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Aspects of the Feeding Ecology of the Bonneville Cisco of Bear Lake, Utah-Idaho

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ASPECTS OF THE FEEDING ECOLOGY OF THE BONNEVILLE

CISCO OF BEAR LAKE, UTAH-IDAHO

by

David C. Lentz

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<div align="right">David C. Lentz</div>

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ABSTRACT

Aspects of the Feeding Ecology of the Bonneville

Cisco of Bear Lake, Utah-Idaho

by

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Utah State University, 1986

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The Bonneville cisco (Prosopium gemmiferum), a small planktivorous whitefish, is an important part of the distinctive fish community of Bear Lake, Utah-Idaho. The Bonneville cisco plays a key role in the trophic structure by converting zooplankton to fish biomass and providing a major forage source for cutthroat and lake trout. Aspects of cisco feeding ecology studied include characterization of the zooplankton community composition and dynamics and cisco feeding habits and prey selection.

Composition and seasonal dynamics of the zooplankton community were determined for a fifteen month period during 1981-1982. The community was dominated by a calanoid copepod, Epischura, and a colonial rotifer, Conochilus. Cladocerans, primarily Bosmina and Diaphanosoma, comprised only a minor portion of the community, never exceeding five percent. The diel vertical distribution of the zooplankton was examined during five months in 1981. Zooplankton were concentrated in the epilimnion and metalimnion and no evidence of diel

vertical migration was detected with the 10 m depth interval sampling scheme used. Some cladocerans were found to utilize refuges in the epilimnion and hypolimnion to avoid intense predation pressure by cisco.

Food habits and prey selection of cisco were examined during five months of 1981. Changes in the zooplankton community were reflected by changes in the food composition of cisco from previously reported studies in 1943. The dominant zooplankter, Epischura, remained an important food item for cisco. Departing from historical information, cladocerans like Diaphanosoma and Daphnia were major food items during periods of seasonal peak abundance. Cladocerans were consistently the most preferred prey items, being utilized in greater proportion than their abundance in the plankton. Also, cladocerans and copepods were nearly always preyed on in size-selective fashion.

Cisco were brought into the laboratory to determine feeding modes they used to capture prey. The reactive distance, or the minimum distance at which the predator can locate specific prey items, was determined for three sizes of Daphnia prey. Cisco were found to have superior prey location ability than other salmonids reported in the literature, having the ability near that of some centrarchids.

Characteristics of copepods and cladocerans such as their repro-ductive strategies, sizes, movement patterns, evasive capabilities and pigmentation were examined in relation to their importance in affecting cisco diets and prey selection. Cisco predation was clearly related to the vertical distribution and dynamics of some zooplankton prey.

(77 pages)

INTRODUCTION

The Bonneville cisco (<u>Prosopium</u> <u>gemmiferum</u>) is an important member of the fish community of Bear Lake, Utah-Idaho. The cisco is one of four endemic Bear Lake fishes, along with two other whitefish (<u>P.</u> <u>spilonotus</u> and <u>P.</u> <u>abyssicola</u>) and a sculpin (<u>Cottus</u> <u>extensus</u>). The cisco is probably the most numerous fish in Bear Lake and represents a significant portion of total fish biomass (McConnell et al. 1957).

The cisco has a key role in the trophic structure of Bear Lake. Cisco remain planktivores throughout life and are very important in converting zooplankton to fish biomass in the limnetic zone of the lake. The Bonneville cisco is a major source of forage for the native cutthroat trout, a large, piscivorous, lacustrine race of <u>Salmo</u> <u>clarki</u> and the introduced lake trout (<u>Salvelinus</u> <u>namaycush</u>). In addition to its importance as a coldwater forage species the cisco provides a sport fishery during its January spawning run in the shallow rocky zones of Bear Lake.

The Bonneville cisco represents a relict population which had a wider distribution in prehistoric Lake Bonneville (Stokes et al. 1964). Behnke (1972) states that the Bonneville cisco with its slim, terete body form, larger mouth and distinctly superior jaw is an excellent example of evolutionary convergence and is phenotypically similar to other pelagic coregonid ciscoes such as <u>Coregonus</u> <u>albula</u>. These characteristics, the shape of its mouth and long, closely spaced gill rakers make the cisco well adapted to life as a limnetic zooplankti-vore.

Previous workers at Bear Lake have provided knowledge on aspects of biology and ecology of the fish and plankton communities. Perry's (1943) study of cisco revealed information on age and growth, food habits, seasonal distribution and spawning. Others (Loo et al. 1964; McConnell et al. 1957; Sigler and Workman 1978) have added to this basic knowledge but many aspects of the life history and ecology of the cisco remain unstudied. The zooplankton was originally studied by Kemmerer et al. (1923) and was restudied by Perry (1943) and Nyquist (1968).

Objectives

An active area of research in aquatic ecology for the past twenty years has been the role of predation in structuring aquatic communities (Brooks and Dodson 1965). The goal of this study was to provide current information about aspects of the feeding ecology of the Bonneville cisco and improve the understanding of trophic structure and interactions in Bear Lake. Specific objectives included:

1) Determine limnetic zooplankton community structure.

2) Determine diel vertical distribution of limnetic zooplankton.

3) Determine the diet composition and prey selection of adult and subadult cisco in the limnetic zone of the lake.

4) Determine the cisco's reactive distance to prey.

METHODS

Bear Lake is a large, old lake on the border of Utah and Idaho. For an estimated 8000 years BP, Bear Lake was a closed basin lake (Robertson 1978). After 1912, the Bear River was diverted through a marsh into Bear Lake for the purpose of irrigation water storage and power generation. The lake is oval-shaped, with a length of 34 km, width of 14 km and shoreline of 81 km. Maximum depth is 63.4 m, mean depth is 30 m and the surface area is 282 km^2. Historical and current water quality and chemical conditions are described elsewhere (Kemmerer et al. 1923; Lamarra et al. 1983).

Collection of cisco for food studies took place during summer stratification. Cisco apparently avoid the epilimnion with temperatures greater than 15 degrees C. The metalimnion, during 1981, was the site of peak chlorophyll a values below 20 m and a metalimnetic maximum of dissolved oxygen (Lamarra et al. 1983). A map with locations of cisco and zooplankton community sampling is presented in Figure 1.

Zooplankton Sampling

To examine limnetic zooplankton community structure, samples were taken with vertical hauls of a Wisconsin type plankton net. The net was constructed of 80 micron mesh Nitex cloth and had a mouth diameter of 11.5 cm. A series of tow samples from several depths were collected biweekly from April 1981 to December 1981 and monthly samples were collected over the winter of 1982, with biweekly sampling resumed April
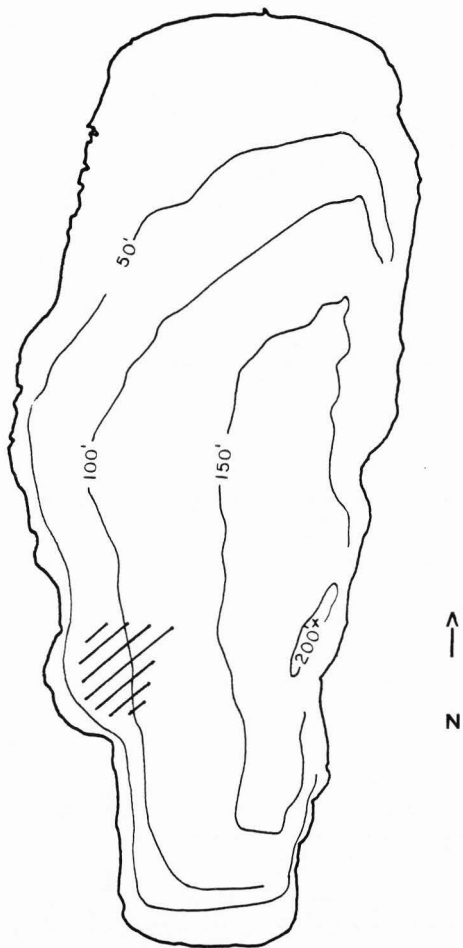
FIG. 1. Bear Lake, Utah-Idaho. Locations of zooplankton (X) and cisco (hatched area) sampling are shown.

to June 1982. All zooplankton samples were preserved in 70 percent ethanol.

In the studies of zooplankton vertical distribution and cisco prey selection, samples were collected with a diaphragm pump system. A weighted diffuser intake was connected to the pump with lengths of 1.6 cm diameter hose. The intake, circular in shape and constructed of transparent plexiglass, was lowered to the desired sampling depth and excurrent water was filtered through the Wisconsin net.

For the vertical distribution studies the water column was divided into five depth intervals: 55 m to 45 m, 45 m to 36 m, 36 m to 21 m, 21 m to 9 m and 9 m to surface. The vertical distribution sampling occurred during a 24 hour period, with single samples from each depth interval collected approximately every four hours. Water from each depth interval was pumped while the intake was raised from the bottom to the top of each interval. Pumping time varied from four to six minutes. During the sampling, the pumping volume was calibrated twice by collecting the excurrent water in a bucket over a measured time period. Twenty-four hour vertical sample series were collected monthly, August through December 1981.

Counting

Zooplankton and cisco stomach contents samples were analyzed with the aid of a compound binocular microscope equipped with an ocular micrometer. Zooplankton samples were poured into graduated centrifuge tubes and their volumes were adjusted depending on density of plankton. Subsamples (1 mL) were obtained with a wide-bore automatic pipet after mixing the sample by repeated filling and emptying of the pipet. Lewis (1979) found this method to produce random subsamples of the total

sample for zooplankters smaller than Chaoborus, a dipteran or small
shrimp. Subsamples were counted in a Sedgwick-Rafter cell.

The lengths of crustacean zooplankton were measured to the nearest
0.05 mm during counts. Length of copepods was measured from the top of
the cephalothorax to the end of the caudal rami (excluding setae).
Nauplii were divided into three size categories: 0.1 mm, 0.2 mm and
0.25 to 0.40 mm. Nauplii of different copepods were not separated.
Carapace length of cladocerans was measured to the base of tail spines.

Population densities of zooplankton for a particular sample date
were estimated by the mean of counts from two vertical tows. In nearly
all cases, the samples analyzed were from tows of 50 m or greater
lengths. The gelatinous matrix of the colonies of the rotifer
Conochilus was dissolved by the ethanol preservative. Thus, counts of
this rotifer were recorded as individuals. Because the numbers of
individual cladocerans in some samples were small, the counts °of as
many as five additional samples were used to improve the estimate of
cladoceran densities for some dates.

The stomach contents of individual cisco were counted and measured
in a Sedgwick-Rafter cell. Entire 1 mL subsamples of the contents were
counted until at least 100 prey items were counted (mean per fish = 134
counted prey items). Counts of the rotifer Conochilus were recorded as
colonies as they tended to remain intact in the formalin preservative.

Cisco Sampling

Monofilament gill nets of 1.9 cm and 1.3 cm square mesh sizes were
used to capture adult and subadult cisco. Echo sounding equipment was
used to determine depths at which cisco schools were frequently located
and to confirm the depths at which gill nets were fished. From August

through November cisco schools were most frequently observed in the metalimnion at depths greater than 15 m during daylight hours. With the goal of capturing feeding schools of cisco, gill nets were fished in midwater sets for periods of two to three hours in daylight. In August, September and October numerous sets of gill nets over a period of several days were required to capture a sample size of at least 40 cisco. Sufficient numbers of cisco were captured in a single day's netting during November and December.

While gill nets were being fished, zooplankton samples were collected to compare with the food of the cisco. O'Brien and Vinyard (1974) criticize the practice of comparing a predator's food with samples of prey from vertical tows which include zooplankton from depths not used by the predator for feeding. To avoid this problem, water was pumped from the six meter depth interval formed by the 2 m of the gill net and the 2 m above and below.

