

# The Temporal Coherence of Zooplankton Population Abundances in Neighboring North-Temperate Lakes

James A. Rusak,<sup>1,\*</sup> Norman D. Yan,<sup>2,†</sup> Keith M. Somers,<sup>2,‡</sup> and Donald J. McQueen<sup>1,§</sup>

1. Department of Biology, York University, Toronto, Ontario M3J 1P3, Canada;

2. Dorset Environmental Science Centre, Ontario Ministry of the Environment, Dorset, Ontario P0A 1E0, Canada

Submitted December 19, 1997; Accepted July 14, 1998

---

**ABSTRACT:** We investigated the temporal coherence (i.e., the correlation or synchrony between time series) of annual abundances among populations of freshwater zooplankton in eight lakes in Ontario, Canada, from 1980 to 1992. We estimated temporal coherence using the intraclass correlation coefficient ( $r_i$ ). While values of  $r_i$  were relatively low among comparisons of all eight lakes, they were statistically significant for three of the seven common cladoceran and copepod taxa (*Bosmina longirostris*, *Leptodiatomus minutus*, and *Mesocyclops edax*). These significant positive correlations imply that a portion of the interannual variation in abundance was produced by factors operating on a scale larger than the individual lake catchments. Because the eight-lake analysis might obscure strong, but conflicting, patterns among lakes in the region, we identified homogeneous and temporally coherent subsets of lakes for each species using an exploratory stepwise deletion procedure. The resultant homogeneous subsets exhibited much greater temporal coherence, accounting for 47% (*Eubosmina*) to 84% (*Leptodiatomus*) of the interannual variation in abundance. Our results suggest that the factors affecting annual variation in zooplankton abundance must be sought both within lakes and beyond their watersheds.

**Keywords:** climate, temporal coherence, intraclass correlation, population regulation, pelagic zooplankton.

---

Magnuson et al. (1990) defined temporal coherence as the phenomenon of synchronous fluctuations in one or more parameters among locations within a geographic region.

\* E-mail: jrusak@yorku.ca.

† E-mail: yanno@ene.gov.on.ca.

‡ E-mail: somers@zoo.utoronto.ca.

§ E-mail: nei@island.net.

The demonstration of such synchrony for populations has theoretical and practical significance. Kratz et al. (1987) interpreted similar regional patterns of population variability as evidence that the population abundances were determined, in some manner, by year-specific factors (e.g., climate) operating on regional scales. In contrast, the absence of synchrony suggested that local-scale (or site-specific) regulators were most important. The degree of temporal coherence can therefore indicate whether populations in a region are influenced more by site-specific (intrinsic) factors or regional (extrinsic) factors, an issue that has been central to the study of temporal variation in populations (e.g., Nicholson 1933; Andrewartha and Birch 1954; Turchin 1995).

Although extrinsic factors such as climate have occasionally been acknowledged as important for controlling population abundances (e.g., Andrewartha and Birch 1954; George and Harris 1985; Sinclair et al. 1993), intrinsic regulation by density-dependent processes is currently the favored paradigm (e.g., Kerfoot and Sih 1987; Carpenter 1988; Wootton 1994; Wellborn et al. 1996). Support for this “intrinsic” view largely originates from the results of strong food-web interactions observed in short-term experiments (e.g., Brett and Goldman 1996). However, such experiments may provide false impressions of nature because of problems arising from their brevity (Taylor 1989; Tilman 1989). To counter these shortcomings, we must turn to long-term experiments or the analysis of large-scale (spatial and temporal) patterns observed in nature (Peters et al. 1991; Brown 1995; Lawton 1996). Herein, we use relatively long-term monitoring data to examine whether the annual abundances of different zooplankton populations in a suite of lakes change synchronously over time. The same analysis could be applied to animal or plant populations in any regional context.

In our study of freshwater zooplankton, we distinguish intrinsic and extrinsic factors on the basis of the lake catchment or watershed. Intrinsic factors include those physical and chemical attributes that characterize zooplankton habitat in a lake (e.g., water depth, temperature, nutrients) as well as the sum of the direct and indirect interactions with

other species (i.e., biological interactions). Extrinsic factors are those that vary on a much larger spatial scale than the watershed. These factors include density-independent climate-related phenomena.

Hairston (1988) demonstrated that the distinction between intrinsic and extrinsic factors may often be ambiguous. He ascribed annual variations in the mortality of a copepod to annual variations in fish predation, an intrinsic factor. However, on a larger scale, Hairston attributed annual variability in fish predation to interannual water-level changes in the pond—the product of large-scale weather patterns, an extrinsic factor. Hence, while the proximate cause of variable copepod mortality was intrinsic, the ultimate cause was extrinsic. When we compare a regional set of populations, Magnuson's concept of temporal coherence provides an "ultimate" estimate of the relative roles of intrinsic and extrinsic factors on the year-to-year variation in abundances. Significant temporal coherence indicates that regional factors contribute a common signal to the interannual fluctuations in abundances. However, insights about the proximate mechanisms involved in transmission of this extrinsic signal cannot emerge from the analysis.

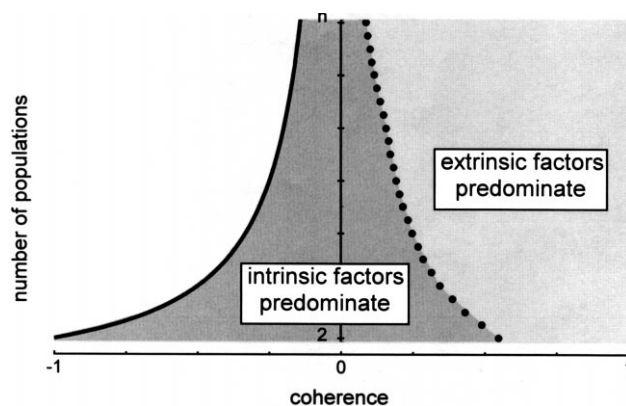
Long-term studies of individual lakes have demonstrated both extrinsic and intrinsic influences on aquatic biota. At one extreme, a 40-yr data set from Lake Windermere was used to correlate total zooplankton abundance with climatic variables, which indicated extrinsic control (George and Harris 1985; George and Taylor 1995). At the other extreme, intrinsic regulation of phytoplankton in Tuesday Lake was evident in the cyclical patterns of algal pigment concentrations that matched the life span of planktivorous fish (Carpenter and Leavitt 1991). Between these extremes, Jassby et al. (1990) reported the interacting effects of climate and food-web dynamics on interannual variation in primary production in Castle Lake. Given the range of factors implicated by these single-lake studies, multiple-lake comparisons provide an opportunity to examine the balance between intrinsic and extrinsic factors.

Magnuson et al. (1990) and Kratz et al. (1998) have completed the only multiple-lake studies of temporal coherence. Using Long-Term Ecosystem Research (LTER) data from seven lakes in Wisconsin, they found that temporal coherence in physical and chemical variables was often strong, but coherence was essentially nonexistent for biotic variables—zooplankton taxa in particular. However, the LTER lakes differed greatly in morphometry and chemistry, and this variation might obscure coherent patterns among these populations. A study of the temporal coherence of zooplankton taxa in more similar lakes is warranted.

Herein, we employ the intraclass correlation coefficient,

$r_i$  (e.g., Fisher 1936; Zar 1984), as our measure of temporal coherence. The  $r_i$  quantifies the degree of synchrony in abundance among two or more populations over time. In a two-population comparison, the intraclass correlation ranges from  $-1$  to  $+1$ , and the point where extrinsic factors are more important than intrinsic factors corresponds to the critical value of  $r_i$  (i.e., where  $P = .05$  for a statistically significant difference from 0). With more than two populations,  $r_i$  is analogous to the "average" correlation among all of the populations. Thus, the critical value and the lower limit for  $r_i$  change as more populations are added (see below). As a result, temporal coherence can be visualized as having two dimensions (fig. 1), where  $r_i$  and the number of populations ( $n$ ) are orthogonal axes that define the coherence plane. Extrinsic and intrinsic influences are balanced along a curve that joins the critical values of  $r_i$  for different numbers of populations. Because there exists the potential to find subregional patterns, this conceptualization also facilitates comparisons among species with varying numbers of temporally coherent populations and varying levels of coherence. The most regionally coherent species will be furthest from the critical value (and away from 0) and include the greatest number of populations.

