

## Disrupted seasonal clockwork in the population dynamics of a freshwater copepod by climate warming

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### Abstract

Life history responses are expected to accompany climate warming, yet little is known how long-term effects of climate and environmental change affect the seasonal dynamics of planktonic organisms. We used an historical data set from Lake Washington (U.S.A.) to quantify population responses of a calanoid copepod (*Leptodiatomus ashlandi*) to long-term changes in temperature and resource availability and explore potential mechanisms for the responses. Increasing water temperatures (annual mean increase of 1.5°C in the upper 10-m water volume) and longer stratification periods (about 4 weeks) were observed between 1962 and 2005, coincident with a pronounced decline in *Leptodiatomus* densities. However, production was maintained because of an increase in the production to biomass ratio and a life cycle shift in *Leptodiatomus* from an annual to a 6-month cycle. Cross-wavelet analyses demonstrated that the annual thermal forcing of copepod recruitment observed during the first two decades of the study weakened substantially, leading to more stochastic population dynamics during the past two decades. This shift from one to two generations per year was most likely produced by a longer and warmer growing period combined with changing fluctuations in resource (phytoplankton) availability. Climate change can lead to higher-frequency voltinism in ectothermic organisms and to temporal reorganization of their population dynamics.

Population dynamics of ectothermic organisms are strongly linked to the seasonality of temperature and resource availability. Subtle variation in extrinsic factors can modify the temporal population fluctuations in these organisms. Temperature is a key parameter affecting physiological rates in ectotherms (Beisner et al. 1997; Gillooly and Dodson 2000; Strecker et al. 2004), and their population growth shows strong coherence with seasonal temperature fluctuations. The direct effect of temperature on metabolic and vital rates have been inferred from experimental manipulations, observations along altitudinal and latitudinal gradients, and correlational studies between distribution patterns and climate variables (Magnuson et al. 1990; Wilhelm and Schindler 2000; Blais et al. 2003). These studies demonstrate that increasing temperature within the tolerance range of a species accelerates both growth and developmental rates of individual organisms given sufficient resources. Changes in these vital parameters caused by elevated temperature ultimately affect population dynamics (McCauley and Murdoch 1987) and have the potential to generate a shift from stable to more fluctuating dynamics (Halbach 1970; Beisner et al. 1997). Larger-amplitude cycles further increase the likelihood of extinction because of stochastic processes, as the population trajectory approaches zero density more closely and more often (Murdoch and McCauley 1985). The emerging view from these research syntheses is that elevated turnover rates, increased number of generations per year, greater population instability, and changes in life history strategies such as dormancy are anticipated for ectotherms with

climate warming (reviewed by Bale et al. 2002; Drake 2005).

The response of ectotherms to climatically driven environmental change, however, will depend not only on the direct effect of temperature on population vital rates but also on the synchronization of key life stages with food availability (Cushing 1990). This is particularly important for pelagic herbivores in temperate regions where quantity and quality of phytoplankton, their major food resource, is highly variable on a seasonal basis (Sommer et al. 1986). Moreover, climate change alters the density gradient of the water column and consequently the relative strength of mixing and stratification. Mixing processes are usually accompanied by changes in phytoplankton resource availability of light and nutrients and affect the seasonal dynamics of consumers (Winder and Schindler 2004b). As a result, climate may indirectly affect population dynamics and life histories of zooplankton through its effect on seasonality of resource availability and other components of the ecosystem, such as the extent of the growing season (Ottersen et al. 2001). Such modifications in the environment are expected to affect life cycle responses particularly in copepods (Chen and Folt 1996; Drake 2005), given the plasticity of their life histories and their extended longevity compared to cladocerans and rotifers (Allan and Goulden 1980).

Copepods are important organisms in both freshwater and marine ecosystems, and their secondary production supports carnivores in many pelagic food webs (Mauchline 1998). Growth and development of these key planktonic taxa are subject to periodic (seasonal) and stochastic environmental variation, and their populations undergo extensive cyclic fluctuations both within and among years (Burns 1992; Twombly et al. 1998). Copepods have distinct reproductive pulses and recurring population oscillations produced through endogenous and exogenous drivers.

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Both temperature and food availability regulate life cycle duration of pelagic copepods, ranging from 1 to several months (Twombly et al. 1998), and, depending on temperature and seasonal time constraints, their life histories can alternate between univoltine or multivoltine strategies among lakes (Allan and Goulden 1980). Environmental conditions also alter life cycle strategies in copepods, which differ from year-round active stages to strong seasonality with resting stages of varying length (Hairston et al. 1996). In addition, copepods are sensitive to climatic change, as evidenced by strong relations between water temperature and biogeographic ranges (Beaugrand et al. 2002), abundances (Roemmich and McGowan 1995), and phenologies (Winder and Schindler 2004b; Adrian et al. 2006). While alterations of the copepod life history are also expected to accompany climate-driven environmental changes (Chen and Folt 1996; Beaugrand et al. 2002; Gerten and Adrian 2002), to date there has been no empirical demonstration of these types of changes.

We investigated the population responses of a calanoid copepod, *Leptodiaptomus ashlandi*, to environmental variation using an extensive data set over a 44-yr time period (1962–2005) from Lake Washington (U.S.A.), where food web structure changed in the mid-1970s (Edmondson 1994; Hampton et al. 2006) and water temperature and the length of the growing season have increased significantly since the early 1960s (Arhonditsis et al. 2004; Winder and Schindler 2004b). We describe shifts in population life cycle dynamics of *Leptodiaptomus* using wavelet analyses and a logistic regression model to assess whether environmental variation of food availability and temperature can explain the dynamics of this species on the basis of the long-term monitoring data. Because Lake Washington has a history of eutrophication and recovery following nutrient diversion that occurred during the early period of our study, we were able to compare the relative importance of climate warming on copepod population dynamics to the effects of detailed changes in their prey community. We find that improved growing conditions due to water temperature warming and changes in resource availability caused a switch in the number of generations per year of this year-round active copepod species. During the first two decades of the study, when the population dynamics were characterized by univoltine life cycle, there was strong 12-month coherence among water temperature, phytoplankton food, and recruitment in the population. As the lake has warmed, the predictable synchrony among these components of the ecosystem eroded such that recruitment in the copepod became only weakly associated with the 12-month seasonality of temperature and essentially independent of the 12-month seasonality in phytoplankton resources. These changes in the temporal organization of the ecosystem were associated with more variable population dynamics as predicted by generic population dynamics models that include environmental stochasticity (Drake 2005; Boyce et al. 2006).

## Methods

**Study site**—Lake Washington is a large (surface area 87.6 km<sup>2</sup>) lake located in the state of Washington (U.S.A.)

(47°83'N, 122°15'W; 4 m asl) with a mean depth of 32.9 m and maximum depth of 65.2 m. The lake has experienced several major changes in the past 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 peak (~100 µg L<sup>-1</sup>) in the mid-1960s and declined thereafter as a consequence of sewage diversion (Edmondson 1997). By 1975, the lake was considered fully recovered from eutrophication, and total phosphorus was constant at an annual average concentration of 14.5 ± 5.7 µg L<sup>-1</sup> between 1975 and 2004.

