PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Photosynthetic Microbial Communities in Aquatic Ecosystems

M. Shilo

Phil. Trans. R. Soc. Lond. B 1982 **297**, 565-574
doi: 10.1098/rstb.1982.0062

Phil. Trans. R. Soc. Lond. B **297**, 565–574 (1982)
Printed in Great Britain

Photosynthetic microbial communities in aquatic ecosystems

By M. Shilo

The Institute of Life Sciences, Division of Microbial and Molecular Ecology, The Hebrew University of Jerusalem, Jerusalem, Israel

A critical reappraisal of our knowledge on the photosynthetic communities of the open oceans and large lakes, and the development of new approaches to measurement of their activity *in situ* have greatly influenced our present views on the structure and function of these communities. Based on the accumulated knowledge of the physiology and molecular biology of the photosynthetic organisms involved we can now understand some of the mechanisms underlying adaptive processes operative in Nature.

The distribution pattern of the photosynthetic communities in the photic zone of aquatic ecosystems is controlled by the nature of the photosynthetic apparatus, the range of antenna pigments formed by the different organisms, and their ability to regulate quantitatively and qualitatively pigment synthesis in response to light intensity and spectral composition. An additional factor controlling distribution is the ability of many of the photosynthetic organisms to escape the oligotrophic conditions prevailing in the water column by adherence to interfaces such as the benthos or the neuston. A major factor governing the ability of organisms to adhere to these interfaces is the hydrophobicity of their cell envelope. Planktonic organisms, on the other hand, have highly hydrophilic envelopes.

Benthic organisms have evolved mechanisms for dispersal, which in many cases involves the formation by the hydrophobic adherent parent cells of hydrophilic progeny cells. This has been confirmed for several hormogonia-producing cyanobacteria. Benthic photosynthetic organisms must in addition be capable of phototactic motility and have versatile metabolic patterns to adapt to the rapid fluctuations in their environment.

The photosynthetic organisms of the neuston and the cyanobacteria that form surface scum share mechanisms enabling the cells to withstand conditions of photooxidation, lethal to most non-resistant organisms.

Introduction

In spite of the great importance of the aquatic photosynthetic communities in global primary production, and the many years of study devoted to the field, our knowledge of these communities and their function in Nature is still incomplete and inaccurate.

In a critical reappraisal of long-accepted notions and concepts, a better understanding of the photosynthetic communities in aquatic ecosystems, their community structure, and interaction with other organisms and with the environment, both temporally and spatially, can now be achieved. Not only have our views on the composition of oceanic communities to be changed and updated, but we will also have to correct data on primary production, rates of growth and turnover of phytoplankton organisms in the oceans.

The second important development in an updated analysis of the picture is the application of knowledge gained from experimental studies with pure cultures. The broad physiological, biological and genetic basis obtained now allows a new approach in the unravelling of the mechanisms underlying regulation and control of the major metabolic functions of the

photosynthetic microorganisms in response to different environments or fluctuations in environmental conditions.

Within the framework of the present symposium, I shall concentrate on the principles that govern the spatial and temporal distribution of photosynthetic communities in natural aquatic ecosystems and discuss ecophysiological mechanisms of their adaptation to the environment.

Distribution pattern of the photosynthetic microbial communities

Most photosynthetic microorganisms have a chlorophyll-based photosynthetic apparatus. The only known exceptions are certain Halobacteria (Archaebacteria), which can use absorbed light to form ATP or proton gradients to meet metabolic requirements, without possessing a chlorophyll-driven photosynthetic mechanism. Instead, these bacteria contain bacteriorhodopsin in their purple membranes (Stockenius 1978). This type of non-chlorophyll photosynthesis is confined to organisms that have a very restricted distribution in extreme halophilic ecosystems.

Functionally, all chlorophyll-type photosynthetic organisms can be divided into two main groups.

(*a*) Those that possess a two-photosystem-driven mechanism (PS I and PS II), in which photolysis of water takes place and oxygen is evolved in the process. All the eukaryotic photosynthesizers and cyanobacteria belong to this group.

(*b*) Those that possess only one photosystem (PS I), and in which the electron donor must be H_2S, H_2 or reduced small organic molecules. In this process no O_2 is evolved. The green and purple photosynthetic bacteria fall into this group.

