THESIS

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Abundance, Structure and Biomass of Nearshore Zooplankton of Northeastern Lake Michigan

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ABUNDANCE, STRUCTURE, AND BIOMASS OF NEARSHORE ZOOPLANKTON OF NORTHEASTERN LAKE MICHIGAN

By

Glenn Lee Barner

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ABSTRACT

ABUNDANCE, STRUCTURE AND BIOMASS OF NEARSHORE ZOOPLANKTON OF NORTHEASTERN LAKE MICHIGAN

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Biotic changes to Lake Michigan and abiotic differences of the northeastern part of Lake Michigan define a need for basic research of these nearshore waters.

Zooplankton were sampled at 10 and 30 meters, at four sites in northeastern Lake Michigan from July to November. Abundances in both individuals^{-2} and individuals^{-3} were measured. Principle component analysis was used to evaluate community structure to the observed variables, depth, month and site. Dry weight biomass was estimated using three methods; counting of instars, length-weight regressions, and volume estimates.

The zooplankton community was dominated by *Diaptomus sp.*, *Cyclops sp.*, and *Bosmina longirostris*. Principle component analysis found site an insignificant variable, and although month was significant, species associations could only be split satisfactorily by the first principal component with the depth variable. Biomass was dominated by species that were the most abundant, except for *Bythotrephes cederstroemi* which averaged 8.4% of the biomass and only 0.1% of the abundance.

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Agricultural Experiment Station; Wildlife Unlimited of Allegan and Ottawa Counties; the Native American Institute at Michigan State University; and the Ludington Charterboat Association.

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INTRODUCTION

Biotic changes to Lake Michigan and abiotic differences of the northeastern part of Lake Michigan define a need for basic research of these nearshore waters. Abundance, community structure and biomass of northeastern Lake Michigan zooplankton are the components of this study.

This study focuses on the zooplankton community of the nearshore waters (<30 meter depth) of northeastern Lake Michigan. Evans et al. (1980) examined relationships between zooplankton abundance (#/m^3) with depth or season. From mid-spring to mid-autumn, zooplankton densities (#/m^3) were strongly related to depth. Maximum densities occurred between the 20 and 30 meter contours, and minimum densities between the 5 and 10 meter contours.

I examined the zooplankton community at two depth contours, 30 meters and 10 meters, from July to November 1991, at four locations so as to assess the influences of these observed variables on zooplankton abundance, structure, and biomass.

The nearshore waters of Lake Michigan tend towards higher productivity than those of the offshore waters because of local inputs that are not readily circulated into the deeper basins of the lake because of water movement differences. The nearshore (<20 m) waters are in a system of currents that run parallel to shore, while the offshore waters are essentially an open lake gyre system separated from the

nearshore (Gannon 1972).

Duffy (1975) studied the vertical distribution and abundance (#/m^3) of nearshore zooplankton off of the Ludington Pumped Storage near Ludington, Michigan.

Other Lake Michigan nearshore studies have focused on the more eutrophic waters of Lake Michigan. Gannon studied the horizontal distribution and abundance of Lake Michigan zooplankton in a cross-lake transect from Milwaukee, Wisconsin to Ludington, Michigan (1975, 1972) and found less distinct inshore and offshore differences off of Ludington (the primary sampling site of this study), than off of Milwaukee.

Roth and Stewart (1973) studied zooplankton abundance (#/m^3) and biomass (mg/m^3) in a study near the of Cook Nuclear Power Plant in southeastern Lake Michigan. Abundances off of Cook were much greater than those near the Ludington Pumped Storage project (Duffy 1975). Waters warmed by the Cook Power plant may be a significant factor in the higher concentrations of zooplankton and the subsequent higher biomass found in that study.

Although total phosphorus concentrations have declined since the early 1970's (Scavia et.al. 1986), it is likely that southern Lake Michigan is still more productive than the northern portions of the lake (Roth and Stewart 1973). Point source inputs of nitrogen and phosphorus from sewage treatment plants and industrial wastes, as well as non-point sources from runoff of animal wastes and storm sewers are more likely to increase phytoplankton growth in the more densely populated southern portion of Lake Michigan, than the sparsely populated northern and northeastern parts.

Biologically, the Great Lakes have been under constant change ecologically for over four decades. The introduction of exotic species has affected the food-web, and changed the species interactions at all trophic levels, including the zooplankton community.

Two invading species, the alewife (*Alosa pseudoharengus*) a planktivorous fish and *Bythotrephes cederstroemi*, a large voracious predatory cladoceran have both, more than any other species, affected the zooplankton community of Lake Michigan.

Alewife can have profound effects on the size-structure of zooplankton communities (Brooks & Dodson 1965), and the alewife directly affected the composition of zooplankton by selectively feeding on the largest zooplankton (Wells 1970).

The alewife is a planktivore throughout its life and is most important to nearshore populations of zooplankton because here they remain primarily a zooplanktivore. In the summer the planktivorous larvae dominate the inshore region of southeastern Lake Michigan (Nash & Geffen 1991), and smaller fish (<140 mm) diets are at least 90% zooplankton (Wells 1980).

Although the bloater chub (*Coregonus hoyi*) can be considered a zooplanktivore, the species generally does not reside in the shallow waters. The bloater was found in the nearshore in southeastern Lake Michigan (Evans and Jude 1986) and has increased in abundance to help replace the forage base (Jude & Tesar 1985), but this species does not spawn or inhabit the nearshore (<30 m) for long periods of time (Crowder 1980). The bloater was found in 20 to 30 meter deep waters off of Saugatuck, Big Sable Point and Ludington only for a few weeks in early July before returning to deeper waters (>40 m)(Rasmussen 1973).

Yellow perch (*Perca flavescens*) were more likely to contribute to zooplanktivory in the nearshore as a result of long residence times in the nearshore waters.

Yellow perch spawn in the very shallow waters (<5 m) in mid-June and the young-of-the-year remain there throughout the summer. Yellow perch inhabit a zone from 0 to 40 meters, but concentrate their activities in 0-25 m depths (Rasmussen 1973).

Yellow perch are more zooplanktivorous when young (<10.2 cm), and increasingly eat more *Mysis* and *Pontoporeia* as they get larger. As adults, yellow perch target *B. cederstroemi* when abundant in both Ludington (Peterson 1993) and in northern Lake Michigan (Schneeberger 1991).

The other species to greatly affect Lake Michigan zooplankton is an invertebrate predator. In 1986 the spined palearctic cladoceran, *Bythotrephes cederstroemi* was first detected in Lake Michigan (Lehman 1987, Evans 1988). The *B. cederstroemi* invasion has coincided with depressed populations of *Leptodora kindti*, another predatory cladoceran, and a subsequent increase of *Bosmina longirostris* populations in the offshore waters off of Grand Haven, Michigan (Branstrator & Lehman 1991). *B. cederstroemi* has also altered the *Daphnia* assemblage by preying on the smaller *Daphnia retrocurva*, and has further suppressed the already declining, larger-sized, *D. pulicaria* (Lehman & Caceres 1993).

This study had four sampling locations. Three were in northeastern Lake Michigan: Ludington, Manitou Passage (part of Sleeping Bear Dunes National Lakeshore), and West Grand Traverse Bay. The fourth location, Holland, was in southeastern Lake Michigan.

The northeastern waters of Lake Michigan from Ludington to Manitou Passage (Carr 1971), and the deep protected waters of West Grand Traverse Bay (Lauff 1957), are cooler, than those of southeastern Lake Michigan. Roth and Stewart (1973) found differences in concentrations of individuals and biomass between their offshore southeastern Lake Michigan study site (11.2 km offshore at 40 m depth) and Gannon's (1972) offshore station, (16 km offshore at 60 m depth) off the coast from Milwaukee. They suggested the difference was because of the less productive waters of northern Lake Michigan.

Zooplankton abundances in Lake Erie have been suggested to vary most with heat content and eutrophication (Patalas 1972), and large scale differences appear to be north-to-south gradients of abundance on lakes Ontario and Erie (Patalas 1969).

This study had two major objectives, first, identify zooplankton community trends with respect to the observed variables: season (month), depth (30 or 10 m), and location. Secondly, look for possible species associations to describe trends within this community. The study utilized the estimation of areal (individuals/m^2) and cubic (individuals/m^3) abundances of each species, principle component analysis (PCA) of the community, and total biomass (mg/m^2) to evaluate both the trends and species associations of the zooplankton community of northeastern Lake Michigan. Vertebrate planktivore populations were not assessed, but *B. cederstroemi* abundance was estimated and its contribution to the zooplankton structure and biomass is described.

STUDY SITES

Four nearshore locations were selected. Three are in northeastern Lake Michigan: Ludington, Manitou Passage, and West Grand Traverse Bay; and one is in southeastern Lake Michigan located off of Holland (Figure 1). Ludington is located in the northwestern part of the State of Michigan. Holland is approximately 140 km south of Ludington and North Manitou Island is about 145 km north of Ludington. The West Grand Traverse Bay location was about 40 km southeast of the Manitou Passage location, over the Leelanau Peninsula.

The study design was to sample at the 10 meter and 30 meter contour at each location. However, because of the steep morphometry of the West Grand Traverse Bay basin, the deeper contour was taken over 110 m of water to allow for a reasonable spatial difference.

The Ludington (LU) 30 m contour (43°:53′:71"N longitude, 86°:31′:09"W latitude) was approximately 10 km southwest of Ludington and the 10 m contour (43°:55′:09"N, 86°:27′W) site was approximately 1.25 km off shore near Butterfield Park. The Ludington sites were the primary sampling sites and were sampled eight times between July 17, and November 14, 1991 (7/17; 7/30 & 8/1; 8/16; 8/29; 9/13; 10/3; 10/18; and 11/14).

The West Grand Traverse Bay (TC) 30 m site (44°:52′N, 85°:36′) was about 1.75 km west off of Marion (Power) Island on the east shore and the 10 m (44°:57′N, 85°:36′W) was located about 4 km NNE off of Lee's Point on the west shore.

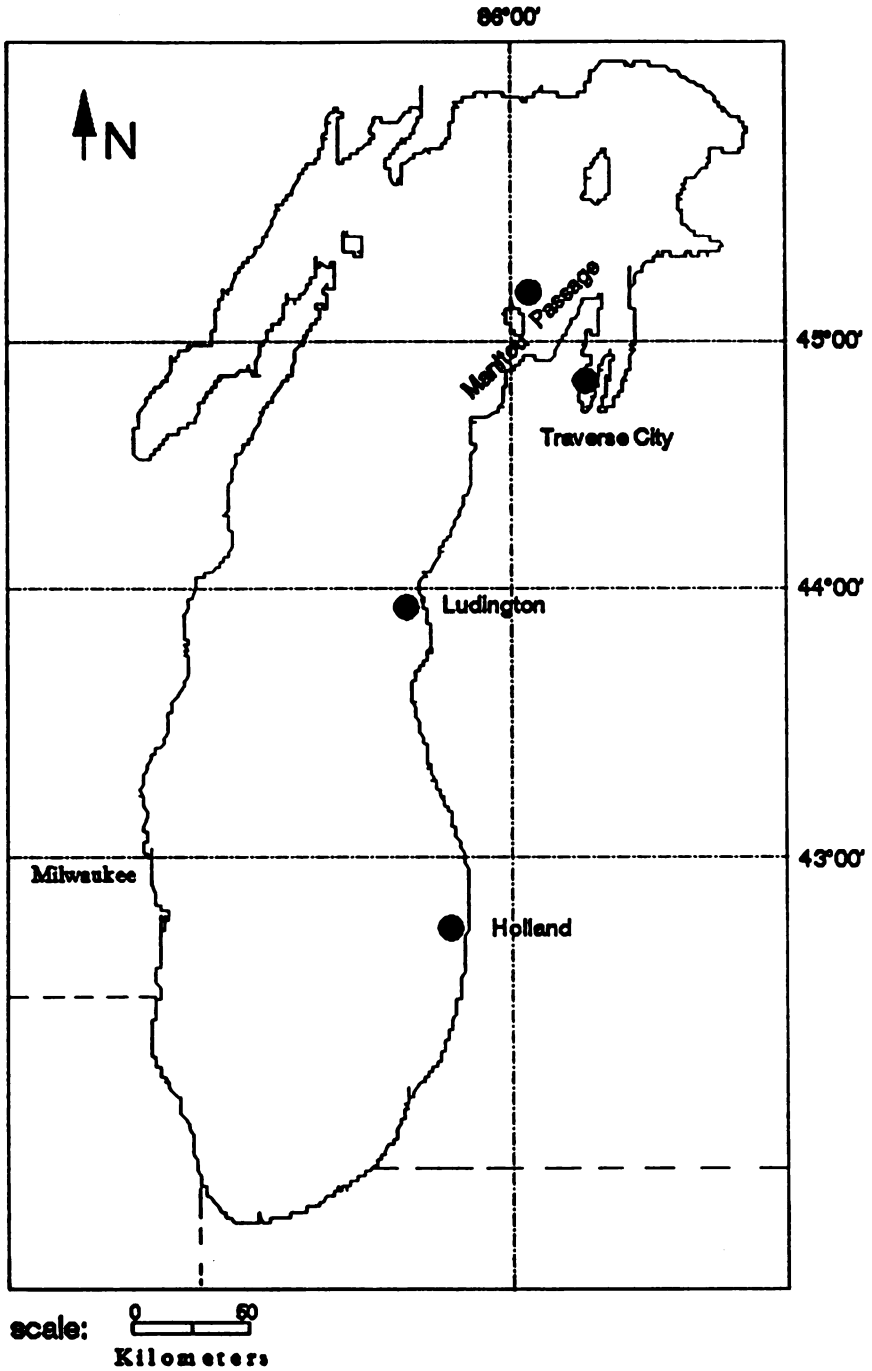


Figure 1. Zooplankton sampling sites on Lake Michigan in 1991.

Both the Manitou Passage (MP) 30 m (45°:04':50"N, 85°:58':39"W) and 10 m (45°:04':50"N, 85°:58':61"W) locations were approximately 25 km NW of Leland. And both were within 1.25 km of the NE side of North Manitou Island.

Each of the West Grand Traverse Bay, and Manitou Passage sites were sampled on two dates in August (8/6 and 8/26) and (8/9 & 8/10 and 8/27) respectively.

The Holland (HO) 30 m (42°46'N,86°14'30") was approximately 2 km offshore of Holland and the 10 m (42°46'N,86°13'20") was about 1 km from shore. Both were sampled only once (8/28).

METHODS

Field Sampling

Vertical tows were taken using a one meter mouth diameter, 153 um mesh Puget Sound closing net (Research Nets, Bothell WA) with a 5:1 length to mouth ratio. The polyethylene cod end had approximately a 5 x 8 cm window of the same mesh. The net has a semi-permeable collar slightly greater than one meter, designed to increase efficiencies by reducing backflow. The towing mechanism was a hydraulically powered drum mounted on the boat deck of the RV Smolt. The net was lowered to the desired depth, just above the sediments (about 1 m). At least a five second delay was allowed (and if necessary, the boat would be repositioned directly above the net) before the net was towed vertically at approximately 0.5 m/sec. After each of the three replicate tows, samples were put in sample jars, preserved with formalin (5-10% by volume), and labeled.

Sampling was mostly during daylight hours, except for July 17, 1991, when sampling took place in the evening before midnight. Patalas (1969) found the capture of zooplankton in Lake Ontario to be unaffected by time of day of sampling. One possible exception was *Limnocalanus macrurus*, which may be reduced in number when sampled in the daylight hours (Balcer et al. 1984).

Temperature Profiles

In August, water temperature profiles (see Appendix A) were taken at each location (except Holland). Temperatures were taken at the surface and at one foot intervals using a thermistor to a depth of about

15 meters. Profiles were again taken at Ludington in September, but to a depth of 30.5 meters.

Surface temperatures were taken at almost every sampling location throughout the study using a hull mounted thermistor.

Surface temperatures detected no upwellings in northeastern Lake Michigan in 1991. Upwellings are caused by sustained winds either from the north or south (Carr 1971). Upwellings cause the colder hypolimnetic waters to surface. An upwelling causes summer epilimnetic temperatures to drop. In 1954, a large upwelling covering several hundred miles of eastern Lake Michigan, dropped surface temperatures from 22°C to only 5°C in less than 3 days (Carr 1971). Such changes in temperature will affect zooplankton abundance, growth, and biomass.

Zooplankton Groups

Fifteen species/groups were counted and converted to numerical abundances. A taxonomic explanation of the abbreviations used in the tables and figures is in Table 1. The rarest species were not estimated and include: *Holopedium gibberum*, *Polyphemus pediculus*, *Pontoporeia hoyi*, *Latona setifera*, and a harpactacoid copepod, probably *Canthocamptus* sp.

The original intent of this study allowed for the grouping of the many species of both Diaptomus sp. and Cyclops sp. Because of these groupings, the dominance by these species groups for the duration of the season may conceal the dominance of one species. The groupings may also conceal a dominance by several species of each grouping, each at different times of the season.

The *Diaptomus* genus, has been split into two genera *Leptodiaptomus* and *Skistodiaptomus* (Balcer et al. 1984), but will be reported here by

Table 1 Taxonomic explanation of abbreviations of species and families used in tables and figures.

Abbreviation	Species	Family
CLADOCERANS		
BYT	Bythotrephes cederstroemi	
BOS	Bosmina longirostris	
GAL	Daphnia galeata mendotae	
RET	D. retrocurva	
PUL	D. pulicaria	
EUB	Eubosmina coregoni	
LEP	Leptodora kindti	
APH	Diaphanosoma sp.	
SPH	Chydorus sphaericus	
CHY		Chydoridae (excluding C. sphaericus)
CYCLOPOID COPEPODS		
CYC	Cyclops sp.	Cyclopidae
CALANOID COPEPODS		
EPI	Epischura lacustris	
LIM	Limnocalanus macrurus	
EUR	Eurytemora affinis	
DIA	Diaptomus sp.	Diaptomidae

the conventional names used by other Great Lakes researchers. In Lake Michigan the genus *Diaptomus* includes up to five possible species: *D. ashlandi*, *D. minutus*, *D. sicilis*, *D. siciloides*, and *D. oregonensis*.

The *Cyclops sp.* group may include the species: *Diacyclops thomasi*, *Acanthocyclops vernalis*, *Mesocyclops edax*, and *Tropocyclops prasinus mexicanus*.

Except for one species of the *Chydoridae* family, *Chydorus sphaericus*, this family was rare and grouped. The remaining *Chydoridae* family was dominated by members of the *Alona* genus, and included the *Alonella* and *Acroperus* genera as well. Species identified included: *Alona rectangula*, *Alona intermedia*, *Alona guttata*, *Alona costata*, *Alonopsis aureola*, and *Acroperus harpae*.The remaining groups in Table 1 are all species and not groups of species.

Numbers of zooplankton are reported both in individuals/m^3, and individuals/m^2. Density abundances are used to facilitate comparisons of total population sizes at sites of differing water depth. Areal abundances are reported because it is assumed that the distribution of zooplankton are primarily in the metalimnion and epilimnion after the establishment of a thermocline. Thermoclines did develope at both Ludington and West Grand Traverse Bay by mid-August. Mean values estimated by dividing these areal abundances by depth will severely underestimate peak densities, and may report a density that does not exist (Lehman 1991).

<u>Zooplankton Abundance</u>

Abundances as both individuals^{-2} (#/m^2) and individuals^{-3} (#/m^3) were measured for use in both the principle component analysis and the biomass estimates.

Previous to subsampling, *B. cederstroemi* were counted and removed from samples for exact abundances and biomass estimates.

In cases where zooplankton density was high, a Folsom plankton splitter was used. Further sub-sampling was done by first bringing the sample up to a known volume, then drawing off a smaller sub-sample using a transfer macro-pipette (1-5 ml).

Each numerous group of animals (in most cases, *Diaptomus sp.*, *Cyclops sp.*, and *B. longirostris*) were counted until at least 100 animals were enumerated. Additional subsamples were taken so that approximately 800-1000 animals were examined, to count the rare taxa.

Samples were enumerated using a plexiglas counting tray, to allow the manipulation of the animals to identify them without dissection. A binocular microscope with a zoom lens (magnification 1-7x), with 15x ocular lenses was used throughout the study.

Identification of zooplankton was made primarily according to Balcer et al. (1984). Brooks (1957) was referenced in the identification of *Daphnia* to species. Brooks (1959) was used for the identification to species of *Chydoridae* and other rare zooplankton. *Chydoridae* were mounted on slides in glycerin and identified to species using a compound microscope.

Principal Component Analysis

Description of the zooplankton community was be done by the multivariate statistical technique, principal component analysis (PCA). Pielou (1984), describes PCA as revealing the "real pattern", of the joint responses of groups of species to persistent features of the environment, separating out the "capricious", unrelated responses of a few individual members of a few species to environmental accidents of

the sort that occur sporadically (such as upwellings in the Great Lakes), and have only local and temporary effects.

The purpose of performing a PCA is to reduce the dimensionality of the data matrix, and find the structure of the matrix, without the sacrifice of eliminating data from the matrix. Structure is here defined as, any systematic pattern that would indicate that species tended to occur together, or that the sampling units, when appropriately arranged, would exhibit a gradual, continuous trend in their species compositions. The chief consequence of a PCA, is the first principle axis is so oriented to make the variance of the first principle component scores as great as possible (and the second PC, second greatest)(Pielou 1984).

Analysis was carried out using the statistical package, SYSTAT 5.02 (Wilkinson 1990). An introductory description of this technique can be found in Sprules (1977), Pielou (1984), and Ludwig & Reynolds (1988).

The matrix of covariances between species was calculated, thus standardizing the normalized abundances by subtraction of species transformed means from the transformed abundances. This preserves the variability of individual species. PCA summarizes the information in the covariance matrix in terms of new components, a small number of which account for most of the variation. From this simplification one can formulate hypotheses about the causes of variation in the system. This reduces the species-quadrat matrix to a species-component matrix (Sprules 1977).

Each component, a linear compound of the transformed proportionate abundances, has an associated eigenvalue giving the amount of variation in species accounted for by each component of the matrix, and eigenvectors (not reported) of component coefficients giving the

weighting of each species in the linear compound (Sprules 1977).

This study had 76 separate samples (quadrats) with abundances (#/m^2) of 15 species, each with the three observed environmental variables of date (month), location, and depth (30m or 10m). Each individual sample is one of the n data points (76) each with *s* (15 species) coordinates. Each coordinate of each point is a function of the species abundance (#/m^2) in the quadrat represented by that point. This produces a 15-dimensional plot, or "swarm" of data points (Pielou 1984). Plotted on the 15 coordinates, the PCA aligns and centers the first principle component (PC) axis where the largest variation occurs.

Before analysis the fifteen species abundances (#/m^2 and #/m^3) were first transformed by $\ln(\#/m^n+1)$. This transformation was used to decrease the dependence of taxa variance on taxa abundance. The transformation allowed rare and abundant taxa to be potentially equal in importance in the analysis while still retaining numerical differences in abundances. Use of the variance-covariance matrix was possible because all abundances had the same measurement units (Pielou 1984).

Correlation Coefficients of PCA

Correlations between principle components (1-4) and the transformed species abundances, species (1-15) were calculated to assist with the interpretation of the PCs. A species was positively correlated with a principle component if the coefficient was >.230, or negatively correlated if the coefficient was < -.230 (df=70, alpha = 0.05).

Multiple Regressions of PCs on Environmental Variables

To determine any environmental interpretation of observed variables, multiple linear regressions of PCs 1 through 4 on month, depth, and site, were performed to determine if there was a hypothetical

trend with these variables and the zooplankton community along the PC ordination axes (Ludwig & Reynolds 1988).

Verification of Zooplankton Environmental Trends on PC's

Transformed abundances of species positively and negatively correlated to both PC 1 and PC 2 were plotted by each significant variable to verify if the species abundance responds in the manner as hypothesized by the regressions and correlations.

Species Partitioning

There are numerous methods for classifying ecological data. The type used here is classified as an ordination-space partitioning method, and is adequate for most, if not all ecological applications (Pielou 1984). Lefkovitch's partitioning method is the most straightforward method for divisively splitting the PCA ordination (Pielou 1984). The data are first ordinated using principle component analysis, then split divisively into positive and negative groups on the first then the second principle component (Pielou 1984). The result of using only the first two PC's, is a two-dimensional partitioning of species into each of the four quadrants of the two axis plot, also called a biplot.

The initial grouping of species into associations was done only for species that were found to be significantly correlated with both components, either positively or negatively on the areal, or cubic biplot.

Zooplankton Dry Weight Methods

It is emphasized that the biomass estimates of this study were not verified. The animals were not weighed, and the accuracy of the estimates are unknown. Therefore the following dry weight estimates are only relative estimates within this study, and can not be applied to

other zooplankton populations.

Aliquots of replicates were mixed and a small subsample was taken for measurement. Measurements of taxon were performed for each month, depth, and location. To reduce the number of measurements of samples, when a sampling occurred within the same month, and at the same location and depth, the measurements of one sample (a combination of three replicates) were applied to taxon within that same month (months began and ended mid-month). Measurement of a species was not done when abundances were low.

Dry weight biomass was estimated only for the most numerous groups found during counting; *Diaptomus sp.*, *Cyclops sp.*, *B. longirostris*, *Daphnia galeata*, and *Epischura lacustris*. Three other species, *L. macrurus*, *D. retrocurva*, and *B. cederstroemi*, whose average abundance was less than one percent of all species/groups over the year, were measured because of their relatively larger size.

Dry weight estimation methods followed three courses of measurement: the counting of instars, length-dry weight regressions, and a volume to dry weight method.

A length-dry weight regression already exists for *B. cederstroemi* (Garton and Berg 1990), but Burkhardt (1991) developed linear regressions of mean dry weights of each of the three instars of *B. cederstroemi* on epilimnetic temperature. Species specific length-dry weight regressions exist for *B. longirostris*, *D. galeata*, *D. retrocurva*, *Epischura lacustris*, and *L. macrurus* and were used. The volume to dry weight method was used for *Diaptomus sp.* and *Cyclops sp.* because these were groupings of many species.

Zooplankton Measurements

Zooplankton dimensions were measured using an ocular micrometer to within 0.02 mm (20 um). Individuals in a sample were measured consecutively as encountered to obtain a random sampling of the population. Those animals that were obviously contorted were not measured.

Copepod length measurements were made from the furthest projection of the head to the insertion of the caudal setae. Lengths of *B. longirostris* were measured from the furthest projection of the head process to the point of insertion of the caudal spine. The cyclomorphotic *D. retrocurva* and *D. galeata* were measured from the eye to the base of the tail spine, or standard length, (Lawrence et al.,1987).

Volume to Dry Weight Estimation

Lawrence et al.(1987) developed estimates of biomass of zooplankton using geometric formulas, and conversion factors to convert volume to dry weight.

Diaptomus sp. and *Cyclops sp.* were measured volumetrically, because they are groupings of several congeneric species. Volume estimates were made by measuring length, width and depth and entering these measurements into formulas, where a=0.5 length, b=0.5 width, and c=0.5 depth:

Cyclops sp. volume= (4/3)abc*pi

Diaptomus sp. volume= (4/3)ab(1.25c)*pi

The volumes were then converted to dry weight by multiplying the average volume of a combined sample by 0.07 (Lawrence et al.1987).

Ninety five percent confidence intervals of the volume measured

species, *Diaptomus sp.* and *Cyclops sp.*, were calculated using the dry weight values (0.07*volume).

Length-Dry Weight Regression Estimation

Species specific length-dry weight regressions (Table 2) used were from: Culver et al. (1985), for *B. longirostris* and both daphnids, *D. galeata* and *D. retrocurva*; Conway (1977), for *L. macrurus*; and Lawrence et al. (1987), for *E. lacustris*.

Biomass estimates from length-dry weight regressions followed the guidelines of Bird and Prairie (1985), except for the use of the bootstrap variance. The bootstrap was performed on 30 dry weights of the most variable species *Diaptomus sp.*, and the resulting confidence interval was nearly symmetrical and differed from both upper and lower limits by less than 0.005 mm. It was decided that the variances using the estimated dry weights would suffice.

Table 2 Length-Dry Weight Regressions

Species	L-W Regression (W in ug)	Range (mm)	r^2
B. longirostris	Ln W= 2.8756+(2.2291LnL)	(.22-.43)	.98
D. galeata	Ln W= 2.3917+(1.5202LnL)	(.36-1.81)	.99
D. retrocurva	Ln W= 2.0213+(2.7552LnL)	(.33-1.45)	.99
L. macrurus	$Log_{10}W$= (0.98L) - 0.79	(1.10-2.83)	.70
E. lacustris	Ln W= 1.4670+(2.4741LnL)	(1.43-2.04)	.86

***Bythotrephes* Dry Weight Estimation**

Burkhardt (1991) developed a linear regression of mean dry weight of the three instars (r_1=.927, r_2=.883, r_3=.930) of *B. cederstroemi* on

epilimnetic temperatures in Lake Michigan (1990 and 1991). The instars are distinguished by the number of lateral spines extending from the caudal spine.

Neonates have no lateral spines, and none were found after August. Average surface temperatures of this study in July and August 1991 ranged from 19.2°C to 21.1°C, and an approximation of 70 ug was used from Burkhardt's (1991) data for neonates at 18°C .

Counts of instars and neonates were done in entirety on every sample to reduce sampling bias. Instars with broken spines were multiplied by the average of the three regression values in order to salvage some estimate of biomass of these animals.

RESULTS and DISCUSSION

Zooplankton Abundance

Abundances are reported as both individuals^{-2} or areal abundances (Table 3) and as individuals^{-3} or cubic abundances (Table 4). Each reporting method has it's advantages. Areal abundances allow for the detection of peak abundances, and density abundances allow for direct comparisons of population abundances at different contours. The density abundance is appropriate when the water column lacks a hypolimnion, because hypolimnetic waters may have low numbers of zooplankton that would artificially lower the zooplankton abundances. The primary sampling location, Ludington, and West Grand Traverse Bay each developed a hypolimnion in August and cubic abundances from that time on should be considered cautiously.

Abundances calculated as #/m^2 were dominated by the four taxon groups; *Diaptomus sp.*, *Cyclops sp.*, *Bosmina longirostris*, and *Daphnia galeata* (Table 3).

Average areal abundances over the entire sampling season were as follows: *Diaptomus sp.* (61.1%), *Cyclops sp.* (21.8%), *B. longirostris* (8.5%), and *D. galeata* (5.7%). Less abundant species areal abundances were, *E. lacustris* (1.5%), *D. retrocurva* (0.7%), and *B. cederstroemi* (0.1%), and the remaining species account for the rest (0.6%).

Total zooplankton areal abundance from a single sample at the 30 meter contour peaked on August 29, 1991 for Ludington (>469,000/m^2: 15,645/m^3), on August 27 for Manitou Passage (>931,000/m^2: 31034/m^3), and on August 26 for West Grand Traverse Bay (>1,222,000/m^2: 40742/m^3)

Table 3. Zooplankton areal abundance (#/m²) at two depths (10 and 30 m) and four sites in northeastern Lake Michigan in 1991.

