ELSEVIER

Water Research 38 (2004) 4013–4027

WATER RESEARCH

www.elsevier.com/locate/watres

Patterns and mechanisms of phytoplankton variability in Lake Washington (USA)

George B. Arhonditsis[a,*], Monika Winder[b], Michael T. Brett[a], Daniel E. Schindler[b,c]

[a]Department of Civil and Environmental Engineering, More Hall, Box 352700, University of Washington, Seattle, WA 98195, USA
[b]School of Aquatic and Fisheries Sciences, University of Washington, Box 355020, Seattle, WA, USA
[c]Department of Biology, University of Washington, Kincaid Hall, Box 351800, Seattle, WA, USA

Received 27 January 2004; received in revised form 28 May 2004; accepted 22 June 2004

Abstract

Temporal variability in lake phytoplankton is controlled largely by a complex interplay between hydrodynamic and chemical factors, and food web interactions. We explored mechanisms underlying phytoplankton interannual variability in Lake Washington (USA), using a 25-yr time series of water quality data (1975–1999). Time-series analysis and PCA were used to decompose chlorophyll data into modes of variability. We found that phytoplankton dynamics in Lake Washington were characterized by four seasonal modes, each of which was associated with different ecological processes. The first mode coincided with the period when the system was light limited (January–March) and phytoplankton patterns were driven by the amount of available solar radiation. The second mode (April–June) coincided with the peak of the spring bloom and the subsequent decline of phytoplankton biomass, and was largely controlled by total phosphorus levels and grazing pressure from cladoceran zooplankton. Evidence of co-dependence and tight relationship between phytoplankton and cladoceran dynamics were also found from July to October when a large portion of the phosphorus supply in the mixed layer was provided by zooplankton excretion. The fourth mode (November–December) was associated with the transition to thermal and chemical homogeneity and the winter phytoplankton minima (2–2.5 μg/l). Finally, we examined the effects of meteorological forcing and large-scale oceanic climate fluctuations (ENSO and PDO) on phytoplankton dynamics and assessed the significance of their role on the interannual variability in the lake.

Keywords: Phytoplankton dynamics; Interannual variability; Lake Washington; Ecological patterns; Phytoplankton–zooplankton interactions; Total maximum daily load (TMDL)

1. Introduction

Phytoplankton seasonal succession is a well-investigated phenomenon in aquatic ecology and several studies have described the patterns and underlying mechanisms of the seasonal dynamics (Sommer et al., 1986; Marshal and Peters, 1989; Vanni and Temte, 1990;

---

[*]Corresponding author. Nicholas School of the Environment and Earth Sciences, Duke University, P.O. Box 90382, Durham, NC 27708-0328, USA. Tel.: +1-919-613-8105; fax: +1-919-684-8741.
E-mail address: georgear@duke.edu (G.B. Arhonditsis).

0043-1354/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.watres.2004.06.030

Hansson et al., 1998; Rothhaupt, 2000). Phytoplankton succession patterns are usually similar in lakes having analogous climatic conditions, morphometric characteristics and trophic status (Reynolds, 1984). In temperate thermally stratified lakes, phytoplankton usually peak in the spring, decrease in early summer and increase slightly in the autumn before decreasing again during the winter minima. The current character of this ordered succession of seasonal events was shown to be widespread in the 1980s by a workshop of the Plankton Ecology Group (Sommer et al., 1986). In north temperate lakes this phytoplankton succession is largely determined by the interactions and the seasonal cycles of chemical (nutrients), biological (grazers), and physical (thermal stratification) factors, the relative importance of which varies at different periods of the year (Sommer et al., 1986).

To have a better understanding of the factors responsible for changes in the annual pattern of phytoplankton, it is important to better understand the link between changes in environmental parameters and phytoplankton dynamics. Knowing which mechanisms operate during different seasonal periods provides informative ways of detecting subtle changes in the structure and function of ecosystems. While traditionally the annual succession of plankton has been treated as discrete phenomenon, in recent years aquatic ecologists have recognized interannual variability in the seasonal dynamics (Jassby et al., 1990, 1992; Goldman et al., 1993; Anneville et al., 2002). Strong interannual variation in the physical, chemical and biological characteristics of lakes seems to have a regulatory role on the phytoplankton dynamics. For example, interannual variation in nutrient supply is an important determinant of year-to-year phytoplankton variability (Baines et al., 2000), since nutrient inputs from water column turnover and seasonal runoff peaks stimulate spring blooms of algae. Evidence that trophic interactions result in interannual variation in phytoplankton dynamics has been provided by experimental food web studies (Carpenter et al., 1987). In addition, climatic and large-scale oceanic fluctuations can influence the interannual phytoplankton patterns (e.g., phytoplankton composition, intensity of spring blooms, timing of clear water phase) as has been shown for northern European lakes (Weyhenmeyer et al., 1999; Straile, 2002).

Goldman (1988) contended that many ecological questions cannot be addressed by short-term data because inherent ecosystem variability conceals patterns and the signature of long-term phenomena may not be apparent in short time series. However, there are only a few studies that observed possible driving forces for phytoplankton interannual variability and attempted to delineate their role at decadal time scales (Jassby et al., 1992, 2002; Goldman et al., 1989). Other studies explored specific events of the seasonal succession (i.e., the spring bloom) over an extended time period (Neale et al., 1991), and generally it is suggested that the analysis of longer time scales provides a powerful tool for studying the factors responsible for the seasonal fluctuation and developing predictive models to forecast future changes (Ives, 1995). Therefore, the conceptualization of the temporal phytoplankton variability in lakes needs to project the complex interplay between hydrodynamic, chemical factors, and food web interactions in both short- and long-time scales.

We conducted a statistical analysis of the intra- and interannual phytoplankton variability in Lake Washington, USA, over a 25-yr period (1975–1999). This period of the lake is characterized by mesotrophic conditions and moderately high *Daphnia* abundance (Edmondson, 1994). Our primary goal was to define the different types of phytoplankton behavior (modes of variability) over the annual cycle and to detect the underlying mechanisms and ecological processes behind those patterns. Environmental variables (air temperature, wind speed, water temperature, solar radiation, total phosphorus, cladoceran and total herbivorous zooplankton biomass) were assessed as predictors (individually and in combinations) of week-to-week phytoplankton community dynamics. The influence of the large-scale climatic processes, such as the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO), on phytoplankton dynamics was also considered. Understanding the basic causal environmental factors of lake phytoplankton patterns is also essential for setting water quality criteria that are more directly linked to the eutrophication-related designated uses, which in turn is likely to reduce the total maximum daily load (TMDL) uncertainty and associated risk.

2. Study site and data description

Lake Washington is the second largest natural lake in the State of Washington, with a surface area of 87.6 km^2 and a total volume of 2.9 km^3. The mean depth of the lake is 32.9 m (maximum depth 65.2 m), the summer epilimnion depth is typically 10 m and the epilimnion: hypolimnion volume ratio during the summer is 0.39. The retention time of the lake is on average 2.4 years (Edmondson, 1994). Lake Washington has been extensively studied and it is perhaps the best example in the world of successful lake restoration by sewage diversion (Edmondson and Lehman, 1981; Edmondson, 1994). The lake received increasing amounts of secondary treated sewage between 1941 and 1963, which resulted in severe eutrophication, cyanobacteria dominance and declining water quality. Sewage was diverted from the lake between 1963 and 1967, with discharge of wastewater treatment plant effluent (except for combined sewer overflows) eliminated by 1968. Rapid water quality improvements followed, cyanobacteria abundance declined dramatically, and a *Daphnia* population resurgence occurred in 1976 and this group has dominated the summer zooplankton community since. Currently, Lake Washington can be characterized as a mesotrophic ecosystem (Edmondson, 1994) with limnological processes strongly dominated by a recurrent diatom bloom, which occurs during March and April with epilimnetic chlorophyll concentration peaks on average at 10 μg/l, which is 3.2 times higher than the concentrations during the summer stratified period (Arhonditsis et al., 2003).

