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

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.

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 (Jurasinski 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 (Colijn 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 sed-

iment 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 epipelic (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 epipelic 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 mg C m^{-2} h^{-1} depending on the sediment (mud $vs.$ sand), water depth and season, and which is generally lower then in tidal systems such as the Ems Dollard Estuary (10—115 mg C m^{-2} 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 (Jurasinski 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 (°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 ± 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 ≤ 0.05).

Station	Latitude	Longitude	Date	Depth (m)	Water temperature (°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]
			Jul 17	5.6	17.4	7.2		16.8±0.3[a]	7.4±0.5[b]	86±24[b]
S25	N 54°13.006'	E 12°9.730'	Apr 17	3.0	8.9	9.2	129	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]
			Jul 17	3.0	17.4	7.6		18.9±0.8[a]	4.1±0.2[c]	4±1[d]
S41	N 54°14.002'	E 12°9.675'	Apr 17	6.2	8.9	9.0	289	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]
			Jul 17	6.2	17.4	7.6		18.3±1.3[a]	9.2±1.0[b]	42±19[d]
S45	N 54°13.717'	E 12°10.354'	Apr 17	4.4	8.9	9.3	131	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).

pling stations. The Warnow has a length of 143 km and an elevation difference from spring to the mouth of 68 m. The river mouth is located 15 km landwards where a weir prevents sea water to travel further upstream. The mean outflow rate is 16.5 m^3 s^{-1} with a mean nitrate concentration of 1.78 mg l^{-1}. During the passage of the Warnow plume through the estuary, inorganic nutrients are entirely consumed or mixed so that only recalcitrant substances like dissolved organic material of the plume are able to reach the study site off the Hütelmoor (Jurasinski et al., 2018).

2.2. Field sampling

Sediment samples were taken by scientific SCUBA divers along the depth gradient (see Figure 1 and Table 1) at three sampling dates in April, June and July 2017. Temperature and salinity were measured in the surface water over the sampling locations (HQ 40d multi, Hach Lange, Düsseldorf, Germany). In order to get undisturbed sediment samples at each sampling location Plexiglas® core liners (height 250 mm, inner Ø 50 mm) were pushed into the sediment and sealed with a rubber plug on the top. The tubes were then pulled out and bottom-sealed with a second rubber plug (always 3 replicates to account for heterogeneity). Afterwards, the sediment cores were transported as fast as possible under undisturbed and dark conditions to the laboratory. Here the samples were kept at 5 or 20°C, respectively, depending on the measured in situ temperature (Table 1). 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.

2.3. Biomass determination and sediment 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 organic 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 x 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 values 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 nitrogen (POC:PON ratio) between 200 and 250 mg dry sediment were homogenized using a mortar, weighted using an analytical scale (accuracy 0.05 mg) (Sartorius MC210P, Göttingen, Germany) and wrapped in silver foil for a treatment with 50 μl 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, Elementar, Langenselbold, 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 μm) in 12 replicates. Size information was summed up to six different size classes (>1000, 1000—500, 500—200, 200—100, 100—63 and <63 μm) which were used to calculate the mean grain size of the sediment samples according to the classification of Wentworth (1922) and the formula provided by Folk and Ward (1957).

2.4. Microphytobenthic community production (ex 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 Ø 50 mm, height 250 mm, volume ~500 cm^3) with intact sediment surface were taken in the field and measured simultaneously in the laboratory.
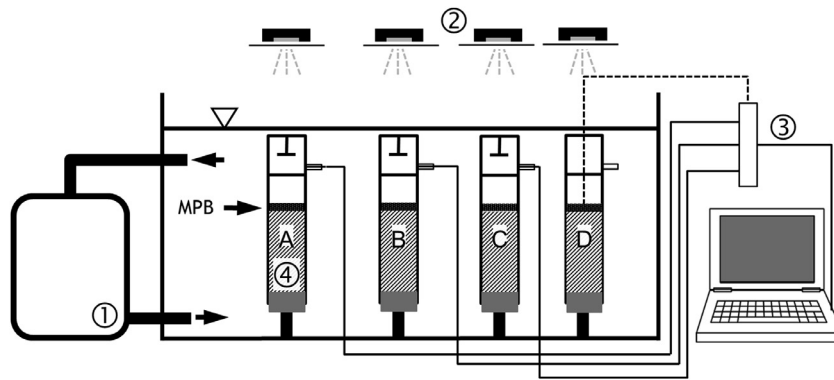
Figure 2   Schematic overview of the experimental setup. Sediment cores were placed inside a plastic tray. Water bath, permanently cooled by a flow-through thermostat (arrows indicate flow direction) (1) and light source (daylight white LEDs) darkened with shading foil to induce different photon fluence 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.

