

Climatic effects on the phenology of lake processes

MONIKA WINDER* and DANIEL E. SCHINDLER*†

*School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA, †Department of Biology, University of Washington, Box 351800, Seattle, WA 98195-1800, USA

Abstract

Populations living in seasonal environments are exposed to systematic changes in physical conditions that restrict the growth and reproduction of many species to only a short time window of the annual cycle. Several studies have shown that climate changes over the latter part of the 20th century affected the phenology and population dynamics of single species. However, the key limitation to forecasting the effects of changing climate on ecosystems lies in understanding how it will affect interactions among species. We investigated the effects of climatic and biotic drivers on physical and biological lake processes, using a historical dataset of 40 years from Lake Washington, USA, and dynamic time-series models to explain changes in the phenological patterns among physical and biological components of pelagic ecosystems. Long-term climate warming and variability because of large-scale climatic patterns like Pacific decadal oscillation (PDO) and El Niño–southern oscillation (ENSO) extended the duration of the stratification period by 25 days over the last 40 years. This change was due mainly to earlier spring stratification (16 days) and less to later stratification termination in fall (9 days). The phytoplankton spring bloom advanced roughly in parallel to stratification onset and in 2002 it occurred about 19 days earlier than it did in 1962, indicating the tight connection of spring phytoplankton growth to turbulent conditions. In contrast, the timing of the clear-water phase showed high variability and was mainly driven by biotic factors. Among the zooplankton species, the timing of spring peaks in the rotifer *Keratella* advanced strongly, whereas *Leptodiptomus* and *Daphnia* showed slight or no changes. These changes have generated a growing time lag between the spring phytoplankton peak and zooplankton peak, which can be especially critical for the cladoceran *Daphnia*. Water temperature, PDO, and food availability affected the timing of the spring peak in zooplankton. Overall, the impact of PDO on the phenological processes were stronger compared with ENSO. Our results highlight that climate affects physical and biological processes differently, which can interrupt energy flow among trophic levels, making ecosystem responses to climate change difficult to forecast.

Keywords: clear-water phase, climate change, *Daphnia*, El Niño–southern oscillation, *Keratella*, *Leptodiptomus*, Pacific decadal oscillation, phenology, phytoplankton, spring bloom, stratification, zooplankton

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Introduction

In environments with strong seasonality, growth and reproduction of many species is usually restricted to a short time window over the annual cycle (Fretwell, 1972). Analysis of historical datasets show that the seasonal dynamics of many plant and animal species have been

affected by climate change during the latter part of the 20th century (Parmesan & Yohe, 2003; Root *et al.*, 2003). Spring phenological patterns of many species have been especially responsive to climate warming (IPCC, 2001), and a number of aquatic and terrestrial species have advanced their vernal activities over the past few decades (Reid *et al.*, 1998; Walther *et al.*, 2002). Whereas phenological shifts of single species are documented, much less is known how physical processes and species at different trophic levels respond simultaneously to climate change.

Correspondence: Monika Winder, fax +1 206 685 7471, e-mail: mwinder@u.washington.edu

Climate variability can affect physical and biological processes differently and can have different impacts on taxonomic groups or on various trophic levels (Inouye *et al.*, 2000; Blenckner & Hillebrand, 2002). Recent studies from a variety of ecosystems give evidence that different responses to climate change can decouple species from favorable food conditions (Post *et al.*, 2001; Visser & Holleman, 2001; Winder & Schindler, 2004), which may have profound consequences for communities (Thomas *et al.*, 2001). Therefore, long-term studies of ecosystems, including physical and multiple trophic levels, are required to develop a holistic understanding of climate-driven responses in ecosystems.

Temperate lake ecosystems are characterized by distinct seasonal patterns in physical and biological processes, and growth and reproduction of any species depends strongly on its relationship with other trophic levels (Sommer *et al.*, 1986; Platt *et al.*, 2003). Because of the high heat capacity of water (Hutchinson, 1957), aquatic systems may be especially sensitive to temperature changes and large-scale climate fluctuations, both of which have been shown repeatedly for physical properties of aquatic ecosystems (Schindler *et al.*, 1990; Magnuson *et al.*, 1997; Livingstone & Dokulil, 2001; Straile, 2002). In turn, alterations to the physical

environment may influence the abundance of planktonic species (e.g., Roemmich & McGowan, 1995; Gerten & Adrian, 2002) and interannual variability in plankton succession (Adrian *et al.*, 1999; George & Hewitt, 1999; Straile, 2002), which ultimately have consequences for higher trophic levels (Hill & Magnuson, 1990; Schindler *et al.*, in review).

In temperate lakes, distinct abiotic and biotic activities are concentrated to the spring period (Sommer *et al.*, 1986; Fig. 1 provides an overview of the sequential processes characterizing temperate lakes). With increasing water temperature in the upper water layer (epilimnion), the stability of the water column increases leading to thermal stratification during the summer, with a warm, surface layer overlaying colder waters. The active growing season in lakes generally coincides with the stratification period. In spring, phytoplankton respond to increasing water stability, temperature, nutrient, and light conditions (Reynolds, 1989) through exponential population growth. The phytoplankton spring bloom is typically short lived because grazing, nutrient depletion, and cell sinking result in a crash of phytoplankton producing a noticeable clear-water phase (Sommer *et al.*, 1986). For zooplankton, the period of suitable growth conditions is largely

