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# Phytoplankton response to a changing climate

**Monika Winder · Ulrich Sommer**

**Abstract** Phytoplankton are at the base of aquatic food webs and of global importance for ecosystem functioning and services. The dynamics of these photosynthetic cells are linked to annual fluctuations of temperature, water column mixing, resource availability, and consumption. Climate can modify these environmental factors and alter phytoplankton structure, seasonal dynamics, and taxonomic composition. Here, we review mechanistic links between climate alterations and factors limiting primary production, and highlight studies where climate change has had a clear impact on phytoplankton processes. Climate affects phytoplankton both directly through physiology and indirectly by changing water column stratification and resource availability, mainly nutrients and light, or intensified grazing by heterotrophs. These modifications affect various phytoplankton processes, and a widespread advance in phytoplankton spring bloom

timing and changing bloom magnitudes have both been observed. Climate warming also affects phytoplankton species composition and size structure, and favors species traits best adapted to changing conditions associated with climate change. Shifts in phytoplankton can have far-reaching consequences for ecosystem structure and functioning. An improved understanding of the mechanistic links between climate and phytoplankton dynamics is important for predicting climate change impacts on aquatic ecosystems.

**Keywords** Light · Water column stratification · Temperature · Phenology · Primary production · Cell size

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## Introduction

Phytoplankton account for <1 % of the photosynthetic biomass on Earth, but are nevertheless responsible for nearly 50 % of global net primary production and are the primary energy source for aquatic ecosystems (Field et al., 1998), and are also of global significance for climate regulation and biogeochemical cycling. The fate of these processes is critically dependent on phytoplankton community composition. Understanding the factors that control species composition and dynamics of these microscopic organisms is a fundamentally important goal in order to predict the impact of environmental change on aquatic ecosystems. Alterations in physical conditions, nutrient input, and

grazing pressure strongly affects the diversity, community structure, and temporal dynamics of phytoplankton. Associated with increasing anthropogenic impacts on ecosystems, the Earth's climate has warmed by approximately 0.6 °C over the past 100 years, which is an unprecedented increase compared with the past 1,000 years (IPCC, 2007), and this rate is expected to accelerate in the current century. Complementing the analyses of long-term trends in global conditions has been the recognition of large coherent spatial and temporal climate variability through changes of the Earth's atmosphere–ocean system (Stenseth et al., 2003). Interannual and subdecadal fluctuations in large-scale climate oscillations can have a strong influence on local climate conditions (Mantua et al., 2002; Stenseth et al., 2003). Long-term climate change and large-scale climate fluctuations are a crucial attribute of global climate change, and a wide range of studies have shown links between fluctuations in climate and ecological processes that affect phytoplankton dynamics (Behrenfeld et al., 2006; Paerl & Huisman, 2008).

Climate-driven physical fluctuations exert strong impacts on aquatic ecosystems because climate is modifying the abiotic and biotic environments. A substantial body of research has demonstrated the sensitivity of phytoplankton to climate change. Consequently, any changes at the base of the aquatic food web can have repercussions for the entire ecosystem. In this review, we illustrate the chain of linked processes from alterations in climate and meteorological conditions to phytoplankton production and taxonomic species composition. This is not a comprehensive review of phytoplankton responses to climate change. Rather, we focus on better-known processes and highlight studies where climate change has had a clear impact on phytoplankton. First, we provide a theoretical framework on climate-driven environmental factors that limit primary production. Then, we review major phytoplankton responses to climate change and discuss how changes in phytoplankton might influence ecosystem functioning.

## Mechanistic links between climate and factors limiting primary production

Phytoplankton dynamics are linked to annual fluctuations of temperature, water column stratification, light availability, and consumption (Sommer et al., 1986; Cloern, 1996). Changing climatic conditions can modify these environmental factors and alter phytoplankton structure and taxonomic composition. Phytoplankton response can be both directly through physiology and indirectly mediated through effects on environmental factors limiting primary production, most notably light and nutrients.

