



LETTER

Environmental stability and lake zooplankton diversity – contrasting effects of chemical and thermal variability

Abstract

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Environmental variability in space and time is a primary mechanism allowing species that share resources to coexist. Fluctuating conditions are a double edged sword for diversity, either promoting coexistence through temporal niche partitioning or excluding species by stochastic extinctions. The net effect of environmental variation on diversity is largely unknown. We examined the association between zooplankton species richness in lakes and environmental variability on interannual, seasonal and shorter time scales, as well as long-term average conditions. We analyzed data on physical, chemical and biological limnology in 53 temperate zone lakes in North America and Europe sampled over a combined 1042 years. Large fluctuations in pH, phosphorus and dissolved organic carbon concentration on different time scales were associated with reduced zooplankton species richness. More species were found in lakes that showed greater temperature variation on all time scales. Environmental variability on different time scales showed similar or, in some cases, stronger associations with zooplankton species richness compared with long-term average conditions. Our results suggest that temporal fluctuations in the chemical environment tend to exclude zooplankton species while temperature variability promotes greater richness. The results indicate that anthropogenic increases in temporal variability of future climates may have profound effects on biodiversity.

Keywords

Diversity, environmental variability, global change, stability, storage effects.

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INTRODUCTION

While projections of future climates vary widely in the direction and magnitude of changes at regional scales, most models agree in forecasting increases in intra-annual variability in conditions such as temperature and precipitation (Knapp *et al.* 2008). Extreme events such as droughts, storms and heat waves have become more common in recent decades (Karl *et al.* 1995; Easterling *et al.* 2000), a trend that climate models predict will continue and intensify (IPCC I.P.o.C.C. 2007). The degree of temporal variability in the environment may be more important than long-term mean conditions in shaping ecosystems and community processes (Knapp *et al.* 2002). The effects of the frequency and intensity of environmental variability on biological systems are poorly understood and present a major challenge for understanding the future of biodiversity in a changing climate (Walther *et al.* 2002; Parmesan 2006).

Fluctuating conditions exert two opposing forces on the coexistence of species in communities (Connell 1978; Chesson & Huntly 1997; Adler & Drake 2008). Large changes in reproduction or survival due to environmental variation can reduce geometric mean fitness and lower diversity by increasing the risk of stochastic extinctions. Alternatively, environmental fluctuations may promote temporal niche partitioning and prevent competitive exclusion when species differ in their response to changing conditions over time (Chesson & Huntly 1997; Shea *et al.* 2004). Such storage effects have been shown to promote coexistence in groups of organisms as diverse as herbaceous plants (Adler *et al.* 2006; Angert *et al.* 2009), zooplankton (Cáceres 1997) and desert rodents (Brown 1989). Whether more species are facilitated or excluded by environmental fluctuations remains an open question, and key to forecasting future biodiversity scenarios under global change. In addition, variation on different time scales (e.g. interannual, seasonal or daily fluctuations) may have distinct consequences for coexistence of species (D'Odorico *et al.* 2008). The matching between the life histories of species and the

pace of environmental change determines whether species can track conditions and maintain populations or are driven extinct.

We asked how species richness of zooplankton in lakes is associated with variability in the physical and chemical environment. We assembled a data set consisting of zooplankton species composition and richness, as well as 10 measures of physical and chemical limnology in 53 lakes sampled over a combined 1042 years for a total of 5932 monthly average observations. Descriptions of the data sets are shown in Table 1. We used a multiplicative time series decomposition approach to partition environmental variability into interannual, seasonal and shorter (residual) time scales. We tested for associations between the 10 commonly measured limnological variables and zooplankton species richness to ask whether and how abiotic variability increased or decreased diversity, which variables were most important and on what time scales. Understanding how different patterns of variation influence species diversity is an important step in forecasting biodiversity under future climate change scenarios.

METHODS

Environmental variables measured include pH, conductivity ($\mu\text{S}\cdot\text{cm}^{-1}$), concentrations of dissolved organic carbon (DOC, in $\text{mg}\cdot\text{L}^{-1}$), chlorophyll-*a* (in $\mu\text{g}\cdot\text{L}^{-1}$), and total nitrogen and total phosphorus (consisting of both particulate and dissolved fractions, $\mu\text{g}\cdot\text{L}^{-1}$). Depth profiles of temperature and dissolved O_2 were also measured and summarized as the maximum and minimum across the water column. When chemical variables were measured at multiple depths, the average value across the water column was used in the analyses as within-lake variation was generally much smaller than that among lakes.

