they live at the sediment-water interface and thus directly influence various exchange processes between these compartments (e.g. Sundbäck et al., 2000). As primary producers they are responsible for a huge proportion of carbon fixation (Ask et al., 2016; Blasutto et al., 2005; Cahoon, 1999; MacIntyre et al., 1996) and thus are an important supplier of organic carbon to grazers as well as sediment feeding macro- and meiofauna (Middleburg et al., 2000; Oakes et al., 2010). The release of dissolved organic carbon by the excretion of extrapolymeric substances (EPS) is common for benthic diatoms and thus an important carbon supply for bacteria (Aslam et al., 2012; Hanlon et al., 2006). In addition, since EPS are sticky these compounds stabilize and modify sediment surfaces (De Brouwer et al.,

2005), thereby reducing hydrodynamic erosion and controlling vertical fluxes of oxygen and other elements at the sediment-water interface (Risgaard-Petersen et al., 1994). Furthermore, benthic diatoms strongly influence bacterial remineralization in the upper sediment layer as oxygen fuels nitrification but inhibits denitrification (Cook et al., 2007). Released nutrients, in turn, are beneficial for benthic algal growth.

Habitat conditions for microphytobenthic communities can be highly diverse, and hence their biomass and productivity varies along multifactorial spatio-temporal environmental gradients such as, for example, small-scale dynamics of sediment grain-size distribution (Orvain et al., 2012). But also other physical and biological gradients such as tides, bathymetry, topography, light availability due to turbidity, deposit-feeders, or sediment nutrient stocks might affect benthic diatom photosynthetic activity (Haro et al., 2020; Jesus et al., 2009; Kromkamp et al., 1995). Benthic diatoms live either epipsamic (attached to sediment grains) or epipellic (in the interspaces between sediment grains) in the uppermost millimeter of sediments (Woelfel et al., 2007). The diatom lifestyle depends on the exposition (e.g. wave energy and currents) and sediment type (e.g. grain size) since exposed sandy sediments typically harbor rather small-sized epipsamic species (Vilbaste et al., 2000; Woelfel et al., 2007) whereas the occurrence of larger epipellic taxa is limited by sand-scouring processes (Sabbe, 1993). Besides seasonality and light conditions, mechanical stress acting on the seafloor such as wind induced currents or waves are important physical factors controlling the establishment of such phototrophic biofilms. Frequent resuspension and deposition of sediment particles at exposed sites lead to recurrent disturbance temporarily enhancing shading effects or even the burial of diatom cells with negative consequences for the development of microphytobenthic biofilms on top of such sediments. On the other hand, raphid benthic diatoms are able to escape unfavorable conditions via vertical migration in or out of the sediment (Harper, 1969). Thus, it is likely that these phototrophs are capable to recover from disturbance events of sediments such as after storms, and resume their photosynthetic activity immediately (Wulff et al., 1997).

Microphytobenthic communities were studied all over the world (Cahoon, 1999). The latter author compiled > 80 studies in his comprehensive review and concluded that previous estimates on microphytobenthic primary production had markedly underestimated their relevance and contribution for coastal shallow water production. Overall, Cahoon (1999) provided for the first time an annual global

estimate of 5×10^8 tons C by microphytobenthic primary production, and indicated marine areas which were relatively well studied (i.e. temperate regions), while others were grossly under-sampled, such as the polar regions at that time. Based on 13 studies [Glud et al. \(2009\)](#) reviewed the importance of microphytobenthic communities for the Arctic shallow water zone and calculated an annual production between 1.1 and 1.6×10^7 tons C. In the temperate zone of Europe there have been many studies undertaken on microphytobenthic primary production in tide-influenced habitats, particularly in the mouth of estuaries and the Wadden Sea (e.g. [Colijn and Dijkema, 1981](#); [Daggers et al., 2018](#); [Frankenbach et al., 2020](#); [Joint, 1978](#); [MacIntyre et al., 1996](#); [Virta et al. 2019](#)), which all confirm their ecological importance for soft bottom coasts. In contrast, the Baltic Sea is much less studied, and hence only very few data exist (Lagoons of German Baltic Sea coast: [Meyercordt and Meyer-Reil, 1999](#); [Wasmund, 1986](#); [Yap, 1991](#); Bay of Gdansk, Poland: [Urban-Malinga and Wiktor, 2003](#); Bay of Riga, Estonia and Latvia: [Vilbaste et al., 2000](#)), which indicate gross primary production rates between 0.2 and 41.8 $\text{mg C m}^{-2} \text{h}^{-1}$ depending on the sediment (mud vs. sand), water depth and season, and which is generally lower than in tidal systems such as the Ems Dollard Estuary (10 – 115 $\text{mg C m}^{-2} \text{h}^{-1}$, [Colijn and de Jonge, 1984](#)). In addition, the rather few Baltic Sea studies are rather old and had been carried out under different environmental settings (sandy beach vs. sheltered lagoon) using different methodological approaches (^{14}C vs. O_2). Consequently, direct comparison of the limited data might be difficult.

Therefore, the focus in the present study was on microphytobenthic primary production at four stations at an exposed sandy coastal site of the Southern Baltic Sea, north east of Rostock in close vicinity to the peatland Hütelmoor at water depths between 3.0 and 6.2 m. This site is characterized by strong wind- and wave-induced mixing of the upper sediment layer along the coastline ([Jurasiński et al., 2018](#)). We hypothesized that with increasing water depths the effects of these physically disturbing factors are dampened and hence favour higher microphytobenthic biomass and primary production. Intact sediment cores were taken by SCUBA divers between April and July 2017, exposed in the laboratory under controlled conditions and measured using oxygen optodes.

2. Material and methods

2.1. Site description

The Hütelmoor sampling stations S21, S25, S41 and S45 are located on near shore exposed sandy sediments at a north-westerly oriented coastline ([Figure 1](#)). They are strongly influenced by westerly winds and the resulting near shore east-west current. Water depth at the four sampling stations ranged from 3.0 to 6.2 m. Water surface temperature measured in 2017 ranged from 8.9°C in April to 17.6°C in June, and absolute salinity varied between 7.2 and 11.5 S_A (S_A : absolute salinity) ([Table 1](#)).

There is no direct river/stream run-off or wastewater discharge in front of the nature reserve Hütelmoor. The nearest estuary is the river Warnow, 10 km west of the sam-

Table 1 Environmental data for the sampling stations in front of the Hütelmoor (Southern Baltic Sea coast, Germany). Samples were taken between April and July 2017. Water depth (m), water temperature ($^\circ\text{C}$) and salinity (S_A) were measured in the field at the respective stations. For water content (WC, % of fresh weight (FW)), organic matter (OM, mg g^{-1} dry weight (DW)) and carbon:nitrogen ratio (C/N, mol/mol) sediment cores were taken at different time points and processed in the laboratory. For these parameters data are expressed as mean values \pm standard deviation ($n = 12$ – 15). The mean grain size of the sediment samples was calculated according to the classification of [Wentworth \(1922\)](#) and the equation of [Folk and Ward \(1957\)](#). Significant differences between means are marked with different letters ($p \leq 0.05$).