LOC	DATE	Z	BYT	CYC	DIA	BOS	GAL	RET	PUL	EPI	EUB	LEP	LIM	APH	CHY	SPH	EUR	TOTAL
LU	07/17/91	30	530	28025	126879	1601	76943	1359	0	314	437	0	1411	0	218	0	0	237718
LU	07/17/91	30	510	13248	95287	3121	79490	4204	318	272	191	1087	1087	0	0	0	0	198815
LU	07/17/91	30	736	11720	263949	2177	59618	3057	602	432	432	0	432	432	0	0	0	343587
LU	07/17/91	10	189	42803	60382	4395	318	413	0	0	138	0	0	92	183	46	0	108959
LU	07/17/91	10	191	37834	83312	3490	510	409	0	82	328	0	82	82	1310	1146	0	128777
LU	07/17/91	10	287	40255	42803	5452	602	340	23	0	57	0	170	113	283	510	0	90895
LU	07/30/91	30	19	142166	237962	1444	34140	2752	0	4127	917	0	4127	0	0	0	0	427653
LU	07/30/91	30	4	51465	68280	1104	20892	2854	594	3669	611	0	0	0	0	0	0	149473
LU	07/30/91	30	14	45401	154140	2335	28306	1834	0	3057	0	0	1834	0	0	0	0	236922
LU	08/01/91	10	22	6837	11771	15338	951	51	0	204	0	0	0	102	34	0	51	35360
LU	08/01/91	10	31	6650	22930	18115	688	41	0	306	102	20	0	102	20	0	143	49147
LU	08/01/91	10	25	11146	21758	31210	951	25	0	535	204	76	0	25	178	76	127	66337
TC	08/06/91	30	745	109656	336917	2155	2766	0	29	1529	127	0	0	0	0	0	0	453924
TC	08/06/91	30	157	12178	177962	801	1547	83	0	375	0	0	0	0	0	0	0	193102
TC	08/06/91	30	284	10043	64204	1076	1552	0	0	170	42	0	0	0	0	0	0	77371
TC	08/06/91	10	74	974	8503	1092	273	9	0	34	8	0	0	9	17	0	0	10993
TC	08/06/91	10	57	611	7813	1077	58	0	0	76	13	0	0	29	38	0	0	9774
TC	08/06/91	10	8	1219	6879	1237	255	0	0	51	13	0	0	0	18	0	0	9680
MP	08/10/91	30	223	37274	152739	3456	3036	0	0	1089	57	57	1318	0	0	0	0	199249
MP	08/10/91	30	113	8548	159745	2763	2883	92	0	642	92	40	1192	0	0	0	0	176110
MP	08/10/91	30	366	18684	110064	2208	4161	85	0	2981	57	0	1548	0	0	0	0	140153
MP	08/09/91	10	5	2994	38726	1110	3694	0	0	65	33	0	33	0	0	0	0	46660
MP	08/09/91	10	3	4251	22828	1070	4637	0	0	102	0	15	0	0	0	0	0	32905
MP	08/09/91	10	5	3626	16140	386	4771	0	0	204	0	0	0	0	0	0	0	25133
LU	08/16/91	30	312	7097	229554	3676	85350	0	801	1468	734	0	2935	0	0	0	0	331928
LU	08/16/91	30	271	71937	139763	2965	39282	0	0	741	371	0	0	0	0	0	0	255330
LU	08/16/91	30	282	8025	245860	5180	105987	0	552	2769	692	0	1384	692	0	0	0	371424
LU	08/16/91	10	111	14522	26879	8471	955	127	0	68	297	0	0	0	442	0	0	51873
LU	08/16/91	10	149	20764	90446	30064	3822	364	0	408	182	0	0	0	34	0	0	146233
LU	08/16/91	10	138	18599	32611	23057	3185	0	0	229	102	25	0	0	25	51	0	78022

Table 3. (cont'd)

LOC	DATE	Z	BYT	CYC	DIA	BOS	GAL	RET	PUL	EPI	EUB	LEP	UM	APH	CHY	SPH	EUR	TOTAL
TC	08/26/91	30	80	130701	279745	122675	138726	0	4169	5837	0	0	0	0	0	0	0	681933
TC	08/26/91	30	84	162038	437962	233885	376051	0	4586	7643	0	0	0	0	0	0	0	1222250
TC	08/26/91	30	73	160510	440510	158132	131975	0	0	3567	1783	5350	0	0	0	0	0	901899
TC	08/26/91	10	33	10919	109045	30064	2912	0	0	0	0	0	0	0	0	0	0	152972
TC	08/26/91	10	22	16194	128408	47236	13901	0	143	1003	0	143	0	0	0	0	0	207050
TC	08/26/91	10	32	28949	131274	69363	12611	0	0	0	0	0	0	0	0	0	0	242229
MP	08/27/91	30	74	189146	361444	25002	60875	0	0	24459	0	0	0	0	0	0	0	661000
MP	08/27/91	30	65	194395	518981	34955	37809	0	0	42803	143	713	0	0	0	0	0	829864
MP	08/27/91	30	80	180042	596178	66705	57441	926	0	28720	0	926	0	0	0	0	0	931020
MP	08/27/91	10	11	25732	95414	17325	4841	535	0	0	0	0	764	0	0	255	0	144878
MP	08/27/91	10	14	42948	164331	20807	13588	212	0	2335	0	212	0	0	0	0	0	244448
MP	08/27/91	10	3	20382	57962	6157	4034	283	0	2052	0	71	0	0	0	71	0	91015
HO	08/28/91	30	18	88280	149045	26083	9745	35828	0	287	2006	3439	0	573	0	0	0	315304
HO	08/28/91	30	11	80255	192611	23977	20212	22987	0	11295	3171	446	0	0	0	0	0	354965
HO	08/28/91	30	31	64204	183694	21191	8183	34480	0	1259	3147	420	0	210	0	0	0	316818
HO	08/28/91	10	43	4222	13248	1295	21	64	0	892	0	42	0	21	42	42	0	19934
HO	08/28/91	10	33	8747	25478	2611	127	446	0	2229	0	159	0	32	96	64	0	40023
HO	08/28/91	10	33	4624	15287	892	0	66	0	727	0	33	0	0	0	0	0	21661
LU	08/29/91	30	19	90955	174777	15032	3567	12484	0	1274	0	0	0	0	0	0	0	298108
LU	08/29/91	30	36	203312	206879	29554	5860	20382	1019	1274	0	1019	0	0	0	0	0	469335
LU	08/29/91	30	23	153376	189045	25223	9427	7389	0	4841	2548	289	0	48	0	0	0	392207
LU	08/29/91	10	37	3742	6316	4618	0	122	0	0	0	122	0	24	0	0	0	14983
LU	08/29/91	10	65	8201	15499	8280	0	142	0	35	0	354	0	71	495	389	0	33531
LU	08/29/91	10	31	3468	5202	2548	0	0	0	71	35	177	0	0	389	495	0	12415
LU	09/13/91	30	19	136433	46213	10230	13052	706	0	0	0	0	1058	0	0	0	0	207711
LU	09/13/91	30	26	60191	142166	7296	15843	834	0	0	0	417	2501	0	0	0	0	229273
LU	09/13/91	30	17	44609	131847	5474	11835	1627	0	0	0	444	0	0	0	0	0	195852
LU	09/13/91	10	4	2644	14910	419	512	16	16	124	0	78	0	0	0	0	0	18720
LU	09/13/91	10	1	4540	25452	734	459	46	0	92	0	46	0	0	0	0	0	31369
LU	09/13/91	10	8	6306	30064	1755	1614	226	0	546	0	109	55	0	0	0	0	40682

Table 3. (cont'd)

LOC	DATE	Z	BYT	CYC	DIA	BOS	GAL	RET	PUL	EPI	EUB	LEP	LIM	APH	CHY	SPH	EUR	TOTAL
LU	10/03/91	30	1	39236	85962	6242	3864	0	0	27643	0	255	0	0	0	0	223	163426
LU	10/03/91	30	4	37452	41376	6658	2259	0	0	23567	235	0	0	0	0	0	235	111786
LU	10/03/91	30	14	37809	43873	8204	238	0	0	0	0	0	0	0	0	0	0	90137
LU	10/03/91	10	32	5401	12433	2955	34	0	0	221	0	0	0	0	0	34	0	21111
LU	10/03/91	10	39	20866	44764	5588	357	0	0	1325	0	0	0	0	0	153	0	73093
LU	10/03/91	10	19	12365	40662	3686	178	0	0	2684	0	34	0	0	0	102	0	59731
LU	10/18/91	10	381	19439	59567	981	30	0	0	1605	0	0	0	0	0	153	76	82232
LU	10/18/91	10	169	44943	127338	1011	0	0	0	1949	0	0	0	0	0	0	0	175409
LU	10/18/91	10	152	46726	85605	5231	0	0	0	1172	0	0	0	51	0	306	0	139243
LU	10/18/91	10	279	88841	225605	20178	0	0	0	459	0	0	0	0	0	0	0	335362
LU	11/14/91	30	113	59134	90803	1168	374	0	0	3325	0	0	0	0	0	0	0	154916
LU	11/14/91	30	80	56892	151618	561	1121	0	0	1656	0	0	0	0	0	0	0	211927
LU	11/14/91	30	28	63618	135363	420	1728	0	0	1911	0	0	0	0	0	0	0	203069
LU	11/14/91	10	103	17707	43312	977	64	0	0	414	64	0	0	0	0	32	0	62673
LU	11/14/91	10	135	12153	26599	0	51	0	0	382	0	0	0	0	0	0	0	39320
LU	11/14/91	10	1003	8662	44841	127	85	0	0	764	0	0	0	0	0	0	0	55482

Table 4. Zooplankton cubic abundance (#/m^3) at two depths (10 and 30 m) and four sites in northeastern Lake Michigan in 1991.

LOC	DATE	Z	BYT	CYC	DIA	BOS	GAL	RET	PUL	EPI	EUB	LEP	LIM	APH	CHY	SPH	EUR	TOTAL
LU	07/17/91	30	18	934	4229	53	2565	45	0	10	15	0	47	0	7	0	0	7924
LU	07/17/91	30	17	442	3176	104	2650	140	11	9	6	36	36	0	0	0	0	6627
LU	07/17/91	30	25	391	8798	73	1987	102	20	14	14	0	14	14	0	0	0	11453
LU	07/17/91	10	19	4280	6038	439	32	41	0	0	14	0	0	9	18	5	0	10896
LU	07/17/91	10	19	3783	8331	349	51	41	0	8	33	0	8	8	131	115	0	12878
LU	07/17/91	10	29	4025	4280	545	60	34	2	0	6	0	17	11	28	51	0	9089
LU	07/30/91	30	1	4739	7932	48	1138	92	0	138	31	0	138	0	0	0	0	14255
LU	07/30/91	30	0	1715	2276	37	696	95	20	122	20	0	0	0	0	0	0	4982
LU	07/30/91	30	0	1513	5138	78	944	61	0	102	0	0	61	0	0	0	0	7897
LU	08/01/91	10	2	684	1177	1534	95	5	0	20	0	0	0	10	3	0	5	3536
LU	08/01/91	10	3	665	2293	1811	69	4	0	31	10	2	0	10	2	0	14	4915
LU	08/01/91	10	3	1115	2176	3121	95	3	0	54	20	8	0	3	18	8	13	6634
TC	08/06/91	30	25	3655	11231	72	92	0	1	51	4	0	0	0	0	0	0	15131
TC	08/06/91	30	5	406	5932	27	52	3	0	13	0	0	0	0	0	0	0	6437
TC	08/06/91	30	9	335	2140	36	52	0	0	6	1	0	0	0	0	0	0	2579
TC	08/06/91	10	7	97	850	109	27	1	0	3	1	0	0	1	2	0	0	1099
TC	08/06/91	10	6	61	781	108	6	0	0	8	1	0	0	3	4	0	0	977
TC	08/06/91	10	1	122	688	124	25	0	0	5	1	0	0	0	2	0	0	968
MP	08/10/91	30	7	1242	5091	115	101	0	0	36	2	2	44	0	0	0	0	6642
MP	08/10/91	30	4	285	5325	92	96	3	0	21	3	1	40	0	0	0	0	5870
MP	08/10/91	30	12	623	3669	74	139	3	0	99	2	0	52	0	0	0	0	4672
MP	08/09/91	10	1	299	3873	111	369	0	0	7	3	0	3	0	0	0	0	4666
MP	08/09/91	10	0	425	2283	107	464	0	0	10	0	2	0	0	0	0	0	3291
MP	08/09/91	10	1	363	1614	39	477	0	0	20	0	0	0	0	0	0	0	2513
LU	08/16/91	30	10	237	7652	123	2845	0	27	49	24	0	98	0	0	0	0	11064
LU	08/16/91	30	9	2398	4659	99	1309	0	0	25	12	0	0	0	0	0	0	8511
LU	08/16/91	30	9	268	8195	173	3533	0	18	92	23	0	46	23	0	0	0	12381
LU	08/16/91	10	11	1452	2688	847	96	13	0	7	30	0	0	0	44	0	0	5187
LU	08/16/91	10	15	2076	9045	3006	382	36	0	41	18	0	0	0	3	0	0	14623
LU	08/16/91	10	14	1860	3261	2306	318	0	0	23	10	3	0	0	3	5	0	7802

Table 4. (cont'd)

LOC	DATE	Z	BYT	CYC	DIA	BOS	GAL	RET	PUL	EPI	EUB	LEP	LIM	APH	CHY	SPH	EUR	TOTAL
TC	08/26/91	30	3	4357	9325	4089	4624	0	139	195	0	0	0	0	0	0	0	22731
TC	08/26/91	30	3	5401	14599	7796	12535	0	153	255	0	0	0	0	0	0	0	40742
TC	08/26/91	30	2	5350	14684	5271	4399	0	0	119	59	178	0	0	0	0	0	30063
TC	08/26/91	10	3	1092	10904	3006	291	0	0	0	0	0	0	0	0	0	0	15297
TC	08/26/91	10	2	1619	12841	4724	1390	0	14	100	0	14	0	0	0	0	0	20705
TC	08/26/91	10	3	2895	13127	6936	1261	0	0	0	0	0	0	0	0	0	0	24223
MP	08/27/91	30	2	6305	12048	833	2029	0	0	815	0	0	0	0	0	0	0	22033
MP	08/27/91	30	2	6480	17299	1165	1260	0	0	1427	5	24	0	0	0	0	0	27662
MP	08/27/91	30	3	6001	19873	2224	1915	31	0	957	0	31	0	0	0	0	0	31034
MP	08/27/91	10	1	2573	9541	1732	484	54	0	0	0	0	76	0	0	26	0	14488
MP	08/27/91	10	1	4295	16433	2081	1359	21	0	234	0	21	0	0	0	0	0	24445
MP	08/27/91	10	0	2038	5796	616	403	28	0	205	0	7	0	0	0	7	0	9101
HO	08/28/91	30	1	2943	4968	869	325	1194	0	10	67	115	0	19	0	0	0	10510
HO	08/28/91	30	0	2675	6420	799	674	766	0	377	106	15	0	0	0	0	0	11832
HO	08/28/91	30	1	2140	6123	706	273	1149	0	42	105	14	0	7	0	0	0	10561
HO	08/28/91	10	4	422	1325	130	2	6	0	89	0	4	0	2	4	4	0	1993
HO	08/28/91	10	3	875	2548	261	13	45	0	223	0	16	0	3	10	6	0	4002
HO	08/28/91	10	3	462	1529	89	0	7	0	73	0	3	0	0	0	0	0	2166
LU	08/29/91	30	1	3032	5826	501	119	416	0	42	0	0	0	0	0	0	0	9937
LU	08/29/91	30	1	6777	6896	985	195	679	34	42	0	34	0	0	0	0	0	15645
LU	08/29/91	30	1	5113	6301	841	314	246	0	161	85	10	0	2	0	0	0	13074
LU	08/29/91	10	4	374	632	462	0	12	0	0	0	12	0	2	0	0	0	1498
LU	08/29/91	10	6	820	1550	828	0	14	0	4	0	35	0	7	50	39	0	3353
LU	08/29/91	10	3	347	520	255	0	0	0	7	4	18	0	0	39	50	0	1241
LU	09/13/91	30	1	4548	1540	341	435	24	0	0	0	0	35	0	0	0	0	6924
LU	09/13/91	30	1	2006	4739	243	528	28	0	0	0	14	83	0	0	0	0	7642
LU	09/13/91	30	1	1487	4395	182	394	54	0	0	0	15	0	0	0	0	0	6528
LU	09/13/91	10	0	264	1491	42	51	2	2	12	0	8	0	0	0	0	0	1872
LU	09/13/91	10	0	454	2545	73	46	5	0	9	0	5	0	0	0	0	0	3137
LU	09/13/91	10	1	631	3006	176	161	23	0	55	0	11	5	0	0	0	0	4068

Table 4. (cont'd)

LOC	DATE	Z	BYT	CYC	DIA	BOS	GAL	RET	PUL	EPI	EUB	LEP	LIM	APH	CHY	SPH	EUR	TOTAL
LU	10/03/91	30	0	1308	2865	208	129	0	0	921	0	9	0	0	0	0	7	5448
LU	10/03/91	30	0	1248	1379	222	75	0	0	786	8	0	0	0	0	0	8	3726
LU	10/03/91	30	0	1260	1462	273	8	0	0	0	0	0	0	0	0	0	0	3005
LU	10/03/91	10	3	540	1243	296	3	0	0	22	0	0	0	0	0	3	0	2111
LU	10/03/91	10	4	2087	4476	559	36	0	0	133	0	0	0	0	0	15	0	7309
LU	10/03/91	10	2	1237	4066	369	18	0	0	268	0	3	0	0	0	10	0	5973
LU	10/18/91	10	38	1944	5957	98	3	0	0	161	0	0	0	0	0	15	8	8223
LU	10/18/91	10	17	4494	12734	101	0	0	0	195	0	0	0	0	0	0	0	17541
LU	10/18/91	10	15	4673	8561	523	0	0	0	117	0	0	0	5	0	31	0	13924
LU	10/18/91	10	28	8884	22561	2018	0	0	0	46	0	0	0	0	0	0	0	33536
LU	11/14/91	30	4	1971	3027	39	12	0	0	111	0	0	0	0	0	0	0	5164
LU	11/14/91	30	3	1896	5054	19	37	0	0	55	0	0	0	0	0	0	0	7064
LU	11/14/91	30	1	2121	4512	14	58	0	0	64	0	0	0	0	0	0	0	6769
LU	11/14/91	10	10	1771	4331	98	6	0	0	41	6	0	0	0	0	3	0	6267
LU	11/14/91	10	14	1215	2660	0	5	0	0	38	0	0	0	0	0	0	0	3932
LU	11/14/91	10	100	866	4484	13	8	0	0	76	0	0	0	0	0	0	0	5548

(Table 3).

Maximum abundance at the 10 meter contour was on the same dates in late August (27 and 26 respectively) for Manitou Passage (>244,000/m^2), and West Grand Traverse Bay (>242,000/m^2), while at Ludington the maximum 10 meter contour abundance was on October 18th (>335,000/m^2: 33,536/m^3)(Table 3).

Obvious differences in areal abundances between the two depths was apparent. For most species, abundance was greater at the 30 meter contour. Much of the difference may be a result of the greater volume of water at the 30 m contour. Areal abundance at the deeper stations was greatest for all three daphnids: *D. pulicaria* (77 X), *D. retrocurva* (43 X), and *D. galeata* (20 X), and a large calanoid copepod, *L. macrurus* (21 X). The daphnid and *L. macrurus* estimates are much greater at the deeper contour than can be explained alone by three times as much volume.

The greater abundance of daphnids at the 30 meter contour than at the 10 meter may be caused by increased predation in shallower waters. *Daphnia sp.* are some of the largest opaque zooplankton found in the Great Lakes and is targeted by visually feeding planktivores.

It is possible that *Bythotrephes cederstroemi*, alewife, or yellow perch, visually feeding predators, may be contributing to the smaller population abundances of daphnids found at the shallower depths.

Greater numbers of *L. macrurus* at the 30 meter contour may be a result of the species affinity to colder waters (Balcer et al. 1984). *L. macrurus* is a cold-water stenotherm that is generally restricted to the hypolimnion (Wells 1960), and is seldom found in waters warmer than 14°C (Balcer et al. 1984).

Differences between seasons are not readily apparent from abundance

estimates alone, and must wait for the following PC analysis.

Principal Component Analysis

A scree diagram is a subjective method of deciding the number of principal components to analyze. The scree diagram (Figure 2) illustrates the declining percent of total variance explained by subsequent principal components. The number of principle components to be analyzed, 4, is one less than the point where the curve flattens at PC 5. This cut off point at PC 4 can also be explained intuitively. Dividing the 15 principle components into 100%, results in 6.66%. If all the variance was random, each component would have no more than 6.66% of the total variance. In both cases, PC 5 explained less than 6.66% for both the areal (6.5%) and the cubic (6.3%) abundance data.

The first four PC's from the areal and cubic abundance data of 15 species account for more than 66% of the total variance in both cases. The first component, PC 1 accounts for 26.1% of the areal and 26.9% of the cubic abundance variance. Principle component 2 accounts for an additional 17.3% of the areal, and 17.2% of the cubic variance. The third accounts for 12.8% areal, and 13.3% cubic variance; and the fourth accounts for 10.1% areal, and 9.4% cubic variance.

The first four principle components were analyzed with multiple regressions and transformed abundances were plotted on each of the significant variables (depth and month) to show slope. However, only the first two PCs were verified and plotted on the two-dimensional biplot. Because the biplot was necessary for the method chosen for species partitioning, correlation coefficients and verification beyond the first two principle components was not done.

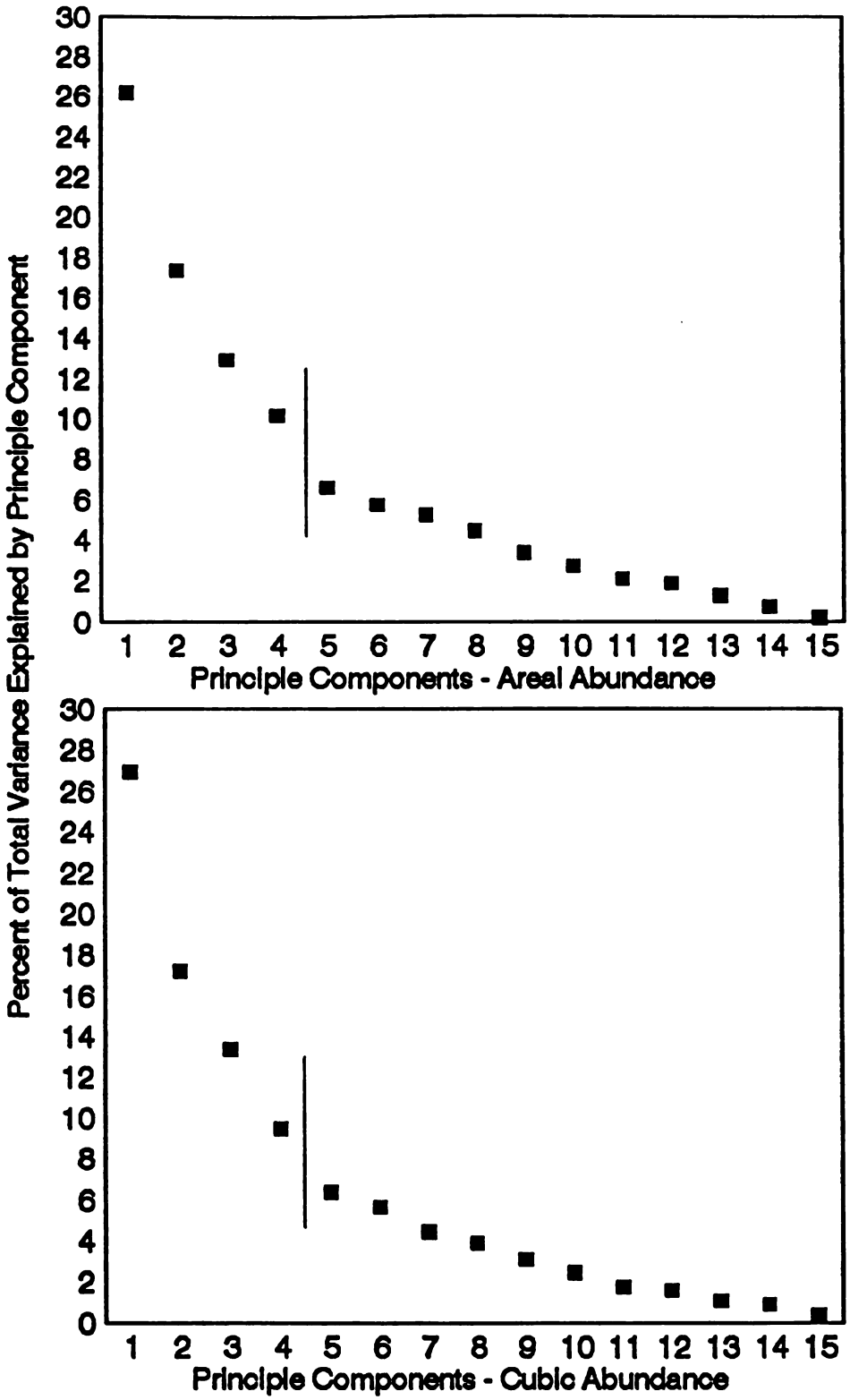


Figure 2. Scree diagrams showing percent of variance explained by each component for both areal and cubic abundance data, and the cutoff line for principle components analyzed.

Correlation Coefficients for PC 1

Correlation coefficients that were significant to each of the principle components of the transformed areal abundances are shown in Table 5. Ten species were positively correlated with PC 1. The species were: *Cyclops sp.*, *Diaptomus sp.*, *B. longirostris*, *D. galeata*, *D. retrocurva*, *D. pulicaria*, *E. lacustris*, *E. coregoni*, *L. kindti*, and *L. macrurus* (Table 5). Only one species, *Chydorus sphaericus*, had a significant negative correlation with the first component.

The cubic abundance data had the same ten positively correlated species, and *C. sphaericus* was joined by *B. cederstroemi* as the only negatively correlated species (Table 6).

Correlation Coefficients for PC 2

Five species were positively correlated with PC 2 of the areal PCA. The species were: *Cyclops sp.*, *Diaptomus sp.*, *D. galeata*, *D. pulicaria*, and *E. lacustris*. Species negatively correlated to the areal abundance PCA include: *D. retrocurva*, *L. kindti*, *Diaphanosoma sp.*, *Chydorus sp.*, and *C. sphaericus* (Table 5).

With the cubic PCA, except for two species, *Cyclops sp.* and *Eubosmina coregoni*, all species reversed significant correlations from negative to positive and from positive to negative (Table 6). *Cyclops sp.* was significant only with the areal PCA (positively) (Table 5) and *E. coregoni* only with the cubic PCA (Table 6).

Regressions and ANOVA of Principal Components

As would be expected with principle component analysis, the regression of the first principle component had the best fit (multiple r^2=.689) (Table 7), and the fourth PC had the worst fit (multiple r^2=.029) (Table 8). The same was true for the cubic abundance data

Table 5. Correlation coefficients of principle components 1 - 4, using areal abundance data. *

SPECIES	PC 1	PC 2	PC 3	PC 4
BYTHOTREPHES	0.036	0.070	0.423 *	0.393 *
CYCLOPS SP.	0.469 *	0.250 *	-.229 *	-.034
DIAPTOMUS SP.	0.611 *	0.463 *	-.058	-.027
BOSMINA	0.404 *	0.017	-.306 *	0.046
DAPHNIA GALEATA	0.802 *	0.431 *	0.083	-.116
D. RETROCURVA	0.674 *	-.608 *	-.140	-.212
D. PULICARIA	0.392 *	0.335 *	0.165	0.056
EPISCHURA	0.229	0.542 *	-.443 *	0.425 *
EUBOSMINA	0.597 *	-.117	0.161	0.656 *
LEPTODORA	0.344 *	-.293 *	-.707 *	-.080
LIMNOCALANUS	0.509 *	-.063	0.667 *	-.165
DIAPHANOSOMA	0.152	-.546 *	0.063	0.425 *
CHYDORUS SP.	-.135	-.606 *	0.183	0.449 *
C. SPHAERICUS	-.330 *	-.478 *	0.072	0.303 *
EURYTEMORA	-.095	0.033	-.178	0.268 *

* Coefficient is significant (α = .05) either positively (> .230) or negitively (< -.230) with the principle components.

Table 6. Correlation coefficients of principle components 1 - 4, using cubic abundance data. *

SPECIES	PC 1	PC 2	PC 3	PC 4
BYTHOTREPHES	-.293 *	0.083	-.163	0.265 *
CYCLOPS SP.	0.359 *	-.077	0.477 *	0.149
DIAPTOMUS SP.	0.502 *	-.323 *	0.176	0.186
BOSMINA	0.400 *	0.067	0.523 *	0.662 *
DAPHNIA GALEATA	0.889 *	-.321 *	-.209	0.144
D. RETROCURVA	0.599 *	0.667 *	0.119	-.349 *
D. PULICARIA	0.411 *	-.265 *	-.121	0.183
EPISCHURA	0.156	-.587 *	0.539 *	-.364 *
EUBOSMINA	0.500 *	0.287 *	0.013	0.016
LEPTODORA	0.332 *	0.254 *	0.550 *	-.170
LIMNOCALANUS	0.375 *	0.149	-.673 *	-.057
DIAPHANOSOMA	0.065	0.540 *	0.092	0.179
CHYDORUS SP.	-.164	0.595 *	0.102	0.393 *
C. SPHAERICUS	-.299 *	0.437 *	0.232 *	0.364 *
EURYTEMORA	-.089	-.072	0.237	0.078

* Coefficient is significant (α = .05) either positively (> .230) or negatively (< -.230) with the principle components.

Table 7. Regression and ANOVA of principle components 1 and 2 using transformed areal abundance data.

Principal Component 1

Regression

N: 76 Multiple R: 0.830 Multiple R^2: 0.689 Adj. Multiple R^2: 0.676
Standard error of estimate: 2.628 Dependent Variable: Factor(1)

Variable	Coefficient	Std. error	Std. coef.	T	P (2 tail)	
CONSTANT	11.586	2.628	0.000	4.410	0.000	
DEPTH	0.284	0.030	0.618	9.372	0.000	**
MONTH	-2.044	0.275	-0.507	-7.433	0.000	**
SITE	0.059	0.313	0.013	0.190	0.850	

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-ratio	P	
REGRESSION	1101.928	3	367.309	53.184	0.000	**
RESIDUAL	497.257	72	6.906			

Principal Component 2

Regression

N: 76 Multiple R: 0.516 Multiple R^2: 0.267 Adj. Multiple R^2: 0.236
Standard error of estimate: 3.285 Dependent Variable: Factor(2)

Variable	Coefficient	Std. error	Std. coef.	T	P (2 tail)	
CONSTANT	-13.445	3.285	0.000	-4.092	0.000	
DEPTH	0.151	0.038	0.404	3.989	0.000	**
MONTH	1.189	0.344	0.363	3.458	0.001	**
SITE	0.287	0.392	0.077	0.732	0.466	

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-ratio	P	
REGRESSION	282.588	3	94.196	8.727	0.000	**
RESIDUAL	777.181	72	10.794			

** - significant at alpha = .05

Table 8. Regression and ANOVA of principle components 3 and 4 using transformed areal abundance data.

Principle Component 3

Regression

N: 76 Multiple R: 0.387 Multiple R^2: 0.150 Adj. Multiple R^2: 0.114
Standard error of estimate: 3.046 Dependent Variable: Factor(3)

Variable	Coefficient	Std. error	Std. coef.	T	P (2 tail)
CONSTANT	7.836	3.046	0.000	2.573	0.012
DEPTH	-0.005	0.035	-0.015	-0.134	0.894
MONTH	-0.675	0.319	-0.239	-2.118	0.038
SITE	-1.204	0.363	-0.373	-3.315	0.001 **

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-ratio	P
REGRESSION	117.621	3	39.207	4.226	0.008 **
RESIDUAL	668.045	72	9.278		

Principle Component 4

Regression

N: 76 Multiple R: 0.170 Multiple R^2: 0.029 Adj. Multiple R^2: 0.000
Standard error of estimate: 2.886 Dependent Variable: Factor(4)

Variable	Coefficient	Std. error	Std. coef.	T	P (2 tail)
CONSTANT	4.174	2.886	0.000	1.446	0.152
DEPTH	-0.018	0.033	-0.062	-0.529	0.599
MONTH	-0.407	0.302	-0.162	-1.346	0.183
SITE	-0.239	0.344	-0.084	-0.694	0.490

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-ratio	P
REGRESSION	17.862	3	5.954	0.715	0.546
RESIDUAL	599.784	72	8.330		

** - significant at alpha = .05

except PC 4 had a better fit than PC 2 and PC 3 (Table 9 and Table 10).

