AN ABSTRACT OF THE THESIS OF

Donald R. Patton for the Master of Science Degree

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Title: Seasonal Population Structures of Two Coexisting Diaptomus Species

Abstract approved: Carl W. Prophet

The Diaptomus siciloides and Diaptomus pallidus populations inhabiting a small Borrow Pit Lake on the Emporia State University campus were observed from March, 1979, through April, 1980. During the first two months of the study, the zooplankton community was recovering from a winter kill; and all copepods appearing in the samples were represented by naupliar stages only. Diaptomus siciloides was the first of the calanoid copepods to undergo development. One generation of Diaptomus siciloides developed during the study. Adult Diaptomus siciloides were first detected in the April, 1979, samples and reached a peak density of 14.3 individuals/liter in May, 1979. Development time for the generation was 55 days. Water temperature ranged from 17°C to 20°C during development. Adults of Diaptomus siciloides were either rare or absent in the samples during the rest of the study.

Three generations of Diaptomus pallidus developed during the study. Development of Diaptomus pallidus generations occurred later than the development of Diaptomus siciloides. The shortest development time observed for a Diaptomus pallidus generation was 46 days and occurred from mid-July to early September with water temperatures between 24°C and 30°C. Development of Diaptomus pallidus was slower at cooler water temperatures and appeared to cease during the winter.

The results of this study indicated that the optimal developmental

time for Diaptomus siciloides occurred during periods of the cool water temperatures experienced during early spring and late fall. Optimal developmental time for Diaptomus pallidus occurred during the warm water temperatures of the summer months.

SEASONAL POPULATION STRUCTURES OF TWO COEXISTING DIAPTOMUS SPECIES

A Thesis
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the Division of Biological Sciences
Emporia State University

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Carl W. Prophet
Approved for Major Department

Harold E. Durst
Approved for Graduate Council

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INTRODUCTION

The competitive exclusion principle recognizes that competition for an essential resource in limited supply may result in the elimination of one of the competing species, but that exclusion is often prevented because of the diversification of coexisting, closely related species. Pennak (1957) believed that the limited species diversity in the limnetic zooplankton community was caused by competition. He stated that it was unusual to find more than one species of the same genus in a limnetic community at the same time, and he considered cases of congeneric coexistence to be a rare event.

Although Pennak's conclusion cannot be entirely rejected, it now appears that congeneric coexistence, especially among members of the calanoid genus *Diaptomus*, is not an uncommon event. Cole (1961) documented 34 cases of coexisting *Diaptomus* species in North America; and in a study of 100 lakes in southern Ontario, Rigler and Langford (1967) found *Diaptomus* species coexisting in 42 % of the lakes studied. Some researchers attempted to explain congeneric coexistence by comparing various physicochemical conditions in lakes inhabited by congeneric species to conditions in lakes inhabited by only one of the species, but such studies were not successful.

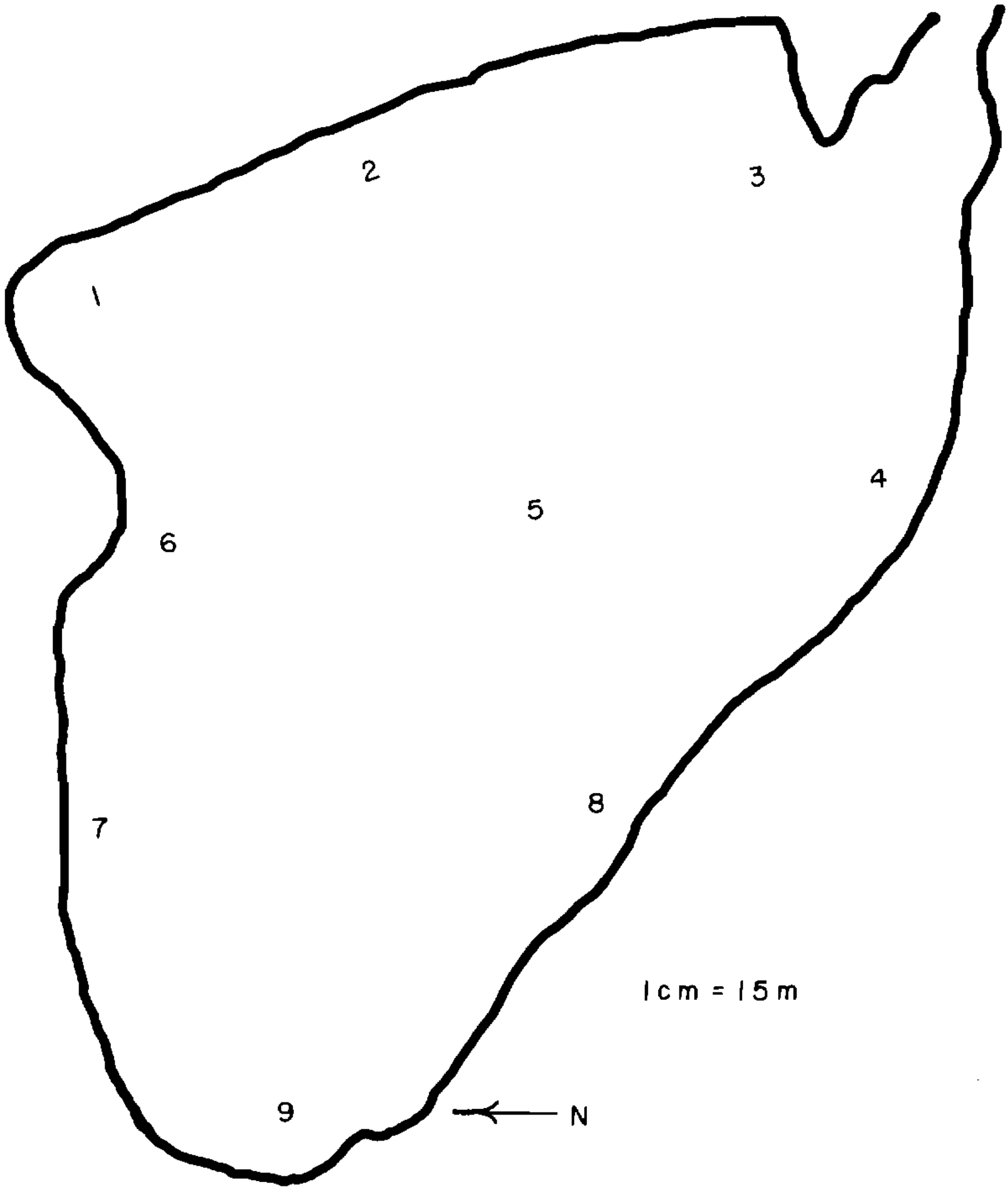
Fryer (1954) and Hutchinson (1951) stated that a size difference between coexisting congeneric species implied a difference in the size of food particles selected by each species, thereby reducing direct competition between the species. Vertical segregation, in which the coexisting species each occupy a different stratum within the water column, was hypothesized as another means of coexistence by Rigler and Langford (1967). Cole (1961) and Pennak (1957) suggested that seasonal separation of *Diaptomus* species, created by differences in their life cycles, would allow coexistence. Sandercock (1967) studied three species of *Diaptomus* coexisting in Clarke Lake, Ontario, and demonstrated evidence for the operation of all three of the above suggested mechanisms of coexistence in *Diaptomus*. Furthermore, Sandercock (1967) proposed that coexistence of the *Diaptomus* species in Clarke Lake was dependent upon the additive effects of two of the mechanisms working together to separate the coexisting species.