Station	Latitude	Longitude	Date	Depth (m)	Water temperature ($^\circ\text{C}$)	Salinity (S_A)	Mean grain size (μm)	WC (% of FW)	OM (mg g^{-1} DW)	C/N ratio (mol/mol)
S21	N 54°13.290'	E 12°9.051'	Apr 17	5.6	8.9	9.6	123	18.4±0.5 ^a	5.1±1.1 ^a	13±9 ^a
			Jun 17	5.6	17.6	11.3		16.1±0.3 ^a	6.1±0.4 ^a	18±7 ^a
S25	N 54°13.006'	E 12°9.730'	Jul 17	5.6	17.4	7.2	129	16.8±0.3 ^a	7.4±0.5 ^b	86±24 ^b
			Apr 17	3.0	8.9	9.2		19.9±0.3 ^a	4.2±0.4 ^c	6±1 ^c
			Jun 17	3.0	17.6	11.4		19.2±0.4 ^a	4.6±0.7 ^c	8±2 ^c
S41	N 54°14.002'	E 12°9.675'	Jul 17	3.0	17.4	7.6	289	18.9±0.8 ^a	4.1±0.2 ^c	4±1 ^d
			Apr 17	6.2	8.9	9.0		13.9±4.3 ^b	8.3±0.1 ^b	14±4 ^a
			Jun 17	6.2	17.6	11.5		18.6±0.5 ^a	6.7±1.1 ^a	6±1 ^c
S45	N 54°13.717'	E 12°10.354'	Jul 17	6.2	17.4	7.6	131	18.3±1.3 ^a	9.2±1.0 ^b	42±19 ^d
			Apr 17	4.4	8.9	9.3		19.4±0.3 ^a	6.0±0.9 ^a	9±2 ^a
			Jun 17	4.4	17.6	11.3		17.5±0.4 ^a	5.4±0.2 ^a	13±4 ^a
			Jul 17	4.4	17.4	7.7		17.0±0.5 ^a	4.1±0.4 ^c	4±1 ^d



Figure 1 Location of the four sampling stations S21, S25, S41 and S45 in front of the site Hütelmoor at the southern Baltic Sea coast, Germany. The isobaths for 3 and 5 m water depth are shown as well. The frame represents the area of a detailed bathymetric study of [Kreuzburg et al. \(2018\)](#).

156 pling stations. The Warnow has a length of 143 km and an
 157 elevation difference from spring to the mouth of 68 m. The
 158 river mouth is located 15 km landwards where a weir pre-
 159 vents sea water to travel further upstream. The mean out-
 160 flow rate is $16.5 \text{ m}^3 \text{ s}^{-1}$ with a mean nitrate concentration
 161 of 1.78 mg l^{-1} . During the passage of the Warnow plume
 162 through the estuary, inorganic nutrients are entirely con-
 163 sumed or mixed so that only recalcitrant substances like
 164 dissolved organic material of the plume are able to reach
 165 the study site off the Hütelmoor ([Jurasinski et al., 2018](#)).

166 2.2. Field sampling

167 Sediment samples were taken by scientific SCUBA divers
 168 along the depth gradient (see [Figure 1](#) and [Table 1](#)) at three
 169 sampling dates in April, June and July 2017. Temperature
 170 and salinity were measured in the surface water over the
 171 sampling locations (HQ 40d multi, Hach Lange, Düsseldorf,
 172 Germany). In order to get undisturbed sediment samples at
 173 each sampling location Plexiglas® core liners (height 250
 174 mm, inner \varnothing 50 mm) were pushed into the sediment and
 175 sealed with a rubber plug on the top. The tubes were then
 176 pulled out and bottom-sealed with a second rubber plug
 177 (always 3 replicates to account for heterogeneity). After-
 178 wards, the sediment cores were transported as fast as possi-
 179 ble under undisturbed and dark conditions to the labora-
 180 tory. Here the samples were kept at 5 or 20°C , respectively,
 181 depending on the measured in situ temperature ([Table 1](#)).
 182 In order to avoid anoxic conditions in the core (due to el-

evated oxygen depletion in the dark) the overlaying water
 columns on top were mildly bubbled with air prior further
 processing.

186 2.3. Biomass determination and sediment 187 characteristics

As proxy for microphytobenthic biomass mg chlorophyll *a*
 per m^2 was estimated for each sample. Always the top first
 cm layer of each sediment core was taken with a scraper,
 well mixed in a Petri-dish and divided into two subsamples.
 One subsample was used for the extraction of chlorophyll
a and the other one was used for the determination of orga-
 nic content, water content and C:N ratio. For chlorophyll
a analysis 1.13 cm^3 sediment was mortared and mixed with
 3 ml of cold 96% ethanol (v/v) plus a spoon tip of MgCO_3
 and left overnight. Afterwards the suspension was centrifuged
 at $6,240 \times g$ for 5 min at 5°C . The centrifuged pellets were
 extracted again with ethanol, but this time incubated for 30
 min to guarantee complete extraction of chlorophyll *a*. The
 supernatants were photometrically measured (UV-2401PC,
 Shimadzu) at wavelength 665 nm for chlorophyll *a* and at
 750 nm for turbidity. The chlorophyll *a* concentration was
 calculated according to [HELCOM protocol \(2015\)](#) and val-
 ues of both extractions were summed up. Always 3 replicate
 samples were used.

Water content (% fresh weight) of sediment cores was
 determined by relative weight loss after drying a defined
 amount (approx. 10 g) of sediment for 12–24 h at 105°C .
 In order to determine the organic content (OC) (% dry
 weight) the dried sediment was combusted at 550°C for
 4h. For the analysis of particulate organic carbon and ni-
 trogen (POC:PON ratio) between 200 and 250 mg dry sedi-
 ment were homogenized using a mortar, weighted using an
 analytical scale (accuracy 0.05 mg) (Sartorius MC210P, Göt-
 tingen, Germany) and wrapped in silver foil for a treatment
 with $50 \mu\text{l}$ 10% hydrochloric acid (v/v) to remove inorganic
 carbon. After drying, the sample was packed air-tight in tin
 foil and combusted in an element analyzer (Vario EL III, El-
 ementar, Langensfeld, Germany). Grain size analysis was
 conducted with a particle size analyzer (Type 1180, Cilas
 Ltd., Orléans, France). Prior to the analysis small amount
 of sediment (tea spoon) was dispersed in deionized water
 and homogenized by sonication for 30 min. For each sample
 sediment grains were split up into 100 size classes (0.37 up
 to $2000 \mu\text{m}$) in 12 replicates. Size information was summed
 up to six different size classes (>1000 , 1000–500, 500–200,
 200–100, 100–63 and $<63 \mu\text{m}$) which were used to calcu-
 late the mean grain size of the sediment samples according
 to the classification of [Wentworth \(1922\)](#) and the formula
 provided by [Folk and Ward \(1957\)](#).

