

Vegetated versus open water zones: *Daphnia* abundance  
across a structural complexity gradient

BIOS 569: Practicum in Aquatic Biology

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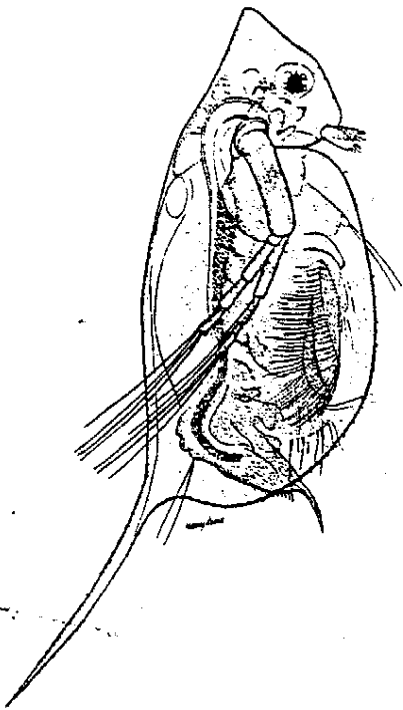


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## Abstract

Shallow eutrophic lakes may exhibit a clear-water stable state, dominated by macrophytes, or a turbid state, dominated by algae. Previous research suggests that the clear-water state in lakes may persist because macrophytes provide a refuge for zooplankton against fish predation. This, in turn, allows large-bodied zooplankton, such as *Daphnia*, to exert stronger grazing pressure on algae. Diel horizontal migration (DHM), in which *Daphnia* hide from predators in vegetated zones during the day and forage in the open water at night, may be an alternative predator avoidance mechanism to diel vertical migration (DVM) in deep lakes, since shallow lakes often lack a hypolimnetic refuge.

Zooplankton were sampled across a macrophyte density gradient in Kickapoo Lake, a eutrophic, highly vegetated lake at the University of Notre Dame Environmental Research Center. During the day, *Daphnia galeata* was found in association with the lower density of macrophytes at the edge of the littoral zone, where the habitat is rapidly changing from vegetated to open water. At night, *D. galeata* density increased linearly with distance from shore.

*Daphnia* show predator-mediated use of macrophytes as a refuge (Lauridsen and Lodge 1996). The congregation of *D. galeata* at the edge zone during the day may be explained by predator-induced migratory behavior. As an ecotonal habitat, the edge of the littoral zone offers a potential refuge from fish predation, complete with access to algae available in the open water. Occupation of this habitat may decrease mortality of *Daphnia* without increasing food limitation. These results are consistent with the predictions of *Daphnia* using DHM as an alternate predation avoidance mechanism in shallow lakes.

## Background

Eutrophication, the anthropogenic enrichment of natural waters with nutrients, is a serious threat in freshwaters today (Edmondson 1992). Traditionally, limnology has focused on reducing external nutrient inputs to deter eutrophication of large, deep lakes (Moss et al. 1997). Yet, most of the world's lakes are shallow (Edmondson 1992), and serve as important habitats for fish and waterfowl. Shallow lakes have the potential to be highly productive due to increased susceptibility to phosphorous loading (Jeppesen 1997, Moss et al. 1997, Beklioglu and Moss 1996, Schindler 1974, Schindler 1977). However, due to internal recycling of phosphorous, external nutrient reduction does not often deter eutrophication (Jeppesen 1997). The biotic interactions in shallow lakes between fish, zooplankton, macrophytes and algae play an important role in determining lake water quality.

Two alternative stable states, turbid and clear-water, have been observed in shallow lakes: a turbid state dominated by algae and small planktivorous fishes, and a clear-water state dominated by submerged macrophytes and large-bodied zooplankton (Scheffer et al. 1993). Several mechanisms are responsible for the increased clarity in the presence of macrophytes, which provide a multitude of ecosystem functions (Carpenter and Lodge 1986). Submerged macrophytes tend to lessen resuspension of sediments and compete with algae, especially for light. Additionally, Scandinavian and European research propose that *Daphnia* can hide from planktivorous fish among aquatic macrophytes (Lauridsen et al. 1997, Timms

and Moss 1984, Scheffer et al. 1993). The presence of macrophytes in shallow lakes has been shown to affect fish predation on the zooplankton community, which in turn relates to the turbidity of lakes (Savino et al. 1992, Jacobsen et al. 1997, Schriver et al. 1995). At PVI (percent volume infested) macrophyte densities of 15-20%, fish predation had less of an impact and large-bodied *Daphnia* were able to persist (Schriver et al. 1995). In the absence of macrophytes, Schriver et al. (1995) found a lower biomass of zooplankton dominated by copepods, and a higher biomass of algae.

In addition to macrophyte presence, fish predation has a strong effect on zooplankton communities (Savino et al. 1992, Jacobsen et al. 1997). Through cascading trophic interactions, large piscivores depress planktivore populations, which then reduces predation pressure on large-bodied zooplankton (Jacobsen et al. 1997, Carpenter et al. 1985). The force of increased predation on planktivores allows large-bodied zooplankton, such as *Daphnia*, to exert stronger grazing pressure on algae, depressing blooms. Size-selective predation on the zooplankton community disproportionately impacts larger species (i.e. *Daphnia*), which are more efficient grazers (Brooks and Dodson 1965). Thus, when planktivores are abundant, *Daphnia* are rare. Smaller-bodied zooplankton (i.e. *Bosmina* and calanoid copepods) increase in abundance in the absence of *Daphnia*. However, these smaller zooplankton do not exert as powerful a predation pressure on algae, with the end result often being blooms of algae. Top-down forces in lakes cascade through the food web to affect the productivity and biomass of phytoplankton (Carpenter

et al. 1985). Thus, lakes containing piscivores and *Daphnia* differ substantially from lakes where planktivores occupy the top trophic level. The presence of piscivores has both direct and indirect effects which influence zooplankton (Jacobsen et al. 1997).

In order to avoid fish predation, large-bodied zooplankton such as *Daphnia* exhibit diel vertical migration (DVM) in deep lakes (Lampert 1993). In DVM, *Daphnia* and other large zooplankters migrate to deep, dark hypolimnetic waters during the day and return to surface waters at night to feed (O'Brien 1979). However, in shallow lakes that do not thermally stratify, a hypolimnetic refuge may not exist (Moss et al. 1997). In shallow lakes, diel horizontal migration (DHM) has been suggested as an alternative predator avoidance strategy to DVM in deep lakes (Lauridsen and Buenk 1996). Instead of seeking a depth refuge, zooplankton may migrate towards vegetated areas where they are less visible to predators by day, and move into the open water to graze by night. Here, in the littoral zone, submerged vegetation may provide refuge from fish predation to large-bodied zooplankton (Timms and Moss 1984, Lauridsen and Buenk 1996, Scheffer et al. 1993, Stansfield et al. 1997). Protected from the full impact of predation, *Daphnia* may be able to exert a larger grazing pressure on algae, which helps to maintain clear-water conditions. Conversely, in the absence of macrophytes, there is increased predation on large zooplankton and less grazing pressure on phytoplankton, often resulting in turbid conditions in the lake (Scheffer et al. 1993).

Limnologists have not often associated *Daphnia* with vegetated

areas, even noting an avoidance of macrophytes (Hasler and Jones 1949). Potentially, there are costs associated with vegetated habitats such as reduced food availability, or greater susceptibility to littoral zone predators. However, the potential benefits of macrophyte refugia could outweigh the costs.

In laboratory experiments, Lauridsen and Lodge (1996) showed that *Daphnia magna* moved into areas occupied by macrophytes in the presence of fish or fish odor. Without the presence of fish, daphnids avoided the plants. Thus, *Daphnia* may respond to predators in shallow lakes by migrating to vegetated areas. In the absence of a hypolimnetic refuge from visual predators, such a response may be adaptive. Daphnids that took refuge in macrophytes may show increased survival and reproduction over daphnids that continued to avoid macrophytes. The littoral zone could also offer increased benefits to reproduction, such as warmer temperatures.

#### Research Goal

Lauridsen and Buenk (1996) found evidence of DHM in their study of two shallow Danish lakes. DHM, as a shallow lake alternative to DVM, has not been tested in North America, and background data is necessary for documenting the occurrence of DHM in North American shallow lakes. The goal of this project was to examine zooplankton taxonomic composition and abundance across a gradient of submerged macrophyte densities. Examining how zooplankton vary spatially from vegetated, near-shore areas to open

water will lend insights into whether large-bodied *Daphnia* are employing DHM as an alternate predation avoidance strategy in shallow lakes.