The surveys varied in the frequency (from weekly to monthly) and duration of sampling throughout the year. To standardize the data across surveys, we calculated monthly means of all richness and abiotic variables. We also limited

Table 1 Descriptions of the data sets included in our analysis

Data set	Location	Lakes (<i>n</i>)	Years sampled mean (range)	Missing variables
Coldwater	Canada	6	8.7 (7–9)	
Dorset	Canada	8	31.4 (29–32)	
Experimental Lakes Area	Canada	12	12.1 (6–30)	DO (five lakes)
Müggelsee	Germany	1	17	Conductivity
North Ontario Lake Size Series	Canada	6	8.1 (3–9)	Temperature (one lake)
Sudbury	Canada	10	26.6 (17–34)	
Washington	USA	1	44	DOC, DO
Wisconsin	USA	8	22.4 (13–28)	Conductivity (three lakes)
Zurich	Switzerland	1	31	

Detailed summary data are presented for the abiotic variables in Appendix S4.

our analysis to data collected between May and October, the minimum period covered by any of the surveys.

The surveys sampled zooplankton community composition using nets or Schindler-Patalas traps and identified and enumerated individuals to genus or species. The number of individuals counted from the samples ranged from around 250 to > 1000 animals. Within this range of variation, sampling intensity has very little effect on the number of species recorded. For instance, Keller & Yan (1991), using data from several of the Sudbury lakes in our data set, found that correcting for the number of individuals counted using rarefaction produced richness estimates that differed from the raw values by only 0.50 species on average. As our estimates of average daily richness ranged from 4 to 16, the variation due to sampling effort is likely to be small. Similarly, examination of the data from four of the lakes in the Experimental Lakes Area (ELA) survey where raw counts of individuals were available found that the number of species identified was independent of the number of individuals examined (Appendix S1). We therefore used raw species richness in our analyses.

We analyzed species richness of crustaceans (copepods and cladocerans) for consistency among data sets. We removed unidentifiable juvenile stages (copepodids and nauplii) from our calculations of species richness. In addition, the surveys varied in taxonomic resolution for small cladocerans. We therefore aggregated members of the genera *Bosmina* (including the closely related genera *Eubosmina* and *Bosminopsis*), *Chydorus* (including *Pseudochydorus*) and *Alona* (including *Alonella*) into single taxonomic units for the purpose of calculating richness.

We calculated three components of zooplankton species richness in order to test their association with environmental variability: average daily richness (the monthly averaged mean number of species recorded in a sample from a single day), average annual richness (the mean number recorded throughout a calendar year of sampling between May and October) and temporal beta diversity (the ratio of annual to daily richness, an indicator of species turnover through time). We present the results for average daily richness in the text and for annual richness and beta diversity in Appendix S2.

We used a multiplicative time series variance decomposition approach to partition environmental variability among three distinct time scales (Chatfield 2004; Cloern & Jassby 2009). A multiplicative model is appropriate when the standard deviation (SD) of the observations scales with the mean with a slope of one on a log-log scale, while an additive model is implied when the slope is zero (see page 20 in Chatfield 2004). Appendix S3 shows the regression of the SD on the mean within and between years for the ten limnological variables. For the within-year SD and mean, the slopes of all variables were greater than zero and often close to one. For the among-year relationships, the slopes were all

greater than zero except for pH and surface temperature. We used the multiplicative model variance decomposition for all variables for the sake of consistency as it was the indicated model in nearly every case. The choice of multiplicative vs. additive model only affects our estimates of residual variability (Chatfield 2004).

For every observation X of each abiotic variable in month j of year i , we calculated the interannual (A_i), seasonal (S_j) and residual (E_{ij}) or unpredictable components of variability as

$$X_{ij} = \overline{X_{LT}} A_i S_j E_{ij} \quad (1)$$

where

$$A_i = \frac{\overline{X_i}}{\overline{X_{LT}}}$$

$$S_j = \frac{\overline{X_{ij}}}{\overline{X_i}}$$

$$E_{ij} = \frac{X_{ij}}{\overline{X_{LT}} A_i S_j}$$

where X_{ij} is the observation in month j of year i , $\overline{X_{LT}}$ is the long-term mean across the data set, $\overline{X_i}$ and $\overline{X_{j}}$ are the means of all samples collected in year i or calendar month j , respectively. S_j is the average seasonal component, the mean of all S_{ij} occurring in the same calendar month across the time series. A_i measures the percent deviation of the annual mean from the long-term mean and S_j is the average seasonal deviation from the annual mean. E_{ij} is the deviation of the observed value from the expected based on the month and year, and can be considered as residual or unpredictable variability (Chatfield 2004).

The variability of different limnological factors on the three temporal scales is measured as the standard deviations of the A_i , S_j and E_{ij} values for the entire time series. This variance decomposition approach has the virtue that it expresses all variables as percent deviations from the appropriate mean, allowing us to compare variables measured in different units. It also separates the influence of the mean values and their variability. Each variance component can be interpreted as standard deviation on the relevant time scale as a fraction of the overall mean. Figure 1 shows an example of the three components for three abiotic factors (pH, surface and bottom temperature) in lakes with different characteristic patterns of variation. The approach has the limitation that the discrete distinctions between scales are somewhat arbitrary (except for the obvious annual periodicity). In addition, the annual component includes both directional trends (which may be interpreted as very long period oscillations, for instance as shown for Clearwater Lake in Fig. 1) and year-to-year fluctuations. These different types