Our analysis was based on standard limnological data, including water temperature, total phosphorus (TP), chl *a* concentrations, zooplankton abundance and community composition (for methodological details about the limnological data, see Scheuerell et al., 2002; Arhonditsis et al., 2004). These data were collected at weekly to monthly intervals from 1975–1999. We focused on the period after 1975, because as previously mentioned after this year cyanobacteria biomass declined and daphnid populations increased markedly (Edmondson, 1994). Two surrogate parameters were used to characterize the zooplankton grazing pressure on phytoplankton: the first included all *Daphnia (D. pulicaria, D. thorata, D. galeata mendotae), Diaphanosoma (D. birgei), Bosmina (B. longirostris)* and *Ceriodaphnia* (*C. reticulata*) species and is referred to as "Cladocerans"; the second parameter also included *Leptodiaptomus ashlandi* (the dominant herbivorous copepod species in Lake Washington) and it will be referred as "Herbivores". Both the parameters were formed as the sum of the species abundances (expressed as organisms per litre) weighted by the respective mean lengths (Carpenter et al., 1996). Solar radiation, air temperature and wind speed data were available as hourly means from the SeaTac Airport (47°45′N–122°30′W and 137 m). Monthly PDO index values were obtained from the Joint Institute for the Study of the Atmosphere and Oceans, University of Washington (http://tao.atmos.washington.edu/data_sets/). Monthly Multivariate ENSO Index (MEI) values were obtained from the Climate Diagnostics Center, National Oceanic and Atmospheric Administration (http://www.cdc.noaa.gov/˜kew/MEI/).

3. Statistical methods

3.1. Time series analysis

Chlorophyll data for the time series and principal component analyses (see following paragraph) were interpolated with the trapezoidal integration and the resulting daily time series was averaged over the months. Depth averages (0–10 m) were also calculated after volume weighting the chlorophyll concentrations, based on morphometric data for Lake Washington (Edmondson and Lehman, 1981). We extracted seasonal patterns by seasonal-trend decomposition using the X-11 (Census II) method, which is an extension and refinement of the classic seasonal decomposition and adjustment method (Census I) containing many ad hoc features that allow for a series of successive refinements and adjustments for outliers and extreme values (Makridakis and Wheelwright, 1989; Kendall and Ord, 1990). The general concept of the seasonal decomposition is that a time series can be separated in three different components: (1) seasonal, (2) trend, and (3) residual components. The most important feature that must be specified for a particular application is the model form, which defines the functional relationship between the three components (additive or multiplicative). We chose the additive model but found little difference in results when using the multiplicative model. After decomposition of the time-series, we subtracted the seasonal component (centering the data) and inspected the residual values for nonstationarity problems.

3.2. Modes of interannual variability

We applied principal component analysis (PCA) for analyzing interannual variability as done in several recent studies (Jassby et al., 1999, 2002) and described in detail by Jassby (1999). The basic rationale behind this application of PCA is that different phases of the intra-annual cycle may be regulated by separate processes and may therefore behave independently of each other, thus impeding the development of clear causal statistical models. For this application of PCA, a chlorophyll data matrix (centered data after the removal of the seasonal component) of 12 columns (months of the year) and 25 rows (years of the study) was formed; each row began with the month of the year where the serial correlation with the preceding month was the weakest (in the present case was between December–January). PCA was used to unravel the number of independent modes of chlorophyll variability, and the time of year in which they were most important (component coefficients), along with their relative strength from one year to the next (amplitude time series). Principal components (PCs) were estimated by singular value decomposition of the covariance matrix of the data. The selection of significant PCs was based on the Monte Carlo technique known as Rule N (Overland and Preisendorfer, 1982), which consisted of applying PCA and computing the eigenvalues of 1000 uncorrelated 12 by 25 data sets formed from a standard normal distribution. Each of the observed eigenvalues (from the real data) was then compared with the 0.95 percentile of the corresponding simulated eigenvalues. We kept the significant PCs and rotated them using the normalized varimax strategy (raw factor loadings divided by the square roots of the respective communalities), calculating the new component coefficients and amplitude time series (Richman, 1986).

3.3. Statistical models

After identifying independent modes of variability in the annual time series, we then computed partial correlation coefficients and developed multiple linear regression models within the resultant seasonal modes of variability, as identified from the PCA. In particular, the ability of air temperature, wind speed, water temperature, solar radiation, TP, cladoceran and herbivore grazing pressure to predict the phytoplankton weekly responses was evaluated for each of the seasonal components of the annual cycle. These cause–effects relationships were based on weekly time resolution; the values of the environmental variables were interpolated with trapezoidal integration and the resulting daily time series were binned by week. The weekly time-series (obviously highly autocorrelated) were initially differenced to achieve stationarity. First-order differencing was found to be sufficient and we then used these differenced data for individually testing the relationship of each variable with chlorophyll after controlling for the other ecological variables effects (partial correlations). We also developed multiple regression models based on the initial (undifferenced) weekly data and we added an autoregressive term to correct for autocorrelation in the errors (Carpenter et al., 1998). So, the general formulation of the multiple regression models is

$$Y_{t+1} = b_{\mathrm{aut}} Y_t + bX_t + E_t,$$

where the subscript t denotes time, b_{aut} is an autoregressive parameter, Y is the response variable (weekly log-transformed chlorophyll values), E is the observation error, b corresponds to the regression parameters and X is a vector that comprises all predictors (log-transformed values) and their interactions. A determination of the best subset of regressors (individual variables and interactions) during model development was based on the Mallows' Cp criterion, which is a measure of the goodness of fit that is less dependent than the coefficient of determination (r^2) on the number of effects in the model; hence, it tends to find the best subset that includes only important predictors for the respective dependent variables thereby providing more parsimonious models (Ronchetti and Staudte, 1994).

4. Results

The seasonal and trend decomposition for the chlorophyll time-series is shown in Fig. 1, where the observed variability at the seasonal scale was filtered out by calculating a centered 13-term moving average (X-11 method). The filtered data indicated that there was a long-term decreasing trend with a Theil slope of $-0.011\,\mu\mathrm{g/l\,yr}$, which however was not significant according to the seasonal Kendall test. The trends for each individual month were also negative and non-significant (not presented here), but interestingly the higher values were calculated for the spring months (March–May) with an average Theil slope of $-0.018\,\mu\mathrm{g/l\,yr}$. The seasonal pattern of the chlorophyll data was bimodal over the last 25 years with a strong chlorophyll maximum in April and a much weaker maximum in October. Another prominent change that can be observed in the seasonal series was an increasing trend in the amplitude from the early 1980s until the year 1990, accompanied by a decrease over the 1990s and the establishment of a seasonal cycle similar to the one observed during the initial years (1975–1980). Partitioning of the contribution of the inter- and intra-annual variation, based on hierarchical analysis of variance, indicated that the annual cycle explains 89% of the overall variability in mean monthly chlorophyll values, with the remaining 11% of variation due to inter-annual variation.

The PCA and subsequent application of Rule N revealed the existence of four eigenvalues that were significantly higher than expected due to random variability. These four eigenvalues accounted for 74% of the total variance in the monthly series. The results for the first four principal components, after rotation with the varimax algorithm, are presented in Fig. 2. The first mode of variability represents the period of the year when the lake is strongly stratified until the time when stratification begins to erode (July–October) and explained 21% of the overall variability in the time-series. The second principal component (mode 2) was characterized by high coefficients during January, February and March and was responsible for nearly 20% of the observed variance. The third mode of variability coincided with the period when the lake was cooling (November–December) and accounted for 17.5% of the overall variability. The fourth component covered the period when the spring diatom bloom (April–May) occurs in the lake and accounts for 14.4% of overall variation in the monthly chlorophyll time-series. The amplitude time-series for all the modes was dominated by interannual variability and no clear long-term trend was identified over the last 25 years (i.e., the r^2 value for the long-term trend was always below 0.05; not presented here).