### Study Site

Zooplankton and macrophyte assemblages were sampled in Kickapoo Lake, located at the University of Notre Dame Environmental Research Center (UNDERC) in the Upper Peninsula of Michigan. Kickapoo Lake is a shallow, north temperate lake, with a highly developed littoral zone. Common macrophytes include *Potamogeton amplifolius*, *P. robbinsii*, and *Ceratophyllum demersum*. Kickapoo Lake is moderately sized, with a surface area of 15 acres (6.1 ha). The lake is roughly circular in shape with a maximum depth of 3.25 meters. Temperature profiles do not change substantially after a depth of 1 m (UNDERC guide). However, the dissolved oxygen quickly drops to 0 after 2.5 m. The sediments of the lake are quite flocculent (personal observation). Kickapoo Lake does support a wide range of piscivores due to continual stocking. However, planktivores, such as crappie, are also present.

### Materials and Methods

Kickapoo was sampled for diel zooplankton composition and abundance, macrophyte species composition and relative abundance, and percent volume infested by macrophytes (PVI). PVI is an expression of macrophyte density taken by dividing the height of the plant by the depth of the water column (Maceina and Shireman 1980). Samples were taken at

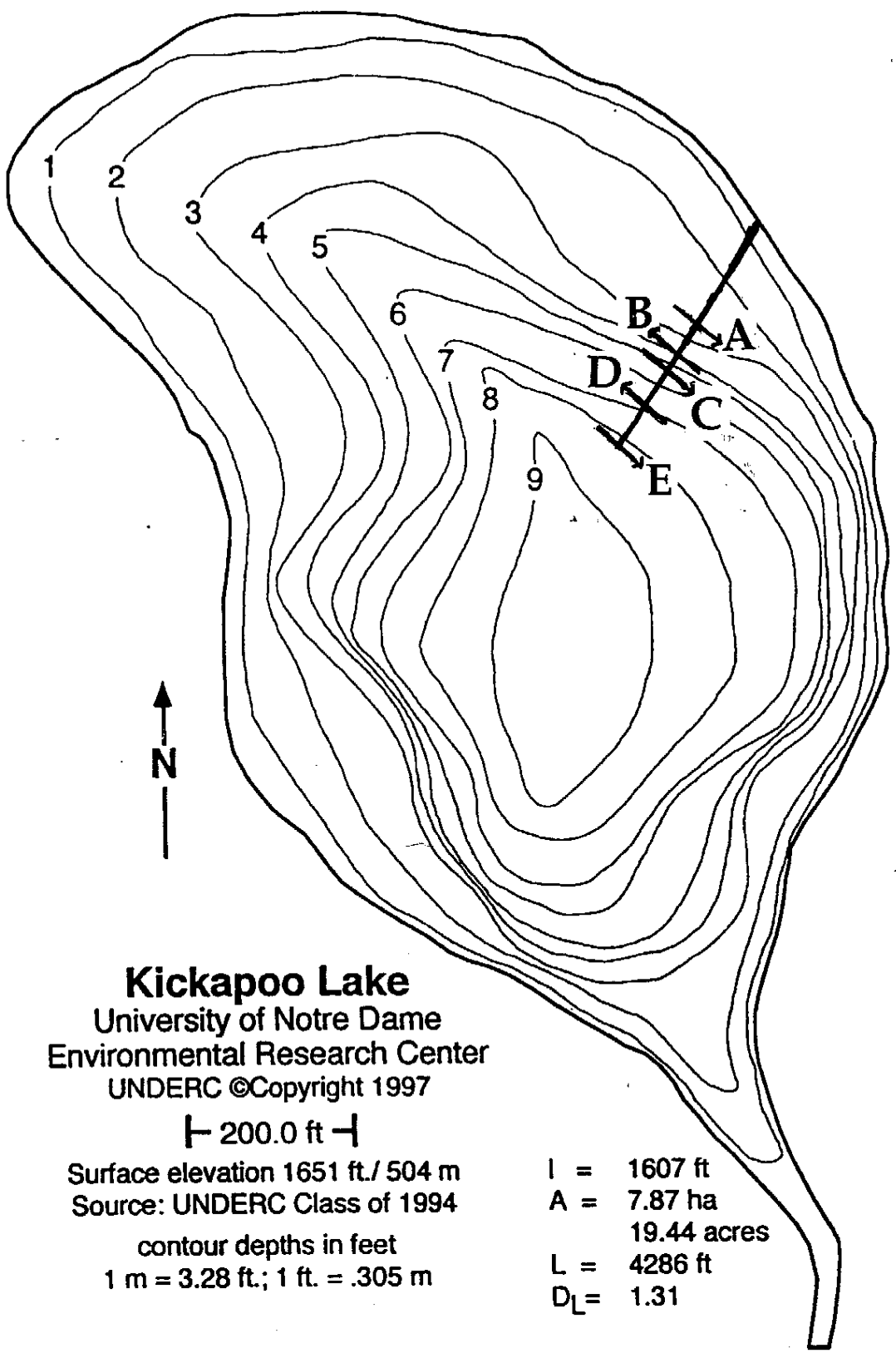


noon and midnight along a transect established in the most dense bed of submerged macrophytes.

A tube sampler constructed as described by Knoechel and Campbell (1991) was used in both the littoral and pelagic zones in order to sample zooplankton quantitatively among submerged macrophytes and in the open water. The sampler filters the volume of water within the tube through an 80  $\mu\text{m}$  zooplankton net with a collection bucket attached to the end. The volume of water sampled was calculated from the length of tube submerged during sampling and the radius of the tube,  $5.74 * 10^{-3}$  m. Error in this volume is due to small leaks in the dryer box and tube, and water leaking from the hinges of the moving flap. Nuts and bolts were attached to weight the sampler, and nails were fastened to the moving flap so that it would fall shut when descent of the sampler halted. Ropes were attached to facilitate sampling from a boat in the open water.

The transect was established on the northeast shore of Kickapoo Lake (Figure 1). One end was tied to a PVC pipe driven into the ground on shore, and a milk gallon float (which was kept in place by a brick anchor) marked the far end of the transect. The transect was established perpendicular to the shoreline, over dense beds of *P. amplifolius*, *P. robbinsii*, and *C. demersum*. Due to the length of rope available and the site selected, the transect extended well into the open water but did not appear to reach the deepest point in Kickapoo (Figure 1).

Sampling sites along the transect were established based on the density of submerged macrophytes. Site A (26.3 m from shore) was selected several meters inside the vegetated area, and sites B (33.9 m from shore) and C (36.0 m from shore) straddled the edge of the vegetated area with two meters separation. Site E (77.7 m from shore) was selected in the open water at the end of the transect, while Site D (57.4 m from shore) was selected halfway between C and E (Figure 1). Each site was marked with a piece of flag tape labeled with its designated letter and tied securely to the rope. The distance of each site from shore was measured after sampling was completed and the transect removed from the water.



**Kickapoo Lake**  
 University of Notre Dame  
 Environmental Research Center  
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┌ 200.0 ft ─┘

Surface elevation 1651 ft./ 504 m  
 Source: UNDERC Class of 1994  
 contour depths in feet  
 1 m = 3.28 ft.; 1 ft. = .305 m

l = 1607 ft  
 A = 7.87 ha  
 19.44 acres  
 L = 4286 ft  
 D<sub>L</sub> = 1.31

**Figure 1**

Bathymetric map of Kickapoo Lake with perpendicular transect and five sampling locations indicated. Sites A is located several meters into the vegetated zone. Sites B and C sample the transitional zone between vegetation and open water, with less than 2 m separation. Sites D and E are located in open water, with site E approximating the maximum depth of the lake.

*Abiotic Conditions:*

Temperature and pH readings were taken at each sample site at noon and at midnight. Secchi disc transparency and light readings were also taken at each site at noon. The weather conditions when samples were taken, on July 2, 1997, were overcast and rainy, so the light on the day of sampling may not be characteristic. Additional light readings, pH, temperature and Secchi disc readings were taken under sunny conditions in order to better characterize the sites. Temperature readings were taken using the Hach conductivity meter. pH readings were taken with a hand-held pH meter, and light readings with a Li-Cor datalogger. Temperature and pH readings were taken just under the water surface, and the submerged light reading was taken at a depth of 1 m, corresponding to the approximate sample depths. Full temperature profiles according to depth were not taken due to technical difficulties.

*Estimating PVI and percent cover:*

At each vegetated site (A, B, & C), the approximate percent cover by each macrophyte species present and the approximate height of the plant and depth of water were determined. Macrophyte samples were taken and identified in lab using Fassett (1940) and Prescott (1980). The percent cover by each species was estimated while snorkeling over the area surrounding the site. The height of each plant species was measured using a rope marked in 10 cm increments with a float at one end and a weight at the other end. Where possible, three plants of the same species were measured to find an

average height. The water depth was measured at each site using a 3 m PVC pipe marked off in 5 cm increments. PVI was calculated by dividing the average plant height by the water depth for each species found at each site.