Coincident with the termination of sewage loading, *Daphnia* became the dominant zooplankton grazer since the mid-1970s as a result of the disappearance of the filamentous blue-green algae *Oscillatoria* and reduced predation by the mysid shrimp *Neomysis mercedis* (Edmondson 1997; Hampton et al. 2006). *Neomysis* decreased in concert with increased densities of longfin smelt (*Spirinchus thaleichthys*) in the 1960s. The most abundant zooplankton crustaceans over the sampling period were the cladocerans *Bosmina longirostris*, *Daphnia* spp., *Diaphanosoma birgei*, *Cyclops bicuspidatus*, the predatory copepod *Epischura nevadensis*, and the herbivorous copepod *Leptodiaptomus ashlandi* (named *Leptodiaptomus* throughout). The most prominent competitors of *Leptodiaptomus* for resource availability were *Daphnia* and the nondaphnid cladocerans (Hampton et al. 2006). Densities of potential *Leptodiaptomus* predators, including *C. bicuspidatus* and *E. nevadensis*, did not show a long-term trend (Hampton et al. 2006). Resting eggs of *Leptodiaptomus* have not been reported in the literature (Torke 2001) and have never been observed in live or sediment samples in Lake Washington (A. Litt pers. obs.). The life cycle of this copepod species is generally characterized by year-round active stages, and their life history has been described as monocyclic or bivoltine (Comita and Anderson 1959; Torke 2001).

**Limnological data**—Limnological data were collected at a central station at weekly to biweekly intervals during the stratified period and monthly during the unstratified winter period from 1962 to 2000 (phytoplankton) and 1962 to 2005 (zooplankton, temperature), respectively. These data include measurements of temperature (at 1-m intervals), zooplankton from 0- to 20-m depth, and phytoplankton biovolume from the surface water, which is a good representative of the upper mixed water layer (Edmondson et al. 2003). Sampling and analysis methods for phytoplankton and zooplankton are fully described in Edmondson (1997) and Edmondson et al. (2003). In short, zooplankton tow nets were taken with a closing Clarke-Bumpus sampler and net mesh size of 130 µm. Phytoplankton abundances were estimated using a modified Utermöhl technique, and biovolume estimates for individual phytoplankton species were based on cell-size measurements and subsequent calculations of biovolume based on geometric solids of known volumes. Copepods were identified to species, sex, and life stage, and volume-weighted average densities of *Leptodiaptomus* were calculated. When stages were not identified (two sampling dates in 1962 and 1963), they were assigned to proportional

densities at the same time the year before or after. In addition, metasomal length of adult females was measured for 50 individuals (if available) per sampling date between 1963 and 1999, and clutch size was enumerated for 175 to 1351 individuals per year (on average for 482 individual per year) between 1962 and 1997. Gut analysis indicated that *Leptodiaptomus* feeds almost exclusively on algae in Lake Washington (Infante and Edmondson 1985), and a recent multivariate approach by Hampton and Schindler (2006) suggested that *Daphnia* and *Leptodiaptomus* compete for the same food sources.

**Leptodiaptomus production**—Secondary production of *Leptodiaptomus* was estimated using the egg ratio method of Paloheimo (1974), a method that has been used successfully to measure copepod secondary production (Kuns and Sprules 2000). Average annual production was calculated as the average of daily production for each sampling interval. Biomass was estimated by using a species specific length-weight regression determined for *Leptodiaptomus* in Lake Washington. For further details on the estimation of *Leptodiaptomus* production and biomass, see the Web Appendix ([www.aslo.org/lo/toc/vol\\_54/issue\\_6\\_part2/2492a.pdf](http://www.aslo.org/lo/toc/vol_54/issue_6_part2/2492a.pdf)).

**Time frequency analysis**—We used the continuous wavelet transform (CWT) (Torrence and Compo 1998) to analyze the frequency components of immature and adult *Leptodiaptomus* abundance over the 44-yr period. Wavelet analysis imitates dynamic Fourier analysis with wavelet functions that are better suited to capture the local behavior of nonstationary time series (Shumway and Stoffer 2000). The CWT quantifies both the amplitude of any periodic signals and how this amplitude varies with time by using short packets of waves that map temporal changes in the cyclicities and is thus advantageous for complex, nonstationary time series. We used the Morlet wavelet (Torrence and Compo 1998) after normalizing average monthly density values by the standard deviation across all years. The CWT applies the wavelet as a band-pass filter to the time series and is stretched in time by varying its scale. This analysis has been used successfully in biological communities to identify fluctuations in abundances (Bjørnstad et al. 1999; Jenouvrier et al. 2005; Vasseur and Gaedke 2007). Because the wavelet transformation showed marked changes in cycle period through time, we split the 44-yr time series of *Leptodiaptomus* abundance into four time periods of each 11 yr representing a single period with elevated cyanobacteria and phosphorus concentration and absence of *Daphnia* (1962–1972) and three subsequent periods with reduced cyanobacteria and otherwise similar algal concentrations (Edmondson 1997), reduced phosphorus concentration, and presence of *Daphnia* (1973–1983, 1984–1994, 1995–2005). Further, this split of the time series separates the approximate time when a shift was observed by the CWT. The frequency spectrum of each time period was analyzed using the global wavelet spectrum (GWS), and the power spectrum was corrected by scale; that is, the produced spectra was divided by the corresponding scale to ensure consistency, as suggested by Liu et al. (2007). The

GWS is the time-averaged wavelet power spectrum for each frequency component and is used to identify the dominant frequency components and to quantify the importance of particular frequencies in the time series.

To explore the dependency of periodicity in *Leptodiaptomus* population dynamics on the seasonality of temperature and food resources, we applied cross-wavelet transform (XWT) between *Leptodiaptomus* abundances and food availability and temperature, respectively. XWT of two time series is useful to examine whether regions in time frequency space with large common power have a consistent phase relationship and finds regions in time frequency space where two time series show high common power (Grinsted et al. 2004). Wavelet software for Matlab was provided by C. Torrence and G. Compo (available at <http://paos.colorado.edu/research/wavelets>) and by A. Grinsted for XWT.

**Statistical analysis**—For trend analysis, a first-order autoregressive term was taken into account if significant autocorrelation was observed (Bence 1995). To evaluate associations between *Leptodiaptomus* voltinism and changes in the thermal structure and food availability, we used generalized linear models with a binomial response distribution and a logit link function. Model selection was based on a stepwise procedure, and the improvement of the fit gained was assessed using the chi-square change in deviance at the 5% level. We used the Akaike information criterion (AIC) corrected for small sample size (AIC<sub>c</sub>) (Burnham and Anderson 2002) to optimize the number and combination of predictive variables to select the best-fit model explaining the occurrence of monocyclic (12-month) or bicyclic (6-month) population dynamics. This was determined on the basis of whether monthly abundances for each calendar year followed a unimodal or a bimodal pattern. A bimodal pattern was chosen when abundances increased in fall after the summer decline. To reduce serial correlation in the residuals, the retained predictor variables were modeled as a first-order autoregressive process using mixed-effects models (Pinheiro and Bates 2000). We tested the hypothesis that a warmer thermal structure and change in food availability allowed the insertion of an additional generation per year in immature copepods. Explanatory variables included degree-days (assuming a lower and upper development thresholds of 8°C and 20°C, respectively, in the upper 20-m water column; Comita and Anderson 1959), duration of summer stratification (Winder and Schindler 2004b), average temperature in the upper 20-m water column, edible phytoplankton biovolume (i.e., phytoplankton excluding cyanobacteria), and phytoflagellates biovolume. Analysis was done using R version 2.7.0 (R Development Core Team 2008).