Partial correlation coefficients between chlorophyll *a* and air temperature, wind speed, solar radiation, water temperature, TP, cladocerans and herbivores for the four modes of variability are presented in Table 1. These results are based on the first order differenced

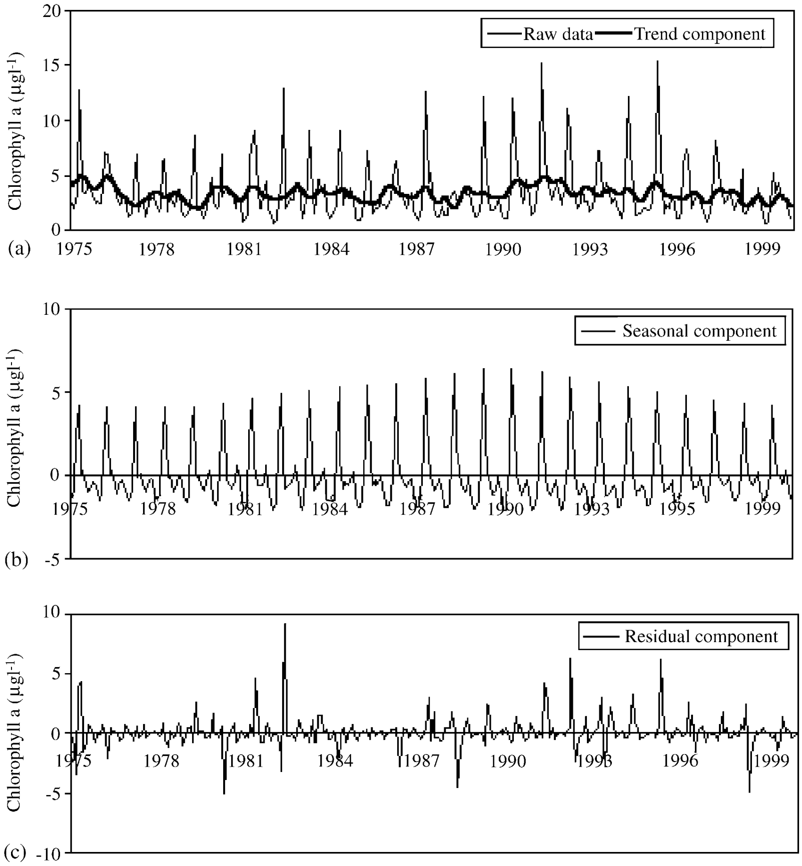

Fig. 1. Trend, seasonal and residual components of chlorophyll in Lake Washington as determined by the X-11 ARIMA method (1975–1999). The values of the seasonal component are plotted as departures from the long-term mean.

weekly data. It should be noted that the modes are presented in a chronological sequence instead of the previous ranking based on the proportion of variability explained. The first mode of variability (January–March) was significantly correlated with solar radiation ($r = 0.235$, $p < 0.001$), air temperature ($r = 0.131$, $p = 0.036$) and herbivore abundance ($r = 0.174$, $p = 0.005$). TP concentrations and cladoceran abundance were significantly correlated with chlorophyll during the second ($r = 0.131$, $p = 0.021$ and $r = -0.181$, $p < 0.001$) and third ($r = 0.104$, $p = 0.032$ and $r = -0.101$, $p = 0.036$) modes, which correspond to the April–June and July–October periods, respectively. Air temperature effects were also significant ($r = -0.148$, $p = 0.002$) during the third mode. Finally, solar radiation ($r = 0.264$, $p < 0.001$) seems to be an important driving force for the months of November and December, as well as air temperature ($r = -0.137$, $p = 0.035$) the cladoceran abundance ($r = -0.222$, $p = 0.001$) and TP concentrations ($r = -0.139$, $p = 0.032$).

Table 2 presents the multiple regression models that include the best subset of predictors (according to the Mallows' Cp) along with the autoregressive term for each of the modes of variability. These models account for high proportions of the weekly variation in chlorophyll, but the b_{aut} coefficients indicate that the largest fraction of the fit is due to the autoregressive term. Nonetheless, significant predictors have been revealed for the individual modes of variability that explain the residual variability after removal of the autoregression effects. The model that describes the first seasonal mode (January–March) included only solar radiation as a regressor and had an r^2 value of 0.905. The second model (April–June), which describes the peak of the spring bloom and subsequent decline of phytoplankton biomass, included TP concentrations and cladoceran abundance and explained 79.5% of the variability observed during this period. The cladoceran abundance and a term that corresponds to their interactions with TP concentrations in the lake were the best predictors of July to October chlorophyll concentrations ($r^2 = 0.711$). Finally, the most important causal factors for describing the period (November–December) when the system becomes physically and

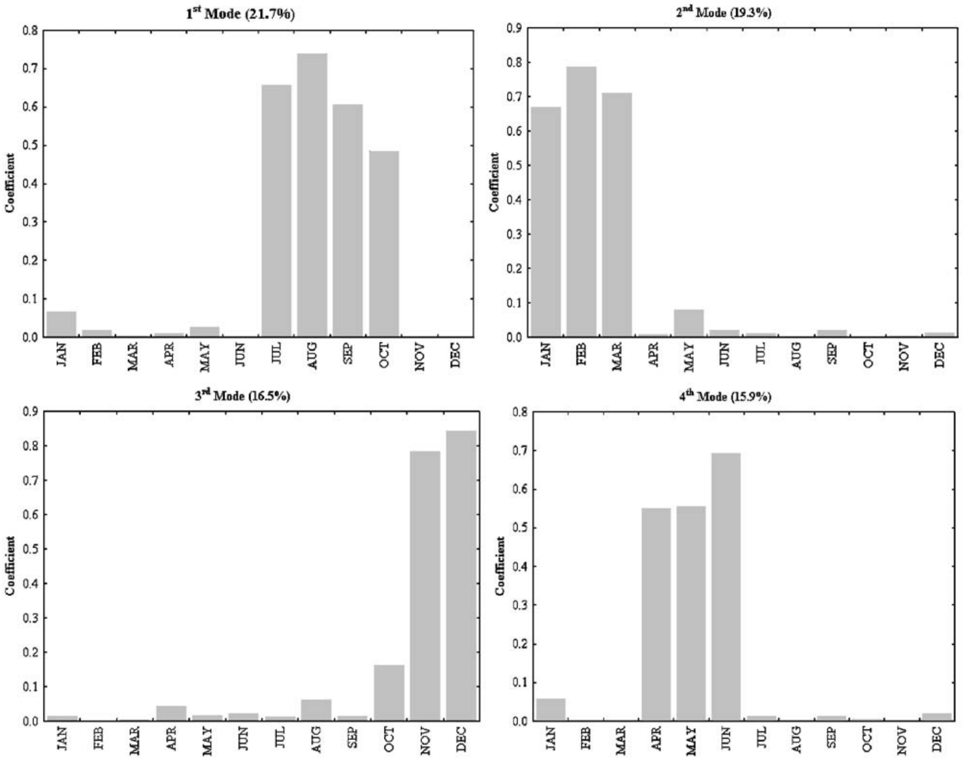

Fig. 2. Squared component coefficients for the first four principal components of chl *a*.

Table 1

Partial correlation coefficients between chlorophyll *a* and air temperature, wind speed, solar radiation, water temperature, total phosphorus, cladoceran and herbivore populations[a] for the four modes of variability (first-order differenced weekly data)

Variables	*r*	*p*	*r*	*p*
	First Mode (January–March) n=264		*Second Mode (April–June) n=312*	
Air temperature	0.131	0.036	0.067	0.238
Wind speed	0.025	0.686	−0.018	0.753
Solar radiation	0.235	<0.001	0.021	0.703
Water temperature	−0.003	0.965	0.047	0.404
Total phosphorus	−0.051	0.413	0.131	0.021
Cladocerans	−0.051	0.413	−0.181	0.001
Herbivores	0.174	0.005	−0.096	0.093
	Third Mode (July–October) n=432		*Fourth Mode (November–December) n=240*	
Air temperature	−0.148	0.002	−0.137	0.035
Wind speed	0.005	0.912	−0.047	0.476
Solar radiation	−0.077	0.113	0.264	<0.001
Water temperature	−0.061	0.205	−0.055	0.401
Total phosphorus	0.104	0.032	−0.139	0.032
Cladocerans	−0.101	0.036	−0.222	0.001
Herbivores	0.048	0.318	−0.021	0.751

[a] Definitions of the two surrogate variables of zooplankton grazing are provided in the text.

chemically homogeneous and phytoplankton biomass declines to the annual minimum were solar radiation and cladoceran abundance ($r^2 = 0.888$).

