Temporal, spatial, and taxonomic patterns of crustacean zooplankton variability in unmanipulated north-temperate lakes

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Abstract

We quantified the spatial and temporal variability of crustacean zooplankton abundance at annual time steps with 261 lake-years of data from 22 lakes in three regions of central North America. None of these lakes had been experimentally manipulated. Using a nested three-way analysis of variance, we apportioned variance among years,

regions, lakes, and their interactions for 10 functional groups and 4 larger taxonomic aggregates. We proposed that relative variation in the abundance of zooplankton would be greatest among regions and lakes and least among years. We also explored how variability differed among functional groups and changed with taxonomic aggregation. Spatial sources of variation dominated the analysis, but a large interaction between lakes and years indicated that time cannot be ignored. Regional variation was half that found among lakes. Relative variance components differed widely among functional groups, which indicates that species will differ in their response to environmental controls and sensitivity to perturbation. Total explained variation also differed widely among zooplankton and decreased with increasing aggregation of taxa. Whether choosing ecological indicators or designing experiments and monitoring programs, these results clearly show that large-scale temporal and spatial variability will be an important consideration.

We must consider the variability in populations and communities in order to understand the relative influence of spatial and temporal processes (McKnight et al. 1996), detect effects of anthropogenic disturbances or experimental treatments (e.g., Carpenter et al. 1998; Olsen et al. 1999; Cottingham et al. 2000), and develop or test ecological theory (e.g., Levin 1992). For example, without an appreciation of spatial variation at multilake scales, we will have problems extrapolating the results of whole-lake experiments beyond the experimental lake (Schindler 1990; Carpenter et al. 1998). Similarly, unless the "normal" range of variability is known, ecological restoration will be difficult to implement and detect (e.g., Inouye 1995; White and Walker 1997), and management and monitoring programs may be compromised (e.g., Cairns 1992; Kratz et al. 1995; Roux et al. 1998; Hughes et al. 1999). We do not yet have a good grasp of natural variation in the abundance of aquatic biota at a variety of temporal and spatial scales. Although the need is evident, the necessary data have seldom been available—such data now exist for the pelagic zooplankton community.

Zooplankton have often been sampled for many years or in many lakes (e.g., Roff and Kwiatkowski 1977; George and Harris 1985; Yan et al. 1996). However, aquatic ecologists have typically examined space and time separately, either sampling several lakes in a single year or one lake for many years. A simultaneous evaluation of spatial and temporal variability allows us to contrast their relative influence and quantify any interaction. Investigations to date have suggested a predominance of spatial over temporal variation (Kratz et al. 1987; Carpenter et al. 1991), but these studies were quite limited in temporal scale, did not partition spatial and temporal variance simultaneously in a single analysis or examine the interaction between space and time, and did not consider variation among regions. Further, Carpenter et al. (1991) included both manipulated and unmanipulated lakes, thus potentially inflating among-lake variability (Rusak et al. 2001). Our knowledge of variability of zooplankton assemblages would be greatly enhanced with increased temporal and spatial coverage as well as a consideration of how these factors interact.

Zooplankton are increasingly being used as ecological indicators (Attayde and Bozelli 1998; Xu et al. 2001) and to set recovery targets (Keller and Yan 1998). Indicator species should have sensitive and specific responses to particular stressors as well as low baseline variability (e.g., Frost et al. 1992; Cottingham and Carpenter 1998). Although a great deal is known about how individual zooplankton taxa respond to a variety of stressors (e.g., Havens et al. 1993;

Jeppesen et al. 2001), comparisons of normal (i.e., baseline) variability among taxa are lacking. We address this deficiency by comparing relative and absolute variability of common zooplankton taxa.

Herein, we contrast variability among regions, lakes, and years in pelagic crustacean zooplankton abundance in unmanipulated lakes. We use a random-effects analysis of variance (ANOVA) to simultaneously estimate temporal and spatial variance components and their interactions. The data set includes 261 lake-years (1978–1996) of ice-free density estimates from 22 lakes in three north-temperate lake regions of North America. We have two objectives. First, we propose that relative variation among regions will be equivalent to or greater than that found among lakes, which will in turn be greater than interannual variation. This hierarchy emerges from our belief that geology, climate, and glacial history influence zooplankton population size, and differences in these factors increase with increasing lake separation. Second, we examine how relative and total explained variance differ among taxa (e.g., Kratz et al. 1987) and change with aggregation. A decrease in variability can arise as a statistical artifact of aggregation (e.g., Doak et al. 1998), but it can also result from compensatory dynamics among competing species (Frost et al. 1995). Either way, a comparison of variance components among common taxa will improve our choice of indicator species as well as our understanding of the relative temporal and spatial controls of zooplankton population dynamics.

Methods

Study area—The study lakes are in three north-temperate regions: northwestern Ontario, south-central Ontario, and northern Wisconsin/Michigan. Zooplankton sampling was coordinated by researchers from, respectively, the Experimental Lakes Area (ELA), the Dorset Environmental Science Centre (DESC), and the University of Wisconsin at Madison (Fig. 1). The study lakes share a number of limnological features, but they have some notable differences—particularly in lake size, depth, productivity, and pH (Table 1).

Precambrian Shield underlies the study lakes, but the thickness of the overburden of glacial till differs among the regions. The till is thinnest in watersheds of the ELA and thickest in Wisconsin watersheds, where bedrock is capped by a thin layer of sedimentary rock (Carpenter and Kitchell 1993). The watersheds in each region are largely forested, but forest composition differs. Conifers dominate at ELA
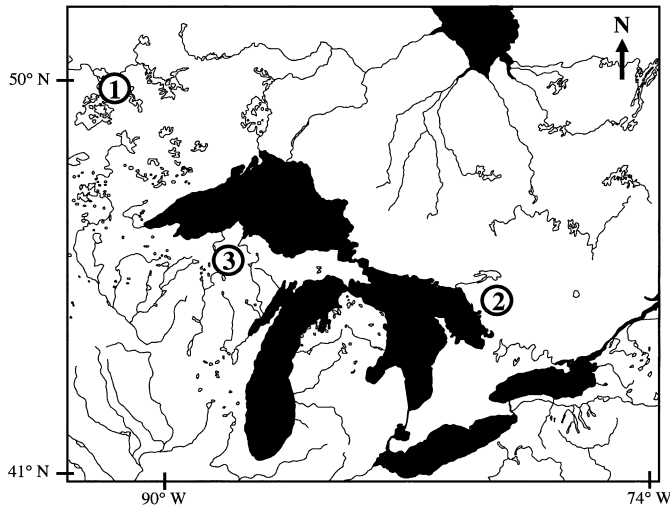
Fig. 1. The study area: (1) Northwestern Ontario—ELA, (2) South-central Ontario—DESC, (3) Wisconsin—North-Temperate LTER sites/Little Rock Lake Acidification Project/Cascade Lakes.

annual air temperatures follow an expected north-south gradient, with ELA at 2.4°C, northern Wisconsin at 3.9°C, and Dorset at 4.5°C. Mean total annual precipitation is greatest in the Dorset area (1034 mm), which is usually downwind of the Great Lakes, intermediate in northern Wisconsin (788 mm), and least at ELA (633 mm). The snowfall portion of this precipitation follows the same pattern, with Dorset receiving 325 cm on average, Wisconsin 252 cm, and ELA 178 cm (Kenora and Muskoka airports—Environment Canada 2001; Minoqua dam—Wisconsin State Climatology Office 2001).

