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

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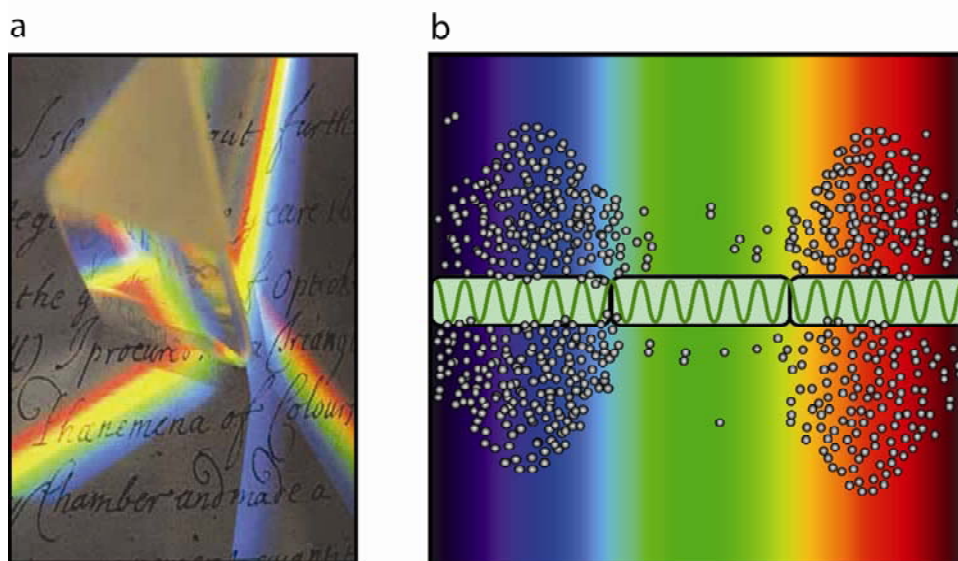
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# Chapter 1

## Introduction

### Utilization of the light spectrum

Light provides the energy source for plants, phytoplankton and other microorganisms capable of photosynthesis. In 1672, Isaac Newton discovered that white light consists of many colours that can be split by a prism glass into a colourful light spectrum (Figure 1.1a). More than 2 centuries later, Professor Theodor W. Engelmann used this colourful light spectrum to illuminate filaments of the green alga *Spirogyra* (Figure 1.1b). Surprisingly, Engelmann discovered that oxygen-dependent bacteria accumulated near those parts of the algal filaments illuminated by red and blue light, but not at the stretches of filament exposed to green light. This demonstrated that selective parts of the light spectrum were used for photosynthesis (Engelmann 1882).



**Figure 1.1** Light colour and its utilization by photosynthesis. (a) Colourful light spectrum created by a prism glass, as discovered by Newton in 1672. White light that passes through the prism is dispersed into a spectrum of light colours, since rays of different wavelengths have different angles of refraction. (b) Utilization of the light spectrum by the green alga *Spirogyra*, as discovered by Engelmann in 1883. Oxygen-dependent bacteria concentrate near those stretches of filament where photosynthesis by *Spirogyra* is most active.

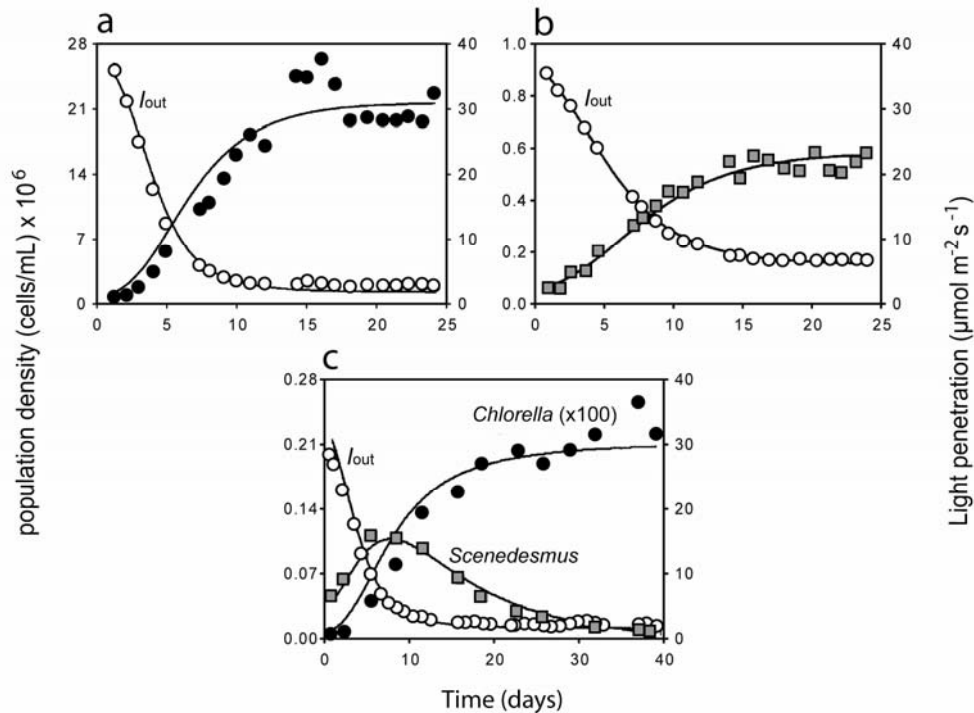
Since then, many phototrophic microorganisms have been discovered that are highly diverse in the utilization of the light spectrum for photosynthesis and growth. This raises the main question of this thesis: how does the colour of light affect competition among phototrophic