Approx. 1/3 of the tube was filled with sediment and 2/3 was filled with overlaying water. The experimental design was similar to the setup published by Woelfel et al. (2010), but with various technical improvements and modifications (Figure 2). A self-constructed "measuring module" was mounted air tight on top of each core without disturbing the sediment surface. This module was equipped with a stirrer (Ø 30 mm, 6—7 rpm) powered by an external rotating magnet, a valve and a commercial contactless oxygen sensor spot (PyroScience, Ø 5 mm, optical isolation). The planar oxygen sensor spots were glued inside the measuring modules and connected across the transparent Plexiglass housing to external optical fibers which transmitted the light signals between the sensor spots and a 4-channel control unit (FireSting O_2, PyroScience, Aachen, Germany). Calibration and measurements were controlled and logged with the software Pyro Oxygen Logger version 3.213 supported by PyroScience. Before measurements, a two-point calibration (0 and 100% oxygen saturation) was carried out using filtered Baltic Sea water from the sampling location. A rubber plug at the bottom of the sediment corer, adjustable for height and a valve on top of the module were used to remove air bubbles from the incubation room and to adjust the incubated water volume above the sediment surface. The latter was determined for each core and integrated in the calculations.

Light was provided by LEDs (Seoul W42182-05LF, daylight white) covering the PAR (photosynthetically active radiation) range of 400—700 nm. LEDs were mounted directly on top of the incubation tubes. The possible maximum photon fluence rate applied in this approach was approx. 800 μmol photons m^{-2} s^{-1}. Each core was irradiated by an individual light source. A fourth tube was filled with fresh in situ water sampled on the same day from the same location as the sediment cores for temperature measurements during the experiment and used as signal for the temperature compensation in the optode software. All cores were placed in a plastic tray (35 × 35 × 53 cm) which was cooled to the measured in situ temperature with a thermostat (Titan 250, Aqua Medic, Bissendorf, Germany). Prior to each

measurement, sediment cores were kept for at least 30 min in the water bath at the respective in situ temperature. Afterwards respiratory oxygen consumption in the dark and photosynthetic oxygen production of the microphytobenthic communities with increasing photon fluence rates were recorded in the original water volume above the sediment surface of the core. The water column above the sediment contained always $<$ 2 μg chlorophyll a L^{-1} which is considered as oligotrophic (Håkanson, 2008), and hence phytoplankton was neglectable. Benthic diatoms were exposed to 5 to 7 increasing light levels ranging from 0 to 750 μmol photons m^{-2} s^{-1} of PAR. Photon fluence rates were measured with a cosine corrected 2π light sensor (light meter LI-250, LI-COR, Lincoln, United States of America) placed directly next to the core on the same height as the sediment surface. Measurements started with a respiration phase of 30 min in the dark followed by a 20 min photosynthesis phase for each light level. The experiment was finished by a final respiration phase for 30 min. Different light levels were achieved by covering the LEDs with combinations of neutral density filter foils. The distance from light source to the sediment surface was kept constant during the measurement. After the experiment the top first cm of each sediment core was harvested and used for chlorophyll a determination as described in detail above. The oxygen consumption and production per time unit was referenced to the surface area (mg O_2 m^{-2} h^{-1}). The resulting photosynthesis irradiance (PI) curve data were fitted to the nonlinear model of Webb et al. (1974) which describes the change in gross production (GPP) with increasing photon fluence rate without photoinhibition:

