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Light penetration and light intensity in sandy marine sediments measured with irradiance and scalar irradiance fiber-optic microprobes

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ABSTRACT: Fiber-optic microprobes for determining irradiance and scalar irradiance were used for light measurements in sandy sediments of different particle size. Intense scattering caused a maximum integral light intensity [photon scalar irradiance, E_0(400 to 700 nm) and E_0(700 to 880 nm)] at the sediment surface ranging from 180% of incident collimated light in the coarsest sediment (250 to 500 µm grain size) up to 280% in the finest sediment (<63 µm grain size). The thickness of the upper sediment layer in which scalar irradiance was higher than the incident quantum flux on the sediment surface increased with grain size from <0.3 mm in the finest to >1 mm in the coarsest sediments. Below 1 mm, light was attenuated exponentially with depth in all sediments. Light attenuation coefficients decreased with increasing particle size, and infrared light penetrated deeper than visible light in all sediments. Attenuation spectra of scalar irradiance exhibited the strongest attenuation at 450 to 500 nm, and a continuous decrease in attenuation coefficent towards the longer wavelengths was observed. Measurements of downwelling irradiance underestimated the total quantum flux available, i.e. scalar irradiance, by >100% throughout the sediment. Attenuation coefficents of scalar irradiance, downwelling irradiance and upwelling irradiance were, however, similar in deeper sediment layers where the light field became more diffuse. Our results demonstrate the importance of measuring scalar irradiance when the role of light in photobiological processes in sediments, e.g. microbenthic photosynthesis, is investigated.

KEY WORDS: Microscale optics · Scattering · Sediments

INTRODUCTION

Coastal sandy sediments are often inhabited by dense populations of microalgae, e.g. tidal flats can be dominated by diatoms or by microbial mats consisting chiefly of cyanobacteria and purple sulfur bacteria (*'Farbstreifensandwatt'*) (Stal et al. 1985). The optical properties of such sediments and the associated microphytobenthos remain virtually unstudied, although light is the key parameter for microbenthic photosynthesis and its regulation. Previous studies of light penetration in sediments have been based on the use of relatively large light collectors covered by sediment layers (Hoffman 1949, Taylor 1964, Taylor & Gebelein 1966, Gomoiu 1967, Haardt & Nielsen 1980) or inserted into the sediment (Fenchel & Straarup 1971). Only recently have techniques based on fiber-optic microprobes with defined light collecting properties become available to study the light field in sediments at high spatial and spectral resolution (Jørgensen & Des Marais 1986, Kühl & Jørgensen 1992, Lassen et al. 1992a). By using microprobes for determining field radiance and scalar irradiance (see definitions in Table 1) the importance of scattered light in the light field in sediments was demonstrated, and basic optical parameters were calculated from measured angular radiance distributions (Kühl & Jørgensen 1994).

Among the surprising effects of the intense scattering on the light field was the formation of a maximum in total light intensity, i.e. scalar irradiance, in the upper 0.0 to 0.5 mm of the sediment reaching up to 200% of the incident light intensity at wavelengths subject to lowest absorption in the sediment. Similar observations have been made for microbial mats, where the high density of microalgal photopigments also resulted in a strong spectral alteration of the surface light field relative to incident light (Jørgensen & Des Marais 1988, Kühl & Jørgensen 1992, Lassen et al. 1992b). Although these studies indicate the importance of measuring scalar irradiance at a high spatial resolution the most commonly used light parameter in studies of microbenthic photosynthesis is still incident downwelling irradiance, measured with a flat cosine collector positioned at the sediment surface (e.g. Pinckney & Zingmark 1993). It is thus important to investigate the relevance of determining the light intensity available for photosynthesis by measuring downwelling irradiance.

In this study we investigated the importance of sediment particle size for the light penetration in sediments and the build-up of a near-surface maximum of scalar irradiance. Furthermore, we used a new fiber-optic microprobe for measuring irradiance, together with scalar irradiance microprobes, in order to quantify upwelling light (i.e. upwelling irradiance) and to quantify the extent to which downwelling irradiance measurements underestimate the light intensity available for photosynthesis in sediments.

