POPULATION DYNAMICS AND PRODUCTIVITY OF ZOOPLANKTON IN TWO SANDHILLS LAKES

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INTRODUCTION

Even though zooplankton has been a favorite subject of limnologists for the past half century, little work has been done in terms of population dynamics or productivity. Reports of population fluctuations are common but few have included an analysis of factors regulating zooplankton populations. A principal reason for this superficial analysis has been the difficulty of monitoring the many environmental variables which might affect zooplankton. I was fortunate in being able to participate in a lake eutrophication project directed by the University of Florida Environmental Engineering Department. In the resulting exchange of lake data, I obtained much valuable environmental information for correlation with zooplankton populations. The eutrophication project and this study involve two small lakes located in the sandhills region about five miles east of Melrose, Florida.

The Florida sandhills region consists of low, rolling hills with small lakes interspersed among them. The soil, of the Lakeland series, is derived from deep quartz sand and is extremely well leached (Laessle, 1958). The vegetation was originally longleaf pine (Pinus palustris) with an understory of turkey oak (Quercus laevis), but selective timbering has removed most of the pine, leaving turkey oak as the apparent dominant. The great porosity of the soil and the rolling topography virtually ensure against any surface runoff in even the heaviest rains.

The numerous small lakes in the sandhills are typically oligotrophic, with soft, slightly acid water not much different in mineral content from rainwater. There are two aquifers associated with the sandhills: an upper perched aquifer in the sand underlain with clays, and a lower, very extensive artesian aquifer in the deeper lying Ocala limestone (Anonymous, 1968). The lakes are sealed in their deeper regions by sediments, but connected into the upper aquifer via the porous sand in the littoral areas. Accordingly, the lakes fluctuate with the upper aquifer except during conditions of drought when they become perched.

The sandhills regions are important to the economy of Florida for three conflicting reasons. First they comprise the main recharge areas for the artesian aquifer upon which nearly all major Florida cities depend for water supply. Second the southern region of the sandhills is the heart of the orange growing area of Florida, where for miles all of the hills are covered with heavily fertilized groves. Third the well-drained land around the lakes is becoming increasingly popular for development of model communities, suburbs, etc. The cultural eutrophication of the sandhills lakes from fertilizer or domestic drainage could seriously impair the quality of Florida's ground water.

The lakes involved in this study are located on private property and receive very little cultural influence. They were initially very similar, being about the same size and only 0.4 miles apart, with the same type of surrounding soil and vegetation. Table 1 shows the similarity of chemical and physical parameters of the lakes at the start of the project. Since March, 1967, nutrients have been added to the experimental lake, Anderson-Cue, at rates comparable to nutrient loading rates known for eutrophic lakes. Nitrogen has been added at a rate of ca. 0.5 mg N $l^{-1}year^{-1}$ and phosphorus at ca. 0.05 mg P $l^{-1}year^{-1}$. These nutrients are added in the form of NH_4Cl and Na_3PO_4 dissolved in secondary sewage effluent so some trace nutrients are being added. Lake McCloud has been kept as a control and comparable measurements of biological, chemical, and physical parameters have been made in both lakes.

The variety and quantity of data available from the eutrophication study made these lakes an excellent area for the study of zooplankton population dynamics. Accordingly, I have attempted to monitor zooplankton populations and biomass and to correlate changes in the zooplankton with probable causative changes in other aspects of the ecosystem. In doing so I have used data collected by the Environmental Engineering staff for temperature (Figures 2-4), chlorophyll concentration (Figure 8), and primary productivity (Figure 9). I have also estimated zooplankton production to make comparisons between the lakes and with other ecosystems.

The study of fresh-water zooplankton began in this country with the descriptive and distributional work of Birge in the late 19th century. It has progressed through seasonal population studies to population dynamics and finally in the late 1950's and 1960's to studies of production.

The number of seasonal studies of zooplankton is too great to permit discussion of each work. Most were quantitatively descriptive, determining variations in population size with time but making no effort to explain population changes other than classifying some organisms as being cold water or warm water forms.

