Effects of the Vertical Distribution of Zooplankton on the Estimation of Abundance and Biovolume Using Deep and Shallow Tows

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INTRODUCTION

Vertical Migration

Vertical migration by zooplankton is one of the earliest and most commonly observed behavioral phenomena in both marine and freshwaters (Cuvier, 1817; Leydig, 1862; Russell, 1927). Alternately referred to as diel or diurnal vertical migration (DVM), this usually involves a migration upward from deeper waters at dusk, resulting in a population maximum in relatively shallow water at night, followed by sinking to deeper water at dawn and a mid-day population maximum at depth. Deviations from this 'nocturnal' DVM include 'reverse' DVM, with a single surface maximum during the day, and a 'twilight' DVM in which surface maxima form both at dawn and dusk (Hutchinson, 1967; for examples, see: Dumont, 1972; Cunningham, 1972; Ohman et al., 1983).

The proximal cause of migration has most often been found to be relative changes in light intensity (Siebeck, 1980; McNaught and Hassler, 1964; Ringelberg, 1964), while the ultimate reason for this behavior is somewhat more obscure. The most common pattern of nocturnal migration involves removal of the animals from a warm, food-rich environment at night to a cold, food-poor environment during the day, at a substantial energetic cost. Most attempts to explain this apparent paradox fall into one of two categories (Lampert, 1989):

1. Vertical migration provides a metabolic or demographic advantage, or
2. Avoidance of surface waters during the day reduces losses from predators.

The first hypothesis, originally proposed by McLaren (1963; 1974) assumes either that a resting period in low temperatures confers a long-term energetic advantage, or that low temperatures allow individuals to reach a larger adult body size, which in turn results in greater fecundity. The second hypothesis, which is probably more widely accepted, holds that migration to a dark refugium in deep waters during daylight hours reduces losses due to visual predators (Zaret and Suffern, 1976).

Within a lake, the pattern and amplitude of DVM can vary from species to species (Wells, 1960; Geller, 1986; Angeli et al., 1995) and within a species with size, age and sex (Stich, 1989). In general, more visually conspicuous individuals (e.g., larger animals, gravid females) exhibit greater amplitudes of migration (Wright et al., 1980; Haney and Hall, 1975). The strength and extent of DVM can also vary seasonally for a given species within the same habitat (Stich and Lampert, 1981; Ringelberg et al., 1991). Often in deep lakes migratory behavior begins soon after the clear water phase in June (Geller, 1986; Stich, 1989). Migratory behavior can vary for a given species from year to year, and from lake to lake, in response to changes in predator abundance. Williamson and Magnien (1982), Stirling et al. (1990), Lehman and Caceres (1993) and Frost and Bollens (1992), have all found interannual variations in the amplitude of zooplankton migration to be related to changes in the size of predator populations, while Gliwicz (1986) found a relationship between amplitude of migration of copepods and the age of the fish populations across a number of lakes that had been stocked with char for different periods of time.

Brief History of the GLNPO Zooplankton Sampling Protocol

The Great Lakes National Program Office (GLNPO) began annual monitoring of the Great Lakes in 1983 for Lakes Michigan, Huron, and Erie. In 1986 sampling was extended to include Lake Ontario, and in 1992 sampling of Lake Superior was added. In 1983 and 1984, two zooplankton tows were taken at each site with a 62 µm mesh net: one from 2 m above the bottom to the surface, and a second from 20 m to the surface, although little analysis was apparently conducted (Makarewicz, 1987; Makarewicz, 1988). In 1985, the deep tow seems to have been discontinued (Makarewicz and Bertram, 1991).

Prior to the summer, 1997 cruise, the zooplankton sampling protocol was changed to include 100 m tows, in addition to the 20 m tows. Unlike previous deep tows, the 100 m tows were taken using a net with a larger mesh size (153 µm) to prevent clogging and to reduce the pressure wave created by the net during sampling. Also, time of day the tows are taken was recorded from 1996 on.

The depth at which zooplankton tows are taken can have a number of possible effects on the estimation of zooplankton abundance and community composition. In species that exhibit nocturnal DVM with a maximum depth greater than 20 m, shallow tows taken during the day can result in an underestimation of abundances. In addition, if larger animals exhibit greater amplitudes of migration than smaller animals, then 20 m tows will have a disproportionately large percentage of smaller animals during the day, and thus individual and total biovolumes of migrating animals will be underestimated in day samples. These two factors can result in the appearance of spurious horizontal spatial patterns in zooplankton community data where in fact none exist, particularly if sites near to each other are sampled at similar times of day, as is often the case. Additionally, populations of deeper-living zooplankton that rarely migrate above 20 m would be consistently underestimated in 20 m tows, whether taken during the day or at night. On the other hand, the abundances of animals whose maximum depth of occurrence is substantially above 100 m would be underestimated, on a volumetric basis, by deeper tows, due to ‘dilution’ of the population by the sampling of deep water which is essentially free of any individuals.

Here we examine the comparability of data collected with the two different tows. In particular, we sought to address the following questions:

1. Are there differences in the net efficiencies of the two mesh sizes (64 µm and 153 µm) to capture specific zooplankters?

2. Do shallow tows result in differences in relative community composition during the day? If so, what species’ abundances are underestimated during the day by shallow tows?

3. Are there lake to lake or within lake differences in the suitability of shallow tows to estimate abundances of specific species?

4. Are there species which are underestimated at all times by shallow tows?

5. Do shallow tows result in low bias in length measurements (and hence biovolume estimates) during the day?
6. Are volumetric estimates of abundance and biovolume underestimated by deep tows?

METHODS

Sample Collection and Processing

Samples used in this study were collected during the summer, 1998 cruise, during which a total of 72 stations were sampled for zooplankton (Fig. 1). Two sampling tows were performed at each site, using a 0.5 m diameter conical net (D:L = 1:3). The first tow was taken from 20 meters below the water surface using a 63 µm mesh net, and the second tow from 2 meters above the bottom of the lake or 100 m, whichever was less, using a 153 µm mesh net. If the station depth was less than 20 m, both tows were taken from one meter above the bottom. Triplicate tows of each depth were taken at the Master Stations.

After collection, samples were immediately narcotized with soda water, and were preserved with sucrose formalin solution (Haney and Hall, 1973) approximately twenty minutes later. Samples were split in the lab using a Folsom plankton splitter, and four stratified aliquots examined per sample. Length measurements were made on the first twenty individuals of each species encountered per sample. Identifications followed Balcer et al. (1984) for adult calanoids, malacostracans, the cladocerans *Leptodora kindtii*, *Polyphemus pediculus*, *Holopedium gibberum*, and *Diaphanosoma birgei*; Hudson et al. (1998) for adult cyclopoids and harpacticoids. Brooks (1957) and Evans (1985) were used for all Daphnidae, and the remaining cladocerans (Chydoridae, Bosminidae, and Macrothricidae) were classified according to Edmundson (1959). Members of Cercopagidae (i.e. *Bythotrephes cedarstroemi*, *Cercopagis pengoi*) were identified according to Rivier (1998).

Analytical Approach

To determine the comparability of data generated from nets with the two different mesh sizes (64 µm and 153 µm), all other factors being equal, sites less than 20 m (i.e. where tows with both nets were taken from the same depth) were examined. There were 12 such sites in the western and central basins of Lake Erie during the summer, 1998 cruise. For each species, estimates of abundances (# m^{-3}) generated from the two different tows were compared to determine if there were any changes in collection efficiency that could be attributed to differences in net mesh size. Comparisons were made using the Wilcoxon signed rank test, a nonparametric paired-sample test which is used to examine data in which measures are repeated only once (e.g. replicate tows with different mesh sizes). The use of a paired-sample test in this case eliminated the influence of inter-site variability on the analysis. Count data tends to follow a Poisson, rather than a normal, distribution, and thus violates the normality assumption of parametric tests.

Differences in relative community composition estimates as a result of different tow depths were assessed using Whittaker's (1952) percent similarity (PSC) index:

$$PSC = 100 - 0.5\sum_{i=1}^{K}|a-b|$$

where *a* and *b* are, for a given species, percentages of the total samples *A* and *B* which that species represents. The absolute value of their difference is summed over all species. This number ranges from 0 to 1, with 0 indicating two samples with no species in common, and 1 indicating two samples with all species present in both samples in the same relative proportions. A relative index, rather than an absolute index (e.g. Pinkham and Pearson's (1976) Biosim index) was used to disregard effects of dilution in cases where the majority of individuals were present substantially above 100 m.

If a substantial portion of the zooplankton community underwent diel migration to depths greater than 20 m, then one would expect similarities between shallow and deep tows to be greater for sites visited at night than for sites visited during the day. This was tested for each lake by first classifying samples according to whether they were collected during the day or at night, where day was defined as being from one hour after sunrise to one hour before sunset. Percent similarities of zooplankton communities estimated with deep and shallow tows were then calculated for each site (in the case of Lake Erie, for the eastern basin only), and differences in similarities between day samples and night samples assessed with a *t*-test where PSC values were both normally distributed and exhibited homoscedasticity, and with a Wilcoxon rank sum test where the assumptions of normality and homoscedasticity were not met.

To determine if individual species were undergoing migration, two-way nested ANOVAs were conducted on species abundances within each of the upper lakes. Here, depth of tow (Depth) was one factor, and time of day (Time), e.g. day or night, the other factor, and the response variable was species abundance m^{-3} for each species within each lake. To isolate the variation due to site differences, Site was included as a factor in the analysis. Since each site was only sampled during one time period (i.e. either day or night), but two tows were taken at each site, factor effects of Site were crossed with depth of tow, but nested within time of day (Fig. 2). If species were undergoing DVM of an amplitude that took them substantially out of the upper 20 m during the day, then the magnitude of difference in numbers of individuals estimated from deep and shallow tows would be dependent on the time of day the tows were taken. This would show up as a significant interaction effect between the factors Depth and Time. Since site was nested within time, and its variance was consequently used as the denominator in tests of significance for factors including time, high site to site variance for a given species within a lake would result in reduced power of the test to detect both Time effects and migration (i.e. Time x Depth interaction) effects. A significant effect of Depth, without a significant interaction effect, could be due to either a preference of the species for depths substantially above the depth of the deep tow, and hence dilution of the organism in the deep tow, or a preference for depths greater than 20 m, and therefore an underestimation of abundance by the 20 m tow.

Separate ANOVAs were conducted for each species within each lake, and the data were assessed for conformance to the assumptions of normality and homoscedasticity. Where these assumptions were not met, one of the following transformations was used, depending on which stabilized variance and resulted in a normal distribution:

$$x' = \sqrt{x + 0.5}$$

$$x' = \ln(x + 1)$$

Sites in both the western basin and the central basin of Lake Erie are relatively shallow, with mean depths of 8.8 m and 25.5 m, respectively. These sites were therefore not included in these analyses. The eastern basin of Lake Erie is deeper, with an average site depth of 47.5 m. However, there were only four sites visited in this basin, three during the day and one at night. Similarly, in Lake Ontario species distributions were uneven enough across the lake to limit the number of sites that could be used for any one ANOVA analysis. As a result, a different approach was used for these two lakes. Here, differences in the abundances of individual species between deep and shallow tows for sites visited during the day were tested for using a paired test. Assumptions of homoscedasticity and normal distribution were met in all cases, so a one-way paired *t*-test was used. The null hypothesis tested was:

$$H_0: \bar{d}_{20-100} \geq 0$$

where: $\bar{d}_{20-100}$ = the average of the differences in abundances between shallow and deep tows at each station. If abundances were greater in deep tows than in shallow tows at stations sampled during the day, this would suggest the possibility that animals were migrating below 20 m during the day.

To compare differences in length between animals captured by the shallow tows and animals captured by the deep tows, average lengths for deep daytime and shallow daytime tows were compared within each lake using either a *t*-test, or the Mann-Whitney rank sum test in the event of non-normality or heteroscedasticity. With this approach, variability due to site to site differences was confounded with variability due to differences in length as a result of depth. However, the considerable non-normality of most the data, and the lack of an appropriate nonparametric method to incorporate site to site differences, particularly given the large differences in sample size within each cell, precluded a better approach. It should be borne in mind, therefore, that the power of this test is probably quite low.

RESULTS

Differences in Net Efficiency Between 64 and 153 μm Mesh Nets

A total of 24 crustacean taxa were found at the 12 sites with depths less than 20 m. Of these, only one taxa, *Mesocyclops* copepodites, showed a significant (α = 0.05) difference between the abundance estimates made with the two different mesh sizes (Table 1). At an α of 0.05, it is expected that one type I error will be committed, on average, for every 20 analyses. Therefore, there appears to be no real difference in the estimates of macrozooplankton abundances collected from a fixed depth using a 64 µm compared to a 153 µm mesh net.

Differences in Relative Community Composition Between Deep and Shallow Tows

Zooplankton community composition by major taxa, as estimated using deep and shallow tows, are shown for all five lakes in Figs 3 through 7. In Lake Superior, nine of 19 stations were sampled during the day (Fig. 3). All sites were dominated by immature copepods. While volumetric abundances differed between shallow and deep tows taken during the day, differences in relative community composition, at least on the basis of broad taxonomic groups, were not apparent. In both Lakes Michigan and Huron (Figs 4, 5), about half of the tows were taken during the day. When shallow tows taken during the day were compared with those taken at night, clear differences in both species composition and abundance where apparent, with day tows showing consistently lower volumetric abundance estimates and a greater proportion of immatures compared to night tows. Deep tows in both lakes showed a remarkable degree of spatial homogeneity, in terms of both species composition and total abundance. In Lake Erie, sites in the western and central basins were by and large 20 m or less in depth, so not surprisingly no substantial differences were noted in community composition between deep and shallow tows taken during the day (Fig. 6). On the other hand, in the eastern basin, the genus *Bosmina*, which was dominant in the deep tows, was almost completely missing from all shallow tows. Lake Ontario, like Lake Erie, exhibited a notable degree of spatial heterogeneity in community composition, with the western three sites dominated by *Bosmina*, and the eastern four sites dominated by *Daphnia* (Fig. 7). A central site was intermediate in species composition between these two communities. Half of the sites were visited during the day, and no systematic differences in community composition were apparent, although abundances tended to be higher in the shallow tows.

To determine if differences in community composition from shallow and deep tows were statistically significant for each lake, PSC similarity values between shallow and deep tows for each site collected during the day were compared to similarity values between shallow and deep tows collected at night (Fig. 8). In Lake Erie, only sites in the eastern basin were compared, since sites in the western and central basins were not substantially deeper than 20 m. Statistically significant differences (α = 0.05) were found for Lakes Huron and Michigan, indicating that shallow and deep tows taken at night were more similar to each other than shallow and deep tows taken during the day. This implies that a substantial portion of the zooplankton community was undertaking nocturnal DVM to a depth greater than 20 m. Although a very large difference in the similarity of deep and shallow tows between day and night was apparent in the eastern basin of Lake Erie, the small sample size precluded a statistically significant difference from being detected. No differences in similarity between day and night samples were detected in Lake Ontario, where similarity values were uniformly high. In Lake Superior, similarities between shallow and deep tows were comparable for day and night samples; however, overall similarities between shallow and deep tows were lower than for other the lakes. This implies that there were differences in the depth distributions of species both day and night.

Species-Specific Differences in Depth Distribution and Migration Behavior

To test for depth preferences and indications of migratory behavior on a species by species basis, ANOVA analyses were conducted on individual species from Lakes Huron, Michigan and Superior. The full results of all ANOVA analyses are presented in Table 2.

Cladocera:

There were five species of cladocera present in sufficient numbers in at least one of the upper lakes to permit analysis: *Bosmina longirostris*, *Eubosmina coregoni*, *Holopedium gibberum*, *Daphnia galeata mendotae* and *Bythotrephes cedarstroemi*. Abundances of *B*. *longirostris* were high enough in both Lakes Huron and Michigan to permit analysis. In both lakes there was a significant interaction effect between Time and Depth, indicating the likelihood of DVM. This can be seen in box plots of abundances of this organism, which show that shallow tows taken at night result in significantly higher abundance estimates than shallow tows taken during the day for both lakes (Fig. 9). Abundances of *E. coregoni* in Lake Huron were substantially greater in both deep day and shallow night samples, compared to shallow day samples (Fig. 10), suggesting nocturnal DVM, although there were no significant factor effects. Failure to find significant differences could have been a result the low power of the performed test, however ($\beta = 0.076$ for Time x Depth). *H. gibberum,* present in Lake Superior, showed significant Depth effects, with abundances estimated from shallow tows consistently higher than those from deep tows (Fig. 11). This suggests that *H. gibberum* prefers upper waters, and therefore that deeper tows consistently underestimate its abundance. There was no evidence of migration in this species. *D. galeata mendotae* was present in substantial numbers in all three upper lakes, although its behavior seemed to differ from lake to lake. In both Lakes Michigan and Huron, significant Depth x Time interaction effects were found, suggesting that *D. galeata mendotae* undergoes DVM in these lakes (Fig. 12). This was particularly pronounced in Lake Michigan, where mean abundances in shallow night tows were nearly two orders of magnitude higher than in shallow day tows. In both lakes, deep tows were greater than day shallow tows, and less than night shallow tows, indicating that though animals were migrating above and below 20 m, most of the population was well above the depth of the deep tows, and so abundances were underestimated by the deep tows. In Lake Superior, in contrast, no significant interaction effects were found, but Depth had a significant effect on abundance estimates. Mean abundance estimates from shallow tows were significantly higher than those from deep tows, indicating that animals were staying above 20 m both day and night, and consequently deep tows underestimated abundance by diluting the samples. *B. cedarstroemi* was common in Lakes Huron and Superior; no evidence of migration below 20 m was found in either lake (Fig. 13).

Paired *t*-test analyses were conducted on the species abundances estimated from deep and shallow tows at the stations sampled during the day in Lakes Erie and Ontario. Full results from these analyses are presented in Table 3. In Lake Erie, a statistically significant difference between abundance estimates from deep and shallow tows was found only for *Bosmina longirostris*. Interestingly, a difference was not found for this organism in Lake Ontario. When the relative abundances of this species in the two lakes are examined (Fig. 30), dramatic differences in its vertical distribution are apparent. The relative abundances of *B. longirostris* estimated from deep and shallow tows at sites in Lake Ontario sampled during the day are essentially identical, while in Lake Erie this organism is almost completely absent from the upper 20 m during the day at sites in which it appears to be the dominant organism, judging from abundances estimated from the deeper tows.

Copepoda:

Of the copepods, there were two species of cyclopoids and seven species of calanoids abundant enough in at least one lake to test. In addition, immatures were tested. The cyclopoid *Tropocyclops prasinus mexicanus* was found in Lake Michigan, and both adult and immatures were significantly more prevalent in the upper 20 m both day and night, with no evidence of migration below 20 m (Fig. 14). Both mature *Diacyclops thomasi* and its copepodites showed evidence of extremely strong DVM in Lake Michigan, with adult abundances in shallow night tows about two orders of magnitude higher than shallow day tows (Fig. 15). The extremely low abundances found in the shallow day tows strongly suggest that most of the adult population was migrating below 20 m during the day. In Lake Superior on the other hand, there was no indication of migration below 20 m during the day for this species (Fig. 16). In fact, both adults and copepodites were more abundant in shallow day tows than in shallow night tows, although this difference was not statistically significant. There was a statistically significant effect of Depth, pointing to dilution of the deep tow samples. *D. thomasi* populations in Lake Huron showed no statistically significant effects of Depth or Time (Fig. 17).

