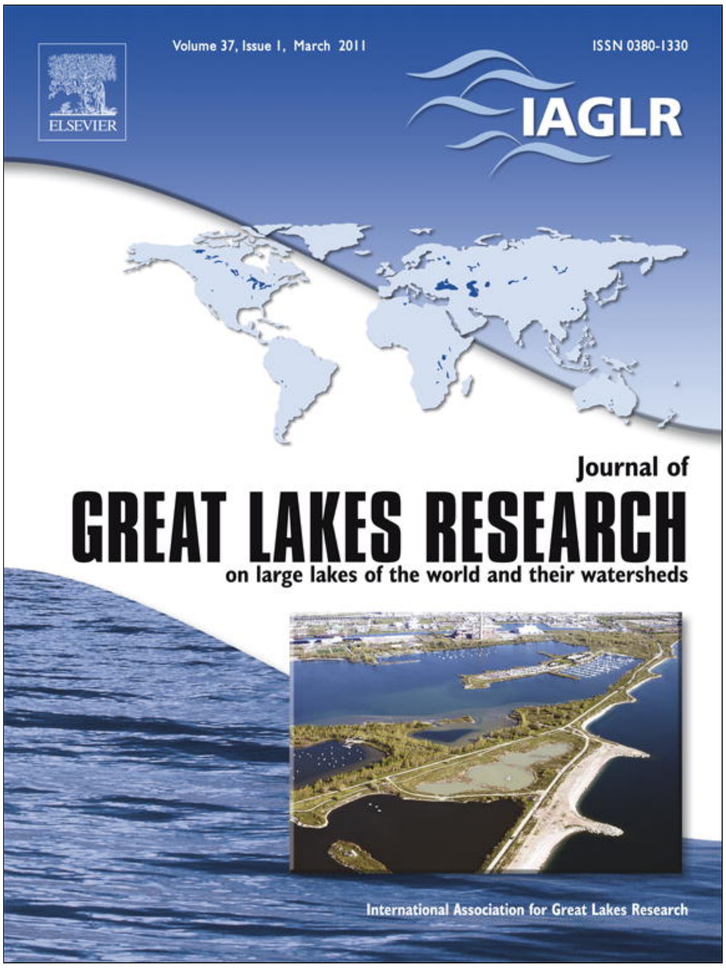
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Review

Our current understanding of lake ecosystem response to climate change: What have we really learned from the north temperate deep lakes?

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ABSTRACT

Climatic change is recognized as an important factor capable of influencing the structural properties of aquatic ecosystems. Lake ecosystems are particularly sensitive to climate change. Several long time-series studies have shown close coupling between climate, lake thermal properties and individual organism physiology, population abundance, community structure, and food-web structure. Understanding the complex interplay between climate, hydrological variability, and ecosystem structure and functioning is essential to inform water resources risk assessment and fisheries management. The purpose of this paper is to present the current understanding of climate-induced changes on lake ecosystem phenology. We first review the ability of climate to modulate the interactions among lake hydrodynamics, chemical factors, and food-web structure in several north temperate deep lakes (e.g., Lake Washington, Lake Tahoe, Lake Constance, Lake Geneva, Lake Baikal, and Lake Zurich). Our aim is to assess long-term trends in the physical (e.g., temperature, timing of stratification, and duration of ice cover), chemical (e.g., nutrient concentrations), and biological (e.g., timing of the spring bloom, phytoplankton composition, and zooplankton abundance) characteristics of the lakes and to examine the signature of local weather conditions (e.g., air temperature and rainfall) and large-scale climatic variability (e.g., ENSO and PDO) on the lake physics, chemistry and biology. We also conducted modeling experiments to quantify the relative effect of climate change and nutrient loading on lake phenology. These modeling experiments focused on the relative changes to the major causal associations underlying plankton dynamics during the spring bloom and the summer stratified period. To further understand the importance of climate change on lakes, we propose two complementary directions of future research. First, additional research is needed to elucidate the wide array of in-lake processes that are likely to be affected by the climate change. Second, it is essential to examine the heterogeneity in responses among different water bodies. The rationale of this approach and its significance for dealing with the uncertainty that the climate signals cascade through lake ecosystems and shape abiotic variability and/or biotic responses have been recently advocated by several other synthesis papers.

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Introduction

The global mean surface air temperature has risen about 0.7 ± 0.2 °C during the 20th century and the last decade was the warmest, during the instrumental record, in the Northern Hemisphere (Intergovernmental Panel on Climate Change, IPCC, 2007). Air temperature is forecasted to increase even more in the future. Specifically, global circulation models, using scenarios that consider a doubling of carbon dioxide (CO_2) and increases in other atmospheric greenhouse gases, predict an increase in the average air temperature of 1.5 to 5 °C by the year 2100. Moreover, there are predictions and evidence that the rise in temperature will cause an increase in the number of areas affected by droughts, a decrease in the number of frost days, longer growing seasons, intense tropical cyclone activity with greater wind speeds and heavier precipitation, significant glacier retreat acceleration, and an increase in the frequency of warm spells, heat waves, and other episodic meteorological events (Timmermann et al., 1999; Urban et al., 2000; Mann and Kump, 2008). Therefore, the key question is how do aquatic ecosystems respond to climate change? This question is essential if scientists are to make predictions to inform environmental management. In his 1997 review, D.W. Schindler clearly stated that "*there has been entirely too much focus on whether or not the recent trends for warming climate are caused by humans or part of a natural cycle. In either case, it is essential to anticipate the consequences for aquatic ecosystems and the human endeavours that depend on them...It is critical that we have the scientific basis for dealing with future water shortages, contamination and biodiversity issues, regardless of whether the problem is natural or manmade*".

Generally, the thermal properties of aquatic ecosystems are more directly governed by the climatic and large-scale oceanic fluctuations, e.g., North Atlantic Oscillation (NAO), El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO), than are the thermal properties of terrestrial ecosystems. The changes in the thermal properties directly and indirectly affect the physiology, distribution, life cycle, and the development of the aquatic organisms, and those of freshwater systems are particularly sensitive because of the localized and relatively static nature of the lacustrine environments (Carpenter et al., 1992; Williamson et al., 2009). The Intergovernmental Panel on Climate Change projected that the negative impacts of climate change on freshwater systems will outweigh any potential benefits (Intergovernmental Panel on Climate Change, IPCC, 2007). Nevertheless, our current understanding of how climate change affects freshwater ecosystem phenology is far behind from that of marine ecosystems. In addition, there is notable geographic imbalance in the available information with respect to the climate-driven changes of the ecosystem functioning, with an overwhelming scarcity of published studies from developing countries.

Climate affects key processes that determine the amount and distribution of freshwater worldwide (La Riviere, 1989). Changes in global climate along with the growing human population will exacerbate existing severe stresses to freshwater resources (Williams, 1989; Ausubel, 1991; Schindler, 2001). There is evidence of a strong relationship between weather conditions, such as air temperature and wind patterns, and lake thermal structure. Specifically, there is evidence of changes in the onset of stratification, thermocline depth, mean epilimnetic temperature, turnover date, and the duration of ice cover (Schindler, 1997; Magnuson et al., 1997). Additionally, the influence of macroscale atmospheric processes and the persistence of their signals vary substantially among lakes with different sizes and mixing regimes, indicating different information storage abilities even under similar climatic conditions (Shuter et al., 1983; Arhonditsis et al., 2004a). The concerted effects of the global climate change and the anthropogenic stressors are also profoundly altering the chemical and biological processes, and several biogeochemical studies have shown a coupling among lake temperatures and water chemistry, individual organism physiology, population abundance, community structure, and food-web dynamics (Weyhenmeyer et al., 1999; Straile, 2000; Gerten and Adrian, 2000; Arhonditsis et al., 2004b). These structural shifts may be more severe in aquatic environments with strong seasonality, where growth and reproduction of many species are usually restricted to short time windows over the annual cycle and the spatiotemporal synchronies largely determine the magnitude of the prey–predator interactions (Stenseth and Mysterud, 2002). Climate change has different effects on various taxonomic groups/trophic levels, and can also decouple species from favourable food conditions, i.e., the match–mismatch hypothesis (Cushing, 1974; Thomas et al., 2001). The rise of the water temperature may also increase bioaccumulation and biomagnification of organic and inorganic contaminants and thus have detrimental ramifications on entire aquatic food webs (Schindler, 2001). Therefore, the acquisition of holistic understanding of the climate-driven aquatic ecosystem responses requires consideration of the complex interactions among physical, chemical factors, and multiple trophic levels at a variety of spatial and temporal scales.

The purpose of this paper is to review the effect of climate changes on lake phenology. We first review what we have learned from several relatively well-studied north-temperate deep lakes (e.g., Lake Washington, Lake Tahoe, Lake Constance, Lake Geneva, Lake Baikal, and Lake Zurich; see Fig. 1) with respect to the ability of climate to modulate the interplay among lake hydrodynamics, chemical factors, and food-web interactions. We intentionally selected deep systems because they offer the opportunity to study the impact of climate change on a range of mixing regimes of the physical lake typology (Hutchinson, 1975). There are three general questions that reflect the anticipated system-specific knowledge and encapsulate the objectives of our review. (i) Are there distinct long-term trends in the physical (e.g., temperature, timing of stratification, and duration of ice cover), chemical (e.g., nutrient concentrations), and biological (e.g., timing of the spring bloom, phytoplankton composition, and zooplankton abundance) characteristics of the lakes? (ii) How strong is the signature of local weather conditions (e.g., air temperature and rainfall) and large-scale climatic variability (e.g., ENSO and PDO) on the lake physics, chemistry and biology? (iii) Which direct and indirect mechanisms drive these ecological patterns? The first two questions are investigated using a thorough literature review of well-studied, north-temperate deep lakes. To address the third question, we use a series of modeling experiments to examine the importance of nutrient loading and its interactions with climate variability on the structure and abundance of plankton communities. Our study concludes with a synthesis of the major findings, pinpoints knowledge gaps, and makes recommendations for future directions of research.

Lake response to climate change: What have we learned from six north-temperate deep lakes?

Lake Washington

Thermal structure

Our current knowledge about the climatic change effects on lake processes has greatly advanced from the monomictic Lake Washington, Washington State, USA (area 87.6 km^2, average depth 32.9 m). In this lake, a series of analyses has highlighted the effects of climate change on the thermal structure, the timing of the spring bloom, the coupling of the trophic interactions between phytoplankton and zooplankton, the interspecific niche differentiation, and the sockeye salmon (*Oncorhynchus nerka*) behavioural patterns (Arhonditsis et al., 2004a,b; Winder and Schindler, 2004a,b; Hampton, 2005; Hampton et al., 2006a). Arhonditsis et al. (2004a) showed that Lake Washington has experienced a warming trend during a 35-yr period (1964–1998), with overall increase of 1.5 °C (0.045 °C yr^{-1}) and 0.9 °C (0.026 °C yr^{-1}) for temperature data weighted over the surface (0–10 m) and entire lake volume, respectively. This warming trend was greatest for the period from March to October and was smallest and non-significant from November to February. The former seasonal mode was mainly driven by the inter-annual variability in air temperature and PDO ($r^2 = 0.65$), whereas the November–February period was more strongly related to air temperature, PDO, relative humidity, solar radiation, and wind speed ($r^2 = 0.83$). The same study also showed stronger PDO relative to ENSO signature in the lake hypolimnion, whereas the ENSO correlation with the epilimnetic temperature ($r^2 = 0.41$) was almost as strong as the one with PDO ($r^2 = 0.46$). The latter finding may suggest that the hypolimnetic warming in large monomictic lakes can be more responsive to longer timescale climatic phenomena like the PDO. Based on a heat budget model, Arhonditsis et al. (2004a) demonstrated that the surface water warming was more closely associated with an

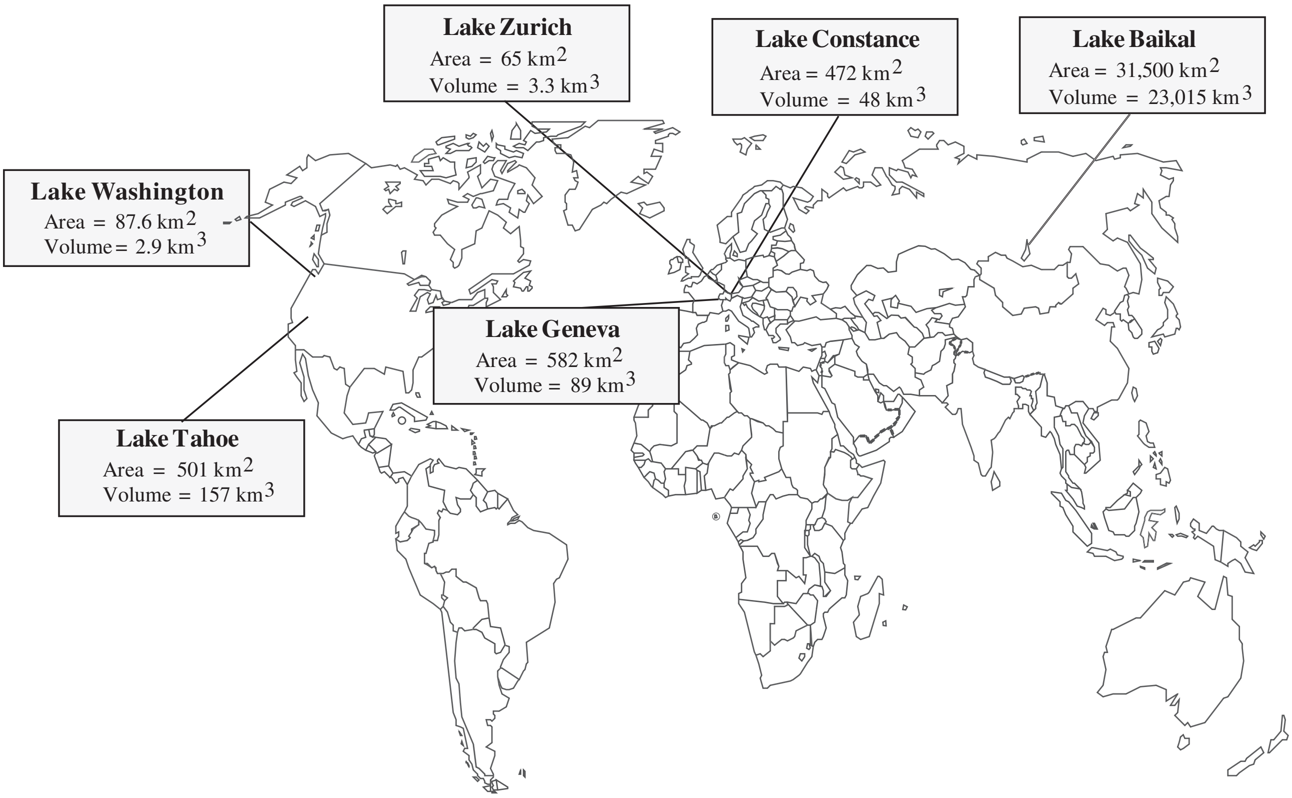

Fig. 1. Locations, surface areas and volumes of the six lakes examined in this study.

increasing linear trend in atmospheric long-wave radiation, which was particularly evident during the March–October period with a slope of 0.525 $\mathrm{W\,m^{-2}\,yr^{-1}}$ ($r^2 = 0.35$). Interestingly, the inter-annual variability in atmospheric long-wave radiation was also strongly related to the maximum and minimum air temperatures with the respective r^2 values being 0.48 and 0.85, while the urban heat island effect in the Seattle area was found to be negligible. Overall, both climate warming and variability associated with the large-scale climatic phenomena PDO and ENSO extended the duration of the stratification period by 25 days over the last 40 years (Winder and Schindler, 2004a). This change was mainly due to earlier spring stratification (16 days) and less to stratification termination in autumn (9 days).

Plankton dynamics

The earlier stratification onset advanced the timing of the phytoplankton spring bloom by about 19 days during the 1962–2002 period, although the initiation of the (diatom-dominated) bloom is not always related to the shallowing of the upper mixed-water layer below a critical depth (Winder and Schindler, 2004a). Arhonditsis et al. (2004b) suggested that the spring bloom in the relatively clear waters of Lake Washington can initiate by a relaxation of turbulent vertical mixing independently of the upper water-column depth (Fig. 2). Namely, under periods of calm winds and/or a temporary warming of the surface layer, the small-single diatom cells can overcome the vertical diffusion rates and maintain their position for sufficient time spans in the upper part of the water column, thereby exploiting the increasingly favourable vernal light conditions (Huisman et al., 1999). The timing of the clear-water phase shifted earlier by about 6 days and was mainly driven by the complex interplay among meteorological (PDO values), chemical (nutrient availability), and biological (*Daphnia* abundance) factors (Winder and Schindler, 2004a; Arhonditsis et al., 2004b). Among the major zooplankton genera, the timing of spring peaks of the copepod *Leptodiaptomus* and the rotifer *Keratella* advanced by 9 and 15 days, respectively. In particular, species of the former genus (e.g., *Leptodiaptomus ashlandi*) have demonstrated a pronounced decline in their densities, although their production was maintained due to an increase in the production to biomass ratio and a life cycle shift from an annual to a 6-month cycle. This higher-frequency voltinism was most likely produced by a longer and warmer growing period combined with changing fluctuations in food availability (Winder et al., 2009). Existing evidence also suggests that the increase of the length of the growing season in Lake Washington offers windows of opportunity for niche differentiation of the colonial rotifers *Conochilus hippocrepis* and *Conochilus unicornis*, whereby the seasonal peaks of the two species have shifted toward fall and spring, respectively. These changes in the phenology of *Conochilus* have allowed to overcome the competition with *Daphnia* (i.e., the dominant herbivores of the summer zooplankton community) and to obtain higher mean annual abundance in recent years (Hampton, 2005).

