Distribution and abundance of zooplankton and *Mysis relicta* in Flathead Lake

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Introduction

During 1960s and early 1970s, *Mysis relicta* were introduced into more that 100 lakes throughout the northwestern U.S. and British Columbia with the primary intention of providing a supplemental prey organism for salmonids, especially kokanee salmon (*Oncorhynchus nerka*) (Lasenby et al. 1986, Martinez and Bergerson 1989). Several lakes in the Flathead Lake catchment, northwest Montana, were stocked with *M. relicta* including Whitefish, Ashley and Swan Lakes. *M. relicta* are voracious predators on zooplankton, and previous studies have reported significant changes in zooplankton communities following other *Mysis* introductions (see reviews by Lasenby et al. 1986, Northcote in press). Kokanee salmon also rely on zooplankton as their principle food resource (Cooper and Goldman 1980, Leathe and Graham 1982, Rieman and Falter 1981, Vinyard et al. 1982). Previous introductions of *M. relicta* have been followed, in some cases, by declines in kokanee abundance. Heightened competition between kokanee salmon and *M. relicta* for declining zooplankton food resources has been implicated as a primary cause for reductions in kokanee abundance (Lasenby et al 1986, Spencer et al. 1991, Northcote in press). In some cases, other factors, including reduction in spawning habitat, have been implicated in kokanee declines (Fraley et al 1986, 1989, Northcote in press).

M. relicta first appeared in Flathead Lake in 1981, presumably the result of downstream movement from previously stocked lakes (Leathe 1984). At that time, kokanee salmon represented the primary sport fish in the Flathead Lake. During the 1970s there were declines in kokanee spawner abundance in portions of the watershed affected by hydropower operations (Fraley et al 1986, 1989). Nevertheless, a sustained kokanee population and fishery existed in Flathead Lake through the mid-1980s, with adult kokanee populations of several hundred thousand fish, and natural kokanee recruitment of 9 million or more fry per year, coming largely from McDonald Creek in Glacier National Park (Beattie et al. 1988, Clancey and Fraley 1986). Then, within a few years after the appearance of *M. relicta*, the kokanee showed signs of decline, and by 1987 the fishery collapsed completely (Beattie et al. 1988). There has been considerable debate over the cause of the kokanee collapse in Flathead Lake, and at this time there is general agreement that several factors were involved. These include the introduction of *M. relicta.*, predation by lake trout which expanded following the *Mysis* introduction, hydropower operations, and angler harvest.

The present cooperative study between the Montana Department of Fish, Wildlife, and Parks and the Flathead Lake Biological Station was developed to provide information on one of these factors, namely the introduction of *M. relicta* and subsequent changes in the zooplankton community in Flathead Lake. The study also includes information on the distribution and abundance of *M. relicta* in Flathead Lake.

Materials and methods

Mysis relicta sampling

The vertical distribution of *M. relicta* was documented through monthly sampling from May through November 1988, at the Mid-Lake Deep site, located in the deepest part of Flathead Lake (Figure 0). Vertical hauls were made with a 1m diameter closing net (mesh size 500um) at towing speeds of 0.4m/sec over the following depth intervals: 50-40m, 40-30m, 30-20m, 20-10m, 10-5m, and 5m-surface. Collections were made both during the day (between 1100-1500 hrs) and on moonless nights (with sample collections commencing at least 1 hour after dark). Similar collections were made on four occasions during 1987, however the net was not rigged as a closing net. Therefore, a series of vertical hauls were made from various depths, up to the surface. Densities of *M. relicta* over mid-depth increments were estimated by difference. Monthly *Mysis* sampling was also conducted in Polson Bay from May through November, 1988. Ten minute horizontal tows were made at night using the same 1m diameter net, at towing speeds of 0.4-0.6 m/sec.

An annual lake-wide census of *M. relicta* was made in late August/early September in 1987 and 1988. A total of 40 sites were selected using a stratified random sampling design in which the lake was divided into three depth strata (<75m, 40-75m, <40m). Single bottom to surface hauls were made at each site with a 1m diameter, 500um mesh net. MDFWP personnel sampled sites at the northern portion of the lake and FLBS personnel sampled the southern portion. Data from all 40 sites were combined to estimate the lakewide density of *M. relicta*.

All *M. relicta* samples were enumerated, separated by sex, and measured. Juveniles (typically less than 15 mm in length) were not separated by sex. Up to 50 individuals of each sex were measured in each sample, from the tip of the rostrum to the fork of the telson, using a dissecting microscope at 6X.

Zooplankton sampling

Monthly sampling of the vertical distribution of zooplankton was carried out at the same location, time, and depth intervals as the *Mysis* sampling described previously. We used a 30cm diameter, 64um mesh closing net. In addition, 50m to surface hauls were made from January through April 1988. For comparison to pre-*Mysis* conditions, I used vertical distribution data collected by David Potter (1978) using identical techniques, from May-December 1972 and January-April 1973. For graphical purposes, I placed Potter's data on a single time line, running from January through December, so that the time line would be comparable to 1988 , when samples were collected over the calender year.

Additional zooplankton sampling locations are shown in Figure 0. Monthly zooplankton samples were collected in Polson Bay from May through September, 1988. Duplicate samples were collected over the entire water column. Each sample consisted of a composite of 3 vertical hauls made from the bottom to the surface.

Monthly, duplicate zooplankton hauls also were made at the Mid-Lake North site, from May through November, 1988. Hauls were made from 50m to the surface except during periods of thermal stratification, when separate hauls were made from 50m to the thermocline, and from the thermocline to the surface.

MDFWP personnel collected zooplankton samples at Lakeside, Somers Bay and Big Arm Bay on a monthly basis from May through September, 1988. Duplicate hauls were made from ~30m to the surface except during periods of thermal stratification, when separate hauls were made from ~30m to the thermocline, and from the thermocline to the surface.

Macrozooplankton were identified to species and duplicate 1 ml subsamples were enumerated using a Sedgwick Rafter counting cell. *Daphnia* were measured from the base of the tail spine to the top of the head, using a Whipple grid.

Results and Discussion

Mysis relicta

Trends in abundance

The population dynamics of *Mysis relicta* in Flathead Lake represent a classic case of a newly invading species. Following their initial appearance in 1981, densities of *M. relicta* increased exponentially reaching a maximum density of $129/m^2$ in 1986 (Figure 1). The maximum density reached by *M. relicta* was well below the level of $1000\text{-}2000/m^2$ predicted by Bukantis (1986), based on densities attained in other large deep oligotrophic lakes in the west, such as Lake Tahoe and Lake Pend Oreille. After peaking in 1986, the density of *M. relicta* declined for three successive years reaching a low of $28/m^2$ in 1989. This decline in abundance is likely a density dependent response caused by over-exploitation of zooplankton prey (to be discussed in detail later in this report), together with increased fish predation on *M. relicta*.

The plankton community in Flathead Lake is beginning to show signs of stabilizing following the appearance of *M. relicta* in 1981. Following three years of decline, the density of *M. relicta* increased slightly in 1990. Several zooplankton species (described later) which disappeared from lake monitoring samples beginning in 1985, have reappeared in the lake.

Life history and Size Frequency analysis of *Mysis relicta*

Previous work on Flathead Lake from 1984-1986 led R. Bukantis (personal communication) to speculate that the Flathead Lake *M. relicta* population was composed of a single cohort of juveniles, released each spring. These juveniles matured over the summer and produced young the following spring. After releasing their young in the spring, adults persisted for several months, before dying in mid-summer. Size frequency data from 1987 supports the single cohort hypothesis (Figure 2). The size frequency distribution of the juvenile cohort appeared to be normally distributed through July; however, by September the distribution was bimodal. The two observed peaks likely resulted from divergence in size of immature males and females, since the mean size of adult females is larger than that of the males as reported by Reynolds and DeGraeve (1972).

In 1988, it appears that two cohorts of juvenile *M. relicta* were released (Figure 3). A large cohort was released in the spring, followed by a much smaller cohort in July. Each of these cohorts showed evidence of a bimodal distribution by August and September, again presumably due to the increased growth and size of females compared to males.

Analysis of the adult data in Figure 3 shows evidence for a bimodal distribution of females from May through November, 1988. Returning to the 1987 data (Figure 2) , there is some evidence for two adult cohorts, particularly on 2 July and 24 July. The extended right shoulder visible for the adult females may represent an older cohort. However, the density of this cohort was quite low.

Given the present data, it is not clear if the bimodal adult distribution, which was distinct in 1988, is due to a subpopulation of adult *M. relicta* which persisted in the lake for an additional year, or if there are simply two subpopulations; an early maturing group and a later maturing group.

Vertical distribution of *M. relicta*

M. relicta typically inhabit the offshore waters of deep lakes and are noted for their nocturnal habits and pronounced diel vertical migrations (Beeton 1960). During the daylight hours, they typically are found in deep waters, on or near the bottom. At night, they migrate up into the water column (Figure 4). Previous studies have shown that *M. relicta* are quite sensitive to even low levels of light, to the extent that they remain depressed vertically in the water column during full moon nights, compared to cloudy or moonless nights (Beeton, 1960). Nevertheless, during the mid-day sample collections in May 1988, we collected a few juvenile *M. relicta* well off the bottom at depths from 5-20m (Figure 4).

In addition to their sensitivity to light, *M. relicta* exhibit marked thermal preferences during their diel migrations. Previous studies indicate that *M. relicta* avoid waters with temperatures above 15 ^{O}C (Beeton 1960). Seasonal vertical distribution patterns from 1988 indicate similar thermal preferences for *M. relicta* in Flathead Lake (Figure 5).

During Spring and Fall nights, when lakewide water temperatures were below 14°C, *M. relicta* occupied the entire water column, and were most abundant in the top 5 to 10 meters (Figure 5). However, during periods of thermal stratification, few *M. relicta* were found in the warm epilimnetic waters. During August and September, when the lake was well stratified and epilimnetic temperatures were from 17-20°C, the thermocline appeared to act as a thermal barrier to most *M. relicta*. At this time of year, the highest densities of *M. relicta* were found just below the thermocline, and very few *M. relicta* were found in the epilimnion. Juvenile *M. relicta* appeared less sensitive to the thermal barrier, especially during July when summer stratification was beginning to set up. Although the greatest density of *M. relicta* in July was from 10-20m where water temperatures remained below 15°C, substantial numbers of juvenile *M. relicta* were found above 10m, where near surface temperatures exceeded 18°C (Figure 5).

Similar vertical distribution patterns were observed in the limited data collections of 1987 (Figure 6). However, enhanced water circulation caused by a mid-July storm produced a decline in surface water temperatures which interrupted the typical seasonal migration pattern of *M. relicta*. By 2 July, a strong thermocline had developed, and epilimnetic water temperatures were from 17-19°C. Most *M. relicta* remained below the thermocline at this time. However, in mid-July a prolonged storm accompanied by 4 days of strong winds caused a drop in epilimnetic temperatures to approximately 16°C on July 24. With this decline in temperature, substantial numbers of juvenile *M. relicta* moved up through the thermocline, all the way to the surface. In September, the epilimnion was 17°C, and again, the majority of *M. relicta* remained just below the thermocline.

Although there could be other factors which also affect the vertical distribution of *M. relicta*, the prevailing evidence from this study together with previous research indicates that temperature is a key determinant in the vertical distribution of *M. relicta*. The thermal preferences of *M. relicta* are relatively narrow. From the data presented in this study, it appears that a water temperature change of 1-2°C may alter their diel migration patterns. Therefore, the distribution *M. relicta* could be affected by of unusually cool summers, or disturbance of natural water temperature regimes by upstream discharge of large volumes of cold hypolimnetic water from Hungry Horse dam during the summer and fall. The latter concern should be considered as part of ongoing discussions and plans concerning the operation of Hungry Horse Dam.

Spatial distribution of *M. relicta*

Densities of *M. relicta* generally increased with increasing water depth, as evidenced by data collected in August, 1987 from 40 stations distributed around Flathead Lake (Figure 7). Few *M. relicta* were collected at sites with water depths < 20m. Based on this information, we eliminated the depth zone <20m from subsequent lakewide *Mysis* census estimates and concentrated our efforts in deeper waters.

The majority of *M. relicta* collected in the shallower sites were juveniles (Figure 8). However, with increasing depth, adults tended to make up a greater percentage of the population (Figure 8). Not only did the percentage of adults increase with depth, but the average size of adults (both males and females) also increased with increasing depth (Figure 9). From these data, it appears that as *M. relicta* grow and age, they move into deeper waters. Another possible explanation is that the observed spatial distribution is the result of size selective predation by fish. *M. relicta* located in shallower waters are likely more vulnerable to predation due to greater visibility. Selective predation by fish on larger *M. relicta* could result in reduced average size and age of nearshore *M. relicta* populations. Without corroborating evidence this latter explanation is speculative.

Although the relationship between depth and body size was highly significant for males and female *M. relicta* , there is one data point that deviates widely from the estimate regression lines (Figure 9). The outlier is from a deep-water site, nearshore, just off the mouth of Yellow Bay. The mean size of *M. relicta* at this deep site was smaller than the other deep sites, and appeared to be more typical of shallower sites (Figure 9). This suggests that distance from shore also may be important in the observed size distribution of *M. relicta* (Figure 9). However, this is speculative due to the lack of additional deep, nearshore samples.

Polson Bay - *M. relicta*

We conducted a number of nighttime horizontal tows with the Mysis net in Polson Bay during 1988. Only a few *M. relicta* were collected in these tows, and these were exclusively juvenile, collected primarily during the Spring; a few individuals were collected in the Fall. No *M. relicta* were collected in tows made from mid-June through September. Unfortunately the density of *M. relicta* collected in these tows was so low that accurate density estimates were not possible.

During the summer period, when Flathead Lake is thermally stratified, Polson Bay is largely made up of near-surface waters of Flathead Lake, flowing into Polson Bay through the Narrows (Figure 0). Since few *M. relicta* are found in surface waters of the lake during the summer (Figure 5), it is not surprising that few *M. relicta* appeared in our Polson Bay collections during the summer. Of course during the Spring and Fall when surface waters of Flathead Lake drop below 15^{o}C, nocturnal migration of *M. relicta* from the deep waters just off the Narrows would likely result in the transport of some individuals into Polson Bay, especially during the spring when *M. relicta* are most abundant in the lake.

ZOOPLANKTON (Mid-Lake Deep)

The results presented here focus on comparison of data collected in 1988 after *M. relicta* was well established in Flathead Lake with data collected in 1972-73, prior to the appearance of *M. relicta.* Although there was considerable zooplankton data collected in the intervening years, these data are beyond the scope of this report. Furthermore, data collected in these other years do not contain comparable vertical distribution data as in 1988 and 1972-73. Rather, these other years contain data from single depth tows, or at most dual tows which are split at the thermocline.

