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Benthic photosynthesis in submerged Wadden Sea intertidal flats

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Abstract

In this study we compare benthic photosynthesis during inundation in coarse sand, fine sand, and mixed sediment (sand/mud) intertidal flats in the German Wadden Sea. In situ determinations of oxygen-, DIC- and nutrient fluxes in stirred benthic chamber incubations were combined with measurements of sedimentary chlorophyll, incident light intensity at the sediment surface and scalar irradiance within the sediment. During submergence, microphytobenthos was light limited at all study sites as indicated by rapid response of gross photosynthesis to increasing incident light at the sea floor. However, depth integrated scalar irradiance was 2 to 3 times higher in the sands than in the mud. Consequently, gross photosynthesis in the net autotrophic fine sand and coarse sand flats during inundation was on average 4 and 11 times higher than in the net heterotrophic mud flat, despite higher total chlorophyll concentration in mud. Benthic photosynthesis may be enhanced in intertidal sands during inundation due to: (1) higher light availability to the microphytobenthos in the sands compared to muds, (2) more efficient transport of photosynthesis-limiting solutes to the microalgae with pore water flows in the permeable sands, and (3) more active metabolic state and different life strategies of microphytobenthos inhabiting sands.

Keywords: benthic photosynthesis; tidal flats; inundation; light availability; advective transport; Germany; North Sea; Wadden Sea

1. Introduction

Microphytobenthos contributes significantly to total primary production in intertidal ecosystems (MacIntyre et al., 1996; Underwood and Kromkamp, 1999). Benthic microalgae are a central component supporting the coastal food chain (Middelburg et al., 2000; Herman et al., 2001), they influence oxygen and nutrient fluxes across the sediment water interface (Bartoli et al., 2003; Tyler et al., 2003) and they are critical for coastal sea bed dynamics through stabilization of sediments by their extracellular polymeric substances (Smith and Underwood, 1998; Widdows et al., 2000; Yallop et al., 2000). Biomass, light- and CO_2 availability have been identified to determine microphytobenthic production (Admiraal et al., 1982; MacIntyre et al., 1996; Barranguet et al., 1998). Nutrients are often not a limiting factor in intertidal sediment (Barranguet et al., 1998; Serôdio and Catarino, 2000; Migne et al., 2004) as the microphytobenthos can assimilate nutrients from both the overlying water and the sediment pore water (MacIntyre et al., 1996; Cahoon, 1999).

In the intertidal regions of the German Wadden Sea, sandy sediments are predominant, while muddy sediments are restricted to relatively narrow low energy zones close to the coastline (Flemming and Ziegler, 1995). Muddy sediments exhibit high rates of benthic primary production (Pomeroy, 1959; Leach, 1970) and tend to have a higher microphytobenthic biomass than sandy sediments (Colijn and Dijkema, 1981; de Jong and de Jonge, 1995). Nevertheless, primary production in intertidal sand flats can be equally high as in mud flats during low tide exposure (Barranguet et al., 1998). In the dynamic intertidal habitat, high microphytobenthic productivity

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can be sustained by regular resuspension events that keep the algal standing stock below the maximum carrying capacity of the system (Blanchard et al., 2001). Resuspension of benthic algae is more likely in high-energy environments like sand flats. More frequent mixing events and higher degradation rates in sand than in mud cause a higher turnover of algal biomass in intertidal sandy sediment of the Dutch Wadden Sea (Middelburg et al., 2000). Therefore, high benthic productivity can possibly be more effectively sustained in sandy sediments than in muds.

As a result of the frequently highly turbid water near the coast, light is the principal limiting factor for primary production in the water column of the Wadden Sea (Veldhuis et al., 1988; Tillmann et al., 2000; Colijn and Cadee, 2003) and may also limit benthic photosynthesis. Therefore, in several studies, microphytobenthos production in intertidal sediments has been assumed to be mostly restricted to the exposure period (e.g. Serôdio and Catarino, 2000; Guarini et al., 2002; Migne et al., 2004). However, photosynthetic production of benthic microalgae can be sustained at low light intensities of about 5–10 μmol photons m^{-2} s^{-1} (Cahoon, 1999 and references therein). Furthermore, the early studies of Cadee and Hegeman (1974, 1977) suggest that benthic primary production takes place also during inundation. Asmus (1982) showed that the microphytobenthos contributed 68% to total primary production during inundation of a sand flat in Sylt, Germany, in an area where water is relatively clear (Asmus et al., 1998).

Light limitation during flooding is possibly more severe over mud flats than sand flats, as fine sediments are more easily resuspended by waves and currents and have much longer settling times than sand. Motile benthic microalgae migrate into the sediment surface layer during inundation to prevent erosion (Janssen et al., 1999; Mitbavkar and Anil, 2004) and consequentially depend on the light availability within the sediment. Light is typically more effectively absorbed in muddy sediment than in sand (Haardt and Nielsen, 1980; Kühl et al., 1994). Thus, benthic microalgae in sand flats may profit from a higher light availability within the sediment as compared to the microphytobenthos in mudflats.

The production of benthic microalgae can be limited by CO_2 availability (Admiraal et al., 1982; Rasmussen et al., 1983). Intense CO_2 assimilation of microphytobenthos can result in pH values above 9 within the photic zone of the sediment (Revsbech and Jørgensen, 1986) and reduced free CO_2 concentrations limiting primary production (Rasmussen et al., 1983; Cook and Røy, 2006). Recent laboratory and field studies suggest that this CO_2 limitation can be relieved by increased advective flushing of the photic zone (Cook and Røy, 2006; Wenzhöfer et al., in preparation).

We hypothesize that during inundation, benthic photosynthesis may be enhanced in intertidal sand flats as compared to mud flats due to higher light availability, more effective solute transport to the algae counteracting CO_2 and nutrient limitation and ensuing more active metabolic state of the microalgal community. We tested this hypothesis by conducting light and dark incubations with advection chambers in coarse, fine, and mixed sand/mud intertidal sediments of the German Wadden Sea. Interpretations of the flux recordings were supported by concurrent measurements of sedimentary chlorophyll, in situ incident light intensity and scalar irradiance within the sediment.

