ZOOPLANKTON IN THE DISCHARGE OF LEWIS AND CLARK LAKE, SOUTH DAKOTA, 1964-73

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ABSTRACT

Crustacean zooplankton collected weekly from the discharge of Lewis and Clark Lake (South Dakota) from 1964 to 1973 with an automatic plankton sampler consisted principally of species from three major groups: cyclopoid copepods (68% of the total), calanoid copepods (20%), and daphnid cladocerans (9%). *Cyclops bicuspidatus thomasi* was the dominant species; its density was highest in spring and fall, and extremely low in summer. Total abundance of cyclopoid copepods was relatively high and similar during the first 6 years of sampling; during the last 4 years abundance was noticeably lower. Numbers of calanoid copepods increased slightly during the later years of the study; daphnid numbers fluctuated little over the entire sampling period. Decreased numbers of cyclopoids in the later years accounted for most of the observed changes in zooplankton abundance. Abundance in the discharge of Lewis and Clark was highly correlated with that in the discharge from Lake Francis Case, a reservoir immediately upstream.

INTRODUCTION

An automatic plankton sampling system enabled us to monitor zooplankton populations in discharges from Lewis and Clark Lake, South Dakota for a 10-yr. period including years when additional upstream reservoirs were filling, and thereafter. Cowell (1970) indicated that the abundance of zooplankton in this reservoir was influenced by zooplankton discharged from Lake Francis Case, the immediate upstream reservoir. We concluded from studies in 1966-70 that the composition and abundance of zooplankton in Lake Francis Case was dependent on events occurring in reservoirs farther upstream in the Missouri River system (Martin and Novotny 1977).

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In this study, zooplankton samples collected in the discharge of Lewis and Clark Lake in 1964-73 were analyzed to determine whether long-term changes in population density and structure occurred. This information was compared with similar data from three upstream main stem reservoirs (Fig. 1). Zooplankton populations monitored in the discharges from Lewis and Clark Lake have been shown to be an accurate indication of changes in species composition and abundance in the reservoir (Cowell 1967).

STUDY AREA

Lewis and Clark Lake is the smallest and farthest downstream of the six Missouri River reservoirs constructed by the U. S. Army Corps of Engineers for flood control, hydroelectric power, navigation, and irrigation. It is shallow, non-stratified, and has rapid rates of water exchange and only minor water-level fluctuations. Because of the rapid rates of water exchange, water temperatures are generally similar throughout the reservoir. At normal pool, mean depth averages 5 m and surface area about 113 km². Ice cover is present for most of 4 months, December through March, and mean water temperatures range from 1.4 C in January to 24 C in July. Average monthly temperatures are similar from year to year.

Additional hydrographic, physical, and chemical characteristics were described by Hudson and Cowell (1966), Cowell (1967), and Benson (1968).

Reservoir Discharge and Water Exchange

Annual discharges from Lewis and Clark Lake ranged from 1,530 million m³/mo in 1964 to 2,870 million m³/mo in 1971, and averaged 2,100 million m³/mo. Generally, discharges were progressively higher from 1964 through 1972. Discharge rates were inversely related to the water exchange rate, the time required for a volume of water equal to the storage capacity of the reservoir to be discharged. The average exchange rate was 9-13 days during 1964-67 when discharges from the Missouri system were low; increased to 7-8 days in 1968-72; and then decreased to 9 days in 1973.

Monthly water releases from Lewis and Clark Lake increased during April-November each year coinciding with the navigation season in the river downstream. Water exchange rates during these months were the most rapid, ranging from 6.1 to 7.2 days for the 10-yr. period, and averaging 4 to 5 days in the later years of sampling, when discharges were high. Exchange rates from December through March were 10-15 days.

Lewis and Clark Lake and the other two reservoirs downstream from Lake Oahe, the largest main stem storage reservoir (Fig. 1),

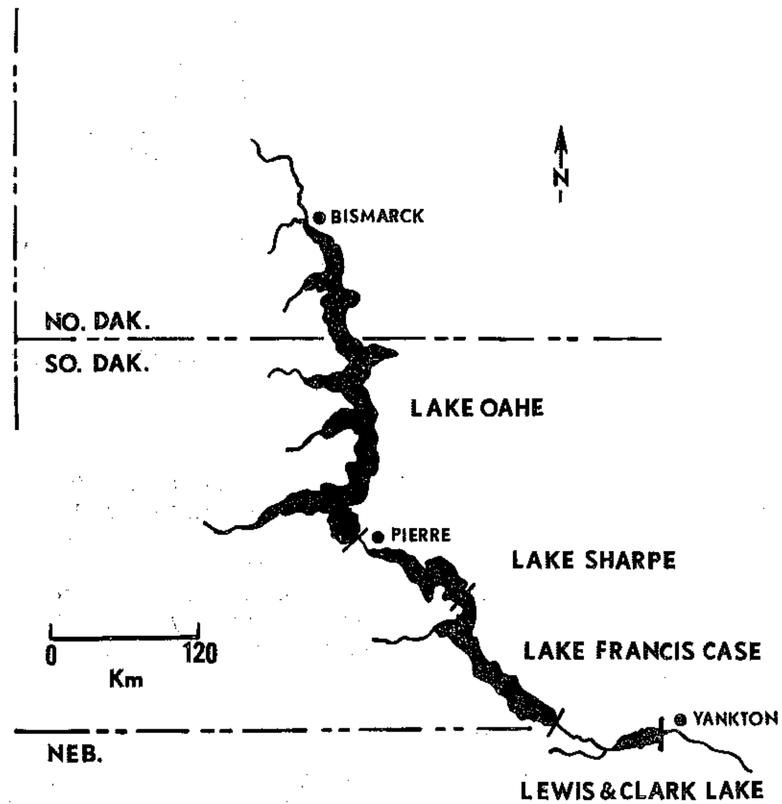

Figure 1. Missouri River reservoirs in South Dakota.

are used primarily for hydroelectric power generation and flow reregulation, and to a lesser extent storage. Flow through these reservoirs is relatively rapid and dependent on discharge from Lake Oahe.