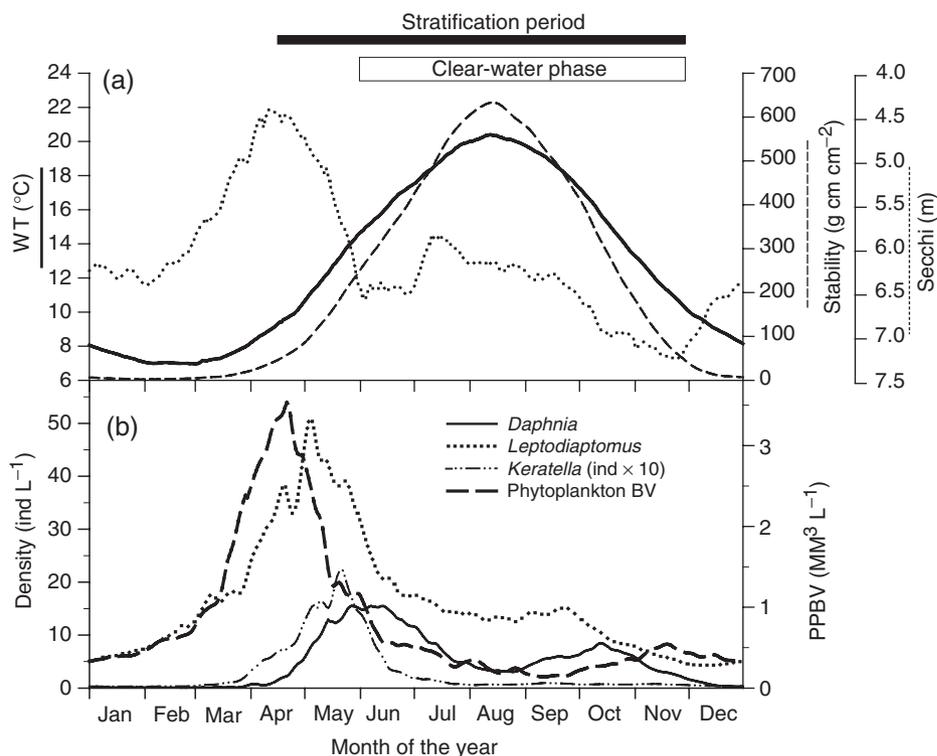


Fig. 1 (a) Seasonal development of water temperature from 0 to 10 m depth, thermal stability and Secchi transparency, and (b) seasonal succession of phytoplankton biovolume (PPBV) and densities of zooplankton species in Lake Washington. Average daily interpolated values were taken from the period 1975 to 2002, which is the period after the lake was recovered from eutrophication.

determined by the timing of phytoplankton growth and water temperature (Sommer *et al.*, 1986), and usually lags the spring phytoplankton bloom.

Because plankton play a central role in trophic transfers through aquatic food webs, it is especially important to understand how climate change affects links between physical processes and plankton dynamics. The goal of our study was to evaluate the effects of long-term changes in climatic and biotic drivers on physical and biological processes in a lake ecosystem. We fit dynamic time-series models (Pole *et al.*, 1994) to a historical dataset of 40 years from a large lake (Lake Washington, USA) to explore the effects of climate and biotic drivers on interannual variability in the timing of several processes characterizing the ecology of temperate lakes. This dataset tracks a period of changing climate, as well as climate variability because of the Pacific decadal oscillation (PDO) (Mantua *et al.*, 2002) and the El Niño–southern oscillation (ENSO) (Philander, 1990). ENSO effects on North America are strongly dependent on the phase of the PDO, such that typical El Niño and La Niña patterns in North America tend to occur during years in which ENSO and PDO extremes are in phase. Positive phases of both the ENSO and PDO are associated with anomalously warm winter temperatures and low winter precipitation along the North American coast, and reverse weather situations are associated with negative ENSO and PDO values (Mantua *et al.*, 1997). ENSO events last for 12–18 months and occur every 2–7 years, whereas PDO persist for 20–35 years and involves abrupt transitions of stable atmospheric conditions (Mantua *et al.*, 2002). While some of the effects of ENSO variation on lakes have been described (e.g., Anderson *et al.*, 1996; Nicholls, 1998), the effects of PDO are virtually unexplored. The PDO has substantial effects on both the physical and biological processes of the North Pacific Ocean (Mantua *et al.*, 1997; Hare & Mantua, 2000). Moreover, PDO is analogous in several ways to the North Atlantic oscillation (NAO) that causes substantial regional coherence in limnological processes of lakes in central Europe and North America (summarized in Straile *et al.*, 2003). Thus, we expect that the PDO has important effects on the temporal organization of aquatic ecosystems in western North America and seek to understand the relative strength of these responses compared with longer-term trends associated with global warming.

Methods

Study site

Lake Washington is a large (surface area 87.6 km²) lake located in the Greater Seattle area in Washington, USA

(47°83'N, 122°15'W; 4 m.a.s.l.) with a mean depth of 32.9 m and maximum depth of 65.2 m. Lake Washington is stratified from early spring until late fall and is mixed entirely during the winter months. The lake has experienced several major changes in the last century, including changes in trophic state and food web structure (reviewed by Edmondson, 1994). Total phosphorus (TP) increased in the early 1940s and reached its highest peak (~100 µg L⁻¹) in the mid-1960s and declined thereafter as a consequence of sewage diversion (Edmondson & Lehman, 1981). By 1975 the lake was considered to be fully recovered from eutrophication. Coincident with the termination of sewage loading, *Daphnia* became the dominant zooplankton grazer as a result of the disappearance of the filamentous blue-green algae *Oscillatoria* and reduced predation from *Neomysis mercedes*, a large predatory crustacean (Edmondson & Litt, 1982). At present, the most abundant zooplankton crustaceans are *Cyclops bicuspidatus*, *Daphnia* (*D. pulicaria*, *D. thorata*, *D. galeata mendotae*), *Leptodiptomus ashlandi*, and the rotifer *Keratella cochlearis*.

Limnological data

Limnological data were collected at a central station over weekly to biweekly intervals during the stratified period and monthly during the unstratified period from 1962 to 2002 (Edmondson, 1994). These data include measurements of temperature at 5 m intervals, Secchi depth transparency, as well as TP and phytoplankton biovolume from the surface water (Edmondson & Lehman, 1981). Phytoplankton were fixed with Lugol's solution prior to enumeration. For each sample, a total of at least 50 cells or colonies were measured to characterize the size range in the population and algal biovolume was estimated using simple geometric analogs (Edmondson, 1997). Zooplankton were collected from 0 to 10 m depth with a Clark–Bumpus sampler fitted with a 130 µm net and a flowmeter to calculate the total sample volume (Edmondson & Litt, 1982). All plankton were identified to species, sex and life stage. Data for rotifer populations were available until 1995 and for *Daphnia* from 1976 to 2002. Monthly averages were determined from the daily interpolated time series of the observed values using the inverse distance weighted method (Watson & Philip, 1985).

