USING TEMPORAL COHERENCE TO DETERMINE THE RESPONSE TO CLIMATE CHANGE IN BOREAL SHIELD LAKES

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Abstract. Climate change is expected to have important impacts on aquatic ecosystems. On the Boreal Shield, mean annual air temperatures are expected to increase 2 to 4 °C over the next 50 years. An important challenge is to predict how changes in climate and climate variability will impact natural systems so that sustainable management policies can be implemented. To predict responses to complex ecosystem changes associated with climate change, we used long-term biotic databases to evaluate how important elements of the biota in Boreal Shield lakes have responded to past fluctuations in climate. Our long-term records span a two decade period where there have been unusually cold years and unusually warm years. We used coherence analyses to test for regionally operating controls on climate, water temperature, pH, and plankton richness and abundance in three regions across Ontario: the Experimental Lakes Area, Sudbury, and Dorset. Inter-annual variation in air temperature was similar among regions, but there was a weak relationship among regions for precipitation. While air temperature was closely related to lake surface temperatures in each of the regions, there were weak relationships between lake surface temperature and richness or abundance of the plankton. However, inter-annual changes in lake chemistry (i.e., pH) were correlated with some biotic variables. In some lakes in Sudbury and Dorset, pH was dependent on extreme events. For example, El Nino related droughts resulted in acidification pulses in some lakes that influenced phytoplankton and zooplankton richness. These results suggest that there can be strong heterogeneity in lake ecosystem responses within and across regions.

Keywords: climate change, long-term data, multiple stressors, phytoplankton, regional drivers, synchrony, temporal coherence, zooplankton

1. Introduction

Human activities are resulting in large-scale changes in aquatic ecosystems (Schindler, 2001). One of the most important stressors is climate change (Schindler, 1998). There is strong evidence of both increasing global air temperatures and increasing temperature variability. Global surface temperatures have increased 0.6 °C since 1861, with the 1990s being the warmest decade and 1998 being the warmest year during the instrumental record (IPCC, 2001). Further increases are anticipated. For example, mean air temperature in the Boreal Shield is expected to increase 2 to

Environmental Monitoring and Assessment **88:** 365–388, 2003.

4 °C over the next 50 years (Hengeveld, 2000). There is also evidence of increased climate variability associated with increased frequency of El Nino events (Urban *et al.*, 2000). An important challenge is to predict how these changes in climate and climate variability will impact our natural systems so that sustainable management policies can be implemented.

The current and anticipated changes in climate will have complex and regionally heterogeneous impacts on the physical, chemical, and biological characteristics of lake ecosystems (Magnuson *et al.*, 1997). There are numerous anticipated effects including potential changes in water clarity and thermal regimes associated with declines in dissolved organic carbon (DOC) inputs (Fee *et al.*, 1996; Snucins and Gunn, 2000), alteration of water chemistry including contaminants (Webster *et al.*, 1996; Yan *et al.*, 1996), and changes in the distribution of organisms (De Stasio *et al.*, 1996; Vander Zanden *et al.*, 1999; Leech and Williamson, 2001). Direct changes in temperature and precipitation and indirect changes resulting from complex responses of the physicochemical environment are likely to impact freshwater ecosystems through changes in species abundance, distribution, and composition. In addition to potential direct influences, there is evidence that climate change may exacerbate the impact of other stressors such as invading species, pollution, and habitat alteration (Schindler, 2001).

To undertake the challenge of predicting biotic responses to complex ecosystem changes associated with climate change, we used long-term databases to evaluate how several physical, chemical, and biotic variables in Boreal Shield lakes have responded to past fluctuations in climate. Our data records span a two decade period where there have been unusually cold years (associated with the Mt. Pinotubo eruption in 1992) and unusually warm years (associated with an exceptionally strong El Nino in 1998). Lakes within a region will experience similar fluctuations in climate and therefore, limnological variables strongly influenced by climate will be expected to vary in a similar way through time. Individual lake characteristics such as water residence time and fish population cycles may create lags and deviations from the general regional response. Therefore, the similarity in lake response within a region will depend on the relative importance of extrinsic (i.e., regional) characteristics versus intrinsic (i.e., individual lake) characteristics (Rusak *et al.*, 1999). We used coherence analyses (e.g., Magnuson *et al.*, 1990; Kratz *et al.*, 1998) to test for regionally operating controls on climate, water temperature, pH, and plankton richness and biomass. Coherence is calculated as the mean Pearson correlation coefficient for all lake-pairs and is a measure of the synchrony or similarity in variability through time. Plankton richness and biomass were chosen because previous studies have indicated they should respond to climatic signals (e.g., George and Harris, 1985; Stemberger *et al.*, 1996) and because this information was available for each of the sites. We have included pH in our analyses because a relationship between El Nino events and pH has been detected for several of our study lakes in previous studies (Keller *et al.*, 1992; Yan *et al.*, 1996; Dillon *et al.*, 1998).

Figure 1. Map of the study areas.

Specifically, we asked the following questions;

1. Do climate variables in different regions change in a similar manner through time?
2. Are lake temperature and pH influenced by air temperature and precipitation, respectively?
3. Are plankton richness and total community biomass related to lake temperature and pH? And
4. Is there evidence of coherence of plankton richness and biomass across regions?

2. Methods

2.1. STUDY SITES

Data for the period from 1980 to 2000 were obtained from three long-term research sites which are part of the Boreal Shield Lakes Climate Change Network; the Experimental Lakes Area, the Cooperative Freshwater Ecology Unit, based in Sudbury, Ontario, and the Dorset Environmental Science Centre (Figure 1). The Experimental Lakes Area (ELA) is located in a sparsely inhabited region of southern Canada and is relatively unaffected by external human influences and industrial activities. Seven lakes were used in this study. Five of the lakes are reference lakes and two, L223 and L302S, were experimentally acidified in 1976 and 1982, respectively and are now recovering (Findlay and Kasian, 1996; Malley and Mills, 1992; Leavitt *et al.*, 1999). The lakes are small (<100 ha) and nutrient-poor (see Table I). More information is available at http://www.umanitoba.ca/institutes/fisheries/#index.

TABLE I

Morphological and limnological characteristics of the study lakes.

Lake	Latitude	Longitude	Surface Area	Max. Depth	*t* (yr)	TP µg/L	DOC mg/L	pH
L223	49°42′	93°42′	27.3	14.4	5.3	6.1	4.1	6.46
L239	49°39′	93°43′	56.1	30.4	10.8	5.6	5.6	7.00
L240	49°39′	93°43′	44.1	13.1	4.4	6.8	6.4	7.17
L373	49°44′	93°47′	27.6	21.5	19.6	5.4	3.9	7.33
L302s	49°40′	93°45′	23.7	13.8	6.6	8.8	3.9	5.97
L382	49°41′	43°41′	36.9	13.3	6.6	7.1	7.4	6.82
Blue Chalk	45°11′	78°56′	52.4	23.0	4.0	5.9	1.8	6.90
Chub	45°13′	78°59′	34.4	27.0	1.9	9.9	4.7	6.0
Crosson	45°05′	78°02′	56.7	25.0	1.5	10.5	4.0	5.94
Dickie	45°09′	79°05′	93.6	12.0	1.5	10.2	5.0	6.14
Harp	45°23′	78°08′	71.4	37.5	2.9	7.1	3.8	6.80
Heney	45°08′	78°06′	21.4	5.8	1.2	6.7	2.8	6.00
Plastic	45°11′	78°50′	32.1	16.3	3.0	5.6	2.2	5.90
Red Chalk	45°11′	78°56′	32.1	38.0	2.4	4.9	2.4	6.83
Clearwater	46°22′	81°03′	75.9	21.5	3.2	3.2	0.9	5.48
Hannah	46°21′	81°02′	27.3	8.5	1.7	5.9	3.3	7.19
Middle	46°26′	81°02′	28.2	15.0	5.7	5.2	3.0	6.85
Lohi	46°23′	81°02′	40.5	19.5	–	3.9	1.2	5.84
Swan	46°21′	81°03′	5.8	8.8	0.6	8.1	2.0	5.39
Sans Chambre	46°43′	81°07′	14.5	15.0	–	8	2.9	5.99
White Pine	47°17′	80°50′	66.9	22	–	5.7	2.5	5.76

TP, DOC, and pH were averaged over the period 1980 to 2000.