The four cause–effect relationships that appear to drive the phytoplankton dynamics during the annual cycle were further explored through their mean weekly

Table 2
Regression models developed for predicting the level of chlorophyll *a* (μg/l) in Lake Washington

Variables	b_{aut}	b_{o}	r^2	s	β	P
First Mode (January–March)	0.849	−0.282	0.905	0.076		
Solar radiation					0.178	<0.001
Second Mode (April–June)	0.766	–	0.795	0.138		
Total phosphorus					0.079	0.039
Cladocerans					−0.217	<0.001
Third Mode (July–October)	0.782	0.114	0.711	0.146		
Cladocerans					−0.516	<0.001
Total phosphorus × Cladocerans					0.525	<0.001
Fourth Mode (November–December)	0.902	−0.287	0.888	0.068		
Solar radiation					0.169	<0.001
Cladocerans					−0.108	<0.001

Symbols b_{aut}, b_{o}, s, β and p denote the coefficient of the autoregressive term, the intercept, the standard error of the estimate, the beta coefficient and the level of significance of each predictor, respectively.

patterns over the respective seasonal modes of variability. Fig. 3 shows the week-to-week evolution of chlorophyll and solar radiation during the first mode of variability (January–March) and verifies the positive correlation between the two variables. An interesting point is that available solar radiation was characterized by an upward shift after the sixth week (middle February), accompanied by a doubling of chlorophyll concentrations (weekly medians from 2–4 μg/l) until the end of March. From late March to early May (12th–18th week of the year), the TP levels were relatively constant (≈15–20 μg/l), which is usually the period when the chlorophyll maximum occurs (weekly medians >8 μg/l between the 15th–18th week; Fig. 4). The TP concentrations decreased markedly after the end of May tending towards a weekly median level of 10 μg/l (sedimentation of the phytoplankton cells where most of the available phosphorus is sequestered), around which concentration fluctuated for the remainder of the stratified period (see also Fig. 5). Meanwhile, a clear response to cladoceran abundance was observed after the end of April–early May (18th week of the year), while the subsequent period (19th–21st week) was clearly associated with high variability and wide range of length weighted weekly abundance. During the remaining period until the end of October–early November, cladocerans were characterized by a local minimum from middle August to early September (30th–34th week of the year) and then a fairly steady level with a weekly median of 10 mm/l (Fig. 5). Relatively high inter-annual variability for cladoceran abundance was observed between the 43rd and 47th week of the year (Fig. 6). Generally, decreasing solar radiation and cladoceran grazing pressure seem to regulate the phytoplankton decline rates during the fourth seasonal mode, while the winter level (2–2.5 μg/l) is usually established during the first days of December (≈48th week of the year).

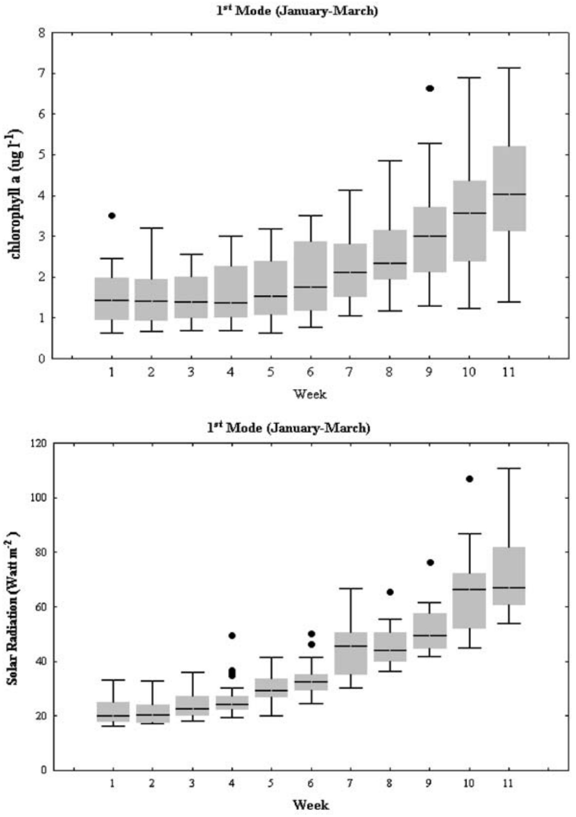

Fig. 3. Box-plots illustrating the variation of weekly averages of chlorophyll (μg/l) and average daily solar radiation (W/m^2) over the first variability mode (January–March).

We also computed correlations between chlorophyll *a* concentrations and PDO and ENSO indices, to assess

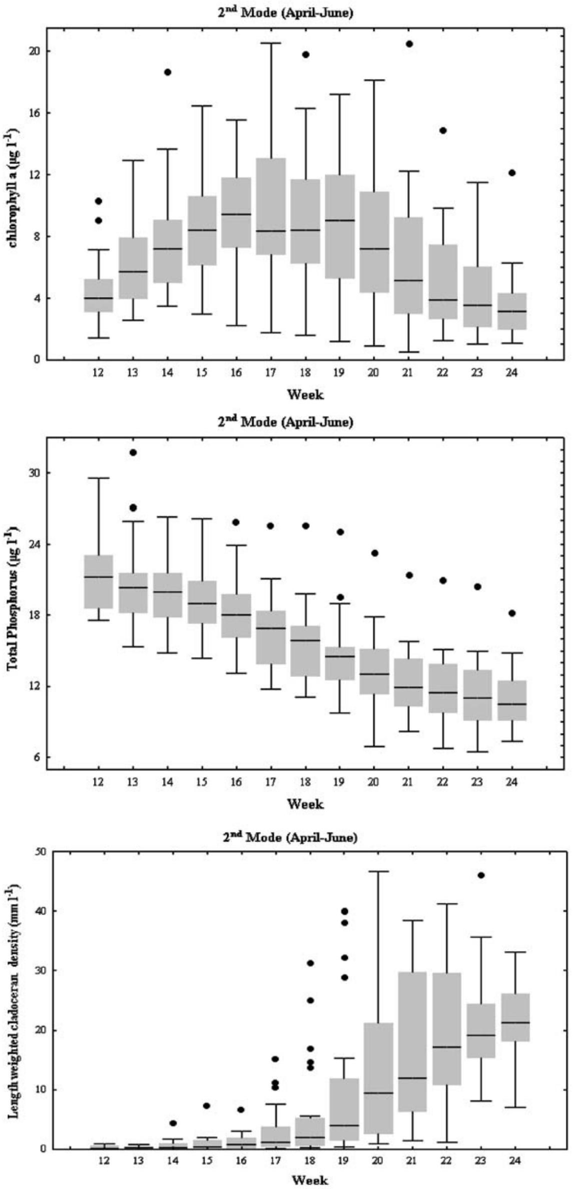

Fig. 4. Box-plots illustrating the variation of weekly averages of chlorophyll (μg/l), total phosphorus (μg/l) and length weighted cladoceran density (mm/l) over the second variability mode (April–June).

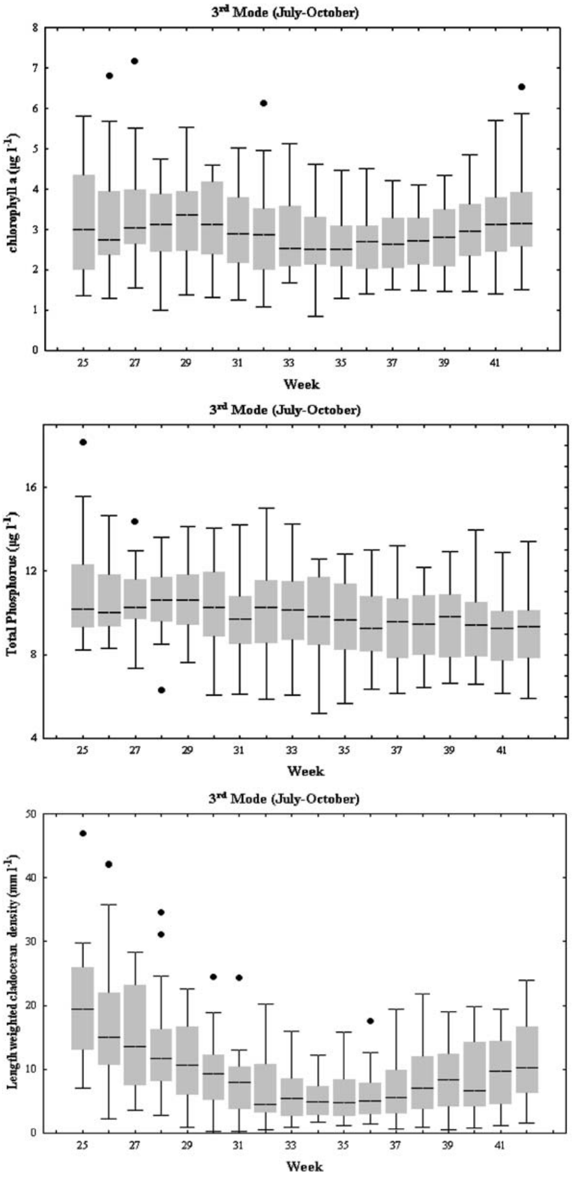

Fig. 5. Box-plots illustrating the variation of weekly averages of chlorophyll (μg/l), total phosphorus (μg/l) and length weighted cladocerans density (mm/l) over the third variability mode (July–October).