2. Methods

2.1. Study sites

In situ measurements and sampling were carried out in two intertidal sand flats and one mixed sand/mud flat in the German Wadden Sea (Fig. 1). The coarse sand site was located on the sand flat "Hausstrand" (55°00′53″ N, 008°26′17″ E) on the island of Sylt. The fine sand site on the intertidal flat "Janssand" (53°44′07″ N, 007°41′57″ E) and the mixed flat near Neuharlingersiel (53°42′09″ N, 007°42′33″ E) were both situated in the backbarrier area of the island of Spiekeroog. Henceforth, the Sylt, Janssand and Neuharlingersiel sites are denoted as coarse sand, fine sand and mud site, respectively. During high tide, the coarse sand and fine sand sites are covered by 1.5–2 m of water, the mud site by 1–1.5 m of water. Investigations took place during spring, summer and autumn 2002, and Summer 2003 (Table 1). In situ measurements with benthic chambers were not possible during winter due to frozen sediments and adverse weather conditions.

2.2. Sediment characteristics

Grain size was analysed by dry-sieving the top 10 cm of the sediment and classified according to Wentworth (1922). Permeability was determined with the constant head method (Klute and Dirksen, 1986) for the top 15 cm of the sediment at the two sandy sites and for the top 4 cm at the mud site. Sediment samples for total carbon (TC) and total inorganic carbon (TIC) measurements were sectioned into 1 cm intervals and stored frozen.

2.3. Chlorophyll analysis

For the measurement of chlorophyll, the top 10 cm of the sediment at the two sandy sites were sectioned in 0.5 cm intervals down to 5 cm depth, and in 1 cm intervals below. At the mud site, the top 5 cm of the sediment were sectioned in 0.2–0.5 cm intervals down to 2 cm depth, and in 0.5 cm intervals below. During spring 2002, the upper 5 cm of the sediment at the mud site were pooled. All sediment samples for chlorophyll analysis were kept frozen and dark until analysis.

2.4. Light measurements in the sediment

A microsensor for scalar irradiance measurement was prepared by placing a 70 μm spherical diffuser on the tapered tip of a 100 μm optical glass fibre (Kühl and Jørgensen, 1992). The same sensor was used for all profiles and connected to a photo-multiplier tube with custom support electronic. Light profiles within the sediment were measured in the laboratory

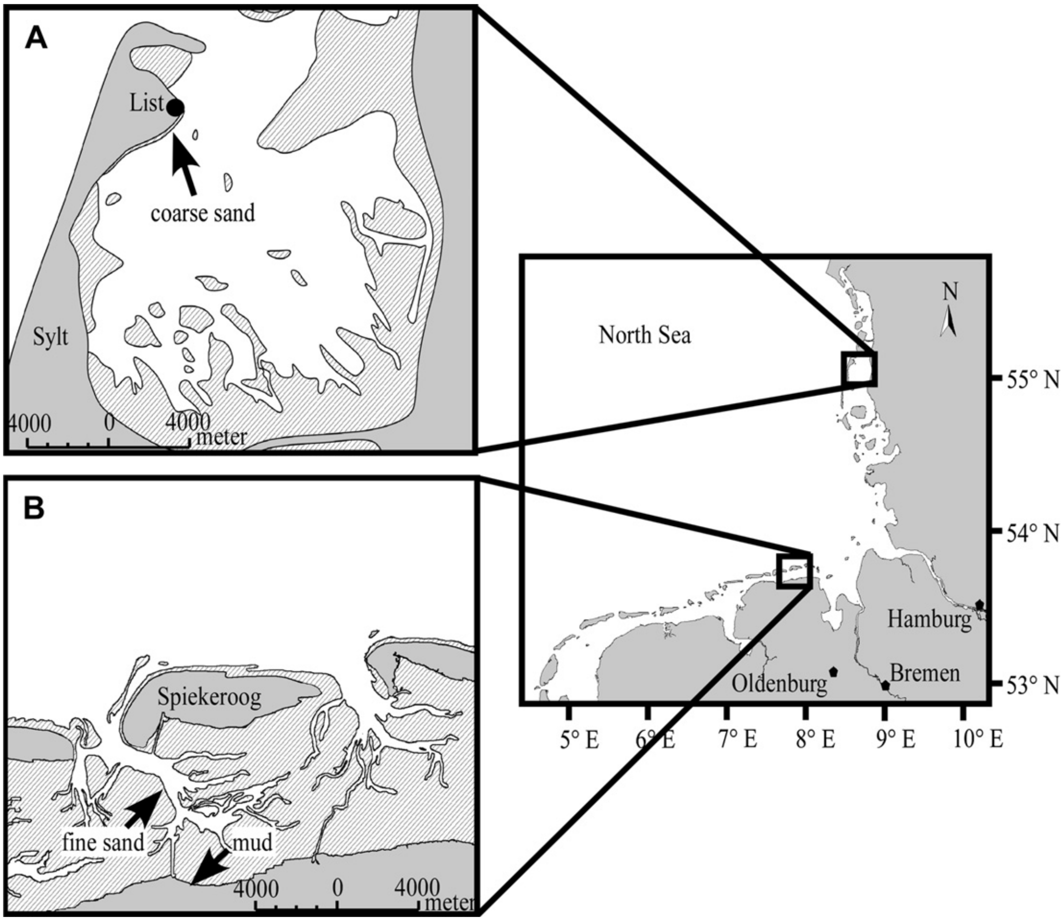

Fig. 1. Intertidal study sites in the German Wadden Sea. (A) The coarse sand site. (B) The fine sand and mixed sand/mud site.

Table 1
Sampling and in situ benthic chamber incubations during the measurement campaigns at the three study sites. Numbers denote replicate measurements (dark/light incubations for benthic chambers)

Campaigns	Sediment parameters			Benthic chambers				
	Permeability	TOC	Chlorophyll	Oxygen	DIC	Nutrients	Br-tracer	Incident light
Coarse sand								
Spring 2002 16./17.04.02	12	13	4	5/4 Optodes	2/2	4/4		1 Only 17.4.
Summer 2002 18./22.08.02	15	13	4	4/2 Winkler		4/2	5	1
Fine sand								
Spring 2002 13.03.02		10		3/2 Optodes	2/2	2/2		
Summer 2002 07.06.2002	9	10	4	2/2 Winkler		2/2	5	1
Autumn 2002 25./26.09.02		10	2	5/4 Optodes	3/2	4/2	5	1
Summer 2003 29.07.2003	6	8	2	3/3 Optodes	3/3	3/3	2	1
Mud								
Spring 2002 04.04.2002	3	10	4 top 0–5 cm	2/2 Winkler		2/1	2	
Summer 2002 19.06.2002		8	4	2/2 Winkler		2/2	4	1
Autumn 2002 30.09.2002		8	2	3/2 Optodes		2/1		1
Summer 2003 02.08.2003		8	2	3/2 Optodes	2/2	2/2		1

in sediment cores (36 mm diameter) from all study sites. The sediment surface was uniformly illuminated with two white light sources placed opposite from each other at 20° zenith angle. The light intensity within the sediment is given normalized to the incident irradiance.