Month, depth and site were regressed on the transformed areal abundance principle components (1-4)(Table 7 and Table 8). Month and depth were found significant ($p<.05$) for PC's 1 and 2 (Table 7). Site was found significant for only PC 3 of the areal data (Table 8). Sites 1, 2, and 3 are Ludington, Manitou Passage, and West Grand Traverse Bay, respectively. Site 4 was Holland, and this site was the only location sampled only once in 1991. Site 4 had a much reduced abundance compared to the other three sites. Because Holland was the only site with a significantly different abundance, and because of the lack of samples from Holland, the site variable was dropped from the verifications and species partitioning sections reported later in the text.

The multiple regressions of the cubic abundance data were significant for PCs 1, 2, and 4 ($p<.05$) for both depth and month, and site was not significant for any of the principle components (Table 9 and Table 10).

Zooplankton Community Trends - Areal

Transformed abundances (ln[# + 1]), of both areal and cubic abundances of the significant variables in the multiple regression models were plotted both temporally (month) and spatially (at different depth contours) to examine trends of significantly correlated species within the zooplankton community.

It is expected, that the zooplankton community would decline in abundance with season (after peaking earlier in the season), or had a negative slope with the month variable. For PC 1 this is true (Figure 3a), but unexpectedly the slope reverses to a positive slope for PC 2 (Figure 3b).

Table 9. Regression and ANOVA of principle components 1 and 2 using transformed cubic abundance data.

Principle Component 1

Regression

N: 76 Multiple R: 0.751 Multiple R^2: 0.563 Adj. Multiple R^2: 0.545
Standard error of estimate: 2.057 Dependent Variable: Factor(1)

Variable	Coefficient	Std. error	Std. coef.	T	P (2 tail)
CONSTANT	8.124	2.057	0.000	3.950	0.000
DEPTH	0.152	0.024	0.502	-6.260	0.000 **
MONTH	-1.347	0.215	-0.506	6.433	0.000 **
SITE	0.149	0.245	0.049	0.607	0.546

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-ratio	P
REGRESSION	392.880	3	130.960	30.965	0.000 **
RESIDUAL	304.506	72	4.229		

Principle Component 2

Regression

N: 76 Multiple R: 0.456 Multiple R^2: 0.208 Adj. Multiple R^2: 0.175
Standard error of estimate: 2.213 Dependent Variable: Factor(2)

Variable	Coefficient	Std. error	Std. coef.	T	P (2 tail)
CONSTANT	8.995	2.213	0.000	4.065	0.000
DEPTH	-0.065	0.025	-0.266	-3.677	0.013 **
MONTH	-0.852	0.232	-0.401	-2.533	0.000 **
SITE	-0.331	0.264	-0.136	-1.255	0.214

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-ratio	P
REGRESSION	92.780	3	30.927	6.316	0.001 **
RESIDUAL	352.527	72	4.896		

** - significant at alpha = .05

Table 10. Regression and ANOVA of principle components 3 and 4 using transformed cubic abundance data.

Principle Component 3

Regression

N: 76 Multiple R: 0.319 Multiple R^2: 0.102 Adj. Multiple R^2: 0.064
Standard error of estimate: 2.076 Dependent Variable: Factor(3)

Variable	Coefficient	Std. error	Std. coef.	T	P (2 tail)
CONSTANT	-2.684	2.076	0.000	-1.293	0.200
DEPTH	-0.038	0.024	-0.177	1.353	0.119
MONTH	0.294	0.217	0.157	-1.580	0.180
SITE	0.552	0.248	0.258	2.230	0.029

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-ratio	P
REGRESSION	35.217	3	11.739	2.724	0.051
RESIDUAL	310.335	72	4.310		

Principle Component 4

Regression

N: 76 Multiple R: 0.464 Multiple R^2: 0.216 Adj. Multiple R^2: 0.183
Standard error of estimate: 1.633 Dependent Variable: Factor(4)

Variable	Coefficient	Std. error	Std. coef.	T	P (2 tail)
CONSTANT	6.092	1.633	0.000	3.730	0.000
DEPTH	-0.060	0.019	-0.333	-2.941	0.002 **
MONTH	-0.503	0.171	-0.319	-3.180	0.004 **
SITE	-0.406	0.195	-0.225	-2.084	0.041

Analysis of Variance

Source	Sum-of-Squares	DF	Mean-Square	F-ratio	P
REGRESSION	52.764	3	17.588	6.596	0.001 **
RESIDUAL	191.994	72	2.667		

** - significant at alpha = .05

For the depth variable, it would intuitively be expected that the slope would be positive if the zooplankton community inhabits all the volume of water at both the 10 and 30 meter contours. The community does have a positive slope for PC 1 (Figure 4a) and PC 2 (Figure 4b) for the areal abundance data.

The site variable was significant only with PC 3 ($p<.05$)(Table 8)(Figure 5).

It is hypothesized that species positively correlated with PC 1 will either tend to decrease markedly with season or be more abundant at the 30 meter depth. Because of the reversal of the seasonal trends between the first and second PC, it is hypothesized that species that are positively correlated with PC 2 will either not be greatly affected by season (because of the reversal of the month trend of PC 2) or more abundant at the 30 meter contour.

Zooplankton Community Trends - Cubic

The expectation that the zooplankton community would decline in abundance with season is also true for the cubic abundance data. Principle components 1, 2, and 4 were all significant and they all had negative slopes as well (Figure 6).

The reporting of the zooplankton community measured as a cubic or volumetric abundance, would not necessarily show an increased abundance at the deeper contour as was expected with the areal abundance data unless the abundances were actually greater at the 30 meter contour. Principle component 1 has a positive slope (Figure 7a), and PCs 2 and 4 have a negative slope (Figure 7b and Figure 7c).

It is hypothesized that species positively correlated with PC 1 of the cubic abundance data will respond in the same way to both depth and

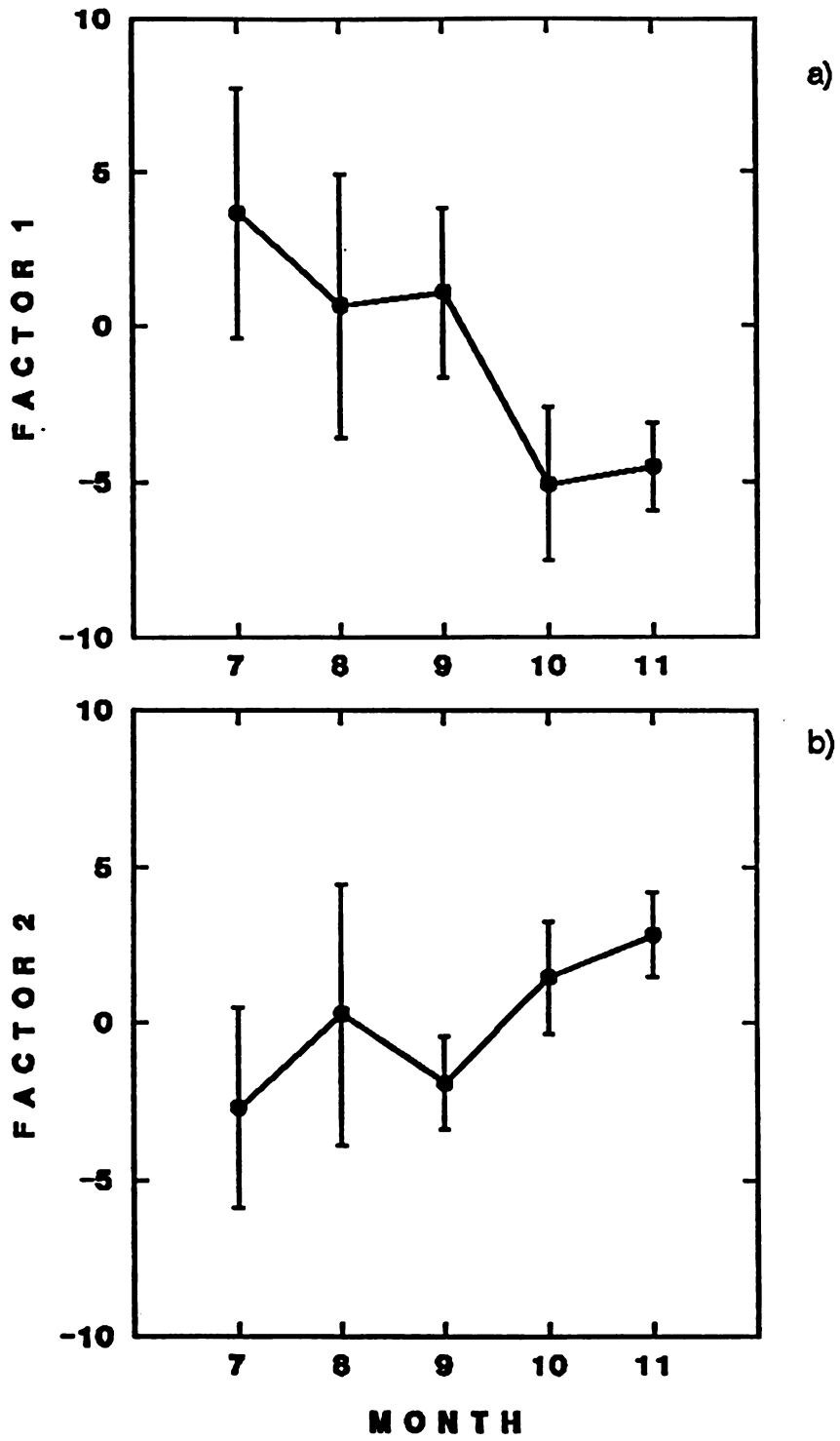


Figure 3. Category plots by month of principle components 1 (a) and 2 (b) using areal abundance estimates.

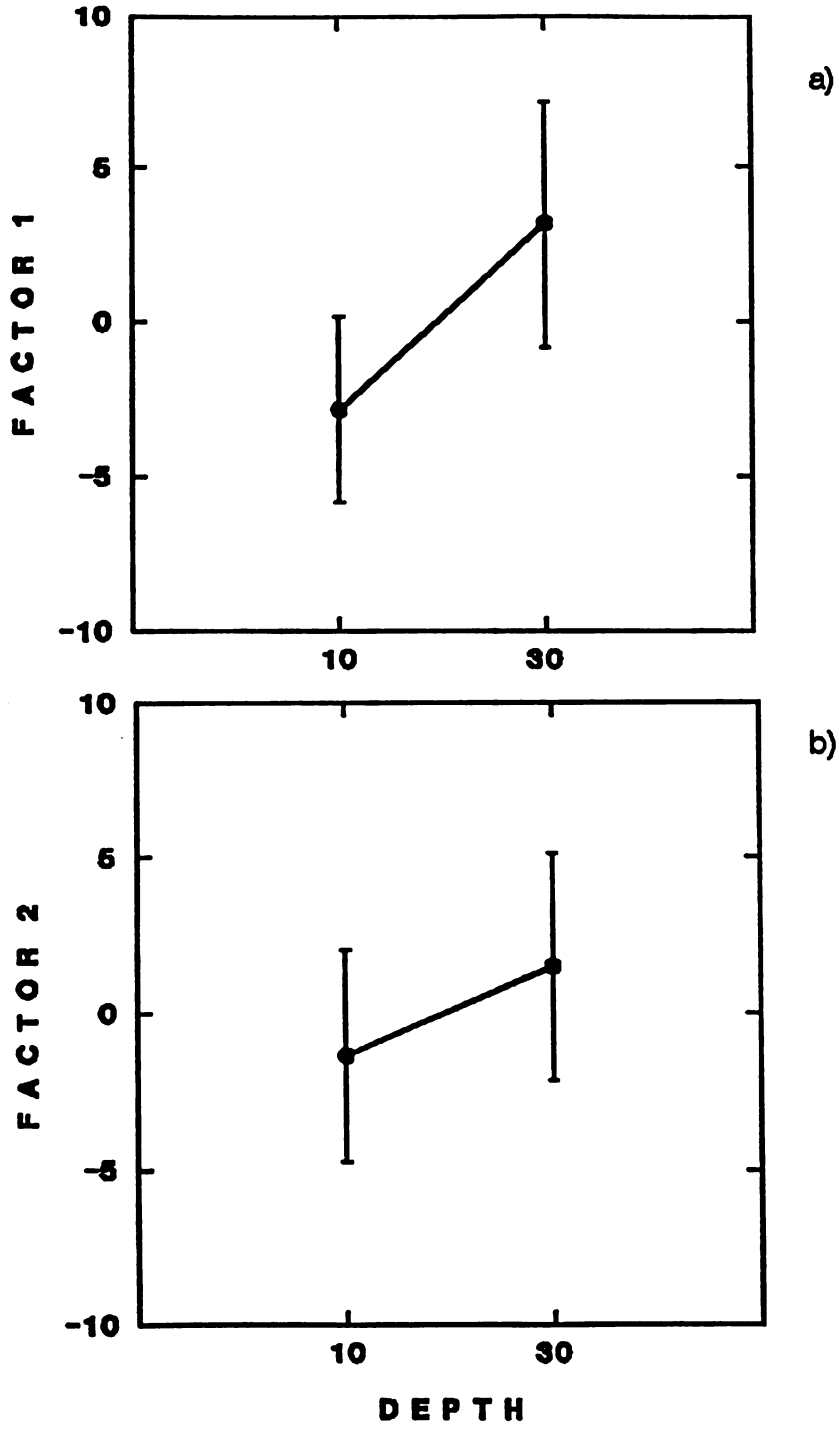


Figure 4. Category plots by depth of principle components 1 (a) and 2 (b) using areal abundance estimates.

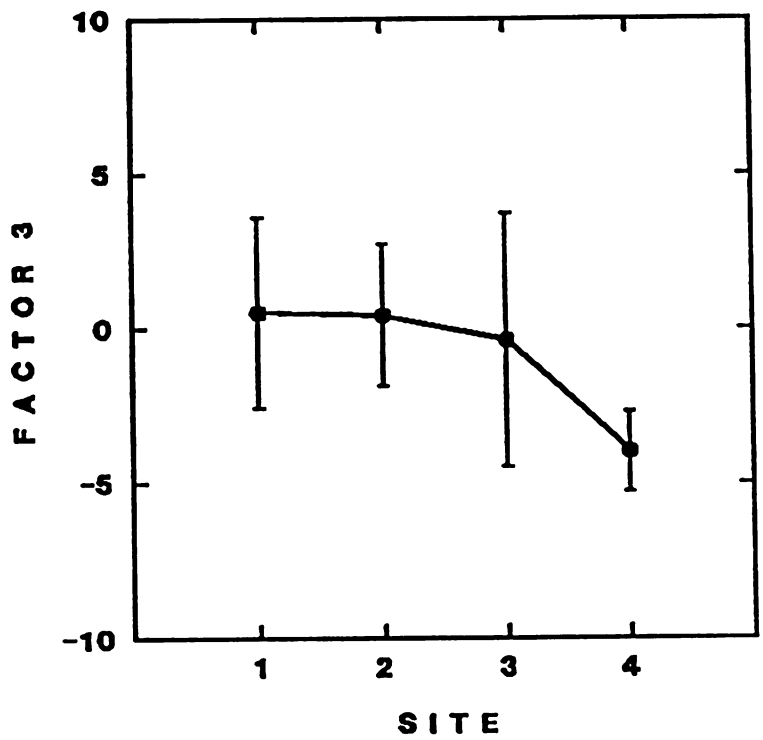


Figure 5. Category plot by site of principle component 3 using areal abundance estimates.

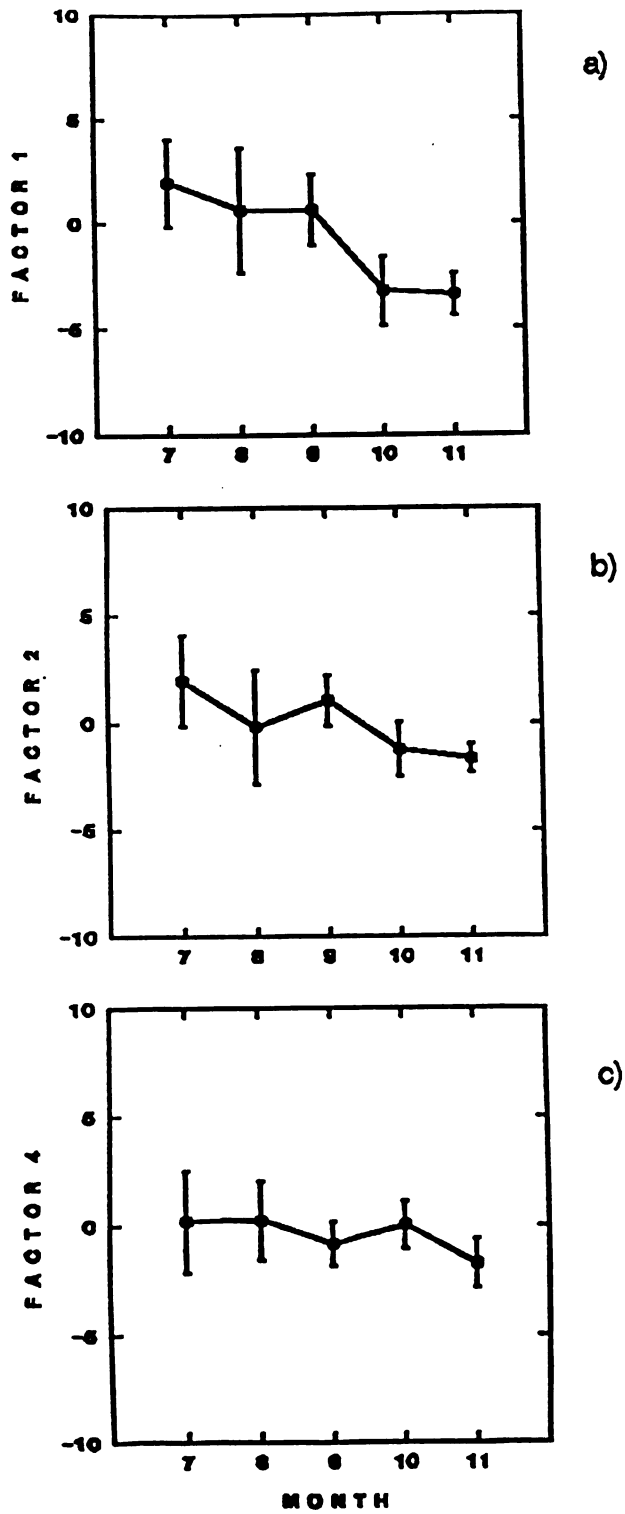


Figure 6. Category plots by month of principle components 1 (a), 2 (b), and 4 (c) using cubic abundance estimates.

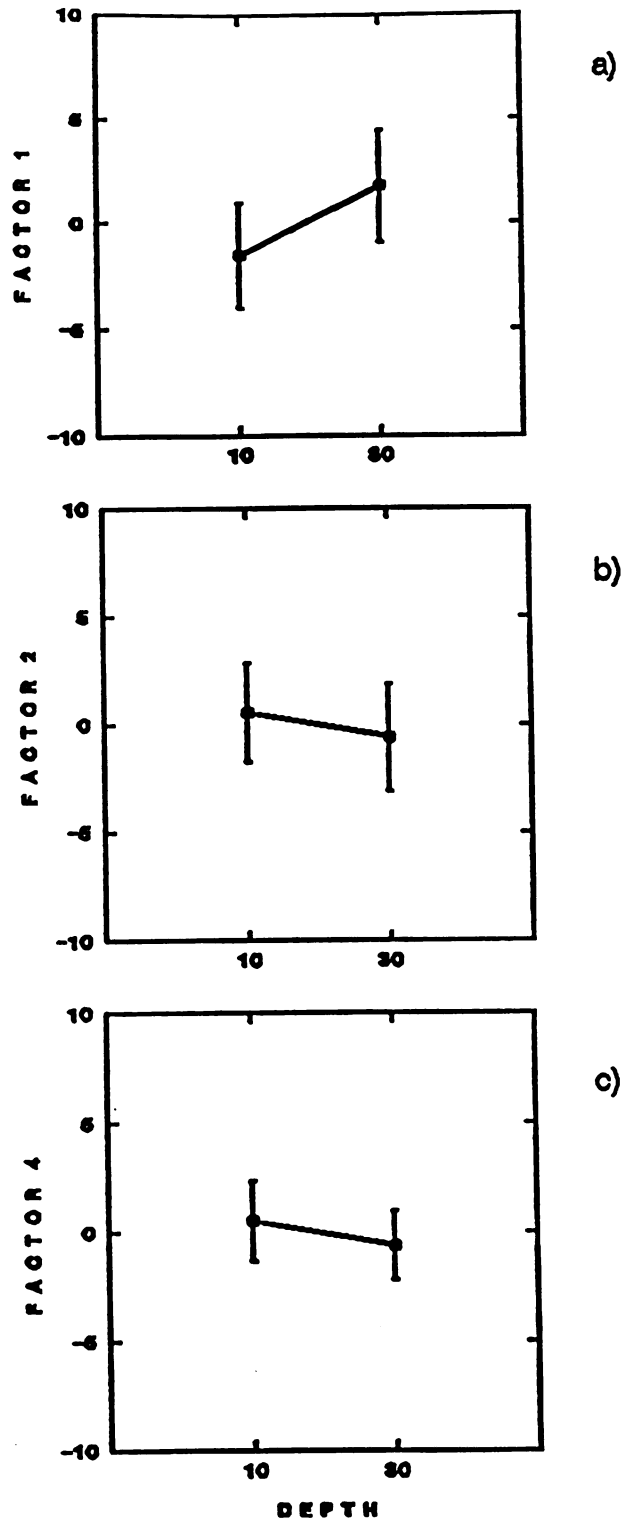


Figure 7. Category plots by depth of principle components 1 (a), 2 (b), and 4 (c) using cubic abundance estimates.

month as with the areal abundance data. In other words, a species positively correlated with PC 1 would be expected to either decline markedly with season or be more abundant at the 30 meter depth.

However, the differences between PC 2 of the cubic PCA are opposites of the seasonal and depth trends of PC 2 of the areal PCA. The month variable of the cubic abundance PCA does not reverse slope from PC 1 to PC 2, as was the case with the areal abundance PCA. And the other variable, depth, unlike the areal PCA, reverses from a negative to a positive slope.

The result is that a species negatively correlated with PC 2 of the cubic PCA ordination would be hypothesized to respond in a like manner (to both the month and depth variables), as a species positively correlated with PC 2 of the areal PCA ordination.

Zooplankton Community Biplots

Each principle component, is a linear compound of the transformed abundances, and has an associated eigenvector of each component coefficient giving the weighting of each species in the linear compound (Sprules 1977). The biplot uses the first two eigenvectors as (x,y) coordinates of the original variables. These coefficients are unitless and the first two principle components of the zooplankton community are plotted on the areal (Figure 8) and cubic (Figure 9) biplots.

Distance and direction of the specie component coefficient has meaning, and species plotting close to the origin would not be expected to have their abundances influenced by the significant variables depth or month, and species abundances plotting far from the origin would be expected to be influenced by these variables.

The biplots use the component coefficients of the principle

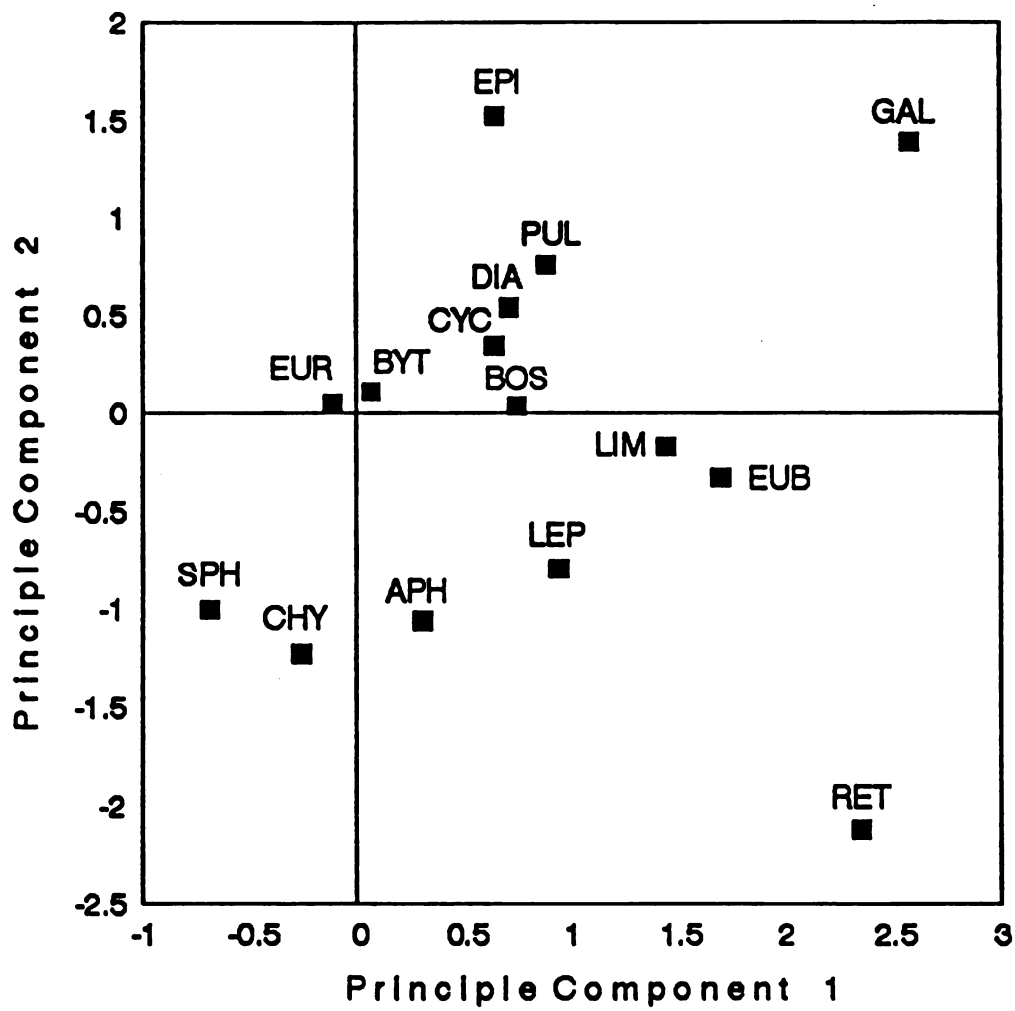


Figure 8. Biplot of first two principle components using areal zooplankton abundance data from Northeastern Lake Michigan in 1991 (axes are unitless).

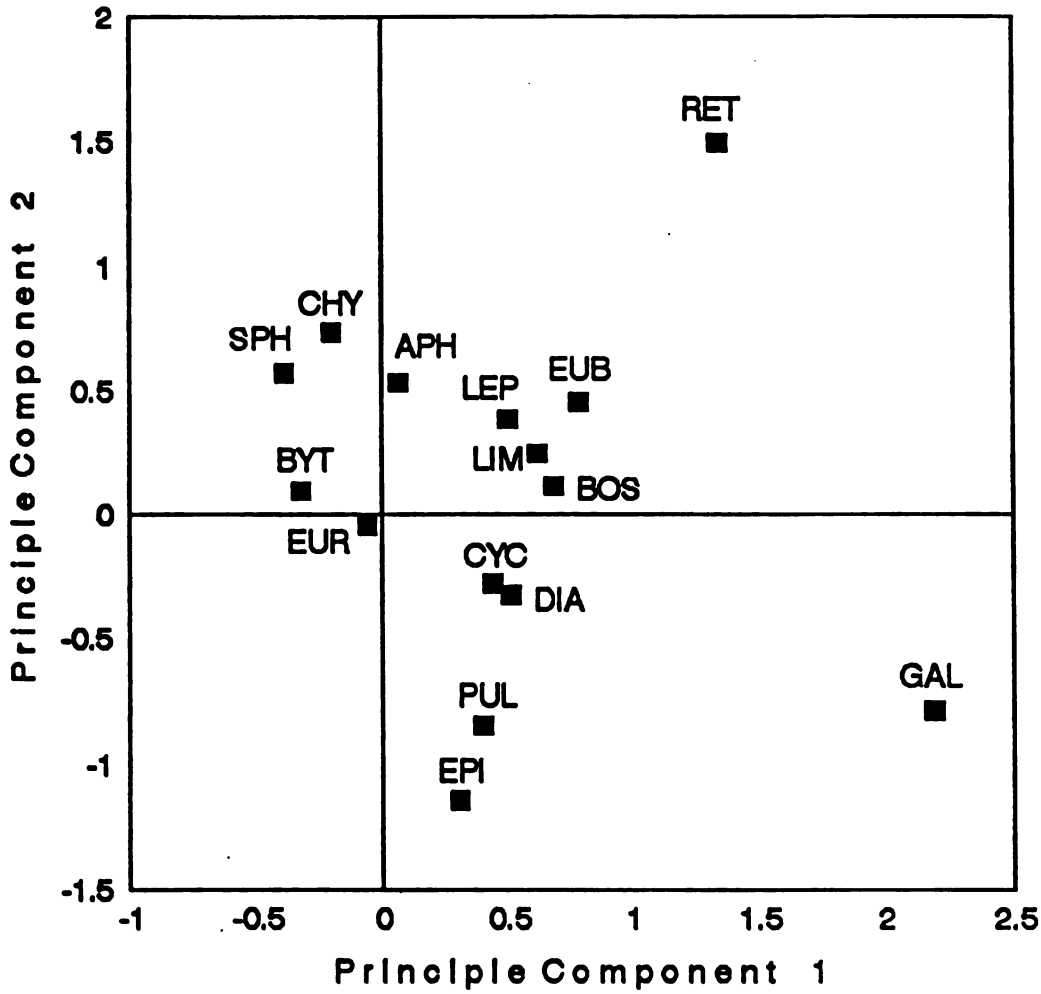


Figure 9. Biplot of first two principle components using cubic zooplankton abundance data from Northeastern Lake Michigan in 1991 (axes are unitless).

components, and the species were assigned correlation coefficients of these components. They both respond in similar intensities either positively or negatively. Because of this, the use of a biplot will visually aid in the verification process and later, in the splitting of the zooplankton community into species associations.

Verification of Zooplankton Environmental Trends

The variables, month and depth, may or may not represent meaningful ecological relationships, and the synthetic principle component variables must now be closely scrutinized. This scrutiny requires that the community trends of the principle components accurately portray the trends of positively correlated species, and that an inverse of the trends is portrayed by the negatively correlated species of the areal abundance data (Table 5), and the cubic abundance data (Table 6).

The regression of the variables depth and month were both significant when regressed on PC 1 with the areal abundance data (Table 7). The hypothetical trends month (Figure 3a) and depth (Figure 4a) of these variables on the zooplankton community with respect to PC 1 is illustrated in Figure 10. These same variables were also significant when regressed on PC 2 and the hypothetical trends of month (Figure 3b) and depth (Figure 4b) are illustrated in Figure 11.