Captured cisco were returned to the Bear Lake Laboratory where their total length was measured, sex was determined and stomach and esophagus dissected. The contents of the cardiac portion of the stomach and the esophagus were removed and preserved in five percent formalin, separately.

To evaluate cisco prey selection, a method comparing rankings of prey utilized and prey available was used (Johnson 1980). Johnson points out that statistical methods based on ranks are nearly as efficient as methods based on the original data. When assumptions necessary to treat the original data such as their measurements are exact and normal distributions are not met, rank methods have desirable advantages of validity and efficiency. As is often the case with

zooplankton, availability values are inexactly measured and the rank methods are preferable.

In the method presented by Johnson (1980), the measure of prey preference is the difference between the rank of usage and the rank of availability. For cisco prey data, the average difference in ranks for each prey item was calculated across all fish in a monthly sample. The most preferred prey item has the lowest (negative) mean difference in ranks and the least preferred has the highest (positive) mean difference.

Johnson's (1980) computer program tests the hypothesis that all prey components are equally preferred using Hotelling's T^2 procedure. If this results in a significant F statistic (P<0.05), multiple comparisons tests are made using the Waller-Duncan procedure to find which pairs of prey items have significantly different mean differences in ranks.

Laboratory Studies

For laboratory studies, captured cisco were brought alive to a temperature controlled facility on the Utah State University campus. Cisco were maintained in tanks and large aquaria in the facility with a constant temperature of 9 degrees C. Cisco were acclimated to laboratory conditions with a light-dark cycle for a period of 2 to 3 months and were fed live zooplankton during this period.

Observations of cisco feeding were made in large glass-fronted aquaria after cisco were accustomed to the presence of the observer. For reactive distance studies, aquaria glass faces were fitted with a centimeter grid system for measurements and fluorescent light fixtures

were suspended over the aquaria allowing control of light intensity. Light intensity was measured with a Licor LI-185 quantum radiometer.

Reactive distance is defined as the minimum distance at which the fish can locate a specific prey (O'Brien 1979). To measure the forward-directed reactive distance of cisco, fish were conditioned to swim in a narrow portion of the front of the aquaria, confined by a plexiglass barrier. Individual cisco cruised back and forth in the confined section, searching for prey. Individual Daphnia were placed into the confined section with an eye dropper while the cisco was swimming away from the prey. As the cisco turned and swam toward the prey, the reactive distance was measured when the fish clearly hesitated and focused on the prey. This hesitation was invariably followed by acceleration, pursuit and capture of the prey. Reactive distance was estimated using the centimeter grid to measure the distance between the eye and the prey at the moment of hesitation and focus. This is essentially the same method used by other researchers to measure the reactive distance for arctic grayling (Schmidt and O'Brien 1982) and small lake trout (Kettle and O'Brien 1978).

Live Daphnia used for prey were netted from the outfall of Willard Bay Reservoir, Box Elder County, Utah and were unpigmented or only lightly pigmented. Daphnia were sized using the ocular micrometer and placed in three size groups: 2 mm, 2.5 mm and 3 mm.

RESULTS

Zooplankton Community Composition

Seven crustaceans and eight rotifers were present in limnetic samples during 1981 and 1982 (Table 1). The calanoid copepod, Epischura, and the colonial rotifer, Conochilus, dominated the zooplankton community as the most numerous members during most of the study period. Other rotifers and cladocerans frequently comprised less than five percent of the total zooplankton (Figure 2).

The zooplankton exhibited a seasonal peak abundance in late spring and a minor peak in late summer-early fall (Figure 3). Population densities of limnetic zooplankton for 1981-1982 are presented in Table 2. The late spring peak in abundance was attributed to rotifers, with more than 95 percent of the zooplankton in late June comprised largely of Conochilus. Rotifers dominated through summer until late fall when their numbers declined and remained low over the winter. Copepods reached peak abundance in late fall and dominated through winter. Cladocera formed only a small part of the community. During late summer and early fall, when cladocerans reached their highest densities, they comprised no more than five percent of the zooplankton.

Rotifera

Figures 4 and 5 show the seasonal abundance patterns for the limnetic rotifers. A brief but prominent appearance in the spring plankton was shown by "A", an unidentified rotifer. This rotifer, averaging about 0.2 mm in length, comprised 81 percent to 99 percent of all rotifers in April and May 1982 (Figure 6). Abruptly disappearing

TABLE 1. Zooplankton collected from Bear Lake limnetic samples, 1981-1982.

Rotifera

    Brachionus

    Collotheca

    Conochilus

    Filinia

    Keratella

    Notholca

    Polyarthra

    "A" (unidentified rotifer)

Cladocera

    Bosmina

    Ceriodaphnia

    Chydorus

    Daphnia

    Diaphanosoma

Copepoda

    Cyclops

    Epischura
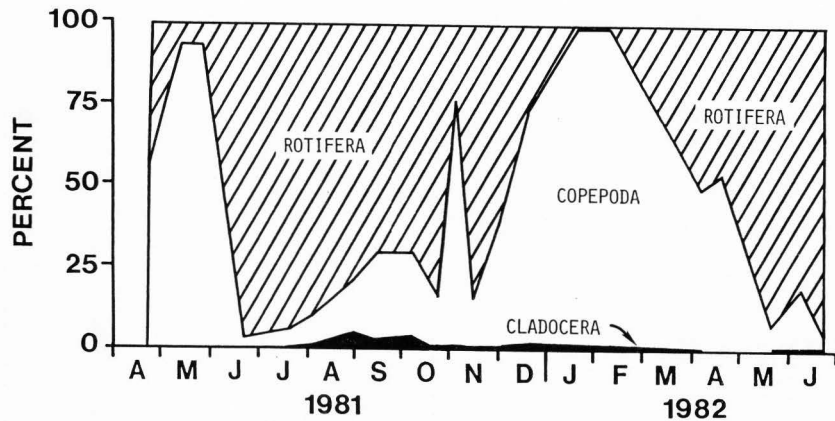
FIG. 2. Zooplankton community composition. Percent composition of total numbers is shown for 1981-1982.
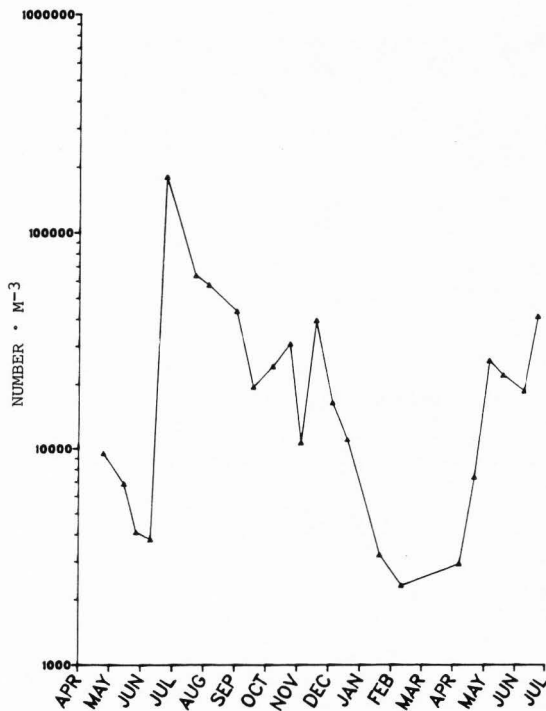
FIG. 3.   Population densities of total zooplankton community, 1981-1982.

Table 2. Population densities (individuals·m^{-3}) of limnetic zooplankton, 1981-1982.

Date	Epischura	Cyclops	Nauplii	Bosmina	Diaphano-soma	Daphnia	Cerio-daphnia	Cono-chilus	"A"	Keratella	Poly-arthra	Other Rotifers	Total
810424	2,327	76	2,794	14	0	0	0	43	651	3,227	361	0	9,493
810514	4,248	241	1,928	9	0	0	0	190	9	240	0	0	6,865
810526	2,881	208	731	0	0	0	0	192	0	83	0	0	4,096
810609	1,039	225	348	21	0	0	0	1,340	0	819	0	0	3,790
810623	2,867	47	390	21	7	0	13	176,229	0	311	0	26	179,911
810721	1,407	133	1,948	75	8	25	0	58,926	0	1,089	17	0	63,630
810804	2,118	369	2,656	101	269	0	0	47,780	0	2,119	2,117	0	57,529
810822*				1,152	401	0	602						
810901*	3,770	56	3,435	1,224	482	16	12	33,922	0	664	0	16	43,598
810917*	2,375	0	2,760	348	134	31	0	12,780	0	941	0	64	19,433
811006	3,579	12	2,343	336	513	12	0	16,902	0	464	0	0	24,162
811023*	3,108	54	1,598	51	29	25	2	25,754	0	43	0	22	30,688
811103	5,229	34	2,874	115	12	22	0	2,305	0	47	0	0	10,638
811117	2,568	49	3,390	93	10	25	0	33,043	0	15	15	196	39,403
811203*	3,060	9	3,030	86	9	0	0	10,119	0	10	0	85	16,409
811218*	3,056	33	4,722	145	9	51	0	3,033	0	0	0	0	11,049
820119	670	13	2,432	34	0	0	0	47	0	17	5	0	3,218
820209	441	43	1,822	7	0	7	0	0	0	3	0	0	2,322
820406	11	83	1,302	0	0	0	0	0	1,505	21	3	4	2,929
820420	196	153	3,574	0	0	6	0	0	3,309	46	89	0	7,371
820504	1,660	342	5,606	0	0	0	0	181	15,713	646	1,577	0	25,725
820518	710	213	710	0	0	9	0	204	16,642	1,193	2,371	0	22,052
820608	2,521	114	635	68	0	0	0	14,640	0	624	0	0	18,602
820622	571	158	508	11	0	0	0	39,817	0	78	0	0	41,143