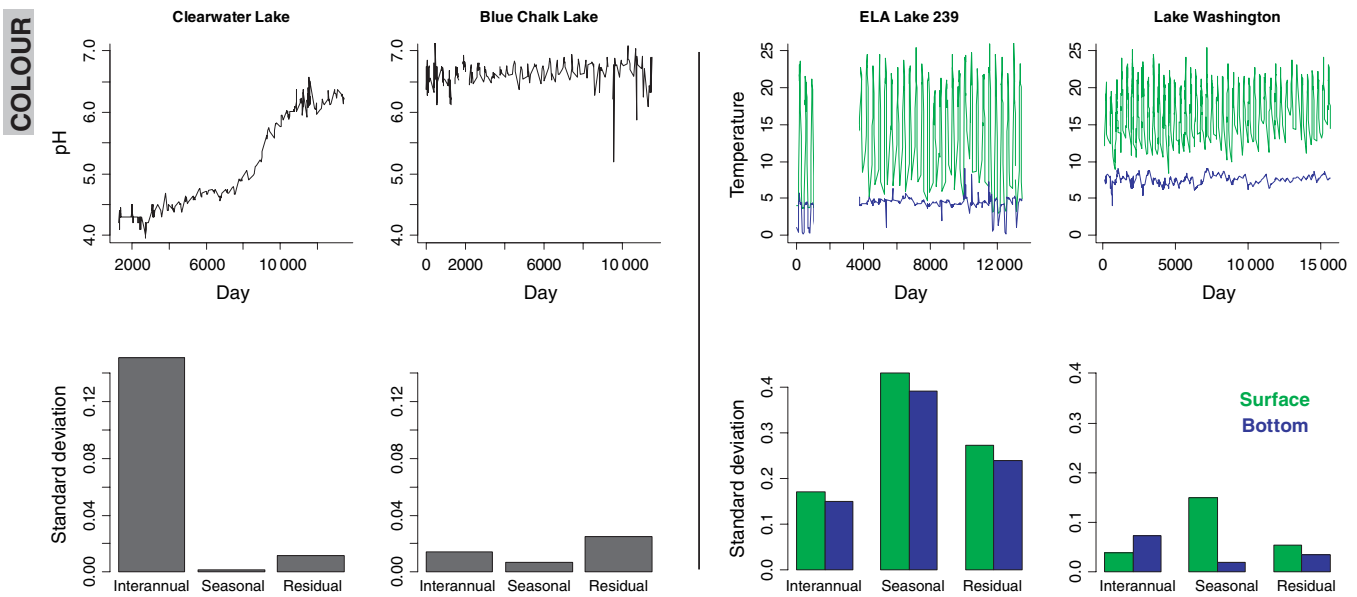


Figure 1 Examples of variance decomposition for abiotic variables showing different temporal patterns. The top row shows time series of pH (two left panels) and temperature (two right panels) in lakes with high (left) and low (right) variability. Clearwater Lake near Sudbury, ON shows a long-term pattern of recovery from acidification, as indicated by the high interannual variability in pH, while Blue Chalk Lake has less interannual variability but higher seasonality and residual variability. ELA Lake 239 shows high variability in surface (green) and bottom (blue) temperatures on all time scales compared to Lake Washington, which is buffered from changes in the atmosphere by its larger size and milder marine climate. The dominant scale of variation in surface temperature is seasonal (bottom two right panels). Lake Washington is always thermally stratified during the sampling period (May–October), leading to lower seasonal variation in bottom temperature compared to Lake 239.

of interannual variability may have different impacts on communities that are not distinguished by our approach.

We used a three-step approach to select models to analyze the association between average daily zooplankton species richness, long-term mean conditions and the three temporal components of variability for the 10 limnological metrics. First, we pre-selected abiotic variables for inclusion in a master model for each time scale (long-term mean, interannual, seasonal and residual variability) by examining independent univariate relationships between zooplankton species richness and variation in each abiotic variable separately using a linear model with normal error distributions. We considered linear, log, and quadratic models in order to identify the function that best described the relationship between the abiotic variable and zooplankton richness. The inclusion of nonlinear models allowed us to detect a range of possible associations between richness and environmental variability, for instance as predicted by the Intermediate Disturbance Hypothesis (Connell 1978). If more than one of these forms of the independent variable showed statistically significant associations with zooplankton richness, we included the model formulation with the lowest AIC value in the master model.

The second step was to select the abiotic variables for inclusion in the best-fit model for each time scale. We

eliminated variables from the master model if doing so resulted in a model with lower AIC using the function ‘stepAIC’ in R (R Core Development Team (R C.D.T.) 2007). This procedure identified the most parsimonious model for a given time scale. Although a number of other approaches to model selection are available (best subsets, stepwise selection based on different criteria), Murtaugh (2009) found that all tended to lead to identify similar best-fit models in ecological data.

The third step was to generate a candidate model to predict richness across all time scales based on the best-fit models from each of the four independent time scales. To achieve this, we included all variables that remained in the final model from step two for each time scale in a second master model for all time scales. Stepwise elimination based on AIC reduction was again used to find the reduced model with the lowest AIC. This model best explained zooplankton richness based on abiotic variables on all time scales.

