HYDRA POPULATION DYNAMICS AND
THE EFFECTS OF SUPPLEMENTAL FEEDING

by

CREIGHTON M. HOOVER

Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in the

Biology Program

signature for Lauren Schroeder 8/25/94
Adviser   Date

signature   8/23/94
Dean of the Graduate School   Date

YOUNGSTOWN STATE UNIVERSITY

August, 1994

THESIS APPROVAL FORM

THESIS TITLE: Hydra Population Dynamics and the Effects of
                Supplemental Feeding

AUTHOR: Creighton M. Hoover

DEGREE: Master of Science in Biological Sciences

ADVISOR: Dr. Lauren A. Schroeder

COMMITTEE MEMBERS   ACCEPT   REJECT

Lauren Schroeder   ✓

James R. Toppen   ✓

Paul C Peterson   ✓

                                    DATE: ___8-10-94___

1 Copy to Accompany Library Copy

1 Copy to Advisor

1 Copy to Departmental Files

ABSTRACT

HYDRA POPULATION DYNAMICS AND
THE EFFECTS OF SUPPLEMENTAL FEEDING

CREIGHTON M. HOOVER

MASTER OF SCIENCE

YOUNGSTOWN STATE UNIVERSITY, 1994

Field studies were conducted in McKelvey Lake throughout the spring and summer of 1993 to examine hydra population dynamics and the related starvation hypothesis. Hydra densities in McKelvey reached a maximum at the end of June 1993 and within three weeks had disappeared from the artificial substrate used for collection. The hydra population declined in conjunction with increasing temperatures and a limited food resource. No other correlation between the decline and the lake's chemical and physical parameters were found. Decreasing hydra to bud ratios and dry weights of the wild hydra suggest a energy deficit was being experienced by the population.

The starvation hypothesis was studied by enclosing hydra in nylon mesh cages suspended in McKelvey Lake and feeding them supplemental rations of zooplankton. All other environmental conditions between the enclosed population and the free-living population were assumed to be similar. If starvation was the reason for the wild population's decline, then the enclosed hydra in the epilimnion would be expected to survive longer into the

summer. However, enclosed hydra in the epilimnion failed to survive, therefore not supporting the starvation hypothesis. Enclosed hydra in the hypolimnion perished in conjunction with the free-living hydra as expected due to anoxic conditions.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Dr. Lauren Schroeder for his invaluable guidance and support during this research. I also wish to thank Drs. Peterson and Toepfer for input during the critical review of this manuscript.

My thanks also go to Kurtis Wilson for assistance rendered during the field work of this study and to Patrica Hoover who assisted in the construction of the enclosures.

Finally, I wish to thank Ohio Water Service for the use of Lake McKelvey and its facilities.

TABLE OF CONTENTS

LIST OF SYMBOLS

SYMBOL	DEFINITION
C	CELSIUS
chla	CHLOROPHYLL a
cm	CENTIMETER
GA	GROWTH AXIS
JD	JULIAN DAYS
KJ	KILOJOULES
mg	MILLIGRAMS
ml	MILLILITERS
ug	MICROGRAMS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Hydra populations in temperate dimictic lakes have been observed to undergo severe fluctuations in densities. Two annual peaks have been observed in shallow fish hatchery ponds in Iowa (Moen, 1951), California ponds (Yu, 1976), Lake Erie (Carrick, 1956), Pine Lake, Ohio (Reeder, 1979), Meander Creek Reservoir, Ohio (Mateja, 1984), Douglas Lake, Michigan (Miller, 1936), and Lake Zurich, Switzerland (Ribi et.al., 1985). A monocyclic fluctuation was recorded by Batha (1974) in Lake Michigan and by Bryden (1952) in Kirkpatrick's Lake, Tennessee. The bicyclic fluctuations are characterized by rapid increases of hydra densities during the spring followed by a rapid decline. A much smaller peak occurs during the late fall. Both of the lakes studied in Ohio, Pine and Meander, exhibited bicyclic peaks. The first occurs by late May to early June and the second occurring by mid November.

Species specific differences have been observed by Yu (1976). He found that populations of H. americana demonstrated bicyclic fluctuations while Chlorhydra viridissiona underwent a monocyclic peak. However, for H. oligactis and H. pseudoligactis, the two species found in this region, species specific differences in seasonal densities have not been recorded (Schroeder, unpublished).

Many hypothesis have been offered to explain the declines in hydra population densities. These include high temperature (Welsh and Loomis, 1924), low temperatures (Batha, 1974), predation and parasitism (Griffing, 1965; Lomnicki and Slobodkin, 1966; Stiven,

1976), competition for substrate space (Miller, 1936), sexuality (Reisa, 1973), depression (Reisa, 1973), rapid sinking in convergences (Batha, 1974), floating (Griffing, 1965), and starvation (Bryden, 1952; Schroeder and Callaghan, 1982). The range of dissolved oxygen, pH, and water pressure conditions observed in temperate lake basins, the definition of which includes local aquatic environments, has not been documented to be harmful to hydra species (Welsh and Loomis, 1924; Miller, 1936; Bryden, 1952; Loomis, 1954; Batha, 1974), except for anoxic conditions (Welsh and Loomis, 1924). High water temperature may limit H. oligactis to cooler waters than H. pseudoligactis but is unlikely to be a direct cause of the observed population declines (Schroeder and Callaghan, 1982).

However, by altering hydra energy balances, high temperatures may have an indirect deleterious effect on the population densities. Schroeder and Callaghan (1982) found that over a temperature range from 10C to 25C, H. pseudoligactis experienced a 61% reduction in assimilation efficiency and a 51% reduction of gross growth efficiency. Furthermore, hydra maintenance costs, on a weight to weight comparison, increased with increasing temperature. At 10C the ingestion rate required for maintenance was found to be 0.04 KJ of zooplankton per KJ of hydra per day. At 20C the maintenance ingestion rate had increased to 0.2 KJ/KJ. Based upon the rate of 0.2 KJ/KJ/day at 20C each hydra must ingest 1.3 zooplankters per day (0.005 mg/GA/day) for maintenance. By determining ingestion rates at low densities, Schroeder and Callaghan (1982) estimated the minimum densities necessary for

maintenance to be 100 zooplankters/liter at 20C and 16-24 zooplankters/liter at 10C. The rising temperatures may also impose a morphological constraint on the hydra feeding rates. Studies have found that hydra sizes decrease in conjunction with increasing temperature (Schroeder and Callaghan, 1982). This decrease in size likely limits the maximum prey size a hydra can capture; therefore limiting the size of the prey population available to the hydra at a time when increased amounts food are needed for maintenance (Stiven, 1965; Griffing, 1965; Bisbee, 1973; Schroeder and Reeder, 1980). Also, as the lake's water column begins to stratify, zooplankton densities naturally tend to decrease (Wetzel, 1983). By driving the hydra populations into a energy deficit, these three factors could be expected to cause the decline in hydra populations (Schroeder and Callaghan, 1982). However, these conditions would not explain the declines in the hypolimnion. The hypolimnion remains considerably cooler than the epilimnion (< 12C) therefore reducing the maintenance requirements of hydra at that depth. The declines in the hypolimnion are likely due to changes in water chemistry e.g. depletion of dissolved oxygen (Schroeder and Callaghan, 1982; Welsh and Loomis, 1924).

The purpose of this study was to determine if hydra populations are indeed food limited. This was done by maintaining isolated experimental populations of hydra which were supplied with supplemental food while remaining in the lake environment and in laboratory aquariums. At the same time the free living hydra population was monitored as a control. Zooplankton densities, chemical limnology, and physical limnology were observed to

determine what, if any, correlation these factors had with the hydra decline.

STUDY SITE

The study was conducted at McKelvey Lake located in Mahoning County, Ohio just east of Youngstown. McKelvey Lake is owned by Ohio Water Service.

HYDRA COLLECTIONS

The hydra traps were similar to those used by Reader (1979). Four glass microscope slides (25mm by 75mm) were inserted into #6 rubber stoppers at right angles to each other. The stoppers were suspended at 2.0, 4.5, and 7.0 meters depth on a line anchored by bricks. Styrofoam floats were attached to the line approximately 0.5 meters below the surface with a second float attached to the end of the line to serve as a marker. The slides were suspended at depths corresponding to the ranges which exhibited distinct population dynamics in prior studies (Schroeder, unpublished; Reader, 1979). Twenty four trap lines were set on May 6, 1991. Subsequently, three lines were collected weekly and reset with clean slides the following week. Collections began May 27 and continued until August 12. The long period between setting and collecting the traps minimized any colonization effects by allowing sufficient time for planktonic hydra to attach to the slides. Slides were transported back to the lab in vials of lake water. All hydra attached to the slides and vials were scraped free and

METHODS

STUDY SITE

The study was conducted at McKelvey Lake located in Mahoning County, Ohio just east of Youngstown. McKelvey Lake is owned by Ohio Water Service.

HYDRA COLLECTIONS

The hydra traps were similar to those used by Reeder (1979). Four glass microscope slides (25mm by 75mm) were inserted into #8 rubber stoppers at right angles to each other. The stoppers were suspended at 2.0, 4.5, and 7.0 meters depth on a line anchored by bricks. Styrofoam floats were attached to the line approximately 0.5 meters below the surface with a second float attached to the end of the line to serve as a marker. The slides were suspended at depths corresponding to the ranges which exhibited distinct population dynamics in prior studies (Schroeder, unpublished; Reeder, 1979). Twenty four trap lines were set on May 5, 1993. Subsequently, three lines were collected weekly and reset with clean slides the following week. Collections began May 27 and continued until August 12. The long period between setting and collecting the traps minimized any colonization effects by allowing sufficient time for planktonic hydra to attach to the slides. Slides were transported back to the labs in vials of lake water. All hydra attached to the slides and vials were scraped free and

poured with the lake water into gridded petri dishes for counting. Counting was done with a dissecting microscope at 10X and a tally counter. The number of basal disks and buds were recorded. Growth axes (GA) equaled the sum of the number of basal disks and buds.

DRY WEIGHTS

Ten hydra were collected haphazardly from hydra pooled by depth. Growth axis (GA) were counted and recorded and the hydra were placed on tared pieces of aluminum foil and dried at 85C for 16 hours in a convection oven. The dried hydra were weighed on a Cahn G-2 electrobalance to a precision of 0.1 ug.

PARASITES

Ten hydra were haphazardly selected from each pooled sample after counting. Each hydra was examined at 100X with a light microscope and examined for the protozoa Hydramoeba hydroxena, Trichodina pedicularis, Kerona polyporum, and Tetrahymena rostrata. The numbers of each species of protozoa per hydra and the number of GA for each hydra were recorded.

HYDRA ENCLOSURES

The enclosures were constructed of 200-300 micron, Nitex nylon mesh. Each enclosure was four sided with the bottom sewn on with nylon filament leaving only the top open which was subsequently

closed with nylon draw ties. The volume of each enclosure was approximately 2 liters. Inside each enclosure 5 microscope slides were held horizontally between two bars of Lexan. The microscope slides served as attachment substrate for the hydra. Each bar of Lexan was 15.0cm*2.0cm*0.5cm. The enclosures were suspended in the lake at the same location, depth, and in the same manner as were the traps. Three enclosures per line comprised one cage line. A feeding tube of 1/4 inch I.D. vinyl tubing was inserted through the top opening of the enclosures using the nylon ties to pinch the mesh around the tube assuring that no openings remained through which hydra could escape. Each feeding tube ran to the surface of the lake and was attached to a styrofoam float. A recorded number of GA (Approximately 10 hydra/cage) were inserted into each enclosure by way of the feeding tube. The hydra were from the Lake McKelvey population that had been collected on May 27 with the slide traps and maintained in the laboratory utilizing the methods described by Loomis (1954). The enclosed hydra were fed supplements of zooplankton once or twice weekly (see section on hydra feeding in Methods).

The first set of 3 cage lines were set June 10, 1993 and the remaining 13 cage lines were set June 15. This group of enclosed hydra were fed once each week. Two cage lines were pulled each week and the number of GA in each cage was recorded. On July 13 six cage lines were reset with fresh hydra and were fed twice a week. On July 27 five cages, all set at 2 meters depth, were place in the lake and the enclosed hydra were fed twice a week. This was done simultaneously with another group of 5 cages set in a

laboratory aquarium. The enclosed hydra were fed from the same zooplankton collections and with the same amounts as the hydra in the lake enclosures.

HYDRA FEEDING

Zooplankton for feeding were collected by towing a conical plankton net from the upper two meters of the lake. The contents of the collection bucket were poured into a 1 liter polyethylene bottle. A 10ml sample of lake water and zooplankton was drawn into a 10ml widemouth pipet and examined to assure approximately 200-300 zooplankters were present in the sample. This was poured down the feeding tube followed by 1-2 liters of lake water to flush the zooplankton into the submerged enclosure. On each feeding date, three subsamples of 10ml of the supplemental zooplankton were placed in vials containing 10% formalin for later counting.

LAKE PRODUCTIVITY

Lake productivity was determined by estimating the concentration of chlorophyll a (chla) by glass filter filtration and acetone extraction (Lind, 1985). Sample collection was done with a Van Dorn water sampler at 2.0, 4.5, and 7.0 meters. Chla was determined by absorbance at 750, 665, 645, and 630 nanometers with a Shimadzu recording spectrophotometer UV-260 was used for the spectral analysis with a cell path of 1.0 cm and a slit width of 2.0 nanometers.

A conical plankton net with a 49.5cm diameter opening was used to collect plankton biomass. Three vertical tows from a depth of 6.5 meters were collected, filtered through a 100 micron mesh, and frozen on dry ice for transportation back to the laboratory. At the lab the samples were dried at 85C and weighed to 0.0004 grams.

A Schindler zooplankton trap was also employed to determine plankton densities. Nine samples, three each from depths of 2.0, 4.5, and 7.0 meters were collected in a plankton bucket and poured, by depth, into 3 polyethylene bottles containing 10% formalin. These were later condensed into smaller volume vials containing 10% formalin by using a 100 micron mesh filter to remove the zooplankton. For counting, the condensed samples were suspended in 100ml of tap water and stirred to assure complete mixing. A 10ml subsample was pipetted into a gridded petri dish where the zooplankton were identified as Cladocera, Copepoda, or Nauplii by using a dissecting microscope at 10X.

CHEMICAL LIMNOLOGY

Water chemistry was determined for samples collected with a Van Dorn water sampler at depths of 2.0, 4.5, and 7.0 meters. Orthophosphate-phosphorus, total soluble phosphorus, and total phosphorus concentrations were determined by the molybdate method described in Lind (1985). The absorbances were measured by a Shimadzu UV-260 recording spectrophotometer with a cell path of 1 cm and a slit width of 2 nm. Ammonium-nitrogen concentrations were measured by using the methods described in Limnological Analyses

(Wetzler and Likens, 1979). Nitrate and nitrite-nitrogen concentrations were determined by a simplified cadmium reduction method using Hach NitraVer VI and Nitriver III powder pillows (Lind, 1985). The Winkler method was used to determine oxygen concentration (Lind, 1985). pH was measured by using a Corning Checkmate 90 portable meter.

PHYSICAL LIMNOLOGY

Transparency was measured using a 8 inch Secchi disk with a cord marked at 10.0cm intervals. Temperature was measured at 0.5 meter intervals from the surface to 8.0 meters depth using a Model 46 TUC Tele-Thermometer. Light transmittance was measured using a LiCor, Inc. Model LI-185B Quantum/Radiometer/Photometer and was recorded every 0.5 meters.