*Additional samples were used to calculate mean densities for cladocerans. All other dates represent mean of two vertical tows.
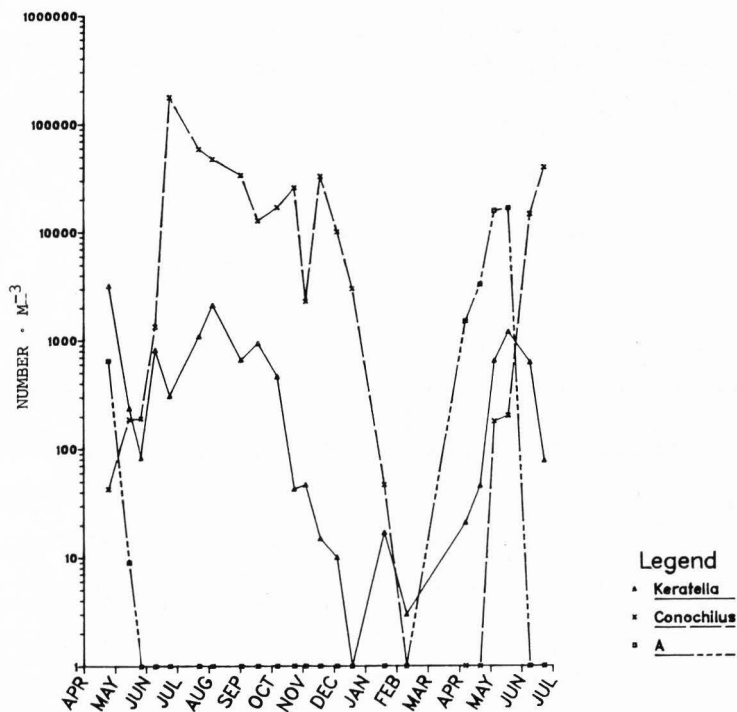
FIG. 4. Population densities of the rotifers Keratella, Conochilus and "A," 1981-1982.
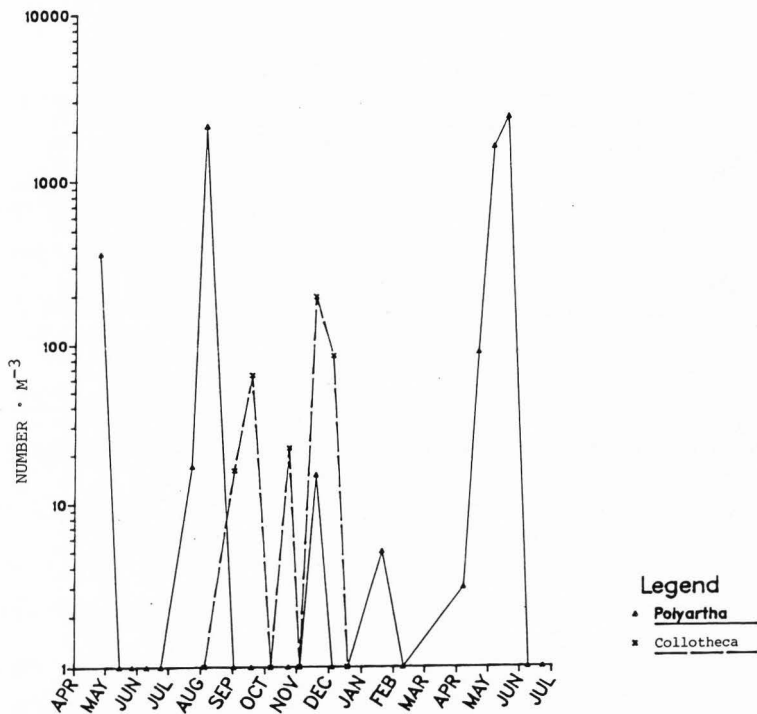
FIG. 5. Population densities of the rotifers <u>Polyarthra</u> and
<u>Collotheca</u>, 1981-1982.
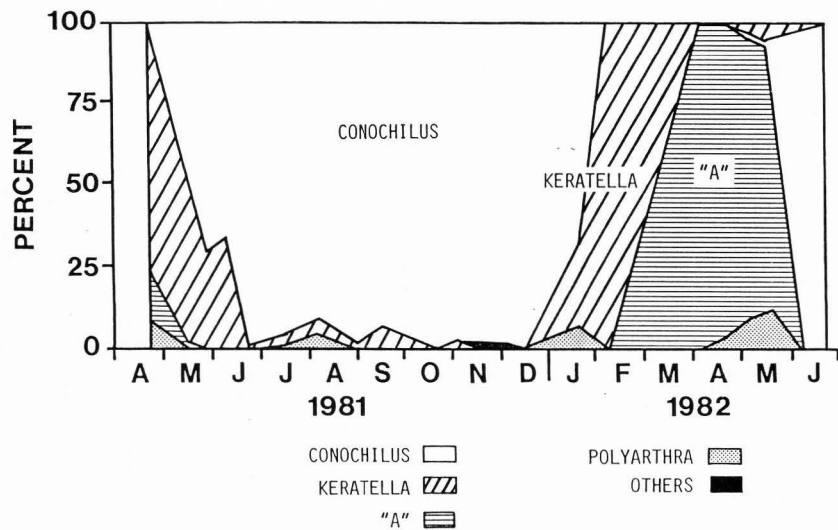
FIG. 6.   Rotifer community composition, percent of numbers, 1981-1982.

from the plankton in June, "A" was suceeded by the rapid increase in
the Conochilus population. After attaining maximum abundance in late
June, Conochilus remained dominant through summer, accounting for over
90 percent of the summer and fall rotifer densities. The Conochilus
population gradually declined and disappeared over winter.

A sample of Conochilus colonies was examined to determine colony
size and numbers of individuals per colony. Table 3 summarizes
Conochilus colony characteristics. Mean diameter of these colonies was
0.94 mm and a mean of 24.1 individuals was determined.

Several other rotifers were less commonly observed in zooplankton
samples. A series of population bursts characterized the seasonal
pattern of Polyarthra, with the strongest peaks occurring in spring and
in midsummer. Keratella, probably the most common freshwater rotifer
genus, persisted in the community throughout the year with lowest
numbers present during winter and like Polyarthra exhibited maxima in
spring and midsummer. Collotheca appeared only in the fall and only

TABLE 3. Summary of Conochilus colony characteristics.

	Individuals per Colony	Diameter of Colony (mm)
Number of Colonies	61	31
Mean	24.1	0.94
Median	23.0	1.00
Standard Deviation	10.0	0.29
Maximum	60	0.45
Minimum	6	1.40
95% Confidence Interval	21.5-26.7	0.83-1.04

once in numbers greater than 100 m^{-3}. The rotifers <u>Filinia</u>, <u>Brachionus</u> and <u>Notholca</u> were present in limnetic samples only rarely.

Cladocera

The seasonal community composition and densities of cladocerans are presented in Figures 7, 8 and 9. These herbivores were the least abundant group in the limnetic zooplankton. The smallest member, <u>Bosmina</u>, was the dominant cladoceran, usually comprising greater than 50 percent of the numbers. <u>Bosmina</u> had the longest duration of occurrence for cladocerans and reached a peak in density in late summer and fall.

Late summer population maxima characterized the seasonal patterns of <u>Ceriodaphnia</u> and <u>Diaphanosoma</u>. However, <u>Daphnia</u> departed from this pattern and was most abundant in December, after fall circulation of the lake had occured. <u>Diaphanosoma</u> was present in the plankton for a brief duration but comprised over 60 percent of the cladocerans at peak density. <u>Ceriodaphnia</u> was present only during summer and early fall. <u>Chydorus</u>, a liitoral form, was only rarely present in limnetic samples. <u>Daphnia</u>, the largest Bear Lake cladoceran, persisted in the community but was sparsely represented in limnetic samples.

Copepoda

Seasonal density patterns of the copepods are shown in Figure 10. Copepodid stages of <u>Epischura</u>, the dominant calanoid, were present on all sample dates. Population peaks occurred in spring and late fall. Copepod nauplii displayed a seasonal pattern similar to <u>Epischura</u> copepodids, with nauplii peaks followed by <u>Epischura</u> peaks. More
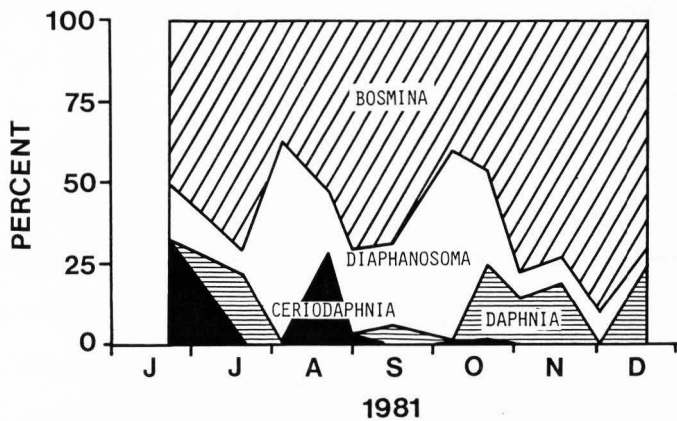
FIG. 7.   Cladoceran community composition, 1981.
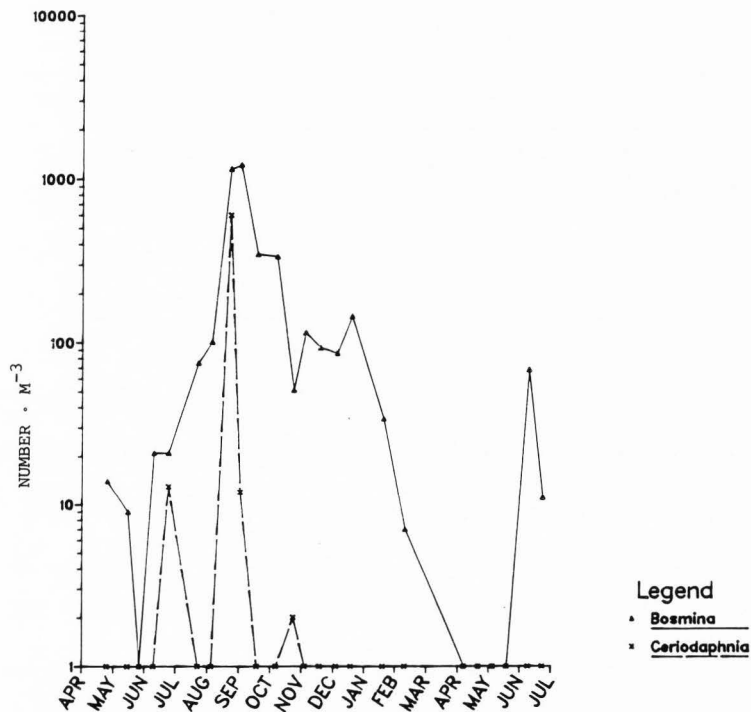
FIG. 8. Population densities of the cladocerans <u>Bosmina</u> and <u>Ceriodaphnia</u>, 1981-1982.
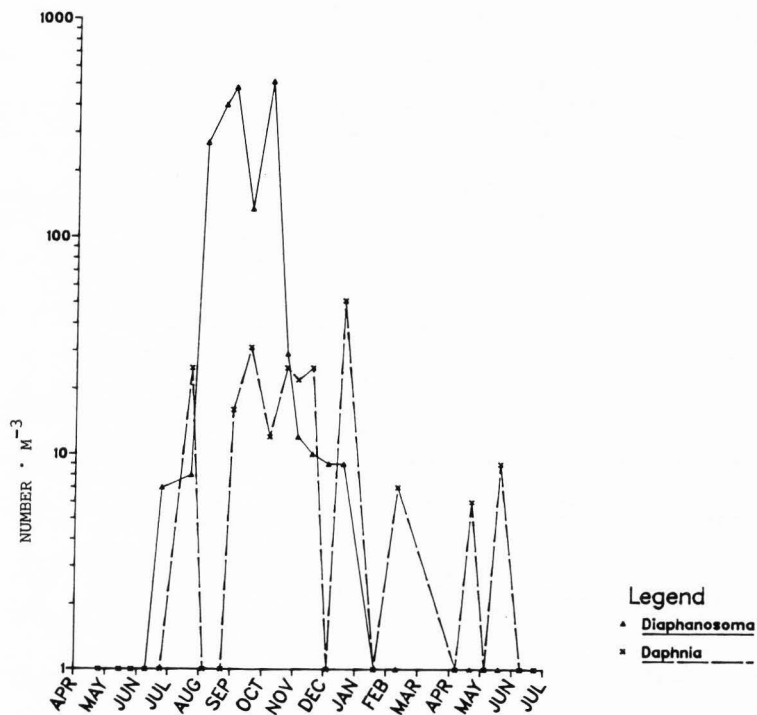
FIG. 9. Population densities of the cladocerans Diaphanosoma and Daphnia, 1981-1982.
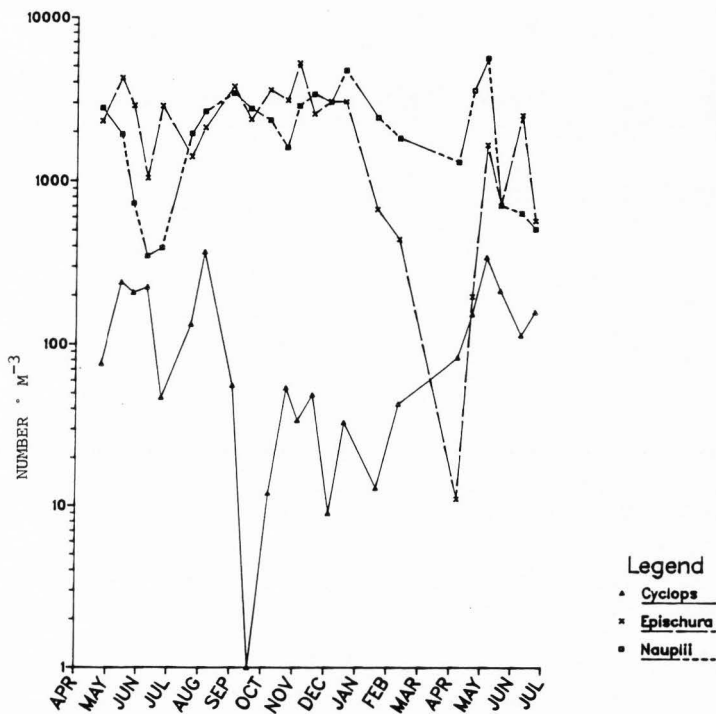
FIG. 10.   Population densities of copepods, 1981-1982.

nauplii were present over winter months than copepodids. Cyclops copepodids showed spring peaks in abundance and comprised less than 15 percent of copepod numbers during these maxima (Figure 11).

