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### Colourful coexistence : a new solution to the plankton paradox

Stomp, M.

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## Summary

Light is the sole energy source for photosynthesis, and hence a key determinant of the primary production of aquatic and terrestrial ecosystems on our planet. Light embodies a spectrum of colours, ranging from blue, green to red light. The colours of light that phytoplankton can absorb depend on their pigment composition. For example, red-pigmented phytoplankton species absorb green light, whereas green-pigmented phytoplankton species absorb red light. This thesis investigates the impact of light colour on the competition between phytoplankton species. In this chapter I will summarize the central questions that underlie this research, accompanied with the answers found during my Ph.D research.

**Question 1:** *Would differences in pigmentation between phytoplankton species allow their coexistence, through a subtle form of niche differentiation?*

To answer this question, we studied competition for light between red and green picocyanobacteria isolated from the Baltic Sea. The red species possesses high quantities of the red pigment phycoerythrin absorbing green light. The green species possesses high quantities of the blue-green pigment phycocyanin absorbing red light. We developed a model describing the spectral aspects of competition for light among phytoplankton species. Monoculture data of the green and red picocyanobacteria were used to parameterize the model. As a next step, the model predictions were tested in competition experiments between the red and the green species. Theory and competition experiments showed:

- The red species excluded the green species when competing for green light.
- The green species excluded the red species when competing for red light.
- The red and green species coexisted when competing in a white light spectrum.

These results provided the first experimental demonstration that interspecific differences in pigmentation allow coexistence of phytoplankton species, through partitioning of the light spectrum. Moreover, the results showed that a single colour of light cannot sustain coexistence under light-limited conditions, but will select for the species that has optimally tuned its pigment composition to the prevailing light colour.

**Question 2:** *Can we explain the distribution of red and green cyanobacteria in natural waters by the underwater light spectra?*

In oceans, seas and lakes the underwater light colour is strongly determined by the concentration of dissolved organic matter (here referred to as ‘turbidity’). With increasing turbidity, the underwater light colour shifts towards the red part of the light spectrum. Hence, in clear oceans blue light dominates whereas red light conditions prevail in turbid lakes. We parameterized our spectral competition model to predict the relative abundances of red and green picocyanobacteria in oceans, seas and lakes. To test the model predictions, we sampled picocyanobacteria of 70 aquatic ecosystems, ranging from clear blue oceans to turbid brown peat lakes.

### Summary

Theory and results from the field survey revealed the following findings:

- Red strains dominated the picocyanobacteria of clear oceans, where blue light prevails.
- Green strains dominated the picocyanobacteria of turbid waters, where red light prevails.
- Coexistence of red and green picocyanobacteria was widespread in waters of intermediate turbidity (e.g., coastal seas, mesotrophic lakes), where the underwater light colour offers suitable conditions for both phycoerythrin and phycocyanin.

The gradual transition from red to green picocyanobacteria along the turbidity gradient indicates that light colour is an important factor that shapes phytoplankton community structure in oceans, seas and lakes. Moreover, niche differentiation gives ample opportunities for coexistence in waters with intermediate turbidities, like coastal waters and clear lakes.

### **Question 3:** Which spectral niches are available for phototrophic microorganisms?

We calculated and measured the underwater light spectra for aquatic ecosystems, ranging from clear oceans to extremely turbid ecosystems representative for microbial mats in sediments. These calculations and measurements showed that:

- Aquatic ecosystems do not offer a continuum of spectral niches ranging smoothly from blue to red underwater light environments. Instead, a series of distinct spectral niches could be identified.
- These spectral niches were shaped by light absorption used for the stretching and bending vibrations of water molecules.
- The distinct spectral niches shaped by the vibrating water molecules match the light absorption spectra of the major photosynthetic pigments on our planet.

Thus, it seems that molecular vibrations of the water molecule have played a key role in the evolution of the light absorption spectra of the phototrophic organisms on Earth.

### **Question 4:** What is the significance of complementary chromatic adaptation in phytoplankton competition?

Some cyanobacteria can adjust the ratio of phycoerythrin and phycocyanin to the prevailing light colour. Thereby, their colour can turn from red to green, and vice versa. This flexibility in pigment composition is called complementary chromatic adaptation. First we studied the competitive performance of the flexible species *Tolypothrix* in competition with either red or green picocyanobacteria in white light. Theory and competition experiments revealed that:

- *Tolypothrix* turned red in the presence of green picocyanobacteria.
- *Tolypothrix* turned green in the presence of red picocyanobacteria.

Hence, *Tolypothrix* absorbed the colour of light not utilized by its competitor. This adaptive niche differentiation allowed coexistence of *Tolypothrix* with either the red or green picocyanobacteria. Thus, *Tolypothrix* seems to benefit from complementary chromatic adaptation. However, chromatic adaptation takes time, and may not be beneficial in environments where light colour fluctuates fast. We studied the time scale of chromatic

adaptation on the flexible species *Pseudanabaena* in competition with red and green picocyanobacteria simultaneously, under conditions where the colour of the incident light switched between red and green at different frequencies (slow, intermediate and fast). Theory and experiments showed that:

- *Pseudanabaena* always competitively excluded the red and green picocyanobacteria.
- Under slow fluctuations, the rate of competitive exclusion of the picocyanobacteria by *Pseudanabaena* was much higher than under fast fluctuations.

The results demonstrated that chromatic adaptation is advantageous in phytoplankton competition, when there is sufficient time for the flexible species to fully adjust its pigmentation to the prevailing light colour.

The answers to the four central questions of this thesis demonstrate that light colour plays a key role in phytoplankton competition. We therefore conclude that it is crucial to take the light spectrum into account in explanations or predictions of the phytoplankton species composition.

*Summary*