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Plankton dynamics under different climatic conditions in space and time

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SUMMARY

1. Different components of the climate system have been shown to affect temporal dynamics in natural plankton communities on scales varying from days to years. The seasonal dynamics in temperate lake plankton communities, with emphasis on both physical and biological forcing factors, were captured in the 1980s in a conceptual framework, the Plankton Ecology Group (PEG) model.
2. Taking the PEG model as our starting point, we discuss anticipated changes in seasonal and long-term plankton dynamics and extend this model to other climate regions, particularly polar and tropical latitudes. Based on our improved post-PEG understanding of plankton dynamics, we also evaluate the role of microbial plankton, parasites and fish in governing plankton dynamics and distribution.
3. In polar lakes, there is usually just a single peak in plankton biomass in summer. Lengthening of the growing season under warmer conditions may lead to higher and more prolonged phytoplankton productivity. Climate-induced increases in nutrient loading in these oligotrophic waters may contribute to higher phytoplankton biomass and subsequent higher zooplankton and fish productivity.
4. In temperate lakes, a seasonal pattern with two plankton biomass peaks – in spring and summer – can shift to one with a single but longer and larger biomass peak as nutrient loading increases, with associated higher populations of zooplanktivorous fish. Climate change will exacerbate these trends by increasing nutrient loading through increased internal nutrient inputs (due to warming) and increased catchment inputs (in the case of more precipitation).
5. In tropical systems, temporal variability in precipitation can be an important driver of the seasonal development of plankton. Increases in precipitation intensity may reset the seasonal dynamics of plankton communities and favour species adapted to highly variable environments.

The existing intense predation by fish on larger zooplankters may increase further, resulting in a perennially low zooplankton biomass.

6. Bacteria were not included in the original PEG model. Seasonally, bacteria vary less than the phytoplankton but often follow its patterns, particularly in colder lakes. In warmer lakes, and with future warming, a greater influx of allochthonous carbon may obscure this pattern.

7. Our analyses indicate that the consequences of climate change for plankton dynamics are, to a large extent, system specific, depending on characteristics such as food-web structure and nutrient loading. Indirect effects through nutrient loading may be more important than direct effects of temperature increase, especially for phytoplankton. However, with warming a general picture emerges of increases in bacterivory, greater cyanobacterial dominance and smaller-bodied zooplankton that are more heavily impacted by fish predation.

Keywords: climate change, PEG model, phytoplankton, seasonal succession, zooplankton

Introduction

With our environment changing at an unprecedented rate, an important challenge is to assess the impact of climate change on the temporal plankton dynamics of lake ecosystems (Christensen *et al.*, 2007). Globally, temperature and precipitation have changed dramatically and are predicted to change even more (Meehl *et al.*, 2007). These changes will affect other environmental conditions such as nutrient loading and water column mixing. Temperature affects nearly all biological process rates, from biochemical kinetics to species generation time, with higher temperatures typically resulting in higher rates until an optimum is reached, above which rate processes usually decrease rapidly (Kingsolver, 2009). Various components of the climate system have been shown to relate to temporal dynamics of natural plankton communities on time scales varying from days (diel periodicity) to years (seasonal periodicity). In a meta-analysis of phytoplankton biomass time-series in temperate and subtropical zones, Winder & Cloern (2010) observed a unimodal pattern (i.e. spring bloom) prevailing at higher latitudes following sinusoidal changes in irradiance and temperature in temperate zones, whereas short-term fluctuation in phytoplankton biomass was more common at low latitudes. Periodicity in temperature at a daily scale has been linked to vertical migration of both phytoplankton and zooplankton in the subtropics (Becker, Cardoso & Huszar, 2009), the tropics (Gliwicz, 1999) and to a lesser degree in temperate regions (Gliwicz & Pijanowska, 1988). On a longer time scale, the typical sinusoidal annual fluctuations of temperature in temperate regions have been related to a multitude of seasonal planktonic events, including the timing of peak biomass in phytoplankton and zooplankton (Straille, 2000, 2002), emergence from resting stages (Gyllström & Hansson, 2004) or hatching

and growth of planktivorous fish (Mooij, de Senerpont Domis & Hülsmann, 2008). Extreme weather events, such as the 2003 and 2006 summer heat waves in central Europe, promoted cyanobacterial blooms (Jöhnk *et al.*, 2008) and shifts in phytoplankton (Wilhelm & Adrian, 2008) and zooplankton succession (Anneville *et al.*, 2010). Climate warming has also induced species-specific changes in the seasonal timing of life-cycle events, resulting in decoupling of trophic relationships (Winder & Schindler, 2004a) and subsequent effects on food-web functioning (de Senerpont Domis *et al.*, 2007); however, in the long term, the importance of such decoupling may be mitigated through to adaptation and microevolution of the plankton (Van Doorslaer *et al.*, 2007).

The seasonal dynamics of lake plankton communities just described have been partially captured in a conceptual framework, the Plankton Ecology Group (PEG) model, published in one of the most highly cited papers in plankton ecology (Sommer *et al.*, 1986). The PEG model has a special emphasis on both physical and biological forcing factors and describes the seasonal succession of phytoplankton and zooplankton in 24 sequential steps based on the well-studied deep, peri-alpine Lake Constance. PEG mainly covers deep stratified lakes and strongly hinges on the assumption that plankton dynamics during winter and spring are under abiotic control (light, nutrients), whereas later in the year biotic interactions (resource competition, herbivory, fish predation) become dominant. The model identifies how basic patterns in plankton seasonality depend on trophic state. Under more eutrophic conditions, seasonal development of phytoplankton biomass follows a bimodal or even trimodal pattern, with a distinct spring clear-water phase and a summer bloom of larger, less edible algae or cyanobacteria. However, under more oligotrophic conditions, both phyto- and zooplankton follow a unimodal

pattern, with the spring bloom as the main event, reflecting reduced availability of nutrients and increased grazing impact on phytoplankton in summer. However, since the PEG model appeared in 1986, this paradigm of bottom-up versus top-down control has shifted (Brett & Goldman, 1997) and the greater complexity of the aquatic food web has been recognised, resulting in a perhaps more nuanced view on plankton seasonality (Jeppesen *et al.*, 1997). Improved knowledge about winter conditions and about shifts in response to recent climate change has opened a debate about one of the basic assumptions underlying the original PEG model: that is, that winter effectively resets the plankton community (Jeppesen *et al.*, 2004; Blank *et al.*, 2009; Hülsmann *et al.*, 2012). Our changed perspectives on aquatic food webs also involve the inclusion of the microbial loop (Sanders, Caron & Berninger, 1992), recognition of the potential impact of parasites on plankton host populations (Wommack & Colwell, 2000; Duffy *et al.*, 2005; Kagami *et al.*, 2007), as well as acknowledgement of the effects of food quality on trophic transfer efficiency and zooplankton dynamics (Elser *et al.*, 2000; Muller-Navarra *et al.*, 2000).

Beyond the absence of such newly appreciated mechanisms, PEG also had limitations because the majority of the lakes used to validate the PEG model were temperate (with the exception of two subtropical lakes located in South Africa) (Sommer *et al.*, 1986). Traditionally, plankton seasonality was assumed to be less prominent in low-latitude than in high-latitude lakes due to the dampened fluctuations in both irradiance and temperature in the tropical zone (Gliwicz, 1999). However, the increasing availability of data on temporal variability in (sub)tropical systems shows that this assumption is not valid for tropical lakes (<23 °C latitude), as many of these are sensitive to seasonal variations in hydrology due to annual cycles of precipitation (de Domitrovic, 2003; Loverde-Oliveira *et al.*, 2009; Ndebele-Murisa, Musil & Raitt, 2010); this seasonality occurs both directly through flushing and indirectly through hydrological effects on nutrient cycling by particle resuspension and run-off.

