Nitrogen Cycling in Coastal Marine Environments
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CHAPTER 4

Benthic Primary Production and Oxygen Profiles

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4.1 INTRODUCTION

The sediment surface at shallow localities is often inhabited by a dense population of photosynthetically active microorganisms utilizing the abundance of both light and nutrients occurring at the sediment–water interface. In a global budget the primary production carried out by benthic communities of microalgae may be of little quantitative importance, but the benthic microalgae are the main primary producers in many shallow areas.

The chemical microenvironment created by the benthic primary producers may have even more pronounced impacts on coastal ecosystems than the photosynthetic production of organic matter itself. The photosynthetic processes can result in large diurnal oscillations in oxygen concentration, pH, etc. near the sediment–water interface, and the impact of these often extreme chemical conditions on, for example, nitrification–denitrification is very significant.

In this chapter we will not try to give a comprehensive review of either the microelectrode methods, which have recently been reviewed elsewhere (Revsbech and Jørgensen, 1986), or of the experimental work on benthic photosynthesis conducted by others, which has also recently been reviewed (Admiraal, 1980; Sundbäck, 1983; Admiraal, 1984). We will instead show some new examples of how benthic photosynthesis can be studied by use of microelectrodes, and we will discuss the impact on the nitrogen cycle of the chemical microenvironment near the sediment surface. Finally we will discuss the factors limiting benthic primary production by microalgae.

4.2 THE CHEMICAL MICROENVIRONMENT AT THE SEDIMENT SURFACE

Until now, microelectrodes have been used to measure O_2, pH, and dissolved sulfide in sediments (Revsbech *et al.*, 1983; Revsbech and Ward, 1983).

No microelectrodes have been used to study profiles of nitrogen species (ammonium, nitrate or amino acids), and there are therefore no direct measurements of nitrogen cycling during photosynthesis. Macroelectrodes for ammonia and nitrate are, however, commercially available, and it might be possible to construct microelectrodes for these species. The production of O_2 in light is more obviously linked to carbon reduction than to nitrogen assimilation, but there is an obvious connection between C and N. This connection is reflected in the relatively constant C:N ratio observed in photosynthetic cell biomass. Rates for carbon assimilation (molar) may thus be converted to nitrogen assimilation by dividing by ~ 6. The oxygen microelectrodes have the smallest sensing tips, with diameters of 2–10 μm, and measurements of oxygen therefore have a very high spatial resolution. The spatial resolution of sulfide and pH measurements is only about 0.1 mm, but that suffices for most applications. The oxygen microelectrodes can be used to analyze for photosynthetic activity (Revsbech *et al.*, 1981) by measuring the decrease in oxygen concentration at each particular depth after darkening. The spatial resolution of the photosynthesis measurements is about 0.1 mm when the rate of decrease after 1 s in the dark is used to calculate the photosynthetic rate (Revsbech and Jørgensen, 1983).

Examples of microprofiles of oxygen, pH, and oxygenic photosynthetic activity in two sediments are shown in Figure 4.1. The sediments had been illuminated for 2 hours before the measurements were performed, and the presented profiles thus represent a close to steady-state condition. The data presented in Figure 4.1a were measured in an extremely active cyanobacterial film living on top of an organic-rich sediment. The sediment contained an abundance of decaying eelgrass, and the flux of dissolved organic and inorganic species (especially sulfide) to the sediment surface must have been very high. The photosynthetically active zone was only 0.4 mm thick, but the photosynthetic rate in the most active layer was as high as 98 mmol $O_2\,dm^{-3}\,h^{-1}$. Rates of up to 200 mmol $O_2\,dm^{-3}\,h^{-1}$ have been measured in other cyanobacterial films, corresponding to a production rate of oxygen per hour equaling 800 times the pool size at air equilibrium. The total photosynthetic activity integrated over all layers was 27 mmol $O_2\,m^{-2}\,h^{-1}$. The photosynthesis resulted in an oxygen concentration of 1420 μM in the most active layer, 0.1 mm below the sediment surface. This oxygen concentration was 5.6 times atmospheric saturation, corresponding to a partial pressure of 1.15 atmospheres. Such oversaturations with oxygen have often been observed in photosynthetically active sediments. Spontaneous bubble formation, by gases such as Ar, N_2, and O_2 dissolved in pure water, occurs only at partial pressures of more than 100 atmospheres (Hemmingsen, 1977), so moderate oversaturation in layers where oxygen is continuously being produced is not surprising. The oxygen concentration decreased sharply at both sides of the photosynthetically active layer. A linear oxygen gradient just above the sediment surface indicated a true diffusive boundary layer (Jørgensen and Revsbech, 1985) ~ 0.25 mm thick, and a vertical oxygen profile indicated that efficient mixing of

