Limnol. Oceanogr., 55(3), 2010, 973–982

doi:10.4319/lo.2010.55.3.0973

Evidence of warming effects on phytoplankton productivity rates and their dependence on eutrophication status

Rémy D. Tadonléké*

Institut National de la Recherche Agronomique, Unité Mixte de Recherche 42, Centre Alpin de Recherche sur les Réseaux Trophiques des Ecosystèmes Lacustres, Thonon-les-Bains, France

Abstract

Using 31-yr data from measurements in a lake that has experienced change in eutrophication status, I showed that the effects of global warming on chlorophyll *a* (Chl *a*)–normalized maximum rates of photosynthesis (P_{max} : Chl *a*) may be positive, nonsignificant, or negative, depending on nutrient availability. The magnitude of P_{max} : Chl *a* change in response to warming showed hyperbolic relationships with phosphorus concentrations; it was positive and constant when total phosphorus (TP) in the lake water exceeded 22 μg P L^{-1} (eutrophic conditions) but was negative when TP was lower (nutrient-poor conditions), indicating direct negative effects of warming on primary productivity (PP) under phosphorus scarcity. Vertically integrated PP responses corroborate those of P_{max} : Chl *a*. These data also showed long-term seasonal variations in the sensitivity of phytoplankton productivity to temperature. The observed hyperbolic curves strongly suggest that the ''limiting-nutrient cell quota''–based mechanism reported so far only in laboratories (by studies analyzing temperature-nutrient effects on microalgal growth or photosynthesis) operates in nature and plays a key role in determining phytoplankton response to warming of waters. The present findings provide insight on how phytoplankton productivity may respond to future warming in lakes of differing eutrophication status.

There is now ecosystem-scale evidence that climate warming affects lake physicochemical characteristics and plankton stocks and phenology (McKnight et al. 1996; Livingstone and Dokulil 2001; Magnusson et al. 2003). Little is known, in contrast, about lake planktonic primary productivity response to increases in water temperature (Gerten and Adrian 2002) and how nutrient conditions may influence this response. Primary productivity (PP) in aquatic systems plays an essential role in element cycling and food production for heterotrophs; it supports the fish stocks and is temperature and nutrient dependent. Warming effects on PP may thus have important consequences for trophic interactions, leading to ecosystem-level changes.

The global average temperature is projected to continue to rise, and the predicted warming range over 1990 to 2100, in the absence of climate mitigation policies, is 1.7°C to 4.9°C (Wigley and Raper 2001). Although laboratory studies have shown nutrient influence on temperature effects on microalgal growth rates or photosynthesis rates (Rhee and Gotham 1981; Raven and Geider 1988; Geider et al. 1998), studies analyzing nutrient influence on warming effects on natural phytoplankton are exceedingly scarce, and they are based on simulation or short-term experiments with a few-degrees increase in temperature and concern shallow nutrient-rich lakes and phytoplankton phenology (i.e., advancements or delays in annually reoccurring events in phytoplankton life cycle, e.g., spring bloom) (Elliott et al. 2006; Staehr and Sand-Jensen 2006; Huber et al. 2008). For example, using the ''Phytoplankton Responses to Environmental Change'' model (that simulates the growth of up to eight phytoplankton species throughout the water column) to study the effects of elevated temperatures and increased nutrient loading, Elliott et al. (2006) found that at low nutrient levels, the effect of water temperature change on phytoplankton was reduced considerably. Likewise, a modeling study simulating warming and using data from a shallow lake has shown that the intensity of diatom spring bloom was higher under hypertrophic than under eutrophic conditions (Huber et al. 2008). Given that lakes (and more generally aquatic systems) are different in terms of eutrophication status and that many of them experience both changes in nutrient supply and warming of waters, proper understanding and forecasting of warming effects on phytoplankton productivity in these ecosystems requires understanding the influence of nutrient conditions and the underlying mechanisms.

Lake Geneva (Switzerland and France) is socioeconomically very important. As the largest freshwater reserve in western Europe, it supplies drinking water to the surrounding towns and contains important stocks of commercially important fish such as Arctic charr, perch, and whitefish. This lake underwent strong cultural eutrophication in the early 1960s, but following implementation of phosphorus reduction measures in 1972, both total phosphorus (TP) and dissolved inorganic phosphorus (DIP) have decreased by more than 60% from a eutrophic period, 1970–1982, to a mesotrophic period, 1989–2005. In parallel, water temperature has increased significantly over time (*see* Results). This has provided a unique opportunity to investigate nutrient (P) influence on phytoplankton productivity responses to warming in a natural environment. Water quality has been monitored in Lake Geneva for more than 30 yr. In this study, using 31-yr data from this monitoring, I have investigated how the responses of phytoplankton productivity to warming of waters vary with nutrient conditions.

* Corresponding author: tadonlek@thonon.inra.fr

Methods

Lake Geneva is located at an elevation of 372 m on the border between Switzerland and France (46°27′N, 6°32′E). It is a semicircular lake with a surface area of 582 km^2, a maximum length of 72 km, and a maximum width of 14 km; the maximum and mean depths are 309 m and 152 m, respectively. This large deep monomictic lake does not freeze; it contains about 89 km^3 of water and has an average residence time of about 11 yr.

