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Coexistence Strategies of *Daphnia* in Lake Reading, Kansas

by

Gregory J. Bruner*

ABSTRACT

Daphnia galeata Sars, 1864 *mendotae* Birge, 1918; *Daphnia ambigua* Scourfield, 1947; and *Daphnia parvula* Fordyce, 1901 inhabited Lake Reading, Kansas, during the 1980 - 1982 spring periods. Some of the probable coexistence strategies employed by the three species in Lake Reading were characterized by comparing standing crops, seasonal occurrences, body lengths, and egg production of each species during the 1980 to 1982 seasons. Water temperatures ranged from approximately 5 to 29°C during the times daphnids were present. Dissolved oxygen varied from 5 to 9 $mg \cdot liter^{-1}$, pH ranged from 8.0 to 8.2 and specific conductance varied from 250 to 300 $\mu mhos \cdot cm^{-1}$ at 25°C.

Daphnia galeata mendotae was the most abundant daphnid during 1980 and 1981, but it shared the role of dominant daphnid species with *Daphnia ambigua* during the 1982 season. The daphnid season in Lake Reading occurred from approximately 15 March to 15 July each year of the study. Peak population densities in 1982 for *D. galeata mendotae* and *D. parvula* occurred in June and July, with the maximum population density of *D. ambigua* occurring in May.

Maximum egg production (mean brood size per gravid female and number of eggs produced per individual per day) for each species occurred 8-16 days prior to the time peak population densities occurred. During the 1982 season *D. parvula* exhibited the highest egg production rate, followed by *D. ambigua* and *D. galeata mendotae*.

The largest species of daphnid inhabiting Lake Reading in 1982 was *D. galeata mendotae*. Ninety-five percent confidence limits for the average body lengths of *D. galeata mendotae, D. parvula,* and *D. ambigua* were 1.18 $\pm$ .03 mm, 1.13 $\pm$ 0.04 mm, and 1.04 $\pm$ .01 mm respectively. Significant differences, at $p = 0.05$, existed between mean body lengths for *D. galeata mendotae* and *D. ambigua,* and for *D. parvula* and *D. ambigua,* but there was no significant difference between mean body lengths for *D. galeata mendotae* and *D. parvula.*

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*This study originated as a master's thesis in the Division of Biological Sciences at Emporia State University under the direction of Dr. Carl W. Prophet.

INTRODUCTION

Microscopic animals suspended in the water of lakes and streams are known as zooplankton. In lakes, zooplankton is predominately composed of Cladocera, Copepoda, and sometimes Rotifera. Cladocerans and copepods are commonly termed microcrustaceans.

The microcrustacean fauna inhabiting a lake during the year may consist of 20 species or more; however, some species of zooplankton are seasonal in occurrence while other species are restricted to either the deep open water (limnetic zone) or the shallow margins (littoral zone) of the lake. Consequently, a single plankton sample will often contain only four or five species, even though the total number of individual plankters may number in the thousands per volume of water. A low species number is characteristic of zooplankton of the limnetic zone, and this condition is usually attributed to a restriction of available niches (Pennak, 1978).

Members of the genus *Daphnia* are often important components of a freshwater zooplankton community and play an important role in the transfer of energy within aquatic food webs. *Daphnia* are either utilized directly or indirectly for food by young and adult fishes; thus, Cladocera have a great impact on aquatic productivity (Lei and Armitage, 1980).

At least eight species of *Daphnia* are known to occur in Kansas. Prophet and Waite (1975) considered *Daphnia parvula* as the most common daphnid species found in eastern Kansas lakes, and Prophet (1970) reported *D. parvula* was the most abundant daphnid species in Lake Reading during 1962-67. Several other species of this genus occasionally appeared in the zooplankton samples, but they were always scarce. During the 1981 spring, Prophet (1982) noted an apparent increase in the abundance of *Daphnia ambigua* and *Daphnia galeata mendotae* relative to *D. parvula,* but he did not verify this observation.

The observations of Prophet (1982) raise several questions. First, was the species composition of the daphnid population inhabiting Lake Reading changing after being relatively stable for two decades? Were the changes in species composition temporary or would they persist?

The occurrence of multiple species of the same genus of microcrustacean in the limnetic zooplankton of a lake also promote some interesting questions. Do the species coexist simultaneously or do their populations only overlap during a short period of their life spans? If these species coexist, what strategies are employed to reduce competition?