## Results

**Long-term trends**—Temperature anomalies from the epilimnion of Lake Washington increased in almost every month between 1962 and 2005 (Fig. 1a). The biovolume of edible phytoplankton (i.e., excluding cyanobacteria) remained at a relatively consistent level throughout the sampling period ( $r = 0.31$ , slope =  $0.01 \text{ yr}^{-1}$ ,  $p = 0.06$ ),

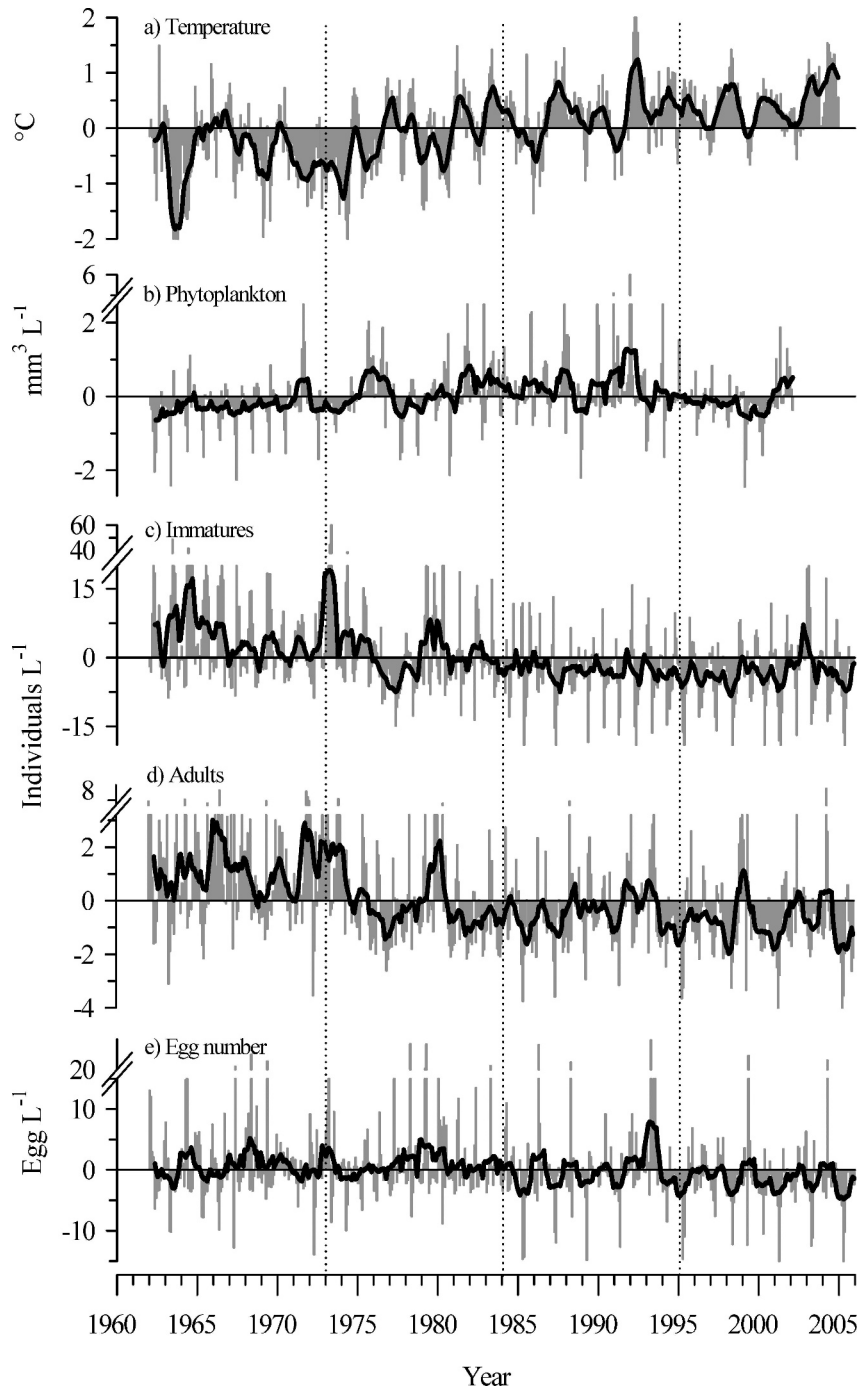


Fig. 1. Monthly anomalies of (a) surface (0–20-m depth) water temperature, (b) phytoplankton biovolume (excluding cyanobacteria), (c) *Leptodiatomus ashlandi* juvenile immature densities, (d) adult densities, and (e) egg numbers in Lake Washington from 1962 to 2005 (phytoplankton to 2000). Gray bars are monthly anomalies; black thick lines represent the 10-month running means. Anomalies were calculated from monthly averages over the respective sampling period. Vertical dotted lines demarcate the time periods for spectral and model analysis.

although values increased slightly from the 1970s to the early 1990s and declined slightly thereafter (Fig. 1b). Interannual variability in *Leptodiatomus* densities was high with pronounced peaks in the 1960s and early 1970s. A Levene test showed that the variance of densities

changed over time ( $p < 0.001$ ). *Leptodiatomus* densities and egg number dropped in the mid-1970s (Fig. 1c–e), and over the sampling period between 1962 and 2005, immatures declined from 15.6 to 4.0 individuals  $L^{-1}$  ( $r = -0.70$ , slope =  $-0.26 \text{ yr}^{-1}$ ,  $p < 0.001$ ), adults from 3.7 to



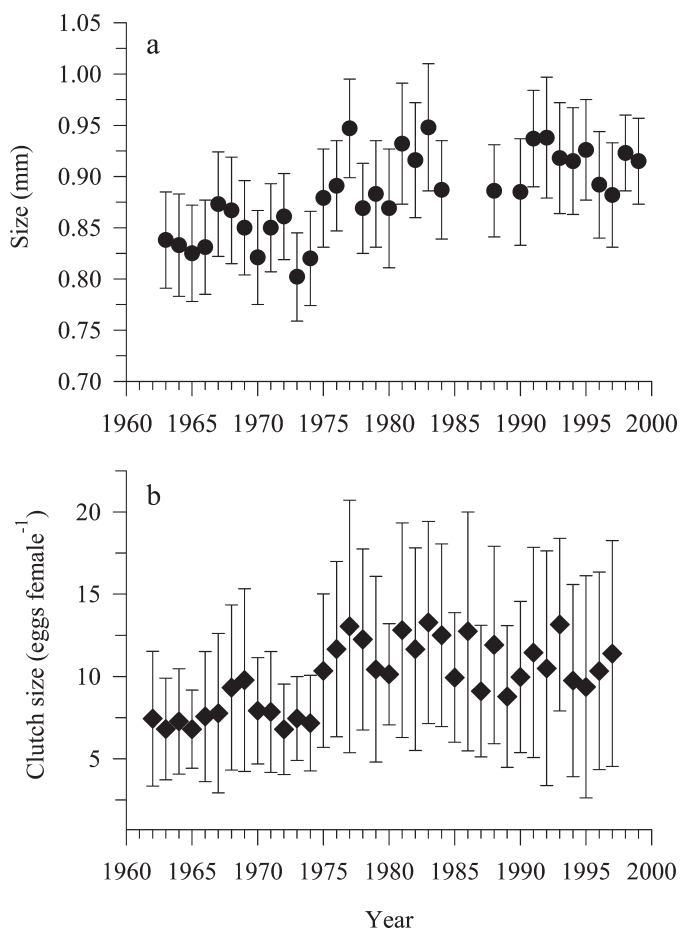


Fig. 2. Average annual (a) adult female length and (b) clutch size of *Leptodiaptomus ashlandi* from 1962 to 1999 and 1997, respectively, in Lake Washington. Female size increased from about 0.84 mm to 0.91 mm and clutch size from about 8 to 11 eggs per female in the mid-1970s (ANOVA separating time periods from 1962 to 1974 and 1975 to 1997–1998; female size:  $F_{1,499} = 87.31$ ,  $p < 0.001$ ; clutch size:  $F_{1,35} = 63.29$ ,  $p < 0.001$ ). Clutch size represents the number of eggs per clutch. Error bars represent standard deviations.