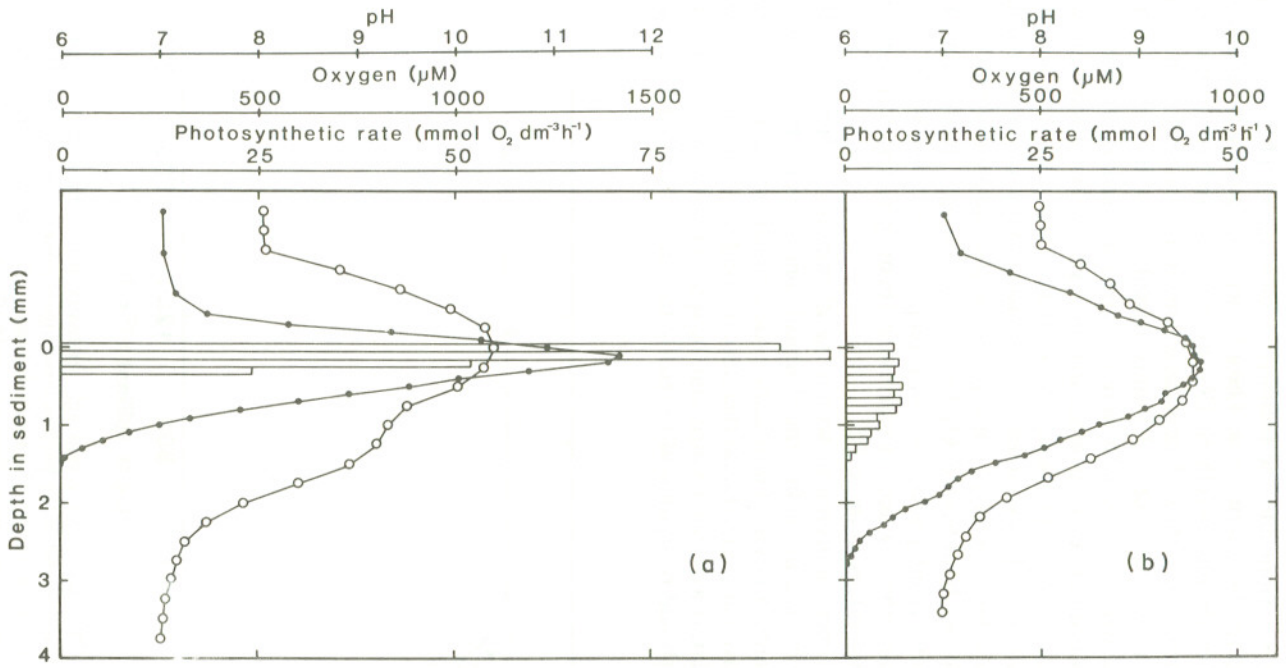

Figure 4.1. Vertical profiles of photosynthetic activity (bars), O_2 (filled circles) and pH (open circles) in an organic-rich, fine grained sediment (a) and in a sandy sediment (b). The sediment was illuminated by a halogen lamp (slide projector), and the light intensity was 1000 μEinst $m^{-2} s^{-1}$ (400–700 nm range) at the sediment surface. The temperature of the water was 16 °C. There was only gentle stirring of the water above the sediment surface. The oxygen profile was recorded in the same position as the profile of photosynthetic activity, but the pH profile may not be from exactly the same place

the overlying water occurred ~1 mm above the sediment surface. Oxygen penetrated only ~1.5 mm into the sediment, indicating a high rate of oxygen consumption below the photic zone. The pH near the sediment surface was severely affected by the photosynthetic CO_2 assimilation, and a maximum value of pH 10.4 was measured at the surface of the sediment. The value at 3.5 mm depth was only 7.1, so a pH difference of 3.3 units existed over a distance of 3.5 mm.

The data presented in Figure 4.1b were measured in a sediment from a tidal sandflat which was inhabited by pennate diatoms. The sediment was typical for many shallow marine areas, and the data presented can thus also be considered to be typical for such areas. This sediment had a considerably lower photosynthetic activity than the sediment analyzed in Figure 4.1a, and the photosynthetic rates were rather uniform, about 6 mmol $O_2\,dm^{-3}\,h^{-1}$ in the uppermost 1 mm of the sediment. The activity integrated over all layers (0–1.5 mm depth) was 7 mmol $O_2\,m^{-2}\,h^{-1}$. This rather low activity still resulted in oxygen concentrations of up to 910 μM and pH values of up to 9.5.

The chemical microenvironment within the illuminated surface layers illustrated in Figure 4.1 is quite unlike the chemical conditions in the surrounding macroenvironments. Analysis of nitrification–denitrification processes in photosynthetically active sediments should therefore be conducted under various light conditions simulating a diurnal change, and the spatial resolution in the topmost few millimeters should be optimized to resolve the fine vertical stratification in

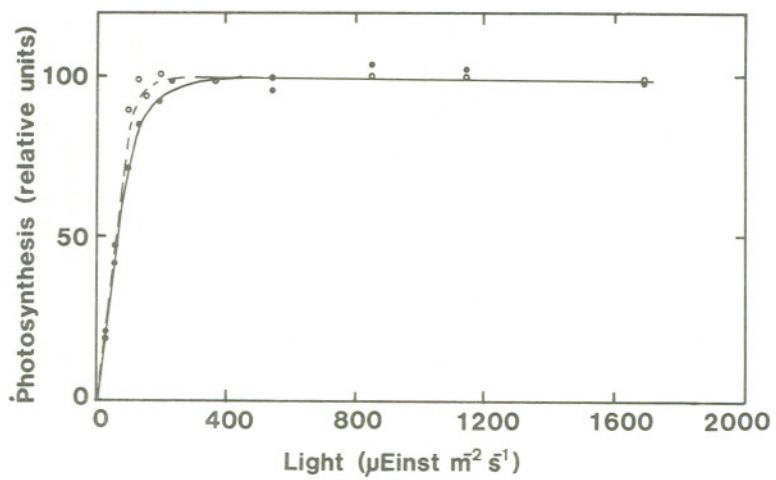

Figure 4.2. Photosynthesis versus light intensity in the uppermost 0.1 mm layer (closed circles) and in the bottom layer (open circles) of a ~1 mm thick diatom film growing on top of a sandy sediment. The measurements in the bottom layer of the film were performed after the film had been turned upside-down. The temperature was 10 °C

transformation rates, which can be expected under these conditions (Andersen *et al.*, 1984; Jensen *et al.*, 1984).