Table 1

Chemical Characteristics of Anderson-Cue and McCloud Lakes

Constituent[1]	Anderson-Cue			McCloud		
	Surf.	Mid.	Bottom	Surf.	Mid.	Bottom
Specific Cond.	28	28	27	32	30	31
pH	4.7	4.8	4.7	4.9	4.8	4.7
Acidity	3.4	3.2	3.4	3.6	3.7	4.5
Alkalinity	0.8	0.7	0.7	---	---	---
Cl^-	5.0	---	5.0	5.2	---	5.5
$SO_4^=$	1.4	1.5	1.4	2.0	2.2	2.0
Ca^{+2}	0,69	0,62	0,80	0.62	0.57	0.65
Mg^{+2}	0.55	0.52	0.55	0.57	0.57	0.55
Na^+	2.43	2.41	2.35	2.95	2.87	2.98
K^+	0.48	0.53	0.53	0.28	0.23	0.26

---

[1] Specific conductance in mho cm^{-1}; acidity and alkalinity in mg/l as $CaCO_3$; other cations and anions in mg/l (Anonymous, 1968).

Other more recent papers have attempted to explain population changes in terms of environmental variables and to describe the ecology of individual plankton species. Pennington (1941) first suggested a relationship of phytoplankton to zooplankton. Pennak (1946, 1949) attempted to relate food to the zooplankton populations but concluded that phytoplankton was probably not the most important food source. This conclusion has not been accepted by subsequent workers such as Gauld (1950, 1951), Gibor (1956), Davis (1958), and George (1966) who have indicated there is a strong relationship between phytoplankton and zooplankton. Further support for phytoplankton being the chief food of zooplankton and also the probability that the relationship between phytoplankton and zooplankton is not one-sided (i.e., grazing by zooplankton may affect both the numbers and species of phytoplankton in a community) has been given by Martin (1965) and Krishnamoorthi and Visvesvara (1963, 1966). Ryther (1954) demonstrated that, in adequately dense cultures, the effect of phytoplankton on zooplankton may take the form of antibiosis. In 1954, Davis summarized the earlier literature on causes of population variation in zooplankton and discussed the lack of consistency and poor general correlations in terms of multiple factor causes.

Some laboratory studies have been very important in understanding zooplankton population dynamics. The first was a study by Ingle, et al. (1937) showing effects of food limitation on Daphnia reproduction and longevity. Another early study (Pratt, 1943) showed that generation time was directly related to temperature but potential population size was greater at lower temperatures. More recently Frank

(1952, 1957, 1960) and Parker (1960, 1961) have demonstrated effects of competition on laboratory populations showing that two species even of different genera may be unable to coexist. Probably the laboratory study having the most bearing on natural population dynamics is that of Slobodkin (1954) demonstrating that populations cannot reach environmental equilibrium unless the environment remains constant for a period of time which may require several generations. Slobodkin also demonstrated that equilibrium population size is directly related to food supply and that environmental changes cause population changes only after time lags.

Recent studies have attempted to apply laboratory techniques and principles to natural populations. Most of these have dealt with only one species of the assemblage of zooplankters. Comita and Anderson (1959) found that reproductive rate in Diaptomus ashlandi was positively correlated with chlorophyll concentration. Edmondson (1962, 1965) and Edmondson, et al. (1962) have shown a similar positive relationship between food and reproduction in rotifers and copepods. There have been several attempts to build models for natural populations using life-table data based on comparisons with laboratory populations, the most notable being those of Smith (1963) and Hall (1964). Hall found that his experimentally determined birth rates would predict spring and fall populations of Daphnia galeata mendotae but gave much too high predictions for the summer. He concluded that death rate, probably due to predation, was much greater in summer.