We used two methods to compare the predictive power of variability on the four time scales. First, we examined the impact of removing each variable on the AIC of the final model after step 3 above. We also compared the best subset of the 10 models containing between one and 10 of the variables included in any of the models for the four time scales using the ‘regsubsets’ function in R. Variables and

time scales that were included in ~~more of~~ these models were the strongest predictors of daily zooplankton species richness.

We used Principal Components Analysis (PCA) to summarize and illustrate the patterns of covariation among the different limnological variables on the different time scales. A separate PCA was performed for each time scale. Lake surface area was included in the analysis to examine the potential dependence of environmental variability on lake size.

RESULTS

Average daily and annual zooplankton richness were correlated with different limnological features on different time scales (Fig. 2, Table 2, Appendix S2). Figure 2 shows correlations between average daily richness and abiotic variables that were retained in the best-fit model for each time scale (step 2 from the procedure above). The number of species generally increased with greater long-term average pH and DOC, and declined with higher surface water temperature (Fig. 2, top row). Richness declined with increasing interannual variability in pH and total phosphorus (TP, which showed a nonlinear but primarily negative relationship), and increased with higher interannual variation in bottom temperature. For seasonal variability, surface temperature had positive effects while DOC and pH had negative effects on zooplankton richness. Residual variation in TP was negatively correlated with richness, while bottom temperature was positively correlated.

Average annual zooplankton richness (the mean number of species observed within a calendar year) was strongly correlated with average daily richness ($r = 0.83$, $P < 0.001$, Appendix S2a), indicating that the lakes showed relatively little variation in temporal beta diversity. Average daily and annual richness were correlated with similar abiotic factors (Table 2, Appendix S2b), although the particular variables retained in the models differed somewhat between the two. Very little variation in temporal beta diversity (annual richness/daily richness) could be explained by any of the abiotic variables on any time scale (results not shown), likely because turnover through time was relatively consistent among the lakes.

The variables selected as predictors of daily zooplankton species richness depended on the time scale of variability. The best-fit model for variables selected from all of the time scales (Step 3) retained mean pH and surface water temperature, interannual variability in bottom temperature and pH, seasonality in pH and DOC and residual variability in bottom temperature and TP (Table 2). This model was selected from among all the variables that remained in the final models for each of the four temporal components (shown in Fig. 2). Residual variation in TP had the highest

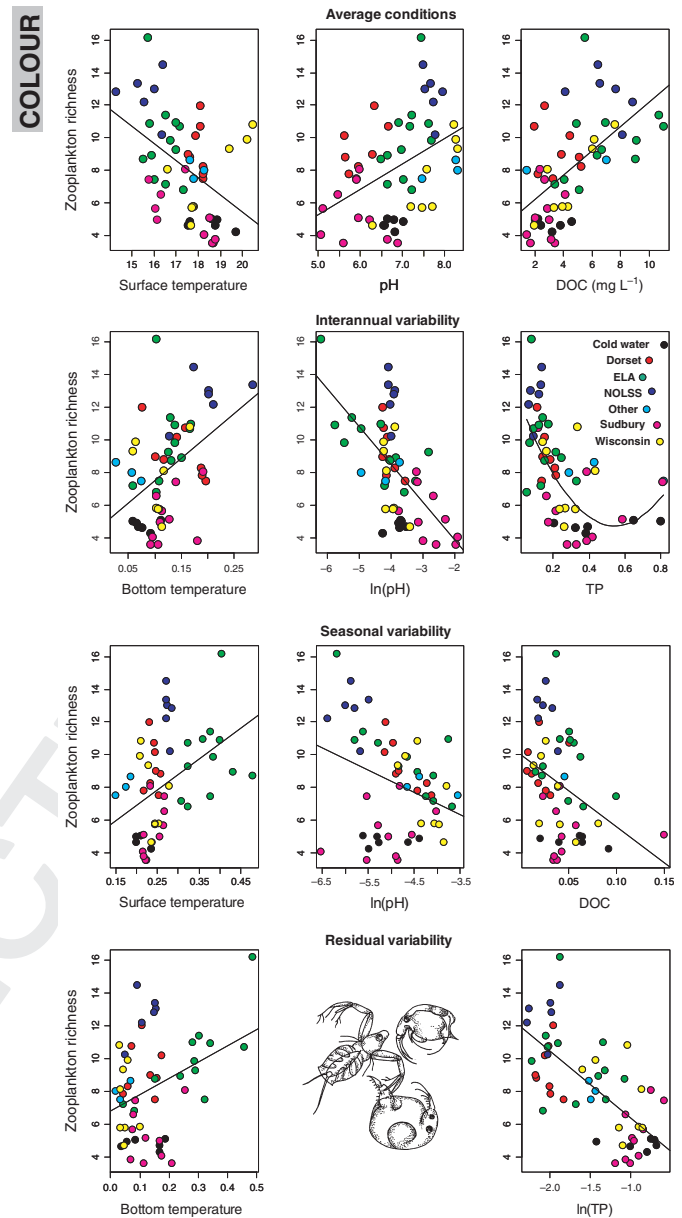


Figure 2 Long-term means and environmental variability of limnological factors included in the best-fit models as predictors of average daily zooplankton species richness. Each point represents a lake and the colour indicates the lake region for the data set. The data set 'other' includes the three singleton lakes in Table 1. Image at the bottom is by Simone Des Roches.