2.5. Benthic chamber incubations

In situ incubations with cylindrical benthic chambers (19 cm inner diameter) were conducted to measure fluxes of oxygen, DIC and nutrients across the sediment water interface. Two transparent and two opaque chambers were used in one or two deployments (Table 1) at each study site. During summer 2003, three transparent and three opaque chambers were used. The stirring of the chamber water by a rotating disc (15 cm diameter) at 20 rpm induces advective flow through the surface layer of permeable sediment (Huettel and Gust, 1992a,b). During low tide, the chambers were placed onto the respective sediment, with the walls of the chambers penetrating down to a sediment depth of 19 cm. After inundation, the chambers were sealed with transparent or opaque lids, each enclosing a water volume of 3.4 L and a sediment area of 0.028 m^2. Twenty milligrams of a 3 mol L^{-1} NaBr inert tracer solution was then injected into each chamber for the assessment of the advective fluid exchange between enclosed sediment and overlying water (Forster et al., 1999). During most incubations (see Table 1), the oxygen concentration inside each chamber was monitored every 2 min for 20 s with fibre-optic optodes inserted through the chamber lid. For oxygen, nutrient and DIC analysis, a total of 80–140 ml volume of chamber water was sampled in 0.5–1 h intervals via a flexible tube (15 ml volume) with one end attached to a sampling port on the chamber lid and the other end reaching above the maximum water level. The first 20 ml of each sample was discarded to account for the sampling tube volume. The sampled water was replaced with ambient seawater via a second port in the chamber lid. Additionally, samples of ambient seawater were taken at each sampling interval. Samples for nutrient analysis were filtered through 0.2 μm nylon syringe filters into plastic vials and kept frozen until analysis. DIC samples were stored without headspace in glass vials and preserved with a saturated mercury chloride solution (end concentration 0.01%) in a refrigerator until analysed in the laboratory. At the end of the chamber incubations, with the water level still above the chambers, sediment cores were retrieved with cut off 60 ml syringes for bromide tracer analysis. The sediment cores were sliced in 0.5 cm intervals (0.2 cm intervals at the mud site) within 30 min after retrieval and kept frozen. Incident light at the sediment surface during the chamber incubations was measured with an Onset® photometric light logger that was sealed watertight into a transparent acrylic tube and positioned close to the sea floor (Table 1). The data, logged in lumen m^{-2}, were transformed into μmol Quanta m^{-2} s^{-1} by calibrating the light logger within the acrylic tube against a Licor® LI-250A quantum light meter in the laboratory.

2.6. Analytical procedures

The sediment samples for TC and TIC analysis were freeze-dried and ground in the laboratory. Sample aliquots were then transferred into tin-cups for TC measurements and analysed with a Heraeus CHNO-rapid elemental analyser using sulphanilamide as a calibration standard. TIC sample aliquots were measured by coulometric titration on a UIC CM5012 and TOC was calculated by subtracting TIC from TC. Pigments were extracted in the laboratory by sonification of sediment subsamples in 10 ml 90% acetone and subsequent measurement of the supernatant on a Shimadzu® UV-160 A spectrophotometer before and after acidification. Phaeopigment concentrations were then calculated according to Lorenzen (1967). Because concentrations of chlorophyll degradation products were very low at the two sandy sites and in some cases produced erroneous results when used for the calculation of chlorophyll *a*, pigment concentrations were given as total chlorophyll (absorption at 665 nm without acidification) for all study sites. For the analysis of bromide, the pore water of the sediment samples was extracted by centrifugation and 100 μl of the pore water then analysed by ion chromatography with a Waters anion-exchange column, using NaBr as a standard for calibration. Nutrient analysis of silicate, phosphate, ammonium, nitrate, and nitrite were performed spectrophotometrically with a Skalar® Continuous-Flow-Analyzer according to Grasshoff et al. (1999). In the following, NO_x fluxes denote the sum of nitrate and nitrite fluxes. Chamber water DIC was determined in the laboratory by flow injection analysis using freshly prepared $NaHCO_3$ calibration standards (Hall and Aller, 1992). In Summer 2003, DIC was measured by coulometric titration on a UIC® CM5012. Oxygen concentrations of the chamber water were determined by Winkler titration and used for calibration of the chamber oxygen optodes (Klimant et al., 1995; Holst et al., 1997). The dilution of the chamber waters due to the sampling was corrected by adding the difference of the solute inventory between the sampled and replaced volume to the chamber volume solute inventory. All solute fluxes are given as calculated from start and end concentrations (lowest end concentration for oxygen was 46 μmol L^{-1} in mud incubations).

3. Results

3.1. Sediment characteristics

At the coarse and fine sand sites, the mud fraction (<63 μm) was below 0.2%, while reaching 12.5% at the mixed sand/mud site. As a consequence, the sediment was highly permeable at the coarse sand, permeable at the fine sand and almost impermeable at the mud site (Table 2). The sandy sites were organic poor, with TOC contents of 0.1% or less in the upper 10 cm of the sediment, whereas the TOC content ranged between 0.5% and 0.7% at the mud flat.

Table 2
Sediment parameters, permeability (top 15 cm at sandy sites, top 4 cm at mud site) and percentage of TOC per sediment weight (top 10 cm) at the three study sites. The standard deviation ($n = 3$–15 for permeability, $n = 8$–11 for TOC) is given in parentheses

	Coarse sand	Fine sand	Mud
Median grain size (μm)	380	176	139
Sorting	Very well	Well	Moderately
Permeability (m^2)			
Spring 2002	4.0×10^{-11} (0.3)		6.0×10^{-14} (0.2)
Summer 2002	3.9×10^{-11} (0.3)	9.0×10^{-12} (0.8)	
Autumn 2002			
Summer 2003		7.2×10^{-12} (0.6)	
TOC (%)			
Spring 2002	0.06 (0.02)	0.05 (0.02)	0.71 (0.28)
Summer 2002	0.08 (0.04)	0.06 (0.01)	0.51 (0.08)
Autumn 2002		0.06 (0.02)	0.52 (0.12)
Summer 2003		0.08 (0.03)	0.56 (0.10)

3.2. Tracer transport

The stirring of the benthic chambers generated an advective flushing of the upper sediment layer. Reflecting the different permeabilities at the three study sites, the tracer was transported down to a sediment depth of 7.0 cm (SD ± 1.6, $n = 5$) in the coarse sand, 2.3 cm (SD ± 0.5, $n = 12$) in the fine sand and 1.3 cm (SD ± 0.4, $n = 6$) at the mud site.

