

Oxygen budgets in subtidal arctic (Kongsfjorden, Svalbard) and temperate (Helgoland, North Sea) microphytobenthic communities

D. S. Sevilgen^{1,2,4,*}, D. de Beer², A. Y. Al-Handal³, T. Brey¹, L. Polerecky^{2,5}

¹Alfred-Wegener-Institut, PO Box 120161, 27515 Bremerhaven, Germany

²Max Planck Institute for Marine Microbiology, Celsiusstraße 1, 28359 Bremen, Germany

³Marine Science Centre, Dept. of Marine Biology, University of Basra, Iraq

⁴Present address: Alfred-Wegener-Institut, Helmholtz Centre for Polar and Marine Research, Am Alten Hafen 26, 27568 Bremerhaven, Germany

⁵Present address: Faculty of Geosciences, Utrecht University, Budapestlaan 4, 3584 CD, Utrecht, The Netherlands

ABSTRACT: We compared primary production and respiration of temperate (Helgoland, North Sea) and subtidal Arctic (Kongsfjorden, Svalbard) microphytobenthic communities during summer. The diatom communities were generally characterized as cosmopolitan, displayed no site specificity, and had similar chl *a* and fucoxanthin concentrations. Their net and gross photosynthesis rates and light adaptation intensities, derived from laboratory microsensor measurements, were also similar, despite differences in water temperature. Daily oxygen fluxes across the sediment–water interface were estimated by combining laboratory microprofile and planar optode measurements with *in situ* data on oxygen penetration and light dynamics. During the study period, the Svalbard sediments were on average net heterotrophic, while the Helgoland sediments were net autotrophic (-22.4 vs. 9.2 mmol O₂ m⁻² d⁻¹). This was due to high infaunal abundance in the Svalbard sediments that caused high oxygen uptake rates in the sediments and consumption below the sediment euphotic zone. Additionally, bioirrigation of the sediment due to infaunal burrow ventilation was reduced by light; thus, the sedimentary oxygen inventory was reduced with increasing light. Conversely, light-enhanced the oxygen inventory in the Helgoland sediments. Oxygen dynamics in the Svalbard sediments were therefore dominated by bioirrigation, whereas in the Helgoland sediments they were dominated by photosynthetic oxygen production.

KEY WORDS: Benthic primary production · Sandy sediments · Microsensors · Planar optodes · Photosynthesis · Respiration · *P-I* curve · Bioirrigation

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The microphytobenthos (MPB) is comprised of communities of photosynthetic microorganisms (diatoms, dinoflagellates and cyanobacteria) that live in the uppermost surface layers of the seafloor (MacIntyre et al. 1996). It constitutes a food source for heterotrophic organisms and can significantly affect solute exchange across the sediment–water interface. The MPB in sandy and muddy habitats is dominated mostly by diatoms (Sundbäck et al.

1991, MacIntyre et al. 1996). In coastal areas, MPB production can be similar to or exceed phytoplankton production, and thus the MPB contributes significantly to ecosystem primary production (MacIntyre et al. 1996, Cahoon 1999, 2006, Underwood & Kromkamp 1999, Glud et al. 2002). On average, benthic microalgae productivity in shallow waters (<30 m) in the Arctic exceeds pelagic productivity (by ~50%; Glud et al. 2009).

Studies on MPB communities range from temperate to tropical regions, and across various habitats,

such as brackish lagoons, salt marshes, intertidal flats and subtidal sediments (MacIntyre et al. 1996, Cahoon 1999, 2006, Underwood & Kromkamp 1999, Glud et al. 2009). MPB organisms are the major primary producers in intertidal flats (Scholz & Liebezeit 2012) and are accordingly well-studied for that habitat (e.g. MacIntyre et al. 1996, Denis et al. 2012, Scholz & Liebezeit 2012). However, studies on subtidal MPB communities are lacking, notably from the German North Sea area, although a few studies have examined MPB and benthic food webs in other parts of the North Sea (Riaux-Gobin et al. 1987, Reiss et al. 2007, Evrard et al. 2010).

Glud et al. (2009) noted that the subtidal MPB, particularly in colder waters and high latitudinal regions like the Arctic, is grossly under-sampled. This is a significant knowledge gap, given that the Arctic continental shelf area accounts for ~1/4 of the global shelf area (areas with less than 200 m water depth; Menard & Smith 1966, Jakobsson 2002), of which ~1/5 receives enough light to support MPB organisms (Gattuso et al. 2006). It is likely that these systems are sensitive and will respond rapidly to global change effects such as ocean warming. The drastic decline of sea ice cover in the Arctic (Serreze et al. 2007, Zhang et al. 2012, Laxon et al. 2013) will change underwater light regimes, with more light becoming available earlier in the year and for longer time periods. As the MPB can quickly adapt to ambient light conditions (Kühl et al. 2001, Glud et al. 2002), these changes could stimulate pelagic and benthic primary production. Increasing temperature will additionally stimulate benthic productivity and remineralization. For example, Hancke & Glud (2004) examined the response of photosynthesis and respiration in benthic communities to short-term elevated temperature in 1 high Arctic and 2 temperate MPB communities. Their results showed that both processes were stimulated, respiration more so than photosynthesis. The response of the MPB was similar at all sites, indicating no latitudinally related temperature adaptation. Similarly, Wieland & Kühl (2000) examined oxygen and sulfide cycling in hypersaline microbial mats from Solar Lake, Egypt, and found that a short-term temperature increase stimulated respiration more than photosynthesis. Thus, it appears that at elevated temperatures benthic systems will gradually become more heterotrophic, and that this trend will hold across large geographical distances.

In this study, we aimed to contribute to the body of available literature that compares the activity of MPB communities from geographical regions characterized by largely different prevailing temperatures. Of

particular interest were subtidal communities, to redress the under-sampling referred to above. As study sites, we chose subtidal sediments from the Arctic (Kongsfjorden, Svalbard) and from a temperate site in the North Sea (Helgoland). Despite the north–south distance of about 2800 km (25° latitude) between the 2 sites, they are oceanographically closely connected by the same North Atlantic water masses. The West Spitsbergen Current transports warm waters of the North Atlantic Current along the western coast of Svalbard, influencing the fjord systems along the coastline (Svendsen et al. 2002, Hop et al. 2012).

Specifically, our aim was to describe and compare habitat characteristics, MPB communities, primary production and oxygen dynamics at the 2 sites. We hypothesized that (1) oxygen dynamics in the sediments are controlled by MPB activity, and that (2) the 2 sites show differences in temperature, light and MPB community composition, but that the photosynthetic performance of the MPB communities is similar as a result of optimal adaptation to local conditions. We conducted laboratory experiments using oxygen microsensors to determine net photosynthesis and respiration rates as a function of light, and planar optodes to measure deeper sediment respiration. Additionally, we monitored *in situ* oxygen distributions in the sediments and incident light intensities over a period of at least 24 h and combined these data with the laboratory results to estimate daily oxygen budgets.

MATERIALS AND METHODS

Study areas and sampling

This study was carried out in shallow subtidal sediments from Svalbard (Arctic, Norway, 78°56' N 11°51' E) and Helgoland (North Sea, Germany, 54°10' N 7°54' E). The Svalbard site, called Brandal, is located in the glacial fjord Kongsfjorden (Fig. 1A). The fjord, located at the western coast of Svalbard, is influenced by water masses of the West Spitsbergen Current, coastal arctic water and, in the inner part, by 4 large tidal glaciers terminating at the east and north sides of the fjord (Svendsen et al. 2002). The estimated annual average water temperature is slightly above 0°C, and the diurnal tidal range is approximately 2 m (Ito & Kudoh 1997, Hop et al. 2002, Svendsen et al. 2002). The Helgoland site, Düne Süd, is located about 100 m south-west from the Helgoländer Düne, which is an island located in the south-

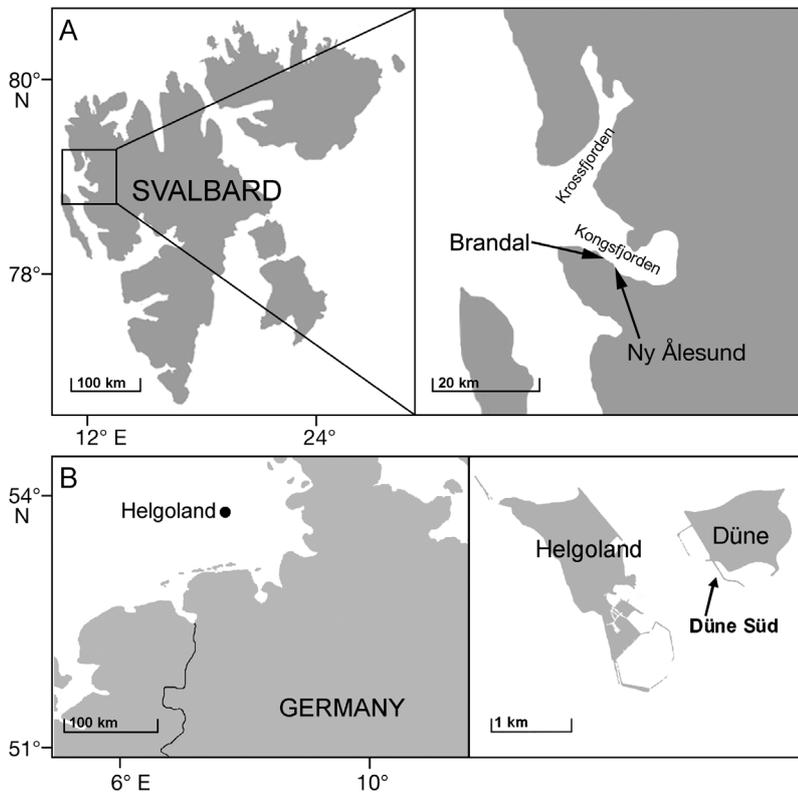


Fig. 1. Locations of the 2 study sites (A) Brandal (Svalbard, Arctic, Norway) and (B) Düne Süd (Helgoland, North Sea, Germany). Modified from <https://maps.google.com>

eastern part of the North Sea (Fig. 1B). Average annual water temperature is around 10°C, and the tidal range is about 2 m (Wiltshire et al. 2008).