*Zooplankton sampling:*

Zooplankton samples were taken using the sampler built as described in Knoechel and Campbell (1991). The dryer tube was marked off in 0.5 m increments, and the depth of the sample was measured from the mark closest to the surface of the water. An attempt was made to sample consistently at a depth of 1 m, without allowing sediment into the sample. Samples were preserved in 50 mL of 4% sugared buffered formalin. The formalin preservative consisted of 2 g Borax, 60 g sucrose, 600 mL 10% buffered formalin phosphate and 400 mL distilled water in 1 L (Haney and Hall 1973). The preservative was diluted approximately 1:1 by the samples in the field. Thus, the final concentration was 2% formalin, 1 g Borax and 30 g sucrose per L. Samples were placed in 500 mL plastic sample bottles, according to the following labeling scheme. Kickapoo Lake was designated KI. Each sample was identified by KI, its site along the transect (A-E), replicate number (1-3) and time (N= 12:00, M= 0:00), and the date of the sample. Thus, KI B3 N 7.2.97 designated the third sample at site B in Kickapoo, at 12:00 PM on July 2. A paper label was placed inside the sample bottle, and lab tape labels were placed on the side of the bottle.

*Zooplankton analysis:*

Zooplankton samples were analyzed for taxonomic composition and abundance under a dissecting microscope. A compound microscope with an ocular micrometer was used for taxonomic resolution when necessary. Dichotomous keys in Thorp and Covich (1991) and Baker et al. (1984) were consulted for identification of zooplankton. The entire sample was emptied into a gridded petri dish, and six 1 cm<sup>2</sup> grids were selected using a random number table. The number of representatives of each taxon per grid was recorded and used to calculate the density of that taxon per liter. The volume of each sample was calculated from the volume of a cylinder of radius equal to 0.005 m (radius of the sampler tube) and height equal to the sample depth in meters [ $\pi(0.005)^2 \times \text{sample depth}$ ]. Sample volume was converted from cubic meters to liters using the relationship [1000 L=1 m<sup>3</sup>]. Thus, the volume sampled for a sample depth of 1 m was 0.1 L. The total number of individual zooplankton in a sample was calculated for all taxa present [average number of organisms (cm<sup>2</sup>)<sup>-1</sup> \* area of petri dish in cm<sup>2</sup>]. The total number of each taxon counted in the sample was then divided by the volume sampled to generate its concentration, in organisms L<sup>-1</sup>. A mean of the concentrations of three replicate samples at each site was determined for densities of all taxa at each sampling site and period (noon or midnight). Juvenile and adult *Daphnia* concentrations were combined in order to calculate one *Daphnia* density.

*Expected results:*

1. Large-bodied zooplankton, such as *Daphnia*, would be found in greater abundances among macrophytes during the day and in the open water zone at night.
2. A preference among daphnids for the edge of the vegetated area is predicted by Lauridsen and Buenk (1996). The edge zone provides the benefits of macrophyte refuge against fish predation and availability of algae in the open water nearby. Thus, a congregation at Sites B and C may be expected.
3. Smaller cladocerans such as *Bosmina* would be found in both vegetated and open water zones. *Chydorus* and *Ceriodaphnia* are expected to associate with the littoral zone more frequently than the open water. Their distributions should be determined more by taxonomic preferences for habitat types than by predation pressure.
4. Other zooplankton groups, including copepods and rotifers, would be present in both littoral and open water zones. As in the small cladocerans, copepod and rotifer distributions should be less dictated by size-selective predation.

## Results

### *Abiotic conditions:*

Data gathered over the course of sampling and analysis at each site included Secchi depth, pH, temperature, and light readings, macrophyte PVI and approximate percent cover by species, and zooplankton densities. Secchi transparency and light readings were taken at each site during the noon sampling period, while pH and temperature were taken at each site at noon and midnight. Weather conditions during the noon sample period on July 2 were overcast and rainy, which may have affected these data. Table 1 presents data taken at transect sampling sites A to E. Secchi depth values indicated that light penetrated to the sediments in the vegetated areas (sites A, B, C). Temperature and pH did not vary greatly between sites. The open water values were quite similar to the littoral zone values at noon, while the open water pH values were slightly more neutral than the littoral zone values at midnight. However, this magnitude of change is unlikely to affect fish-zooplankton-macrophyte interactions (Beklioglu and Moss 1995). Values taken during sunny weather conditions showed the same essential relationships.



## Abiotic Conditions at Sites A-E during sampling

Sample Site	A	B	C	D	E
Secchi depth (m)	1.4	1.5	1.5	1.75	2.0
Maximum depth at site (m)	1.65	2.0	2.0	2.1	2.4
Light ( $\mu\text{M}$ ) Terrestrial	318.8	392.2	283.1	140.3	317.8
Light ( $\mu\text{M}$ ) 1 m depth	13.54	9.15	24.1	-60.53	5.26
pH (noon)	6.3	6.4	6.6	6.5	6.5
pH (midnight)	6.4	6.4	6.5	6.9	7.1
Temperature ( $^{\circ}\text{C}$ ), noon	21.6	22.0	21.7	21.2	21.7
Temperature ( $^{\circ}\text{C}$ ), midnight	20.3	21.1	20.3	20.0	20.0

Table 1: Secchi depth, light readings (terrestrial and submerged), pH and temperature data from Kickapoo Lake sampling sites A-E.

*Macrophyte Assemblages:*

The littoral zone of Kickapoo Lake supports a dense growth of macrophytes. Sampling sites A, B, and C were dominated by *Potamogeton amplifolius*, *Potamogeton robbinsii*, and *Ceratophyllum demersum*.

Approximate percent cover, PVI, and macrophyte species composition are given in Table 2 for sites A, B, and C. The overall PVI for each site is the average PVI weighted by percent abundance of each species. Thus, total PVI at sites A, B, and C is 54%, 11%, and 5%, respectively.

The difference in PVI among the three sites characterizes macrophyte abundance in the littoral (Site A) and edge zones (Sites B and C). Overall, PVI fell sharply in the littoral zone border area.

#### Macrophyte Assemblages

Sample Site	Macrophyte Species	approximate percent cover	PVI (%)
A	<i>P. amplifolius</i>	35	56
A	<i>P. robbinsii</i>	65	33
A	<i>C. demersum</i>	15	87
B	<i>P. robbinsii</i>	40	21
B	<i>C. demersum</i>	7	37
C	<i>C. demersum</i>	10	54

Table 2: Approximate percent cover and PVI for macrophyte species at sampling sites A, B, and C.

#### *Zooplankton composition:*

*Daphnia galeata mendotae* was the largest cladoceran species present in the samples from Kickapoo. Other zooplankters included *Bosmina longirostris*, cyclopoid copepods, calanoid copepods, nauplii, *Keratella*, *Brachionus*, *Trichocera*, *Ceriodaphnia*, *Chydorus*, and *Diaphanosoma*. Several rare forms were observed in occasional samples. These included *Eurycercus*, *Asplanchna*, and *Kellicottia*. Kickapoo Lake supports a diverse zooplankton fauna with great variance in patterns of abundance and distribution.

#### *Zooplankton abundance:*

According to DHM theory, *Daphnia* was expected among the macrophytes during the day and in the open water at night (Expected Result

1). The greatest noontime *Daphnia* density was at PVI slightly greater than 10% (Site B). The greatest density of *Daphnia* at midnight was in areas with PVI less than 10%. Noon and midnight concentrations of *Daphnia galeata* were plotted against PVI to look for relationships between time and association with macrophytes (Figure 2). As predicted, *Daphnia* were found only near macrophytes during the day, while the highest *Daphnia* density was observed in open water sites D and E at night.

At noon, *Daphnia* was only found in association with macrophytes at Site B, which was located at the edge of the vegetated area with PVI of 11%. No *Daphnia* were observed at Sites A, C, D, and E during the day. Site C had very few macrophytes, one of which was *Utricularia*, a carnivorous submerged macrophyte which probably depressed *Daphnia* numbers. The congregation of *Daphnia* at the edge of the littoral zone agrees with Expected Result 2 and the findings of Lauridsen and Buenk (1996). The density of *D. galeata* at noon and midnight was also plotted against distance from shore (Figure 3). A linear regression was done for *Daphnia* midnight concentrations ( $R^2=0.8559$ ), in which density increased linearly from shore to open water at midnight.