None of the study lakes were experimentally manipulated, nor were they subjected to damaging accidents, such as the invasion of an exotic species. Hence, we refer to them as "reference" or "unmanipulated" systems. However, the lakes are certainly influenced by climatic fluctuations, acid precipitation, and differences in nutrient supply from recreational shoreline development. Hence, the variability of zooplankton abundance in these lakes is best regarded not as typifying "undisturbed" systems but as typical of temperate lakes in eastern North America during the late twentieth century.

Northwestern Ontario lakes—Long-term reference data sets (Table 1) are available for lakes of the ELA in northwestern Ontario (Fig. 1). Lake 239 has been monitored for the past 30 yr. We used a 19-yr subset of Lake 239 data for

(Brunskill and Schindler 1971), whereas the Wisconsin and Dorset forests are a mix of deciduous and coniferous species (Brezonik et al. 1986; Magnuson et al. 1990; Carpenter and Kitchell 1993; Dillon and Molot 1996).

The climate of the three regions differs somewhat. Mean

Table 1. Selected sampling and limnological characteristics of unmanipulated lakes from three north-temperate lake regions (FRS, flushing rate series). Water chemistry values are all means ($\pm$SE) of annual epilimnetic summer values for the period of sampling, with the exception of Little Rock Lake TP (1984–1990) and ELA-FRS chlorophyll *a* (1989–1990).

Lake (abbreviation)	Region	Sampling period	Gear type	Area (ha)	Mean depth (m)	Max depth (m)	Chl *a* (μg L^{-1})	pH (μg L^{-1})	TP (μg L^{-1})
Dorset									
Blue Chalk (BC)	Dorset	1978–1996	Net	52.4	8.5	23.0	1.9 ± 0.1	6.7 ± 0.02	6.6 ± 0.1
Chub (CB)	Dorset	1978–1996	Net	34.4	8.9	27.0	3.2 ± 0.3	5.7 ± 0.03	10.1 ± 0.4
Crosson (CN)	Dorset	1978–1996	Net	56.7	9.2	25.0	4.0 ± 0.9	5.6 ± 0.02	10.9 ± 0.3
Dickie (DE)	Dorset	1978–1996	Net	93.6	5.0	12.0	3.8 ± 0.3	5.9 ± 0.02	10.7 ± 0.6
Heney (HY)	Dorset	1978–1996	Net	21.4	3.29	5.8	2.4 ± 0.2	5.8 ± 0.04	6.7 ± 0.2
Plastic (PC)	Dorset	1978–1996	Net	32.1	7.9	16.3	2.3 ± 0.2	5.8 ± 0.02	4.3 ± 0.3
Red Chalk (RC)	Dorset	1978–1996	Net	44.1	16.7	38.0	2.0 ± 0.1	6.3 ± 0.02	5.0 ± 0.1
ELA									
Lake 239	ELA	1979–1995	Net	56.1	10.5	30.4	2.3 ± 0.2	7.0 ± 0.03	7.1 ± 0.5
Lake 149	ELA (FRS)	1988–1993	Tube	26.9	2.0	4.1	3.9 ± 1.0	7.6 ± 0.03	11.3 ± 0.5
Lake 164	ELA (FRS)	1988–1993	Tube	20.3	4.9	7.1	2.8 ± 1.1	7.2 ± 0.02	9.7 ± 0.6
Lake 165	ELA (FRS)	1988–1993	Tube	18.4	3.4	4.6	2.5 ± 0.8	7.2 ± 0.02	10.6 ± 0.5
Lake 373	ELA (FRS)	1988–1993	Tube	27.6	11.0	21.0	1.0 ± 0.4	7.5 ± 0.04	5.6 ± 0.4
Lake 377	ELA (FRS)	1988–1993	Tube	26.9	9.2	17.9	1.5 ± 0.6	7.4 ± 0.02	7.3 ± 0.3
Lake 442	ELA (FRS)	1988–1993	Tube	16.0	9.0	17.8	1.7 ± 0.4	7.4 ± 0.02	7.2 ± 0.3
Lake 938	ELA (FRS)	1988–1993	Tube	19.2	2.0	6.0	1.8 ± 0.7	7.6 ± 0.02	8.7 ± 0.5
Wisconsin									
Paul (L)	Cascade	1984–1995	Net	1.5	3.9	15.0	5.3 ± 0.5	5.6 ± 0.34	10.2 ± 1.7
Little Rock (LRLR)	Little Rock	1983–1995	Trap	8.1	3.1	6.5	3.1 ± 0.3	6.1 ± 0.03	13.1 ± 1.5
Big Musky (BM)	LTER	1981–1989	Trap	396	7.5	21.3	3.1 ± 0.5	7.6 ± 0.06	7.5 ± 0.5
Crystal (CR)	LTER	1981–1995	Trap	36.7	10.4	20.4	1.8 ± 0.1	6.3 ± 0.04	5.7 ± 0.5
Crystal Bog (CBL)	LTER	1981–1987	Trap	0.5	1.7	2.5	12.4 ± 4.3	5.1 ± 0.09	13.5 ± 1.8
Sparkling (SP)	LTER	1981–1989	Trap	64	10.9	20	2.2 ± 0.3	7.8 ± 0.04	6.5 ± 0.9
Trout (TR)	LTER	1981–1989	Trap	1608	14.6	35.7	3.1 ± 0.4	7.9 ± 0.04	7.5 ± 0.5

which the sampling protocol was constant. We also used a 6-yr ELA data set from seven lakes chosen to vary widely in flushing rates (Salki 1995).

South-central Ontario lakes—The Ontario Ministry of the Environment's DESC has monitored eight south-central Ontario lakes for >20 yr. These lakes were chosen to range in alkalinity (Dillon et al. 1987) and anthropogenic phosphorus supply (Dillon and Molot 1996). Seven lakes, most sampled continuously since 1978, were used in our analysis (Fig. 1). We excluded the eighth lake, Harp Lake, which has recently been invaded by *Bythotrephes* (Yan and Pawson 1997).

