

AN ABSTRACT OF THE THESIS OF

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Title: Calanoid recovery in Lake Reading eight years
after termination of threadfin shad stocking

Abstract approved: Carl W. Probst

The Kansas Department of Wildlife and Parks stocked threadfin shad (Dorosoma petenense) in Lake Reading, Kansas, each spring from 1980 through 1983. Introductions of this planktivore altered the calanoid population structure by reducing the length of the calanoid season and reducing the standing crops of D. siciloides and D. pallidus. These changes resulted in D. pallidus replacing D. siciloides as the dominant calanoid species in this lake.

The primary objective of this study was to determine if the D. siciloides population had recovered as the dominant calanoid. Nested ANOVAs and t-tests indicate that the D. pallidus population had recovered to pre-shad levels and that the D. siciloides population had not recovered to pre-shad levels. Calanoid mean standing crops show that D. pallidus outnumbered D. siciloides overall during 1991-1992 sampling dates 15 to 1. Approximately 95% of adult calanoids identified in 1991 and 89% in 1992 were D. pallidus. Eight years after termination of the KDWP threadfin shad stocking project the length of the calanoid season was again similar to pre-shad levels. The D. siciloides population failed to recover as the dominant

calanoid. Introductions of many new species of fish, higher fish densities, and the presence of another planktivore (gizzard shad, Dorosoma cepedianum) may have suppressed the D. siciloides population.

CALANOID RECOVERY IN LAKE READING EIGHT YEARS
AFTER TERMINATION OF THREADFIN SHAD STOCKING

A Thesis

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the Division of Biological Sciences

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INTRODUCTION

Threadfin shad (*Dorosoma petenense*) were stocked in Lake Reading, Kansas, (Lyon County State Fishing Lake) by fisheries biologists of the Kansas Fish and Game Commission, now the Kansas Department of Wildlife and Parks (KDWP), each spring from 1980 to 1983. The purpose of stocking this planktivorous fish in Lake Reading was to evaluate the use of threadfin shad as added forage for game fishes. Although this stocking program interrupted a study of coexistence strategies of *Diaptomus siciloides* and *Diaptomus pallidus* which was in progress, it presented an opportunity to monitor the response of these two calanoid species to the presence of a new predator (Prophet 1982). It was subsequently determined that the stocking of threadfin shad altered the calanoid population structures and standing crops (Prophet 1985). Threadfin shad do not survive winter conditions in Kansas lakes, and a preliminary comparison of the calanoid populations during 1984 and 1985 failed to reveal evidence that they were recovering to pre-threadfin shad population levels (Prophet 1988).

The persistence of impacts of planktivorous fish on zooplankton and phytoplankton communities is a rarely studied facet of what is otherwise an increasingly well-documented set of trophic interactions between fish and plankton (Drenner and DeNoyelles 1982; Threlkeld and Drenner 1987). That is, if the addition of fish has an effect on a

planktonic community, it is assumed that the removal of the fish will reverse the effect, even though the earlier planktivory may have strong persistent effects on future plankton community structure (Kohler and Ney 1981). Planktivorous fish can exert a significant impact on standing crops and species composition of zooplankton communities (Brooks and Dodson 1965; Threlkeld 1988). Threlkeld and Drenner (1987) demonstrated in the laboratory that gizzard shad (Dorosoma cepedianum), introduced into tanks that formerly lacked their presence, reduced the number of crustacean zooplankton in all of their experiments. Analysis of data on microcrustacean zooplankton in two Arizona lakes provided field evidence that large populations of threadfin shad are capable not only of causing declines in zooplankton abundance, but also of virtually eliminating zooplankton communities for extended periods as long as two years (Ziebell et al. 1986).

From 1963 to 1979 at least 70% of the limnetic microcrustacean fauna of Lake Reading was copepods, with calanoids outnumbering cyclopoids (Prophet 1982). Cladocerans made up the remainder of the microcrustacean zooplankton. A rather sudden disappearance of all large species of zooplankton during the late summers of 1980 and 1981 was the first indication that the zooplankton community structure of this lake was being affected by the presence of threadfin shad (Bruner 1984; Prophet 1985). Previous

studies have documented that selection for larger bodied zooplankters by introduced planktivores causes a shift in zooplankton community structure to smaller bodied zooplankters (Brooks and Dodson 1965; Ziebell et al. 1986; DeVries and Stein 1990).

When relative abundances of D. siciloides and D. pallidus in Lake Reading were compared for periods before, during, and immediately after the threadfin shad stocking program, it was obvious that the calanoid populations had undergone marked changes (Prophet 1985). Total standing crops for calanoids were greater before than during the threadfin shad stocking project (Prophet 1985). Prior to 1980, D. siciloides outnumbered D. pallidus throughout most of a season, and it was the dominant calanoid in Lake Reading (Prophet 1982). During the shad stocking project D. pallidus became the more abundant of these two calanoid species, and during the two years following termination of the shad stocking project D. pallidus remained the dominant calanoid, in that total standing crops increased for D. pallidus but not for D. siciloides (Prophet and Perry 1984; Prophet 1988).

Assuming that the reduction in abundance of large bodied zooplankton and the shift in dominance from D. siciloides to D. pallidus was caused by added predation pressure from threadfin shad, it was hypothesized that these relationships would eventually revert to their former status

in the absence of threadfin shad. The primary objective of my research was to test this hypothesis by analyzing the structure of the zooplankton community eight years after threadfin were eliminated from Lake Reading, and by comparing the current standing crops of calanoids to standing crops prior to and during the period threadfin shad were being stocked.

Description of Study Area

Lake Reading (Lyon County State Fishing Lake) is a 55 ha lake located 19 km northeast of Emporia, Kansas. The lake drains 583 ha of grassland composed primarily of little bluestem (Andropogon scoparius), big bluestem (Andropogon geradi), indian grass (Sorghastrum nutans), switch grass (Panicum virgatum), and side-oats grama (Bouteloua curtipendula). It was constructed for the Kansas Forestry, Fish and Game Commission (now Kansas Department of Wildlife and Parks) in 1934 by the Civilian Conservation Corps and first reached spillway elevation in 1937 (Prophet 1970). At spillway level the lake had an original maximum depth of 13 m. Sedimentation has since reduced the maximum depth to approximately 11 m and the volume to $2.33 \times 10^6 \text{ m}^3$ with a mean depth of 4.2 m (Prophet 1988).

Lake Reading is holomictic with wind-driven circulation mixing the entire lake for much of the year. From early June to late September the lake is thermally stratified, with the thermocline between 4 and 6 meters. Compared to other Kansas lakes Lake Reading is relatively clear with Secchi disc visibility of 1.5 to 2.5 meters, indicating that the depth of the euphotic zone generally exceeds four meters. During the period of thermal stratification, the hypolimnion becomes anoxic (Bruner 1984).

MATERIALS AND METHODS

A total of 256 separate vertical plankton tows was collected from Lake Reading during 16 sampling days from 6 September to 14 December 1991 and from 25 April to 1 August 1992. Zooplankton samples were collected and processed by the methods described by Prophet (1988) to estimate the standing crops of D. pallidus and D. siciloides in Lake Reading. Vertical tows were made from a depth of 5.0 m to the surface using a 30 cm diameter, 64 μ mesh plankton net. Assuming that 100% straining occurred, 350 l of water were strained by each tow. Each sample set consisted of paired vertical tows collected from eight locations within the lake where water depth was 5.0 m or greater. Conditions permitting, sample sets were collected at two week intervals.

Zooplankters were preserved in the field using 20% Bioperm biological preservative. In the laboratory, four paired tows from each sample set were randomly selected for examination. Each tow was analyzed by first making its volume to 100 ml (50 ml when zooplankton was scarce), mixing, and then transferring 1 ml of the sample to a Ward's plankton counting wheel for examination at 40X, using a Stereozoom binocular microscope. Numbers of adults of each species of calanoid, calanoid nauplii, and calanoid copepodids in the subsample were recorded. Three subsamples from each tow were processed (Prophet 1988).

Depending upon their abundance, the first 10 to 20 copepod adults counted in each subsample were transferred to slides and examined at 440X for identification as either cyclopoid or calanoid, and calanoid adults to either D. pallidus or D. siciloides based on Fresh-water Invertebrates of the United States, 2nd Edition, Pennak (1978). The same method was used to identify copepod nauplii as either calanoid or cyclopoid. The proportion of each species identified at 440X was considered equal to the percentage of each species from each subsample in which it was taken.

For each tow examined, the number of individuals of a species in each subsample was multiplied by the volume (ml) of the composite sample and then divided by the volume (l) of lake water strained by the tow to yield the number of individuals per liter.