The cyanobacteria occupy a unique position among the photosynthetic microorganisms and form a bridge between the two groups. They possess the two-photosystem mechanism for oxygenic photosynthesis, but many of them have the capacity to shift under appropriate conditions to non-oxygenic photosynthesis in which only PS I is operative and in which H_2S is the electron donor (Cohen *et al.* 1975*a*, *b*; Padan 1979*a*). This shift occurs after an induction period and without loss of the inoperative PS II system (Oren & Padan 1978). The distribution pattern of the photosynthetic microorganisms in aquatic ecosystems is first and foremost based on the nature of the photosynthetic apparatus and its function.

The euphotic zone in aquatic ecosystems can be clearly divided into (i) regions maintaining constantly aerobic conditions, (ii) layers where permanently anaerobic conditions prevail, and (iii) regions in which aerobic and anaerobic conditions fluctuate.

Organisms capable only of oxygenic photosynthesis are found exclusively in the first type of region, including all the eukaryotic algae and many of the cyanobacteria.

The second biotope, that of the permanently anaerobic layers of the euphotic zone, below the thermocline or chemocline of stratified waterbodies, is colonized exclusively by the non-oxygenically photosynthesizing green and purple bacteria. These communities depend on H_2S, hydrogen or small organic molecules as electron donors for their photosynthetic activity.

The third type is colonized by cyanobacteria, which can shift between oxygenic and non-oxygenic photosynthesis. They are dominant in conditions that fluctuate between the aerobic and anaerobic, often in a diurnal rhythm. Cyanobacterial sediment mats, marine marshes, rice paddies, sediment layers of shallow ponds and lakes, and the interface between the aerobic

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

and anaerobic layers in certain stratified lakes, are among the typical biotopes in which organisms belonging to this group are widely found (Padan 1979*b*).

A second major factor determining the distribution of the photosynthetic communities is the quantity and quality of light reaching the different layers of the euphotic zone. Different organisms will position themselves in the light gradient according to their ability to synthesize suitable antenna pigments, and their capacity to respond to changes in the light gradient (diurnal, seasonal or sporadic) by a change in the total amount of pigments, brought about by a change in number or size of the photosynthetic centres (Falkowsky & Owens 1978). Another response to change in light quality is the selective regulation of synthesis of specific pigments, as in chromatic adaptation (Bogorad 1975).

The great variety of antenna pigments found in different photosynthetic microorganisms, and the regulatory potential to adapt to changes in the light conditions, explain the fact that the entire photic zone can be colonized along the gradient of different light quantities and colours. Often this leads to a positioning effect whereby discrete layers or plates of photosynthetic organisms are formed, one overlaying the other. This is true for the water column in the euphotic zone of lakes, lagoons and oceans, as well as for mats of photosynthetic communities. The famous 'Farbstreifen' on the shores of the Baltic Sea are an example of such sequential layers of different photosynthetic microorganisms.

A common adaptation to rhythmical diurnal or seasonal changes in light quantity and quality is the ability of many of the photosynthetic microorganisms to change their position in the water column. This can occur through active flagella-driven phototactic or photophobic motility in the water column itself, by gliding movement of benthic organisms or by change in buoyancy found in the gas-vacuolated cyanobacteria.

Some planktonic cyanobacteria stratify at a particular depth in some lakes, (Walsby & Klemer 1974; Reynolds & Walsby 1975), and change their position in response to changes in the light gradient (Walsby & Booker 1980). The physiological mechanism underlying this buoyancy regulation seems to be the controlled collapse of gas vacuoles caused by the increasing turgor pressure resulting from the interacellular build-up of photosynthates (Dinsdale & Walsby 1972) and light-stimulated accumulation of potassium at increase of light intensity (Allison & Walsby 1981).

The main aquatic ecosystems and, most typically, the open oceans are characterized by their oligotrophic conditions, with nutrient levels and fluxes approaching very low levels or even zero. Under such conditions, organisms must adapt and develop extremely efficient uptake, storage and growth control mechanisms (Poindexter 1979, 1981*a*), or escape into niches providing higher nutrient concentrations, or both. Such conditions are indeed found at the various interfaces in the aquatic ecosystems, e.g. the water–air interface, the sediment–water interface or surfaces on immersed particles, plants or animals. We thus find high concentrations and great diversity of special neuston organisms at the water–air interface (Geitler 1942), epiphytes on algal surfaces and benthic organisms at the sediment–water interface (Marshall 1976).