The present data cover the period 1970–2005. All in-lake measurements were done at the deepest station of the lake. Samples were collected once a month from 1970 to 1981 and two or three times a month thereafter. The water temperatures (T, in °C) measured from the surface to the bottom waters were used to estimate water density (ρ) with the formula $\rho(T) = 1000 - 7 \times 10^{-3}(T - 4)^2$ (Lerman 1978). An index of water column stability, the Brünt–Vaisälä frequency, was calculated from water density using the equation $N^2 = (g/\rho)/(d\rho/dz)$, where N^2 is the stability coefficient (s^{-2}), g the gravity (m s^{-2}), and z the depth. Precipitations data were analyzed but not presented because they were not significantly related to the studied variables. Samples for nutrients were collected at 12–20 depths ranging from the surface to the bottom of the lake (0–309 m). Nutrients were analyzed by standard colorimetric methods (Association Française de Normalisation 1990). Chlorophyll *a* (Chl *a*) and primary productivity (PP) were measured at 0, 1, 2, 3.5, 5, 7.5, 10, 15, 20, and 30 m of depth. Chl *a* was analyzed spectrophotometrically (Strickland and Parsons 1968). PP was measured using the carbon 14 method (Steeman-Nielsen 1952). The Chl *a*–normalized maximum rates of photosynthesis (maximum production rates per unit of chlorophyll $a = P_{max}$: Chl *a*) was calculated by dividing the maximum volumetric rate of PP recorded in the water column on any given date by the value of Chl *a* recorded at the same depth on this date. This ratio is a sensitive physiological indicator of algal responses to ambient conditions (Eppley 1972; Behrenfeld and Falkowski 1997). Because nutrient concentrations were generally not significantly different between depths in the zone where P_{max} : Chl *a* was observed (0–5 m in general) for each sampling date and because PP is generally lower at 0 m than at 1–3.5 m in Lake Geneva, the recorded maximum photosynthesis rates were likely light saturated. Least-squares regressions and Kendall's tau statistics were used to detect long-term trends in data. Given the strong decrease in phosphorus concentrations over time in Lake Geneva, two groups of data were considered, according to total phosphorus (TP) concentration in the 0–20-m zone (where almost all the phytoplankton productivity occurred): data for which TP was ≥ 22 μg P L^{-1} (P-rich conditions) and data for which TP was < 22 μg P L^{-1} (P-poor conditions). This limit (22 μg P L^{-1}) was chosen for two reasons. First, it is close to the limit values used to separate mesotrophic and eutrophic lakes in the Organization for Economic Cooperation and Development (OECD) management model (20 μg P L^{-1} for categories that are management oriented or 25 μg P L^{-1} for categories used for diagnostic purposes; Vollenweider and Kerekes 1982). Note that other OECD trophic categories based on TP could not be defined (e.g., oligotrophic [TP: 2.5–8 μg P L^{-1}] or hypereutrophic [TP ≥ 80 μg P L^{-1}]) because TP is this study ranged from ~ 16 μg P L^{-1} to ~ 56 μg P L^{-1}. Second, this limit (22 μg P L^{-1}) allowed splitting the data according to DIP concentration at a threshold (10 μg P L^{-1}) below which phytoplankton is reported to become phosphorus limited during reoligotrophication of lakes (Sas 1989; Manca and Ruggiu 1998). Indeed, mean annual DIP concentration was < 11 μg P L^{-1} when mean annual TP was < 22 μg P L^{-1} (except in 1995) and > 11 μg P L^{-1} when mean annual TP was ≥ 22 μg P L^{-1}. The effects of warming on PP were analyzed by two different methods, the data belonging to these two groups (eutrophic vs. metrotrophic conditions) being compared. One of the methods involved the Arrhenius plot of P_{max} : Chl *a* against temperature, the slopes of which allowed calculation of Q_{10} and thus evaluation of P_{max} : Chl *a* sensitivity to temperature. Significant relationships in the Arrhenius plot were considered indicative of P_{max} : Chl *a* sensitivity to temperature. The Arrhenius plot is widely used to evaluate the dependence of biological processes on temperature. The second method concerned log–log regression analyses. The latter involved the coupling between temperature and vertically integrated primary production (using individual sampling date data) and that between annual mean temperatures and the slope of the P_{max} : Chl *a*-temperature relationships calculated for each year using data from all individual sampling dates of that year. This slope, here referred to as S_{PT}, is the magnitude of PP response to temperature and represents the average production per unit biomass per degree Celsius for each year. For these regressions, the effect of temperature on PP was assessed using analysis of covariance (ANCOVA), and the pooled data in which the eutrophic conditions were coded as TP ≥ 22 and the less nutrient-rich conditions as TP < 22. The null hypothesis tested in the ANCOVA was that there are no differences among these two groups of data (TP < 22 μg P L^{-1} and TP ≥ 22 μg P L^{-1}) for means of vertically integrated PP or P_{max} : Chl *a* when these are adjusted for a common mean of temperature and a common regression line.

Results

As mentioned earlier, phosphorus concentrations in Lake Geneva have decreased by more than 60% from the period 1970–1982 to the period 1989–2005. Since 1990, annual means of TP and DIP in the 0–20-m zone (the productive zone) are below 19 μg P L^{-1} and 10 μg P L^{-1}, respectively, except in 1995 and 1996 (Fig. 1A). Moreover, the duration of DIP depletion in this zone has been extended into early spring and late fall (Fig. 1B,C).

The present data revealed significant increase in annual mean water temperature during the study period (1970–2005) in both the epilimnetic and the hypolimnetic layers (Fig. 1D). The linearized rate of temperature increase in the 0–5-m zone was 0.5°C per decade ($r^2 = 0.42$, Kendall's tau $= 0.46$, $p < 0.0001$), while that in the hypolimnion was ~ 0.2°C per decade at 100 m ($p < 0.05$) or at 250 m ($p <$