METHODS

Throughout the 10-yr. study period, weekly average standing crops and composition of the Copepoda and Cladocera were determined, and population fluctuations of the various taxa were defined. Water from the reservoir discharge was sampled for 15 min., four times daily at 6-hr. intervals with an automatic plankton sampler (Swanson, 1965) located in the Gavins Point Dam powerhouse. The reliability of this system for sampling zooplankton populations in the discharges from Missouri River reservoirs was shown by Cowell (1967, 1970), Selgeby (1968), and Martin and Novotny (1977).

The intakes of the powerhouse draw from a water stratum 10 m thick, from about 3 m below the surface to the bottom of the reservoir. Zooplankton was filtered from 5,000 to 15,000 liters of water per week and preserved automatically in the sampler. Once per week it was washed from the stainless steel filtering screen (140 μm mesh) and preserved with modified Lugol's solution for laboratory analysis.

We used procedures given by Cowell (1967, 1970) and Martin and Novotny (1977) to identify and count plankton in the samples. Copepod nauplii were not counted because the catch efficiency of the sampling apparatus for these small organisms was low. No effort was made to identify copepodites to species.

Hydrographic information was obtained from the U. S. Army Corps of Engineers (Omaha District).

RESULTS

Cyclopoid copepods, calanoid copepods, and daphnid cladocerans made up about 95% of the crustacean zooplankton in Lewis and Clark Lake during 1964-73 (Table 1). Miscellaneous cladocerans accounted for most of the remainder; harpacticoid copepods and parasitic copepods were present in trace numbers. The three major zooplankton groups showed similar seasonal cycles-a dominant spring pulse in June and a secondary winter pulse in December and January (Fig. 2).

Annual and Seasonal Distribution of Cyclopoid Copepods

Cyclopoid copepods were the most numerous organisms collected during the 10 years. Weekly densities averaged 6,986/m^3 and ranged from 1,719/m^3 in 1971 to 13,681/m^3 in 1964 (Table 1). Standing crops were highest in 1964, generally decreased through 1971, and then increased slightly in 1972 and 1973 (Fig. 3). Annual numbers of cyclopoid copepods discharged were highest from 1964 to 1969, a 6-yr. period during which they accounted for 76% of the total zooplankton; numbers were much lower in 1970-73 when they accounted for 54% of the total (Fig. 4).

Cyclops bicuspidatus thomasi was numerically the dominant cyclopoid species during all years, making up 46% of the total adult zooplankton collected (Table 1). Its density was highest during 1964-67, and considerably lower in 1968-73. Standing crops were highest in 1967 and lowest in 1972.

This species made up 74-95% (average, 87%) of the total adult cyclopoids. Although its density diminished during the later years, no other cyclopoid species became dominant. The contribution of adult *C. bicuspidatus thomasi* to the total zooplankton diminished from 56% in 1964-67 to 27% in 1968-73.

TABLE 1

Estimated mean numbers (no./m^3 per week) of zooplankters in the discharge waters of Lewis and Clark Lake, 1964-73

(Percent of yearly total in parentheses.)

Group and taxon	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Cyclopoid copepods										
Cyclops bicuspidatus thomasi	3,363	2,188	4,230	5,002	1,287	1,082	769	495	462	637
C. vernalis	304	208	157	372	20	153	28	18	12	139
Mesocyclops edax	56	50	59	104	54	41	42	55	49	85
Eucyclops agilis	492	3	4	15	8	9	4	6	8	4
E. agilis montanus	3	0	0	0	T	T	T	0	2	2
E. prionophorus	0	0	0	0	0	0	0	0	2	0
Tropocyclops prasinus	0	1	0	T	0	0	0	0	0	T
Paracyclops fimbriatus poppei	0	0	0	0	0	0	0	0	0	T
Macrocyclops albidus	0	0	T	1	0	0	0	0	0	0
C. varicans rubellus	5	0	T	0	1	6	4	4	1	T
Copepodites	9,458	8,787	2,919	4,622	6,071	5,951	2,431	1,141	1,973	4,339
Total	13,681 (74)	11,237 (83)	7,369 (82)	10,116 (82)	7,441 (65)	7,242 (73)	3,278 (63)	1,719 (45)	2,509 (51)	5,206 (58)
Calanoid copepods										
Diaptomus siciloides	230	249	155	149	70	45	383	527	396	1,079
D. ashlandi	222	87	90	200	699	482	261	229	174	114
D. forbesi	62	71	72	39	104	104	89	121	234	72
D. clavipes	142	40	12	45	33	8	8	17	17	29
D. sicilis	49	20	50	36	31	6	9	13	13	15
Copepodites	265	215	364	488	1,804	980	629	825	896	989
Total	970 (5)	682 (5)	743 (8)	957 (8)	2,741 (24)	1,625 (16)	1,379 (27)	1,732 (45)	1,730 (35)	2,298 (26)

