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a common ecology

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ABSTRACT

Picocyanobacteria (Pcy) single-cells and microcolonies are common in lakes throughout the world, and abundant across a wide spectrum of trophic conditions. The single-celled Pcy populations tend to be predominant in large, deep oligo-mesotrophic lakes, while the microcolonies find optimal conditions in warmer, shallower and more nutrient rich lakes. Microcolonies of different size (from 5 to 50 cells) constitute a gradient without a net separation from single-celled types. Considering microcolonies as transitional forms from single-cells to colonial morphotypes it is conceivable to propose a common ecology where local communities are not isolated but linked by dispersal of multiple, potentially interactive, species. In this review abiotic forcing and biotic regulation of Pcy community structure and dynamics are examined to offer an updated view of Pcy ecology.

Key words: picocyanobacteria, freshwaters, Synechococcus*, microcolonies, single-cells*

1. INTRODUCTION

A phylogenomic study of the evolution of cyanobacterial traits shows that the earliest lineages were probably unicellular cells in terrestrial and/or freshwater environments (Sánchez-Baracaldo *et al*. 2005; Blank & Sánchez-Baracaldo 2010) rather than in the marine habitat as suggested by Honda *et al*. (1999). This discovery opens new prospects for the study of freshwater picocyanobacteria (Pcy) and provides impetus and relevance for future phylogenetic and ecological investigations to clarify many uncertainties in the literature.

One of the most striking differences between freshwater and marine Pcy lies in the extraordinary richness of morphotypes and the unresolved phylogeny of Pcy in lakes. However, despite marked phylogenetic differences, Pcy have a similar pattern in their absolute and relative importance in freshwater and marine systems along the trophic gradient (Bell & Kalff 2001).

Although studies of the ecology of microcolonies and colonial forms are few, there have been sufficient studies within the past 25 y of Pcy in lakes and their role in food webs to warrant synthesis and further review (Stockner *et al*. 2000; Callieri 2008).

The picocyanobacteria exhibit two common morphologies: single cells, (coccoid, rods) and microcolonies. Under favorable environmental conditions some Pcy can develop mucilage or a sheath and remain near to the mother cell forming a clump. Here Pcy is designated as the single cells (0.2-2.0 µm) which are the major component of the picophytoplankton community. Microcolonies of different size (from 5 to 50 cells) constitute a gradient without a clear separation from the single-celled type and should be considered Pcy.

The introduction of molecular biology and of single-cell analysis to microbial ecology has revolutionized our knowledge of taxonomy, dynamics and ecology of these organisms. The emergence of Pcy as an important research topic for limnologists and oceanographers provides an opportunity to discuss to what extent this large and diverse group of cyanobacteria shares a common ecology. The current challenge is to better understand the relationship between the diversity and ecology of Pcy and microcolonies and their interaction with the environmental factors that allow the proliferation of the most competitive genotypes. The study of genome divergence, lateral gene transfer and genomic islands will provide new opportunities for a better understanding of niche adaptation (Dufresne *et al*. 2008; Scanlan *et al*. 2009).

2. TAXONOMY AND PHYLOGENETIC DIVERSITY

Even more than for most prokaryotes (Komárek *et al.* 2004), the morphological features of Pcy are insufficiently distinct to provide a reliable basis for discriminating taxa. The criteria used for the definition of genera of single-celled Pcy e.g., *Cyanobium*, *Synechococcus* and *Cyanothece dianae/cedrorum*-type (Komárek 1996) have been supplanted by molecular methods which focus on clade divergence in the phylogenetic tree rather than on morphological differences. The clade containing Pcy (*Synechococcus*/*Prochlorococcus*/*Cyanobium sensu* Sánchez-Baracaldo *et al*. 2005) is formed by coccoid and rod-shaped cells with a diameter <3 µm. Analysis of 16S ribosomal DNA (rDNA) of freshwater *Synechococcus* shows it is polyphyletic genus and cannot be considered a natural taxon (Urbach *et al*. 1998; Robertson *et al*. 2001). In the phy-

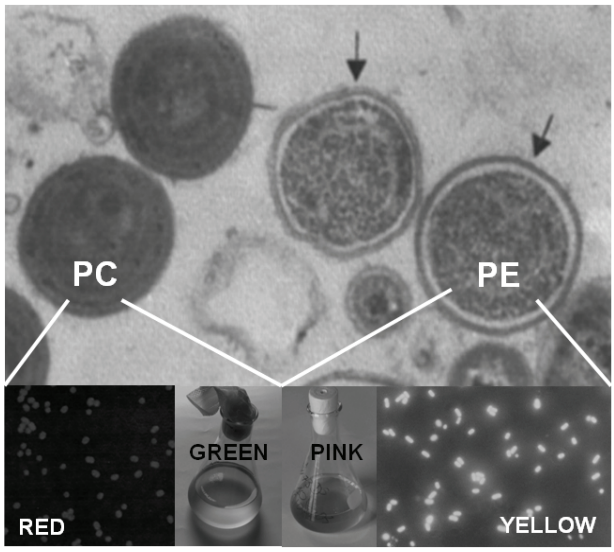

Fig. 1. Three different views of Pcy: liquid cultures (green: PC-cells, pink: PE-cells), epifluorescence photographs (under blue excitation: red cells: PC-cells, yellow cells: PE-cells), transmission electron microscope photo (showing the different internal structure of PC- and PE-cells).

logenetic tree the Antarctic strains represent a unique and highly adapted clade related only peripherally to *Synechococcus* sp. Cluster 5.2 (Marine Cluster B) (Vincent *et al*. 2000; Powell *et al*. 2005).

Over a decade has passed since the acknowledgement of the necessity that phenotypic diversity should be evaluated in conjunction with genotypic analysis in order to resolve whether a similar morphology also reflects a phylogenetic relationship. Even though many genetically distinct *Synechococcus* strains have been found (Robertson *et al*. 2001), it is still helpful to broadly classify Pcy into the two cell-types: the first with yellow autofluorescing phycoerythrin (PE-rich cells), and the second with red autofluorescing phycocyanin (PC-rich cells) as the major light-harvesting pigment (Wood *et al*. 1985; Ernst 1991) (Fig 1). Phycoerythrin-rich strains have an absorption peak at ~560 nm, and hence absorb green light effectively. Phycocyanin-rich strains have an absorption peak at ~625 nm, and absorb orange-red light effectively (Callieri *et al*. 1996; Haverkamp *et al*. 2008).

Phylogenetic studies are basically performed using sequence data derived from 16S rDNA which is a conserved gene but shows high pair-wise similarity in freshwater Pcy (Crosbie *et al*. 2003a) and cannot resolve the actual genetic variation that accompanies their physiological diversity (Urbach *et al*. 1998). Less conserved genetic markers can offer a more detailed definition of the diversity of Pcy (Haverkamp *et al*. 2009). In particular the spacer between the 16S and 23S rDNA (ITS-1) exhibits a great deal of length and sequence variation and can be used to differentiate marine and freshwater Pcy ecotypes using fingerprinting techniques (T-RFLP, DGGE or ARISA) (Rocap *et al*. 2002; Becker *et al*. 2002; Ernst *et al*. 2003). The study of functional genes as, for example, those encoding for phycocyanin and phycoerythrin (*cpcBA* and *cpeBA*) can offer another perspective on the evolution of Pcy, grouping the strains on the basis of pigment composition (Haverkamp *et al*. 2008). Indeed, it has been found that phylogenies based on phycobiliprotein rod gene components are not congruent with the 16S rRNA phylogeny whilst those based on the allophycocyanin core are congruent (Six *et al*. 2007; Haverkamp *et al*. 2009).

The phylogenetic approach combined with quantitative real-time PCR has been successfully used to assess Pcy community structure both in oceans (e.g., Ahlgren *et al*. 2006) and freshwaters (e.g., Becker *et al*. 2000, 2007). Using small subunit (ssu) rDNA sequences from novel culture isolates together with environmental samples from the Baltic Sea and seven freshwater lakes, Sánchez-Baracaldo *et al*. (2008) showed that freshwater Pcy communities encompass much greater diversity than is found in marine systems. They hypothesised a more rapid speciation in lakes allowed by geographical barriers and noticed that most of the Baltic Sea-derived sequences were closely related to freshwater lineages.

To provide a more realistic phylogenetic tree of cyanobacteria Sánchez-Baracaldo *et al*. (2005) used a combination of different molecular sequence data instead of individual genes. Flanking a selection of morphological traits into the backbone cyanobacterial tree they showed that the ancestral cyanobacterium was a single cell and that filamentous/colonial forms appeared later in time. The presence of a well-defined sheath, associated with the colonial lifestyle, is a trait which has been lost and attained several times during evolution. In Arctic lakes the Pcy isolated strains appeared to be closely related to *Microcystis elabens* (Vincent *et al*. 2000) now reclassified as a species of *Aphanothece* (Komárek & Anagnostidis 1999). Thus, it is tempting to suggest that microcolonies, which are

frequently found in freshwater, may be considered transitional forms from single-cells to true colonial. In this sense the investigations done by Crosbie *et al*. (2003a) confirm the existence of single-cell/single-colony strains, with different degrees of aggregation, possibly belonging to the group H and group B sub-alpine cluster I.