The seasonal variation in length of Epischura is presented in Table 4. Epischura copepodids averaged less than 1 mm during April and May of both years. Mean length increased until midsummer when a decline occurred and was followed by a pattern of gradual increase in length through November. Epischura mean lengths remained over 1.0 mm until the following spring.

Vertical Distribution of Zooplankton

The twenty-four hour vertical distribution of the zooplankton was studied monthly, from August to December 1981. Table 5 summarizes the densities of zooplankton groups in five depth intervals of the water column from midday samples. This distribution shows that zooplankton were concentrated in the upper 36 m of the water column, with the bottom 20 m sparsely populated. Rotifers and cladocerans were especially numerous in the top 21 m. The vertical distribution of the large cladoceran, Diaphanosoma, is shown for a 24 hour period in September (Figure 12). Diaphanosoma was most abundant in the epilimnion and was seldom encountered in depths below 21 m.

Unlike other cladocerans, Daphnia showed highest densities in the bottom depth intervals. Figure 13 presents vertical distribution of Daphnia in late November, when this large cladoceran was increasing in numbers. No Daphnia individuals were sampled in the top 21 m of water for this 24 hour series. The small herbivore, Bosmina, was the most frequently encountered cladoceran in the hypolimnion but highest densities were in the upper depth intervals.
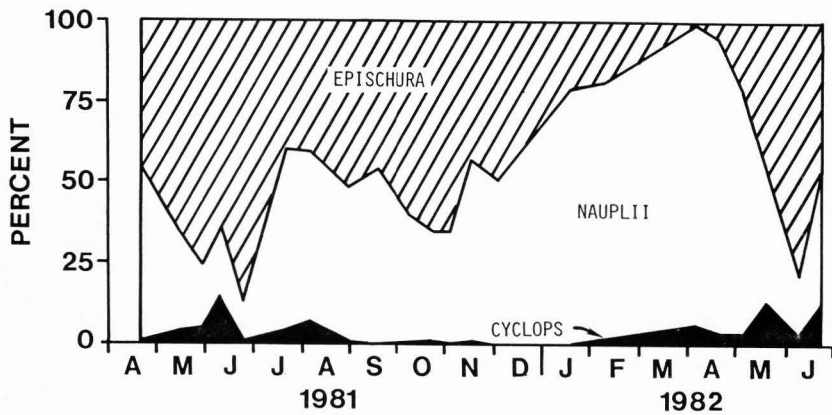
FIG. 11. Copepod community composition, 1981-1982.

TABLE 4. Length measurements of <u>Epischura</u> copepodids, 1981-1982.

Date	Number of Individuals	Mean Length (mm)	Standard Deviation	Minimum Length (mm)	Maximum Length (mm)
810424	348	0.645	0.132	0.50	1.35
810514	543	0.824	0.229	0.50	1.55
810526	377	0.779	0.181	0.50	1.55
810609	153	0.948	0.159	0.60	1.40
810623	299	1.057	0.157	0.55	1.50
810721	168	1.194	0.223	0.50	1.50
810804	189	0.964	0.321	0.40	1.50
810901	397	0.867	0.253	0.10	1.40
810917	111	0.920	0.218	0.50	1.45
811006	291	0.960	0.170	0.50	1.40
811023	272	1.025	0.162	0.50	1.35
811103	457	1.047	0.150	0.50	1.30
811117	209	1.111	0.141	0.50	1.35
811203	325	1.134	0.105	0.50	1.30
811218	268	1.107	0.090	0.45	1.25
820119	164	1.103	0.090	0.65	1.25
820209	135	1.080	0.090	0.75	1.25
820406	4	0.813	0.333	0.50	1.10
820420	50	0.982	0.237	0.50	1.20
820504	200	0.650	0.178	0.50	1.25
820518	133	0.730	0.157	0.50	1.25
820608	222	1.125	0.222	0.50	1.60
820622	157	1.298	0.177	0.50	1.60

TABLE 5. Vertical distribution of zooplankton groups for five months,
1981. Densities of midday samples are presented.

Month	Depth (m)	Density (numbers·m^{-3})			Total
		Copepods	Cladocerans	Rotifers	
Aug	09-00	6,524	2,646	4,246	13,415
31	21-09	15,152	3,515	110,915	129,582
	36-21	8,023	87	14,477	22,587
	45-36	1,966	56	1,396	3,419
	55-45	950	196	615	1,760
Sep	09-00	3,536	365	13,567	17,470
16	21-09	4,629	927	31,172	36,728
	36-21	5,439	31	4,501	9,969
	45-36	1,438	125	3,688	5,250
	55-45	1,312	125	1,251	2,688
Oct	09-00	5,568	366	13,113	19,048
22	21-09	6,691	509	50,740	57,939
	36-21	11,848	108	9,710	21,667
	45-36	2,310	108	1,589	4,007
	55-45	576	144	2,015	2,770
Nov	09-00	2,906	76	7,283	10,264
20	21-09	1,849	113	7,849	9,811
	36-21	5,397	38	2,227	7,660
	45-36	2,641	19	75	2,736
	55-45	1,036	113	38	1,186
Dec	09-00	5,939	382	1,555	7,878
17	21-09	1,813	153	76	2,042
	36-21	3,293	197	478	3,968
	45-36	2,688	73	768	3,528
	55-45	1,642	18	237	1,898
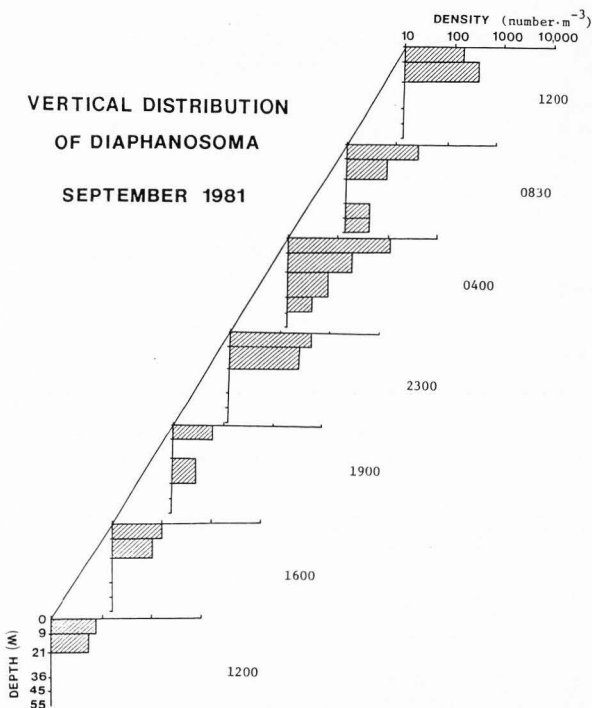
FIG. 12. Twenty-four hour vertical distribution of Diaphanosoma, September 16, 1981. Sampling times are shown to the right of the density bars.
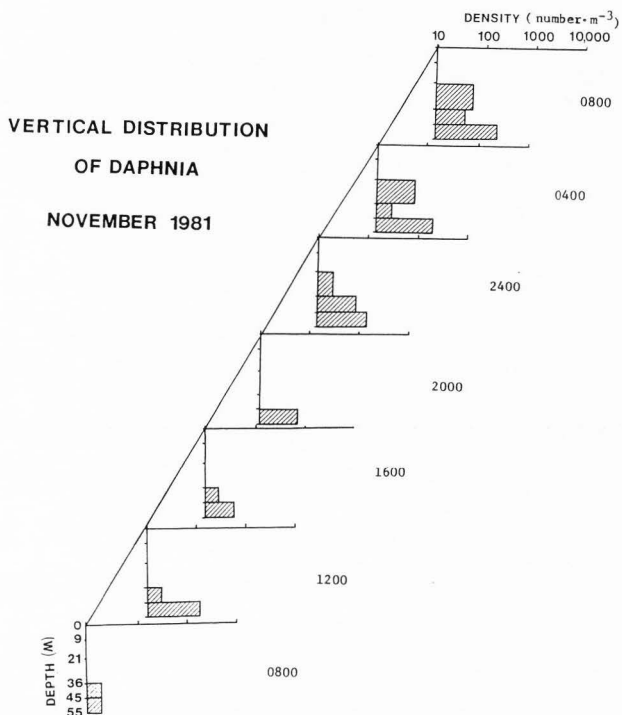
FIG. 13. Twenty-four hour vertical distribution of Daphnia, November 20, 1982. Sampling times are shown on right.

Epischura also showed highest densities in the top 36 m of the water column. In August, greater than 90 percent of Epischura copepodites were found in the top three depth intervals (Figure 14). This pattern was found again in September and October but, in December, numbers in the bottom depths increased such that distribution was more uniform across depths (Table 6).

The diel light-dark cycle is generally accepted as being an important factor in regulating diel vertical migration of zooplankton. The timing of the 24 hour sampling series was set up to help detect possible vertical migration, especially around sunset and sunrise when light conditions changed rapidly. Samples were collected approximately two hours before and after the onset of darkness at sunset. Because of this design, sampling occurred at different hours each month and necessitated the partitioning of samples into light "treatments" for statistical analyses. For a 24 hour period, two samples were grouped into each of three light treatments: full daylight at midday, darkness at night and a transitional period close to sunset or sunrise. In analysis of variance methods, more than one observation per cell allows for the test of interaction between factors (e.g. light and depth).

The pattern of zooplankton concentration in the upper depth layers did not change when the vertical distributions were plotted by light treatment (Figures 15 and 16). For both total zooplankton and for Epischura high percentages of the numbers were located in the top 36 m from August through November. In December, after fall turnover, the distribution became more uniform, although the smallest percentage was in the bottom depth interval.
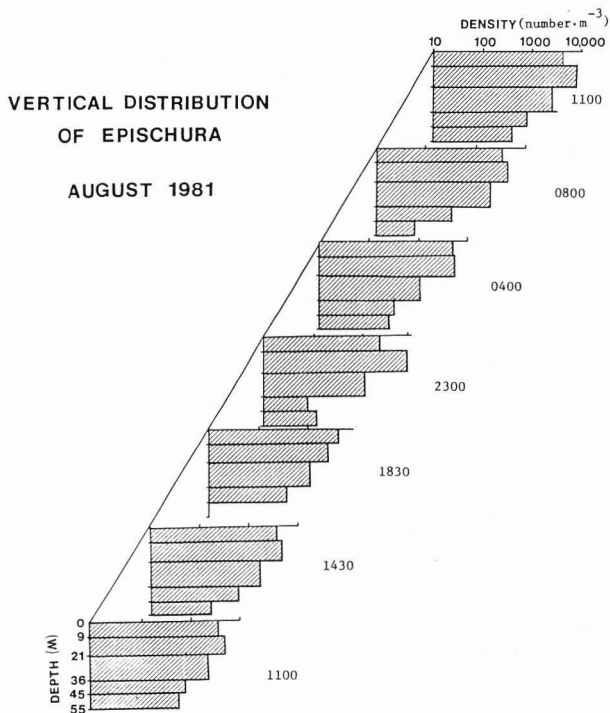
FIG. 14. Twenty-four hour vertical distribution of Epischura copepodites, August 31, 1981. Sampling times are shown on right.