Calanoid copepods were the most diverse group of the macrozooplankton, with a total of seven species found. Four species of the family Diaptomidae were found in the lakes: *Leptodiaptomus ashlandi*, *Leptodiaptomus minutus*, *Skistodiaptomus oregonensis* and *Leptodiaptomus sicilis*. Abundances of *L. ashlandi* from shallow tows in both Lakes Huron and Michigan were several times higher at night than during the day, strongly suggesting DVM (Fig. 18). However, these differences were not statistically significant. A similar, but stronger, pattern was found in both lakes for *L. minutus*, indicating strong DVM below 20 m during the day (Fig. 19). Deep tows were similar both day and night, and were lower than shallow night tows and higher than shallow day tows. This indicates that most of the population was probably well above 100 m at all times. Substantial populations of *S. oregonensis* were found only in Lake Michigan, and while shallow night tows were much higher than shallow day tows, there was no statistically significant difference (Fig. 20). Since deep tows were always less than shallow tows, indicating dilution of these population in deep tows, it appears that both shallow day and all deep tows underestimate these populations. *L. sicilis* was present at a substantial number of sites in all three lakes, and its populations were always significantly greater in deep tows than in shallow tows (Fig. 21). There was some suggestion of migration into the upper 20 m at night in Lakes Huron and Michigan, although this was not statistically significant. Percent abundance data of *L. sicilis* clearly indicate that shallow tows greatly underestimate abundances of this species in Lake Michigan and Superior (Fig. 22). Diaptomid copepodites showed evidence of migration in Lake Michigan, and of increased numbers with depth in Lake Superior (Fig. 23). No patterns were noted in Lake Huron. Since this group probably represented a mix of species with different behaviors, however, conclusions regarding differences between lakes are of limited value.

Limnocalanus macrurus was found in both Lakes Michigan and Superior, and in both lakes relative abundances were significantly higher in deep tows, both day and night, than shallow tows taken at any time (Fig. 24). In addition, animals were nearly absent from the upper 20 m during the day, but not at night, suggesting migration into the upper 20 m at night (Fig. 25), although a significant interaction effect was noted only in Lake Superior. The lack of an interaction effect in Lake Michigan was probably due to the high variability in that lake. In both lakes, abundances estimates were higher from deep night tows than deep day tows, suggesting that perhaps a portion of the population was residing in waters deeper than 100 m during the day and migrating up at night. *Senecella calanoides*, also present in both Lakes Superior and Michigan, showed an even more extreme distribution, being completely absent from surface waters both day and night (Fig. 26). Somewhat more individuals were found in deep night tows than in deep day tows, suggesting again that perhaps some of the population was migrating below 100 m during the day, but numbers of individuals were too low to permit confident conclusions. As with *L. macrurus*, estimates of the relative abundance of *S. calanoides* made with deep and shallow tows were very different (Fig. 27).

Epischura lacustris was present at a substantial number of sites in all lakes, and showed some evidence of migration in Lake Michigan, but not in the other lakes (Fig. 28). *Epischura* copepodites, present both in Lake Michigan and Lake Huron, were significantly more abundant in the upper 20 m in both lakes (Fig. 29).

In Lake Ontario, diaptomid copepodites showed a slightly significant difference in abundances estimated from the two tows (Table 3). None of the other copepods tested in the two lower lakes exhibited any differences in vertical distribution, indicating that DVM below 20 m was not occurring for these species.

Differences in Animal Lengths Between Deep and Shallow Tows

Full results of length comparisons between shallow and deep day tows are presented in Table 4. Of the twenty species tested, eleven showed significant differences in length between individuals captured in the deep tows compared to the shallow tows in at least one lake. Only in the case of *D. thomasi* were larger individuals found in the shallow tows. Differences in length, though significant, were in most cases relatively minor, often amounting to less than a one percent change in lengths between the two tows. However, for some organisms, in particular the cladocerans *B. longirostris* and *D. galeata mendotae*, the differences were substantial. In the case of Lake Huron, differences in length of *Bosmina longirostris* and *D. galeata mendotae* between shallow and deep tows would have lead to an underestimation in biovolume of approximately 50%, even if abundances calculated from the two tows were identical.

DISCUSSION

Migration

A number of different patterns of depth distribution were found for the zooplankton in the Great Lakes. In general, cladocerans exhibited nocturnal DVM in Lakes Michigan and Huron, with patterns being stronger in the former lake. *B. longirostris*, the dominant cladoceran in eastern Lake Erie, also appeared to be undergoing migration in that lake, being virtually absent from 20 m tows during the day. In contrast, where sufficient organisms were present to test, migratory behavior was not apparent in cladoceran populations in Lake Superior or Lake Ontario. In Lake Superior in particular, cladocerans exhibited a strong tendency to remain in the upper 20 m both day and night.

Finding comparable data in the literature is difficult since most lakes are much shallower than the Great Lakes, and therefore migration patterns tend to be much more restricted with respect to depth. Surprisingly, little work on migratory behavior has been done on the Great Lakes, although some studies have been conducted which have addressed vertical distribution. Wells (1960), in an extensive study of the zooplankton of Lake Michigan, found that *D. galeata mendotae* undertook diel migrations, but that populations did not descend below 20 m. In contrast to the present study, his data indicated that migration took place almost entirely between the surface and 10 m. McNaught and Hasler (1966), on the other hand, found that populations of *D. retrocurva* in Lake Michigan had an amplitude of migration of over 20 m, with population mean density at a depth of 34 m during the day. Conway et al. (1973) in a study of zooplankton distribution in Lake Superior found that abundances of cladocerans declined notably between 20 and 30 m, which is consistent with the present findings. Wilson and Roff (1973) observed variable migration in *Bosmina* in Lake Ontario. During September there was notable migration below 20 m during the day, although the majority of the population remained above that depth. In contrast, *D. retrocurva* exhibited stronger migration below 20 m in their study. Migration ranges for the two species in September were about 20 m and 14 m, respectively.

In Lake Geneva, Angeli et al. (1995) found that migration of small individuals of *D. hyalina* was limited to the upper 15 m, while larger individuals undertook migrations with an amplitude of greater than 30 m. Makino et al. (1996), working on a caldera lake in Japan, observed population maxima of *D. longispina* between 25 – 50 m during the day in spring, but mostly above 30 m in October. Similar depth maxima were found for *Bosmina* (*Eubosmina*) *coregoni*.

In contrast to the smaller cladocerans, the large invertebrate predators *Leptodora kindtii*, *Bythotrephes cedarstroemi* and *Cercopagis pengoi* did not exhibit substantial migratory behavior in any of the lakes. This seems paradoxical, since the size of these zooplankton would appear to make them more vulnerable to sight-feeding planktivores. However, *Leptodora kindtii* is extremely transparent, and it is possible that even in epilimnetic waters during the day it is not visible to fish. Both *Bythotrephes* and *Cercopagis* have very long barbed spines which can get caught in the gill rakers of planktivorous fish (Barnhisel and Harvey 1995), thus reducing their vulnerability to predation. Stich (1989), working on Lake Constance, also found that migratory behavior of the species *Leptodora kindtii* and *Bythotrephes longimanus* was either slight or absent.

Our study also found evidence of migration in many copepod species, although in some cases site to site variability prevented this from being statistically significant. Of the cyclopoids, only *D. thomasi* showed evidence of migration, and then only in Lake Michigan. On the other hand, most of the calanoids, and in particular the diaptomids, exhibited depth distributions in Lakes Michigan and Huron suggestive of migratory behavior, although in some cases these were not statistically significant. Evidence of migration of these organisms was not apparent in the other lakes. Wells (1960) similarly found nocturnal DVM, extending to below 20 m, for the diaptomids *L. minutus*, *L. ashlandi* and *S. oregonensis*. No evidence of migration was found for these organisms in the lower lakes, which agrees with Wilson and Roff's (1973) observations on Lake Ontario.

There are a number of possible explanations for the differences observed in migration patterns from lake to lake. The lack of observable migration in Lakes Superior and Ontario could be due to a smaller amplitude of migration in those lakes. If movements were largely confined to the top 20 m, migratory behavior would not have been apparent from our analyses. These differences could also be due to differences in predation pressure by juvenile or small fish. There is a great deal of literature documenting the influence of the presence of predators on the extent of DVM in freshwater zooplankton. In field studies of Polish lakes, Gliwicz (1986) found that *Cyclops abssorum* migrates only where Arctic char are present, and this behavior can be induced through planktivorous fish stocking. The initiation of vertical migration in *Daphnia hyalina* in Lake Maarsseveen has been observed to coincide with the appearance of active juvenile perch, and to cease when these predators disappeared from the open water (Ringelberg et al., 1991). Similarly, migration of *Diaptomus kenai* in Gwendoline Lake, British Columbia ceased when the predator *Chaoborous* was removed from the lake by an invasion of small trout, but when *Chaoborous* were added in an *in situ* enclosure, DVM resumed within 4 hours (Neill 1990). Stirling et al. (1990) found that DVM of *Daphnia galeata mendotae* in Lake St. George increased in amplitude by a factor of 2 during years in which planktivorous fish recruitment was high, while *Daphnia pulex* responded to *Chaoborous* additions in Ranger Lake, Ontario by initiating migratory behavior (Nesbitt and Riessen, 1996).

Laboratory work has provided evidence that the induction of DVM in zooplankton is a response to the presence of chemical exudates produced by predators. Dodson (1988) first demonstrated that several different species of *Daphnia* could be induced to ascend or descend when added to water that was preconditioned by the presence of a vertebrate or invertebrate predator, and that this response was both predator- and prey-specific. This initial observation has been corroborated by a number of subsequent laboratory studies (e.g., Ringelberg, 1991; Loose, 1993; Watt and Young, 1994; Van Gool and Ringelberg, 1998), and recent attempts have been made to chemically characterize the fish exudates responsible for this behavior (Von Elert and Loose, 1996). The response of zooplankton exposed to such predator exudates is typically rapid (Neill, 1990) but short-lived (Dodson, 1988; Loose, 1993). In general, contact with vertebrate predators, which are mainly visual feeders, induces ‘normal’ DVM, while invertebrate predators, which are mainly tactile feeders and often undergo normal DVM themselves, induce reductions in mean population depths or reverse migrations (Leibold, 1990; Nesbitt and Riessen, 1996; Dodson, 1988; Brancelj and Blejec, 1994). In this way contact time with the two predator groups is reduced.

The intensity of response to predator cues appears to have a genetic component (Young and Watt, 1994), and it has been supposed that this serves to set a limit on the maximum extent of behavioral response to predator cues. So populations from environments historically subject to greater predation pressure might be genetically predisposed to exhibit greater behavioral responses to predator fish cues than those populations which have been subject to less intense pressure (cf. Young and Watt, 1996). These genetic differences can even be exhibited within a given habitat between genetically distinct populations of a single species. Field studies have found distinct migratory behaviors between co-occurring but genetically distinct populations of *Daphnia longispina* (King and Miracle, 1995), *Daphnia galeata* x *hyalina* (Spaak and Ringelberg, 1997; Van Gool and Ringelberg, 1998) and *Daphnia pulex* (Weider, 1984).

It is possible that the differences in migratory behavior observed in the present study could be the result of differences in predation pressure between the lakes. This would suggest that predation pressure by zooplanktivorous fish is greater, for example, in Lake Erie, where migration by *Bosmina longirostris* was observed, than in Lake Ontario, where such behavior was not apparent. Similarly, zooplanktivory by vertebrates might be expected to be more intense in Lakes Michigan and Huron than in Lake Superior. Dorazio et al. (1987) have reported differences in the migratory behavior of *Daphnia* species in Lake Michigan that they attributed to interannual differences in planktivore populations. In 1985, during which the planktivore *Coregonus hoyi* was present in large numbers, all zooplankton grazers displayed pronounced vertical migrations, while in 1983, a year of low planktivore numbers, the dominant herbivore, *D. pulicaria*, did not exhibit vertical migration.

The lack of apparent migration in Lakes Superior and Ontario, on the other hand, might be the result of predation pressure by invertebrates. The main invertebrate predator in the lakes, *Bythotrephes cedarstroemi*, was present at most sites in Superior, albeit at very low abundances. However, populations of this predator were much higher in eastern Erie than in western Ontario, which is the opposite of what would be expected on the basis of the migration patterns of *B. longirostris* in these two areas. Alternatively, nocturnal diurnal migration by planktivores can result in static populations of zooplankton in shallow waters. Levy (1990) has shown that *Bosmina* populations remained in shallow waters in British Columbia lakes where juvenile sockeye salmon migrated vertically, but undertook vertical migrations where sockeye vertical migrations were reversed and sticklebacks were present. More concrete conclusions about the possible causes for the differences in vertical distributional patterns observed in our study will have to await an analysis of fish census data in the lakes.

Depth Distribution

A number of calanoid species were found to exhibit depth preferences that resulted in a majority of the population residing below 20 m at all times. *Limnocalanus macrurus*, present at a substantial number of sites in both Lakes Michigan and Superior, was significantly more abundant in the 100 m tows, both day and night, while *Senecella calanoides*, also present in both lakes, was virtually absent from the 20 m tows at all times. *Leptodiaptomus sicilis*, which was present at most sites in all three upper lakes, was also always more abundant in the deeper tows, although the difference in abundance between deep and shallow tows was not as pronounced as for the other two species.

Other studies have documented the deep water preferences of these species. In Wells' (1960) study of Lake Michigan, *L. macrurus* was almost completely absent from the top 20 m during a period of strong thermocline delineation, but when thermal structure was weaker animals were found in surface waters at night, suggesting that a sharp temperature gradient could restrict its movements. McNaught and Hasler (1966) also found evidence that a sharp thermal gradient presented a hindrance to *L. macrurus* movement in L. Michigan. Wilson and Roff (1973) reported a mean depth of 50-62 m for the *L. macrurus* population in Lake Ontario. While usually below 20 m, the animals did reach the surface waters at night through the summer and fall, although apparently a distinct epilimnion did not form during their study. Conway et al. (1973), working in Lake Superior, found that *L. macrurus* was present at all depths from June through early August, but was restricted to depths below the thermocline when it was present. *L. macrurus* appeared to be restricted to a temperature below 12° C. Wells (1960) found that abundances of *S. calanoides* in Lake Michigan were usually highest below 20 m. This species was rare in his collections, but since his tows only extended to 40 m, it is possible that the majority of its populations were missed. Conway et al. (1973) rarely found this animal above 40 m in Lake Superior. It is clear, therefore, that shallower tows run the risk of substantially underestimating the abundances of these species, or missing them altogether.

Lengths of Migrating Individuals

In Lakes Michigan and Huron where migration was occurring, the larger cladocerans appeared to exhibit greater amplitudes of migration than the smaller organisms. This phenomenon was first suggested by Wilson and Roff (1973) when they suggested a relationship between zooplankton body weight and range of migration. Haney and Hall (1975) found that for *Daphnia pulex* and *Daphnia galeata mendotae*, filtering activity at the surface at night was up to 25x higher due to the presence of larger-bodied animals, which were absent from surface waters during the day. Wright et al. (1980) used a model to predict that larger individuals and gravid females of *Daphnia parvula* would exhibit stronger migrations, and this has been observed for *Daphnia hyalina galeata* and *Daphnia galeata mendotae*, respectively (Guisande et al., 1991; Lampert, 1992)

Both cyclopoid and diaptomid copepodites, as well as mature *Leptodiaptomus minutus*, also showed a significant relationship between body length and depth of migration. Wells (1960) found that diaptomus copepodites in Lake Michigan did not migrate as strongly as the adults. For the calanoid copepod *Limnocalanus macrurus*, both Carter (1969) and Wilson and Roff (1973) found that later copepodite instars occurred deeper in the water column than earlier instars.

CONCLUSIONS

Members of both the cladocera and the copepoda were found to undertake vertical migrations below 20 m. These migrations were largely confined to Lakes Michigan and Huron, although the dominant cladoceran in eastern Lake Erie, *Bosmina longirostris*, was found to migrate almost entirely out of the top 20 m during the day. Therefore, care should be taken when interpreting data from these lakes at sites sampled during the day with 20 m tows. Given the plasticity of migratory behavior documented in the literature, even data from lakes in which migration was not documented in the present study should be approached with caution, since differences in predator community structure could have induced migration in the past in species not presently exhibiting such behavior. Underestimates of abundances resulting from 20 m tows are likely to be exaggerated when abundances are converted to biovolumes, particularly for cladocerans, by the tendency of larger animals to undertake deeper migrations. Previous findings of spatial patterns in zooplankton data generated from 20 m tows should be approached with extreme caution. In cases where the time of sample collection is known, a possible ameliorative measure is to exclude historical data collected during the day from any future trends analysis. However, the large copepods *Limnocalanus macrurus*, *Senecella calanoides* and *Leptodiaptomus sicilis* have depth preferences substantially below 20 m, and have most likely always been underestimated by 20 m tows, regardless of time of collection.

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Table 1. Summary of results of Wilcoxon Signed Rank Test comparison between zooplankton samples collected with 64 μm and 153 μm mesh nets.

Species	W	T+	T-	P(est.)	P(exact)	P<0.05
Bosmina longirostris	-28	25	-53	.29	.301	
Bythotrephes cederstroemi	-4	12	-16	.8	.813	
Cyclops copepodites	-6	36	-42	.845	.85	
Cyclops vernalis	4	16	-12	.8	.813	
Daphnia galeata mendotae	-25	15	-40	.221	.232	
Daphnia longirostris	1	8	-7	1	1	
Daphnia retrocurva	-8	10	-18	.554	.578	
Diacyclops thomasi	4	16	-12	.8	.813	
Diaphanosoma birgei	-13	4	-17	.208	.219	
Diaptomid copepodites	-14	32	-46	.61	.622	
Epischura copepodites	12	45	-33	.666	.677	
Epischura lacustris	7	26	-19	.722	.734	
Eubosmina coregonii	-8	29	-37	.756	.765	
Eurytemora affinis	-9	3	-12	.281	.313	
Leptodiaptomus ashlandi	6	17	-11	.673	.688	
Leptodiaptomus minutus	-8	29	-37	.756	.765	
Leptodiaptomus sicilis	-15	3	-18	.142	.156	
Leptodiaptomus siciloides	-9	3	-12	.281	.313	
Leptodora kindtii	-9	18	-27	.636	.652	
Mesocyclops copepodites	-56	11	-67	.031	.027	*
Mesocyclops edax	-28	25	-53	.29	.301	
Skistodiaptomus oregonensis	-17	19	-36	.415	.432	
Tropocyclops copepodites	14	21	-7	.272	.297	
Tropocyclops prasinus mexicanus	-10	34	-44	.724	.733	

Table 2. Summary of ANOVA results testing for depth preferences and indications of zooplankton migratory behavior in Lakes Huron (HU), Michigan (MI), and Superior (SU). All species with an adequate sample size were tested. Probabilities for factor effects are presented. **Bold** type indicates a significant factor effect at $\alpha=0.05$.

