

Chapter V

Short-term effects of storm runoff on stream chemistry

Based on hydrochemical data, Emerald Lake and the streams in its watershed do not show evidence of chronic acidification (Chapters II and III). However, episodic acidification of surface waters in the watershed may result from two types of events: the elution of an ionic pulse during the initial phase of snowmelt (Galloway et al. 1987, Stottlemeyer 1987, Dozier et al. 1989), and the runoff of acidic rainfall from summer storms (Marmorek et al. 1986). Episodic exposure to low pH can adversely affect fishes (Gunn and Noakes 1987, Cooper et al. 1988a), benthic invertebrates (Hall et al. 1980, Hopkins et al. 1988, Cooper et al. 1988b), and zooplankton (Chapter VI).

In this chapter, we examine the effects of storm runoff on the chemistry of inflowing streams at Emerald Lake during two summer storms in 1987. Short-term effects of storm runoff on surface waters are of interest to us not only because of the potential for effects on the aquatic biota, but also because comparison of the chemistry of runoff with that of rainfall can reveal chemical processes that occur as runoff travels through the watershed. Investigation of the processes that modify the chemical composition of rain before storm runoff reaches surface waters is important for understanding the effects of acidic deposition on alpine ecosystems.

Methods

The two storms occurred on 1 and 2 September 1987. With the exception of a light rain (1.5 mm) on 31 August, there had been no significant rainfall for 2.5 months prior to the storms, and soils were very dry at the surface. These storms were typical of convective summer storms at Emerald Lake, although smoke from extensive forest fires burning at lower elevations within 40 km of the lake had been visible in the watershed for several days before the storms.

Rain was collected in 25-cm polypropylene funnels mounted 1.2 m above the ground in a treeless area close to the lake. When rain appeared imminent, four acid-washed collection funnels and their attached reservoir bottles were taken from storage, copiously rinsed with deionized water, and mounted at the collection site. A manual rain gauge was installed near the funnels. Rain depth was also recorded automatically near the lake and at the upper cirque

of the watershed by Belfort rain gauges. The rain samples were collected immediately after the rain stopped. Samples from the four funnels were combined into one composite sample, from which unfiltered and filtered subsamples were taken. Duplicate subsamples were collected for analysis of pH. Subsamples were filtered immediately in the field, and chemical analyses were performed according to our routine protocol (Chapter II).

Inflows #1 and #4 were sampled at the routine sites close to the lake shore (Chapter I) shortly before and then throughout the spates that resulted from storm runoff. Staff gauge heights were recorded when samples were collected. At the peak of runoff during each storm, we also sampled water flowing off the bedrock (non-channelized overland runoff) at the foot of a small sub-basin (Aplite Dike), located 25 m to the east of the mouth of Inflow #1. This site was dry before and after the storms. All water samples were filtered in the field and analyzed according to our routine protocol. Discharge was determined for each sampling time from staff gauge heights using the rating curves of Dozier et al. (1987).

Results and Discussion

The chemistry of rain during the two storms is given in Table V-1. The rain was acidic, as is common for summer storms in the Sierra (Melack et al. 1982, Stohlgren and Parsons 1987), with substantial amounts of calcium, ammonium, nitrate, and sulfate. The first storm was considerably more acidic than the second one. The large anion deficit is normal for Sierran rain samples (ionic charges in lake and stream samples usually balance within 10 $\mu\text{eq L}^{-1}$), and was likely to be caused by organic anions, which were not measured.

Figure V-1 shows the changes in concentrations of major solutes in Inflow #1 during the 1 September spate. The spate was small: peak discharge was only 1.3 times the baseflow discharge. Changes in solute concentrations are clearly visible over the course of the spate; during peak runoff, acid neutralizing capacity (ANC) first decreased then increased, pH and silica decreased slightly, sodium showed little change, and the other major solutes increased. The observed changes are much greater than could be accounted for by analytical variation (Chapter II).

Figure V-2 contains chemical data for Inflow #4 during the 1 September spate. The peak discharge of Inflow #4 during this spate (0.4 L s^{-1}) was much

less than that of Inflow #1 (5 L s^{-1}), but the proportional increase in discharge over baseflow was greater in Inflow #4. The smaller watershed of Inflow #4 compared with Inflow #1 is evident from the hydrographs of the two streams during the storm; the runoff peak occurred sooner and was shorter in duration in Inflow #4. Chemical patterns in Inflow #4 during the spate are similar but not identical to those in Inflow #1. In particular, Inflow #4 differed from #1 in the patterns for ANC, which first increased then decreased in concentration (the reverse of the pattern in Inflow #1), and silica, which increased slightly in concentration at peak discharge.

Figures V-3 and V-4 show the chemistry during spates in the two inflows that resulted from the storm on 2 September. This storm was larger than the one on 1 September (Table V-1), and its effects on discharge in the two inflows were greater and longer-lasting. Chemical changes in the two inflows during the resulting spates were also greater, as expected, because storm runoff comprised a greater proportion of the peak discharge in the streams. Most solutes in the two inflows showed similar patterns of increased concentrations at peak discharge. However, silica decreased in concentration in both inflows (as in Inflow #1 on 1 September), and ANC increased in concentration at first, then decreased (as in Inflow #4 on 1 September).

Table V-2 compares solute concentrations in the rain with those in the non-channelized overland runoff for each storm. Most solutes increased in concentration in the runoff during both storms. The concentration of ammonium increased in runoff during the first storm, but decreased during the second storm. These results generally agree with the changes observed in the streams.

Changes in the chemistry of the inflowing streams during these spates are not likely to adversely affect the aquatic biota (Marmorek et al. 1986). The observed depression in pH is small, entailing only $<1 \mu\text{eq L}^{-1}$ of change in H^+ . Although other solutes show strong patterns of change during the spates, these are probably not great enough to be biologically important. However, comparison of the solute concentrations in rain during the two storms (Table V-1) with that of the streams before the spates suggests that simple conservative mixing of the two waters does not explain the changes in solute concentrations observed in the streams during the spates. The possibility that the chemistry of storm runoff was altered during passage through the watershed merits closer examination.

Direct comparison of the solute concentrations in the inflows with concentrations in the rain is complicated by several factors. First, even at peak discharges, baseflow probably contributed significantly to the total discharge, and the relative proportions of water from baseflow and storm runoff varied between inflows and between storms. Second, the rain samples were composites for the entire storm, and therefore do not show changes in rain chemistry that may have occurred during the storm.

In order to interpret the chemical patterns without these complications, we formulated a simple null model of mass transport in the streams that integrates the patterns over time. Assumptions of the model are:

- 1) the initial sampling time represents baseflow discharge and chemistry;
- 2) stream baseflow was stable over the course of the storms;
- 3) increases in discharge after the initial sampling were caused solely by overland (Hortonian) runoff, because there was very little pre-existing soil water in the watershed that could have been purged out by rainwater percolating through soils; and
- 4) for the model predictions, storm runoff into the streams has the same chemical composition as the rain.

Each sampling time was taken as the midpoint of a time interval. Transport of water and solutes over the time interval was calculated from stream discharge and chemistry at each sampling time. Total transport over the course of the spate was obtained by summation of the transport over each interval. Baseflow transport during the spate, as determined from the initial sampling, was then subtracted from the total transport to give transport resulting from storm runoff. This is the observed transport for each solute: the corresponding predicted transport was calculated from the chemistry of the rain sample and the storm runoff discharge.

The predicted transport assumes that rain water passes through the watershed to the streams without change in chemical composition. Comparison of observed with predicted transport allows us to examine changes in the chemistry of rain water during runoff through the watershed. For example, if runoff dissolves materials from the rock surfaces, observed transport would exceed predicted transport for those materials. Conversely, runoff may lose solutes by processes such as adsorption in soils; losses would cause the observed transport to be less than predicted.

Several caveats concerning the model deserve mention here. First, the rain samples are from a single site near the lake. Consequently, spatial heterogeneity in the chemistry of rain over the Emerald Lake watershed could affect the model predictions of solute transport. However, the amount of rain was uniform throughout the watershed: the Belfort gauges located across the lake and in the upper watershed showed no differences in rain depth for the 1 September storm, and only 0.8 mm difference (< 10%) for the 2 September storm. Second, the error in the estimates of observed and predicted transport is directly related to errors in the discharge estimates, which are likely to be greater than our analytical error. The discharge estimates would have to be very inaccurate to affect our conclusions, however. Finally, another source of error is our assumption that the initial sample represents the baseflow chemistry for the stream over the course of the spate. Sampling and analytical errors as well as normal temporal variation in stream chemistry affect the accuracy of this assumption.

In two cases the chemistry of the initial sample could not be used to represent baseflow chemistry: in Inflow #4 on 2-3 September, initial concentrations of nitrate and ammonium appeared anomalously high, so concentrations from the end of the sampling period were used to estimate baseflow transport. The storm may have already affected these variables in Inflow #4 before the initial sample was taken; rain began at 1615 h and the sample was collected at 1634 h. The stage had not yet increased when the sample was collected.

Table V-3 summarizes the results of the mass transport modelling. The ratios of observed to predicted transport generally show that strong changes in the content of solutes in rain water occurred during runoff. Runoff from both storms consistently lost H^+ and ammonium and gained ANC, sodium, and silica. The data for both inflows show that runoff from the 1 September storm also gained calcium, magnesium, and potassium. Other solutes show greater variation in the ratios between the two inflows and the two storms, although substantial change is indicated in most cases.

Changes in the chemistry of runoff are most likely to result principally from interaction with rock surfaces, soils, and other surficial material. The long drought prior to the storms and the short residence time of runoff in the watershed during the stream spates make weathering and biotic uptake likely to be less important than ion exchange in soils and dissolution of materials from

previously dry surfaces. The watershed of Inflow #4 is mainly exposed rock, while that of Inflow #1 contains significant soil areas as well as exposed rock. Comparison of the modelling results for these two inflows can therefore provide an indication of the influence of soils on runoff chemistry. The ratios of observed to predicted transport in Table V-2 indicate that the major changes in the solute content of runoff, when they occurred, were similar in magnitude in the two inflows, despite the differences in soil coverage. Comparable changes in the solute content of rain were also observed in the non-channelized runoff from Aplite Dike (Table V-2), which originated in a small watershed with very little soil cover.

The observed changes in solute content of runoff could have resulted from contact of rainwater with material on rock and vegetation surfaces, possibly including material that was deposited by atmospheric dry deposition. The long dry period preceding the two storms would have resulted in the accumulation of dry deposition on exposed surfaces (Bytnerowicz and Olszyk 1988). The first storm (1 September) may not have been large enough to thoroughly wash the surfaces, leaving enough material to affect runoff in the following storm. This hypothesis is consistent with the modelling results, which show that gains in solutes were relatively greater during runoff from the first storm than from the second one. The non-channelized runoff data also show this pattern, although the higher acidity of the first storm could also explain this difference. The hypothesis that dry deposition caused the chemical changes in runoff is speculative, however, and the problem requires additional investigation.

Conclusions

Changes in concentrations of major solutes occurred during spates that resulted from two summer storms in 1987. However, acidification of the streams was much less severe than expected on the basis of rain chemistry, and was unlikely to be of biological significance. A null model of mass transport in the streams during the spates is used to show that the solute chemistry of rain changed substantially during runoff through the watershed. The net effect of these changes was to neutralize acidity and to increase ANC in storm runoff before it reached the lake. Chemical changes during runoff in the watershed of Inflow #4, which is dominated by exposed rock, resembled those during runoff in the watershed of Inflow #1, which contains more soil and vegetation. This

observation implies that the changes may be caused by contact of runoff with material on surfaces, possibly including dry deposition, rather than by reactions in soils. Comparison of rain chemistry with the chemistry of non-channelized overland runoff from a small sub-basin mainly composed of rock also supports the observation that chemical changes in rain water occur during runoff over rock surfaces. If this hypothesis is correct, the magnitude of these changes would presumably decrease with increasing intensity and frequency of precipitation, because the supply of material on surfaces would be limited.

Table V-1. Chemistry of rain collected during the stream spates.
 Concentration units are $\mu\text{eq L}^{-1}$ except silica ($\mu\text{M Si}$).

	1 Sept. 1987	2 Sept. 1987
duration	1645-1715 hr	1630-2000 hr
depth (mm)	3.8	8.4
pH	4.29	5.12
H ⁺	50.7	7.6
ANC	0	0
Ca ²⁺	16.8	56.8
Mg ²⁺	3.8	9.0
Na ⁺	6.1	6.2
K ⁺	4.8	6.9
Cl ⁻	5.9	6.4
SO ₄ ²⁻	35.5	49.5
NO ₃ ⁻	25.6	54.2
NH ₄ ⁺	17.0	93.2
Si	0.5	3.6
conductance ($\mu\text{S cm}^{-1}$; 25°C)	24.2	34.9
sum of cations	99	180
sum of anions	67	111
cations:anions	1.5	1.6

Table V-2. Comparison of rain chemistry with the chemistry of non-channelized overland runoff from the Aplite Dike, a small sub-basin composed mainly of exposed bedrock. The runoff was sampled near the lake at the peak of the storm. Concentration units are $\mu\text{eq L}^{-1}$ except silica ($\mu\text{M Si}$).

	1 September 1987		2 September 1987	
	rain	runoff	rain	runoff
pH	4.29	5.60	5.12	5.76
H ⁺	50.7	2.5	7.6	1.7
ANC	0	48.2	0	61.3
Ca ²⁺	16.8	124.8	56.8	101.1
Mg ²⁺	3.8	26.2	9.0	22.0
Na ⁺	6.1	26.6	6.2	17.3
K ⁺	4.8	61.9	6.9	47.7
Cl ⁻	5.9	47.0	6.4	29.3
SO ₄ ²⁻	35.5	67.5	49.5	60.8
NO ₃ ⁻	25.6	87.9	54.2	84.0
NH ₄ ⁺	17.0	34.9	93.2	63.8
Si	0.5	16.7	3.6	10.0
conductance ($\mu\text{S cm}^{-1}$; 25°C)	24.2	51.5	34.9	47.9
sum of cations	99	277	180	254
sum of anions	67	251	111	235
cations:anions	1.5	1.1	1.6	1.1

Table V-3. Comparison of observed chemical transport during the spates with that predicted by the null model of mass transport.

solute		1 September 1987		2-3 September 1987	
		Inflow #1	Inflow #4	Inflow #1	Inflow #4
H ⁺ (meq)	observed	19	0.7	102	5
	predicted	350	24.4	931	56
	ratio	0.05	0.03	0.11	0.08
ANC (meq)	observed	203	17	4020	223
	predicted	0	0	0	0
	ratio	--	--	--	--
Ca ²⁺ (meq)	observed	487	22.1	4872	172
	predicted	116	8.1	6961	419
	ratio	4.19	2.73	0.70	0.41
Mg ²⁺ (meq)	observed	107	5.2	1001	33
	predicted	26	1.8	1103	66
	ratio	4.07	2.89	0.91	0.50
Na ⁺ (meq)	observed	139	8.5	1934	77
	predicted	42	2.9	760	46
	ratio	3.29	2.93	2.54	1.67
K ⁺ (meq)	observed	184	6.3	935	12
	predicted	33	2.3	846	51
	ratio	5.56	2.74	1.11	0.24
Cl ⁻ (meq)	observed	143	5.1	1533	22
	predicted	41	2.8	784	47
	ratio	3.51	1.82	1.95	0.47
SO ₄ ²⁻ (meq)	observed	258	7.1	1713	29
	predicted	245	17.1	6066	365
	ratio	1.05	0.42	0.28	0.08
NO ₃ ⁻ (meq)	observed	377	6.3	4028	32
	predicted	177	12.3	6642	399
	ratio	2.13	0.51	0.61	0.08
NH ₄ ⁺ (meq)	observed	85	0.1	222	5
	predicted	118	8.2	11423	687
	ratio	0.72	0.01	0.02	0.01
Si (mmoles)	observed	157	21.8	3758	269
	predicted	3	0.2	441	27
	ratio	45.5	109.0	8.52	9.96

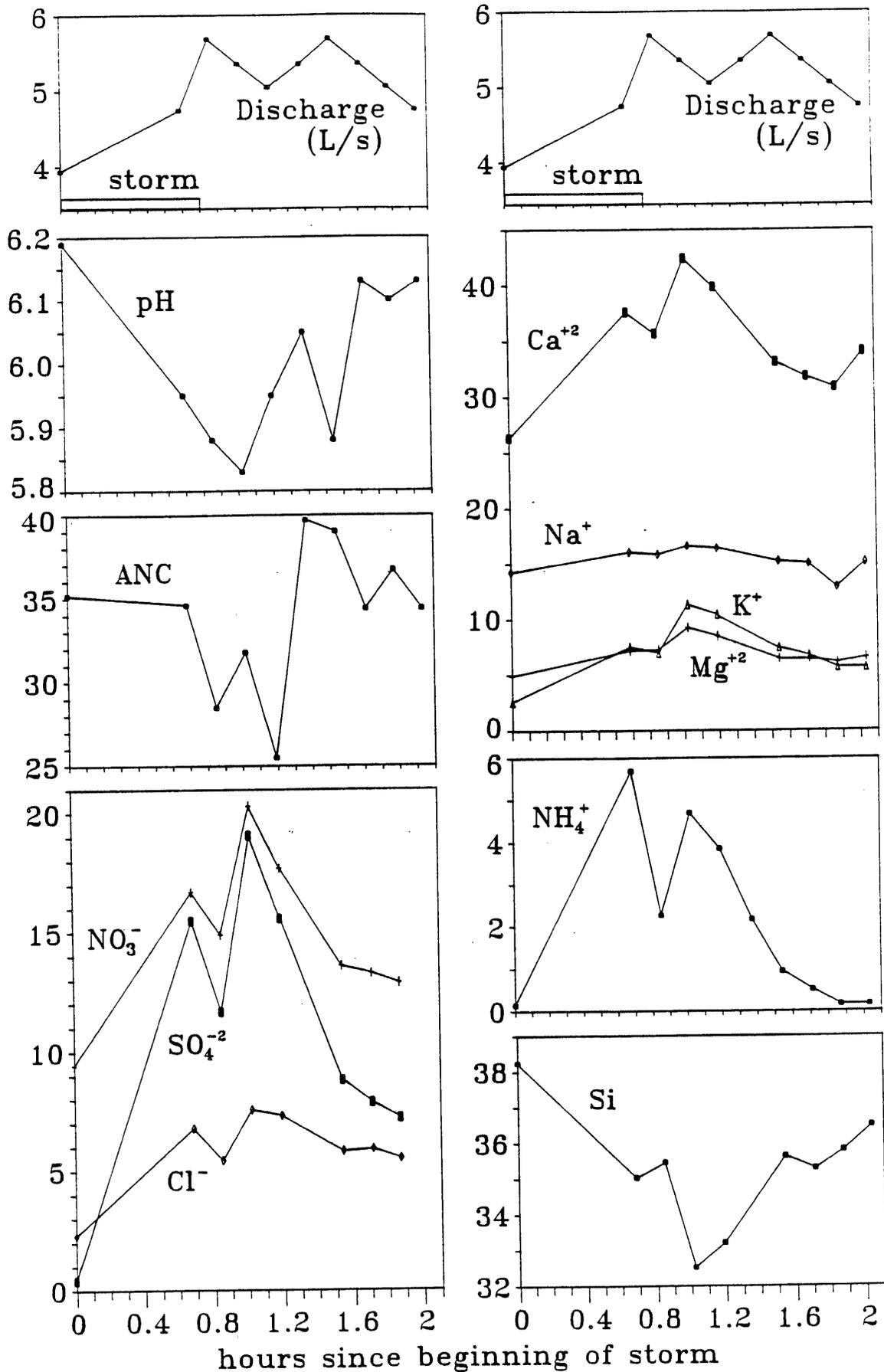


Fig. V-1. Chemistry of Inflow #1 during the 1 September 1987 spate. Concentration units are $\mu\text{eq L}^{-1}$ except Si (μM).

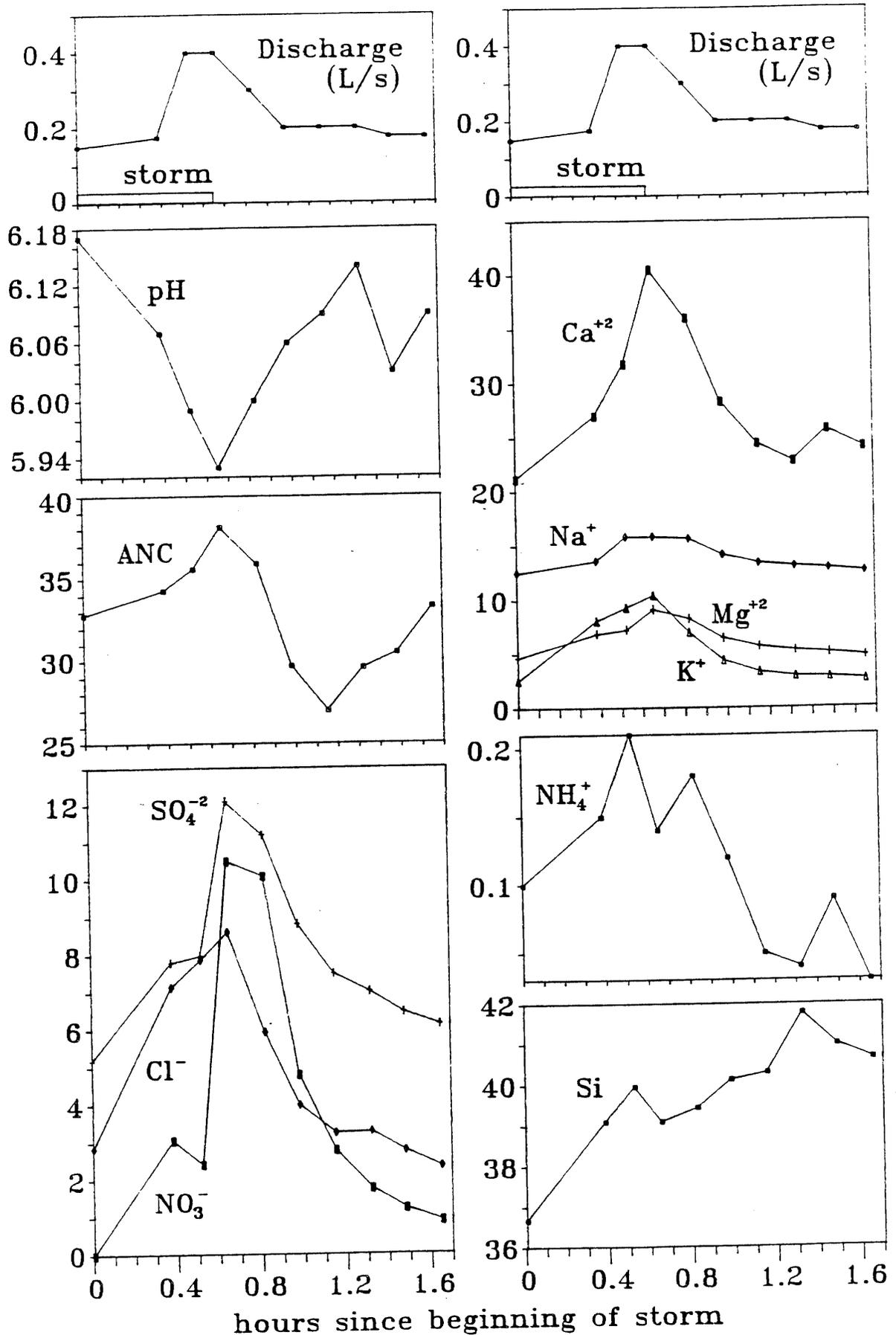


Fig. V-2. Chemistry of Inflow #4 during the 1 September 1987 spate. Concentration units are $\mu\text{eq L}^{-1}$ except Si (μM).

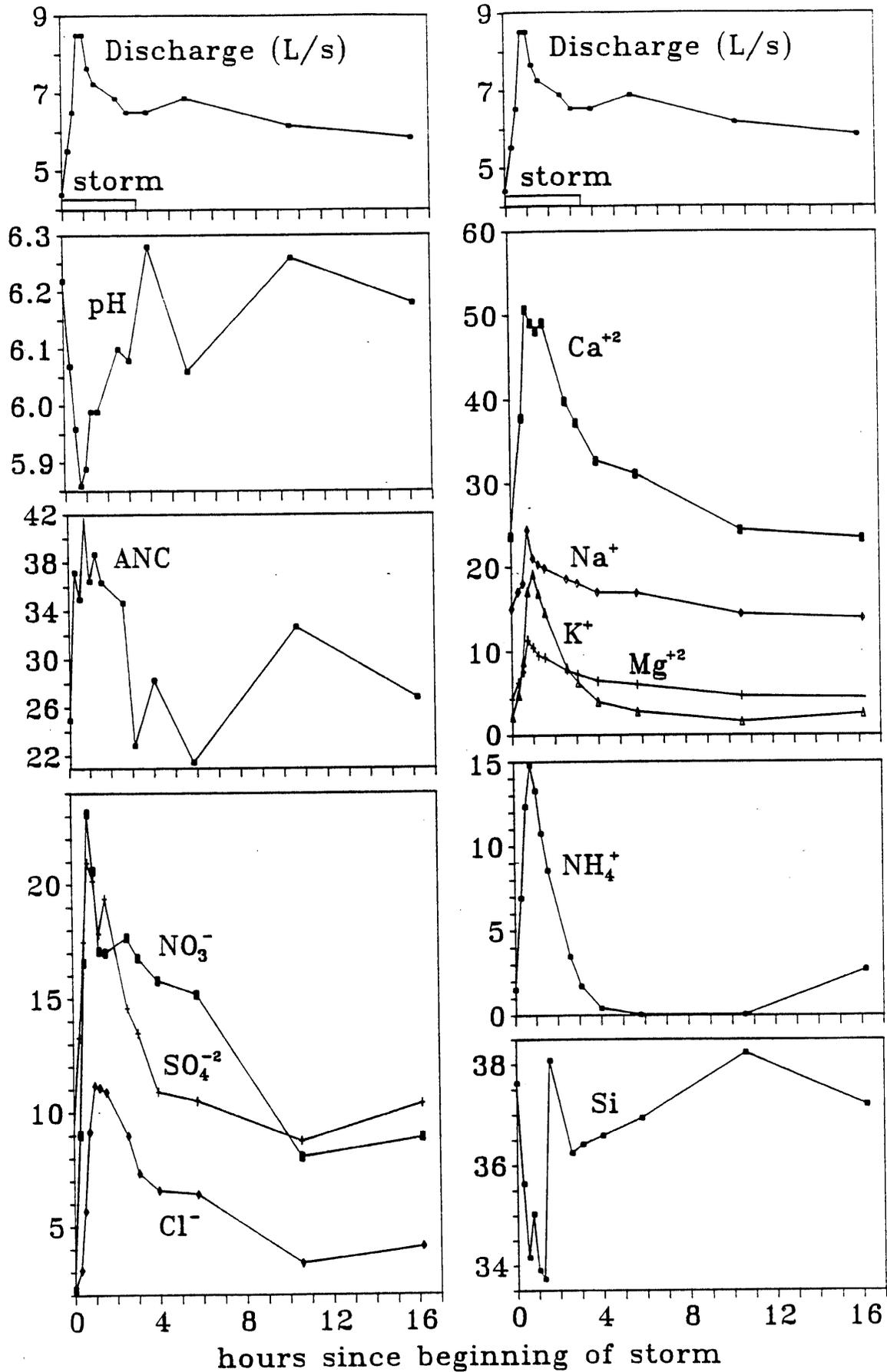


Fig. V-3. Chemistry of Inflow #1 during the 2-3 September 1987 spate. Concentration units are $\mu\text{eq L}^{-1}$ except Si (μM).

