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Zooplankton spatial patterns in two lakes with contrasting fish community structure

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Abstract

Horizontal and temporal patterns in crustacean zooplankton communities were analyzed in two small, oligotrophic lakes which were morphologically and chemically similar, but had contrasting fish communities. Ranger Lake was dominated by two bass species and the planktivores numbered <25 ind. ha^{-1}. Mouse Lake had no large piscivores and planktivores numbered >1200 ind. ha^{-1}. There were significant differences in the distribution of zooplankton taxa and size classes between sampling stations. In Ranger Lake, the smallest size classes were more abundant at the deeper stations and the larger individuals were more abundant at the shallower stations. In Mouse Lake, the smaller individuals were more common at the shallow stations and the larger individuals were more common at the deeper stations. These differences suggest medium scale patterns induced by vectorial forces, but modified by species specific migration patterns. We tested the hypothesis that horizontal heterogeneity should be influenced by planktivore density and found that none of the taxa showed significant between-lake differences in the variance-mean regressions. We also tested the hypothesis that larger taxa should be more heterogeneous and we found that cladocerans were more heterogeneous than copepods and nauplii. In terms of sampling methodology our data suggest that the between-station variability was so high that a single mid-lake sample would certainly lead to completely unacceptable errors in the estimation of population densities and biomasses.

Introduction

Horizontal patchiness in zooplankton spatial distributions has been recognized for almost 100 years (Reighard, 1894; Ward, 1896; Birge, 1987; Moberg, 1918, 1921; Southern & Gardiner, 1926; Naber, 1933; Ricker, 1937; Langford, 1938; reviewed by Baldi *et al.*, 1945; Welch, 1951). Malone & McQueen (1983) grouped some of the more recent studies into four categories representing: (1) large scale patterns induced by vectorial forces (Patalas, 1969; Stavn, 1971) or by seasonal (Watson, 1976; Gannon, 1975; Urabe, 1989) and morphometric factors (Davis, 1969; Urabe & Murano, 1986), (2) medium scale patterns caused by wind induced currents (Ragotzkie & Bryson, 1953; Tonelli & Tonelli, 1960; Colebrook, 1960a; McNaught & Hasler, 1961; Dumont, 1967; George & Edwards, 1976; Riley, 1976) or by the combined effects of shore avoidance and vertical migration (Burckhardt, 1910; Siebeck, 1964, 1968; Healey, 1967; Ringleberg, 1969), (3) small scale patterns associated with Langmuir (1938) circulation cells (Neess, 1949; Stommel, 1949; Stavn, 1970, 1971; George & Edwards, 1973), and (4) swarms caused by behavioural interactions (Birge, 1897; Moberg, 1918; Kunne, 1925; Southern & Gardiner, 1926; Tonelli, 1958; Colebrook, 1960b; Steven, 1961; Klemetsen, 1970; Nie *et al.*, 1980). Recently, Pinel-Alloul *et al.* (1988) used a factorial design to investigate zooplankton distribution patterns and found that variability increased with density (Downing *et al.*, 1987), depth and sampling area, but decreased with body size. They noted that these patterns were consistent with the hypothesis that heterogeneity should be positively related to predation pressure (May, 1978; Rasmussen & Downing, 1988) and negatively related to competition (Diamond, 1979).

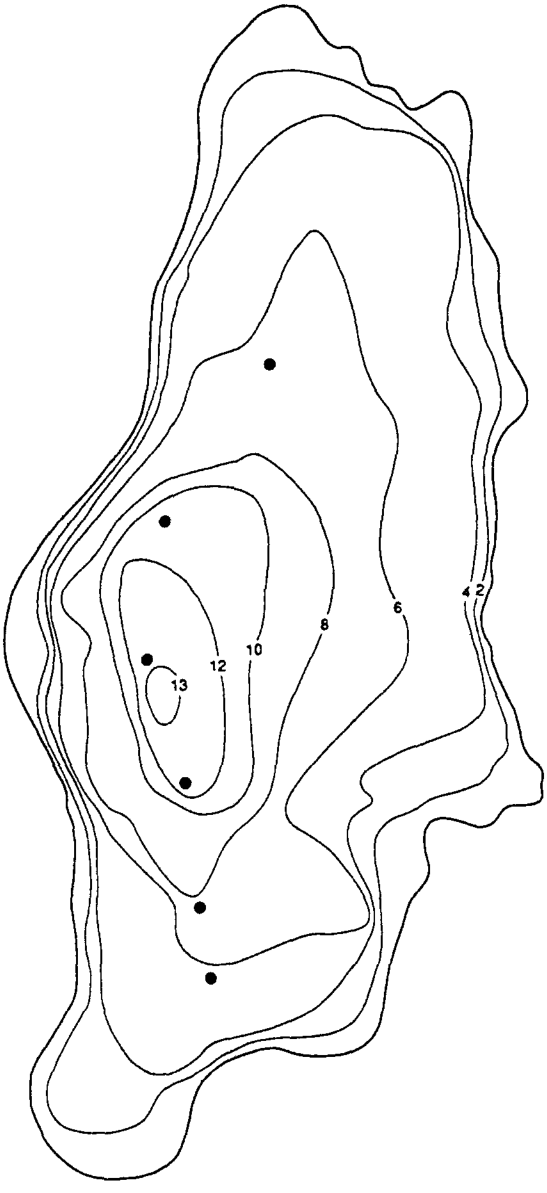

Fig. 1. Bathymetric map of Ranger Lake. The total surface area is 11.25 ha and the mean depth is 5.62 m. Stations 1 (bottom) through 6 (top) are shown as solid dots.

In the study that follows we have examined seasonal changes in the distribution patterns of crustacean zooplankton in two small, oligotrophic lakes located in south-central Ontario. The two lakes are morphologically and chemically similar, but have very different fish communities which are associated with zooplankton assemblages that appear to be strongly structured by top-down (McQueen *et al.*, 1986, 1989, 1992) food web cascades (Carpenter *et al.*, 1985, 1987). These food web differences provide an opportunity to explore between-lake and within-lake spatial and temporal variations in zooplankton distributions.

Our hypotheses are: (1) that horizontal zooplankton distributions should be more heterogeneous in Mouse Lake, which contains very high planktivore densities, and (2) that this effect should be stronger for larger zooplankton. At an empirical level, we also examine the relationship between sampling effort (samples per ha) and the level of precision required to adequately quantify population abundance, species composition, biomass and size frequency.

Site description

Both Ranger and Mouse Lakes are small, moderately humic, oligotrophic lakes located in south-central Ontario. Ranger Lake (Fig. 1) has a surface area of 11.25 ha, a mean depth of 5.62 m, a maximum depth of 13.0 m and a shoreline length of 1.63 km. The littoral substrate is predominately sand, the profundal substrate sedimentary mud and the macrophyte cover sparse. Mouse Lake (Fig. 2) has a surface area of 8.99 ha, a mean depth of 4.88 m, a maximum depth of 9.0 m and a shoreline length of 1.60 km. The littoral substrate is a mixture of sand and organic material, the profundal substrate sedimentary mud and the macrophyte cover moderate. During the ice-free season, both lakes strongly stratify and have anoxic hypolimnia. They have similar chemical compositions (Table 1) although epilimnetic pH is higher in Ranger Lake and chlorophyll *a* lower in Mouse Lake. The prevailing wind during the sampling season was from the SSW (Ontario Ministry of the Environment and Energy unpublished climatic records – Dorset Research Centre).

