Chapter V.1

ZOOPLANKTON

Introduction

Zooplankton assemblages show a variety of responses to acidic inputs. Surveys conducted in Scandinavia, Canada, and the United States show that the number of zooplankton species declines with decreasing pH (Sprules 1975, Almer et al. 1974, 1978, Leivestad et al. 1976, Wright et al. 1976, Roff and Kwiatkowski 1977, Raddum et al. 1980, Confer et al. 1983, Yan and Strus 1980, Fryer 1980, Brezonik et al. 1984, Siegfried et al. 1984, Carter et al. 1986, Keller and Pitbaldo 1984). A number of studies also indicate that zooplankton abundance or biomass is lower in acidic than in non-acidic lakes (Yan and Strus 1980, Roff and Kwiatkowski 1977, Almer et al. 1978, Dillon et al. 1979, Brezonik et al. 1984, Confer et al. 1983).

Experimental and survey data show shifts in zooplankton community structure with decreasing pH. Among microcrustaceans, daphnids, *Epischura*, *Leptodora*, and *Tropocyclops* appear to be very sensitive to acidic inputs (require pH > 5.0); *Holopedium*, *Diaphanasoma*, *Mesocyclops*, and *Cyclops* seem to tolerate pHs to the mid to low 4's; and bosminids and some diaptomid copepods often dominate in the most acidic conditions (Almer et al. 1974, 1978, Raddum et al. 1980, Sprules 1975, Roff and Kwiatkowski 1977, Carter 1971, Marmorek 1984, Janicki and DeCosta 1979, Yan and Strus 1980, Keller and Pitbaldo 1984, Brezonik et al. 1984, Confer et al. 1983, Carter et al. 1986, DeLisle et al. 1984, Blouin et al. 1984, Chengalath et al. 1984). *Polyphemus pediculus* and *Chydorus sphaericus* are also commonly collected in acidic waters (Sprules 1975, Roff and Kwiatkowski 1977, Yan and Strus 1980, Keller and Pitbaldo 1984, Confer et al. 1983). There are many exceptions, however, to this general tolerance scheme. For example, *Daphnia catawba* and *Daphnia ambigua* seem relatively tolerant of low pH, whereas most other species of daphnids are absent in acidic waters (Keller and Pitbaldo 1984, Sprules 1975, Carter 1971, Brezonik et al. 1984). *Diaptomus sicilis*, *D. tyrrelli*, and *D. oregonensis* often disappear as pH decreases, whereas *D. minutus*, *D. reighardi*, *D. floridanus*, and *D. gracilis* often dominate in acidic lakes, depending on geographical area (Sprules 1975, Carter 1971, Almer et al. 1974, 1978, Marmorek 1984, Keller and Pitbaldo 1984, Confer et al. 1983, Brezonik et al. 1984). In Norway, the large copepod *Heterocope saliens* often dominates acidic lakes, whereas in Sweden, *H. appendiculata* is restricted to

lakes with pH > 5.5 (Almer et al. 1974, Henrikson et al. 1980, Eriksson et al. 1980). Similarly, in eastern Canada Epischura lacustris is only found in circumneutral lakes, and E. nordenskioldi is found at low pHs (Carter et al. 1986). Although cyclopoids are often reported to be sensitive to acidic inputs (Nilssen 1980, Confer et al. 1983, Roff and Kwiatkowski 1977, Keller and Pitbaldo 1984), a number of studies have reported Mesocyclops edax, Cyclops bicuspidatus thomasi, and Cyclops vernalis in fairly acidic conditions (pH < 4.8, Sprules 1975, Yan and Strus 1980, Keller and Pitbaldo 1984, Brezonik et al. 1984). Even within a species there are discrepancies in reported acid tolerances. For example, Confer et al. (1983) found Bosmina coregoni and B. longirostris only in Adirondack lakes with pH's > 5; however, these species have been reported from much more acidic lakes in many other areas (Marmorek 1984, Keller and Pitbaldo 1984, Almer et al. 1974, 1978, DeCosta and Janicki 1982, Yan and Strus 1980). Yan and Strus (1980) found that Cyclops vernalis was abundant at some times in acidic lakes, whereas Carter et al. (1986) found that this species was more common in non-acidic than in acidic lakes.

Among the rotifers, Keratella serrulata, K. taurocephala, Polyarthra remata, or P. minor are common or dominant in acidic waters; Keratella cochlearis, Kellicottia longispina, and Polyarthra vulgaris tolerate mildly acidic pHs (to 4.4 - 5.4); and Asplanchna, Filinia, Ascomorpha, and Ploesoma are found primarily in circumneutral lakes (Siegfried et al. 1984, Chengalath et al. 1984, Brezonik et al. 1984, Almer et al. 1978, Roff and Kwiatkowski 1977). In eastern Canada Asplanchna priodonta, Keratella crassa, K. cochlearis, Polyarthra dolichoptera, and Trichocerca cylindrica were more common in non-acidic than acidic lakes, and Keratella taurocephala was the major rotifer in acidic waters (Carter et al. 1986). Although Almer et al. (1974, 1978) report that the colonial rotifer Conochilus unicornis was reduced in acidified waters in Sweden, Siegfried et al. (1984) found it in abundance in some acidic, clear lakes in the Adirondack Mountains of the U.S.

Results of some of these studies indicate that, not only the relative, but also the absolute abundances of tolerant species increase as acidification proceeds. Marmorek (1984) found that, relative to controls, Chydorus, Bosmina, and Diaphanasoma increased in abundance then declined in in situ bags to which acid and fertilizer were added, whereas these taxa showed

little response in bags to which only fertilizer was added. Marmorek (1983) reported the results of another experiment where in situ bags were acidified to pH 5.5, 5.0, and 4.5. Daphnia rosea disappeared at pHs between 5.2 - 5.3, Diaptomus tyrrelli was nearly as sensitive, and Bosmina disappeared at the lowest pH. Chlorophyll a and rotifers (Keratella, Polyarthra) increased with increasing acidic inputs, and all crustaceans except for Diaptomus kenai and Holopedium gibberum were removed at pH 4.5. Havens and DeCosta (1985) found that Bosmina increased in in situ bags that were acidified to pH 4.2, whereas most other microcrustacean taxa declined. In these cases increases in tolerant species were attributed to releases from competition or predation by other zooplankton species. Similarly, Henrikson et al. (1980) and Eriksson et al. (1980) hypothesized that the appearance and dominance of large Heterocope saliens in increasingly acidified lakes was owing to the elimination of fish predators.

The literature, then, suggests generalizations in the acid tolerances of different zooplankton taxa. In most cases, however, acid sensitivity is species-specific, so patterns in the distributions and abundances of zooplankton relative to pH will depend on the species pool available in an area. In some cases, there are differences in the reported sensitivity of a given species from area to area. These discrepancies can be attributed to differential sensitivity of different races, subspecies, or sibling species within a species; to other changes brought about by acidification, such as regional differences in trace metal concentrations or other chemical species; or to different complements of co-occurring species. Similarly, the population responses of zooplankton taxa to acidic inputs will depend on their pH tolerances, their interactions with other species in the community, and the effects of acidification on these co-occurring species.

It is necessary, then, to determine the responses of zooplankton communities to acidification for each region separately, because zooplankton species composition and water chemistry will vary from region to region. To date, very little work has examined the distribution and abundances of zooplankton in the Sierra Nevada, or the effects of acidification on these zooplankton assemblages. Stoddard (1986) surveyed 75 high elevation lakes in the Sierra Nevada mountains of California and found that the species composition of zooplankton assemblages showed little relationship to lake pH; however, almost no lakes had a pH < 6. Instead, the distribution of

zooplankton in the Sierra seemed primarily related to the presence of fish. The microcrustacean assemblage in Emerald Lake is typical of that Stoddard (1986) observed in high elevation lakes containing brook trout (Salvelinus fontinalis), i.e., it is dominated by Daphnia rosea, Diaptomus signicauda, Bosmina longirostris, and Holopedium gibberum. Furthermore, the Emerald Lake assemblage is generally similar to British Columbia systems investigated by Neill and his associates (Neill 1982, 1984, Marmorek 1983, 1984). There is evidence, then, that our results for Emerald Lake will have implications for many montane waters of the West Coast.

Prior to our studies, Tonnessen (1984) conducted the only studies on the effects of acidic inputs on Sierran zooplankton. Working in laboratory microcosms, Tonnessen (1984) found that lowering the pH to 4.0 resulted in decreased population levels of rotifers, nearly eliminating Keratella spp. in one experiment. Marmorek (1983, 1984), working with a British Columbia zooplankton assemblage similar to that at Emerald Lake, found that Daphnia rosea, Diaptomus tyrrelli, and Bosmina longirostris were sensitive to acidic inputs, that Diaptomus kenai and Holopedium gibberum tolerated pHs as low as 4.5, and that rotifers (particularly Keratella and Polyarthra) increased with decreasing pH.

Our investigations had two major purposes: (1) To characterize the zooplankton assemblage and its population dynamics in Emerald Lake. (2) To conduct in situ experiments to determine the effects of increased acid and nutrient inputs on zooplankton populations. As part of the second objective, we also attempted to determine the effects of sediment on zooplankton responses to acidification, and to distinguish the effects of the various ions associated with acid deposition (H^+ vs. NO_3^- and SO_4^{2-}).

Methods

Zooplankton in Emerald Lake were quantitatively sampled with vertical tows taken with a 0.3 m diameter, 64 µm mesh net. Duplicate samples were taken from each of seven or eight stations at biweekly intervals from late June to October in 1985 and from early July to late October, in 1984 (Figure I-3). Duplicate samples were taken from each of one to two stations at monthly intervals from November, 1984, to late March, 1985. Tows encompassed the water column from the bottom to the surface and tow lengths

varied with station, ranging from 2 to 10 m. Zooplankton in each sample were preserved in 10% formalin.

Zooplankton in samples were diluted and subsampled with a Stempel pipette and identified and counted at 25 X under a dissecting microscope. Subsampling for microcrustaceans was treated separately from subsampling for rotifers because of the generally higher numerical abundance of the latter. Subsample dilutions were adjusted so that at least 100 individuals were counted for each subsample, at least three subsamples were counted per sample, and from 0.05 to 10% and from 0.05 to 5% of microcrustacean and rotifer samples, respectively, were counted in each subsample, with a few exceptions. In the few exceptions the entire sample was counted. After calculation of numbers per sample, numbers per volume were calculated from data on net mouth area and tow length. No correction for net capture efficiency was used. Zooplankton density for each station was calculated as the average of the densities for the duplicate tows taken from each station. Mean zooplankton abundance and associated measures of variation for each date were calculated treating density estimates for stations as the replicates.

Field experiments were conducted during the summer of 1985 in large bags suspended in the middle of Emerald Lake. Bag construction and experimental treatments are described in Chapter II.4. In Experiment 1 zooplankton were sampled directly following acid additions and eight and seventeen days thereafter. In Experiments 2, 3, and 4 zooplankton were sampled in each bag just before chemical additions and after eight days in Experiment 2, after 1, 9, 23, and 35 days in Experiment 3, and after 11 and 24 days in Experiment 4. Zooplankton samples were taken with a 0.12 m diameter, 64 μm mesh plankton net. Vertical tows were taken from 5 m depth in Experiments 1 through 3, and from 9 m in Experiment 4. Single tows were taken from each bag on each sampling date in Experiments 1, 2, and 4, and duplicate tows were taken from each bag and pooled in Experiment 3. From 1 to 2.6% of each bag's volume was sampled on each sampling date. Zooplankton samples were preserved in 10% formalin. Depending on zooplankton densities, either all zooplankton were counted in samples or subsamples were taken as outlined above.

For each sampling date a mean and variance was calculated for the bags assigned to each treatment. We pooled the data for all dates within an experiment to examine relationships between the mean and variance for each taxon. By using the slope of the regression line describing the relationship

between log variance and log mean we were able to calculate appropriate transformations for meeting the assumptions of parametric statistical tests (Taylor 1961, Downing et al. 1986). If variance - mean relationships are determined from data pooled for all experiments and taxa, the best transformation is the fifth root transformation, confirming the analyses of Downing et al. (1986). There was considerable variation in the slope of the log variance - log mean relationship, however, depending on the experiment and taxon. The transformations we used varied from the square root to the $\log_{10}$ transformation.

After appropriate transformation, we subjected our data to several levels of analyses. For experiments where samples were taken prior to manipulations (Experiments 2, 3, 4) we performed a one way (Experiments 2, 3) or two way (Experiment 4, acid X sediment) analysis of variance to determine if there were any a priori differences among bags assigned to different treatments. We also performed a one way analysis of variance on data taken directly after chemical additions (Day 0 in Experiment 1, Day 1 in Experiment 3) to see if there were any immediate effects of treatment on the abundances of different zooplankton taxa. In Experiment 2, which was terminated after 8 days, we performed a one way ANOVA on data collected at experiment termination. In all of these cases, we performed Duncan's multiple range test for taxa showing significant responses to treatment, as determined from the ANOVAs, to discern which treatments were significantly different. In experiments containing time series data (Days 8 and 17 in Experiment 1, Days 9, 23, and 35 in Experiment 3, and Days 11 and 24 in Experiment 4) we performed repeated measures ANOVAs to determine the effects of treatment, time, and their interaction on plankton abundances. In these cases we also calculated a mean abundance for each taxon in each bag over these sampling dates. The mean values for each bag were then used in subsequent ANOVAs and multiple range tests to determine which treatments were significantly different in each experiment. Finally, to help explain any significant time X treatment interactions evident in the results of the repeated measures ANOVAs, we performed one way (Experiments 1 and 3) or two way ANOVAs (Experiment 4) and subsequent multiple range tests for each date separately. All analyses were run using the ANOVA or GLM programs in the SAS statistical package (SAS Institute 1985).

To examine overall relationships between pH and zooplankton responses we calculated mean pH values and zooplankton densities for each bag over experimental periods. A mean density for control bags was calculated for each experiment using the bag means. Abundance of individual zooplankton taxa in each bag to which acid was added was divided by the appropriate mean control density then multiplied by one hundred to obtain the percentage response of each zooplankton taxon in each bag to acid addition. The response of zooplankton in each bag, measured as percentage of relevant controls, was then plotted against the associated mean pH of each bag. To avoid the confounding influence of phosphate addition, the only experimental treatments used from Experiment 3 were the acid, HCl (pH 5.2), and HCl (pH 5.8) treatments. We did not fit lines to relationships between zooplankton responses and pH using, e.g. multi-polynomial regression analyses, because the magnitude of zooplankton responses to acid treatment depended on experiment duration and different experiments differed in duration.

Results

The zooplankton assemblage in Emerald Lake was dominated by one copepod (*Diaptomus signicauda*), three cladocerans (*Daphnia rosea*, *Holopedium gibberum*, *Bosmina longirostris*), and three rotifers (*Keratella cochlearis*, *Polyarthra vulgaris*, *Conochilus unicornis*). *Diaptomus* copepodite and adult densities remained high from July through mid-August in 1984, then declined to December (Figure V-1). In 1985 *Diaptomus* abundance increased abruptly from late June to early August, then remained at high levels through September (higher levels than in 1984) (Figure V-2). Abundances of *Diaptomus* nauplii fluctuated widely in both years, but peaked in the summer. All cladocerans greatly increased in early summer, but *Holopedium* reached higher levels sooner than *Daphnia* or *Bosmina* then declined precipitously after late August, 1984, or early July, 1985 (Figure V-1). *Holopedium* peaked and declined earlier, and had a briefer period of high abundance, in 1985 as opposed to 1984. In both years *Holopedium* declines coincided with large increases and population peaks in *Daphnia* and *Bosmina*. After peaking in early to mid-September the *Daphnia* population declined to low levels by winter. *Bosmina* showed similar population fluctuations except that it peaked later in 1984 and earlier in 1985 than *Daphnia* (Figures V-1 and V-2). *Bosmina* also showed a second peak in abundance in December 1984 - January

1985. Keratella's population dynamics were the mirror image of Daphnia's in 1984, peaking in August, declining in September and October, then increasing again in late October and early November. Keratella's abundance was generally higher in summer 1985 than in summer 1984, whereas Polyarthra showed the opposite pattern. Polyarthra's abundance peaked in late August, 1984, whereas two peaks were evident in 1985, one in late June, the other in early September. Abundances of Conochilus were highest in July and August, and Polyarthra, Keratella cochlearis, and Conochilus reached low levels in winter and spring. Keratella quadrata, on the other hand, was commonly collected in winter, spring, and early summer but was largely absent at other times. The rotifer Trichocerca capucina was abundant in late summer. A variety of other taxa were occasionally collected (Table V-1).

Congruence Between the Lake and Control Bags, Pre-Manipulation Analyses--Because bags enclosed the water column before being tied off by SCUBA divers, zooplankton abundance was the same between the lake and the bags at the outset. In general, zooplankton populations inside bags faithfully mimicked zooplankton dynamics outside of the bags. For example, large population crashes in Diaptomus nauplii and Polyarthra occurred both in the lake and inside bags in early July. In Experiments 1, 3, and 4 copepod and rotifer abundances inside and outside control bags were similar; however, population increases in cladocerans were greater in the lake than in the control enclosures in Experiment 1, perhaps owing to recruitment from ephippia in the lake (Figures V-2 - V-5). Daphnia abundance tended to be higher in the lake than in the bags in all experiments, perhaps owing to similar reasons. In Experiment 2, densities of nauplii, Holopedium, and Polyarthra were similar between the lake and bags; however, abundances of most other taxa were less in the bags. This discrepancy was not owing to any enclosure effects; rather it was owing to lower densities of zooplankton in the center of the lake where experiments were performed than in other parts of the lake which were sampled as part of the monitoring program. For example, mean densities of Bosmina, Keratella, and Conochilus in the center of the lake at experiment initiation were 155, 6522, and 155/m^3, whereas mean lakewide densities a few days later were 3492, 77247, and 1648/m^3. Although most taxa increased or decreased in the bags as in the lake, Holopedium always decreased in bags in July even during the time of increasing population densities in the lake.

ANOVAs performed on pre-manipulation data generally showed no significant effect of treatment on the abundances of individual taxa. There were two exceptions, however. In Experiment 3 initial abundances of Diaptomus nauplii were significantly higher in nitrate + sulfate and nitric + sulfuric acid treatments than in the phosphate and acid + phosphate treatments. In Experiment 4 initial densities of Diaptomus copepodites and adults were significantly lower in the acid, no sediment treatment than in all other treatments. In both cases, these initial biases appeared to have no effect on treatment results. In general, densities of zooplankton taxa were similar in bags assigned to different treatments before manipulations began.

Experiments 1 and 2--The results of the repeated measures ANOVAs and multiple range tests for Experiment 1 revealed that Keratella, Conochilus, and all stages of Diaptomus were significantly less abundant in bags to which acid was added than in control bags (Figure V-3, Table V-2). ANOVAs performed on data collected immediately after acid additions showed that Diaptomus responded immediately to acidification whereas rotifers began showing significant responses only after a week. There was also a tendency for Holopedium and Bosmina to be more abundant in control than in acidified bags, and for Polyarthra to be more abundant in acidic (pH 4.8) than control treatments (Figure V-3, Table V-2).

In Experiment 2 Conochilus, Daphnia, and Diaptomus nauplii were significantly more abundant in control than in acidified bags, Holopedium and Bosmina were more abundant in control and pH 5.2 bags than in pH 4.2 bags, and Diaptomus copepodite and adult densities showed the significant responses: controls > pH 5.2 > pH 4.2 (Table V-2, Figure V-4). Polyarthra was significantly more abundant in pH 5.2 than pH 4.2 treatments, and Keratella was significantly more abundant in pH 5.2 bags than in control bags and more abundant in control bags than in pH 4.2 bags. In general, then, Conochilus, Daphnia, and Diaptomus were very sensitive to acidic inputs, Holopedium and Bosmina were significantly reduced only at low pH levels (pH < 5), and the rotifers Keratella and Polyarthra increased in bags reduced to intermediate pH levels (pH ~5), relative to controls, then declined at low pH levels (pH < 4.8).

Experiment 3--The repeated measures ANOVAs revealed that all common taxa showed significant responses to treatment (Table V-2). Daphnia, Conochilus, and Diaptomus copepodites and adults were more abundant in high pH treatments

(pH > 5.5, NO_3 + SO_4, HCl (pH 5.8), and control treatments) than in low pH treatments (pH < 5.5, acid, acid + phosphate, and HCl (pH 5.2) treatments) (Table V-2, Figure V-5). Keratella showed the opposite pattern. Diaptomus nauplii were significantly more abundant in HCl (pH 5.8), acid + phosphate, and control treatments than in acid or HCl (pH 5.2) treatments, and Polyarthra was significantly more abundant in the HCl (pH 5.8) than in the acid + phosphate, phosphate, and nitrate + sulfate treatments. Bosmina was more abundant in the acid + phosphate, phosphate, and HCl (pH 5.2) treatments than in the control treatment, and Holopedium densities were higher in the HCl (pH 5.8) than in the phosphate, nitrate + sulfate, and acid + phosphate treatments, and higher in the acid, control, and HCl (pH 5.2) treatments than in the acid + phosphate treatment. Daphnia showed the largest increases in response to phosphate addition, reaching densities several times higher than those in controls. Bosmina abundances increased in phosphate + acid and phosphate addition bags through the first 23 days following experiment initiation, then levelled off in phosphate bags but continued increasing in phosphate + acid bags (Figure V-5). Copepods and rotifers showed no significant responses to phosphate addition relative to controls.

Experiment 4--The two-way repeated measures ANOVA revealed a significant effect of sediment and treatment on transformed abundances of Keratella, and significant interaction effects of treatment X day for Diaptomus and sediment X day for Bosmina (Table V-2). Examination of population patterns indicate that the interaction effect for Diaptomus was owing to generally lower densities on Day 11 and higher densities on Day 24 in acid than in control treatments. The interaction effect for Bosmina was primarily owing to lower densities on Day 11 and higher densities on Day 24 in sediment (particularly sediment + acid) than in no sediment treatments (Fig. V-6). There was a nearly significant sediment X treatment interaction effect on Daphnia densities, with treatment effects being much more pronounced in sediment bags than in bags without sediment. ANOVAs and multiple range tests using mean abundances for each bag over the experimental period showed that Daphnia were significantly more abundant in control than in acidified bags, whereas Keratella and Polyarthra showed the opposite pattern. Keratella was also significantly more abundant in bags without sediment than in bags containing sediment. ANOVAs and multiple range tests conducted separately for each date revealed that Daphnia were significantly more abundant in

control than in acidified bags and Polyarthra were significantly more abundant in acidified than in control bags on Day 11, whereas neither taxon showed a significant response on Day 24 (Figure V-6). Keratella were significantly more abundant in no sediment than in sediment bags only on Day 24. Other taxa showed no significant responses to acid addition or the presence of sediments.

Overall Analyses

Diaptomus, Daphnia, and Conochilus were very sensitive to acid addition (Figure V-7). Diaptomus and Daphnia densities were relatively unaffected by acid additions to pH 5.6, then declined precipitously at ca. pH 5.5 and remained low at lower pHs. Bosmina and Keratella abundances in acidified bags were greater than those in associated controls between pH 5.1 - 5.5, but declined to low levels below pH 5.0. Although there was considerable scatter in data on Holopedium responses, apparent "releases" (i.e., acidified bags > controls) were apparent in some bags with pH > 5.1. At pHs below 5.0 Holopedium densities were usually < 25% of controls. Responses of Polyarthra were quite variable over the pH range tested.

Discussion

These experimental results indicate that Sierra Nevada zooplankton assemblages are very sensitive to acid and nutrient inputs, and will show significant changes in community structure if nutrient or acid loading rates change. Daphnia rosea, Diaptomus signicauda, and Conochilus unicornis are very sensitive to acidification, declining abruptly at approximately pH 5.5. Keratella cochlearis, Bosmina longirostris, and Holopedium gibberum were more tolerant of low pH, but also declined below pH 5.0. Polyarthra vulgaris appeared to be the most tolerant taxon, and often remained abundant even at the lowest pHs tested (pH = 4.0). In general, these results agree with zooplankton pH tolerances reported from survey and experimental work (see references in Introduction).

Between pH 5.1 and 5.5 Bosmina and Keratella, and, in some experiments, Polyarthra and Holopedium, actually increased relative to controls, indicating a release from competition or predation by more sensitive taxa (Daphnia, Diaptomus). Marmorek (1983) and Havens and DeCosta (1985) obtained similar results for rotifers and Bosmina and attributed them to releases from competition with cladocerans or from predation by copepods. Neill (1984,

1985), working with a similar assemblage in British Columbia, found that the removal of Daphnia rosea, but not Diaptomus spp., resulted in large increases in the densities of rotifers and other cladocerans (including Bosmina and Holopedium). We conclude from our results and those of Neill (1984, 1985, see also Vanni 1986) that the increases in rotifers, Bosmina, and Holopedium observed when Daphnia was diminished by acidification were owing to a release from competition with Daphnia.

The results of Experiment 4 indicate that some zooplankton taxa respond to relatively modest, short-term changes in pH. In this experiment sediment bags were initially acidified to pH 5.3 - 5.5 and bags without sediment to pH 5.4 - 5.6, and pH increased throughout the experiment to 5.6 - 6.1 in sediment bags and 5.6 - 5.8 in bags without sediment. On Day 11 but not Day 24 Daphnia densities were significantly reduced in acidified bags relative to controls, indicating a temporary response to acid reductions. Similarly, the time X treatment interaction effect for Diaptomus was owing to a temporary Diaptomus response to acid inputs. Because Daphnia and Diaptomus seem to respond drastically to pH drops from 5.6 to 5.5, it is possible that these taxa showed initial responses because pH dropped below the critical level. As the pH of bags increased above this critical threshold densities of Daphnia and Diaptomus rebounded, so that no significant differences were apparent at experiment termination. Responses of other taxa, i.e., increases in rotifers in acidified bags vs. controls, were probably owing to releases from competition with Daphnia (see above).

The Experiment 4 results also indicate that the presence of sediment can affect the responses of zooplankton to acidification, perhaps owing to release of metals from sediments. Daphnia responses to acidification were much more pronounced in sediment bags than in bags without sediment, especially when expressed as percent of controls (Fig. V-7). The sediment X time interaction for Bosmina was owing primarily to a temporary reduction and subsequent large increase in population size in acidified sediment bags, the bags in which Daphnia's densities were lowest. Bosmina's response indicates a temporary reduction owing to acid stress, followed by increases owing to alleviation of competition with Daphnia. Although not tested directly, other survey and experimental studies indicate that zooplankton responses to acidification may be modified or enhanced by increased metal concentrations (Yan and Strus 1980, DeLisle et al. 1984).

The addition of orthophosphate resulted in consistent, significant increases in the abundance of Daphnia. Bosmina increased in phosphate addition treatments through the first 23 days then levelled off, and rotifers and copepods showed no responses to nutrient addition. Because previous experiments have shown that orthophosphate is the major nutrient limiting algal growth in Emerald Lake, these results indicate a hierarchy of competitive abilities. Daphnia, probably owing to its rapid numerical and functional responses to increased food, appears to rapidly sequester food resources resulting in large population increases (Neill 1984). Bosmina also increases during those times when food is less limiting, but show slowed population growth as Daphnia populations diminish the available food. Other taxa show no demographic responses because of slow numerical responses (copepods) or because excess food is quickly ingested by rapidly increasing densities of superior competitors (i.e., Daphnia). Similarly, Neill (1984) found that moderate nutrient additions resulted in only increases in abundances of cladocerans (particularly Daphnia rosea), whereas large nutrient inputs were necessary to elicit a rotifer population response.

The addition of acid, however, overwhelmed the effects of nutrient addition on Daphnia population growth, and Daphnia densities in acid + phosphate bags were as low as those in acid or HCl (pH 5.2) bags. As a consequence, chlorophyll a levels were higher in the phosphate + acid treatment than in other treatments, because nutrient levels were high and densities of the dominant exploiter were low (as in Marmorek 1984). These results indicate that declines in Daphnia when acid is added are direct responses to acid toxicity, rather than indirect responses mediated through the food supply. Roff and Kwiatkowski (1977) suggest that declines in phytoplankton biomass with declining pH result in declining zooplankton biomass. In our experiments, however, there was little change in the size structure of phytoplankton assemblages among treatments, and there was increased phytoplankton biomass in the acid + phosphate as compared to other treatments. Despite high food levels in the acid + phosphate treatment, sensitive taxa (Daphnia, Diaptomus) exhibited abundances as low as those in other acid treatments. These results, coupled with very rapid population responses to acid addition, indicate that acid was directly toxic to sensitive taxa.

Bosmina reached its highest densities in the acid + phosphate treatment, benefiting from reduced densities of the superior competitor (Daphnia) and enhanced food levels (similar to Marmorek's 1984 results). Because Bosmina levels were similar in the HCl (pH 5.2) and phosphate addition treatments, enhanced growth owing to competitive release approximately equalled enhanced growth due to increased food supplies. Similarly, densities of Diaptomus nauplii were similar in control and acid + phosphate treatment. In this case the production or survival of nauplii was probably enhanced by increased food levels in the acid + phosphate treatment which compensated for the negative consequences of acid stress. On Day 23 densities of Keratella were much higher in the acid, HCl, and acid + phosphate treatments than in the other treatments; however, by Day 35 Keratella densities in the acid + phosphate treatment had declined to control levels probably owing to the continued population growth of Bosmina in this treatment. In general, population growth in Keratella showed the opposite patterns of population growth in Bosmina for Days 23 - 35 in Experiment 3. Population responses of Polyarthra and Holopedium were less consistent but densities tended to be greatest at pH 5.8, where Daphnia levels had declined somewhat but Keratella and Bosmina levels had not increased. The densities of both of these species tended to be lowest in treatments to which nutrients were added indicating suppression by superior competitors which increased when phosphate (Daphnia) or phosphate + acid (Bosmina, Keratella) were added.

Our results also indicate that the effects of acidification are primarily the result of responses to proton addition, rather than responses to nitrate or sulfate addition. In Experiment 3, there were no significant differences in abundances of individual zooplankton taxa in control bags vs. bags to which nitrate and sulfate were added. On the other hand, reduction of pH by addition of hydrochloric acid produced very similar results as comparable reductions of pH by addition of sulfuric and nitric acids.

In summary, these experiments indicate that the effects of acidification will depend on the exact pHs involved, the species assemblage present, and biological interactions among zooplankton species. Few changes will occur as pH declines from 6.3 to 5.6; however, between 5.6 and 5.5 a number of zooplankton taxa will abruptly decline, owing to direct toxic effects, including the competitive dominant (Daphnia rosea). As pH declines from 5.5 to 5.1 Bosmina longirostris and Keratella cochlearis will dominate, owing to

release from competition with Daphnia. This is not to say that Bosmina and Keratella do not experience physiological stress between pH 5.5 and 5.1; rather, it indicates that the advantages these taxa accrue from competitive release more than compensates for any deleterious effects of acidification. Below pH 5.0 even these taxa will decrease. Addition of limiting nutrients will favor the dominance of Daphnia, whereas additions of both nutrients and acid will favor the dominance of Bosmina. Responses of zooplankton to acidification appear to be responses to protons rather than nitrate or sulfate ions. The presence of sediments can affect the responses of some zooplankton taxa to acidification. Finally, short-term depressions of pH can result in temporary population responses of zooplankton.

The abundance of Diaptomus signicauda and Daphnia rosea in Emerald Lake indicates that short-term depressions of pH have not been of sufficient duration or intensity to have long-term effects on the Emerald Lake zooplankton assemblage. The Emerald Lake zooplankton assemblage will show sensitive responses to acidic inputs, underlining their importance as monitors of acid stress.

Table V-1. Emerald Lake zooplankton

CLADOCERA

- *Holopedium gibberum**
- *Bosmina longirostris**
- *Daphnia rosea**
- *Scapholeberis kingii*
- *Diaphanosoma brachyurum*
- *Moina* sp.
- *Polyphemus pediculus*
- *Chydorus sphaericus*
- *Eurycercus lamellatus*
- *Camptocercus* sp.
- *Alona affinis*
- *Graptoleberis* sp.

COPEPODA

- *Diaptomus signicauda**
- *Cyclops* sp.
- *Bryocamptus* sp.

MISCELLANEOUS

- *Hydra*
- Nematoda
- Oligochaeta
- Tardigrada
- Neorhabdocoela
- Ostracoda
- Acari

ROTIFERA

- *Keratella cochlearis**
- *Polyarthra vulgaris**
- *Conochilus unicornis**
- *Trichocerca capucina*
- *Trichotria* sp.
- *Keratella quadrata*
- *Gastropus stylifer*
- Bdelloida

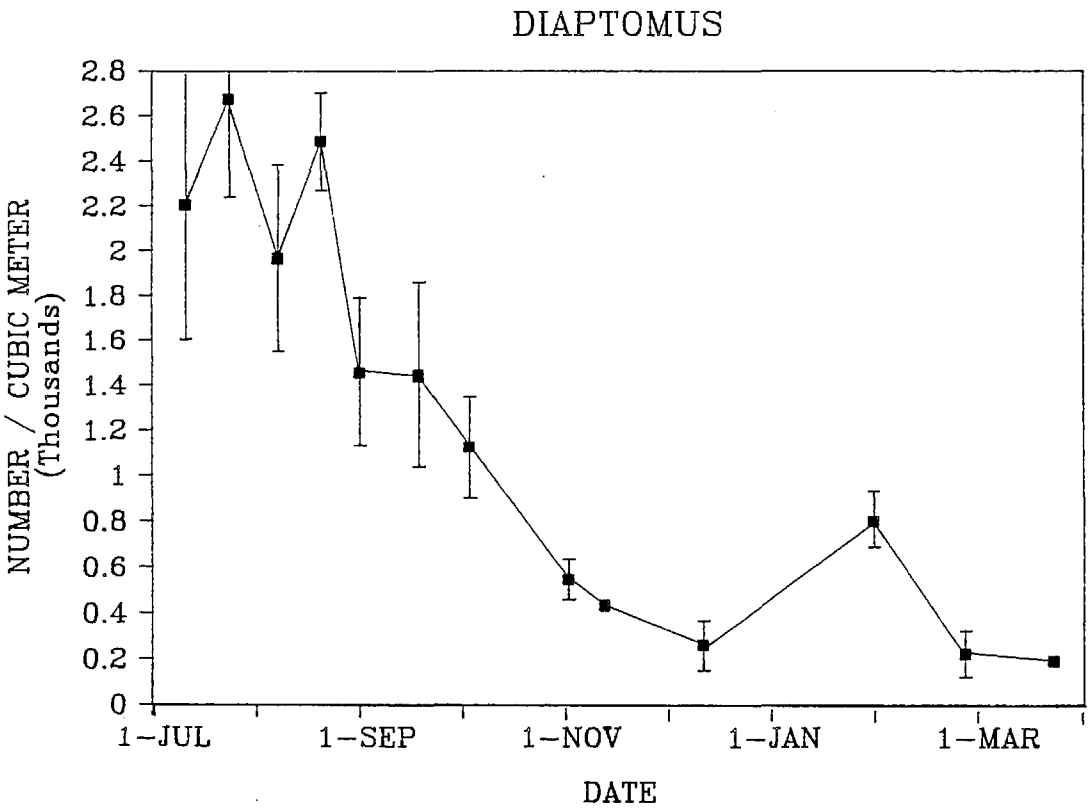
INSECTA

- *Chaoborus*
- Chironomidae

*Dominant species

Table V-2. Results of statistical analyses of bag experiments. F values and probability (P) levels for F tests for one-way ANOVAs (Expt. 2) or for one-way (Expts. 1 and 3) or two-way (Expt. 4) repeated measures ANOVAs are shown. Underlying letters show the results of Duncan's multiple range tests on mean values for individual bags assigned to different treatments over the experimental period. Treatments connected by an underline are not significantly different (P>0.05). Treatment codes are: Expt. 1: C = control, HP = +acid (pH=4.8), LP = +acid (pH=4.2). Expt. 2: C = control, HP = +acid (pH=5.2), LP = +acid (pH=4.2). Expt. 3: C = control, N = +NO_3 and SO_4, P = +PO_4, HH = +HCl (pH=5.8), HL = +HCl (pH=5.2), Ac = +H_2SO_4 and HNO_3, AP = +H_2SO_4, HNO_3, PO_4. Expt. 4: Top - A = +acid, C = control; Bottom - N = no sediment, S = sediment.

Expt	Source	Diaptomus copepodids and adults		Diaptomus nauplii		Holopedium		Bosmina		Daphnia		Keratella		Polyarthra		Conochiloides	
		F	P	F	P	F	P	F	P			F	P	F	P	F	P
1	Trt	67.2	0.0001	9.0	0.007	1.6	0.2	2.3	0.2			5.4	0.03	2.4	0.1	13.4	0.002
	Time	0.06	0.8	0.01	0.9	13.5	0.005	1.0	0.3	Rare		19.0	0.002	0.5	0.5	1.4	0.3
	Trt*Time	0.2	0.8	0.8	0.5	2.0	0.2	0.3	0.7			8.7	0.008	1.2	0.4	0.05	0.9
		C HP LP		C LP HP		C HP LP		C HP LP				C LP HP		HP LP C		C HP LP	
2	Trt	108.8	0.0001	18.4	0.0007	9.0	0.007	12.0	0.003	9.5	0.006	50.7	0.0001	5.4	0.03	5.0	0.04
		C HP LP		C HP LP		C HP LP		HP C LP		C HP LP		HP C LP		HP C LP		C LP HP	
3	Trt	14.1	0.0001	3.0	0.04	5.4	0.003	2.9	0.04	28.1	0.0001	10.9	0.0001	3.0	0.03	5.1	0.004
	Time	16.4	0.0001	1.6	0.2	9.3	0.0006	4.0	0.03	3.8	0.03	9.2	0.0007	4.7	0.02	7.1	0.003
	Trt*Time	1.4	0.2	2.5	0.02	1.9	0.07	2.4	0.02	3.3	0.003	2.2	0.03	0.9	0.5	1.1	0.4
		N C HH P AP Ac HL		HH AP C N P Ac HL		HH Ac C HL P N AP		AP P HL HH Ac N		C P N C HH AP Ac HL		Ac HL AP HH C P N		HH Ac C HL AP P N		C HH N P AP Ac HL	
4	Sed	0	1.0	0	1.0	Absent		0.02	0.9	0.4	0.5	8.6	0.01	1.5	0.2	3.1	0.1
	Trt	0	1.0	1.8	0.2			0.2	0.6	1.7	0.2	7.6	0.02	0.4	0.5	1.1	0.3
	Time	0.2	0.7	8.0	0.02			16.6	0.002	1.3	0.3	1.9	0.2	1.1	0.3	1.3	0.3
	Sed*Trt	3.2	0.1	1.5	0.2			0.2	0.7	4.5	0.06	0.9	0.4	0.05	0.8	0.08	0.8
	Sed*Day	0.8	0.4	0.1	0.8			5.3	0.04	2.5	0.1	2.9	0.1	1.0	0.3	0.1	0.7
	Trt*Day	6.4	0.03	1.8	0.2			2.8	0.1	1.6	0.2	0.2	0.7	2.2	0.2	1.2	0.3
	Sed*Trt*Day	0.01	0.9	1.6	0.2			3.3	0.9	0.4	0.6	0.7	0.4	1.1	0.3	0.09	0.8
		C A / S N		C A / N S				A C / S N		C A / S N		A C / N S		A C / N S		C A / N S	



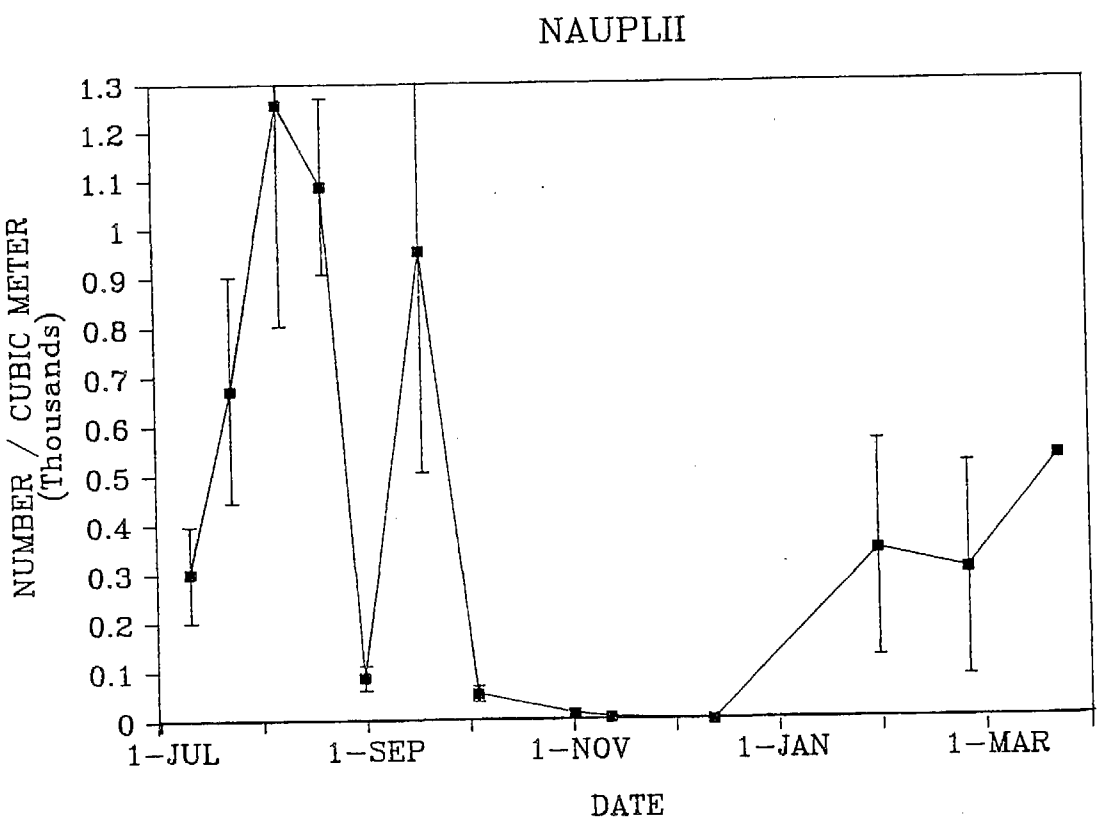
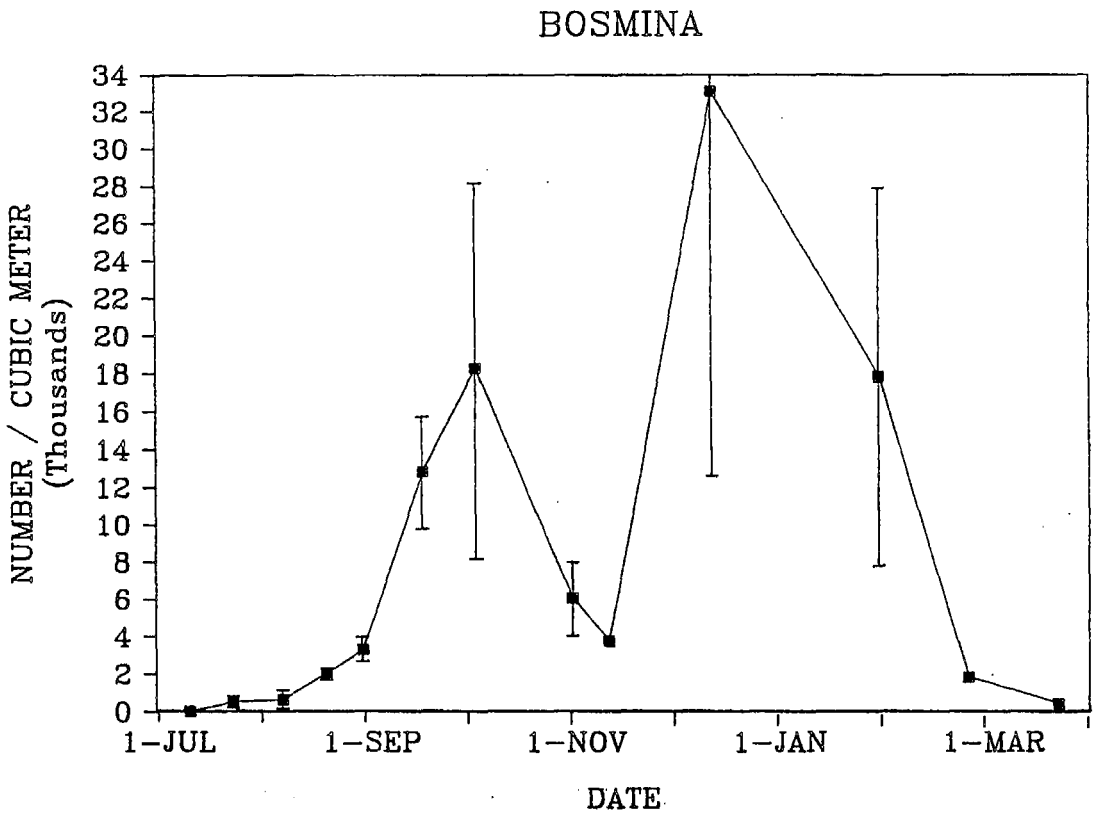
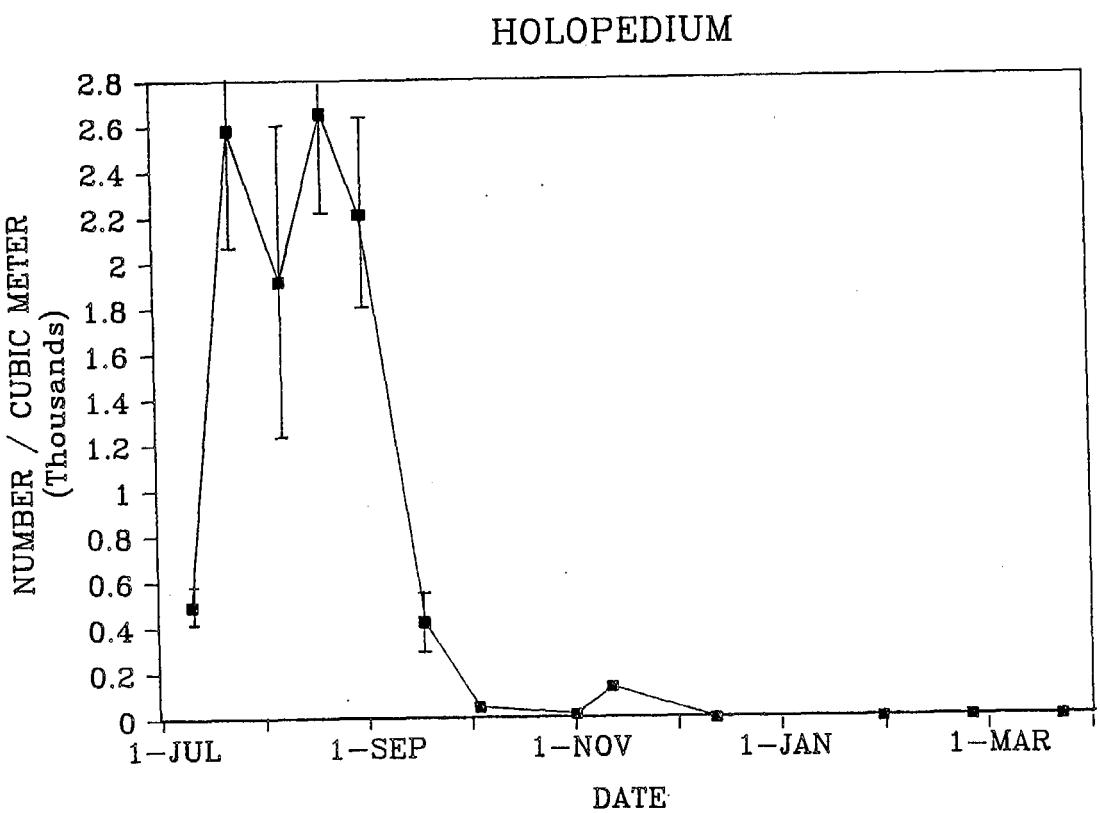


Figure V-1. Abundance of common zooplankton taxa (thousands/m^3) in Emerald Lake from July, 1984, to March, 1985. Points are means and error bars are ± 1 SE.