	TIME			DEPTH			TIME x DEPTH		
Species	**HU**	**MI**	**SU**	**HU**	**MI**	**SU**	**HU**	**MI**	**SU**
Cladocerans									
Bosmina longirostris	**0.015**	0.823		**0.003**	**0.017**		**0.012**	**0.015**	
Bythotrephes cedarstroemi	0.261		0.140	0.102		**0.01**	0.932		0.598
Daphnia galeata mendotae	**0.005**	**0.050**	0.655	0.009	0.227	**0.014**	**0.001**	**<0.001**	0.556
Eubosmina coregoni	0.736			0.612			0.285		
Holopedium gibberum			0.803			**<0.001**			0.108
Calanoid copepods									
Diaptomid copepodites	0.161	0.121	0.834	0.839	0.435	0.097	0.566	**0.015**	0.855
Epischura lacustris	0.249	0.070	0.715	0.192	0.492	0.054	0.578	**0.006**	0.775
Epischura copepodites	0.692	0.115		**<0.001**	**0.015**		0.761	0.070	
Leptodiaptomus ashlandi	**0.034**	0.055		0.104	0.407		0.121	0.058	
Leptodiaptomus minutus	**0.021**	**0.019**		**0.031**	**0.012**		**0.011**	**<0.001**	
Leptodiaptomus sicilis	0.258	0.185	0.552	**<0.001**	**0.002**	**0.021**	0.305	0.366	0.609
Limnocalanus macrurus		0.239	**0.004**		**<0.001**	**<0.001**		0.743	**0.016**
Senecella calanoides		0.155	0.369		**0.036**	**<0.001**		0.155	0.369
Skistodiaptomus oregonensis		0.100			0.054			0.117	
Cyclopoid copepods									
Cyclops copepodites	0.136	**0.002**	0.312	0.605	0.142	**<0.001**	0.460	**<0.001**	0.555
Diacyclops thomasi	0.062	**<0.001**	0.226	0.164	**0.002**	**0.004**	0.170	**<0.001**	0.198
Tropocyclops prasinus		0.383			**0.007**			0.380	
Tropocyclops copepodites		0.637			**0.019**			0.568	

Table 3. Results of paired *t*-test comparison of zooplankton abundances estimated from shallow and deep tows at stations sampled during the day in Lakes Erie and Ontario. The following one-tailed hypothesis was tested: $H_0 : \bar{d}_{20-100} \geq 0$

Lake Erie

Species	t	p
Bosmina longirostris	-3.812	**0.03**
Bythotrephes cedarstroemi	0.571	NS
Cyclops copepodite*s*	1.035	NS
Daphnia galeata mendotae	-0.082	NS
Diaptomid copepodites	1.794	NS
Epischura copepodites	2.481	NS
Epischura lacustrus	1.335	NS
Leptodiaptomus minutus	1.621	NS
Leptodiaptomus oregonensis	-0.244	NS
Leptodora kindti	2.969	NS
Mesocyclops copepodite*s*	1.147	NS
Mesocyclops edax	2.179	NS
Tropocyclops copepodites	2.029	NS
Tropocyclops prasinus mexicanus	2.945	NS

Lake Ontario

Species	t	p
Bosmina longirostris	1.486	NS
Daphnia retrocurva	1.909	NS
Diacyclops thomasi	1.266	NS
Diaptomid copepodites	-2.354	**0.05**

Table 4. Results of *t*-tests or Mann-Whitney rank sum tests comparing zooplankton length in deep and shallow day tows. Probabilities of $H_0 : \overline{length}_{deep} - \overline{length}_{shallow} = 0$ are shown, with bold type denoting significance (=0.05). *indicates *t*-test used.

	Huron	Michigan	Superior	Ontario
Bosmina longirostris	**<0.001**	**<0.001**	0.380	0.724
Bythotrephes cedarstroemi	**0.006***		0.262	
Cercopagis pengoi				0.484
Cyclops copepodites	0.241	**<0.001**	0.510	0.620
Daphnia galeata mendotae	**<0.001**	**0.028**	**<0.001**	
Daphnia retrocurva				0.369
Diacyclops thomasi	0.309	0.331	**0.008**	0.914
Diaptomid copepodites	**<0.001**	**<0.001**	0.001	0.152
Epischura copepodites	**0.035**	0.379	0.080	
Epischura lacustris	0.641	0.308	0.407	
Eubosmina coregoni	**<0.001**			0.782
Holopedium gibberum	0.112		0.902	0.862*
Leptodiaptomus ashlandi	0.355	0.068		
Leptodiaptomus minutus	0.319	**0.016**		
Leptodiaptomus sicilis	0.380	**<0.001**	0.340	
Leptodora kindtii				0.203*
Limnocalanus macrurus			**0.025**	**0.020**
Polyphemus pediculus				0.300*
Tropocyclops copepodites		0.061		
Tropocyclops prasinus mexicanus	0.686	0.694		

	Huron	Michigan	Superior	Ontario
Bosmina longirostris	**29.9%**	**13.6%**		
Bythotrephes cedarstroemi	**-3.3%**			
Cyclops copepodites		**0.4%**		
Daphnia galeata mendotae	**23.3%**	**1.0%**	**0.7%**	
Diacyclops thomasi			**-0.1%**	
Diaptomus copepodites	**0.8%**	**49.2%**	**0.3%**	
Epischura copepodites	**0.4%**			
Eubosmina coregoni	**0.5%**			
Leptodiaptomus minutus		**4.5%**		
Leptodiaptomus sicilis		**0.8%**		
Limnocalanus macrurus			**3.3%**	**9.2%**

Figure 1. Summer 1998 GLNPO Zooplankton Sampling Stations

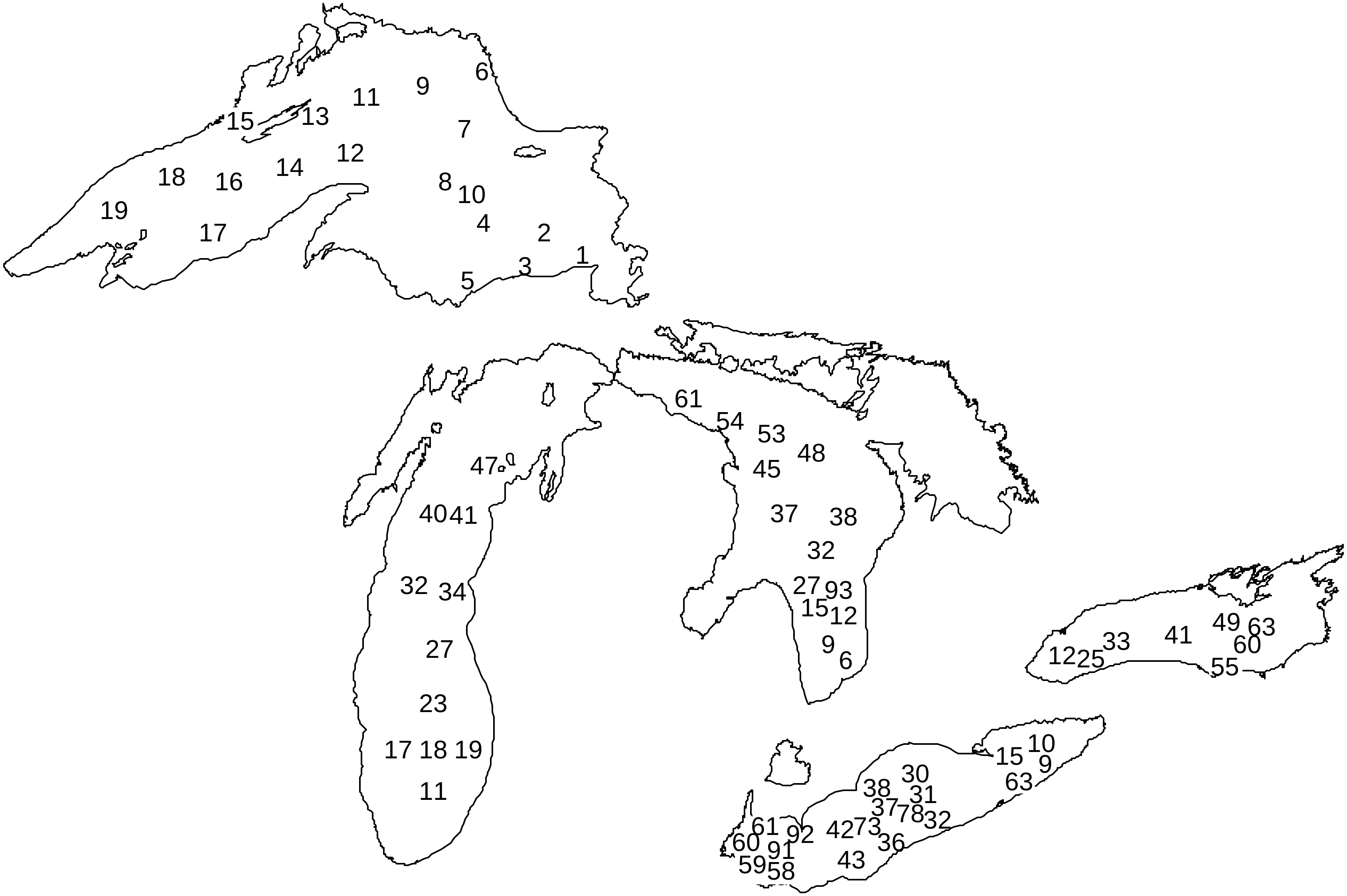

Figure 2. Factor structure of ANOVA analyses. Depth of tow (Depth) and time of day (Time) are the two factors, with species abundance the response variable. Note that sample site is crossed with depth of tow, but nested within time of day.

		TIME OF DAY							
		DAY				NIGHT			
		Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
TOW DEPTH	SHALLOW	—	—	—	—	—	—	—	—
	DEEP	—	—	—	—	—	—	—	—

Figure 3. Differences in Zooplankton Abundance and Community Composition Between Shallow and Deep tows, Lake Huron, Summer 1998

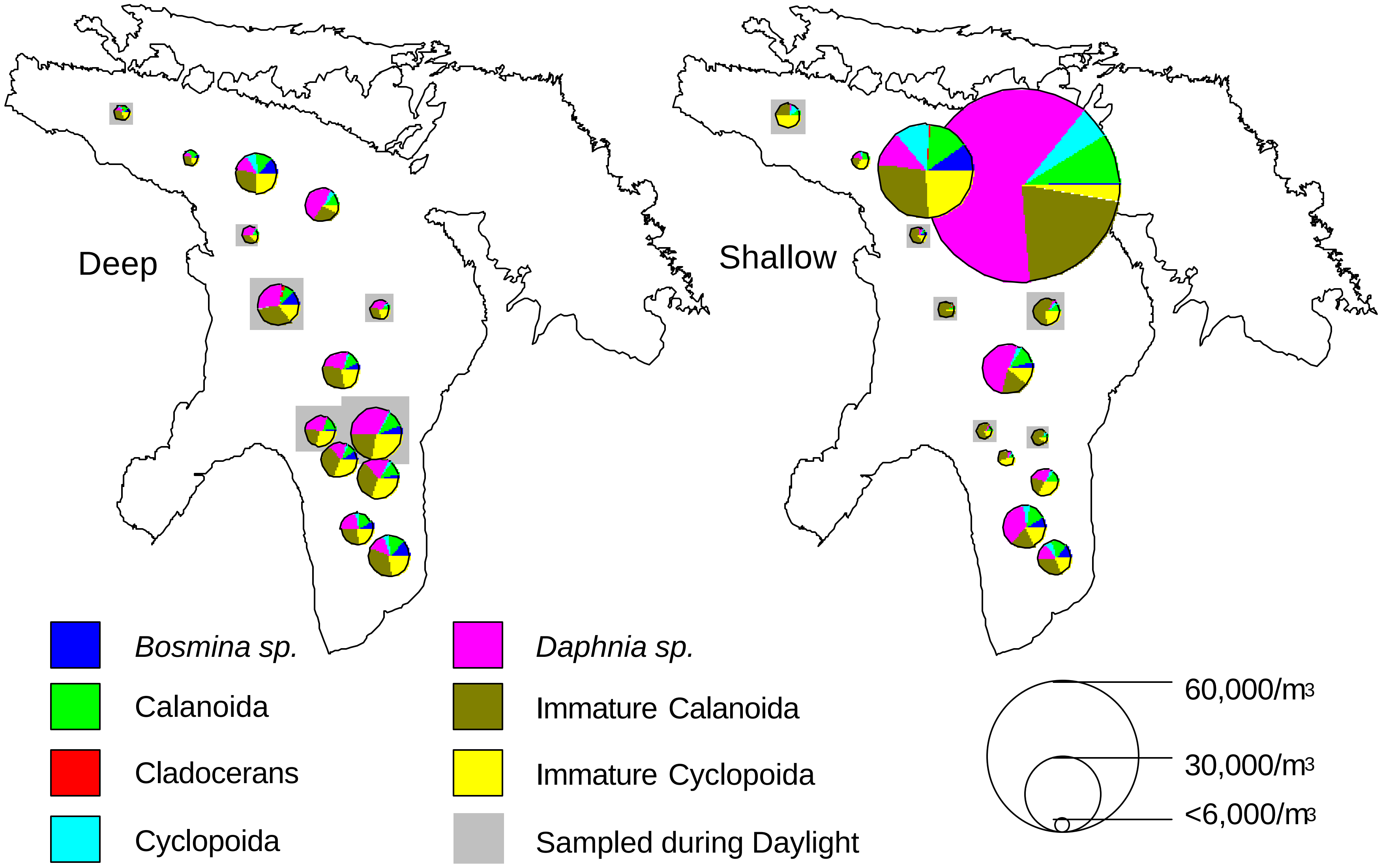

Figure 4. Differences in Zooplankton Abundance and Community Composition Between Shallow and Deep tows, Lake Michigan, Summer 1998

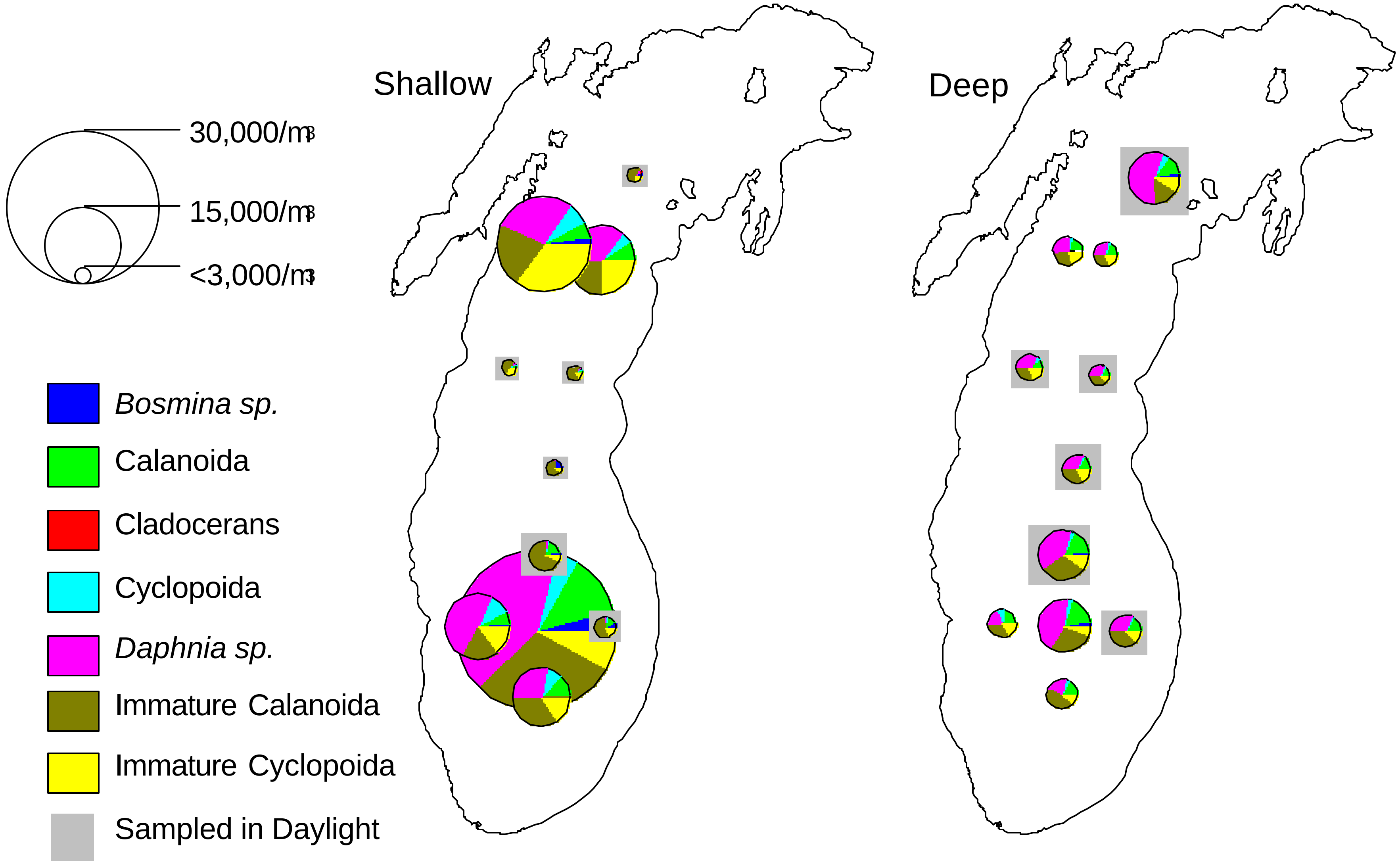

Figure 5. Differences in Zooplankton Abundance and Community Composition Between Shallow and Deep tows, Lake Ontario, Summer 1998