The high resolution of the microelectrode measurements in both space and time enables us to investigate some aspects of the physiological ecology of the microorganisms without removing them from their natural environment at the sediment surface. One intriguing question is whether the microalgae living at some depth in the sediment are physiologically adapted to the lower light intensities when compared to the microalgae living at the very surface. Such an adaptation could result in a change in the light intensity necessary to saturate the photosynthesis (the I_k value; see Talling, 1957). Experiments were performed with cyanobacterial and diatom films sufficiently coherent to be peeled off the sediment and turned upside-down. The photosynthesis–irradiance curve was first recorded with the electrode inserted in the topmost layer of the undisturbed film, the film was then inverted, and a new curve was recorded in the bottom layer

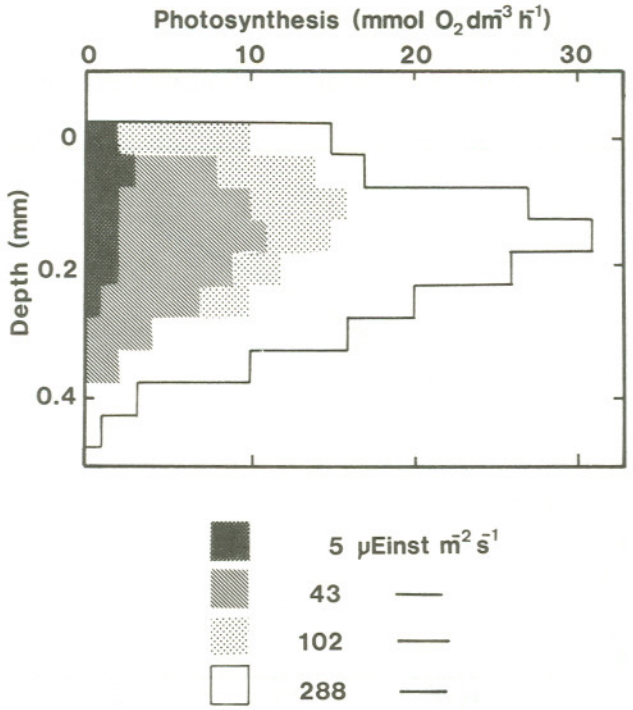

Figure 4.3. Depth profiles of oxygenic photosynthesis in a muddy sediment inhabited by diatoms as a function of light intensity. The sediment was preincubatet at 20 μEinst m^{-2} s^{-1} for 2 h before the start of the experiment. The photosynthesis profiles were measured after about 10 min at each light intensity. The temperature was 10 °C

immediately after the inversion. Data from such an experiment conducted on a diatom film are shown in Figure 4.2. There seemed to be a slightly lower I_k value in the surface layer as compared to the bottom layer, but other experiments showed the opposite, and the difference was always very small. Experiments with cyanobacterial films gave the same answer. We could thus not demonstrate any difference in light adaptation between microorganisms living at the very surface and at some depth.

The depth distribution of photosynthesis under various environmental conditions can also be easily analyzed by use of the microelectrodes. Figure 4.3 shows the photosynthesis profiles at various light intensities in a sediment covered by a dense diatom mat. Both the diameter of the photosynthetically active zone and the rates of photosynthesis in the individual layers increased with increasing light intensity. Figure 4.4 shows the integrated rate of photosynthesis versus light intensity. The progressive activation of deeper layers at increasing light intensities normally results in increasing values for photosynthesis integrated over all layers at even very high light intensities (up to 2090 μEinst $m^{-2} s^{-1}$, Revsbech and Ward (1983); up to 1800 μEinst $m^{-2} s^{-1}$, Revsbech *et al.* (1983).

The photosynthetic rates may also change during the light period. A decrease

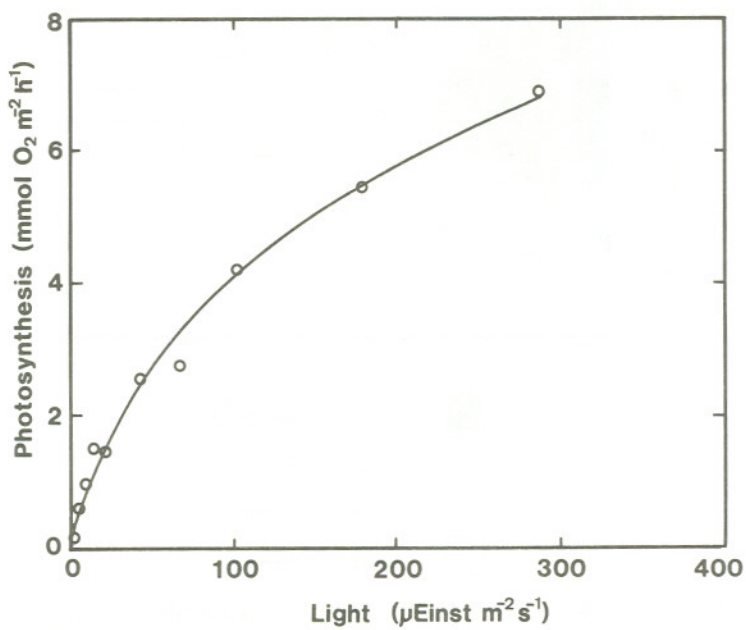

Figure 4.4. The photosynthetic rates from Figure 4.3 and some additional light intensities integrated over all depths and plotted as a function of light intensity