These latitudinal contrasts suggest that comparison of seasonal patterns in plankton dynamics across different regions may give us much-needed insight into the coupling between climate and seasonality, which will be helpful in predicting the possible effects of climate-change scenarios. Here, we seek an overview of patterns in plankton dynamics, highlighting those in different climatic zones in the light of our improved, post-PEG, understanding of plankton ecology. Rather than updating the PEG model to the newest scientific insights (for this, see Sommer *et al.*, 2012), we will use the PEG approach as

a framework for synthesising available data on temporal plankton dynamics in different climate zones. We emphasise that the degree of change in the different climate components will result in the creation of new climate regimes, rather than just warmer climates. In the light of this, we discuss the role of bottom-up versus top-down processes and trophic state in determining plankton dynamics. In addition to phytoplankton and zooplankton, we will discuss the role of the microbial food web, parasites and fish in governing these seasonal events.

Projected changes in climate components

Temperature

Warming over land is expected to be greater than global annual warming due to the smaller thermal inertia and less available water for evaporative cooling on land. Thus, climate warming will likely affect inland waters more than oceans (Christensen *et al.*, 2007). Based on modelling output from Atmosphere-Ocean General Circulation Models as well as data on recent changes in climate, regional patterns in warming are emerging: most of the Americas and all of Africa, Europe, the polar regions and Northern and Central Asia are likely to warm more than the global average. These projections suggest that the warming will be least in South-East Asia, Australia and New Zealand and southern South America (Christensen *et al.*, 2007).

Projected warming also differs by season: in the northern part of Europe and North America, warming will be largest in the winter, whereas in the southern areas of North America and Europe warming will be largest in summer (Christensen *et al.*, 2007). In the polar regions, warming in winter will be larger than in the summer as a result of a reduction in sea ice and snow (Meehl *et al.*, 2007). This phenomenon will be more pronounced in the Arctic, and consequently, snow and (sea) ice content will continue to decrease. In most of Asia, warming in winter will be more pronounced than in summer, but in South America the projected seasonal differences in warming may not be so distinct (Christensen *et al.*, 2007).

Beyond these model projections, data records can also be examined to assess the patterns of climatic change. In most regions of the world, long-term records have shown a decrease in the number of very cold days and nights and an increase in the number of very hot days and nights (Trenberth *et al.*, 2007); this trend will most likely continue. Indeed, global climate projections indicate that heat waves will be more intense, more frequent and longer lasting (Meehl *et al.*, 2007). Likewise, the frost-free season

has increased in length at mid- and high latitudes in both hemispheres during the past several decades; this translates to shorter duration of ice cover in lakes. In the next hundred years, the number of frost days will continue to decrease (Meehl *et al.*, 2007). On a global scale, the diurnal temperature range will decrease, as daily minimum temperatures are projected to increase faster than daily maximum temperatures (Meehl *et al.*, 2007). While regional information is too sparse to make global statements on temperature variability, most model projections agree that projected temperature variability will be lower in winter in most of Europe, whereas in summer both interannual and daily temperature variability are predicted to increase (Christensen *et al.*, 2007).

Precipitation

Precipitation has shown a significant upward trend over the past few decades as a consequence of a warming-driven increase in the water-holding capacity of the atmosphere. This increase has affected mainly regions that are already receiving a considerable amount of precipitation, for example eastern parts of North and South America, northern Europe and northern and central Asia (Trenberth *et al.*, 2007). In contrast, during the last century, historically low precipitation areas, such as the Mediterranean, southern Africa and Asia and the Sahel, have experienced decreased precipitation. Due to the temperature rise over the recent decades, more precipitation has fallen as rain rather than snow in mid- and high-latitude regions. All these trends are predicted to continue under current climate model projections (Christensen *et al.*, 2007). In addition, it is very likely that precipitation will increase in areas with monsoon regimes, such as tropical parts of Asia and South America (Meehl *et al.*, 2007).

How precipitation intensity will change at local and regional scales is to a large extent governed by changes in atmospheric circulation patterns such as the El Niño Southern Oscillation and the North Atlantic Oscillation. In areas predicted to experience increases in mean precipitation, such as some tropical and high-latitude areas, the intensity of precipitation events will grow. This projection also holds true for areas that are expected to experience a decrease in mean precipitation, such as large parts of the subtropics, but the interval between subsequent rainfall events will be longer (Meehl *et al.*, 2007). In these areas, this precipitation variability translates not only to a higher incidence of flooding but also to extended drought. In Asia in particular (Christensen *et al.*, 2007), tropical storms and hurricanes are likely to become more intense,

producing stronger peak winds and increased rainfall over some areas due to warming sea surface temperatures that can energise these storms.

Climate-induced changes in physical characteristics of lakes and biogeochemical cycling

Stratification

Thermal stratification has long been accepted as a prime environmental variable steering plankton succession in deep lakes (Sommer, 1985). There is increasing evidence that a warmer climate will result in earlier, stronger and longer stratification (DeStasio *et al.*, 1996; Peeters *et al.*, 2002). This might even lead, for some lakes at least, to a scenario in which dimictic lakes become warm monomictic lakes (Gerten & Adrian, 2002) and monomictic ones become oligomictic.

While such shifts in stratification are relevant mostly to deeper lakes that can establish stable thermal gradients, in shallow waters (typically waterbodies with average depths <2 m) higher temperatures and an increase in solar energy input can also lead to stronger (micro)stratification, strengthening of water column stability and resistance to complete mixing. In warm shallow waters, even small differences in water temperature between upper and lower water layers can result in the water column becoming stably stratified (Huszar & Reynolds, 1997). In tropical lakes, superficial stratification occurs during the daytime followed by nocturnal mixing, a process that is sometimes called *atelmixis*. In deeper tropical lakes, this diurnal stratification may result in a situation where the hypolimnion stays intact, whereas the epilimnion splits up in multiple isolated layers, each with its own physical and chemical properties (Lewis, 1973; Barbosa & Padisák, 2002). Particularly during warmer episodes, this pattern of alternating periods of stabilisation and mixing, operating at the diel scale, has been observed in temperate lakes as well (Riley & Prepas, 1984; Kallio, 1994). Reduced convective cooling during the night under future, warmer conditions will render this type of microstratification more stable, especially in small, wind-sheltered lakes (Hanson *et al.*, 2008). Since microstratification can have important implications for lake metabolism with net ecosystem production being significantly higher on days with microstratification (Coloso, Cole & Pace, 2010), future climate change could significantly alter ecosystem dynamics in lakes that are subject to such microstratification. Under future climate change, oxygen depletion of the hypolimnion is likely to be aggravated by the projected longer period of summer

stratification. As a result, earlier and longer phosphorus release from anoxic sediments is expected (Jankowski *et al.*, 2006). In shallower lakes, this hypolimnetic nutrient accumulation might fuel phytoplankton blooms, especially when periods of stability come to an end by an increased number of mixing events that introduce nutrient pulses (Wilhelm & Adrian, 2008).