232 2.4. Microphytobenthic community production (ex 233 situ)

The production and consumption of oxygen was used as
 proxy for microphytobenthic community production and
 respiration, respectively. Always three replicate sediment
 cores per station (inner \varnothing 50 mm, height 250 mm, vol-
 ume $\sim 500 \text{ cm}^3$) with intact sediment surface were taken
 in the field and measured simultaneously in the labora-

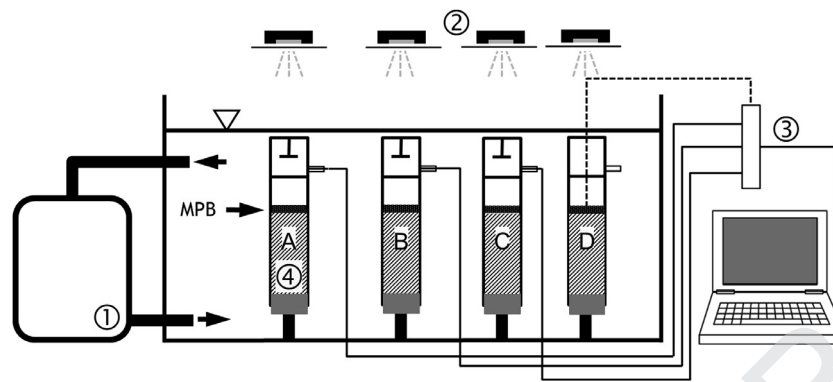


Figure 2 Schematic overview of the experimental setup. Sediment cores were placed inside a plastic tray. Water bath, permanently cooled by a flow-through thermostat (arrows indicate flow direction) (1) and light source (daylight white LEDs) darkened with shading foil to induce different photon fluence rates (2). Light came only from the top. Three sediment cores with mounted measuring module (A–C) equipped with magnetic stirrer and fluorescent sensor spot (3) are connected to a control unit (4) via optical fiber. A fourth dummy core filled with in situ surface water (D) is used for temperature measurement and compensation during the experiment. MPB: Microphytobenthic biofilm on top of the sediment.

240 tory. Approx. 1/3 of the tube was filled with sediment and
 241 2/3 was filled with overlaying water. The experimental design
 242 was similar to the setup published by [Woelfel et al.](#)
 243 (2010), but with various technical improvements and modifi-
 244 cations (Figure 2). A self-constructed “measuring module”
 245 was mounted air tight on top of each core without disturb-
 246 ing the sediment surface. This module was equipped with
 247 a stirrer (Ø 30 mm, 6–7 rpm) powered by an external ro-
 248 tating magnet, a valve and a commercial contactless oxy-
 249 gen sensor spot (PyroScience, Ø 5 mm, optical isolation).
 250 The planar oxygen sensor spots were glued inside the mea-
 251 suring modules and connected across the transparent Plexi-
 252 glass housing to external optical fibers which transmitted
 253 the light signals between the sensor spots and a 4-channel
 254 control unit (FireSting O₂, PyroScience, Aachen, Germany).
 255 Calibration and measurements were controlled and logged
 256 with the software Pyro Oxygen Logger version 3.213 sup-
 257 ported by PyroScience. Before measurements, a two-point
 258 calibration (0 and 100% oxygen saturation) was carried out
 259 using filtered Baltic Sea water from the sampling location. A
 260 rubber plug at the bottom of the sediment corer, adjust-
 261 able for height and a valve on top of the module were used
 262 to remove air bubbles from the incubation room and to adjust
 263 the incubated water volume above the sediment surface.
 264 The latter was determined for each core and integrated in
 265 the calculations.

266 Light was provided by LEDs (Seoul W42182-05LF, daylight
 267 white) covering the PAR (photosynthetically active radi-
 268 ation) range of 400–700 nm. LEDs were mounted directly on
 269 top of the incubation tubes. The possible maximum pho-
 270 ton fluence rate applied in this approach was approx. 800
 271 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. Each core was irradiated by an in-
 272 dividual light source. A fourth tube was filled with fresh in
 273 situ water sampled on the same day from the same loca-
 274 tion as the sediment cores for temperature measurements
 275 during the experiment and used as signal for the tempera-
 276 ture compensation in the optode software. All cores were
 277 placed in a plastic tray (35 × 35 × 53 cm) which was cooled
 278 to the measured in situ temperature with a thermostat (Ti-
 279 tan 250, Aqua Medic, Bissendorf, Germany). Prior to each

280 measurement, sediment cores were kept for at least 30 min
 281 in the water bath at the respective in situ temperature. Af-
 282 terwards respiratory oxygen consumption in the dark and
 283 photosynthetic oxygen production of the microphytoben-
 284 thic communities with increasing photon fluence rates were
 285 recorded in the original water volume above the sediment
 286 surface of the core. The water column above the sediment
 287 contained always < 2 $\mu\text{g chlorophyll } a \text{ L}^{-1}$ which is con-
 288 sidered as oligotrophic ([Håkanson, 2008](#)), and hence phy-
 289 toplankton was neglectable. Benthic diatoms were exposed
 290 to 5 to 7 increasing light levels ranging from 0 to 750 μmol
 291 $\text{photons m}^{-2} \text{ s}^{-1}$ of PAR. Photon fluence rates were measured
 292 with a cosine corrected 2π light sensor (light meter LI-250,
 293 LI-COR, Lincoln, United States of America) placed directly
 294 next to the core on the same height as the sediment sur-
 295 face. Measurements started with a respiration phase of 30
 296 min in the dark followed by a 20 min photosynthesis phase
 297 for each light level. The experiment was finished by a fi-
 298 nal respiration phase for 30 min. Different light levels were
 299 achieved by covering the LEDs with combinations of neutral
 300 density filter foils. The distance from light source to the sed-
 301 iment surface was kept constant during the measurement.
 302 After the experiment the top first cm of each sediment core
 303 was harvested and used for chlorophyll *a* determination as
 304 described in detail above. The oxygen consumption and pro-
 305 duction per time unit was referenced to the surface area
 306 ($\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$). The resulting photosynthesis irradiance
 307 (PI) curve data were fitted to the nonlinear model of [Webb](#)
 308 [et al. \(1974\)](#) which describes the change in gross production
 309 (GPP) with increasing photon fluence rate without photoin-
 310 hibition:

$$GPP(PFD) = NPP_{max} \cdot \left(1 - e^{-\frac{\alpha \cdot PFD}{NPP_{max}}}\right) + R$$

311 with NPP_{max} as light saturated net production, α as the
 312 slope of net production increase during initial photon flu-
 313 ence rates (light limiting range), PFD as photon fluence rate
 314 and R as dark respiration. Fitting of the data was conducted
 315 with the Excel add-in Solver (MS Office 2013, Microsoft Co-
 316 operation).