Δ AIC in the final model (8.6, Table 2), followed by mean pH (7.8), interannual variability in bottom temperature (4.4) and pH (3.3), and seasonal variability in DOC (3.1). All other variables had Δ AIC < 2 , indicating that their exclusion had minimal impact on the fit of the model (Burnham & Anderson 2002).

Of the top 11 best-fit models containing between one and 11 of the variables from the models on each time scale

Table 2 The best-fit model for average daily zooplankton species richness

Time scale	Variable	Estimate	SE	<i>P</i>	Δ AIC	
Long-term mean* ($R^2 = 0.48$)	Intercept	12.93	5.06	0.01		
	DOC	0.46	0.16	0.005	6.5	
	Surface temp	-0.76	0.26	0.005	6.6	
	pH	0.92	0.42	0.04	2.9	
Interannual† ($R^2 = 0.57$)	Intercept	3.40	2.33	0.15		
	Bottom temp	20.54	7.10	0.007	6.6	
	$\log_e(\text{pH})$	-1.22	0.44	0.009	6.0	
	TP	-19.06	6.00	0.003	8.1	
	TP ²	18.77	6.77	0.009	6.0	
Seasonal‡ ($R^2 = 0.42$)	Intercept	-2.01	2.82	0.48		
	DOC	-41.05	13.20	0.003	7.6	
	Surface temp	19.93	5.01	0.0002	12.8	
	$\log_e(\text{pH})$	-1.33	0.47	0.007	6.0	
Residual§ ($R^2 = 0.45$)	Intercept	2.15	0.95	0.03		
	Bottom temp	7.83	3.70	0.04	2.6	
	$\log_e(\text{TP})$	-2.86	0.59	$2.75e^{-5}$	17.5	
	Intercept	-1.84	4.59	0.69		
All ($R^2 = 0.77$)	Mean	Surface temp	-0.33	0.20	0.10	1.3
	Mean	pH	0.92	0.31	0.005	7.8
	Interannual	Bottom temp	12.61	5.31	0.02	4.4
	Interannual	$\log_e(\text{pH})$	-0.83	0.39	0.04	3.3
	Seasonal	$\log_e(\text{pH})$	-0.50	0.34	0.15	0.6
	Seasonal	DOC	-20.40	9.70	0.04	3.1
	Residual	Bottom temp	3.49	2.57	0.18	0.2
	Residual	$\log_e(\text{TP})$	-1.76	0.57	0.003	8.6

'Time scale' indicates average conditions, interannual, seasonal and residual variability, and 'Variable' is the abiotic factor measured. Δ AIC shows the change in AIC value as a result of excluding the variable from the model. 'Variables excluded' lists the variables that showed significant univariate relationships with zooplankton richness, but were excluded by the model selection procedure. Higher order variables (e.g. 'TP²') are included as quadratic terms in the same model with the first-order term. The top four models are the best-fit model for the ten abiotic variables on the time scale indicated. The model labelled 'All' is the best-fit model selected from all of the variables included in each of the final models for the four time scales.

*Variables excluded: surface temperature².

†Variables excluded: conductivity, DOC, TN.

‡Variables excluded: none.

§Variables excluded: chlorophyll-*a*, chlorophyll-*a*², conductivity, DOC, pH, TN.

(Appendix S5, TP and TP² were considered together as a single variable), residual variability in TP was included in all 11, followed by interannual variability in pH (10 models) and bottom temperature (9), long-term means of pH (8) and surface temperature (7), and finally seasonality in pH (6). Thus, environmental variability on interannual and residual

time scales showed correlations with daily zooplankton species richness that were comparable with or stronger than those of long-term average conditions, while seasonality showed relatively weak associations.

Many of the abiotic features showed correlated patterns of variability across time scales. The first two PC axes explained between 38 (residual variability) and 51 (mean conditions) percent of the overall variation among the lakes in the 10 abiotic variables (Fig. 3). In all four cases, the first PC axis was most closely related to indicators of lake productivity (TN, TP, chlorophyll-*a*, conductivity) and pH, while the second axis was mostly associated with thermal stratification (temperature and, in some cases, dissolved oxygen, DO). Residual variability in pH and conductivity were closely associated with those of temperature, in contrast with the other time scales. These multivariate correlations indicate that lakes that are stable or variable in terms of one physical or chemical factor tend to exhibit similar temporal patterns in other features. Thus, the correlations we show between zooplankton richness and univariate aspects of environmental stability likely reflect broader patterns of variability in multiple abiotic factors.