After counting, all organisms from each vertical tow were placed in crucibles, dried, and ashed at 500° C for one hour. The D. siciloides and D. pallidus data were analyzed using four-tiered nested analysis of variance (ANOVA) in order to test multisample hypotheses (Zar 1984). Nested ANOVA was used to compare mean annual standing crops between all of the sampling years of 1978, 1979, 1980, 1981, 1984, 1985, 1991, and 1992. Variation was tested, using the statistical package Biostat2, between years, sampling dates, sampling sites, and between tows of each of the paired tows, for D. siciloides and D. pallidus. T-tests were used to

compare calanoid mean annual standing crops during (1980, 1981) and after (1991, 1992) threadfin shad stocking, and to compare before (1978, 1979) and after (1991, 1992) threadfin shad stocking. Zooplankter mean annual standing crop trends were analyzed using mean annual standing crop densities plotted against time.

Water temperatures, dissolved oxygen, specific conductance, and pH were measured at 1.0 m intervals from surface to bottom in the deepest portion of the lake on each sampling date by using a Hydrolab Surveyor II water quality analyzer.

RESULTS

Physicochemical Characteristics of Lake Reading During 1991-1992 Sampling Dates

Selected physicochemical conditions measured on sampling days during 1991 and 1992 are summarized in Tables 1 and 2. Secchi disk visibility during sampling dates varied from 0.6 m on 18 July 1992 to 3.9 m on 23 May 1992 and averaged 1.6 m. Temperature at a depth of 1.0 m varied from 4.1 to 28.6° C, and pH was 7.9 to 8.7. Dissolved oxygen at 1.0 m ranged from 6.2 to 11.2 ppm and specific conductance was 280 to 295 $\mu\text{mhos cm}^{-1}$. From the initial date of sampling in 1991 thermal stratification persisted until 20 September 1991. Thermal stratification re-established 21 May 1992 and was present through the end of this study on 1 August 1992. During stratification the hypolimnion was anoxic, pH was lower (7.3 to 7.6), and specific conductance was higher (355 to 419 $\mu\text{mhos cm}^{-1}$) in the hypolimnion than in the epilimnion.

Species Composition of Zooplankton in Lake Reading During 1991-1992 Sampling Dates

Ten species of Cladocera and eight species of Copepoda were identified in samples during this study (Table 3). Any

Table 1. Physicochemical conditions at selected depths in Lake Reading on 1991 sampling dates.

Date	Depth	Water Temp.	Diss. O ₂	Sp. Cond.	pH
	m	°C	ppm	μmhos cm ⁻¹	
9/6/91	1	25.5	6.2	287	7.9
	4	25.0	4.9	287	7.9
	8	19.6	0.0	355	7.6
9/12/91	1	26.7	6.7	280	7.7
	4	26.5	6.3	280	7.6
	8	19.6	0.0	355	7.6
9/20/91	1	20.9	6.0	288	7.5
	4	20.9	5.9	291	7.6
	8	20.8	5.2	290	7.7
9/27/91	1	17.5	7.9	300	8.2
	4	17.4	7.4	299	8.2
	8	17.2	6.9	299	8.2
10/4/91	1	18.9	7.6	296	7.8
	4	18.9	7.3	298	8.1
	8	18.3	5.5	298	8.0
10/18/91	1	15.7	7.8	310	7.9
	4	15.7	7.6	310	8.0
	8	15.6	6.9	311	8.1
11/9/91	1	4.2	11.0	331	7.9
	4	4.2	10.3	326	8.1
	8	4.1	10.2	323	8.2
12/14/91	1	4.1	11.2	328	8.0
	4	4.1	10.5	326	8.1
	8	4.0	10.3	322	8.3

Table 2. Physicochemical conditions at selected depths in Lake Reading on 1992 sampling dates.

Date	Depth	Water Temp.	Diss. O ₂	Sp. Cond.	pH
	m	°C	ppm	μmhos cm ⁻¹	
4/25/92	1	14.5	9.9	360	7.9
	4	14.4	9.9	360	7.9
	8	12.6	8.7	365	7.6
5/9/92	1	18.5	9.2	395	7.9
	4	18.4	8.9	392	8.0
	8	17.5	6.2	398	7.8
5/21/92	1	22.5	8.6	379	7.9
	4	22.4	8.4	378	8.0
	8	16.6	0.9	404	7.4
6/6/92	1	20.1	10.4	366	8.1
	4	18.3	8.4	370	8.2
	8	17.4	0.6	376	7.7
6/19/92	1	24.5	9.2	334	8.7
	4	22.5	4.6	344	7.9
	8	17.3	0.0	378	7.3
7/4/92	1	26.5	8.1	329	8.5
	4	24.7	3.5	336	8.1
	8	17.1	0.0	376	7.3
7/18/92	1	28.2	8.2	315	8.6
	4	26.4	5.6	315	8.1
	8	17.9	0.0	375	7.4
8/1/92	1	25.5	7.3	316	8.2
	4	25.4	7.2	316	8.3
	8	18.2	0.0	373	7.5

given plankton sample usually contained a total of six species of microcrustacea, of which three species were cladocerans and three species were copepods. Three species were found in samples year-round during this study:

Diaphanosoma brachyurum, Diaptomus pallidus, and Mesocyclops edax. Bosmina longirostris, Daphnia ambigua, D. galeata mendotae, Pleuroxus hamulatus, Alona sp., Diaptomus siciloides, and Diacyclops bicuspidatus thomasi were present in samples collected during the spring only. Leptodora kindti, Daphnia parvula, Ceriodaphnia lacustris, Chydorus sphaericus, Acanthocyclops vernalis, Mesocyclops leuckarti, Ergasilus chatauquaensis, and Eucyclops agilis were observed only in summer samples.

Organic Biomass Content of 1991-1992

Tow Net Samples From Lake Reading

Although the organic biomass values presented in Figures 1 and 2 actually represent total organic matter in the tow net samples, they are used to indicate the biomass of zooplankton because the amounts of phytoplankton and non-zooplankton particles contained in the samples were negligible. During the 1991-1992 sampling dates the organic zooplankton biomass varied from 1.1 to 8.1 milligrams liter⁻¹ and averaged 3.4 milligrams liter⁻¹. Organic biomass

Figure 1. Lake Reading standing crop biomass for 1991
sample dates.