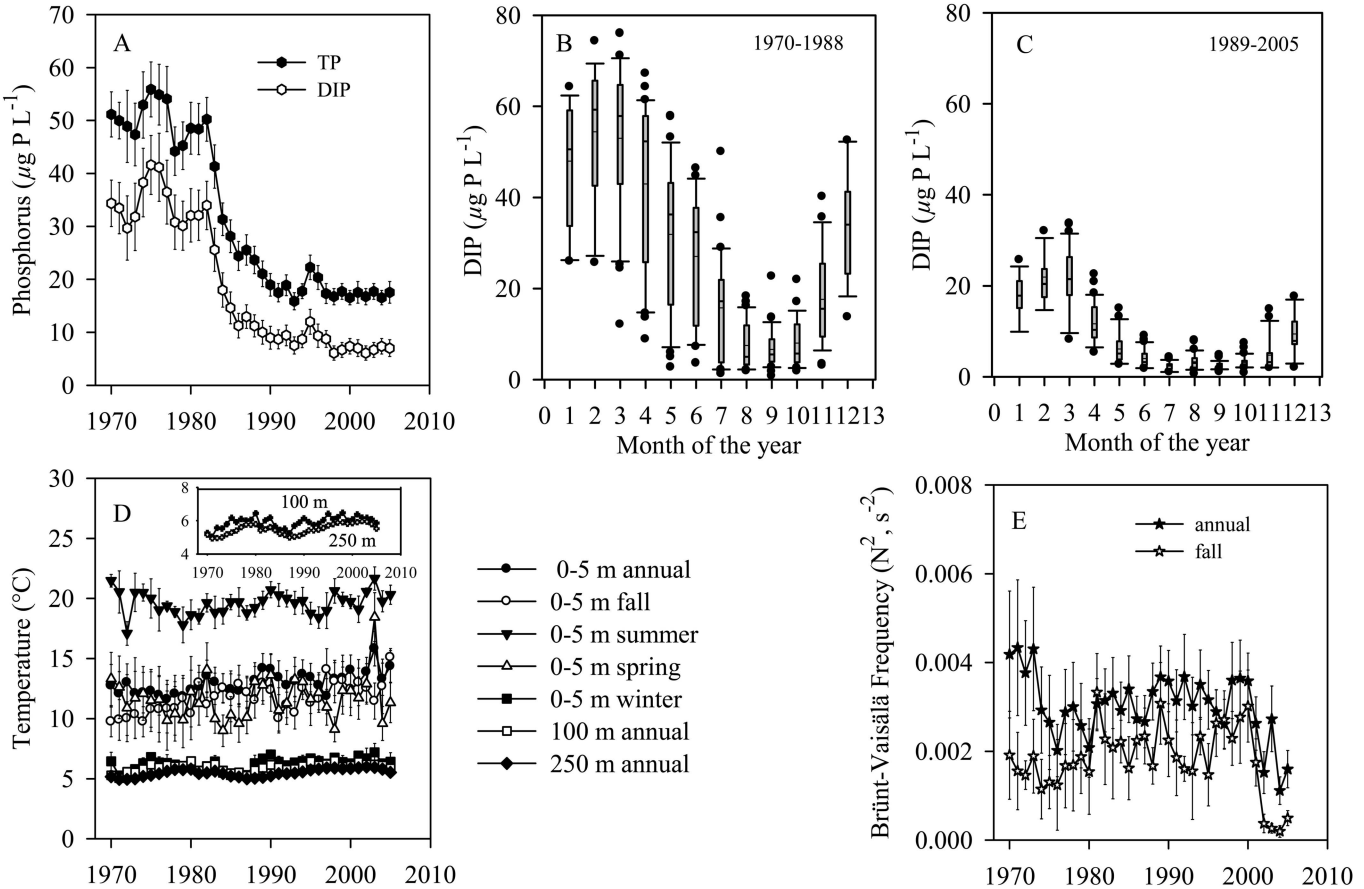

Fig. 1. (A) Long-term changes in annual mean of total and dissolved inorganic phosphorus (TP and DIP). (B) Seasonal variations and 90% confidence intervals for monthly mean dissolved inorganic phosphorus concentrations during 1970–1988, when total phosphorus (TP) was ≥ 22 μg P L^{-1}, and (C) during 1989–2005, when TP was < 22 μg L^{-1} (exception in 1995). (D) Long-term changes in water temperature and (E) in the water column stability as determined by the Brünt–Vaisälä frequency. For (B, C), the numbers on the x-axis correspond to months: 1 corresponds to January, 6 to June, and 12 to December. For (D), the inset shows detail on variations at 100 m (filled cross) and 250 m (opened cross). The vertical bars on data points are error bars; they are not visible when they are smaller than the points.

0.0005). At the seasonal scale, the rates of warming of the top 5 m in Lake Geneva were higher for the fall period, October–December (0.8°C per decade, Kendall's tau = 0.53, $p < 0.0001$), than for the two other seasons that also exhibited significant long-term trends in water temperature (winter and summer: 0.2°C [$p < 0.01$] and 0.3°C [$p < 0.05$] per decade, respectively; Fig. 1D).

As a consequence of this warming, annually calculated water column stability (WCS) increased significantly between 1974 and 2001 (Fig. 1E, 0.00026 s^{-2} per decade; Kendall's tau = 0.27, $p < 0.05$), and fall mean values of WCS showed an even higher increase during this period (0.00031 s^{-2} per decade; Fig. 1E). The reasons for the strong decrease in WCS after 2001 are unclear, especially since the annual means of wind speed and the number of days with high wind speed (> 5 m s^{-1}) were higher in 2000 and 2001 (2 m s^{-1} and 2.14 m s^{-1} and 45 d and 58 d, respectively) than during 2002–2005 (1.78 m s^{-1}–1.99 m s^{-1} and 26–36 d). The lake overturned in 1999, which is rare; the magnitude of the overturn was also very high in 2000 (Blanc et al. 2000; P. Blanc pers. comm.). Maybe these processes observed between 1999 and 2001 affected the WCS during the following years. The observed increase in WCS likely reduced mixing and thus exchanges between deeper and upper waters and restricted internal supplies of nutrients to phytoplankton, as suggested by the low and vertically stratified inorganic nutrient concentrations in the 0–5-m zone in fall, despite vertical homogeneity in water temperatures (Fig. 2A–C). Note that the sampling dates shown in Fig. 2 were selected on a random basis because it was not possible to show the vertical homogeneity or stratification of the variables in these zones of the water column (0–50 m and 0–100 m) using all these sampling depths and the seasonal means.

Temperature is a key factor driving cellular metabolic processes, including P_{max}:Chl *a* (the Chl *a*–normalized maximum rates of photosynthesis). Using data from all individual sampling dates, I found that the intercept (TP term = code) of the relationship between temperature and P_{max}:Chl *a* was significantly higher under strongly eutrophic conditions (0.52 for TP ≥ 22 μg P L^{-1}, $r^2 = 0.21$, $p < 0.0001$) than when the lake was less nutrient rich (0.29 for TP < 22 μg P L^{-1}, $r^2 = 0.13$, $p < 0.0001$), while the slopes (logTemperature $\times$ TP term) were similar (0.51

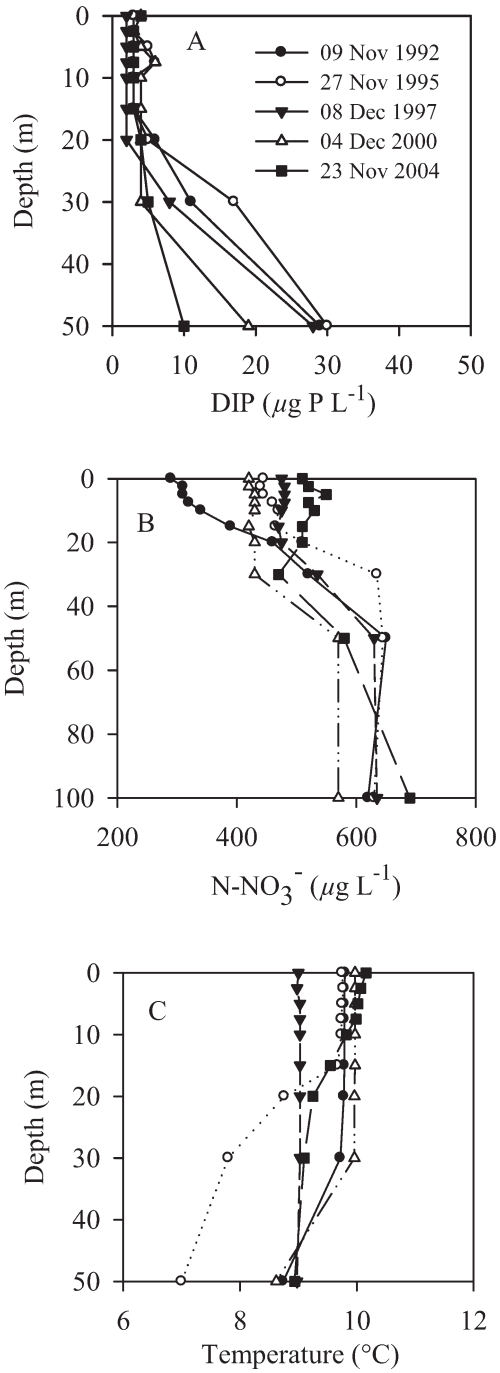

Fig. 2. Examples of vertical profiles of (A) dissolved inorganic phosphorus (DIP), (B) nitrates ($N\text{-}NO_3^-$), and (C) temperature during late fall after 1990. Note that for (A–C), the y-axis scale was restricted to 50 m or 100 m in order to provide greater internal detail.