Paired t-tests were performed on the noon and midnight *D. galeata* concentrations at each sampling site (Figure 4). Due to the high variation within samples, no significant differences between noon and midnight were detected (Site A,  $p=0.18$ ; Site B,  $p=1$ ; Site C,  $p=0.23$ ; Site D,  $p=0.12$ ; Site E,  $p=0.25$ ). A 2-way ANOVA was performed to test for differences between sites

Figure 2:

### Daphnia Density per Macrophyte Density

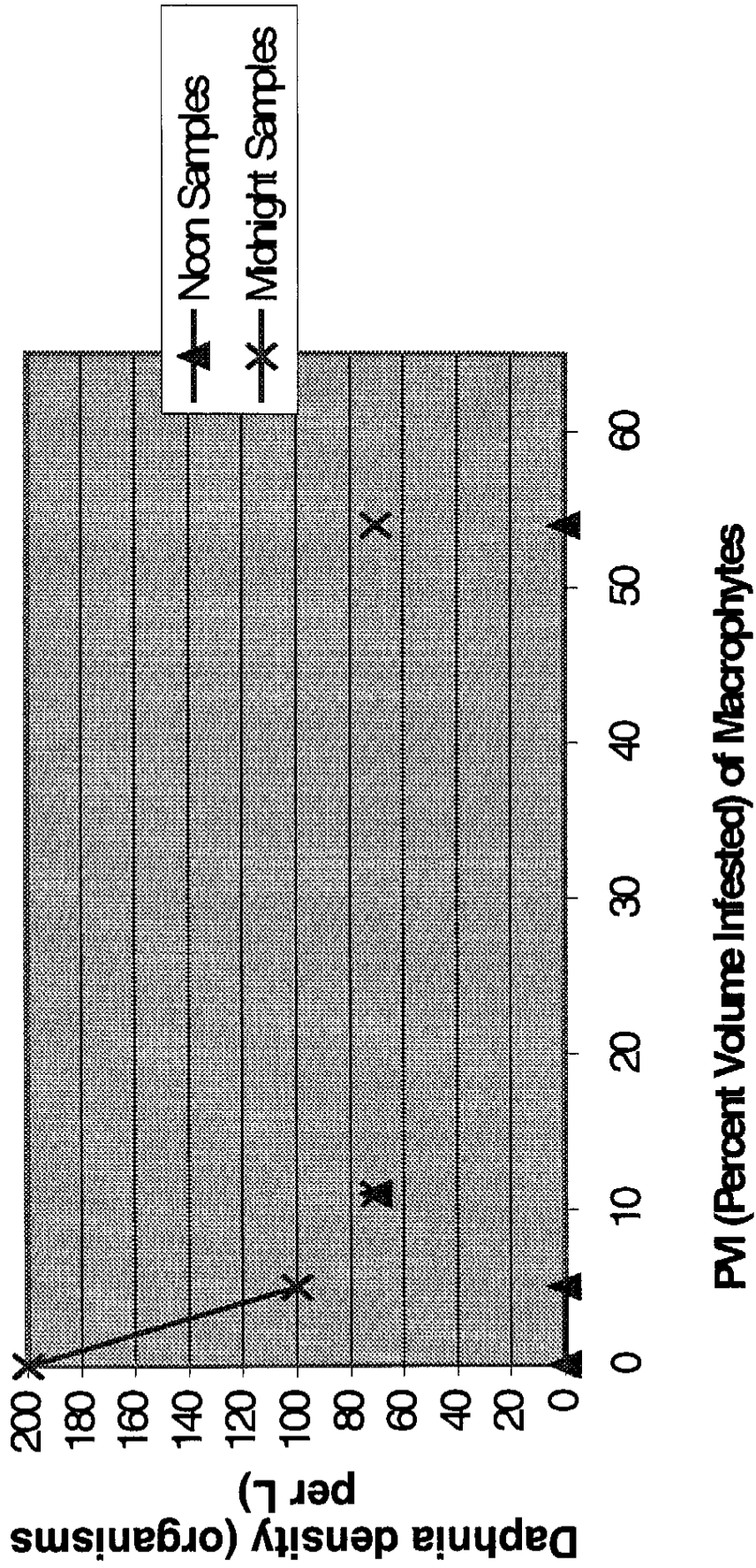
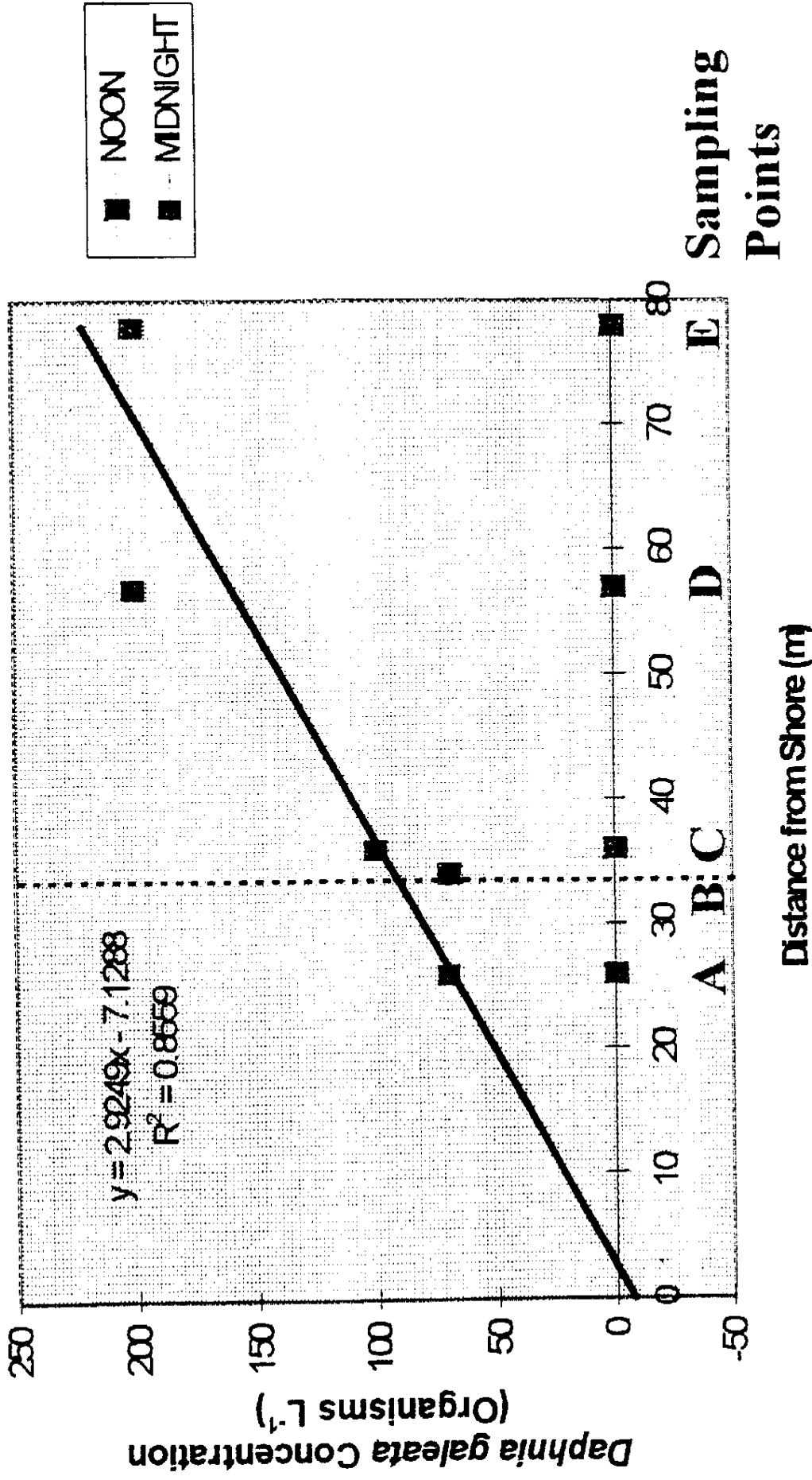


Figure 2: *D. galeata* density at noon and midnight, as a function of macrophyte abundance (PVI). Triangles represent noon points, and Xs represent midnight.

Figure 3:

### *Daphnia galeata* Abundance versus Distance from Shore



----- = Macrophyte Edge Zone

Figure 3: *D. galeata* density versus distance from shore. To the left of the dotted line macrophytes were present. Both noon and midnight points are shown. A linear regression was performed on midnight *Daphnia* abundance resulting in  $R^2=0.8559$ .