TABLE 6. Depth distribution of _Epischura_ for five months, 1981. Densities (numbers·m^{-3}) for midday samples and means of 24-hour series are presented.

Depth (m)	August 31	September 16	October 22	November 20	December 17
Midday samples					
09-00	3,371	2,378	5,275	1,698	577
21-09	4,929	2,654	5,018	906	1,162
36-21	2,194	1,063	942	642	604
45-36	682	344	397	1,132	841
55-45	517	531	252	358	611
Means of 24-hour sample series					
09-00	3,729	1,493	4,124	1,152	983
21-09	5,239	2,251	2,944	978	958
36-21	1,642	571	891	1,049	1,160
45-36	451	240	369	469	1,032
55-45	148	186	277	219	671
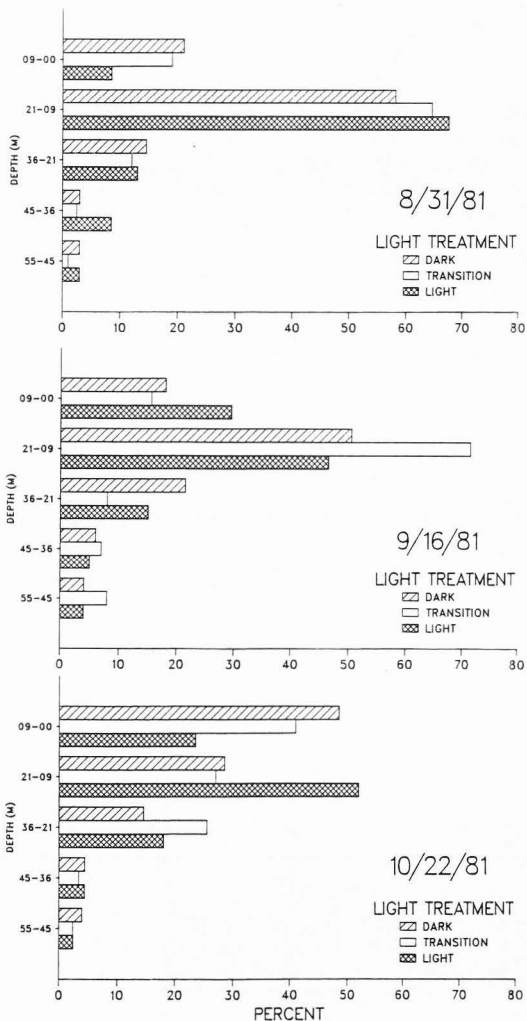
FIG. 15. Vertical distribution of total zooplankton separated into light treatments.
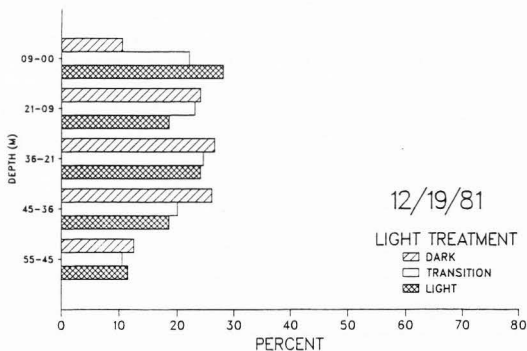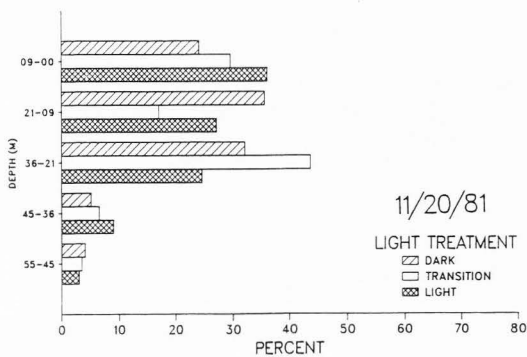
FIG. 15. Continued.
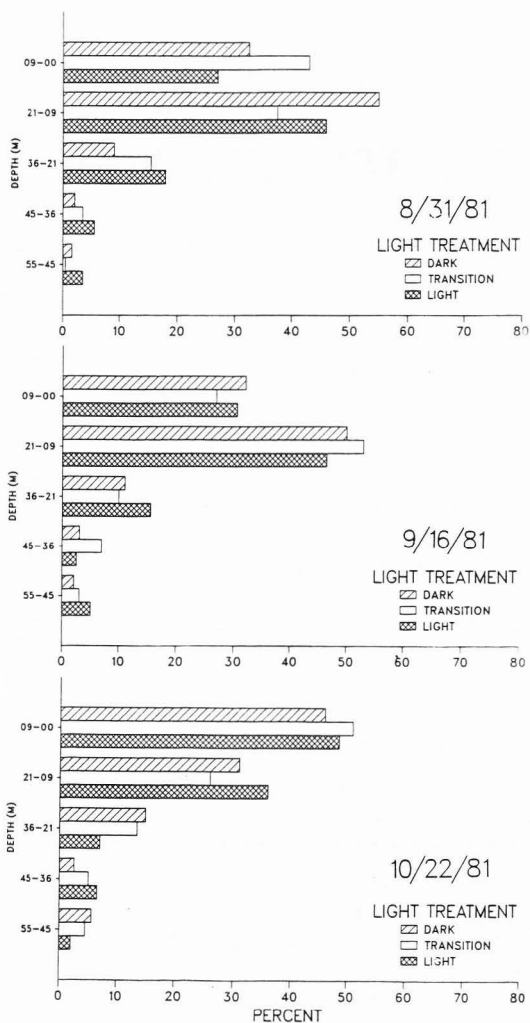
FIG. 16. Vertical distribution of _Epischura_ separated into light treatments.
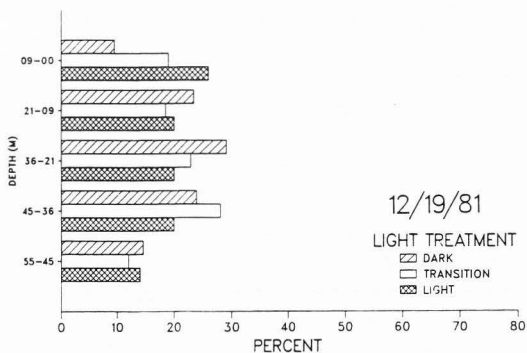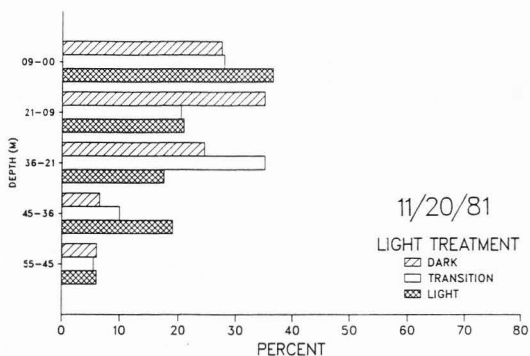
FIG. 16. Continued.

Results of the three-way analysis of variance on 24 hour vertical distribution samples are presented in Table 7. A 5x5x3 design was used for the main effects of date, depth and light. A log transformation (LN x+1) of the zooplankton numbers was used because of large variation between summer and winter zooplankton densities and to ease detection of significant interactions.

Evidence for vertical migration of zooplankton was not present in these analyses. Obvious significant differences ($P \leq 0.05$) were present by date and by depth interval, but, in no case, was the interaction between light and depth significant. Thus, obvious vertical movements of zooplankton numbers with changes in light treatment were not detected.

Differences in the sizes of crustacean zooplankton with depth were examined by comparing mean lengths. Table 8 shows the mean lengths of Epischura at depth intervals from midday samples. As for zooplankton numbers, significant differences in mean size were noted by date and by depth but light-depth interactions were not detected (Table 7).

Cisco Diet Composition

Cisco captured during five months of 1981 were used to determine diet composition. The sampling locations in the water column and the associated physical conditions where cisco were presumably feeding are reported in Table 9. Temperature and light intensity were estimated from diel sampling in closest proximity to cisco sampling.

Cisco utilized all of the limnetic crustaceans and the rotifer Conochilus as food items. The frequency of occurrence of these prey items from sampled fish is shown in Table 10. All cisco stomachs examined contained Epischura.

TABLE 7. Summary of three-way analysis of variance results. F-statistics and significance (P) presented for _Epischura_ and total zooplankton analyses.

| | | Main Effects | | | | Two-way Interactions | | |
		Date	Light	Depth		Date-Light	Date-Depth	Light-Depth
Numbers Total Zooplankton (LN X+1	F	23.045	4.713	77.707		3.261	5.187	0.331
transforms)	P	<0.000	0.011	<0.000		0.002	<0.000	0.952
Numbers _Epischura_ (LN X+1	F	3.793	0.973	43.845		2.613	4.428	0.922
transforms)	P	0.006	0.381	<0.000		0.012	<0.000	0.502
Mean Lengths Total Zooplankton	F	70.964	1.942	7.486		3.456	2.704	0.753
	P	<0.000	0.148	<0.000		0.001	0.001	0.644
Mean Lengths	F	22.225	0.754	2.482		1.385	1.426	1.468
Epischura	P	<0.000	0.473	0.048		0.211	0.143	0.177

TABLE 8. Mean lengths of _Epischura_ copepodites from midday samples of vertical distribution.

Date	Depth (mm)	Number	Mean Length	Standard Deviation	Minimum Length	Maximum Length
	09-00	118	0.806	0.239	0.45	1.50
	21-09	173	0.699	0.186	0.30	1.35
Aug	36-21	77	0.936	0.150	0.60	1.35
	45-36	18	0.967	0.174	0.70	1.30
	55-45	13	0.958	0.117	0.70	1.15
	09-00	78	0.753	0.236	0.50	1.45
	21-09	68	0.859	0.198	0.50	1.40
Sep	36-21	34	0.943	0.151	0.65	1.30
	45-36	11	0.941	0.122	0.70	1.10
	55-45	17	0.988	0.210	0.60	1.35
	09-00	72	0.928	0.160	0.50	1.30
	21-09	69	0.948	0.149	0.65	1.30
Oct	36-21	26	1.063	0.158	0.70	1.30
	45-36	11	1.205	0.061	1.10	1.30
	55-45	7	1.007	0.219	0.70	1.30
	09-00	66	1.037	0.131	0.70	1.30
	21-09	51	1.048	0.159	0.60	1.30
Nov	36-21	34	1.107	0.130	0.70	1.25
	45-36	60	1.102	0.103	0.80	1.30
	55-45	19	1.087	0.127	0.85	1.25
	09-00	30	1.008	0.136	0.70	1.20
	21-09	61	1.089	0.085	0.80	1.20
Dec	36-21	32	1.069	0.070	0.90	1.20
	45-36	45	1.088	0.087	0.85	1.25
	55-45	33	1.080	0.077	0.90	1.20

TABLE 9. Capture depths, temperature and estimated light conditions during cisco sampling for five months, 1981.

Month	Sample Dates	Depth Range (meters)	Temperature Range (°C)	Light Intensity $\mu E \cdot m^{-2} \cdot s^{-1}$
August	20-22	15 to 20	15 to 11	51 to 20
September	23-27	17 to 25	12.7 to 9	47 to 17
October	19-Nov 2	17 to 22	12 to 10	23 to 8
November	17	20 to 22	9.3 to 9.1	9 to 7
December	19	20 to 22	5.5	5 to 3

TABLE 10. Frequency of occurrence of prey items in cisco stomachs, 1981, expressed as number of stomachs a prey item occurred in (N) and percent of stomachs examined containing at least one prey item (%).