Lake size explained some of the variation in the stability of the physical and chemical environment (Fig. 3). Large lakes have greater thermal mass and are therefore buffered against temperature changes in the atmosphere. Surface area was weakly correlated with the mean conditions in the lakes; however, it was strongly negatively associated with thermal variability on all three time scales. In addition, larger lakes showed low interannual variability in conductivity and less residual variability in both pH and conductivity (Fig. 3).

DISCUSSION

The number of zooplankton species found in lakes is closely related to the degree of variability in the physical and chemical environment as well as average environmental conditions experienced over time. Fewer zooplankton species occur in lakes showing larger fluctuations in water chemistry, while variability in temperature is positively correlated with richness. The results suggest that instability in water chemistry tends to exclude more species than are facilitated by temporal niche partitioning. By contrast, thermal instability may favour coexistence and promote greater richness through storage effects. Potential impacts of ongoing global change on lake zooplankton biodiversity depend on the relative magnitudes and interactions between shifts in chemistry and temperature. Patterns of association between diversity and environmental stability indicate that increasing frequency of extreme events and greater ranges of variability may be as or more important than changes in average conditions as drivers of zooplankton community diversity.

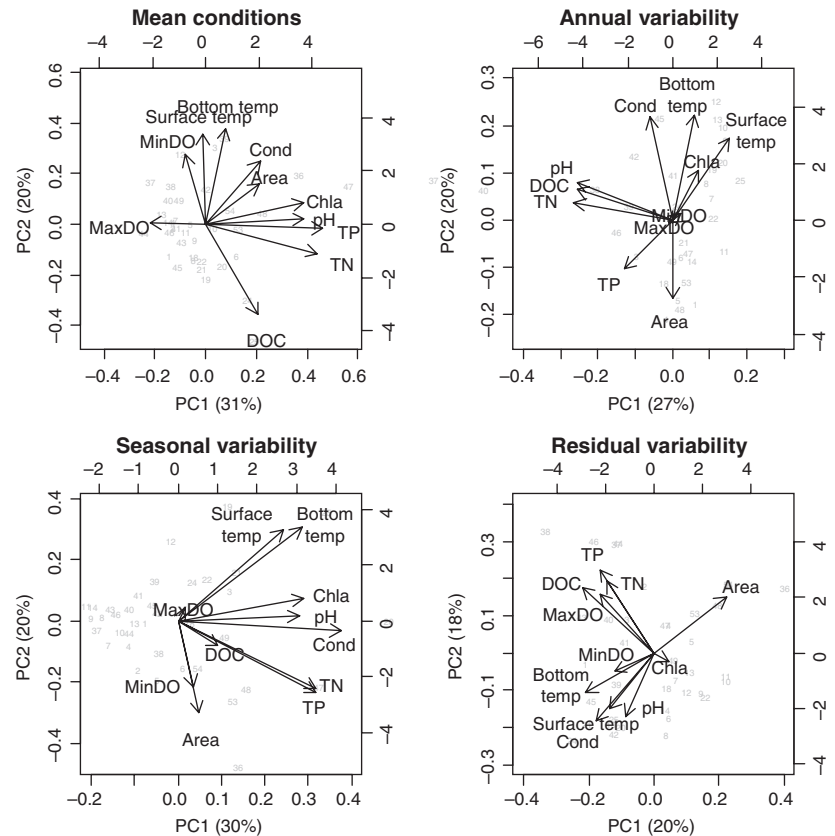


Figure 3 Principal component analysis (PCA) for the means and variability of the 10 limnological variables plus lake surface area. The small numbers indicate the position of individual lakes, and the direction and length of the arrows indicate the correlation for each limnological variable with the first two PC axes. ‘Surface temp’ and ‘Bottom temp’ indicate the maximum and minimum temperature across the water column. The axis labels indicate the proportion of total variation explained by each PC axis.

Different temporal scales of variability have distinct impacts on the richness of zooplankton communities found in lakes. Very few species were found in lakes showing strong variability in pH on interannual and seasonal time scales. High interannual variation in pH tended to occur in lakes with low intrinsic chemical buffering capacity subjected to industrial acidification (Dillon *et al.* 1984). This was particularly apparent in the Sudbury Lakes, although fluctuations in pH tended to reduce zooplankton richness across the entire range of variability. A number of species show sensitivity to low pH and declines in richness with acidification are commonly observed (Yan *et al.* 1996). Although declines in diversity are often only observed below pH around 6 (Keller & Yan 1991), our results indicate that even modest increases in pH variability are associated with reduced zooplankton species richness (Fig. 2). Many of the patterns associated with the interannual time scale (particularly in pH) reflect long-term trends such as acidification or eutrophication (or recovery from them) rather than random year-to-year fluctuations. The interannual time scale includes both directional and non-directional changes, which may have distinct effects on communities. Further work is needed to separate the influence of these two types of changes on diversity.