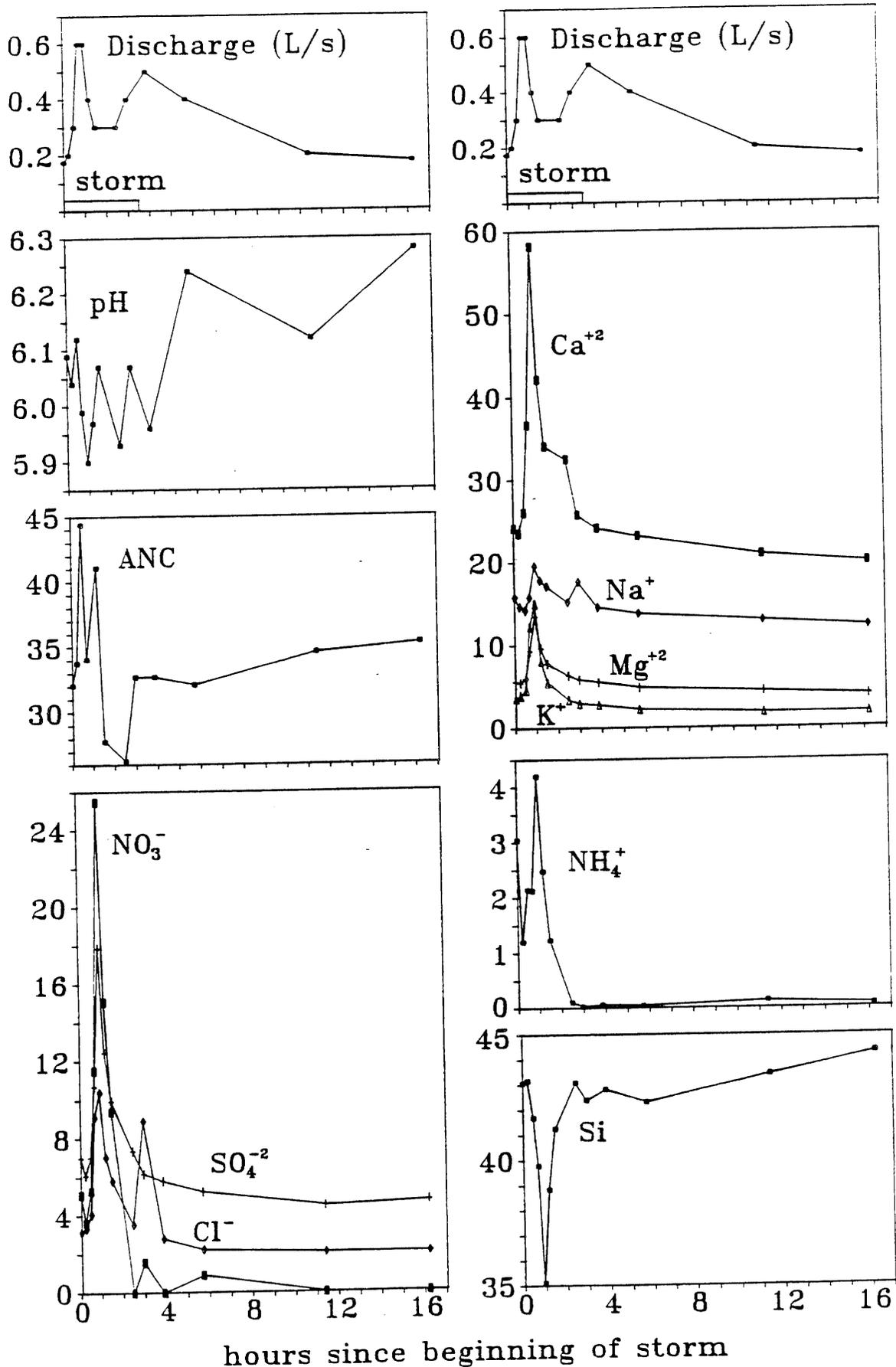


Fig. V-4. Chemistry of Inflow #4 during the 2-3 September 1987 spate. Concentration units are $\mu\text{eq L}^{-1}$ except Si (μM).

Chapter VI

Experimental acidification of enclosures in Emerald Lake

Acidification of lakes and streams by atmospheric deposition can seriously affect the aquatic biota (Schindler et al. 1985). Responses of zooplankton to acidification commonly include a reduction in species diversity and biomass and a shift in the dominant species (Yan and Strus 1980, Marmorek 1984, Havens and DeCosta 1985, Malley and Chang 1986, Havens and DeCosta 1987). The zoobenthos also includes taxa that are sensitive to acidification, although most experimental studies have focussed on streams (Hall et al. 1980, Burton et al. 1985, Hall and Ide 1987, Ormerod et al. 1987, Hopkins et al. 1988) rather than on lakes (Schindler et al. 1985).

In the Sierra Nevada of California, acidic deposition has been reported in the Tahoe basin and on both the eastern and western slopes (Leonard et al. 1981, Dozier et al. 1987, Stohlgren and Parsons 1987, California Air Resources Board 1988). The lakes and streams of the Sierra Nevada are among the most weakly buffered in the world (Landers et al. 1987), and are thus potentially susceptible to acidification by atmospheric deposition, although chronic acidification of Sierran lakes has not been documented (Melack et al. 1985).

The biological effects of lake acidification have been studied primarily in eastern North America and Europe. Application of the results of these studies to the high-altitude lakes of the Sierra Nevada may not be appropriate because of differences in climate, hydrology, and biotic assemblages. Consequently, in situ experimental investigations are necessary to predict the consequences of increased acid loading to Sierran lakes. Study of the pH tolerances of aquatic biota may also reveal particularly sensitive species that could serve as early-warning indicators of acidification in future monitoring programs (Mills and Schindler 1986).

Melack et al. (1987) acidified large enclosures in Emerald Lake to examine the responses of phytoplankton and zooplankton. Additions of various combinations of strong acids and neutral salts showed that the effects of acid addition on zooplankton were caused by the hydrogen ion rather than by indirect effects of fertilization with nitrate or sulphate. These experiments suggested that the crustaceans Daphnia rosea Sars emend. Richard and Diaptomus signicauda Lilljeborg and the rotifer Conochilus unicornis (Rousselet) were adversely affected by acidification below pH 5.5, while the cladocerans Bosmina

longirostris (Müller) and Holopedium gibberum Zaddach and the rotifer Keratella taurocephala Ahlstrom were tolerant of acidic conditions until the pH dropped below 5.0.

We here report results of an enclosure experiment designed to determine the responses of the zooplankton and zoobenthos of Emerald Lake to decreased pH. The purpose of this experiment was to corroborate the findings of earlier experiments and to define more precisely the pH tolerances of key species of crustacean zooplankton in Emerald Lake. In contrast to earlier experiments, we included the lake sediments in the enclosures, thereby making the environmental conditions of the experiment more realistic. The inclusion of sediments also permitted us to examine the responses of the zoobenthos to experimental acidification of the overlying water column.

Methods

Design and installation of enclosures

Eighteen cylindrical enclosures made of clear polyethylene (4 mil) were suspended vertically through the water column from floating platforms anchored in the east-central part of the lake. Each enclosure was kept taut by hoops of PVC pipe (1.3-cm dia) secured at 1-m intervals, and a circular frame of PVC pipe (2.5-cm dia) at the base of the enclosures facilitated their insertion into the sediments. The enclosures were 1 m in diameter and extended from above the lake surface through the 9.7-m water column to the sediments, enclosing approximately 7.6 m³ of water.

The enclosures were allowed to leach underwater for seven days while tied near the surface of the floating platforms. On 29 July 1987, SCUBA divers pulled the bottoms of the enclosures down from the surface to the sediments, taking care to enclose the water column as evenly as possible, and gently implanted the bases of the enclosures in the soft mud to a depth of 0.2-0.5 m. We sampled the enclosures twice (30 July and 4 August) before acidification.

On each sampling date, vertical profiles of temperature and dissolved oxygen were measured in each enclosure, as well as in the open water near the enclosures, using a polarographic oxygen electrode and a thermistor. Samples for chemical analyses were collected with a Kemmerer sampler from depths of 1 and 7 m. A subsample was filtered in the boat through 24- μ m Nitex mesh with the intent of size-fractionating the phytoplankton, removing large forms that

are less likely to be consumed by zooplankton. We also sampled the zooplankton (see below).

To facilitate efficient mixing of acid we attempted to destratify the enclosures on 31 July and 4 August by pulling a mixer consisting of plastic baskets (0.4-m wide) on a weighted line through the water column twenty times in each enclosure. The temperature in the enclosures was 16.3°C at 1 m and 13.9°C at 8 m before mixing, and 15.9° at 1 m and 15.2° at 8 m immediately afterward.

Each enclosure was randomly assigned an experimental treatment. There were six treatments, each with three enclosures: control (pH ca. 6.3), and pH 5.8, 5.4, 5.3, 5.0, and 4.7. These treatments were chosen on the basis of our earlier experiments to define precisely the pH tolerances of the zooplankton. The enclosures were acidified with a 0.5-N stock solution of nitric and sulfuric acids (1:1 by equivalents). The acid was added by pumping a measured volume of the stock solution through a 6-mm Tygon tube that was attached to the mixer; addition of acid as the mixer was raised ensured that the acid solution was mixed immediately and evenly into the enclosure. The acid addition was followed by another twenty mixings, after which samples were taken from depths of 1, 5, and 8 m for field measurement of pH. We added two-thirds of the required quantity of acid on 4 August and the remaining third on the following day, which was designated as Day 0 of the experiment.

The enclosures were sampled for chemistry and zooplankton on 7 August (Day 2), two days after pH adjustment, and again on 12 August (Day 7). Beginning on 12 August, we collected an additional water sample from 9 m in each enclosure to ensure that vertical differences in pH were adequately documented. Sampling continued at approximately weekly intervals through 9 September (Day 35). The pH of the enclosures was maintained within 0.1 unit of the target pH by adding acid after each weekly sampling; addition of base was never required. One of the pH 5.0 enclosures was lost when it was dislodged from the sediments by high winds; consequently, there were only two replicates for this treatment on the last two sampling dates.

Chemistry

In the laboratory, water samples were analyzed for pH (electrode), acid neutralizing capacity (Gran titration), major cations (flame atomic absorption), major anions (ion chromatography), ammonium (indophenol method), phosphate

(molybdenum blue method), silica (silico-molybdate method), and iron and aluminum (graphite furnace atomic absorption). Analytical methods are detailed in Melack et al. (1989). We first analyzed samples from the control and pH 4.7 treatments for all major solutes from before acid addition on 3 August (i.e. Day -1) and Days 2, 14, and 35; additional treatments and dates were analyzed only for variables that showed substantial differences resulting from acidification. To provide an indication of phytoplankton biomass, material collected on filters was analyzed for particulate carbon and nitrogen with an Elemental Analyzer, and for chlorophyll-a by fluorometric measurement after the filters were soaked overnight in 90% acetone. The subsamples filtered through the 24- μ m mesh were analyzed for chlorophyll-a and particulate carbon and nitrogen.

Zooplankton

Zooplankton in the enclosures was sampled by taking a vertical tow from the bottom to the top of each enclosure using a 0.12-m diameter net with 64- μ m mesh. Samples were immediately preserved with 5% formalin. In addition to the weekly samples from the enclosures, zooplankton was sampled fortnightly at five stations in the lake by taking vertical net tows from the bottom to the surface. These samples were compared with those taken from the control enclosures to determine whether zooplankton densities in the lake and enclosures were similar.

In the laboratory, zooplankton samples were diluted and subsampled with a Stempel pipette, and zooplankters were identified and counted at 25 X under a dissecting microscope. Microcrustaceans and rotifers were subsampled separately 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 each subsample usually comprised from 0.05 to 10% and from 0.05 to 5% of microcrustacean and rotifer samples, respectively. In several cases the entire sample was counted.

Zoobenthos

On 22 July, before the enclosures were pulled down through the water column, divers used a PVC core sampler (15-cm dia, 30-cm long) to collect duplicate benthic samples from the future site of each enclosure, then marked the core sites with small plastic flags to ensure that identical spots would

not be resampled later. At the end of the experiment divers slit the enclosures near the sediments and again collected duplicate cores from within each enclosure. Samples were concentrated in the field using a 250- μ m mesh sieve and preserved in 70% ethanol. In addition, zoobenthos at six sites in the lake was sampled with an Ekman grab (one sample per site) near the beginning and end of the experiment; these samples were compared with those from the enclosures. In the laboratory, Rose Bengal was added to stain the invertebrates, which were then sorted using dissecting microscopes, and identified to species when possible.

Data analysis

In order to compare the depth-integrated zooplankton samples to the chemical data for discrete depths, volume-weighted means of the chemical variables for each enclosure on each date were calculated. Thermal profiles in the enclosures were used to estimate the volumes of the epilimnion and hypolimnion during thermal stratification. Thermal layering inside the enclosures resembled that of the water column outside. During the first three weeks of the experiment, there was a pronounced thermocline at 7-8 m; the enclosures were isothermal during the last two weeks (Fig. VI-1).

Analyses of variance (ANOVA) were performed on the response variables to check for significant differences among the enclosures assigned to the different treatments before acidification. For chemical data, only the samples from 4 August (Day -1) were included. Zooplankton data from both 30 July (Day -6) and 4 August (Day -1) were included. Statistical analyses of the zooplankton data were limited to the most abundant taxa. Heterogeneity of between-treatment variances was checked using the F_{\max} test and, where appropriate, data were log-transformed and the analysis repeated.

Since this experiment was a split-plot or repeated measures design, post-acidification data were analyzed using profile analysis, which is a multivariate alternative to repeated measures ANOVA. Profile analysis was used because it has less restrictive assumptions than conventional univariate repeated measures ANOVA and is generally considered a more robust technique (Harris 1985). This technique treats observations on each day as dependent variables in a multivariate analysis of variance (MANOVA) to test for effects due to the repeated factor (i.e., Day) and its interaction with pH, while the main effect due to pH is tested with a univariate ANOVA (Harris 1985, Morrison 1976). As

in repeated measures ANOVA, a non-significant interaction indicates that the shape of the profile of the response variable over time is parallel between levels of pH, and permits valid testing for significant differences between days and between levels of pH. The F-ratios reported for the multivariate test statistics were calculated using Pillai's trace since this is among the most robust of the multivariate test statistics (Green 1979, Harris 1985).

Profile analysis was used on the zooplankton and chemical data to identify variables which responded consistently to manipulation after acidification. For those zooplankton species showing responses to acidification, the nature of their response was investigated using regression rather than by testing contrasts within the ANOVA design. This was done because the pH of replicate enclosures within treatments varied over the course of the experiment. The pH values were transformed to H^+ concentrations for calculation of means. The mean pH for each enclosure over each time interval was calculated from samples taken at the beginning and end of each interval (i.e. from the pH measured after adding acid in the previous week and from the pH measured immediately before readjustment of the pH by acid addition). The appropriateness of the regression models was checked by inspecting residuals, and the data were log-transformed where necessary.

Zoobenthic responses were examined using multivariate analysis of variance with the most abundant taxa as dependent variables. We also used exploratory techniques (multidimensional scaling and cluster analysis) using data on all of the taxa collected to see whether there were any changes in overall community composition that were not reflected by the common species alone. The latter techniques were based on the Kulczynski dissimilarity coefficient, which has been shown to be suitable for use with ecological data (Faith et al. 1987).

Results

Chemistry

For each treatment, the volume-weighted mean pH for each time period, as well as the overall means for the duration of the experiment, are presented in Table VI-1. Table VI-2 compares the concentrations of major solutes and trace metals in the control treatment with those in the most acidified (pH 4.7) treatment during the experiment. Only concentrations of magnesium ($P = 0.04$) and ammonium ($P = 0.02$) showed significant, but small ($<0.3 \mu\text{eq L}^{-1}$), differences

among enclosures assigned to different treatments before acidification; these differences did not persist for the rest of the experiment (Table VI-2). Addition of nitric and sulfuric acids directly affected pH, ANC, and concentrations of nitrate and sulphate. Of the other solutes, only potassium and aluminum showed significant differences in concentration between treatments ($P = 0.03$ and $P < 0.001$, respectively). The concentration of potassium also showed a significant interaction; it was higher in the pH 4.7 enclosures on Day 2, but lower than the control at the end of the experiment. The concentration of aluminum was consistently higher (mean difference, $0.4 \mu\text{M}$) at pH 4.7 throughout the experiment.

The data for nitrate and sulphate permit estimation of the importance of reduction reactions that might have decreased the concentrations of these anions in the enclosures. Such reactions are important because the reduction of nitrate or sulphate results in ANC generation, which in turn contributes to the recovery of water bodies from acidification (Schnoor and Stumm 1985, Schindler 1985). Nitrate and sulphate were added to the enclosures in a 1:1 ratio, by equivalents. Loss processes, which at a particular depth are unlikely to affect nitrate and sulphate equally, will change the ratio of these anions over time.

A t-test comparing the deviations of the observed ratios from 1:1 in the pH 4.7 enclosures was used to test the hypothesis that concentrations of nitrate and sulphate in this treatment were unaffected by differential loss processes. Before computing the ratios, the mean concentrations of the anions in the controls on each date were subtracted from the concentrations in the acidified treatment. There were no significant deviations from a 1:1 ratio ($P > 0.10$) for any of the dates after acidification. There was no tendency for the difference in concentrations to be greater close to the sediments (at 9 m), as would be expected if dissimilatory reduction were important, or in the lower water column (at 7 m), as would be expected if nitrate assimilation by phytoplankton were important.

Concentrations of particulate carbon, particulate nitrogen, and chlorophyll-a over the course of the experiment are presented in Figure VI-2. These variables were measured to assay phytoplankton biomass in the enclosures. Concentrations of particulate carbon and nitrogen did not differ significantly among the treatments at the beginning of the experiment ($P > 0.25$) and, although these variables fluctuated over time, there were no consistent patterns

attributable to pH treatment (Fig. VI-2). However, the volume-weighted mean concentrations of chlorophyll-a on Day -1 indicate that phytoplankton biomass differed significantly among the treatments at the beginning of the experiment ($P = 0.022$). The profile analysis showed that these differences persisted throughout the experiment. A posteriori tests (Tukey's HSD) among the treatment means show that only the pH 6.3 and 5.2 treatments differed significantly from each other, and that there was no direct correspondence between chlorophyll-a concentration and the level of acidification (Fig. VI-2).

Data for the samples filtered through a 24- μm Nitex mesh are not presented here. Chlorophyll-a concentrations for a representative subset of mesh-filtered samples ($n = 85$) were compared with chlorophyll-a in the corresponding unfiltered samples using a t-test for paired comparisons. Filtration through the mesh had no significant effect ($P > 0.10$) on chlorophyll-a concentrations. Algae large enough to be retained by a 24- μm mesh were evidently not a significant component of the phytoplankton in the enclosures. The t-test for particulate carbon and nitrogen in a smaller subset of samples ($n = 65$) showed that filtration significantly reduced concentrations of these variables ($P < 0.001$). We attribute this to the removal of zooplankton by the mesh; in the field, we observed that nearly all the material retained by the mesh was zooplankton.

Zooplankton

The major taxa of zooplankton were the cladocerans Daphnia rosea, Bosmina longirostris and Chydorus cf. sphaericus, the calanoid copepod Diaptomus signicauda and its nauplii, and three species of rotifers: Trichocerca capucina (Wierzejski), Polyarthra vulgaris Carlin, and Keratella taurocephala. The latter species was incorrectly identified as K. cochlearis in Melack et al. (1987). Several taxa, including the cladoceran Holopedium gibberum, the cyclopoid copepod Cyclops sp., and the rotifer Conochilus unicornis, were also found in the enclosures, but they were not abundant enough for their responses to acidification to be quantified.

Prior to adding acid, Diaptomus signicauda was the only taxon that differed significantly ($P = 0.005$) in abundance with respect to the pH treatments assigned to the enclosures; it was more abundant in the enclosures assigned to the pH 6.3, 5.0 and 5.4 treatments compared to the pH 5.8 and 4.7 treatments.

The profile analyses are summarized in Table VI-3. Five species showed significant effects due to pH, and four of these also changed in abundance over the duration of the experiment. Examples of the different sorts of responses to the treatments over time are shown in Figure VI-3. In the case of Daphnia rosea, the effect of time was significant, but there was no simple temporal trend; the same was true of Diaptomus signicauda and Polyarthra vulgaris. Nevertheless, the effects due to pH, where present, were consistent on each date as evidenced by the lack of significant interactions between time and pH (Table VI-3), although the effects were not fully apparent until after Day 7 (Fig. VI-3).

To summarize the relationship with pH, the mean abundances of each species in each enclosure over the period Day 7 to Day 35 inclusive were plotted against the mean pH of that enclosure over the same period (Fig. VI-4). Daphnia rosea and Diaptomus signicauda both declined with decreased pH, whereas Keratella taurocephala showed the opposite trend. Bosmina longirostris showed the most complex pattern of response, being least abundant in the control and most acidic enclosures, but increasing as pH dropped from 6.3 to ca. 5.2. Copepod nauplii showed a significant response to acidification in the profile analyses, and Figure VI-4 indicates that this was due to reduced abundances in the lowest pH treatments; above pH 5.0, however, there was no strong relationship.

The abundance of Keratella was log-linearly related to pH throughout the experiment; the regression was highly significant ($P < 0.001$; $r^2 = 0.57$). The shape of the responses for Daphnia and Diaptomus suggest that there were threshold pH values above which response to pH was essentially linear. We used a simplex, least-squares model-fitting procedure to estimate these thresholds and the slopes of the responses (Wilkinson 1988); this is similar to piece-wise linear regression (Neter, Wasserman and Kuter 1985), except that the point at which the slopes changed was unknown a priori. This procedure allowed us to calculate confidence limits around the threshold as well as limits for the slope of the regression.

The models fitted were of the form:

$$Y = X_0 [b_1 (X_1 - b_0)] + \epsilon$$

where Y is the abundance of Daphnia or Diaptomus; b_0 is the threshold pH; X_0 is an "indicator variable" that is zero if the pH (denoted by X_1) is below the threshold, and is one if the pH is above the threshold; b_1 is the slope of the regression of Y on X_1 ; and ϵ is the error.

Both regressions were highly significant (Table VI-4), and both species had thresholds close to pH 5.0, below which they were virtually absent. Since the profile analyses showed significant effects due to time for these taxa, the regressions were repeated for each date separately. Day 2 was the only date to show substantial differences in the estimate of the threshold, indicating that the response to acidification may take a few days to manifest itself. The slope of the regression above the threshold also changed on the last day, reflecting lowered abundances in all enclosures at the end of the experiment relative to the preceding weeks.

To determine whether there were any artifacts due to the experimental design, abundance data for the samples from the control enclosures and from the five monitoring stations were converted to volumetric densities and the results compared graphically, since the sampling dates did not coincide for the two series of samples. Figure VI-5 indicates that the mean abundances of zooplankton were similar in the enclosures and in the lake at the beginning of the experiment. Thereafter, densities of Daphnia and Diaptomus increased in the lake relative to the enclosures, while Trichocerca disappeared more quickly in the enclosures than in the lake. Conversely, Chydorus became more numerous in the enclosures, while the other species generally behaved similarly in the two series of samples.

Zoobenthos

A total of 33 species were found in the benthic cores from the enclosures (Table VI-5). No additional species were found in the samples taken from soft sediments elsewhere in the lake using the Ekman grab. Because the two sampling techniques have different biases, direct comparison of densities is inappropriate. Instead, the rank abundances of all taxa in the two types of samples were compared using the Wilcoxon signed-ranks test. There was no

significant difference ($P = 0.82$) between rank abundances in the cores and in the Ekman grab samples. Overall, there were eight taxa collected in the cores that were not present in the Ekman grab samples (Table VI-5). Seven of these were the rarest taxa in the core samples, occurring in fewer than 9 of the 68 cores analyzed. Bosmina longirostris was moderately abundant in the cores, but was absent from the Ekman samples.

Fourteen species were sufficiently abundant for statistical analyses. Two-way MANOVA (i.e., date by pH treatment) showed no significant interaction (Pillai's trace, $P > 0.27$) or response to pH treatment ($P > 0.40$). There was, however, a significant change in the abundances of several species between the two dates. To ensure that there were no species showing a significant response to pH treatment, separate one-way ANOVAs were performed on the data from the end of the experiment for each of the fourteen taxa. Only Bosmina longirostris showed a significant result ($P = 0.04$). Variances for this species remained heterogeneous even after transformation; this and the significant result of the ANOVA were due to its absence from the pH 6.3 and 4.7 treatments, a pattern which was also found for this species in the zooplankton samples.

The other multivariate analyses performed on all taxa from all cores showed no discrete groupings or systematic patterns related to pH treatment. The only pattern to emerge from these analyses was that the two sampling dates were slightly different, as would be expected from the significant time effect in the MANOVA on the abundant taxa.

Discussion

Chemistry

The only solutes that changed significantly in concentration with the addition of acid were the hydrogen ion, nitrate, sulphate, potassium and aluminum. Although elevated levels of aluminum might be anticipated as a result of acidification, its concentration and that of potassium were both well within the annual range of concentrations in Emerald Lake (Chapter II). The concentrations of aluminum in the enclosures were less than those found to have deleterious effects on Daphnia magna Straus and D. catawaba Coker in laboratory assays, and concentrations an order of magnitude greater than those found in Emerald Lake do not affect Holopedium gibberum and Chironomus anthrocinus (Zetterstedt) (Havas and Hutchinson 1982, Havas 1985, Havas and

Likens 1985). Consequently, aluminum toxicity was unlikely to be a proximal factor mediating faunal change in this experiment. The lack of deviation of the ratio of nitrate to sulphate from 1:1 indicated that there was probably little reduction of these anions. This is not surprising given the oxic conditions in the water column, which would preclude dissimilatory reduction reactions, and the strong phosphorus limitation of Emerald Lake phytoplankton (Melack et al. 1987), which would limit assimilation of nitrate.

Before acid addition, there were some differences among the treatments with respect to chlorophyll-a, and these differences persisted for the duration of the experiment. The volume- and time-weighted mean concentrations of chlorophyll-a in the treatments varied from 0.36-0.53 $\mu\text{g L}^{-1}$. There was no apparent relation between these differences and the observed responses of zooplankters sensitive to acidification.

Zooplankton

Most of the abundant taxa of zooplankton showed patterns of population change in the enclosures that resembled those in the lake, albeit at reduced densities in the enclosures for some species. We attribute the higher abundances of Daphnia, Diaptomus, and Trichocerca in the lake to the opportunity for continued recruitment from resting eggs in the lake. Chydorus, which increased in abundance in the enclosures relative to the lake, is epibenthic and probably used the sides of the enclosures as an extension of its habitat. The scarcity of Holopedium gibberum in this experiment compared to our previous trials was most likely due to its normal seasonal decline towards the end of summer in Emerald Lake (Melack et al. 1987); furthermore, this species is known to be adversely affected by enclosures (Tessier 1986).

Of the taxa examined in this experiment, three showed relatively simple responses to pH. Daphnia rosea and Diaptomus signicauda were both virtually eliminated below ca. pH 5.0, whereas Keratella taurocephala reached much higher abundances in the most acidic enclosures. Bosmina longirostris also increased in abundance with increased acidity, but was almost absent from the pH 4.7 treatment. These patterns are consistent with our earlier experiments (Melack et al. 1987), and also resemble the patterns found in several studies that have compared the zooplankton assemblages in acidic and circumneutral lakes (Yan and Strus 1980, Havens and DeCosta 1987). The positive responses of Bosmina and Keratella to decreased pH in the enclosures probably resulted from

decreased competition with Daphnia, which has been shown to be competitively dominant in similar zooplankton assemblages (Neill 1984 and 1985, Vanni 1986, cf. Schaffner 1989). Thus the increased abundances of Keratella and Bosmina were probably mediated by interspecific interactions rather than by direct physiological benefits of higher acidity.

Not all of the patterns observed in our earlier experiments were reproduced here, however. Previously we had found that Keratella taurocephala tolerated pH between 5.0 and 6.0, but declined at more acidic levels. We are unable to explain this discrepancy; however, the fact that K. taurocephala increased steadily in abundance in the most acidified treatment over the course of the experiment suggests that it is generally tolerant of low pH in Emerald Lake. Surveys in eastern Canada have showed that this species was more abundant in acidic lakes than its congeners K. cochlearis (Gosse) and K. crassa Ahlstrom, which were more common in circumneutral waters (Carter et al. 1986).

As with all such analyses, however, care must be exercised when extrapolating either to wider ranges of pH or to different systems. Tonnessen (1984), for example, found that in laboratory microcosms, Keratella species were eliminated at very low pH (ca. 4.0), while Havens and DeCosta (1985) found that Bosmina longirostris continued to be numerous at pH 4.2 in West Virginia. Marmorek (1984), working in British Columbia with a fauna similar to that of Emerald Lake, found that Chydorus cf. sphaericus also increased in abundance at lower pH, together with Bosmina longirostris, and attributed this to competitive release from Daphnia. In Emerald Lake, Chydorus showed no such behavior. Inconsistencies in the relation between species abundances and pH have also been reported from studies based on surveys. For example, Conochilus unicornis is less abundant in acidic waters in Sweden (Almer et al. 1976 and 1978), but Siegfried et al. (1986) found that it was more abundant in acidic than in circumneutral lakes of the Adirondack Mountains, U.S.A. Such differences could be due to intra-specific variations in acid tolerance (e.g. different clones or sibling species predominating at different localities), faunal and physicochemical differences between localities, and variations in experimental technique.

We should also emphasize that the results of this experiment apply to the latter part of summer, when the crustacean zooplankton assemblage is normally dominated by Daphnia rosea. Seasonal differences in zooplankton community structure (Chapter VIII) must be considered when designing monitoring

programs. Nevertheless, the results indicate that several zooplankters are sensitive and reliable indicators of acid stress in Emerald Lake.

Zoobenthos

In contrast to the zooplankton, there was no firm evidence to suggest that the zoobenthos was affected by acidification in this experiment. There are two possible explanations for this. First, the zoobenthos may have been so patchily distributed that two cores were insufficient to estimate reliably its abundance within each enclosure; thus, intra-treatment variation could have obscured any inter-treatment effects. Second, the benthic sediments may have buffered the effects of acid addition (Schindler et al. 1985, Okland and Okland 1986).

