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Increased niche differentiation between two *Conochilus* species over 33 years of climate change and food web alteration

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Abstract

Long-term data from Lake Washington are used to ask whether zooplankton population dynamics can be predicted on the basis of abiotic gradients and potential food resources. I used Dynamic Linear Models to examine effects of fluctuations in temperature and five algal groups on population dynamics of two rotifer species over a 33-yr period in which climate has warmed, anthropogenic nutrient loading has changed dramatically, and *Daphnia* has become established. Dynamics of the colonial rotifers *Conochilus hippocrepis* and *Conochilus unicornis* were both best predicted by temperature and the density of single-celled bacterio- and phytoplankton smaller than 10 μm, but their seasonal peaks have become dramatically offset toward fall and spring, respectively, in recent years. Both species have been extirpated from the summer months in which they once flourished, seemingly because of midsummer declines in their food resources, which have been depressed by *Daphnia* since its establishment. However, climate warming has increased the length of the plankton growing season in Lake Washington, such that spring and fall offer greater abundance of food resources for *Conochilus,* offsetting modern exclusion of *Conochilus* from midsummer months. Additionally, greater distinction in temporal niches presumably has reduced possibilities for intrageneric competition, and both *Conochilus* species have achieved higher mean annual abundances in recent years.

A strong historical emphasis on experimentation in limnology has promoted a rich understanding of many aspects of zooplankton ecology (Kerfoot 1980), such as life history variation, reproductive ecology, and feeding preferences, but we have surprisingly little ability to predict zooplankton population dynamics in nature. Extrapolation from the laboratory to the field is complicated by the temporal and spatial heterogeneity of the natural environment (Kareiva et al. 1996), particularly because short generation times allow zooplankton to respond rapidly to changing abiotic conditions or biotic interactions (e.g., Kirk 1997). Although we have a deep understanding of the importance of phytoplankton quality as food for zooplankton (Brett and Müller-Navarra 1997), there is still very poor connection in models linking the dynamics of phytoplankton taxa to zooplankton population dynamics. Use of long-term ecological data can increase the probability of detecting such species interactions in natural communities, and population responses to a broader natural range of abiotic and biotic conditions can be observed (Edmondson 1993; Kratz et al. 2003). Time series analysis allows us to characterize population relationships to environmental variables over the long term, and we can draw on mechanistic studies to infer cause and effect that underlie natural patterns (Edmondson 1993). Here, I ask whether responses of rotifer populations to abiotic gradients and food resources can be detected in a long-term field study.

Long-term research in Lake Washington (Seattle, Washington) was initiated primarily to document the lake's response to anthropogenic nutrient loading and reduction in the 1960s, but over the past four decades, several other major disturbances have also occurred. Secondary sewage effluent prior to 1968 and subsequent diversion radically affected primary producers, and concurrent human alterations to the fish community reduced zooplanktivory by the invertebrate predator *Neomysis* (Edmondson 1994). Primarily as a result of these changes in food resources and predatory environment, *Daphnia* became established in Lake Washington in 1976 (Edmondson and Litt 1982). Overlying these anthropogenic disturbances to the Lake Washington community has been a gradual increase in temperature, creating longer periods of more intense stratification (Arhonditsis et al. 2004; Winder and Schindler in press).

The establishment of *Daphnia* led to an immediately pronounced clear-water phase in Lake Washington (Edmondson and Litt 1982), and the associated reduction of common algal food resources could be expected to result in declining abundance of other grazers (Edmondson 1985). In addition to competing effectively for food, *Daphnia* also can affect microzooplankton through mechanical interference (Gilbert 1988), whereby rotifers in particular can be damaged by being drawn into *Daphnia*'s feeding apparatus. Thus *Daphnia* generally suppresses rotifers through both exploitative and interference competition (Gilbert 1988). In Lake Washington, however, rotifers have shown no detectable declines in annual mean abundance. In fact, the colonial rotifer *Conochilus* has increased in annual mean abundance over the past four decades in Lake Washington (Fig. 1).

