Climate Change Uncouples Trophic Interactions in an Aquatic Ecosystem
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CLIMATE CHANGE UNCOUPLES TROPHIC INTERACTIONS IN AN AQUATIC ECOSYSTEM

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Abstract. The largest uncertainty in forecasting the effects of climate change on ecosystems is in understanding how it will affect the nature of interactions among species. Climate change may have unexpected consequences because different species show unique responses to changes in environmental temperatures. Here we show that increasingly warmer springs since 1962 have disrupted the trophic linkages between phytoplankton and zooplankton in a large temperate lake because of differing sensitivity to vernal warming. The timing of thermal stratification and the spring diatom bloom have advanced by more than 20 days during this time period. A long-term decline in *Daphnia* populations, the keystone herbivore, is associated with an expanding temporal mismatch with the spring diatom bloom and may have severe consequences for resource flow to upper trophic levels.

Key words: Daphnia pulicaria; *diatoms; energy flux; food web;* Keratella cochlearis; *match; mismatch; phenology; plankton; timing.*

INTRODUCTION

Climate change may cause dramatic perturbations to food webs if interacting species respond differently to shifting environmental conditions (Stenseth and Mysterud 2002). These perturbations may be especially spectacular in seasonal environments where there are only short periods of the annual cycle suitable for growth and reproduction (Fretwell 1972) or in aquatic ecosystems where trophic interactions are typically strong (Sommer et al. 1986, Platt et al. 2003). A shift in synchrony between trophic levels due to climate change has been demonstrated for migratory bird species, in which a growing disjunction between phenology in overwintering areas and their summer breeding grounds occurred (Inouye et al. 2000, Both and Visser 2001, Thomas et al. 2001), and thus they arrive at an inappropriate time to match peak food availability. Adaptation to match food supply and demand may also be hampered in species that rely on environmental stimuli unrelated to climate change (Visser and Holleman 2001). Except for these few notable exceptions from terrestrial ecosystems, there has been no evidence for such trophic decoupling in response to recent climate warming in freshwater or marine ecosystems.

In aquatic ecosystems, the fitness of a predator depends on its temporal and spatial synchrony with the production of its prey (match–mismatch hypothesis [Cushing 1974]). In these ecosystems, seasonal changes in temperature and radiation lead to a predictable succession of physical processes, and phytoplankton and zooplankton growth in pelagic ecosystems (Sommer et al. 1986). Growth of phytoplankton in the spring is strongly controlled by temperature, turbulence, and the strength of thermal stratification in the water column. Spring conditions favor fast growing diatoms, with high nutrient, but low light and temperature requirements (Reynolds 1984). Zooplankton often lag the physically driven dynamics of diatoms, which provide most of the high quality food for herbivore growth in the spring (Brett and Muller-Navarra 1997). Increasing nutrient limitation (especially by phosphorus and silica), cell sinking, and eventually grazing, cause a collapse of the spring phytoplankton bloom and often a shift from small single-celled diatoms to larger sized algae of lower nutritional quality for zooplankton. It has been hypothesized that population growth of predators depends strongly on the ability to match the timing of reproduction to optimal food availability (Cushing 1974, Beaugrand et al. 2003, Platt et al. 2003). We analyzed several phenological processes from a long-term plankton data set for Lake Washington (USA) to examine how temperature warming since the 1960s has affected the synchrony between phytoplankton and zooplankton populations. We show that changes in the degree of synchrony between these trophic levels have reduced the spring densities of certain herbivorous zooplankton taxa in this ecosystem during the last four decades.

