Gross growth efficiency For a given organism, the efficiency of conversion of carbon intake into new carbon growth.

Heterotrophs Organisms that utilize organic sources of carbon (particulate or dissolved) for metabolic synthesis.

Microplankton Planktonic organisms in the size range 20–200 μm; includes single-celled as well as multicellular organisms.

Mixotrophic Organisms with a mixed mode of nutrition, typically combining the ability to derive significant nutrition from photosynthesis as well as feeding directly on other organisms (or dissolved substrates).

Nanoplankton Planktonic singled-celled organisms in the size range 2–20 μm.

Oligotrophic System characterized by low concentrations of nutrients and plankton biomass.

Picoplankton Planktonic singled-celled organisms in the size range 0.2–2 μm.

See also

Bacterioplankton. Photochemical Processes. Phytoplankton Blooms. Primary Production Distribution. Primary Production Methods. Primary Production Processes.

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MICROPHYTOBENTHOS

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Introduction

Microphytobenthos is a descriptive term for the diverse assemblages of photosynthetic diatoms, cyanobacteria, flagellates, and green algae that inhabit the surface layer of sediments in marine systems. Microphytobenthos occur wherever light penetrates to the sediment's surface, and are abundant on intertidal mud and sandflats and in shallow subtidal regions. Microphytobenthic primary production may be high, matching that of phytoplankton in the overlying water column, yet this activity is compressed into a biofilm only a few millimeters thick. The relationship between irradiance and rates of microphytobenthic photosynthesis is fairly well understood, but new methods are revealing fine-scale effects of microspatial distribution within the vertical light profile and migration of cells throughout the diel illumination period. Patterns of biomass distribution and seasonal and spatial changes in species composition are well described, but studies differ on the relative importance of the factors influencing microphytobenthic biomass (irradiance, resuspension, nutrients, grazing, exposure, desiccation, etc.). Microphytobenthic biofilms play an important role in mediating the exchange of nutrients across the sediment–water interface, and microphytobenthos both stimulate and compete with various bacterial sediment processes. The presence of biofilms rich in extracellular polysaccharides alters the erosional properties of sediments, termed biostabilization.

Types of Microphytobenthos

Sediment properties play a major role in determining the type of microphytobenthic assemblage present in a particular environment. Sediments consisting of fine silts and clays (less that 63 μm) are termed cohesive sediments. The fine nature of such material and the lack of suitable attachment points result in assemblages dominated by motile micro-

Table 1 Genera of photoautotrophs commonly found in microphytobenthic communities

Algal group	*Epipelic*	*Epipsammic*
Cyanobacteria	*Oscillatoria*	*Oscillatoria* *Microcoleus* *Spirulina*
Bacillariophyta	*Navicula* *Amphora* *Fallacia* *Staurophora* *Gyrosigma* *Pleurosigma* *Nitzschia* *Diploneis* *Cylindrotheca*	*Opephora* *Raphoneis* *Achnanthes* *Cocconeis* *Fragilaria* *Navicula* *Nitzschia* *Amphora*
Euglenophyta	*Euglena*	*Euglena*
Chlorophyta		Many

phytobenthic species. These are termed 'epipelic' biofilms (epipelic: living on mud), and the microphytobenthos are sometimes termed 'epipelon.' Sediments consisting of larger particles, silty sands, and sands are noncohesive, with greater pore space, and are generally more often disturbed. Growing attached to individual sand and silt particles are found 'epipsammic' taxa (epipsammic: living on sand). Epispammic assemblages usually contain a substantial proportion of epipelic taxa as well.

Epipelic biofilms The commonest epipelic microphytobenthos are biraphid diatoms, with the genera *Navicula*, *Gyrosigma*, *Nitzschia* and *Diploneis* usually well represented (**Table 1**). In fine sediment habitats, light penetration is very limited and, in order to photosynthesize, cells need to be able to position themselves at the sediment surface. Biraphid diatoms move by excreting extracellular polymeric substances (EPS) from the raphe slit present in each of the silica cell walls (valves) that make up the cell. Cyanobacterial filaments move by gliding and nonflagellated euglenids move by amoeboid movement. In dense biofilms of epipelic diatoms, the concentrations of EPS can become high (200–300 $\mu g\,g^{-1}$ dry weight of sediment), providing a carbon source to the sediment system. High concentration of EPS can increase the force needed to erode sediments, termed 'biostabilization.' Epipelic biofilms can be very extensive on intertidal estuarine mudflats, where they can contribute up to 50% of estuarine carbon budgets.