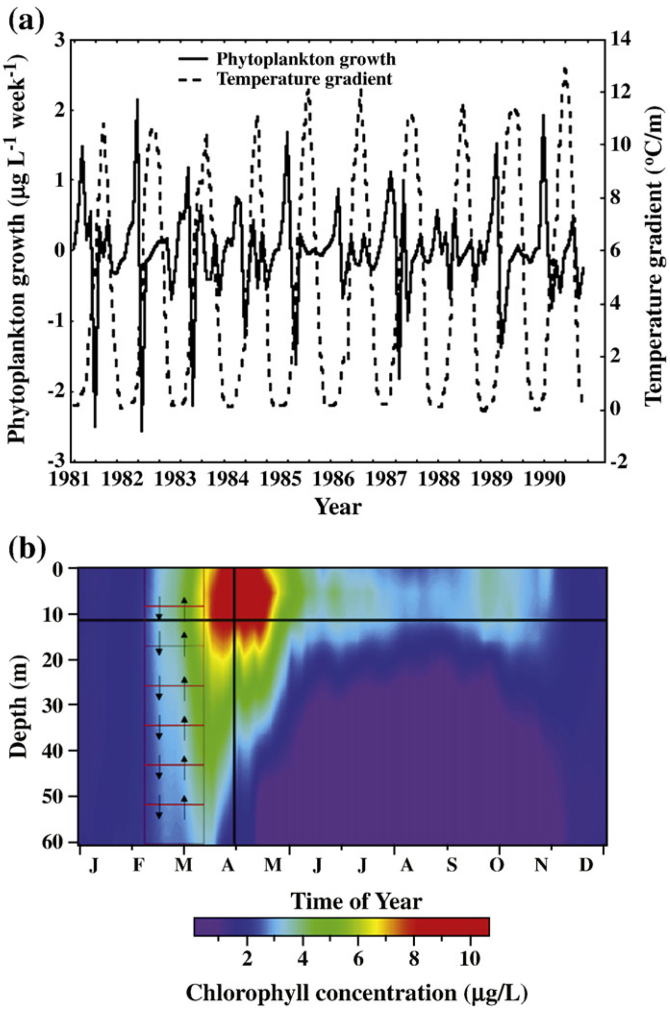

Fig. 2. (a) Seasonal cycles of phytoplankton growth and surface (0–10 m)—hypolimnion (10 m-bottom) temperature differences; (b) mean vertical profiles of chlorophyll *a* ($\mu g\,L^{-1}$) in Lake Washington (1975–1998). Note that the initiation of the spring bloom (e.g., the years 1982, 1985 and 1990) can precede the water-column stratification.

Reprinted with permission from Arhonditsis, G.B., M. Winder, M.T. Brett, and D.E. Schindler 2004b. Patterns and mechanisms of phytoplankton variability in Lake Washington (USA). Water Research 38: 4013–4027. Copyright 2004 Elsevier.

By contrast, the *Daphnia* spring peaks showed significant inter-annual variability but no systematic temporal trends, which generated a growing mismatch between peak phytoplankton densities and *Daphnia* populations in Lake Washington (Winder and Schindler, 2004b). The lack of response in *Daphnia* to increasing water temperature may stem from the stimuli that usually trigger the start of seasonal reproduction in Lake Washington. That is, *Daphnia* almost disappear from the water column during the winter, and the recruitment of the population in spring relies on the emergence of diapausing eggs from sediments. Photoperiod and temperature are the main cues stimulating *Daphnia* diapausing eggs to develop, while the Winder and Schindler (2004b) study surmised that the increase in water temperature may have less effect on the hatching rate of resting eggs than the photoperiod. The latter factor, however, is independent of climate change and such reliance upon hatching cues disconnected from water temperature increase may explain the absence of a response in *Daphnia* to match peak food availability (i.e., the spring diatom bloom). By refining the resolution at the species level, Hampton et al. (2006a) further discerned species-specific differences in *Daphnia* phenology in that the relatively unpredictable—with respect to its timing and abundance—*D. thorata* is gaining competitive advantage over the large-bodied and nutritious *D. pulicaria* in Lake Washington. These structural shifts in the zooplankton community could conceivably decrease the reliability of daphnid resources for sockeye fry (*O. nerka*) and may induce feeding shifts upon less profitable prey (e.g., copepods).

Apart from the earlier timing of the spring bloom and the possible uncoupling of the phytoplankton–zooplankton interactions, Law et al. (2009) suggested that the Lake Washington may also experience stronger phosphorus limitation along with greater dependence on the internal nutrient regeneration mechanisms (i.e., bacterial mineralization, zooplankton excretion) due to the prolongation of the stratified period. The year-to-year variability of the strength of the recycling feedback loop appears to be moderately related to climate forcing, while other biotic factors such as the zooplankton community composition and the succession patterns among groups with higher (rotifers) or lower (cladocerans and copepods) phosphorus excretion rates may also be equally important (Gulati et al., 1989; Kowalezewska-Madura et al., 2007). In this context, Hampton et al. (2006b) also proposed a food-web conceptualization that highlights the role of the “bottom–up” control mediated by picoplankton in Lake Washington phenology. Because of their functional properties (higher surface-area-to-volume ratio, more area of membrane per cell), the small-sized algal cells can easily adapt and potentially dominate the resource-limited environments expected due to the intensified lake stratification (Reynolds, 2006). This hypothesis offers a new perspective on the anticipated responses of the system to a changing climate in that the integrity of the zooplankton community may be compromised due to its increasing dependence on the mixture of widely edible but nutritionally variable picoplankton. Importantly, a possible decline of the *Daphnia* abundance and/or undesirable shifts to the zooplankton community composition could limit the transfer of energy to the higher trophic levels with dire repercussions on the highly selective sockeye salmon populations.

Lake Tahoe

Thermal structure

Lake Tahoe is a large, ultra-oligotrophic, monomictic, and ice-free lake lying at an elevation of 1898 m in the central Sierra on the California–Nevada border, USA (area 501 km^2, average depth 313 m). The lake is renowned for its deep blue color and clarity. Most of the recent research has focused on the climate-induced changes in the lake thermal dynamics as well as on the long-term trends in the phytoplankton biomass and taxonomic size structure (Goldman et al., 1989; Coats et al., 2006; Winder and Hunter, 2008; Kamenir et al., 2008). Coats et al. (2006) examined the effects of climate variability on the thermal structure of Lake Tahoe between 1970 and 2002. The volume-weighted mean temperature of the lake increased at an average rate of 0.015 °C yr^{-1}, which would amount to an increase of 0.49 °C over the 33-yr study period. However, the lake temperature did not rise at a constant rate, characterized by periods of cooling and periods of very rapid rise. The upward trend in annual mean total heat was significant (Mann–Kendall test, $p<5\times10^{-5}$), resulting in an increase in heat storage of 0.71 ± 0.02 W m^{-2}. Interestingly, the warming rates varied with the depth and were higher near the surface (0 and 10 m) and at 400 m, although the time required for a climatic event at the surface to affect the temperature at 400 m was approximately 1.4 years. In contrast with Lake Washington, the upward temperature trends by month vary slightly with the highest warming rate (0.019 °C yr^{-1}) in October and the lowest (0.014 °C yr^{-1}) in January–February. Using multiple regression analysis, Coats et al. (2006) showed that the daily lake surface temperature is positively related to the air temperature, short wave radiation, ENSO and PDO, whereas wind was associated with cooler temperatures ($r^2=0.17$–0.19). A significantly higher proportion of the observed annual lake temperature variability was also explained by the maximum and minimum air temperature, wind, short wave radiation, the ENSO and PDO indices along with the interactions of wind with minimum daily temperature and short wave radiation ($r^2=0.74$). The warming of the lake also increased its thermal stability and resistance to mixing, as the upward trends in the annual averages of the seasonally detrended Schmidt Stability ($p<0.06$), Birge Work ($p<4.9\times10^{-7}$), and Total Work ($p<7.9\times10^{-4}$) were all significant. The latter finding also implies that the lake has undergone changes in its thermal structure, such as the significant decline of the October thermocline depth (Coats et al., 2006).

Plankton dynamics

The long-term changes in the thermal structure of Lake Tahoe may affect the lake's clarity and primary productivity, although Goldman et al. (1989) argued that the inter-annual variability in primary production is mainly associated with the local weather conditions occurring in the late winter–early spring period rather than the large-scale climatic events. Winder and Hunter (2008) documented shifts in phytoplankton structure and vertical distribution that have been probably induced by the intensified long-term stratification in Lake Tahoe over a 23-yr period of records. The phytoplankton community composition significantly differed among the 1980s (1982–1989), the early/mid 1990s (1992–1997), and from 1998 till present (ANOSIM $r=0.79$, $p<0.001$). The phytoplankton community structure in the former period was more closely associated with the resource availability (low nitrogen to phosphorus ratios and relatively higher phosphorus concentrations) as well as with the deeper euphotic zone. The primary regulatory factor of the phytoplankton composition during the latter period was the intensified stratification and the reduced turbulent diffusion. In particular, filamentous and coenobial chlorophytes with morphological adaptations to reduce sinking velocities were favoured under the reduced mixing conditions and warmer water temperatures currently prevailing in Lake Tahoe (Reynolds, 2006). Likewise, the increased water-column stability also promoted the dominance of small-sized slow-sinking diatoms and indicative of their predominance is that the bulk of the diatom biomass in Lake Tahoe is about 10 m shallower in recent years (ANOVA, $p=0.004$) (Winder and Hunter, 2008). The filamentous and coenobial chlorophytes were not characterized by significantly different vertical positions in the water column between the two time periods (ANOVA, $p=0.9$). Generally, the phytoplankton community patterns in Lake Tahoe render support to the notion that the intensified stratification should offer competitive advantage to small-sized species and species with the capability of buoyancy regulation, which subsequently may alter the primary productivity, nutrient recycling, and the integrity of the higher trophic levels of the system.

The zooplankton community of Lake Tahoe has changed dramatically since the 1960s, due to the introduction of the planktivorous kokanee salmon (*O. nerka*) and the opossum shrimp (*Mysis relicta*) (Threlkeld, 1981). Coats et al. (2006) surmised that the increased stability and decreased thermocline depth along with biological factors, such as the shifts in the algal community structure and the change in the primary productivity patterns, may affect the feeding behaviour and population structure of zooplankton. Moreover, the thermocline provides a thermal refugium that protects cladocerans and copepods from predation (Richards et al., 1991), and thus it was hypothesized that a greater thermal gradient associated with the lake warming may strengthen this barrier. However, no long-term changes in zooplankton communities in response to climate change have been reported so far.

Lake Constance

Thermal structure

Lake Constance is a large and deep monomictic lake at the northern fringe of the European Alps (area 472 km^2, mean depth 101 m). Straile et al. (2003) reported that the positive phase of NAO and the resulting winter warming over Central Europe strongly influence the thermal structure of Lake Constance. Volumetrically weighted water temperatures increased by an average of 0.017 °C yr^{-1} ($p<0.01$) during a 37-yr study period (1962–1998), which was strongly related to the variability in winter air temperature ($r=0.88$, $n=37$, $p<0.0001$). Furthermore, both winter air temperature and annual mean water temperature were significantly correlated with NAO ($r=0.53$, $n=37$, $p<0.001$ and $r=0.42$, $n=37$, $p<0.01$, respectively), although the NAO signature on water temperature was more persistent than its influence on air temperature. The seasonal persistence of the NAO signal increased with water depth, and the strong association between deep-water temperatures and NAO exhibited a “sawtooth” pattern: periods of gradual temperature increase of several years (associated with high-NAO winters) followed by an abrupt decrease (Livingstone, 1997). NAO-related warming can also induce a positive feedback on the water-column stability, whereby mild winters stemming from high-NAO years usually result in persistent vertical gradients of temperature and incomplete mixing. This pattern of reduced vertical transport in the winter suggests that NAO can potentially regulate the upward mixing of nutrients, accumulating in the hypolimnion during the previous stratification period as well as the downward fluxes of oxygen in Lake Constance (Straile et al., 2003).

Plankton dynamics

Understanding the effects of climate variability on plankton phenology in Lake Constance requires delineation of the structural changes induced from the re-oligotrophication processes that followed the substantial reduction of the exogenous nutrient loading (Bauerle and Gaedke, 1998). First, consistent with the trends in Lake Washington, model-based analyses and empirical evidence suggest that the onset of the spring phytoplankton bloom in Lake Constance would occur earlier in response to climate warming (Peeters et al., 2007a). The timing of the spring phytoplankton bloom is primarily determined by the magnitude of the turbulent diffusivity, rather than the oligotrophication or the photosynthetically active radiation variations, the phytoplankton sinking velocity, and the effect of water temperature on biological process rates (Peeters et al., 2007b). Tirok and Gaedke (2007) offered further insights into the effects of surface irradiance, vertical mixing, and temperature on algal dynamics based on a long-term dataset (1979–1998). They argued that the spring primary production can be 40–80% lower due to light limitation, while phytoplankton biomass can decrease by 10–30% due to losses by vertical mixing. The response of the spring phytoplankton to abiotic and biotic forcing factors differed among the different functional groups, i.e., small, fast-growing and edible algae fluctuated more strongly than the larger, less-edible algae. This pattern was attributed to the prompt response of the small algae to mixing and light conditions due to their short generation time as well as due to their higher grazing susceptibility. The summer algal biomass has been significantly reduced by the declining phosphorus concentrations in Lake Constance, and cryptophytes/chrysophytes have gained competitive advantage in the summer community along with species (e.g., *Ceratium*) that have the ability to vertically migrate between the euphotic zone and deeper P-enriched water layers (Sommer et al., 1993; Anneville et al., 2005).

The annual average daphnid biomass remained relatively constant throughout the re-oligotrophication process, partly due to the persistence of the small and edible phytoplankton species in the summer community (Straile and Geller, 1998). To elucidate the influence of climate variability on daphnid population dynamics, Straile (2000) suggested a sequence of events connecting NAO together with the winter and early spring meteorological conditions to planktonic events in summer. Namely, high-NAO years were associated with warmer spring temperatures that enabled high phytoplankton growth rates and high daphnid biomass in May. Consequently, the exceedance of a critical threshold of *Daphnia* biomass was reached earlier in high-NAO years, causing an earlier recession of the spring phytoplankton bloom and subsequently a longer lasting clear-water phase. Because of the earlier summer decline of *Daphnia* in July, the relationship between *Daphnia* biomass and the NAO index was negative ($r = -0.58$, $p < 0.05$). Seebens et al. (2007) recently reported a relatively stable abundance of the calanoid copepod *Eudiaptomus gracilis* over a 26-yr study period (1970–1995). The impact of oligotrophication was mainly manifested as a seasonal shift in the timing of peak abundance from spring to late summer, and this change was most evident within the early copepodid stages rather than the adult animals. Similar to the *Daphnia* seasonal patterns, the effects of climate variability on population dynamics involved again faster vernal growth rates in years with warmer conditions, and subsequently earlier occurrence of the summer population minimum along with earlier abundance increase in late summer/early fall. Generally, the interplay of the spring environmental variability with the dynamics of two major residents of the zooplankton community in Lake Constance highlights the remarkable memory of the system, whereby the winter NAO signals can affect the lake phenology for more than half of the year.

Whereas most of the studies on zooplankton dynamics in Lake Constance focused mainly on cladocerans and copepods, Tirok and Gaedke (2006) offered a different perspective by examining the influence of all major zooplankton groups (including rotifers and ciliates) on the initiation of clear-water phase under different weather and climatic conditions. Using 19 years of observations, they showed that regardless of the daphnid biomass levels, clear-water phase occurred regularly due to strong grazing by a diverse assemblage of zooplankton community including daphnids and/or micro- and mesozooplankton. Ciliates accounted for most of the grazing pressure exerted on phytoplankton throughout the spring period maintaining high abundance levels for up to two months. According to the Tirok and Gaedke (2006) study, the timing of the clear-water phase was unrelated to the NAO levels, but was correlated with the wind-dependent vertical mixing intensity of three months earlier. Lower mixing intensity triggered early growth of phytoplankton followed by earlier appearance of ciliates and rotifers, while the lower water temperature prevented a significant increase in daphnid growth. The latter mechanism should be relevant for other large and deep water bodies, where mixing-sensitive phytoplankton and small zooplankton growth may be temporarily disconnected from temperature-sensitive growth of crustaceans. This pattern contrasts the synchronous development of small and large zooplankton in shallow lakes, promoted by the water temperature increase and/or by the relative independence of phytoplankton and small zooplankton growth to mixing (Tirok and Gaedke, 2006).

Lake Geneva

Thermal structure

Lake Geneva is an elongated, warm-monomictic lake located on the border between France and Switzerland at an elevation of 372 m (area 582 km^2, mean depth 152 m). Winter temperatures rarely drop below 5 °C and the maximum mixing depth can be more than 50 m. Gillet and Quetin (2006) reported a mean annual temperature increase of 1 °C for both air and surface water of Lake Geneva recorded from 1983 to 2000. The warming trend varied seasonally with the lowest temperature increase (+0.5 °C) being recorded at the end of the winter and at a depth of 30 m, while the highest increase (+2 °C) occurred in May at the surface water of the lake. Molinero et al. (2007) further investigated the connections between the subtropical Atlantic climate variability and the summer water temperature in Lake Geneva. It was found that the long-term water temperature was significantly related to the Tropical North Atlantic pattern ($r = 0.32$, $p < 0.005$), the Atlantic Multi-decadal Oscillation ($r = 0.59$, $p < 0.01$), the air temperature ($r = 0.62$, $p < 0.01$), and humidity ($r = -0.57$, $p < 0.01$). Most recently, Perroud et al. (2009) also examined the capability of a 1-D model in successfully reproducing the water temperature profiles.