Figure 4:

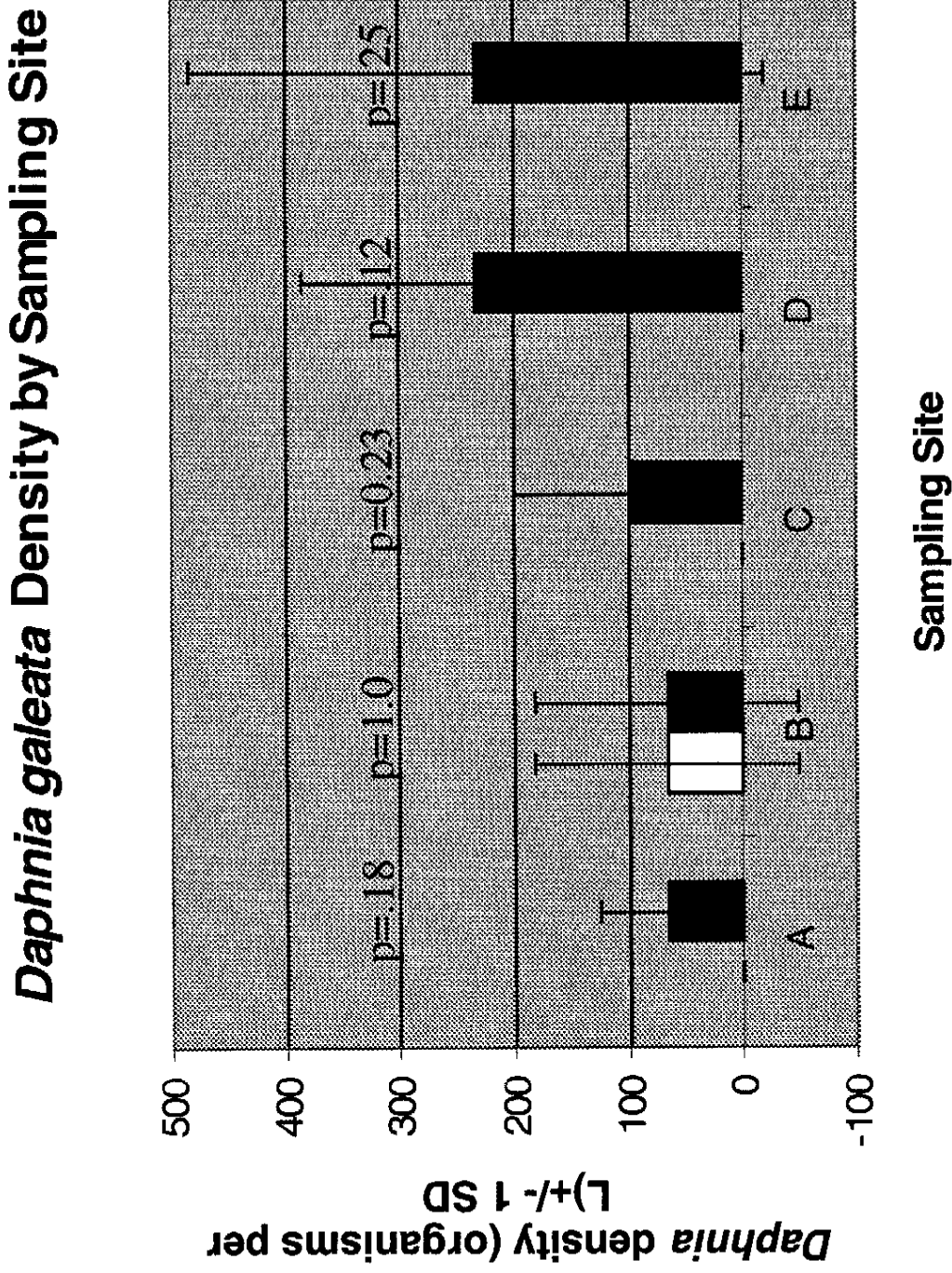


Figure 4: *Daphnia* density by sampling site for both day and night. p-values above bars are a result of paired t-tests. White bars represent noon sampling, dark bars are midnight.

for both noon and midnight *D. galeata* abundances. Site did not have a significant effect on variation in *Daphnia* abundance ( $F=0.697$ ,  $p=0.603$ ), but time was found to have a significant effect ( $F=9.50$ ,  $p=0.006$ ). Results of the ANOVA and Tukey's MCT showed that noon variation in *D. galeata* abundance was significantly different from midnight. The lack of difference among sites may be due to the generally low densities of *D. galeata* and high variation among replicates. These findings are consistent with predictions for diel habitat selection by *Daphnia*. More sampling dates or increased replication may improve confidence in diel differences at individual sample sites in future studies.

The density of other zooplankton groups by sampling site is shown in Figures 5-9. T-tests were performed for each taxa at each sampling site to detect differences in distributions between vegetated and open water zones (Table 3). Figure 5 represents *Bosmina longirostris*. Figure 6 represents abundances of the other small cladocerans. *B. longirostris* was found in greater abundance than *D. galeata*, but it did not show a pronounced trend in its use of the littoral and pelagic habitats (Figure 7). Likewise, the smaller cladocerans *Diaphanosoma*, *Ceriodaphnia*, and *Chydorus* did not show clear diel preference of habitats. *Chydorus* densities, however, were slightly larger at vegetated Sites A and B. Major differences between noon and midnight were not detected by t-tests (Table 3). The spike in *Ceriodaphnia* density at site A during midnight may be due to contamination of one site A sample with

Figure 5:

*Bosmina longirostris* Density by Sampling Site

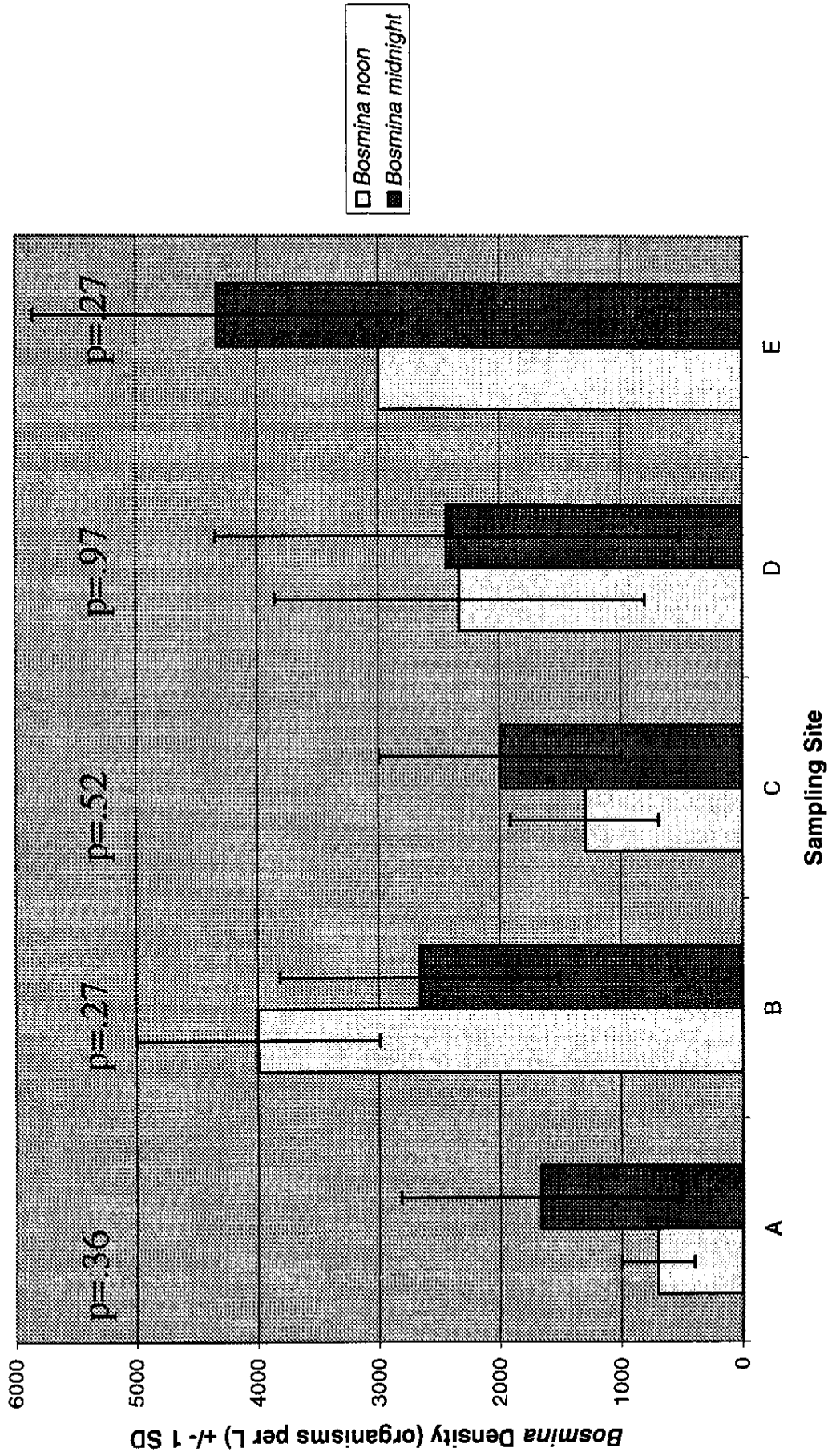


Figure 5: *Bosmina* density by sampling site for both day and night. p-values above bars are a result of paired t-tests. Light bars show noon samples, dark bars represent midnight.