3. SINGLE-CELLS *VS* MICROCOLONIES

In the last ten years a growing interest in Pcy microcolony presence in lakes of different trophic state has been rekindled (Crosbie *et al*. 2003c; Callieri 2008). The abundance of microcolonies found under nutrient depleted conditions in mid-summer in temperate lakes suggests that colony formation may be a strategy for more efficient nutrient recycling, providing a self-sustaining microcosm that offers a competitive advantage over the free-living condition. This hypothesis has been considered unlikely for Pcy (Crosbie *et al*. 2003c), in the light of results obtained with the colony-forming marine alga *Phaeocystis* sp., where the formation of a diffusive boundary layer can strongly limit nutrient diffusion into the colonies (Ploug *et al.* 1999). At low phosphorus concentrations the colonial forms actually grow slower than the single-cell forms (Veldhuis & Admiraal 1987), due to the lower cell-specific nutrient fluxes in colonies (Ploug *et al*. 1999). But in microcolonies, formed by 5-10 cells in one plane, the duplication should not be depressed as much as in a large, thick colony, where the diffusion of nutrients is impeded. In this case, exudates adsorbed to the cell surface can act as rich metabolite pools. Therefore, during the initial stage of its formation a microcolony can have a selective advantage in nutrient depleted waters.

Crosbie *et al*. (2003c) observed an increase of microcolonies in nutrient-poor surface waters in Lake Mondsee and attributed their formation to the production of photosynthate-rich mucilage in Pcy single-cells, that were actively photosynthesising organic carbon. As the leakage or excretion of photosynthate has been considered one protection mechanism against photochemical damage (Wood & van Valen 1990), it is likely to also consider the effect of irradiance, at near-surface depths, as a stressor promoting clumping of daughter cells during duplication. Among the exudates produced by cyanobacteria the siderophores, iron-chelating compounds, are of great importance (Murphy *et al*. 1976). It has been hypothesized that siderophore production can provide a competitive advantage to cyanobacteria over other algae during iron stress, and can alter the bioavailabity of iron to the aquatic community (Wilhelm 1995). Nevertheless in diluted environments (open oceans) the loss of siderophores is highly probable and the cost of production not justified (Hopkinson & Morel 2009). Particles are therefore considered the hotspots for siderophore production, mainly by heterotrophic bacteria (Hopkinson & Morel 2009).

To better understand genus-specific microcolony formation one must consider the factors influencing cell aggregation, despite the many differences between microcolonies and aggregates. The results by Koblížek *et al*. (2000) suggest that, in culture at least, *Synechococcus elongatus* aggregates rapidly if exposed to blue light (30 minutes, 1000 μmol m^{-2} s^{-1}) due to the effect of electron transfer downstream of PSI, with reactive oxygen radicals (ROS), likely triggering the aggregation. The production of glutathione, which is an important antioxidant of superoxide radicals, may be the metabolite inducing aggregation at high irradiance (Koblížek *et al*. 2000). PSI may therefore have an important role to play in the first stages of microcolony formation in lakes, but this hypothesis requires further study.

As well as cell metabolism alterations caused by external factors such as light, other important structural changes of Pcy single-cells must be mentioned as a causative factor inducing microcolony formation. Aggregation is an ATP-independent process without any de novo protein synthesis (Koblížek *et al*. 2000), and this indicates that some structures responsible for the aggregation must be present on the cell surface before irradiation. For example, in selected strains with different genotypes isolated from Lake Constance; Ernst *et al*. (1996) found that they possess a surface S-layer composed of regularly ordered globular protein layers that would facilitate colony formation. Also, in grazing (by *Ochromonas* sp.) induced microcolonies of PC-rich *Cyanobium* sp., rigid tubes from 100 nm to 1 μm long (spinae) have been observed on the cell surface (Jezberová & Komárková 2007). To what extent the formation of microcolonies is due to the presence of specific *Synechococcus* genotypes or is the result of a specific survival strategy is presently not fully understood (Ernst *et al*. 1999; Passoni & Callieri 2000).

A fascinating hypothesis on microcolony formation is related to the observation by Postius & Böger (1998) that exo-polysaccharides, exudated by Pcy, stimulate nitrogen fixation constituting microzones for diazotrophic bacteria growth. This finding opens new perspectives for the study of consortial, synergistic interactions that may be of critical importance to our understanding of colony formation in Pcy. Also, inside large microcolonies anoxic microsites can form and enable nitrogenase functioning. The negative relationship between the concentrations of available nitrogen forms (NH_4-N, NO_3-N, urea-N) and large microcolonies in Lake Balaton (Mózes *et al*. 2006) induce to think over the role of nitrogen limitation on microcolonies increase in summer.

4.SINGLE-CELL AND MICROCOLONY DYNAMICS

4.1. Seasonal dynamics

Sufficient information is now available to delineate the different patterns of Pcy, single-cells and microcolonies, in lakes of different morphology, thermal regime and trophic state (Callieri 2008). In lakes of temperate regions maxima generally conform to a typical bimodal pattern, with a spring or early summer peak

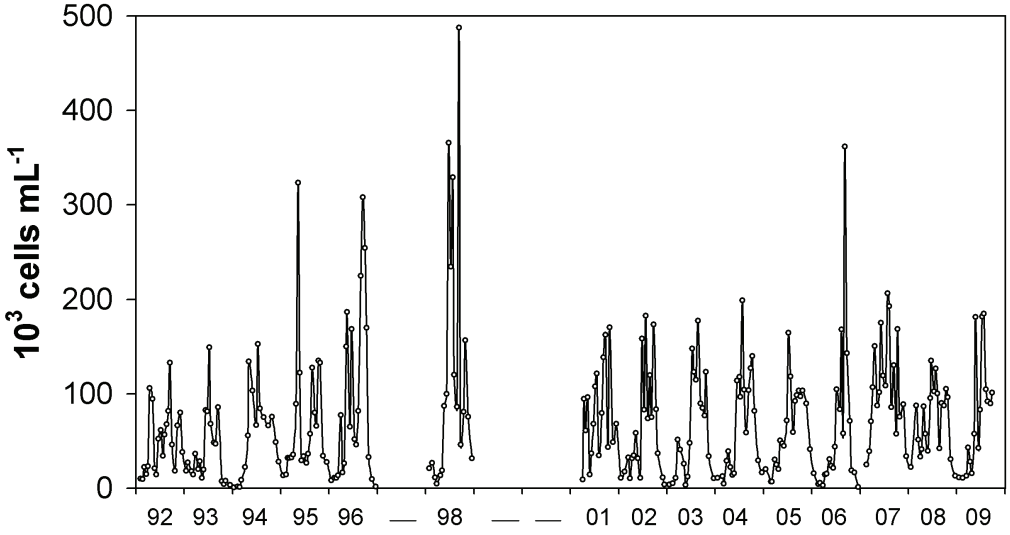

Fig. 2. Long-term Pcy abundance dynamics in Lake Maggiore, Northern Italy.

and a second peak during summer-autumn (Stockner *et al*. 2000). This is the case of most of the subalpine large lakes (e.g., Lake Maggiore, Lake Constance) without ice-cover, but also of Lake Stechlin, a deep oligo-mesotrophic lake in the Baltic Lake District where ice-cover occurs (Padisák *et al*. 2003). Nevertheless looking at the long-term series of Pcy abundance in Lake Maggiore (Fig. 2) (Callieri & Piscia 2002), Lake Costance (Gaedke & Weisse 1998), and Lake Stechlin (Padisák *et al*. 2003) not all the years are clearly bimodal. The interannual variability of Pcy dynamics is mainly related to differences in weather conditions which cause different spring mixing regimes and timing of water column stabilization (Weisse 1993). Studies in British Columbia's temperate oligotrophic lakes have shown a clear trend in both magnitude and timing of Pcy seasonal maxima related to levels of seasonal nutrient supplementation (Stockner & Shortreed 1994).

Large spring peaks are also common in eutrophic, hypereutrophic and dystrophic shallow lakes (Sime-Ngando 1995; Jasser 1997; Mózes *et al*. 2006). The seasonal patterns found in Danish lakes (Søndergaard 1991), Canadian lakes (Pick & Agbeti 1991), Lake Biwa, Japan (Maeda *et al*. 1992), English lakes (Hawley & Whitton 1991; Sánchez-Baracaldo *et al.* 2008), Lake Mondsee, Austria (Crosbie *et al*. 2003c), lakes Bourget and Geneva, France (Personnic *et al*. 2009a) all lack the spring peak, there being only a summer or autumnal maximum. The lack of Pcy spring peak in these lakes was likely due to weak stratification in March-April and to relatively deep vertical mixing. This interpretation is further strengthened by recent studies of Lake Baikal, where owing to winter ice-cover and extended spring isothermal conditions, Pcy can reach high abundance only in summer months and lack a spring peak (Belykh *et al.* 2006).

In Arctic and Antarctic lakes Pcy are widely distributed, despite the fact they are generally present in low abundance the marine polar environment (Vincent 2000). In continental Antarctica in meromictic saline Ace Lake Pcy reached concentrations of one order of magnitude higher than in temperate lakes in summer - 8 $\times$ 10^6 cells mL^{-1} (Vincent 2000). In the Antarctic Peninsula in Lake Boeckella (Izaguirre *et al*. 2003) Pcy abundance were as high as 3.6 $\times$ 10^5 cells mL^{-1} and represented up to 80% of phytoplankton biomass (Allende & Izaguirre 2003). Nevertheless very low Pcy concentrations (10^2-10^3 cells mL^{-1}) were recorded in a set of shallow lakes and ponds in the Byers peninsula of maritime Antarctica (Toro *et al*. 2007).