Congeneric species obviously have more similar niche requirements than less closely related species. It is expected that competition for food and other limited essential resources would be so severe that one or more of the congeneric species would be eliminated, or at least greatly reduced in abundance. Recent observations of coexisting species of *Daphnia* by Seitz (1980) and Applegate and Mullan (1969) suggest that some cladocerans have diversified their niche requirements sufficiently that coexistence is possible.

The primary objectives of my research were to verify which species of *Daphnia* were inhabiting Lake Reading, to determine whether the periods of occurrence of these species overlapped throughout their populations' life spans, and to characterize life strategies which reduced direct competition among these species to allow coexistence.

DESCRIPTION OF STUDY AREA

Lake Reading is located approximately 19 km northeast of Emporia, Kansas. It is in the Missouri River Drainage Basin which drains the northern half of the state. The lake drains 583 ha of the little bluestem *(Andropogon scoparius),* big bluestem *(Andropogon gerardi),* indian grass *(Sorghastrum nutans),* switch grass *(Panicum virgatum),* and side-oats grama *(Bouteloua curtipendula)* association. It was constructed for the Kansas Forestry, Fish and Game Commission in 1934 by the Civilian Conservation Corps and first reached spillway capacity in 1937. At capacity elevation, the lake had a surface area of 55 ha and a maximum depth of 13 m. Sedimentation has reduced the present maximum depth to less than 12 m. The lake is approximately 1200 m long with a maximum breadth of 500 m; its long-axis is oriented in a southwesterly to northeasterly direction (Prophet, 1970). The earthen dam impounding the lake is 640 m long and 14.6 m high (Brooks, 1947).

After its initial stocking, Lake Reading maintained a relatively high fish production for nearly 20 years, but by 1962 fishing success had so declined that the State Fisheries Division initiated a program to rehabilitate the lake's fisheries (Prophet, 1970). Drawdown was commenced during the 1962 summer, and by October the impoundment was reduced to a small, shallow pool which was first seined and then treated with fish toxicant to destroy the remaining fishes. During February and March 1963, the lake was restocked with channel catfish *(Ictalurus punctatus)*, largemouth bass *(Micropterus salmoides)*, and bluegill *(Lepomis macrochirus)*; it was reopened to fishing in early spring 1966 (Prophet, 1970).

METHODS AND MATERIALS

Beginning in March and extending through July, plankton samples were collected at selected time intervals to estimate population standing crops and to obtain information concerning egg production for each species. Initially, samples were taken at two to three day intervals until each of the species reached its maximum population density. Sampling frequency was then reduced to every four to five days until the species disappeared. When the plankton samples were collected, physicochemical conditions (pH, dissolved oxygen, specific conductance, and temperature) were measured using a Hydrolab water analyzer, while light transmittance was estimated using a Secchi disc.

Plankton samples were collected from 12 different regions on the lake (Figure 1). Each sample set consisted of 12 vertical tows from a depth of two meters to the surface using a 30 cm diameter plankton net (64 µ mesh). Zooplankters were preserved with a four percent formaldehyde-sucrose solution to reduce loss of eggs from the brood chamber (Prepas, 1978).

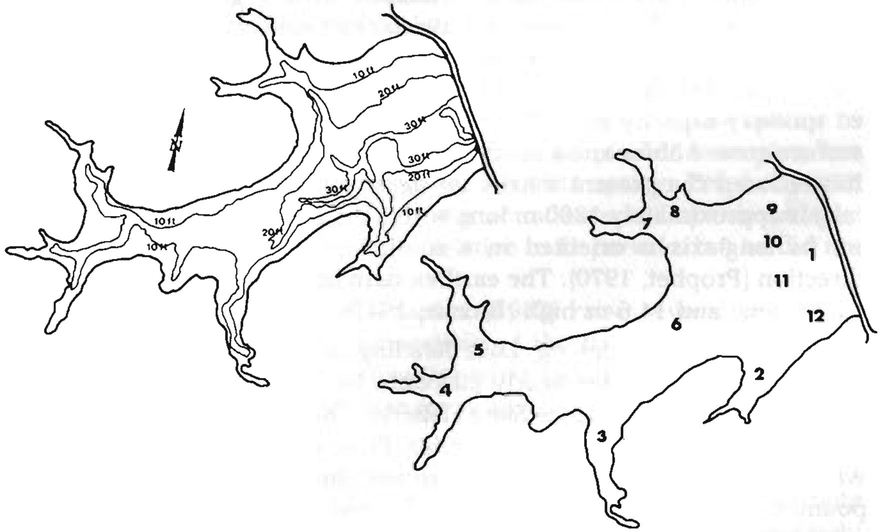

Figure 1. Map of Lake Reading showing general sampling areas and depth contours.