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

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

2.5. Scanning electron microscopical investigation

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

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

2.6. Statistics

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

3. Results

3.1. Environmental settings of both study sites

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

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

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

3.2. Microphytobenthic standing stock biomass

The areal chlorophyll *a* concentration was determined as widely used proxy for phototrophic biomass in all sediment
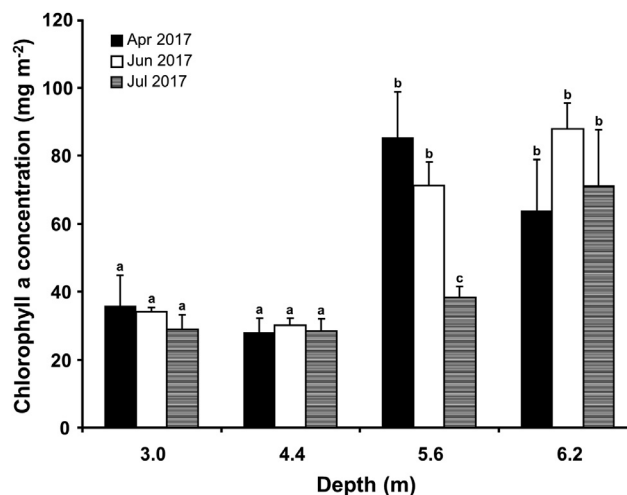

Figure 3 Areal chlorophyll *a* concentration as proxy for phototrophic biomass (chlorophyll *a* mg m^{-2}) in all sediment samples, as measured in different water depths (m) and at three sampling dates in April, June and July 2017. All values represent the mean values with standard deviation (n=12—15).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

samples. A distinct depth gradient with significantly lower chlorophyll *a* values was observed ranging from 28.5 mg Chl. *a* m^{-2} at 3 m depth to 87.7 mg Chl. *a* m^{-2} at 6.2 m depth (p < 0.05, Figure 3). Both shallow water stations at 3.0 and 4.4 m depth exhibited very similar chlorophyll *a* concentrations (28.0 to 35.8 mg Chl. *a* m^{-2}) in April, June and July 2017 (Figure 3). In contrast, at both deeper stations the chlorophyll *a* values were always higher, but also more variable. Particularly the July sample at 5.6 m exhibited a strong decline in chlorophyll *a* concentration from 71.2—85.2 mg Chl. *a* m^{-2} in April/June to 38.3 mg Chl. *a* m^{-2} (Figure 3).

3.3. Microphytobenthic primary production and respiration

Net primary production strongly varied across the sampling dates and along the depth gradient from 3 to 6.2 m, ranging from 29.4 to 178.9 mg O$_2$ m^{-2} h^{-1} (Figure 4). At the shallowest station (3.0 m water depth) net primary production was the highest in April 2017 (129.9 mg O$_2$ m^{-2} h^{-1}) and the lowest in June 2017 (39.7 mg O$_2$ m^{-2} h^{-1}), while in July 2017 an intermediate rate was measured (68.8 mg O$_2$ m^{-2} h^{-1}) (Figure 4). A similar pattern could be determined at the 5.6 m station, where in April and June 2017 the highest production rates were estimated (178.8 and 151.0 mg O$_2$ m^{-2} h^{-1}, respectively), followed by a sharp decline to 29.4 mg O$_2$ m^{-2} h^{-1} in July 2017 (Figure 4). At the deepest station (6.2 m) net primary production was more similar across the sampling dates, ranging from 68.5 to 104.6 mg O$_2$ m^{-2} h^{-1} (Figure 4).