The seven study lakes around Sudbury, Ontario were intensively sampled since the 1970s. The area was historically subjected to severe acid deposition from local mining and smelting activities, but legislated reductions in sulphur dioxide emissions have resulted in increased pH over the past two decades (Keller, 1992; Keller *et al.*, 1992). The lakes are located on the Precambrian Shield where thin soils and low buffering capacity made them susceptible to acidification. All lakes are small ($<$100 ha), softwater (28–75 µS/cm, except Middle (230 µS/cm) and Hannah (330 µS/cm)), and nutrient-poor. Five of the lakes are headwater lakes and two (Middle and Lohi lakes) are second order lakes. All lakes are dimictic, with the occasional exception of Swan Lake which has had incomplete stratification during some years. Three of the lakes, Middle, Lohi, and Hannah, were experimentally limed in the 1970s. Calcium carbonate ($CaCO_3$) and Calcium hydroxide ($Ca(OH)_2$) were added to Middle and Lohi lakes in 1973 and to Hannah Lake in

1975. Small amounts of phosphorus were added to Middle in 1975–1978 and to Hannah from 1976–1978 (Yan and Lafrance, 1984).

The eight Dorset lakes are located in mixed deciduous-coniferous forests with extensive wetlands and have been monitored since 1975. The lakes are located in south-central Ontario and are small (<100 ha), soft water (23–34 μS/cm), and nutrient-poor. All of the lakes are headwater lakes, except Red Chalk Lake which is downstream of Blue Chalk Lake. Six of the lakes are dimictic, and one, Heney Lake does not stratify. One of the lakes, Harp was invaded by an exotic invertebrate predator, *Bythotrephes*, in the early 1990s resulting in dramatic changes to the zooplankton community (Yan and Pawson, 1997; Yan *et al.*, 2002).

The lakes used in our study are part of routine long-term monitoring programs at each of the sites (Table II). In all lakes the sampling station was located over the deepest part of the lake. Annual values of each parameter were generated by averaging monthly values, except phytoplankton from Dorset and Sudbury lakes where biweekly to monthly samples were pooled and phytoplankton from the composite were identified and enumerated (Table III). More detailed information on the study sites and sampling programs can be found in Brunskill and Schindler (1971), Dillon *et al.* (1991, 1994), Dillon and Molot (1996), Fee *et al.* (1996), Keller (1992), Nicholls *et al.* (1992), Yan *et al.* (1996), and Girard *et al.* (2001).

2.2. COHERENCE ANALYSES

We used the Pearson correlation coefficient to estimate temporal coherence. A year-by-lake matrix was developed for each of the variables with each cell containing an estimate of the mean annual value for that variable. Pair-wise correlation coefficients were then calculated for lakes within regions and among regions. Note that not all lakes were used in the analyses for each of the parameters and the number of years of data varied among lakes according to data availability (Table IV). Coherence in air temperature among ELA, Sudbury and Dorset regions was assessed by calculating the correlation of mean annual (Jan–Dec), spring (Mar–May), summer (June–Aug), fall (Sept–Nov), and winter (Dec–Feb) air temperatures. Similarly, correlations between region-pairs was calculated for total annual, hydrological (June–May), spring, summer, fall, and winter precipitation. Correlations were calculated for summer lake surface temperature between lakes in each region, as well as across regions. The correlation between summer air temperature and summer lake surface temperature for each lake was calculated within each region. Likewise, the relationship between precipitation and lake pH was determined for each region. The coherence of summer lake surface temperature and plankton annual richness and total biomass was calculated within and across regions. Finally, coherence in annual richness and total biomass of zooplankton and phytoplankton was assessed by calculating the mean correlation within and among regions.

Because different lakes might respond to regional signals in different ways, we analyzed between-lake coherence of zooplankton and phytoplankton for subsets of

TABLE II

General methodology for sampling in each of the three regions.

Variables	Site	Time Period	Months	Methods
Air temperature	ELA	1980–2000	Jan. to Dec.	Local meteorological station, 2 daily measurements
	Dorset	1980–2000	Jan.–Dec.	Local meteorological station, daily measurements
	Sudbury	1980–2000	Jan.–Dec.	Sudbury Airport, daily measurements
Precipitation	ELA, Dorset, Sudbury	1980–2000	Jan. to Dec.	Local meteorological station, daily measurements
Surface water	ELA, Dorset, Sudbury	1980–2000*	June–Aug.	Time-weighted average of 1–3 m, bi-weekly to monthly measurements
temperature				
PH	ELA	1980–2000*	May–Oct	Integrated sample from epi- and metalimnion, bi-weekly measurements
	Dorset	1980–2000*	May–Oct	Volumn-weighted sample from epi-, meta-, and hypolimnion, bi-weekly to monthly measurements
	Sudbury	1980–2000*	May–Oct	Volume-weighted water column sample, bi-weekly to monthly measurements
Phytoplankton	ELA	1980–1998*	May–Oct	Euphotic zone, average of monthly values
	Dorset, Sudbury	1981–1996*	May–Nov	2x secchi disk, ice-free season composites pooled from bi-weekly to monthly samples
Zooplankton	ELA	1980–2000*	May–Oct	Double-barrel closing net from lake bottom, 53 um mesh, bi-weekly samples
	Dorset, Sudbury	1980–2000*	May–Oct	**Metered net, 80 um, from 1m off bottom, bi-weekly to monthly samples

*some years missing in some lakes.

**except Swan Lake where discrete samples from 3 stations were combined for 1m and also for 4 m. A discrete sample was taken at 7 m for 1 station and then data from all three depths were pooled, accounting for differences in lake volume at each depth strata.

TABLE III

The average number of samples used to calculate annual means. The number of samples used to generate phytoplankton biomass also reflect the number of samples used to calculate mean annual pH.

Taxa	Parameter	Region	No. samples	95% CI
Phytoplankton	Richness	ELA	7	Na
		Dorset	11	1.0
		Sudbury	5.8	0.26
	Biomass	ELA	11	0.6
		Dorset	11	1.0
		Sudbury	5.8	0.26
Zooplankton	Richness	ELA	6	Na
		Dorset	6	Na
		Sudbury	6	Na
	Biomass	ELA	11	0.5
		Dorset	8	0.4
		Sudbury	6	0.3

lakes following Brien *et al.* (1984) and Rusak *et al.* (1999). Four steps are used to determine if subsets of the correlation matrix of lakes are significantly coherent. They include testing for homogeneity (i.e., H_{01}, all correlations are equal), interactions between rows and columns of the matrix (H_{02}), equal correlations in rows or columns (H_{03}), and finally that the grand mean of the correlation matrix is equal to zero (H_{04}). Lakes were grouped by finding the 3-lake subset with the highest mean correlation. We considered lakes to be a synchronous subset if the correlation matrix was homogeneous (accepting H_0s 1-3) and coherent (rejecting H_{04}). Lakes were added to this subset until the resulting subset was found to be heterogeneous or the grand mean correlation was not different from zero ($P < 0.05$). Lakes in each subset are, therefore, significantly correlated to each other.