Plankton dynamics

Anneville et al. (2002a) used STATIS analysis to describe the general phytoplankton succession patterns and to delineate the relative importance of the intra- versus inter-annual variability. The phytoplankton seasonal patterns in the first part of the year (December–June) were in agreement with what is predicted by the Plankton Ecology Group (PEG) model. The dominant functional groups of this period were mainly diatoms and cryptophytes (e.g., *Rhodomonas minuta*, *Fragilaria crotonensis*, *Asterionella formosa*, *Stephanodiscus minutulus*, *Gymnodinium helveticum*, and *Aulacoseira islandica*); the majority of those being fast-growing small species ('r' strategists) with high surface:volume ratios that allow rapid nutrient transfer through the cell surface. The second part of the year (July–November) comprised much larger forms including colonial species and filamentous forms. These species are typically characterized as 'K' strategists with slow growth rates and high nutrient storage capacities (e.g., *Aphanothece clathrata v. rosea*, *Dinobryon sociale*, *Mougeotia gracillima*, *Peridinium willei*, *Ceratium hirundinella*, and *Planktothrix rubescens*). However, the temporal evolution of the summer phytoplankton community demonstrated significant inter-annual variability. Specifically, Anneville et al. (2002a) identified three distinct periods for the annual phytoplankton patterns in Lake Geneva. During the 1974–1985 period, the phytoplankton succession followed the general seasonal patterns described by the PEG model (see their Fig. 8b), demonstrating a remarkable resilience to meteorological perturbations and environmental changes. Following a sudden shift in the seasonal phytoplankton structure in 1986, there was another period (1986–1991) of resistance to changes in the environmental conditions characterized by a longer persistence of the summer species (*C. hirundinella*, *P. willei*, *A. clathrata v. rosea*, and *Cryptomonas* sp.) and an absence of the typical autumnal community. An interesting exception to the phytoplankton community of that period was the year 1988, suggesting that the resistance was not an intrinsic property of the system, but rather the result of the interplay among several mechanisms which under extreme perturbations can potentially lead to a sudden shift. During the third period (1992–1996), the annual structure was similar to that of the year 1988 and the summer community was dominated by species usually characteristic of late summer and autumn (*Diatoma tenuis*, *M. gracillima*, *P. rubescens*, and *Oscillatoria limnetica*). The third period recorded in Lake Geneva coincided with the worldwide warming and an extreme phase of NAO that was a major driver of weather and climate variability in the northern hemisphere (Hurrell, 1995; Hurrell and VanLoon, 1997). The warmer conditions favoured earlier spring phytoplankton growth and consequently an earlier depletion of the epilimnetic phosphorus concentrations. Because of this earlier timing along with the deepening of the phosphorus-depleted layer, the authors opined that species adapted to low light intensity that can more effectively exploit nutrient-rich deeper water layers were promoted.

Molinero et al. (2006) investigated the impacts of climatic and anthropogenic forcing on the long-term changes in the community of rotifers during the period 1969–98 in Lake Geneva. Canonical correlation analysis (CCA) showed that the North Atlantic Climate (NAC), i.e., a proxy of the North Atlantic climate signal obtained by the composition of the key modes of low-frequency atmospheric variability such as the Arctic Oscillation (AO), North Atlantic Oscillation (NAO), East Atlantic pattern (EA), Gulf Stream/Northern Current Index (GSI), East Atlantic Western Russian (EA/WRUS) and the Northern Hemisphere Temperature (NHT), was positively correlated with the water temperature ($r = 0.77$), phytoplankton ($r = 0.75$), and nanophytoplankton ($r = 0.71$) inter-annual variability. Similarly, the inter-annual variability of rotifers was tightly associated with the NAC ($r = 0.87$), water temperature ($r = 0.93$), phosphorus ($r = 0.95$), and nanophytoplankton ($r = 0.82$). A more detailed picture was revealed when testing the relationships between the two main rotifer size classes (small and large) and the climate or other local environmental factors: a significant link was found between the small size class (<0.5 mm) and NAC ($r = 0.88$), water temperature ($r = 0.93$), phosphorus ($r = 0.96$), and nanophytoplankton ($r = 0.80$). The large size class (>0.5 mm) appeared to be related only to water temperature ($r = 0.63$), highlighting the importance of other factors (i.e., food-web interactions) to modulate their inter-annual variability. The authors also proposed a conceptual model (see their Fig. 6), whereby both anthropogenic influences and large-scale climate variability associated with the North Atlantic Ocean regulate the long-term dynamics of the rotifer community in Lake Geneva. According to this model, the concerted effects of the North Atlantic climate and human-induced disturbances could affect not only the abundance of the rotifer populations but also their size structure, which in turn might have major implications on the lake ecosystem functioning (e.g., energy flow and food-web interactions) (Alvarez-Cobelas and Rojo, 2000). The ramifications of the climatic forcing on the functioning of the pelagic ecosystem were also illustrated by the long-term increase in the *Leptodora kindtii* abundance and the decrease in the *Bythotrephes longimanus* biomass (Molinero et al., 2007).

Lake Zurich

Thermal structure

Lake Zurich is a long, narrow lake (area 65 km^2, mean depth 51 m) situated at 406 m above sea level in the northern peri-alpine region of Switzerland. Lake Zurich is separated into two basins by a natural dam: the lower basin and the upper basin. Both lakes are also located downstream from Lake Walen, and thus are not only affected by similar local meteorological conditions but are also hydrologically linked. Lower Zurich and Lake Walen are deep lakes and the corresponding maximum depths are 136 m and 145 m, while the Upper Zurich is 48 m deep. In recent years, the three lakes underwent re-oligotrophication and the average phosphorus concentrations in Lake Walen, Upper and Lower Lake Zurich approximately lie around the levels of 5, 10 and 20 μg TP L^{-1}, respectively. The Lower Zurich has undergone a so-called “secular increase” in the water temperature at all depths, reflecting the high degree of regional warming in the European Alpine area during the 20th century (Livingstone, 2003). From the 1950s to the 1990s, the temperature in the upper 20 m of the lake increased by 0.24 °C decade^{-1}, whereas the hypolimnetic temperature increased by 0.13 °C decade^{-1}. This discrepancy between the epi/metalimnion and the hypolimnion warming resulted in a 20% increase of the (Schmidt) thermal stability and a consequent 2–3 weeks prolongation of the stratification period. The temporal variability of the temperature structure of the surface mixed layer of Lake Zurich is more closely associated with the regional daily minimum air temperature, but not with the daily maximum. Thus, the processes responsible for the changes in the thermal structure of Lake Zurich more likely operate during the night, presumably by controlling the nighttime convective cooling of the surface mixed layer (Livingstone, 2003). Another important facet of the thermal structure in the facultatively dimictic Lake Zurich is the importance of the heat carryover during the winter. Peeters et al. (2002) used the 1-D SIMSTRAT model to simulate the thermal structure of the lake from 1948 to 1997, and the continuous modeling approach adopted overcame the defect of the commonly employed discontinuous modeling approach (with no heat carryover during winter), i.e., the substantial underestimation of the long-term hypolimnetic warming typically induced from the air temperature increase. The significant degree of hypolimnetic warming found in this study suggests that the response of the stratification intensity to the air temperature increase is likely to be less affected in facultatively dimictic lakes (i.e., only rarely freeze over) rather than in strictly dimictic systems (i.e., lakes that freeze over each year). In addition, Peeters et al. (2002) hypothesized that the elevated air temperature (+4 °C) will likely induce a switch from facultative dimixis to facultative monomixis with potentially dire repercussions on the ecological processes in Lake Zurich, given that the suppression of the deep convective mixing events can conceivably exacerbate the hypolimnetic oxygen depletion and the subsequent nutrient release from the anoxic sediments.

Plankton dynamics

Despite the difference in their trophic status, the re-oligotrophication process along with the contemporary warming trends resulted in an earlier appearance and a deepening of the phosphorus-depleted zone in the Upper and Lower Lake Zurich as well as in Lake Walen (Anneville et al., 2004). However, the warmer and somewhat shallower epilimnion, and possibly the higher TP levels, segregated the Lower Zurich from the other two lakes in regards to the phytoplankton community composition (Anneville et al., 2004). Namely, while the toxic cyanobacterium *P. rubescens* represented approximately 25% of the total phytoplankton biomass in the lower basin of Lake Zurich, the same species has been nearly absent in Upper Zurich and Lake Walen (Anneville et al., 2004). Interestingly, the *P. rubescens* abundance increase in the Lower Zurich phytoplankton community was mainly manifested after 1987, and the same pattern has been observed in many other European lakes (e.g., Lake Geneva and Lake Constance) despite the gradual decrease of the ambient nutrient levels (Morabito et al., 2002;

Anneville et al., 2005; Legnani et al., 2005). Because the occurrence of *P. rubescens*-dominated communities temporally coincides with the strongly positive NAO phase, it has been hypothesized that a sequence of causal associations may be responsible for this structural shift, i.e., lower TP concentrations stemming from the protracted stratification (or other climate-related factors; see following paragraph) along with the reduced external nutrient loading resulted in lower epilimnetic phytoplankton biomass; the subsequent increase in light penetration created a more favourable metalimnetic environment, where the higher nutrient levels can be exploited by species adapted to lower light intensities, such as the *P. rubescens* (Legnani et al., 2005). Notably, unless the mixing depth in the winter exceeds the mean critical pressure depth for the gas vesicles collapse (≈90 m), this species has the capacity to persist throughout the warm winters, when most of the *P. rubescens* filaments remain buoyant and form the inocula for the spring growth (Walsby et al., 1998).

Another noteworthy structural change of the phytoplankton community in Lakes Walen and Upper Zurich was the shift from a diatom-dominated community by a new assemblage composed of mixotrophic species or species with high affinity to nutrients (Anneville et al., 2004). The latter pattern is a typical response of the phytoplankton community to re-oligotrophication and is probably unrelated to the regional climate variability (Gaedke, 1998; Anneville et al., 2005). Generally, the delineation of climate change vis-à-vis the nutrient loading reduction effects suggests that the oligotrophication has been the main regulatory factor of the phenology of the European peri-alpine lakes, while the climate appears to have an indirect role on the synchrony (i.e., the correlation between concurrent time series of a variable measured in several lakes) and temporal coherence (i.e., the degree to which variables behave similarly over time) of the systems (Anneville et al., 2005). Regarding the climate-related influence, potentially important mechanisms that can contribute to more severe epilimnetic phosphorus depletion and thus modulate the plankton dynamics are the incomplete winter mixing which reduces the nutrient replenishment of the trophogenic zone from the hypolimnion; the higher spring phytoplankton growth due to the warmer temperatures that increases the contemporary nutrient consumption; and the earlier spring *Daphnia* growth which can be a significant drain of phosphorus for phytoplankton (Sommer et al., 2003; Salmaso, 2005; Anneville et al., 2005).

Lake Baikal

Thermal structure

Hampton et al. (2008) recently reported significant warming of the surface water and long-term changes in the lower food web in Lake Baikal, the world's deepest, largest (by volume), and most ancient lake (area 31,500 km^2, mean depth 730 m). The annual mean air temperature in the Baikal area increased by 1.2 °C over the past century, which is a rate similar to those reported in higher latitudes and roughly twice the global average (Serreze et al., 2000; Shimaraev et al., 2002). In response to this intense warming, surface water temperature increased at an average rate of approximately 0.20 °C decade^{-1}, while the mean temperature at 25 m increased by 0.12 °C decade^{-1} over the 60-yr period of records. The warming trend was more evident in data averaged by season, as the surface water temperature increased by 0.38 °C decade^{-1} in the summer, and the deeper waters (25 m) increased by 0.22 °C decade^{-1} in the fall. The ice-free season in Lake Baikal is also known to have lengthened by 16.1 days over the past 137 years mainly due to later ice onset (Magnuson et al., 2000; Todd and Mackay, 2003).

Plankton dynamics

Chlorophyll *a* concentrations in Lake Baikal increased by 300% on average in the summer period since 1979 (slope = 0.04 µg chl *a* L^{-1} yr^{-1}, $r^2 > 0.30$, $p < 0.01$), possibly driven by a suite of mechanisms associated with the thermal structure changes, such as the increased nutrient loading from the watershed, wind-induced mixing of nutrients from deeper depths into upper waters, and warming effects on primary production and nutrient recycling (Hampton et al., 2008). Interestingly, the increase of the summer phytoplankton biomass in Lake Baikal is in sharp contrast with the Lake Tanganyika, where the stronger stratification patterns along with the different water-circulation regimes have reduced the vertical mixing of nutrients and consequently the algal biomass and primary productivity (O'Reilly et al., 2003; Verburg et al., 2003). The Secchi disc depth did not demonstrate a significant long-term trend which suggests that the water clarity is not primarily affected by the chlorophyll *a* concentrations in the ultra-oligotrophic Lake Baikal (Hampton et al., 2008). The dynamics of the phytoplankton community are strongly dominated by a recurrent under-ice spring diatom bloom that mainly consists of endemic *Cyclotella* species, which may experience severe stresses (i.e., exposure to different light and temperature conditions) should the trends of reduced snowfall and ice formation persist over time (Hampton et al., 2008). Although the spatiotemporal phytoplankton distribution is primarily determined by the temperature and stratification patterns in Lake Baikal, Fietz et al. (2005) provided evidence of compositional shifts induced by the enhanced phosphorus loading from the Selenga River. The same study also argued that further global warming would favour the dominance of picoplankton along with small pigment-rich *Bacillariophyceae* and *Chrysophyceae* cells in near-shore areas, whereas the offshore phytoplankton community will probably be more resistant (Fietz et al., 2005).

The longer ice-free season and warmer summer temperatures in Lake Baikal were also associated with increasing trend of cladoceran densities in summer and fall, and decreasing copepod and rotifer abundance during the colder months of the year (Hampton et al., 2008). In particular, untransformed data of cladoceran densities (dominated by *Bosmina* and *Daphnia*) demonstrated a 334% increase since 1946, while primarily rotifers (slope = −0.02 ln(individuals L^{-1} + 1) yr^{-1}, $r^2 = 0.07$, $p < 0.01$) and secondarily copepods (slope = −0.01 ln(individuals L^{-1} + 1) yr^{-1}, $r^2 = 0.22$, $p < 0.03$) showed significant decline. The gradual predominance of cladocerans over the historically dominant copepods may also have important implications for nutrient recycling and food-web dynamics in an oligotrophic system like Lake Baikal, as cladocerans graze a wider range of cells and are characterized by lower rates of phosphorus excretion per unit of biomass (Sommer and Sommer, 2006). In support of the latter assertion, Hampton et al. (2008) presented results from multivariate autoregressive (MAR) modeling in which cladocerans had significantly negative relationships with green algae, cryptophytes, and chrysophytes.

Structural changes in lake functioning induced from nutrient loading and climate variability: What do the models predict?

Objectives and modeling experiments

After more than two decades of research focus on the climate-induced changes in lake phenology, we have sufficient evidence that most of the north temperate deep lakes have experienced a warming trend, with temperature increase approximately ranging between 0.01 and 0.11 °C yr^{-1} (Table 1). In general, this warming trend is much stronger in the epilimnion or metalimnion than in the hypolimnion, and is also associated with long-term increase in thermal stability, lengthening of stratification period, and shortening of the ice cover period (Table 1). The temperature is strongly correlated with the large-scale climatic variability (e.g., NAO, PDO and ENSO) as well as with regional and local meteorological variables (e.g., air temperature, wind speed, precipitation, humidity and solar radiation). To that end, Livingstone (2008) challenged the traditional view of the lakes as individual unconnected systems influenced by statistically stationary local meteorological conditions. Rather, he proposed a new conceptual model founded upon the explicit recognition of spatial

Table 1
Summary of climate-induced changes in the thermal structure of some north temperate deep lakes.

Lake	Observed change	Time period (yr)	Reference
Increase in lake temperature (°C yr^{-1})			
Lake Washington	0.045 (epilimnion) 0.026 (average ^{a})	1964–1998	Arhonditsis et al. (2004a)
Lake Tahoe	0.015 (average ^{a})	1970–2002	Coats et al. (2006)
Lake Constance	0.017 (average ^{a})	1962–1998	Straile et al. (2003)
Lake Geneva	0.059 (epilimnion)	1983–2000	Gillet and Quetin (2006)
Lake Baikal	0.02 (epilimnion) 0.012 (>25 m)	1945–2005	Hampton et al. (2008)
Lake Zurich	0.016 (average^{a}) 0.024(epi/metalimnion) 0.013 (hypolimnion)	1950–1990	Livingstone (2003)
Lake Superior	0.01 (near-shore)	1906–1992	McCormick and Fahnenstiel (1999)
	0.11 (epilimnion)	1979–2006	Austin and Colman (2007)
Lake Michigan	0.065 (epilimnion)	1979–2006	Austin and Colman (2007)
Lake Huron	0.086 (epilimnion)	1979–2006	Austin and Colman (2007)
Lake Erie	0.01 (near-shore)	1918–1992	McCormick and Fahnenstiel (1999)
	0.037 (average)	1983–2002	Burns et al. (2005)
Lake Ohrid	0.025 (hypolimnion)	2001–2004	Matzinger et al. (2006)
Lake Garda	0.1 (hypolimnion)	1990–2003	Salmaso (2005)
Increase in stratification period (days)			
Lake Washington	25	1962–2002	Winder and Schindler (2004b)
Lake Zurich	14–21	1947–1998	Livingstone (2003)
Lake Superior	14–18	1906–1992	McCormick and Fahnenstiel (1999)
	17 ^{b}	1979–2006	Austin and Colman (2007)
Lake Huron	17 ^{b}	1979–2006	Austin and Colman (2007)
Increase in ice free season (days decade^{-1})			
Lake Baikal	1.61	1869–1996	Todd and Mackay (2003)
Lake Ontario	10	1973–2002	Assel (2005)
Lake Superior	13	1973–2002	Assel (2005)
Lake Huron	2.3	1973–2002	Assel (2005)
Lake Michigan	8.5	1973–2002	Assel (2005)
Lake Erie	5.9	1973–2002	Assel (2005)
Lake Mendota	1.35	1853–1995	Magnuson et al. (2000)
Lake Paijanne	1.02	1855–1995	Magnuson et al. (2000)

[a] Average volume-weighted temperatures of the entire lake.
[b] Average of several locations of the lakes. Values indicate the advancement of the stratification onset.

interconnectedness and temporal change of lake properties. According to this paradigm, the thermal structure of a lake should be primarily viewed as a local response to large-scale climatic forcing, whereby a strong climate signal leads to large-scale spatial coherence, while the existence of long-term trends in climatic variability (associated with climate change) leads to non-stationary thermal properties (Livingstone, 2008). Viewing the emergence of this conceptual framework as the norm in future climate research, the question arises of how possible it is to draw similarly definitive conclusions regarding the chemical and biological properties of freshwater ecosystems? Admittedly, this is a more challenging task given that the impact of human activities (e.g., nutrient enrichment), restoration efforts (e.g., biomanipulations), and other external perturbations (e.g., invasive species) along with the intricate nature of the ecological processes is often confounded with the climate signals.