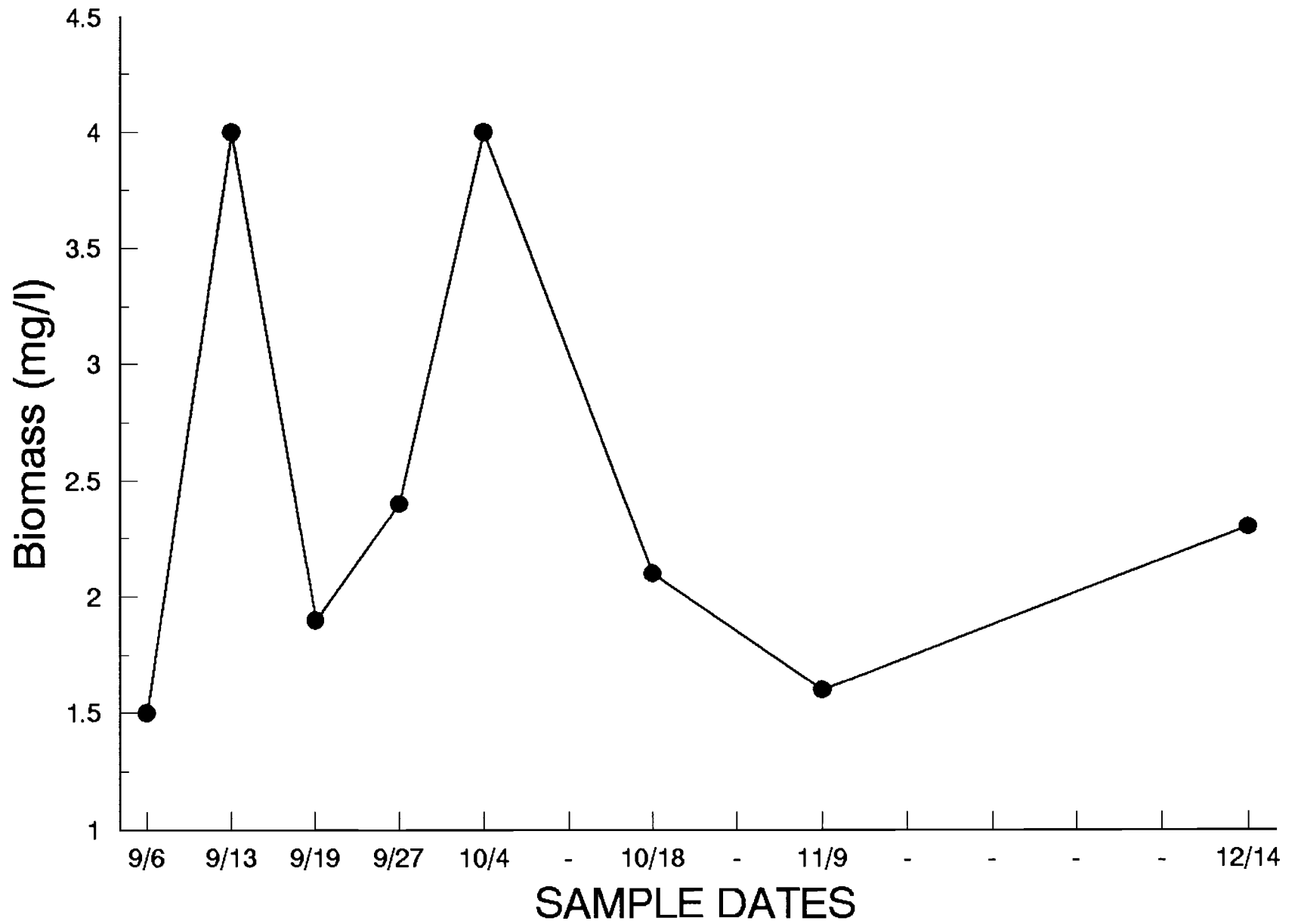
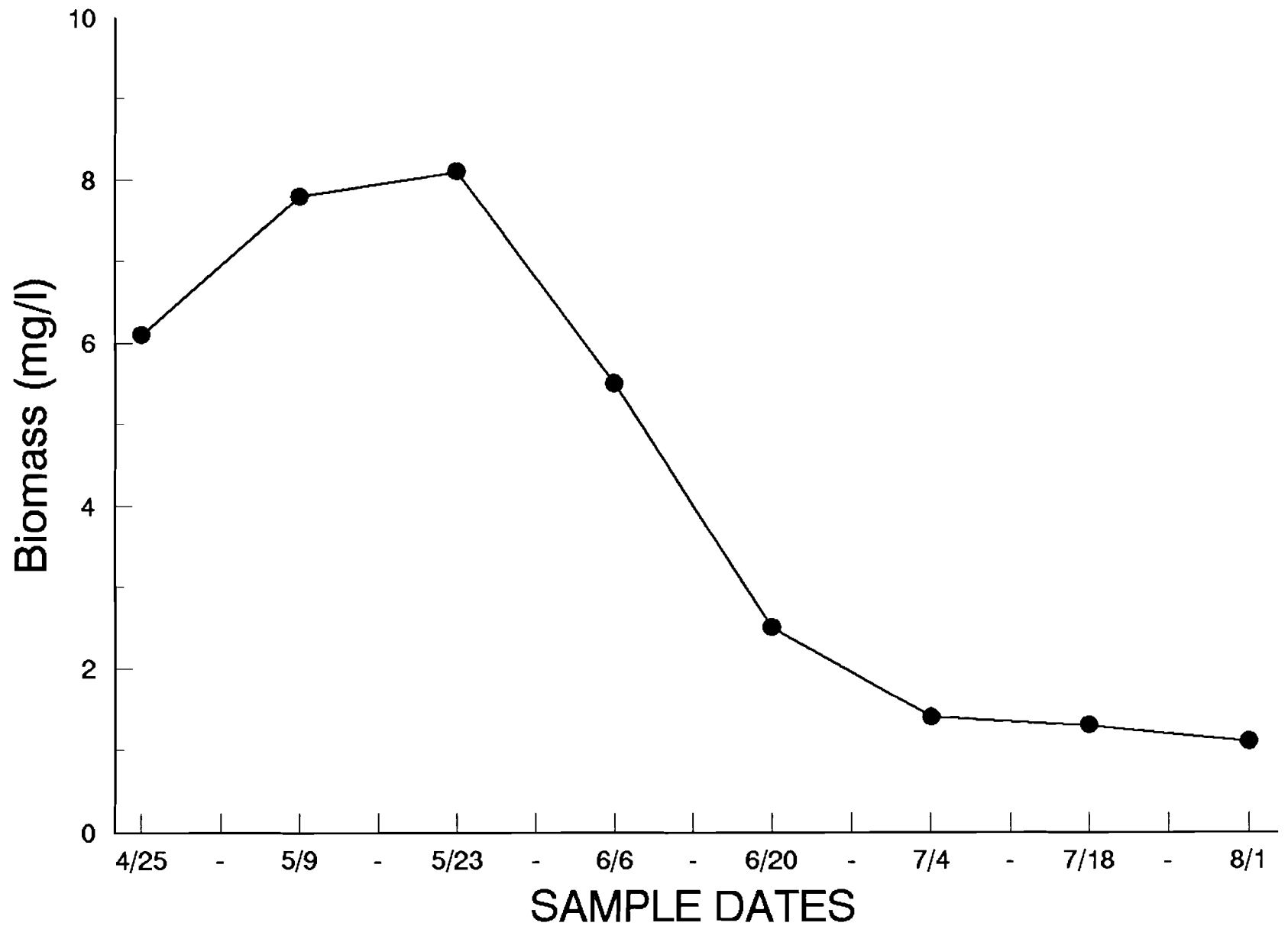


Figure 2. Lake Reading standing crop biomass for 1992
sample dates.

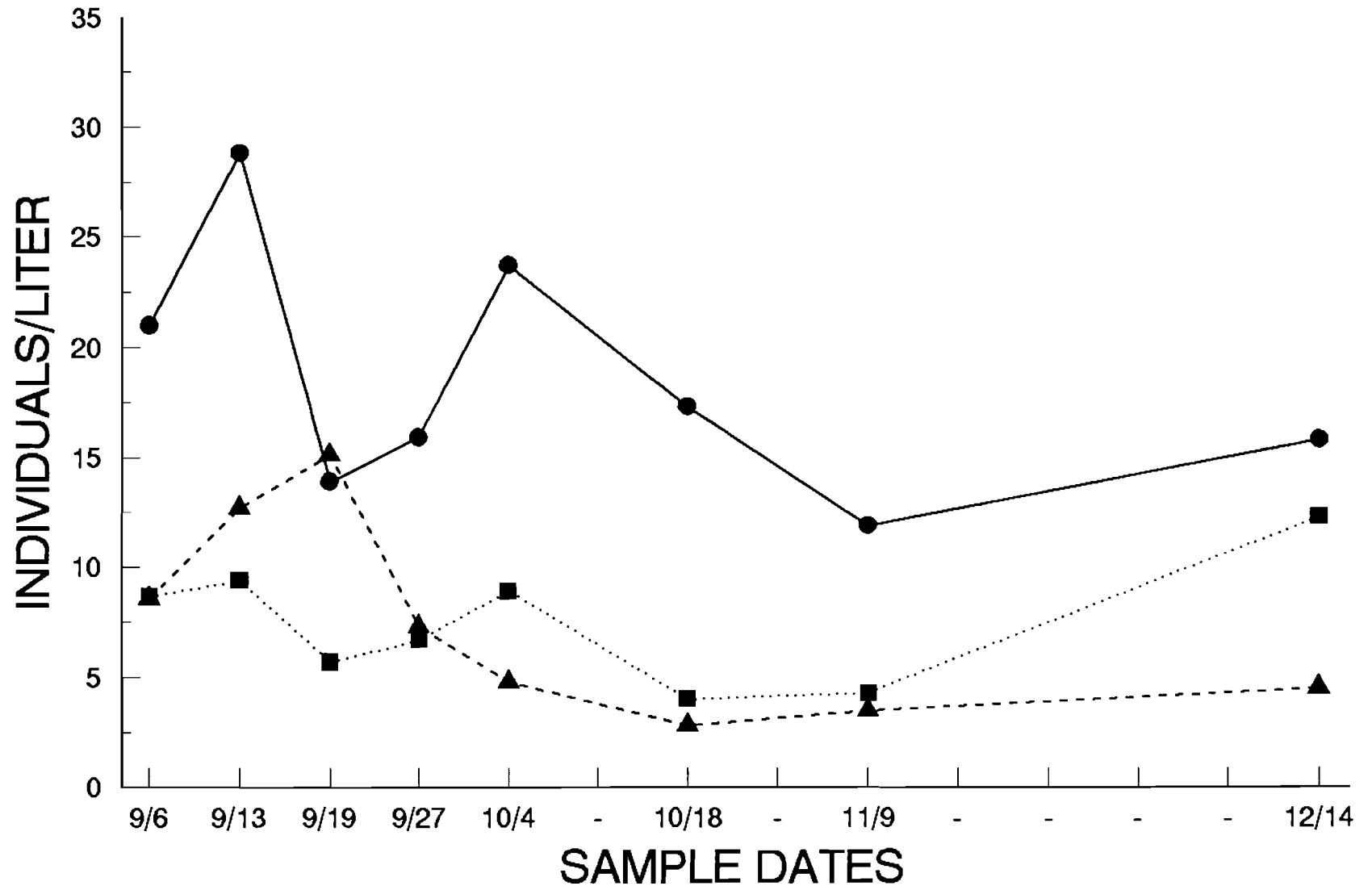


increased as total zooplankton densities increased during April and May. Organic biomass peaked in late May as did total zooplankton densities.