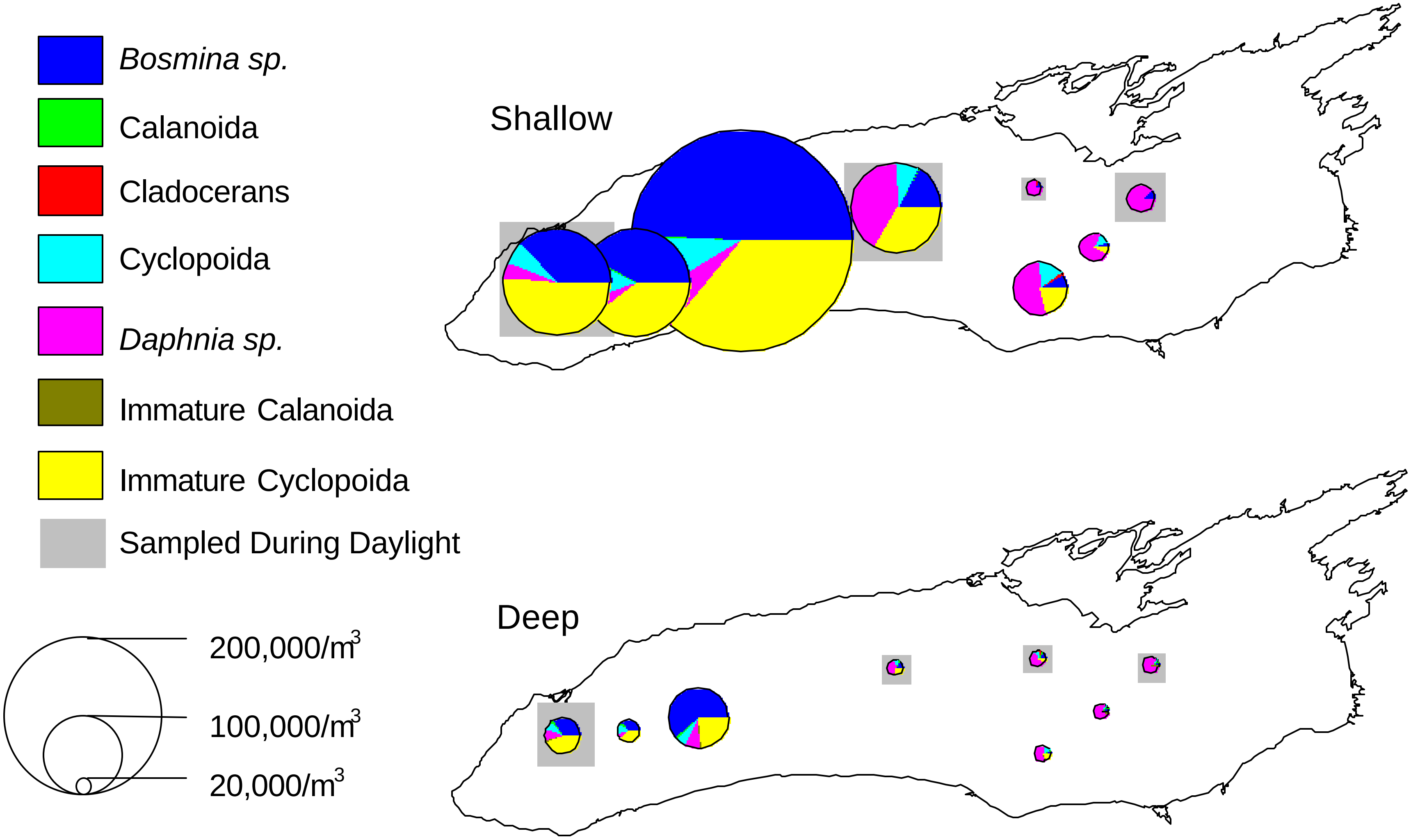

Figure 6. Differences in Zooplankton Abundance and Community Composition Between Shallow and Deep tows, Lake Superior, Summer 1998

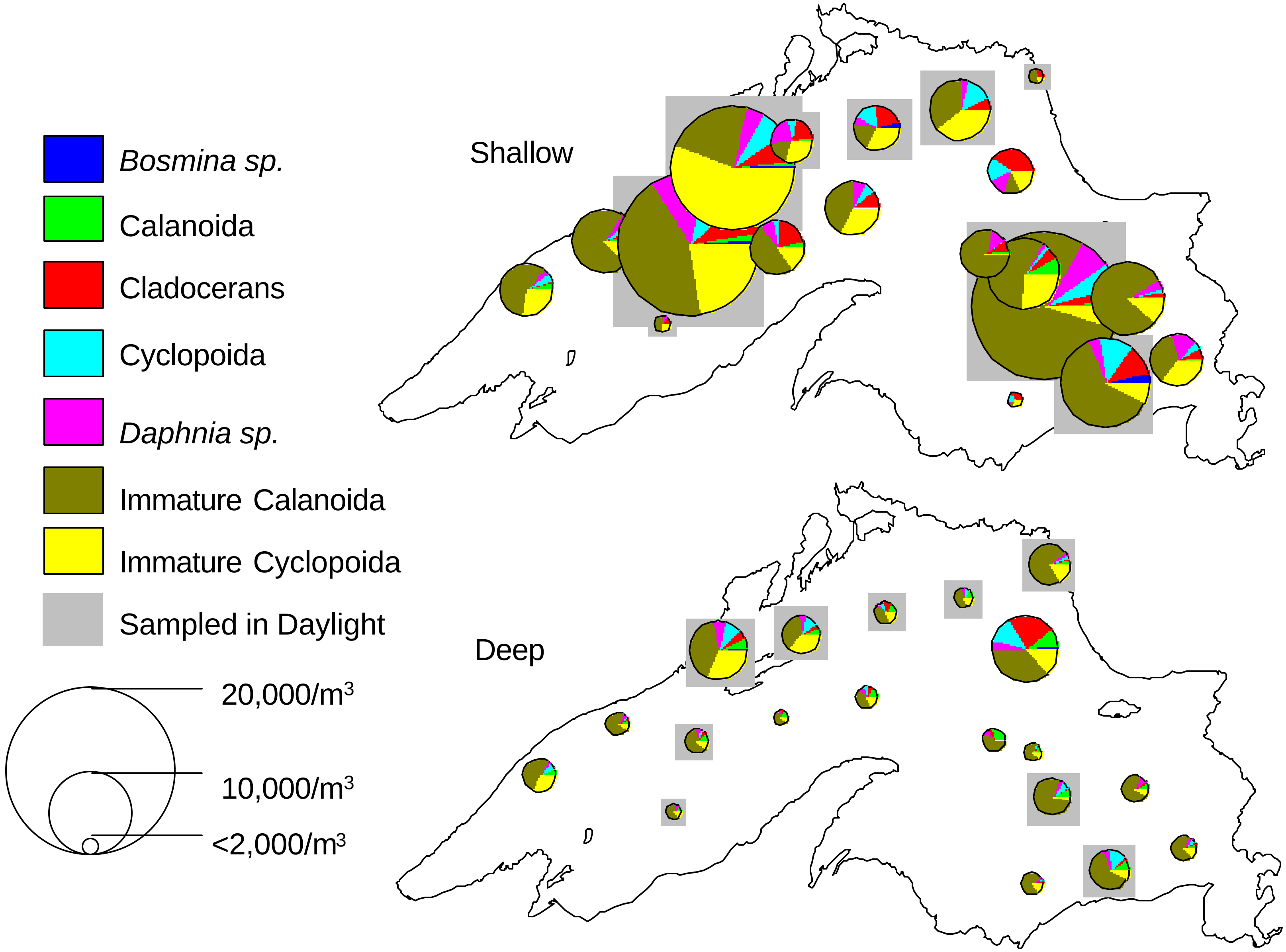

Figure 7. Differences in Zooplankton Abundance and Community Composition Between Shallow and Deep tows, Lake Erie, Summer 1998

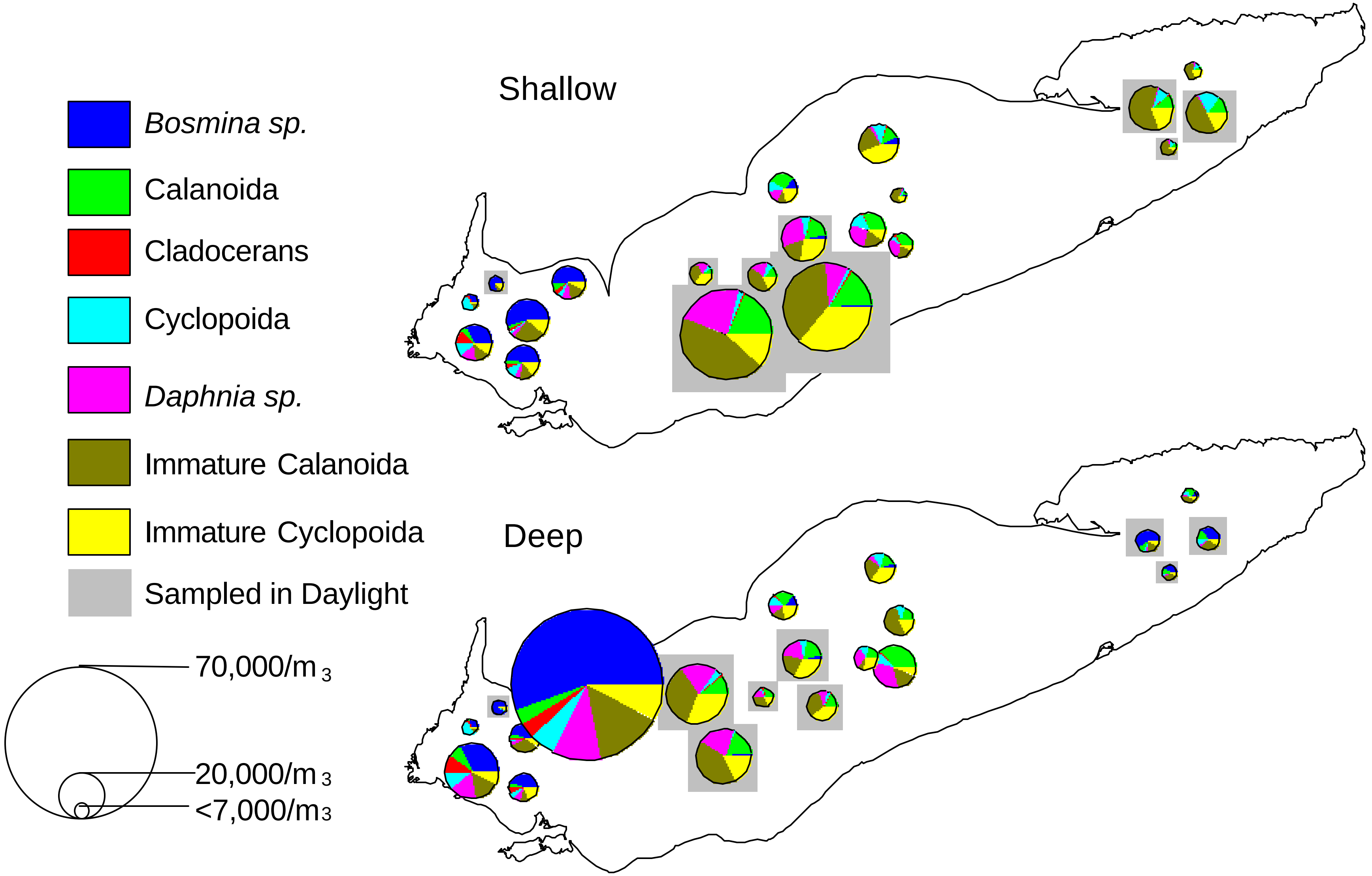

Figure 8. Average relative similarity between zooplankton communities from shallow and deep tows for tows taken at night and during the day. An * indicates a significant difference between day and night comparisons (a=0.05).

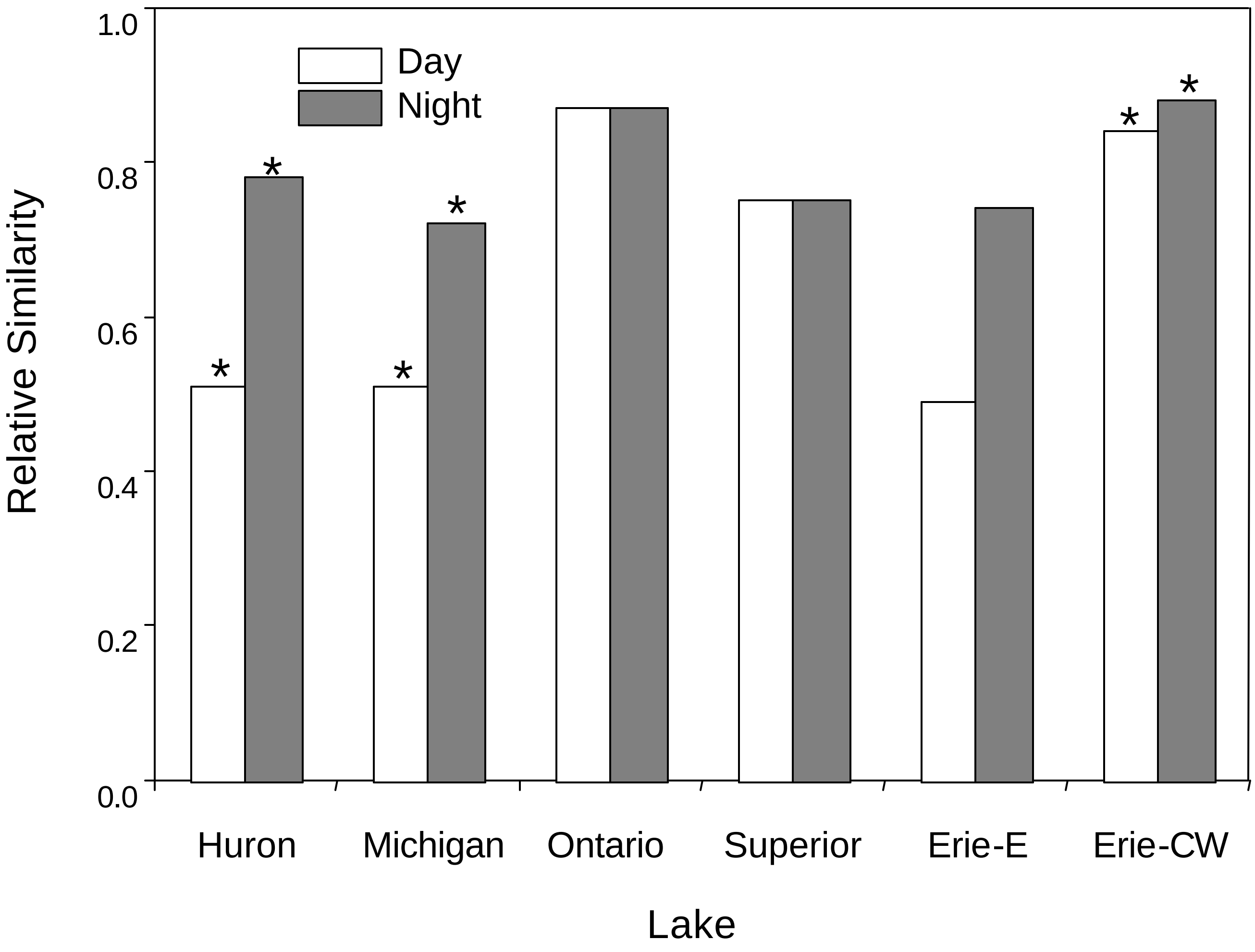

Figure 9. Box plots of *Bosmina longirostris* abundance for both shallow and deep tows taken during the day and during the night. The solid line in the box represents the median abundance while the top and bottom edges of the box are the 25th and 75th percentile values. The whiskers represent the 10th and 90th percentile values, and the solid black dots are outliers.

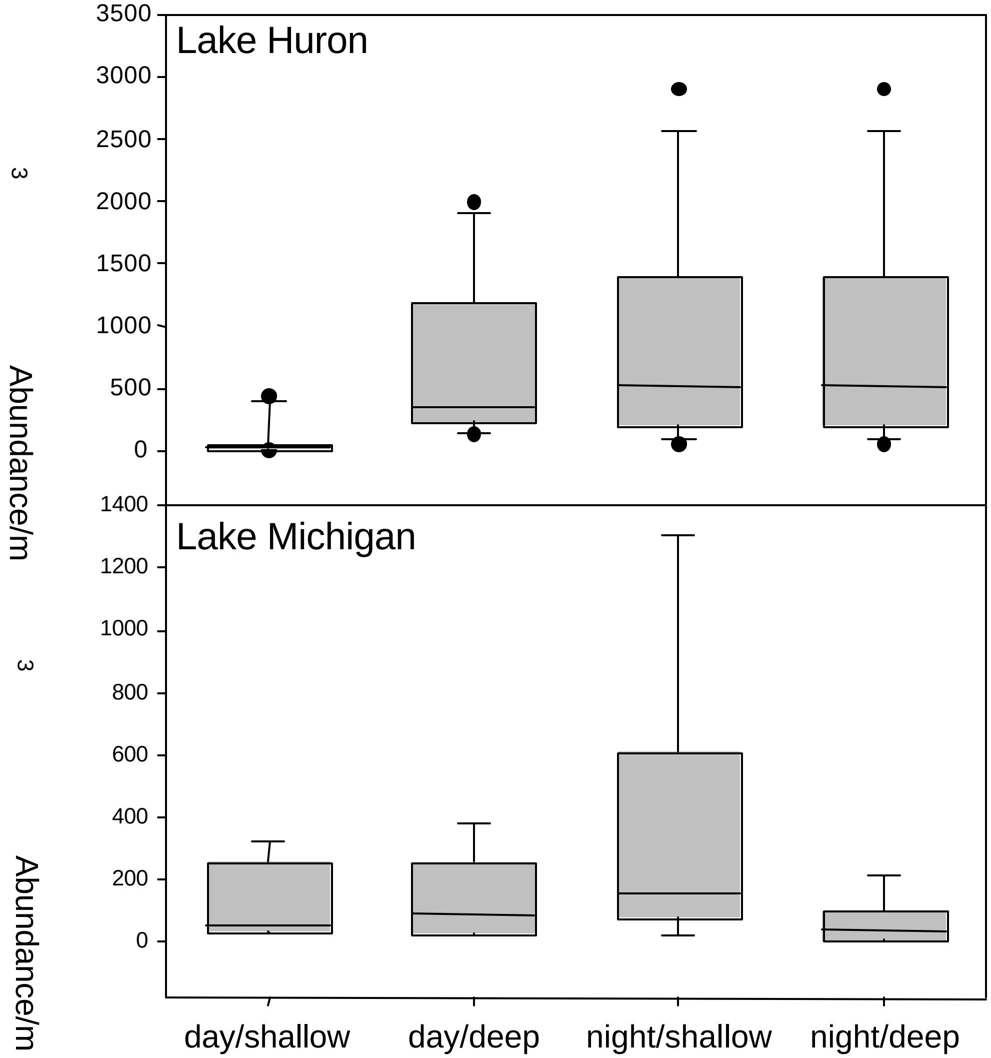

Figure 10. Box plot of *Eubosmina coregoni* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