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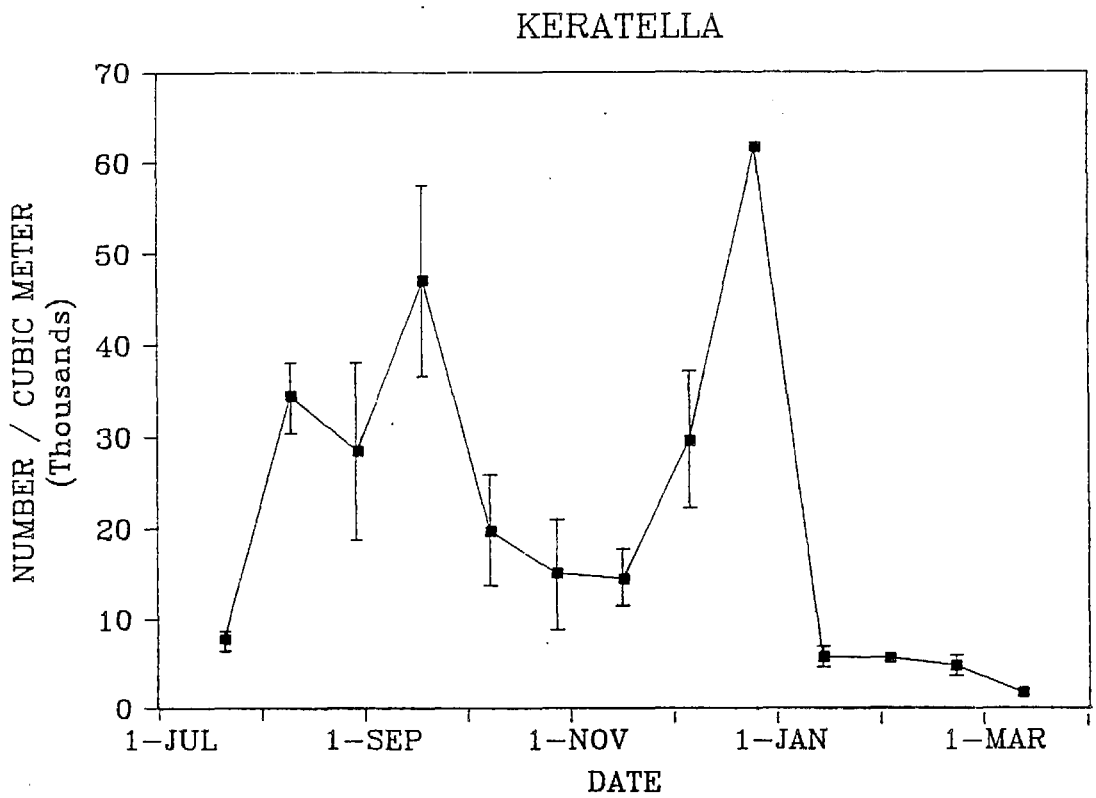

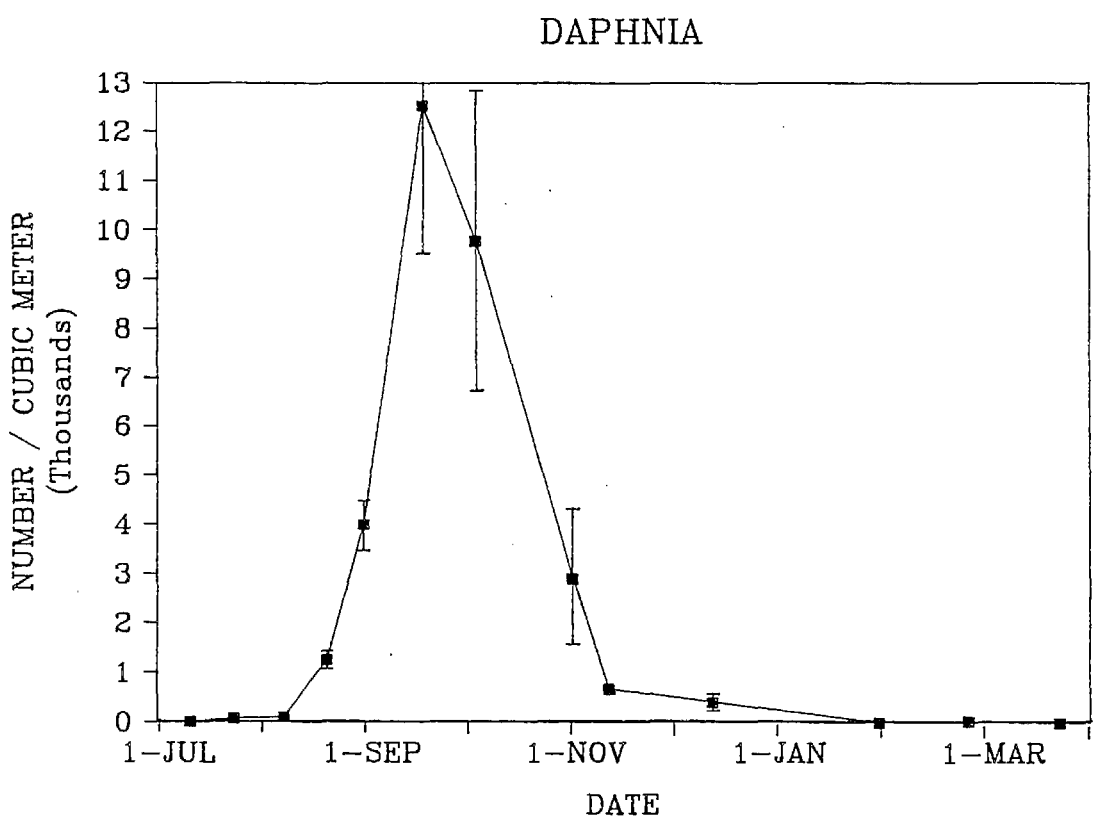

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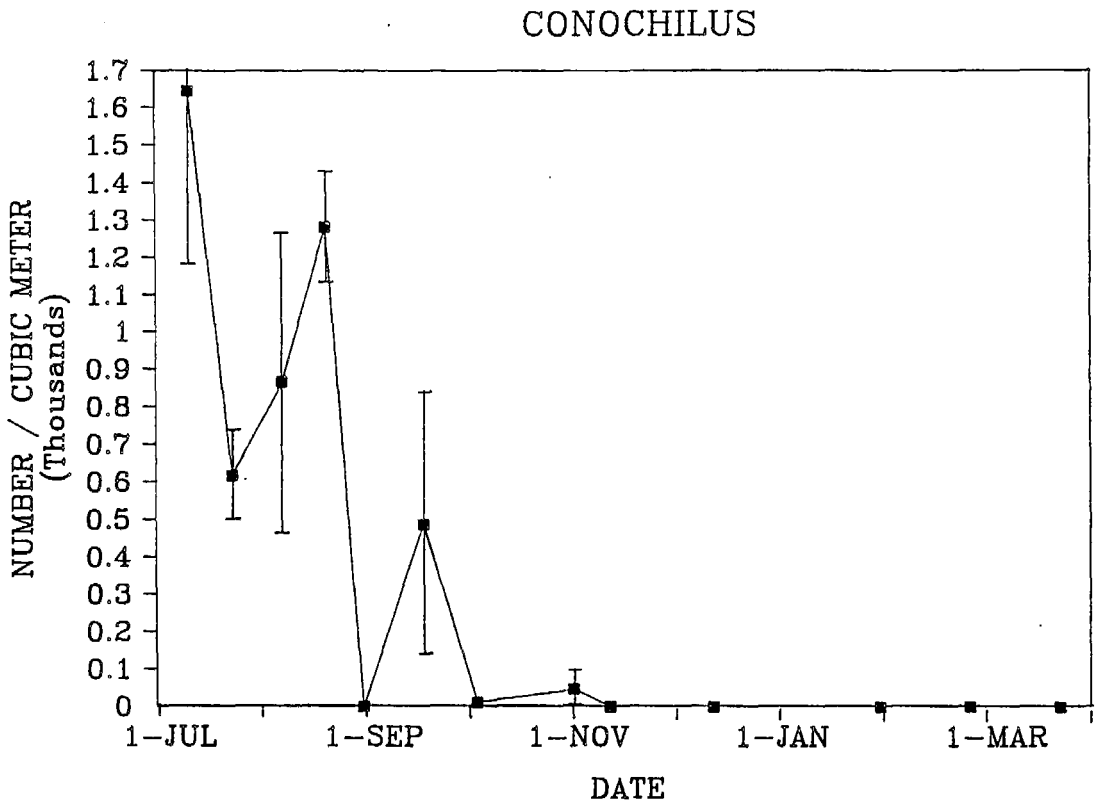

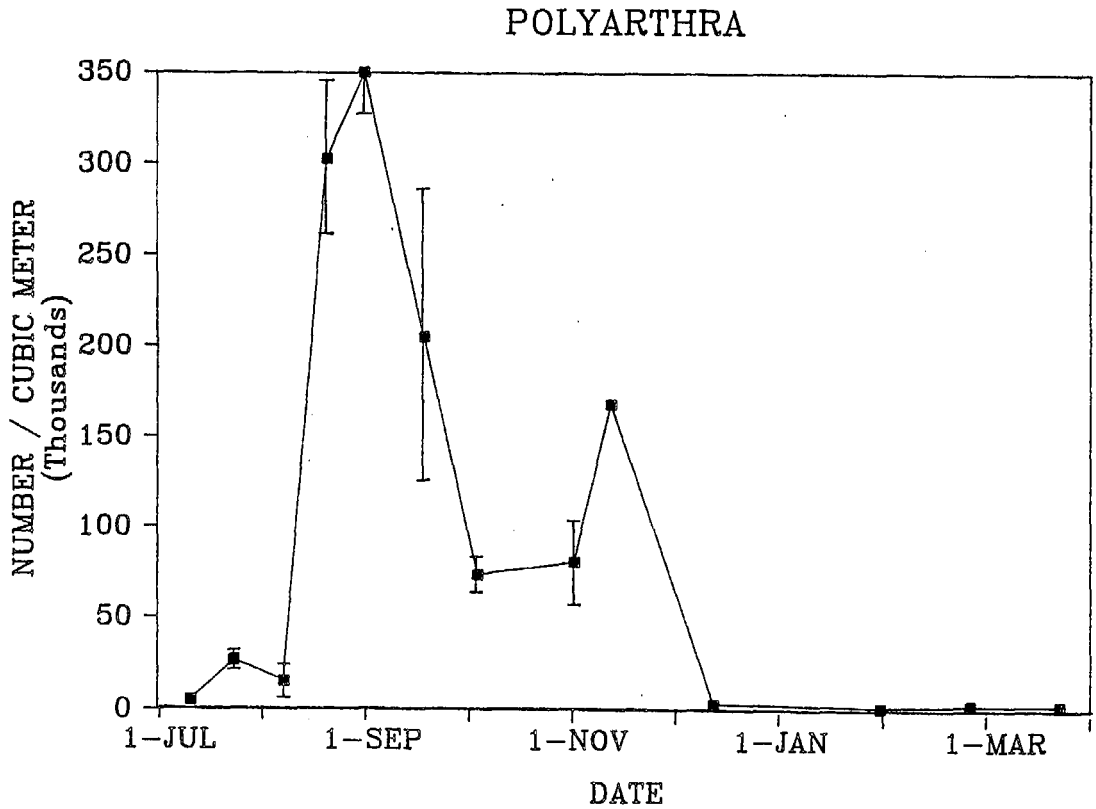

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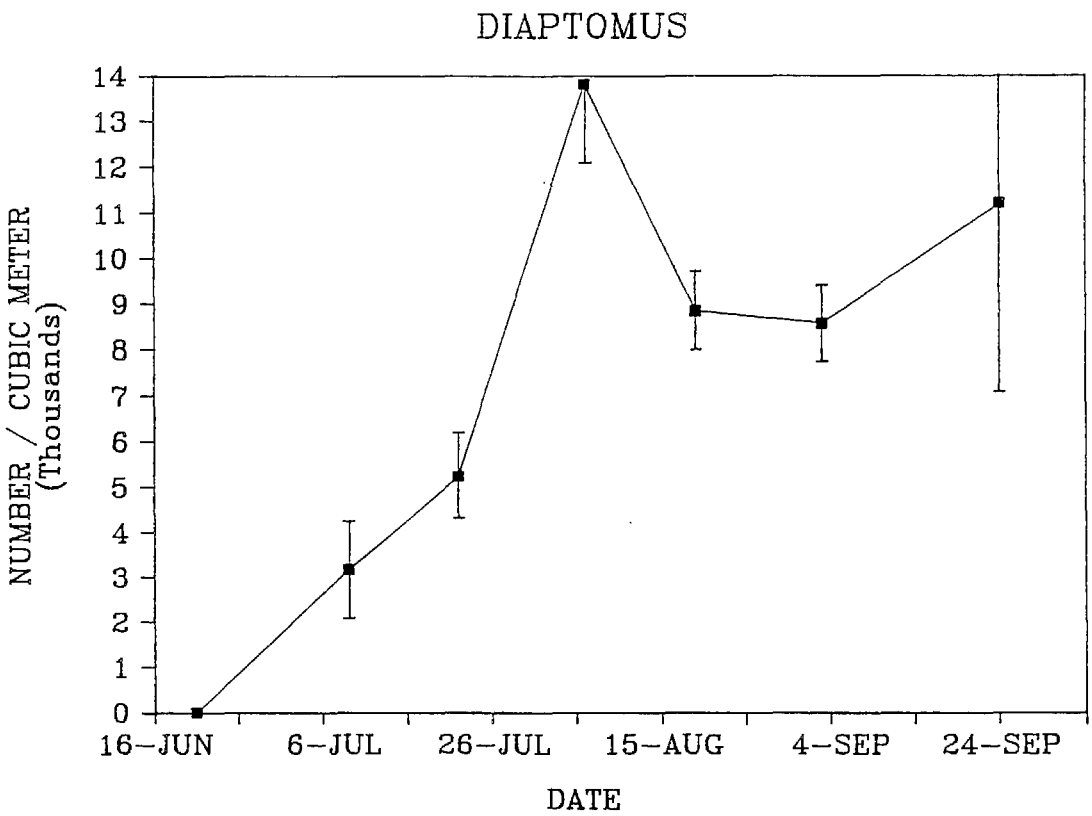


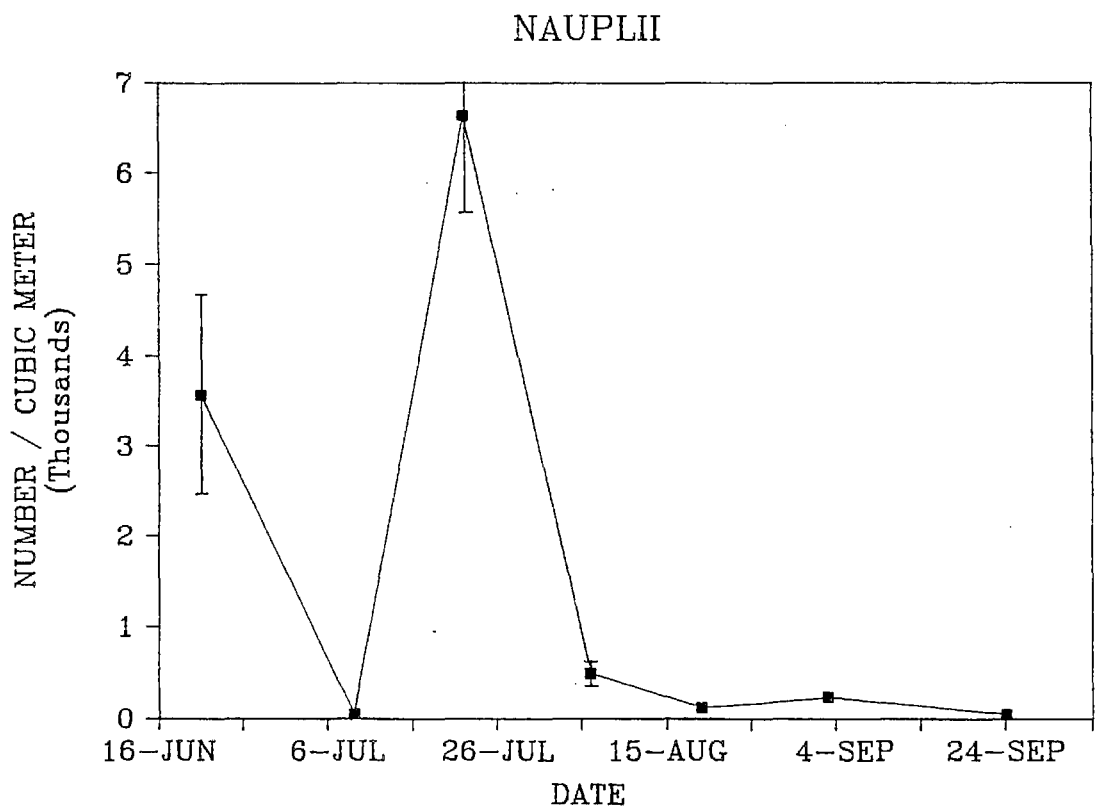
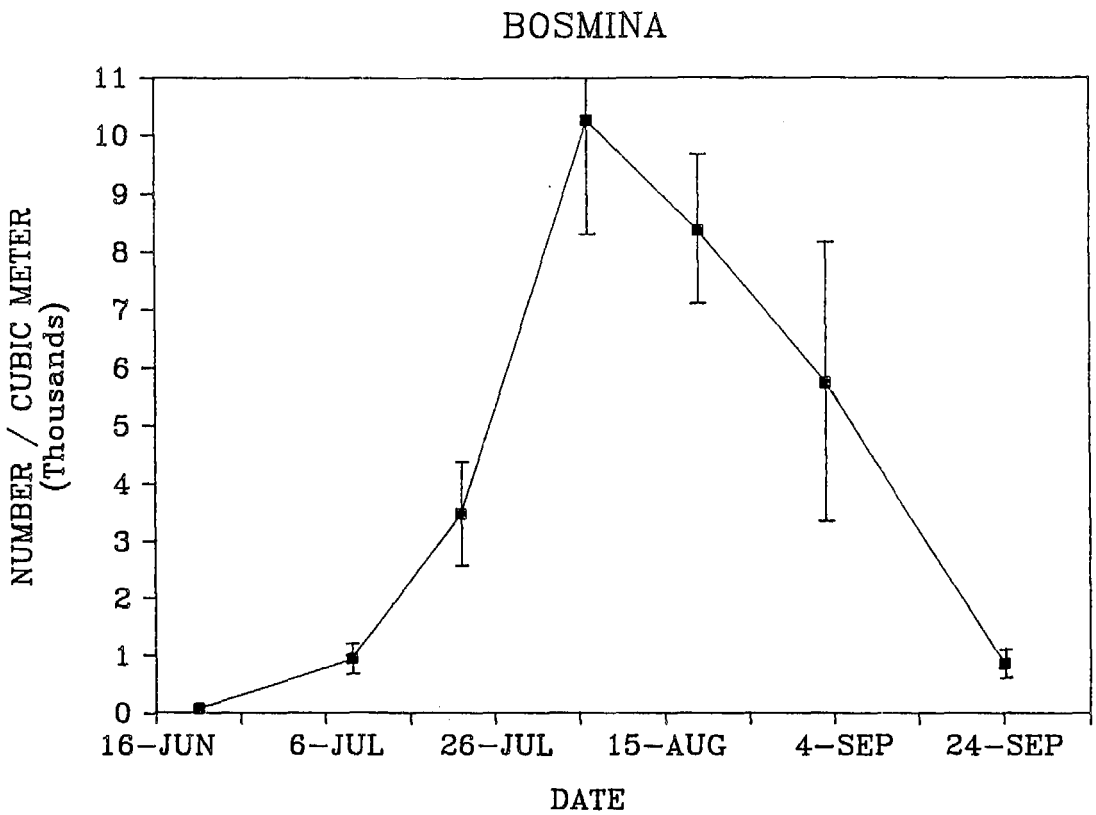
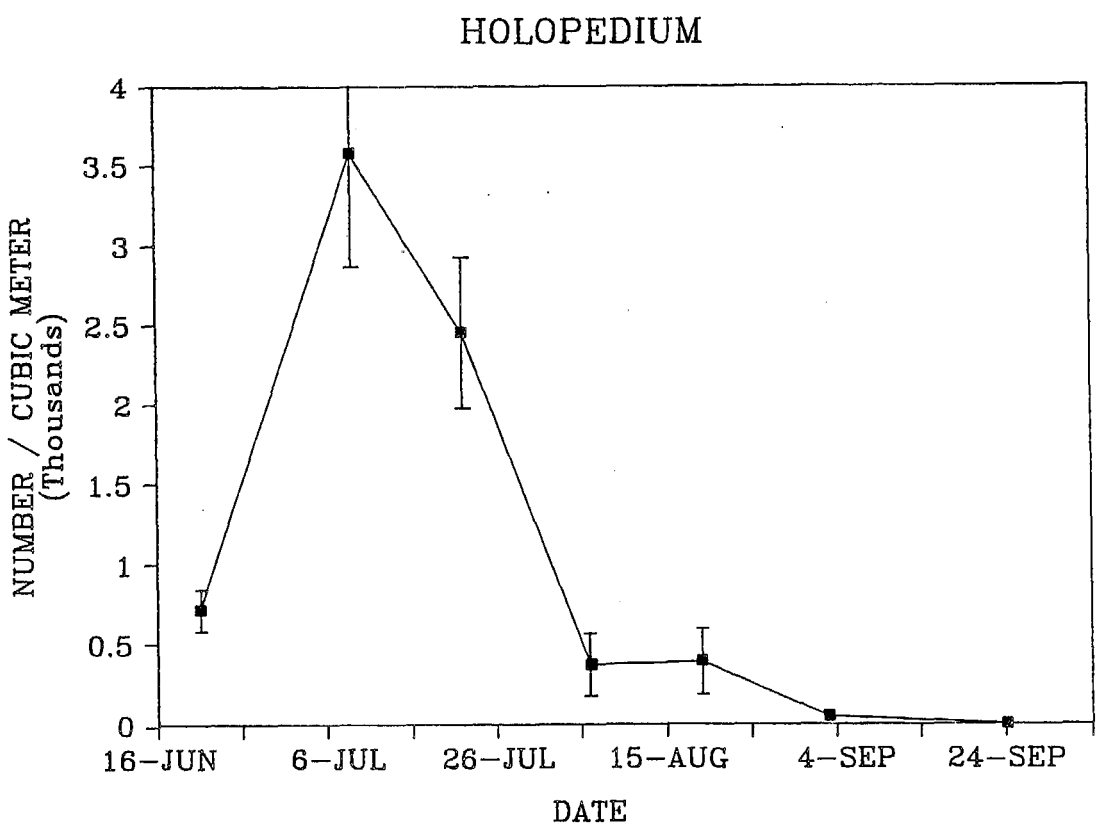


Figure V-2. Abundances of common zooplankton taxa (thousands/m^3) in Emerald Lake from June to September, 1985. Values are means $\pm$ 1 SE.





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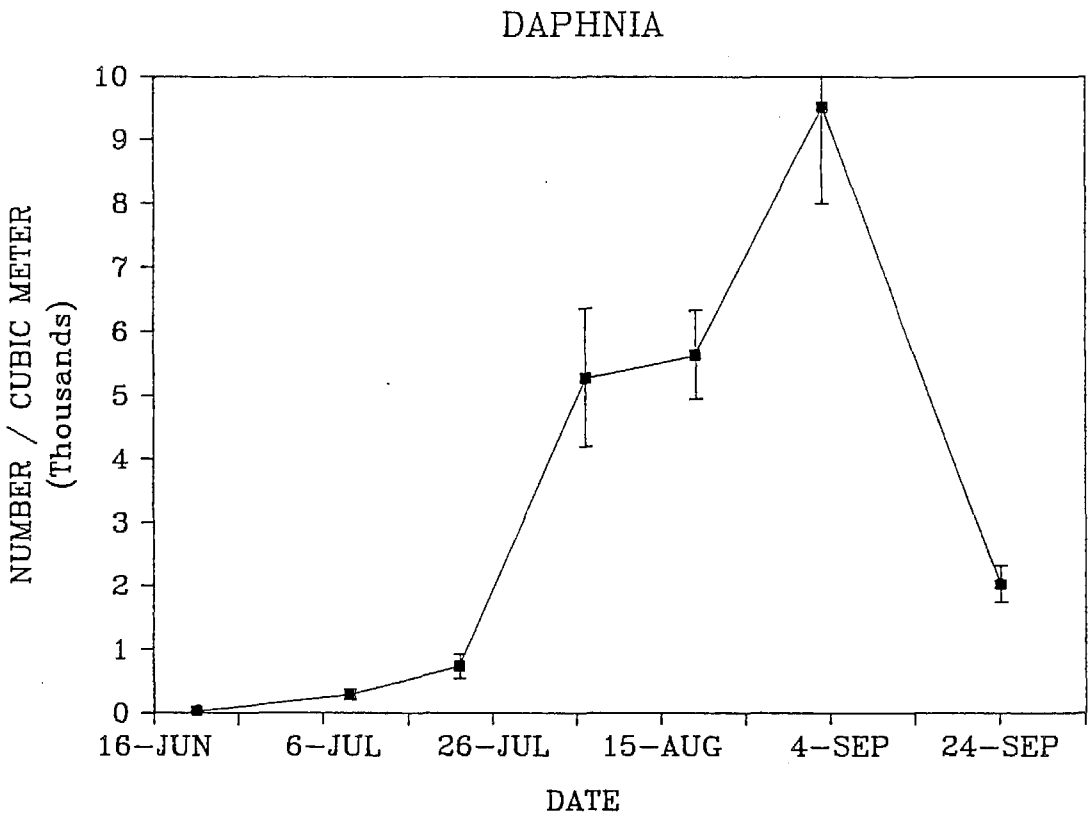

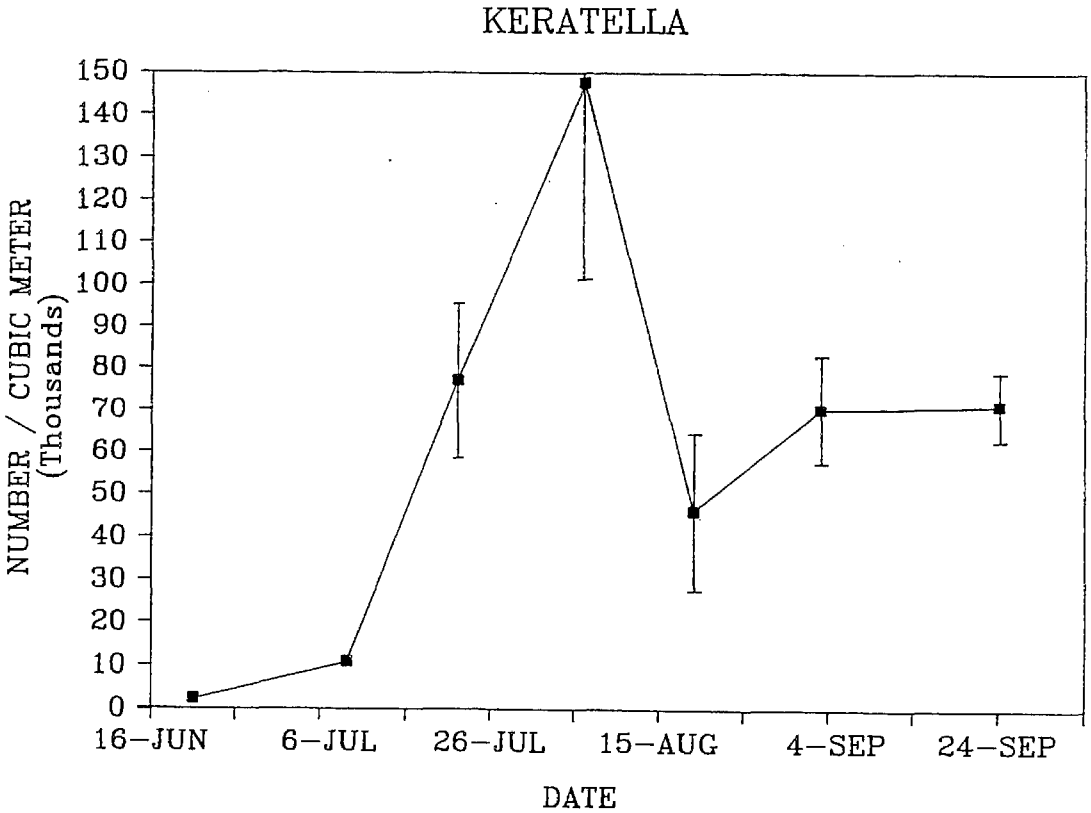

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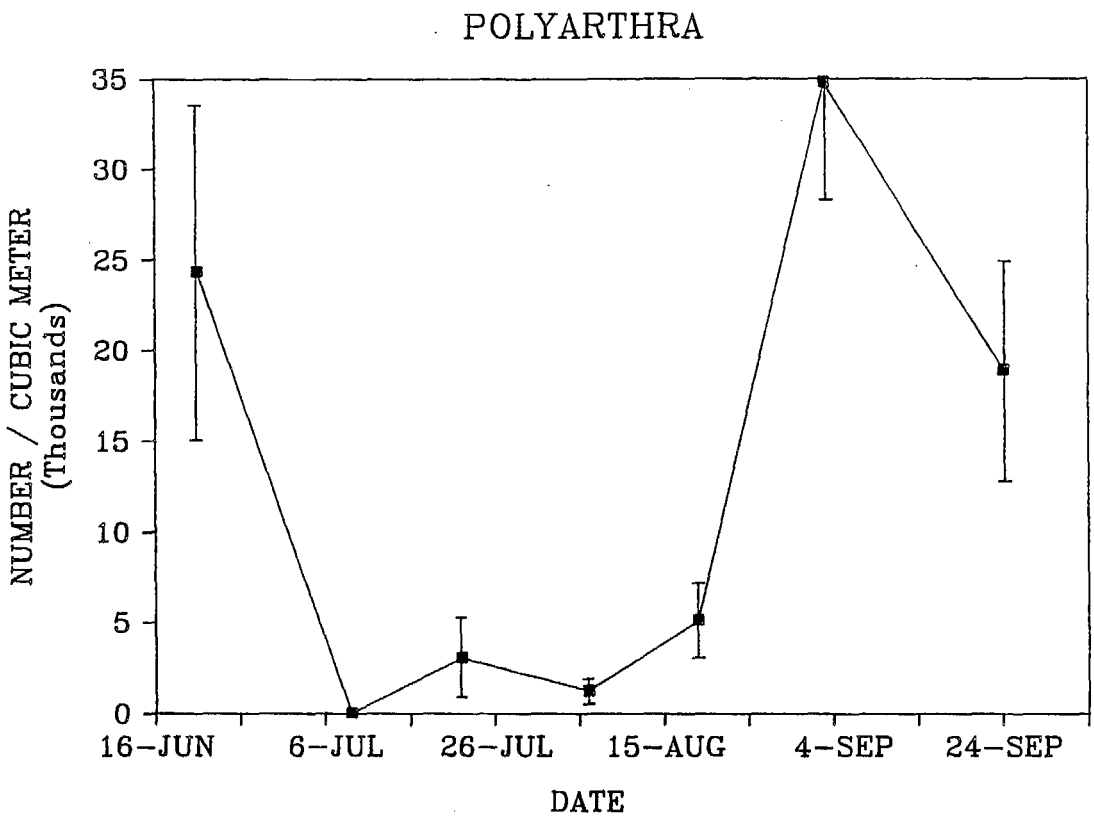

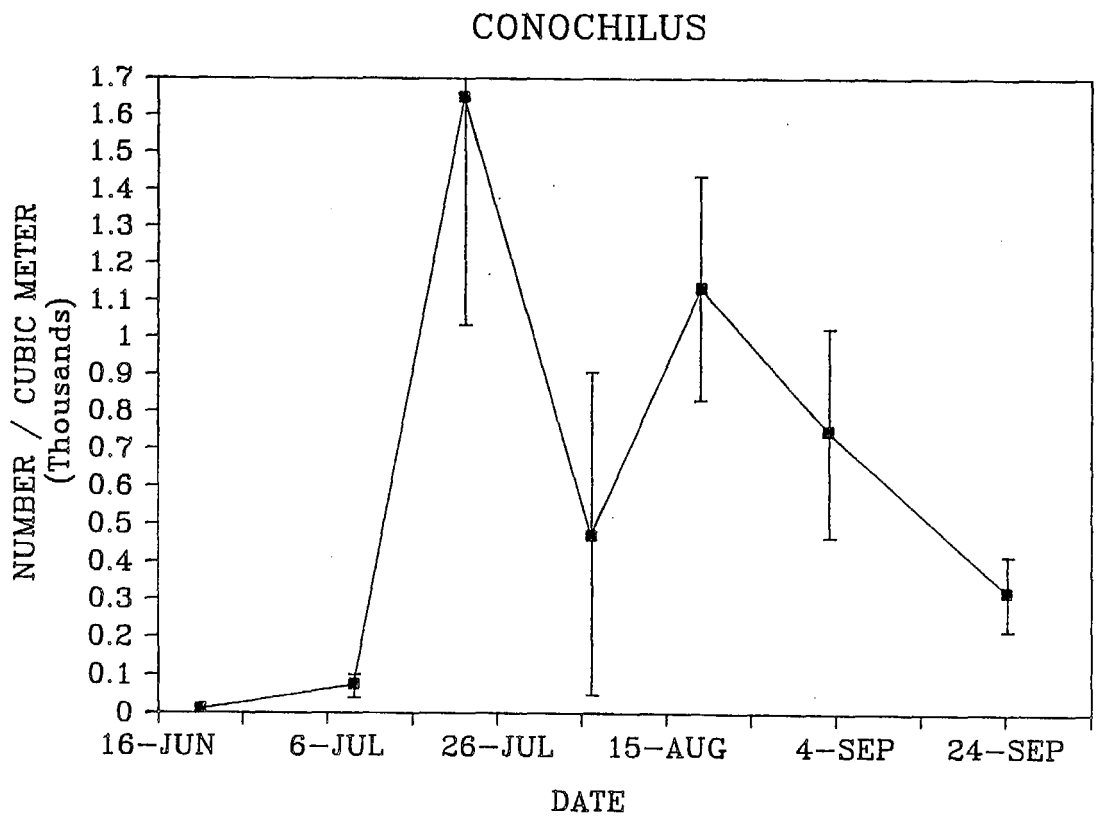

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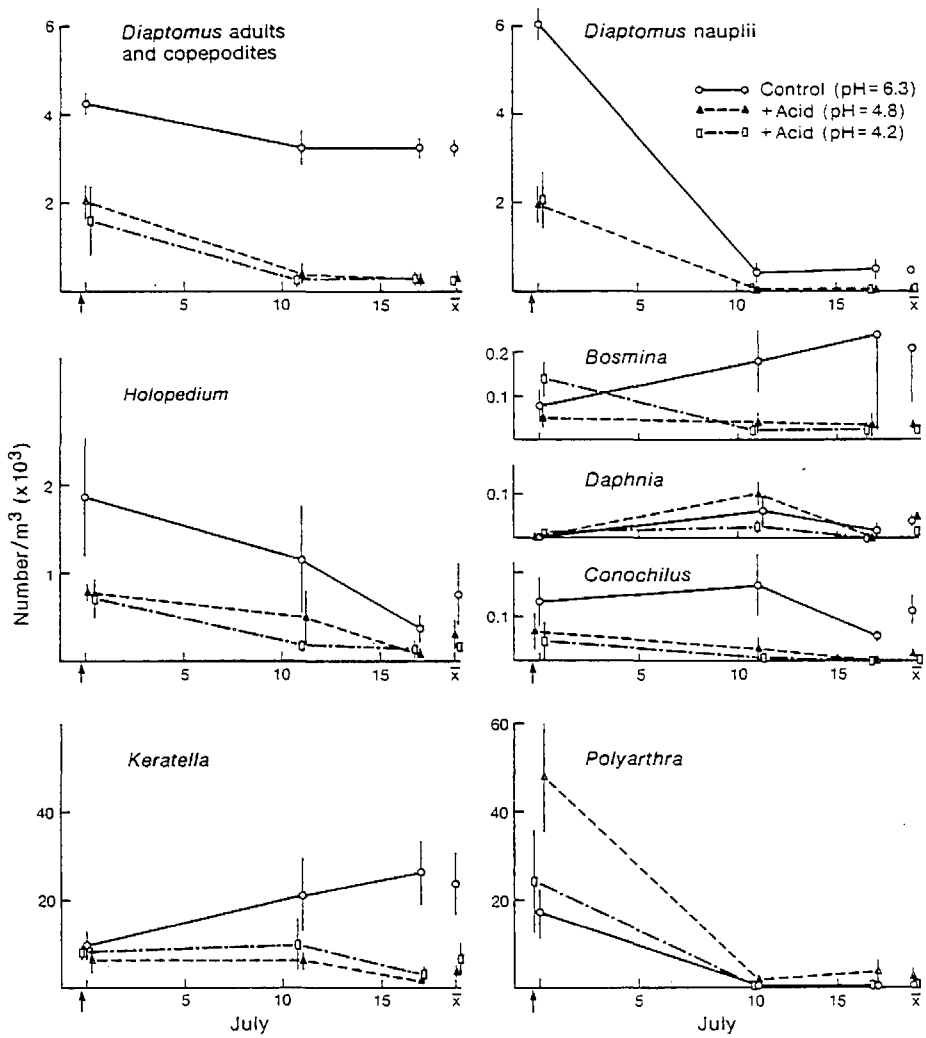


Figure V-3. Densities of common zooplankton taxa ($X \pm 1$ SE) in bags assigned to different treatments in Experiment 1. The arrow denotes the time the experiment began. X indicates the mean (± 1 SE) of the individual bag means for each treatment for the last two sample dates.

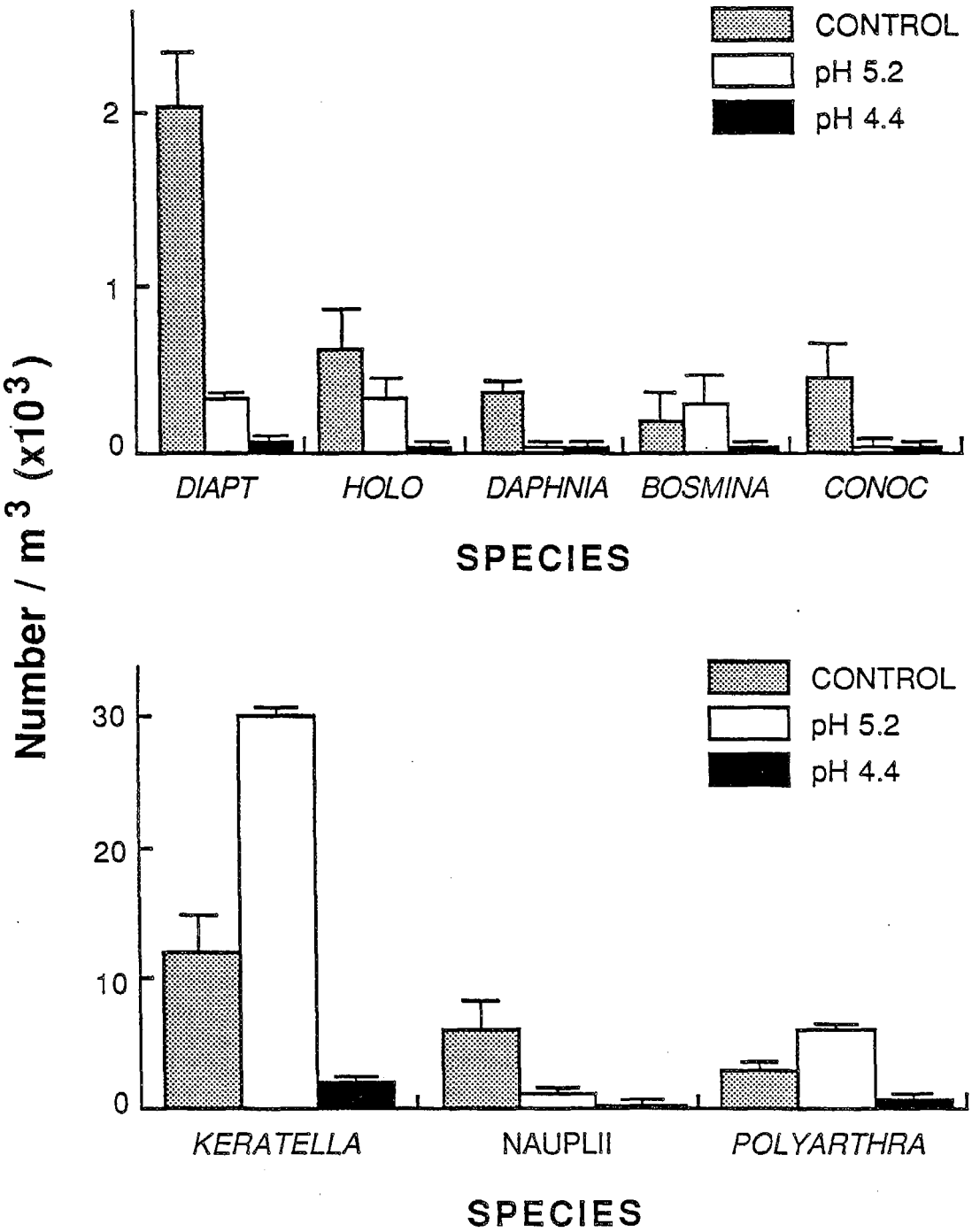


Figure V-4. Densities of common zooplankton taxa (X ± 1 SE) in bags assigned to different treatments at the end of Experiment 2.

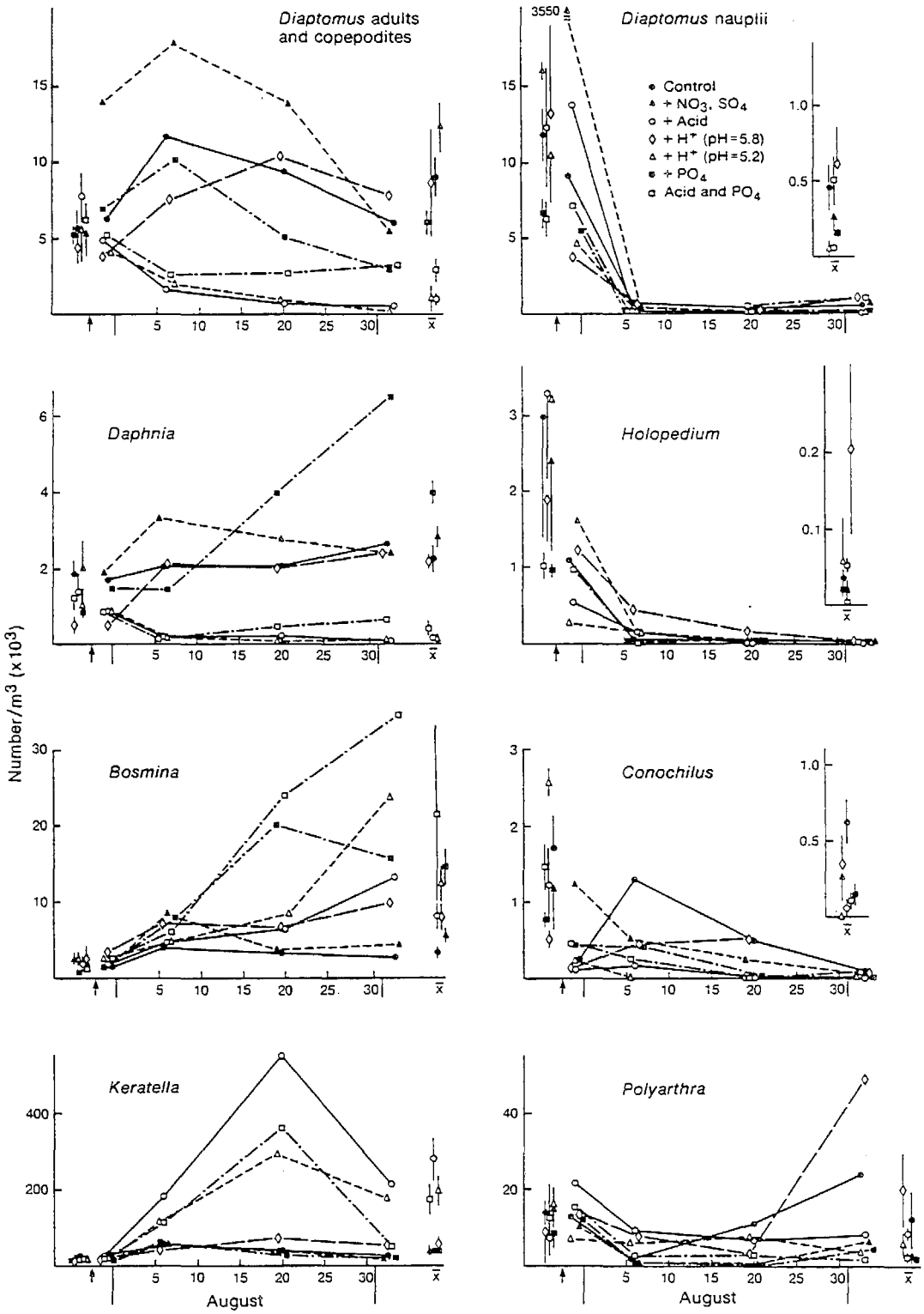


Figure V-5. Densities of common zooplankton taxa (X) in bags assigned to different treatments in Experiment 3. The arrow denotes the time the experiment began. X indicates the mean (± 1 SE) individual bag means for each treatment for the last three sample dates.

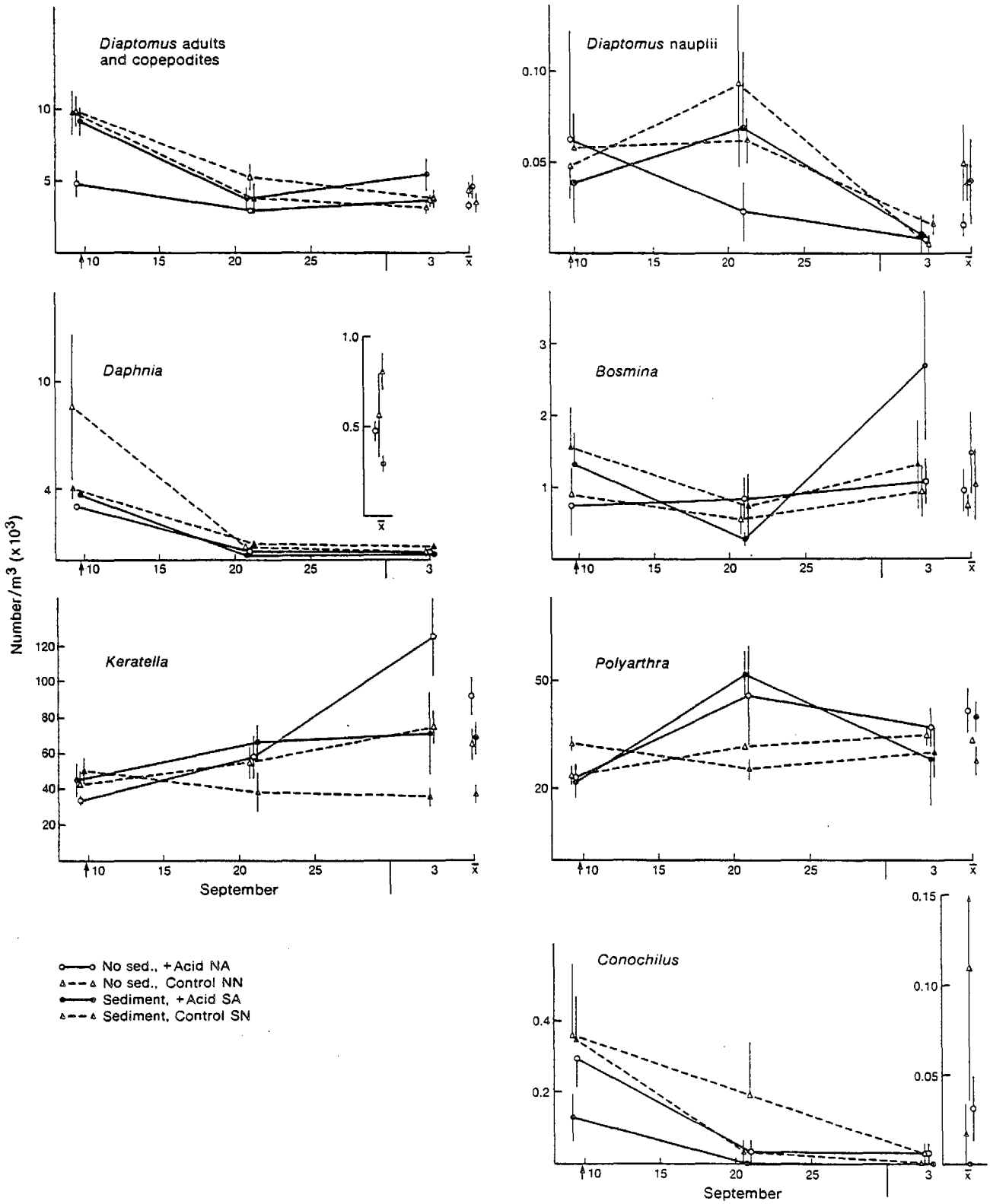


Figure V-6. Densities of common zooplankton taxa (X ± 1 SE) in bags assigned to different treatments in Experiment 4. The arrow denotes the time the experiment began. X indicates the mean (± 1 SE) individual bag means for each treatment for the last two sample dates.

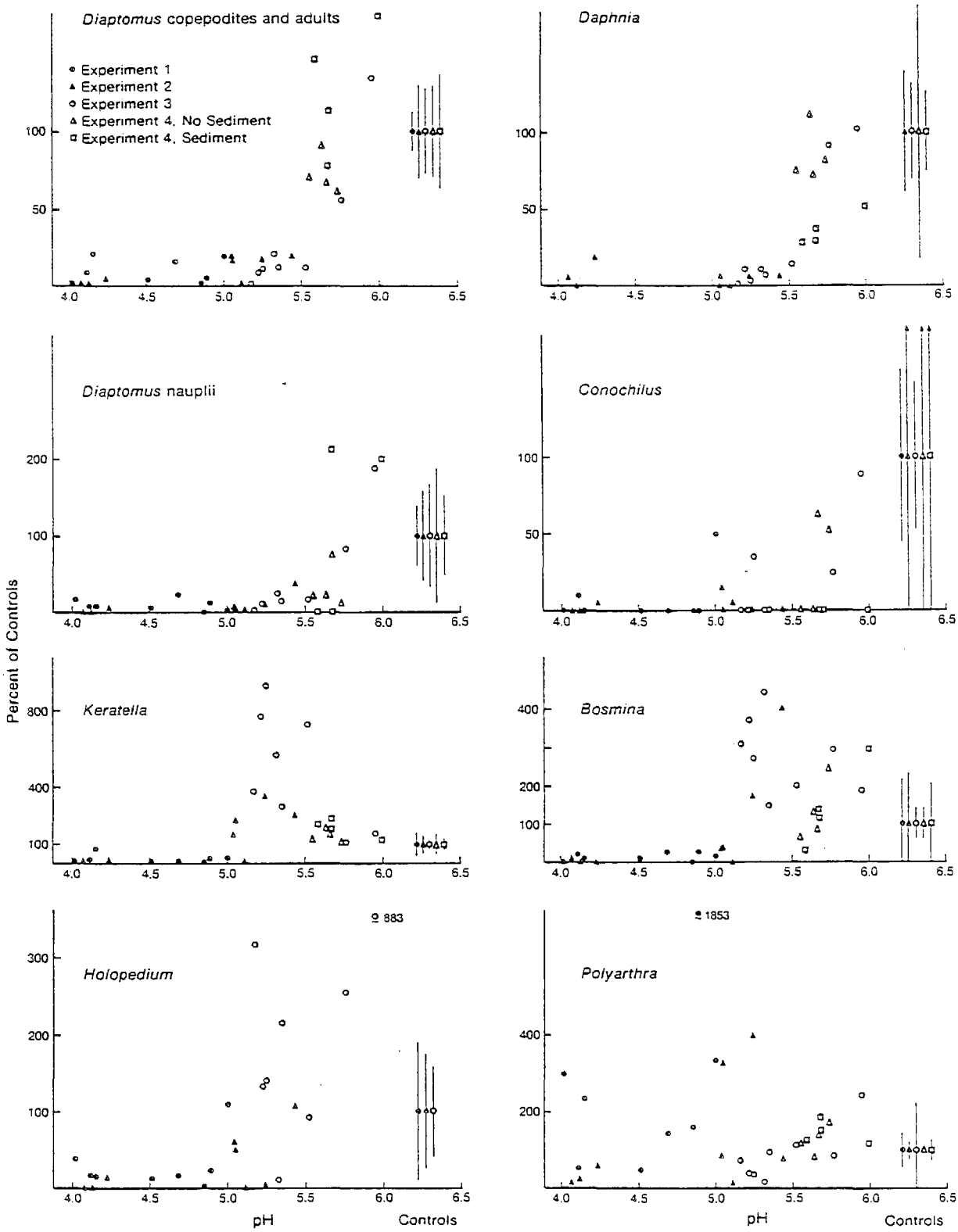


Figure V-7. Relationships between percentage response to acid addition and pH for common zooplankton taxa over all experiments. Mean densities and pHs were calculated for each bag over times > 1 week in the experimental period. Mean density in each acid addition bag was divided by mean density for all control bags and multipled by 100 to obtain a percentage response in each bag. Error bars around control means (100%) are ± 2 SEs.

Chapter V.2

ZOOBENTHOS

Introduction

Reduction of pH in stream waters, caused by acidic deposition, can have several adverse effects on benthic invertebrate communities (Hall et al. 1980, Raddum 1980, Burton et al. 1982, 1985, Hall and Ide in press). Increased acidity has been shown to decrease the diversity (Friberg et al. 1980, Roff and Kwiatkowski 1977, Almer et al. 1978, Okland and Okland 1980, Mackay and Kersey 1985, Simpson et al. 1985, NRC Canada 1981) and abundance (Fiance 1978, Hall and Likens 1979, Howells et al. 1983) of benthic invertebrate communities, and to alter invertebrate life histories (Bell 1971, Fiance 1978, Zischke et al. 1983, Burton et al. 1985, Lacroix 1985). Increased acidity can change community composition and predator-prey relationships, as sensitive organisms are replaced by more tolerant ones (Leivestad et al. 1976, Henrikson et al. 1980, Eriksson et al. 1980, Burton et al. 1982, Zischke et al. 1983, Hunter et al. 1985, and Hall and Ide in press). In addition, acidic inputs can affect organisms through their influence on other organisms in the trophic web. For example, fish can be eliminated by acid deposition with important repercussions for the invertebrates on which they prey (Henrikson and Oscarson 1978, Eriksson et al. 1980).

Acidic precipitation (pH ca. 4-5) sometimes falls on the Sierra Nevada of California during the summer and autumn (Melack et al. 1982). During periods of heavy rainfall, watersheds may not be able to assimilate acidic inputs and short-term pH depressions of lake and stream waters may occur (Dillon et al. 1984). These episodic depressions may have a substantial impact on the aquatic biota well before long-term declines in pH are detectable (Servos and Mackie 1986).

A variety of approaches have been used to assess the effects of increased acidity on invertebrate assemblages. Many studies on the effects of acidification on benthic invertebrates have been primarily surveys (Sutcliffe and Carrick 1973, Singer 1981, Raddum 1980, Okland 1980, Okland and Okland 1980, Roff and Kwiatkowski 1977) or laboratory bioassays (Bell 1970). The survey approach involves comparisons of the distribution and abundance of aquatic organisms in relation to the pH of the waters in which

they live. However, causation cannot be inferred from correlation, for relationships can be confounded or obscured by the effects of other, perhaps unmeasured, variables. In the same geographical area, streams and lakes not affected by acidification may be different in many ways from those experiencing decreases in pH, thus obviating the usefulness of comparisons.

Laboratory bioassays, in which pH tolerances of various organisms are determined (Bell 1971, Hollet et al. 1986) cannot adequately represent the complex biological and chemical interactions that occur in an organism's natural habitat. It is difficult to extrapolate the results obtained in the laboratory to organisms in their natural environments. Laboratory microcosms and mesocosms, which mimic natural assemblages, sediments, and water (Tonnessen 1983) have been used as compromises between bioassay-type and field experiments. Although certainly an improvement, in some cases microcosms quickly diverge from larger natural systems as some processes, such as mixing, are hindered or modified by the small size of the container. Also, other natural conditions, such as weather changes, are difficult to simulate.

Stream ecologists have increasingly used cages to analyze species interactions (Peckarsky and Dodson 1980). It is becoming increasingly apparent, however, that cages alter abiotic conditions, such as current and sediment conditions, and provide increased surfaces for insect and algae attachment, thereby confounding the interpretation of experimental results (Waide and Davies 1984). Furthermore, chemicals added to _in situ_ cages are quickly washed to other parts of the stream, making cages useless for examining the effects of chemical stresses on stream organisms. Although minimizing variability among samples (Rosenberg and Resh 1982), results from studies using artificial substrates, cannot always be extrapolated to natural substrate conditions.

As alternatives, whole system acidification experiments have been performed (Hall and Likens 1979, Hall et al. 1980, Schindler 1980a, b, Schindler et al. 1985) but it is difficult to find replicate systems both for examining inter-system variability and for concurrent controls. Using separate streams or lakes as controls does not provide good replication because of stream to stream or lake to lake variability. It is often difficult to determine densities of the biota of whole lakes and streams because the organisms in these systems are highly aggregated (Allan 1984,

Hurlbert 1984, Morin 1985). A number of studies have indicated that large numbers of samples are needed to calculate density estimates for many freshwater, particularly benthic, organisms (Resh 1979, Allan 1984). Whole stream experiments often utilize a down-stream manipulative versus upstream control experimental design. The problem with this design is that it does not allow for the replication of treatments (Allan 1984, Hurlbert 1984). Furthermore, upstream and downstream areas are not independent, as upstream processes affect downstream results. Finally, whole system manipulations are logistically difficult, requiring large amounts of manpower, money and time. They can also have effects that are biologically and socially unacceptable, potentially altering whole system irreversibly.

Experimental stream channels and large lake enclosures, then, seem to constitute good compromises between the naturalness of whole system manipulations and the control and replication of laboratory experiments; they approximate natural conditions while providing the replication needed for statistical analyses. Artificial stream channels have been successfully used in past studies to examine the effects of increased acidity on stream systems (Zischke et al. 1983, Burton et al. 1985, Servos and Mackie 1986). Large bags in lakes have been used to examine the effects of acidic inputs on plankton (Marmorek 1983, 1984, Yan and Stokes 1978, see Zooplankton chapter), but have not been used to examine effects on zoobenthos. Based on our analysis of the literature and our experience with stream and lake experiments we felt that the stream channels or lake bags used in these studies provided the best compromise in terms of replicability, ease of manipulation and size, and duplication of nearly natural conditions.

Simulations of acidic rain events (containing sulfuric and nitric acids), of similar acidity to those known to occur during convective storms occurring in the Sierran dry season (Melack et al. 1982), were performed in stream channels operated near Emerald Lake. These acidic rains, characteristic of early phases of acid deposition, comprise the primary acidic inputs into Sierra Nevada aquatic systems. Except during these events, the pH of freshwater habitats in the western Sierra Nevada is near a pH of 6.2-6.5. Most previous stream or stream channel experiments have added acid continuously to stream sections or channels for long periods of time (Hall et al. 1980, Burton et al. 1985). Although these experiments may indicate biotic responses to severe, continuous acid exposure, they provide

us with little information regarding the effects of early phases of acid deposition on streams.

We measured invertebrate benthic densities and drift rates in response to decreased pH, because benthic densities and drift are sensitive indicators of acid stress (Fiance 1978, Hall and Likens 1980, Hall et al. 1980, Howells et al. 1983, Hall et al. in press). The replicated stream channels used in this study allowed more precise evaluation of the effects of acid deposition on the stream biota and allowed us to predict the effects of increased acidic input on this system.

We also acidified a series of large bags in Emerald Lake which enclosed the water column including sediments. At experiment termination we sampled the benthos inside acidified and non-acidified bags to examine the responses of the lake zoobenthos to acidification. A variety of survey data indicate that the species composition, abundance, and distribution of lake benthic macroinvertebrates are affected by pH levels (Raddum 1980, Okland 1980, Okland and Okland 1980, Roff and Kwiatkowski 1977).

Information from these stream channel and lake bag experiments revealed which invertebrates in Sierra Nevada aquatic habitats were particularly sensitive to acid stress. These indicator organisms are being closely observed, together with changes in stream chemistry, in order to monitor the effects of acidic inputs on this system. In this section we describe the results of our monitoring program characterizing the zoobenthos of the Emerald Lake system, and the results of lake bag and stream channel experiments examining the affects of acidification on stream and lake benthos and stream drift.

Methods

Stream Benthos

Benthic samples were taken from inlet and outlet streams at monthly intervals from early July to late October in 1984, from early July to early October in 1985, and, in the outlet only, in mid-December, 1984, and late March and late November, 1985. In 1984 each inlet sample consisted of a composite of four (July 8) or five (other dates) quadrat subsamples (8 X 10 cm in July, 6 X 5 cm on other dates) of hard substrates. In 1985 each inlet sample consisted of a composite of five 10 X 10 cm quadrat subsamples of hard substrates. Samples were taken by clearing quadrat areas into 500 μm

mesh hand nets placed immediately downstream. In July 1984 and 1985, August 5, 1984, and October 1985 a composite sample was taken from each of the four inlet streams (Fig. V-8). Because one or two of the inlet streams were dry on other dates, two samples were taken from one inlet stream and one sample from each of the two others in late August, September, and October, 1984. One sample was taken from each of the three flowing streams in August, and from each of the two flowing streams in September, in 1985.