Group and taxon	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Daphnid cladocerans										
*Daphnia pulex-schödleri**	353	584	591	699	1,086	870	387	296	529	968
D. galeata mendotae	451	177	113	157	130	61	56	36	78	18
D. retrocurva	50	50	35	147	5	69	39	7	10	275
Total	854	811	739	1,003	1,221	1,000	482	339	617	1,261
	(5)	(6)	(8)	(8)	(11)	(10)	(9)	(9)	(12)	(14)
Miscellaneous cladocerans										
Bosmina longirostris	2,957	822	51	191	39	63	8	5	24	56
Diaphanosoma brachyurum	15	0	34	25	26	28	36	48	79	57
Chydorus sphaericus	1	0	0	4	T	0	T	1	5	6
Alona costata	0	0	0	0	0	0	T	0	0	0
Ceriodaphnia pulchella	T	0	0	T	T	6	T	T	T	3
Alonella rostrata	T	0	0	T	0	0	0	T	0	0
Leptodora kindtii	3	T	1	2	5	1	1	T	1	6
Moina brachiata	45	0	2	5	2	11	2	1	3	31
Simocephalus serrulatus	0	0	0	0	0	0	0	T	0	0
Pleuroxus denticulatus	0	0	0	0	0	T	0	T	0	0
Macrothrix laticornis	0	0	0	0	2	0	0	T	0	0
Sida crystallina	0	0	0	T	T	0	0	0	0	0
Total	3,021	822	88	227	74	109	47	55	112	159
	(16)	(6)	(1)	(2)	(1)	(1)	(1)	(1)	(2)	(2)
Grand Total	18,526	13,552	8,939	12,303	11,477	9,976	5,186	3,845	4,968	8,924

(*) **Daphnia pulex** and **D. schodleri** have been included in one group because of the close similarity of these two species in Missouri River reservoirs. This complex has recently been referred to as a separate species, **D. pulicaria.** (Brandlova et al., 1972; personal communication, A. Repsis, Nalco Environmental Sciences, Lincoln, Nebraska).

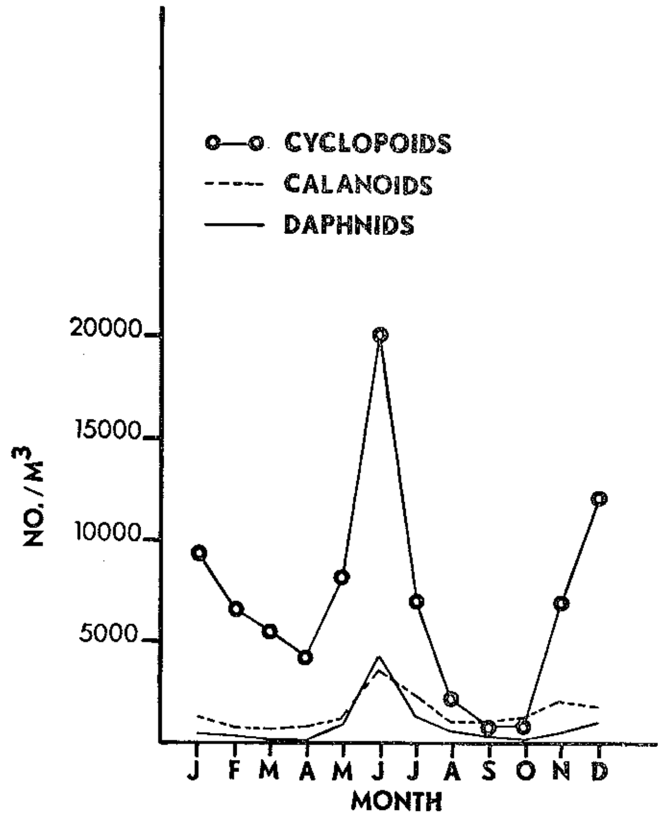

Figure 2. Seasonal distribution of cyclopoids, calanoids, and daphnids in Lewis and Clark Lake discharges, 1964-73.

The seasonal distribution of adult *C. bicuspidatus thomasi* in 1964-73 was characterized by maximum standing crops in spring, when water temperatures were between 19-24 C, and reduced standing crops in most of the summer and fall (Fig. 5). In most years, an additional pulse occurred during late fall or in winter, when water temperatures were rarely above 5 C. Because the timing of this second pulse was somewhat variable, occurring randomly during a 4-mo. period from November through February, the average seasonal distribution of *C. biscuspidatus thomasi* appeared to be only weakly bimodal; the irregularity in time of occurrence of the second pulse tended to obscure the secondary maxima.

Cyclops vernalis was the second most abundant cyclopoid species, composing 6% of the adult cyclopoid population (Table 1).