0.7 individuals  $L^{-1}$  ( $r = -0.71$ , slope =  $-0.06 \text{ yr}^{-1}$ ,  $p < 0.001$ ), and egg numbers from 6.7 to 1.3 eggs  $L^{-1}$  ( $r = -0.37$ , slope =  $-0.06 \text{ yr}^{-1}$ ,  $p = 0.01$ ) as indicated by linear regressions of annual mean abundances versus year. The abundance decline in the mid-1970s coincided with an increase in female length ( $r = 0.41$ ,  $p < 0.001$ ) and clutch size ( $r = 0.77$ ,  $p < 0.001$ ) (Fig. 2). Whereas *Leptodiaptomus* abundances showed a pronounced decline, their overall annual production rates were markedly constant throughout the entire duration of the study ( $r = 0.09$ , slope =  $-0.02 \text{ yr}^{-1}$ ,  $p = 0.6$ ) (Fig. 3a). Thus, coincident with the decline in population density in the mid-1970s was a distinct increase in the production : biomass (P : B) ratio for this copepod population ( $r = 0.38$ , slope =  $0.01 \text{ yr}^{-1}$ ,  $p = 0.01$ ) (Fig. 3b) that maintained secondary production by *Leptodiaptomus* in this ecosystem.

Adding to the pronounced decline in *Leptodiaptomus* densities, a change in the dominant seasonal cycle was

observed in the early to mid-1980s as supported by wavelet analysis over the entire sampling period (Fig. 4a,b). We split the time series into two distinct periods, each subdivided into two subperiods to highlight this response (see Methods for details). Average seasonal abundances of *Leptodiaptomus* revealed a clear distinction between the periods 1962–1983 and 1984–2005 (Figs. 4, 5). During the period 1962–1983, the average seasonal dynamics of *Leptodiaptomus* immatures were characterized by high densities during spring and summer (especially in the first period) and low densities during fall and winter, indicative of a monovoltine life cycle. A univoltine population dynamic was demonstrated by the global wavelet spectrum, indicating a strong cyclic component corresponding to a 12-month oscillation and from 1973 to 1983 an additional but weaker 6-month cycle (Fig. 6a,b). Between 1984 and 2005, the seasonal dynamics of immatures shifted, however, and showed a clear bimodal pattern with a distinct spring and fall peak (Fig. 5a). During this latter time period, immature *Leptodiaptomus* were already at considerable densities late in the winter or early spring compared to the first two decades of the study (Fig. 5a). This shift in population dynamics was confirmed by spectral analysis of measured densities within this period, indicating that the power of the 12-month cycle declined and disappeared in the last time interval (1995–2005), when 6-month oscillations became the only significant cycle components (Fig. 6c,d).

A similar change in the seasonal dynamics was observed for adult *Leptodiaptomus*. During the first period (1962–1972), densities peaked in spring, generally declined until July, then increased slowly after this period with relatively high densities during the winter (Fig. 5b), indicating that the population is overwintering as adults. This increase in winter was indicated by the global wavelet spectrum, which showed significant 12-month and 6-month cycles (Fig. 6a). Over the next 11-yr interval (1973–1983), dynamics were similar, although with a less intense density increase in fall and winter, and the global wavelet spectrum showed a strong cyclic component corresponding to a 12-month and 6-month oscillation (Fig. 6b). After 1983, the seasonal pattern of adults was comparable to immatures and characterized by peak densities in spring and fall and a significant 6-month oscillation (Figs. 5b, 6).

Major *Leptodiaptomus* reproductive pulses occurred in spring throughout the entire time period (Fig. 5c), which is also indicated by the dominant 12-month oscillation in clutch size (Fig. 7). Since the mid-1970s, pulses of egg production occurred over a prolonged period that extended into fall and declined in October for a short time. The relative strength of the 6-month oscillation increased during the last time period (1995–2005), indicative of more consistent egg production in spring and fall (Fig. 7d).

In comparison, average seasonal succession of phytoplankton biomass was relatively consistent over the sampling period both for total phytoplankton and for the edible fraction with a distinct spring peak and a slight increase in fall, particularly during the last three time periods (Figs. 4c,d, 5d). A significant cyclicity of edible phytoplankton with a consistent dominant 12-month cycle and a less dominant 6-month cycle was observed in all four

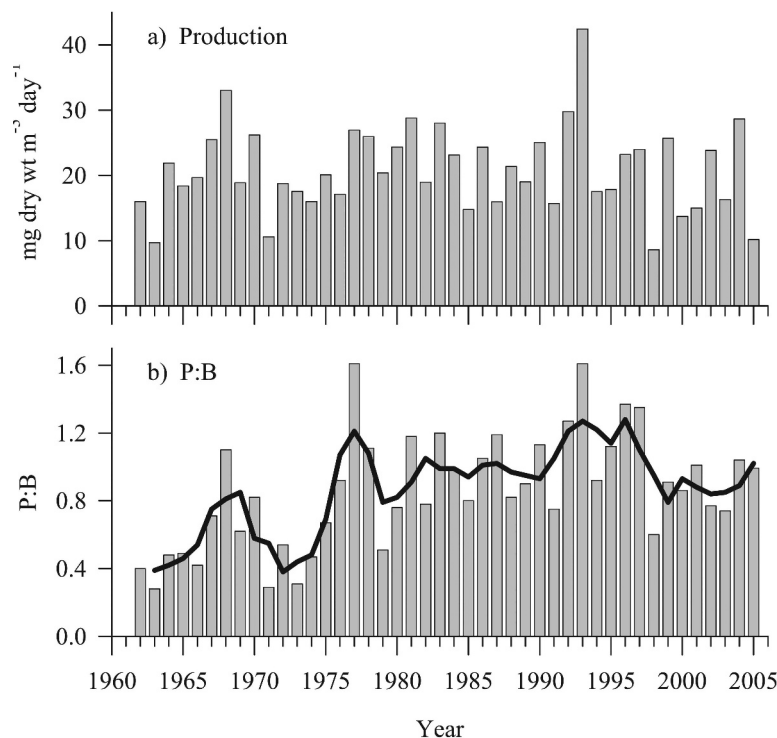


Fig. 3. (a) Annual production in mg dry weight carbon  $\text{m}^{-3} \text{d}^{-1}$  and (b) annual production:biomass ratio (P:B) of *Leptodiaptomus ashlandi* between 1962 and 2005 in Lake Washington. The solid line represents a 3-yr moving average. The P:B ratio is a measure of the rate of *Leptodiaptomus* turnover.

time periods (Fig. 7). The relative strength of the 6-month cycle, however, increased particularly during the last 11-yr time period, suggesting more consistent phytoplankton peaks in fall and winter over this period of record. In addition to more distinct phytoplankton peaks in fall, species composition changed after the mid-1970s to the end of the 1970s, likely as a response to phosphorus reduction (for detailed changes in the phytoplankton community, see Edmondson et al. 2003). The most striking change was an increase in phytoflagellate biovolume (including dinoflagellates, chlorophytes, and cryptophytes) particularly during summer, fall, and winter since the early 1980s. Note that Fig. 5 shows daily averages over the four 11-yr time periods and thus may mask seasonal abundances in individual years.