Temperature effects on phytoplankton

Temperature directly affects plant metabolism, which consists of both photosynthetic and respiratory activity, while metabolic rates of primary producers are primarily limited by photosynthesis (Dewar et al., 1999). Phytoplankton blooms on ice margin in polar and subpolar seas (Smith & Nelson, 1985) and under clear ice in lakes (Vehmaa & Salonen, 2009) indicate that low temperature does not prevent exponential growth of phytoplankton in liquid water. Light-limited rates of photosynthesis are insensitive to temperature, but light-saturated ones increase with temperature, which indirectly increases the light level where light saturation begins (Tilzer et al., 1986). Therefore, it is expected that global warming increases light-saturated rates of photoautotrohic production, but not light-limited ones. As a result, a temperature increase should lead to greater plant growth rates and biomass accumulation under adequate resource supply (Padilla-Gamino & Carpenter, 2007). However, compared to photosynthesis rates, the metabolism of heterotrophic organisms is more sensitive to temperature (Allen et al., 2005; Lopez-Urrutia et al., 2006). Consequently, warming should increase consumption by herbivores more strongly than primary production. This can strengthen top-down control over primary production by increasing grazing rates (O'Connor et al., 2009; Sommer & Lewandowska, 2011), and thus affect phytoplankton production and taxonomic composition.

The most significant climatic effects on phytoplankton species composition will very likely be mediated through changes in thermal stratification patterns such as the extent of the growing season and vertical mixing processes (Schindler et al., 1996; Rodriguez et al., 2001; Diehl et al., 2002; Smol et al., 2005) (Fig. 1). Vertical mixing is one of the key variables that conditions the growth performance of phytoplankton within the water column (Diehl et al., 2002; Salmaso, 2005), because mixing processes are

**Fig. 1** The effect of increasing temperature on water column stratification (*blue arrows*), associated nutrient redistribution (*black arrows*), and phytoplankton production and cell size
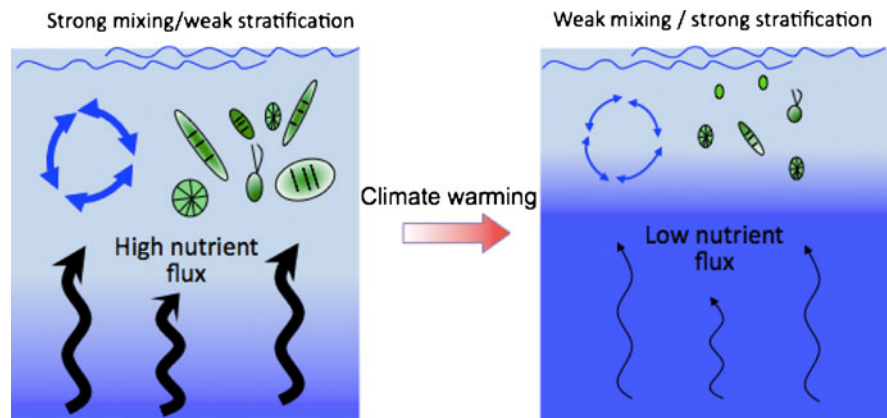


usually accompanied by changes in resource availability of light and nutrients. Vertical mixing of natural waters is largely determined by meteorological variables. Heat exchange processes and wind action create two opposing tendencies—the tendency to stratify and suppress mixing, and the tendency for inputs of turbulent kinetic energy to promote mixing (Wetzel, 2001). The seasonal cycle of summer stratification and winter mixing is a product of the time-varying nature of these two tendencies. Changes in meteorological forcing result in a modification of the balance between stratification and mixing (King et al., 1997; Boyd & Doney, 2002; Livingstone, 2003).

A change in the intensity or duration of thermal stratification has a direct impact on turbulent diffusion and phytoplankton cell sedimentation, which are the major mechanisms causing vertical displacement for non-motile cells (Livingstone, 2003; Huisman et al., 2006). Thermal stratification and vertical mixing therefore has an immediate influence on phytoplankton sinking velocities, which increase non-linearly with size (Smayda, 1969), giving smaller and buoyant species an advantage in an environment where turbulence is not present to resuspend all planktonic species (Findlay et al., 2001; Huisman et al., 2004; Strecker et al., 2004).

