

## LOCAL AND REGIONAL ZOOPLANKTON SPECIES RICHNESS: A SCALE-INDEPENDENT TEST FOR SATURATION

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**Abstract.** Assemblages of coexisting species are formed by immigration from a regional pool of colonists and local interactions among species and with the physical environment. Theory suggests that the shape of the relationship between regional and local species richness may indicate the relative roles of dispersal and local interactions in limiting local diversity. Here we examine patterns of regional and local species richness in freshwater crustacean zooplankton to test whether linear (suggesting dispersal limitation) or curvilinear (suggesting saturation, via strong local control) functions best fit the data. Local richness appeared saturated when regions of different spatial extents were included on the same graph. However, this pattern was influenced by differences in scale among surveys. We corrected for the effects of regional scale by plotting mean local richness against the residuals of the species–landscape area relations. Controlling for the extent of the regional scale produced much more linear patterns, suggesting strong dispersal limitation. We present a simple graphical model to explain how variation among surveys in the geographic size of regions can produce apparent saturation of local diversity even if the underlying pattern of local and regional richness is linear. We also compare the predictive power of residual regional richness on local richness with that of several local features in a multiple regression model. Local richness exhibits strong relationships with both residual regional richness and pH.

We argue that the relative strengths of local and regional processes depend on the definition of the regional scale. A variety of evidence suggests that local processes play a major role in generating differences in zooplankton diversity among lakes within a biogeographic region. Evidence for the importance of dispersal limitation comes largely from comparisons of lakes across very large scales. Our analysis suggests that linear patterns of local and regional diversity are not incompatible with strong local interactions.

**Key words:** *cladocerans; copepods; dispersal limitation; diversity; saturation; scale-dependence; species richness.*

### INTRODUCTION

Theories of community structure come from one of two broad perspectives: regional and local. The regional approach considers the role of movement of species among habitat patches in shaping local communities. The local view focuses on interactions within patches, both among species and with the abiotic environment. Clearly these explanations for species composition are not mutually exclusive; in order to occupy a site a species must both arrive there by dispersal and maintain positive population growth in the local environment. The question of interest is then, to what extent do colonization and local interactions limit local diversity and generate differences in species composition among sites? Here we adopt a comparative approach to estimating the roles of local interactions and

dispersal limitation in determining the species richness of freshwater zooplankton communities.

The method we use is based on the hypothesis that, if local processes place intrinsic upper limits on the number of species that may coexist, then local and regional richness will be independent of one another at high levels of regional richness (Terborgh and Faaborg 1980, Cornell and Lawton 1992). Factors that might limit local diversity include the physiological tolerance of organisms to environmental conditions and species interactions that prohibit the coexistence of certain species combinations. If mean local richness approaches an upper asymptote with increasing regional richness, then local processes may play a dominant role in structuring local communities relative to colonization from the region. Alternatively, if species are frequently absent from suitable habitats due to dispersal limitation, then local richness is expected to show a linear dependence on the size of the regional pool. Linear, or unsaturated, patterns of local and regional diversity may indicate that communities are under strong regional control as dispersal greatly limits local

Manuscript received 21 April 1999; revised 30 September 1999; accepted 6 October 1999.

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FIG. 1. Locations of the surveys included in the data set. Numbers refer to the study numbers in Table 1.

species richness (Cornell and Lawton 1992, Cornell and Karlson 1997). The patterns predicted in the cases of strong local vs. regional control provide a testable, qualitative contrast for examining unsaturation in natural communities.

Several issues may complicate the interpretation of patterns of local and regional diversity in terms of the importance of dispersal limitation or local interactions. First, moderate levels of disturbance in saturated communities can produce linear patterns that are indistinguishable from highly dispersal-limited scenarios (Caswell and Cohen 1993). Second, communities may be unsaturated on evolutionary time scales yet saturated in ecological time (Rosenzweig 1995). That is, communities may be open to "invasion" by the evolution of new species but still resist colonization from the existing pool of species. Third, the relationship between local and regional diversity depends on the definition of the local scale. Environmental heterogeneity within a presumed local site can lead to the apparent coexistence of species that occupy distinct habitats and bias studies in favor of finding linear relationships (Westoby 1998, Huston 1999). Fourth, the choice of the regional scale also affects the relationship between local and regional richness (Caley and Schluter 1997, Angermeier and Winston 1998, Karlson and Cornell 1998, Srivastava 1999). Fifth, regional richness is not independent of the local environment but is likely to reflect broad-scale gradients in local features such as productivity (Huston 1999). Covariance between regional richness and aspects of the local environment may inflate the apparent importance of regional pro-

cesses if local factors are not also considered. In the present study, we explore the effects of the fourth and fifth issues listed above on patterns of local and regional species richness.

We compiled data from published and unpublished surveys to examine the relationship between local and regional species richness in freshwater crustacean zooplankton. The complete data set included lists of species found in samples taken from 2832 lakes, ponds, and reservoirs (hereafter "lakes") in 27 geographic regions around the world (Fig. 1, Table 1). We used these data to explore three broad questions. (1) Is the qualitative pattern of local and regional richness in zooplankton more consistent with hypotheses of local or regional control? That is, does mean local richness approach an upper asymptote or increase continuously with increasing regional richness? (2) What is the effect of variation in the extent of the regional scale on patterns of local and regional diversity (the fourth issue listed previously)? (3) How does variation in the local environment among regions influence the relationship between local and regional diversity (the fifth issue listed previously)? In addition, we review the literature on dispersal limitation in zooplankton to compare the conclusions suggested by this analysis with those of other studies.

The first question asks whether local diversity in zooplankton is primarily limited by dispersal of species among lakes or by aspects of the local environment that exclude some members of the regional pool. A variety of observational evidence suggests that local and regional factors jointly regulate diversity in zoo-

TABLE 1. The studies included in the analysis.