In the outlet, five benthic samples were taken from soft (gravel, organic debris or sand) substrates, three to five were taken from hard (bedrock or boulder) substrates, and one sample was taken from cobble with a Hess sampler (mesh, 390 µm; area, 0.10 m^2) on each sample date in the summer and fall of 1984. In addition, four supplementary 10 X 10 cm quadrat samples were taken, as in the inlet, from hard substrates largely covered with moss or macroalgae in September and October 1984. Three hard and three soft substrate samples were taken in December, 1984, and one hard substrate sample was taken in March, 1985, all with a Hess sampler. In 1985 fourteen samples were taken on each date including five Hess samples on soft substrates, one Hess sample on cobble, five mini-Hess samples (mesh, 250 µm; area, 81 cm^2) from hard substrates, and three mini-Hess samples from hard substrates covered with moss or macroalgae. Owing to low flows, three hard substrate samples taken in late November, 1985, were taken with a 10 X 10 cm quadrat. All benthic samples were preserved in 70% ethanol.

Stream drift

Drift samples were taken by drift net from the outflow stream of Emerald Lake on July 7-8, August 3-4, August 28-29, September 29-30, and October 29-30, 1984, and from the two main inflows and outflow stream on August 4-5 and September 2-3, 1985. Drift samples were taken over a twenty-four hour period on each of the collection dates. The four to five drift sets taken on each date in 1984 bracketed dusk and dawn and periods during day and night. The six sampling periods for each date in 1985 bracketed dusk and dawn and two periods each during the day and night. Drift sets lasted between ca. 2 and 4 hours each in 1984, and were ca. two hours each in 1985.

Collection days were always bright and clear. Dawn and dusk would normally occur earlier and later, respectively, than the rising and setting of the sun. However, due to shading by the steep mountains forming the basin

around the lake, dawn and dusk occurred at approximately the same times as the rising and setting of the sun. Moons were in the new to quarter phases during the dark periods of 1984 sampling, but in 1985 night sampling coincided with periods of bright moonlight (3/4 to nearly full moon).

Organisms were collected in fine (250 µm) nets with mouth areas of 1350 cm^2 (30 x 45 cm) in 1984, and 400 cm^2 (20 x 20 cm) in 1985, set in the thalweg (principal current pathway), on the bottom of each stream. Drift nets extended above the air-water interface on all dates in 1984 and inflow collections in 1985, but were entirely submerged in outflow collections in 1985. Two drift collection sites were located in the outflow stream; the upper site approximately 58 meters below the lake and the lower site approximately 27 meters further downstream. Because the drift sites were separated by this distance, it is unlikely that the abundance of drift in the downstream site was impoverished by the upstream drift net (Wilzbach et al. 1986). Current speeds, measured with Bentzel tubes (Everest 1967), and depth were measured in three positions across the front of each drift net before and after each sampling period. These measurements were used to calculate discharge through the drift nets for each time period. Water temperature was also measured at each sampling period in 1985.

Drift samples were preserved in 70% ethanol and were later counted and identified (Merrit and Cummins 1984) to family or genus under a dissecting microscope at 12 X. Samples containing high numbers of invertebrates (greater than 500) were subsampled (50 or 25%) using a wheel plankton splitter (Allan and Russek 1985) after separation (by 2 mm sieve) from coarse materials such as leaves and twigs. Inspection of replicate subsamples indicated close correspondence between counts. Drift rates were calculated in two forms: (1) number of organisms per hour passing into drift nets and (2) number of organisms per unit volume (corrected for flow) passing into the drift net (Wilzbach et al. 1986). As diel discharge was relatively constant on most drift collection dates, data are presented in numbers per hour.

Lake benthos

Benthic samples were taken from Emerald Lake in July 1984 and 1985, August 1984, and September 1985. In early July 1984 one soft substrate (silt, mud, sand) and four hard substrate (bedrock, boulder) samples were taken with a suction sampler (mesh, 250 µm; area, 0.18 m^2) operated by SCUBA

divers (Gale and Thompson 1975). In late August two soft substrate and four hard substrate samples were taken with the suction sampler, and two soft substrate samples were taken with an Ekman dredge (area, 0.023 m^2). In conjunction with the suction sampling, SCUBA divers made qualitative observations of substrate and macrophyte distributions and took samples of aquatic macrophytes.

In 1985 sixteen benthic samples were taken from Emerald Lake. Four samples were taken from hard substrates with the suction sampler and four samples were taken from soft substrates with an Ekman dredge at each of two times (July 11 and September 6-8). All lake benthic samples were preserved in 70% ethanol.

In the laboratory preserved benthic samples were generally scanned under a dissecting microscope at 12 X and any invertebrates were removed from leaf litter, twigs, moss, macroalgae, and sediment. In some cases, where numbers of invertebrates in samples exceeded 500, samples were subsampled with a plankton splitter as outlined above. In these cases 25% of each sample was processed. Aquatic insects were identified under a dissecting microscope at 25 to 50 X using Merritt and Cummins (1984) and counted at 12 to 25 X.

Stream channel experiment

Twelve experimental stream channels were set up next to the Marble Fork of the Kaweah River, in Sequoia National Park on the western side of the Sierra Nevada, California, U.S.A. (elevation 2780m, latitude 36°35'N, longitude 118°40'W), in early July, 1985. Each channel was 2 m long, 20 cm wide and had 20 cm high side walls, with six channels in each of two sets. The base was a 2.5 cm thick plywood sheet, treated with three coats of Varathane® (non-toxic), with Plexiglas partitions between channels (Fig. V-9). A 6 cm high Plexiglas plate was affixed to the down-stream end of each channel to insure adequate water depth throughout the channel. Immediately in front of each downstream plate were small retainers on the sides of the Plexiglas walls to hold drift nets (mesh, 250 µm). The gradient in each set of stream channels was adjusted by placing lumber under the channels to provide a drop of 5 cm from the upstream to the downstream end of each channel (2-1/2% drop).

Water was supplied to these channels by diverting water from a pool in the Marble Fork approximately 40 m upstream and elevated ca. 2 m above the

channels. Two flexible plastic pipes (20 cm internal diameter) transported the unfiltered water 40 m to a one cubic meter reservoir constructed of 1.25 cm Varathane-treated plywood. Three PVC pipes (ca. 13 cm internal diameter, each 5 m long) carried water from the bottom of the front panel of the reservoir to the stream channels. Water flow to these pipes was regulated by gate valves inside the reservoir. A 30 liter plastic vessel supplied acid to the appropriate delivery pipes via Tygon tubing regulated by stopcocks. Four PVC T's were attached at intervals of approximately 0.6 m along each delivery pipe, and flexible plastic pipes (internal diameter 12 cm) carried water from each T to the stream channels. Flow into each channel was regulated by the valves inside the reservoir and by plastic collars placed over the ends of each of the pipes delivering water from the T's to the channels. Tying off these collars allowed the regulation of flow into each stream channel.

Water leaving the channels was carried in a trough back to the stream except during acid addition when water leaving the channels was allowed to return to the Marble Fork via natural channels in order to buffer the low pH water. There was negligible effect of our acid additions on the pH of the Marble Fork below the outfall of the stream channels.

The stream channels were stocked with natural substrates and associated flora and fauna from the Marble Fork. Care was taken to insure that each channel received similar substrates and invertebrates. Six large rocks (ca. 9 cm diam.) and ca. 2 cm of gravel (0.5-2.0 cm) and sand were placed in each channel. Insects, after collection by kick sampling into drift nets (mesh, 250 μm), were gently suspended in buckets of water and equally divided among the stream channels. Invertebrates were stocked twice (approximately once a week) into stream channels during the ensuing 2 weeks, but were not stocked for one week prior to experimental acidification. Periphyton became dense after ca. 1 week of acclimation.

A drought during the acclimation period resulted in low flows, sufficient to feed only four of the twelve channels. On August 7, acid was added to two of the stream channels for approximately 6 hours in order to simulate an acid rain event. Experiments were conducted in late morning and afternoon (1123 hours to 1728 hours) because movements (Waters 1962) and drift (Muller 1974) of aquatic invertebrates are at a minimum during this time and thus most increased macroinvertebrate drift could be interpreted as

a stress response induced by acid addition. Most acid precipitation events occur in the afternoon in the summer months, so the timing of the acidification is representative of a natural rain event. Sufficient quantities of acid (sulfuric and nitric in equivalent volumetric proportions) were added to two experimental channels to reduce the pH to ca. 5.0 for the six hour experimental period. Acid was added to two of the delivery pipes, where mixing occurred, each delivering water to a single channel. Acid was not added to the third delivery pipe which supplied water to two channels which acted as undisturbed controls (pH 6.4).

The pH of each of the four channels was measured shortly before, during (1/2 and 3 hours after the start of acid addition), and after acid additions (immediately after and ca. 18 hours after additions stopped). Water samples were periodically taken for major anion (Cl^-, NO_3^-, SO_4^{2-}, and PO_4^{3-}) and alkalinity analyses before, during, and after acidification (same times as for pH). Trace metal (aluminum, iron, and manganese) samples were taken once before acidification started and once just before the end of acid addition. Methods of analysis are described in section II-1.

The stream benthos was sampled one day before and two days after acid additions. Stream benthos was sampled by cleaning all substrates in a 10 x 20 cm area on the bottom of each channel into a drift net (250 µm) placed just downstream. Two such samples were collected from each channel at each sampling time and combined for analyses. Invertebrate drift was monitored for 24 hours before acid additions (four sets of ca. 4 hours each), six hours during acid additions (two sets of ca. 3 hours each), and for 36 hours after acid addition (six sets of 4-8 hours each). Invertebrate drift was sampled by placing drift nets (mesh, 250 µm) at the downstream end of each channel. Discharge was measured in each channel before and after each drift sample was taken, by collecting the discharge in a calibrated bucket set at the end of each channel. Drift rates were calculated as numbers per unit volume (m^3) to correct for flow difference among channels (Wilzbach et al. 1986).

Live vs. dead counts were recorded for the drift of the most abundant ephemeropteran and plecopteran taxa, i.e., Baetis spp. and Isoperla sp., respectively, immediately upon pulling the drift nets at the end of each sampling period. This was done by gently washing drift organisms from the drift net into a white bucket where the number (number of first 100 or total number counted) of alive (showed some movement or response when nudged) and

dead insects was recorded. Invertebrate samples were preserved in 70% ethanol and were later counted and identified (Merrit and Cummins 1984) to family or genus under a dissecting microscope at 12 X. Analyses of variance and t-tests were performed with appropriately transformed data (Allan 1984, Allan and Russek 1985) to determine if significant differences in drift rates, benthic densities, and percentage dead in drift, existed between control and experimental channels. Surface flows were almost absent in the Marble Fork two days after acid additions, so the experiment was discontinued 36 hours after acid addition.

Lake benthos experiment

In conjunction with Experiment 4 described in section II.4 of this report, we also examined the effects of acidic inputs on the benthos of Emerald Lake. At experiment termination SCUBA divers cut bags approximately 1 m from the bottom, then reached inside bags and sampled the benthos with hand corers. Hand corers, which were 10.3 cm in diameter, were pushed into the bottom sediments to a depth of 10 cm then capped for removal of sediments. Sediment samples were then strained through 250 µm mesh to remove macroinvertebrates from sediments. Two cores were taken from each bag and pooled.

Results

Stream benthos

The dominant macroinvertebrates in the inlet and outlet streams were chironomid larvae. Simuliid larvae (*Simulium* sp., *Prosimulium* sp., *Twinnia* sp.), *Baetis* nymphs, and *Rhyacophila* larvae were commonly collected in both the inlet and the outlet streams. In addition, larvae of ephemerellid and leptophlebiid mayflies (*Drunsella spinifera*, *Serratella* sp., *Paraleptophlebia* sp.), nemourid stonefly nymphs (*Malenka* sp., *Amphinemoura* sp., *Zapada* sp.), tipulid larvae (*Dicranota* sp., *Hexatoma* sp.), water mites (Acaridae), oligochaetes, and sphaeriid clams (*Pisidium* sp.) were often collected in the outflow stream. In general, the outflow stream had a much higher diversity of invertebrates than the inflow streams, perhaps because only hard substrates were sampled in the inflow streams and both hard and soft substrates were sampled in the outflow stream. A variety of other taxa were occasionally collected (Table V-3).

There was a large amount of variability in the densities of common macroinvertebrates collected from the inflow streams. Chironomid densities tended to increase through July or August, depending on the stream, in 1984 then declined to low levels by mid-September (Fig. V-10). Channel A (Fig. V-8) was an exception, as chironomid abundance increased through August then remained steady at ca. 9000/m^2 through September and October. In 1985 chironomid densities in Channels B and D (Fig. V-B) tended to decline from July through August (Channel B) or September (Channel D) (Fig. V-11). Chironomid abundance in Channel A in 1985 remained low through July and early August, increased to a peak in early September, then declined somewhat by the first of October (Fig. V-11). Simuliid larvae were present in all channels in early July of 1984 and 1985, but were generally absent at other times of the summer and early fall. Particularly in 1984, however, simuliid densities in Channel A did not peak until later in the year (early August in 1984). Baetis was rare in Channels C and D, but reached high abundances in Channels A and B. Baetis densities increased through August and September in Channel A in both years and Channel B in 1984, peaking in early to late September (Figs. V-10 and V-11). Densities of the free-living caddis larvae Rhyacophila were higher in Channel A in both years, and Channel B in 1984, than in other channels at other times. Rhyacophila abundance peaked in late August - early September in Channel A in both years and Channel B in 1984. Densities of all common taxa in Channel B, and of simuliids and chironomids in Channels C and D, were higher in 1984 than in 1985. This was probably owing to the lower discharges in 1985 as opposed to 1984. Channel B flowed throughout the 1984 field season but dried in August of 1985, and Channel C dried earlier in 1985 than in 1984.

There were consistent differences in the abundances of some taxa collected from hard vs. soft substrates in the outlet stream. For example, sphaeriid clams and tipulid larvae were much more common in soft than on hard substrates, whereas simuliid larvae and baetid nymphs, particularly early in the summer, showed the opposite pattern. In addition, almost all taxa were much more abundant on hard substrates with moss or macroalgal covering than on hard substrates without mass or macroalgae (Figs. V-17 and V-13). The high variability in the hard substrate data from 1984 probably reflects our random sampling of all hard substrate habitats (Fig. V-14). Although the preponderance of hard substrate Hess samples taken in 1984 came from

relatively clean substrates, some were covered by substantial amounts of moss or macroalgae. Our preliminary examination of differences in invertebrate abundance on hard substrates with and without moss (Fig. V-12), indicated much higher abundances on moss. As a consequence, our 1985 sampling regime was stratified so that moss or macroalgal habitats were treated separately from hard substrates that lacked these plants.

It was often difficult to discern the population dynamics of many taxa in the outlet stream, because of high sampling variability. Chironomid larvae and mites were generally more abundant in early summer than in autumn on hard substrates, but showed the opposite pattern on soft substrates (Figs. V-14 - V-17). In both years simuliid and Rhyacophila larvae were most abundant in early summer on clean hard substrates, but were largely absent in the autumn (Figs. V-15 and V-18). On clean hard substrates Baetis declined from July through August in 1984 then remained at low densities through the autumn, whereas Baetis was commonly collected from July through September in 1985, but was absent in October. On hard substrates oligochaete dynamics were similar to those of Baetis in 1984, and ephemerellid nymphs were common through the summer but rare or absent in autumn. In 1984 Baetis, chironomid, mite, and oligochaete densities remained high in moss habitats through September and October, and simuliid densities increased and Rhyacophila and ephemerellid densities decreased from September to October (Fig. V-12). In 1985 most common taxa peaked in moss habitats in August; however, oligochaete densities generally declined in moss habitats from July through September (Fig. V-12). Baetis was usually rare on soft substrates, but tended to increase to a peak in late August then declined to December in 1984 (Fig. V-16). On soft substrates oligochaetes were generally more abundant in the summer than in the autumn. Sphaeriid clams showed an abrupt peak in abundance on soft substrates in late September, 1984, and remained at densities of 50 - 200/m^2 from July through September in 1985 (Figs. V-16 and V-17). With the exception of chironomid larvae, mites, and clams on soft substrates, most taxa exhibited summer population peaks on soft and hard substrates and were rare or absent in the autumn. There was considerable interannual variation in the densities of common taxa in moss habitats.

Stream drift

Water temperatures showed a daily fluctuation at all sites in 1985, with maxima reached at ca. 1500 hours for both dates, and the minima at ca. 0600 hours in August, and 0700 hours in September (Figs. V-18A and B). The outflow stream was warmer than the inflow streams. The outflow stream and Inflow D showed less diel fluctuation in temperature than Inflow A, which showed diel fluctuations of over 12°C in September. Inflow D was usually a few degrees colder than Inflow A, because the water in Inflow D came from a nearby permanent snow bank whereas the water in Inflow A was warmed by insolation as it flowed over bedrock from snow banks further away.

There was little change in diel current velocity and stream discharge through the nets at each site (Figs. V-19A-D) during collection periods except for the outflow sites in July, 1984. On this date the highest discharge occurred during the day, possibly due to increased snowmelt and decreased through the night. Stream discharge decreased from July to October in 1984 and was lower in September than August in all streams in 1985, (Fig. V-19E). Change in stream discharge did not appear to effect diurnal changes in invertebrate drift rates. Some seasonal changes in drift rates may have been due to changes in discharge, although this pattern was not consistent. For example, discharge and drift rates were higher in August than in September, 1985, but July, which had the highest discharge values for 1984, did not consistently show the highest drift values for that year.

Drift fauna from the inflows and the outflow was composed largely of Chironomidae (57% of the total number of benthic insects in drift nets; not separated further than family in this study), Simuliidae (24%; Prosimulium and Simulium spp.), Baetis spp. (7%; primarily Baetis bicaudatis and B. tricaudatis counted together), aquatic mites (4%), and terrestrial insects (13% of total drift collected; Table V-4). Zooplankton from the lake were present in the outflow drift collections, but were not counted. Among other organisms present in the vicinity of the sampling sites were those that were common in the benthos but not susceptible to drifting, such as cased caddisflies and tubiculous chironomids, burrowing dipteran larvae (e.g. tipulids), and clams of the genus Pisidium in the outflow. Also present but not captured in high numbers in the drift were organisms with low benthic densities such as Hydra, coleopteran larvae, Sialis, miscellaneous dipteran larvae, and predatory stoneflies (Waters 1962, Cooper, unpublished data).

Total invertebrate drift, in general, rose nocturnally for all collection dates in 1984, at both outflow sites (Fig. V-20A and B). Mean drift values for July and August were substantially higher than for the autumn months in 1984. The total number of invertebrates in the outflow drift reached a peak of approximately 3X the mean daytime drift level shortly after dusk in the August, 1985, (Fig. V-20C). The total number of organisms drifting per hour in Inflow A peaked at about 0200 hours but remained relatively constant and low for Inflow D in August, 1985 (Fig. V-20D). The total number of aquatic organisms in the drift in the lower outflow site in September and October, 1984, and at all sites in September, 1985, remained fairly constant and low.

Chironomids nearly always displayed nocturnal increases in drift rates when their numbers were high enough for analyses (V-21 A-D). Chironomid larvae in the outflow showed a distinct nocturnal rise (approximately 3 X daytime level) at the lower outflow site on August 28-29, 1984 and August, 1985, and at the upper site on October 29-30, 1984. Most other dates showed small nocturnal increases in chironomid drift (outflow). Chironomid larvae drift rates rose at night to ca. 4 X mean daytime level in Inflow A in August, 1985. Drift rates for chironomid larvae were low and displayed no diel periodicity for other inflows.

Blackfly larvae (Simuliidae) were common in the outflow drift only on collection dates in July and August, 1984, and August, 1985. In both years, Simuliid drift was generally highest at night (Figs. V-22 A-C), showing nighttime peaks of up to 10 X the daytime drift rates.

Baetis (B. bicaudatus and B. tricaudatus), were present in high enough numbers (7% of total benthic organisms) in the lower outflow site in September of 1984, and August of both years and in Inflow A in both months in 1985, for an analysis of diel trends. In general, Baetis drift peaked at night and fell in the day. Baetis drift rates rose shortly after dusk at the lower outflow site in August of both years, peaking at approximately 5-10 X that of the mean daytime level (Figs. V-23 A and B). However, closer to the lake itself, drift was constant and very low on all collection dates. This may be due to the proximity of the upper site to the lake as well as the geomorphology of the outflow stream. Baetis is primarily a riffle taxon, so is probably more abundant above the downstream site. Also, riffles tend to produce more drift than do pools in certain stream systems (Bailey 1966).

Baetis drift rate in Inflow A displayed a nocturnal peak in both August and September (1985) of approximately 3 X and 2 X the mean daytime drift rates, respectively (Fig. V-23C).

Stream experiment

The total stream channel discharge showed a general decrease over the course of the experiment owing to the drying of the Kaweah (Fig. V-27A). The discharge in the channels tended to decrease in the late afternoons. Discharge per channel dropped from a mean of 20.8 to 13.0 liters per minute during acid addition (38% mean decrease in discharge for all four channels). Discharge became very low in the afternoon and evening on the third day of the experiment, as the Kaweah dried (mean discharge of 7.6 liters per minute for all four channels). Variability in discharge among stream channels was often high owing to difficulties in regulating the relatively low stream flow from the Kaweah.

The pH of the experimentally acidified stream channels (2 and 4) was lowered by acid addition to a mean of 5.0 (target pH of 5.0) during the acidification period (Fig. V-27B), and returned to pre-addition levels shortly after acid addition was stopped. The pH of the control channels (1 and 3) remained relatively constant (ca. 6.4) during the entire experiment. Alkalinity fell to zero during acidification in the experimental channels but rose to pre-acid levels after acid additions stopped, whereas the alkalinity in the control channels remained at approximately 54 μeq/l throughout the experiment (Fig. V-27C). NO_3^- and SO_4^{2-} rose in the experimental channels during addition of nitric and sulfuric acid (Figs. V-27D and 27E). Mean phosphate concentrations were near the detection limit in all channels at all sampling times. Chloride ion concentrations were not substantially different between control and acidified channels. Dissolved iron, manganese, and aluminum were not significantly (ANOVA) different between control and acidified channels during acid addition (Fig. V-27F). This lack of mobilization of metals is likely due to the relatively short stretch of stream channel used in these experiments.

Stream invertebrates found in the benthos and drift of the experimental stream channels are listed in Table V-5. Benthic densities of common taxa (Baetis spp., Simulium, Isoperla sp., Rhyacophila spp., and Chironomidae) were not significantly (ANOVA) different between control and experimental

stream channels before the acidification (Fig. V-28). Coefficients of variation for common benthic taxa before acidification were low (e.g. chironomids, 0.15; Baetis, 0.44), and somewhat higher for less abundant taxa (e.g. Rhyacophila, 0.54; Simuliids, 1.64). No Isoperla were present in stream channels before acidification, but were present in the drift collected at this time.

There was no significant effect of acid addition on any of the stream invertebrate benthic densities measured as benthic numbers were small and there was much variation in the data. Drifting organisms coming from the Kaweah River may have swamped the benthos in the channels, for the total number of Baetis leaving each acidified stream channel in the drift during the acid addition period (437) was well above the number of Baetis calculated to be in the benthos of each experimental channel (285).

Pre-acidification drift rates for Baetis, chironomid larvae, water mites, Isoperla, Simulium, and trichopterans were very similar in both control and experimental channels (Figs. V-29A-29F). Mean coefficients of variation for common taxa in the drift among channels were very low prior to acidification (e.g. mean of 0.20 for Baetis, 0.36 for chironomids, and 0.32 for water mites), and somewhat higher for other taxa (e.g. mean of 0.54 for plecopterans, 0.62 for simuliids). Baetis showed a sensitive drift response to acid additions (Fig. V-29A), having drift rates approximately 7 times higher in acidified channels than in control channels shortly after acid addition commenced ($F=39$, $p<0.025$; fourth root transformation, ANOVA). The number of Baetis drifting from the acidified channels was approximately 3 X the number drifting from the control channels over the acidification period. Other stream invertebrates, including Isoperla, Rhyacophila spp., Simulium, and water mites (Figs. V-29B-29F) show no substantial drift responses to acidification, owing to the large variation among replicate stream channels in some cases (e.g. Simuliids).

Before acid addition, ca. 2.5% of Baetis in the drift were dead (mean of four channels combined). Immediately after acid addition the percent of drifting Baetis that was dead in the acidified channels was higher than in control channels (46% vs. 0%; $F = 29.86$, $p<0.05$, arcsin square root transformed data, ANOVA; Fig. V-30). Fifty-four percent of the enhanced drift in the acidified over the control channels can be attributed to death (e.g. toxic drift), 46% to behavioral drift. Acidification had no

measurable effects on the survival of the plecopteran, Isoperla, found in the drift.

Lake benthos and bag experiment

Observations made by SCUBA divers show that substrates in the southeast corner of the lake are dominated by sand. Granitic bedrock dominates at the lake's edges, large boulders are found in the northwestern part of the lake, and flocculant mud dominates the lake's central areas. Quillwort (Isoetes cf. bolanderi var. pygmaea) grows on sand in the southeastern section of the lake, whereas clumps of moss (Drepanocladus sp.) are found on mud in mid-lake. Low densities of a sponge (Spongilla lacustris) are found on or under hard substrates in the lake. The dominant benthic invertebrates in the lake include chironomids, water mites, and sphaeriid clams (Pisidium sp.), and oligochaetes and chydorid cladocerans are commonly collected. Summer densities of chironomids range from 211 to 4960/m^2 on hard substrates, and from 1739 to 3750/m^2 on soft substrates (Table V-6). Acidification of large bags had no effect on the densities of chironomids or clams (Fig. V-31).

Discussion

Stream benthos

Numbers of benthic taxa varied greatly through space and time in both the inlet and outlet streams. The inlet streams were quite different from one another in terms of benthic densities, and the outlet stream was quite heterogeneous in the relative and absolute densities of benthic taxa, both among habitats (soft vs. hard clean vs. hard moss vs. cobble) and among spots within a habitat. Although numerous investigators have noted high variation in stream benthic densities, the causes of this variation are not certain (Needham and Usinger 1956, Allan 1984). Many studies have shown that stream invertebrates are responsive to substrate size and heterogeneity, including substrates modified by the presence of plants (Rabeni and Minshall 1977, Minshall 1984, Reice 1980, 1981). Furthermore, invertebrate densities are affected by current speed, temperature, light, and availability of food resources (Hynes 1970). Even when our sampling design was stratified by substrate types, we observed high variation in the densities of many common taxa.

Many of the benthic taxa observed in this study showed large temporal variation in densities, both from season to season and from year to year. Particularly on clean hard substrates, most taxa exhibited summer population peaks and declined to low levels in the autumn. Some taxa, such as chironomid larvae and mites, however, remained at high levels through the autumn. Most of these insects complete one to several generations each year, so large seasonal variation in densities is expected. It is not clear, however, if changes in invertebrate densities among habitats is owing to the substrate specificity of invertebrates or to shifts in the habitats preferences of invertebrates as they grow.

It is apparent that the inlet and outlet streams contain taxa which are known to be sensitive to acidic inputs. The mayflies (Baetis, Serratella, Drunella) and sphaeriid clams, in particular, are often rare or absent in acidic waters (Hall and Ide in press, Okland 1980, Bell 1971, Sutcliffe and Carrick 1973, Friberg et al. 1980, Singer 1982). Because these taxa are common in the Emerald Lake system, it is unlikely that acid deposition has had a long-term effect on the biota of these streams.

Stream drift

Stream benthic invertebrates in the Emerald Lake streams displayed diverse patterns of diel periodicity in their drift rates, while others were aperiodic. Simuliids, Baetis, Malenka, and chironomids generally showed nocturnal increases in their drift rates, mites showed differing drift patterns depending on the date or stream sampled, and trichopterans appeared to be aperiodic. Despite the variability of abiotic factors between months and years sampled, certain taxa of invertebrates displayed drift patterns that remained fairly consistent over time.

The diel periodicity which characterizes behavioral drift was first observed by Tanaka (1960) in the drift patterns of the mayfly genus Baetis, and it has since been substantiated in many studies throughout the world (Elliot 1967a, b, McLay 1968, Waters 1968, Hynes 1970, Allan 1984). Most stream invertebrates, including Baetis, that exhibit diel periodicity have much higher drift activity at night than during daylight hours, often with a strong peak immediately after nightfall (Anderson and Lehmkuhl 1968, Bailey 1981). Some species, including certain trichopterans (Anderson 1967) and mites (Elliot and Minshall 1968, Bishop and Hynes 1969), have been shown to

be primarily day-active and other species (i.e., Chironomidae) aperiodic (Waters 1972).

It has been postulated that higher nocturnal drift is associated principally with increased nocturnal foraging activity of stream invertebrates (Waters 1962). The nocturnal foraging behavior of stream insects presumably evolved as an adaptation to minimize mortality due to visually feeding vertebrate predators (Allan 1978, 1984). An unequivocal test of this hypothesis is difficult, however, since invertebrate behavior should be fixed and thus would not be expected to change in the short-term absence of predators (Allan 1982). No obvious differences in drift rates between the fishless inflow streams and the outflow stream could be attributed to the presence or absence of fish, as the three streams studied were too different in other features (e.g. geomorphology, discharge, and benthic invertebrate community structure) to be directly compared. The streams were also too close to another to be directly compared, as most adult aquatic insects are very mobile and the insects in the different streams were probably genetically similar.

The proximate cause of the observed diel periodicity is light, which has been shown to trigger insects' increased activity as it falls to some threshold intensity level (Holt and Waters 1967, Bishop 1969, Haney et al. 1983). Moonlight has been shown to suppress nocturnal drift (Anderson 1966, Bishop and Hynes 1969). Peaks in drift rates may occur as the moon is occluded (Waters 1962). Nearly full moons were occluded on the evenings on both dates in 1985, and may account for the second peaks observed in drift rates of chironomids, Simuliids, and Malenka.

Stream invertebrates exhibiting diel periodicity in drift rates may drift as a passive (accidental) consequence of nocturnal foraging activity (Elliot 1967b). Their drift patterns may be due to an active (behavioral) process of habitat or food search, (Hildebrand 1974, Otto 1976, and Kohler 1985) or a means of dispersal related to over-crowding or resource depletion (Allan 1985). The question of whether active or passive entry into the water column is actually occurring is still controversial, and evidence supporting either hypothesis has been largely circumstantial. Different invertebrate taxa, owing to their differing functional roles (Merrit and Cummins 1984), habits and habitat preferences, will likley exhibit variable drift mechanisms (Otto and Sjostrom 1986).

Stream invertebrate drift may be biologically important as part of a "colonization cycle" (Muller 1954) in which adults fly to upstream reaches of streams for oviposition, while larval forms are distributed downstream by the current. Drift may also function in dispersal of benthic invertebrates over the streambed (Lehmkuhl and Anderson 1972). Given these important biological functions of drift, increased acidification of stream waters could have severe consequences on invertebrate behavior and community structure as increased acidity affects drift.

Macroinvertebrate drift also functions as an important food source for stream-dwelling fish species such as salmonids (Jenkins et al. 1970, Allan 1980, Wilzbach et al. 1986), whose stomach contents have a similar composition to the percent composition of drift organisms (Elliot 1973). Visual observation has shown stream invertebrate drift to be a major source of the brook trout diet in the Emerald Lake outflow (Jenkins, unpublished data). This relationship between drifting invertebrates and fish could have important implications for the brook trout inhabiting the Emerald Lake outflow, should cultural acidification decrease the abundance of stream invertebrates. Past studies have shown that increased acidification can affect community structure through trophic web interactions (Henrikson et al. 1980, Burton et al. 1985, Hunter et al. 1986).

Drift patterns of benthic invertebrates have been used as indicators of disturbed systems (Hall et al. 1980). For example, survival rate of drifting animals has been measured to evaluate the effectiveness of an insecticide on target species in pest or disease vector control programs, for example on blackflies carrying onchocerciasis (Cummins 1985). Lennon (1941) reported increased drift upon a rise in water temperature, and, under experimentally controlled temperatures in a small stream, higher temperatures resulted in higher drift for Baetis vagans nymphs (Wotjalik and Waters 1970).

Increase in the rate of vertebrate drift has been observed under unusually low discharge and reduced current velocity conditions, in both natural and experimental conditions (Carlsson 1967, Minshall and Winger 1968, and Pearson and Franklin 1968, Campbell 1985). This result is apparently due to an active swimming response of the organism seeking greater currents for respiratory facilitation. Others (Anderson and Lemkuhl 1968, Bishop and Hynes 1969, and Ciborowski 1983) have found drift rates to be proportional to

stream flow, benthic invertebrates being passively dislodged from substrates more often as current velocity increases.

In the present study, drift rates do not appear to be correlated with daily fluctuations in stream discharge, but appear to be correlated with seasonal changes in flow for some dates and sites. For example, both drift rates and discharge were, in general, much higher in August than in September, 1985. Other dates, however, did not show this direct correlation between drift rates and flow. For example, although the highest discharge was observed in July, 1984, higher mean drift rates were recorded for September of that year. The differences in annual stream discharges between 1984 and the drought year of 1985 emphasize the need for long-term monitoring.

Stream invertebrate drift has been shown to be a sensitive indicator of pH stress, often displaying a short-term increase following experimental acidification of stream waters (Hall and Likens 1979, Hall et al. 1980, Overrein et al. 1980, Singer 1982, Zischke et al. 1983). It is not clear if this short-term increase in drift observed in field acidification studies is the result of increased "toxic" drift (i.e., dead individuals in the drift) passively entering the water column (Griffiths and Sardella 1984), or is due to a behavioral "stress" response (Allan et al. 1986). Mayflies have been demonstrated to be especially sensitive to reductions in pH of stream waters (Bell 1970, Fiance 1978, Hall et al. 1980) and often show a more dramatic drift rate response to acid than other invertebrates (Overrein et al. 1980, Hall et al. in press).

Several authors have concluded cultural acidification of streams can have severe effects on benthic invertebrate communities, decreasing both the diversity and abundance of organisms (Bell 1971, Sutcliffe and Carrick 1973, Hendrey 1976, Fiance 1978, Hall and Likens 1979, Friberg et al. 1980, Hall et al. 1980, Muller 1980, Haines 1981, NRC 1981, Burton et al. 1982, 1985, Singer 1982, Zischke et al. 1983, Howells et al. 1983a, Mackay and Kersey 1985, Hall et al. in press, Hall and Ide in press). These adverse effects on invertebrate communities can occur either through direct physiological damage to the organisms or by indirect means mediated through the food chain (Burton et al. 1982, Henrickson et al. 1980, Leivestad et al. 1976, Hall et al. 1980, Muller 1980). For example, sensitive organisms can have their numbers reduced directly from chemical toxicity, or be outcompeted or preyed upon by

more tolerant competitors or predators. Similarly, more tolerant organisms may be reduced in number through the trophic web if their sensitive prey have been decreased due to acidification. Some taxa can benefit because increased acidity eliminates predators or competitors, e.g. invertebrate grazes can be eliminated by acid deposition with important repercussions for the algae on which they feed (Hendrey 1976, Hall et al. 1980).

The waters of the Sierra Nevada are particularly sensitive to aluminum leaching due to the granitic nature of their watersheds. Increased leaching of aluminum from sediments as a consequence of cultural acidification has been shown to have deleterious effects on stream communities (Howells et al. 1983b, Brown 1981). Aluminum has been found to be toxic to stream fish, including the brook trout Salvelinus fontinalis (Schofield and Trojnar 1980, Driscoll et al. 1980, Baker and Schofield 1980), and may affect invertebrate populations in acidified surface waters (Hall et al. 1980, 1985, Burton and Allan 1986, Hall et al. in press).

In conclusion, long-term data sets on benthic invertebrate drift in the Emerald Lake streams are important in providing biotic measures that may be used to evaluate the effects of future environmental changes. The collection of baseline invertebrate drift and benthic data along with water chemistry data will allow us to separate natural fluctuations in aquatic invertebrate populations from fluctuations caused by anthropogenic perturbations, such as increased acidity of stream waters.

Stream experiment

Past studies on the effects of acid deposition on aquatic communities have been primarily either surveys (Singer 1981), laboratory bioassay experiments (Bell 1971), or whole stream acidifications (Hall et al. 1980). Experimental stream channels provide an excellent compromise between these methods in terms of similarity to natural conditions, replicability needed for statistical analyses, ease of manipulation, and size. The experimental stream channels used in this study were representative of the natural system, containing similar substrates, and algal and invertebrate populations found in the Kaweah River. Species composition for invertebrate and algal populations were very similar (Cooper, unpublished data). Water chemistry was identical to the Kaweah River as water was diverted directly from the natural stream into the channels.

The replicability of the stream channels was excellent as neither drift rates nor benthic densities were significantly different between control and experimental channels prior to acid addition. Coefficients of variation for pre-acid benthos and drift in all channels were reflective of high to satisfactory precision (Allan 1984). Increased variability between channels near the end of the experiment was probably owing to the drying of the Kaweah River. This experimental design eliminates pseudoreplication as described by Hurlbert (1984) as treatments were spatially randomized and had independent supply systems. Because we can manipulate channels before experiment initiation to insure that they have similar abiotic (substrates, current) conditions and similar algae and invertebrate densities, we can circumvent many of the problems associated with high sampling variability.

To date, artificial channels have not been used extensively to examine the effects of increased acidity on stream systems. Studies that have been done, however, show that stream channel experiments are sensitive indicators of periphyton and invertebrate responses to chemical stress (Hendrey 1976, Zischke et al. 1982, Burton et al. 1985, Lamberti and Resh 1983). For example, Lamberti and Resh (1983) were able to separate the effects of temperature and chemical concentration on the composition of a stream benthic community using stream microcosms, whereas large _in situ_ experiments failed to do the same. Preliminary results, then, indicate that stream channel experiments are the most tractable, manageable, rigorous, and sensitive methods to determine and predict the effects of acid stress on the chemistry and biota of streams.

Stream channel designs used to test the effects of reduced pH on stream invertebrates in the past have had limited replicability, and thus were not adequate for rigorous statistical analyses (Zischke et al. 1983, Burton et al. 1985, Servos and Mackie 1986). Replicate channels used in some studies have been dissimilar at the outset of experimental manipulation, channels being of different material and size (Burton et al. 1985). Other stream channels have not been representative of the natural environment, having unnatural substrates (Servos and Mackie 1986), or being indoors, with artificial, recirculating stream water and unnatural assemblages of invertebrates (Burton et al. 1985).

In our experiments a significant increase in _Baetis_ drift rates occurred following acidification of experimental stream channels. Increased drift of

benthic invertebrates has been reported to follow acidification of streams (Hall and Likens 1979, Hall et al. 1980, Overrein et al. 1980, Zischke et al. 1983). This acceleration in macroinvertebrate drift activity is often an initial reaction to lowered pH and levels off to pre-acid rates over time (Hall and Likens 1979, Hall et al. 1980). Ephemeroptera are especially sensitive to low pH waters (Bell 1971, Sutcliffe and Carrick 1973, Fiance 1978, Howells et al. 1983, Mackay and Kersey 1985) and often have a higher drift rate in response to lowered pH than other benthic invertebrates (Overrein et al. 1980).

The increased drift of stream invertebrates during acidification may be due to a passive, "toxic" drift; i.e., an increased number of killed individuals in the drift (Griffiths and Sardella 1984). Increases in drift in response to insecticide spraying have been shown to result from an increase in the number of dead invertebrates in the drift (Eidt and Weaver 1983). The increased drift may be due to an active, behavioral response of the drifting organisms (Hall et al. 1980), or may be due to an increase in the insects' susceptibility to being accidently dislodged. The high percentage of dead Baetis (46%) in the drift immediately following acidification of stream channels compared to the controls (0%) indicates that some "toxic" drift occurred. 54% of the enhanced drift seen shortly after the start of acid addition in the acidified channels can be attributed to "toxic" drift, the remainder to behavioral drift. The mechanisms of stream drift during acid pulses is most likely species specific, as is drift behavior in unmodified waters (Otto and Sjostrom 1986).

The low discharges observed in this experiment, which occurred because of the drying of the Kaweah, most likely confounded the interpretation of our results. Past studies have shown increased drift rates when stream flow decreased rapidly, due to an active "swimming" response of benthic invertebrates (Minshall and Winger 1968). Other authors (Anderson and Lehmkuhl 1968, Bishop and Hynes 1969, Ciborowski 1983) have found that drift rates are proportional to stream flow, benthic invertebrates being dislodged from substrates more often as current velocity increases. Both rapidly decreasing discharge, as occurring during a drought, and exceptionally high discharge, for example during a flood, can be viewed as stresses which increase drift. The drift rates of some (e.g. Simuliids, which live in rapidly flowing waters) taxa increased in the afternoon of the third day when

stream channel discharge fell to very low levels. This increase in drift rate was most likely due to a response to rapidly dropping discharge.

The lack of significant differences in benthic invertebrate densities between acidified and control channels was possibly due to the influx of drift organisms from the Kaweah River. As post-acid benthic densities were not measured until two days after acidification, it is likely that any effects were swamped by drifting inputs. The enhanced Baetis drift seen in the acidified channels, compared to the base drift level of Baetis in the control channels, can be viewed as the net loss of this taxon from the stream channels caused by the effects of acidification. If incoming invertebrate drift had been blocked from entering the stream channels during acidification, the net loss of Baetis from the acidified channels would have far exceeded the number in the benthos. Thus, the benthic density of Baetis would have significantly decreased during acid addition.

Drift has been shown to play a major role in the dispersal of organisms over streambeds (Lehmkuhl and Anderson 1972), and recovery of bottom fauna has been rapid in other streams following chemical disturbance (Dimond 1967). Benthic densities of stream invertebrates have been shown to decrease following long-term acidification of stream waters (Hall et al. 1980).

Since aquatic communities often show the first and most drastic effects of cultural acidification (Cowling and Linthurst 1981, Almer et al. 1974, Hall et al. in press), it is important to be able to make predictions as to which organisms will be the most sensitive to acid stress. Baseline monitoring data (Hall and Ide 1986) are important in order to differentiate between natural (e.g. seasonal and annual) variation in community structure, and variations caused by anthropogenic perturbations. Experiments such as this can help us to pinpoint the early-warning signals of stream stress so that we will know which aspects or processes in Sierra Nevada streams to concentrate our attention and efforts on in future monitoring efforts. The results suggest that Baetis, in particular, may be a good "early-warning" indicator of the effects of acid deposition on Sierra Nevada streams.

Lake benthos

The dominant benthic organisms are chironomids and sphaeriid clams. Oligochaetes and water mites are commonly collected, and a population of the sponge Spongilla lacustris is present in Emerald Lake. The clams and sponges

are of particular interest because of their known or presumed sensitivity to acid deposition. Because of the close relationship between calcium and pH, decreases in pH will probably result in the disappearance of the clam population (Roff and Kwiatkowski 1977, Okland and Okland 1980). Okland (1980) found that few sphaeriid clams were found in lakes having pHs < 5.7. Because certain groups of sponges require $CaCO_3$ for spicule formation, Haines (1981) postulated that acidic precipitation may affect sponge distribution and abundance. Raddum (1980) reported that chironomids were reduced in acidic waters.

Our preliminary acidification experiment indicated that chironomid and clam populations would not respond to small reductions in pH. This lack of response can be attributed to three causes: (1) pH in acidified bags was only reduced to pH 5.3 - 5.5 for a brief period of time and pH had rebounded to 5.6 - 6.1 by the end of the experiment. It is likely that pH was not reduced sufficiently, or for long enough periods of time, to elicit population responses from the benthos. Although previous experiments revealed that the zooplankton assemblage exhibits clear, sensitive responses to acidic inputs, only one common zooplankton taxon was significantly affected by treatment at the end of this experiment. Furthermore, an analysis of the time course of zooplankton responses to acidification in this experiment indicated that some taxa showed only subtle, temporary responses to pH reductions. (2) The sediments that lake benthos live in may generate alkalinity and buffer zoobenthos from increases in acidity. Because the sediments may neutralize acidic inputs, organisms which live in the sediments may be less vulnerable than organisms which live in the water column. (3) Lake zoobenthic taxa live for much longer than most zooplankton taxa. Because many population effects of temporary reductions in pH are mediated through effects on growth and reproduction, it is probably necessary to run experiments longer when examining effects of acidic inputs on zoobenthos than when examining effects on zooplankton. It is not clear that this experiment was run long enough to elicit population responses from the zoobenthos.

In general, then, our sampling program indicates the presence of a number of sensitive benthic taxa in Emerald Lake. Our pilot experiment indicates, however, that these taxa will probably not be affected by moderate, temporary reductions in pH.

Table V-3. Emerald Lake Outlet and Inlet Macroinvertebrates

Class Insecta

- Order Collembola (0)
- Order Plecoptera
  - Family Chloroperlidae
    - *Alloperla* (0)
    - *Sweltsa* (0)
    - *Sweltsa pacificum* (0)
  - Family Nemouridae
    - *Malenka* (0)
    - *Zapada* (I,0)
  - Family Perlodidae
    - *Cultus* (0)
    - *Isoperla* (0)
- Order Ephemeroptera
  - Family Baetidae
    - *Baetis* (I,0)
  - Family Ephemerellidae
    - *Daunella spinifera* (0)
    - *Ephemerella* (I,0)
    - *Ephemerella spinifera* (I,0)
    - *Serratella* (0)
  - Family Leptophlebiidae
    - *Paraleptophlebia* (0)
  - Family Siphlonutidae
    - *Ameletus* (0)
- Order Diptera
  - Family Chironomidae
    - *Halocladius* (0)
    - *Hydrobaenus* (0)
    - *Microspectra* (0)
    - *Neozavrelia* (0)
    - *Parametriocnemus* (I,0)
    - *Paratanytarsus* (0)
    - *Psectrocladius* (0)
    - *Synorthocladius* (0)
    - *Thienemannia* (0)
    - *Thienemannimyia* (0)
  - Family Ceratopogonidae
    - *Forcipomyia* (0)
  - Family Empididae
    - *Chelifera* (0)
    - *Clinocera* (I,0)
    - *Wiedemannia* (0)
  - Family Muscidae
    - *Limnophora* (0)
  - Family Simuliidae
    - *Prosimulium* (I,0)
  - Family Stratiomyidae
    - *Euparyphus* (0)
  - Family Tipulidae
    - *Dicranota* (0)
    - *Hexatoma* (0)
    - *Pedicia* (0)
    - *Tipula* (I)
- Order Lepidoptera (0)
- Order Hemiptera
  - Family Saldidae (0)
- Order Megaloptera
  - Family Sialidae
    - *Sialis* (0)
- Order Trichoptera
  - Family Brachycentridae
    - *Amiocentrus* (0)
    - *Micrasema* (0)
    - *Oligoplectrum* (0)
  - Family Lepidostomatidae
    - *Lepidostoma* (0)
  - Family Limnephilidae
    - *Apatania* (0)
    - *Desmona* (I)
    - *Ecclisomyia* (0)
    - *Hesperophylax* (0)
    - *Manophylax* (I)
  - Family Polycentropodidae
    - *Polycentropus* (0)
  - Family Rhyacophilidae
    - *Rhyacophila* (I,0)
  - Family Sericostomatidae
    - *Grumaga* (0)
- Order Coleoptera
  - Family Dytiscidae
    - *Deronectes* (0)
    - *Hydroporus* (0)
    - *Rhantus gutticolis* (I)
  - Family Hydrophilidae (0)

Phylum Arthropoda

- Class Crustacea
  - Order Amphipoda
    - Family Talitridae
      - *Hyalella azteca* (0)
- Class Arachnida
  - Order Acarina (0)

Phylum Mollusca

- Class Pelecypoda
  - Family Pisididae
    - *Pisidium* (0)

Table V-4. List of organisms found in the Emerald Lake stream drift in July, August, September, and October, 1984, and August and September of 1985. 1 -outflow stream, 2 -Inflow A stream, and 3 -Inflow D stream. Percent composition of benthic invertebrate drift in ( )'s (excluding terrestrials).

Class Insecta

Order Collembola 1,2

Order Ephemeroptera

Baetidae

Baetis 1,2,3 (7%)

Ephemerellidae

Drunella 1

Heptageniidae

Cinygmula 1,2

Leptophlebiidae

Paraleptophlebia 1,3

Siphlonuridae

Ameletus 1,2

Order Hemiptera

Gerridae

Gerris 1

Order Plecoptera (1%)

Chloroperlidae

Alloperla 1,2

Nemouridae

Malenka 1,2

Zapada 1,2

Perlodidae

Isoperla 1,2

Order Trichoptera (0.5%)

Lepidostomidae

Lepidostoma-quercina type 1,3

Limnephilidae

Ecclisomyia 1,2

Dicosmoecus 3

Psychoglypha 2

Rhyacophilidae

Rhyacophila 1,2,3

Order Diptera

Chironomidae 1,2,3 (57%)

Dixidae

Dixa 1,2

Simuliidae (24%)

Prosimulium 1

Simulium 1,2,3

Tipulidae

Dicranota 2

Order Coleoptera

Dytiscidae

Hydroporus 1,2

Gyrinidae

Gyrinus 2

Hydrophilidae

Ametor 1

Class Arachnida

Hydracarina 1,2,3 (4%)

Phylum Cnidaria

Hydroids

Phylum Nematoda 1,2

Phylum Oligochaeta 1,2,3

Terrestrials 1,2,3 (13% of total drift collected in 1985)

Table V-5. Stream invertebrates found in benthic and drift samples collected from experimental stream channels in July, 1985.

Phylum Arthropoda
Class Insecta

Order Collembola

Order Ephemeroptera
- Baetidae
  - *Baetis*
- Ephemerellidae
  - *Attenella*
  - *Drunella*
  - *Ephemerella*
- Heptageniidae
  - *Cinygmula*
  - *Epeorus*
- Leptophlebiidae
  - *Paraleptophlebia*

Order Plecoptera
- Leuctridae
  - *Perlomyia*
- Nemouridae
  - *Nemoura*
  - *Malenka*
  - *Zapada*
- Perlidae
  - *Isoperla*
- Periodidae
  - *Megarcys*

Order Trichoptera
- Brachycentridae
  - *Amiocentrus*
- Hydropsychidae
  - *Hydropsyche*
- Limnephilidae
  - *Ecclisomyia*
- Polycentopidae
  - *Polycentropus*
- Rhyacophilidae
  - *Rhyacophila*

Order Diptera
- Chironomidae
- Dixidae
  - *Dixa*
  - *Meringodixa*
- Simuliidae
  - *Prosimulium*
  - *Simulium*
  - *Twinnia*
- Tipulidae

Order Coleoptera
- Dytiscidae
  - *Oreodytes*
  - *Uvarus*

Class Arachnida
- Hydracarina

Phylum Nematoda
Phylum Annelida
Class Oligochaeta

Table V-6. Densities of common benthic macroinvertebrates collected from Emerald Lake in 1984 and 1985. Values presented are the range of densities (no./m^2) encountered. n is the number of replicate samples taken.