RESULTS

HYDRA DENSITIES

Maximum hydra densities at 2.0 meters occurred June 17 (JD=168) at 85 ±70 GA/slide (Figure 1; Table 1). The greatest densities for all depths were observed at 4.5 meters on June 24 (JD=175) at 510 ±200 GA/slide. At 7 meters a maximum of 120 ±33 GA/slide occurred on July 1 (JD=182). The hydra at 2.0 meters peaked and declined first with no hydra being found on the artificial substrate by July 1 (Figure 1). No hydra were found at 4.5 meters after July 8 (JD=189). The hydra at 7.0 meters reached their maximum density later and persisted longer into the summer than the other depths. No hydra were found on the 7.0 meter slides after July 15 (JD=196). Hydra at all depths demonstrated rapid declines and lasted no longer than three weeks after the maximum densities were reached. Hydra did not re-appear on the slides until August 12 (JD=224) when 4 slides at 7 meters were found with hydra attached.

The pattern observed for hydra populations dynamics in McKelvey Lake is a rapid growth to a maximum density, occurring first in the epilimnion and proceeding with time to the metalimnion and then the hypolimnion. Persistence in the metalimnion, observed in previous studies (Reeder, 1979; Schroeder, unpublished), was not recorded in Lake McKelvey.

Figure 2 shows the change in the number of growth axis per

FIGURE 1. Hydra densities: expressed as change in the mean number of growth axes (GA) per slide over time (Julian Day) for each depth. Bars denote standard deviation.

MCKELVEY HYDRA 1993
GROWTH AXIS

MEAN GROWTH AXIS PER SLIDE

800
700
600
500
400
300
200
100
0

2 METERS
4.5 METERS
7 METERS

147 154 161 168 175 182 189 196 203 210 217 224

COLLECTION TIME (JULIAN DAYS)
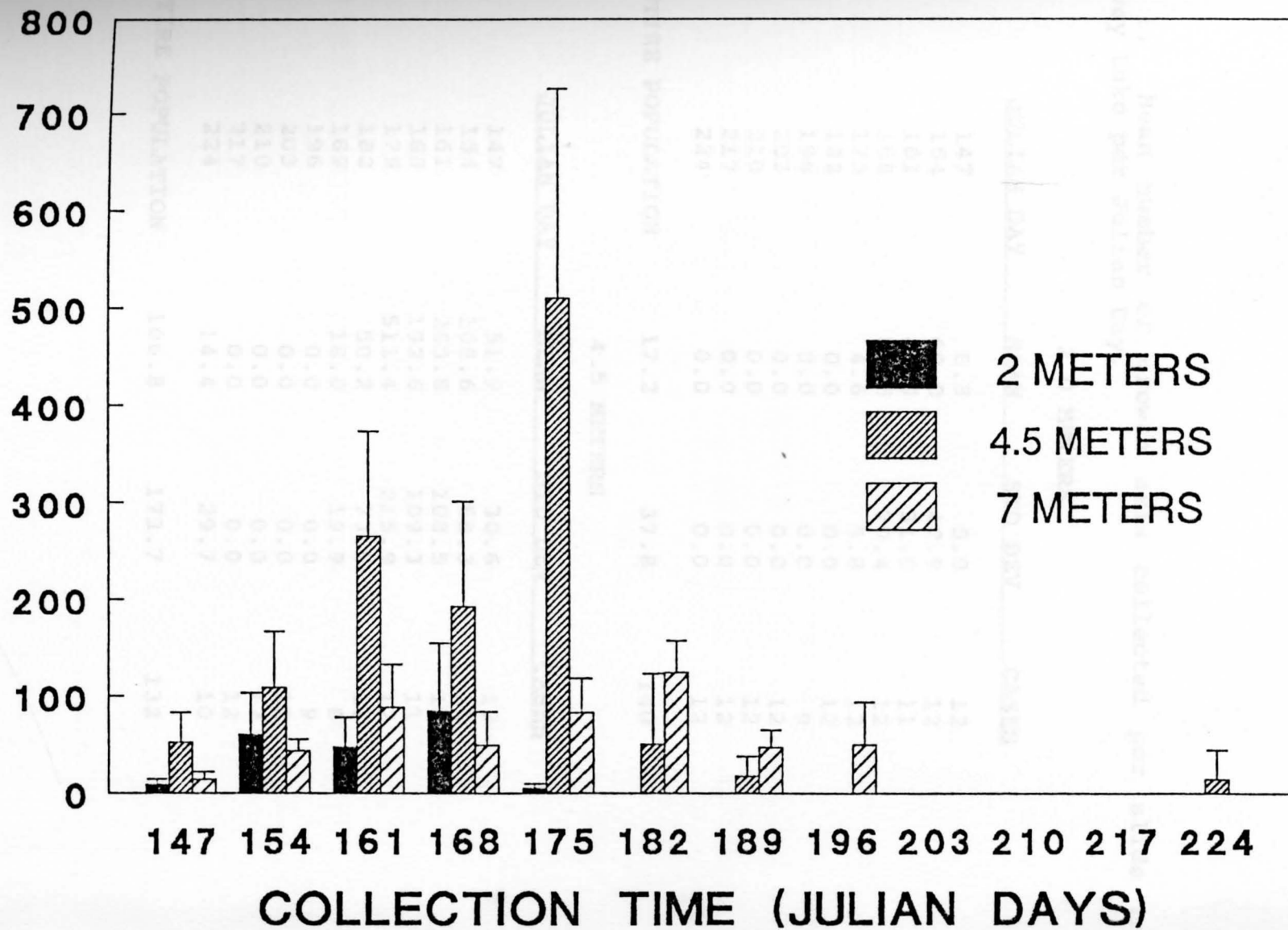
TABLE 1. Mean number of growth axis collected per slide in McKelvey Lake per Julian Day.

2.0 METERS

JULIAN DAY	MEAN	STD DEV	CASES
147	8.8	5.9	12
154	60.0	42.9	12
161	47.0	31.5	11
168	84.5	70.4	12
175	4.6	5.8	12
182	0.0	0.0	12
196	0.0	0.0	9
203	0.0	0.0	12
210	0.0	0.0	12
217	0.0	0.0	12
224	0.0	0.0	12
FOR ENTIRE POPULATION	17.2	37.8	140

4.5 METERS

JULIAN DAY	MEAN	STD DEV	CASES
147	51.9	30.6	12
154	108.6	58.3	11
161	265.8	108.5	12
168	192.6	109.3	11
175	511.4	215.9	12
182	50.2	73.5	11
189	18.0	19.9	8
196	0.0	0.0	9
203	0.0	0.0	12
210	0.0	0.0	12
217	0.0	0.0	12
224	14.4	29.7	10
FOR ENTIRE POPULATION	106.8	173.7	132

hydra over time (Table 2). Data from all three depths, analyzed by One way ANOVA (p<0.05), exhibited a significant decrease in the number of growth axes per hydra at the same time the hydra densities were decreasing (Figures 1 and 2). The mean number of growth axes per hydra at 2.0 meters for all sample dates is 1.9 ±0.6 GA/hydra with the highest number occurring on June 17 (JD=168) at 2.1 ±0.3 GA/hydra. At 4.5 meters the mean for all dates is 1.9 ±0.4 GA/hydra. The highest ratio occurred on June 24 (JD=175) at

TABLE 1 (CONTINUED).

2.2 ±0.3 GA/hydra. For the samples taken from 7.0 meters the average for all dates is 1.3 ±0.3 GA/hydra. The highest recorded mean GA/hydra for one date occurred on June 10 (JD=161) at 1.9 ±0.1.

7.0 METERS

JULIAN DAY	MEAN	STD DEV	CASES
147	14.2	7.9	12
154	43.2	12.9	12
161	88.3	44.8	12
168	49.3	35.6	12
175	83.2	35.2	12
182	124.5	33.3	11
189	47.2	18.0	12
196	49.8	44.7	9
203	0.0	0.0	12
210	0.0	0.0	12
217	0.0	0.0	12
224	0.0	0.0	12
FOR ENTIRE POPULATION	40.9	46.4	140

The mean weight per hydra per GA at 2.0 and 4.5 meters decreased simultaneously with the decrease of hydra densities (Figures 1 and 2). The 7.0 meter hydra dry weight data did not correspond with the fluctuations in the weights from the other depths. The greatest mean dry weight per GA recorded at 2 meters was 41 ug/GA on June 10 (JD=161). The mean dry weight recorded for all collections at 2.0 meters is 35 ug/GA ±5. At 4.5 meters the greatest recorded weight was 55 ug/GA and occurred on June 17 (JD=168). The mean weight for all collections at 4.5 meters was 40 ug/GA ±13. The greatest recorded weight for the 7.0 meter data was 40 ug/GA and occurred on June 24 (JD=175) and July 1 (JD=182). The mean weight for all collections at 7.0 meters was 37 ug/GA ±2.

hydra over time (Table 2). Data from all three depths, analyzed by One Way ANOVA (p<0.05), exhibited a significant decrease in the number of growth axes per hydra at the same time the hydra densities were decreasing (Figures 1 and 2). The mean number of growth axes per hydra at 2.0 meters for all sample dates is 1.9 $\pm$0.5 GA/hydra with the highest number occurring on June 17 (JD=168) at 2.3 $\pm$0.3 GA/hydra. At 4.5 meters the mean for all dates is 1.9 $\pm$0.4 GA/hydra. The highest ratio occurred on June 24 (JD=175) at 2.2 $\pm$0.3 GA/hydra. For the samples taken from 7.0 meters the average for all dates is 1.3 $\pm$0.3 GA/hydra. The highest recorded mean GA/hydra for one date occurred on June 10 (JD=161) at 1.8 $\pm$0.2.

DRY WEIGHTS

The mean dry weight of hydra per GA at 2.0 and 4.5 meters decreased simultaneously with the decrease of hydra densities (Figures 1 and 3). The 7.0 meter hydra dry weight data did not exhibit obvious fluctuations as the weights from the other depths. The greatest mean dry weight per GA recorded at 2 meters was 43 ug/GA on June 10 (JD=161). The mean dry weight recorded for all collections at 2.0 meters is 35 ug/GA $\pm$5. At 4.5 meters the greatest recorded weight was 58 ug/GA and occurred on June 17 (JD=168). The mean weight for all collections at 4.5 meters was 40 ug/GA $\pm$13. The greatest recorded weight for the 7.0 meter data was 40 ug/GA and occurred on June 24 (JD=175) and July 1 (JD=182). The mean weight for all collections at 7.0 meters was 37 ug/GA $\pm$2.

FIGURE 2. Change in the number of growth axes per hydra over time (Julian Days). Bars denote standard deviation.

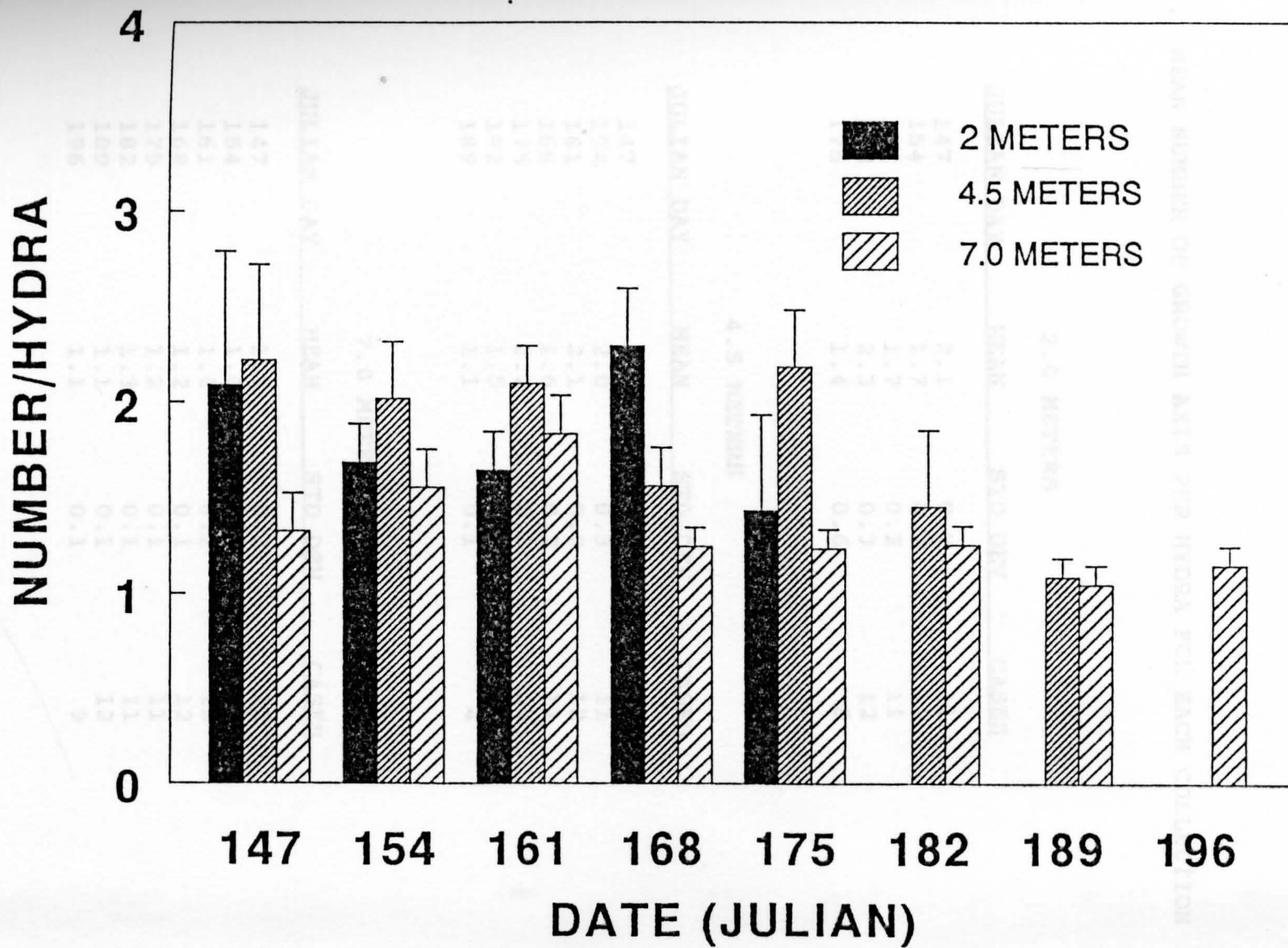TABLE 2. MEAN NUMBER OF GROWTH AXIS PER HYDRA FOR EACH COLLECTION DATE.

2.0 METERS

JULIAN DAY	MEAN	STD DEV	CASES
147	2.1	0.7	11
154	1.7	0.2	12
161	1.7	0.2	11
168	2.3	0.3	12
175	1.4	0.6	8

4.5 METERS

JULIAN DAY	MEAN	STD DEV	CASES
147	2.2	0.5	12
154	2.0	0.3	11
161	2.1	0.2	12
168	1.6	0.2	11
175	2.2	0.3	12
182	1.5	0.4	6
189	1.1	0.1	4

7.0 METERS

JULIAN DAY	MEAN	STD DEV	CASES
147	1.3	0.2	12
154	1.6	0.2	12
161	1.8	0.2	12
168	1.2	0.1	12
175	1.2	0.1	11
182	1.3	0.1	11
189	1.1	0.1	12
196	1.1	0.1	9

FIGURE 3.   Mean dry weight of hydra expressed as change in micrograms per growth axis over time (Julian Days).