the significance of the role of climatic and large-scale oceanic fluctuations as regulatory factors of the inter-annual phytoplankton variability in Lake Washington (Table 3). The temporal resolution of the study was increased from weekly intervals to moving-average windows equal to the mode duration, to identify possible memory effects of these climatic phenomena. Hence, a 3-month window was used for the first and the second modes, a 4-month window for the third and a 2-month window for the fourth mode (Fig. 7). Furthermore, we tested the impacts of these climatic processes on the chlorophyll stability by correlating the chlorophyll coefficient of variation (standard deviation of weekly chl*a* values/average chl*a*) with the respective PDO and ENSO values. A statistically significant correlation between chlorophyll and PDO ($r = -0.461$, $p = 0.020$) was found during the second mode, while the ENSO index ($r = -0.391$, $p = 0.053$) in the same period

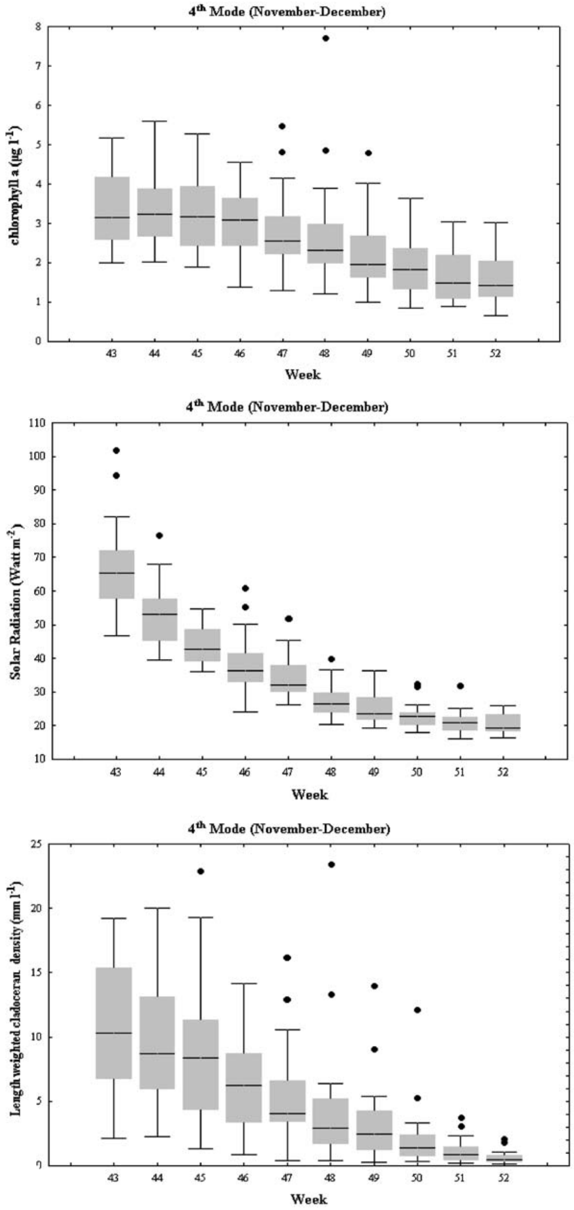

Fig. 6. Box-plots illustrating the variation of weekly averages of chlorophyll (μg/l), average daily solar radiation (W/m^2) and length weighted cladoceran density (mm/l) over the fourth variability mode (November–December).

was marginally significant. A significant correlation with the ENSO index ($r = 0.451$, $p = 0.022$) was observed for the fourth mode (November–December). Finally, positive ENSO effects on phytoplankton weekly variability were found during the second mode ($r = 0.401$, $p = 0.048$), while the remainder of the correlations was not significant.

5. Discussion

We have attempted to delineate the intra- and interannual phytoplankton variability in Lake Washington and to identify the mechanisms that drove these dynamics from 1975 to 1999. The study period is characterized by the establishment of *Daphnia* as a result of bottom-up (due to the disappearance of filamentous cyanobacteria, i.e., *Oscillatoria*) and top-down (due to reduced predation by mysid shrimp) biotic control (Edmondson, 1994). The ‘‘traditional’’ concept of a physically (i.e., temperature, light, nutrients) controlled phytoplankton community can describe portions of the lake’s current seasonal patterns, but there are at least two periods of the annual cycle when arguments for a dominant role of zooplankton and significant interactions with the phytoplankton community can be supported (Arhonditsis et al., 2003). The first period is associated with the spring phytoplankton maximum and the subsequent collapse of the spring bloom, while the second occurred during the summer period when the system is strongly stratified and total phosphorus concentrations reach their lowest levels. Here, by using a longer time-series and higher temporal resolution we were able to ‘‘unfold’’ phytoplankton dynamics and assess the relative importance of the abiotic factors and grazing pressure for week-to-week phytoplankton variability over the annual cycle.

5.1. Seasonal phytoplankton patterns in Lake Washington

The annual phytoplankton cycle was split into four independent seasonal ‘‘modes’’ of variability that together accounted for 74% of the total observed variance for Lake Washington’s phytoplankton dynamics over the last 25 years. The first mode (January–March) represented the period of the year when the system is light-limited and the phytoplankton patterns were driven by the amount of the available solar radiation. Hence, increased surface irradiance and day-length are the main regulatory factors for the phytoplankton responses, while the observed upward shift after the middle of February corresponds to a 9.5-h day length at Lake Washington’s latitude which—given the local climatic conditions—appears to be a photoperiod threshold for triggering phytoplankton growth. During the same period, another important factor for the spring bloom, especially in deep aquatic ecosystems, is thought to be the onset of the thermal stratification and the shallowing of the upper mixed-water layer below a critical depth (Sverdrup, 1953; Horn and Paul, 1984; Nelson and Smith, 1991; Mann and Lazier, 1996). We tested Lake Washington’s consistency with this concept by contrasting the weekly phytoplankton growth rates with the respective temperature vertical gradients over a

Table 3
Correlation matrix between chlorophyll *a*, the Pacific Decadal Oscillation (PDO) and the Multivariate ENSO Index (MEI) Indices

Variables	Average	Coefficient of variation[a]	Average	Coefficient of variation
	First Mode (January–March)		*Second Mode (April–June)*	
PDO	−0.247(−2)	0.132	−0.461(−2)	0.260
	0.234	*0.539*	*0.020*	*0.221*
ENSO	0.325 (0)	−0.129	−0.391(−3)	0.401
	0.112	*0.549*	*0.053*	*0.048*
	Third Mode (July–October)		*Fourth Mode (November–December)*	
PDO	−0.076(−3)	0.327	0.191(−3)	−0.116
	0.719	*0.119*	*0.36*	*0.59*
ENSO	−0.188(0)	0.299	0.451(0)	−0.349
	0.368	*0.156*	*0.022*	*0.095*

A 3-month average was used for modes 1 and 2, a 4-month average was used for mode 3 and a 2-month average for mode 4. The parentheses indicate the lag (months) that yielded the most significant correlation coefficients and the numbers with italics the respective level of significance ($n = 25$).

[a] Computed for each mode as standard deviation of weekly chl*a* values/average chl*a*.