3.3. Light availability in the sediment

Light distributions within the sediment of the three study sites are shown in Fig. 2. The increase above the sediment surface of the coarse and fine sand is due to reflection by the quartz sand. The irradiance peak below the surface is due to multiple scattering within the sediment. These features are less pronounced at the mud site due to less reflection and higher light absorption of the mud. The depth integrated scalar irradiance in the coarse sand was factor 3.45 higher and in the fine sand factor 2.04 higher than in the mud.

3.4. Sediment total chlorophyll

Total chlorophyll concentrations decreased with sediment depth at the three study sites and were generally higher at the muddy site than at the two sandy sites (Fig. 3). Total chlorophyll in the uppermost cm of the sediment was on average 185 mg m^{-2} (range 176–194 mg m^{-2}) in the coarse sand, 150 mg m^{-2} (range 134–172 mg m^{-2}) in the fine sand and 291 mg m^{-2} (194–356 mg m^{-2}) in the mud during the study seasons. At the two sandy sites, phaeophytin was never detectable in the top 3 cm and did not exceed 10% of the total chlorophyll below. At the mud site, phaeophytin was present at all sediment depths reaching up to 18% of total chlorophyll in the uppermost cm of the sediment and up to 38% below.

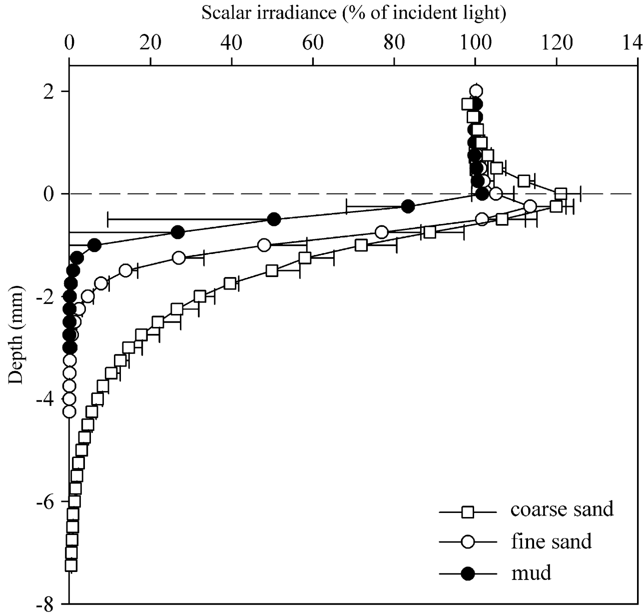

Fig. 2. Depth profiles of scalar irradiance normalized to incident light at the coarse sand, fine sand and mud site. Error bars indicate standard deviation of 3–6 measurements.

3.5. Oxygen and DIC fluxes

Oxygen and DIC fluxes revealed that benthic microalgae photosynthesized during inundation at all stations during all seasons (Fig. 4). Despite the higher total chlorophyll concentrations in the upper sediment layer of the mud site, areal gross photosynthesis was about 4-fold higher in the fine sand and 10-fold higher in the coarse sand compared to the mud site (Table 3). Fig. 5 shows the direct response of areal gross photosynthesis rates to the changing incident light regime at all study sites. During Summer 2002, areal gross photosynthesis rates in the coarse sand were much higher than those in the fine sand and mud, despite similar or even lower in situ photon flux at the coarse sand site compared to the two other sites (Fig. 5). The high photosynthetic activity at the two sandy study sites led to an efflux of oxygen during daytime inundation, whereas the oxygen produced at the mud site was completely consumed within the sediment (Fig. 4A). Production in the water column measured with in situ bottle incubations during July 2003 at the fine sand and mud sites was less than 3% of the benthic production.

3.6. Nutrient fluxes

Benthic photosynthesis affected the chamber nutrient fluxes (Fig. 6). While phosphate and ammonium were generally released from the sediment in the dark incubations, the light chamber fluxes indicated an uptake of inorganic nutrients by the microphytobenthos (Fig. 6B, C). Silicate was generally released in the dark incubations at all sites and the light fluxes indicated photosynthetic assimilation of silicate in the fine sand (Fig. 6A). Nitrate + nitrite (NO_x) was usually taken up by the sediment in both dark and light incubations during all

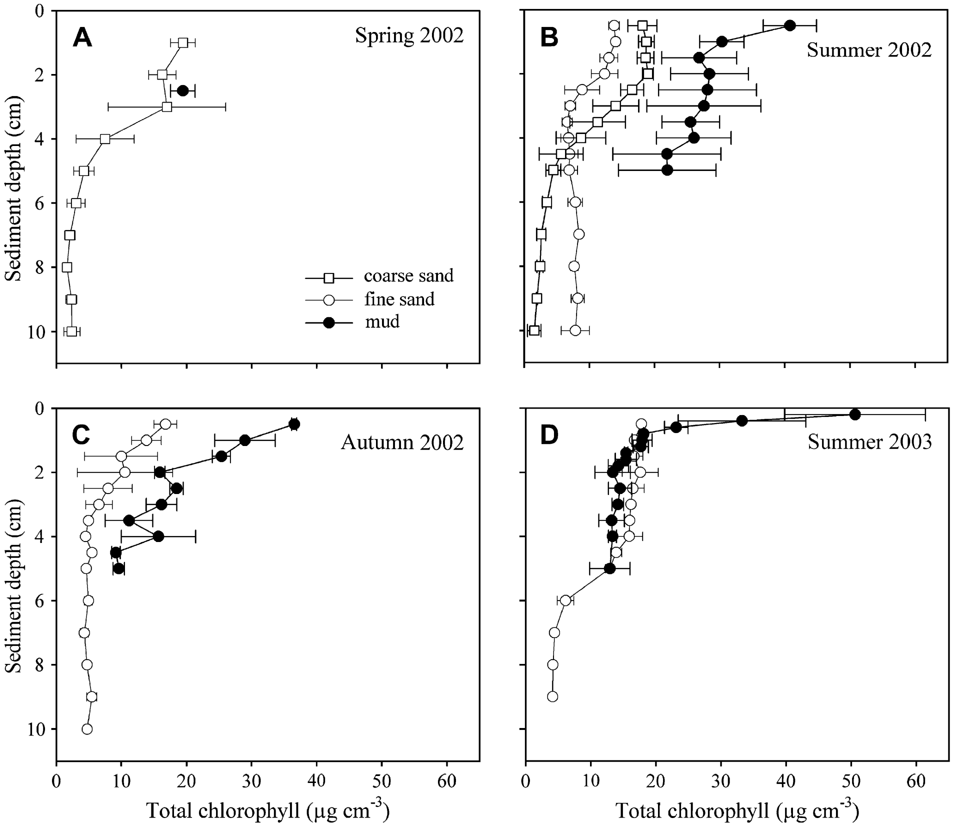

Fig. 3. Total chlorophyll concentration of the sediment at the study sites (μg cm^{-3}) with the standard deviation ($n = 2–4$) as error bars.