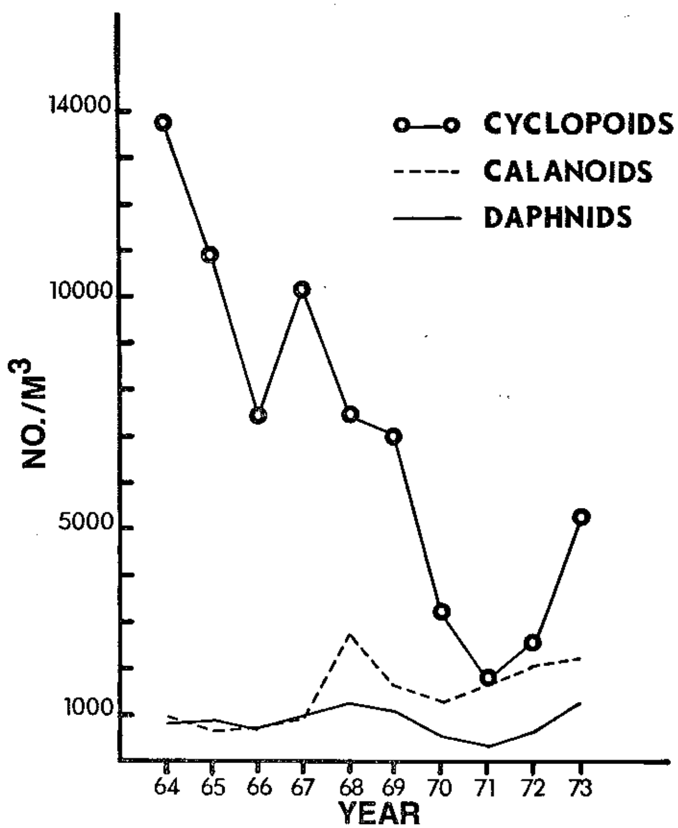

Figure 3. Annual mean numbers of cyclopoids, calanoids, and daphnids, from Lewis and Clark Lake between 1964-73.

Numbers of this species collected varied among years, but densities were generally higher in 1964-67 than in 1968-73. Over 80% were collected in a 9-wk. period during the summer when water temperatures were above 23 C (Fig. 5). Nearly all the rest were taken in spring and fall; few were collected in winter.

The only other cyclopoid species that occurred in significant numbers were *Eucyclops agilis* and *Mesocyclops edax* (Table 1). These species (combined) made up about 5% of the total cyclopoids. *E. agilis* was most abundant in 1964 with few found thereafter. *M. edax* was present in nearly constant numbers throughout the 10 years; its seasonal abundance was bimodal, the population maxima occurring in spring and in fall when water temperatures

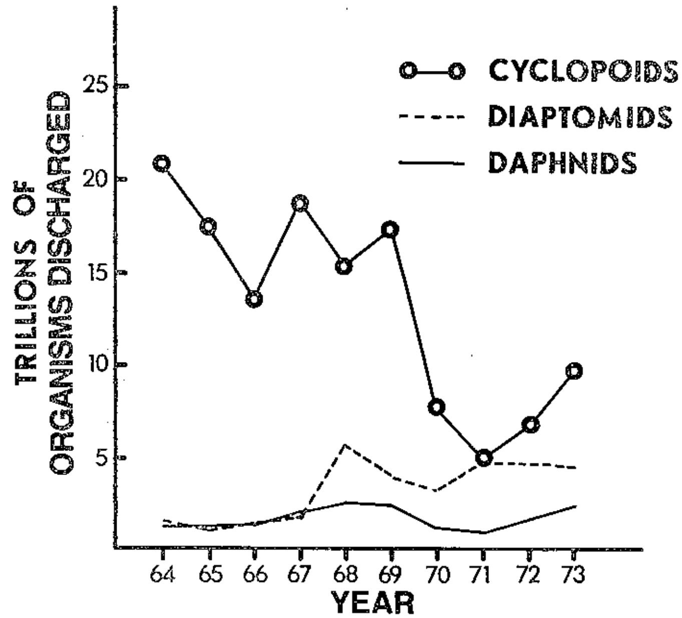

Figure 4. Total numbers of cyclopoids, calanoids, and daphnids discharged from Lewis and Clark Lake, 1964-73.

were 19-20 C (Fig. 5). No *M. edax* were collected from December through March, when water temperatures were lower than 5 C. Six other cyclopoid species *(Eucyclops agilis montanus, E. prionophorus, Tropocyclops prasinus, Paracyclops fimbriatus poppei* and *Macrocyclops albidus)* were identified, but considered incidental because they accounted for less than 1% of the total adult cyclopoids.

Copepodites made up 68% of the total number of cyclopoid copepods. In general, the abundance of copepodites was greatest in the earlier years and lowest in 1970-72 (Table 1). The seasonal distribution of cyclopoid copepodites closely resembled that of *C. bicuspidatus thomasi* (Fig. 5), peak numbers occurring in spring and in mid-winter. The spring peak was the more pronounced, but the winter peak was the more prolonged. About 30% of the copepodites were captured during each peak period and the rest were distributed through the rest of the year.