317 2.5. Scanning electron microscopical investigation

318 Sand grains with attached diatoms from the sediment cores
 319 were visualized and photographed by a field emission scanning
 320 electron microscopy (SEM) operated at 5 kV (FE-SEM,
 321 MERLIN® VP Compact, Carl Zeiss, Oberkochen Germany,
 322 Faculty for Medicine, University of Rostock). Individual sand
 323 grains were picked and washed gently in ultrapure water
 324 several times to remove salt and other small particles. The
 325 so prepared sand particles were mounted onto Aluminium
 326 SEM-carriers with adhesive conductive carbon tape (Co.
 327 PLANO, Wetzlar, Germany), coated with carbon (5–10 nm
 328 layer) and exposed to a vacuum (EM SCD 500, Co. BALTEC,
 329 Balzers, Liechtenstein).

330 From the shallowest station 25 one sediment core was
 331 used for getting a crude overview on benthic diatom abundances
 332 according the methodological approach of [Woelfel
 333 et al. \(2010\)](#). Species were morphologically identified using
 334 taxonomic literature given by [Woelfel et al. \(2014a\)](#).

335 2.6. Statistics

336 Statistical significance of the mean values of the respective
 337 abiotic data, chlorophyll values, net primary production
 338 and respiration rates were tested with one-way ANOVA,
 339 followed by a Tukey's multiple comparison test ($P < 0.05$).
 340 Prior to this, a test for equality of variances ([Levene et al.,
 341 1960](#)) and a normality test ([Shapiro and Wilk, 1965](#)) was
 342 conducted. Analyses were performed with InStat (GraphPad
 343 Software Inc., La Jolla, California, USA). Photosynthesis versus
 344 photon fluence rates and respiration rates were fitted to
 345 the model of [Webb et al. \(1974\)](#) using the Excel module
 346 Solver.

347 3. Results

348 3.1. Environmental settings of both study sites

349 The Hütelmoor sampling stations S21, S25, S41 and S45 are
 350 brackish with fluctuating salinities between 7.2 and 11.5 S_A
 351 (absolute salinity) and temperatures ranging from 8.9°C to
 352 17.6°C in April to July 2017 ([Table 1](#)) due to irregular up-
 353 welling of cool, saline deep water at the outer Baltic Sea
 354 coast ([Jurasinski et al., 2018](#)).

355 The mean grain size of the sediment particles was very
 356 similar at the study site, ranging from 123 to 289 μm (fine
 357 to medium sand particles).

358 The water content of all sediment samples was very similar
 359 with an average value of 18% of fresh weight ([Table 1](#)).
 360 The organic matter (OM) content of the sediments ranged
 361 from 4.1 to 9.2 mg g^{-1} dry weight, and the respective C/N
 362 ratio (mol/mol) varied between 4 and 86 ([Table 1](#)). Partic-
 363 ularly at both deeper stations (5.6 and 6.2 m) C/N ratio in-
 364 creased 3 to 6-fold from April/June to July 2017 ([Table 1](#)).

365 3.2. Microphytobenthic standing stock biomass

366 The areal chlorophyll *a* concentration was determined as
 367 widely used proxy for phototrophic biomass in all sediment
 368 samples. A distinct depth gradient with significantly lower

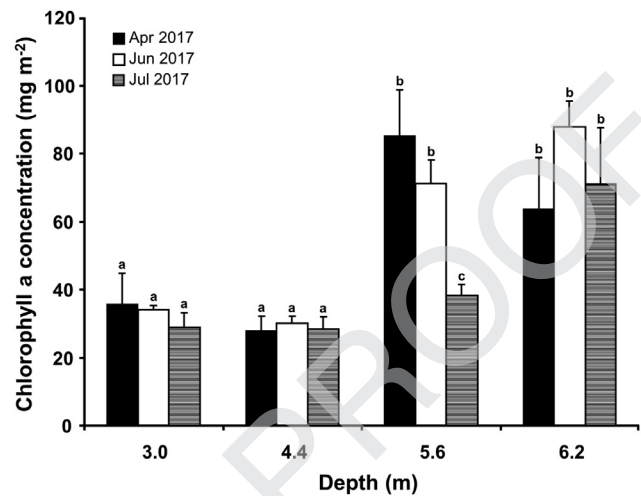


Figure 3 Areal chlorophyll *a* concentration as proxy for phototrophic biomass (chlorophyll *a* mg m^{-2}) in all sediment samples, as measured in different water depths (m) and at three sampling dates in April, June and July 2017. All values represent the mean values with standard deviation ($n=12-15$). Different letters indicate significantly different means (Tukey's test, $P < 0.05$).

369 chlorophyll *a* values was observed ranging from 28.5 mg Chl.
 370 a m^{-2} at 3 m depth to 87.7 mg Chl. a m^{-2} at 6.2 m depth (p
 371 < 0.05 , [Figure 3](#)). Both shallow water stations at 3.0 and 4.4
 372 m depth exhibited very similar chlorophyll *a* concentrations
 373 (28.0 to 35.8 mg Chl. a m^{-2}) in April, June and July 2017
 374 ([Figure 3](#)). In contrast, at both deeper stations the chloro-
 375 phyll *a* values were always higher, but also more variable.
 376 Particularly the July sample at 5.6 m exhibited a strong de-
 377 cline in chlorophyll *a* concentration from 71.2–85.2 mg Chl.
 378 a m^{-2} in April/June to 38.3 mg Chl. a m^{-2} ([Figure 3](#)).

