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Cyanobacterial surface blooms formed by *Aphanizomenon* sp. and *Nodularia spumigena* in the Baltic Sea: Small-scale fluxes, pH, and oxygen microenvironments

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Abstract

Summer blooms of filamentous cyanobacteria, mainly *Aphanizomenon* sp. and *Nodularia spumigena*, are characteristic for the Baltic Sea, where they accumulate at the sea surface in calm weather. The chemical microenvironment, and thus the actual growth conditions within these cyanobacterial surface blooms of the Baltic Sea, are largely unknown. Using microsensors, it is shown that photosynthesis is substantial within these millimeter-thin cyanobacterial layers accumulating at the air–water interface. Net oxygen fluxes at the air–sea interface were on average 2.7-fold higher than those at the aggregate–water interface beneath the layers. Net photosynthesis at light saturation was 1.7–2.4 mmol O_2 m^{-2} h^{-1}. Dark respiration varied between 0.21 ± 0.12 mmol O_2 m^{-2} h^{-1} and 0.50 ± 0.30 mmol O_2 m^{-2} h^{-1}. There is a tight coupling of O_2-producing and O_2-consuming processes within aggregates of these large, heterocystous, nitrogen-fixing cyanobacteria and their associated heterotrophic microbial community. It is suggested that the close association of autotrophic and heterotrophic organisms and processes creates a pH microenvironment that is favorable for iron uptake for the cyanobacteria, which in turn may release surplus nitrogen to the heterotrophic community. The pH varied between 7.4 and 9.0 between darkness and saturating light intensities. Decaying aggregates were anoxic up to 12 h. The volumetric oxygen consumption rate in an anoxic aggregate was 1.2 μmol O_2 cm^{-3} h^{-1}. During the initial 12 h of decay, aggregate sinking velocity increased 10-fold, concurrent with a decrease in volumetric oxygen consumption to 0.67 μmol O_2 cm^{-3} h^{-1}.

The Baltic Sea is characterized by summer blooms of two large, heterocystous, N_2-fixing cyanobacteria species, *N. spumigena* and *Aphanizomenon* sp., of which the former species is toxic (Bianchi et al. 2000). It has been proposed that gas vesicles within filaments make these cyanobacteria positively buoyant to reach high light intensities at the sea surface, where they cover the energy needed for N_2 fixation through photosynthesis (Walsby et al. 1997). In calm weather, a significant fraction of these cyanobacteria accumulate at the sea surface and cover very large areas of the Baltic Sea where the N : P ratio is low (Kononen et al. 1996; Moisander et al. 2003; Stal et al. 2003). *N. spumigena* and *Aphanizomenon* sp. often compose 20–30% of the cyanobacterial biomass, the remaining being represented by picocyanobacteria. However, the contribution to primary production by large cyanobacteria was 44% (Stal et al. 1999; Stal and Walsby 2000). The large cyanobacteria are the main N_2-fixing organisms in the Baltic Sea (Stal and Walsby 2000; Boström et al. 2007). The large cyanobacteria fix excess N_2 relative to their own nitrogen demand and channel the surplus nitrogen through the microbial food web and to picocyanobacteria (Larsson et al. 2001).

Cyanobaterial aggregates *N. spumigena* and *Aphanizomenon* sp. are colonized by a diverse community of bacteria that show high ectoenzymatic activities (Hoppe 1981; Stoecker et al. 2005; Tuomainen et al. 2006). The tight physical association of autotrophic and heterotrophic organisms implies tight couplings of biological processes. Up to 40% of the primary production measured by the use of $H^{14}CO_3$ in *N. spumigena* aggregates from the Baltic Sea was incorporated in the associated bacteria (Hoppe 1981). Blooms of *N. spumigena* and *Aphanizomenon* sp. thus support a large and active food web dominated by microheterotrophs, which also appear to remineralize much of the cyanobacterial biomass within the water column (Forsskåhl et al. 1982; Sellner 1997). Isotopic signatures of sedimenting organic matter, however, have revealed that a large fraction of nitrogen fixed by pelagic cyanobacteria is exported to sediments in the Baltic Sea (Struck et al. 2004). Hence, large cyanobacteria play an important role for primary production and input of nitrogen to the pelagic surface waters and sediments.

The accumulation of millimeter-thin layers of cyanobacterial biomass at the air–water interface in lakes leads to significant gradients of oxygen and pH within these aggregates (Ibelings and Maberly 1998). The physical and chemical microenvironment and growth conditions for the cyanobacteria and their associated heterotrophic community are, therefore, significantly different from that of the

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bulk. The mass transfer of CO_2 at the sea–air interface, where the cyanobacteria accumulate, may be significantly more efficient than that through a diffusive boundary layer surrounding cyanobacterial aggregates deeper in the water column. In the present study of cyanobacterial surface blooms in the Baltic Sea, microsensors of oxygen and pH were used to test the hypotheses that (1) photosynthesis rates can be substantial within millimeter-thin layers of cyanobacteria at the air–water interface because of high light intensities and an efficient gas exchange with the atmosphere, (2) the oxygen production and consumption is tightly coupled within aggregates, (3) CO_2 uptake and production leads to pH microenvironments with potential impact on iron uptake, and (4) cyanobacterial aggregates can be anoxic during decay.