*Factors affecting Leptodiaptomus voltinism*—We used the cross-wavelet power analysis to explore whether the coherence in the periodicity of *Leptodiaptomus* population dynamics and the periodicity of environmental drivers (i.e., phytoplankton biovolume and water temperature) changed over the course of the study. Cross-wavelet power for population dynamics of immatures and water temperature showed strong covariation between the time series corresponding to a 12-month period until the late 1980s, and this strength of coherence decreased substantially thereafter (Fig. 8a). Covariation between population dynamics of immatures and phytoplankton was strong at the 12-month frequency until the early 1980s and disappeared thereafter

except for a short time in the late 1980s (Fig. 8c). After the early 1980s, covariation between food and immatures increased in strength at the 6-month period. *Leptodiaptomus* adult oscillation showed strong covariation with temperature at the 12-month period throughout the period (Fig. 8b), although the direction varied over the sampling period between linear (in-phase) and nonlinear (out-of-phase) relations. Similar to immatures, the coherence of adult population dynamics with phytoplankton was disrupted in the early 1980s at the 12-month scale with few years of coherence at that period afterward (Fig. 8d). At the 6-month scale, adult dynamics displayed coherence with phytoplankton in the mid-1960s, and more consistent relations appeared since the 1980s, similar to the pattern for immatures. Taken together, the results of the cross-wavelet analyses indicated that the seasonal population dynamics of adult and immature became increasingly disconnected from the seasonal, 12-month variation in temperature and food availability.

Logistic regression models for immature *Leptodiaptomus* support that change in the thermal structure was primarily responsible for the shift from a 12-month to a 6-month cycle (Table 1). The best-fit models suggest additive effects associated with annual degree-days and phytoflagellate biovolume. The probability of a 6-month cycle increased with higher degree-days and increased phytoflagellate biovolume. The change in the thermal environment was, however, always a better predictor compared to change in food availability as differences in

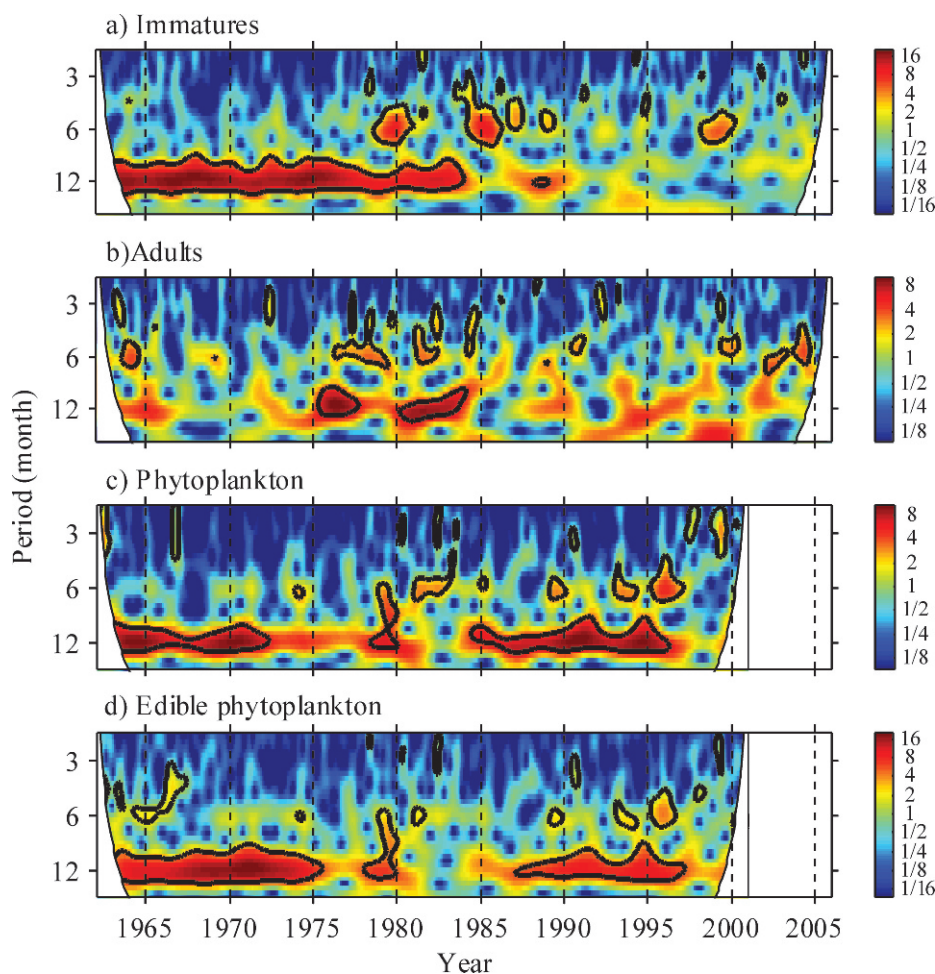


Fig. 4. Wavelet power spectrum of (a) juvenile immature and (b) adult *Leptodiaptomus ashlandi* abundances (power [individuals L<sup>-1</sup>]<sup>2</sup>), (c) phytoplankton biovolume, and (d) edible phytoplankton biovolume (i.e., excluding cyanobacteria) in Lake Washington from 0- to 20-m depth between 1962 and 2005. The power of the wavelet spectrum decreased considerably after 1983 owing to extensive population fluctuations, resulting in low resolution after that period. The cone of influence (black curve) indicates the region without edge effects. The power values are coded from dark blue for low power to dark red for high power, as shown in the right panels.

AIC<sub>c</sub> increased substantially in models using only food availability as predictor variables (Table 1). This suggests that enhanced growing conditions due to a longer period of warmer temperature, in particular due to the increasing trend in degree days ( $r_p = 0.82$ , slope = 8.8 yr<sup>-1</sup>,  $p < 0.001$ ) and water temperature ( $r_p = 0.79$ , slope = 0.03 yr<sup>-1</sup>,  $p < 0.001$ ), were the primary driver for the addition of a second generation per year in *Leptodiaptomus* and that improved food quality was secondarily important for this shift.

## Discussion

One of the main mechanisms by which environmental stochasticity may induce changes in ecosystem structure and function is by disrupting the life history strategies of key component species (Rhodes et al. 1996; Bale et al. 2002). Here, we demonstrated that a long-term shift in thermal conditions (Arhonditsis et al. 2004; Winder and

Schindler 2004b), coupled with change in resource availability (Edmondson et al. 2003; Winder and Schindler 2004b), was associated with a shift in the seasonal dynamics of a copepod species from one generation to two generations per year. Associated with this shift in the dominant life cycle was a decoupling of population dynamics from the seasonal forcing of the annual temperature cycle. Adding to this life history shift, the P:B ratios of this copepod species increased over the same period, thereby resulting in a conservation of secondary production by this species despite reduced abundance. The most parsimonious models we considered suggested that the process underlying this shift in population dynamics was an additive effect of increasing annual degree-days and availability of high-quality food.