When daphnids first appeared, the entire composite sample was used to determine standing crops of the species present. As daphnids became more abundant only a portion of the composite sample was examined. This technique consisted of making the volume of each sample to 100 ml; the sample was then thoroughly mixed, and three 1.0 ml subsamples were withdrawn using a Hensen-Stemple plankton pipet. The subsamples were then transferred to a Sedgwick-Rafter counting chamber and examined with a steroscopic binocular microscope at 10X-30X for counting. The average number of individuals in the subsamples was substituted in the following equation to estimate the density$\cdot m^{-3}$ of each species.

$$\text{Density}\cdot m^{-3} \text{ of Species A} = \frac{(\bar{x})\,(c)}{s} \times 1000$$

where $\bar{x}$ was the average number of individuals$\cdot ml^{-1}$ based on the three subsamples examined, *c* was the volume in milliliters of the composite plankton sample, and *s* was the total liters of water strained when the sample was collected.

The number of parthenogenic eggs per gravid female and body lengths for 20-25 randomly selected individuals per sample were also recorded. Body lengths were measured from the base of the posterior spine to the top of the head (Anderson, 1932). Significant differences, if any, between mean body lengths were determined by Student's t-test at $p = 0.05$.

RESULTS AND DISCUSSION

Physicochemical Characteristics of Lake Reading

Although small in area, 55 ha, Lake Reading has a mean depth of approximately four meters. There is at least one known active spring in the basin, but runoff is the primary source of inflowing water. However, since there is virtually no outflow, evaporation and seepage account for most of the water loss (Prophet, 1970).

The physicochemical data reported in this study, when possible, were based on measurements during the 1982 sampling period. Compared to other Kansas impoundments, Lake Reading was relatively clear with Secchi disc visibility usually 1.0 to 2.0 m. Prophet (1970) estimated light transmittance using a Secchi disc and a Whitney Underwater Photometer. His comparison of simultaneously obtained readings indicated that the depth to which one percent of the surface illumination penetrated (depth of the euphotic zone) was about 3.5 times the depth at which the Secchi disc became invisible, indicating the depth of the euphotic zone generally exceeded four meters.

The lake was holomictic throughout most of the year. Ice covers formed during the winter but were of short duration, and the lake was rarely ice bound for more than a few weeks at a time. Winter water temperatures increased during the spring, and thermal stratification was established by the first week of June and persisted into September. Maximum surface temperatures of 27-29°C occurred during late July and early August.

Top to bottom differences in physicochemical conditions were most pronounced during thermal stratification, indicating the lake also became chemically stratified. During stratification, dissolved oxygen was depleted in the hypolimnion, while specific conductance and bicarbonate alkalinity decreased in the epilimnion and increased in the hypolimnion. The pH generally ranged from 8.0 to 8.2 throughout the lake, but it decreased in the hypolimnion during stratification. Dissolved oxygen was usually greater than 6 mg•liter^{-1} in the upper two meters (Figure 2). Specific conductance tended to range from 250 to 300 µmhos•cm^{-1} at 25°C. No attempt was made to identify phytoplankton, but visual examination of the plankton samples indicated a low to moderate species diversity of phytoplankters. Annual means for chlorophyll concentrations from 1963 to 1967 ranged from 1.81 to 6.73 µg•liter^{-1} (Prophet, 1970).