METHODS

Site description and history

Our analyses are based on a historical data set (1962–2002) for Lake Washington, situated in the northwest of the United States (47°83′ N, 122°15′ W). Lake Washington does not freeze, and the water column mixes completely during the winter but develops thermal stratification from April to November when a warm
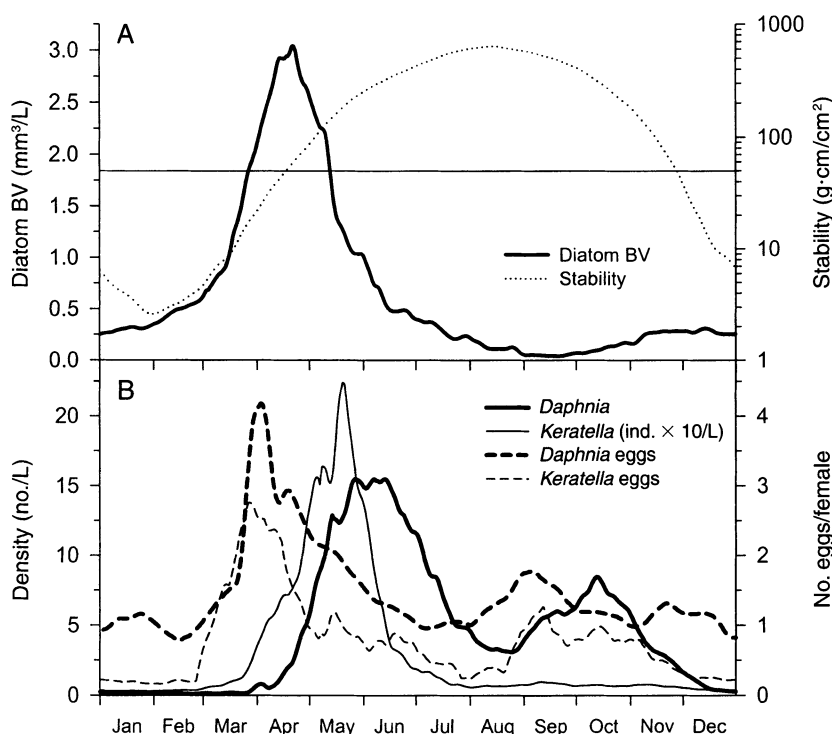
FIG. 1. Seasonal succession patterns in Lake Washington. (A) Seasonal development of water stability (log scale) and diatom biovolume (BV). The straight line indicates the threshold that was chosen for determining stratification onset. (B) Seasonal succession of *Keratella* and *Daphnia* densities and egg numbers. *Keratella* eggs are given per individual (right-hand axis) and per 10 liters (left-hand axis), and *Daphnia* eggs are reported per female (right-hand axis). Lines in panel (A) show average values from the period 1969–2002, and lines in panel (B) show average values for *Keratella* (1962–1995) and for *Daphnia* (1977–2002).

water layer (~10 m) overlays the colder deep water (Fig. 1A). Lake Washington experienced a period of eutrophication (the biological response to increased inputs of secondary sewage effluent) during the 1940–1960s, recovered entirely from sewage inputs between 1969 and 1975, and has since been characterized by stable nutrient inputs (Edmondson 1994). In 1976, the zooplankter *Daphnia* established abruptly as the dominant summer herbivore in the system as a result of reduced predation pressure from the crustacean *Neomysis* and the disappearance of the inedible and nutritionally poor cyanobacterium *Oscillatoria* (Edmondson and Litt 1982). Since that time, high-food quality diatoms have dominated the annual phytoplankton composition (~64%) and comprise the main fraction (~80%) of the spring bloom (Fig. 1A). Since 1976, the dominant zooplankton species have been the rotifer *Keratella cochlearis*, the cladoceran *Daphnia pulicaria*, and the two copepod species *Cyclops biscuspidatus thomasi* and *Leptodiaptomus ashlandi*. *Keratella* and *Daphnia* show a pronounced seasonal succession that coincides with or lags the phytoplankton spring bloom (Fig. 1B).

Data collection

Physical and biological data were collected over 1–2 week intervals during the stratified period (April–November) and monthly during the mixing period (December–March) in Lake Washington since 1962. Water temperature was recorded in 1-m intervals above the thermocline and 5-m intervals below the thermocline to 60 m depth. Phytoplankton and crustacean zooplankton were continuously measured in 0–10 m depth from 1962 to the present and rotifers from 1962 to 1995. All taxa were identified to species and crustacean zooplankton also to life stages (i.e., juvenile, adult). Sampling and analysis methods for phytoplankton and zooplankton are fully described elsewhere (Edmondson and Litt 1982, Edmondson 1997). Monthly averages were determined from the daily interpolated time series of the observed values using the inverse distance weighted method (Watson and Philip 1985).