Month		EP	CY	NA	BO	CE	CH	DA	DI	CO
						Prey Item[*]				
August	N	25	1	1	25	25	0	0	25	1
	%	100	4	4	100	100	0	0	100	4
September	N	25	1	0	23	25	0	0	24	2
	%	100	4	0	92	100	0	0	96	8
October	N	25	3	1	24	4	0	0	24	16
	%	100	12	4	96	16	0	0	96	64
November	N	25	1	0	25	1	0	0	20	1
	%	100	4	0	100	4	0	0	80	4
December	N	24	19	1	17	0	2	24	0	24
	%	100	79.2	4.2	70.8	0	8.3	100	0	100
Five months	N	124	25	3	114	55	2	24	93	44
	%	100	20.2	2.4	91.9	49.4	1.6	15.6	75	35.5

*Key: EP = Epischura, CY = Cyclops, NA = nauplii, BO = Bosmina, CE = Ceriodaphnia,
CH = Chydorus, DA = Daphnia, DI = Diaphanosoma, CO = Conochilus colonies

The monthly food composition determined for adult and subadult cisco (140-210 mm total length) is presented in Figure 17. During August, cisco captured from the metaliminion had Epischura as the most abundant prey item, but three cladocerans accounted for 59.5 percent of the total prey consumed. The cladoceran Diaphanosoma comprised nearly 73 percent of the food items in late September, corresponding to its peak abundance in the plankton. During the last two weeks of October, Epischura composed 78 percent of the food, while in mid-November, it increased to 93.8 percent of all prey items sampled.

December food composition was markedly different from other months. Epischura decreased to its lowest observed monthly proportion of 12.8 percent. Daphnia, which became more available after fall circulation, comprised 48.3 percent and Conochilus colonies contributed over one-third of the prey items consumed. Both of these prey were minor items in other months. Cisco stomachs contained noticeably less food than in other months although volumes were not measured.

Measurements of zooplankton during counting and stomach analyses permitted examination of prey size selection. Length-frequency distributions of prey items in cisco stomachs and potential prey available in the plankton revealed size-selective feeding occurred in four of the five months examined. Figure 18 shows lengths frequencies of all crustacean prey excluding nauplii. Distributions of the available prey and the prey consumed for November showed considerable overlap. Their mean lengths compared with a two-sample t test showed no significant difference (t=0.29, P=0.77; Table 11). Significant differences for the other four months were observed at P<0.05.
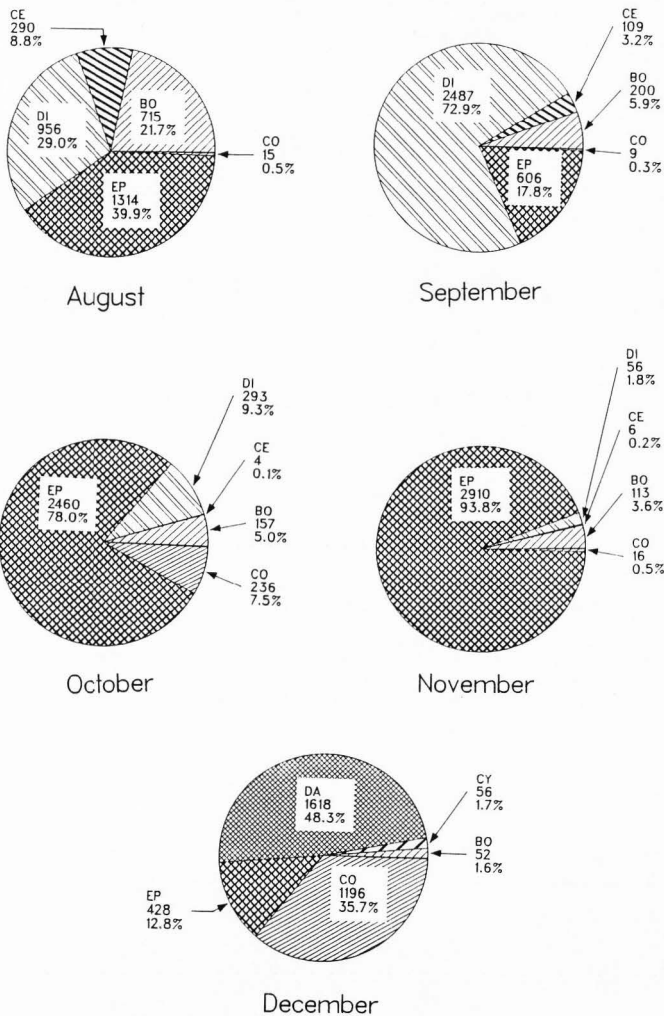
FIG. 17. Cisco food composition for five months, 1981. Numbers of prey items counted and percentages are shown. Prey item code is same as in Table 10.

FIG. 18. Length-frequencies of crustacean prey items in available plankton and in cisco stomachs for five months, 1981.

TABLE 11. Summary of all crustacean prey lengths, excluding Nauplii, from cisco stomachs and from the plankton.

Month		Number of Prey	Mean Length (mm)	Standard Deviation	Minimum Length (mm)	Maximum Length (mm)	t Statistic	P
August	Plankton	576	0.63	0.23	0.25	1.50	23.07	<0.0000
	Stomachs	3276	0.89	0.34	0.25	1.65		
September	Plankton	743	0.81	0.24	0.25	1.40	10.74	<0.0000
	Stomachs	3403	0.91	0.22	0.30	1.60		
October	Plankton	510	0.98	0.25	0.25	1.40	2.45	0.014
	Stomachs	2917	1.01	0.20	0.30	1.50		
November	Plankton	147	1.03	0.18	0.30	1.30	0.29	0.77
	Stomachs	3080	1.02	0.16	0.30	1.40		
December	Plankton	124	1.05	0.16	0.40	1.55	9.91	<0.0000
	Stomachs	2156	1.20	0.27	0.40	2.15		

Food items smaller than 0.4 mm were seldom consumed by cisco. The smallest prey items found in stomachs were Bosmina and nauplii of 0.25 mm length. Nauplii were very rare in stomach contents. The length of the largest food items, however, often exceeded the length of the largest prey sampled from the plankton (Table 10).

The length-frequency distributions of Epischura showed temporal variablity in size-selective feeding (Figure 19). August and September distributions showed clear separations in the ranges of prey lengths consumed and in the plankton. Cisco clearly favored the largest individuals which were a small proportion of the total population. As length groups of smaller Epischura copepodids increased body size through growth, the stomach and plankton distributions showed increasing overlap for October through December. The mean lengths of Epischura in stomachs and in the plankton were not significantly different for these three months (Table 12).

Cladocerans were consistently fed on in size-selective fashion during the months when they were abundant (Figure 20). Mean lengths of ingested cladocerans were significantly larger than those of available prey (Table 13), even in the case of Bosmina, the smallest crustacean prey item.

Prey Selection

The question of whether cisco selectively consumed various prey was examined using the resource preference program of Johnson (1980). Use of this program resulted in a ranking of prey items from "most preferred" to "least preferred" according to the differences between use and availability of each prey (Table 14). Although Epischura was the dominant prey item in cisco diets, cladocerans were most preferred
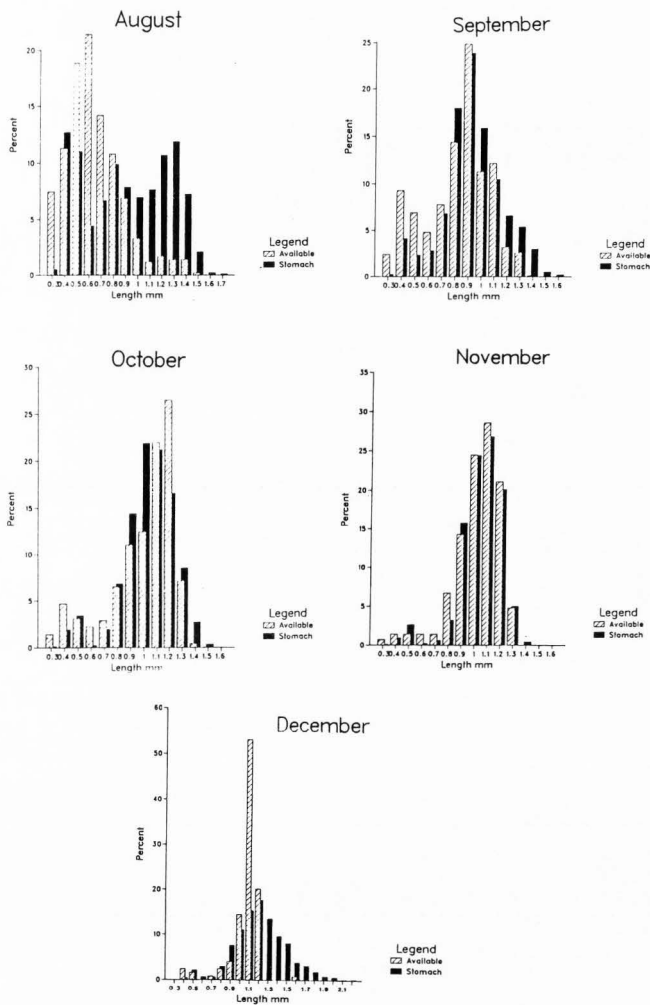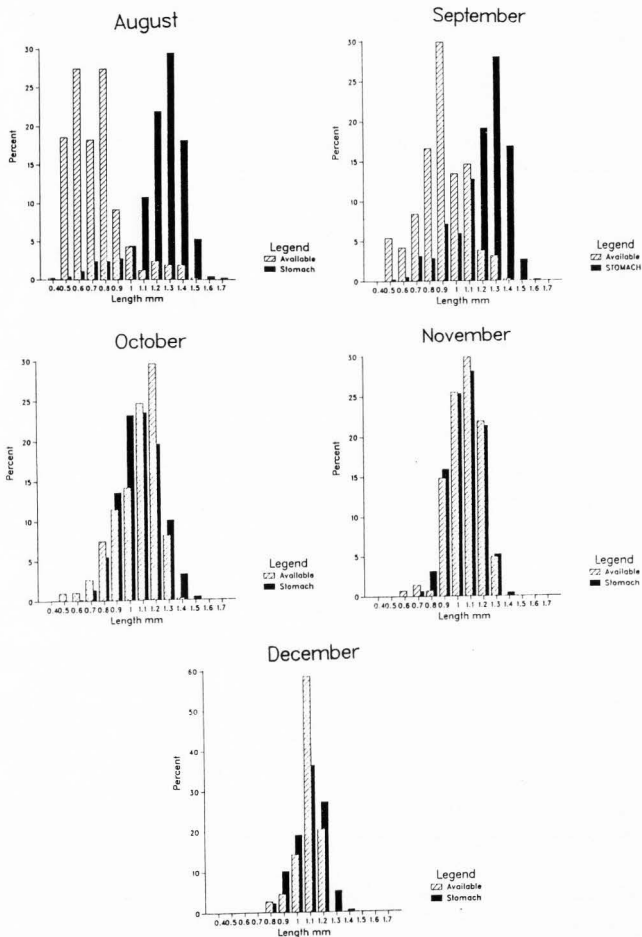
FIG. 19. Length-frequencies of _Epischura_ copepodites in available plankton and in cisco stomachs for five months, 1981.

TABLE 12. Summary of *Epischura* lengths from cisco stomachs and the plankton.

