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Climatic forcing and primary productivity in a subalpine lake: Interannual variability as a natural experiment

Abstract—We analyzed a 42-yr record of primary productivity in small, subalpine Castle Lake to determine how climatic variability might influence lake primary productivity. A Pacific Decadal Oscillation (PDO) polarity reversal in 1977 significantly affected winter air and summer water temperatures in Castle Lake. The timing of lake ice-out was explained by spring air temperature and winter total precipitation ($r^2 = 0.72$) and significantly affected water temperature ($r^2 = 0.74$). Primary productivity was negatively correlated with ice-out date and positively correlated with primary productivity during the previous year ($r^2 = 0.47$). Alternatively, primary productivity was positively correlated with water temperature and primary productivity during the previous year ($r^2 = 0.49$). Ammonium availability immediately after ice-out was significantly related to primary productivity from the previous and the current year, suggesting that nutrient availability is an important mechanism for the serial correlation. *Daphnia* and cyanobacteria biomass also increased during warmer years. Our results suggest that variability in air temperature and precipitation from global warming, PDO, and the El Niño Southern Oscillation (ENSO) influence primary productivity and plankton communities in North American dimictic lakes.

There is considerable concern that human activities are transforming the global climate and that anthropogenically driven global climatic warming might alter biological processes (IPCC 2001). During the last 100 years, global mean surface temperature has increased by ~0.6 ± 0.2°C (IPCC 2001), while anthropogenic greenhouse gas loading has increased markedly. General circulation models (GCMs) predict that doubling atmospheric concentrations of the greenhouse gas CO_2 could cause global temperature increases of 1.7–4.9°C over the next century (Wigley and Raper 2001). This projected change in global temperatures has also increased scientific interest in the relationship between climate and basic biological processes in natural ecosystems.

Recent simulation studies have predicted that doubling CO_2 would shorten the ice cover period and increase water temperatures in lakes (Fang and Stefan 1999). One of the most important biological processes that have the potential to be affected by climatic change is primary productivity. Primary production is also important because it consumes CO_2 and thus sequesters some of this greenhouse gas and plant nutrients, especially at the scale of the world's oceans. Despite the tremendous interest in this topic, there is limited empirical evidence indicating how lake primary productivity might respond to global warming (Carpenter et al. 1992; Magnuson et al. 1997; however, *see* Byron and Goldman 1990; Findlay et al. 2001). Because primary production provides the energetic basis for almost all ecosystems, it is essential to know how interannual variability of primary productivity is controlled by the underlying mechanisms that drive this process at longer time scales. This study investigates the effects of climate variability, especially in air temperature, on interannual variability of primary production and the plankton community in a small subalpine lake.

The primary productivity and general limnology of Castle Lake, a small subalpine lake in the Siskiyou Mountains of northern California, have been monitored every 5–7 d for 4 months (from June to September), as well as monthly in the spring and in fall since 1959. Primary productivity was measured weekly at 2.5-m increments from 0 to 30 m depth on each sampling date using standard light/dark ^{14}C uptake methods. Daily primary productivity was calculated as depth-weighted averages for the summer period and was averaged into monthly means by trapezoidal integration (Jassby et al. 1990). Summer means were calculated from the four monthly averages per summer season. In early summer, Castle Lake typically has two primary productivity peaks at ~3 and 20 m. The deeper primary productivity peak disappears as summer progresses. The thermocline usually occurs between 6 and 13 m in Castle Lake (Strub et al. 1985). In this study, we defined the epi-metalimnion as a layer between 0 and 12.5 m and the hypolimnion as the layer between 12.5 and 30 m. We used whole-column averages for primary productivity and water temperature. Climate data comprising continuous daily records for the entire study period were obtained from a weather station in McCloud, California, which is ~20 km from Castle Lake. Ammonium was analyzed within 24 h of sample collection with the phenol-hypochlorite method. Phytoplankton were counted and measured with a Wild inverted microscope by the Utermöhl technique to generate biovolume estimates for each taxon. Other procedural details are described in Goldman and de Amezaga (1984) and Jassby et al. (1990).