Material and methods

Sampling of aggregates—Aggregates formed by *Aphanizomenon* sp. and *N. spumigena* were collected during two cruises on R/V *Aranda*, held in July–August, 1993 and 1994, at the entrance to the Gulf of Finland. Several transects were done between Finland and Estonia, where horizontal, vertical, and temporal variability of chlorophyll *a*, stratification, currents, and pelagial biology were studied during July–August 1994 (Kononen et al. 1998). Aggregates were positively buoyant and accumulated at the sea surface during this period. They could thus be directly collected from the sea surface by use of a bucket. The in situ temperature was 21°C and the salinity was 4. The in situ light intensity at noon was 1,200 μmol photons m^{-2} s^{-1}. Aggregates composed of coherent bundles of filaments and their associated mucus were transferred to a smaller container with water collected in situ for microsensor measurements at room temperature (21°C). The aggregates accumulated at the air–water interface as in their natural environment. The aggregates covered <1% of the water surface to ensure steady state of oxygen concentration and pH below the aggregates, i.e., avoid artificial O_2 depletion or supersaturation due to a high concentration of cyanobacterial biomass relative to surrounding water. In 1993, during which no surface bloom occurred, cyanobacteria from the deeper water column were collected using a plankton net. Aggregates of these were formed in roller tanks within 2 h (Shanks and Edmondson 1989). The flux of oxygen to an anoxic aggregate potentially increases when it sinks due to advection in the vicinity of the aggregate (Kiørboe et al. 2001; Ploug 2001). Aggregates were transferred to a vertical flow system in which it is possible to measure oxygen gradients at hydrodynamic conditions similar to those experienced by aggregates sinking through the water column (Kiørboe et al. 2001). Sinking velocity was calculated from the flow velocity, which balanced sinking velocity (Ploug and Jørgensen 1999).

pH and oxygen measurements—pH was measured using a pH microsensor calibrated at a pH of 6.88, 9.18, and 10 (Revsbech and Jørgensen 1986). Its sensing tip was 20 μm wide and 150 μm long. A calomel electrode was used as a reference. Its signal was measured by a millivoltmeter connected to a strip chart recorder. Oxygen concentration gradients were measured at steady state using a Clark-type microelectrode with a tip diameter of 5 μm. Its 90% response time was <0.3 s and its stirring sensitivity was <1% (Revsbech 1989). Its signal was measured by a picoamperemeter connected to a strip chart recorder. It was calibrated at air-saturation and at anoxic conditions. The microsensors were mounted in a micromanipulator. The surface of aggregates was determined visually as observed under a dissection microscope with an ocular micrometer. Steady-state gradients of pH and oxygen occurred after 10–15 min of light exposure. Measurements of O_2 concentrations and gross photosynthesis were measured at 100-μm-step intervals. Gross photosynthesis rates were measured using the light–dark shift technique (Revsbech et al. 1981). A 150-W halogen lamp with an infrared cutoff filter (Schott KL 1500) was used as the primary light source, which was suddenly shaded during light-to-dark shifts and vice versa. The light intensity was calibrated using an underwater scalar irradiance sensor (Biospherical Instruments QLS 100). The natural background light intensity in the laboratory was <5 μmol photons m^{-2} s^{-1}.

Flux calculations—In surface scums, the upward and downward oxygen fluxes were calculated from the one-dimensional oxygen distribution using Fick's first law of diffusion:

$$J = -D\frac{dC}{dx} \quad (1)$$

where J is the flux (nmol O_2 cm^{-2} s^{-1}), D is the diffusion coefficient of O_2 in the bulk water (2.15×10^{-5} cm^2 s^{-1} at a salinity of 4 and 21°C; Broecker and Peng 1974), and dC/dx is the concentration gradient of O_2 (nmol O_2 cm^{-4}). The apparent diffusivity of O_2 within aggregates was assumed to be 0.95 times that in the surrounding water (Ploug and Passow 2007). Surface area and volume of sinking aggregates was calculated assuming ellipsoid geometry (Mass 1994).

Results

The trichomes and filaments of the cyanobacteria were positively buoyant and occurred close to the sea–air interface. A mucus layer extended underneath the filaments. The aggregates were colonized by bacteria and protozoa (*Bodo ovatus*). Examples of oxygen distributions in light and darkness and the distributions of gross photosynthesis rates as measured with the light–dark shift method within aggregates are shown (Fig. 1). Oxygen concentrations varied between 260 μmol O_2 L^{-1} and 450 μmol O_2 L^{-1}, depending on the light conditions. Gross photosynthesis was only detected in the uppermost 1.1 mm. Gross photosynthesis rates increased when the light intensity increased from 110 μmol photons m^{-2} s^{-1} to 270 μmol photons m^{-2} s^{-1}. The saturating light intensity of gross photosynthesis measured at the surface of a few individual filaments positioned close to each other was found at ~160 μmol photons m^{-2} s^{-1} (Fig. 2A). Oxygen