Attempts at measuring zooplankton production are also recent. Earlier workers such as Elster (1955) and Davis (1958) did not distinguish between standing crop and production. One of the first attempts to determine zooplankton production was an excellent study by Wright (1958). He made accurate calculations of zooplankton standing crop from counts of each species and mean dry weight per individual of a species, determining production from changes in standing crop and turnover rates. Unfortunately his study covered only two months. Stross, *et al*. (1961) used total zooplankton biomass and turnover time for the dominant species to calculate zooplankton production. Their estimates are crude due to error in determining biomass; they weighed net catches assuming that the net would retain all zooplankton and pass all phytoplankton. Ilkowska *et al*. (1966) used reproductive rates and wet weights based on volume to calculate zooplankton production. Shuskina (1966a, 1966b) has devised a mathematical formula for calculating secondary production from zooplankton biomass; this method is at best an approximation. Chemyr (1966) has attempted to extend the use of carbon-14 to include measurements of secondary production but his method ignores respiration in both phytoplankton and zooplankton. Most recently, McAllister (1969) has made calculations of secondary production based on primary production, changes in phytoplankton standing crop and correction factors for zooplankton assimilation.

While there have been few direct studies showing changes in species composition and abundance with changes in the trophic nature of a lake, faunal comparisons of different lakes as by Lang (1931) and sediment studies such as those by Deevey (1942) and Goulden (1964) strongly suggest that such changes do occur. There have been several fertilization experiments involving fish ponds: Hepher (1962) found increased primary productivity up to a compensation point following fertilization, and Glonti and Tskhomelidze (1963) found an increase in zooplankton biomass. There have been two related experiments with lakes. Stross and Hasler (1960) and Stross, et.al. (1961) reported that lime added to a bog lake caused no increase in zooplankton standing crop but apparently caused a more rapid turnover resulting in increased production. Nelson and Edmondson (1955) reported that inorganic fertilizer applied to Bare Lake, Alaska, induced an increase in primary production, no change in zooplankton biomass but again, presumably, an increase in turnover rate and thus in secondary production.

The present study will evaluate the interrelationships of zooplankton populations and environmental factors in Anderson-Cue and McCloud lakes with respect to food limitation, competition, predation upon, and production by zooplankton.

MATERIALS AND METHODS

Sampling

Zooplankton samples were taken from January, 1967, through December, 1968, in Lake Anderson-Cue and from May, 1967, through December, 1968, in Lake McCloud. From January to August, 1967, samples were taken biweekly with a Wisconsin closing plankton net (125 meshes/inch) towed horizontally for a known distance at three depths corresponding to just below the surface, mid-depth and just above the bottom. Aliquots from these samples were counted; counts were adjusted to No./m^3 and integrated over depth to obtain No./m^2. After August, 1967, weekly samples were taken with a vertical-tow plankton net (125 meshes/inch) pulled from bottom to surface. When using the vertical-tow net, samples were taken from three stations in the lake and each sample concentrated to 35 ml. The three samples were combined, mixed thoroughly, and a subsample of 35 ml taken from the mixture for preservation with formalin and counting. This procedure provided a physical means of averaging samples from three areas of the lake while counting only one sample, thus providing a more representative sample from the lake.

Zooplankters were counted using a compound microscope at a magnification of 21 diameters. Each sample was shaken thoroughly; a 1 ml aliquot was then taken with a graduated syringe and placed in a Sedgewick-Rafter counting chamber. Three such aliquots were counted for each sample and all zooplankters in the chambers were identified and counted. Occasionally, when phytoplankton was especially numerous, it was necessary to dilute a sample before counting. Counts from samples taken with a vertical-tow net were converted directly to No./m^2 based on the area of the net mouth; e.g., a net with a 0.2 m^2 mouth area towed from bottom to surface would collect the plankton under 0.2 m^2 of lake surface.