Most statistical analyses were performed with S-Plus 6 for Windows, whereas multicollinearity diagnoses using the variance inflation factor (VIF) were done with SAS 6.12 for Macintosh. Serious multicollinearity (VIF $>$ 10) was not detected in our analyses. To check for autocorrelation in the time series, we carried out Durbin–Watson (DW) tests with our multiple regressions and reported the probability of having a significant autocorrelation ($P <$ DW). For each variable in the multiple regression analyses, we calculated squared semipartial correlation coefficients that describe the proportion of unique variance accounted for by each predictor relative to total variance for the dependent variable. For intervention analyses, we tested a step intervention at the

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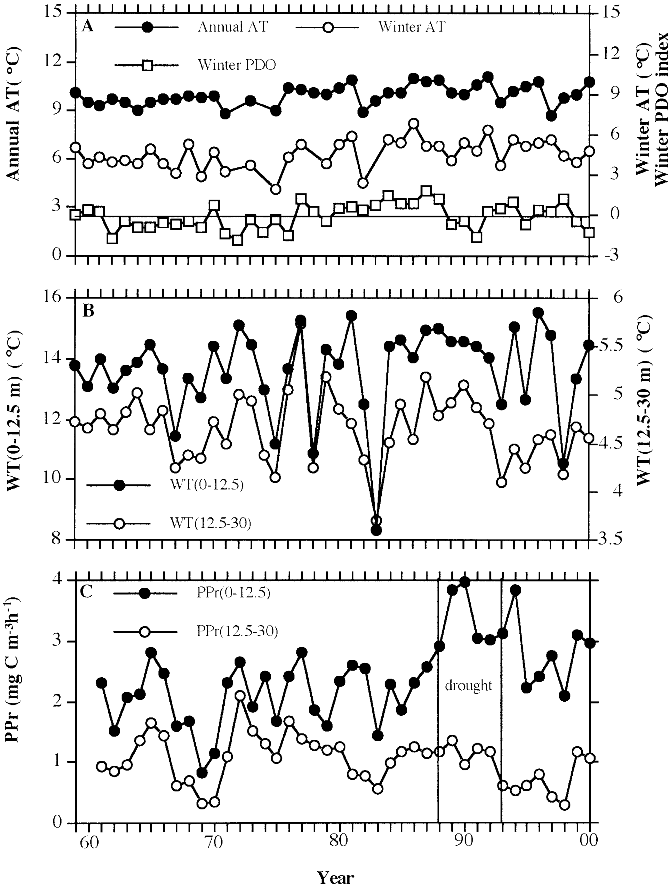

Fig. 1. (A) Mean annual air temperature and mean winter air temperature (AT) at the McCloud Weather Station located 20 km from Castle Lake and the average winter (November–March) Pacific Decadal Oscillation (PDO) index. (B) Water temperature (WT) in the epi-metalimnion, WT(0–12.5 m), and in the hypolimnion, WT(12.5–30 m). (C) Primary productivity (PPr) in the epi-metalimnion and in the hypolimnion. Before we examined the long-term trends for these variables, we conducted Durbin–Watson tests to ascertain whether these time series had autocorrelations. A multi-year ''drought'' from 1988 to 1993 is shown in panel C.