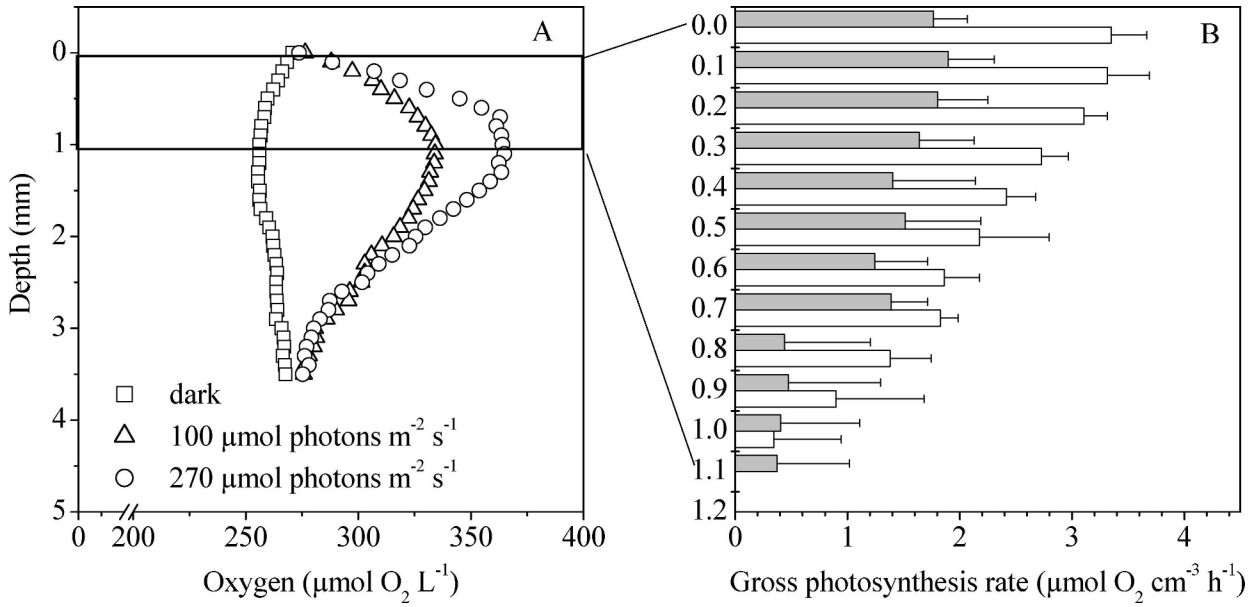

Fig. 1. (A) Oxygen distributions in dark, at light intensities of 110 μmol photons m^{-2} s^{-1} and 270 μmol photons m^{-2} s^{-1}. The data points represent the average value of three series of measurements. (B) Gross photosynthesis rates measured with the light–dark shift method at 110 μmol photons m^{-2} s^{-1} and 270 μmol photons m^{-2} s^{-1}. The bars represent the average value of three series of measurements with the standard deviation of the mean value.

concentrations did not increase at light intensities >250 μmol photons m^{-2} s^{-1}, and net photosynthesis of the whole aggregate community was thus saturated at these light intensities (Fig. 2B). The compensating light intensity at which all O_2 produced by photosynthesis was consumed by respiration, including that by heterotrophic microorganisms, was found at 33 μmol photons m^{-2} s^{-1} (Fig. 2B). Net fluxes of oxygen at different light conditions and depth-integrated gross photosynthesis rates are summarized in Table 1. Gross photosynthesis as calculated from the difference of the oxygen fluxes in light and dark was similar to the depth-integrated gross photosynthesis measured by the light–dark shift method.

The oxygen distribution within aggregates varied dependent on aggregate thickness, and the relative contribution of photosynthesis and respiration. An example of a 6-mm-thick aggregate in which the dark respiration rate was relatively high compared to net photosynthesis at light saturation is shown (Fig. 3). Oxygen concentrations varied between 135 μmol O_2 L^{-1} and 420 μmol O_2 L^{-1}, depending on the light conditions. Gross photosynthesis occurred in the uppermost 3 mm only, and the average rates were higher than those shown in the previous example (Fig. 1). Net fluxes of oxygen at different light conditions and depth-integrated gross photosynthesis are summarized in Table 2. The net fluxes measured at 270 μmol photons m^{-2} s^{-1} were similar to those measured in the thinner aggregate previously shown (Fig. 1; Table 1). However, gross photosynthesis calculated from the difference in the oxygen fluxes measured in light and dark was significantly lower than the depth-integrated gross photosynthesis measured by the light–dark shift method in the thicker aggregate.