In contrast to net primary production rates, respiration rates were more similar at all stations and sampling dates. The respiration values ranged from −9.9 to −20.8 mg O$_2$ m^{-2} h^{-1} (Figure 5). The measured respiratory rates were low since at each depth and sampling date net primary produc-
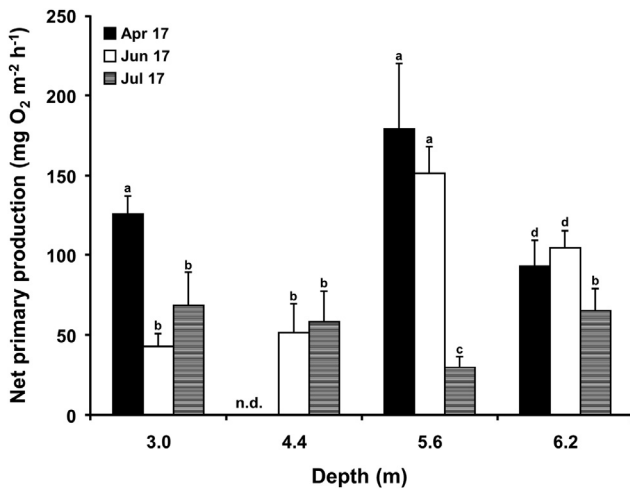
Figure 4   Rates of ex situ net primary production expressed as mg O_2 m^{-2} h^{-1} along the depth gradient from 3.0 to 6.2 m and at three sampling dates in April, June and July 2017. All values represent mean values with standard deviation (n=3). Different letters indicate significantly different means (Tukey's test, $P < 0.05$). n.d.: not detected.
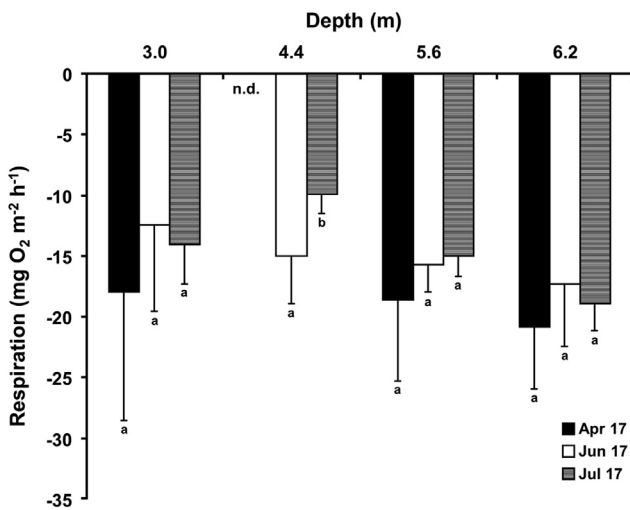
Figure 5   Rates of ex situ respiratory oxygen consumption expressed as mg O_2 m^{-2} h^{-1} along the depth gradient from 3.0 to 6.2 m and at three sampling dates in April, June and July 2017. All values represent the mean values with standard deviation (n=3). Different letters indicate significantly different means (Tukey's test, $P < 0.05$). n.d.: not detected.

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

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

3.4. Diatoms colonizing sediment particles

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.

4. Discussion

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 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 turbu-

Table 2   Gross primary production (mg C m^{-2} 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 (PQ = $\triangle O_2/\triangle C$) of 1 (Hargrave et al., 1983).