MATERIALS AND METHODS

Light parameters. Definitions of the basic light parameters used in this study are given in Table 1. All parameters are a function of wavelength and can be integrated over a range of wavelengths. In this study we present photon irradiance and photon scalar irradiance data integrated from 400 to 700 nm (visible light, VIS or PAR) and from 700 to 880 nm (infrared light, IR). The fundamental light field parameter is the field radiance, which measures the radiant flux from a defined direction. From the radiance, various integral measures of light intensity can be defined. The most commonly measured light parameter is downwelling irradiance, E_d, which is the total downwelling radiant flux per unit area of a horizontal surface element. A similar measure for the upwelling light is upwelling irradiance, E_u. The ratio of upwelling to downwelling irradiance is called irradiance reflectance, R. In most oceanic waters and

Table 1. Basic optical parameters for light measurements in sediments

Parameter	Symbol	Definition	Microscale measuring technique
Field radiance	$L(\theta, \phi) = d^2\Phi/(dA\, d\omega)$	The radiant flux, Φ, from a certain direction (θ, ϕ) in a spherical coordinate system per unit solid angle, $d\omega$, per unit area perpendicular to the direction of light propagation, dA	Measured by a simple, flat-cut untapered or tapered optical fiber. The radiance fiber probe has a directional response defined by the acceptance angle of the optical fiber. Tip diameter 10 to 125 µm. (Jørgensen & Des Marais 1986, Kühl & Jørgensen 1992)
Downwelling irradiance and upwelling irradiance	$E_d = \int_{2\pi} L(\theta, \phi) \cos\theta\, d\omega$ $E_u = \int_{-2\pi} L(\theta, \phi) \cos\theta\, d\omega$	The integral radiant flux incident from the upper or lower hemisphere per unit area of a horizontal surface element	Measured by a coated optical fiber with a diffusing disk fixed at the flat cut end of the fiber. The irradiance fiber probe weights the incident radiance, $L(\theta, \phi)$, with the cosine of the incident zenith angle, θ. Tip diameter 40 to 125 µm. (C. Lassen unpubl.)
Scalar irradiance	$E_0 = \int_{4\pi} L(\theta, \phi)\, d\omega$ $= E_{0d} + E_{0u}$	The integral radiant flux incident from all directions about a point in the sediment. E_0 consists of a downwelling (E_{0d}) and an upwelling (E_{0u}) component corresponding to the integral flux incident from the upper or lower hemisphere respectively	Measured by a coated and tapered optical fiber with a diffusing sphere fixed on the tip. The fiber probe has an isotropic response for light incident from +160° to −160° zenith angle. Tip diameter 50 to 100 µm. (Kühl & Jørgensen 1992, Lassen et al. 1992a)

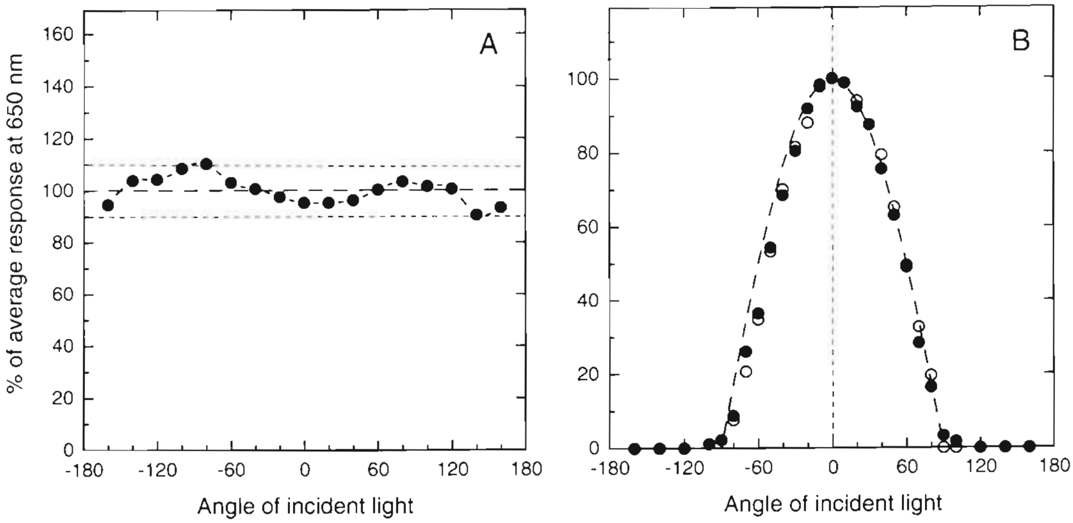

Fig. 1 Light collecting properties of fiber-optic microprobes for scalar irradiance (A; sphere diameter 80 µm) and irradiance (B; tip diameter 125 µm) measured by rotating the fiber probe relative to a collimated light beam with the tip fixed at the same position and distance relative to the light source. The acceptance function of the irradiance probe was determined at 2 different orientations (solid and open symbols) by rotating the fiber 90° after the first series of measurements. Thick dotted lines represent the theoretical response of an ideal scalar irradiance and irradiance sensor respectively