Two of the most widespread species of calanoid copepods in Kansas are *Diaptomus siciloides* Lilljeborg and *Diaptomus pallidus* Herrick (Siefken and Armitage, 1968; Prophet and Waite, 1974). Both species are common in lakes, ponds, and roadside ditches (Palavanchuk, 1975) and are known to coexist in several Kansas lakes. Yet, nothing is known of the strategies utilized by these two species to reduce competition to levels which favor coexistence. This study was undertaken to compare the variations in the population structure of *D. siciloides* and *D. pallidus* inhabiting a small Kansas lake and to obtain some preliminary insights into the ways in which they are partitioning their basic niche resources.

DESCRIPTION OF STUDY AREA

The lake selected for this study was located on the north edge of the Emporia State University campus and originated as a borrow pit area formed during construction of Interstate 35 during 1966 to 1967. Commonly known as the Borrow Pit Lake, it has a surface area of approximately 3.2 hectares, a relatively flat bottom, steep sides, and an average depth of 1.5 meters (Figure 1). The drainage area consists of approximately 16 hectares. Inflow is mainly storm water runoff from parking lots located on the north end of campus. Outflow of the lake is by an uncontrolled spillway located at the southeast end of the lake. During the summer months of this study, water was pumped from the lake to irrigate portions of the Emporia State University campus.

Figure 1. Outline of the Emporia State University Borrow Pit Lake showing the location of the nine sample sites.


1
2
3
4
5
6
7
8
9
1cm = 15m
N

METHODS AND MATERIALS

Tow net samples were taken at intervals of seven to ten days from 21 March 1979 to 23 April 1980 from nine separate locations scattered throughout the lake. Samples consisted of vertical tows using a 30 cm diameter tow net (64 microns mesh). The net was allowed to sink to the bottom and slowly retrieved to reduce back-wash. Each sample was preserved in a 5 % formalin solution.

In the laboratory, four samples of each sample set were selected randomly for examination. A sample was first made to a known volume, usually 100 ml, and after mixing three 1.0 ml subsamples were withdrawn with a Hensen-Stemple plankton pipette and placed in a Sedgewick-Rafter counting cell. With the aid of a binocular dissecting microscope, the numbers of males and females of each Diaptomus species in each subsample were recorded. Adult individuals were identified to species based on Wilson (1959) and Pennak (1953). Nauplii and copepodite stages also were counted, but were not identified as to species.

Population densities for adults of each species and each copepodite stage were estimated by using the formula:

$$\text{population/l} = \frac{\text{average of the 3 subsamples x 100 ml}}{\text{total liters in sample}}$$

Temperature and oxygen were measured at each sample station on each sampling date with the aid of a YSI Oxygen, Temperature Meter (Model 51B) and electrode. Also, water was collected with a Kemmerer water sampler for determining total alkalinity by standard titration with 0.02 N sulfuric acid.

RESULTS AND DISCUSSION

Physicochemical Characteristics of Borrow Pit Lake

Water temperature

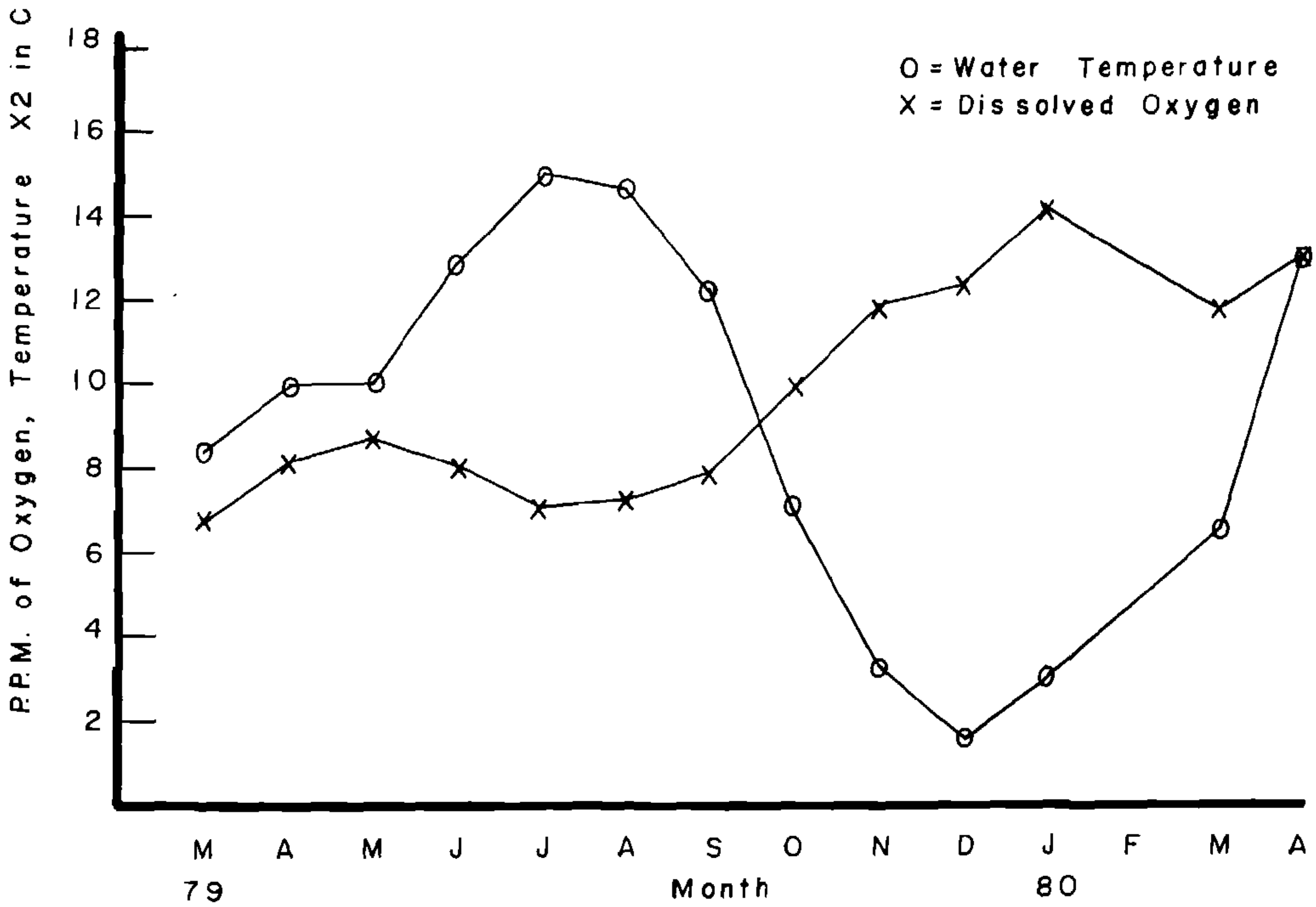
Water temperature within the lake during the study tended to be uniform from the surface to the bottom of the water column; at no time during the study did thermal stratification occur, and there were virtually no differences in water temperatures between the different sampling stations on any given sampling date. The uniform water temperatures throughout the lake probably were the result of the lake's exposed shoreline and shallow depth which allowed wind action to maintain circulation.