Cladocera

The zooplankton community changed dramatically in Flathead Lake following the appearance of the voracious planktivore, *M. relicta* (Bukantis 1986, Beattie et al. 1988, Spencer et al. 1991). Cladocerans are preferred prey for *M. relicta* (Grossnickle 1982, Nero and Sprules 1986, Cooper and Goldman 1980), and previous *Mysis* introductions have been linked to disappearance of various Cladoceran species in other lakes including Lake Tahoe and Lake Pend Oreille (Richards et al. 1975, Rieman and Falter 1981). The three dominant Cladoceran species in Flathead Lake all declined in abundance following the appearance of *M. relicta.* However, there were marked differences in the pattern of decline exhibited by the three species. The differential responses may be explained by differences in vertical distribution patterns together with life history traits among the three species.

In 1972, prior to the appearance of *M. relicta*, *Daphnia longiremis* were present in the water column throughout the year (Figure 10). Maximum densities reached levels of approximately 1/L during spring and early summer. *D. longiremis* virtually disappeared from plankton samples from Flathead Lake, beginning in late 1985 and 1986 (Bukantis 1986). No *D. longiremis* were collected at the Mid Lake Deep sampling site in 1988 (Figure 10).

The vertical distribution of *D. longiremis* makes it especially vulnerable to predation by *M. relicta*. As shown in Figure 11, *D. longiremis* appears adapted to colder waters as it is concentrated below the thermocline during summer stratification. In the spring and fall, it is concentrated closer to the surface. The year-round vertical distribution pattern illustrated in Figure 11, shows remarkable overlap with the night-time distribution of the plankton predator, *M. relicta* (Figure 5). Thus the dramatic decline in abundance of *D. longiremis* in 1985, concurrent with greatly increased densities of *M. relicta,* is likely the result of predation by *M. relicta.*

Another disadvantage for *D. longiremis* with respect to vulnerability to predation from *M. relicta,* is that this Cladoceran does not appear to produce ephyppia (resting eggs) in Flathead Lake. This is not uncommon for limnetic Cladocerans in large lakes (Pennak 1978). *D. longiremis* overwinters in the adult stage, and overwintering individuals remain suspended in the water column throughout the winter (Figure 11). Thus *D. longiremis* is exposed to predation by *M. relicta* throughout the year.

The seasonal population dynamics of *Daphnia thorata* also have changed since the introduction of *M. relicta* (Figure 12). Although mid-summer densities of *D. thorata* before and after the *M. relicta* introduction are comparable, the total period of dominance by *D. thorata* has been truncated during both spring and fall. Prior to the appearance of *M. relicta, D. thorata* were present in substantial quantities (>1/L) from mid-May through late November (Figure 12). In 1988, *D. thorata* were only present at those densities from mid-July through early October.

The life history and vertical distribution characteristics of *D. thorata* make it much better adapted to co-existance with the potential predator, *M. relicta*, than *D. longiremis*. *D. thorata* has characteristics typical of warm water adapted species. Historically, *D. thorata* first appeared in the water column in early spring and then rapidly increased in abundance reaching peak densities by early June (Figure 12). Densities declined slightly during mid-summer and then increased to a second peak in October. These twin peaks correspond to spring and fall turnover, and are likely the result of increased food availability resulting from stimulation of primary production in Flathead Lake during these periods (Stanford et al. 1983).

D. thorata reside in the upper 20m of the water column from May through November (Figure 13). During summer stratification, they are almost exclusively restricted to the epilimnion. Since the appearance of *M. relicta, D. thorata* populations now only develop when the lake in thermally stratified. It is during this time that a thermal refuge for *D. thorata* exists in the epilimnion, which is relatively free of *M. relicta*. During Spring and Fall, *M. relicta* occupy the entire water column thus there is no refuge for *D. thorata*, and populations are decimated. Unlike *D. longiremis*, produce ephyppia in the Fall which likely provides *D. thorata* with an effective means of escaping predation by *M. relicta* over the winter months, when no thermal refuge exists. For most of the year, *D. thorata* populations are made up exclusively of females, which reproduce via parthenogenesis. However, during the fall, male *D. thorata* appear in the population. Sexually produced ephyppia appear in females by late fall. The ephyppia serve as the overwintering stage for *D. thorata*. Adult *D. thorata* are essentially gone from the water column by January. The thick walled ephyppia sink to the bottom or accumulate along the shoreline. They can withstand drying and freezing (Pennak 1978). Ephyppia hatch in early spring and the cycle begins again.

The response of *Bosmina longirostris* to *M. relicta* appears to be intermediate between the other two Cladocerans. The abundance of *B. longirostris* was reduced throughout the year in 1988 compared to 1972 (Figure 14); however, substantial numbers of this Cladoceran, up to 2/L, still develop in mid-summer. Even so, peak summer densities declined ~50% in 1988 compared to 1972. Densities throughout the remainder of the year declined 10 fold or more.

Prior to the appearance of *M. relicta, B. longirostris* tended to be concentrated in the upper portion of the water column throughout the year (Figure 15). However, the distribution of *B. longirostris* was not as restricted to the warm epilimnetic waters as *D. thorata* (Figure 13). For example, the highest densities of *B. longirostris* during the summer of 1972 were often found within the metalimnion. While few *D. thorata* were ever found below 30m, *B. longirostris* densities in excess of 1/L were measured from 30-40m during June and July, 1972, and measurable densities were found as deep as 60m during August (Figure 15). Given this vertical distribution, a substantial portion of the *B.*

longirostris population appeared to be exposed to predation by *M. relicta* during the summer.

In 1988, *B. longirostris* still did not appear to take advantage of the epilimnetic refuge, as a significant portion of the population remained near or below the thermocline. Like *D. longiremis*, *B. longirostris* do not appear to produce ephyppia in Flathead Lake, or in Lake Tahoe (Threlkeld 1981). Thus they too overwinter as adults suspended in the water column where they have no apparent refuge from *Mysis* predation. This undoubtedly contributed to the dramatic decline in *B. longirostris* densities observed in 1988, from late fall through winter and spring.

Copepods

Cyclopoid copepods, primarily *Diacyclops thomasii*, declined markedly following the appearance of *M. relicta* (Figure 16). In fact, next to *Daphnia longiremis*, *Diacyclops thomasii* was the macrozooplankton species which showed the greatest decline following the appearance of *M. relicta.* While declines in Cladocera have been reported following other *M. relicta* introductions (Richards et al. 1975), similar declines in copepods have not been reported. Order of magnitude declines in *D. thomasii* abundance were documented in Flathead Lake. In 1972, cyclopoid densities at Mid-lake Deep remained above 9/L throughout the year and reached levels up to 25/L (Figure 16). In 1988 following the appearance of *M. relicta*, the highest cyclopoid density recorded all year was only 2.4/L.

The vertical distribution of *Diacyclops thomasii* shown in Figure 17 suggests a cold-water distribution, similar to *D. longiremis* (Figure 11). In 1972 *Diacyclops thomasii* generally remained below the thermocline during summer stratification. Peak summer densities of *Diacyclops thomasii* were concentrated from the thermocline down to depths of 40 meters or more. Substantial numbers of *Diacyclops thomasii* were found as deep as 70-80m.

Given this year-round vertical distribution, *Diacyclops thomasii*, together with *D. longiremis*, likely represented the most abundant plankton food resource available for *M. relicta* during the summer. Feeding experiments indicate that next to Cladocera, cyclopoid copepods are the next most preferred macrozooplankton prey (Vanderploeg et al. 1982, Grossnickle 1982). The data suggest that following depletion of the preferred

Cladoceran prey, *M. relicta* likely have preyed heavily on *Diacyclops thomasii* in Flathead Lake.

The response of *Leptodiaptomus ashlandii* to the appearance of *M. relicta*, offers a distinct contrast to *Diacyclops thomasii.* Densities of *L. ashlandii* were comparable in 1972 and 1988 (Figure 18), and the mean annual density in 1988 was 4.9/L compared to 3.71/L in 1972. *L. ashlandii* were concentrated in the upper portion of the water column prior to the *Mysis* introduction (Figure 19). The highest densities occurred in mid-summer and were found in the upper portion of the epilimnion. As such, this species may benefit from the development of the epilimnetic refuge from *M. relicta.* Nevertheless, substantial number of *L. ashlandii* were found below the thermocline during the summer of 1988. Feeding studies indicate that calanoid copepods are less vulnerable to *Mysis* predation than either Cladocera or cyclopoid copepods (Vanderploeg et al.1982, Grossnickle 1982). In fact, these studies report that adult calanoid copepods were the least preferred of all zooplankton prey.

Following the appearance of *M. relicta L. ashlandii* apparently has replaced *D. thomasii* as the dominant copepod in Flathead Lake. Likely explanations for the success of *L. ashlandii* are that it is not a preferred prey of *Mysis* together with its vertical distribution which favors the epilimnion where *Mysis* predation is greatly reduced.

Diel zooplankton distributions

Like *M. relicta*, cladocerans and copepods also may exhibit pronounced diel vertical migrations in lakes (Pennak 1978). However, monthly sampling conducted from May through November 1988 suggest that the zooplankton in Flathead Lake do not undergo marked diel migrations. Vertical profiles of *D. thorata* and *B. longirostris* show only small differences in day and night distributions (Figures 20,21). Copepods (not shown) also exhibited minor differences between day and night distributions.

Mid-Lake North

The 1988 population dynamics of zooplankton at the Mid-lake North (MLN) station were similar to patterns observed at our primary sampling station at Mid-lake Deep (MLD). However, the density of the various zooplankton groups was slightly lower at MLN (Figure 22).

Zooplankton densities from the epilimnion and hypolimnion at MLN indicate that densities of most of the the zooplankton groups were higher in the epilimnion than the hypolimnion (Figure 23). This was especially true for *D. thorata*, which was found almost exclusively in the epilimnion at MLN (Figure 23), as was the case at MLD (Figure 13). *Bosmina*, and both major copepods groups, were generally more abundant in the epilimnion than the hypolimnion at MLN; however, substantial numbers of each of these groups were found below the thermocline. This lends additional support for the hypothesis that the vertical distribution of these zooplankton groups makes them more vulnerable than *D. thorata* to predation by *M. relicta.*

Polson Bay

The zooplankton community in Polson Bay was similar to MLD in 1988 (Figure 24, 25. This is to be expected given the short retention time of Polson Bay waters, which are continually being replaced by waters flowing in through the Narrows. In late June, 1988, the density of *D. thorata* declined dramatically in Polson Bay (Figure 24). This reduction was preceded by a large storm, accompanied by high winds. Strong water circulation during the storm resulted in a $4^{o}C$ drop in temperature in Polson Bay which was observed throughout the 7m deep, water column (Figure 24) The most likely explanation for this rapid decline in temperature is that water circulation during the storm resulted in upwelling of cold hypolimnetic waters from the Narrows into Polson Bay. As discussed previously, the hypolimnetic waters of Flathead Lake have very low zooplankton densities (Figures 11,13,15,17,23). This would appear to explain the concurrent decline in abundance of zooplankton in Polson Bay in late June 1988.

Nearshore verses offshore sites

For purposes of this report, the offshore zone is defined as the central deep pelagic zone of the lake with water depths from 50 to 100m. Offshore sites in this study include MLD and MLN (Figure 0). Nearshore sites are located less than 1km from shore in water depths generally less than 30m. Historical zooplankton data collected by David Potter (1978) suggest that nearshore zooplankton populations were comparable to offshore populations in 1972, prior to the appearance of *M. relicta*. For example, *D. thorata* densities were comparable at MLD and Lakeside in 1972 (Figure 26). The densities of cyclopoid copepods also were comparable between these two sites in 1972 (Figure 27). In 1988, there was a sharp contrast between zooplankton populations at the nearshore station at Lakeside, compared to the deep offshore station at MLD. Both cyclopoid copepods and *D. thorata* were drastically reduced at Lakeside, compared to MLD in 1988 (Figure 26,27). When the additional sites at MLN, Somers Bay and Big Arm are added, the nearshore decline in zooplankton is also apparent (Figure 28, 29).

While most of the emphasis on *Mysis* impacts in other lakes have focused on the offshore zone, the limited data presented above indicate that nearshore zooplankton populations have declined even more than offshore populations in Flathead Lake. This is in contrast to Lake Tahoe, where large bays reportedly serve as refuges for Cladocera following the introduction of *Mysis* (Threlkeld, 1981). Unfortunately, few nearshore/offshore zooplankton comparisons have been made in other *Mysis* lakes.

Direct predation by *Mysis* may only be partially responsible for the observed declines in macrozooplankton in Flathead Lake. The remarkable decline in all macrozooplankton in the nearshore zone, where temperature and light generally exclude *Mysis* (Beeton and Bowers 1982) suggest that changes in the fish community may have contributed to the community-wide zooplankton changes. Unfortunately quantitative data on nearshore fish populations, pre and post-*Mysis* are lacking. Nevertheless, qualitative visual observations suggest that yellow perch populations have increased greatly since the appearance of *M. relicta*. Large schools of yellow perch are now quite noticeable throughout the summer along the shoreline of Flathead Lake. These large schools were apparently not present prior to the *Mysis* invasion.

At this time, we suspect that burgeoning populations of yellow perch may be responsible for the dramatic decline in nearshore zooplankton populations observed in the lake. Comparable expansions in yellow perch populations occurred in Lake Michigan following the introduction of coho and chinook salmon and the subsequent decline in alewife abundance. Expansion of yellow perch in Lake Michigan together with the other fisheries changes also appear linked to dramatic changes in nearshore zooplankton populations there (Scavia et al. 1986, Evans 1986).

Additional studies are needed before drawing definite conclusions about the nearshore fish/zooplankton interactions in Flathead Lake. Ongoing studies at FLBS are focusing on interactions between *M. relicta*, yellow perch, and other fish species in the food web of Flathead Lake.

Conclusions

This report along with previous studies (Bukantis and Bukantis 1987, Beattie et al. 1988, Spencer et al. 1991, Beattie and Clancey 1991) documents significant changes in the zooplankton community of Flathead Lake following the appearance of the voracious zooplankton predator, *M. relicta*. *Daphnia longiremis* virtually disappeared from the lake, while cyclopoid copepods have declined in abundance by an order of magnitude. Both of these organisms are poorly adapted to co-existance with *M. relicta*. They do not have a dormant, winter resting stage and, like *M. relicta*, these organisms occupy the cold-water regions of the lake. Thus both organisms are vulnerable to predation by *M. relicta* throughout the year.

Daphnia thorata and the calanoid copepods are better adapted to co-existance with *M. relicta*. Both of these organisms are concentrated in the warm waters of the epilimnion during summer thermal stratification of Flathead Lake. *M. relicta* generally remain below the thermocline, thus the epilimnion serves as an effective refuge from *Mysis* predation for warm water zooplankters like *Daphnia thorata* and the calanoid copepods. This epilimnetic refuge lasts only for 3-4 months during the summer, and for the remainder of the year, *M. relicta* are found throughout the entire water column. Consequently, few Cladocerans are now found in the water column from October through June.