Water temperature in Lake Washington increased by about 1.5°C in the upper 10-m water volume (Fig. 1a; Arhonditsis et al. 2004), and the period of stratification was extended by about 4 weeks over the past four decades

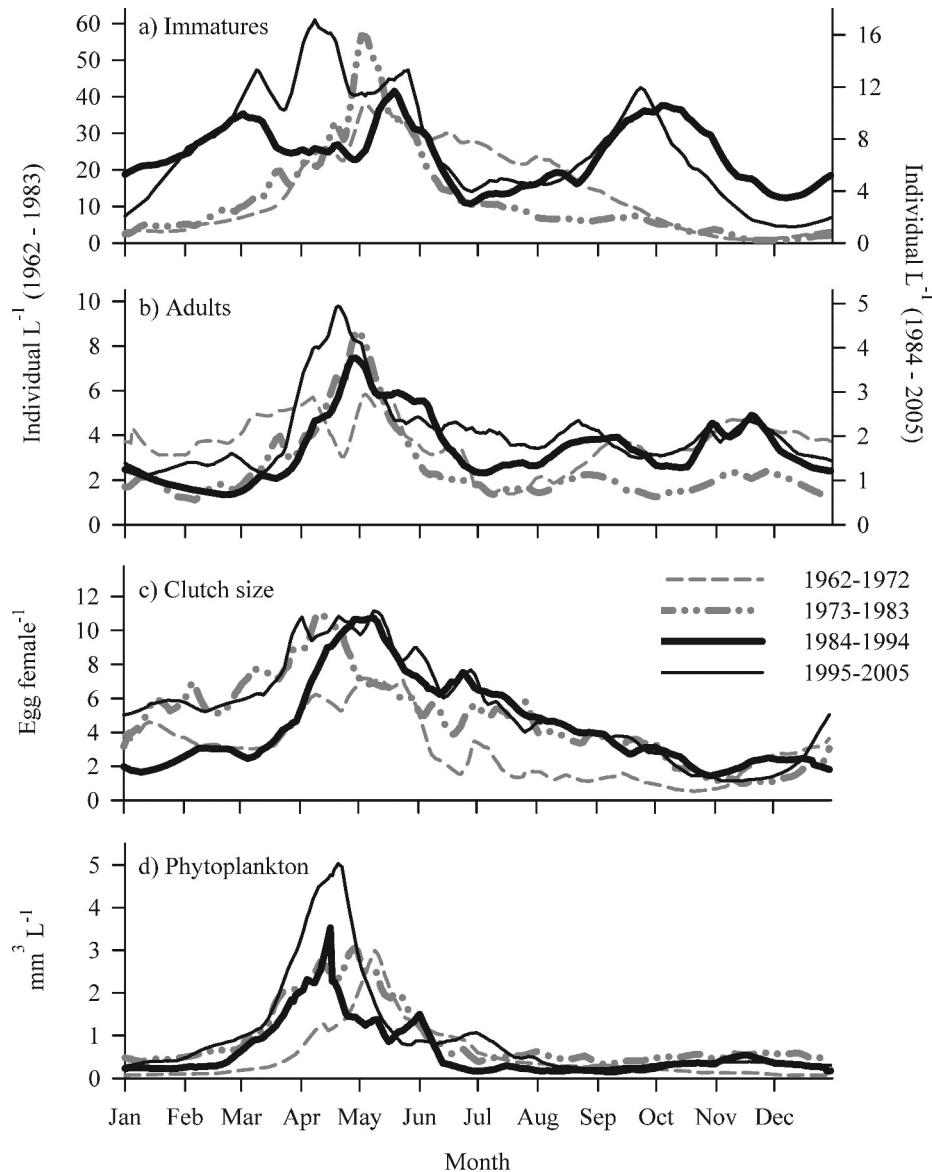


Fig. 5. Seasonal succession of (a) juvenile immature and (b) adult *Leptodiatomus ashlandi* abundances, (c) *Leptodiatomus* clutch size calculated as egg per female, and (d) phytoplankton biovolume excluding cyanobacteria in Lake Washington during four successive time periods between 1962 and 2005 (phytoplankton to 2000). Values represent averages of daily linear interpolated data over the 11-yr time periods. A trend toward earlier timing of spring peaks in *Leptodiatomus* densities and clutch size was observed over the past four decades. Note the secondary y-axis in (a) and (b) for *Leptodiatomus* abundances between 1984 and 2005.

(Winder and Schindler 2004b). Phytoplankton spring peaks were strongly linked to the onset of stratification, and both processes progressively advanced in spring over the sampling period (Winder and Schindler 2004a). Thus, climate increased the duration of the stratified period, which extended the period of elevated temperature in the upper water column as indicated by an increasing trend of annual degree-days and hence extended the growing period for planktonic organisms. Furthermore, the change in the cyclic nature of edible phytoplankton suggests that in addition to spring peaks, phytoplankton increased more consistently in fall and winter in recent years. This increase

in phytoplankton can be particularly attributed to diatoms and phytoflagellates, a key resource for copepods (Infante and Edmondson 1985; Demott 1995). Cross-wavelet spectra between *Leptodiatomus* oscillation, temperature, and phytoplankton further demonstrated that historically there was a strong covariation between immature abundances and the 12-month cycle associated with temperature. However, in recent years, the seasonality of the temperature driver was diminished in terms of its importance for juvenile seasonal abundances, which is now more related to the 6-month cycle associated with biannual changes in food availability. These overall improved



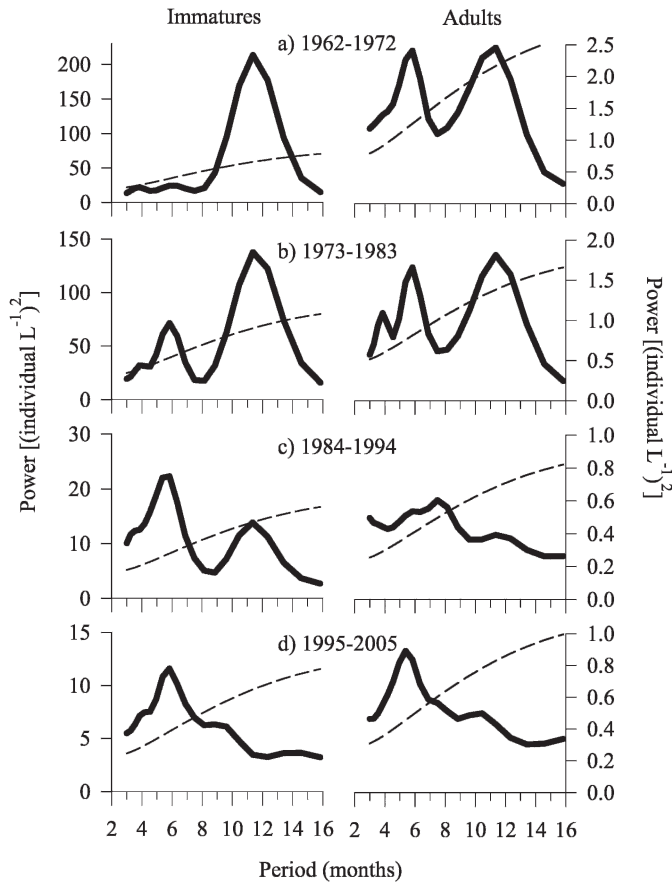


Fig. 6. Global wavelet spectrum of juvenile immature (left panels) and adult (right panels) *Leptodiaptomus ashlandi* abundances within four successive time periods in Lake Washington between 1962 and 2005. Dashed lines represent the 95% significance level; values above that line are significant. The y-axes give the distribution of power (or, equivalently, variance) among different periodicities; that is, it quantifies the importance of a particular cyclic fluctuation in the time series.

growing conditions allowed for increased development of *Leptodiaptomus*, which is in agreement with studies from field and laboratory observations documenting that temperature and food stimulate the development of copepods (Huntley and Lopez 1992; Twombly et al. 1998).