We analyzed a 13-yr record of changes in the annual abundances of several common crustacean zooplankton



**Figure 1:** A conceptual diagram of coherence space. The dotted line joins the critical coherence values (at  $P = .05$ ) for comparisons involving differing numbers of populations. The line divides the plane into areas where intrinsic and extrinsic factors predominate. Species to the right of this curve have their abundances determined by extrinsic factors, while species to the left are predominately intrinsically regulated. The solid line joins points that delineate the lower limit of negative coherence values for different numbers of populations. In an  $n$ -lake comparison, the minimum possible coherence value is  $-1/(n - 1)$  because of the correction that must be made to the lower limit of a correlation coefficient when more than two variables are involved (Zar 1984). Values to the left of this line are not possible.

species in eight neighboring lakes in south-central Ontario, Canada. Our first objective was to quantify the temporal coherence of common zooplankton taxa across all eight lakes. The extrinsic factors responsible for any such coherence will be examined in a later article. Our second objective was to search for temporally coherent patterns in subsets of the eight lakes. This approach explores the nature of temporal coherence for individual zooplankton taxa and ensures that strong patterns among subsets of lakes, that may have been obscured in a regional setting, were not missed. Our third objective was to investigate whether individual species differed in their temporal coherence, as might be predicted by differences in generation time (e.g., Kratz et al. 1987).

## Methods

### *Study Area*

Eight lakes in south-central Ontario, Canada, within 50 km to the south and west of the Dorset Environmental Science Centre, were sampled from 1978 to 1992. These are small (<100 ha), soft water (23–34  $\mu\text{S}/\text{cm}$ ), nutrient-poor lakes in forested watersheds underlain by the Precambrian shield (table 1). Seven of the lakes are headwater lakes, with the exception of Red Chalk Lake, which is downstream of Blue Chalk Lake. Six lakes are dimictic, with the exception of Dickie Lake, which stratifies weakly, and Heney Lake, which does not stratify (Dillon et al. 1993). The lakes vary in their sensitivity to acid deposition; Gran alkalinity ranges from 9.6  $\mu\text{eq}/\text{L}$  in Plastic Lake to 86.0  $\mu\text{eq}/\text{L}$  in Blue Chalk Lake (Dillon and Molot 1996; P. Dillon, unpublished data). The lakes also differ substantially in the abundance of the phantom midge, *Chaoborus* (table 1), the most common macroinvertebrate zooplankton predator in temperate lakes (Yan et al. 1991).

A climatic exposure index (lake area to mean depth,

which is equivalent to  $\text{area}^2/\text{volume}$ ) was one of the primary criteria used by Magnuson et al. (1990) to distinguish lakes. Less than an order of magnitude separated the climatic exposure extremes in our lakes (table 1). In contrast, this index differed by more than two orders of magnitude among the LTER lakes (Magnuson et al. 1990).

Overlain on this among-lake variability was considerable among-year variation in climate (table 2). During the 13 study years, there were three El Niño events (1983, 1987, and 1992), the first two of which produced hot, dry summers in central Ontario (Dillon et al. 1997). The effects of the 1992 El Niño were apparently overridden by the eruption of Mount Pinatubo in 1991. This volcanic eruption contributed to cooler and wetter summer weather across much of North America (Thompson 1995). These global phenomena have local implications. For example, Dillon et al. (1997) demonstrated that the summer droughts in El Niño years have delayed the recovery of Plastic Lake from acidification as falling water tables led to sulfur oxidation and acid generation in wetlands in the lake's catchment.

### *Sampling Design and Data Preparation*

Zooplankton samples were taken monthly throughout the ice-free season at a single station located over the deepest spot in each lake (Yan et al. 1996). A single station provides an accurate estimate of mean open-water zooplankton biomass on an annual basis in these lakes (Yan 1986). Each sample was a composite of three to seven vertical hauls taken from fixed depths to the lake's surface with an 80- $\mu\text{m}$  mesh, conical, metered net (McQueen and Yan 1993). The depths of each vertical haul were chosen so that the various lake strata contributed to the composite sample in proportion to their respective volumes (Girard and Reid 1990). Samples were preserved in a 6% sucrose-formalin

Table 1: Selected physical, chemical, and biological attributes of the study lakes

Lake	Northern latitude	Western longitude	$A_0$ (ha)	$Z_{\text{max}}$ (m)	$A_0/z$ (m)	$t$ (yr)	Secchi (m)	pH	$TP$ ( $\mu\text{g}/\text{L}$ )	<i>Chaoborus</i> (number/ $\text{m}^3$ )
Blue Chalk	45°12'	78°56'	52.4	23.0	6.2	4.0	6.4	6.7	5.9	8.0
Chub	45°13'	78°59'	34.4	27.0	3.9	1.9	3.5	5.7	9.9	133.2
Crosson	45°05'	79°02'	56.7	25.0	6.2	1.5	3.7	5.7	10.5	8.6
Dickie	45°09'	79°05'	93.6	12.0	18.7	1.5	2.7	5.8	10.2	65.1
Harp	45°23'	79°07'	71.4	37.5	5.8	2.9	4.0	6.6	7.1	.1
Heney	45°08'	79°06'	21.4	5.8	6.5	1.2	4.7	5.8	6.7	.3
Plastic	45°11'	78°50'	32.1	16.3	4.1	3.0	7.6	5.6	5.6	58.8
Red Chalk	45°11'	78°56'	44.1	38.0	2.6	2.4	6.6	6.5	4.9	.2

Note:  $A_0$  = lake area,  $Z_{\text{max}}$  = maximum depth,  $A_0/z$  = area/mean depth (climatic exposure index; Magnuson et al. 1990),  $t$  = water residence time, Secchi = mean Secchi disk depth during summer stratification, and  $TP$  = long-term mean annual whole-lake total phosphorus (Yan et al. 1985; Dillon et al. 1993; Dillon and Molot 1996). Secchi, pH, and  $TP$ -values are ice-free means of volume-weighted samples. *Chaoborus* abundance is calculated as mean density, weighted by lake area and volume, from a fall sampling of 10 stations (Pawson and McEachern 1987).

**Table 2:** Selected meteorological attributes and the number of monthly zooplankton samples for each year in the data set

Year	Months included	ENSO index <sup>a</sup>	Mean ice-out date	Mean wind speed (m/s)	Total precipitation (mm)	Mean air temperature (°C)
1980	6	-2.9	April 21	1.37	567.7	15.1
1981	7	-3.6	April 4	1.32	535.3	15.2
1982	6	1.2	April 29	1.22	506.4	15.5
1983	6	-20.4	April 20	1.37	450.5	16.0
1984	6	-.2	April 17	1.41	492.8	14.7
1985	6	-.1	April 25	1.35	641.1	14.8
1986	7	-1.6	April 13	1.19	608.6	14.9
1987	7	-7.6	April 13	1.22	341.9	16.3
1988	6	-2.5	April 16	1.33	440.9	16.1
1989	6	8.0	May 1	1.07	396.9	15.7
1990	6	-4.3	April 26	.95	429.5	15.0
1991	7	-2	April 20	1.04	480.1	16.2
1992	6	-12.4	May 1	1.15	491.4	13.8

Note: Wind speed, precipitation, and air temperature are summer values (May–September inclusive) estimated from daily readings provided by the Atmospheric Environment Service weather station of Environment Canada at Muskoka Airport, Bracebridge, Ontario.