Besides an earlier onset of stratification due to climate change, changes in the depth of the mixed layer are also expected in temperate waters (Hondzo & Stefan, 1993). The direction of change will depend on the interplay between lake morphometry, transparency and radiative balance (Magnuson *et al.*, 1997). For example, wind-exposed lakes in regions experiencing an increase in wind velocity (a likely scenario for some coastal regions in the temperate zone) will probably see a deepening of the thermocline during the summer months (Hondzo & Stefan, 1991). As a result of this, regeneration of nutrients within the epilimnion should increase as particles would be retained longer (Fee *et al.*, 1994). In contrast, warming will probably result in a shallower epilimnion during summer stratification in smaller lakes with their short fetch (Hondzo & Stefan, 1993). For lakes with heat carry-over during the winter from 1 year to the next (e.g. lakes that are not strictly dimictic), warmer winter temperatures may result in hypolimnetic warming (Peeters *et al.*, 2002; Livingstone, 2003; Straile *et al.*, 2010). This deep-water warming might not only enhance the solubilisation of accumulated phosphorus from the sediments but also the mineralisation of hypolimnetic organic matter. This would increase the likelihood of anoxia (Gudasz *et al.*, 2010). Conversely, in strictly dimictic lakes, earlier and more rapid onset of stratification may shield deeper water from warming, resulting in colder hypolimnetic temperatures (Hondzo & Stefan, 1993).

Increases in precipitation may also disrupt stratification for many aquatic systems due to washout. For example, extreme events of precipitation are projected for the entire east coast of South America (Marengo *et al.*, 2009); as a consequence, thermal stratification in small- and medium-sized reservoirs in this region is likely to be disrupted due to the effects of hydrological flushing on thermal conditions (Bouvy *et al.*, 2003).

Changes in nutrient cycling and hydrology

Ongoing global climate change will likely intensify the hydrological cycle, consistent with ongoing global increases in evaporation and thus precipitation (Huntington, 2006) (Fig. 1). However, the hydrological response to climate change of drainage basins strongly depends on

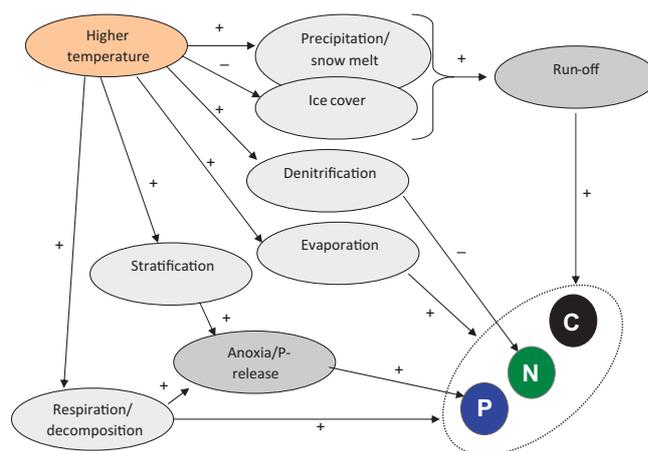


Fig. 1 Schematic overview of the effect of temperature on physical and chemical processes influencing nutrient cycling of phosphorus (P), carbon (C) and nitrogen (N).

latitude. Whereas increased run-off is predicted for the Arctic, mid-latitude humid and some tropical regions, decreased run-off is predicted for semi-arid and arid regions (Solomon *et al.*, 2007; Praskievicz & Chang, 2009). In the northern temperate zone, the expected climate change will most probably boost the nitrogen (N) and phosphorus (P) load to lakes, predominantly in winter due to higher winter rainfall (Jeppesen *et al.*, 2009). As erosion is generally a major contributor of P to lakes, increased surface flow will result in increased P loading (Praskievicz & Chang, 2009). Climate change-induced land-use shifts may modulate or further strengthen the loss of nutrients, depending on the scenario (Jeppesen *et al.*, 2009).

In warm temperate and arid climates, the projected reduction in precipitation and the higher evaporation will lead to a severe drop in run-off. Whereas diffuse loadings may consequently decrease, concentrations of nutrients in inflows may increase (Jeppesen *et al.*, 2009, 2011). Furthermore, enhanced evaporation and water extraction for irrigation in warm regions will aggravate salinisation (Jeppesen *et al.*, 2009, 2011). The resulting lower water levels and increased lake residence times could promote the internal release of nutrients and dominance of cyanobacteria and chlorophytes (Beklioglu *et al.*, 2007). On the other hand, in a drier climate, lakes might also completely disappear (Schindler, 2009), a possibility exacerbated by likely compensatory increases in water extraction for irrigation (Jeppesen *et al.*, 2011). A modelling exercise based on projected local run-off indicated that, while the overall distribution of lakes will change regionally, total global lake area will not be altered by 2050 (Tranvik *et al.*, 2009). Nonetheless, a significant reduction in total lake area is expected in North America, Western Europe, the Mediterranean, Russia and Australia (Tranvik *et al.*, 2009).

Global change scenarios predict that atmospheric CO₂ concentrations will rise to ~750 ppm by the year 2100 (Solomon *et al.*, 2007). Increased atmospheric CO₂ concentrations may affect the inorganic carbon chemistry of freshwater ecosystems and themselves alter elemental composition and species interactions in freshwater phytoplankton communities. Many studies have reported an increase in phytoplankton productivity under increased atmospheric CO₂ (Hein & Sand-Jensen, 1997; Ibelings & Maberly, 1998; Schippers, Lurling & Scheffer, 2004). Furthermore, the species composition of phytoplankton may also change substantially (Verschoor *et al.*, 2013), depending on the magnitude of change in CO₂ (Low-Décarie, Fussmann & Bell, 2011).

The effects of climate on water quality are clearly complex, since warming and different temperature-related drivers influence interacting physical, biogeochemical and biological processes (Kosten, 2010). Nonetheless, the projected increase in overall lake nutrient levels has been identified as an important contributor to predicted deterioration of lake water quality under future climate scenarios (Genkai-Kato & Carpenter, 2005; Bicudo *et al.*, 2007).

Climate-induced patterns in plankton dynamics

Phytoplankton

With anticipated changes in length of growing season and nutrient loading, we expect that the seasonality of phytoplankton will be altered with warming. However, such changes will likely vary in different regions and latitudes.

Polar lakes and ponds. In polar lakes and ponds, maximum productivity during the warmer summer months results in a single biomass peak. Extended periods of snow and ice cover strongly hamper photosynthesis, favouring dominance of mixotrophic species that are able to actively survive cold and dark periods, such as *Dinobyron*, *Chrysochromulina* and *Ochromonas* (Laybourn-Parry, 2002; Laybourn-Parry & Marshall, 2003). With warming, an earlier onset and longer duration of the growth period may result in higher biomass. Several studies have shown that climate warming, that is, change in ice cover and/or enhanced thermal stratification, is a prime determinant of recent changes in diatom assemblages in arctic lakes (Smol, 2005; Keatley, Douglas & Smol, 2008; Ruhland, Paterson & Smol, 2008). More specifically, a pronounced increase in the abundance of planktonic diatoms such as *Cyclotella* has been noted at the expense of benthic species of *Fragilaria* and *Achnantes*, and tychoplanktonic genera

such as *Aulacoseira* (Smol, 2005; Keatley *et al.*, 2008; Ruhland *et al.*, 2008). Phytoplankton growth in arctic lakes often shows concurrent N and P limitation; thus, phytoplankton productivity should increase in response to changes in climate that increase nutrient loading, such as increased landslides, erosion and thawing of the permafrost (Levine & Whalen, 2001). Enhanced temperatures may also significantly boost nutrient acquisition and phytoplankton biomass accumulation in arctic lakes (Ogbebo *et al.*, 2009).