Study	No. lakes	Area (km <sup>2</sup> )	Local richness	Regional richness	Description	Mean lake surface area (ha)†
1) Leibold (1999)	35	2910	5.5	28	ponds	...
<b>2) Pinel-Alloul et al. (1995)</b>	54	$3.0 \times 10^5$	8.5	32	lakes	208 (36–721)
3) Keller and Conlon (1994)	60	560	9.1	28	lakes	30 (1.8–175)
<b>4) Kling et al. (1992)</b>	45	24 300	3.9	9	lakes	50 (0.1–422)
5) Tessier and Horwitz (1990)	147	$1.2 \times 10^5$	7.8	69	lakes	82 (5–1620)
6) Keller and Pitblado (1989)	137	$1.2 \times 10^5$	11.3	38	lakes	2915 (90–65 506)
<b>7) Sutherland (1989)</b>	50	5 940	7.9	44	lakes	...
8) Carter et al. (1986), a) Labrador	93	$1.7 \times 10^5$	5.6	15	lakes	165 (5–1215)
b) Newfoundland	107	$3.3 \times 10^5$	5.4	19	lakes	153 (21–2500)
c) New Brunswick–Nova Scotia	142	$2.7 \times 10^5$	7.7	24	lakes	...
9) Keller and Pitblado (1984)	249	$1.5 \times 10^5$	9.0	39	lakes	...
10) Carter et al. (1980)	696	$2.9 \times 10^6$	10.4	45	lakes	...
11) Jacobi and Meijering (1978)	35	270	...	...	lakes and ponds, no copepods	...
12) Halvorsen and Gullestad (1976)	31	60 400	2.9	6	lakes and ponds	...
13) LaBarbera and Kilham (1974)	48	$6.1 \times 10^5$	...	...	lakes, no cladoc- cerans	...
14) O'Brien and Huggins (1974)	44	52 700	4.3	18	lakes and ponds	...
15) Carter (1971)	32	500	6.7	21.1	ponds	3 (0.1–17)
16) Patalas (1971)	45	210	8.5	28	lakes	69 (1.3–1007)
17) Roen (1968)	34	640	1.2	6	lakes and ponds	...
18) Patalas (1964)	52	...	4.8	38	lakes	16 (0.1–151)
19) Reed (1963)	105	$1.2 \times 10^7$	4.1	57	lakes and ponds	...
20) Roen (1962)	207	$3.5 \times 10^6$	4.5	29	lakes and ponds	...
21) Patalas (1954)	28	28 300	10.6	23	lakes	338 (3–1862)
22) J. E. Havel, unpublished data	203	$6.9 \times 10^5$	10.7	62	reservoirs and oxbow ponds	...
<b>23) K. Swadling, R. Pienetz, and T. Nogrady, unpublished data</b>	30	377 800	3.8	19	lakes	94.9 (1.1–1260)
24) K. Swadling, unpublished data	37	133	...	...	lakes and ponds, no cladocerans	...
<b>25) A. J. Tessier, unpublished data</b>	86	$5.4 \times 10^5$	7.5	45	lakes	10 (0.4–142)

Notes: Area is the landscape area over which lakes were sampled (defined in the text). Patalas (1964) did not present a map of the study lakes; therefore landscape area is not given. Local and regional richness are for planktonic crustacean species (cladocerans plus calanoid and cyclopoid copepods). Studies for which local and regional richness are not given did not report data for one or more taxonomic groups. Studies in boldface are included in the multiple regression to predict local richness (Table 5).

† Minimum–maximum is in parentheses.

plankton communities. Patterns in zooplankton diversity and species composition have been correlated with gradients in pH (Sprules 1975, Keller and Pitblado 1984, Carter et al. 1986), productivity (Dodson 1992, Leibold 1999), chemical ion concentrations (Pinel-Alloul et al. 1990, Tessier and Horwitz 1990), and predator communities (Brooks and Dodson 1965, Mazumder 1994). These results suggest that the local environment plays a major role in structuring communities, a conclusion that is supported by a number of experiments (Brezonik et al. 1993, Carpenter and Kitchell 1993, Lukaszewski et al. 1999, Shurin, 2000). However, even in studies that exhaustively sample local biotic and abiotic features of many lakes, considerable residual variation in zooplankton species composition remains unexplained (Pinel-Alloul et al. 1995). The influence of past colonization history is one potential explanation for the limited power of local features to predict species composition (Hubbell and Foster 1986, Jenkins and Buikema 1998). In addition, community membership is often related to lake surface area and geographical location (Carter et al. 1980, Hebert and

Hann 1986, Dodson 1992, Pinel-Alloul et al. 1995, Stemberger 1995), further suggesting that regional processes may be important in shaping zooplankton communities (Bengtsson 1991, Jenkins and Buikema 1998). A variety of evidence supports both local and regional hypotheses of zooplankton community structure; however the relative contributions of local and regional processes remain unknown.

The second question deals with the influence of the extent of the regional scale on the shape of the relationship between local and regional diversity. The definition of the regional scale clearly influences the estimate of regional richness and may therefore affect the shape of local–regional richness patterns as well (Caley and Schluter 1997, Angermeier and Winston 1998, Karlson and Cornell 1998, Srivastava 1999). Regional richness increases as more sites are sampled over greater areas according to the species–area relationship whereas local richness is not expected to vary systematically with the regional scale. The choice of regional scale should ideally reflect the pool of colonists available to invade local sites and therefore depends on the

geographic ranges and characteristic distances over which the component species disperse. Since little is known about the dispersal abilities of zooplankton, we used both scale-dependent and scale-independent estimates of regional richness to test for saturation. The contrast between the conclusions suggested by the two tests indicates the effect of variation among studies in geographic extent on patterns of local and regional diversity.