Tropical lakes behave differently and show high cell numbers (10^5-10^6 cell mL^{-1}) throughout the season with higher early-spring peaks (Peštová *et al*. 2008) or summer peaks (Malinsky-Rushansky *et al*. 1995), depending upon the interactions of Pcy with other phytoplankton.

In Lake Maggiore the pronounced late summer peak of Pcy is composed by different morphotypes, including microcolonies (Passoni & Callieri 2000) (Fig. 3a). Microcolonies are generally present throughout the euphotic zone, albeit in low abundance in all oligotrophic lakes e.g. representing only 25% of the single-cell forms in Lake Maggiore (Passoni & Callieri 2000). The peak of the colonial coccoid cyanobacteria showed a seasonal distribution pattern similar to that of the microcolonies with maximum values in September-October (Fig. 3b). *Aphanothece* spp. has been recognised to dominate the natural population of colonial coccoid cyanobacteria in late summer-autumn, whereas the spring peak observed in 1996 was due to the presence of *Microcystis* sp. (Fig. 3b).

The peak abundance of Pcy microcolonies appears in summer or autumn in a variety of freshwater systems

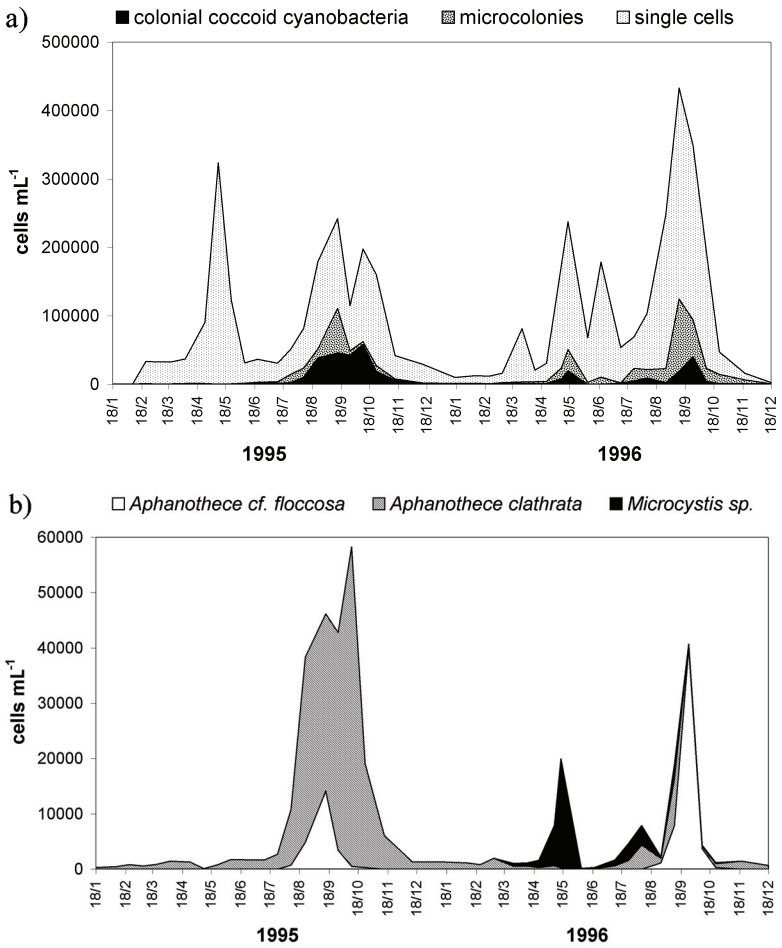

Fig. 3. Seasonal dynamics of: (**a**) single-cell picocyanobacteria, microcolonies and colonial coccoid cyanobacteria, (**b**) *Aphanothece clathrata*, *A.* cf. *floccosa* and *Microcystis* sp., in Lake Maggiore (from Passoni & Callieri 2000, modified).

(Komárková 2002; Szelag-Wasielewska 2003; Crosbie *et al*. 2003c; Mózes *et al*. 2006; Ivanikova *et al.* 2007). Such a variety of morphotypes reflects a genotypic diversity among Pcy communities that accounts for the different Pcy composition observed in spring and summer assemblages (Callieri *et al.* 2007; Caravati 2008) (Fig. 4).

Using quantitative PCR, a sort of rapid succession of individual clades of Pcy shows the patchy structure of the community over quite small spatial/temporal scales (Sánchez-Baracaldo *et al*. 2008). At the same time the co-existence of genetically and physiologically diverse *Synechococcus* spp. found in the pelagic zone of Lake Constance (Postius & Ernst 1999; Ernst *et al*. 2003) indicates possible niche partitioning exploited by the different strains. In marine systems distinct Pcy lineages have also been shown to partition between waters having different environmental characteristics (Fuller *et al*. 2006), a feature evident over large spatial scales (Zwirglmaier *et al*. 2007, 2008). In the Sargasso Sea the community composition of Pcy varied during the season with the highest numbers of *Synechococcus* in spring and *Prochlorococcus* in summer and autumn (DuRand *et al*. 2001). I suggest that the new perspective of habitat-related distribution pattern of *Synechococcus* proposed for Lake Constance (Becker *et al*. 2007) and North Patagonian Andean lakes (Caravati *et al*. 2010) could be generalized to other aquatic systems.

Furthermore, there is strong evidence that Pcy of the cyanobacterial evolutionary lineage VI *sensu* Honda *et al*. (1999) are not exclusively pelagic organisms, but can also inhabit periphytic biofilm in the euphotic zone of temperate lakes (Becker *et al*. 2004). We should integrate our knowledge of Pcy diversity in pelagic and littoral zone habitats to better explain the dominance of certain genotypes in the water column, because the adaptability of these microorganisms may likely be the key feature for their ubiquity (Becker *et al*. 2004).

4.2. Spatial dynamics

Studies of the vertical distribution of populations of Pcy have provided important information about their response to changing physical and biological variables within the euphotic zone. Though Pcy cells are small and their settling rate negligible, their abundance and

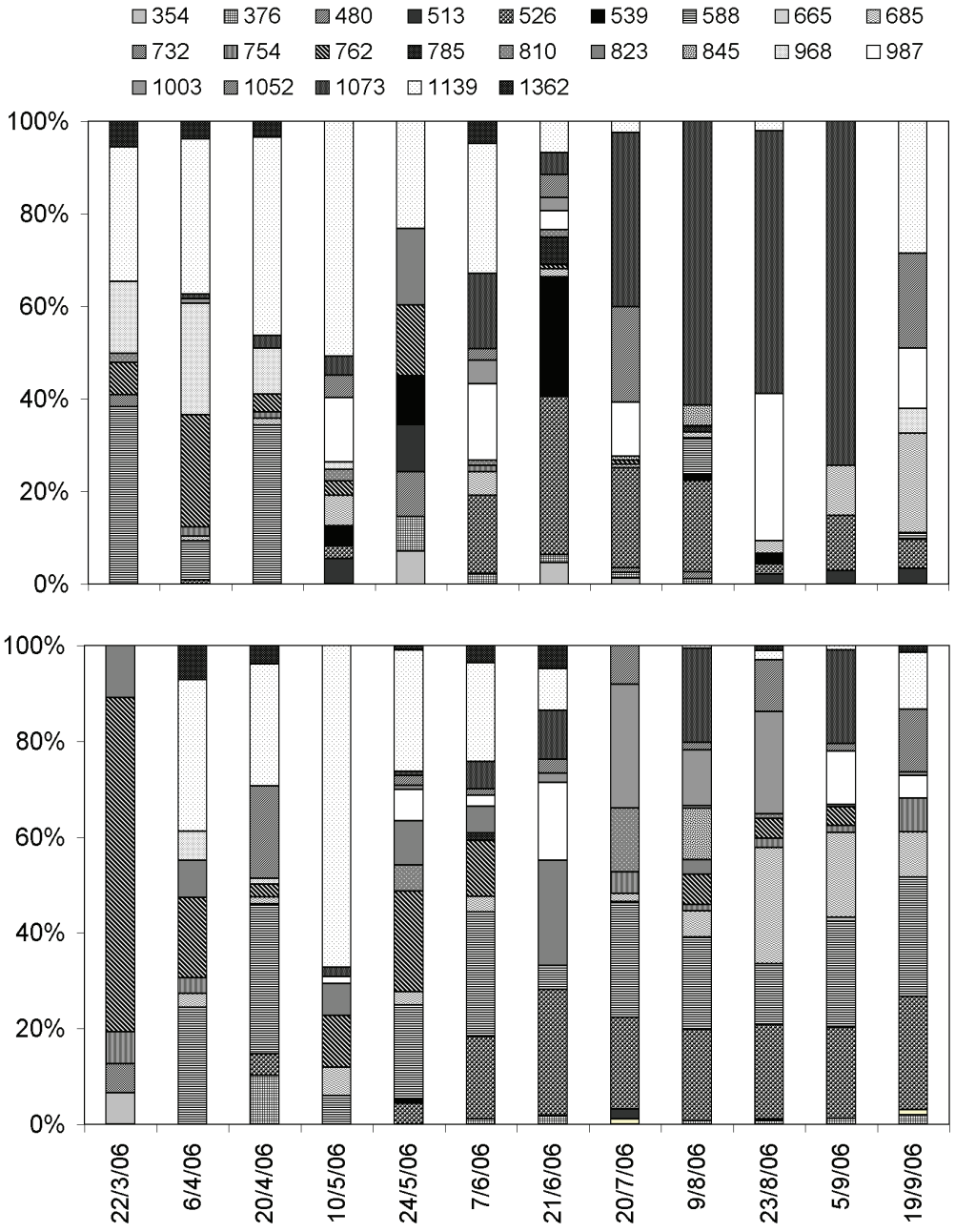

Fig. 4. Dynamics of the percentage of the Operational Taxonomic Units (OTU) of Pcy in Lake Maggiore obtained with ARISA on the ITS-1 (3 m: upper panel, 20 m: lower panel) (from Caravati 2008).

distribution within the water column can change rapidly with different thermal and light regimes, and to the presence of predators or viruses (Pernthaler *et al*. 1996; Muhling *et al*. 2005). Water column depth, which is often inversely related to the trophic state of the lake, is an important indicator of the presence of Pcy and/or of its abundance relative to larger species of phytoplankton.