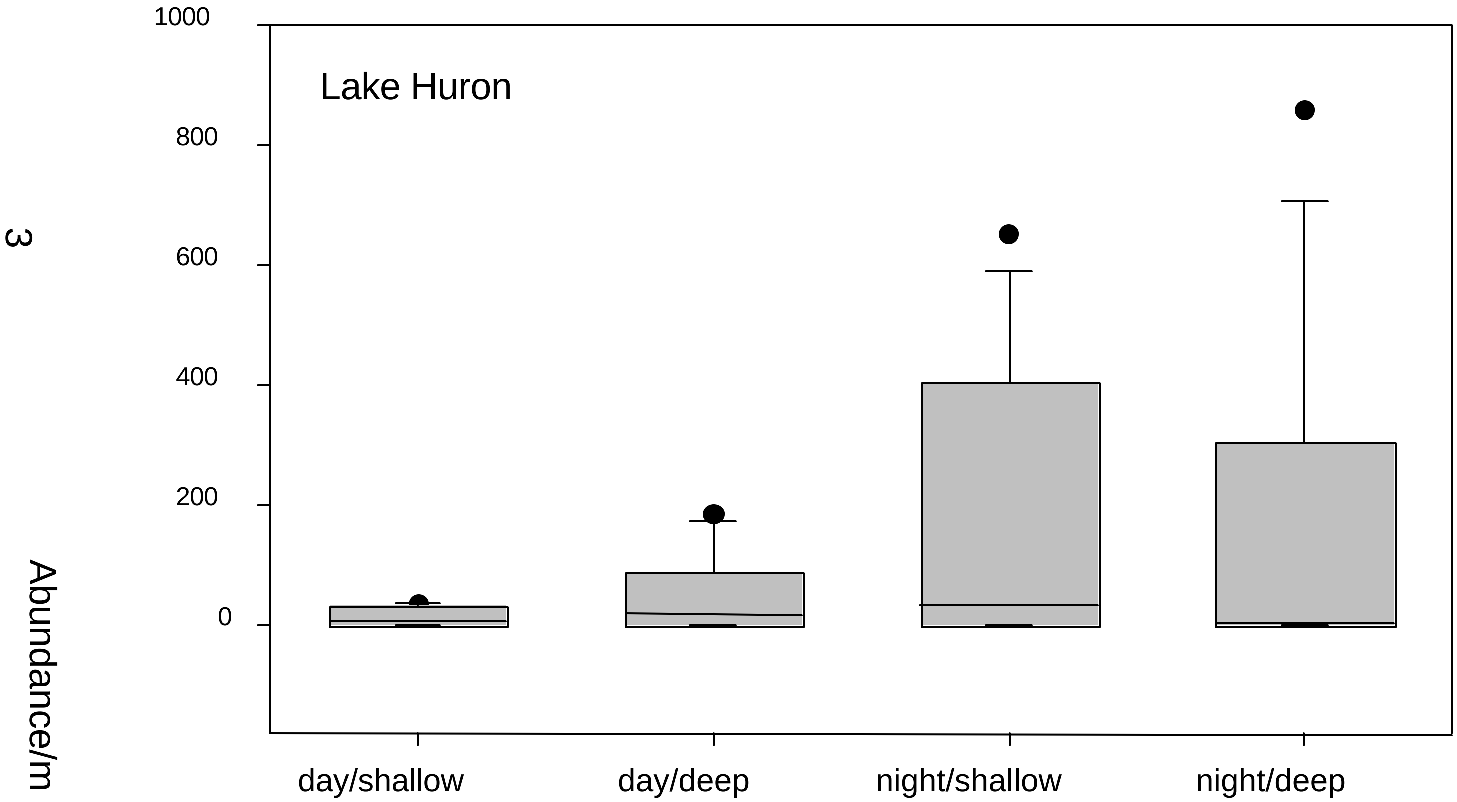

Figure 11. Box plot of *Holopedium gibberum* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

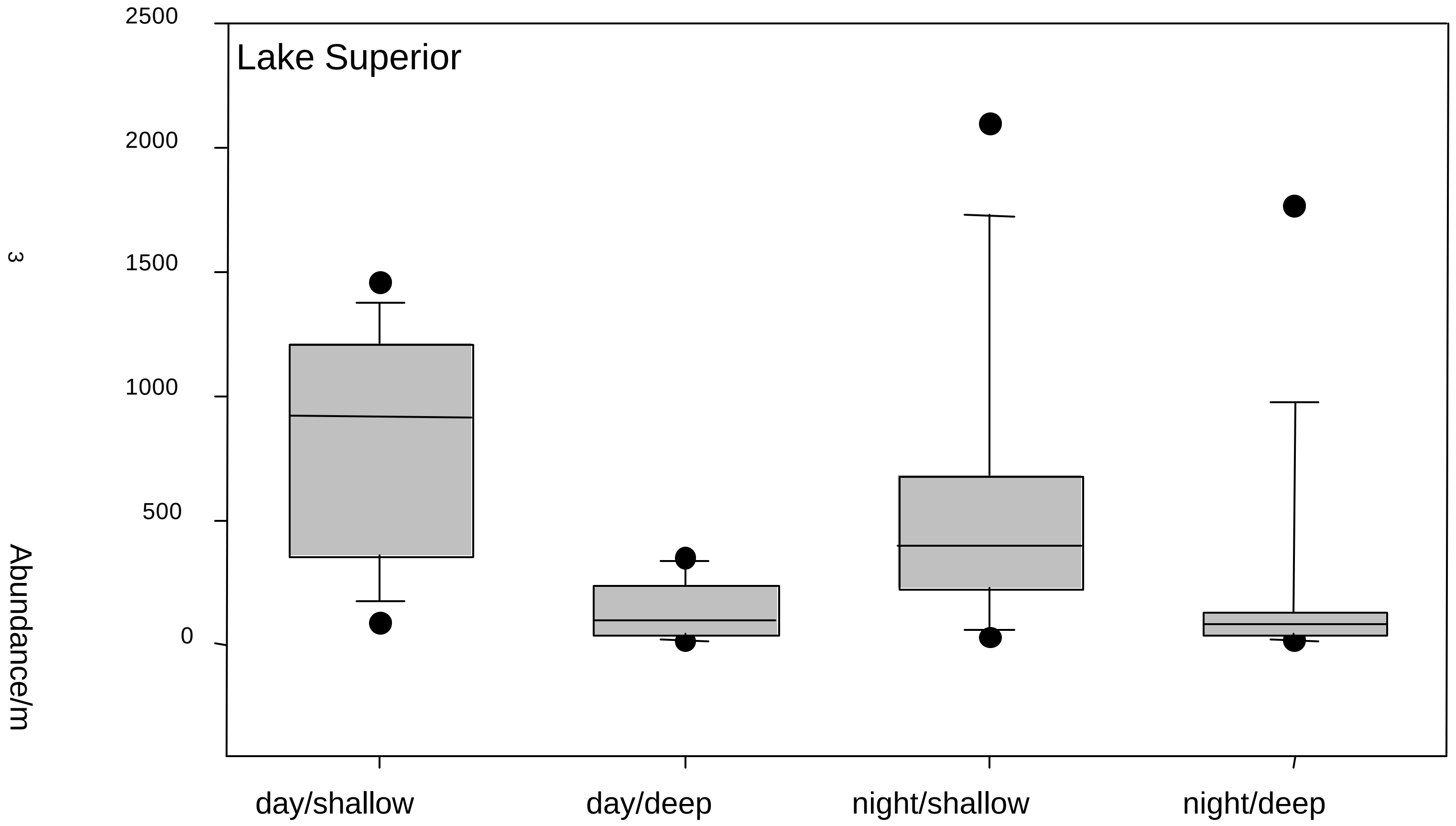

Figure 12. Box plots of *Daphnia galeata mendotae* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

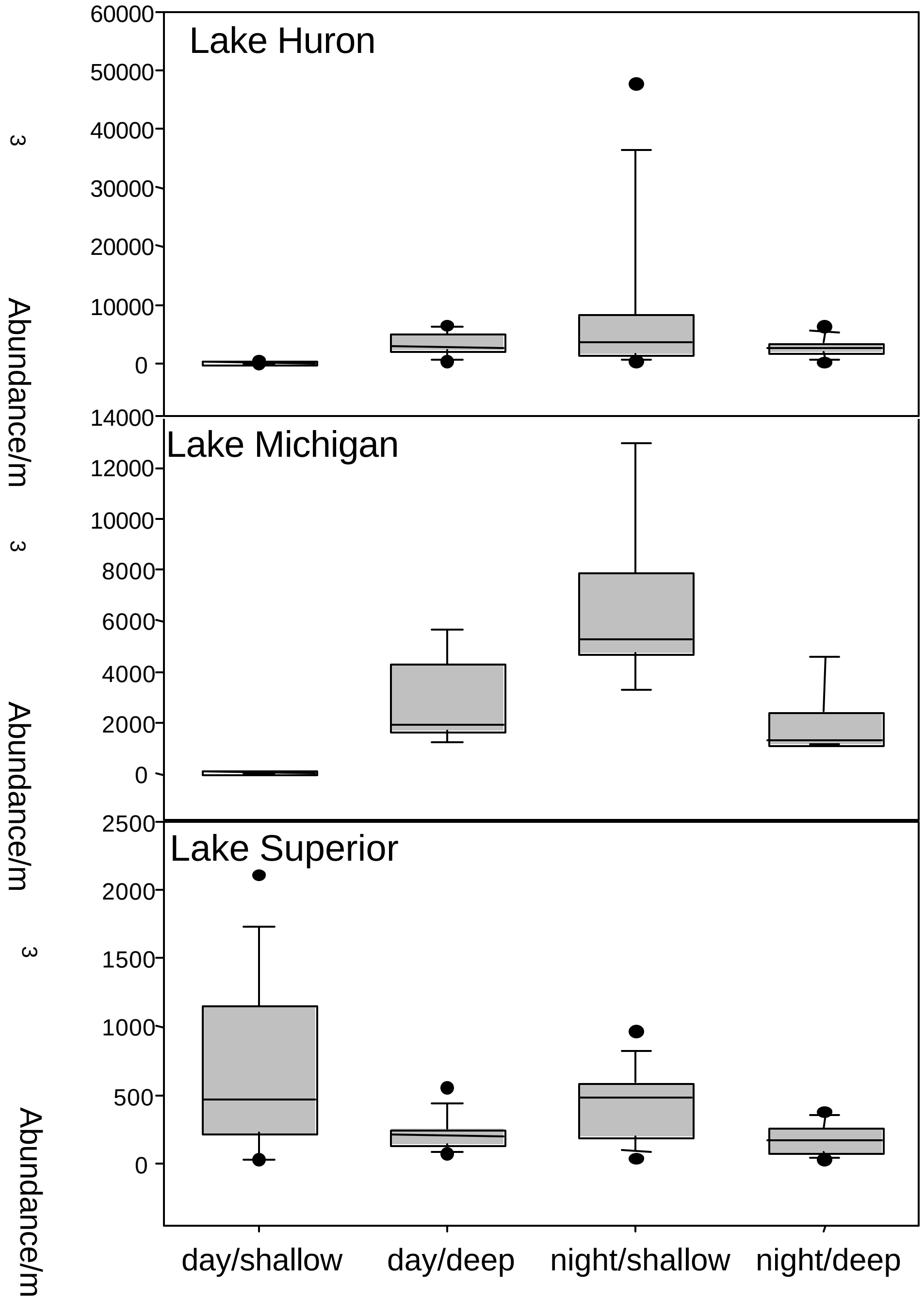

Figure 13. Box plots of *Bythotrephes cedarstroemi* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

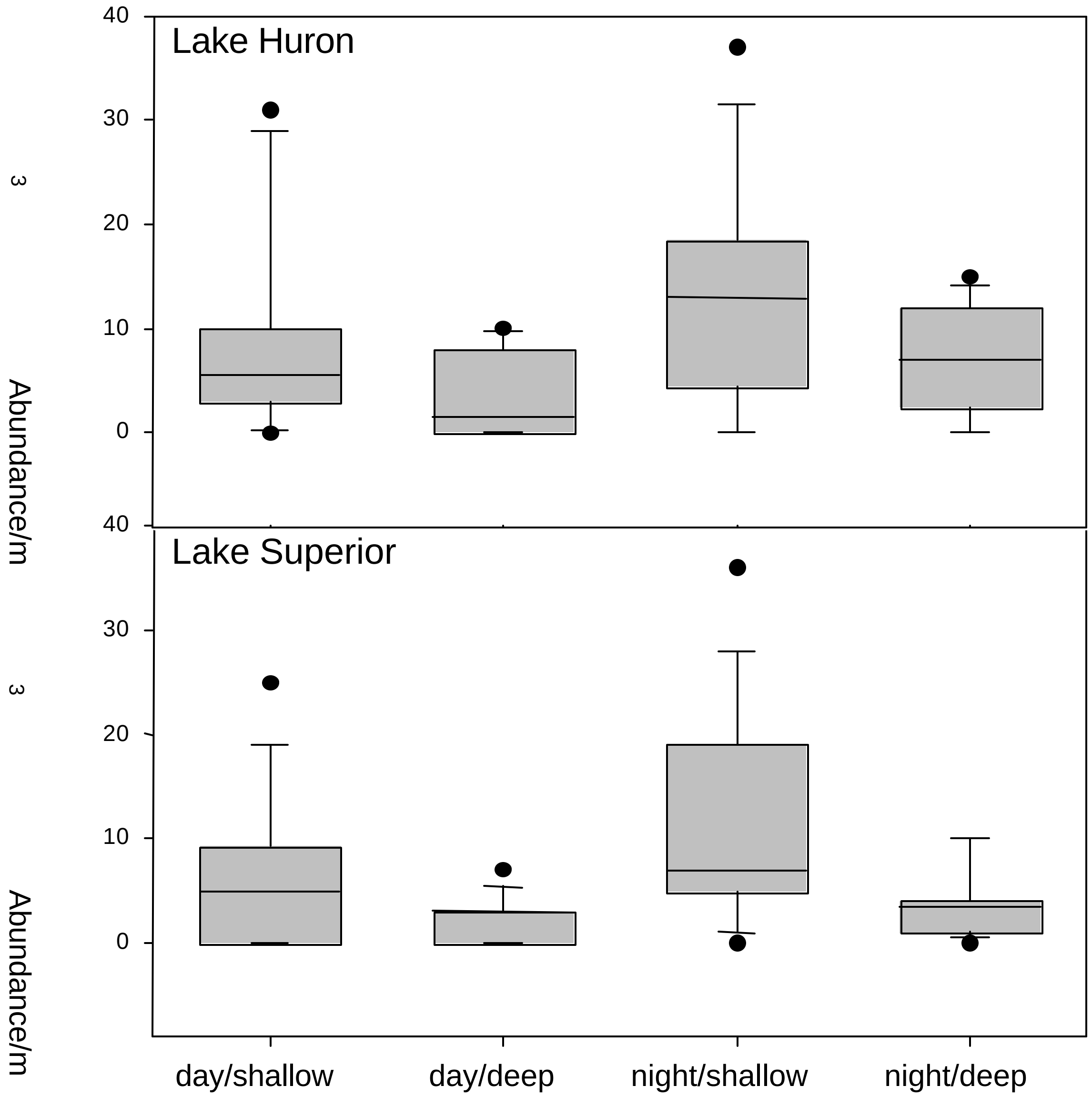

Figure 14. Box plots of *Tropocyclops prasinus mexicanus* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

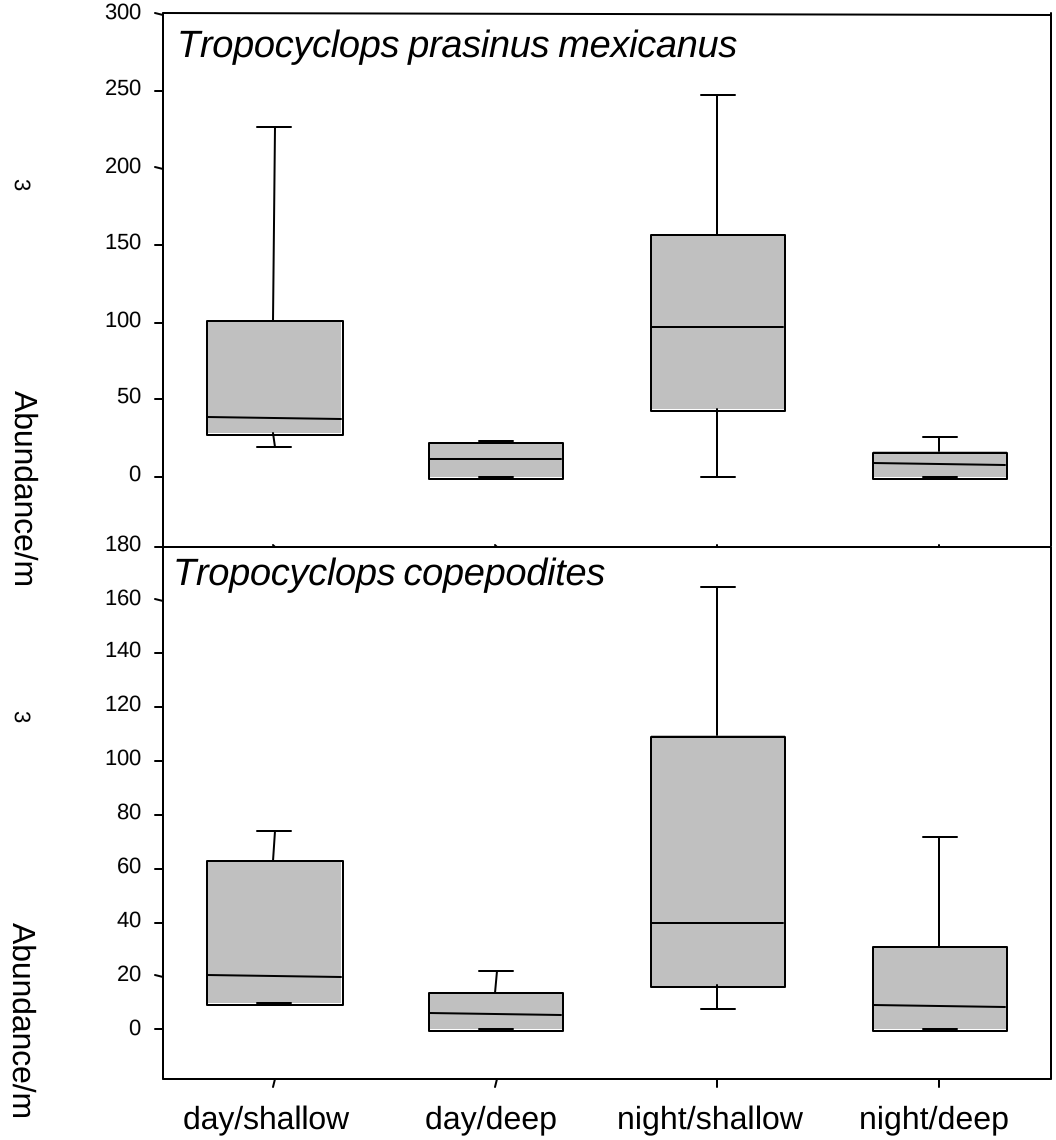

Figure 15. Box plots of *Diacyclops thomasi* and Cyclops copepodite abundance in Lake Michigan for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