Daphnia thorata produce ephyppia in autumn, and these lie dormant in the lake sediments over the winter. These resting eggs appear to provide an effective refuge from predation for *D. thorata* from fall through spring when *M. relicta* forage throughout the water column.

Nearshore zooplankton populations have declined even more than offshore populations following the appearance of *M. relicta* in Flathead Lake. Densities of all macrozooplankton in this region in 1988 were severely depressed throughout the year compared to 1972. Since few *M. relicta* occupy the nearshore zone, direct predation by *M. relicta* does not appear to be responsible for the nearshore zooplankton decline. We suspect that changes in the fish community of Flathead Lake following the *Mysis* invasion, have resulted in increased zooplankton predation in the nearshore environment by planktivorous fish such as yellow perch. However, further studies are needed before definitive conclusions can be drawn on food web interactions in the nearshore environment.

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APPENDIX

Figures 0-29

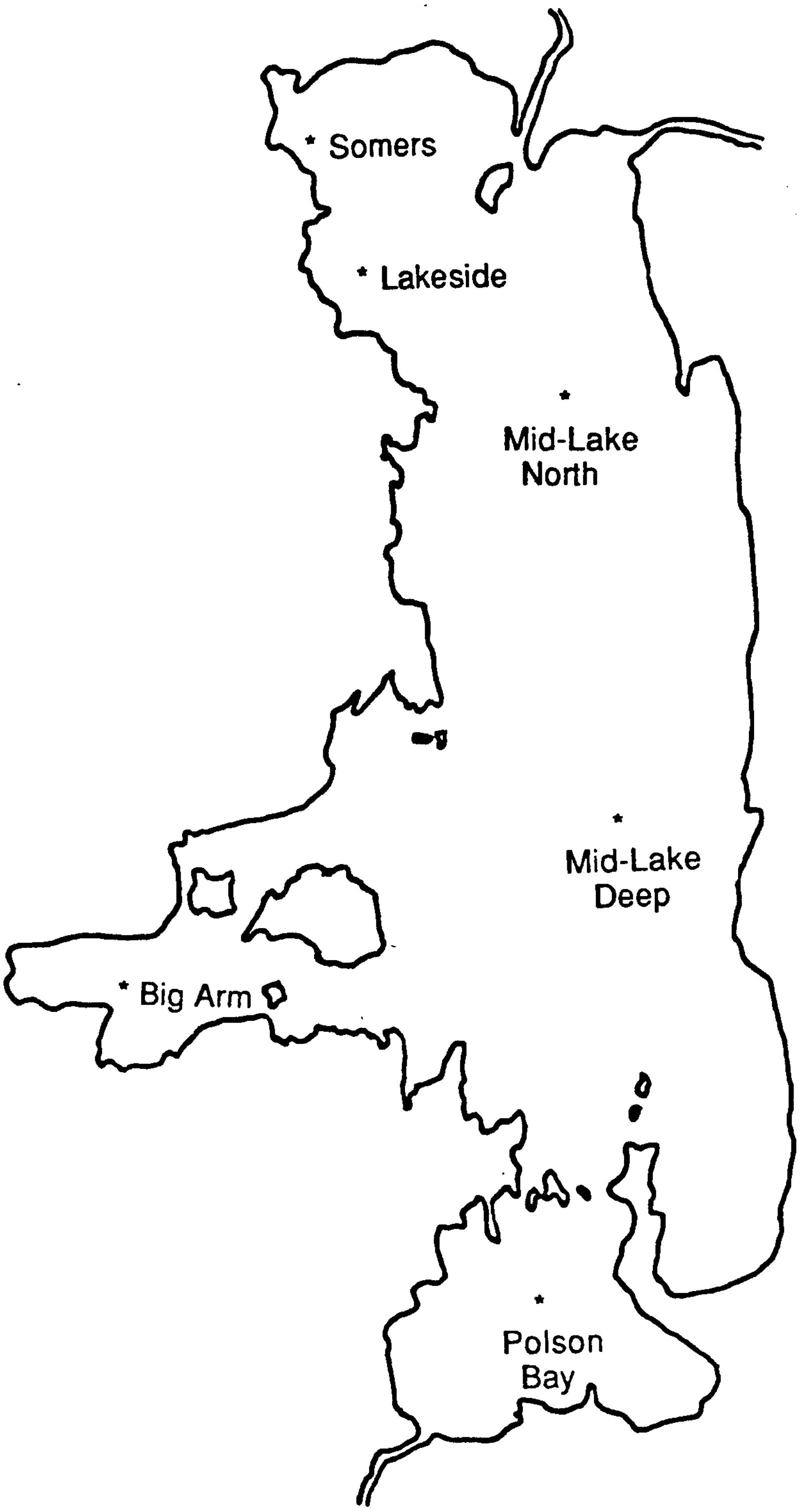


Figure 0. Map of Flathead Lake showing primary sampling stations.

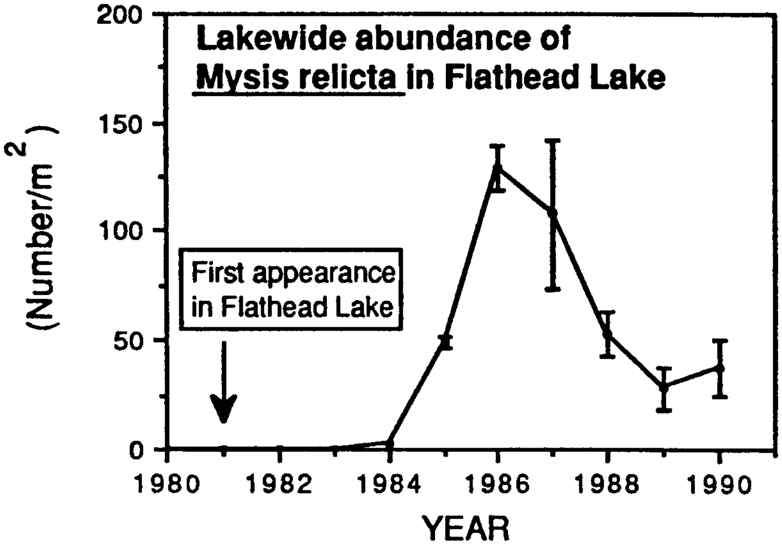


Figure 1. Annual autumn census of *M. relicta* abundance in Flathead Lake. Error bars represent 95% confidence intervals.

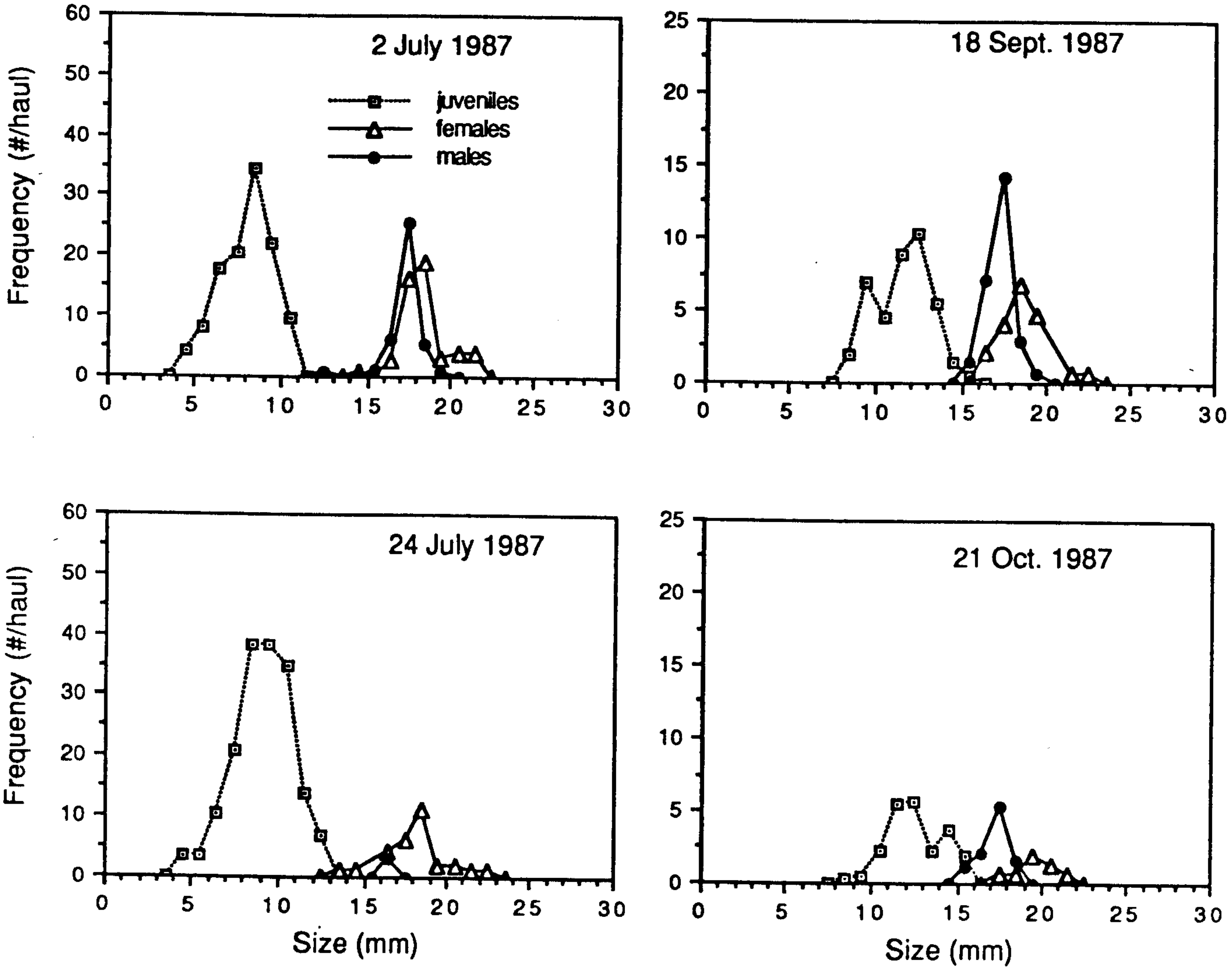


Figure 2. Size frequency distribution of *M. relicta* collected in 1987 at the Mid-Lake Deep station in Flathead Lake.

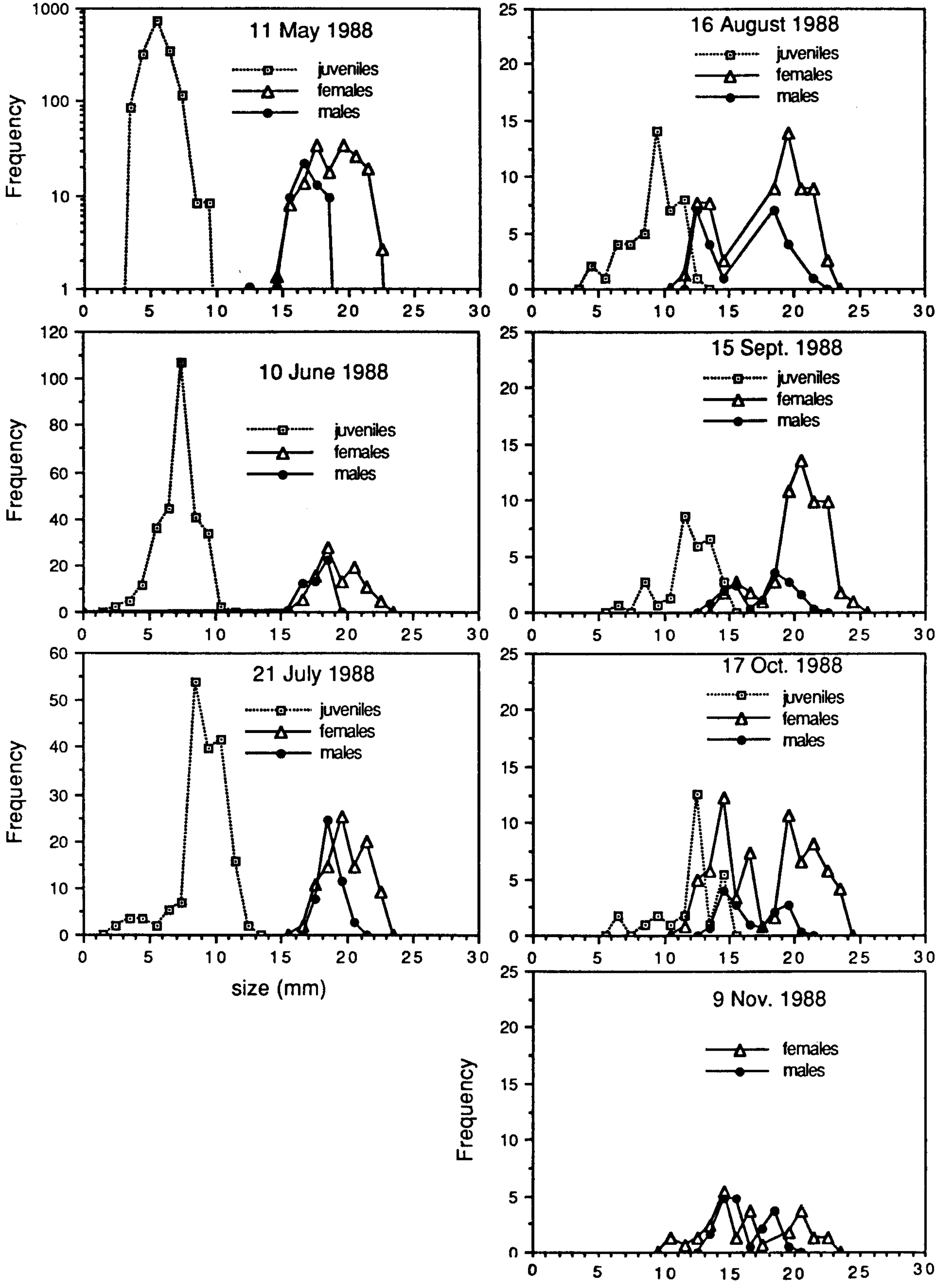


Figure 3. Size frequency distribution of *M. relicta* collected in 1988 at the Mid-Lake Deep station in Flathead Lake.