Wisconsin northern highland lakes—From Wisconsin, we included five unmanipulated lakes monitored by the North Temperate Lakes Long-Term Ecological Research (LTER) site and two reference basins from whole-lake experiments (Fig. 1). These were the reference basin from the Little Rock Lake acidification experiment and Paul Lake from trophic cascade experiments conducted at the University of Notre Dame Environmental Research Center (UNDERC). These lakes are within 40 km of each other.

Zooplankton sampling—Zooplankton sampling and counting methods have been described elsewhere for ELA (Chang et al. 1980; Chang and Malley 1987; Malley et al. 1988; Salki 1995), Dorset (Yan et al. 1996), and Wisconsin (Frost and Montz 1988; Carpenter and Kitchell 1993). Although protocols differed among lakes (Table 1), zooplankton density was always weighted by lake volume, with the exception of Paul Lake. This consistency is of considerable importance given the morphometric differences among lakes and the fact that zooplankton composition and abundance almost always vary with depth. In Paul Lake, density was expressed as numbers per unit volume of pelagic water column. Because Paul Lake is a kettle lake, volume- and nonvolume-weighted abundance estimates are probably quite similar.

Data preparation—To balance the benefits of taxonomic resolution with the disadvantages of sparse data matrices, we aggregated counts of species into 10 functional groups. Species membership in the groups was based on body size, food web position, and taxonomy (Table 2). We split functional groups into large and small categories where their creation resulted in a wide range of body sizes. The groups were nauplii (NAU), large calanoids (LCA), small and copepodite calanoids (SCA), large cyclopoids (LCY), small and copepodite cyclopoids (SCY), chydorids and other littoral species (CHY), *Holopedium* (HOL), large *Daphnia* (LDA), small *Daphnia* (SDA), and other small cladocerans (SCL). Large predators (*Polyphemus pediculus* and *Leptodora kindtii*) were presumed to be poorly sampled and were excluded.

To determine how differences in taxonomic aggregation affected patterns of variability we constructed four larger taxonomic aggregates, i.e., adult calanoid copepods (CAL), adult cyclopoid copepods (CYC), small cladocerans (SMCL), and large cladocerans (LGCL; Table 2). We excluded immature copepods in an attempt to ensure that trophic relationships remained relatively homogeneous within

Table 2. Zooplankton genera found in the study lakes and the functional groups and taxonomic aggregates to which they belong. Species are indicated when a genus did not fit entirely within a single taxonomic unit.

Species	Functional group	Taxonomic aggregate
Algladiaptomus sp.	LCA	CAL
Epischura sp.	LCA	CAL
Limnocalanus sp.	LCA	CAL
Senecella sp.	LCA	CAL
Calanoid copepodids and copepodites	SCA	
Leptodiaptomus sp.	SCA	CAL
Skistodiaptomus sp.	SCA	CAL
Acanthocyclops sp.	LCY	CYC
Diacyclops sp.	LCY	CYC
Macrocyclops sp.	LCY	CYC
Mesocyclops sp.	LCY	CYC
Cyclopoid copepodids and copepodites	SCY	
Eucyclops sp.	SCY	CYC
Orthocyclops sp.	SCY	CYC
Paracyclops sp.	SCY	CYC
Tropocyclops sp.	SCY	CYC
Nauplii	NAU	
Acantholeberis sp.	CHY	
Acroperus sp.	CHY	
Alonella sp.	CHY	
Alona sp.	CHY	
Camptocercus sp.	CHY	
Chydorus sp.	CHY	
Drepanothrix sp.	CHY	
Eurycercus sp.	CHY	
Ilyocryptus sp.	CHY	
Macrothrix sp.	CHY	
Ophryoxus sp.	CHY	
Pleuroxus sp.	CHY	
Scapholeberis sp.	CHY	
Chydorus sphaericus	CHY	SMCL
Bosmina sp.	SCL	SMCL
Ceriodaphnia sp.	SCL	SMCL
Diaphanosoma sp.	SCL	SMCL
Eubosmina sp.	SCL	SMCL
Daphnia ambigua	SDA	SMCL
Daphnia longiremis	SDA	SMCL
Daphnia parvula	SDA	SMCL
Daphnia retrocurva	SDA	SMCL
Daphnia rosea	SDA	SMCL
Latona sp.		SMCL
Sida sp.		LGCL
Holopedium sp.	HOL	LGCL
Daphnia catawba	LDA	LGCL
Daphnia dubia	LDA	LGCL
Daphnia galeata mendotae	LDA	LGCL
Daphnia pulex	LDA	LGCL
Daphnia pulicaria	LDA	LGCL
Daphnia catawba	LDA	LGCL
Daphnia schoedleri	LDA	LGCL

categories. Cladocerans were apportioned into large and small aggregates to examine differences in variability that might be correlated with body size. We chose a mean body size of 1 mm, using individuals measured in the Dorset and UNDERC lakes, to group the cladocerans. This body size

represents a perceived consumption threshold between invertebrate and vertebrate planktivores (Dodson 1974). *Polyphemus* and *Leptodora* were again excluded from these aggregates.

We used May through October samples to derive ice-free means for each of the lakes. During the summer, rare taxa are often missed in routine counts; hence, zeroes were accommodated by adding the minimum density observed for a given aggregate to its annual mean. These constants ranged from 0.0004 to 0.002 animals L^{-1}. Arnott et al. (1998) noted that most species occurred in all Dorset lakes at some time, but the majority of species were very rare. In the few instances when an aggregate was never found in a particular lake, we assumed that it was absent and a missing datum resulted. This occurred in two functional groups: CHY (Little Rock Lake) and LCA (Big Musky, Little Rock, and Sparkling lakes and Crystal Bog). All annual means were log-transformed after aggregation to derive relative estimates of abundance; hence, the final data were of the form $\log_{10}(x + x_{min})$.

Statistical analysis—We used variance components from a Model II ANOVA (all factors random) to apportion variation in zooplankton density among regions, lakes within regions, and years. The model we used was

$$Y_{yrl} = \mu + A_y + B_r + (AB)_{yr} + C_{l(r)} + e_{yrl}$$

where Y_{yrl} is the density of a zooplankton variable in the *l*th lake in the *r*th region of the *y*th year, μ is the overall mean density of the variable, A_y is the effect of the *y*th year, B_r is the effect of the *r*th region, $(AB)_{yr}$ is the effect of the interaction between the *y*th year and the *r*th region, $C_{l(r)}$ is the effect of the *l*th lake in region *r*, and e_{yrl} is the error term. In this unreplicated case, e_{yrl} incorporates the interaction between years (A_y) and the nested effect of lakes within regions ($C_{l(r)}$). When comparing variance components, one is frequently just as interested in relative (expressed as a percentage of the total variation) as absolute (total variation explained by the model) values (e.g., Sokal and Rohlf 1995). We calculated both forms in our analysis with SAS PROC MIXED (SAS version 6.12). Because of our unbalanced design, we estimated our variance components using the recommended residual maximum-likelihood method (Robinson 1987).