Sampling and measurements were carried out at water depths of about 5 m through the summer months of 2009–2012. They included sediment characterization, *in situ* measurements of oxygen and light, sampling for porewater nutrients and MPB biomass, and laboratory measurements of photosynthesis and respiration in freshly collected sediment samples (Table 1).

Sediment characterization

Sediments were collected by scuba divers using cylindrical acrylic cores (inner diameter: 50 mm, length: 200 mm). The cores were sliced into 2 cm sections and each section was desalinated and dried at 80°C until constant weight. The grain size distribution, sorting and skewness were determined as described in Wentworth (1922) and Friedman & Sanders (1978), using a sieve-column with mesh sizes of 63, 125, 250, 500, 1000 and 2000 µm. Porosity was

determined from weight loss on drying. Sediment permeability was measured in 2 cores per site with a constant head permeameter (Klute & Dirksen 1986).

Biogeochemical characterization of sediments and porewaters

Total carbon (TC), nitrogen and sulfur contents in freeze-dried and ground samples of the sediment (depth intervals 0–1, 1–2, 2–4, 4–6, 6–8, 8–10 cm) were determined by high temperature combustion (Carlo Erba NA-1500 CNS analyzer). Total inorganic carbon (TIC) was measured in a CO₂ Coulometer (CM 5012, UIC) after acidification with 20% (w/v) phosphoric acid (CM 5130 Acidification module UIC). Total organic carbon was calculated as TOC = TC – TIC.

Porewater for the analysis of nutrients (NO₂⁻, NO₃²⁻, NH₄⁺, PO₄²⁻, Si²⁺) was sampled *in situ* by scuba divers using soil moisture samplers (10 cm Rhizon samplers, pore size 0.1 µm). For vertical profiles, a bottomless plastic

bucket (30 cm diameter) was pushed 20 to 25 cm into the sediment, emptied and left to rest for between 24 and 72 h. Subsequently, rhizons were inserted horizontally from the inside of the bucket outwards into the sediment through holes made at 2 cm vertical intervals down to a maximum depth of 12 cm. Porewater was extracted either with a syringe or into vacuum vials. Samples were immediately transported to the laboratory and analyzed for nutrients using a 5 channel QuAAtro nutrient analyzer (Seal) equipped

Table 1. Overview of the measurement and sampling activities conducted at the Arctic ('Brandal', Kongsfjorden, Svalbard, Norway) and temperate ('Düne Süd', Helgoland, North Sea) study sites. nd: not determined

Activity	Svalbard	Helgoland
Oxygen profiles/ incident light (<i>in situ</i>)	Jun 2010	Aug 2009
Sediment	Jun 2010	Aug 2009
Porewater nutrients	Jun 2010	nd
Photosynthesis and respi- ration rates (laboratory)	Jun–Jul 2011	Jun–Aug 2009
MPB pigments	Jun 2012	May 2012

with a Jasco fluorometer for NH_4^+ analyses. NH_4^+ was analyzed as described in Kerouel & Aminot (1997), and specific analytical protocols for the remaining nutrients were applied (Seal Analytical).

Photopigment analyses

Concentrations of chl *a* and fucoxanthin were used as a measure of MPB biomass. The upper 3 mm of the sediment in the sampled sediment cores (area 19.6 cm²) were freeze-dried and weighed. To extract the pigments, 1.5 ml 99.8% acetone was added, the samples were vortexed for 5 s, left in an ultrasound bath with iced water for 3 min, and then stored at -28°C for 24 h in the dark. The extracts were filtered (Acro disc CR 4 mm syringe filters with a 0.45 µm PTFE membrane) and analyzed by high performance liquid chromatography (HPLC) as described in Wright et al. (1991). The HPLC system consisted of a Waters 2695 separation module and a Waters 996 photodiode array detector (Waters, MA). Pigment standards supplied by DHI, Denmark, were used for calibration. The MPB samples were originally taken from the same cores where photosynthesis and respiration rates were measured by microsensors (see 'Materials and methods: *Ex situ* oxygen microprofile measurements' below). However, because these samples were lost, pigments were analyzed from a later measurement campaign (Table 1).

Diatom identification

Sub-samples of the upper 5 mm of sediment cores (2 per site) were taken and fixed in Lugol's solution for the identification and quantification of diatoms. Diatom samples were first washed with deionized water to remove salts, and then cleaned by boiling in 30% hydrogen peroxide. A few drops of 50% hydrochloric acid were added to the diatom suspension to ensure the removal of the hydrogen peroxide, which was followed by several rinses with distilled water. Cleaned diatoms were allowed to settle on cover slips, which were placed on a metal tray that was kept stable, protected from any disturbance. After air-drying at room temperature, permanent diatom slides were made using Naphrax diatom mountant medium. Diatoms were identified and photographed using a Zeiss Axioplan 2 light microscope (Carl Zeiss AB) with differential interference contrast. Relative occurrence of species was estimated on 3 levels: (1) very rare (observed only once per slide), (2) rare (a

few specimens per slide) and (3) frequent (at least 1 value in each microscope field and up to 10% of all values in a slide). Diatom taxonomic identification was mainly based on Hustedt (1958, 1961–1966), Hendey (1964), Germain (1981), Krammer & Lange-Bertalot (1986, 1988, 2000), Witkowski et al. (2000) and Scott & Thomas (2005).

In situ light and temperature measurements

In situ intensities of downwelling photosynthetically active radiation (PAR) were measured in 30 or 60 s intervals using submersible light-loggers (Odyssey Dataflow Systems) positioned at the sediment surface close to the points where the microsensor measurements were done. *In situ* temperature at the Svalbard site was measured at 5 m depth in 20 min intervals over 1 year (June 2011–June 2012) using HOBO Pendant and TidbiT loggers (ONSET). Because similar measurements could not be done at Helgoland, temperature data for this site were taken from the Helgoland Roads data series (Wiltshire et al. 2008).

In situ oxygen microprofile measurements

Vertical oxygen microprofiles in the sediment were measured *in situ* with amperometric Clark-type oxygen microelectrodes (Revsbech 1989) connected to a diver-operated microsensor profiler (Weber et al. 2007). Sensors had a tip diameter of 10 to 50 µm and a stirring sensitivity of <1.5%. Linear calibration of the sensors was derived from *in situ* measurements in the anoxic parts of the sediment and from laboratory measurements in air-bubbled seawater at *in situ* temperature. Subsequently, *in situ* O₂ concentrations were calculated based on the measured salinity and temperature (Li & Gregory 1974, Garcia & Gordon 1992). Profiles were continuously measured during at least 24 h, with 2 replicate time-series in Svalbard and one in Helgoland. Measurements were done on sand plains with a visible cover of diatoms, as identified by the light red-brown color of the sediment surface. A semi-circular steel grid (10 cm height) was set up ~15 cm in front of the sensor to prevent possible entanglement with floating macroalgae.

Ex situ oxygen microprofile measurements

Laboratory microsensor measurements were carried out in the Marine Laboratory at Ny Ålesund,

Svalbard, and at the Biologische Anstalt Helgoland. Sediment samples were randomly collected in close vicinity to the *in situ* microsensor measurements and transported to a climate room, where they were stored for a maximum of 48 h in a flow-through system with natural seawater. During storage, temperature and light conditions mimicked those determined *in situ*, the latter achieved by a programmable illumination system (GHL Profilux PLUS II). The Helgoland samples were illuminated with a stepless light:dark cycle of 15:9 h with a maximum light intensity of 100 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (higher maximum light intensities could not be reached due to set-up limitations). In contrast, continuous illumination was applied to the Svalbard samples, with intensities varying between 30 and 130 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ over a 24 h period.

Vertical profiles of oxygen were measured in 3 replicate sediment cores for each site. During the measurements, the samples were kept at *in situ* temperature using a thermostat (Julabo F32) or by using water that was continuously pumped from a water tank in the climate room. Illumination was provided by a halogen lamp (Schott KL 1500), and the measurements were made at downwelling light intensities increasing from 0 to 600 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$. At each intensity level, oxygen profiles were measured at 3 to 5 randomly selected positions in the core after a delay of 30 to 60 min to ensure steady state. The Svalbard sediments contained large numbers of bio-irrigating infauna, which disturbed the microsensor measurements. To minimize this disturbance, the overlying water was made anoxic (by purging with N_2) before the measurement, which temporarily stopped bioirrigating activity. Alternatively, the upper 5 mm of the sediment were removed, and the rest of the sediment was sieved to remove the larger animals. After reestablishing the sediment layers, the core was let to rest for 12 h in the climate room at *in situ* light and temperature conditions before the measurement. This treatment was not required for the Helgoland samples.