379 3.3. Microphytobenthic primary production and respiration

380
 381 Net primary production strongly varied across the sampling
 382 dates and along the depth gradient from 3 to 6.2 m, ranging
 383 from 29.4 to 178.9 $\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ([Figure 4](#)). At the shallow-
 384 est station (3.0 m water depth) net primary production was
 385 the highest in April 2017 (129.9 $\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$) and the low-
 386 est in June 2017 (39.7 $\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$), while in July 2017
 387 an intermediate rate was measured (68.8 $\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$)
 388 ([Figure 4](#)). A similar pattern could be determined at the 5.6
 389 m station, where in April and June 2017 the highest pro-
 390 duction rates were estimated (178.8 and 151.0 $\text{mg O}_2 \text{ m}^{-2}$
 391 h^{-1} , respectively), followed by a sharp decline to 29.4 mg
 392 $\text{O}_2 \text{ m}^{-2} \text{ h}^{-1}$ in July 2017 ([Figure 4](#)). At the deepest station
 393 (6.2 m) net primary production was more similar across the
 394 sampling dates, ranging from 68.5 to 104.6 $\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$
 395 ([Figure 4](#)).

396 In contrast to net primary production rates, respiration
 397 rates were more similar at all stations and sampling dates.
 398 The respiration values ranged from -9.9 to -20.8 $\text{mg O}_2 \text{ m}^{-2}$
 399 h^{-1} ([Figure 5](#)). The measured respiratory rates were low
 400 since at each depth and sampling date net primary produc-

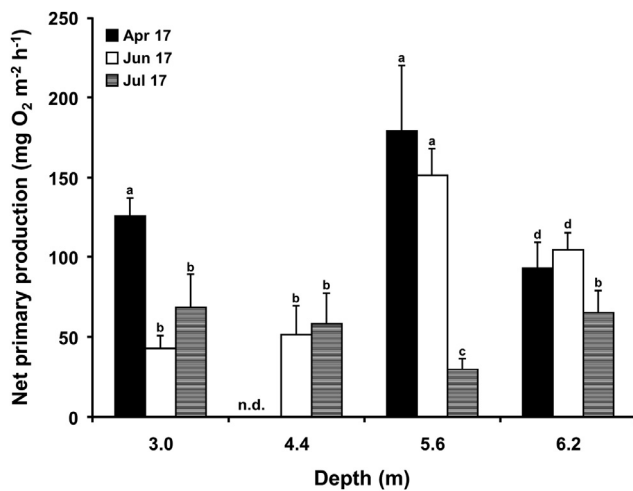


Figure 4 Rates of ex situ net primary production expressed as $\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$ along the depth gradient from 3.0 to 6.2 m and at three sampling dates in April, June and July 2017. All values represent mean values with standard deviation ($n=3$). Different letters indicate significantly different means (Tukey's test, $P < 0.05$). n.d.: not detected.

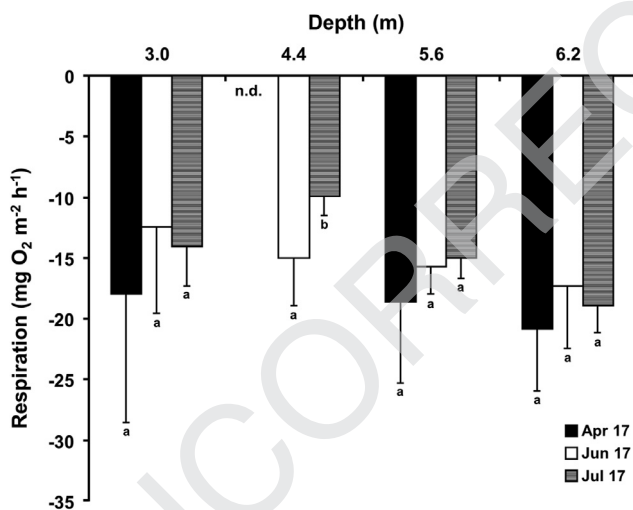


Figure 5 Rates of ex situ respiratory oxygen consumption expressed as $\text{mg O}_2 \text{ m}^{-2} \text{ h}^{-1}$ along the depth gradient from 3.0 to 6.2 m and at three sampling dates in April, June and July 2017. All values represent the mean values with standard deviation ($n=3$). Different letters indicate significantly different means (Tukey's test, $P < 0.05$). n.d.: not detected.

401 tion rates always exceeded respiratory oxygen consumption
402 rates by a factor of 2.1 to 9.7.

403 From these oxygen measures gross primary production
404 ($\text{mg C m}^{-2} \text{ h}^{-1}$) was calculated, by converting the O_2 values
405 into C using a photosynthetic quotient ($\text{PQ} = \Delta\text{O}_2 / \Delta\text{C}$)
406 of 1 (Hargrave et al., 1983). For the study site next to the
407 Hütelmoor along the depth gradient from 3.0 to 6.2 m and
408 across the sampling dates from April to July 2017 a gross
409 primary production of 16.3 to 74.0 $\text{mg C m}^{-2} \text{ h}^{-1}$ was calcu-
410 lated (Table 2).

3.4. Diatoms colonizing sediment particles

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Benthic diatoms were attached to the sandy sediment particles collected at the exposed sites. Sand grains generally exhibited an intermediate sphericity with a smooth and rounded surface without sharp edges, and they were inhabited by only few diatoms of ca. 10 μm length, with *Planothidium delicatulum* as most abundant species (25% of the community). They preferentially occurred in some cracks and crevices (Figure 6 b, c and d). Many cells belong to araphid taxa, hence cannot move and rather stick to the surface by mucus coming from special pores at the cell poles.

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4. Discussion

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This is the first study in which primary production of microphytobenthic communities were measured in intact sediment cores taken at different depths and sampling dates at a sandy coastal site of the southern Baltic Sea using oxygen planar optodes. The sediment cores were incubated under controlled and undisturbed conditions in the laboratory to evaluate potential maximum primary production. This, however, does not necessarily reflect in-situ conditions, since the study site can be characterized as exposed location with strong meteorological and hydrodynamic effects on shallow water microphytobenthic communities. Wind-induced waves and currents along with water-level changes shape the sediment properties, i.e. the sand grains are highly mobile and hence rounded, both preventing attachment of enhanced cell numbers of benthic diatoms. This is well reflected in the low chlorophyll *a* values at 3 and 4.2 m depth (Figure 3) and the generally low organic content of these sediments (Table 1). At greater depth (5.6–6.2 m) the influence of waves and currents are dampened and hence the sediments are less erosive resulting in doubled chlorophyll *a* concentrations compared to the shallower stations (Figure 3) (Ubertini et al., 2012; Van der Wal et al., 2010). The prevailing wind direction and speed have been documented for all seasons for the wind flat system Bock (Zingst Peninsula, German Baltic Sea coast, 55 km east of Hütelmoor), which temporarily induce even an irregular and unpredictable pattern of emersion and flooding (Karsten et al., 2012). These authors reported that over 2.5 years continuous measurements frequent short time intervals of flooding occurred up to 20 and 50 cm water height, particularly during storm events (wind speed $>8 \text{ m s}^{-1}$), with strong forcing of sediment resuspension and erosion. In addition, at the exposed site the temperature amplitude was rather small (8.9–17.6°C) compared to more sheltered sites, because there is irregular upwelling at the open coast (Jurasinski et al., 2018; Lehmann and Myrberg, 2008). The surface water at sheltered sites warms more quickly as there is less mixing. Consequently, microphytobenthic communities experience more hydrodynamic stress and more unfavorable temperature conditions at exposed sites like in front of Hütelmoor compared to, for example, shallow coastal lagoons of the southern Baltic Sea, such as the Darss Zingst Bodden Chain (Meyercordt and Meyer-Reil, 1999). Vertical mixing and wave action are key factors controlling benthic diatom growth on an exposed beach (Steele and Baird, 1968), and wave-generated shear stress and turbulence can cause re-