<sup>a</sup> The El Niño–Southern Oscillation (ENSO) index represents the 6-mo (October–March) mean of unstandardized monthly sea-level air pressure differences between Darwin, Australia, and Tahiti. The annual value is applied to the year represented by the January–March data (National Oceanic and Atmospheric Administration data: <http://www.pmel.noaa.gov/toga-tao/el-nino/>). Large negative values indicate the potential for strong El Niño effects at northern latitudes during that year.

solution. A minimum of 250 crustacean zooplankton were identified, measured, and counted from a series of subsamples with volumes that were adjusted to be inversely proportional to the abundance of taxa in the sample (Allen et al. 1994). Cladocera and the mature Copepoda were identified to species. Immature Copepoda were identified to suborder but are not used herein.

Species were included in our data set if the annual sum of their monthly counts was greater than or equal to 10 individuals and if they were found in all of the eight lakes over the 13 yr. We then removed species that had abundances of 0 in more than two of the eight lakes in any given year. Of the eight common species initially identified, only *Daphnia galeata mendotae* was removed to satisfy this latter criterion. The final data set included the cladocerans *Holopedium gibberum*, *Bosmina longirostris*, *Eubosmina tubicen*, and *Diaphanosoma birgei*; the cyclopoids *Mesocyclops edax* and *Tropocyclops extensus*; and the calanoid *Leptodiaptomus minutus*. *Tropocyclops extensus* is the renamed *Tropocyclops prasinus mexicanus* (Dussart and Fernando 1990).

Although most of the eight lakes have been sampled since 1978, we chose to begin this study in 1980 because this was the first year that all of the lakes were sampled concurrently and samples were identified and counted according to the same protocol by the same technician. For each year, we ensured that the number of samples from each lake was identical, but this number was allowed to vary among years in accordance with the length of the ice-

free season (table 2). Because of our desire to work with equivalent sample sizes among lakes in a given year, the occasional missing monthly sample necessitated the estimation of a monthly abundance for a total of 12 samples of the 656 possible samples (i.e., 1.8%). To make this estimate, we duplicated the sample taken nearest (in time) to the missing monthly data for a given lake. In only one instance did this involve more than a single estimate within a given year (two monthly estimates were used for Red Chalk Lake in 1989). In addition, no 1982 data were available for Heney Lake. To avoid complications associated with missing data, we estimated abundances for this single lake-year by averaging the observed abundances in 1981 and 1983. These annual sums of monthly samples for each species were the data we then analyzed.

#### Statistical Approach

We used the intraclass correlation coefficient ( $r_i$ ; e.g., Fisher 1936; Zar 1984) to estimate temporal coherence. This metric has three advantages over the more traditional Pearson's correlation ( $r$ ). First,  $r_i$  is not restricted to pairwise comparisons but can simultaneously estimate the relationship between  $n$  sets of time series data. Second, it is the recommended method when it is impossible to designate dependent and independent series in a pairwise comparison (Zar 1984). Finally, because  $r_i$  is an estimate of the among-year variance component (Haggard 1958),

the intraclass correlation can be obtained from an ANOVA table and any missing data can be accommodated.

In an  $n$ -lake comparison, the intraclass correlation coefficient was estimated as

$$r_i = \frac{MS_Y - MS_E}{MS_Y + (n - 1)MS_E},$$

where  $MS_Y$  and  $MS_E$  are the mean squares for years and error from a two-way ANOVA without replication (Haggard 1958; Somers et al. 1996). By utilizing a two-way ANOVA, we factored out a component of variation that may confound the analysis, namely, variation due to differences among lakes. When used in this way,  $r_i$  quantifies synchrony in zooplankton abundances over time, excluding any variation due to differences in means among lakes. When population fluctuations in different lakes are increasingly synchronous, the  $MS_E$  term from the two-way ANOVA approaches 0 and  $r_i$  approaches 1. Conversely, with increasingly dissimilar fluctuations among lakes, the variance apportioned to the error term (which includes the interaction term given no replication) will increase until greater than the  $MS_Y$  (in essence, there is more variability within years than among years), and the correlation will become negative. Because of this relationship, the intraclass correlation can only fall to  $-1$  when  $n = 2$ , otherwise its theoretical lower limit is  $-1/(n - 1)$  (see Zar 1984 for further details).

The intraclass correlation assumes samples are drawn from normal distributions with equal variances (Zar 1984). While the "lake" factor in the two-way design removes variation due to differences among lake means, it does nothing to equalize variance among lakes. To ensure that large differences in zooplankton variance did not unduly influence our estimate of coherence, we standardized our annual counts to unit variance, following Somers et al. (1996). When the data are transformed to  $z$ -scores (i.e., a mean of 0 and a standard deviation of 1), the resultant intraclass correlation is equivalent to the mean Pearson correlation for all pairwise, between-lake comparisons (Haggard 1958). Coherence values obtained after this standardization measure the "parallel" or synchronous nature of year-to-year changes in abundance, irrespective of whether there are long-term trends or not.

Because variation in abundances typically scales as a function of the mean, we initially analyzed both raw and  $\log_{10}(x + 1)$ -transformed data to examine differences between these measures. We also used a Levene's test to examine the homogeneity of the residuals from these two analyses.

To look for coherent patterns among lakes, we tested the null hypothesis  $r_i = 0$ . Given our modest number of data points (i.e., years) and the initial nonrandom selection

of study lakes, we tested the null hypothesis with a randomization test (e.g., Manly 1991). After calculating the observed  $r_i$  for a given species, we randomly permuted abundances among years within each lake and calculated coherence values for 999 random reshuffles of the data. To determine the level of significance ( $P$ ), we counted the number of randomly generated coherence values that were greater than (less than for negative  $r_i$ ) or equal to the observed coherence value and divided this sum by 1,000 (i.e., 999 times plus the observed value; Manly 1991). These  $P$ -values were deemed significant using the Bonferroni inequality ( $P = .05/7 = .007$ , as there were seven species).

Like other correlation and regression parameters,  $r_i$  may be unduly influenced by outliers. We quantified the influence of each individual year on our estimate of coherence by recalculating the intraclass correlation obtained when that particular year was deleted from the matrix (Girau-deau et al. 1996).

Because opposing patterns among different lakes might obscure synchrony in smaller subsets of the eight lakes, we examined the pairwise, between-lake coherence matrix for each species following Brien et al. (1984). This methodology exposes structure in a correlation matrix in four sequential steps. It first tests for the homogeneity of the entire correlation matrix, that is,  $H_{01}$ , all correlations are equal. If heterogeneity is detected, its source is then sought with null hypotheses of  $H_{02}$ , no interaction between rows and columns, and  $H_{03}$ , row (or column) means are equal. Last, this technique tests  $H_{04}$ , the grand mean of the correlation matrix equals 0.

To further explore the results of this coherence-matrix analysis, we deleted lakes from the full correlation matrix until a subset of the eight-lake matrix remained that was both homogeneous (accepting  $H_0$ 's 1–3) and coherent (rejecting  $H_{04}$ ). To achieve this goal, we first tested for homogeneity. If any of  $H_0$ 's 1–3 were rejected ( $P < .05$ ), we deleted the lake with the lowest mean correlation and then recalculated the matrix. Lakes were sequentially deleted until we were able to accept all three homogeneity hypotheses. We then tested for significant coherence ( $P < .05$ ) via  $H_{04}$  and continued to delete lakes with the lowest mean correlation if this hypothesis was accepted. Rejection of  $H_{04}$  identified the homogeneous and most strongly correlated subset of the original eight-lake matrix. While this procedure relies on levels of significance to derive homogeneous subsets, it is, in essence, an exploratory approach to matrix decomposition. As a result of this exploration, we were able to position each species in a conceptual temporal coherence space (fig. 1).

Coherence values summarize the synchronous nature of fluctuations in interannual abundances but do not illustrate the underlying patterns. Hence we plotted ( $z$ -score

transformed) species abundances for individual lakes over time to characterize patterns among lakes and identify atypical years within a given series.