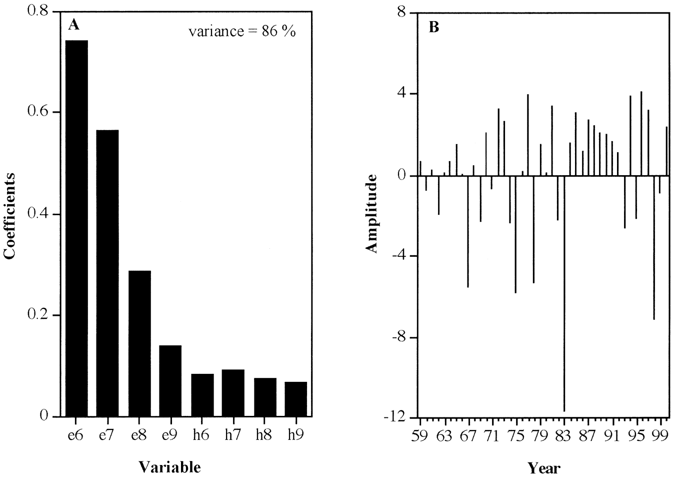

Fig. 2. (A) Mode and (B) amplitudes determined by a PCA of the eight time series (i.e., two layers and 4 months) of monthly mean water temperature from June to September in the epi-metalimnion and the hypolimnion. Panel A: e, epi-metalimnion; h, hypolimnion. Numerals indicate months. For example, e6 indicates epi-metalimnion in June.

Pacific Decadal Oscillation (PDO) polarity reversal year (1977) for winter (January–April) air temperature, annual air temperature, the winter El Niño Southern Oscillation (ENSO) index, water temperature, winter precipitation, and summer primary productivity (Wei 1990). Monthly PDO data from November to March were averaged to produce a winter PDO index (Mantua et al. 1997).

During the 42-year study period, Castle Lake and the surrounding region experienced a significant increase in mean annual air temperatures of 0.91°C (Fig. 1). Mean annual air temperature and mean winter (January–April) air temperature showed significant increasing trends over time (yr) (for mean annual air temperature [°C], slope = 0.0218, intercept = −33.124, $n = 40$, $r^2 = 0.195$, $P = 0.0044$; for mean winter air temperature [°C], slope = 0.031, intercept = −57.724, $n = 40$, $r^2 = 0.141$, $P = 0.017$). However, mean summer water temperature and primary productivity did not show any clear trends after removing a serial correlation (1-yr autocorrelation). This is probably attributable to a greater influence of short-term climatic processes relative to the direct effects of warming through air temperature on the Castle Lake ecosystem.

Large-scale climate events prevalent in the western United States include ENSO and PDO. Previous studies found that ENSO was associated with unusually low or high primary productivity in Castle Lake (Strub et al. 1985; Jassby et al. 1990). In the present study, we also investigated the influence of the PDO on air and water temperatures and primary productivity. Intervention analyses suggested that a PDO polarity reversal (which occurred in 1977) significantly affected winter air and summer water temperatures in Castle Lake, whereas there was no evidence of correlation of the PDO with annual air temperature or primary productivity. PDO index was correlated with winter air temperature ($r^2 = 0.18$, $P = 0.0063$, $n = 40$), but further correlations of PDO were not detected.

From principal component analyses (PCA) (*see* Jassby 2000 for details), we found that the majority of interannual variability in water temperature took place in June and July and in the epi-metalimnion (Fig. 2). This pattern suggests a connection between water temperature and presummer processes such as ice-out and spring warming. A Monte Carlo test showed that there is only one statistically significant mode (i.e., the layers and months vary together). This supports the use of mean water temperature over the entire water column during the summer season.

On the basis of a 27-yr data set of primary productivity and other climatic and limnological variables, Goldman et al. (1989) proposed a conceptual model in which summer primary productivity is regulated by snowfall (thickening snow-ice pack delaying ice-out timing), winter total precipitation (through hydraulic flushing), and a serial correlation (autocorrelation from previous year's primary productivity)