Photosynthesis and respiration rate calculations

Areal rates of net photosynthesis, P_{net} , and respiration, R_{phot} , in the euphotic layer of the sediment were calculated from the measured oxygen gradients as described in Kühl et al. (1996). The molecular diffusion coefficient of oxygen, D_0 , corrected for temperature and salinity in accordance with the Unisense gas tables (Li & Gregory 1974, Garcia & Gordon 1992),

was used to calculate the O_2 fluxes in the diffusive boundary layer, whereas the effective diffusion coefficient, D_e , calculated as $D_e = D_0\Phi$, where Φ is sediment porosity (Kühl et al. 1996), was used for flux calculations in the sediment. The measured rates of P_{net} were plotted against the incident light intensities, I , and fitted with the function $P_{\text{net}} = P_{\text{gross, sat}} \{1 - \exp[-\ln(2) \times I / I_{1/2}]\} + R_{\text{phot}}$ (Webb et al. 1974) where R_{phot} was the rate derived from microsensor measurements. During the fit, the value of the parameter R_{phot} was forced to equal the measured rate R_{phot} . Assuming that the rates of respiration in the dark and in the light were equal, the parameters $P_{\text{gross, sat}}$ and $I_{1/2}$ obtained from the fit represent the areal rate of gross photosynthesis at light saturation and the half-saturation light intensity, respectively. This fitting was done separately for P - I curves measured in each core, and the fitted values were averaged.

Sedimentary oxygen consumption rates

Potential sedimentary oxygen consumption rates (OCR) were measured as described in Polerecky et al. (2005) and Volkenborn et al. (2010). Freshly collected square sediment cores (width and breadth 70 mm, length 200 mm) equipped with a planar optode (Precht et al. 2004) were set up in a climate room, and the measurements were carried out at *in situ* temperature and in the dark. Oxygenated water was carefully injected next to the optode into the anoxic sediment regions at depths from 3.0 to 8.5 cm below sediment surface, and depletion in porewater O_2 concentration was monitored at 30 s intervals. This was done simultaneously in 2 to 3 spots in each core. In 3 of the 4 cores measured, this was repeated twice, resulting overall in 3 to 6 measurements per core. The average size of the measured spots (as seen by the optode) was $0.33 \pm 0.14 \text{ cm}^2$, with one area exceptionally large (0.68 cm^2) and one exceptionally small (0.07 cm^2). The values of OCR, expressed per volume of sediment, were calculated as rates of the porewater O_2 depletion multiplied by sediment porosity (Polerecky et al. 2005). These measurements were made only for Svalbard sediments because of the evidence of deeper subsurface sediment oxygenation (see 'Results'), and not for the Helgoland sediments.

Statistical analyses

Statistical analyses in this study were performed using JMP 9.0 (SAS Institute, USA) with the signifi-

cance level α set to 0.05. Analysis of variance (1-way ANOVA) was performed to test whether the 2 study sites differed significantly with respect to sediment characteristics, pigment biomass, measured and calculated photosynthesis and respiration rates. Furthermore, we tested if volumetric oxygen consumption rates in the sub-surface sediments of the Svalbard site were significantly correlated with depth and if there were significant correlations between the *in situ* oxygen inventories (in and below the euphotic sediment zone) and the respective *in situ* light intensities in the sediments of both study sites.

RESULTS

General settings

The Svalbard and Helgoland sites are generally characterized as cold and temperate, with annual

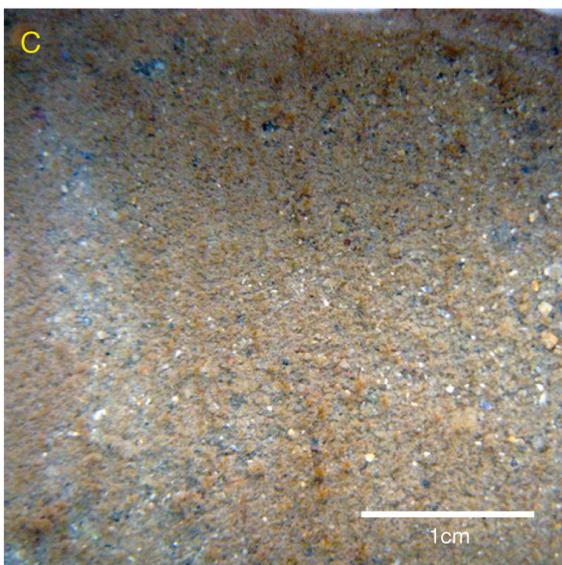
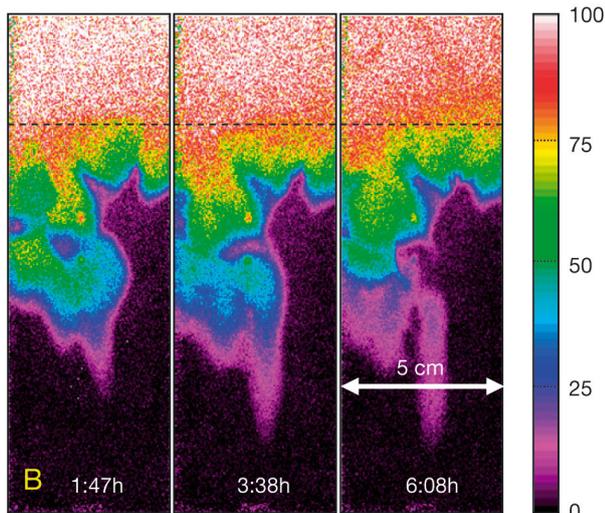
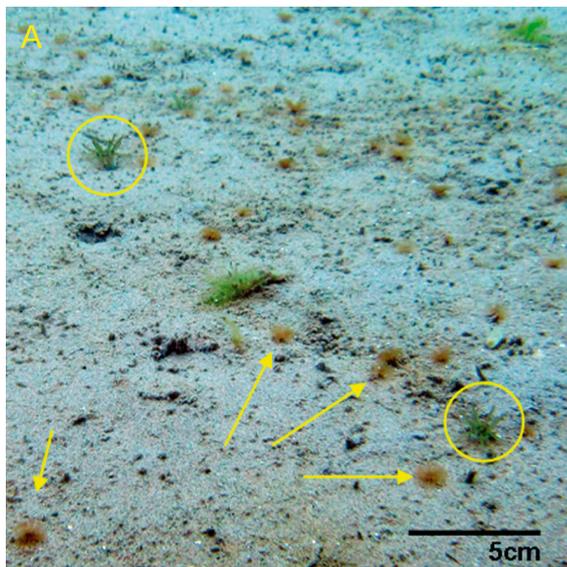
average water temperatures during the studied years of 2.4°C and 10.1°C, respectively. During the *in situ* study period (June 2010 for Svalbard and August 2009 for Helgoland), average water temperatures in Svalbard and Helgoland were 4.8°C and 18.3°C, respectively. Over a 24 h day period, light was present continuously in Svalbard, whereas there were 9 h of darkness in Helgoland (Table 2).

Sediment characteristics

Sediments at the sites were similar and generally characterized as well sorted, fine, porous, permeable sands (Table 2). Permeability did not significantly differ with depth down to 10 cm between the 2 sites (Table S1 in the Supplement at www.int-res.com/articles/suppl/m504p027_supp.pdf). Porosity decreased with depth in Svalbard and was significantly higher than in the Helgoland sediment (Table S1).

Table 2. Characteristics of the sites in Svalbard and Helgoland. Shown are mean \pm SD values for N replicate measurements. TC: total carbon, TN: total nitrogen, TS: total sulfur, TIC: total inorganic carbon, TOC: total organic carbon, LOD: limit of detection, wt: weight, dw: dry weight. The carbon, nitrogen, sulfur and pigment data are normalized to sediment dry weight. Unless otherwise stated, all data were collected during the study periods 22 Jun–12 Jul 2010 for Svalbard and Aug 2009 for Helgoland

Characteristic	Svalbard	Helgoland	N
Environment			
Sampling depth (m)	5 \pm 0.2	4.5 \pm 0.2	
Water temperature (°C)			
Annual	2.4 \pm 2.1 [Jun 2011–Jun 2012]	10.1 \pm 5.7 [Jun 2009–Jun 2010] ^a	26 375, 242
During study period	4.8 \pm 1.6	18.3 \pm 0.3 ^a	28 080, 20
Salinity	31 \pm 2	34	
Light:dark duration (h)	24:0	15:9	
<i>In situ</i> PAR ($\mu\text{mol photons m}^{-2} \text{s}^{-1}$)	[22–23 (23–24) Jun 2010]	[11–12 Aug 2009]	
Min	4 (12)	0	2, 2
Max	230 (73)	339	2, 2
Average \pm SD ^b	49 \pm 46 (33 \pm 21)	62 \pm 78	2, 2
Sediment			
Median grain size (μm)	147 \pm 3	224 \pm 12	6, 3
Sorting	0.50 \pm 0.01	0.49 \pm 0.06	6, 3
Skewness	0.061 \pm 0.004	-0.09 \pm 0.02	6, 3
Porosity (vol%), 0–10 cm	0.44 \pm 0.02	0.41 \pm 0.02	5, 2
Permeability k [10^{-11}m^{-2}]	0.95 \pm 0.17	1.37 \pm 0.06	2, 2
TC (%wt)	2.56 \pm 0.18	1.12 \pm 0.30	6, 5
TN (%wt)	0.019 \pm 0.005	0.012 \pm 0.003	6, 5
TS (%wt)	0.033 \pm 0.008	< LOD (0.001)	6, 5
TIC (%wt)	0.10 \pm 0.02	0.06 \pm 0.02	6, 5
TOC [= TC–TIC], (%wt)	2.46 \pm 0.20	1.06 \pm 0.32	6, 5
C:N	137 \pm 50	95 \pm 31	6, 5
MPB biomass			
Chl <i>a</i> ($\mu\text{g g}^{-1} \text{dw}$)	13.9 \pm 5.6	12.9 \pm 6.0	5, 6
Fucoxanthin ($\mu\text{g g}^{-1} \text{dw}$)	7.6 \pm 2.2	8.7 \pm 3.5	5, 6
^a Data taken from the Helgoland Roads Series (Wiltshire et al. 2008).			
^b Downwelling PAR intensities are calculated for the 24 h time frame starting at 14:00 h local time. Values after ‘ \pm ’ represent measurement uncertainty related to the vertical non-alignment of the 2 light loggers used			



The most striking difference was a large abundance of macrofauna in the Svalbard sediments (mainly visible as polychaetes, crustaceans and sedimentary anemones), which were largely absent in Helgoland sediments (Fig. 2).