microorganisms? We tried to answer this question by theory, laboratory experiments and field surveys.

## Competition for light

When light energy limits the rate of photosynthesis, competition for light between different phototrophic microorganisms is likely to play an important role. That is, photons absorbed by an organism are not available for its competitors any longer. To describe this competition process, the theory presented in this thesis extends the competition theory developed by Huisman and Weissing (1994, 1995). In their model, there is a direct coupling between changes in phytoplankton population densities and changes in light availability caused by phytoplankton shading. When there is an ample availability of light, phytoplankton populations will increase. An increased phytoplankton population will absorb more light, and thus the light intensity that reaches the bottom of the water column,  $I_{out}$ , is reduced (Figure 1.2a and 1.2b).

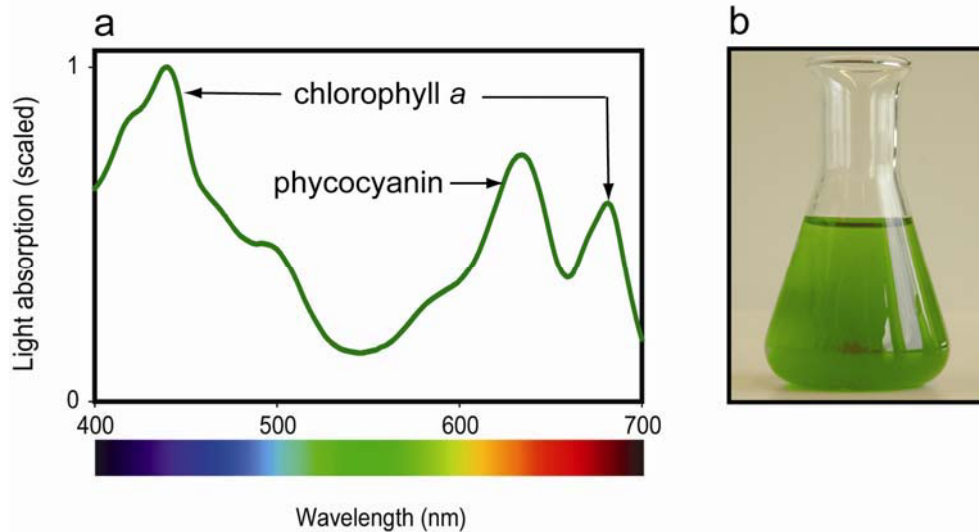
Hence, in monoculture, a growing phytoplankton population will increase its own shading, and thereby temper its growth until a steady state is reached. The light intensity at the bottom of the water column at which the net population growth ceases has been termed the ‘critical light intensity’ (Huisman & Weissing 1994). The critical light intensity is species specific and plays a crucial role when phytoplankton species compete for light. Theory predicts that the species with lowest critical light intensity should be the superior competitor for light (Weissing & Huisman 1994). The experiment in Figure 1.2, considers two green algae, *Chlorella* and *Scenedesmus*. Comparison of the steady-state  $I_{out}$  levels in the monocultures of the two species revealed that the critical light intensity of *Chlorella* ( $2 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Figure 1.2a) was lower than the critical light intensity of *Scenedesmus* ( $6 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ; Figure 1.2b). Hence, the model predicts that *Chlorella* should be the better competitor. Indeed, the competition experiment revealed that both species initially increased, as long as  $I_{out}$  exceeded their critical light intensities. However, as soon as  $I_{out}$  was reduced below the critical light intensity of *Scenedesmus*, *Scenedesmus* started to decline (Figure 1.2c). Hence, as predicted, *Chlorella* won the competition (Huisman *et al.* 1999a). This theory has also been successfully applied in other phytoplankton competition experiments (Litchman 2003; Passarge *et al.* 2006; Agawin *et al.* 2007). However, in all these experiments the competing species had similar light absorption spectra. In fact, the theory developed by Huisman & Weissing (1994, 1995) treats light as a single resource, and thus ignores the spectral distribution of light. Yet, the critical light intensity might be a poor predictor for the outcome of competition, when species differ in the colours of light they absorb. In this thesis, therefore, we extend the existing theory by including the spectral aspects of light and light absorption.



