

Marine cyanobacteria in tropical regions: diversity and ecology

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(Received 15 January 1999; accepted 17 June 1999)

Tropical marine ecosystems are characterized by a specific cyanobacterial flora, temperature most probably being the major factor limiting the geographic distribution of the species. When compared with the open ocean, the highest biodiversity of cyanobacteria is observed in the littoral zones where they form intertidal and infralittoral mats, live as endoliths in carbonate substrates or form symbiotic associations, especially with sponges and ascidians. Their diversity, which especially in the less accessible infralittoral is still largely unknown, is also a source of diverse bioactive compounds, some of which are important as herbivore deterrents. As photosynthetic organisms, cyanobacteria *sensu lato* (including Prochlorophyta) are important contributors to benthic and open ocean primary production, but their main role in the tropical marine ecosystems appears to be as nitrogen fixers. Of primary importance in the often oligotrophic tropical oceans is the non-heterocystous, planktonic bloom-forming *Trichodesmium*, which probably represents a major nitrogen source for the marine and global nitrogen cycle.

Key words: biodiversity, biogeography, Cyanobacteria, Cyanophyta, marine, nitrogen fixation, secondary metabolites, tropics

Introduction

The existence of Precambrian fossil stromatolites containing evidence of oxygenic photosynthesis and fossil endoliths similar to living species (Golubic & Knoll, 1993) indicates the long evolutionary and biochemical history of marine cyanobacteria. Contemporary marine cyanobacteria still play important roles, especially in tropical ecosystems (the phytogeographical subdivisions of the oceans as defined by Van den Hoek (1984) for macroalgae are applied here: the tropical oceanic area is thus limited by the 20 °C winter isotherm of the seawater, whereas in the temperate regions water temperature drops to 10 °C), where they have a high biodiversity, are widespread, and may sometimes occur in striking abundance. It was probably a red-pigmented bloom-forming species of the genus *Trichodesmium* which gave the Red Sea its name (Fogg, 1982). The assessment of the biodiversity of cyanobacteria depends on a reliable taxonomy in order definitively to recognize genetically different entities in nature. Modern molecular phylogenetic studies are currently restricted to axenic cultures and DNA mixtures extracted from natural populations. Ecological research will, therefore, continue to depend on the phenotypic identification of cyanobacteria. On the other hand, taxonomic studies of cyanobacteria have neglected marine environments, especially in tropical regions. Identification manuals include only a small fraction of genuine marine cyanobacterial taxa. Consequently, floristic surveys have frequently applied names of freshwater taxa when reporting cyanobacteria from marine habitats.

Renewed interest in marine cyanobacteria was generated in conjunction with the study of marine picoplankton and its contribution to oceanic primary production (Waterbury *et al.*, 1979; Johnson & Sieburth, 1979), while

planktonic filamentous cyanobacteria attracted attention as important contributors to the nitrogen cycle in the ocean as well as toxin producers (see e.g. Sellner, 1997). In contrast, interest in marine benthic cyanobacteria has mostly been limited to intertidal environments, which were used as model systems for the interpretation of fossil stromatolites.

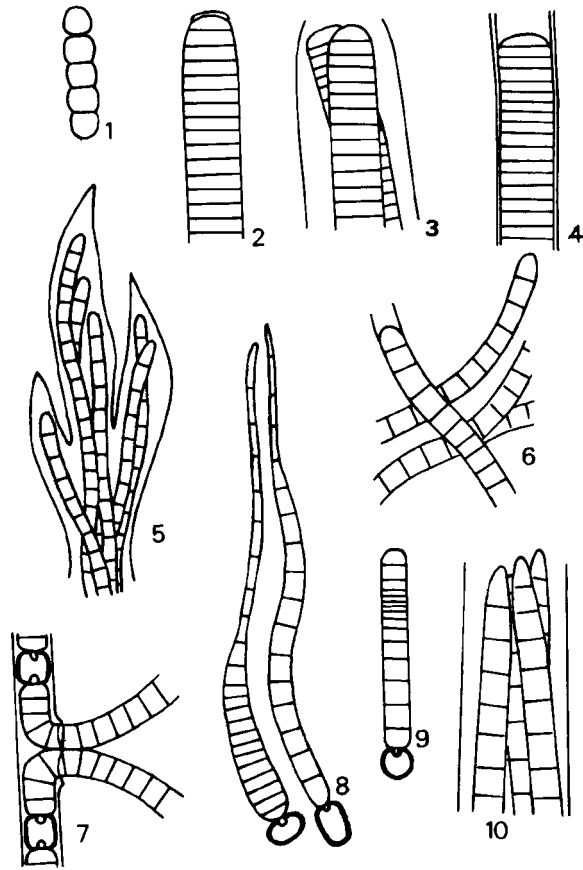
Oxygenic photosynthetic prokaryotes have been placed in two divisions: cyanobacteria (Cyanophyta) characterized by the presence of chlorophyll *a* and phycobiliproteins, and the Prochlorophyta, also called Oxychlorobacteria, characterized by the possession of chlorophylls *a* and *b*, and the absence of phycobilisomes. Sequence analyses have shown, however, that the prochlorophytes are a polyphyletic group residing within the cyanobacterial lineage (Turner, 1997). In the following review, the term 'cyanobacteria' is used in a wide sense, including all oxygenic, photosynthetic prokaryotes (= oxyphotobacteria *sensu* Murray, 1989). The nomenclatural system followed is that of Geitler (1930–2).