To explore the effects of variation in local features among regions (the third question), we selected studies in the survey that reported limnological data from the lakes sampled. The most commonly reported variables were pH, conductivity, total dissolved solids, maximum depth, surface area, and elevation. Local features were entered into a stepwise multiple regression model, along with residual regional richness, as predictors of local species richness. The goal of this analysis was to compare the predictive power of regional richness on local richness with several aspects of the local environment. Because only limited limnological information was available for the lakes in our data set, the actual contribution of local features, relative to regional richness, could not be completely assessed. However, the data allowed us to ask how the power of residual regional richness to predict local richness compares to that of several key local features.

#### METHODS

##### *Study selection and data extraction*

We searched the literature for studies that surveyed zooplankton in at least 20 lakes, ponds, and reservoirs within a geographic region. A minimum of 20 lakes was required because Patalas (1990) found that >90% of the species present in a region were generally found by sampling 20 lakes. We used electronic databases (BIOSIS and Web of Science) to find recent studies and searched the literature cited in those studies for older references. Surveys were included that reported the incidence or abundance of species by lake or the proportion of lakes in which each species in the region was found. Data from four unpublished lake surveys were also included. One was a survey of lakes, reservoirs, and oxbow ponds throughout Missouri, Arkansas, and Oklahoma (J. E. Havel, *unpublished data*). The others were surveys of high elevation lakes in Maine (A. J. Tessier, *unpublished data*), lakes in the Yukon and Northwest Territories of Canada (K. Swadling, R. Pienitz, and T. Nogrady, *unpublished manuscript*), and lakes and ponds near Kuujuarapik in Quebec (K. Swadling, *unpublished data*). Each study was considered a single, independent "region" except for Carter et al. (1986) who reported data from three regions (Labrador, Newfoundland, and New Brunswick–Nova Scotia) separately. Only the lakes in northwestern Ontario from Keller and Pitblado (1989) were included since the others did not meet our selection criteria.

Table 1 gives a list of all studies included in the data set and Fig. 1 shows their location.

Mean local and regional richness were calculated for each study in the data set (Table 1). We defined local richness for each lake as the number of species found at a single sampling location within the lake on one date. Zooplankton show pronounced seasonal succession (Hutchinson 1967, Sommer 1989) as well as strong spatial segregation among habitats within lakes (Patalas and Salki 1993, Arnott et al. 1998). The number of species found very often increases with both the number of dates and the number of stations sampled per lake (Patalas and Salki 1993, Arnott et al. 1998). The hypothesis that local interactions limit the diversity of local assemblages is based in part on interactions among coexisting species. Temporal or spatial segregation can permit species to occupy the same lake that would otherwise be excluded by interspecific interactions. We therefore represented local richness as the number of species coexisting in the water column at the same time. Although zooplankton tows might sample multiple vertical habitats, especially in stratified lakes, many species migrate vertically (Hutchinson 1967) and potentially interact with other species found throughout the water column. We therefore considered the number of species found in a sample from one station to be the most reasonable representation of local richness.

Mean local richness was calculated by averaging among all lakes in each study and regional richness was the cumulative number of species identified. For studies that reported the percentage of lakes in which each species was found, mean local richness was calculated as the sum of the proportional lake occupancies for all species in the region. For studies that reported the results of multiple sampling dates from each lake, local and regional richness were calculated for each sampling period separately and then averaged across sampling dates. One older study (Patalas 1954) differentiated among a number of subspecies that are now considered to be a single species showing variable morphologies. These subspecies were combined into a single species in our data set. Studies also varied somewhat in their taxonomic resolution in that a few reported single taxa that likely included groups of species. However, variance due to taxonomic resolution, as well as other methodological differences, was likely to have been small relative to the range in diversity seen on a global scale. In addition, it is unlikely that such variance was biased in any particular direction but probably only weakened our ability to detect patterns by adding noise.

The extent of the regional scale was estimated for each survey as both the area of the landscape (hereafter "landscape area") and the number of lakes sampled. Landscape area was measured by drawing a rectangle around the lakes on the map and measuring the area enclosed by the rectangle. That is, we drew north–south

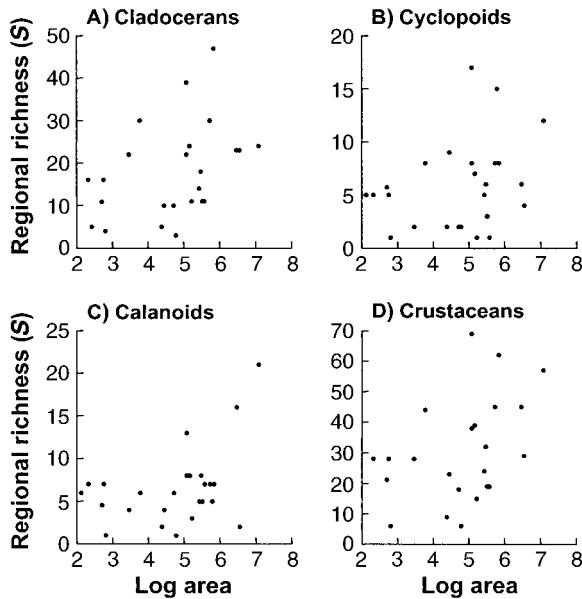


FIG. 2. Regional richness vs. landscape area (measured in square kilometers) over which lakes were sampled for (A) cladocerans, (B) cyclopoid copepods, (C) calanoid copepods, and (D) all planktonic crustaceans. Landscape area is defined in the *Methods: Study selection*. The equations for the species–area relations are given in Table 2.