Epipsammic assemblages The 'epipsammon' are generally nonmotile, or only partially mobile. Diatoms are the major constituents, with araphid and monoraphid genera common (e.g., *Opephora*, *Achnanthes*, *Amphora*, and *Cocconeis*) (**Table 1**).

Table 2 Daily and annual rates of primary production for epipelic and epipsammic microphytobenthos from a number of different habitats.

Site	*Daily production* ($mg\,C\,m^{-2}\,d^{-1}$)	*Annual production* ($g\,C\,m^{-2}\,a^{-1}$)
Epipelon		
Ems-Dollard, Netherlands[a]	600–1370	62–276
Tagus Estuary, Portugal[b]	5–32 (h^{-1})	47–178
North Inlet, SC, USA[c]	–	56–234
Langebaan Lagoon, South Africa[d]	17–69	253 (mud)
Epipsammon		
Langebaan Lagoon, South Africa[d]	17–69	63 (sand)
Laholm Bay, Sweden[e]	10–200	0.3–20
Ria de Arosa, Spain[f]	–	54
Weeks Bay, AL, USA[g]	10–750	90.1

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Epipsammic cells attach themselves to sand particles by a pad or short stalk of EPS, though many cells are also capable of movement. Filamentous and colonial cyanobacteria (*Oscillatoria*, *Microcoleus*), coccal green algae and motile flagellates and chlorophytes are common in epipsammic assemblages. Thus epipsammic assemblages often have a greater taxonomic diversity (at the level of algal groups). Light penetration is greater into sandy sediments, which are also disturbed by tidal and wind-induced currents. Cells are therefore frequently mixed within the sediment photic zone, and the requirement for motility is less. Indeed, in highly mixed systems, nonattached, motile taxa may be absent, and only attached species are found, often within depressions present on the surface of sand grains, where they receive protection from abrasion.

Primary Production

Photosynthesis

Microphytobenthos are photoautotrophic organisms. Hourly rates of primary production are high, with annual primary production ranging between 0.3 and 234 $g\,C\,m^{-2}\,a^{-1}$ (**Table 2**). Different tech-

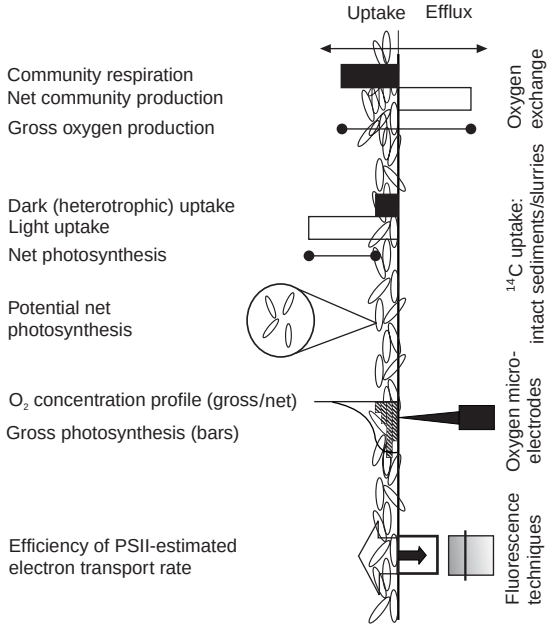

Figure 1 Techniques used to determine microphytobenthic primary production measure different aspects of photosynthesis in microphytobenthic biofilms, and have varying scales of vertical and horizontal resolution. Thus comparison of data needs to be made with care. PSII, photosystem II.

niques are used to measure microphytobenthic primary production: (1) oxygen exchange across the sediment–water interface; (2) (^{14}C)bicarbonate uptake in intact biofilms; (3) (^{14}C)bicarbonate uptake in slurries; (4) oxygen production within biofilms using oxygen microelectrodes; and more recently (5) modulated chlorophyll *a* fluorescence techniques (**Figure 1**). These techniques all measure slightly different aspects of photosynthesis, making intercomparisons difficult.