It would be premature to conclude that acidification would not affect the benthos at Emerald Lake. Congeners of species found in this study have been found to be detrimentally affected in other studies (e.g., Heterissocladius, Tanytarsini, reviewed by Okland and Okland 1986), while other species of Chironomus have been recorded from waters with pH as low as 2.8 (Havas and Hutchinson 1982). Nevertheless, the benthic taxa most frequently cited as being good indicator species (Mills and Schindler 1986) are either absent from Emerald Lake (e.g., Orconectes virilis (Hagen), Lepidurus arcticus Pallas, Asellus aquaticus L.) or are found only occasionally (e.g., Hyalella azteca). Thus our results, combined with the extra effort of processing benthic samples compared with zooplankton samples, suggest that lacustrine benthos would make poor indicator species for acidification at Emerald Lake.

Amongst the zooplankton, Daphnia rosea, Diaptomus signicauda, Bosmina longirostris, and Keratella taurocephala are evidently reliable indicators of acidification in late summer in Emerald Lake. If the pH remains above about 6.0, we predict the dominant crustaceans in August and September will be Daphnia and Diaptomus; moderate acidification will result in Bosmina dominating the crustaceans, with Keratella becoming increasingly numerous. Below pH 5.0 (but above pH 4.7), we expect both cladocerans and Diaptomus to be absent, with Keratella dominating the rotifers. This latter scenario, however, would only occur after serious and prolonged acidification.

Table VI-1. Volume-weighted means for pH in each treatment over the course of the experiment, and the overall time-weighted means for each treatment. Day numbers represent days since the initial acidification. The mean pH over each interval was calculated from samples taken at the beginning and end of the interval.

Interval	Experimental treatment					
	Ctrl	pH 5.8	pH 5.4	pH 5.3	pH 5.0	pH 4.7
Day -1	6.37	6.41	6.35	6.32	6.34	6.32
Days 2-7	6.23	5.86	5.25	5.26	4.97	4.84
7-14	6.21	5.86	5.40	5.25	5.02	4.79
14-21	6.33	5.82	5.45	5.28	5.02	4.78
21-28	6.30	5.77	5.45	5.30	5.03	4.74
28-35	6.27	5.81	5.48	5.34	5.05	4.70
mean (time-weighted)	6.27	5.82	5.39	5.28	5.01	4.77

Table VI-2. Concentrations of major solutes in the control and pH 4.7 treatments during the experiment. Data are volume-weighted means averaged over all post-acidification sampling dates. Units are $\mu\text{eq L}^{-1}$ except Si, Fe, and Al, which are μM . Results of the statistical analyses are given; "before" denotes the ANOVA amongst enclosures prior to acidification. Significant effects ($P < 0.05$) are underlined.

Solute	Experimental treatment		Probabilities (F-test)			
	Control	pH 4.7	Before	pH	Day	Day by pH
ANC	30.5	0.0	0.200	<u>0.002</u>	<u>0.047</u>	0.616
Ca ²⁺	23.6	23.3	1.000	0.947	<u>0.015</u>	0.079
Mg ²⁺	4.1	4.0	<u>0.036</u>	0.633	0.099	0.062
Na ⁺	17.7	18.2	0.165	0.147	0.804	0.225
K ⁺	3.7	3.8	0.212	<u>0.028</u>	<u>0.005</u>	<u>0.008</u>
Cl ⁻	2.5	2.4	0.098	0.898	0.119	0.706
SO ₄ ²⁻	7.1	30.6	0.495	<u>0.000</u>	0.101	0.097
NO ₃ ⁻	2.6	24.8	0.078	<u>0.000</u>	0.124	<u>0.050</u>
NH ₄ ⁺	0.7	0.4	<u>0.022</u>	0.165	<u>0.001</u>	0.147
PO ₄ ³⁻	0.0	0.0	--	--	--	--
Si	25.0	25.8	0.626	0.138	<u>0.004</u>	0.296
total Fe	0.8	0.9	0.610	0.763	0.079	0.780
total Al	0.6	1.0	0.946	<u>0.000</u>	<u>0.050</u>	0.093

Table VI-3. F-values from profile analyses of the responses of selected zooplankton taxa to acidification (see text for explanation); *** P < 0.001, ** P < 0.01.

* P < 0.05, ns P > 0.05.

Taxon	Source		
	pH	Day	Day by pH
<u>Daphnia</u>	35.90***	5.89*	1.34 ^{ns}
<u>Diaptomus</u>	14.18***	96.08***	1.38 ^{ns}
<u>Keratella</u>	10.66***	2.66 ^{ns}	1.35 ^{ns}
<u>Bosmina</u>	5.07*	9.58**	1.48 ^{ns}
<u>Nauplii</u>	4.41*	29.86***	1.22 ^{ns}
<u>Chydorus</u>	0.55 ^{ns}	9.58**	1.02 ^{ns}
<u>Polyarthra</u>	2.43 ^{ns}	6.78**	1.06 ^{ns}

Table VI-4. Results of regressions performed to define the responses of Daphnia rosea and Diaptomus signicauda to acidification (see text for explanation). The regression coefficients (r^2) were highly significant; 95% confidence limits for the estimated threshold pH's are given in parentheses.

	<u>Daphnia</u>	<u>Diaptomus</u>
r^2	0.869	0.794
F (2,16)	118.116	10.583
Threshold pH (b_0)	5.01 (4.84, 5.17)	4.74 (4.50, 4.97)
Slope of regression (b_1)	299 (228, 369)	311 (244, 399)

Table VI-5. List of benthic taxa found in core samples from inside the enclosures:
 a + indicates that the taxon was not also found in the Ekman samples taken
 outside the enclosures.

Taxon	Mean abundance (per 0.02 m ²)
NEMATODA	45.5
NEMATOMORPHA	
<u>Gordius</u> sp. +	0.03
OLIGOCHAETA	38.6
MOLLUSCA	
Bivalvia	
<u>Pisidium</u> sp.	1.5
ACARINA	
<u>Trimalaconothrus</u> sp.	1.0
<u>Nanahermannia nana</u> (Nicolet)	1.2
CRUSTACEA	
Harpacticoida	6.8
Cyclopoida	
<u>Macrocylops albidus</u> (Jurine)	47.2
Calanoida	
<u>Diaptomus signicauda</u> Lilljeborg	37.0
Amphipoda	
<u>Hyalella azteca</u> (Saussure) +	0.5
Cladocera	
<u>Alona</u> spp.	2.3
<u>Bosmina longirostris</u> (Muller) +	4.7
<u>Chydorus sphaericus</u> (Muller)	14.6
<u>Daphnia rosea</u> Sars emend. Richard	6.4
<u>Eurycercus glacialis</u> Lilljeborg	8.6
<u>Ilyocryptus sordidus</u> (Lieven)	6.9
<u>Polyphemus pediculus</u> (Linné)	1.5
DIPTERA (CHIRONOMIDAE)	
Tanypodinae	
<u>Ablabesmyia</u> sp.	0.7
<u>Procladius</u> sp.	1.2
Chironominae	
<u>Chironomus</u> sp.A	5.3
<u>Chironomus</u> sp.B	7.3
? <u>Cladotanytarsus</u> sp.	3.1
<u>Paracladopelma</u> sp. +	0.8
? <u>Phaenopsectra</u> sp. +	0.3
<u>Tanytarsus</u> sp.	1.2

Table VI-5 (continued).

Taxon	Mean abundance
Orthoclaadiinae	
<u>Corynoneura</u> sp.;	2.7
<u>Cricotopus</u> sp.	0.09
?Eukiefferiella sp. +	0.5
<u>Heterissocladius</u> sp. +	0.5
Orthoclaadiinae sp.4 +	0.1
<u>Psectrocladius</u> sp.	4.3
LEPIDOPTERA +	0.09

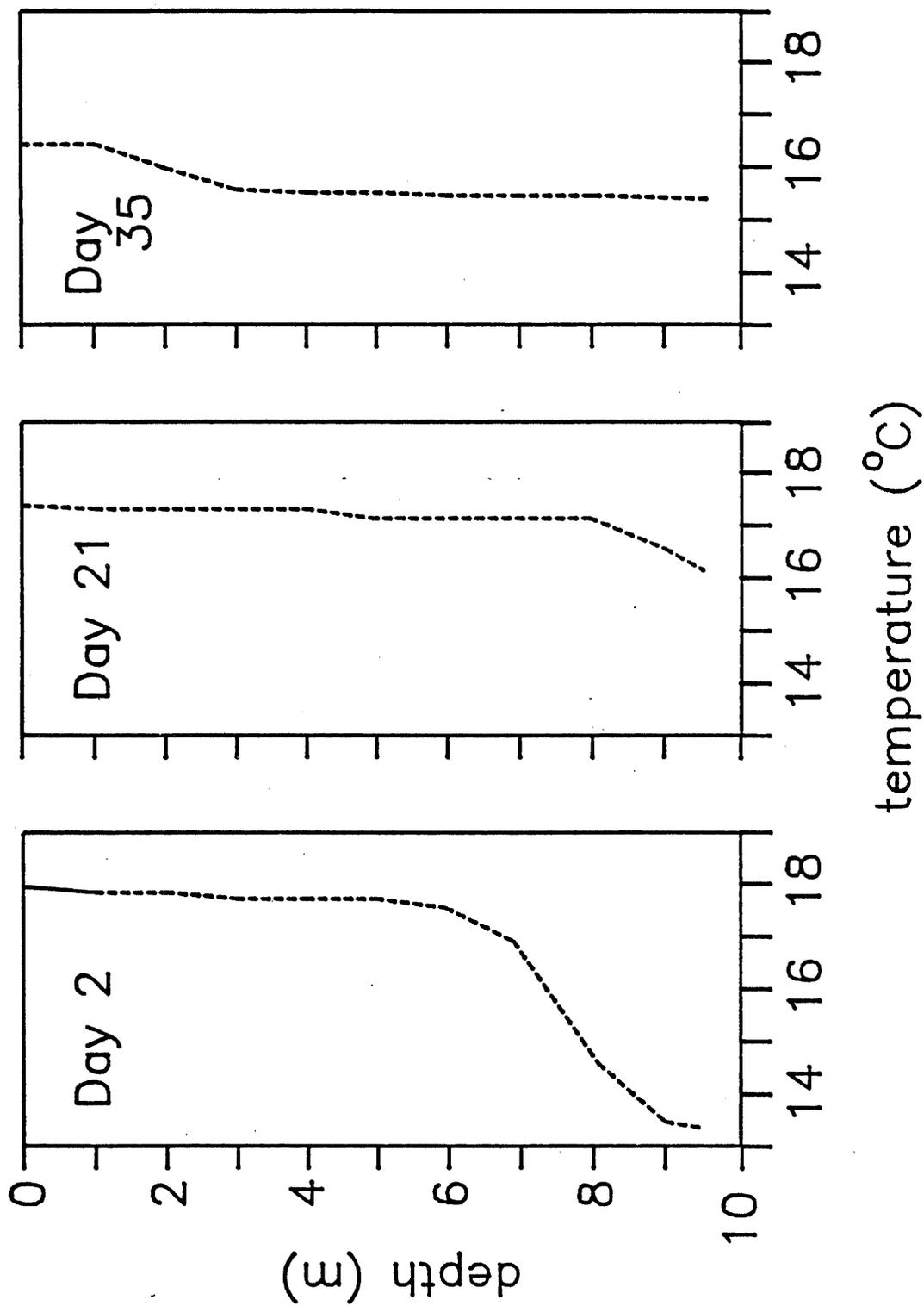
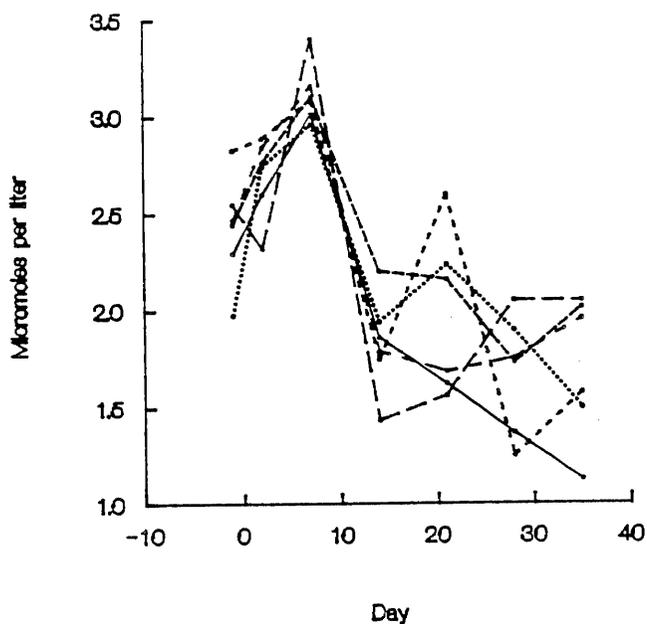
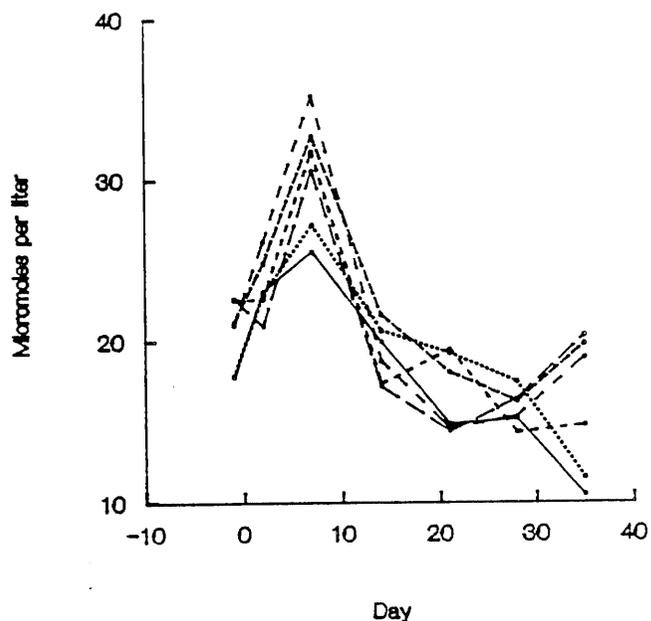


Fig. VI-1. Thermal profiles in Emerald Lake during the experiment. Thermal layering inside the enclosures resembled that of the water column outside.

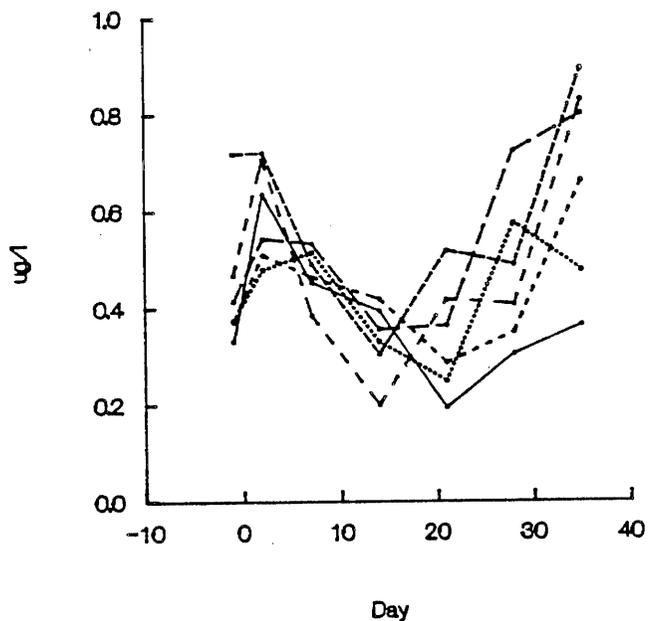
Particulate Nitrogen



Particulate Carbon



Chlorophyll-a



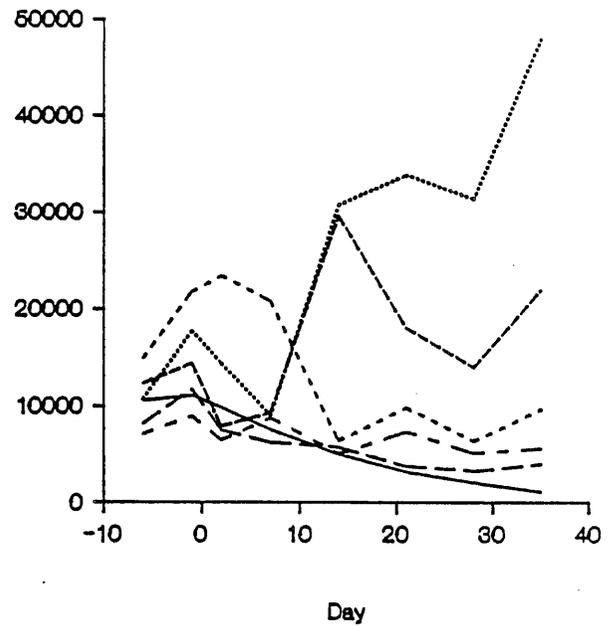
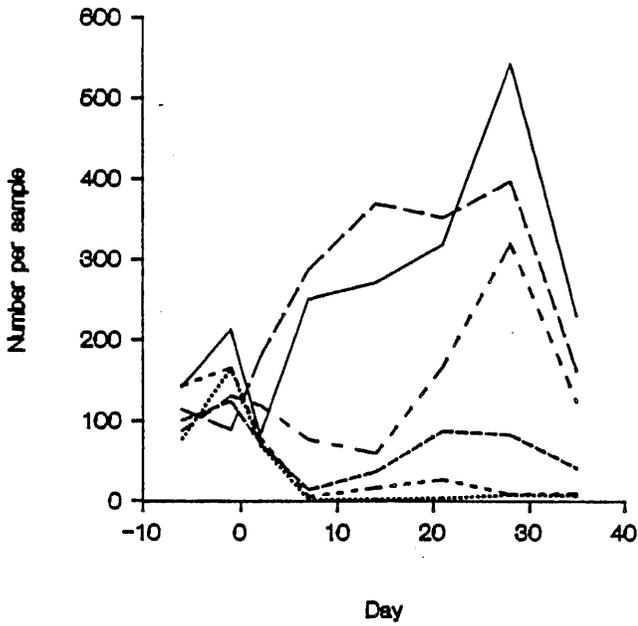
Legend

- pH 6.3
- pH 5.8
- - - - - pH 5.4
- - - - - pH 5.2
- - - - - pH 5.0
- pH 4.7

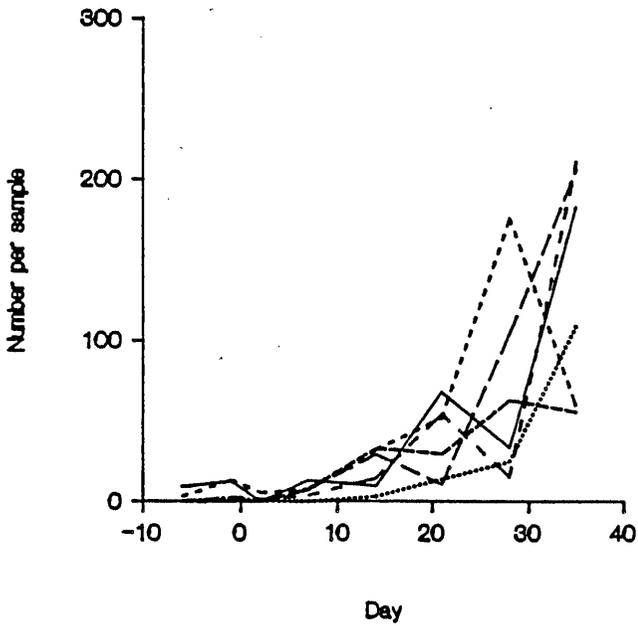
Fig. VI-2. Concentrations of chlorophyll-a, particulate nitrogen and particulate carbon in each treatment. Acidification was completed on Day 0.

Daphnia rosea

Keratella taurocephala



Chydorus cf. sphaericus

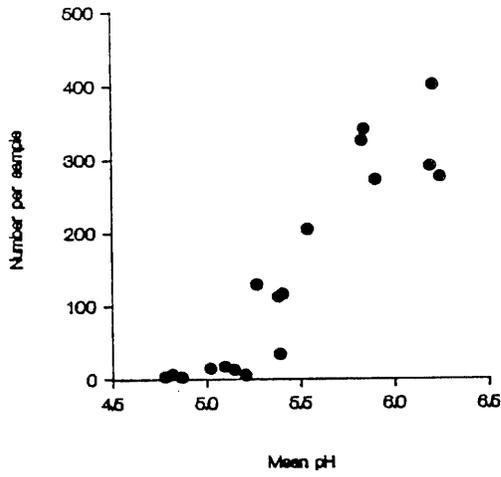


Legend

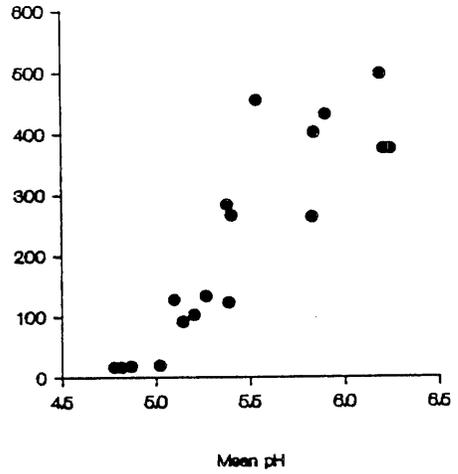
- pH 6.3
- pH 5.8
- - - - - pH 5.4
- pH 5.2
- - - - - pH 5.0
- pH 4.7

Fig. VI-3. Mean densities of *Daphnia rosea*, *Keratella taurocephala* and *Chydorus cf. sphaericus* in each treatment. Acidification was completed on Day 0.

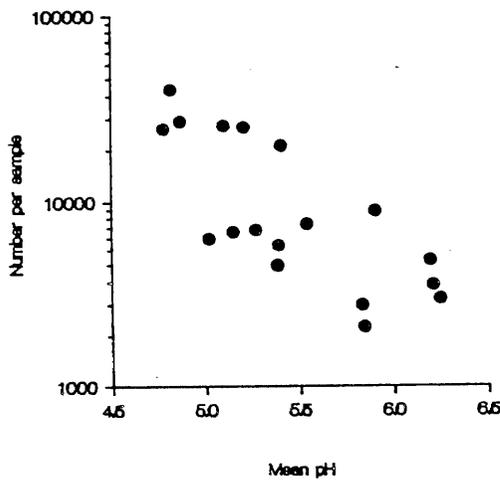
Daphnia rosea



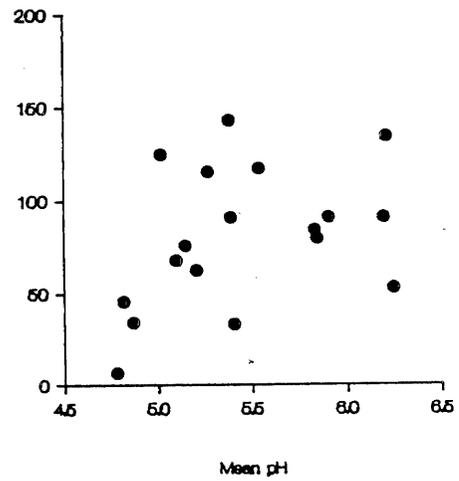
Diaptomus signicauda



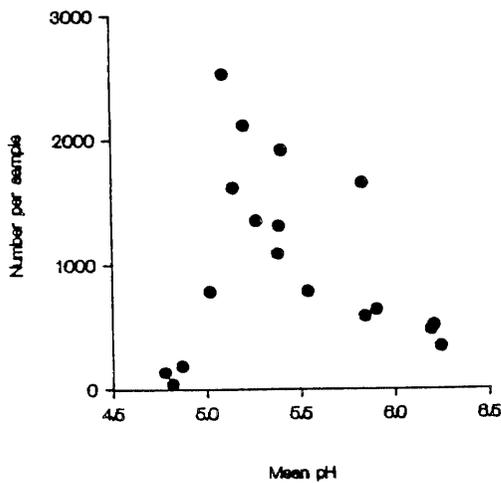
Keratella taurocephala



Diaptomid nauplii



Bosmina longirostris



Polyarthra vulgaris

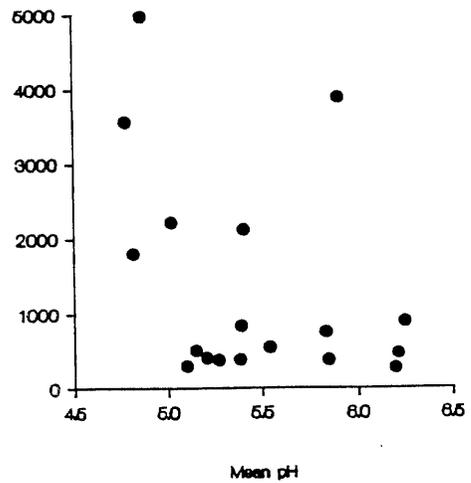
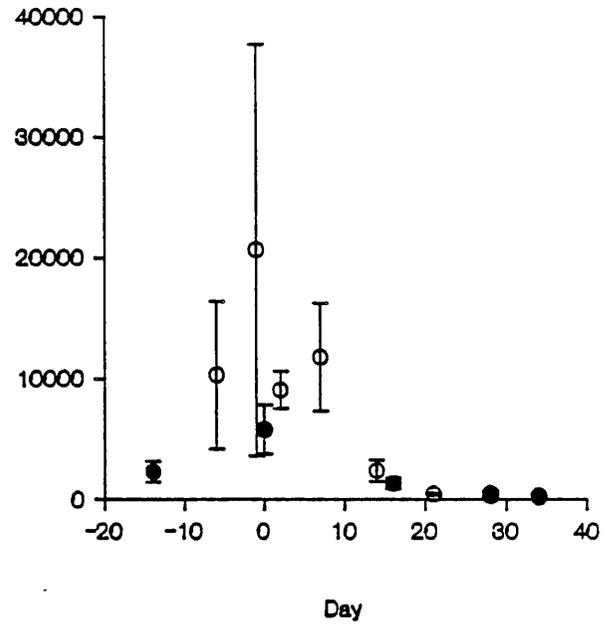
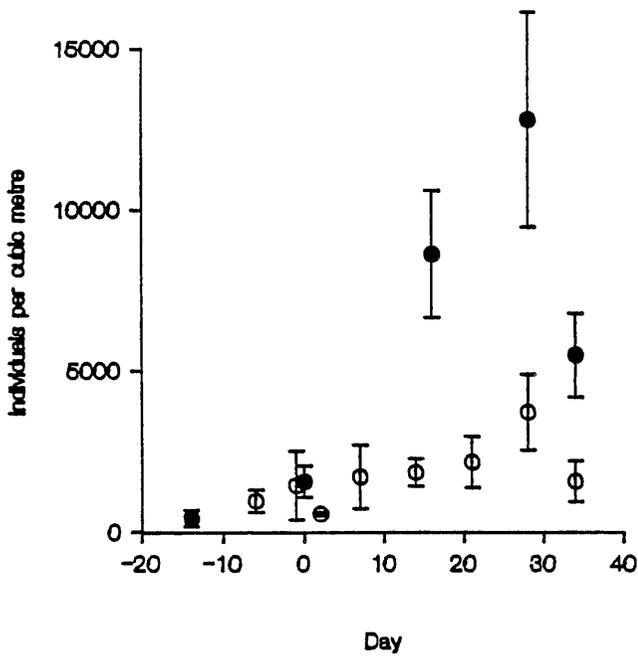


Fig. VI-4. Mean abundance of each species in each enclosure vs. mean pH of each enclosure after acidification.