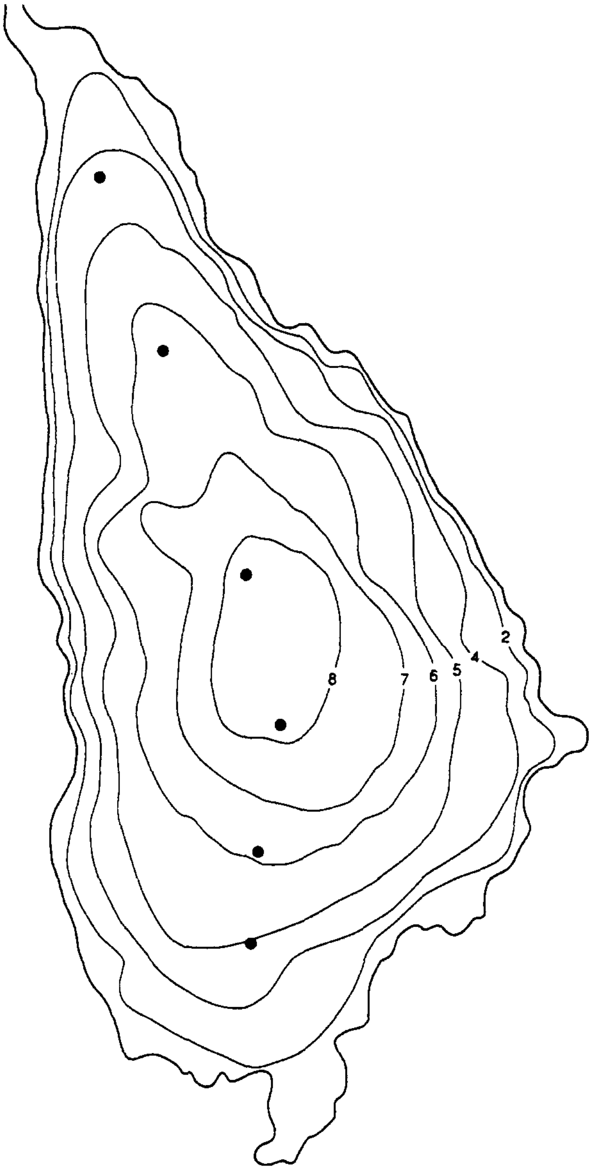

Fig. 2. Bathymetric map of Mouse Lake. The total surface area is 8.99 ha and the mean depth is 4.88 m. Stations 1 (bottom) through 6 (top) are shown as solid dots.

The fish communities are very different. Ranger Lake is dominated by two piscivorous species (Table 2) and planktivores number less than 25 ind. ha^{-1}. Mouse Lake has no large piscivores and planktivores number more than 1200 ind. ha^{-1}.

The major crustacean zooplankton species common to both lakes include the cladocerans *Bosmina longirostris*, *Daphnia catawba*, and *Holopedium gibberum*, the calanoid copepod *Leptodiaptomus minutus*, and the cyclopoid copepods *Mesocyclops edax* and *Tropocyclops extensus*. In addition, Ranger Lake contains *Daphnia retrocurva* while Mouse Lake contains *Eubosmina coregoni*, *Diaphanosoma brachyurum*, *Diaphanosoma birgei*, *Diacyclops bi. thomasi*, and *Orthocyclops modestus*.

Methods

Zooplankton samples were collected at midday from six stations in each lake on ten sampling periods between May 15 and October 15, 1991

Table 1. Mean 1991 ice-free season selected water chemistry summary for Ranger and Mouse Lakes. Epi. = epilimnion, Meta. = metalimnion and Hypo. = hypolimnion, TP = total phosphorus (μg l^{-1}), DOC = dissolved organic carbon (mg l^{-1}). Chl-c and Chl-t (μg l^{-1}) = corrected and total chlorophyll *a* (one standard deviation). In all cases $n = 9$.

Water chemistry	Ranger			Mouse		
	Epi.	Meta.	Hypo.	Epi.	Meta.	Hypo.
Ph	6.27	5.74	5.85	5.74	5.46	5.60
TP	5.93	22.12	26.58	6.19	9.83	36.60
DOC	5.04	5.80	6.29	4.15	4.34	5.61
Chl-c	1.48 (1.22)			1.11 (0.71)		
Chl-t	4.17 (1.86)			3.30 (0.88)		

Table 2. Summary of 1991 fish population estimates for Ranger and Mouse Lakes. Data are recorded as number ha^{-1} (standard deviation). All recorded fish are 1+ or older. NE = no estimate because the population was so small that there were no recaptures.

Species	Ranger Lake	Mouse Lake
Micropterus salmoides (Largemouth bass)	15.4 (8.1)	absent
Micropterus dolomieui (Small mouth bass)	23.3 (12.9)	absent
Perca flavescens (Yellow perch)	3.1 (1.2)	525.8 (457.8)
Lepomis gibbosus (Pumpkinseed sunfish)	21.4 (16.3)	478.1 (378.4)
Catastomus commersoni (Common white sucker)	32.8 (28.5)	26.8 (21.8)
Notemigonus chrysoleucas (Golden shiner)	10.0	223.8 (170.7)
Phoxinus spp. (Dace)	absent	NE
Culaea inconstans (Brook stickleback)	NE	absent
Semotilus atromaculatus (Creek chub)	absent	NE
Ictalurus nebulosus (Brown bullhead)	absent	81.4 (48.5)

Table 3. Sampling dates for Ranger Lake and Mouse Lake. All dates refer to 1991. The indicated date codes are used in subsequent tables and figures.

Date code	Sampling date	
	Ranger Lake	Mouse Lake
1	May 15	May 16
2	June 2	May 30
3	June 13	June 15
4	June 22	June 24
5	July 7	July 9
6	July 26	July 27
7	August 9	August 10
8	August 24	August 27
9	September 17	September 19
10	October 10	October 15

(Table 3). The stations were located along a horizontal transect. In Ranger Lake, two stations were 5 m deep, two were 8 m deep, and two were 13 m deep. The Mouse Lake stations were represented by two stations at each of 4 m, 6 m and 9 m depth. Samples were collected using a vertical tow net (80 μm mesh size) 143 cm long with a square mouth of 30 x 30 cm (Filion, 1991). Each tow was calibrated with a Rigosha flow meter and density calculations were corrected for actual volume filtered (McQueen & Yan, 1993). Zooplankton samples were preserved in a 4% formaldehyde-sugar solution (Prepas, 1978) and were brought into the laboratory for processing.

Subsamples from each tow net were counted under magnifications of 25 x or 50 x, dependent upon the size of the animals. Measurements were made using a computer based (Sprules *et al.*, 1981) video overlay (ZCOUNT) system capable of estimating individual zooplankton masses from length measurements. Copepods were identified as either calanoid or cyclopoid copepodids, or adults, and the length of each individual from head to setae was measured. Copepod nauplii were categorized as one group and measured from head to setae. Cladocera were identified to genus and carapace length was measured. A minimum of 170 animals were measured and counted per sample (typical number of animals was > 250 per sample). The sample taken from Ranger Lake, station 1, on June 22 was not available for processing and is therefore not included in the analyses.

Water chemistry samples were taken every two weeks at the deepest point in each lake. The samples were analyzed at the Ontario Ministry of

Table 4. Summary of repeated measures ANOVA with one grouping factor (Lake) for Time and Lake main effects and Time * Lake interaction effects on zooplankton biomass (log transformed data). The Greenhouse-Geisser epsilon was applied to the degrees of freedom for all time effects and interactions.

Source	d*f*	Mean square	*F*	*p*
Lake	1	17.0	21.3	0.001
Error	9	0.8		
Time	9	0.5	1.5	0.241
Time * Lake	9	2.5	7.8	0.001
Error (Time)	81	0.3		
Greenhouse-Geisser epsilon = 0.39				

the Environment Laboratories located in Dorset and Toronto, Ontario using the methods of (Anon, 1983). Volume weighted mean concentrations for the epilimnion, metalimnion and hypolimnion were estimated using the methods of Girard & Reid (1990). Depth profile temperatures and oxygen concentrations were recorded with a YSI Model 51 DO meter and oxygen concentrations were later confirmed with Winkler titrations (Girard & Reid, 1990).

The fish community densities were estimated from sequential mark and recapture methods (McQueen *et al.*, 1989). The estimates were made over two week time intervals in May 1991 and the sampling sites were randomized during each sampling cycle. The fishing gears that were used included 100 m (1 cm mesh) beach seines and six foot box trap nets (2 cm mesh).