Definition of phenological processes

The onset and termination of thermal stratification were calculated using Schmidt's stability index (Hutchinson, 1957). Water density changes in response to temperature were calculated from the Tilton and Taylor approximation

assuming no conductivity effects (Likens, 1985). Schmidt's stability index is a measurement of the water column stability (g cm cm^{-2}) and indicates the amount of work per unit area required to mix the entire lake to an isothermal condition. The value is zero when the water column is isothermal and maximum when the lake is most strongly stratified. Average water column stability was calculated from every sampling date and daily interpolated over the sampling period. An arbitrary threshold of 50 g cm cm^{-2} was taken to estimate the timing of stratification onset and termination. However the choice of this threshold had no effect on the significance of the long-term trend (Winder & Schindler, 2004). The timing of the phytoplankton spring bloom (day of year) was defined as the date when maximum diatom biovolume was observed, because the spring peak is usually dominated by diatoms ($\sim 80\%$ of total phytoplankton biovolume). By using diatoms as a proxy we were able to include the years with high phosphorus concentration in the lake (i.e., years before 1969), when the phytoplankton bloom was prolonged and usually peaked in mid-summer. However, the timing of the diatom bloom was strongly synchronized with the timing of the total phytoplankton bloom not only since 1969 ($n = 34$, $r^2 = 0.97$, $P < 0.001$), but also over the whole sampling period ($n = 41$, $r^2 = 0.75$, $P < 0.001$). Clear-water timing (CWT) was defined by the date when Secchi depth reached 5 m after diatom blooms, which is the smallest Secchi depth observed when a distinct clear-water phase was visible. According to this definition no CWT was observed before 1973, presumably a symptom of eutrophication. The timing of the zooplankton spring peak was defined as the date when maximum density of each taxon was reached. When zooplankton developed multiple peaks in spring, the timing of the peak with the maximum density was taken. In addition, we examined whether a sampling resolution of every second week affected the observed trend in stratification onset, diatoms and rotifers spring peaks. This was done by comparing Schmidt's stability indices or spring peaks of diatoms and rotifers over a sampling period when samples were taken every week (1973–1983) with the exclusion of every second sampling over the same time period. The timing of stratification onset ($r = 0.96$, $P < 0.001$), spring peaks for diatoms ($r = 0.85$, $P < 0.001$), and rotifers ($r = 0.94$, $P < 0.001$) were highly correlated between both temporal resolutions, indicating that the sampling interval of weekly to biweekly observations captures the observed trends.

Climate data

Data on air temperature were obtained from the SeaTac Airport weather station (47°45'N, 122°30'W, 137 m a.s.l.)

(<http://www.ncdc.noaa.gov/>). The ENSO effects were characterized by using the monthly values for the multivariate ENSO index (MEI) obtained from <http://www.cdc.noaa.gov/~kew/MEI/>. Monthly values of the PDO index were provided at <http://tao.atmos.washington.edu/pdo/PDO.latest>. This index is derived as the leading principal component of monthly sea surface temperature anomalies in the North Pacific Ocean, and is highly correlated with other ocean-climate indices, such as the North Pacific index, and Aleutian low-pressure index (Mantua *et al.*, 2002). The PDO is strongly pronounced from October to March. The PDO index is a decadal-scale oscillation that shifted from a cold to a warm phase in the mid-1970s (Fig. 2a). Additional regime shifts occurred in 1989 (Hare & Mantua, 2000) and likely again back to a negative (cold) phase in 1998 (Mantua *et al.*, 2002).

Time-series analysis

For detecting trends in the temperature and the phenological time-series data we used dynamic linear models (DLMs, Pole *et al.*, 1994). Trends were observed from the underlying level of a single-parameter random-walk model, consisting only of an intercept term and no regression effects. DLMs were also used to determine how the observed patterns for physical and biological events were related to environmental drivers (e.g., climate, nutrients) and to the phenology of related processes. The strength of this method is that DLMs recognize that the sequencing of the data is critical such that the level of the response variable at a given time step may be related to its level at earlier time steps in the data. In these models, parameter estimates are influenced only by prior and current data, not by subsequent data. Furthermore, DLMs allow parameters to vary through time to reflect shifts in both the dynamics of the system (i.e., the level of the response variable) and processes that drive these dynamics. For each response variable of interest, several competing models were fit to identify potential explanatory variables and using an information theoretic approach, the performance of these competing alternative models were evaluated. Detailed descriptions of the DLM methodology have been described elsewhere (e.g., Cottingham & Carpenter, 1998; Lamon *et al.*, 1998; Scheuerell *et al.*, 2002). Here, we give only a brief overview of the ideas and concepts of the Bayesian analysis of the DLM.

DLMs are related to the general linear model

$$\mathbf{Y} = \mathbf{X}\theta + v, \quad (1)$$

where \mathbf{Y} is the response variable (e.g., stratification onset), \mathbf{X} are predictor variables (e.g., air temperature),