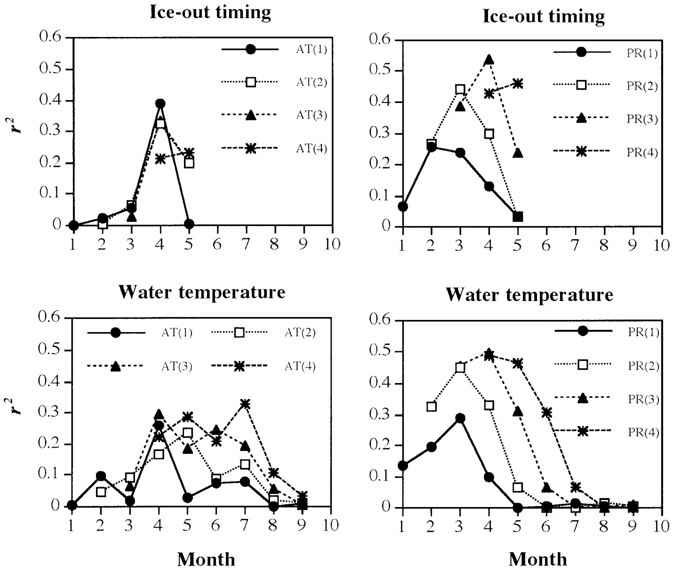

Fig. 3. Coefficients of determination (r^2) between monthly means and moving averages of (A) air temperature (AT) and (B) precipitation (PR) with ice-out date, (C) air temperature, and (D) precipitation with water temperature PCA amplitudes for Castle Lake. Numbers in parentheses indicate the number of months averaged. Moving averages were plotted on the last month. For example, the moving average between March and June for air temperature was plotted as June on the x-axis.

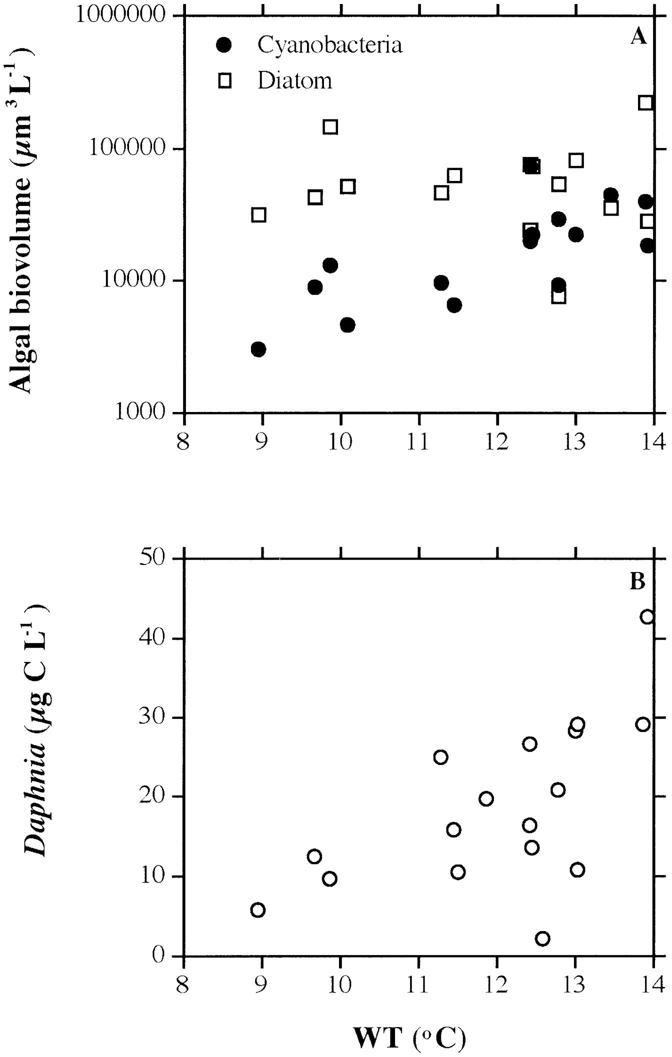

Fig. 4. Water temperature (WT) versus (A) mean annual diatom and cyanobacteria biovolume and (B) mean annual *Daphnia rosea* biomass in the whole-water column of Castle Lake. Cyanobacteria biovolume had a significant positive relationship ($y = -56{,}462.8 + 6597.0x$; $r^2 = 0.306$; $n = 15$; $P = 0.0326$) with water temperature while diatom biovolume was not significantly correlated. *Daphnia* biomass was significantly correlated with water temperature ($y = -34.79 + 4.46x$; $r^2 = 0.373$; $n = 17$; $P = 0.0092$).

