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Colourful coexistence : a new solution to the plankton paradox

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Chapter 7

Afterthoughts

The main purpose of this thesis has been to identify the significance of the colour of light for the competitive dynamics of phytoplankton species. A combined approach of theory and experiments led to the first experimental evidence that phytoplankton species can coexist by utilizing different parts of the light spectrum (Stomp *et al.* 2004). Moreover, extensive field surveys on a global scale showed that the underwater light colour in oceans, seas and lakes is an important selective factor for phytoplankton communities. For instance, red picocyanobacteria are favored in clear oceans and lakes, while green picocyanobacteria are selected in more turbid waters (Stomp *et al.* 2007*a*; Haverkamp *et al.* 2008). In Stomp *et al.* (2007*b*), we identified the various spectral niches available for photosynthetic organisms in aquatic habitats. Interestingly, vibrations of water molecules require light energy of specific wavelengths, and thereby create large gaps in the underwater light spectrum. The wavebands between these gaps define a series of distinct niches, ranging from the blue light niche in clear blue oceans to the infra-red light niche in turbid microbial mats. The pigments of photosynthetic organisms seem to be tuned to these distinct niches, thus avoiding intense competition for light with the surrounding water molecules. Some cyanobacteria can actively adjust their pigment composition to the prevailing light spectrum, by the process called complementary chromatic adaptation. In Chapter 6, we showed that this strategy of adaptation is beneficial in competition for light, but only if fluctuations in the prevalent light colour are slow relative to the time needed for chromatic adaptation.

Although this thesis demonstrates that light colour plays an important role in phytoplankton competition, there are still many open questions. In this chapter I would like to put forward several ideas for further exploration of competition in the light spectrum.

Does ‘sharing the light spectrum’ resolve the Paradox of the Plankton?

In this thesis we showed that phytoplankton species can coexist by partitioning of the light spectrum, thereby promoting phytoplankton diversity. However, what is the maximum number of species that is able to coexist by partitioning of the light spectrum? As a case study, let’s focus on the green light environment of the Baltic Sea. Our field survey and model simulations showed that red and green picocyanobacteria coexist in the Baltic Sea (Stomp *et al.* 2007*a*; Haverkamp *et al.* 2008). However, diatoms and chlorophytes are abundant in the Baltic Sea as well (Stal *et al.* 2003). Can we explain their coexistence based on sharing of the light spectrum? To answer this question, we used the parameterized model of Stomp *et al.* (2007*a*) to simulate competition between red and green picocyanobacteria (*Synechococcus* strains BS4 and BS5), diatoms (*Phaeodactylum tricornutum*), and chlorophytes (*Chlorella vulgaris*) (Figure 7.1). Although red picocyanobacteria become most abundant, the model simulations predict stable coexistence of all four species in the Baltic Sea based on partitioning of the light spectrum. Thus, indeed, these simulations show that our findings extend beyond the mere coexistence of

red and green cyanobacteria. A wide diversity of phytoplankton species can coexist in coastal waters, simply by utilizing different parts of the light spectrum in different ways.

In a similar way, we can make predictions on the major phytoplankton groups that coexist in other aquatic ecosystems. Besides the ‘green light niche’ of coastal waters, we identified four other niches in the light spectrum (Stomp *et al.* 2007*b*), ranging from the blue light environment in the clear blue oceans to the infra-red light niche in turbid microbial sediments. To predict which phototrophic groups are dominant in which niche, one could run simulations of competition along a gradient of turbidity (as in Stomp *et al.* 2007*a*). Instead of the four species used in the simulations of Figure 7.1, one could use a much larger pool of species covering the full suite of photosynthetic pigments on Earth (as in Figure 5.6). Which phototrophic microorganisms will coexist in which spectral niches? And will there be changes in diversity of phototrophic microorganisms along the turbidity gradient?

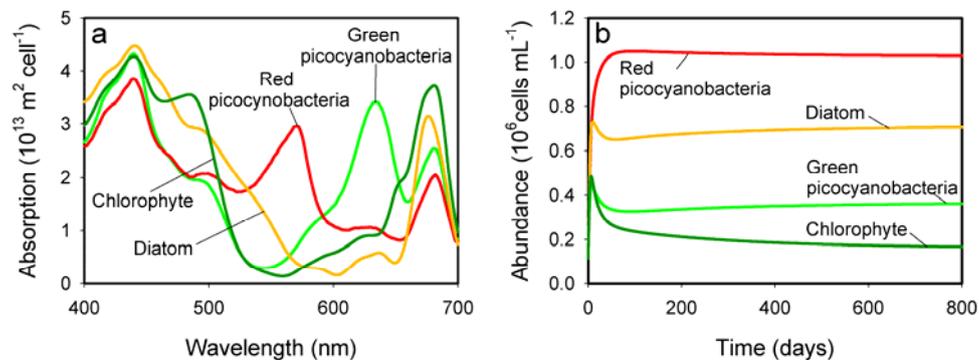


Figure 7.1 Model predictions of four phytoplankton species competing for light in the Baltic Sea. (a) Absorption spectra of the phytoplankton species, normalized to surface area. (b) Model simulation of competition between the species. Environmental parameters describing the light spectrum in the Baltic Sea: spectrum of incident light $I_m(\lambda)$, see Figure 4.1c; background turbidity $K_{bg}(484) = 1.1 \text{ m}^{-1}$; mixing depth Z_m set to the euphotic depth (17 m). Species parameters: $P_{max} = 1.8, 1.5, 1.9$ and 2.1 d^{-1} for the red cyanobacteria, green cyanobacteria, diatom and chlorophyte respectively; $\phi = 2.8 \times 10^8 \text{ cells } (\mu\text{mol photons})^{-1}$ for all species; $L = 0.6 \text{ d}^{-1}$ for all species.