Deep, clear oligotrophic lakes typically support Pcy comprising mainly PE-rich cells; on the contrary PC-rich cells prevail in shallow, turbid lakes (Callieri & Stockner 2002). This disparity in the distribution of PE- and PC-rich cells is due to their characteristic spectral signature (Everroad & Wood 2006), which has been associated with particular underwater light quality (e.g., Hauschild *et al*. 1991; Vörös *et al*. 1998). In the blue-green North Patagonian lakes (Pérez *et al*. 2002), PE-rich cells typically dominate the Pcy that forms deep chlorophyll maxima (DCM) at the base of the euphotic zone (Callieri *et al*. 2007). In Lake Baikal at offshore stations the Pcy are mainly PE-rich cells, whereas PC-rich cells are found at near shore stations (Katano *et al*. 2005, 2008), suggesting water quality differences in

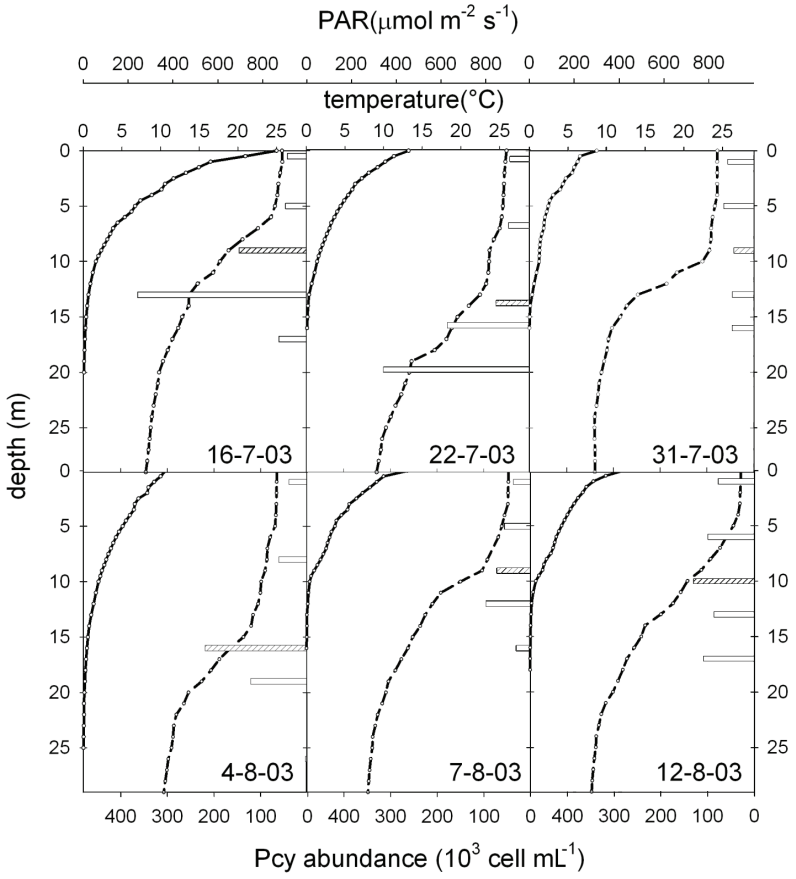

Fig. 5. Six vertical profiles of Pcy abundance, temperature and PAR in Lake Maggiore, during 30 days of summer stratification (Callieri C. and Oboti L., unpublished data). In solid line the photosynthetic active radiation (PAR), in dashed line the temperature, and in histogramms the Pcy abundances. The striped histogramms refer to the depth of thermocline, below there are depths of around 0.1-4% of surface PAR, above depths of around 25-75% of surface PAR.

various zones of the lake. Similar situations have been described for Lake Balaton where in the eastern basin PE-rich cells dominate, while in the western basin PC-rich cells are dominant (Mózes *et al*. 2006). It is the establishment of a pronounced thermocline at depth which likely favours the development of DCM, largely made up of Pcy which are suited both to low nutrient and light conditions (Modenutti & Balseiro 2002; Gervais *et al*. 1997; Camacho *et al*. 2003; Callieri *et al*. 2007). In Lake Tahoe Pcy dominated in the nutrient deficient upper water column during the stratified season, in a distinct vertical niche with respect to picoeukaryotes which peaked at DCM (Winder 2009), as has been found in the Oceans (Vázquez-Domínguez *et al*. 2008). The dynamics of DCM formed by Pcy is quite unstable and its duration is unpredictable, depending upon the strength of hydrodynamic and biotic interactions. A good example is provided by Pcy communities in Lake Maggiore where DCM can appear, and also suddenly disappear, in just a few days (Fig. 5).

Further, it has been shown that the interaction of different biotic and abiotic factors within the water column can affect Pcy vertical distribution patterns, with peaks of abundance in the lower metalimnion and upper hypolimnion of Lake Stechlin (Padisák *et al.* 1997, 1998); in the metalimnion, beneath the steepest part of the thermocline, in Lake Constance and Lake Maggiore (Weisse & Schweizer 1991; Callieri & Pinolini 1995); in the metalimnion of Lake Baikal (Nagata *et al*. 1994); and in the epilimnion of Lake Biwa (Maeda *et al*. 1992), Lake Kinneret (Malinsky-Rushansky *et al*. 1995) and Lake Alchichica, Mexico (Peštová *et al*. 2008).

Microcolonies followed the Pcy single-cell vertical abundance in Lake Maggiore, with a significant correlation between the two distribution patterns in summer (Passoni & Callieri 2000). This provides further evidence of the importance of a common approach to the ecology of single-cells and microcolonies in freshwaters.

5. ECOLOGICAL ASPECTS OF PCY COMMUNITY

5.1. Morphometry and temperature

In order to interpret Pcy single cells and microcolonies dynamics in freshwaters it is imperative to take into consideration the morphometric characteristics and thermal regime of a lake. The community composition of the Pcy can strongly depend on lake typology and

morphogenesis. In a survey covering 45 lakes and ponds, Camacho *et al*. (2003) found that picocyanobacterial development was favoured by the stability of the vertical structure of the lake; that is by the inertial resistance to complete mixing owing to vertical density differences and to a long hydrological retention time. In lakes with relatively high water inflow and short retention time, Pcy are scarce. Far from this situation are deep lakes with a complex basin morphometry such as large sub-alpine lakes. In one of these lakes (Lake Maggiore, Northern Italy) the Pcy population densities during summer stratification are high but with a pronounced North-South gradient due to a high retention time and peculiar characteristics along the lake axis (Fig. 6) (Bertoni *et al*. 2004). Lake Constance, with a different basin morphometry, has a less pronounced gradient (Weisse & Kenter 1991).

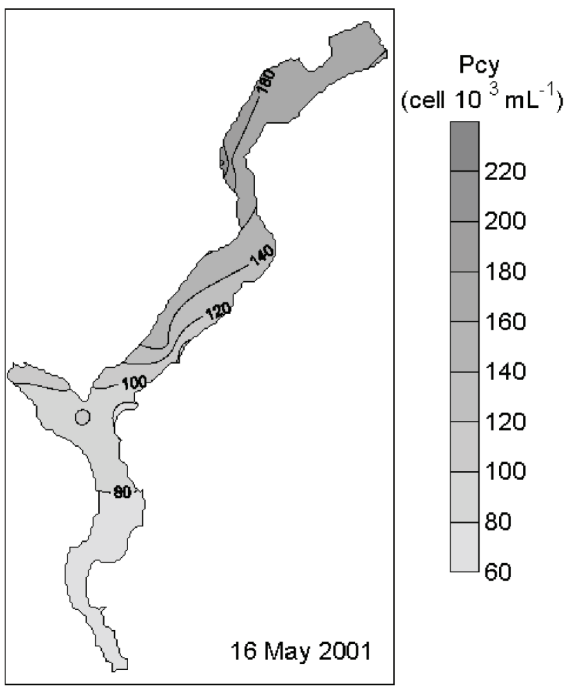

Fig. 6. Map of the spatial heterogeneity of picocyanobacteria (Pcy) abundance in Lake Maggiore during spring sampling. The Northern basin of the lake has a lower contribution of total nitrogen and total phosphorus from the drainage basin respect to the other part of the lake (Bertoni *et al*. 2004, modified).