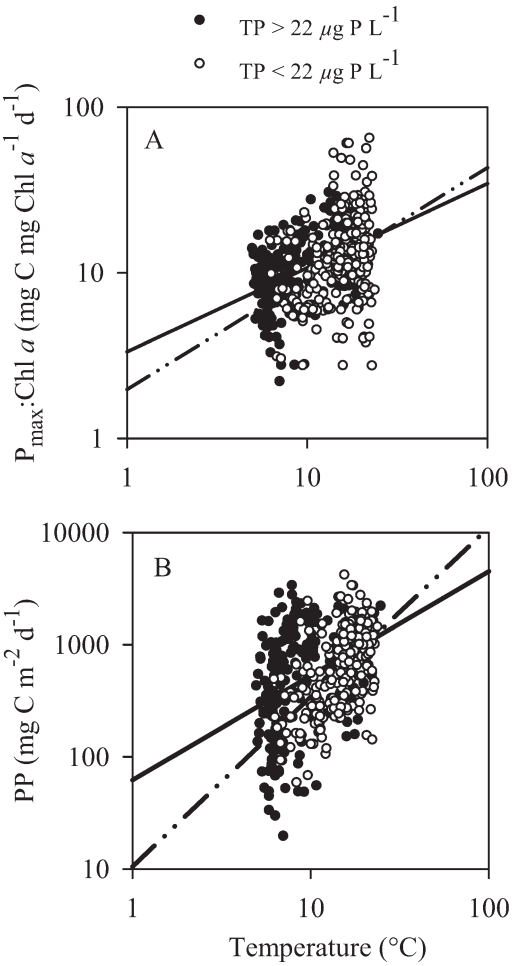

Fig. 3. Relationships between temperature and (A) Chl *a*–normalized maximum rates of photosynthesis (P_{max} : Chl *a*) and (B) the vertically integrated primary production (PP). The regression lines were extended to the axes because regression lines restricted to the data regions were not visible. For (A), the equations, including standard error of estimates (in parentheses), are $\log[P_{max}:\text{Chl } a] = 0.67(0.10) \times \log[\text{Temperature}] + 0.29(0.12)$, $p < 0.0001$, for TP < 22 μg P L^{-1} and $\log[P_{max}:\text{Chl } a] = 0.51(0.06) \times \log[\text{Temperature}] + 0.52(0.06)$, $p < 0.0001$, for TP ≥ 22 μg P L^{-1}. For (B), the equations are $\log[PP] = 1.51(0.12) \times \log[\text{Temperature}] + 1.02(0.14)$, $p < 0.0001$, for TP < 22 μg P L^{-1} and $\log(PP) = 0.93(0.16) \times \log[\text{Temperature}] + 1.79(0.16)$, $p < 0.0001$, for TP ≥ 22 μg P L^{-1}. *See* Table 1 for results of ANCOVA.

vs. 0.67; Fig. 3A; ANCOVA; Table 1). The null hypothesis that the two regressions had similar intercepts was thus rejected at the probability level = 0.05. Lake Geneva thus exhibited a significantly higher production per unit biomass when phosphorus was abundant than when it was scarce for the same temperature. For the relationship between temperature and vertically integrated primary production (mg C m^{-2} d^{-1}), the two groups of data were significantly different in terms of both intercepts and slopes (intercepts = 1.79 and 1.02 for TP ≥ 22 μg P L^{-1} and TP < 22 μg P L^{-1}, respectively; slopes [logTemperature × TP term] = 0.93 vs. 1.51; Fig. 3B; ANCOVA; Table 1). This indicated strong interactions between temperature and TP and showed that temperature effects on vertically integrated primary production under eutrophic conditions were significantly different from those under less nutrient-rich conditions. Temperature and P_{max} : Chl *a* or vertically integrated primary production were not correlated when more coarsely scaled annual means values were used.

Table 1. Analyse of covariance for $\log_{10}$ P_{max} : Chl *a* and $\log_{10}$ vertically integrated primary production (PP). Log_{10}temperature is the covariate, and the data are coded as either TP < 22 μg P L^{-1} or TP > 22 μgP L^{-1}. For P_{max} : Chl *a*, $r^2 = 0.187$, adjusted $r^2 = 0.183$; for PP, $r^2 = 0.247$, adjusted $r^2 = 0.243$.

Dependent variable	Source	Sum of squares	df	Mean square	*F*	Significance level
P_{max} : Chl *a*	Model	5.304	3	1.768	39.358	<0.0001
	Intercept				38.44	<0.0001
	Code (=TP term)	0.235	1	0.235	5.24	<0.05
	$\log_{10}$temperature	4.409	1	4.409	98.139	<0.0001
	TP term$\times\log_{10}$temperature	0.083	1	0.083	1.856	0.173
	Error	23.003	512	0.044		$p>F$
	Corrected total	28.307	515			
PP	Model	20.649	3	6.883	54.225	<0.0001
	Intercept				154.534	<0.0001
	Code (=TP term)	1.596	1	1.596	12.573	<0.0005
	$\log_{10}$temperature	18.131	1	18.131	142.838	<0.0001
	TP term$\times\log_{10}$temperature	1.027	1	1.027	8.093	<0.005
	Error	62.833	495	0.127		$p>F$
	Corrected total	83.483	498			

The Arrhenius plot of the data confirmed these differences at seasonal scale (Fig. 4). In winter, P_{max} : Chl *a* showed no obvious sensitivity to temperature ($p > 0.05$) across the very narrow range of 5–8°C (Fig. 4A). In contrast, P_{max} : Chl *a* appeared to be stimulated by temperature during the fall: its associated Q_{10} (2.33) was higher when TP was ≥ 22 μg P L^{-1} ($\ln[P_{max} : \text{Chl } a] = -6.26\ (2.3) \times [1000/T] + 24.02(8.37)$, $p < 0.02$) than when TP was < 22 μg P L^{-1} ($Q_{10} = 1.89$) ($\ln[P_{max} : \text{Chl } a] = -4.72\ (1.02) \times [1000/T] + 18.75(3.58)$, $p < 0.001$) (Fig. 4B). Inorganic phosphorus availability was also higher when TP was ≥ 22 μg P L^{-1} (mean DIP = 23.9 μg P L^{-1}, range 8.8–52.3) than when TP was < 22 μg P L^{-1} (mean DIP = 5.3, range 1–17.7; 90% of these DIP concentrations were $<$ 12 μg P L^{-1}) (Fig. 1B,C).