in photosynthetic activity should be expected after some time in the light due to the high oxygen concentrations and pH values developing in the photic zone. Figure 4.5 shows the photosynthesis profiles in a cyanobacterial mat after various durations of light incubation. The activity was actually lowest at the beginning of the light period; it then increased until a steady high rate was obtained after about 1 hour. The rate did not decrease again after several hours of illumination, and the high oxygen concentrations and pH values developing in the light consequently did not seem to have any negative effects on the photosynthetic rates. Other workers have found a negative effect of high pH on benthic diatoms (Rasmussen *et al.*, 1983). The ecological significance of great tolerance by benthic diatoms to high oxygen concentrations and pH values was discussed by Admiraal (1984). The apparent initial low rate of photosynthesis (Figure 4.5) may be an artifact due to an utilization of sulfide as electron-donor by the cyanobacteria in the beginning of the light period. This ('anoxygenic') mode of photosynthesis does not result in a production of oxygen and would consequently not be monitored by the oxygen microelectrode method. A switch from sulfide-

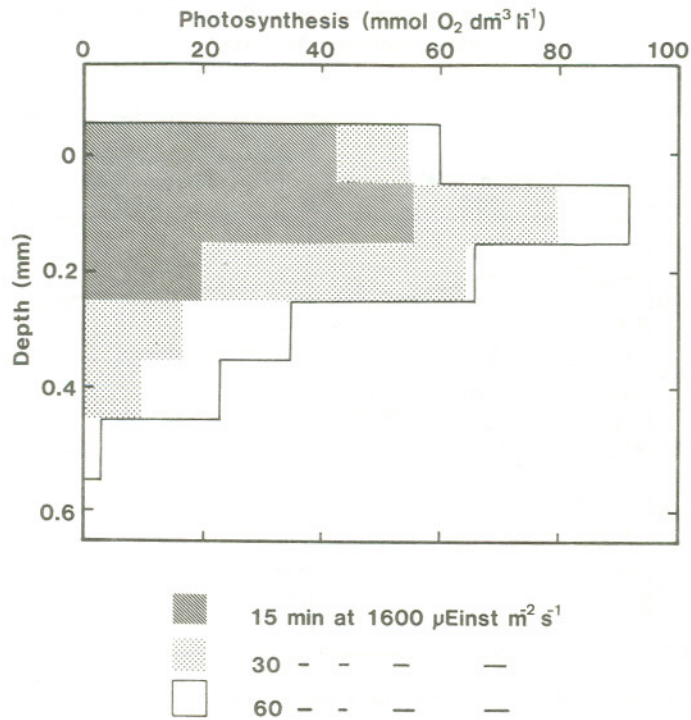

Figure 4.5. Photosynthesis profiles in a cyanobacterial mat found on top of a muddy sediment from a Danishfjord as a function of time in the light. The temperature was 20 °C

utilizing (anoxygenic) to water-utilizing (oxygenic) photosynthesis in a natural cyanobacterial mat has previously been observed (Jørgensen *et al.*, 1986). The theory of a sulfide-caused lower rate of oxygenic photosynthesis in the beginning of the light period was also supported by the observation that photosynthesis in diatom-covered sediments with less sulfide started up at maximum speed immediately after turning on light.

It is possible to calculate profiles of oxygen consumption from the oxygen profiles when the oxygen production (photosynthesis) profiles, the diffusion coefficients and the porosities are known. Computer-iterations on diffusion models have been used to obtain the best possible profiles of oxygen consumption (Revsbech *et al.*, 1986). Figure 4.6 shows a set of oxygen and photosynthesis data used to calculate the oxygen consumption profile shown in Figure 4.7. The data shown in Figure 4.6 were measured in a sediment covered by cyanobacteria in which there was a high flux of reduced substances from below towards the oxic region. The oxygen consumption, originating from the oxidation of reduced substances at the oxic–anoxic interface, is reflected in Figure 4.7 as a very high peak of oxygen consumption. The peak in oxygen consumption in the photosynthetically active layer is probably due to high rates of respiration both by cyanobacteria and non-photosynthetic bacteria.