clear coastal waters the irradiance reflectance is only a few percent, and the light field is highly forward-directed (Jerlov 1976, Kirk 1983). Downwelling irradiance is thus an appropriate light intensity parameter to measure in combination with photosynthesis measurements in the water column of clear waters. In turbid waters and near the sea floor, irradiance reflectance can increase up to 20–30% as the light field becomes more diffuse due to higher scattering intensity (Kirk 1983). In sediments this effect is even more pronounced due to the high density of scattering material (Kühl & Jørgensen 1994). In turbid waters and sediments irradiance measurements thus underestimate the total quantum flux available for phototrophs. Furthermore, irradiance weights incident radiance with the cosine of the incident angle (see Table 1) and thus weights scattered light travelling at an oblique angle less than directional collimated light. Sediment microalgae live, however, in a highly diffuse light field and receive light from all directions around the cells (Jørgensen & Des Marais 1988, Kühl & Jørgensen 1994). The scalar irradiance, E_0, is an integral measure of light incident from all directions about a point and thus quantifies the total amount of light available for photosynthesis at a given depth. Scalar irradiance is therefore the most relevant light parameter to measure in combination with studies of microbenthic photosynthesis.

Fiber-optic microprobes. Fiber-optic microprobes for measuring irradiance and scalar irradiance were developed in our laboratory. The scalar irradiance microprobe had an isotropic (± 10%) response for light incident from −160° to +160° (Fig. 1A) and consisted of a small diffusing sphere (80 µm diameter) cast on the coated tip of a tapered optical fiber (Lassen et al. 1992a). The irradiance microprobe was made by fixing a small diffusing disk of TiO_2-doped methacrylate on the end of an untapered optical fiber (tip diameter 125 µm), which was coated on the sides with black enamel paint. The angular response of the irradiance microprobe closely matched the theoretical response curve for a cosine collector (Fig. 1B). A description of the manufacturing procedure of irradiance microprobes and their light collecting properties is given elsewhere (Lassen unpubl.).

Experimental setup. Light penetration was measured in quartz sand of different grain sizes. Sediment was collected at the upper littoral zone at a beach near Rønbjerg, Limfjorden, Denmark, and was sieved into particle sizes of <63, 63–125, 125–250, and 250–500 µm. Animals and organic material adherent to the sand grains were removed by washing, and the sand was dried at 105°C before use. Light measurements were done in 7 to 8 mm thick sediment samples transferred to black coring tubes, which were sealed at the bottom with a plug of solidified agar. Measurements in wet material were done with 3 to 5 mm of water on top of the sediment. Homogeneous vertical illumination was provided by a fiber-optic tungsten-halogen light source (Schott KL-1500, Germany) equipped with a collimating lens. A detailed description of the measuring setup is given elsewhere (Kühl & Jørgensen 1992, 1994). Microscale spectral light measurements were done at a spatial resolution of 0.1 mm using fiber-optic microprobes for irradiance and scalar irradiance connected to an optical multichannel analyser (Kühl & Jørgensen 1992, Lassen et al. 1992a). The position of the microprobes was controlled by a motorized micromanipulator (Märtzhäuser, Germany) interfaced to a computer via a custom-built controller card and software. Depth profiles of spectral scalar irradiance, E_0, were measured by inserting the scalar irradiance microprobe into the sediment from above at a zenith angle of 135° relative to the incident collimated light beam. Depth profiles of spectral downwelling irradiance, E_d, and upwelling irradiance, E_u, were measured by inserting the irradiance microprobe from below through the agar plug at 0° zenith angle and from above at 175° zenith angle respectively. Integrated values for VIS (400 to 700 nm) and IR (700 to 880 nm) photon irradiance or photon scalar irradiance were obtained by integrating measured spectra corrected for the spectral sensitivity of the detector system (Kühl & Jørgensen 1992, Lassen et al. 1992b).

Attenuation coefficients. The diffuse vertical attenuation coefficient, K, for irradiance or scalar irradiance is defined as:

$$K = -\frac{d\ln E}{dz} = -\frac{1}{E}\frac{dE}{dz} \qquad (1)$$

where z = depth. Attenuation coefficients for downwelling irradiance, K_d, upwelling irradiance, K_u, and scalar irradiance, K_0, were calculated in 2 ways. Attenuation coefficients for integral VIS or IR irradiance and scalar irradiance were calculated by linear regression from the slope of linear parts of ln-transformed depth profiles, i.e. equivalent to the right hand side of Eq. (1). Attenuation spectra of scalar irradiance were furthermore calculated over a sediment layer of 0.5 to 1.5 mm by the formula:

$$K = \frac{\ln(E_1/E_2)}{z_1 - z_2} \qquad (2)$$

using the spectral irradiance or scalar irradiance, E, measured at depths z_1 and z_2, in the sediment, where $z_2 > z_1$. All attenuation coefficients presented here have the unit mm^{-1}.