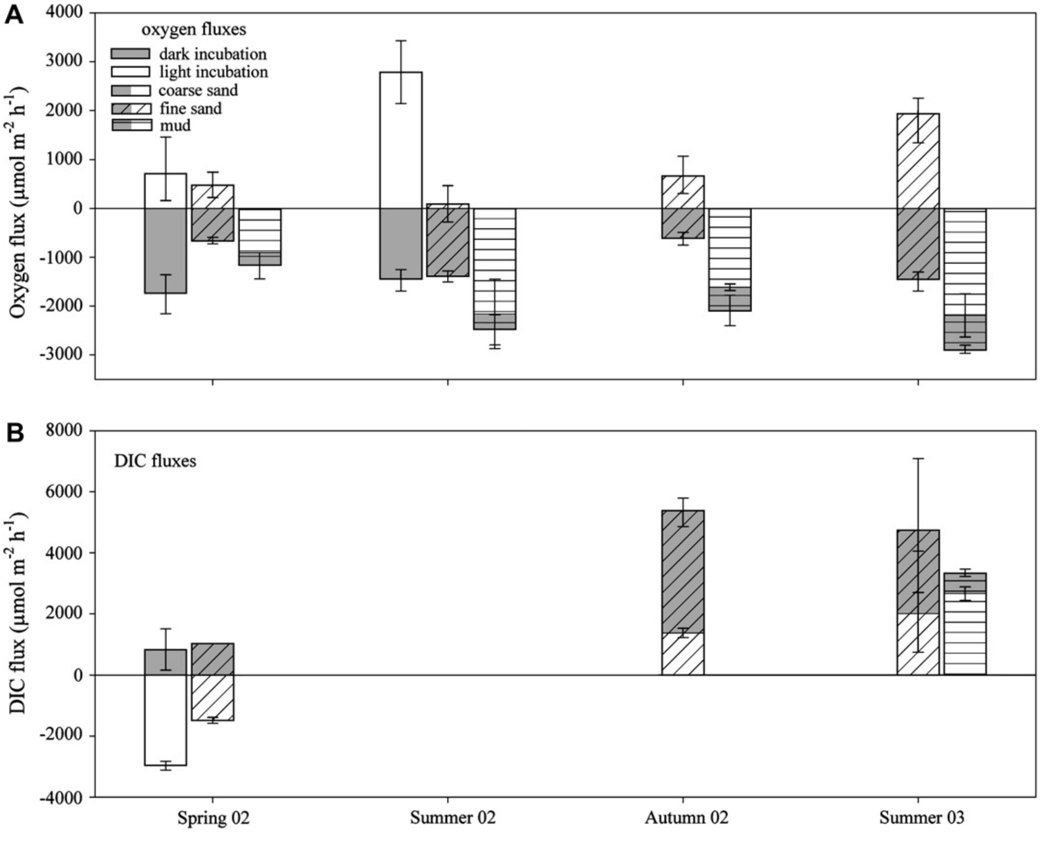

Fig. 4. Average benthic chamber fluxes of (A) oxygen and (B) DIC at the three study sites with range as error bars. Negative and positive values denote influx and efflux via the sediment surface, respectively.

Table 3
Net oxygen and DIC fluxes in µmol m^{-2} h^{-1} in dark and light incubations at the three study sites and calculated gross photosynthetic production of oxygen and consumption of DIC (GP). Negative and positive values denote influx and efflux via the sediment surface, respectively

	Coarse sand			Fine sand			Mud		
	Dark	Light	GP	Dark	Light	GP	Dark	Light	GP
Oxygen									
Spring 2002	−1737	718	2455	−676	482	1158	−1169	−903	266
Summer 2002	−1453	2788	4241	−1394	94	1488	−2483	−2159	325
Autumn 2002				−617	668	1284	−2098	−1613	485
Summer 2003				−1456	1942	3398	−2901	−2191	710
DIC									
Spring 2002	834	−2968	−3803	1035	−1486	−2521			
Summer 2002									
Autumn 2002				5499	1534	−3965			
Summer 2003				4751	2008	−2743	3350	2665	−684