MCKELVEY HYDRA 1993
MEAN DRY WEIGHT
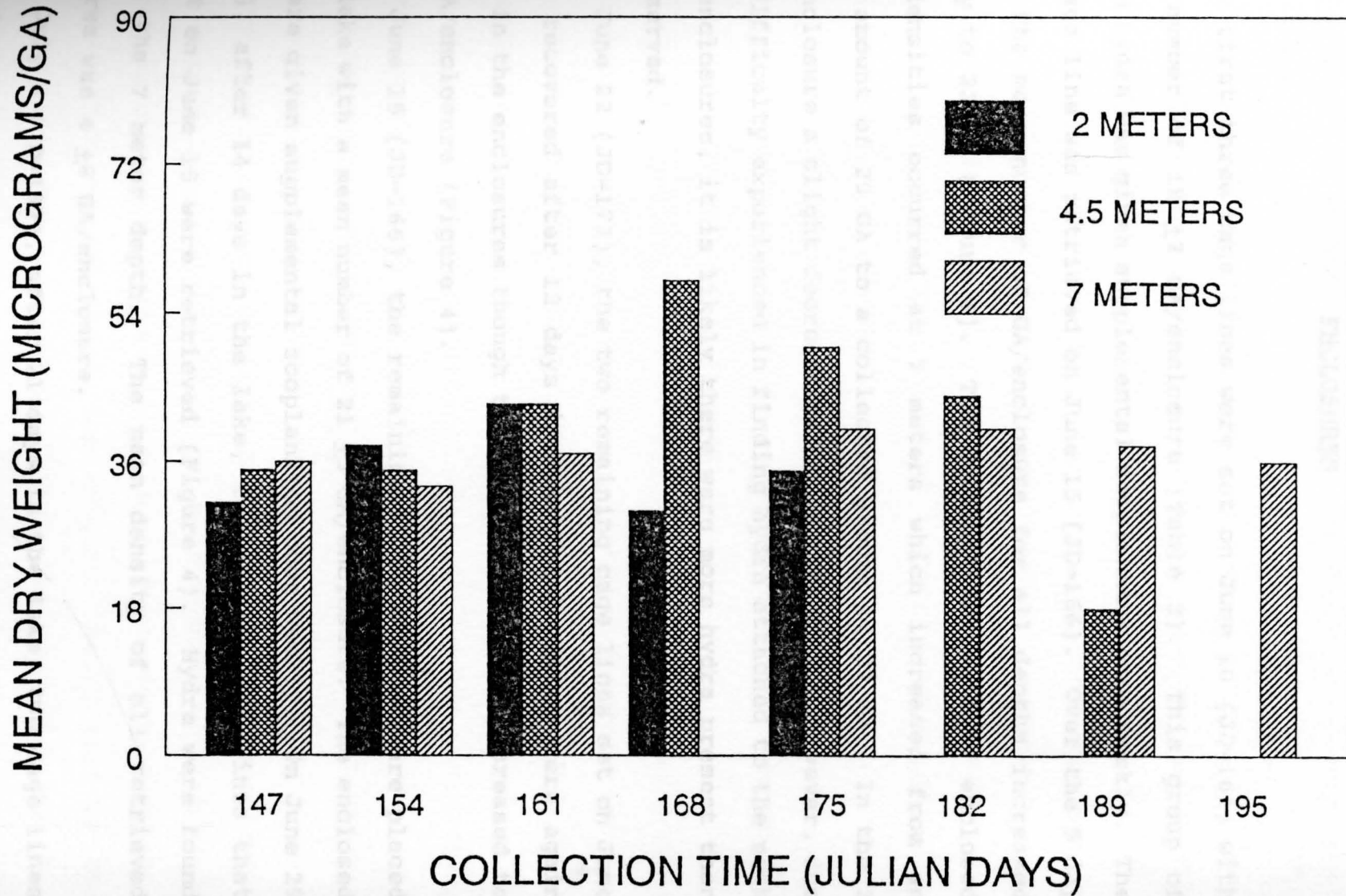
ENCLOSURES

The first three cage lines were set on June 10 (JD=161) with a mean number of 18 ±2 GA/enclosure (Table 3). This group of enclosed hydra was given supplemental zooplankton once weekly. The first cage line was retrieved on June 15 (JD=166). Over the 5 day period, the mean number of GA/enclosure for all depths increased slightly to 22 ±9 (Figure 4). The greatest increase of enclosed hydra densities occurred at 7 meters which increased from an initial amount of 20 GA to a collected amount of 27 GA. In the 2 meter enclosure a slight decrease of GA was observed. However, due to the difficulty experienced in finding hydra attached to the mesh of the enclosures, it is likely there were more hydra present than were observed.

On June 22 (JD=173), the two remaining cage lines set on June 10 were recovered after 12 days in the lake. Hydra were again present in the enclosures though the mean density had decreased to 13 ±9 GA/enclosure (Figure 4).

On June 15 (JD=166), the remaining 13 cage lines were placed in the lake with a mean number of 21 ±3 GA/enclosure. The enclosed hydra were given supplemental zooplankton once weekly. On June 29 (JD=180), after 14 days in the lake, two of the cage lines that were set on June 15 were retrieved (Figure 4). Hydra were found only at the 7 meter depth. The mean density of all retrieved enclosures was 4 ±8 GA/enclosure.

On July 6 (JD=187), after 21 days in the lake, two cage lines set on June 15 were retrieved. Nine GA were observed in one

enclosure from 4.5 meters (Figure 4). No other enclosures were found to contain hydra.

On July 13 (JD=194), after 28 days in the lake, two cage lines set on June 15 were recovered. No hydra were found in the enclosures (Figure 4).

At this time, due to the difficulty being experienced in maintaining hydra in the cages, it was decided to reset 6 cage lines and increase the feeding intervals to twice a week. The cages were set with a mean density of 15 ±3 GA/enclosure and placed in the lake on July 13 (JD=194).

On July 20 (JD=201), after 7 days in the lake, two cage lines set on July 13 were retrieved. One cage at the 2 meter depth had 2 GA while all other cages were empty.

On July 27 (JD=208), after 14 days in the lake, two cage lines were retrieved. Hydra were found at 2.0 and 4.5 meters but the mean densities had still declined from 15 ±3 GA/enclosure to 3 ±5 GA/enclosure (Figure 4).

Due to the poor survival rate of the hydra in the enclosures, even when provided supplemental zooplankton twice a week, an experiment was conducted to determine if the enclosures themselves were the cause of the hydra's inability to survive. Five enclosures were placed at 2 meters depth in the lake on July 27 (JD=208) with a mean density of 13 ±2 GA/enclosure. On July 29 (JD=210) 5 enclosures were placed in a lab aquarium containing aged tap water. The enclosures in the aquarium functioned as the control group for the experiment. The mean densities for the control group was 15 ±3 GA/enclosure. On August 12 (JD=224) all

FIGURE 4. Change in the number of growth axes collected per enclosure over time. Number over bars for each date denotes duration (Days) of the enclosures in the lakes. Bars denote standard deviation.
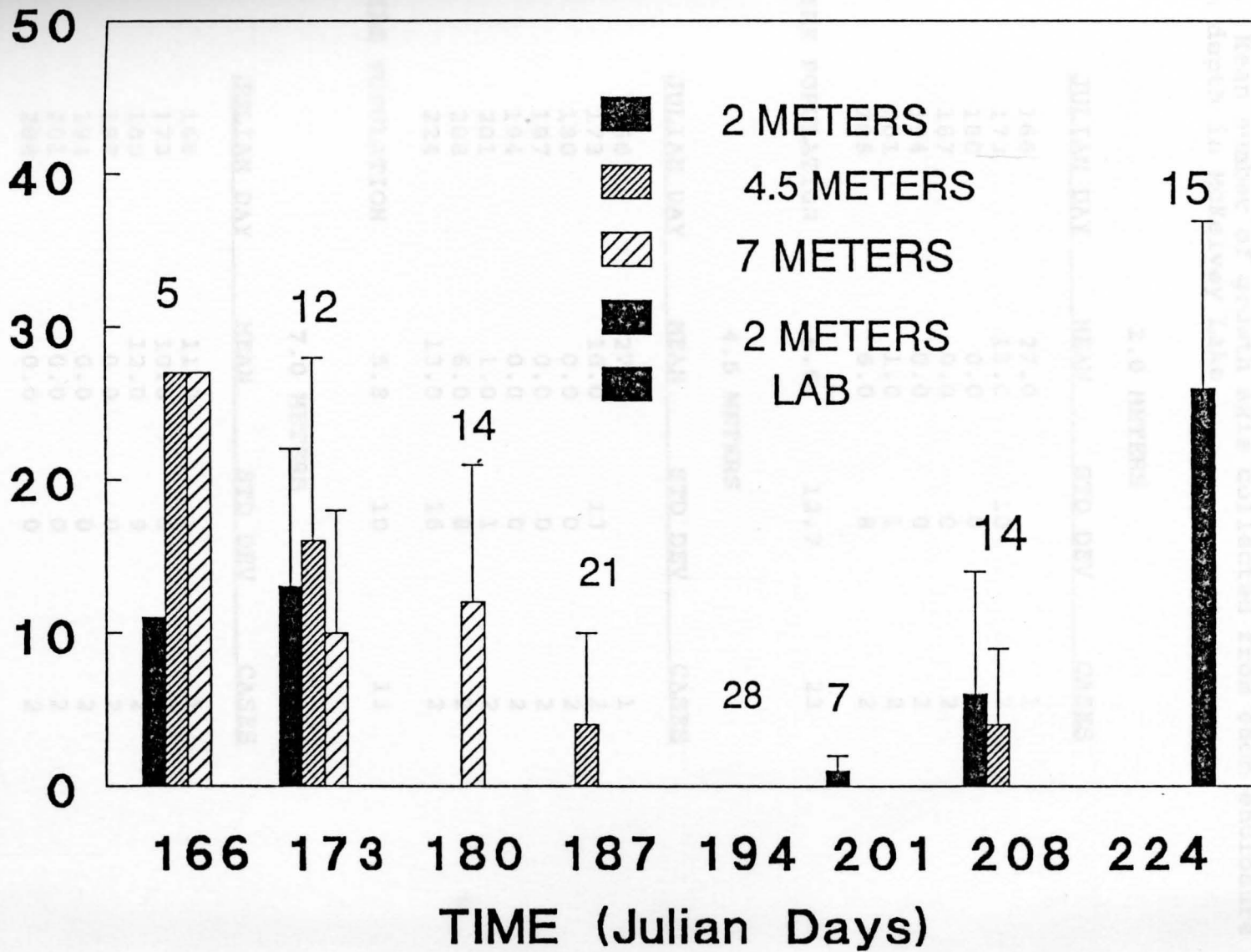
HYDRA IN ENCLOSURES

TABLE 3. Mean number of growth axis collected from each enclosure for each depth in McKelvey Lake.

2.0 METERS

JULIAN DAY	MEAN	STD DEV	CASES
166	27.0		1
173	13.0	10	2
180	0.0	0	2
187	0.0	0	2
194	0.0	0	2
201	1.0	1	2
208	6.0	8	2
FOR ENTIRE POPULATION	8.6	12.7	23

4.5 METERS

JULIAN DAY	MEAN	STD DEV	CASES
166	27.0		1
173	16.0	13	2
180	0.0	0	2
187	0.0	0	2
194	0.0	0	2
201	1.0	1	2
208	6.0	8	2
224	13.0	16	2
FOR ENTIRE POPULATION	5.8	10	13

7.0 METERS

JULIAN DAY	MEAN	STD DEV	CASES
166	11.0		1
173	10.0	8	2
180	12.0	9	2
187	0.0	0	2
194	0.0	0	2
201	0.0	0	2
208	0.0	0	2
FOR ENTIRE POPULATION	4.3	7	13

TABLE 3 (CONTINUED).

RESET: 2.0 METERS AND LABORATORY

	JULIAN DAY	MEAN	STD DEV	CASES
2.0 METERS (LAKE)	224	0.0	0	5
LABORATORY	224	26.0	12	5

enclosures were recovered and examined for hydra (Figure 4). No hydra were found in the lake enclosures while a mean of 26 ±12 GA/enclosure was found for the control group.

LAKE PRODUCTIVITY

The maximum for chlorophyll a (chla) at 2.0 meters occurred on June 17 (JD=168) to June 24 (JD=175) at 19 ug/liter (Figure 5). The maximum chla at 4.5 meters occurred on June 24 at 23 ug/liter. The chla concentrations at 7.0 meters were generally similar to those at 4.5 meters but produced no obvious maximums (Figure 5). The mean for all concentrations at 2.0 meters is 10 ±6 ug/liter; at 4.5 meters, 14±5 ug/liter; at 7 meters, 11 ±5 ug/liter. These data were found to be positively correlated with zooplankton dry weight data (Pearson's correlation coefficient = 0.7638, N=10, p=0.01) (Table 4). The correlation is likely caused by the dependance of the zooplankton densities on their food source i.e. photosynthetic algae.

Densities of zooplankton were measured by dry weight in milligrams/liter. The maximum dry weight was recorded on June 24 (JD=175) at 0.245 mg/liter (Figure 6). This maximum was followed by a rapid decrease so that by July 1 (JD=182) the dry weight was recorded at 0.145 mg/liter. Zooplankton densities fluctuated during the following weeks never exceeding 0.152 mg/liter. The mean dry weight for all samples was 0.16 ±.04 mg/liter.

Schindler zooplankton trap data at two meters reach a maximum on June 17 (JD=168) to June 24 (JD=175) exceeding 70

PEARSON'S CORRELATION COEFFICIENT
TABLE 4
N=10 FOR ALL CORRELATIONS

	SRP	TP	TSP	BIO	CHLA	DO	SECCHI	TDS	pH
SRP	N/A	0.0009 p=0.998	0.0583 p=0.873	0.2869 p=0.422	0.1791 p=0.620	0.2341 p=0.515	0.064 p=0.861	0.2944 p=0.409	0.298 p=.403
TP		N/A	0.4639 p=0.177	-0.1112 p=0.76	0.0213 p=0.954	0.3424 p=0.333	-0.8083 p=0.005	-0.1888 p=0.601	-.1847 p=.609
TSP			N/A	0.0770 p=0.832	0.1835 p=0.612	-0.269 p=0.452	-0.6865 p=0.028	-0.5668 p=0.088	-.5458 p=.103
BIO				N/A	0.7638 p=0.01	0.1109 p=0.76	0.1266 p=0.728	-0.1929 p=0.593	-.1553 p=.668
CHLA					N/A	0.497 p=0.144	-0.0928 p=0.799	0.0767 p=0.833	0.1218 p=.738
DO						N/A	-0.1492 p=0.681	0.6173 p=0.057	0.6215 p=.055
SECCHI							N/A	0.4329 p=0.211	0.4375 p=.206
TDS								N/A	0.9940 p=0.0
pH									N/A

(N/A) INDICATES COEFFICIENT CANNOT BE COMPUTED

SYMBOLS: AMM=AMMONIUM   SRP=SOLUBLE REACTIVE PHOSPHORUS   TP=TOTAL PHOSPHORUS
               TSP=TOTAL SOLUBLE PHOSPHORUS   CHLA=CHLOROPHYLL A   DO=DISSOLVED OXYGEN
               TDS=TOTAL DISSOLVED SOLIDS   BIO=BIOMASS