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Table 2 Gross primary production ($\text{mg C m}^{-2} \text{ h}^{-1}$) estimates and standing stock biomass expressed as chlorophyll *a* concentration (mg m^{-2}) of benthic microalgae for temperate regions of the North Sea and Baltic Sea as determined by ^{14}C fixation or O_2 production. The O_2 values were converted into C using a photosynthetic quotient ($\text{PQ} = \Delta\text{O}_2 / \Delta\text{C}$) of 1 (Hargrave et al., 1983).

Location	GPS data	Depth (m)	Sediment mean grain diameter (μm)	Method	GPP ($\text{mg C m}^{-2} \text{ h}^{-1}$)	Chl. <i>a</i> content (mg m^{-2})	Reference
Westerschelde, The Netherlands	N 51°26.5' E 3°57.9'	intertidal	224–301	^{14}C	15–80	15–32	Barranguet et al. (1998)
Wadden Sea, Germany, two locations	N 55°00.8' E 8°26.3' N 53°44.1' E 7°41.9'	Intertidal	139–380	O_2	29–51	176–194	Billerbeck et al. (2007)
Ems Dollard Estuary, The Netherlands	N 53°22.4' E 6°54.1'	intertidal	80–110	^{14}C	10–115	5–560	Colijn and de Jonge (1984)
Coastal lagoon, Southern Baltic Sea, Germany	N 54°32.3' E 13°07.5'	2.5	100–490	O_2	6–18	135–209	Meyercordt and Meyer-Reil (1999)
Sandy beach, Southern Baltic Sea, Poland	N 54°27.1' E 18°34.1'	< 0.5	1,120–1,310	O_2	0.2–41.8	20–122	Urban-Malinga and Wiktor (2003)
Laholm Bay, Kattegat, Sweden	N 56°35.1' E 12°50.0'	2–20	muddy sand	^{14}C	1–17.3	1–87	Sundbäck and Jönsson (1988)
Gulf of Riga, Baltic Sea, Estonia and Latvia	N 58°21.0' to N 57°15.0' E 22°10.0' to E 24°24.0'	0.2–5	Muddy sand	^{14}C	0.1–2.8	15–66	Vilbaste et al. (2000)
Ythan Estuary, Scotland, UK	N 57°19.9' W 1°59.9'	< 1	336	^{14}C	9–226	163–221	Leach (1970)
Lynher Estuary, England, UK	N 50°21.9' W 4°12.2'	< 2	< 63	^{14}C	163–523	5–115	Joint (1978)
Southern Baltic Sea, Germany	see Table 1	3–6.2	123–289	O_2	16.3–74.0	28.0–87.7	This study

469 suspension of surface sediments and their associated organ- 491
 470 isms resulting in lower microalgal biomass (de Jonge and van 492
 471 Beusekom, 1995). 493

472 The sediment organic matter (OM) content ranged be- 494
 473 tween 4 and 9 mg g^{-1} dry weight across all stations and sam- 495
 474 pling dates which is similarly low to 3–6 mg g^{-1} dry weight 496
 475 measured in a nearby wind flat at a station with very low 497
 476 numbers of phototrophic microorganisms (Woelfel et al., 498
 477 2007). Assemblages of benthic diatoms and cyanobacteria, 499
 478 however, increase the OM values in the wind flat to 12–17 500
 479 mg g^{-1} dry weight (Woelfel et al., 2007). 501

480 The C/N ratios measured in April and June 2017 502
 481 amounted between 6 and 18 across all stations, and are in 503
 482 the same range as previously published ratios (10–12) for 504
 483 sediments sampled in a shallow coastal lagoon at Hog Island 505
 484 Bay, Virginia, USA (Hardison et al., 2013). In July 2017, a 506
 485 strong change in the C/N ratios could be observed. While 507
 486 at both deeper stations the C/N ratios increased to 42– 508
 487 86, at both shallower stations the opposite was observed 509
 488 with a strong decline of the C/N ratio to 4. High C/N ratios 510
 489 generally indicate carbon-rich organic matter, which is 511
 490 relatively poor in nitrogen. The study site is connected to 512

a coastal peatland, which stretches into the shallow wa- 491
 492 ter zone (Kreuzburg et al., 2018). These authors reported 493
 494 also organic-rich layers further offshore with C/N ratios 495
 496 <71, which are similar to the data of the present study. 497
 498 The submerged peat and organic-rich layers at the study 499
 500 site are not always exposed to the water column, depend- 501
 502 ing on wave-induced sediment movement which results in 503
 504 erosion or burial (Jurasinski et al., 2018). C/N ratios of 4 505
 506 are rather unusual, but have been described for unialgal 507
 508 cultures (Falkowski and Owens, 1980) and for early spring 509
 510 cyanobacterial plankton in the Baltic Sea (Walve and Lar- 511
 512 son, 2010). A cyanobacterial phytoplankton bloom did not
 happen in July 2017 in front of Hütelmoor and hence can
 be neglected as cause for the low C/N ratio in the shal-
 low water stations. There is, however, significant subma-
 rine groundwater discharge with dissolved nitrate from the
 peatland into the nearshore Baltic Sea sediments (Jurasinski
 et al., 2018), which might explain the temporarily reduced
 C/N ratios.