We plotted the z-score transformed total biomass and richness (x-x/stdev) for each of the significant subsets.

3. Results

3.1. COHERENCE OF CLIMATE AND PHYSICOCHEMICAL VARIABLES

Air temperature was highly coherent across all three regions (Figure 2). There were seasonal differences in coherence, with summer being the most coherent season and fall being the least (Figure 3). The Pearson correlation coefficient was

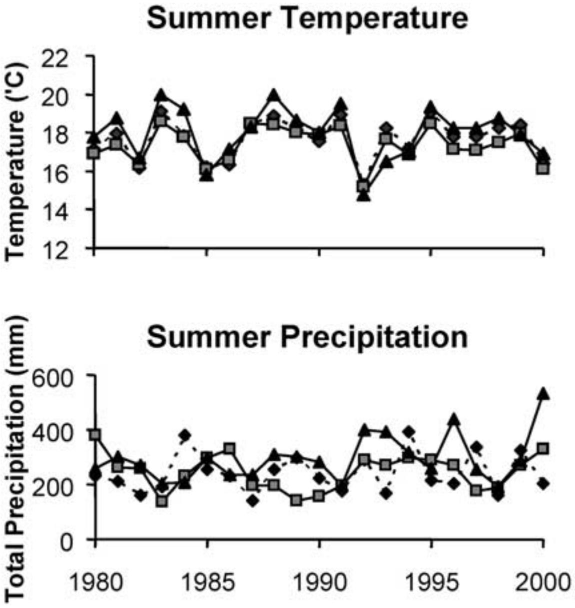

Figure 2. Mean summer temperature and precipitation at Sudbury (♦), Dorset (■), and the ELA (▲).

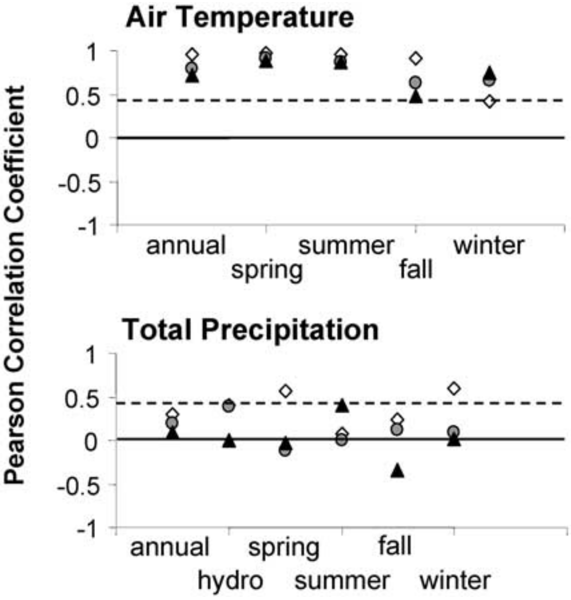

Figure 3. Pairwise Pearson correlation coefficients (i.e., coherence) for Sudbury-Dorset (◇), Sudbury-ELA (●), and Dorset-ELA (▲). The dashed line indicates the value for significance at the 0.05 level.

TABLE IV

The number of years of data for correlation analyses for each of the study lakes. Note that not all lakes had data available for every analysis

Lake Name	Lake Temperature	pH	Phytoplankton	Zooplankton
L223	19	21	20	19
L239	21	21	20	21
L240			17	
L302	21	21	20	21
L373	18	18	15	12
L382	17	14	19	
L442		14		12
Blue Chalk	19	21	15	21
Chub	19	21	14	20
Crosson	19	21	15	20
Dickie	19	20	15	20
Harp	19	21	15	21
Heney	19	19	15	19
Plastic	19	20	17	21
Red Chalk	18	21	15	21
Clearwater	17	21	16	20
Hannah	16	21	15	20
Lohi	17	21	14	14
Middle	17	21	13	20
Sans Chambre		21		16
Swan	19	19	15	18
White Pine				20

significant ($P < 0.05$) for all regional pairs in each season except fall where the correlation between air temperature in Dorset and ELA was positive but not significant ($r = 0.42$). Precipitation patterns among regions were less coherent than air temperature, with the highest coherence being in winter and the lowest being in the fall (Figure 3). Most correlations were positive with only 3 of the 18 possible pairs being negative. However, only two of the positive correlations were significantly different from zero.

Air temperature and lake surface temperature were highly correlated within a region, particularly for Dorset and ELA where correlations were all significantly positive (Figure 4). For the Sudbury lakes, the correlations between air temperature and lake temperature were all positive, but significant for only three of the six lakes. At the ELA and Dorset, lake surface temperatures varied synchronously within the

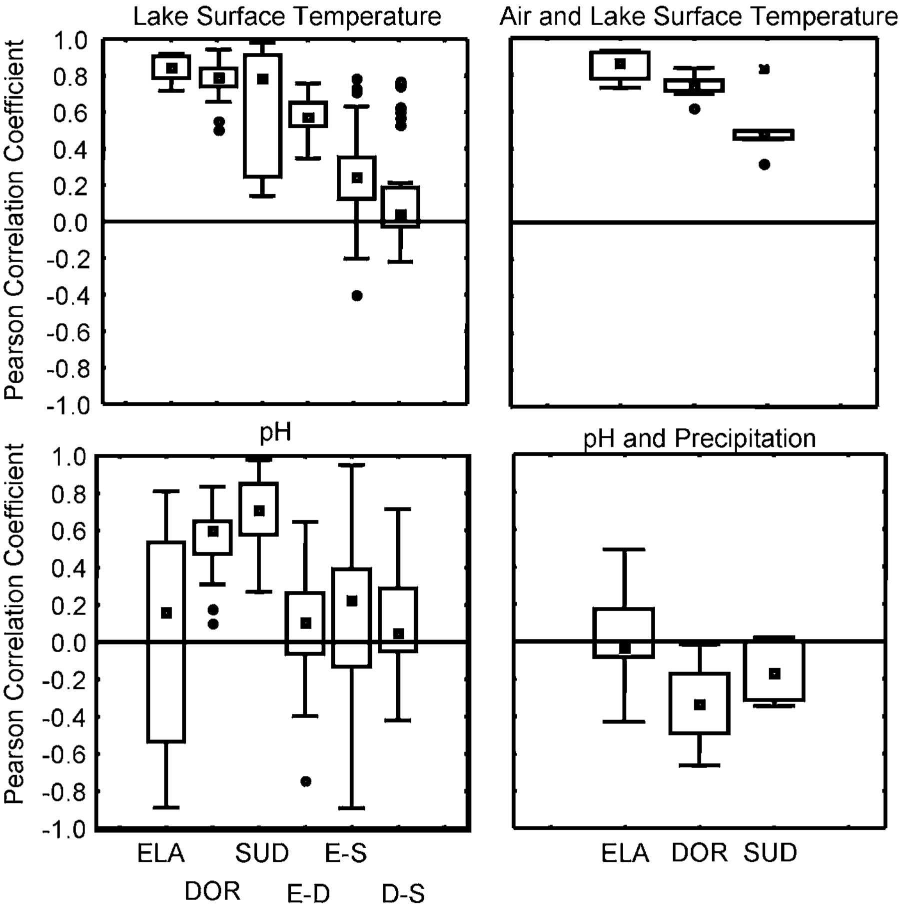

Figure 4. Box plot diagrams of pairwise Pearson correlation coefficients, within and among regions, for lake surface temperature, pH, the relationship between air and lake surface temperature, and the relationship between pH and precipitation. The center square indicates the median, the box represents the 25th and 75th quartiles, the bars indicate the range excluding outliers, and the points outside the bars indicate outliers.