**Figure 1.2** Time course of monoculture experiments of (a) *Chlorella vulgaris* (black circles) and (b) *Scenedesmus protuberans* (grey squares), and (c) time course of competition between the two species. The light intensity,  $I_{out}$ , penetrating through the cultures is indicated by white circles. After Huisman *et al* Ecology 1999a.

## Spectral light absorption

Phytoplankton harvest light with photosynthetic pigments (Falkowski & Raven 1997). These photosynthetic pigments come in many colours, and absorb photons in specific regions of the light spectrum, while reflecting or scattering photons in other regions of the spectrum. The latter determines the colour of the pigment. The set of pigments in a species determines which part of the light spectrum the species can utilize for photosynthesis. For example, green cyanobacteria contain the green pigment chlorophyll *a* with absorption peaks in the blue part (430 nm) and red part (680 nm) of the light spectrum. In addition, they contain the blue pigment phycocyanin which absorbs red light at 620-630 nm (Figure 1.3a). These cyanobacteria absorb poorly in the bluegreen part of the spectrum, and hence they have a bluegreen appearance (Figure 1.3b). That is why these cyanobacteria are also called bluegreen algae.



**Figure 1.3** Optical characteristics of green cyanobacteria, also know as bluegreen algae. (a) Absorption spectrum of the cyanobacterium. (b) Culture of the cyanobacterium showing its bluegreen appearance.

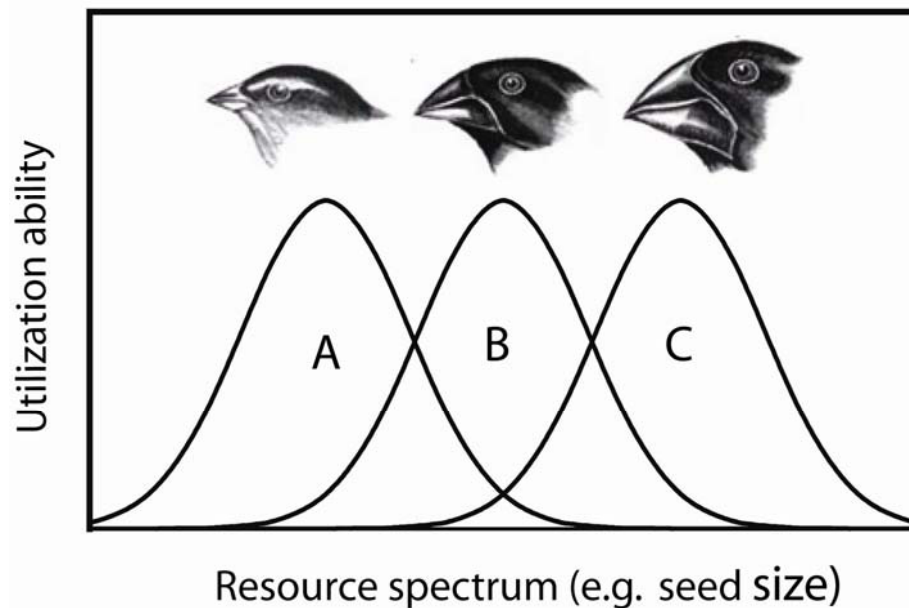
In addition to bluegreen cyanobacteria, there are also red cyanobacteria. They have the same absorption peaks at 430 nm and 680 due to light absorption by the pigment chlorophyll *a*. They also contain a little bit of phycocyanin, but their main accessory pigment is the red pigment phycoerythrin that absorbs green light at 560-570 nm. Red cyanobacteria absorb relatively poorly in the red part of the spectrum, hence they have a red appearance. Note the complementary aspect in the light absorption by these species: red species absorb green light, while green species absorb red light.