Location	GPS data	Depth (m)	Sediment mean grain diameter (μm)	Method	GPP (mg C m^{-2} h^{-1})	Chl. *a* 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
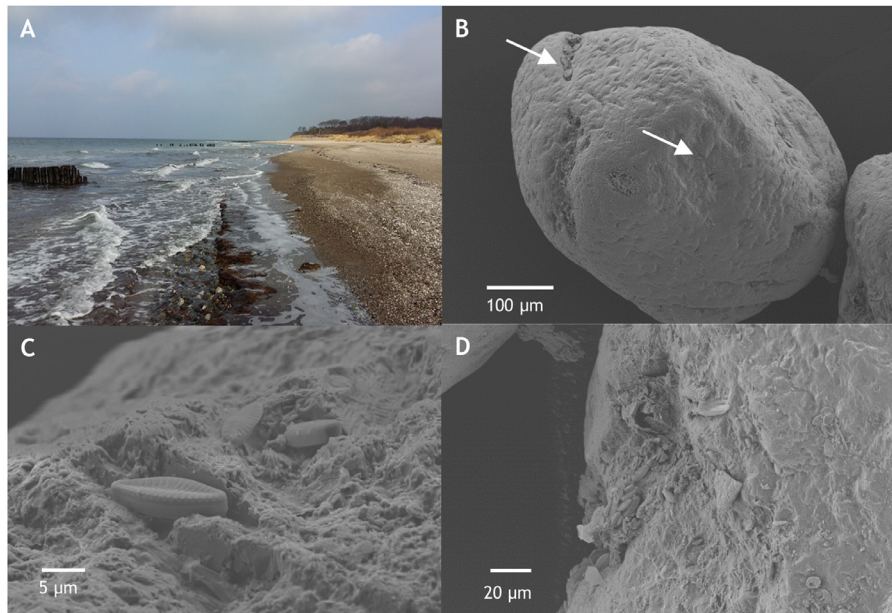
Figure 6   Representative habitat picture of the exposed sampling site in front of the Hütelmoor on 18th February 2016 (A). This site is a near shore sandy beach, which is strongly influenced by westerly winds and a coastal parallel east-west current leading to high hydrodynamic, erosive forces. Scanning 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).

lence can cause resuspension of surface sediments and their associated organisms resulting in lower microalgal biomass (de Jonge and van Beusekom, 1995).

The sediment organic matter (OM) content ranged between 4 and 9 mg g^{-1} dry weight across all stations and sampling dates which is similarly low to 3—6 mg g^{-1} dry weight measured in a nearby wind flat at a station with very low numbers of phototrophic microorganisms (Woelfel et al., 2007). Assemblages of benthic diatoms and cyanobacteria, however, increase the OM values in the wind flat to 12—17 mg g^{-1} dry weight (Woelfel et al., 2007).

The C/N ratios measured in April and June 2017 amounted between 6 and 18 across all stations, and are in the same range as previously published ratios (10—12) for sediments sampled in a shallow coastal lagoon at Hog Island Bay, Virginia, USA (Hardison et al., 2013). In July 2017, a strong change in the C/N ratios could be observed. While at both deeper stations the C/N ratios increased to 42—86, at both shallower stations the opposite was observed with a strong decline of the C/N ratio to 4. High C/N ratios generally indicate carbon-rich organic matter, which is relatively poor in nitrogen. The study site is connected to a coastal peatland, which stretches into the shallow water zone (Kreuzburg et al., 2018). These authors reported also organic-rich layers further offshore with C/N ratios <71, which are similar to the data of the present study. The submerged peat and organic-rich layers at the study site are not always exposed to the water column, depending on wave-induced sediment movement which results in erosion or burial (Jurasinski et al., 2018). C/N ratios of 4 are rather unusual, but have been described for unialgal cultures (Falkowski and Owens, 1980) and for early spring cyanobac-

terial plankton in the Baltic Sea (Walve and Larsson, 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 shallow water stations. There is, however, significant submarine 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 radiation due to the optical properties of the water column (yellow substances, re-suspended particles, phytoplankton etc.). Maximum solar radiation during spring and summer 2017 ranged from approximately 1,900 to 2,100 μmol photons m^{-2} s^{-1} (own measurements). Vertical snapshot light measurements at the deeper stations at noon in June and July 2017 down to the seafloor resulted in calculated attenuation coefficients (K$_d$) between 0.26 and 0.41 m^{-1}. These rather low K$_d$ values point to a high to medium transmittance of the water column in the PAR range, resulting in 135 to 157 μmol photons m^{-2} s^{-1} at noon at 6 m depth (own measurements). Such PFDs are usually sufficient to saturate the light requirements for photosynthesis in benthic diatoms. This is supported by measurements of the photosynthetic performance of eight clonal benthic diatom strains, which were isolated from the study site, and which exhibited light saturation points between 32 and 151 μmol photons m^{-2} s^{-1} (Prelle et al., 2019). Similar low light requirements (34 to 100 μmol photons m^{-2} s^{-1}) were reported for three benthic diatom species isolated from a sheltered sediment of the southern Baltic Sea