Oxygen exchange measurements on intact biofilms measure net community production, and if the oxygen uptake rate (negative) in the dark is subtracted from the net community production, then a measure of gross oxygen production is obtained (assuming that respiration in the light and dark do not differ). (^{14}C)Bicarbonate uptake into intact biofilms measures net photosynthesis, and tends to underestimate carbon fixation rates as it is not possible to measure accurately the specific ^{14}C activity within the thin photosynthetically active layer. In noncohesive sediments, percolation of sea water of known specific ^{14}C activity into the biofilm through the application of a slight vacuum to the bottom of a sediment core results in higher estimates of carbon fixation. Percolation techniques cannot be used with cohesive sediments. Oxygen exchange and ^{14}C methods require the microphytobenthic community to be submerged and this may underestimate intertidal primary production, where the majority of the photosynthesis occurs during low tide exposure. ^{14}C slurry techniques are a rapid method for measuring photosynthetic parameters, with photosynthesis versus light curves generated in a 'photosynthetron.' However, existing microgradients in the sediment are destroyed in slurries, and this technique therefore measures maximum potential primary production, in the absence of structure within the biofilm.

Oxygen microelectrodes measure gross primary production rates at small-scale (100–200 μm) depth intervals down a profile into the sediment. Construction of complete photosynthesis profile curves is time-consuming; the time taken to generate sufficient replicate production profiles is greater than some of the temporal properties of the biofilm (e.g., endogenous vertical migration). To avoid this, production rates can be calculated from the profile of oxygen concentration with depth under a fixed irradiance, assuming diffusion and porosity coefficients. Net oxygen production can be calculated from the slope in oxygen concentrations out of the sediment, but with exposed sediments this can be problematic. Significant amounts of variation in oxygen production profiles can be due to patchiness in the distribution of microphytobenthic biomass. Oxygen microelectrodes are an important tool for measuring the microspatial distribution of photosynthesis within sediments and response of photosynthesis to environmental variation, but scaling-up of these measurements to larger areal rates is contentious.

Variable fluorescent techniques measure the activity of the photosystem II (PSII) reaction centre, thus providing an estimate of the rate of production of electrons by the water-splitting system of PSII (electron transport rate). Being noninvasive, fluorescence techniques can be used to rapidly and repeatedly measure *in situ* activity. As oxygen is a product of the water-splitting process, there is a relationship between oxygen production and PSII electron transport rate (ETR), and also reasonable linearity between ^{14}C-fixation rates and ETR, especially in sediment slurries. Thus fluorescence techniques can provide an indirect (but nondestructive and rapid) measurement of microphytobenthic primary production. However, the relationship between ETR and oxygen evolution or ^{14}C fixation can become nonlinear at high irradiances, and vertical migration of cells within the biofilm can complicate the interpretation of results. Variable fluorescence measurements can also be made on single cells, using a modified fluorescence microscope and image analysis techniques, allowing the photosynthetic response of single cells within a mixed population to be measured in undisturbed biofilms (**Figure 2**).