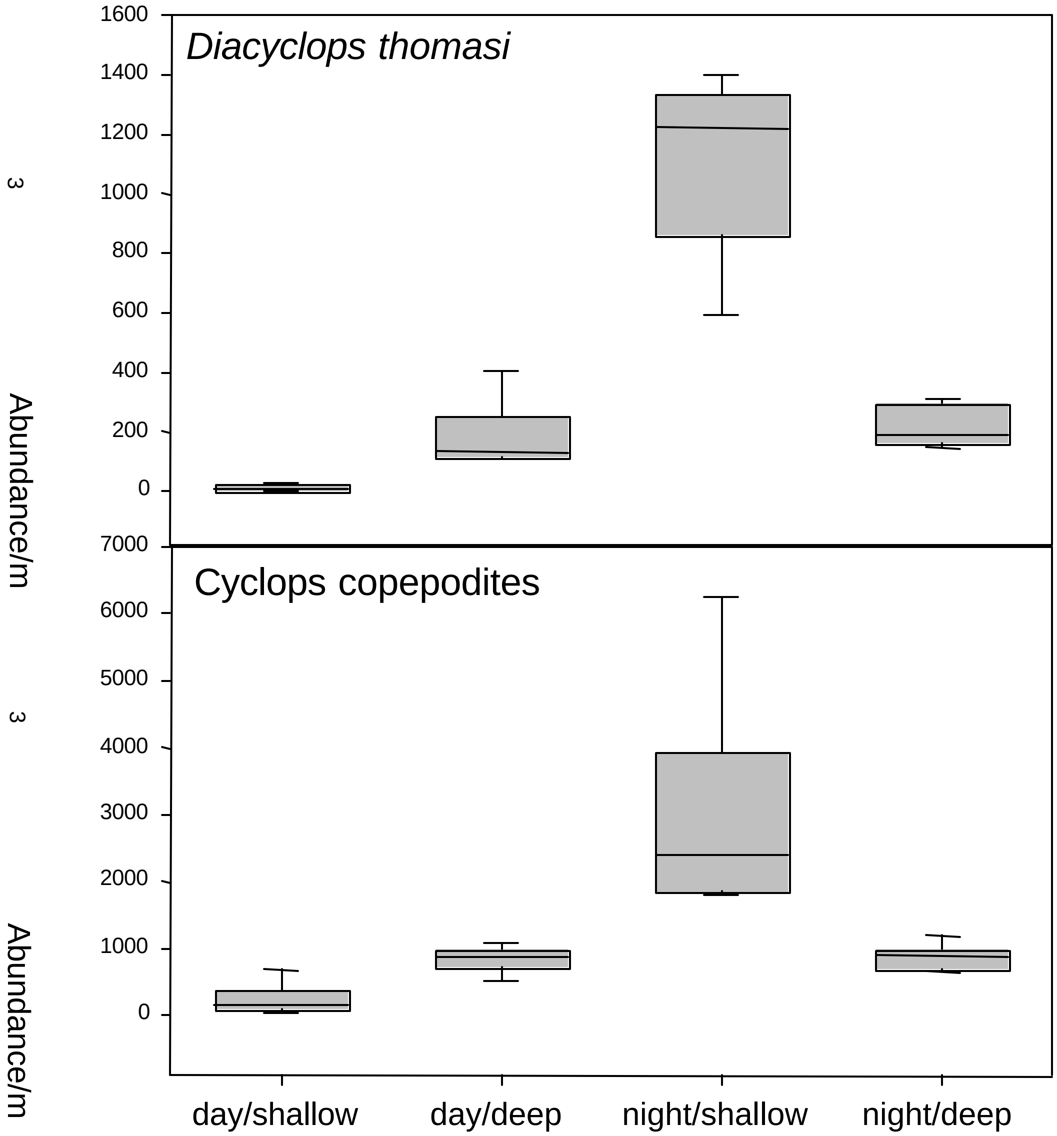

Figure 16. Box plots of *Diacyclops thomasi* and Cyclops copepodite abundance in Lake Superior for both shallow and deep tows taken during the day and during the night. Box plot explanations follow figure 9.

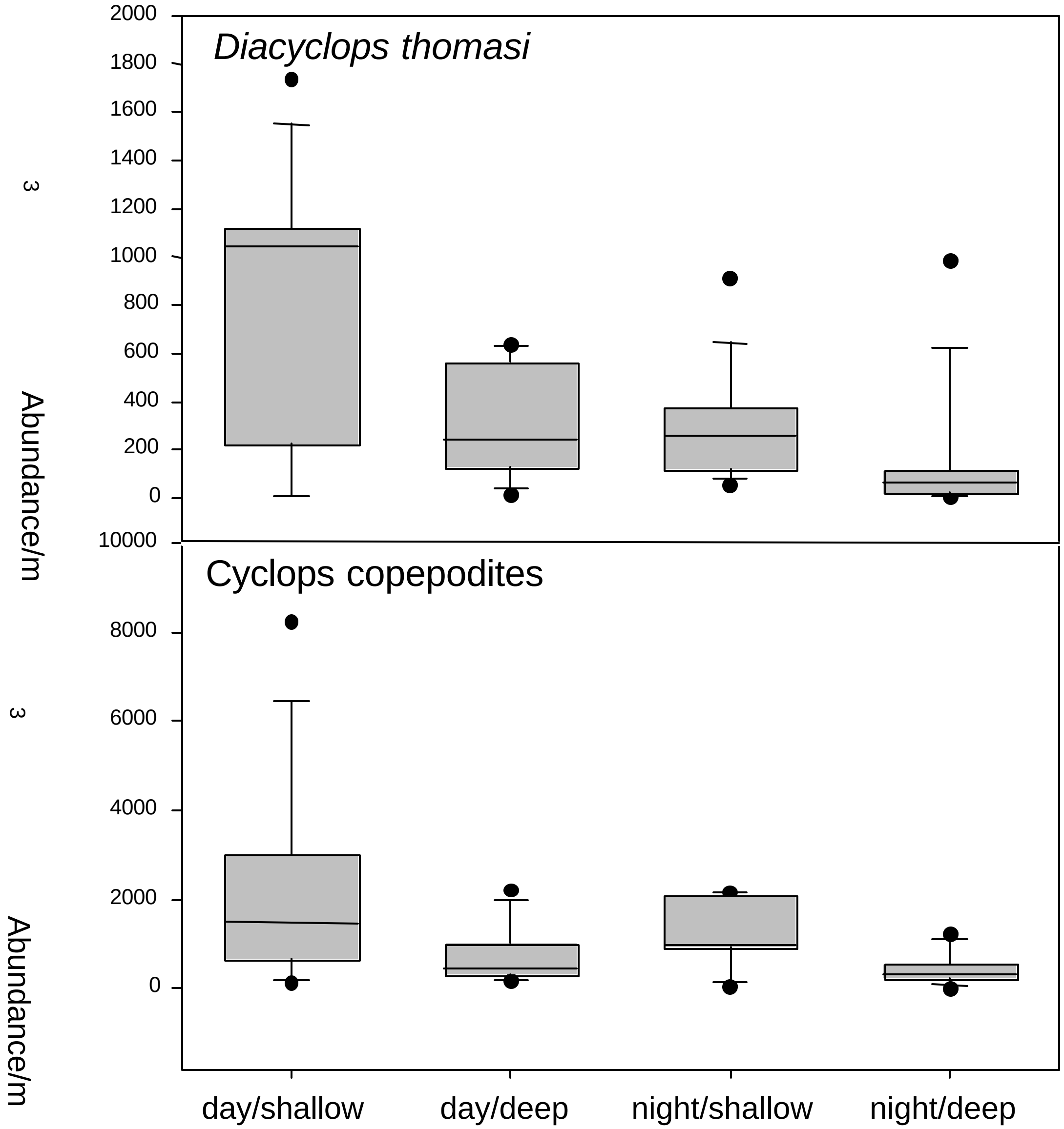

Figure 17. Box plots of *Diacyclops thomasi and C*yclops copepodite abundance in Lake Huron for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

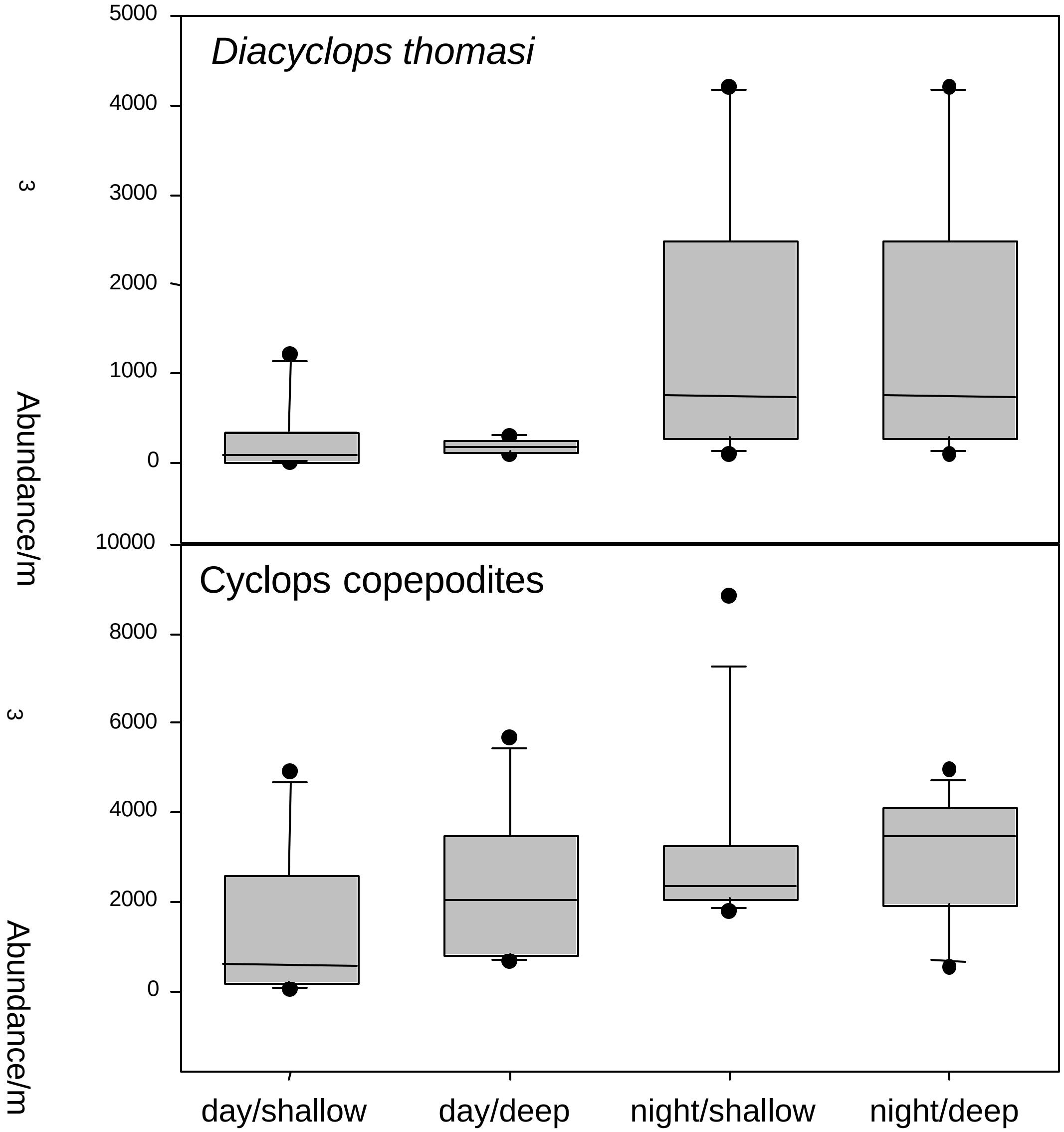

Figure 18. Box plots of Leptod *iaptomus ashlandi* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9

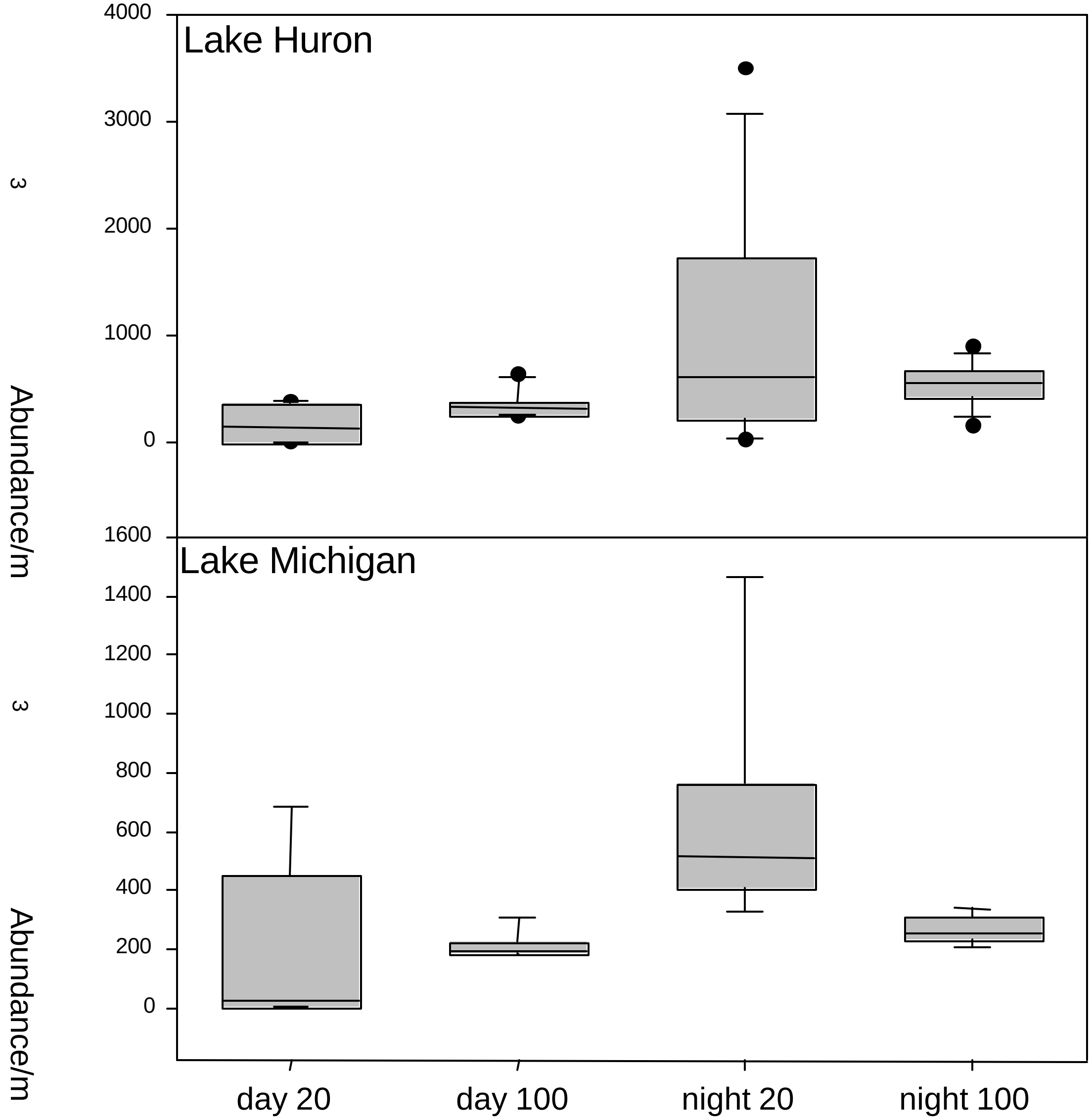

Figure 19. Box plots of *Leptodiaptomus minutus* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow figure 9.

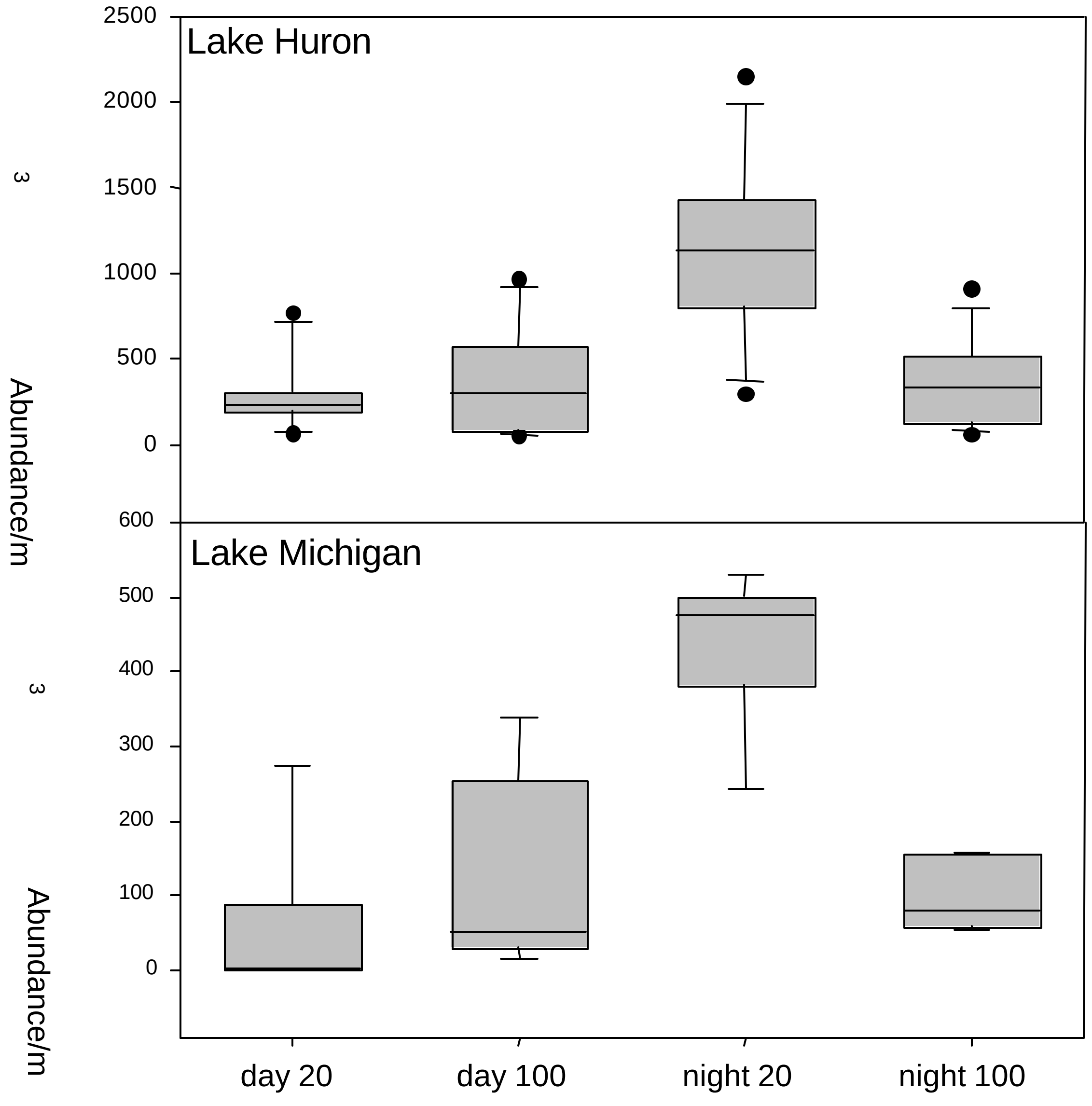

Figure 20. Box plot of *Skistodiaptomus oregonensis* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