Standard contingency table chi-square analyses (Zar, 1984) were used to test null hypotheses pertaining to the distribution of size classes and individual taxa with respect to station and lake. Repeated measures analyses of variance (Winer, 1971) were used to test the hypothesis that the two lakes had similar zooplankton biomasses through time and to test the hypothesis that there were between-lake differences in zooplankton size with respect to time. For both analyses, stations were used as replicates (fixed effects) and the Greenhouse-Geisser epsilon was applied to the degrees of freedom for all time effects and interactions. Taxa specific differences in dispersion were assessed by fitting the function $s^2 = Am^b$ (Taylor, 1984) and by using ANCOVA to test for equivalence between coefficients (Downing, 1986; Downing *et al.*, 1987; Rasmussen & Downing, 1988). Effects were considered to be significant at $\alpha = 0.05$.

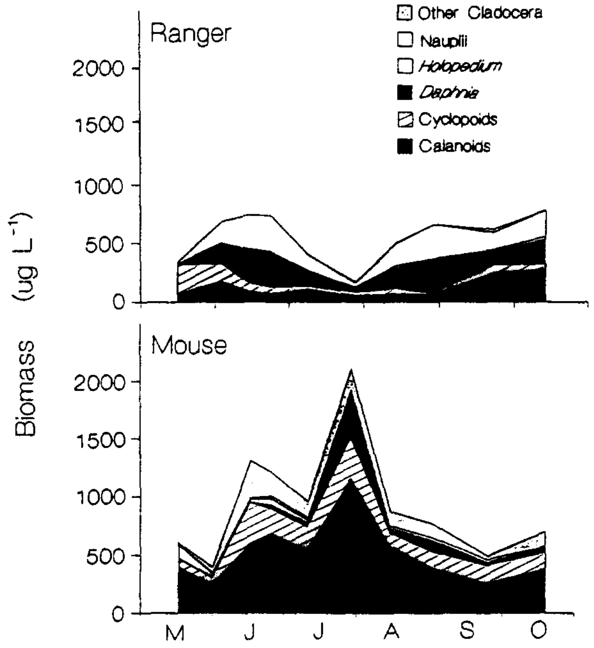

Fig. 3. Cumulative zooplankton biomass in Ranger Lake and Mouse Lake. The taxa plotted are: calanoids, cyclopoids, copepod nauplii, daphnids, *Holopedium*, and other cladocera.

Results

Zooplankton spatial and temporal trends

Ranger Lake had consistently lower crustacean biomass than Mouse Lake (Table 4, Fig. 3). Both lakes showed distinct temporal trends in biomass. The biomass in Ranger Lake reached a peak in May, declined in July, and then increased after reaching a minimum on July 26. The Mouse Lake biomass increased from the start of the sampling season, reached a peak on June 24, and steadily declined.

To explore between-lake temporal trends, re-

Table 5. Between-lake differences: Lake simple effects on taxonomic distribution of zooplankton by sampling date. All Chi-Square values are significant at $p < 0.001$.

Sample date	Chi-square	*df*
1	3124.0	6
2	485.5	6
3	747.7	6
4	635.6	6
5	473.6	6
6	644.1	6
7	862.2	6
8	544.6	6
9	352.5	6
10	1303.1	6

peated measures analysis of variance was applied to the total biomass data from both lakes (Table 4). As expected, there was a highly significant lake main effect on biomass that was independent of time (Lake main effect, $p = 0.001$) indicating that Mouse Lake had higher crustacean biomass than Ranger Lake. The overall (time * lake) interaction effect was also significant ($p = 0.001$), suggesting that the between-lake temporal trends are also different. Repeated measures analysis of variance using lake and station depth (littoral, pelagic or intermediate) as grouping factors revealed that, in general, within-lake variability in total biomass could not be accounted for by station location along the littoral-pelagic depth gradient (depth main effect: $F = 0.01$, d$f = 2,3$, $p = 0.99$), and that this lack of effect was common to both lakes (depth * lake interaction: $F = 0.42$, d$f = 2,3$, $p = 0.69$).

The temporal distribution of biomass in each

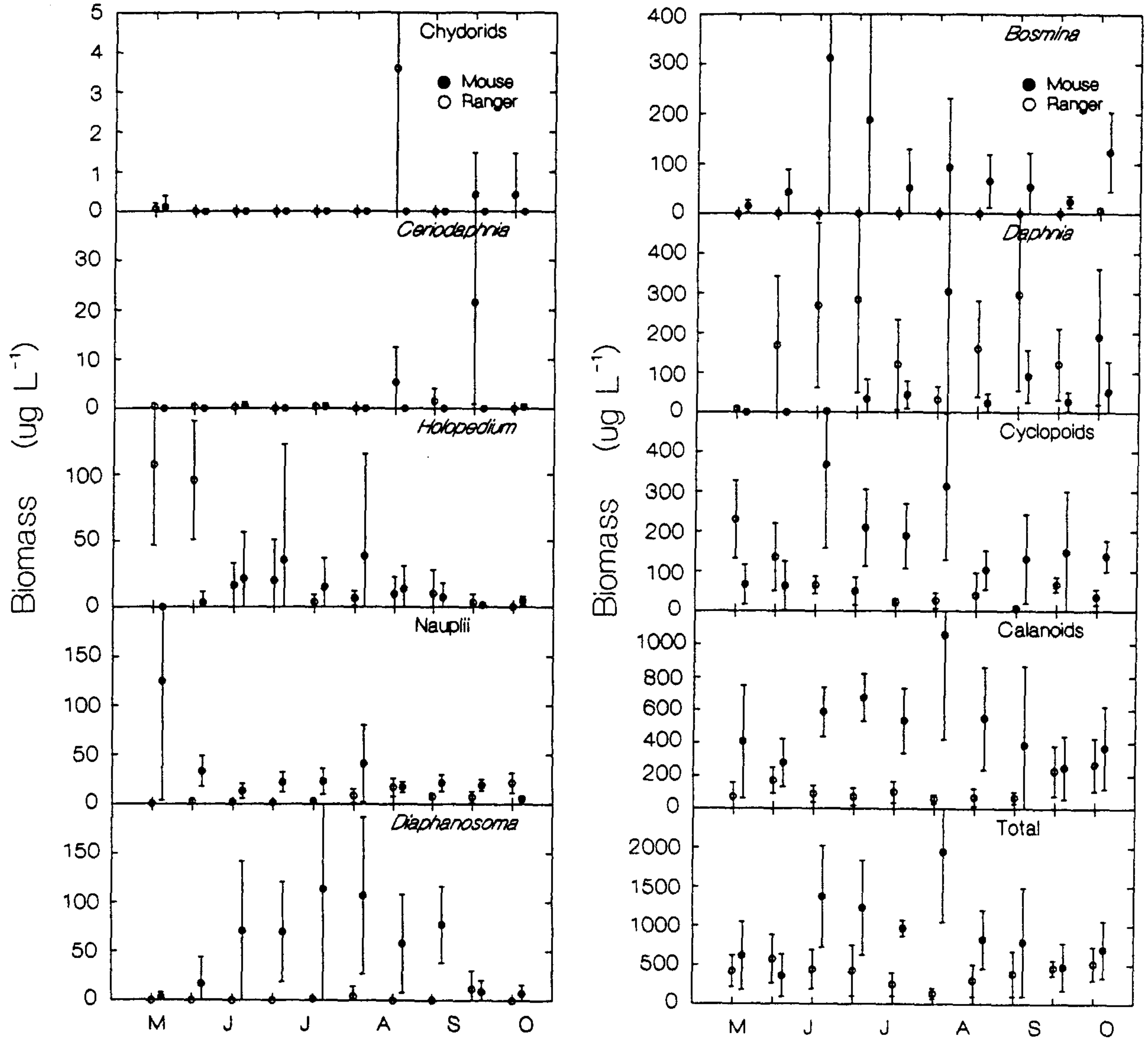

Fig. 4. Temporal trends in the biomass of the principal zooplankton taxa in Ranger and Mouse Lakes. The between-station ranges are shown for each biomass mean.

lake by taxonomic group (Fig. 4) suggests that there were significantly different species-specific abundance patterns in the two lakes (Table 5). Calanoid copepodid biomass was higher in Mouse Lake and peaked during late June, while calanoid biomass at Ranger Lake increased during September and October. Cyclopoid copepodid biomass was also higher in Mouse Lake and generally decreased over time in both lakes. There were distinct differences in the trends in copepod nauplii biomass. Not only was the biomass much higher in Mouse Lake, but the Mouse Lake population peaked in May while the Ranger Lake population peaked in October. Daphnids were present in Ranger Lake throughout the season, but did not appear until June in Mouse Lake. Bosminids and *Diaphanosoma spp.* were rare in Ranger Lake, but were both present throughout the season in Mouse Lake with a distinct bosminid peak in June. The *H. gibberum* populations were similar in both lakes except for the May peak in Ranger Lake.