During spring and summer, the temperature–P_{max} : Chl *a* relationship was not significant when TP was < 22 μg P L^{-1} ($p > 0.05$; Fig. 4C,D). Interestingly, when TP was ≥ 22 μg P L^{-1}, the coupling between these variables was significant and positive in spring ($\ln[P_{max} : \text{Chl } a] = -5.06\ (1.13) \times [1000/T] + 20.42(4.02)$, $p < 0.001$) or negative in summer ($\ln[P_{max} : \text{Chl } a] = 4.95\ (1.9) \times [1000/T] - 14.34(6.68)$, $p < 0.02$). Hence, when TP was ≥ 22 μg P L^{-1}, an activation Q_{10} (stimulation) of 2.41 was found for spring data, whereas an inactivation Q_{10} (inhibition) of 1.91 was found for summer data. Again, P availability was lower when temperature inhibition of photosynthesis was found (mean DIP = $\sim$16 μg P L^{-1}, range 2–37) than when temperature stimulation was observed (mean DIP = 26 μg P L^{-1}, range 4–67) (Fig. 1B,C). For these data, neither the temperature nor P_{max} : Chl*a* was correlated with phosphorus concentrations ($0.09 > p < 0.84$). Even though P_{max} : Chl *a* was correlated with nitrogen for summer data, the relationship was positive ($r^2 = 0.19$, $p < 0.005$), and, on the other hand, nitrogen was not correlated at all with temperature ($p > 0.05$). These results suggest that the observed response of PP to temperature in spring or in summer was likely not due to the direction of changes in nutrient (especially P) concentrations over the course of the study. Similar conclusions were reached for fall data based on results from similar analyses. For example, P_{max} : Chl *a* showed no significant relationships with DIP and TP ($r^2 = 0.00009$ and 0.012, respectively, $p > 0.26$) but was positively related to temperature (T) when TP was < 22 μg P L^{-1} ($\log [P_{max} : \text{Chl } a] = 0.66(0.15) \times \log[T] + 0.25(0.16)$, $r^2 = 0.17$, $p < 0.001$). When TP was ≥ 22 μg P L^{-1}, P_{max} : Chl *a* was related positively to temperature ($\log [P_{max} : \text{Chl } a] = 0.87(0.32) \times \log[T] - 0.026(0.33)$, $r^2 = 0.24$, $p < 0.02$) but negatively to phosphorus (e.g., $\log [P_{max} : \text{Chl } a] = -0.61(0.15) \times \log[\text{DIP}] + 1.66(0.20)$, $r^2 = 0.38$, $p < 0.0005$).

Annual-scale analyses showed that S_{PT} (the magnitude of PP response to warming = slope of the temperature–P_{max} : Chl *a* relationships calculated for each year) significantly increased with increase in annual mean water temperature when annual mean TP was ≥ 22 μg P L^{-1} ($r^2 = 0.44$, $p < 0.01$) but tended to decrease (even though the decline was not significant) when TP was < 22 μg P L^{-1} (Fig. 4E). Moreover, S_{PT} exhibited a saturating relationship with phosphorus concentrations (Fig. 4F,G), that resembles the hyperbolic relationship commonly observed between microalgal growth rates or photosynthetic rates and cell quotas of the growth-limiting nutrient (Rhee and Gotham 1981; Smith 1983; Raven and Geider 1988). S_{PT} increased as phosphorus in lake waters increased below 22 μg P L^{-1} of TP and then leveled off when TP became $\geq$ 22 μg P L^{-1}. This saturating relationship provided additional support to the view that the long-term responses of PP to temperature were likely not due to the direction of changes in nutrient concentrations over the course of the study. The years exhibiting negative values of S_{PT} also had the lowest vertically integrated production values recorded since TP and DIP have dropped below 19 μg P L^{-1} and 10 μg P L^{-1}, respectively (696 mg C m^{-2} d^{-1} and 716 mg C m^{-2} d^{-1} in 1998 and 2002, respectively), indicating that PP response was negative when P availability was lowest (Figs. 1A, 4F,G).

In contrast, tests of the coupling of S_{PT} with other potential controlling factors (nitrogen, N : P ratios, light, WCS, zooplankton) yielded no significant relationships or