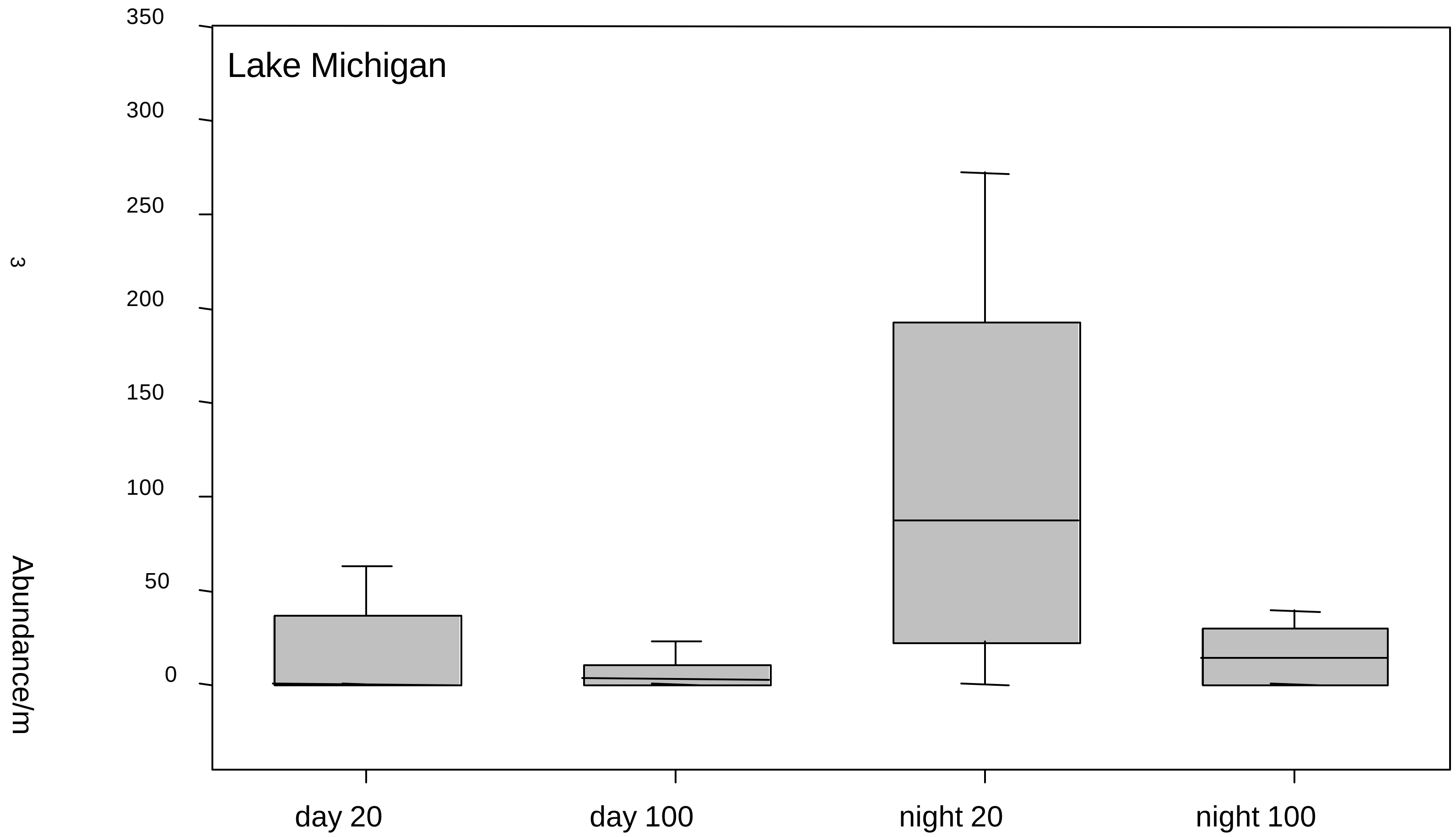

Figure 21. Box plots of abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

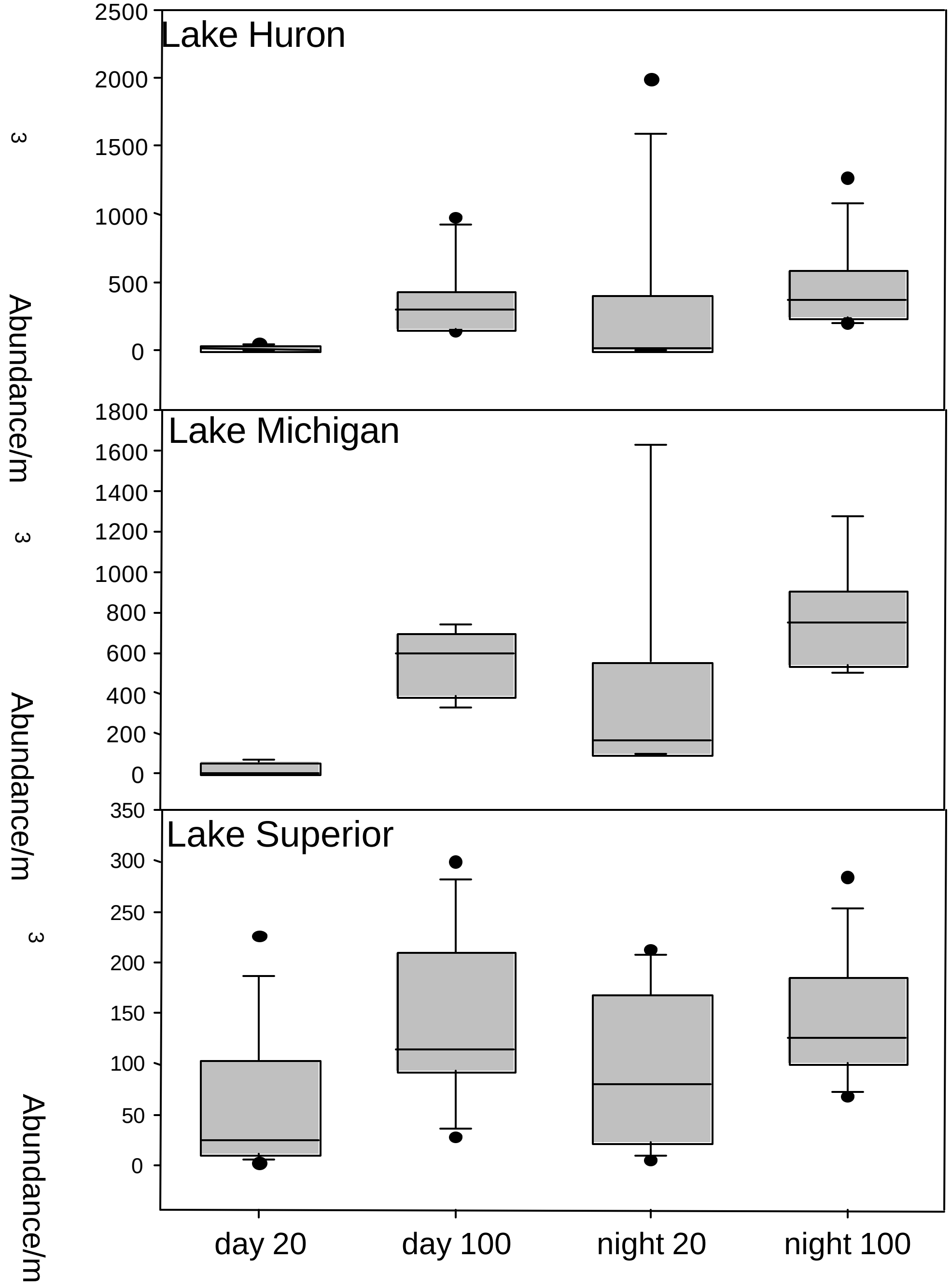

Figure 22. Relative abundance of *Leptodiaptomus sicilis*, as percent of total crustacean abundance at sites in Lakes Superior, Michigan and Huron, estimated by shallow and deep tows, Summer 1998.

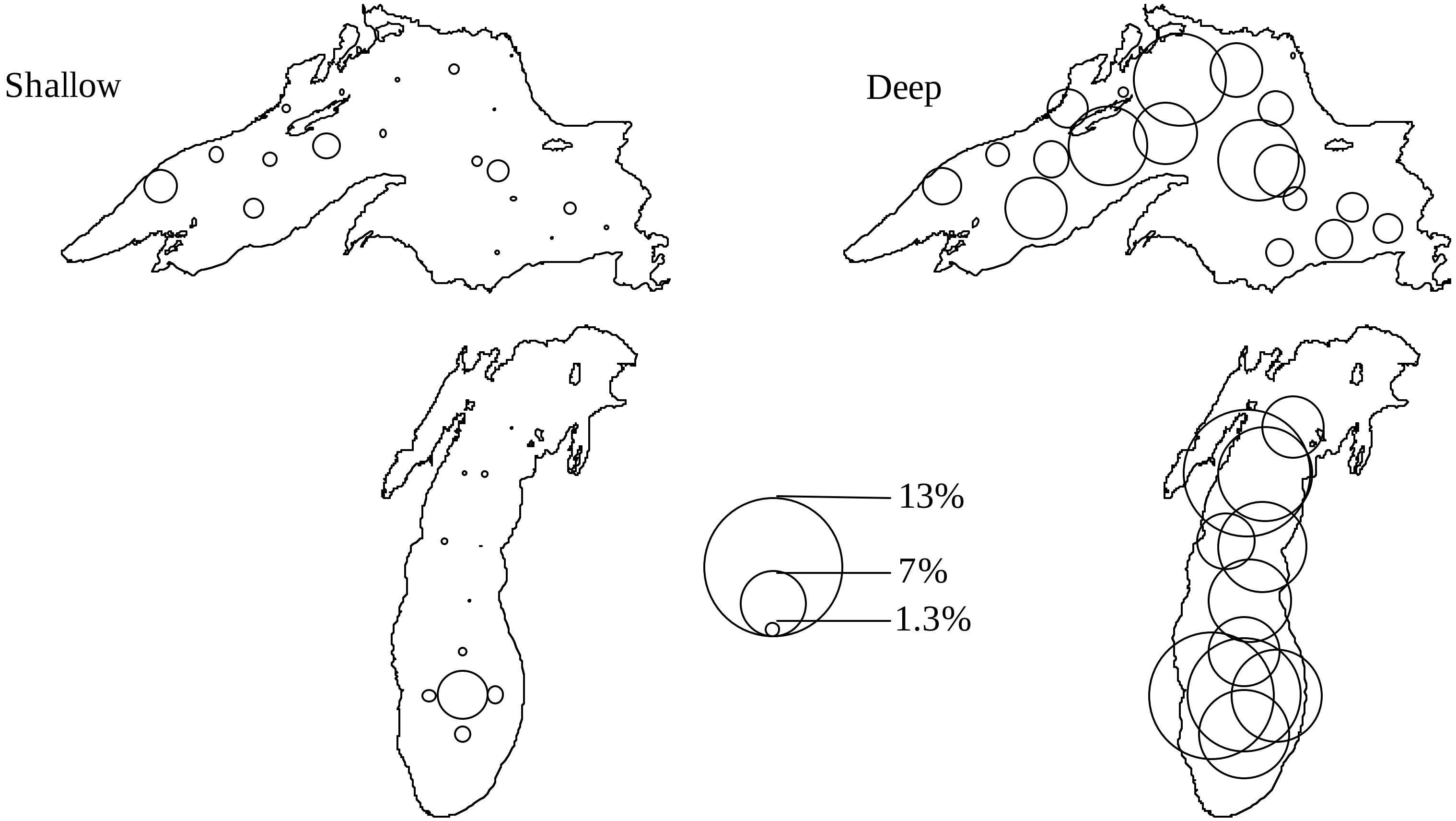

Figure 23. Box plots of Diaptomid copepodite abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

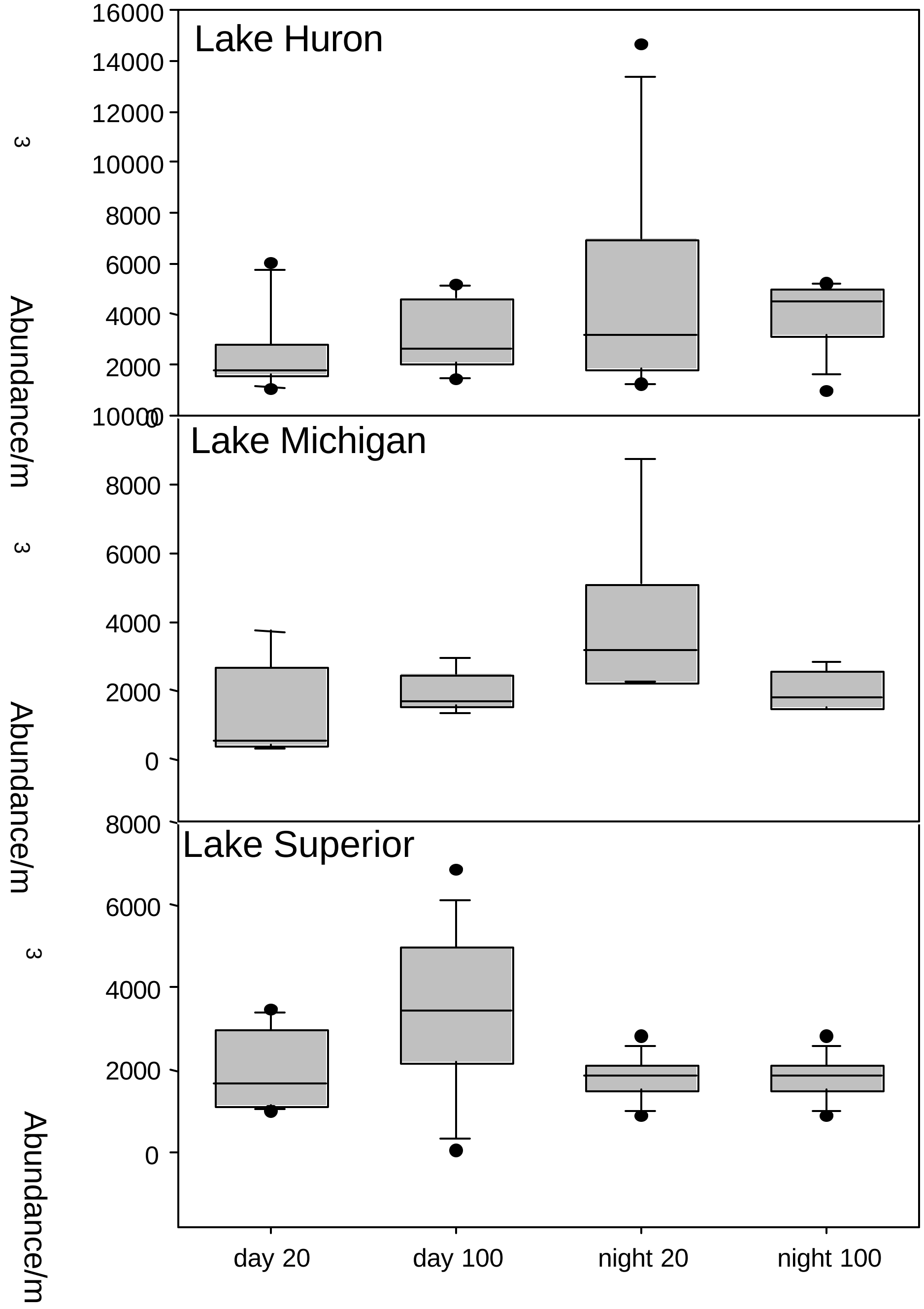

Figure 24. Relative abundance of *Limnocalanus macrurus*, as percent of total crustacean abundance at sites in Lakes Superior, Michigan and Huron, estimated by shallow and deep tows, Summer 1998.

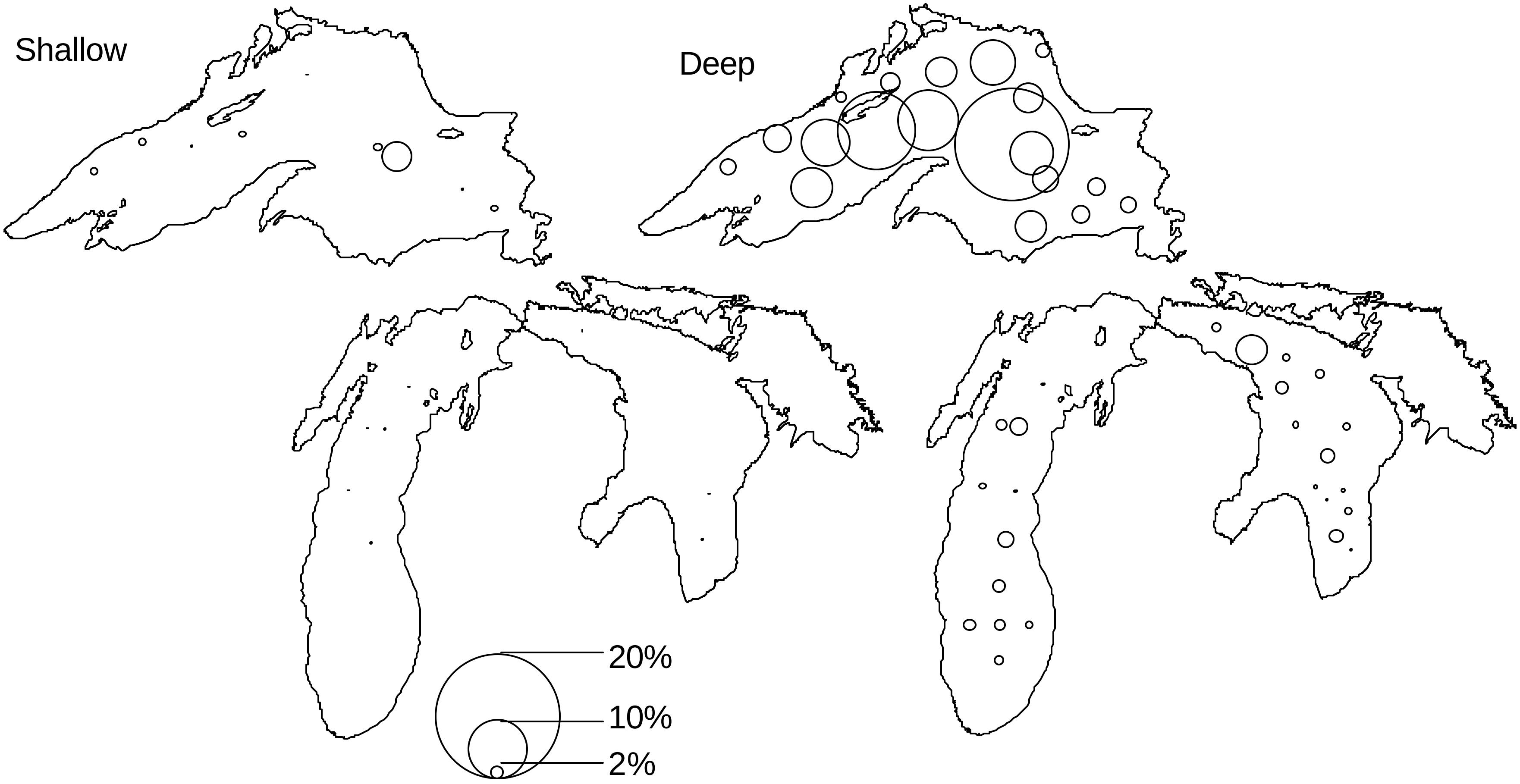

Figure 25. Box plots of *Limnocalanus macrurus* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