of unknown origin. Furthermore, Jassby et al. (1990) showed that early and later summer primary productivity were regulated by different variables. The model of Jassby et al. (1990) is quite comprehensive and includes both climatic and trophic factors to explain summer primary productivity at Castle Lake. However, mechanisms for the serial correlation in primary productivity remained unknown, and the model did not directly include air and water temperatures, two important factors in predicting ecosystem responses to future climate change. Recent studies on the North Atlantic Oscillation (NAO) suggest that both winter and spring weather conditions (e.g., air temperature) influence water temperature and thus biological interactions in lakes (Gerten and Adrian 2000). To extend these studies, we chose to examine the relative importance of the prevailing weather, such as precipitation and air temperature, on lake water temperatures.

In Castle Lake, the timing of ice-out is an important factor regulating primary productivity via its influence on algal biomass (chlorophyll) accumulation during the phytoplankton growing season and nutrient supply from the hypolimnion as a result of vertical mixing (Jassby et al. 1990). Ice-out date at Castle Lake is related to winter snowfall (Goldman et al. 1989) and total precipitation (Goldman and de Amezaga 1984). Because the climatic data used in this study came from a weather station located at a lower elevation (where it sometimes rains when it snows in the Castle Lake area), we regard total precipitation data as more representative of hydrological inputs to Castle Lake than snowfall or rainfall. Because air temperature might influence the thickness of the ice-snow pack in addition to snowfall (Livingston 1999), we built a two-factor (air temperature and total precipitation) regression model for the ice-out date. Of monthly and multimonthly averages of air temperature and total precipitation, April mean air temperature (T_{AIR4}, °C) and total precipitation between February and April (PREC_{24}, mm) showed the highest correlation with ice-out date (day of year) (Fig. 3A,B). With the use of these variables ($P = 0.0001$ for T_{AIR4} and $P < 0.0001$ for PREC_{24}), our model explained 72% of the variation in the ice-out date in our 42-yr data set ($n = 35$).

$$D_{\text{ice-out}} = 141.79 + (-4.97) \times T_{\mathrm{AIR4}} + 0.148 \times \mathrm{PREC}_{24} \quad (1)$$

Squared semipartial correlation coefficients for T_{AIR4} and

$PREC_{24}$ were 0.166 and 0.324, respectively. Autocorrelation in the residuals was checked with the Durbin–Watson test, and the probability of autocorrelation ($P < \mathrm{DW}$) was 0.31. Similarly, T_{AIR47} and $PREC_{24}$ exhibited the highest correlation with the amplitudes for the PCA of summer water temperature (Fig. 3C,D). Winter total precipitation and spring air temperature appear to be important in determining the ice-out date and summer air temperature at Castle Lake.

Using ice-out date and the serial correlation in primary productivity, we were able to explain 47% of the variation in the long-term primary productivity record. This regression model comprised a positive serial correlation (e.g., the previous year's primary productivity, PPr_{t-1}; $P = 0.0009$) and a negative correlation with ice-out date ($P = 0.0009$; $n = 37$; $P < \mathrm{DW} = 0.1661$).

$$\mathrm{PPr}_t = 531.37 + (-2.42) \times D_{\text{ice-out}} + 0.47 \times \mathrm{PPr}_{t-1} \quad (2)$$

PPr_t is the mean summer primary productivity (mg C m^{-2} d^{-1}). Squared semipartial correlation coefficients for $D_{\text{ice-out}}$ and PPr_{t-1} were 0.204 and 0.205, respectively. Primary productivity tended to be high when the previous year's primary productivity and winter air temperature were high and the previous winter's total precipitation was low.