Among these specialized interface communities, many are photosynthetic. The communities adhering to interfaces possess a number of characteristic properties that clearly differentiate them from planktonic organisms floating freely in the water column.

One of the most characteristic features of the benthic or neuston organisms is their adherence to interfaces; hydrophobicity of the outer cell surface, or of special localized sites on the cell envelope, is one of the most important mechanisms for such adherence (Norkraus 1980; Marshall 1976).

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Envelope hydrophobicity can now be easily demonstrated by using the selective partitioning of the cells in a biphasic system of water and immiscible non-polar solvants (Rosenberg *et al.* 1980).

A survey of the hydrophobicity or hydrophilicity of many cyanobacteria taken from fresh water, marine and hypersaline conditions, showed (Shilo & Fattom, unpublished) that, while all planktonic types had a hydrophilic envelope, the benthic types tested all had a hydrophobic external surface, which caused the selective movement of the cells into the non-polar solvent phase of the biphasic partitioning systems. This property may therefore be a very important factor in explaining the free flotation of plankton organisms and the exclusion of neuston and benthic forms from the water body, and their adherence instead to immersed hydrophobic surfaces.

Adaptive consequences of positioning of the phototrophic microbial communities

The segregation of aquatic microorganisms into neuston, benthic and plankton types also defines three different types of environments in which these organisms live. Each of these environments imposes conditions, often extreme, to which organisms have to adapt. Survival and multiplication in the three above-mentioned habitats have adaptive consequences for the organisms, which can be predicted and which can be tested experimentally.

One such consequence is that for organisms fixed to substrates, a complex life-cycle can be expected to include the production of a morphological and physiological cell type which can function as a dispersal unit, allowing colonization of new surfaces.

This mode of securing spread of progeny should be particularly important for benthic organisms living in currents, streams or turbulent waters where adherence to substrate is especially strong.

Indeed, for all of the neuston organisms studied, including eukaryotic algae and heterotrophic bacteria such as *Nevskia*, *Hyphomicrobium*, *Caulobacter* and the phototrophic *Rhodomicrobium*, production by the adherent cells of progeny that act as motile swarmer or dispersal cells has been shown. If hydrophobicity characterizes the cells in their attached adherent phase, we would expect the swarmer cells to be hydrophilic.

Many benthic filamentous cyanobacteria form special short trichome fragments, the hormogonia, which seem to function as dispersal forms (Rippka *et al.* 1979). For several filamentous cyanobacteria of the Pasteur Institute Collection, including *Calothrix desertica* (strain 7102), *Anebaenopsis circularis* (strain 6720), and *Plectonema boryannum* (strain 6306), it was shown (Shilo & Fattom, unpublished) that the hormogonia are hydrophilic, while the mature filaments were highly hydrophobic. It seems that similarly to the *Caulobacter* system (Poindexter 1981 *b*), in these cyanobacteria, separation of hormogonia could become an easy means of synchronization of populations.

In certain planktonic marine cyanobacteria, such as *Oscillatoria* (*Trichodesmium*) *thiebautii*, which may form massive blooms in tropical oceans, the ability of these organisms to fix atmospheric nitrogen has been shown (Carpenter & McCarthy 1975). In one case of *O. erthraea* blooming in the Red Sea, there seemed to be a correlation between nitrogen fixation and the ability of the filaments to clump together to form bundles. This 'bundledness' was enhanced by wind-driven filament concentration (Bryceson & Fay 1979). It would be interesting to test whether this phenomenon of filament aggregation is also the expression of a transient change in the cell envelope to a state of increased hydrophobicity triggered under conditions of nitrogen deprivation.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

A consequence of the adherence of benthic phototrophs is the continuous danger to the organisms of burial under the rain of precipitating particles and thus of being light-deprived. It is therefore not surprising to find that special mechanisms have evolved to cope with this situation, namely the ability of benthic filamentous cyanobacteria to remain always on the surface of the sediment by gliding phototactic mobility.

Of the many additional consequences of adherence of phototrophs to surfaces I shall mention two more.

One is the exposure of most benthic organisms to the drastic fluctuations in environmental conditions of the water–sediment interface involving O_2, H_2S, pH and *Eh*. This creates selective conditions for organisms with versatile metabolic capabilities (Oren & Shilo 1979) and with the capacity to shift from oxygenic to non-oxygenic photosynthesis (Shilo 1980). As already mentioned, this capacity is found in many cyanobacteria (Padan 1979*a*, *b*) and thus explains their dominance in recent and in earlier geological periods in biotopes where fluctuating conditions have prevailed.