Table 6. Within-lake differences: Station simple effects on taxonomic distribution of zooplankton by sampling date. All Chi-Square values are significant at $p<0.001$.

Lake	Sampling day	Chi-square	d*f*
Ranger Lake	1	264.0	20
	2	226.0	25
	3	210.2	20
	4	174.9	16
	5	226.1	25
	6	266.4	25
	7	243.6	25
	8	177.2	25
	9	407.9	30
	10	214.5	25
Mouse Lake	1	55.1	20
	2	125.6	25
	3	213.0	30
	4	677.5	30
	5	306.1	30
	6	556.9	30
	7	325.3	30
	8	629.9	30
	9	517.3	30
	10	240.5	30

Table 7. Between-lake differences: lake simple effects on zooplankton size distribution by sampling date. All Chi-Square values are significant at $p<0.001$.

Sample date	Chi-square	d*f*
1	2886.8	5
2	769.6	5
3	304.4	5
4	418.1	5
5	249.4	5
6	365.8	5
7	341.9	5
8	434.1	5
9	179.2	5
10	455.8	5

Within each lake, there were significant differences in the taxonomic distribution across stations (Fig. 4) (Ranger Lake: Chi-square = 681.6, d*f* = 30, $p<0.001$; Mouse Lake: Chi-square = 1807.5, d*f* = 30, $p<0.001$) and over time (Ranger Lake: Chi-square = 7370.7, d*f* = 54, $p<0.001$; Mouse Lake: Chi-square = 5124.5, d*f* = 54, $p<0.001$). These within-lake differences were also significant for each individual sampling date (Table 5, station simple effects). In addition, the lakes showed differences in taxonomic distribution on each sample date (Table 6, lake simple effects).

Between lake (station * time) differences were also found for the zooplankton size distributions (Figs 5, 6). There was a significant overall station effect in both Ranger Lake (Chi-square = 464.9, d*f* = 25, $p<0.001$) and Mouse Lake (Chi-square = 1048.9, d*f* = 25, $p<0.001$). In addition, there were significant differences between stations on all sampling dates in both lakes (Table 7) and between stations within lakes on all dates (Table 8). The inclusion of station depth (littoral, pelagic, and intermediate) as a categorical variable in the analysis reveals that between-station variability in size distribution may indeed be accounted for by the station's location along the littoral-pelagic depth gradient (Mouse Lake: Chi-square = 902.5, d*f* = 10, $p<0.0005$; Ranger Lake: Chi-square = 377.2, d*f* = 10, $p<0.0005$). Finally, there were differences in the overall size distribu-

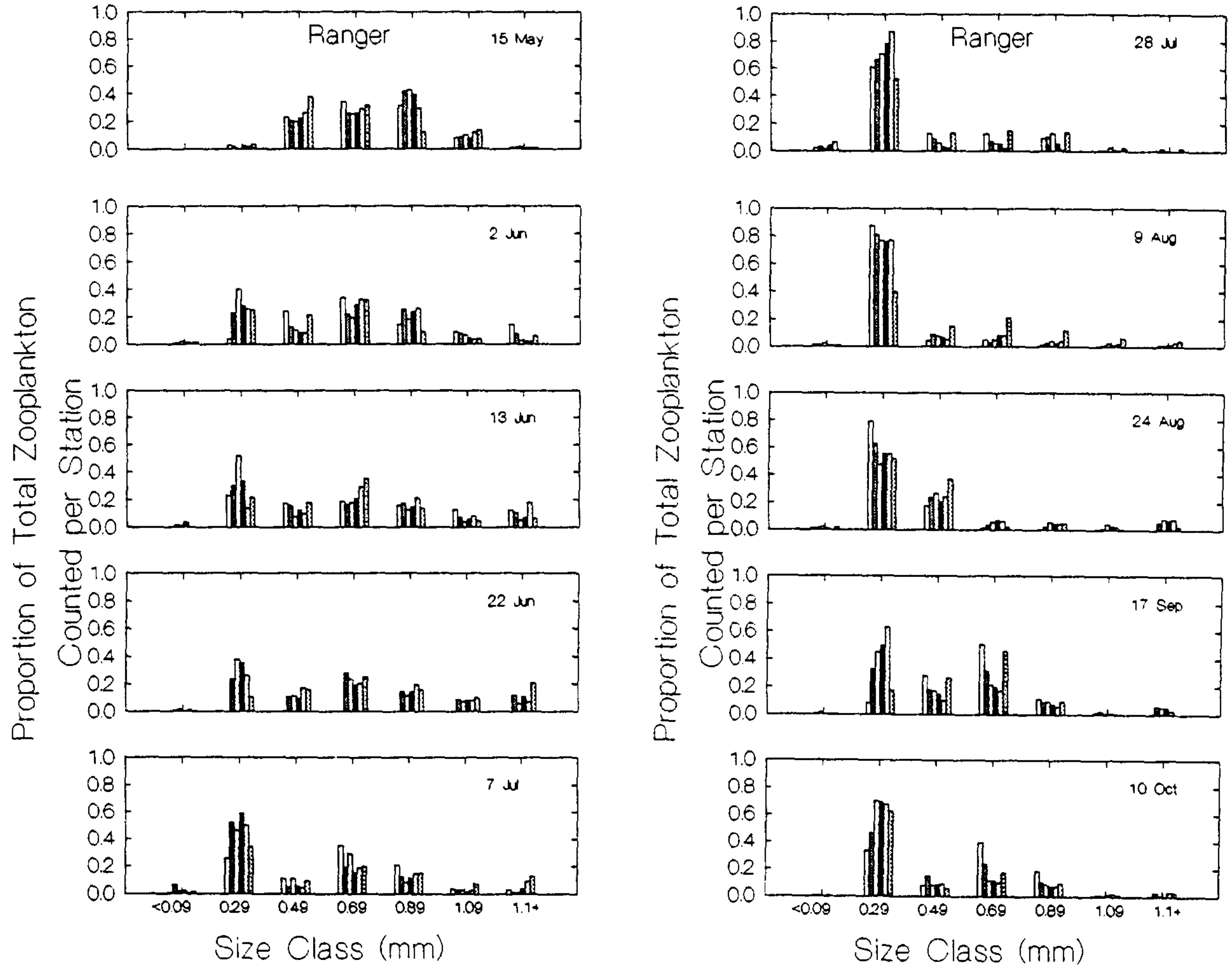

Fig. 5. Size distributions of zooplankton in Ranger Lake. Size classes are designated by the upper size limit of the class. For each date the stations are plotted from station 1 on the left to station 6 on the right. Stations 1 and 6 are littoral, stations 2 and 5 are intermediate, and stations 3 and 4 are pelagic.

tions over time (Ranger Lake: Chi-Square = 4558.5, d$f = 45$, $p < 0.001$; Mouse Lake: Chi-square = 2977.1, d$f = 45$, $p < 0.001$).

These results suggest that the size structure of the crustacean zooplankton communities in Ranger and Mouse Lakes was different over space and time, but it remains possible that these results were an artifact of differences in species assemblies between the two lakes. In order to ascertain the relative magnitude of the taxonomic effects on the difference in community size structure between lakes, repeated measures analysis of variance was performed on the average body length ($\log_{10}$ mm) recorded for each taxonomic group (Table 9). This analysis suggests that while a substantial proportion of variation in size could be attributed to taxonomic affiliation, there were also significant differences in mean body length between the two lakes. The analysis also showed that the temporal patterns in mean size were different in each lake (indicated by the significant (time * lake) interaction) and that each taxon exhibited different temporal patterns in mean size. The lack of an interaction between time, lake and taxon suggests that overall, the temporal trend in mean size for a given taxon does not differ between lakes.