The decline in zooplankton species richness with higher long-term average surface temperature (Fig. 2) is likely a

consequence of lower seasonal temperature variability in warmer lakes. The lakes with higher average surface temperatures tended to be thermally stratified throughout the entire sampling period (May–October). This is reflected by negative correlations between long-term average surface temperature and interannual ($r = -0.28$, $P = 0.04$), seasonal ($r = -0.63$, $P < 0.001$) and residual variation ($r = -0.34$, $P = 0.01$) in surface temperature. Periods of thermal mixing can introduce nutrients from the sediments and hypolimnion to the surface and cause large phenological changes in plankton community structure (Sommer *et al.* 1986). As stratified and mixed seasons support distinct communities, lakes that are always stratified have lower potential for temporal niche partitioning and, our data suggest, lower average species richness. The negative correlation between average surface temperature and richness may therefore not reflect a direct negative influence of warmer temperatures on zooplankton diversity but rather the inverse correlation between mean temperature and its variability.

It is interesting that indicators of lake primary productivity (chlorophyll-*a* and TN) other than TP showed very few associations with zooplankton species richness. This result contrasts with findings of mostly unimodal associations between primary productivity and richness in several groups of lake organisms (Dodson *et al.* 2000). Differences among lakes in the depths at which nutrients and

1 chlorophyll were measured may have introduced error
2 because these factors often show strong depth gradients
3 (Fee 1976). Higher interannual and residual variation in TP
4 tended to be associated with low zooplankton richness. TP
5 is not a mortality agent or source of physiological stress for
6 zooplankton in the same way as, say, pH or conductivity;
7 therefore, it seems unlikely that fluctuations in TP would
8 tend to exclude species directly. Instead, fluctuations in
9 productivity may favour small subsets of species with high
10 growth rates. Many of the lakes with greatest interannual
11 variation in TP were ones that underwent periods of cultural
12 eutrophication or recovery due to nutrient abatement
13 efforts. The mechanistic basis for the correlation between
14 TP variability and zooplankton richness is unclear.

15 Environmental stability of lakes was related to their size.
16 Smaller lakes are more sensitive to changes in atmospheric
17 temperature (Gerten & Adrian 2001) and therefore show
18 greater thermal variability on all three time scales (Fig. 3).
19 Most aspects of water chemistry variability were weakly
20 related to lake surface area, although conductivity and pH
21 tended to be somewhat more stable in large lakes. These
22 patterns illustrate an interesting mechanism by which habitat
23 size influences species diversity; because they have more
24 stable thermal regimes, large lakes may present fewer
25 opportunities for temporal niche partitioning. This effect
26 may explain the inverse species–area relationship observed
27 in some groups of freshwater organisms (Scheffer *et al.*
28 2006). Our data showed a weak species–area curve for
29 zooplankton (for average daily richness, $y = 6.0 + 0.48 \cdot \log_e(\text{Area})$, $P = 0.03$), indicating that positive effects of area
30 on richness outweigh the greater temperature stability of
31 large lakes.
32

33 Our results support a previous study that found lower
34 species turnover through time in more speciose zooplank-
35 ton assemblages (Shurin *et al.* 2007). Similar patterns have
36 been documented for a diverse range of taxa from a number
37 of different biomes (White *et al.* 2006). Possible explana-
38 tions for these patterns include direct effects of diversity on
39 community stability (McCann 2000; Shurin 2007) or
40 negative effects of environmental instability on species
41 coexistence (Adler & Drake 2008). The patterns shown here
42 indicate that if storage effects or temporal niche partitioning
43 promote diversity in zooplankton, they do so mainly
44 through temperature rather than chemical variability.
45 MacArthur (1972) proposed that more stable environmental
46 conditions and dampened seasonality in the tropics com-
47 pared to the temperate zone are a possible explanation for
48 the latitudinal gradient in species diversity. Our results
49 suggest that different forms of environmental instability can
50 either facilitate coexistence or reduce diversity by excluding
51 species.

52 The patterns of association between zooplankton rich-
53 ness and abiotic stability can help inform the task of

forecasting future biodiversity scenarios under ongoing
global change. Warmer air temperatures may lead to longer
stratified periods (Winder & Schindler 2004), which may
reduce productivity in some lakes. Higher temperature
variability on all time scales was generally associated with a
greater number of zooplankton species; however, the effects
of future changes in patterns of temperature variation will
depend on the interaction with a number of processes
including ice formation and melting, vertical mixing and
re-suspension of nutrients from the sediments. Our results
also agree well with Drake (2005) who found that greater
temperature variability tended to increase population growth
rate among zooplankton, potentially leading to persistence
of rare species and greater diversity. Greater variability in
precipitation will likely lead to changes in runoff and the
input of allochthonous materials such as terrestrial plant
matter, the source of much DOC in lakes (Wetzel 1995).
A warmer climate may increase the export of DOC from
terrestrial to aquatic ecosystems (Worrall *et al.* 2004), and
our results showed that variability in DOC is strongly
associated with zooplankton species richness (Fig. 2). More
mechanistic studies are needed to identify the processes
responsible for the correlations between abiotic variability
and species richness, and to forecast community effects of
future climatic regimes.