Month		Number of Prey	Mean Length (mm)	Standard Deviation	Minimum Length (mm)	Maximum Length (mm)	t Statistic	P
August	Plankton	414	0.71	0.21	0.40	1.50	43.66	<0.0000
	Stomachs	1314	1.21	0.19	0.40	1.65		
September	Plankton	594	0.88	0.18	0.45	1.40	27.23	<0.0000
	Stomachs	606	1.18	0.19	0.50	1.60		
October	Plankton	447	1.04	0.17	0.45	1.35	1.85	0.064
	Stomachs	2460	1.06	0.15	0.60	1.50		
November	Plankton	141	1.05	0.12	0.60	1.30	0.62	0.54
	Stomachs	2910	1.05	0.12	0.60	1.40		
December	Plankton	113	1.07	0.08	0.80	1.20	0.65	0.52
	Stomachs	428	1.08	0.11	0.75	1.40		
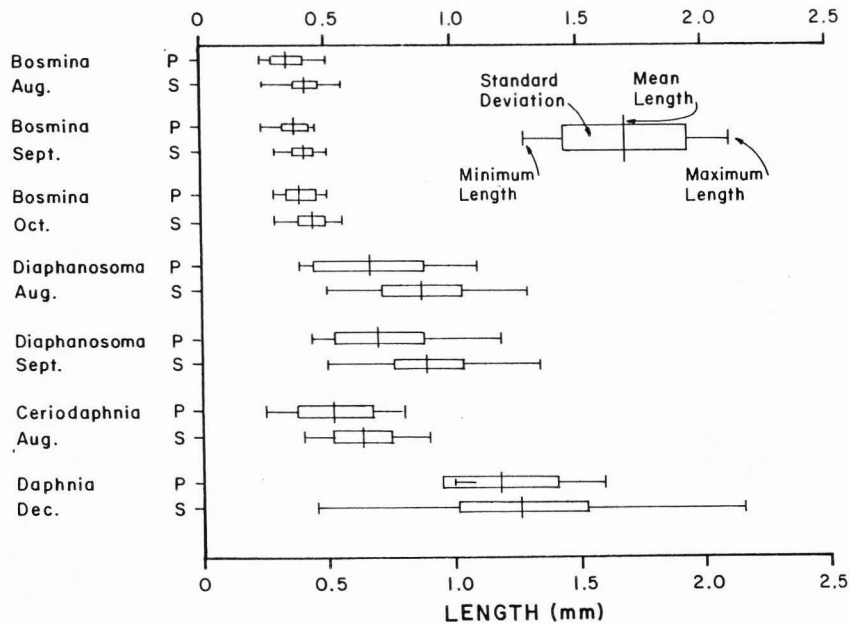
FIG. 20. Lengths of cladoceran prey in cisco stomachs (S) and in the plankton (P).

TABLE 13. Summary of _Cladoceran_ lengths from cisco stomachs and the plankton.

Month		Number of Prey	Mean Length (mm)	Standard Deviation	Minimum Length (mm)	Maximum Length (mm)	t Statistic	P
Bosmina								
August	Plankton	116	0.35	0.06	0.25	0.50	11.73	<0.0000
	Stomachs	715	0.42	0.05	0.25	0.55		
September	Plankton	95	0.38	0.05	0.25	0.45	5.73	<0.0000
	Stomachs	200	0.41	0.04	0.30	0.50		
October	Plankton	21	0.40	0.06	0.30	0.50	3.81	0.0009
	Stomachs	157	0.44	0.05	0.30	0.55		
Diaphanosoma								
August	Plankton	17	0.67	0.22	0.40	1.10	3.94	0.0012
	Stomachs	956	0.88	0.16	0.50	1.30		
September	Plankton	44	0.71	0.18	0.45	1.20	6.90	<0.0000
	Stomachs	2487	0.90	0.14	0.50	1.35		
Ceriodaphnia								
August	Plankton	15	0.52	0.15	0.25	0.80	2.81	0.013
	Stomachs	290	0.63	0.12	0.40	0.90		

TABLE 14. Mean differences between ranks of prey items utilized and ranks of prey available.[a]

Month	Prey Item[b] Mean Difference in Rank								
August	DI −3.85	CE −2.46	BO −1.00	EP −0.12	CY 0.12	CO 2.58	NA 4.73		
September	CE −4.19	DI −2.54	DA −0.42	BO −0.31	DY 0.29	EP 0.88	CO 2.00	NA 4.29	
October	DI −4.04	BO −1.28	EP −1.24	DA −0.70	CE −0.34	CH 0.30	CY 0.72	CO 1.70	NA 4.88
November	DI −3.20	BO −1.80	CE −1.16	EP 0.00	CY 0.38	CO 2.32	NA 3.46		
December	CY −2.81	CO −1.87	DA −1.02	CH −0.84	DI 0.81	BO 1.27	EP 1.54	NA 4.75	
All months	DI −2.75	CE −1.87	DA −1.02	CH −0.84	BO −0.61	CY 0.15	EP 0.19	CO 1.72	NA 5.02

[a]Underscored difference values were not significantly different (Waller Duncan procedure).

[b]Key: Same as Table 10.

in nearly all cases. Prey with lowest (negative) differences were utilized in greater proportion to their ranking of availability.

In November, each cisco analyzed had Epischura as the highest ranked prey consumed and the highest ranked prey available, which resulted in a mean difference in rank of 0.00 (Figure 21). In December, Daphnia was the prey item most utilized, but Cyclops received the highest preference ranking because of its rarity in sampled zooplankton. For most months, the array of cladocerans ranked more preferable than copepods and Conochilus colonies. Copepod nauplii, ranked last in all months, were rarely present in stomachs but common in the plankton. It is likely that nauplii were only incidentally ingested because of their small size.

Laboratory Studies

Planktivorous fishes may use three modes of plankton feeding. These modes have been described for alewives (Alosa pseudoharengus) and ciscoes (Coregonus hoyi and C. artedii) from the Great Lakes (Janssen 1978). The particulate or visual mode involves locating individual prey by sight, pursuing it, and capture by sucking it into the fish's mouth by rapid expansion of the buccal cavity (O'Brien 1979). Filter feeding is characterized by the fish swimming ahead with mouth held open so that water is strained through its gill rakers continuously. Gulping or pump filtering consists of the fish opening and closing the mouth 2-3 times per second, filtering out food particles (Janssen 1976).

Like most freshwater planktivorous fish, the Bonneville cisco uses the particulate feeding mode to capture individual prey. Cisco were also observed using the gulping or pump filtering mode in laboratory

Average Difference in Ranks for Prey Items
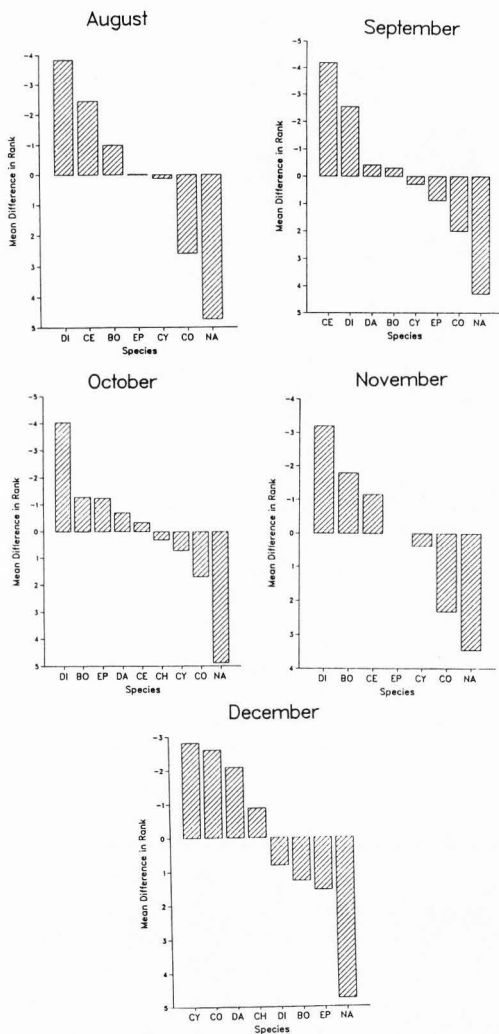
FIG. 21. Mean differences in ranks of preference for cisco prey items for five months, 1981. Prey code is same as in Table 10.

feeding. As live zooplankton were introduced into an aquarium, cisco gulped repeatedly at the dense assemblage of plankters, not directing their attacks at individual prey until the plankton cloud dispersed. The prey density which triggered feeding mode shifts was not measured.

Results of reactive distance measurements with three sizes of Daphnia prey are presented in Figure 22. The line was fitted by least squares regression with 51 observations of reactive distance (cm) vs. prey size (mm). The regression equation is $y = -4.34 + 11.35 x$ ($r^2 = 0.614$). Light intensity measured during the observations varied from 3.0 to 3.2 μE m^{-2} s^{-1} (250 to 267 lux). These photon units were converted to photometric units (lux) with approximate conversion factors from McCree (1981) to facilitate comparison of cisco reactive distance with other planktivores.
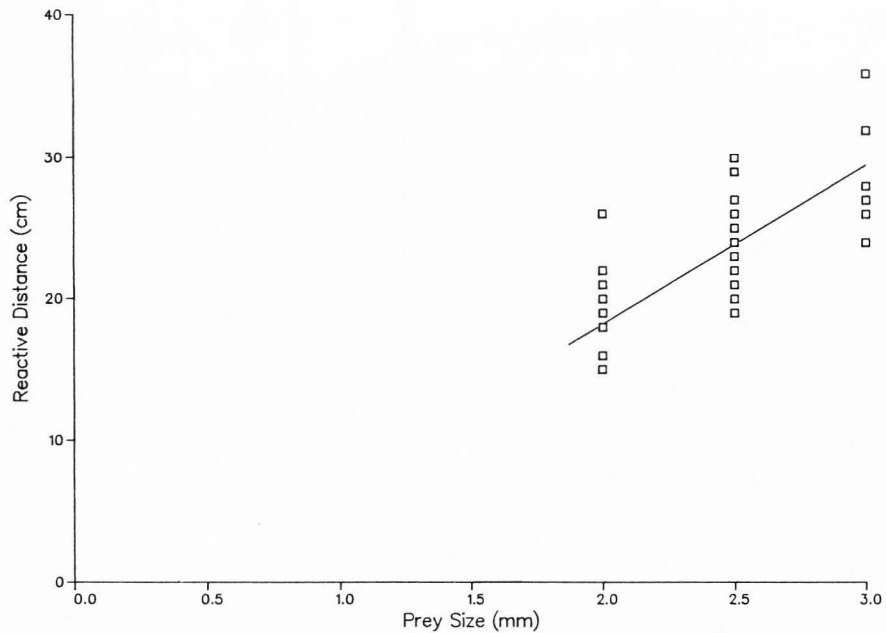
FIG. 22. Reactive distance of Bonneville cisco for three sizes of Daphnia prey. Reactive distances measured at light intensity of approximately 250 lux.

DISCUSSION

The findings of this study revealed several points of interest to the feeding ecology of the Bonneville cisco. First, changes in the zooplankton of Bear Lake have been reflected in the cisco's food habits compared to previous knowledge of cisco diet. Cladocerans were found to be an important food source in some months, whereas they played only a minor food role in the study by Perry (1943). Second, the reactive distance of cisco was determined and allowed comparisons to be drawn to other planktivorous fishes. Also, the vertical distribution and community structure of the zooplankton were determined. At the magnitude of the depth intervals sampled, no evidence of diel vertical migration by the zooplankton was detected.

Feeding Selectivity

Perry (1943) found that as a food item, Epischura was "monotonously abundant" and was a significant food at all times of the year. At times when Epischura was in low abundance, as in the winters of 1938 and 1940 and spring, 1940, cisco ate some cladocerans, mostly Bosmina and Chydorus. Perry's collections included cisco captured near the bottom and, thus, small numbers of food items such as harpacticoid copepods (Canthocamptus) and chironomid larvae were reported. Also, adult chironomids were found in 10 of 60 stomachs examined for June, 1941. However, during comparable seasons with this study, summer and fall, Perry found Epischura to comprise 90 to 100 percent of the food by volume.

An important prey in this study, Diaphanosoma, was not present in the zooplankton during Perry's study. Diaphanosoma is apparently a new member in the community, first reported by Nyquist (1968). A likely explanation for the increased contribution of prey like Diaphanosoma, Ceriodaphnia and Daphnia to the cisco diet is that cladocerans have become more numerous in the community since 1943, although comparative densities are not available for cladocerans. Increases in zooplankton densities are likely consequences of observed increases in nutrient loading and chlorophyll a (Lamarra et al. 1983). McConnell et al. (1957) reported no cladocerans were present in their plankton net hauls, but some were found in cisco stomach contents. Perry reported the zooplankton to be dominated by Epischura and Conochilus and their patterns of vertical distribution appeared similar to this study. His data show several cladocerans in cisco stomachs but cladocerans were not included in his plankton results.