### Results

The common and ubiquitous species that were retained for analysis had representatives from both cladocerans and copepods (table 3). The cladocerans included both large (*Holopedium gibberum*) and small (*Bosmina longirostris*, *Diaphanosoma birgei*, *Eubosmina tubicen*) herbivorous species, while the copepods included both a large predaceous (*Mesocyclops edax*) and a small omnivorous (*Tropocyclops extensus*) cyclopoid and a herbivorous calanoid (*Leptodiaptomus minutus*). Together, these seven species composed 74% of the total annual counts for all cladocerans and adult copepods (immature copepods were not included). *Leptodiaptomus* was the most abundant of these species, making up 27% of the total count for all adult crustacean zooplankton. The annual sums of individual species ranged widely, both within and among lakes. For a given species, the ratio of maximum to minimum mean abundance spanned almost two orders of magnitude, while the same ratio for mean variance spanned more than two orders of magnitude.

Analyses of log-transformed and raw data provided similar results (table 4). Using raw data, we observed significant temporal coherence among all eight lakes for *Bosmina*, *Leptodiaptomus*, and *Mesocyclops*; the pattern for *Holopedium* was significant at  $P < .05$  but not at the significance level dictated by the Bonferroni inequality (table 4). As expected, interspecific differences were apparent. With logged data, *Leptodiaptomus* was the only species significant with a Bonferroni-corrected  $P < .007$ , but *Bosmina*, *Holopedium*, and *Mesocyclops* were all significant at a  $P < .05$ . None of the remaining three species produced coherence values that approached significance in either analysis. The largest difference in  $r_i$  between the analyses occurred for *Leptodiaptomus*. The log transformation in-

creased its coherence. The residuals from analyses of both data sets were homogeneous for all species (table 4). For simplicity, results that follow are from analyses of the raw data.

Plots of the multilake time series (standardized raw data) were useful visual aids (fig. 2). Because temporal coherence estimates the “parallel” nature of among-lake patterns, it can be helpful to note the number of times temporal profiles cross when attempting to interpret a particular  $r_i$ . The plot of *E. tubicen*, a temporally “incoherent” species (fig. 2A), exhibits many line crosses. In contrast, *L. minutus* displayed synchronous behavior over time across many of the lakes (fig. 2B). However, for the two other species with significant eight-lake coherence (*B. longirostris* and *M. edax*), overall patterns do not appear synchronous (fig. 2C, 2D). Rather, influential points, generated by exceedingly large abundances in several lakes in 1980 (followed by a subsequent decrease in 1981), appear to contribute unduly to the significant intraclass correlations. Indeed, the removal of 1980 drops the  $r_i$  for *Mesocyclops* to  $-0.003$ , while sequentially deleting each other year in turn only decreased the correlation to a minimum of 0.16 (fig. 3A). The values for *Bosmina* were similar although not as extreme. Temporal coherence fell to 0.08 when 1980 was deleted and to a minimum of 0.17 when any other year was omitted from the series (fig. 3B). The influence exerted by this single year was disproportionate when the complete temporal record was considered. In contrast to *Mesocyclops* and *Bosmina*, the  $r_i$  value for *Leptodiaptomus* increased when 1980 was deleted (fig. 3C).

Despite the observation of significant temporal coherence for several species across all lakes, most of the variance remained unexplained. Only 20% of the temporal variation in the data was explained for *Mesocyclops*, the most coherent species. Our attempts to reduce this heterogeneity by deriving both homogeneous and coherent subsets of lakes produced different results for each species (table 5). The *M. edax* subset was the largest, consisting of five lakes. Among-year variation accounted for 57% of the variance

**Table 3:** Descriptive statistics of the lake  $\times$  year matrices for the selected zooplankton species

Species	$a_{ij \text{ min}}$	$a_{ij \text{ max}}$	$\bar{k}_{\text{max}}/\bar{k}_{\text{min}}$	$\sigma_k^2 \text{ max}/\sigma_k^2 \text{ min}$	$\bar{a}_{ij}$	$\sigma_{a_{ij}}$
<i>Bosmina longirostris</i>	0	5,437.0	36	11,1267	213.1	634.7
<i>Diaphanosoma birgei</i>	0	4,080.0	16	5,313	94.8	398.5
<i>Eubosmina tubicen</i>	0	1,061.8	305	25,060	128.4	184.6
<i>Holopedium gibberum</i>	0	639.0	6	168	75.9	95.0
<i>Leptodiaptomus minutus</i>	29.0	3,147.3	10	192	372.1	530.0
<i>Mesocyclops edax</i>	1.0	274.0	12	223	36.2	39.4
<i>Tropocyclops extensus</i>	1.0	4,808.0	49	44,447	102.7	475.2

Note: The data populating the matrices are annual counts ( $a_{ij}$ ) for each species.  $\bar{k}$  = the mean of all counts for a given lake, and  $\sigma_k^2$  = variance of all counts for a given lake.

**Table 4:** Eight-lake intraclass correlation coefficients ( $r_i$ ) and their associated significance levels for standardized raw and  $\log_{10}(x + 1)$ -transformed data

Species	Raw data				$\log_{10}(x + 1)$ data			
	$r_i$	$P$	$F_{\text{residual}}$	$P_{\text{residual}}$	$r_{i(\log)}$	$P_{(\log)}$	$F_{\text{residual}}$	$P_{\text{residual}}$
<i>Bosmina longirostris</i>	.199	.006	.404	.898	.138	.024	1.252	.283
<i>Diaphanosoma birgei</i>	.028	.277	.915	.498	.018	.347	.322	.942
<i>Eubosmina tubicen</i>	.030	.261	.042	.999	-.003	.547	.229	.978
<i>Holopedium gibberum</i>	.143	.022	1.066	.391	.140	.012	1.086	.378
<i>Leptodiptomus minutus</i>	.181	.007	.312	.947	.257	.002	.659	.706
<i>Mesocyclops edax</i>	.201	.004	1.978	.066	.149	.017	1.667	.126
<i>Tropocyclops extensus</i>	-.016	.430	.627	.732	-.029	.300	.659	.706

Note: The  $F$  ratio and its associated  $P$  value test the homogeneity of the residuals arising from the analysis of each data set.

in this subset. Smaller subsets of lakes were identified for *L. minutus* and *H. gibberum*, but these patterns accounted for a larger proportion of the variation (approximately 85%). Lake membership in subsets typically differed among species, although Crosson (in four of the six subsets), Blue Chalk, Chub, and Heney (each in three of six subsets) Lakes were most often included in the subsets. Dickie Lake was unique. It was never a member of any homogeneous coherent subset.

The decomposition of the eight-lake matrix reduced the problem of influential years but did not eliminate it (fig. 4). *Leptodiptomus minutus* and *H. gibberum* were not affected by 1980 (although 1992 had a similar influence on *Holopedium*), but the temporal trajectories of *B. longirostris*, *D. birgei*, *M. edax*, and *T. extensus* were strongly influenced by 1980. The three-lake coherence observed for *L. minutus* is thus unique among the homogeneous subsets in its absence of influential years (the sequential deletion of years decreased the intraclass correlation to a minimum of 0.79). This temporal coherence is apparent notwithstanding the relatively large fluctuations in annual abundances (fig. 4).

When portrayed in the two-dimensional space spanning the range of temporal coherence values, the homogeneous subsets for many species indicated some degree of extrinsic influence on interannual abundances (i.e., observed coherence above the critical coherence value at  $P = .05$ ; fig. 5). That most species subsets fell in the extrinsic area of this space is not surprising. The homogeneous and coherent subset for a given species represents a distillation of the eight-lake data set into the strongest temporally coherent subset in the largest number of lakes. Thus, our protocol actively sought subsets that were significantly coherent. However, this search is not a self-fulfilling prophecy (e.g., see *Eubosmina*) but rather a necessary step in investigating the prevalence of climatic impacts on lake ecosystems.