Total carbon and nitrogen contents were about 2-fold higher in Svalbard than in Helgoland. Nitrogen contents were very low. Total organic carbon content was high at both sites, representing about 95 % of the total carbon (Table 2). Bulk sediment C:N ratios ranged from 76 to 198 in Svalbard and from 63 to 145 in Helgoland, and were not significantly different between the sites (Table S1).

Porewater nutrient concentrations in the upper 12 cm in Svalbard sediments were generally low (see Fig. S1 in the Supplement). Silicate and nitrate concentrations were mostly $\leq 10 \mu\text{M}$, whereas ammonium and phosphate usually ranged between 1 and 5 μM . Nitrite concentrations were low, varying between 0.1 and 0.2 μM . Especially in the upper 5 to 6 cm of the sediment, nitrogen compounds displayed notably low concentrations. Below these depths, only a single profile showed an increase, and overall no general trends with depth were detected. With the exception of silicate, nutrient concentrations in the overlying water were ~ 10 -fold lower than in the top centimeter of the sediment. For silicate the difference was ~ 4 -fold. Thus, porewater nutrients could not be considered as limiting for microphytobenthos. Due to sample loss during transport, porewater nutrient profiles are not available for the Helgoland site.

MPB community

MPB biomass was highly variable within both sites, and there was no significant difference between the Svalbard and Helgoland site with respect to chl *a* and

Fig. 2. (A) Photo of the sublittoral Arctic sediment from Brandal (Svalbard, 5 m depth, June 2010), showing the dense infaunal population. Arrows indicate the visible, extended, feather-like tentacle crowns of sedimentary polychaetes; circles highlight tentacles of sedimentary anemones. (B) Examples of oxygen distributions in the highly bioirrigated Svalbard sediment at specific times during a 24 h measurement. Dashed lines indicate the approximate location of the sediment surface; the color bar gives oxygen concentrations in percentage of air saturation. (C) Close-up photo of the sediment surface in a sediment core from Düne Süd (Helgoland, 4.5 m depth, August 2009) showing the relative lack of infaunal organisms compared to Svalbard. Photographs by D. S. Sevilgen

fucoxanthin concentrations in the top 3 mm of the sediment (Table S1 in the Supplement). With respect to the MPB community composition, both sites were dominated by diatoms. Overall, 40 diatom species were identified, of which 18 were exclusively found in Svalbard, 11 exclusively in Helgoland, and 11 at both sites (see Table S2 & Fig. S2 in the Supplement). All species belonged to the classes Bacillariophyceae (39 species) and Coscinodiscophyceae (1 species). They were distributed amongst 19 genera, of which 11 are known to have species commonly found in polar regions. Three of these 11 genera were *Amphora*, *Diploneis* and *Navicula*, which cover 50% of all identified species in the studied sediments. Frequently found species exclusive to the Svalbard sediments were *Plagiotropos lepidoptera*, *Donkina carinata*, *Planothidium delicatulum*, *Amphora sulcata*, *Pleurosigma normanii* and *Navicula directa*. These species have been reported from polar regions previously but are also common in marine and brackish waters of the North Sea, the western Baltic and the NW Atlantic. Frequently observed species exclusive to the Helgoland sediments included *Navicula cancellata* and *Petroneis humerosa*, which are widespread in temperate marine and brackish waters, in coastal areas and on sandy shores but also in polar regions. Likewise, the species frequently found at both sites, *Diploneis smithii*, *Petroneis marina* and *Amphora marina*, are described as ubiquitous and have also been previously identified in polar habitats.

***In situ* light and oxygen measurements**

In Svalbard, ambient light was present 24 h per day (June 2010). Light intensities generally followed a day:night cycle, with higher intensities during the day hours and lower intensities during the night, but sometimes weather conditions (cloud cover) caused intensities during the day to be lower than during the night (Fig. 3C). *In situ* oxygen microprofiles showed a small but detectable peak close to the sediment surface (Fig. 3A), indicative of photosynthetic activity by MPB organisms in the euphotic zone of the sediment. However, the most striking features of the profiles were elevated oxygen concentrations several centimeters below the sediment surface (Fig. 3A), demonstrating intensive bioirrigation of the sediment due to the ventilation activity of the infauna present. The average thickness of the oxygenated sediment layer was 2.25 cm over 24 h. However, the complete set of measured profiles

(data not shown) suggested that the bioventilation-induced oxygen penetration likely reached down to 6 cm. O₂ inventory in the euphotic zone of the sediment, obtained by depth-integration of the *in situ* O₂ profiles over the top 2.5 mm, varied from 0.1 to 0.3 mmol O₂ m⁻², whereas the O₂ inventory below the euphotic zone was larger, by up to 10-fold (Fig. 3C). The latter inventory values were likely underestimated, since the O₂ concentrations were measured away from infaunal burrows (i.e. where they are known to be lower) and they often did not reach zero at the deepest points of the profiles. Unexpectedly, the O₂ inventories in the sediment euphotic zone were significantly negatively correlated with light ($R = -0.43$, $p < 0.001$; Fig. 3E). When integrated over a 24 h period, the O₂ inventories below the euphotic zone constituted between 77% (first measuring day) and 92% (second measuring day) of the total sedimentary O₂ inventory, indicating a highly significant impact of the infauna on the sediment biogeochemistry at this site.

In Helgoland, *in situ* light intensities followed a 15:9 h day:night cycle (Fig. 3D). In the light, oxygen showed a clear peak slightly below the sediment surface and penetrated down to 5 mm (Fig. 3B), indicative of photosynthetic activity by MPB organisms in the sediment euphotic zone and respiration below. In contrast, oxygen concentrations in the dark steeply declined with depth due to respiration, penetrating at most 2 mm. During the day, the O₂ inventory in the euphotic zone of the sediment were between 0.2 and 0.6 mmol O₂ m⁻² and about 2- to 10-fold higher than during the night. As expected, the O₂ inventory in and below the sediment euphotic zone were significantly positively correlated with ambient light ($p < 0.0001$; Fig. 3F). When integrated over a 24 h period, the O₂ inventory in the euphotic zone constituted about 92% of the total sedimentary O₂ levels, suggesting the dominant role of light in the sedimentary O₂ dynamics at this site.

Laboratory rate measurements of photosynthesis and respiration

Because the oxygen profiles measured *in situ* were not in steady state and (due to the highly significant animal activity in Svalbard) not diffusive, the rates of photosynthesis and respiration in the sediments were determined by laboratory micro-sensor measurements in treated cores. The net photosynthesis rates increased in relation with incident intensity of PAR and reached saturation at high