For the shallow regions close to ocean and lake shores, drastic fluctuations in temperature, salinity and light intensity are also found frequently, often creating a combination of several extreme conditions with differing fluctuation rhythms to which native organisms have to adapt.

Laboratory simulations as well as direct measurements *in situ* in Nature have been carried out to follow the changes in the environment and their effect on the photosynthetic communities. Work on cyanobacterial mats (Jørgensen *et al.* 1979*b*) and the chemocline communities of Solar Lake (Jørgensen *et al.* 1979*a*) serves as a typical example.

High resistance to photooxidative death must be expected in neuston organisms and in scum-forming surface cyanobacteria. This was verified in photosynthetic cyanobacterial communities in surface blooms in fishponds (Eloff *et al.* 1976).

Another case of drastic fluctuation in the environmental conditions with concomitant fluctuations in metabolic activity, can be seen in the cyanobacterial communities of *Scytonema*, which colonize the pneumatophores of mangrove trees in Sinai and are wetted at high tides only. The filaments are well protected from photooxidation by a dark pigmentation of the colony exterior. Maximal metabolic activity, as well as nitrogen fixation, is limited to short periods of wetting during high tide (Potts 1979).

Composition and function of the photosynthetic microbial communities in the aquatic ecosystems and their role in oceanic primary production

In spite of the vast area of the lakes and oceans, covering 70 % of the biosphere, we still do not know the role of the photosynthetic communities that live in these ecosystems in global net production (Peterson 1980).

The accumulating evidence resulting from the work of many scientists has caused a change in our views about the composition, overall activity and growth rate of the photosynthetic communities in the oceanic ecosystems, and we are in the midst of a reassessment of the entire problem. It has become evident that our knowledge of community composition was incomplete and that our data on overall productivity were inaccurate.

Recently the discovery was made of a new widespread chroococcalean cyanobacterium (*Synechococcus* types) in several oceans (Waterbury *et al.* 1979; Johnson & Sieburth 1979). These small cyanobacteria, which have escaped notice until recently, appeared in such high

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

concentrations as to suggest that they are major contributors to primary production. Evidence has been produced to show that at least some of these *Synechococcus* types isolated from oceans are capable of nitrogen fixation (Duerr & Mitsul 1981).

Experimental and field work has repeatedly shown that the estimated and computed values for the primary productivity of the oceans are open to question. It has become clear that the methodology used up to now for measuring primary production was inadequate and has led to gross underestimates of the activity of primary production of the open oligotrophic oceans, possibly as much as by fivefold or more (for review see Peterson 1980).

The idea that measurement of $^{14}CO_2$ uptake in oligotrophic waters may underestimate primary production and carbon flow rates has also found support in studies of oligotrophic lakes such as Lake Superior (Verduin 1975). Primary production measurements with the ^{14}C uptake method simultaneously with other independent methods showed that the values obtained were an order of magnitude greater than those obtained with the ^{14}C uptake method.

Additional evidence that has led to a reappraisal of our long-held views on the subject has come from several independent sources. Estimation of heterotrophic bacterial populations in the tropical Pacific was found to be several times greater than photosynthetic $^{14}CO_2$ uptake (Sorokin 1971). Work of Sieburth & Johnson (1977) on rates of heterotrophy in the Azor plateau of the Atlantic Ocean supported this contention.

Measurement of ATP increase in phytoplankton from samples taken from the Saragass Sea led Sheldon & Sutcliffe (1978) to conclude that ^{14}C uptake values were gross underestimates and that the generation times calculated for the phytoplankton were unexpectedly short.

We thus may also have to change our views about the physiological state of the photosynthetic microorganisms in the open oceans. The dogma that photoplankton turnover and growth rates are low was also found to be contradictory to recent findings based on comparison of cell composition from open ocean samples and from defined continuous culture experiments (Goldman *et al.* 1979; McCarthy & Goldman 1979). They have therefore put forward the hypothesis that even in the oligotrophic conditions of the ocean, continuous small fluxes of nutrients, efficiently utilized by the oligotrophically adapted organisms, allow rapid rates and high turnover.

A critical review of the methodology used for many years to measure primary productivity of oceanic phytoplankton has shown that the most commonly used method of ^{14}C uptake (Steemann-Nielsen 1952) is inadequate unless coupled with other tools now available to the aquatic ecologist (Peterson 1980).