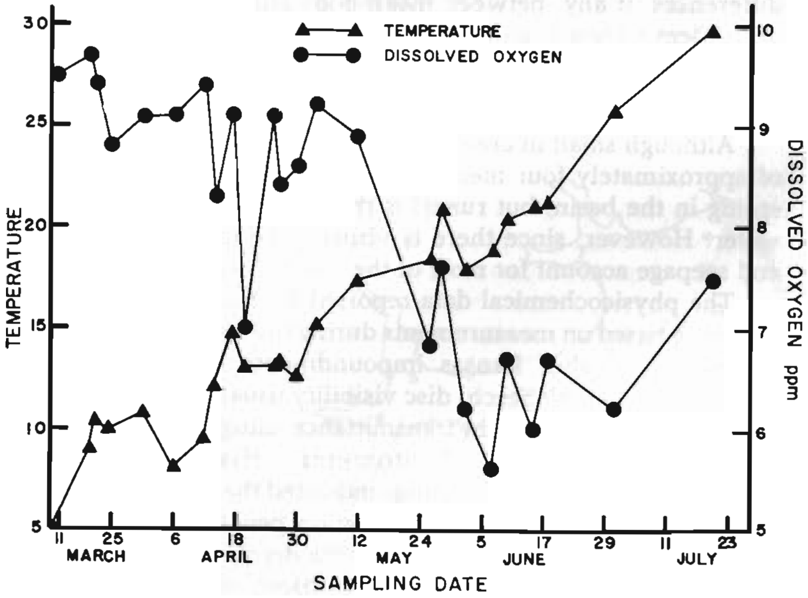

Figure 2. Temperature and dissolved oxygen in the upper two meters of Lake Reading during the 1982 sampling period.

Composition of Zooplankton

The zooplankton in Lake Reading during the study was composed primarily of cladocerans, copepods, rotifers, and protists. Although no attempt was made to quantify species of either phylum, rotifers and protists tended to reach peak population densities during the summer months. Two genera of protists *Ceratium* and *Difflugia* were especially abundant in July. Rotifera were represented by numerous genera including *Keratella, Filinia, Hexarthra, Asplanchna, Polyarthra, Ascomorpha,* and *Brachionus.*

The species composition and standing crops of the zooplankton community in Lake Reading from fall 1979 through summer 1982 were described by Prophet (1982). He idenified 18 species of Cladocera and 11 species of Copepoda in 535 separate plankton samples collected during that three year period and reported the microcrustacean fauna in Lake Reading was dominated by the copepods, which usually accounted for 70% or more of the adult and immature individuals observed in the samples. The most abundant species of copepods were *Diaptomus pallidus, Diaptomus siciliodes, Mesocylops edax, Diacyclops biscuspidatus thomasi,* and *Acanthocyclops vernalis.* The more numerous cladocerans were represented by *Daphnia* spp., *Diaphanosoma leuchtenbergianum,* and *Ceriodaphnia lacustris.* Although population densities were low, *Leptodora kindti* was a conspicuous component of the zooplankton from approximately June through September.

Lake Reading Daphnidae

The first record of the species composition of zooplankton in Lake Reading was compiled by Brooks (1947). Two of the 19 species of Cladocera reported by Brooks were daphnids, *Daphnia pulex* and *Daphnia longispina.* Prophet and Waite (1975) questioned Brooks' records of these two species. They concluded that the *D. pulex* identified by Brooks may have been *D. parvula,* since the latter species was more common in lakes in the vicinity of Emporia and was the most common daphnid in Lake Reading from 1962 to 1967 (Endicott, 1965; Prophet, 1970). Prophet and Waite (1975) stated that *D. longispina* does not occur in North America, but it was impossible to determine which other species of *Daphnia* Brooks had observed.

A preliminary examination of the Lake Reading *Daphnia* was conducted during the 1981 fall by analyzing plankton samples that had been collected during the period March 1978 through August 1981 by personnel from the Emporia State University Limnology

Laboratory. I established that *Daphnia* populations appeared in Lake Reading from March through mid-July and that the daphnid fauna at that time consisted of three species: *Daphnia parvula* Fordyce, 1901; *Daphnia ambigua* Scourfield, 1947; and *Daphnia galeata* Sars, 1864 *mendotae* Birge, 1918.

Although Prophet (1982) listed seven species of *Daphnia* that were collected from Lake Reading during 1962-79, only *D. parvula* was abundant while the other species recorded were rare. *Daphnia ambigua* and *Daphnia galeata mendotae,* as well as *D. parvula,* have been collected from other lakes in eastern Kansas (Armitage, 1961; Tash and Armitage, 1960) although never from the same lake.