Generally, although it is acknowledged that failure to explicitly account for the multitude of stressors impacting system behaviour can provide conflicting results (Scheffer et al., 2001a; Van Donk et al., 2003; Jeppesen et al., 2005), the delineation of climate change vis-à-vis nutrient loading effects on freshwater ecosystem phenology has not been unequivocally addressed in the literature. Controlled experimentation with numerical models predicts that the interplay between climate forcing and nutrient supply may induce changes in the seasonal succession plankton patterns, alter the relative importance of the bottom–up and top–down control, favour prolonged cyanobacteria blooms, and ultimately lead to significant loss of the diversity of plankton communities (Horn, 2003; Elliott et al., 2006; Huber et al., 2008). Yet, empirical evidence suggests that the control exerted from nutrient loading management (e.g., re-oligotrophication signals) is much stronger and can be the main driver of the synchrony in geographically isolated plankton communities (McKee et al., 2003; Moss et al., 2003; Anneville et al., 2005; Jeppesen et al., 2005; Law et al., 2009). Thus, considering that many of the ominous ecological forecasts of climate warming are arguably controversial and still remain in the realm of speculation, we believe that concerted experimental and modeling efforts to separate the effects of climate change from the influence of other external stressors will be instrumental in impartially improving our contemporary understanding. In this context, we undertake modeling experiments that examine the changes in lake phenology induced from two climatic (present and warming) regimes on three trophic states (i.e., oligotrophic, mesotrophic, and eutrophic conditions). Our intent is not to provide deterministic predictions of future ecosystem response, but rather to illuminate to what extent structural changes in lake functioning induced from increasing nutrient enrichment can be further accentuated from climate warming. Special emphasis is placed on two particularly critical periods of the seasonal plankton variability, i.e., the spring bloom and the mid-summer plankton dynamics.

Our numerical experiments are based on the aquatic biogeochemical model presented by Arhonditsis and Brett (2005a,b). The model simulates five biogeochemical cycles, i.e., organic carbon, nitrogen, phosphorus, silica and oxygen, while its spatial structure consists of two compartments representing the lake epilimnion and hypolimnion. The phytoplankton community of the model comprises three functional groups (diatoms, green algae, and cyanobacteria) and the herbivorous zooplankton community consists of two functional groups, i.e., cladocerans and copepods. The group-specific configurations along with the rest model parameterization were based on the calibration vector presented in the Lake Washington application (see Appendix B in Arhonditsis and Brett, 2005a). Similarly, the reference conditions for our Monte Carlo analysis correspond to the average epilimnetic and hypolimnetic temperature, solar radiation, vertical diffusive mixing, and current hydraulic/nutrient loading in Lake Washington (Arhonditsis and Brett, 2005a,b; Brett et al., 2005). In the second phase of our analysis, we used structural equation modeling (SEM) to elucidate some of the key causal relationships underlying the interplay among physical environment, nutrients, and plankton community under the nutrient enrichment and climatic conditions examined (Fig. 3). A brief description of the aquatic biogeochemical model, the design of our modeling experiments, and the basic concepts of structural equation modeling (Bollen, 1989; Arhonditsis et al., 2006, 2007a,b) are provided in the Electronic Supplementary Material (ESM).

Physiological adaptation of cyanobacteria to warming temperature

Although cyanobacteria dominance is generally associated with nutrient enrichment, climate change has been hypothesized to be a potential catalyst for more frequent cyanobacteria blooms in the summer (Legnani et al., 2005; Paerl and Huisman, 2008; Johnk et al., 2008). For example, the cyanobacteria outbursts during the extreme summer heat wave (locally 5 °C higher than average) of 2003 in Europe have been interpreted as a warning signal for a potentially important causal link between global warming and cyanobacteria dominance (Beniston, 2004; Johnk et al., 2008). Cyanobacteria have higher optimal temperature for their growth relative to other algal species, which offers a competitive advantage when lakes experience elevated temperatures (e.g., Dokulil and Teubner, 2000; Johnk et al., 2008). Moreover, high water temperatures coupled with reduced wind speed and cloudiness can also increase the stability of the water column, thereby creating a favourable hydrodynamic environment (i.e., reduced vertical turbulent mixing) for buoyant cyanobacteria (Johnk et al., 2008). Thus, evidence from both empirical and modeling studies suggests that climate change is likely to increase the threats to the integrity of the phytoplankton communities of eutrophic freshwater ecosystems by promoting the occurrence of harmful cyanobacteria blooms. The relationship between climate warming and cyanobacteria abundance in oligo- and mesotrophic environments also has important management implications, but the expected system response is inherently difficult to be unequivocally predicted. That is, the combination of a warmer climate with reduced phosphorus levels entails a delicate competition balance among the typical residents of the epilimnetic phytoplankton assemblage, given that the aforementioned favourable setting for cyanobacteria dominance will be counterbalanced by their inferior phosphorus kinetics.

To gain insights into the relative importance of the major regulatory factors of the phytoplankton community composition, we conducted a preliminary sensitivity test whereby different levels of physiological adaptation of cyanobacteria to warming temperature were combined with a range of nutrient loading conditions. The unimodal response introduced by Arhonditsis and Brett (2005a) was replaced by a piecewise monotonic temperature–cyanobacterial growth relationship to entertain the competitive advantage of cyanobacteria at warmer temperatures. Then, the coefficient KT_2 that represents the control exerted on the cyanobacteria growth rates at high water temperatures (>20 °C) was varied from 0.04 to 0.20 °C^{-2}, while the temperature effects on diatoms and green algae growth were described by the same piecewise monotonic approach but the KT_2 values were set at 0.004 and 0.005, respectively (Arhonditsis and Brett, 2005a, Appendix B). Under the warming scenario (+2 °C), the influence of the KT_2 values on the simulated phytoplankton community structure was tested against a broad range of exogenous TP loading levels (50–250% of the reference conditions) that approximately correspond to 7–30 µg TP L^{-1} during the summer stratified period. Our numerical experiments highlight the ability of the exogenous loading to shape the phytoplankton community response to increased temperatures (Fig. 4). Namely, the slope of the cyanobacteria biomass–KT_2 relationship varies significantly dependent

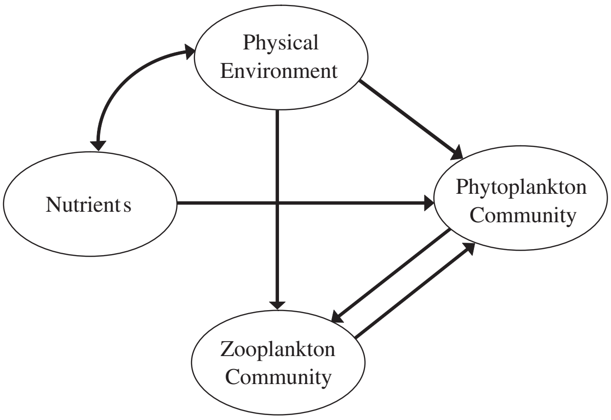

Fig. 3. Conceptual model that represents the main causal links underlying plankton dynamics in an epilimnetic environment.

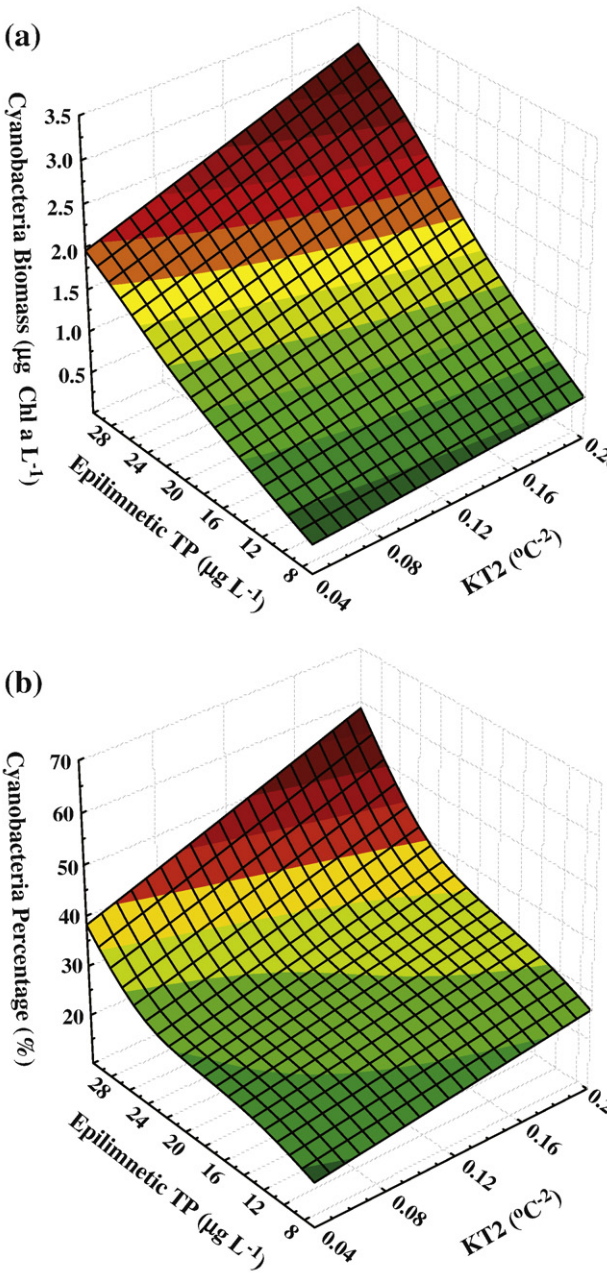

Fig. 4. Cyanobacteria biomass variability as a function of the summer epilimnetic TP concentration and the temperature effects on cyanobacteria growth (KT_2) when the reference temperature of 20 °C is exceeded.

Table 2
Average timing and chlorophyll *a* values (μg L^{-1}) associated with the spring phytoplankton bloom and the subsequent clear-water phase of the six simulated epilimnetic environments.

	Present	Warming	Advancement
Spring bloom			
Oligotrophic environment			
Julian day	125.4 ± 7.6	115.6 ± 7.1	10 days
Chlorophyll *a*	9.26 ± 1.86	8.54 ± 1.62	
Mesotrophic environment			
Julian day	124.7 ± 7.3	115.2 ± 6.8	9 days
Chlorophyll *a*	12.66 ± 1.65	11.63 ± 1.47	
Eutrophic environment			
Julian day	125.0 ± 7.4	115.1 ± 8.0	10 days
Chlorophyll *a*	19.57 ± 2.67	17.07 ± 2.39	
Clear-water phase			
Oligotrophic environment			
Julian day	170.5 ± 10.8	159.7 ± 14.6	11 days
Chlorophyll *a*	2.71 ± 0.43	2.43 ± 0.31	
Mesotrophic environment			
Julian day	161.1 ± 9.8	149.0 ± 9.5	12 days
Chlorophyll *a*	3.01 ± 0.58	2.55 ± 0.45	
Eutrophic environment			
Julian day	154.6 ± 8.3	143.8 ± 9.3	11 days
Chlorophyll *a*	2.04 ± 0.54	1.71 ± 0.43	

upon the epilimnetic TP concentrations, while the relative (percentage) cyanobacteria abundance profoundly increases at TP levels higher than their half saturation constant for phosphorus uptake assigned (>20 μg TP L^{-1}). Thus, the model predicts that the severity of the phosphorus limitation alone can potentially negate a suite of mechanisms that favour cyanobacteria dominance (i.e., increasingly higher temperature optima, buoyancy, lower light requirements and higher shading effects, lower mortality, superior nitrogen kinetics), and therefore delineates the domain where the cyanobacteria adaptability to warmer temperatures may undermine the resilience of the phytoplankton assemblages.

Warming trends, nutrient enrichment, and plankton phenology

Spring bloom and clear-water phase

Spring planktonic events seem to be particularly sensitive to climate change and their seasonal timing appears to have advanced over the past few decades (Parmesan and Yohe, 2003; Peeters et al., 2007a,b; Thackeray et al., 2008). Yet, the question arising is to what extent the effects of climate warming on the spring phytoplankton phenology are intertwined with the changes induced from nutrient enrichment? According to our numerical experiments, the spring phytoplankton bloom will advance by an average of 10 days in response to the earlier stratification onset and the thermal stability increase, regardless of the

Table 3
Summary statistics of the major limnological variables in May.

Variables		Oligotrophic environment		Mesotrophic environment		Eutrophic environment	
		Present	Warming	Present	Warming	Present	Warming
Diatoms (μg chl *a* L^{-1})	Mean	3.27	1.99	3.64	2.08	4.00	1.94
	Std. dev.	1.06	0.74	1.34	0.91	1.81	1.11
	Skewness	0.19	0.59	0.20	0.63	0.25	0.93
	Kurtosis	−1.05	−0.64	−1.09	−0.70	−1.10	−0.32
Greens (μg chl *a* L^{-1})	Mean	1.95	1.46	2.55	1.70	3.32	1.78
	Std. dev.	0.38	0.41	0.64	0.62	1.26	0.94
	Skewness	0.10	0.35	−0.25	0.40	−0.04	0.76
	Kurtosis	−0.75	−0.75	−1.00	−0.97	−1.20	−0.65
Cyanobacteria (μg chl *a* L^{-1})	Mean	1.11	1.07	2.17	1.64	4.36	2.27
	Std. dev.	0.32	0.26	0.41	0.54	1.69	1.34
	Skewness	−0.07	0.40	0.03	0.24	−0.10	0.73
	Kurtosis	−0.71	−0.55	−0.49	−0.93	−1.14	−0.72
Chlorophyll *a* (μg L^{-1})	Mean	6.34	4.51	8.35	5.41	11.68	6.00
	Std. dev.	1.42	1.30	2.27	2.05	4.73	3.38
	Skewness	0.13	0.43	−0.11	0.43	0.03	0.80
	Kurtosis	−0.79	−0.65	−1.02	−0.92	−1.18	−0.59
Copepods (μg C L^{-1})	Mean	91.9	73.0	147.4	112.3	272.9	184.2
	Std. dev.	22.1	21.7	33.2	38.1	69.2	87.4
	Skewness	0.5	0.5	0.3	0.2	−0.2	0.2
	Kurtosis	0.0	−0.4	−0.4	−1.0	−0.9	−1.3
Cladocerans (μg C L^{-1})	Mean	61.8	75.3	87.0	105.2	135.8	151.5
	Std. dev.	20.9	14.3	32.2	20.2	53.9	32.1
	Skewness	0.2	0.3	0.1	0.0	−0.1	0.0
	Kurtosis	−0.8	−0.4	−1.2	−0.6	−1.3	−0.8
PO_4 (μg L^{-1})	Mean	3.17	3.65	4.80	5.96	13.51	17.57
	Std. dev.	0.68	0.90	1.10	1.78	3.34	5.41
	Skewness	0.58	0.63	0.59	0.59	0.63	0.36
	Kurtosis	0.48	−0.03	0.13	−0.41	−0.24	−0.85
TP (μg L^{-1})	Mean	12.81	12.22	19.55	18.78	43.16	42.68
	Std. dev.	1.79	1.77	2.02	2.11	3.79	4.75
	Skewness	0.05	0.04	0.14	0.09	0.07	0.34
	Kurtosis	−0.76	−0.68	−0.59	−0.38	−0.36	−0.08
NO_3 (μg L^{-1})	Mean	228.8	222.4	161.3	160.2	39.9	55.4
	Std. dev.	20.2	19.1	17.5	18.5	16.7	29.8
	Skewness	0.0	−0.1	−0.2	−0.5	0.2	0.3
	Kurtosis	−0.8	−0.7	−0.3	0.0	−0.2	−1.0
NH_4 (μg L^{-1})	Mean	12.6	15.9	12.4	17.1	13.4	20.0
	Std. dev.	2.4	2.7	3.7	4.0	5.7	5.4
	Skewness	0.4	0.1	0.6	0.1	0.6	−0.2
	Kurtosis	−0.6	−0.8	−0.6	−1.0	−0.7	−1.0
TN (μg L^{-1})	Mean	241.4	238.2	173.7	177.4	53.3	75.4
	Std. dev.	20.0	18.9	17.2	19.9	19.7	34.1
	Skewness	0.1	−0.1	−0.2	−0.4	0.5	0.2
	Kurtosis	−0.8	−0.7	−0.4	−0.3	−0.2	−1.2

nutrient loading regime considered (Table 2). [Note that the spring bloom timing herein was determined by the day of the year when the chlorophyll *a* peak occurs.] Our model also predicts that the warmer spring weather will result in somewhat lower chlorophyll *a* maximum values due to the earlier appearance and faster zooplankton grazing rates in the system. The increased spring zooplankton activity and secondarily the earlier nutrient depletion in the mixing layer (e.g., the greater variability of clear-water phase timing in the oligotrophic environment) are also associated with the advancement of the clear-water phase by approximately 11 days under the warming scenarios (Fig. 1-ESM). [The clear-water phase timing represents the Julian day between the spring bloom and June 30, when the chlorophyll *a* minimum value occurs.] Notably, because of the present model configuration (see description in Zhao et al., 2008a,b), the epilimnetic nutrient depletion in the spring mainly refers to the nitrogen and phosphorus availability, although we acknowledge that the silica limitation can frequently modulate the diatom bloom recession (Reynolds, 2006; Thackeray et al., 2008). Interestingly, the earliest timing of the clear-water phase as well as the lower average chlorophyll *a* values were recorded in the eutrophic environment (<2 μg chl *a* L^{-1}). This—somewhat counterintuitive—pattern stems from the emergence of increased oscillatory behaviour in the system in response to the increased nutrient loading; the so-called Rosenzweig's enrichment paradox (Roy and Chattopadhyay, 2007; Zhao et al., 2008a,b). In addition, our analysis herein provides evidence that the warming conditions may accentuate the destabilizing effects on the system, thereby increasing the amplitude and the frequency of the prey–predator oscillations (Fig. 2-ESM). This finding is in complete alignment with other predictions that the effects of global warming on plankton dynamics will mimic those of nutrient enrichment (Kilham et al., 1996; Porter et al., 1996). Although Rosenzweig's concept has been severely criticized in the literature as being of merely theoretical interest (Abrams and Walters, 1996), we believe that it highlights the possibility of a climate-induced restructuring of biotic communities and/or an increasing uncertainty on the dynamics of consumer–food systems (Scheffer, 1998; Mooij et al., 2005).