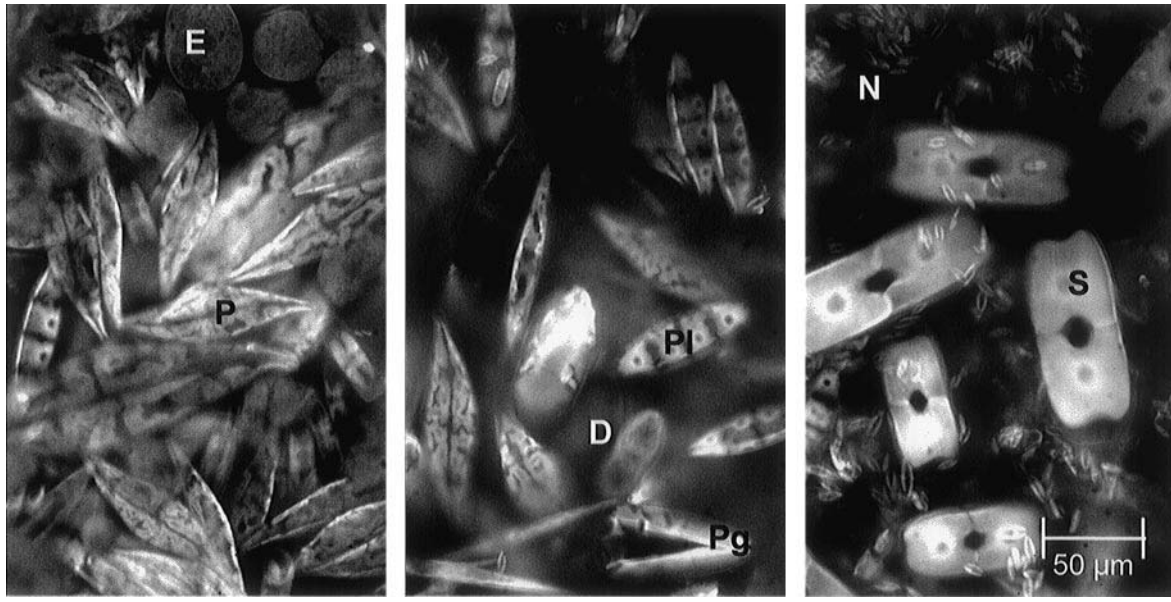

Figure 2 Fluorescence images of intact epipelic microphytobenthic biofilms, showing patchiness at a microscale in cell distribution, and differences in cell size (E = *Euglena* sp.; P = *Pleurosigma angulatum*; P1 = *Plagiotropis vitrea*; D = *Diploneis didyma*; Pg = *Petrodictyon gemma*; S = *Staurophora* sp.; N = small *Navicula* species). Fluorescence imaging techniques can calculate the photosynthetic efficiency of individual cells within the biofilm, allowing taxonomic differences to be determined. (Images courtesy of ARM Hanlon, University of Essex.)

Light Penetration and Photosynthesis

There are substantial spatial and temporal gradients in light availability in microphytobenthic habitats. Irradiance can exceed 2000 μmol photons $m^{-2} s^{-1}$ on exposed intertidal sediments, while in clear shallow water sufficient light can penetrate to depths of 20–30 m, permitting microphytobenthic growth. Steep gradients of irradiance occur within sediments, where the attenuation of light is rapid (attenuation coefficients (k) between 1 and 3.5 mm^{-1} for sandy and cohesive sediments, respectively). Thus the euphotic zone depth in sediments (1% of incident light) is usually much less than 1 cm (less than 2 mm in cohesive muddy sediments) (**Figure 3**). Light intensity just beneath the sediment surface, particularly at wavelengths > 700 nm can be greater than the incident light, owing to backscatter effects within the sediment. The spectral quality of light also changes within sediments and is further modified by increased light attenuation of specific wavelengths (particularly blue and red) due to absorption by microalgal photopigments.

There is a fairly clear relationship between biomass-normalized primary production (μg C (μg Chl*a*)$^{-1}$ h^{-1}, termed P^B) and irradiance in microphytobenthic systems, up to saturating irradiances (P^B_{max}). Irradiance accounts for between 30% and 60% of the variability in primary production, and biomass explains another 30–40%. Within cohesive sediments the majority of photosynthesis occurs within the top 200–400 μm of the sediment. In sandy sediments, where light penetration is greater, gross photosynthesis can occur deeper than this (up to 2 mm) (**Figure 3**) and may even show a biomodal distribution owing to distinct vertical separation of diatoms and cyanobacterial layers. Isolated microphytobenthos (i.e., in slurries, lens tissue preparations or cultures) reach P^B_{max} at light intensities between 100 and 800 μmol photons $m^{-2} s^{-1}$ and show photoinhibition of P^B at higher light intensities. Depth-integrated rates of sediment photosynthesis obtained from *in situ* oxygen microelectrode measurements saturate at higher irradiances than slurries and show little or no evidence of photoinhibition. In undisturbed sediments, the peak of gross oxygen production occurs deeper in the sediment at high light intensities (> 1200 μmol photons $m^{-2} s^{-1}$) than at lower light intensities, mainly because of migration of the bulk of the microalgal population down into the sediment away from high surface irradiance. Microphytobenthos are sensitive to light intensity and UVB radiation, with surface biomass varying with irradiance. Some subtidal assemblages are shade-adapted and migrate down into the sediment at midday to avoid high light levels. Taxonomic differences occur with regard to positioning with the light field. The euglenophyte *Euglena deses* commonly occurs on intertidal flats and at high irradiance occurs on the surface of