The limits of this analysis are that it does not

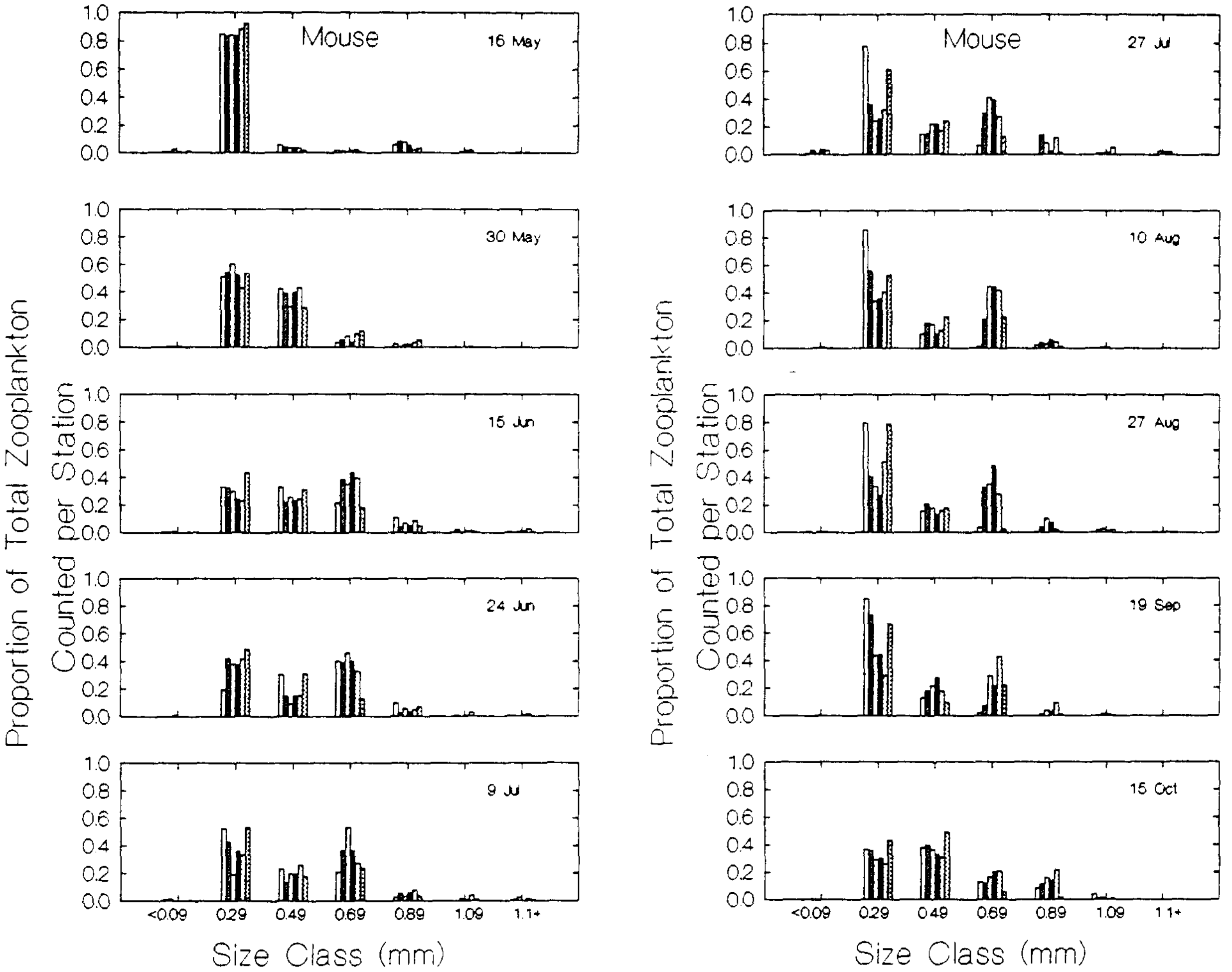

Fig. 6. Size distributions of zooplankton in Mouse Lake. Size classes are designated by the upper size limit of the class. For each date the stations are plotted from station 1 on the left to station 6 on the right. Stations 1 and 6 are littoral, stations 2 and 5 are intermediate, and stations 3 and 4 are pelagic.

identify which species contribute most to the observed patterns. Therefore, repeated measures analysis of variance was applied to each taxon that was sufficiently abundant in both lakes (Fig. 7) to permit analysis (Table 10). Bosminids were found to exhibit significant temporal changes in mean size, and these trends were different in each of the two lakes. Bosminids were larger at the beginning of the season in Ranger Lake and the decline in size over the season was more rapid than in Mouse Lake. The overall mean size of bosminids did not, however, differ between lakes. Daphnids were significantly smaller in Mouse Lake than in Ranger Lake overall; and also showed temporal trends that were different between lakes. Mean Daphnid size remained relatively constant over time in Ranger Lake, but increased in Mouse Lake. Calanoid copepodids exhibited significantly different trends over time in each lake. Overall, cyclopoids were larger in Ranger Lake than in Mouse Lake and showed a similar decline in size over the season. Copepod nauplii did not differ in mean overall size between lakes, but they did show significant temporal trends that differed between lakes. This may be attributed to the initial large size of the Ranger Lake nauplii during May and the subsequent rapid decrease in their mean size in June.

Zooplankton heterogeneity

Tests of zooplankton heterogeneity using ANCOVA analysis (Pinel-Alloul *et al.*, 1988; Rasmussen & Downing, 1988) of the between-sample variances for both densities and biomasses plotted with respect to the means revealed that: (1) Mouse Lake had more zooplankton biomass and higher densities (Fig. 8), (2) there were no significant between-lake differences in the variance-mean relationships ($p > 0.05$) for all taxa except *Daphnia*, (3) that for biomasses (but not densities), the combined plots for the six major taxonomic groups (Fig. 9) showed significant differences ($p = 0.02$) in the variance-mean relationships, and (4) that the combined biomass plots for cladocera (*Holopedium*, daphnids and *Bosmina*), copepods (calanoids and cyclopoids) and nauplii (Fig. 10) revealed that cladocerans were more heterogeneous than copepods and nauplii (Table 11).

Table 8. Within-lake differences: station simple effects on size distribution of zooplankton by sampling date. All Chi-Square values are significant at $p < 0.001$ unless otherwise indicated.

Lake	Sampling day	Chi-square	d*f*
Ranger Lake	1	104.6	25
	2	189.3	25
	3	192.0	25
	4	93.4	20
	5	210.2	25
	6	202.5	25
	7	217.1	25
	8	132.6	25
	9	267.9	25
	10	204.5	25
Mouse Lake	1	76.8	25
	2	50.1 ($p = 0.002$)	25
	3	100.2	25
	4	206.8	25
	5	136.4	25
	6	345.1	25
	7	246.4	25
	8	408.8	25
	9	342.8	25
	10	145.3	25

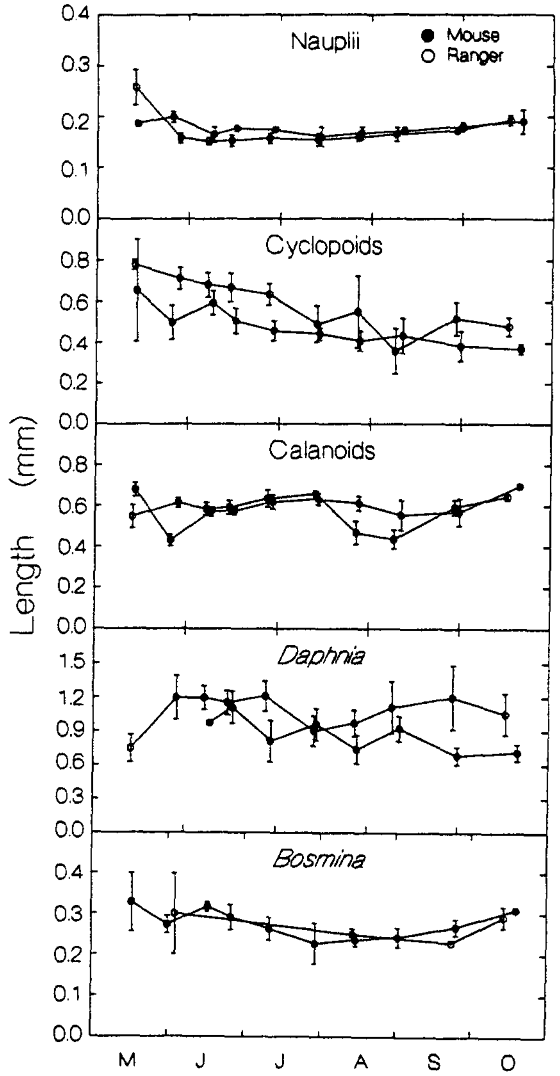

Fig. 7. Mean length of the major zooplankton species over time in Ranger and Mouse Lakes. The between-station ranges are shown for each mean length.