RESULTS

Comparison of irradiance and scalar irradiance

Depth profiles of downwelling irradiance, E_d, and of scalar irradiance, E_0, in wet quartz sand of 125 to 250 µm particle size are shown in Fig. 2. At the sediment surface the incident light was collimated and the downwelling irradiance was thus equal to the downwelling scalar irradiance at the sediment surface. The

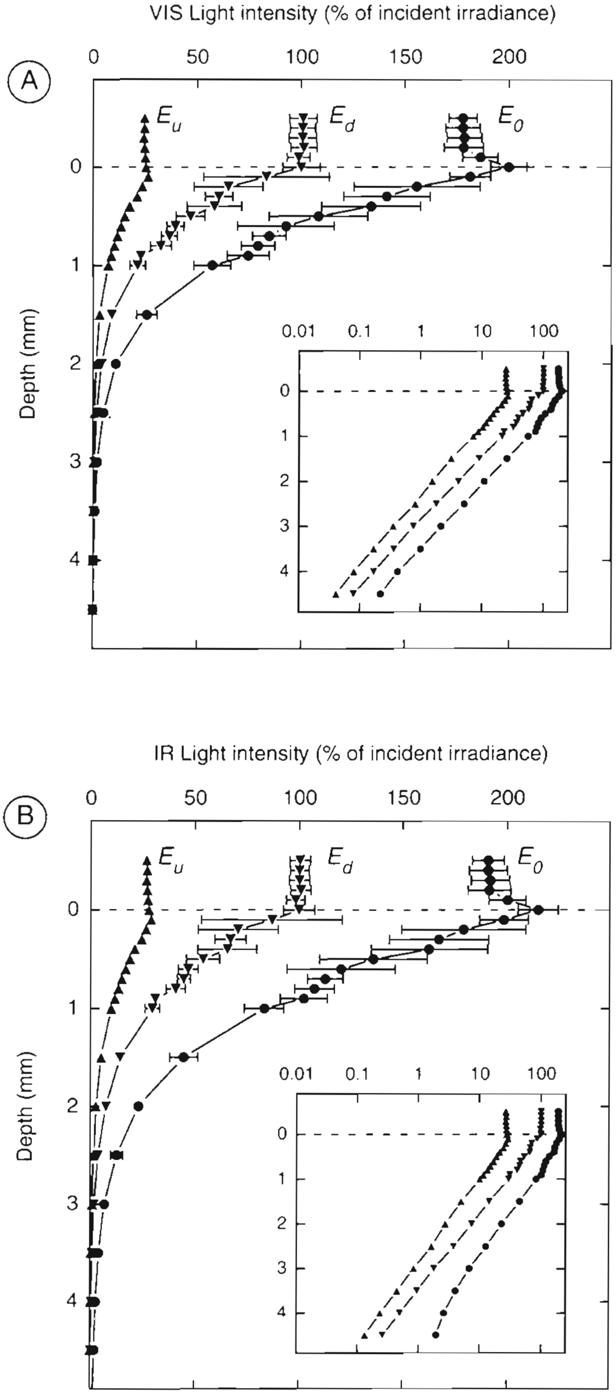

Fig. 2. Depth profiles of (A) VIS (400–700 nm) light and (B) IR (700–880 nm) light, in wet quartz sand (particle size 125 to 250 µm). Light intensity measured as downwelling irradiance, E_d (▼), upwelling irradiance, E_u (▲), and scalar irradiance, E_0 (●). Insets show depth profiles of log transformed data. Light intensities are expressed as % of incident collimated light at the sediment surface [E_0(surface) = E_d(surface)]. Error bars indicate the standard deviation and data points represent the arithmetic mean of 3 to 5 measurements

Table 2. Attenuation coefficients (± SD) of VIS and IR light in wet and dry quartz sand (particle size 125 to 250 µm)

Sediment	Attenuation coefficients		
	Downwelling irradiance, K_d	Upwelling irradiance, K_u	Scalar irradiance, K_0
Dry sand			
VIS light (400–700 nm)	2.73 (± 0.05)	2.71 (± 0.04)	2.65 (± 0.09)
IR light (700–880 nm)	2.42 (± 0.05)	2.43 (± 0.03)	1.94 (± 0.09)
Wet sand [a]			
VIS light (400–700 nm)	1.61 (± 0.04)	1.46 (± 0.02)	1.59 (± 0.02)
IR light (700–880 nm)	1.36 (± 0.03)	1.22 (± 0.01)	1.21 (± 0.02)

[a] Calculated from log-linear part of the depth profiles in Fig. 2 ($r^2 > 0.98$ to 0.99)