Pcy composition and abundance vary conspicuously among shallow lakes, with a strong dependence on lake trophic condition (Søndergaard 1991; Stockner 1991), on lake altitude (see Straškrabová *et al*. 1999, and references cited therein), on oxidized-reduced conditions (Camacho *et al*. 2003), and on the presence of dissolved humics (Drakare *et al*. 2003). Therefore it is very difficult to predict Pcy abundance in shallow lakes without considering the physico-chemical characteristics of their waters. In a study of shallow humic lakes of the Boreal Forest Zone, Jasser & Arvola (2003) found Pcy to be light and temperature limited whereas in humic Swedish lakes dissolved organic carbon (DOC) concentration was the factor most influencing Pcy composition (Drakare *et al*. 2003).

The effect of lake thermal structure on the abundance and dynamics of Pcy must take into consideration both the effect of temperature per se and the water mass movements due to the formation of density gradients. In general the increase of temperature enhances the potential growth rate of phytoplankton, increasing the reaction rate of RUBISCO (Beardall & Raven 2004). Marine *Synechococcus* reacts promptly to the temperature increase in laboratory experiments (Fu *et al*. 2007), and in a five year study on Lake Balaton Pcy abundance was positively correlated to water temperature (Vörös *et al*. 2009). Nevertheless the influence of temperature on the abundance of Pcy in the field is difficult to separate from seasonality effects and biogeographic location. The general consensus that temperature is the driving force for growth and development of many different microorganisms does not apply so plainly for Pcy in the field. In diverse marine habitats Li (1998) found a direct relation of the Pcy yearly mean abundance with temperature below 14 °C, and noticed that above 14 °C nitrate concentrations were very low and therefore could replace temperature as the most significant factor affecting Pcy growth. At higher temperatures, other factors can become dominant and control Pcy growth. Weisse (1993) proposed the importance of temperature as triggering the onset of Pcy growth in marine and freshwaters, but not for regulating their population dynamics. In Lake Maggiore the maximal concentrations of Pcy were observed at an optimum temperature of between 18 °C and 20 °C and at the depth of the thermocline (Callieri & Piscia 2002). In this case thermal conditions were important, not only for the ambient water temperature per se, but for the maintenance of a density gradient resisting further settlement and the further deepening of the Pcy peak (Callieri 2008). In general it is possible to state that vertical density gradients in lakes have a very profound effect on the distribution and diversity of Pcy abundance peaks reported in the metalimnion, upper hypolimnion and mixolimnion.

5.2. Nutrients

Nutrient co-limitation can occur in oligotrophic systems (Mills *et al*. 2004), where more than one nutrient may effectively co-limit biomass production (Mackey *et al*. 2009). Thus, past assumptions about whether the N or P is the proximate or ultimate nutrient limiting the productivity of phytoplankton populations in both marine and freshwater systems are re-opened to debate.

As regard Pcy it may be inferred from the Stockner model that as lakes or oceans become more nutrient

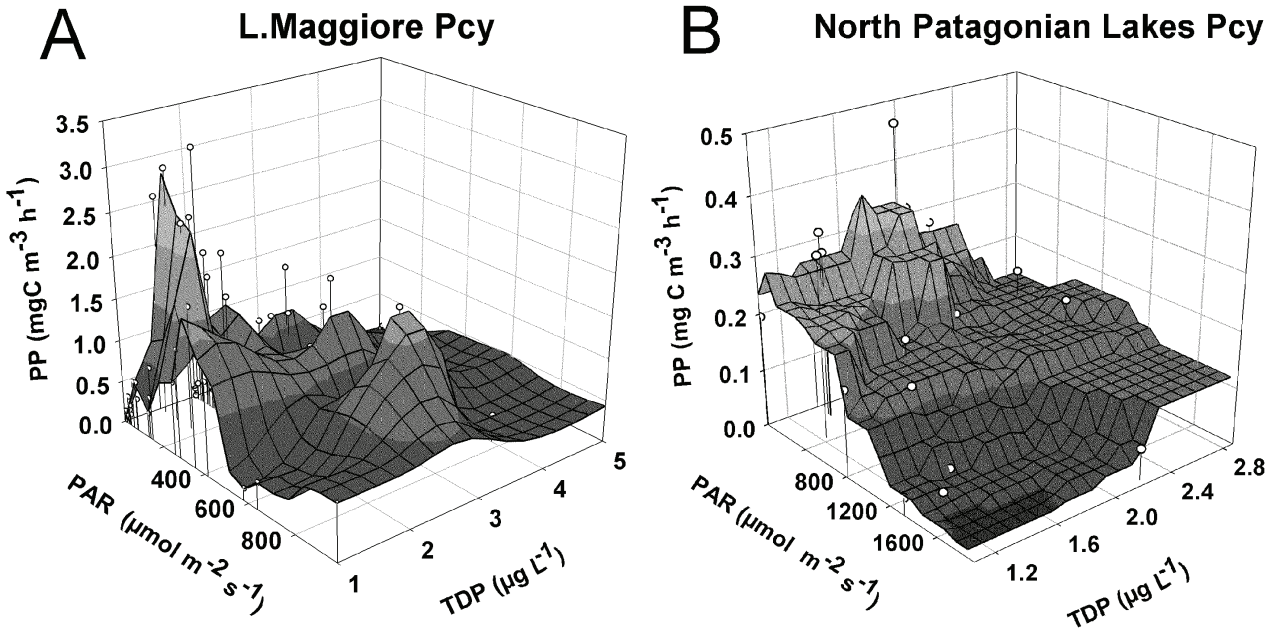

Fig. 7. Multiple linear regression analysis of the Pcy primary production (PP) vs irradiance (PAR) and P (TDP) in: (A) Lake Maggiore, (B) six North Patagonian Lakes (partly from Callieri *et al*. 2007, modified).

depleted, i.e. oligotrophic, then the greater the importance and relative contribution of Pcy to total autotrophic biomass (Bell & Kalff 2001). The success of *Synechococcus* spp. in oligotrophic systems can also be explained by their high affinity for orthophosphate (Moutin *et al*. 2002) and their maximum cell specific P-uptake rates that are competitively superior to algae and other bacteria under a pulsed supply (Vadstein 2000). Actually it has been demonstrated that growth rates of marine Pcy, under limitation by NH_4^+, PO_4^{3-}, Fe or light, are seldom completely stopped; moreover, cell quotas are low as can be expected for such small cells (Timmermans *et al*. 2005).

An alternative explanation for the relative success of Pcy to grow at low inorganic P concentrations is given by the ability of cells to utilise, in addition to PO_4^{3-}, organic sources of phosphate. Under orthophosphate limitation, algae hydrolyse ambient organic phosphates using extracellular phosphatases and transport the orthophosphate thus liberated into their cells (Jansson *et al*. 1988). The extracellular phosphatase activity (APA) in several phytoplankton species has been demonstrated by the enzyme-labelled fluorescence (ELF) technique (Nedoma *et al*. 2003; Štrojsová *et al*. 2003).

There are other alternative ways for Pcy to overcome P limitation. Two pathways are of interest: one has been discovered from the presence of genes necessary for phosphonate utilization in the genome of Pcy (Palenik *et al*. 2003). This suggests that in P limiting conditions *Synechococcus* is able to survive utilizing this refractory form of DOP, derived also from a common herbicide. The other alternative derives from the ability of marine cyanobacteria to substitute sulphate (SO_4^{2-}) for PO_4^{3-} in lipids, thus minimising their phosphorus requirement by using a 'sulphur-for-phosphorus' strategy (Van Mooy *et al*. 2006).

There is evidence that ammonium is the preferred form of nitrogen for *Synechococcus* in culture (Glibert & Ray 1990), but when ammonium is exhausted *Synechococcus* can take up nitrate, thanks to a regulatory mechanism that can induce expression of nitrate reductases (Bird & Wyman 2003). Also, under severe N-limitation Pcy can alternatively use the nitrogen reserve that exists in phycobiliproteins as amino acids storage molecules (Grossman *et al*. 1993).

The success of Pcy under low light conditions is tightly coupled with competition for limiting nutrients. Good evidence on the interplay between P, irradiance and primary production of Pcy and how it is mediated in the field is difficult to envisage, but some clues come from the comparison of six ultra-oligotrophic North Patagonian lakes and from the sub-alpine Lake Maggiore (Fig. 7) (Callieri *et al*. 2007). In the ultra-oligotrophic lakes Pcy production was inversely significantly related to PAR but not to P, indicating that in such extremely nutrient deplete ecosystems, low P concentrations were not the limiting resource driving Pcy production. Conversely, in the oligo-mesotrophic Lake Maggiore both P and light were not significantly correlated to Pcy production. One interpretation of these results is that high irradiance is likely photo-inhibiting Pcy production and hence is the key driving variable and not phosphorus concentration. Similar finding are reported by Lavallée & Pick (2002) who found a lack of correlation between pico-phytoplankton growth rates and any form of dissolved phosphorus.