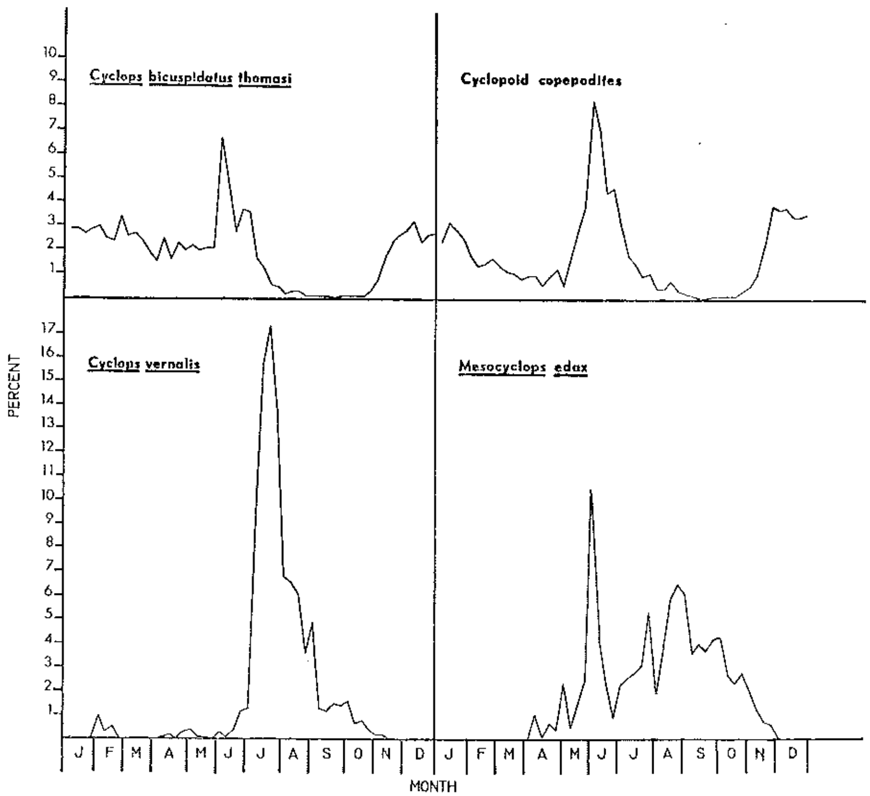

Figure 5. Seasonal distribution (percent by week) of cyclopoids in Lewis and Clark Lake discharges, 1964-73.

Annual and Seasonal Distribution of Calanoid Copepods

Calanoid copepods were the second most abundant zooplankton group, and were the only group whose numbers generally increased over the 10-yr. period (Figs. 3 and 4). Standing crops ranged from 682 to 970/m^3 in 1964-67 but more than doubled in 1968 and remained relatively high through 1973, averaging 1,918/m^3 (Table 1). Calanoids accounted for 8% of the total zooplankton taken in 1964-67 and for more than 30% in 1968-73. The shift resulted from the combined effects of reduced cyclopoid populations and increased calanoid populations during 1968-73.

Diaptomus siciloides and *D. ashlandi* made up 55% and 35% of the adult calanoids, respectively (Table 1). Annual densities of *D. siciloides* were highest in 1970-73, whereas, *D. ashlandi* varied randomly with no apparent long-term trend. These two species combined, accounted for about 15% of the total adult zooplankton throughout the 10 year study.

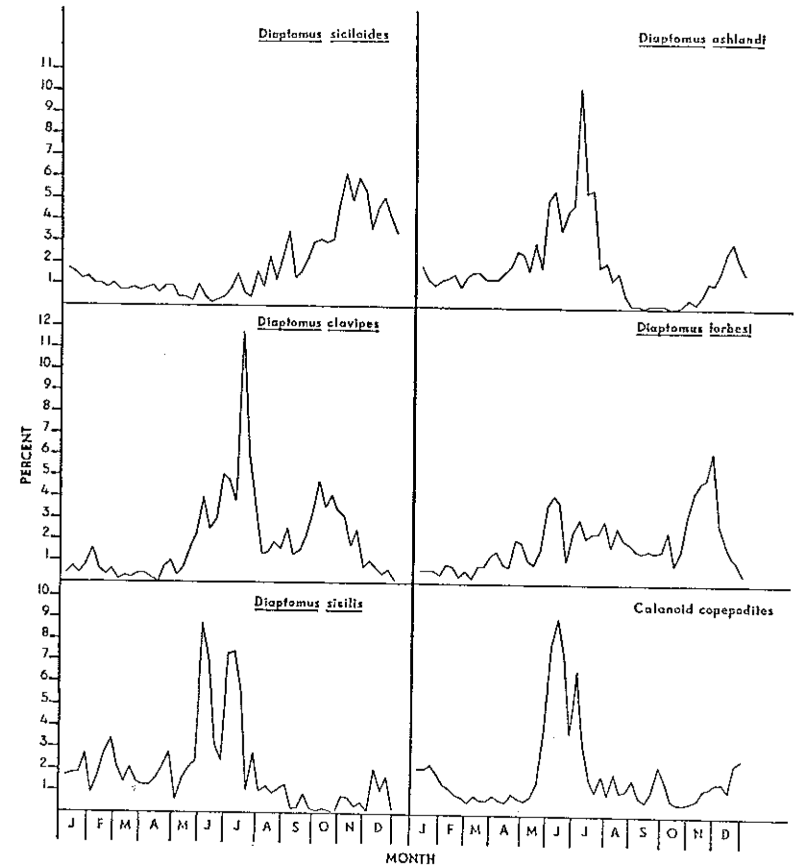

Figure 6. Seasonal distribution (percent by week) of calanoids in Lewis and Clark Lake discharges, 1964-73.