Assessment of the significance of variance components in an unbalanced design is difficult. The proposed tests of significance for the contribution of the different factors are not exact and the violation of assumptions concerning homogeneity and normality are more likely to affect probabilities of type I error than when data are balanced (e.g., Sokal and Rohlf 1995). For these reasons, we do not attempt tests of significance, although we do calculate approximate standard errors on each variance component. In this context, our ANOVA design is simply an effective and interpretable way of apportioning long-term and large-scale variance.

A variance component describes the amount of variation in the dependent variable attributable to a given random factor (e.g., Sokal and Rohlf 1995). With reference to plots of illustrative data sets (simulated abundances in two regions each with five lakes for 5 yr with a constant total variance
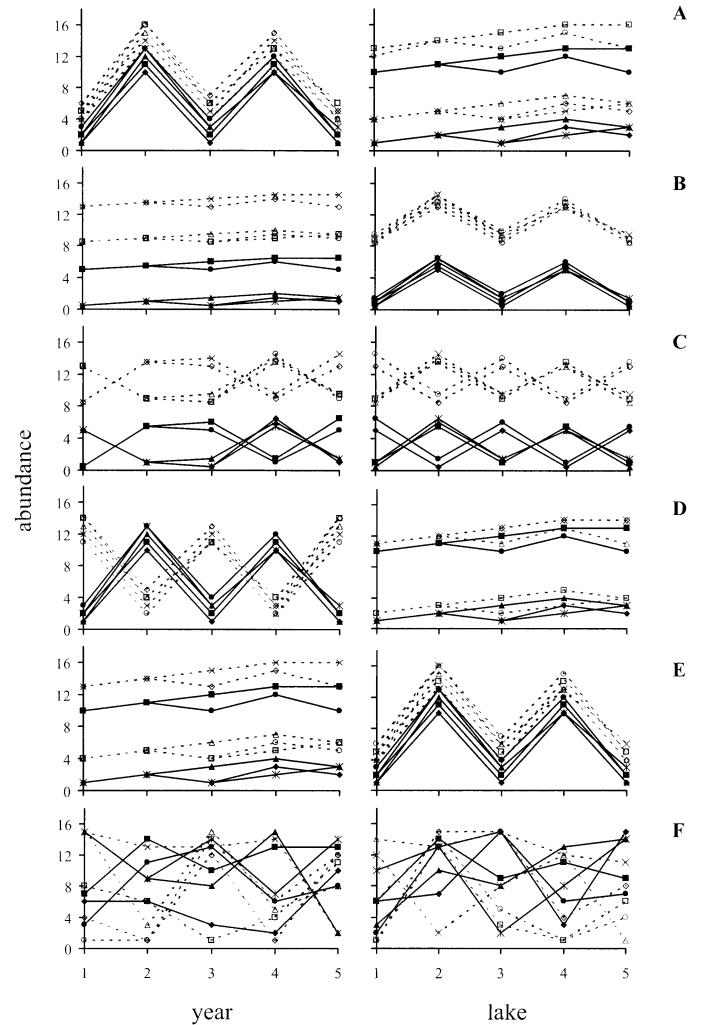

Fig. 2. Plots of simulated abundance data (5 yr from two different regions, as indicated by dotted and black lines with open and solid symbols, for five lakes per region) in time (left panels—each line represents one lake) and space (right panels—each line represents 1 yr). The relative variance components for each data set are as follows: (A) large year variance component ($\sigma_Y^2 = 83\%$, $\sigma_R^2 = 14\%$), (B) large regional variance component (with a moderate lake component—$\sigma_R^2 = 82\%$, $\sigma_{L(R)}^2 = 17\%$), (C) large regional variance component (with a moderate residual component—$\sigma_R^2 = 85\%$, $\sigma_E^2 = 15\%$), (D) large year-region interaction ($\sigma_{YR}^2 = 96\%$), (E) large lake variance component ($\sigma_{L(R)}^2 = 96\%$), (F) large residual, or year-lake interaction, variance component ($\sigma_E^2 = 93\%$).

of ~25 in each lake by year matrix; see Fig. 2), our variance components can be interpreted as follows:

Year—For a given variable, a large σ_Y^2 implies that most of the variance in annual density is temporal in origin (Fig. 2a). Expressed in its relative form as a percentage of total variation [i.e., $\sigma_Y^2/(\sigma_Y^2 + \sigma_R^2 + \sigma_{YR}^2 + \sigma_{L(R)}^2 + \sigma_e^2)$], this component is analogous to the intraclass correlation among time series (Rusak et al. 1999; see Kratz et al. 1995 for a similar estimate). σ_Y^2 thus estimates the synchrony of fluctuations in zooplankton density among lakes. This phenomenon of pop-

ulation synchrony has been termed "temporal coherence" by Magnuson et al. (1990).

Region—The regional variance component, σ_R^2, estimates the covariation between the densities of a particular taxa in different regions (Fig. 2b,c). Expressed relative to total explained variation, it indicates the similarity in zooplankton densities among regions. However, because lakes are nested within regions, it is only large when differences among regional means exist. For the same reason, σ_R^2 is unlikely to ever be the sole source of all spatial variance. Covariation among regions will also necessarily imply some covariation among lakes (Fig. 2b) or an interaction between lakes (within regions) and years (Fig. 2c).

Year-region interaction—σ_{YR}^2 estimates the additional variation due to the dependence between year and region after these factors have been estimated independently. The more one has to keep track of years to estimate zooplankton density in a given region, the larger this variance component is (Fig. 2d). In its relative form, the year-region interaction estimates the proportion of the total variation that is due to this interdependence.

Lakes (within region)—In a nested design, $\sigma_{L(R)}^2$ estimates the amount of variance among lakes within regions, beyond the variation among regions. As in any hierarchical analysis of variance, this nested term also includes the variation associated with the interaction between lakes and regions (Sokal and Rohlf 1995). Relative $\sigma_{L(R)}^2$ is large when densities in individual years fluctuate in synchrony among lakes, thus minimizing interaction terms, and differences among lake means (within regions) are large (Fig. 2e).

Year-lake interaction (residual)—Because we are using mean annual abundances and have no replication in any given lake-year, σ_e^2 estimates the portion of total variance not accounted for by the effect of the above three factors and their interactions. The equation estimating this component is the same as that used to calculate the interaction between years and lakes (within regions) in a replicated design (e.g., Sokal and Rohlf 1995); thus, we do not have an independent estimate of random error in an unreplicated model. The more density depends on particular combinations of lakes and years, the larger this component will be (Fig. 2f). This term has additional implications for the interpretation of σ_Y^2—a large residual variance component in an unreplicated design may also indicate the potential for synchronous variations in abundance among populations over time (large σ_Y^2) in subsets of lakes within regions (e.g., recalculating variance components after removing the regional difference in abundance from Fig. 2c results in a relative σ_e^2 of 100%). In a similar two-factor ANOVA design (lakes and years), Larsen et al. (1995) indicated that this lake-year interaction may also be of interest as an indicator of stress or change in an ecosystem.