The underwater light field along the depth gradient is
 complex because of the attenuation of incident solar ra-
 diation due to the optical properties of the water column

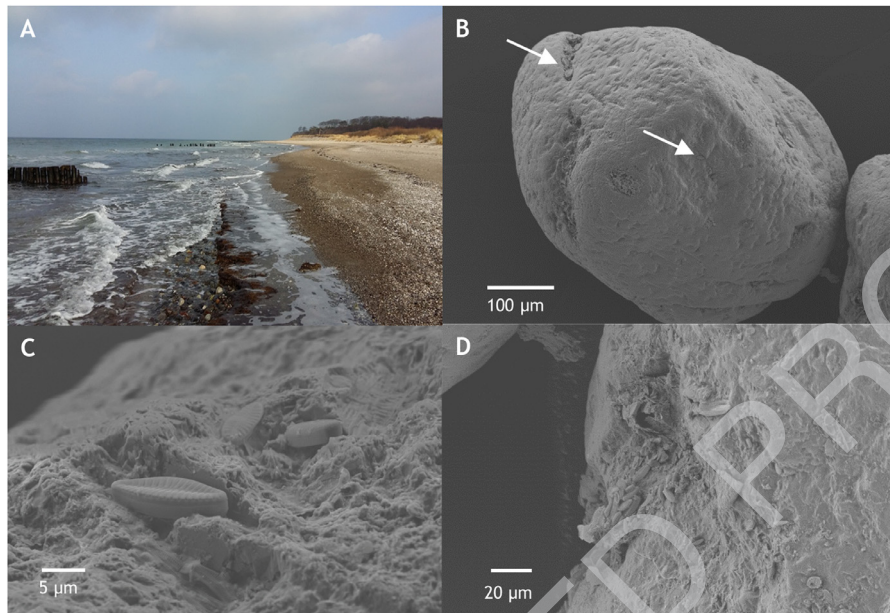


Figure 6 Representative habitat picture of the exposed sampling site in front of the Hütelmoor on 18th February 2016 (A). This site is a near shore sandy beach, which is strongly influenced by westerly winds and a coastal parallel east-west current leading to high hydrodynamic, erosive forces. Scanning electron microscopic pictures of sand grains with attached diatoms from the from this exposed site (B, C, D). The sand grains are rounded with low numbers of attached, mainly araphid diatoms, and they occurred mainly in cracks and crevices (C, D).

513 (yellow substances, re-suspended particles, phytoplankton
 514 etc.). Maximum solar radiation during spring and summer
 515 2017 ranged from approximately 1,900 to 2,100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$
 516 (own measurements). Vertical snapshot light
 517 measurements at the deeper stations at noon in June and
 518 July 2017 down to the seafloor resulted in calculated atten-
 519 uation coefficients (K_d) between 0.26 and 0.41 m^{-1} . These
 520 rather low K_d values point to a high to medium transmit-
 521 tance of the water column in the PAR range, resulting in 135
 522 to 157 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ at noon at 6 m depth (own
 523 measurements). Such PFDs are usually sufficient to satur-
 524 ate the light requirements for photosynthesis in benthic di-
 525 atoms. This is supported by measurements of the photosyn-
 526 thetic performance of eight clonal benthic diatom strains,
 527 which were isolated from the study site, and which exhib-
 528 ited light saturation points between 32 and 151 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$
 529 (Prelle et al., 2019). Similar low light require-
 530 ments (34 to 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) were reported for
 531 three benthic diatom species isolated from a sheltered sedi-
 532 ment of the southern Baltic Sea (Woelfel et al., 2014a).
 533 Benthic diatoms are well known for their high photophysio-
 534 logical plasticity and their capability for vertical movement
 535 into or out of the sediment to avoid photodamage (Ezequiel
 536 et al., 2015). Physiological and behavioral photoprotection
 537 are thus the two major mechanisms by which natural mi-
 538 crophytobenthic communities protect themselves against
 539 high incident solar radiation (Cartaxana et al., 2011). They
 540 are able to adjust their photosynthetic apparatus relatively
 541 quickly to a new light regime (Glud et al., 2002; Köhl et
 542 al., 2001). The underlying mechanisms include, for exam-
 543 ple, alterations of the size or composition of the photosyn-
 544 thetic units with consequences for electron transport ca-

545 pacity (Richardson et al., 1983). However, as mentioned be-
 546 fore, most of the benthic diatoms observed were araphid
 547 and epipsamic, and hence immobile.

548 As mentioned in the introduction microphytobenthic
 549 biomass can strongly vary in space and time at all scales
 550 on shallow coastal sediments (Ubertini et al., 2012). There
 551 are many reports indicating benthic diatom biomass changes
 552 even on diurnal to bi-weekly tidal cycles and over the course
 553 of the seasons (Koh et al., 2007; Orvain et al., 2012; van
 554 der Wal et al., 2010). Besides light, temperature and wind
 555 conditions (Ubertini et al., 2012), also nutrient concentra-
 556 tions can control microphytobenthic biomass and primary
 557 production (Cibic et al., 2007), although sediment pore wa-
 558 ter is generally considered as nutrient-enriched compared
 559 to the overlying water column (Garcia-Robledo et al., 2016;
 560 Sundbäck et al., 1991). In addition, sediment grain-size is
 561 not homogenous within tide-influenced coastal areas, lead-
 562 ing to differential distribution of particle size-groups with
 563 different degrees of erodibility which of course affects
 564 benthic diatom biomass and activity (Orvain et al., 2012;
 565 Ubertini et al., 2012). The sediment types determine the
 566 preferential occurrence of epipsamic or epipellic benthic di-
 567 atoms causing related variation in their biomass (Ubertini et
 568 al., 2012). Microphytobenthos have mostly been studied in
 569 temperate tidal-influenced estuaries (Serôdio et al., 2020),
 570 while for the Baltic Sea with its specific hydrographic and
 571 environmental conditions only few data exist.

572 The used ex-situ planar oxygen optode approach, i.e.
 573 to sample intact sediment cores as intact microecosystem
 574 from the field and to undertake incubations under controlled
 575 and simulated conditions in the laboratory, opens
 576 many possibilities to estimate benthic production rates un-
 577

der various environmental settings. The advantage of this set-up is the possibility to measure community respiration and net production from many replicate sediment samples with a defined area without subsampling or destructing. The disadvantage of the core incubations is the fact that although they well integrate total activity of the whole sediment dwelling community they provide only a limited insight into their vertical distribution and activity. It should be mentioned, however, that during the laboratory incubations, the impact of shear stress and turbulence induced sediment resuspension, which frequently occur at the natural site, was ignored, and hence the productivity data reflect only the potential optimum under calm in-situ conditions. In addition, to overcome the problem with the limited vertical distribution and activity, the best methodological approach is the application of vertical oxygen micro-electrode profiling, which, although time-consuming, allows a three-dimensional determination of oxygen production and consumption at any given depth point in the sediment (e.g. Glud et al., 2002; Kühl et al., 1996; Revsbech and Jørgensen, 1983). However, the extrapolation of such fine-scaled results on a mm scale to larger sediment areas might be challenging because of sediment heterogeneity and biomass patchiness. Our *ex-situ* benthic incubation set-up might be a feasible compromise as it integrates the patchiness of microorganisms corresponding to the covered sediment area of c. 20 cm². In addition and in contrast to the microsensor approach, the respective biomass parameter (chlorophyll *a* per sediment area) can be easily estimated, and thus a comparison with other studies facilitated.