Date	Substrate	Sampler	n	Chironomids	Sphaeriid clams	Mites	Oligochaetes
July 11, 1984	Hard	Suction	3	211-1972	67-2333	22-3011	6-472
Aug. 28, 1984	Hard	Suction	4	2100-4956	94-833	22-433	0-150
Aug. 28, 1984	Gravel, sand	Suction	1	3750	61	422	156
Aug. 28, 1984	15cm silt over rock	Suction	1	3150	389	1778	22
Aug. 30, 1984	Soft	Ekman	1	1739	50	0	609
July 11, 1985	Hard	Suction	2	950-1806	33-533	6-44	0-17

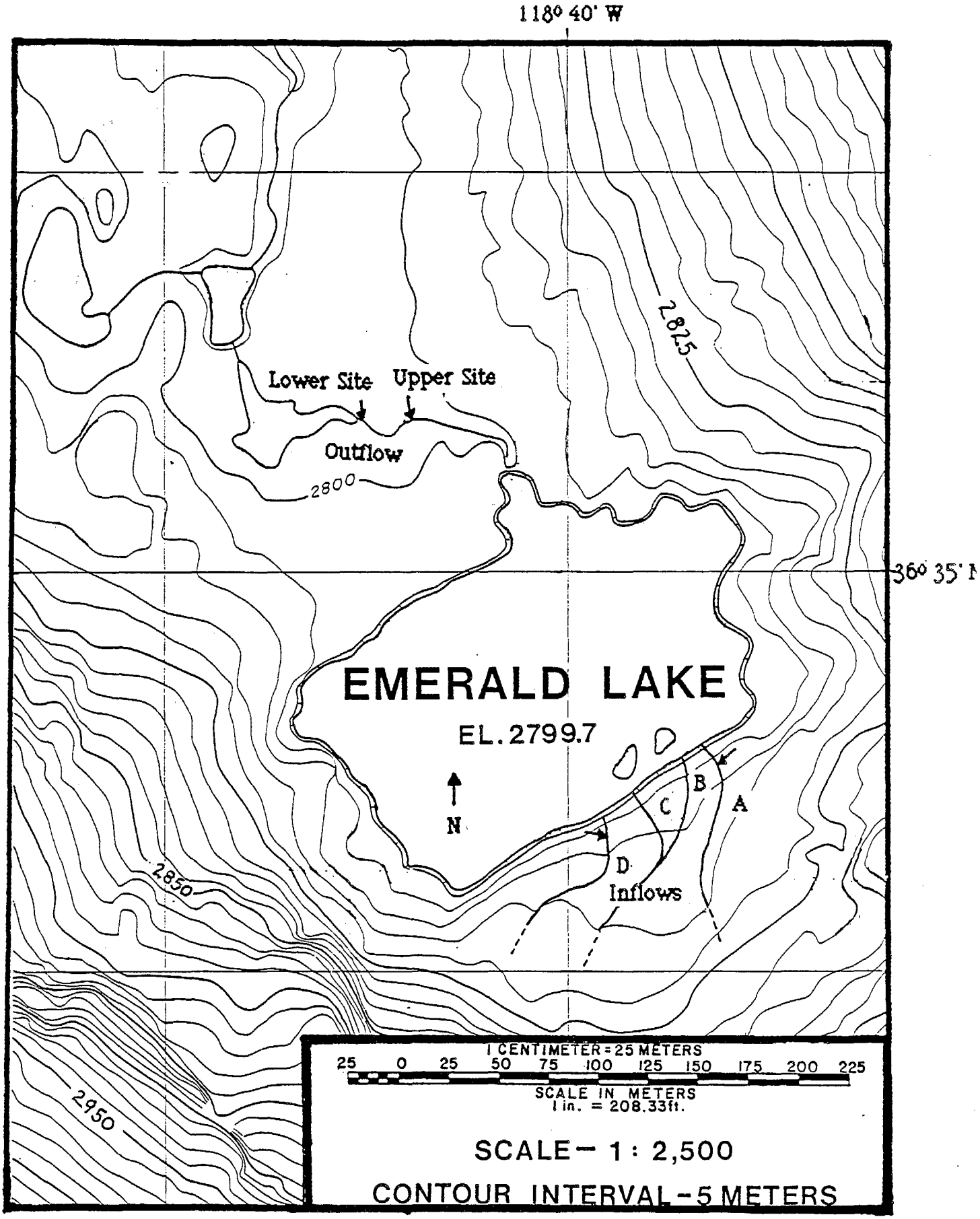
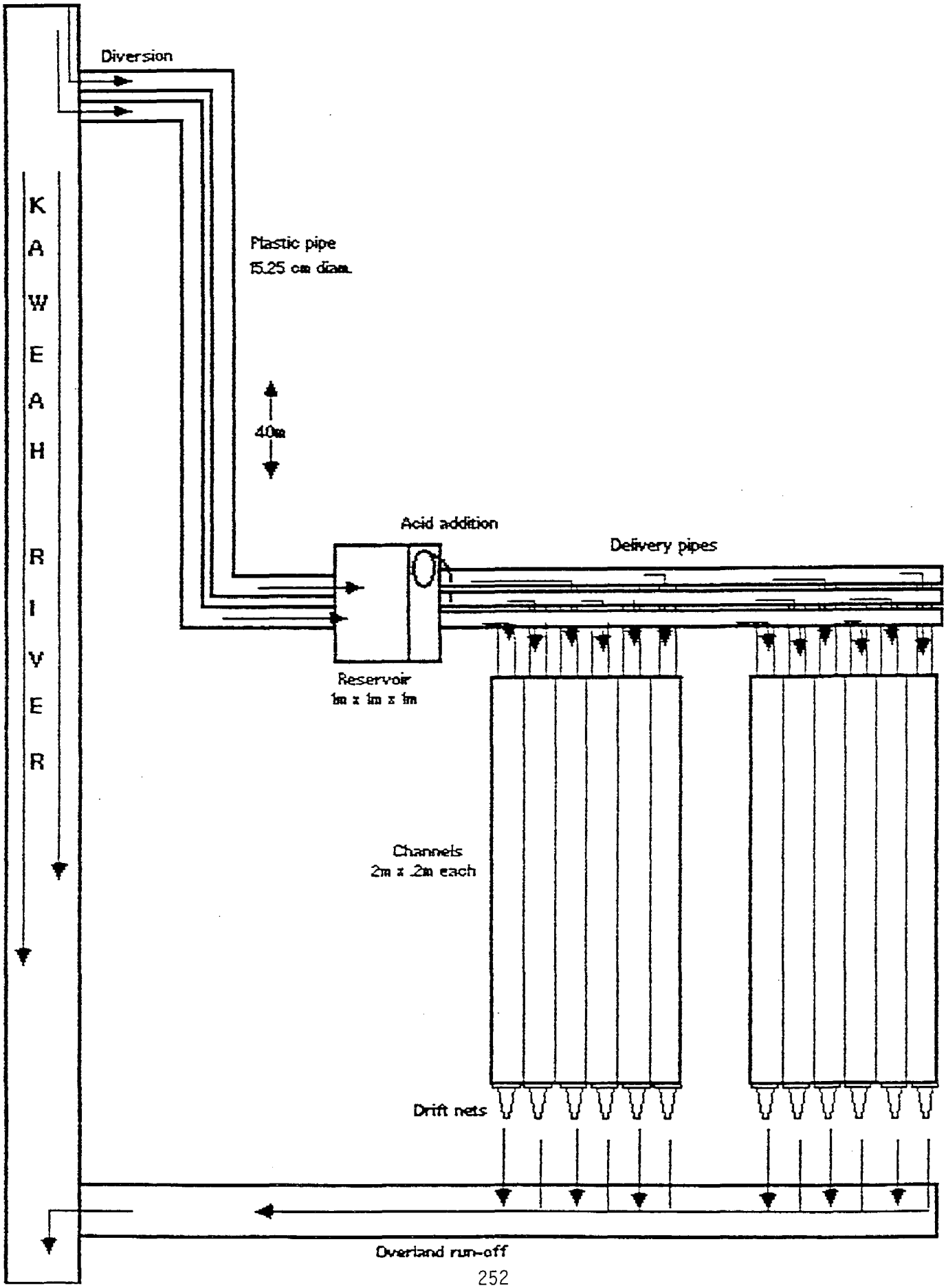
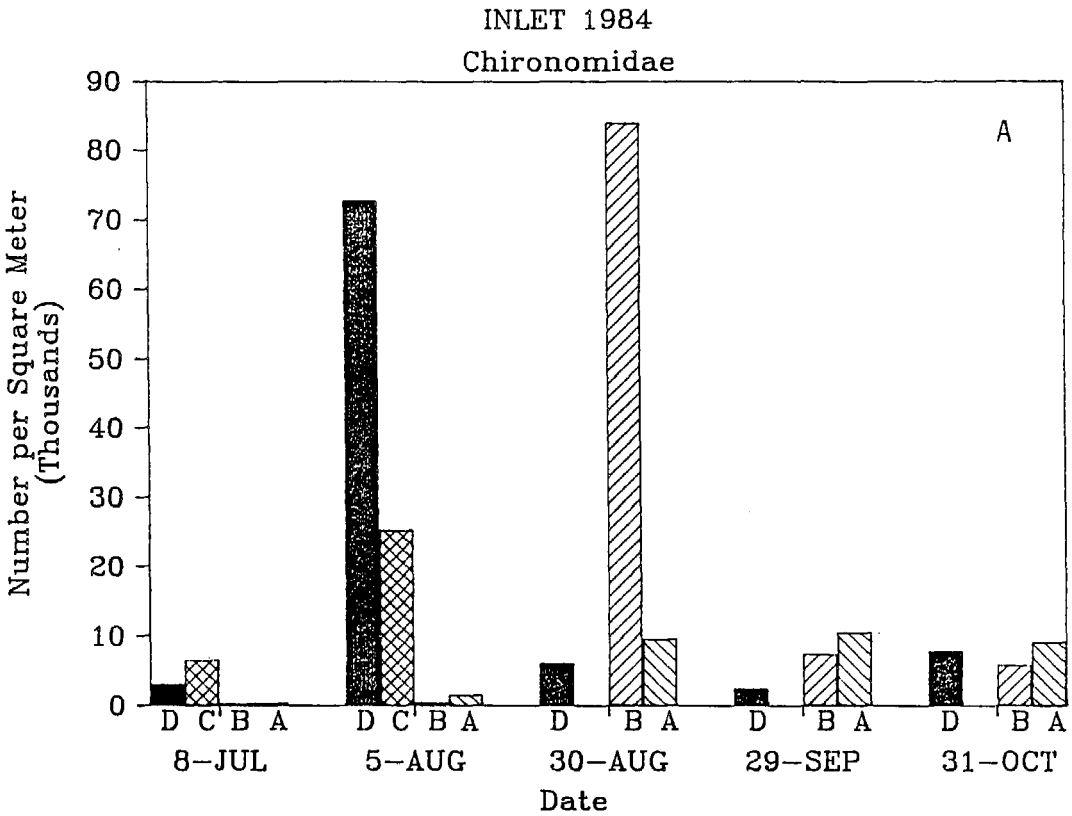


Figure V-8. Map of Emerald Lake, Kings County, California, U.S.A. Arrows indicate the two inflow and two outflow drift collection sites.

Figure V-9. Design of the replicate experimental stream channels set up along the Marble Fork of the Kaweah River in July, 1985. Arrows indicate the direction of water flow.





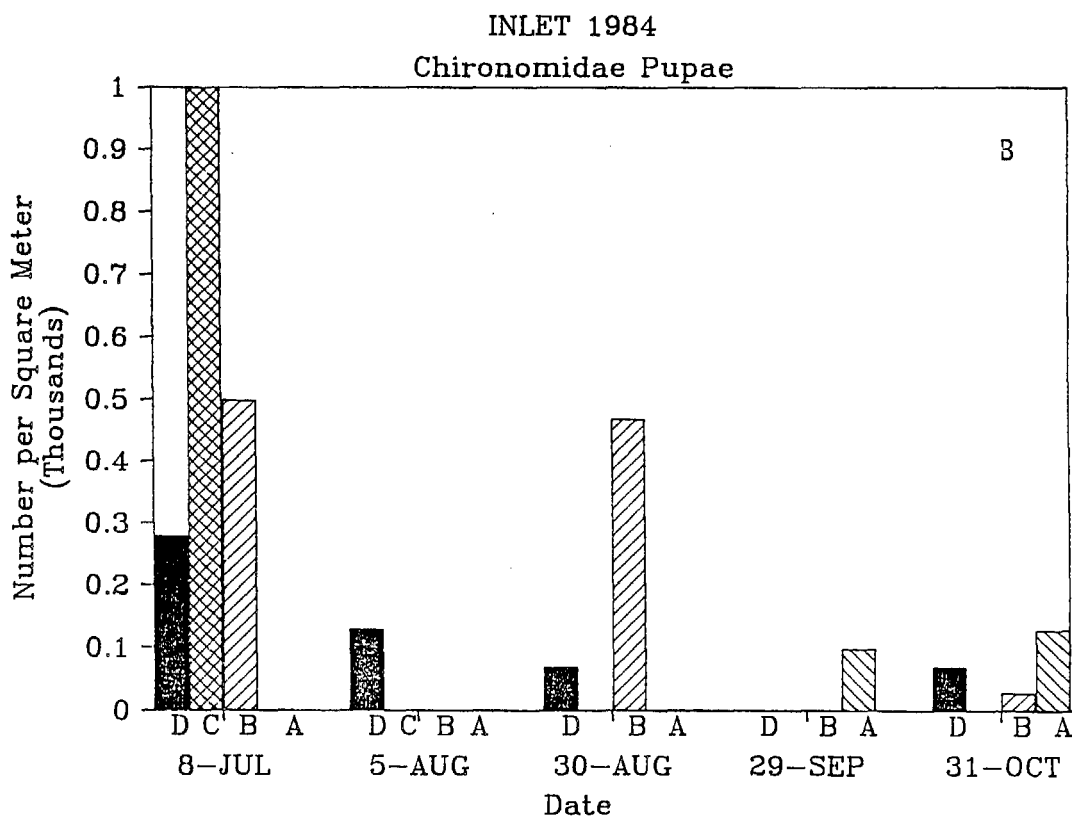
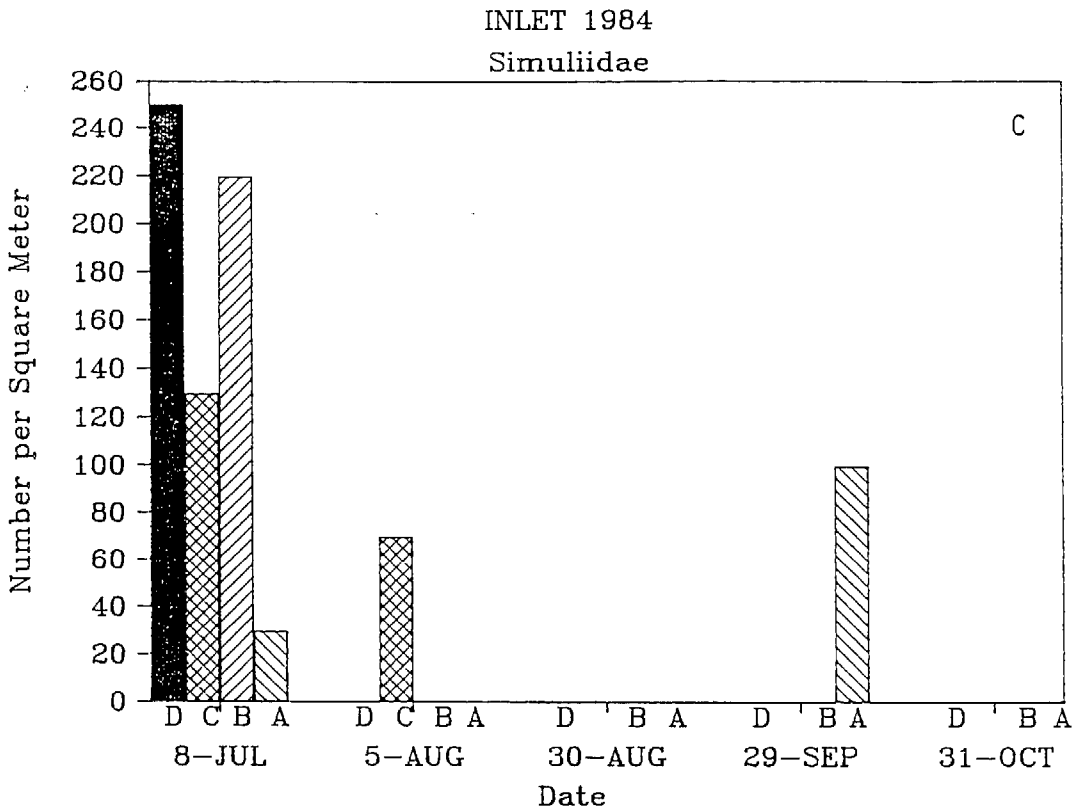


Figure V-10. Densities of common benthic macroinvertebrates in inlet channels A, B, C, D (see Fig. V-8) in the summer and autumn of 1984. If the letter designation for a channel on a particular date has no histogram above it, the channel was dry.



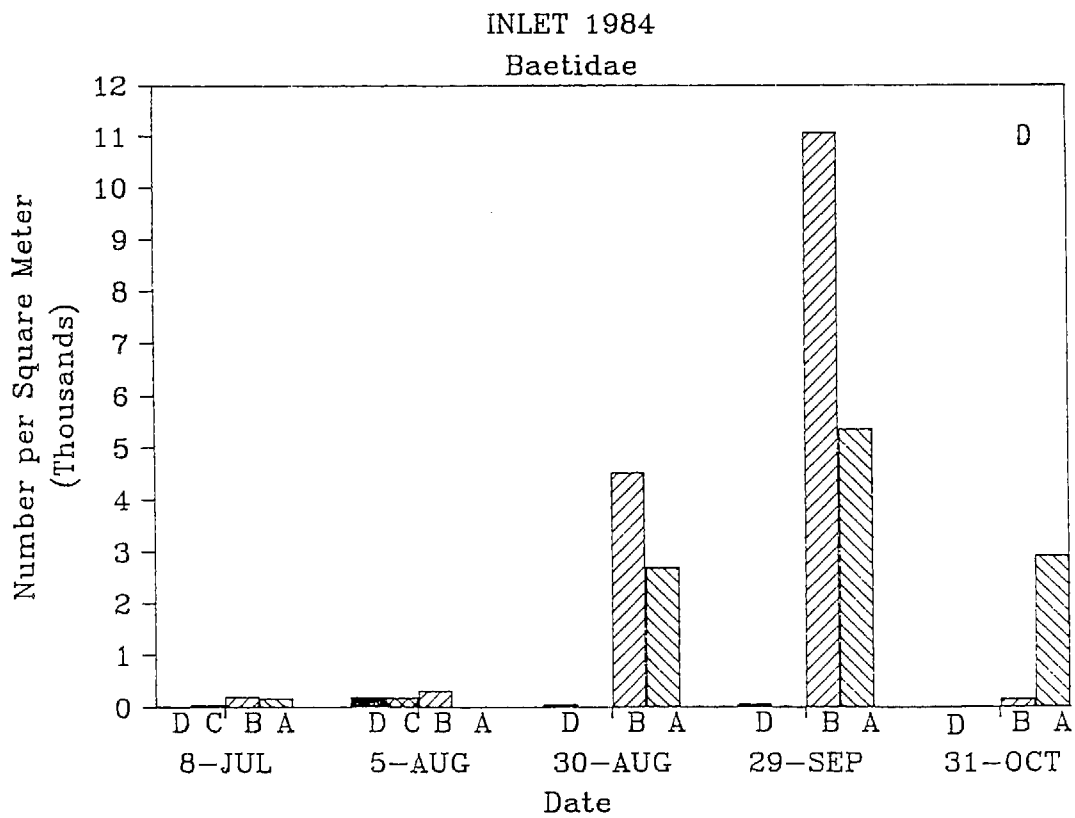


Figure V-10. (continued).

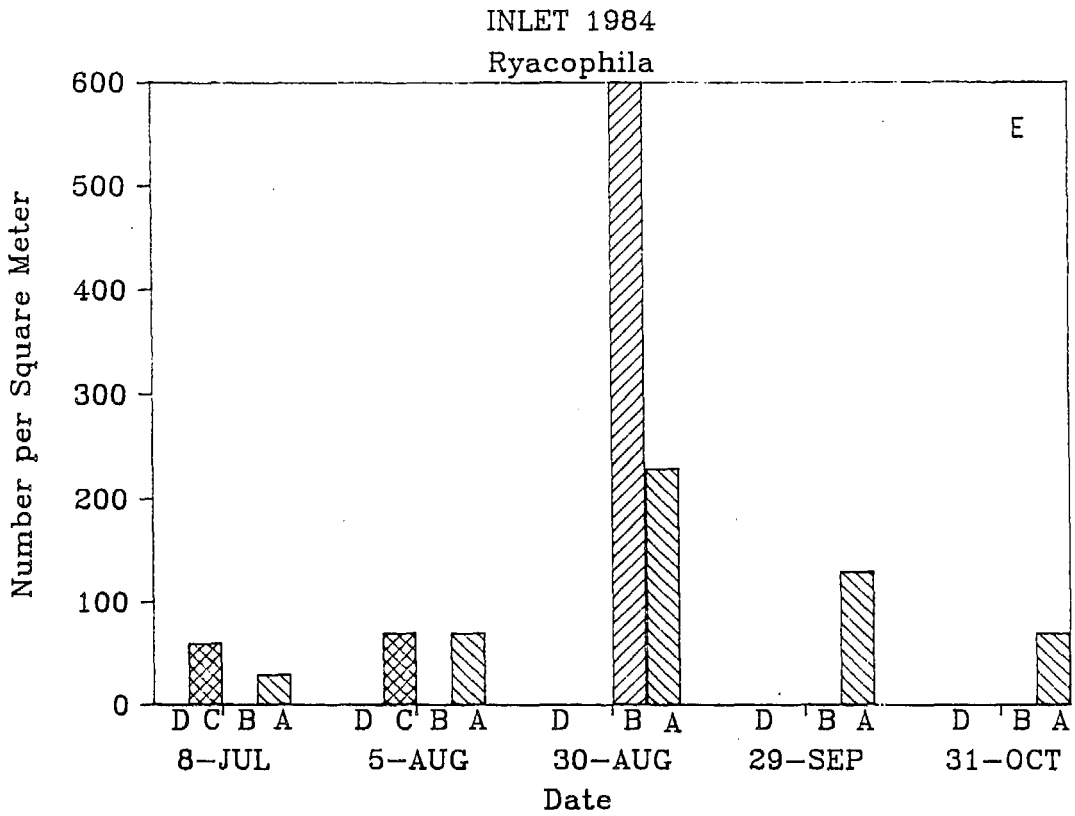
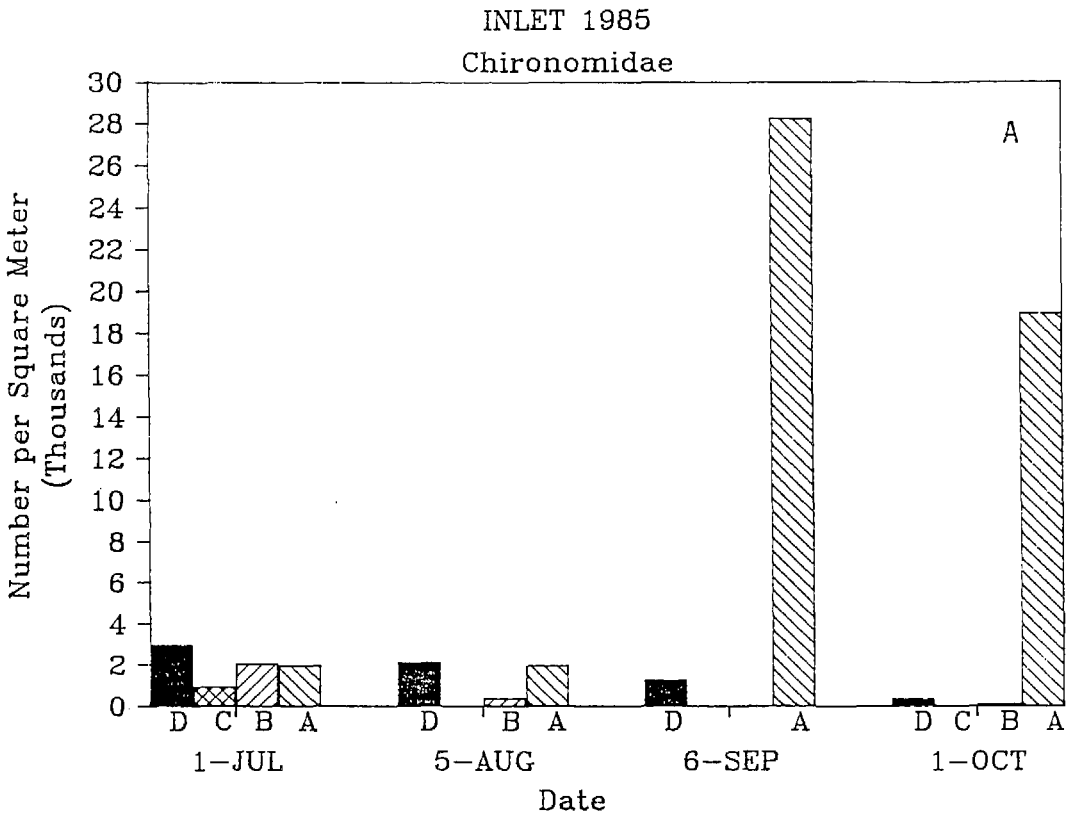


Figure V-10. (continued).



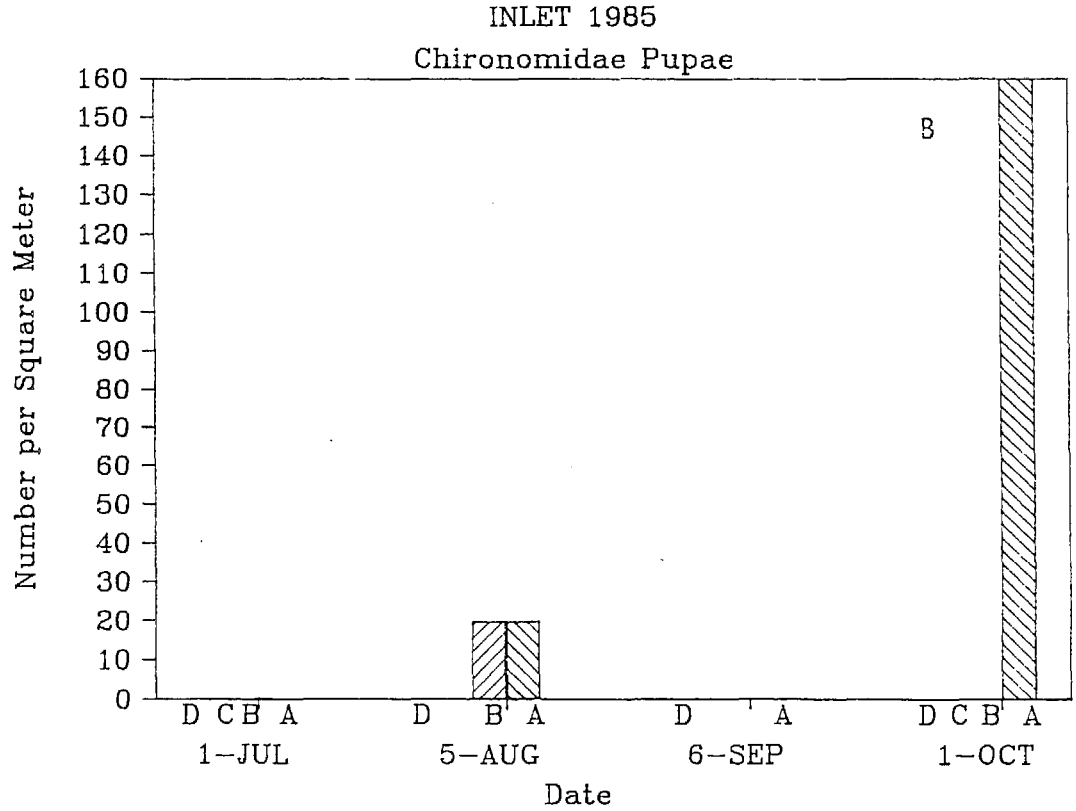
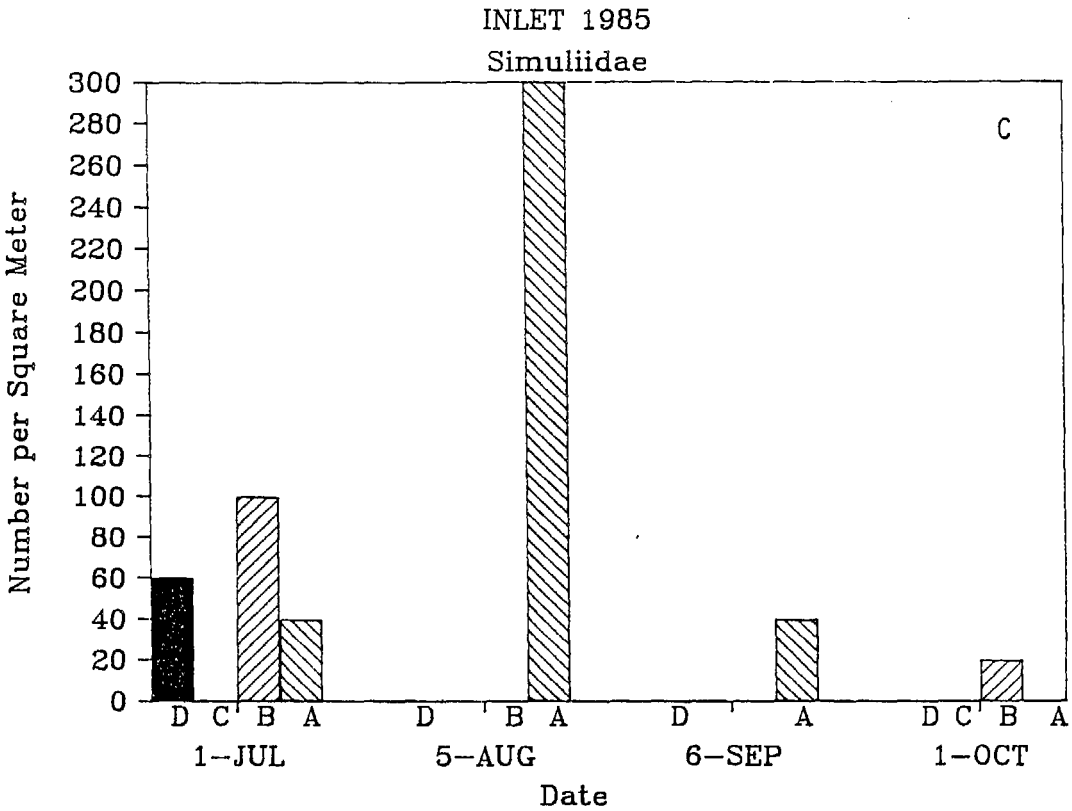


Figure V-11. Densities of common benthic macroinvertebrates in inlet channels A, B, C, and D in the summer and early autumn of 1985. Letter designations as in Figure V-10.



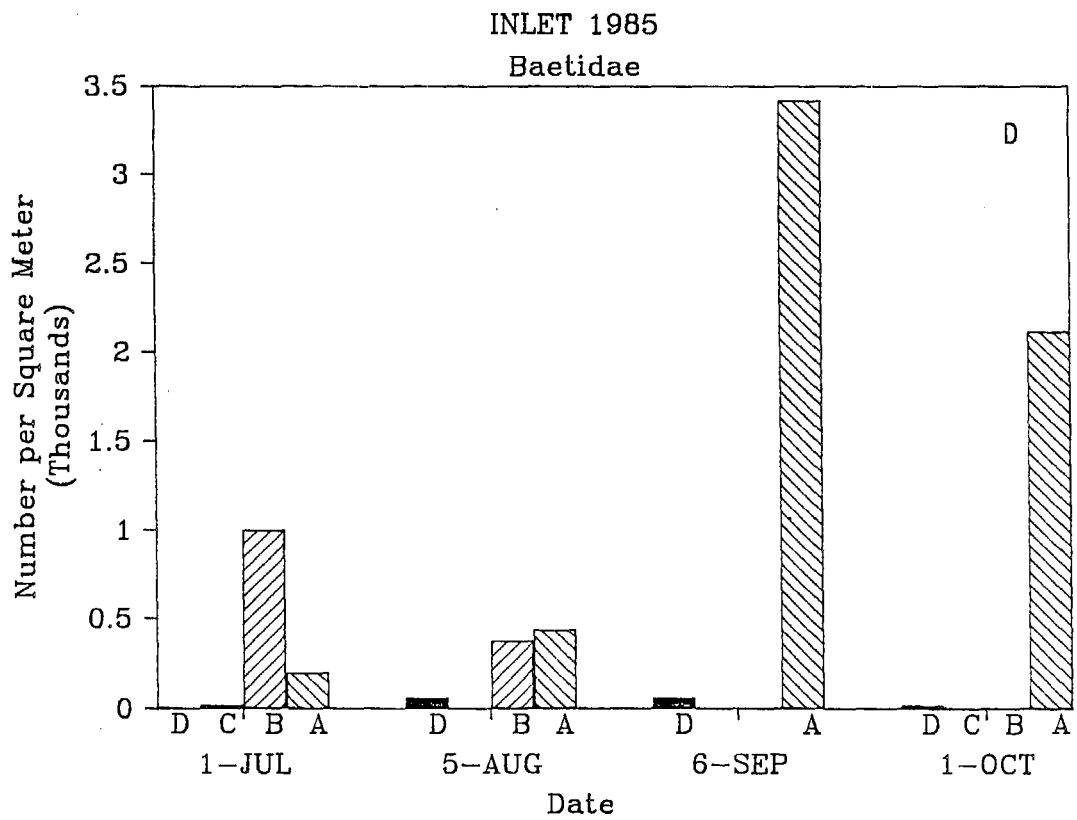


Figure V-11. (continued).

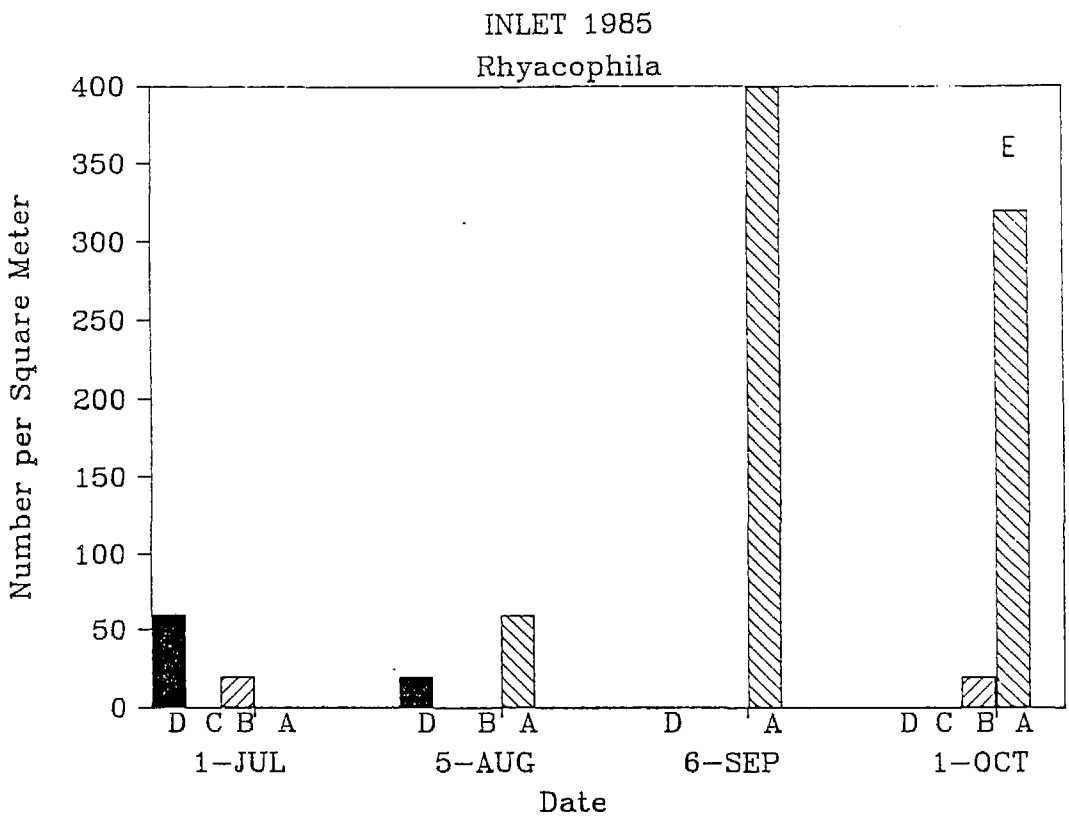
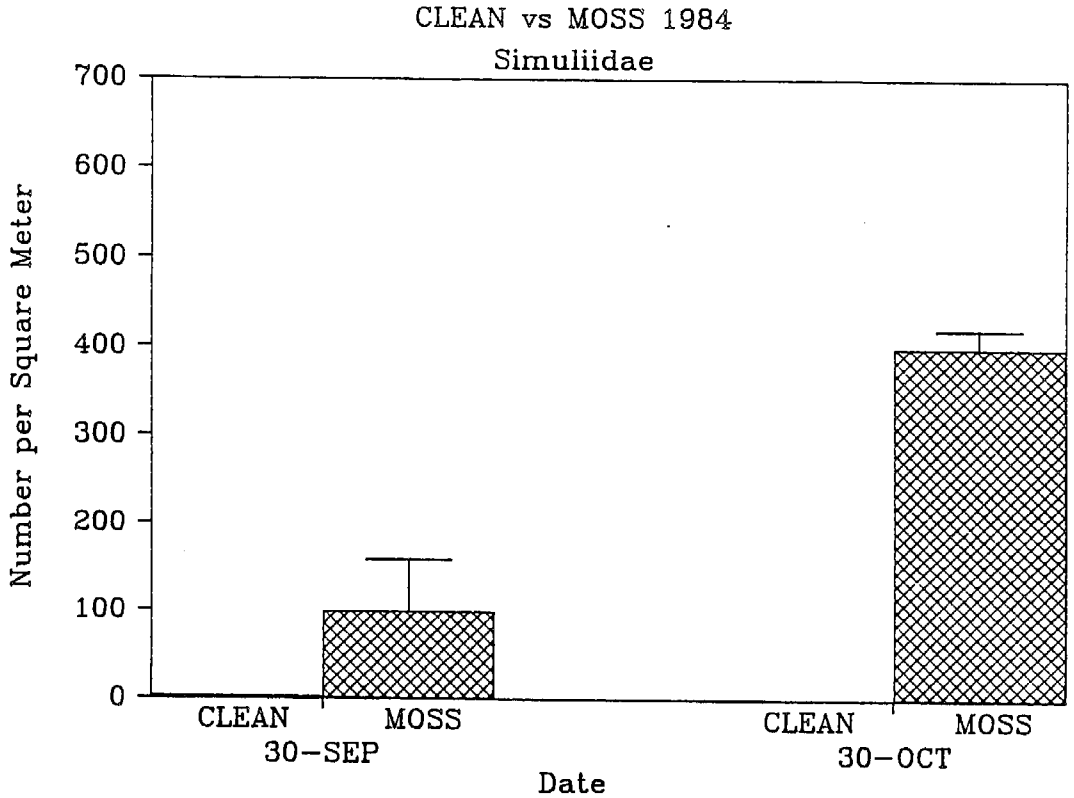


Figure V-11. (continued).



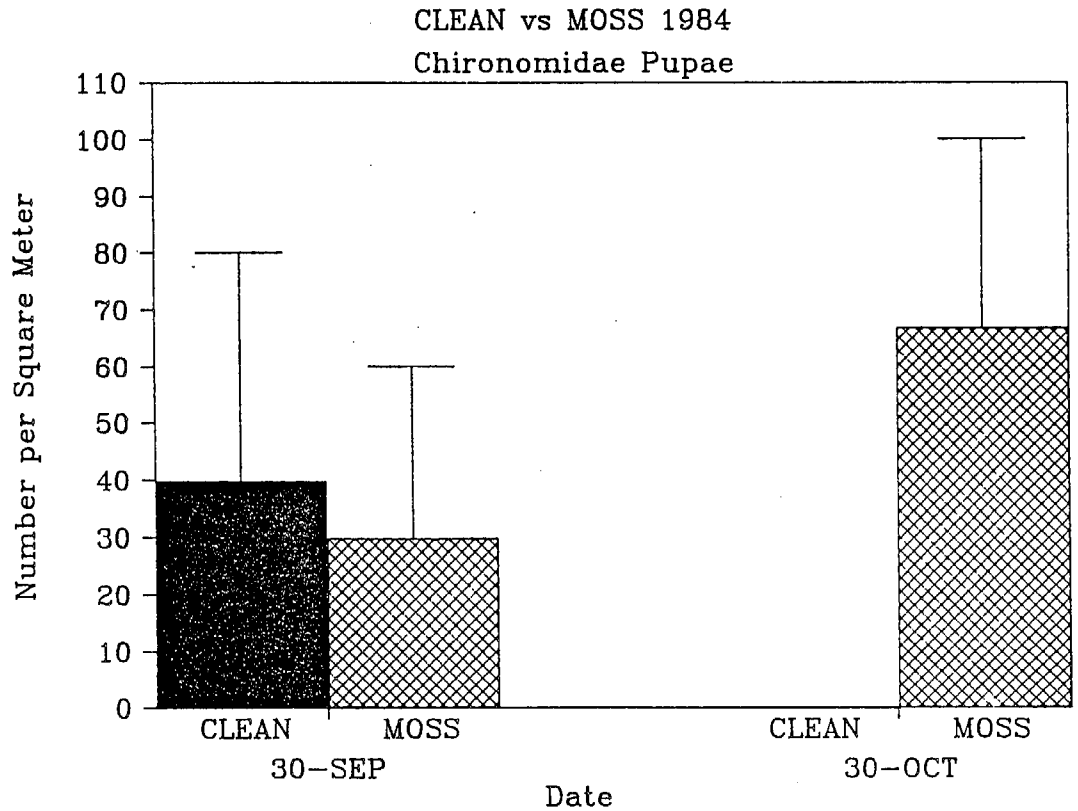
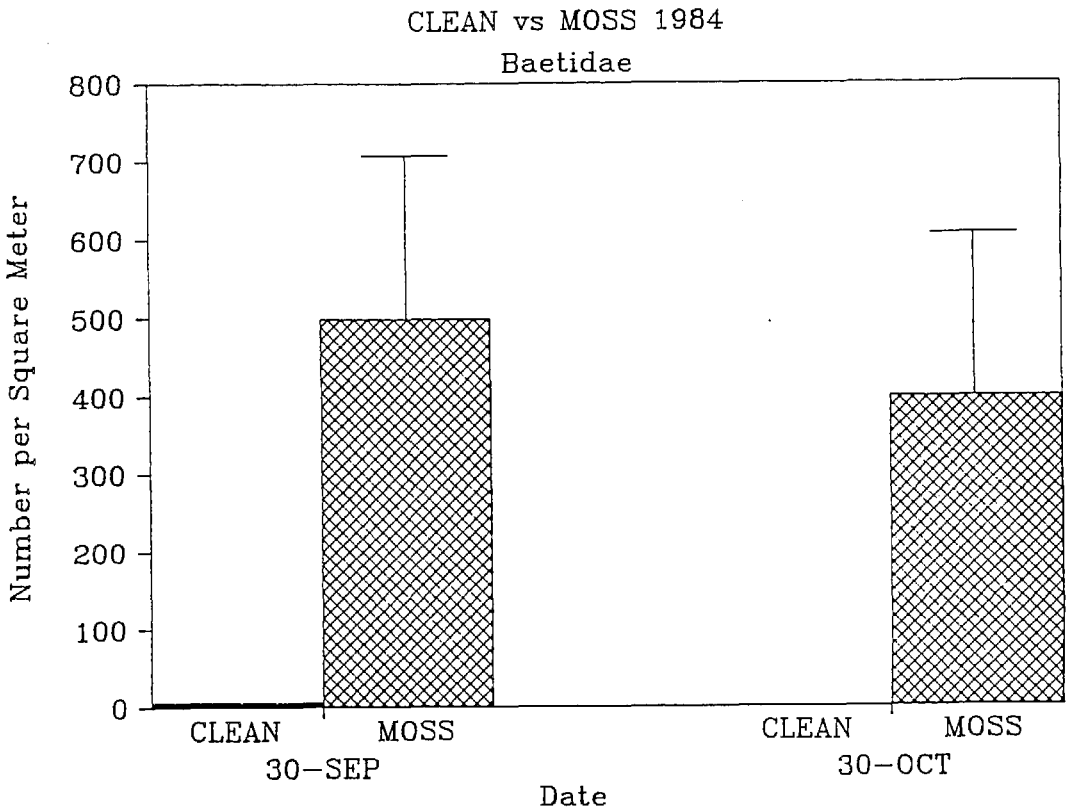


Figure V-12. Mean densities (± 1 SE) of common benthic macroinvertebrates on hard substrates lacking plant cover (clean) vs. hard substrates covered by moss or macroalgae (moss) in the Emerald Lake outlet on two dates in 1984.



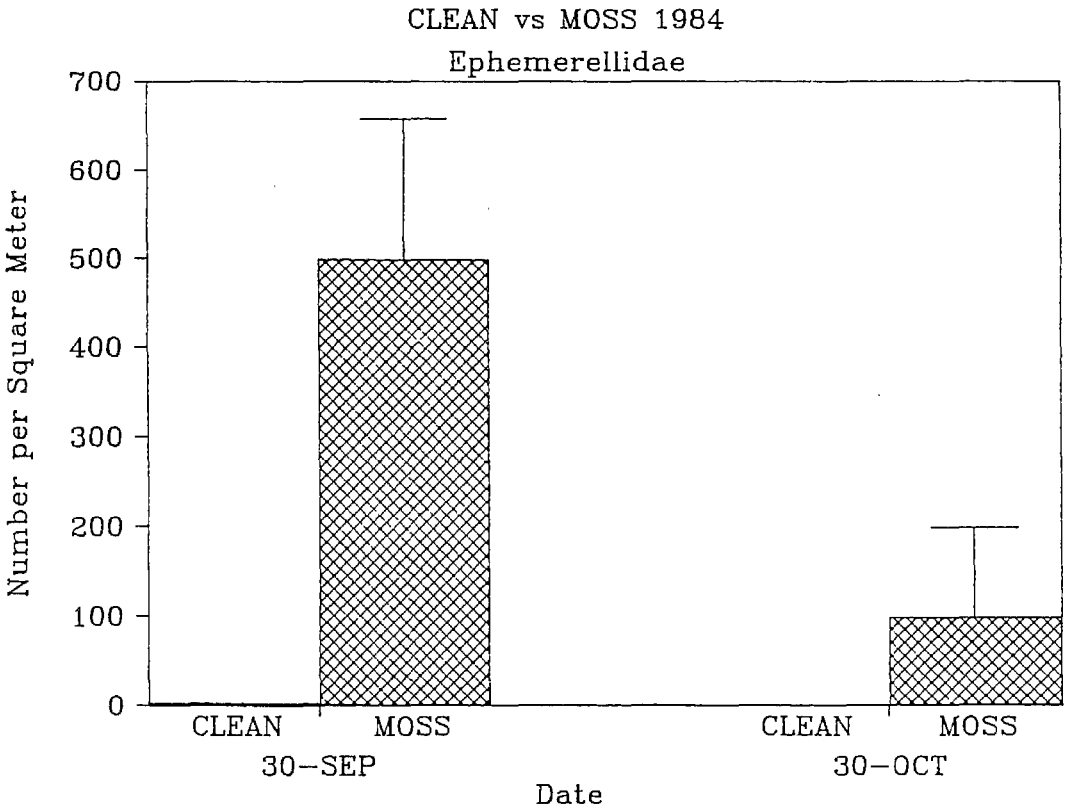
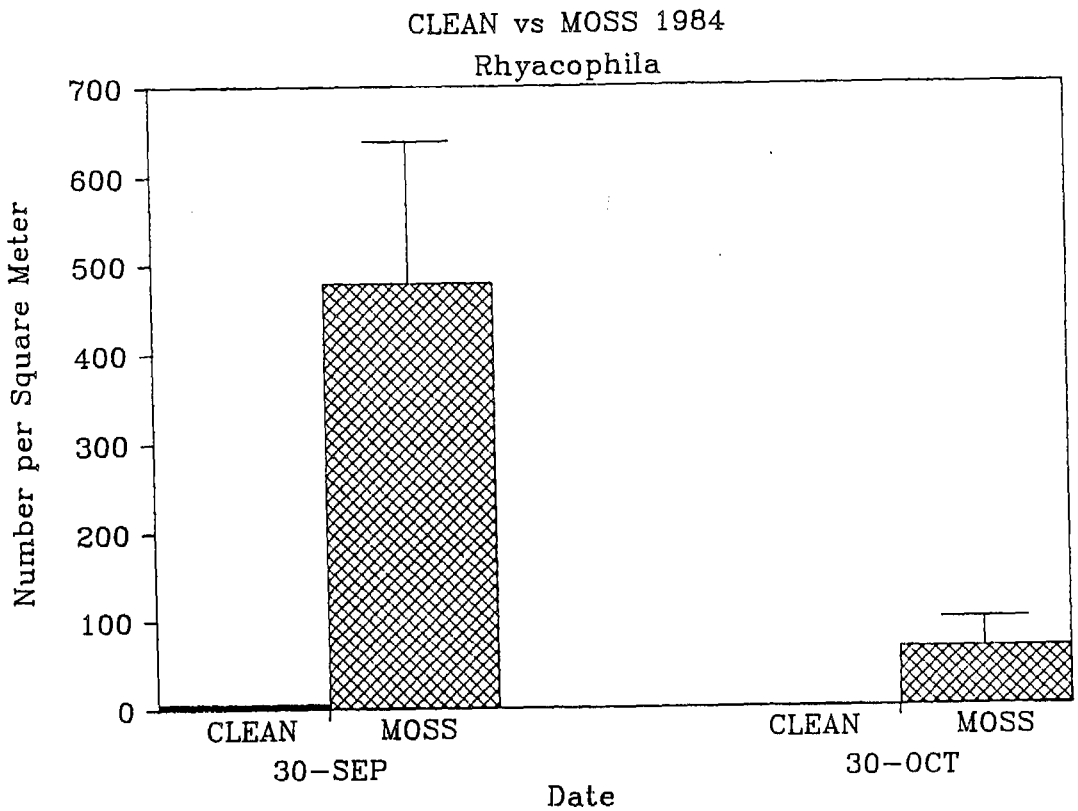


Figure V-12. (continued).



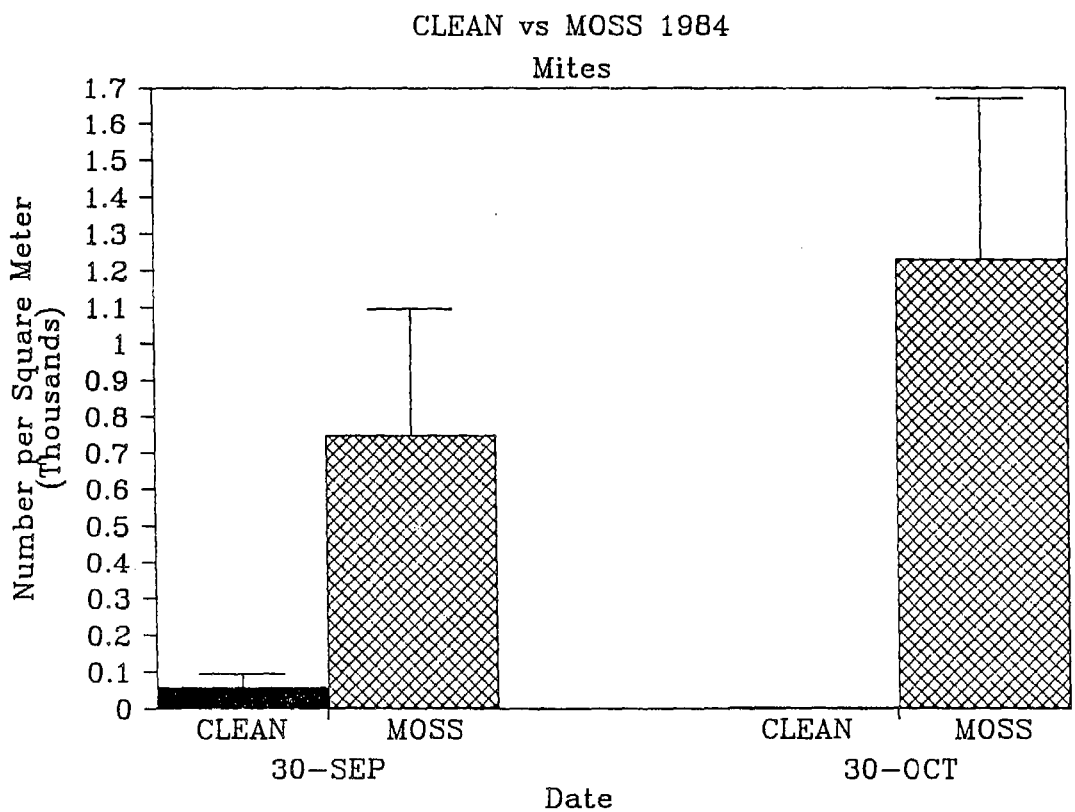
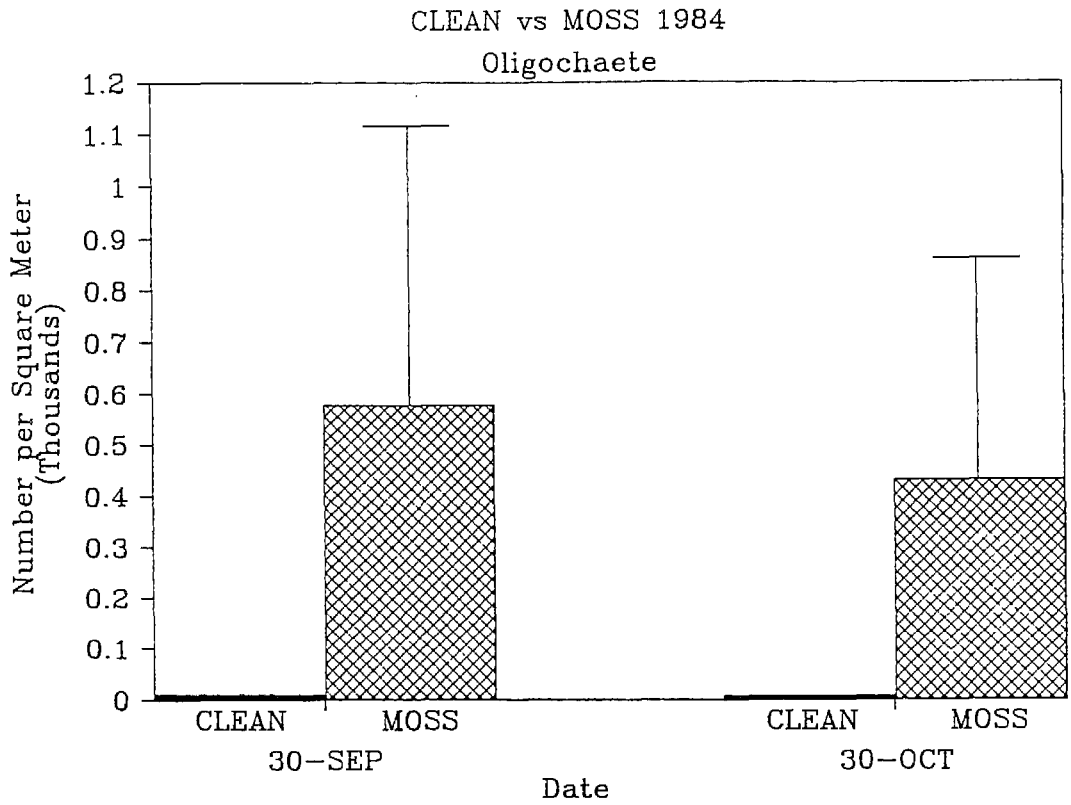


Figure V-12. (continued).



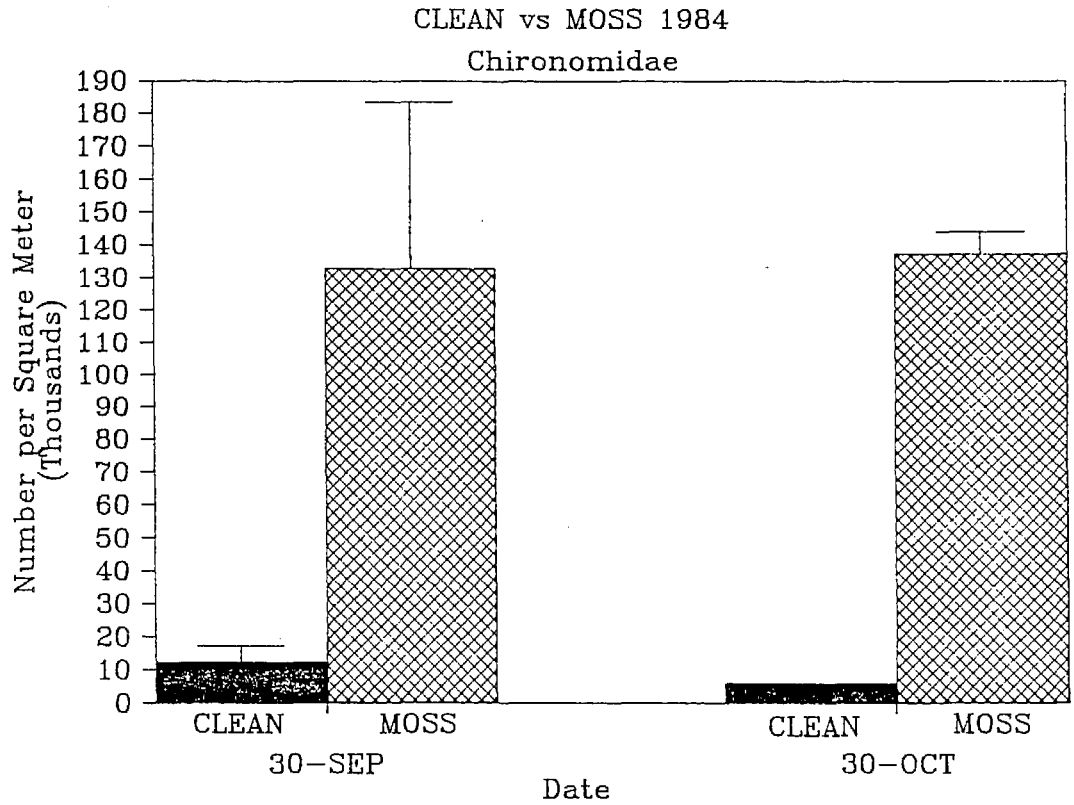
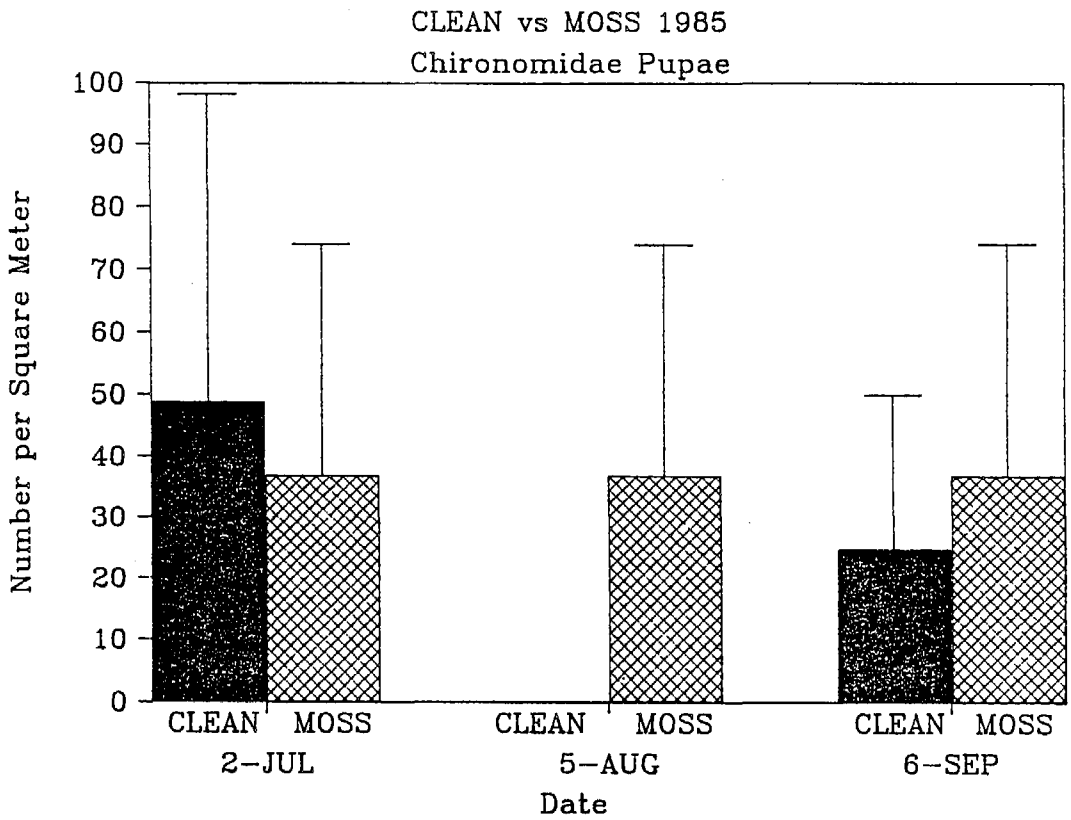


Figure V-12.(continued).