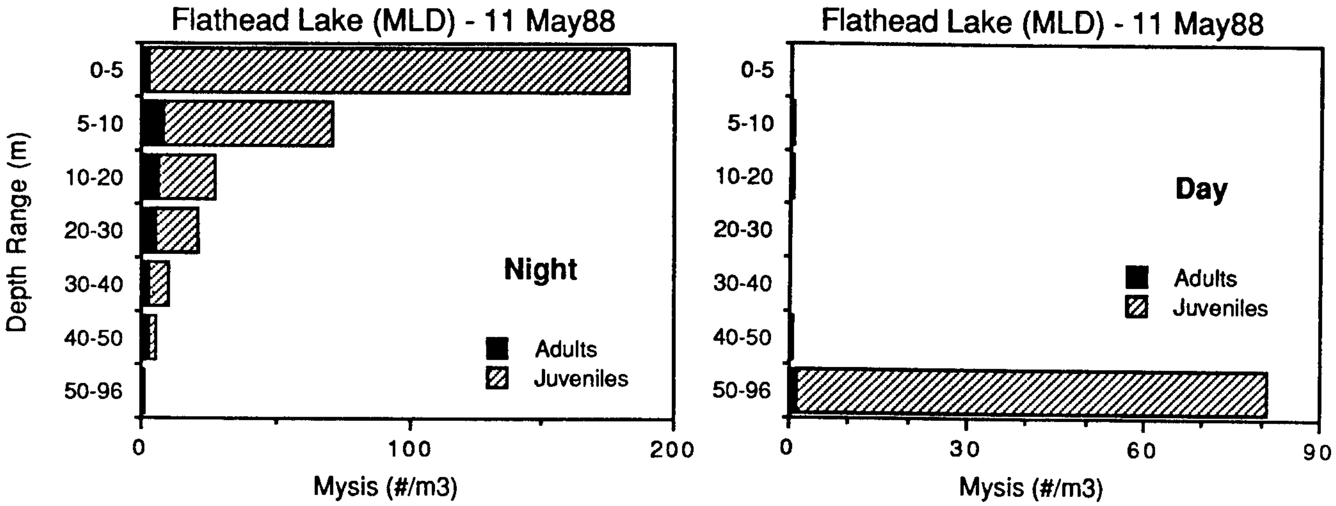


Figure 4. Vertical distribution of *M. relicta* on May 11, 1988 at mid-day and mid-night at the Mid-Lake Deep station in Flathead Lake. The organisms observed between 20m and 5m during the daytime samples are juvenile *M. relicta*.

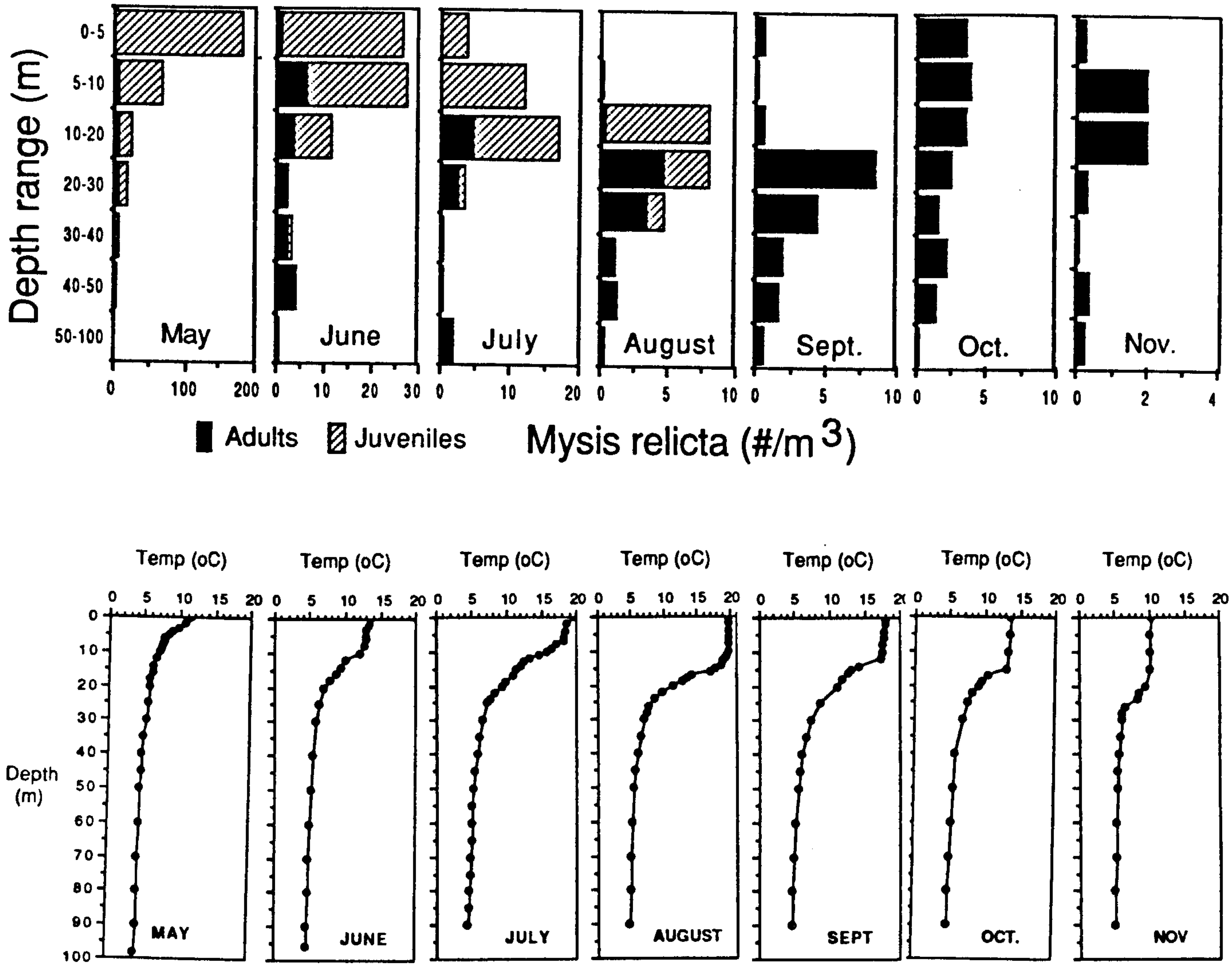


Figure 5. Temperature profiles and vertical distribution of *M. relicta* from May through November, 1988 on moonless nights at the Mid-Lake Deep station in Flathead Lake.

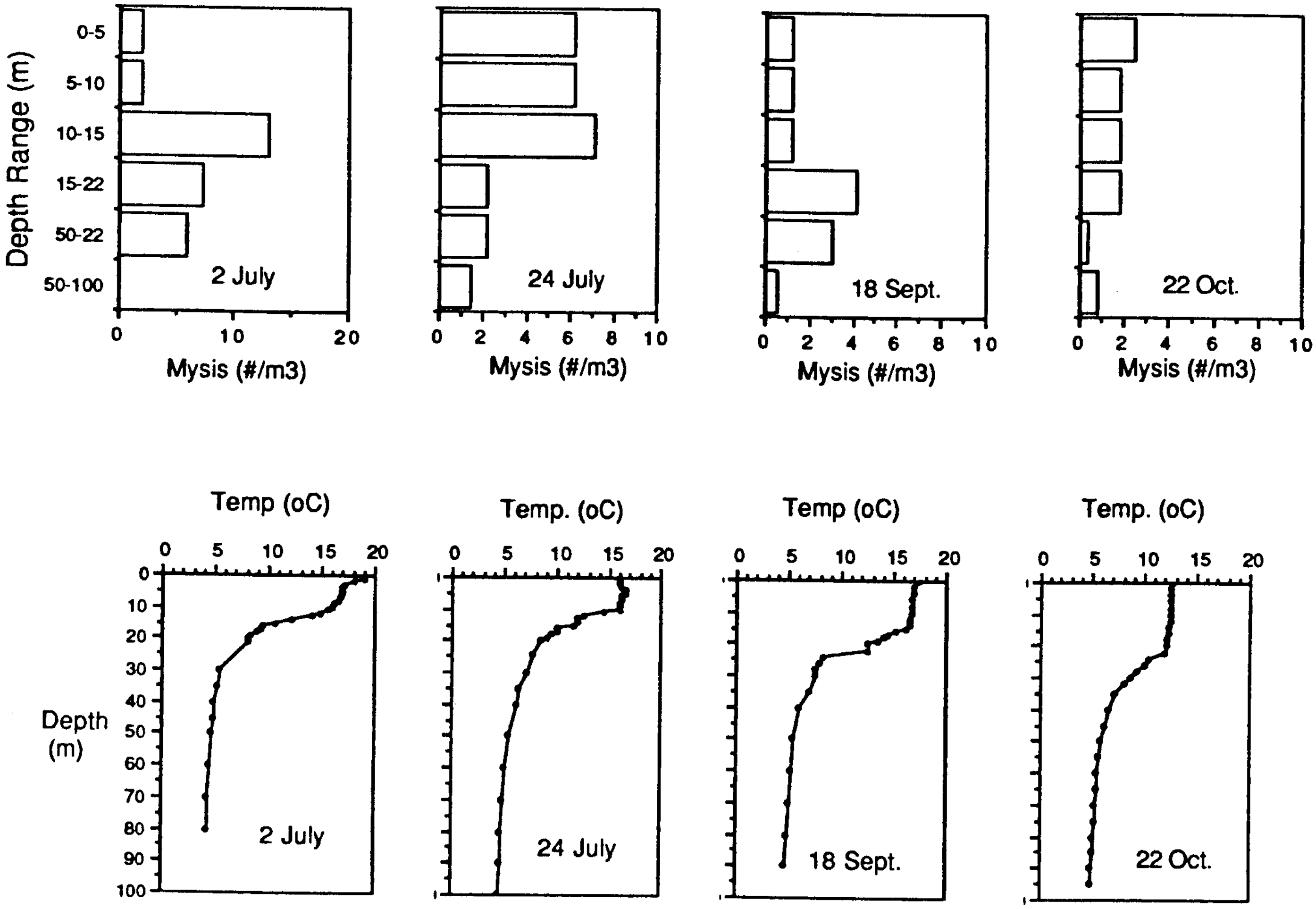


Figure 6. Temperature profiles and vertical distribution of *M. relicta* from July through October, 1987 on moonless nights at the Mid-Lake Deep station in Flathead Lake.

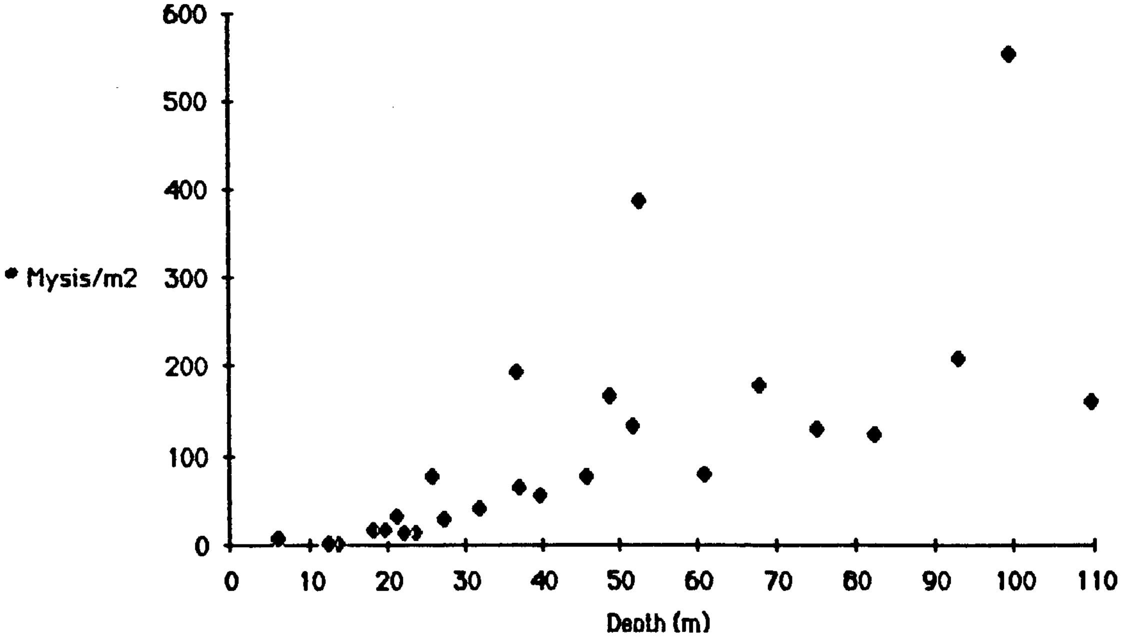


Figure 7. Relationship between sampling site depth and Mysis abundance at 40 randomly selected sites in Flathead Lake during the August 31, 1987 *Mysis* census.

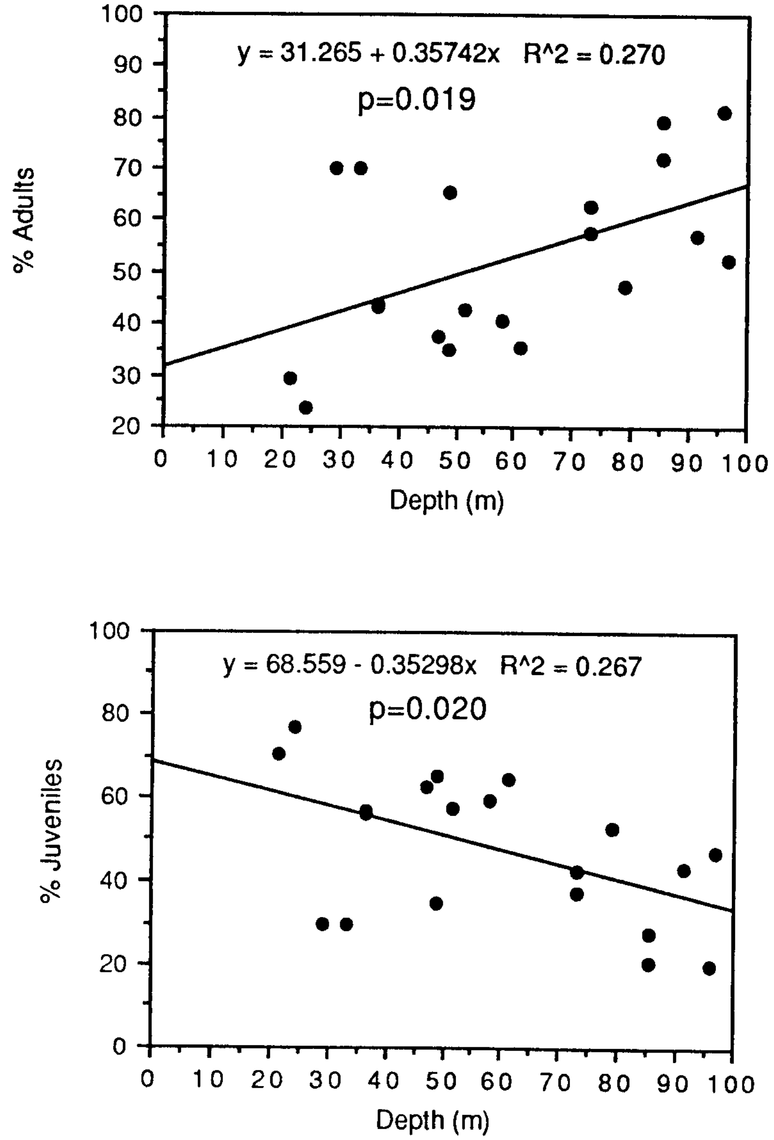


Figure 8. Relationship between sampling depth and the % of adult and juvenile *M. relicta* at FLBS sampling sites during the 1988 autumn *Mysis* census.