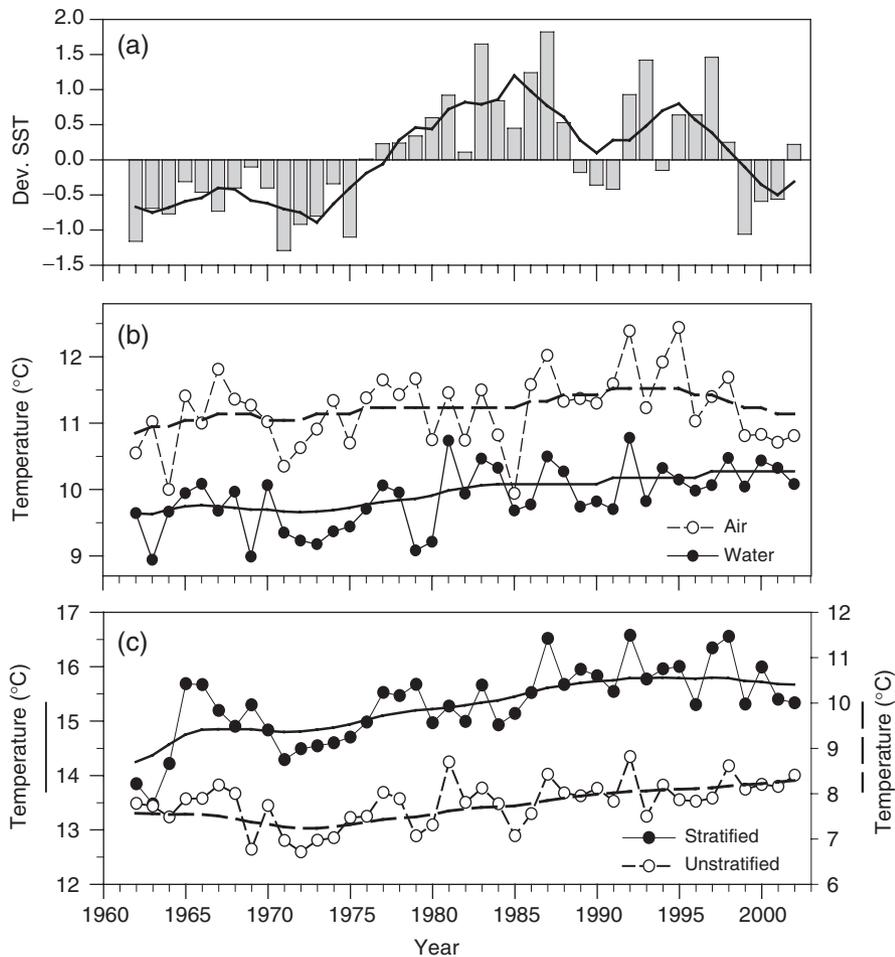


Fig. 2 (a) Time series of the standardized annual Pacific decadal oscillation index and 5-year running means (line) derived as the leading principal component of monthly sea surface temperature (SST) anomalies in the North Pacific Ocean (Mantua *et al.*, 2002). (b) Volume-weighted mean annual water temperature from the period 1962 to 2002 throughout the whole water column in Lake Washington and mean annual air temperature around Lake Washington. (c) Volume-weighted mean lake water temperature from 0 to 10 m depths during the stratified period (April–November) and during the unstratified period (December–March) from 1962 to 2002. Circles in (b) and (c) indicate the observed values; lines indicate the trend predicted from the random-walk model (for more details see text).

θ are the parameters describing the relationship between \mathbf{X} and \mathbf{Y} , and v are observation errors. For DLMS, models are defined by two equations: an observation equation that relates parameters to the observed data with an explicit time ordered index t (i.e., Y_1, Y_2, \dots, Y_t)

$$Y_t = \mathbf{X}_t \theta_t + v_t, \quad v_t \sim N[0, V_t]. \quad (2)$$

The observation errors v_t have a normal distribution with mean zero and a time-dependent variance V_t . Further, a system equation (autoregressive process) that defines the evolution of the parameters through time according to a first-order Markov process

$$\theta_t = \mathbf{G}_t \theta_{t-1} + w_t, \quad w_t \sim N[0, W_t], \quad (3)$$

where \mathbf{G}_t is a matrix of known coefficients that describe the configuration of the model and w_t is an unobservable stochastic term.

Parameters are updated and one-step forecasts are generated at each time step. Thus the values of parameters evolve as the model progresses through the time series. Discount factors determine how influential old data are when updating parameter estimates. A discount of 1 (its maximum value) means that all of the prior information is used by the model, and one of 0 that no prior information is used. Our analyses were composed of a two-step process: first a forecast model was fitted to determine the most appropriate discount factors in the range between 1 and 0.8 (Pole *et al.*, 1994) and choosing the discount that

minimizes the negative log likelihood of the forecast model. Using the information learned from this model, a retrospective model was fitted to describe historical relationships among the time series. The retrospective fits of predictor variables were compared with the retrospective reference model, containing only an underlying level that varies randomly but may have a trend (i.e., an autocorrelated random walk), using the test statistic (R) as twice the difference in negative log likelihood (Scheuerell *et al.*, 2002). Competing models for explaining the dynamics of any simple response variable were ranked according to the Bayesian information criterion (BIC)

$$\text{BIC} = 2L(x|\cdot) + P \log_e(n), \quad (4)$$

where L is the negative log likelihood of the model, P the number of parameters in the model, and n the sample size (Box *et al.*, 1994). Models with the lowest BIC represent the most parsimonious (best) representations of the data.

Results

Long-term temperature trends

A random-walk model predicted that the mean annual air temperature around Lake Washington increased about 0.32°C between 1962 and 2002 (Fig. 2b). The strongest increase in air temperature occurred in January (1.48°C) and April (0.49°C) over this time period. Annual mean air temperature was significantly correlated with raw values of the volume-weighted annual mean water temperature of Lake Washington ($r = 0.42$, $n = 40$, $P < 0.01$; Fig. 2b). In the last four decades, annual mean water temperature increased by 0.65°C . The epilimnion water temperature increased by 1.41°C during the stratified period (April–November) and by 0.71°C during the unstratified period (December–March) as predicted by a random-walk model (Fig. 2c).

Thermal stratification

Annual water column stability, expressed as Schmidt's stability index, increased over the last four decades by 32% from 179.4 to $237.2 \text{ g cm cm}^{-2}$, as indicated by a random-walk model. The overall increase in water column stability is also reflected in an increase of the duration of summer stratification by 25 days over the study period, i.e., about 6 days per decade (Fig. 3a). This trend primarily reflected earlier onset of stratification in spring and to a lesser extent later termination of stratification in fall. The timing of stratification onset occurred between the end of March and early May and