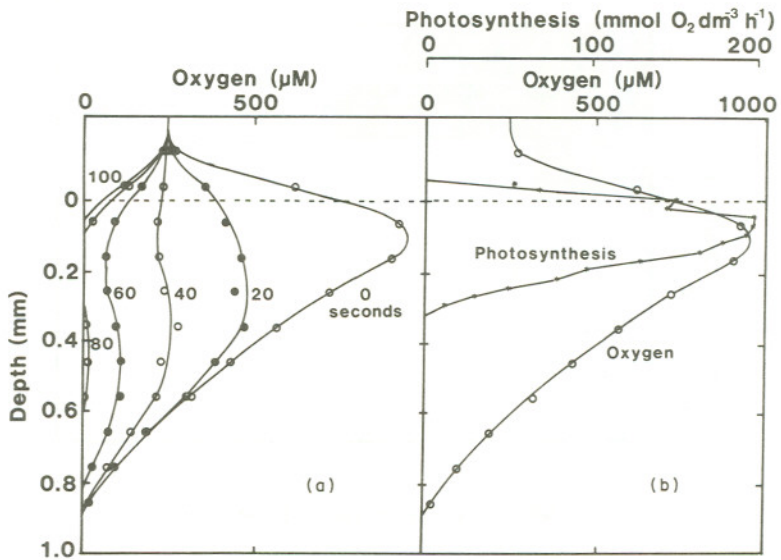

Figure 4.6. (a) Oxygen profiles in a cyanobacterial mat at various times (seconds) after darkening. (b) Steady-state oxygen profile in the light (250 μEinst $m^{-2} s^{-1}$) and profile of photosynthetic activity. The cyanobacterial mat was sampled from the same site (but a different year) as analyzed in Figure 4.1. The temperature was 20 °C

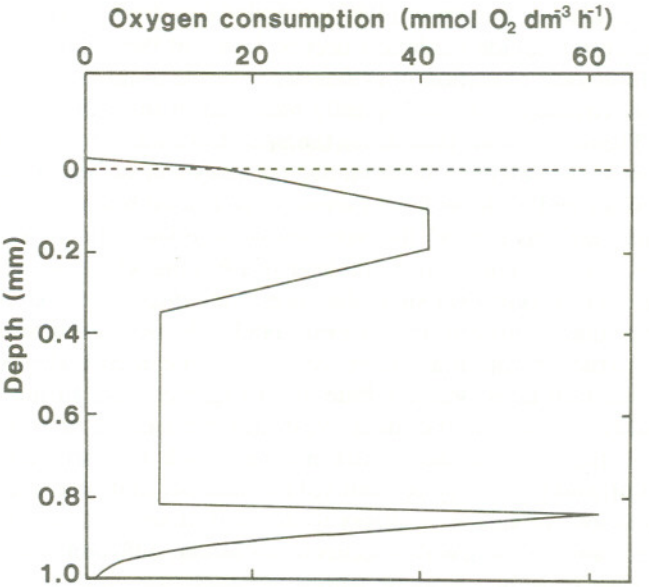

Figure 4.7. Profile of oxygen consumption calculated from the data shown in Figure 4.6

4.3 THE NITROGEN CYCLE IN THE CHEMICAL MICROENVIRONMENT NEAR THE SEDIMENT SURFACE

The microalgae assimilate combined nitrogen according to the Redfield ratio of microbial biomass, i.e., ~ 1 N for every 6 or 7 C fixed. The effect of the chemical microenvironment created by the microalgae on the nitrification–denitrification processes may, however, have larger impacts on the nitrogen cycle of coastal areas than the N-incorporation itself. Diurnal variations in nitrification–denitrification, as well as in the pool sizes of combined nitrogen, have been observed in the surface layers of sediments inhabited by microalgae (Koike and Sørensen, this volume; Henriksen and Kemp, this volume).

One intriguing question is, how tightly coupled are the nitrification–denitrification processes at the oxic–anoxic interface (Aller, this volume). We know that sulfide oxidation in sediments where sulfide diffuses up to the oxic zone can be restricted to a 50–100 μm thick layer, in which a dense population of sulfide-oxidizing bacteria mediates the process (Jørgensen and Revsbech, 1983; Revsbech *et al.*, 1983). The peak in oxygen consumption at the oxic–anoxic interface shown in Figure 4.7 was probably due to sulfide oxidation. Could ammonium oxidation be equally significant at some oxic–anoxic interfaces? It might be worthwhile to compare the processes of sulfide oxidation and

ammonium oxidation. Jørgensen (1982) compiled data from three environments in which extensive sulfide oxidation occurs. Some of these data are shown in Table 4.1. Biological oxidation of sulfide seems to be insignificant in the Black Sea, but was virtually 100% biologically mediated in the sediment covered by *Beggiatoa*. The oxic–anoxic interface in the Solar Lake was intermediate between these extremes. The difference between the mechanism of sulfide oxidation in the Black Sea water and in the sediment seems to be caused mainly by the physical transport mechanisms around the oxic–anoxic interfaces. In the sediment the transport of solutes occurs only by molecular diffusion, which is a very efficient mechanisms of transport over small distances, but which is comparatively slow over larger distances (Purcell, 1977; Crank, 1983). The steady diffusion of sulfide and oxygen to the interface thus enables relatively dense microbial populations to develop in the thin layer where sulfide and oxygen coexist. In the Black Sea, however, eddy diffusion is the most important mechanism of transport. The turbulence in the water masses results in a very thick zone where oxygen and sulfide coexist, and the energy per unit volume and per unit time does not allow dense populations of sulfide oxidizers to develop. It seems that a high flux of reductant (e.g. ammonium), which occurs by molecular diffusion, is most likely to result in a high microbial biomass within the oxidation zone, thus allowing a rapid biologically mediated oxidation of the reductant.