Diatomus signicauda

Diatomid nauplii

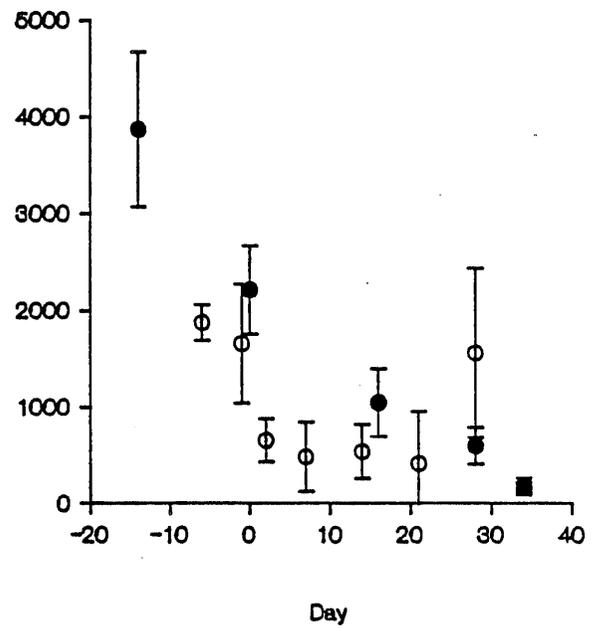
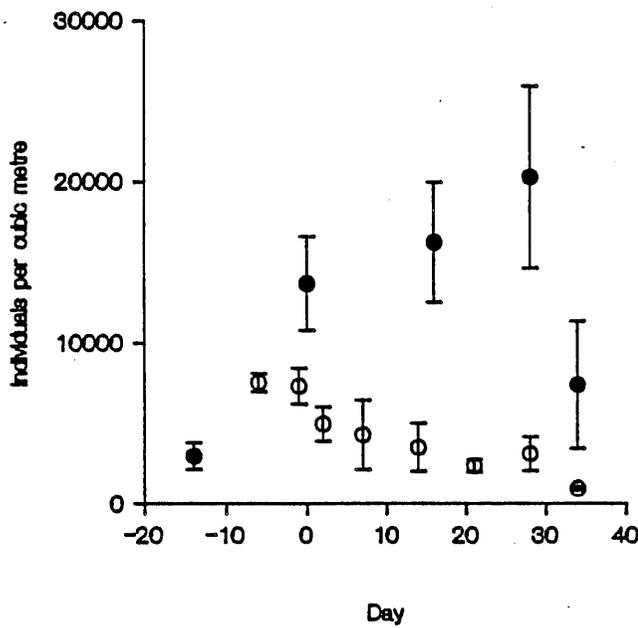
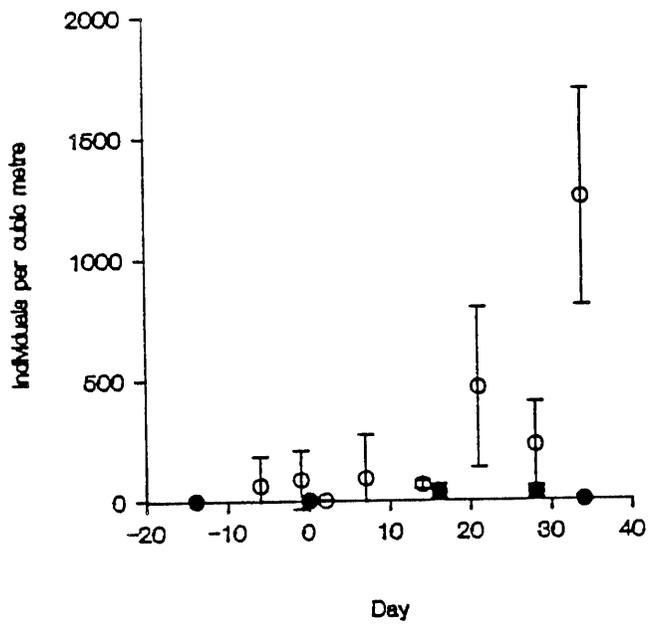
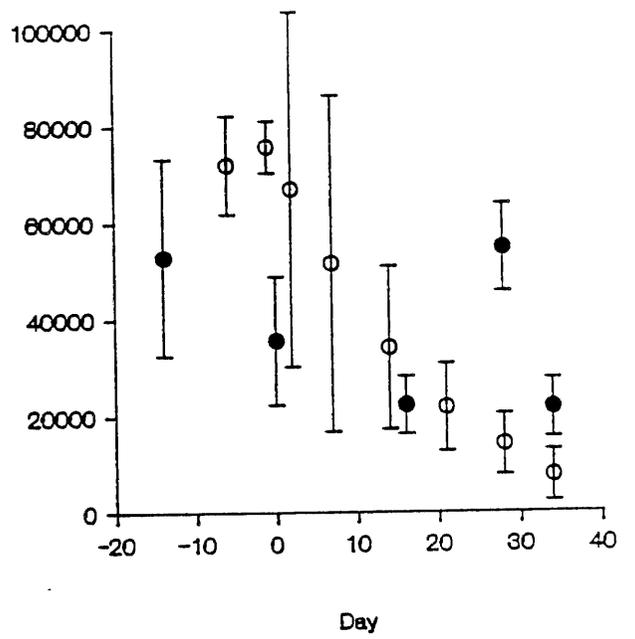


Fig. VI-5. Mean abundances of zooplankton species in the enclosures (open symbols) and in the lake (closed symbols); vertical lines are ± 2 standard errors of the mean. Continued on following page.

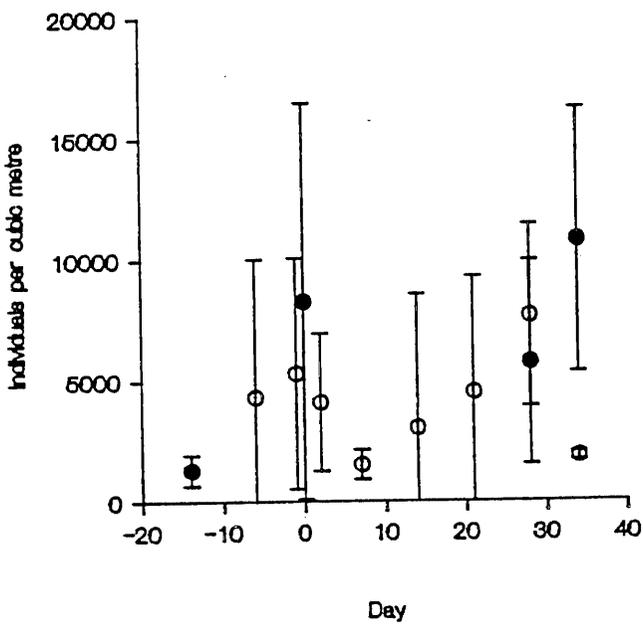
Chydorus cf. sphaericus



Keratella taurocephala



Polyarthra vulgaris



Trichocerca capucina

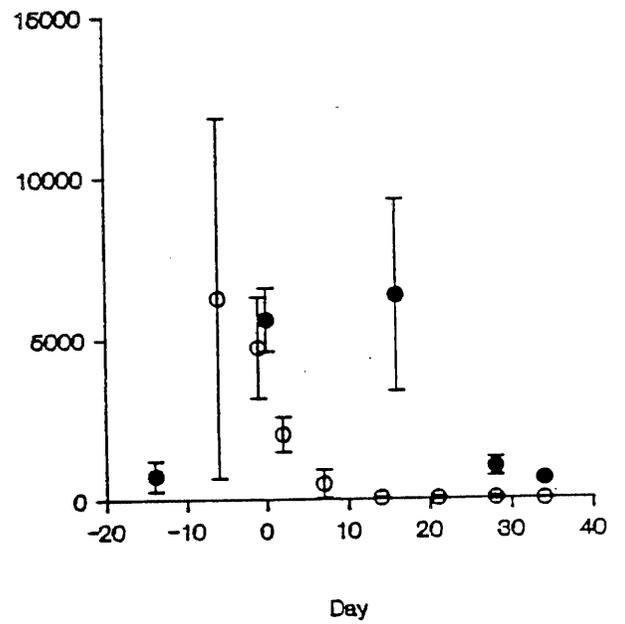


Fig. VI-5. Continued.

Chapter VII

Primary Productivity in Emerald Lake

Primary production and algal standing crop are related to community structure, nutrient availability, zooplankton grazing and water transparency (Redfield 1980, Reynolds 1984, Harris 1986) and these factors can be altered by acidification (Kring and O'Brien 1976, Almer et al. 1978, Jansson et al. 1986, Havens and Decosta 1987, Schenck et al. 1988). Algal production may therefore integrate the many chemical and biological changes induced by lake acidification.

Carbon uptake by phytoplankton was measured using a radioisotope tracer technique. Small amounts of labelled inorganic carbon (^{14}C) were added to water samples which were incubated under a range of light intensities. After filtration, the particulate fraction was collected on filters and its radioactivity was measured. A hyperbolic tangent function was fit to the relationship between photosynthetic carbon production (normalized to chlorophyll-*a*) and light irradiance (Fee 1973). The initial slope of this curve is a measure of the photosynthetic efficiency (α) of the phytoplankton. In addition, the upper asymptote of the production-irradiance (P vs. I) curve is an index of the photosynthetic potential of the plankton, termed P_m^B . These P vs. I curve parameters, along with measurements of lake temperature and transparency, were coupled with a continuous record of solar radiation at Emerald Lake in a numerical model of integral primary production. Integral production is defined as the amount of carbon fixed below a meter of lake surface overlying the deepest portion of the lake. These techniques are extremely sensitive, allow for rapid processing of samples, and avoid the problem of gross enrichment of nutrient concentrations. Tests of the accuracy of these techniques in the Experimental Lakes Area have shown that ^{14}C productivity measurements employing small samples of lake water agree well with data from whole-lake experiments (Bower et al. 1987).

In this study we discuss the environmental factors affecting the P vs. I relationship and the physical and biological controls of integral production. Additionally, we will examine these data in terms of their value in long-term monitoring programs and their ability to indicate lake changes induced by acidification.

Methods

Experiments were conducted during the ice-free seasons of 1984, 1985, and 1987. Samples were collected from the center of the lake using either a 2-L acrylic Kemmerer sampler (for epilimnion and hypolimnion sampling) or a 10-m length of 2.5-cm diameter Tygon tubing used as an integrating sampler. The entire water sample was then placed in an opaque plastic container. During 1987 water from two discrete depths (1 and 7 m) was collected and analyzed separately. Immediately after collection the water was backpacked 8 km to a trail head, then driven by automobile 45 kilometers to the laboratory. Elapsed time between collection and start of an experiment was about 5 hours.

Lake water was measured into 125-ml borosilicate glass bottles, inoculated with 5 μCi of $\text{NaH}^{14}\text{CO}_3$, and thoroughly mixed. Initial activity was determined by immediately removing 0.5 mL of sample from a subset of bottles and adding each to a scintillation vial containing 0.1 N NaOH and 10 mL of fluor (PCS or Ecoscint). Samples were illuminated at a series of light levels by cool-white, power groove, fluorescent lamps (GE F48PG17CW). A range of light intensities was obtained by enclosing the bottles in layers of neutral density screen. The incubations took place in an insulated container which was kept at lake temperature. The usual incubation time was 4 to 5 hours. After incubation, samples were filtered through glass fiber filters (Gelman A/E) at a pressure not exceeding 125 mm Hg and rinsed with 30 mL of filtered Emerald Lake water. The perimeter of the filters was also rinsed by removing the upper part of the filter holder and pipetting an additional 10 mL of filtered lake water around the edge. The filters were then placed in 10 mL of fluor. The ^{14}C activity on the filters and the initial activity was determined with a Rackbeta 1217 automatic scintillation counter. The dissolved inorganic carbon content of the lake water was determined by Gran titration (Talling 1973); virtually all of the dissolved inorganic carbon in Emerald Lake exists as bicarbonate. Chlorophyll-a was determined by filtering 1 L of the water used in the ^{14}C experiment through a glass fiber filter. The filter was macerated with a Teflon homogenizer and the pigment extracted in the dark for at least 45 minutes with 90% acetone. After extraction the filter-acetone slurry was centrifuged and the fluorescence of the extracted pigments measured on a fluorometer, which was calibrated against a spectrophotometer using spinach pigments and/or commercially available chlorophyll-a standards. The

concentrations were corrected for phaeopigments. The carbon uptake rate ($\mu\text{g C L}^{-1} \text{ hr}^{-1}$) was then calculated by the following equation:

$$\text{C uptake} = \left(\frac{{}^{14}\text{C assimilated}}{{}^{14}\text{C available}} \right) \left(\frac{{}^{12}\text{C available}}{\text{time}} \right) (K)$$

where ${}^{14}\text{C assimilated}$ = sample activity in disintegrations per minute (dpm) from scintillation counter $\times 1.06$; ${}^{14}\text{C available}$ = the initial activity (dpm) of the sample times a dilution factor based on the size of the initial activity aliquot and the original sample volume; ${}^{12}\text{C available}$ = Gran alkalinity in $\mu\text{M C}$; K = a dimension factor to convert $\mu\text{M C}$ to $\mu\text{g C L}^{-1}$; and time = elapsed time (hours) of the experiment.

A continuous record of photosynthetically active radiation (PAR, 400 to 700 nm) was calculated from a total solar radiation sensor (Licor LI200S pyranometer) located at a National Park Service meteorological station (Log Meadow: 2050 m ASL) approximately 7 km from Emerald Lake. A regression was performed between the total radiation sensor at Log Meadow and a PAR sensor operative intermittently during 1987 at Emerald Lake. The regression was performed on data from cloudless days and was based on more than 500 data pairs. The correlation coefficient was 0.94. This regression equation was used to estimate PAR at Emerald Lake for 1984, 1985, 1986 and 1987 from the Log Meadow total radiation measurements. However there were gaps in the records during each of the years. In order to have complete records, we calculated an average yearly PAR record using the four years of data and applied this average to gaps in an individual year's record.

PAR was measured during sample collection at each meter of the water column with a Licor LI-185B quantum sensor. These data were used to calculate light extinction coefficients for use in the integral productivity calculations. PAR was also measured during incubations with the same sensor.

Light-saturated, chlorophyll-specific carbon uptake rates (P_m^B) were estimated by the following procedure. Carbon uptake rates (P) were normalized to chlorophyll-a and plotted against light intensity (I). The parameters of the P vs. I curves were then estimated by fitting the hyperbolic tangent equation:

$$P^B(I) = P_m^B * \tanh(\alpha^B / P_m^B) - R$$

where $P_m^B(I)$ = the specific carbon uptake rate ($\mu\text{g C } (\mu\text{g Chla})^{-1}$) per $\mu\text{Einstein m}^{-2} \text{ s}^{-1}$; P_m^B = the light-saturated specific-uptake rate (same units as $P_m^B(I)$), which is an index of the photosynthetic potential of the phytoplankton; α^B = the initial slope of the P vs. I curve, which is an index of the photosynthetic efficiency of the phytoplankton; and R = the Y intercept. The fitting routine minimizes the sum of the squared residuals by searching the entire 3-dimensional parameter space defined by P_m^B , α^B , and R (see Gallegos and Platt, 1981).

Estimates of daily integral production were made using the P vs. I curve parameters (P_m^B , α^B and R) estimated above and a modification of the methods suggested by Fee (1973). Inputs into the interpolative numerical model include insolation, light extinction, and photosynthetic rates at different light levels of the samples, which were either integrated samples of the water column or from two discrete depths. The photosynthetic parameters of the integrated water samples (1984, 1985) were taken to be representative of the entire euphotic zone. The discrete depth samples from 1987 were assumed to be representative of a region of the euphotic zone delineated by the thermal structure of the lake on the sampling date. The calculated uptake was modified, in the model, to incorporate differences in algal abundance and temperatures by using measured profiles of chlorophyll-a (4 depths) and temperature (1-m intervals). Uptake rates are very sensitive to temperature effects (Jellison and Melack 1988); therefore the rates were corrected to the temperature at the meter intervals using an exponential correction factor:

$$P_m^B(t_2) = P_m^B(t_1) * \exp((0.107 * (t_2 - t_1))).$$

In practice, these modifications were small because incubations were done near ambient lake temperatures, and chlorophyll-a concentrations were nearly uniform in Emerald Lake. To assess the effect of light variability on production, estimates were made between sampling dates by linear interpolation of the uptake parameters and light extinction values, and combining these with the continuous record of surface insolation. The integration was performed by summing hourly values over 1-m thick layers in the water column. The first layer was 1.5-m thick since it extends from the surface to 1.5-m depth.

In order to evaluate the accuracy of using the average light data to drive the production model, a regression of integral production estimates

derived from average and calculated light was performed. Integral production from 158 days was calculated using both types of light and the data sets were regressed against one another. The following regression equation was obtained ($r^2 = 0.98$, standard error = 10.58):

$$P_{CL} = (1.005 * P_{AL}) - 2.508$$

where P_{CL} = integral primary production calculated using light data derived from Log Meadow pyranometer; P_{AL} = integral primary production calculated using light data which is the average of P_{CL} from 1984, 1985, 1986 and 1987.

Results

Carbon-14 uptake was measured 24 times during the ice-free seasons of 1984, 1985 and 1987. Figures VII-1 through VII-4 contain the P vs. I curves for all three years. Time series for the curve parameters and measurements of primary production are presented in Figures VII-5 and VI-6. Data for the light saturation curve parameters for 1987 are the average of the measurements from the 1-m and 7-m samples. The values for the two depths showed very little difference (see Figures VII-3 and VII-4). In the following description of the seasonality of the P vs. I curve parameters and production, I define spring to be period just following the peak of the snowmelt hydrograph, and autumn to mean the period after lake turnover.

Light-saturated carbon uptake normalized to chlorophyll concentration provides an index of the photosynthetic potential of chlorophyll-a at high light intensities. Time series for P_m^B for the three years are shown in Figure VII-5. In 1984, P_m^B showed an increase after snowmelt with a peak of $1.8 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$ on 1 September. There was a gradual decline in the photosynthetic potential through the remainder of the summer and autumn. In 1985 a different pattern was observed. As in 1984 P_m^B increased until late August (peak: $3.6 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$) but this high photosynthetic potential was maintained through the remainder of September and October. In 1987 P_m^B peaked very early, 23 July, at $2.4 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$. A gradual decline in photosynthetic potential followed until the lake mixed in early September when P_m^B rose slightly to $1.9 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$. This intermediate level was maintained for the remainder of the 1987 season. Overall, 1984 and 1987 were similar in photosynthetic potential in that the rates were low and varied

only slightly during the period. The ice-free season of 1985 was unusual compared to 1984 and 1987 because there was a threefold variation in P_m^B and relatively high rates were maintained throughout the summer and autumn.

The term α^B describes the efficiency with which chlorophyll-a uses light energy in carbon fixation. It is calculated from the initial slope of the P vs. I curve and is a measure of the ability of the plankton to fix carbon at low light levels. During 1984, relative quantum yield increased after snowmelt and peaked in early September ($0.016 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$ per $\mu\text{Einsteins m}^{-2} \text{ s}^{-1}$; Figure VII-5). From this point till late October α^B declined to post-snowmelt levels; however, it increased sharply in early winter to $0.014 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$ per $\mu\text{Einsteins m}^{-2} \text{ s}^{-1}$. The pattern observed in 1985 was similar, with a post-snowmelt increase (peak = $0.015 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$ per $\mu\text{Einsteins m}^{-2} \text{ s}^{-1}$) followed by a short decline then an autumn peak. The autumn peak in α^B was, however, about one month earlier and relatively very large ($0.045 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$ per $\mu\text{Einsteins m}^{-2} \text{ s}^{-1}$). The relative quantum yield in 1987 showed a different pattern. As in other years, α^B exhibited a steady increase after snowmelt with a peak in early August ($0.021 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$ per $\mu\text{Einsteins m}^{-2} \text{ s}^{-1}$) but a decline in efficiency was measured for only a brief period in the late summer. In the autumn photosynthetic efficiency peaked again ($0.022 \mu\text{g C } (\mu\text{g Chla})^{-1} \text{ h}^{-1}$ per $\mu\text{Einsteins m}^{-2} \text{ s}^{-1}$) and exceeded post-snowmelt levels. This intermediate level of quantum yield was sustained through the rest of the autumn season.

Light-saturated carbon uptake is a measure of the gross carbon fixation in a liter of lake water at high light levels. Integral primary production is the amount of carbon fixation below a square meter of lake surface overlying the deepest portion of the lake (10 m). Integral production is therefore a measure of the carbon fixation occurring in the entire lake at all light levels. Figure VII-6 is a time series of these measures of production for the ice-free seasons of 1984, 1985 and 1987. Light-saturated carbon uptake (unnormalized) displayed a very consistent pattern during all three years. The data show a classic spring and autumn peak in carbon production separated by relatively low mid-summer productivity. There were, however, large differences in the magnitude of the peaks and in their relative sizes. The 1985 spring peak in carbon uptake ($2.0 \mu\text{g C l}^{-1} \text{ h}^{-1}$) was much larger than those in 1984 and 1987 (1.1 and $0.7 \mu\text{g C l}^{-1} \text{ h}^{-1}$ respectively) and larger than measured in the autumn of the same year ($1.5 \mu\text{g C l}^{-1} \text{ h}^{-1}$). In 1984 and 1987 the autumn

peaks in carbon fixation ($2.1 \mu\text{g C l}^{-1} \text{ h}^{-1}$ in both years) were 2 to 3 times higher than the spring peaks.

Integral production (IP) also reflected this classic pattern and generally correlated with P_m. In 1984, peak IP occurred in late August ($106 \text{ mg C m}^{-2} \text{ d}^{-1}$) and was slightly greater than that observed in the autumn ($80 \text{ mg C m}^{-2} \text{ d}^{-1}$). The pattern in 1985 was very similar to that in 1984 except that the relative difference between the spring and autumn peaks was greater ($138 \text{ mg C m}^{-2} \text{ d}^{-1}$ in spring, $66 \text{ mg C m}^{-2} \text{ d}^{-1}$ in autumn). In 1987 the opposite pattern was observed. The highest IP reached during the ice-free season was in the autumn ($168 \text{ mg C m}^{-2} \text{ d}^{-1}$) and this was the highest rate of integral production measured during the three years of the study. The peak integral production in the spring of 1987 was $86 \text{ mg C m}^{-2} \text{ d}^{-1}$, slightly smaller than that in 1984 and 1985.

Table VII-1 contains a summary of the results from the integral production model. Despite the differences in the magnitude and timing of peaks of IP, mean daily production and total carbon production were very similar between the three years. The highest mean daily production was $70 \text{ mg C m}^{-2} \text{ d}^{-1}$ and the highest total integral production was $7,368 \text{ mg C m}^{-2}$; both occurred in 1985. Total integral production is the amount of carbon fixation below a square meter of lake surface during the ice-free season (June through October). The seasonal lake production was calculated on the basis of lake volume and was largest in 1985 (118 kg C). This term represents the amount of carbon fixation during the ice-free season for the entire lake volume.

Discussion

Environmental controls of P_m^B , α^B and production

Many environmental parameters have been shown to be significant in modelling phytoplankton production. Côté and Platt (1984) attributed most of the variation in α^B and P_m^B in a coastal marine environment to factors relating to community structure. In hypersaline Mono Lake, Jellison and Melack (1988) found that 68% of the seasonal variation in P_m^B could be explained by a regression on temperature. Heyman (1986) normalized the P vs. I parameters to carbon instead of chlorophyll and found that in oligotrophic Lake Siggeforajön (Sweden), P_m^B was dependent on temperature, stratification, biomass, and species composition. Previous work on lakes in the Sierra Nevada has demonstrated that α^B and P_m^B correlate significantly with nitrate concentration (Lake Tahoe:

Williams 1978). And lastly, a correlate unique to mountain lakes, snow deposition, was found to be significant in predicting integral primary production in Castle Lake (Goldman and De Amezaga 1984). Guided by these studies, an attempt was made at explaining the seasonality and year to year variation in the light saturation curve parameters and carbon production in Emerald Lake. Figures VII-7 through VII-9 contain data on potential environmental correlates of P_m^B , α^B and carbon production.

Incident light drives the IP model and has been found to be a factor controlling specific uptake (through enzymatic processes: Beardall and Morris 1976) and α^B (plankton adaptation to sun and shade: Yentsch and Lee 1966). Figure VII-7 contains time-series data on daily insolation (as PAR) and the PAR extinction coefficient for the ice-free seasons of 1984, 1985 and 1987. Relatively high carbon production (P_m and IP) in the spring may be explained, in part, by the higher photon flux density during June and July. The light records show that daily insolation in October is only 50% of that measured in the period following snowmelt.

The waters of Emerald Lake are usually very clear, with the euphotic zone extending to the bottom during ice-free periods. PAR extinction is in general small, $\sim 0.4 \ln \text{ PAR units } m^{-1}$. There was however some seasonality to these measurements. In 1985 and 1987 the relative trends in P_m and IP generally followed those of the PAR extinction coefficient. In addition chlorophyll-a concentration (Figure VII-8) varied closely with PAR extinction, implying that the turbidity in Emerald Lake was mainly due to phytoplankton biomass during those years. The extinction coefficient during the ice-free season of 1984 did not show this agreement because of a large rain event in July of that year. Water turbidity was very high (due to allochthonous materials) and did not correlate well with any of the P vs. I curve parameters, indices of production, or chlorophyll-a. Instead, P_m^B and α^B exhibited very similar patterns. This indicates that the phytoplankton may have been experiencing light limitation since P_m^B was being controlled by the light-limited slope of the P vs. I curve. This storm had long-lasting, multifarious affects on lake chemistry and carbon productivity. In the early winter of 1984, chlorophyll-a reached the highest recorded concentration ($5-6 \mu\text{g L}^{-1}$; Chapter III) after breakdown of an unusually persistent stratification (see Figure VII-9), which could have increased the supply of nutrients to the euphotic zone. This large standing crop, along with other detrital materials,

must have supported a large bacterial biomass which may explain the unusually high carbon uptake (both P_m and IP) in the spring of 1985.

As stated before, temperature may have an important effect on primary production, not only due to a direct effect on enzymatic processes but also by inducing lake thermal stratification. Data on mean lake temperature and a lake stability index derived from density are presented in Figure VII-9.

Temperature shows a very smooth progression during the period following snowmelt. Higher temperatures in the immediate post-snowmelt period may explain peaks in P_m^B , P_m and IP observed in 1984 and 1987, and to a lesser extent those in 1985. It is interesting to note that while temperature follows a very smooth course, the time series for P_m^B , P_m and IP are quite variable both in magnitude and direction. This implies that temperature may be important not in predicting seasonal patterns but in setting the upper and lower bounds of production. Warmer than usual autumn lake temperatures in 1987 and an early breakdown of stratification may help explain the exceptional P_m and IP measured that autumn. Mean lake temperature did not drop below 12°C until well into October. In addition, the lake stability reached zero upon mixing sometime in August, about a month earlier than normal. This meant that when nutrients from hypolimnetic waters became available to phytoplankton in surface waters, the lake temperature was high enough to support high rates of production. Thus in 1987 the combination of nutrients, lake stability and temperature were important in controlling primary production.

When comparing the seasonality of IP to the standing crop of phytoplankton we see an agreement of trends but not in the magnitude of the changes. For instance, why is the standing stock of phytoplankton low in the spring while IP is relatively high? One possible explanation for the lack of biomass buildup in the spring is the flushing of the lake by inflowing waters. During a typical snowmelt period Emerald lake may be flushed several times (Figure VII-8). In addition, during summer thermal stratification, small inflow discharge may have a large effect on phytoplankton biomass. This is because inflowing waters, being close to the surface water temperature, do not mix with the hypolimnion but instead flush the epilimnion of the lake. This portion of the water column is where carbon fixation is greatest due to favorable conditions (light saturation and higher temperature). Another possible reason for the lack of biomass buildup is that zooplankton grazing pressure may be high due to higher temperatures. A final possibility is that a large portion

of P_m and IP may be due to bacteria. These plankton may pass through the filters used for the chlorophyll assay and cause an underestimation of chlorophyll-a biomass.

Another seeming contradiction in biomass and production levels is the high phytoplankton biomass in the autumn of 1984 when IP is relatively small. This low carbon production relative to chlorophyll biomass may be due to a combination of low temperature and light. The phytoplankton community at that time was large but very slow growing and possibly under lower grazing pressure (due to low temperature affecting zooplankton grazing activity).

Phytoplankton as an Indicator of Acidification

After this analysis of environmental correlates of the production model it is evident that no one factor is dominant. In certain years the stratification appears important (1984 and 1987) while in others it appears to have little effect (1985). Temperature and light clearly influence production but are more important in establishing the range of possible values than in predicting the patterns of change. Patterns in water clarity may parallel those of α^B and be controlled by chlorophyll biomass, but this relationship can break down under the influence of transient physical disturbances. Furthermore, these transient disturbances (i.e., snowmelt, large rain events, wind-induced mixing) may be so important to the short-term dynamics of the phytoplankton-production system that modelling the effects of environmental factors on production may be impossible (see Côté and Platt 1984). However carbon production may still be a valuable index of acidification effects. When looking at longer time periods, such as the entire ice-free season, we see much less annual variation. Mean daily production and seasonal lake production in Emerald Lake are very similar in all three years despite large variations in P_m^B , P_m , chlorophyll-a, and peak IP rates. Additionally, 80 to 90% of the annual production in mountain lakes occurs during the ice-free period (Goldman and De Amezaga 1984, Shearer et al. 1987). There is not, however, a consensus on the effect of increasing acidity on phytoplankton community production. When examining a single species, acidification has been shown to be detrimental (Schenck et al. 1988) and has been demonstrated to alter the balance between phytoplankton and macrophyte production (Grahn 1986). Studies on lakes contaminated with acid mine wastes have shown a decrease in lake fertility which was also associated with metal toxicity (Yan 1979, DeCosta and Preston

1980. Cabecadas and Brogueira 1987). Early studies of lakes in Scandinavia (Grahn 1974, Hendrey et al. 1974) showed declines in biomass due to acidification as did selected lakes in the La Cloche region of Ontario (Bleiwas et al. 1984), softwater lakes in Florida (Brezonik et al. 1984) and lakes in Finland (Ilmavirta et al. 1984).