Temperate lakes. In most temperate lakes, ample nutrient and light availability towards the end of winter triggers an initial spring bloom of small- to medium-sized algae (e.g. centric and pennate diatoms and cryptophyceae). In shallow lakes, this initial bloom of small algae is soon replaced by large pennate diatoms, such as *Asterionella*, and in summer by green algae and/or cyanobacteria (Sommer *et al.*, 1986; Reynolds, 1989). Heavy grazing by zooplankton may strongly reduce phytoplankton biomass (the 'clear-water phase'). However, whether a clear-water phase actually occurs in temperate lakes depends on fish predation (Carpenter *et al.*, 2008); indeed, no clear-water phase occurs in hypertrophic shallow lakes with high fish predation (Jeppesen *et al.*, 1997).

How might climate change alter these typical dynamics? As in polar lakes and ponds, extension of the growing season can lead to larger phytoplankton biomass, as indicated by a correlative study of Weyhenmeyer, Peter & Willen (2013) on variations in the length of the ice-free season and phytoplankton species richness and biomass patterns over a latitudinal gradient. Their results suggest that this shift in biomass corresponds to a shift in nutrient conditions. In a cross-lake comparison of shifts in phytoplankton phenology over 58 years, Feuchtmayr *et al.* (2012) found that locally variable phosphate levels had a more consistent effect on phenology than temperature.

As a consequence of changes in thermal stratification in warming climates, the spring phytoplankton bloom is likely to start earlier, as is the case in arctic lakes (Muller-Navarra, Guss & Von Storch, 1997; Winder & Schindler, 2004b; Christoffersen *et al.*, 2008). This would then be followed by an earlier zooplankton peak and clear-water phase or by a decoupling of trophic interactions in which zooplankton is no longer able to make optimal use of its food source (Edwards & Richardson, 2004; Winder & Schindler, 2004a; de Senerpont Domis *et al.*, 2007). At present, it is not clear how frequently trophic uncoupling will occur, as we have insufficient understanding of the consequences of an earlier spring bloom for later stages of the seasonal plankton succession. Furthermore, changes

in (fish) predation need to be taken into account. For example, the study by Wagner *et al.* (2013) on warming-induced changes in trophic coupling between the key herbivore *Daphnia* and both a vertebrate and invertebrate predator underlines the importance of a mechanistic understanding of temperature-driven changes in trophic interactions.

The extended period of thermal stratification under climate warming seems to open a window for prolonged summer blooms of cyanobacteria or large dinoflagellates and also for invasive species (Blenckner *et al.*, 2007; Paerl & Huisman, 2008; Masclaux *et al.*, 2009). In a more stable water column, positively buoyant cyanobacteria will more easily disengage from turbulent mixing and use their buoyancy-controlled vertical migration to position themselves in the water column nearer to the surface (Ibelings, Mur & Walsby, 1991), promoting their dominance (Jöhnk *et al.*, 2008). Consistent with this scenario, Blenckner *et al.* (2007) showed that cyanobacteria responded positively to positive NAO years, increasing their abundance in response to both higher temperatures (on the basis of a supposedly superior Q_{10} of cyanobacteria, but see Lürling *et al.*, 2013) and enhanced stratification, benefitting from efficient buoyancy (Ibelings *et al.*, 1991). Also in support of such shifts is a regression analysis on data from numerous Danish lakes (Jeppesen *et al.*, 2009). This study found that dominance of cyanobacteria and dinophytes increased with warming, while the contribution of green algae and diatoms decreased. Finally, the earlier seasonal increase in water temperature under climate warming permits earlier germination from cyanobacterial resting stages, potentially promoting the spread of invasive cyanobacteria such as *Cylindrospermopsis raciborskii* in the temperate zone (Wiedner *et al.*, 2007).

In historically low precipitation areas, such as the Mediterranean, anticipated decreases in precipitation will lead to longer water residence times. Romo *et al.* (2013) found that, during dry years in the large shallow Lake Albufera, stagnant water columns as well as long residence time led not only to higher total cyanobacterial biomass but also to increased amounts of cyanotoxins. Segura *et al.* (2013) used a mechanistic model based on morphology-based functional groups to confirm these observations, showing that, compared to other functional groups, the competitive ability of large cyanobacteria with gas vesicles was highest under low flushing rates.

In temperate floodplain areas prone to inundation (Roozen *et al.*, 2008), the projected intensification of annual precipitation may reset the seasonal dynamics of plankton communities. Timing of inundation seems to play an important role: spring inundation synchronised plankton

dynamics in different waterbodies in a floodplain, while winter inundation did not have the same effect (Roozen *et al.*, 2008). Through increases in run-off, increased precipitation can lead to higher external nutrient loading (Rip *et al.* 2007), boosting phytoplankton growth. Extreme rainfall events cause even higher run-off during winter periods when catchment vegetation lacks foliage (Andersen *et al.* 2006).

In eutrophic shallow lakes in the temperate zone, higher temperatures in winter and spring will enhance the internal loading of P (Jensen & Andersen, 1992; Søndergaard, Jensen & Jeppesen, 2003), which in turn will reinforce a warming-induced stimulation of phytoplankton in spring and autumn (E. Jeppesen, unpublished data). Higher temperature can also boost summertime internal loading in shallow lakes (Jensen & Andersen, 1992; Søndergaard *et al.*, 2003) and thus potentially lead to higher phytoplankton biomass (Jeppesen *et al.*, 2009).

Tropical lakes. A comparison of phytoplankton dynamics in tropical lakes spanning three continents (Melack, 1979) suggests that in most tropical lakes, seasonality is usually dominated by either hydrological (water input and output) or hydrographical features (water column stratification and mixing), both of which are also related to climate (Talling, 1986). In addition, both Melack (1979) and Gliwicz (1999) have suggested that the diel cycles of physical, chemical and biological processes in tropical productive lakes can have a much stronger periodicity than the seasonal cycle. Seasonal fluctuations in plankton biomass and species composition are also strongly governed by the hydrological and hydrographical cycle in tropical floodplain lakes, such as in the Amazon region (equatorial latitudes) or in the Pantanal wetlands (Huszar & Reynolds, 1997; Bozelli & Garrido, 2000; Loverde-Oliveira *et al.*, 2009).

High flushing rates during high water and low flushing rates during low water favour species better adapted to those conditions and also influence the structure, metabolism and productivity of communities. The pattern of hydrographical variability is driven by seasonal differences in the distribution of local precipitation and precipitation in the headwaters and, in case of Amazonian floodplain lakes, also by seasonality in the glacial melting in Andean regions (Junk *et al.*, 2006). Phytoplankton seasonal patterns in floodplain lakes at intermediate subtropical latitudes (such as in the Paraná River basin in South America, $\sim 31^{\circ}\text{S}$, where there is a considerable variability in temperature and irradiance) are also explained by interactions between hydrology and climatology (de Emiliani, 1997). Precipitation is also an

important driver of plankton communities in other regions. For example, rain events disrupt the long-standing cyanobacterial dominance in man-made lakes in semi-arid regions ($\sim 8^{\circ}\text{S}$), leading to decreases in biomass and changes in species composition (Bouvy *et al.*, 2003). With anticipated higher precipitation intensities in these systems, higher flushing rates may result in a stronger reset of the biomass build-up as well as a community dominated by species more closely adapted to variable environments.