Water temperatures recorded during the study ranged from 3°C on 13 December 1979 to 30.5°C on 28 July 1979 (Figure 2). The average water temperature recorded during the spring months of March, April, and May was 18°C. During the summer months of June, July, and August water temperatures averaged 27.8°C. The average fall and winter temperatures recorded were 15.8°C and 4.3°C, respectively. An ice cover approximately 2 cm thick was observed on 13 December 1979, and persisted at various thicknesses until 25 January 1980.

Dissolved oxygen

The concentration of dissolved oxygen during the course of the study ranged from 6.8 ppm to 14 ppm (Figure 2). The lowest concentration of dissolved oxygen was recorded on 21 March 1979. In studies of two other Kansas lakes, Osborne (1968) and Gamache (1977) found dissolved oxygen concentrations of 10 ppm or greater during a comparable period. The low oxygen concentration recorded during March may have been due to a devastating winter kill experienced in the lake during the winter prior to the start of the study, which would have removed most of the oxygen

Figure 2. Average monthly water temperatures and dissolved oxygen concentration recorded during the study.


P.P.M. of Oxygen, Temperature X2 in C
18
16
14
12
10
8
6
4
2
O = Water Temperature
X = Dis solved Oxygen
M A M J J A S O N D J F M A
79
Month
80

from the lake.

Dissolved oxygen concentrations increased throughout the spring until a concentration of 8.8 ppm was recorded on 26 May 1979. The concentration of dissolved oxygen then decreased until September, 1979, and began to increase to the maximum observed concentration of 14 ppm on 25 January 1980.

Alkalinity

Total alkalinity ranged from 65 ppm to 125 ppm, with a mean of 102 ppm for the entire study. Both phenolphthalein alkalinity and methyl orange alkalinity were present at times during the study. Phenolphthalein alkalinity was detected during 10 of the 13 months of the study and averaged 15.2 ppm for the entire study. The highest monthly average obtained for phenolphthalein alkalinity was 35.7 ppm during June, 1979, (Figure 3). This value was higher than the maximum of 30 ppm reported for a Kansas pond by Griffith (1961) but less than 75 ppm phenolphthalein alkalinity reported for a Kansas farm pond by Tiemeier and Moorman (1957).

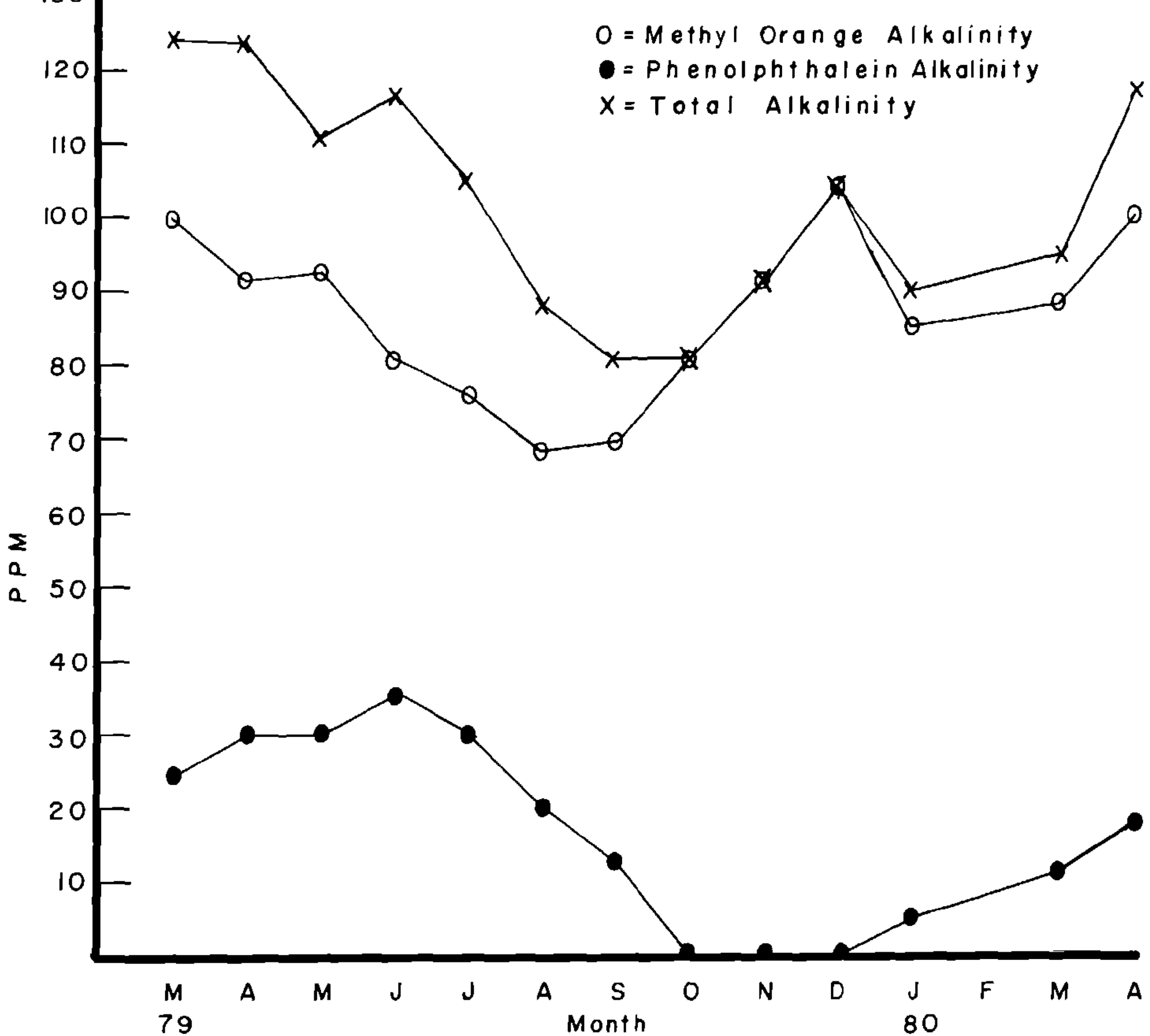
Methyl orange alkalinity was present at all times during the study. It varied from 67.2 ppm in August, 1979, to 104 ppm in December, 1979. The mean methyl orange alkalinity concentration for the entire study was 86.7 ppm.