Estimated Standing Crops

Estimated monthly standing crops of each species during the 1980, 1981 and 1982 seasons are compared in Table 1. Standing crops were greatest during May and June of each season. Both *D. parvula* and *D. ambigua* tended to be less abundant during the 1980 and 1981 seasons than during 1982, while the standing crops of *D. galeata mendotae* were high during all three seasons.

The maximum monthly standing crops for *D. parvula* and *D. ambigua* observed during this study were 2,397 *D. parvula*•m^{-3} in June 1982 and 20,090 *D. ambigua*•m^{-3} in May 1982. During these same months *D. galeata mendotae* averaged 4,216 and 7,668 individuals•m^{-3}, respectively. The greatest monthly average standing crop of *D. galeata mendotae,* 15,796 individuals•m^{-3}, occurred in May 1980.

The observed standing crops fall within ranges reported in other studies. Endicott (1965) estimated the *Daphnia parvula* standing crop in Lake Reading at approximately 15,000 individuals•m^{-3} during June and July 1964, and Applegate and Mullan (1969) estimated standing crops of 1,000 *D. parvula*•m^{-3} and 16,199 *D. galeata mendotae*•m^{-3} in large Missouri River reservoirs. Tash and Armitage (1960) estimated the density of *D. galeata mendotae* in Leavenworth County State Lake to be 24,975 individuals•m^{-3} on 21-22 June 1959. The greatest densities recorded during my study were 24,762 *D. galeata mendotae*•m^{-3} on 14 May 1980 and 33,410 *D. ambigua*•m^{-3} on 14 May 1982.

Based on the relative abundance of species observed during the seasons covered by this study, it is obvious that there has been a marked change in the structure of the daphnid population in Lake Reading since approximately 1978. Prior to that season the bulk of the *Daphnia* population consisted of *D. parvula* (Endicott, 1965;

Table 1. Mean monthly standing crops (individuals•m^{-3}) for *Daphnia ambigua, Daphnia parvula,* and *Daphnia galeata mendotae* for the 1980-1982 seasons.

MONTH	*Daphnia parvula*			*Daphnia ambigua*			*Daphnia galeata mendotae*		
	1980	1981	1982	1980	1981	1982	1980	1981	1982
MARCH	R	*	969	R	*	135	R	*	R
APRIL	R	*	969	R	*	7666	R	*	156
MAY	905	298	1270	238	2500	20090	15796	4772	4216
JUNE	R	R	2397	R	R	3193	4404	5438	7668
JULY	R	R	642	R	R	50	R	204	2076

R—present but fewer than 20 individuals m^{-3}
*—no data

Prophet, 1982), and populations of *D. ambigua* and *D. galeata mendotae* which were occasionally present remained sparse. Now the relationships among these three species appears to be reversed.

Population Growth and Development

Temporal separation of species in terms of periods of peak reproductive activity and population densities is considered to be a partitioning mechanism which might reduce competition (Applegate and Mullan, 1969; Jacobs, 1977; Seitz, 1980). Growth and development of each species population were monitored during the 1982 season to determine the degree of overlap between species.

The *D. ambigua* population developed approximately four weeks earlier than the population of *D. galeata mendotae* (Figure 3). All species of *Daphnia* were scarce prior to April, then the abundance of *D. ambigua* began increasing, finally peaking during the middle of May. The density of this species then decreased until the first week in June when its season was completed. The *D. galeata mendotae* population began growing about the time *D. ambigua* had peaked. It attained peak density during June and apparently completed its season by mid-July. Although lower in number, standing crops of *D. parvula* paralleled those of *D. galeata mendotae*, growing and reaching peak densities in June and completing its season by mid-July. All species of *Daphnia* were absent in samples collected after mid-July.