Mesozooplankton

As with phytoplankton, zooplankton have characteristic seasonal cycles that are strongly linked to the seasonality of temperature (arctic and temperate regions), hydrology (tropical regions), food availability and predation pressure. Variation in these factors can modify the population fluctuations in these organisms. Indeed, the interplay between seasonal increases in temperature, resource availability and predation pressure results in the typical unimodal and bimodal patterns in zooplankton seasonality often observed in temperate lakes (Jeppesen *et al.*, 1997; Angilletta, Huey & Frazier, 2010), whereas a combination of year-round strong predation pressure and hydrological forcing seems to govern zooplankton seasonality in warmer lakes (Havens *et al.*, 2009).

Zooplankton population growth shows strong coherence with seasonal temperature fluctuations as evidenced by latitudinal gradients (Gillooly & Dodson, 2000; Straile, 2002) and seasonal timing or phenologies (Adrian, Wilhelm & Gerten, 2006): peaks in biomass typically occur earlier with warmer temperatures. Given sufficient resources, an increase in temperature within the tolerance range of a species accelerates growth, developmental and reproductive rates. For zooplankton, changes in phenology and life-history strategies, increased turnover rates, increased number of generations per year and greater population instability can be anticipated with climate warming (Drake, 2005). In addition, seasonality is governed to a large extent by the structure of the predator communities (fish and macroinvertebrates); this impact of predation seems to be stronger in warmer climates than in colder climates (Meerhoff *et al.*, 2007).

Polar lakes and ponds. In polar lakes and ponds, the short duration of the growing season and the absence of strong predation typically result in a unimodal pattern of zooplankton biomass over time, regardless of trophic state. Here, the lack of food, but not the cold temperature, seems to be dominant in driving zooplankton dynamics

(Van Geest *et al.*, 2007); therefore, increased food availability under warmer conditions, rather than the direct effect of warmer temperatures on vital rates, is likely to result in higher zooplankton productivity. Whether this higher zooplankton productivity translates into higher annual biomass will likely depend on the predation pressure. For example, arctic lakes that contained fish did not support significant populations of *Daphnia middendorffiana*, although growth and survivorships experiments indicated that this species could do well in these environments (Yurista & O'Brien, 2001). Low density of large-bodied zooplankton is also characteristic for lakes in Greenland hosting fish, while they are abundant in fishless lakes (Lauridsen *et al.*, 1999; Davidson *et al.*, 2011). Studies of Greenlandic lakes have further shown that warming may result in fish colonisation of lakes when enhanced precipitation as rain enhances connectivity to the sea, and consequently, large-bodied zooplankton are lost (Bennike *et al.*, 2008).

Temperate lakes. In temperate lakes, the annual cycles in zooplankton biomass and grazing pressure on phytoplankton represent a bimodal pattern with high grazing pressure in spring and autumn in oligo-mesotrophic lakes. In contrast, a unimodal pattern with relatively low grazing pressure prevails throughout the year in hypertrophic lakes (Jeppesen *et al.*, 1997). This difference in modality has been attributed to a shift from mid-summer high fish predation [particularly by young-of-the-year (YOY) fish] creating bimodality in oligo-mesotrophic lakes to high predation by planktivorous fish of all size classes throughout the year in hypertrophic lakes (Jeppesen *et al.*, 1997).

However, the pattern in seasonality (i.e. unimodal versus bimodal) might not be directly regulated by temperature, but rather by top-down regulation. Lake comparisons by Straile (2002) suggest that the timing of the zooplankton peak(s) seems to be influenced by temperature: increases in temperature advance the timing of peak zooplankton abundance. The effect of temperature on zooplankton phenology might also be modified by trophic state as suggested by the large differences observed in the response of two peri-alpine lakes to heat waves (Anneville *et al.*, 2010). These data showed that, during the heat waves, zooplankton in oligotrophic Lake Annecy followed the usually observed succession from herbivorous zooplankton to carnivorous zooplankton, whereas dominance of herbivorous zooplankton was maintained throughout the summer in meso-eutrophic Lake Geneva. Further evidence comes from a fish-free mesocosm experiment in the U.K. (Feuchtmayr *et al.*,

2010). The experiment tested the combined effects of warming (4 °C above ambient) and increased nutrient loading on plankton communities and found warming to advance zooplankton phenology. However, this advance could be dampened in systems with high nutrient concentrations. The experiment revealed high peak zooplankton abundances with warming at high nutrient loadings; these high abundances induced a clear-water phase due to heavy zooplankton grazing, despite high nutrient concentrations.

The synchronisation of key zooplankton life stages with resource availability plays an important role in governing seasonality, particularly in temperate regions where quantity and quality of phytoplankton are highly variable on a seasonal basis (Sommer *et al.*, 1986; Cushing, 1990; de Senerpont Domis *et al.*, 2007). As a result, climate warming may indirectly affect population dynamics and life histories of zooplankton in temperate regions through its effect on the seasonality of resource availability and other components of the ecosystem, such as the duration of the growing season (Ottersen *et al.*, 2001; Stenseth *et al.*, 2004). These modifications in the environment are especially likely to affect life-cycle responses in longer-lived species such as copepods (Chen & Folt, 1996; Drake, 2005), but the effects may be quite complex (Adrian *et al.*, 2006; Winder *et al.*, 2009). For example, shifts in the number of generations (voltinism) were observed for copepod species concurrent with warming and lengthening of the growing period (Adrian *et al.*, 2006; Winder *et al.*, 2009), as predicted by generic population dynamics models (Drake, 2005). Shifts in voltinism are important from an ecological and evolutionary perspective because an additional generation per unit time may strongly accelerate population growth or adaptation.

Tropical lakes. In low-latitude lakes, zooplankton dynamics seem to be characterised by an almost perennial but low biomass (Havens *et al.*, 2009). Meerhoff *et al.* (2007) argue that this observed difference in seasonality in low-latitude lakes versus high-latitude lakes for cladocerans (Gillooly & Dodson, 2000) cannot be primarily ascribed to direct temperature effects on zooplankton performance. Instead, it more likely reflects temperature-mediated shifts in the community preying on zooplankton. Indeed, fishes in tropical lakes likely exert a stronger predation pressure on large zooplankton due to enhanced reproduction rates, early reproduction and a high degree of omnivory. This leads to cascading effects promoting water turbidity (van Leeuwen *et al.*, 2007; Meerhoff *et al.*, 2007; Jeppesen *et al.*, 2010). The experiments of Lacerot *et al.* (2013) support the view that the small-bodied cladocerans

generally present in (sub)tropical lakes have limited abilities to exert top-down control of the phytoplankton biomass. Consistent with this, Iglesias *et al.* (2011) showed that large zooplankton dominated in a subtropical lake after a fish kill and also appeared in fish-free enclosures open to the sediment but were missing in similar enclosures with fish. They also found resting eggs of *Daphnia* in the surface sediment of many subtropical Uruguayan lakes even when *Daphnia* were missing in contemporary samples, demonstrating that *Daphnia* potentially are capable of developing populations but are kept low by high fish predation. In addition, unlike in higher-latitude lakes, submerged macrophytes in low-latitude lakes do not seem to offer zooplankton refuge from predation due to abundant littoral predators, as indicated by weak diel horizontal migration (Meerhoff *et al.*, 2007). Furthermore, the impact of a cold-water refuge from predation by planktivorous fish is larger in temperate lakes than in tropical and arctic lakes, in which temperature differences between stratified water layers are smaller. Regression analysis of Danish lakes also indicates a reduction in both the abundance and the size of zooplankton and an increase in proportion of small fish with increasing temperature, which is consistent with a view that the low-latitude dominance of small zooplankton species cannot be attributed to biogeographical or evolutionary issues (Jeppesen *et al.*, 2009, 2010).