oriented lines at the eastern- and western-most lakes and east–west oriented lines at the northern- and southern-most lakes. The size of the rectangle was measured with a ruler, the area calculated and converted to square kilometers using the scale given on the map. By this measure, the studies in our data set varied in area over almost five orders of magnitude (Table 1, Fig. 2). More sophisticated measures of extent would not significantly alter our conclusions over such a large range of variation. We used both landscape area and the number of lakes sampled as measures of regional extent since surveys varied in the density (number per area) of lakes sampled. The number of species is expected to increase with the number of lakes sampled; however the slope of the sampling curve depends on the spatial distribution of the lakes (Patalas 1990). We corrected for scale using both number of lakes sampled and landscape area in order to determine whether the metric of regional extent influenced our conclusions. The map for Sutherland (1989) was taken from Siegfried et al. (1989). State maps were used to calculate landscape area for the ponds in Leibold (1999) and the ponds and reservoirs in J. E. Havel (*unpublished data*). A map of the lakes in the Maine survey (A. Tessier, *unpublished data*) was generated from the geographic coordinates for the lakes using ARC/INFO (ESRI 1995).

#### Data analysis

The relationship between local and regional richness was tested by linear regression. All analyses were performed using SYSTAT version 8.0 (Wilkinson 1998).

Curvilinearity or decreasing slope was tested by inclusion of a quadratic term in the regression of local on regional richness. Although curvilinearity does not necessarily imply saturation (i.e., further increases in regional richness will not result in greater local richness), we consider evidence for decreasing slope to indicate that local richness approaches some upper limit. We use the terms “saturated” and “curvilinear” interchangeably to describe a function with a decreasing slope. A quadratic function does not accurately describe the relationship between local and regional richness in the case of saturation since mean local richness is not expected to decrease at high levels of regional richness (the downward portion of the hump-shaped curve produced by a second-order term). However, the significance of the inclusion of the quadratic term provides a convenient statistical test for a declining slope (Caley and Schluter 1997, Karlson and Cornell 1998).

The relationships between regional richness and both landscape area (the species–area curve of the form  $S = cA^z$ ) and number of lakes sampled ( $S = cN^z$ ) were determined by nonlinear regression for each taxonomic group. The parameters  $c$  and  $z$  represent the slope and the intercept of the log–log relationship between species richness and area, and were estimated by maximum likelihood methods using the NONLIN routine in SYSTAT (Wilkinson 1998). The residuals of the species–area (“residual regional richness”) and species–lakes (“lakes residual richness”) curves were plotted against mean local richness and the significance of the quadratic term was examined as a scale-independent test for saturation. The effect of variation among studies in the extent of the regional scale on patterns of local and regional species richness is shown by the contrast between the scale-dependent and scale-independent tests.

To compare the power of residual regional richness to predict local richness with that of several local features, we performed a stepwise regression using backward elimination procedure for 204 lakes from the data set for which limnological information was available. The local features that were evaluated included lake surface area, maximum depth, elevation, pH, and specific conductance. We estimated conductance for several studies reporting total dissolved solids (TDS) by using the data in Rohde (1949) to generate a regression equation for the relationship between TDS and conductance. Residual regional crustacean richness was used as a scale-independent estimate of regional richness. All of the limnological variables were found to be non-normally distributed by a Lilliefors’ test and so were  $\log_{10}$ -transformed. Residual regional richness was also non-normal; however, because negative values were common, residual regional richness could not be log-transformed. A number of other transformations were attempted but all failed to produce a normal distribution. Because the normal probability plot for residual regional crustacean richness did not appear to

TABLE 2. The relationship between regional richness of cladocerans, cyclopoid and calanoid copepods, and all planktonic crustaceans and (A) landscape area (Fig. 2) and (B) the number of lakes sampled.

Group	No. regions	$c$	$z$	$R^2$
A) Species–landscape area relations ( $S = cA^z$ )				
Cladocerans	24	$7.01 \pm 3.76$	$0.08 \pm 0.04$	0.77
Cyclopoids	25	$2.55 \pm 1.59$	$0.07 \pm 0.05$	0.71
Calanoids	25	$0.93 \pm 0.64$	$0.16 \pm 0.05$	0.77
All crustaceans	23	$10.88 \pm 5.67$	$0.09 \pm 0.04$	0.81
B) Species–lakes relations ( $S = cN^z$ )				
Cladocerans	25	$4.84 \pm 2.48$	$0.30 \pm 0.11$	0.81
Cyclopoids	26	$2.73 \pm 1.86$	$0.18 \pm 0.15$	0.71
Calanoids	26	$1.34 \pm 0.75$	$0.36 \pm 0.11$	0.77
All crustaceans	24	$8.67 \pm 4.13$	$0.29 \pm 0.10$	0.84

Note: Parameter values are  $\pm 1$  SE.

be extremely non-normal, we used raw values of residual regional richness. All independent variables, including residual regional richness, were standardized to the same scale after transformation by subtracting the mean for that variable and dividing by the standard deviation. Each variable and its quadratic were first entered together into a linear regression as predictors of local crustacean richness. Variables or second-order terms that showed no relationship ( $P > 0.05$ ) were eliminated from the overall model. The remaining variables were then included in the backwards stepwise regression model. Correlations among the variables were tested by Pearson correlation coefficient.