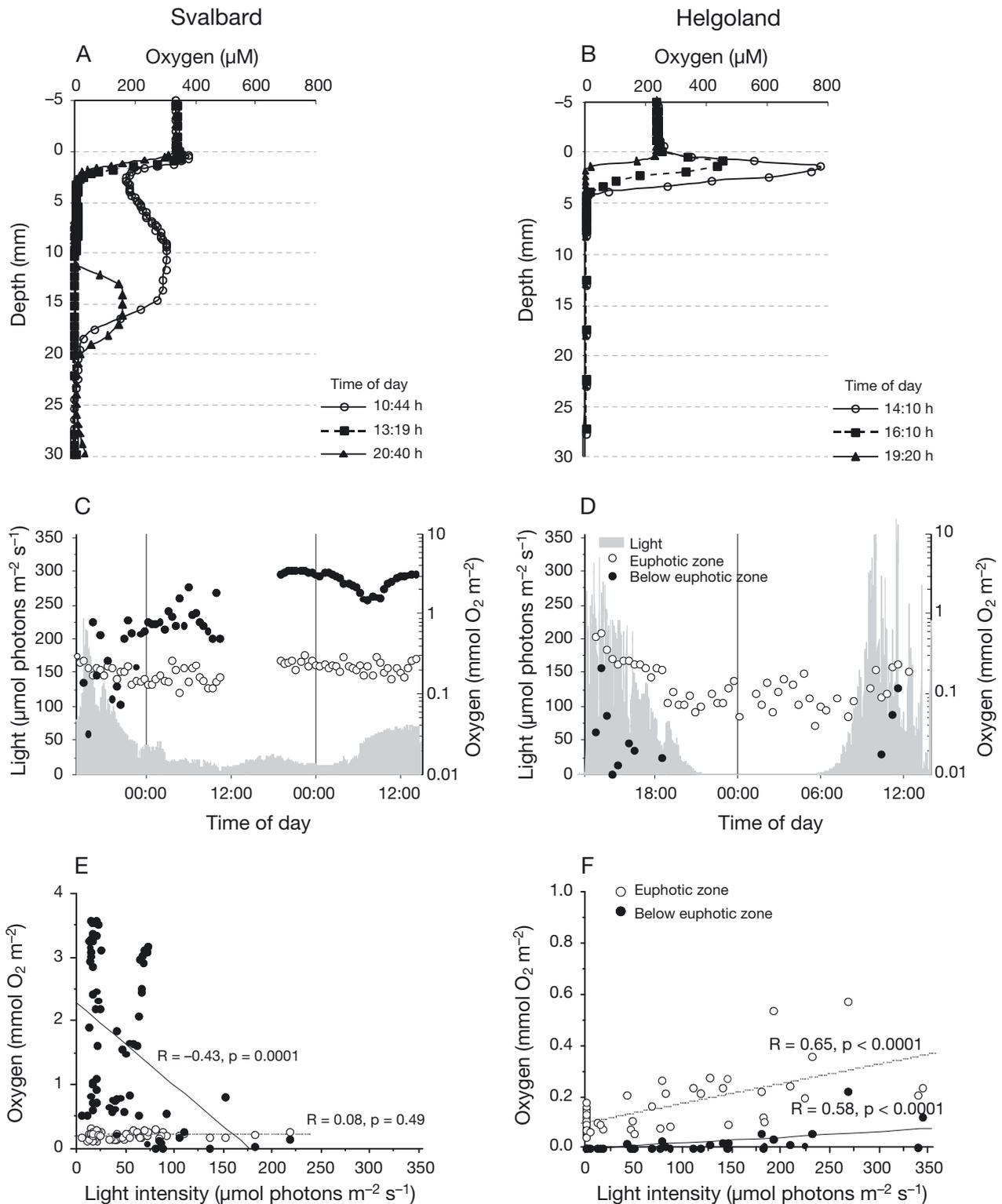


Fig. 3. (A,B) Selected *in situ* oxygen profiles in the Svalbard and Helgoland sediments, measured at the time of day (Svalbard: 23 Jun 2010, Helgoland: 11 Aug 2009) indicated in the key. Zero depth corresponds to the sediment–water interface. (C,D) *In situ* downwelling PAR intensity, overlaid with the oxygen concentrations in and below the euphotic zone, as a function of time of day (Svalbard: 22–24 Jun 2010, Helgoland: 11–12 Aug 2009). Vertical solid lines indicate midnight. (E,F) Correlations between the oxygen concentrations and downwelling PAR intensities, derived from the time-series measurements shown in (C,D)

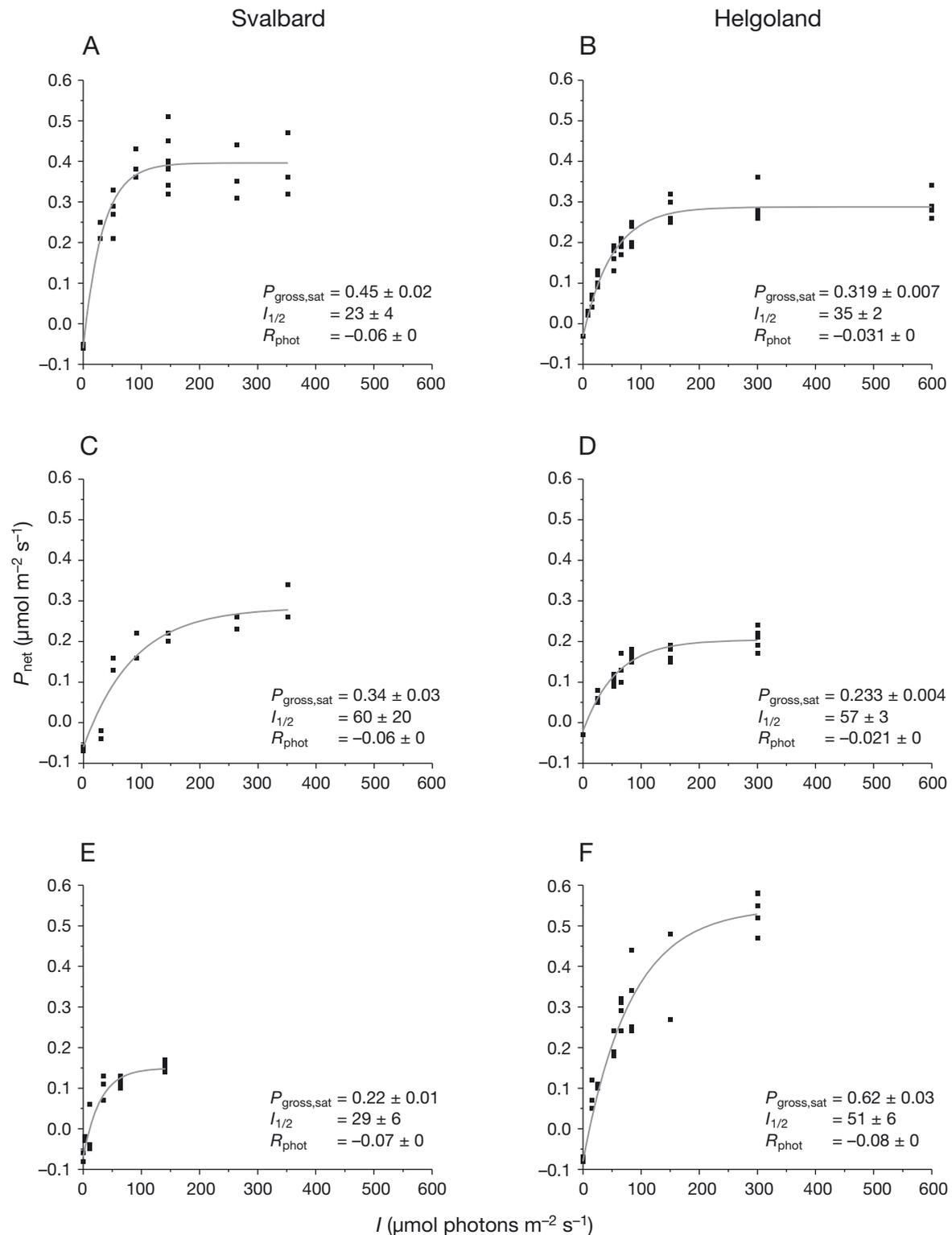


Fig. 4. Net photosynthesis (P_{net}) rates as a function of downwelling irradiance (P - I curves), obtained from laboratory micro-sensor measurements in replicate sediment cores from Svalbard (A,C,E; June 2010) and Helgoland (B,D,F; August 2009). Symbols in each graph show replicate values obtained in random locations within one core; lines show the least-square fit by the model $P_{\text{net}} = P_{\text{gross,sat}} \{1 - \exp[-\ln(2) \times I/I_{1/2}]\} + R_{\text{phot}}$, with the values (means \pm SE) of the corresponding fitting parameters given in the graph. $P_{\text{gross,sat}}$ = areal rate of gross photosynthesis at light saturation, $I_{1/2}$ = half-saturation light intensity, R_{phot} = respiration in the euphotic zone

PAR intensities (Fig. 4). High variability between the measurements at each light intensity was most likely due to pronounced heterogeneity in the surface chl *a* concentration within the samples. Fitting of the *P-I* curves revealed that photosynthetic parameters (net and gross photosynthesis and the rates of respiration in the sediment euphotic zone) were not significantly different between the 2 sites (Table 3, Table S1 in the Supplement). The average half-saturation PAR intensities, $I_{1/2}$ (which characterize the adaptation of the community to light), and the average compensation PAR intensities, I_c (the intensities at which the community photosynthesis equals respiration), were comparatively low and similar for both sites (Table 3). Thus, the MPB at both sites was low-light adapted and showed similar photosynthetic performance.

Volumetric rates of oxygen consumption in subsurface sediments from Svalbard were highly variable within and between the sediment cores, and ranged from ~ 8 to $44 \mu\text{mol O}_2 \text{ m}^{-3} \text{ s}^{-1}$ (Table 3). No significant trends ($p = 0.48$) with depth in the top 8 cm of sediment were observed. The areal respiration rates, obtained by integration of the volumetric rates over the average O_2 penetration depth determined *in situ* (2.25 cm), were about 6-fold higher than the areal respiration rates in the sediment euphotic zone and similar to the areal gross photosynthesis rates at light saturation (Table 3). Because oxygen is most likely present also below 3 cm depth, areal respiration rates below the euphotic zone are probably underestimated.