Cladoceran Density by Sampling Site

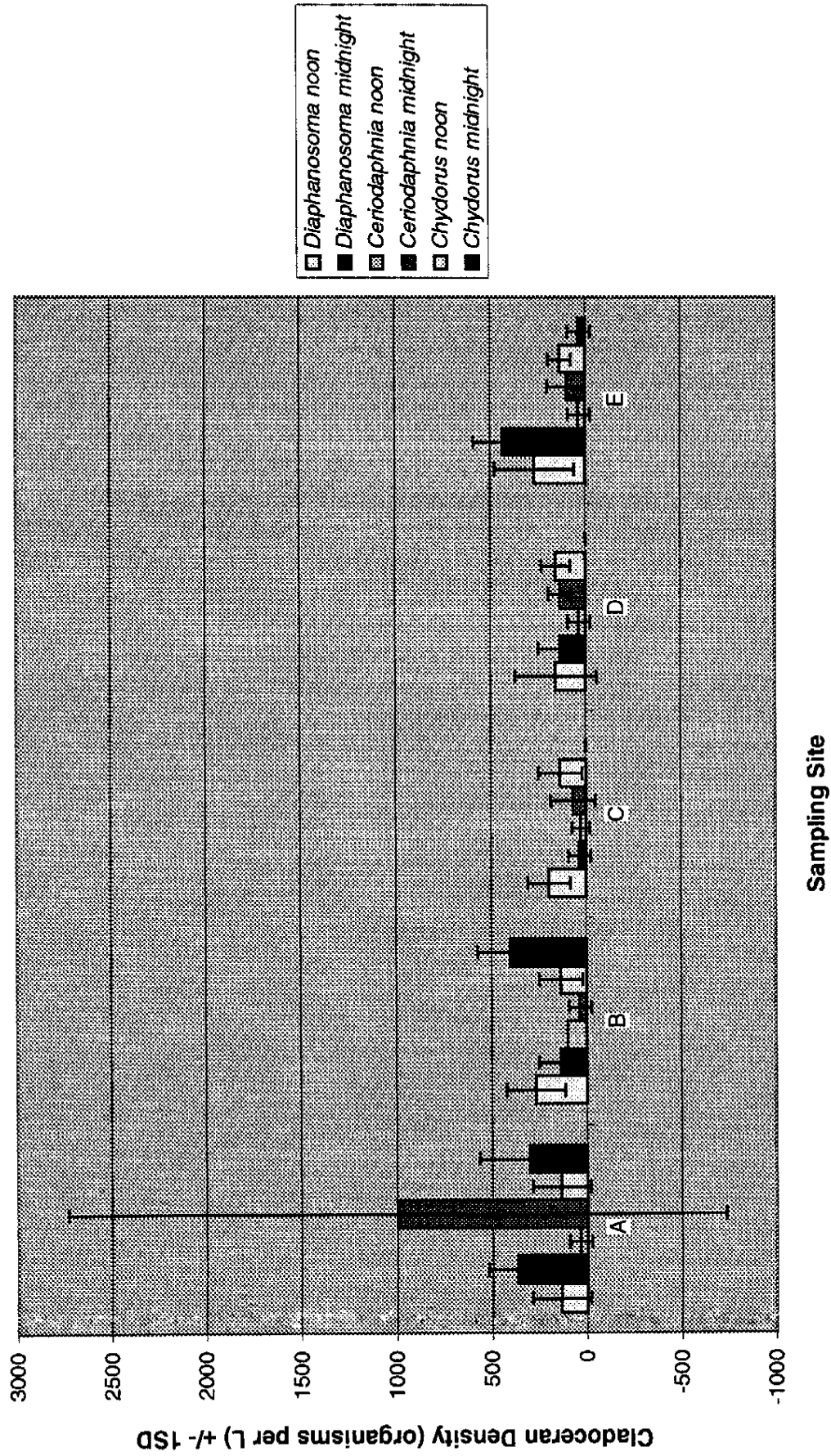


Figure 6: Density of *Diaphanosoma*, *Ceriodaphnia*, and *Chydorus* by sampling site for both day and night. Light bars represent noon abundance, dark bars are midnight.

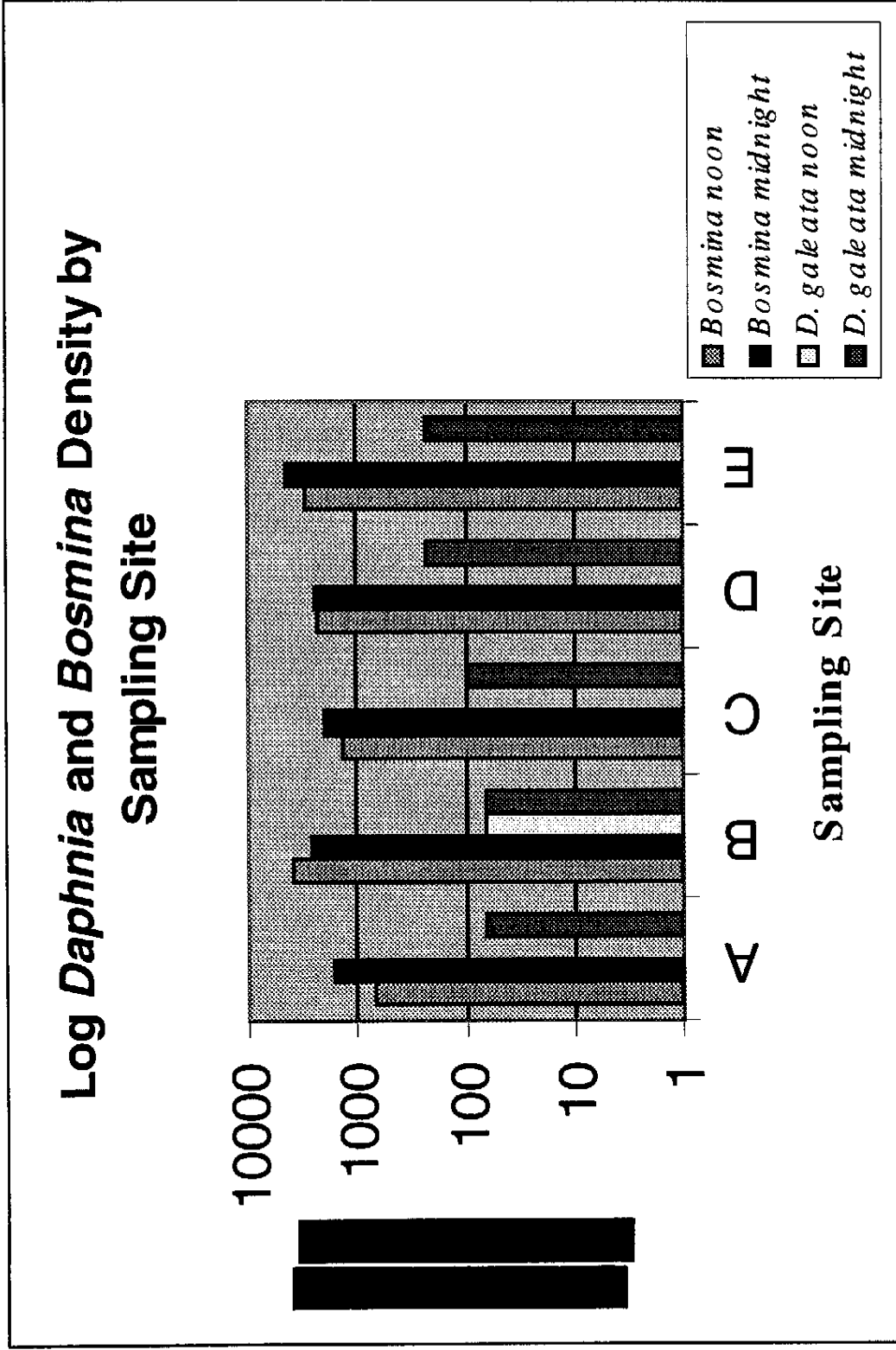


Figure 7: *D. galeata* and *Bosmina* density by sampling site for day (light bars) and night (dark bars) with density on a log-scale to emphasize diel differences in distribution.