The free energy yields by sulfide and ammonium oxidation, and the growth yields of the bacteria when grown in pure cultures, are shown in Table 4.2. About four times as much ammonium as sulfide should be oxidized to give the same microbial biomass. Anaerobic degradation of organic matter by sulfate reduction will result in about four times as much sulfide as ammonium. The potential formation of biomass by 100% utilization of both ammonium and sulfide at the oxic–anoxic interface is thus about sixteen times higher for the sulfide oxidizers than for the ammonium oxidizers. The ammonium oxidizers at the interface will thus be very sensitive to the high grazing pressure by the meiofauna in this zone (Reise, 1981), and a complete oxidation of all the ammonium diffusing into the oxic zone may not occur. Also, the build-up of dense ammonium-oxidizing

Table 4.1. Data for hydrogen sulfide oxidation in three environments where extensive oxidation of sulfide occurs

	Black Sea	Solar Lake	Beggiatoa mat
Overlap zone thickness	35 m	10 cm	50 μM
H_2S residence time	5 days	15 min	0.6 s
Oxidation rate (μmol dm^{-3} min^{-1})	0.8	250	250000

The overlap zone is the zone where both oxygen and hydrogen sulfide were found in measurable quantities. (Data from Jørgensen, 1982.)

Table 4.2. Growth yields of chemolithoautotrophic bacteria and free energy yields by oxidation of hydrogen sulfide or ammonium with oxygen

	$H_2S \rightarrow SO_4^{2-}$	$NH_4^+ \rightarrow NO_2^-$
$\Delta G'_0$	-190 kcal/mol	-66 kcal/mol
Growth yield	8 g biomass/mol	~2 g biomass/mol

Data from D. C. Nelson *et al.* (in preparation) and Fenchel and Blackburn (1979).

populations at new oxic–anoxic interfaces, for example around a new infaunal burrow, can be anticipated to be much slower than for the sulfide oxidizers. There will consequently always be a significant release of ammonium from bioturbated sediments. Ammonium is continuously being formed by mineralization of organic matter within the oxic zone, where the diffusion path to the overlying water may be very short, and some of this ammonium will also end up in the overlying water.

At those oxic–anoxic interfaces, where ammonium is effectively being oxidized, denitrification is likely to be closely coupled to nitrification. In such systems, high rates of denitrification should occur within 100 μm from the zone where nitrification occurs. Because of the sharp diffusion gradient most of the nitrite and nitrate formed immediately above the oxic–anoxic interface will diffuse down to the anoxic layers and be denitrified.

The oxic–anoxic interface moves up and down in diurnal cycles in photosynthetically active sediments. It is therefore advantageous for microorganisms utilizing chemical species found near the interface, to be motile, so that they can follow the interface when it moves. Many sulfide-oxidizing microorganisms, e.g. *Beggiatoa* spp. and *Thiovolum* spp., are motile, and ammonium-oxdizing microorganisms are also mostly motile (Watson *et al.*, 1981).

4.4 FACTORS REGULATING BENTHIC PHOTOSYNTHESIS

Relatively few investigations of benthic photosynthesis in shallow marine and estuarine areas have been made. The thesis of Admiraal (1980), including the papers by Admiraal (1977a, b, c, d), and Admiraal and Peletier (1979a,b, 1980a,b), the thesis of Sundbäck (1983) and the review by Admiraal (1984) compile most of the information known about the factors limiting benthic photosynthesis. All investigators seem to agree that light and temperature can limit the photosynthetic activity. Combined nitrogen seems to have a stimulatory effect on some benthic photosynthetic communities, and must therefore be limiting in some cases (Van Raalte *et al.*, 1976; Sullivan and Daiber, 1975; Darley *et al.*, 1981). Excess ammonia may also be inhibitory (Admiraal, 1977d). In view of the high pH

values measured in illuminated sediments (Figure 4.1; Gnaiger, 1978; Revsbech *et al.*, 1983; Rasmussen *et al.*, 1984), where the ammonium is transformed into toxic ammonia, this may not be surprising. Phosphate rarely seems to be limiting, but the oxidized surface layer inhabited by the microalgae may be an efficient trap for phosphate diffusing up from below, and may thus regulate pelagic primary production (Sundbäck, 1983). CO_2 may be in short supply in dense algal mats (Ludden *et al.*, 1985). This is indicated by the high pH values (Figure 4.1), and it has also been verified by experiments (Admiraal, 1980). The concurrent high oxygen concentration does not improve the situation, as it creates competition about the active site of the RUBP-carboxylase, which is also an oxygenase (Lorimer *et al.*, 1977). Extensive grazing by protozoa (Fenchel, 1975), meiofauna (Admiraal *et al.*, 1983) and macrofauna (Darley *et al.*, 1981; Sundbäck, 1983) may decrease the population to suboptimal levels and thereby decrease primary production. The standing stock of benthic microalgae is thus often highest in early spring, before grazers get too abundant. A slight grazing may on the contrary increase the primary production by mobilization of nutrients (Fenchel and Kofoed, 1976). Instability of the substratum may be a very important limiting factor in many environments (Admiraal, 1980). Light is extinguished at a few mm depth in the sediments, and resuspension–sedimentation cycles may bury the microalgae below the photic zone. A factor which is very little investigated, but which may be important for supporting dense microalgal communities, is the assimilation of organic matter by microalgae. Many diatoms (Admiraal and Peletier, 1979a) are able to assimilate low molecular weight organic molecules.