Other researchers have found no decrease in biomass and primary production during acidification experiments (Havens and DeCosta 1987, Melack et al. 1987) or in acidified lakes (ELA Lake 223: Shearer et al. 1987, Tibbs Run Lake, W. Virginia: Shellito and DeCosta 1981, northern Ontario lakes: Kwiatkowski and Roff 1976). Fortunately some of the discrepancies in the data have been explained. Many of the differences are due to sampling methodologies and the manner in which production units are expressed. Under acidifying conditions, water transparency can increase (Shearer et al. 1987). Thus the euphotic zone increases such that biomass and productivity measurements made with single subsurface samples underestimate these parameters. Areal measurements of carbon production, as opposed to volumetric, give more accurate estimates of the phytoplankton response to acidification. There is, however, some general agreement among these studies. The one clear indication of acidification has been the strong decrease in the diversity of the phytoplankton communities, both in acidified lakes and artificial enclosures which were acidified (Kwiatkowski and Roff 1976, Yan 1979, Brezonik et al. 1984, Seigfried et al. 1984, Havens and DeCosta 1984, Bleiwas et al. 1984, Blouin et al. 1984, Melack et al. 1987). This trend was evident in all the above lakes despite substantial differences in the study sites and in the methodology.

It is uncertain whether the results of these studies can be extrapolated to Emerald Lake. The transparency is very high in Emerald Lake and given its shallow depth, the entire water column is euphotic. Moreover, the transparency of Emerald Lake is already as high as that found in acidified lakes in Canadian Shield (Shearer et al. 1987). Photoinhibition of phytoplankton production occurs in mountain lakes (Priscu 1984) and probably occurs in Emerald Lake. The average value of the derived parameter I_k (the ratio of $P_m^B : \alpha^B =$ optimum light level) in Emerald Lake is $140 \mu\text{Einsteins m}^{-2} \text{s}^{-1}$, the light level usually found at a depth of 4 to 7 m (Figure VII-10). This makes it unlikely that increased water transparency would enhance carbon production. There is also the possibility that lower water turbidity would interfere with summer thermocline formation, a potentially important correlate of integral

production in Emerald Lake. Data from enrichment experiments at Emerald Lake have demonstrated the potential importance of the nutrients associated with acid deposition in the Sierra Nevada (inorganic nitrogen) in enhancing phytoplankton biomass. Work conducted at Emerald Lake indicates that carbon production is potentially useful in detecting acidification affects.

Table VII-1. Summary of primary production data for the ice-free seasons of 1984, 1985 and 1987. The units for daily production are $\text{mg C m}^{-2} \text{d}^{-1}$. The units for total integral production are mg C m^{-2} per season. The units for seasonal lake production are kg C per season and represent the entire volumetric carbon production of the lake.

Year	Mean Daily Prod.	Max. Daily Prod.	Season Integral Prod.	Season Lake Prod.	Days In Season
1984	57	106	5973	96	103
1985	70	138	7368	118	105
1987	60	168	6459	103	107

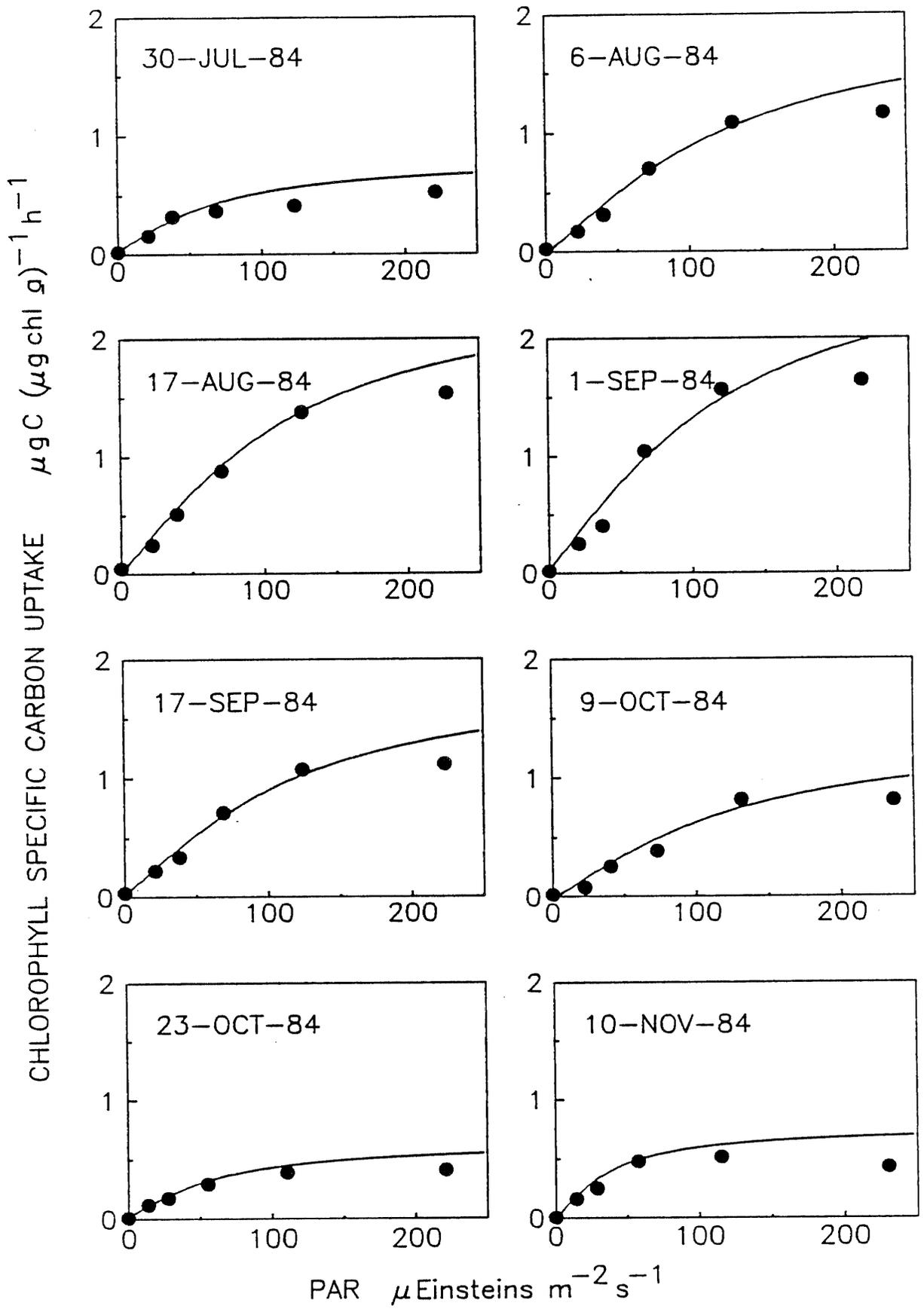


Figure VII-1. P/I curves for 1984.

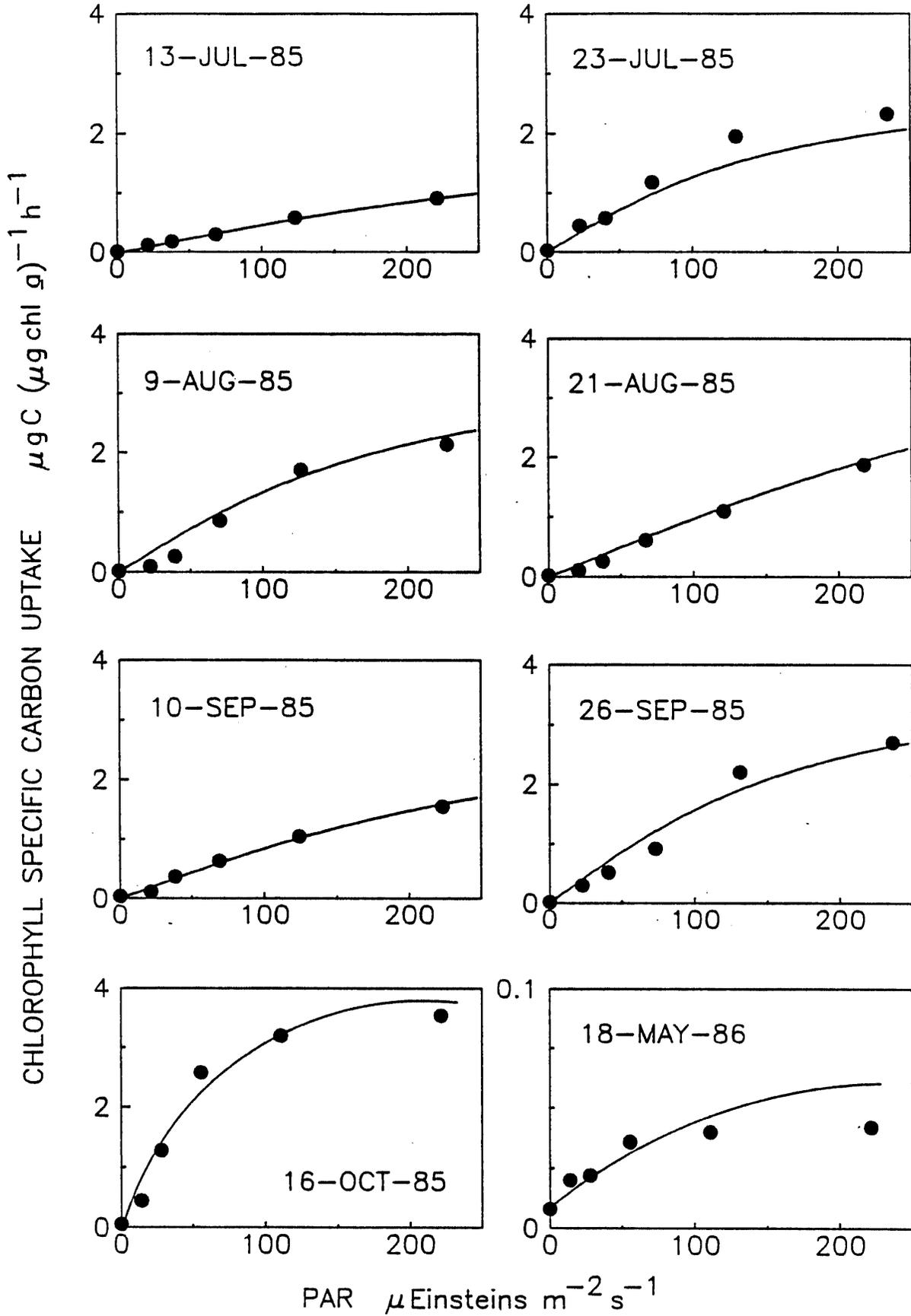


Figure VII-2. P/I curves for 1985 and 1987.

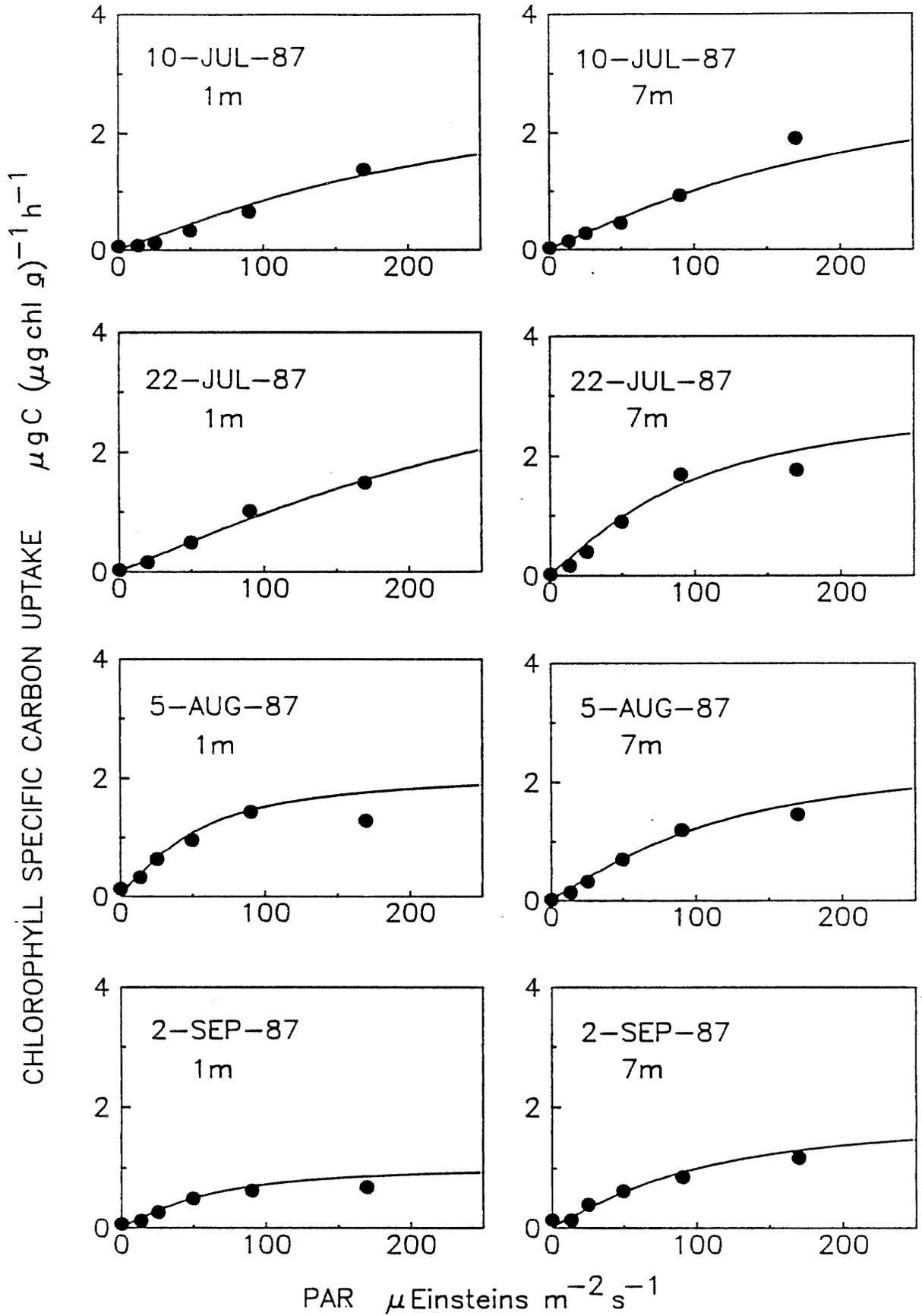


Figure VII-3. P/I curves for 1987.

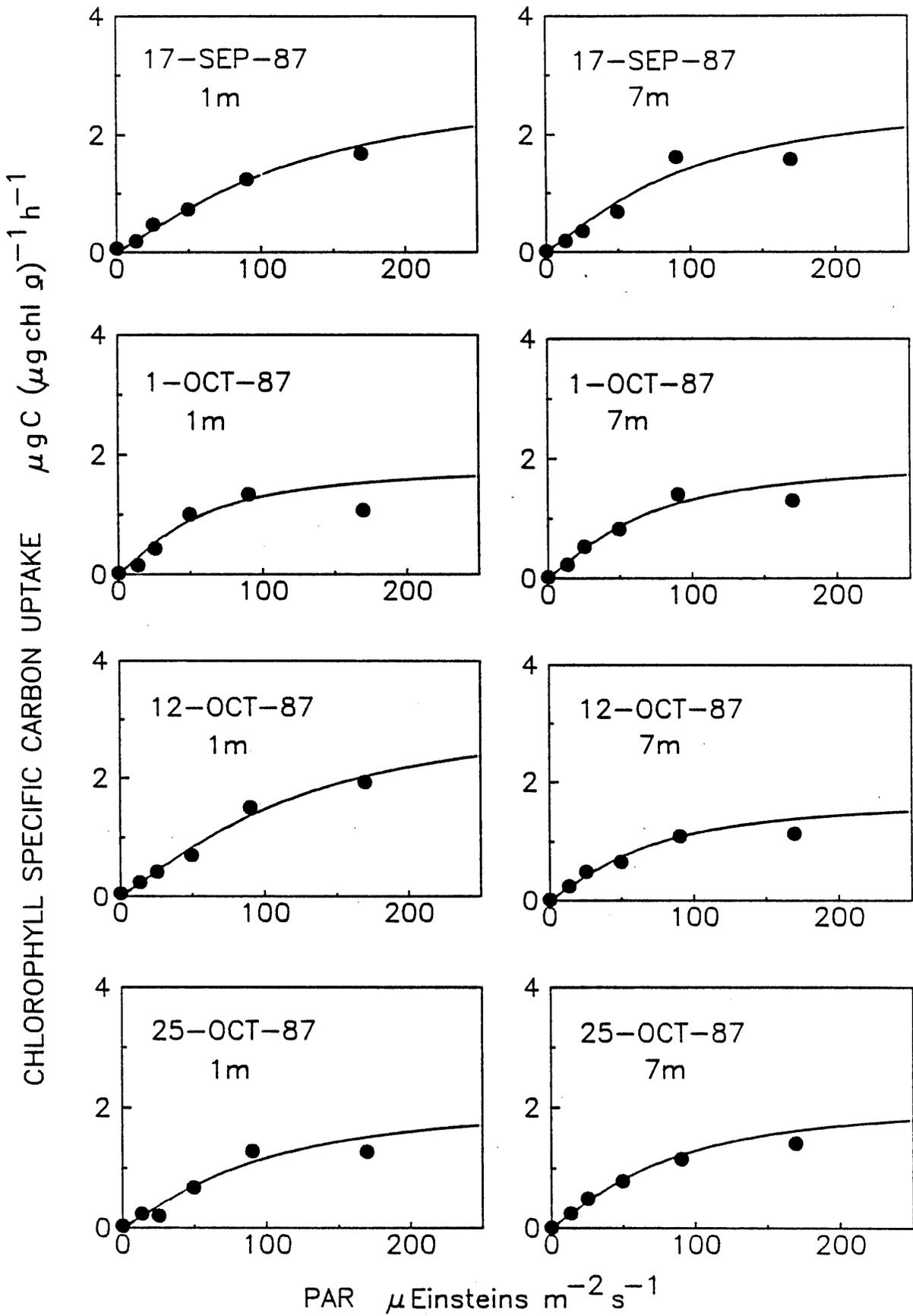


Figure VII- 4. P/I curves for 1987.

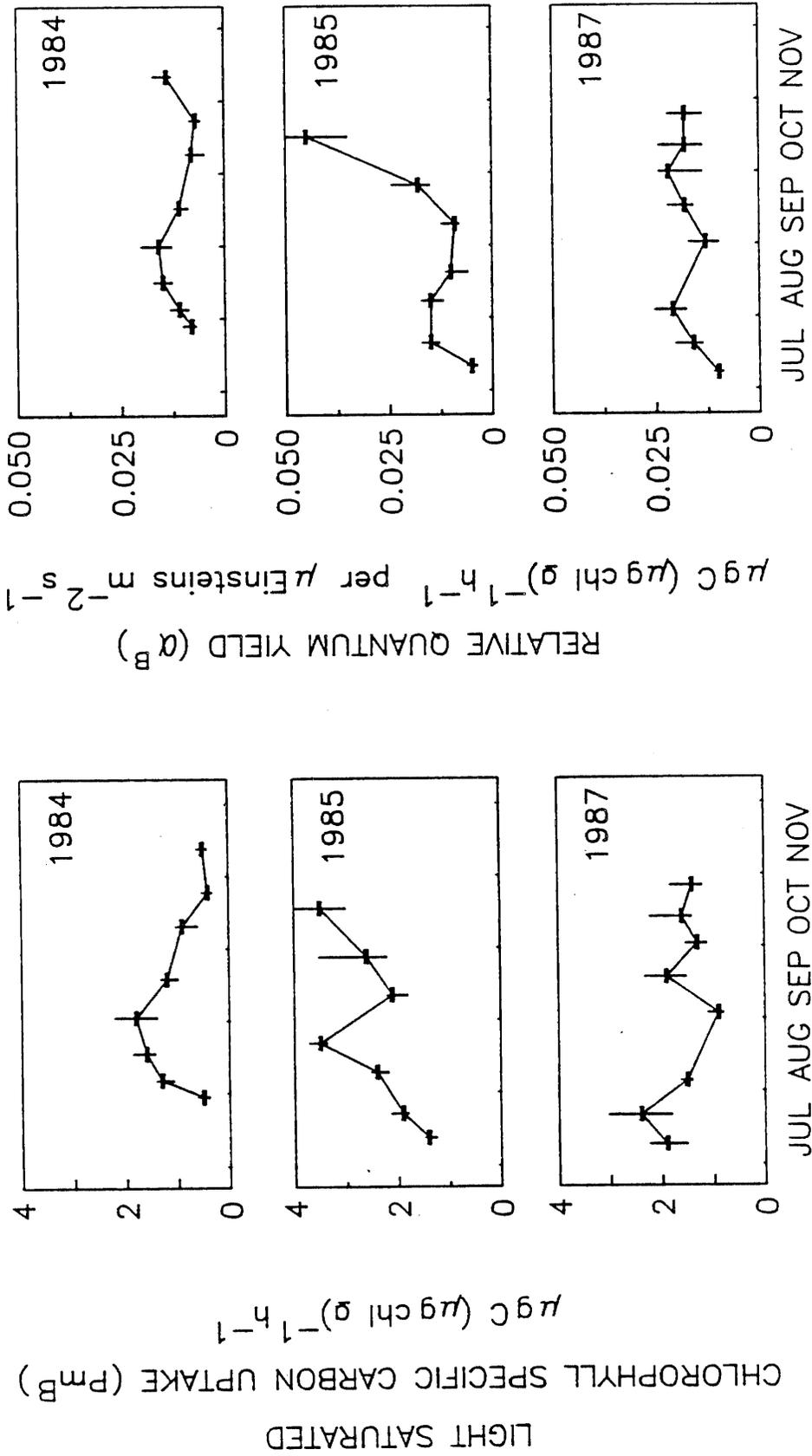


Figure VII-5. Light saturated carbon uptake and relative quantum yield for the ice free periods of 1984, 1985 and 1987. The vertical lines indicate the 90% confidence interval.

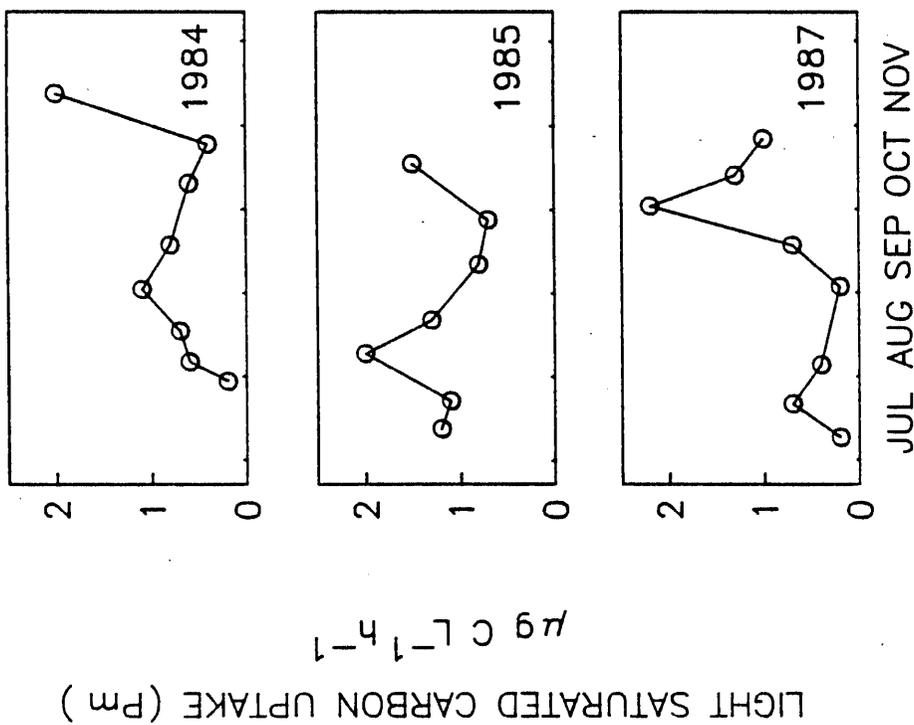
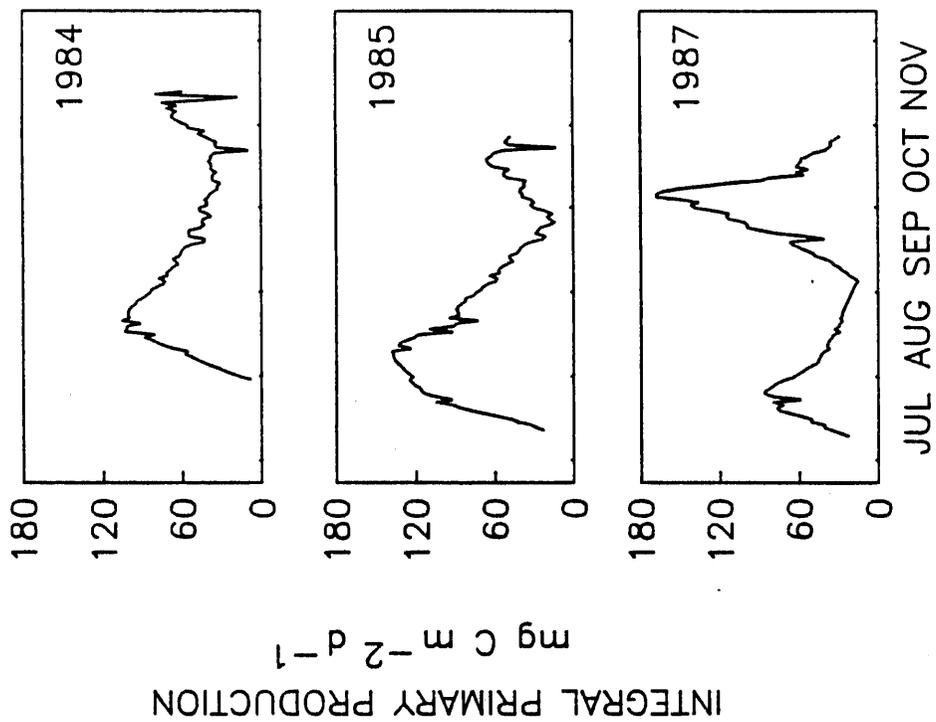


Figure VII-6. Light saturated carbon uptake and integral primary production for the ice free seasons of 1984, 1985 and 1987.

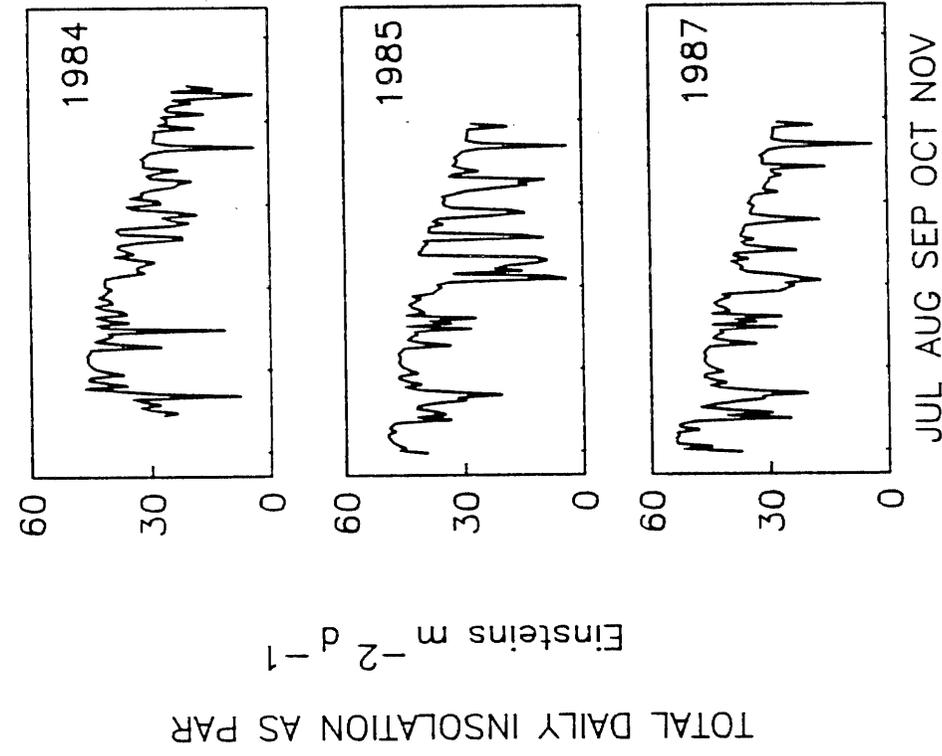
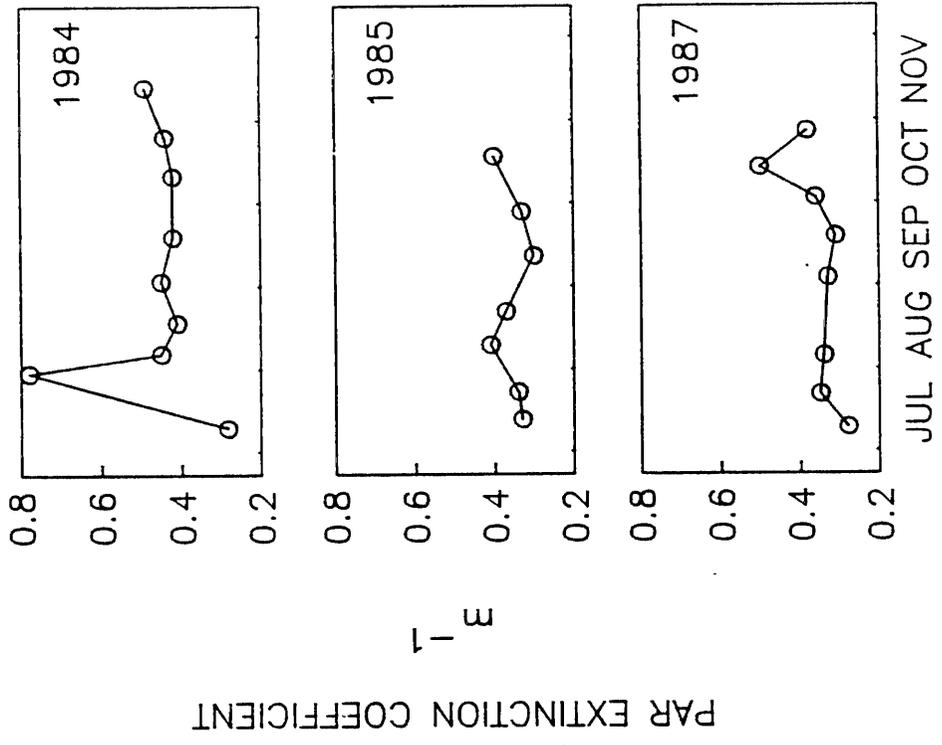


Figure VII-7.
Total daily insolation as PAR (400-700 nm) and the PAR extinction coefficient for the ice free seasons of 1984, 1985 and 1987.