### Copepod Density by Sampling Site

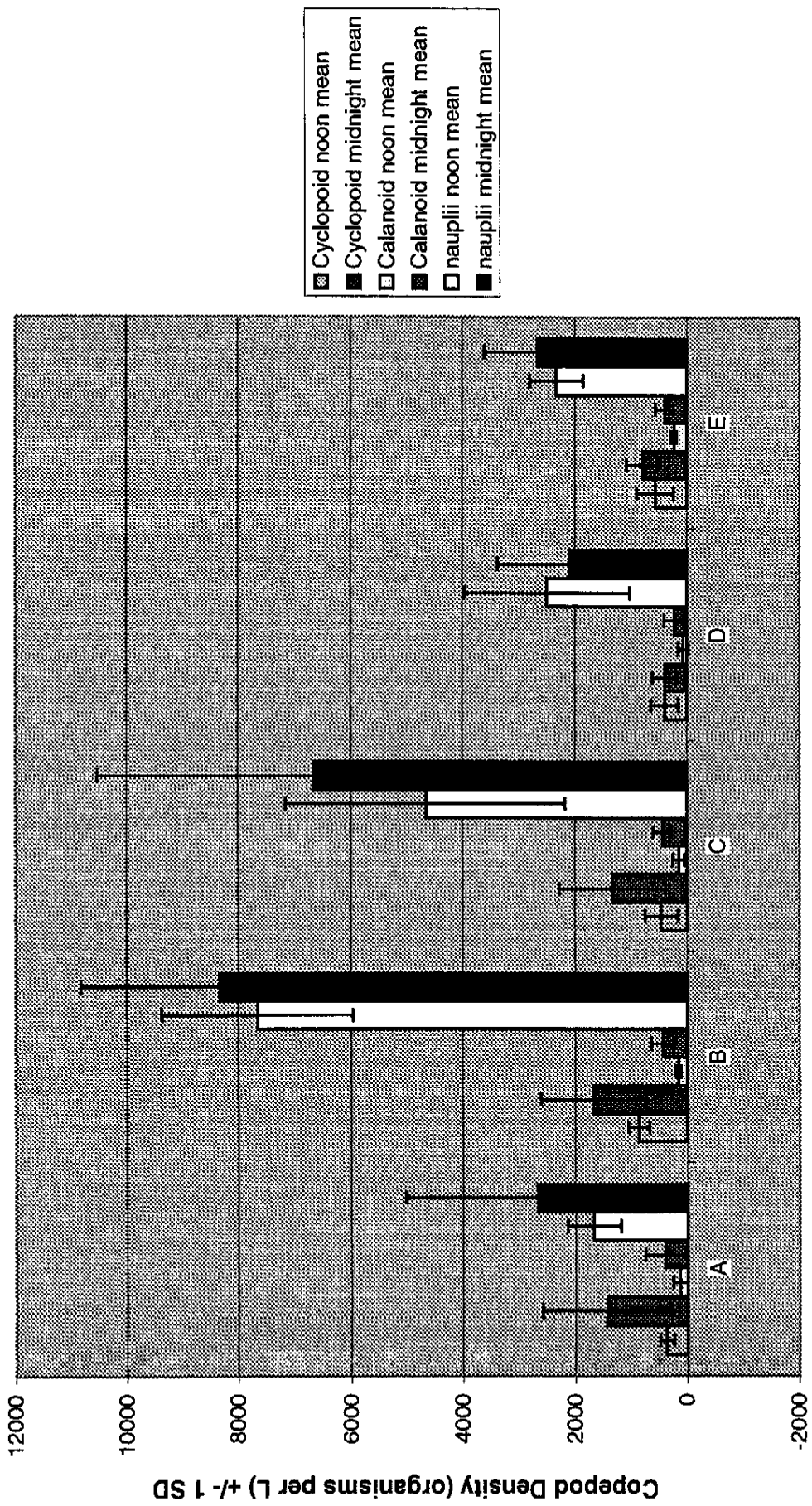


Figure 8: Cyclopoid and Calanoid copepod density and nauplii density by sampling site for both day and night. Light bars represent noon samples and dark bars show midnight.

Rotifer Density by Sampling Site

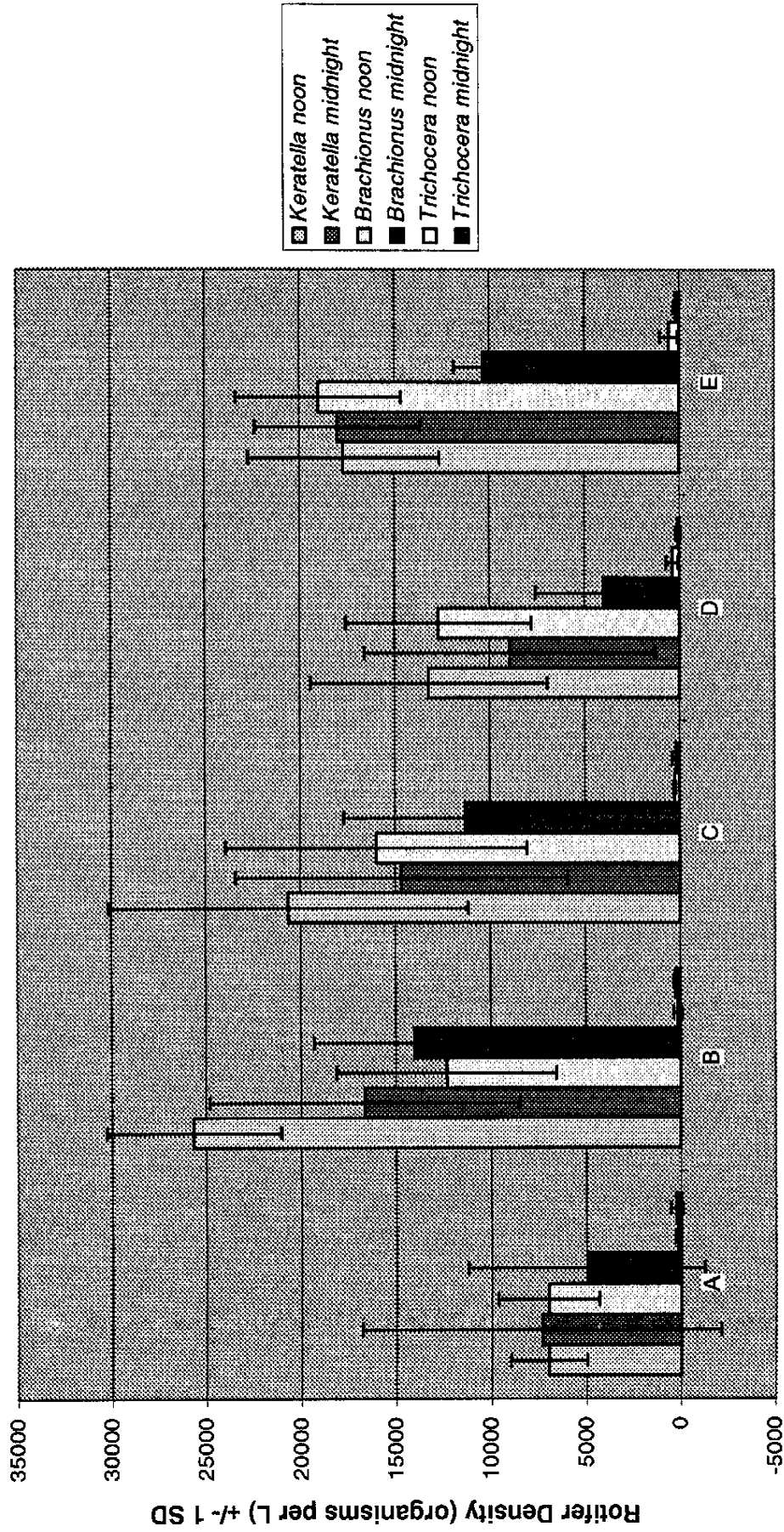


Figure 9: Rotifer densities by sampling site for both noon and midnight. Light bars represent daytime samples, dark bars show night.

sediment, which may have harbored those *Ceriodaphnia*, rather than the water column.

Figure 8 shows the concentration of copepods and nauplii by sampling site. Nauplii were present in higher densities than adult cyclopoid and calanoid copepods, which could be due to seasonal dynamics. The highest densities of nauplii were found at sites B and C, with little difference from day to night. T-test results were not significant (Table 3). Cyclopoid copepods were present in greater numbers than calanoid copepods. The pattern of their habitat use is unclear. Fairly uniform distribution over sampling sites was expected, with little diel change in abundance. As expected, t-test results were not significant (Table 3). Figure 9 presents rotifer density and distribution by sampling site. The rotifers *Keratella* and *Brachionus* dominated the zooplankton community by numbers (with some densities upwards of 20,000 L<sup>-1</sup>). Their distribution was relatively uniform across sites B to E. Rotifer density was lower at site A, suggesting an avoidance of heavy macrophyte infestations.