FIGURE 5. Change of chlorophyll a concentrations (mg/liter) over time (Julian Days) at each depth.
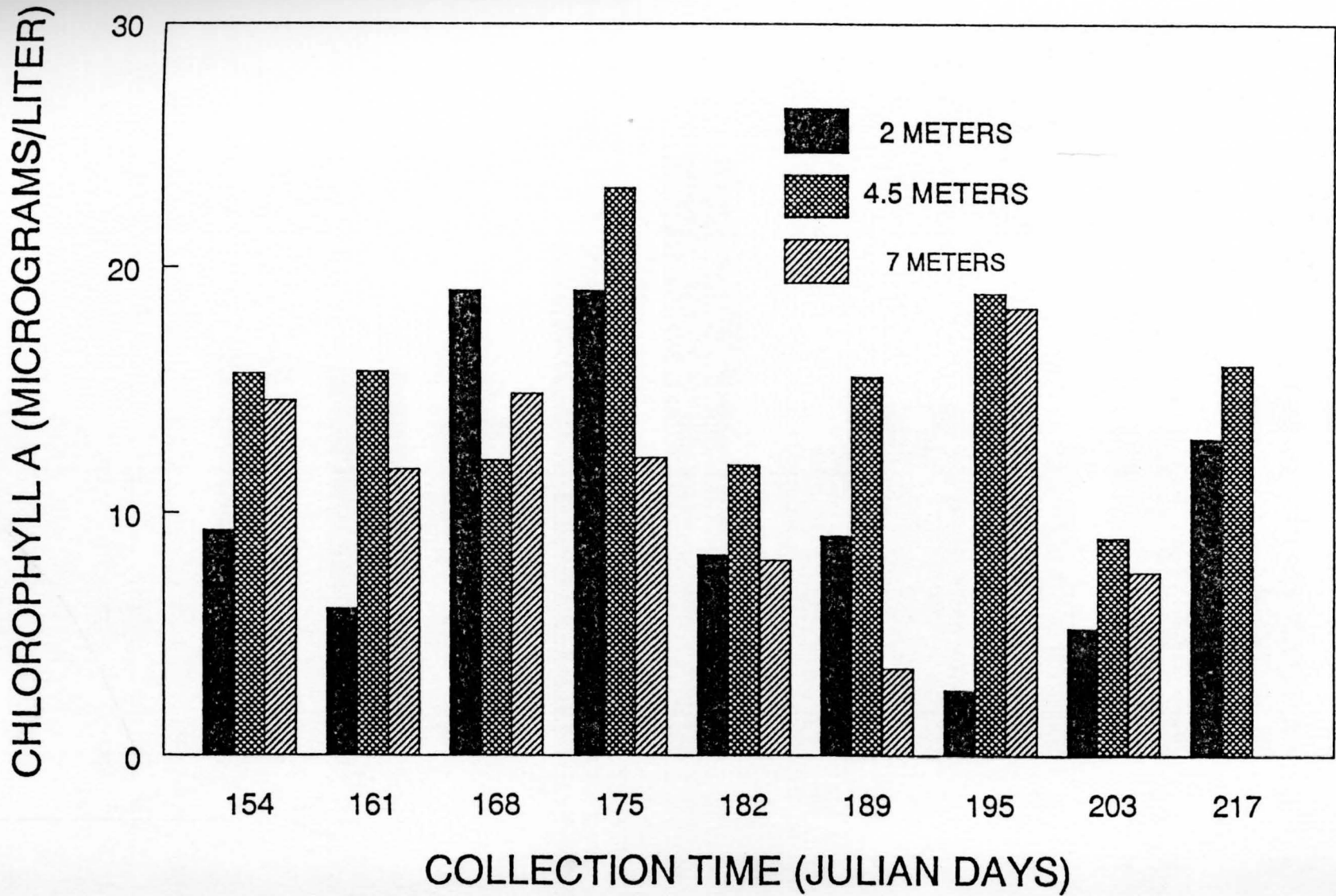
MCKELVEY PRODUCTIVITY
CHLOROPHYLL (A)

Bar chart. Y-axis: CHLOROPHYLL A (MICROGRAMS/LITER), ranging 0 to 30. X-axis: COLLECTION TIME (JULIAN DAYS) with values 154, 161, 168, 175, 182, 189, 195, 203, 217.

Legend:
- 2 METERS
- 4.5 METERS
- 7 METERS

FIGURE 6.   Dry weight of biomass (mg/liter) collected by
vertical tows from 6.5 meters with a conical net and its change
over time (Julian Days).

MCKELVEY BIOMASS
DRY WEIGHT

BIOMASS (GRAMS/LITER)

COLLECTION TIME (JULIAN DAYS)
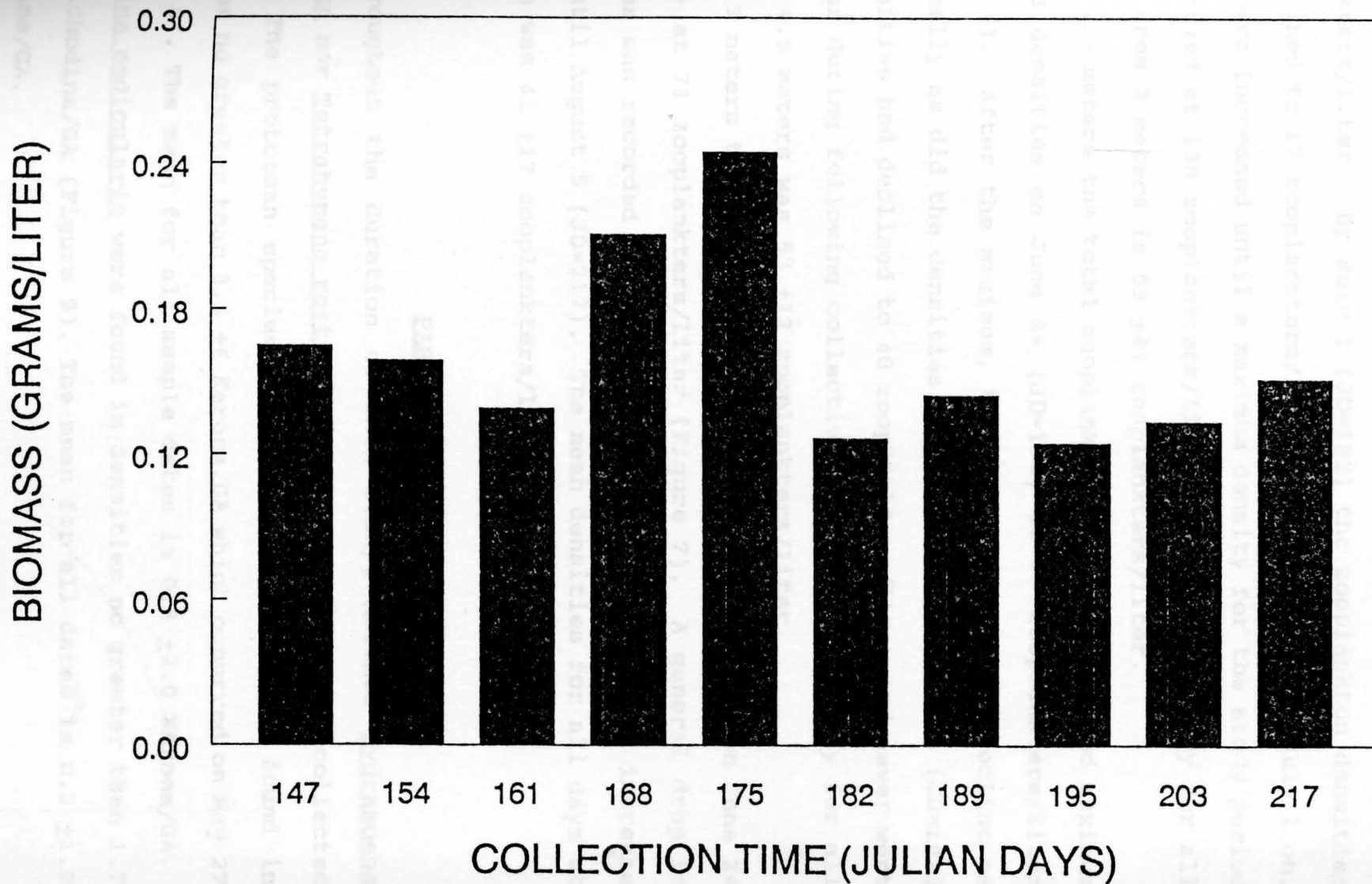
zooplankters/liter. By July 1 (JD=182) the zooplankton densities had declined to 17 zooplankters/liter (Figure 7). From July 1 on, the numbers increased until a maximum density for the study period was observed at 130 zooplankters/liter. The mean density for all samples from 2 meters is 59 ±41 zooplankters/liter.

At 4.5 meters the total zooplankton densities reached maximum recorded densities on June 24 (JD=175) at 73 zooplankters/liter (Figure 7). After the maximum, the densities did not decline as dramatically as did the densities at 2 meters. On July 1 (JD=182) the densities had declined to 40 zooplankters/liter and never went any lower during following collections. The mean density for all days at 4.5 meters was 53 ±17 zooplankters/liter.

At 7 meters the peak densities were again observed on June 24 (JD=175) at 71 zooplankters/liter (Figure 7). A general drop in densities was recorded on July 1 and the numbers did not increase again until August 5 (JD=217). The mean densities for all days at 7 meters was 41 ±17 zooplankters/liter.
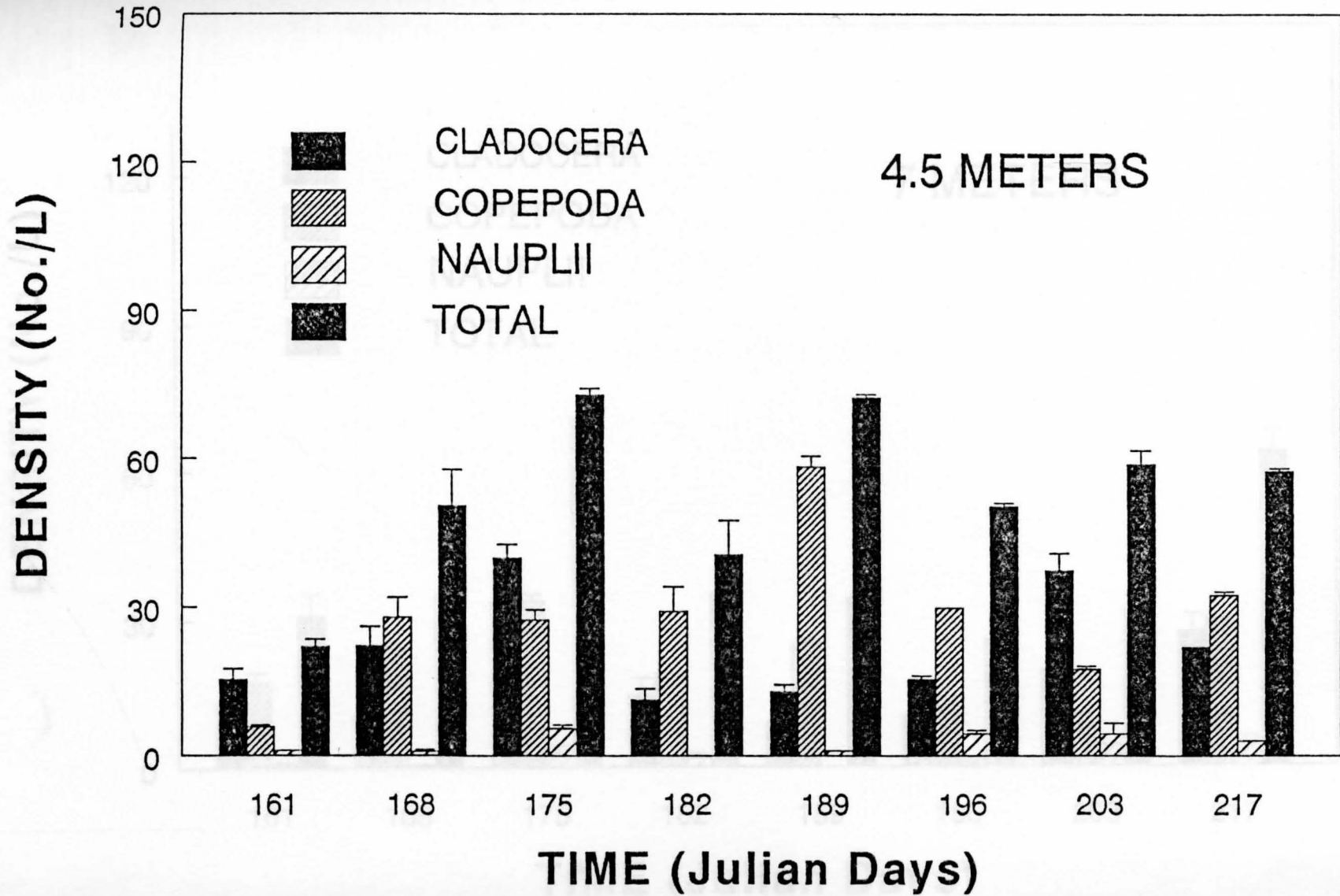
PARASITES

Throughout the duration of this study, neither Hydramoeba hydroxena nor Tetrahymena rostrata, were observed on the collected hydra. The protozoan species, Kerona polyporum, were found in densities no greater than 3.8 ±6 Kerona/GA which occurred on May 27 (Figure 8). The mean for all sample dates is 0.8 ±2.0 Kerona/GA. Trichodina pedicularis were found in densities no greater than 1.7 ±3.6 Trichodina/GA (Figure 9). The mean for all dates is 0.3 ±1.0 Trichodina/GA.

