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Shades of red and green : the colorful diversity and ecology of picocyanobacteria in the Baltic Sea

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Chapter 7

English summary

The open water of aquatic ecosystems offers a rather homogenous environment with little spatial structure compared to, for instance, tropical rain forests or coral reefs. Yet, surprisingly, aquatic environments are inhabited by a highly diverse phytoplankton community with numerous coexisting species competing for only a limited number of nutrients. One potential niche axis contributing to the species diversity of the plankton might be the underwater light spectrum. This thesis describes the ecology and phylogeny of coexisting picocyanobacteria in relationship to the color of light. In particular, it was investigated how the color of light affects the distribution, diversity and pigment composition of the cyanobacteria *Synechococcus* and *Pseudanabaena* in the Baltic Sea.

In Chapter 2 the distribution of red and green pigmented picocyanobacteria was investigated in relation to the light regime in natural waters. Previously, it was found in laboratory experiments that red and green picocyanobacteria can coexist under white light. Here, a parameterized competition model was used to describe the coexistence of red and green phytoplankton species in relation with the underwater light color of lakes and seas. To test the predictions of the model, picocyanobacteria were sampled from 70 aquatic ecosystems, ranging from clear blue oceans to turbid brown peat lakes. As predicted, red picocyanobacteria dominated in clear waters whereas green picocyanobacteria dominated in turbid waters. Widespread coexistence of red and green picocyanobacteria occurred in waters of intermediate turbidity. These data support the hypothesis that niche differentiation along the light spectrum promotes phytoplankton biodiversity, thus providing a colorful solution to Hutchinson's plankton paradox.

In Chapter 3 the distribution and diversity of differently colored picocyanobacteria in the Baltic Sea is reported. It was found that coexistence of red and green picocyanobacteria in the Baltic Sea is widespread. The diversity and phylogeny of red and green picocyanobacteria was analyzed using three different genes: 16S rRNA-ITS, the *cpeBA* operon of the red pigment phycoerythrin (PE), and the *cpcBA* operon of the blue pigment phycocyanin (PC). Sequencing of 209 environmental clones from the Baltic Sea showed that picocyanobacteria exhibit high levels of microdiversity. The partial nucleotide sequences of the *cpcBA* and *cpeBA* operons from the clone libraries of the Baltic Sea revealed two distinct phylogenetic clades: one clade contained mainly sequences from cultured PC-rich picocyanobacteria, while the other clade contained only sequences from cultivated PE-rich strains. A third clade of phycourobilin (PUB) containing strains of PE-rich *Synechococcus* spp. did not comprise sequences from the Baltic Sea clone libraries. These findings differ from previously published phylogenies based on 16S rRNA gene analysis. Our data suggest that, in terms of their pigmentation, *Synechococcus* spp. represent three different lineages occupying different ecological niches in the underwater light spectrum. Strains from different lineages can coexist in light environments that overlap with their light absorption spectra.

Chapter 4 describes the isolation of 46 closely related picocyanobacterial strains from the Baltic Sea. The isolates show considerable variation in their pigmentation phenotypes. Furthermore, small differences between the strains were observed with respect to cell volume and preference for either ammonium or nitrate as the main source of nitrogen. At the molecular level we found that 39 strains, designated BSea1, had almost identical 16S rRNA-ITS sequences

with *Synechococcus* strain WH5701. Despite having similar 16S rRNA–ITS sequences, the BSea1 strains could be separated into several different clusters when comparing the phycocyanin (*cpcBA*) operon. This separation corresponds to the pigmentation of the different BSea1 strains. The majority of PC-rich Bsea1 strains clustered with WH5701. Remarkably, the PE-rich strains of BSea1 formed an as yet unidentified cluster within the *cpcBA* phylogeny, distantly related to other PE-rich groups. Detailed analysis of the *cpcBA* operon using neighbour net analysis indicated that the PE-rich BSea1 strains are probably endemic for the Baltic Sea. Comparison of the phylogenies obtained by using the 16S rRNA–ITS, the *cpcBA* as well as the concatenated 16S rRNA-ITS and *cpcBA* operon sequences, revealed possible events of horizontal gene transfer among different *Synechococcus* lineages. Our results show that microdiversity is widespread in *Synechococcus* populations, and that it can reflect different phenotypes with different ecological roles.

The topic discussed in chapter 5 is the isolation and diversity of *Pseudanabaena* strains from two different ecosystems. *Pseudanabaena* species are poorly known filamentous bloom-forming cyanobacteria closely related to *Limnothrix*. Because of their small size, the importance of *Pseudanabaena* has been overlooked and they have not been recognized as dominant organisms in blooms. We isolated 28 *Pseudanabaena* strains from the Baltic Sea and the Albufera de Valencia (Spain). By combining phenotypic and genotypic approaches the phylogeny, diversity, biogeography and evolutionary diversification of these isolates were explored. Analysis of the *in vivo* absorption spectra of the *Pseudanabaena* strains revealed two coexisting pigmentation phenotypes: (i) phycocyanin-rich strains, and (ii) strains containing both phycocyanin and phycoerythrin. Strains of the latter phenotype were all capable of complementary chromatic adaptation (CCA). We compared the different *Pseudanabaena* strains using a multi-locus sequence approach which spanned the 16S and 23S rRNA genes, the ribosomal intergenic spacer ITS-1, the *cpcBA* operon encoding phycocyanin, and the intergenic spacer (IGS) between *cpcA* and *cpcB*. In addition, the presence of *nifH*, one of the structural genes of nitrogenase, was investigated. Sequence analysis of ITS and *cpcBA*-IGS allowed for the differentiation between *Pseudanabaena* isolates exhibiting high levels of microdiversity. This multi-locus sequencing approach revealed specific clusters for the Baltic Sea, the Albufera de Valencia, and a mixed cluster with strains from both ecosystems. The latter comprised exclusively CCA phenotypes. The phylogenies of the 16S and 23S rRNA genes were consistent, but analysis of other loci indicated loss of substructure, suggesting that recombination between these loci has occurred. Population genetic analyses of the phycocyanin genes suggest an evolutionary diversification of *Pseudanabaena* through purifying selection.

Summarizing this research, we have found that picocyanobacteria of the Baltic Sea show an extensive genetic differentiation that enables them to display a wide variety of physiological and morphological characteristics. This extensive microdiversity allows cyanobacteria to occupy a variety of different ecological niches. In particular, the light spectrum offers an important axis for niche differentiation in pelagic ecosystems that can be occupied by cyanobacteria with different photosynthetic pigments. It was demonstrated that picocyanobacteria with the pigments phycocyanin and phycoerythrin have different abundances related to the light

quality. Interestingly, while the differently pigmented picocyanobacteria could not be separated phylogenetically on the basis of the 16S rRNA gene, they were clearly separated into different endemic and ecologically important groups when using the genes encoding for their pigment proteins phycocyanin and phycoerythrin. For *Pseudanabaena* it was found that the non-coding regions separated endemic and cosmopolitan groups. More ecological data will be required to fully understand the ecological niches of *Pseudanabaena* in aquatic environments.

In conclusion, our results show that functional genes can be used to identify a rich microdiversity of genotypes occupying different niches in the environment. A major ingredient in our approach is that the genotypes can be linked to distinct phenotypes, for which a dedicated collection of cultured isolates is indispensable.