Conochilus could be relatively safe from mechanical in-

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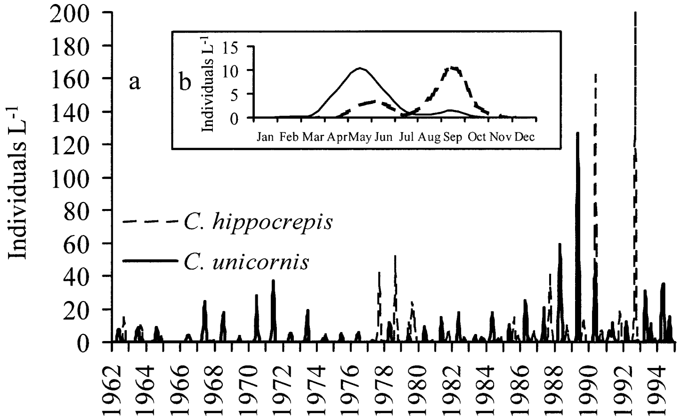

Fig. 1. Abundances of *Conochilus* species in the upper 10 m of Lake Washington from 1962 to 1994, expressed as (a) daily averages on each sampling date, and (b) monthly averages for all years.

terference because of its colonial habit, which likely prevents it from becoming entrained in *Daphnia*'s feeding current, but it is probably still susceptible to exploitative competition from *Daphnia.* Little is known of the ecology of *Conochilus* in nature, except that its jaw morphology restricts it to eating food particles less than ~12 μm (Pourriot 1977). *Daphnia* suppresses algae of this size in Lake Washington (Hampton and Schindler unpubl.) and other systems (Modenutti et al. 2003; Sommer et al. 2003), so it is puzzling that *Daphnia*'s dominance has not resulted in *Conochilus* declines. I analyzed abundance patterns of *Conochilus* from 1962 through 1994 to determine whether *Conochilus* population dynamics can be predicted from changing temperature patterns and potential food resources in Lake Washington and to help us understand how *Conochilus* has withstood modern dominance by the influential grazer *Daphnia.*

Methods

I analyzed dynamics of *Conochilus hippocrepis* and *Conochilus unicornis* abundance (individuals L^{-1}) in the long-term data collected in Lake Washington from 1962 to 1994 in relation to temperature (°C), total chlorophyll (μg L^{-1} chlorophyll [Chl] *a*), and biovolume of potential food resources (μm^3 L^{-1}). Detailed methods for long-term sample collection and enumeration can be found in Edmondson and Lehman (1981), Edmondson and Litt (1982), and Edmondson et al. (in press). Here, I restrict the study to monthly arithmetic means of samples from 10 to 0 m at only the central Madison Park sampling station to provide the most continuous data set for these variables, resulting in 396 observations for each species. Phytoplankton samples and Chl *a* measurements are less frequent than zooplankton samples throughout the time series, so zooplankton averages are often based on a greater number of values. For seven dates, missing values were linearly interpolated for either the zooplankton or phytoplankton.

Categories of potential algal food were assigned on the basis of known nutritional and edibility qualities for the Lake Washington phytoplankton. Diatoms, cryptomonads, and green algae are known to be the most nutritious zooplankton foods (Brett and Müller-Navarra 1997), and taxa in this study were further restricted to those of edible size and shape for Lake Washington zooplankton on the basis of gut content studies (Infante and Edmondson 1985). Furthermore, I included free-living cells between 1 and 10 μm as a potential food group, hereafter called Unicells, a category composed of noncolonial algal taxa too difficult to have been consistently enumerated separately over the entire history of Lake Washington collections. The Unicells category includes common bacterial and algal pico- and nanoplankton such as *Synecocchus*, *Chlamydomonas,* and *Chlorella.*

I used dynamic linear models (DLMs) to characterize the individual dynamics of the two *Conochilus* species, to determine which algal resources best predict abundance for each, and to examine changes in the importance of resources and environmental variables for each species. For a reference model, I fit one model with no regressors for each species, against which other models with predictors were compared. This model was simply an autocorrelated random walk, in which the trend of *Conochilus* abundance was subject only to an error term over time. For each species, I also built six competing models that variously included temperature, Chl *a,* and the algal categories as predictors. Finally, for all seven models for each species, I fit a corresponding model that included the variable Daylength (average hours of daylight per day) to control for seasonality.

All DLMs were fit with the use of Bayesian Analysis of Time Series (BATS) software (Pole et al. 1994). The application of DLMs to ecological time series has been described in detail elsewhere (e.g., Lamon et al. 1998; Cottingham et al. 2000), and my methods closely follow those of Scheuerell et al. (2002), so I describe DLMs only briefly here.