Analyses

All analyses were performed with linear regression using two-tailed P values. For detecting trends in the time series of annual phenological processes, the data were first checked for normality of residuals and serial correlations using the lag-1 autocorrelation function. If significant autocorrelation was observed (i.e., for stratification onset and diatom peak), a first-order autoregressive term was taken into account (Bence 1995).
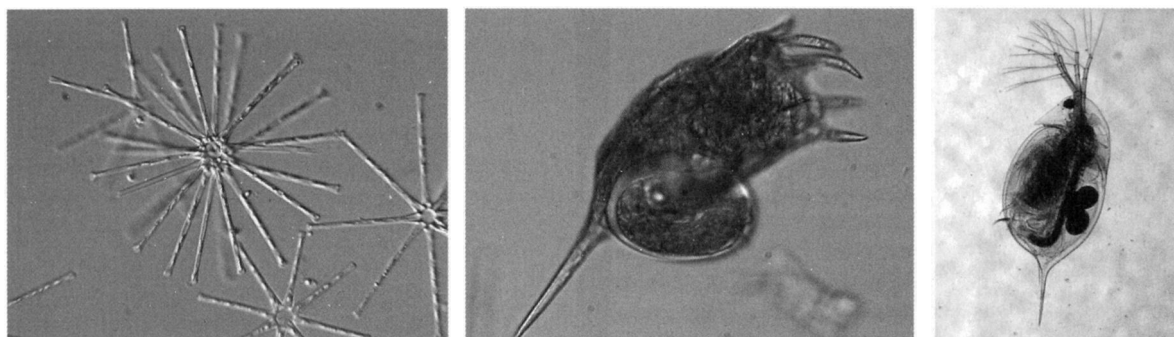
PLATE 1. Zooplankton species in Lake Washington: (A) the rotifer *Keratella cochlearis* (143 μm lorica length) carrying a parthenogenetic egg, (B) the cladoceran *Daphnia pulicaria* (2.18 mm carapace length) with three parthenogenetic eggs in the brood pouch, and (C) cells of the diatom *Asterionella formosa* (2–3 μm diameter). Photo credit: M. Winder.

The timing of thermal stratification onset was calculated from the Schmidt's stability index S (Hutchinson 1957, Idso 1973) as follows:

$$S = A_0^{-1} \sum_{z_0}^{z_m} (z - z^*)(p_z - p^*)A_z dz$$

where A_0 is surface area of the lake, A_z is the lake area at depth z, p_z is density as calculated from the temperature at depth z, p^* is the lake's mean density, and z^* is the depth where the mean density occurs. The summation is taken over all depths (z) at an interval (dz) of 1 m from the surface (z_0) to the maximum depth (z_m). Water density changes in response to temperature were calculated from the Tilton and Taylor approximation assuming no conductivity effects (Likens 1985). This index is a measurement of the water column stability and indicates the amount of mechanical work required to mix the lake to an isothermal condition. The value is zero when the water column is isothermal and maximum when the lake is most strongly stratified. An arbitrary threshold of 50 g·cm·cm^{-2} was taken to estimate the timing of stratification onset in spring. This threshold approximately reflects the establishment of a thermocline (temperature difference >1°C within a 1-m interval) in the upper 10-m water layer. However, choice of this particular threshold had no effect on the significance of the long-term trend (see Appendix A for trend comparison using different stability thresholds). The timing of the phytoplankton spring bloom was defined as the day of year when maximum diatom biovolume was reached because diatoms represent the dominant fraction (~80%) of the phytoplankton community during the spring peaks. By using diatoms as a proxy, we were able to include the years with high phosphorus concentration in the lake (i.e., years before 1969), when the phytoplankton bloom was prolonged and usually peaked in midsummer. However, the timing of the diatom bloom was strongly synchronized with the timing of the total phytoplankton bloom not only since 1969 ($r^2 = 0.97$, $P < 0.001$, $n = 34$), but also over the whole sampling period ($r^2 = 0.75$, $P < 0.001$, $n = 41$). The diatom spring peak occurs after a stability