The summary statistics of the major limnological variables in May, depicting the conditions that arise from the combination of the three nutrient loading regimes with the two climatic scenarios, is provided in Table 3. Generally, the total phytoplankton biomass has decreased by 30–50% from the present to the warming conditions, which probably reflects the fact that the third month of the spring consistently coincides with the recession of the phytoplankton bloom under the latter setting. The same decreasing trend characterizes the biomass levels of the three phytoplankton groups, although the "cyanobacterium-like" species appears to be the least affected functional group by the warmer spring temperatures. This pattern is primarily driven by the attributes of preferential grazing assigned to the two zooplankton groups that allow to selectively feed upon higher food quality seston (i.e., diatoms and green algae) and/or upon the most abundant food sources (Arhonditsis and Brett, 2005a). Moreover, our model predicts that the cyanobacteria can potentially dominate the end-of-spring phytoplankton community in the eutrophic environment, as a result of the higher phosphate and the lower inorganic nitrogen ambient levels that offer a competitive advantage over the other two functional groups. Under the warming scenario, the end-of-spring zooplankton community is consistently characterized by a significant cladoceran biomass increase and an approximately proportionate decrease of the copepod abundance. The latter change in the zooplankton succession patterns stems from an earlier appearance of the temperature-sensitive cladocerans, triggered by the warmer ambient conditions, which subsequently outcompete the other resident of the simulated zooplankton community due to their superior grazing kinetics. Finally, we note the somewhat higher dissolved phase nutrient concentrations (NO_3, NH_4, and PO_4) with the warming scenario, which suggests that the earlier recession of the spring phytoplankton bloom along with the stronger top–down control may allow a secondary build-up of the nutrient stock towards the end of the spring, assuming that the contemporary rates of the external nutrient supplies to the system will not quantitatively change.

Table 4 provides the fit statistics of the twelve SEMs selected to reproduce the ecological structures underlying the end-of-spring and mid-summer plankton dynamics under different weather and nutrient enrichment conditions, while the relative strengths of the different causal links considered are shown in Tables 1-ESM and 2-ESM. The best performing structural equation models in the oligotrophic environment highlight the causal association between TP and the two phytoplankton groups in May under both climatic scenarios (Figs. 5a and b). The importance of this path is plausible given that the underlying nutrient loading regime was designed to reproduce strongly phosphorus limiting conditions. It is interesting to note though that the TP-cyanobacteria (standardized) path becomes stronger as we shift from the present to the warming conditions, whereas the corresponding TP-diatom paths follow the opposite trend. This result consolidates the aforementioned evidence of increasing importance of the cyanobacterium-like species during warmer springs, when the ambient phosphorus levels primarily modulate its competitive balance relative to other phytoplankton functional groups, e.g., diatoms. Not surprisingly, the structural equation models selected to represent the mesotrophic and eutrophic environments consider the role of both phosphorous and nitrogen on phytoplankton dynamics (Figs. 5c–f). Although the paths among these models are not directly comparable because of the different nitrogen forms included (TN, DIN, and NO_3), we note that the causal links from nitrogen become relatively stronger in response to the increasing nutrient loading compared to the ones from phosphorus. Interestingly, the latter standardized paths get weaker in the warmer environments which may also be associated with the most distinctive difference between the two climatic conditions, i.e., the replacement of copepods by cladocerans to represent the role of the zooplankton community in the optimal structural equation models developed. This prediction raises the critical issue of identifying the factors that can potentially determine the responsiveness of the dominant herbivores (e.g., *Daphnia*) to the abiotic variability during the spring succession in north temperate lakes.

Table 4
SEM fit statistics for the six simulated epilimnetic environments.

Fit statistics	χ^2	*p*-value	RMR	GFI	PGFI	RMSEA	AIC
MAY							
Oligotrophic environment							
Present	3.626	0.057	0.000	0.998	0.067	0.061	31.63
Warming	0.398	0.528	0.001	1.000	0.067	0.000	28.39
Mesotrophic environment							
Present	0.391	0.532	0.000	1.000	0.048	0.000	40.39
Warming	0.020	0.888	0.000	1.000	0.048	0.000	40.02
Eutrophic environment							
Present	0.185	0.667	0.001	1.000	0.048	0.000	40.18
Warming	4.373	0.037	0.003	0.998	0.048	0.069	44.37
JULY							
Oligotrophic environment							
Present	0.044	0.834	0.000	1.000	0.048	0.000	40.04
Warming	2.906	0.088	0.001	0.998	0.067	0.052	30.91
Mesotrophic environment							
Present	0.404	0.817	0.000	1.000	0.095	0.000	38.41
Warming	0.262	0.609	0.000	1.000	0.048	0.000	40.26
Eutrophic environment							
Present	5.770	0.016	0.000	0.998	0.067	0.069	33.77
Warming	7.519	0.023	0.004	0.995	0.095	0.074	45.52

χ^2: chi-square test; RMR: Root Mean Square Residual; GFI: Goodness of Fit Index; PGFI: Parsimony Goodness of Fit Index; RMSEA: Root Mean Square Error Approximation; AIC: Akaike Information Criterion. More information on the fit statistics is provided in the Electronic Supplementary Material.

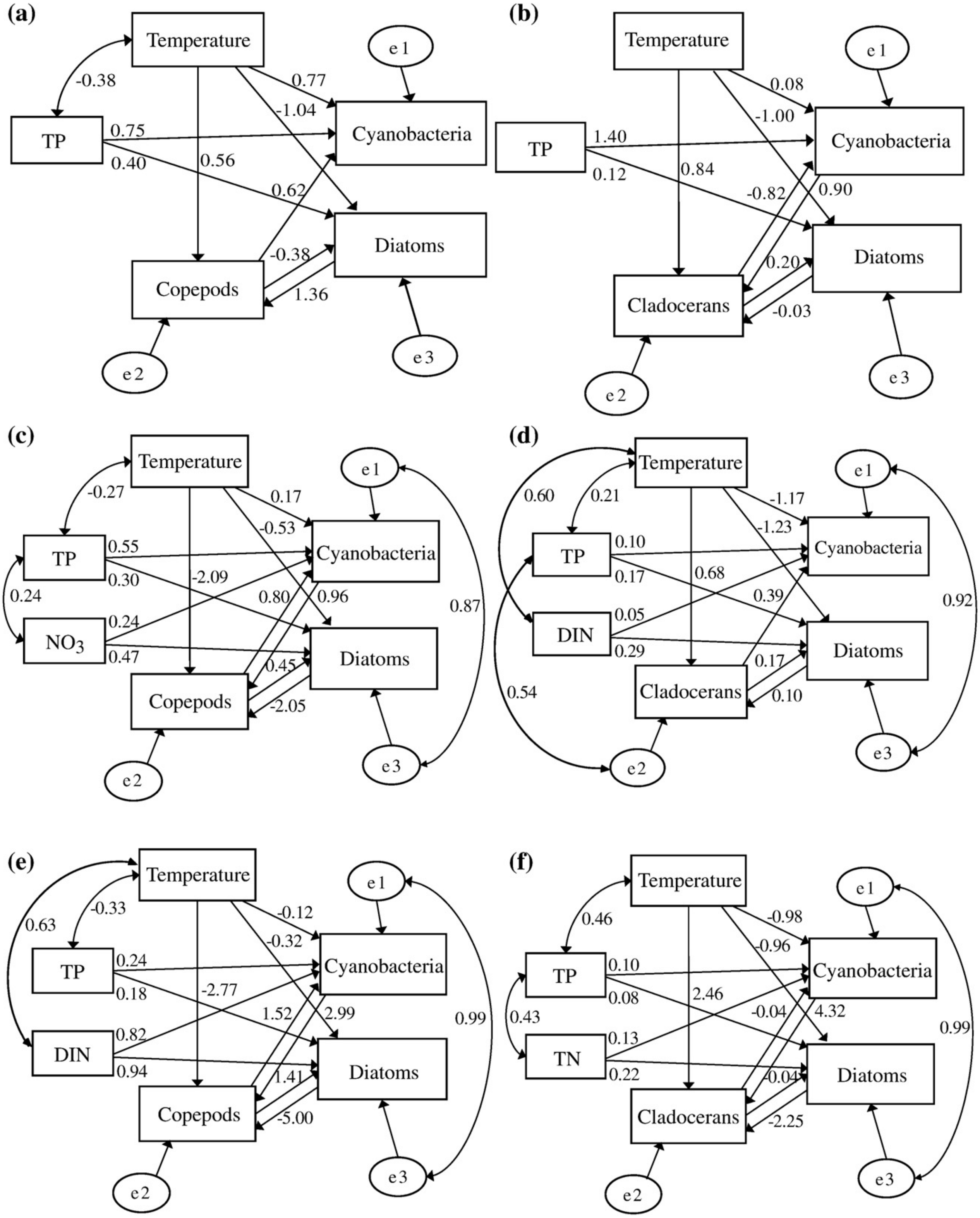

Fig. 5. Structural equation models of plankton dynamics for the month of May in the oligotrophic (a,b), mesotrophic (c,d), and eutrophic simulated environments (e,f). Left and right panels represent the current conditions and 2 °C lake temperature increase, respectively. The numbers correspond to the standardized path coefficients (i.e., the unstandardized partial regression coefficients multiplied by the ratio of the standard deviation of the explanatory variable to the standard deviation of the variable it affects).

Existing evidence suggests that the spring *Daphnia* abundance is determined by the hatching rates of diapausing eggs and/or by the fecundity rates of the overwintering populations (Sommer et al., 1986). While the population fecundity is directly related to the algal food quantity and quality as well as to the spring temperature rise, the former strategy is primarily controlled by the photoperiod (Gyllstrom, 2004; Vandekerkhove et al., 2005); although the importance of the incubation and hatching temperatures, the storage period length, and the maternal effects have also been acknowledged (Schwartz and Hebert, 1987; De Meester et al., 1998). Because of the different stimuli associated with the spring zooplankton community composition, it has been hypothesized that the potential for climate warming to induce a disparity between the photoperiod and temperature seasonal cycles is also likely to have different effects on the overwintering versus emerging population of daphnids (Domis et al., 2007). That is, the development of an overwintering population of daphnids may parallel shifts in phytoplankton phenology due to climate warming (e.g., the Lake Constance patterns presented in Straile 2000), whereas a mismatch between zooplankton and their phytoplankton prey is likely to occur when photoperiod is the dominant cue for termination of diapauses (e.g., the Lake Washington trends reported in Winder and Schindler 2004a,b). To address this question, a modeling exercise by Domis et al. (2007) examined combinations of hatching versus emerging daphnid populations, showing that climate change will not significantly alter the algal–zooplankton interactions or decouple trophic relationships in lake communities. The same study also argued that the refuge availability and the deep locations of the resting egg banks typically experienced in deep lakes should likely promote overwintering strategies, and therefore the reported absence of major overwintering inocula of daphnids in deep systems, such as the Lakes Windermere and Washington, is probably unusual (George and Taylor, 1995; Winder and Schindler, 2004a,b). Our analysis is on par with Domis et al.'s (2007) assertions in that we postulate an active overwintering inoculum of cladocerans which can potentially follow the phenological shifts of the phytoplankton populations, although we also found that the earlier timing of their spring abundance increase may not always guarantee access to the window of opportunity for the high quality food (see following discussion). Given that our experiments also predict a substantial restructuring of the end-of-spring phytoplankton community, the latter pattern pinpoints another important question regarding the nature of the phytoplankton–zooplankton interactions during the transient phase leading to the summer stratified period and their resilience to the climate warming.

Generally, our structural equation modeling analysis revealed positive (uni- or bidirectional) associations between herbivorous zooplankton and cyanobacteria under both climatic scenarios. These positive paths may reflect the competitive benefits indirectly gained from cyanobacteria through the preferential control exerted on the other two functional groups (i.e., diatoms and green algae) or via the internal subsidies of bioavailable phosphorus of the contemporary zooplankton excretion. Two notable exceptions were the bidirectional causal link between cyanobacteria and cladocerans in the oligo- and eutrophic environments (Figs. 5b and f), where the positive path from cyanobacteria to cladocerans reflects the strength of the bottom–up forcing and the negative sign of the opposite path highlights the increasing importance of the top–down control under the warming conditions; especially in the oligotrophic setting. While the generic "cyanobacteria" group can encompass a variety of K strategists and is not necessarily related to noxious algae, the prospect that daphnids may experience earlier low availability of high food quality casts doubts on the integrity of the zooplankton community structure. For example, the presence of filamentous cyanobacteria is generally associated with shifts in zooplankton size spectra (Adrian and Deneke, 1996; Dupuis and Hann, 2009). By contrast, Domis et al. (2007) argued that the likelihood of shifts in the genetic composition of populations and/or phenotypic adaptations may optimize the timing of consumers and their ability to effectively select food resources. Finally, we note the counterintuitive signs derived for some of the recursive relationships between diatoms and copepods (Figs. 5c and e) or cladocerans (Figs. 5b and f). The negative paths from diatoms to the corresponding zooplankton group probably stem from a lagged response of the predator to the prey variability, i.e., the increase of the copepod or cladoceran biomass typically coincides with the recession of the diatom spring bloom. The positive sign of the opposite ecological paths though may imply a positive feedback induced from the subsequent zooplankton recycling rates that can account for a substantial proportion of the ambient dissolved phase nutrient stock readily available for phytoplankton utilization towards the end of the spring in oligo- and mesotrophic environments. The positive copepods → diatoms path in the eutrophic environment may stem from their competition with the dominant herbivores (cladocerans) of our simulated zooplankton community that alleviate the grazing pressure exerted on diatoms.

Summer plankton dynamics

Contrary to predictions that higher temperatures will affect physiological processes and can potentially result in a larger carrying capacity of primary producers (Mooij et al., 2005), the standing phytoplankton biomass in the mid-summer (July) demonstrated a slight decrease with the warming scenarios under all nutrient enrichment conditions (Table 5). This decrease of the total phytoplankton biomass stems from a proportionate decline of the diatoms and the greens, whereas the cyanobacteria biomass remained relatively constant between present and warming conditions in the oligo- and mesotrophic environments or even increased in the eutrophic setting. The cyanobacteria tolerance primarily reflects the superior adaptive capacity to warmer temperature postulated in this exercise ($KT_2 = 0.20\ ^\circ\mathrm{C}^{-2}$). Similar to Johnk et al.'s (2008) predictions, the present analysis shows that this competitive advantage combined with a favourable bottom–up (i.e., nitrogen decrease, phosphorus increase, and reduced vertical turbulent mixing) and top–down (i.e., preferential grazing on other competing species) forcing leads to a gradual increase of their relative contribution to the total phytoplankton biomass in eutrophic systems. In our structural equation modeling analysis, the stronger paths of the recursive relationship between diatoms and cladocerans (relative to the ones with cyanobacteria) emphasize the beneficial role of the high food quality algae for the dominant herbivores, especially when the mesotrophic and eutrophic epilimnetic environments become warmer (Figs. 6d and f), which in turn through their grazing pressure on the phytoplankton community can pave the way for cyanobacteria increase and ultimately dominance.

Interestingly, the structural equation models selected to represent the oligotrophic and eutrophic states under the warming scenario have the following features: (*i*) cyanobacteria is the only phytoplankton functional group considered in the oligotrophic SEM, with a particularly strong causal connection with TP (Fig. 6b); and (*ii*) both the inorganic nitrogen forms are used to depict the influence of nutrients on phytoplankton dynamics in the eutrophic environment, where the NO_3 → diatoms path is also quite strong (Fig. 6f). That is, the relationship between the potentially limiting nutrient in a given trophic state and the phytoplankton functional groups possessing inferior kinetics for that nutrient becomes stronger in warmer summers. These results probably stem from the increased species-specific growth rates (associated with the higher temperatures) that consequently increase their intrinsic responsiveness to the availability of the limiting nutrients, i.e., a pattern implying that the climate warming can possibly act as a limit-cycle amplifier (Scheffer et al., 2003).

We also highlight the consistent decrease of the abundance of the two zooplankton functional groups across all the experiments, driven by the assumption that the warmer climate induces a shift to suboptimal levels for their growth (Table 5). The zooplankton response to thermal stress and its adaptive capacity to a warmer environment have recently received considerable attention (Mitchell et al., 2004; Masclaux et al., 2009), but little has been done to elucidate the impact of a reduced zooplankton growth on the ecosystem functioning. Our analysis suggests that the decline of the summer zooplankton biomass driven by unfavourably high temperatures and the consequent decrease of the nutrient subsidies from the zooplankton metabolism may negate the anticipated increase in lake productivity due to enhanced nutrient mineralization (Blenckner et al., 2002). Evidence of the latter hypothesis is the relatively constant ambient nutrient levels between the two climatic scenarios (Table 5). Generally, the total amount and the relative importance of the phosphorus recycled depend on the trophic status of

Table 5
Summary statistics of the major limnological variables in July.