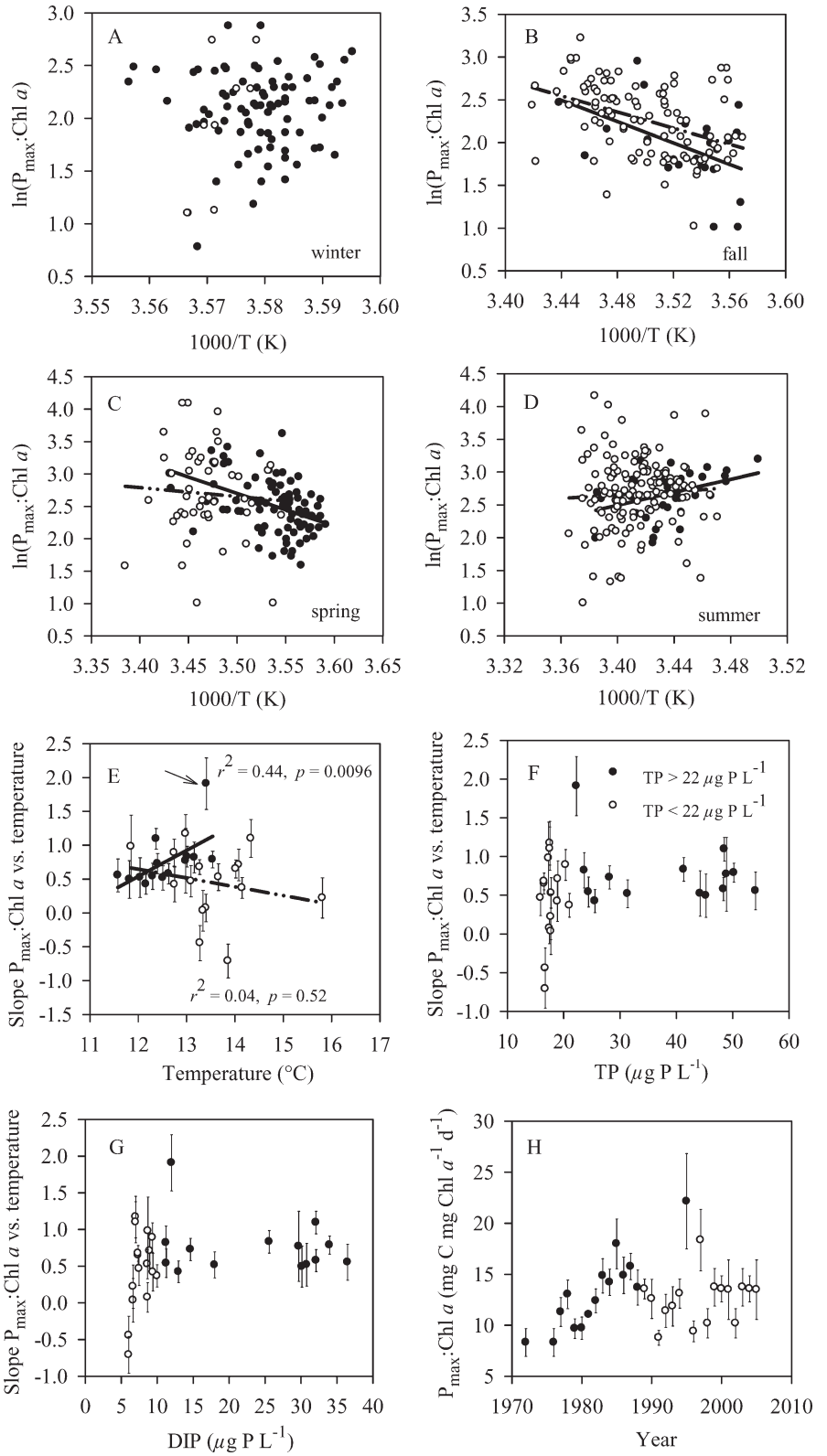

Fig. 4. Arrhenius plots of temperature and P_{max} : Chl *a* (Chl *a*–normalized maximum rates of photosynthesis, in mg C mg Chl^{-1} d^{-1}) for (A) winter, (B) fall, (C) spring, and (D) summer. Relationships between S_{PT} (slope of the P_{max} : Chl *a*–temperature relationship, in mg C mg Chl a^{-1} d^{-1} $°C^{-1}$, calculated for each year using data from all individual sampling dates of that year) and (E) annual mean temperature, (F) total phosphorus concentration, and (G) dissolved inorganic phosphorus concentration. (H) Long-term changes in P_{max} : Chl *a* between 1970 and

consistent trends (data not shown). In agreement with these results, annual mean P_{max} : Chl *a* increased annually when TP was ≥ 22 μg P L^{-1} ($r^2 = 0.79$, $p < 0.0001$) but not when TP was below this value ($r^2 = 0.05$, $p > 0.05$) (Fig. 4H). These findings at the annual scale emphasized the influence of lake eutrophication status on PP responses and confirmed results at the seasonal scale; that is, photosynthetic responses to temperature were strongly constrained when phosphorus was scarce (negative responses being observed when P availability was lowest) and were positive when P was abundant, these positive responses being stronger when nutrient availability was higher.

Discussion

This study has shown significant long-term increase in water temperature in Lake Geneva from 1970 to 2005. The observed rate of epilimnetic warming is consistent with increases in annual mean air temperature calculated for Western Europe during the period 1976–2000 (+ 0.5°C to + 1°C per decade) (Intergovernmental Panel on Climate Change 2001), and the rate of hypolimnetic warming is higher than or similar to the observed rates of warming of deep waters in several large African lakes (O'Reilly et al. 2003). At the seasonal scale, the rates of warming of the top 5 m were higher for the fall period than for winter and summer, and no significant long-term increase in water temperature was observed for spring. Similar to these results, long-term warming of surface waters was detected in eight Austrian lakes in fall but not in the other seasons (Livingstone and Dokulil 2001). Recent studies in Lake Geneva have found links between climate change indexes and either the warming of hypolimnetic waters (Dokulil et al. 2006) or the variability of summer temperature (Molinero et al. 2007).

Phytoplankton productivity was sensitive to warming of waters at different seasons in Lake Geneva. This response to water temperature was positive in fall and spring and negative in summer. These results showed for the first time both long-term seasonal variations in P_{max} : Chl *a* sensitivity and possible evidence of negative physiological responses of lake PP to warming (inactivation Q_{10}) based on natural phytoplankton communities in situ. Inactivation Q_{10} (inhibition) for microalgae, as found here for summer data, has been reported so far only in laboratories (Gao et al. 2000). While studies of long-term changes in water temperature in temperate lakes have often neglected the fall months (Gerten and Adrian 2003; Magnusson et al. 2003; Molinero et al. 2007), the present results demonstrated that the warming of fall waters in Lake Geneva was accompanied by a significant increase in phytoplankton productivity rates and that this photosynthetic response was stronger when phosphorus availability was higher. This influence of nutrient conditions on PP response to temperature was also observed at annual scale (in addition to the seasonal scale), highlighting the influence of lake eutrophication status. Overall, when phosphorus was abundant, photosynthetic responses to temperature were positive and were stronger when nutrient availability was higher. In contrast, when phosphorus was scarce, photosynthetic responses to temperature were strongly constrained, negative responses being observed when P availability was lowest. The apparent insensitivity of P_{max} : Chl *a* to temperature in summer (Fig. 4D, open circles) while P was scarce (TP $<$ 22 μg P L^{-1}, mean DIP = 3.4 μg P L^{-1}, range = $\sim$ 1–9) suggested that besides P uptake capacities of species, species-specific differences in susceptibility to temperature (Raven and Geider 1988; Coles and Jones 2000; Elliott et al. 2006) also affected photosynthetic responses during this season. To my knowledge, this is the first study showing direct effects of warming on rates of phytoplankton productivity and their dependence on nutrient availability based on long-term direct and in situ measurements of variables and using both the biomass-normalized maximum rates of photosynthesis and the vertically integrated primary production.

Phytoplankton is an important determinant of water quality and is a key compartment in carbon cycling and food production for heterotrophs, supporting the fish stocks in aquatic systems. Climatic effects on these autotrophs are thus of considerable interest (theoretical knowledge, management). How warming will affect phytoplankton productivity is still a matter of debate for oceans (Doney 2006). Using nearly 10 yr data derived from satellite records of ocean color, Behrenfeld et al. (2006) found that ocean phytoplankton productivity (mg C m^{-2} d^{-1}) increases during 1997–1998 and then decreases gradually to 2005, which coincided with an increase (1997–1998) and a decrease (1999–2005) in climate-related thermal stratification indexes. These authors argued that this long-term decline occurred because climate-induced increase in water stratification reduced the supply of nutrients needed for phytoplankton growth in the upper waters (they did not examine nutrient conditions, however). Other authors have argued that in ocean regions where light rather than nutrient limits phytoplankton (i.e., higher latitudes), future warming may actually increase phytoplankton productivity because reduced mixing maintains plankton in the illuminated surface

←

2005. In panels (A–D), T is temperature in degrees Kelvin (K). Note that for panel (E), the regression was performed with $\log_{10}$-transformed data; the equation, including standard error of estimates (in parentheses), is $\log [S_{PT}] = 5.6\ (1.80) \times \log[\text{Temperature}] - 6.26(1.98)$; $r^2 = 0.44$, $p < 0.01$. The point indicated by an arrow is not an outlier, and the regression remains significant if this point is excluded: $\log [S_{PT}] = 3.6(1.49) \times \log[\text{Temperature}] - 4.17(1.63)$; $r^2 = 0.35$, $p < 0.05$. Outliers were checked by plotting residuals with the predicted variable. For panels (E–H), the vertical bars on data points are error bars.

waters with abundant nutrients (Doney 2006). Our results agree well with these observed and predicted trends (Behrenfeld et al. 2006; Doney 2006).