Successful life cycle completion requires both synchrony with food availability and synchrony between development time and the time window of the available growing season (Cushing 1990). Calanoid copepods are energetically efficient grazers under low food availability (Lampert and Muck 1985) and often persist during low food concentration. In Lake Washington, an extended growing period and warmer water temperature, combined with sufficient fall and winter food since the mid-1970s, were apparently able to accelerate ontogenetic development to enable the completion of a fall generation. Favorable fall and winter conditions are especially important in temperate regions and likely influence strongly the reproductive success of females and development of juveniles (Twombly et al. 1998).

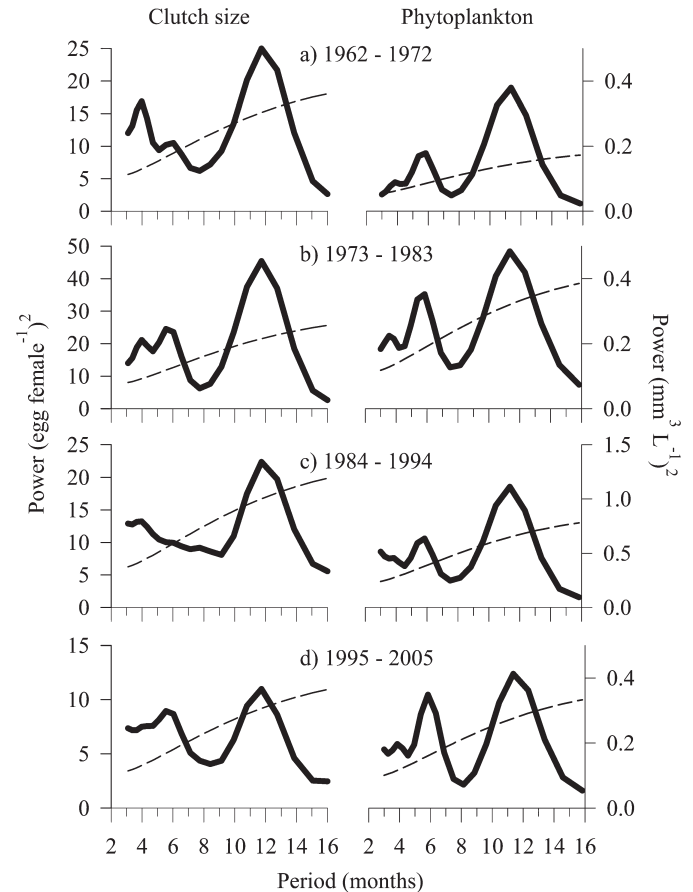


Fig. 7. Global wavelet spectrum of *Leptodiaptomus ashlandi* clutch size calculated as egg per female (left panels) and phytoplankton biovolume excluding cyanobacteria (right panels) within four successive time periods in Lake Washington between 1962 and 2005 (phytoplankton to 2000). Dashed lines represent the 95% significance level; values above that line are significant. The y-axes give the distribution of power (or, equivalently, variance) among different periodicities.

If the change in the seasonal life cycle of *Leptodiaptomus* was solely a response to the food web changes in the mid-1970s (Edmondson 1997), we would expect a similar rapid response as was observed in their morphological and life history characteristics at that time. Cross-wavelet analysis also demonstrated that change in phytoplankton dynamics had no effect on *Leptodiaptomus* seasonal cycles in the mid-1970s. However, the change in the dominant seasonal cycle in *Leptodiaptomus* occurred in the early to mid-1980s, about 10 yr after Lake Washington recovered from eutrophication. A rapid response would have been likely because copepod species have the potential to be multivoltine (Allan and Goulden 1980) and *Leptodiaptomus* has active stages year-round in Lake Washington. A detailed life cycle study of *Leptodiaptomus* in 1949–1950, that is, before the lake showed changes related to eutrophication, also documented a monocyclic life history (Comita and Anderson 1959) in this lake and showed that this species overwintered as adults. Moreover, a food web analysis of the historical Lake Washington plankton community

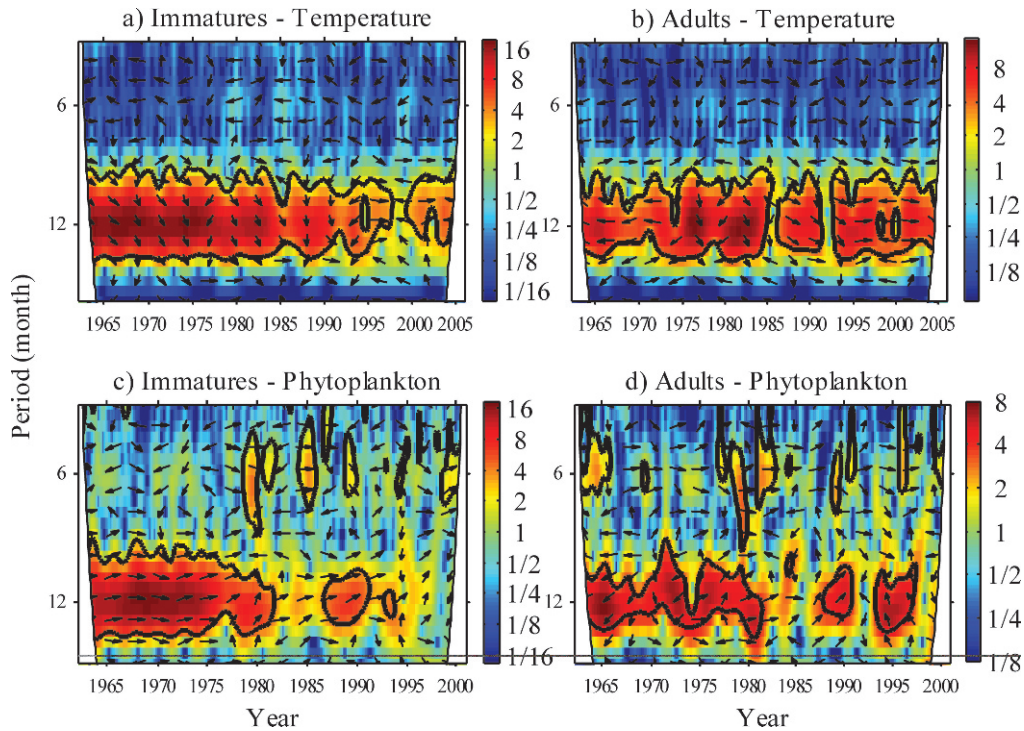


Fig. 8. Cross-wavelet spectrum between *Leptodiatomus ashlandi* and environmental variables in Lake Washington between 1962 and 2000 or 2005: (a) between immatures and temperature, (b) adults and temperature, (c) immatures and edible phytoplankton (i.e., excluding cyanobacteria), and (d) adults and edible phytoplankton. The direction of the arrows indicates the phase between the two time series involved: horizontal right is 0° and corresponds to an in-phase situation, and horizontal left is 180° and corresponds to an antiphase situation; both situations imply a linear relation between the phenomena; vertical up (90°) and vertical down (270°) arrows correspond to an out-of phase situation, that is, a nonlinear relation. The black contours indicate the 95% significance level.

confirmed that *Leptodiatomus* dynamics was not affected by altering cyanobacteria abundances (Hampton et al. 2006). This historical food web study also showed that food web linkages with potential invertebrate predators were not apparent. In addition, *Daphnia* size is relatively large (>2.0–2.5 mm) in Lake Washington, and fish prey electivity for *Leptodiatomus* is low (Beauchamp et al. 2004), both of which indicate overall low fish predation

pressure. Therefore, this shift in *Leptodiatomus* was likely not caused by any change in predation pressure.