Variables		Oligotrophic environment		Mesotrophic environment		Eutrophic environment	
		Present	Warming	Present	Warming	Present	Warming
Diatoms (μg chl a L^{-1})	Mean	1.09	1.01	1.43	1.26	1.19	0.97
	Std. dev.	0.11	0.10	0.12	0.12	0.28	0.12
	Skewness	−0.01	0.06	0.27	0.21	0.73	0.27
	Kurtosis	−0.67	−0.77	−0.49	−0.88	−0.73	0.72
Greens (μg chl a L^{-1})	Mean	0.81	0.74	1.13	1.01	1.47	1.30
	Std. dev.	0.10	0.09	0.10	0.09	0.27	0.13
	Skewness	0.01	−0.03	0.41	0.49	0.46	0.43
	Kurtosis	−0.63	−0.79	−0.48	−0.30	−0.86	−0.56
Cyanobacteria (μg chl a L^{-1})	Mean	0.64	0.65	1.01	1.00	1.74	2.02
	Std. dev.	0.12	0.13	0.12	0.13	0.34	0.55
	Skewness	0.08	0.19	0.38	0.32	1.23	0.66
	Kurtosis	−0.43	−0.49	−0.02	−0.21	1.05	−0.87
Chlorophyll a (μg L^{-1})	Mean	2.53	2.39	3.56	3.26	4.39	4.29
	Std. dev.	0.33	0.28	0.31	0.20	0.81	0.50
	Skewness	0.00	−0.13	0.56	0.53	1.01	0.42
	Kurtosis	−0.63	−0.90	−0.27	0.23	−0.18	−0.82
Copepods (μg C L^{-1})	Mean	21.8	14.9	33.9	24.8	46.4	33.5
	Std. dev.	7.6	3.9	9.8	4.4	14.0	7.6
	Skewness	0.9	0.4	1.0	0.5	1.1	0.8
	Kurtosis	0.5	−0.2	0.5	−0.2	0.5	−0.3
Cladocerans (μg C L^{-1})	Mean	35.8	33.6	54.8	54.5	102.8	95.7
	Std. dev.	5.4	5.2	7.9	6.7	18.7	10.8
	Skewness	0.3	0.05	0.7	0.6	0.3	0.7
	Kurtosis	−0.1	−0.6	0.6	0.1	−0.1	0.4
PO_4 (μg L^{-1})	Mean	2.79	3.06	3.70	4.16	11.09	12.28
	Std. dev.	0.38	0.32	0.51	0.60	1.81	1.99
	Skewness	−0.01	0.26	0.02	0.77	0.16	0.15
	Kurtosis	−0.60	−0.16	−0.43	0.23	−0.65	−0.39
TP (μg L^{-1})	Mean	8.18	8.65	12.38	13.25	30.99	33.57
	Std. dev.	1.21	1.31	1.41	1.85	3.21	4.95
	Skewness	0.22	0.28	0.26	0.53	0.24	0.36
	Kurtosis	−0.36	−0.38	−0.31	−0.08	−0.49	−0.50
NO_3 (μg L^{-1})	Mean	192.8	189.2	109.6	105.2	4.6	5.7
	Std. dev.	22.2	22.82	17.8	16.9	3.2	4.0
	Skewness	0.13	0.10	0.0	0.1	0.8	0.6
	Kurtosis	−1.09	−1.09	−0.9	−1.0	0.4	−0.2
NH_4 (μg L^{-1})	Mean	13.96	14.43	12.0	13.4	14.3	14.9
	Std. dev.	0.99	0.84	1.0	1.2	2.6	1.8
	Skewness	0.48	0.25	0.4	0.1	0.1	0.8
	Kurtosis	−0.35	−0.43	−0.3	−1.1	0.0	0.5
TN (μg L^{-1})	Mean	363.1	363.3	306.0	308.0	213.5	225.0
	Std. dev.	14.9	14.6	13.5	13.1	9.1	18.1
	Skewness	0.08	0.05	−0.2	−0.3	0.6	0.4
	Kurtosis	−1.05	−1.06	−0.6	−0.6	−0.3	−1.0

the lake, the water temperature as well as on the abundance and composition of the zooplankton community, with the smallest organisms being associated with higher rates of phosphorus excretion per unit of biomass (Gulati et al., 1989; Teubner et al., 2003; Ejsmont-Karabin et al., 2004; Kowalezewska-Madura et al., 2007). Thus, given the uncertainty associated with the competition patterns among coexisting zooplankton species under changing environmental conditions (Johnson and Havel, 2001), we hypothesize that the year-to-year variability of the zooplankton community composition and the succession patterns among groups with higher (rotifers) or lower (cladocerans, copepods) phosphorus excretion rates may become an important regulatory factor in phosphorus-depleted epilimnetic environments (Law et al., 2009).

Synthesis–future perspectives

Thermal structure

In his 2008 review paper, D.M. Livingstone argued that “the old, stationary lake typology of Hutchinson (1975) may be one of the first real limnological casualties of climate change”. Indeed, more than anything else, our analysis shows that the primary response to external meteorological forcing has been the increase in overall lake and (especially) epilimnetic temperatures, the increase in thermal stability, the lengthening of stratification period and/or shortening of the ice cover period of several well-studied north temperate deep lakes (Table 1). Thus, if the contemporary warming trends persist, it is not unreasonable to expect that strictly dimictic deep lakes will more frequently behave as ice-free monomictic systems or that monomictic lakes are likely to switch to meromictic hydrodynamic regimes due to the increasing suppression of deeply penetrative mixing during mild winters. Moreover, the realisation that lakes as physical systems demonstrate a remarkable spatial coherence while undergoing these changes may also invite a gradual shift in the focus of future lake physics research (Livingstone, 2008). Namely, rather than overemphasizing the importance of retrospective analysis based on data series from individual systems, the emerging paradigm of spatial interconnectedness and temporal change suggests that more weight should be placed in improving our understanding of the small-scale aspects of lake mixing and consequently in describing the complex interactions among the mechanisms that most likely modulate the shifts in lake mixing regimes (Goudsmit et al., 1997; Fer et al., 2002; Wuest and Lorke, 2003). Yet, while the change in the physical behaviour of the deep lakes is indisputable, the climate-induced alterations in their chemical and biological properties are still less clear and quite often incongruous.

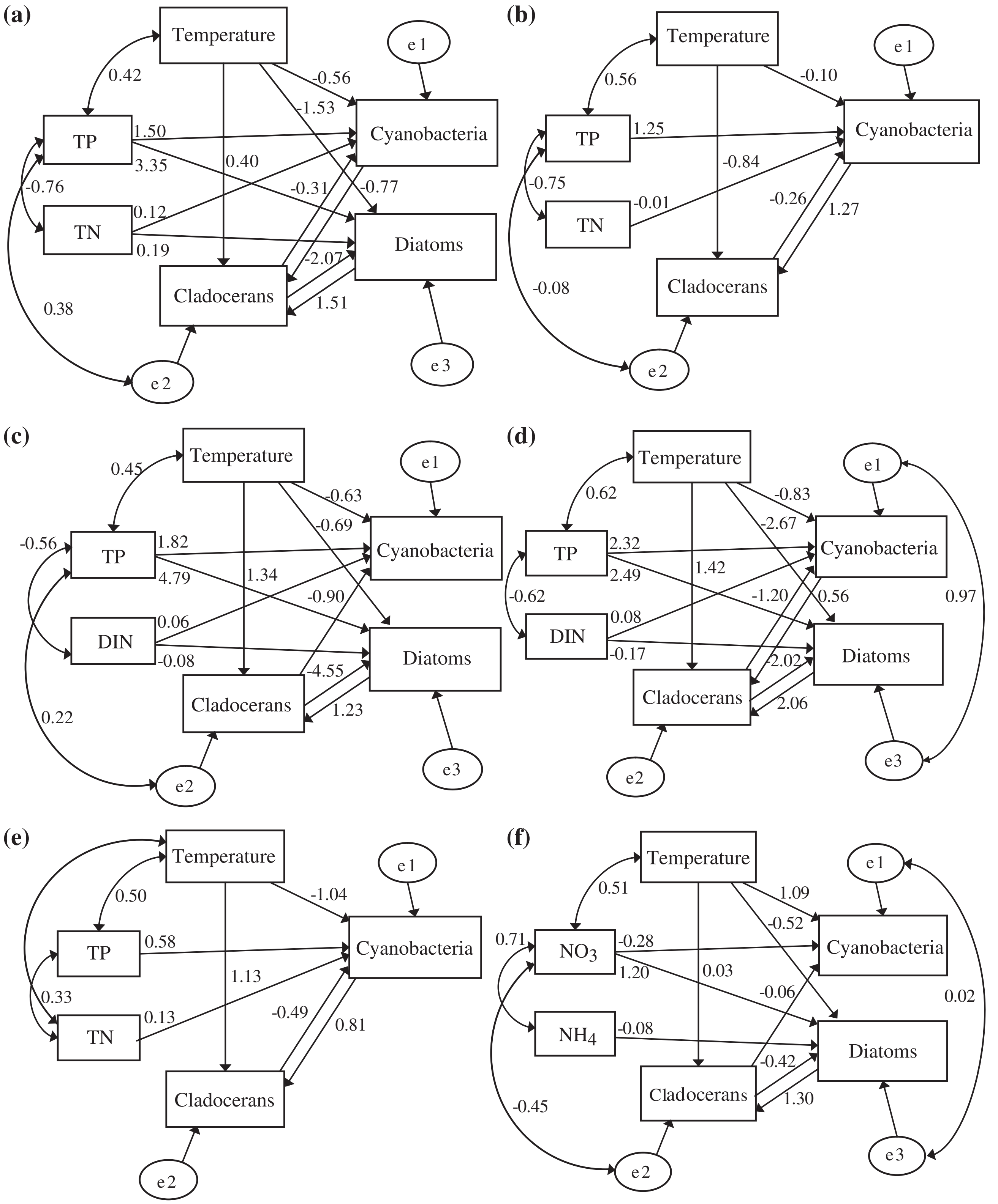

Fig. 6. Structural equation models of plankton dynamics for the month of July in the oligotrophic (a,b), mesotrophic (c,d), and eutrophic simulated environments (e,f). Left and right panels represent the current conditions and 2 °C lake temperature increase, respectively.

Spring plankton dynamics

Both empirical evidence and model predictions show that the advancement of the spring phytoplankton bloom timing is an established pattern in north temperate deep water bodies regardless of their trophic status (Winder and Schindler, 2004a; Arhonditsis et al., 2004b; Peeters et al., 2007a,b). Whether responding to the earlier stratification onset or to a relaxation of turbulent vertical mixing independently of the upper water-column depth, the spring phytoplankton bloom has advanced by an average of 1–2 weeks (Table 3). Although the initiation and the temporal evolution of the phytoplankton biomass are primarily determined by the physical forcing for most of the spring (Peeters et al., 2007a,b), our analysis also suggests that the warmer vernal weather may result in lower chlorophyll *a* maximum values due to an earlier appearance and faster zooplankton grazing rates. Generally, our model predictions appear on par with empirical evidence that the causal link between spring zooplankton activity (especially daphnid biomass) and meteorological forcing is closely related to the spatiotemporal patterns of the clear-water phase (Gaedke, 1998; Straile, 2002). Yet, we underscore Tirok and Gaedke's (2006) finding that the clear-water phase in large and deep water bodies, where mixing-sensitive phytoplankton and small zooplankton growth may be temporarily disconnected from temperature-sensitive growth of crustaceans, can occur either by a daphnid-dominated zooplankton community or by a diverse assemblage consisting of ciliates, rotifers or other micro- and meso-zooplankton. In the latter case, the wind-dependent intensity of deep vertical mixing, and not the water temperature, becomes a good predictor of the clear-water phase timing (Tirok and Gaedke, 2006). Finally, as warming progresses, it is expected that the earlier epilimnetic nutrient depletion (e.g., the end-of-spring phosphorus or silica availability) will become an increasingly important driver of the phytoplankton community dynamics and the clear-water phase timing in north temperate deep lakes; especially in systems where nutrient loading reductions reinforce oligotrophication (Huppert et al., 2002; Winder and Schindler, 2004b; Thackeray et al., 2008).

Climate change has brought about asynchronies in biotic communities that are likely to result in a phenological decoupling of trophic relationships (Stenseth and Mysterud, 2002). Spatiotemporal mismatches of trophic interactions typically stem from the sensitivity differences in the phenology of a predator and its preys to the physical forcing changes. Given the critical role of daphnids within the aquatic food webs, the factors that determine their timing and biomass levels in the spring have recently received considerable attention (Domis et al., 2007). The severity of the problem was illustrated in the case of Lake Washington (Winder and Schindler, 2004a,b), where a long-term decline in daphnid populations was associated with a growing temporal mismatch with the spring diatom bloom, and this undesirable shift to their diet has been hypothesized to have dire ramifications on food-web interactions. Domis et al. (2007) though surmised that the refuge availability and the unfavourable locations of the resting egg banks typically characterizing the deep lakes may promote overwintering daphnid strategies with a flexibility to track shifts in phytoplankton phenology due to climate warming and therefore to minimize trophic discontinuities. The same study also predicted that climate change will not significantly alter the algal–zooplankton interactions unless daphnids depend on hatching from very small inocula of ephippia. Another reassuring prospect about the integrity of the food-web interactions is the likelihood of phenotypic adaptations and/or genetic modifications of populations, which in turn may optimize the timing of consumers and their ability to effectively access good quality food (Domis et al., 2007). Yet, the patterns reported in Lakes Windermere and Washington indicate that the predominance of emerging daphnid populations from diapausing eggs in large and deep lakes should not be ruled out (George and Taylor, 1995; Winder and Schindler, 2004a,b). Thus, because the relationship between lake morphology and daphnid strategies to escape adverse ambient conditions is not straightforward, we believe that the objective assessment of their reliability as a food source for fish populations invites a shift in the focus on elucidating the long-term interspecific phenological differences (Hampton et al., 2006a).

Summer phytoplankton communities

Several of the deep lakes reviewed (Lake Washington, Lake Constance, Lake Geneva, and Lake Zurich) have undergone changes that are primarily associated with the substantial reduction of the external nutrient loading during the last 20–30 years (Jeppesen et al., 2005). Despite the inherently difficult task to parcel out the effects of climate change from the influence of external nutrient loading, there is evidence that the structural changes in lake functioning induced from the nutrient enrichment variability can be modulated by climate warming. Generally, the re-oligotrophication signals in deep lakes include the decrease of annual and summer TP concentrations, decrease of the summer PO_4:TP ratios, lower chlorophyll *a* concentrations, increased water clarity, and cyanobacteria biomass decline (Jeppesen et al., 2005, see their Table 5). Building upon these conditions, the climate-induced intensification of lake stratification can presumably magnify the severity of nutrient limitation, thereby promoting changes in the summer phytoplankton community composition in oligo- and mesotrophic epilimnetic habitats (Anneville et al., 2005; Law et al., 2009). Such resource-limited environments are typically dominated by CS strategists, i.e., stress-tolerant species that can survive at low nutrient levels while growing faster than S species (Elliott et al., 2000). This assemblage usually includes species capable of mixotrophy and motility (or increased resistance to sinking associated with their irregular shapes) that allows them to retain in the euphotic zone and to exploit favourable microenvironments of nutrients (Reynolds, 2006). In more eutrophic deep systems though, a somewhat different response has been the transition to summer phytoplankton communities dominated by disturbance-tolerant R strategists (Anneville et al., 2005). This supposedly paradoxical response appears to be related to the gradual deepening and the longer duration of the nutrient-depleted upper zone vis-à-vis the relatively nutrient-rich deeper layers. Namely, this setting offers opportunities for hypolimnetic intrusions that intermittently provide nutrient pulses in the metalimnion, whereby nutrient-deprived species with appropriate adaptations to low light intensity (e.g., light-harvesting antennae) and increased cell-specific photosynthetic capacity are able to gain advantage (Anneville et al., 2002b). Finally, given that the prolonged lake stratification may also increase the dependence on nutrient regeneration mechanisms, another interesting research question is how an epilimnetic environment subject to rapid nutrient turnover rates and to periodic partial mixing due to episodic meteorological events can shape the interspecific plankton competition patterns and ultimately the configuration of food-web dynamics (Capblancq, 1990; Jorgensen and Padisak, 1996; Teubner et al., 2003; Becker et al., 2008).

Cyanobacteria dominance

Warmer water temperatures coupled with favourable hydrodynamic conditions will increase the likelihood of cyanobacteria dominance in nutrient enriched freshwater ecosystems (Johnk et al., 2008). Our modeling analysis also shows that the relative contribution of cyanobacteria to the total phytoplankton biomass can potentially increase by the end-of-spring in the eutrophic epilimnetic environments, but this pattern does not differ significantly between present and warm conditions. However, Shatwell et al. (2008) provided evidence that the lagged response between phytoplankton and cladoceran abundance peaks, a mechanism that is not faithfully captured by our model, offers a window of opportunity for filamentous cyanobacteria to establish dominance after the diatoms in warm springs. Importantly, our model predicts that the strength of the phosphorus limitation alone can delineate the domain where the cyanobacteria adaptability to warmer temperatures may undermine the stability domain of phytoplankton assemblages. In this regard, recent theoretical work has revealed critical indicators (autocorrelation coefficients, variance, skewness, and kurtosis) that can potentially serve as warning signs to forthcoming transitions in the phytoplankton community (Carpenter et al., 2009).

System resilience and catastrophic shifts

Climate change impact to lake dynamics should also be viewed under the prism of a lurking threat for the system resilience that can ultimately lead to catastrophic shifts to undesirable states (Scheffer et al., 2001b). In addition, the increasing frequency of extreme meteorological events (e.g., hurricanes) associated with climate change may also provide the perturbations needed to bring the systems into the basin of attraction of alternative states (McCook, 1999; Wagner and Adrian, 2009). Because of the costly interventions required to restore desired ecosystem states and the substantial loss of ecological or economic resources that such state shifts entail, recent research efforts have focused on the identification of early-warning signals of approaching massive changes (Scheffer et al., 2009). In the context of lake eutrophication, the increased variance in the pattern of fluctuations has been proposed as an early-warning signal of impending shifts to eutrophic conditions, stemming from the limited capacity of the systems to equilibrate after external perturbations, when we move closer to a regime shift (Carpenter and Brock, 2006). Likewise, the predictions that the impact of global warming on plankton dynamics can mimic the effects of nutrient enrichment imply that these destabilization patterns may also be manifested (or even be amplified) in a warmer climate (Fig. 2-ESM). That is, the projected higher growth rates are likely to increase the nonlinearity in trophic interactions and therefore to drive populations faster to threshold crossings (Anderson et al, 2008). While this ominous prospect may not hold true in the near future of large water bodies, we believe that our study renders support to Scheffer et al.'s (2001b) assertions that an emerging imperative in the management of lake ecosystems is to maintain the resilience of desired states by focusing on factors (e.g., nutrient loading) that can actually be controlled and, most importantly, appear to be particularly influential on their stability domain. Considering that the transfer of mass overrides the energetic regulation of most of the lake processes (Doscher et al., 2009), we argue that the level of anthropogenic disturbances on lake mass balance is the key covariate in predicting the climate warming effects.

Future perspectives

We conclude by emphasizing the importance of two complementary directions of future research: first, the need to elucidate the wide array of in-lake processes that are likely to be affected by climate change; and, second, the need to examine the heterogeneity in responses among different water bodies. The rationale of this approach and its significance for dealing with the uncertainty that the climate signals cascade through lake ecosystems and shape abiotic variability and/or biotic responses have been recently advocated by several other review papers (Schindler, 2009; Adrian et al., 2009). Lakes have a strong potential as sentinels of climate change, because they have a number of variables with response times that allow them to reflect the rapid and (quite often) non-linear rates of current changes in climate (Wagner and Adrian, 2009; Adrian et al., 2009). Yet, not all indicator variables can be used broadly across all lakes; there are certain indicators that are particularly suitable for different lake types and geographical regions.