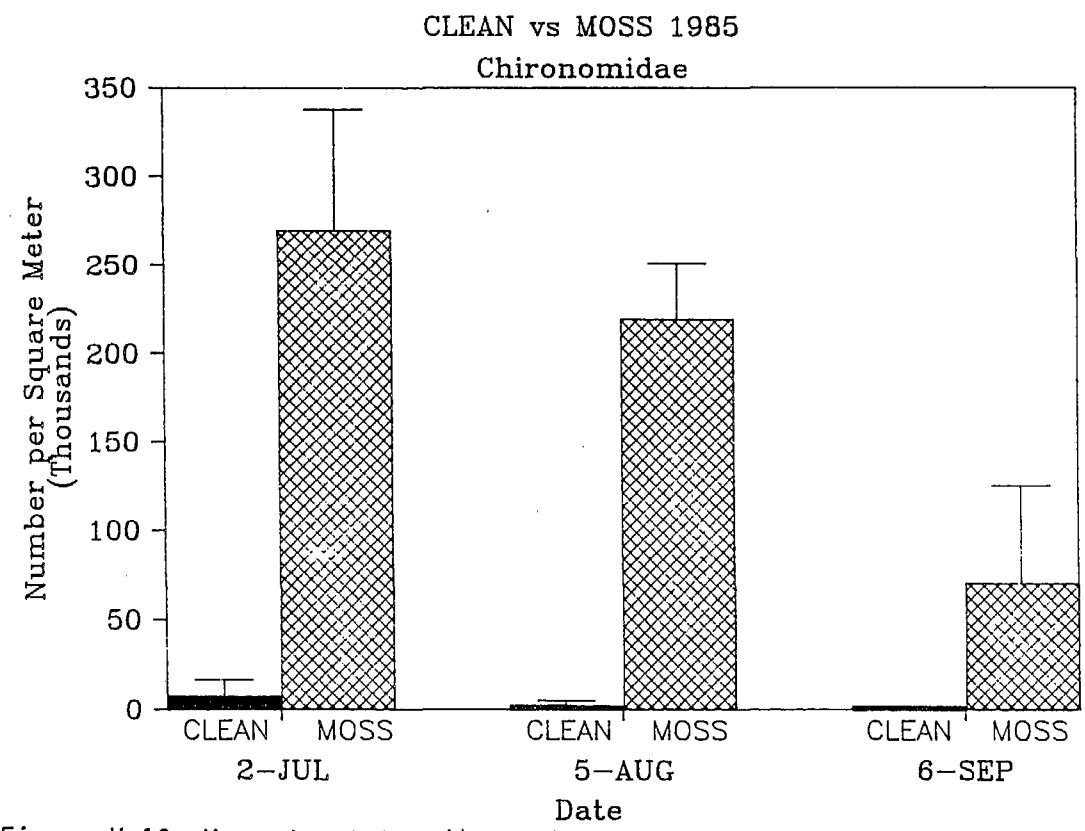
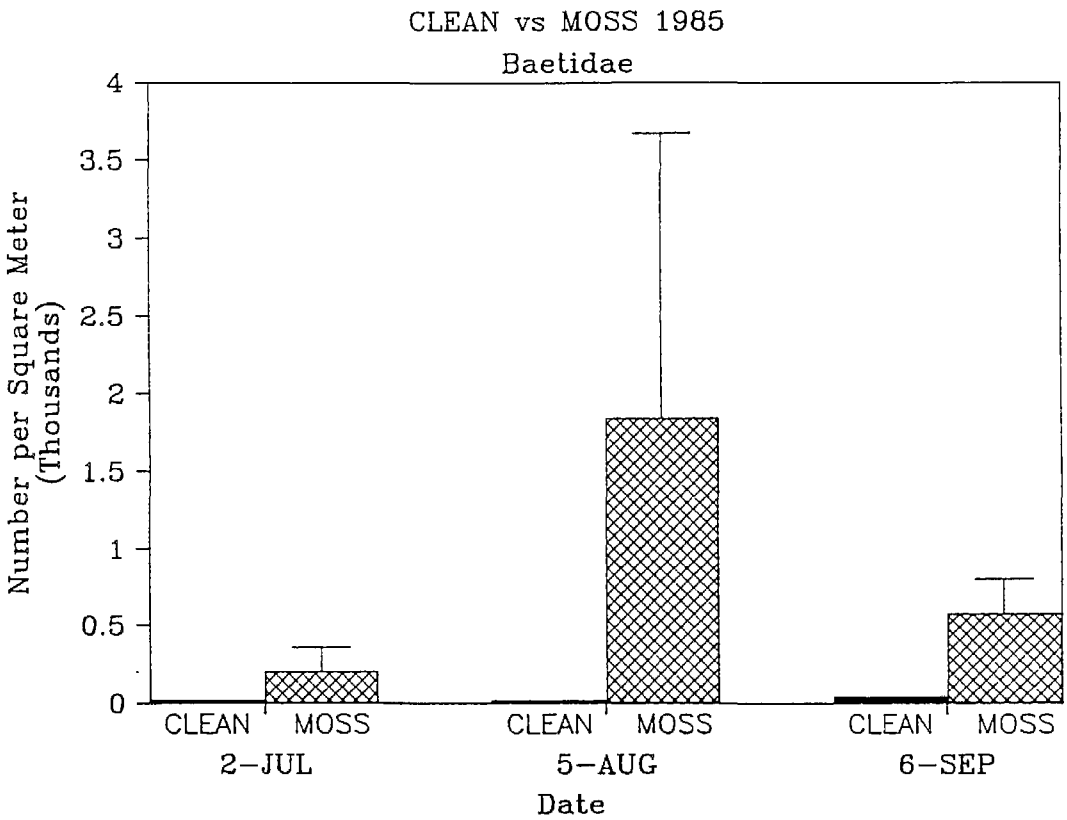


Figure V-13. Mean densities (± 1 SE) of common benthic macroinvertebrates on hard substrates lacking plant cover (clean) vs. hard substrates covered by moss or macroalgae (moss) in the Emerald Lake outlet on three dates in 1985.



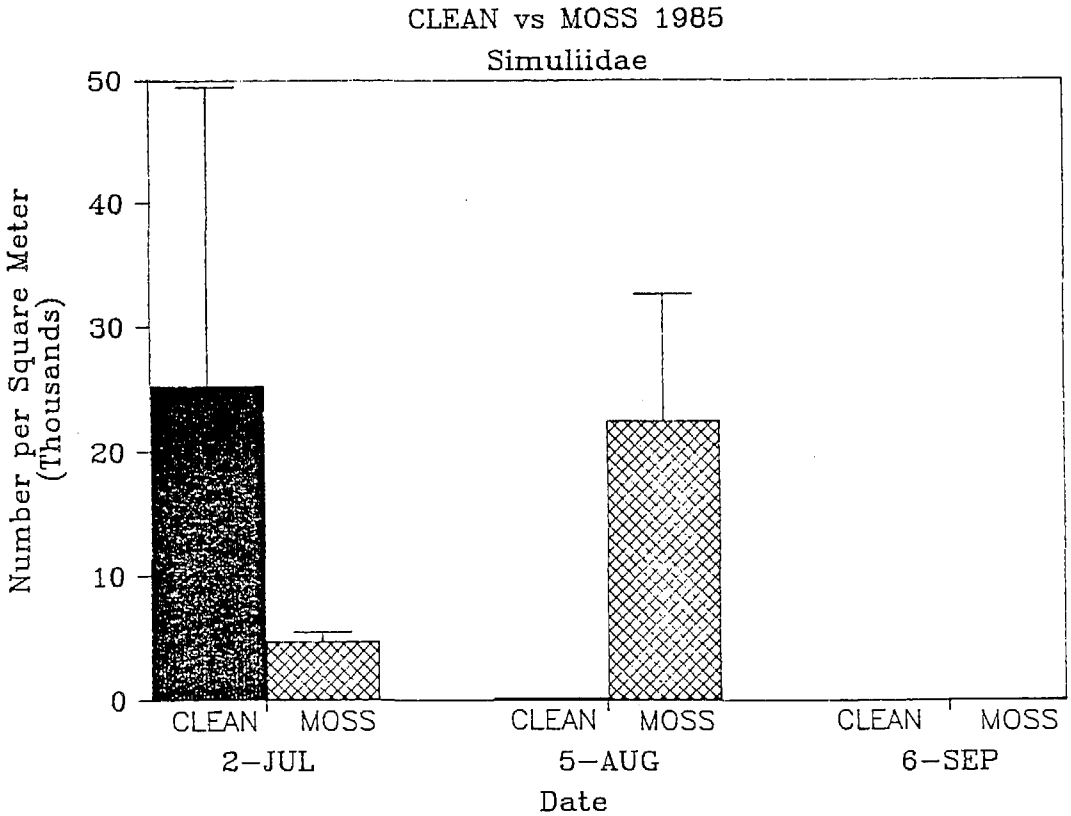
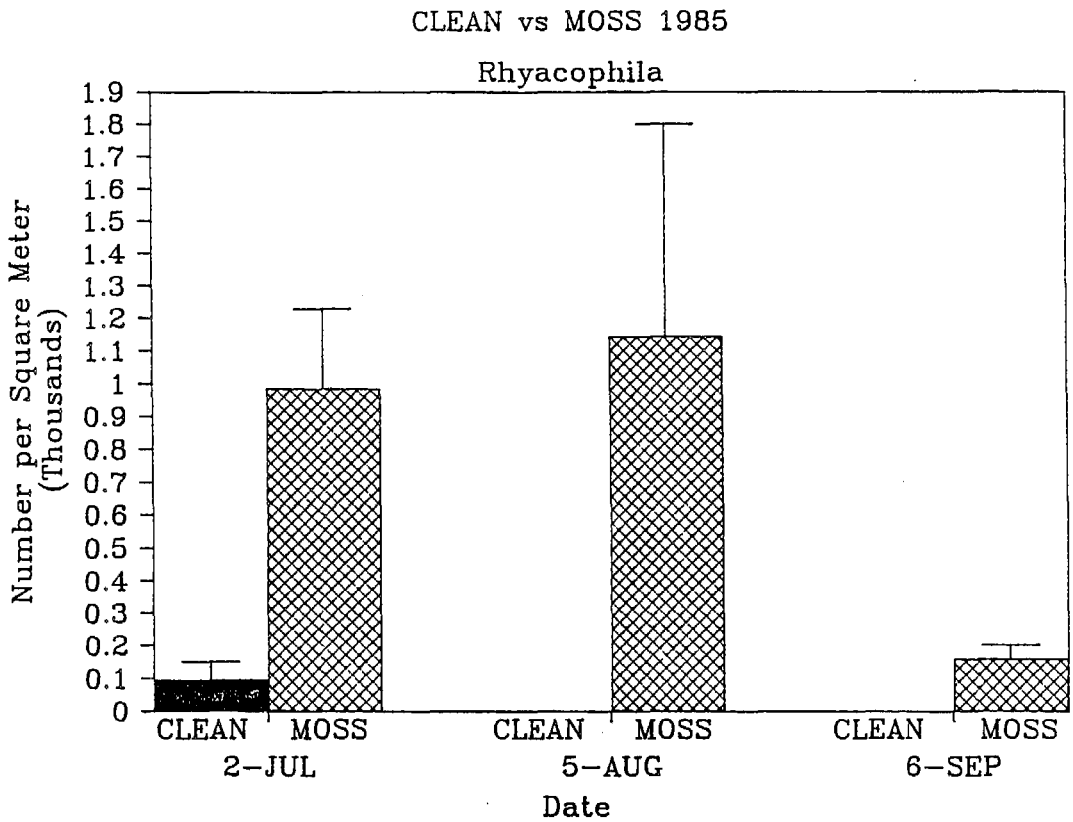


Figure V-13. (continued).



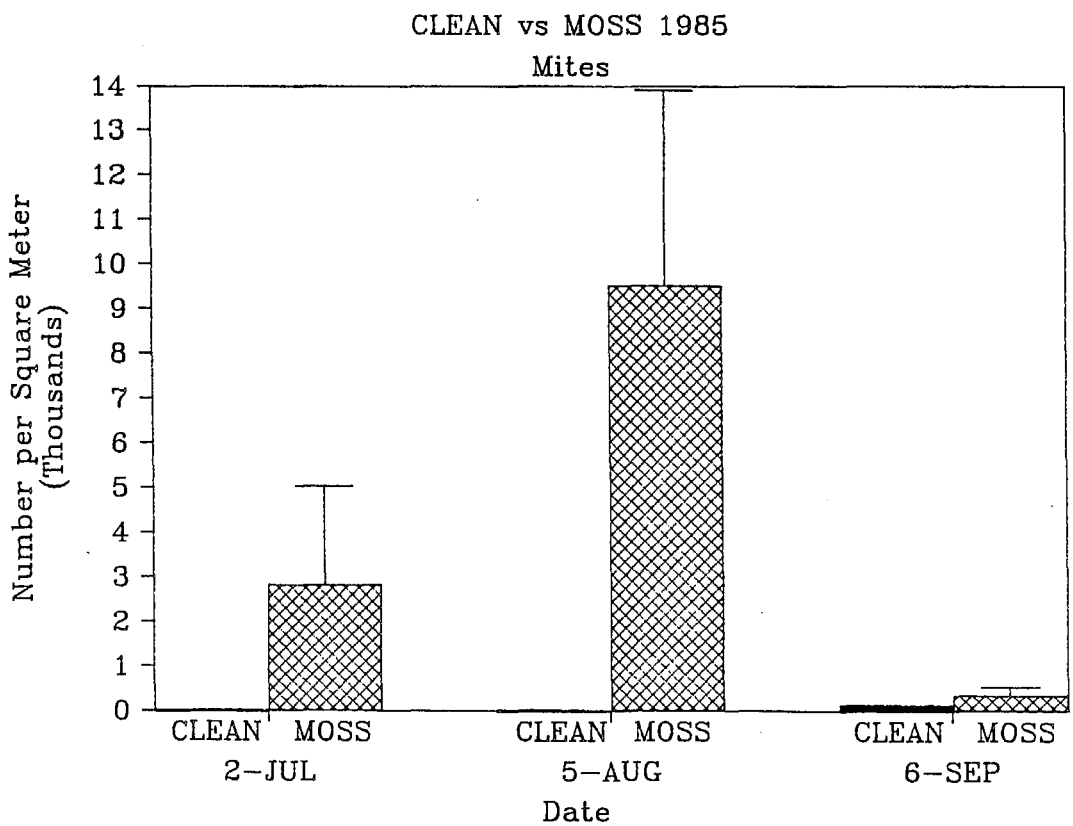


Figure V-13. (continued).

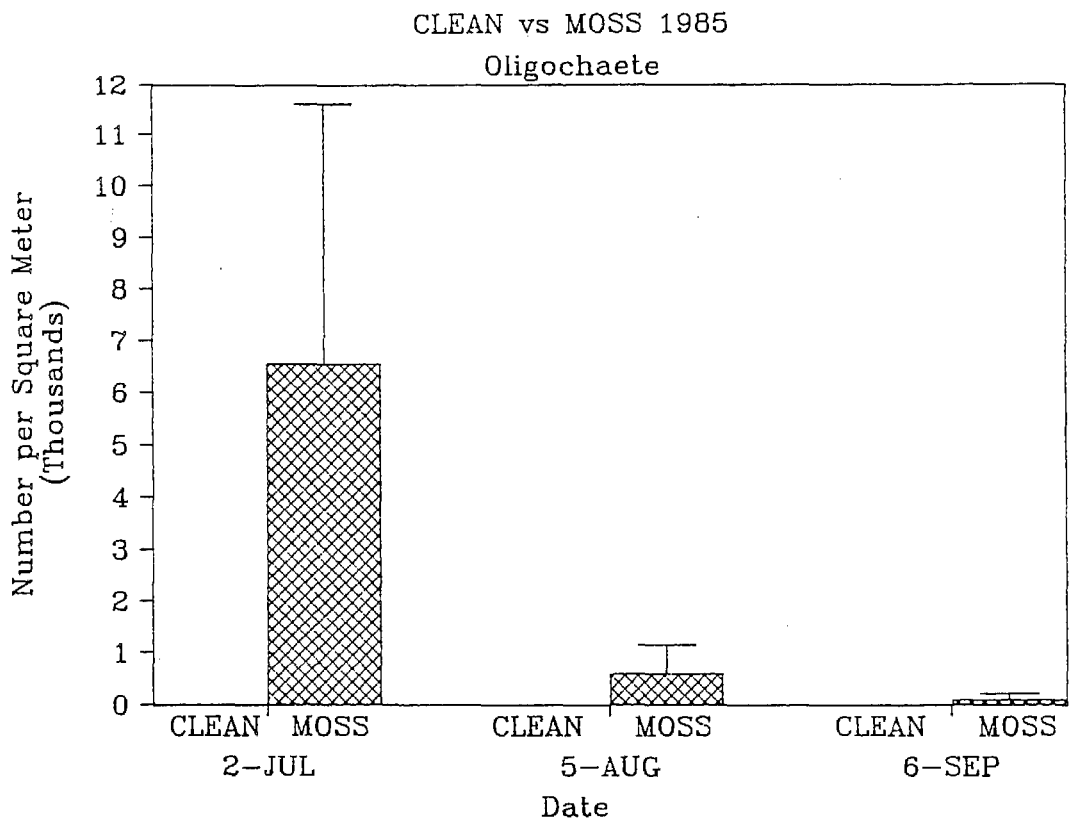
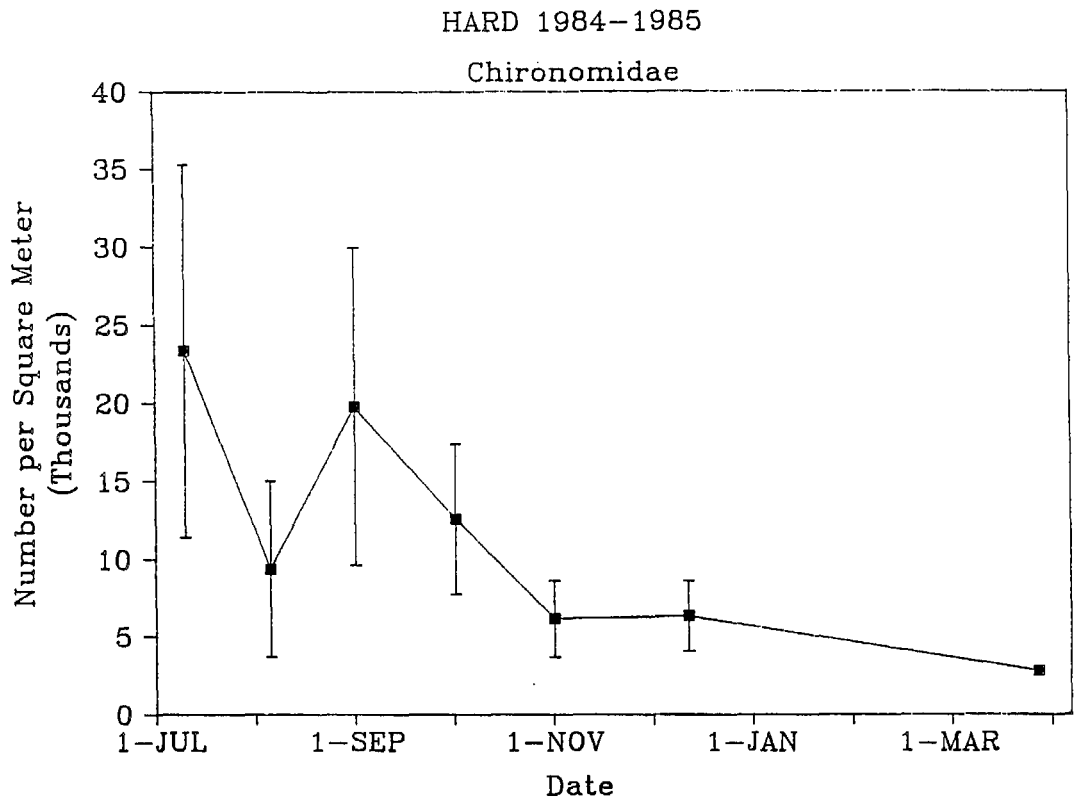


Figure V-13. (continued).



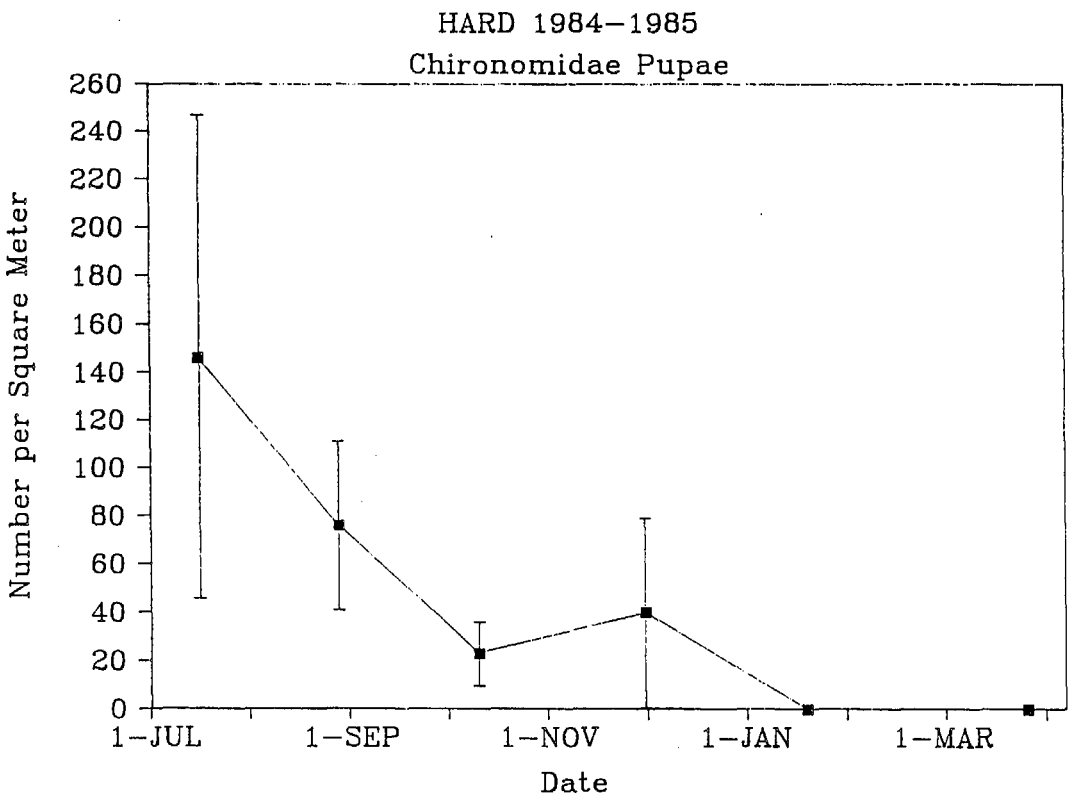
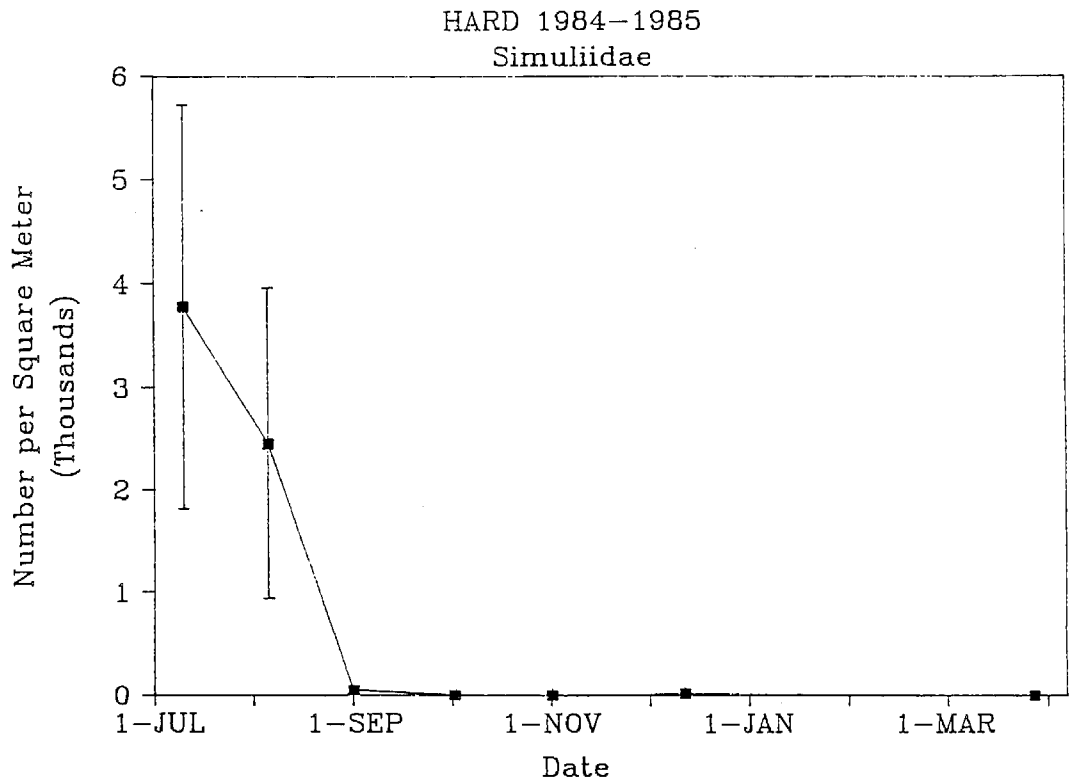


Figure V-14. Mean densities (± 1 SE) of common benthic macroinvertebrates on hard substrates in the Emerald Lake outlet in summer and autumn of 1984.



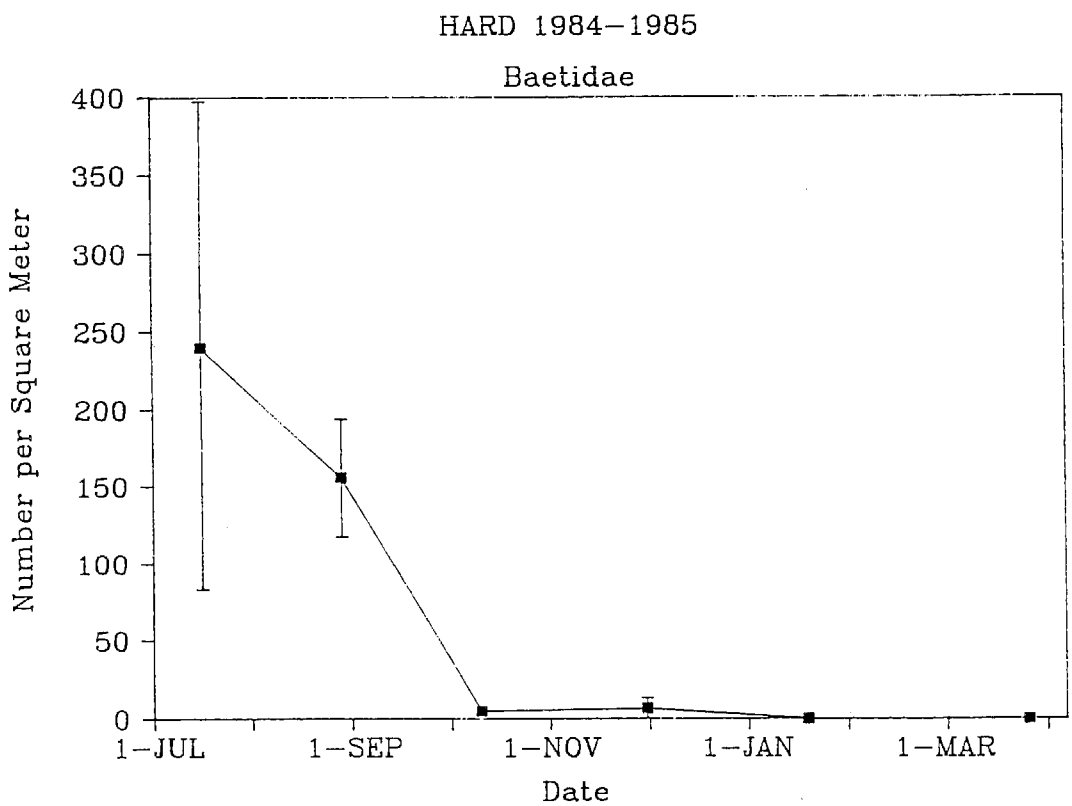
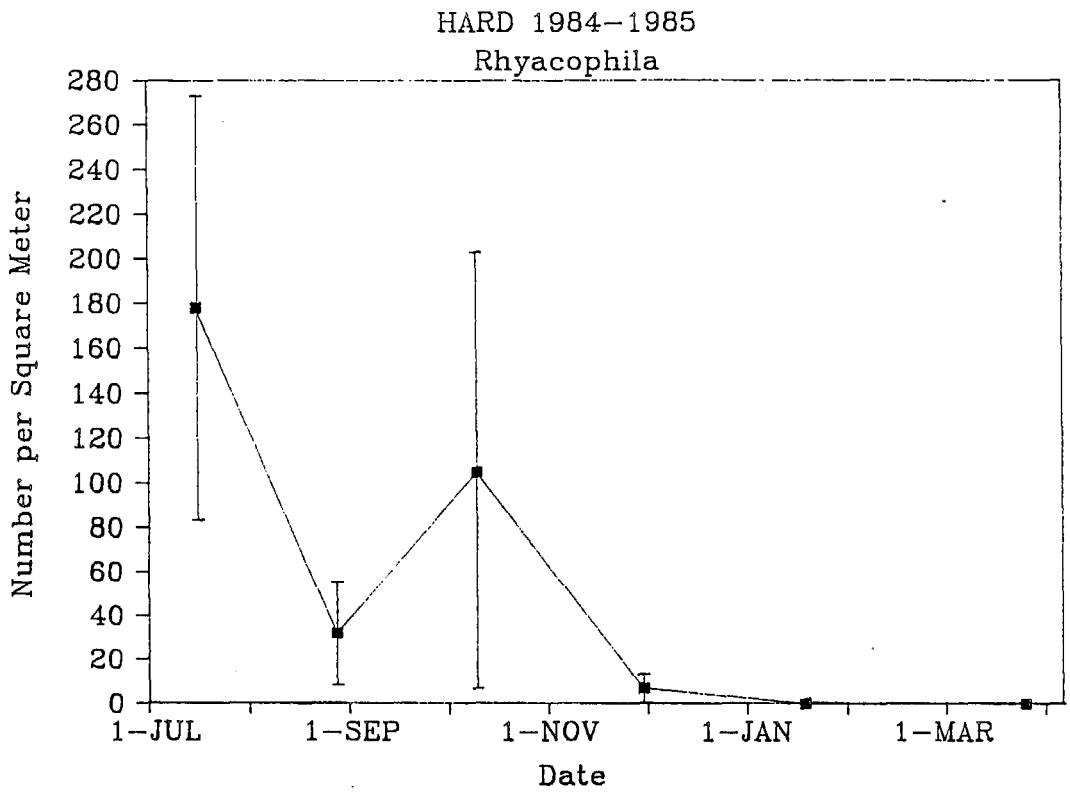


Figure V-14. (continued).



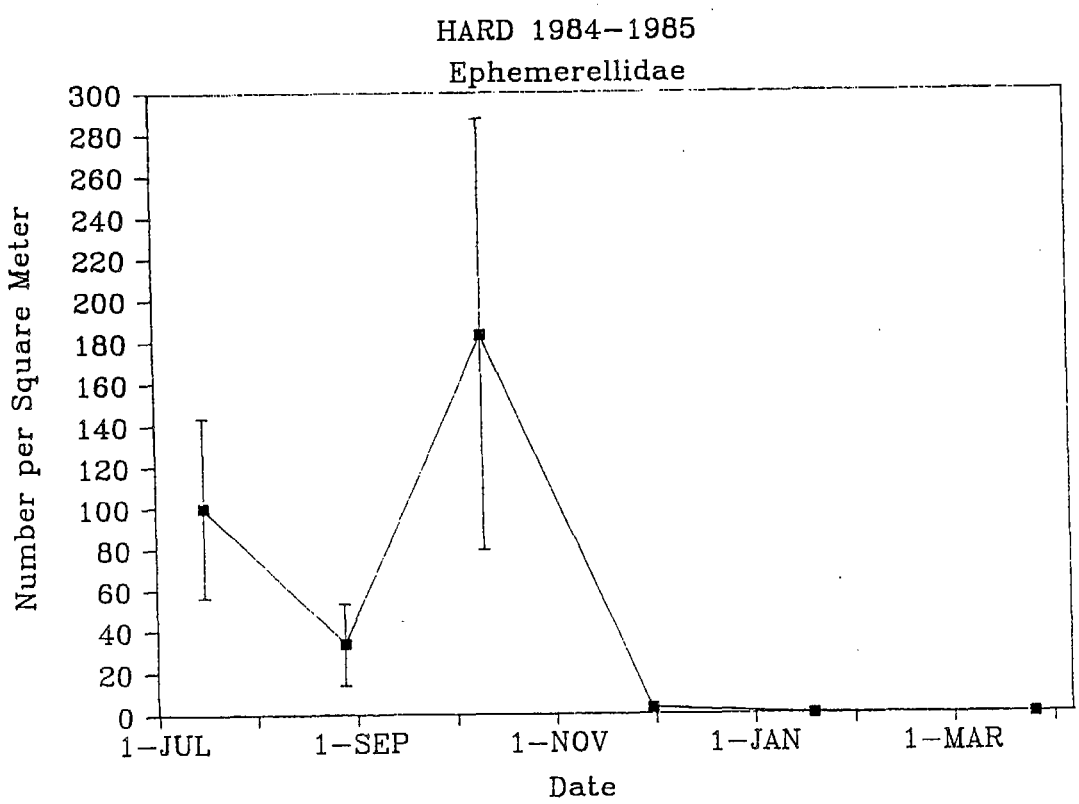
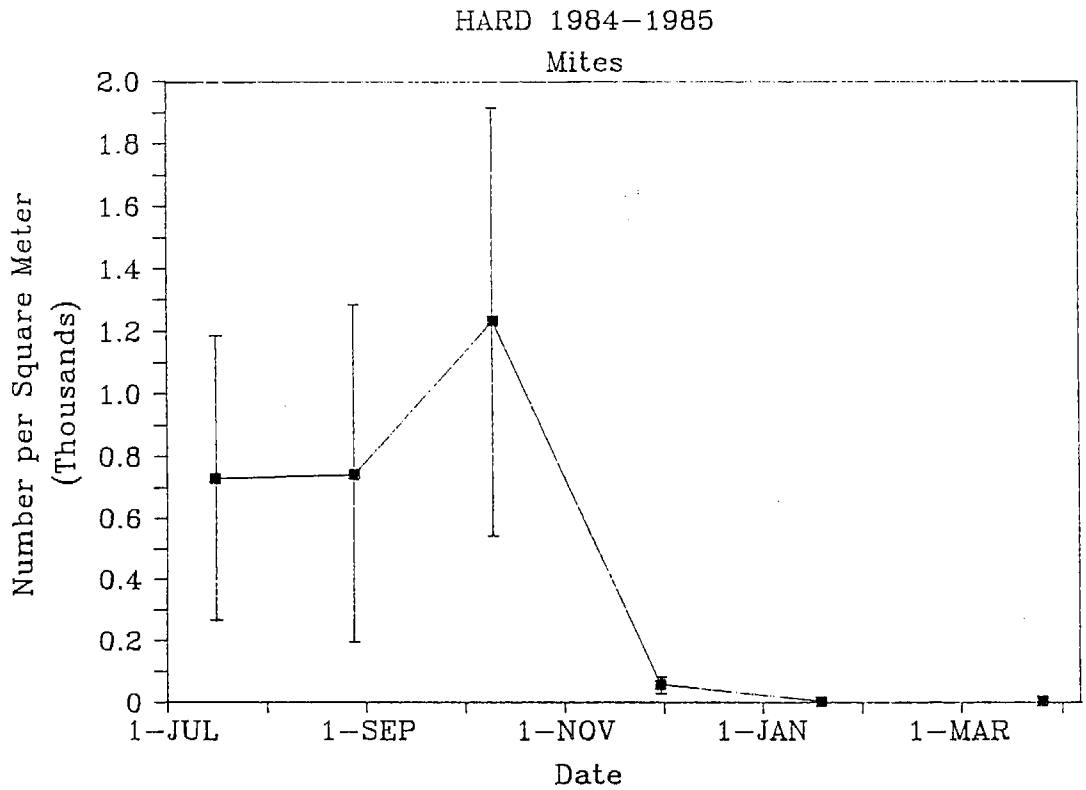


Figure V-14. (continued).



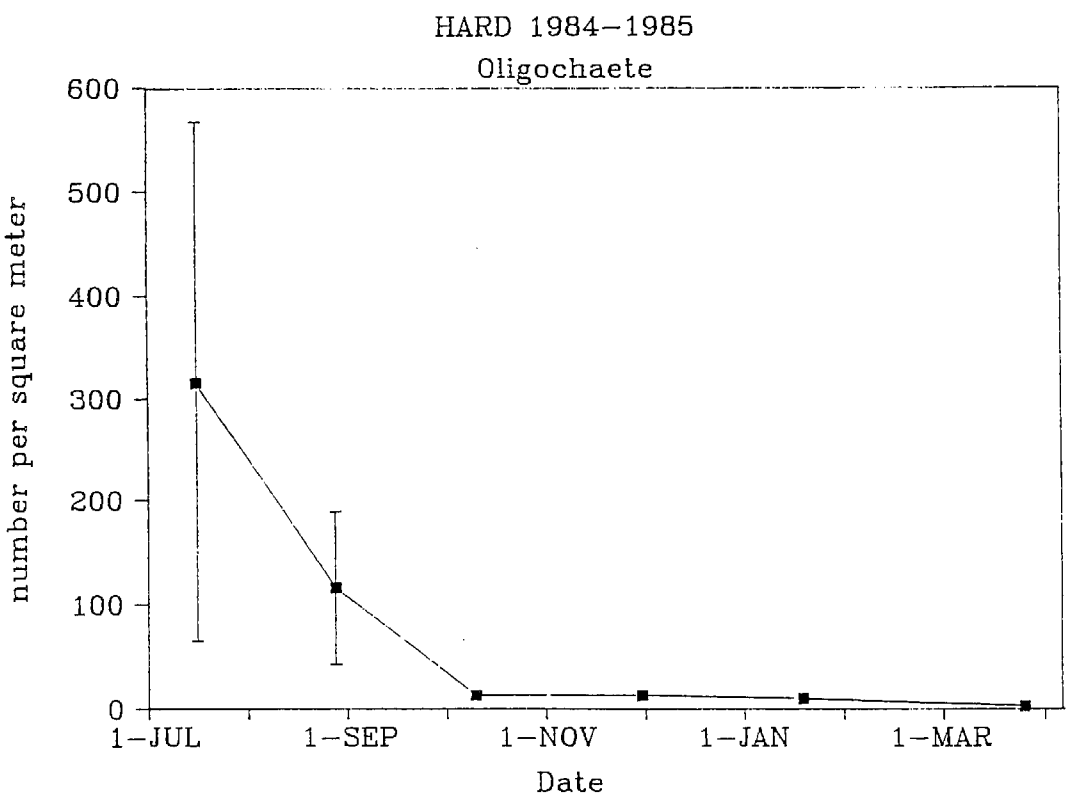
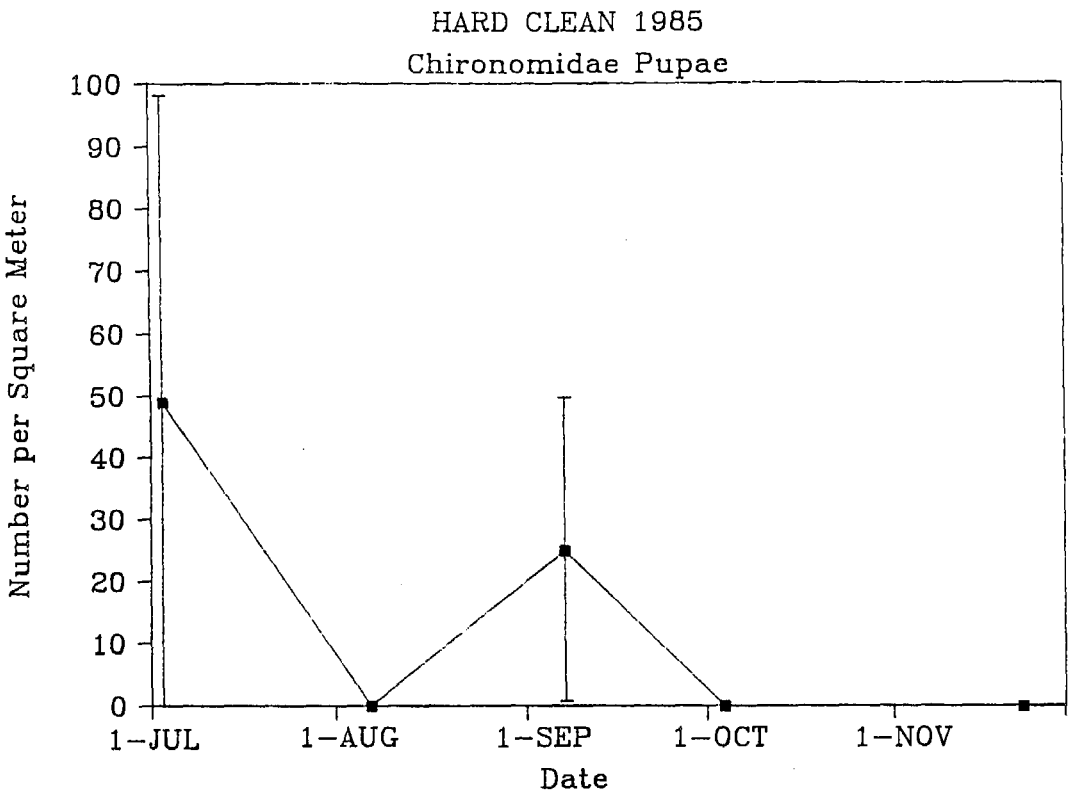


Figure V-14. (continued).



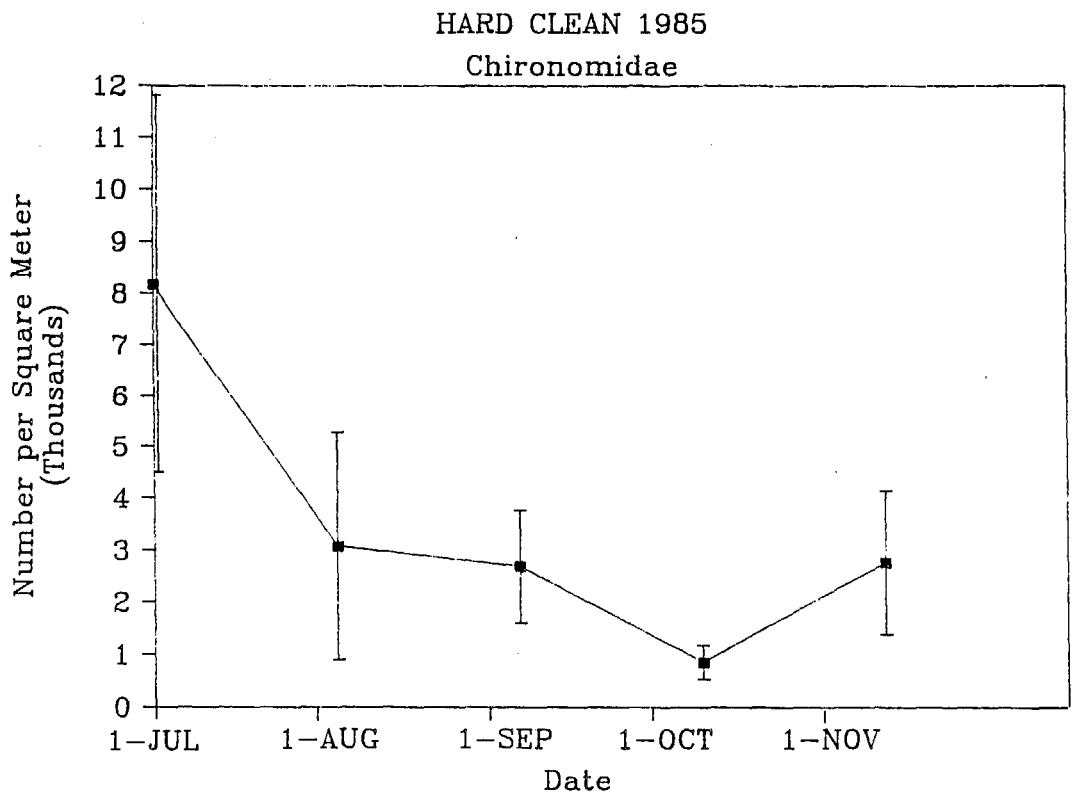
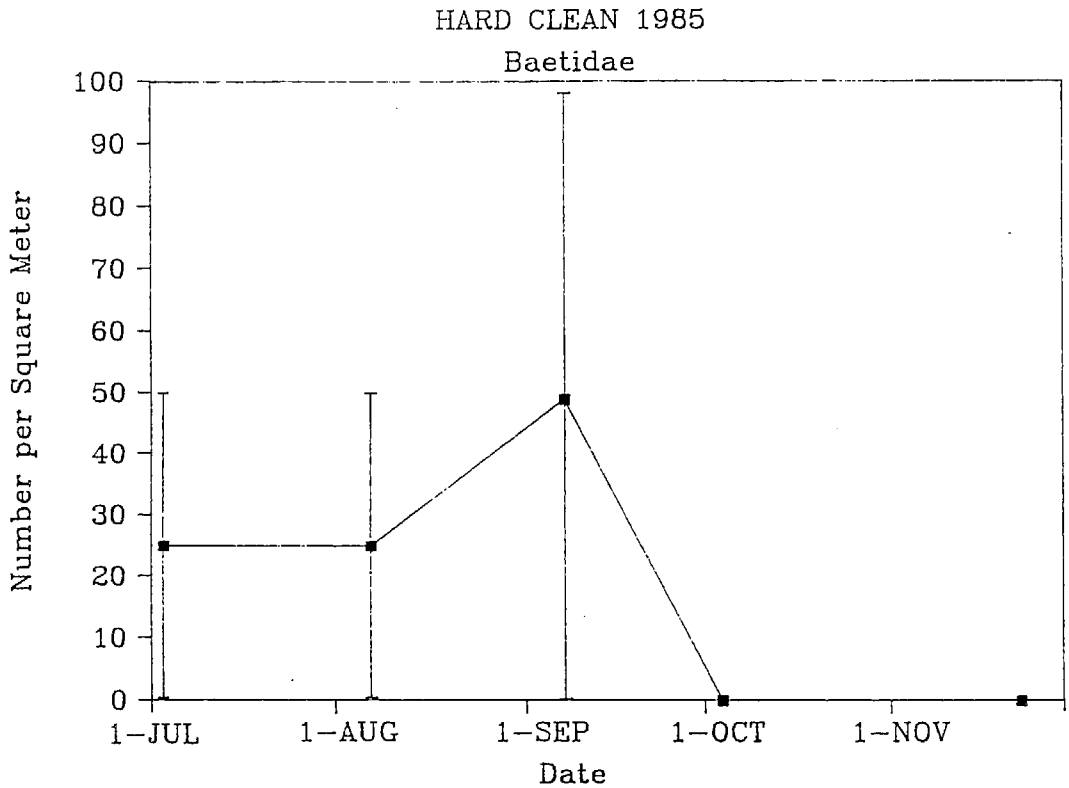


Figure V-15. Mean densities (± 1 SE) of common benthic macroinvertebrates on (clean) hard substrates in the Emerald Lake outlet in summer and autumn of 1985.



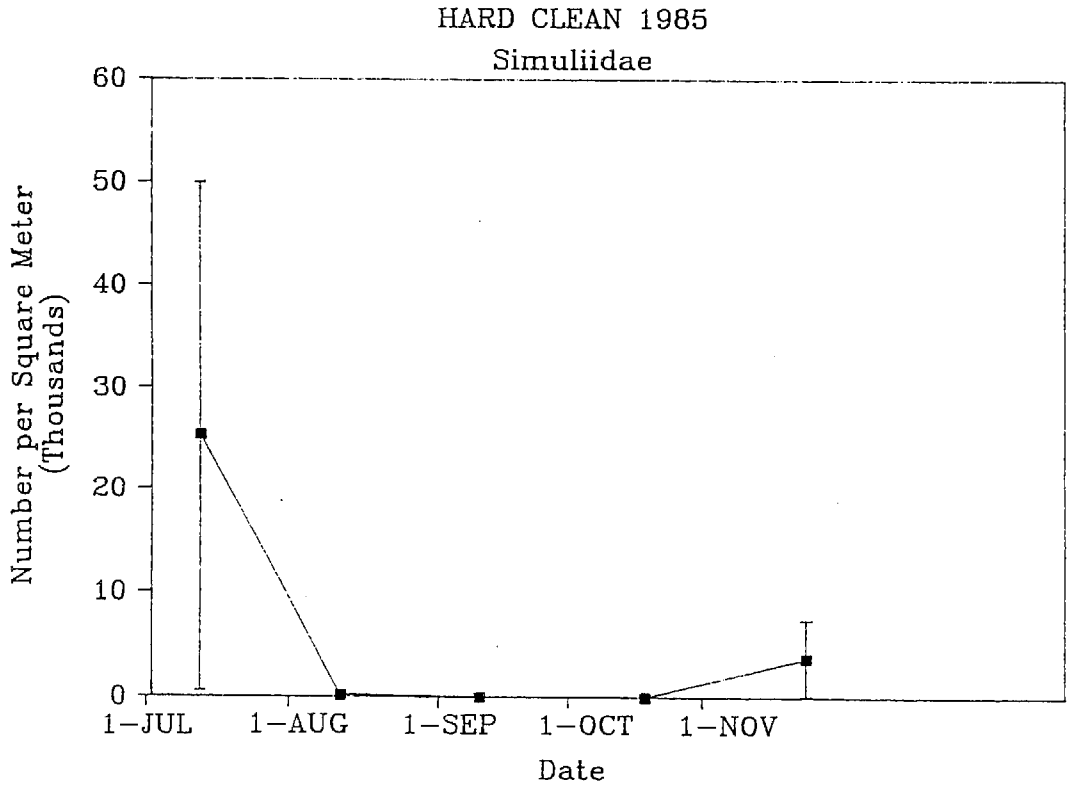
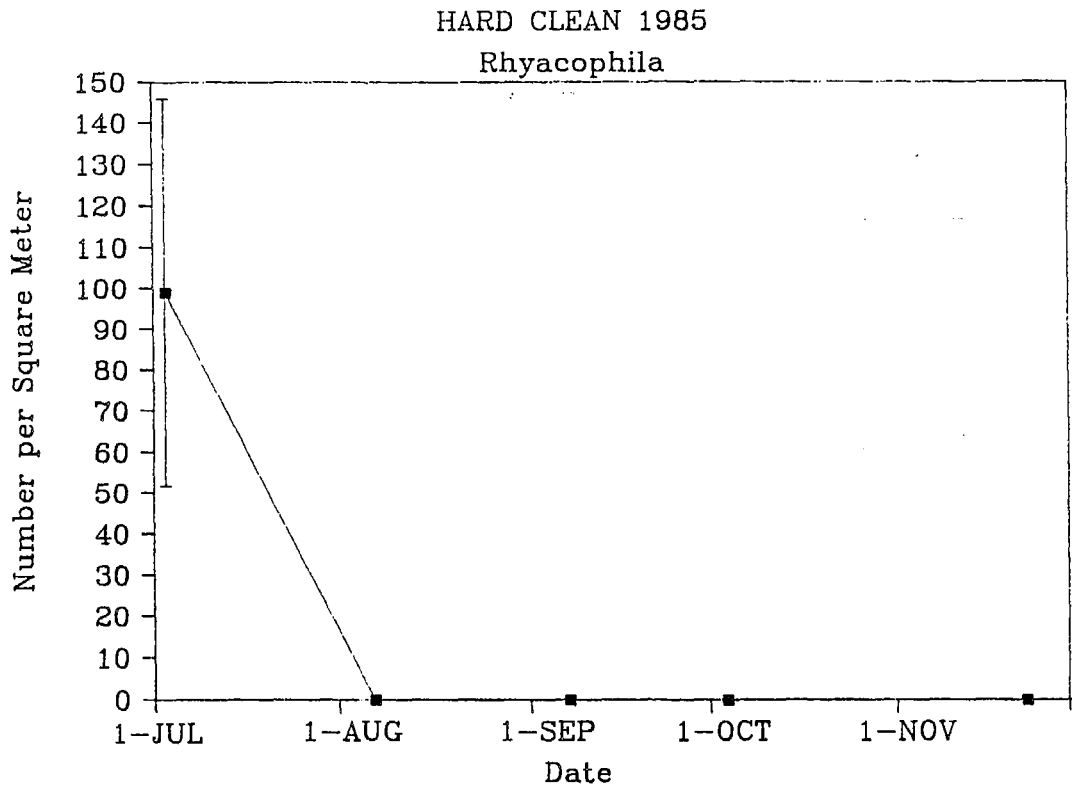


Figure V-15. (continued).