threshold of ~50 g·cm·cm^{-2} has been established in the water column, but before the water column develops strong stratification (see Appendix B for relation between the timing of different Schmidt stability thresholds and the timing of diatom peaks). The timing of each zooplankton spring peak was determined when maximum abundance of the taxon was reached. When multiple peaks were developed in spring for diatoms and *Daphnia*, the timing of the last diatom peak, except in 2000, and the timing of the first *Daphnia* peak was taken. However, the choice of the peaks did not affect the significance of the trends. In 2000, a second diatom bloom of indigestible colonies (mainly *Tabellaria fenestrate* and *Fragilaria crotonensis*) for *Daphnia* (Infante and Edmondson 1985) developed in June; therefore, the first peak was taken. Overall stratification onset (mean day of year = 110), preceded the diatom peaks (mean day of year = 116), which were followed by *Keratella* (mean day of year = 133) and *Daphnia* peaks (mean day of year = 151). *Daphnia* length was measured for at least 50 individuals in each sampling event from May through August to the nearest 0.01 mm over the period 1981–1999.

RESULTS AND DISCUSSION

Spring water temperatures in Lake Washington have shown significant warming trends and values in the upper 10-m water layer from March to June and have increased, on average, 1.39°C since 1962 (slope = 0.04 ± 0.02 [mean ± 1 SD], $P < 0.001$, $n = 41$; Fig. 2A). This trend affected the onset of spring thermal stratification in Lake Washington, which showed a significant advancement of spring warming from 1962 to 2002 (Fig. 2B). Stratification onset now occurs 21 days earlier than it did four decades ago. This shift is associated with the pronounced vernal warming observed over the American northwest (Cayan et al. 2001). In Lake Washington, the timing of the spring phytoplankton bloom changed in accordance with earlier stratification and has advanced 27 days over the entire study period (1962–2002), or 20 days over the period 1977–2002, when the trophic state of Lake Washington was
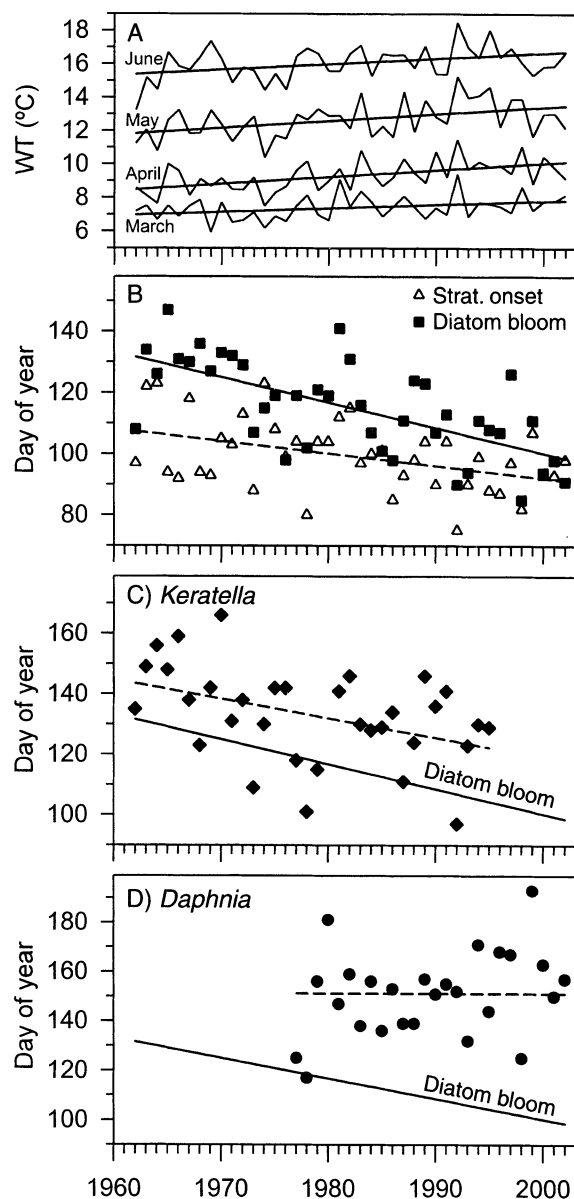
FIG. 2. Physical and biological trends in Lake Washington. (A) Average monthly volume-weighted temperature (WT) of the upper 10-m water layer during spring with linear regression lines ($n = 41$): March, $+0.92°C$ (slope $= 0.02 \pm 0.018$ [means ± 1 SD], $r^2 = 0.13$, $P = 0.019$); April, $+1.74°C$ (slope $= 0.04 \pm 0.02$, $r^2 = 0.30$, $P < 0.001$); May, $+1.76°C$ (slope $= 0.04 \pm 0.02$, $r^2 = 0.21$, $P = 0.002$); June, $+1.41°C$ (slope $= 0.03 \pm 0.02$, $r^2 = 0.16$, $P = 0.009$). (B) Onset of spring stratification (dashed line, slope $= -0.43 \pm 0.28$, $r_p = -0.39$, $P = 0.003$, $n = 41$) and timing of diatom bloom (solid line, slope $= -0.39 \pm 0.19$, $r_p = -0.49$, $P < 0.001$, $n = 41$; for the period 1977–2002, slope $= -0.81 \pm 0.6$, $r^2 = 0.22$, $P = 0.015$, $n = 26$). For stratification onset and diatom bloom, significant autocorrelations were detected; therefore, the partial coefficient of determination (r_p) is given. (C) Timing of diatom bloom (solid line) relative to annual timing of Keratella peaks (diamonds, dashed line; slope $= -0.65 \pm 0.51$, $r^2 = 0.17$, $P = 0.018$, $n = 34$). (D) Timing of diatom bloom (solid line) relative to annual timing of Daphnia peaks (circles, dashed line; $r^2 = 0.11$, $P = 0.10$, $n = 26$).