FIGURE 7.   Change in zooplankton densities at each depth
collected with a Schindler zooplankton trap over time (Julian
Days).   Bars denote standard deviation of counting procedures.
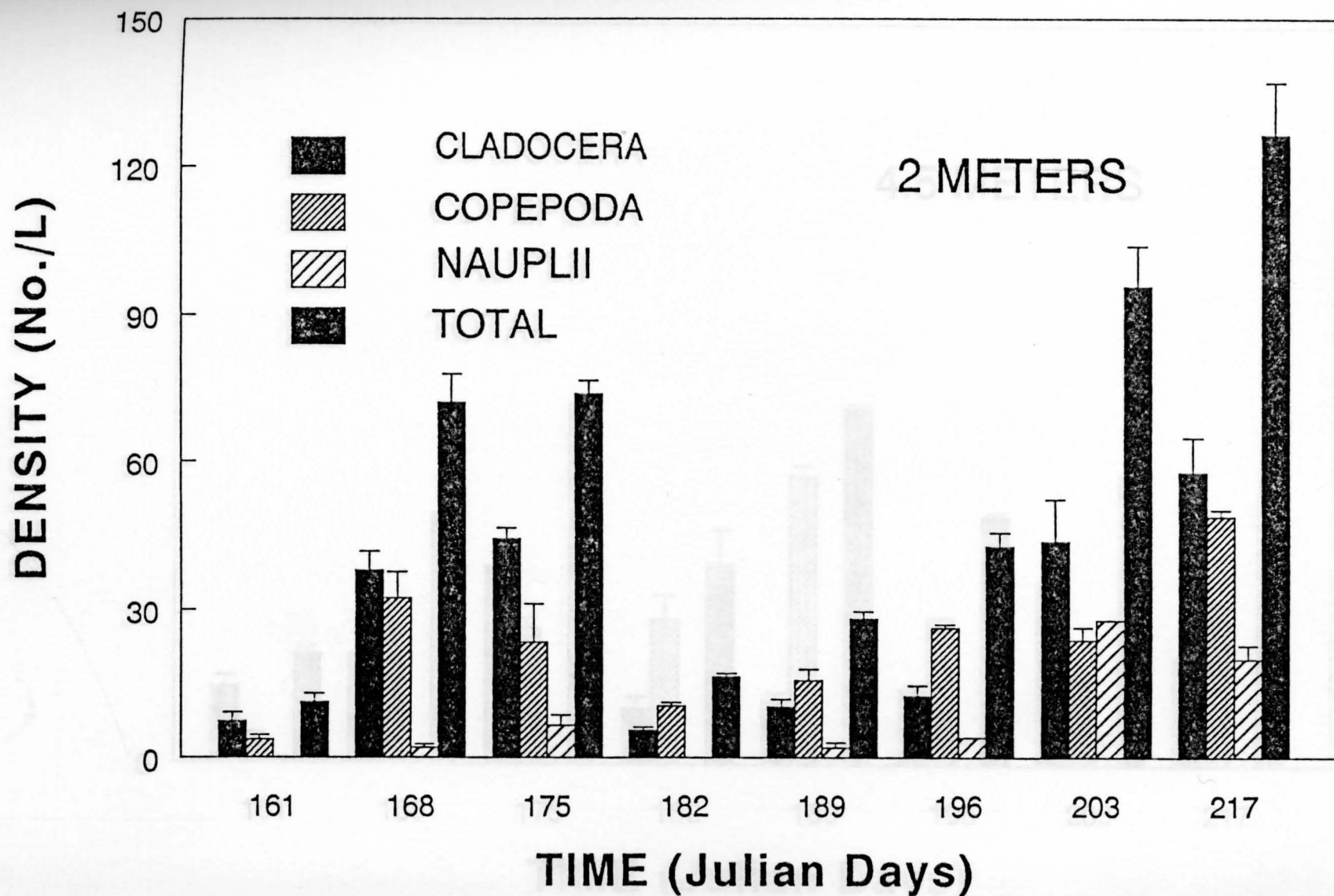
ZOOPLANKTON DENSITY
LAKE MCKELVEY
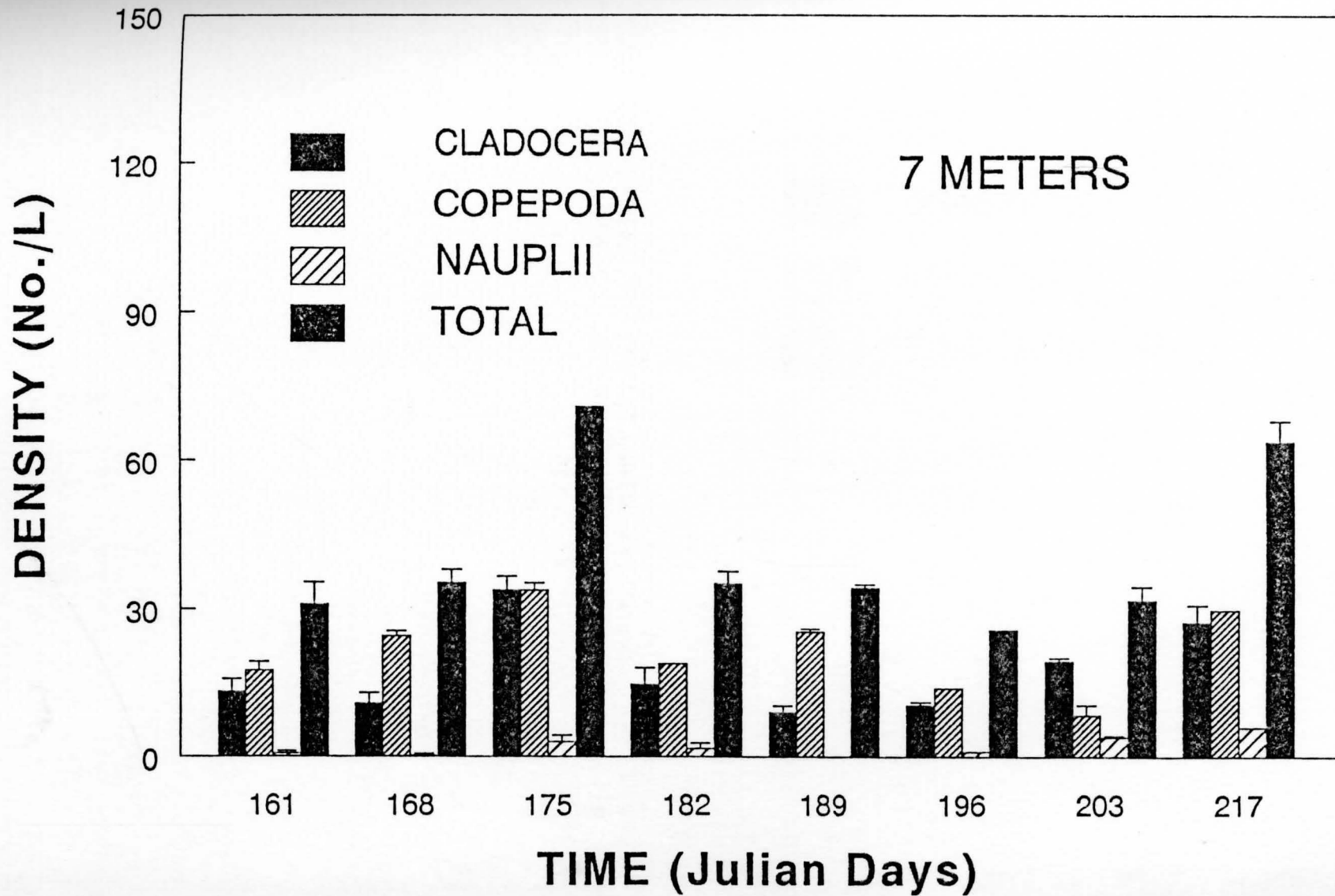
ZOOPLANKTON DENSITY
LAKE MCKELVEY

4.5 METERS

Legend:
- CLADOCERA
- COPEPODA
- NAUPLII
- TOTAL

DENSITY (No./L)

TIME (Julian Days)

161 168 175 182 189 196 203 217

ZOOPLANKTON DENSITY
LAKE MCKELVEY

FIGURE 8. Change of mean number of <u>Kerona polyporum</u> per growth axis over time at each depth. Bars denote standard deviation.

HYDRA PARASITES 1993
KERONA POLYPORUM

Figure showing MEAN PARASITES PER GROWTH AXIS versus COLLECTION TIME (JULIAN DAYS).

Legend:
- 2 METERS
- 4.5 METERS
- 7 METERS

Y-axis values: 0.00, 2.10, 4.20, 6.30, 8.40, 10.50

X-axis (Julian Days): 147, 154, 161, 168, 175, 182, 189, 196
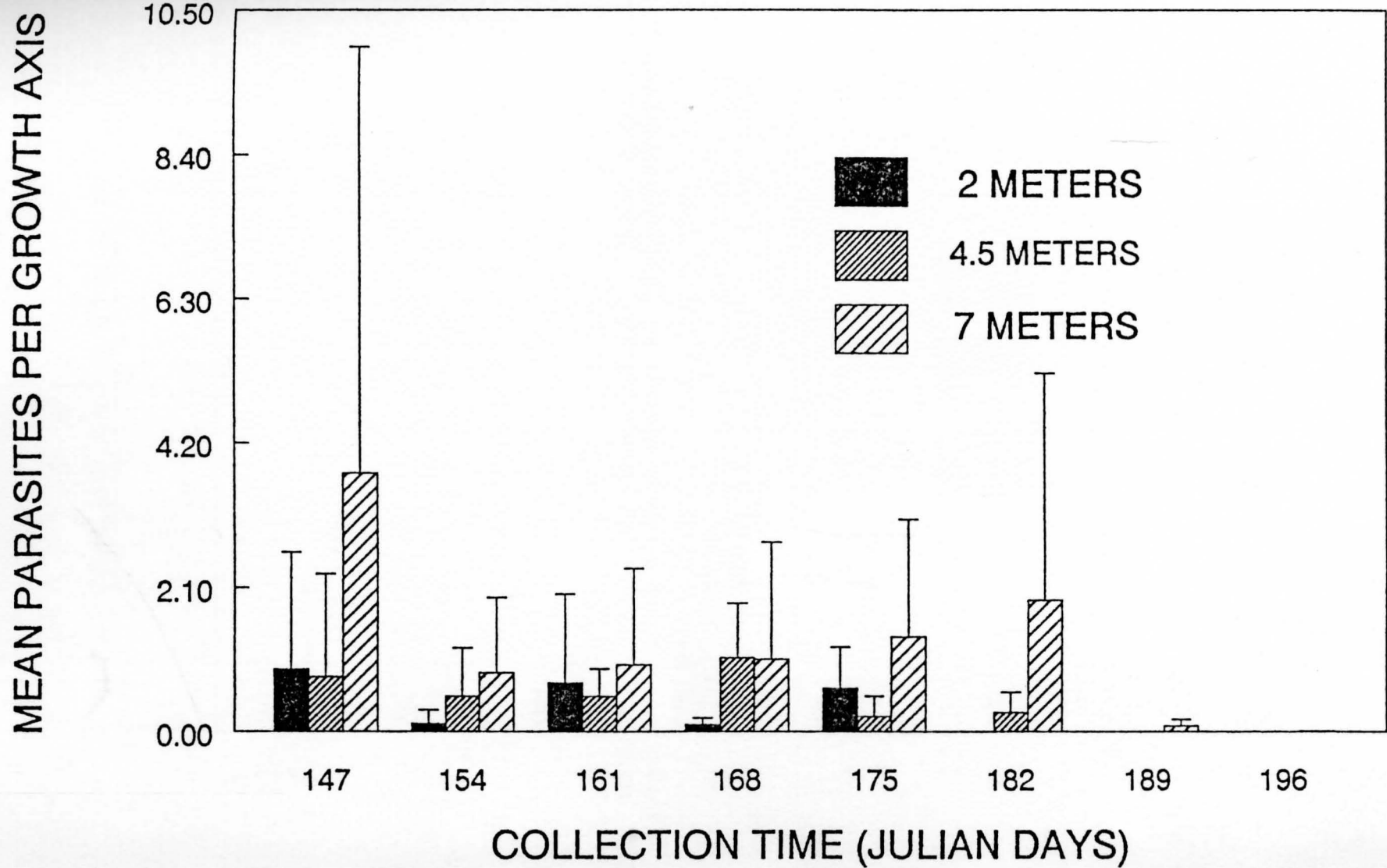
FIGURE 9. Change of mean number of <u>Tricodina pedicularis</u> per growth axis over time at each depth. Bars denote standard deviation.

HYDRA PARASITES 1993
TRICHODINA PEDICULARIS
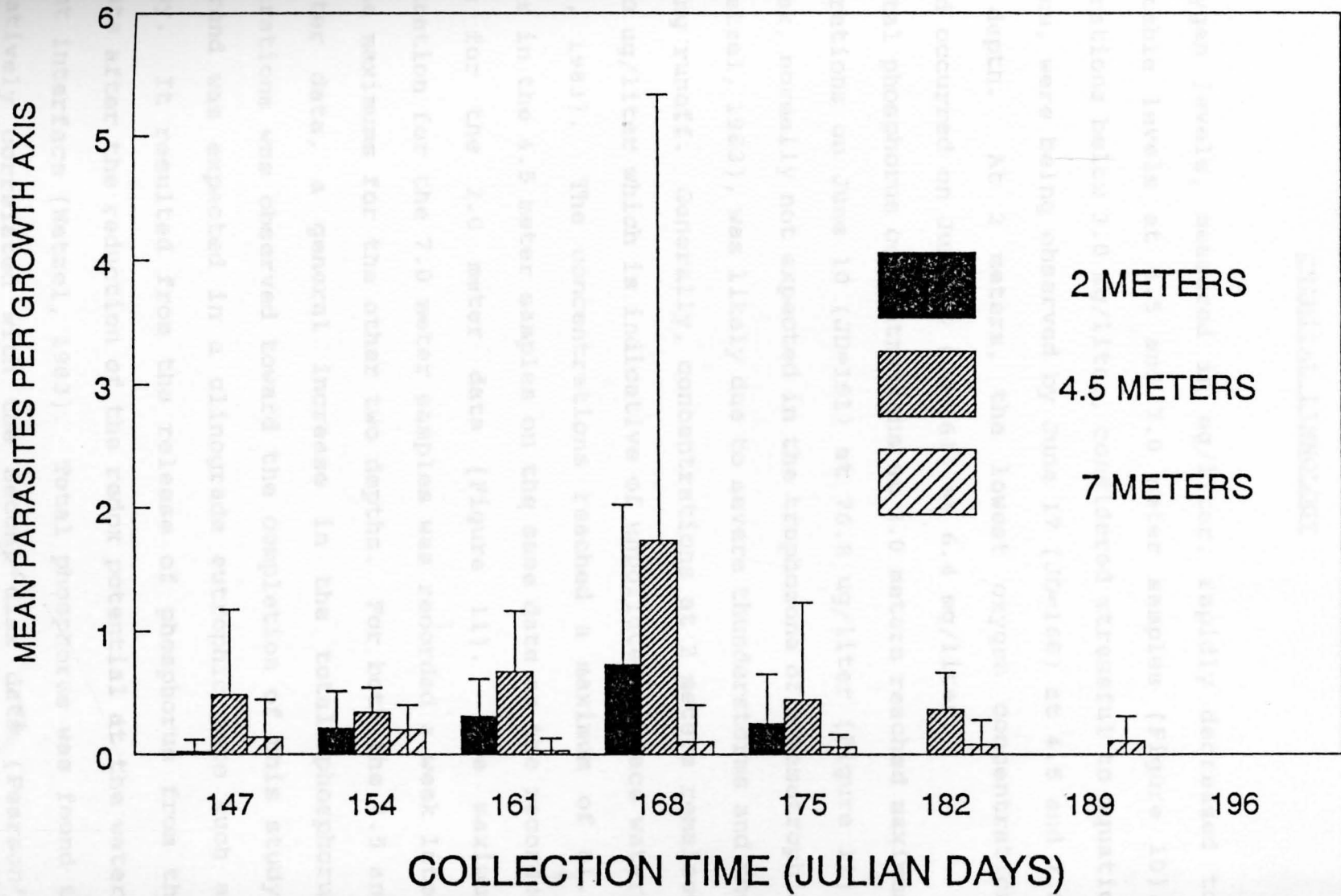
CHEMICAL LIMNOLOGY

Oxygen levels, measured in mg/liter, rapidly decreased to undetectable levels at 4.5 and 7.0 meter samples (Figure 10). Concentrations below 3.0 mg/liter, considered stressful to aquatic organisms, were being observed by June 17 (JD=168) at 4.5 and 7.0 meters depth. At 2 meters, the lowest oxygen concentration recorded occurred on June 10 (JD=161) at 6.4 mg/liter.

Total phosphorus concentrations at 2.0 meters reached maximum concentrations on June 10 (JD=161) at 76.8 ug/liter (Figure 11). This peak, normally not expected in the trophozone of a mesotrophic lake (Wetzel, 1983), was likely due to severe thunderstorms and the resulting runoff. Generally, concentrations at 2 meters remained below 30 ug/liter which is indicative of unpolluted surface waters (Wetzel, 1983). The concentrations reached a maximum of 61.4 ug/liter in the 4.5 meter samples on the same date as the recorded maximum for the 2.0 meter data (Figure 11). The maximum concentration for the 7.0 meter samples was recorded a week later than the maximums for the other two depths. For both the 4.5 and 7.0 meter data, a general increase in the total phosphorus concentrations was observed toward the completion of this study. This trend was expected in a clinograde eutrophic lake such as McKelvey. It resulted from the release of phosphorus from the sediments after the reduction of the redox potential at the water-sediment interface (Wetzel, 1983). Total phosphorus was found to be negatively correlated with the Secchi disk data (Pearson's correlation coefficient =-0.8083 N=10 p=0.005). Secchi disk