Cyanobacteria occupy a wide range of niches in marine ecosystems in tropical regions where they occur along maritime coasts as well as in the open ocean. The environmental constraints to which they are exposed vary widely in these two habitat categories, so that their biodiversity and ecology in the benthic and planktonic environments will be considered separately.

Littoral cyanobacteria

Cyanobacteria of intertidal and supratidal zones

Benthic cyanobacteria are widespread along maritime coasts, often forming visually conspicuous growths on rocks and sediments as mats and epilithic growths. A

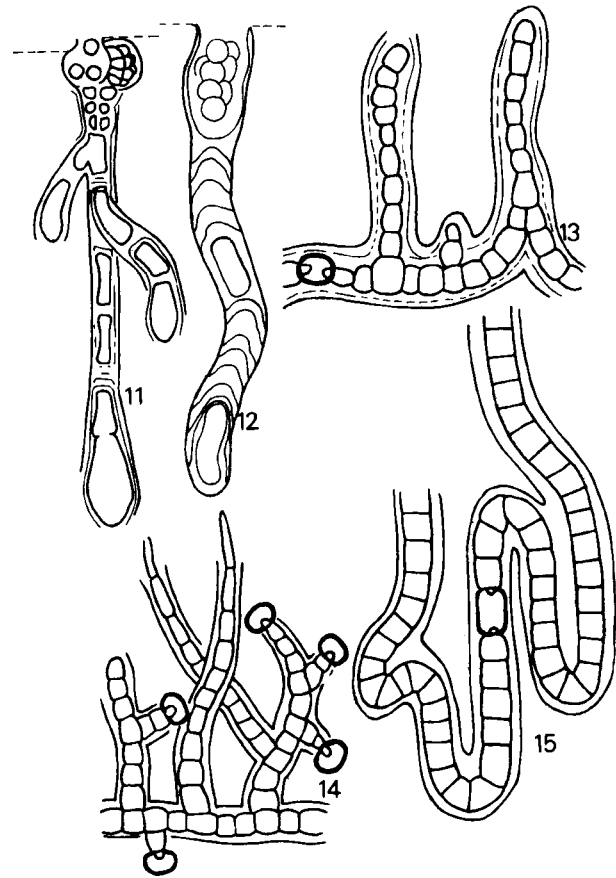


Figs 1–10. Representative cyanobacterial genera of the tropical marine benthos. Fig. 1. *Borzia* Gomont. Fig. 2. *Oscillatoria* Gomont. Fig. 3. *Hydrocoleum* Gomont. Fig. 4. *Lyngbya* Gomont. Fig. 5. *Schizothrix* Gomont. Fig. 6. *Phormidium* Gomont. Fig. 7. *Scytonema* Bornet et Flahaut. Fig. 8. *Calothrix* Bornet et Flahaut. Fig. 9. *Microchaete* Bornet et Flahaut. Fig. 10. *Microcoleus* Gomont.

littoral fringe containing lichens and cyanobacteria is of almost universal occurrence on rocky shores (Stephenson & Stephenson, 1949) and has also been described from tropical regions such as around the Seychelles (Taylor, 1968).

The occurrence of extensive mats of cyanobacteria is observed on or in much tropical coastal sand and silt. Many of the more complex types play an important role in building and trapping sediments and/or in carbonate precipitation (Golubic, 1973). Some of these littoral communities dominated by cyanobacteria are restricted to warm waters; this is especially true for those which form well-developed stromatolites, which are lithified mats. Many examples of stromatolites have been described (Walter, 1976). They are most abundant in lagoons and sheltered coastal localities; some of the best-developed examples, such as those at Shark Bay (Western Australia) or in the Persian Gulf, are found in hypersaline waters.