stable (Fig. 2B). Similar trends of advancing vegetation phenologies have been observed in terrestrial, marine, and freshwater systems in the Northern Hemisphere over the past few decades (Reid et al. 1998, Weyhenmeyer et al. 1999, Walther et al. 2002, Parmesan and Yohe 2003). In Lake Washington, a significant trend towards earlier timing of peak densities was also observed for the herbivorous rotifer *Keratella*, which advanced 21 days between 1962 and 1995 (Fig. 2C). In contrast, the timing of the annual spring peaks of *Daphnia* exhibited no significant trend over the period from 1977 to 2002 (Fig. 2D). Even though the variation in intensity of diatom blooms was high (ranging from 0.7 to 15.5 mm³/L), diatom biovolumes in April, May, or June did not influence the timing of *Daphnia* peaks ($r^2 < 0.06$, $P > 0.27$), whereas the timing of *Keratella* peaks was influenced by diatom biovolume in May ($r^2 = 0.19$, $P = 0.01$).

Changes in the timing of thermal stratification in Lake Washington were transmitted through primary producers to herbivorous zooplankton. However, the ability to respond to changes in the timing of phytoplankton blooms differed among zooplankton species. The phenology of *Keratella* paralleled the advance in timing of the phytoplankton peak. The temporal offset in this predator–prey relationship did not exhibit any long-term trends (slope $= 0.18 \pm 0.51$, $P = 0.50$; Fig. 2C). In distinct contrast, a growing mismatch between peak algal densities and *Daphnia* populations in the water column has developed since 1977. The offset in timing between the peak of the spring diatom bloom and the peak of the spring *Daphnia* bloom has increased significantly over the past 26 years (slope $= 1.57 \pm 0.8$, $P < 0.001$; Fig. 2D), corresponding to a significant long-term decline in spring/summer *Daphnia* densities (Fig. 3D, F). Coupled with the observation that peak diatom biovolume has not decreased over this time period, these trends demonstrate that advancement of the spring diatom bloom has produced a situation where peak algal abundance occurs too early in the spring for *Daphnia* populations to exploit maximum food availability.