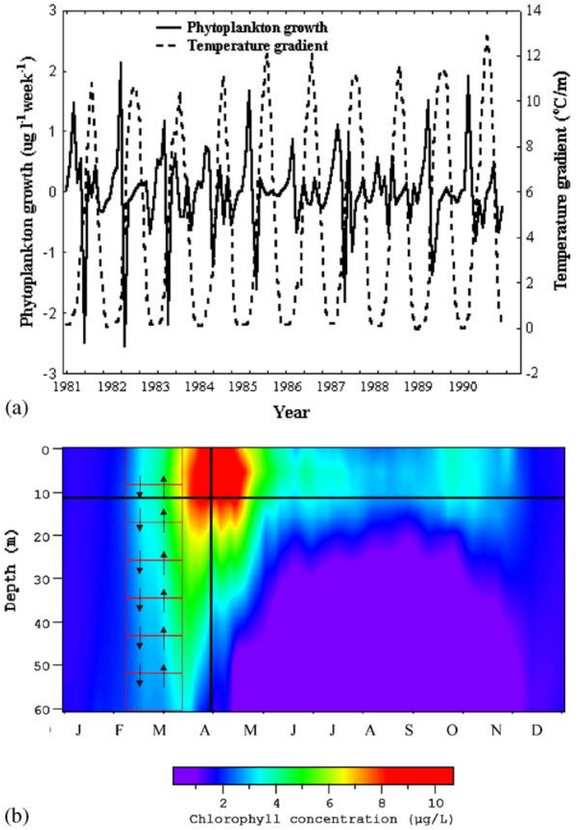

Fig. 7. (a) Annual cycles of phytoplankton growth and surface (0–10 m)—hypolimnion (10 m-bottom) temperature differences, and (b) annual variability of the mean vertical profiles of chlorophyll (μg/l) in Lake Washington (1975–1998).

period of 10 consecutive years (Fig. 8a). It can be seen that the initiation of the spring bloom (for example, see the years 1982, 1985 and 1990) can precede water-column stratification. This finding supports the field observations of several studies (Townsend et al., 1992; Eilertsen, 1993). Huisman et al. (1999) provided the theoretical explanation for these observations with the so-called ''critical turbulence concept''. Fig. 8b depicts the mean annual phytoplankton cycle throughout the water column and the two black lines correspond to the mean timing (vertical) and depth (horizontal) of the epilimnion. Apparently, the spring bloom in the relatively clear waters of Lake Washington can initiate by a relaxation of turbulent mixing (resulting from a period with calm winds and/or a temporary warming of the surface layer) independently of the upper water column depth. Under these conditions, water masses (boxes in Fig. 8b) can maintain their position for sufficient time spans in the upper part of the water column and phytoplankton in this water can exploit the increasingly favorable light conditions. Consequently, phytoplankton growth rates in the upper part of the water column can overcome vertical mixing rates (Huisman et al., 1999). Furthermore, sufficient light transmission and turbulent diffusion magnitudes along with the positive diatom sinking rates, the dominant fraction of the phytoplankton community during February–March (Arhonditsis et al., 2003), generate fairly uniform vertical phytoplankton distribution over the entire water column. Similar vertical profiles were also predicted from Huisman's et al. turbulent diffusion model (see their Figs. 1 and 5) under realistic parameter ranges that coincide with diffusivity values reported for Lake Washington (Walters, 1980).

The second component (April–June) described the peak of the spring bloom and the subsequent decline in phytoplankton biomass is largely controlled by the levels of total phosphorus and grazing pressure from cladocerans. Earlier work by Edmondson and Litt (1982) suggested the spring phytoplankton maximum probably

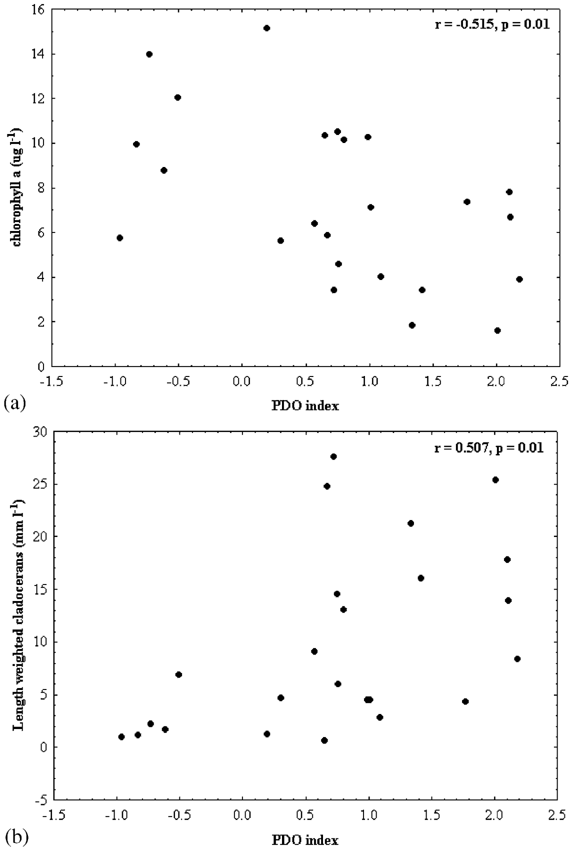

Fig. 8. Scatter plot of the average (a) chlorophyll and (b) cladoceran abundance from the 17th–21st week of the year vs. the March PDO index (1975–1998).

occurs very close to the time when the *Diaptomus* population climbs above a point of 25 ind/l, where its density is sufficient to produce grazing rates that exceed phytoplankton growth rates. Indeed, the significant positive correlation ($r = 0.174$, $p = 0.005$) between the herbivores and chlorophyll *a* during the first mode (January–March) indicates that the small herbivores respond rapidly to the initial increase in phytoplankton biomass and their grazing pressure along with the phytoplankton growth regulate the progress of the spring bloom until the end of April–early May. However, inspection of the system's dynamics with a weekly resolution indicated that this period (see Fig. 4, plots between 17th and 21st week) was also characterized by high interannual phytoplankton variability closely related with the cladoceran abundance. It appears therefore that depending on the year *Diaptomus* grazing rates and/or significant *Daphnia* populations along with decreasing phytoplankton growth rates (due to the exhaustion of the epilimnion phosphorus stock) can reduce phytoplankton biomass; whereas, the subsequent period (middle May–June) is mostly driven by cladoceran grazing. Additional evidence for the latter was provided from Devol (1979), where the highest proportion ($\approx$60%) of the primary production respired by zooplankton was measured in late May. Several recent studies from European lakes have associated interannual variability in the timing of the late spring *Daphnia* population outburst with water temperatures, which in turn were associated with climatic forcing and large-scale meteorological phenomena, such as the North Atlantic Oscillation (Müller-Navarra et al., 1997; Straile, 2000). In Lake Washington, both PDO and ENSO were negatively correlated with the chlorophyll concentrations during the same period, while positive ENSO years seem to have an impact on phytoplankton stability (standard deviation of weekly chl*a* values/average chl*a*) in the system (see Table 3). In addition, the period with the highest phytoplankton and cladoceran variability (17th–21st week) was even more closely correlated ($r = -0.515$ and 0.507, respectively) with the March PDO values (Fig. 8), underlying the tight relationship between weather conditions, the timing of *Daphnia* increase and the collapse of the spring phytoplankton bloom. Winder and Schindler (in press) verified these findings and also showed a significant signature of the local climatic conditions and large-scale meteorological phenomena on the general phenology of the lake (i.e., onset of stratification, maximum algal bloom, clear-water phase). Interestingly, the phytoplankton biomass and the water temperature were not significantly correlated ($r = 0.047$, $p = 0.404$), which is probably due their indirect association—through water temperature effects on *Daphnia* timing—along with the weekly resolution of our study that might have dampened their relationship. In conclusion, a complex interplay between meteorological, chemical and biological factors seems to regulate the interannual variability of phytoplankton dynamics during the spring in Lake Washington.

Another interesting hypothesis about the system dynamics during the same period (April–June) is not directly related with the results of the present statistical analyses, but can be raised from the existing literature of Lake Washington. Arhonditsis et al. (2003) described structural shifts in phytoplankton community composition from the prevalent diatoms (i.e., *Aulacoseira, Stephanodiscus, Asterionella, Fragilaria)* in the spring to chlorophytes *(Oocystis, Sphaerocystis)* and cyanobacteria *(Anabaena, Anacystis, Microcystis)* in early summer. Steady and nonsteady competition experiments under phosphorus limited conditions—the existing regime during the summer in Lake Washington—suggested that only silica limitation could prevent diatoms from displacing cyanobacteria and green algae (Sommer, 1991). Conditions of silica depletion and higher sedimentation rates were also proposed by the

PEG-model as the cause of diatom replacement by dinoflagellates or cyanophyta in lakes (Sommer et al., 1986). Unfortunately, silica concentrations for the entire study period are not available for Lake Washington, but reported values from 1986–1992 (see Fig. 12 of Edmondson, 1997) showed a substantial interannual variability. Mean summer silica levels were between 20 and 500 μg/l, while Si:P atomic ratios varied from 2 to 60. These values are similar to those reported for Lake Constance and Lake Schöhsee where seasonal phytoplankton succession patterns (i.e., *Fragilariaceae* fluctuations) closely followed the Si:P ratio with a lag time of 1–2 weeks (Lampert and Sommer, 1997). Also, considering that the optimum Si:P for *Asterionella formosa* and *Fragilaria crotonensis*—two dominant diatom species during the Lake Washington spring bloom—are 92 and 20, respectively (Tilman, 1981; Hecky and Kilham, 1988), it can be claimed that the late vernal–early summer structural shift of the phytoplankton community can—at least partially—be related to silica limitation and that more consistent monitoring of silica concentrations in Lake Washington is warranted.