(Woelfel et al., 2014a). Benthic diatoms are well known for their high photophysiological plasticity and their capability for vertical movement into or out of the sediment to avoid photodamage (Ezequiel et al., 2015). Physiological and behavioral photoprotection are thus the two major mechanisms by which natural microphytobenthic communities protect themselves against high incident solar radiation (Cartaxana et al., 2011). They are able to adjust their photosynthetic apparatus relatively quickly to a new light regime (Glud et al., 2002; Kühl et al., 2001). The underlying mechanisms include, for example, alterations of the size or composition of the photosynthetic units with consequences for electron transport capacity (Richardson et al., 1983). However, as mentioned before, most of the benthic diatoms observed were araphid and epipsamic, and hence immobile.

As mentioned in the introduction microphytobenthic biomass can strongly vary in space and time at all scales on shallow coastal sediments (Ubertini et al., 2012). There are many reports indicating benthic diatom biomass changes even on diurnal to bi-weekly tidal cycles and over the course of the seasons (Koh et al., 2007; Orvain et al., 2012; van der Wal et al., 2010). Besides light, temperature and wind conditions (Ubertini et al., 2012), also nutrient concentrations can control microphytobenthic biomass and primary production (Cibic et al., 2007), although sediment pore water is generally considered as nutrient-enriched compared to the overlying water column (Garcia-Robledo et al., 2016; Sundbäck et al., 1991). In addition, sediment grain-size is not homogenous within tide-influenced coastal areas, leading to differential distribution of particle size-groups with different degrees of erodibility which of course affects benthic diatom biomass and activity (Orvain et al., 2012; Ubertini et al., 2012). The sediment types determine the preferential occurrence of epipsamic or epipelic benthic diatoms causing related variation in their biomass (Ubertini et al., 2012). Microphytobenthos have mostly been studied in temperate tidal-influenced estuaries (Serôdio et al., 2020), while for the Baltic Sea with its specific hydrographic and environmental conditions only few data exist.

The used ex situ planar oxygen optode approach, i.e. to sample intact sediment cores as intact microecosystem from the field and to undertake incubations under controlled and simulated conditions in the laboratory, opens many possibilities to estimate benthic production rates under 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 microelectrode 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 Jorgensen, 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 cm^2. 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 O$_2$ 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 O$_2$ m^{-2} h^{-1}, other authors reported much higher values (−48.6 mg O$_2$ m^{-2} h^{-1}, Urban-Malinga and Wiktor, 2003; −46.0 mg O$_2$ m^{-2} h^{-1}, Woelfel et al., 2010; −37.2 mg O$_2$ 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 O$_2$ values were converted into C equivalents using a photosynthetic quotient (PQ = ΔO$_2$/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 Longphuirt 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}, Vilbaste 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).

5. Conclusion

In conclusion, our hypothesis could be confirmed that with increasing water depths the effects of strong wind- and wave-induced mixing of the upper sediment layer are dampened and hence they support higher microphytobenthic biomass and primary production. Consequently, microphytobenthic communities play an important ecological role at the shallow southern Baltic Sea coast, and hence their contribution to the total primary production should be much better evaluated in space and time. Such data are important for the calculation of a realistic complete Baltic Sea carbon budget, as reported so far only for the Bothnian Bay (Ask et al., 2016). In addition, if the mi-

crophytobenthic primary production contributes with one third to the total Baltic Sea production, its biogeochemical fate under global change scenarios should be much better evaluated because of future weather and climate change scenarios for the southern Baltic Sea region. Dryer summers with more frequent and occasional extreme storm events are to be expected (BACC II Author Team, 2015), leading to higher disturbance of exposed sandy sediments with negative effects on microphytobenthic primary production.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at https://doi.org/10.1016/j.oceano.2021.02.002.

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