A 2-way ANOVA was performed to test whether there were differences in rotifer abundance between sites. Site had a significant effect on *Keratella* abundance ( $F=3.983$ ,  $p=0.016$ ) while the effect of time was not significant ( $F=2.12$ ,  $p=0.161$ ). Tukey's post-hoc test results showed that *Keratella* abundance was significantly different between sites A and B ( $p=0.013$ ), and sites B and D ( $p=0.013$ ), and nearly significant between sites A and E ( $p=0.085$ ). The smallest *Keratella* densities were observed at Site A, and the highest at

Site B. Site D also had low *Keratella* abundance, while Site E abundance was fairly high, with the lowest standard deviation.

These differences do not amount to a clear pattern; they could merely reflect underestimation of the populations at certain sites due to inexperience in sampling rather than meaningful results. As *Keratella* are not selectively preyed upon, other explanations must be invoked differences are, in fact, biologically meaningful. T-tests also detected significant differences between noon and midnight *Keratella* abundance, at sites B ( $p=0.05$ ) and D ( $p=0.03$ )(Table 3). A diel difference at Site B remains questionable due to the large errors and likelihood of underestimating *Keratella* density during sampling, counting, or both. The same holds for Site D, where relative error in the densities was even greater.

A 2-way ANOVA test of *Brachionus* abundance indicated significant effects of both site ( $F=3.188$ ,  $p=0.035$ ) and time ( $F=5.576$ ,  $p=0.028$ ) without a significant interaction (site\*time  $F=1.104$ ,  $p=0.382$ ). Tukey's MCT results showed one near-significant difference, between Sites A and E ( $p=0.092$ ). Site A exhibited the lowest *Brachionus* densities. Those at Site E were the greatest. However, *Brachionus* density does not appear to increase from shore to open water, and interpretation of this result is difficult. ANOVA and Tukey's MCT detected a significant difference in *Brachionus* abundance between day and night. This is most likely the effect of the large diel differences in *Brachionus* density at Sites D and E. For Site D, the t-test also returned a significant

difference between noon and midnight ( $p=.01$ ). One replicate sample from Site D midnight had extremely low densities of all zooplankton, and may have skewed the mean, apparently underestimating the actual zooplankton densities. Diel changes and differences among sites were not expected for *Brachionus*, which should not be limited in its distribution by predation. No other factors accounting for significant differences in its distribution are known at this time. The distributions of *Brachionus* and *Keratella* do not exhibit clear patterns of habitat choice, despite the significant differences detected. This stands in contrast to *D. galeata*, which may often be forced to take refuge from predators.

#### T-test Results

Taxa	Site	p-value returned from T-test between day and night sampling	Significant ns=non-significant *=significant
<i>Diaphanosoma</i>	A	0.12	ns
	B	0.46	ns
	C	0.06	ns
	D	0.83	ns
	E	0.5	ns
<i>Ceriodaphnia</i>	A	0.44	ns
	B	0.18	ns
	C	0.68	ns
	D		
	E	0.53	ns
<i>Chydorus</i>	A	0.13	ns
	B	0.21	ns
	C	0.18	ns
	D	0.07	ns
	E	0.22	ns
Cyclopoid copepods	A	0.28	ns
	B	0.32	ns

Taxa	Site	p-value returned from T-test between day and night sampling	Significant ns=non-significant *=significant
Cyclopoid copepods	C	0.28	ns
	D	1	ns
	E	0.25	ns
Calanoid copepods	A	0.27	ns
	B	0.21	ns
	C	0.28	ns
	D	0.20	ns
	E	0.20	ns
Nauplii	A	0.58	ns
	B	0.73	ns
	C	0.67	ns
	D	0.32	ns
	E	0.74	ns
<i>Keratella</i>	A	0.96	ns
	B	0.05	*
	C	0.55	ns
	D	0.03	*
	E	0.94	ns
<i>Brachionus</i>	A	0.72	ns
	B	0.13	ns
	C	0.56	ns
	D	0.01	*
	E	0.08	ns
<i>Trichocera</i>	A	0.80	ns
	B	0.38	ns
	C	0.84	ns
	D	0.12	ns
	E	0.38	ns

Table 3: Results of t-tests comparing noon and midnight zooplankton abundance.



## Discussion

The zooplankton fauna of Kickapoo Lake was dominated by *Keratella*, *Brachionus*, *B. longirostris*, and nauplii. *D. galeata*, copepods, and several other small cladocerans were present at lower densities in samples. Of the zooplankton taxa present, *D. galeata* showed the most pronounced use of littoral and pelagic habitats. As the only large cladoceran species found, *D. galeata* is likely to experience the greatest predation pressure from the planktivores and any juvenile piscivores present in the lake. *D. galeata* was not observed in pelagic samples during the day (Figure 4), while *B. longirostris* and other small cladocerans (Figures 5, 6) did not show a clear avoidance or preference for any habitat. T-test results for these groups were not significant.

*B. longirostris* is considerably smaller than *Daphnia*, and thus experiences much less predation pressure than large-bodied zooplankton. Its distribution and abundance are less subject to the danger of planktivory. *Bosmina* may occupy any zone of the lake without the high costs associated with occupation of a size-selective predator's habitat. *Daphnia* is subject to these costs due to its larger size, and thus daphnids are more likely to seek a refuge to avoid predation than other groups, such as *Bosmina*.

During the day, *Daphnia* was restricted to Site B, while *Bosmina* was more uniformly distributed (Figure 7). At night, *Daphnia* exhibited a markedly broader distribution while *Bosmina* did not appear to change in distribution. These results are consistent with Expected Results 1 and 2. The

differences in abundance and time-dependent presence across the macrophyte density gradient are partially due to the effect of size-selective predation. The effect of time was significant in variation of *D. galeata* abundance ( $F=9.5$ ,  $p=0.006$ ). There may have also been differences among sites that were not significant due to high variation and low *D. galeata* densities.

Due to their greater vulnerability to size-selective predation, large-bodied zooplankton may exhibit a migratory behavioral response (Brooks and Dodson 1965, O'Brien 1979). In unstratified lakes, macrophytes may provide an alternative refuge in the absence of the hypolimnetic refuge. The presence of macrophytes may lessen the impact of predation on zooplankton (Jacobsen et al. 1997, Schriver et al. 1995). Cladoceran biomass (including *Daphnia*) was positively related to PVI, and negatively related to fish abundance (Schriver et al. 1995). Kickapoo supports piscivores (yellow perch, northern pike) due to stocking, as well as some planktivores (crappie). Thus, there may be fairly high levels of predation pressure on large-bodied zooplankton from planktivores and juvenile piscivores. At 3 m maximum depth, Kickapoo could possibly stratify, but it is unlikely. Macrophyte refugia from predation could increase the fitness of migrating daphnids, especially those which occupy the edge zone (Lauridsen and Buenk 1996).

Although there was high variability in the samples taken and *D. galeata* were present in low numbers, a congregation of *Daphnia* was observed at site B during the day. Density increased linearly with distance from shore at midnight (Figure 3). The presence of *Daphnia* in vegetated

areas may be in response to detection of predators, as *Daphnia* otherwise tend to avoid macrophytes (Lauridsen and Lodge 1996). The daytime association of *Daphnia* with the edge zone macrophytes is consistent with the pattern of DHM. This congregation is more difficult to explain in diel vertical migration theory. As all samples were taken at approximately 1 to 1.5 m depth, sampling half or more than half of the water column at most points, these findings may indicate migratory behavior.

If Kickapoo Lake does stratify, the abundance at sites A-E would result from a combination of DHM and DVM. We are confident that DVM is not the only predator avoidance mechanism since *D. galeata* was found during the day only at the macrophyte edge. Even if Kickapoo Lake were unstratified, some DVM may nevertheless occur. *D. galeata* may have occupied the sediment-water interface, hiding near flocculent particles of sediment, in addition to the macrophyte edge zone. The observed abundance of *D. galeata* is likely the result of a combination of DHM and DVM with possible use of the sediment as a refuge.

DHM and occupation of the edge zone during the day may be adaptive to large-bodied zooplankton, which are selectively preyed upon. The littoral zone may offer other benefits such as warmer temperatures. The presence of macrophytes in a lake may allow *Daphnia* to persist in the presence of planktivores. Thus, algae would experience greater grazing pressure in a lake with macrophytes, and water clarity could be maintained. The interactions among macrophytes and the pelagic food web may lead to a better

understanding of the factors needed to control algal biomass and improved management of eutrophied shallow lakes.

### Acknowledgments

I would like to acknowledge the Bernard J. Hank family for their generous support of the UNDERC program, which has made this project possible. I would also like to recognize Romi Burks and Dr. David Lodge for their great assistance in the development and realization of this project. Thanks to Jeff Runde and to Gerry Schoesser for their assistance in my project during the summer. Special thanks go to Pam Japlit, Molly McCracken and Noah Gray for their invaluable assistance in field sampling, at all hours. Finally, I would like to recognize the excellent customer service provided by Ace Hardware in Woodruff, WI for driving to UNDERC with an item I purchased which was inadvertently left out of my bag at the cash register.

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