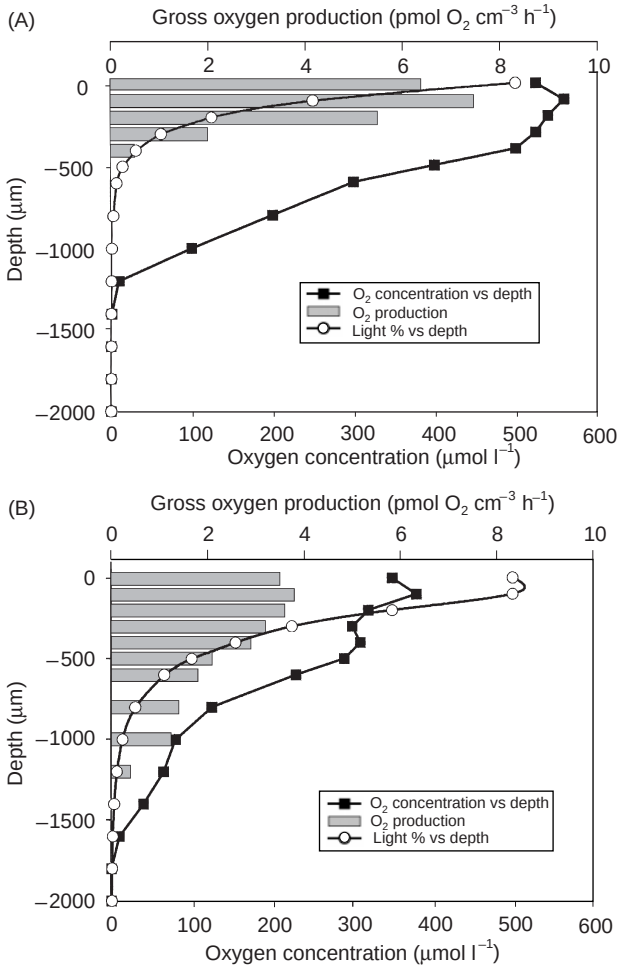

Figure 3 Typical oxygen concentration profiles and rates of gross oxygen production in an epipelic (A) and epipsammic (B) microphytobenthic biofilm. Light attenuation is less steep in sandier sediments, and thus oxygen production occurs to a greater depth.

sediments, with epipelic diatoms underneath. Mixed assemblages of filamentous cyanobacteria and epipelic diatoms also show vertical positioning, with cyanobacteria positioned beneath the diatom layer. The ability of cells to migrate away from high irradiance allows microphytobenthos to respond to the light climate and position themselves at optimal irradiances.

Vertical migration Following disturbance and/or deposition of fresh sediment, microphytobenthos need to reposition themselves back within the euphotic zone to photosynthesize. In many intertidal habitats the microphytobenthos exhibit endogenous rhythms of vertical migration, with migration remaining in synchrony with the daily shift of the tidal cycle within the diel light frame. These endogenous rhythms can be maintained for between 3 and 4 days in the absence of any light or tidal stimuli. Intertidal sites are also subject to varying patterns of diel illumination periods. The shifting pattern of tidal exposure (≈ 55 min per day) within diel light curves, and the fortnightly cycle of spring and neap tides can result in periods when microphytobenthos are exposed to very high irradiance during low tide at solar noon (exceeding 2000 μmol photons $m^{-2} s^{-1}$) and at other times (several days for some regions of the intertidal) when little or no light reaches the sediment surface. Thus cells need to be able to cope with periods of darkness, when they rely on intracellular carbon storage compounds (glucans) as an energy source.

Temperature effects on microphytobenthic photosynthesis The temperature of a mudflat can change rapidly during a tidal emersion period, at up to 2–3°C h^{-1}, with daily ranges of 20°C and seasonal ranges between 0 and 35°C. There is a clear relationship between P^{B}_{max} and temperature, with an optimal temperature for intertidal diatoms of 25°C, while at temperatures above 25°C there can be significant inhibition (30%) of microphytobenthic photosynthesis, particularly on upper shore intertidal regions. This can lead to reductions of biomass on upper shores.