Some cyanobacterial species can change their pigment composition by a quite spectacular process called complementary chromatic adaptation (Gaidukov 1902; Tandeau de Marsac 1977; Grossman *et al.* 1993; Kehoe & Gutu 2006). In the presence of green light, they make phycoerythrin and turn red. Conversely, in the presence of red light, they make phycocyanin and turn green. Species capable of complementary chromatic adaptation can achieve optimal light absorption by fine-tuning of their pigment composition to the prevailing light spectrum, which favors their photosynthesis and growth.

### Sharing of the light spectrum?

Classic ecological theory predicts that two species competing for a single resource cannot stably coexist (Gause 1934). As in the theory of Huisman & Weissing, one of the two competitors will always have an advantage over the other that leads to the extinction of the inferior competitor (Figure 1.2). However, if there are multiple resources, species may specialize, so that one species does not out-compete the other. Resource partitioning facilitates coexistence (MacArthur & Levins 1967; Hutchinson 1978). Darwin's finches are a famous

example (Darwin 1859; Lack 1974). On the Galápagos Islands a rich variety of finch species coexist. The species are highly diverse in their beak morphology, enabling niche differentiation of the finch species along a spectrum of different seed sizes (Figure 1.4). Similar to the resource spectrum of seed sizes, light offers a resource spectrum of wavelengths ranging from blue light at short wavelengths, via green and yellow, to red light at long wavelengths (Figure 1.3). Therefore, analogous to the coexistence of finch species on different seed sizes, one might hypothesize that phytoplankton species can share the light spectrum by specialization on different colours of light.

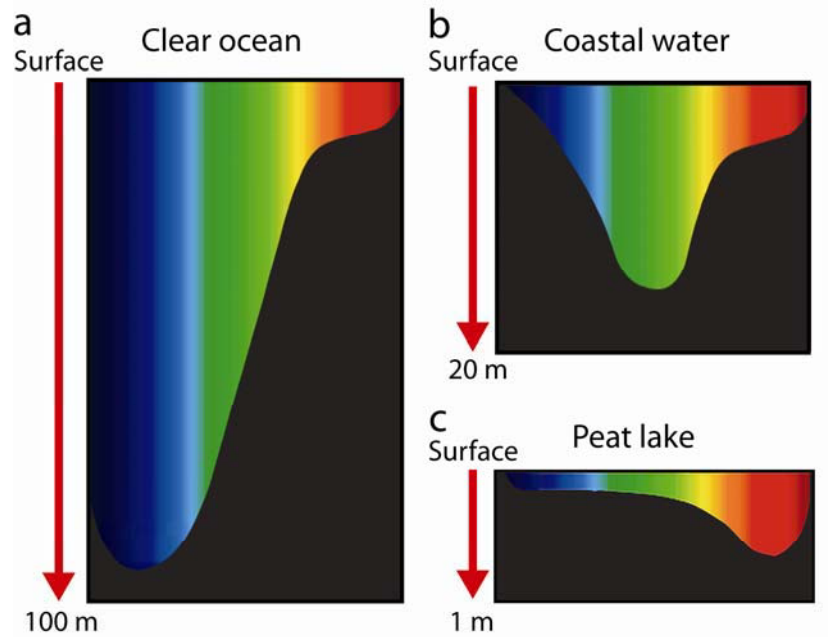


**Figure 1.4** Three seed-eating birds (species A, B and C) inhabit an environment that contains seeds of various sizes. Each species is specialized on a specific range of seed sizes, depending on its beak morphology. Hence, the birds species exploit different parts of the resource spectrum of seed-sizes. After Nee & Colegrave 2006.

## Underwater light colour in lakes, seas, and oceans

What colours of light are available for phytoplankton in their natural habitat? White light is provided by solar irradiance, entering the water column. The absorption of solar light in the water column takes place at different rates for different parts of the spectrum. Hence, the underwater light spectrum alters rapidly with increasing depth. For example, water itself absorbs strongly in the red part of the light spectrum. As a result, in clear oceans red light is attenuated more rapid than other colours of light such that eventually only blue light is left over at greater depths (Figure 1.5a). In more turbid waters, like coastal waters and clear lakes, the presence of organic material is responsible for absorption in the blue part of the light spectrum. The combination of blue light absorption by organic material, and red light

absorption by water itself, results in a green light environment at greater depths (Figure 1.5b). In very turbid waters, like peat lakes, absorption of blue light by organic material overrules the absorption of red light by water. Consequently, in these waters red light is penetrating the deepest (Figure 1.5c). Generally, with increasing turbidity the light spectrum is shifted towards the red part of the light spectrum (Kirk 1994).