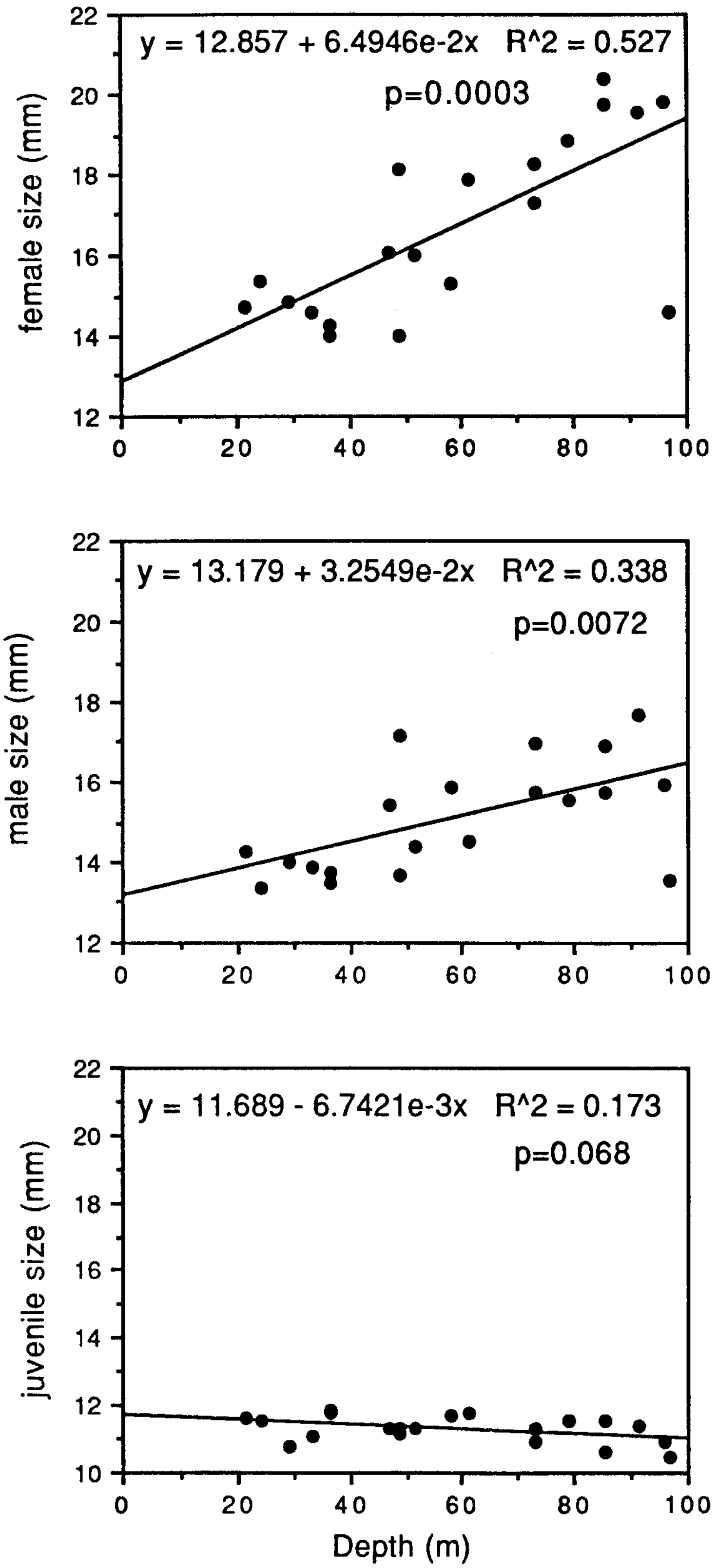


Figure 9. Relationship between sampling depth and the size of female, male, and juvenile *M. relicta* at FLBS sampling sites during the 1988 autumn *Mysis* census.

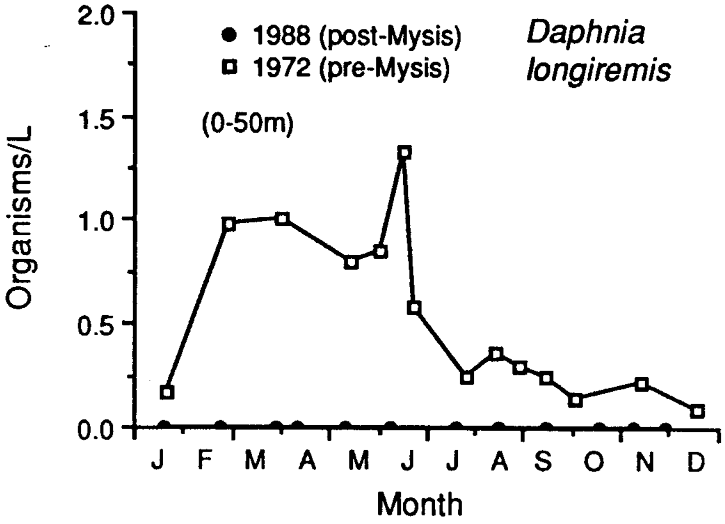


Figure 10. Seasonal abundance of *Daphnia longiremis* in 1972 (open symbols) and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake. Densities were calculated by summing up incremental 10m hauls from 50m to the surface. No *D. longiremis* were collected in 1988.

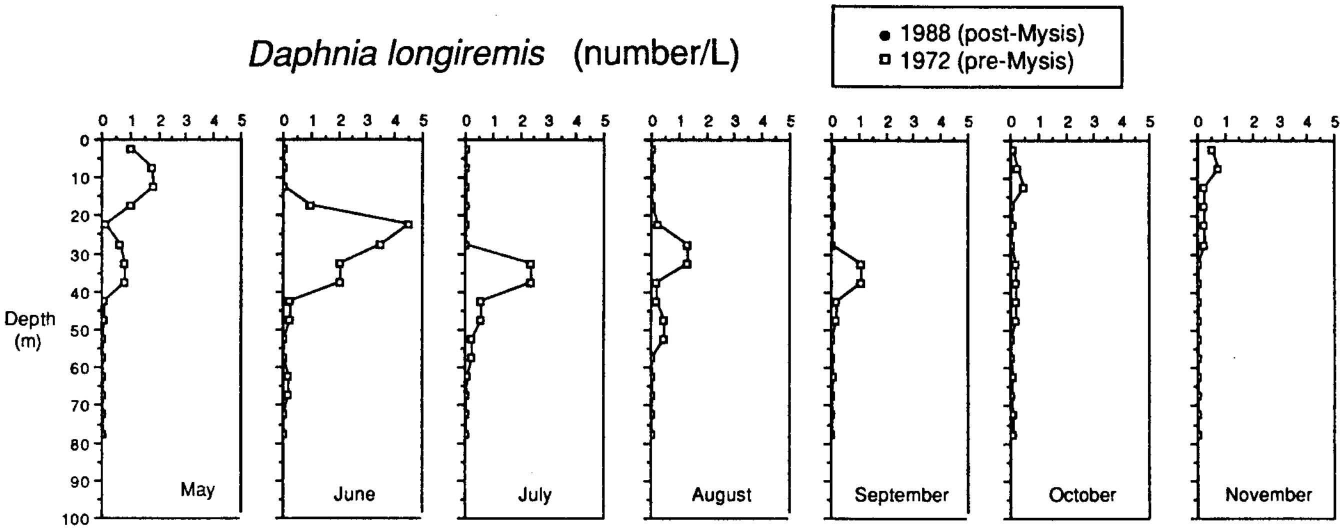


Figure 11. Vertical distribution of *Daphnia longiremis* (#/L) from May through November, in 1972 (open symbols), and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake. No *D. longiremis* were collected in 1988.

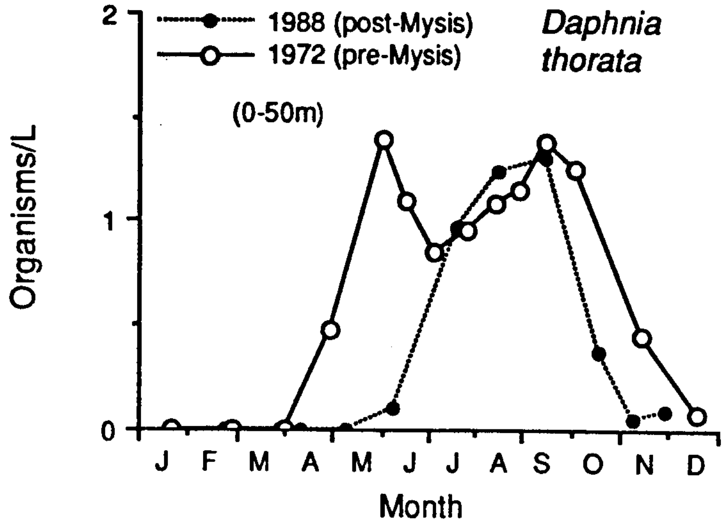


Figure 12. Seasonal abundance of *Daphnia thorata* in 1972 (open symbols) and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake. Densities were calculated by summing up incremental 10m hauls from 50m to the surface.

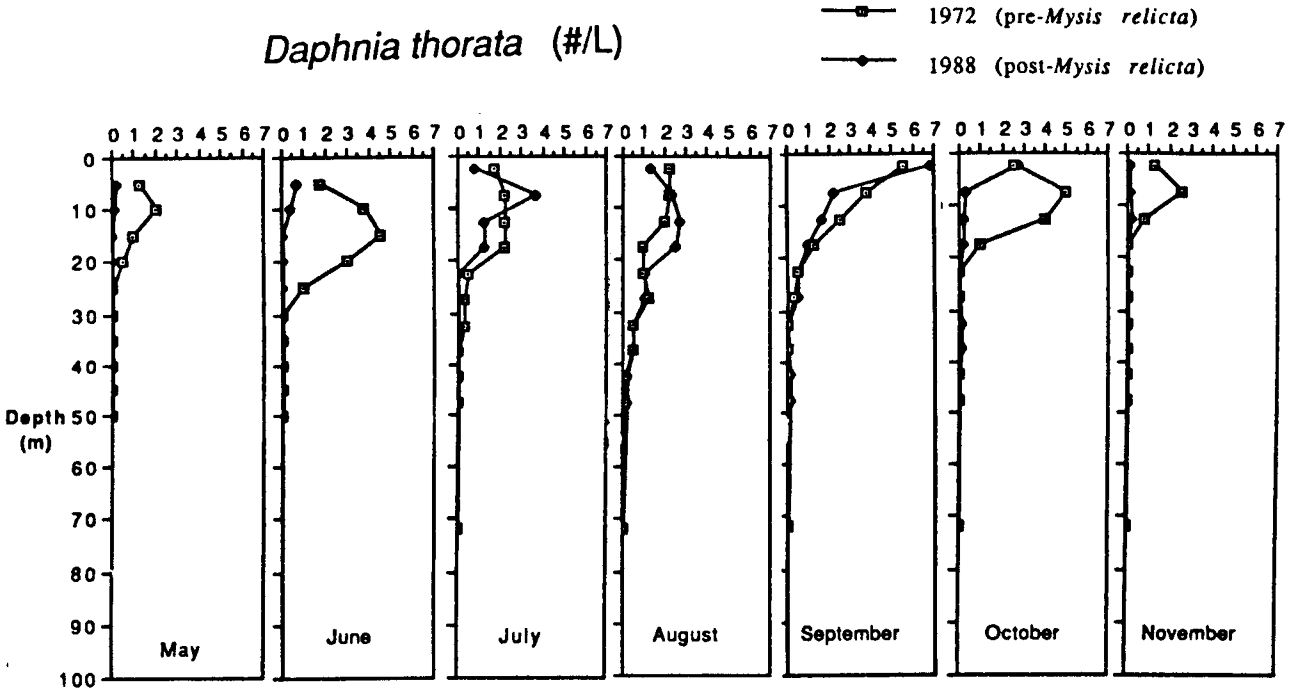


Figure 13. Vertical distribution of *Daphnia thorata* (#/L) from May through November, in 1972 (open symbols), and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake.

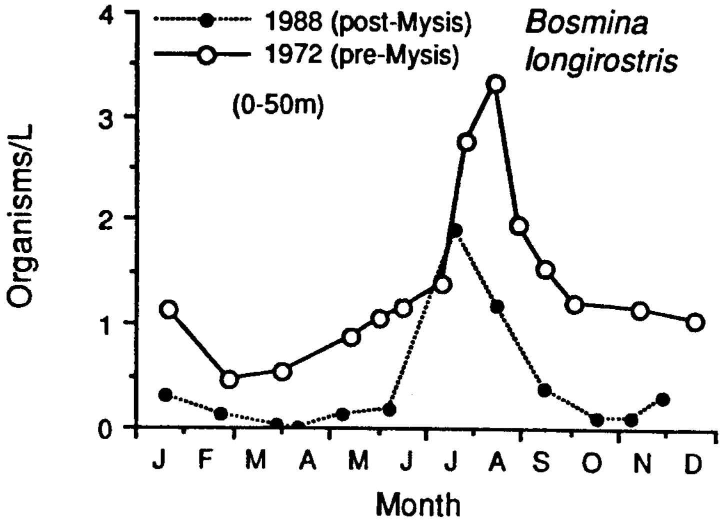


Figure 14. Seasonal abundance of *Bosmina longirostris*in 1972 (open symbols) and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake. Densities were calculated by summing up incremental 10m hauls from 50m to the surface.