Evidence for co-dependence and the tight relationship between the phytoplankton community and cladoceran grazing was also found from July to October (third mode of variability), when a significant portion of the phosphorus supply in the mixed layer is provided by zooplankton excretion (model interaction term between total phosphorus and cladocerans). These results are in agreement with earlier studies by Lehman (1978) and Richey (1979), who estimated that zooplankton nutrient recycling (mostly by *Daphnia pulicaria* and *D. thorata*) provided 60–90% of the phosphorus supply to the mixed layer during the summer stratified period. During the same period, the fraction of primary production respired by the zooplankton community was 25% and remained at this level from June to September, indicative of an equilibrium between phytoplankton–zooplankton that sustains the algal biomass around a level of 3 μg chl *a*/l (Devol, 1979). Interestingly, cladoceran biomass is typically at its lowest level at the end of summer–early fall (see Fig. 5), when *Daphnia* fecundity also decreases from an average spring level of 3 to 1 egg per female (Scheuerell et al., 2002). Good predictors for the observed variability of daphnid growth and fecundity in Lake Washington were found among a variety of surrogate parameters of algal quality and quantity (chlorophyll *a*, proportion of cyanobacteria, particulate carbon, particulate nitrogen, particulate phosphorus, C:N and eicosapentaenoic acid) (Scheuerell et al., 2002; Ballantyne et al., unpublished data). Hence, the nature of the summer phytoplankton/herbivorous zooplankton relationships in the lake needs to be further explored, to delineate the relative importance of algal biochemical, elemental composition and algal quantity as well as assessing the interannual variation of their role.

Finally, the fourth seasonal component (November–-December) was associated with the conditions (solar radiation, zooplankton population) under which the system becomes homogeneous and the phytoplankton reached winter minimum (2–2.5 μg chl*a*/l). An interesting insight into this cooling period requires a three-dimensional projection of the system dynamics and was provided by Walters (1980). This modeling study suggested that rapid cooling rates in the shallow bays of Lake Washington can cause deepening of the mixed layer. These water masses are of intermediate density between the epilimnion and the deeper layers of the lake and can flow beneath the thermocline, and thus hasten the lake's thermal homogenization. In addition, convective penetration of the cooled surface water was discussed as another important process for the temperature vertical profiles of this period. In general, the fourth mode of variability is associated with the combined effects of the weather conditions and hydrodynamic processes that regulate the biological rates at which the system approximates its winter state.

5.2. Management implications and conclusions

Knowledge about the mechanisms that underlie phytoplankton patterns can be particularly useful in the water quality criteria development process and for management planning decisions. For example, Reckhow et al. (2002) pointed out that a water quality criterion, which is a poor surrogate for the designated use of a water body, increases the TMDL forecast uncertainty and is associated with greater risk in water management decisions. It is suggested that a balanced combination of both causal (e.g., nutrients) and response (e.g., chlorophyll *a*, Secchi depth; algal taxa) variables in the criteria together with careful attention to seasonal variability is more appropriate for yielding definitive and comprehensive criteria (Office of Water, 2000). Therefore, elucidation of the role of various ecological mechanisms and understanding the way several physical, chemical and biological variables are interrelated in time (and possibly space; see Arhonditsis et al., 2003), as was provided by this study, is an essential prerequisite for establishing regional and water-body-specific criteria. In addition, our analysis indicated that a set of simple overlapping equations (e.g., spring chlorophyll peak=$f_1(TP_{\text{January-March}}, Cladocerans_{\text{May}})$; $Cladocerans_{\text{May}} = f_2(\text{Temperature}_{\text{April-May}})$) can describe several aspects of phytoplankton dynamics in Lake Washington. Using this conceptualization of the system to formulate structural equation models might reduce predictive error or—at least—enable explicit assessment of the residual uncertainty (Malaeb et al., 2000). Hence, it can assist the TMDL development process, which requires robust methodologies to determine the maximum pollutant loading that will allow a water body to comply with quality standards and attain its designated uses (Reckhow, 1999; Borsuk et al., 2002). Finally, it should be noted that this study mostly focused on total phytoplankton biomass dynamics and we did not include in our statistical analyses individual taxa (or species) variations. For example, we did not take into account the risk of cyanobacteria dominance in the lake. However, the lake has experienced structural shifts in the summer phytoplankton composition (*Aphanizomenon* dominance in 1988); and thus evaluation of the environmental conditions (i.e., meteorological conditions, physical characteristics of the water column, see Soranno, 1997) that can cause such episodic events is warranted and has significant management implications (Edmondson, 1997).

To conclude, statistical analyses of the intra- and interannual phytoplankton variability of Lake Washington, USA, revealed four different types of phytoplankton behavior (modes of variability) over the annual cycle. Direct and interactive effects of available solar radiation, total phosphorus concentrations and cladoceran populations were found to be the best predictors of phytoplankton seasonal patterns. Significant signature of the large-scale climatic fluctuations (ENSO, PDO) was mostly identified during the spring period, when they possibly regulate the interannual variability of the phytoplankton bloom dynamics (timing of the phytoplankton peak and clear water phase). An interesting next step will be the use of this information to develop a linked set of simple equations based on these ecological relationships. This structural approach can provide a comprehensive assessment of the water quality endpoints (i.e., chlorophyll *a*); and thus can be used to predict the trophic state of a water body and assist TMDL decisions.

Acknowledgments

We wish to thank Laura Steinberg (Department of Civil and Environmental Engineering, Tulane University) and Curtis L. DeCasperi (King County, Department of Natural Resources and Parks) for very helpful comments to an earlier draft of this manuscript. This study was supported by a grant from the King County, Department of Natural Resources and Parks, Wastewater Treatment Division. Monika Winder was funded by the Swiss National Science Foundation and the Austrian Science Fund. Support from the Andrew W. Mellon Foundation funded much of the data collection and development of the database.

References

Anneville, O., Ginot, V., Druart, J.C., Angeli, N., 2002. Long-term study (1974–1998) of seasonal changes in the phytoplankton in Lake Geneva: a multi-table approach. J. Plankton Res. 24, 993–1007.

Arhonditsis, G.B., Brett, M.T., DeGasperi, C.L., Schindler, D.E., 2004. Effects of climatic variability on the thermal properties of Lake Washington. Limnol. Oceanogr. 49, 256–270.

Arhonditsis, G., Brett, M.T., Frodge, J., 2003. Environmental control and limnological impacts of a large recurrent spring bloom in Lake Washington, USA. Environ. Manage. 31, 603–618.

Baines, S.B., Webster, K.E., Kratz, T.K., Carpenter, S.R., Magnuson, J.J., 2000. Synchronous behavior of temperature, calcium, and chlorophyll in lakes of northern Wisconsin. Ecology 81, 815–825.

Borsuk, M.E., Stow, C.A., Reckhow, K.H., 2002. Predicting the frequency of water quality standard violations: a probabilistic approach for TMDL development. Environ. Sci. Technol. 36, 2109–2115.

Carpenter, S.R., Kitchell, J.F., Cottingham, K.L., Schindler, D.E., Christensen, D.L., Post, D.M., Voichick, N., 1996. Chlorophyll variability, nutrient input, and grazing: evidence from whole-lake experiments. Ecology 77, 725–735.

Carpenter, S.R., Cole, J.J., Kitchell, J.F., Pace, M.L., 1998. Impacts of dissolved carbon, phosphorus and grazing on phytoplankton biomass and production in experimental lakes. Limnol. Oceanogr. 43, 73–80.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Cochran, P.A., Elser, J.J., Elser, M.M., Lodge, D.M., Kretchmer, D., He, X., Von Ende, C.N., 1987. Regulation of lake primary productivity by food web structure. Ecology 68, 1863–1876.

Devol, A.H., 1979. Zooplankton respiration and its relation to plankton dynamics in two lakes of contrasting trophic state. Limnol. Oceanogr. 24, 893–905.

Edmondson, W.T., 1997. *Aphanizomenon* in Lake Washington. Arch. Hydrobiol. Suppl. 107, 409–446.