Variations in the Zooplankton Community

Zooplankton Population Composition

When the study was initiated on 21 March 1979, the lake zooplankton was just beginning to recover from a devastating winter kill that had virtually wiped out the aquatic biota of the lake. During the first two months of the study the zooplankton population was reestablishing itself in the lake and consisted primarily of rotifers of the genera *Brachionus*, *Keratella*, and *Asplanchna*. Adult cladocerans and copepods were rare.

Figure 3. Average monthly alkalinity recorded during the study.


O = Methyl Orange Alkalinity
● = Phenolphthalein Alkalinity
X = Total Alkalinity
120
110
100
90
80
70
60
50
40
30
20
10
PPM
M
79
A
M
J
J
A
S
O
N
D
J
80
F
M
A
Month

As the study progressed, various species of zooplankters dominated the population at different times during the study until August, 1979, when an equilibrium seemed to be established with *Bosmina longirostris*, *Daphnia parvula*, and *Diaptomus pallidus* being the dominant species.

Variations in *Diaptomus* Standing Crops

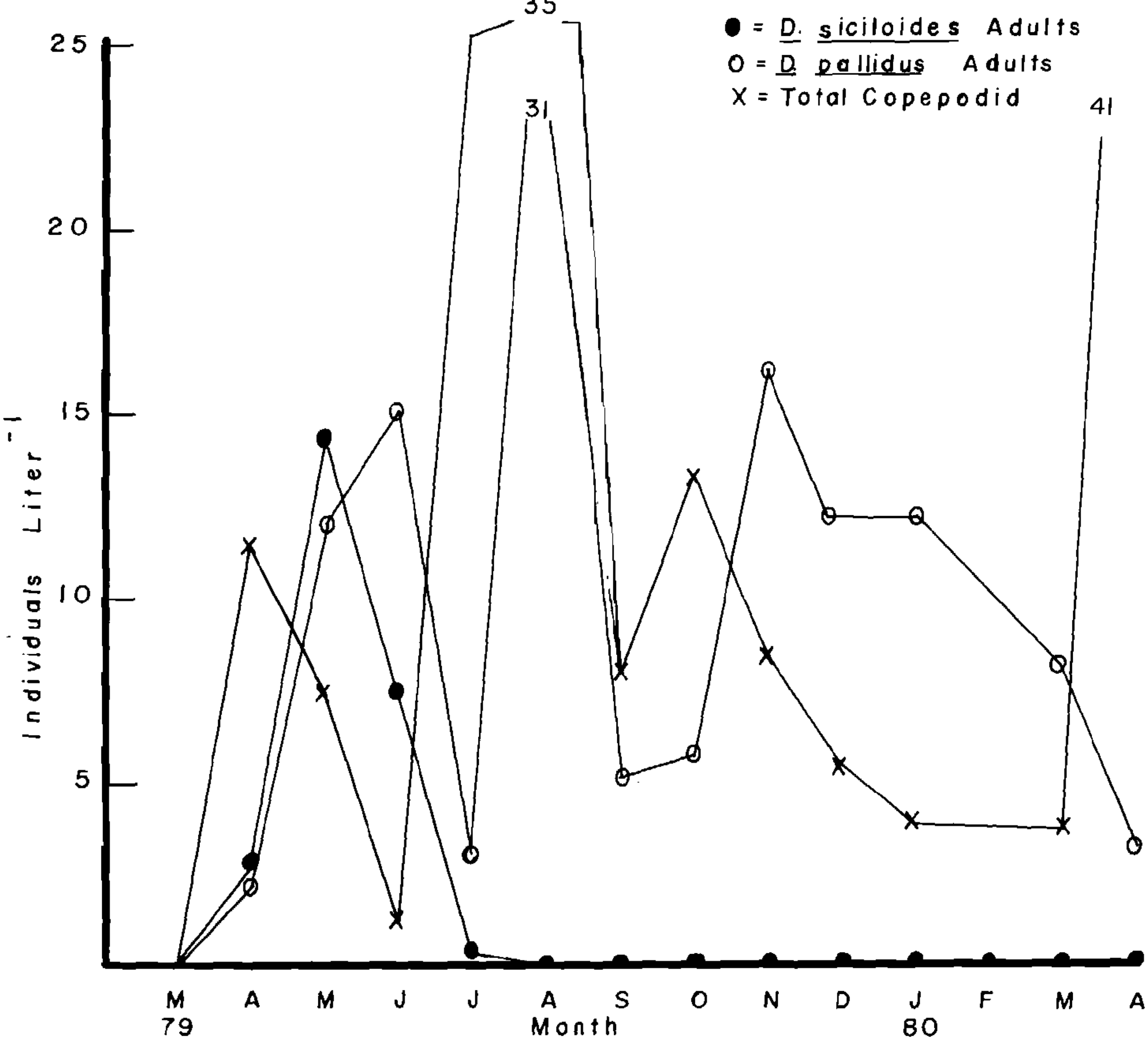
Copepodid stages

The *Diaptomus* population at the start of the study was represented by individuals in the naupliar stages of development; adults were absent. No distinction was made between nauplii of the different *Diaptomus* species and nauplii of the cyclopoid copepods. Samples taken in April showed that some of the *Diaptomus* nauplii present during March had matured to the copepodid stage of development. A majority of the immature copepods were copepodid stages CI, CII, and CIII (Wilson, 1959). The average density of copepodids in April was 11.5 individuals/liter. Density of the copepodid stages decreased to 1.2 individuals/liter in June. From June to August the standing crops of copepodid stages increased from 1.2 individuals/liter in June to a total of 35 individuals/liter in August. A decrease in the number of copepodid stages was again observed in September, followed by another increase in the density of copepodids in October. The density of the copepodid stages decreased after the October peak until March, 1980. Samples taken in April, 1980, showed an increase in abundance of copepodid stages. The standing crop of 41.1 individuals/liter recorded in April, 1980, was the highest density recorded for the copepodid stages during the study.