region (Figure 4), with all correlations being positive and significant. In Sudbury, correlations for surface temperature were positive for all 10 lake pairs, but significant for only six. As a result, correlations with lake surface temperature among regions were high for Dorset-ELA (all 40 possible pairs were positive, with 33 being statistically significant) but lower when Sudbury was compared to the other regions (27 of 40 pairs positive and 8 significantly positive for Dorset-Sudbury, 22 of 25 pairs positive and 5 significantly positive for ELA-Sudbury).

Coherence in lake pH was examined because there have been changes in pH in some of the lakes at each site over the past two decades (Table V). This was most pronounced in the Sudbury lakes where reductions in sulphur dioxide emissions from local smelters have resulted in increased pH in many of the area's

TABLE V

Directional changes in pH, results of Mann-Kendall test

ELA		Dorset		Sudbury	
Lake	*P*-value	lake	*P*-value	Lake	*P*-value
L223	<0.001	Blue Chalk	0.43	Clearwater	<0.001
L239	0.07	Chub	0.45	Hannah	<0.001
L302s	0.35	Crosson	0.50	Lohi	<0.001
L373	0.15	Dickie	0.01	Middle	<0.001
L382	0.19	Harp	0.33	Sans Chambre	0.003
L442	0.09	Heney	0.003	Swan	0.01
		Plastic	0.40		
		Red Chalk	0.12		

lakes (Keller *et al.* 1992). As a result of this increasing pH trend, lake pH is highly correlated among the Sudbury lakes (Figure 4). All 15 lake pairs were positively correlated and 12 were statistically significant. The weakest correlations were associated with Swan Lake, which underwent a dramatic drought-related re-acidification event in the late 1980s (Yan *et al.*, 1996). In the Dorset area, pH was also positively correlated among all lakes with 23 of the 28 lake-pairs being positively significant. Despite moderate acid deposition in this area, two lakes, Dickie and Heney, had increasing pH trends over the past two decades (Table V). In Heney Lake some of the pH fluctuations have been associated with El Nino related drought events (Dillon *et al.*, 1997). At ELA, an area of low acid deposition, pH in lakes were both positively and negatively correlated (9/15 were positive with 4 of these being significant, 6/15 were negative with 5 being significant). Coherence among regions was lower than within regions with only 55 to 65% of the correlations being positive (Figure 4).

Previous studies have indicated that pH in lakes can be influenced by precipitation, i.e., droughts (Webster *et al.*, 1990; Keller *et al.*, 1992; Yan *et al.*, 1996; Dillon *et al.*, 1997). When we looked at the relationship between total annual precipitation and lake pH, there was evidence of negative correlations, particularly in Dorset and Sudbury (Figure 4). That is, when precipitation is high, pH tends to be low. This is probably the result of lag effects; drought causes the re-oxidation of sulphur stored in exposed sediments, wetlands, and the catchment (Devito *et al.*, 1999). The re-oxidized sulphur is then flushed back into lakes and streams when precipitation increases after the drought. Therefore, the low pH, although caused by a drought period, is expressed when precipitation increases.

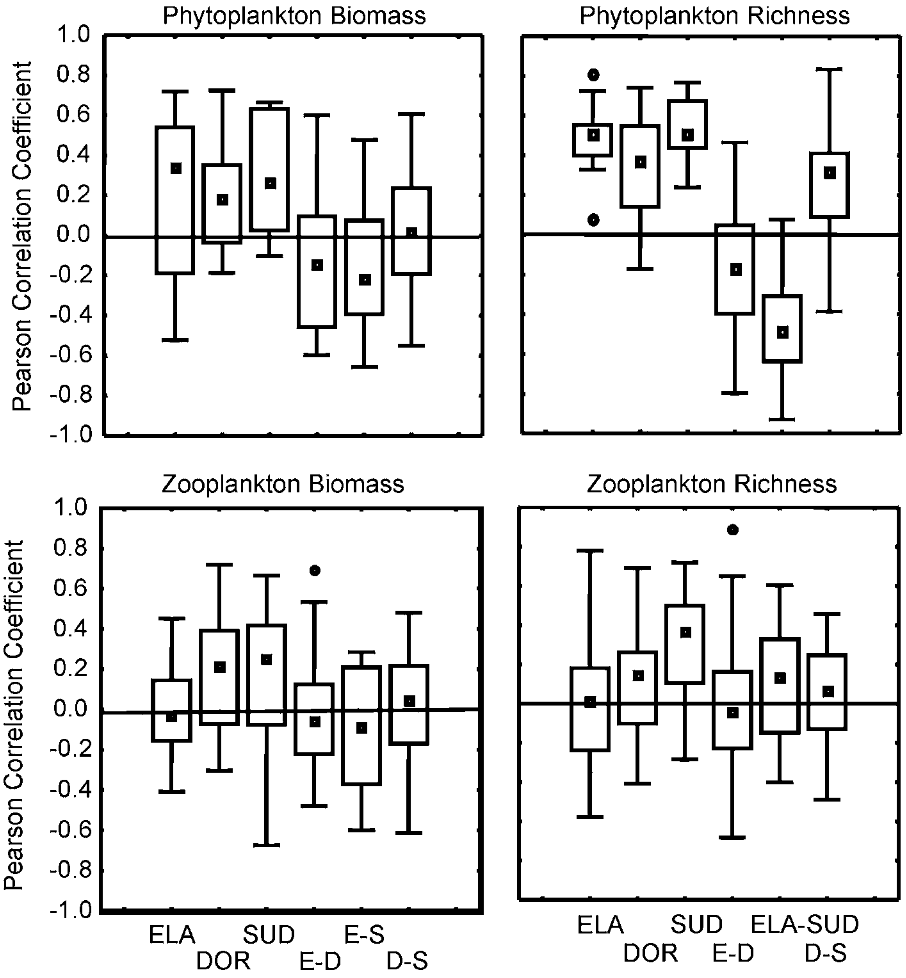

Figure 5. Box plot diagrams of pairwise Pearson correlation coefficients, within and among regions, for phytoplankton biomass, phytoplankton richness, zooplankton biomass, and zooplankton richness.