FIGURE 10. Oxygen concentrations expressed as change in milligrams of oxygen per liter over time (Julian Days) at each depth.
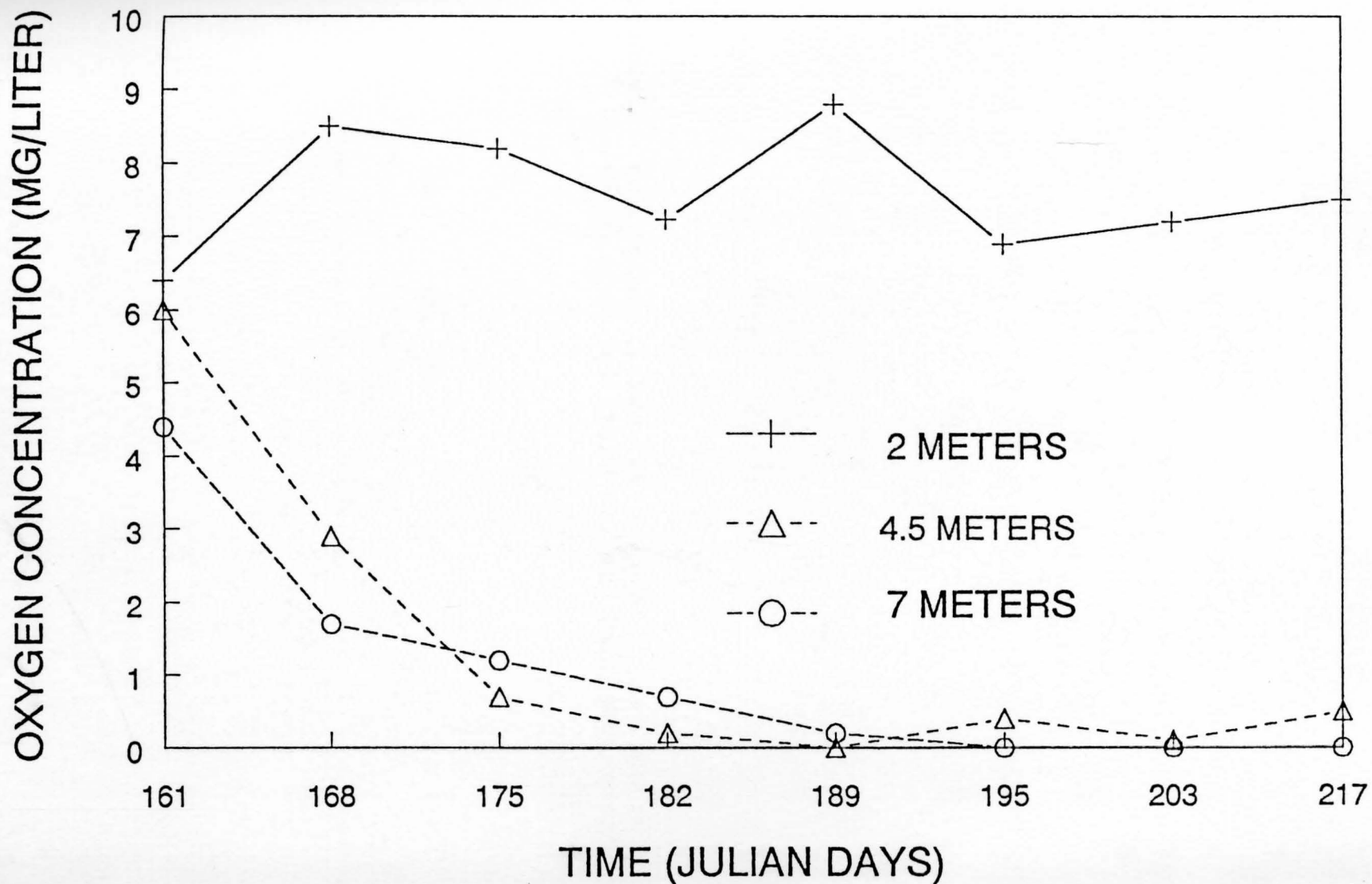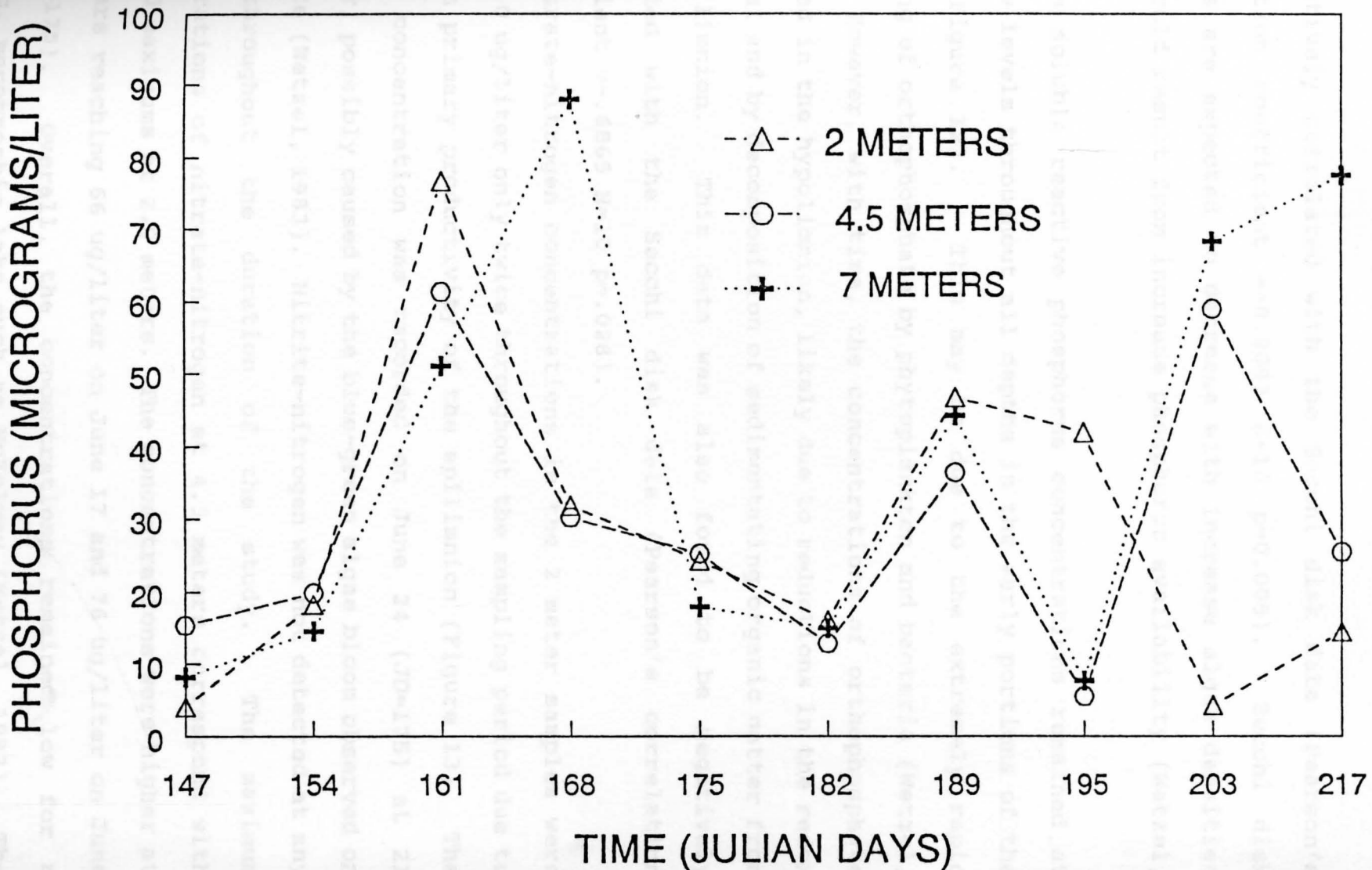
OXYGEN PROFILE
MCKELVEY LAKE 1993

FIGURE 11.   Change of total phosphorus concentrations
(ug/liter) over time (Julian Days) for each depth.

TOTAL PHOSPHORUS
MCKELVEY LAKE 1993

be negatively correlated with the Secchi disk data (Pearson's correlation coefficient =-0.8083 N=10 p=0.005). Secchi disk readings are expected to decrease with increase algae densities which would result from increase phosphorus availability (Wetzel, 1983).

The soluble reactive phosphorus concentrations remained at very low levels throughout all depths in the early portions of the study (Figure 12). This may be due to the extremely rapid recycling of orthophosphate by phytoplankton and bacteria (Wetzel, 1983). However, with time, the concentrations of orthophosphate increased in the hypolimnion, likely due to reductions in the redox potential and by decomposition of sedimentating organic matter from the epilimnion. This data was also found to be negatively correlated with the Secchi disk data (Pearson's correlation coefficient =-.6865 N=10 p=.028).

Nitrate-nitrogen concentrations in the 2 meter samples were above 0.0 ug/liter only twice throughout the sampling period due to the high primary productivity of the epilimnion (Figure 13). The highest concentration was recorded on June 24 (JD=175) at 21 ug/liter, possibly caused by the blue-green algae bloom observed on this date (Wetzel, 1983). Nitrite-nitrogen was not detected at any depth throughout the duration of the study. The maximum concentrations of nitrate-nitrogen at 4.5 meters correspond with observed maximums at 2.0 meters. The concentrations were higher at 4.5 meters reaching 66 ug/liter on June 17 and 76 ug/liter on June 24 (JD=175). Overall, the concentrations remained low for a dimictic, mesotrophic lake such as McKelvey (Wetzel, 1983). The

FIGURE 12. Change of soluble reactive phosphorus
concentrations (ug/liter) over time (Julian Days) at each depth.

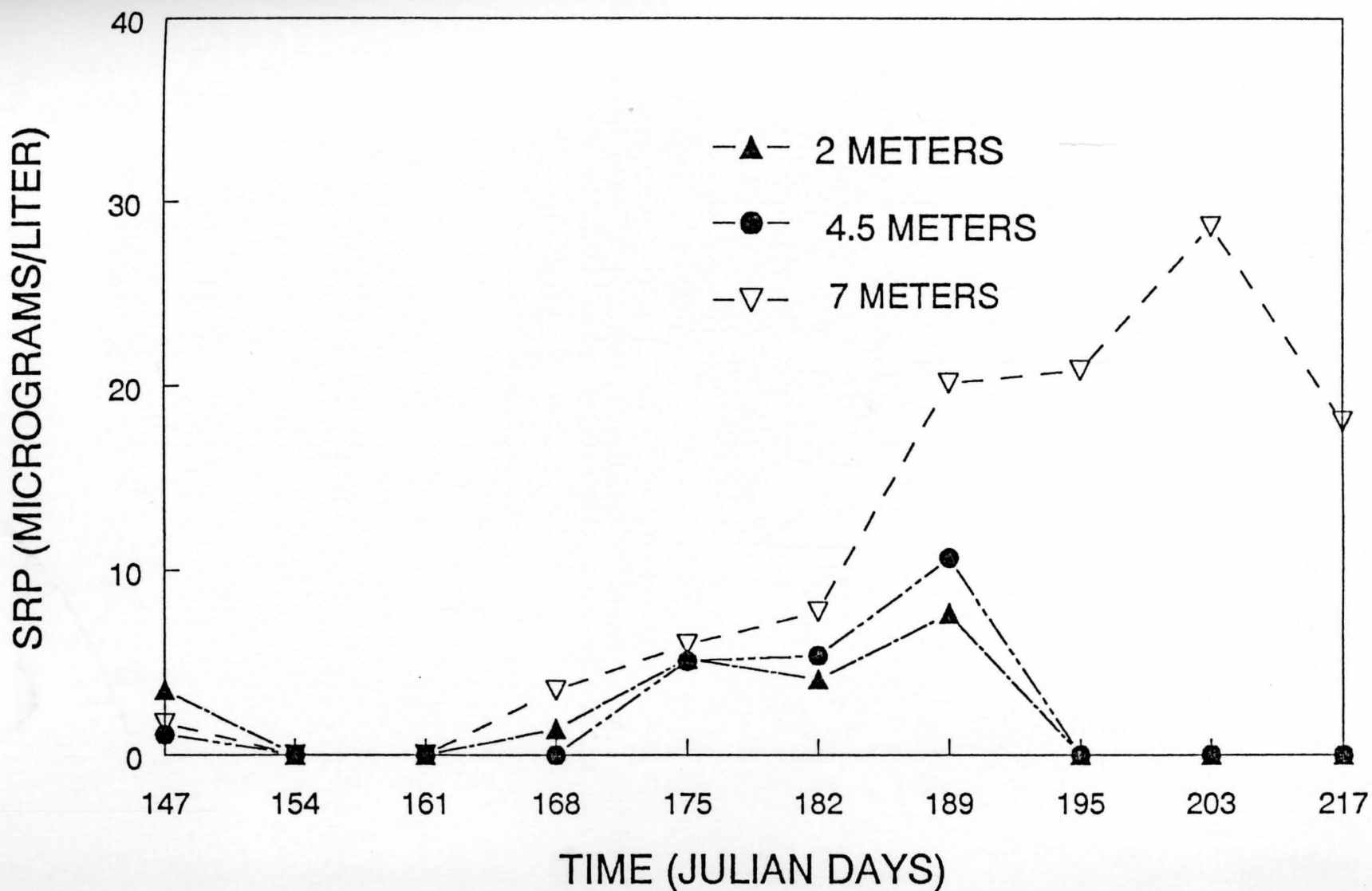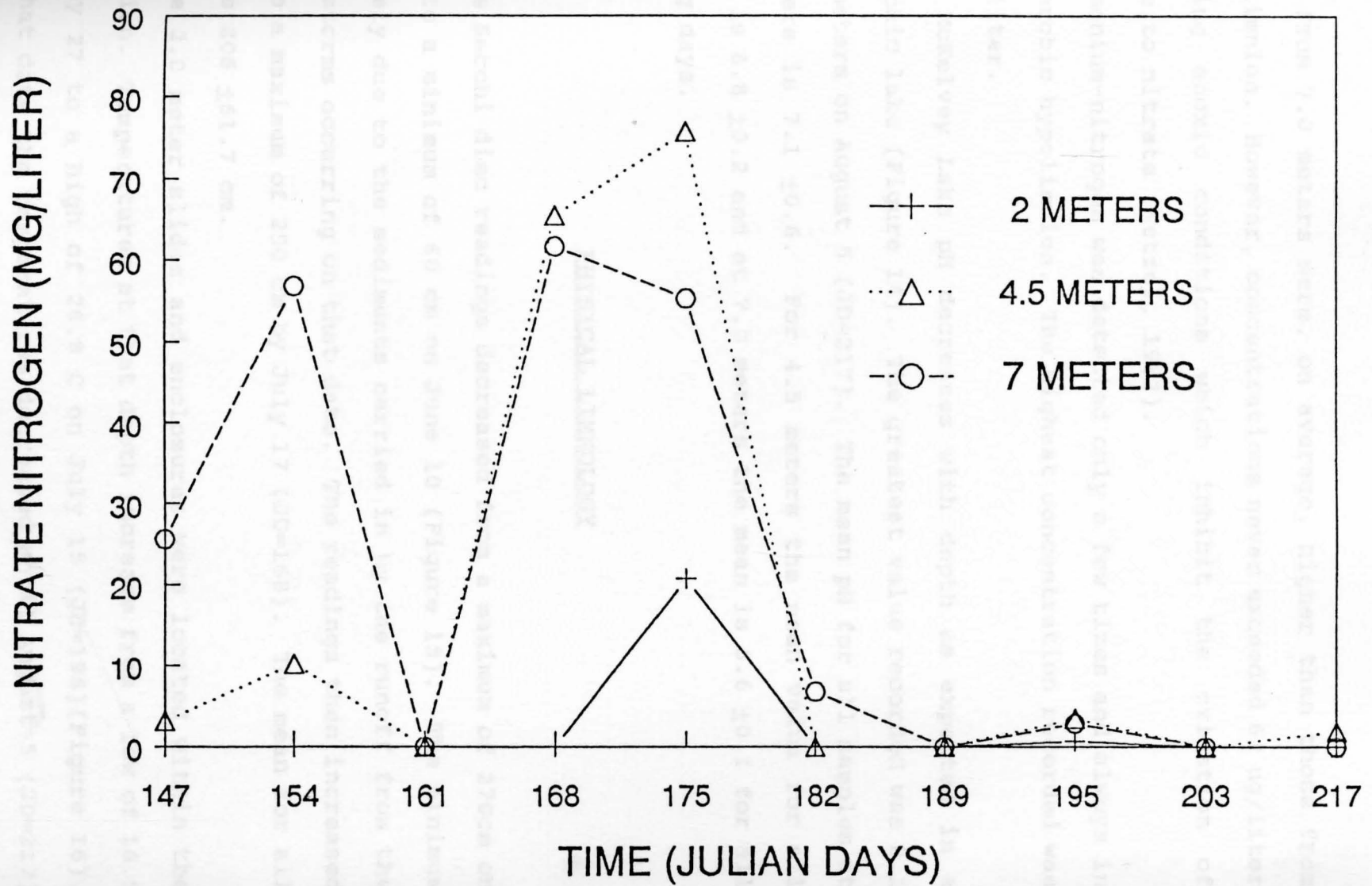# SOLUBLE REACTIVE PHOSPHORUS
MCKELVEY LAKE 1993

FIGURE 13. Nitrate nitrogen concentrations expressed as change in miligrams per liter over time (Julian Days) at each depth.

