



Title: Freshwater phytoplankton responses to global warming[☆]



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ABSTRACT

Global warming alters species composition and function of freshwater ecosystems. However, the impact of temperature on primary productivity is not sufficiently understood and water quality models need to be improved in order to assess the quantitative and qualitative changes of aquatic communities. On the basis of experimental data, we demonstrate that the commonly used photosynthetic and water chemistry parameters alone are not sufficient for modeling phytoplankton growth under changing temperature regimes. We present some new aspects of the acclimation process with respect to temperature and how contrasting responses may be explained by a more complete physiological knowledge of the energy flow from photons to new biomass. We further suggest including additional bio-markers/traits for algal growth such as carbon allocation patterns to increase the explanatory power of such models. Although carbon allocation patterns are promising and functional cellular traits for growth prediction under different nutrient and light conditions, their predictive power still waits to be tested with respect to temperature. A great challenge for the near future will be the prediction of primary production efficiencies under the global change scenario using a uniform model for phytoplankton assemblages.

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1. Introduction: Global change and its influence on freshwater phytoplankton growth and ecology

Long-term weather observations indicate that global changes in temperature patterns have occurred over recent decades due to the rising anthropogenic emissions of greenhouse gases (Meehl et al., 2007). Global warming is only one of the numerous components of climate change, but probably one of the most deleterious for freshwater systems (Woodward et al., 2010). Additionally, future scenarios include a high risk for extreme weather events, such as heat waves, in combination with extended drought periods or flooding (IPCC, 2014). This will lead, especially in those freshwater systems with a high surface to volume ratio, to wide fluctuations of the water level and to drastic short-term changes in hydrological retention times, which will strongly influence salinity as well as the mobilization and efflux of nutrients (Jeppesen et al., 2015).

The temporal coincidence of high solar radiation and low water level can lead to unusual high water temperature. This may exceed the physiological tolerance of certain phytoplankton taxa and therefore change the whole community structure. It has been proposed that under climate change scenarios those taxa which are physiologically adapted to high temperature will become dominant (Paerl, 2014). Recently, Rasconi et al. (2015) reported that increasing water temperature will favor the development of small phytoplankton species, altering the usual succession patterns and community structures. Paerl and Huisman (2008) also predicted a link between global warming and the proliferation of harmful cyanobacteria, because of their high growth potential at elevated temperatures (Elliott et al., 2006; Jöhnk et al., 2008). Since many freshwater systems are used for irrigation or drinking water supply, the risk of toxin production by cyanobacteria needs special care and preventive plans (Carmichael, 2001; Paerl and Otten, 2013). The higher stability of the water column, due to a temperature increase would be a further advantage for cyanobacteria, because of their ability to regulate buoyancy. On the other hand, heavy thunderstorms during summer can disturb stratification. Thus, the increased mixing could selectively promote the growth of eukaryotic algae such as chlorophytes or summer diatoms (Andersen et al., 2006; Becker et al., 2006). Mixing of the water column is further accompanied by nutrient mobilization, which in turn influences growth and production

Abbreviations: APX, Ascorbate peroxidase; CCM, carbon concentrating mechanisms; ETR, electron transport rate; NPQ, non photochemical quenching; PSII, photosystem II; ROS, reactive oxygen species; SOD, superoxide dismutase.

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rates in a species-specific way (Moss, 2012). For instance, nutrients that are generally limiting in summer (i.e. depleted from the water column) may become available and stimulate species typically not present to flourish. In addition, other parameters indirectly related to climate change that will influence phytoplankton growth are the water used in agricultures for irrigation and the nutrient loads present in it. These two factors can be responsible for further eutrophication events in freshwater habitats, which strongly influence the food-web structure therein (Bruce et al., 2012, 2010; Jeppesen et al., 2010; Meerhoff et al., 2007). Overall, it is clear that the effects of temperature with respect to freshwater reservoirs are incredibly diverse, thus, freshwater phytoplankton will respond in a very sensitive way to climate change in space and time (De Senerpont Domis et al., 2013; Jeppesen et al., 2012).

In order to better describe the behavior of phytoplankton in response to global warming, powerful mathematical models have been recently developed. For example, the Plankton Ecology Group (PEG) model has been used to describe system-specific consequences for polar, temperate and tropical lakes (De Senerpont Domis et al., 2013). The authors hypothesized that indirect effects, such as nutrient loading, food-web structure and stratification patterns are more important than the direct effects caused by temperature on cell metabolism. In addition, increased metabolic rates, changed growth seasons and temperature response curves of physiological traits are necessary ingredients to understand and predict the future development of ecosystems (AQUASHIFT project; Sommer et al., 2012). Although very useful for the identification of future trends, simulation and predictive models do not give any explanation behind their outcomes in physiological terms regarding the response of phytoplankton communities to global warming. For this reason, it is still a matter of debate if the predicted dominance of specific algal groups under high temperature scenarios is mainly due to peculiar physiological profiles or has to be attributed to altered physico-chemical characteristics of the water column such as thermal stratification patterns and nutrient concentrations (Elliott, 2012).