Species significantly correlated with a principle component either positively or negatively would be expected to be influenced (by relative abundance) by one or both of the variables found significant in the regressions. Species that were not correlated with both principle components may or may not be influenced, and for this reason the uncorrelated species of both PC 1 and PC 2 will not be used in the verification process or the delineation of species into species

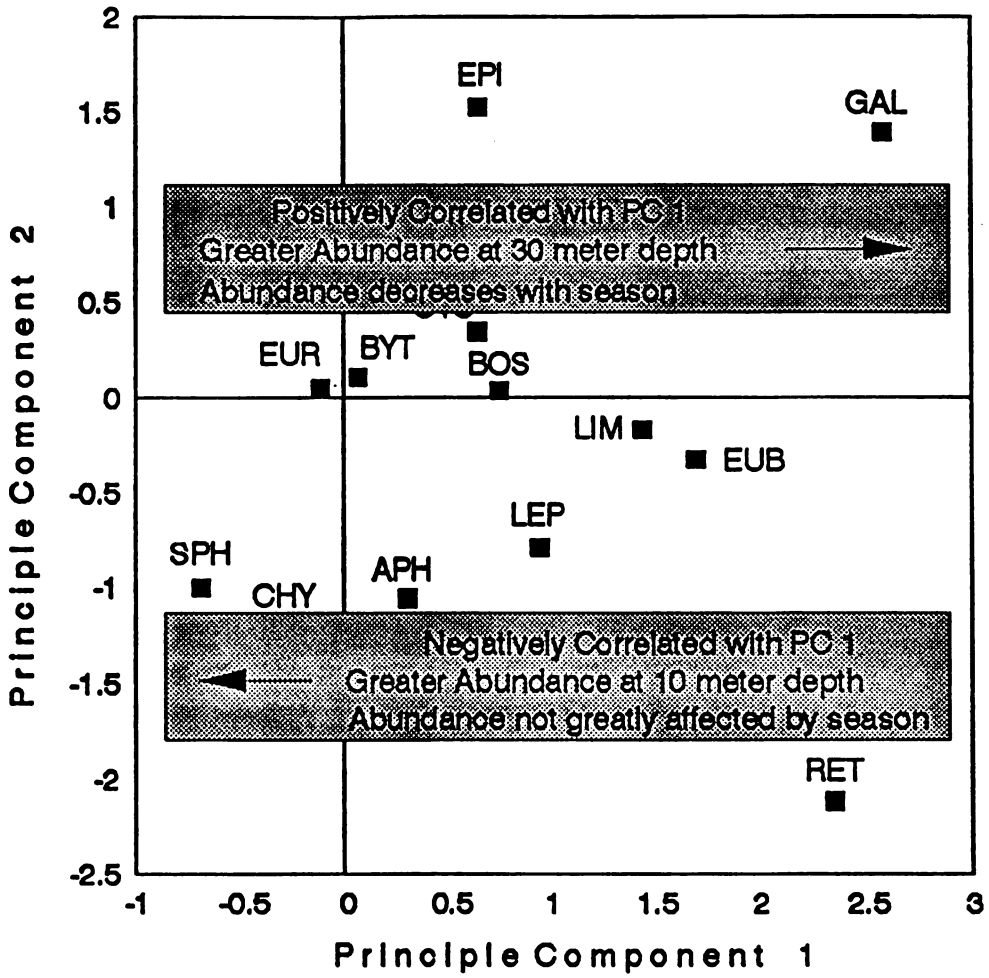


Figure 10. Illustration of the significantly correlated variables, depth and month, of principle component 1, expected to influence a species position on both the areal and cubic abundance biplots.

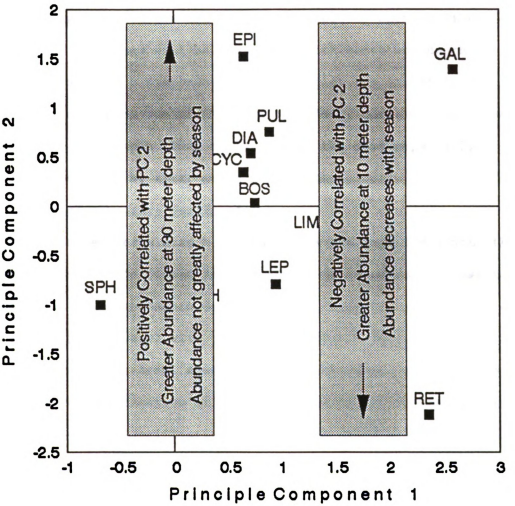


Figure 11. Illustration of the significantly correlated variables, depth and month, of principle component 2, expected to influence a species position on the areal abundance biplot.

associations. Figure 12 illustrates only those species that were significantly correlated with both PC 1 and PC 2 (Table 5).

Following are the areal, then the cubic abundance verifications. Because it is unknown which variable, either month and depth (or both), is affecting the relative abundance of a species, each species transformed abundance will be plotted by both month and depth. Verification of each component will first plot the transformed abundances of one or two of the most positively correlated species by first month then depth. Then one or two of the most negatively correlated species by first month than depth.

Areal Abundance Verification

Most species correlated both positively and negatively with the areal abundance data (Table 5) were also correlated in the same manner as with the cubic abundance data (Table 6). Only *B. cederstroemi* was correlated (negatively) with the cubic abundance data, and not correlated with the areal abundance data. Therefore, except for *B. cederstroemi*, verification of PC 1 for the areal abundance data will also represent the verification of the cubic abundance data as well.

The first two plots are the log transformed abundances of the two species with the highest positive correlation with PC 1, *D. galeata* and *D. retrocurva* (Table 5). It is hypothesized that these species would either decrease in abundance with season, or be in greater abundance at the 30 meter contour (Figure 10). A plot of these two species by month (Figure 13) shows that only *D. retrocurva* is much affected by season. *D. retrocurva* was no longer found in the community after September, while *D. galeata* was present in abundances similar to samples taken in July, and was present until November. The graph of these two species plotted

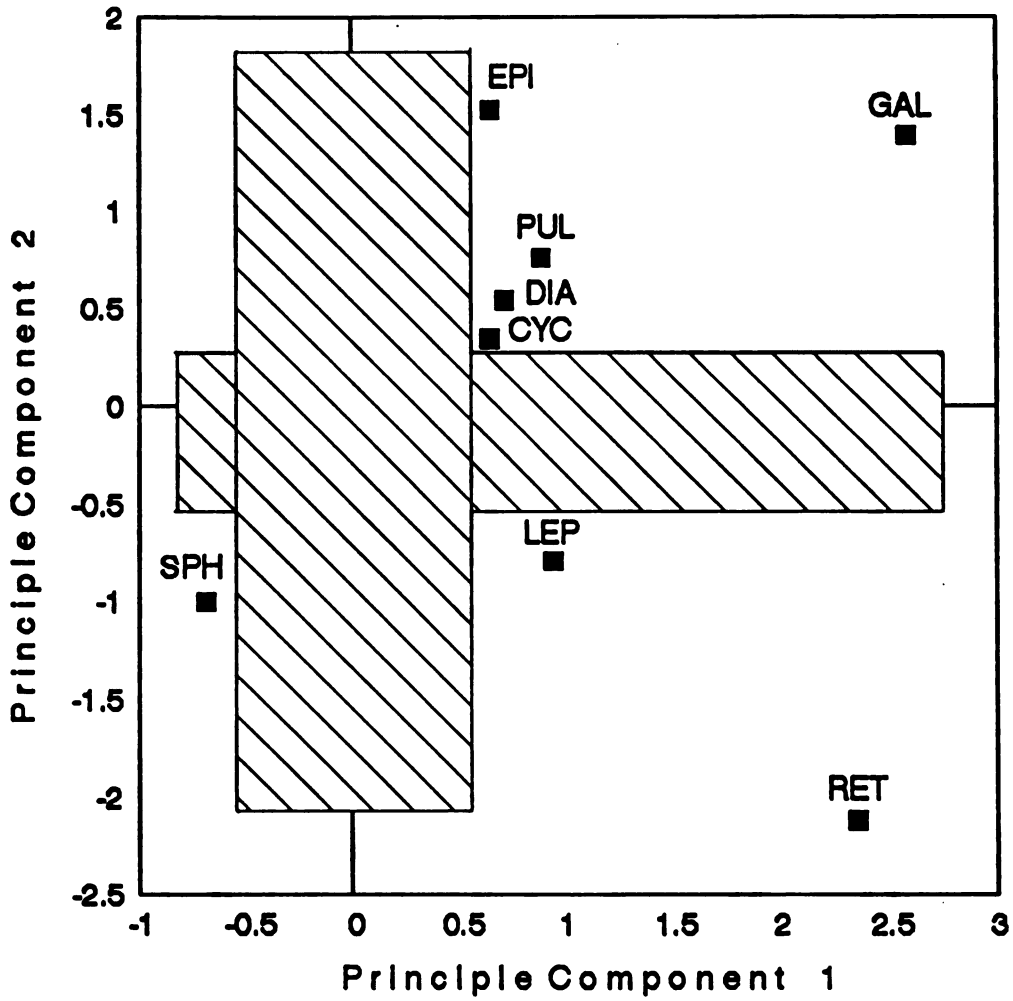


Figure 12. Biplot illustrating species that are significantly correlated with principle components 1 and 2 using the areal abundance data.

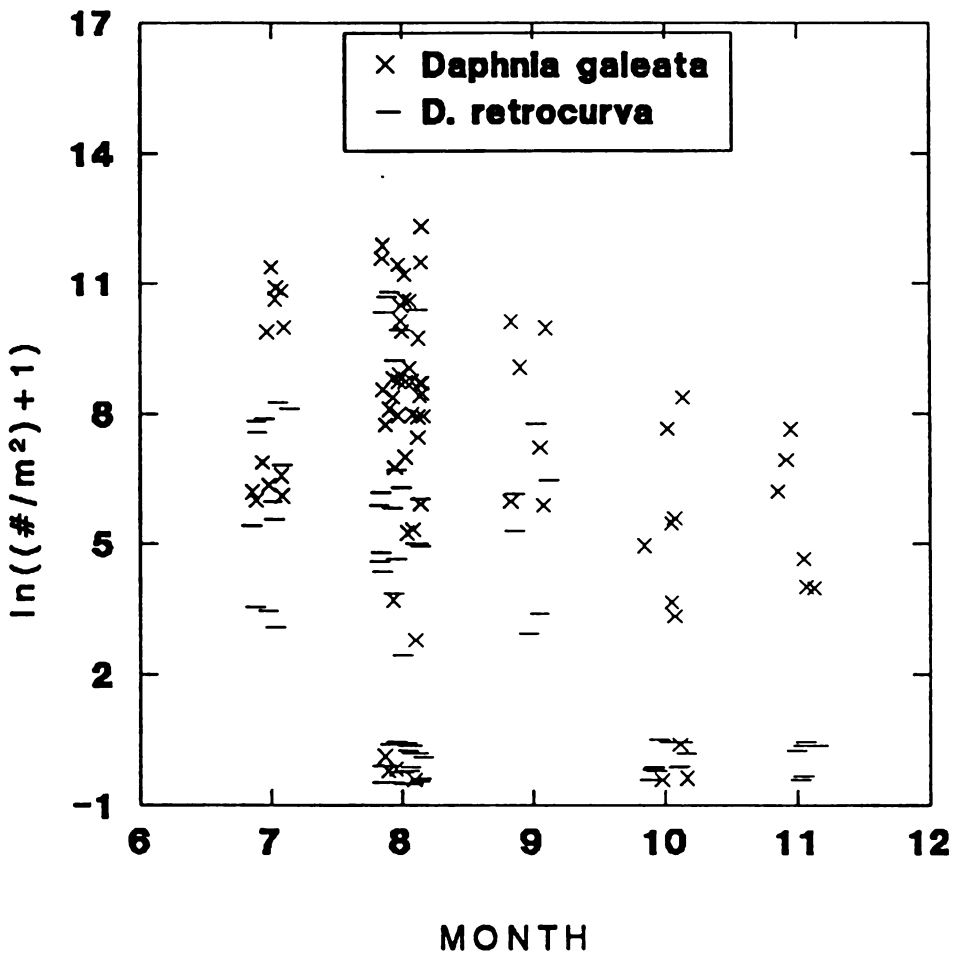


Figure 13. Log transformed (ln) areal abundances of Daphnia galeata and D. retroourva for the months of July through November in 1991.

by depth (Figure 14) shows both species appear to have greater abundances at the 30 meter contour. Many samples for both species had absences, however, *D. galeata* was absent only at the 10 meter contour which may indicate the species is more affected by depth than by season.

The only species with a significant negative correlation to PC 1 was *C. sphaericus*. It is hypothesized that this specie's abundance would either not differ much throughout the season or has a greater abundance at the 10 meter contour (Figure 10). When this species was plotted against month (Figure 15), the species does not appear to follow the seasonal trend of PC 1. However, abundances were highest in August and October and absent in September. It appears that this species is indeed not greatly affected by season. A plot of this species by depth (Figure 16) clearly shows that *C. sphaericus* corresponds very well with the second part of the hypothesis, that it is more abundant at the 10 meter contour. The species was totally absent at the 30 meter depth.

The next two plots are the log transformed abundances of the two species with the highest positive correlation with PC 2, *D. galeata* and *E. lacustris*. It is hypothesized that these species would either decline markedly with season or have greater abundance at the 30 meter depth (Figure 11). The first plot, is the graph of the two species by month (Figure 17). Neither species shows decline in the later months and both are present in all samples in November. The next plot of the two species is by depth (Figure 18), and it appears that both species are present at greater abundances at the 30 meter contour.

The next two plots are of the two species most negatively correlated with PC 2, *D. retrocurva* and *C. sphaericus*. It is hypothesized that these two species would declined markedly with season

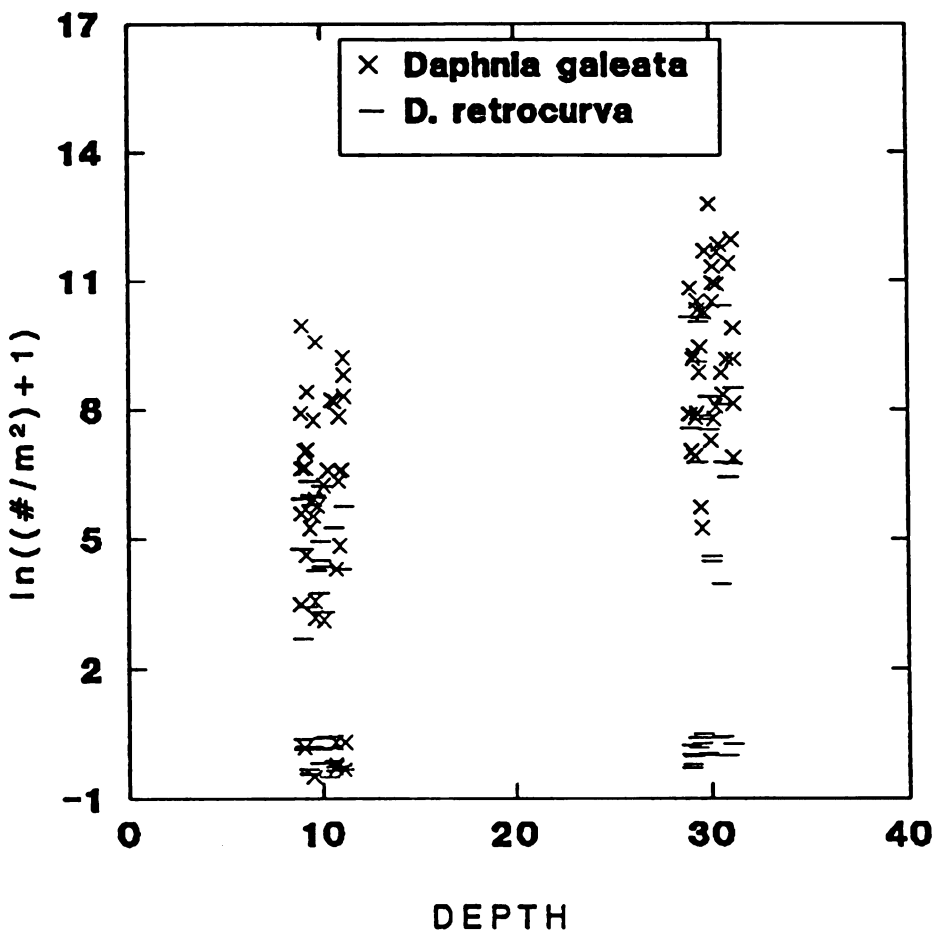


Figure 14. Log transformed (ln) areal abundances of Daphnia galeata and D. retrocurva at two depths, 10 and 30 meters.

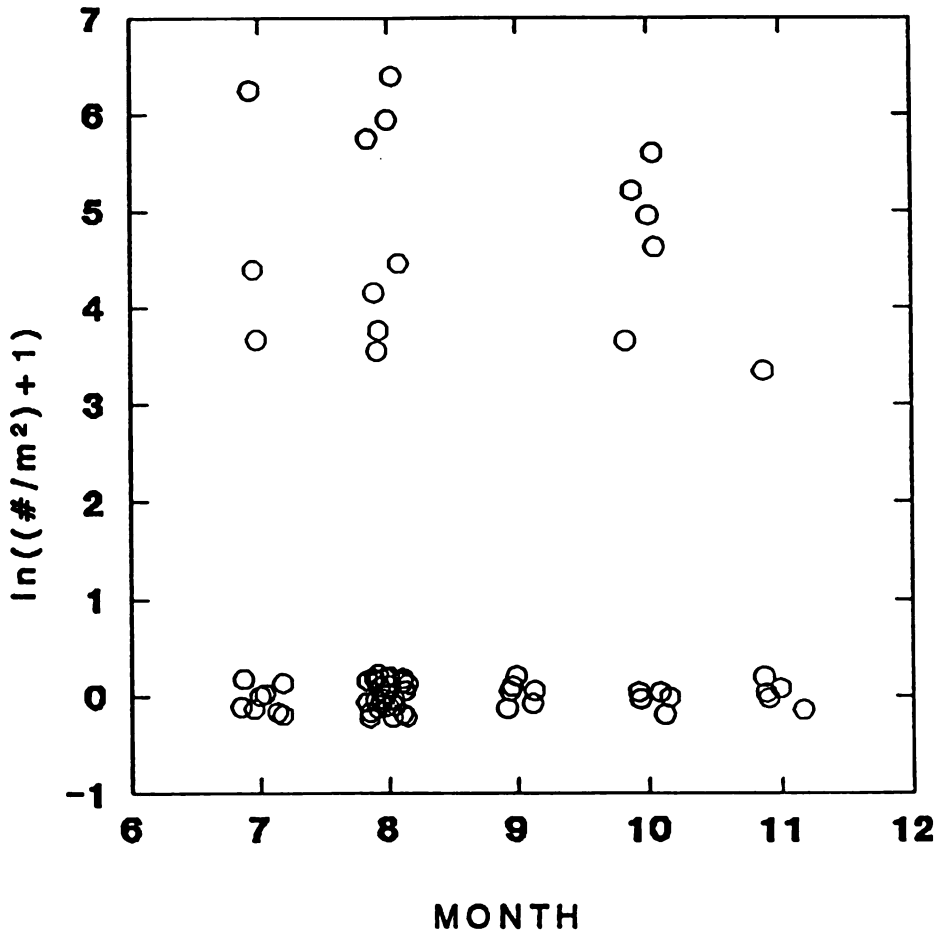


Figure 15. Log transformed (ln) areal abundances of Chydorus sphaericus for the months of July through November in 1991.

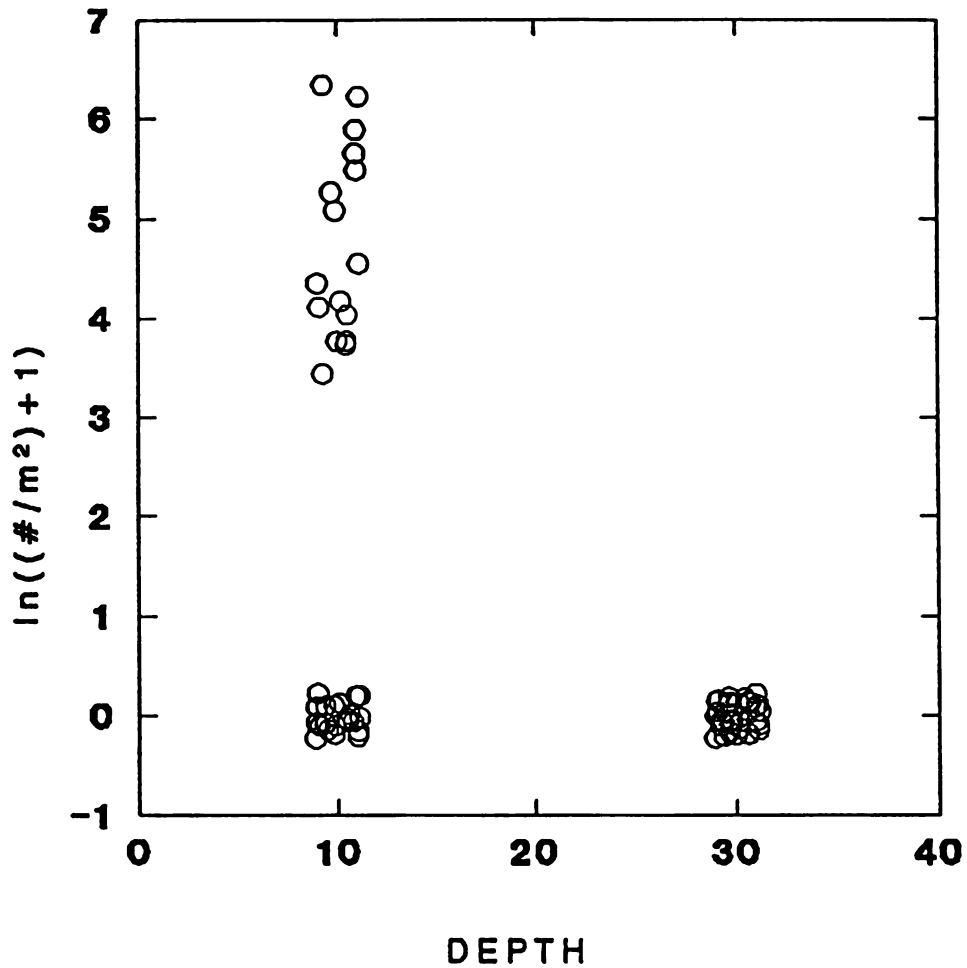


Figure 16. Log transformed (ln) areal abundances of Chydorus sphaericus at two depths, 10 and 30 meters.

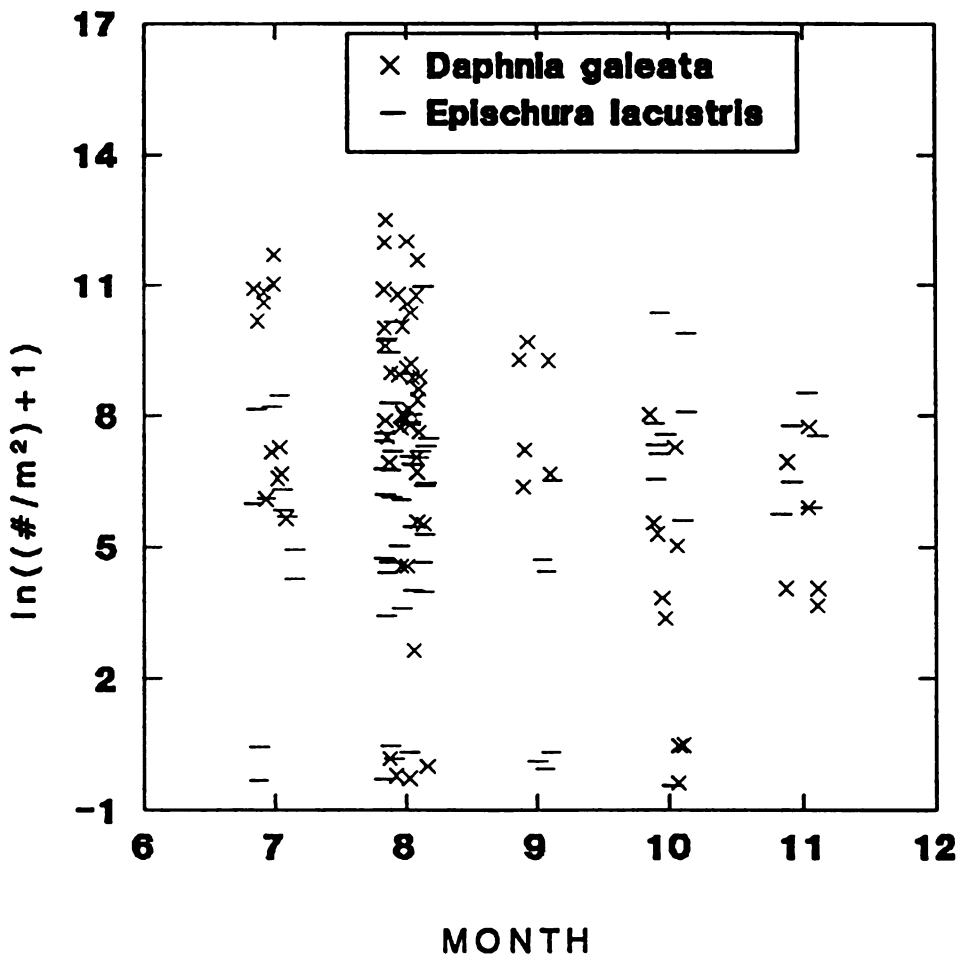


Figure 17. Log transformed (ln) areal abundances of Daphnia galeata and Epischura lacustris for the months of July through November in 1991.

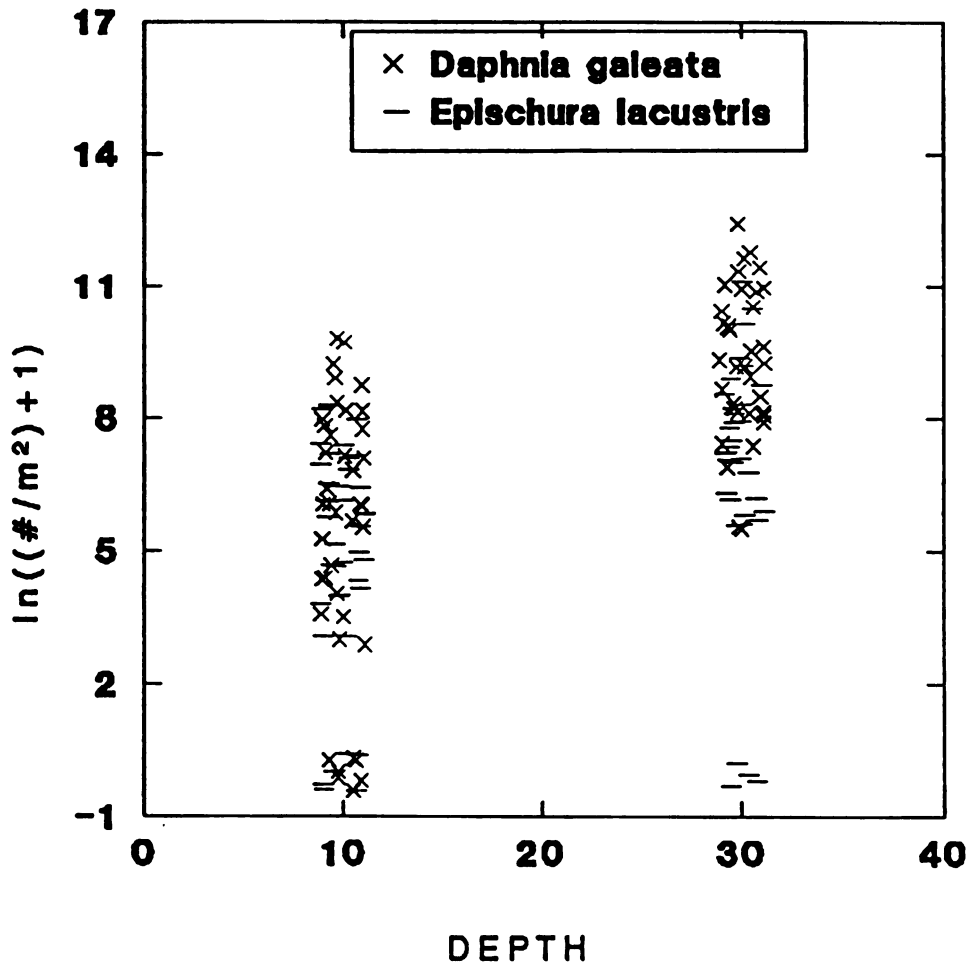


Figure 18. Log transformed (ln) areal abundances of Daphnia galeata and Epischura lacustris at two depths, 10 and 30 meters.

or have a greater abundance at the 10 meter depth (Figure 11). The plot of the two species by month (Figure 19) shows that only *D. retrocurva* decreases with season and is absent in the samples after September. The plot of the two species by depth (Figure 20) shows that only *C. sphaericus* is more abundant at the 10 meter contour.

Cubic Abundance Verification

As was mentioned above, the only species whose correlation coefficient was found significant in the cubic and not in the areal abundance, was *B. cederstroemi*. This species was negatively correlated with PC 1 of the cubic abundance data (Table 6). It is hypothesized that this species either does not decline markedly with season or it is more abundant at the 10 meter contour (Figure 10). When *B. cederstroemi* was plotted by month (Figure 21) the species showed no decline with season, instead the species was absent in the September samples then in October and November rebounded to areal abundance levels similar to July and August. When *B. cederstroemi* was plotted by depth (Figure 22), it showed no greater abundance at either the 10 or the 30 meter contour.

Hypotheses of the species responses to principle component 2 of the cubic abundance data (Figure 23) are reversals of the PC 2 areal abundance hypotheses (Figure 11). In other words, most species in the upper two quadrants on the areal biplot (Figure 8) will be in the bottom two quadrants of the cubic biplot (Figure 9) and vice versa. However, positively and negatively correlated species from PC 2 of the cubic PCA (Table 6) also reverse direction (positive to negative and vice versa) from the areal (Table 5). This results in both biplots grouping many of the same species into groups with hypothetically similar responses to both month and depth, or species associations. Therefore the following

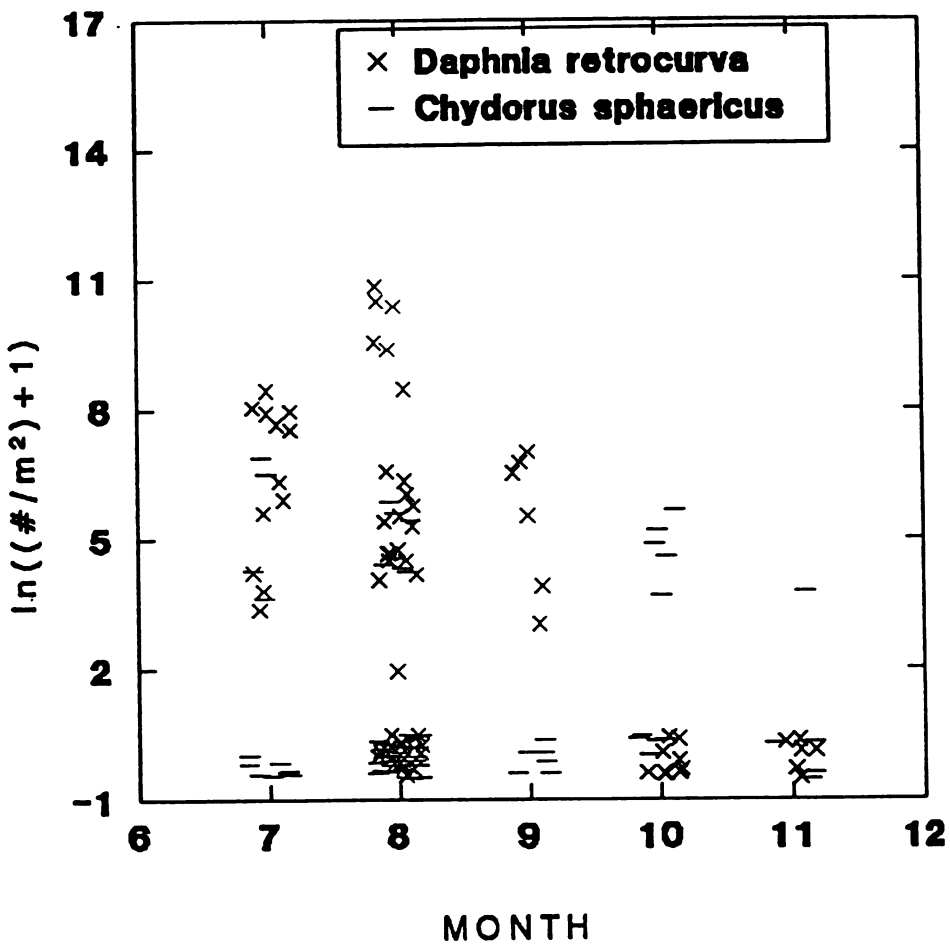


Figure 19. Log transformed (ln) areal abundances of Daphnia retrocurva and Chydorus sphaericus for the months of July through November of 1991.