Discussion

Ranger and Mouse Lakes represent quite different patterns of zooplankton community structure. Mouse Lake had crustacean zooplankton biomasses that were almost twice as large as the biomasses recorded for Ranger Lake (Fig. 3) (Table 4). The temporal patterns (Figs 3, 4) were also different (Table 4) with Ranger Lake showing midsummer declines and Mouse Lake showing a late spring increase and then a gradual summer decline. The species abundances were also different with small species (bosminids and copepods) being much more abundant in Mouse Lake and *Daphnia* and *Holopedium* being much more abundant in Ranger Lake (Figs 3, 4). Finally, within-taxa (bosminids, daphnids, copepods and *Holopedium*), the Ranger Lake individuals were always larger (Figs 6, 7).

Given the high planktivore numbers found in Mouse Lake and the low abundances of > 1 + planktivores in Ranger Lake (Table 2), these patterns are not unexpected. At Mouse Lake, during the month of May, the majority of the zooplankton community (Fig. 6) fell into the smaller size classes. There was an early spring size increase and then the size structure favored relatively small individuals for the remainder of the season. At Ranger Lake (Fig. 5), the sizes were large in the spring, but there was a substantial decrease in total biomass during late June and early July which was accompanied by a significant decrease in large-bodied zooplankton (*Daphnia* and *Holopedium*). This corresponds with the time (July) when YOY (bass) started foraging on zooplankton. These were followed by YOY pumpkinseeds which also consumed zooplankton. Analyses of the gut contents of YOY bass showed that their period of planktivory was short-lived and that they started to feed on small fish once they reached only a few cm in length. However, the YOY pumpkinseeds remained

Table 9. Summary of repeated measures ANOVA with two grouping factors (Lake, Taxa) and one trial factor (Time) for Lake, Taxa and Time main effects, and their interaction effects on mean zooplankton length (log transformed data). The Greenhouse-Geisser epsilon was applied to the degrees of freedom for all time effects and interactions.

Source	df	Mean square	F	p
Lake	1	0.2	24.6	0.0001
Taxa	6	4.5	462.3	0.0001
Lake * Taxa	3	0.1	13.9	0.0001
Error	43	0.01		
Time	9	0.1	14.1	0.001
Time * Lake	9	0.02	5.1	0.001
Time * Taxa	54	0.02	4.9	0.001
Time * Lake * Taxa	27	0.02	3.2	0.001
Error (Time)	387	0.01		
Greenhouse-Geisser Epsilon = 0.56				

Table 10. Summary of repeated measures ANOVA with one grouping factor (Lake) for Time and Lake main effects, and Time * Lake interaction effects on mean zooplankton length (log transformed data) by taxonomic group. The Greenhouse-Geisser epsilon was applied to the degrees of freedom for all time effects and interactions.

Source	df	Mean square	F	p
(A) Taxon: *Bosmina*				
Lake	1	0.003	5.9	0.058
Error	5	0.0006		
Time	2	0.01	13.7	0.001
Time * Lake	2	0.01	10.8	0.004
Error (Time)	10	0.001		
Greenhouse-Geisser Epsilon = 0.93				
(B) Taxon: *Daphnia*				
Lake	1	0.18	46.8	0.001
Error	5	0.003		
Time	6	0.015	5.7	0.011
Time * Lake	6	0.018	6.8	0.005
Error (Time)	30	0.002		
Greenhouse-Geisser Epsilon = 0.45				
(C) Taxon: Calanoid copepodids				
Lake	1	0.002	1.44	0.261
Error	9	0.001		
Time	9	0.018	19.95	0.001
Time * Lake	9	0.017	19.02	0.001
Error (Time)	81	0.001		
Greenhouse-Geisser Epsilon = 0.49				
(D) Taxon: Cyclopoid copepodids				
Lake	1	0.23	17.76	0.002
Error	9	0.01		
Time	9	0.07	14.60	0.001
Time * Lake	9	0.01	2.24	0.097
Error (Time)	81	0.005		
Greenhouse-Geisser Epsilon = 0.37				
(E) Taxon: Copepod nauplii				
Lake	1	0.01	9.57	0.012
Error	9	0.001		
Time	9	0.02	24.35	0.001
Time * Lake	9	0.01	12.73	0.001
Error (Time)	81	0.001		
Greenhouse-Geisser Epsilon = 0.36				

planktivorous through the remaining portion of the season until colder mid-September temperatures slowed metabolic rates and the zooplankton began to recover and large individuals became common again.

Within and between the lakes, there were significant differences in the distribution of individual taxa between stations (Tables 5, 6). *Daphnia* were more common at the shallow stations in Ranger Lake, but showed no station affinity in Mouse Lake. *Holopedium* were more common at the central stations at Ranger Lake and at the shallow stations in Mouse Lake. Calanoids were more common at the shallow stations in Ranger Lake and more common at the central stations at Mouse Lake. Cyclopoids showed spring preferences for shallow stations in both lakes, and nauplii showed no station preference.

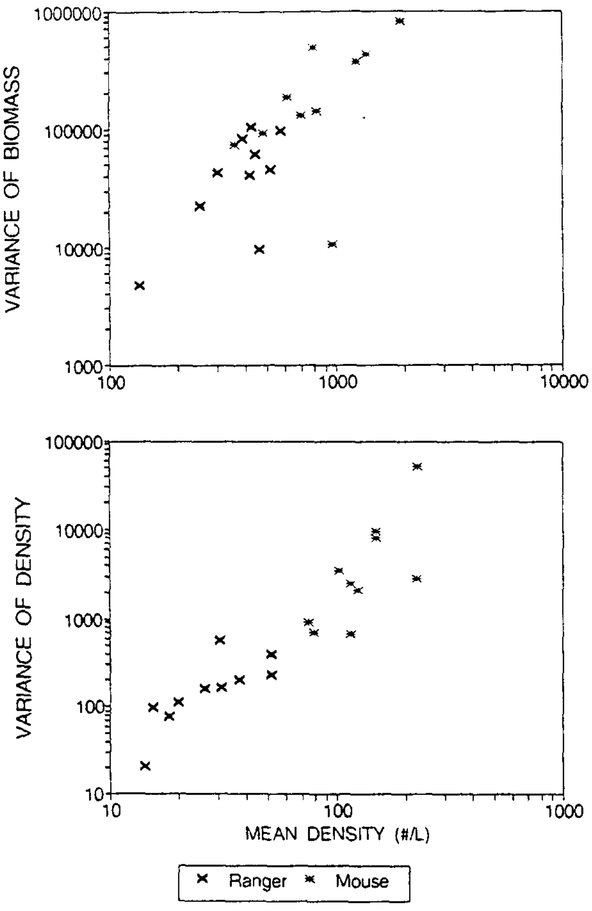

Fig. 8. Mouse Lake and Ranger Lake variances plotted with respect to sample mean biomass (top panel) and density (bottom panel) for each sampling date during 1991.

Table 11. ANCOVA comparisons of mean – variance regressions for taxa from Ranger and Mouse Lake. Both density l^{-1} and biomasses l^{-1} were tested.