Estimates of daily oxygen budgets

We estimated daily light and oxygen budgets in the Svalbard and Helgoland sediments using the values of gross photosynthesis, respiration and light adaptation intensity estimated from the laboratory measure-

Table 3. Photosynthesis (*P*) and respiration (*R*) rates, and irradiance (*I*), derived from laboratory measurements by oxygen microsensors and planar optodes. P_{net} and P_{gross} : net and gross photosynthesis, R_{phot} : respiration in the euphotic zone, $I_{1/2}$: half saturation downwelling PAR irradiance, I_c : compensation irradiance, $R_{\text{below_phot}}$: respiration below the euphotic zone. Shown are averages \pm SD (minimum, maximum) values of *N* replicate measurements. nd: not determined

Parameter	Unit	Svalbard	Helgoland	N
Microprofiles				
P_{net}	($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.28 ± 0.12 (0.15, 0.39)	0.34 ± 0.17 (0.20, 0.54)	3, 3
R_{phot}	($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)	-0.062 ± 0.007 (-0.055, -0.070)	-0.048 ± 0.032 (-0.029, -0.085)	3, 3
P_{gross}	($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)	0.34 ± 0.11 (0.22, 0.45)	0.39 ± 0.21 (0.23, 0.62)	3, 3
$I_{1/2}$	($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	34 ± 22 (23, 60)	43 ± 11 (35, 55)	3, 3
I_c	($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	7 ± 2 (5, 8)	14 ± 9 (6, 23)	3, 3
Planar optodes (= $R_{\text{below_phot}}$)				
$R_{\text{below_phot, volumetric}}$	($\mu\text{mol O}_2 \text{ m}^{-3} \text{ s}^{-1}$)	-16.4 ± 15.8 (-8.3, -44.3)	nd	5
$R_{\text{below_phot, areal}}^a$	($\mu\text{mol O}_2 \text{ m}^{-2} \text{ s}^{-1}$)	-0.37 ± 0.36 (-0.19, -1)	nd	3

^aValues calculated for the average depth of oxygen penetration of 2.25 cm, as derived from *in situ* oxygen profiles during a 24 h interval (N = 43 profiles)

Table 4. Estimated *in situ* daily oxygen budgets for the 2 sites. Shown are averages \pm SD (minimum, maximum) values of *N* replicate measurements. The Svalbard budgets were estimated using the average *in situ* oxygen penetration depth of 2.25 cm (section A) and values ranging from 2 to 6 cm (section B). Daily (24 h) light doses were Svalbard: $3.5 \pm 1.0 \text{ mol photons m}^{-2} \text{ d}^{-1}$ ($n = 2$) and Helgoland: $5.3 \text{ mol photons m}^{-2} \text{ d}^{-1}$ ($n = 1$). nd: not determined

(A) Oxygen budgets ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$)				
Parameter	Svalbard	Helgoland	N	
P_{gross}	14.8 ± 7.0 (9.9, 22.9)	13.4 ± 5.7 (8.5, 19.7)	6, 3	
R_{phot}	-5.4 ± 0.6 (-4.8, -6.1)	-4.2 ± 2.7 (-2.5, -7.3)	3, 3	
$R_{\text{below_phot}}$	-31.8 ± 30.8 (-16.2, -86.2)	nd	3, -	
P_{net}	-22.4 ± 31.6 (-82.4, 1.9)	9.2 ± 6.3 (1.1, 17.2)	3, 3	
(B) Oxygen budgets for different depths of O_2 penetration ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$)				
Depth (cm)	Svalbard	Helgoland	N	
2	-18 ± 13 (-73, 4)	-	3, -	
4	-47 ± 23 (-149, -11)	-	3, -	
6	-75 ± 34 (-226, -25)	-	3, -	

ments, and the values of available downwelling PAR intensity and depths of sediment oxygenation determined *in situ*. Because each parameter was estimated with some uncertainty, we combined the values so as to estimate the average, as well as the minimum and maximum values, for the daily oxygen budgets.

For the Svalbard site, the PAR dose during the 24 h period was about $3.5 \text{ mol photons m}^{-2} \text{ d}^{-1}$. In comparison, the daily PAR dose at the Helgoland site was ~50% higher, despite the extended period (9 h) of darkness (Table 4).

The estimated daily gross primary production was very similar for the Svalbard and Helgoland sites (Table 4). This is somewhat counterintuitive considering the roughly 50% higher daily PAR dose and about 15% higher rates of gross photosynthesis at light saturation in Helgoland (Table 3), and is related to the combined effects of the generally low-light adaptation of the 2 communities and to the continuous illumination at Svalbard, which led to an additional 9 h of primary productivity per day.

Considering only the sediment euphotic zone, about 40% of the daily primary production at Svalbard would be remineralized by aerobic respiration. However, due to the much deeper O_2 penetration linked to sediment bioirrigation, the total estimated aerobic remineralization at this site exceeded production at least 2-fold, possibly up to about 5-fold, leading to a grossly negative daily O_2 budget (Table 4). In contrast, remineralization by aerobic processes occurred only within the upper 5 mm of sediment at the Helgoland site, and the estimated net daily O_2 budget was positive (about $9.17 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$; Table 4).

DISCUSSION

Microphytobenthic communities

During the study period, the Svalbard and Helgoland MPB communities were dominated by diatoms. The large overlap (28%) of identified species at both study sites and the dominance of cosmopolitans can be linked to the specific oceanographic setting of Kongsfjorden (Svalbard). A distinct Atlantic influence renders Kongsfjorden in the sub-Arctic rather than in the Arctic realm. Correspondingly, endemic species are rare, and North Atlantic species are present at all trophic levels of the fjord ecosystem (Hop et al. 2002, 2012). Some of the identified diatom species occur at both poles (e.g. *Navicula directa* and *Actinocyclus actinochilus*). However, morphological species analyses alone are sometimes not sufficient to decide on species identity (Mann 2010). Molecular biological tools are needed to check for the existence of cryptic species, which are likely to have developed due to the large geographical distance between the sites.

Microphytobenthic photosynthesis

Our data show that the concentrations of chlorophyll *a* and fucoxanthin, the half-saturation and compensation light intensities, and the productivity at light saturation are similar for the studied MPB communities in Svalbard and Helgoland. Thus, despite the differences in ambient water temperatures, the 2 communities have similar photosynthetic potential and performance, and thus seem to be adapted to the prevailing local conditions.

With respect to light adaptation, MPB communities from both of our studied sites showed low-light adaptation, similar to results obtained previously for comparable communities. For example, our half-saturation irradiance values, $I_{1/2}$, for the Svalbard community ($34 \pm 22 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) include the average value of $19 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ obtained by Glud et al. (2009) for another arctic MPB community (from Greenland) during summer, while the slightly larger $I_{1/2}$ values determined for the Helgoland community ($43 \pm 11 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) are comparable to those found previously for a temperate subtidal site in Brest, France ($40\text{--}58 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$; Ni Longphuir et al. 2007). Compared to previously reported values in photosynthesis research (Kuhl et al. 1996, Denis et al. 2012), the compensation irradiances were also generally low (7 and $14 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for Svalbard and Helgoland, respectively), although somewhat larger than those reported previously for an Arctic fjord in Greenland ($4.7 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$; Glud et al. 2009) or for diverse coastal MPB communities ($2.8 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$; Gattuso et al. 2006).

With respect to MPB photosynthesis, our data are also similar to those available in the literature for comparable communities (Table 5). For example, daily benthic primary production estimated for our Svalbard site ($10\text{--}23 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) lies within the range determined for other sites in Kongsfjorden ($2\text{--}48 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$; Woelfel et al. 2010), although it is smaller than previous estimates for the same site (Brandal, 37 to $47 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$; Woelfel et al. 2010). This discrepancy is likely due to differences in light conditions used to estimate the daily O_2 budgets. While we used the naturally variable light intensities measured *in situ* to estimate daily oxygen budgets in this study, our calculations for budgets of the study of Woelfel et al. (2010) were based on a fixed light intensity they used ($100 \text{ } \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and thus on a higher daily light dose ($8.6 \text{ mol photons m}^{-2} \text{ d}^{-1}$) than that measured by us ($3.5 \text{ mol photons m}^{-2} \text{ d}^{-1}$, Table 4). It is known that when *in*

Table 5. Comparison of daily oxygen budgets in sublittoral MPB communities from different Arctic and temperate sites

Site	Depth (m)	Gross O ₂ production (mmol O ₂ m ⁻² d ⁻¹)	O ₂ consumption (mmol O ₂ m ⁻² d ⁻¹)	Method	Date	Source
All sites, Kongsfjorden Brandal, Kongsfjorden	≤5 to 30 5	2 to 48 ^a ~ 38 to 47 ^a	-2 to -35 ^b ~ -35 ^b	Planar O ₂ optode sensor spots	Summer 2007	Woelfel et al. (2010)
Nivå Bay, Denmark Adventfjord, Svalbard/Arctic	0.4 ± 0.3 1.3 ± 0.6	28.8 ^a -	-8 to -9 ^c ~ -9 to -17 ^c	O ₂ microsensors	February 2001 May 2000	Hancke & Glud (2004)
Brandal, Kongsfjorden	5	10 to 23 10 to 23	-5 to -6 ^c -16 to -86 ^b	O ₂ microsensors Planar O ₂ optodes	Summer 2010/2011	Present study
Düne Süd, Helgoland	5	9 to 20	-3 to -7 ^c	O ₂ microsensors		

^aValues are estimated based on the data in the respective study. Daily gross production rates from our study are calculated using 24 h *in situ* light intensities, whereas calculations for the other studies are extrapolated from production rates at fixed experimental light intensities (see 'Discussion' for details)

^bIntegrated sediment O₂ consumption (euphotic & below euphotic zone)

^cO₂ consumption estimates within the sediment euphotic zone from 0 to 3°C

situ conditions are not taken into account, extrapolations can lead to overestimated budgets (Denis et al. 2012). Regarding the temperate site in Helgoland, our estimated daily O₂ budget (9 to 20 mmol O₂ m⁻² d⁻¹) was similar to but somewhat lower than that which we determined for the study by Hancke & Glud (2004) for a comparable site in Nivå Bay, Denmark (28.8 mmol O₂ m⁻² d⁻¹) (Table 5). The difference could be due to local conditions or again due to differences in light conditions applied when calculating the budget (i.e. constant incident light intensity of 140 μmol photons m⁻² s⁻¹ resulting in a daily light dose of 12 mol photons m⁻² d⁻¹ vs. variable light intensity measured *in situ* with a daily light dose of 5.3 mol photons m⁻² d⁻¹ for the study of Hancke & Glud [2004] and our study respectively).