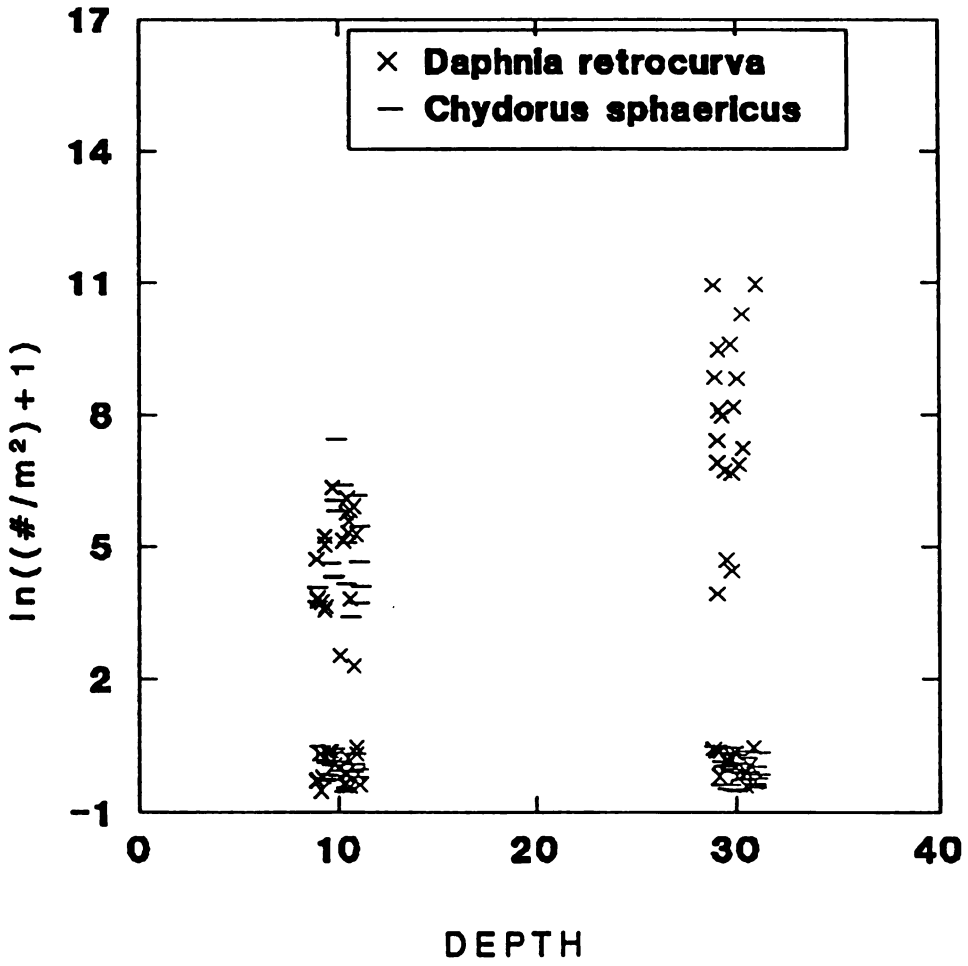


Figure 20. Log transformed (ln) areal abundances of Daphnia retrocurva and Chydorus sphaericus at two depths, 10 and 30 meters.

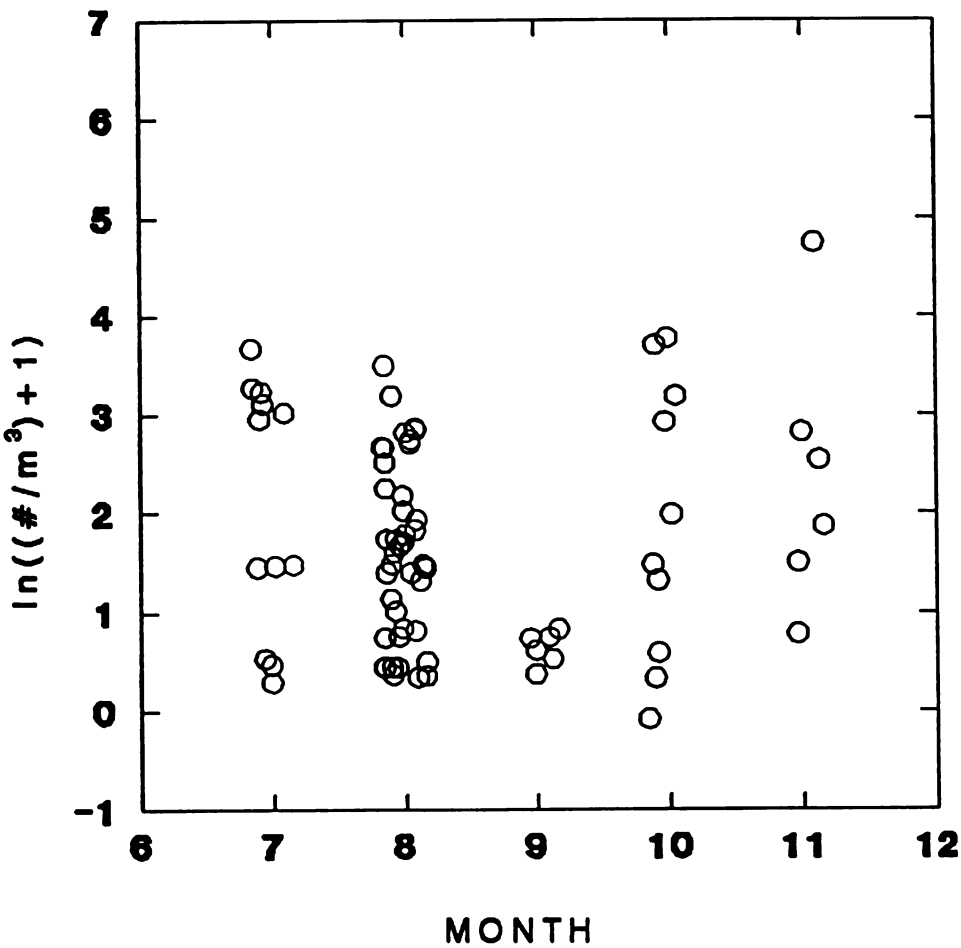


Figure 21. Log transformed (ln) cubic abundances of Bythotrephes cederstroemi for the months of July through November in 1991.

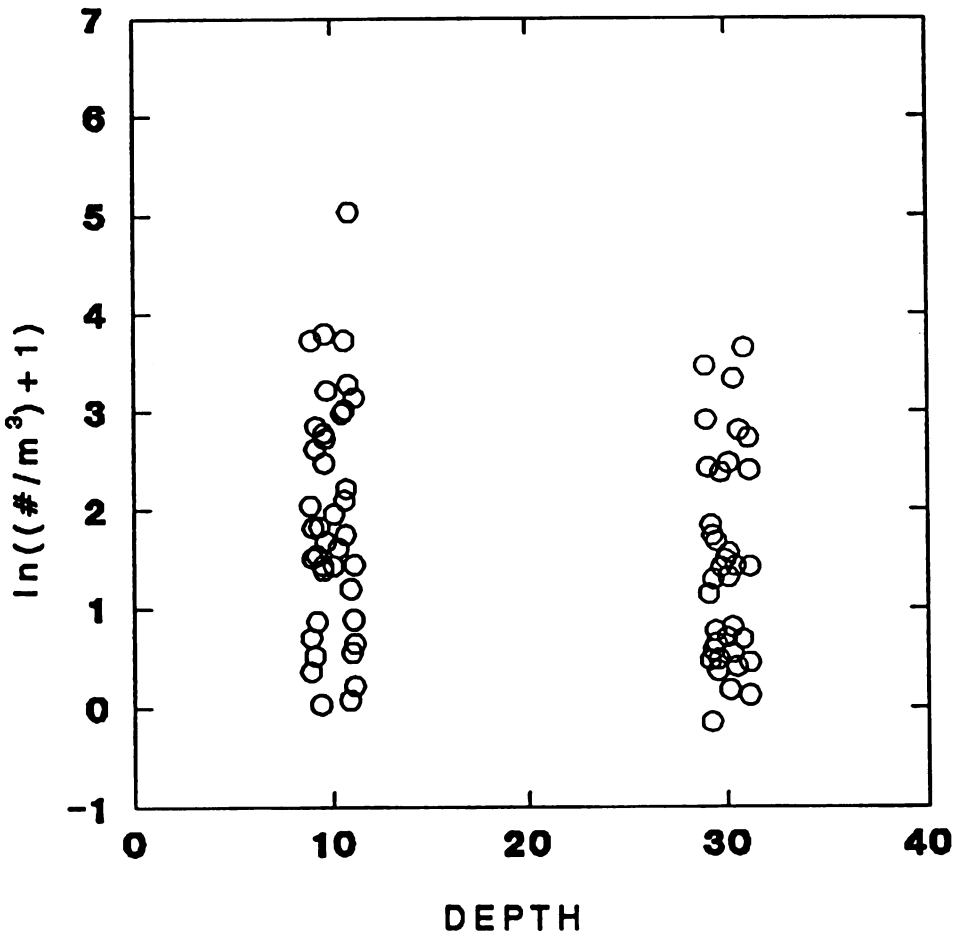


Figure 22. Log transformed (ln) cubic abundances of Bythotrephes cederstroemi at two depths, 10 and 30 meters.

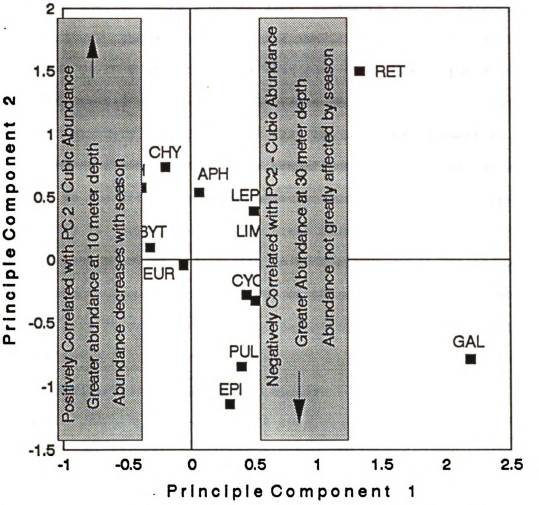


Figure 23. Illustration of the significantly correlated variables, depth and month, of principle component 2, expected to influence a species position on the cubic abundance biplot.

verifications of the cubic abundance environmental trends need only be compared to the areal abundance verifications to ensure that the significantly correlated species respond in a like manner.

The next two plots (month and depth) are of the most positively correlated species to PC 2 of the cubic abundance PCA, *D. retrocurva* and *C. sphaericus*. These species are the same as the two most negatively correlated to PC 2 with the areal abundance PCA. The response of the cubic (Figure 24) and the areal abundance (Figure 19) of the two species to season are very similar, except that the cubic measurement is less marked than the areal. Next is the comparison of these same two species response to the different depth contours, and again the cubic response (Figure 25) is very similar to the areal response (Figure 20). The two most negatively correlated species to PC 2 of the cubic PCA are *D. galeata* and *E. lacustris*. Comparison of the cubic responses to both month (Figure 26 and Figure 17) and depth (Figure 27 and Figure 18) are also similar.

Verification of Correlated Species

If the grouping of species into species associations is reduced to using only the significantly correlated species of the first two principle components, then the two types of species associations, will differ by only a few species (Figure 12 and Figure 28). In other words, *Cyclops sp.* and *E. lacustris* are in the proposed areal association illustration but not the cubic, and *E. coregoni* is in the cubic association illustration, but not in the areal.

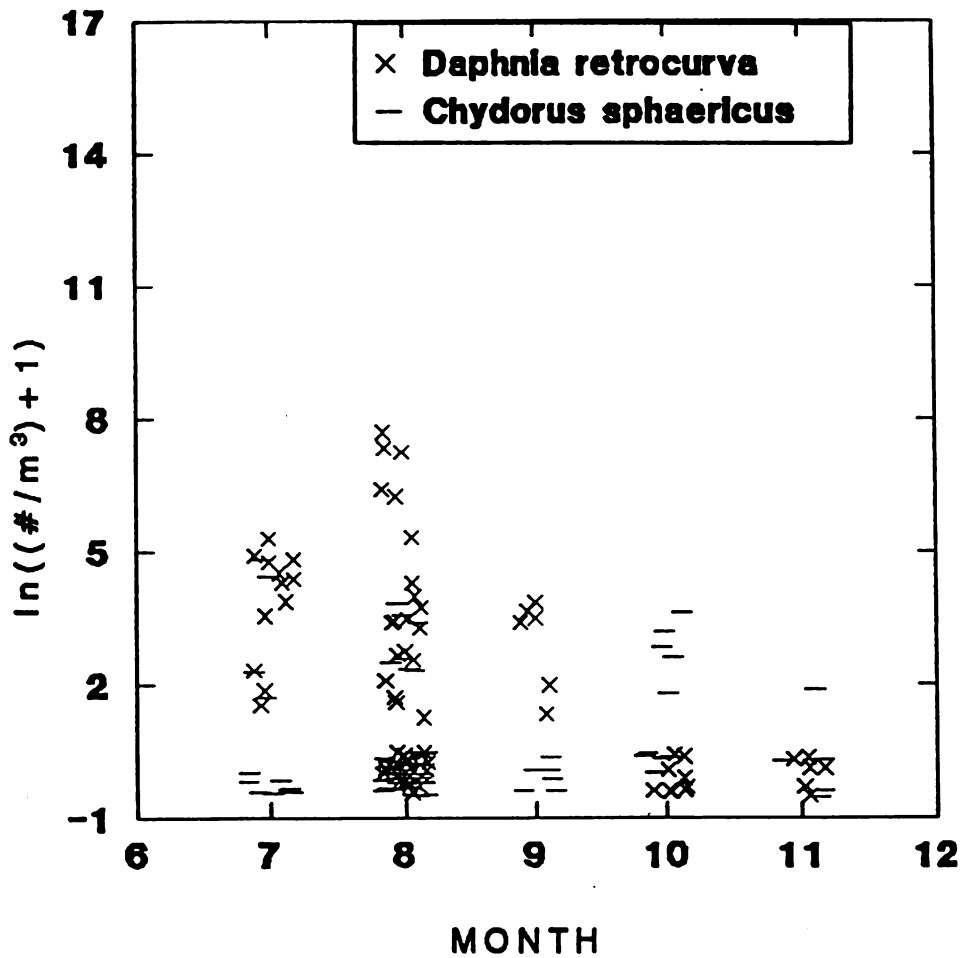


Figure 24. Log transformed (ln) cubic abundances of Daphnia retrocurva and Chydorus sphaericus for the months of July through November of 1991.

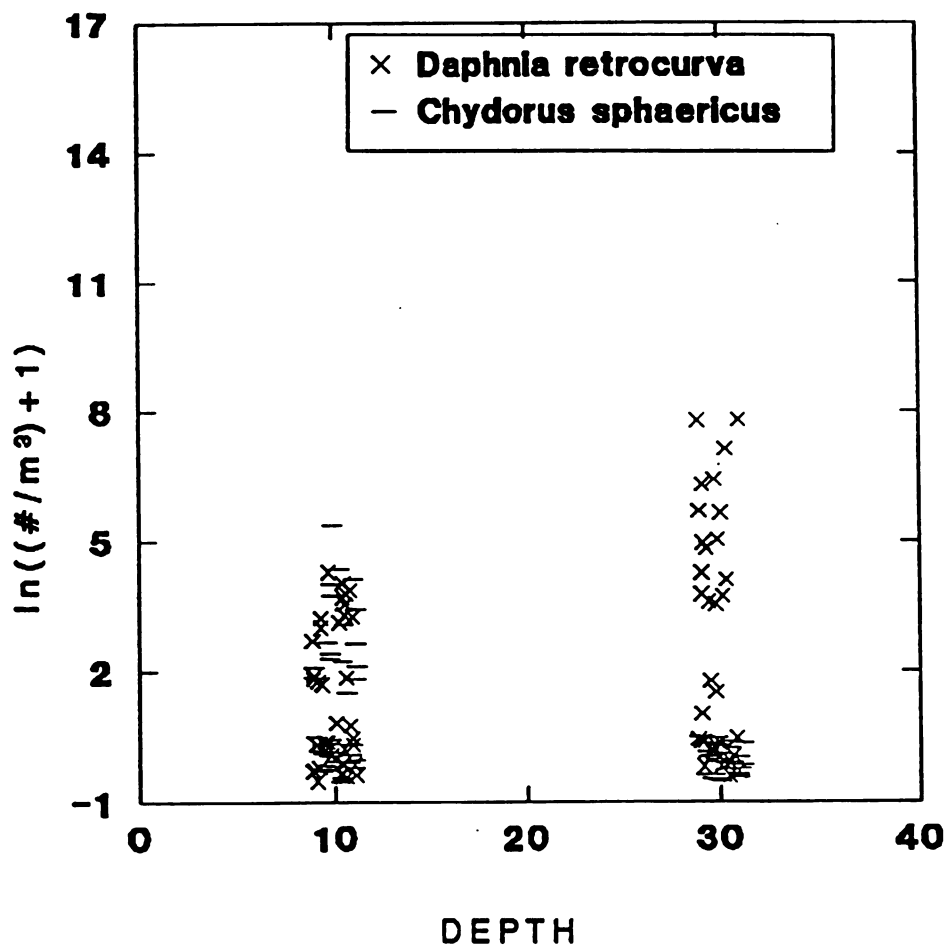


Figure 25. Log transformed (ln) cubic abundances of Daphnia retrocurva and Chydorus sphaericus at two depths, 10 and 30 meters.

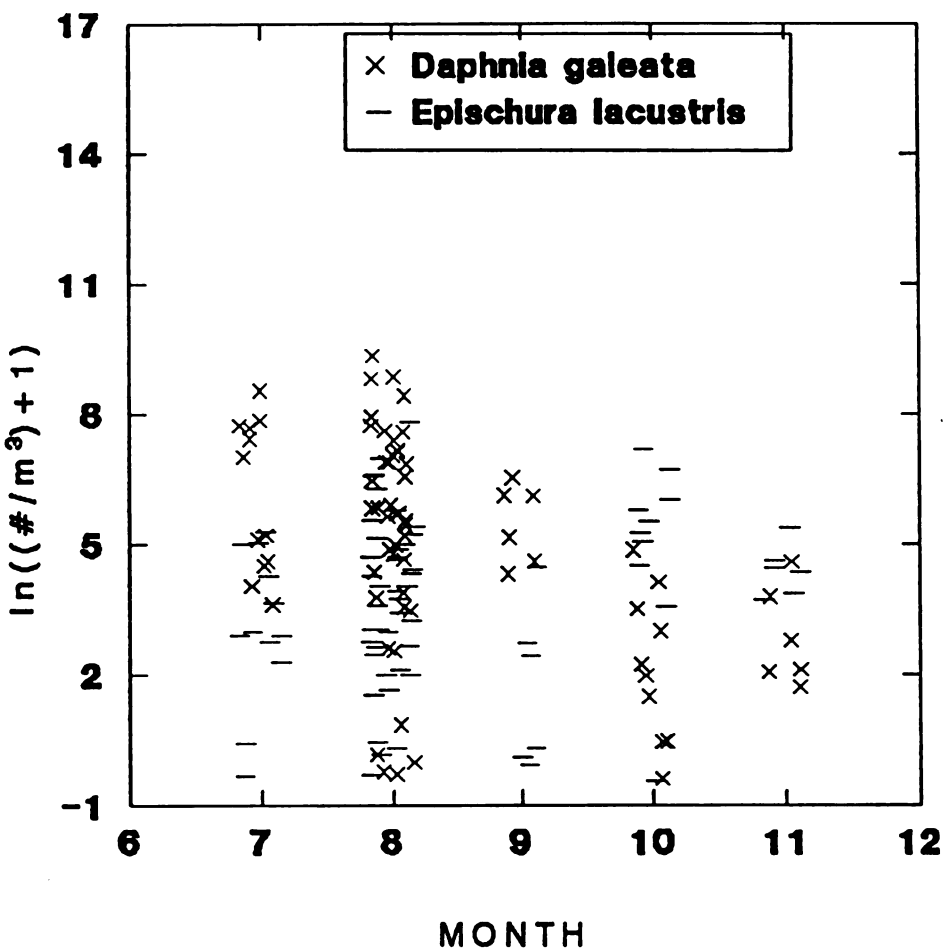


Figure 26. Log transformed (ln) cubic abundances of Daphnia galeata and Epischura lacustris for the months of July through November in 1991.

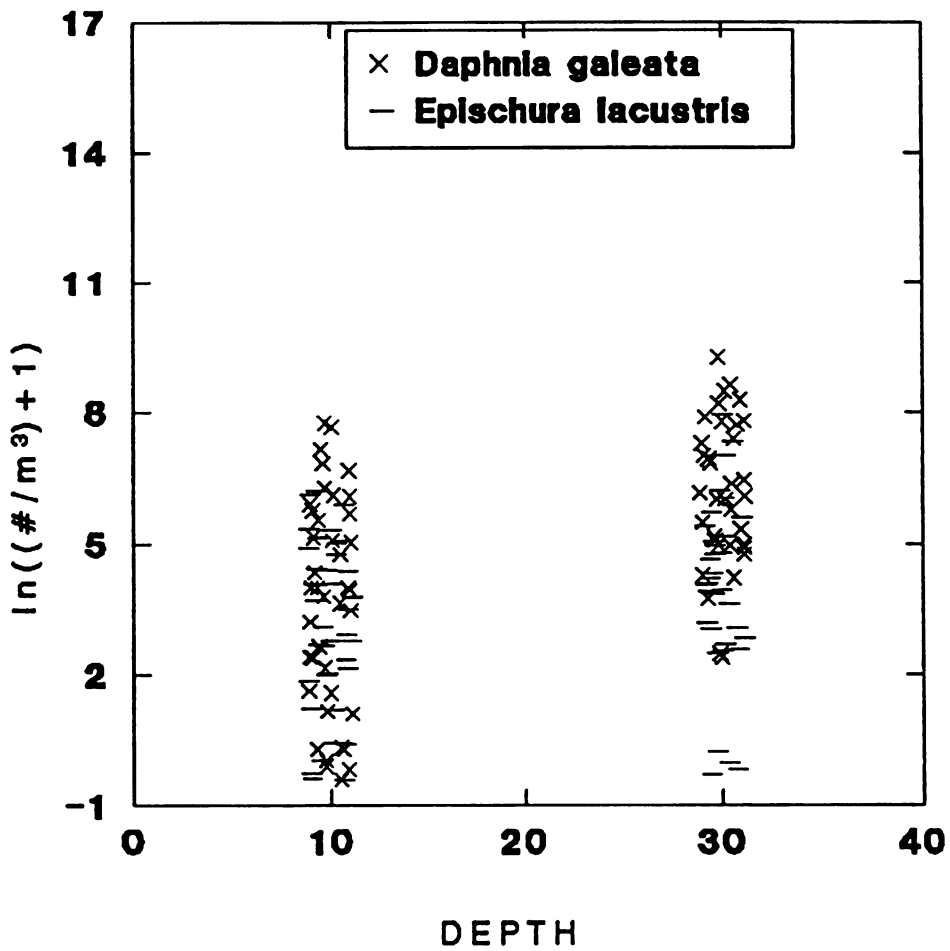


Figure 27. Log transformed (ln) cubic abundances of Daphnia galeata and Epischura lacustris at two depths, 10 and 30 meters.

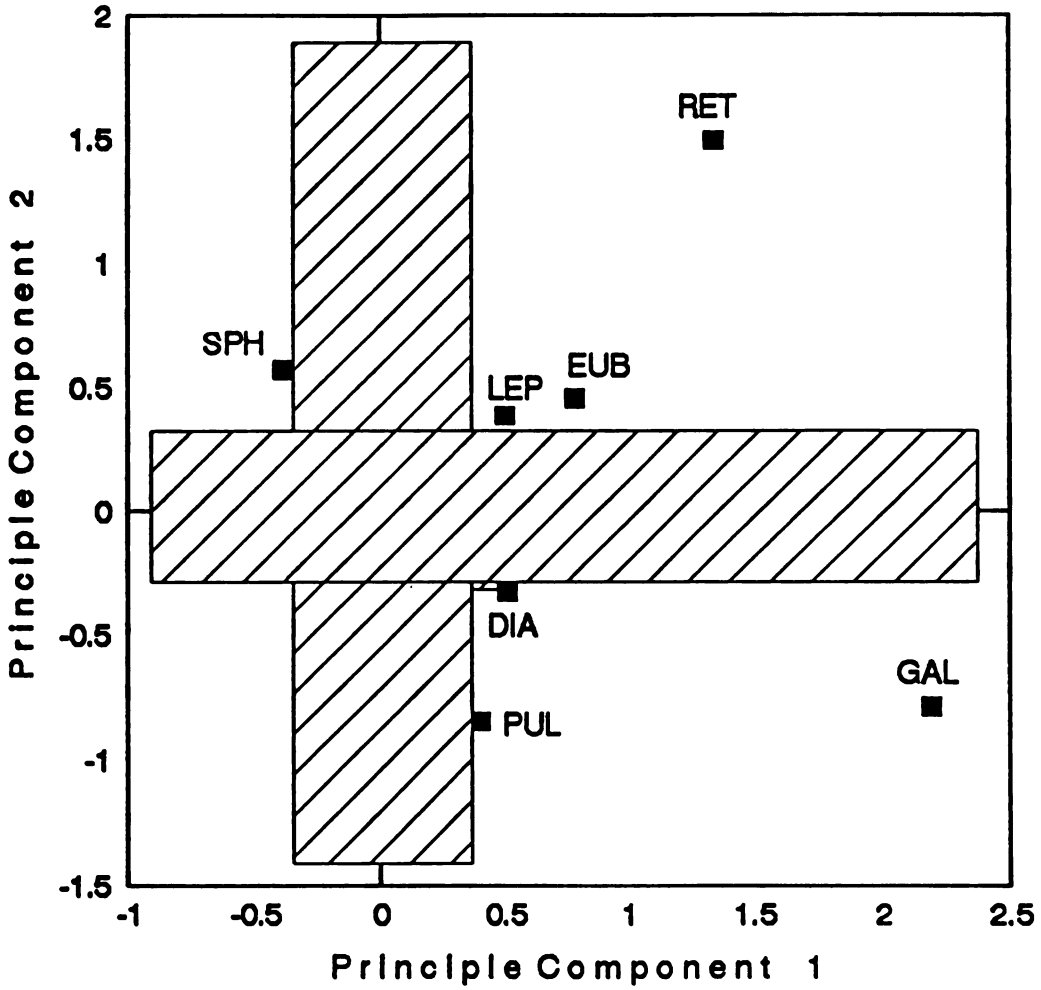


Figure 28. Biplot illustrating species that are significantly correlated with principle components 1 and 2 using cubic abundance data.

Species Groups

Areal Species Groups

Species will first be assembled into quadrants until the actual species associations are described later in the text.

Figure 29 illustrates the species that are hypothesized to be in the areal species associations. Each quadrant has text that describes what the hypotheses are for each quadrant and the responses of the verified species to each of the variables of the hypotheses. The unverified species (uncircled) are species that are significantly correlated to both PC 1 and PC 2.

The verified quadrant I species of the areal PCA, *E. lacustris* and *D. galeata* were both more abundant at the 30 meter contour and did not decline markedly with season. It is therefore hypothesized that *D. pulicaria*, *Diaptomus sp.* and *Cyclops sp.* will respond in a similar manner and the species could then be characterized by these environmental trends. Both *Diaptomus sp.* and *Cyclops sp.* did not decline markedly with season (Figure 30), and were more abundant at the 30 meter contour (Figure 31). *D. pulicaria* differed from the other quadrant I species with respect to month and declined with season and was absent from the samples by October (Figure 32). However, *D. pulicaria* did respond similarily to the depth variable (Figure 33).

The verified quadrant II species of the areal PCA, *D. retrocurva* declined markedly with season and was more abundant at the 30 meter contour. The other hypothesized quadrant II species, *L. kindti* also declined with season and was absent from four of six samples in October and totally absent by November (Figure 32). Like *D. retrocurva*, *L. kindti* when present in the samples, was more abundant at the 30 meter

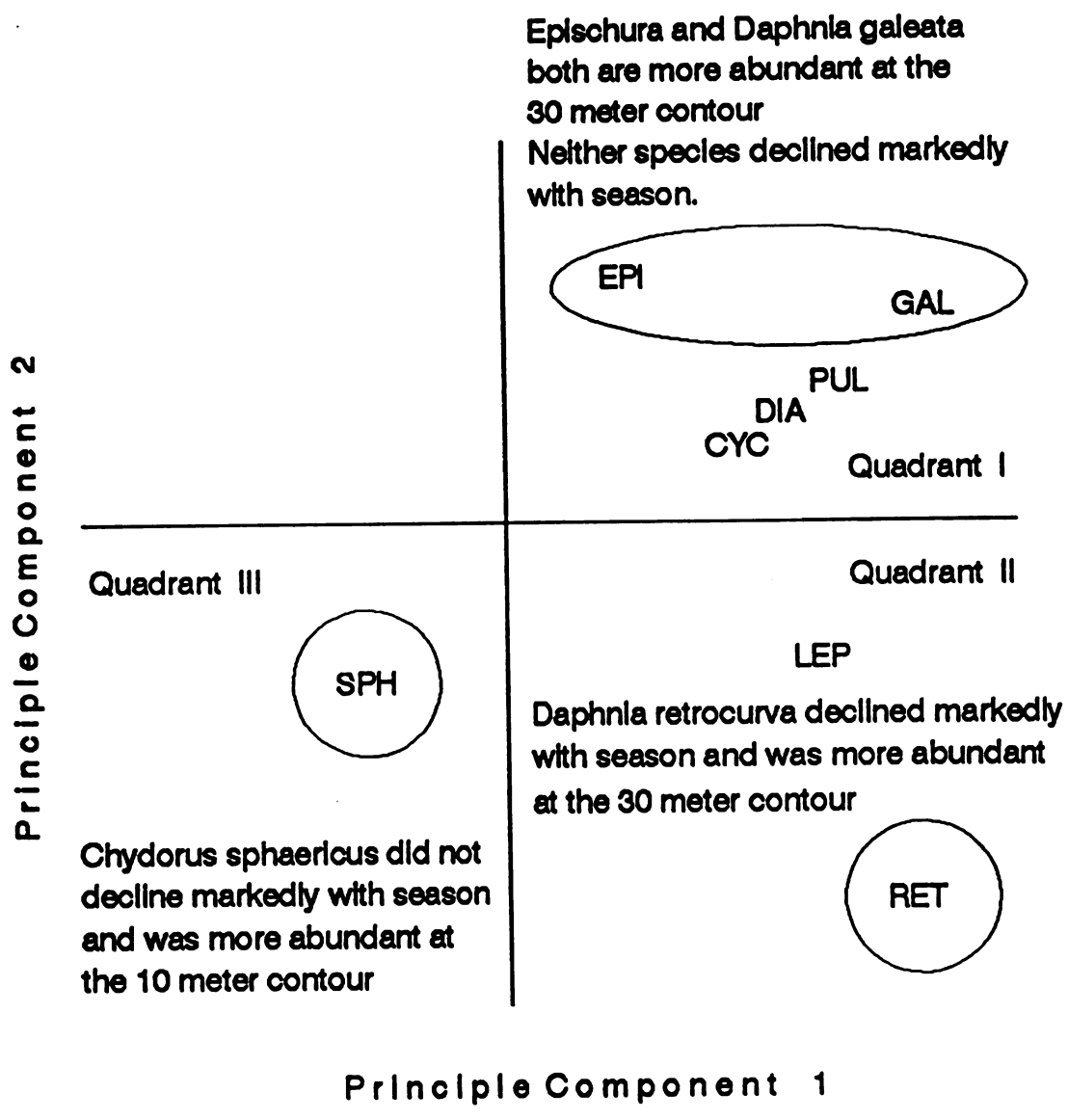


Figure 29. Illustration of significantly correlated species of the areal abundance biplot. Verified species and their responses to hypothetical expectations related to month and depth in the verification process (circled), and unverified species (uncircled) within proposed species associations or quadrants.