The basic model formulation

$$\mathbf{Y}_t = \mathbf{X}_t\theta_t + \mathbf{v}_t \qquad \mathbf{v}_t \approx N(0, \mathbf{V}_t)$$

is similar to a familiar general linear model in which the response vector **Y** is a function of the predictor variable matrix **X** and the error vector **v**. Explicit time-ordering of the data and evolution of model parameters over time differentiate DLMs from the standard general linear model. Both the regression parameter vector θ, describing the effects of **X** on **Y**, and the error term **v** evolve with the addition of "new" data as the model is updated sequentially at each time step (t). The error term **v** has variance **V** that changes over time with the addition of new information. The regression parameter vector θ uses Bayesian learning to change over time with consideration of prior information, according to a first-order Markov process.

$$\theta_t = \mathbf{G}\theta_{t-1} + \omega_t \qquad \omega_t \sim N(0, \mathbf{W}_t)$$

The evolution matrix **G** dictates how the parameters change systematically over time, whereas the variance vector ω_t allows for stochastic change, as the system variance matrix $\mathbf{W}_t$ evolves with the addition of new information at each new time step.

Model performance is improved by the adjustment of each model's discounting scheme. Discounts describe the amount of prior information that is considered in parameterizing the model at each new time step. We can expect that the usefulness of information from prior time steps deteriorates as

Table 1. Model results for *C. hippocrepis,* with the random walk model as the reference model listed first, against which other models, ranked from best to worst fit according to BIC, are compared. Model ranks correspond to BICs for models that excluded daylength (bold type) because these nonseasonal models outcompeted their seasonal counterparts for *C. hippocrepis.*

	Predictors				Daylength model	
Rank	X_1	X_2	Parameters	BIC	Parameters	BIC
Reference			4	942	5	828
1	Temperature	Unicells	7	**630**	8	670
2	Temperature	Diatoms	7	**634**	8	717
3	Temperature		6	**686**	7	796
4	Temperature	Cryptomonads	7	**714**	8	733
5	Temperature	Green algae	7	**715**	8	808
6	Temperature	Chl *a*	7	**719**	8	778
7	Chl *a*		6	**822**	7	841

it gets older until it is obsolete, so discounts allow the influence (or weight) of data to degrade as it gets older until it can reach zero, such that the oldest data can be disregarded entirely. For example, a discount of 1 includes all prior data points when choosing parameter values, and a discount of 0 excludes all prior information, relying only on information for that discrete time step. This weighting of prior information directly affects both **v** and ω. I systematically varied discounts between 0.8 and 0.99 (sensu Pole et al. 1994) and chose those values that minimized the negative log-likelihood for each model.

Once the discounting scheme was chosen for each model, I used the retrospective model-fitting feature of BATS to derive the best fitting model given consideration of all time-ordered data points together. Predicted values from the retrospective analyses were used to assess the relative fit of all models for each *Conochilus* species. The models were ranked according to fit as determined by the Bayesian information criterion (BIC; Box et al. 1991), which awards parsimony, evaluating fit of the model to the data but penalizing models for increasing numbers of parameters.

Results

C. hippocrepis models generally were not improved by inclusion of Daylength (Table 1), but Daylength models outcompeted their nonseasonal counterparts for *C. unicornis* (Table 2). Models that used Temperature and Unicells as predictors were the best fit for both *C. hippocrepis* (Table 1) and *C. unicornis* (Table 2), followed by models that used Temperature and Diatoms, but interesting differences between the species emerged in the ordering and relative fit of models. For *C. hippocrepis,* the Temperature and Unicells model was only moderately better than the Temperature and Diatoms model (Table 1), but for *C. unicornis,* the Temperature and Unicells model fit substantially better than any model (Table 2).

For *C. hippocrepis,* Temperature remained in all of the top models, with Chl *a* being the worst of the predictive models (Table 1). Conversely, Chl *a* remained among the top models for *C. unicornis,* and Temperature alone provided the worst model (Table 2).

To better understand how *Conochilus* species have re-

Table 2. Model results for *C. unicornis,* with the random walk model as the reference model listed first, against which other models, ranked from best to worst fit according to BIC, are compared. Models including daylength outcompeted their nonseasonal counterparts, but provided the same ranking order (bold type) for models.