Climate impacts on nutrient regimes

Water column mixing also affects nutrient availability for phytoplankton growth. Enhanced water column stratification suppresses the upward flux of nutrients from deep-water layers through vertical mixing, resulting in more nutrient-depleted conditions in surface waters (Livingstone, 2003; O'Reilly et al.,

2003; Schmittner, 2005). As a consequence, altered mixing regimes affects the competitive advantage of specific algal cell types, that are better competitors for nutrients (Falkowski & Oliver, 2007) and that are able to maintain their vertical position in the surface water (Huisman et al., 2004).

On the other hand, for more eutrophic systems, mechanistic models predict that reduced vertical mixing will shift the competitive advantage between buoyant cyanobacteria and sinking phytoplankton species (Huisman et al., 2004). Intensified stratification can also lead to increased hypolimnetic oxygen depletion, which has widespread consequences for internal nutrient loading both for lakes and oceans (Jankowski et al., 2006; Shaffer et al., 2009). Thus, climate change might increase phosphorus concentration in concert with extended anoxic conditions (Wilhelm & Adrian, 2008), and effects of climate change may be similar to processes associated with eutrophication.

In addition, the frequency of extreme rainfall and severe drought has increased since the late 1970s (IPCC, 2007), affecting nutrient runoff from terrestrial sources (Briceño & Boyer, 2010). Increasing runoff can also modify the resource ratio in certain types of systems, depending on the nature of the geochemistry in the catchment and thus modifying the competitive advantage of phytoplankton species. For example, phytoplankton and bacterioplankton biomass is related to air temperature that controls the export of nitrogen and dissolved organic carbon from the catchment across subarctic Swedish lakes, indicating that climate may affect the balance between phytoplankton and bacterial production (Jansson et al., 2010). For coastal regions, enhanced upwelling due to an increasing

temperature gradient between land and sea are anticipated, which will increase nutrient availability and stimulate phytoplankton production (Rabalais et al., 2002). Similarly, melting ice at the poles can act as a nutrient source and can locally stimulate phytoplankton production (Smith et al., 2007). Overall, climate-associated changes in the nutrient environment vary strongly among ecosystems (Adrian et al., 2006).

### Climate impacts on the underwater light environment

Light is essential for photosynthesis and therefore for food webs depending upon phototrophic production. The light experienced by phytoplankton is not independent of climatic conditions of temperature, wind, and precipitation. These climatic variables act on stratification, cloud cover, and—in coastal seas and lakes—runoff from land, which might transport suspended solids and dissolved humic substances that influence the underwater light climate. The impact of these variables can be demonstrated by calculating the mean light intensity of the mixed surface water layer $I_{mix}$ ("epilimnion" in lakes) (Riley, 1957):

$$I_{mix} = I_0(1 - e^{-Kz})(Kz)^{-1}$$

where $I_0$ is the surface irradiance, $K$ the vertical attenuation coefficient, and $z$ the depth in meters. Under usual values of $z$ and $K$, the term $(1 - e^{-Kz})$ approaches 1, thus making $I_{mix}$ inversely proportional to $z$ and $K$. Each of the independent variables is under different climatic influences as discussed below.

The role of the mixing depth is the core of Sverdrup's (1953) classic "critical depth" concept for deep-water bodies. Vernal phytoplankton growth can only start when spring warming leads to a thermal stratification with a mixing less than a critical limit: at mixing depths ($z_m$) beyond that limit, water column respiration would be higher than water column photosynthesis, thus preventing an increase in biomass. In deep oceans and lakes, the onset of stratification easily leads to an order-of-magnitude decrease of $z_m$ and thus an order of magnitude increase in mean mixed water column irradiance. The onset of stratification has thus been viewed as the big light switch that initiates the onset of the phytoplankton growth period. In accordance with this idea, Siegel et al. (2002) identified a minimal mixed water daily light dose of

1.3 mol photons $m^{-2}$ days$^{-1}$ (0.96–1.75) PAR for the onset of the spring bloom from remote sensing data of the North Atlantic. This threshold value was independent of latitude and, therefore, sea surface temperature. Siegel's threshold value was confirmed by mesocosms experiments with Baltic Sea plankton with temperature scenarios ranging from 2 to 8 °C warming (Sommer & Lengfellner, 2008).