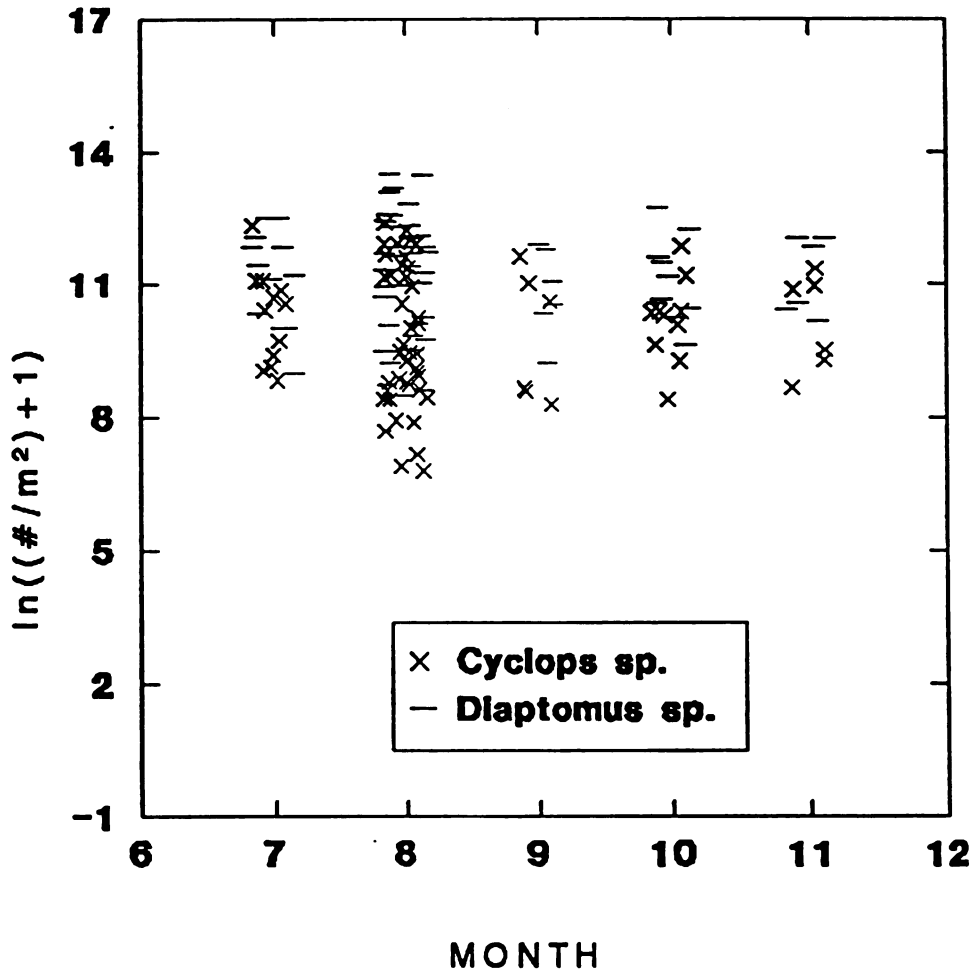


Figure 30. Log transformed (ln) abundances of the significantly correlated quadrant I groups, Cyclops sp. and Diaptomus sp., for the months of July through November in 1991.

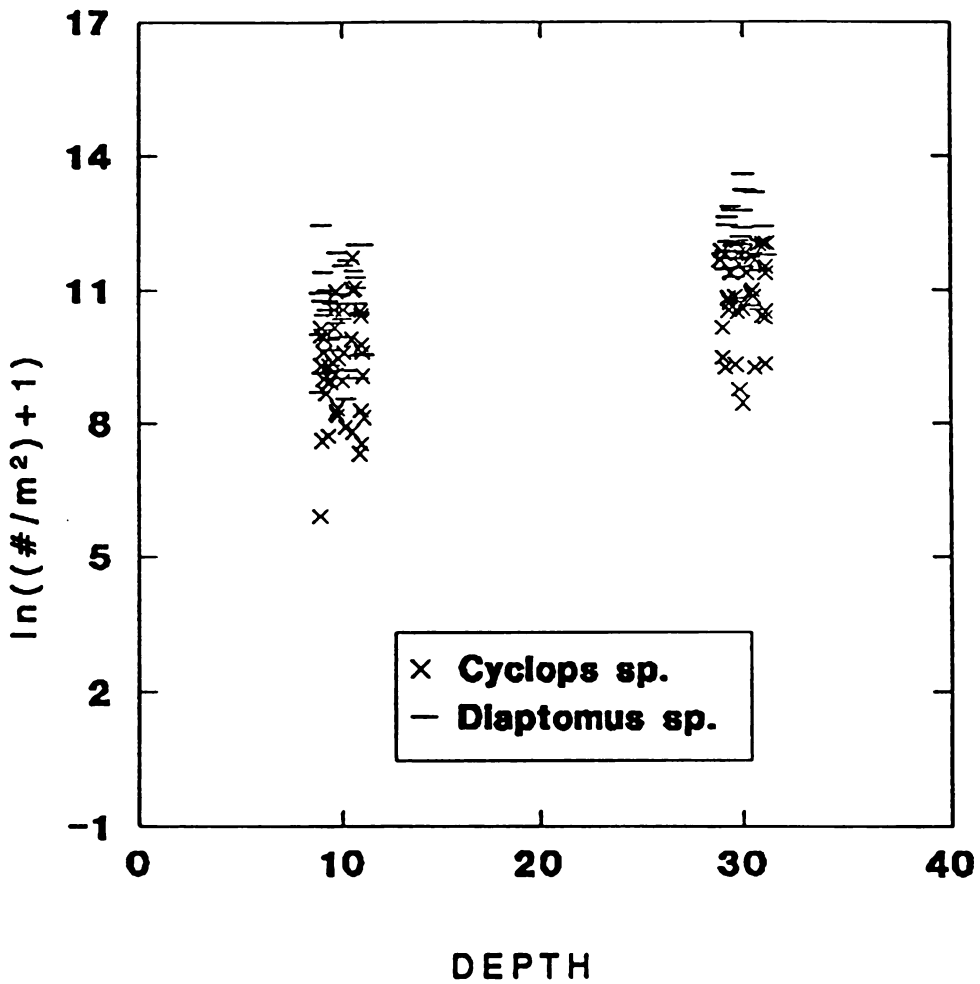


Figure 31. Log transformed (ln) abundances of the significantly correlated quadrant I groups, Cyclops sp. and Diaptomus sp., at two depths, 10 and 30 meters.

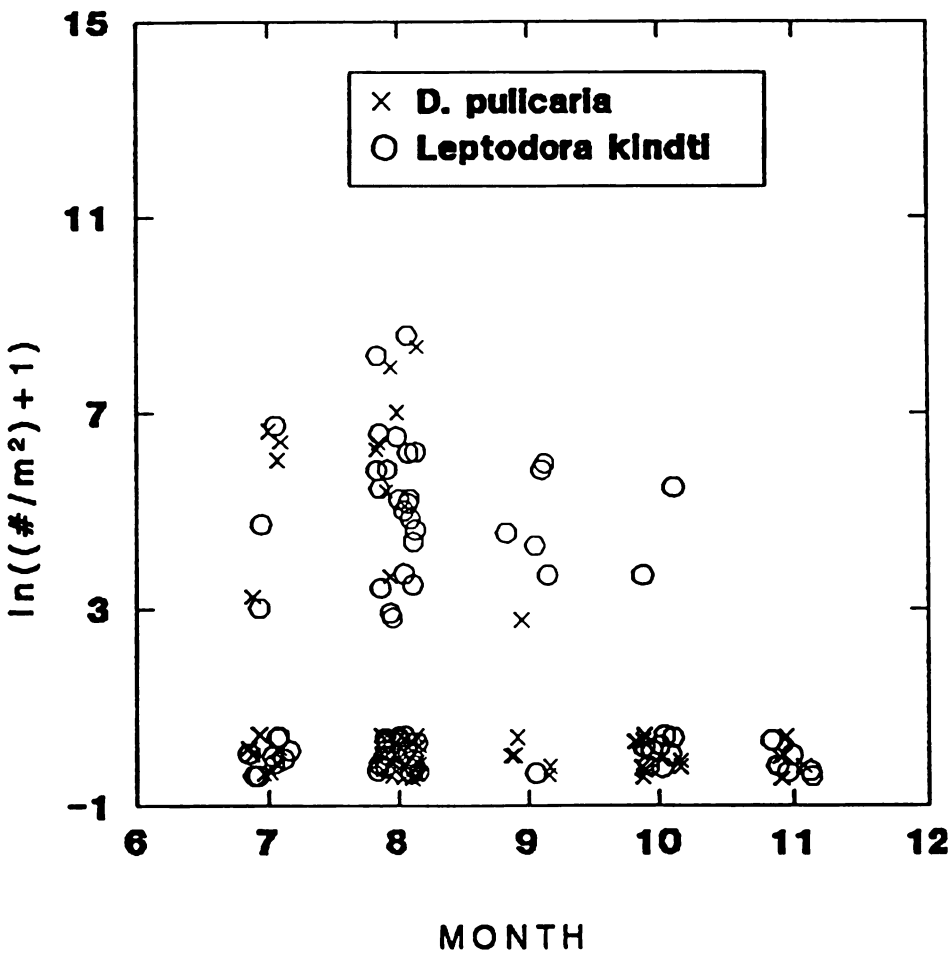


Figure 32. Log transformed (ln) abundances of the significantly correlated quadrant I species, Daphnia pulicaria and the quadrant II species, Leptodora kindti for the months of July through November in 1991.

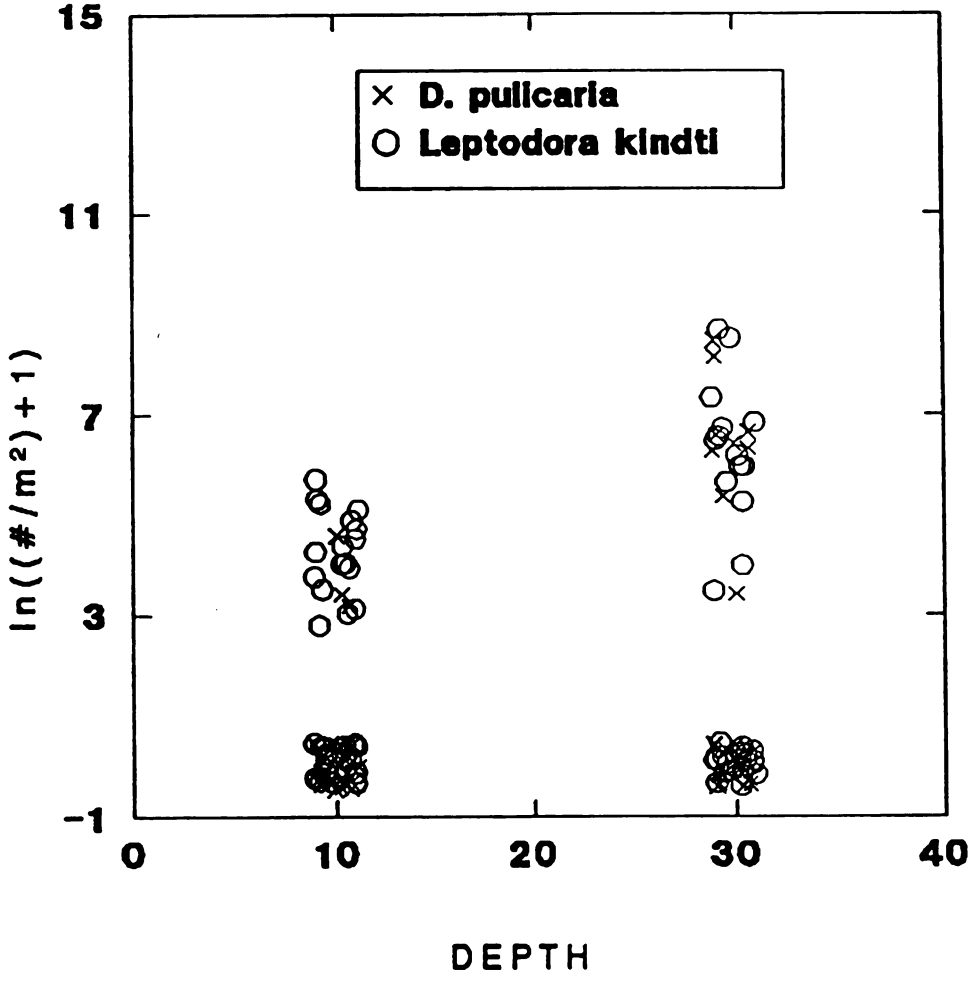


Figure 33. Log transformed (ln) abundances of the significantly correlated quadrant I species, Daphnia pulicaria and the quadrant II species, Leptodora kindti at two depths, 10 and 30 meters.

contour.

Quadrant III contains only *C. sphaericus* and this species declined with season (Figure 15), but not as drastically as other species such as *D. retrocurva*, *D. pulicaria* or *L. kindti*. This species placement on the left side of the biplot is more likely because of the remarkable characteristic of having a greater abundance at the 10 meter contour.

Cubic Species Groups

Figure 34 illustrates the species that are hypothesized to be in the cubic species associations. The unverified quadrant I species, *L. kindti* and *E. longirostris* are hypothesized to decline markedly with season and be more abundant at the 30 meter contour (Figure 34). *L. kindti* declines gradually. In September and October, two of six samples, then four of six samples lack this species, respectively, and in November the species was totally absent from the samples (Figure 35). *E. coregoni* also declined, but not gradually. It was totally absent in September, and one in six samples had the species present in both October and November (Figure 35). Both species, when present, were more abundant at the 30 meter contour (Figure 36).

The unverified quadrant II species, *D. pulicaria* and *Diaptomus sp.* are hypothesized to not decline markedly with season and be more abundant at the 30 meter contour. Only *Diaptomus sp.* responded in this manner to both season (Figure 37) and to depth (Figure 38). *D. pulicaria*, when present, was more abundant at the 30 meter depth (Figure 38), but declined significantly with season and was absent by September.

Species Associations

Only two variables, month and depth, were significant in the regressions of the principle components on the zooplankton community.

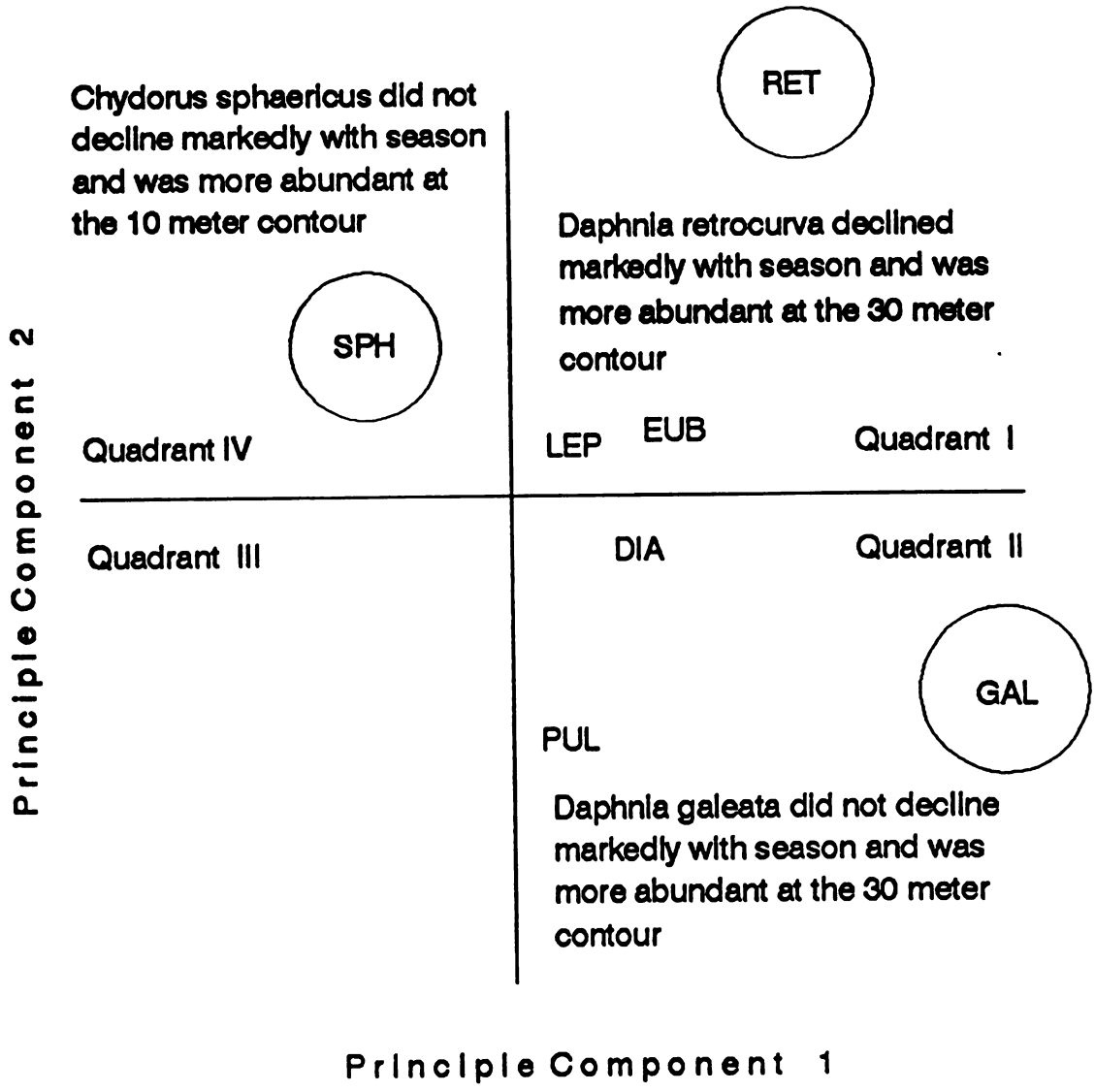


Figure 34. Illustration of significantly correlated species of the cubic abundance biplot. Verified species and their responses to hypothetical expectations related to month and depth in the verification process (circled), and unverified species (uncircled) within proposed species associations or quadrants.

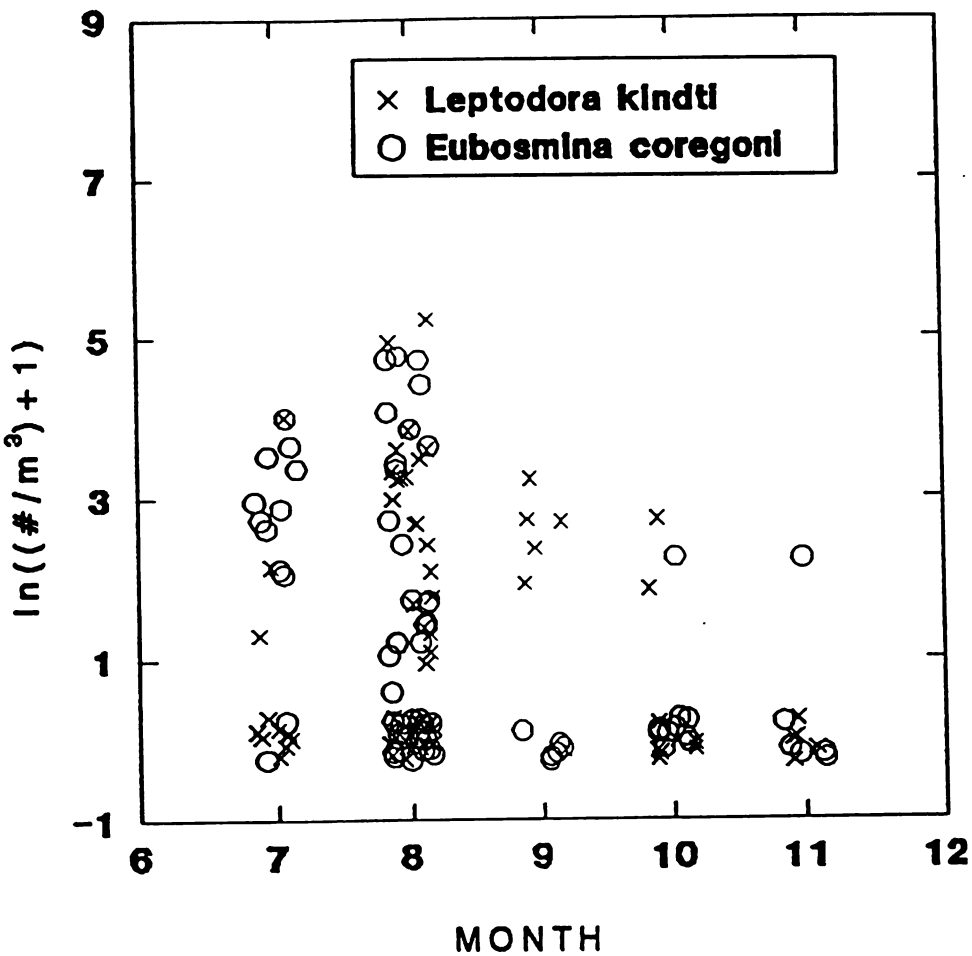


Figure 35. Log transformed (ln) cubic abundances of the significantly correlated quadrant I species, Leptodora kindtl, and Eubosmina coregoni for the months of July through November in 1991.

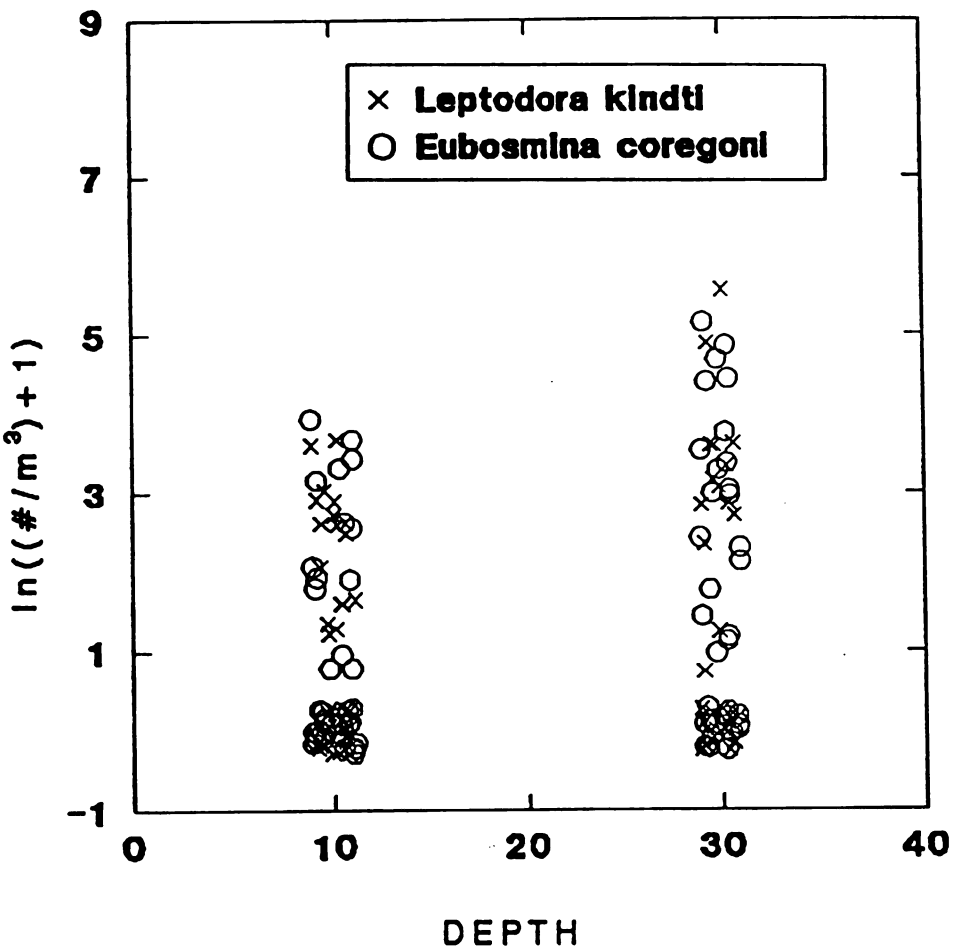


Figure 36. Log transformed (ln) cubic abundances of the significantly correlated quadrant I species, Leptodora kindti, and Eubosmina coregoni at two depths, 10 and 30 meters.

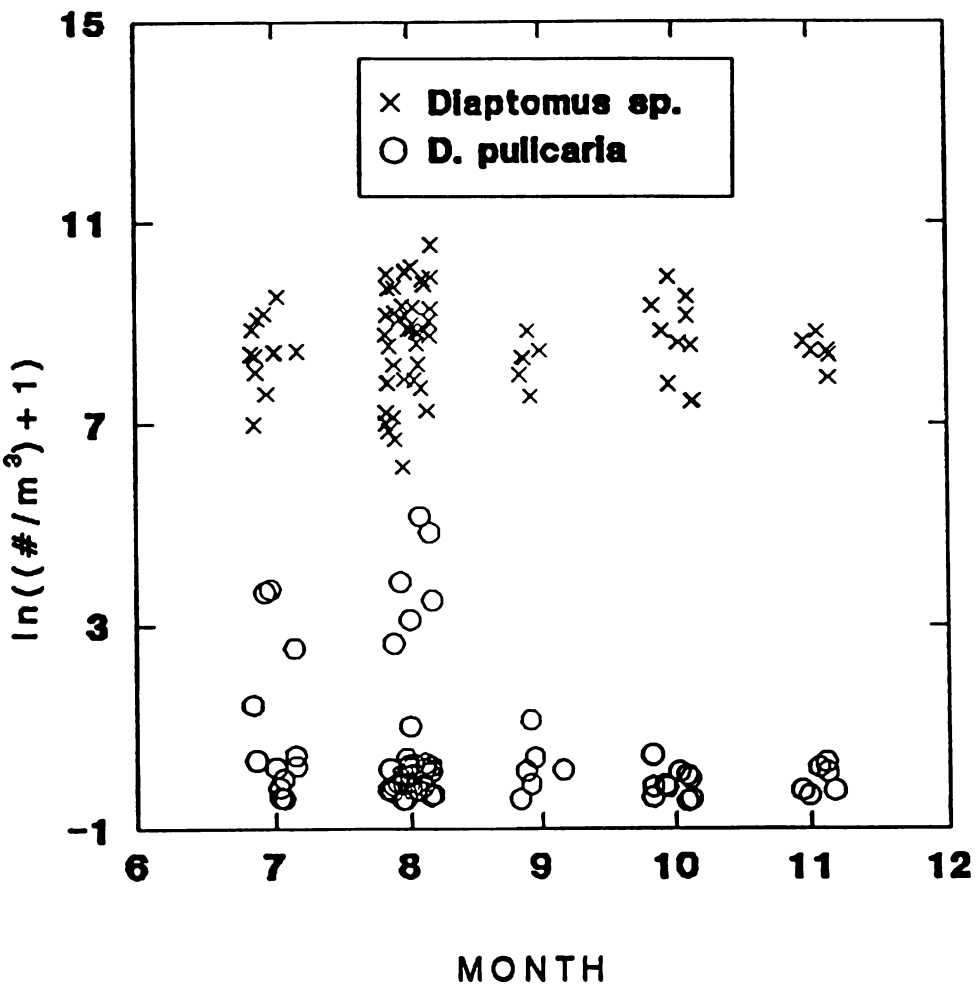


Figure 37. Log transformed (ln) cubic abundances of the significantly correlated quadrant II species, Diaptomus sp, and D. pulicaria for the months of July through November in 1991.

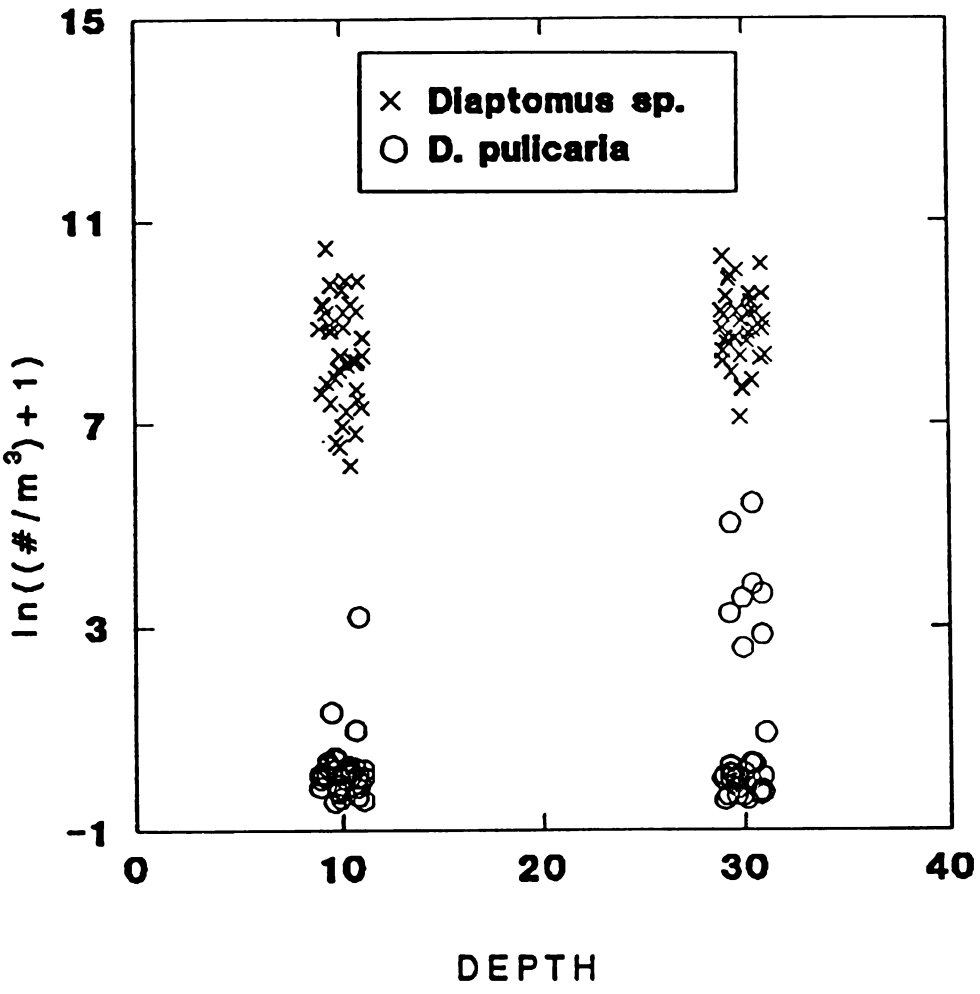


Figure 38. Log transformed (ln) cubic abundances of the significantly correlated quadrant II species, Diaptomus sp, and D. pulicaria at two depths, 10 and 30 meters.