The light–dark shift method to measure gross photosynthesis rates is based on the fact that the production of oxygen is exactly balanced by oxygen consumption and diffusion away from the measuring point when the oxygen concentration distribution is constant during time and thus at steady state (Fig. 4A). Photosynthesis stops when the light is turned off and the oxygen concentration therefore decreases due to oxygen consumption and diffusion away from the measuring point. The initial rate of decrease of oxygen after darkness thus equals the gross photosynthesis rate before the light was turned off, assuming the oxygen consumption and diffusion to be constant within the first seconds after darkness. The pH showed a similar response to light (Fig. 4B). This method therefore detects any close coupling between O_2-producing and -consuming processes in light, e.g., where O_2 and CO_2 is recycled within the community of autotrophic and heterotrophic organisms. The gross photosynthesis detected by the light–dark shift method was 3.9 mmol O_2 m^{-2} h^{-1} higher than the gross photosynthesis calculated from the sum of the net O_2 fluxes measured in light and dark. This difference in O_2 production is recycled and thus immediately consumed during light. Hence, the O_2 consumption in light was 5.6 times higher than the total O_2 flux into the aggregates measured during darkness.

Net fluxes of oxygen and depth-integrated gross photosynthesis measured in different aggregates at different light conditions are summarized in Table 3. The upward oxygen fluxes at the air–sea interface were on average 2.7-fold higher than the downward flux at the aggregate–water interface beneath the aggregate.

A decaying aggregate was anoxic even at a light intensity of 350 μmol photons m^{-2} s^{-1} (Fig. 5). The aggregate was ellipsoidal in shape, the longest axis being 5 mm and the shortest 3 mm. The aggregate had up to 2-mm-long extensions of filaments pointing toward the water phase

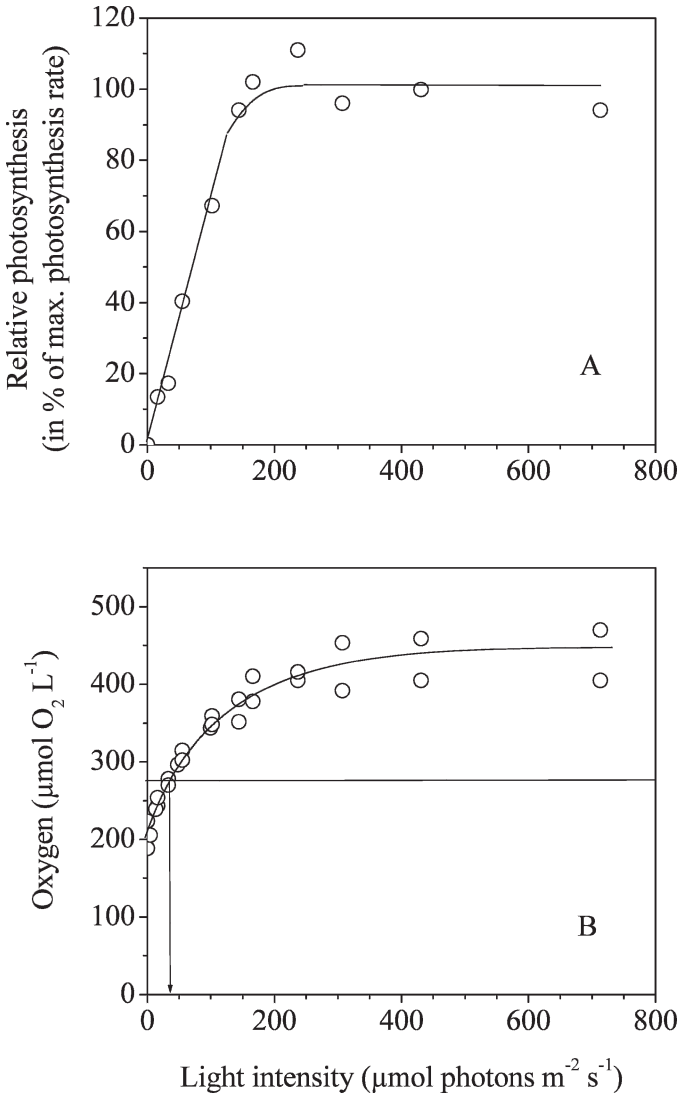

Fig. 2. (A) Gross photosynthesis measured at the surface of aggregates as a function of light intensity. (B) Oxygen concentration measured at the surface of aggregates as function of light intensity. The horizontal line represents the bulk concentration.