Phytoplankton blooms have also been found before the onset of stratification when calm conditions permitted a sufficiently long residence of near surface phytoplankton in favorable light conditions (e.g., in Lake Constance; Tirok & Gaedke, 2007). Accordingly, the "critical depth" concept has been developed further into the "critical turbulence concept" (Huisman & Sommeijer, 2002). Such pre-stratification blooms in deep waters are, however, unstable, because any wind might induce deep mixing and distribute phytoplankton to greater depths and reduce the light supply. In shallow to medium deep-water bodies and non-stratifying systems, where either the bottom or a halocline is above Sverdrup's critical limit, phytoplankton blooms are strongly coupled to the external light regime, which is influenced by ice cover, cloud cover, or day length, and blooms can occur independently of temperature change (Sommer & Lengfellner, 2008).

The attenuation coefficient $K$ depends on light attenuation by phytoplankton pigments through most of the growth season in waters where riverine input of turbidity or resuspension of sediments are unimportant, factors that are influenced by climate. The increase of $K$ with chlorophyll acts as a negative feedback loop ("self shading") on phytoplankton growth, but at the start of the seasonal growth period, the background light attenuation is decisive for the light climate. In the open ocean, $K$ is close to the value for clear water (0.02 $m^{-1}$), while it can reach values >1 $m^{-1}$ in brown-water lakes or turbid estuaries. In shallow waters, where wind can stir up the bottom sediment, sudden increases of $K$ can happen any time of the year, creating an "optical winter". The same applies to suspended solids transported by floods of tributaries.

This means that the different aspects of the anticipated climate change will influence the light availability for phytoplankton differently and in partly counteracting ways: warming will lead to an earlier onset of thermal stratification in stratified water bodies, an earlier ice-melt, and a reduced mixing

depth in summer. All these tend to increase light availability. Increased windiness will partially counteract the effect of warming in deep-water bodies, i.e. delay the onset of stratification and increase mixing depth, and will increase the resuspension of sediments in shallow water bodies. Overall, the effect of wind on light availability is negative. Increased runoff from land will increase the transport of suspended particulate matter, and in certain geological settings (acidic bedrocks) increase the transport of humic matter to lakes and coastal seas. Due to their regional and episodic character, the changes in wind and runoff will increase the variance of light availability and thus phytoplankton production.

## Climate effects on phytoplankton processes

Interactions between climate and phytoplankton are complex, because other factors such as resource availability, density dependence, and predation strongly control the abundance, distribution, and size structure of the community. Despite these complexity of interacting processes, some widespread climate-related responses have emerged, and the mechanisms involved in climate-related changes are becoming better understood (Richardson, 2008; Adrian et al., 2009). Impacts of climate change on plankton are mainly manifested as shifts in seasonal dynamics, species composition, and population size structure.

### Phenology

Plankton blooms are important features in seasonal aquatic environments, where they drive many ecosystems and community processes, and are a major source of energy input for higher trophic levels (Smayda, 1997; Winder & Cloern, 2010). Seasonal phytoplankton succession is a community phenomenon that is controlled by processes that regulate population dynamics of various primary producers and consumers (Sommer, 1989). Blooms are triggered by individual species' life history and physiological responses to changing abiotic conditions. Timing and magnitude of blooms are controlled by population feedbacks and mediated through resource dynamics and predator–prey interactions (Sommer et al., 1986; Carpenter et al., 2001; Jäger et al., 2008). The onset of plankton

spring blooms is usually initiated by changes in water temperature and light supply. In deep systems, spring phytoplankton blooms are coupled to the onset of thermal stratification, which increases the mean light exposure of phytoplankton cells in the mixed surface layer. Under these conditions, spring blooms are triggered by correlated increases in temperature and seasonal light availability (Edwards & Richardson, 2004; Winder & Schindler, 2004b; Peeters et al., 2007). In shallow, well-mixed systems, phytoplankton blooms are strongly coupled to the external light regime, that is influenced by ice cover, cloud cover, or day length, and can occur independently of temperature change (Sommer & Lengfellner, 2008).