Microbial plankton

Climate-induced increases in carbon and nutrient loading (see above) might have consequences for the relative roles of bacteria and bacterivores in the aquatic food web, especially in oligotrophic systems. Based on cross-system observations, Cotner & Biddanda (2002) argued that, in eutrophic systems, phytoplankton and phagotrophic heterotrophs (i.e. most ciliates and flagellates, rotifers and mesozooplankton) are favoured over bacteria due to both the high overall inorganic nutrient availabilities and the dominance of inorganic nutrients relative to dissolved nutrients in organic form. Support for the role of climate-induced changes in the nutrient loading rather than climate warming itself comes from a mesocosm study that manipulated nutrient levels along with temperature in the simulation of shallow-lake warming towards the end of this century. The data showed that the abundances of picoalgae, bacteria and heterotrophic nanoflagellates were far more affected by the nutrient state than by temperature and that the temperature effect was highest at the low nutrient level (Christoffersen *et al.*, 2006).

Polar lakes and ponds. The truncated food webs of these extreme habitats are often dominated by the microbial loop (Laybourn-Parry, 1997; Laybourn-Parry & Marshall, 2003). In these oligotrophic systems, large input of labile allochthonous dissolved organic matter with snowmelt water can result in high bacterial productivity in early spring. In the ultra-oligotrophic arctic Lake Toolik, seasonal changes in the source of organic matter (allochthonous versus autochthonous) were related to shifts in bacterial community composition (Crump *et al.*, 2003). Typically, the low productivity of these lakes cannot sustain high microzooplankton biomass, so the higher levels of the microbial food web cannot control flagellates and bacteria (Hobbie, Bahr & Rublee, 1999). Mixotrophy can provide a survival mechanism to survive the cold, dark winter months (Laybourn-Parry, 2002). Mixotrophic and heterotrophic flagellates typically peak in abundance during winter and early spring, whereas rotifers and ciliates are the dominant bacterivores in late spring to early summer (Rautio, Mariash & Forsstrom, 2011). With the anticipated changes in nutrient loading and temperature in these systems, most likely a shift will occur from bottom-up control of the bacterioplankton to top-down control of the bacterioplankton. In a long-term study on the effects of warming and nutrients, Özen *et al.* (2013) found the bacteria/phytoplankton ratio to be lowest in nutrient-rich warm mesocosms, which had the highest heterotrophic nanoflagellate/bacteria ratio as well as the highest rotifer/bacteria ratio. Their results suggest stronger grazer control of bacterioplankton under warmer, more nutrient-rich conditions.

Temperate lakes. While bacterial production and abundance in most temperate systems show a more dampened seasonal variation than phytoplankton and zooplankton, overall abundances are lowest in winter and highest in summer (Sanders *et al.*, 1989, 1992; Christoffersen *et al.*, 2006). Furthermore, bacteria sometimes exhibit a time lag in their response to changes in chlorophyll *a* biomass, which is usually highest in later winter–early spring and decreases over the summer (with the exception of the above-mentioned summer nuisance algal blooms). The correlation between phytoplankton and bacterioplankton biomass seems to be predominantly strong and positive in temperate systems (unless the grazing pressure by zooplankton on phytoplankton is high, Jeppesen *et al.*, 1997; Jürgens & Jeppesen, 2000). As in polar systems, warmer and more nutrient-rich conditions could potentially lead to stronger grazer control of the bacterioplankton with consequently lower bacteria/phytoplankton ratios (Özen *et al.*, 2013).

Tropical lakes. In contrast to colder lakes, the correlation between phytoplankton biomass and bacterial biomass appears to be much weaker in (sub)tropical lakes (Roland *et al.*, 2010). Bacterial abundance in deep tropical African Lake Kivu and Lake Tanganyika was constant throughout the year, whereas chlorophyll *a* was strongly seasonal with the alternation of dry and wet seasons (Sarmiento *et al.*, 2008). This difference may reflect a larger influence of terrestrial, allochthonous carbon subsidies in tropical lakes due to impacts of flooding or it may reflect higher abundances of small heterotrophs such as flagellates and ciliates due to the absence of large-bodied zooplankton (Roland *et al.*, 2010).

A comparison of ciliate dynamics in 20 subtropical lakes with varying trophic states found that seasonal patterns were modified by trophic state: oligotrophic and mesotrophic systems had ciliate biomass peaks in fall, whereas eutrophic and hypertrophic systems showed biomass maxima during summer (Beaver & Crisman, 1990). Compared to their high-latitude counterparts, low- and mid-latitude lakes often maintain a higher abundance of smaller zooplankton, including rotifers, ciliates and nanoflagellates, resulting in a higher degree of bacterivory (Crisman & Beaver, 1990; Jeppesen *et al.*, 2007). This higher productivity may be because higher temperatures and the longer growing season allow sustained productivity or because of higher fish predation on large-bodied zooplankton (Roland *et al.*, 2010; Havens & Beaver, 2011).

Parasites

Parasites (including viruses and fungi) are often missing links in (aquatic) food webs (Lafferty *et al.*, 2008) and can, for instance through parasitising otherwise inedible large phytoplankton, unlock nutrients that would otherwise be unavailable for grazers (Kagami, Helmsing & van Donk, 2011). As the abundance of parasites is hard to quantify, their occurrence is often underestimated (Lefèvre *et al.*, 2008). Parasitism is argued to be a more common life strategy than traditional predation (Lafferty *et al.*, 2008), and parasites are suggested to exert a comparable or even stronger influence on the wax and wane of their (planktonic) host than other consumers (Gerla *et al.*, 2013). Compelling evidence from humans and wildlife shows that seasonal variation in temperature, precipitation and sunlight can cause changes in parasite abundance through determining seasonality in host abundance and host immunity to infection (Altizer *et al.*, 2006). The projected climate change-induced prolongation of the growing season for parasites may increase the potential for faster generation cycles and year-round transmission

(Marcogliese, 2001); however, such year-round transmission does not necessarily result in higher overall parasite abundances. Effects of increasing temperature on host–parasite interactions may generally cause faster parasite population growth and earlier maturation but also increased mortality of transmission stages (Marcogliese, 2001). Differential responses to temperature change of host and parasite may lead to a mismatch in life-cycle time between hosts and parasites (Lafferty, 2009) and to asynchrony between hosts and parasite phenology, distribution and abundances in a changing climate (Marcogliese, 2001; Parmesan, 2006).

Polar lakes and ponds. While only few studies are available on seasonality of parasites in these extreme habitats, existing data reveal the importance of the viral loop for the carbon cycle in polar lakes and ponds (Laybourn-Parry, Hofer & Sommaruga, 2001). The viral loop makes particulate organic carbon and nutrients available again for the production of new bacterial populations through virus-induced lysis of bacteria (see Sawstrom *et al.*, 2007). In polar lakes and ponds, viruses seem to be particularly important during the winter months as more than 60% of the carbon supplied to the DOC pool originates from viral lysis, even though bacterial abundance is lowest in winter. In contrast, during the summer months, <20% of DOC originates from viral lysis; grazers likely play a bigger role (Sawstrom *et al.*, 2007). As mentioned in the previous section, the role of these bacterivores might even become larger with warmer temperatures.