Predictive models (Schöl et al., 1999; Walsby, 1997) include fixed or measured physiological parameters, such as cell chlorophyll content, the carbon to chlorophyll ratio, the ratio photons demand per carbon, the nutrient uptake rates and the internal nutrient quotas, to quantitatively assess changes in water quality under changing environmental conditions. Here we discuss why and how some of these parameters, under changing temperature, may fail to predict phytoplankton growth. We further summarize the current gaps of knowledge, and how they can be, at least in part, closed in the near future. We present also some new aspects of the acclimation process with respect to temperature and how contrasting responses found in the literature may be explained by a more complete physiological knowledge about the energy flow from photons to new biomass.

2. Acclimation syndrome: simultaneous, joint appearance of acclimation responses to environmental changes

When environmental conditions change (e.g. light quality/quantity, nutrient availability and temperature), a self-reorganization of the cell metabolic network occurs. The re-organization is triggered by an input signal that induces modification of the gene expression profile, resulting into a new proteome, which fits more to the new environmental settings (McKew et al., 2013; Raven et al., 2011; Talmy et al., 2013). Interestingly, a series of studies revealed that phytoplankton cells exhibit comparable acclimation symptoms in response to various unfavorable exter-

nal conditions. This is particularly evident when considering their energy and carbon partitioning preferences among different cellular processes and pools, respectively (Fanesi et al., 2016; Halsey and Jones, 2015; Jakob et al., 2007; Wagner et al., 2006). Typically, the percentage of energy allocated to biomass formation decreases in parallel to growth limitation. As a consequence, cells have to redirect their metabolic network towards the dissipation of excess energy (Fanesi et al., 2016). Such energy dissipation can take place at different levels of the energy flux from photons to biomass (Jakob et al., 2007), resulting in a very complex acclimation syndrome.

The first and most efficient pathway to cope with excess energy is heat dissipation occurring at the light harvesting pigment-protein complexes; it can be estimated as non-photochemical chlorophyll fluorescence quenching (NPQ) (Goss and Jakob, 2010). A second prominent mechanism acts at the level of the photosynthetic electron transport chain and allows energy dissipation by different alternative electron pathways: cyclic electron transport around both photosystems, pseudo-cyclic electron transport via the water-water cycle and photorespiration (Wilhelm and Selmar, 2011). Finally, under conditions of energy and carbon overflow, cells can also excrete compounds as an additional safety valve (Kozłowska-Szerenos and Zieliński, 2000). Despite the wide range of excretion rates reported in literature, the loss of carbon is typically lower than 10% of the newly fixed carbon (Halsey and Jones, 2015; Zlotnik and Dubinsky, 1989).

The re-distribution of energy among different processes occurs in parallel with a re-allocation of carbon between intracellular pools to facilitate the synthesis and breakdown of cellular constituents (Halsey and Jones, 2015). Under N-limitation, biosynthesis of N-rich compounds, such as proteins, is typically inhibited, in order to optimize energy and nutrient usage for growth with respect to their supply (Schmollinger et al., 2014). The result is an intracellular accumulation of N-poor storage compounds, such as lipids or carbohydrates (Palmucci et al., 2011; Feng et al., 2012). Therefore, N-limited algae produce proteins aimed at synthesizing storage compounds (e.g. for lipid or polysaccharide synthesis) and/or reactive oxygen species (ROS) protecting components to detoxify the cell. On the other hand, N-replete cells showing high metabolic rates are characterized by a higher amount of proteins and ribosomes per cell (50% and 60% more, respectively) (Schmollinger et al., 2014). Analogue responses have been reported under conditions of P-limitation (Dean et al., 2008; Heraud et al., 2008).

The regulation of energy and carbon metabolism in phytoplankton cells has been described in detail under nutrient limitation and fluctuating light conditions (Wagner et al., 2006; Jakob et al., 2007; Palmucci et al., 2011). However, the energy balance from absorbed photons to consumed electrons in response to temperature is much less studied. To the best of our knowledge, only few studies showed how phytoplankton cells balance the energy partitioning to growth and excess energy dissipation at different growth temperatures (Fanesi et al., 2016; Szyszka et al., 2007). These approaches are, however, essential for the identification of conserved acclimation strategies and for the understanding of phytoplankton population dynamics, which in turn may help to improve water quality monitoring under changed environmental conditions (e.g. climate change).

3. Filtering important cellular traits with respect to temperature

Selection of appropriate cellular traits to model phytoplankton growth is a crucial aspect for water quality monitoring. A defined set of parameters may be particularly suitable for a specific environmental setting or species composition, but might be

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