Extracellular Polysaccharide (EPS) Production and Sediment Biostabilization

Epipelic and epipsammic diatoms produce EPS either during motility or as an attachment structure. Microphytobenthos also excrete surplus photoassimilated carbon as carbohydrates when they are nutrient limited and subject to high irradiance. In diatom-rich biofilms, between 20% and 40% of the extracellular carbohydrate material present is polymeric, i.e., EPS. The remainder consists of nonpolymeric material, mainly simple sugars, leachates, and other photoassimilates. These low molecular weight exudates are rapidly utilized by bacteria, and may play a significant role in the ecology of cohesive sediments by providing bacteria with a readily available carbon source. Carbohydrate concentrations in sediments are much more a function of the epipelic rather than epipsammic (attached) diatom biomass, and within more mixed assemblages of photosynthetic microorganisms (cyanobacterial mats, high-saltmarsh algal assemblages), the close relationship between colloidal carbohydrate and chlorophyll *a* concentrations present in diatom-dominated sediments is not present.

In epipelic diatoms, production of EPS requires between 0.1% and 16% of photosynthetically fixed

carbon. EPS is produced both during illuminated and darkened periods. In conditions of darkness, the relative amounts of EPS produced increase, possibly linked to increased cellular motility. Extrusion of EPS by pennate diatoms is an active metabolic process, as vesicles filled with polymeric material are transported from the Golgi body to the raphe. Motility is generated by the extrusion of polymers through the cell membrane within the raphe, and the polymer strand is moved along the raphe by actin fibres. In dark conditions, internal storage carbohydrates (glucans) are metabolized to provide the carbon and energy sources needed to produce EPS.

These mechanisms provide a route for the production of extracellular carbohydrate material into the surrounding sediments. The EPS produced by microphytobenthos diatoms binds together sediment particles and can form smooth surface layers. The binding strength of exopolymers varies with chemical composition and the degree of cross-linkage; and as polymers dehydrate during tidal exposure, their binding strength increases. Thus during tidal exposure there is an increase in concentrations (due to diatom photosynthesis and motility) and a reduction in sediment water content. This can significantly increase the critical shear required for sediment erosion (by up to 300%) when the tide covers the site. In epipsammic biofilms, sand particles can be stuck together by pads and fibers of EPS, as well as by filaments of cyanobacteria. These processes all result in biostabilization, and the presence of microphytobenthos significantly changes the sedimentological properties of their habitat.

Distribution and Biomass

Small-scale Heterogeneity in Microphytobenthos

Microphytobenthos show a high degree of spatial heterogeneity in biomass and species composition. This patchiness occurs on a scale of micrometers to many tens of meters. There are also patterns of vertical distribution within sediments, with the bulk of the active biomass (determined as chlorophyll *a*) found within the top few millimeters of cohesive sediments, and the top centimeter of sandy sediments. However, viable cells and chlorophyll *a* can be isolated from deeper layers, up to 10–15 cm. Given the shallow photic depth in most sediments, only the algae in the uppermost depths of the sediments will be photosynthetically active. Yet many microphytobenthos can survive prolonged periods (2–3 weeks) of darkness, and there is some limited evidence of heterotrophy. Thus buried cells may, if mixed back to the surface, resume photosynthesis.

Large-scale Heterogeneity

Sediment type is a major determining factor in the abundance and biomass of microphytobenthos. Sandy silts and sands support significantly lower concentrations of microalgal biomass than sites with fine cohesive sediments (chlorophyll *a* concentrations ranging from 1 to 560 $\mathrm{mg\,m^{-2}}$ or 0.1–460 $\mu\mathrm{g\,g^{-1}}$ sediment). As sediment grain size increases, the proportion of epipelic, motile taxa decreases and microphytobenthic assemblages in intertidal sands consist predominantly of smaller epipsammic taxa. Sands tend to have lower nutrient concentrations and are more frequently resuspended than are cohesive sediments, and all of these characteristics contribute toward lower microphytobenthic biomass.