**Seasonal Variation in the Zooplankton Community
Structure of Lake Reading During
1991-1992 Sampling Dates**

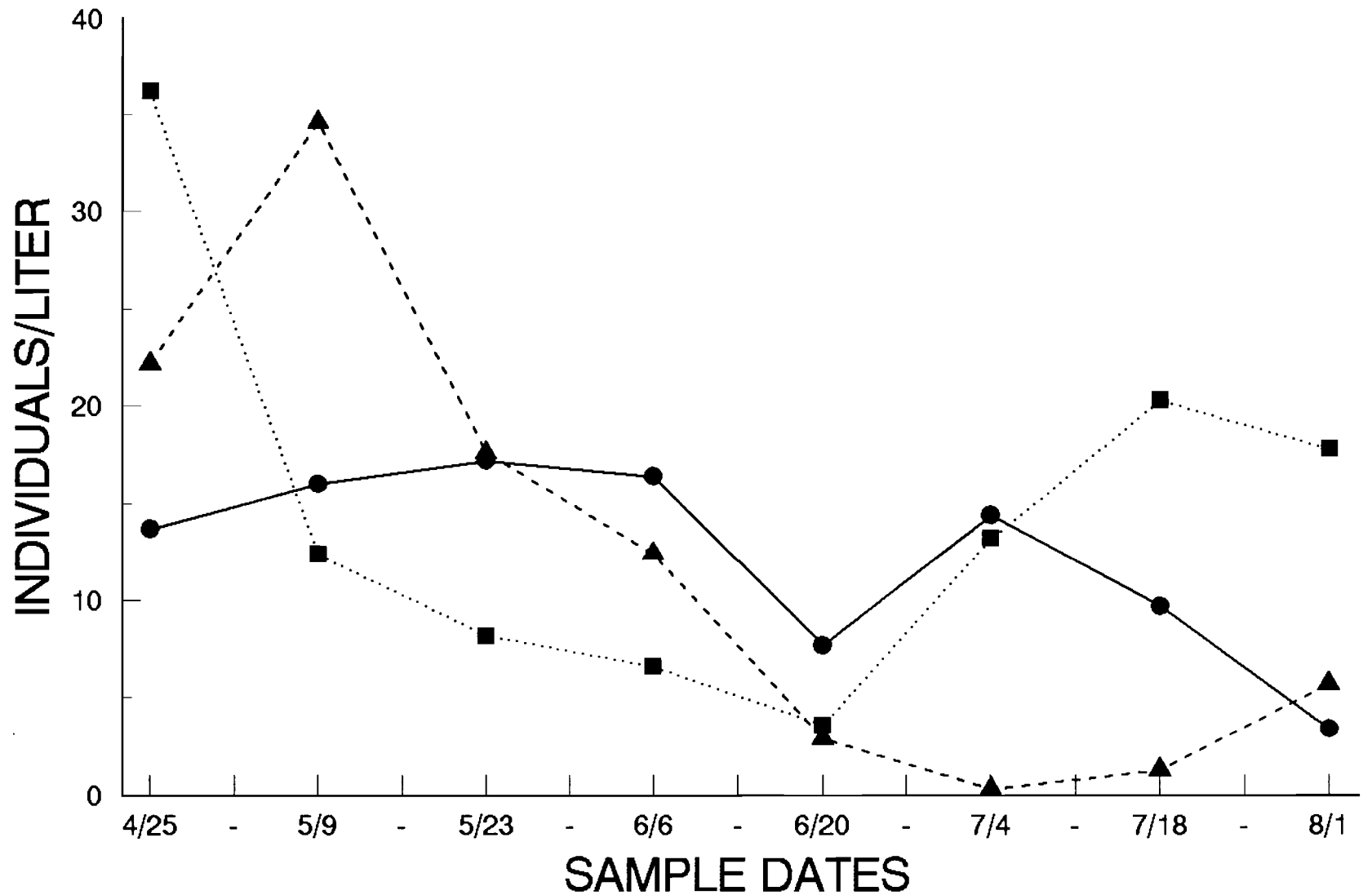
Comparison of the three main groups of zooplankton in Lake Reading, calanoids, cyclopoids, and cladocerans, shows the calanoid population had the highest density during the 1991 sampling dates (Figure 3). The cyclopoid population had the highest relative density at the beginning of the sampling dates during the spring of 1992 followed by peak densities of the cladoceran population. The calanoid population reached peak densities next, followed by another maximum value of cyclopoids. The two peaks of cyclopoids were due to different cyclopoid species reaching their greatest densities at different times in a season. The most abundant zooplankter during 64% of the 1991-1992 sampling dates were the calanoids. Cladocerans were the most abundant zooplankter on 18% of the sampling days and cyclopoids were most abundant on 18% of the sampling days. Figures 3 and 4 demonstrate the seasonal variation of the three main groups of zooplankton in Lake Reading during the

Figure 3. Zooplankton seasonal pattern in Lake Reading for 1991 sample dates.



Calanoids Cyclopoids Cladocerans
—●— ■..... - - -▲- - -

Figure 4. Zooplankton seasonal pattern in Lake Reading for 1992 sample dates.



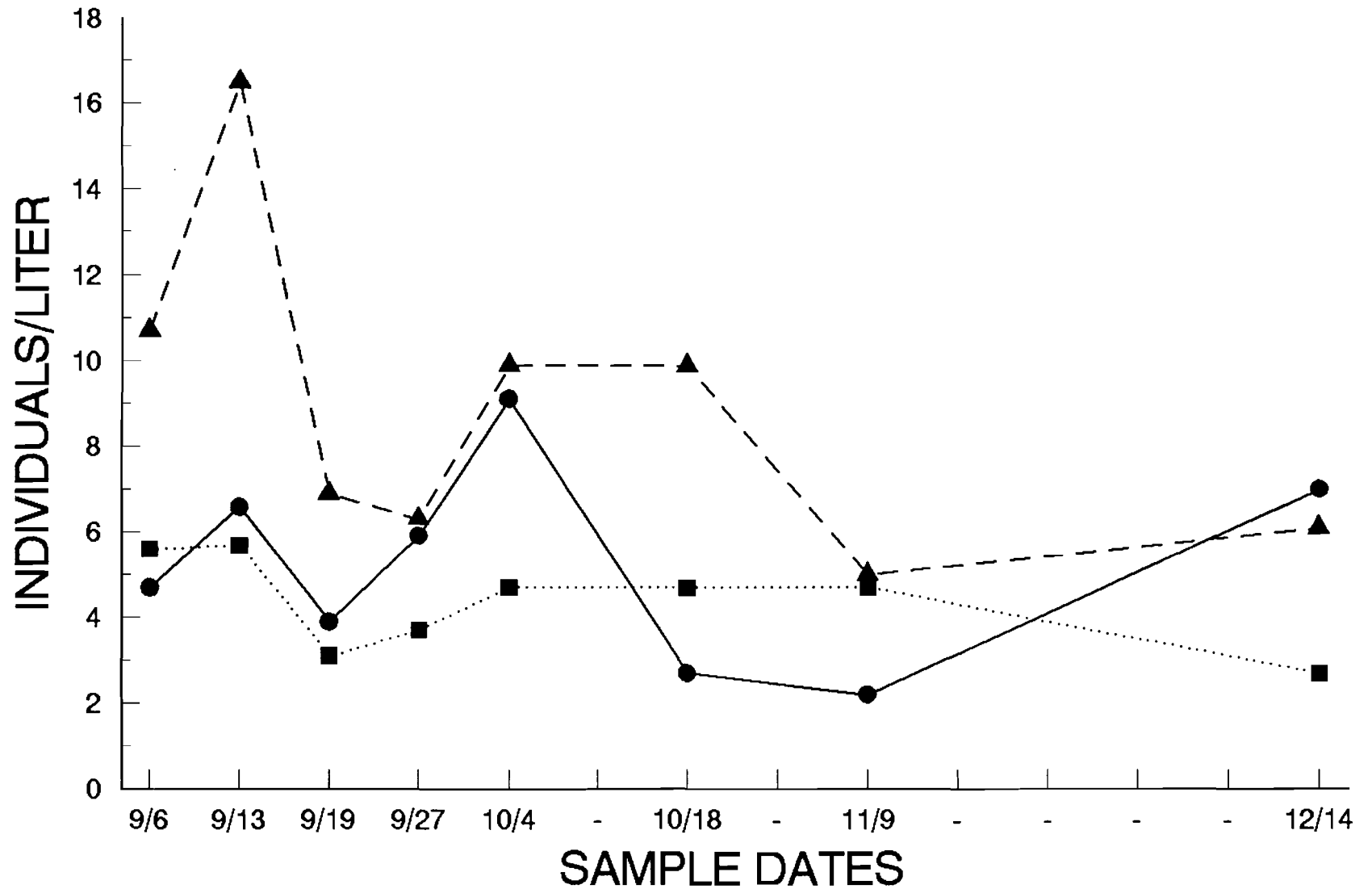
Calanoids Cyclopoids Cladocerans
—●— ■..... - - -▲- - -

1991-1992 sampling dates. Copepods were more numerous than cladocerans on all sampling dates but one. Copepods constituted 73% of all zooplankters collected during this study, and 58% of the copepods were calanoids.