## Discussion

Given what appears to be the first documentation of a regionally coherent pattern of zooplankton abundance for *Leptodiptomus minutus*—numerically, the most important zooplankton in Precambrian shield lakes—our first task must be to ensure that this result is real. Because of our small sample size and nonrandom selection of lakes, we relied on a randomization test to evaluate the significance of the intraclass correlation in our eight-lake comparisons. The randomization approach is an appropriate technique given our potential violations of standard parametric assumptions (Manly 1991).

Temporal coherence could also reflect autocorrelation among time series. Significant lag-one autocorrelation in a time series can be made up of trend, where increases follow increases, or drift, where high and low values occur in sequence (Norman and Streiner 1986). Both autocorrelated trend and drift might influence coherence estimates among lakes, either obscuring or enhancing the patterns we wish to detect. For example, if a single time series was changing monotonically because of a lake-specific disturbance, temporal patterns in common with other lakes could be obscured. Alternatively, lag-one autocorrelation in stationary time series among lakes might be a pattern generated by regional factors and worthy of investigation. We tested for significant lag-one autocorrelation in each species  $\times$  lake time series combination using the Box-Ljung  $Q$ -statistic (StatSoft 1997). Six of 56 time series revealed significant autocorrelation (at  $P < .05$ ), affecting three different species. In five of these lakes, the autocorrelation was due to a significant linear trend. We removed these trends and analyzed the residuals from the regression of species abundance against time in place of the original lake time series. The eight-lake intraclass correlations derived from this residual analysis were essentially unchanged ( $r_i$  *Bosmina*, removal of Heney Lake trend = 0.25 [an increase of 0.05];  $r_i$  *Holopedium*, removal of Dickie and Red

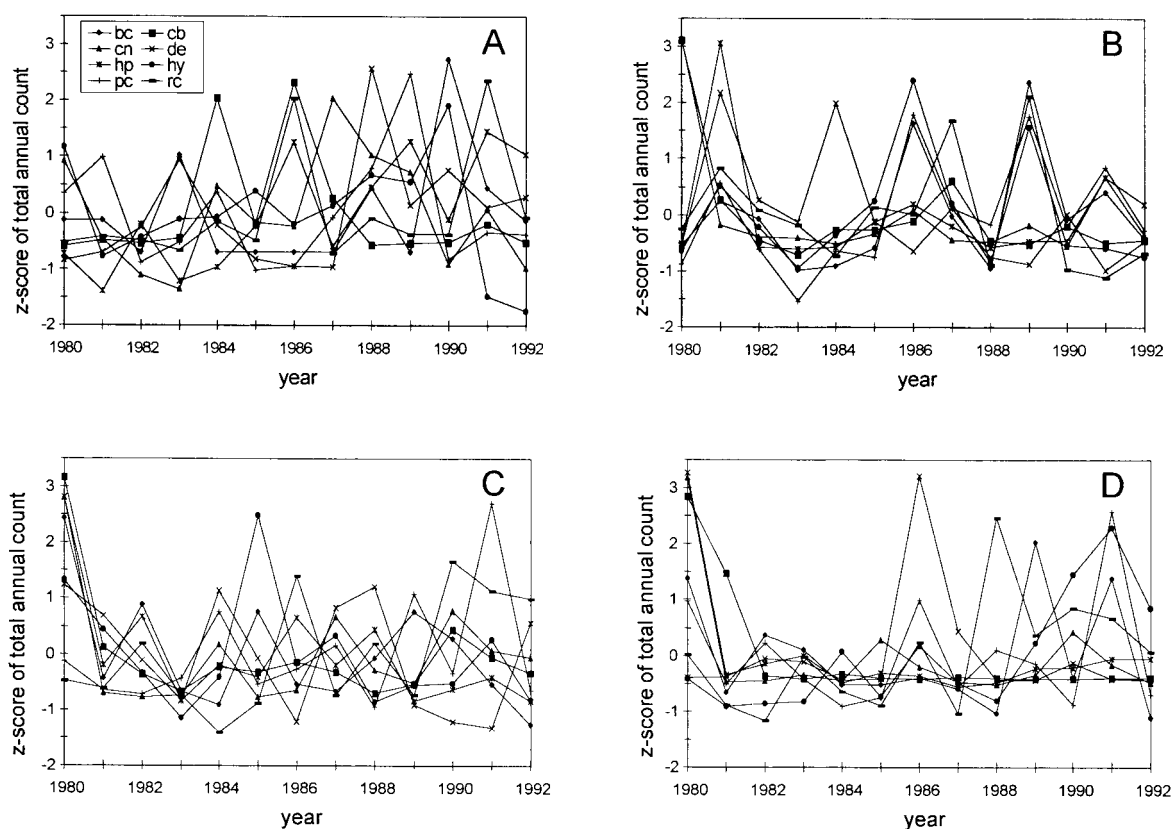


Figure 2: Long-term changes in standardized abundances of (A) *Eubosmina tubicen*, (B) *Leptodiptomus minutus*, (C) *Mesocyclops edax*, and (D) *Bosmina longirostris* in the eight study lakes. Annual abundances were estimated as the sum of monthly counts (6 or 7 mo/yr depending on the length of the ice-free season). The annual abundances in Heney Lake for 1982 were estimated as the mean of 1981 and 1983 counts. The lakes are abbreviated as *bc*, Blue Chalk; *cb*, Chub; *cn*, Crosson; *de*, Dickie; *hp*, Harp; *hy*, Heney; *pc*, Plastic; and *rc*, Red Chalk.

Chalk trends = 0.12 [a decrease of 0.02]; and  $r_i$  *Diaphanosoma* removal of Blue Chalk and Chub trends = 0.05 [a decrease of 0.02]). As a result, we concluded that temporal autocorrelation was not responsible for unduly inflating or reducing our coherence estimates and that our ability to detect significant temporal coherence was not compromised by simple lag-one autocorrelations.

While several investigators have examined long-term patterns in zooplankton in multiple lakes (Schindler et al. 1985; Kratz et al. 1987; Walters et al. 1990; Stemberger et al. 1996), the only previous analyses of the temporal coherence of zooplankton abundance per se are those of Magnuson et al. (1990) and Kratz et al. (1998). Magnuson et al. (1990) did not find coherent patterns between 1982 and 1988 for any of the biological variables they studied in their seven LTER lakes. *Leptodora* and *Chaoborus* were the two species of zooplankton considered. That analysis has since been enlarged to include aggregates of cladoc-

eran, copepod, and rotifer species and extended to include a longer time span (1982–1994), but the results were similar (Kratz et al., 1998).

Given the range in  $r_i$  values that we observed among species, it seems unlikely that our contrasting results depend on our choice of taxa. However, differences could arise from the use of aggregated taxa. When we aggregated taxa into total cladoceran and adult copepod groups, coherence remained high ( $r_i$  Cladocera = 0.12,  $r_i$  Copepoda = 0.19) when compared with LTER aggregates ( $\bar{r}_{\text{Cladocera}} = 0.07$ ,  $\bar{r}_{\text{Copepoda}} = 0.00$ ; Magnuson et al. 1990).