Diaptomus siciloides was most abundant during late fall and early winter with few collected during the spring and early summer (Fig. 6). Numbers increased irregularly throughout the summer, toward a maximum in November and December.

Diaptomus ashlandi was most abundant during late spring and early summer (Fig. 6), when water temperatures increased from 15 to 23 C. The species was practically absent from the plankton during August, September, and October, when water temperatures were decreasing from 23 to 6 C. A weak population pulse occurred in early winter.

Other calanoid species collected were *D. forbesi, D. clavipes* and *D. sicilis,* which made up 13, 5, and 3% of the total adult calanoids, respectively. None of these species displayed distinct overall trends in annual abundance. Generally, *D. clavipes* and *D. sicilis* were more abundant during the early years, and *D. forbesi* was more abundant during the later years (Table 1).

The standing crop of *D. forbesi* varied throughout the year; moderate peaks occurred during a 3-wk. period in spring, and a 6-wk. period in late fall. About 50% of the yearly numbers were taken in spring, when water temperatures were above 19 C, and 25% in late fall, when water temperatures were between 4 and 9 C.

Diaptomus clavipes and *D. sicilis* were most abundant in mid-summer, when water temperatures were 20-23 C. *D. clavipes* showed a late-fall pulse, whereas *D. sicilis* was abundant only during summer; few of either species were taken during the rest of the year.

About 50% of the total calanoid copepods collected during the study were in the copepodite stage, and nearly 50% of the copepodites occurred in an 8-wk. period in June and July. Reduced numbers of copepodites were distributed randomly throughout the rest of the year.

Annual and Seasonal Distribution of Cladocerans

Daphnid standing crops averaged 833/m³ and ranged from 339 to 1,261/m³ during 1964-73 (Table 1). Standing crops varied irregularly among years, and no trends were noted during the 10 years. Because cyclopoid densities were reduced and fluctuations in daphnid standing crops were relatively minor, daphnids made up slightly higher percentages of the total zooplankton during the later sampling years.

Daphnia pulex and *Daphnia schödleri* could not be reliably separated because certain morphological characteristics overlap in specimens from the Missouri River reservoirs (Cowell, 1970; Martin and Novotny, 1977). Therefore, these species were treated as a single taxon. Recently, some workers have referred to these two forms as *D. pulicaria* (Brandlova et al. 1972; personal communication, A. Repsis, Nalco Environmental Sciences, Lincoln, Nebraska).

The *Daphnia pulex-schödleri* complex made up 76% of the daphnids and 14% of the total adult zooplankton. Annual abundance was variable, and no trend with time was evident during the 10 years (Table 1). About 70% of the organisms of this complex were taken during an 8 wk. interval in May, June, and early July, when water temperatures were between 15 and 23 C (Fig. 7).

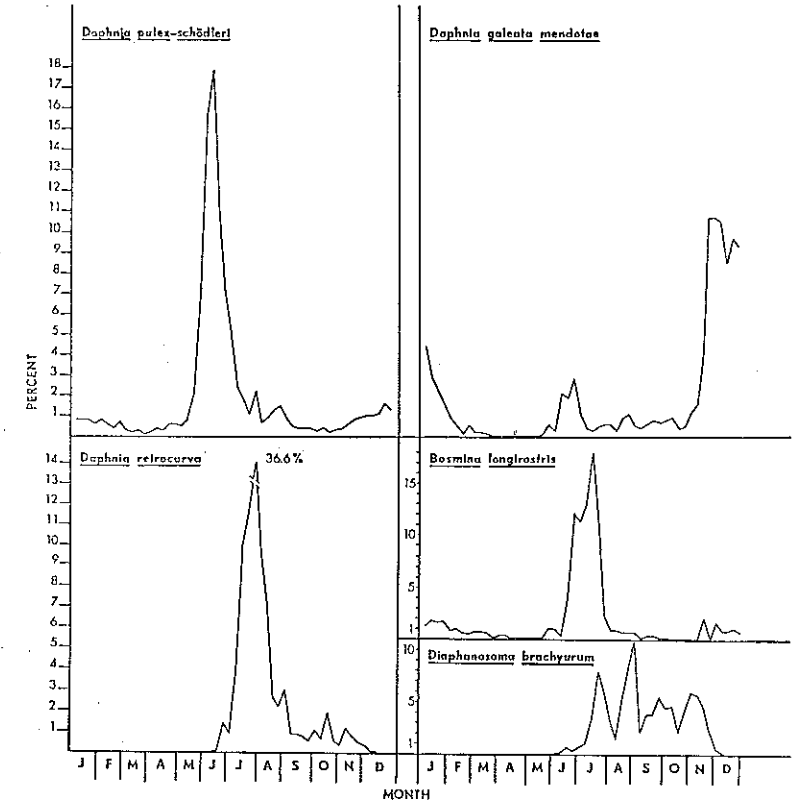

Figure 7. Seasonal distribution (percent by week) of cladocerans in Lewis and Clark Lake discharges, 1964-73.

This early-summer maximum was followed by a weak pulse in December.