An alternative explanation for the changes in the characteristics of population dynamics in *Leptodiatomus* is a delayed response to the changing food web structure in Lake Washington. Associated with phytoplankton quality and quantity changes in Lake Washington in the mid-1970s, densities of *Daphnia* increased (Edmondson 1997),

Table 1. Results of logistic regression models testing whether change in thermal conditions and/or food availability affected occurrence of a 12- or 6-month cycle in *Leptodiatomus* immatures, ranked by their level of support. In comparison to the three most parsimonious models, additional best-fit bivariate models for thermal and phytoplankton predictors, respectively, are shown. The significance level of explanatory variables is corrected for autocorrelation (\*\*\*  $p < 0.001$ , \*\*  $p < 0.05$ , ns  $p > 0.05$ ).

Model†	AIC <sub>ci</sub>	$\Delta_i$ ‡	Rel lik.§	W <sub>i</sub>	McFadden's rho¶
Degree-days** + phytoflagellates <sup>ns</sup>	38.51	0.0	1.00	0.34	0.47
Degree-days***	39.37	0.9	0.65	0.22	0.42
Degree-days** + phytoflagellates** + temperature <sup>ns</sup>	39.60	1.1	0.58	0.20	0.37
Temperature***	44.65	6.1	0.05	0.02	0.27
Phytoflagellates**	47.27	8.8	0.01	0.00	0.23

† The full model included the following predictor variables: degree-days + duration of summer stratification + temperature (volume weighted between 0- and 20-m depth) + edible phytoplankton (i.e., total phytoplankton excluding cyanobacteria) + phytoflagellates. Other model combinations with these predictor variables had  $\Delta_i > 2.2$  and  $w_i < 0.12$ .

‡ Change in AIC<sub>c</sub> between selected and minimum model (AIC<sub>ci</sub> – minAIC<sub>c</sub>).

§ Relative likelihood

|| Akaike weight (exp[-1/2Δ<sub>i</sub>]): the likelihood of the model, given the data, normalized to sum 1 across all models.

¶ McFadden's rho estimates the proportion of variation explained by a logistic regression model and conceptually is similar to an r-squared in linear regression.

while *Leptodiatomus* densities dropped, likely as a result of exploitative and/or interference competition with *Daphnia* (Hampton et al. 2006). This density decline in the mid-1970s coincided with an increase in female length and clutch size, which probably is linked to declining densities of cyanobacteria and hence improved food conditions (Twombly and Tisch 2000) or decreasing predation pressure by *Neomysis* (Edmondson 1997) that likely prey on larger-sized individuals (Murtaugh 1981), both food web changes happening in the mid-1970s. However, exploitative competition with *Daphnia* and relaxation of the predation pressure from *Neomysis* should slow down the development of *Leptodiatomus* life stages because of reduced food availability and therefore should contrast with our findings that voltinism of *Leptodiatomus* increased. Competition with *Daphnia* for resources is a possibility because both species capitalize on similar food items (Bowers 1977; Infante and Edmondson 1985). It is likely that the change in food web structure had an important indirect effect on the doubling of the generations per year inasmuch as food conditions improved; however, the intimate link between advanced stratification onset and phytoplankton peak (Winder and Schindler 2004a), the delayed stratification termination, and changes in the spectral properties of phytoplankton suggest that a prolonged growing season, combined with availability of high-quality food, was the main driver for this life cycle change. These arguments support the notion that growing conditions for *Leptodiatomus* surpassed a threshold level in the mid-1980s that allowed for an additional generation per year.

Our results further demonstrate that the predictability of *Leptodiatomus* population cycles decreased over time. This is indicated by decreasing strength in the cyclical component of the wavelet spectrum, which declined especially since the early to mid-1980s. Increasing seasonal variability matched with increasing variability in the timing and magnitude of the spring peak after 1983 (Winder and Schindler 2004b), which was best explained by increasing temperature and large-scale climate patterns. Reduced population predictability indicates that population oscillations became less stable with a prolonged growing period, which is in accordance with experimental studies (Beisner et al. 1997) and model predictions (Bjørnstad et al. 1999; Drake 2005) for invertebrates affected by temperature warming. Less predictable population dynamics in *Leptodiatomus* are likely caused by the direct effect of temperature on vital rates that destabilize the phytoplankton–copepod interaction. It remains to be determined whether the overall declining trend in *Leptodiatomus* densities is linked to a temporal disruption with their food resource. Experimental work indicated that temperature-induced instability in herbivorous zooplankton increases the likelihood of population extinction (Beisner et al. 1997). Although experimental work and theoretical population models predict that climate-induced environmental change should alter population dynamics, our results show that these shifts can occur relatively abruptly with changes in the underlying physical environment (Levin 1992).

Similar life cycle shifts associated with climate-driven environmental changes have been proposed for copepods in other freshwater and marine ecosystems (Beaugrand et al. 2002; Gerten and Adrian 2002). However, extensive cyclic population fluctuations and complex life cycles complicate the analysis of population dynamic in planktonic organisms, and consequently, despite their importance as a trophic link in the pelagic system, little is known about how seasonal population dynamics are affected by extrinsic factors, such as climate-driven environmental changes. Using an extensive time series of copepod densities and resource data, combined with a statistical modeling approach, we were able to resolve these problems and clarify the role of environmental factors in this life cycle switch.

Our study does not reveal whether the observed changes in the dynamical characteristics of *Leptodiatomus* populations demonstrate phenotypic plasticity or a shift in the dominant genotypes in the population. The shift in *Leptodiatomus* population dynamics in the early 1980s suggest that this shift is triggered after critical levels of developmental parameters are surpassed because of overall improved growing conditions. Similar threshold-like responses in population growths and life cycles are typical along thermal latitudinal and longitudinal gradients in ectotherms (Wilhelm and Schindler 2000), and nonlinear responses to future climate change also are predicted in vertebrate species (Saether et al. 2000). In addition, threshold responses are common features in phenotypic traits caused by stochastic gene expression (Nijhout 2004). However, our study does not provide insights into whether the change in the seasonal dynamics of *Leptodiatomus* is under environmental (such as growing conditions) and/or genetic (selection for specific genotype) control. Thus, whether the nonlinear response in *Leptodiatomus* is a physiological or genetic adaptation to the enhanced growing season remains an important hypothesis for future exploration.

Our study demonstrates that changes in environmental conditions can disrupt the seasonal dynamics of species with prolonged life cycles. An increased number of generations per year has been predicted with temperature elevation for aquatic and terrestrial ectotherms (Bale et al. 2002; Gerten and Adrian 2002) as well as bird species (Saether et al. 2000), and our results demonstrate that such a shift occurred concurrently with the warming trend over the past four decades. A consequence of this response includes a decoupling of the seasonal dynamics of *Leptodiatomus* reproduction with the seasonal dynamics of the thermal regime in this lake. The effect of climate is mainly indirect through altering the extent of the growing season and the dynamical properties of copepod food resources, although direct effects due to enhanced metabolic rates are also expected. These results demonstrate that climate-induced life history changes are likely to be complex because climate warming effects can be mediated through other components of the ecosystem, such as resource availability. The mechanisms through which variability in climate and its effect on plankton demography are transmitted to other ecosystem components remain



unknown. Further, our results highlight that population responses to climate warming likely alter the temporal organization of ecosystems (Levin 1992). The generality of such responses and their implications for ecosystem processes should be an important priority for climate change science.

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