Adult *Diaptomus siciloides*

Adult *Diaptomus siciloides* specimens were first detected in the April, 1979, samples (Figure 4). A population density of 2.7 individuals/liter existed at this time. Abundance of *Diaptomus siciloides* adults

Figure 4. Monthly population densities of adult *Diaptomus siciloides*, adult *Diaptomus pallidus*, and all copepodid stages.



● = D. siciloides Adults
O = D. pallidus Adults
X = Total Copepodid
35
31
41
25
20
15
10
5
Individuals Liter⁻¹
M
A
M
J
J
A
S
O
N
D
J
F
M
A
79
Month
80

increased in May to 14.3 individuals/liter. This was the highest density of adults recorded for Diaptomus siciloides during this study. From May to July the adult Diaptomus siciloides population declined to such a level that Diaptomus siciloides adults were rarely found in samples collected during the remainder of this study.

Adult Diaptomus pallidus

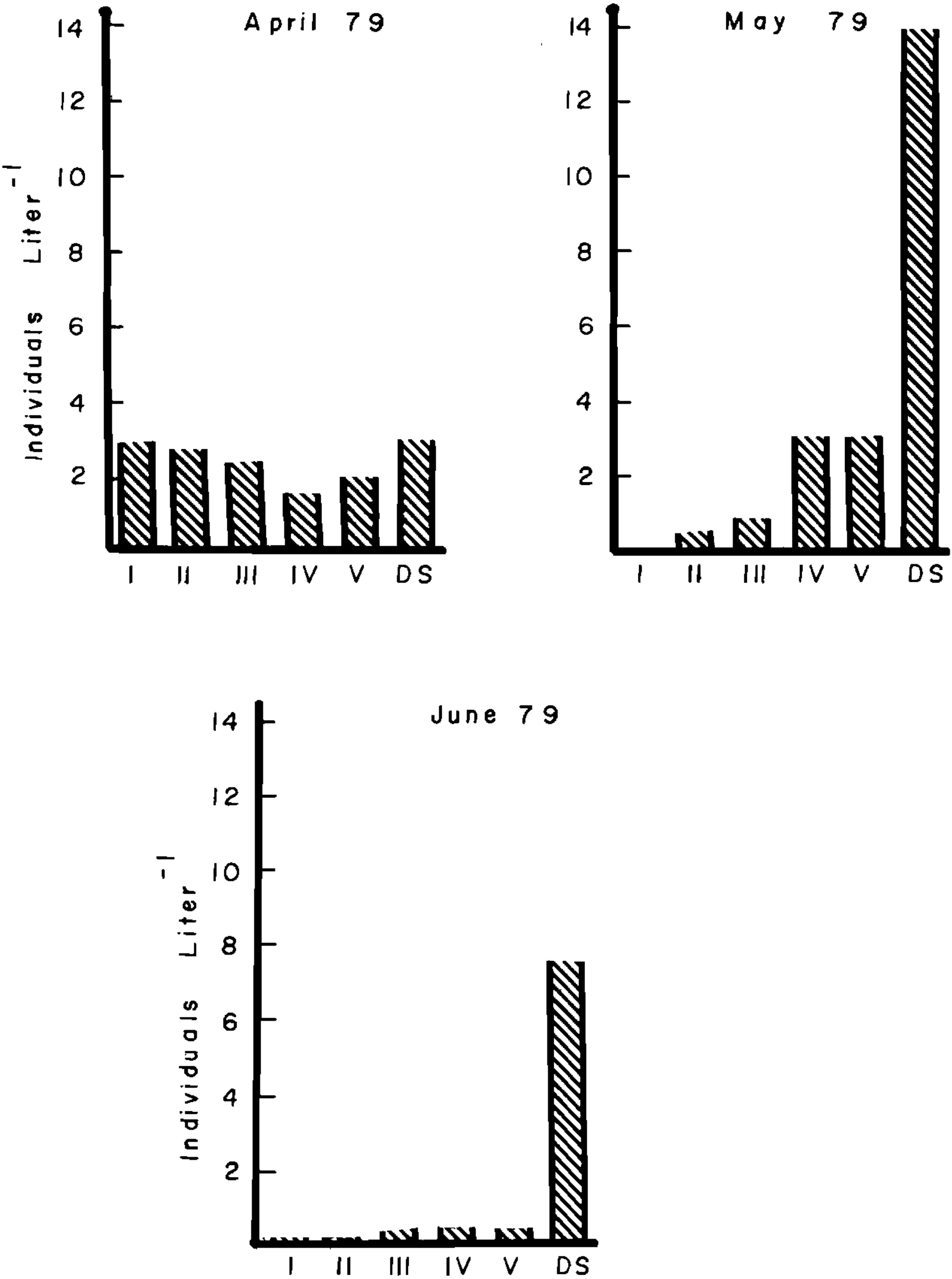
Adult Diaptomus pallidus were first observed during April, 1979; a density of 2.4 individuals/liter was estimated to exist at that time. The abundance of adult Diaptomus pallidus increased throughout May and June to a density of 15.1 individuals/liter. However, samples collected during July showed that the density of Diaptomus pallidus adults had decreased to 4.1 individuals/liter. The highest density of adult Diaptomus pallidus recorded during the study was 31.4 individuals/liter which occurred during August, 1979. After the August peak, the standing crop decreased to 5.2 individuals/liter by September and October and then increased to 16.1 individuals/liter in November, 1979. From November, the abundance of Diaptomus pallidus adults decreased throughout the remainder of the study. The estimated standing crop for this species during the last month of this study was 3.2 adults/liter (Figure 4).