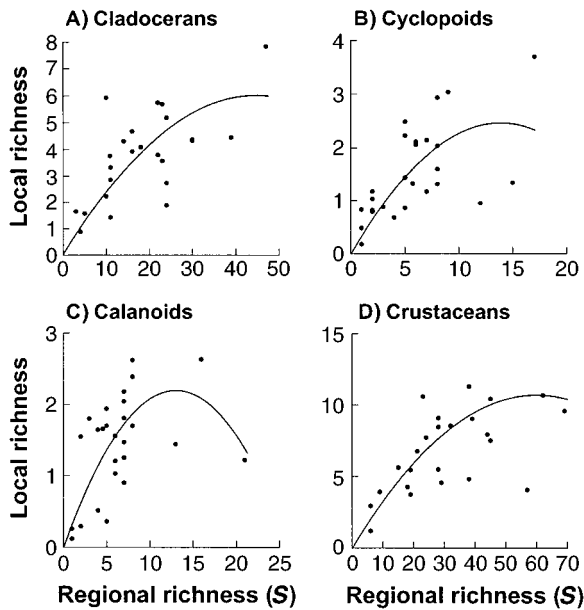


FIG. 3. Local vs. regional species richness for (A) cladocerans, (B) cyclopoid copepods, (C) calanoid copepods, and (D) all planktonic crustaceans. The second-order term is significant in each case. The equations and significance levels for the regressions are given in Table 3.

## RESULTS

Regional richness, the cumulative number of species found, was strongly related to both landscape area (Fig. 2, Table 2A) and the number of lakes sampled (Table 2B). All three groups of crustacean taxa showed increases in regional richness as more lakes were sampled over larger areas. Studies varied over nearly five orders of magnitude in landscape area (Table 1, Fig. 2) and over two orders of magnitude in the number of lakes sampled (Table 1). Landscape area and the number of lakes sampled were strongly correlated among studies (Pearson correlation, after both variables were  $\log_{10}$ -transformed,  $R_s = 0.63$ ,  $P < 0.001$ ).

When each study in the survey was considered an independent region, local richness showed strong evidence for saturation at high levels of regional richness (Fig. 3). The quadratic term contributed significantly to the fit of the regression for each taxonomic group (Table 3). However, when mean local richness was plotted against residual regional richness (the residuals of the species–area curve), the quadratic term was insignificant in every case although the first-order terms were highly significant (Fig. 4, Table 4). Using the relationship between regional richness and the number of lakes sampled to correct for variation in regional extent produced similar patterns (Table 4B). When lakes residual richness was plotted against mean local richness, the second order term was insignificant for

TABLE 3. The regression equations for the local vs. regional richness curves ( $Y = bX + cX^2$ ; Fig. 3)

Group	$b$	$c$	$R^2$
Cladocerans	$0.27 \pm 0.04^{***}$	$-0.003 \pm 0.001^{**}$	0.89
Cyclopoids	$0.36 \pm 0.05^{***}$	$-0.013 \pm 0.004^{**}$	0.85
Calanoids	$0.34 \pm 0.03^{***}$	$-0.013 \pm 0.002^{***}$	0.89
All crustaceans	$0.36 \pm 0.04^{***}$	$-0.003 \pm 0.001^{***}$	0.92

Notes: No constant was included because the relationship is expected to pass through the origin. None of the intercepts were significant when they were included. All regression models are significant at  $P < 0.0001$ . Notation is as in Table 2.

\*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

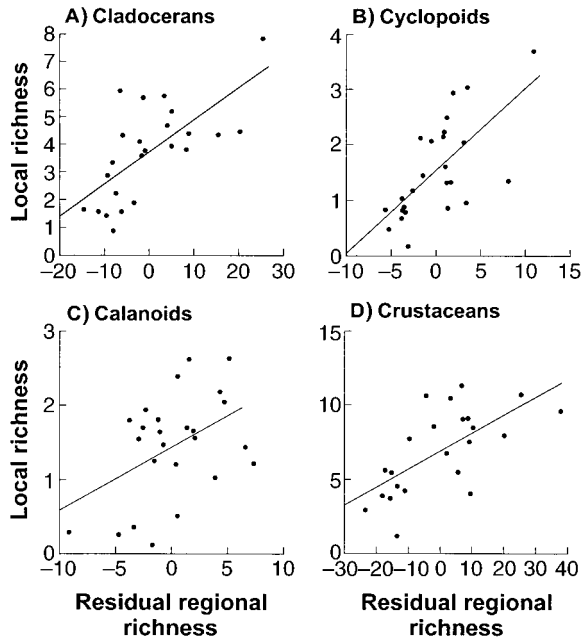


FIG. 4. Local richness vs. residual regional richness for (A) cladocerans, (B) cyclopoid copepods, (C) calanoid copepods, and (D) all planktonic crustaceans. The equations and significance levels for the regressions are given in Table 4.

every group except calanoid copepods (Table 4B). Residual regional richness was not significantly correlated with the number of lakes sampled for any taxonomic group, nor was lakes residual richness correlated with landscape area (Pearson correlation, after both measures of extent were  $\log_{10}$ -transformed, all  $P$  values  $>0.1$ ).

The stepwise multiple regression model for the 204 lakes from which limnological data were available retained pH,  $\text{pH}^2$ , and residual regional richness as predictors of local crustacean richness (Table 5). These variables, as well as elevation and conductivity, showed significant relationships with total crustacean richness when entered into simple linear regressions. Lake depth, surface area, and their quadratics, did not

TABLE 5. Multiple regression for the effect of local features and residual regional richness on local richness in 204 lakes in five regions. (A) ANOVA for the complete multiple regression model. (B) Parameter estimates and  $t$  test for the deviation of fitted values from zero.

A) Analysis of variance					
Source	ss	df	$F$	$P$	$R^2$
Model	892.3	3	62.1	<0.0001	0.48
Error	958.0	200			
Total	1850.3	203			
B) Parameter estimates					
Variable	df	Estimate	$t$	$P$	
Intercept	1	6.65	26.86	<0.0001	
pH	1	0.99	3.71	0.0003	
$(\text{pH})^2$	1	-0.45	-2.84	0.005	
Residual regional richness	1	2.40	10.44	<0.0001	

show significant regressions on local richness and were therefore eliminated. In the final model, residual regional richness contributed most strongly to predicting local richness, followed by pH and its second order term (Table 5). Correlation coefficients among the predictor variables are given in Table 6. Although there were significant correlations among the independent variables included in the final model, the tolerance values (one minus the multiple correlation coefficient between each predictor and all the others) were all  $>0.1$  and the absolute  $t$  values for all of the predictors were  $>2$  (Table 5). In this situation, multicollinearity among the independent variables does not have a large influence on the regression coefficients (Wilkinson 1998).