The measured chlorophyll *a* concentrations at the sampling site (28.0–87.7 mg m⁻²) was similar to those of benthic microalgae from coastal temperate regions of the North Sea and Baltic Sea (Table 2). Meyercordt and Meyer-Reil (1999) and Urban-Malinga and Wiktor (2003) reported chlorophyll *a* values of 135–209 and 20–122 mg m⁻², respectively, from sediment samples taken further east in a coastal lagoon, southern Baltic Sea, Germany, and from a sandy beach, southern Baltic Sea, Poland. The conspicuous decline in chlorophyll *a* concentration from April/June to July 2017 at the 5.6 m station compared to the unchanged values at 6.2 m station can be explained by patchy distribution of microphytobenthic communities and different prevailing physical forces affecting sediment structure. Both sampling points are < 1.3 km distant, and hence it might be possible that at 5.6 m sediments were more disturbed due to wind and waves.

The respiration rates measured across all sampling stations and dates amounted -9.9 to -20.8 mg O₂ m⁻² h⁻¹, and hence were less variable compared to the net primary production rates. While Sundbäck et al. (1991) determined very similar respiration rates up to -19.5 mg O₂ m⁻² h⁻¹, other authors reported much higher values (-48.6 mg O₂ m⁻² h⁻¹, Urban-Malinga and Wiktor, 2003; -46.0 mg O₂ m⁻² h⁻¹, Woelfel et al., 2010; -37.2 mg O₂ m⁻² h⁻¹, Yap, 1991). Benthic respiration strongly depends on OM content as substrate for bacterial mineralization in combination with high abundances of micro- and meiofauna (Yap, 1991). The rather low OM values of the Hütelmoor stations together with the regular sediment disturbance would reduce such heterotrophic activities.

The measured O₂ values were converted into C equivalents using a photosynthetic quotient (PQ = ΔO₂/ΔC) of 1 (Hargrave et al., 1983), although other authors used PQ values between 0.9 and 1.3 depending on light and nutrient availability (Cahoon and Cooke, 1992; Glud et al., 2009; Ni Longphurt et al., 2007). Based on our approach we calculated gross primary production of 16.3–74.0 mg C m⁻² h⁻¹ along the depth gradient and across the sampling dates (Table 2). These values are higher compared to sediments of a coastal lagoon, southern Baltic Sea, Germany (6–18 mg C m⁻² h⁻¹, Meyercordt and Meyer-Reil, 1999), to those of a sandy beach, southern Baltic Sea, Poland (0.2–41.8 mg C m⁻² h⁻¹, Urban-Malinga and Wiktor, 2003) and to those in the Gulf of Riga (0.1–2.8 mg C m⁻² h⁻¹, Villabaste et al., 2000), but similar to other locations in the Kattegat and Wadden Sea (Table 2).

For the Baltic Sea a total C budget based on all primary producers is still missing, because microphytobenthic communities have been largely ignored so far and because the pelagial is considered as the main compartment for C fixation (Schiewer, 2008). However, coastal areas are considered among the most productive ecosystems worldwide, and here a combination of benthic and pelagic habitats contribute to total primary production (Ask et al., 2016, and references therein). Benthic diatoms can be responsible for up to 20% of the ocean gross primary production although occupying only 0.03% of the ocean surface area, i.e. shallow coastal regions (Pinckney, 2018). Compared to the water column, sediments are typically enriched in pore water nutrients and if sufficient light is available, such coastal soft bottom ecosystems are often dominated by benthic primary production from polar to tropical regions (Cahoon, 1999; Glud et al., 2002, 2009). The nearest data set to the Hütelmoor of the southern Baltic Sea is from the Gulf of Gdańsk, where the average primary production of the phytoplankton comprises 3.3 mg C mg Chl. *a*⁻¹ h⁻¹ (Renk and Ochocki, 1998) and that of the microphytobenthos around 1 mg C mg Chl. *a*⁻¹ h⁻¹ (Urban-Malinga and Wiktor, 2003), i.e. 23% of the total primary production originated from benthic diatoms. A recent study on the Bothnian Bay (Northern Baltic Sea) reported similar values with a share of 31% of the total annual primary production by microphytobenthic communities (Ask et al., 2016), and these authors also pointed to the lack of data regarding benthic primary production in the Baltic Sea.

Compared to earlier studies (e.g. Woelfel et al., 2010) the community respiration rates were always very low at the study site, generally representing < 20% of the photosynthesis signals (Figure 5). Therefore, it is reasonable to assume that the heterotrophic activity based on bacteria and meiofauna was strongly reduced, which is well reflected in the low organic matter content, and can be explained by the strong prevailing hydrodynamic forces.

We are aware that the data shown represent only a snapshot under optimal conditions, and hence it would be very important to consider all seasons (as in Urban-Malinga and Wiktor, 2003) with their strongly fluctuating environmental conditions to better understand the in-situ net primary production of shallow water benthic diatoms of the Baltic Sea. A modelling approach, as reported for Arctic microphytobenthic primary production, might be highly useful to address this task (Woelfel et al., 2014b).

701 **5. Conclusion**

702 In conclusion, our hypothesis that with increasing water
703 depths the effect of strong wind- and wave-induced mix-
704 ing of the upper sediment layer are dampened and hence
705 support higher microphytobenthic biomass and primary pro-
706 duction could be confirmed. Consequently, microphytoben-
707 thic communities play an important ecological role at the
708 shallow southern Baltic Sea coast, and hence their contri-
709 bution to the total primary production should be much bet-
710 ter evaluated in space and time. Such data are important
711 for the calculation of a realistic complete Baltic Sea carbon
712 budget, as reported so far only for the Bothnian Bay (Ask
713 et al., 2016). In addition, if the microphytobenthic primary
714 production contributes with one third to the total Baltic
715 Sea production, its biogeochemical fate under global change
716 scenarios should be much better evaluated because of fu-
717 ture weather and climate change scenarios for the southern
718 Baltic Sea region. Drier summers with more frequent and
719 occasional extreme storm events are to be expected (BACC
720 II Author Team, 2015), leading to higher disturbance of ex-
721 posed sandy sediments with negative effects on microphy-
722 tobenthic primary production.

Q2 723 **Uncited References**724 [HELCOM 2018](#)725 **Declaration of Competing Interest**

726 None

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740 **Supplementary materials**

741 Supplementary material associated with this article can be
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743 [02.002](#).

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