Finally, regarding the former direction of research, we caution that much of our contemporary understanding has been based on empirical evidence from offshore areas, while the interactions with the nearshore zones have largely been neglected. In many large lakes, the most degraded areas are nearshore zones above the summer thermocline adjacent to the mouths of large rivers and enclosed embayments with restricted mixing with offshore water. These areas are intermediate zones in that they can receive polluted inland waters from watersheds with significant agricultural, urban and/or industrial activities while mixing with offshore waters having different biological and chemical characteristics (Kalff, 2002). Climate-induced shifts in air temperature, rainfall and wind forcing can potentially influence lake mixing and currents, because they determine both the rate and magnitude of warming/cooling and the magnitude and frequency of runoff. Runoff also affects water level which in turn strongly drives nearshore dynamics. Winds produce coastal upwelling events forcing deeper, cooler water often with different water quality, up to depths where they can interact with shallow water intakes. Surface waves can resuspend bottom sediments in the shallow zones of large lakes, and as sediments tend to be repositories of both nutrients and contaminants, resuspension events are highly important in predicting water quality. The interaction of surface hydrological patterns with in-lake hydrodynamics thus dictates to a large degree the in-lake dispersal of pollutants and consequently the spatial extent and magnitude of associated ecological impacts that incoming inflows are likely to have. We believe that the classical two dimensional conceptualization (time and depth in an offshore site) has been sufficient to bring us here, but any further advancements of our understanding of the climate-induced changes on lake phenology should be based on more integrative frameworks that consider as one of the focal points the interplay among watershed, nearshore and offshore lake areas.

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Appendix A. Supplementary data

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OUR CURRENT UNDERSTANDING OF LAKE ECOSYSTEM RESPONSE TO CLIMATE CHANGE: WHAT HAVE WE REALLY LEARNED FROM THE NORTH TEMPERATE DEEP LAKES?

(Electronic Supplementary Material)

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Methodology

1. Aquatic biogeochemical model

Our numerical experiments are based on the aquatic biogeochemical model presented by Arhonditsis and Brett (2005a; b). Its spatial structure consists of two compartments representing the lake epilimnion and hypolimnion. The model simulates five biogeochemical cycles, i.e., organic carbon, nitrogen, phosphorus, silica and oxygen. The particulate phase of the elements is represented from the state variables particulate organic carbon, particulate organic nitrogen, particulate organic phosphorus, and particulate silica. The dissolved phase fractions comprise the dissolved organic (carbon, nitrogen, and phosphorus) and inorganic (nitrate, ammonium, phosphate, silica, and oxygen) forms involved in the five elemental cycles. The major sources and sinks of the particulate forms include plankton basal metabolism, egestion of excess particulate matter during zooplankton feeding, settling to hypolimnion or sediment, bacterial-mediated dissolution, external loading, and loss with outflow. Similar processes determine the levels of the dissolved organic and inorganic forms along with the bacterial mineralization and the vertical diffusive transport. The model also explicitly simulates denitrification, nitrification, heterotrophic respiration, and the water column–sediment exchanges. The external forcing encompasses river inflows, precipitation, evaporation, solar radiation, water temperature, and nutrient loading.

The phytoplankton community of the model comprises three functional groups (diatoms, green algae, and cyanobacteria) that differ with regards to their strategies for resource competition (nitrogen, phosphorus, light, temperature) and metabolic rates as well as their morphological features (settling velocity, shading effects). Diatoms are modelled as r-selected organisms with high maximum growth rates and higher metabolic losses, superior phosphorus and inferior nitrogen kinetics, lower tolerance to low light availability, low temperature optima, silica requirements, high sinking velocities, and high food quality preferably grazed from herbivorous zooplankton (Zhao et al., 2008a). By contrast, cyanobacteria are modelled as K-strategists with low maximum growth and metabolic rates, inferior phosphorus and superior nitrogen kinetics, higher tolerance to low light availability, low settling velocities, high temperature optima, higher shading effects (i.e., filamentous cyanobacteria), and inferior food quality for zooplankton (Zhao et al., 2008a). The parameterization of the third functional group (labelled as ‘‘Green

Algae'') aimed to provide an intermediate competitor that more realistically depicts the continuum between diatom- and cyanobacteria dominated communities in our numerical experiments.

The herbivorous zooplankton community consists of two functional groups, i.e., cladocerans and copepods, and their biomass is controlled by growth, basal metabolism, higher predation, and outflow losses. Copepods are parameterized as having a wider temperature tolerance relative to cladocerans. We also consider copepods to have higher feeding rates at low food abundance, whereas cladocerans become feeding saturated at higher food concentrations and consequently have a competitive advantage at greater food levels (Zhao et al., 2008b). Cladocerans are filter-feeders with an equal preference between the four food-types (diatoms, green algae, cyanobacteria and detritus), whereas copepods are assumed to be capable of selecting on the basis of food quality (Arhonditsis and Brett, 2005a). Copepods have slightly higher nitrogen and much lower phosphorus content relative to cladocerans. These differences drive their succession patterns along with their interactions with the phytoplankton community.

2. Monte Carlo analysis

We consider a hypothetical large lake with morphological characteristics, average epilimnetic and hypolimnetic temperature, solar radiation, vertical diffusive mixing, hydraulic and nutrient loading that correspond to those of Lake Washington (Arhonditsis and Brett, 2005a, b; Brett et al., 2005). Specifically, the lake volume is 2.9 km^3, the surface area is 87.6 km^2, and the mean depth is 33 m. The hydraulic renewal rate in our hypothetical system is 0.384 yr^{-1}, the fluvial and atmospheric total nitrogen inputs are 1114×10^3 kg yr^{-1}, and nitrate and ammonium loading supplies are 561 and 34×10^3 kg yr^{-1}, respectively. The exogenous total phosphorus loading contributes approximately 74.9×10^3 kg yr^{-1}, while 23.9 and 17.3 $\times 10^3$ kg yr^{-1} are entering the system as dissolved phosphorus and phosphate. In our analysis, the average input phosphorus concentrations for the oligo-, meso-, and eutrophic environments correspond to 50 (32.5 μg *TP* L^{-1}), 100 (65 μg *TP* L^{-1}), and 250% (162.5 μg *TP* L^{-1}) of the reference conditions, respectively. The present average epilimnetic (14 ^oC) and hypolimnetic (10 ^oC) temperatures were increased approximately by 2^oC for epilimnion and 1^oC for hypolimnion under the warming scenarios. To accommodate the interannual variability in the system, we introduced perturbations of the reference conditions uniformly sampled from the ±20% range for nutrient loading, water temperature, and the stratification onset, whereas the vertical diffusion varied within a ±5% range of the present levels. In our analysis, the climate warming was assumed to advance the timing of the stratification onset by an average of two weeks relative to the present conditions, while the diffusion mixing and stratification timing were negatively correlated with temperature response based on observed patterns from Lakes Washington and Tahoe (Winder and Schindler, 2004b; Coats et al., 2006). Following this scheme, we generated 3000 input vectors for each of the six trophic state-temperature regime combinations. Finally, all the external forcing functions were also assigned random daily noise to account for the day-to-day variability.

3. Structural equation modeling

In the second phase of our analysis, we used structural equation modeling (*SEM*) to elucidate the key causal relationships underlying the interplay among physical environment, nutrients, and plankton community under the nutrient enrichment and climatic conditions examined. *SEM* is a multivariate statistical method that encompasses both factor and path analysis, which allows to decompose multiple causal pathways and to quantify direct and indirect relationships among variables (Bollen, 1989; McCune et al., 2002; Arhonditsis et al., 2006; Kenney et al., 2009). Another advantage of *SEM* is that it can explicitly incorporate uncertainty due to measurement error and/or accommodate the discrepancy between conceptual ecosystem properties and observed variables that can be actually measured in the real world (Malaeb et al., 2000). *SEM* is also an *a priori* statistical method whereby a hypothetical structure of the system studied, reflecting the best knowledge available, is tested against the observed covariance structure (Arhonditsis et al., 2006; Kenney et al., 2009). Unlike other statistical methods, *SEM* is used to accept the hypothesized model by minimizing the residuals between the observed and model covariance matrices (McCune et al., 2002).

In this study, we tested datasets obtained through our Monte Carlo Analysis to examine the significant causal relationships between climate warming and lake phenology within our hypothetical system. The surrogate variables examined to reproduce the physical epilimnetic environment were the water temperature and vertical diffusivity, whereas all the dissolved phase (PO_4, NO_3 NH_4 and *DIN*) or total nitrogen and phosphorus forms were tested for their ability to account for the role of nutrients on phytoplankton dynamics. Being the two extremes of the simulated phytoplankton community, diatoms and cyanobacteria were also explicitly considered to assess how the interplay between climate and nutrient loading shapes the competition patterns in the epilimnetic environment. The trophic interactions between phytoplankton community and herbivorous zooplankton were assumed to have a recursive nature, i.e., bottom-up and top-down forces. The chi-square (χ^2) test was primarily used to examine the model fit; when the minimum χ^2 value was achieved (i.e., a probability level supporting acceptance of the model structure), the model was evaluated for fit and parsimony with multiple test statistics. The model assessment started with the Akaike Information Criterion (*AIC*) that evaluates model performance while accounting for model complexity. Amongst different structures of relatively similar performance, we chose the most parsimonious model with the lowest *AIC*; that is, the model that optimally balances between performance and complexity. A total of six test statistics were used to evaluate the models, such as the Root Mean Square Residual (*RMR*), the Goodness of Fit Index (*GFI*), the Root Mean Square Error Approximation (*RMSEA*), and the Parsimony Goodness of Fit Index (*PGFI*) (Bollen, 1989). *RMR* is the square root of the average squared amount by which the sample variances and covariances differ from their estimates obtained under the assumption that the model is correct. A *RMR* of zero indicates a perfect fit. There are analogies between the r^2 and *GFI*; the former is interpreted as the percent of variability explained by the model, whereas the latter reflects the proportion of observed covariances explained by the covariances implied by the model. *GFI* values should be approximately equal to or greater than 0.90 to accept the model. *RMSEA* incorporates model complexity by taking the square root of the ratio of the population discrepancy function with the number of degrees of freedom. *RMSEA* of about 0.05 or less would suggest a close model fit. *PGFI* is a modification of the *GFI* that takes into account the degrees of freedom and *PGFI* values close to 1 indicate good model fit.

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Table 1-ESM. SEM path coefficients and relative strengths in May

Scenarios	***Generic Path***			***SEM Path***			***Relative strength***[a]
Oligotrophic Environment							
Present	Physical	→	Phytoplankton	Temperature	→	Diatoms	⇩
	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇧
	Physical	→	Zooplankton	Temperature	→	Copepods	⇧
	Nutrients	→	Phytoplankton	TP	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Zooplankton	→	Phytoplankton	Copepods	→	Diatoms	⇩
	Zooplankton	→	Phytoplankton	Copepods	→	Cyanobacteria	⇧
	Phytoplankton	→	Zooplankton	Diatoms	→	Copepods	⇧
Warming	Physical	→	Phytoplankton	Temperature	→	Diatoms	⇩
	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇧
	Physical	→	Zooplankton	Temperature	→	Cladocerans	⇧
	Nutrients	→	Phytoplankton	TP	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Zooplankton	→	Phytoplankton	Cladocerans	→	Diatoms	⇧
	Zooplankton	→	Phytoplankton	Cladocerans	→	Cyanobacteria	⇩
	Phytoplankton	→	Zooplankton	Diatoms	→	Cladocerans	⇩
	Phytoplankton	→	Zooplankton	Cyanobacteria	→	Cladocerans	⇧
Mesotrophic Environment							
Present	Physical	→	Phytoplankton	Temperature	→	Diatoms	⇩
	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇧
	Physical	→	Zooplankton	Temperature	→	Copepods	⇩
	Nutrients	→	Phytoplankton	TP	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Nutrients	→	Phytoplankton	NO_3	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	NO_3	→	Cyanobacteria	⇧
	Zooplankton	→	Phytoplankton	Copepods	→	Diatoms	⇧
	Zooplankton	→	Phytoplankton	Copepods	→	Cyanobacteria	⇧
	Phytoplankton	→	Zooplankton	Diatoms	→	Copepods	⇩
	Phytoplankton	→	Zooplankton	Cyanobacteria	→	Copepods	⇧
Warming	Physical		Phytoplankton	Temperature	→	Diatoms	⇩
	Physical		Phytoplankton	Temperature	→	Cyanobacteria	⇩
	Physical		Zooplankton	Temperature	→	Cladocerans	⇧
	Nutrients		Phytoplankton	TP	→	Diatoms	⇧
	Nutrients		Phytoplankton	DIN	→	Diatoms	⇧
	Nutrients		Phytoplankton	TP	→	Cyanobacteria	⇧

	Nutrients		Phytoplankton	DIN	→	Cyanobacteria	⇧
	Zooplankton		Phytoplankton	Cladocerans	→	Diatoms	⇧
	Zooplankton		Phytoplankton	Cladocerans	→	Cyanobacteria	⬆
	Phytoplankton		Zooplankton	Diatoms	→	Cladocerans	⇧
Eutrophic Environment							
Present	Physical	→	Phytoplankton	Temperature	→	Diatoms	⬇
	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇩
	Physical	→	Zooplankton	Temperature	→	Copepods	⬇
	Nutrients	→	Phytoplankton	TP	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Nutrients	→	Phytoplankton	DIN	→	Diatoms	⬆
	Nutrients	→	Phytoplankton	DIN	→	Cyanobacteria	⬆
	Zooplankton	→	Phytoplankton	Copepods	→	Diatoms	⬆
	Zooplankton	→	Phytoplankton	Copepods	→	Cyanobacteria	⬆
	Phytoplankton	→	Zooplankton	Diatoms	→	Copepods	⬇
	Phytoplankton	→	Zooplankton	Cyanobacteria	→	Copepods	⬆
Warming	Physical	→	Phytoplankton	Temperature	→	Diatoms	⬇
	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⬇
	Physical	→	Zooplankton	Temperature	→	Cladocerans	⬆
	Nutrients	→	Phytoplankton	TP	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Nutrients	→	Phytoplankton	TN	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TN	→	Cyanobacteria	⇧
	Zooplankton	→	Phytoplankton	Cladocerans	→	Cyanobacteria	⇩
	Zooplankton	→	Phytoplankton	Cladocerans	→	Diatoms	⇩
	Phytoplankton	→	Zooplankton	Diatoms	→	Cladocerans	⬇
	Phytoplankton	→	Zooplankton	Cyanobacteria	→	Cladocerans	⬆

Table 2-ESM. SEM path coefficients and relative strengths in July.

Scenarios	*Generic Path*			*SEM Path*			*Relative strength* [a]
Oligotrophic Environment							
Present	Physical	→	Phytoplankton	Temperature	→	Diatoms	⇩
	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇩
	Physical	→	Zooplankton	Temperature	→	Cladocerans	⇧
	Nutrients	→	Phytoplankton	TP	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Nutrients	→	Phytoplankton	TN	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TN	→	Cyanobacteria	⇧
	Zooplankton	→	Phytoplankton	Cladocerans	→	Diatoms	⇩
	Zooplankton	→	Phytoplankton	Cladocerans	→	Cyanobacteria	⇩
	Phytoplankton	→	Zooplankton	Diatoms	→	Cladocerans	⇧
	Phytoplankton	→	Zooplankton	Cyanobacteria	→	Cladocerans	⇩
Warming	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇩
	Physical	→	Zooplankton	Temperature	→	Cladocerans	⇩
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Nutrients	→	Phytoplankton	TN	→	Cyanobacteria	⇩
	Zooplankton	→	Phytoplankton	Cladocerans	→	Cyanobacteria	⇩
	Phytoplankton	→	Zooplankton	Diatoms	→	Cladocerans	⇧
Mesotrophic Environment							
Present	Physical		Phytoplankton	Temperature	→	Diatoms	⇩
	Physical		Phytoplankton	Temperature	→	Cyanobacteria	⇩
	Physical		Zooplankton	Temperature	→	Cladocerans	⇧
	Nutrients		Phytoplankton	TP	→	Diatoms	⇧
	Nutrients		Phytoplankton	TP	→	Cyanobacteria	⇧
	Nutrients		Phytoplankton	NO_3	→	Diatoms	⇩
	Nutrients		Phytoplankton	NO_3	→	Cyanobacteria	⇧
	Zooplankton		Phytoplankton	Cladocerans	→	Diatoms	⇩
	Zooplankton		Phytoplankton	Cladocerans	→	Cyanobacteria	⇩
	Phytoplankton		Zooplankton	Diatoms	→	Cladocerans	⇧
Warming	Physical	→	Phytoplankton	Temperature	→	Diatoms	⇩
	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇩
	Physical	→	Zooplankton	Temperature	→	Cladocerans	⇧
	Nutrients	→	Phytoplankton	TP	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Nutrients	→	Phytoplankton	DIN	→	Diatoms	⇩