3.2. COHERENCE IN BIOLOGICAL VARIABLES

Phytoplankton richness and biomass within each region were moderately coherent – i.e., the correlations tended to be positive within regions (Figure 5). Within regions, 66 to 80% of the correlations for phytoplankton biomass were positive, and 82 to 100% of the correlations for phytoplankton richness were positive. Between regions correlations for phytoplankton biomass tended to be negative (62 to 70% for ELA-Dorset and ELA-Sudbury, respectively, but 48% for Dorset-Sudbury). Correlations in phytoplankton richness between regions were variable; 85% of the correlations between Dorset and Sudbury were positive, although only two were significant; 97% of the correlations between ELA and Sudbury were negative, with 43% being significant (richness increased in Sudbury but decreased in ELA during

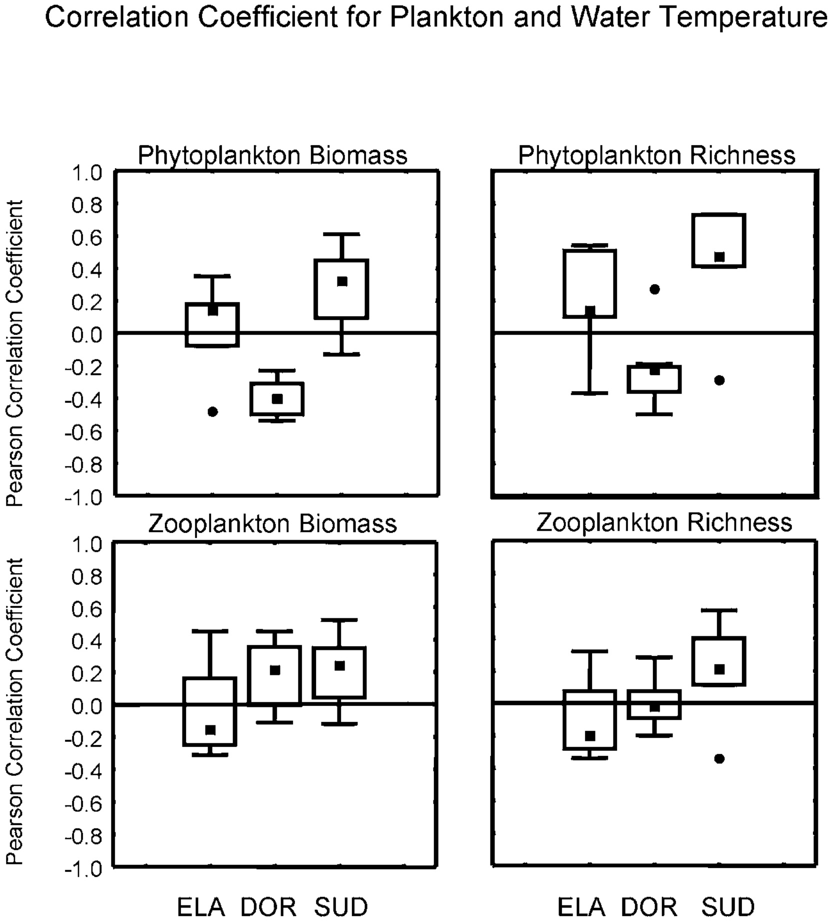

Figure 6. Box plot diagrams of the pairwise Pearson correlation coefficients between surface water temperature and plankton biomass and richness for each of the three study regions.

this time); and 71% of the correlations between ELA and Dorset were negative, with 12% being significant. This suggests that there are strong regional controls on phytoplankton that are probably different across large regions. For example, trend tests suggest that both phytoplankton richness and biomass decreased in ELA during our two-decade study (biomass: $P = 0.02$ for L223, $P = 0.03$ for L239, $P = 0.02$ for L240; richness: $P = 0.04$ for L223, $P = 0.003$ for L239, $P = 0.03$ for L302s, $P = 0.01$ for L382; Mann-Kendall trend test). There were no significant decreases in phytoplankton biomass in any of the Dorset or Sudbury lakes. However, phytoplankton richness in three Sudbury lakes significantly increased in response to increased pH ($P = 0.01$ for Clearwater, $P = 0.04$ for Hannah, and $P = 0.02$ for Middle Lake; Mann-Kendall trend test).

Neither zooplankton biomass nor richness was coherent within the ELA region. For Dorset and Sudbury within region zooplankton coherence was moderate.

In most cases, coherence among regions was low (Figure 5). Only 40% of the correlations for zooplankton biomass were positive for the ELA and none were statistically significant. Coherence was higher for Dorset (68% positive, 14% significant) and Sudbury (67% were positive, 24% significant). Richness tended to be more coherent; 60 to 86% of the correlations within regions were positive with 10 to 14% significant. Between regions, there was little evidence for coherence; the percent positive correlations for biomass and richness ranged from 37 to 61% with only 0 to 9% being significantly different from zero. Some lakes exhibited declines or increases in species richness or biomass over the two decade period. In Sudbury, Middle Lake zooplankton increased in both richness and total biomass ($P = 0.04, 0.02$, respectively; Mann-Kendall trend test). In Dorset, zooplankton biomass decreased in Heney Lake and richness decreased in Harp Lake ($P = 0.03$, 0.02, respectively; Mann-Kendall trend test). At the ELA, zooplankton richness and biomass increased in L223 ($P = 0.02$; Mann-Kendall trend test) and zooplankton richness decreased in L373 and L442 ($P = 003$; Mann-Kendall trend test).

The phytoplankton response to water temperature was different in each of the regions. In the Dorset lakes both phytoplankton biomass and richness tended to be negatively correlated with surface water temperature (Figure 6). In both Sudbury and the ELA, phytoplankton richness tended to increase in years with warmer lake temperatures. The relationships between phytoplankton biomass and lake surface temperature for Sudbury and the ELA were weak. In general, there were more positive than negative correlations, but only two significant correlations (positive) between water temperature and phytoplankton richness in both ELA and Sudbury and only one significant correlation (positive) between water temperature and phytoplankton biomass in Sudbury.

Little evidence of a relationship between zooplankton richness and biomass and surface temperature was apparent. Zooplankton biomass in the Dorset and Sudbury lakes was positively correlated with lake surface temperature in 75 and 80% of the lakes, respectively, although the relationship was statistically significant in only one lake (Middle). At the ELA, 75% of the correlations were negative, although none were statistically significant. In the Sudbury lakes, zooplankton richness tended to be higher when surface temperature was warmer, but the relationship was significant for only Middle Lake. In the Dorset and ELA lakes, the relationship was negative for over half of the lakes, but correlations were low and not significant. There was little evidence that lake temperature was influencing either biomass or richness in most lakes.

In Sudbury lakes, plankton richness and biomass were correlated with changes in pH (Figure 7). Increases in richness and biomass have occurred with increased pH associated with decreases in sulphur dioxide emissions over the past several decades (Table V). In Dorset, a region with lower historic acid deposition, a relationship between plankton and pH was less apparent. Zooplankton biomass, however, was positively related to pH in 75% of the lakes, but only one lake (Plastic)