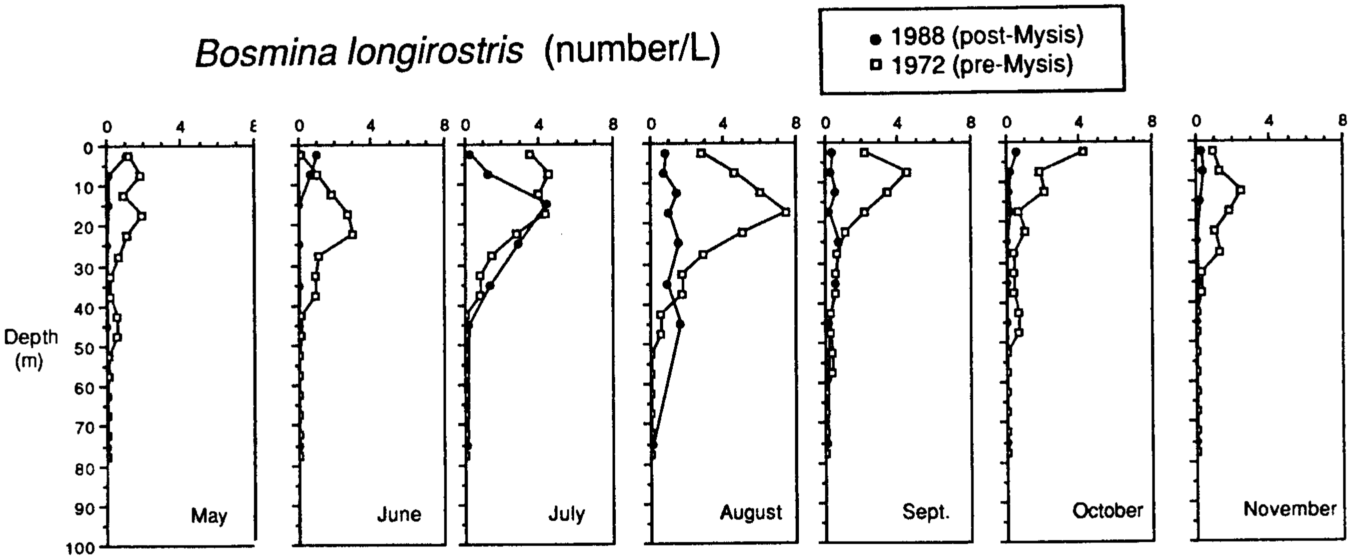


Figure 15. Vertical distribution of *Bosmina longirostris* (#/L) from May through November, in 1972 (open symbols), and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake.

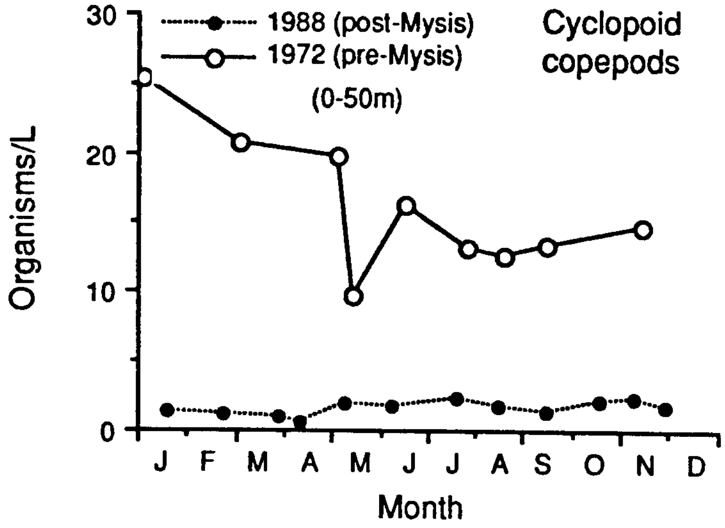


Figure 16. Seasonal abundance of cyclopoid copepods in 1972 (open symbols) and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake. Densities were calculated by summing up incremental 10m hauls from 50m to the surface.

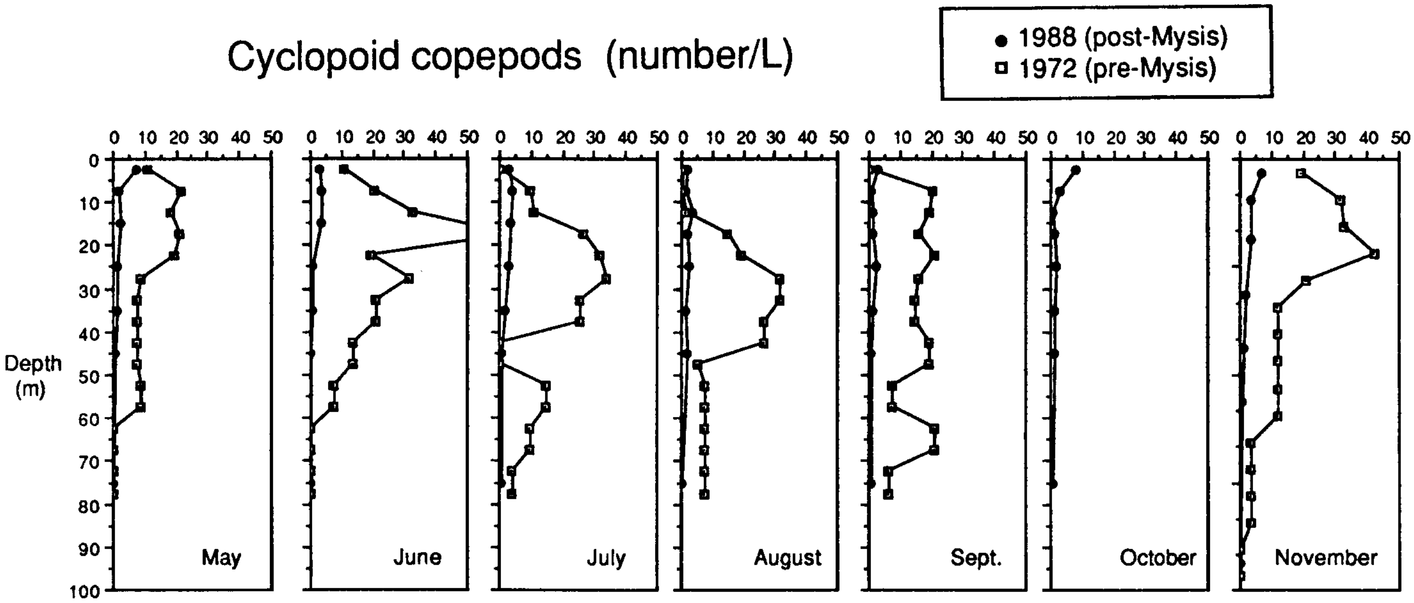


Figure 17. Vertical distribution of cyclopoid copepods (#/L) from May through November, in 1972 (open symbols), and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake.

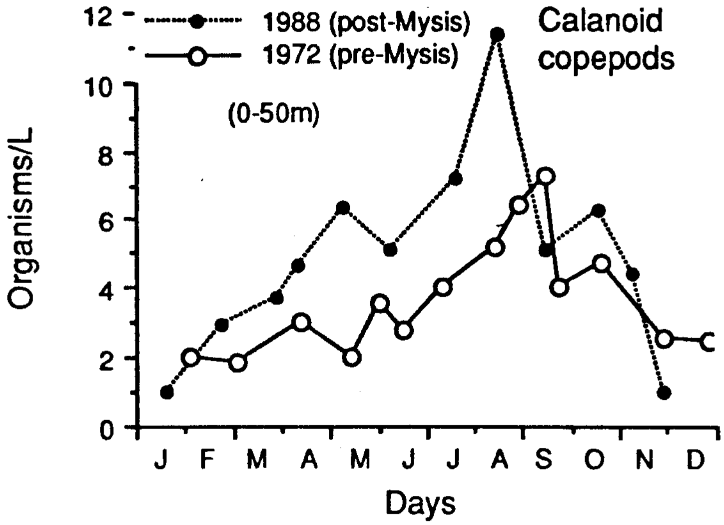


Figure 18. Seasonal abundance of calanoid copepods in 1972 (open symbols) and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake. Densities were calculated by summing up incremental 10m hauls from 50m to the surface.

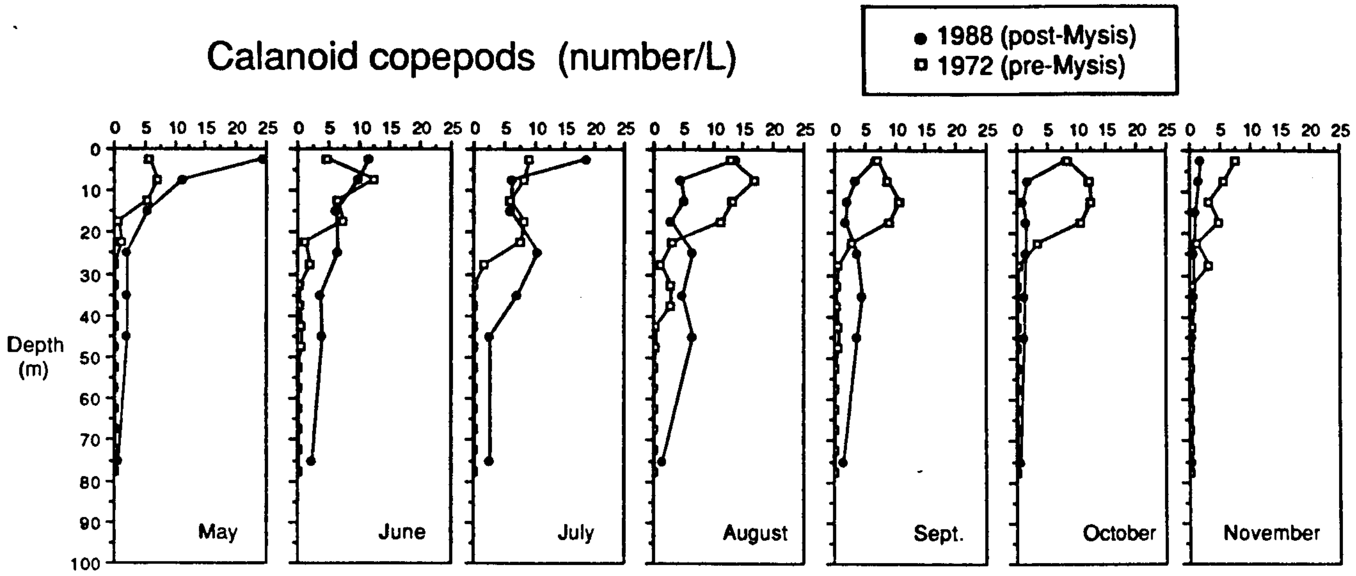


Figure 19. Vertical distribution of calanoid copepods (#/L) from May through November, in 1972 (open symbols), and 1988 (closed symbols) at the Mid-Lake Deep station in Flathead Lake.

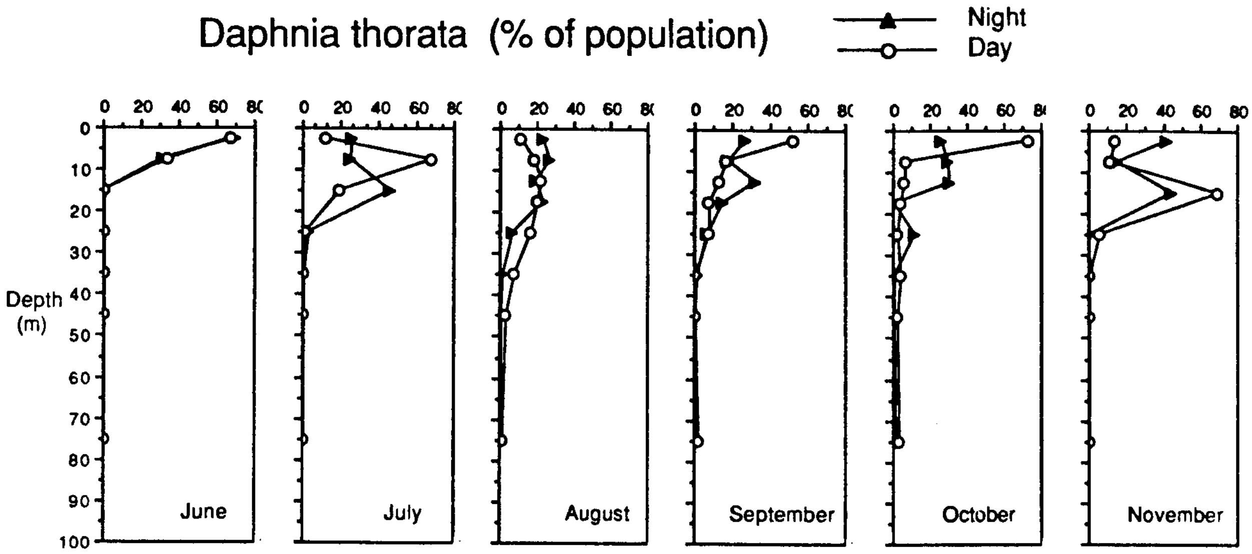


Figure 20. Vertical distribution of *Daphnia thorata* (#/L) from May through November, 1988 at mid-day (open symbols), and mid-night (closed symbols) at the Mid-Lake Deep station in Flathead Lake. Note, no *Daphnia thorata* were collected in the May 1988 samples.

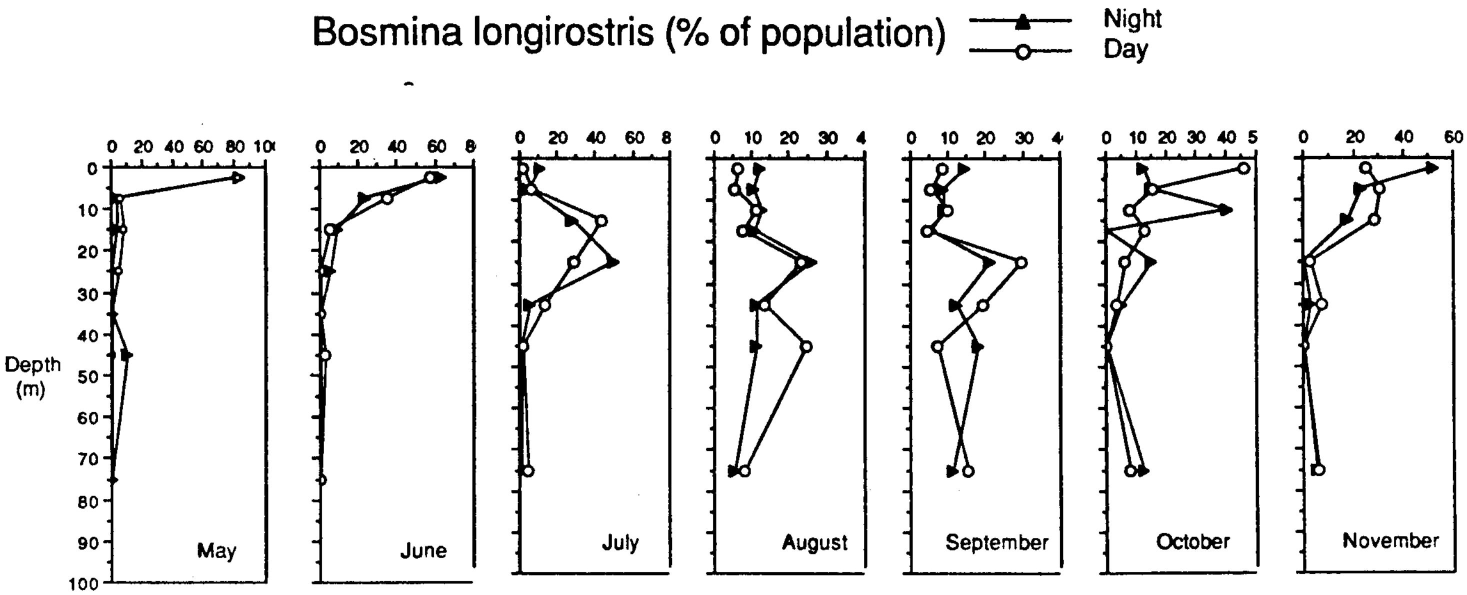


Figure 21. Vertical distribution of *Bosmina longirostris* (#/L) from May through November, 1988 at mid-day (open symbols), and mid-night (closed symbols) at the Mid-Lake Deep station in Flathead Lake.