Biomass Determination

To determine the mean individual biomass of a zooplankton species, individuals were sorted from a sample under a dissecting microscope, blotted, dried under vacuum desiccation, and weighed on a calibrated quartz helix. From 5 to 200 dry individuals were weighed at a time to get an adequate deflection of the helix. To avoid bias in unconsciously selecting only the larger individuals, several drops of plankton sample were placed on a watch glass and all individuals of a species were removed for drying. The total individuals weighed of any species were taken from several samples in case a species might average larger in some samples than in others. Due to the small size and relative scarcity of planktonic rotifers in these lakes, only the biomass of the most abundant species, Keratella americana, could be determined. For conversion of population estimates to biomass, all other rotifers were considered to be the same size as K. americana. The obvious error involved is quite small in terms of total zooplankton biomass since K. americana, when most abundant, comprised only ca. 7 percent of the total biomass.

After the mean dry weight/individual of a species had been determined, the species biomass for any sample date was calculated by multiplying individuals/m^2 by mg/individual. The species biomasses were summed to obtain total zooplankton biomass.

Secondary Production

An estimate of yearly production was made for each zooplankton species except that rotifers other than K. americana were lumped. In order to put limits on secondary production, three calculations were made: a minimum estimate, a maximum estimate, and a "best estimate." The minimum estimate for a species was obtained by summing the net positive change in population size over a year, then multiplying by the average mass per individual of the species. The other two estimates were unrelated to the minimum estimate, except that all were based on the same population data and biomass data.

The classical sigmoid growth curve for a population is described by the equation $\frac{dN}{dt} = rN(\frac{K-N}{K})$ where:

N = No. of individuals

t = time

r = instantaneous rate of increase

K = carrying capacity of the environment

If N is very small relative to K the expression $\frac{K-N}{K}$ simplifies to 1.0 and the resulting equation, $\frac{dN}{dt} = rN$ describes the logarithmic phase of the growth curve. In this study N was considered to be very much smaller than K for several reasons:

1. The relative density of zooplankton in oligotrophic lakes such as those studied is very low. For example, maximum cladoceran densities in Anderson-Cue and McCloud are in the order of 50-100/liter. Ward

(1940) reported up to 2,000 cladocera/l in a small pond and Borecky (1956) reported 3,500 cladocera/l in Pymatuning Reservoir.

2. Density dependent effects on laboratory populations of Daphnia were not seen by Frank, et al. (1957) until densities of 1,000-2,000/l were reached.

3. A plot of r vs. N for data from Anderson-Cue shows no tendency for r to decline as N gets large (Figure 1). If N were approaching K, r should be approaching zero.

The equation $\frac{dN}{dt} = rN$ can be written in its integrated form: $N_t = N_o e^{rt}$, and taking natural logarithms: $\ln N_t = rt + \ln N_o$, which, when $\ln N_t$ is plotted against t, gives a straight line with r as the slope.

In this study logarithms of population were plotted against time and each slope was considered to be an estimate of r over that time period. For any species the maximum positive slope observed was considered to approximate r_m, the intrinsic rate of increase for that species. To determine maximum production, each species was considered to be reproducing at r_m at all times during the year so that observed differences between r and r_m were considered to be due entirely to a variable death rate. The maximum productivity at any time was calculated from the equation, $\rho_m = N_t \, r_m \, B$, where:

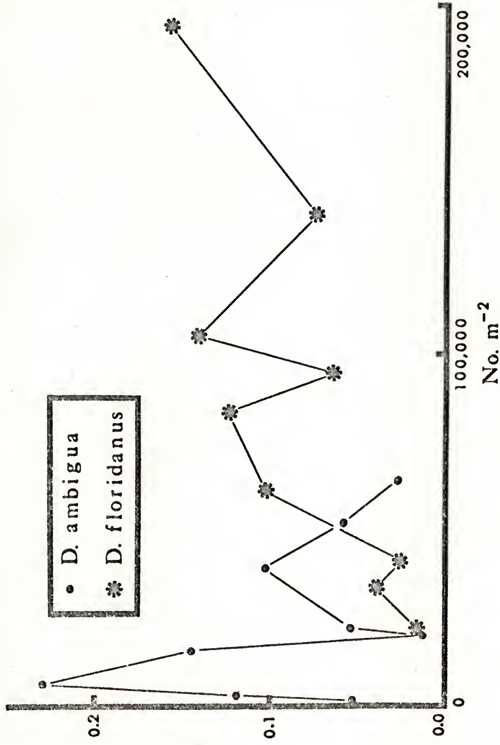
ρ_m = maximum productivity

N_t = population size at time t

r_m = maximum observed instantaneous rate of increase

B = average biomass per individual.