## DISCUSSION

We found that local species richness in freshwater crustacean zooplankton was positively related to the number of species in the surrounding area, a result that may suggest a large role for dispersal limitation in shaping community structure. Saturated patterns of local and regional richness for crustacean zooplankton were driven by the artifact of differences among surveys in the size of the geographical region in which

TABLE 4. The regression equations for local richness vs. (A) residual regional richness (see Fig. 4) and (B) lakes residual richness.

Group	Constant	$b$	$c$	$R^2$
A) Local vs. residual regional richness ( $Y = \text{constant} + bX + cX^2$ )				
Cladocerans	$3.88 \pm 0.35^{***}$	$0.13 \pm 0.03^{***}$	$-0.001 \pm 0.002$	0.48
Cyclopoids	$1.60 \pm 0.17^{***}$	$0.16 \pm 0.04^{***}$	$-0.004 \pm 0.006$	0.46
Calanoids	$1.56 \pm 0.16^{***}$	$0.08 \pm 0.03^*$	$-0.008 \pm 0.006$	0.27
All crustaceans	$7.46 \pm 0.57^{***}$	$0.14 \pm 0.03^{***}$	$-0.003 \pm 0.002$	0.49
B) Local vs. lakes residual richness ( $Y = \text{constant} + bX + cX^2$ )				
Cladocerans	$3.49 \pm 0.41^{***}$	$0.07 \pm 0.04$	$0.002 \pm 0.003$	0.26
Cyclopoids	$1.67 \pm 0.18^{***}$	$0.17 \pm 0.05^{**}$	$-0.010 \pm 0.007$	0.38
Calanoids	$1.57 \pm 0.14^{***}$	$0.10 \pm 0.04^*$	$-0.010 \pm 0.004^*$	0.23
All crustaceans	$7.59 \pm 0.71^{***}$	$0.11 \pm 0.04^{**}$	$-0.004 \pm 0.003$	0.26

Notes: Notation is as in Table 2. The independent variables are defined in the Results.  
\*  $P \leq 0.05$ ; \*\*  $P \leq 0.01$ ; \*\*\*  $P \leq 0.001$ .

TABLE 6. Pearson correlation coefficients among the standardized independent variables that were examined for inclusion in the multiple regression model shown in Table 5.

Variable	Elevation	Area	Depth	Conductivity	pH
Area	-0.268**				
Depth	0.173	0.484***			
Conductivity	-0.327***	-0.034	-0.187		
pH	-0.185	0.120	0.041	0.616***	
Residual richness	0.282**	-0.219*	-0.084	-0.593***	-0.733***

Note: *P* values are Bonferroni probabilities.  
 \* *P* ≤ 0.05; \*\* *P* ≤ 0.001; \*\*\* *P* ≤ 0.0001.

lakes were sampled. Using the residuals of the species–landscape area or species–lakes relations as scale-independent estimates of regional richness produced linear patterns of local vs. regional richness. This result supports the contention of Cornell and Karlson (1997) that unsaturated patterns of local and regional richness are common among a diverse array of organisms. Many studies have taken linear patterns of local and regional diversity to indicate that communities are open to invasion by species from the region as dispersal exerts dominant influence, relative to local interactions, in constraining species distributions and limiting local diversity (Cornell and Karlson 1997 and references therein). However, a number of observational and experimental studies have concluded that local interactions play a dominant role to dispersal limitation in shaping zooplankton species richness. Below we discuss evidence for the importance of dispersal and local processes in structuring zooplankton communities and its implications for the present study.

Several lines of observational evidence suggest that zooplankton are highly effective dispersers over distances on the order of 100 km. For instance, Pinel-Alloul et al. (1995) used an ordination approach to determine how much of the variation in zooplankton community structure among 54 lakes could be explained by an exhaustive list of local chemical, biological, and morphometric features, spatial location (the geographic coordinates of the lakes), and an interaction between the two (spatial gradients in physical conditions). The spatial component can be interpreted as a proximity effect or contagion arising from neighborhood dispersal patterns. Using several different methods, Pinel-Alloul et al. (1995) found that the purely spatial component explained considerably less of the variance in community structure than did either the local or local by spatial interaction terms and that the spatial term was often not significantly different from zero. Their results suggest that zooplankton dispersal is fairly uniform among lakes within a geographic area of  $\sim 3 \times 10^5$  km<sup>2</sup>. In addition, the rapid spread of some invasive zooplankton species into new habitats across broad geographic areas suggests that these species are highly effective dispersers over long distances (Havel and Hebert 1993, Havel et al. 1995).

Several experiments also suggest that zooplankton disperse rapidly within relatively restricted geographic

areas and that local interactions play a dominant role in structuring communities. Jenkins and Buikema (1998) constructed artificial ponds and allowed them to be colonized naturally over time. The number of zooplankton species found in the ponds increased over the first 6–7 months after the ponds were filled, after which local richness remained constant, although new species continued to appear for the entire year of the study (Fig. 3 and Table 4 in Jenkins and Buikema 1998). This result suggests that colonization events for many species occur on the order of days to months rather than years and that sites rapidly achieve colonization–extinction balance. Similarly, J. B. Shurin and G. M. Cohen (*unpublished data*) placed artificial pools at four distances (5, 10, 30, and 60 m) from two natural ponds to serve as targets for colonists. An average of 0.25 species per day colonized the pools. These experiments suggest that zooplankton move rapidly over fairly short distances, and that dispersal only limits the diversity of very young communities.