On intertidal mudflats, microphytobenthic biomass tends to be greater toward the upper shore. Lower shore sediments have a higher water content and are less stable than sediments at the middle and upper shore, partly owing to the energy of tidal flow and regular resuspension of sediments. Periods of illuminated exposure are shorter on the low intertidal where light penetration is restricted by highly turbid estuarine waters. Thus low shore microphytobenthos are probably light limited (in terms of available photoperiod per 24 h), while biomass accumulation is prevented by frequent disturbance. At higher tidal heights on a shore, the pattern of illuminated emersion periods and reduced resuspension contribute to create conditions favorable for epipelic microphytobenthos. However, upper shore stations are also subject to greater desiccation and temperature effects, the effect of which can be increased by long periods of exposure during neap tide periods. These factors usually result in a unimodal distribution of biomass across an intertidal flat, with the peak somewhere between mid-tide level and mean high water neap tide level, and not necessarily at the highest bathymetric level. In subtidal habitats, microphytobenthic biomass tends to decrease with increasing water depth owing to increasing light limitation. However, very shallow (< 1 m) sediments in exposed situations are more prone to mixing and disturbance due to wave action or tidal flows, and thus biomass decreases in such sites.

Temporal Variation

In temperate latitudes, increases in epipelic microphytobenthic biomass tend to occur during the summer months. However, peaks of biomass also occur frequently at other times of the year, and in many estuarine systems epipelic diatom assemblages are less seasonally influenced than are phytoplankton communities. High temporal variability in biomass

is a common feature of epipelic microphytobenthos, with biomass dependent on local environmental changes such as erosion and deposition events, desiccation linked to tidal exposure and weather conditions, and periods of rapid growth. Rapid doubling times (1–2 days) permit microphytobenthos to increase rapidly in density during favorable conditions. Subtidal microphytobenthos are not subjected to the extremes of exposure present on the intertidal, with irradiances ranging from very high during exposure to virtually nil during immersion in turbid overlying water. Subtidal microphytobenthos tends to show greater degrees of seasonality, with peaks of biomass and activity following the annual pattern of irradiance.

Response of Microphytobenthos to Nutrients

Nutrient Limitation

The potential for nutrient limitation of microphytobenthos depends in part on the sediment type concerned. Fine cohesive sediments usually have high organic matter contents, with high rates of bacterial mineralization and high porewater concentrations of dissolved nutrients, while sand flats are more oligotrophic. There is therefore an increased possibility that microphytobenthos inhabiting sediments of a larger grain size will be nutrient limited. The spatial distribution of sediments within estuaries is also pertinent to whether nutrient limitation will occur, in that many estuaries exhibit significant nutrient gradients along their length and areas of extensive mudflats supporting microphytobenthos may coincide with regions of high nutrient concentration.

There are few experimental data showing nutrient effects on intertidal microphytobenthos independently of other covarying factors that also affect primary production and biomass (shelter, salinity, etc.). Nutrient enrichment experiments on mudflats have found no consistent short-term pattern of increased photosynthesis or biomass, though long-term reductions (over 16 years) in nutrient inputs in estuaries have been shown to result in declines in biomass. In contrast, enrichment experiments in subtidal epipsammic microphytobenthos and cyanobacterial mats in nutrient-poor habitats have shown varying degrees of stimulation of microphytobenthic photosynthesis and biomass. It is generally considered that epipelic microalgae are not nutrient limited and that they obtained nutrients both from within the sediment, particularly during migration during tidal immersion, and from the overlying water. However, the term 'nutrient limitation' includes both Liebig-type limitation (on final biomass) and short term (Monod type) effects on rates of photosynthesis/growth. To what extent short-term nutrient dynamics within biofilms influence the rate of photosynthesis and growth of microphytobenthos is not known. As porewater concentrations of many nutrients (e.g., ammonium, phosphate) increase with depth within the sediment, cells exhibiting vertical migration may obtain nutrients when they have migrated away from the surface. Although this seems logically sound, there is as yet no experimental evidence to support this hypothesis.