Number of Generations of Each Diaptomus Species

Diaptomus siciloides

Only one distinct generation of Diaptomus siciloides was seen to develop during the study. Members of that generation were present only in naupliar stages in the first sample taken 21 March 1979. Samples taken in April, 1979, contained individuals of the various copepodid stages of development as well as the adult stage (Figure 5). Development continued through May, 1979, at which time most of the individuals had reached the

Figure 5. Population structure and density of _Diaptomus siciloides_ from April, 1979 through June, 1979. I through V represent the five copepodid stages. DS represents the adult stage.


April 79
May 79
June 79
Individuals Liter⁻¹
14
12
10
8
6
4
2
I
II
III
IV
V
DS

adult stage of development with only a few individuals remaining in the late copepodid stages (Figure 5). The total adult Diaptomus siciloides population density for May, 1979, was calculated to be 14.3 individuals/ liter, which was the highest population density recorded for Diaptomus siciloides during the study. Adult population density decreased in the June, 1979, samples; and few copepodid stages were found in the June samples (Figure 5). The decrease in the adult population density and the absence of copepodid stages indicated that development of the Diaptomus siciloides generation had been concluded. No other generations of Diaptomus siciloides were observed to develop during the study.

The developmental time for the generation of Diaptomus siciloides in this study was approximately 55 days. Topping (1971) reported a developmental time of 32 days for Diaptomus siciloides maintained under laboratory conditions. Possible explanations for the longer developmental time observed in this study may be due to the winter kill which occurred prior to the start of the study. The physicochemical conditions, such as a decrease in dissolved oxygen concentration created by the severe winter kill may have stressed the Diaptomus siciloides population to an extent that development was temporarily slowed or stopped. Siefken and Armitage (1968) suggested an optimal temperature range for Diaptomus siciloides of 4-11°C, a temperature range that indicates that Diaptomus siciloides was perhaps a early spring, late fall species. Water temperatures recorded at the beginning of this study were in excess of 11°C. The absence of the adult and copepodid stages of Diaptomus siciloides at the start of this study suggested that the Diaptomus siciloides population had been prevented from developing during the optimal period.

Diaptomus pallidus

Three generations of *Diaptomus pallidus* were observed to develop during the course of this study. The first generation occurred from March, 1979, through June, 1979. Both copepodid stages and adult *Diaptomus pallidus* were first observed in samples collected during April, 1979, when densities of 2.4 adult *Diaptomus pallidus*/liter and 11.4 copepodids/liter were estimated to exist. The majority of the copepodids were of the CI, CII, and CIII stages of development which indicated that development of the first generation was just beginning (Figure 6). Development continued through May, 1979, at which time most of the copepodids were in the late stages of development. The absence of first stage copepodids in the samples suggested that the first generation of *Diaptomus pallidus* was nearing completion. Standing crops of copepodid stages at that time was calculated to be 7.2 individuals/liter. The population density of adult *Diaptomus pallidus* was 12 individuals/liter (Figure 6). By June, 1979, development of the first *Diaptomus pallidus* generation was completed and the adult population density reached 15.1 individuals/liter. The approximate developmental time for the first generation was 80 days (Figure 6).

The second generation of *Diaptomus pallidus* was initially observed in the July, 1979, samples. Members of the second generation were represented by the increased numbers of first and second copepodid stages in the July samples (Figure 6). Total copepodid population density was 25.3 individuals/liter. During August, 1979, individuals were maturing through the copepodid stages, and copepodid density was 35 individuals/liter. A density of 31.5 individuals/liter was calculated for the adult *Diaptomus pallidus*. This was the highest population density recorded for adult *Diaptomus pallidus* during the study (Figure 7).

Figure 6. *Diaptomus pallidus* population structure and density from April, 1979 through July, 1979. I through V represent the five copepodid stages. DP represents the adult stage.