Temperate lakes. Seasonality in the occurrences and impacts of microparasites on host populations and nutrient cycling is well documented: viruses have population maxima in late summer to autumn and minima in winter (Wommack & Colwell, 2000). This pattern is likely to be a density-dependent response to summer increases in phytoplankton and bacterioplankton populations, with increases in chlorophyll *a* and bacterial populations preceding increases in viral populations (Wommack & Colwell, 2000). Parasitic fungi, such as chytrids, can also be an important factor in controlling plankton seasonal succession in temperate lakes (Van Donk & Ringelberg, 1983; Kagami *et al.*, 2007). Many chytrids show a distinct seasonality with maxima in late winter/early spring (Van Donk & Ringelberg, 1983; Johnson *et al.*, 2006) that reach densities sufficient to regulate and even terminate peaks in the planktonic host abundance. Such strong seasonal patterns may be brought about by the seasonality of the host populations, but parasites also directly respond to external environmental conditions (Gsell *et al.*, 2013). This

is illustrated in the diatom host–chytrid parasite system of *Asterionella formosa* – *Zygorhizidium planktonicum* where warmer temperatures result in a constant infection of the host population, preventing the build-up of host blooms (Ibelings *et al.*, 2011). In the *Daphnia*–*Metschnikowia*–bluegill system (Hall *et al.*, 2006), warmer temperatures need not lead to higher prevalence, as higher temperature allows stronger predation on infected *Daphnia* by bluegill sunfish.

Tropical lakes. Few studies have examined the effects of climate on plankton–parasite dynamics in tropical lakes, but most studies to date support the expected picture of host density-dependent parasite dynamics. In an Amazonian floodplain lake, close coupling of viral and bacterial abundances as well as a low virus/bacterium ratio suggests that viral abundance in this system tends to be driven by the reduction of hosts for viral infection (Barros *et al.*, 2010). Overall, the authors argued that, while viruses are strongly controlled by host abundances in this system, bacteria are regulated both by predation losses and by physical processes associated with turbidity, which affects the underwater light distribution and dissolved organic carbon availability (Barros *et al.*, 2010). In another example, the bacterium that induces cholera, *Vibrio cholerae*, is associated with warm conditions and with high abundances of chitinous plankton such as copepods and cladocerans (Huq *et al.*, 1983). Indeed, its abundance has been observed to follow copepod seasonal populations, which in turn again follow their prey populations (Colwell, 1996).

Synthesis and implications

Our climate is changing; however, the (projected) rate and impact of this change depends on region and season. Areas exposed to a strong sinusoidal annual cycle in temperature (temperate and polar regions) will be exposed to stronger relative increases in temperature. In these higher-latitude areas, the anticipated warming will extend the growing season (Fig. 2, upper left and right). Higher runoff in summer (polar regions) and winter (temperate regions) will most likely increase the overall external loading of nutrients; furthermore, in shallow systems, warmer temperatures may also increase internal nutrient loading. The projected higher incidence of heat waves in temperate systems will intensify thermal stratification.

In subtropical systems (Fig. 2, lower right), drier summers will increase water residence times and increased evapotranspiration will result in more saline waters (Beklioglu *et al.*, 2007). The intensification of precipitation

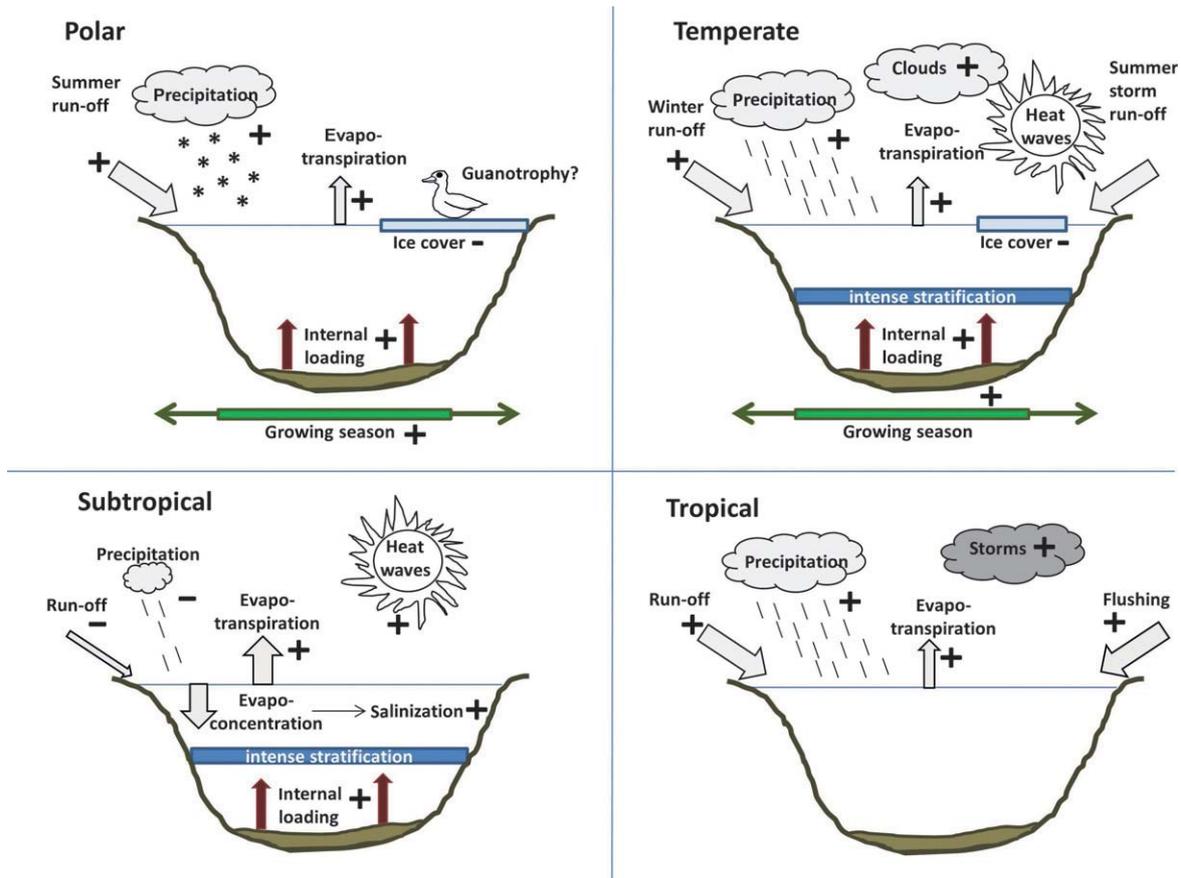


Fig. 2 Increased temperature as an important climate stressor leading to higher evapotranspiration in all climate regions (polar to tropics), more precipitation in all regions except subtropical areas and, consequently, more run-off except in the subtropical areas where evapoconcentration leads to salinisation (lower left panel). Expected effects in polar regions are shorter ice cover, thawing of permafrost, fewer glaciers, but more melt water, summer run-off, a longer growing season, potentially more nutrient release from sediments and more resident water birds (upper left panel); in temperate waters, intensified stratification is expected, more summer heat waves and heavy summer storms (upper right panel), while more storms are also expected in the tropics (lower right panel).

events will have stronger consequences for hydrology-driven systems, characteristic of some tropical areas (Fig. 2, lower left). In these systems, increased incidence of flooding events will lead to elevated washout.