Following are the three proposed species associations. Species significantly correlated to the first two principle components can hypothetically be grouped together in these associations as a means of describing the groups of species within the zooplankton community.

The Littoral Species Association

There was one species, *C. sphaericus*, that showed a negative correlation to both PC1 and PC2. In both the areal and the cubic PCA the species had abundances greater at the 10 meter contour, and was never found at the 30 meter contour (Table 3 and Table 4).The rest of the *Chydoridae* family, though not significantly correlated with PC 1 in both the areal (Table 5) or the cubic PCA (Table 6), was significantly correlated with PC 2. The species was in the same quadrant as *C. sphaericus* in both biplots (Figure 8 and Figure 9), and was absent at the 30 meter depth in all but one sample in July (Table 3 and Table 4).

It is proposed that these two species be grouped in a species association on the basis of their affinity to the shallower depths in the Great Lakes (Balcer et al. 1984).

The seasonal trends of the pair differ. Both groups had their highest abundance in July. *C. sphaericus*, although rare, was found in the samples until November, and *Chydorus sp.* was no longer found in the samples after August. The known life history and habitat preferences for the sediment and littoral zones of both species conforms with this association (Balcer et al. 1984).

Limnetic Non-persistent Species Association

It was hypothesized from both the areal and cubic abundance PCA's that because *D. retrocurva* was in greater abundance at the 30 meter depth and declined significantly in the fall months, that the other

species included within a quadrant with this species would also react similarily to the variables.

L. kindti was in this quadrant for both the areal and cubic PCA. *L. kindti* both declined gradually with season (Figure 32) and was more abundant at the 30 meter depth (Figure 33). Another species, *E. coregoni* found significant only in the cubic PCA, though more abundant at the 30 meter depth (Figure 36) persisted in one of six samples in both October and November (Figure 35).

D. pulicaria is another species that should be included in this grouping although the species was never placed in the same quadrant as *D. retrocurva*. In each of the biplots, *D. pulicaria* was placed on the other side of the x-axis, in the quadrant that is proposed to be the persistent species.

For the areal PCA, *D. retrocurva, L. kindti*, and *D. pulicaria*; and in the cubic PCA, *D. retrocurva, L. kindti, E. coregoni*, and *D. pulicaria* are grouped in the limnetic non-persistent species association.

Limnetic Persistent Species Association

It was hypothesized from both the areal and cubic abundance PCA's that because *D. galeata* (and *E. lacustris* in the areal PCA), was in greater abundance at the 30 meter depth and persisted into the fall months, and that the other species included within a quadrant with this species would also react similarily to the variables. As mentioned above, *D. pulicaria* was included within these quadrants, yet declined appreciably with season.

The other two species within the respective quadrants, *Diaptomus sp.* in both biplots, and only *Cyclops sp.* in the areal biplot, did

however persist. However, it is impossible to tell what is happening with both of these large groupings of species with respect to season. It may be many species peaking at different times within the genus, or one species dominating over the entire season.

For the areal PCA, *D. galeata*, *Diaptomus sp.*, *Cyclops sp.*, and *E. lacustris*; and in the cubic PCA, *D. galeata*, *Diaptomus sp.*, and *E. lacustris* are grouped in the limnetic non-persistent species association.

Estimations of Dry Weight Biomass

Volume Estimations of Biomass

Mean dry weights (ug) (used to estimate biomass), and 95% confidence intervals (n=30) for the volume estimated species *Diaptomus sp.* and *Cyclops sp.* are shown in Table 11.

Both of these species dry weight estimates were based on both length and either depth or width measurements. Because of this, size differences of many different sized adults and copepodid stages can give widely differing dry weight estimates. Compounding these variations is that both the *Diaptomus sp.* and *Cyclops sp.* groupings are composed of different sized species.

The significantly smaller dry weight average estimates of *Diaptomus sp.* and *Cyclops sp.* at the 10 meter contour in West Grand Traverse Bay on 8/26/91 (Table 11) was because the population was dominated by the shorter and thinner early copepodid stages. *Diaptomus sp.* lengths ranged from 0.38-0.64 mm, and *Cyclops sp.* from 0.34-0.60 mm. These measured lengths were less than half the measured dimensions of *Diaptomus sp.* and *Cyclops sp.* on comparable dates at Ludington on 8/29 and at Manitou Passage on 8/27 (Table 11). This lag in development was expected because

Table 11. Unverified estimates of mean dry weight (μg), standard error, and 95% confidence intervals for Diaptomus sp. and Cyclops sp.

			Diaptomus sp.			Cyclops sp.		
LOC.	DATE	Z	Mean	SE	CI (n=30)	Mean	SE	CI (n=30)
LU	07/17/91	30	3.9636	0.501	(2.980,4.947)	2.2304	0.243	(1.752,2.708)
LU	07/17/91	10	4.8217	0.401	(4.036,5.606)	2.8891	0.262	(2.373,3.404)
LU	07/30/91	30	3.9636	0.501	(2.980,4.947)	2.2304	0.243	(1.752,2.708)
LU	08/01/91	10	4.8217	0.401	(4.036,5.606)	2.8891	0.262	(2.373,3.404)
TC	08/06/91	30	1.8086	0.220	(1.377,2.239)	1.1114	0.101	(0.914,1.308)
TC	08/06/91	10	2.0496	0.608	(0.857,3.242)	0.9938	0.114	(0.769,1.219)
MP	08/10/91	30	2.8853	0.537	(1.889,2.885)	1.3110	0.186	(0.947,1.675)
MP	08/09/91	10	2.3865	0.254	(1.832,3.938)	4.1827	1.753	(0.745,7.620)
LU	08/16/91	30	3.1849	0.429	(2.344,4.023)	2.0995	0.971	(0.196,4.003)
LU	08/16/91	10	2.7573	0.294	(2.180,3.334)	1.2696	0.181	(0.914,1.624)
TC	08/26/91	30	2.4532	0.220	(2.021,2.885)	1.7381	0.208	(1.329,2.147)
TC	08/26/91	10	0.9466	0.083	(0.783,1.110)	0.8895	0.067	(0.758,1.021)
MP	08/27/91	30	2.0913	0.241	(1.619,2.563)	1.1684	0.151	(0.873,1.464)
MP	08/27/91	10	1.7573	0.208	(1.350,2.164)	0.8451	0.084	(0.681,1.009)
HO	08/28/91	30	2.1378	0.339	(1.473,2.802)	1.1472	0.155	(0.843,1.452)
HO	08/28/91	10	1.8402	0.193	(1.461,2.219)	0.9183	0.043	(0.835,1.002)
LU	08/29/91	30	3.1849	0.429	(2.344,4.023)	2.0995	0.971	(0.196,4.003)
LU	08/29/91	10	2.7573	0.294	(2.180,3.334)	1.2696	0.181	(0.914,1.624)
LU	09/13/91	30	5.4913	1.264	(3.013,7.969)	0.7973	0.119	(0.565,1.030)
LU	09/13/91	10	1.6961	0.226	(1.253,2.140)	1.0322	0.139	(0.759,1.305)
LU	10/03/91	30	5.4913	1.264	(3.013,7.969)	0.7973	0.119	(0.565,1.030)
LU	10/03/91	10	1.6961	0.226	(1.253,2.140)	1.0322	0.139	(0.759,1.305)
LU	10/18/91	10	3.6026	0.411	(2.796,4.409)	1.0466	0.114	(0.823,1.270)
LU	11/14/91	30	3.9796	0.589	(2.826,5.132)	0.7528	0.075	(0.606,0.899)
LU	11/14/91	10	3.2603	0.602	(2.081,4.440)	1.2455	0.300	(0.847,1.644)

of observed differences in both temperature and zooplankton abundances between Grand Traverse Bay and other locations on Lake Michigan the previous year (Barner unpub. data). In addition, the previous sample at West Grand Traverse Bay (8/6/91) contained the largest proportion of nauplii of all the samples. It was suspected to be an important component to the total biomass, but estimates found the estimated weight to be insignificant (922 ug), or less than 0.2% of the total biomass for that sample.

Length-Weight Regression Estimations

Dry weights were split into two tables because *B. longirostris* and *D. galeata*, in most cases, had at least 30 animals measured and there is a higher degree of confidence in the length measurements than in the case of *D. retrocurva*, *E. lacustris*, and *L. macrurus*.

Mean dry weights (ug) used to estimate biomass from length-dry weight regressions, the number of animals measured (n), standard error and 95% confidence intervals are shown in Table 12 for *B. longirostris* and *D. galeata*, and Table 13 for *D. retrocurva*, *E. lacustris*, and *L. macrurus*.

The biomass weights of this study are similar to those estimated by Hawkins and Evans (1979). The exception, was the weight of *D. galeata*, which averaged from 3.7 to 9.6 ug per individual in this study, and just 4.0 ug in the Hawkins and Evans (1979) study.

The discrepancy may be explained by the differing methods of estimation. Hawkins and Evans (1979) estimates should be the most accurate because they were done directly using a microbalance, whereas in this study they were only estimated by a length-dry weight regression and unverified.

Table 12. Unverified estimates of mean dry weight (μg), standard error, and 95% confidence intervals of Bosmina coregoni and Daphnia galeata.

			Bosmina coregoni				Daphnia galeata			
LOC.	DATE	Z	Mean	N	SE	CI	Mean	N	SE	CI
LU	07/17/91	30	1.2464	30	0.071	(1.11,1.39)	8.6719	30	0.696	(7.31,10.04)
LU	07/17/91	10	1.2508	30	0.075	(1.10,1.40)	9.6331	8	0.651	(8.36,10.91)
LU	07/30/91	30	1.2464	30	0.071	(1.11,1.39)	8.6719	30	0.696	(7.31,10.04)
LU	08/01/91	10	1.2508	30	0.075	(1.10,1.40)	9.6331	8	0.651	(8.36,10.91)
TC	08/06/91	30	1.2481	21	0.121	(1.10,1.40)	4.0213	28	0.131	(3.88,4.16)
TC	08/06/91	10	1.0678	30	0.052	(0.96,1.17)	3.9326	17	0.252	(2.95,4.92)
MP	08/10/91	30	1.8909	23	0.203	(1.49,2.29)	5.7113	35	0.240	(4.15,5.09)
MP	08/09/91	10	1.2971	30	0.085	(1.13,1.46)	4.6217	30	0.366	(4.99,6.43)
LU	08/16/91	30	2.1844	16	0.257	(1.68,2.69)	8.5142	30	0.552	(7.43,9.60)
LU	08/16/91	10	1.2140	30	0.090	(1.04,1.39)	5.4933	23	0.243	(5.02,5.97)
TC	08/26/91	30	1.9105	30	0.168	(1.58,2.24)	5.0360	9	0.337	(4.38,5.70)
TC	08/26/91	10	1.5681	30	0.126	(1.32,1.81)	3.7216	9	0.208	(3.31,4.13)
MP	08/27/91	30	1.0329	22	0.054	(0.93,1.14)	4.1203	30	0.162	(3.80,4.44)
MP	08/27/91	10	0.9467	30	0.050	(0.85,1.05)	4.1948	30	0.196	(3.81,4.58)
HO	08/28/91	30	1.3847	30	0.082	(1.22,1.55)	5.6220	30	0.325	(4.99,6.26)
HO	08/28/91	10	0.8922	11	0.059	(0.781,1.01)				
LU	08/29/91	30	2.1844	16	0.257	(1.68,2.69)	8.5142	30	0.552	(7.43,9.60)
LU	08/29/91	10	1.2140	30	0.090	(1.04,1.39)	5.4933	23	0.243	(5.02,5.97)
LU	09/13/91	30	1.1253	7	0.107	(0.91,1.34)	6.4845	22	0.493	(5.52,7.45)
LU	09/13/91	10	1.0532	7	0.098	(0.86,1.24)	5.3452	17	0.551	(4.26,6.43)
LU	10/03/91	30	1.1253	7	0.107	(0.91,1.34)	6.4845	22	0.493	(5.52,7.45)
LU	10/03/91	10	1.0532	7	0.098	(0.86,1.24)	5.3452	17	0.551	(4.26,6.43)
LU	10/18/91	10	1.2164	12	0.048	(1.12,1.31)				
LU	11/14/91	30					8.3894	2		
LU	11/14/91	10	1.4914	15	0.103	(1.29,1.69)				

Table 13. Unverified estimates of mean dry weight (μg), standard error, and 95% confidence intervals for Daphnia retrocurva, Epischura lacustris and Limnocalanus macrurus.

			Daphnia retrocurva				Epischura lacustris				Limnocalanus macrurus			
LOC.	DATE	Z	Mean	N	SE	CI	Mean	N	SE	CI	Mean	N	SE	CI
LU	07/17/91	30	1.5832	4	0.199	(1.19,1.97)	10.0544	4	4.646	(0.95,19.16)	41.1655	12	4.232	(33.87,49.46)
LU	07/17/91	10	4.1967	9	1.138	(0.26,3.10)	8.8251	2						
LU	07/30/91	30	1.5832	4	0.199	(1.19,1.97)	10.0544	4	4.646	(0.95,19.16)	41.1655	12	4.232	(33.87,49.46)
LU	08/01/91	10	4.1967	9	1.138	(0.26,3.10)	8.8251	2						
TC	08/06/91	30	1.0158	2			2.3767	7	0.477	(1.44,3.31)				
TC	08/06/91	10					1.4086	6	0.233	(0.46,2.36)				
MP	08/10/91	30					7.6190	7	1.036	(5.59,9.65)	28.0967	13	4.730	(18.83,37.37)
MP	08/09/91	10					7.5603	4	0.559	(6.46,8.66)	18.4850	2		
LU	08/16/91	30					9.1133	4	1.485	(6.20,12.02)	16.1173	3		
LU	08/16/91	10					5.4209	2						
TC	08/26/91	30					7.1789	1						
TC	08/26/91	10					2.0586	1						
MP	08/27/91	30					4.2458	14	0.522	(3.22,5.27)				
MP	08/27/91	10					2.5318	3						
HO	08/28/91	30	2.5749	30	0.212	(2.16,2.99)	6.1754	8	0.963	(4.29,8.06)				
HO	08/28/91	10					7.3832	1						
LU	08/29/91	30	2.8003	23	0.425	(1.97,3.63)	6.3129	10	0.864	(4.62,8.01)				
LU	08/29/91	10					5.4209	2						
LU	09/13/91	30	1.2261	2			7.9071	2			31.3584	7	6.854	(17.93,44.79)
LU	09/13/91	10	3.1956	2			4.5001	13	0.680	(3.17,5.83)				
LU	10/03/91	30	1.2261	2			5.1328	30	0.446	(4.26,6.01)				
LU	10/03/91	10	3.1956	2			4.5001	13	0.680	(3.17,5.83)				
LU	10/18/91	10					4.9543	11	0.403	(4.16,5.74)				
LU	11/14/91	30					9.0211	20	0.312	(8.41,9.53)				
LU	11/14/91	10					8.4914	12	0.584	(7.35,9.64)				

***Bythotrephes* Biomass Estimations**

Bythotrephes dry weights (ug), derived from regressions of instar weights on epilimnetic temperatures (Burkhardt 1991) are reported in Table 14. Weights are reported for each instar, and neonates. Animals that had broken spines could not be aged and were multiplied by the average of all instar weights of the sample. Counts of instars and temperatures (°C) used are in APPENDIX B.

Total Biomass - All Locations (mg/m^2)

Biomass (mg/m^2) for each contributing species, from all three methods are combined in Table 15. Total biomass for individual samples ranged from 24 mg/m^2 to 3782 mg/m^2. Total biomass for each location, date, and depth, (averaged over replicates), ranged from a low of 53 mg/m^2 in Ludington on both August 29th and September 13th to a high of 2691 mg/m^2 in West Grand Traverse Bay on August 26th.

Copepods dominated the biomass over the entire season. *Diaptomus sp.* averaged 60.5% of the total biomass, followed by *Cyclops sp.* with 11.1%. The third most abundant species, *Bosmina longirostris*, ranked fifth in total biomass (4.8%), and the fourth most abundant, *D. galeata* ranked third in total biomass (10.5%).

B. cederstroemi was only 0.1% of the total abundance, yet it was ranked fifth in biomass with 8.4% of the total biomass. The remaining species measured for biomass were: *E. lacustris* 3.0%, *L. macrurus* 0.8%, and *D. retrocurva* 0.7%.

Both Manitou Passage and West Grand Traverse Bay increased at the 30 meter depth, and decreased in average biomass at the 10 meter depth in August of 1991. Grand Traverse Bay began at a very low average biomass (210 mg/m^2) on August 6th at the deeper station, and increased

Table 14. Estimated dry weight biomass (μg) of three instars, neonates, and broken spine animals of Bythotrephes cederstroemi at two depths and four sites in northeastern Lake Michigan in 1991.

				Instar					
Loc.	Date	Z	#/m²	3rd	2nd	1st	neonate	broken*	total (mg)
LU	07/17	30	530	96800	31565	14840	70	11808	155.1
LU	07/17	30	510	88000	36580	10360	1190	11480	147.6
LU	07/17	30	736	112750	42480	17920	1960	19352	194.5
LU	07/17	10	287	63800	14455	3780	1540	8856	92.4
LU	07/17	10	191	34650	7965	4900	560	5576	53.7
LU	07/17	10	189	25300	7965	7000	210	4264	44.7
LU	07/30	30	4	0	0	100	0	542	0.6
LU	07/30	30	19	5170	490	100	0	0	5.8
LU	07/30	30	14	2350	735	200	0	271	3.6
LU	08/01	10	25	4230	245	900	70	0	5.4
LU	08/01	10	31	5640	1225	700	0	0	7.6
LU	08/01	10	22	4700	735	100	0	813	6.3
TC	08/06	30	157	22000	10325	5880	0	1968	40.2
TC	08/06	30	745	134750	40120	23240	490	11480	210.1
TC	08/06	30	284	50600	17700	7280	70	4920	80.6
TC	08/06	10	57	7150	3540	1400	350	2296	14.7
TC	08/06	10	74	8800	4720	1820	280	1312	16.9
TC	08/06	10	8	550	885	0	0	656	2.1
MP	08/10	30	113	26950	5015	2240	210	1968	36.4
MP	08/10	30	366	107250	14455	2800	70	6560	131.1
MP	08/10	30	223	66550	10325	1820	140	1640	80.5
MP	08/09	10	5	1650	0	0	0	328	2.0
MP	08/09	10	5	1650	295	0	0	0	1.9
MP	08/09	10	3	1100	0	0	0	0	1.1
LU	08/16	30	271	32775	17325	11250	0	4056	65.4
LU	08/16	30	312	54625	16695	11500	0	5070	87.9
LU	08/16	30	282	41400	12915	10500	630	5070	70.5
LU	08/16	10	138	25875	8820	2625	0	3718	41.0
LU	08/16	10	149	27600	13545	1750	0	3718	46.6
LU	08/16	10	111	24150	7245	1250	0	3380	36.0
TC	08/26	30	73	16875	4550	1485	0	1850	24.8
TC	08/26	30	84	21875	5600	2565	0	740	30.8
TC	08/26	30	80	16250	4900	1620	0	3700	26.5
TC	08/26	10	22	5000	1750	540	0	0	7.3
TC	08/26	10	33	10000	1400	270	0	1850	13.5
TC	08/26	10	32	10625	350	405	280	740	12.4
MP	08/26	30	80	8750	3150	3915	0	740	16.6
MP	08/27	30	65	11875	4900	2160	0	1480	20.4
MP	08/27	30	74	9375	5250	2835	0	740	18.2
MP	08/27	10	3	0	350	135	0	0	0.5
MP	08/27	10	14	3125	1400	270	0	0	4.8
MP	08/27	10	11	625	1750	135	0	740	3.3
HO	08/28	30	11	0	2820	525	0	0	3.3
HO	08/28	30	18	2340	2350	700	0	950	6.3
HO	08/28	30	31	7020	2820	1050	0	950	11.8

Table 14. (cont'd)

				Instar					
Loc.	Date	Z	#/m²	3rd	2nd	1st	neonate	broken*	total (mg)
HO	08/28	10	33	6240	3760	1050	0	1900	13.0
HO	08/28	10	43	6240	6110	1575	0	1900	15.8
HO	08/28	10	33	3120	6580	1050	0	950	11.7
LU	08/29	30	23	4800	1320	650	0	353	7.1
LU	08/29	30	36	9000	660	1300	0	706	11.7
LU	08/29	30	19	3600	990	260	0	1412	6.3
LU	08/29	10	65	18600	2310	1300	0	1412	23.6
LU	08/29	10	37	12000	660	780	0	353	13.8
LU	08/29	10	31	5400	1650	780	0	1412	9.2
LU	09/13	30	17	940	0	800	0	813	2.6
LU	09/13	30	25	1880	245	1200	0	813	4.1
LU	09/13	30	19	2350	490	400	0	1084	4.3
LU	09/13	10	8	940	0	300	0	271	1.5
LU	09/13	10	1	470	0	0	0	0	0.5
LU	09/13	10	4	1410	0	0	0	0	1.4
LU	10/03	30	4	0	85	150	0	0	0.2
LU	10/03	30	1	265	0	0	0	0	0.3
LU	10/03	30	14	265	85	400	0	133	0.9
LU	10/03	10	19	265	425	300	0	399	1.4
LU	10/03	10	39	2650	510	600	0	532	4.3
LU	10/03	10	32	1590	595	400	0	532	3.1
LU	10/18	10	169	16100	2220	855	0	999	20.2
LU	10/18	10	381	22080	4800	1980	0	6660	35.5
LU	10/18	10	152	3220	2580	1260	0	3552	10.6
LU	10/18	10	279	6210	4140	2565	0	6993	19.9
LU	11/14	30	113	1900	2080	165	0	416	4.6
LU	11/14	30	80	1000	1400	90	0	572	3.1
LU	11/14	30	28	200	640	30	0	104	1.0
LU	11/14	10	103	3900	680	90	0	468	5.1
LU	11/14	10	135	3900	1600	60	0	884	6.4
LU	11/14	10	1003	14400	9600	1440	0	14352	39.8

Table 15. Unverified estimated biomass (mg/m²) of measured species at two depths (10 and 30 m) and four sites in northeastern Lake Michigan in 1991.

Loc	Date	Z	BYT	CYC	DIA	BOS	GAL	RET	EPI	LIM	Tot (mg)	Avg (mg)
LU	07/17/91	30	155	63	503	2	667	2	3	58	1453	
LU	07/17/91	30	148	30	378	4	689	7	3	45	1302	1523
LU	07/17/91	30	194	26	1046	3	517	5	4	18	1813	
LU	07/17/91	10	45	124	291	5	3	2	0	0	470	
LU	07/17/91	10	54	109	402	4	5	2	1	0	576	492
LU	07/17/91	10	92	116	206	7	6	1	0	0	429	
LU	07/30/91	30	6	122	609	3	11	4	4	0	759	
LU	07/30/91	30	1	14	322	1	6	5	1	0	349	512
LU	07/30/91	30	4	11	116	1	6	3	0	0	142	
LU	08/01/91	10	6	1	14	1	1	0	0	0	24	
LU	08/01/91	10	8	1	17	1	1	0	0	0	28	65
LU	08/01/91	10	5	1	16	1	0	0	0	0	24	
TC	08/06/91	30	210	15	39	1	22	0	2	0	288	
TC	08/06/91	30	40	13	92	1	17	0	0	1	165	210
TC	08/06/91	30	81	18	54	1	21	0	1	0	176	
TC	08/06/91	10	17	24	318	4	24	0	23	43	453	
TC	08/06/91	10	15	11	461	5	16	0	5	33	547	520
TC	08/06/91	10	2	49	441	7	17	0	8	37	561	
MP	08/10/91	30	80	20	57	19	9	0	2	0	187	
MP	08/10/91	30	36	32	105	39	9	0	5	0	227	236
MP	08/10/91	30	131	19	111	23	7	0	3	0	293	
MP	08/09/91	10	2	115	271	1	181	0	37	0	607	
MP	08/09/91	10	1	101	611	3	245	0	31	75	1068	1149
MP	08/09/91	10	2	317	943	2	296	0	41	170	1771	
LU	08/16/91	30	56	17	783	11	902	0	25	22	1817	
LU	08/16/91	30	88	15	731	8	727	0	13	47	1629	1469
LU	08/16/91	30	17	151	445	6	334	0	7	0	961	
LU	08/16/91	10	47	26	249	36	21	0	2	0	382	
LU	08/16/91	10	26	24	90	28	17	0	1	0	187	238
LU	08/16/91	10	36	18	74	10	5	0	0	0	144	

Table 15. (cont'd)

Loc	Date	Z	BYT	CYC	DIA	BOS	GAL	RET	EPI	LIM	Tot (mg)	Avg (mg)
TC	08/26/91	30	25	279	1081	302	665	0	26	0	2377	
TC	08/26/91	30	31	282	1074	447	1894	0	55	0	3782	2691
TC	08/26/91	30	26	227	686	234	699	0	42	0	1915	
TC	08/26/91	10	7	14	122	74	52	0	2	0	271	
TC	08/26/91	10	14	10	103	47	11	0	0	0	184	258
TC	08/26/91	10	12	26	124	109	47	0	0	0	318	
MP	08/27/91	30	17	210	1247	69	237	0	122	0	1901	
MP	08/27/91	30	18	221	756	26	251	0	104	0	1376	1661
MP	08/27/91	30	20	227	1085	36	156	0	182	0	1707	
MP	08/27/91	10	5	36	289	20	57	0	6	0	412	
MP	08/27/91	10	0	17	102	6	17	0	5	0	148	263
MP	08/27/91	10	3	22	168	16	20	0	0	0	229	
HO	08/28/91	30	6	101	319	36	55	92	2	0	611	
HO	08/28/91	30	3	92	412	33	114	59	70	0	783	681
HO	08/28/91	30	12	74	393	29	46	89	8	0	650	
HO	08/28/91	10	16	4	24	1	0	0	7	0	52	
HO	08/28/91	10	13	8	47	2	1	0	16	0	87	63
HO	08/28/91	10	12	4	28	1	0	0	5	0	50	
LU	08/29/91	30	7	322	602	55	80	21	31	0	1118	
LU	08/29/91	30	12	427	659	65	50	57	8	0	1277	1085
LU	08/29/91	30	6	191	557	33	30	35	8	0	860	
LU	08/29/91	10	9	4	14	3	0	0	0	0	31	
LU	08/29/91	10	14	5	17	6	0	0	0	0	42	53
LU	08/29/91	10	24	10	43	10	0	0	0	0	87	
LU	09/13/91	30	4	48	781	8	103	1	0	78	1023	
LU	09/13/91	30	3	36	724	6	77	2	0	0	847	789
LU	09/13/91	30	4	109	254	12	85	1	0	33	497	
LU	09/13/91	10	2	7	51	2	9	1	2	0	73	
LU	09/13/91	10	0	5	43	1	2	0	0	0	52	53
LU	09/13/91	10	1	3	25	0	3	0	1	0	33	

Table 15. (cont'd)

Loc	Date	Z	BYT	CYC	DIA	BOS	GAL	RET	EPI	LIM	Tot (mg)	Avg (mg)
LU	10/08/91	30	1	30	241	9	2	0	0	0	283	
LU	10/03/91	30	0	31	472	7	25	0	142	0	678	454
LU	10/03/91	30	0	30	227	7	15	0	121	0	400	
LU	10/03/91	10	4	22	76	6	2	0	6	0	116	
LU	10/03/91	10	1	13	69	4	1	0	12	0	100	83
LU	10/03/91	10	3	6	21	3	0	0	1	0	34	
LU	10/18/91	10	36	20	215	1	0	0	8	0	280	
LU	10/18/91	10	20	47	459	1	0	0	10	0	537	
LU	10/18/91	10	11	49	308	6	0	0	6	0	380	537
LU	10/18/91	10	20	93	813	25	0	0	2	0	952	
LU	11/14/91	30	3	43	603	1	9	0	15	0	674	
LU	11/14/91	30	5	45	361	2	3	0	30	0	445	580
LU	11/14/91	30	1	48	539	1	14	0	17	0	620	
LU	11/14/91	10	5	22	141	1	1	0	4	0	174	
LU	11/14/91	10	6	15	87	0	0	0	3	0	112	163
LU	11/14/91	10	40	11	146	0	1	0	6	0	204	

over 12 times to the greatest average biomass of all stations to 2,691 mg/m^2 on August 26th (Table 15). The large increase in both abundance (Table 3 and Table 4) and average biomass over replicates (Table 15) may illustrate that Grand Traverse Bay lags behind Lake Michigan in the timing of plankton blooms and that this study was able to capture the first population peak of zooplankton in Grand Traverse Bay in the 1991 season. It may also demonstrate that Grand Traverse Bay, like other embayments in Lake Michigan, may have a higher productivity than the other nearshore waters of Lake Michigan.

In 1990, the year previous to the study, nearshore water temperatures at numerous sites on Lake Michigan had already increased above 4 °C by the end of April, and Grand Traverse Bay was still at 4°C throughout the water column in the shallow nearshore waters at the southern end of the bay, where the first warming of the bay would be expected. Warming of Grand Traverse Bay is inhibited by depth and a lack of water movement with the open waters of Lake Michigan (Lauff 1957). Spring mixing, and the subsequent primary and secondary production, occurs much later in Grand Traverse Bay than in Lake Michigan (Lauff 1957).

Ludington Seasonal Biomass Trends

Ludington was the only station that was sampled more than twice and will be used to examine seasonal community biomass trends in 1991.

The 30 meter contour at Ludington showed the greatest seasonal decline in biomass. The first samples taken (on 7/17/91) was the season high average biomass (over replicates) for the 30 meter site with 1523 mg/m^2. The low for Ludington was on October 3rd (454 mg/m^2) and the last sample on November 14th, the average biomass rose slightly to 580 mg/m^2

(Table 15).

The 10 meter contour at Ludington also declined in biomass as the season progressed. An outlier to this declining seasonal trend was the highest average biomass at the shallower station in Ludington on October 18th (537 mg/m^2). On that day, *Diaptomus sp.*, *Cyclops sp.*, *B. longirostris*, and *B. cederstroemi* all greatly increased in abundance from the previous sample at the site just 15 days earlier (Table 3 and Table 4). The increase was too sudden to be explained by growth or reproduction in the cold waters (13 °C), and most likely reflects a combination of offshore and nearshore animals that were concentrated by stormy weather that day, because the 30 meter sample could not be taken that day because of high seas.

The decreasing average biomass in Ludington reflects the decrease in abundance of all species (Table 3 and Table 4). This decline may indicate that the 1991 field season either started at peak productivity or some time after maximum abundance.

In 1974, Duffy (1975) studied the nearshore zooplankton adjacent to the Ludington Pumped Storage facility. The sampling for that study started in June and the numbers of zooplankton ($\#/m^3$) were similar to the present study except the samples in June found about ten times as many *Cyclops sp.* than in any other samples of Duffy's, or this study. This considerable increase to the zooplankton community from a single species suggests that the Duffy (1975) study may have sampled the spring peak of zooplankton abundance and the present study did not (Figure 39).