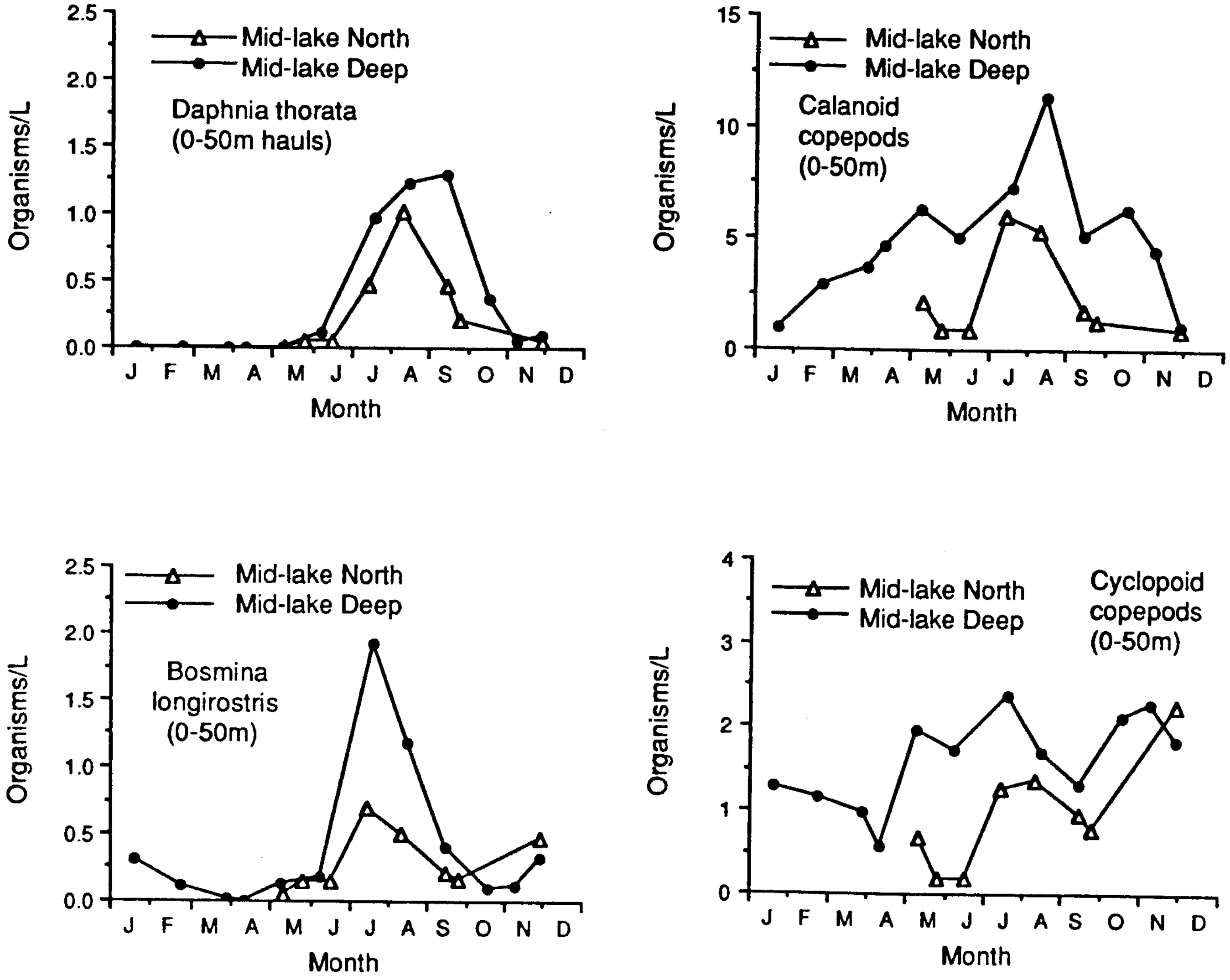


Figure 22. Seasonal abundance of the dominant macrozooplankton at the Mid-Lake North and Mid-Lake Deep stations in Flathead Lake during 1988. Densities at MLD were calculated by summing up incremental 10m hauls from 50m to the surface. Densities at MLN were calculated from 50m to surface hauls from January-June and November, and on the other dates by summing up incremental hauls from 50m to the thermocline and from the thermocline to the surface.

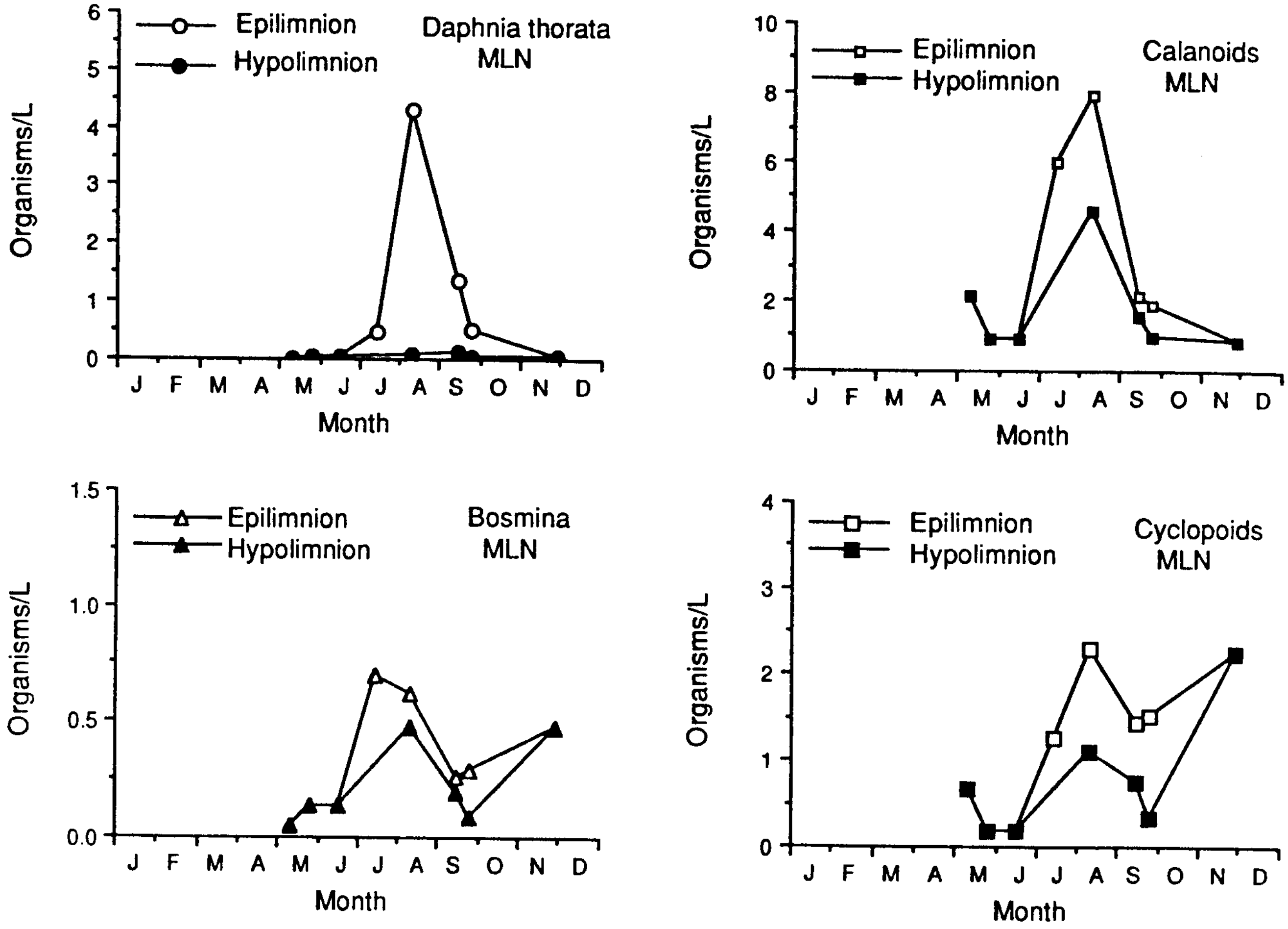


Figure 23. Seasonal abundance of the dominant macrozooplankton in the hypolimnion (50m to the thermocline) and epilimnion (thermocline to the surface) at the Mid-Lake North station in Flathead Lake during 1988. Densities at MLD were calculated by summing up incremental 10m hauls from 50m to the surface. Densities at MLN were calculated from 50m to surface hauls from January-June and November, and on the other dates by summing up incremental hauls from 50m to the thermocline and from the thermocline to the surface.

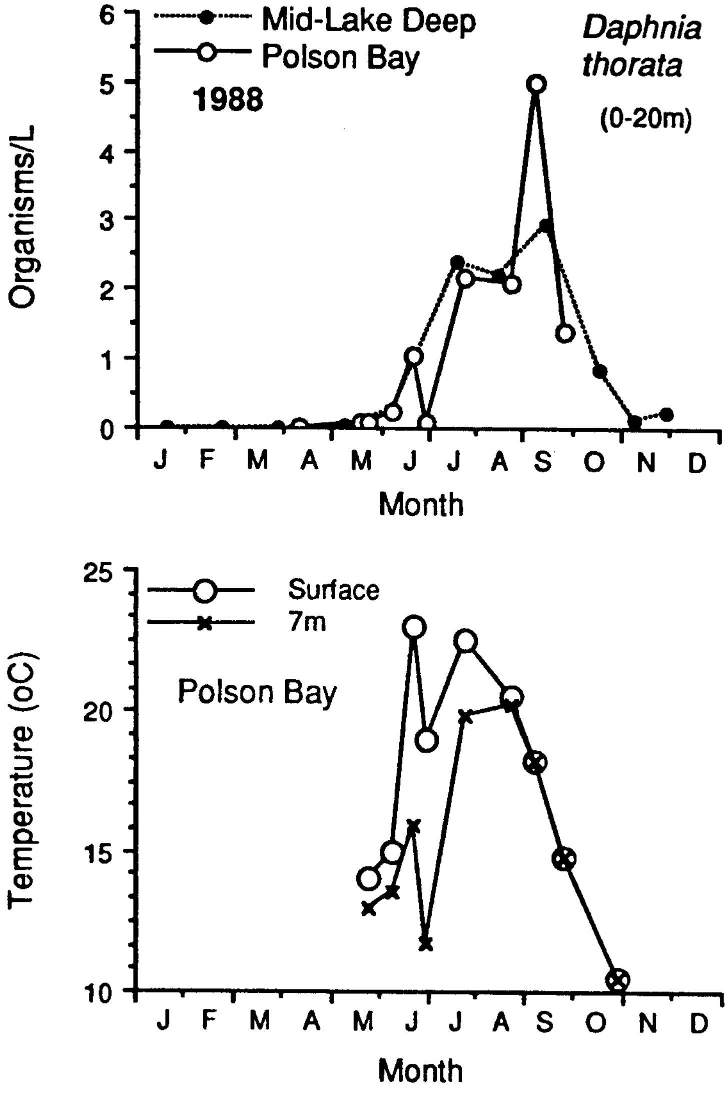


Figure 24. Seasonal abundance of the dominant macrozooplankton at Polson Bay and Mid-Lake Deep stations in Flathead Lake during 1988. Densities at MLD were calculated by summing up incremental 10m hauls from 20m to the surface. Densities at Polson Bay were calculated from bottom (~6m) to surface hauls.

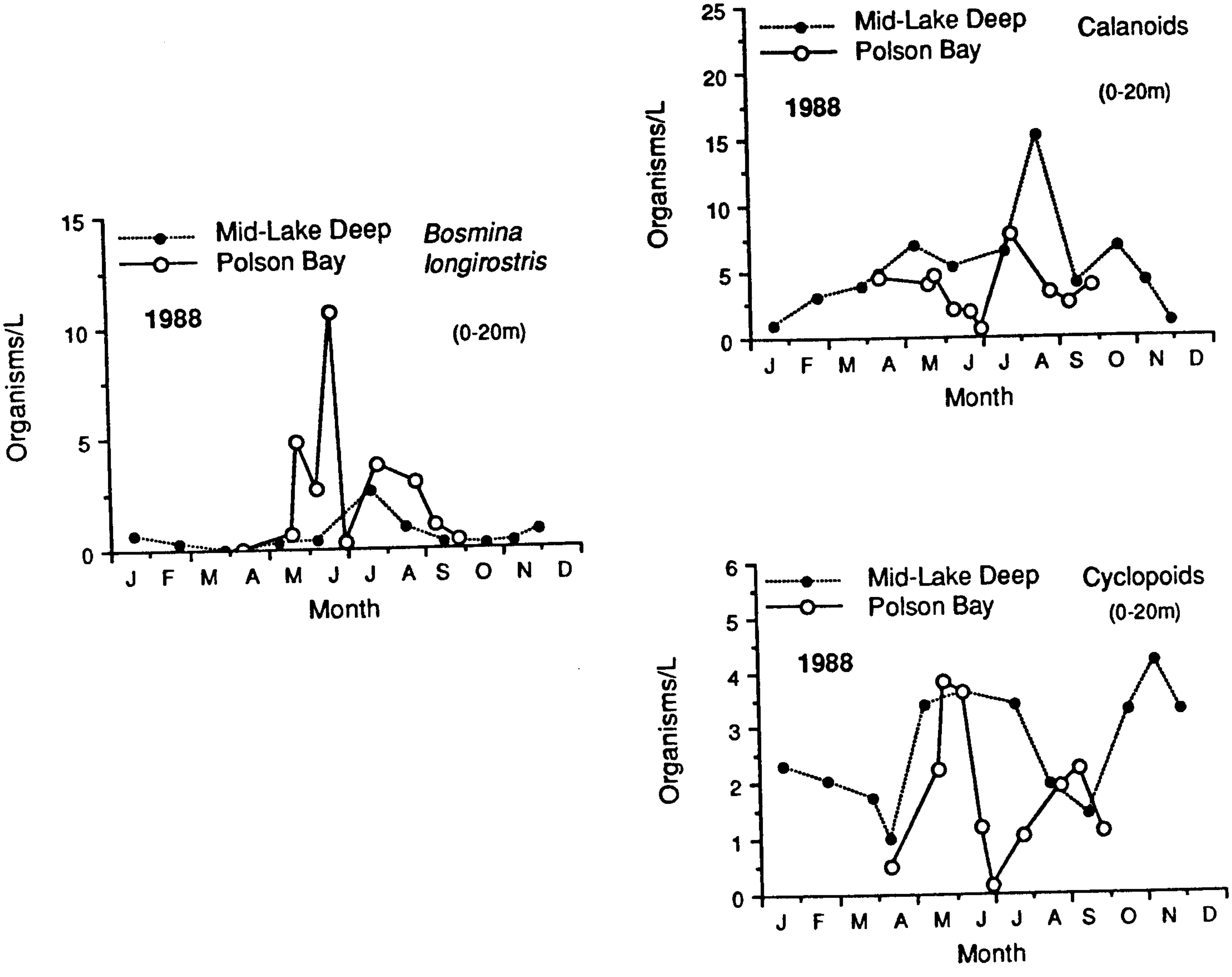
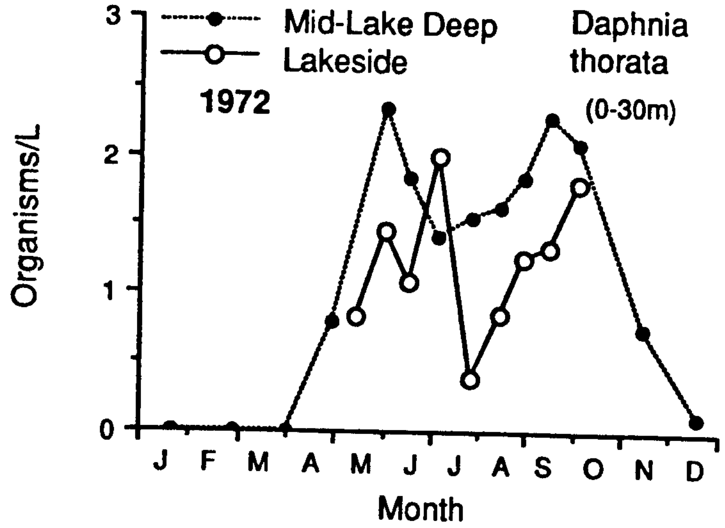