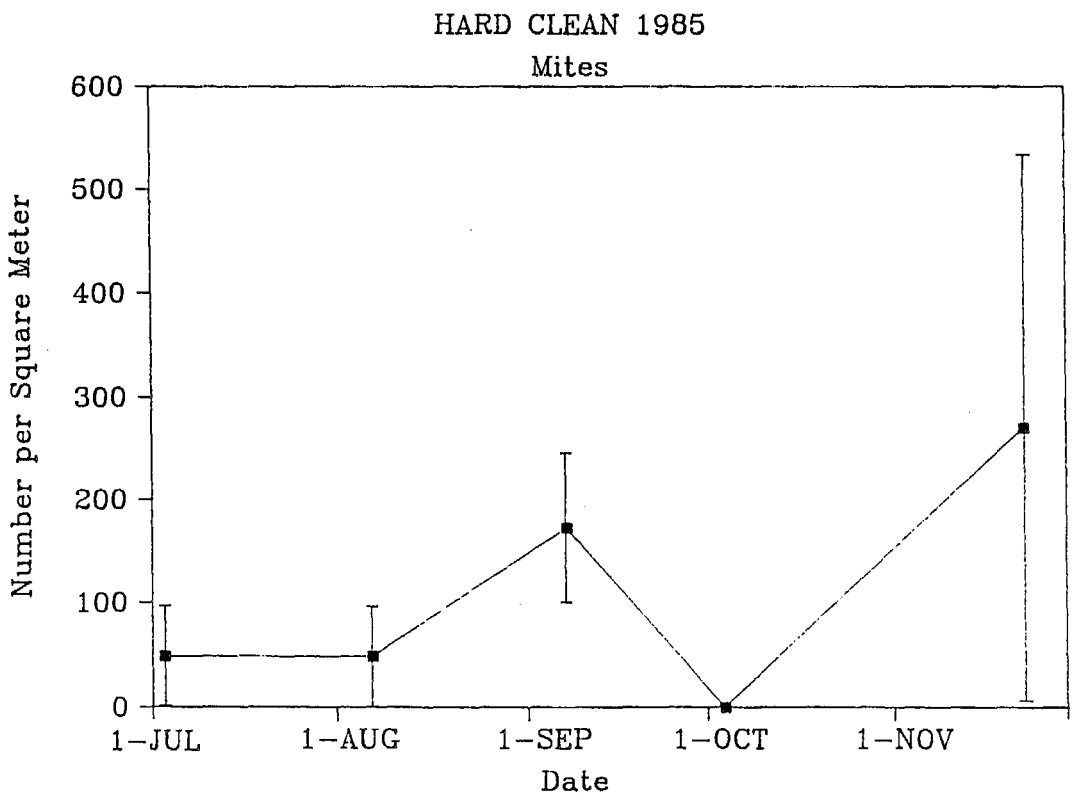


Figure V-15. (continued).

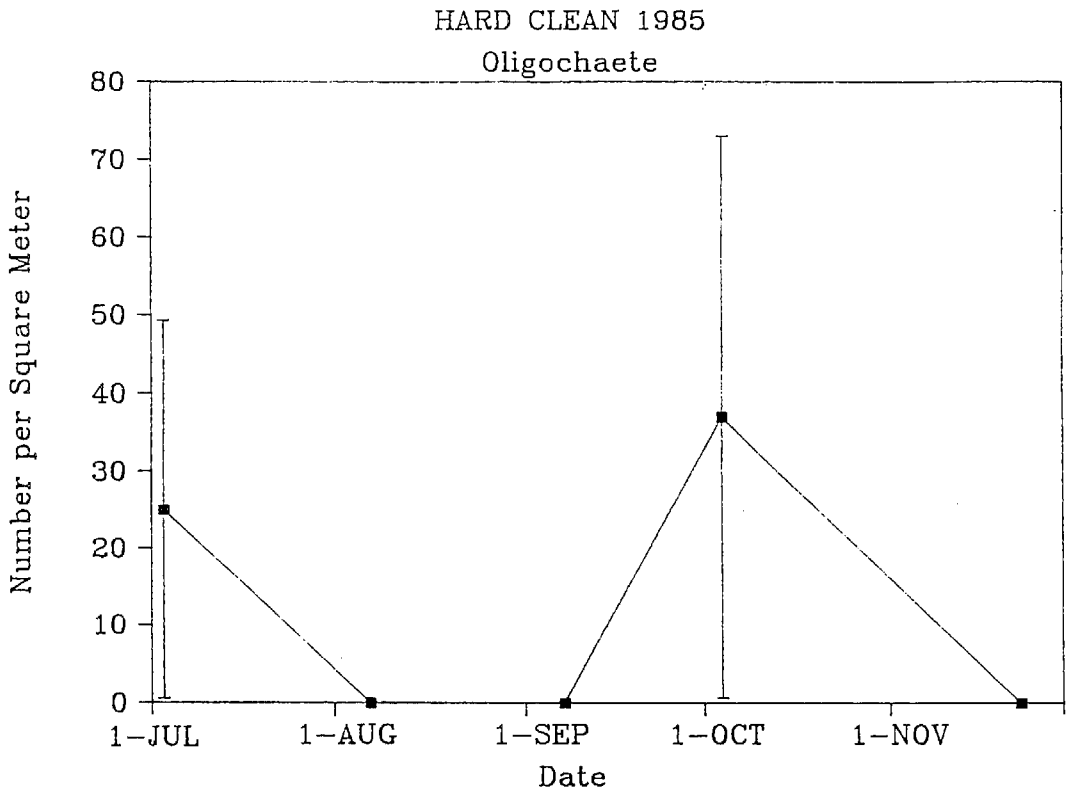
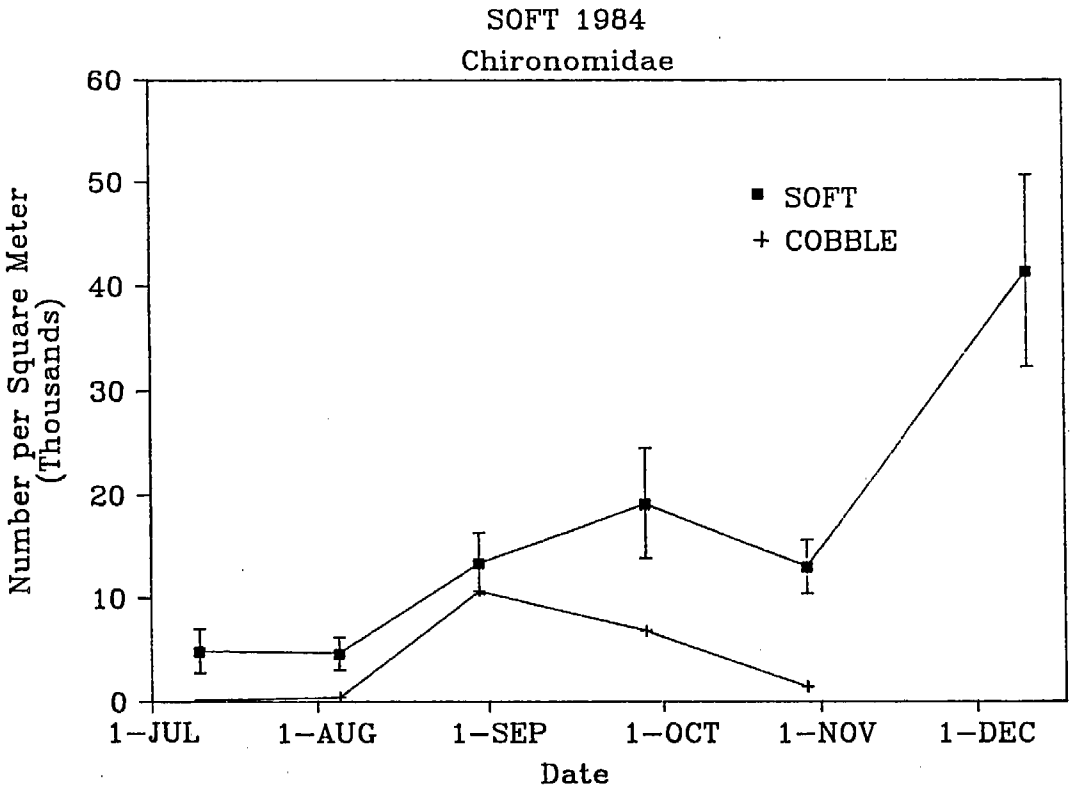


Figure V-15. (continued).



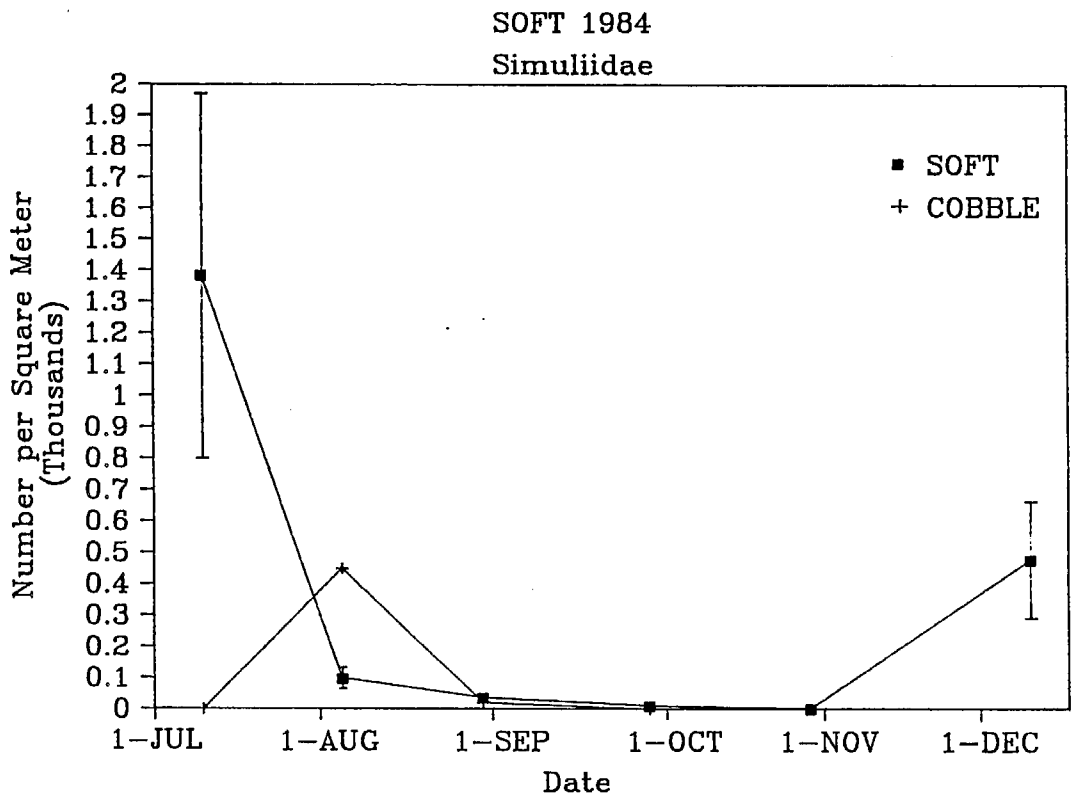
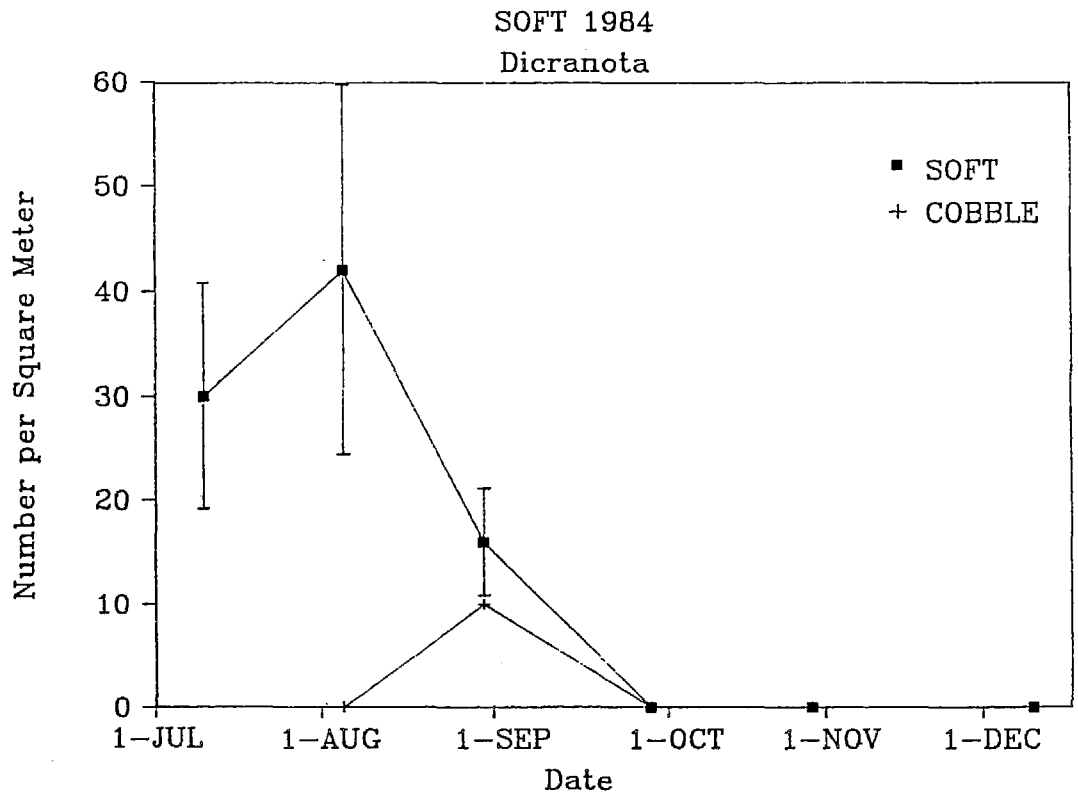


Figure V-16. Densities of common benthic macroinvertebrates on soft and cobble substrates in the Emerald Lake outlet in the summer and autumn of 1984. Values for soft substrates are Xs ± 1 SE, whereas values for cobble are a density estimate from one sample on each date.



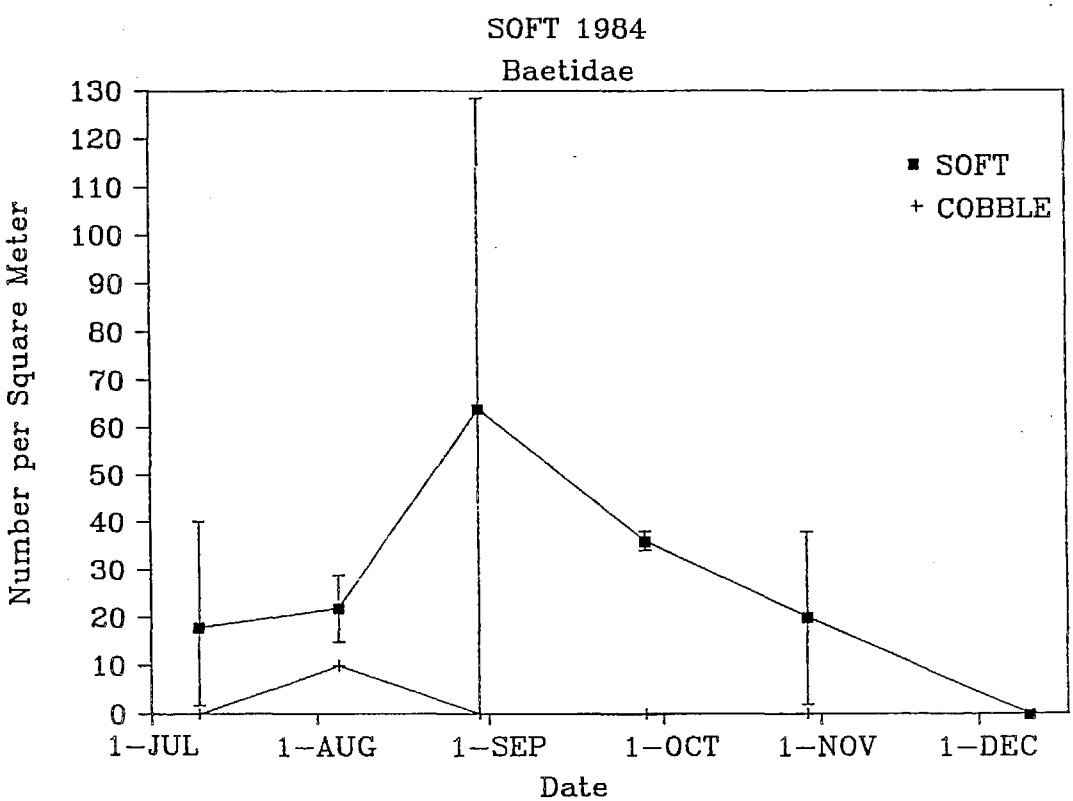
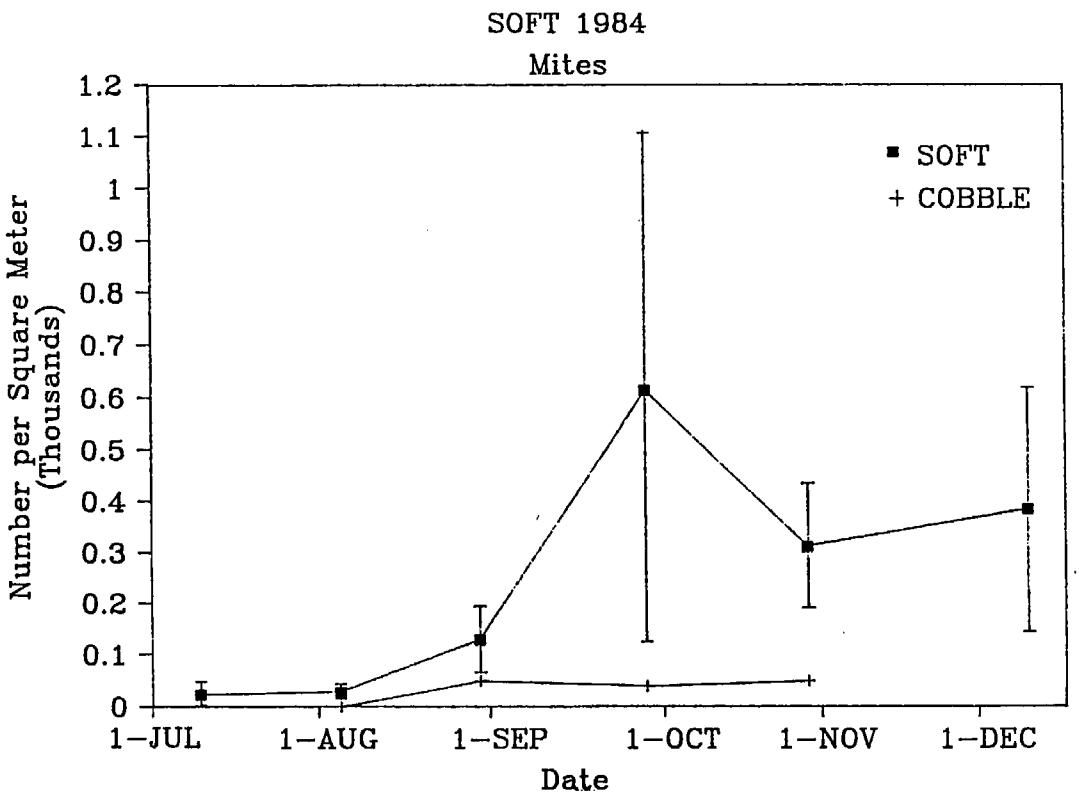


Figure V-16. (continued).



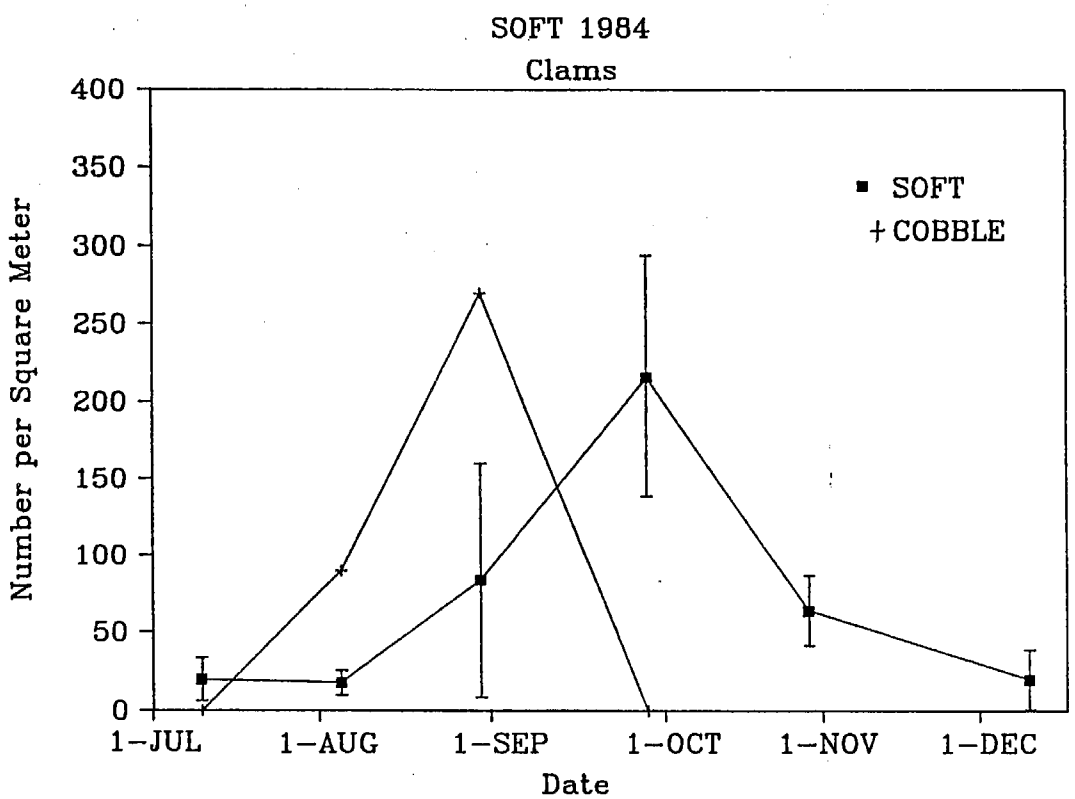
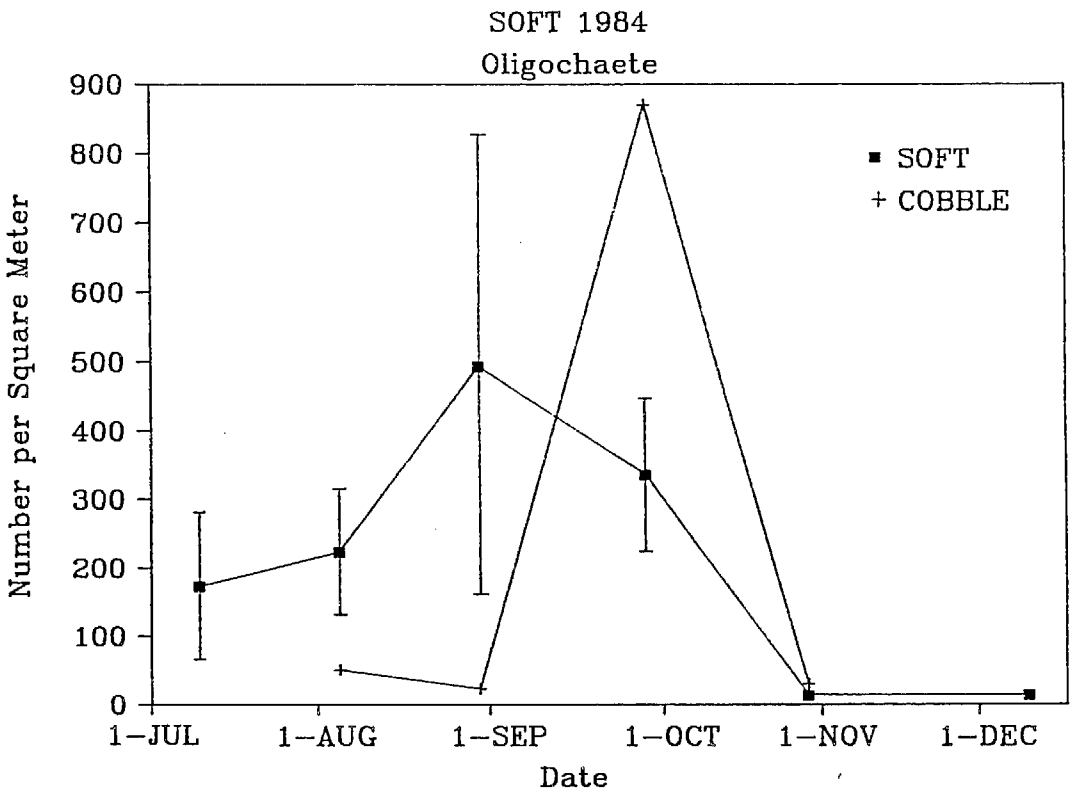


Figure V-16. (continued).



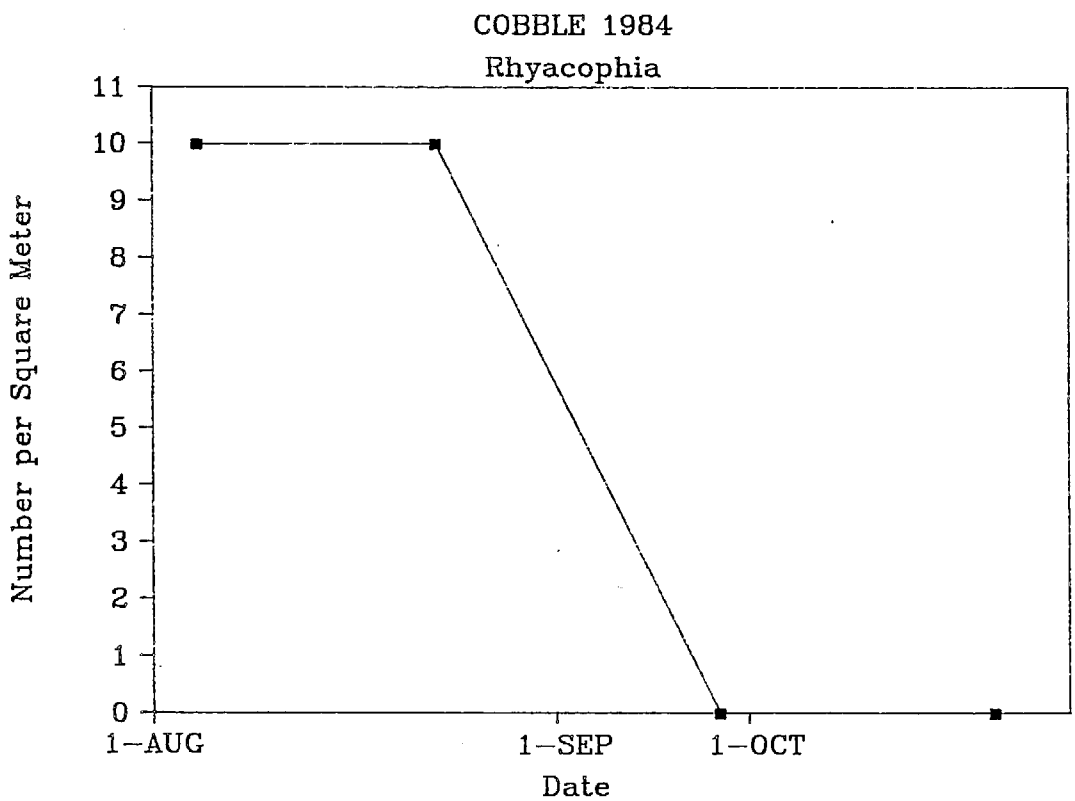
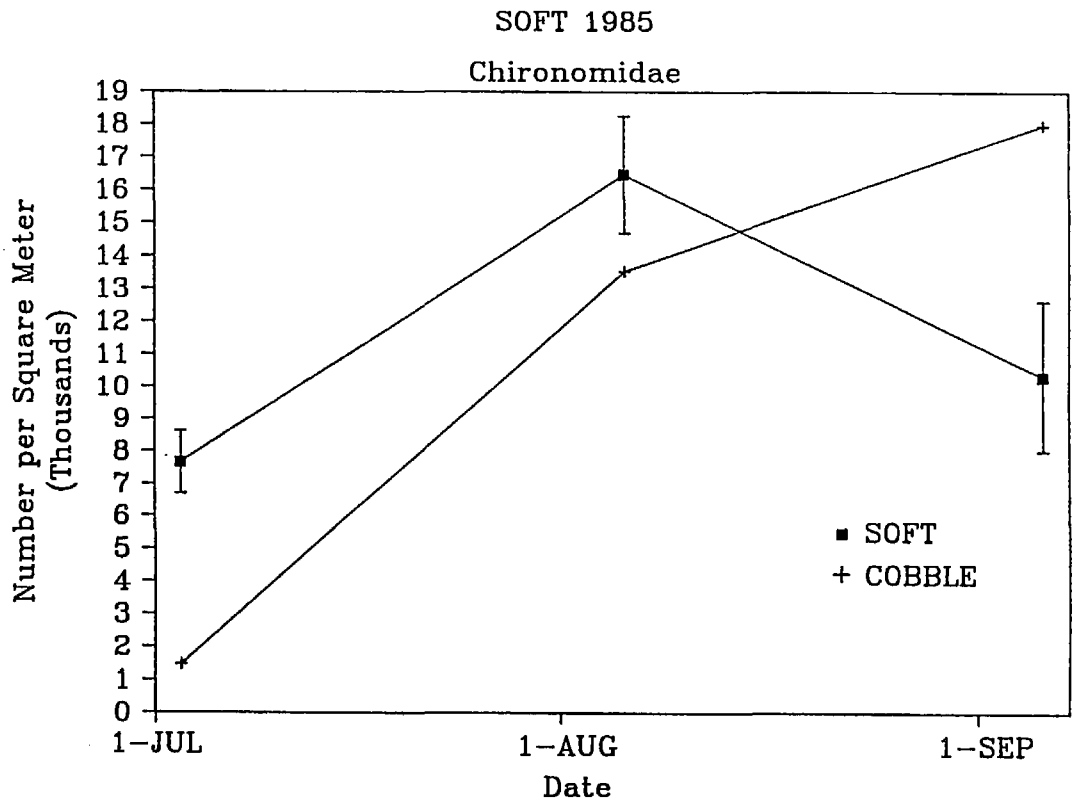


Figure V-16. (continued).



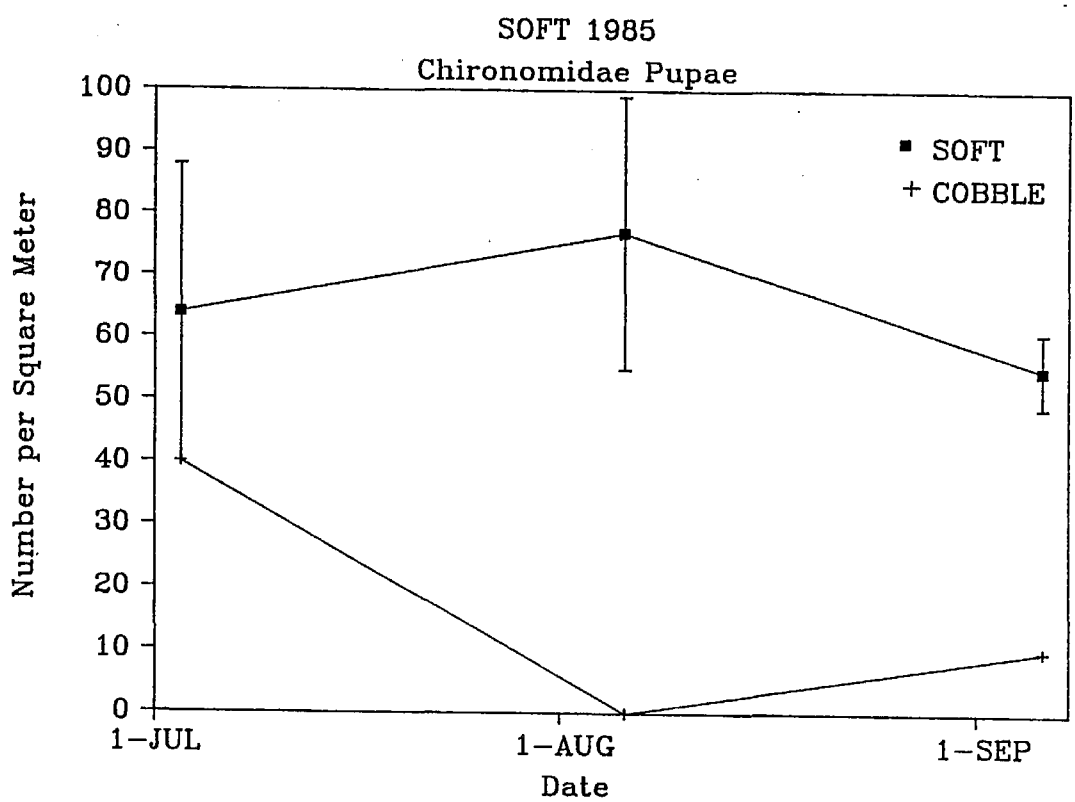
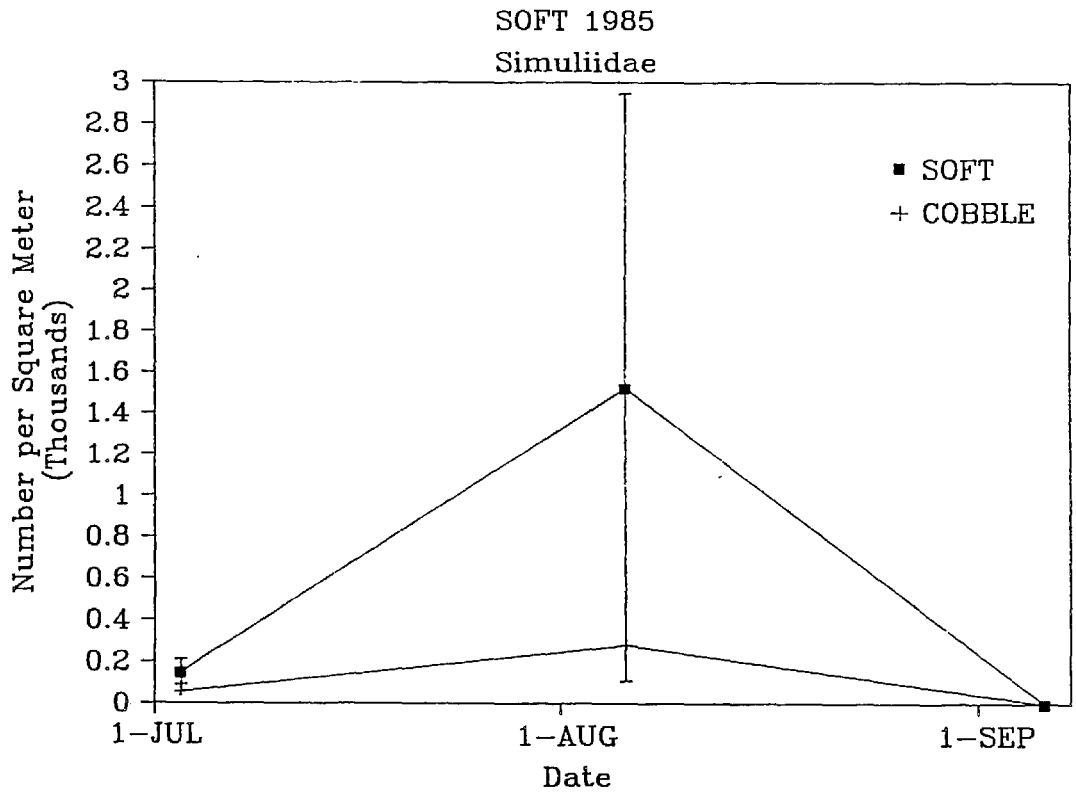


Figure V-17. Densities of common benthic macroinvertebrates on soft and cobble substrates in the Emerald Lake outlet in the summer and early autumn of 1985. Values as in Figure V-16.



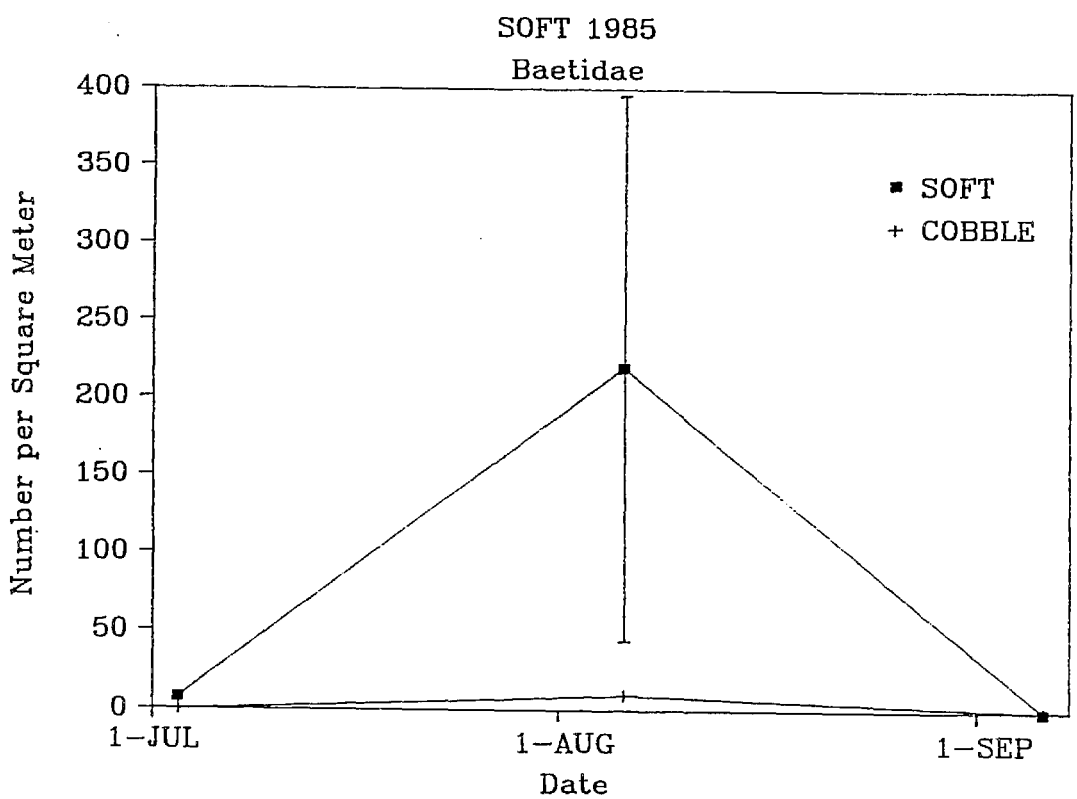
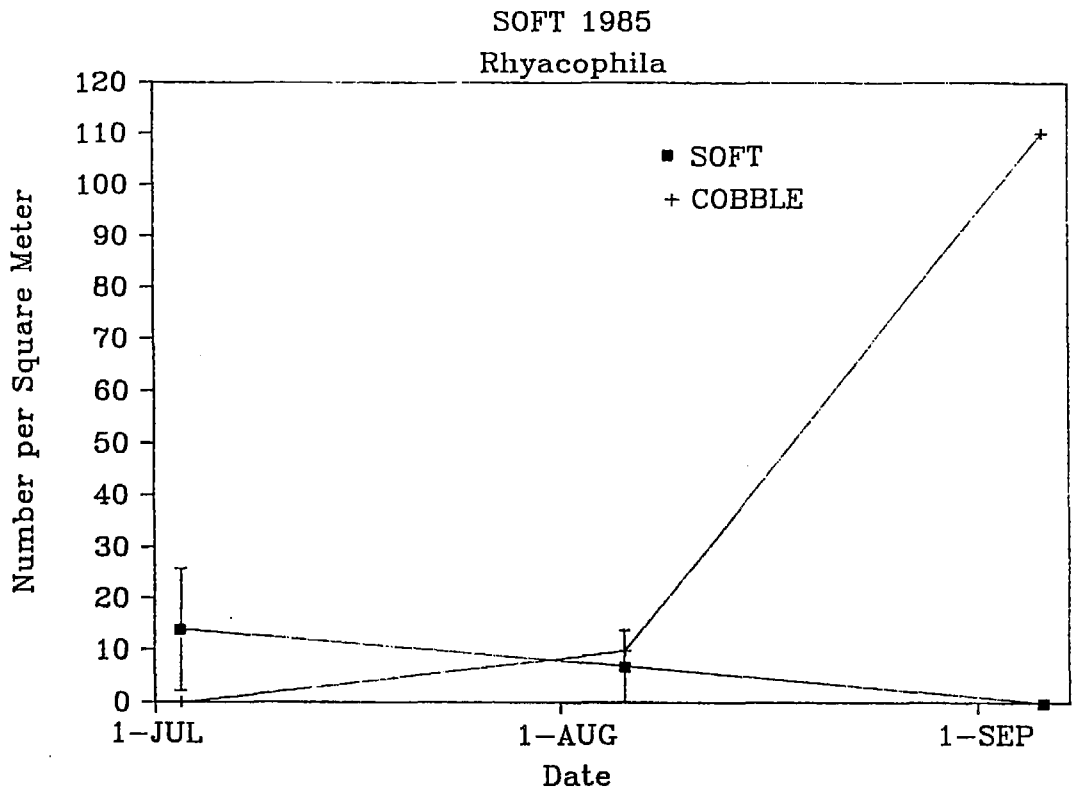


Figure V-17. (continued).



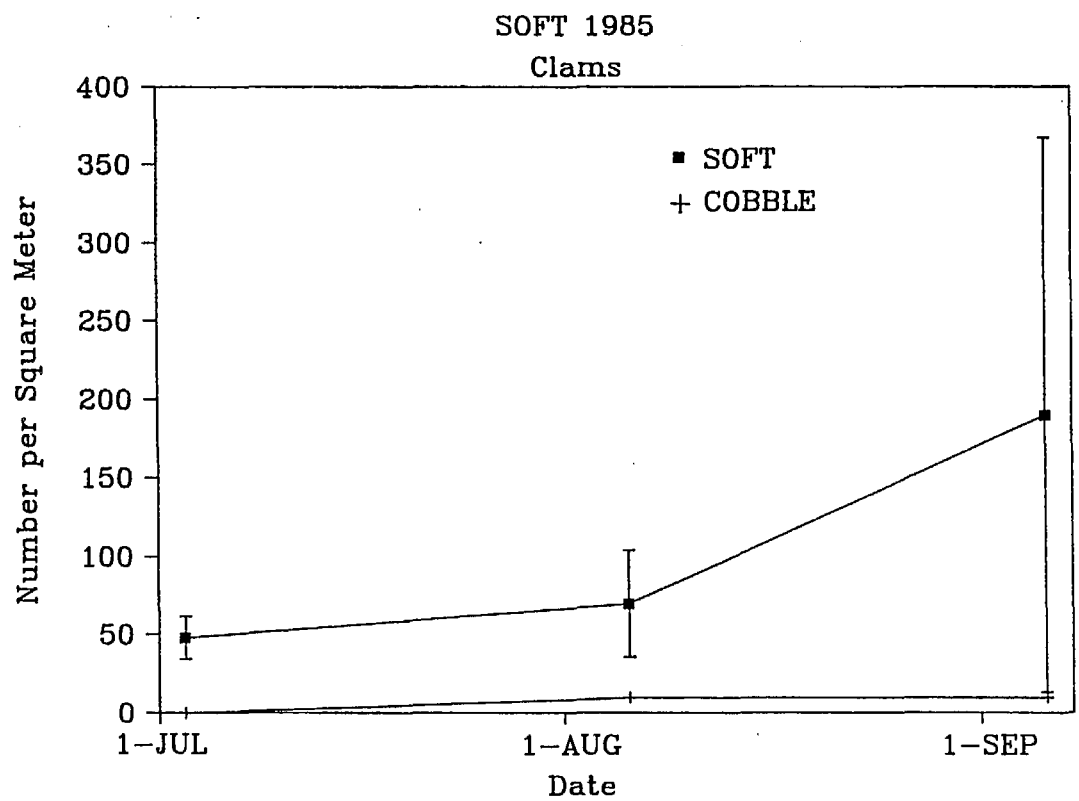
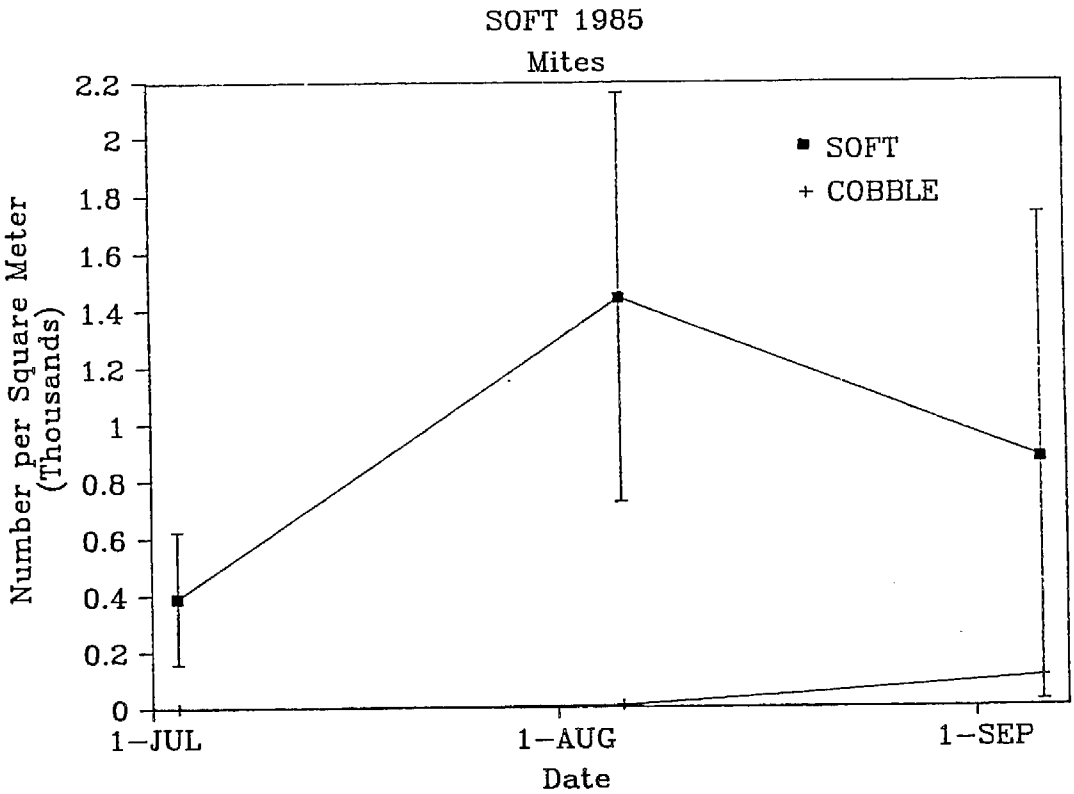


Figure V-17. (continued).



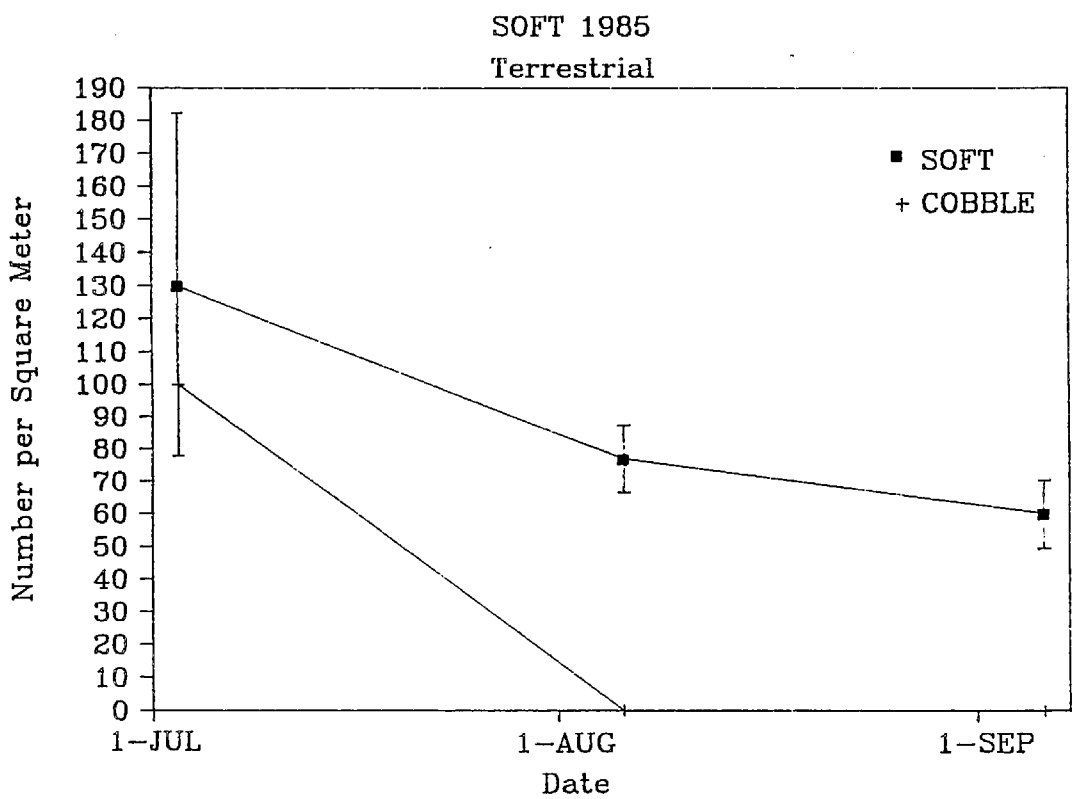
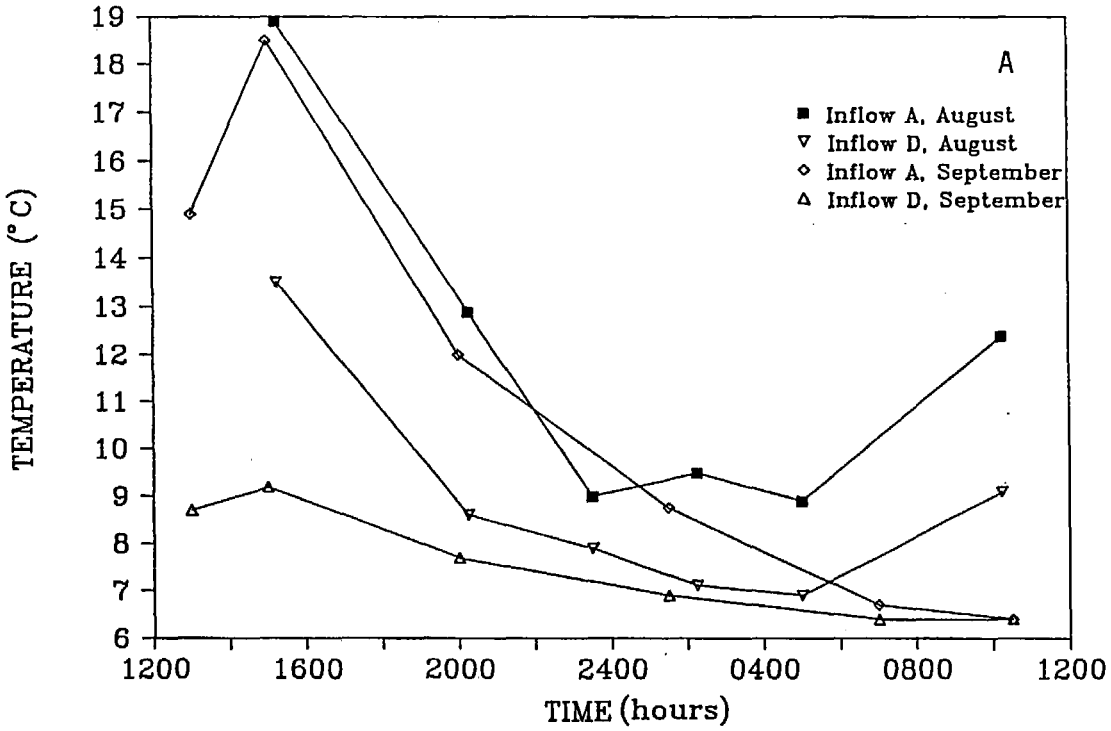


Figure V-17. (continued).



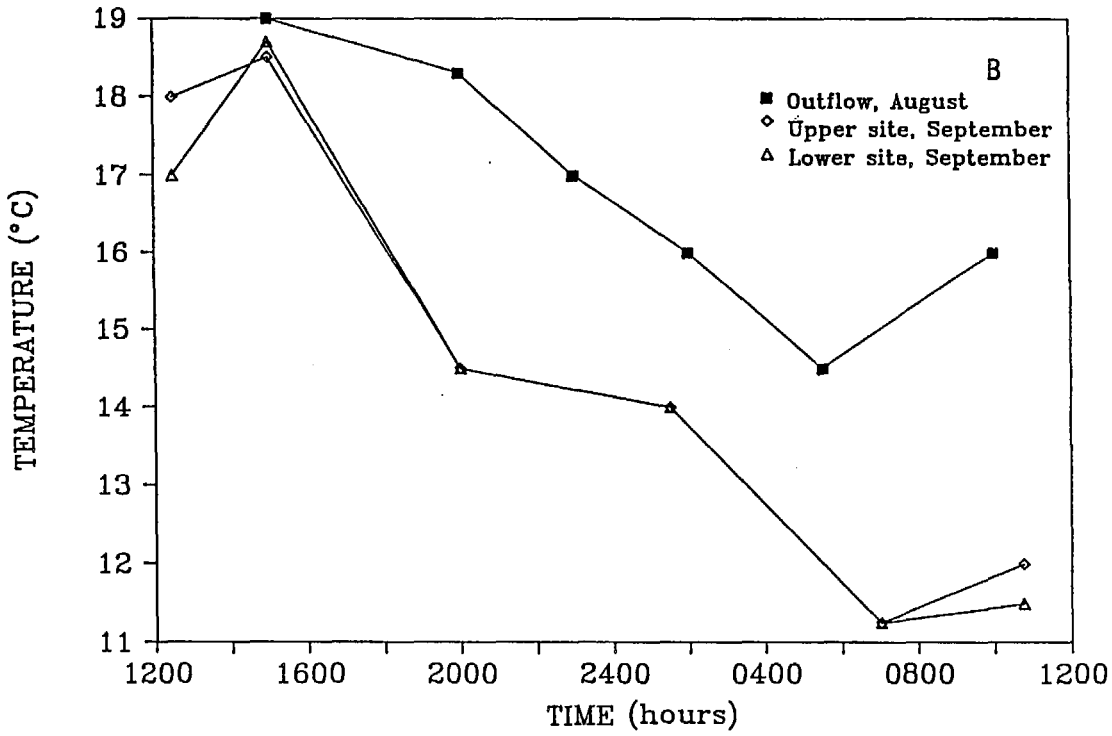
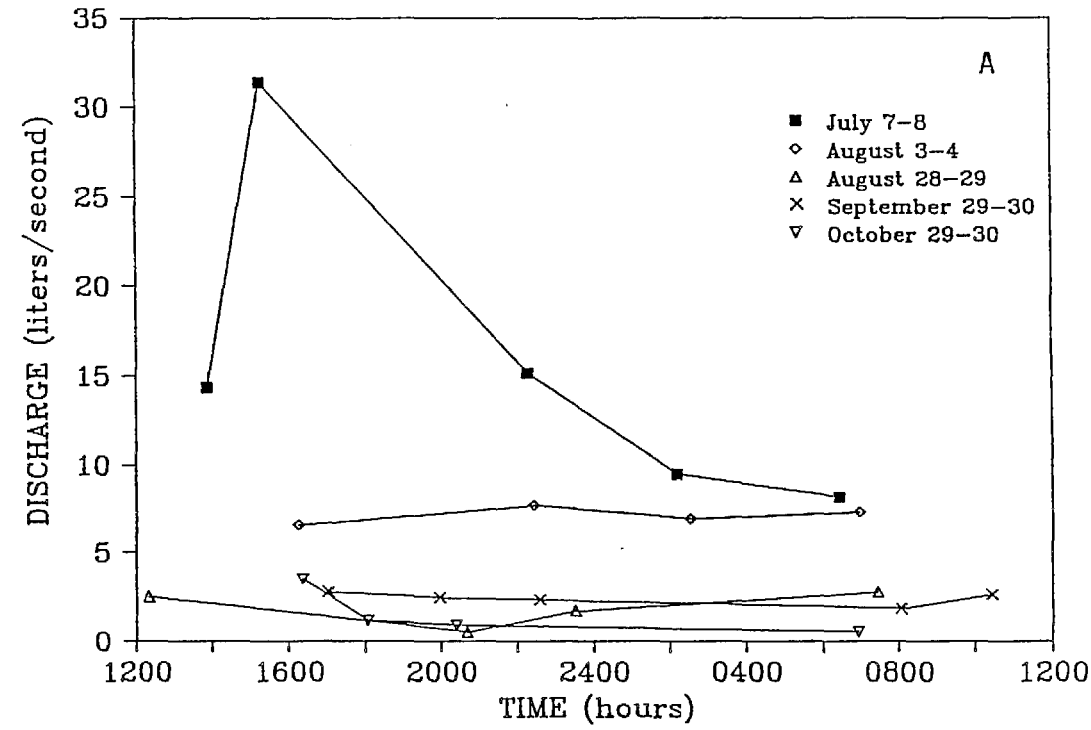


Figure V-18. Diel temperatures (°C) of Emerald Lake (A) Inflow, 1985 and (B) Outflow streams, 1985.