but was not transparent towards the center. *N. spumigena* and *A. flos-aquae* were the dominating phototrophic species. Compared to the species composition of the water column, it was highly enriched in *A. flos-aquae* and the heterotrophic flagellate *B. ovatus*. Some fecal pellets were trapped in the aggregate as well. Net respiration depleted the aggregate in O_2, although the measurements of O_2 distribution were done in light, and photosynthesis thus cannot be excluded. Hence, the aggregate was a highly heterotrophic microenvironment, indicating that the cyanobacteria were being decomposed. The aggregate was initially sinking at 4.4 m d^{-1}. The longest axis was oriented perpendicular to the sinking velocity. The sinking velocity increased 10-fold during 12 h, which indicate that the gas vesicles were being degraded. At sinking rates of 4.4 m d^{-1} and 11 m d^{-1}, the aggregate was anoxic in a 0.5-mm-wide zone in its interior, and the availability of oxygen for microbial respiration was thus limited by the diffusive flux of oxygen from the surrounding water. Oxygen was present throughout the aggregate at a sinking rate of 40 m d^{-1}. The potential diffusive oxygen flux to an aggregate increases with increasing aggregate sinking velocity because advection occurs in the vicinity of the aggregate when it sinks (Kiørboe et al. 2001). In the present case, however, the oxygen consumption rates decreased with increasing sinking velocity or time. The oxygen uptake was 100 nmol O_2 cm^{-2} h^{-1}, 110 nmol O_2 cm^{-2} h^{-1}, and 120 nmol O_2 cm^{-2} h^{-1}, respectively, at sinking rates of 40 m d^{-1}, 11 m d^{-1}, and 4.4 m d^{-1}. At low sinking rate, the average volume-specific oxygen uptake was 1.20 μmol O_2 cm^{-3} h^{-1}. At the highest sinking rate, oxygen was present throughout the aggregate, and the average specific oxygen uptake was ~0.7 μmol O_2 cm^{-3} h^{-1}. The highest respiration rates thus occurred during the early degradation process at lowest sinking velocity.

Discussion

This is the first time that O_2 evolution and O_2 consumption, and the pH microenvironment of aggregates formed by *Aphanizomenon* sp. and *N. spumigena* from the Baltic Sea, have been studied under physical conditions similar to those in the field, when they accumulate at the sea surface in calm weather. The use of microsensors made it possible to study these parameters during contact with air as in the natural environment. During incubation in closed bottles, aggregates are often destroyed, or diffusion-limited gas exchange between the aggregates and the surrounding water may occur (Stal and Walsby 1998). Oxygen consumption in marine *Oscillatoria* spp. aggregates has

Table 1. Oxygen fluxes and depth-integrated photosynthesis rates measured as mmol O_2 m^{-2} h^{-1} in the aggregate shown in Fig. 1 at three different light conditions measured as μmol photons m^{-2} s^{-1}. The values represent the mean with the standard deviation of the mean value (n = 3–5).

O_2 fluxes	0	110	270
Upward flux	−0.14±0.05	0.75±0.09	1.37±0.35
Downward flux	−0.07±0.07	0.44±0.32	0.42±0.09
Total flux	−0.21±0.13	1.19±0.24	1.79±0.37
Gross photosynthesis*	0	1.40±0.35	2.01±0.50
Gross photosynthesis†	0	1.49±0.59	2.30±0.20

* Calculated as the sum of the total fluxes measured in light and in dark.
† Measured by the light–dark shift technique.

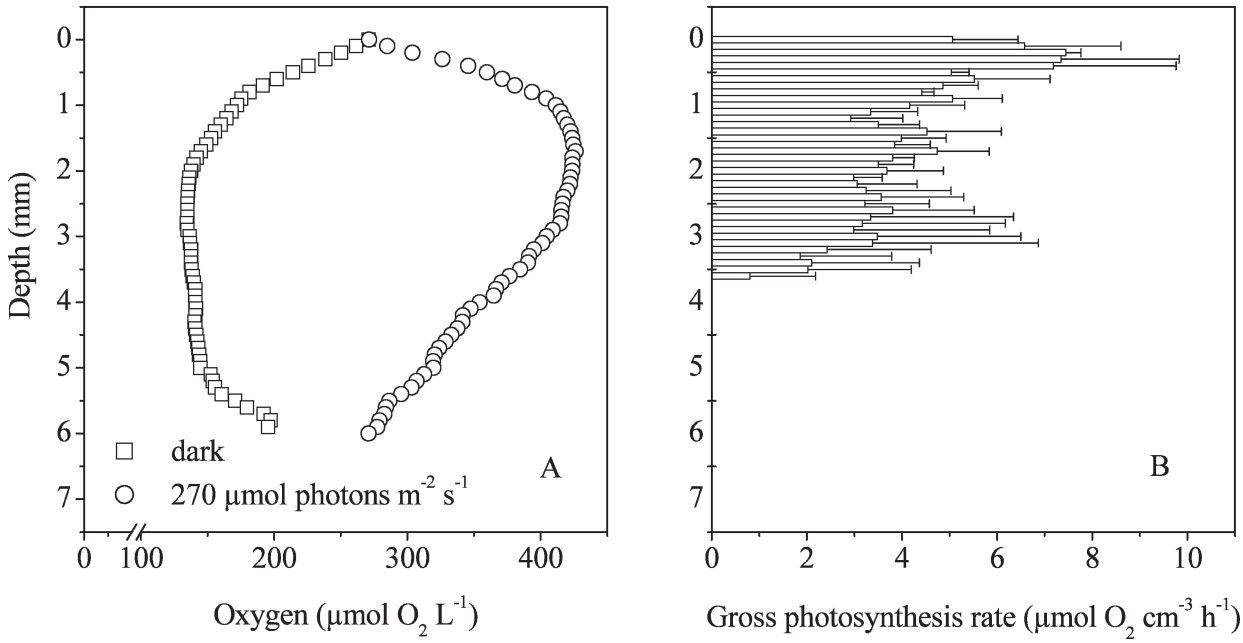

Fig. 3. (A) Oxygen distributions in dark and at 270 μmol photons m^{-2} s^{-1}. The data points represent the average value of three series of measurements. (B) Gross photosynthesis rates measured with the light–dark shift method at a light intensity of 270 μmol photons m^{-2} s^{-1}. The bars represent the average value of three series of measurements with the standard deviation of the mean value.