Figure 25. Seasonal abundance of the dominant macrozooplankton at Polson Bay and Mid-Lake Deep stations in Flathead Lake during 1988. Densities at MLD were calculated by summing up incremental 10m hauls from 20m to the surface. Densities at Polson Bay were calculated from bottom (~6m) to surface hauls.



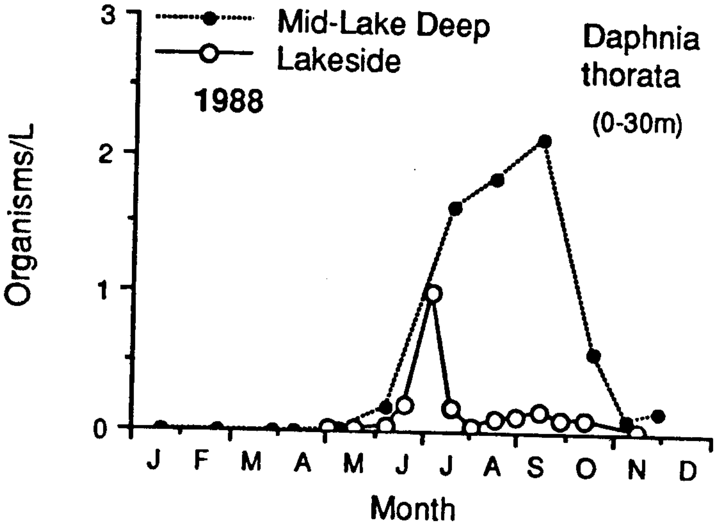
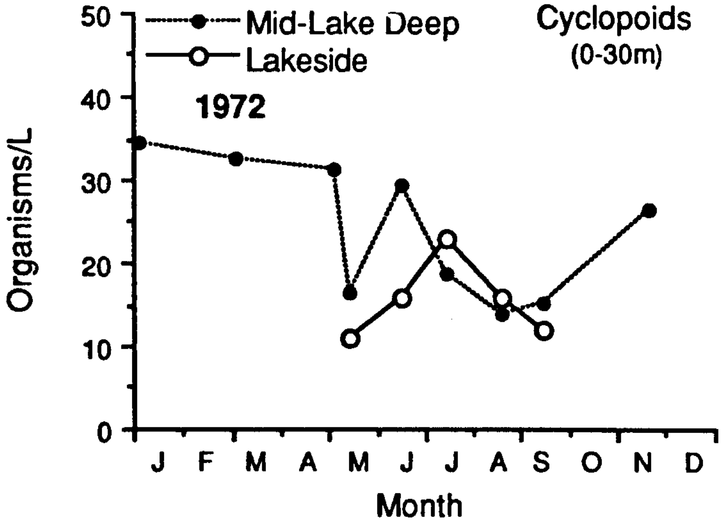


Figure 26. Seasonal abundance of *Daphnia thorata* at the Lakeside and Mid-Lake Deep stations in Flathead Lake during 1972 (top graph) and 1988 (bottom graph). Zooplankton densities were calculated by summing up incremental 10m hauls from 30m to the surface.



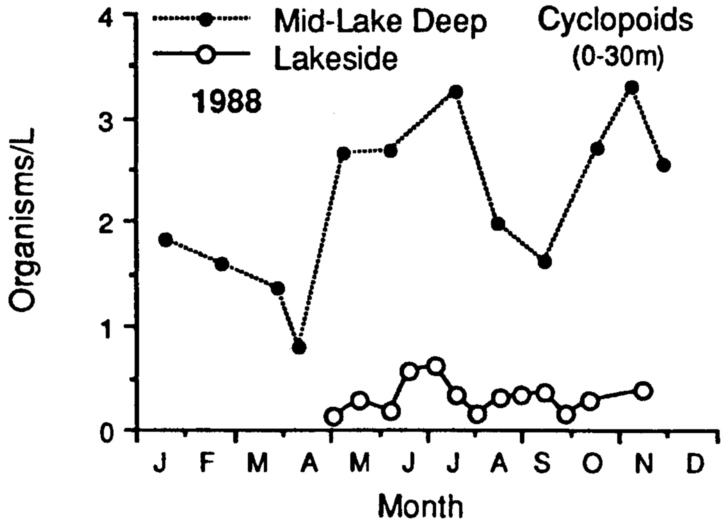


Figure 27. Seasonal abundance of Cyclopoid copepods at the Lakeside and Mid-Lake Deep stations in Flathead Lake during 1972 (top graph) and 1988 (bottom graph). Zooplankton densities were calculated by summing up incremental 10m hauls from 30m to the surface.

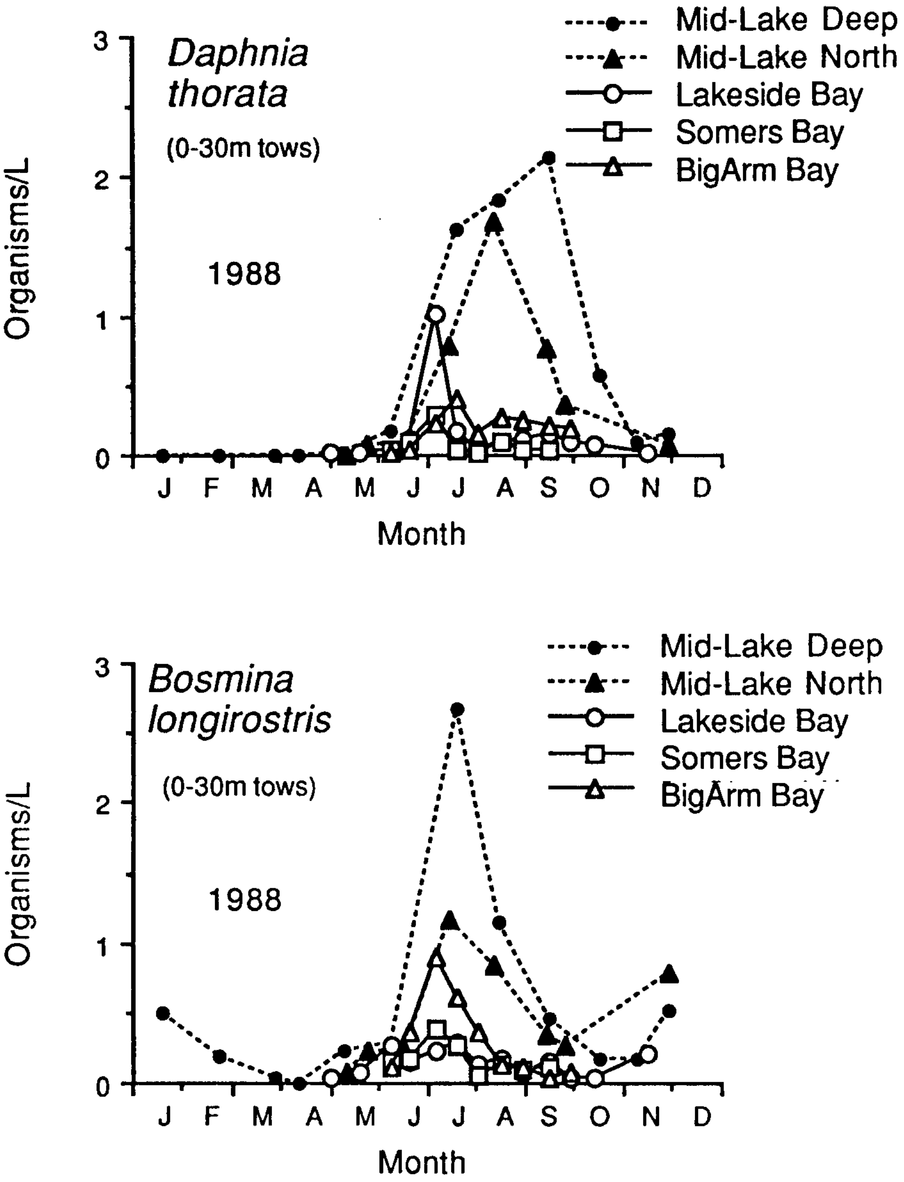


Figure 28. Seasonal abundance of *Daphnia thorata* and *Bosmina longirostris* at two offshore deep sites and 3 nearshore bay sites in Flathead Lake during 1988. Zooplankton densities at MLD and Lakeside were calculated by summing up incremental 10m hauls from 30m to the surface. Zooplankton densities at Somers Bay, and Big Arm Bay were estimated during summer stratification by adding vertical hauls from 25-30m to the thermocline and the thermocline to the surface, and for the rest of the year from 25-30m to surface hauls.

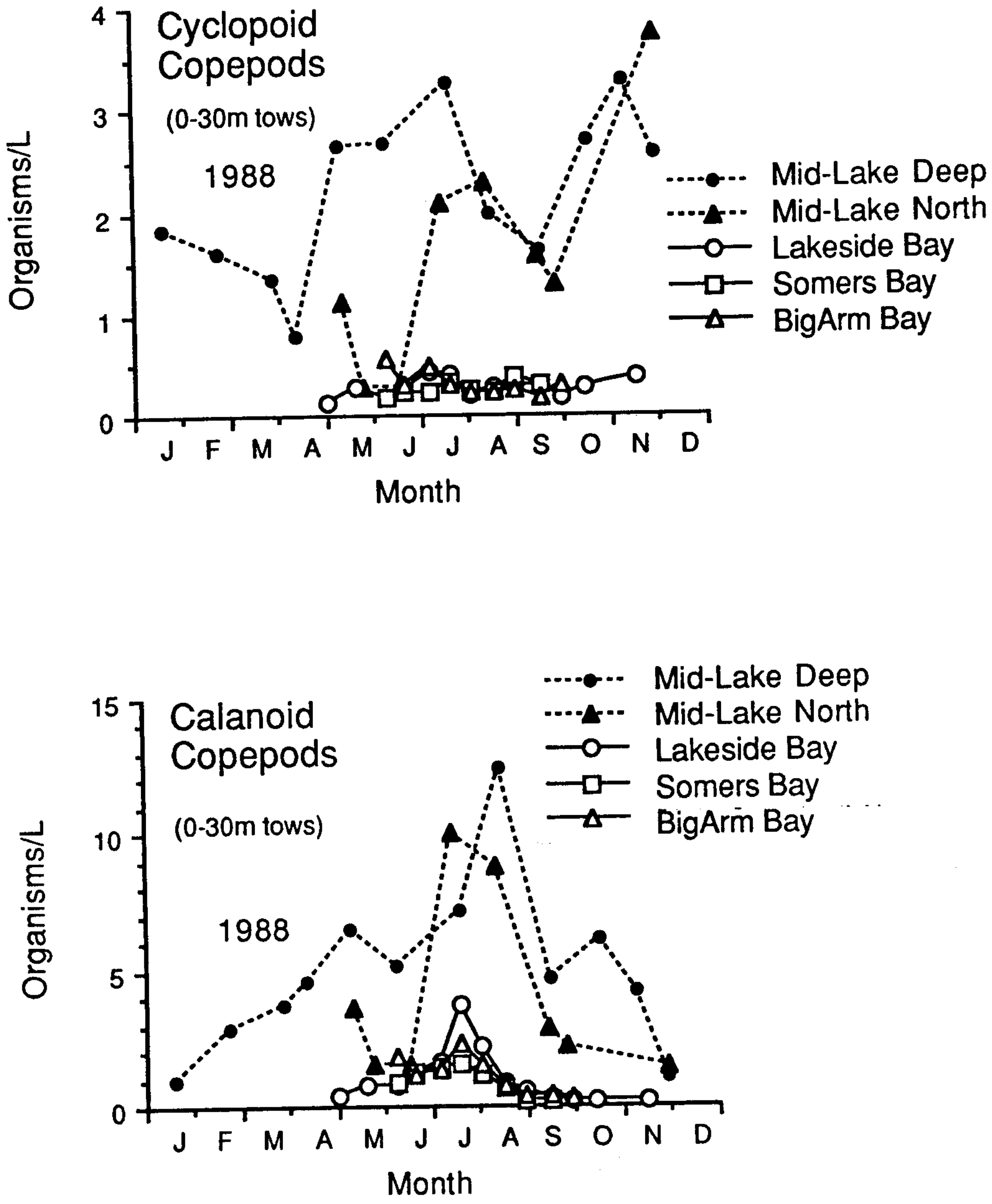


Figure 29. Seasonal abundance of cyclopoid and calanoid copepods at two offshore deep sites and 3 nearshore bay sites in Flathead Lake during 1988. Zooplankton densities at MLD and Lakeside were calculated by summing up incremental 10m hauls from 30m to the surface. Zooplankton densities at Somers Bay, and Big Arm Bay were estimated during summer stratification by adding vertical hauls from 25-30m to the thermocline and the thermocline to the surface, and for the rest of the year from 25-30m to surface hauls.