Table 3. Attenuation coefficients (K_0, ± SD) of VIS and IR scalar irradiance in wet quartz sand of different particle size. K_0 was calculated from log-linear parts of depth profiles in Fig. 3 ($r^2 > 0.99$)

	Particle size			
	< 63 µm	63–125 µm	125–250 µm	250–500 µm
VIS light (400–700 nm)	3.46 (± 0.02)	1.64 (± 0.02)	1.60 (± 0.02)	0.99 (± 0.03)
IR light (700–880 nm)	2.84 (± 0.02)	1.38 (± 0.01)	1.18 (± 0.02)	0.81 (± 0.02)

total light intensity, i.e. the scalar irradiance, was, however, much higher. For VIS and IR light, scalar irradiance exhibited a distinct maximum of 200 % and 215 % of the incident irradiance at the sediment surface, respectively. Throughout the sediment, scalar irradiance was >2× higher than the downwelling irradiance measured at the same depths.

The upwelling VIS and IR irradiance, E_u, in wet quartz sand is also shown in Fig. 2. The upwelling light was a significant component of the total light intensity and upwelling irradiance was on the order of 20 to 40 % of the downwelling irradiance at corresponding depths in the sediment. As the data were normalised to the incident downwelling irradiance, the surface value of E_u corresponds to the surface irradiance reflectance, $R = E_u/E_d$. Surface irradiance reflectance, also called the albedo of the sediment, was 25 % and 28 % for VIS and IR light respectively. From a similar data set in dry quartz sand (data not shown), sediment albedos of 35 % and 40 % for VIS and IR light were calculated.

The depth profiles of upwelling and downwelling irradiance as well as scalar irradiance showed an exponential light attenuation with depth below 1 mm in the wet quartz sand (see insets in Fig. 2), with similar diffuse attenuation coefficients (Table 2). In dry quartz sand of the same particle size we found a higher attenuation of VIS and IR light than in the wet sand (Table 2; depth profiles not shown). In both cases VIS light was attenuated more strongly than IR light.

Scalar irradiance as a function of particle size

Depth profiles of VIS and IR scalar irradiance in wet sediment with different grain sizes are shown in Fig. 3. In all sediments a pronounced surface maximum of scalar irradiance was found. The surface maximum of scalar irradiance increased, while the light penetration decreased, with decreasing particle size. IR light exhibited both a higher surface maximum of scalar irradiance and deeper light penetration than VIS light in all sediments. Highest values of scalar irradiance maxima were found in wet quartz sand of <63 µm particle size, where the VIS and IR scalar irradiance reached up to 260 % and 280 % of the incident light intensity respectively. The near-surface zone of the sediment, where scalar irradiance values were higher than the incident irradiance, varied in thickness from <0.3 mm in the finest to >1 mm in the coarsest sediment. Light (E_0) was attenuated exponentially with depth starting from the surface in the finest sediment (<63 µm), while exponential attenuation of light started below a depth of 0.5 mm in 63 to 125 µm sand, 1 mm in 125 to 250 µm sand, and >1 mm in 250 to 500 µm sand. The attenuation coefficient of scalar irradiance increased with decreasing particle size of the sediment (Table 3). Attenuation coefficients of the 63 to 125 µm and the 125 to 250 µm sediment were almost identical as both sediment types had their major grain size fraction near 125 µm.