NITRATE NITROGEN
MCKELVEY LAKE 1993

Figure: Nitrate Nitrogen (mg/liter) versus Time (Julian Days) for McKelvey Lake 1993 at depths of 2 meters, 4.5 meters, and 7 meters.

samples from 7.0 meters were, on average, higher than those from the epilimnion. However, concentrations never exceeded 62 ug/liter indicating anoxic conditions which inhibit the oxidation of ammonium to nitrate (Wetzel, 1983).

Ammonium-nitrogen was detected only a few times and always in the anaerobic hypolimnion. The highest concentration recorded was 0.1 mg/liter.

In McKelvey Lake pH decreases with depth as expected in a mesotrophic lake (Figure 14). The greatest value recorded was 8.1 at 2.0 meters on August 5 (JD=217). The mean pH for all samples at 2.0 meters is 7.1 ±0.6. For 4.5 meters the mean value for all samples is 6.8 ±0.2 and at 7.0 meters the mean is 6.6 ±0.1 for all sampling days.

PHYSICAL LIMNOLOGY

The Secchi disc readings decreased from a maximum of 270cm on May 27 to a minimum of 60 cm on June 10 (Figure 15). The minimum was likely due to the sediments carried in by the runoff from the thunderstorms occurring on that date. The readings then increased again to a maximum of 250 cm by July 17 (JD=168). The mean for all dates is 206 ±61.7 cm.

The 2.0 meter slides and enclosures were located within the epilimnion. Temperatures at that depth increase from a low of 16.5 C on May 27 to a high of 26.8 C on July 15 (JD=196)(Figure 16). After that date the temperatures decreased until August 5 (JD=217) where it was recorded at 24.1 C. The mean temperature for all days

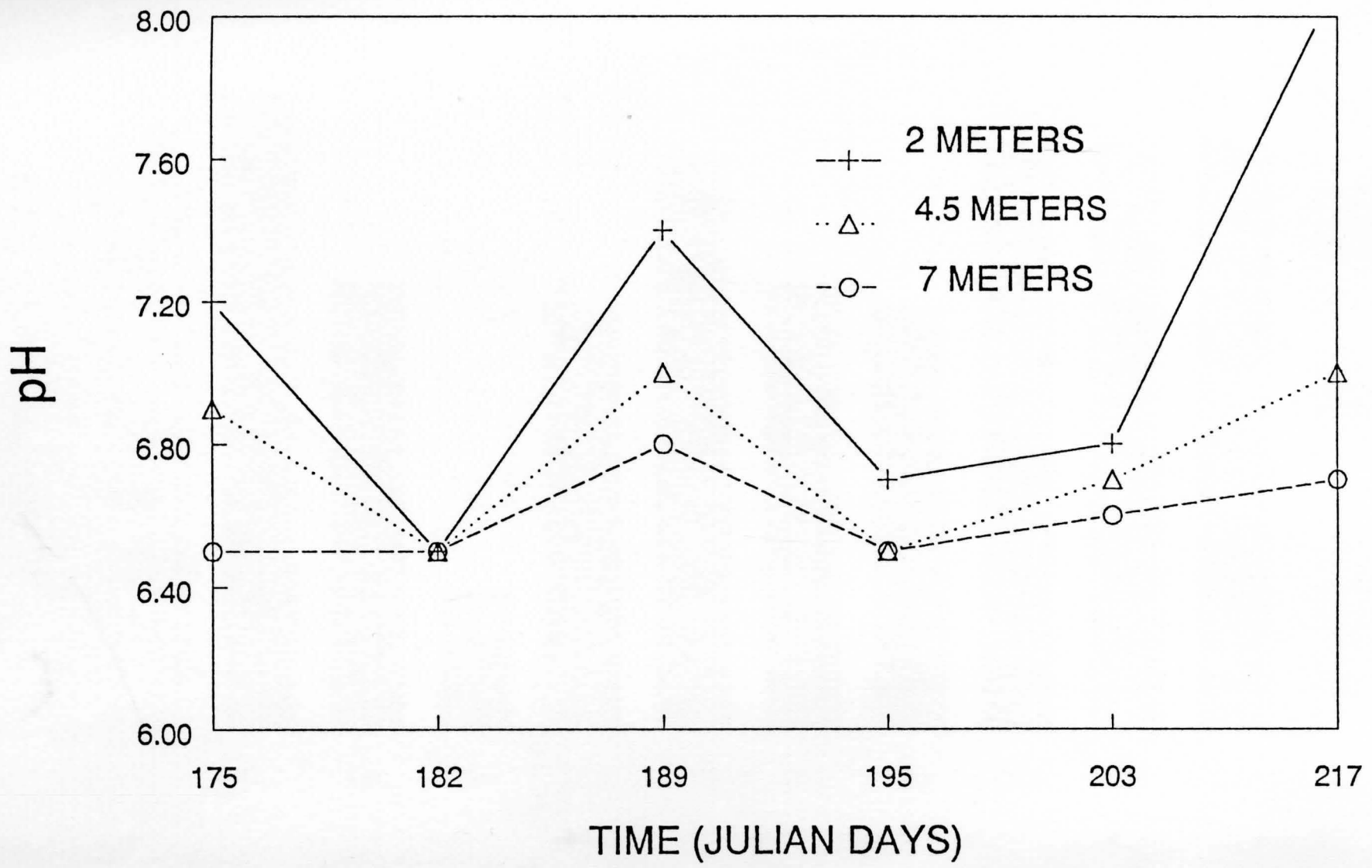FIGURE 14. Change of pH values over time at each depth.

MCKEEVER LAKE pH

FIGURE 15.   Change of Secchi transparency values (cm) over time (Julian Days).
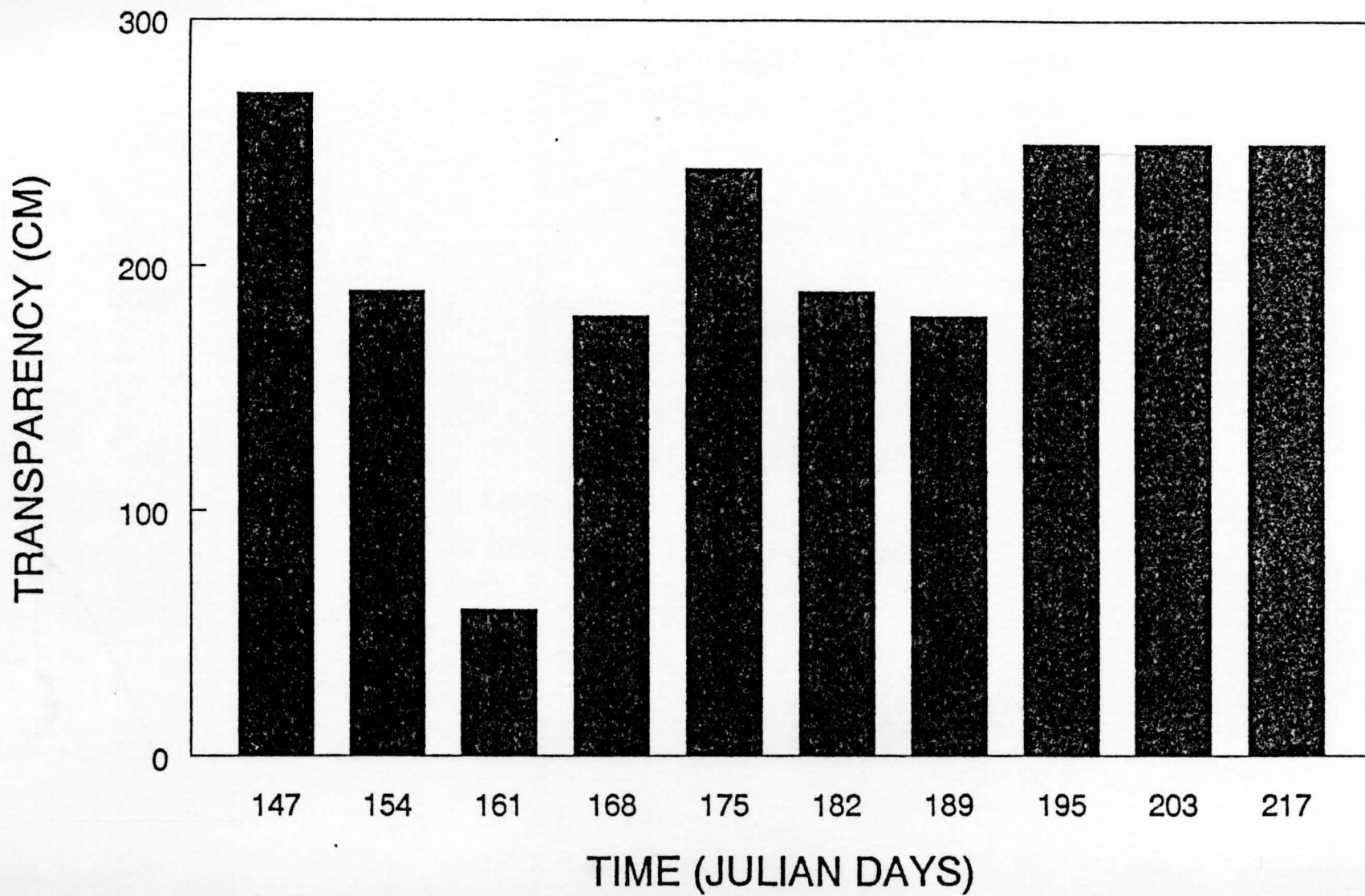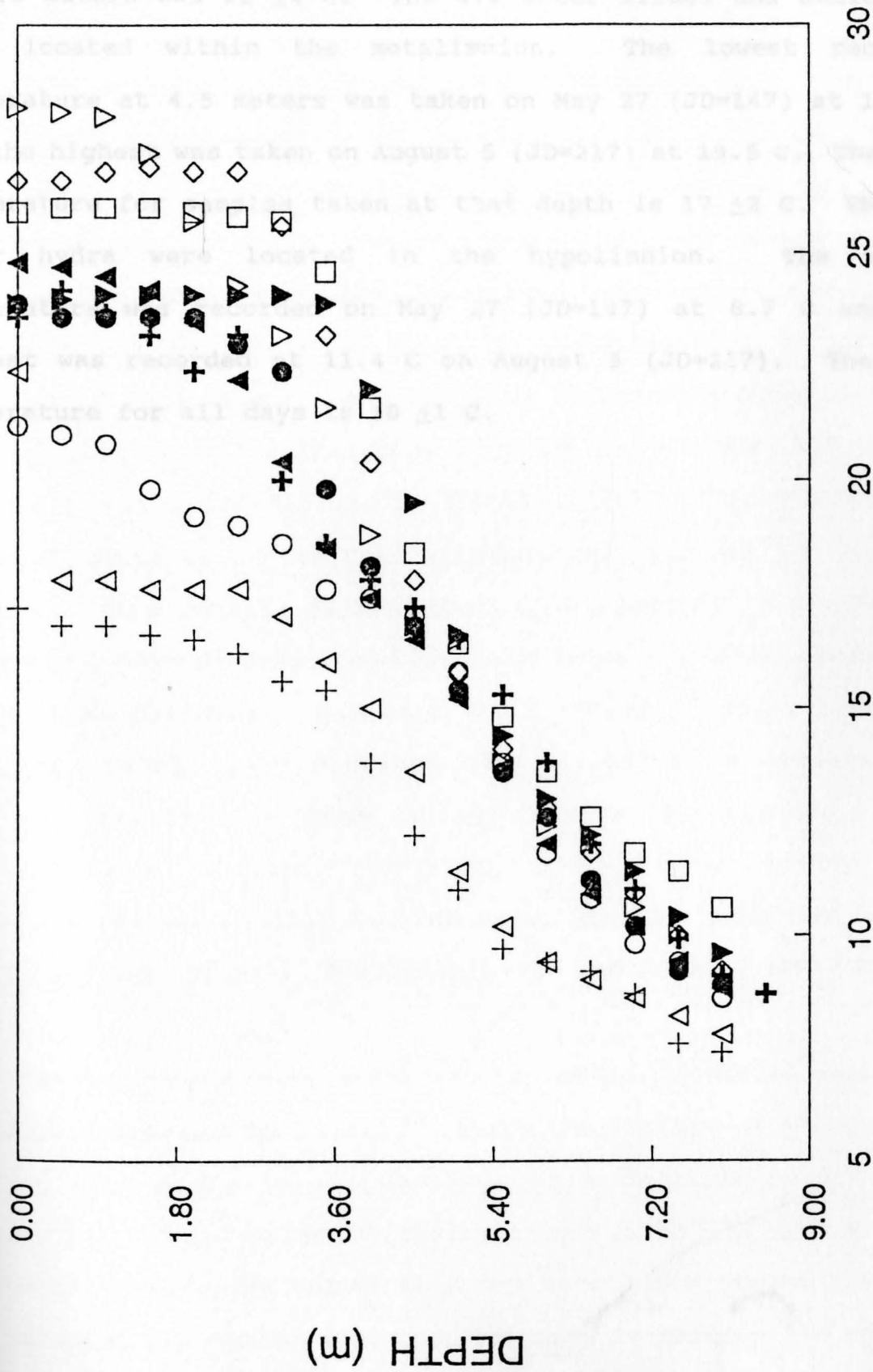
SECCHI DISK TRANSPARENCY
MCKELVEY LAKE 1993

FIGURE 16.   Temperature profile of water column expressed as change in degrees celsius for each depth over time (Julian Days).

TEMPERATURE 1993

TEMPERATURE

DEPTH (m)

at 2.0 meters was 22 ±4 C. The 4.5 meter slides and enclosures were located within the metalimnion. The lowest recorded temperature at 4.5 meters was taken on May 27 (JD=147) at 12.2 C and the highest was taken on August 5 (JD=217) at 19.5 C. The mean temperature for samples taken at that depth is 17 ±2 C. The 7.0 meter hydra were located in the hypolimnion. The lowest temperature was recorded on May 27 (JD=147) at 8.7 C and the highest was recorded at 11.4 C on August 5 (JD=217). The mean temperature for all days is 10 ±1 C.

DISCUSSION

Lake McKelvey is a typical mesotrophic lake with relatively high secchi transparencies and moderate levels of phosphorus and chlorophyll a. Chlorophyll a, a direct measure of algae concentrations, tracked the concentrations of phosphorus as expected if phosphorus were limiting. Similarly, zooplankton densities tracked the chlorophyll a concentrations as would be expected if food (algae) were limiting zooplankton densities.

Spring population densities of hydra in McKelvey Lake exhibit a rapid increase and decline in density. This is consistent with observed dynamics of natural populations recorded by previous studies; Pine Lake in Northeastern Ohio (Reeder, 1979), Meander Creek Reservoir, Northeastern Ohio (Schroeder, unpublished; Mateja, 1984), Lake Zurich and Maggiore (Ribi, et.al., 1985), Lake Erie (Carrick, 1956), Lake Michigan (Batha, 1974), a shallow fish hatchery lake in Iowa (Moen, 1951), California ponds (Yu, 1976), Pickeral Lake, Michigan (Griffing, 1956), Kirkpatrick's Lake, Tennessee (Bryden, 1952), Toolick Lake, Alaska (Cukor and Mozley, 1981), and Lake Douglas, Michigan (Welch and Loomis, 1924; Miller, 1936).

The decline in hydra densities following the spring maximum is rapid in McKelvey Lake. At 2.0 meters the decline is the quickest falling from close to 100 GA/slide to 0 GA/slide in two weeks (Figure 1). In and below the thermocline the decline took a longer period of three weeks before no hydra were found on the slides.

Several hypotheses have been proposed to explain the observed

declines. Miller (1936) proposed wave action could dislodge the hydra from substrate causing the hydra to perish when washed into unfavorable environments. However, this hypothesis is not consistent with the observed dynamics of the hydra decline. Wave action would effect only those hydra in the shallow depths and does not explain the decline of hydra populations below the reach of wave energy. Furthermore, the declines occur at approximately the same time annually, again not consistent with a random environmental event.