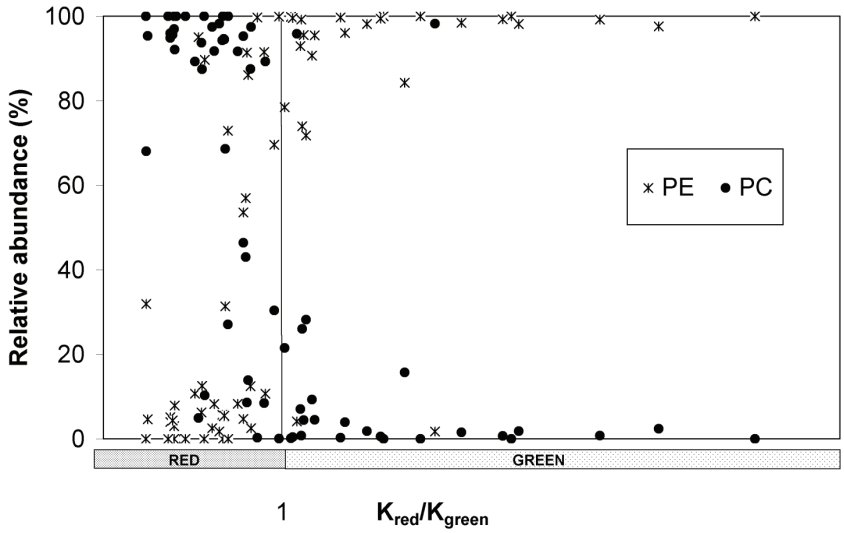

Fig. 8. Relative abundance of PC-cells and PE-cells in different aquatic systems in relation to the underwater light climate expressed as the ratio between the extinction coefficient of red and green wavelengths (K_{RED}/K_{GREEN}). When the K_{RED}/K_{GREEN} ratio is >1 the extinction of red light is high and the dominant underwater light is green. Very low values of K_{RED}/K_{GREEN} ratio indicate a red dominant underwater radiation (modified from Vörös *et al*. 1998).

5.3. Light

Light is well known as an important factor in niche differentiation for Pcy and can modulate the balance between single-cells and microcolonies. The response of Pcy to different light intensity has been studied both in laboratory experiments and *in situ*, and it has been shown that the optimum growth rate of *Synechococcus* occurs at low light intensities, notably at a quantum flux of 45 μE m^{-2} s^{-1} where their highest growth has been observed (Morris & Glover 1981). These findings agree with field observations where the maximum peak abundance has been found deep in the Atlantic mixed layer (Glover *et al*. 1985), and in the DCM (deep chlorophyll maximum) of Lake Stechlin (Gervais *et al*. 1997) and of North Patagonian ultra-oligotrophic Andean lakes (Callieri *et al*. 2007). In lakes worldwide Pcy have been found at a variety of depths and light irradiance (Nagata *et al*. 1994; Callieri & Pinolini 1995; Callieri & Piscia 2002), confirming the classification of *Synechococcus* as a euryphotic organism (Kana & Glibert 1987). One explanation of Pcy tolerance and adaptation to high irradiance is the identification of a process that prevents photo-damage in open ocean Pcy by maintaining oxidized PSII reaction centres, channeling the electrons from PSI to oxygen through a specific oxidase (Mackey *et al*. 2008). As a results of this process Pcy possess an efficient mechanism for dissipating PSII excitation energy, decreasing any potential photo-damage. Nevertheless the relative phylogenetic complexity of the *Synechococcus* and *Cyanobium* genera does not presently permit the simple discrimination of high light- and low light-adapted ecotypes, as has been attained for *Prochlorococcus* (Scanlan & West 2002; Ahlgren & Rocap 2006).

Synechococcus ecotypes exhibit differences in their accessory pigments that affect their adaptation to spectral light quality. It was found that in highly coloured (humic) lakes, non-phycoerythrin cells dominated numerically, while in clearer, oligotrophic hard-water lakes, phycoerythrin-rich cells were the most abundant (Pick 1991). The influence of underwater light quality on the selection of Pcy types having different pigment content has been studied in many aquatic systems, covering a wide spectrum of trophic states and underwater light quality (Vörös *et al*. 1998; Stomp *et al*. 2007). Vörös *et al*. (1998) found that the percentage of PE-rich cells in the total Pcy community (PE + PC) increased with increasing values of the K_{RED}/K_{GREEN} (vertical attenuation coefficient) ratio (Fig. 8). When this ratio is >1 the extinction of the red light is high and therefore the dominant underwater light is green (and blue). On the other hand very low values of this ratio indicate a red dominant underwater radiation. This finding has been resumed by Stomp *et al.* (2007) who considered turbidity instead of light climate. Light quality is actually the primary reason of the prevalence of PC- or PE-rich Pcy, due to their different pigment composition.

In laboratory experiments, it has been shown that Pcy grow better when they have a phycobiliprotein whose absorption spectrum is complementary to that of the available light (Callieri *et al*. 1996) and subsequent experiments showed that PE-rich cells prevail in green light and PC-rich cells in red light but when grown together in white light, can co-exist, absorbing different parts of the light spectrum (Stomp *et al*. 2004). The importance of red light for phycocyanin and biomass production has been shown in laboratory experiments with a PC-rich *Synechococcus* strain (Takano *et al*. 1995), while blue and green wavelengths of light are

used more efficiently than red of similar intensity by PE-rich *Synechococcus* (Glover *et al*. 1985).

The pigment composition of Pcy represents a characteristic spectral signature that can define individual strains, but closely related strains can have different pigment composition (Everroad & Wood 2006). In particular both pigment types have been found in several non-marine Pcy clusters (Crosbie *et al*. 2003a). A new clade, sister to *Cyanobium*, was recently reported from oceanic waters, based upon phylogenetic analysis of concatenated 16S rDNA and *rpo*C1 data sets (Everroad & Wood 2006). This large clade includes both PE-rich and PC-rich strains. Similarly, marine cluster B (MC-B) also contains PE-rich and PC-rich strains, and this cluster is polyphyletic, consisting of at least 2 different subclusters (Chen *et al*. 2006). The phylogeny derived from the *cpc*BA operon of the green PC pigment was better able to separate differently pigmented Pcy than 16S rRNA-ITS phylogeny (Haverkamp *et al*. 2008). The ecological implication of these findings is that *Synechococcus* from different lineages can occupy different niches; or alternatively, if the environment offers greater variability and more suitable niches, like in the Baltic Sea (Haverkamp *et al*. 2009) or in Lake Balaton (Mózes *et al*. 2006), they can coexist.

Laboratory experiments with freshwater strains from different phylogenetic groups acclimated at low and medium irradiance, showed that photosynthetic responses are strain-specific and sensitive to photo-acclimation (Callieri *et al*. 2005; Moser *et al*. 2009) (Fig. 9). PE-rich Pcy from Group B, subalpine cluster I (*sensu* Crosbie *et al*. 2003a), are more sensitive to photo-acclimation than PC-rich cells from Group I and from Group A, *Cyanobium gracile* cluster. Therefore eco-physiological differences seem to be more related to the pigment type. Nevertheless the extent of photo-adaptation is strain-specific and depends on the duration of the photo-acclimation (Moser *et al*. 2009).

5.4. Ultraviolet radiation (UVR)

Picoplankton are thought to be particularly vulnerable to UVR because: 1) their small size does not permit the intracellular production of sunscreen compounds (Garcia-Pichel 1994); 2) the small 'package' effect leads to higher pigment-specific absorption (Morel & Bricaud 1981) and 3) the distance between the cell surface and the nucleus (DNA) is shortened and the DNA damage induced by UV-B is increased. Thymine dimers like cyclobutane pyrimidine dimer (CPD) are frequently built upon DNA lesions under UV-B radiation and have been recovered in marine phytoplankton (Buma *et al*. 1995) and in Argentinian lakes (Helbling *et al*. 2006).

Although the higher vulnerability of picoplankton is theoretically predictable, contrasting results have been obtained in field studies. Laurion & Vincent (1998) studying size-dependent photosynthesis in a sub-arctic lake have shown that cell size is not a good index of UVR sensitivity. Further, they indicated that Pcy are less sensitive to UVR fluxes and that genetic difference between taxa, more than size, are important in determining the tolerance to UVR; while other authors obtained evidence of an higher vulnerability of smaller algae to UVR (Kasai *et al*. 2001; Van Donk *et al*. 2001).

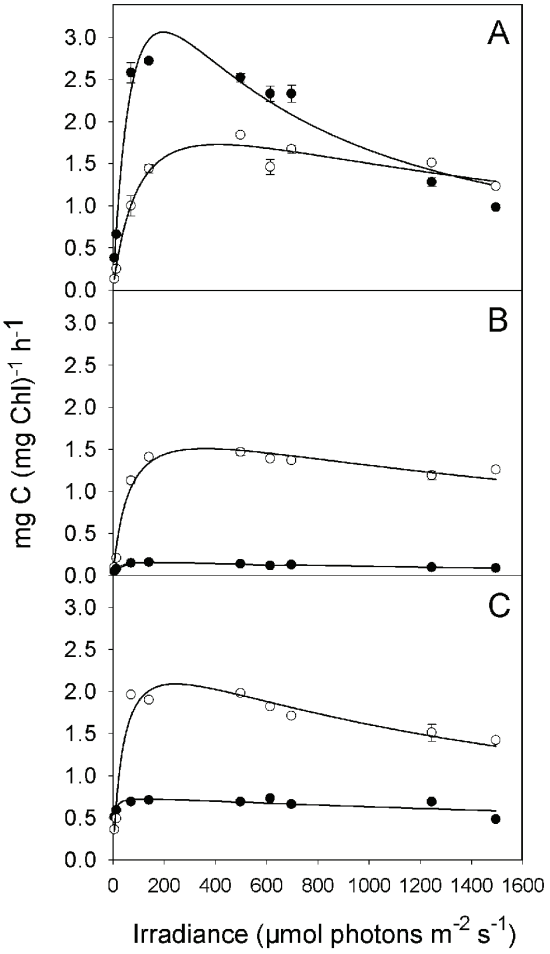

Fig. 9. P/E curves of three Pcy strains: (A) PE-cells MW4C3 from the Group B, Subalpine cluster; (B) PC-cells MW100C3 from Group I; (C) PC-cells BO8801 from Group A, *Cyanobium* cluster. Open symbols refer to medium light acclimation (100 µmol m^{-2} s^{-1}), filled symbols refer to low light acclimation (10 µmol m^{-2} s^{-1}). (from Moser *et al*. 2009, modified).