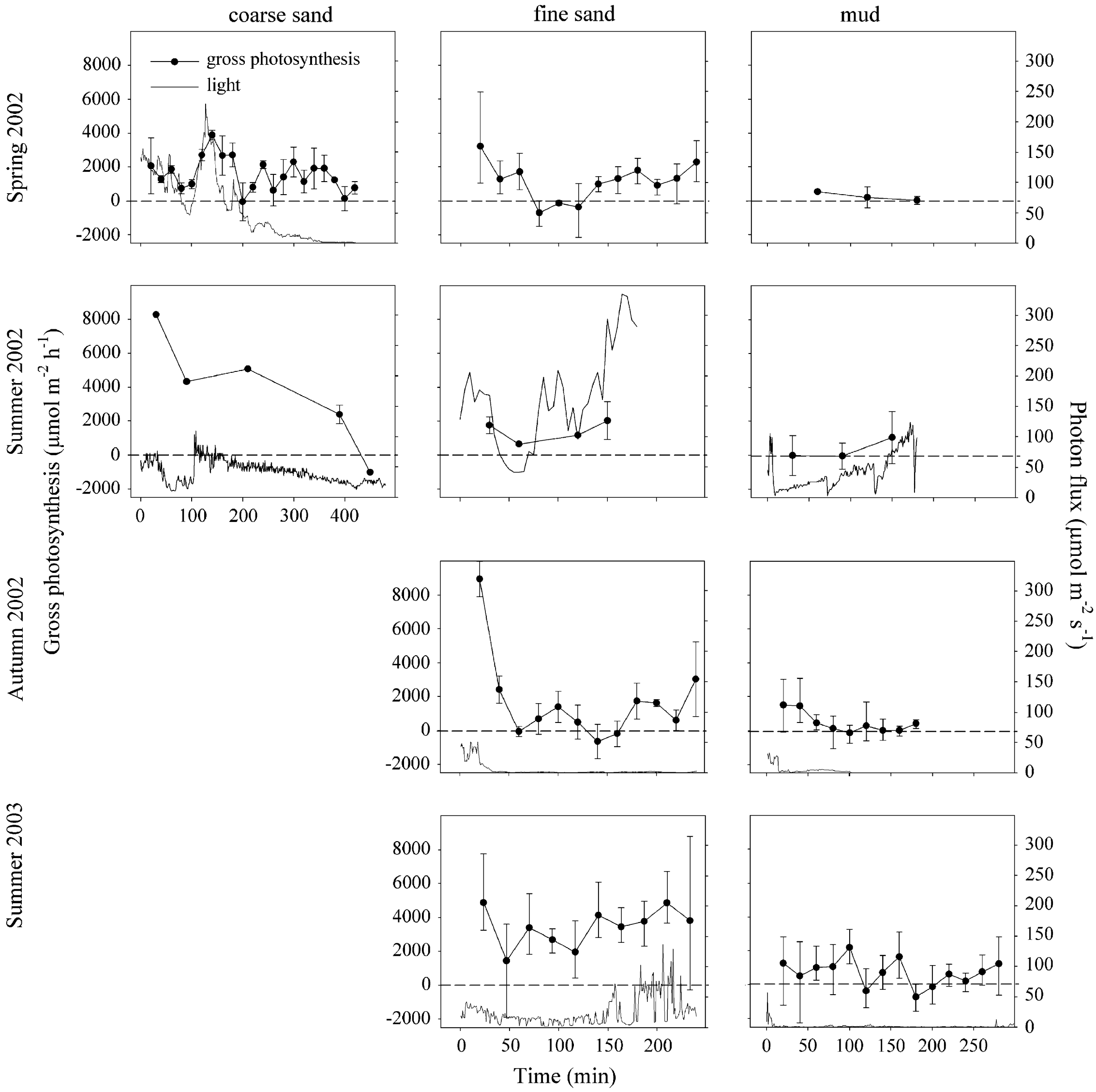

Fig. 5. Average gross photosynthesis (µmol m^{-2} h^{-1}) calculated from dark and light chamber incubations and in situ photon flux (µmol m^{-2} s^{-1}) at the three study sites. Error bars denote minimum and maximum estimates of gross photosynthesis. Dashed lines denote zero gross photosynthesis.

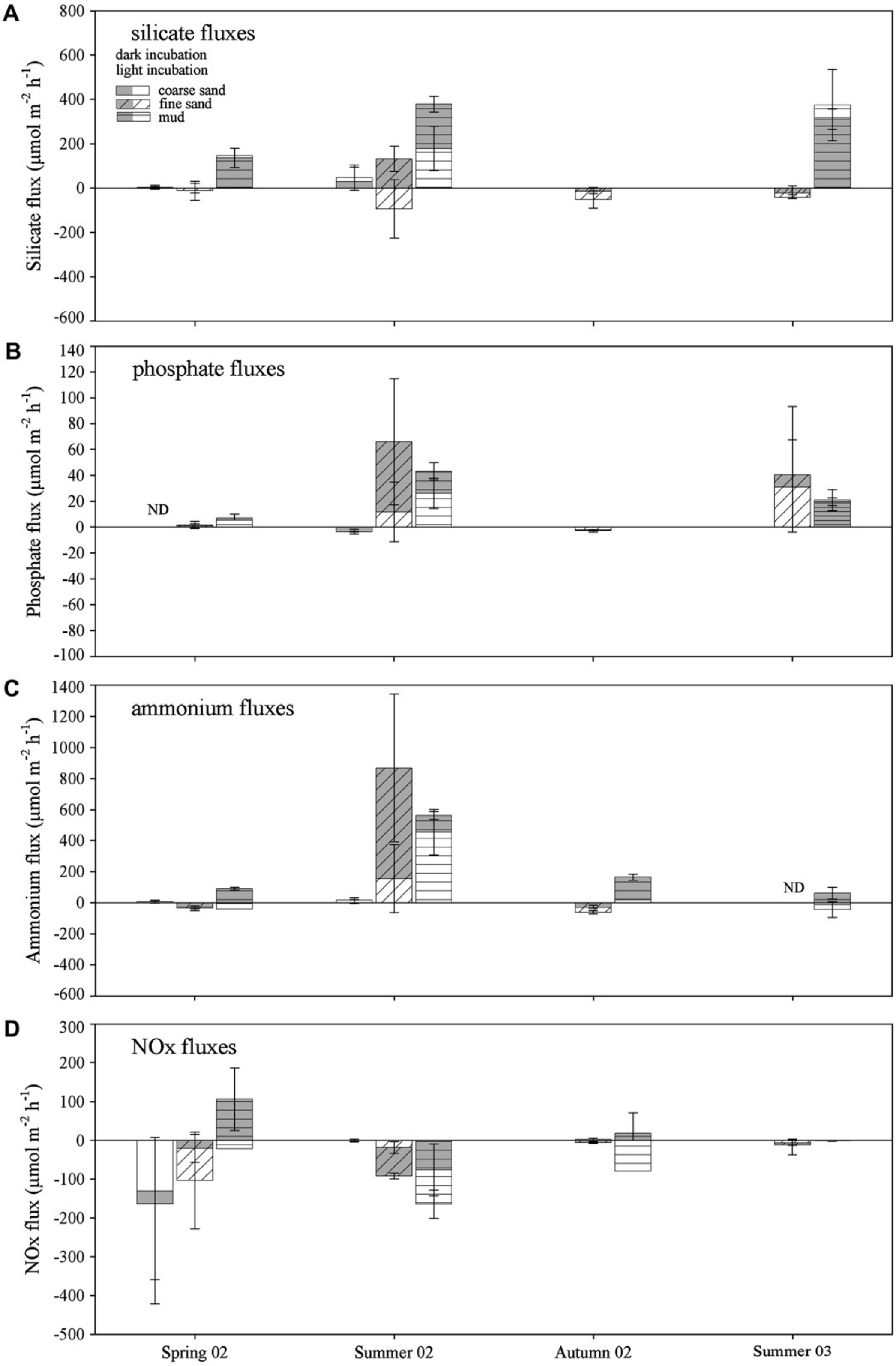

Fig. 6. Average benthic chamber fluxes of (A) silicate, (B) phosphate, (C) ammonium, (D) nitrate + nitrite (NO_x) at the three study sites with range as error bars. Negative and positive values denote influx and efflux via the sediment surface, respectively. ND denotes not detectable fluxes.