Benthic respiration

Our respiration rates, integrated for the whole sediment community of Brandal, are in the same range as those determined previously for intact sediment cores of the same site, although our maximum estimate (-86 mmol O₂ m⁻² d⁻¹) exceeds previously determined maximum rates by Woelfel et al. (2010) by a factor of about 2.5. These differences may be related to heterogeneity of the studied system. Our sediment dark respiration rates of the euphotic zone determined from microsensor measurements are slightly lower but well comparable with rates measured by Hancke & Glud (2004) using the same method (Table 5) and show no differences between the arctic and temperate site.

While respiration in the sediment euphotic zone was similar at Svalbard and Helgoland, total respiration in the Svalbard sediment greatly exceeded respiration in the Helgoland sediments due to high infaunal activity. Laudien et al. (2007) reported high infaunal biomass in Brandal/Kongsfjorden (2260 infauna ind. m⁻² at 5 m water depth), with macrozoobenthos composed of annelids (79%), molluscs (11%) and crustaceans (8%), and the shallow (5 m) soft sediment fauna dominated by suspension-feeding or surface and sub-surface detritivorous polychaetes and deposit-feeding amphipods. It has been suggested that macrozoobenthos communities in the intertidal and shallow subtidal zones in the Arctic develop seasonally, and that community development (species richness, diversity and biomass) in the shallow subtidal zone is mainly affected by ice scouring (Bick & Arlt 2005, Laudien et al. 2007). Therefore, the macrozoobenthos community found at the Arctic site in the present study will likely not persist throughout all seasons but may be present only during summer months. Owing to bioirrigation and oxygenation of deeper sediment layers by this fauna, biotic oxygen respiration and the abiotic oxidation of reduced inorganic compounds are stimulated. This stimulation results in elevated oxygen consumption, which in our study was roughly 10-fold higher in Svalbard than in the Helgoland sediments. Macrozoobenthos (as present in the Svalbard sediments) was not observed in the Helgoland sediments, and our measurements indicated no bioirrigation at the Helgoland site. No infauna studies on shallow subtidal sandy sediments around Helgoland are available.

To enable quantification of rates from the micro-sensor measurements, the measured profiles had to be diffusion controlled. For this, the infauna in the Svalbard sediments had to be eliminated or have its activity stopped. This was achieved by sieving the sediment or purging the overlaying water with N_2 , which may have affected our measurements. However, we expect that these effects were insignificant. Regarding the MPB, the sediment cores were illuminated to enable ongoing photosynthesis during N_2 purging and the upper 5 mm of the sediments (in contrast to the rest of the core that was sieved) were left intact. Regarding the infauna, the exclusion or reduction of infauna activity was not selective and likely included meiofauna activity. Microsensor-derived respiration rates for Svalbard may thus be underestimated, and accordingly the net photosynthesis rates may be overestimated.

Drivers of high infauna abundance and respiration in Svalbard sediments

Total organic carbon content and C:N ratios were higher in the Svalbard than in the Helgoland sediments but not significantly different. The TOC content detected in Svalbard is similar to previous descriptions of marine surface sediments in the Kongsfjorden-Krossfjorden system (Kim et al. 2011). Organic matter in marine sediments can originate from benthic, pelagic and also sea-ice production, or from terrestrial input. The high C:N ratios indicate terrestrial organic matter input (e.g. coal), representing refractory (i.e. not bio-available) carbon. Recently, Kim et al. (2011) analyzed single organic matter contributors to sediments of the Kongsfjorden-Krossfjorden system. They documented high coal-derived organic matter content in the marine surface sediments in close vicinity to Ny Ålesund, which is a former coalmining site. Ancient organic matter is much less or not degradable compared to fresh organic matter. Thus, it can elevate carbon concentrations, supporting very high C:N ratios, but will not be available as a food source for the infauna.

Spring blooms in Kongsfjorden produce a great amount of bioavailable organic matter (e.g. 27 to 35 g C m^{-2} during the spring bloom from April 18th to May 13th 2002; Hodal et al. 2012), which can be either grazed in the water column or sink to the sea floor where it is grazed or buried. Hodal et al. (2012) showed that the spring bloom production in April–May was highest in shallow water depths (0–10 m), usually showing maxima at 5 m. The high pelagic

organic matter input represents an increased food supply. This, in turn, can support high abundance of infauna, which bioirrigate the sediment through ventilation of their burrows and thus increase the extent and depth of oxygen penetration into the sediment. As the interfacial oxygen uptake increased, sedimentary oxygen consumption rates increased. Additionally, sediment reworking, which is another effect of bioturbation by animals, returns reduced compounds from anoxic layers to the oxic part of the sediment, allowing these compounds to contribute to oxygen consumption through biotic and abiotic oxidation.

CONCLUSION

For the studied Arctic (Svalbard, Norway) and temperate (Helgoland, North Sea, Germany) sites, MPB communities and their photosynthetic potential showed no site specificity and were similar during the studied summer months. A dense infauna population was observed in the Svalbard sediments that may have been fueled by organic matter input from previous pelagic (spring) blooms. Oxygen budgets of the Svalbard sediments are therefore highly controlled by infauna activity and result in net heterotrophy, whereas the net positive oxygen budget in the Helgoland sediments is primarily governed by the photosynthetic oxygen production and thus controlled by light. Thus, we decline the first hypothesis that oxygen dynamics are controlled by MPB activity at both sites, and confirm the second hypothesis that both MPB communities show similar photosynthesis performance.

Acknowledgements. This study was supported by the POLMAR graduate school, the Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research (AWI); and the Max Planck Institute for Marine Microbiology (MPI). We are grateful for the support of the AWIPEV and Kings Bay staff in Ny Ålesund, and our colleagues at the Biologische Anstalt Helgoland. We thank Max Schwanitz, Sebastian Baumgarten, Philipp Fischer, Stephanie Wehkamp, Matthias Wehkamp, Elisa Bayraktarov and Antje Klawon for their diving support. We gratefully acknowledge all the technicians of the microsensor department for provision of the microsensors.

LITERATURE CITED

- Bick A, Arlt G (2005) Intertidal and subtidal soft-bottom macro- and meiofauna of the Kongsfjord (Spitsbergen). *Polar Biol* 28:550–557
- Cahoon LB (1999) The role of benthic microalgae in neritic