Seasonal Variation in Calanoid Stages During 1991-1992 Sampling Dates

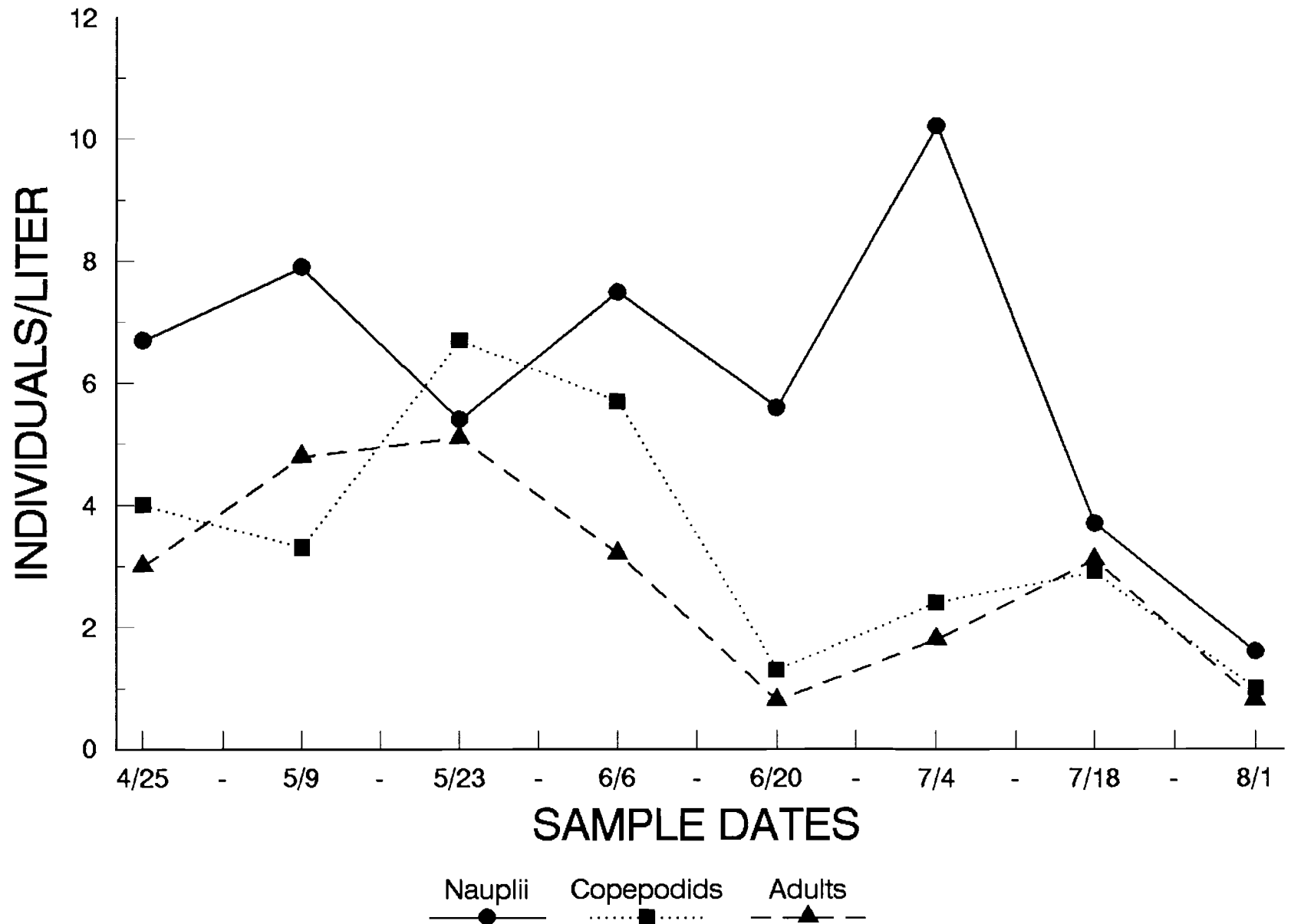
Temporal variation in the calanoid seasonal population structure of Lake Reading during 1991-1992 sampling dates is summarized in Figures 5 and 6. During the 1991-1992 sampling dates, seasonal variation in densities of calanoid nauplii ranged from 1.6 to 10.2 individuals per liter. Calanoid copepodid densities ranged from 1.0 to 6.7 individuals per liter. The 1992 calanoid season extended from April through the end of sampling in August. Population growth began in late April as indicated by increased numbers of adults and copepodids appearing in samples after 25 April. The calanoid population reached its apogee approximately one month later (Figure 6). Adults and copepodids became scarce in August 1992.

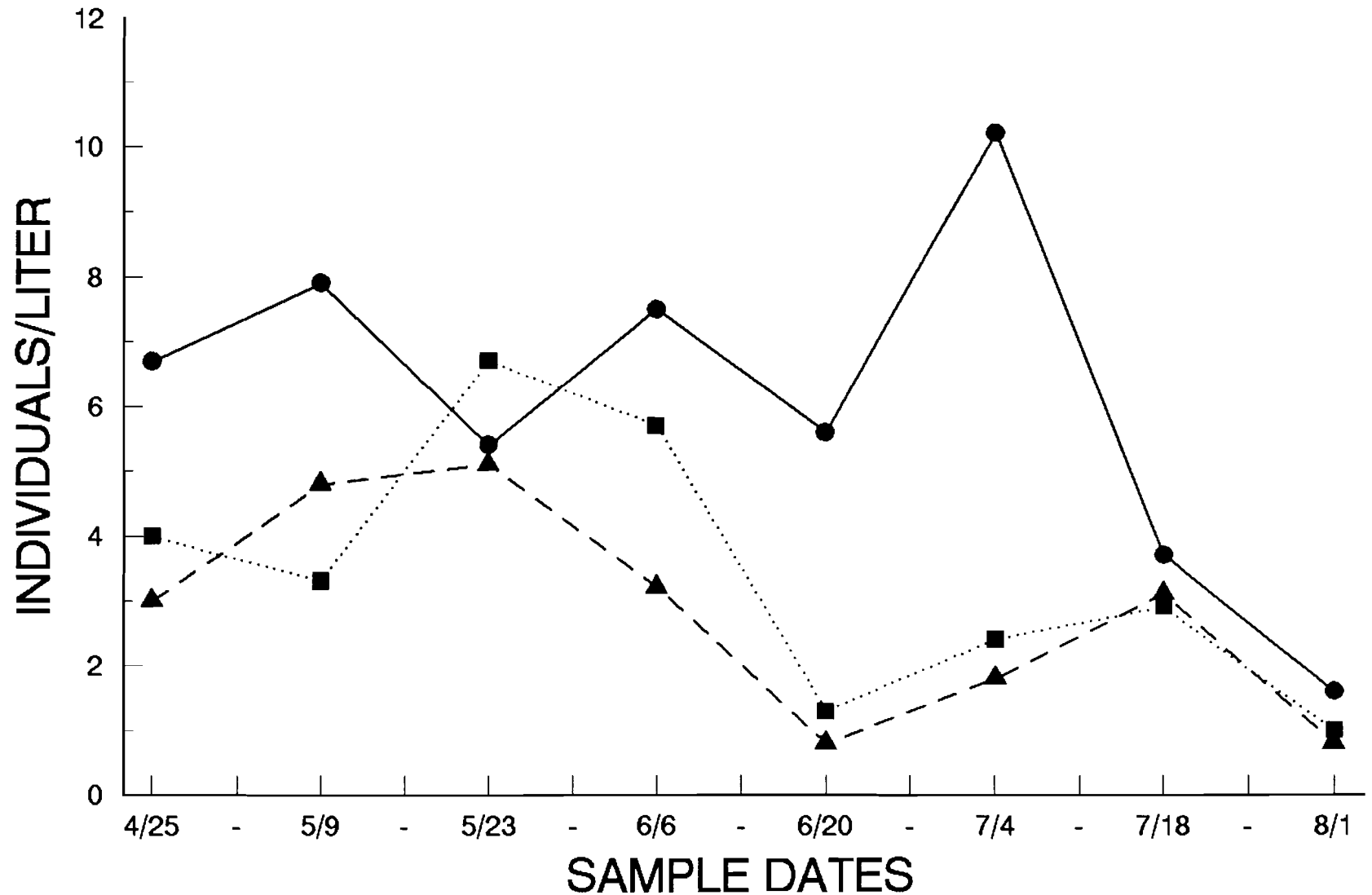
Figure 5. Calanoid seasonal population structure in Lake Reading for 1991 sample dates.