A large number of studies have reported that the timing and magnitude of seasonal plankton blooms are shifting in response to climate change (Straile, 2002; Edwards & Richardson, 2004), which agrees with predictions from dynamical models of pelagic producer–grazer systems (De Senerpont Domis et al., 2007). Particularly, shifts in plankton spring phenology related to climate have been shown in several ecosystems, whereas later in the season other factors like biotic interactions often complicate the extraction of a clear climate signal. For example, vernal warming advanced the timing of stratification onset and the spring bloom in Lake Washington by 20 days over the last four decades (Winder & Schindler, 2004b). Shifts in bloom timing have also been observed in the Western Scheldt Estuary, where earlier onset of blooms have paralleled increasing temperature over the last 30 years (Kromkamp & Van Engeland, 2009). Similarly, a shift to the warm phase of the North Atlantic Oscillation (NAO) caused advancement of stratification onset and the spring bloom in the Baltic Sea (Smayda et al., 2004; Alheit et al., 2005), and shifted the timing of various phytoplankton taxa in the North Sea. Earlier timing of the spring bloom was also observed across central European lakes during the warm NAO phase as a result of accelerated early summer algal suppression due to faster growth of herbivores in warmer water (Straile, 2002). Similarly, new autumn phytoplankton blooms developed in San Francisco Bay through a trophic cascade induced by a shift of the east Pacific to its 'cool' phase in 1999 (Cloern et al., 2007). These studies are consistent with widespread observations in freshwater and marine systems (Blenckner et al., 2007; Thackeray et al., 2010).

Similar to field observations, increasing temperature advances the timing of phytoplankton spring peaks consistently in marine and freshwater systems and in taxonomic groups in mescosm experiments (McKee and Atkinson, 2000; Winder et al., 2012). These studies showed that, in well-mixed systems, earlier occurrence of phytoplankton peaks at high temperatures are independent of light intensity and are primarily driven by increased grazing pressure at higher temperatures that terminated the phytoplankton bloom earlier (Sommer & Lewandowska, 2011; Winder et al., 2012). Intensified grazing at increased temperature can also affect phytoplankton species composition and size structure, as has been shown in mesocosm experiments dominated by copepod grazers that prey preferentially on intermediate phytoplankton size classes (Lewandowska & Sommer, 2010).

The degree of advance varies, however, among taxonomic groups. For example, mesocosm experiments have demonstrated that cryptophytes and diatoms showed the strongest response to warming (Winder et al., 2012), which is in agreement with their physiological characteristics (Gervais, 1997; Litchman et al., 2007). In the North Sea, diatom taxa showed large phenologial variation, whereas the timing of total diatom biomass did not change (Edwards & Richardson, 2004), which is likely associated with the diatom community composition that is dominated by taxa forming resting stages that are triggered by the photoperiod and thus are not coupled to shifts in water column stratification. Differential responses to climate change can be expected and largely depend on the life strategies of the community.

In addition to peak timing, climate also affects phytoplankton peak magnitudes (Berger et al., 2010); the effects are, however, strongly sensitive to changes in algal carrying capacity as mediated by light supply (Jäger et al., 2008; Schalau et al., 2008). High light intensity typically increases phytoplankton bloom magnitude in mesocosm experiments (Berger et al., 2010; Winder et al., 2012). In contrast, intensified grazing at higher temperatures can create opposite patterns in phytoplankton bloom dynamics. This suggests that light limitation can have pronounced effects on plankton succession and that tight predator–prey coupling can suppress a response of phytoplankton to increased temperature.

Phytoplankton production

While climate-related phenological shifts towards earlier spring events are broadly observed, there has been a lack of consensus on how climate affects plankton production (Boyce et al., 2010; Taucher and Oschlies, 2011). Satellite and long-term field observations show that phytoplankton in the Pacific Ocean oscillate with large-scale climate patterns, and chlorophyll concentrations are typically lower during warm periods (Behrenfeld et al., 2006). Using a combination of water transparency and chlorophyll measurements, Boyce et al. (2010) extended the historical dataset and showed that ocean chlorophyll concentration decreased in large parts of the North Pacific and North Atlantic that parallelled increases in surface temperature. In contrast, long-term chlorophyll observations from continuous sampling programs showed that concentration increased in certain regions of the Pacific and Atlantic Oceans (McQuatters-Gollop et al., 2011). Simulation studies suggest that increased phytoplankton metabolism with increasing temperature may counteract the reduced nutrient redistribution into surface water, yielding a net increase in ocean productivity (Taucher & Oschlies, 2011). However, a temperature increase will also enhance the metabolism of heterotrophs that can intensify top-down control and may reduce phytoplankton production.