On moving from the supralittoral down to the intertidal zone, mats often show a zonation. The distribution of the types of mats is determined by the frequency and duration of subaerial exposure, wave energy, and the type and amount of sediment transported by tidal currents (e.g. Golubic, 1985). The surface morphology of mats depends on the prevailing environmental conditions, but also on



Figs 11–15. Representative genera of tropical marine endolithic cyanobacteria. Fig. 11. *Hyella* Bornet et Flahaut. Fig. 12. *Solentia* Ercegovic. Fig. 13. *Herpyzonema* Weber-van Bosse. Fig. 14. *Mastigocoleus* Bornet et Flahaut. Fig. 15. *Kyrtuthrix* Ercegovic.

the dominant species (Golubic & Focke, 1978; Zhang & Hoffmann, 1982).

The intertidal zone is often dominated by sheath-producing taxa of filamentous non-heterocystous (*Lyngbya*, *Microcoleus*, *Phormidium*, *Schizothrix*) and heterocystous (*Rivularia* Bornet et Flahaut, *Calothrix*, *Scytonema*) genera (Figs 1–10). Vertical sections of mats usually include various groups of prokaryotes in discrete coloured layers. The surface layer is often dominated by the cosmopolitan *Lyngbya aestuarii* Gomont. This species seems to be protected from excessive radiation by the brown extracellular sheath pigment 'scytonemin' (Garcia-Pichel & Castenholz, 1991). Another common and geographically widespread member of microbial mats is *Microcoleus chthonoplastes* Gomont.

Mangrove forests, common along many tropical and some subtropical coastal lagoons are inhabited by diverse cyanobacterial communities which reside on leaf and root litter, live roots, and often form extensive mats on the surrounding sediments (e.g. Potts, 1979, 1980; Potts & Whitton, 1980; Sheridan, 1991; Hussain & Khoja, 1993; Toledo *et al.*, 1995; Phillips *et al.*, 1996); many of these communities are capable of N₂ fixation. The genera *Oscillatoria*, *Lyngbya*, *Phormidium* and *Microcoleus* are widespread in these habitats, as are heterocystous genera, such as *Scytonema*, in some areas (Potts, 1979). Vertical

Table 1. Floristic survey of marine cyanobacteria in Papua New Guinea (Hoffmann, 1989, 1993; Hoffmann & Demoulin, 1991, 1993).

	No. of genera	No. of species and subspecies	No. of new taxa
CHROOCOCCALES	14	20	5
Chamaesiphonaceae	2	4	2
Chroococcaceae	1	1	—
Dermocarpellaceae	1	1	—
Hydrococcaceae	4	7	3
Microcystaceae	4	5	—
Prochloraceae	1	1	—
Xenococcaceae	1	1	—
OSCILLATORIALES	9	41	17
Oscillatoriaceae	9	41	17
NOSTOCALES	5	13	3
Microchaetaceae	1	2	1
Nostocaceae	1	2	—
Rivulariaceae	2	7	1
Scytonemataceae	1	2	1
STIGONEMATALES	3	3	—
Mastigocladaceae	2	2	—
Nostochopsidaceae	1	1	—

zonation is often observed on the pneumatophores or prop roots.

Cyanobacteria that live inside limestone rocks are also an important feature of intertidal habitats (Radtke *et al.*, 1997). The colonization of marine rocks by endoliths can be very rapid (Perkins & Tsentas, 1976; Potts & Whitton, 1980). The cyanobacterial endolithic assemblages exhibit a well-defined zonation pattern which is recognized by changes in the dominance and abundance of the different species and can be correlated with differences in tidal range and the vertical distribution of the macroflora and macrofauna (Hoffman, 1985; Radtke *et al.*, 1996; Taton & Hoffmann, 1999). The upper ranges are generally dominated by *Herpyzonema*, *Hormathonema* Ercegovic, *Scytonema*, *Solentia* and *Kyrtuthrix*, whereas *Mastigocoleus* (Figs 11–15) generally appears only in the lower intertidal zone. The major difference between temperate and tropical carbonate coasts seems to lie in the presence and often dominance of *Herpyzonema intermedium* Weber-van Bosse in tropical regions (Hoffman, 1985; Taton & Hoffmann, 1999), whereas in temperate regions such as the Mediterranean Sea (Le Campion-Alsumard, 1979), *Hyella balani* Lehmann seems to occupy the niche of the latter species in the intertidal zone.

Cyanobacteria of the infralittoral zone

Conspicuous growths of sublittoral benthic mats are frequently recorded from warmer waters, where films of filamentous species overlying sand in shallow water appear to be relatively common. In contrast to those found in the intertidal, they are simpler, generally do not show a vertical zonation, and consist of films of interwoven filaments, often of single species. Thick mats can

extend to the lower part of the shore in sheltered, moderately hypersaline conditions (Potts & Whitton, 1980; Bauld *et al.*, 1992) and can even form stromatolites (Golubic & Browne, 1996). Mats with cyanobacteria have been observed to depths of 50 m, but in general growth appears to be most rapid in depths of less than 10 m. These superficial mats become established where rates of sediment movement and turnover by grazers and especially by burrowers are low (Whitton & Potts, 1982).

In the infralittoral zone a very high biodiversity is found, especially near coral reefs, where the oscillatorian genera (*Oscillatoria*, *Hydrocoleum*, *Microcoleus*) are represented by many taxa, some of which remain to be described (e.g. Hoffmann & Demoulin, 1993; see also Table 1). Little information is available about their ecology, including their interactions with herbivores, although some reports mention that they are heavily grazed, for instance by holothurians (Sournia, 1976).

Epiphytic cyanobacteria (especially *Calothrix*, *Microchaete*, *Lyngbya*) are present on pelagic macroalgae such as *Sargassum* C. Agardh (Phlips *et al.*, 1986), and on benthic macroalgae and seagrasses (e.g. Brouns & Heijs, 1986; Klumpp *et al.*, 1992; Hoffmann, 1993), together with diatoms, Chlorophyta and Rhodophyta. These epiphytic communities are important contributors to the overall productivity (Moncreiff *et al.*, 1992) and are a major food source for macroinvertebrate grazers (Klumpp *et al.*, 1992; Mukai & Iijima, 1995). Many of these epiphytic cyanobacteria are heterocystous and thus fix N₂, which may contribute to the marine nitrogen budget (e.g. the estimated nitrogen input by epiphytic cyanobacteria on *Sargassum* amounts to 0.018 10⁹ g N year⁻¹, Capone & Carpenter, 1982).

The tropical regions are also characterized by particularly diverse endolithic cyanobacterial communities (including e.g. the genera *Hyella*, *Solentia*) (Figs 11, 12) which can be found in the skeletons of living and dead coral (Le Campion-Alsumard *et al.*, 1995) and in other limestone substrata, contributing substantially to the dissolution of carbonates of coral reefs (Chazottes *et al.*, 1996) and to the bioerosion of limestone coasts. Recent studies demonstrate a high diversity of endolithic cyanobacteria in shallow tropical and subtropical seas. Many new taxa, especially within the genus *Hyella*, have thus been described in the last 20 years, for example from the Bahamas, Florida and the Arabian Gulf (Golubic *et al.*, 1996 and references cited therein).

Black-band disease is a widespread phenomenon found on coral reefs (Richardson, 1996). The disease consists of a microbial community dominated by the filamentous cyanobacterium *Phormidium corallyticum* (Rützler & Santavy, 1983) associated with bacteria and fungi. It normally forms a band 1 mm thick between the coral skeleton and the living coral tissue. Black-band disease can cause the death of entire coral colonies due to tissue destruction as the bands migrate, and is thought to be a factor contributing to the observed global degradation of coral reefs (Williams & Bunkley-Williams, 1990).

A noteworthy feature of tropical regions, especially of coral reefs, is the presence of a number of cyanobacterial species belonging to the genera *Aphanocapsa* Nägeli, *Prochloron* Lewin ex Florenzano *et al.*, *Synechocystis* Sauvageau, *Borzia* and *Oscillatoria*, which live in symbiosis with sponges (Wilkinson, 1992) or ascidians (Pardy & Royce, 1992). Recently, a new type of unicellular oxygenic photosynthetic prokaryote was isolated from a tropical colonial ascidian, *Lissoclinum patella*, and provisionally named *Acaryochloris marina* Miyashita *et al.* Chihara gen. *et* sp. *in*edit. (Miyashita *et al.*, 1996). Its most distinctive feature is the presence of a unique light-harvesting system which uses chlorophyll *d* as the major antenna pigment and chlorophyll *a* as a minor pigment. Like other species commonly included in the Prochlorophyta (Goerick & Repeta, 1992; Larkum *et al.*, 1994), it also contains a chlorophyll *c*-like pigment (Miyashita *et al.*, 1997) which is absent in cyanobacteria *sensu stricto*. Some of these organisms, especially *Prochloron* and *Acaryochloris*, are interesting models for the studies on the origin of the different algal plastid types (Lewin & Cheng, 1989; Matthijs *et al.*, 1994; Turner, 1997).

Coral reefs are one of the tropical marine habitats in which cyanobacterial diazotrophs appear to play a critical role in ecosystem functioning. Cyanobacteria are found in monospecific mats, mixed 'algal' turfs and as macroalgal epiphytes. Cyanobacteria play an important role in the nitrogen budget of coral reefs (Mague & Holm-Hansen, 1975; Webb *et al.*, 1975; Wiebe *et al.*, 1975; Burris, 1976), where N₂ fixation can account for 20–40% of the annual nitrogen requirements (Borowitzka & Larkum, 1986). The estimated annual contribution of coral reefs to the global nitrogen cycle amounts to 2.8 Tg, with a mean areal N₂ fixation rate of 25 g m⁻² year⁻¹ (Capone & Carpenter, 1982).

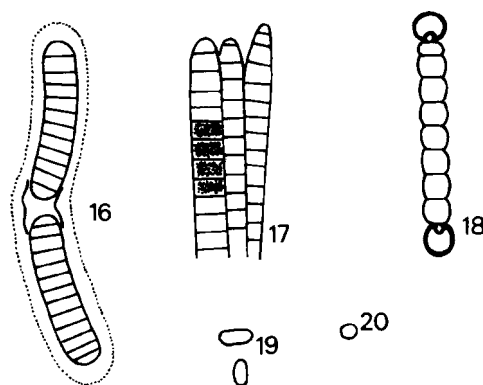
Although benthic cyanobacteria are periodically very common in reef habitats subject to high levels of herbivory, and although they lack structural defences (e.g. calcification) like various macroalgae, they seem to be a low-preference food item for many marine herbivores. Some of these cyanobacteria, such as the genera *Hormothamnion* Bornet *et* Flahaut (Pennings *et al.*, 1997) and *Lyngbya* (Pennings *et al.*, 1996; Nagle *et al.*, 1996; Orjala & Gerwick, 1996), are unpalatable to most, but not all, potential consumers, probably because of the presence of secondary metabolites which effectively deter feeding. Marine cyanobacteria have been a productive source of novel secondary metabolites (Moore, 1981; Faulkner, 1995) with varying bioactivities. They present a diversity of structural classes: cyclic peptides, depsipeptides, linear peptides, guanidines, phosphonates, purines, lipids and macrolides. They often contain nitrogen (in striking difference to those found in macroalgae) and often are halogenated (e.g. brominated pyrrole derivatives, chlorinated amides) (Moore, 1981). Some secondary metabolites from marine cyanobacteria have been examined for pharmacological activity (e.g. cytotoxicity to tumour cells, inhibition of proteases) (Shimizu, 1996). Several

bioactive peptides found in cyanobacteria have structural features of metabolites described from ascidians and sponges living in coral reefs (Namikoshi & Rinehart, 1996), which suggests the latter compounds may be derived from dietary or symbiotic cyanobacteria (Williams *et al.*, 1993), but transfer of genes cannot completely be ruled out (Shimizu, 1996).

One of the richest cyanobacterial source of secondary metabolites is the benthic filamentous *Lyngbya majuscula* Gomont (Mermaid hair) (Moore, 1981; Moore *et al.*, 1984; Sitachitta & Gerwick, 1998; Graber & Gerwick, 1998; Hooper *et al.*, 1998), one of the largest cyanobacteria known, which caused an outbreak of severe contact dermatitis in fishermen due to the presence of prenylated amino acid derivatives, called lyngbyatoxins (Cardellina *et al.*, 1979). Another *Lyngbya* species, *L. bouillonii*, recently described from coral reefs in Papua New Guinea (Hoffmann & Demoulin, 1991) where it forms extensive mats, strongly attached to madrepores in the infralittoral, proved also to be a rich source of novel macrolides and peptides (Klein *et al.*, 1996, 1997, 1999). *Hormothamnion enteromorphoides* contains a series of at least 15 related cyclic peptides (Gerwick *et al.*, 1989). Their chemical defences thus are probably a key factor allowing these cyanobacteria to persist in reefs.

Planktonic cyanobacteria

In contrast to their abundance in freshwater habitats, there are few truly planktonic cyanobacterial species in the sea. There are four groups of cyanobacteria known to be present in the plankton of tropical oceans in numbers sufficient to make a measurable ecological contribution: the picoplanktonic *Synechococcus* and *Prochlorococcus* (see e.g. Ferris & Palenik, 1998) and the filamentous genera *Trichodesmium* (Capone *et al.*, 1997) and *Richelia* (Villareal, 1992) (Figs 16–20). There are, of course, many other reports of cyanobacteria of various genera (Sournia, 1970), such as *Katagnymene* (Wille, 1904), but none of these seems to make a consistent major input into the ecosystem.



Figs 16–20. Representative cyanobacterial genera of the tropical marine plankton. Fig. 16. *Katagnymene* Lemmermann. Fig. 17. *Trichodesmium*: Ehrenberg ex Gomont. Fig. 18. *Richelia* Schmidt. Fig. 19. *Synechococcus* Nägeli. Fig. 20. *Prochlorococcus* Chisholm *et al.*

Trichodesmium

During the past few decades, *Trichodesmium* has been one of the most intensively studied cyanobacteria of the open tropical oceans. The main reasons for this interest are that *Trichodesmium* can occur in great abundance (as surface blooms) and it can fix N₂ (Dugdale *et al.*, 1961) during the day without the formation of thick-walled heterocysts (Bergman & Carpenter, 1991).

Trichodesmium includes a number of filamentous forms which, apart from their general tendency to aggregate in bundles, closely resemble species of *Oscillatoria*. Five marine species are included in the genus *Trichodesmium*, distinguished by trichome dimensions and colony morphology. On the basis of ultrastructure (Janson *et al.*, 1995b), *T. erythraeum* Gomont and *T. tenue* Wille, with spherical colony shape and narrow trichomes, can be distinguished from *T. thiebautii* Gomont, *T. hildebrandtii* Gomont and *T. contortum* Wille. The presence of several distinct morphotypes is consistent with the results from nitrogenase nifH and 16S rDNA sequence analyses (Capone *et al.*, 1997), which also show that all *Trichodesmium* clones studied so far form a monophyletic group.

Species of *Trichodesmium* are primarily found in tropical and subtropical surface waters, especially during calm conditions. These waters have low nutrient concentrations and deep euphotic zones (Capone *et al.*, 1997). Under calm conditions, filaments accumulate as surface blooms known to sailors as 'sea sawdust'. Such blooms are often large enough to be detected by satellite.

The positive buoyancy of *Trichodesmium* depends on the presence of very strong gas vesicles (Walsby, 1978), a possible adaptation to the great hydrostatic pressures to which *Trichodesmium* can be exposed at depth in the sea (e.g. about 20 bars at 200 m). When highly gas-vacuolated, they can migrate to the surface at a velocity of 0.5–3 mm s⁻¹ (40–250 mm day⁻¹). In addition to providing buoyancy, the gas vacuoles may shield the cells from excessively strong radiation (Janson *et al.*, 1995b).

Trichodesmium is well adapted to living in oligotrophic waters. It fixes atmospheric nitrogen, thus avoiding nitrogen limitation, and uses buoyancy reversals to migrate below the nutricline to acquire phosphorus (Carpenter & Romans, 1991; Karl *et al.*, 1992). In oligotrophic waters removed from terrestrial influences and unaffected by upwelling, where N₂-fixing planktonic or benthic cyanobacteria are of importance, additional nutrient limitations may occur. In particular the availability of iron, essential for N₂ fixation, NO₃⁻ assimilation and photosynthetic activity, may be restricted (Rueter *et al.*, 1992; Paerl *et al.*, 1994).

The enigmatic situation of having an oxygen-generating photosystem II functioning at the same time as the highly oxygen-sensitive process of nitrogen fixation is one of the most interesting traits of *Trichodesmium*. At least in certain *Trichodesmium* species, cells containing nitrogenase are clustered into groups (Janson *et al.*, 1995b).

A recent model (Fredriksson & Bergman, 1997) proposes (a) that *Trichodesmium* is capable of differentiating a cell type which is specific for nitrogenase; (b) that these nitrogenase-containing cells are grouped into small subsets, possibly one or more subsets in each filament; and (c) that these cells are structurally and functionally modified to harbour the oxygen-sensitive nitrogenase.

Trichodesmium aggregates often harbour diverse eukaryotic and prokaryotic organisms: bacteria, cyanobacteria, diatoms, dinoflagellates, fungi, protozoa, hydroids and copepods (O'Neil & Roman, 1992; Siddiqui *et al.*, 1992). The association of most organisms with *Trichodesmium* colonies appears to be mutualistic, but larger planktonic and nektonic organisms (fish, crabs) may graze on *Trichodesmium* filaments. There are also associations of the juvenile harpacticoid copepod *Macrosetella gracilis* with *Trichodesmium*. It not only ingests *Trichodesmium* colonies but rapidly incorporates cyanobacterial organic matter into its own cellular material (O'Neil, 1998). The neurotoxins identified for some *Trichodesmium* blooms (Hawser *et al.*, 1991; Hawser & Codd, 1992) may have a role in determining the susceptibility or resistance of *Trichodesmium* to grazers (Hawser *et al.*, 1992).

A rapid disappearance of *Trichodesmium* blooms has been observed in the natural environment. Though the grazing action of zooplankton is considered a potential cause, recent observations (Ohki, 1997) suggest that *Trichodesmium* harbours a temperate virus leading to lysis. As for the picoplanktonic *Synechococcus* (Suttle & Chan, 1994), viruses may play an important role in this component of the food web of the oligotrophic tropical ocean (Fuhrman & Suttle, 1993).

There seems to be little doubt that *Trichodesmium* is the principal source of N₂ fixation in marine pelagic ecosystems, contributing an estimated 80 Tg (Capone *et al.*, 1997) of fixed nitrogen per year, which could support up to half of the new production in oligotrophic oceans (Karl *et al.*, 1997).

Richelia intracellularis and other cyanobacteria–diatom symbioses

Two types of cyanobacteria–diatom symbioses are common in the tropical marine plankton. The most frequently reported is the association of the heterocystous filamentous cyanobacterium generally referred to as *Richelia intracellularis* Schmidt (Nostocaceae) with the diatom genera *Rhizosolenia*, *Hemiaulus*, *Bacteriastrum* and *Chaetoceros* (Villareal, 1992). Besides *R. intracellularis*, an additional taxon, *Calothrix rhizosoleniae* (Rivulariaceae), was described by Lemmermann (1905). The similarity of the two symbionts may have led to misidentifications and it would be interesting to establish their genetic relationship. *R. intracellularis* has short unbranched filaments with heterocysts at one end or, less commonly, both ends. There are usually two to four filaments per diatom cell but the number increases with the size of the host (up to 32;

Sundström, 1984). The cyanobiont is usually located at the apex of the host *Rhizosolenia* cell outside the host cytoplasm and there is no evidence for the presence of gas vesicles (Janson *et al.*, 1995a). The filament breaks into two halves, one half migrating into each daughter cell (Taylor, 1982). The division cycles of the diatom host and of the *Richelia* symbiont seem to be largely uncoupled (Villareal, 1989).

Richelia is primarily found in warm tropical and subtropical waters, with a latitudinal range from approximately 38°N to 36°30'S (Sournia, 1970; Villareal, 1992). Its abundance varies with season, being low in winter (10 cells l⁻¹) and high in late summer (10⁴ cells l⁻¹) in the central North Pacific gyre (Venrick, 1974).

Together with *Trichodesmium* these intracellular diatom cyanobionts contribute to nitrogen fixation in oligotrophic tropical oceans (Mague *et al.*, 1974; Venrick, 1974; Carpenter & Romans, 1991). Nitrogenase is found only in heterocysts in *Richelia* and nitrogen is fixed during the day with rates ranging up to 18 mg N m⁻² day⁻¹, supporting up to 36% of total phytoplankton production during some blooms (Sellner, 1997).

A second type of symbiosis occurs between unicellular, coccoid cyanobacteria and the diatom genus *Neostreptotheca*, an association for which few data are available (Villareal, 1992).

Synechococcus and *Prochlorococcus*

Picoplanktonic cyanobacteria are an important component of the marine plankton community (e.g. Ferris & Palenik, 1998). Biomass and photosynthesis measurements in different tropical and equatorial oceans show that the bulk of the chlorophyll *a* is in organisms of less than 1 µm and 3 µm respectively, and that this contributes 20–90% of the photosynthetic productivity (e.g. tropical North Atlantic: Platt *et al.*, 1983; eastern tropical Pacific Ocean: Li *et al.*, 1983; subtropical Hawaiian waters: Takahashi & Bienfang, 1983). These cyanobacteria are an important food source for planktonic heterotrophic flagellates and ciliates, as well as macroinvertebrates (Yahel *et al.*, 1998).

The two important picoplanktonic groups are *Synechococcus*, discovered 20 years ago (Waterbury *et al.*, 1979; Johnson & Sieburth, 1979), and *Prochlorococcus* (Chisholm *et al.*, 1988; Chisholm *et al.*, 1992), identified 10 years ago. *Prochlorococcus* is a unicellular oxygenic photosynthetic prokaryote that contains divinyl chlorophyll *b* as its main pigment (Goericke & Repeta, 1992) rather than the phycobiliproteins typical of cyanobacteria. At least two ecotypes, adapted to grow at either low or high light intensities, can be distinguished (Moore *et al.*, 1998).

While the coccoid *Synechococcus* is virtually ubiquitous in all marine environments, ranging in abundance over three orders of magnitude from 500 to 500 000 cells ml⁻¹, *Prochlorococcus* is virtually ubiquitous in the latitudinal band 40°N–40°S where it comprises a significant proportion of the photosynthetic biomass (Campbell *et al.*, 1994). North of 40°N and south of 40°S it can still be

found but its concentrations decline fairly rapidly (Partensky *et al.*, 1999). It is found throughout the photic zone, but in contrast to *Trichodesmium* often dominates the deep chlorophyll maximum at densities of 10⁴–10⁵ cells ml⁻¹ (Post & Bullerjahn, 1994). It was suggested (Vaulot *et al.*, 1995) that, in contrast to *Synechococcus*, *Prochlorococcus* may not be severely limited by nutrients, including iron.

Geographical distribution of tropical cyanobacteria

The study of the distribution of cyanobacteria is hampered by difficulties in recognizing the different taxa due to their simple morphology. To date, only floristic lists using the traditional geitlerian approach and Drouet's system (Drouet, 1981) (e.g. Humm & Wicks, 1980; Zaneveld, 1988) have appeared in the literature. However, it has been shown that the latter system does not reflect the natural cyanobacterial diversity (e.g. Stam, 1978; Waterbury & Stanier, 1978). The main identification guide is still Geitler (1930–2), which mostly deals with taxa described from temperate regions. Many taxonomists working on tropical collections and encountering populations which did not correspond well to any described species often simply referred these to the most similar taxon known from temperate regions (Komárek, 1985). Such misinterpretations led to an overestimate of the distribution area of many species originally described from temperate zones. This situation will improve with the new edition of the *Süßwasserflora von Mitteleuropa*, which also includes non-European species as is already the case in the first published part treating the unicellular cyanobacteria (Komárek & Anagnostidis, 1999). Notwithstanding these methodological difficulties, it seems that apart from cyanobacterial species with a (sub)cosmopolitan distribution (e.g. *Lyngbya aestuarii*, *Microcoleus chthonoplastes* Gomont), as confirmed by a phenotypic and phylogenetic analysis of *M. chthonoplastes* by Garcia-Pichel *et al.* (1996), some seem to be limited almost exclusively to warm-water regions (e.g. the planktonic genera *Trichodesmium* (Capone *et al.*, 1997) and *Prochlorococcus* (Partensky *et al.*, 1999) and the benthic genera *Prochloron* (Lewin & Cheng, 1989), *Herpyzonema* and *Hormothamnion* (Hoffmann, 1993)). The distribution of these taxa suggests that temperature is probably a major factor limiting their distribution (Hoffmann, 1994). This has been confirmed by culture studies, for example, of two clones of the genus *Prochlorococcus* that showed minimum growth temperatures of 15 and 12.5 °C, respectively (Moore *et al.*, 1995). In the same way, the growth and activity of the genus *Trichodesmium*, which is occasionally found in waters colder than 20 °C, are usually restricted to waters above 20 °C (Capone *et al.*, 1997).

Conclusions

As photosynthetic organisms, cyanobacteria *sensu lato* are important contributors to benthic and open ocean primary production, but their main role in tropical marine ecosystems appears to be as nitrogen fixers. Of primary

importance in the often oligotrophic tropical oceans is the non-heterocystous, planktonic bloom-forming *Trichodesmium*. N₂ fixation associated with *Trichodesmium* probably represents a major nitrogen source to the marine and global nitrogen cycle. Tropical marine ecosystems are characterized by a specific cyanobacterial flora and nature seems to have provided all possible combinations of photosynthetic pigments, thus presenting interesting model systems for the study of the evolution of plastids. The largely unknown biodiversity, especially in the less accessible infralittoral, may also in the future be an important renewable source for hitherto undescribed bioactive compounds, some of which may have potential as antibiotics, antitumour agents and related pharmaceuticals (Rossi *et al.*, 1997).

Acknowledgements

The author is a research associate of the Belgian National Fund for Scientific Research whose financial support is also acknowledged in the framework of FRFC grants 2.9006.86, 2.9001.90 and 2.4521.96 which allowed the author, in cooperation with professor V. Demoulin, to get acquainted with the tropical marine cyanobacteria of Papua New Guinea.

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