Nauplii Copepodids Adults

Figure 6. Calanoid seasonal population structure in Lake Reading for 1992 sample dates.





Nauplii Copepodids Adults

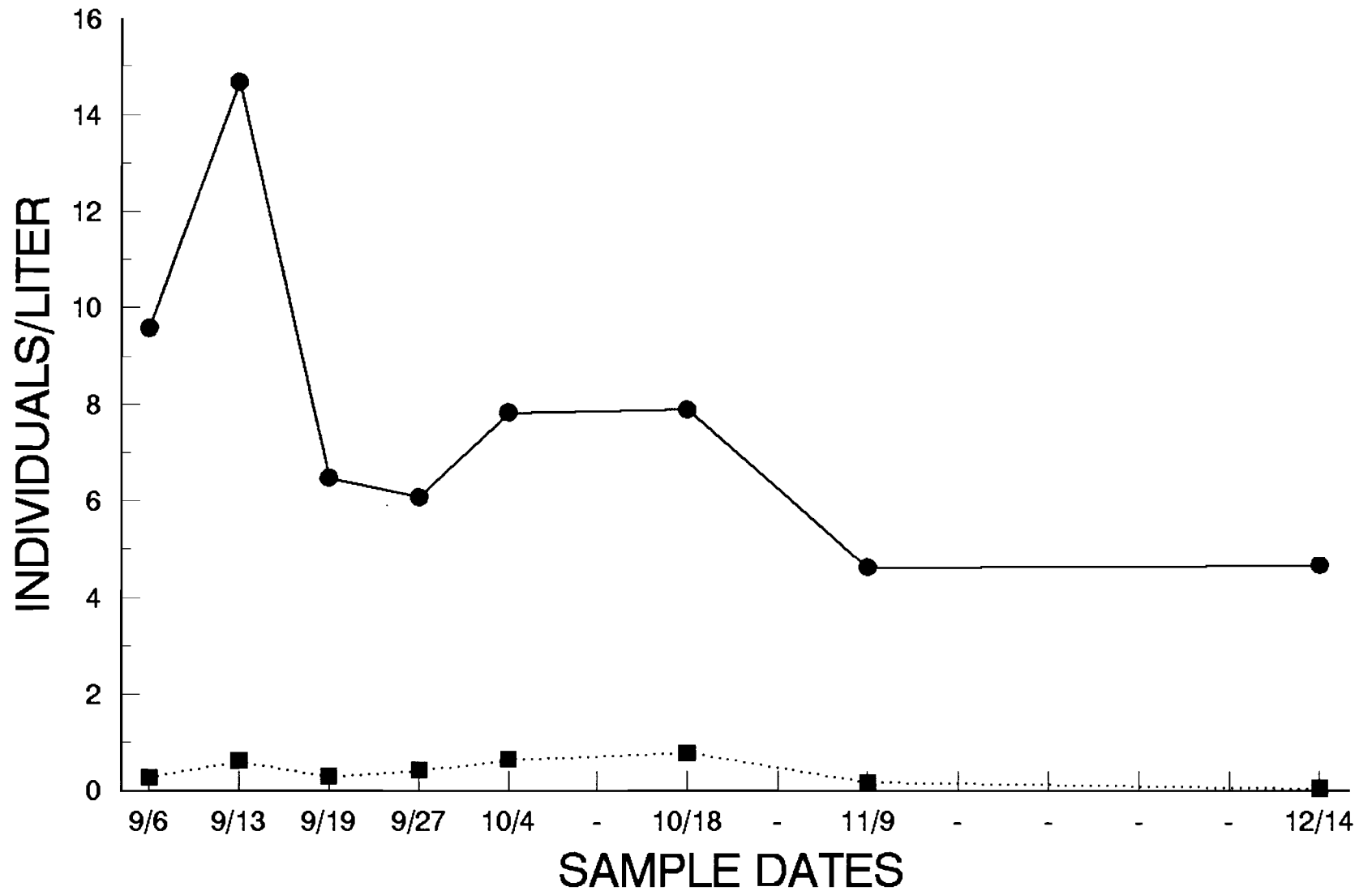
**Standing Crops of Diaptomus pallidus and D. siciloides
During 1991-1992 Sampling Dates**

Comparison of the standing crops of Diaptomus pallidus and D. siciloides shows that D. pallidus greatly outnumbered D. siciloides on most sampling dates (Figures 7 and 8). In fact D. pallidus outnumbered D. siciloides overall 15 to 1. Mean standing crops during the 1991-1992 sampling dates for D. pallidus was 4.83 individuals per liter and ranged from 0.41 individuals per liter on 4 July 1992 to 14.83 individuals per liter on 13 September 1991. Mean standing crops during 1991-1992 sampling dates for D. siciloides was 0.33 individuals per liter and ranged from 0.0 individuals per liter on 4 July and 20 June 1992 to 0.78 individuals per liter on 18 October 1991. Approximately 95% of adult calanoids identified in 1991 and 89% in 1992 were D. pallidus.

**Comparisons of Calanoid Mean Annual Standing Crops
Before, During, and After Threadfin Shad Stocking**

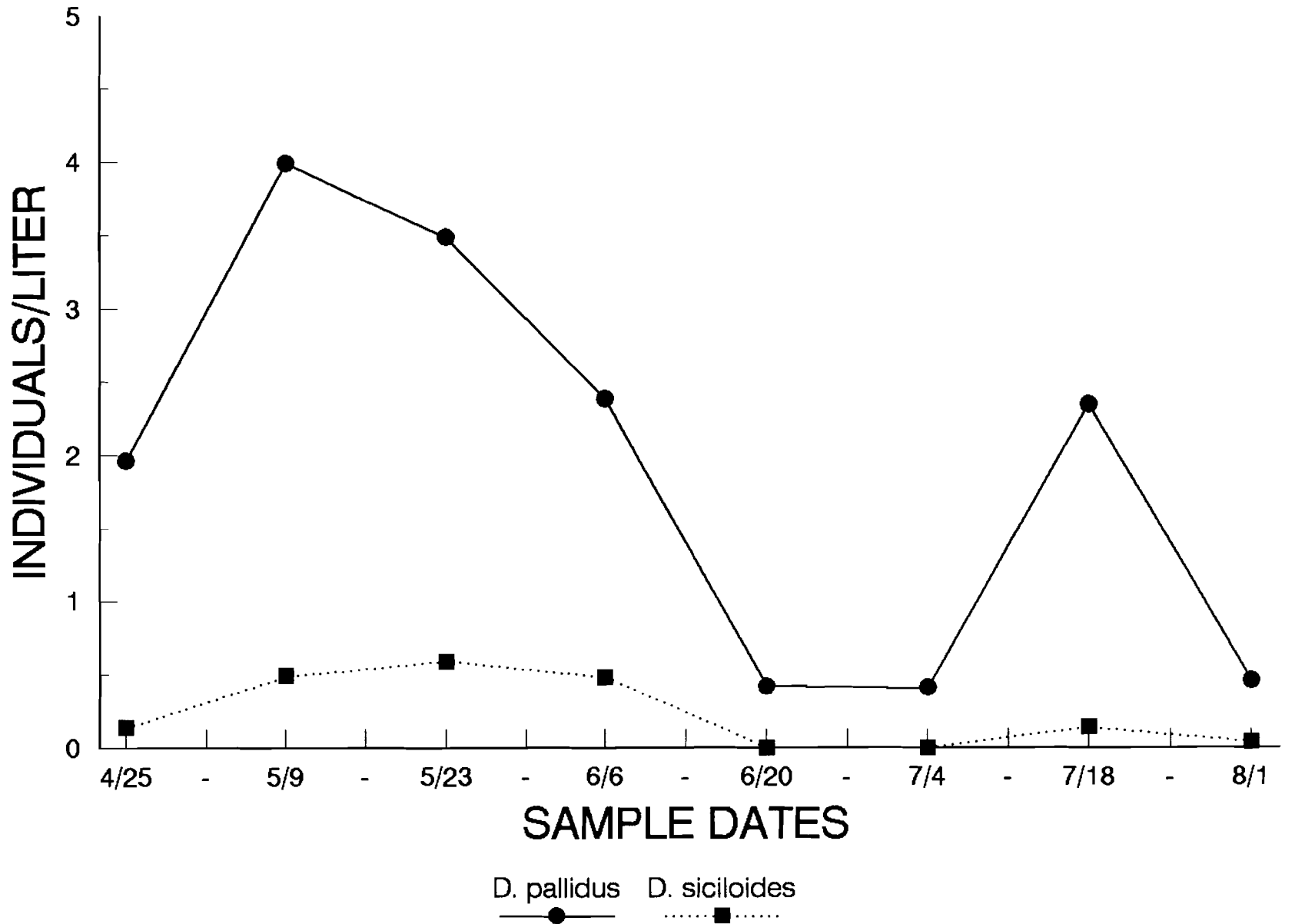
Calanoid mean annual standing crops were compared using nested ANOVA between all sample years of 1978, 1979, 1980, 1981, 1984, 1985, 1991, and 1992. Year to year differences in D. pallidus mean annual standing crops between all sampling years were highly significant ($P < 0.00001$). There