	Predictors				Daylength model	
Rank	X_1	X_2	Parameters	BIC	Parameters	BIC
Reference			4	1,053	5	938
1	Temperature	Unicells	7	887	8	**854**
2	Temperature	Diatoms	7	927	8	**881**
3	Temperature	Chl *a*	7	931	8	**886**
4	Chl *a*		6	943	7	**895**
5	Temperature	Cryptomonads	7	1,010	8	**906**
6	Temperature	Green algae	7	1,027	8	**910**
7	Temperature		6	1,032	7	**914**

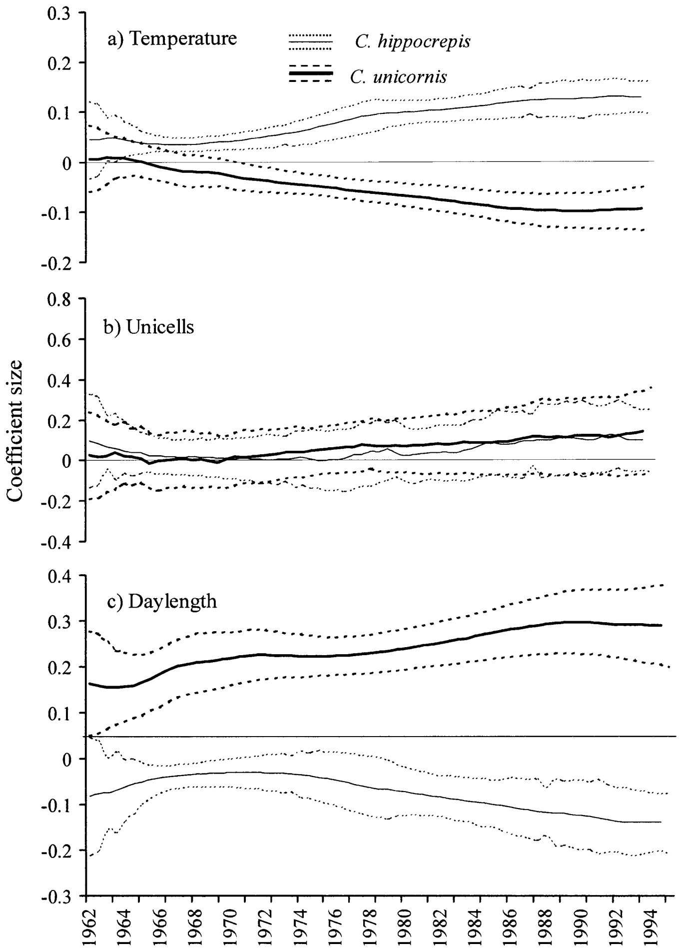

Fig. 2. Coefficients (with 95% confidence intervals) from the Daylength + Temperature + Unicells models for *Conochilus* species, expressing the effects of (a) average temperature, (b) the biovolume of Unicells (phyto- and bacterioplankton between 1 and 10 μm), and (c) the seasonal indicator Daylength (average hours of daylight) on abundance of each *Conochilus* species. Daylength was not a significant predictor of *C. hippocrepis* abundance, but values from this model are presented in panel c for comparison.