Daphnia galeata mendotae and *D. retrocurva* were the only other daphnid species collected; they accounted for 15 and 8% respectively of the total daphnids (Table 1). Densities of *D. galeata mendotae* were higher during the earlier years of sampling than during the later years. Annual densities of *D. retrocurva* varied; numbers were highest in 1973 and low in 1968 and 1971. Numbers of *D. galeata mendotae* were highest from November to January (Fig. 7); over 75% occurred during this winter pulse (water temperature < 5 C). A minor pulse in June accounted for another 10% of the total; this secondary peak coincided roughly with peak densities of *D. pulex-schödleri.* The abundance of *D. galeata mendotae* was low during the rest of the year. About 90% of the *D.*

retrocurva were collected during July and August, when water temperatures were above 23 C (Fig. 7). This species was not collected from mid-December through May in any year.

Bosmina longirostris and *Diaphanosoma brachyurum* were minor components of the total zooplankton. The seasonal occurrences of these species were similar to those of the daphnids in that the major portion of each population was characteristically restricted to certain periods of the year (Fig. 7). Nearly 75% of the *B. longirostris* were taken during June and July; numbers were small during the rest of the year. *D. brachyurum* occurred in a series of sporadic pulses from July through December.

The occurrence of *B. longirostris* in unusually high densities during 1964 and part of 1965, especially during the cold-water months of December to March (Table 1) was considered an anomaly. Normally, the species was most abundant during June and July (Fig. 7). Other miscellaneous species of Cladocera accounted for about 1% of the total zooplankton.

Relation of Zooplankton in Lewis and Clark Lake to that in Upstream Reservoirs

Over 98% of the variation in the total zooplankton abundance in the discharge from Lewis and Clark Lake was associated with similar variation in zooplankton discharged from Lake Francis Case, the reservoir immediately upstream. Cyclopoids were most highly correlated (98.6%); calanoids only slightly less (93.1%); and daphnids the least (75%).

June (1974) and Martin and Novotny (1977) showed that similar trends in abundance of all three major groups of zooplankton occurred in corresponding years in Lake Oahe (the first large storage reservoir upstream), Lake Francis Case, and Lewis and Clark Lake (Fig. 8). Daphnids and calanoids were most abundant in 1968 and cyclopoids in 1967. These trends were observed during 1966-70, the only years when comparable data were available in all three reservoirs.

Total quantitative estimates of the three zooplankton groups were highest in Lake Oahe, and progressively diminished downstream (Fig. 8). June and O'Bryan (unpublished, U. S. Fish and Wildl. Serv., North Central Reservoir Investigations, Yankton, S. D.) indicated that zooplankton densities in Lake Sharpe were lower than in Lake Oahe, and higher than in the downstream reservoirs in 1966-70. Densities in Lewis and Clark Lake discharges were substantially lower; cyclopoids and calanoids averaged 40% fewer and daphnids 25% fewer than in the Lake Francis Case discharges. Kallemeyn and Novotny (1977) showed that the progressive down-

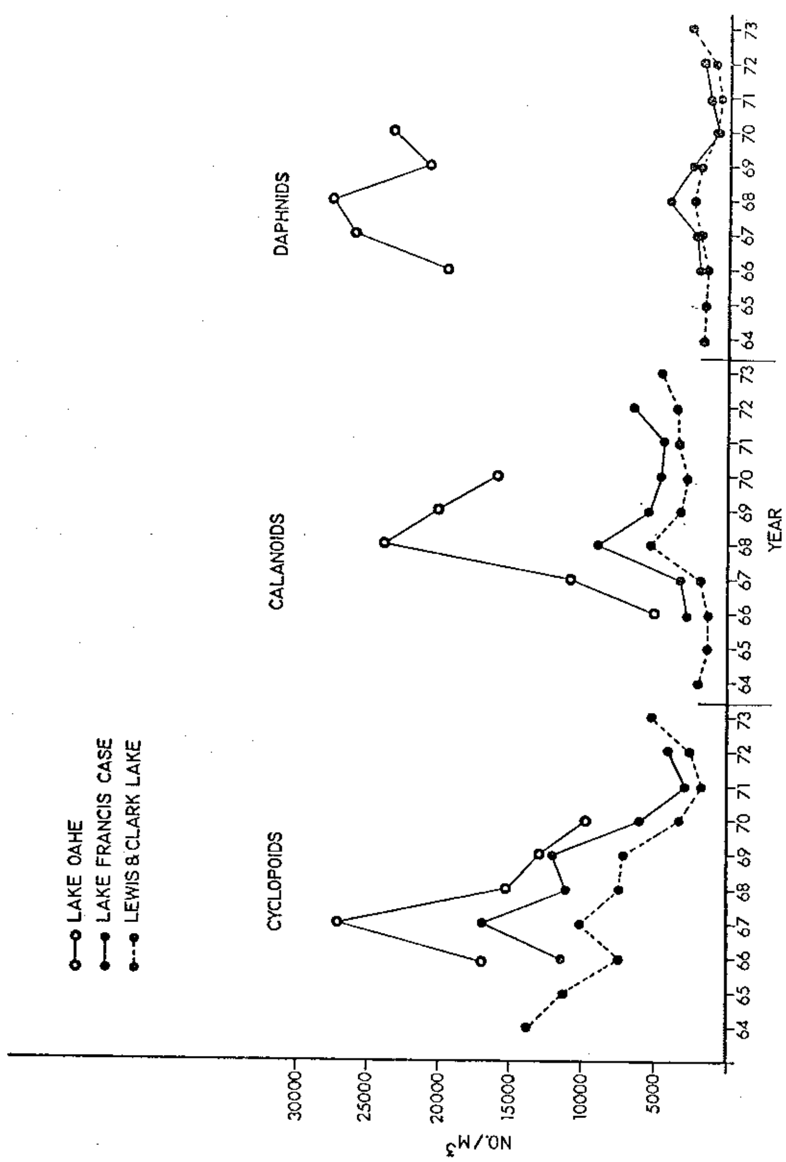

Figure 8. Abundance of zooplankton in the discharges from Lakes Oahe, Francis Case, and Lewis and Clark, 1964-73.

stream reduction in densities observed between reservoirs continued downstream in the Missouri River, below Lewis and Clark Lake.