These contradictory results indicate the necessity for controlled observational programs. Phytoplankton production is a complex function of physical and physiological effects on predator–prey interactions, and effects of climate change on phytoplankton production will likely vary among sites, depending on resource limitation and species composition.

Species composition and size structure

The performance of individual phytoplankton species is strongly governed by the thermal stratification's impact on vertical mixing within the water column, which alters the position of phytoplankton relative to nutrients and light. Margalef (1978) proposed an empirical relationship between the interplay of turbulence, nutrient supply, and taxonomic composition. Based on this model, specific phylogenetic morphotypes (r versus K growth strategists) are selected along a continuum of habitat mixing and nutrient conditions.

The model predicts that, in marine systems, dinoflagellates are favored at weak mixing and diatoms at intensified mixing. In a further elaboration of his concept, Margalef separated the prediction under low turbulence: dinoflagellates will dominate under eutrophic and coccolithophore under oligotrophic conditions. For freshwater phytoplankton, Reynolds (1987) suggested a distinct association of phytoplankton key genera and morphological properties with the nutrient and turbulence environment. Similarly, experimental (Reynolds et al., 1983; Diehl et al., 2002; Ptacnik et al., 2003; Berger et al., 2007) and theoretical (Diehl et al., 2002; Huisman et al., 2004) work documented shifts in algal community structure and dynamics related to physical mixing processes.

Thermal stratification and vertical mixing has an immediate influence on phytoplankton sinking velocities that give smaller species an advantage in an environment where turbulence is not present to resuspend all planktonic species (Bopp et al., 2005). In contrast, buoyant species and flagellates have relatively low net sinking velocities (Findlay et al., 2001; Huisman et al., 2004; Strecker et al., 2004), and the latter are highly motile and are capable of selecting an appropriate light and nutrient environment in the water column (Fee, 1976). Similarly, bloom-forming phytoplankton species (e.g., cyanobacteria) may contain gas vesicles to decrease their density. These functional species traits have a distinct competitive advantage at reduced vertical mixing (Findlay et al., 2001; Huisman et al., 2004; Strecker et al., 2004).

In line with these predictions, several studies have shown that bloom-forming cyanobacteria have a competitive advantage over other phytoplankton taxa at higher temperatures in eutrophic systems (Jöhnk et al., 2008; Paerl & Huisman, 2008). Cyanobacteria have a higher maximum specific growth rate compared to diatoms and green algae at temperatures above 23 °C (Reynolds, 2006; Jöhnk et al., 2008), which makes cyanobacteria a strong competitor at high temperatures. Many cyanobacteria have the ability to form intracellular gas vesicles, which provide them with the ability to exploit habitats under intensified stratification and to outcompete other taxa (Paerl & Huisman, 2008). In addition, under eutrophic conditions, increasing temperatures will lead to steeper nutrient gradients in the thermocline, which gives an advantage to effective vertically migrating phytoplankton, such as cyanobacteria and dinoflagellates. The increase in cyanobacteria at higher temperatures has been reported in several lakes with different mixing regimes (Jöhnk et al., 2008), and along a latitudinal gradient in shallow lakes (Kosten et al., 2011).

Enhanced water column stratification and subsequently more nutrient-depleted conditions in surface waters is also expected to affect phytoplankton size structure (O'Reilly et al., 2003; Schmittner, 2005). Under a low nutrient concentration, small-sized algal taxa are expected to be favored because their high surface area to volume ratio enables rapid nutrient exchange through the cell surface (Litchman et al., 2007). In addition, small cells exhibit lower sinking rates and divide more rapidly, which is favorable under reduced mixing conditions.