Finally, Shurin (2000) performed field enclosure experiments in southwestern Michigan in which an average of 15.0 new crustacean and rotifer species from the region were introduced into the resident communities of 11 fishless ponds. The number of new species found in each of the ponds averaged only 0.5 throughout the experiments, suggesting that most species capable of invading the ponds were already present. In addition, four times as many species invaded when the resident assemblage was experimentally perturbed by filtering than when the local community was intact. This treatment showed that local biotic interactions played a major role in excluding invaders. Taken together, these results support the hypothesis that species richness in zooplankton communities is under strong local control and that dispersal at fairly small regional scales is of minor importance in generating differences among lakes.

In contrast, a number of studies have shown high genetic differentiation among zooplankton populations in lakes separated over very short distances (reviewed in Boileau et al. 1992 and De Meester 1996). High divergence among lake populations may suggest that gene flow is restricted due to limited dispersal. However, differences in the local selective environments may favor some genotypes in certain lakes but not others. Strong site-specific selection is another viable ex-

planation for the pattern of large genetic differentiation at small spatial scales. A number of studies have documented high genetic variability for ecologically important traits (De Meester 1996, Tessier et al. 2000), suggesting that selection may favor different genotypes in different environments. In addition, Tessier et al. (1992) showed rapid evolution of body size in *Daphnia* in response to fluctuating selection within a season, indicating that natural selection can produce local adaptation over very short time scales. The experimental studies described above provide support in favor of local selection over dispersal limitation as an explanation for high among-population genetic differentiation in zooplankton.

Observational evidence for dispersal limitation comes largely from the postglacial colonization of lakes across broad geographic scales (Carter et al. 1980, Hebert and Hann 1986, Boileau and Hebert 1991, Stemmerger 1995). Distributions of some species, particularly calanoid copepods, appear to be defined by patterns of glaciation and surface water movement, suggesting that these species recolonize slowly following the retreat of glaciers. The contrast between such large-scale patterns and the results of studies at smaller scales described above suggests that strong dispersal limitation in zooplankton is only evident at very broad scales. That is, communities may be ecologically saturated with respect to the pool of species within a relatively restricted area. Yet species in different biogeographic regions may still be excluded by limited long-distance dispersal. In this case, it makes little sense to ask whether local or regional processes dominate in structuring communities. Rather, the question becomes at what scale do regional processes contribute to determining species composition? In the example of zooplankton, the available evidence suggests that dispersal limitation only plays a detectable role at very large scales and that local interactions dominate in generating differences in composition among lakes separated over shorter distances.

To understand why including studies at different regional extents should produce saturated patterns, it is helpful to employ a graphical approach using species-area relations. If the underlying relationship between local and regional richness is positive over some or all of its range, then large regions are expected to have shallower slopes to their local-regional diversity curves than smaller regions (Fig. 5). This pattern results from the expectation that the cumulative number of species found ( $S$ ) will increase according to  $cA^z$  whereas local richness remains constant as the extent of the regional scale ( $A$ ) expands. Since the curves must pass through the origin, the slope of the relationship decreases at broader regional scales. In this case, highly diverse regions with large areas will fall to the right on the  $x$ -axis of Fig. 5 while regions of low diversity, whatever their area, will cluster to the lower left. If regions of variable extents are included on the same

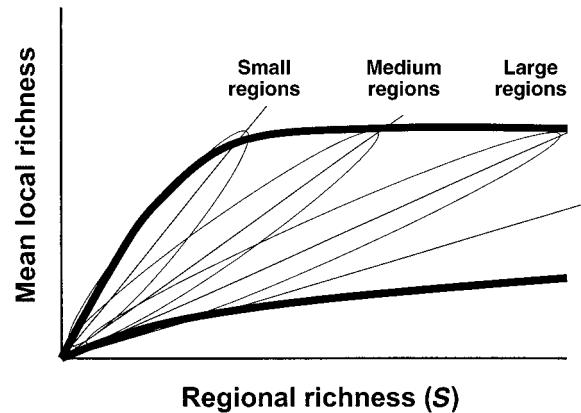


FIG. 5. A graphical model for patterns of local and regional richness with variable regional scales. The lines radiating out from the origin represent local vs. regional curves for small (steep slopes) to large (shallow slopes) regions. The ellipses represent the range of data expected for each curve, and the heavy lines show the area where points are expected to fall if regions of different sizes are included on the same graph.

graph, then most regions will fall within the area bounded by the thick lines in Fig. 5, resulting in apparent saturation of local diversity. Srivastava (1999) has recently provided a rigorous mathematical formulation for this simple graphical model. The pattern predicted by this model is remarkably similar to that observed for zooplankton in Fig. 3 and the one shown by Angermeier and Winston (1998) for fishes in rivers. It is interesting to note that although dispersal limitation becomes more important at broad scales (i.e., species are better able to disperse short distances than long distances), the slope of local vs. regional richness functions become shallower with increasing regional extent (Fig. 5), and may eventually become indistinguishable from zero (Angermeier and Winston 1998). Patterns of local and regional richness may therefore suggest saturation at broad scales but not at smaller regional scales, whereas the importance of dispersal in limiting local diversity is expected to increase at larger regional scales.