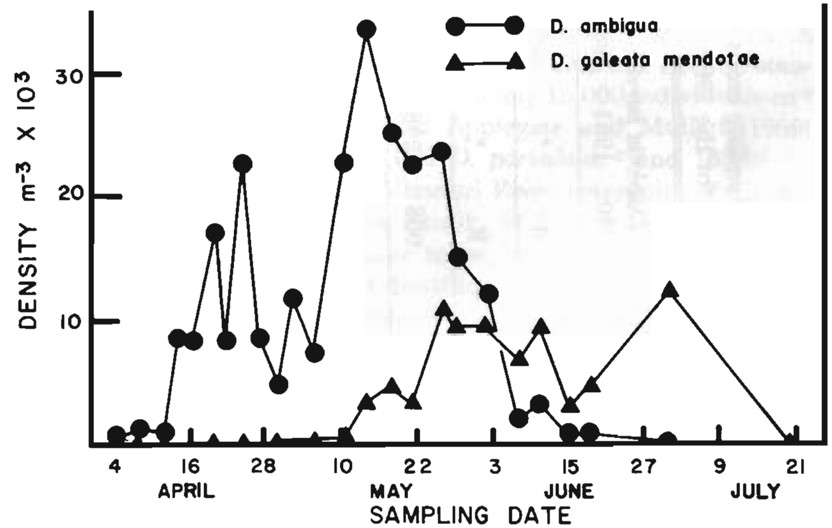

Figure 3. Comparison of estimated standing crops of *Daphnia ambigua* and *Daphnia galeata mendotae* per sampling date in Lake Reading for 1982.

Vertical Distribution of Species

Vertical distribution of daphnid species in Lake Reading was analyzed by taking multiple 10 liter samples with a Juday Plankton Trap. Three series of vertical samples were collected from 22 April to 7 May 1982 at one meter intervals from the surface to the bottom in the limnetic region of the lake. Although a comprehensive analysis was not possible during the course of this study, examination of the vertical samples collected revealed the *Daphnia* populations were concentrated in the top two meters of the lake and did not exhibit a vertical separation of the three species; however, additional work is needed to verify these preliminary observations.

Reproduction

Life Cycle. Daphnia populations usually winterover in ephippial eggs. During favorable conditions,the ephippial eggs develop into parthenogenic females. There then follows numerous broods of parthenogenic females. Eventually, in response to environmental conditions, some of the females produce eggs which develop into males; haploid eggs that become fertilized are encased by an ephippium which is derived from the dorsal part of the carapace (Edmondson, 1955; Pennak, 1978). Ephippial eggs are resistant to the adverse effects of desiccation and freezing and are well adapted for carrying the population through either winter or drought.

Development of the diploid, parthenogenic eggs occurs in the dorsal brood chamber of the female. Newly developed parthenogenic females are released during the molting process, and a new clutch of eggs enters the brood chamber. Clutch size and developmental times are variable and depend upon factors such as water temperature, age or size of the individual, food abundance, and chemical quality of the water (Hall, 1964; Lynch, 1978).

Mean Brood Size. Mean brood size per gravid female was based on the mean number of eggs for all females carrying eggs rather than for all mature females in the sample, because there is no morphological distinction between a reproductively mature female and a reproductively immature female (Hall, 1964). Population reproduction during 1982, in terms of mean brood size per gravid female, for *Daphnia parvula* and *D. ambigua* was greatest from mid-March to mid-April, and from late April to late May for *D. galeata mendotae.* Maximum brood sizes for each species occurred 8-16 days prior to the time that peak population densities occurred (Figures 4-6). Each population curve appeared to be unimodal, and reproductive efforts were greatest during the early part of the population's life and then declined, rapidly at first, and finally leveled-off at 1-2 eggs per gravid female for the remainder of the population's life span.

During the peak reproductive period for each species in 1982, *Daphnia parvula* had a larger mean brood size per gravid female than either *D. ambigua* or *D. galeata mendotae.* The mean brood size for *D. parvula* during peak reproduction was 9.5 eggs per gravid female, with brood sizes ranging from 6 to 18 eggs, and more than 40% of the population carried parthenogenic eggs. *Daphnia ambigua* broods averaged 8.6 eggs per gravid female during peak reproductive activity and approximately 20% or more of the population carried eggs. Brood sizes during this time span ranged from 7 to 12 eggs per gravid female. Less than 25% of the *D. galeata mendotae* population carried eggs during maximum reproduction. The mean brood size for this period was 4.8 eggs, with brood sizes ranging from 3 to 7 eggs per gravid female.

Population Reproduction. Egg production for all individuals in a population on a sampling date, regardless of whether or not they carried eggs, was determined by dividing the total number of eggs produced by the total number of individuals examined in samples on that date. During the 1982 reproductive season, *Daphnia parvula* produced approximately 2.2 eggs per individual per day, while *Daphnia ambigua* and *D. galeata mendotae* individuals produced 1.0 and 0.2 eggs, respectively. Values for egg production per individual per day during maximum reproductive activity for *D. parvula, D. ambigua,* and *D. galeata mendotae* were 6.8, 1.8, and 0.7, respectively.