In support of this hypothesis, shifts in size structure have been observed in planktonic organisms, including diatoms, dinoflagellates, and foraminifera, over geological and centennial time scales (Schmidt et al., 2004; Smol et al., 2005; Finkel et al., 2007; Rühland et al., 2008), and these shifts have been linked to changing water column stratification related to changing climate. Fossil records document that diatom community structure has been altered by environmental change over their evolutionary history (Finkel et al., 2005). On a geological time scale, macro-evolutionary changes coincide with changing hydrodynamic mixing processes, such as changes in sea-level and ocean thermal structure that are climate driven (summarized in Falkowski & Oliver, 2007). Marine diatom size structure and diversity shifted towards a smaller size in response to intensified thermal stratification linked to increasing ocean temperatures (Burckle et al., 1981; Finkel et al., 2005). Similarly, paleolimnological studies from high latitude and altitude systems indicate a widespread expansion of pelagic and small-sized diatoms in more recent decades (Sorvari et al., 2002; Saros et al., 2003; Rühland & Smol, 2005; Roberts et al., 2006), which is largely attributed to a longer ice-free season and increased stratification in deep lakes (Smol et al., 2005; Rühland et al., 2008).

Changes in temperature and physical mixing have also affected the competitive advantage of small-sized diatom cells in Lake Tahoe, as a response to contemporary climate warming (Winder et al., 2009). Small-sized cells within the *Cyclotella* genus increased with intensified stratification, whereas large-sized diatoms

dominated under stronger turbulent mixing conditions and decreased over the record of sampling. The selection for small-sized diatoms was accompanied with a shoaling trend in their vertical position in the water column (Winder & Hunter, 2008). In the North Atlantic, the dominance of pico-phytoplankton (<2 μm) increased with temperature and picophytoplankton cell size decreased with temperature (Moran et al., 2010). A trend towards smaller phytoplankton size under warming has also been reported from mesocosm experimental studies (Daufresne et al., 2009); however, its universal applicability is still controversial (Gardner et al., 2011; Rüger and Sommer 2012).

## Conclusions

A floristic shift can have cascading ecosystem effects and, consequently, climate-driven changes likely alter important ecosystem functions, including primary production, biogeochemical cycling (Richardson & Jackson, 2007), energy transfer through the food web, and plankton community structure via size-dependent species interactions (Sommer et al., 2002). Shifting phytoplankton phenologies are critical for ecosystem production if phenological responses differ among primary producers and consumers (Edwards & Richardson, 2004; Winder & Schindler, 2004a; Seebens et al., 2007). The different degrees of change in phytoplankton peaks and zooplankton growth can lead to a decoupling of zooplankton food requirements and peak food availability. Asynchronization between peak food availability and requirements can result in predator–prey mismatches that can affect energy transfer to higher trophic levels (Cushing, 1974). Differences in the temporal match of a predator with its prey have been observed in algal–herbivore interactions (Edwards & Richardson, 2004; Winder & Schindler, 2004a; Adrian et al., 2006).

Reorganizations within the phytoplankton community with changing thermal structure of the water column will shift the dominance towards small-sized algal cells and species that are able to regulate their buoyancy (Findlay et al., 2001; Huisman et al., 2004; Strecker et al., 2004; Bopp et al., 2005; Smol et al., 2005). A shift towards small-sized cells will result in lower export production, which can have positive feedbacks on the climate system. These changes in primary producers will have associated effects on primary production and biogeochemical cycling of carbon and other elements. In addition, blooms of cyanobacteria or dinoflagellates have large ecosystem impacts on trophic transfer, water quality, and fish production.

Phytoplankton variability is a key driver of biogeochemical variability (Cloern, 1996; Behrenfeld et al., 2006) and fluctuations in annual fish recruitment (Platt et al., 2003). An improved understanding of the inherent natural variability of phytoplankton is therefore important for forecasting the extent of global change impact on aquatic ecosystem functioning. A current challenge is to predict how compositional shifts propagate up to higher trophic levels, and how synergistic effects of climate warming and other environmental changes will affect ecosystem functioning. The extent of physical changes and potential for species to adapt to changing environmental conditions will greatly influence food-web dynamics as the future climate warms and becomes more variable.

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