Edmondson, W.T., 1994. Sixty years of Lake Washington: a curriculum vitae. Lake Reserv. Manage. 10, 75–84.

Edmondson, W.T., Litt, A.H., 1982. *Daphnia* in Lake Washington. Limnol. Oceanogr. 27, 272–293.

Edmondson, W.T., Lehman, J.T., 1981. The effect of changes in the nutrient income on the condition of Lake Washington. Limnol. Oceanogr. 26, 1–29.

Eilertsen, H.C., 1993. Spring blooms and stratification. Nature 363, 24.

Goldman, C.R., Jassby, A.D., Hackley, S.H., 1993. Decadal, interannual, and seasonal variability in enrichment bioassays at Lake Tahoe, California-Nevada, USA. Can. J. Fish Aquat. Sci. 50, 1489–1496.

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

Goldman, C.R., 1988. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada. Limnol. Oceanogr. 33, 1321–1333.

Hansson, L-A., Annadotter, H., Bergman, E., Hamrin, S.F., Jeppesen, E., Kairesalo, T., Luokkanen, E., Nilsson, P.A., Søndergaard, M., Strand, T., 1998. Biomanipulation as an application of food-chain theory: constraints, synthesis, and recommendations for temperate lakes. Ecosystems 1, 558–574.

Hecky, R.E., Kilham, P., 1988. Nutrient limitation of phytoplankton in fresh-water and marine environments—a review of recent evidence on the effects of enrichment. Limnol. Oceanogr. 33, 796–822.

Horn, H., Paul, L., 1984. Interactions between light situation, depth of mixing and phytoplankton growth during the spring period of full circulation. Int. Rev. Ges. Hydrobiol. 69, 507–519.

Huisman, J., Oostveen, P., Weissing, F.J., 1999. Critical depth and critical turbulence: Two different mechanisms for the development of phytoplankton blooms. Limnol. Oceanogr. 44, 1781–1787.

Ives, A.R., 1995. Predicting the response of populations to environmental change. Ecology 76, 926–941.

Jassby, A.D., Cloern, J.E., Cole, B.E., 2002. Annual primary production: Patterns and mechanisms of change in a nutrient-rich tidal ecosystem. Limnol. Oceanogr. 47, 698–712.

Jassby, A.D., Goldman, C.R., Reuter, J.E., Richards, R.C., 1999. Origins and scale dependence of temporal variability in the transparency of Lake Tahoe, California-Nevada. Limnol. Oceanogr. 44, 282–294.

Jassby, A.D., 1999. Uncovering mechanisms of interannual variability from short ecological time series. In: Scow, K.M., Fogg, G.E., Hinton, D.E., Johnson, M.L. (Eds.), Integrated Assessment of Ecosystem Health. CRC Press, Boca Raton, FL, pp. 285–306.

Jassby, A.D., Goldman, C.R., Powell, T.M., 1992. Trend, seasonality, cycle, and irregular fluctuations in primary productivity at Lake Tahoe, California-Nevada, USA. Hydrobiologia 246, 195–203.

Jassby, A.D., Powell, T.M., Goldman, C.R., 1990. Interannual fluctuations in primary production: direct physical effects and the trophic cascade at Castle lake, California. Limnol. Oceanogr. 35, 1021–1038.

Kendall, M., Ord, J.K., 1990. Time Series. third ed. Griffin.

Lampert, W., Sommer, U., 1997. Limnoecology: the ecology of lakes and streams. Oxford University Press, Oxford.

Lehman, J.T., 1978. Aspects of nutrient dynamics in freshwater communities. Ph.D. Thesis, University of Washington.

Makridakis, S.G., Wheelwright, S.C., 1989. Forecasting methods for management, fifth ed. Wiley, New York.

Malaeb, Z.A., Summers, J.K., Pugesek, B.H., 2000. Using structural equation modeling to investigate relationships among ecological variables. Environ. Ecol. Stat. 7, 91–111.

Mann, K.H., Lazier, J.R.N., 1996. Dynamics of marine ecosystems: biological–physical interactions in the oceans, second ed. Blackwell, Oxford.

Marshal, T.C., Peters, R.H., 1989. General patterns in the seasonal development of chlorophyll *a* for temperate lakes. Limnol. Oceanogr. 34, 856–867.

Müller-Navarra, D.C., Güss, S., Storch, H., 1997. Interannual variability of seasonal succession events in a temperate lake and its relation to temperature variability. Global Change Biol. 3, 429–438.

Neale, P.J., Talling, J.F., Heaney, S.I., Reynolds, C.S., Lund, J.W.G., 1991. Long-time series from the English Lake District—irradiance dependent phytoplankton dynamics during the spring maximum. Limnol. Oceanogr. 36, 751–760.

Nelson, D.M., Smith Jr., W.O., 1991. Sverdrup revisited: Critical depths, maximum chlorophyll levels, and the control of Southern Ocean productivity by the irradiance-mixing regime. Limnol. Oceanogr. 36, 1650–1661.

Office of Water, 2000. Nutrient Criteria Technical Guidance Manual. Lakes and Reservoirs. United States Environmental Protection Agency, Washington, DC.

Overland, J.E., Preisendorfer, R.W., 1982. A significance test for principal components applied to a cyclone climatology. Mon. Weather Rev. 110, 1–4.

Reckhow, K.H., Stow, C.A., Borsuk, M.E., 2002. Uncertainty between the criterion and the designated use: implications for standards and TMDL margin of safety. Proceedings of the Water Environment Federation National TMDL Science and Policy Conference, Phoenix, Arizona, November 13–16, 2002.

Reckhow, K.H., 1999. Water quality prediction and probability network models. Can. J. Fish Aquat. Sci. 56, 1150–1158.

Reynolds, C.S., 1984. The Ecology of Freshwater Phytoplankton. Cambridge University Press, Cambridge, UK.

Richey, J.E., 1979. Patterns of phosphorus supply and utilization in Lake Washington and Findley Lake. Limnol. Oceanogr. 24, 906–916.

Richman, M.B., 1986. Rotation of principal components. J. Climatol. 6, 293–335.

Ronchetti, E., Staudte, RG., 1994. A robust version of Mallows' Cp. J. Am. Stat. Assoc. 89, 550–559.

Rothhaupt, K.O., 2000. Plankton population dynamics: food web interactions and abiotic constraints. Freshwater Biol. 45, 105–109.

Scheuerell, M.D., Schindler, D.E., Litt, A.H., Edmondson, W.T., 2002. Environmental and algal forcing of *Daphnia* production dynamics. Limnol. Oceanogr. 47, 1477–1485.

Sommer, U., 1991. Growth and survival strategies of planktonic diatoms. In: Sandgren, C.D. (Ed.), Growth and Reproductive Strategies of Freshwater Phytoplankton. Cambridge University Press, London, pp. 227–260.

Sommer, U., Gliwicz, Z.M., Lampert, W., Duncan, A., 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Arch. Hydrobiol. 106, 433–471.

Soranno, P.A., 1997. Factors affecting the timing of surface scums and epilimnetic blooms of blue green algae in a eutrophic lake. Can. J. Fish Aquat. Sci. 54, 1965–1975.

Straile, D., 2002. North Atlantic oscillation synchronizes food-web interactions in central European lakes. Proc. Roy. Soc. London B 269, 391–395.

Straile, D., 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. Oecologia 122, 44–50.

Sverdrup, H.U., 1953. On conditions for the vernal blooming of phytoplankton. J. Cons. Perm. Int. Explor. Mer. 18, 287–295.

Tilman, D., 1981. Test of resource competition theory using four species of Lake Michigan algae. Ecology 62, 802–815.

Townsend, D.W., Keller, M.D., Sieracki, M.E., Ackleson, S.G., 1992. Spring phytoplankton blooms in the absence of vertical water column stratification. Nature 360, 59–62.

Vanni, M.J., Temte, J., 1990. Seasonal patterns of grazing and nutrient limitation of phytoplankton in a eutrophic lake. Limnol. Oceanogr. 35, 697–709.

Walters, R.A., 1980. Time and depth-dependent model for physical, chemical and biological cycles in temperate lakes. Ecol. Model 8, 79–96.

Weyhenmeyer, G.A., Blenckner, T., Petterson, K., 1999. Changes of the plankton spring outburst related to the North Atlantic Oscillation. Limnol. Oceanogr. 44, 1788–1792.

Winder, M., Schindler, D.E., Climate impact on the phenology of lake processes. Global Change Biology, in press.