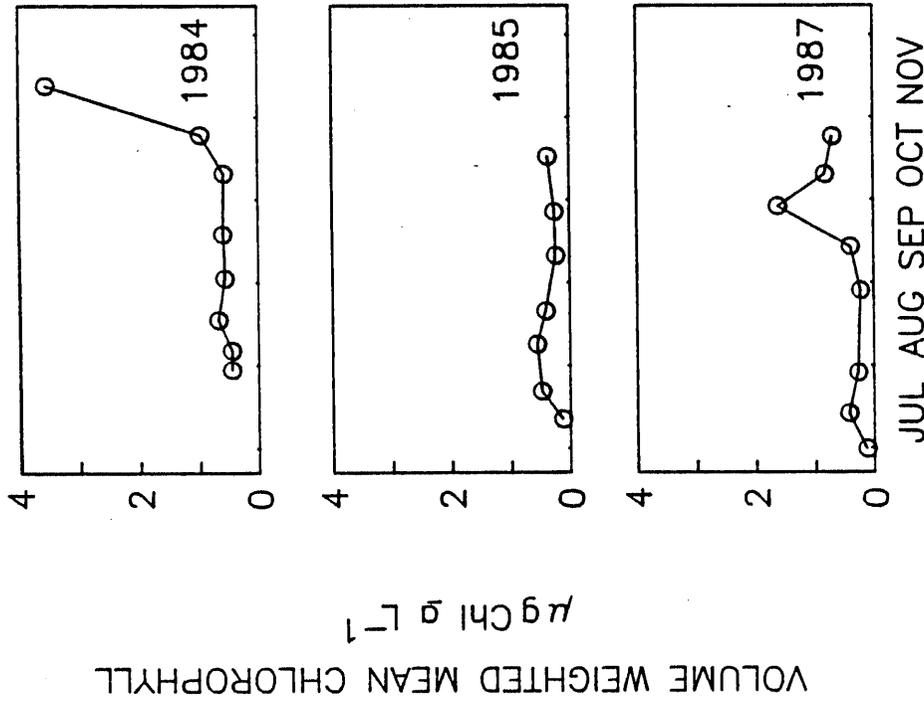
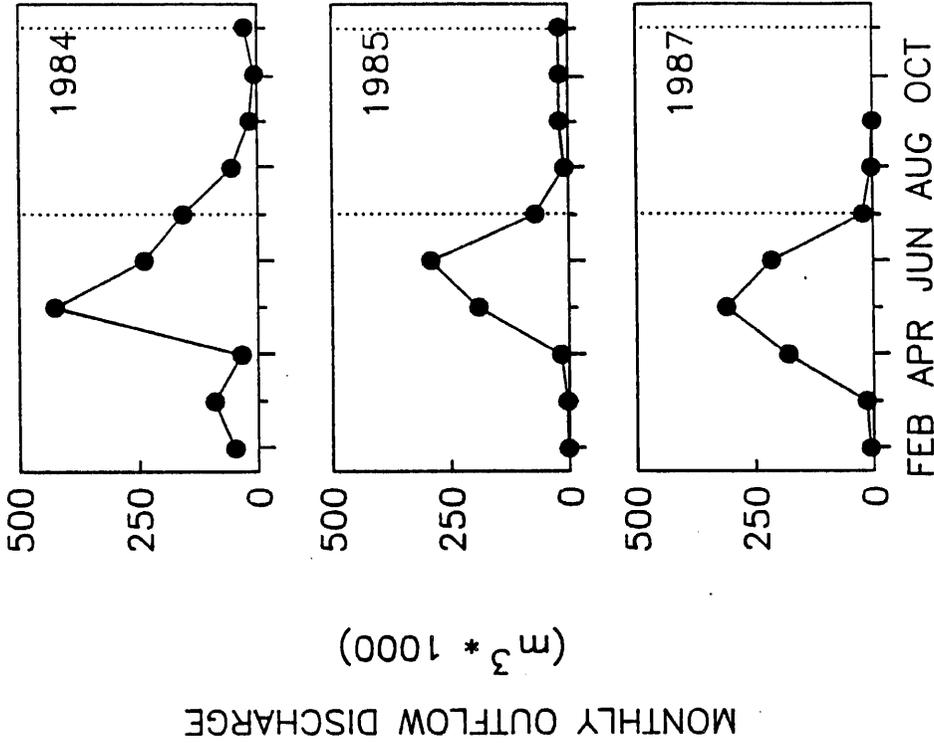


Figure VII-8. Volume weighted mean chlorophyll concentrations for the ice free seasons of 1984, 1985 and 1987 and monthly outflow discharge for the period from February through November for the same years. The tic marks for the date on the discharge figures indicate the beginning of months. The vertical dotted lines indicate the period July through November.

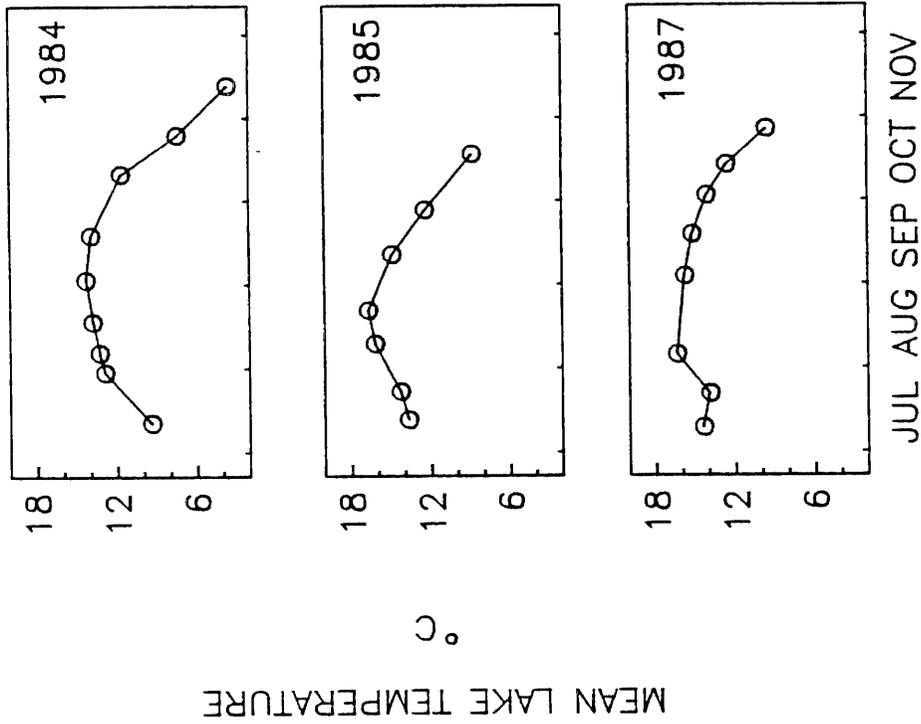
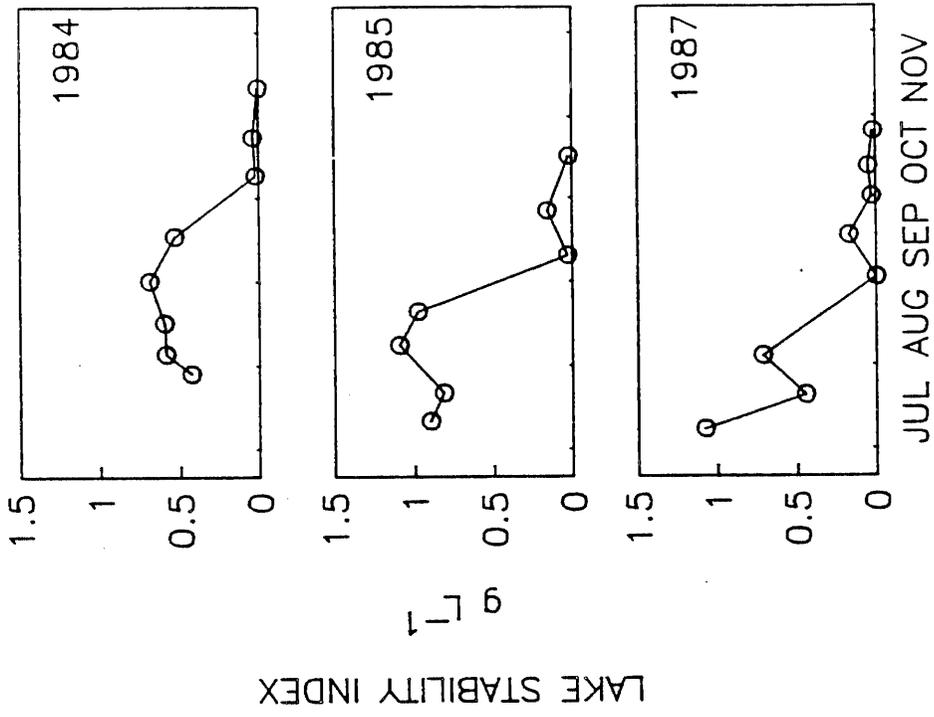


Figure VII-9.
 Mean lake temperature and lake stability for the ice free seasons of 1984, 1985 and 1987. Mean lake temperature was calculated as the average of temperature measurements made at one meter depth intervals. Lake stability is defined as the density difference between one and ten meters.

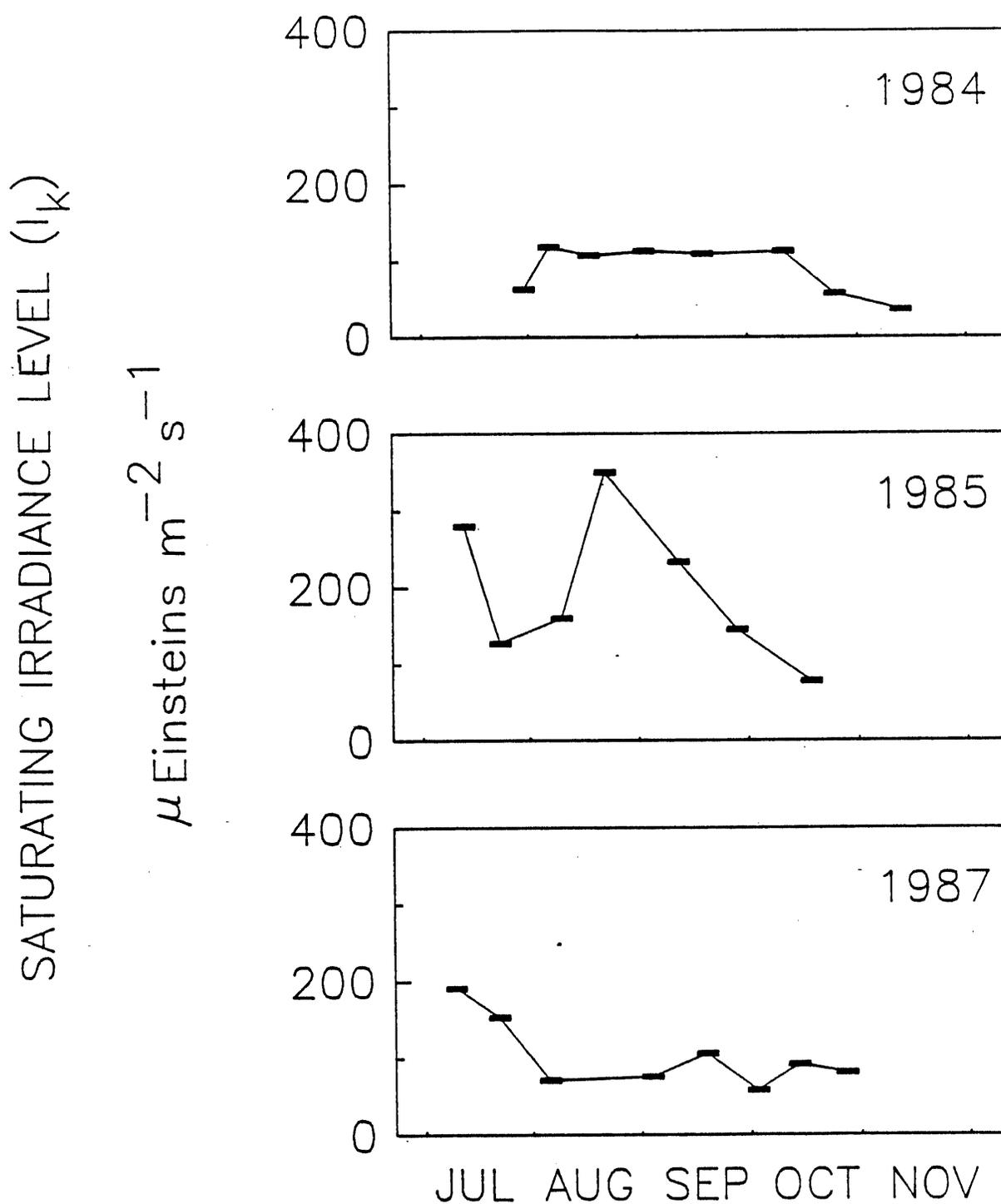


Figure VII-10.

Saturating irradiance level for the ice free periods of 1984, 1985 and 1987. This parameter is defined as the ratio of light saturated chlorophyll specific uptake to relative quantum yield.

Chapter VIII

Zooplankton and Zoobenthos

Of the aquatic invertebrate groups, the zooplankton shows the clearest and most consistent responses to acidification, commonly including a reduction in species diversity and marked changes in the relative abundances of species (Schindler et al. 1985, Mierle et al. 1986, Okland and Okland 1986). The zoobenthos also includes acid-sensitive taxa; surveys and experiments in streams have documented particularly sensitive responses to acidification in mayflies (Ephemeroptera) and stoneflies (Plecoptera) (Hall et al. 1980, Hall and Ide 1987, MacKay and Kersey 1985, Ormerod and Edwards 1987). Field experiments in which pH is rapidly reduced in flowing waters have shown increases in drift of invertebrate benthos and decreases in emergence of adults (e.g. Hall et al. 1980); presumably densities of sensitive taxa would be reduced in following years if the pH remained low. The lacustrine zoobenthos has received less attention, especially in experimental studies. Nevertheless, several species have been shown to be sensitive to acidification (e.g. Hyaella azteca, Orconectes virilis). Mollusks as a group are regarded as being intolerant of acidic conditions, although gastropods are generally more sensitive than pelecypod bivalves (Okland and Okland 1986).

There is clearly a role for descriptive or survey data in assessing and monitoring the effects of acidification in ecosystems. Data collected over a long time period can be useful in detecting any chronic or cumulative effects of acidification in lakes and streams (Likens 1983). However, acidic deposition is not the only factor that will influence the distribution and abundance of aquatic invertebrates, and baseline monitoring of the biota will document the natural variation in the community (Green 1979).

We commenced sampling the invertebrate communities of Emerald Lake and its outflow in July 1984. The principal aim of these monitoring studies was to produce a substantial baseline of biological data. This baseline can then be used to establish the magnitude of seasonal and year-to-year variations against which to judge future changes in the aquatic biota. In addition, we can suggest which communities would be most useful for continued monitoring to assess the effects of acidification, together with methods and frequency of future sampling.

We examined two major communities in detail: the zooplankton of Emerald Lake itself and the zoobenthos of its outflow. The zoobenthos was collected by direct sampling of the stream bed and by sampling drifting organisms. The latter approach was explored because drift samples are less costly to process, and because drift is an important component of fish diets in this system. In our analyses we paid particular attention to those taxa which were found to be sensitive to acidification in our experimental studies (Melack et al. 1987, Hopkins et al. 1988, Cooper et al. 1988b).

Methods

Zooplankton

Regular zooplankton sampling began in July 1984. The number of stations sampled on each date, and the frequency of sampling are summarized in Table VIII-1. At each station on each date duplicate vertical tows were taken from near the bottom to the surface of the lake using a 64- μ m mesh net. Zooplankton samples were preserved in the field with 10% formalin. From July 1984 through February 1986 a 0.2-m diameter net was used; after February 1986 we used a 0.12-m diameter net because it was easier to manipulate in winter and was identical to the net used in the lake experiments. The depth of each tow was recorded (range 2 to 10 m) and numbers per sample were converted to numbers per cubic meter prior to averaging across all stations for each date. The filtration efficiency of the net was assumed to be 100%. Methods of zooplankton subsampling and enumeration are given in Chapter VI.

Stream zoobenthos and drift

The benthic sampling program changed during the course of the project as methodological improvements were made, and as distinct habitats became apparent. The sampling devices and the area sampled were changed to reduce the effect of sampling on the stream habitat, and to accommodate low water levels during the late summer (see below). By the end of 1984, we were sampling four habitats in the outflow:

- 1) Soft - substrate consisting of fine gravel, sand or organic debris;
- 2) Hard - bedrock or boulders;
- 3) Cobble - large rocks and cobbles;
- 4) Moss - hard substrate covered either with moss or filamentous algae.

In 1984, samples were taken monthly from July to October inclusive from soft, hard, and cobble habitats using a Hess sampler (mesh size 390 μm , area 0.10 m^2) (Hess 1941). Five replicates were taken from soft substrates, between three and five from hard substrates, and one from cobbles on each date. Three replicate Hess samples were taken from each of the soft and hard substrates in December as well. Moss habitats were inaccessible in winter but were sampled in September and October by scraping four 0.1 m X 0.1 m quadrats into a hand-net (effective mesh size 250 μm).

In 1985 all substrates were sampled monthly from July to October inclusive. Five replicate samples were taken from soft and hard substrates, three from moss and one from cobbles on each date. Soft and cobble habitats were sampled with the Hess sampler, while the hard and moss samples were taken with a mini-Hess device (a smaller version of the Hess sampler: mesh size 250 μm , area 0.081 m^2). In addition, one Hess sample was taken from hard substrates in March, and, because of low flows, three replicate 0.1 m X 0.1 m quadrats from each of soft and hard habitats in November.

In 1986 and 1987 the mini-Hess sampler was used to sample soft and cobble substrates while all hard and moss samples were collected using 0.1 m X 0.1 m quadrats. For July-October 1986 and July-September 1987, the number of replicates for each habitat was the same as in July-October 1985. In addition three replicates were collected from soft and hard habitats in May, June and December 1986, and on 1 and 29 April 1987.

Stream drift was sampled monthly from July-October 1984, August-September 1985, November 1985-December 1986, and March-September 1987. One additional drift sample was taken at the end of August 1984. Sampling runs were conducted over 24 hours and were divided into 4 to 6 sampling periods on each date; sampling periods were timed so that they encompassed dusk and dawn when drift rates are usually maximal (Waters 1972, Brittain and Eikeland 1988). In 1984 the drift nets had a mouth area of 0.135 m^2 (0.3 X 0.4 m). After 1984, 0.04 m^2 (0.2 m X 0.2 m) nets were used on all dates; all nets had a mesh of 250 μm . One net was set at each of two sites: the upper site was 58 m downstream of the lake and the lower site was a further 27 m downstream, which is a sufficient distance for the downstream samples to be free of interference from the upstream net (Waters 1972). Each time the nets were set, stream velocities were measured using Bentzel tubes to determine discharge through the net. These data were used to see whether flow through the net

varied during the sampling period due to clogging or short-term variations in stream discharge.

All benthic and drift samples were preserved in 70% ethanol in the field and were returned to the laboratory where they were sorted and identified using dissecting microscopes at 25 to 50 X. Where necessary materials finer than 1 mm were subsampled with a plankton splitter.

Identification of invertebrates followed Merritt and Cummins (1984) and various taxonomists (listed in the Acknowledgments) were consulted to confirm identifications where necessary. For samples taken from 1986 and 1987 we attempted to identify the Chironomidae and Simuliidae to genus or species for all samples. Unfortunately, this proved impossible to do routinely for all Chironomidae since several taxa of two subfamilies could only be separated reliably by dissection, maceration and mounting of head capsules for examination under a compound microscope. As a compromise, chironomids were split into the following groups to see if more information could be gained from using a finer taxonomic resolution: 1) Orthocladiinae and Diamesinae, 2) Tanypodinae, 3) Tanytarsini, and 4) Chironomini.

There were insufficient resources to process all the drift and benthic samples collected. Instead, we attempted to process samples from early and late summer in all years, since summer was when the fauna was most abundant, and, in the case of drift, we had a complete set of samples (during the winter, we occasionally lost samples because of overnight freezing of the stream).

Results

Zooplankton

A complete list of the taxa of zooplankton collected from Emerald Lake is given in Table VIII-2. Numerically, the fauna was dominated by rotifers: Polyarthra vulgaris reached mean abundances near $800,000 \text{ m}^{-3}$ whereas the most abundant crustacean, Daphnia rosea, had maximal abundances of around $20,000 \text{ m}^{-3}$ (Figs. VIII-1 and VIII-2). Most of the species collected, however, were too rare or occurred too sporadically for statistical analyses of abundance patterns. The species that were sufficiently abundant for analysis are listed in Table VIII-2 and include a calanoid copepod and its nauplii, four species of cladoceran crustaceans, and five species of rotifers.

The data from July 1984 through October 1987 are presented in Figure VIII-1 for the crustaceans and Figure VIII-2 for the rotifers. Diaptomus

signicauda usually peaked in abundance in late summer and early fall (i.e. August-September), and these peaks were generally preceded by elevated numbers of diaptomid nauplii. Daphnia rosea also peaked in late summer and early fall, whereas Holopedium gibberum reached its maximum earlier in summer (June-July). Bosmina longirostris showed more erratic patterns, but typically was more abundant in winter than in summer. Chydorus cf. sphaericus was substantially less common than the other crustaceans; it was restricted mostly to summer but showed no other obvious patterns of variation.

The rotifers showed substantial interannual variation both in abundance and in the timing of peaks. Generally, however, they were most abundant in late summer and fall (i.e., after July). Keratella taurocephala was most numerous in November 1985 and October 1987. This species, together with Polyarthra vulgaris and the less abundant Trichocerca capucina usually peaked between July and November. Conochilus unicornis showed the most consistent patterns from year to year, rising sharply to high abundances in summer and gradually declining through fall. Keratella quadrata, although rarer, showed similar timing of maxima.

In summary, the typical pattern of seasonal change in species composition of zooplankton in Emerald Lake is as follows. From January until late March all species are at low densities except for the cladoceran Bosmina longirostris. In late May or early June Holopedium gibberum dominates the crustaceans, and is followed later in summer and early fall by high numbers of Daphnia rosea and Diaptomus signicauda. Concomitantly, the colonial rotifer Conochilus unicornis reaches its peak abundance together with Polyarthra vulgaris. Keratella taurocephala may come to dominate the zooplankton later in fall, before Bosmina longirostris becomes dominant during winter.

The most obvious exception to this scenario was in 1986. The peaks in abundance for Holopedium and Conochilus were delayed, and all the other species which typically reached maximum abundances in August-October were severely reduced in abundance, in some cases by an order of magnitude (e.g. Diaptomus, Daphnia). We attribute these changes to the persistence of ice in 1986 (Fig. VIII-3). Emerald Lake was not completely free of ice until mid-July, and, consequently, the timing of zooplankton life cycles was shifted to later in the year. The onset of winter, however, was not delayed in 1986, resulting in a shortened growing season for the plankton species characteristic of late summer.

Stream zoobenthos

The composition of the fauna is given in Table VIII-3. The stream benthos is diverse with dipteran taxa, especially the Chironomidae, making up the bulk of the species. Table VIII-3 probably underestimates the total benthic diversity because the Oligochaeta could not be identified to species since our sampling and processing techniques usually damaged taxonomically important features of these animals. Furthermore, there could possibly be additional sibling species within the dipteran taxa that could only be identified reliably using more complicated techniques (e.g. electrophoresis).

Previously we found that the densities of benthic invertebrates were highly variable, but that generally the mossy substrates supported the highest densities (Melack et al. 1987). This pattern was reiterated in 1986-87 (Fig. VIII-4). Simultaneous confidence intervals around the medians (McGill et al. 1978) for each type of substrate over all sampling dates processed in 1986-87 showed that the hard and moss substrates had significantly ($P < 0.05$) higher abundances than either the soft or cobble substrates; hard and moss substrates did not differ significantly from each other ($P > 0.05$), nor did cobble and soft habitats. Numerically, the fauna was dominated by chironomid larvae on all substrates except the hard, where filter-feeding Simuliidae were presumably able to take advantage of the firm substrate and unimpeded flow to harvest food (Fig. VIII-4). However, this preference for hard substrates by Simuliidae was only recorded on one other date in our earlier study (July 1985; Melack et al. 1987).

Temporal variation of invertebrate abundance over the 1986-87 samples showed no consistent pattern across substrates. Total numbers and numbers of chironomids were highest in moss in fall 1986, whereas soft substrates showed highest abundances of invertebrates in July 1987 (Fig. VIII-5). Simuliids tended to be more numerous in spring and summer in their preferred habitat, and some of the non-dipteran taxa (e.g. Baetis, Rhyacophila) also peaked in summer and early fall. Other insects (Ephemereididae, Nematouridae) and the major non-insect taxa (mites and oligochaetes) showed erratic variations in abundance, with no clear seasonal patterns; this was probably due to the scarcity of these organisms resulting in imprecise estimates of population densities.

Examination of the finer taxonomic divisions of the Chironomidae and Simuliidae showed no further spatial or temporal patterns for the 1986-87 samples (Fig. VIII-6). The Chironomidae were dominated by species in the

subfamilies Orthocladiinae and Diamesinae: the latter is typically common in cold-water streams (Coffman and Ferrington 1984). Of the Simuliidae the genus Simulium was more abundant than Prosimulium on most dates, especially on hard substrates (Fig. VIII-6).

To determine whether there were any interannual changes in the benthos we examined the full data set from 1984 to early 1987. Figure VIII-7 shows the data for the two most abundant taxa, the Chironomidae and Simuliidae, as well as Baetis spp. and the bivalve mollusc Pisidium sp. Baetis was chosen because our earlier experiments indicated this taxon was the most sensitive of the local fauna to acidic inputs (Melack et al. 1987; Hopkins et al. in press); Pisidium was graphed because it was the most abundant mollusk in the stream, and other studies have found that mollusks are good indicators of long-term acid stress (e.g. Servos and Mackie 1986, reviews by Mierle et al. 1986, Okland and Okland 1986).

Although the data are variable, Figure VIII-7 indicates that 1986 had lower abundances of chironomids and simuliids than previous years. From the limited number of winter samples processed, it also appears that large numbers of chironomids sometimes persist during winter, whereas simuliids all but disappear. However, since mossy substrates were not sampled during winter, it is difficult to verify the pattern for this habitat. Variations in sampling techniques from year to year may further account for some of the patterns in Figure VIII-7.

Baetis spp. appear to be most abundant in summer and in moss; however, their overall abundances were very low (usually < 20 individuals per sample) and variable, and no interannual trends were apparent in the data (Fig. VIII-7). Pisidium was virtually absent from all habitats but the soft substrates. Although variable in abundance, it seemed to peak regularly in summer and fall in all years.