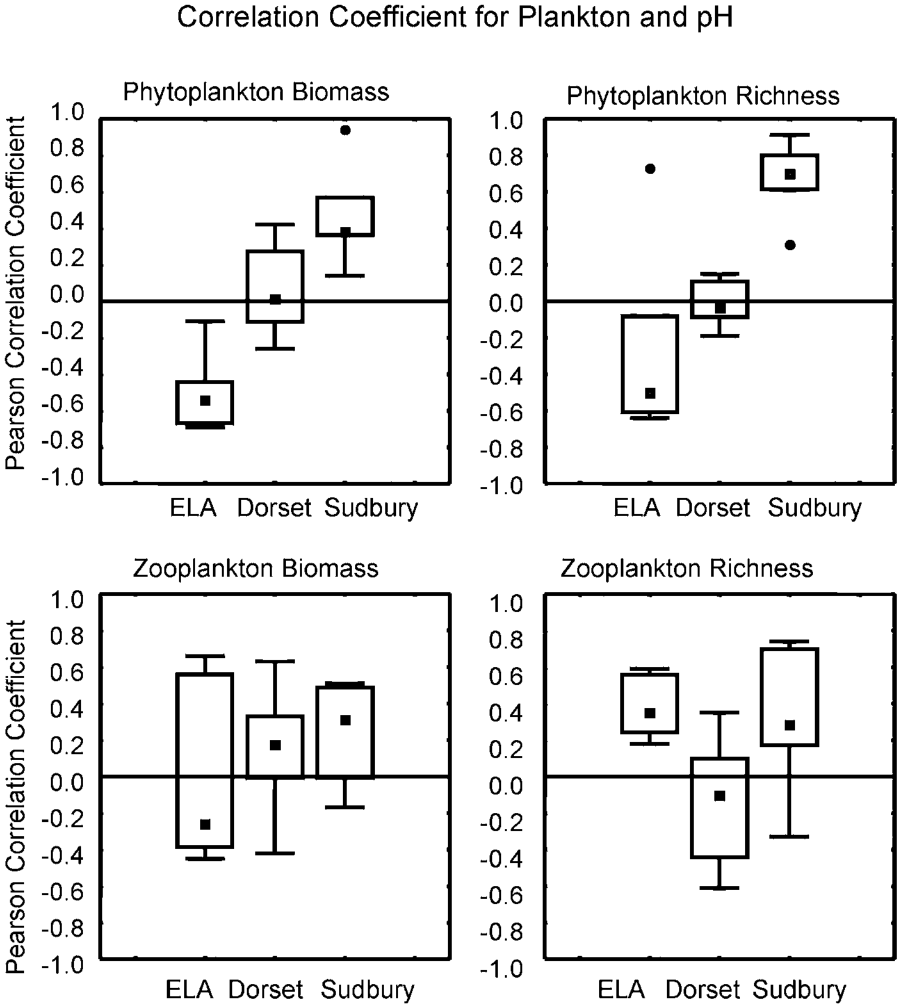

Figure 7. Box plot diagrams of the pairwise Pearson correlation coefficients between pH and plankton biomass and richness for each of the three study regions.

had a significantly positive correlation. Zooplankton richness was negatively correlated with pH in two lakes, Harp and Red Chalk. This is probably not a causal relationship in Harp Lake because it was invaded by an exotic invertebrate predator, *Bythotrephes longimanus*, in the mid-90s, which resulted in a decline in richness, concurrent with a slight increase in pH (Yan *et al.*, 2002). Interestingly, at the ELA phytoplankton richness and biomass were negatively correlated with pH. However, in all lakes except L223 and L302s, pH fluctuations were small and mean pH tended to remain above 6, which is considered a critical threshold for many sensitive species (Marmorek and Korman, 1993). In L223 and L302s, pH increased through time reflecting recovery from experimental acidifications. Phytoplankton richness

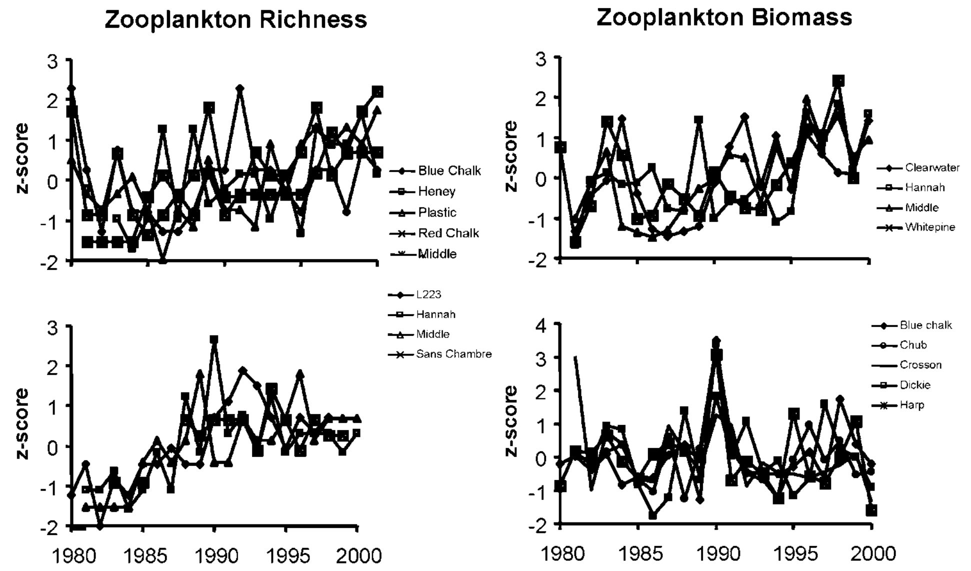

Figure 8. Z-scores of zooplankton richness and zooplankton biomass for homogeneous subsets of lakes.

was positively correlated with pH in L302s, suggesting a recovery response from previous manipulations.

Although coherence in phytoplankton and zooplankton was low in many cases, we produced several homogeneous and coherent subsets of lakes for both richness and biomass (Table VI, Figures 8, 9). Phytoplankton richness had a large subset of lakes, consisting of lakes from both Sudbury and Dorset. Other subsets for phytoplankton richness consisted of subsets of three lakes, all within the same region. Phytoplankton biomass had a large homogeneous and coherent subset of lakes that spanned Dorset and Sudbury although they were different lakes than those that were coherent in richness. Two other subsets were detected; three lakes in ELA and three lakes in Dorset.

Coherent homogeneous subsets in zooplankton richness were detected in two groups of lakes. In both cases the subsets were comprised of lakes from two regions; Dorset and Sudbury, Sudbury and ELA. In contrast the two coherent subsets for zooplankton biomass consisted solely of lakes within a single region.

4. Discussion

We estimated temporal coherence of several climatic and limnological variables in an effort to reveal regional climatic signals in Boreal Shield lake ecosystems. We interpret high temporal coherence as an indication of the importance of regional drivers such as climate. Low temporal coherence suggests that within lake processes mediate regional climate changes. Air and water temperature had high