The nutrient environment is important in determining species composition. Ammonium concentrations in sediments influence the distribution of diatom species in both saltmarshes and mudflats. Concentrations of ammonium between 500 and 1000 $\mu mol\,l^{-1}$ are selective for some taxa of microalgae, with the toxic effects of ammonia being enhanced in high pH conditions. Sediment organic content and tolerance to sulfide also influence the species composition of microalgal biofilms. Given the steep gradients in pH, oxygen and sulfide within fine cohesive sediments, these are likely to be impor-

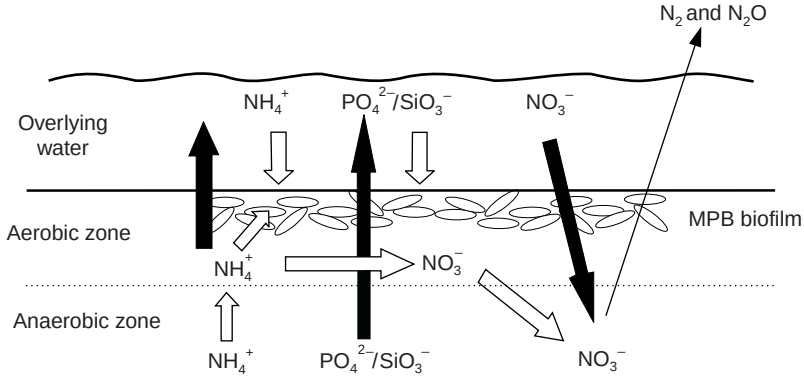

Figure 4 Interactions between microphytobenthos and nutrient fluxes across the sediment–water interface. Open arrows indicate fluxes/processes stimulated by the action of microphytobenthic primary production. Solid arrows represent processes reduced by microphytobenthic activity.

tant selective factors determining the species diversity of microphytobenthic assemblages.

Interaction between Microphytobenthos and Nutrient Cycling

The activity of microphytobenthos biofilms can significantly affect the fluxes of nutrients across the sediment–water interface (**Figure 4**). This is due to assimilation of nutrients by the algae from the overlying water and underlying porewaters, and to the high oxygen concentrations present in the surface sediments during photosynthesis. Photosynthetic production of oxygen increases the depth of the surface oxic layer, which increases the oxidation of vertically diffusing reduced molecules such as sulfide, ammonium, and phosphate. Thus the export fluxes of these compounds across the sediment–water interface can be significantly reduced compared to the fluxes under dark conditions (**Figure 4**). Assimilation by the algae of nutrients (ammonium, nitrite, nitrate, phosphate, CO_2, dissolved organic carbon) diffusing into the biofilm both from overlying water and from deeper layers within the sediments also alters the pattern of exchange fluxes. On intertidal mudflats, microphytobenthic biofilms develop an ammonium demand during periods of tidal exposure and photosynthesis that persists for up to 4 h after tidal cover.

Bacterial denitrification (the reduction of nitrate to nitrogen gas) is an important process in coastal sediments as it is the only mechanism by which nitrogen can be permanently removed from the marine environment. Microphytobenthos influence denitrification in a number of ways (**Figure 4**). The position of the microphytobenthos on the surface of the sediment allows them to assimilate nitrate from the overlying water column and reduce the amount diffusing into the sediment. Denitrification is an anaerobic process, and photosynthetic oxygen production increases the depth in the sediments at which it can occur, thereby increasing the diffusional path length for nitrate. By these processes, microphytobenthos reduce denitrification of nitrate from the water column. However, oxygen production can stimulate nitrification (production of nitrate from ammonium), and this nitrate can then be denitrified. Stimulation of this 'coupled nitrification–denitrification' pathway can be particularly significant, especially in low-nutrient environments. By these processes, microphytobenthos influence the nutrient dynamics of shallow water sediments (**Figure 4**). These processes will be affected by spatial and temporal (both diel and seasonal) differences in biofilm biomass, activity, and species composition. There is some evidence to suggest that differences in species composition effect the ability of biofilms to sequester C and N compounds from the overlying water.

See also

Benthic Boundary Layer Effects. Geomorphology. Marine Mats. Microbial Loops. Nitrogen Cycle. Phytobenthos. Primary Production Methods. Salt Marshes and Mud Flats. Sandy Beaches, Biology of.

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MICROPLATES

See **PROPAGATING RIFTS AND MICROPLATES**