Taxon comparison	*p*	
Density		
Copepods *vs* cladocerans	$p < 0.001$	
Cladocerans *vs* nauplii	$p < 0.004$	
Copepods *vs* nauplii	$p > 0.386$	NS
Biomasses		
Copepods *vs* cladocerans	$p < 0.001$	
Cladocerans *vs* nauplii	$p < 0.001$	
Copepods *vs* nauplii	$p > 0.549$	NS

Within and between the lakes there were significant differences in the distribution of size classes between stations (Tables 7, 8). In Ranger Lake the smallest size classes were more abundant at the deeper stations and the larger individuals (often daphnids) were frequently more abundant at the shallower stations. In Mouse Lake the smaller individuals were more common at the shallow stations and the larger individuals were more common at the deeper stations (Figs 5, 6). These within and between lake differences with respect to size and taxa (Tables 9, 10)

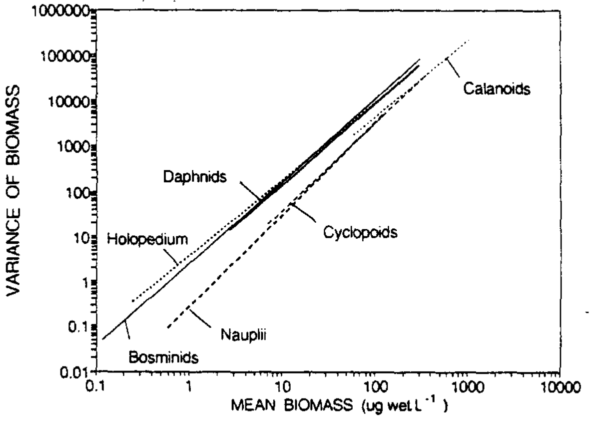

Fig. 9. Combined Ranger Lake and Mouse Lake regressions for variance in biomass plotted with respect to mean biomass for *Holopedium*, daphnids, bosminids, calanoids, cyclopoids and nauplii.

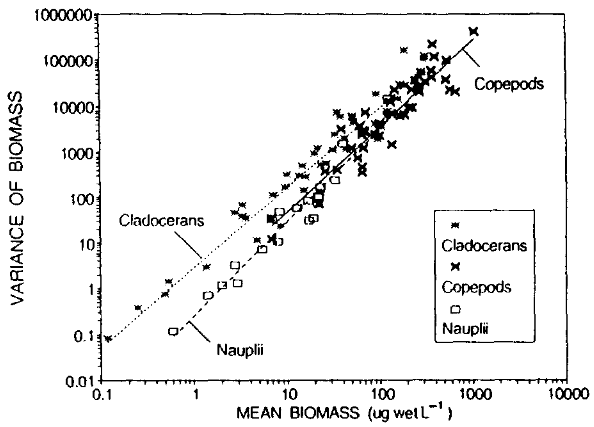

Fig. 10. Ranger Lake and Mouse Lake combined regressions for variance in biomass plotted with respect to mean biomass for all cladocerans, copepods and nauplii.

suggest medium scale patterns (Malone & McQueen, 1983) induced by vectorial forces, but modified by species specific migration patterns.

It has been suggested that horizontal heterogeneity should be positively related to predation pressure (May, 1978; Rasmussen & Downing, 1988) and negatively related to competition (Diamond, 1979). We found that none of the taxa showed significant between-lake differences in the variance-mean regressions with respect to both biomass and density. However, because the predation hypothesis suggests the presence of predator-induced behavioural modification it is likely that this would be recognized only at the smallest scales (swarms). Given that we sampled only six stations per lake, it is possible that our sampling regimen was too course-scaled and therefore it is not surprising that we found no change in the variance-mean relationship.

Pinel-Alloul *et al.* (1988) suggested that in the presence of predators, large zooplankton should be less heterogeneous than smaller ones. They also noted that Peters (1983) and Calder (1984) predicted the opposite. Our results for cladocerans (*Holopedium*, daphnids and *Bosmina*), copepods (calanoids and cyclopoids) and nauplii (Fig. 10) revealed that cladocerans were more heterogeneous than copepods and nauplii (Table 11). These results also suggest the existence of medium scale patterns (Malone & McQueen, 1983) induced by vectorial forces, but modified by species specific migration patterns.

In terms of sampling methodology our data suggest that the temporal between-station, within-taxa, variability was high and that a single mid-lake sample might lead to unacceptable errors. This is exemplified by an analysis (Table 12) of the biomass estimates from Ranger Lake for three abundant taxa (*Holopedium*, daphnids and cyclopoids). It is clear that the between sample variation was so large that population estimates from single midlake stations are seen to lead to completely unacceptable errors.

Table 12. Biomass estimates from the deepest station compared to the mean estimate from all six stations in Ranger Lake. Percent deviation = (larger value divided by the smaller value) x (100).

Date (d–m)	*Holopedium*			*Daphnia*			Cyclopoid copepods		
	Deep	Mean	*d*	Deep	Mean	*d*	Deep	Mean	*d*
5–5	21	116	552%	7	8	114%	121	241	200%
2–6	89	95	106%	74	180	243%	63	146	231%
13–6	10	18	180%	116	290	250%	45	68	151%
22–6	0	22	%	113	303	268%	24	52	216%
7–7	0	5	%	20	132	660%	14	24	171%
26–7	1	7	700%	3	35	1166%	19	26	136%
9–8	5	11	220%	50	173	346%	7	43	614%
24–8	26	8	325%	252	287	113%	1	7	700%
17–9	0	2	%	84	123	146%	53	65	122%
10–10	0	1	%	25	216	864%	22	35	159%

References

Anon., 1983. Handbook of analytical methods for environmental samples. Laboratory Service and Applied Research Branch. Ontario Ministry of the Environment Report.

Baldi, E., L. L. Cavalli & L. Pirocchi, 1945. Condizioni della distribuzione del mesoplancton nel pelago di un grande lago oligotrofo (Lago Maggiore). Mem. Ist. ital. Idrobiol. 2: 253–289.

Birge, E. A., 1897. Plankton studies on Lake Mendota. II. The crustacea of the plankton in July, 1894–December 1896. Trans. Wis. Acad. Sci. Arts Lett. 11: 274–448.

Burckhardt, G., 1910. Hypothesen und Beobachtungen über die Bedeutung der vertikalen Planktonwanderung. Int. Revue ges. Hydrobiol. 3: 156–172.

Calder, W. A. III, 1984. Size, function and life history. Harvard University Press, Cambridge, Massachusetts, USA.

Carpenter, S. R., J. F. Kitchell & J. R. Hodgson, 1985. Cascading trophic interactions and lake productivity. BioScience 35: 634–639.

Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He & C. N. von End, 1987. Regulation of lake primary productivity by food web structure. Ecology 68: 1863–1867.

Colebrook, J. M., 1960a. Plankton and water movements in Windermere. J. anim. Ecol. 29: 217–240.

Colebrook, J. M., 1960b. Some observations of zooplankton swarms in Windermere. J. anim. Ecol. 29: 241–242.

Davis, C. C., 1969. Seasonal distribution, constitution and abundance of zooplankton in Lake Erie. J. Fish. Res. Bd Can. 26: 2459–2476.

Diamond, J. M., 1979. Community structure: is it random or is it shaped by species differences and competition? In R. M. Anderson, B. D. Turner & L. R. Taylor (eds), Population Dynamics. Blackwell, Oxford: 165–181.

Downing, J. A., 1986. Spatial Heterogeneity: evolved behaviour or mathematical artefact? Nature 323: 255–257.

Downing, J. A., M. Perusse & Y. Frenette. 1987. Effect of interreplicate variance on zooplankton sampling design and data analysis. Limnol. Oceanogr. 32: 673–680.

Dumont, H. J., 1967. A five day study of patchiness in *Bosmina coregoni* Baird in a shallow eutrophic lake. Memorie del'Istituto Italiano di Idrobiologia 22: 81–103.

Filion, 1991. Improving zooplankton samplers with simple electronics. Limnol. Oceanogr. 36: 204–210.