Discovery of new pigments

Recently, a new photosynthetic pigment was discovered in oceanic bacteria (Béjà *et al.* 2000). This new pigment, bacterial proteorhodopsin, is similar to the light-absorbing pigment called rhodopsin that is associated with vision in animals. However, the pigment proteorhodopsin acts as proton pumps in bacteria, enabling them to obtain energy from sunlight that stimulates their growth (Gómez-Consarnau *et al.* 2007). Two types of marine proteorhodopsin have been found so far, a blue-light absorbing type and a green-light absorbing type. Their distribution is stratified with depth, with green-absorbing pigments at the surface and blue-absorbing pigments in deeper waters, in accordance with the light spectra available at these depths (Béjà *et al.* 2001; Sabehi *et al.* 2007). Surprisingly, the difference in light absorbing properties of these two pigments is based on a single amino-acid substitution in the structure of the pigment (Man

et al. 2003). This suggests that, in an evolutionary perspective, proteorhodopsins might be quite flexible in their spectral tuning to any light colour. Accordingly, it is very likely that these proteorhodopsin-containing bacteria are not restricted to marine ecosystems only. Would they persist in freshwater ecosystems as well? And would their light absorption spectra be shifted towards green light in mesotrophic lakes and red light in turbid peat lakes? Indeed, a recent search using a broad range of suitable primers discovered that proteorhodopsin-containing bacteria are widely distributed in many freshwater lakes and estuaries (Atamna-Ismaeel *et al.* 2008). The amino acid composition of these freshwater proteorhodopsins seems largely consistent with green-absorbing proteorhodopsins, but shows a higher variability than the marine proteorhodopsins described earlier. Accordingly, the light absorption properties of these freshwater proteorhodopsins have not yet been fully revealed. It would be highly interesting to investigate whether a new type of red-absorbing proteorhodopsins can be found in turbid lakes.

The different spectral niches identified in Stomp *et al.* (2007b) may guide the search for more new pigments. It could be even more challenging maybe, to select for new pigments. As described above, the difference between blue-absorbing and green-absorbing proteorhodopsins is based on only a single amino-acid substitution (Man *et al.* 2003). Similarly, the pigments phycocyanin and phycoerythrin differ in just a double bonding (Falkowski & Raven 1997). Hence, it seems that evolutionary tuning to a new light colour requires only a few simple molecular modifications. Can we force spectral evolution to select for mutants with new absorption spectra, for example with an absorption peak at 600 nm? Thus far, no such pigments exist, which makes sense because the waveband at 600 nm corresponds to the fifth harmonics of the stretching vibrations of the water molecule, and therefore this colour of light is relatively less available for phytoplankton photosynthesis (Stomp *et al.* 2007b). It would be fascinating to see what happens if we expose a variety of phytoplankton species to wavelengths of 600 nm in a long-term laboratory experiment. Long-term selection experiments with *Escherichia coli* have shown adaptation and divergence of *E. coli* strains within 2000 generations (Lenski *et al.* 1992). For phytoplankton species with a doubling time of about twice a day, this would correspond to a long-term experiment of more than three years in order to observe evolution in action. Will these experiments lead to mutants with new photosynthetic pigments that shift their absorption peak to 600 nm? Will the spectral evolution be gradual, wavelength per wavelength, or will changes in absorption spectra occur more abruptly? Answers to these questions may improve our insight in the evolution of photosynthesis on Earth.

Competition in the light spectrum and nutrient limitation

Phytoplankton absorb light by photosynthetic pigments. However, pigments contain nutrients. Chlorophyll *a* and carotenoids, for example, are rich in carbon, whereas phycoerythrin and phycocyanin are rich in nitrogen. Therefore, the pigment content of a species, and hence its absorption spectrum, depends on nutrient availability (Dolganov & Grossman 1999). Hence,

competition for light and competition for nutrients are likely to be tightly coupled. Theoretical studies that combine nutrient and light competition predict that a trade-off in competitive ability for nutrients and light may lead to coexistence (Tilman 1982; Huisman & Weissing 1995; Passarge *et al.* 2006). However, recent competition experiments of Passarge and colleagues (2006), didn't show any trade-offs in competitive abilities for phosphorus and light. Of the five species tested, strong competitors for phosphorus were strong competitors for light as well. As a result, all their competition experiments led to competitive exclusion.