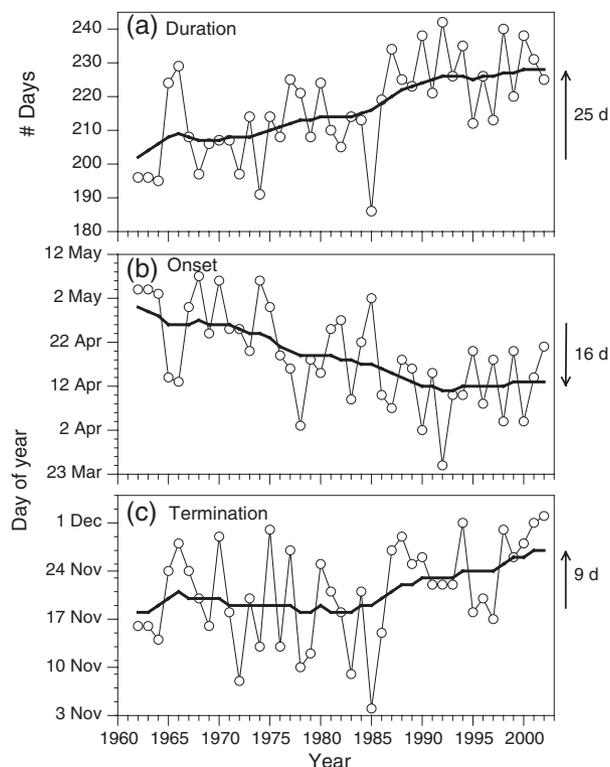


Fig. 3 (a) Duration of summer stratification, (b) timing of spring stratification onset, and (c) stratification termination in fall from 1962 to 2002 in Lake Washington. Open circles indicate the observed values; solid lines indicate the trend predicted from the random-walk model (for more details see text). On the right side of each plot the direction of change and intensity (day number, d) are shown.

was shifted earlier by about 16 days (4 days per decade) over the last 40 years, as indicated by the underlying trend of the random-walk model (Fig. 3b). The termination of summer stratification was shifted 9 days later from mid-November to the end of November (Fig. 3c); i.e., a shift of 2 days per decade. The underlying trend showed that stratification termination was stable until mid-1980s and showed an increasing trend afterwards.

Air temperature in April best explained the observed variation in stratification onset as indicated by the smaller BIC value relative to the random-walk model (Table 1) and accounted for a high proportion of the variation in stratification onset ($r^2 = 0.69$). The negative effect across years indicated that earlier stratification onsets were associated with high air temperature. In addition, PDO significantly explained the variation in stratification onset, as did the combinations of air temperature with PDO and ENSO (Table 1). For stratification termination, the only significant model included a positive effect of fall air temperature and the strength of PDO in fall and explained 84% of the

Table 1 DLM results from the analysis of the timing in stratification onset and termination from 1962 to 2002

Rank	Predictor variable		<i>P</i>	−Log (<i>L</i>)	BIC	<i>P</i> -value
	<i>X</i> ₁	<i>X</i> ₂				
<i>Stratification onset</i>						
Ref.			4	145.4	305.7	–
1	AT₄(−)		6	140.9	304.1	0.011
2	PDO₄(−)		6	142.4	307.1	0.048
3	AT₄(−)	ENSO (−)	7	140.6	307.2	0.021
4	AT₄(−)	PDO₄ (−)	7	140.9	307.8	0.028
5	ENSO		6	143.1	308.4	0.092
<i>Stratification termination</i>						
Ref.			4	132.1	279.0	–
1	PDO_{10,11}(−/ +)	AT_{10,11}(+)	7	123.9	273.8	0.001
2	PDO _{10,11}		6	129.3	280.9	0.062
3	ENSO		6	131.5	285.3	0.560
4	AT _{10,11}		6	132.5	287.3	–
5	AT _{10,11}	ENSO	7	134.9	295.8	–

Models are ranked in terms of decreasing overall performance (increasing BIC) relative to the reference model (Ref.). The models in bold perform significantly better than the random walk model. For each significant model the sign of the regression coefficients for the predictor variables over the time period is given in parentheses. The *P*-value is based on a likelihood ratio test comparing each model to the reference model. *P*, number of parameters in the model; −Log (*L*), negative log likelihood; AT, air temperature; lower case numbers refer to month of the year.

DLM, dynamic linear model; BIC, Bayesian information criterion; PDO, Pacific decadal oscillation; ENSO, El Niño–southern oscillation.

variation (Table 1), while these weather variables alone or ENSO did not perform better than the random-walk model.

Timing of phytoplankton processes

During the period 1962–2002, the timing of phytoplankton spring blooms varied between early March and early June (Fig. 4a). The random-walk model predicted that the timing of phytoplankton spring bloom shifted earlier by about 19 days, from early May to mid-April, or 5 days per decade. The onset of stratification best explained the observed variation based on BIC ($r^2 = 0.53$; Table 2), and had positive effects across years. In addition, the strength of ENSO, TP, and spring PDO were also significant, but only after correction for stratification onset, while weather variables alone as well as TP and temperature did not perform better than the random-walk model (Table 2).

From 1962 to 1972 no clear-water phase was observed in Lake Washington because of eutrophic conditions, but since 1972 the clear-water phase appeared between mid-April and mid-June (Fig. 4b). During the period 1973–2002 the clear-water timing has progressed 6 days or 2.2 days per decade. The observed variation was best explained by a model that included the timing of the phytoplankton spring bloom ($r^2 = 0.56$; Table 2) and indicated that clear-water phases were progressed with

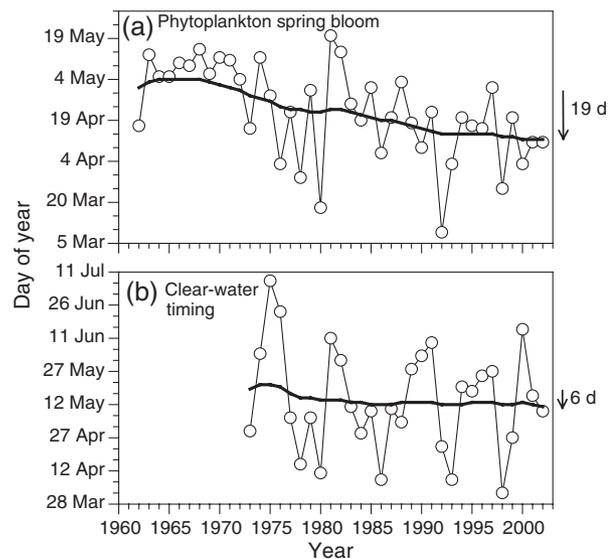


Fig. 4 Timing of (a) diatom spring blooms from 1962 to 2002 and (b) timing of clear-water phases from 1973 to 2002 in Lake Washington. Open circles indicate the observed values; solid lines indicate the trend predicted from the random-walk model (for more details see text). On the right side of each plot the direction of change and intensity (day number, d) are shown.

earlier phytoplankton blooms. Other significant models for predicting the clear-water phase included a negative effect of PDO and of *Daphnia* abundance in May.