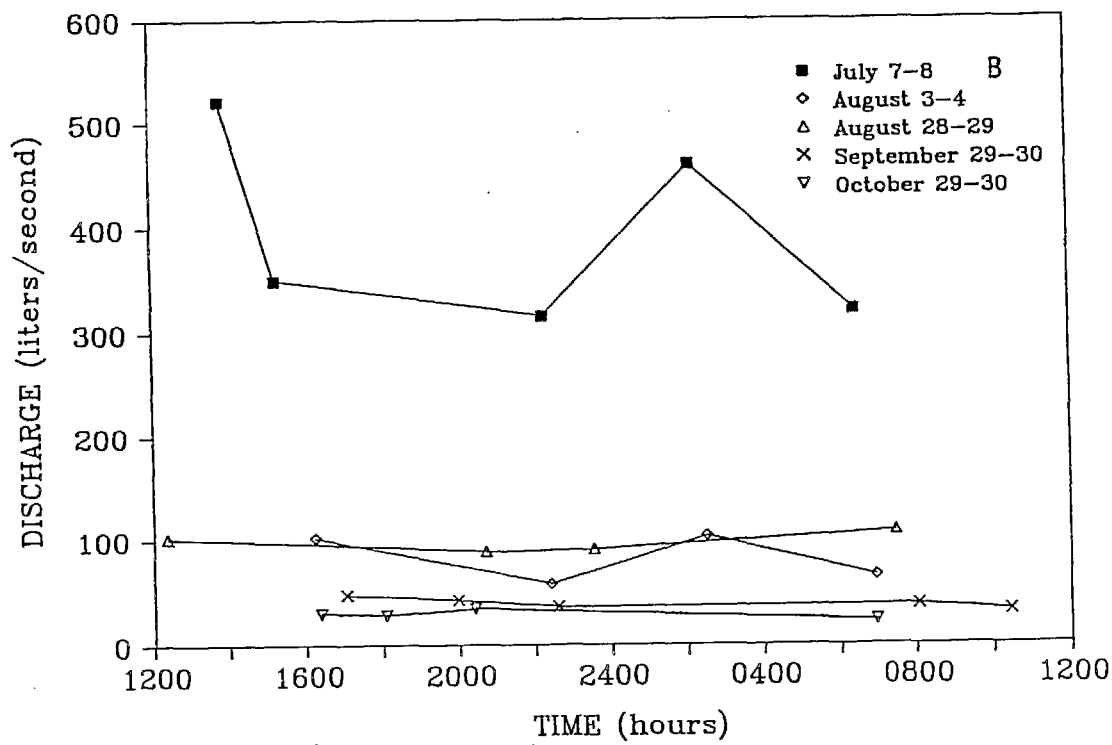
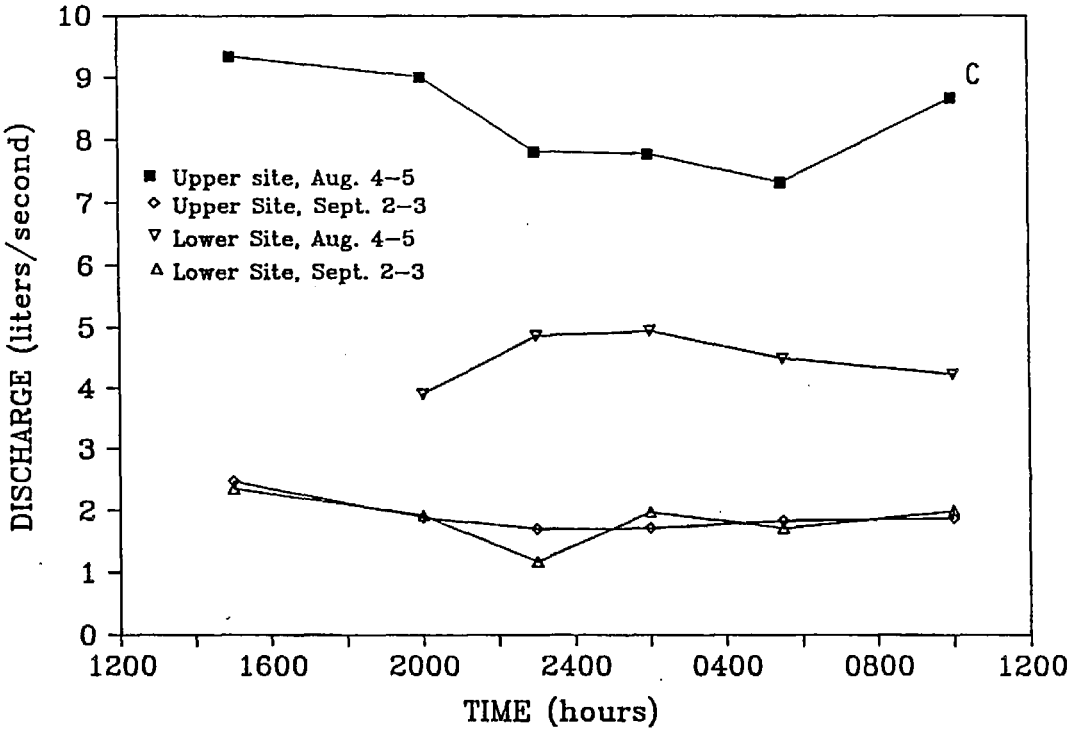
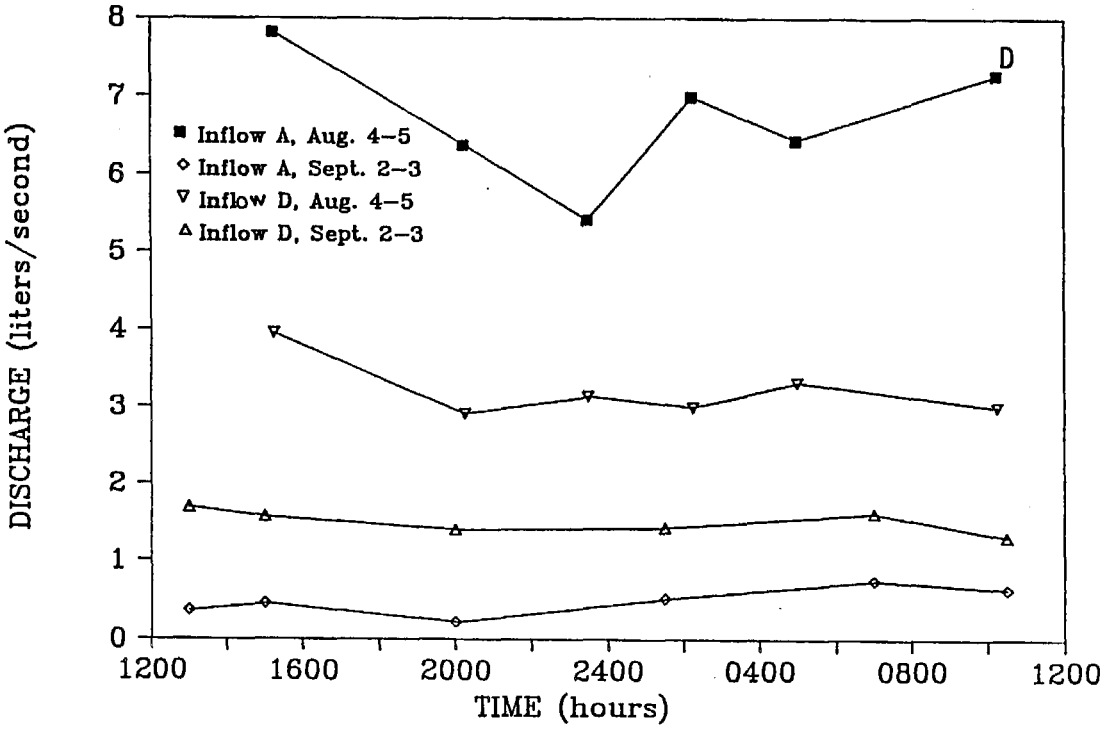


Figure V-19. Discharge (liters/second) through drift nets at Emerald Lake streams. A and B: Upper and lower outflow sites, 1984. C: Outflow stream, and D: inflows, on August 4-5 and September 2-3, 1985. Data was not taken for lower outflow site on August, 1985. E: Mean daily discharge volumes for Emerald Lake outflow on 1984 and 1985 collection dates. Numbers are means for 2 weeks of daily measurements around each date.





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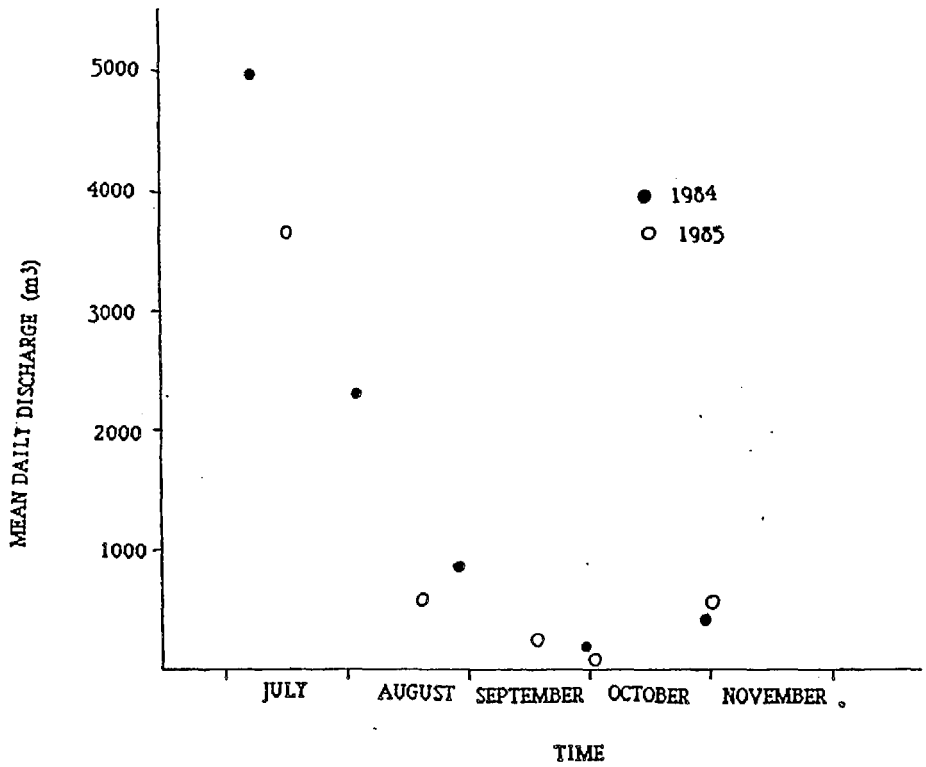

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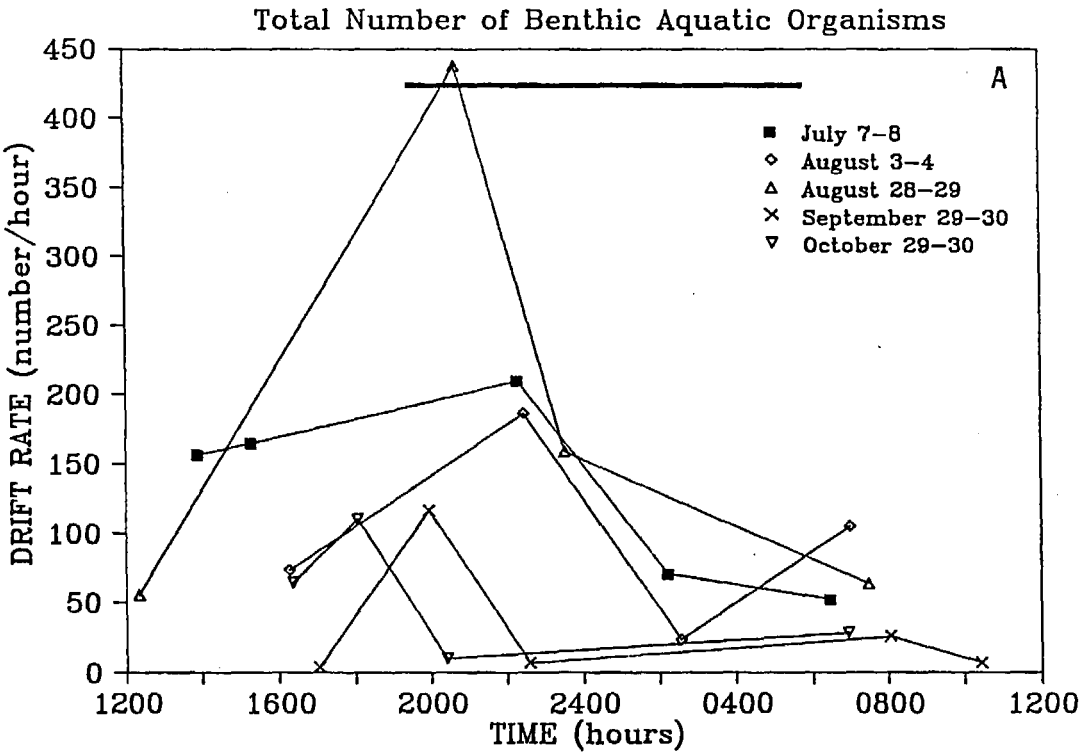


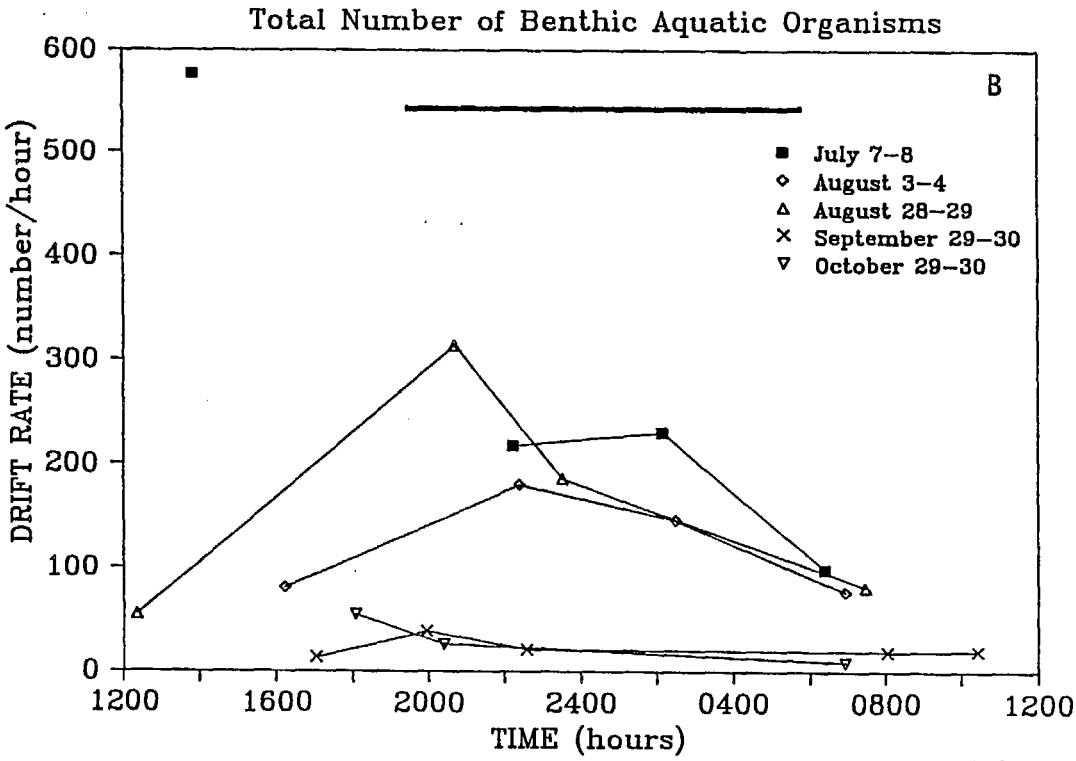
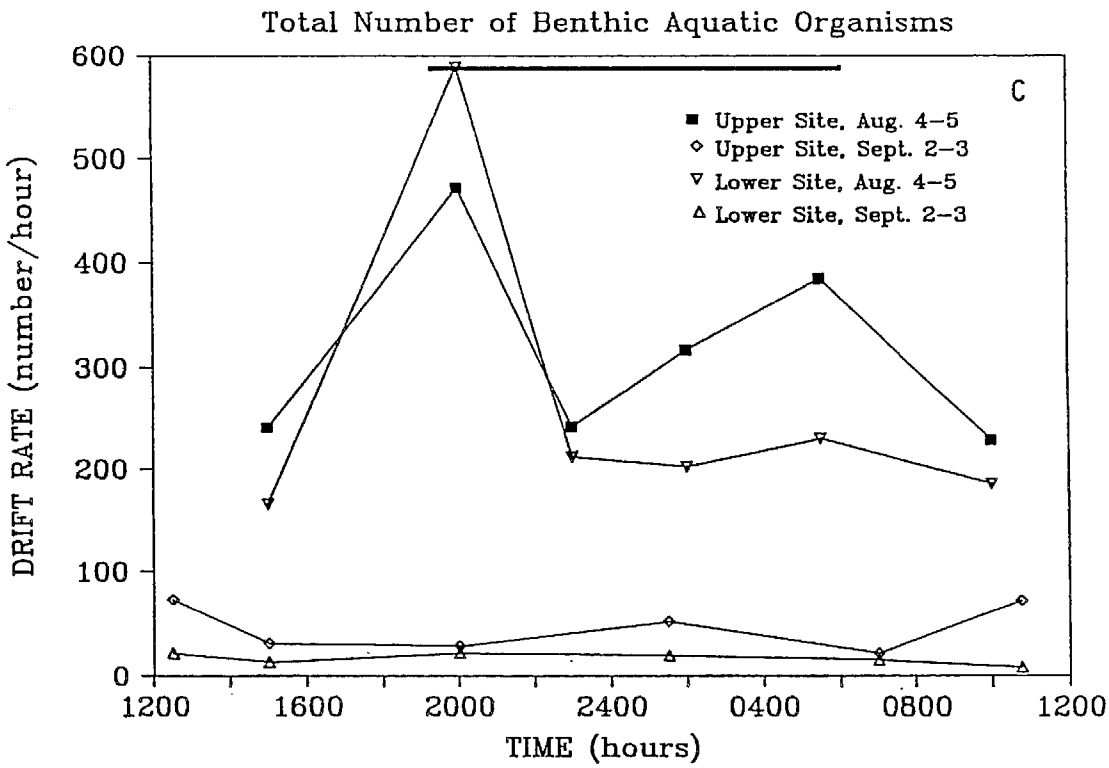
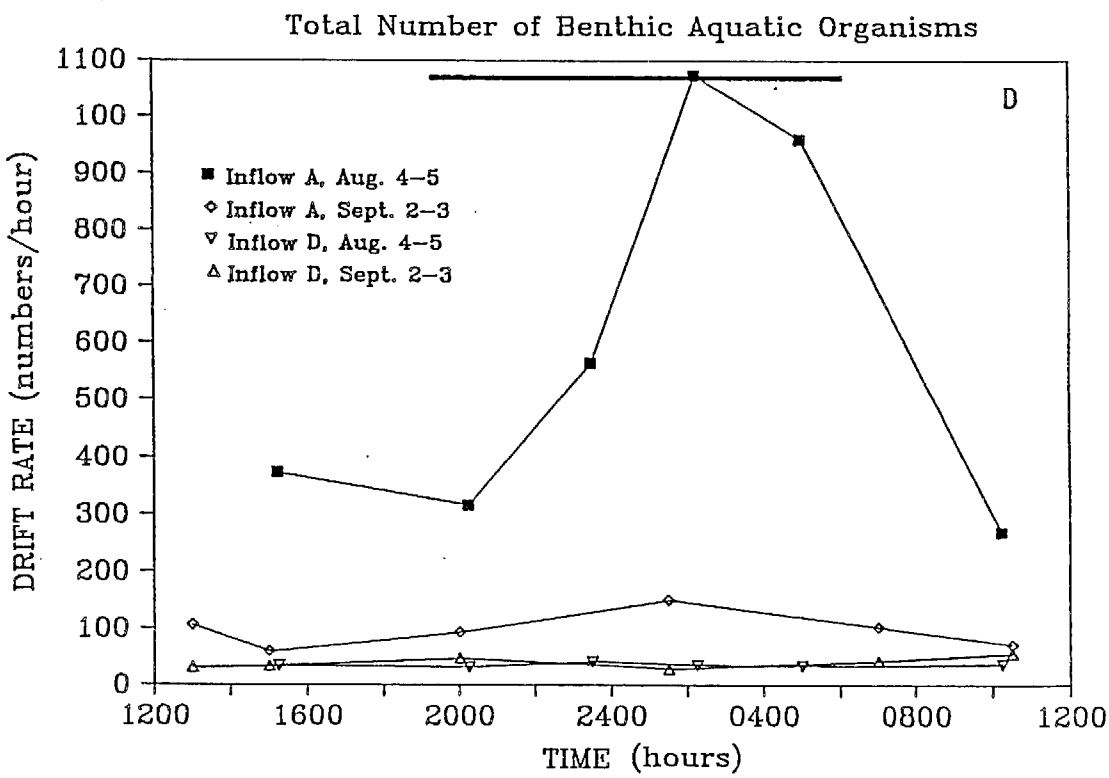


Figure V-20. Total number of benthic aquatic organisms captured in drift nets per hour in the Emerald Lake streams. A and B: Upper and lower outflow sites, 1984. C: Outflow stream, and D: inflows, on August 4-5 and September 2-3, 1985. The dark bars represent periods of darkness.





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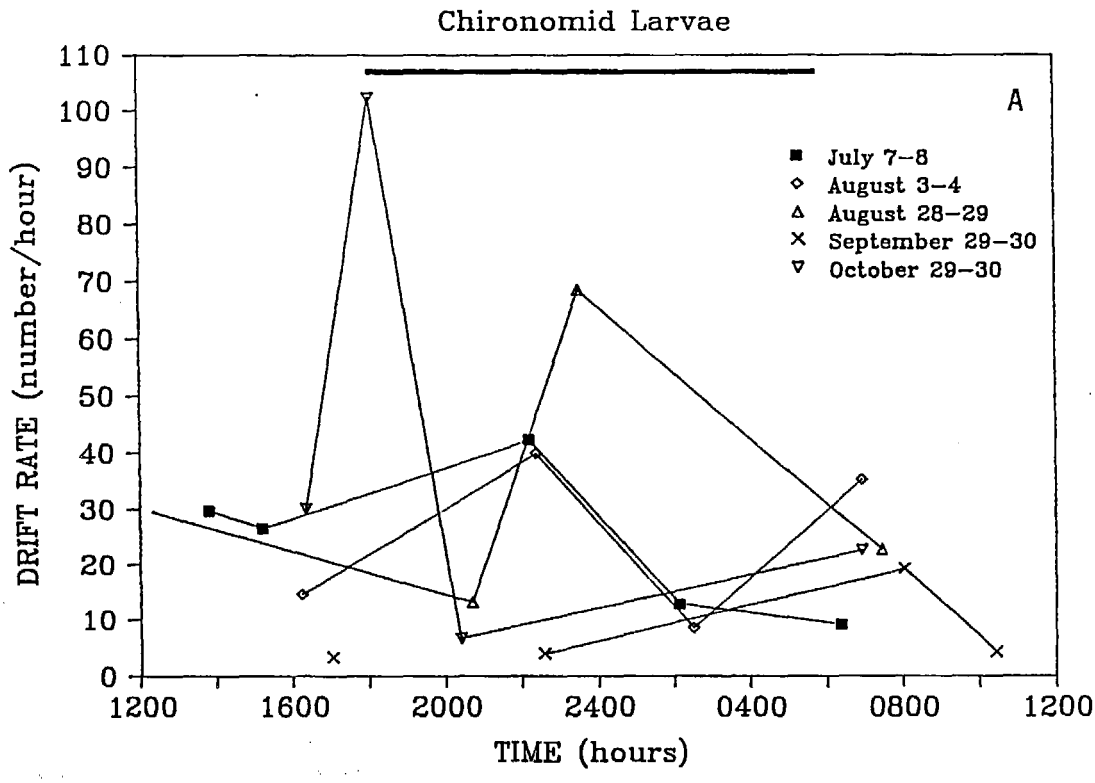


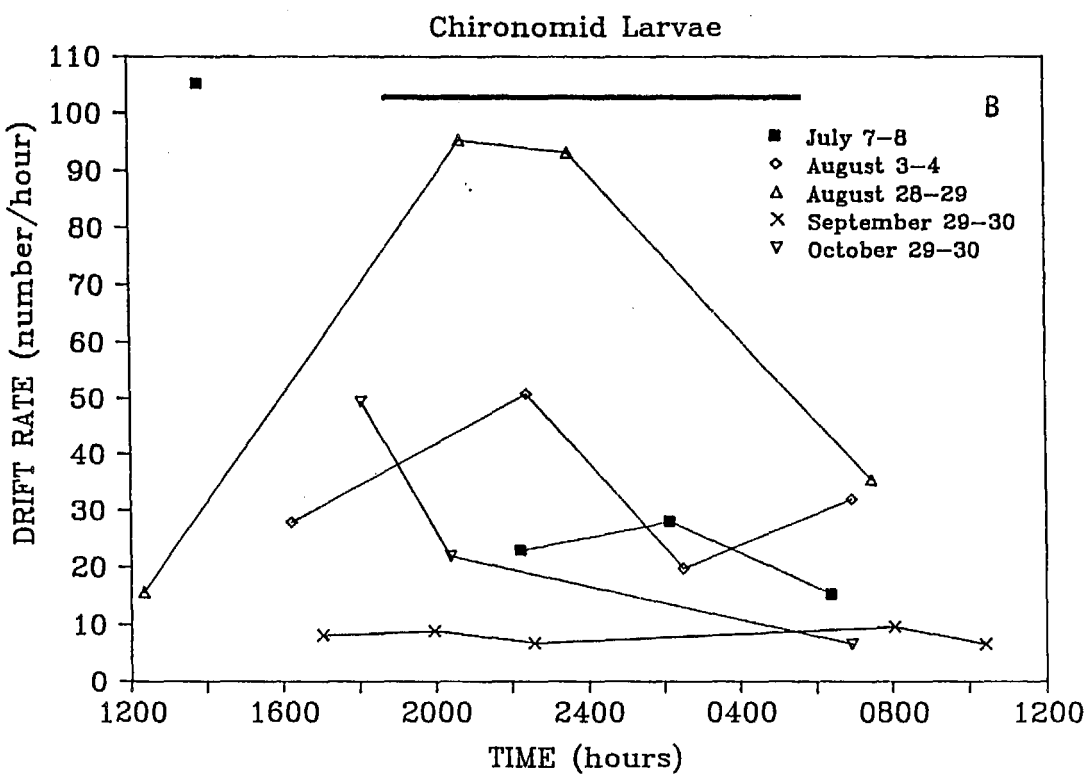
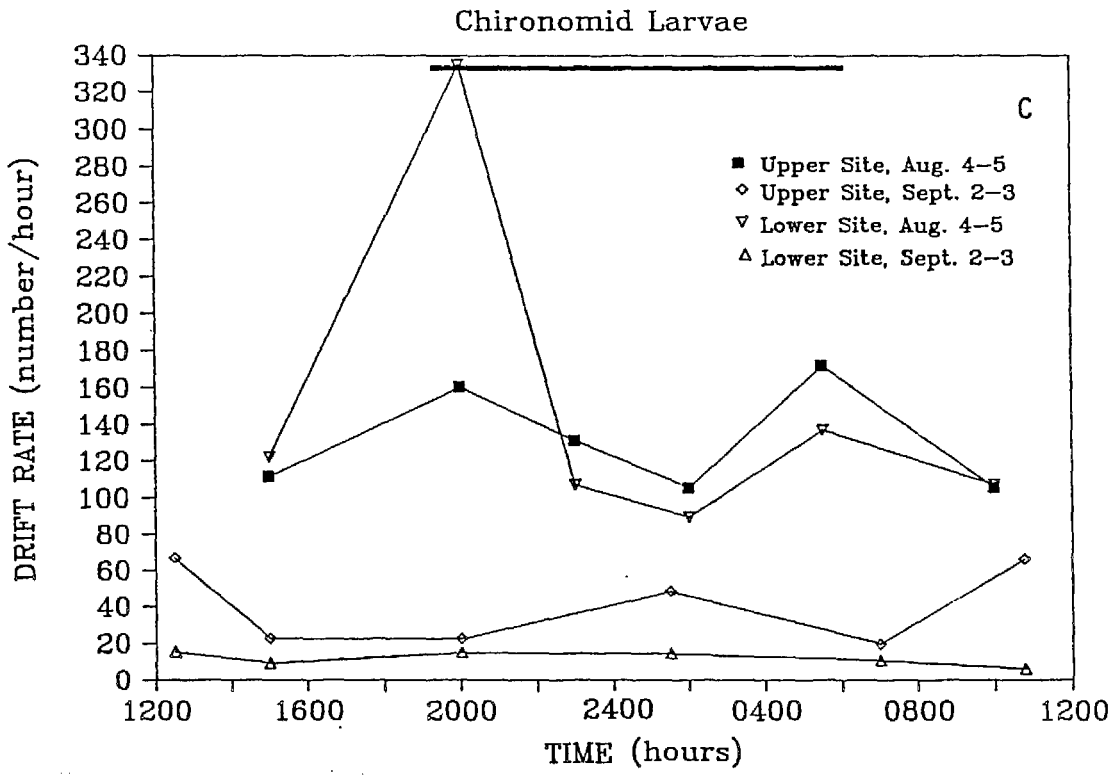
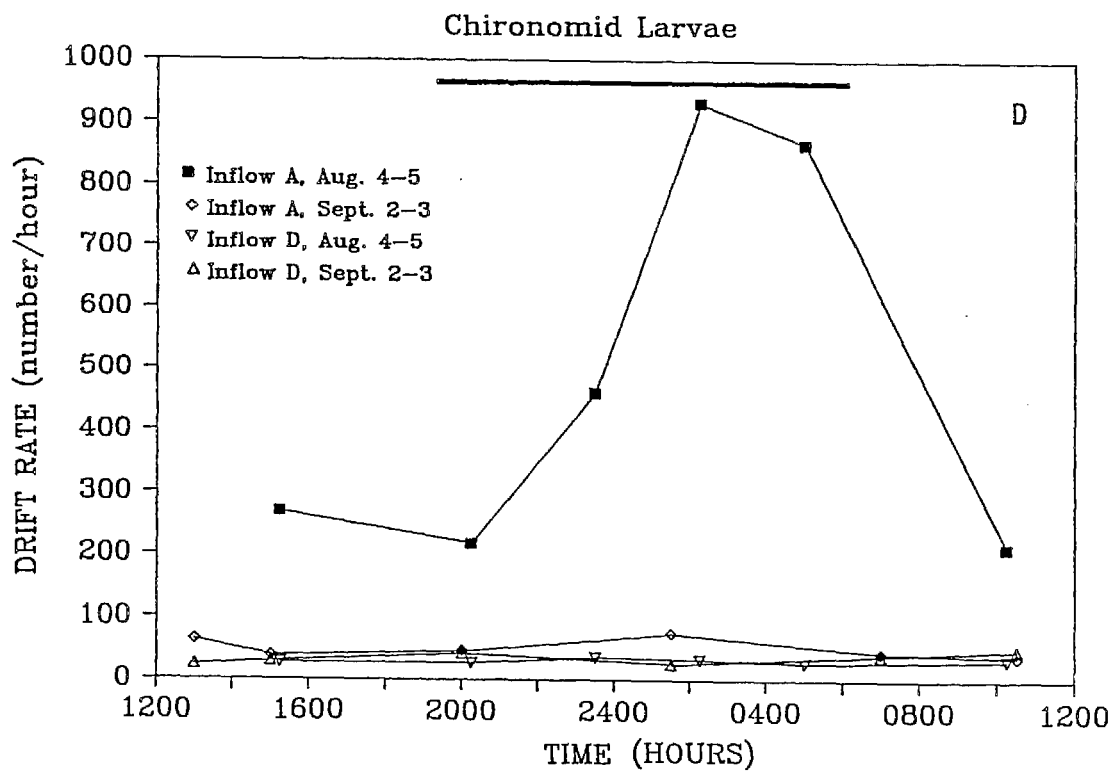


Figure V-21. The number of chironomid larvae captured in drift nets per hour in the Emerald Lake streams. A and B: Upper and lower outflow sites, 1984. C: Outflow stream, and D: Inflow streams, on August 4-5 and September 2-3, 1985. The dark bars represent periods of darkness.





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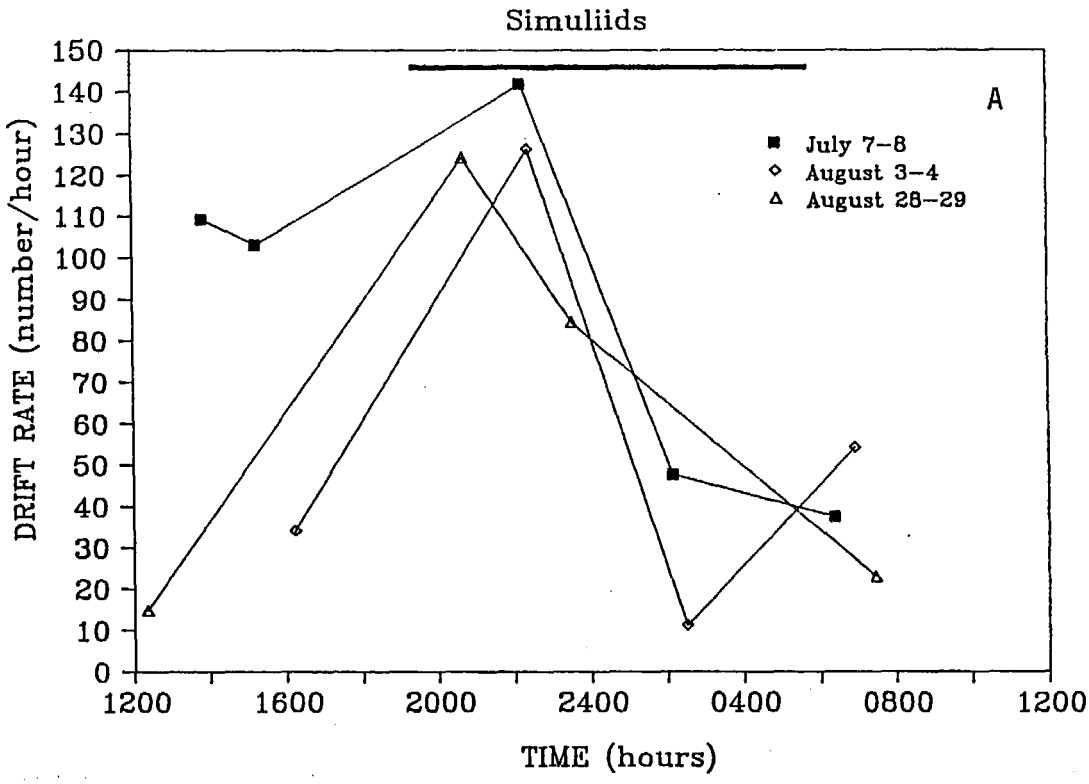


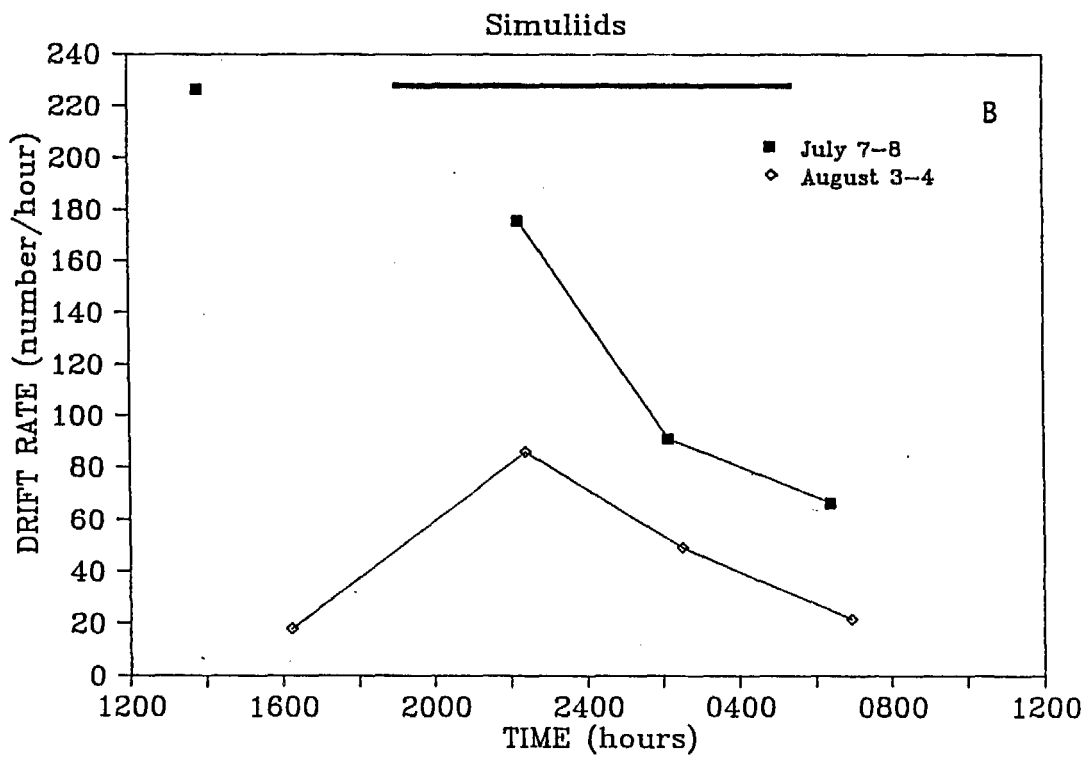
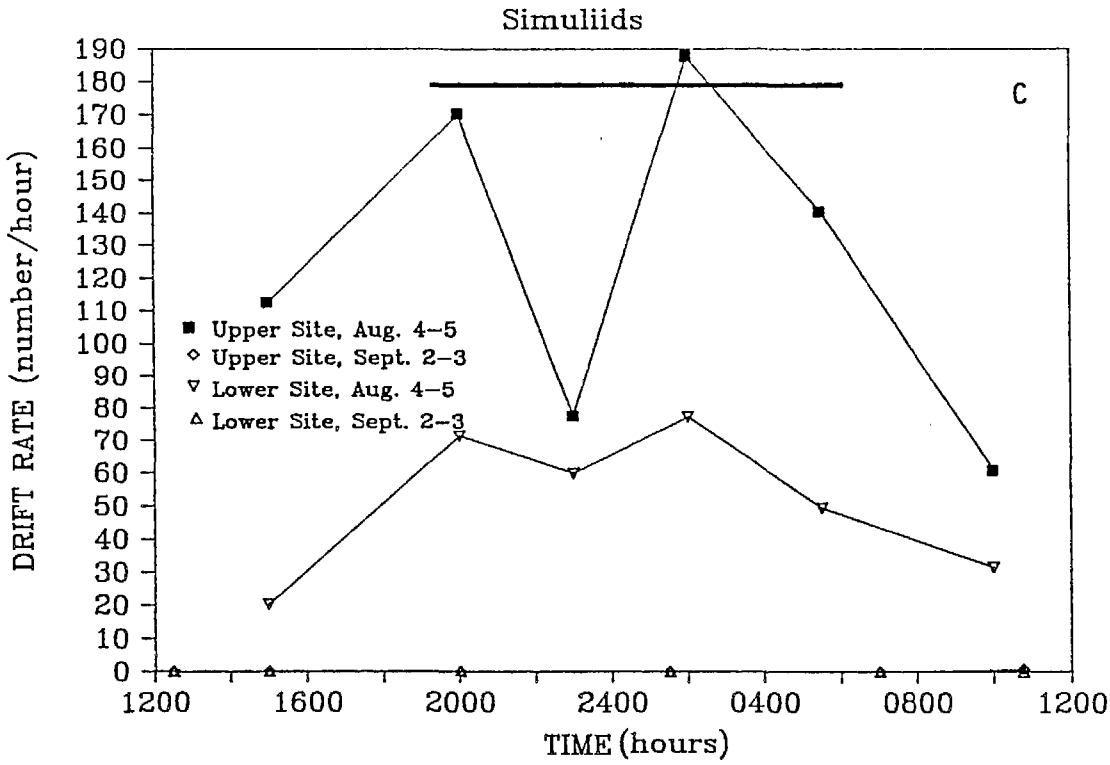


Figure V-22. The number of Simuliids captured in drift nets per hour in the Emerald Lake outflow. A and B: Upper and lower outflow sites, 1984, C: Outflow stream on August 4-5, 1985. The dark bars represent periods of darkness.



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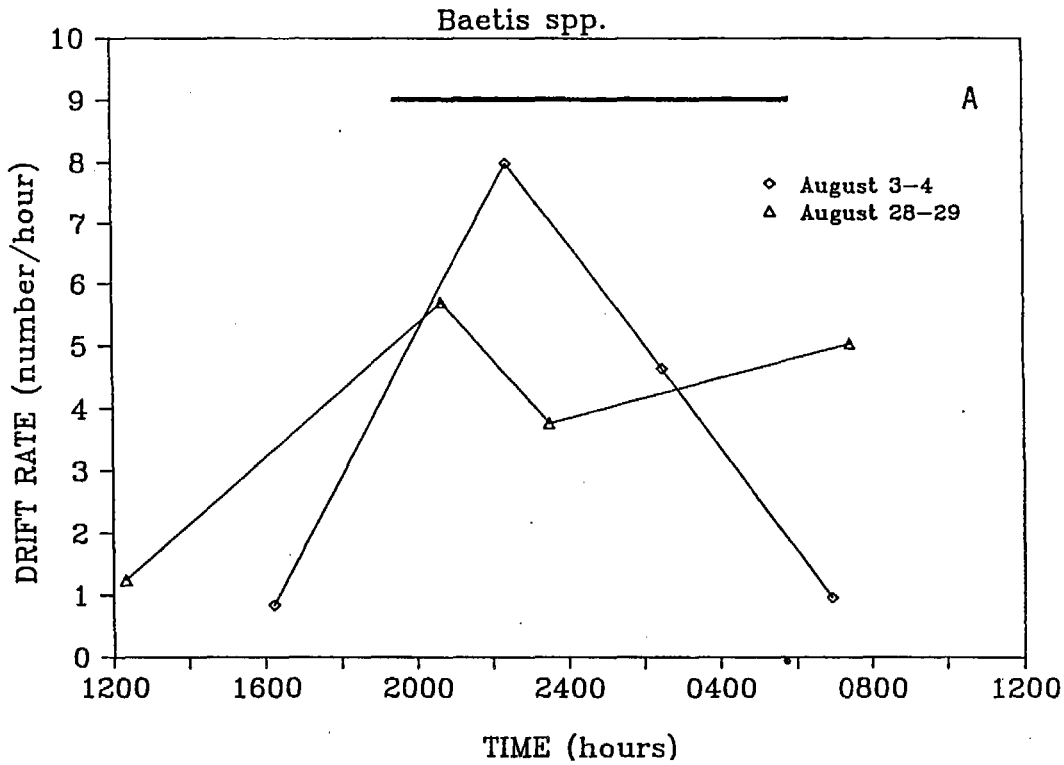


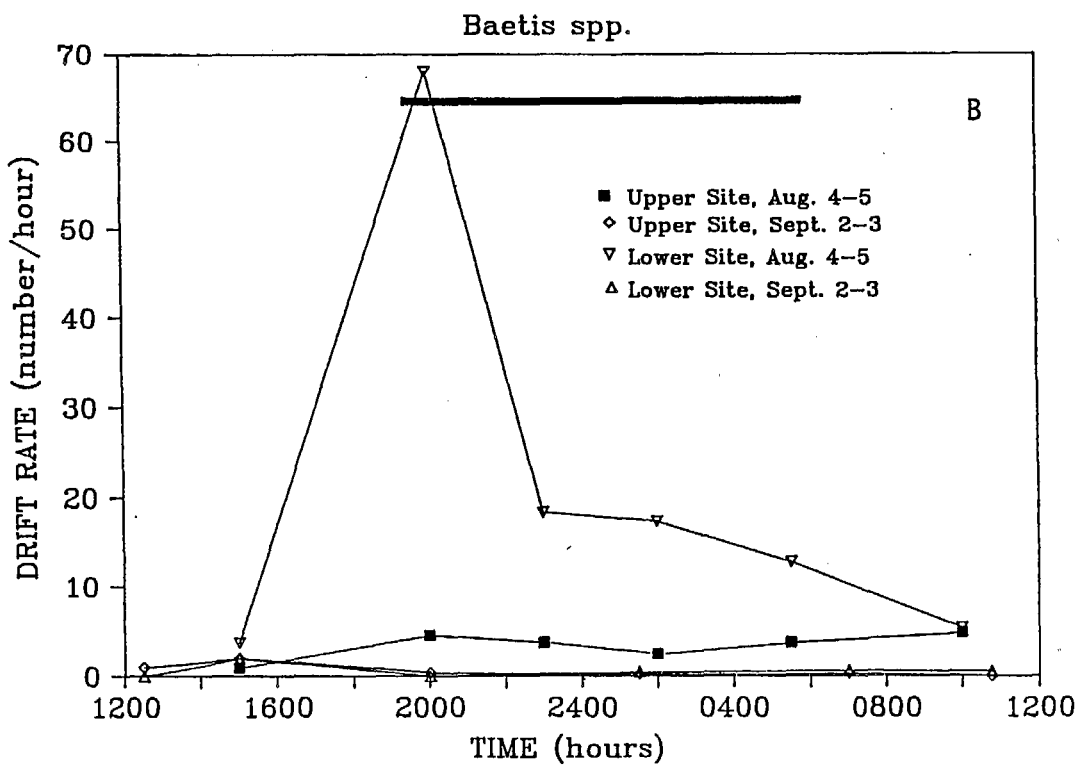
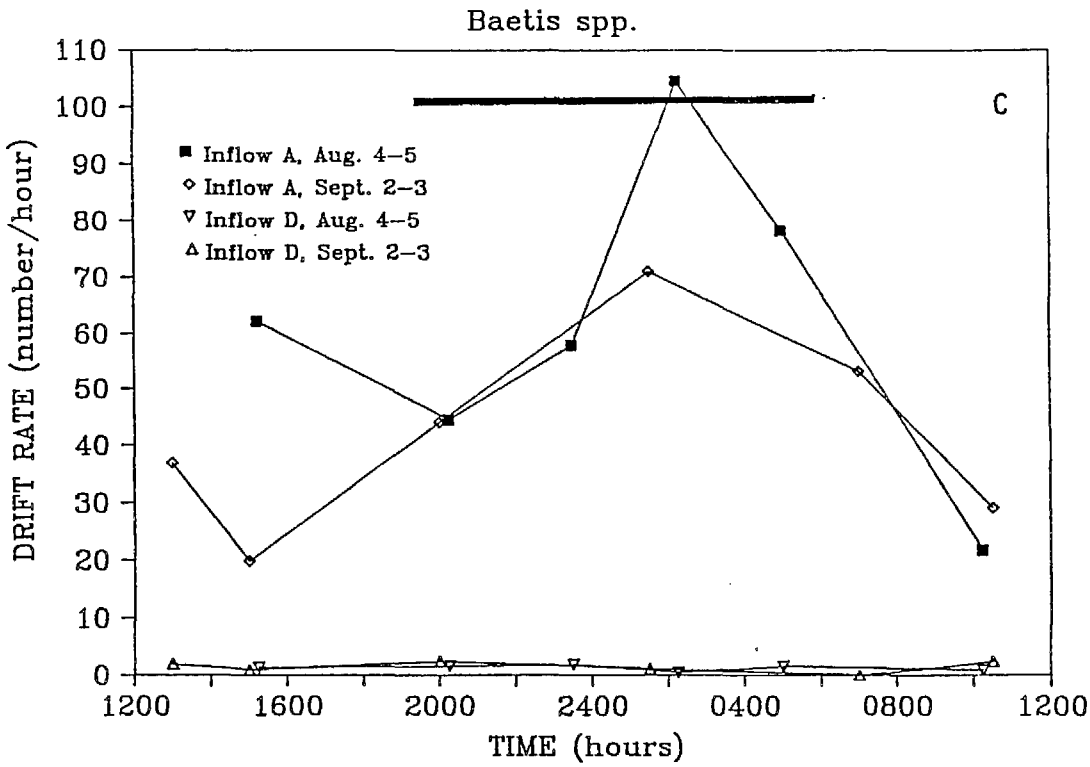


Figure V-23. The number of Baetis spp. captured in drift nets per hour in the Emerald Lake streams. A: Lower outflow site in 1984. B: Outflow stream and C: inflows, on August 4-5 and September 2-3, 1985. The dark bars represent periods of darkness.



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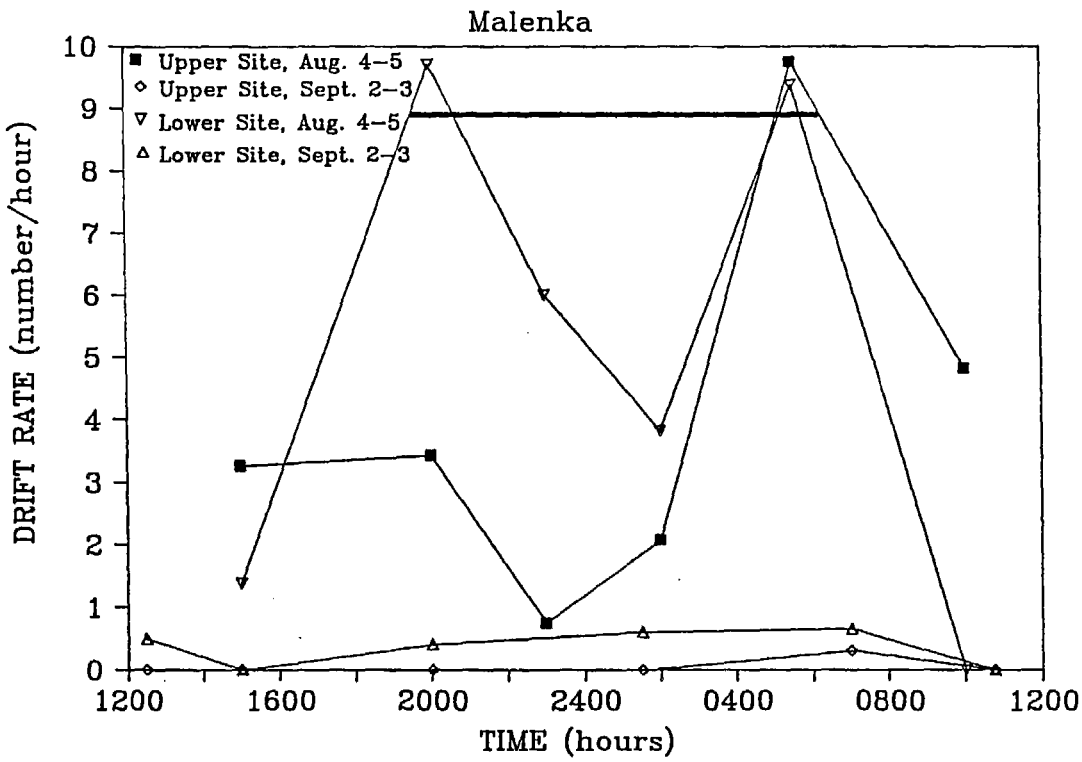


Figure V-24. The number of Malenka captured in drift nets per hour in the Emerald Lake outflow on August 4-5 and September 2-3, 1985. The dark bar represents the period of darkness.