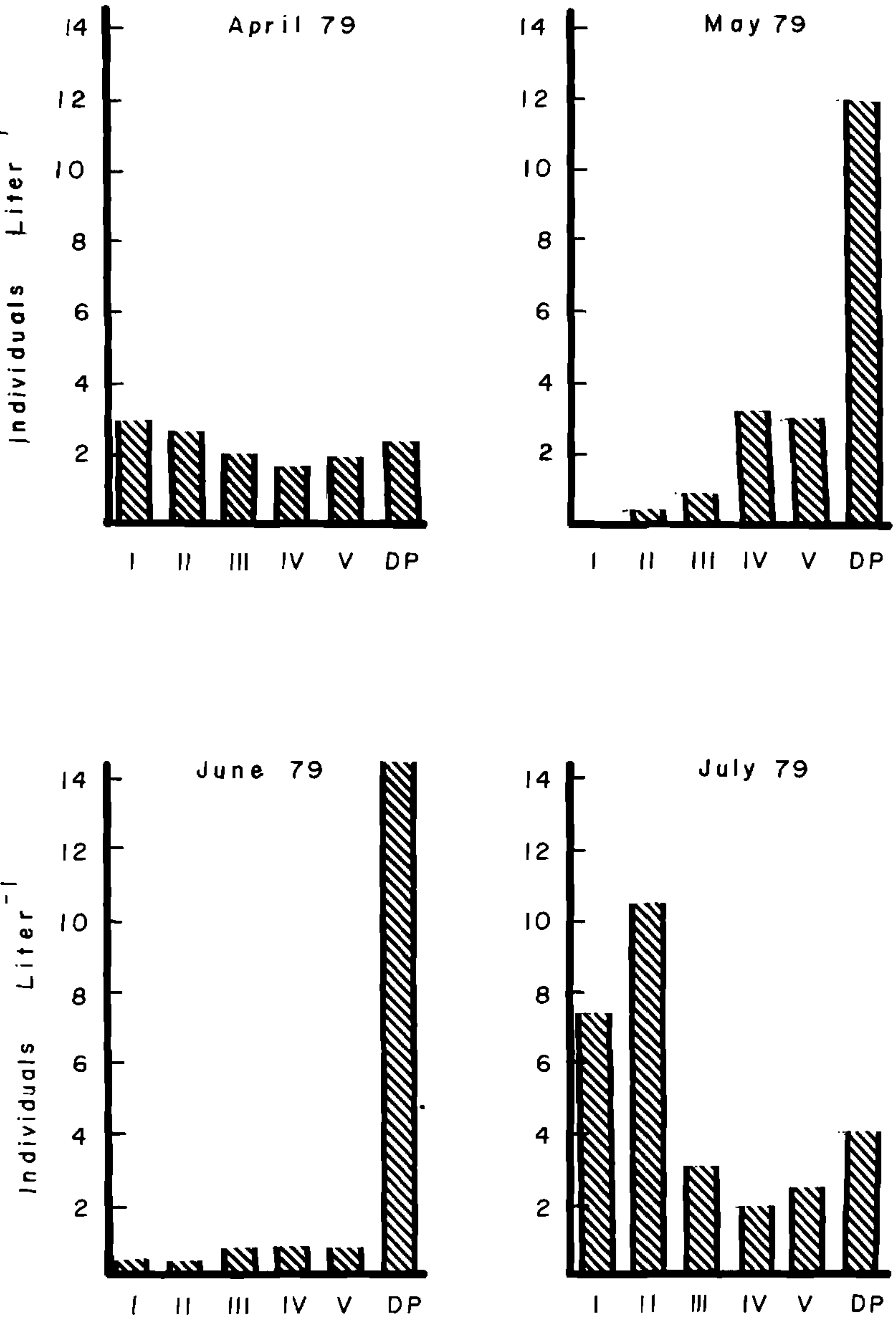
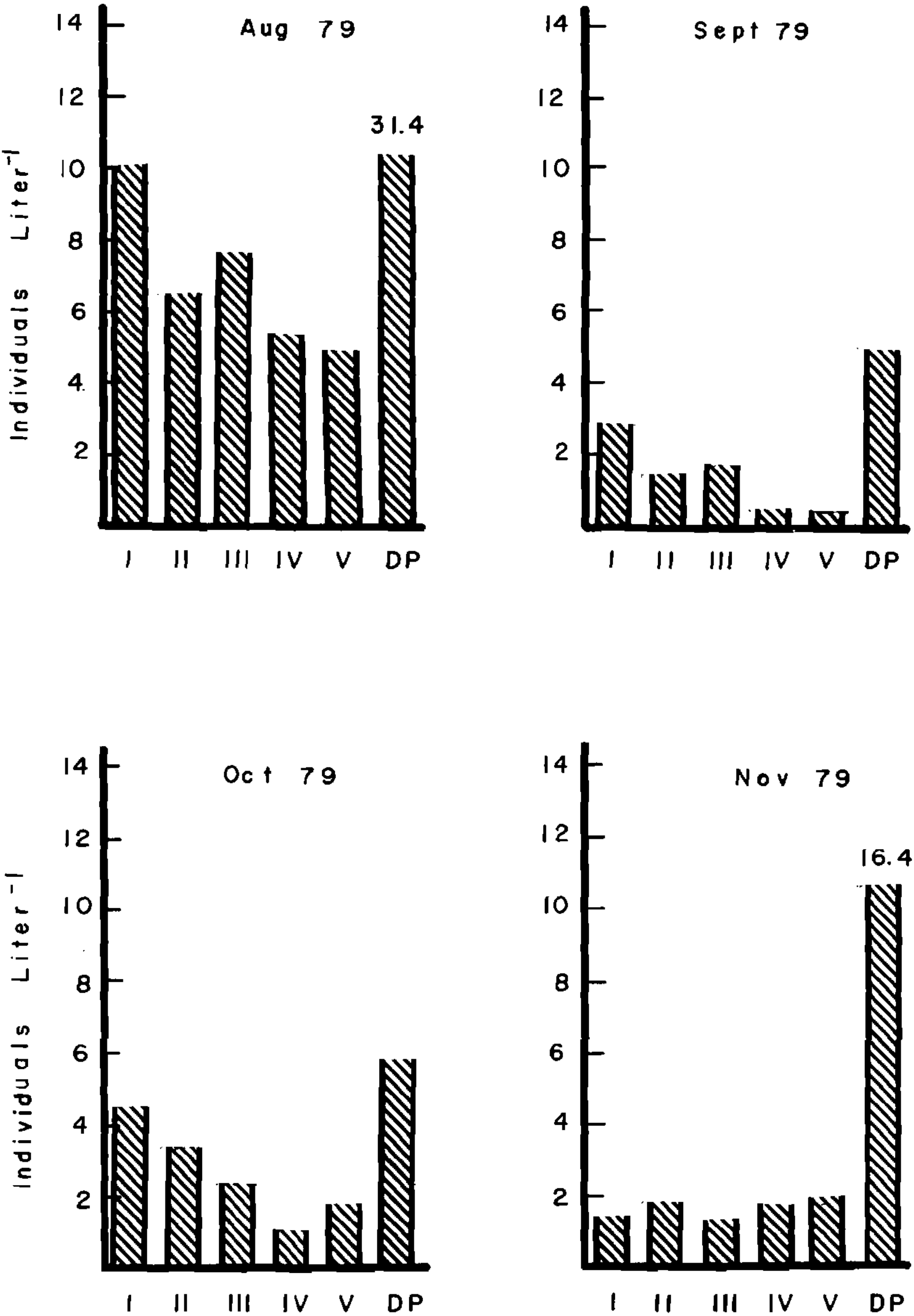

April 79
May 79
June 79
July 79
Individuals Liter -1
14
12
10
8
6
4
2
I
II
III
IV
V
DP

Figure 7. Population density and structure of *Diaptomus pallidus* recorded from August, 1979 through November, 1979. I through V represents the five copepodid stages. DP represents the adult stage.


Aug 79
Sept 79
Oct 79
Nov 79
Individuals Liter^{-1}
14
12
10
8
6
4
2
31.4
16.4
I
II
III
IV
V
DP

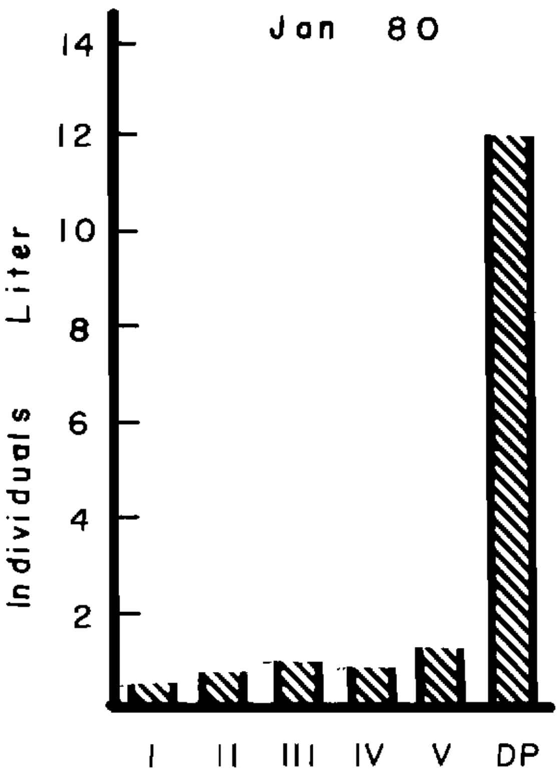
The second generation of Diaptomus pallidus completed development by September, 1979, and the third generation was represented by an increase in the abundance of the first copepodid stages appearing in the October samples (Figure 7). During October, 1979, the population density of the copepodid stages increased to 13.1 individuals/liter (Figure 7). Development of this third generation of Diaptomus pallidus was near completion by November, 1979, as evidenced by a shift of individuals from copepodid stages to the adult stage (Figure 7). Average adult population density recorded in November was 16.1 individuals/liter, while the average density for the copepodid stages was 3.8 individuals/ liter. Approximate development time for the third generation of Diaptomus pallidus was fifty days.

