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 basic biological processes in natural ecosystems.

Increased scientific interest in the relationship between climate and basic biological processes in natural ecosystems.

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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, r² = 0.195, P = 0.0044; for mean winter air temperature [°C], slope = 0.031, intercept = −57.724, n = 40, r² = 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 (r² = 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)
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 Amzaga 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 ($T_{\text{AIR4}}$, °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 $T_{\text{AIR4}}$ 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 ($n = 35$).

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

Squared semipartial correlation coefficients for $T_{\text{AIR4}}$ and

![Graph showing 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.](image1)

![Graph showing 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 ($y = -34.79 + 4.46x; r^2 = 0.373; n = 17; P = 0.0092$).](image2)
for by seasonal mean water temperature (WT; variability for primary productivity could also be accounted replacing ice-out date accordingly (n = 0.219 and 0.242, respectively. Probability for PPr 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, [µg N L⁻¹]) explained summer production much better than spring nitrate concentrations (NOX, [µg N L⁻¹]) (P = 0.003 for NHX; P = 0.330 for NOX).

\[ \text{PPr}_t = \text{NHX}_t + \text{NOX}_t, \quad (4) \]

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

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

\[ \text{PPr}_t = (-82.01) + (32.00) \times \text{WT}_t + (15.90) \times \text{NHX}_t \quad (6) \]

The substitution of NHX, for the serial correlation term (\(\text{PPr}_{t-1}\)) 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 (\(P < \text{DW} = 0.8022\) and 0.4410 for Eqs. 5 and 6, respectively). Squared semipartial correlation coefficients for \(D_{\text{ice-out}}\) and \(\text{PPr}_{t-1}\) 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 (\(n = 41, P < \text{DW} = 0.2494\)).

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

This statistical model explained 49% of interannual variability for Castle Lake primary productivity and squared semipartial correlation coefficients for WT and \(\text{PPr}_{t-1}\) were 0.219 and 0.242, respectively. Probability for \(\text{PPr}_{t-1}\) 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 growth 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.
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, [μg DW L⁻¹]) using mean summer water temperature (WT) and primary productivity (PPr) (n = 17, P < DW = 0.1271):

\[ \text{DAPHNIA} = \text{PPr} + \text{WT}, \]  

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 Strale (2000). Squared semipartial correlation coefficients for PPr and WT 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 (Strale 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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**References**


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