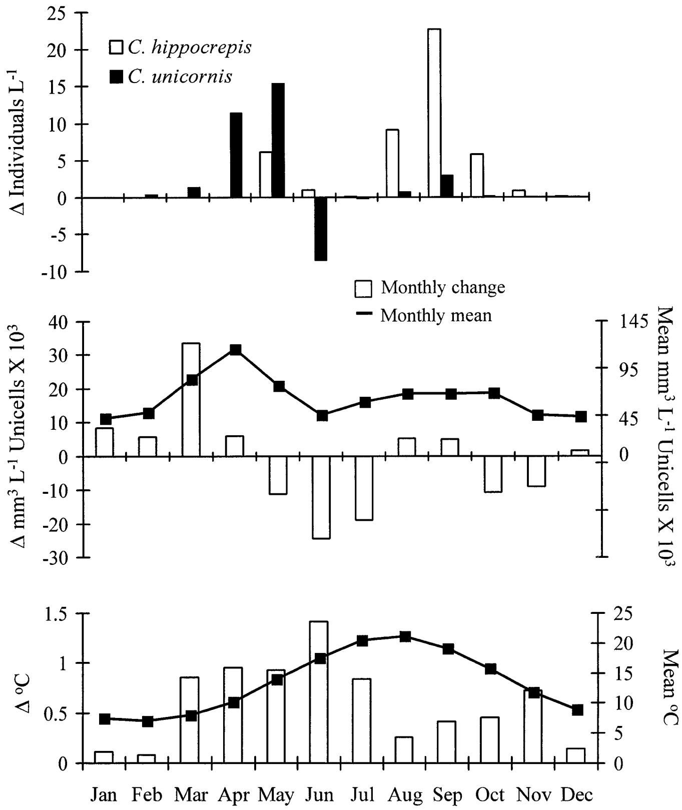

Fig. 3. Increases and decreases in *Conochilus* species, abundance of Unicells (phyto- and bacterioplankton between 1 and 10 μm), and temperature since August 1977. Average values from the period from 1972 to 1977 were used as the "baseline" condition for this comparison, as described in "Results." The mean values are averages over the entire time series.

sponded through the time series to the factors indicated as being most important, I examined DLM parameter evolution over time for Temperature, Unicells, and Daylength (Fig. 2). Temperature has become a stronger predictor for both species, with *C. hippocrepis* becoming more strongly associated with higher temperatures and *C. unicornis* with somewhat lower temperatures (Fig. 2a). For both species, the positive influence of Unicells became similarly greater over time, although there was less certainty in the predictive power of Unicells than other variables, as indicated by relatively wide confidence intervals that overlap with zero (Fig. 2b). The Temperature + Unicells model was a better fit for *C. hippocrepis* than was the Temperature + Unicells + Daylength model (Table 1), but the Daylength coefficient from the latter model is included in Fig. 2c for comparison to that in the corresponding *C. unicornis* model. Daylength seems to have always been positively correlated with *C. unicornis* abundance and has become more so over time, whereas *C. hippocrepis* abundance has become somewhat negatively associated with Daylength (Fig. 2c).

To illustrate how the influence of Temperature and Unicells on *Conochilus* have changed over the last 40 yr, I examined monthly mean values before and after 1977. To calculate modern day differences in monthly values, I had to choose an interval of the time series to be considered "baseline" against which modern averages for the variables were compared. Biotic variables were affected by eutrophication from 1962 until ~1972, after which the lake was widely considered "recovered" in a practical sense (Edmondson 1994), so I only considered post-1972 years as candidates for baseline conditions. To find the end of a period to be considered baseline conditions in this study, I used the Automatic Monitoring feature of BATS to define a time period of major deviation from previous pattern (Pole et al. 1994). For a Temperature and Unicells model with total *Conochilus* as the response variable, 1977 was the only time step flagged by Automatic Monitoring in the model. Therefore, I used the high-resolution Lake Washington data (i.e., normally more than one date per month, rather than monthly averages used in the DLMs) to calculate averages of *Conochilus* species abundances, Temperature, and Unicells for each month from 1973 to 1977 to use as baselines against which post-1977 values were compared (Fig. 3).

Both *Conochilus* species have become less abundant during summer months in which *C. unicornis* used to be particularly abundant. Whereas *C. unicornis* once regularly reached its peak abundance in June, it abruptly stopped doing so in 1976 (S.E. Hampton unpubl.). Instead, *C. unicornis* typically peaks in May now (Fig. 3). *C. hippocrepis* has not experienced declines in any month but has become much more common in the late summer months (Fig. 3) after the clear-water phase presently occurs in Lake Washington (Winder and Schindler in press). Modern declines in Unicell abundance in the summer months were clear, but Unicells appeared to have become more abundant in the spring, as well as late summer and early fall (Fig. 3). Modern Temperature in Lake Washington was greater than baseline in all months but showed the greatest increases during spring and early summer (Fig. 3). Peak Temperature has typically been achieved in late summer.

Discussion

Both *Conochilus* species appear to require similar algal resources, in that Unicells biovolume was a superior predictor in models for both, but the two species show strong differences in response to temperature, a result that corresponds to their observed offset seasonal distributions. Over time, their seasonal distributions have in fact become more distinct, with *C. unicornis* peaking predictably now in May and *C. hippocrepis* occupying primarily August and September, when water temperature is highest, and neither species being abundant in the midsummer months. This modern *Conochilus* distribution could be a response to (1) a longer warm season that encourages a longer growing season for them and their resource Unicells and (2) a depression of their resource during the clear water phase, which has intensified in the past 20 yr since *Daphnia* became established in Lake Washington.