Table 2 DLM results from the analysis of the timing in phytoplankton spring blooms from 1962 to 2002 and of clear-water timing from 1973 to 2002

Rank	Predictors		<i>P</i>	–Log (<i>L</i>)	BIC	<i>P</i> -value
	<i>X</i> ₁	<i>X</i> ₂				
<i>Phytoplankton spring bloom</i>						
Ref.			4	166.7	348.3	–
1	StratOnset (+)		6	163.1	348.5	0.012
2	StratOnset (+)	ENSO (–)	7	162.2	350.4	0.029
3	StratOnset (+)	TP_{4,5}(+)	7	162.3	350.6	0.032
4	StratOnset (+)	PDO_{1–4} (–)	7	162.7	351.4	0.046
5	ENSO		6	165.2	352.7	0.223
6	PDO _{1–4}		6	166.2	354.7	0.607
7	WT _{4,5}		6	168.9	360.1	–
8	AT ₄		6	169.3	360.9	–
9	TP _{4,5}		6	169.3	360.9	–
<i>Clear-water timing</i>						
Ref. walk			4	136.0	285.6	–
1	<i>Daphnia</i> ₅ (–)	TP _{2–5} (+)	7	126.2	276.2	0.000
2	PhytoBloom (+)		6	129.3	279.0	0.001
3	PDO _{1–5} (–)		6	130.1	280.6	0.003
4	TP _{2–5} (+)		6	131.9	284.2	0.017
5	<i>Daphnia</i> ₅ (–)	PDO (–)	7	131.7	287.2	0.035
6	<i>Daphnia</i> ₅ (–)		6	132.9	286.2	0.045
7	<i>Daphnia</i> peak		6	133.2	286.8	0.061
8	WT _{4–6}		6	135.2	290.8	0.449
9	ENSO		6	135.6	291.6	0.670
10	AT _{4–6}		6	136.7	293.8	–

For more details see Table 1.

StratOnset, stratification onset; PhytoBloom, timing of phytoplankton spring bloom; *Daphnia*, *Daphnia* density; WT, water temperature; TP, total phosphorus; DLM, dynamic linear model; BIC, Bayesian information criterion; PDO, Pacific decadal oscillation; ENSO, El Niño–southern oscillation.

Timing of zooplankton peaks

The timing of *Keratella* peaks occurred about 15 days earlier in 1995 than in 1962 (Fig. 5a) as indicated by the random-walk model. According to the BIC, water temperature performed best and explained 98% of the observed variance in the timing of *Keratella* spring peaks (Table 3). In addition, high water temperature combined with earlier phytoplankton spring peaks or with ENSO and PDO was associated with earlier occurrence of *Keratella* peaks (Table 3).

The timing of spring peaks of the copepod *Leptodiaptomus* was shifted about 9 days earlier over the past 38 years (Fig. 5b). A model with water temperature and PDO as regressors best explained the variation in timing of *Leptodiaptomus* peaks ($r^2 = 0.69$; Table 3); both predictor variables had negative coefficients. Also, a water temperature only model was better than the random-walk model. The timing of spring peaks of the cladoceran *Daphnia* showed high variability among years, but there was no systematic change in timing

across the study period (Fig. 5c). The timing of *Daphnia* spring peaks was best explained by a model with a negative effect of water temperature combined with the timing of the phytoplankton bloom ($r^2 = 0.98$; Table 3). In addition, models with PDO and water temperature were favored over the random-walk model.

Discussion

Phenology of lake processes

A strong climate signal was observed on the duration of the stratification period of Lake Washington, which was about 25 days longer in 2002 than it was in the early 1960s (Fig. 3). Most of this increase is a result of a strong advancement in the timing of spring stratification onset rather than delayed fall termination, which is in accordance with other aquatic as well as terrestrial ecosystems (Schindler *et al.*, 1990; Magnuson *et al.*, 2000; Walther *et al.*, 2002). Much of the advancement in stratification onset occurred in the mid-1970s to 1990s,

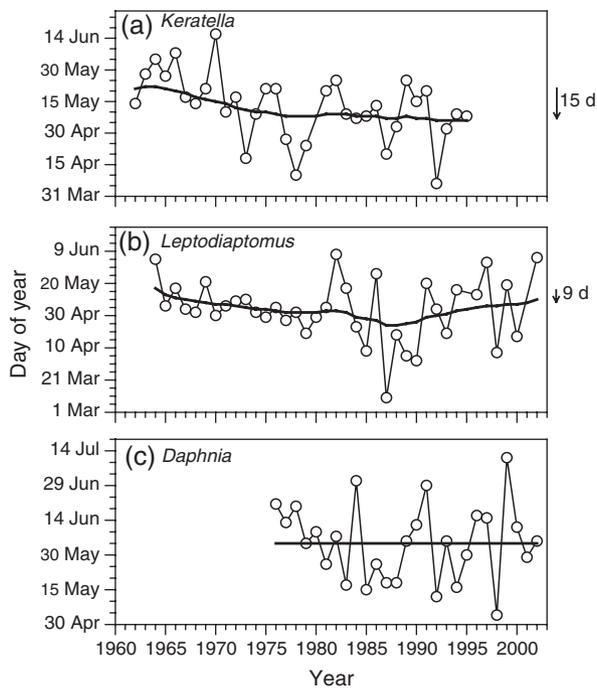


Fig. 5 Timing of spring peaks in (a) *Keratella* from 1962 to 1995 (1980 is excluded because no peak was observed in spring) and (b) *Leptodiatomus* from 1964 to 2002, and in (c) *Daphnia* from 1976 to 2002. Open circles indicate the observed values; solid lines indicate the trend predicted from the random-walk model (for more details see text). On the right side of each plot the direction of change and intensity (day number, d) are shown.

which coincided with the warm phase of the PDO (Mantua *et al.*, 2002). April air temperature, which increased 0.49°C over the last four decades, was however, a better predictor than PDO. Both variables were sufficient to explain the advance (Table 1), presumably because they co-vary ($r^2 = 0.40$, $P = 0.01$). This suggests that a long-term trend of vernal temperature increase strongly affected the physical change of the water column, which was overlaid by large-scale climate fluctuation. For stratification termination, only the combined model of air temperature and PDO index for the fall was a strong model describing the delayed termination, whereas individual climatic drivers performed poorly at describing the observed interannual variation. Thus PDO is an important driver for physical processes in Lake Washington.