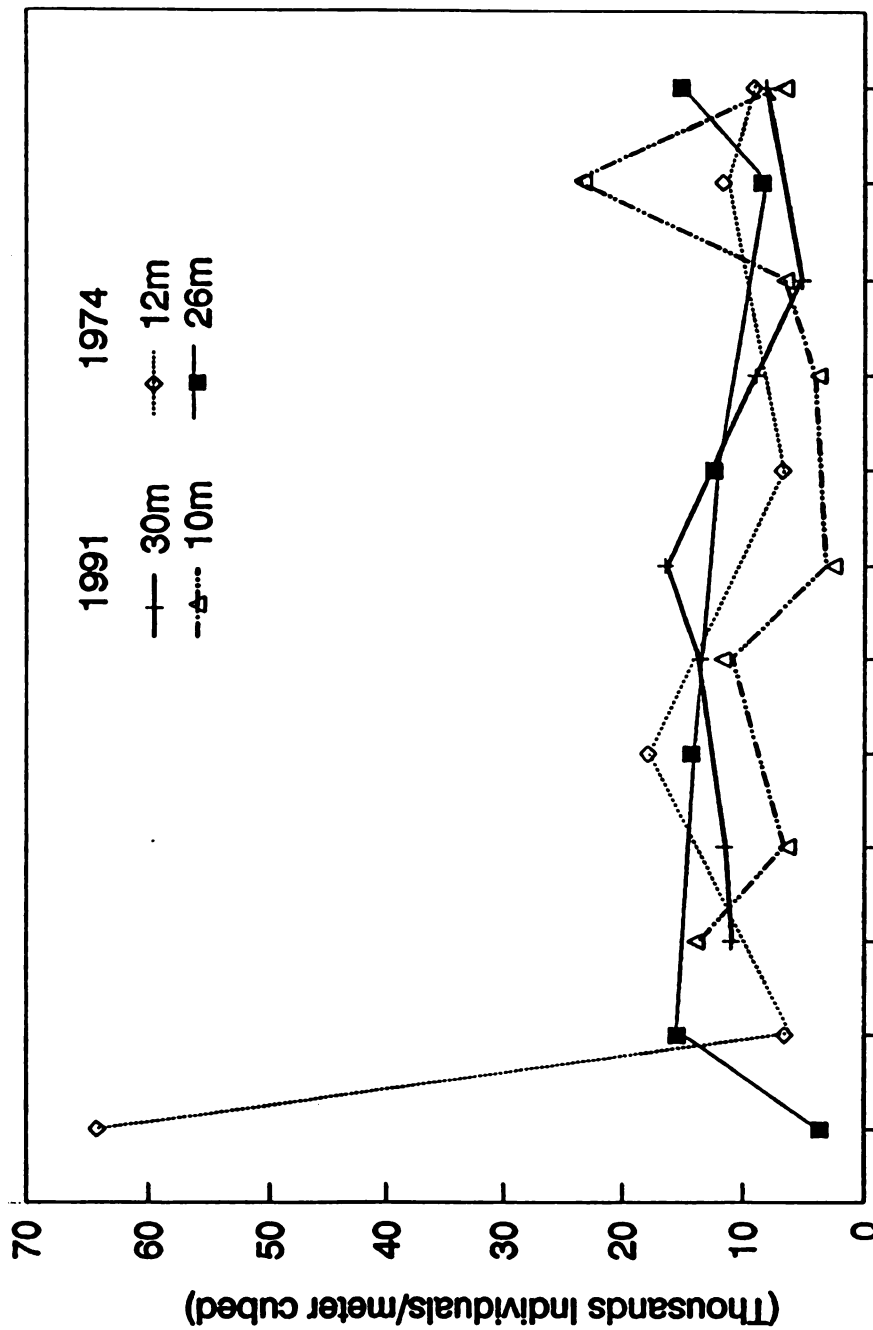


Figure 39. Comparison of Ludington total zooplankton cubic abundances (#/m^3) between this study (1991), and Duffy's (1974).

SUMMARY

Zooplankton Abundance

The zooplankton community was dominated by three species/groups, *Diaptomus sp.*, *Cyclops sp.*, and *Bosmina longirostris*. However, because *Diaptomus* and *Cyclops* were groups of possibly many species, it can only be concluded that the two families, *Diaptomidae* and *Cyclopoidae* and one species, *B. longirostris* dominated.

Abundances of species/groups were found in greater number at the deeper contour even if the zooplankton were measured as individuals^{-3}. When replicates were averaged, and same day comparisons made between depths, the 30 m:10 m ratio was 7.81 for the areal abundance and 2.60 for the cubic abundance.

The daphnids, *D. galeata*, *D. retrocurva*, *D. pulicaria*, and one copepod *Limnocalanus macrurus* were found at much greater abundances at the deeper station.

Species Associations

The proposed species associations utilized the first two PC's. Although the first PC of to both PCA's, #/m^2 and #/m^3, were significantly correlated to both month and depth, the split appears to be more influenced by depth than by month. All of the positively correlated species of PC 1 are more abundant at the 30 meter contour and negatively correlated species, more abundant at 10 meters.

The second PC split was less definitive and involved different degrees of relative abundance as the season progressed and water temperatures became cooler. One group included the species, *D.*

retrocurva and *L. kindti*, (and *E. coregoni* only with the cubic PCA) which were characterized as declining markedly as the season progressed.

The other group was characterized as having abundances that did not decline rapidly with season. All the species except one, *D. pulicaria*, did not decline appreciably as the season progressed. *D. pulicaria* declined precipitously with season. Because of this *D. pulicaria* could not be included in the limnetic persistent species association.

Regarding the attempt to twice split the species into groups, it is deduced that the second split is inconclusive, and only the first split is acceptable.

Differences between the analyses of the areal and cubic data were minor, and because of this the analysis could have been done adequately with one measurement or the other.

Dry Weight Biomass

In almost every case the 30 meter contour total biomass (mg/m^2) is at least 3 times that of the 10 meter contour. A declining seasonal trend is also evident at both contours. The total biomass at the 10 meter stations declines very gradually. The 30 meter contour decline is much steeper (Table 15), and between August 16 (1469 mg/m^2), and October 3 (83 mg/m^2), the decline is sharp.

Grand Traverse Bay Biomass

Peak zooplankton biomass values at Grand Traverse Bay exceeded peak biomasses at both Ludington and Manitou Passage, but were less than the biomass peaks of other nearshore studies (Evans et al. 1980, Roth and Stewart 1973, Gannon 1972) in southern Lake Michigan. This indirectly supports the generalization by Stoermer et al. (1972), that the primary productivity and phytoplankton standing stock in Grand Traverse Bay were

intermediate between high values of inshore waters in Lake Michigan and those of the offshore.

Bythotrephes cederstroemi

In 1987, on Lake Michigan (Lehman 1991), *Bythotrephes* was characterized as more abundant (#/m^2) offshore (>40 m) than inshore. Lehman suggested that a gradient of fish planktivory exists from inshore to offshore, and that this factor may be responsible for the lower abundances nearshore. It is of interest that this new invading species, could not be characterized by PCA as occurring in greater numbers at the deeper stations.

High abundances (>100/m^2) occurred sporadically from mid-July to mid-August, particularly at the deeper station at Ludington, Manitou Passage, and West Grand Traverse Bay (Table 3). High abundances were also found at the shallower station in October and November.

A possible explanation for the similarity of abundances (>100/m^2) between the nearshore of this study and the offshore (Lehman 1991) may be that wave and wind actions concentrate the animals in the nearshore, and sampling was done before the dispersal of the physically developed swarm. In July 1991 samples were taken when waves were 2-4 feet, and winds were out of the southwest at 5-15 knots. Wave and wind action, however cannot explain the high average abundances at 30 meters in mid-August at Manitou Passage (234/m^2 on 8/10) when waves were 1-2 feet and the wind was only 0-5 knots.

Another proposed suggestion may be that in 1987, *B. cederstroemi* might not have reached equilibrium yet, or that the species had not yet increased to the point where the predation by fish could no longer control the population in the nearshore region.

Bythotrephes also could not be characterized as having a seasonal gradient from July to November, or a summer maximum density. Sprules et.al. (1990) reported maximum densities of *B. cederstroemi* in Lake Michigan in 1987 as 29/m^3 during August and September, and Mordukhai-Boltovskaya (1958) reported August maximum densities in Rybinsk reservoir in the USSR as 44.3/m^3. The maximum values at the two depths of this study were found not in mid-summer, but at the beginning and end of the sampling season. Densities were averaged over replicates, and resulted in 20.0/m^3 on July 17 at 30 meters, and 42.6/m^3 on November 14 at 10 meters (Table 4). Densities in August and September were for the most part much lower in these months. Except for mid-August at Ludington, and at 30 m in early August at Manitou Passage and West Grand Traverse Bay, densities were less than 5/m^3.

Also of interest is the large proportion of biomass *Bythotrephes* is estimated to contribute. *Bythotrephes* abundance, on average, was less than 0.1% of the total abundance, yet was fifth highest in average biomass, comprising 8.4% of the total biomass.

Copepod Dominance

Cladocerans, primarily the smaller cladoceran *Bosmina longirostris*, reached summer maximums and dominated over all species in southeastern Lake Michigan (Evans et.al. 1980, Roth & Stewart 1973), and off of Milwaukee Wisconsin (Gannon 1972).

Dominance by *Bosmina* may be the result of a more prolific nearshore phytoplankton population. Nearshore phytoplankton standing stocks were reported to be higher than offshore in southeastern Lake Michigan by Ayers & Siebel (1973), and inshore carbon fixation (measured as mgC/m^3/hr), is twice that of the offshore (Schelske and Callender 1970).

Gannon (1975) described *Bosmina* as the best adapted organism to rapidly respond to nutrient loading conditions in the nearshore waters.

Diaptomus sp. dominated over *Bosmina*, or at the least, copepods dominated over cladocerans in both abundance (Table 3 and Table 4) and biomass (Table 15) at both depths and throughout the season in 1991. In the earlier study (1974) at Ludington (Duffy 1975), this same dominance by copepods also existed. Although *Bosmina* dominated once on July 1, 1974 at the shallower station (12 m), the seasonal peak in Ludington that year was attributed to a large abundance of the copepod *Cyclops sp.*, not *Bosmina*.

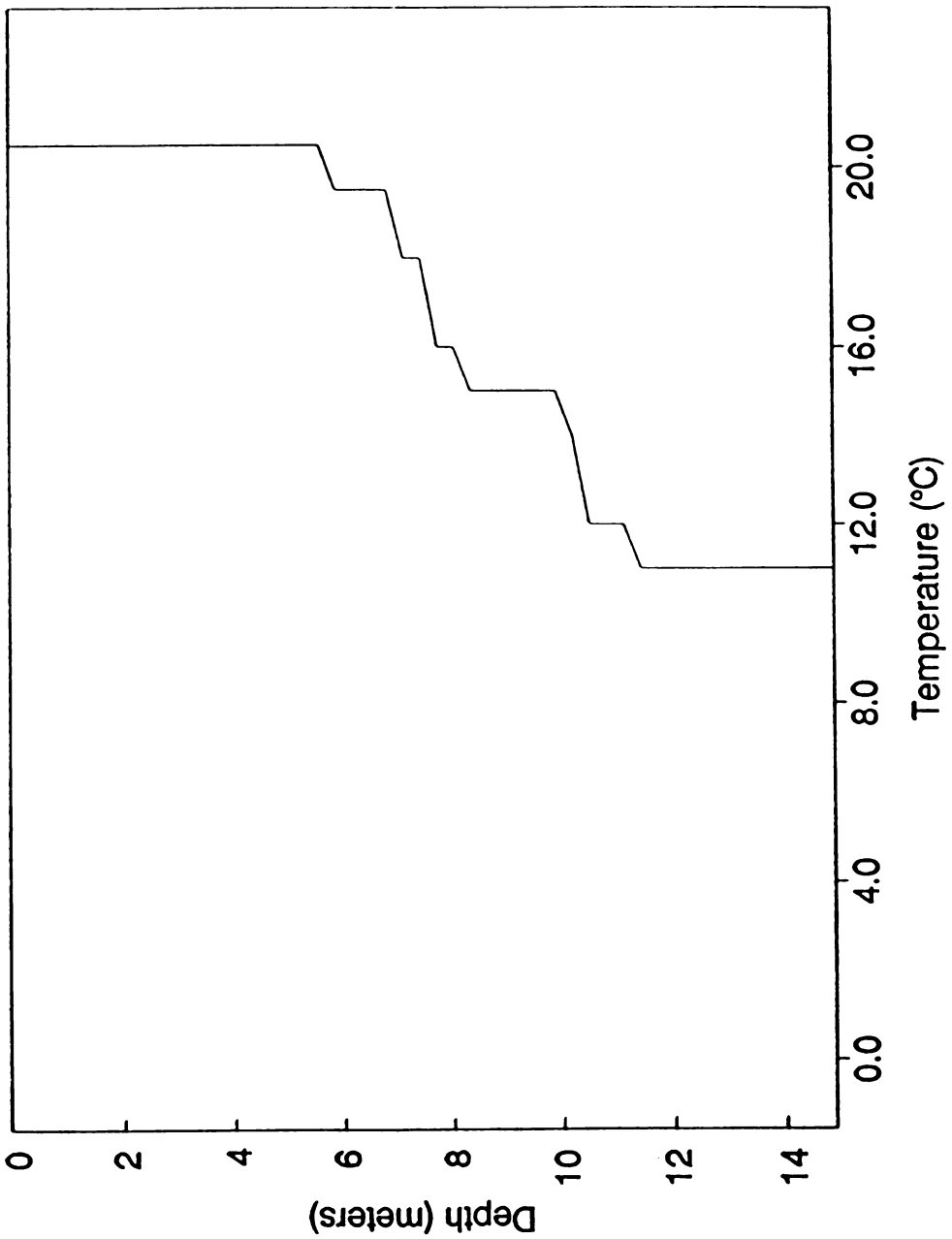
Diaptomids use chemoreception (smell) and are more selective than cladocerans, preferring phytoflagellates over the less edible blue-green and green algae (Sterner 1989). Cladoceran morphology, with their appendages enclosed in a carapace, is a source of interference that limits their selectivity. Cladocerans use their thoracic legs to produce a constant current of water between the valves of the carapace (Pennak 1989), and has a much higher ingestion rate of phytoplankton than do the Diaptomids (Scavia et.al. 1988). Theoretically, these differences in preferences and feeding rates can affect the seasonal succession of phytoplankton (Sterner 1989).

B. longirostris responds to local conditions of temperature and food abundance that controls growth rate and fecundity (it determines a monocyclic or dicyclic reproductive pattern) (Balcer et al. 1984). Therefore, low abundance of phytoplankton will result in lower abundances of cladocerans, particularly *Bosmina*.

APPENDICES

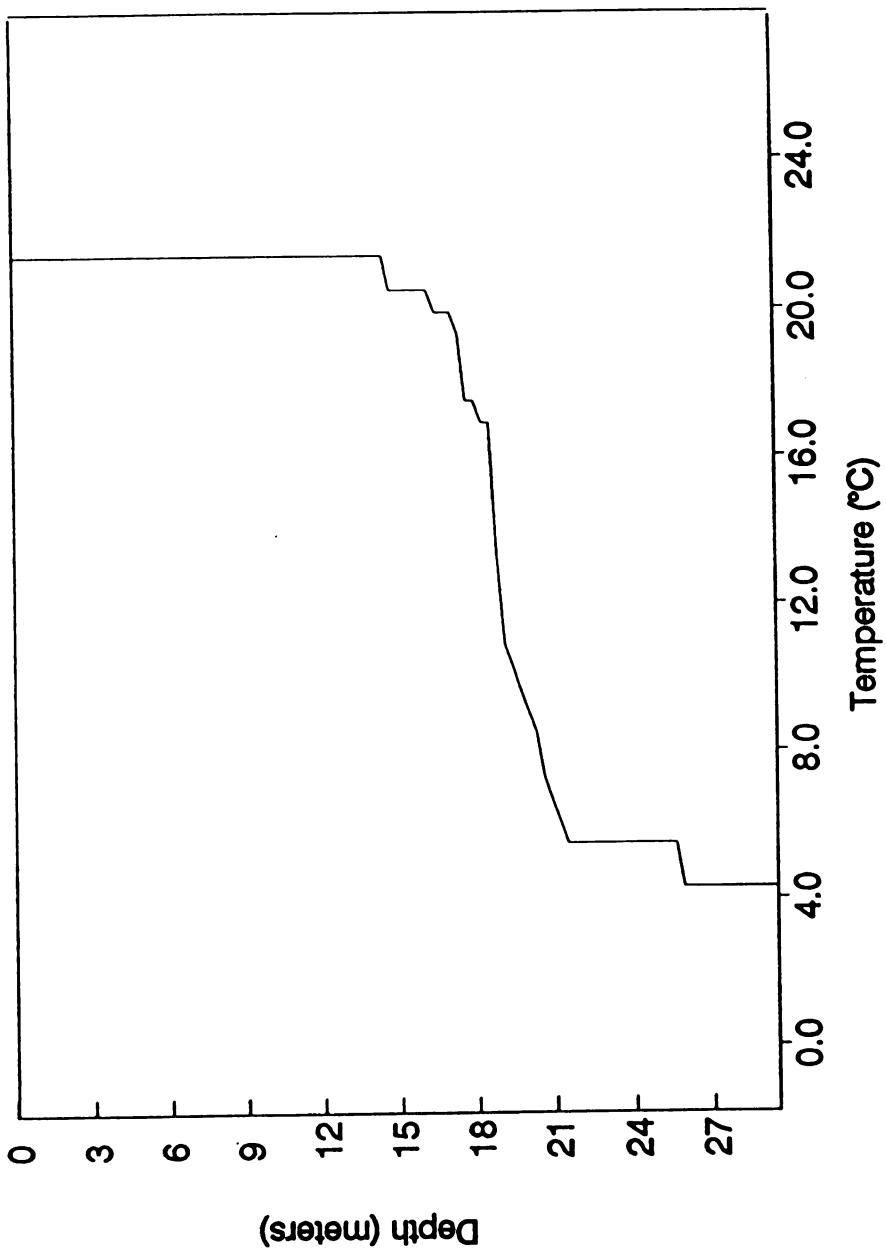
APPENDIX A. Temperature Profiles.

Figure 40. Temperature (°C) profile at 30 meter depth at Ludington on August 16, 1991.



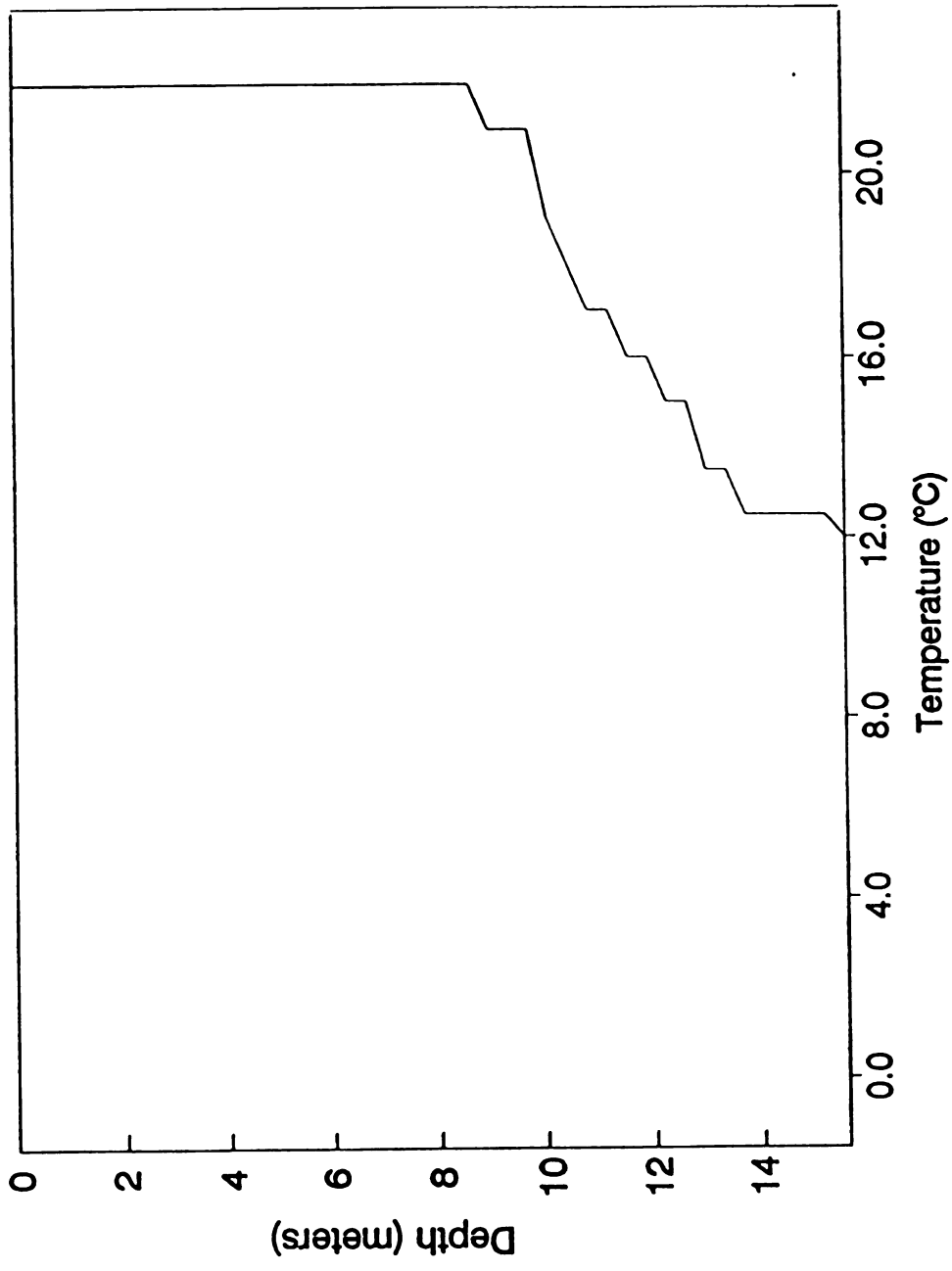
APPENDIX A. Temperature Profiles.

Figure 41. Temperature (°C) profile at 30 meter depth at Ludington on September 13, 1991.



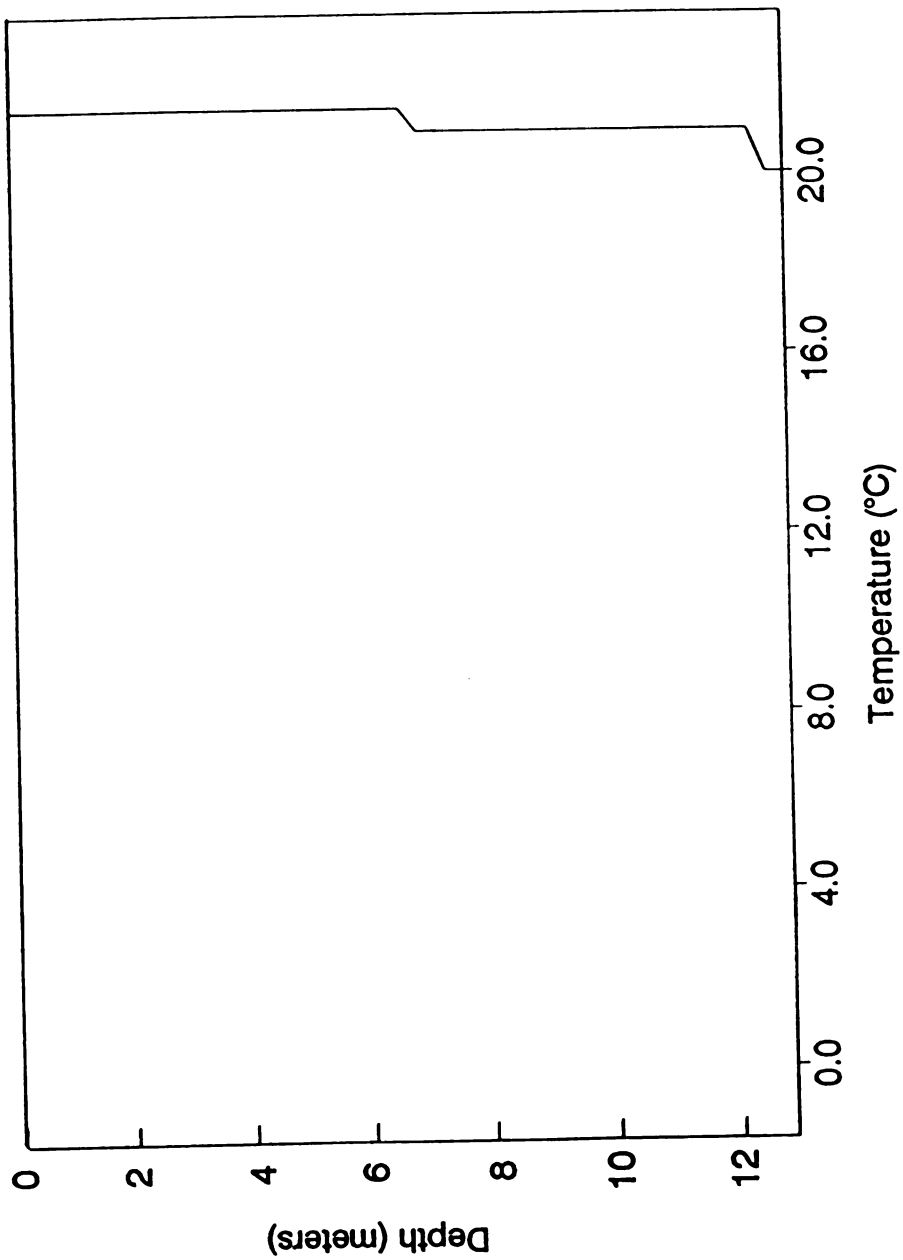
APPENDIX A. Temperature Profiles.

Figure 42. Temperature (°C) profile at 30 meter station (over 110 m of water) at West Grand Traverse Bay on August 26, 1991.



APPENDIX A. Temperature Profiles.

Figure 43. Temperature (°C) profile at 30 meter station at Manitou Passage on August 27, 1991.



APPENDIX B

Table 16. Counts of three instars, neonates, and broken spine animals of Bythotrephes cederstroemi at two depths and four sites in northeastern Lake Michigan in 1991.

				Instar					
Loc	Date	Z	#/m²	3rd	2nd	1st	neonate	broken	total
LU	07/17	30	530	176	107	106	1	36	416
LU	07/17	30	510	160	124	74	17	35	400
LU	07/17	30	736	205	144	128	28	59	578
LU	07/17	10	287	116	49	27	22	27	225
LU	07/17	10	191	63	27	35	8	17	150
LU	07/17	10	189	46	27	50	3	13	148
LU	07/30	30	4	0	0	1	0	2	3
LU	07/30	30	19	11	2	1	0	0	15
LU	07/30	30	14	5	3	2	0	1	11
LU	08/01	10	25	9	1	9	1	0	20
LU	08/01	10	31	12	5	7	0	0	24
LU	08/01	10	22	10	3	1	0	3	17
TC	08/06	30	157	40	35	42	0	6	123
TC	08/06	30	745	245	136	166	7	35	585
TC	08/06	30	284	92	60	52	1	15	223
TC	08/06	10	57	13	12	10	5	7	45
TC	08/06	10	74	16	16	13	4	4	58
TC	08/06	10	8	1	3	0	0	2	6
MP	08/10	30	113	3	0	0	0	1	4
MP	08/10	30	366	3	1	0	0	0	4
MP	08/10	30	223	2	0	0	0	0	2
MP	08/09	10	5	49	17	16	3	6	89
MP	08/09	10	5	195	49	20	1	20	287
MP	08/09	10	3	121	35	13	2	5	175
LU	08/16	30	271	57	55	90	0	12	213
LU	08/16	30	312	95	53	92	0	15	245
LU	08/16	30	282	72	41	84	9	15	221
LU	08/16	10	138	45	28	21	0	11	108
LU	08/16	10	149	48	43	14	0	11	117
LU	08/16	10	111	42	23	10	0	10	87
TC	08/26	30	73	27	13	11	0	5	57
TC	08/26	30	84	35	16	19	0	2	66
TC	08/26	30	80	26	14	12	0	10	63
TC	08/26	10	22	8	5	4	0	0	17
TC	08/26	10	33	16	4	2	0	5	26
TC	08/26	10	32	17	1	3	4	2	25
MP	08/26	30	80	14	9	29	0	2	63
MP	08/27	30	65	19	14	16	0	4	51
MP	08/27	30	74	15	15	21	0	2	58
MP	08/27	10	3	0	1	1	0	0	2
MP	08/27	10	14	5	4	2	0	0	11
MP	08/27	10	11	1	5	1	0	2	9

APPENDIX B

Table 16. (cont'd)

Loc	Date	Z	#/m²	Instar 3rd	2nd	1st	neonate	broken	total
HO	08/28	30	11	0	6	3	0	0	9
HO	08/28	30	18	3	5	4	0	2	14
HO	08/28	30	31	9	6	6	0	2	24
HO	08/28	10	33	8	8	6	0	4	26
HO	08/28	10	43	8	13	9	0	4	34
HO	08/28	10	33	4	14	6	0	2	26
LU	08/29	30	23	8	4	5	0	1	18
LU	08/29	30	36	15	2	10	0	2	28
LU	08/29	30	19	6	3	2	0	4	15
LU	08/29	10	65	31	7	10	0	4	51
LU	08/29	10	37	20	2	6	0	1	29
LU	08/29	10	31	9	5	6	0	4	24
LU	09/13	30	17	2	0	8	0	3	13
LU	09/13	30	25	4	1	12	0	3	20
LU	09/13	30	19	5	2	4	0	4	15
LU	09/13	10	8	2	0	3	0	1	6
LU	09/13	10	1	1	0	0	0	0	1
LU	09/13	10	4	3	0	0	0	0	3
LU	10/03	30	4	0	1	3	0	0	3
LU	10/03	30	1	1	0	0	0	0	1
LU	10/03	30	14	1	1	8	0	1	11
LU	10/03	10	19	1	5	6	0	3	15
LU	10/03	10	39	10	6	12	0	4	31
LU	10/03	10	32	6	7	8	0	4	25
LU	10/18	10	169	70	37	19	0	9	133
LU	10/18	10	381	96	80	44	0	60	299
LU	10/18	10	152	14	43	28	0	32	119
LU	10/18	10	279	27	69	57	0	63	219
LU	11/14	30	113	19	52	11	0	8	89
LU	11/14	30	80	10	35	6	0	11	63
LU	11/14	30	28	2	16	2	0	2	22
LU	11/14	10	103	39	17	6	0	9	81
LU	11/14	10	135	39	40	4	0	17	106
LU	11/14	10	1003	144	240	96	0	276	787

APPENDIX B

Table 17. Temperatures (°C) used to estimate dry weight biomass (μg) of three instars and neonates of Bythotrephes cederstroemi based on Burkhardt's (1991) linear regression of mean dry weight on epilimnetic temperatures in Lake Michigan.

			Instar				
Loc.	Date	°C	3rd	2nd	1st	0	broken
LU	07/17	20.0	550	295	140	70	328
LU	07/30	18.5	470	245	100	70	271
TC	08/06	20.0	550	295	140	70	328
MP	08/10	20.0	550	295	140	70	328
LU	08/16	20.5	575	315	125	70	338
TC	08/26	22.0	625	350	135	70	370
MP	08/27	22.0	625	350	135	70	370
HO	08/28	25.0	780	470	175	70	475
LU	08/29	21.3	600	330	130	70	353
LU	09/13	18.5	470	245	100	70	271
LU	10/03	14.0	265	85	50	70	133
LU	10/18	13.5	230	60	45	70	111
LU	11/14	10.3	100	40	15	70	52

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