DISCUSSION

The zooplankton populations in Lewis and Clark Lake generally differed from the typical lake zooplankton community; which, for example, could be expected to have one or two species of copepods and two or three species of cladocerans, among which one species was dominant (Pennak 1957). In Lewis and Clark Lake discharges, it was common to have four to six species of copepods and two to five species of cladocerans present at any given time, especially during the summer. Two similarities did occur between Pennak's "typical" community structure and the zooplankton collected during this study: (1) during months of low reservoir discharge there were brief periods when the zooplankton community did resemble the typical situation; and (2) one species, *Cyclops bicuspidatus thomasi*, dominated the plankton in the discharge during most of the 10-yr. period.

Cyclops bicuspidatus thomasi was the most common zooplankton species found in other Missouri River reservoir studies (Selgeby 1968; Cowell 1967, 1970; Martin and Novotny 1977). It was especially abundant in 1964-67, whereas standing crops after 1969 were greatly reduced in all reservoirs. These reductions were not associated with offsetting increases in other species.

Predation by young-of-the-year fish has been shown to alter the structure and abundance of zooplankton populations (Johns 1964; Galbraith 1967). However, no significant relations were found between the abundance of young-of-the-year fish (Walburg 1976) and that of zooplankton in Lewis and Clark Lake.

Previous investigations have indicated that the composition and dynamics of zooplankton in the discharge of Lewis and Clark Lake were closely correlated with those in the discharge of Lake Francis Case, the reservoir immediately upstream (Cowell 1967, 1970). We confirmed that abundance of zooplankton in the discharges of the two reservoirs was closely correlated throughout the 10 years of sampling. In addition, studies by Martin and Novotny (1977) led to a hypothesis that the abundance of zooplankton in Lake Francis Case was influenced by that in reservoirs upstream.

A series of lakes can be closely linked, especially if water exchange rates are rapid (Tonolli, 1955). Trophic conditions occurring upstream can be transported throughout the system, and accompanying biotic factors respond accordingly.

Lake Oahe, which has three times more storage capacity than

the three downstream reservoirs combined (Benson 1973), was filling during the early years of the present study and therefore discharges in the system downstream were reduced. The inundation of vegetation and organic debris as Lake Oahe filled resulted in an influx of nutrients that affected the lower three reservoirs as the water moved downstream (Martin and Novotny 1977). Reduced rates of water exchange and increased supplies of organic matter and nutrients provided the potential for higher zooplankton densities along the entire system in 1964-69.

After 1969, the flooding of additional shoreline areas of Lake Oahe was limited, and inundation of previously unflooded land was essentially halted. Consequently, the influx of large amounts of organic matter into the system was stopped. When the system reached operational pool levels in late 1967 (June 1974), the amount of water discharged from Lake Oahe increased. The amount of water discharged through the system has since been related to the amount of runoff in the upper Missouri River drainage basin.

The effects of these upstream perturbations were evident in the zooplankton standing crops in the discharge from Lewis and Clark Lake. Densities of cyclopoid copepods appeared to be the most strongly influenced by changes in the system. In 1964-69, total cyclopoid standing crops were relatively high, but as discharges remained high or increased, standing crops decreased (Fig. 4). The effects of the upstream conditions on standing crops of calanoid copepods were more subtle. Calanoids increased gradually during the 10 years, and accounted for a higher percentage of the zooplankton population in the last four years. Daphnid standing crops were apparently unaffected by factors that influenced the cyclopoids and calanoids.

Trophic conditions in lakes are influential in determining numbers and structure of the zooplankton standing crops. In lakes with high productivity, zooplankton standing crops are dominated by cyclopoids and cladocerans, whereas in those of lower productivity, the plankton is less abundant and is dominated by calanoids (Zyblut 1970; Patalas 1972). No evaluation of the trophic conditions in Lewis and Clark Lake is available for the 10 years of our study. We hypothesize, however, that the increased organic materials coming from Lake Oahe during the first six years were at least partly responsible for the higher standing crops of cyclopoid copepods downstream. Likewise, the lower standing crops during the last four years of our study were partly a response to a reduction in organic matter in the system.

Factors affecting the zooplankton standing crops in Lewis and Clark Lake discharges probably originated in Lake Oahe and continued through the system. Specific cause-and-effect relations were difficult to establish because of the lack of supplemental long-term data. However, the combination of varying rates of discharge and organic influx into the upstream reservoirs could have affected the densities of zooplankton in Lewis and Clark Lake discharges and resulted in reduced standing crops in the later years of the sampling period. These reduced densities were due to decreases in cyclopoids, primarily *C. bicuspidatus thomasi.*

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