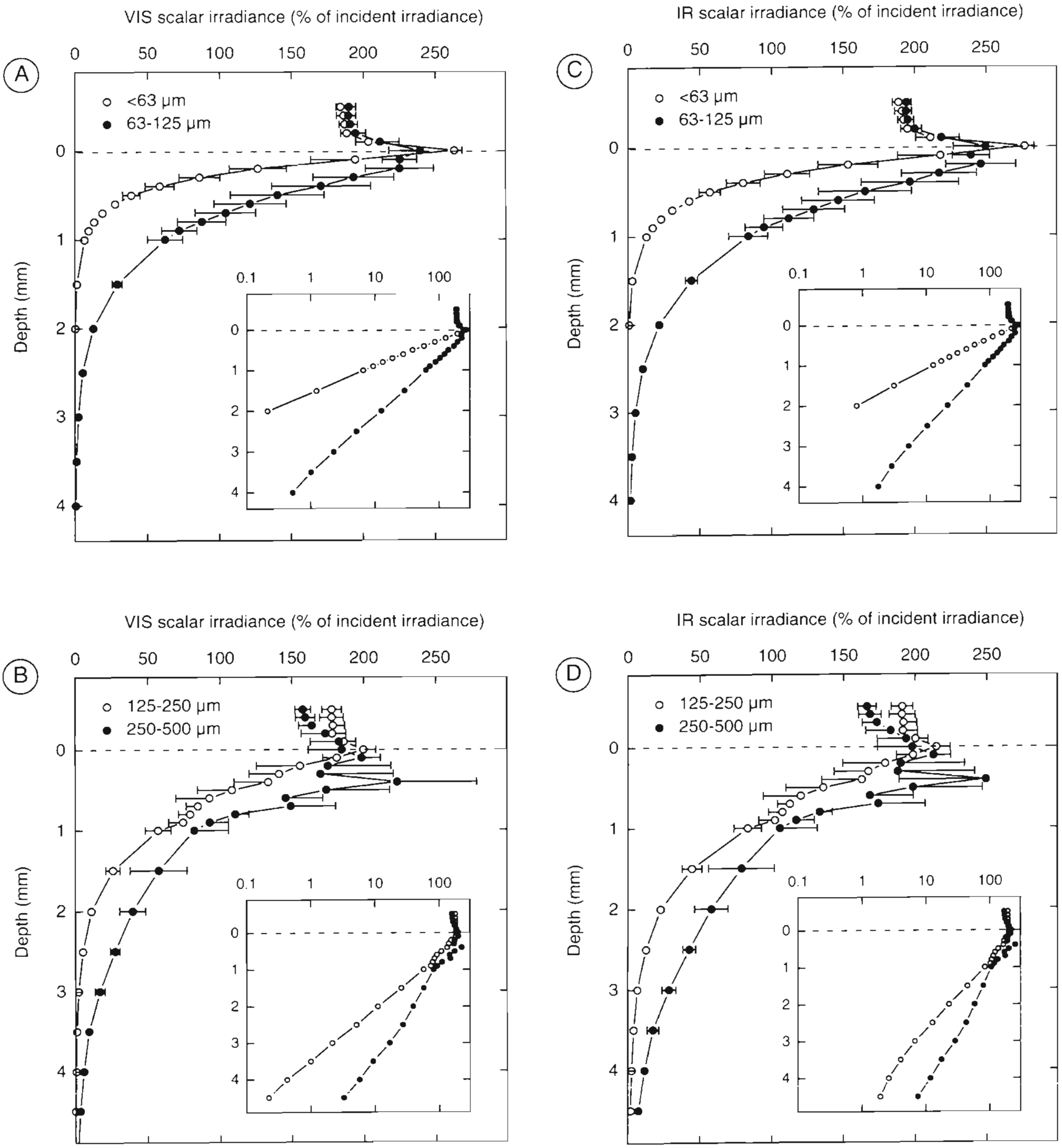

Fig. 3. Depth profiles of (A, B) VIS (400 to 700 nm) and (C, D) IR (700 to 880 nm) scalar irradiance in wet quartz sand of different particle size. Light intensities are expressed as % of incident collimated light at the sediment surface [E_{0d}(surface) = E_d(surface)]. Error bars indicate the standard deviation and data points represent the arithmetic mean of 3 to 5 measurements

The spectral attenuation of scalar irradiance in sediments of different grain size is shown in Fig. 4. In all sediments, 450 to 500 nm light was attenuated most strongly, and the attenuation coefficients decreased continuously towards longer wavelengths, with IR light exhibiting the lowest attenuation. This spectral variation in attenuation coefficient was most pronounced in the <63 µm grain size sediment and gradually decreased in the coarser sediments.

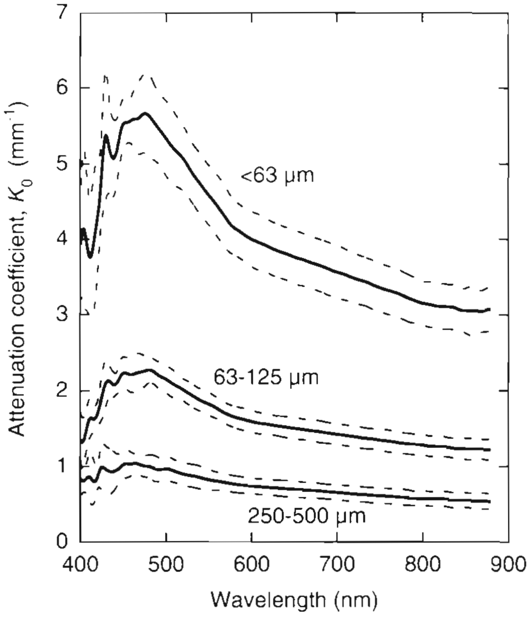

Fig. 4. Attenuation spectra of scalar irradiance, E_0, in quartz sand of 3 different particle sizes. The spectra represent the mean of 3 to 5 measurements (continuous lines) ± SD (dotted lines)