For lakes, the few studies that have examined nutrient influence on phytoplankton response to warming showed that the response of phytoplankton (i.e., the intensity of diatom spring bloom, the biomass or the photosynthesis rates in mg C mg Chl^{-1} h^{-1}) to the simulated warming was stronger under very rich than under rich nutrient conditions (Elliott et al. 2006; Staehr and Sand-Jensen 2006; Huber et al. 2008). The few ecosystem-scale studies of primary productivity response to warming of waters have generally reported nonsignificant or positive correlations between temperature and lake PP, and in these cases, nutrients were abundant (Schindler et al. 1990; Gerten and Adrian 2002). Positive effects of warming of waters on PP as found here (Figs. 3, 4; Table 1), undoubtedly result from the combined effects of nutrient availability and direct increase in temperature-dependent physiological rates in the primary producers (Eppley 1972; Raven and Geider 1988). Long-term decline in lake PP with increase in water temperature has been reported, to my knowledge, only for the oligotrophic tropical and deep Lake Tanganyika (O'Reilly et al. 2003; Verburg et al. 2003). In this lake, PP was measured as $\delta^{13}C$ (‰) isotopes in sediment cores, and its decline was more pronounced during the period of P scarcity (1950–2000; phosphorus values at times were as low as 0.31 μg P L^{-1}, mean = $\sim$ 8.99 μg P L^{-1}) (O'Reilly et al. 2003; Verburg et al. 2003). In Lake Tanganyika and in lakes where a long-term positive relationship was found between annual PP (mg C m^{-2} d^{-1}) and spring mixing depth (e.g., the ultraoligotrophic Lake Tahoe; Goldman et al. 1989), results have generally been attributed, as mentioned previously for oceans, to indirect effects of warming, that is, changes in thermal stratification that affect vertical mixing and supply of nutrients to upper waters (Goldman et al. 1989; O'Reilly et al. 2003; Behrenfeld et al. 2006). Although direct negative effects of increase in water temperature on phytoplankton have often been evoked, this has not been demonstrated in nature. By showing unprecedented inactivation Q_{10} (possible negative physiological response) for phytoplankton in situ and negative values of S_{TP} and the lowest vertically integrated production values when phosphorus availability was lowest (Fig. 4D–G), the present results not only agree with those from the previously cited deep lakes but also provide indication that under strong and prolonged nutrient scarcity in lakes, PP may be directly affected negatively by long-term increase in water temperature.

The responses of phytoplankton P_{max} : Chl *a* or specific growth to increase in temperature under nutrient-limited conditions has been studied extensively but generally in laboratories (Rhee and Gotham 1981; Raven and Geider 1988). In an experimental field study in reservoirs, the nutrient-limited growth rates of phytoplankton have also been found to decrease with increases in water temperature, and this was explained by competition with bacteria for nutrients (Chzarnowski and Grover 2001). The laboratory studies suggest that in such conditions, phytoplankton responses depend on the limiting-nutrient cell quota (Rhee and Gotham 1981; Raven and Geider 1988). Modeling and laboratory studies have shown that under light saturation and/or nutrient limitation, photosynthesis products in phytoplankton cells are accumulated mainly in energy-storage polymers (Geider et al. 1998). Since the 1990s, DIP concentrations in the productive zone of Lake Geneva have dropped below the value (10 μg P L^{-1}; Fig. 1B,C) below which P limitation of phytoplankton is expected to occur during reoligotrophication of lakes (Sas 1989; Manca and Ruggiu 1998). In such a context, P cell quota in phytoplankton might have decreased since increase in temperature may increase P demand in the cells and has been found to cause decrease in minimum P cell quota in culture (Rhee and Gotham 1981). Hence, increased P demand may have negative effects on phytoplankton metabolism, given that P can represent a small fraction of cell dry weight (Raven and Geider 1988; Karl 2000) and that important P-rich compounds such as nucleic acids or sugar phosphates cannot be substituted by non–P-containing compounds in cells in response to P scarcity. Respiration rates of cells and species susceptibility to photoinhibition may also increase with temperature (Staehr and Sand-Jensen 2006); this might have occurred in summer in Lake Geneva, as high temperature and high light intensities prevail during this season. At saturating light intensities, enzymatic rather than photochemical reactions are rate limiting and regulated by temperature (Davison 1991). Hyperbolic relationships similar to those found here describing nutrient influence on photosynthesis response to temperature have so far been reported only in the laboratory (Rhee and Gotham 1981; Raven and Geider 1988). The occurrence of such curves here strongly suggests that the limiting-nutrient cell quota–based mechanism also operates in natural environments and plays a key role in determining phytoplankton productivity response to warming of waters. The present observations undoubtedly result from both the direct (effects of temperature on physiological rates) and the indirect (changes in the water column stability) effects of warming. I suggest that phytoplankton respond positively to warming of waters when nutrient cell quota is high and that the responses decline with this nutrient cell quotas to become negative when the nutrient content of cells is very low.

To summarize, this study has shown, using several approaches (Arrhenius plot, calculation of the slopes corresponding to the magnitude of the responses, analyse of covariance) and both Chl *a*–normalized maximum rates of photosynthesis rates and vertically integrated production, that it is important to consider nutrient conditions in a lake when analyzing the mechanisms underlying the effect of global warming on phytoplankton productivity. This likely also holds for ocean and marine ecosystems since nutrients are essential for phytoplankton. The limiting-nutrient cell quota–based mechanism seemed to play a key role in PP responses. These findings are likely one important step in this challenge; they strongly suggest that the long-term responses of PP to warming of waters might be quite different in nutrient-rich vs. nutrient-poor lakes. Future warming might thus have different consequences on trophic interactions and ecosystem function and services in

these two types of ecosystems. However, given that ecosystem dynamics are complex and nonlinear, that site specificity may be important, and that mesocosms or microcosms cannot mimic all aspects of climate change, full understanding of climate effects on lakes will likely require more ecosystem-scale studies.

Acknowledgments

I thank Val H. Smith and John A. Raven for their critical comments on versions of the manuscript. Discussions with Val H. Smith stimulated and improved this work. The long-term record of data on Lake Geneva was financially supported by the Commission Internationale pour la Protection des Eaux du Léman (CIPEL) and comes from the work of many people, including P. Blanc, J. P. Bosse, J. Pelletier, J.-P. Moille, J. C. Hustache, P. Chifflet, P. Perney, C. Leboulanger, and J. Lazzarotto. I thank the two anonymous reviewers for their constructive comments.

References

Association Française de Normalisation. 1990. Water assessment methods, 4th ed. Association Française de Normalisation.