- ecosystems. *Oceanogr Mar Biol Ann Rev* 37:47–86
- Cahoon LB (2006) Upscaling primary production estimates: regional and global scale estimates of microphytobenthos production. In: Kromkamp JC, de Brower JFC, Blanchard GF, Forster RM, Créach V (eds) *Functioning of microphytobenthos in estuaries*. Royal Netherlands Academy of Arts and Sciences, Amsterdam
- Denis L, Gevaert F, Spilmont N (2012) Microphytobenthic production estimated by in situ oxygen microprofiling: short-term dynamics and carbon budget implications. *J Soils Sediments* 12:1517–1529
- Evrard V, Soetaert K, Heip CHR, Huettel M, Xenopoulos MA, Middelburg JJ (2010) Carbon and nitrogen flows through the benthic food web of a photic subtidal sandy sediment. *Mar Ecol Prog Ser* 416:1–16
- Friedman GM, Sanders FE (1978) *Principles of sedimentology*. Wiley, New York, NY
- Garcia HE, Gordon LI (1992) Oxygen solubility in seawater—better fitting equations. *Limnol Oceanogr* 37:1307–1312
- Gattuso JP, Gentili B, Duarte CM, Kleypas JA, Middelburg JJ, Antoine D (2006) Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. *Biogeosciences* 3:489–513
- Germain H (1981) *Flore des diatomées d'eaux douces et saumâtres du Massif Armoricaïn et des contrées voisines d'Europe occidentale*. Société Nouvelle des Éditions Boubée, Paris
- Glud RN, Kuhl M, Wenzhöfer F, Rysgaard S (2002) Benthic diatoms of a high Arctic fjord (Young Sound, NE Greenland): importance for ecosystem primary production. *Mar Ecol Prog Ser* 238:15–29
- Glud RN, Woelfel J, Karsten U, Kuhl M, Rysgaard S (2009) Benthic microalgal production in the Arctic: applied methods and status of the current database. *Bot Mar* 52:559–571
- Hancke K, Glud RN (2004) Temperature effects on respiration and photosynthesis in three diatom-dominated benthic communities. *Aquat Microb Ecol* 37:265–281
- Hendey NI (1964) *Bacillariophyceae (diatoms)*. In: *Great Britain. Ministry of Agriculture, Fisheries and Food. Fishery investigations, Series 4. An introductory account of the smaller algae of British coastal waters. Part V*. HMSO, London
- Hodal H, Falk-Petersen S, Hop H, Kristiansen S, Reigstad M (2012) Spring bloom dynamics in Kongsfjorden, Svalbard: nutrients, phytoplankton, protozoans and primary production. *Polar Biol* 35:191–203
- Hop H, Pearson T, Hegseth EN, Kovacs KM and others (2002) The marine ecosystem of Kongsfjorden, Svalbard. *Polar Res* 21:167–208
- Hop H, Wiencke C, Vogebe B, Kovaltchouk NA (2012) Species composition, zonation, and biomass of marine benthic macroalgae in Kongsfjorden, Svalbard. *Bot Mar* 55:399–414
- Hustedt F (1958) *Diatomeen aus der Antarktis und dem Südatlantik*. In: *Deutsche Antarktische Expedition 1938/39, Vol 2. Geogr.-Kartogr. Anstalt „Mundus“, Hamburg*, p 103–191
- Hustedt F (1961–1966) *Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete, Vol 7. Akademische Verlagsgesellschaft, Leipzig*
- Ito H, Kudoh S (1997) Characteristics of water in Kongsfjorden, Svalbard. *Proc NIPR Symp Polar Meteorol Glaciol* 11:211–234
- Jakobsson M (2002) Hypsometry and volume of the Arctic Ocean and its constituent seas. *Geochem Geophys Geosyst* 3(5):1–18, doi:10.1029/2001GC000302
- Kerouel R, Aminot A (1997) Fluorometric determination of ammonia in sea and estuarine waters by direct segmented flow analysis. *Mar Chem* 57:265–275
- Kim JH, Peterse F, Willmott V, Kristensen DK, Baas M, Schouten S, Damste JSS (2011) Large ancient organic matter contributions to Arctic marine sediments (Svalbard). *Limnol Oceanogr* 56:1463–1474
- Klute A, Dirksen C (1986) Hydraulic conductivity and diffusivity: laboratory methods. In: Klute A (ed) *Methods of soil analysis. Part 1. Physical and mineralogical methods*. American Society of Agronomy and Soil Science Society of America, Madison, WI, p 687–734
- Krammer K, Lange-Bertalot H (1986) *Bacillariophyceae 1. Teil. Naviculaceae*. Gustav Fischer Verlag, Stuttgart
- Krammer K, Lange-Bertalot H (1988) *Bacillariophyceae 2. Teil. Bacillariaceae, Epithemiaceae, Surirellaceae*. Gustav Fischer Verlag, Stuttgart
- Krammer K, Lange-Bertalot H (2000) *Bacillariophyceae 3. Teil. Centrales, Fragilariaceae, Eunotiaceae*. Spektrum Akademischer Verlag, Heidelberg
- Kühl M, Glud RN, Ploug H, Ramsing NB (1996) Microenvironmental control of photosynthesis and photosynthesis-coupled respiration in an epilithic cyanobacterial biofilm. *J Phycol* 32:799–812
- Kühl M, Glud RN, Borum J, Roberts R, Rysgaard S (2001) Photosynthetic performance of surface-associated algae below sea ice as measured with a pulse amplitude-modulated (PAM) fluorometer and O₂ microsensors. *Mar Ecol Prog Ser* 223:1–14
- Laudien J, Herrmann M, Arntz WE (2007) Soft bottom species richness and diversity as a function of depth and iceberg scour in Arctic glacial Kongsfjorden (Svalbard). *Polar Biol* 30:1035–1046
- Laxon SW, Giles KA, Ridout AL, Wingham DJ and others (2013) CryoSat-2 estimates of Arctic sea ice thickness and volume. *Geophys Res Lett* 40:732–737
- Li YH, Gregory S (1974) Diffusion of ions in sea water and in deep-sea sediments. *Geochim Cosmochim Acta* 38:703–714
- MacIntyre HL, Geider RJ, Miller DC (1996) Microphytobenthos: the ecological role of the “secret garden” of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. *Estuaries* 19:186–201
- Mann DG (2010) Discovering diatom species: Is a long history of disagreements about species-level taxonomy now at an end? *Plant Ecol Evol* 143:251–264
- Menard HW, Smith SM (1966) Hypsometry of ocean basin provinces. *J Geophys Res* 71:4305–4325
- Ni Longphuiert S, Clavier J, Grall J, Chauvaud L and others (2007) Primary production and spatial distribution of subtidal microphytobenthos in a temperate coastal system, the Bay of Brest, France. *Estuar Coast Shelf Sci* 74:367–380
- Polerecky L, Franke U, Werner U, Grunwald B, de Beer D (2005) High spatial resolution measurement of oxygen consumption rates in permeable sediments. *Limnol Oceanogr Methods* 3:75–85
- Precht E, Franke U, Polerecky L, Huettel M (2004) Oxygen dynamics in permeable sediments with wave-driven

- pore water exchange. *Limnol Oceanogr* 49:693–705
- Reiss H, Wieking G, Kroencke I (2007) Microphytobenthos of the Dogger Bank: a comparison between shallow and deep areas using phytopigment composition of the sediment. *Mar Biol* 150:1061–1071
- Revsbech NP (1989) An oxygen microsensor with a guard cathode. *Limnol Oceanogr* 34:474–478
- Riaux-Gobin C, Llewellyn CA, Klein B (1987) Microphytobenthos from two subtidal sediments from North Brittany. II. Variations of pigment compositions and concentrations determined by HPLC and conventional techniques. *Mar Ecol Prog Ser* 40:275–283
- Scholz B, Liebezeit G (2012) Microphytobenthic dynamics in a Wadden Sea intertidal flat—Part I: Seasonal and spatial variation of diatom communities in relation to macro-nutrient supply. *Eur J Phycol* 47:105–119
- Scott FJ, Thomas DP (2005) Diatoms. In: Scott FJ, Marchant HJ (eds) Antarctic marine protists. Australian Biological Resources Study and Australian Antarctic Division, Canberra, p 13–201
- Serreze MC, Holland MM, Stroeve J (2007) Perspectives on the Arctic's shrinking sea-ice cover. *Science* 315: 1533–1536
- Sundbäck K, Enoksson V, Granéli W, Pettersson K (1991) Influence of sublittoral microphytobenthos on the oxygen and nutrient flux between sediment and water: a laboratory continuous-flow study. *Mar Ecol Prog Ser* 74: 263–279
- Svendsen H, Beszczynska-Moller A, Hagen JO, Lefaucon-nier B and others (2002) The physical environment of Kongsfjorden-Krossfjorden, an Arctic fjord system in Svalbard. *Polar Res* 21:133–166
- Underwood GJC, Kromkamp J (1999) Primary production by phytoplankton and microphytobenthos in estuaries. *Adv Ecol Res* 29:93–153
- Volkenborn N, Polerecky L, Wetthey DS, Woodin SA (2010) Oscillatory porewater bioadvection in marine sediments induced by hydraulic activities of *Arenicola marina*. *Limnol Oceanogr* 55:1231–1247
- Webb W, Newton M, Starr D (1974) Carbon dioxide exchange of *Almus rubra*: a mathematical model. *Oecologia* 17:281–291
- Weber M, Faerber P, Meyer V, Lott C, Eickert G, Fabricius KE, De Beer D (2007) In situ applications of a new diver-operated motorized microsensors profiler. *Environ Sci Technol* 41:6210–6215
- Wentworth CK (1922) A scale of grade and class terms for clastic sediments. *J Geol* 30:377–392
- Wenzhöfer F, Glud RN (2004) Small-scale spatial and temporal variability in coastal benthic O₂ dynamics: Effects of fauna activity. *Limnol Oceanogr* 49:1471–1481
- Wieland A, Kühl M (2000) Short-term temperature effects on oxygen and sulfide cycling in a hypersaline cyanobacterial mat (Solar Lake, Egypt). *Mar Ecol Prog Ser* 196: 87–102
- Wiltshire KH, Malzahn AM, Wirtz K, Greve W and others (2008) Resilience of North Sea phytoplankton spring bloom dynamics: An analysis of long-term data at Helgoland Roads. *Limnol Oceanogr* 53:1294–1302
- Witkowski A, Lange-Bertalot H, Metzeltin D (2000) Diatom flora of marine coasts. *Iconographia diatomologica: annotated diatom micrographs, Vol 7*. ARG Gantner Verlag, Vaduz, Liechtenstein
- Woelfel J, Schumann R, Peine F, Flohr A and others (2010) Microphytobenthos of Arctic Kongsfjorden (Svalbard, Norway): biomass and potential primary production along the shore line. *Polar Biol* 33:1239–1253
- Wright SW, Jeffrey SW, Mantoura RFC, Llewellyn CA, Bjornland T, Repeta D, Welschmeyer N (1991) Improved HPLC method for the analysis of chlorophylls and carotenoids from marine phytoplankton. *Mar Ecol Prog Ser* 77:183–196
- Zhang JL, Lindsay R, Schweiger A, Rigor I (2012) Recent changes in the dynamic properties of declining Arctic sea ice: a model study. *Geophys Res Lett* 39:L20503, doi: 10.1029/2012GL053545

Editorial responsibility: Erik Kristensen,
Odense, Denmark

Submitted: March 28, 2013; Accepted: November 28, 2013
Proofs received from author(s): April 15, 2014