DISCUSSION

Heterogeneity of the light field

Light measurements with fiber-optic microprobes have the advantage of high spatial resolution, enabling the characterisation of the light field on the same scale at which microbenthic photosynthesis can be quantified by microelectrodes (Revsbech & Jørgensen 1983). This, however, results in inherent problems with heterogeneous sediment structure, which makes repetitive measurements necessary. Thus, due to the small size of the fiber probes, measurements at the sediment surface depend on the sediment structure and microtopography, and the measurement resolution cannot be much better than half the average grain size of the sediment. The depth profiles of irradiance and scalar irradiance presented in this study exhibited the highest variability, i.e. the highest standard deviation, in the upper mm of the sediment (Figs. 2 & 3). In this near-surface layer interactions with individual sand grains, for example the presence of a transparent (quartz) or a coloured (e.g. felspar) sand grain at the probe tip, can cause large variations in the detected light intensity. There may also be a slight physical disturbance of the sediment due to penetration by the fiber probe. The described effects were most pronounced in the coarsest sediment, which exhibited a relative standard deviation of scalar irradiance of ±20 to 25% near the surface. The relative standard deviations of the measured light intensities near the sediment surface decreased with particle size and were ±15% in the finest sediment. In deeper sediment layers the standard deviation was generally lower as the intense scattering of light smoothed out effects of near-surface heterogeneities in the light field.

Sediment optics

We found surface maxima of photon scalar irradiance ranging from 180% of incident irradiance in the coarsest sediment (250 to 500 µm grain size) up to 280% in the finest sediments (<63 µm grain size) where scattering was most intense (Fig. 3). Although the measurements in pure sand represent an extreme situation, with high scattering intensity and little absorption, similar scalar irradiance maxima have also been calculated from measured radiance distributions or have been measured directly in microbial mats and biofilms (e.g. Jørgensen & Des Marais 1988, Lassen et al. 1992b, Kühl 1993, Kühl & Jørgensen 1994) as well as in plant and animal tissue (e.g. Vogelmann & Björn 1984, Star et al. 1987, Profio 1989). A near-surface maximum of scalar irradiance thus seems to be an inherent property of compact light-scattering media in which multiple scattering is important for the radiative transfer.

Although a build-up of light intensity to >100 to 200% of incident light intuitively may appear to be in conflict with the laws of thermodynamics, this phenomenon can be explained by the internal reflection and refraction properties of scattering media (e.g. Vogelmann & Björn 1986, Kaufmann & Hartmann 1988, Anderson et al. 1989). Light attenuation in sediments is due to both absorption and multiple scattering, where scattering enhances the probability of absorption. If absorption is low, however, strong scattering maintains a high flux density at a given depth in the sediment (i.e. light is travelling a longer distance per vertical distance traversed). This effect of multiple scattering is especially enhanced near optical boundaries, e.g. the sediment-water interface or interfaces between different layers in a sediment, where differences in refractive index could result in internal reflection at the boundaries. This results in apparent light trapping phenomena such as the local maximum of light intensity relative to the incident light from above. A more detailed discussion of the optical mechanisms behind the observed scalar irradiance maximum can be found elsewhere (e.g. Vogelmann & Björn 1986, Kaufmann & Hartmann 1988, Anderson et al. 1989, Seyfried 1989, Kühl & Jørgensen 1994).

In the investigated sandy sediments, scattering predominated and resulted in a significant amount of upwelling light as seen from the depth profiles of upwelling irradiance (Fig. 2). The sediments exhibited a high irradiance reflectance of 20 to 40 %. In dry sand a higher irradiance reflectance was found than in wet sand, accompanied by a stronger light attenuation in dry sand (Table 2). Similar results were obtained by calculating irradiance reflectance from measured radiance distributions in the same type of sediment (Kühl & Jørgensen 1994). A higher reflectance and light attenuation in dry versus wet sand is due to a change in the scattering properties of the sand particles upon wetting (Bohren 1983, Twomey et al. 1986). Light scattering in sand becomes more forward-directed, and light thus penetrates deeper when the difference in refractive index between the quartz particles and the surrounding medium is lowered by wetting. Light must therefore travel a longer distance, i.e. be scattered more times, before being redirected towards the surface (Bohren 1983). Increasing the light path does, however, also increase the probability of absorption of upwelling light, thus resulting in a lower reflectance of wet sediments.

Measurements of spectral irradiance reflectance, R, can be used to describe the spectral scalar irradiance at the sediment surface from measurements of spectral downwelling irradiance. Kühl & Jørgensen (1994) found a good approximation to measured scalar irradiance values for single wavelengths, λ, at the sediment surface, z_0, by using the simple model of Anderson et al. (1989):

$$E_0(z_0,\lambda) = E_d(z_0,\lambda)\,[1 + 2R(z_0,\lambda)] \qquad (3)$$

Surface photon scalar irradiance for VIS and IR light calculated by Eq. (3) from the measured irradiances in this study was 150 % and 156 % of downwelling irradiance in wet quartz sand, while directly measured values reached 200 % and 215 % of downwelling VIS and IR irradiance, respectively. The use of Eq. (3) for integral measurements of VIS and IR light is thus inappropriate as it does not take the spectral variation of light attenuation within the VIS and IR range into account.