Behrenfeld, M. J., and P. G. Falkowski. 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr. **42:** 1–20.

———, and others. 2006. Climate-driven trends in contemporary ocean productivity. Nature **444:** 752–755, doi:10.1038/nature05317

Blanc, P., C. Corvi, S. Khim-Heang, and F. Rapin. 2000. Evolution physico-chimique du Léman. Rapport de la Commission Internationale Pour la Protection des Eaux du Léman, campagne 1999, 33–58. Available from http://www.cipel.org

Chrzanowski, T. H., and J. P. Grover. 2001. Effects of mineral nutrients on the growth of bacterio- and phytoplankton in two southern reservoirs. Limnol. Oceanogr. **46:** 1319–1330.

Coles, J. F., and R. C. Jones. 2000. Effect of temperature on photosynthesis-light response and growth of phytoplankton species isolated from a tidal freshwater river. J. Phycol. **36:** 7–16, doi:10.1046/j.1529-8817.2000.98219.x

Davison, R. I. 1991. Environmental effects on algal photosynthesis: Temperature. J. Phycol. **27:** 2–8, doi:10.1111/j.0022-3646.1991.00002.x

Dokulil, M. T., and others. 2006. Twenty years of spatially coherent deepwater warming in lakes across Europe related to North Atlantic Oscillation. Limnol. Oceanogr. **51:** 2787–2793.

Doney, S. C. 2006. Plankton in a warmer world. Nature **444:** 695–696, doi:10.1038/444695a

Elliott, J. A., I. D. Jones, and S. J. Thackeray. 2006. Testing the sensitivity of phytoplankton communities to changes in water temperature and nutrient load, in a temperate lake. Hydrobiologia **559:** 401–411, doi:10.1007/s10750-005-1233-y

Eppley, R. W. 1972. Temperature and phytoplankton growth in the Sea. Fish. Bull. **70:** 1063–1085.

Gao, Y., G. J. Smith, and R. S. Alberte. 2000. Temperature dependence of nitrate reductase activity in marine phytoplankton: biochemical analysis and ecological implications. J. Phycol. **36:** 304–313, doi:10.1046/j.1529-8817.2000.99195.x

Geider, R. J., H. L. MacIntyre, and T. M. Kana. 1998. A dynamic regulatory model of phytoplankton acclimation to light, nutrient and temperature. Limnol. Oceanogr. **43:** 679–694.

Gerten, D., and R. Adrian. 2002. Effects of climate warming, North Atlantic Oscillation, and El Niño-Southern Oscillation on thermal conditions and plankton dynamics in Northern Hemispheric lakes. Sci. World J. **2:** 586–606.

———, and ———. 2003. Difference in the persistency of the North Atlantic Oscillation signal among lakes. Limnol. Oceanogr. **46:** 448–455.

Goldman, C. R., A. Jassby, and T. Powell. 1989. Interannual fluctuations in primary productivity: Meteorological forcing at two subalpine lakes. Limnol. Oceanogr. **34:** 310–323.

Huber, V., R. Adrian, and D. Gerten. 2008. Phytoplankton response to climate warming modified by trophic state. Limnol. Oceanogr. **53:** 1–13.

Intergovernmental Panel on Climate Change. 2001. Climate change 2001—synthesis report. Intergovernmental Panel on Climate Change.

Karl, D. M. 2000. Phosphorus, the staff of life. Nature **406:** 31–33, doi:10.1038/35017683

Lerman, A. 1978. Lakes, chemistry, geology, physics. Springer-Verlag.

Livingstone, D. M., and M. T. Dokulil. 2001. Eighty years of spatially coherent Austrian lake surface temperatures and their relationship to regional air temperature and the North Atlantic Oscillation. Limnol. Oceanogr. **46:** 1220–1227.

Magnuson, J. J., and others. 2003. Historical trends in lake and river ice cover in the Northern Hemisphere. Science **289:** 1743–1746, doi:10.1126/science.289.5485.1743

Manca, M., and D. Ruggiu. 1998. Consequences of pelagic food web changes during a long-term lake oligotrophication process. Limnol. Oceanogr. **43:** 1368–1373.

McKnight, D., D. F. Brakke, and P. J. Mulholland. 1996. Freshwater ecosystems and climate change in North America. Limnol. Oceanogr. **41:** 815–1149.

Molinero, J. C., O. Anneville, S. Souissi, L. Lainé, and D. Gerdeaux. 2007. Decadal changes in water temperature and ecological time series in Lake Geneva, Europe—relationship to Atlantic climate variability. Clim. Res. **34:** 15–23, doi:10.3354/cr034015

O'Reilly, C. M., S. R. Alin, P.-D. Plisnier, A. S. Cohen, and B. A. McKee. 2003. Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. Nature **424:** 766–768, doi:10.1038/nature01833

Raven, J. A., and R. J. Geider. 1988. Temperature and algal growth. New Phytol. **110:** 441–461, doi:10.1111/j.1469-8137.1988.tb00282.x

Rhee, G. I., and J. Gotham. 1981. The effects of environmental factors on phytoplankton growth: temperature and interactions of temperature with nutrient limitations. Limnol. Oceanogr. **26:** 635–648.

Sas, H. [ed.]. 1989. Lake restoration by reduction of nutrient loading: Expectations, experiences and extrapolations. Academia Verlag Richarz.

Schindler, D. W., and others. 1990. Effects of climatic warming on lakes of the central boreal forest. Science **250:** 967–970, doi:10.1126/science.250.4983.967

Smith, V. H. 1983. Light and nutrient dependence of photosynthesis by algae. J. Phycol. **19:** 306–313, doi:10.1111/j.0022-3646.1983.00306.x

Staehr, P. A., and K. Sand-Jensen. 2006. Seasonal changes in temperature and nutrient control of photosynthesis, respiration and growth of natural phytoplankton communities. Freshw. Biol. **51:** 249–262, doi:10.1111/j.1365-2427.2005.01490.x

Steeman-Nielsen, E. 1952. The use of radio-active carbon for measuring organic production in the sea. J. Cons. Int. Explor. Mer. **18:** 117–140.

Strickland, J. D. H., and T. W. Parsons. 1968. A practical handbook for sea water analyses. Bull. Fish. Res. Board Can. **167:** 1–311.

Verburg, P., R. E. Hecky, and H. Kling. 2003. Ecological consequences of a century of warming in Lake Tanganyika. Science **301:** 505–507, doi:10.1126/science.1084846

Vollenweider, R. A., and J. Kerekes. 1982. Eutrophication of waters: Monitoring, assessment and control. Organization for Economic Cooperation and Development.

Wigley, T. M. L., and S. C. B. Raper. 2001. Interpretation of high projections for global-mean warming. Science **293:** 451–454, doi:10.1126/science.1061604

Associate editor: Anthony Larkum

Received: 26 June 2009
Accepted: 07 December 2009
Amended: 31 December 2009