Figure 7. Calanoid standing crops in Lake Reading
for 1991 sample dates.



D. pallidus *D. siciloides*
—●—■.....

Figure 8. Calanoid standing crops in Lake Reading
for 1992 sample dates.



was additional variance due to differences among sample dates ($P < 0.00001$; 40% of total variance), sample sites ($P = 0.00150$; 22% of total variance), and tows ($P < 0.00001$; 38% of total variance) (Table 4). There was an obvious decrease in the D. pallidus mean annual standing crop when threadfin shad were stocked (Figure 9). The standing crop of D. pallidus during 1991 was similar to the 1978 level. The difference between mean annual standing crops of D. pallidus during (1980, 1981) and after (1991, 1992) threadfin shad stocking was significant ($P < 0.02$). The difference between mean annual standing crops of D. pallidus before (1978, 1979) and after (1991, 1992) stocking of threadfin shad was not significant ($P > 0.1$) (Table 5).

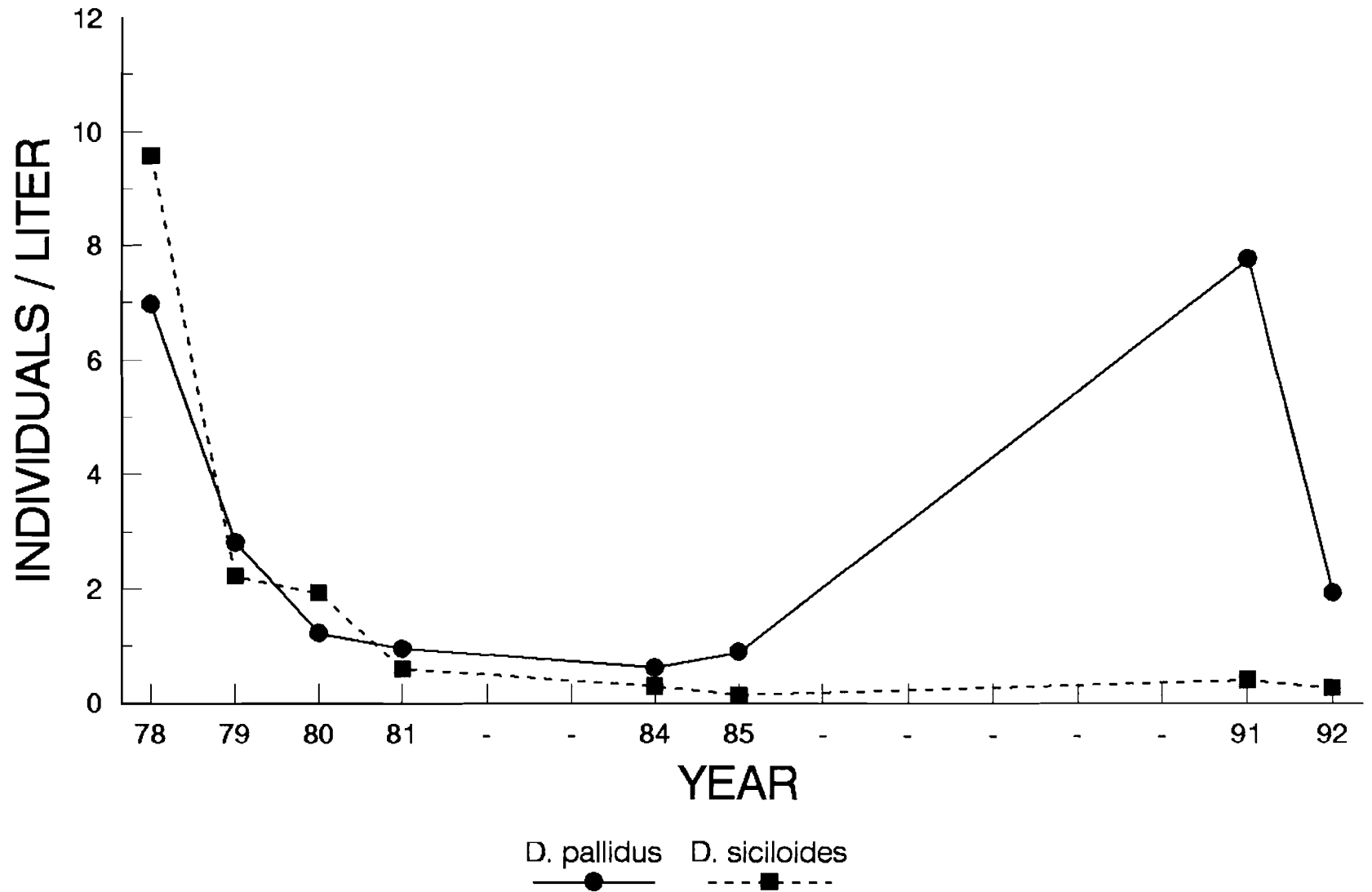
Year to year differences in D. siciloides mean annual standing crops between all sampling years were highly significant ($P < 0.00001$). There was additional variance due to differences among sample dates ($P < 0.00001$; 24% of total variance), sample sites ($P < 0.00001$; 41% of total variance), and tows ($P < 0.00001$; 35% of total variance) (Table 4). There was an obvious decrease in the D. siciloides mean annual standing crop after threadfin shad were stocked (Figure 9). The difference between mean annual standing crops of D. siciloides during (1980, 1981) and after (1991, 1992) threadfin shad stocking was not significant ($P < 0.1$). The difference between mean annual standing crops of D. siciloides before (1978, 1979) and

after (1991, 1992) stocking of threadfin shad was highly significant ($P < 0.005$) (Table 5).

Table 4. Results from four-tier nested ANOVAs of Diaptomus siciloides and D. pallidus in Lake Reading for sampled years 1978, 1979, 1980, 1981, 1983, 1984, 1985, 1991, and 1992.

Tier		df	Probability	% of variance
<u>D. siciloides</u>				
4	year	7	$P < 0.00001$	
3	date	91	$P < 0.00001$	24
2	site	395	$P < 0.00001$	41
1	tow	122	$P < 0.00001$	35
0		1382		
<u>D. pallidus</u>				
4	year	7	$P < 0.00001$	
3	date	91	$P < 0.00001$	40
2	site	395	$P = 0.00150$	22
1	tow	122	$P < 0.00001$	38
0		1382		

Figure 9. Calanoid mean annual standing crops in Lake Reading before, during, and after threadfin shad stocking.



Before - 1978,1979
During - 1980,1981
After - 1984,85,91,92

Table 5. Results from t-tests of Diaptomus siciloides and D. pallidus in Lake Reading for sampled years before (1978, 1979), during (1980, 1981), and after (1991, 1992) threadfin shad stocking.