previously been measured using microsensors (Paerl and Bebout 1988). During these measurements, the aggregates were placed in a petri dish and were in direct contact with a solid surface. Under these experimental conditions, the oxygen exchange is limited by the solid surface, leading to significantly different oxygen gradients compared to those measured when aggregates are suspended in water phase (Ploug and Jørgensen 1999). In the present study, the uppermost filaments were covered by a micrometer-thin water film through which the gas exchange with the atmosphere is most efficient, and net O_2 fluxes at the air–sea interface on average were 2.7-fold higher than the downward flux through the mucus matrix within aggregates. The maximum oxygen concentration inside aggregates was 600 μmol L^{-1} at a light intensity of 714 μmol photons m^{-2} s^{-1} (data not shown).

The buffering capacity of brackish water is larger than that of freshwater and lower than that of seawater. The pH within cyanobacterial surface blooms of the brackish water in the Baltic Sea varied dramatically in response to light conditions where salinity was 4. The pH of $\geq$9 at saturating light intensities implies that the CO_2 concentration is low within surface blooms and bicarbonate must be a major essential carbon source, which has also been observed in lakes (Ibelings and Maberly 1998). These authors, however, demonstrated that a steep gradient of pH at the air–water interface promotes influx of CO_2 from the atmosphere in cyanobacterial surface blooms of *Aphanizomenon flos-aquae*, *Anabaena flos-aquae*, and *Gomphospheria naegeliana* in lakes.

It has been shown that only ~10% of the filamentous cyanobacterial community occurs at the sea surface during blooms (Stal and Walsby 1998), and photoinhibition may be severe after a longer residence time at depth. Photoinhibition of photosynthesis has been demonstrated in surface blooms of *Aphanizomenon flos-aquae*, *Anabaena flos-aquae*, and *G. naegeliana*, as well as in *Microcystis* colonies in lakes (Ibelings and Mur 1992; Ibelings and Maberly 1998). Photoinhibition was not detected in surface blooms at light intensities <800 μmol photons m^{-2} s^{-1}, but it may occur at longer exposure to higher light intensities. At moderate light intensities, net photosynthesis occurred at substantial rates within these millimeter-thin cynaobacterial layers. Concentration ratios of particulate organic carbon, nitrogen, and phosphorus in cyanobacterial aggregates from the Baltic Sea have previously been demonstrated to be highly enriched in carbon relative to the Redfield ratio (Engel et al. 2002). A large fraction of the primary production may be channeled into mucus, which apparently was a large component of the aggregates. Mucus was mostly located beneath the filaments, presumably due to differential buoyancy of cells and mucus. Photosynthesis was not detected all through the cyanobacterial mucus layer, which may reflect light gradients or the

Table 2. Oxygen fluxes and depth-integrated photosynthesis rates measured as mmol O_2 m^{-2} h^{-1} in the aggregate shown in Fig. 2 in darkness and at 270 μmol photons m^{-2} s^{-1}. The values represent the mean with the standard deviation of the mean value (n = 3–5).

O_2 fluxes	0	270
Upward flux	−0.40±0.11	1.43±0.20
Downward flux	−0.38±0.25	0.48±0.15
Total flux	−0.78±0.30	1.91±0.41
Gross photosynthesis*	0	2.69±0.71
Gross photosynthesis†	0	6.60±0.96

* Calculated as the sum of the total fluxes measured in light and in dark.
† Measured by the light–dark shift technique.