months at the two sandy sites (Fig. 6D). An efflux of NO_x was recorded in the dark incubations during Spring and Autumn at the mud site. There was no apparent causal connection between benthic photosynthesis and chamber NO_x fluxes (Fig. 6D). At the coarse sand site, very low nutrient fluxes resulted from the low organic content in this sediment (Table 2), and an effective nutrient cycling within the sediment by a very active microphytobenthic community, as reflected in the high

Table 4
Average nutrient concentrations (μmol L^{-1}) of the ambient seawater at the three study sites during the chamber incubations

Campaign	Coarse sand				Fine sand				Mud			
	Si	PO_4	NH_4	NO_x	Si	PO_4	NH_4	NO_x	Si	PO_4	NH_4	NO_x
Spring 2002	0.2	0.0	0.5	23.3	26.1	0.6	2.7	53.8	23.1	1.2	14.9	29.5
Summer 2002	2.5	0.4	2.7	0.8	8.5	0.6	5.9	2.6	15.1	1.5	10.6	2.6
Autumn 2002					8.2	1.1	5.9	1.9	31.5		7.0	3.7
Summer 2003					5.9	1.8	0.2	0.3	14.9	2.6	2.9	0.4

rates of gross photosynthesis at this site (Table 3). Relatively high release rates of phosphate and ammonium from the fine sand and mud during summer reflected higher mineralization and ensuing remobilization of bound phosphate due to a lowering of the oxygen penetration depths. The nutrient concentrations of the ambient seawater were generally highest at the mud site, intermediate at the fine sand and lowest at the coarse sand site (Table 4).

4. Discussion

Our study demonstrates that during inundation rates of benthic photosynthesis in sandy intertidal zones can be similar to those in mud flats, despite higher total chlorophyll content in the top cm of the mud sediment. Relatively high gross photosynthesis rates in the investigated tidal flats were associated with coarse grain size and high permeability of the sediment and resulted in a net-autotrophy for the two sandy study sites (Fig. 3). The mud site had lower photosynthesis rates and higher mineralization rates, which led to a net heterotrophy of the benthic community during inundation. The higher gross photosynthesis at the two sandy sites was surprising, as the total chlorophyll content of the top cm of the sediment was highest at the mud site. Thus, photosynthetic yield per unit chlorophyll was much higher in the sand than in the mud. Possible mechanisms causing the higher yield per chlorophyll in the sandy sediments that will be discussed here are (1) differences in metabolic state and life strategies of sand and mud microphytobenthos, (2) differences in light availability to the microphytobenthos, and (3) site specific nutrient limitation.

4.1. Metabolic state and sediment-dependent life strategies of the microphytobenthos

The higher gross photosynthesis at the sandy study sites may have been produced by a more active microphytobenthic community and different life strategies of the microphytobenthos in sands compared to muds. The measurement of phaeophytin content at the three study sites indicated an accumulation of chlorophyll degradation products in the muddy sediment, whereas no chlorophyll degradation products were measured in the top 3 cm of the sediment at the sandy sites. This is in agreement to other studies of intertidal flats (Cadee and Hegeman, 1977; Barranguet et al., 1997; Lucas and Holligan, 1999; Middelburg et al., 2000). Sandy sediments are sites of high organic matter turnover (Forster et al., 1996; Huettel and Rusch, 2000; D'Andrea et al., 2002) and algal cells can be rapidly degraded within these sediments (Ehrenhauss et al., 2004). Additionally, dead algal cells can be removed by advective flushing and resuspension of the permeable sand during inundation (de Jonge and van Beusekom, 1995; Lucas et al., 2000; Rusch et al., 2001). This is in contrast to fine grained sediments that accumulate organic matter (Table 2). This possibly involves settling of phytoplankton cells (Lucas and Holligan, 1999) that may not meet favourable conditions upon sedimentation on the mud flat and, hence, are less active.

More frequent resuspension and mixing in sandy sediment may also relocate the phototrophic community into deeper, dark layers, while cells from the aphotic sediment zone may end up in the photic surface layer. Relative constant chlorophyll concentrations (Fig. 3) indicate that this mixing affects the upper 3 to 6 cm of the sands and only the uppermost 1 to 2 cm in the mud (see also MacIntyre et al., 1996; Lucas and Holligan, 1999). Because many diatoms can survive over long time periods in the dark (Steele and Baird, 1968; French and Hargraves, 1980) and benefit from the higher nutrient concentrations at depth (Saburova and Polikarpov, 2003), frequent mixing of the sediment can keep a phototrophic community alive and active down to the mixing depth. The mixing may also reduce the potentially benthic-photosynthesis-diminishing effect of grazing (Hargrave, 1970; Connor et al., 1982), which is most intense at the sediment surface. In sands, the mixing of the sediment may quickly compensate for the grazing effect, while the recovery may take longer in muds, where phototrophs have to move or grow into the grazed surface areas.

Aside from the physical mixing, many benthic diatoms migrate vertically in synchrony with the solar and tidal cycle (Janssen et al., 1999; Mitbavkar and Anil, 2004). These diatoms move to the sediment surface during daylight exposure and descent during inundation to avoid resuspension (Round and Palmer, 1966; Paterson, 1989). Typically, a higher fraction of these mobile diatoms are associated with muddy sediment, while relatively immobile diatoms living firmly attached to the sediment grains are more common in sandy sediments (Barranguet et al., 1997). The migration of diatoms into deeper sediment layers during inundation may result in decreased photosynthesis in muddy sediment, which is characterized by strong light adsorption. In sandy sediments, the deeper light penetration and physical mixing of the microphytobenthos community during inundation can result in enhanced photosynthesis.

4.2. Light availability

The turbidity of the seawater increases from the relatively clear open North Sea towards the turbid near-shore areas (Postma, 1961). Light therefore limits primary production in the water column of the Wadden Sea (Colijn and Cadee, 2003) and likely also benthic primary production during inundation. Integral primary productivity of intact sediment has been previously shown to be saturated at a wide range of light intensities between 100 and 1260 μmol photons m^{-2} s^{-1} (MacIntyre et al., 1996 and references therein). Incident light intensities at the sea floor were generally below this level in our study, which caused a quick response of gross photosynthesis to incident light. Incident light intensities during inundation were generally lower at the mud site than at the fine sand site during all investigated study seasons (Fig. 5), which can partly explain the lower gross photosynthesis during inundation at the mud site as compared to the only 4 km distant fine sand site. The consequence of the more severe light limitation in the mud is a higher chlorophyll specific production at the sandy site during submersion.