The observed differences between the LTER lakes and our lakes were not attributable to the time period studied. The Magnuson et al. (1990) data spanned a subset of our time period. When we reanalyzed our data using the same 1982–1988 period, our eight-lake  $r_i$  *Leptodiptomus* increased to 0.39, and its three-lake homogeneous subset to 0.91, thus enhancing the difference between the two studies. Because

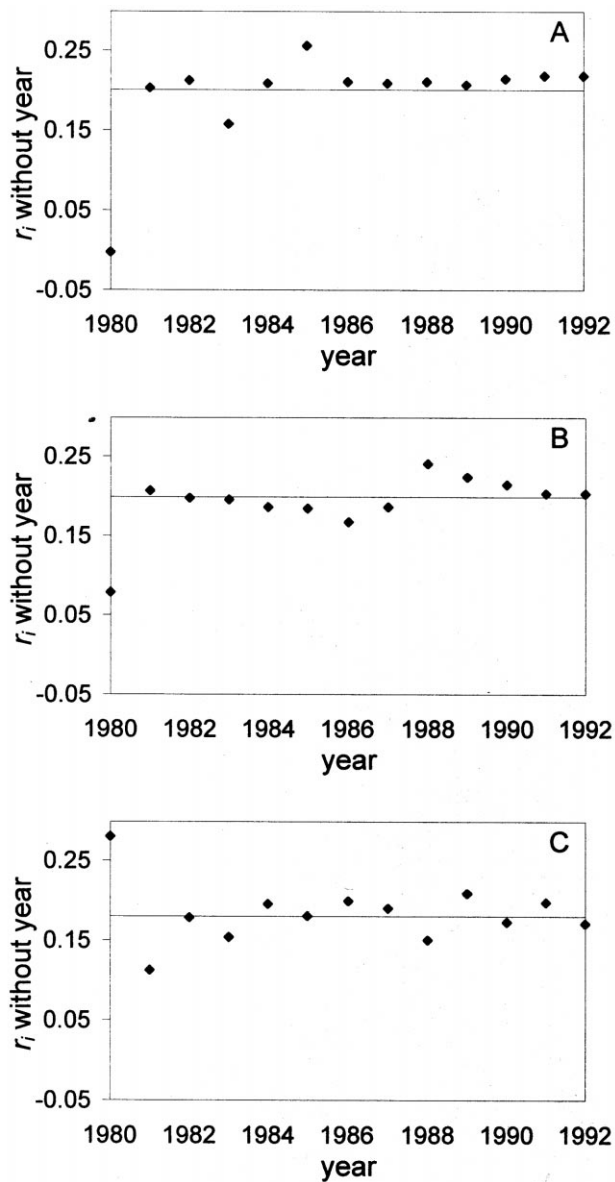


Figure 3: Influence of individual years on coherence of (A) *Mesocyclops edax*, (B) *Bosmina longirostris*, and (C) *Leptodiptomus minutus* in the eight-lake data set.

of the 11-yr overlap between our data and those analyzed by Kratz et al. (1998), it is unlikely that two additional years would have much effect on among-region comparisons of temporal coherence.

We believe that the discrepancy between these two sets of results stems from differences in the two sets of study lakes. The LTER lakes differ in area and climatic exposure by over two orders of magnitude and in maximum depth by one order of magnitude. Our lakes were generally

smaller, differing by only a factor of five in area and climatic exposure and approximately sevenfold in maximum depth. Surprisingly, we observed coherence in lakes at the lowest end of the climatic exposure scale. Magnuson et al. (1990) predicted that these lakes would be least affected by a changing climate. While it may seem intuitive that small deep lakes should be less affected by variations in climate than large shallow lakes, a recent study has provided conflicting evidence. Fee et al. (1996) predicted that, under an atmospheric doubling of  $\text{CO}_2$ , transparency increases would cause deeper epilimnia in small lakes ( $A_0 < 500$  ha), but large lakes would be unaffected. Similarly, Goldman et al. (1989) showed that El Niño events were associated with extreme values of annual primary production in Castle Lake ( $A_0 = 20$  ha,  $z = 11.4$  m) but not in Lake Tahoe ( $A_0 = 50,100$  ha,  $z = 313$  m). Clearly, the relationship between the effect of climate and lake size is not the simple positive correlation predicted by the climatic exposure index.

Instead of the LTER lakes being too dissimilar, the converse is also possible; our lakes might be so similar in intrinsic attributes that synchrony might be expected. Given the large differences in *Chaoborus* abundance and thermal regimes observed in our lakes, it is clear that our observation of coherence is not a product of the absence of variance in intrinsic factors. For temporally coherent species, the effect of extrinsic factors may be large, so large, in fact, that even strong experimental manipulations, whether pulse or press (sensu Bender et al. 1984), can be dampened. For example, Walters et al. (1990) recorded abundances of *Holopedium* and *Daphnia* in four oligotrophic lakes subjected to fish introductions, fertilization, and zooplankton harvesting over the course of 10 yr. These manipulations did not alter among-lake patterns for annual rates of spring increase in plankton abundances. Similarly, the annual patterns of zooplankton abundance in acidic Bowland Lake in Ontario paralleled those in two of

Table 5: Homogeneous coherent subsets extracted from the eight-lake data set

Species	$n$	Lake membership	$r_i$	$P$
<i>Bosmina longirostris</i>	2	cn, hp	.948	<.001
<i>Diaphanosoma birgei</i>	4	cb, cn, hp, rc	.455	<.001
<i>Eubosmina tubicen</i> <sup>a</sup>	2	cn, pc	.471	.105
<i>Holopedium gibberum</i>	3	bc, hy, rc	.837	<.001
<i>Leptodiptomus minutus</i>	3	bc, hy, pc	.850	<.001
<i>Mesocyclops edax</i>	5	bc, cb, cn, hp, hy	.574	<.001
<i>Tropocyclops extensus</i>	2	cb, cn	.926	<.001

Note:  $P$  is the significance value from the test of  $H_{0i}$ , the grand mean of the matrix equals 0 (Brien et al. 1984). Lake abbreviations are provided in the legend to fig. 2.

<sup>a</sup> A significant result was not obtained, and the last two lakes are listed.

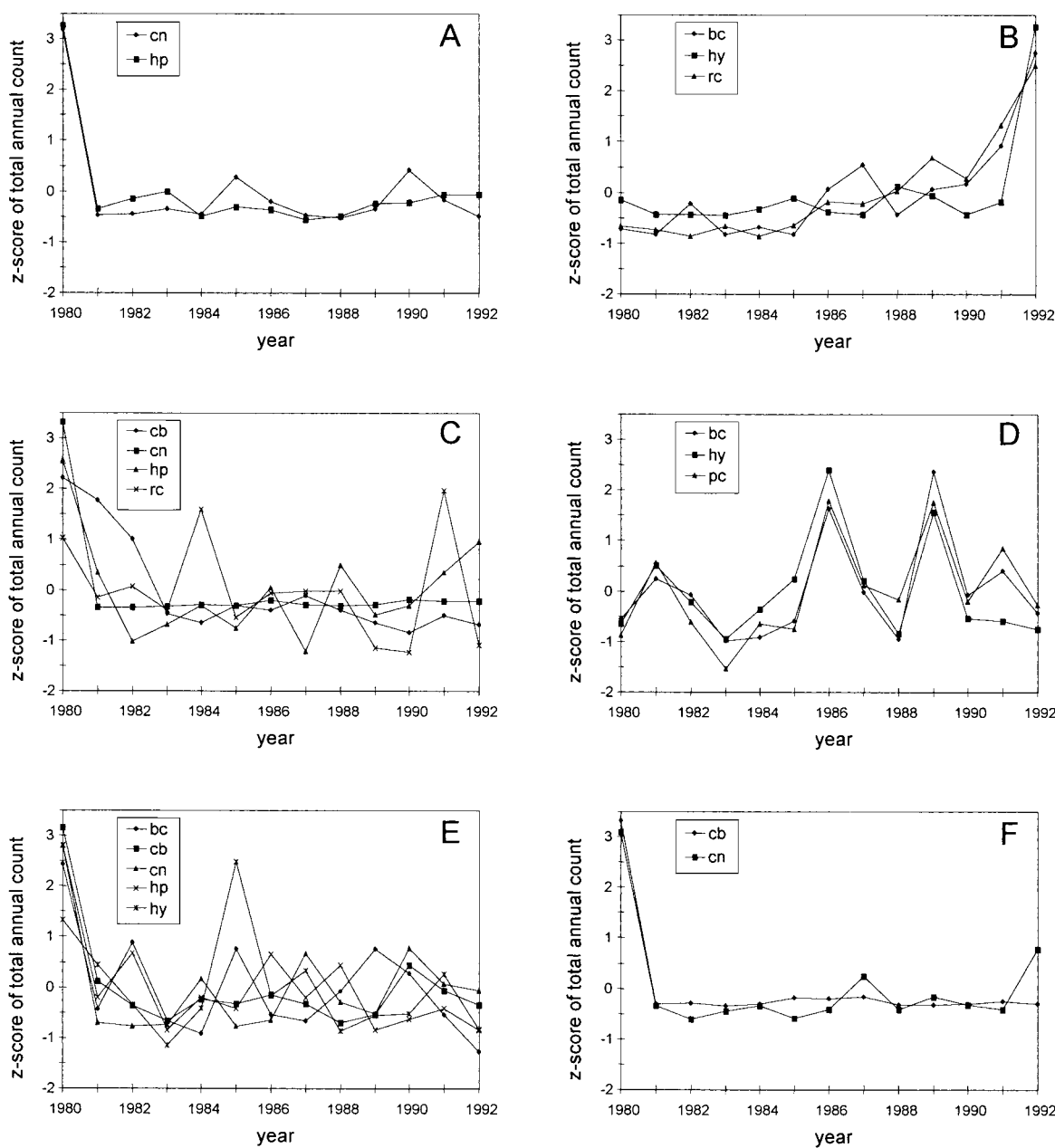
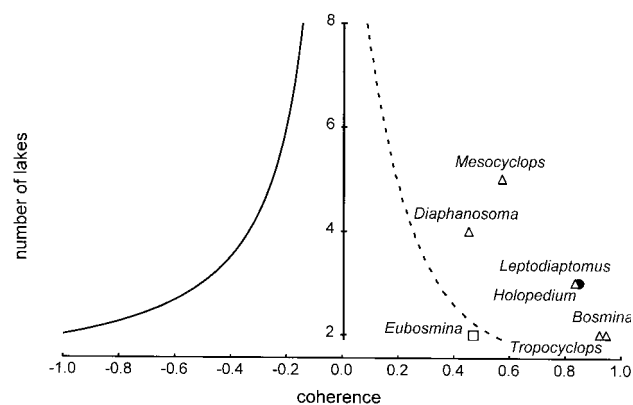