A high Pcy sensitivity to UVR radiation in comparison to nano-phytoplankton was observed in the biological weighting functions (BWF) in a high altitude alpine lake by Callieri *et al*. (2001). A possible interpretation of these contrasting results is that small cells are likely more susceptible to DNA damage than large cells but they are able to acclimate faster, within hours (Helbling *et al*. 2001), and are more resistant to photosystem damage (Villafañe *et al*. 2003).

The spectral quality of the UVR exposure, its duration and photon flux density, strongly influences the effect on phytoplankton communities (Harrison & Smith 2009). The damaging power of radiation generally increases from PAR through UV-A into the UV-B wavebands, but this general pattern may still be questioned (Harrison & Smith 2009). There is evidence that many aquatic organisms react promptly to UV-B stress by producing protective substances such as mycosporine-like amino acid compounds (MAAs) (Sinha & Hader 2008), which have absorption maxima ranging from 310 to 359 nm (Carreto *et al*. 1990; Karentz *et al.* 1991). In particular cyanobacteria react in response to UV-A radiation by producing an extracellular yellow-brown pigment - scytonemin, that absorbs most strongly in the UV-A spectral region (315-400 nm) (Garcia-Pichel & Castenholz 1991; Dillon *et al*. 2002). The sunscreen capacities of MAAs and scytonemin are higher if they are present concurrently, and their production is considered an adaptive strategy of photo-protection against UVR irradiance (Garcia-Pichel & Castenholz 1993). Also it is recognized that the UV-B induced production of CPD is counterbalanced by repair mechanisms based on the production of enzymes known as photolyases (Jochem 2000).

Therefore aquatic organisms have numerous mechanisms of protection against UVR which influence their global community responses in nature. Recently it has been recognized that many of the effects of solar UVR are caused by wavelengths in the UV-A range, which are not affected by changes in stratospheric ozone (Sommaruga 2009). The higher photo-inhibiting effect of UV-A than UV-B on different size fractions of phytoplankton has been described in several different lakes (Callieri *et al*. 2001; Villafañe *et al*. 1999; Callieri *et al*. 2007) and in marine habitat as well (Villafañe *et al*. 2004; Sommaruga *et al*. 2005). Callieri *et al*. (2001) explain the negligible impact of UV-B on *in situ* phytoplankton production with the lower weighted irradiance brought about by the high K_d at short wavelengths and low incident flux, whereas with UV-A the weighted irradiance is higher due to a greater incident flux and lower K_d.

Mixing is an important factor affecting the degree of plankton exposure to UVR. Vertical mixing transports the cells to depth where active repair takes place and subsequently re-exposes them to higher UVR, upon transport again to near surface depths. Species which form surface blooms, like colonial *Microcystis aeruginosa*, can also withstand high UVR, synthesizing carotenoids and MAAs (Liu *et al*. 2004). To explain the resistance of colonial Pcy to UVR it is interesting to note that the colonial morphotype of *Microcystis* can synthetize substances such as D-galacturonic acid, which is the main component of the slime layer of *Microcystis* (Sommaruga *et al*. 2008), and which may hence provide a protective function. In *Nostoc commune* UV-B exposure induced the synthesis of a glycan sheath around the filaments to provide a matrix for the MAAs (Ehiling-Schulz et al. 1997). Similarly microcolonies, here considered as transitional forms from single-cell to colonial, may have a selective advantage under UVR exposure due to the presence of a sheath matrix. To better understand the role of microcolonies in lakes Callieri & Bertoni (in preparation) used a PE-rich *Synechococcus* strain which does not form aggregates in culture, and exposed the strain to different levels of UVR and PAR radiation under controlled conditions (Fig. 10). They observed that the culture previously acclimated to high light (HL) did not form microcolonies, even if exposed to UVR, but the culture acclimated to low light (LL) reacted to UVR by forming microcolonies, likely finding a refuge through a morphological adaptation, inclusive of slime layer protection, similar to that noted in *Microcystis* (Sommaruga *et al*. 2008). Therefore, in the equilibrium between single cells *vs* microcolonies or even larger colonial morphologies, the importance of solar radiation (UVR and PAR) should not be underestimated but considered together with other important factors like the nutrient status of the ecosystem.

5.5. Biotic interactions

Heterotrophic and mixotrophic nanoflagellates and small ciliates have been recognised as the most important grazers of Pcy (Stockner & Antia 1986; Christoffersen 1994; Sanders *et al*. 2000). Despite the importance of ciliate grazing on Pcy in some systems (Šimek *et al*. 1995), it is generally recognized that among protozoa, both heterotrophic and mixotrophic nanoflagellates are responsible for 90% of the grazing of Pcy and bacteria; whereas ciliates accounted for only 10% (Pernthaler *et al*. 1996b; Callieri *et al*. 2002). The size of the prey, its morphological characteristics and nutritional value have been indicated as important factors in the selection carried out by the predators (Šimek & Chrzanowski 1992; Jezberová & Komárková 2007; Shannon *et al*. 2007). In particular the involvement of the proteinaceous cell surface (S-layer) as grazing protection has also recently been suggested for freshwater *Actinobacteria* (Tarao *et al*. 2009). Morphological characteristics can therefore be considered as group-specific traits and can greatly influence the success of the group in their ecosystems. The presence of a gelatinous matrix in the Pcy microcolonies (like for the larger colonial Pcy), acts as an effective anti-grazing agent. Protozoa grazing and in particular nanoflagellates can influence the characteristics of bacterial and Pcy communities and lead to changes in their structural and taxonomic composition. In a laboratory study, using 37 *Synechococcus* strains it was clearly demonstrated that prey selection discriminates at the strain-specific level (Zwirglmaier *et al*. 2009).

The selection of food as described for metazooplankton generally takes place during food capture and

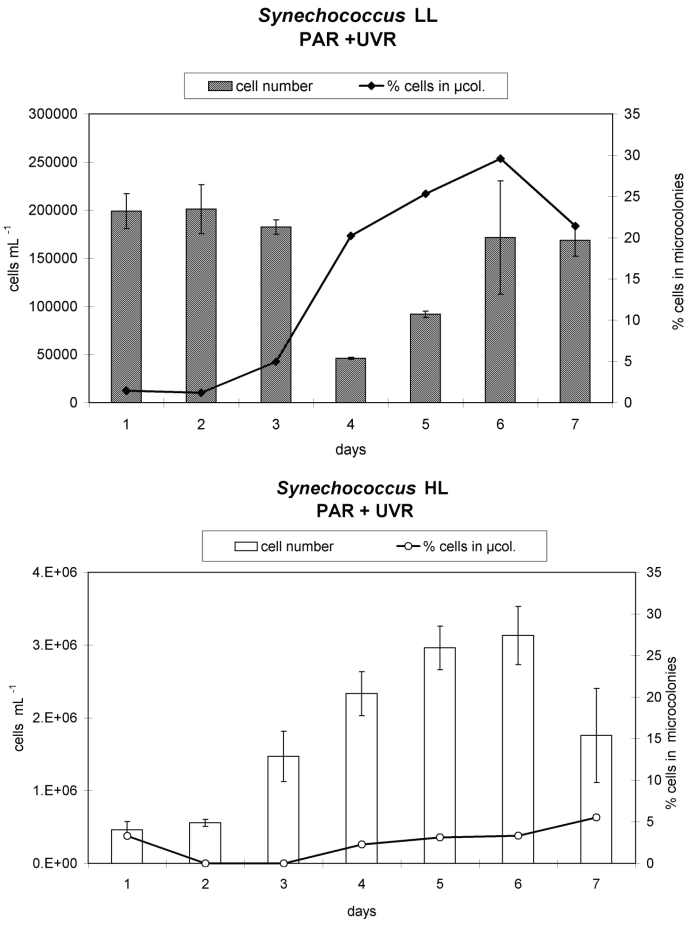

Fig. 10. Selected results of experiments done with *Synechococcus* sp. (PE-cells) acclimated at low light (LL) 10 µmol m^{-2} s^{-1} (upper panel) and high light (HL) 100 µmol m^{-2} s^{-1} (lower panel) exposed to UV (Q panel 30 µW cm^{-2} nm^{-1}) and HL. The percent of cells in microcolonies increase beginning from the 4 days in the LL culture, but not in the HL (from Callieri & Bertoni, in preparation).

processing (Porter 1973). According to the theory of 'selective digestion' prey selection takes place inside the food vacuoles (Boenigk *et al*. 2001). The fate of the prey is decided at the moment of digestion, with the possibility of very fast prey-excretion after the uptake. Knowledge of the mechanism of Pcy consumption and excretion/digestion is species-specific both for prey and predator. Also, amoebae can perform food selection in the food vacuole and excrete the toxic or unpalatable prey items similarly to nanoflagellates (Liu *et al*. 2006; Dillon & Parry 2009).