**Figure 1.5** The underwater light colour in (a) clear oceans, (b) coastal waters of intermediate turbidity and (c) extremely turbid lakes. With increasing turbidity, the light spectrum is shifted towards red wavelengths.

Together with other factors, like nutrients, temperature and grazing, the underwater light colour could be a potential selective force for shaping the phytoplankton community. However, what is the importance of light colour as a selective factor in aquatic ecosystems? And, does partitioning of the underwater light spectrum mediate the coexistence of a colourful mixture of phytoplankton species in lakes and oceans?

## This thesis

The aim of the work presented in this thesis is to determine the impact of light colour on the competitive interactions among phytoplankton species. For this purpose, we develop new theory, run numerous laboratory experiments, and confronted our model predictions against extensive field surveys. Below follows the outline of the thesis.

In **chapter 2** we develop our theory describing competition among phytoplankton species in the light spectrum. We parameterized the competition model using monoculture experiments with green and red picocyanobacteria isolated from the Baltic Sea. The green species is efficient in absorbing red light, whereas the red species is efficient in absorbing green light. Model predictions and competition experiments revealed stable coexistence of the two picocyanobacteria, through a subtle form of niche differentiation in the light spectrum. Furthermore, additional competition experiments were performed with a species capable of complementary chromatic adaptation. In competition, this species persisted by adopting the opposite colour of its competitor. Hence, it tuned its pigment composition to absorb the light colour left over by its competitor.

As a next step, we tested the theory in the field. In **chapter 3**, we show that coexistence of red and green picocyanobacteria is widespread in the Baltic Sea. Furthermore, we reconstructed the phylogenetic tree of the natural community of picocyanobacteria from the Baltic Sea, by constructing clone libraries of the operons encoding for phycoerythrin and phycocyanin. Red and green picocyanobacteria appeared as separate clades in the tree, matching their pigment composition.

In **chapter 4** we further extended the field survey to 70 different aquatic ecosystems, ranging from clear blue oceans to turbid brown peat lakes. As predicted by our model, red picocyanobacteria dominated in clear waters whereas green picocyanobacteria dominated in turbid waters. We found widespread coexistence of red and green picocyanobacteria in waters of intermediate turbidity (like the Baltic Sea). This showed that the underwater light colour is a major selective factor in shaping the phytoplankton community.

This brings us to the next question: Which spectral niches are available for phototrophic microorganisms? Is there a continuum of spectral niches, or do environmental conditions constrain part of the resource spectrum, such that only a few distinct niches are available? In **chapter 5**, we tackled this question by calculating and measuring many underwater light spectra at the euphotic depth of waters ranging from clear blue oceans to extreme turbid systems representative for microbial mats in sediments. Contrary to our expectation, the data did not show a smooth shift from blue to red wavelengths with increasing turbidity. Instead, a series of distinct spectral niches in the underwater light spectrum could be identified, separated by large gaps. Strikingly, these gaps appeared to originate from light absorption by the stretching and bending vibrations of water molecules. Moreover, 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, the molecular properties of the water molecular have played a key role in the evolution of the light absorption spectra of the phototrophic organisms on Earth.

In **chapter 2** we showed that, under continuous white light, chromatic adaptation allowed the adaptive species to persist with its competitor. However, chromatic adaptation requires reconstruction of the pigment machinery, and this takes time. Is chromatic adaptation still beneficial when the colour of light experienced by the adaptive species changes frequently? In **Chapter 6** we addressed this question by model simulations and competition experiments.



## *Chapter 1*

Green and red picocyanobacteria with a fixed pigment composition, and an adaptive species, were exposed to light that switched between red and green at different frequencies (slow, intermediate and fast). The adaptive species competitively excluded the green and red picos in all competition experiments. Strikingly, the rate of competitive exclusion was much faster when the adaptive species had sufficient time to adjust its pigment composition. That is, the adaptive species benefitted from chromatic adaptation when fluctuations in prevailing light colour were relatively slow. These results demonstrate that the time scale of phenotypic plasticity can be decisive in the competitive interactions between species in a fluctuating environment.

Finally, in **chapter 7** I summarize the work in this thesis. The work presented in this thesis showed that the colour of light plays a key role in the competitive dynamics of phytoplankton species. However, some important and interesting issues remain to be solved. In this chapter, I will suggest several ideas for future research.