The influence of scale on the test of the main hypothesis (saturation vs. unsaturation) in studies where the region is defined by the observer raises the question of the appropriate choice of the regional scale. Regions ideally represent the pool of species from which local sites draw colonists. If the range over which species disperse is unknown, then it will likely prove impossible to operationally define the regional scale. In addition, if species vary greatly in their dispersal abilities, then any given regional scale may include many metapopulations (groups of patches connected by dispersal) of some species and still be smaller than the average size of a metapopulation for other species. The first set of species are poor dispersers while the second consists of good dispersers with wide-ranging propa-

gules. In this case, there is no appropriate geographical definition of the region and tests of saturation may either overestimate or underestimate regional richness. Because dispersal, especially long-range or highly infrequent colonization, is difficult to measure directly in many organisms, geographically defined regional pools may be inadequate for estimating the degree of unsaturation in communities.

Westoby (1998) presents an approach similar to ours that entails comparing species–area relations for different regions. He proposed that, if the species–area curves for different regions converge on similar values at small scales, then this suggests that biotic interactions limit diversity among coexisting species. Westoby's method deals with the issue of identifying the correct local scale when the set of species comprising a local assemblage is unknown. Our data do not allow us to explore variation in the definition of the local scale because the volume of water sampled is unknown for the majority of surveys. However, the studies included employed a standard sampling method of drawing a plankton net through the water column, usually at the site of maximum known depth. The species found by this approach are the group most likely to interact with one another. Although there is often considerable habitat segregation by depth, many species also migrate vertically so that species typically found at different depths will often overlap in their habitat use to different degrees (Hutchinson 1967). Our definition of the local species pool is the most consistent that is possible with data drawn from such a large variety of sources. Caley and Schluter (1998) point out that convergence at very small scales may result from rarefaction or underrepresentation of rare species when sample sizes are small. Our estimates of local richness were unlikely to have been affected by rarefaction as zooplankton samples, even those from small ponds, typically contain very large numbers of individuals.

Residual regional richness was an important predictor of local richness relative to the few local environmental factors for which data were available for comparison. Only pH and its quadratic improved the fit of the model to predict local crustacean richness relative to that with only residual regional richness (Table 5). The multiple regression model indicates that the power of residual regional richness to predict local richness was large relative to the few local environmental parameters considered. However, many important features, including productivity and aspects of the biota, were not accounted for in this analysis. Estimating the actual contributions of local factors and residual regional richness would require much more complete limnological information.

It is interesting to note that surface area was not a major predictor of local richness among the lakes in this survey. Dodson (1992) found that surface area was the most important predictor of local species richness for pelagic crustacean zooplankton. However, the range

of surface areas among the lakes in our data set is much smaller than the range of lakes considered by Dodson; therefore our ability to detect area effects is weaker. In addition, Dodson's survey included only pelagic species whereas we included all free-living crustacea. Many more littoral species are encountered when sampling lakes with small surface areas, perhaps elevating the estimate of local diversity for small lakes. The differences between the results of the present study and Dodson (1992) are therefore likely due to methodologies and the selection of study lakes.

Another explanation for linear patterns of local and regional diversity in the presence of strong local interactions is that zooplankton communities are unsaturated on evolutionary time scales but not in ecological time (Cornell and Lawton 1992, Rosenzweig 1995). That is, the size of the regional pool is limited by its history of extinction and speciation events. In this case, communities may be open to invasion by the evolution of new species, although existing species, either within the region or present globally, are excluded by local conditions. Whether we expect to see saturation on an evolutionary time scale is a different issue from ecological saturation; however, the process of speciation may influence patterns of local and regional diversity. Evolutionary unsaturation is therefore one potential explanation for unsaturated patterns of species richness in organisms such as zooplankton that interact strongly within local sites.

The issues that arise when drawing inferences from local vs. regional diversity curves illustrate the common problem in ecology of multiple potential explanations for any given pattern. The available evidence suggests that unsaturated patterns of diversity in freshwater zooplankton reflect either dispersal limitation at very broad geographic scales or unsaturation in evolutionary time. However, such patterns have often been interpreted as suggesting that local processes in general and interspecific interactions in particular exert weak influence in structuring communities (Cornell and Karlson 1997 and references therein). Zooplankton present a somewhat unique case in that we can compare evidence from geographic patterns of local and regional diversity with experimental and observational studies for the importance of dispersal and local interactions. A range of evidence suggests that dispersal only limits the diversity of local zooplankton communities at the broadest regional scales. The unsaturated pattern of local and regional diversity also did not reflect the large body of evidence showing that local processes, including interspecific interactions, play major roles in shaping zooplankton species composition. Comparing the results of different approaches indicates that caution is warranted when using local vs. regional diversity curves to draw inferences about the roles of dispersal and local processes in limiting local diversity. We argue that unsaturated patterns of diversity provide relatively weak evidence for the importance of dispersal limita-

tion and local interactions when compared with the larger body of experimental and observational work in zooplankton community structure. A pluralistic approach combining observational and experimental tests with theoretical explorations allows for much more robust conclusions about the control of community structure.

#### ACKNOWLEDGMENTS

Steve Kahl, William Keller, Clifford Siegfried, and Alan Tessier generously provided raw data from published studies and Thomas Nogrady, Reinhard Pienitz, Kerrie Swadling, and Alan Tessier provided unpublished data. Shelley Arnott, Joy Bergelson, Sarah Gergel, Michael Huston, Cathy Pfister, Jack Sepkoski, James Servidea, Alan Tessier, William Tonn, Tim Wootton, and the U.C. Enlightenment at Noon group made many helpful suggestions for the analysis and manuscript. Kashka Kubzdela translated a paper from Polish, Sarah Gergel created a map of the Maine lakes, and Spencer Hall created the map of the world. J. Shurin was supported by a Grant in Area of National Need from the U.S. Dept. of Education and by NSF Dissertation Improvement Grant DEB 99-72656, J. Havel by NSF grant DEB 93-17869 and by the Missouri Department of Conservation, and M. Leibold was supported by NSF grant DEB 95-09004. This is Kellogg Biological Station contribution no. 892.

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