Results

The limnology of the three regions differed. A null hypothesis of no difference among regions for the six parameters in Table 1 was rejected by a MANOVA (multivariate analysis of variance) (Wilk's λ, $P = 0.012$). However, individual one-way ANOVAs identified pH as the single significant variable distinguishing the regions. Neary and Dillon (1988) have found similar regional differences in mean pH (5.99 and 6.65 for soft-water lakes in south-central and north-western Ontario, respectively).

Differences in how variance in zooplankton abundance was apportioned were evident both among factors (i.e. time, space, and their interaction terms) and functional groups (Table 3). Relative variation due to year was one of the smallest components for all taxa (mean, 0.81%). A number of taxa had no discernible variance associated with σ_Y^2, and it peaked at 1.73% for the nauplii. Thus, there was no evidence for temporal coherence or synchrony among all the study lakes. In contrast, there was a regional signal in the data. σ_R^2 was substantial (mean, 22.0%) and often quite large (i.e., maximum of 48% for the large cyclopoids). Although usually substantial, the regional variance component was zero for HOL and SCL, and it often had large standard errors. The relative amount of variance associated with σ_{YR}^2 was similar to the year component in that its contribution to total variation was small (mean, 2.6%), with a maximum of 9.5% in the nauplii. $\sigma_{L(R)}^2$ was the largest source of relative variation for 7 of the 10 functional groups (mean, 46.9%). Only the two large copepod groups (LCA and LCY) and the nauplii differed. In these cases, the regional component was largest. The relative values of σ_e^2, which estimate the interaction between years and lakes within regions, were large and of a magnitude similar to the regional component (mean, 27.7%; range, 14.6–47.4%). However, σ_e^2 generally had smaller standard errors relative to the size of the variance component.

We found many similar patterns in the larger taxonomic aggregates (Table 4). Relative measures of σ_Y^2 were consistently small (mean, 0.55%) as were those for σ_{YR}^2 (mean, 1.3%). σ_R^2 accounted for a somewhat smaller portion of the total variation (mean, 16%) in these larger aggregates but spanned a wider range (up to 55%) of relative variability. Adult cyclopoids were again atypical in that the relative contribution of regional variation was greatest. $\sigma_{L(R)}^2$ was by far the largest relative variance component for the taxonomic aggregates (mean, 53%). Relative variance in σ_e^2 was also quite substantial (mean, 30%).

Spatial variation exceeded temporal variation in both the functional groups and larger aggregates. Generally, relative variation ranked as lakes (within regions) > regions ≫ year. One unexpected feature of the data was the magnitude of the σ_e^2 term. This interaction between years and lakes within regions indicates an additional source of variation that was not accommodated by the main factors and demonstrates considerable dependence between space and time. Although σ_Y^2—the pure temporal effect—explained little of the variation in zooplankton density, time is also captured by σ_e^2. This large residual component can also indicate that there is potential for synchronous subsets of lakes in the data (Fig. 3)—an aspect of variation that Rusak et al. (1999) consider in detail but is not considered herein.

The sum of all variance components represents the total variability of a given functional group or taxonomic aggregate. Large calanoids, chydorids, *Holopedium,* and large and

Table 3. Variance components and mean densities for each of the functional groups (FG).

Functional group	Factor	Mean density (No. L^{-1})	Variance component	Standard error	Total variance	Relative variance
LCA	Year	0.09	0.022	0.033	1.29	1.70
	Region		0.593	0.633		45.83
	Year × region		0.046	0.042		3.52
	Lake (region)		0.182	0.079		14.06
	Residual		0.451	0.050		34.89
LCY	Year	4.54	0.003	0.004	0.55	0.53
	Region		0.260	0.290		47.69
	Year × region		0.002	0.005		0.35
	Lake (region)		0.201	0.068		36.88
	Residual		0.079	0.008		14.55
CHY	Year	0.29	0.015	0.033	1.54	1.00
	Region		0.479	0.559		31.06
	Year × region		0.060	0.054		3.88
	Lake (region)		0.469	0.178		30.44
	Residual		0.518	0.056		33.63
HOL	Year	1.58	0.017	0.014	1.38	1.20
	Region		0.000	—		0.00
	Year × region		0.000	—		0.00
	Lake (region)		1.104	0.350		79.73
	Residual		0.264	0.025		19.06
LDA	Year	1.52	0.000	—	1.68	0.00
	Region		0.400	0.526		23.76
	Year × region		0.039	0.024		2.34
	Lake (region)		0.844	0.292		50.14
	Residual		0.400	0.040		23.76
N	Year	23.15	0.003	0.005	0.16	1.73
	Region		0.063	0.069		39.79
	Year × region		0.015	0.007		9.52
	Lake (region)		0.029	0.011		18.75
	Residual		0.047	0.005		30.21
SCA	Year	11.29	0.003	0.004	0.68	0.48
	Region		0.093	0.163		13.74
	Year × region		0.000	—		0.00
	Lake (region)		0.481	0.161		70.80
	Residual		0.102	0.010		14.98
SCL	Year	4.42	0.000	—	0.49	0.00
	Region		0.000	—		0.00
	Year × region		0.013	0.015		2.70
	Lake (region)		0.246	0.083		49.91
	Residual		0.234	0.024		47.39
SCY	Year	4.67	0.013	0.017	0.93	1.45
	Region		0.064	0.149		6.88
	Year × region		0.025	0.021		2.74
	Lake (region)		0.554	0.190		59.85
	Residual		0.269	0.027		29.08
SDA	Year	0.70	0.000	—	1.60	0.00
	Region		0.180	0.314		11.25
	Year × region		0.020	0.022		1.23
	Lake (region)		0.928	0.318		58.07
	Residual		0.471	0.047		29.46

Table 4. Variance components and mean densities for each of the large taxonomic aggregates.