Primary production rates were usually estimated from single endpoint measurements taken after relatively long incubation periods. The kinetics of the process, however, are linear for only very short time intervals (Taylor *et al.* 1981), especially in the oligotrophic conditions prevailing in the open oceans.

Furthermore the recent work of Gieskes & Baars (1979) indicates that in the small incubation bottles used a severe underestimation of primary production can result from massive mortality of the photosynthetic organisms in the sample. Similar conclusions have also been reached in the work on *Peridinium cinctum fawestii* involving ^{14}C uptake measurements in Lake Kinneret (Dubinsky & Berman 1976).

Now new methods are being developed in which multiple measurements can be taken *in situ* during the incubation of the sample, and the necessary precautions are taken to overcome the intrinsic pitfalls of the method (Peterson 1980). A sophisticated automatic unit, which takes a

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

large water sample, injects the $^{14}CO_2$ *in situ*, and which periodically extracts multiple aliquots, has been constructed by Taylor *et al.* (1981). Another important development is the continuous simultaneous measurement of pH, O_2 and sulphides by microelectrodes (Revsbech *et al.* 1981 *a*, *b*). This method is especially important in taking measurements in algal and cyanobacterial mats (Jørgensen *et al.* 1979 *b*), and in sediments in which environmental conditions fluctuate rapidly. Use of this newly introduced method has allowed accurate determination of fluxes of O_2 and sulphides, and special and temporal measurements of photosynthesis and respiration within the mats.

Using these new methods, we may now expect correct determinations of productivity rates and realistic estimations of global primary production. Recently, constructed models for primary production in open oceans take into consideration the complex interactions of predation, grazing, heterotrophy, secondary production and heterotrophic respiration (Marra *et al.* 1981). These models may therefore also aid in reaching more realistic values of primary production.

The waxing and waning of photosynthetic communities

Great fluctuations are characteristic for the photosynthetic communities in most aquatic ecosystems.

In many lakes and oceans, periodic mass development can lead to 'bloom' formation causing water discolouration of extended areas (e.g. red tide or cyanobacterial surface scums). We know little about the factors that trigger the blooms and regulate the size and species compositions of these populations in Nature, or which control their succession (Shilo 1975). Mass development of certain photosynthetic microorganisms can occur as a permanent, year-round phenomenon (as in African equatorial lakes, e.g. Lake George, Uganda (Ganf 1974)), as a seasonal phenomenon (fish ponds, lakes and reservoirs in subtropical regions), or as a sporadic event. Often the physical concentration of the organisms caused by wind (e.g. *Oscillatoria* (*Trichodesmium*) *thiebautii*) by convection currents or internal waves (e.g. 'red tide' streaks) or by buoyancy (e.g. surface scums or gas-vacuolated cyanobacteria) plays an important part in the starting of the 'blooms' and in their locational delineation.

An important aspect of our interest in the photosynthetic communities in Nature are the economic consequences of their mass development. Important benefits as well as great damage and harm are connected with algal and cyanobacterial blooms.

Photosynthetic blooms may be used as food for man (e.g. *Spirulina platensis* from lakes in Tchad or Mexico) or for animal feed, or they may cause damage, intoxication and losses. In some of the equatorial lakes in Africa (Lake Nakuro, Kenya) mass development of *Spirulina* sustains extremely dense populations of flamingo populations. Sporadic sudden unexplained collapses of the cyanobacterial blooms, cause the birds to scatter and disperse or even die. Toxigenic algae ('red tide' dinoflagellates and chrysophytes) and cyanobacteria (e.g. *Microcystis*, *Anabaena* and *Aphenozomenon*) have widespread distributions in oceans, lakes and brackish water lagoons and fish ponds, and cause human intoxication, domestic animal mortalities and extensive 'fish kills' (for reviews see Shilo 1967, 1972; Carmichael 1981). Furthermore these blooms of photosynthetic organisms are related to problems of bad taste and odour in drinking water (Shilo 1972).

The appearance and degree of damaging effects are often closely related to the collapse of the community and the sudden massive release of intracellular components from the organisms.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Because of their economic impact on human life, concentrated efforts have been directed to the study of the factors that trigger bloom formation and which affect their maintenance, as well as to the agents and conditions that cause mass mortality and community collapse of the photosynthetic blooms.