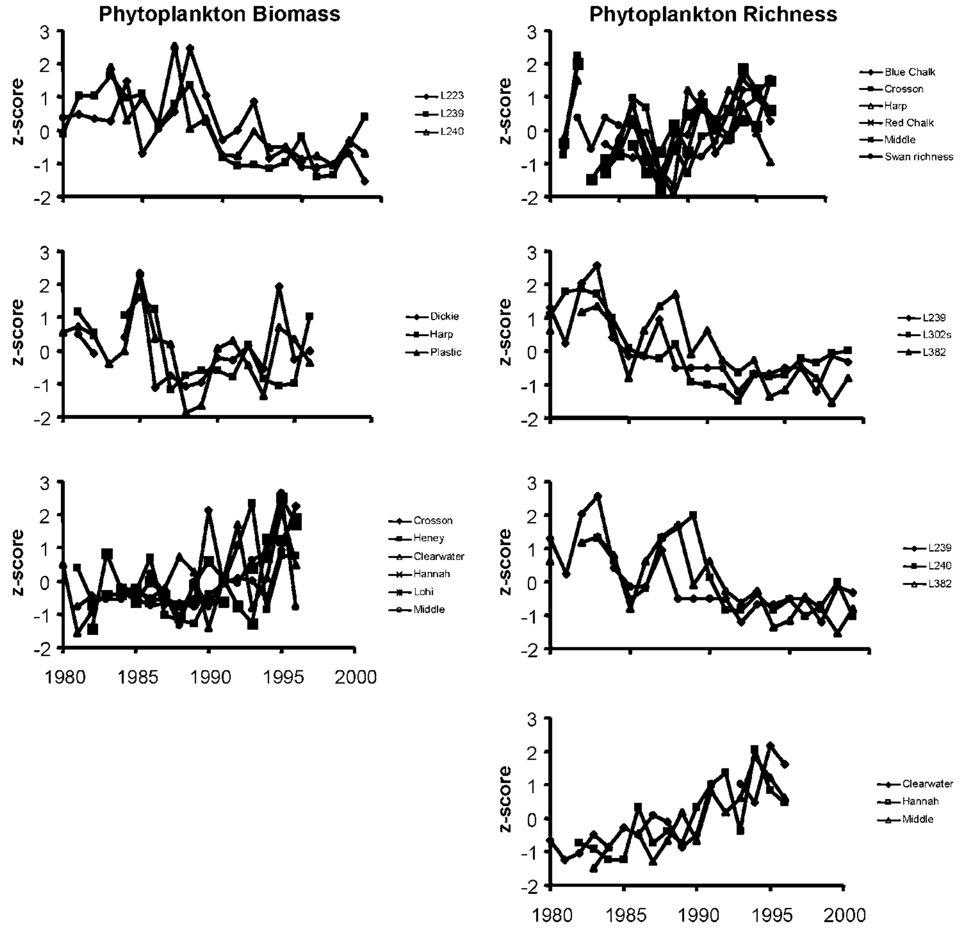

Figure 9. Z-scores of phytoplankton richness and phytoplankton biomass for homogeneous subsets of lakes.

coherence, indicating the importance of regional controls. Biotic variables tended to have low coherence. However, we found evidence of homogeneous subsets of lakes with high coherence, suggesting that regional controls exist but are modified by individual lake-types.

Air temperature followed very similar trajectories among regions but precipitation was less coherent through time, although correlations were generally greater than zero. Low temporal coherence of total precipitation was not surprising because cloud cover and precipitation patterns tend to be localized. Similar results were observed by Benson *et al.* (2000), who compared climatic variables (temperature and solar radiation) among four sites in the Great Lakes region, including the ELA and Dorset, two of our study sites. In a coarser analysis, we examined precipitation anomalies (i.e., deviations from the 1980–2000 mean) and found that there were similar cycles of dry and wet years, droughts associated with El Nino events in

TABLE VI

Homogeneous and coherent subsets of lakes.

Parameter	*r*	*P*	Lakes*
Phytoplankton richness	0.52	<0.001	BC, CR, HP, *MD*, RC, *SW*
	0.66	<0.001	L239, L302s, L382
	0.62	<0.001	L239, L240, L382
	0.68	<0.001	CW, HA, MD
Phytoplankton biomass	0.51	<0.001	DK, HP, PL
	0.55	<0.001	L223, L239, L240
	0.36	<0.001	*CW*, CR, *HA*, HN, *LO, MD*,
Zooplankton richness	0.56	<0.001	L223, HN, *MD, SC*
	0.34	<0.001	BC, HN, *MD*, PL, RC
Zooplankton biomass	0.45	<0.001	BC, CH, CR, DK, HP
	0.51	<0.001	CW, HA, MD, WP

'r' indicates the average correlation for the subset, i.e., the grand mean and P indicates the significance for H_0, the grand mean correlation is significantly different from zero. Lakes in italics are in the Sudbury area, numbered lakes are at the ELA, the remainder are in the Dorset area. Abbreviations: BC=Blue Chalk, CR=Crosson, CH=Chub, DK=Dickie, HP=Harp, HN=Heney, PL=Plastic, RC=Red Chalk, *CW=Clearwater, HA=Hannah, LO=Lohi, MD=Middle, SW=Swan, SC=Sans Chambre, WP=Whitepine*

1983–84, 1985–87, 1993–94, and 1998. However, the span of time the droughts covered often differed among regions, and they were sometimes offset by one or more years, resulting in low temporal coherence. The level of coherence in limnological variables across the region, therefore, will depend on the relative importance of air temperature and precipitation as environmental drivers and will depend on lags in response (e.g., the relationship between precipitation and re-acidification).

Surface water temperature, an important environmental variable for aquatic biota, was strongly related to summer air temperature. In general, coherence in water temperature was high, a result that is shared with other studies (Baines *et al.*, 2000; Benson *et al.*, 2000). There was, however, variation in the strength of these relationships among our study regions. The mean coherence among Sudbury lakes water temperature was low, resulting from low coherence when lakes were paired with Swan Lake. Variation in surface water temperature may be different in Swan Lake because it is morphologically quite different from the other study lakes; it is small, shallow, has a high DOC concentration, and a short water renewal time. Interestingly, it is the other Sudbury lakes that contribute to low coherence when lakes from other regions were paired with the Sudbury lakes. Swan Lake behaved in a similar manner to the lakes in Dorset and the ELA. There is no obvious explanation for this as Swan Lake is morphologically distinct from all of our other study lakes. This demonstrates that despite similar climatic forcings (i.e., air temperature) lakes within a region can have asynchronous surface temperatures. These differences could have implications for detecting biological responses to climate change.

In our study lakes, pH changes were the result of both regional and local drivers, depending on the study region. In Sudbury, the high level of temporal coherence was the result of lakes responding to the legislated decreases in sulphur emissions from local smelters as well as declines in long range transport; i.e., regional controls. Lakes in the Dorset area probably responded to both the regional signal of acid deposition as well as localized heterogeneity among the lakes. Variation in pH of some of the Dorset lakes was the result of re-acidification events induced by droughts (Dillon *et al.*, 1997). The strength of these events tends to be associated with individual lake characteristics such as flushing rates and the amount of wetlands in the catchment (Yan *et al.*, 1996; Devito *et al.*, 1999). Therefore, changes in pH depend on the interaction between local lake characteristics and regional drivers. The wide range in correlation coefficients at the ELA results from the inclusion of two lakes that received experimental acid additions; i.e., localized control. When we compared the percentage of positive correlations in our study with those of Pace and Cole (2002) for the UNDERC (University of Notre Dame Environmental Research Center) lakes, we found that the temporal coherence of pH for the ELA lakes was very similar to UNDERC (27% for ELA vs. 25% for UNDERC with positive correlations) and much lower than Dorset and Sudbury (82% and 80% with positive correlations, respectively). The difference in coherence among these regions is the result of differences in the strength of the pH trend resulting from changes in regional acid deposition, indicating the role that regional differences play in determining the level of synchrony among lakes.

Studies have found that regional heterogeneity limits synchrony in temporal dynamics. Temporal coherence in water temperature (Benson *et al.*, 2000) and water chemistry (Webster *et al.*, 2000) were influenced by regional differences in climate and hydrology. For example, Webster *et al.* (2000) found that water chemistry dynamics were most similar among lakes in regions where the hydrology was similar throughout the region (spatially unstructured), such as at the ELA where hydrology is dominated by overland run-off. In areas, such as northern Wisconsin, where the hydrology was more complex and dominated by groundwater flow (spatially structured), water chemistry dynamics were influenced by spatial patterns related to landscape position and therefore synchrony among lakes was reduced. In such a heterogeneous hydrological setting, individual lake characteristics tended to drive temporal dynamics, obscuring regional climate signals. Likewise in our study, regional heterogeneity (e.g., hydrology and lake morphology) probably obscured the effects of large-scale climate signals.