Taxonomic aggregate	Factor	Mean density (No. L^{-1})	Variance component	Standard error	Total variance	Relative variance
CAL	Year	3.61	0.002	0.004	0.486	0.31
	Region		0.000	—		0.00
	Year × region		0.0003	0.006		0.07
	Lake (region)		0.374	0.120		77.06
	Residual		0.110	0.011		22.56
CYC	Year	6.27	0.000	0.004	0.478	0.05
	Region		0.262	0.285		54.91
	Year × region		0.010	0.006		2.06
	Lake (region)		0.150	0.051		31.47
	Residual		0.055	0.006		11.50
LGCL	Year	2.89	0.004	0.009	0.332	1.06
	Region		0.025	0.050		7.52
	Year × region		0.006	0.010		1.87
	Lake (region)		0.152	0.054		45.70
	Residual		0.146	0.014		43.85
SMCL	Year	5.16	0.002	0.004	0.235	0.77
	Region		0.000	—		0.00
	Year × region		0.003	0.007		1.32
	Lake (region)		0.132	0.044		56.27
	Residual		0.098	0.010		41.64

small *Daphnia* had the highest total variation among the functional groups (Table 3), with the large *Daphnia* the most variable of all. Both the overall mean and maximum variance components decreased as aggregation increased from the functional group (mean, 1.03; max, 1.68) to the taxonomic aggregates (Table 4; mean, 0.38; max, 0.49). All taxonomic aggregates had lower total variation than their component functional groups.

Potential influence of gear type and protocol—Because of the synthetic nature of our study and its need to draw on many sources of data, we explored the extent to which our results could be influenced by differences in gear type or sampling protocol. The effect that differences in gear type (Table 1) had on our analysis was found to be minimal. First, Johannsson et al. (1992) have quantified potential differences among all of the gear types except the tube sampler used in seven ELA lakes (Table 1). They noted that the various nets and traps sampled zooplankton comparably—of the six cladoceran and copepod taxa found, only *Holopedium gibberum* and *Diaphanosoma birgei* were less abundant in Schindler-Patalas trap collections. A recent comparison of the tube sampler and ELA and Wisconsin-type nets detected no gear bias (M. J. Paterson unpubl. data). Second, spatial variance was not elevated by the use of two different gear types at ELA and Wisconsin. To examine this potential bias, we deleted Lake 239 and Paul Lake in turn, then reanalyzed the 21-lake data sets. Variance components averaged across all taxonomic aggregates and functional groups changed little—only 1.5% and 1.7% without Lake 239 and only 1.3% and 2.2% without Paul Lake, respectively. In summary, we believe that our comparisons of variance are not unduly affected by gear differences among lakes or regions.

There were also differences in protocol among regions,

but these did not have a substantial effect on our derivation of variance components. The first difference relates to the tube sampler being deployed at both littoral and pelagic stations, whereas the net and trap samples were obtained only at midlake stations. Thus, the tube-sampler data may be biased to littoral species. Inspection of regional time-series plots for the four large aggregates (Fig. 3) does reveal more cyclopoids in ELA lakes (as well as in most of the Wisconsin trap data) relative to Lake 239 and the Dorset lakes. The same is true for ELA chydorids. Although real, this bias had only a small influence on our variance components and changed none of our conclusions. We reduced cyclopoid densities in all those lakes sampled with either a tube or a trap (seven ELA lakes and six Wisconsin lakes) and chydorid densities in the seven ELA lakes sampled with a tube by 50%—the maximum annual density differences of the time series for net- and tube-derived samples in ELA lakes (M. J. Paterson unpubl. data). When the variance components were recalculated, the relative regional variation in the LCY and CHY functional groups was only slightly reduced (2% and 4%, respectively), and a moderate reduction was observed in the cyclopoid taxonomic aggregate (12%), but the rank order of variance components was not changed.

The second protocol difference concerns sampling frequency, which varied from weekly to monthly among lakes. We calculated the number of samples required to estimate mean annual zooplankton density (Cattaneo and Prairie 1995) with a standard error of ≤20% as ranging from 8 to 14 (using 173 lake-years of monthly ELA data; M. J. Paterson unpubl. data). Given our May–October sampling period, a monthly sampling regimen is close to the lower indicated sampling frequency. Yan and Welbourn (1990) also demonstrated that weekly and monthly sampling provided very similar annual zooplankton density estimates from Dor-
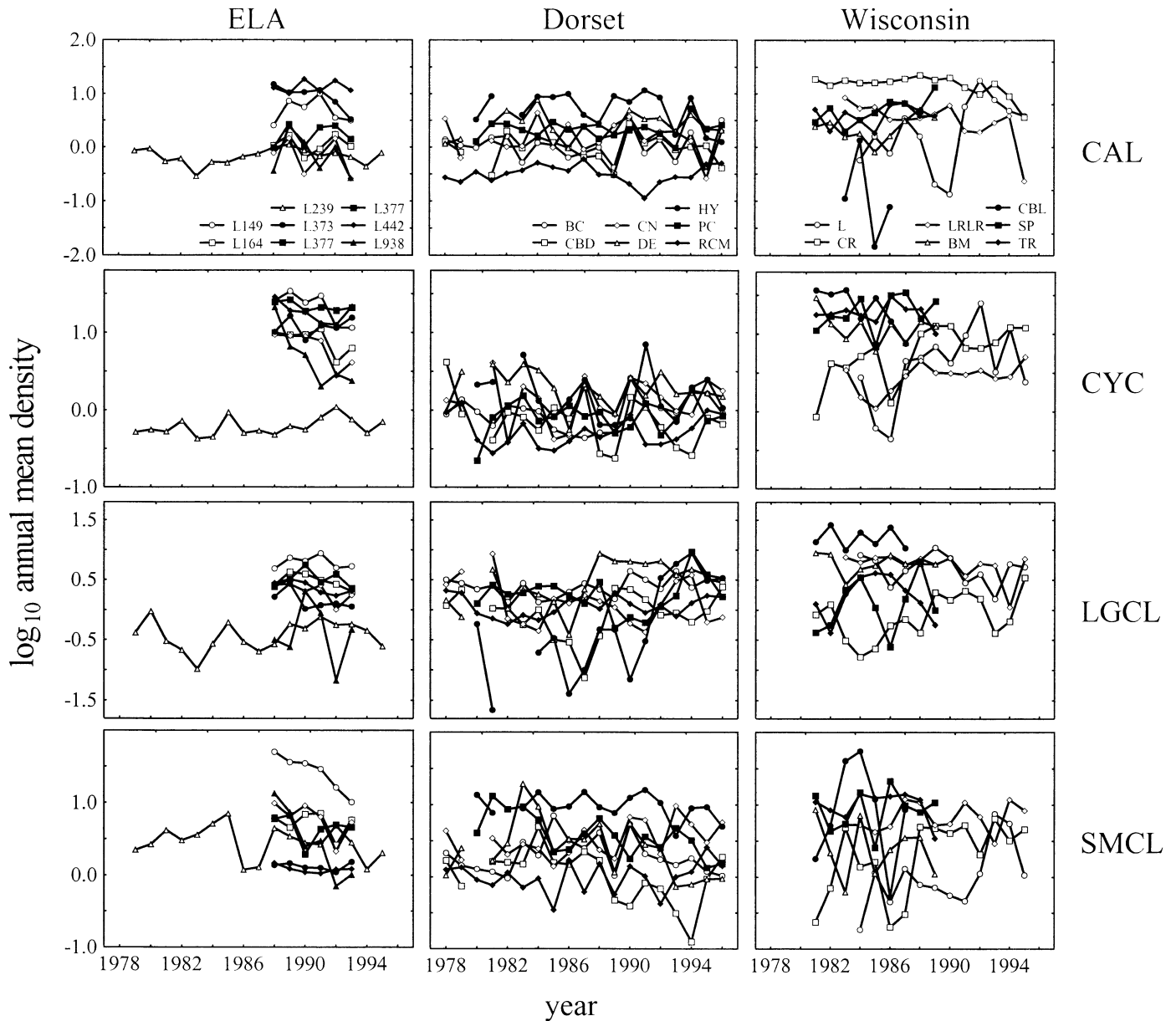
Fig. 3. Plots of changes in $\log_{10}$ annual mean density over time for each of the four taxonomic aggregates (adult Calanoida, CAL; adult Cyclopoida, CYC; large Cladocera, LGCL; and small Cladocera, SMCL).