Our comparison of plankton dynamics under different climatic conditions suggests that the consequences of these changing climates for plankton dynamics are to a large extent system specific and depend on characteristics such as food-web topology, trophic state, lake morphometry and catchment area. Some of these characteristics show a strong relationship with geographical location and latitude, thus obscuring or even confounding our comparison. Other non-climate-related factors, such as day length, covary with latitude and have a strong effect on both phytoplankton and zooplankton. This further complicates prediction of climate-related forcing of plankton dynamics. Stochasticity in species composition adds another complicating factor in predict-

ing plankton succession, although time-series analyses such as those of Bauer, Sommer & Gaedke, (2013) suggest that internal feedback mechanisms will make spring development of plankton succession in temperate systems more predictable.

We took the conceptual PEG model (Sommer *et al.*, 1986) as a starting point for framing our review. A recent update of the PEG model with the newest scientific insights (Sommer *et al.*, 2012) gives a more nuanced view of plankton succession, although the core patterns of the original PEG model still hold. Seasonality of bacteria seems to be more muted than phyto- or zooplankton, but a significant correlation exists between microbial and phytoplankton dynamics, especially in colder lakes. In warmer lakes, and with future warming, a greater influx of allochthonous carbon may obscure the association between phytoplankton and bacteria. Existing data show that parasites can strongly control plankton succession,

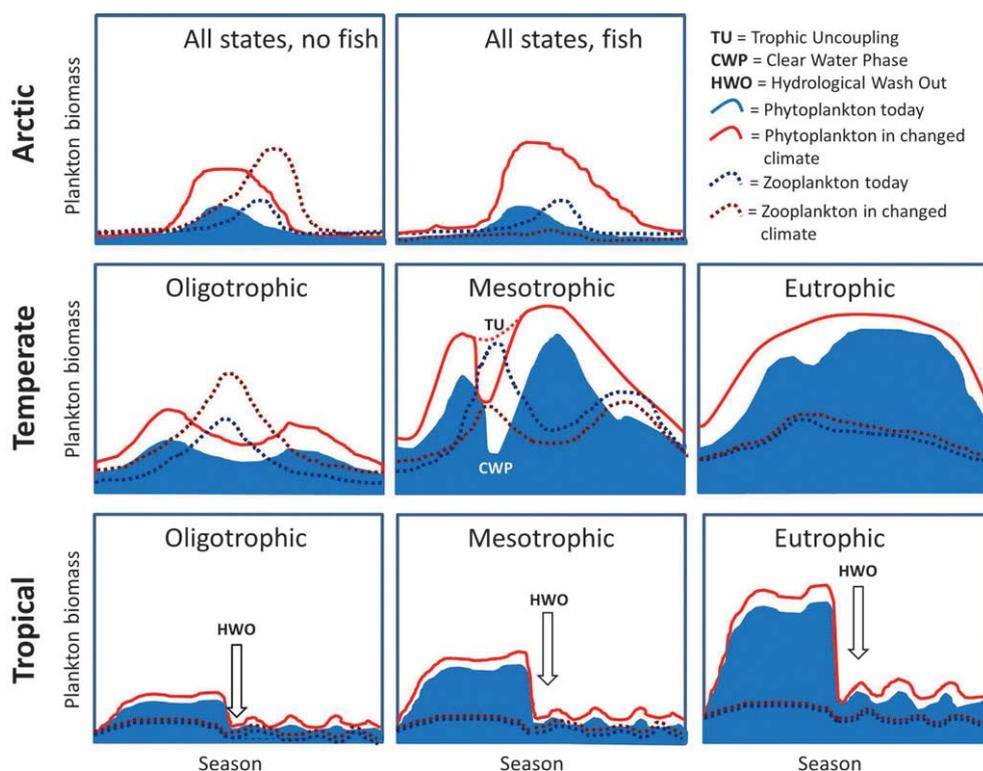


Fig. 3 Generalised seasonal development of current (blue area) and future (red solid line) phytoplankton biomass in polar lakes (upper panel), temperate lakes of different trophic states (middle panel) and tropical systems (lower panel). The generalised expected zooplankton biomass in current and future climate scenarios is indicated by dark blue and brown dotted lines.

but limitation of available data constrains our potential to generalise.

Despite the difficulties that complicating factors present for predicting plankton dynamics under different climatic conditions, some general patterns based on lake experiments, mesocosm experiments and field observations emerge (Fig. 3). Importantly, the patterns depicted in Fig. 3 are stylised and need to be further elaborated. In general, we propose that the indirect consequences of warmer climates will exceed the direct effects of warmer temperatures on vital rates.

In polar systems, warming-induced lengthening of the growing season may lead to higher and prolonged phytoplankton productivity (Fig. 3, upper panel). In addition, increased nutrient input in these predominantly oligotrophic waters will lead to higher phytoplankton biomass. For systems without high predation pressure on zooplankton, this higher algal food availability will result in higher zooplankton productivity and abundance (Fig. 3, upper panel).

In temperate systems, the response of the plankton to climate change is seen to depend strongly on the trophic state of the system (Fig. 3, middle panel), with two biomass peaks – in spring and summer – in oligotrophic systems,

but a lengthier and larger biomass peak in more eutrophic systems. With anticipated increases in external loading (precipitation) and internal loading (warming) of nutrients, a shift from two biomass peaks to a single biomass peak with associated higher populations of zooplanktivorous fish seems more likely in the temperate region. Increased water column stability and nutrient loading with climate change may likely intensify the frequency and duration of nuisance phytoplankton blooms in temperate lakes; whether trophic uncoupling will occur is likely to be lake system specific (Wagner *et al.*, 2013).

In warmer low-latitude systems, high grazing pressure by fish on large-bodied zooplankton may shift the zooplankton community towards small-bodied zooplankton, such as rotifers, ciliates and small cladocerans. In areas with projected decreases in precipitation, such as the Mediterranean lakes, decreases in flushing rates may increase the dominance of cyanobacteria (Romo *et al.*, 2013; Segura *et al.*, 2013). We propose that climate pressures on these semi-arid to arid shallow systems are likely strong (salinisation, increased nutrient loading, high water residence times), and the need for more data on these understudied systems is therefore urgent. In tropical systems where temporal variability in precipitation inten-

sity is an important driver in plankton dynamics, we suggest that the anticipated increases in precipitation intensity will result in resetting the seasonal dynamics of plankton communities, selecting for species adapted to highly variable environments (Fig. 3, lower panel). In these systems, the existing intense predation by fish on large-bodied zooplankton may increase further, resulting in a perennially low zooplankton biomass.

Our review aimed at outlining some general predictions on plankton dynamics under different climatic conditions now and in the future. With warming, a general picture emerges of increases in bacterivory, greater cyanobacterial dominance and smaller-bodied zooplankton that is more heavily impacted by fish predation. Our picture reflects gross biomass changes in trophic groups; however, species-specific differences in response to anticipated climate changes could have a strong impact on aquatic food webs in which a key role is reserved to single species. Typically, freshwater food webs are characterised by a high degree of redundancy and trophic generalism, indicating a high degree of functional similarity among species, with a small proportion of species exerting disproportionately strong effects on lake ecosystem functioning (Woodward, 2009). In these cases, differential responses to the anticipated changes in climate between species might weaken or intensify the match between trophic groups. Sublethal warming of ectotherm herbivores, for instance zooplankton, can potentially strengthen top-down control, resulting in a more intense match (O'Connor, 2009), although enhanced top-down control by fish and higher degree of fish omnivory (González-Bergonzoni *et al.*, 2012) may alter such relationships. Importantly, indirect effects of climate change, for example, through increases in nutrient loading and changes in stratification pattern may be more important than the direct effects of temperature on vital rates, especially for phytoplankton.

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