Recently, studies of agents and processes involved in the sudden collapse of cyanobacterial blooms have given insight into the mechanisms underlying this phenomenon. In these investigations the complex interaction of the 'blooming' organisms with cyanophages (Padan & Shilo 1973) and with cyanobacteria-lysing Lysobacteria (Shilo 1970, 1971) have been studied. However, in spite of the wide occurrence of both cyanophages and Lysobacteria and their great activity in experimental conditions, their role in Nature seems to be a limited one (Padan & Shilo 1973).

A major factor involved in mortality and cyclic collapse of cyanobacterial communities in natural environments seems to be light and oxygen. Conditions supporting photooxidative killing of the photosynthetic microbial communities are found in the tropical and subtropical regions, where light intensities can be very high, oxygen in the surface water layer is often supersaturated and CO_2 depleted owing to the photosynthetic activity of the 'bloom'. Any cyanobacteria that can appear and persist in these conditions must have special mechanisms of increased resistance to photooxidative damage.

A detailed analysis of one typical bloom form, *Microcystis marginate*, common in Israeli fish ponds, proved to be highly resistant to experimental photooxidation (0.1 J cm^{-2} s^{-1}) in an O_2 atmosphere under laboratory as well as field conditions (Eloff *et al.* 1976; Steinitz & Shilo 1976). Indications were found suggesting that the mechanism underlying this resistance may be attributed to a change in the ratio between the two superoxide dismutase (SOD) isoenzymes. In the resistant types there seems to be a dramatic shift in this ratio whereby extremely high (more than 95 %) manganese SOD proportion occurs, while in the sensitive strains most of the SOD activity is due to the ferric SOD enzyme. The high resistance of the manganese enzyme to H_2O_2 may be an important factor in the survival of these cells, which lack catalase (Steinitz *et al.* 1976).

The periodic die-off of even the photooxidation-resistant cyanobacteria may be related to physiological conditions of the blooms at peak development, which affect SOD turnover in the cells. Such conditions can indeed be simulated experimentally by stopping all protein synthesis by addition of chloramphenicol (Steinitz & Shilo 1976).

References (Shilo)

Allison, E. M. & Walsby, A. E. 1981 The role of potassium in the control of turgor pressure in a gas vacuolate blue-green algae. *J. exp. Bot.* **32**, 241–249.

Bogorad, L. A. 1975 Phycobiliproteins and complementary chromatic adaptation. *A. Rev. Pl. Physiol.* **26**, 369–401.

Bryceson, I. & Fay, P. 1979 Nitrogen fixation associated with surface blooms of *Oscillatoria* (*Trichodesmium*) *erythraea* in the coastal waters of Dar Es Salaam. In *Abstr. Int. Symp. on Photosynthetic Prokaryotes*, Oxford, p. D2.

Carmichael, W. W. 1981 Freshwater blue-green algae (cyanobacteria) toxins – a review. In *The water environment*. New York: Plenum. (In the press.)

Carpenter, E. J. & McCarthy, J. J. 1975 Nitrogen fixation and uptake of combined nitrogenous nutrients by *Oscillatoria* (*Trichodesmium*) *thiebautii* in the Western Saragasso Sea. *Limnol. Oceanogr.* **20**, 389–401.

Cohen, Y., Jørgensen, B. B., Padan, E. & Shilo, M. 1975*b* Sulfide-dependent anoxygenic photosynthesis in the cyanobacterium *Oscillatoria limnetica*. *Nature, Lond.* **257**, 489–492.