The quantitative importance of benthic photosynthesis, of course, varies between localities. Many authors (Pomeroy, 1959; Cadée and Hegeman, 1974; Van Raalte *et al.*, 1976) have found annual primary productivities of the benthic microalgae, which were comparable to the planktonic productions normally measured in relatively nutrient-rich, coastal waters (100–200 $g\,C\,m^{-2}\,y^{-1}$). The normally applied oxygen and 14C methods for measuring benthic photosynthesis, however, tend to underestimate the actual rates (Revsbech *et al.*, 1981; Revsbech and Jørgensen, 1983; Admiraal, 1984).

A very interesting question, which has to be considered when dealing with the photosynthesis of benthic microalgae, is that of ecological efficiency. The concurrent respiration of the microalgae themselves, and of the associated bacteria, may account for the mineralization of a very significant proportion of the daily carbon fixation, and only a small proportion of the gross primary production as measured by the applied techniques may be available for higher trophic levels. The algal mats of hot springs at 50 °C or above constitute an extreme in this respect, as they contain no grazers.

4.5 SUMMARY

The benthic microalgae may cause a significant primary productivity in shallow waters. Their activity is confined to a narrow stratum being 0.3–2 mm thick, but

this narrow stratum may exhibit extremely high rates of photosynthesis and respiration per unit volume. The high rates of photosynthesis during illumination may cause supersaturation with pure oxygen and pH values above 10 within the active layers. The microorganisms in the uppermost sediment layers thus influence the nitrogen cycle by high rates of both incorporation and mineralization of nitrogen compounds, and also by changing the chemical microenvironment. Both total photosynthetic activities and oxygen penetrations increase when the light intensity is increased. The oxygen consumption is very high at the lower boundary of the oxic zone where intense biologically mediated oxidation of reduced sulfur compounds, and probably also ammonium, takes place. The information obtained by microelectrode studies of sulfide oxidation in microgradients is used for a discussion of the depth distribution of nitrification and denitrification near the oxic–anoxic boundary.

REFERENCES

Admiraal, W. (1977a). Influence of light and temperature on the growth rate of estuarine benthic diatoms in culture. *Mar. Biol.*, **39**, 1–9.

Admiraal, W. (1977b). Salinity tolerance of benthic estuarine diatoms as tested with a rapid polarographic measurement of photosynthesis. *Mar. Biol.*, **39**, 11–19.

Admiraal, W. (1977c). Influence of various concentrations of orthophosphate on the division rate of an estuarine benthic diatom, *Navicula arenaria*, in culture. *Mar. Biol.*, **42**, 1–8.

Admiraal, W. (1977d). Tolerance of estuarine benthic diatoms to high concentrations of ammonia, nitrite ion, and orthophosphate. *Mar. Biol.*, **43**, 307–15.

Admiraal, W. (1980). Experiments on the ecology of benthic diatoms in the Eems-Dollard estuary. Ph.D. Thesis, University of Groningen, The Netherlands.

Admiraal, W. (1984). The ecology of estuarine sediment-inhabiting diatoms. In: Round, F. E. (ed.), *Progress in Phycological Research*, Vol. 3, pp. 269–322. Biopress Ltd.

Admiraal, W., and Peletier, H. (1979a). Influence of organic compounds and light limitation on the growth rate of estuarine benthic diatoms. *Br. Phycol. J.*, **14**, 197–206.

Admiraal, W., and Peletier, H. (1979b). Sulphide tolerance of benthic diatoms in relation to their distribution in an estuary. *Br. Phycol. J.*, **14**, 185–96.

Admiraal, W., and Peletier, H. (1980a). Distribution of diatom species on an estuarine mudflat and experimental analysis of the selective effect of stress. *J. Exp. Mar. Biol. Ecol.*, **46**, 157–75.

Admiraal,W., and Peletier, H. (1980b). Influence of seasonal variations of temperature and light on the growth rate of cultures and natural populations of intertidal diatoms. *Mar. Ecol. Prog. Ser.*, **2**, 35–43.

Admiraal, W., Bouwman, L. A., Hoekstra, L., and Romeyn, K. (1983). Qualitative and quantitative interactions between microphytobenthos and herbivorous meiofauna on a brackish intertidal mudflat. *Int. Rev. Ges. Hydrobiol.*, **68**, 175–91.

Andersen, T. K., Jensen, M. H., and Sørensen, J. (1984). Diurnal variation of nitrogen cycling in coastal, marine sediments I. Denitrification. *Mar. Biol.*, **83**, 171–6.

Cadée, G. C., and Hegeman, J. (1974). Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. *Neth. J. Sea. Res.*, **8**, 260–91.

Crank, J. (1983). *The Mathematics of Diffusion.* Oxford University Press, London.

Darley, W. M., Montague, C. L., Plumley, F. C., Sage, W. W., and Psalidas, A. T. (1981).

Factors limiting edaphic algal biomass and productivity in a Georgia salt marsh. *J. Phycol.*, **17**, 122–8.

Fenchel, T. (1975). The quantitative importance of the benthic microflora of an arctic tundra pond. *Hydrobiologia*, **46**, 445–64.

Fenchel, T., and Blackburn, T. H. (1979). *Bacteria and Mineral Cycling*. Academic Press, London.