Similar findings of greater reproductive activity early in a population's life span were reported by Seitz (1980) for *Daphnia hyalina, Daphnia galeata gracilis,* and *Daphnia cucullata.* In laboratory studies of *D. galeata mendotae,* Hall (1964) found mean brood sizes to range from 2.0 to 4.0 eggs with the maximum being 7.5 parthenogenic eggs per gravid female. Lei and Armitage (1980), reported laboratory populations of *D. ambigua* cultured at 10°C produced 1.3 eggs per individual per day. The greater reproductive rate estimated for Lake Reading during peak reproduction probably resulted, in part, from higher water temperatures which existed in the lake when *D. ambigua* was present. It is well documented that reproduction of many microcrustaceans is directly affected by water temperatures.

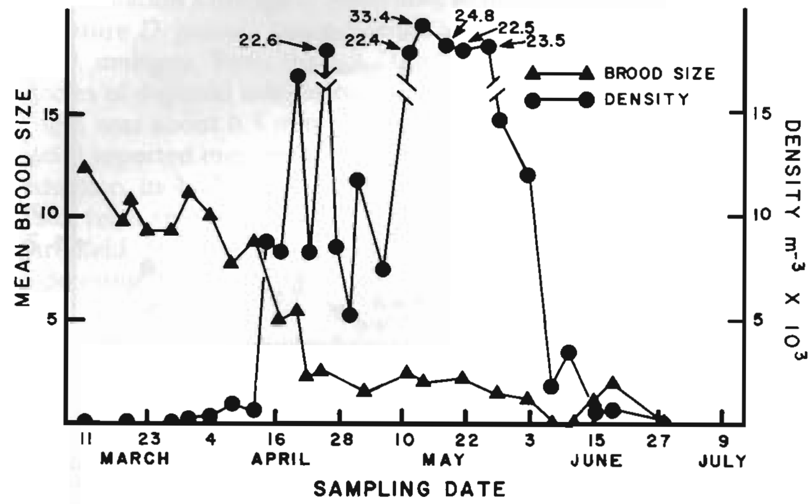

Figure 4. Comparison of mean brood size for gravid females and estimated standing crops per sampling date of *Daphnia ambigua* in 1982.

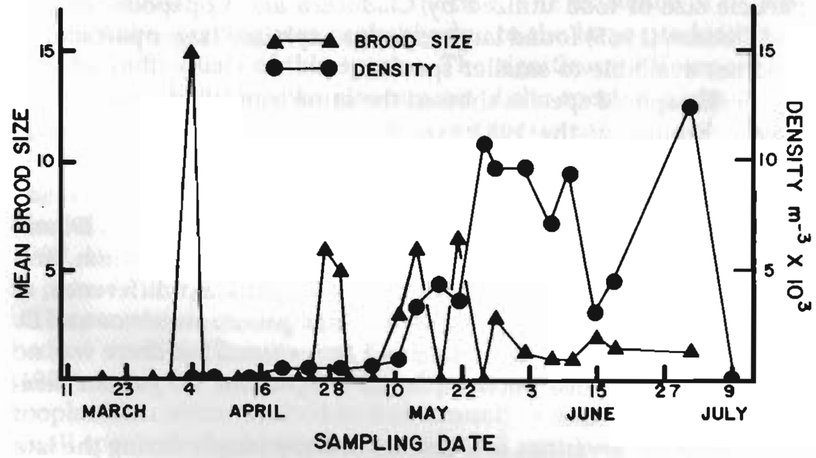

Figure 5. Comparison of mean brood size for gravid females and estimated standing crop per sampling date of *Daphnia parvula* in 1982.