set lakes. Hence, we conclude that differences in sampling frequency did not bias our results.

Finally, given the potential for climate to determine zooplankton abundance (e.g., George and Harris 1985; Rusak et al. 1999), it is possible that the particular years sampled might have influenced our results. To determine the influence of temporal coverage, we calculated variance components for the 1984–1993 time period. This 10-year subset included 67% of the original data. These variance components were very similar to those derived from the complete data set and did not alter our conclusions whatsoever. On average, the percentage of change (either positive or negative) in relative variance components between the full data set and the 10-year window was only 2.1% and 1.8% for functional groups

and large aggregates, respectively. As was the case with sampling gear and protocol, we conclude that our variance components were not unduly influenced by the particular combination of years sampled.

Discussion

Our analysis demonstrates that the majority of variation in interregional zooplankton density in small, unmanipulated, north-temperate Shield lakes is spatial in origin and is apportioned primarily among lakes and regions rather than among years. However, our hypothesized regional dominance of variation was not generally observed, and the interaction between time and space was often substantial. The

patterns of relative and total variation differed considerably among zooplankton taxa—the latter decreasing with increasing aggregation.

Temporal and spatial patterns of variation—Our results indicate a dominance of spatial over temporal controls in north-temperate zooplankton communities at annual time steps but do not explain this pattern. Historically, zooplankton species-environment relationships have been sought in single lakes over many years (e.g., Hairston 1988; Adrian and Denke 1996) or in many lakes in a single year (e.g., Auclair et al. 1993; Rodriguez et al. 1993; Pinel-Alloul et al. 1995; Currie et al. 1999). Given our observed dominance of spatial variance components, studies that have maximized spatial extent may be more fruitful in identifying mechanisms underlying large-scale, interregional variability in zooplankton abundance at annual time steps. Pinel-Alloul et al. (1995) examined spatial relationships between zooplankton abundance and 101 environmental variables (32 limnological variables, 61 phytoplankton taxa, and 8 fish species) in 54 boreal lakes. They found that the strongest environmental gradients were related to vertebrate predation (piscivory and planktivory) and acid sensitivity, hardness, and eutrophy in Quebec lakes. Similarly, Auclair et al. (1993) found that acidity (which was a strong correlate of piscivory) was an important determinant of zooplankton community structure in Quebec lakes, whereas Rodriguez et al. (1993) demonstrated the importance of fish community composition on zooplankton community structure in 43 lakes, once the effects of abiotic variables were removed. Alternatively, Currie et al. (1999) were unable to find a relationship between piscivory and the biomass of various zooplankton aggregates in 29 north-temperate lakes, although zooplankton biomass was correlated with total phosphorus and chlorophyll *a* concentrations. Collectively, this literature suggests that spatial patterns in zooplankton are influenced by chemical (phosphorus and acidity), physical (lake size and depth), and biological (productivity and planktivory) factors.

Of these limnological variables, only lake pH differed significantly among regions in our analysis. The study lakes are generally acid-sensitive, but their exposure to acid precipitation and their resultant acidity vary widely. Therefore, lake- and region-specific differences in pH may explain a good portion of the predominance of spatial variation in the data set. Indeed, the small calanoid functional group, which generally consists of more acid-tolerant organisms (Sprules 1975), had one of the lowest estimates of total variation, whereas the large *Daphnia,* a group of generally acid-sensitive species (Havens et al. 1993) had the highest total variation. Even though the lakes have pH values typical of their regions (Neary and Dillon 1988), damage from acidity can appear as pH falls near or just below 6.

Interregional differences in planktivory may also contribute to the dominance of spatial variance in our analysis. We lack planktivory estimates for all but a few of our lakes, but we do have information on fish species composition. Fish species richness varied from 1 to 25 in the Wisconsin lakes (Swenson et al. 1987; Carpenter and Kitchell 1993; Kratz et al. 1997), from 8 to 15 (N. D. Yan unpubl. data) in the Dorset lakes, and from 4 to 10 in the ELA lakes (B. Fudge

and K. Mills unpubl. data). Both the Dorset and Wisconsin regions have lakes that lack piscivores. Ranges in fish species richness and composition of this magnitude could produce large differences in zooplankton among lakes within regions and possibly also among regions (e.g., Brooks and Dodson 1965).

Although lake size was not identified as a significant factor among regions, there are considerable size differences among the Wisconsin study lakes. Crystal Bog and Trout Lake are the smallest and largest lakes in the data set, and they are in the same region, thus potentially increasing $\sigma^2_{L(R)}$ and decreasing σ^2_R. However, when these two lakes were removed, our results were not altered. Overall, the relative magnitudes of variance components from this subset changed little (mean, ~3%; median, ~1%) when compared with the full analysis. The predominant influence of interlake variability suggests that local factors have a greater effect on zooplankton densities in small oligotrophic lakes on the Precambrian Shield than do regional factors.

The observed dominance of spatial over temporal variability was as predicted; however, the virtual absence of an unconfounded temporal component was unexpected. The nauplii functional group had the largest relative σ^2_Y at a mere 1.7%. These small σ^2_Y values were not a product of the duration of our data sets. Although temporal variation increases with time (e.g., Pimm 1991), this increase slows appreciably for most freshwater zooplankton populations after a decade of monitoring (Cyr 1997). Among the Dorset lakes, Rusak et al. (1999) found that an analogous estimate of temporal variability was never dominant when all lakes were considered. However, many species did display a significant degree of synchrony (maximum of 20%) among lakes over time. Differences in spatial scales between our study and Rusak et al. (1999) likely explain this discrepancy. Although Rusak et al. (1999) sought synchrony in zooplankton abundance in neighboring lakes *within* a region, we quantified σ^2_Y among three north-temperate regions. To test whether our larger scale obscured σ^2_Y, we partitioned variance within each region separately using a two-way ANOVA with year and lake as random factors. As a result, relative σ^2_Y increased more than sevenfold when averaged across all functional groups in the three within-region analyses (from a mean of 0.8 among regions to 5.7 within regions). Thus, the interregional nature of our analysis diminished the importance of σ^2_Y. We suspect that regional climatic differences around the Great Lakes explain this result.