Phenology of Conochilus *and potential algal resources*—Edmondson and Litt (1987) noted the long-term increases in Lake Washington *Conochilus* abundance and the temporal separation of the two populations' peaks but were unable to correlate population size with total phytoplankton biomass. Differences between that work and this study are likely a result of two factors. Statistical models accounting for temporal autocorrelation are necessary to detect some relationships in community time series data, and *Conochilus* species appear to track a very specific component of phytoplankton such that *Conochilus* dynamics are not readily related to total phytoplankton biomass, as illustrated by the inability of Chl *a* to predict *Conochilus* dynamics in the present work.

Models that included the algal group Unicells outperformed all other models for both species. The strong distinction between the Unicells and Diatoms models for *C. unicornis* was particularly surprising because its peaks coincide with the spring diatom bloom in Lake Washington. Unicell biovolume is high during this time as well, so the strong difference in performance between the Unicells and Diatom models suggests a very tight tracking of the pico- and nanoplankton rather than diatoms. The increasingly negative influence of Temperature on *C. unicornis* over time, with concurrent increase in the positive effects of Unicells and Daylength, describes the shift of *C. unicornis* peaks away from warm summer months, now depleted of Unicells, and toward the late spring months when Unicells are more abundant than they were in the mid-1970s. Similarly, Unicells have had increasingly positive influence on *C. hippocrepis* dynamics, and the now regular occurrence of *C. hippocrepis* in August and September corresponds with recent increases in biovolume of Unicells for those months.

Causes of phenological changes—Two disturbances to the lake stand out as important for *Conochilus* phenology and abundance: long-term warming and the establishment of *Daphnia*. Long-term Lake Washington data, beginning with observations in 1933, provide clear evidence of a long-term warming trend throughout the year (Arhonditsis et al. 2004). Winter is no longer as cold as it was as recently as the 1960s, and the stratified period is longer by an average of 25 d, beginning earlier and persisting later in the year (Winder and Schindler in press). Algal blooms can start earlier in the year, which is likely the reason that the Unicells in this study have increased in the spring months, a pattern also seen for diatoms (Winder and Schindler in press). Although nutrients are depleted in later summer months after the clear-water phase (Arhonditsis et al. 2003), continuing warm temperatures likely allow for growth of the taxonomically diverse Unicells group in months that were once too cold for rapid growth. Overall, the longer season of warm temperatures appears to have created a longer growing season for both *Conochilus* and its resource.

The longer growing season might have provided some refuge for the rotifers from *Daphnia* competition that began with its population explosion in the 1970s. The *Daphnia* establishment in Lake Washington appears to have been caused by concurrent human manipulations of upper trophic levels and radical taxonomic changes in the primary producers after sewage diversion (Edmondson 1994). After *Daphnia* became established in the lake in 1976, the clear-water phase immediately became much more pronounced (Edmondson and Litt 1987). Although the clear-water phase in Lake Washington is attributable in large part to depletion of nutrients, *Daphnia*'s contribution as an added stressor to phytoplankton growth is apparent (Arhonditsis et al. 2003). In recent multivariate time series analyses, we have found that *Daphnia*'s most dramatic grazing effect in Lake Washington is in the depression of Unicells (Hampton and Schindler unpubl.). Other studies have also found *Daphnia* to strongly suppress bacterial and algal picoplankton (Jürgens 1994; Modenutti et al. 2003; Sommer et al. 2003). Although this study does not conclusively implicate *Daphnia* in the modern summer decline of *Conochilus*, circumstantial evidence strongly suggests that *Daphnia* has extirpated *Conochilus* from the summer months by removing its food source, the Unicells.

Thus, although *Conochilus* has suffered competitive effects of *Daphnia*'s sudden and persistent establishment, the long-term warming trend has unexpectedly allowed *Conochilus* to persist in the lake by offering it a larger window of time in which to grow without its new competitor *Daphnia*. This temporal refuge could be ephemeral, however, as climate continues to change and bring more ''surprises'' (sensu Carpenter et al. 1992) that alter community dynamics. New statistical tools allow us to use long-term ecological records to look back in time at the natural responses of complex ecosystems to a suite of interacting stressors, and thus enhance our appreciation for fairly subtle effects, such as the changes in phenology reported here, which will influence future community dynamics under multiple stresses.

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