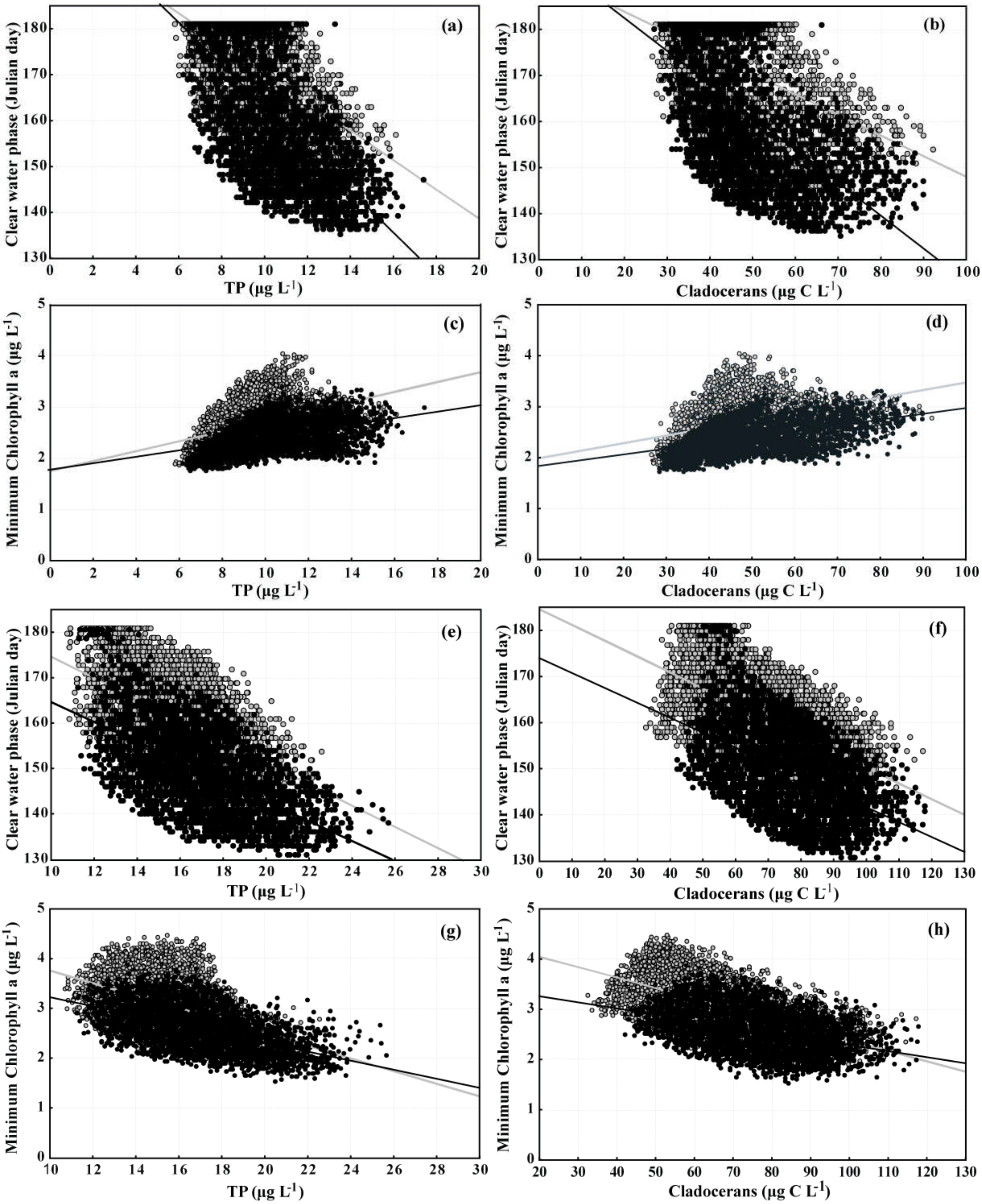
	Nutrients	→	Phytoplankton	DIN	→	Cyanobacteria	⇧
	Zooplankton	→	Phytoplankton	Cladocerans	→	Diatoms	⇩
	Zooplankton	→	Phytoplankton	Cladocerans	→	Cyanobacteria	⇩
	Phytoplankton	→	Zooplankton	Diatoms	→	Cladocerans	⇧
	Phytoplankton	→	Zooplankton	Cyanobacteria	→	Cladocerans	⇧
Eutrophic Environment							
Present	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇩
	Physical	→	Zooplankton	Temperature	→	Cladocerans	⇧
	Nutrients	→	Phytoplankton	TP	→	Cyanobacteria	⇧
	Nutrients	→	Phytoplankton	TN	→	Cyanobacteria	⇧
	Zooplankton	→	Phytoplankton	Cladocerans	→	Cyanobacteria	⇩
	Phytoplankton	→	Zooplankton	Cyanobacteria	→	Cladocerans	⇧
Warming	Physical	→	Phytoplankton	Temperature	→	Diatoms	⇩
	Physical	→	Phytoplankton	Temperature	→	Cyanobacteria	⇧
	Physical	→	Zooplankton	Temperature	→	Cladocerans	⇧
	Nutrients	→	Phytoplankton	NO_3	→	Diatoms	⇧
	Nutrients	→	Phytoplankton	NO_3	→	Cyanobacteria	⇩
	Nutrients	→	Phytoplankton	NH_4	→	Diatoms	⇩
	Zooplankton	→	Phytoplankton	Cladocerans	→	Diatoms	⇩
	Zooplankton	→	Phytoplankton	Cladocerans	→	Cyanobacteria	⇩
	Phytoplankton	→	Zooplankton	Diatoms	→	Cladocerans	⇧

[a] Relative strength of paths in Table 7 and 8 is shown in four levels with different width of the arrow; the widest as the strongest relationship (coefficient > 0.75), second strongest (0.5 < coefficient < 0.75), third strongest (0.25 < coefficient < 0.5), the weakest (0 < coefficient < 0.25). Direction of the arrows indicates positive and negative relationships; upwards and downwards, respectively.

FIGURES LEGENDS

Figure 1: Relationships between the clear water phase timing (Julian day) and the corresponding chlorophyll a concentrations with Total Phosphorus (μg *TP* L^{-1}) and Cladoceran biomass (μg C L^{-1}) in three trophic states: oligotrophic (*a*–*d*), mesotrophic (*e*–*h*), and eutrophic (*i*–*l*) environments. Grey and black dots correspond to the present and warming conditions, respectively.

Figure 2: Seasonal variability of the phytoplankton (μg chl *a* L^{-1}) and zooplankton (μg C L^{-1}) community under the six scenarios examined. In these experiments, the input phosphorus concentrations for the oligo-, meso-, and eutrophic environments correspond to 32.5, 65, and 162.5 μg *TP* L^{-1}, respectively. The present epilimnetic (14 ^{o}C) and hypolimnetic (10 ^{o}C) temperatures were increased by approximately 2^{o}C and 1^{o}C under the warming scenario. Panels correspond to oligotrophic (*a*, *b*), mesotrophic (*c*, *d*), and eutrophic (*e*, *f*) states, and present (*a*, *c*, *e*) & warming (*b*, *d*, *f*) conditions


(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
Clear water phase (Julian day)
Minimum Chlorophyll a (μg L^{-1})
TP (μg L^{-1})
Cladocerans (μg C L^{-1})
130
140
150
160
170
180
0
1
2
3
4
5
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
40
50
60
70
80
90
100
110
120
130

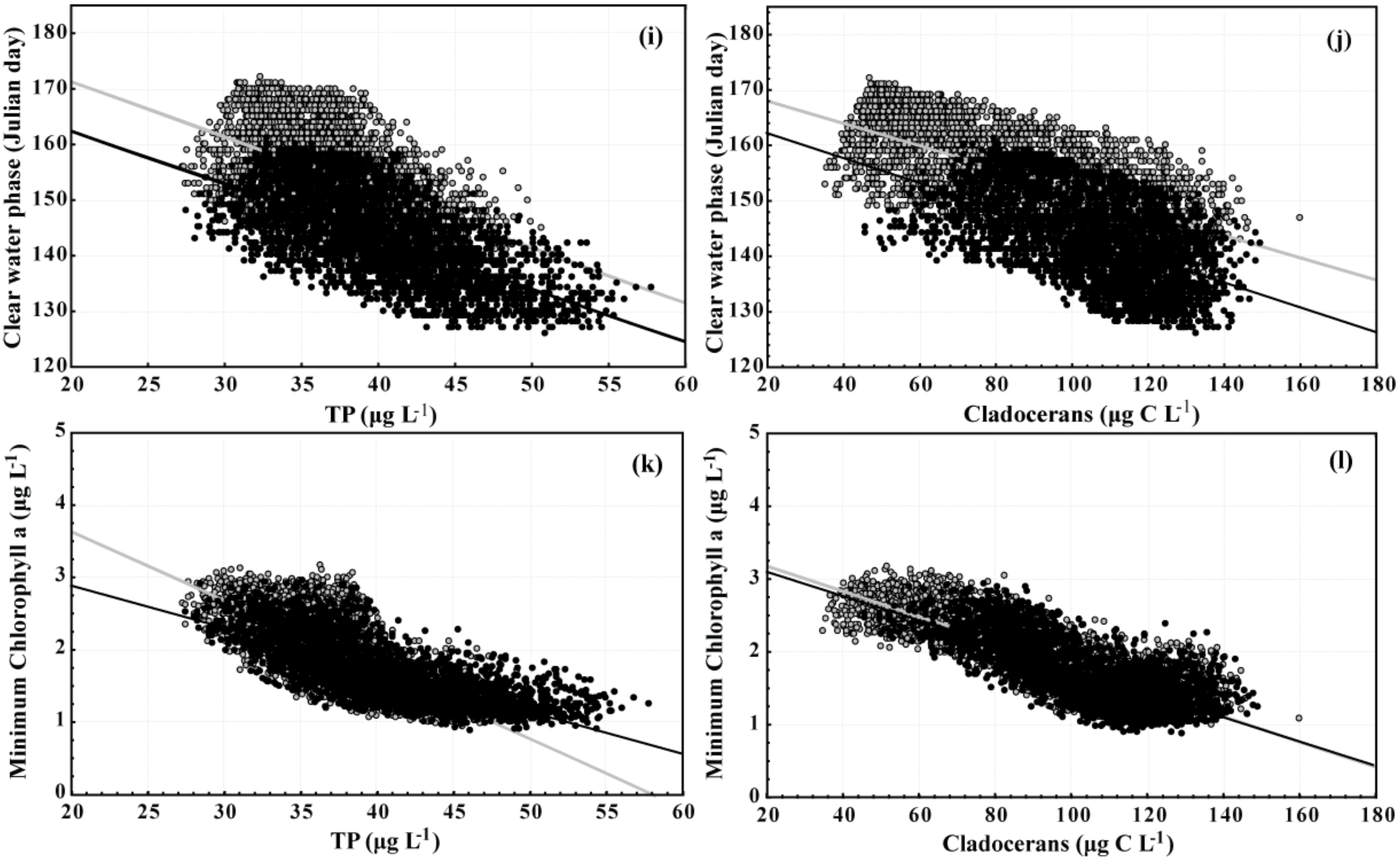
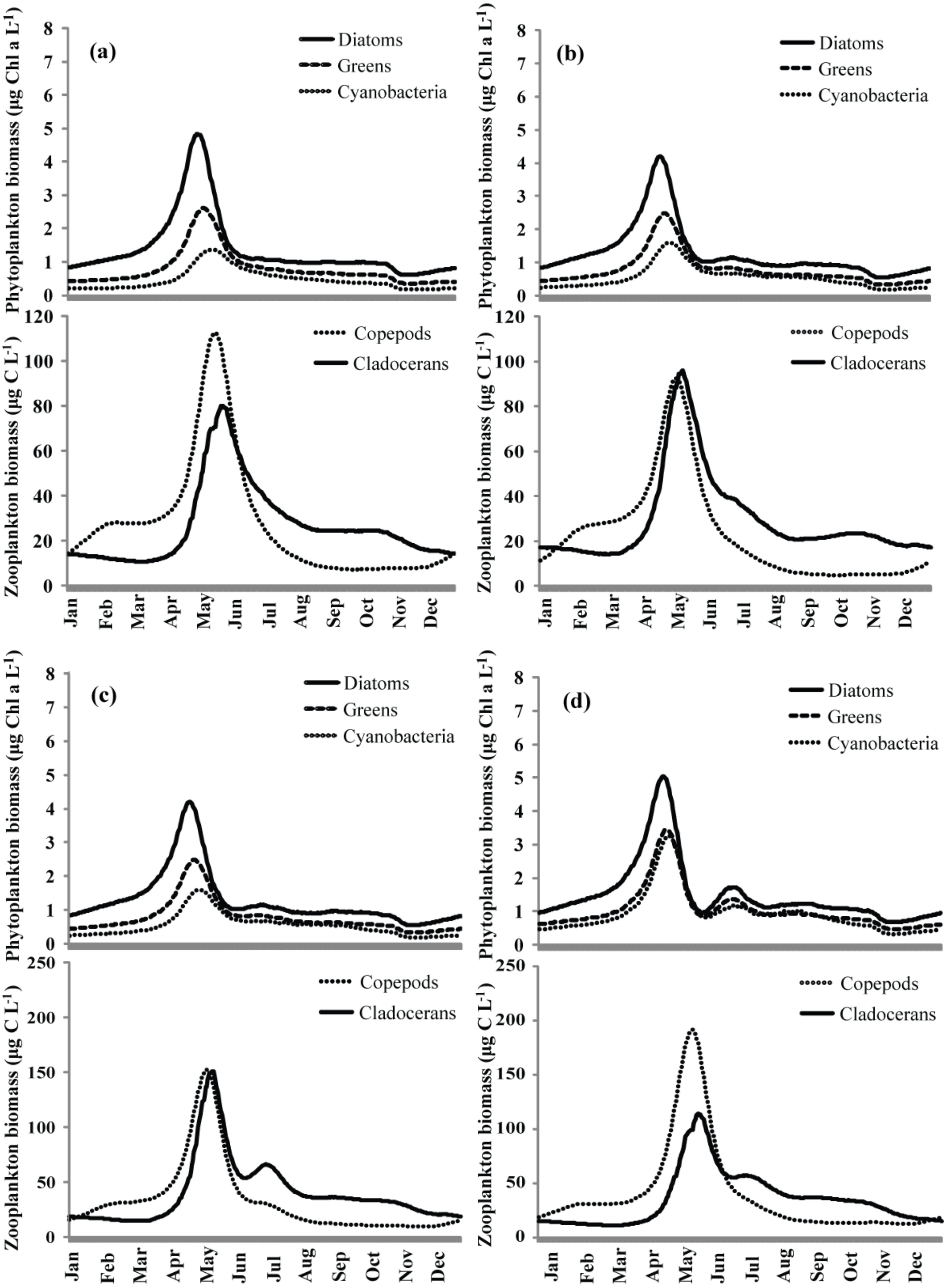

(i)
Clear water phase (Julian day)
120
130
140
150
160
170
180
TP (μg L-1)
20
25
30
35
40
45
50
55
60
(j)
Clear water phase (Julian day)
Cladocerans (μg C L-1)
20
40
60
80
100
120
140
160
180
(k)
Minimum Chlorophyll a (μg L-1)
0
1
2
3
4
5
TP (μg L-1)
(l)
Minimum Chlorophyll a (μg L-1)
Cladocerans (μg C L-1)

Figure 1


(a)
(b)
(c)
(d)
Diatoms
Greens
Cyanobacteria
Copepods
Cladocerans
Phytoplankton biomass (µg Chl a L^{-1})
Zooplankton biomass (µg C L^{-1})
0
1
2
3
4
5
6
7
8
0
20
40
60
80
100
120
0
50
100
150
200
250
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

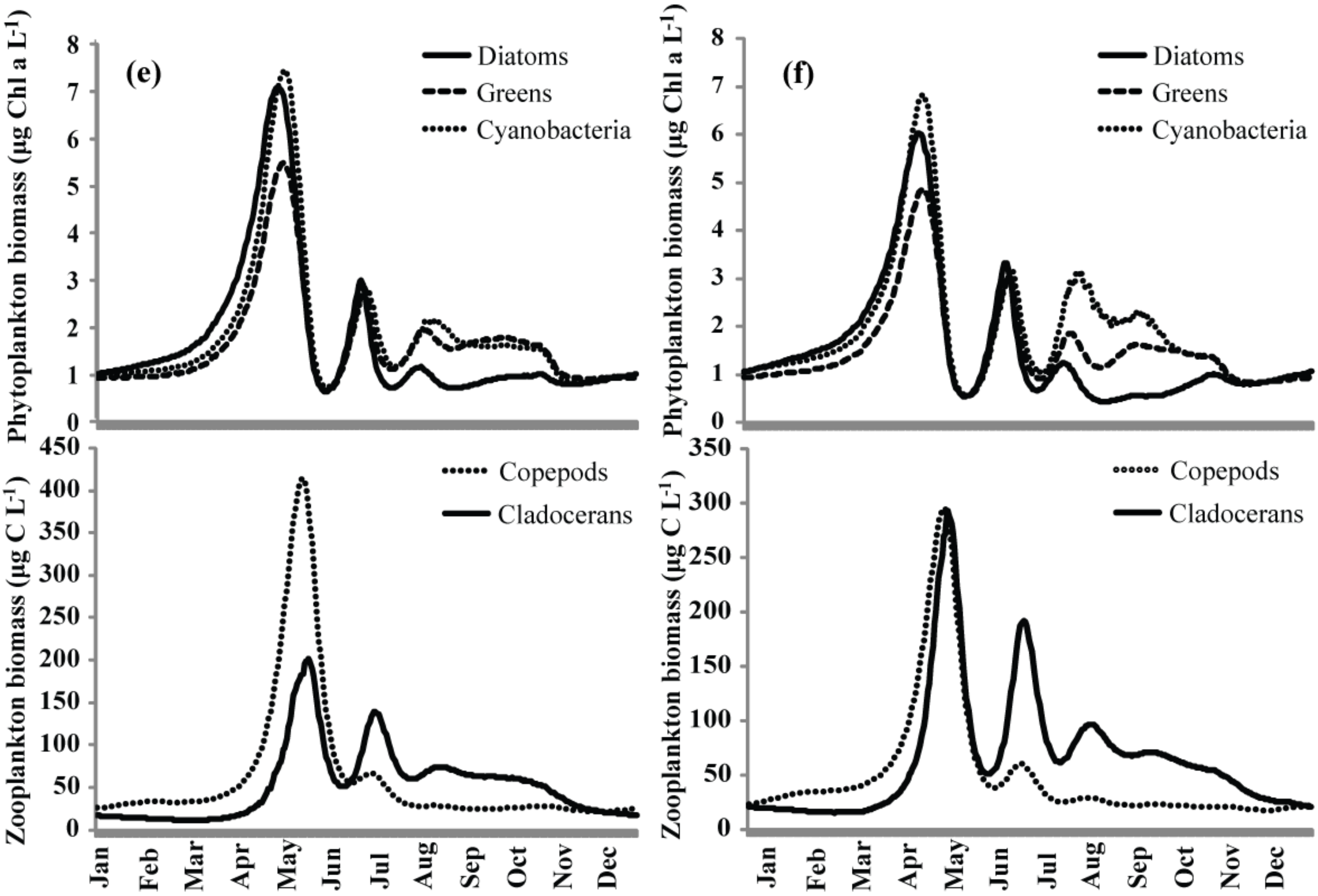

(e)
(f)
Phytoplankton biomass (µg Chl a L-1)
Zooplankton biomass (µg C L-1)
Diatoms
Greens
Cyanobacteria
Copepods
Cladocerans
0
1
2
3
4
5
6
7
8
0
50
100
150
200
250
300
350
400
450
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 2