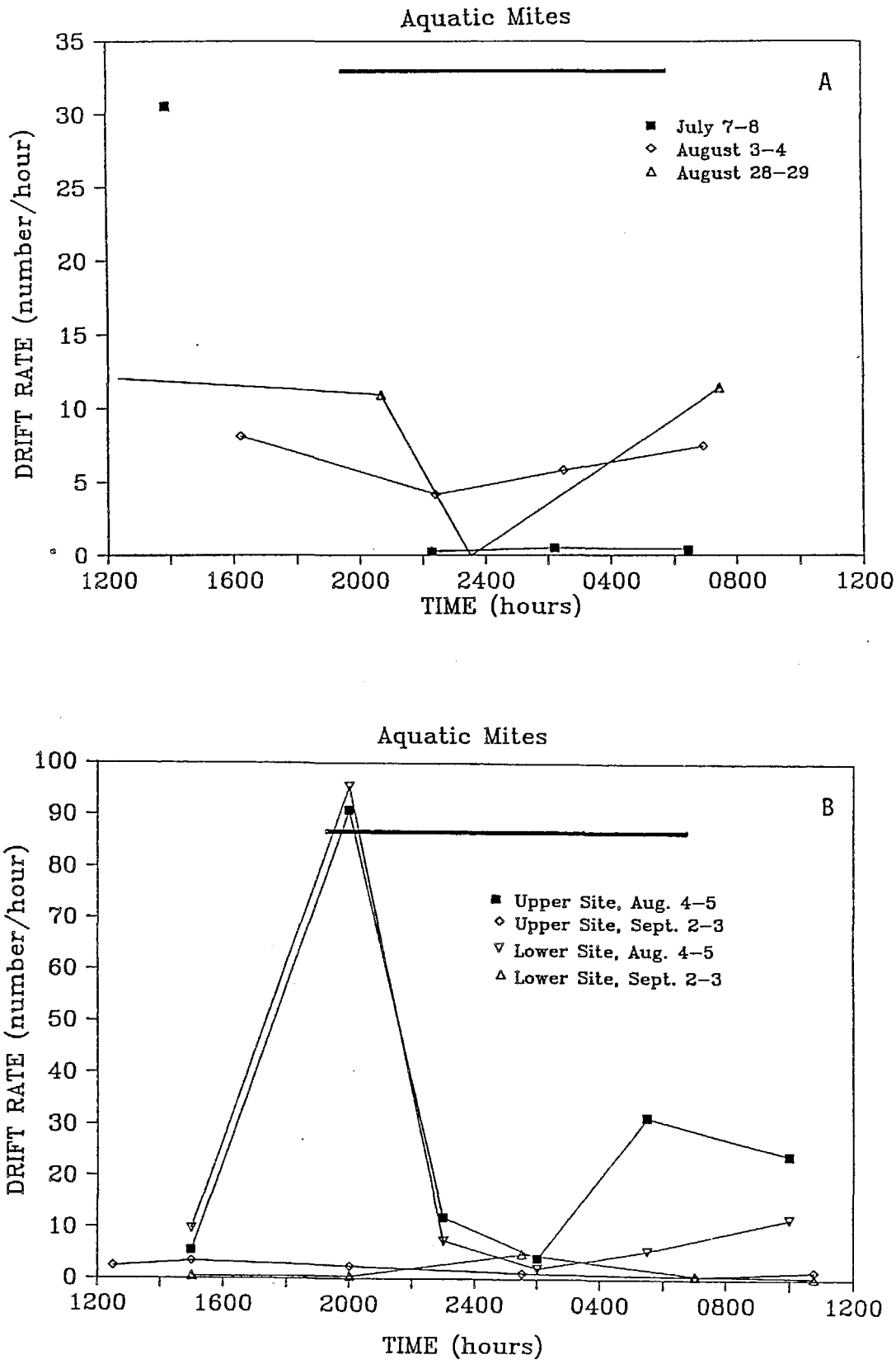
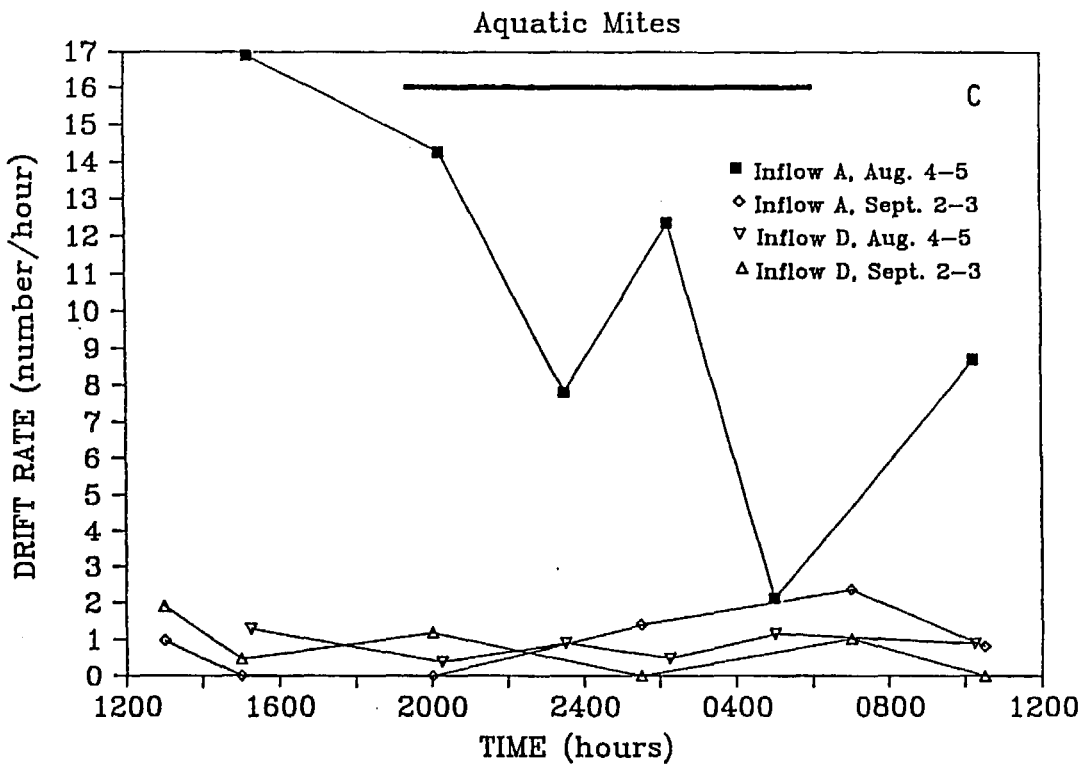


Figure V-25. The number of aquatic mites captured in drift nets per hour in the Emerald Lake outflow. A: Lower outflow site in 1984. B: Outflow stream, and C: Inflows, on August 4-5 and September 2-3, 1985. The dark bars represent periods of darkness.



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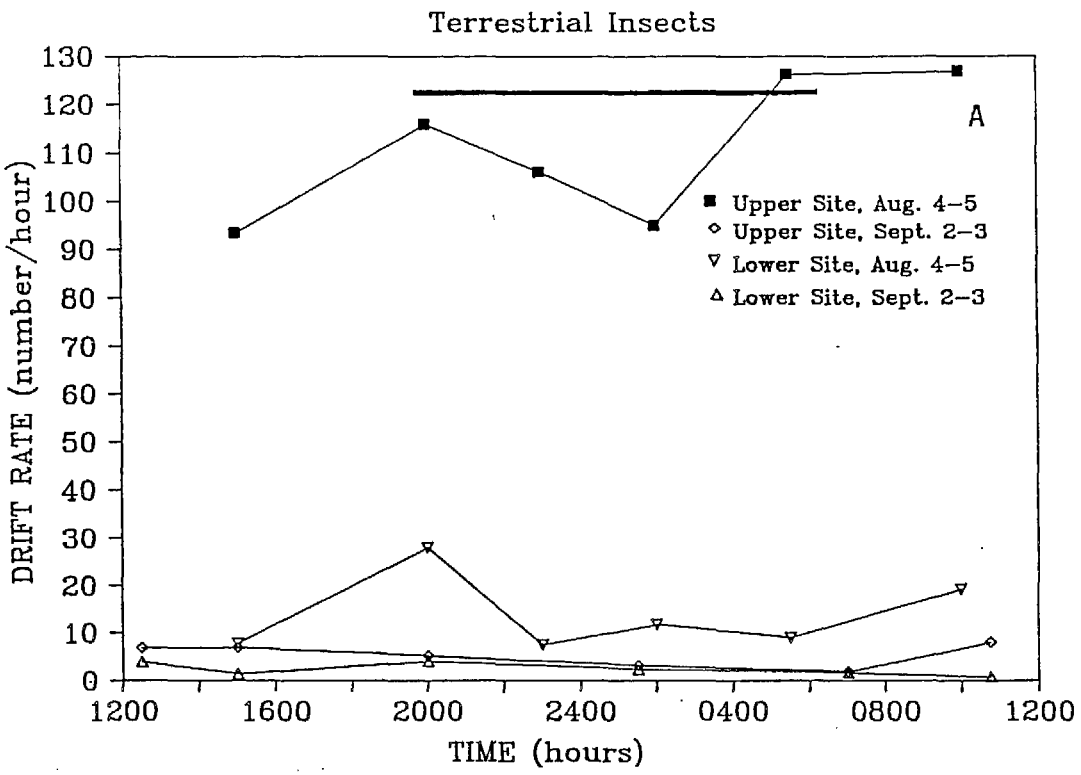

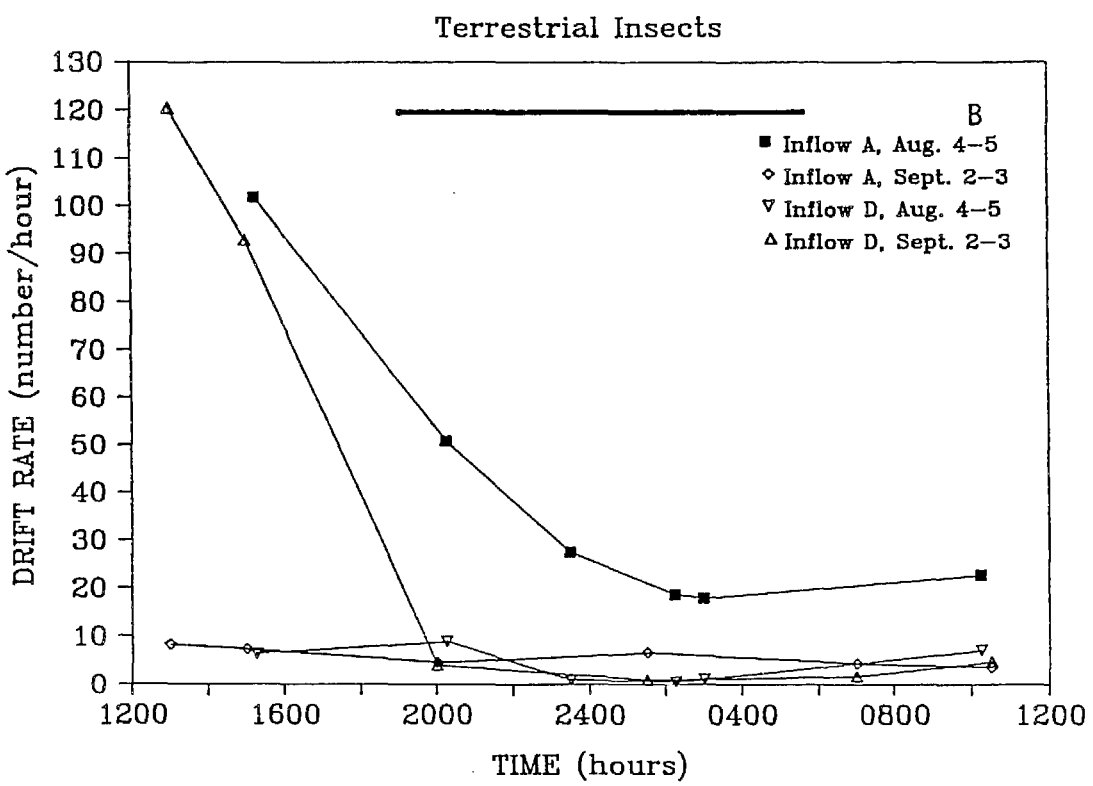

Figure V-26. The number of terrestrial insects captured in drift nets per hour in the Emerald Lake streams. A: outflow, and B: inflows, on August 4-5 and September 2-3, 1985. The dark bar represents the period of darkness.

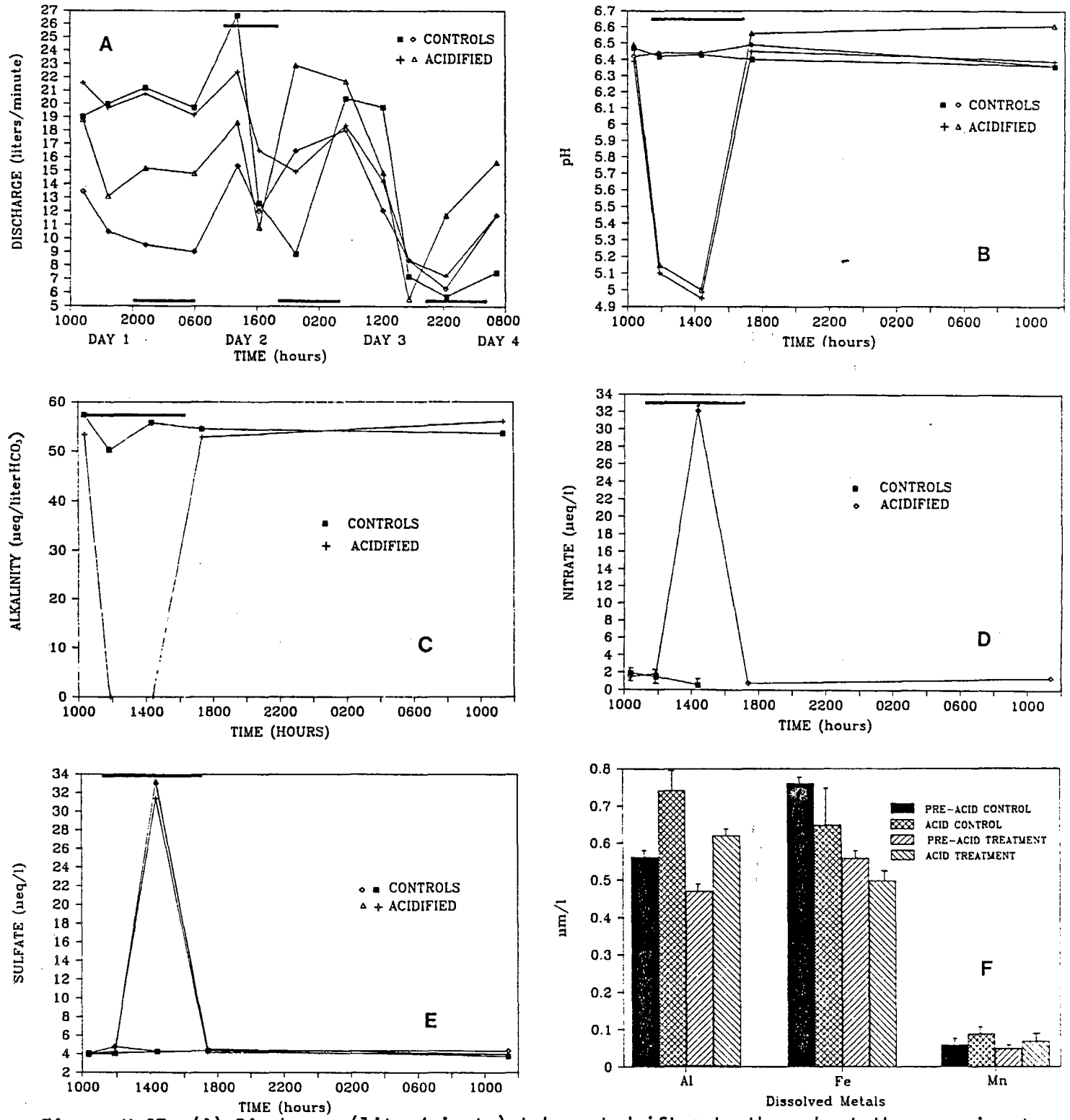

Figure V-27. (A) Discharge (liter/minute) taken at drift sets throughout the experiment (August 6-9, 1985). Lower bars indicate periods of darkness. (B) pH, (C) Alkalinity, (D) Nitrate concentrations, (E) Sulfate concentrations before, during, and after acid addition ±1 SE. Upper bar indicates period of acid addition. (F) Dissolved aluminum, iron, and manganese concentrations (um/l) before and during acid addition in control and acidified channels + 1 SE.

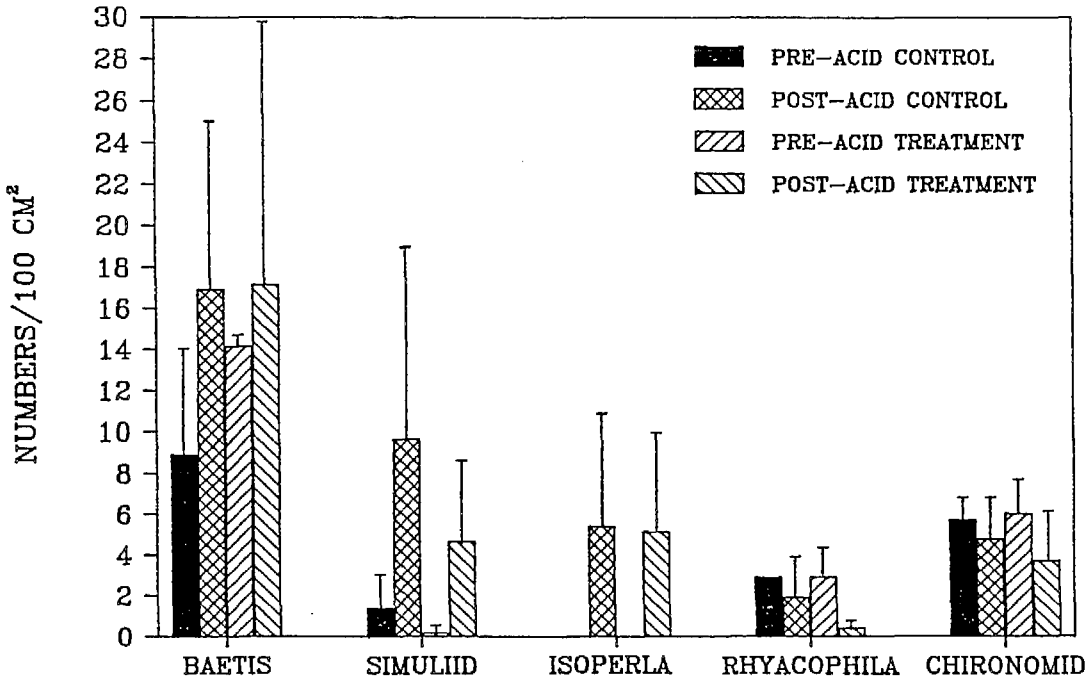

Figure V-28. Stream invertebrate benthic densities for Baetis, Simuliidae, Isoperla, Rhyacophila, and Chironomidae before and after acid addition in control and acidified channels (+ 1 SE).

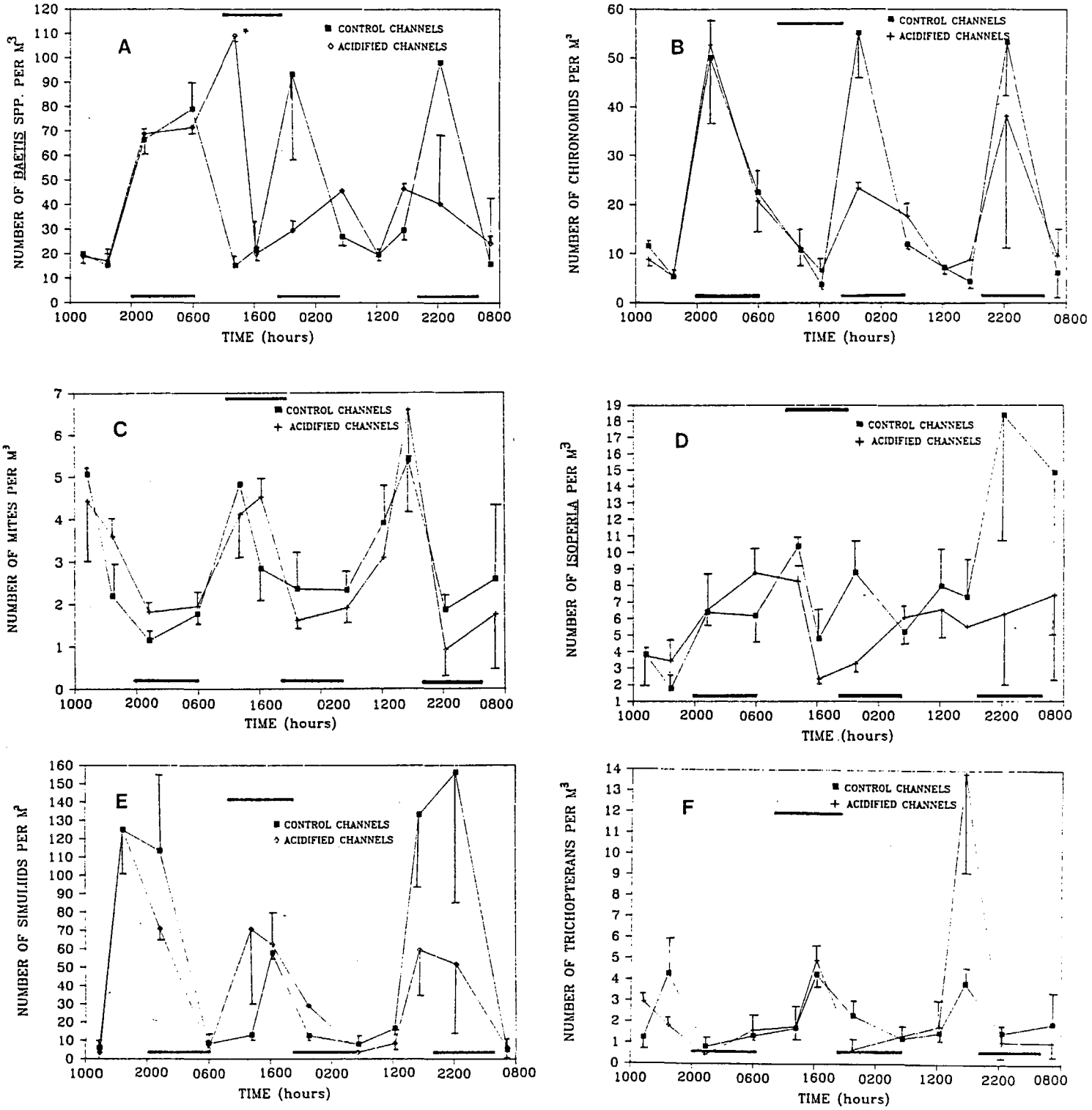

Figure V-29. (A) Baetis, (B) Chironomid larvae, (C) aquatic mites, (D) Isoperla, (E) Simuliidae, and (F) trichopteran drift rates (number/m^3) throughout the experiment + 1 SE. Upper bar indicates period of acid addition. Lower bars indicate periods of darkness. Asterisk denotes a significant effect of acid addition on Baetis drift rates (*$p < 0.025$, ANOVA).

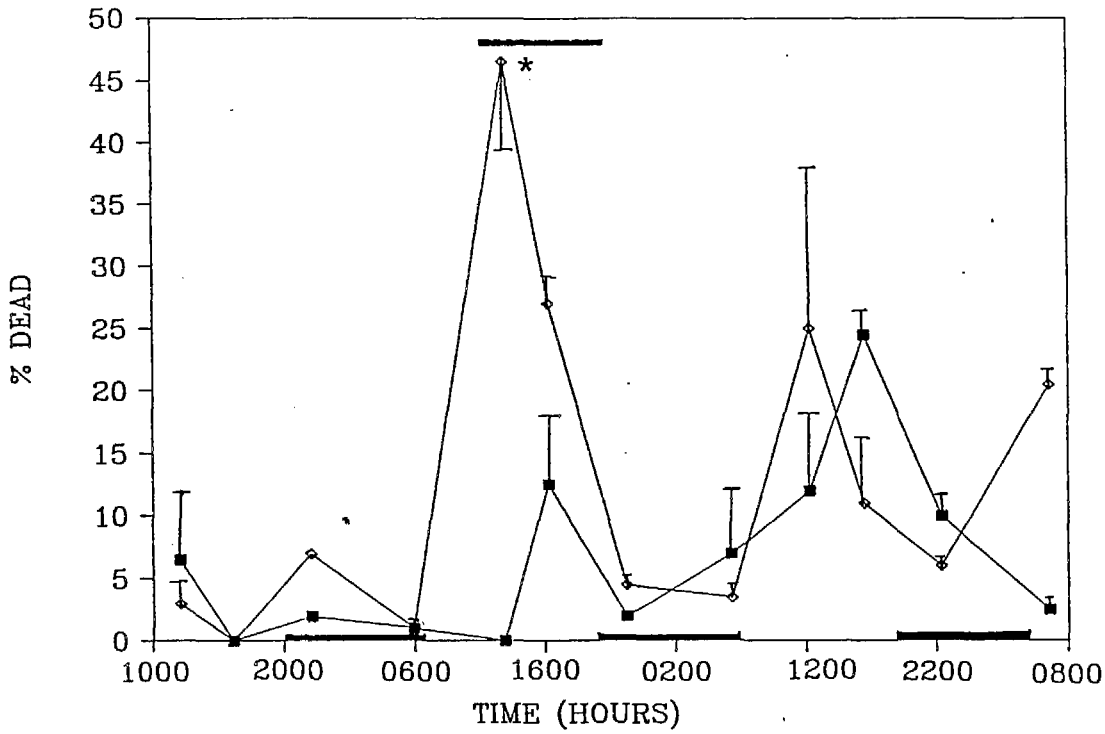

Figure V-30. Percent of drifting Baetis that were dead throughout the experiment (+1 SE). Upper bar indicates period of acid addition. Lower bars indicate periods of darkness. Asterisk denotes a significant effect of acid addition on drifting Baetis mortality (* $P < 0.05$, ANOVA).

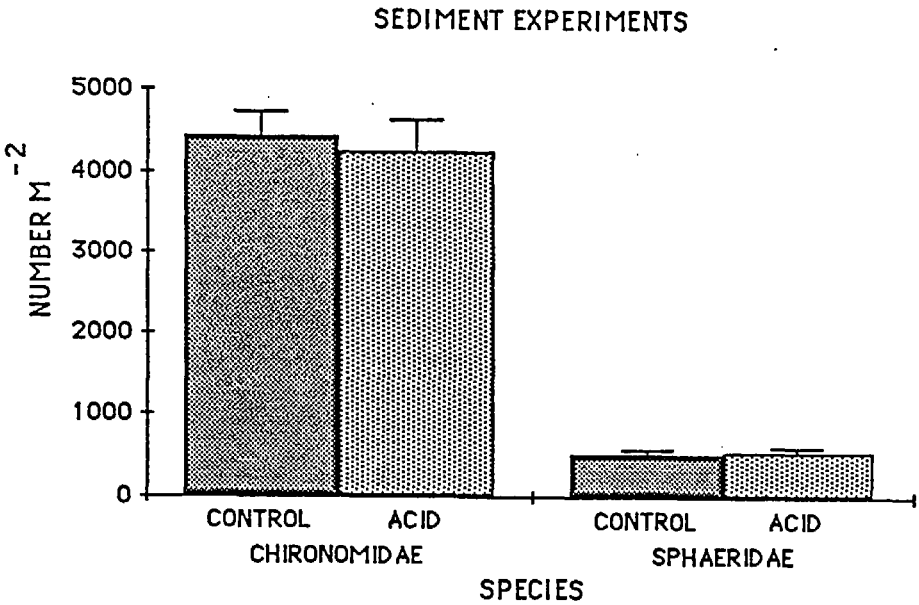

Figure V-31. Mean densities (± 1 SE) of chironomid larvae and sphaeriid clams in acidified (acid) and nonacidified (control) bags in Experiment 4. Mean densities are the means for the four replicate bags assigned to each treatment.

Chapter V.3
FISH

Introduction

The brook trout (Salvelinus fontinalis) is the most widely distributed (and usually only) fish in high elevation Sierra Nevada lakes and is of considerable recreational importance. The brook trout is the only fish species present in the Emerald Lake system and nearby lakes. Brook trout were last stocked in Emerald Lake and its outlet stream in 1959, and the current population is being maintained by natural reproduction. Although brook trout are common in Emerald Lake and its outlet stream, the inflowing streams contain no fish. The inflows are too shallow, small, and steep to provide adequate fish habitat during the severe ice and snow scouring in the winter months and severe flooding in the spring. Fish cannot migrate from the lake into the inflow streams as they are connected by small (ca. 5 m high) waterfalls.

The brook trout and its relatives in the genus Salvelinus are among the species most affected by acidification in the European and Atlantic seaboard areas, so their physiological tolerances have been extensively investigated. Brook trout can be harmed by direct effects of low pH, or through indirect effects on habitat and trophic structure. All individuals are killed within hours at pH 4.1 or less, and young fish are less able to tolerate temporary exposure to low pH than adults (Robinson et al. 1976). When exposure to acid conditions is frequent or chronic the tolerance of brook trout is far less, and they are not found in natural habitats with pH lower than 4.7 (Lennon 1967). At pH 5.2 growth of reproductive adults is reduced considerably, which reduces their egg production. Although gametogenesis proceeds normally down to pH 4.5, ovulation, and thus spawning time, is delayed significantly at 5.6 (Tam and Payson 1986). The production of viable zygotes by natural spawning declines below pH 6.5, and drops rapidly below 5.5. Hatching success also declines at pH 6.5 and is negligible below 5.1. Growth and survival of sac fry after hatching and alevins after emergence from the natal gravel are reduced at pH 6.5, and mortality approached 100% at 5.0 (Menendez 1976).

These direct responses of trout to increased acidification are reflected in changes in their population structure. Many population parameters of fish

including recruitment, survival, size or age structure, and growth, change in response to changes in pH (Fish and Wildlife Service 1982 a,b; Johnson 1982, D'Itri 1982, NRC Canada 1981, Frenette and Dodson 1984). The reduced abundance or disappearance of brook trout from acid-stressed systems is usually related to recruitment failure (Haines 1981, Spry et al. 1981), although mortalities of juveniles and adults have been reported in some studies (Schofield 1977). In an 8-year lake acidification experiment, Schindler et al. (1985) found complete reproductive failure in lake trout (Salvelinus namaycush) at pH 5.4. At pH 5.1 the condition of adult trout declined drastically with the collapse of their food supply. Because of recruitment failure, the size structure of fish populations often changes to one dominated by larger, older fish (Ryan and Harvey 1980, 1981, Schofield 1976). In some instances, however, older fish may be absent from systems exposed to increased acidity because of increased mortality following spawning (Frenette and Dodson 1984, Rosseland et al. 1980). Most laboratory studies indicate that fish grow more slowly at lower pHs (Muniz and Leivestad 1979, Rodgers 1984). In the field, however, some fish populations will actually grow at higher rates following acidification because lowered fish densities reduce competition (Almer et al. 1974, Jensen and Snekvik 1972). Field growth rates, then, will represent the results of antagonistic responses to metabolic stress and decreased competition. The effects of low pH on fish are also influenced by the concentration of other ions (Brown 1981, Fromm 1980). Increased acidification may also affect fish indirectly by altering the abundance and species composition of prey assemblages, and by altering habitat characteristics (USFWS 1980). In the latter case, increased growths of filamentous algae, fungi, and mosses following acidification may make gravel beds unsuitable for spawning.

Because of the recreational importance of brook trout, and because of their sensitivity to acidic inputs, we conducted pilot surveys of brook trout in Emerald Lake and its outlet stream in the summer of 1984. The primary purpose of these surveys was to test sampling methodologies in anticipation of more detailed studies of brook trout populations, and to obtain some data on brook trout abundances, and size and age structures. Since July 1985 a much more detailed examination of the behavior, size and age structures, reproductive success, growth, abundances, and diets of brook trout populations in the Emerald Lake system has been conducted under a separate ARB

grant. The 1984 data, then, is regarded as a pilot analysis of the size and age structure of fish in the Emerald Lake system, and as an introduction to more detailed studies that have followed.

Methods

Brook trout (*Salvelinus fontinalis*) populations were censused in the outlet stream, from the outlet to the ponds 100 m downstream, in early July and early October, 1984, by electroshocking. Three electroshocking passes were made on each sample date. From the collected fish, 12 trout in July and 10 trout in October were sacrificed for otolith (Brothers et al. 1976) and diet analyses. In early October brook trout in the inlet and outlet of Aster Lake were censused using similar procedures, and six trout from the outlet and five trout from the inlet were sacrificed. Visual observations of the size and number of fish missed by the electroshocking procedure were noted for each sample date at each study site. Trout in Emerald Lake were censused using snorkelling transects in early July, and three fish from the lake were captured using hook and line. These three fish were sacrificed for aging analyses.

Results and Discussion

Eighty-three fish were collected or sighted in three electroshocking passes in the Emerald Lake outlet in July 1984. In October 1984, 90 fish were collected or sighted in three similar passes. The size structure of the outlet population was bimodal: the left-hand mode represented young-of-the-year and the right-hand mode represented older fish (Fig. V-32). From early July to early October, brook trout young-of-the-year grew from 3 - 4 cm to 5 - 8 cm in total length. Trout in the right-hand mode were often quite old; otolith analyses indicate many fish from four to eight years old. Trout densities in the Aster Lake outlet and inlet were lower than in the Emerald Lake outlet, but the size structures of these populations were similar. There was a lot of variation in individual trout growth rates. For example, two fish collected on Oct. 1, 1984, were both 20.5 cm. in total length; one fish, however, was 4 years old and the other was 7 years old. The age structures of these populations (i.e., domination by older age classes) indicate populations with high juvenile mortality, perhaps owing to intense intraspecific interactions among age classes. Such an age structure is

typical of populations that receive little fishing pressure (i.e., low adult mortality).

The sex ratio of mature fish was approximately 50:50. Eggs and milt were released by trout captured in early October, and males were breeding at a much smaller size than females. Trout larvae were collected in benthic samples taken in early July 1984. These data suggest a protracted egg and larval duration for trout in this high-altitude system. Spawning apparently occurs in October or November, and alevins emerge from the gravel in late spring or early summer.

One hundred seventy-seven trout were counted along snorkelling transects in Emerald Lake in early July 1984, and 81% of these fish were sighted near the lake inflows. The three fish collected from the lake by hook and line (21 - 23 cm TL) were 5, 6, and 8 years old. A more detailed analysis of the demographics, life history, behavior, movement patterns, and feeding habits of the trout in the Emerald Lake system requires an intensive study incorporating mark-recapture, egg basket, alevin cage, netting, electro-shocking and snorkelling techniques. Such a study is currently underway.

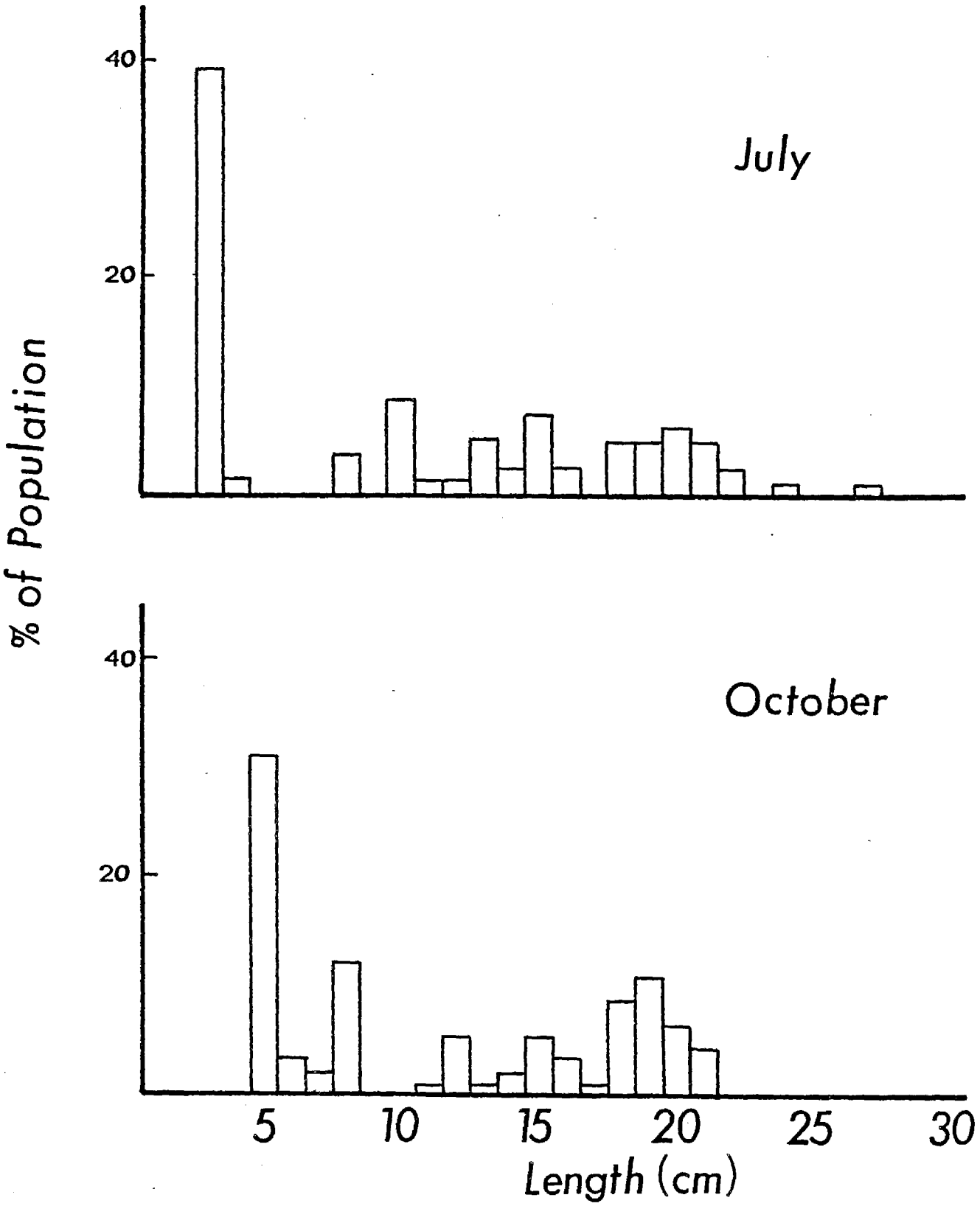

Figure V-32. The size structure of the brook trout population in the Emerald Lake outlet in July and October of 1984.

Chapter VI
KAWEAH RIVER, MARBLE FORK, DRAINAGE SURVEY

Introduction

An intensive monitoring system is necessary to define seasonal and annual population fluctuations so that natural variation can be distinguished from the effects of anthropogenic acid perturbation. However, habitat heterogeneity increases the sampling intensity required to accurately determine the population dynamics of component species. Because sampling is so intensive and time-consuming investigators are often constrained to studying a single representative system. Any results must be extrapolated to other systems. It is the purpose of this study to determine if the Emerald Lake biotic community is representative of the Marble Fork of the Kaweah River drainage.

Methods

Chemical or biological characteristics of 8 lakes and a vernal pond in the Kaweah River drainage were monitored on an annual basis beginning in 1984. The lakes and elevations are as follows: Aster-2933 m, Emerald-3067 m, Heather-2933 m, Pear-3200 m, Hidden-3333 m, Topaz-3467 m, Frog-3333 m, Lyness-3400 m, and a vernal pond-3433 m. The first 5 lakes have reproducing populations of brook trout (*Salvelinus fontinalis*), the last 4 are fishless. Lakes were sampled on 21-22 September 1984 and 21-22 and 26-28 August 1985. Surface water samples were collected from each lake for analyses of pH, alkalinity, µS, NH_4, PO_4, Ca, Mg, Na, Ca, NO_3, SO_4, Cl, and silica, in 1984 and 1985, and trace metals (Fe, Mn, Al) in 1985. Samples were immediately filtered, and then returned to the laboratory for analyses (see Chapter II.1 for methods). Temperature and dissolved oxygen profiles were taken from a boat at a single site in each lake.

Two replicate vertical zooplankton tows were taken with a 0.12 meter, 64 µm mesh net at each sampling date. Samples were preserved in 10 percent formalin until identification and enumeration. Qualitative sweep net samples were taken with a 150 µm mesh, D shaped-ring-net. Samples were collected from the outflow streams of each lake (except Heather where the outlet ceased to flow) in 1984 and 1985, using the net as a modified "kick net."

Additionally, sweep samples were taken from the margins of each lake in 1985. Invertebrates were preserved in 70 percent ethanol.

Results

Chemistry

All six lakes sampled in the Marble Fork survey were similar to Emerald Lake (Table VI-1). Acid neutralizing capacities ranged from 22 to 69 μeq l^{-1}, and calcium was the dominant cation. pH's ranged from 6.4 to 6.8. Nitrate values were lower than Emerald Lake in some cases and similar in others. Phosphate and ammonium concentrations were low as expected for oligotrophic lakes.

Zooplankton

Twenty-two species of zooplankton were collected including two calanoid copepods, two cyclopoid copepods, 10 cladocerans, and eight rotifers (Table VI-2). The number of species collected from lakes ranged from 4 (Lyness Lake) to 15 (Heather Lake). Depending on the year, from 9 to 10 species were collected from Emerald Lake, including one copepod, five cladocerans, and four rotifers. The number of species collected in lakes tended to decline with increasing elevation, both across all lakes and across those lakes containing fish (Spearman's r_s = -0.87 and -0.82, respectively, $P < 0.05$). Most of the increase in species richness with declining elevation was owing to increases in the species richness of cladocerans and rotifers. There were also differences in the species composition of zooplankton assemblages in lakes containing vs. lacking fish. The large calanoid copepod *Diaptomus eiseni* and the large cladoceran *Daphnia middendorffiana* were collected in all fishless lakes but were absent in all lakes containing fish. On the other hand, *Daphnia rosea* was a dominant zooplankter in all lakes with fish but was absent from lakes lacking fish. Although small species such as *Bosmina longirostris*, *Keratella cochlearis*, *Polyarthra vulgaris*, and *Trichocerca capucina* were collected in low numbers in fishless lakes, they only reached high relative abundance in lakes containing brook trout. The cladoceran *Ceriodaphnia affinis* was present in only the two lowest lakes, and only dominant in Aster Lake. *Diaptomus signicauda* was an important member of the zooplankton assemblage in all lakes.

The Emerald Lake zooplankton assemblage was very similar to that found in Pear Lake, a lake of similar elevation with trout. Despite elevational

gradients, the dominant species found in Emerald Lake (Diaptomus signicauda, Daphnia rosea, Bosmina longirostris, Keratella cochlearis, Polyarthra vulgaris) were dominant or common in other lakes containing brook trout.

Macroinvertebrates

A total of 25 macroinvertebrate taxa were identified from qualitative samples from lakes in the Kaweah River drainage (Table VI-3). Identification was resolved to genera in 19 taxa, family in 4 cases, and order in 2 cases. The most widespread taxon in the watershed was the Chironomidae, present in all lakes and the vernal pond, followed by clams (Pisidium sp.), water mites (Hydracarina) (absent only from the vernal pond) and alderfly larvae (Sialis) (present in 6 of 8 communities).

The number of macroinvertebrate taxa collected in sweep samples from the lakes ranged from 5 (Pear Lake) to 11 (Frog Lake) with an approximate mean of 8 (s.d. 2). A total of 7 taxa were collected from Emerald Lake. The Emerald community contained all of the most common taxa (those found in over 50 percent of the other lakes). It shared 86 percent of its taxa with at least 2 other lakes, and 57 percent with 5 or more of the remaining aquatic communities.

Emerald Lake community composition is most similar to those lakes which also have brook trout populations, containing 76 percent of the taxa found in those communities in comparison to only 43 percent in fishless environments. There was a significant absence of Callibaetis from communities with fish and a similar trend in hemipterans (Fisher exact test, $p = 0.1$ and $p = .07$, respectively). Other taxa largely, but not exclusively restricted to fishless lakes included dytiscid beetles and caddisflies. Conversely, the odonates were most closely associated with fish communities.

Amphibians were observed in three of the lakes. Single mountain red legged frogs (Rana aurora) adults were seen in Heather and Emerald lakes, and Pacific tree frog (Hyla regilla) larvae in Topaz Lake.

A greater number of taxa (36) were collected in the outlet streams than in the lakes. Taxon richness ranged from 5 (Lyness Lake) to 21 (Aster Lake) with an approximate mean of 12 (s.d. = 5). Emerald outlet samples contained 11 taxa (Table VI-4). The Chironomidae and Oligochaeta were present in all stream communities. Slightly less widespread were the blackflies (Simulium), mayflies (Baetis), and the predatory caddisfly (Rhyacophila), present in 6, 6, and 5 outflows, respectively. The Emerald Lake outflow stream shared all

the most common species found throughout the drainage. Of the 7 taxa found in over 4 of the stream communities, 5 were found in Emerald's outflow. Missing was a stonefly (Zapada), and water mites (Hydrocarina). Although the latter were not collected in these samples they have been observed on subsequent occasions (pers. obs. K. Kratz).

Outlet stream invertebrate compositions were less suggestive of a fish and fishless community dichotomy. Hemipterans were significantly absent, and fewer dytiscid beetle species were collected, from communities with fish (Fisher exact test, $p = .05$ and $p = .11$, respectively). The remaining taxa were apparently not constrained to either community type.

Discussion

Elevation and presence of fish seem to be the most important determinants of zooplankton community composition in lakes in the Marble Fork watershed. These results agree with those of Stoddard (1986) who sampled 75 lakes in the Sierra Nevada including Emerald, Pear, and Heather Lakes. Stoddard (1986) reported similar species complements in Emerald, Pear, and Heather Lakes to the ones that we found, indicating that the species composition of Sierran lakes may remain relatively constant. In accordance with our results, a number of investigators have observed decreasing zooplankton species richness with increasing elevation (Stoddard 1986, Patalas 1964, Reed and Olive 1958). In addition, the presence of fish had an affect on the distribution of zooplankton species with large species (maximum size > 2 mm) found only in fishless lakes, and some small species (maximum size < 1.2 mm) being only present or dominant in lakes with fish. It has long been known that large zooplankton will be eliminated by fish predation to the benefit of some small species (Brooks and Dodson 1965).

The zooplankton assemblage found in Emerald Lake is typical of those found in high elevation lakes containing brook trout (Stoddard 1986). In addition, the species found in Emerald Lake are widely distributed in the western U.S. and Canada (Stoddard 1986, Neill 1984, 1985). In general, then, the results of our zooplankton investigations in Emerald Lake should have wide implications for lake systems in western North America.

The pattern in the distribution of macroinvertebrates in the Kaweah drainage is related to the presence of brook trout. The capacity of fish predation to influence the community assemblage has been well documented

(Zaret 1980, Allan 1983). Prey vulnerability to severe cropping or extinction is generally positively related to size, mobility and conspicuousness (Healy 1981, Hemphill and Cooper 1984). Species absent from trout communities in this study are large or mobile, conspicuous taxa, e.g. baetids, hemipterans, dytiscid beetles, and caddisflies. The possibility of an elevational gradient determining the observed distributions of these species can be discounted as most are present in the outlet streams where greater habitat structure presumably confers a refuge from fish predation (Crowder and Cooper 1982).

Despite the influence of trout predation there is a large number of macroinvertebrate species in Emerald Lake with a broad distribution in the Kaweah drainage. These include the Ephemeroptera, sphaeriid clams, and plecopterans, all known to be intolerant of acidic input (Roff and Kwiatkowski 1977, Friberg et al. 1980, Singer 1982, Mackay and Kersey 1985).

In conclusion, Emerald Lake and its associated outflow stream contain zooplankton and benthic macroinvertebrate communities representative of other lakes in the Kaweah system. Therefore, conclusions based on Emerald Lake monitoring and experiments should be applicable to the remaining lakes in the Kaweah River drainage, and probably to lakes throughout the Sierra Nevada.

Table VI-1. Chemistry of six lakes within the Marble Fork of the Kaweah River drainage in late summer 1984 and 1985. Concentrations are in μeq l^{-1}.

SITE	DATE	DEPTH	pH	NH_4	NO_3	PO_4	HCO_3	Ca	Mg	Na	K	SO_4	Cl
Aster Lake	21 Sep 1984	SURF	6.4	0.3	0.2	0.4	35	24.7	5.5	11.0	3.5	5.5	3.6
	21 Aug 1985	SURF	6.6	0.7	0.3	0.5	45	23.7	5.6	24.7	4.4	7.1	4.6
Topaz Lake	22 Sep 1984	SURF	6.6	0.2	0.0	0.05	43	33.8	5.2	10.7	3.7	6.3	3.1
	22 Aug 1985	SURF	6.6	0.2	2.7	0.02	31	24.4	4.5	17.1	2.2	5.8	6.3
Frog Lake	22 Sep 1984	SURF	6.8	1.1	1.3	0.05	69	54.1	4.6	16.0	5.4	5.4	5.5
	22 Aug 1985	SURF	6.8	1.4	1.2	0.04	61	45.1	4.1	14.8	3.2	4.9	3.6
Heather Lake	21 Sep 1984	SURF	6.4	0.6	0.1	0.03	46	33.2	7.4	11.7	8.2	3.7	10.6
	21 Aug 1985	SURF	6.5	0.3	2.0	0.04	46	28.8	6.4	20.5	3.5	4.4	5.9
Hidden Lake	22 Aug 1985	SURF	6.6	0.3	0.2	0.02	44	31.9	3.7	11.1	2.5	2.8	1.8
Pear Lake	21 Sep 1984	SURF	6.4	0.2	0.1	0.03	22	16.8	3.4	7.0	2.2	3.8	2.4
	21 Sep 1984	INFLOW	6.5	0.3	14.8	0.03	32	36.4	4.5	12.0	2.1	5.3	3.4
	21 Aug 1985	SURF	6.4	0.2	2.5	0.02	25	16.8	4.0	14.6	3.2	4.8	2.9

Table VI-2. Zooplankton taxa and number of species collected from lakes in the Kaweah (or Tokopah) drainage in September, 1984, and August, 1985. D denotes dominant species, C indicates common species and X denotes species present.

		Lake	Date	Diaptomus signicauda	Diaptomus eiseni	Macrocyclops albidus	Tropocyclops prasinus	Daphnia rosea	Daphna middendorffiana	Ceriodaphnia affinis	Diaphanasoma brachyurum	Holopedium gibberum	Bosmina longirostris	Polyphemus pediculus	Macrothrix montana	Chydorus sphaericus	Alona sp.	Keratella cochlearis	Keratella quadrata	Polyarthra vulgaris	Conochilus unicornis	Trichocerca capucina	Ploesoma sp.	Lepadella sp.	Ascomorpha sp.	Salvelinus fontinalis	Number of species
FISHLESS	Lakes	Topaz Lake	22 Sep 84	X	D				C							X		X			D	X					7
			22 Aug 85	D	X	X							X							X	X	X					7
		Frog Lake	22 Sep 84	D	D				D				X		X	X		X		X							8
			22 Aug 85	D	D				X									X		X							5
		Lyness Lake	28 Aug 85	D	D				X												C						4
FISH	Lakes	Hidden Lake	22 Aug 85	X				D										D	X	C		X				X	6
		Pear Lake	21 Sep 84	X		X		D					X			X		X		C	X	C	C		X	X	11
			21 Aug 85	X				D			X		D	X				D		D		D	X			X	9
		Emerald Lake	15 Sep 84	C				D				X	D	X				D		D	X	X				X	9
			19 Aug 85	D				D				X	D	X		X		D		X	X	X				X	10
		Aster Lake	21 Sep 84	C		X		D		D	X		C				X	D		D		X	X		X	X	12
			21 Aug 85	D				X		D	C		X	X		X		D		X		X	C			X	11
		Heather Lake	21 Sep 84	D				D		X	X		X			C	X	D	X	D		X	X		X	X	13
			21 Aug 85	C		X	X	D		X	X	X	X			X	X	D		C		X	X	X		X	15

Table VI - 3. Taxa collected using qualitative sweep nets from Tokapah Drainage lakes, August 1985.

	Fish lakes				Fishless lakes			
Taxa	Aster	Emerald	Heather	Pear	Topaz	Frog	Lyness	Vernal
O. Ephemeroptera								
F. Baetidae								
g. Callibaetis					X	X	X	X
O. Odonata								
F. Libellulidae								
g. Sympetrum	X							X
F. Coenegrionidae								
g. Zoniagrion	X	X	X					
O. Hemiptera								
F. Corixidae								
g. Sigara					X	X		X
F. Notonectidae								
g. Notonecta								X
O. Megaloptera								
F. Sialidae								
g. Sialis	X	X	X	X			X	X
O. Trichoptera								
F. Limnephilidae			X					
g. Dicosmoecus							X	
g. Ecclisomyia						X		
g. Hesperophylax					X			
g. Onocosmoecus							X	
F. Rhyacophilidae								
g. Rhyacophila						X		
O. Coleoptera								
F. Dytiscidae								
g. Acilius								X
g. Agabus					X			
g. Deronectes	X					X		X
g. Hydroporus						X	X	X
g. Oreodytes			X			X		
O. Diptera								
F. Chironomidae	X	X	X	X	X	X	X	X
F. Ceratopogonidae								
g. Bezzia		X						
F. Simulidae								
g. Simulium						X		
O. Hydrocarina	X	X	X	X	X	X	X	

Table VI - 3 (continued). Taxa collected using qualitative sweep nets from Tokapah Drainage lakes, August 1985.

	Fish lakes				Fishless lakes			
Taxa	Aster	Emerald	Heather	Pear	Topaz	Frog	Lyness	Vernal
O. Heterodonta								
F. Sphaeridae								
g. Pisidium	X	X	X	X	X	X	X	
O. Oligochaeta		X	X	X			X	
F. Hirudinea	X		X		X			

Table VI - 4. Taxa collected using qualitative net sweeps of Tokapah Lake outlet streams, Sept. 1984 and Aug. 1985.

	Fish lakes					Fishless lakes		
Taxa	Aster	Emerald	Heather	Pear	Hidden	Topaz	Frog	Lyness
O. Ephemeroptera								
F. Baetidae								
g. Baetis	X	X		X	X		X	X
F. Ephemerellidae								
g. Caudatella	X							
g. Drunella	X							
g. Ephemerella	X							
F. Heptageniidae								
g. Cinygmula	X	X						
F. Siphlonuridae								
g. Ameletus							X	
O. Odonata								
F. Coenegrionidae								
g. Zoniagrion	X							
O. Plecoptera								
F. Nemouridae								
g. Malenka	X							
g. Nemoura		X			X			
g. Zapada	X			X	X	X		X
F. Perlodidae								
g. Kogotus							X	
g. Isoperla	X	X						
O. Hemiptera								
F. Corixidae								
g. Sigara						X	X	
F. Notonectidae								
g. Notonecta							X	
O. Megaloptera								
F. Sialidae								
g. Sialis	X			X			X	
O. Trichoptera								
F. Lepidostomidae								
g. Lepidostoma	X							
F. Limnephilidae								
g. Dicosmoecus		X		X				
g. Ecclisomyia		X		X			X	
g. Hesperophylax						X	X	
F. Rhyacophilidae								
g. Rhyacophila	X	X		X	X		X	

Table VI - 4 (continued). Taxa collected using qualitative net sweeps of Tokapah Lake outlet streams, Sept. 1984 and Aug. 1985.

	Fish lakes					Fishless lakes		
Taxa	Aster	Emerald	Heather	Pear	Hidden	Topaz	Frog	Lyness
O. Coleoptera								
F. Dytiscidae								
g. Agabus					X			X
g. Deronectes						X	X	X
g. Hydroporus							X	
g. Hydrovatus						X		
g. Oreodytes				X			X	
F. Elmidae								
g. Narpus	X			X				
g. Rhizelmus	X							
F. Hydrophilidae								
g. Helophorus							X	
g. Tropisternus	X							
O. Diptera								
F. Chironomidae	X	X		X	X	X	X	X
F. Empididae								
g. Clinocera	X							
F. Simulidae								
g. Prosimulium		X		X				
g. Simulium	X	X		X	X	X	X	
O. Hydrocarina	X			X	X		X	
O. Heterodonta								
F. Sphaeridae								
g. Pisidium	X			X			X	
O. Oligochaeta	X	X		X	X	X	X	X

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