Fluctuations in the chemical environment on all time
scales, particularly in pH and TP, most often led to lower
diversity (Fig. 2). The impacts of global change on the
chemical stability of lakes are likely to vary regionally. For
instance, warming and reduced precipitation at the
Experimental Lakes Area in Ontario produced more forest
fires, more wind mixing, higher nitrogen concentrations,
lower DOC and a suite of associated changes in lake
communities (Schindler *et al.* 1990). The relative magni-
tudes of potential changes in richness due to variability in
temperature vs. water chemistry remain important open
questions. The negative effects of chemical variability on
richness likely come about because local- and regional-
scale pollution (acidification and eutrophication) creates
conditions that far exceed of the natural range found in
lakes. For instance, acid rain lowered the pH of Clearwater
lake to 4–4.5 (Fig. 1). By contrast, temperature variation,
even in lakes that have shown recent warming trends (e.g.
Lake Washington, Fig. 1) is mostly within the range of
normal seasonal patterns. Finally, while our data set is a
fairly comprehensive accounting of water chemistry and
temperature, many aspects of the lake environment that
are important to zooplankton were not measured. Vari-
ability in predator, phytoplankton and microbial commu-
nities are certainly important factors but were absent from
our data. Future studies linking variability among different
parts of lake food webs will likely improve our predictive
capacity.

Niche segregation along gradients of variability in the environment has been invoked as a primary explanation for the coexistence of species ever since Hutchinson (1961) posed the question of how planktonic diversity is maintained. Diverse forms of niche partitioning have been identified even in organisms occupying environments with little apparent spatial structure such as plankton (Chase & Leibold 2003; Stomp *et al.* 2004). The temporal dynamism of the lake environment has long been appreciated (Forbes 1887; Sommer *et al.* 1986); however, its consequences for diversity (and vice versa) have rarely been explored. Our results suggest that fluctuating thermal conditions have largely positive effects on zooplankton diversity, while instability in the chemical environment mostly reduces richness. We propose that temperature variation provides opportunities for niche partitioning, whereas chemical variability most often excludes species. Our results also raise concern about the future of lake biodiversity in a changing global environment. Increasingly variable and unpredictable conditions have been observed (Karl *et al.* 1995; Easterling *et al.* 2000) and are forecasted to continue by many climate models (IPCC I.P.o.C.C. 2007). Our data indicate that these patterns of variability may have profound implications for biological diversity that are comparable in magnitude to changes in long-term average conditions and need to be incorporated in models to predict future scenarios.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 The relationship between number of zooplankton individuals counted per sample and the number of species identified in four ELA lakes. Numbers on the panels indicate the lake number. Richness was calculated by the method of Dodson (1992), which excludes littoral species and is therefore slightly different from the one we use. A mixed-effects model with only an intercept and a random term for ‘Lake’ provided a superior fit to models with a fixed effect for the number of individuals with either the same ($P = 0.0002$) or different ($P = 0.0042$) slopes for each lake. Thus, lakes differ in species richness and the number of animals counted had no discernable effect on the estimate of species richness.

Appendix S2 (a) The correlation between average daily and annual zooplankton species richness. (b) The best-fit models for average annual richness on the four time scales, and for all variables on all time scales.

Appendix S3 The scaling between the mean and standard deviation for each of the ten limnological variables on a log-log scale. The top rows are the relationships between the annual mean and the standard deviation among monthly averages, the bottom rows are for the long-term mean and the standard deviation of annual averages. The parameter values shown are for the mixed-effects models with the following random effects: none, Lake, or Lake nested within Data set. A likelihood ratio test was used to select among the three models with different random terms included. The parameter values shown are for the

1 fixed effects of the $\log(\text{mean}(x))$ on $\log(\text{StDev}(x))$. A slope
2 of 1 indicates that a multiplicative model is appropriate
3 form of variance decomposition, while an additive model
4 is appropriate for a slope of 0 (Chatfield 2004). The slopes
5 were significantly greater than zero in every case except for
6 the relationship between the long-term mean and annual
7 standard deviation for pH and Surface Temperature. We
8 therefore applied a multiplicative variance decomposition
9 model for all of the variables in our data set.

10 **Appendix S4** Summary statistics on environmental variables.
11 Each column indicates the mean and 95% bootstrapped
12 confidence intervals for each variable. Units are given in the
13 text.

14 **Appendix S5** Comparison of the best subset models con-
15 taining between one and 11 of the variables included in any
16 of the final models for each time scale (in Table 2). The first
17 and second order terms for interannual variability in TP
18 were removed together from the model. The models are
19 ranked from best (top) to worst (bottom) based on AIC
20 (indicated in the first column). Each row indicates a model,
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and the shaded rectangles indicate the variables included in
the model. The colour indicates the time scale as shown by
the top row. The number of models containing a variable is
an indication of its importance as a predictor of average
daily zooplankton species richness after accounting for
variance explained by all of the others.

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