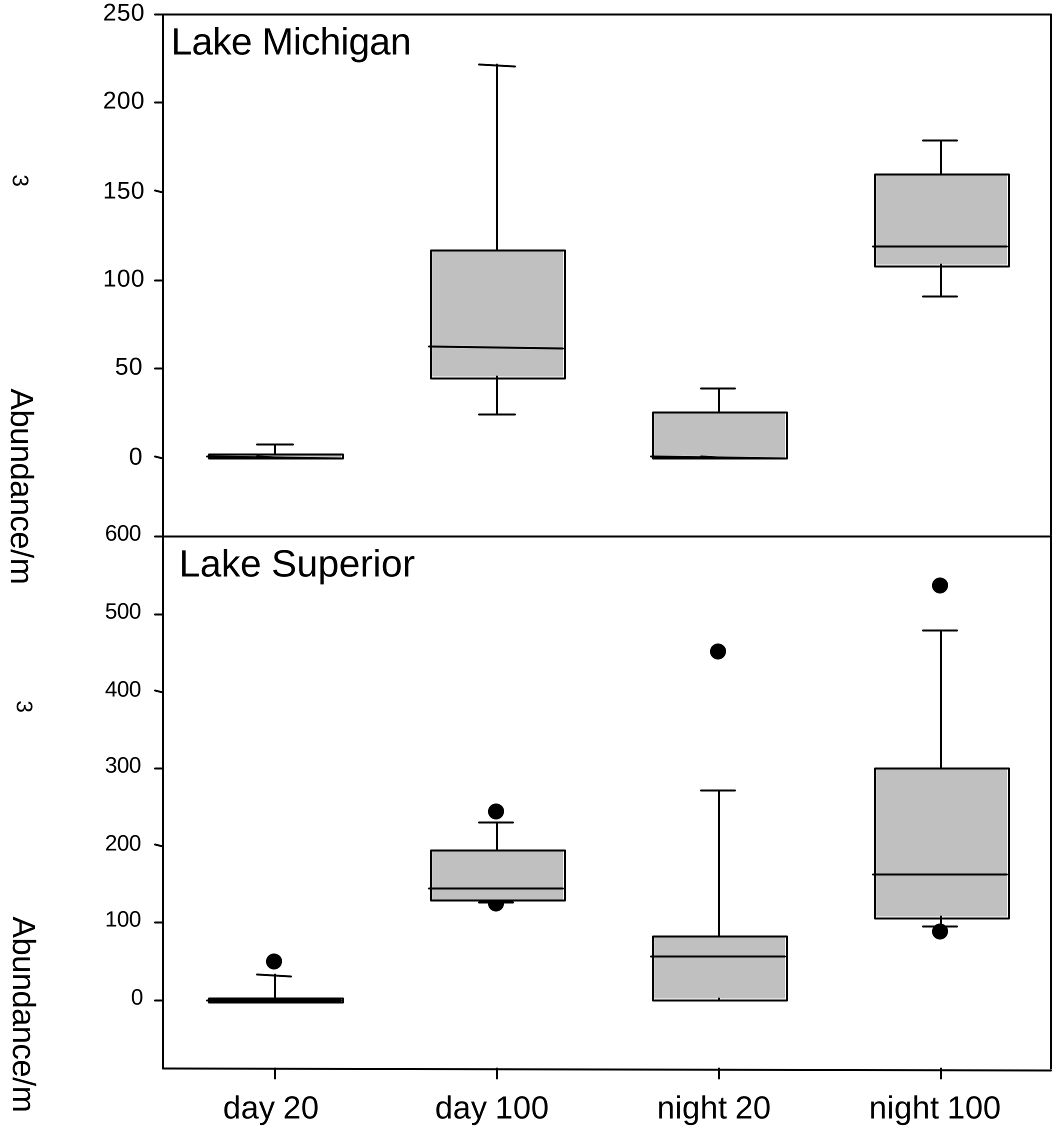

Figure 26. Box plots of *Senecella calanoides* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

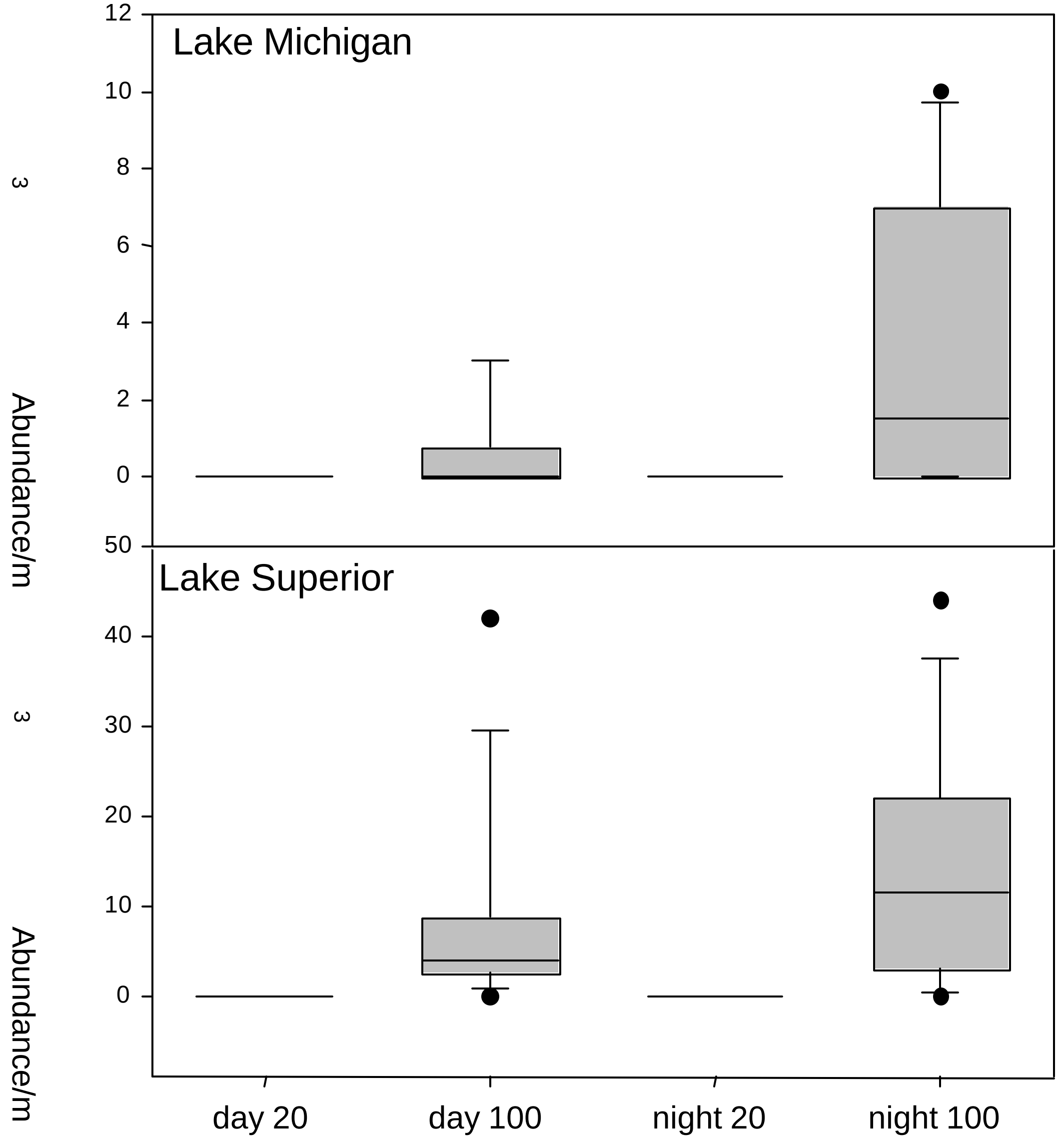

Figure 27. Relative abundance of *Senecella calanoides*, as percent of total crustacean abundance, at sites in Lakes Superior and Michigan, estimated by shallow and deep tows, Summer 1998.

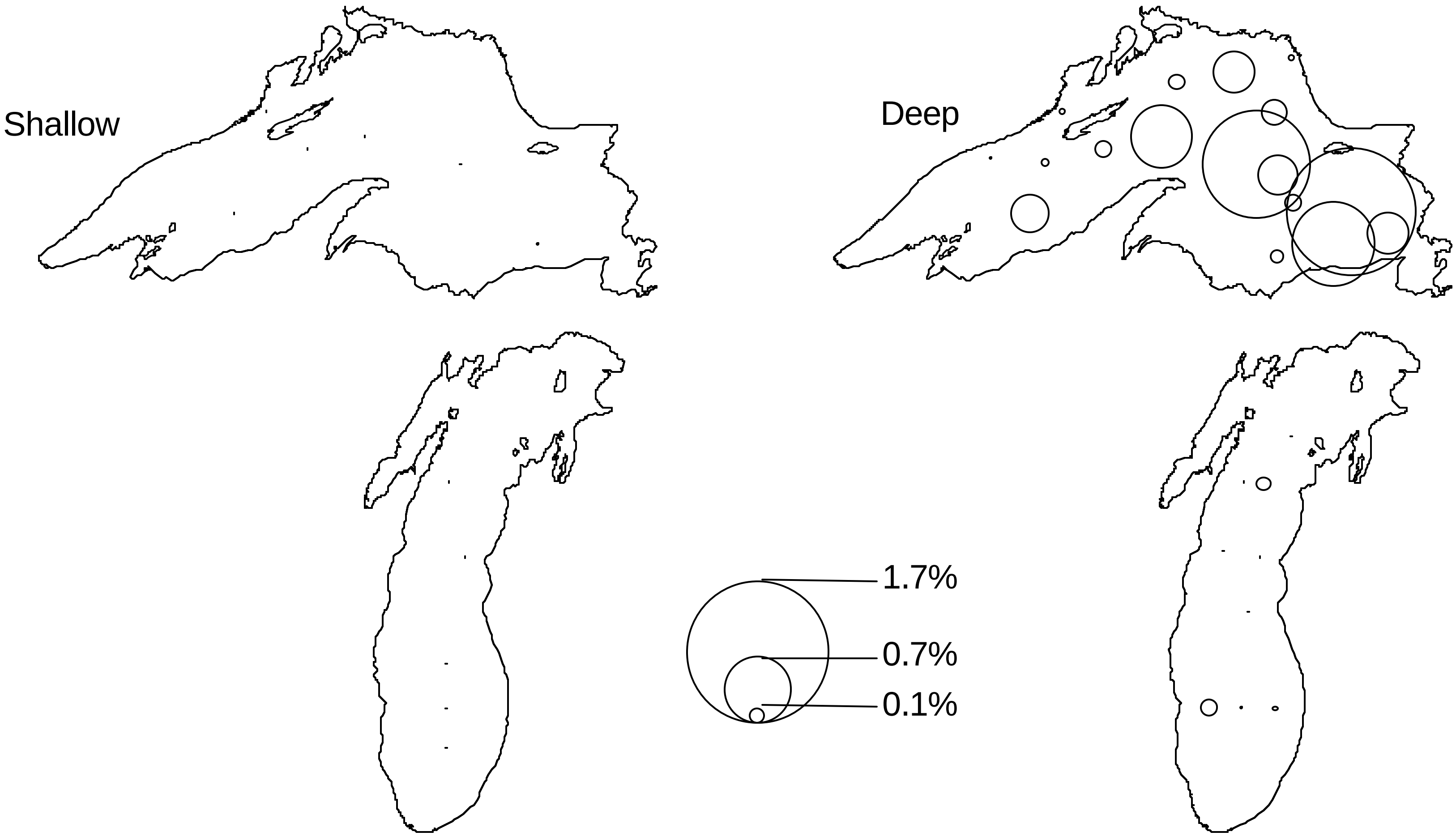

Figure 28. Box plots of *Epischura lacustris* abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow figure 9.

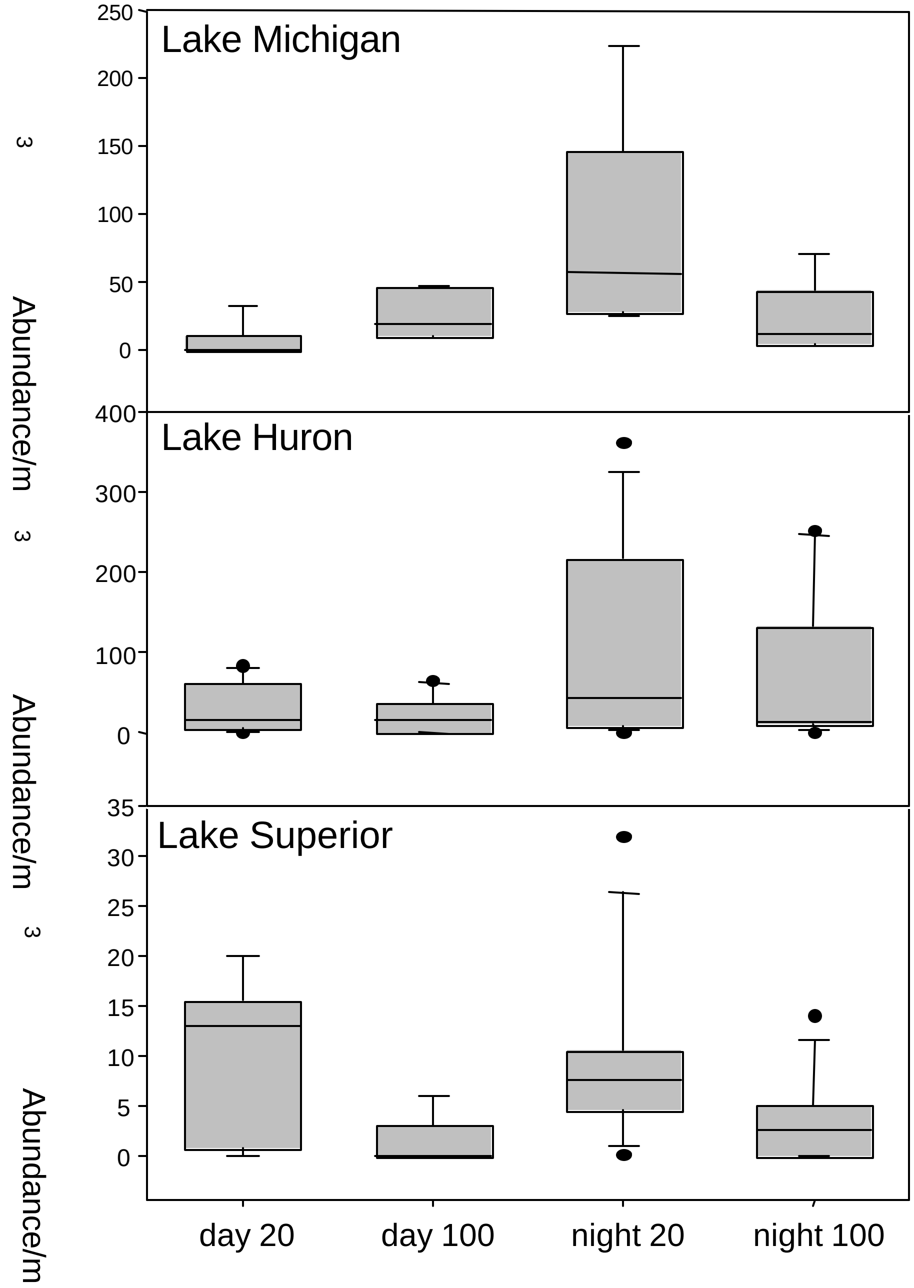

Figure 29. Box plots of *Epischura copepodites*, abundance for both shallow and deep tows taken during the day and during the night. Box plot explanations follow Figure 9.

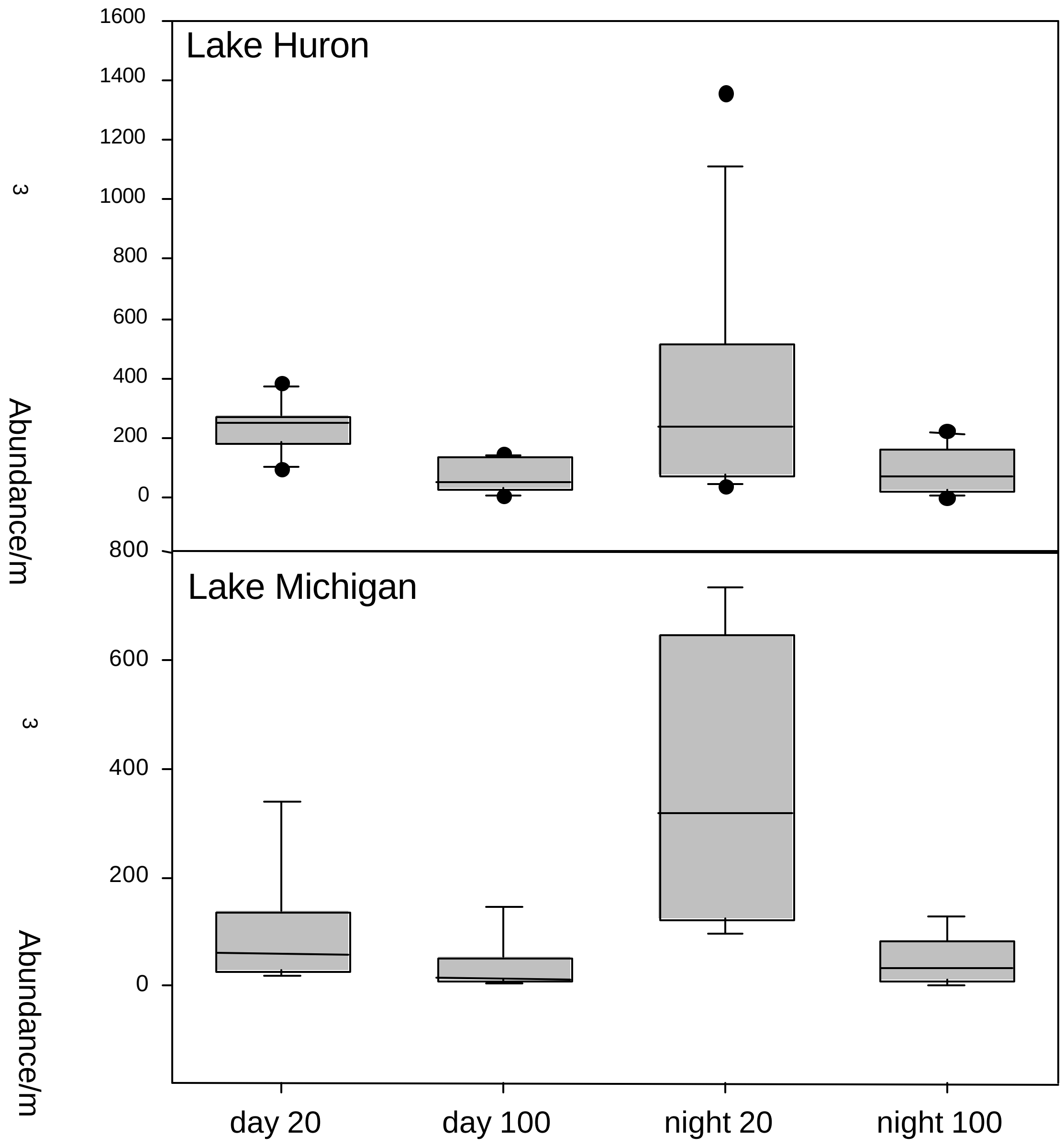

Figure 30. Percent abundance of *Bosmina longirostris* in shallow and deep tows taken during the day