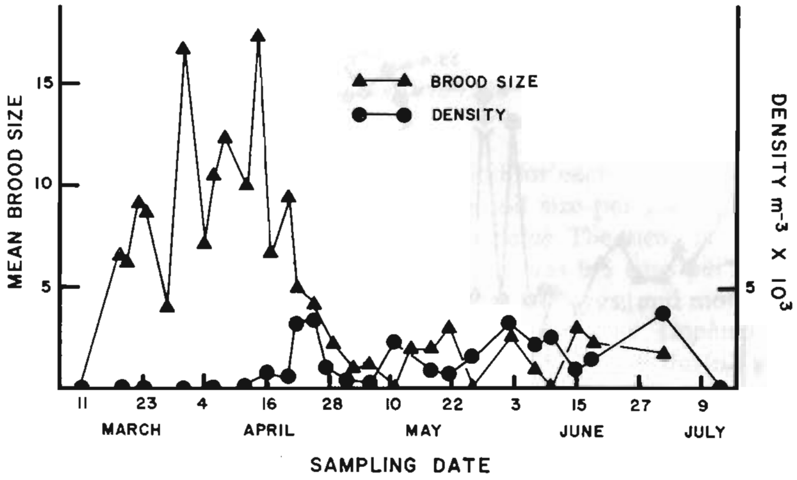

Figure 6. Comparison of mean brood size for gravid females and estimated standing crop per sampling date of *Daphnia galeata mendotae* in 1982.

Body Size

Growth is discontinuous in *Daphnia,* since size increases only during and immediately following ecdysis. Although numerous age and size categories are usually present in any natural population, the maximum length attained by *Daphnia* is apparently determined by the abundance of food (Hall, 1964). In studies completed on the particle size of food utilized by Cladocera and Copepoda, Brooks and Dodson (1965) found larger species exploited larger particles of food not available to smaller species.

Each daphnid species showed the same trends in terms of body length throughout the 1982 sampling period, a decrease in body length which coincided with a decline in population standing crops late in the season. During 1982, 95% confidence limits for mean body lengths for adult *D. galeata mendotae, D. parvula,* and *D. ambigua* in Lake Reading were 1.18 ± .03 mm, 1.13 ± .04mm, and 1.04 ± .01mm, respectively. There was a significant difference, at $p = 0.05$, between mean body lengths for *D. galeata mendotae* and *D. ambigua,* and between *D. parvula* and *D. ambigua,* but there was no significant difference between mean lengths for *D. galeata mendotae* and *D. parvula.*

Similar observations of a decline in body length during the late phases of a population's season of occurrence were reported by Applegate and Mullan (1969) and Brooks (1965). Applegate and Mullan (1969) found body lengths for reproductive adult *D. galeata*

mendotae, in Bull Shoals Reservoir, averaged 1.0 to 1.2 mm during the population's life span. According to Brooks (1957), body lengths of mature *D. parvula* range from .75 to 1.0 mm and about 1.0 mm for *D. ambigua.* Even though *D. galeata mendotae* was the largest species of daphnid inhabiting Lake Reading in 1982, its mean body length was about 0.5 mm less than during 1980 and 1981. Brooks (1957) reported members of this species reach 2.0 mm in length. A reduction in body size among individuals of a population may result from an adaptation which decreases predation (Brooks, 1965; Threlkeld, 1981). It was not possible during the course of my study to determine if the reduced body size of *D. galeata mendotae,* from 1980 to 1982, was an adaptation for greater utilization of the available food resource or a result of predation pressure.

CONCLUSIONS

The periods of occurrence for the three daphnid species inhabiting Lake Reading during 1982 overlapped. However, there was a separation among the species in terms of occurrence of peak population densities. Based on the data collected and analyzed during 1982, *D. ambigua* appeared to have taken over the role of dominant species of daphnid inhabiting Lake Reading. Even though *D. galeata mendotae* standing crops were large in 1982, the low egg production for this species suggests a reduction in relative abundance in future years could be expected. The existence of *D. parvula* in Lake Reading was probably due to the large production of eggs by individuals of this species. The significant differences between mean body lengths also suggested the species might utilize different particle sizes of food to allow coexistence.

A factor which may have caused the fluctuations of the daphid populations in Lake Reading was the introduction of the planktivorous threadfin shad *(Dorosoma pretense)* in the lake during 1980, 1981, and 1982 by Kansas Fish and Game fisheries biologists to provide forage for some game species of fish. Fish predation can influence a shift in zooplankton community structure to a smaller-bodied species (Brooks and Dodson, 1965). O'Brien and Kettle (1979) reported intense feeding by planktivorous fish on large zooplankton often resulted in a community composed primarily of small species, which may be less than 1.2 mm long as adults. This evidence suggests changes in the *Daphnia* community structure Lake Reading may have been a result of predation rather than competition among the species.

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