Among numerous effects of ice-out timing, the most obvious is on water temperature. Ice-out date explained 74% of the interannual variability for summer water temperatures ($y = 19.31 - 0.05x$; $r^2 = 0.744$, $n = 37$, $P < 0.0001$). Thus, variability for primary productivity could also be accounted for by seasonal mean water temperature (WT; $P = 0.0003$), replacing ice-out date accordingly ($n = 41$, $P < \mathrm{DW} = 0.2494$).

$$\mathrm{PPr}_t = -270.58 + (37.86) \times \mathrm{WT} + (0.51) \times \mathrm{PPr}_{t-1} \quad (3)$$

This statistical model explained 49% of interannual variability for Castle Lake primary productivity and squared semipartial correlation coefficients for WT and PPr_{t-1} were 0.219 and 0.242, respectively. Probability for PPr_{t-1} variable was 0.0001.

Both ice-out timing and water temperature are associated with plausible causal pathways, but we do not have enough data to resolve which is most important. Ice-out timing affects phytoplankton standing crop by changing the phytoplankton growing season, providing turbulent conditions for diatom growth (Gerten and Adrian 2000), reducing initial phytoplankton biomass by hydraulic flushing after ice-snow pack melting (Goldman et al. 1989), and modifying nutrient supply via the extent of spring mixing (Jassby et al. 1990). Elevated water temperature can increase primary productivity either by metabolically enhancing photosynthesis or by increasing nutrient availability by accelerating nutrient regeneration rates (Rustad et al. 2001). To understand how the spring ice-out process affects interannual variability of primary productivity via flushing, water temperature, and the length of the growth period, it will be necessary to focus future sampling between the ice-out date and the start of the summer growing season.

Primary productivity in Castle Lake has previously been shown to have a strong positive correlation with the previous year's primary productivity (Goldman et al. 1989; Jassby et al. 1990); however, the mechanism behind this strong serial correlation was not clear. We hypothesized that higher primary productivity might increase nutrient supplies in the following year. Castle Lake is nitrogen and phosphorus colimited and inorganic nutrient concentrations in the photic zone decrease rapidly immediately after ice-out and spring mixing (Elser et al. 1995). Of available nitrogen forms, spring ammonium concentration (mean ammonium concentration during the month after ice-out, NHX_t [μg N L^{-1}]) explained summer primary production much better than spring nitrate concentrations (NOX_t [μg N L^{-1}]) ($P = 0.003$ for NHX; $P = 0.330$ for NOX).

$$\mathrm{PPr}_t \approx \mathrm{NHX}_t + \mathrm{NOX}_t \quad (4)$$

Spring inorganic phosphorus data were not available for many years. Therefore, we used NHX_t as a surrogate for spring nutrient availability for primary production in the summer and substituted the serial correlation term (PPr_{t-1}) in Eqs. 2 and 3 with NHX_t.

$$\mathrm{PPr}_t = 648.31 + (-2.46) \times D_{\text{ice-out}} + (13.62) \times \mathrm{NHX}_t \quad (5)$$

$$\mathrm{PPr}_t = (-82.01) + (32.00) \times \mathrm{WT}_t + (15.90) \times \mathrm{NHX}_t \quad (6)$$

The substitution of NHX_t for the serial correlation term (PPr_{t-1}) improved the primary productivity model, explaining 73% (Eq. 5) and 63% (Eq. 6) of the variation in the long-term primary productivity record without causing autocorrelations in the residuals ($P < \mathrm{DW} = 0.8022$ and 0.4410 for Eqs. 5 and 6, respectively). Squared semipartial correlation coefficients for $D_{\text{ice-out}}$ ($P = 0.0004$) and NHX_t ($P = 0.0060$) were 0.313 and 0.156 for Eq. 5, and those for WT_t ($P = 0.0060$) and NHX_t ($P = 0.0052$) were 0.224 and 0.214 for Eq. 6. Higher primary productivity significantly contributed to a larger anoxic layer (depths with DO < 1 mg O_2 L^{-1}; $r^2 = 0.231$, intercept $= 1.719$, slope $= 0.009$, $n = 35$, $P = 0.0035$), which should result in greater releases of ammonium and dissolved phosphorus from the sediments. Higher water temperatures also could have enhanced nutrient regeneration throughout the water column. Both mechanisms could result in a greater nutrient supply being available for the next year's production.