Nevertheless, there might be trade-offs in the competitive ability for light and nitrogen, because of the high nitrogen content of phycocyanin and phycoerythrin. If so, competition for nitrogen and light between red and green cyanobacteria may even lead to higher diversity than expected based on the light spectrum alone. An interesting approach for investigation of this hypothesis could be provided by the experimental setup used in Chapter 6. In this setup, red and green picocyanobacteria competed with a species that was flexible in its pigment composition. The three species competed in chemostats where the incoming light colour switched between green and red. All competition experiments led to competitive dominance by the flexible species, which was able to tune its pigment composition to the fluctuating light colours and thereby displaced the red and green picocyanobacteria. However, it is likely that frequent switching between phycoerythrin and phycocyanin pigments requires a significant amount of nitrogen. Therefore, it would be highly interesting to see what the outcome of competition would be under nitrogen-depleted conditions. Possibly, the best competitor for light (the flexible species) is a weak competitor for nitrogen, giving more opportunities for the red and green picocyanobacteria to persist. This could explain the coexistence of all three species in the Baltic Sea, where nitrogen is the most important limiting nutrient (Granéli *et al.* 1990).

Brownification: shifts toward the red by global change

Studies of the underwater light spectrum can be very useful in predicting changes in species composition in response to global change. The pool of dissolved organic matter (gilvin) in lakes and many coastal waters is dominated by terrestrial sources. There are strong indications that changes in land use and global warming enhance the export of gilvin from terrestrial ecosystems into lakes, seas and oceans, increasing their turbidity (Freeman *et al.* 2001; Monteith *et al.* 2007). Increased gilvin concentrations will cause a shift in the underwater light colour towards the red part of the spectrum (Kirk 1994; Stomp *et al.* 2007*b*). This process has been described as the 'brownification' of aquatic ecosystems (Granéli 2008).

Field measurements on a global scale identified that a red shift in underwater light colour with turbidity is accompanied by a shift in phytoplankton community composition. More precisely, green species gradually replace red species with increasing turbidity (Stomp *et al.* 2007*a*; Figure 4.5). Based on these results, it seems plausible that brownification could favour an increased dominance of green cyanobacteria. This effect will be most pronounced in aquatic ecosystems where the underwater light spectrum is near a transition point from green to red light

conditions, as might apply to many inland lakes in rural and forested areas. Thus, in addition to the strong positive effect of global warming on cyanobacterial bloom formation (Elliott *et al.* 2006; Jöhnk *et al.* 2008; Paerl & Huisman 2008), brownification could possibly be a mechanism that further promotes the dominance of green (and potentially harmful) cyanobacteria.

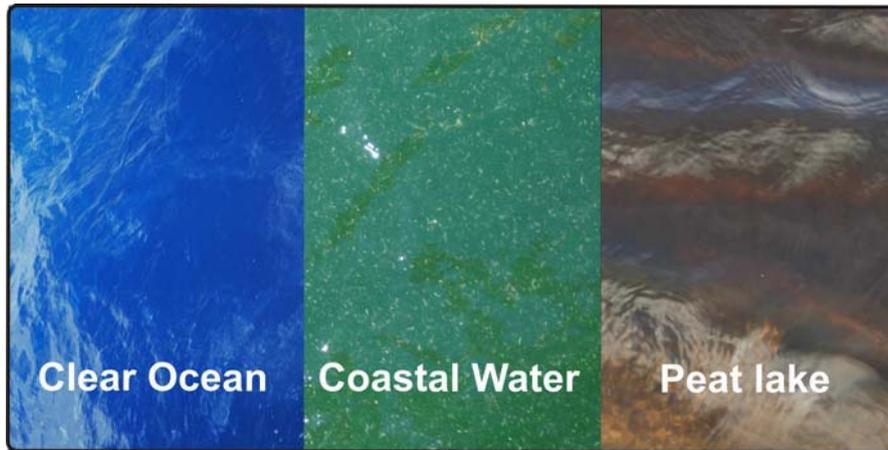


Figure 7.2 The colour of water is strongly determined by the concentration of dissolved organic matter, also known as gilvin in the optics literature (Kirk 1994; Stomp *et al.* 2007a,b). With increasing turbidity the colour of water shifts from blue (clear oceans), via green (coastal water), towards brownish red (peat lakes). Global change will possibly lead to increasing concentrations of gilvin, shifting the light colour in aquatic ecosystems towards the red part of the spectrum.

Conclusions

The work presented in this thesis has demonstrated that the light spectrum plays a crucial role in the distribution of phytoplankton species. We have shown that species can coexist by partitioning of the light spectrum, which provides a novel solution for Hutchinson's paradox of the plankton. We have also shown that the underwater light spectrum has a strong selective effect, and may determine which species will disappear and which will remain. Yet, this Discussion has also indicated that there are still several open questions that need further investigation. Nowadays, the underwater light spectrum of lakes and seas can be measured relatively easily. Therefore, we hope this work will encourage microbiologists, oceanographers, aquatic ecologists and water managers to routinely measure underwater light spectra in studies of phytoplankton growth.