Ciliates and nanoflagellates can also serve as a trophic link between Pcy production and *Daphnia* production, thereby upgrading the nutritional value of Pcy as a food source by producing essential lipids such as sterols (Bec *et al*. 2006; Martin-Creuzburg & Von Elert 2006). Among mesozooplankton, *Daphnia* has the capacity of feeding on a wide particle size range (1 µm to 50 µm), filtering Pcy as well (Gophen & Geller 1984; Stockner & Porter 1988). An important effect of *Daphnia* grazing on Pcy functioning was observed in laboratory experiments (Callieri *et al*. 2004), where there was an increase in P and C cell-specific uptake of Pcy and in their photosynthetic efficiency. This increase in activity could have been related to the release of P by *Daphnia*, which was measured to be around 5% of the total P-pool per day (Boersma & Wiltshire 2006). Another possible conjecture is that nutrients are replenished during the passage of Pcy through the digestive tracts of consuming daphnids (Porter 1975; Stockner 1991). There is evidence that nutrient-limited green algae pass through the gut of *Daphnia* intact and alive (Van Donk & Hessen 1993) and that during passage some of the P is released in the gut (Boersma & Wiltshire 2006).

Among lake studies of Pcy, only a few refer to the impact of copepod grazing, particularly calanoid copepods. It has been shown that copepods have a stronger negative effect on ciliates than do *Daphnia* (Burns & Schallenberg 1996) and that top-down effects in the short term are stronger in oligotrophic ecosystems than in eutrophic ones (Burns & Schallenberg 2001). The mesocosm experiments of Zöllner *et al*. (2003) showed the structuring and cascading effects of the cladoceran *Daphnia hyalina* cf. *galeata* and copepods on microbial food web structure. Copepods prey selectively and efficiently on ciliates and algae in the size range 20 to 40

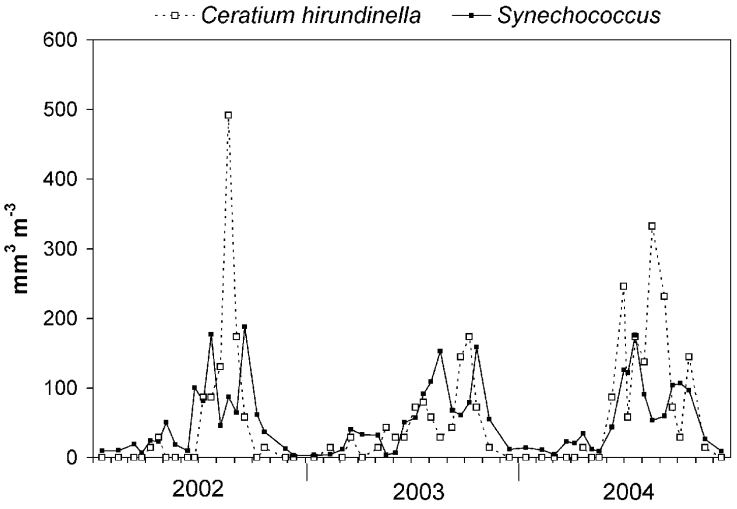

Fig. 11. Seasonal dynamics (2002, 2003, 2004) of the *Synechococcus* spp. – *Ceratium hirundinella* functional association (from Callieri *et al*. 2006, modified).

µm (Yoshida *et al*. 2001), thereby triggering a trophic cascade, enabling high numbers of HNF and the potential for a greater mortality of Pcy (Zöllner *et al*. 2003). Sundt-Hansen *et al*. (2006) have shown that in marine mesocosms, copepods have a profound structuring effect on the pelagic food web, and thus directly and indirectly, regulate the abundance of Pcy predators. In this way, the strength of the trophic cascade downward to Pcy depends substantially on the structure of the food web and the inventory of zooplankton species present (Gismervik 2006; van Grenberghe *et al*. 2008).

Rotifers can either act directly on Pcy populations by grazing or indirectly by preying on nanoflagellates and small ciliates (Stockner & Shortreed 1989; Arndt 1993; Pernthaler *et al.* 1996a). It has been found that many planktonic rotifers (*Keratella cochlearis*, *K. quadrata*, *Polyarthra dolichoptera*) feed on particles in the size-range 0.5 to 3 µm, interspecific variation in food selection being dependent on differences in the corona sizes of the consuming species (Ronneberger 1998).

While predation has been recognised as an important top-down structural and dynamic control of Pcy, very little attention has been directed towards the study of other ecological interactions such as symbiosis (Adams 2000). In the sea, the cyanobacterial symbionts (or 'cyanobionts': Taylor 1982) provide an example of proto-cooperation. Foster *et al*. (2006) used molecular methods to amplify prokaryotic symbiont rRNA sequences from individual marine cells of various marine eukaryotes. The same symbiont was found capable of forming associations with a variety of organisms, thus opening up the possibility of consortial interconnections. Another approach to the study of biological interactions is to consider the in situ occurrence of groups of species that share similar requirements or even show proto-cooperative interaction. The natural co-occurrence and simultaneous increase or decrease in the numbers of some species may indicate the existence of 'functional associations' (Reynolds *et al*. 2002) that help us to interpret and predict their dynamics. The supposition at the base of such associations is that common morphological or physiological properties offer relative, dynamic advantages of component species of the association. Recently, a new association was proposed that comprises *Synechococcus* spp. and potentially mixotrophic flagellates e.g., *Rhodomonas lacustris*, *Ceratium hirundinella*, *Cryptomonas erosa* (Callieri *et al*. 2006). Co-occurrence of Pcy and *Ceratium* spp. has been reported from mesotrophic lakes (Kasprzak *et al*. 2000), from Lake Kinneret (Berman *et al*. 1992) and Lake Maggiore (Callieri *et al*. 2006). In the latter lake, a three-year study showed a phase of co-existence in which the organisms might each benefit from the association, followed by a phase of predation in which one member of the association prevailed over the other (Fig. 11). At low levels of physical and biological disturbance, the cycle can restart with prey recovery driven by nutrient excretion of phagotrophs. The association indicates that assemblages that form a functional group may not only have similar adaptations and requirements, but can exhibit predator-prey interactions, as was recently shown in a marine lagoon in France where the quasi simultaneous appearance of both Pcy and the dinoflagellate *Alexandrium catenella* was observed (Collos *et al*. 2009). These authors hypothesised that Pcy can make up for a particulate nitrogen form during periods of limiting nutrients, thus providing *A. catenella* an ecological advantage over strictly autotrophic phytoplankton. The co-domination of a desirable prey organism, such as *Synechococcus* with its potential grazers opens up new perspectives on the interaction between the ecological categories of phytoplankton and the components of the microbial food web. We cannot refrain from conjecturing that these functional associations may be an

advanced phase of a symbiotic association of cyanobacteria with eukaryotic plankton hosts, similar to those observed in the ocean (Carpenter & Foster 2002; Foster *et al*. 2006).

In the consideration of biological interactions, it is also opportune to refer to viral infections (Weinbauer 2004). The occurrence of viruses that infect *Synechococcus* is widespread and there is agreement that phages exert a significant selection pressure on *Synechococcus* (Mann 2003). Cyanophages are ubiquitous in aquatic environments, and can occur at abundances in excess of 10^6 mL^{-1} (Suttle 2000). Recent findings indicate that cyanophage infections can exert a major influence on the direction of Pcy succession in the sea (Muhling *et al*. 2005), and that marine viruses can act as intermediates for exchanging genes (Zeidner *et al*. 2005). Transduction is the phage-mediated gene transfer between a donor and a host, and has been recognized as is an important factor for bacterial evolution (e.g., Doolittle 1999). In three peri-alpine lakes viral impact on Pcy exceeded predation in autumn, but was highly variable throughout the early season (Personnic *et al*. 2009b). However, the interplay between viruses and nanoflagellates and their control of prokaryotes is not completely understood, largely due to a lack of knowledge of the direct interactions of viruses on predators and vice-versa (Jacquet *et al*. 2007; Massana *et al*. 2007; Pradeep-Ram & Sime-Ngando 2008).

The extent of lysogeny in 19 freshwater *Synechococcus* strains indicated a high level within PC-rich *Synechococcus* (Dillon & Parry 2008). These authors found that the majority of cyanophages in the eutrophic lake they studied were temperate, that is they exist in a lysogenic association with their hosts. In the majority of the strains cell lysis by the phage was only triggered by an inducing agent used experimentally to assess the level of temperate phage infection in the host population. On the other hand viral DNA might also have a protective role on the host (Baley *et al*. 2004). An example is provided by the discovery of a cyanophage encoding polypeptide D1 and D2 of the PSII, inducing repair cycles after photo-damage (Baley *et al*. 2004). Nevertheless it is not known at which extent the phage modifies the properties of PSII and therefore manipulates the photosynthetic physiology of the infected cells.

6. CONCLUDING REMARKS

Important advances in our perception of the significance of picocyanobacteria in freshwaters and oceans have occurred only within the last few decades, and these findings have come largely from an improved understanding of phylogenetic evolution of this major group. We now know that evolution of earliest cyanobacterial lineages were not marine, but likely were of terrestrial or freshwater origin and were unicellular.

The form-genus *Synechococcus* likely represents the ancestral morphology from which other types, including colonial forms, evolved. To what extent the formation of microcolonies is due to the presence of specific *Synechococcus* genotypes or is the result of survival strategy is presently not fully understood. The current challenge is to better understand the relationship between the diversity and ecology of Pcy and microcolonies and their interaction with the environmental factors that allow the proliferation of the most competitive genotypes.

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