Further analyses could not elucidate the mechanism underlying the connection between primary productivity and nutrient availability with our current data set. For example, both water temperature (WT_{t-1}) and the anoxic layer depth (ANOXIA_{t-1} [m]) during the previous year did not significantly improve a model using the previous year's primary production (PPr_{t-1}) ($P = 0.183$ for WT_{t-1}; $P = 0.683$ for ANOXIA; $P = 0.006$ for PPr_{t-1}).

$$\mathrm{NHX}_t \approx \mathrm{PPr}_{t-1} + \mathrm{WT}_{t-1} + \mathrm{ANOXIA}_{t-1} \quad (7)$$

Similarly, we could not detect significant contributions from winter climate variables such as winter precipitation (PRCP_t [mm]) or winter snowfall (SNOW_t [mm]) to explain NHX_t ($P = 0.253$ for PRCP_t; $P = 0.118$ for SNOW_t; $P = 0.005$ for PPr_{t-1}).

$$\mathrm{NHX}_t \approx \mathrm{PPr}_{t-1} + \mathrm{PRCP}_t + \mathrm{SNOW}_t \quad (8)$$

Winter climate variables such as winter precipitation and winter air temperature affect summer primary productivity through ice-out timing and water temperature. In addition, nutrient availability in the spring is influenced by the previous year's primary productivity and influences summer primary productivity in the following summer.

Studies of producer communities in other systems have shown that climate warming affects species composition (Nehring 1998). For Castle Lake, we found that increasing water temperatures were accompanied by increasing mean summer cyanobacteria biovolume, whereas the mean summer diatom biovolume was unrelated to summer water temperatures (Fig. 4A). Other phytoplankton groups also did not show significant trends with water temperature. Changes in producer community composition, such as the relative increase in cyanobacteria biomass observed in Castle Lake, can affect a multitude of ecosystem processes, including trophic transfer efficiencies at the producer–consumer interface (Park et al. 2003).

To explore how climate-induced variability in water temperature and primary productivity affect *Daphnia rosea* biomass, we constructed a multiple regression model for mean summer *D. rosea* biomass (DAPHNIA$_t$ [μg DW L^{-1}]) using mean summer water temperature (WT$_t$) and primary productivity (PPr$_t$) ($n = 17$, $P <$ DW $= 0.1271$):

$$\mathrm{DAPHNIA}_t \approx \mathrm{PPr}_t + \mathrm{WT}_t \tag{9}$$

We found WT explained *Daphnia* biomass significantly (Fig. 4B), whereas PPr did not ($P = 0.003$ for WT; $P = 0.105$ for PPr), supporting the results reported by Straile (2000). Squared semipartial correlation coefficients for PPr$_t$ and WT$_t$ were 0.199 and 0.483, respectively. These results are consistent with findings from European lakes, where warm winter air temperatures caused by the NAO enhanced *Daphnia* biomass (Straile and Adrian 2000).

Our analyses of the long-term Castle Lake data set showed that climatic forcings such as spring air temperature and winter precipitation were related to variability in the timing of lake ice-out and that, in turn, ice-out timing influenced water temperature, primary productivity, phytoplankton community composition, and *Daphnia* biomass. Our results suggest that changes in air temperature and precipitation as a result of global warming, PDO, and ENSO could substantially affect primary productivity and plankton communities in North American dimictic lakes.

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