Cohen, Y., Padan, E. & Shilo, M. 1975*a* Facultative anoxygenic photosynthesis in the cyanobacterium *Oscillatoria limnetica*. *J. Bact.* **123**, 858–861.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Dinsdale, M. T. & Walsby, A. E. 1972 The interactions of cell turgor pressure, gas vacuolation and buoyancy in a blue-green algae. *J. exp. Bot.* **23**, 561–570.
Dubinsky, Z. & Berman, T. 1976 Light utilization efficiencies of phytoplankton in Lake Kinneret. *Limnol. Oceanogr.* **21**, 226–230.
Duerr, E. D. & Mitsul, A. 1981 Aerobic growth characteristics of two marine unicellular N_2 fixing cyanobacteria. In *Abstr. Annual Meeting of the A.S.M.* K85.
Eloff, J. N., Steimitz, Y. & Shilo, M. 1976 Photooxidation of cyanobacteria in natural conditions. *Appl. environ. Microbiol.* **31**, 119–126.
Falkowsky, P. G. & Owens, T. G. 1978 Effects of light intensity on photosynthesis and dark respiration in six species of marine phytoplankton. *Mar. Biol.* **45**, 289–295.
Ganf, G. G. 1974 Phytoplankton biomass and distribution in a shallow eutrophic lake (Lake George, Uganda). *Oecologie* **16**, 9–29.
Geitler, L. 1942 Zur kenntnis der Bewohner des Oberflächenhëutchens einheimischer gewässer. *Biologia gen.* **36**, 460–475.
Gieskes, W. W. C. & Baars, G. W. 1979 Current ^{14}C methods for measuring primary production, gross underestimates in oceanic waters. *Neth. J. Sea Res.* **13**, 58–78.
Goldman, J. C., McCarthy, J. J. & Peavey, D. G. 1979 Growth rate influence on the chemical composition of phytoplankton in ocean waters. *Nature, Lond.* **279**, 210–215.
Johnson, K. M. & Sieburth, J. 1979 Chroococcoid cyanobacteria in the sea in a ubiquitous and diverse phototrophic biomass. *Limnol. Oceanogr.* **24**, 928–935.
Jørgensen, B. B., Kuenen, J. G. & Cohen, Y. 1979*a* Microbial transformations of sulfur compounds in a stratified lake (Solar Lake, Sinai). *Limnol. Oceanogr.* **24**, 799–822.
Jørgensen, B. B., Revsbech, N. P., Blackburn, T. H. & Cohen, Y. 1979*b* Diurnal cycle of oxygen and sulfide microgradients and microbial photosynthesis on a cyanobacterial mat sediment. *Appl. environ. Microbiol.* **38**, 46–58.
McCarthy, J. J. & Goldman, J. C. 1979 Nitrogenous nutrition of marine phytoplankton in nutrient depleted waters. *Science, N.Y.* **203**, 670–673.
Marra, J., Landrian, G., Jr & Ducklow, H. W. 1981 Tracer kinetics and plankton rate processes in oligotrophic oceans. *Mar. Biol. Lett.* **2**, 216–223.
Marshall, K. C. 1976 *Interfaces in microbial ecology*. Harvard University Press.
Norkraus, B. 1980 Surface microlayers in aquatic environments. *Adv. microb. Ecol.* **4**, 51–85.
Oren, A. & Padan, E. 1978 Induction of anaerobic photoautotrophic metabolism on ecology of cyanobacteria. *Adv. microb. Ecol.* **3**, 1–48.
Oren, A. & Shilo, M. 1979 Anaerobic heterotrophic dark metabolism in the cyanobacterium *Oscillatoria limnetica*: Sulfur respiration and lactate fermentation. *Arch. Microbiol.* **122**, 77–84.
Padan, E. 1979*a* Facultative anoxygenic photosynthesis in cyanobacteria. *A. Rev. Pl. Physiol.* **30**, 27–40.
Padan, E. 1979*b* Impact of facultatively anaerobic photoautotrophic metabolism on ecology of cyanobacteria. *Adv. microb. Ecol.* **3**, 1–48.
Padan, E. & Shilo, M. 1973 Cyanophages – viruses attacking blue-green algae. *Bact. Rev.* **37**, 343–370.
Peterson, B. J. 1980 Aquatic primary productivity and the ^{14}C–CO_2 method. A history of the productivity problem. *A. Rev. ecol. Syst.* **11**, 359–385.
Poindexter, J. S. 1979 Morphological adaptation to nutrient concentration. In *Strategies of microbial life in extreme environments* (ed. M. Shilo), pp. 341–356. Weinheim and New York: Verlag Chemie.
Poindexter, J. S. 1981*a* Oligotrophy: fast and famine existence. *Adv. microb. Ecol.* **5**. (In the press.)
Poindexter, J. S. 1981*b* The caulobacters: ubiquitous unusual bacteria. *Microbiol. Rev.* **45**, 123–179.
Potts, M. 1979 Nitrogen fixation (acetylene reduction) associated with communities of heterocystous and non-heterocystous blue-green algae in mangrove forests of Sinai. *Oecologia* **39**, 359–373.
Revsbech, N. P., Jørgensen, B. B. & Brix, O. 1981*a* Primary production of microalgae in sediments measured by oxygen microprofile, $H^{14}CO_3$-fixation and oxygen exchange methods. *Limnol. Oceanogr.* **26**, 717–730.
Revsbech, N. P., Jørgensen, B. B. & Cohen, Y. 1981*b* Oxygen, sulfide, and pH microelectrode measurements of photosynthetic and respiratory processes in a cyanobacterial mat sediment. *Limnol. Oceanogr.* (In the press.)
Reynolds, C. S. & Walsby, A. E. 1975 Water blooms. *Biol. Rev.* **50**, 437–481.
Rosenberg, M., Gutnick, D. & Rosenberg, E. 1980 Adherence of bacteria to hydrocarbons: a simple method for measuring cell surface hydrophobicity. *FEMS Lett.* **9**, 29–33.
Rippka, R., Deruelles, J., Waterbury, J. B., Herdman, M. & Stanier, R. Y. 1979 Generic assignments, strain histories and properties of pure cultures of cyanobacteria. *J. gen. Microbiol.* **111**, 1–61.
Sheldon, B. F. & Sutcliffe, W. H. 1978 Generation time of 3 h for Saragano Sea microplankton determined by ATP analysis. *Limnol. Oceanogr.* **23**, 1051–1054.
Shilo, M. 1967 Formation and mode of action of algal toxins. *Bact. Rev.* **31**, 180–193.
Shilo, Miriam 1970 Lysis of blue-green algae by myxobacter. *J. Bact.* **104**, 453–461.
Shilo, M. 1971 Biological agents which cause lysis of blue-green algae. *Proc. Soc. int. Limnol.* **19**, 206–213.
Shilo, M. 1972 Toxigenic algae. *Prog. ind. Microbiol.* **11**, 235–265.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Shilo, M. 1975 Factors involved in dynamics of algal blooms in nature. In *Unifying concepts in ecology* (ed. W. H. van Dobben & R. H. Lowe-McConnell), pp. 127–132. The Hague: W. Junk.