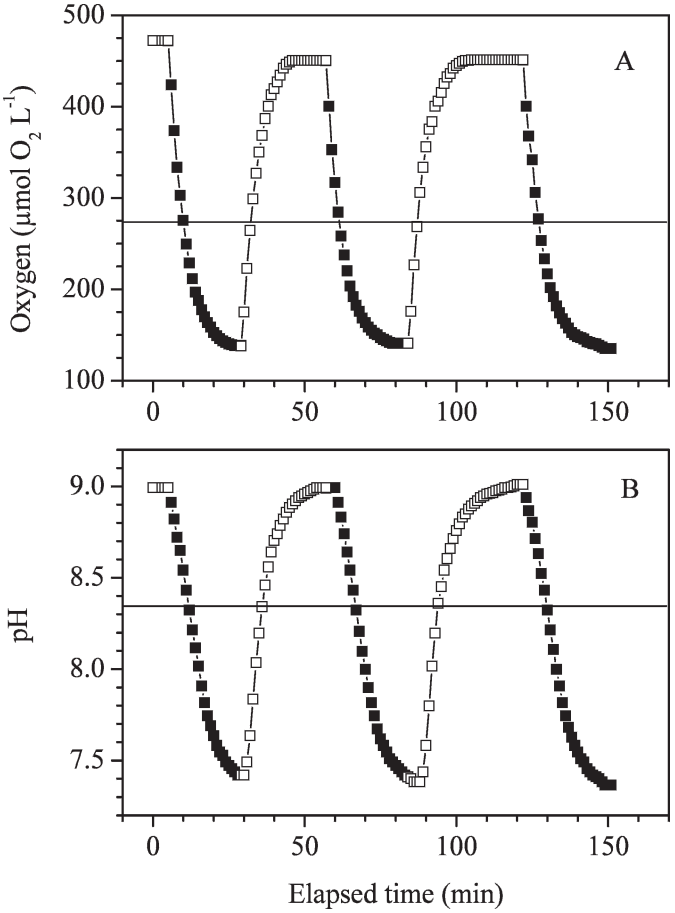

Fig. 4. (A) Oxygen and (B) pH as a function of time measured 200 μm below the aggregate surface during sudden shifts between light (open symbols) and darkness (closed symbols). The horizontal lines represent the bulk values.

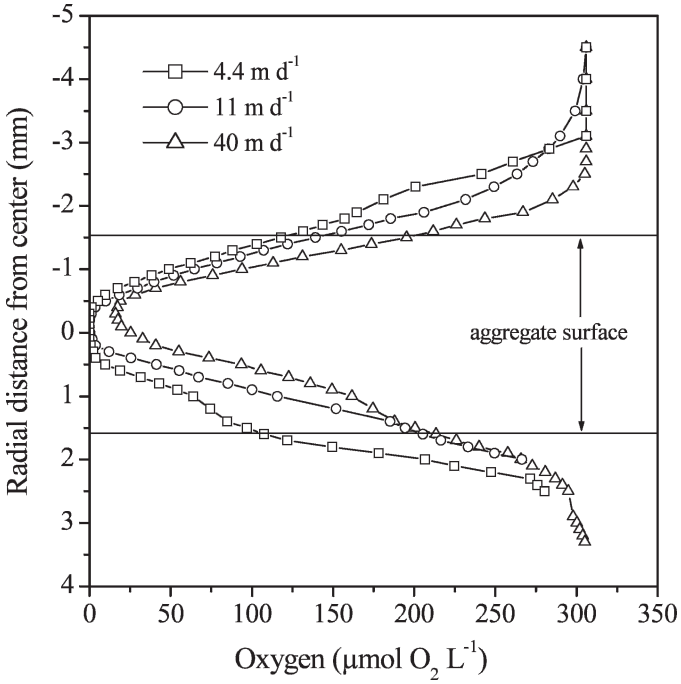

Fig. 5. Radial distributions of oxygen in a 2-mm-deep aggregate, the longest axis being 5 mm and oriented perpendicular to the flow, measured at sinking rates of 4 m d^{-1}, 11 m d^{-1}, and 44 m d^{-1}. Each profile represents the average of three series of measurements.

abundance of trichomes (Ibelings and Maberley 1998; Prufert-Bebout et al. 1993).

Assuming a day length with 10 h of saturating light intensities at this high latitude, maximum net and gross photosynthesis within patches of these surface blooms were 24 mmol O_2 m^{-2} d^{-1} and 66 mmol O_2 m^{-2} d^{-1}, respectively. The depth-integrated net photosynthesis from dawn to dusk in the Baltic Sea during cyanobacterial summer blooms has previously been shown to vary between 1.77 mmol O_2 m^{-2} d^{-1} and 14.2 mmol O_2 m^{-2} d^{-1} in a 21-m-deep water column (Walsby 1997). The distribution of cyanobacterial surface scums at the sea surface is often highly patchy. The present study shows that the depth-integrated production within 1–3-mm-thin layers of filamentous cyanobacteria at the sea surface can locally be higher than the depth-integrated photosynthesis within a 20-m-deep water column.

The light–dark shift technique was originally developed to study gross photosynthesis at high spatial resolution within sediments and microbial mats (Revsbech et al. 1981). Gross photosynthesis rates of cyanobacterial surface blooms of the present study were similar to those of sediments as well as to those measured within cyanobacterial surface blooms in lakes (Ibelings and Maberly 1998). In those systems, the depth-integrated gross photosynthesis measured with the light–dark shift technique was consistently higher than that calculated from the sum of the

Table 3. Oxygen fluxes and depth-integrated photosynthesis rates measured as mmol O_2 m^{-2} h^{-1} in various aggregates at four different light intensities (μmol photons m^{-2} s^{-1}). The values represent the mean with the standard deviation of the mean value (n = 3–12).