Death caused by high temperatures (Griffing, 1965) is unlikely to be a direct cause of hydra declines. Schroeder and Callaghan (1981) maintained Hydra pseudoligactis indefinitely at 30C in a laboratory, a temperature rarely seen in the epilimnion of a lake and never reached below the thermocline. Hydra oligactis was found to have a upper lethal temperature of 26C. The highest temperature recorded in the epilimnion of Lake McKelvey was observed on July 8 at 28 C (Figure 15), therefore possibly limited H. oligactis to the metalimnion which never exceeded 20C. Nevertheless, the hydra population decline occurred in the metalimnion as well as throughout the lake, indicating temperature is an unlikely cause.

Predation and parasitism have been used as a hypothesis to explain the hydra declines (Bryden, 1952; Griffing, 1965; Reynolds and Looper, 1968). Predators include the flatworm Microstomum, an amoeba, Hydramoeba hydroxena, and the cladoceran, Ankistropus minor. Three species of protozoans are considered commensals with hydra and include: Trichodina pedicularis, Kerona polyporum, and Tetrahymena rostrata. However, predation and parasitism is an

unlikely factor in the annual and rapid hydra declines. The species of amoeba, protozoan, flatworm, and cladoceran have not been found to be associated with the hydra in densities high enough or regular enough to explain hydra declines (Schroeder and Callaghan, 1982). In McKelvey Lake Hydramoeba and Microstomum were never observed in association with hydra prior to or during the crash. The other protozoan species did not exhibit increases in densities that could have been associated with the decline at their respective depth (Figure 8 and 9).

Competition for substrate space has also been suggested as a mechanism in the decrease of hydra abundance (Miller, 1936). Competition with photosynthetic aufwucks can be severe but is not a likely cause of the declines. Below the compensation point the aufwuck densities decrease dramatically but no changes in hydra population dynamics are observed. Furthermore, the studies in Meander Creek Reservoir utilized microscope slides as substrate for the hydra. Since these slides were renewed at regular intervals the aufwucks did not colonize the substrate at rates where hydra would be adversely effected. Nevertheless, the hydra decline occurred on these slides as well, indicating competition for substrate space was not a factor.

Another hypothesis used to explain hydra population dynamics is the hydra becoming sexual (Reisa, 1973). Sexual reproduction in hydra occurs in response to unfavorable environmental conditions and is metabolically very costly for the hydra, often resulting in death. However, sexual hydra are very rare and are unlikely to cause the observed declines (Schroeder, unpublished; Batha, 1978;

Slobodkin and Bossert, 1991; Ribi et. al., 1985). In McKelvey Lake less than ten sexual hydra were observed prior to and during the decline making it very unlikely for sexuality to have any association with the decline.

Floating to avoid unfavorable environmental conditions has been suggested as a possible cause of the decline (Lomnicki and Slobodkin, 1966; Griffing, 1965; Batha, 1974). Hydra are able to become planktonic by secreting a gas bubble which is trapped in a mucus film at the bottom of the basal disk. Hydra could use this capability to vacate unfavorable conditions therefore causing a abrupt decrease in local populations. However, if the entire hydra population suddenly began floating in order to avoid unfavorable conditions, an increase in the number of planktonic hydra observed in the lake would be expected. This has not been recorded in previous studies of local populations, (Schroeder, unpublished; Reeder, 1979; Mataja, 1985) nor was this observed in the McKelvey population. Also, if floating is occurring, sudden increases in the colonization rate of freshly set artificial substrate (slides) in the lakes would be expected. This too has not been observed. Therefore, it is unlikely hydra populations are merely changing from sessile to planktonic organisms and are actually experiencing a decrease in densities.

Depression is another hypothesis used to explain the observed decreases in hydra populations (Reisa, 1973). This is defined as a reduced metabolic state induced in the hydra by environmental stress. This remains a possible explanation but evidence has not yet been produced in support of this suggestion. The physical

indicators of depression include: a severe reduction in the length of tenticals, reduced overall hydra length, and decreased feeding rates. While this condition was observed a number of times in the laboratory population, the McKelvey Lake hydra did not exhibit these morphological characteristics before or during the decline.

Starvation is considered as another possible cause of hydra declines (Bryden, 1952; Schroeder and Callaghan, 1982). The negative energy budget must be severe enough to cause the decimation of the hydra population within two to three weeks. However, hydra tolerate starvation by reduction in body size (Schroeder and Callaghan, 1982; Heckler and Slobodkin, 1965) and are able to survive 10-12 weeks without food at low temperatures (Griffing, 1965; Schroeder, unpublished). Obviously, this time period is not consistent with the observed declines which last no longer than 3 weeks. At high temperature (25 C), new buds survived only 5.4 days and adult hydra less than two weeks (Schroeder and Reeder, 1979; Griffing, 1965). High temperatures have been reported to play a decisive role in inducing starvation in hydra populations (Schroeder and Callaghan, 1982). The amount of food required by hydra for maintenance (unchanging body size and no bud growth) can be temperature dependent. The minimal food required for maintenance in a weight specific estimation was found to increase from 0.02 ug/ug to 0.10 ug/ug of zooplankton within a temperature range of 10 C to 25 C. Nevertheless, the daily maintenance cost of H. pseudoligactis was found to remain at 0.004 KJ/GA over the same temperature range despite the increasing weight specific costs. This is attributed to the overall decrease in

hydra size as temperature increases (Schroeder and Callaghan, 1981).

Furthermore, increasing temperatures have been attributed to cause decreases in assimilation and growth efficiencies (Schroeder and Callaghan, 1981). Schroeder and Callaghan (1981) found that over a 10 C to 25 C temperature range, hydra experience a 61% reduction in assimilation efficiency and a 51% reduction of gross growth efficiency. Therefore, as temperatures increase in the lake, hydra must increase ingestion rates to compensate for the decreased efficiencies. If zooplankton abundances decrease at the same time, the hydra could be driven into an energy deficit.

As lakes warm and stratify, zooplankton densities in temperate lakes tend to decrease (Wetzel, 1983). Also, hydra size decreases in the warmer water possibly reducing the size of prey the hydra could capture and digest thus reducing the size of the prey population available to the hydra (Schroeder and Callaghan, 1982). Both factors may contribute to the reduction of the size of the prey population available to the hydra. The results which would have supported the starvation hypothesis, would have been the occurrence of the zooplankton maximum a week prior to the hydra density maximum at each depth respectively, therefore driving the hydra into a food deficit. However, the densities of zooplankton did not decrease prior to the hydra declines in McKelvey Lake. The maximum densities of zooplankton at 2.0 and 4.5 meters occurred on the same dates the hydra were reaching their maximum densities (Figure 1 and 7). Furthermore, the zooplankton densities decreased in conjunction with the decreases in the hydra population. The

expected time lag between the two groups did not occur.

Schroeder and Callaghan (1982) calculated the minimum zooplankton density necessary for hydra to meet maintenance requirements to be approximately 100 zooplankters/liter at 20 C and 16-24 zooplankters/liter at 10 C over a twenty four hour period. This was estimated from ingestion rates at low food densities. Densities of zooplankton in the epilimnion of McKelvey, where the temperature exceeded 20 C (Figure 7 and 15), never reached 100 zooplankters/liter until August 5 when all hydra at that depth had previously disappeared. Despite the increased densities of zooplankton at the end of the study, the hydra did not reappear on the 2.0 meter slides. The peak and decline of hydra at that depth occurred in the absence of the minimum densities of zooplankton required by the hydra. In the hypolimnion, the temperature never exceeded 12 C and the minimum required densities of zooplankton were present (Figure 7 and 15), yet the hydra on the 7.0 meter slides disappeared (Figure 1).

Nevertheless, this can still be explained under the temperature induced starvation hypothesis. The hydra in the epilimnion could have been driven into a energy deficit by the climbing temperatures despite the increased food resource. Therefore, the decline occurred even with the increasing food availability. This would, however, apply only to the hydra in the epilimnion and not in the hypolimnion which remains much colder (<12 C) throughout the summer. Hydra declines in the hypolimnion have been attributed to the anoxic conditions experienced in eutrophic lakes such as McKelvey (Schroeder and Callaghan, 1982;

Welsh and Loomis, 1924). The recorded oxygen concentrations of McKelvey dropped below 1 mg/liter on June 24 (JD= 175) for both 4.5 and 7.0 meter samples and remained there for the duration of the study (Figure 10). Oxygen concentration levels below 3 mg/liter is considered harmful to aquatic life (Wetzel, 1983). These factors would cause an expectation for the hydra located in the metalimnion to persist longer into the summer than hydra in the other depths. This has been recorded in previous studies (Reeder, 1979; Schroeder, unpublished) and has been attributed to the lower temperatures found in the metalimnion than in the epilimnion, while also having greater oxygen saturation than the hypolimnion (Schroeder and Callaghan, 1982). However, in McKelvey Lake, the hydra in the metalimnion disappeared after the hydra in the epilimnion and before the hydra in the hypolimnion (Figure 1). This was likely caused by the oxygen concentrations in the metalimnion which decreased simultaneously with those recorded in the hypolimnion. The hydra in the hypolimnion persisted longer due only to the colder temperatures.

Hydra subjected to starvation would be expected to experience a decrease in overall size during the decline. Previous studies have recorded a decrease of up to 90% of body mass while remaining viable (Schroeder and Callaghan, 1982, Heckler and Slobodkin, 1965). The McKelvey hydra at 2.0 and 4.5 meters did experience a reduction in weight during but not prior to the decline, indicating starvation was possibly occurring (Figure 3).

Another indication that the McKelvey hydra were experiencing a food deficit was a reduction of their budding rates. Starved

hydra are expected to produce fewer buds than well fed hydra. Therefore, hydra should experience a decrease in the number of buds they contain during the decline if starvation is the cause. This has been recorded in previous studies conducted on hydra in Meander Creek Reservoir (Schroeder, unpublished) and in Lake Zurich (Ribi et. al., 1985). The hydra to bud ratio in McKelvey Lake (Figure 2) did peak on the same date as the hydra densities reached their maximum (Figure 1) for each depth respectively. Following the peak the number of growth axis per hydra significantly decreased (One Way ANOVA) on the same date the hydra densities decreased, providing a indication the hydra were experiencing starvation.

If hydra declines are caused by temperature induced starvation, enclosed hydra in the epilimnion fed supplemental amounts of zooplankton would be expected to survive longer into the summer than the free-living hydra, while enclosed hydra in the hypolimnion should perish in the same time frame as the free-living hydra due to the anoxic conditions found in the deeper waters. The enclosed hydra in the hypolimnion and metalimnion of McKelvey did exhibit the expected results and disappeared at approximately the same time the free-living hydra were declining (Figure 1 and 4). However, the enclosed hydra in the epilimnion did not survive as expected. Initially, on June 22, the enclosed hydra at 2.0 meters were surviving while the free-living hydra at the same depth had almost completely disappeared from the slides by June 24. In the following weeks, there were no hydra to be found in the enclosures. Even after the enclosures had been reset and the hydra fed twice what they had been previously, the enclosed hydra were unable to

survive.   The survival of the enclosed hydra in the laboratory aquariums while the enclosed hydra in McKelvey perished (Figure 4), suggests the cause of the decline is a condition found in McKelvey and not in the enclosures.   Therefore the enclosure data does not support the starvation hypothesis.

If starvation alone was the cause, then the enclosed hydra should have survived in the lake as they did in the laboratory.   If temperature induced starvation is the cause, then the critical temperature is between 23.5 C (The temperature at 2.0 meters at the time the hydra could no longer survive in the enclosures) and 21 C (Room temperature).   It is possible the enclosed hydra were not being fed enough. One factor which points to this as a possibility is the enclosed hydra in the laboratory had a very low bud to hydra ratio, an indication of starvation.   If the enclosed hydra in the aquariums were on the verge of starvation, the few degrees difference between the two could have been sufficient to cause an energy deficit.

REFERENCES

Batha, JV (1974): The Distribution and Ecology of the Genus Hydra in the Milwaukee Area of Lake Michigan. Ph.D. Thesis, The University of Michigan. 196 p.

Bisbee, JW (1973): Size determination in Hydra: The roles of growth and budding. J Embryol Exp Morph. 30, 1-19.

Bryden,RR (1952): Ecology of Pelmatohydra oligactis in Kirkpatrick's Lake, Tennessee. Ecol. Mono. 22, 45-68.

Carrick,LB (1956): A Study of Hydras in Lake Erie. Ph.D. Thesis, The Ohio State University. 318 p.

Cukor,BE; Mozley,SC (1981): Summer population fluctuations, feeding and growth of Hydra in an Arctic lake. Limnol. Oceanogr. 26, 697-708.

Griffing,TC (1965): Dynamics and Energetics of Populations of Brown Hydra. Ph.D. Thesis, The University of Michigan. 67 p.

Hecker,B; Slobodkin,LB (1976): Response of Hydra oligactis to temperature and feeding rate. In: Coelenterate Ecology and Behavior. Plenum, New York, 175-186.

Lind, Owen T. (1985): Handbook of common methods in Limnology. Kendal/Hunt Publishing Co. Dubuque, Iowa. 199pp.

Lomnicki,A; Slobodkin,LB (1966): Floating in Hydra littoralis. Ecol. 47, 881-889.

Loomis,WF (1954): Experimental factors controlling growth in hydra. J. Exp. Zool. 126, 223-234.

Mateja, G.B. (1984): Effects of Food Limitation on the Population Dynamics of Hydra. MA Thesis, Youngstown State University. 140 p.

Miller,DE (1936): A limnological study of Pelmatohydra with special reference to their quantitative seasonal distributioni. Trans. Am. Micros. Soc. 55, 123-193.

Moen,T (1951): Hydra in an Iowa lake. Proc. Iowa Acad. Sci. 58, 501-505.

Park,JD (1972): Growth and differentiation in Hydra II. The effect of temperature on budding in Hydra littoralis. J. Exp. Zool. 1979, 283-288.

Reeder,PS (1979): Population Dynamics of Hydras in Pine Lake. MA Thesis, Youngstown State University. 103 p.

Reynolds,BD; Looper,JB (1925): Infection experiments with *Hydramoeba* *hydroxena* nov. gen. J. Parasit. 15, 23-30.

Ribi,G; Tardent,R; Tardent,P; Scasighini,C (1985): Dynamics of hydra populations in Lake Zurich, Swizerland, and Lake Maggiore, Italy. Schweizerland Zeitschriftt Hydrologie 47, 45-56.

Riesa,JJ (1973): Ecology. In: Biology of Hydra. (Ed: Burnett,AL) Academic Press, Inc, New York, 466.

Schroeder,LA (1969): Population growth efficiencies of laboratory populations of *Hydra* *psuedoligactis* populations. Ecol. 50, 81-86.

Schroeder,LA; Callaghan,WM (1981): Thermal tolerance and acclimation of two species of hydra. Limnol. Oceanogr. 26, 690-696.

Schroeder,LA; Callaghan,WM (1982): Effects of temperature on the energy budgets of *Hydra* *psuedoligactis*. Oecol. 53, 238-244.

Schroeder,LA; Reeder,PS (1979): Effects of temperature and fasting on the rate of sinking of *Hydra* *psuedoligactis*. L i m n o l. Oceanogr. 24, 1092-1103.

Stiven,A (1976): The quantitative analysis of the *Hydra* *Hydramoeba* host-parasite system. In: Coelenterate Ecology and Behavior. (Ed: Mackie,GO) Plenum, New York, 389-400.

Stiven,AE (1965): The relationship between size, budding rate, and growth efficiency in three species of Hydra. Res. Pop. Ecol. 7, 1-15.

Welch,PS; Loomis,HA (1924): A limnological study of *Hydra* *oligactis* in Douglas Lake, Michigan. Am. Micros. Soc. 43, 203-235.

Wetzel, Robert G. (1983). Limnology. Saunders College Publishing. 767pp.

Wetzel, Robert G. and Gene E. Likens (1979). Limnological Analyses. W.B. Saunders Co. Philadelphia. 84 pp.

Yu,H (1976): Bioecological studies of freshwater Hydra and planaria. Ph.D. Thesis, University of California Riverside. 152 p.