Populations compared	df	t-value	Probability
<u>D. pallidus</u>			
After vs. During	852	2.354	$\underline{P} < 0.02$
After vs. Before	858	0.158	$\underline{P} > 0.1$
<u>D. siciloides</u>			
After vs. During	852	1.428	$\underline{P} > 0.1$
After vs. Before	858	2.827	$\underline{P} < 0.005$

DISCUSSION

Each of the eighteen species of microcrustaceans identified in the tow net samples during this study has been observed previously in Lake Reading (Prophet 1982; Bruner 1984). There was little variation in the species composition of zooplankton in Lake Reading before (1978, 1979), during (1980, 1981), and after (1984, 1985, 1991, 1992) threadfin shad stocking. No attempt was made to quantify species other than Diaptomus pallidus and D. siciloides. The remaining zooplankter species were qualitatively identified as either scarce, common, or abundant. While the species present before, during and after threadfin shad stocking were the same, their relative abundances changed. Larger bodied zooplankters became scarce during threadfin shad stocking and smaller bodied zooplankters became more abundant (Prophet 1982, 1985, 1988; Bruner 1984). For example, Leptodora kindti, a large bodied zooplankter, was abundant before and after threadfin shad stocking but scarce during threadfin shad stocking. Bosmina longirostris, a small bodied zooplankter, was scarce before (since 1975) and after threadfin shad stocking but became abundant during threadfin shad stocking (Prophet 1982; Bruner 1984). Zooplankton species composition of Lake Reading during this study was similar to that observed in other lakes in eastern Kansas (Prophet 1978).

D. siciloides and D. pallidus coexisted before the shad stocking project even though D. siciloides was the more abundant of the two species and constituted approximately 60% of all adult calanoids identified to species (Prophet 1988). During and after threadfin shad stocking in Lake Reading, D. pallidus was the more abundant of the two species of calanoid. Although the observed changes in the structure of the calanoid populations in Lake Reading may have been produced by the interactions of numerous variables, increased predation by threadfin shad was considered the most important factor by Prophet (1988).

Threadfin shad are predominately planktivores. Examination of the stomach contents of threadfin shad in central Arizona lakes revealed that rotifers and crustaceans were the major food items with lesser quantities of algal forms (Haskell 1959). The results of planktivory are density reductions of the more easily captured species and density increases for some of the remaining species. Changes in the densities of zooplankton populations may be the consequences of a planktivore's foraging selectivity of either large or small zooplankters. Prey selectivity depends upon the age structure and feeding mechanism of the planktivore (Drenner et al. 1982). Miller (1967), and Holanov and Tash (1978) demonstrated that threadfin shad prey upon zooplankton both as particulate and filter feeders, depending upon the prospective prey individuals.

Threadfin shad are particulate feeders until they become approximately 5 cm in length and then they are predominately pumpfilter feeders (Haskell 1959; Miller 1967). All young-of-year fishes feed on zooplankton in their first few weeks after hatching, but threadfin shad feed almost exclusively on zooplankton throughout their lives (Guest et al. 1990). When threadfin were introduced into lakes where they did not naturally occur they had a great impact on zooplankton community structure (Elmore 1983; Miura 1990; Turner and Mittelbach 1990; Guest et al. 1990). Young-of-year threadfin shad have a greater impact on zooplankton community structure than adult threadfin because of their abundance during the early summer and their tendency to select for larger bodied zooplankters (Holanov and Tash 1978). Drenner and DeNoyelles (1982) reported experimental ponds containing young gizzard shad (8 to 20 cm standard length) had a higher density of D. pallidus, but lower densities of smaller size zooplankton, than did control ponds with no gizzard shad. Drenner and McComas (1980) demonstrated that D. pallidus exhibited a significantly lower capture probability ($P = 0.07$) than either cyclopoids ($P = 0.28$) or cladocerans ($P = 0.88$) when tested with a fish suction simulator. Prophet and Frey (1987) demonstrated that the capture probability for D. siciloides (P varied from 0.092 to 0.391) was significantly greater ($P < 0.025$) than that for D. pallidus (P varied from 0.047 to 0.210).

Since D. siciloides has a higher capture probability than D. pallidus, D. siciloides would be selected for over D. pallidus during threadfin shad predation. This would increase the predation rate for D. siciloides compared to that for D. pallidus, causing a shift in the calanoid population structures.

Why has D. siciloides not become more abundant and recovered as the dominant calanoid in the absence of the threadfin shad? Possibly the D. siciloides population was so depleted by threadfin shad predation that it can no longer compete favorably with D. pallidus for available resources. The D. pallidus population was not nearly as depleted by threadfin shad predation as was D. siciloides and that may be why D. pallidus was able to recover in numbers to pre-shad levels. Finding that D. siciloides had not recovered as the dominant calanoid in the absence of threadfin shad was not expected. Factors shaping community structure are perhaps more complex than just the presence or absence of one species of fish.

During the period threadfin shad were being stocked in Lake Reading, a few gizzard shad were also accidentally released during other stocking operations by KDWP. Gizzard shad are still present and apparently reproducing, but the population is not expanding (T. D. Mosher, KDWP Fisheries Biologist, Pers. Comm.). Even though the gizzard shad population is not expanding, their young-of-year in spring

and early summer could have a significant impact on the zooplankton community.

There were more species of fish in Lake Reading during this study (1991, 1992) than before threadfin shad were stocked. Some of the species of fish now present in Lake Reading that were not there before 1980 are: carp (Cyprinus carpio), drum (Aplodinotus grunniens), black crappie (Pomoxis nigromaculatus), white crappie (P. annularis), orangespotted sunfish (Lepomis humilis), black bullhead (Ameiurus melas), yellow bullhead (A. natalis), and flathead catfish (Pylodictis olivaris). There is now a larger population of largemouth bass (Micropterus salmoides) in the lake than there was before the threadfin shad stocking project (T. D. Mosher, KDWP Fisheries Biologist, Pers. Comm.). Because fishes tend to be zooplanktivorous during the few weeks after hatching, the presence of additional species of fish plus the higher densities of some of these fishes, there may be little difference between the total predation pressure on the zooplankton community presently and during the threadfin stocking project. Thus, the D. siciloides population may have had little opportunity to recover to pre-project levels.

During the 1991 sampling season there was a drought and the water level in Lake Reading was 2 m below the spillway. During the 1992 sampling season heavy rains every week or two caused the lake level to rise to the spillway and

repeatedly overflow. This constant flushing was unusual for Lake Reading and led to much lower zooplankton numbers than usual, because Lake Reading rarely overflows the spillway (Prophet 1970). Rooted macrophytes were abundant in 1991 but were scarce in 1992. Also, turbidity was higher in 1992 due to increased runoff even though most of the watershed is non-tilled and native prairie. This increase in erosion may have been the result of spring burning of most of the land immediately surrounding the lake by KDWP personnel. Loss of protective habitat by scarcity of macrophytes and higher turbidity may have led to the lower densities of zooplankton in 1992.

Threadfin shad manipulation studies are more likely (10 to 1) to report the effects of shad introductions than the effects of shad removal. This is probably due to threadfin shad's small maximum size which makes it an ideal forage species. DeVries and Stein (1990) stated that if they were attempting to assess shad effects on ecosystem processes, effects are more likely to result from additions than from removals. The majority of shad removal studies deal with the shad removal effects on the sport fish that prey upon the shad (Huish 1958; Ellis 1981; Kirk et al. 1986). The few studies I found that do deal with shad (planktivore) removal effects on zooplankton densities were short term studies.

Previous studies suggest a correlation between changes in zooplankton densities and planktivore load. When planktivore load is reduced or removed, zooplankton densities tend to increase, though the rate of increase varies. Threlkeld and Drenner (1987) found that zooplankton increased moderately after a die-off of gizzard shad during changeover experiments in large outdoor tanks in Oklahoma to evaluate the persistence of effects of predation on plankton community structure. Threadfin shad introductions into Lake Alamo, Arizona in 1979 virtually eliminated the zooplankton community for two years, 1980 and 1981. An unusual cold spell in January 1982 killed many of the threadfin shad. An increase in zooplankton occurred in February 1982 and continued the upward trend in March when the study was terminated. The same species of zooplankton that were present before threadfin shad introductions (1978) were again identified in the 1982 samples (Ziebell et al. 1986). Kohler and Ney (1981) found that zooplankton increased rapidly in 1978 following an alewife (Alosa pseudoharengus) die-off in Claytor Lake, Virginia. All of these studies are consistent with my findings in that after the winter kill of threadfin shad in Lake Reading the zooplankton densities increased. The calanoid season lengthened back to pre-shad levels and larger zooplankters became common again. The only result I found in my study that is not consistent with these other studies is that the D. siciloides population did

not recover to pre-shad levels.

The only change observed in the calanoid populations in Lake Reading since 1985 has been an increase in mean annual standing crops of D. pallidus (Figure 9) and a lengthening of the calanoid season to pre-shad levels. The Lake Reading D. siciloides population failed to recover to pre-shad levels, and failed to recover as the dominant calanoid. D. siciloides was the dominant calanoid before the shad stocking project but D. pallidus became the dominant calanoid during the shad stocking project and remains so even in the absence of threadfin shad.

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