Figure 4: Long-term changes in standardized abundances of populations belonging to homogeneous subsets of (A) *Bosmina longirostris*, (B) *Holopedium gibberum*, (C) *Diaphanosoma birgei*, (D) *Leptodiaptomus minutus*, (E) *Mesocyclops edax*, and (F) *Tropocyclops extensus*.

three unmanipulated reference lakes over a 7-yr period with two El Niño years, 1983 and 1987, despite its experimental neutralization (the pH was raised from 5.0 to 6.5; Keller et al. 1992). In our study, one of the lakes in the temporally coherent *Leptodiaptomus* subset was Plastic Lake, a lake that underwent gradual acidification from the late 1970s to the mid-1980s (Dillon et al. 1987). By con-

trast, the pH of Blue Chalk and Heney Lakes, the other two members of the subset, has remained relatively stable.

Our analyses indicated that different species vary substantially in their degree of temporal coherence. Individual species ranged from those displaying no coherent behavior across all eight lakes (*Eubosmina*) to those that were highly coherent (*Leptodiaptomus*). That species differed comes as



**Figure 5:** Homogeneous subsets of common zooplankton species plotted in coherence space. Both the open triangles and solid circle identify species for which a significant correlation was observed, but only the latter was unaffected by influential years. The open square identifies a species that was not significantly coherent. The critical values of  $r_i$  used to explore coherence in species subsets were obtained from the test of  $H_{0a}$ , the grand mean of the matrix equals 0 (Brien et al. 1984) at  $P = .05$ .

no surprise, but the range of values was noteworthy, especially when the homogeneous subsets were examined. Patterns in coherent subsets of *Eubosmina* (two lakes) and *Leptodiatomus* (three lakes) explained 47% and 85% of the temporal variation respectively, a range that spans the intrinsic and extrinsic portions of the coherence space (fig. 5). Woiwod and Hanski (1992) similarly report large differences in density-dependent behavior among insect species.

Lake membership in the homogeneous subsets differed among species. Chub, Blue Chalk, and Heney were the lakes most frequently found in the homogeneous and coherent subsets, but their individual characteristics suggest little in common (table 1). This indicates that within-lake attributes with the potential to filter regional forces may also vary among species.

Our results have implications for the duration, design, and interpretation of whole-lake experiments. First, our results provide additional evidence (see Tilman 1989) for conducting whole-lake experiments over a relatively long period of time. Short-duration experiments risk missing the emergence of treatment effects from regionally coherent ephemera. Second, they reiterate the need for replication of both treatment and reference lakes, a rare design element for experiments conducted at the whole-lake scale (Schindler 1988; Yan et al. 1996). Such replication is necessary to ensure that regionally coherent patterns are not mistakenly ascribed to treatment effects (Schindler et al. 1985; Keller et al. 1992). Third, because regional coherence is not a uniform characteristic of all taxa, our results imply

that our ability to detect treatment effects differs among species. Comparisons of reference and treatment basins may be compromised for species with strong regional coherence (e.g., *L. minutus*), unless this pattern is extracted prior to testing for treatment effects. Alternatively, reference and treatment comparisons should be straightforward for asynchronous taxa (e.g., *Tropocyclops extensus*).

The two techniques (intraclass correlation and correlation matrix decomposition) we have described in this article should prove useful to a wide variety of ecologists. The intraclass correlation detects synchrony among populations in a region while the matrix decomposition explores its subregional structure. Our temporal coherence space provides a conceptual framework for identifying the relative influence of intrinsic and extrinsic factors.

Using these tools, we have observed evidence of a temporally coherent pattern in the population abundances of a very common zooplankton species in north-temperate lakes. Two of the remaining six zooplankton species also exhibited coherence, a product of periods of exceptional abundances in different subsets of the eight lakes. These results suggest that ecologists, plankton ecologists in particular, must broaden their search for an understanding of temporal variability in populations and communities. While intrinsic factors are often important, extrinsic ones cannot be ignored. Sorting out the environmental correlates associated with the transmission of climatic signals to zooplankton populations is our next step in understanding the intrinsic and extrinsic controls on zooplankton abundances in north-temperate lake communities.

#### Acknowledgments

We thank M. Futter for many statistical discussions, R. Girard and T. Pawson for many years of zooplankton sampling and database management, and W. Geiling for counting the samples. T. Kratz kindly provided a copy of an in press manuscript. We thank K. Cottingham, T. Kratz, R. Sterner, and two anonymous reviewers for many helpful comments. We also thank participants in the Community Dynamics Working Group supported by the National Center for Ecological Analysis and Synthesis, a center funded by the National Science Foundation, the University of California, Santa Barbara, and the State of California, for useful discussions. The primary author thanks C. Rusak for support and advice. This work was supported by the Ontario Ministry of the Environment, a Natural Sciences and Engineering Research Council postgraduate scholarship to J.A.R., and NSERC operating grants to N.D.Y. and D.J.M.

#### Literature Cited

Allen, G., N. D. Yan, and W. T. Geiling. 1994. ZEBRA2, zooplankton enumeration and biomass routines for