O_2 fluxes	0	110	270	714
Upward flux	−0.46±0.28	0.85±0.16	1.40±0.25	1.97±0.68
Downward flux	−0.18±0.22	0.44±0.32	0.44±0.11	0.61±0.34
Upward : downward flux	2.6	1.9	3.2	3.2
Total flux	−0.64±0.50	1.29±0.49	1.85±0.37	2.39±0.61
Gross photosynthesis*	0	1.93±0.99	2.49±0.88	3.14±0.83
Gross photosynthesis†	0	1.49±0.59	4.40±2.40	4.10±2.40

* Calculated as the sum of the total fluxes measured in light and in dark.
† Measured by the light–dark shift technique.

oxygen fluxes measured in light and darkness, respectively. High oxygen consumption rates in light due to the Mehler reaction have been demonstrated in *Trichodesmium* aggregates using membrane inlet mass spectroscopy (Kana 1993). To what extent enhanced oxygen consumption in light in aggregates formed by *Aphanizomenon* sp. and *N. spumigena* from the Baltic Sea is due to photorespiration, the Mehler reaction, and enhanced heterotrophic activity during light is not known. In cyanobacterial surface blooms of the present study, however, gross photosynthesis measured with the light–dark shift technique was similar to that calculated from the difference in oxygen fluxes at the aggregate–water interfaces measured in light and darkness when dark respiration was low. A tight coupling and enhancement of gross photosynthesis and respiration during light was thus only observed when the ratio of dark respiration to net photosynthesis at saturating light intensities was high. Using radioisotopes, it has been demonstrated that up to 40% of the primary production in *N. spumigena* aggregates from the Baltic Sea is incorporated in the associated bacteria (Hoppe 1981). Hence, the density and activity of microbial heterotrophic community associated with the autotrophs may be responsible for the enhanced oxygen consumption in light in these aggregates.

A close autotrophic–heterotrophic association in cyanobacterial aggregates can lead to efficient nutrient uptake and recycling within these communities. It has been shown that filamentous cyanobacteria, e.g., *Trichodesmium*, fix surplus dinitrogen, as is the case for *Aphanizomenon* sp. and *Nodularia* sp. In *Trichodesmium*, this surplus nitrogen is leaked to the microbial community as dissolved organic nitrogen and ammonium (Glibert and Bronk 1994; Mulholland and Capone 2001). This will increase growth and respiration of the microbial community, which produces inorganic carbon to be assimilated by the cyanobacteria. It has also been demonstrated that growth of large, heterocystous, N_2-fixing cyanobacteria such as *Aphanizomenon* sp. and *N. spumigena* can be iron-limited in the Baltic Sea (Stal et al. 1999; Stolte et al. 2006). A large fraction of iron enters the Baltic Sea from rivers partly bound to dissolved organic matter (Stolte et al. 2006). The accumulation of large cyanobacteria at the air-water interface, as observed in various geographical locations, may be an advantage to collect iron-rich organic matter or dust from the atmosphere, if these sources are trapped within the mucus of these aggregates. High light intensities, including those of ultraviolet at the sea surface, promote photoreduction of iron (Sunda 2001). The present study furthermore demonstrates that respiration by cyanobacteria and heterotrophic microorganisms results in a pH of 7.4 inside aggregates during darkness. Such a low pH significantly enhances the solubility of iron to become available to the cyanobacteria (Waite 2001). The heterotrophic community may therefore enhance iron uptake by the cyanobacteria. Hence, the close association of autotrophic and heterotrophic organisms creates a microenvironment that is favorable for iron uptake for the cyanobacteria, which in turn may release surplus nitrogen to the heterotrophic community.

A decaying aggregate was demonstrated to be anoxic for approximately 12 h in its interior. The highest volumetric respiration rate was 24-fold higher than those measured in similar-sized marine snow (Ploug et al. 1999; Ploug 2001). Cyanobacterial aggregates isolated from the Baltic Sea contain bacteria with genes encoding for key enzymes of nitrification and denitrification (Tuomainen et al. 2003). Denitrification rates measured using the ^{15}N-isotope pairing technique, however, were very low (Hietanen et al. 2002). It has previously been argued that anoxic conditions may be an ephemeral phenomenon only in suspended and sinking aggregates when the aggregate carbon content is the substrate to be respired and the O_2 concentration in the surrounding water is at air-saturation. Under these conditions, the organic carbon pool of marine aggregates can only last for approximately 1 d before it is turned over by respiration at such high rates. Anoxia in aggregates is more likely to occur for longer time periods in O_2-depleted bottom waters of the Baltic Sea (Ploug et al. 1997; Ploug 2001). The short time during which anoxic conditions occur inside aggregates may limit nitrification and denitrification to be quantitatively unimportant within these aggregates in the upper water column with high O_2 concentrations. The overall carbon turnover by respiration relative to aggregate sinking velocity during this relatively short time period, however, is substantial and can explain the observation that a large fraction of cyanobacterial biomass appears to be remineralized within the water column.

In recent years, recognition of small- and large-scale heterogeneities of organic matter, nutrients, and organisms, e.g., thin layers and aggregates, in aquatic systems has increased our understanding of the function of ecosystems. The present study shows that cyanobacterial surface blooms in the Baltic Sea compose highly productive patches with a physical/chemical microenvironment that is significantly different from that of the bulk. These chemical microenvironments can have profound implications for gas exchange as well as for uptake and release of micro- and macronutrients through a tight association of autotrophic and heterotrophic organisms and their biological activities.

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