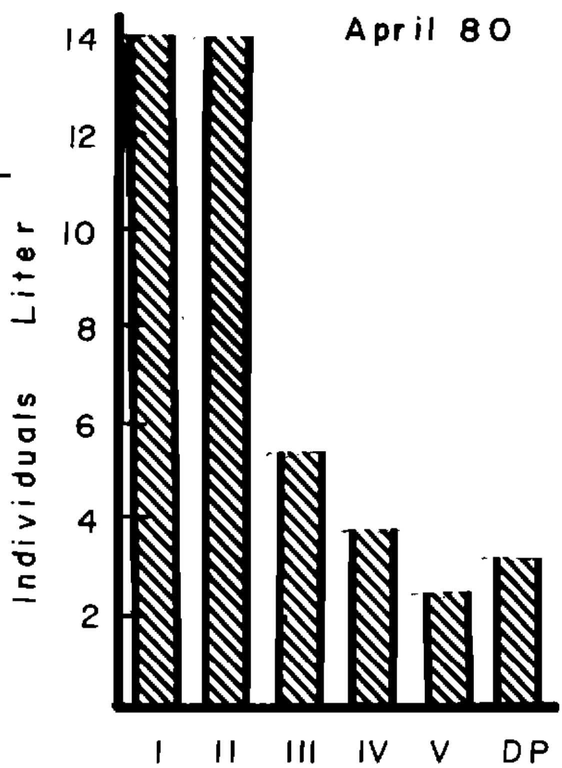
The structure of the Diaptomus pallidus population showed little change from November, 1979, to January, 1980 (Figure 8). The stability of the Diaptomus pallidus population exhibited during that period may have been due to a resting or dormant period in which development had slowed or ceased, or to an equilibrium reached by the Diaptomus pallidus population in which replacement of new individuals equaled the mortality rate.

Final samples collected in April, 1980, contained an average of 41.3 copepodids/liter (Figure 8). These individuals represented the beginning of the first generation of 1980 Diaptomus pallidus population.

The development time for the Diaptomus pallidus generations observed during this study was estimated to have been 80 days for the first generation, 46 days for the second and 50 days for the third generation. The developmental times observed during this study compared favorably with developmental times of 14.6 and 66.2 days reported for Diaptomus pallidus under controlled conditions by Geiling and

Figure 8. Population structure and density of *Diaptomus pallidus* in January, 1980 and April, 1980. I through V represent the five copepodid stages. DP represents adult *Diaptomus pallidus*.


Jan 80
Individuals Liter^{-1}
14
12
10
8
6
4
2
I
II
III
IV
V
DP


April 80
Individuals Liter^{-1}
14
12
10
8
6
4
2
I
II
III
IV
V
DP

Campbell (1972). Geiling and Campbell also found that faster development occurred at higher water temperatures. The shortest development time obtained during this study was 46 days and occurred from mid-July to late August when the highest water temperatures were recorded. Siefken and Armitage (1968) suggested an optimal temperature range of 16°C and 21°C, a temperature range that indicated Diaptomus pallidus was perhaps a summer species whose development was slowed or stopped during periods of cold water temperature.

Niche Partitioning Strategy

Environmental events prior to and during the early phases of this study inhibited the accumulation of sufficient data to describe the nature and scope of the mechanisms employed by Diaptomus siciloides and Diaptomus pallidus which allowed simultaneous coexistence. However, results of this study indicate the reproductive seasons of these two species are different, which, at the least, reduces the opportunity for competition between their developmental stages.

The virtual absence of Diaptomus siciloides in the Borrow Pit Lake after the 1979 spring was not characteristic of the seasonal occurrence of this species in Kansas. In other lakes in which Diaptomus siciloides and Diaptomus pallidus coexist, Diaptomus siciloides exhibits population peaks during the May-June and September-October periods while Diaptomus pallidus tends to peak during July-August. It is hypothesized that the winter kill occurring in the Borrow Pit Lake during January-March, 1979 delayed the development of the spring population of Diaptomus siciloides consequently, Diaptomus pallidus gained a competitive advantage and threatened to eliminate the Diaptomus siciloides population from the lake. It is impossible to predict at this time if the Diaptomus siciloides population will recover its original status in the Borrow Pit Lake.

SUMMARY

The Diaptomus siciloides and Diaptomus pallidus populations inhabiting a small Borrow Pit Lake on the Emporia State University campus were observed from March, 1979 through April, 1980. During the first two months of the study, the zooplankton community was recovering from a winter kill; and all copepods appearing in the samples were represented by naupliar stages only. Diaptomus siciloides was the first of the calanoid copepods to undergo development. One generation of Diaptomus siciloides developed during the study. Adult Diaptomus siciloides were first detected in the April, 1979, samples and reached a peak density of 14.3 individuals/liter in May, 1979. Development time for the generation was 55 days. Water temperature ranged from 17°C to 20°C during development. Adults of Diaptomus siciloides were either rare or absent in the samples during the rest of the study.

Three generations of Diaptomus pallidus developed during the study. Development of Diaptomus pallidus generations occurred later than the development of Diaptomus siciloides. The shortest development time observed for a Diaptomus pallidus generation was 46 days and occurred from mid-July to early September with water temperatures between 24°C and 30°C. Development of Diaptomus pallidus was slower at cooler water temperatures and appeared to cease during the winter.

The results of this study indicated that the optimal developmental time for Diaptomus siciloides occurred during periods of the cool water temperatures experienced during early spring and late fall. Optimal developmental time for Diaptomus pallidus occurred during the warm water temperatures of the summer months.

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