Fenchel, T., and Kofoed, L. H. (1976). Evidence for exploitative interspecific competition in mud snails (*Hydrobiidae*). *Oikos*, **27**, 367–76.

Gnaiger, E., Gluth, G., and Weiser, W. (1978). pH fluctuations in an intertidal beach in Bermuda. *Limnol. Oceanogr.*, **23**, 851–7.

Hemmingsen, E. A. (1977). Spontaneous formation of bubbles in gas-supersaturated water. *Nature*, **267**, 141–2.

Jensen, H. B., Jørgensen, K. S., and Sørensen, J. (1984). Diurnal variation of nitrogen cycling in coastal, marine sediments. II. Nitrous oxide emission. *Mar. Biol.*, **83**, 177–83.

Jørgensen, B. B. (1982). Ecology of the bacteria of the sulfur cycle with special reference to anoxic–oxic interface environments. *Phil. Trans. R. Soc. Lond. B*, **298**, 543–61.

Jørgensen, B. B., and Revsbech, N. P. (1983). Colorless sulfur bacteria, *Beggiatoa* spp. and *Thiovolum* spp. in O_2 and H_2S microgradients. *Appl. Environ. Microbiol.*, **45**, 1261–70.

Jørgensen, B. B., and Revsbech, N. P. (1985). Diffusive boundary layers and the oxygen uptake of sediments and detritus. *Limnol. Oceanogr.* **30**, 11–21.

Jørgensen, B. B., Cohen, Y., and Revsbech, N. P. (1986). Transition from anoxygenic to oxygenic photosynthesis in a *Microcoleus·chtonoplastes* cyanobacterial mat. *Appl. Environ. Microbiol.*, **51**, 408–17.

Lorimer, G. H., Badger, M. R., and Andrews, T. J. (1977). D-ribulose-1, 5-biphosphate carboxylase–oxygenase. *Anal. Biochem.*, **78**, 66–75.

Ludden, E., Admiraal, W., and Colijn, F. (1985). Cycling of carbon and oxygen in layers of marine microphytes; a simulation model and its eco-physiological implications. *Oecologia*, **66**, 50–9.

Pomeroy, L. R., (1959). Algal productivity in salt marshes of Georgia. *Limnol. Oceanogr.*, **4**, 386–97.

Purcell, E. M. (1977). Life at low Reynolds number. *Am. J. Phys.*, **45**, 3–11.

Rasmussen, M. B., Henriksen, K., and Jensen, A. (1983). Possible causes of temporal fluctuations in primary production of the microphytobenthos in the Danish Wadden Sea. *Mar. Biol.*, **73**, 109–14.

Reise, K. (1981). Gnathostomulida abundant alongside polychaete burrows. *Mar. Ecol. Prog. Ser.*, **6**, 329–33.

Revsbech, N. P., and Jørgensen, B. B. (1983). Photosynthesis of benthic microflora measured with high spatial resolution by the oxygen microprofile method: capabilities and limitations of the method. *Limnol. Oceanogr.*, **28**, 749–56.

Revsbech, N. P., and Jørgensen, B. B. (1986). Microelectrodes: their use in microbial ecology. In: Marshall, K. C. (ed.), *Advances in Microbial Ecology*, vol. 9, pp. 293–352. Plenum, New York.

Revsbech, N. P., and Ward, D. M. (1983). Oxygen microelectrode that is insensitive to medium chemical composition: use in an acid microbial mat dominated by *Cyanidium caldarium*. *Appl. Environ. Microbiol.*, **45**, 755–9.

Revsbech, N. P., Jørgensen, B. B., and Brix, O. (1981). Primary production of microalgae in sediments measured by oxygen microprofile, $H^{14}CO_3$ fixation and oxygen exchange methods. *Limnol. Oceanogr.*, **26**, 717–30.

Revsbech, N. P., Jørgensen, B. B., Blackburn, T. H., and Cohen, Y. (1983). Microelectrode studies of photosynthesis and O_2, H_2S, and pH profiles of a microbial mat. *Limnol. Oceanogr.*, **28**, 1062–74.

Revsbech, N. P., Madsen, B., and Jørgensen, B. B. (1986). Oxygen production and consumption in sediments determined at high spatial resolution by computer simulation of oxygen microelectrode data. *Limnol. Oceanogr.*, **31**, 293–304.

Sullivan, M. J., and Daiber, F. C. (1975). Light, nitrogen, and phosphorus limitation of edaphic algae in a Delaware salt marsh. *J. Exp. Mar. Biol. Ecol.*, **18**, 79–88.

Sundback, K. (1983). Microphytobenthos on sand in shallow brackish water, Oresund, Sweden. Ph.D. thesis, University of Lund, Sweden.

Talling, J. F. (1957). Photosynthetic characteristics of some freshwater plankton diatoms in relation to underwater radiation. *New Phytol.*, **56**, 1–50.

Van Raalte, C. D., Valiela, I., and Teal, J. M. (1976). The effect of fertilization on the species composition of salt marsh diatoms. *Water Res.*, **10**, 75–86.

Watson, S. W., Valois, F. W., and Waterbury, J. B. (1981). The family *Nitrobacteraceae*. In: Starr, M. P., Stolp, H., Trüper, H. G., Balows, A., and Schlegel, H. G. (eds), *The Procaryotes*, Vol. 1, pp. 1005–22. Springer, New York.