Shilo, M. 1980 Strategies of adaptation to extreme conditions in aquatic microorganisms. *Naturwissenschaften* **67**, 384–389.

Sieburth, J. McN. & Johnson, K. M. 1977 Estimation of in situ rates of heterotrophy using diurnal changes in dissolved organic matter and growth rates of picoplankton in diffusion culture. *Helgoländer wiss. Meeresunters.* **30**, 565–574.

Sorokin, Y. L. 1971 On the role of bacteria in the productivity of tropical oceanic waters. *Int. Res. ges. Hydrobiol.* **56**, 1–48.

Steemann-Nielsen, E. 1952 The use of radioactive C^{14} for measuring organic production in the sea. *J. Cons. int. Explor. Mer.* **18**, 117–140.

Steinitz, Y., Mazor, Z. & Shilo, M. 1979 A mutant of the cyanobacterium *Plectomena boryanum* resistant to photooxidation. *Pl. Sci. Lett.* **16**, 327–335.

Steinitz, Y. & Shilo, M. 1976 Study of photodynamic damage in cyanobacteria and mechanisms of their resistance to photooxidative death. In *Abstr. Int. Symp. on Photosynthetic Prokaryotes*, Dundee, pp. 18–21.

Stockenius, W. 1978 Bacteriorhodopsin. In *The photosynthetic bacteria* (ed. R. K. Clayton & W. R. Sistrom), pp. 521–592.

Taylor, C. D., Molongoski, J. J., Doherty, K. W. & Ljungdahl, P. O. 1981 Instrumentation for the in situ, time-course measurement of phytoplankton production. *Limnol. Oceanogr.* (In the press.)

Verduin, J. 1975 Photosynthetic rates in Lake Superior. *Verh. int. Verein. theor. angew. Limnol.* **19**, 689–693.

Walsby, A. E. & Booker, M. J. 1980 Changes in buoyancy of a planktonic blue-green algae in response to light intensity. *Br. phycol. J.* **15**, 311–319.

Walsby, A. E. & Klemer, A. R. 1974 The role of gas vacuoles in the microstratification of a population of *Oscillatoria agardhii* var. *isothrix* in Demming Lake, Minnesota. *Arch. Hydrobiol.* **74**, 375–392.

Waterbury, J. B., Watson, S. W., Guillard, R. R. L. & Brand, L. E. 1979 Widespread occurrence of a unicellular marine planktonic cyanobacteria. *Nature, Lond.* **277**, 293–294.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES