Differential distribution and ecology of *Prochlorococcus* and *Synechococcus* in oceanic waters: a review

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ABSTRACT

Photosynthetic prokaryotes evolving oxygen are a major component of oceanic ecosystems. The diversity of these micro-organisms in the picoplanktonic fraction of open oceans appears to be very limited, since they are represented almost exclusively by two genera : *Synechococcus* and *Prochlorococcus*.

Synechococcus is virtually ubiquitous in all marine environments with concentrations ranging from 5×10^2 to 1.5×10^6 cell ml^{-1} (or 0.01 to > 1.3 $\times 10^9$ cells per cm^{-2}). It is much more abundant in nutrient-rich than in oligotrophic areas and its distribution is generally restricted to the upper well-lit layer. *Synechococcus* has also been reported at fairly high abundances from environments with low salinities and (or) low temperatures. In contrast, *Prochlorococcus* appears to be less ubiquitous. Although it is by far the most abundant group in the central oligotrophic part of oceans, with concentrations of 1-4 10^5 cell ml^{-1} (or 1 to 4 10^9 cells per cm^{-2}), cell numbers drop dramatically at latitudes higher than 45°N. Moreover, this organism is generally absent from brackish or well-mixed waters. Nevertheless, it is not strictly restricted to oligotrophic areas, but can be found in mesotrophic conditions as well. In the Equatorial Pacific, for instance, there are no drastic changes of *Prochlorococcus* abundance between the oligotrophic warm pool and the high nutrient-low chlorophyll (HNLC) areas. Another peculiarity of this

organism is its ability to colonize the water column down to depths of 150-200 m, which are reached by less than 0.1% of the surface irradiance.

Thus, although *Synechococcus* and *Prochlorococcus* often co-occur, they have different types of adaptation with regard to biogeochemical conditions. Recent literature provides some clues about the biological and genetic bases of these differential behaviours. In terms of carbon biomass, *Prochlorococcus*, despite its narrower geographical distribution, seems to be more important than *Synechococcus* on a global scale since it is ca. 100 times more abundant (i.e. account for about 22 times more C) in warm oligotrophic areas, which correspond to a major part of the world ocean. An estimation of their relative contributions to the carbon biomass in the northern Atlantic ocean is proposed.

INTRODUCTION

In less than twenty years, the view of the community structure of oceanic phytoplankton has drastically changed. Apart from the premonitory work of Wauthy *et al.* (1967) and a few incidental reports on small-sized cells (Stockner, 1988), the central parts of the oceans were generally considered as being biological deserts only inhabited by very scarce phytoplanktonic cells. The generalized use of epifluorescence microscopy and later, flow cytometry demonstrated the huge abundance and the ubiquitous distribution of coccoid photosynthetic prokaryotes. The first organism of this kind to be detected was the cyanobacterium *Synechococcus*, which is easily distinguishable by fluorescence techniques due to the intense orange fluorescence emitted by its phycoerythrin under blue light (Waterbury *et al.*, 1979; Murphy & Haugen, 1985; Olson *et al.*, 1988). The second was *Prochlorococcus*, which differs from *Synechococcus* by virtue of its smaller size and very low or lack of orange fluorescence (Chisholm *et al.*, 1988, 1992; Hess *et al.*, 1996). Surprisingly, with the exception of *Trichodesmium* (Carpenter *et al.*, 1993) which does not belong to the picoplankton, the diversity of picoplanktonic prokaryotes in oceanic ecosystems is almost exclusively limited to these two genera. Few other free-living photosynthetic oceanic prokaryotes of ecological significance have been reported to date, even at a local scale. These include phycocyanin-rich *Synechococcus* found in estuarine and coastal areas (see e.g. Shimada *et al.*, 1995) and potentially nitrogen-fixing *Gloeocapsa*-like cells observed in the North Atlantic Ocean by Johnson & Sieburth (1979) using electron microscopy. Also, Neveux *et al.* (1999) observed in the subtropical Pacific Ocean some non-motile round cells, about 2-3 µm in size, containing an unusual phycoerythrin. These are possibly the same micro-organisms as those observed previously by flow cytometry by Ishizaka *et al.* (1994) in the central north Pacific and Campbell *et al.* (1997) at station Aloha, and that were tentatively identified as *Synechocystis*.

Because of its rapidity and sensitivity, flow cytometry proved a very useful instrument for the study of photosynthetic prokaryotes. In the past ten years, the number of biological oceanographers using flow cytometry to study marine picophytoplankton has increased tremendously and a large amount of data has been collected on picoplankton abundance. The greatest set of data

concerns the inter-tropical area. Nevertheless, some data are available up to 60°N (Buck *et al.*, 1996). A decade after the discovery of *Prochlorococcus*, the aim of the present paper is mainly to review the recent literature on the distribution of *Synechococcus* and *Prochlorococcus*. We tried to determine some global patterns and draw some general considerations on physico-chemical and biological factors which regulate their respective abundance. This will complement previous extensive reviews on various aspects of *Synechococcus* ecology, biology and physiology (e.g. Glover, 1985; Stockner & Antia, 1986; Waterbury *et al.*, 1986; Stockner, 1988; Carr & Mann, 1994) and reviews on "prochlorophytes" which included a few preliminary data on *Prochlorococcus* (Bullerjahn & Post, 1993; Matthijs *et al.*, 1994).

DISTRIBUTION PATTERNS

Descriptions of the community structures of picophytoplankton and ancillary parameters have been published for the Atlantic, Pacific (including the Tuamotu archipelago) and Indian oceans as well as for the Red and Mediterranean seas. Most reports concern tropical oceanographic cruises, with transects and times series. In a few cases, temporal studies have been made such as at station OFP off Bermuda (Olson *et al.*, 1990a), three stations off the Mauritanian coast (Partensky *et al.*, 1996) or the several year-long survey at Aloha station, in the north Pacific central gyre (Campbell *et al.*, 1997). The rapid analysis of this extensive literature demonstrates unambiguously that *Prochlorococcus* is often much more abundant than *Synechococcus* in areas where they co-occur. The most notable exceptions are areas seasonally or permanently enriched with nutrients by strong upwellings and (or) coastal inputs. The highest concentrations of *Synechococcus* have been reported in the euphotic zone at the Costa Rica Dome (1.5×10^6 cell ml^{-1}; Li *et al.*, 1983), in the upwelling area off the Mauritanian coast (4×10^5 cell ml^{-1}; Partensky *et al.*, 1996), along the coast of Arabia (3.7×10^5 cell ml^{-1}, Gradinger *et al.*, 1992, 4.5×10^5 cell ml^{-1}; Burkill *et al.*, 1993) and in coral reef water lagoon water of the Haraiki atoll (3.7×10^5 cell ml^{-1}; Charpy & Blanchot, 1998). *Synechococcus* is always present in nutrient-depleted areas such as the central gyres of Atlantic and Pacific oceans but at very low abundance (ca. 1-4 10^3 cell ml^{-1} or 1.3-8.5 10^7 cell cm^{-2}; Olson *et al.*, 1990b, Blanchot *et al.*, 1992, Campbell & Vaulot, 1993; Li, 1995; Blanchot & Rodier, 1996). Its distribution also extends to low salinity environments (down to 12‰; Jochem, 1988; Vaulot & Ning Xiuren, 1988). Moreover, *Synechococcus* appears to be an eurytherm organism, since it has been reported to bloom at temperatures down to 6-8°C (Waterbury *et al.*, 1986; Neuer, 1992) and to be abundant even at 2°C (Shapiro & Haugen, 1988), although it was almost absent in the Arctic in low salinity polar waters at –1.5°C (Gradinger & Lenz, 1989). Nevertheless, the thermal preferendum of *Synechococcus* is in general significantly higher, even for species from cool areas, since it preferentially thrives during the summer months in the Baltic Sea (Jochem, 1988). Similarly, Hall and Vincent (1990) showed that concentrations increased from cool coastal (10.4°C) to warmer offshore waters (> 13°C) of South Island (New Zealand) as long as the nitrates concentration was higher

than 3 µM. On another hand, it is in winter that *Synechococcus* abundance peaks are observed in subtropical areas like Bermuda (Olson *et al.,* 1990a) and off Hawaii (Campbell *et al.,* 1997), but in both cases, seawater temperature was above 19°C.

In contrast to *Synechococcus*, *Prochlorococcus* occurs at abundances exceeding 10^5 cells per ml throughout much of its distribution area. Record abundances (4.4×10^5 cell ml^{-1}, Blanchot unpublished data) of *Prochlorococcus* have been observed in the western equatorial Pacific, slightly above the nitracline. In coral atoll lagoons, high concentrations (2.8×10^5 cell ml^{-1}) have been observed in the Hiti atoll (Charpy & Blanchot, 1998). At last, a record of integrated concentration of *Prochlorococcus* (4.1×10^9 cells cm^{-2}) has also been observed in a downwelling structure at 14°S-165°E, during an El Niño year (1992), where abundances of over 3×10^5 cell ml^{-1} were observed on a 60 m thick layer above the nitracline (Blanchot & Rodier, 1996). Integrated *Prochlorococcus* concentrations in tropical, oligotrophic areas typically stand around 1-2.5 $\times 10^9$ cell cm^{-2} (Campbell & Vaulot, 1993; Partensky *et al.,* 1996). In contrast to that of *Synechococcus, Prochlorococcus* distribution seems to be limited by low temperatures. Although *Prochlorococcus* cells have been detected to latitudes as high as 60°N in the North Atlantic at a temperature of 10.2°C, Buck *et al.* (1996) noted that maximum concentrations decreased fairly regularly from 3.5 10^5 cells ml^{-1} at 15°N down to 5.3 10^4 cells ml^{-1} at 50°N and then dropped dramatically above this latitude. Another limiting factor appears to be the stability of the water column. Lindell & Post (1995) observed that deep mixing in winter in the Red Sea prevented *Prochlorococcus* growth. Similarly, in the northwestern Mediterranean Sea, the stability of the water column seems to be a prerequisite for *Prochlorococcus* bloom development (Bustillos-Guzman *et al.,* 1995). *Prochlorococcus* is in general absent from eutrophic areas and (or) low salinity waters, with the notable exception of the Mediterranean Sea, where a few cells were observed in the Rhône river outflow (Vaulot *et al.,* 1990). Although *Prochlorococcus* is the dominant genus in oligotrophic areas, its distribution extends to warm mesotrophic, stratified areas (i.e. waters with a detectable level of nutrients in the upper layer), such as the equatorial Pacific, with only small changes of abundance. This apparent insensibility toward nutrients appears clearly on Fig. 1, which illustrates the variations of integrated concentrations of *Prochlorococcus* and *Synechococcus* and inorganic forms of nitrogen in surface, along a transect in the equatorial Pacific between the "warm pool" (West of the date line) and high nutrient-low chlorophyll (HNLC) waters (from the date line to the Galapagos archipelago). In contrast, there was a tremendous increase in *Synechococcus* integrated abundance in the transition zone, which was clearly concomitant with the raise in $NO_3 + NO_2$ concentrations.

Because of their ubiquity and abundance, both *Prochlorococcus* and *Synechococcus* appear to play a significant ecological role in the biomass and production of oceans. However, the relative importance of these two microorganisms on a global scale is still poorly assessed. This results from historical facts : for almost ten years, *Synechococcus* was thought to be the only photosynthetic organism smaller than 1 µm and this has sometimes led to overestimate its contribution when it was estimated by such methods as size

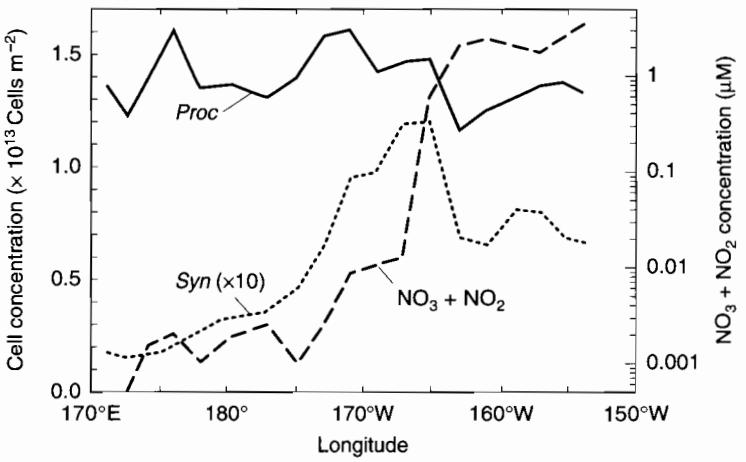

Figure 1. Integrated concentrations of *Prochlorococcus* and *Synechococcus* and concentration of nitrate and nitrite in surface, along a transect in the equatorial Pacific between the warm pool (165°E) and HNLC waters (150°W). Data were collected during the FLUPAC cruise, held during fall 1994 (Blanchot, unpublished data; nutrient data are from Eldin *et al.* 1997).

fractionation. With the discovery of *Prochlorococcus*, the previous picture has changed as it has become obvious that *Prochlorococcus* may be 100 times denser and account for ca. 22 times more carbon than *Synechococcus* in oligotrophic areas. However, considering that *Synechococcus* is still more important than *Prochlorococcus* in terms of biomass in meso- and eutrophic areas, the picture of the relative contribution of these two prokaryotes to global carbon is unclear. Using typical integrated concentrations for different well-defined zones, the area of these zones, and assuming an average carbon content per cell of 53 fg for *Prochlorococcus* and 250 fg for *Synechococcus* (Campbell *et al.*, 1994), it is theoretically possible to roughly compute global carbon stocks for each of these two prokaryotes. In practice however, many areas of the world ocean either have been little studied (e.g. the south parts of Atlantic or Indian oceans) or are too variable (e.g. the equatorial Pacific) to make such simple estimations. Therefore, we have tried to make a preliminary estimate of the contribution of *Prochlorococcus* and *Synechococcus* to carbon in the N Atlantic (0-60°N) for which usable integrated values are available through recent literature (see Table I). Most of our computation was based on integrated values reported for a S-N transect by Buck *et al.* (1996), but we have checked that they were in the same range as data from other authors, such as those obtained during a transatlantic transect by Li (1995). Results of the computation suggest that, in summer, *Prochlorococcus* accounts for ca. 3/4 of the picophytoprokaryotic carbon between 0° and 60°N. The relative contribution of *Synechococcus* is far from negligible and would be even higher in winter, when it dominates the subtropical and temperate zones. It seems to be much higher than intuitively suggested by a rapid

Table 1. Computation of the relative contributions of *Prochlorococcus* and *Synechococcus* to the carbon of the North Atlantic ocean in summer.

Area of North Atlantic	Areas ($\times 10^4$ km^2)			Proc ($\times 10^{11}$ cells/m^2)		Syn ($\times 10^{11}$ cells/m^2)		Biomass (Mt C/zone)		References used for integrated concentrations
	Oligo	Meso	Eu	Meso	Oligo	Eu+Meso	Oligo	Proc	Syn	
Equatorial 0°-5°N	307	39	10	125	208	17.6	5.20	3,81	0,62	Buck *et al.* (1996)
Tropical 5°N-25°N	1,340	150	29	48	187	64.0	6.25	14,8	4,97	id for Oligo/ Partensky *et al.* (1996) for Meso
Subtropical 25°N-40°N	997	134	7	138	138	4.30	4.30	8,3	1,22	Buck *et al.* (1996)
40°N-45°N	33	244	2	74	74	6.66	6.66	1,1	0,46	*id.*
45°N-50°N	0	226	8	37	na	12.8	na	0,44	0,75	*id.*
50°N-55°N	0	190	26	9.3	na	12.6	na	0,09	0,68	*id.*
55°N-60°N	0	236	43	1.0	na	16.0	na	0,01	1,11	*id.*
Total 0°-60°N	**2,680**	**1,220**	**125**					**28,5**	**9,82**	

Conversion coefficients were 53 and 250 fg C / cell, respectively. In the equatorial and tropical zones, we used different values for integrated concentrations in the oligotrophic zone (Oligo : Chl < 0.2 mg.m^{-3}), and the mesotrophic (Meso : 0.2 < Chl < 2.0 mg.m^{-3}) + eutrophic (Eu : Chl > 2.0 mg.m^{-3}) zones. *Prochlorococcus* were neglected in the eutrophic zones. Areas of the different trophic zones were computed using a chlorophyll datafile obtained from satellite images (annual average) and a software kindly provided by D. Antoine (Villefranche/mer).

comparison of abundances of the two prokaryotes. Values for *Synechococcus* carbon should however be looked at with more caution than those for *Prochlorococcus*, because the limits of its occurrence at high concentrations are much more difficult to set and our delimitation of the oligo- and mesotrophic areas were somewhat arbitrary (see Table I).

VERTICAL DISTRIBUTIONS

Vertical profiles of picophytoplanktonic cells are strongly influenced by hydrological conditions and dramatic changes have been reported both on spatial and seasonal scales. In well-mixed waters, when the mixing layer is deeper than the euphotic layer (i.e. the depth that is reached by > 1% of the incident light in surface), a situation currently found in upwelling areas, both populations are present at low concentrations (< 10^3 cells ml^{-1}; see e.g. Fig. 2A in Partensky *et al.*, 1996). In coastal waters and oceanic areas with a nutrient-replete mixed layer, the shape of the vertical profiles of *Prochlorococcus* and *Synechococcus* are generally parallel, with an homogeneous distribution in the upper layer and a dramatic decrease below the thermocline. In these circumstances, the concentrations of these two genera in the mixed layer are equivalent or slightly in excess for *Synechococcus* (e.g. Fig. 2; station EU;

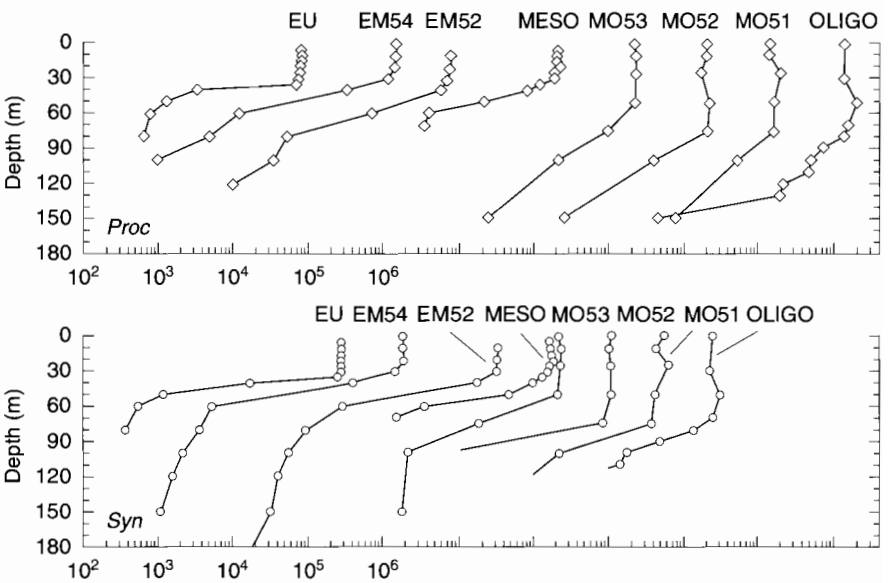

Figure 2. Vertical profiles of *Prochlorococcus* (*Proc*) and *Synechococcus* (*Syn*) cell concentrations along the transect from the EU (20°32'N 18°34'W) to OLIGO site (21°02'N 31°08'W) during December 1992 (EUMELI 5). For each profile, the abcissa ranges from 10^2 to 10^6 cells ml^{-1}, but consecutive profiles are shifted by one decade. Modified from Partensky *et al.* (1996) with permission.

see also Shimada *et al.,* 1995, Fig. 5). In intermediate situations between this and the typical oligotrophic structure, a case which is observed in the tropical Atlantic (e.g. Fig. 2, station MESO), in the equatorial Pacific HNLC zone (Landry *et al.,* 1996) or in temperate open sea areas when the stratification has been recently established after winter mixing (Olson *et al.,* 1990a; Li 1995), the shape of the vertical profiles of the two populations are again parallel, but they both exhibit a clear abundance maximum at or slightly above the nitracline level. In this situation, the integrated concentration of *Synechococcus* as well as the amplitude of the abundance peak are in general inversely related with the depth of the nitracline (Olson *et al.,* 1990a; Campbell & Vaulot, 1993). In contrast, *Prochlorococcus* integrated concentrations slightly increase with the nitracline depth. Finally, in oligotrophic waters, the vertical structure of picophytoplankton does not show any clear variation between Atlantic and Pacific oceans at a given latitude but it does vary for a given ocean between tropical, subtropical and temperate areas. In the latter two cases in summer-autumn, the profiles correspond to the extreme of the previous situation, with the nitracline depth located at the bottom of the euphotic layer. In these circumstances, there is a marked *Prochlorococcus* abundance peak just above the nitracline and much fewer cells in the surface waters, while for *Synechococcus*, the abundance is low all along the vertical profile (~1-3 10^3 cell ml^{-1}) and the abundance peak is reduced (Olson *et al.,* 1990a; Li, 1995). In tropical areas, the vertical structure is fairly stable throughout the year although a slight seasonal cycle can be observed (Campbell *et al.,* 1997). It is about the same as the previous one for *Synechococcus*, but for *Prochlorococcus*, the abundance peak is often much less marked than in the previous case, because the abundance layer extends up to the surface (e.g. Fig. 2, stations MO52 to OLIGO; see also Campbell & Vaulot, 1993). Consequently, the integrated concentrations of *Prochlorococcus* are generally higher under the tropics than at higher latitude (see above). It is frequent however that, in both cases, counts of *Prochlorococcus* cells in near surface are inaccurate, because the weak fluorescence of cells make them hardly distinguishable by flow cytometry, unless a special configuration is used (Olson *et al.,* 1990a, 1990b; Dusenberry & Frankel, 1994).

Figure 2 illustrates the dramatic variations of the shape of vertical profiles of *Prochlorococcus* and *Synechococcus* occurring along a sharp nutrient gradient off the Mauritanian coast. Another good example of the variation of the vertical structure of photosynthetic prokaryotes in response to hydrological changes is given by the comparison of typical profiles from the warm pool and from HNLC waters (Fig. 3). In the low salinity, low nutrient upper layer of the warm pool (Lindström *et al.,* 1987; Mackey *et al.,* 1995; Radenac & Rodier, 1996), the cell concentration (i.e. $\approx 10^3$ *Synechococcus* cells ml^{-1} and $\approx 10^5$ *Prochlorococcus* cells ml^{-1}) and the shape of the profiles is typical of oligotrophic waters with a slight maximum of *Prochlorococcus* above the nitracline (Blanchot, unpublished). In the high salinity high nutrient under layer, *Synechococcus* disappears abruptly while *Prochlorococcus* abundance decreases regularly down to around 200 m. In the HNLC area, the photic zone is also shared in two layers but the upper one is not nitrate-depleted. The shape of the profiles are typical of mesotrophic waters. They have a smaller

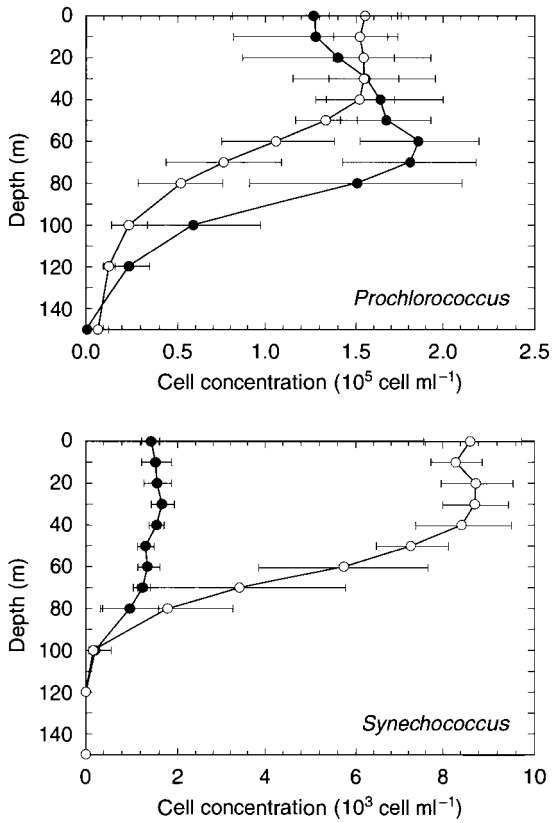

Figure 3. Typical vertical profiles of *Prochlorococcus* and *Synechococcus* in the warm pool (0°-167°E, filled circles) and in HNLC waters (0°-150°W, outlined circles). Samples were collected during two one-week time series during fall 1994. Data show average abundances ± SE (n = 7) at 4:00 a.m. local time, when cell division is completed (FLUPAC cruise; Blanchot unpublished data).

vertical extension than in the warm pool, but the main difference is the increase of the *Synechococcus* abundance by one order of magnitude, while the abundance of *Prochlorococcus* is rather stable (i.e. ≈ 10^4 *Synechococcus* ml^{-1} and ≈ 10^5 *Prochlorococcus* ml^{-1}; Blanchot unpublished).

FACTORS CONTROLLING THE ABUNDANCE OF *PROCHLOROCOCCUS* AND *SYNECHOCOCCUS*

Differences in the distributions of the two picophytoplankters clearly show that, although they are under similar controls, they are responding at very different degrees to biological (specific growth rate, grazing, viral mortality, genetic variability, etc.) and/or physico-chemical factors (stability of the

water column, light, temperature, micro- and macronutrients, etc.). However, several of these factors are interconnected (e.g. a well-mixed water body is generally colder and richer in nutrients than a stratified water body and may also have a different grazer community), and it is not easy to determine with certainty which factor is the most important to condition the distribution of these two prokaryotes in the field.

Tremendous progress has been made in the recent years about the determination of growth rates of natural populations of *Synechococcus* and *Prochlorococcus* (Landry *et al.,* 1995b; Vaulot *et al.,* 1995; Liu *et al.,* 1997; Shalapyonok *et al.,* 1998; Jacquet *et al.,* in press; Furnas & Crosbie, this book; Navarette *et al.,* this book). These studies tend to prove that, beside the fact that cells are highly synchronized by the diel cycle, growth rates of both prokaryotes are high (generally close to one division per day or even higher), i.e. their growth does not seem to be drastically limited, even in oligotrophic areas. The quasi-constancy of cell concentrations from one day to another, which is a characteristics of stable environments such as the tropical oligotrophic zones, suggests that loss rates are, on the time scale of one to a few days, almost exactly compensating growth rates (Burkill *et al.,* 1993; Landry *et al.,* 1995a). For instance, Jacquet *et al.,* (in press) showed that grazing rates adjusted within one day to changes in intrinsic growth rates of coastal populations of *Synechococcus*. Little is however known on the relative importance of grazers, viruses and other causal agents in picophytoprokaryotic mortality. In oceanic waters off Japan Kudoh *et al.* (1990) found that mortality of *Synechococcus* populations due to small ciliates was higher (0.06 h^{-1}) than that by heterotrophic flagellates (0.04 h^{-1}), these two rates exactly balancing the population growth rate. Furthermore, experiments with mixtures of *Prochlorococcus*, *Synechococcus* and ciliates showed that these grazers preferentially feed on the latter (Christaki *et al.,* in press). Differential grazing on *Synechococcus* and *Prochlorococcus* also probably occurs in situ, and this may partly explain differences in the relative abundance of these two prokaryotes, in particular in oligotrophic systems. Other possible causes of mortality include grazing by larger filter feeders such as appendicularians (Gorsky *et al.,* 1999), but the true ecological impact of these predators on prokaryotes is not known yet. Viral lysis may also be an important mortality factor since cyanophages are very abundant in the marine environment. Proctor and Fuhrman (1990) observed that up to 5% of cyanobacteria contain mature phages. Suttle (1994) also estimated that 3% of *Synechococcus* biomass may be lysed daily, but Waterbury and Valois (1993) considered that phages have a negligible impact in regulating the densities of marine *Synechococcus*. However, the potential impact of these viruses on *Prochlorococcus* has not been studied yet.

Among physico-chemical factors, light is the most probable to play a role in itself in the differential distribution of *Synechococcus* and *Prochlorococcus* along the vertical gradient in oligotrophic areas. The fact that *Synechococcus* does not grow below the euphotic zone, in contrast to *Prochlorococcus* which can be found at significant concentrations at 150 m or deeper, clearly indicates that the former but not the latter organism is limited by low irradiances. This is corroborated by studies in culture (Moore *et al.,* 1995) which show that *Synechococcus* compensation point for growth is higher than that of

Prochlorococcus, although differences in growth irradiance optima also exist between pigment types of *Prochlorococcus* (see below). The role of nutrients is much more tricky to evaluate. In general, there is a positive relationship between nitrogen and *Synechococcus* concentrations (see e.g. Blanchot *et al.*, 1992, Figs. 1-2) and an inverse relationship between *Synechococcus* and *Prochlorococcus* integrated concentrations (Campbell & Vaulot, 1993). However, although it is tempting to speculate that nitrogen could directly drive *Synechococcus* abundances, at least in surface waters where light is not limiting, things might not be that simple. First, as mentioned above, other parameters covary at the same time as nitrogen and their role might also be predominant. Second, the fact that *Synechococcus* can grow in highly oligotrophic areas at near-maximum rates (one division per day or more) and often higher than *Prochlorococcus* (Liu *et al.*, 1995) is puzzling. The influence of nitrogen on *Prochlorococcus* is even more complex to understand. In the Mediterranean Sea in winter (Vaulot & Partensky, 1992) as well as in the subtropical northern Atlantic in late spring (Graziano *et al.*, 1996), enrichment experiments pointed out that *Prochlorococcus* growth was limited by nitrogen (nitrate and/or ammonium). Similarly, Olson *et al.* (1990a), while observing the evolution of vertical profiles of photosynthetic prokaryotes during the onset of stratification off Bermuda, speculated that *Prochlorococcus* had a more stringent requirement for nitrate (or other nutrients which covary with nitrate) than did *Synechococcus*. However, this is clearly not true for populations from tropical oligotrophic areas, where *Prochlorococcus* abundance peak is in general located significantly above the nitracline. Moreover, high integrated concentrations of this organism have been reported on a very large range of nitrate surface concentrations (0.001-3 μM), suggesting a relative indifference toward inorganic forms of nitrogen (see Fig. 1). The only way to reconcile this apparent contradiction is to assume that there are several physiological types of *Prochlorococcus*, inhabiting different geographical areas and behaving differently with regard to nitrogen assimilation. This is also possibly true with *Synechococcus*, since different pigment types dominate in nutrient-enriched and oligotrophic waters but, in this case, the quality of light (green or blue) is probably also involved (see "biological adaptations").

Among micro-nutrients, only the effects of iron limitation has been studied to date. Zettler *et al.* (1996) showed that iron addition increased the scatter (i.e. the size) and red fluorescence (i.e. the chlorophyll content) of *Synechococcus* and, although not very significantly, *Prochlorococcus*, but not their cell concentration. These results were confirmed by flow cytometric measurements made directly on field populations during the IronExII experiment (Cavender-Bares *et al.*, unpublished). So either iron addition did not boost the growth of these prokaryotes, because they were already growing at near maximal rates, or grazers were able to quasi-instantaneously increase their pressure to compensate an increase in intrinsic growth rate.

As already evoked (see distribution patterns), temperature is another potential limiting factor, although its effects are sometimes hard to uncouple from that of other factors, like mixing. For *Prochlorococcus*, it essentially plays a limiting role for growth when it is too low (< 15-18°C) and an inhibiting role below 10°C (Olson *et al.*,1990a, Buck *et al.*, 1996). Temperature

therefore restricts its *Prochlorococcus* distribution to inter-tropical areas year-round or to summer and early autumn months in temperate latitudes, although low concentrations may be detected also in winter in the northwestern Mediterranean Sea (Vaulot *et al.*, 1990). The growth of individual *Prochlorococcus* strains is inhibited at temperatures higher than 25°C (Moore *et al.*, 1995), but this does not seem to occur in the field where high concentrations ($> 2\ 10^5$ cells ml^{-1}) of *Prochlorococcus* have been recorded in waters > 29°C (Blanchot & Rodier, 1996). For *Synechococcus*, the very large range of temperature at which it has been reported to bloom, suggests that there are several ecotypes in the field having different temperature growth optima. The reference strain WH8103, for instance, grows best at 28°C (Moore *et al.*, 1995), which is probably not the case for natural populations from e.g. the Baltic sea. However, generally speaking, in areas where *Synechococcus* co-occurs with *Prochlorococcus*, the former prokaryote seems to preferentially bloom when temperature is lower (Shimada *et al.*, 1995) and can tolerate a lesser stability of the water column (Lindell & Post, 1995).

BIOLOGICAL ADAPTATIONS TO LIGHT

An important factor which may explain the overall distribution of both *Synechococcus* and *Prochlorococcus* is their ability to either acclimate (in the physiological sense) or adapt (in the evolutionary sense) to changes in their environment and, especially the light quality and (or) intensity. For both organisms, at least two main pigment families can be distinguished in oceanic waters by flow cytometry. Several (generally two) populations of *Synechococcus*, distinguishable by their different orange and green fluorescences, are often observed to co-occur in coastal waters (Olson *et al.*, 1990b; Veldhuis & Kraay, 1993). It has been shown that these populations possess a phycoerythrin having different proportions of the two chromophores phycourobilin (PUB) and phycoerythrobilin (PEB), which have in vivo absorption maxima at ca. 495 and 545 nm, respectively (Olson *et al.*, 1988). The population which has the lowest orange fluorescence has a phycoerythrin with a low PUB to PEB ratio, whereas that of the brightly orange population has a high PUB to PEB ratio. In the field, the PEB-rich population dominates in mesotrophic or coastal green waters, whereas the PUB-rich population is the only detectable one by flow cytometry in oligotrophic areas (Olson *et al.*, 1988) as well as in HNLC waters (Neveux *et al.*, 1999). Low PUB cells may be present in open ocean areas at very low abundances (escaping flow cytometric detection) since strains with this pigmentation have been isolated by culturing (Waterbury *et al.*, 1986; Toledo & Palenik, 1997). This is why early studies on *Synechococcus* mistakenly considered that the low PUB isolate WH7803 (also called DC2) was representative of open ocean waters (see e.g. Glover 1985). Flow cytometry might therefore oversimplify the picture of the pigment and genetic diversity within marine *Synechococcus*. Isolates currently available in culture show a wide range in PUB to PEB ratios ($A_{495\ nm}/A_{545\ nm}$ from 0.37 to 2.40) whereas, for a single isolate, PUB to PEB ratio only vary two-fold (Waterbury *et al.*, 1986). Molecular studies show that low and high PUB types of *Synechococcus* are genetically distinct (Palenik, 1994; Urbach *et al.*,

1998). Toledo & Palenik (1997) have also shown that low PUB strains from the California current (CCLPUB strains) and from the Atlantic (such as WH7803) were more distinct genetically than were the latter from high PUB isolates from either the Atlantic or Pacific. The fact that low PUB populations do not belong to a single homogeneous gene pool is consistent with the hypothesis that low PUB populations are less cosmopolitan than are high PUB ones.

Flow cytometry also has resolved two sub-populations of *Prochlorococcus* characterized by different red fluorescences. This differentiation is observed at depth in oligotrophic areas (Campbell & Vaulot, 1993; Veldhuis & Kraay, 1993; Blanchot & Rodier, 1996; Partensky *et al.,* 1996). The dim sub-population tends to dominate in the well lit upper layer and the bright population at the base of the euphotic zone. Sub-populations of each sorted by flow cytometry and brought into culture, have been shown to maintain their differences in red fluorescence after being in culture for several years (Moore *et al.,* 1998). This work also confirmed previous studies on isolates from different geographical areas (Moore *et al.,* 1995) which suggested that the dim population was adapted to grow at higher irradiances and had a much lower divinyl-Chl *b* to *a* ratio than the bright population. This pigment differentiation mainly translates a difference in the antenna proteins of these two organisms. Light harvesting complexes are more abundant and bind more divinyl-Chl *b* in the low light-adapted type (Partensky *et al.,* 1997). The genetic characterization of low- and high-light adapted isolates has demonstrated that they belong to different clusters (Palenik & Haselkorn, 1992; Hess *et al.,* 1996; Laroche *et al.,* 1996; Urbach *et al.,* 1998). Amazingly, the genetic distance between high and low light *Prochlorococcus* strains, isolated from close areas or even from a given water sample, is wider than that between two strains isolated from surface waters of very remote sites (Scanlan *et al.,* 1996; Moore *et al.,* 1998). This is apparently not true for *Synechococcus*, since Toledo & Palenik (1997) found that deep and surface populations from a same oligotrophic site were genetically very close. This low genetic variation of *Synechococcus* populations in oligotrophic areas may explain why this organism is more confined to the upper layer than is *Prochlorococcus.*

CONCLUSION

The extensive literature on *Synechococcus* and *Prochlorococcus* allows to draw some general conclusions on their ecological distribution. Although these prokaryotes co-occur on a wide part of the world ocean, particular adaptations have allowed the former organism to colonize cold areas and the second one low light niches. Even in areas where light and temperature are not limiting, there is a clear differentiation between these micro-organisms : *Synechococcus* proliferates in nutrient-rich (generally near coastal) waters whereas *Prochlorococcus* is most abundant in offshore nutrient-depleted areas. These adaptations are even more remarkable when one consider that these organisms are phylogenetically very close and probably have diverged near-simultaneously from a single ancestor (Palenik & Haselkorn, 1992;

Urbach *et al.*, 1992, 1998). Among the most significant (or visible?) divergences existing between these prokaryotes, one must note their different cell sizes (ca. 0.6 µm *vs.* 0.9 µm for *Prochlorococcus* and *Synechococcus*, respectively; Morel *et al.*, 1993; Sieracki *et al.*, 1995) and light harvesting complexes (divinyl-Chl *a/b* antenna *vs.* phycobilisomes). The differentiation of cell size has direct consequences on nutrient assimilation (Chisholm, 1992) and grazer efficiency, although for the latter, other factors such as differences in cell surfaces are also probably implicated (Christaki *et al.*, in press). The specialization of light-harvesting systems, has allowed *Synechococcus* to thrive in either green (high PEB cells) or blue (high PUB cells) waters and *Prochlorococcus* to adapt to blue light waters from surface (high-light adapted cells) down to depths receiving 0.1% of the irradiance incident in surface (low-light adapted cells). However, although this is not clearly established yet, there might also exist differences between these organisms in other biological processes, such as nutrient assimilation. Furthermore, the differential behaviour of natural populations of *Prochlorococcus* from tropical areas and from more temperate areas suggest that isolates truly representative of these two nutrient types may have not been isolated in culture yet.

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