In accordance with stratification onsets, a progressive earlier onset of phytoplankton growth occurred in Lake Washington, which is consistent with patterns seen in marine and terrestrial ecosystems over the Northern Hemisphere (Reid *et al.*, 1998; Walther *et al.*, 2002). Timing of stratification onset was the best predictor of phytoplankton blooms and was a co-variable in every

significant model (Fig. 6). The strong predictor of stratification onset for phytoplankton bloom indicates the tight connection of diatom growth with turbulent water conditions during the stratification onset, which prevent these small-single cells from sinking out of the euphotic zone (Huisman *et al.*, 1999). Thus, climate has an indirect effect on the timing of phytoplankton blooms through its effects on the timing of the development of thermal stratification; however, models with only weather variables, water temperature or TP as a predictor were not significant. Others have documented the influence of climate variability on phytoplankton growth and phytoplankton species composition via its effect on ice-cover dynamics and light availability (Schindler *et al.*, 1990; Adrian *et al.*, 1999; Weyhenmeyer *et al.*, 1999). Here we show that temperature warming influenced the timing of phytoplankton blooms through its effect on stratification. A similar mechanism has been hypothesized to account for changing phytoplankton growth in Lake Windermere (George & Taylor, 1995) and the North Atlantic Ocean (Drinkwater *et al.*, 2003).

The timing of the seasonal decline of the phytoplankton and the noticeable clear-water phase showed weak changes in Lake Washington. Among several central European lakes, Straile (2002) found a coherent pattern of the timing of the clear-water phase that was synchronized by the NAO, which strongly influenced spring *Daphnia* density via water temperature. *Daphnia* species are able to suppress algal growth, and thus initiate the clear-water phase and control its timing. In Lake Washington, *Daphnia* density and PDO had a negative effect on CWT, suggesting that *Daphnia* densities and PDO have similar extensive effects on lake ecosystems as the NAO does on European ecosystems (Straile *et al.*, 2003). However, *Daphnia* density was only the best model for predicting the phytoplankton crash in Lake Washington in combination with phosphorus concentration, and the model with TP concentration alone performed better than the *Daphnia* density only model. This indicates the importance of nutrients availability for phytoplankton succession, and thus the difficulty of separating climatic effects from changes in the trophic state of the ecosystem for predicting CWT dynamics.

Interannual variation in timing of zooplankton peaks was high over the study period; however, the timing of spring peaks advanced only in the rotifer *Keratella* and slightly in the copepod *Leptodiatomus*, while phenological patterns of the cladoceran *Daphnia* did not show a trend (Fig. 5). Spring water temperature was a significant predictor for all of the observed zooplankton species and their peaks occurred earlier at higher spring water temperature (Fig. 6). This is in accordance with

Table 3 DLM results from the analysis of the timing in spring peaks of *Keratella cochlearis*, *Leptodiatomus ashlandi*, and *Daphnia* sp

Rank	Predictors		P	-Log (L)	BIC	P-value
	X ₁	X ₂				
<i>Keratella</i> spring peak						
Ref.			4	132.5	279.0	–
1	WT ₄ (–)		6	121.1	263.2	0.000
2	WT ₄ (–)	PhytoBloom (+)	7	121.2	266.9	0.000
3	WT ₄ (–)	ENSO (–)	7	121.3	267.1	0.000
4	WT ₄ (–)	PDO _{1–5} (–)	7	121.3	267.1	0.000
5	PhytoBloom		6	130.9	282.8	0.202
6	PDO _{1–5}		6	131.0	283.0	0.223
7	PhytoBloom	PDO _{1–5}	7	130.2	284.9	0.204
8	ENSO		6	133.9	288.8	–
<i>Leptodiatomus</i> spring peak						
Ref.			4	157.5	329.4	–
1	WT _{4,5} (–)	PDO _{1–5} (–)	7	149.9	325.1	0.002
2	WT _{4,5} (–)		6	153.5	328.7	0.018
3	WT _{4,5}	ENSO	7	157.1	339.5	0.849
4	PDO _{1–5}		6	158.9	339.5	–
5	PhytoBloom		6	159.0	339.7	–
6	ENSO		6	159.4	340.5	–
7	WT _{4,5}	PhytoBloom	7	158.2	341.7	–
<i>Daphnia</i> spring peak						
Ref.			4	113.7	240.6	–
1	WT ₅ (–)	PhytoBloom (–/ +)	7	101.6	226.3	0.000
2	PDO _{1–5} (–)		6	109.7	239.2	0.018
3	WT ₅ (–)		6	110.3	240.4	0.033
4	ENSO		6	112.0	243.8	0.183
5	PhytoBloom	PDO _{1–5}	7	112.7	248.5	0.572
6	PhytoBloom		6	113.6	247.0	0.905

For more details see Table 1.