Gannon, J. E., 1975. Horizontal distribution of crustacean zooplankton along a cross lake transect in Lake Michigan. J. Gt. Lakes Res. 1: 79–91.

George D. G. & R. W. Edwards, 1973. *Daphnia* distribution within Langmuir circulations. Limnol. Oceanogr. 18: 798–800.

George D. G. & R. W. Edwards, 1976. The effect of wind on the distribution of chlorophyll A and crustacean plankton in a shallow eutrophic reservoir. J. appl. Ecol. 13: 667–690.

Girard, R. & R. A. Reid, 1990. Dorset Research Centre Study Lakes: Sampling methodology (1986–1989) and lake morphometry. Ontario Ministry of the Environment Data Report, DR 90/4.

Healey, M. C., 1967. The seasonal and diel changes in distribution of *Diaptomus leptopus* in a small eutrophic lake. Limnol. Oceanogr. 12: 34–39.

Klemetsen, A., 1970. Plankton swarms in Lake Gjökvatn, East Finmark. Astarte, J. arct. Biol. 3: 83–85.

Künne, C., 1925–26. Über Schwarmbildung bei *Bosmina longirostris* O.F.M. Arch. Hydrobiol. 16: 508.

Langford, R. R., 1938. Diurnal and seasonal changes in the distribution of limnetic crustacea in Lake Nipissing, Ontario. Univ. Toronto Stud. Biol. Ser. 45: 1–142.

Langmuir, I., 1938. Surface motion of water induced by wind. Science 87: 119–123.

Malone, B. J. & D. J. McQueen, 1983. Horizontal patchiness in zooplankton populations in two Ontario kettle lakes. Hydrobiologia 99: 101–124.

May, R. M., 1978. Host-parasitoid systems in patchy environments: a phenomenological model. J. anim. Ecol. 47: 833–843.

McNaught, D. C. & A. D. Hasler, 1961. Surface schooling and feeding behaviour in white bass. Limnol. Oceanogr. 6: 53–60.

McQueen, D. J. & N. D. Yan, 1993. Metering filtration efficiency of freshwater zooplankton hauls: reminders from the past. J. Plankton Res. 15: 57–65.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart & D. R. S. Lean, 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecol. Monogr. 59: 289–309.

McQueen, D. J., E. L. Mills, J. L. Forney, M. R. S. Johannes & J. R. Post, 1992. Trophic level relationships in pelagic food webs: Comparisons derived from long-term data sets for Oneida Lake, New York (USA), and Lake St. George, Ontario (Canada). Can. J. Fish. aquat. Sci. 49: 1588–1596.

McQueen, D. J., J. R. Post & E. L. Mills, 1986. Trophic relations in freshwater pelagic ecosystems. Can. J. Fish. aquat. Sci. 43: 1571–1581.

Moberg, E. G., 1918. Variation in the horizontal distribution of plankton in Devils Lake, North Dakota. Trans. am. Microsc. Soc. 37: 239–267.

Moberg, E. G., 1921. Horizontal distribution of the zooplankton in Devils Lake, North Dakota. Int. Revue ges. Hydrobiol. Hydrogr. 9: 153–159.

Naber, H., 1933. Die Schichtung des Zooplanktons holsteinischen Seen und der Einfluss des Zooplanktons auf den Sauerstoffgehalt der bewohnten Schichten. Arch. Hydrobiol. 25: 81–132.

Neess, J. C., 1949. A contribution to aquatic population dynamics. Ph. D. Thesis, Univ. Wis., Madison, 103 pp.

Nie. H. W. de, H. J. Bromley & J. Vijverberg, 1980. Distribution patterns of zooplankton in Tjeukemeer, the Netherlands. J. Plankton Res. 2: 317–334.

Patalas, K., 1969. Composition and horizontal distribution of crustacean plankton in Lake Ontario. J. Fish. Res. Bd Can. 26: 2135–2164.

Peters, R. H. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, England.

Pinel-Alloul, B., J. A. Downing, M. Pérusse & G. Codin Blumer, 1988. Spatial heterogeneity in freshwater zooplankton: Variation with body size, depth and scale. Ecology 69: 1393–1400.

Prepas, E., 1978. Sugar-coated *Daphnia*: an improved fixation technique for cladocera. Limnol. Oceanogr. 23: 557–559.

Ragotzkie, R. A. & R. A. Bryson, 1953. Correlation of currents with the distribution of adult *Daphnia* in Lake Mendota. J. mar. Res. 12: 157–172.

Rasmussen, J. B. & J. A. Downing, 1988. The spatial response of chironomid larvae to the predatory leech, *Nephelopsis obscura*. Am. Nat. 131: 14–21.

Reighard, J. E., 1894. A Biological Examination of Lake St. Clair. Bulletin of the Michigan Fish Commission. No. 4. 61 pp.

Ricker, W. E., 1937. Statistical treatment of sampling processes useful in the enumeration of plankton organisms. Arch. Hydrobiol. 31: 68–84.

Riley, G. A., 1976. A model of plankton patchiness. Limnol. Oceanogr. 21: 873–880.

Ringelberg, J., 1969. Spatial orientation of planktonic crustaceans: II The swimming behaviour in a vertical plane. Verh. int. Ver. Limnol. 17: 841–847.

Siebeck, O., 1964. Ist die 'Uferflucht' planktischer Crustaceen eine Folge der Vertikalwanderung. Arch. Hydrobiol. 60: 419–427.

Siebeck, O., 1969. Spatial orientation of planktonic crustaceans. I. The swimming behaviour in a horizontal plane. Verh. int. Ver. Limnol. 17: 831–840.

Southern, R. & A. C. Gardiner, 1926. The seasonal distribution of the crustacea of the plankton of Lough Derg and the R. Shannon. Sci. Invest. Minist. Fish. Irish. Free St. #1. 171 pp.

Sprules W. G., L. B. Holtby & G. Griggs, 1981. A microcomputer-based measuring device for biological research. Can. J. Zool. 59: 1611–1614.

Stavn, R. H., 1971. The application of the dorsal light reaction for orientation in water currents by *Daphnia* distributions. Limnol. Oceanogr. 16: 453–466.

Steven, D. M., 1961. Shoaling behaviour in a Mysid. Nature Lond. 192: 280.

Stommel, H., 1949. Trajectories of small bodies sinking slowly through convection cells. J. mar. Res. 8: 24–29.

Taylor L. R., 1984. Assessing and intrepreting the spatial distribution of insect populations. Annu. Rev. Entomol. 29: 321–357.

Threlkeld, S. T., 1988. Planktivory and planktivore biomass effects on zooplankton, phytoplankton, and the trophic cascade. Limnol. Oceanogr. 33: 1362–1375.

Tonolli, V., 1958. Zooplankton Swarms. Verh. int. Ver. Limnol. 13: 776–777.

Tonolli, V. & L. Tonolli, 1960. Irregularities of distribution of plankton communities: Considerations and methods. In A. A. Bussati-Traverso (ed.), Marine Biology, University of California Press, Berkeley: 137–143.

Urabe, J., 1989. Relative importance of temporal and spatial heterogeneity in the zooplankton community of an artificial reservoir. Hydrobiologia 184: 1–6.

Urabe, J. & M. Murano, 1986. Seasonal and horizontal variations in the zooplankton community of Ogochi reservoir, Tokyo. Bull. Plankton Soc. Jap. 33: 101–112.

Ward, H. B., 1896. A biological examination of Lake Michigan. Bull. Michigan Fish Comm. 6: 62–64.

Ward, J., 1955. A description of a new zooplankton counter. Quart. J. micros. Sci. 96: 371–373.

Watson, N. H. F., 1976. Seasonal distribution and abundance of crustacean zooplankton in Lake Erie, 1970. J. Fish. Res. Bd Can. 33: 612–621.

Welch, P. S., 1951. Limnology, 2nd edn. McGraw Hill, New York, 471 pp.

Winer, B. J., 1971. Statistical Principles in Experimental Design. McGraw-Hill.

Zar, J. H., 1984. Biostatistical Analysis, Second Edition. Prentice Hall, New Jersey, 718 pp.