Stream drift

Water flow through the nets varied little during the course of any given sampling date, although there were substantial differences among dates. The data presented in Figures VIII-8 and VIII-9, however, are expressed as drift rates (i.e. numbers of organisms drifting into the nets per hour) because this is a useful indicator of food availability for fish.

Faunal composition of the drift (Fig VIII-8) was similar to that of the benthos: numerically it was dominated by chironomid and simuliid larvae. Occasionally, large numbers of terrestrial invertebrates were also washed into the stream. For 1986 we examined the abundances in the drift of the two most abundant groups (Chironomidae and Simuliidae), the most numerous acid-sensitive species (Baetis spp.), and terrestrial invertebrates because they can comprise a large proportion of fish diets.

Trends in drift rate were usually the same at the upper and lower outflow sites for the aquatic invertebrates, with abundances typically elevated after dusk and declining again after dawn. Diel changes in the abundance of terrestrial invertebrates were less regular, probably because their input is unrelated to diel changes in light. Drift rates of simuliids and chironomids were highest in August. Benthic densities of simuliids were highest for August, but chironomids were more numerous in September. Baetis, which is the stream invertebrate most sensitive to acidic inputs, was absent from the drift in both July and August. This reflects reduced benthic densities in these two months in 1986; when benthic densities increased in September, numbers also rose in the drift.

Comparison of year-to-year differences (Fig. VIII-9) showed that peak drift rates were shifted to later in the year in 1986: rates were lower in early summer than in previous years, but were higher in early fall (September). It appears that Baetis is usually absent from the drift early in summer (July), and its drift rate peaked later in 1986 than in previous years. There were also substantial differences in drift rate between the upper and lower sites in mid-summer of 1985.

Discussion

The zooplankton of Emerald Lake is typical of oligotrophic, high altitude lakes in the Sierra Nevada containing brook trout (Stoddard 1987). Similarly, the stream benthos is diverse, numerically dominated by dipteran larvae, and has a species composition similar to that found in other streams in the Kaweah catchment (Chapter X). The continued presence of taxa known to be acid-intolerant in the lake (e.g. Daphnia rosea, Diaptomus signicauda; see Chapter VI) and in the stream (e.g. Pisidium, Baetis, other Ephemeroptera, and some Plecoptera; see Cooper et al. 1988b) suggests that neither habitat is currently suffering chronic acid stress.

Our data indicate a marked seasonality in the zooplankton assemblage which is repeated regularly from year to year, unless prolonged winter conditions delay life cycles and diminish abundances of species characteristic of late summer. The data also suggest that the extreme conditions in 1986 may have reduced the density of Bosmina longirostris over the winter of 1986-87 in comparison with previous winters. However, most species seemed to have recovered in 1987, indicating that the zooplankton are resilient to this sort of climatic stress.

The stream benthos also showed some evidence of reduced densities in 1986. This is consistent with the observation of scouring of the outflow resulting from the 1986 avalanche, and the poor recruitment of brook trout in this year. We conclude that interannual variations in climate and disturbance regime can significantly affect zooplanktonic and benthic community structure, and such effects need to be considered in any long-term quantitative monitoring program.

Because of its high abundance and relatively predictable occurrence from year to year, the zooplankton is the most promising invertebrate group for routine, long-term monitoring. Our experiments suggested four species were good indicators of acidity: Daphnia rosea, Diaptomus signicauda, Bosmina longirostris, and Keratella taurocephala. The former two decline with decreasing pH, while the latter increase, at least down to pH 5.0 (see Chapter VI). Apart from the effects of prolonged winter, the monitoring data presented in Figs. VIII-1 and VIII-2 also indicate interannual variations in abundance that are difficult to explain. Abundances of Keratella taurocephala and Polyarthra vulgaris seem to have a loose inverse relationship while the abundance of Diaptomus signicauda was similarly low in 1984 and 1986. It would be prudent, therefore, to continue monitoring the abundances of all the common zooplankters since interactions between them and with other environmental variables are still poorly understood in this lake. Sustained simultaneous declines of acid-intolerant species and increases of acid-tolerant ones would provide strong evidence of acidification.

Reducing the cost of zooplankton monitoring could be achieved by reducing the duration or frequency of sampling or by reducing the number of stations sampled. Since most of the abundant zooplankters reach their maxima between June and November each year, it seems reasonable to restrict sampling to the ice-free period. Figures VIII-1 and VIII-2 also suggest that sampling

once per month would usually detect these maxima, whereas the standard errors around the mean are still sufficiently large to recommend against reduction of the number of stations sampled on a date.

By contrast, the stream benthos varied more erratically. The substantial differences in abundance among habitats are consistent with the literature (Hynes 1970, Minshall 1984). However, some taxa altered their preferences from year to year (e.g. Simuliidae), and all taxa showed wide variations about their mean densities within a habitat on any given date. Such variability is not unusual in stream benthos and can only be compensated for by substantially increasing the number of replicate sampling units for each habitat (Chutter 1972, Elliott, 1977, Allan 1984).

Unfortunately, the small size of the Emerald Lake outflow channel and the limited extent of some of the habitats precludes this because the intensity of sampling required would deplete benthic populations. Moreover, such a sampling regime would be prohibitively expensive. Most of the acid-sensitive insects were usually most abundant in habitats with moss or filamentous algae. Samples from these habitats were the most time-consuming to sort, and subsampling was often impossible because much of the fauna was entangled in the moss and algae. In addition, the densities of the acid-sensitive taxa were low.

Drift samples offer a less costly alternative to benthic samples since they are easier to process. Drift samples included relatively high numbers of Baetis spp. when they were present but, as the data from 1986 indicate, the time of peak occurrence can be delayed by a long winter. There is some controversy about whether drift accurately reflects benthic densities (see Brittain and Eikeland 1988); sampling specifically directed at this question needs to be undertaken in this stream before using drift as a substitute for benthic sampling.

Acute acidification usually increases drift rates of sensitive taxa (e.g. Hall et al. 1980, Cooper et al. 1988b). However, this response is relatively short-lived and, during the early stages of chronic acidification, may be difficult to separate from increases resulting from spates (Waters 1972). Consequently, a monitoring program based on drift collections requires a complex sampling regime that is related both to flow and seasonal events; this presents substantial logistic difficulties.

Although our experiments have established that some of the benthic species of streams in the Kaweah catchment are likely to be good indicators of

acidic deposition. biological monitoring based on regular quantitative sampling either of drift or benthos will be difficult and expensive. However, qualitative samples collected less frequently could document the disappearance or appearance of species, thereby corroborating other biological and physicochemical data. The material we have processed so far does provide a solid benchmark for comparison with samples taken in the future. Hall and Ide (1987), for example, inferred changes in stream benthos due to acidification from samples taken nearly 50 years apart in Ontario, Canada, and Ormerod and Edwards (1987) used extensive qualitative survey data to identify species sensitive to acidity.

We conclude that the zooplankton of Emerald Lake is the most reliable and easiest group of aquatic invertebrates to use for continued biological monitoring. The major species are taxonomically well known, samples are easy to collect, and they can be processed more rapidly and inexpensively than benthic samples. Conversely, the stream benthos, whether sampled directly or by using the drift, presents major logistic and interpretive problems for reliable quantitative sampling. Less frequent qualitative surveys may, however, provide corroborative information over the long term.

Table VIII-1. Summary of zooplankton sampling regime. Frequency of sampling given as number of times per month; *= no samples taken in March 1986.

Date	Number of stations	Frequency of sampling
Jul 84 - Oct 84	7 - 8	2
Nov 84 - Mar 85	1 - 2	1
Jun 85 - Oct 85	7 - 8	2
Jan 86 - Jun 86	1 - 3	1*
Jul 86 - Oct 86	5	2
Feb 87 - Mar 87	3	1
May 87 - Oct 87	5	2

Table VIII-2. List of zooplankton collected from Emerald Lake.

CLADOCERA

Holopedium gibberum
Bosmina longirostris
Daphnia rosea
Scapholeberis kingii
Diaphanosoma brachyurum
Moina sp.
Polyphemus pediculus
Chydorus cf. sphaericus
Camptocercus sp.
Alona affinis
Alona sp.
Graptolebris sp.

COPEPODA

Diaptomus signicauda
Cyclops sp.
Bryocamptus sp.

ROTIFERA

Keratella taurocephala
Keratella quadrata
Polyarthra vulgaris
Conochilus unicornis
Trichocerca capucina
Trichotria sp.
Gastropus stylifer
Bdelloidea

INSECTA

Chaoborus sp.
Chironomidae

MISCELLANEOUS

Hydra sp.
Nematoda
Oligochaeta
Tardigrada
Neorhabdoceola
Ostracoda
Acari

Table VIII-3. List of zoobenthos collected from the Emerald Lake outflow.

PHYLUM NEMATODA

PHYLUM ANNELIDA

CLASS OLIGOCHAETA

PHYLUM MOLLUSCA

Order Bivalvia

Family Sphaeriidae

Pisidium sp.

PHYLUM ARTHROPODA

CLASS CRUSTACEA

Order Amphipoda

Family Talitridae

Hyaella azteca

CLASS ARACHNIDA

Order Acari

Hydrozetes terrestris

Nanhermannia nana

Trimalacothonrus sp.

CLASS INSECTA

Order Collembola

Order Plecoptera

Family Chloroperlidae

Alloperla sp.

?Suwalia sp.

Sweltsa pacificum

Sweltsa sp.

Family Nemouridae

Malenka californica.

Zapada cinctipes

Zapada

?oregonensis/haysi

Family Perlodidae

Cultus sp.

Isoperla

quingepunctata

Order Ephemeroptera

Family Baetidae

Baetis bicaudatus

Baetis tricaudatus

Order Ephemeroptera (cont.)

Family Ephemerellidae

Caudatella hystrix

Drunella doddsi

Drunella grandis

Drunella spinifera

Epeorus grandis

Ephemerella sp.

Seratella sp.

Family Heptageniidae

Cinygma sp.

Cinygmula sp.

Family Leptophlebiidae

Paraleptophlebia sp.

Family Siphonuridae

Ameletus sp.

Order Neuroptera

Family Sialidae

Sialis sp.

Order Coleoptera

Family Dytiscidae

Agabus sp.

Hydroporus sp.

Deronectes sp.

Family Gyrinidae

Gyrinus sp.

Family Hydrophilidae

Ametor sp.

Hydrobius sp.

Hydrophilus sp.

Order Trichoptera

Family Lepidostoma

Lepidostoma cf.

quercina

Family Limnephilidae

Dicosmoecus sp.

Ecclisomyia sp.

Psychoglypha sp.

Family Polycentropodidae

Polycentropus sp.

Family Rhyacophilidae

Rhyacophila sp.

Table VIII-3. (continued).

Order Diptera

Family Chironomidae

Subfamily Chironominae

Tribe Chironomini

Chironomus sp.AChironomus sp.B

Tribe Tanytarsini

?Cladotanytarsus sp.Paratanytarsus sp.

Subfamily Diamesinae

Diamesa sp.Pagastia sp.Pseudodiamesa sp.

Subfamily Orthocladiinae

?Chaetocladius sp.Corynoneura sp.Diplocladius sp.Eukiefferiella sp.Halocladius sp.Heterisocladius sp.Hydrobaenus sp.Microspectra sp.Neozavrelia sp.?Orthocladius sp.Parametriocnemus sp.Psectrocladius sp.Synorthocladius sp.Thienemannia sp.Thienemannimyia sp.

Subfamily Tanypodinae

?Ablabesmyia sp.Procladius sp.

Order Diptera (cont.)

Family Ceratopogonidae

Forcipomyia sp.

Family Dixidae

Dixa sp.

Family Empididae

Chelifera sp.Clinocera sp.Wiedamannia sp.

Family Muscidae

Limnophora sp.

Family Simuliidae

Prosimulium sp.Simulium sp.Twinnia sp.

Family Stratiomyidae

Euparyphus sp.

Family Tipulidae

Dicranota sp.Hexatoma sp.Limnophora sp.Pedicia sp.Tipula sp.

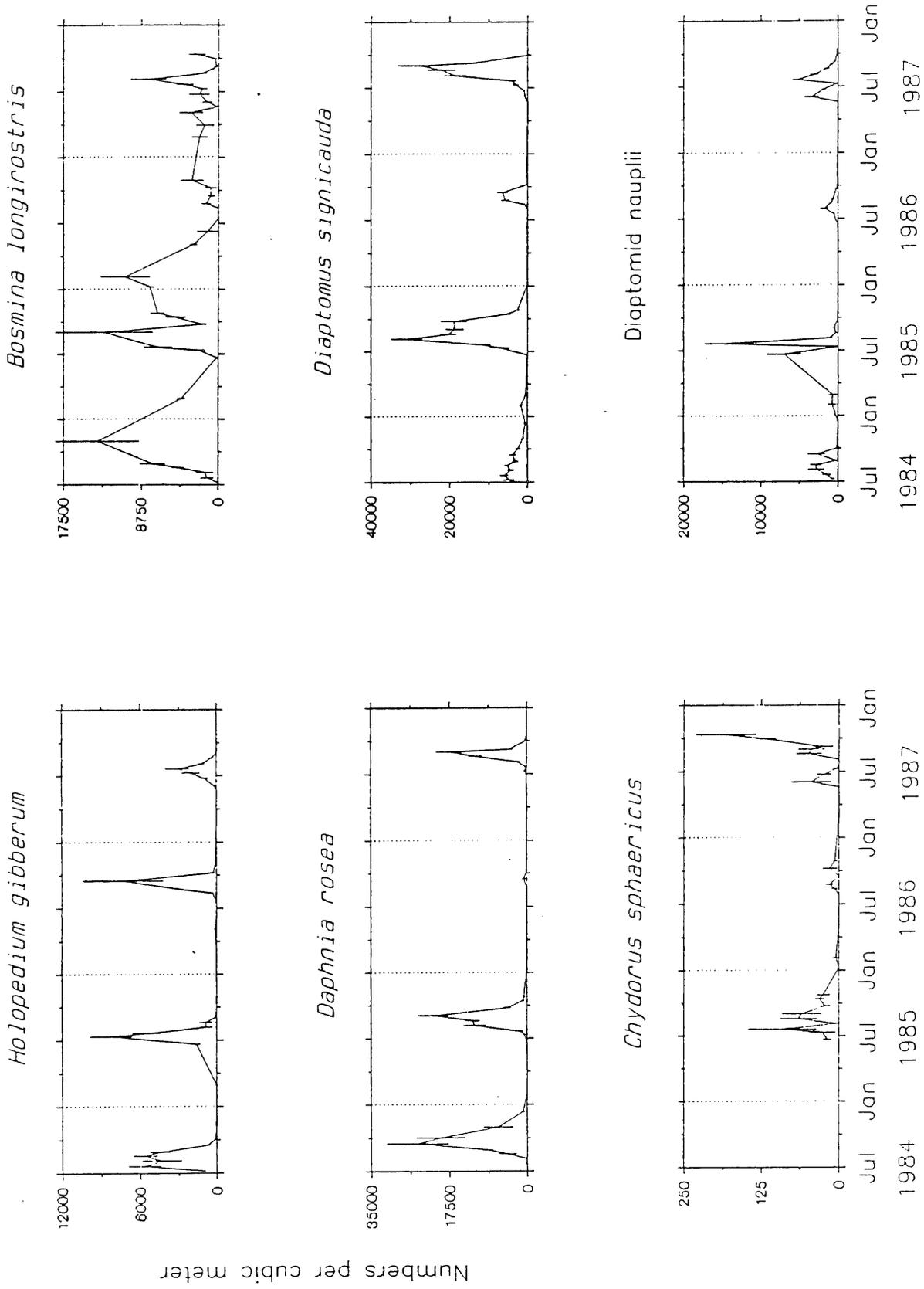


Figure VIII-1. Time-series plots of the abundance of the most abundant crustacean zooplankton species in Emerald Lake from July 1984 through October 1987. Vertical bars are ± 1 standard error of the mean. Abundances of *Chydorus* cf. *sphaericus* were too low to be estimated reliably from samples taken before June 1985.

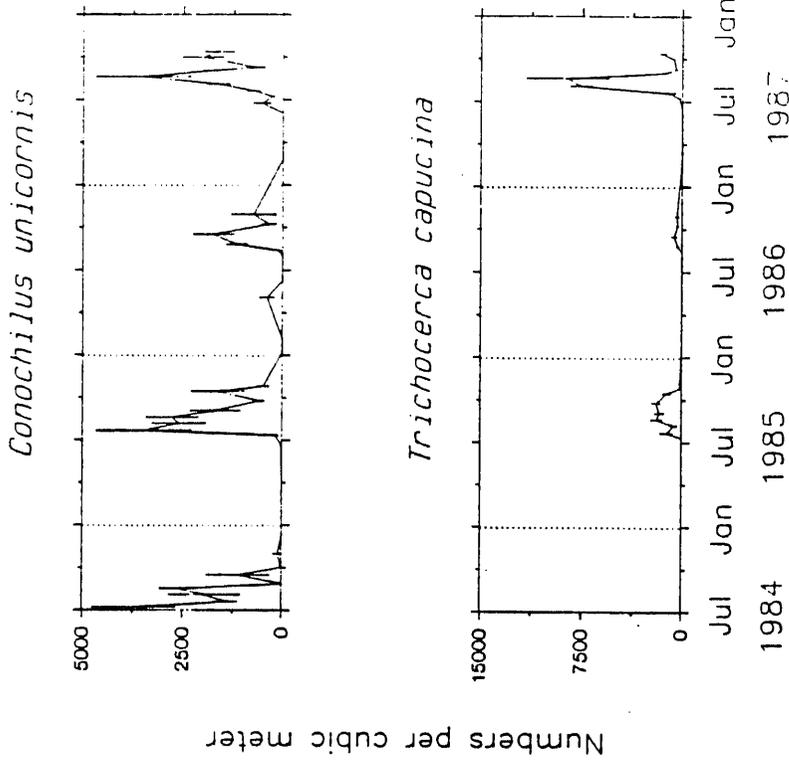
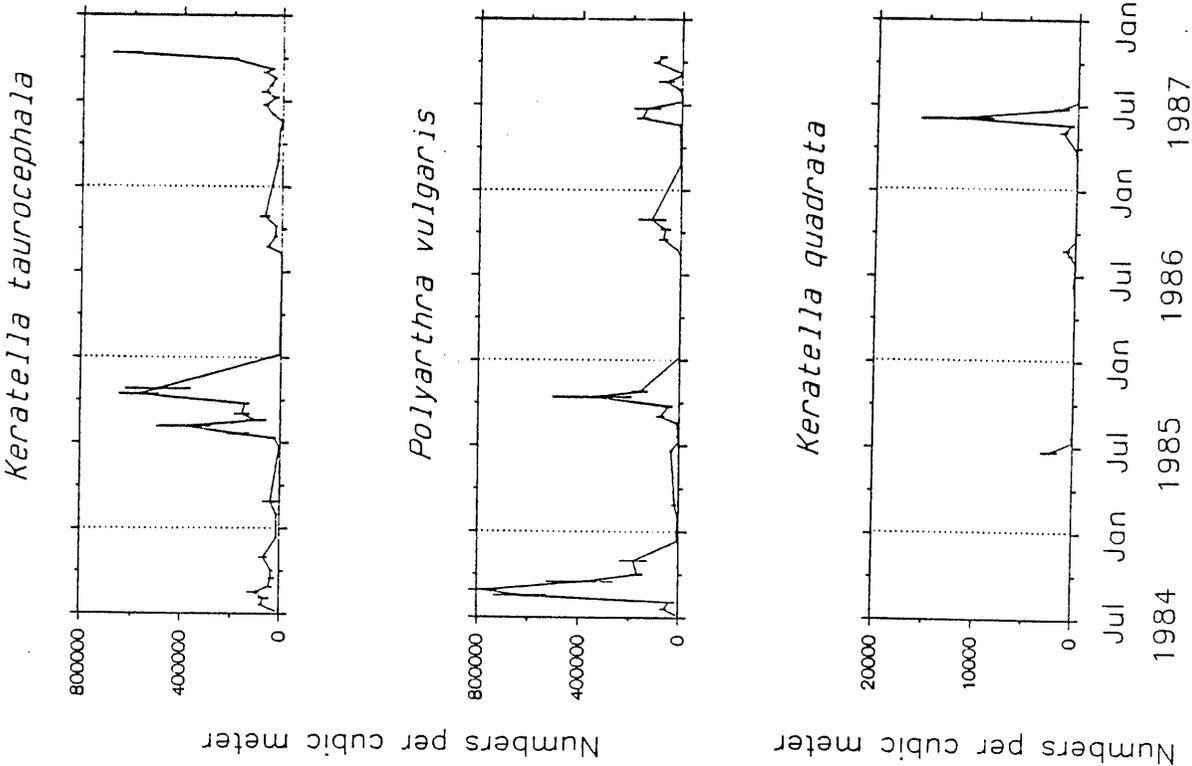


Figure VIII-2. Time-series plots of the abundance of the most abundant species of rotiferan zooplankton in Emerald Lake from July 1984 through October 1987. Vertical bars are ± 1 standard error of the mean. Abundances of *Trichocerca capucina* and *Keratella quadrata* were too low to be estimated reliably from samples taken before June 1985.

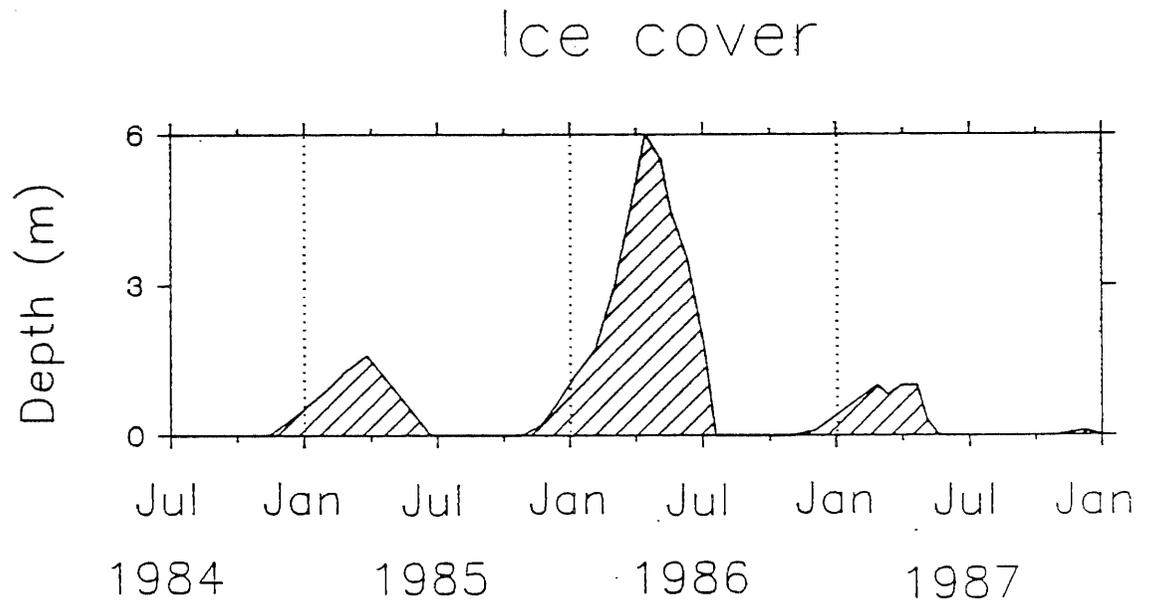


Figure VIII-3. The thickness of the ice layer on Emerald lake.

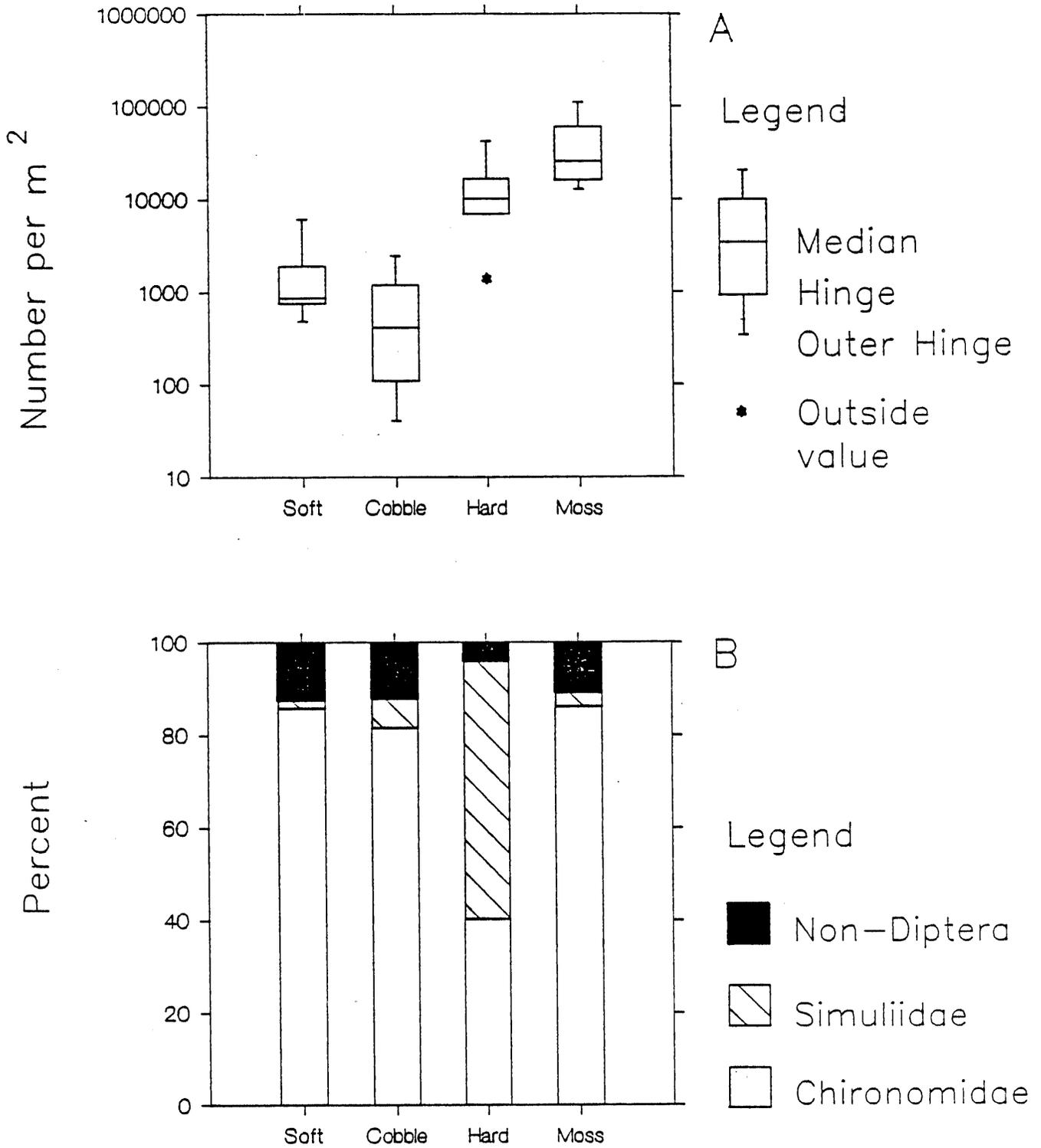


Figure VIII-4. Summary of total benthic abundances (A) and gross faunal composition (B) of the Emerald Lake outflow in 1986-87; data are pooled across sampling dates for each substrate. A: Boxplots show the median abundances and variation and skewness about the median; note the logarithmic scale. B: Percentage composition of all aquatic invertebrates.