In addition to differences in incident light, also the light distribution within the sediment varies between the mud site and the sands. Due to less adsorption in the sand, the benthic photic zone here was 2 to 3 times larger at same incident light intensities than in the mud (Fig. 2). The higher light absorption in the mud sediment cannot be explained by the higher total chlorophyll content, as chlorophyll was maximal 42 μg g^{-1} dry sediment in the mud. Note that the light availability in the mud is less than half of that in the sand, but that the chlorophyll content is doubled. Potentially, these effects cancel each other out with respect to total production, but again cause a higher chlorophyll specific production in the sand. The different optical properties of the sediments help explain why at the coarse sand site gross photosynthesis during inundation was 3 and 13 times higher during Summer 2002 than at the fine sand and mud site, respectively, despite relatively low incident light intensity at the sea floor (Fig. 5).

4.3. Potential nutrient limitation

Cook and Røy (2006) showed that advective flushing enhanced benthic primary production in a photosynthetically active permeable sand layer, because this flushing reduced CO_2 limitation of the microphytobenthos. Likewise, flushing may reduce limitation of nutrients due to high local photosynthetic rates. This effect may explain in situ observation of enhanced photosynthesis with increased sediment flushing (Wenzhöfer et al., in preparation). The flushing rates in our benthic chambers induced by the radial stirring (Huettel and Gust, 1992a,b; Janssen et al., 2005) reflected the different permeabilities of the three sediment types. The bromide tracer measurements documented the higher flushing rates in the coarse sand compared to the fine sand and mud sites. Enhanced transport of solutes with the advective pore water flows in the sands, thus, may have contributed to higher

Table 5
Comparison of annual rates of photosynthesis (g C m^{-2} a^{-1}) between sandy, mixed sand/mud and muddy sediments measured during inundation and exposure. Measurements in the laboratory study were conducted under conditions of light saturation, similar to the conditions during exposure

Study site	Sand	Sand/Mud	Mud	In situ/lab	Method	Authors
Exposure/laboratory						
Wadden Sea Ems Dollard estuary	99	108	314	In situ	Bell jars	van Es (1982)
Netarts Bay, Oregon, USA	129	153	72	In situ	Core incubation	Davis and McIntire (1983)
Bay of Fundy, Canada			20–84	In situ	^{14}C	Hargrave et al. (1983)
Wadden Sea Ems Dollard estuary	70–81	51–106	200–256	In situ	^{14}C	Colijn and de Jonge (1984)
Halifax Harbour, Nova Scotia, Canada	22			In situ	Core incubation	Grant (1986)
Savin Hill Cove, Boston, USA			250	In situ	^{14}C	Gould and Gallagher (1990)
Island of Fyn, Denmark	150–175			Laboratory	Core incubation	Kristensen (1993)
North Inlet Estuary, USA	93		191	Laboratory	Microsensors	Pinckney and Zingmark (1993)
Wadden Sea Westerschelde estuary			136	Laboratory	P/B estimate	de Jong and de Jonge (1995)
Wadden Sea Westerschelde estuary			2–28	Laboratory	Microsensors	Kromkamp et al. (1995)
Wadden Sea Sylt Königshafen	367	336	241	Laboratory	Core incubation	Kristensen et al. (1997)
Gironde Estuary, France			37–42	Laboratory	P/B estimate	Santos et al. (1997)
Wadden Sea Sylt Königshafen	329–362		355	Laboratory	Core incubation	Asmus et al. (1998)
Wadden Sea Westerschelde estuary	95[a]	111[a]		Laboratory	^{14}C	Barranguet et al. (1998)
Tagus Estuary, Portugal			156	Laboratory	Microsensors	Serodio and Catarino (2000)
Wadden Sea Büsum/Hedwigenkoog		42	35	Laboratory	Photosyn. light display	Wolfstein et al. (2000)
Douro River Estuary, Portugal	274–441		374	Laboratory	Core incubation	Magalhaes et al. (2002)
Colne Estuary, United Kingdom			53–191	Laboratory	Core incubation	Thornton et al. (2002)
Seto Inland Sea, Japan	434			Laboratory	Algae incubation	Montani et al. (2003)
Bay of Somme, France		110–147		In situ	Closed chamber CO_2 flux	Migne et al. (2004)
Inundation						
Wadden Sea Sylt Königshafen	68			In situ	Bell jars	Asmus (1982)
Wadden Sea Sylt Königshafen	39–67[a]			In situ	Bell jars	Asmus et al. (2000)
Ria Formosa, Portugal	64[a]		5	In situ	Bell jars	Asmus et al. (2000)
Sylt/Spiekeroog	24–65[a]	4[a]		In situ	Advection chambers	This study

[a] Calculated by multiplying the reported daily rates by 270 for temperate regions according to Cahoon (1999).

photosynthesis rates in these sands during inundation. Due to the relatively low stirring rates employed in our experiments, advective flushing and benthic photosynthesis may be even higher at in situ flow conditions than measured in the benthic chambers.

With the advection chambers we could measure only during inundation of the tidal flats and these measurements cannot be transferred to the exposure period. Table 5 compares potential annual productivity for different intertidal sediment types during inundation with rates during exposure or measured under saturating light conditions in the laboratory. Our calculated annual rates are in good range of values reported for the inundation period in other studies. Higher productivity in submerged intertidal sands than muds was also measured by (Asmus et al., 2000). During exposure and in laboratory studies, annual photosynthesis rates during exposure or measured in the laboratory generally exceed the rates during inundation as can be expected from the higher light availability during low tide. When comparing the different sediment types, some studies show muddy sediments to be more productive than sandy sediments during exposure. However, high photosynthesis in muddy sediments was in some studies associated with extraordinarily high nutrient concentrations produced e.g. by nearby wastewater outlets (van Es, 1982; Colijn and de Jonge, 1984; Thornton et al., 2002). Other studies reported little differences in productivity between sandy and muddy sediments or even higher productivity in sandy sediments during exposure (Table 5). Therefore, a budget over the entire tidal cycle is difficult to establish and subject to further studies.

5. Conclusions

For the period of inundation, our study demonstrated that benthic photosynthesis may be enhanced in intertidal sands compared to muds, mainly because of the higher availability of light and nutrients. Considering that sands can be equally productive as muds during the exposure period, sand flats thus can act as islands of net autotrophy in the heterogeneous Wadden Sea system that is generally considered net-heterotrophic (Gattuso et al., 1998; van Beusekom et al., 1999).

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