Despite the negligible ''pure'' temporal variance component, the residual component was often quite large. This component (σ^2_e) incorporates the extent to which years and lakes within regions interact and was often ranked as the second largest variance component. σ^2_e can also suggest the potential for synchronous subsets of lakes within regions, and such patterns seem apparent in our data (e.g., Fig. 3). We explored this potential further by examining the interaction between year and lake from the within-region, two-way ANOVA results. This interaction, averaged across all functional groups in the three within-region analyses, almost doubled when compared with overall results. When combined with the noted increase in the ''pure'' temporal component within regions, these larger relative values of σ^2_e re-

inforce the idea that temporal variability becomes more important as we narrow our spatial coverage. σ_e^2 also suggests that climatic effects on zooplankton abundance will not be uniform among lakes within a region.

The observed dominance of spatial variance in north-temperate zooplankton populations has important implications for the design of monitoring programs. Variance components can be used to indicate the scale at which our sampling efforts should be concentrated—the most variable factor needing the greatest replication (Sokal and Rohlf 1995). For monitoring programs designed to assess the effect of management decisions for large regions (e.g., effects of reductions in SO_2 emissions on ecological recovery from lake acidification), our results suggest that reference conditions may best be quantified when several different lakes are used. Similarly, the overriding influence of spatial variation also cautions against the extensive use of single "sentinel" monitoring sites, a conclusion also reached by Jassby (1998). Burke and Laurenroth (1993) proposed that simulation models could be a solution for extrapolating from individual sites to larger regions if relationships between control variables and ecological responses can be determined from site-level experiments and observations. Our results suggest that, even with knowledge of critical ecosystem features, the large spatial component of variation may make extrapolation a difficult task.

In an experimental context, the observed dominance of spatial variation may help explain some of the apparent contradictions in the response of zooplankton among whole-lake food web manipulations (e.g., DeMelo et al. 1992). This problem is particularly acute for treatments that do not increase variability in zooplankton abundance beyond that in unmanipulated systems (Rusak et al. 2001). Given the spatial variability we have documented, this may be a frequent occurrence. The consistent dependence between year and lake may also confound the application of results from zooplankton manipulation experiments to other lakes, particularly if the observed changes in population dynamics are subtle ones.

Taxonomic patterns of variation—We anticipated differences in relative variance components among taxa because food requirements, growth rates, predator vulnerability, and habitat requirements will vary both among species and among lakes. Nonetheless, the magnitude of this difference is instructive. For example, *Holopedium* is a widely distributed species with relative σ_R^2 equal to zero and relative $\sigma_{L(R)}^2$ of almost 80%. In contrast, the large calanoids have relative σ_R^2 of 45% and a $\sigma_{L(R)}^2$ of only 14%. Reid et al. (1995) also found large differences in relative temporal and spatial variation among macroinvertebrate taxa within a season. Why such large differences might arise among taxa is not always obvious, but it is clear that the relative influence of spatial and temporal controls of zooplankton abundance are strongly taxa-specific. Whether changes in zooplankton abundance are used to define perturbations (e.g., Yan et al. 1996; Attayde and Bozelli 1998) or to test ecological hypotheses (e.g., Rusak et al. 2001), aquatic ecologists must be aware of and control for this inter-specific variability.

Total variation also differed widely among taxa. For ex-ample, large *Daphnia* were the most variable functional group of the 10 we surveyed. This group's sensitivity to low pH (Havens et al. 1993), size-selective predation from vertebrate planktivores (e.g., Carpenter and Kitchell 1993), and food quality (e.g., Elser et al. 1998) all have the potential to contribute to its large variability. In contrast, total variation for the small cyclopoids, another acid-sensitive group (Sprules 1975), was almost half that observed in the large *Daphnia*. Clearly, the functional group chosen to quantify the regional effects of acidification could influence our interpretation of damage.

The observed trend of decreasing variability with increasing aggregation also has important implications for recent attempts to employ zooplankton species as ecological indicators. Efforts aimed at deriving meaningful ecological indicators have centered on finding a balance between natural variability and sensitivity to stressors (e.g., Frost et al. 1992; Cottingham and Carpenter 1998), with the most suitable scale of aggregation deemed to have low baseline variability but high sensitivity. In general, we found total variation to decrease as species were increasingly aggregated from their functional groups to larger taxonomic units. Although statistical averaging can play a role in this reduction (Doak et al. 1999), compensatory dynamics operating among competing taxa (Frost et al. 1995) appear to have a larger effect. For example, the two most variable functional groups (large and small Daphnia) were contained in the two least variable larger aggregates (large and small Cladocera), which indicates that compensatory dynamics outweighed any effect of statistical averaging. This suggests that biological interactions can suppress variability in species aggregates, a desirable quality for an indicator group.

In summary, we have demonstrated that spatial (primarily lake-specific) processes controlled the natural variation in north-temperate zooplankton at a subcontinental scale during the past two decades. This finding is robust because it is based on a data set that includes much greater temporal and spatial coverage than has been examined elsewhere, it excludes all manipulated lakes, and it uses an analysis that effectively partitions time and space simultaneously. The fact that this conclusion might match "conventional wisdom" does not lessen its significance, given that the conventional wisdom has not been substantiated elsewhere. We also detected a previously unquantified interaction between space and time—an interaction that was relatively important for most taxa. Furthermore, the role of time increased as we looked at patterns within regions. Monitoring or management programs that focus on time or space exclusively do so at their peril, particularly at a subregional scale.

One of our next tasks is to examine the relationship between zooplankton variability and its environmental covariates in space and time and extend this type of analysis to other aquatic organisms. Given the strong food web interactions in aquatic ecosystems and the consistency in patterns of temporal variance found between zooplankton, phytoplankton and fish (Cyr 1997), we predict that similar patterns exist in other freshwater communities. Another task is to examine the use of variance, in itself, as a dependent variable in tests of population-level responses to perturbation (e.g., Underwood 1991; Rusak et al. 2001) or in detection of stress

at the community and ecosystem level (e.g., Micheli et al. 1999; Cottingham et al. 2000). A better grasp of natural background variance, the sort we have provided for north-temperate lake zooplankton, will help us to determine whether both means and variances are useful indicators of environmental stressors.

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