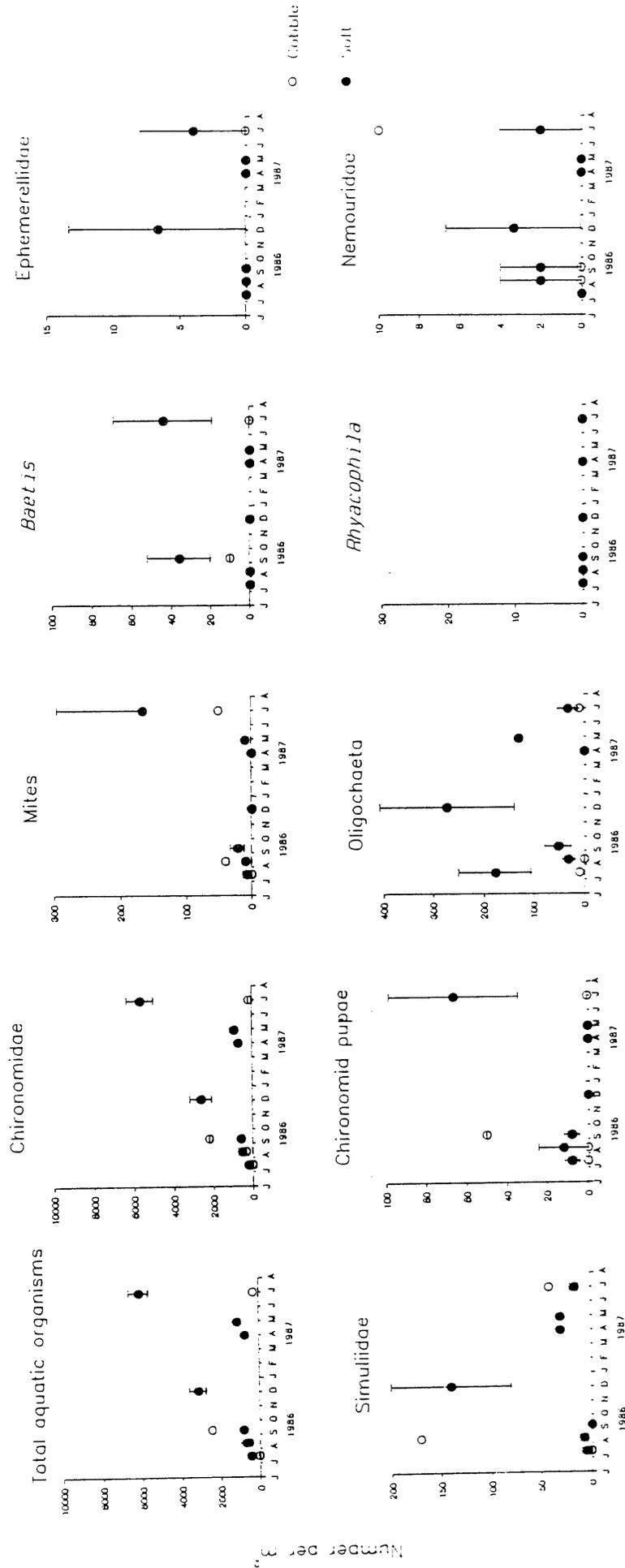


Figure VIII-5. Densities of aquatic benthos in the four habitats of the Emerald Lake outflow. Vertical bars are ± 1 standard error of the mean; there is no standard error for the cobble habitat because only one sample was taken on each date. Continued on following page.

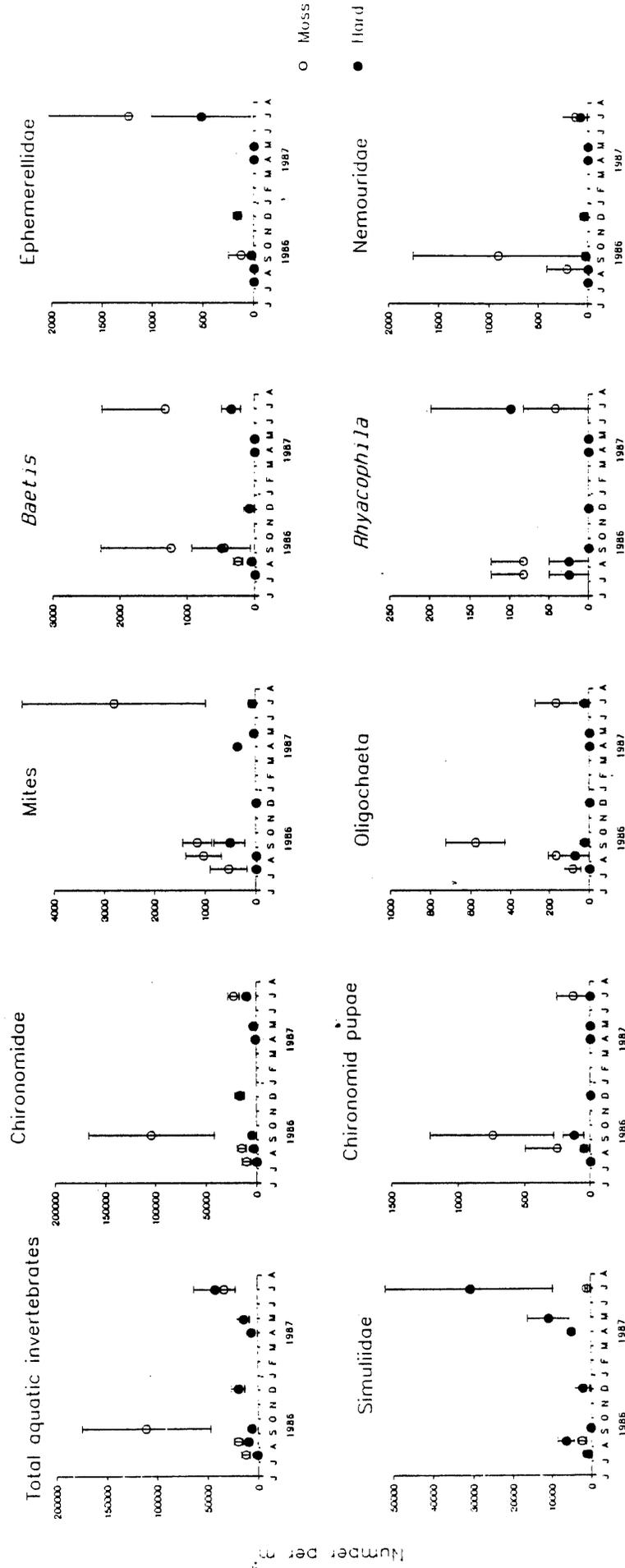


Figure VIII-5 (Continued). Densities of aquatic benthos in the four habitats of the Emerald Lake outflow. Vertical bars are ± 1 standard error of the mean; there is no standard error for the cobble habitat because only one sample was taken on each date.

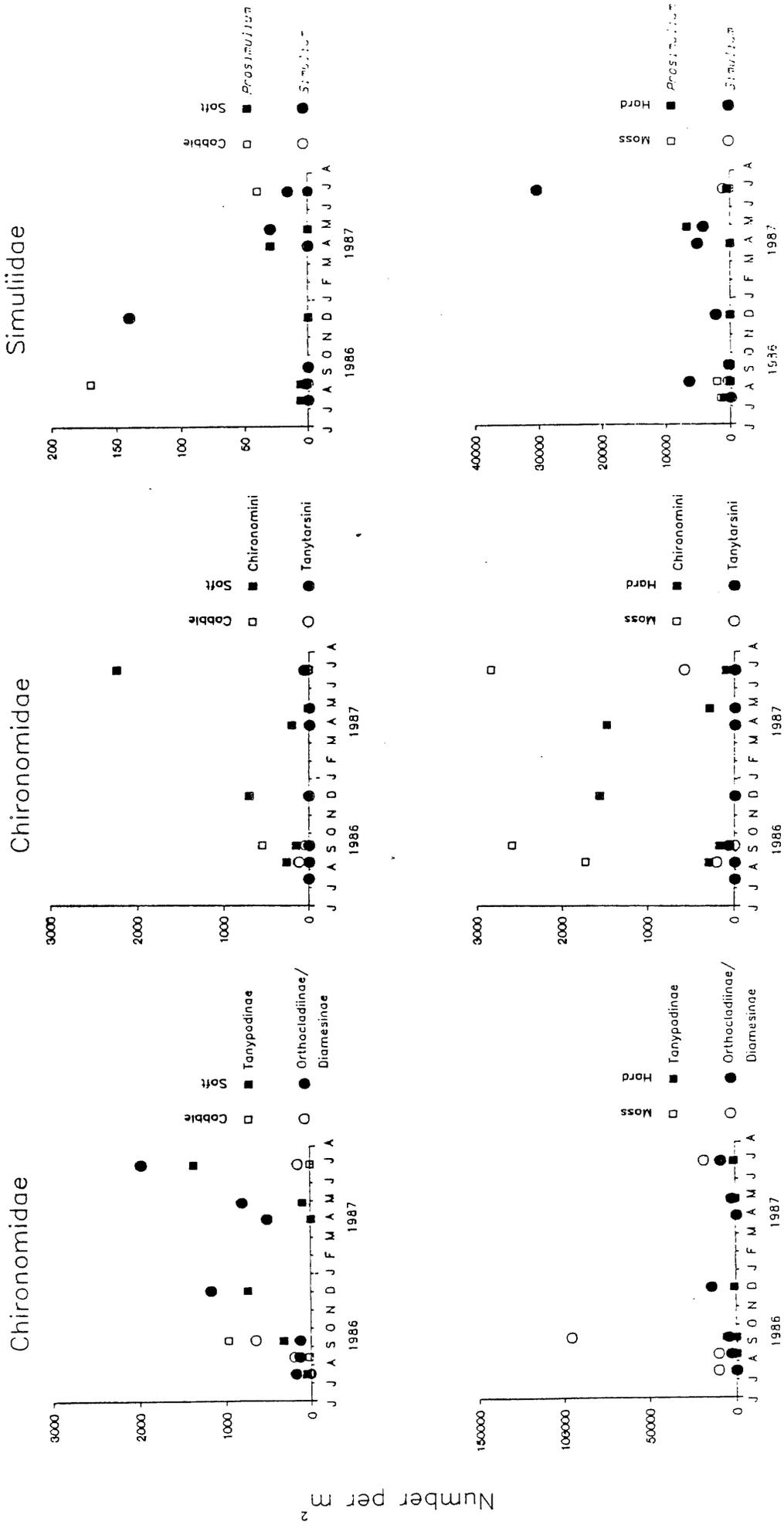


Figure VIII-6. Mean densities of finer taxonomic categories of chironomids and simuliids in the Emerald lake outflow in 1986-87. Error bars omitted for clarity.

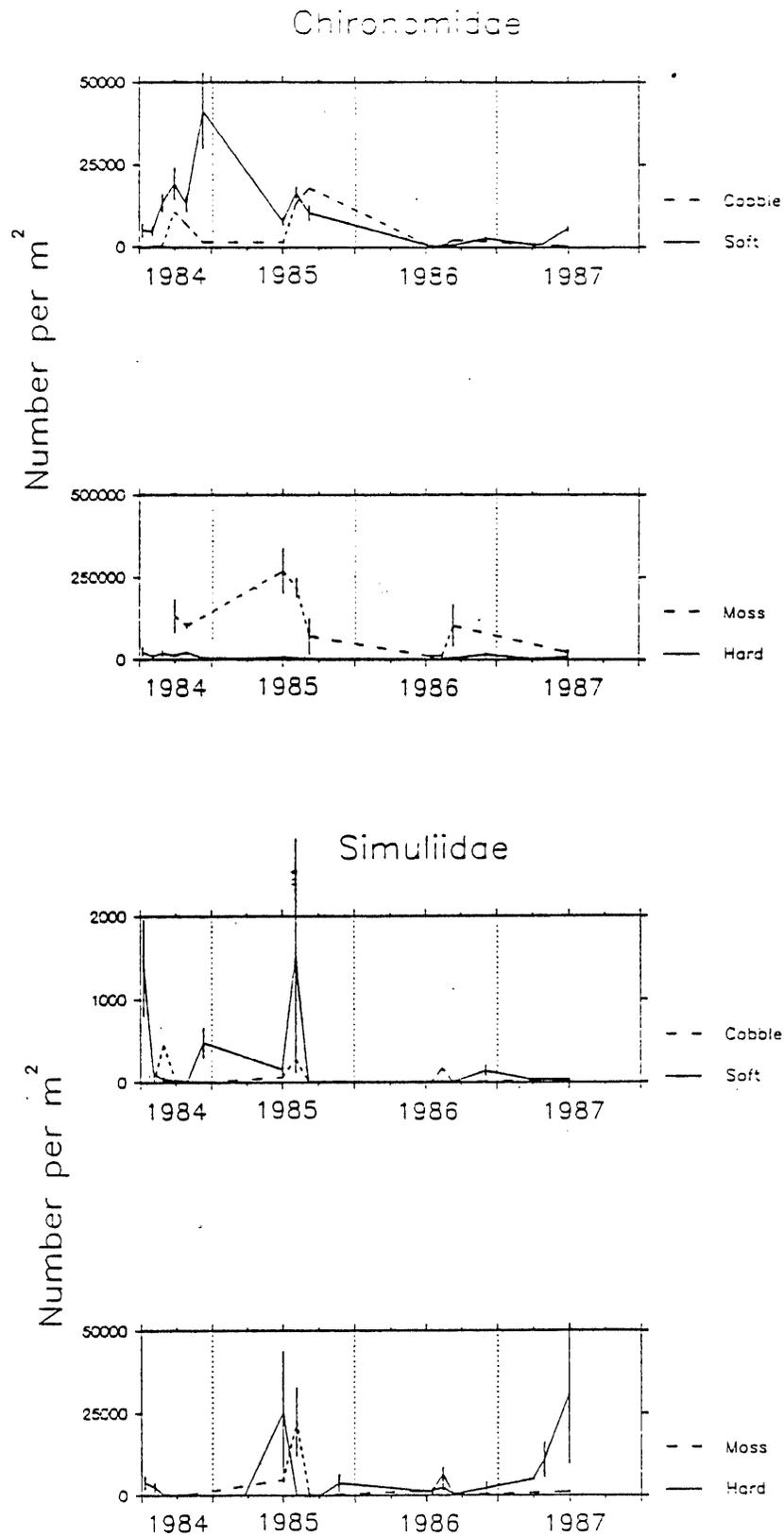


Figure VIII-7. Time-series plots of benthic invertebrates from the Emerald Lake outflow from July 1984 through July 1987. Vertical bars are ± 1 standard error of the mean; there is no standard error for the cobble habitat because only one sample was taken on each date. Continued on following page.

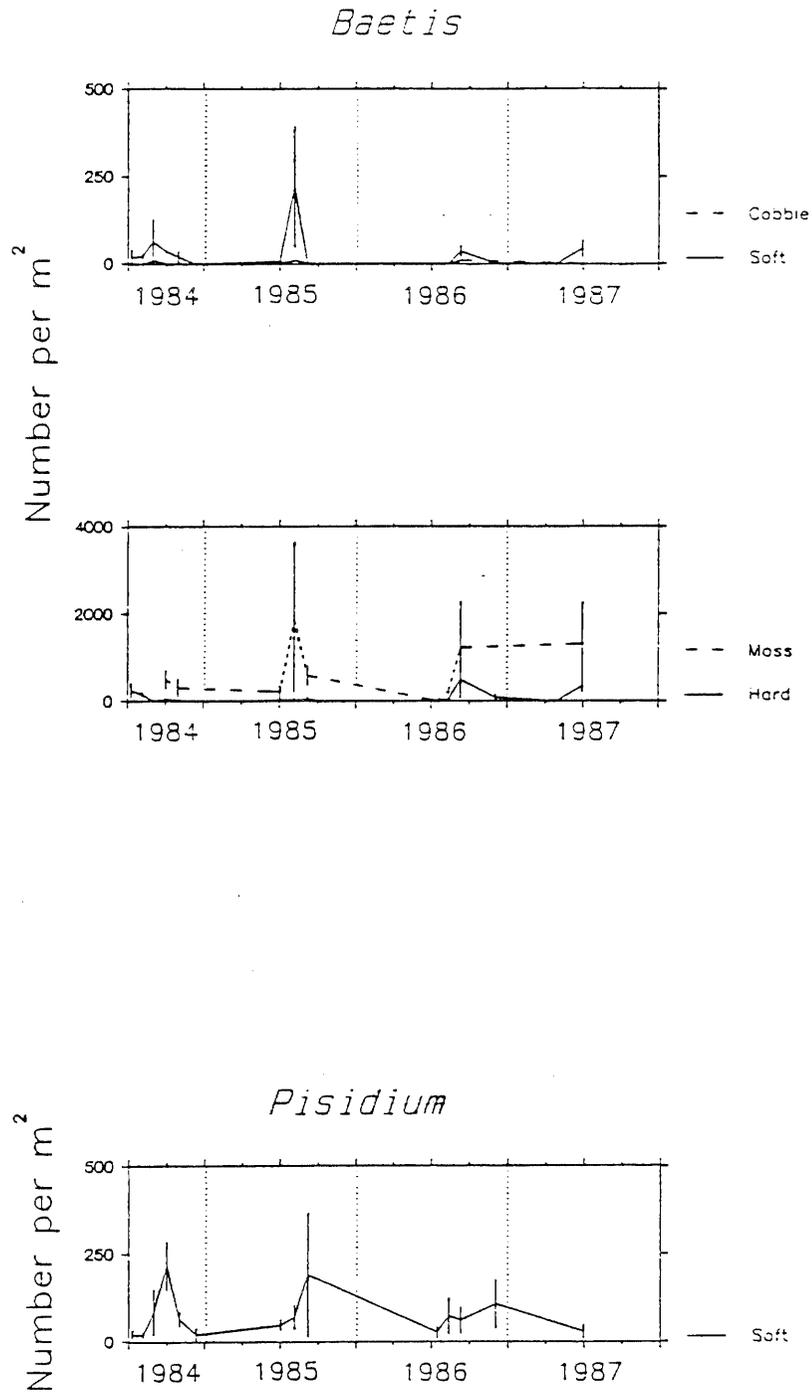
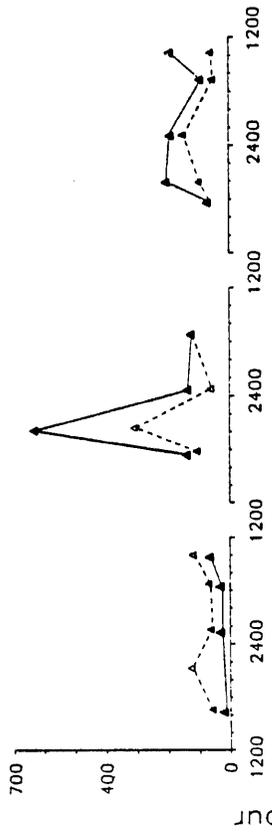


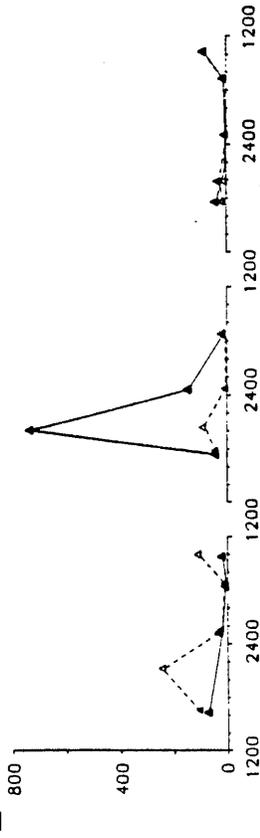
Figure VIII-7 (Continued). Time-series plots of benthic invertebrates from the Emerald Lake outflow from July 1984 through July 1987. Vertical bars are ± 1 standard error of the mean; there is no standard error for the cobble habitat because only one sample was taken on each date.

Total aquatic invertebrates

July August September

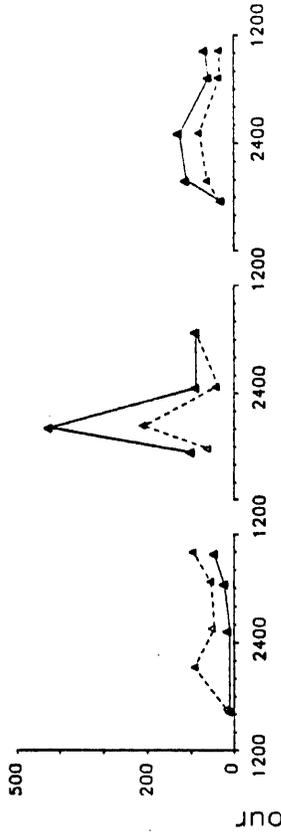


Terrestrial invertebrates

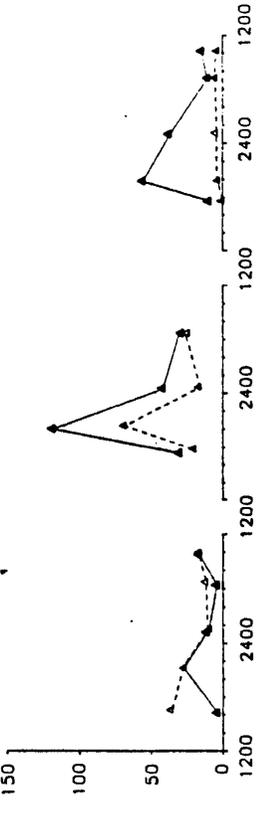


Chironomidae

July August September



Simuliidae



Baetis spp.

July August September

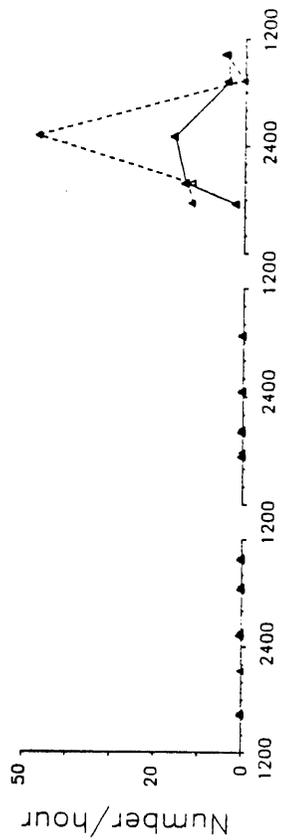


Figure VIII-8. Drift rates in the Emerald Lake outflow in 1986. Solid line denotes upper site, broken line denotes the lower site.

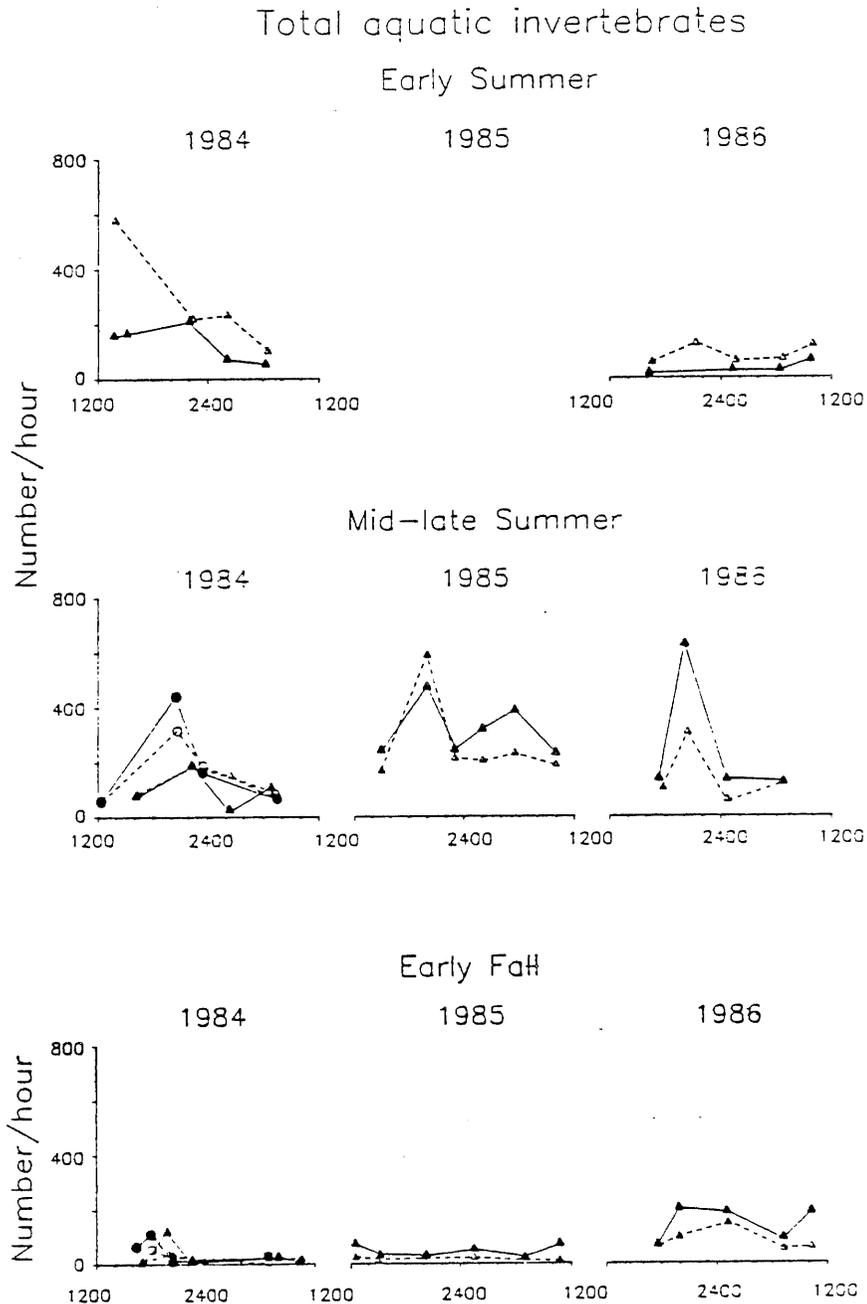


Figure VIII-9. Drift rates compared between years for total aquatic invertebrates and *Baetis* spp. Solid line denotes upper site, broken line denotes the lower site. "Early Summer" = June and July; "Mid-late Summer" = August; "Early Fall" = September and early October. In 1984, additional dates were sampled in mid-late summer and early fall and are represented with circular symbols. Continued on following page.

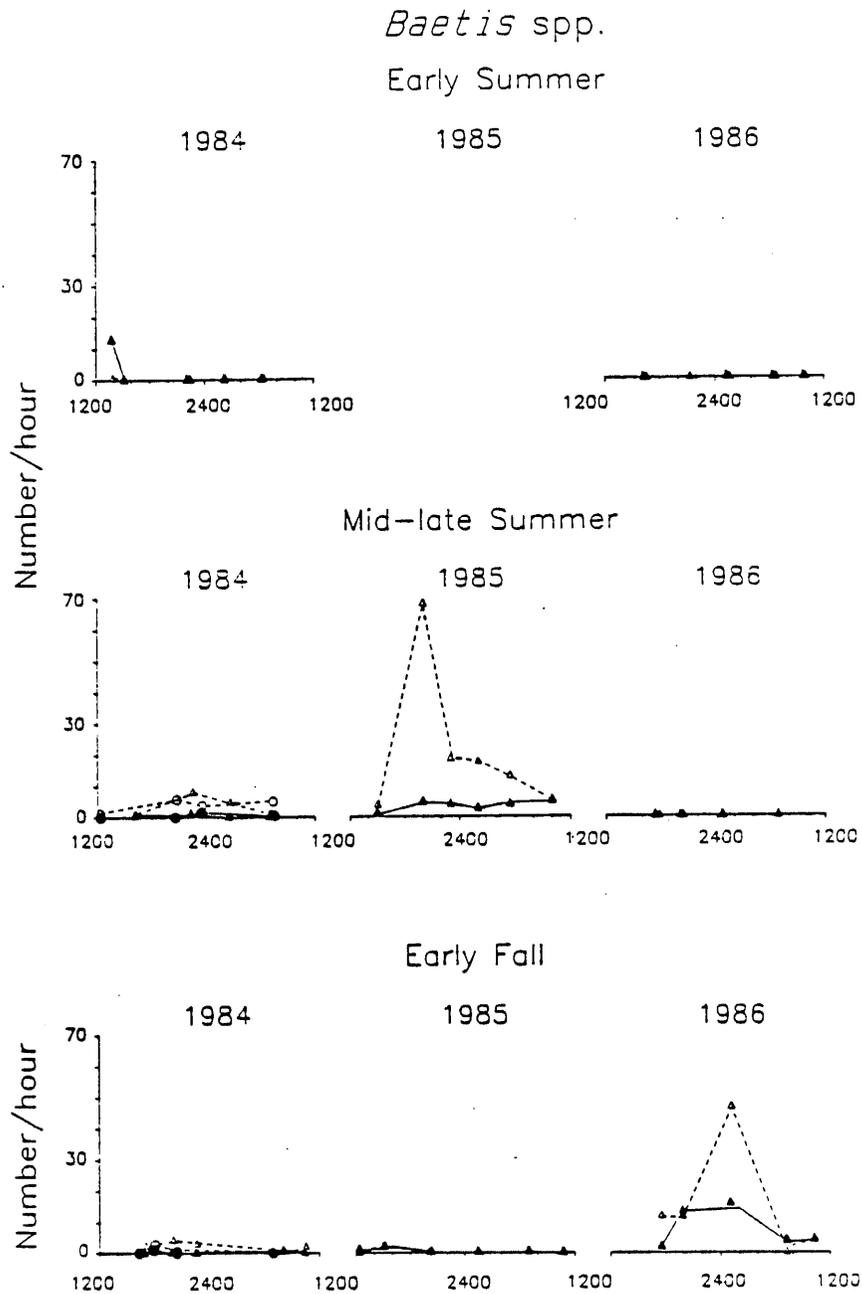


Figure VIII-9 (Continued). Drift rates compared between years for total aquatic invertebrates and *Baetis* spp. Solid line denotes upper site, broken line denotes the lower site. "Early Summer" = June and July; "Mid-late Summer" = August; "Early Fall" = September and early October. In 1984, additional dates were sampled in mid-late summer and early fall and are represented with circular symbols.