The strong light attenuation in sediments is the combined result of absorption and multiple scattering of light. Near the sediment surface the light field is highly anisotropic and consists mainly of collimated light from above and diffuse scattered light from below (Kühl & Jørgensen 1994). With increasing depth in the sediment, the collimated light is scattered, and the light field thus becomes more diffuse and can finally approach an asymptotic state, where the spatial light distribution no longer changes with depth and the attenuation coefficents of radiance, irradiance, and scalar irradiance thus become identical. The depth profiles of irradiance and scalar irradiance presented in this study confirm these fundamental properties of the light field, which have also been determined from measured radiance distributions in similar sediments (see Kühl & Jørgensen 1994). The near-surface zone, where the anisotropic light field changes with depth, had a thickness of <1 mm in sand of 125 to 250 µm particle size. Below this depth the attenuation coefficients of photon irradiance and photon scalar irradiance became almost identical (Fig. 2, Table 2) indicating a diffuse and near-asymptotic light field.

An increasing scattering intensity with decreasing sediment particle size resulted in a higher attenuation of light in the fine grained sediments (Figs. 3 & 4, Table 3). At the same time, however, the increased scattering intensity resulted in a higher surface maximum of scalar irradiance and a narrower anisotropic zone in the fine grained sediments (Fig. 3). Light attenuation in the sediments was generally highest for blue light, probably due to the presence of iron oxides and coloured sand grains in the sediments (Fig. 4). The spectral variation in the attenuation of scalar irradiance was most pronounced in the fine grained sediment, although the absorption was expected to be more or less independent of particle size (Fig. 4). With decreasing particle size the scattering intensity is increased, resulting in a longer pathlength travelled by the photons in order to penetrate a certain vertical distance into the sediment. Photons are thus scattered more times and, as there is a given probability for absorption at each encounter with a sediment particle, the overall result is a higher attenuation of light even though the absorption properties of the sediment have not changed. This mechanism will be most pronounced at wavelengths which are absorbed most strongly by the sediment. Increased multiple scattering thus tends to amplify relatively small spectral variations of absorption in sandy sediments.

Measurement of light intensity in sediments

This study presents the first comparison of direct microscale measurements of irradiance and scalar irradiance in sediments. The results demonstrate the importance of choosing the correct light parameter in studies of benthic photobiology. Measurements of downwelling photon irradiance, which is the most commonly measured light parameter in benthic studies, can underestimate the total light intensity, i.e. the scalar irradiance, in the sediment by >100 %, for both visible and infrared light. Although this represents an extreme value measured in scattering sand with little absorption, similar results have been obtained in other sediments or biofilms exhibiting much higher light absorption. Visible photon scalar irradiance measurements in coastal sediments covered by cyanobacteria or diatoms showed a maximum light intensity of 120 to 130 % of incident irradiance at the mat surface (Lassen et al. 1992b). In a laminated coastal sandy sediment (*'Farbstreifensandwatt'*; Stal et al. 1985), visible photon scalar irradiance was higher than incident irradiance in the upper 0.4 mm of the sediment, with a surface maximum of 120 % of incident irradiance (Kühl & Jørgensen 1992). Even in a very dense cyanobacterial biofilm without significant amounts of light-scattering mineral particles, photon scalar irradiance was 120 % of the incident downwelling irradiance at the biofilm surface (Kühl 1993) The values mentioned represent integral light intensities for 400 to 700 nm light, i.e. VIS photon scalar irradiance. Spectral scalar irradiance measurements have shown even higher maxima ranging from 120 % for blue light to >200 % for IR light in coastal marine sediments and microbial mats (Kühl & Jørgensen 1992, Lassen et al. 1992b). Therefore, in detailed studies of the regulatory role of light for microbenthic photosynthesis, measurements of scalar irradiance at high spatial resolution are essential. The photosynthetic performance of the microphytobenthos should thus be related to the scalar irradiance when measuring light saturation curves (P-I curves) or action spectra of photosynthesis (Jørgensen et al. 1987, Ploug et al. 1993).

In conclusion, the use of the fiber-optic microprobes described here, in combination with oxygen microelectrodes, now makes it possible to investigate sediment optics, microbenthic photosynthesis, and the photophysiology of benthic photosynthetic microorganisms at a level comparable to that of aquatic optics and plankton research.

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