- APIOs: a semiautomated sample processing system for zooplankton ecologists. Ontario Ministry of the Environment and Energy, Dorset.
- Andrewartha, H. G., and Birch, L. C. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1–13.
- Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. *Proceedings of the National Academy of Sciences of the USA* 93:7723–7726.
- Brien, C. J., W. N. Venables, A. T. James, and O. Mayo. 1984. An analysis of correlation matrices: equal correlations. *Biometrika* 71:545–554.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Carpenter, S. R., ed. 1988. *Complex interactions in lake communities*. Springer, New York.
- Carpenter, S. R., and P. R. Leavitt. 1991. Temporal variation in a paleolimnological record arising from a trophic cascade. *Ecology* 72:277–285.
- Dillon, P. J., and L. A. Molot. 1996. Long-term phosphorus budgets and an examination of a steady-state mass balance model for central Ontario lakes. *Water Research* 30:2273–2280.
- Dillon, P. J., R. A. Reid, and E. deGrosbois. 1987. The rate of acidification of aquatic ecosystems in Ontario, Canada. *Nature (London)* 329:45–48.
- Dillon, P. J., R. A. Reid, and H. E. Evans. 1993. The relative magnitude of phosphorus sources for small, oligotrophic lakes in Ontario, Canada. *Verhandlungen Internationale Vereinigung für Limnologie* 25:355–358.
- Dillon, P. J., L. A. Molot, and M. Futter. 1997. The effect of El Niño-related drought on the recovery of acidified lakes. *Environmental Monitoring and Assessment* 46:105–111.
- Dussart, B. H., and C. H. Fernando. 1990. A review of the taxonomy of five Ontario genera of freshwater cyclopoid Copepoda (Crustacea). *Canadian Journal of Zoology* 68:2594–2604.
- Fee, E. J., R. E. Hecky, S. E. M. Kasian, and D. R. Cruikshank. 1996. Effects of lake size, water clarity, and climatic variability on mixing depths in Canadian Shield lakes. *Limnology and Oceanography* 41:912–920.
- Fisher, R. A. 1936. *Statistical methods for research workers*. Oliver & Boyd, London.
- George, D. G., and G. P. Harris. 1985. The effect of climate on long-term changes in the crustacean zooplankton of Lake Windermere, UK. *Nature (London)* 316:536–539.
- George, D. G., and A. H. Taylor. 1995. UK plankton and the Gulf Stream. *Nature (London)* 378:139.
- Girard, R., and R. A. Reid. 1990. *Dorset Research Centre study lakes: sampling methodology (1986–1989) and lake morphometry*. Ontario Ministry of the Environment, Dorset.
- Giraudeau, B., A. Mallet, and C. Chastang. 1996. Case influence on the intraclass correlation coefficient estimate. *Biometrics* 52:1492–1497.
- Goldman, C. R., A. Jassby, and T. Powell. 1989. Interannual fluctuations in primary production: meteorological forcing at two subalpine lakes. *Limnology and Oceanography* 34:310–323.
- Haggard, E. A. 1958. *Intraclass correlation and the analysis of variance*. Dryden Press, New York.
- Hairton, N. G., Jr., 1988. Interannual variation in seasonal predation: its origin and ecological importance. *Limnology and Oceanography* 33:1245–1253.
- Jassby, A. D., T. M. Powell, and C. R. Goldman. 1990. Interannual fluctuations in primary production: direct physical effects and the trophic cascade at Castle Lake, California. *Limnology and Oceanography* 35:1021–1038.
- Keller, W., N. D. Yan, T. Howell, L. A. Molot, and W. D. Taylor. 1992. Changes in zooplankton during the experimental neutralization and early reacidification of Bowland Lake near Sudbury, Ontario. *Canadian Journal of Fisheries and Aquatic Sciences* 49:52–62.
- Kerfoot, W. C., and A. Sih, eds. 1987. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, N.H.
- Kratz, T. K., T. M. Frost, and J. J. Magnuson. 1987. Inferences from spatial and temporal variability in ecosystems: long-term zooplankton data from lakes. *American Naturalist* 129:830–846.
- Kratz, T. K., P. A. Soranno, S. B. Baines, B. J. Benson, J. J. Magnuson, T. M. Frost, and R. C. Lathrop. 1998. Interannual synchronous dynamics in north temperate lakes in Wisconsin, USA. Pages 273–287 in D. G. George, J. G. Jones, P. Puncochar, C. S. Reynolds, and D. W. Sutcliffe, eds. *Management of lakes and reservoirs during global change*. Kluwer, Hingham, Mass.
- Lawton, J. 1996. Patterns in ecology. *Oikos* 75:145–147.
- Magnuson, J. J., B. J. Benson, and T. K. Kratz. 1990. Temporal coherence in the limnology of a suite of lakes in Wisconsin, USA. *Freshwater Biology* 23:145–159.
- Manly, B. F. J. 1991. *Randomization and Monte Carlo methods in biology*. Chapman & Hall, London.
- McQueen, D. J., and N. D. Yan. 1993. Metering filtration efficiency of freshwater zooplankton hauls: reminders from the past. *Journal of Plankton Research* 15:57–65.
- Nicholson, A. J. 1933. The balance of animal populations. *Journal of Animal Ecology* 2:132–178.
- Norman, G. R., and D. L. Streiner. 1986. *PDQ Statistics*. B. C. Decker, Toronto.

- Pawson, T. W., and L. J. McEachern. 1987. *Chaoborus* abundance in Muskoka-Haliburton lakes: 1986 methods and data. Ontario Ministry of Environment and Energy, Dorset.
- Peters, R. H., J. J. Armesto, B. Boeken, J. J. Cole, C. T. Driscoll, C. M. Duarte, T. M. Frost et al. 1991. On the relevance of comparative ecology to the larger field of ecology. Pages 46–63 in J. J. Cole, G. M. Lovett, and S. E. G. Findlay, eds. *Comparative analyses of ecosystems: patterns, mechanisms, and theories*. Springer, New York.
- Schindler, D. W. 1988. Experimental studies of chemical stressors on whole lake ecosystems. *Verhandlungen Internationale Vereinigung für Limnologie* 23:11–41.
- Schindler, D. W., K. H. Mills, D. F. Malley, D. L. Findlay, J. A. Shearer, I. J. Davies, M. A. Turner, G. A. Linsey, and D. R. Cruikshank. 1985. Long-term ecosystem stress: the effects of years of experimental acidification on a small lake. *Science (Washington, D.C.)* 228:1395–1401.
- Sinclair, A. R. E., J. M. Gosline, G. Holdsworth, C. J. Krebs, S. Boutin, J. N. M. Smith, R. Boonstra, and M. Dale. 1993. Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? evidence from tree rings and ice cores. *American Naturalist* 141:173–198.
- Somers, K. M., R. A. Reid, S. M. David, and R. Ingram. 1996. Are the relative abundances of orconectid crayfish better indicators of water quality changes than cambarid abundances? *Freshwater Crayfish* 11:249–265.
- StatSoft. 1997. *STATISTICA for Windows*. Tulsa, Okla.
- Stemberger, R. S., A. T. Herlihy, D. L. Kugler, and S. G. Paulsen. 1996. Climatic forcing on zooplankton richness in lakes of the north-eastern United States. *Limnology and Oceanography* 41:1093–1101.
- Taylor, L. R. 1989. Objective and experiment in long-term research. Pages 20–70 in G. E. Likens, ed. *Long-term studies in ecology*. Springer, New York.
- Thompson, R. D. 1995. Volcanic eruptions and global temperatures. *Ambio* 24:320–321.
- Tilman, D. 1989. Ecological experimentation: strengths and conceptual problems. Pages 136–157 in G. E. Likens, ed. *Long-term studies in ecology*. Springer, New York.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19–40 in N. Cappuccino and P. W. Price, eds. *Population dynamics: new approaches and a synthesis*. Academic Press, San Diego, Calif.
- Walters, C. J., D. C. E. Robison, and T. G. Northcote. 1990. Comparative population dynamics of *Daphnia rosea* and *Holopedium gibberum* in four oligotrophic lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 47:401–409.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics* 27:337–363.
- Woiwod, I. P., and I. Hanski. 1992. Patterns of density-dependence in moths and aphids. *Journal of Animal Ecology* 61:619–629.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443–466.
- Yan, N. D. 1986. Empirical prediction of crustacean zooplankton biomass in nutrient-poor Canadian Shield lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 43:788–796.
- Yan, N. D., R. W. Nero, W. Keller, and D. C. Lasenby. 1985. Are *Chaoborus* larvae more abundant in acidified than in non-acidified lakes in central Canada? *Holarctic Ecology* 8:93–99.
- Yan, N. D., W. Keller, K. M. Somers, T. W. Pawson, and R. E. Girard. 1996. Recovery of crustacean zooplankton communities from acid and metal contamination: comparing manipulated and reference lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 53:1301–1327.
- Zar, J. H. 1984. *Biostatistical Analysis*. Prentice Hall, Englewood Cliffs, N.J.