PhytoBloom, phytoplankton bloom; WT, water temperature; DLM, dynamic linear model; BIC, Bayesian information criterion; PDO, Pacific decadal oscillation; ENSO, El Niño–southern oscillation.

other studies that showed an earlier development of specific zooplankton species in anomalous warm spring periods or short ice durations (Adrian *et al.*, 1999, Gerten & Adrian, 2000, Straile, 2000), which is most probably a physiological response of egg development and growth rates to increased water temperatures (Bottrell *et al.*, 1976). Most studies also show a strong relationship between spring water temperature and the interannual variability of zooplankton density in spring (Gerten & Adrian, 2000; Straile, 2000). In Lake Washington, March and April water temperature explained about 23% and 33%, respectively, of the variance in *Keratella* densities in these months when the spring peak occurred ($n = 33$, $P_{\text{Mar}} = 0.004$, $P_{\text{Apr}} = 0.004$), and *Leptodiatomus* negatively correlated with water temperature in May and June ($n = 34$, $r^2 < 0.12$, $P < 0.048$). However, *Daphnia* densities in May and June, when they were most abundant, did not correlate with water temperature ($n = 24$, $r^2 < 0.08$, $P > 0.17$). These contrasting results

indicate that the response of zooplankton growth to increased temperature is site specific and may strongly depend on the local adapted life-history characteristics of each species. In addition, temperature influences growth rates of the parthenogenetic species *Keratella* and *Daphnia* in a similar way (Bottrell *et al.*, 1976; Stemberger & Gilbert, 1985), whereas for the more slowly developing copepods, temperature change may take a longer time to affect the dynamics (but see Weyhenmeyer *et al.*, 1999; George, 2000). Therefore, only detailed life-history studies may determine how temperature change affects the seasonal dynamics of copepods (Chen & Folt, 1996, Gerten & Adrian, 2002).

Climate change and trophic interactions

Physical and biological processes in Lake Washington responded in different ways to climate change. The timing of *Leptodiatomus* and *Daphnia* peaks did not

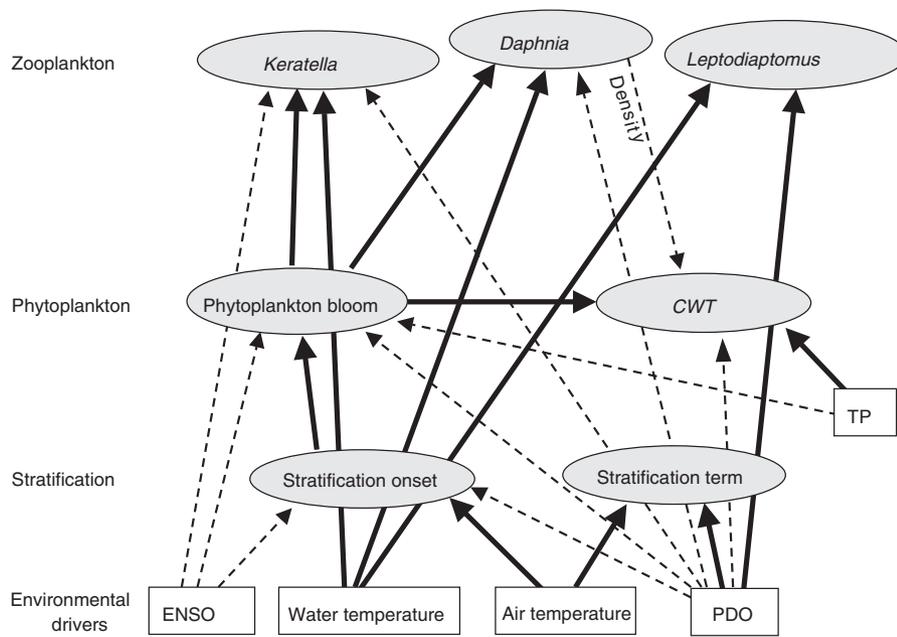


Fig. 6 Schematic summary of environmental drivers (white boxes) affecting the observed physical and biological patterns (grey boxes) in Lake Washington. Solid lines represent the best-fit models; dashed lines represent additional significant effects (see Tables 1–3).

change in parallel with thermal structure and phytoplankton blooms, and the different degree of change in diatom peaks and zooplankton growth may lead to a decoupling of zooplankton food requirements and peak food availability (Winder & Schindler, 2004). A decoupling from favorable food conditions can be especially critical for *Daphnia*, because reproduction rates depend strongly on the availability of high-quality food sources like diatoms (Brett & Muller-Navarra, 1997). Because *Daphnia* is an important energy link between phytoplankton and fish, low *Daphnia* abundance can have profound consequences for the entire food web. The match or mismatch of fish population development with peak food availability has long been realized in the ocean (Cushing, 1974). Recently it has been shown that climate change can create asynchronization between peak food availability and requirement in terrestrial taxa (Inouye *et al.*, 2000; Thomas *et al.*, 2001; Visser & Holleman, 2001). Because zooplankton in general, and *Daphnia* in particular, are such critical links in pelagic food webs, responses of zooplankton to climate change have substantial consequences for entire ecosystems.

In addition, predation from planktivorous fish may affect the dynamics of zooplankton development in spring. In this study, we did not include fish predation as a potential driver of zooplankton phenology. Increased fish predation in spring could delay population growth of zooplankton and shift their peak backwards, which could result in a progressive longer

time between food availability and food requirements. However, in Lake Washington the highest consumption rate of planktivorous fish is later in the season (Beauchamp and Mazur, unpublished data), after the spring peaks of zooplankton species. Therefore, we do not expect that fish predation affects the spring dynamics of zooplankton species in Lake Washington.

Summary

Our results demonstrate that subtle changes in temperature can translate into very substantial changes in the phenology of ecological processes in lakes. Long-term climate change and interannual climate variability have strong effects on the thermal structure of the water (Fig. 6) column, which in turn controls spring dynamics of phytoplankton and zooplankton in Lake Washington (Fig. 6). In general, PDO had stronger effects on the phenological processes compared with ENSO. This is in accordance with other recent studies demonstrating that the temporal organization of aquatic (Hilborn *et al.*, 2003; Arhonditsis *et al.*, in press; Schindler *et al.*, in press) and terrestrial (Vandenbosch, 2003) ecosystems in western North America is strongly affected by the PDO. However, at higher trophic levels and later in the year, during the clear-water phase for example, regulating mechanisms of population dynamics are more complicated as biotic factors like competition and predation become more important (Sommer *et al.*, 1986) and obscure ecology–climate links. Because the degree

to which individual species respond to climate varies, it is likely that climate change can significantly alter trophic flows among trophic levels in aquatic ecosystems in unpredictable ways. Further, the effect of warming on food web structure and ecosystem function may depend strongly on the local adaptation of life-history traits in species, which can be quite rapid in zooplankton (Hairston *et al.*, 1999). We conclude that the extent of physical changes and the potential for species to adapt to changing environmental conditions will greatly influence food web dynamics as future climate warms and becomes more variable.

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