Coherence in biotic variables tends to be lower than in physical and chemical variables (Magnuson *et al.*, 1990; Kratz *et al.*, 1998; Baines *et al.*, 2000). In general, it is expected that biological variables have low levels of synchrony because they are influenced by a combination of mechanisms that include species specific growth rates, species specific tolerances to stressors, nutrient dynamics, predation pressure, and other food web dynamics. These factors will be of varying importance across our lakes. For example, fish predation is a major driver of zooplankton community structure in lakes (Zaret, 1980), and could potentially have important influences on annual zooplankton richness and biomass. Although we do not have complete fish records for our study lakes, we know that the number and kind of fish species are variable across the lakes, ranging from fishless lakes to moderately diverse assemblages containing 9–10 species. We expect that high inter-annual variation in fish populations in individual lakes would play an important role in plankton dynamics, thus contributing to low coherence across lakes. Environmental stressors are also an important factor determining biotic temporal dynamics. There are several stressor gradients across our site; historic acidification (highest at Sudbury, lowest at ELA), nutrient loading (highest at Dorset, lowest at ELA), forest fires (highest at ELA, lowest at Sudbury). Variation in these stressors is likely to interact with climate and potentially modify biotic responses.

It is therefore somewhat surprising that we were able to detect some coherence in biotic variables, given the potential importance of local drivers. One possible explanation for this 'higher than expected' coherence is that some local drivers are influenced by regional climate signals. While other studies have indicated that fish populations do not tend to be synchronous (Magnuson *et al.*, 1990), preliminary studies on over 350 lakes in Ontario suggest that walleye recruitment is strongly driven by extreme climate events such as El Nino (G. Morgan, unpublished data). Large, climatically-driven recruitment events could influence plankton composition and biomass through increased predation pressure when walleye are the dominant species, or if the walleye response is representative of other northern fishes. This merits further investigation.

Climatic changes may result in biotic synchrony in subsets of lakes where local controlling factors respond to climate in a similar way. For example, Baines *et al.* (2000) found that chlorophyll a, a measure of phytoplankton biomass, was synchronous among lakes with similar thermal stratification; i.e., deep, strongly stratified lakes. In these lakes, nutrient loading, controlled by precipitation inputs may influence chlorophyll *a* levels from year to year, more so than in-lake processes. Similarly, Findlay *et al.* (2001) found strong coherence in phytoplankton richness and biomass in four lakes that were similar in morphology; small, deep, strongly stratified. Likewise, Rusak *et al.* (1999) observed synchrony in the abundance of several species of zooplankton in subsets of the Dorset lakes. Initial analyses by Rusak *et al.* (1999) indicated that, for at least one zooplankton species, changes in abundance were correlated with ENSO (El Nino/Southern Oscillation index, a regional climatic signal). Our results are consistent with these general findings. Despite low mean coherence among lakes, within subsets of similar lakes there were detectable regional signals. Further analyses that are beyond the scope of this paper are required to determine the lake characteristics and mechanisms responsible for coherent lake subsets.

Precipitation may be an important climatic driver in lake ecosystems because it influences nutrient loading, DOC inputs (Schindler *et al.*, 1996), and therefore lake productivity and water clarity. In turn, lake productivity and water clarity can have important influences on biological variables such as richness and biomass (e.g., Dodson *et al.*, 2000). We found that the biological response to precipitation, namely drought, varied among regions. At the ELA, an exceptionally dry decade (1980–89) resulted in an increase in phytoplankton richness and biomass, despite decreased nutrient inputs (Findlay *et al.*, 2001). Although previous studies have predicted decreased phytoplankton richness and biomass associated with drought (Magnuson *et al.*, 1997), the increase in richness and biomass at the ELA was associated with an increase in mixotrophic species that were able to migrate into deeper water layers with lower light, and higher nutrients, utilizing bacteria as an additional carbon source (Findlay *et al.*, 2001). In other regions (Sudbury and Dorset), drought cycles have negative impacts on phytoplankton richness through interactions with anthropogenic stressors such as acidification (Arnott *et al.*, 2001).

The interaction between stressors occurring at local and regional levels may influence coherence among lakes. Drought-driven re-acidification events have been documented in Dorset and Sudbury, areas of historic acid deposition, although the impact of acidification was much greater in Sudbury (Keller *et al.*, 1992; Yan *et al.*, 1996; Dillon *et al.*, 1997). These climate-driven re-acidification events can have important impacts on local biota (Arnott *et al.*, 2001; Arnott and Yan, 2002). Our analyses indicate that changes in pH were highly correlated with phytoplankton richness and biomass in the Sudbury area (Figure 7). For many aquatic taxa, including phytoplankton, zooplankton, macroinvertebrates, and fish, when pH decreases, sensitive species are lost (Nicholls *et al.*, 1992; Keller *et al.*, 1992; Keller and Gunn, 1995). The relationship between pH and zooplankton richness is not as strong as phytoplankton richness, primarily because of an unexpected indirect response of zooplankton in Swan Lake to a drought-induced re-acidification event (Arnott and Yan, 2002). These results emphasize the importance of considering climate effects in association with other regional and local stressors that may modify biological responses.

5. Conclusions

Can we make generalizations about the effects of climate change on aquatic ecosystems using coherence analyses? The answer depends both on the variable and the spatial scale considered. Some variables such as surface water temperature tended to be synchronous over large regions (e.g., the 1500 km span of our study sites), suggesting that regional drivers, such as climate, control year to year variation. Other variables such as pH had responses that were regionally (lake district) and locally (individual lake) dependent. We found that precipitation can influence lake pH, but this was dependent on the region (i.e., historic acid deposition) and individual lake characteristics within the region (wetlands and flushing rates). Climatic events such as drought can have important influences on biota by influencing nutrient availability (e.g., lakes at the ELA) and through interactions with additional stressors such as acidification (e.g., Swan Lake in Sudbury). Interestingly, drought produced a different response at different sites; at the ELA there was an increase in phytoplankton richness and in Swan Lake there was a decrease in phytoplankton richness.

One of the limitations in assessing climatic responses using coherence analyses is that the dominant regional drivers may vary across the landscape. At the ELA, climatic changes appeared to have an important role in determining biotic responses. In Sudbury, however, regional-scale reductions in sulphur emissions appeared to be the dominant driver of biotic responses. Therefore, determining a causal link between coherent community responses and climate may be problematic, particularly in a multiple-stressor environment.

Coherence analyses do, however, provide insights into the relative importance of regional versus within lake processes in determining community composition. We were able to find homogenous subsets of lakes where changes in the biota were similar through time. This suggests that regional-level drivers are important in determining community dynamics, but that the response to these drivers may be modified by individual lake characteristics.

Acknowledgements

Funding was provided by Environment Canada's Environmental Monitoring and Assessment Network (EMAN), the Ontario Ministry of the Environment, and NRCan's Climate Change Action Fund. The collection, analyses, and management of data were provided by D. Findlay, M. Paterson, K. Beaty, S. Kasian, K. Nicholls, B. Keller, J. Heneberry, N. Yan, P. Dillon, B. Girard, J. Binks, M. Futter... and many others at the Freshwater Institute, the Cooperative Freshwater Ecology Unit, and the Dorset Environmental Science Centre. Comments by B. Benson and T. Kratz improved the manuscript.

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