In this study, when cladocerans were present at their peak numbers they formed only a very small percentage of the total zooplankton. Yet, they were selectively fed upon by cisco and formed significant proportions of the diet. A number of factors are involved in the selective feeding of planktivorous fishes. Predation can be broken into four steps: location, pursuit, capture and retention and factors come into play that affect the success of each step (Wright and O'Brien 1984; O'Brien 1979).

The ability of the predator to locate prey can be measured by its reactive distance to various prey items. Reactive distance is clearly affected by prey size and always increases in a linear fashion with prey size. Other factors affecting the location of prey include prey

movements, pigmentation, light intensity, turbidity, body shape and orientation. Ware (1973) found rainbow trout to locate moving prey more sucessfully than stationary prey, with other characteristics being equal. Most cladocerans have movement patterns of conspicuous and constant motion. An exception is _Diaphanosoma_ which behaves more like copepods and may remain motionless or move intermittently a great percentage of time (Zaret 1980; Wright and O'Brien 1984). Colored zooplankton are more easily detected than clear unpigmented prey (Mellors 1975; Vinyard and O'Brien 1975). Environmental conditions like turbidity of water and light intensity also influence the reactive distance of planktivores (Vinyard and O'Brien 1976).

Selective feeding is also impacted by the zooplankter's ability to evade capture. Copepods have been shown to be consistently more successful at evading the suction attack of particulate planktivores than cladocerans (Drenner et al. 1978). Selectivity is further affected by the predator's learning ability to distinguish which prey may be more vulnerable to capture (Drenner and McComas 1980). This learning may result in the predator selecting a smaller non-evasive cladoceran over a larger evasive copepod (Vinyard 1980).

In this study, size selectivity was observed in most cases (Tables 11-13). The cisco's preference for cladoceran prey with smaller sizes than the more abundant, larger _Epischura_ was also observed. Most likely, factors like prey motion and evasiveness contributed to this pattern of prey preference. Further feeding studies and reactive distance measurements with _Epischura_ and smaller sized prey would prove enlightening in the matter of prey preference.

Reactive distance (RD) measured for Bonneville cisco placed its prey location ability ahead of other tested salmonids and close to that of centrarchids. The cisco's mean RD of 18.2 cm for 2 mm Daphnia was greater than the arctic grayling's mean RD of about 17 cm for the copepod Heterocope, measured at 748 lux. Grayling tended to locate all prey types equally on the basis of core body size (Schmidt and O'Brien 1982). Cisco and grayling had superior RD measurements compared to lake trout and brook trout (Kettle and O'Brien 1978; Confer et al. 1978). The cisco's RD for three sizes of Daphnia measured at light intensities of about 250 lux was very close to the white crappie's RD for Daphnia magna measured at 106 lux (Wright and O'Brien 1984). For all planktivores tested except grayling, maximum visual acuity (RD values) appeared to occur at intensities around 100 lux. One might expect that cisco, which remain planktivores throughout life would have developed superior prey location ability to grayling and trout which switch to eating larger prey when they grow to adults. Further measurements with different prey sizes and light intensities would be needed to confirm if cisco can match the centrarchids' abilities at prey location.

Zooplankton Distribution

Vertical distribution sampling showed that during summer stratification, zooplankton were concentrated in the epilimnion and metalimnion (depth intervals above 36 m). Often, the greatest densities were in the top of the metalimnion and coincided with the depths where cisco were most frequently captured in feeding studies. When the epilimnion was warmer than 15 degrees C, an apparent refuge from cisco predation was present. Cisco schools were not observed in

these warmer waters with echo sounding equipment, confirming previous netting studies of cisco depth distribution, however, no attempt at determining distribution was made in this study.

A number of hypotheses have been offered to explain the adaptive significance of diel vertical migration, swimming upward during or around sunset and swimming downward around sunrise. Hutchinson (1967) reviewed many of these. Avoidance of visually oriented planktivores is one popular explanation and many studies offer evidence (Zaret and Suffern 1976; Zaret 1980; Wright et al. 1980). A second major explanation states that migrating zooplankton benefit energetically by entering a cool hypolimnion and then returning upward to their food source (Enright 1977; McLaren 1974). It is unlikely that either hypothesis will fully explain vertical migration and Wetzel (1983) states that they probably interact to varying degrees.

Amplitude of vertical migration varies with species and environments. In turbid and productive lakes, migration distance is slight, often only a few meters. In oceans and oligotrophic lakes with high light penetration, amplitude of migration of the same species is markedly greater (Wright et al. 1980). In Lake Michigan, some cladocerans showed migration amplitudes of 10 m to 25 m and the copepod Limnocalanus migrated a maximum of 24 m (Wells 1960; McNaught and Hasler 1966). Pseudodiaptomus in an African lake migrated as much as 40 m (Hart and Allanson 1976). During midsummer stratification, in Bear Lake, Nyquist (1968) reported that volumes of total zooplankton at night increased by as much as six times over daylight samples collected at the surface and top 7 m of the lake. Nyquist sampled with a Van Dorn bottle of 8 L.

In this study, no evidence of vertical migration was detected by sampling at approximately 10 m intervals. Possible vertical migrations of less than 10 m amplitude within a depth interval were not able to be detected. Eggers (1978) reported that nocturnal vertical migration patterns of zooplankton were lacking in Lake Washington and in Great Central Lake and Babine Lake, British Columbia. Lake Washington supported a large population of juvenile sockeye salmon that selectively preyed on Epischura and Diaphanosoma. Zooplankton in Lake Washington was concentrated in the top 20 m except in late fall and winter. Eggers suggested that vertical migration of zooplankton was absent because the planktivores' vertical movements were controlled by piscivorous fishes in these lakes.

Predation and Zooplankton
Community Structure

The composition of the Bear Lake zooplankton fits some general rules about zooplankton community structure. The Bear Lake community is considered a small-bodied community with individuals rarely exceeding 1.5 mm in length. This type of community is generally found in the presence of vertebrate planktivores (O'Brien et al. 1979). Large-bodied communities with many individuals over 2 mm length are generally associated with an absence of planktivorous vertebrates. The dominant zooplankter of Bear Lake, Epischura is probably the most capable zooplankter at evading fish predation. Like other copepods, the strategy of Epischura in the face of predation pressure is to be swift and evasive.

Cladocerans have developed a different strategy to deal with predation pressure from planktivorous fish. Cladocerans have much

higher reproductive rates than copepods because they can reproduce by parthenogenesis, producing clones rapidly when environmental conditions are favorable. Bosmina also counters predation with small body size. Smaller instars may escape some predators by passing through their gill rakers (Schmidt and O'Brien 1982). Diaphanosoma has also adopted more effective motion patterns to counter predation.

The influence of predation on the structure of zooplankton communities is widely recognized (Brooks and Dodson 1965; Zaret 1980; Goldman et al. 1979; Lane 1978). In Bear Lake, aspects of the community structure and vertical distribution of zooplankters are clearly affected by cisco predation. Selective feeding by cisco in the limnetic zone influences both the composition and the location of zooplankton in the water column.

The zooplankton of Bear Lake is dominated by Epischura, a calanoid copepod with the greatest ability to evade capture by cisco relative to other zooplankters of the lake. The success of Epischura is aided by inconspicuous motion patterns, sensitive receptors for detecting suction currents in the water and rapid acceleration for evasive swimming. Some copepods may evade as much as 40 percent of the suction attacks of simulated fish predators (Drenner et al. 1978).

There are other possible factors which may contribute to the dominance of Epischura. The evasive skills of this copepod allow it to remain high in the water column where food resources are greatest, despite strong predation pressure from cisco in the metalimnion. The epilimnetic refuge from cisco predation is utilized by a large portion of the Epischura population during summer. Smaller individuals with presumably lesser evasive skills are located in these upper waters

while larger individuals are found in deeper waters utilized by cisco
(Table 8). Inspection of the seasonal patterns of mean lengths (Table
4) suggests that the life cycle of Epischura may possibly include a
bivoltine pattern of reproduction, producing two generations per year.
Main (1962) demonstrated this pattern for Epischura lacustris in a
Michigan lake using instar analysis. Also, Epischura nevadensis in
Bear Lake is at the extreme short end of its reported range in body
size (Wilson 1959). At Bear Lake, its mean length is just over 1 mm,
while in Pend Oreille Lake, mean length is 1.6 mm (Rieman and Bowler
1980). and in Lake Washington it is nearly 2 mm (Kerfoot 1977).
Further investigation of these factors is needed to determine what role
they play in Epischura's dominance.

Although rotifers are abundant in the plankton, they provide only
a minor contribution to the diet of cisco. When present, the rotifer
Conochilus substantially outnumbers all other zooplankters. Conochilus
has the ability to foil tactile invertebrate predators such as copepods
by forming large colonies in a gelatinous matrix (Gilbert 1980). Low
predation pressure from cisco and invertebrate predators surely
influences the dominance of this rotifer.

Rotifers are located in large numbers in the upper part of the
water column close to food resources. Invertebrate predators are
important in structuring zooplankton communities and are significant
factors in rotifer ecology (Williamson 1983; Dodson 1974; Lane 1979).
Further knowledge of invertebrate predators' usage of rotifers is
needed to improve understanding of the structure and distribution of
Bear Lake rotifers.

The increases in cladoceran populations over historical abundances may be tied to increased productivity of the lake. In highly oligotrophic Lake Tahoe, _Bosmina_ persists in shallower, more productive Emerald Bay. In the main part of the lake _Bosmina_ is extremely limited spatially and temporally by predators (Byron et al. 1984). Predators are present in Emerald Bay but increased food in this part of the lake allows the higher reproductive rate of the cladoceran to counter selective predation. _Bosmina_ in Bear Lake is the most numerous cladoceran and may do well against the cisco's selective feeding because of its small size and ubiquitous vertical distribution.

Other Bear Lake cladocerans combine reproductive strategy and vertical distribution patterns to counter cisco predation. _Diaphanosoma_ is a highly preferred cisco prey item when available. The vertical distribution of this cladoceran with large concentrations in the epilimnetic refuge helps provide replacement of individuals selectively fed on in the metalimnion. Rapid reproduction and copepod-like motion patterns help this herbivore maintain population numbers near those of _Bosmina_ despite greater preference by cisco. _Daphnia_ remain in the zooplankton community in low numbers nearly year-round by utilizing the hypolimnion. When conditions permit populations to increase and _Daphnia_ use more of the water column cisco predation pressure becomes intense and, most likely, is too great to allow _Daphnia_ to become numerous.

Future Research

Knowledge of cisco feeding ecology may benefit from more detailed looks at certain facets of this study. Further, understanding of

relationships between predation and community structure may be improved by investigating the role of invertebrate predation on zooplankton.

Determination of the cisco's reactive distance to Bear Lake planktonic prey would be interesting. Comparisons of RD for Epischura and Bear lake cladocerans may provide some insightfull benefits. Clarifying the cisco's relative prey location abilities compared to other salmonids and centrarchids would require further RD measurements with smaller prey and lower light intensities.

Also of interest is a refined view of vertical distribution of Epischura and some of the cladocerans. A finer scale than 10 m depth intervals should provide a closer look at zooplankton location and may reveal vertical migrations of smaller amplitudes.

A gap in predation information is the feeding habits of Epischura. Epischura is known to be omnivorous in Lakes Tahoe and Washington (Goldman et al. 1979; Kerfoot 1975). In these lakes rotifers and prey as large as Bosmina may be utilized. Determination of the food of Epischura in Bear Lake may provide insight on the rotifers and other members of the zooplankton community.

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