The contrasting responses of these two zooplankton species in Lake Washington may result from different sensitivity to temperature warming. *Keratella* densities were significantly positively correlated with water temperature in March and April ($r^2 > 0.23$, $P < 0.004$), whereas *Daphnia* showed no response to water temperature variation ($P > 0.05$). A lack of response in *Daphnia* could also result from different stimuli that trigger the start of seasonal reproduction. Both *Keratella* and *Daphnia* reproduce by cyclical parthenogenesis (Hughes 1989). However, *Keratella* remains in the water column for the entire annual cycle and produces no diapausing eggs in Lake Washington. The advance in *Keratella* peak abundance may reflect a response to variation in the timing of food availability and/or a physiological response to temperature warming. In
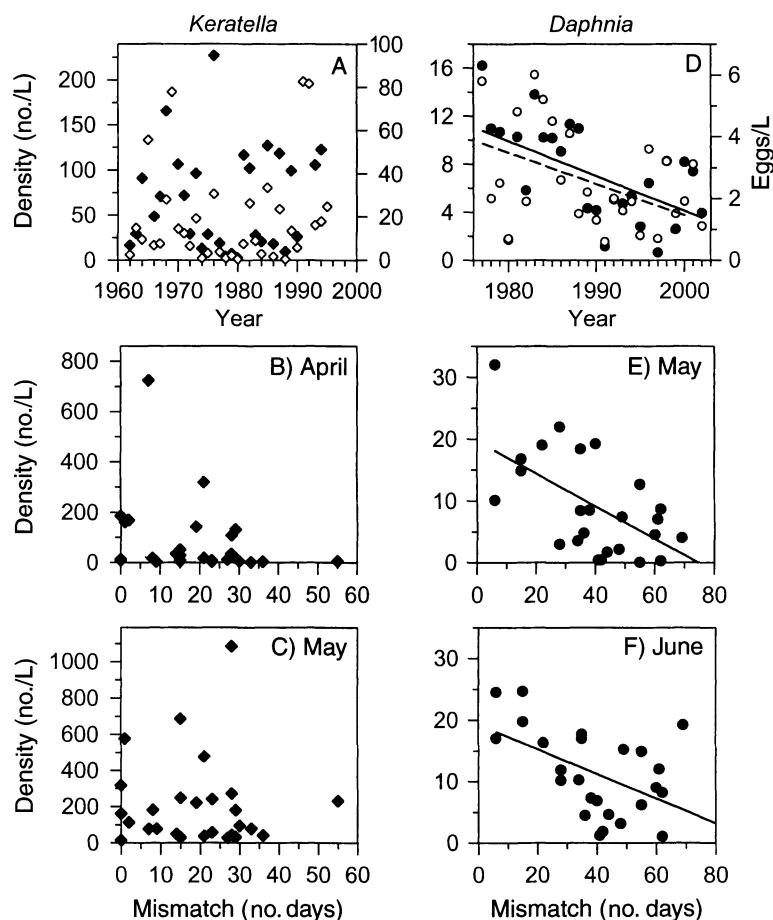
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FIG. 3. Performance of *Keratella* and *Daphnia* over the study period and densities in relation to the mismatch between diatom bloom and zooplankton peaks. (A) Average *Keratella* densities (solid diamonds, solid line; slope = 1.61 ± 3.9 [means ± 1 SD], $P = 0.30$, $n = 34$) and *Keratella* egg number (open diamonds, dashed line; slope = 0.32 ± 0.79, $P = 0.44$) from April until June during 1962–1995. (B) Relation of *Keratella* April densities ($r^2 = 0.03$, $P = 0.33$) and (C) May densities ($r^2 = 0.01$, $P = 0.65$) densities to the offset over the period 1962–1995. (D) Average *Daphnia* density (solid circles, solid line; slope = −0.29 ± 0.18, $P = 0.0037$, $n = 26$) and egg number (open circles, dashed line, right-hand axis; slope = −0.09 ± 0.08, $P = 0.033$) from May until August over the period 1977–2002. (E) Relation of *Daphnia* densities in May ($r^2 = 0.42$, $P < 0.001$) and (F) June to the offset during 1977–2002 ($r^2 = 0.29$, $P = 0.005$).

contrast, *Daphnia* populations are represented in very low numbers or disappear completely from the plankton during winter (average$_{Feb-Mar}$ = 0.09 ± 0.13 *Daphnia*/L [mean ± 1 SD]; in 13 out of 26 years densities declined to zero), and the recruitment of the population in spring may rely on the emergence of diapausing eggs from sediments. Experiments suggest that photoperiod and temperature are the main cues (Stross 1966) stimulating *Daphnia* diapausing eggs to develop, and, thus, emergence usually occurs only over a narrow window in spring (Cáceres 1998). The water temperature increase may have less effect on the hatching rate of resting eggs, and a photoperiod cue is independent of climate change. Thus, the absence of a response in *Daphnia* to match peak food availability may be explained by the use of hatching cues disconnected from water temperature increase. Although we do not know

why the phenology of *Daphnia* populations have not responded to climate change in Lake Washington compared to what has been observed in other ecosystems (Gerten and Adrian 2000, Straile 2002), their inability to track the change in spring warming has produced a growing mismatch with their food resources that is decoupling this critical trophic linkage in this ecosystem.

In Lake Washington, average *Keratella* densities and *Keratella* egg number have remained fairly constant during spring/summer when they are most abundant (Fig. 3A). Additionally, the offset between the *Keratella* peak and diatom peak did not correlate with *Keratella* densities in spring over the period 1962–1995 (Fig. 3B, C). In contrast, average *Daphnia* density and egg number have shown a significant decline in the spring/summer over the past 26 years (Fig. 3D). The increased mismatch between timing of the diatom

bloom and *Daphnia* peak explained a high variance in *Daphnia* population decline during the spring peak (Fig. 3E, F).

The key alternative explanation for the long-term decrease in *Daphnia* densities may be increased predation by planktivorous fishes, which should be reflected in the size structure of the population through a disproportional loss of large females (Brooks and Dodson 1965, Hrbáček 1969, Mills and Schiavone 1982). We tested this alternative hypothesis by evaluating for demographic changes and shifts in size structure in the *Daphnia* population of Lake Washington. Over the study period, the decline of juveniles from May to August was steeper than for adults (slope$_{juv}$ = -0.21 ± 0.14, $P = 0.009$; slope$_{ad}$ = -0.08 ± 0.04, $P = 0.005$; $n = 26$) suggesting the smaller juveniles responded more strongly than the larger adults. Moreover, average adult female length did not change in May through August over the period 1981–1999. The presence of large-sized species and individuals indicates that fish predation can be excluded as the primary driver in the decline of *Daphnia* densities. Furthermore, predation pressure by planktivorous fish is highest during late summer (August–September) in Lake Washington (D. A. Beauchamp and M. M. Mazur, *unpublished manuscript*). In addition, invertebrate predation can be excluded because of low densities in spring (i.e., for *Leptodora*: average density = 0.004/L) or the preference for large-sized *Daphnia* individuals (i.e., for *Neomysis*: average *Daphnia* prey size = 2.21 mm [Murtaugh 1981]). For *Daphnia*, it is well known that low food availability negatively effects juvenile growth and fecundity (Lampert et al. 1986), suggesting that the increased interval between high-quality diatoms and the *Daphnia* peak, forced by climate warming, caused the population decline in *Daphnia* by uncoupling this trophic interaction.

A fundamental concept within aquatic ecology poses that the fitness of a predator depends on its temporal and spatial synchrony with the production of its prey (Cushing 1974). Ecologists have also observed drastic population declines in predators when predator–prey relationships are disrupted through climate-related perturbations (e.g., the decadal shift from anchovies to sardines in the Pacific Ocean [Chavez et al. 2003], changes in the community composition of the Sonoran desert [Brown et al. 1997]). Here we show that climate change over the latter part of the 20th century has produced a mismatch in the timing of favorable environmental conditions in an algal–herbivore interaction. Such mismatching may have critical consequences for all ecosystems, especially if keystone species are affected. In pelagic ecosystems, algae–zooplankton interactions form the basis for energy flux to higher trophic levels (Platt et al. 2003), and decoupling of this predator–prey relationship may be transmitted to all trophic levels, causing drastic ecological and economical consequences. Whether or not the life history strategy of *Daphnia* can adapt to continuing climate change will have crucial effects on the future trajectory of this predator–prey interaction, and the ecosystem it is embedded within.

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APPENDIX A

A trend comparison of stratification onset on Lake Washington using different thresholds of the Schmidt's stability index is available in ESA's Electronic Data Archive: *Ecological Archives* E085-060-A1.

APPENDIX B

Figures showing the relation between the timing of different Schmidt stability thresholds and the timing of diatom peaks are available in ESA's Electronic Data Archive: *Ecological Archives* E085-060-A2.