Figure 1. Relationship of observed rate of increase "r" to population density for *Daphnia ambigua* and *Diaptomus floridanus*.


D. ambigua
D. floridanus
r
0.2
0.1
0.0
0
100,000
200,000
No. m^{-2}

Values of ρ_m were integrated over a year's time to get maximum yearly production.

The "best estimate" of production was determined similarly to maximum production except that all positive r values were used to determine productivity: $\rho = N_t r_t B$.

N_t and B are the same as above.

r_t = the observed rate of increase at time t.

ρ = productivity.

Productivity was integrated over time to get a "best estimate" for yearly production. Finally production values for all species were summed to get total zooplankton production.

Predation

Labidesthes sicculus was considered to be the chief zooplankton predator in these lakes. The population size of L. sicculus was estimated using the Peterson mark-recapture method as described by Ricker (1958). Fish were captured individually at night with dipnets and each fish was immediately marked by clipping a pectoral fin and released. Since L. sicculus will lie at the surface in shallow water on a dark night, the marking procedure was fairly simple. The brief period of handling ensured minimum damage to the fish. Recaptures were made after one week.

At numerous times during the year, samples of L. sicculus were collected with a dipnet or seine and preserved in 10 percent formalin for later analysis. To determine food habits, each fish was measured and its gut contents analyzed. The entire gut was removed, carefully pulled apart, and washed with a few drops of water in a Sedgewick-Rafter counting chamber. All recognizable organisms in the gut were counted under 21X magnification with frequent use of higher magnification to check identification. The counts of zooplankton in the gut were converted to total mass of zooplankton eaten by multiplying the number of each species by the mean individual biomass for the species.

Statistics

Statistical tests were used to evaluate apparent trends in the results. Since sampling frequency was arbitrarily chosen, samples were considered to be random with respect to population size or biomass. Total biomass values were assumed to have an approximately normal distribution. In determining correlation coefficients between species, only samples in which both species occurred were used, as inclusion of zero values would constitute a significant departure from a normal distribution and thus invalidate the test statistic "r." All statistical tests used are described by Mendenhall (1967). A significance level of 0.05 was used throughout.

RESULTS

Population Density

The densities (No./m^2) of zooplankton species are shown in Tables 2-9. Species of which only one or two individuals were seen during the study are not included since their contribution to the biomass of zooplankton is negligible. Most of such occasional sightings represent strays from the littoral zone. Sample dates where a species was not seen are indicated by dashes in the tables.

Biomass

Table 10 shows the mean (with 95 percent confidence interval) individual biomass of the common zooplankton species. These values represent average dry weights for individuals of each species. The scarcity of Holopedium amazonicum in these lakes is reflected in the few individuals obtained for weighing and the consequent inaccuracy of weight determination for this species. The total zooplankton biomass is shown in Figures 2-4; and the biomasses of copepods, cladocera, and rotifers are shown in Figures 5, 6, and 7, respectively.

Table 2

Population Densities (No./m^2) of Zooplankton -- Microcrustacea of Anderson-Cue, 1967

	Cyclopoid (2 sp.)	*Diaptomus floridanus*	Larval Copepods	*Bosmina coregoni*	*Daphnia ambigua*	*Diaphanosoma brachyurum*	*Holopedium amazonicum*
7 Jan	2,895	37,406	79,645	803	2,389	-----	1,664
21 Jan	3,676	235,270	78,743	1,182	39,991	636	3,617
4 Feb	5,226	111,280	79,465	4,131	49,925	2,054	2,462
18 Feb	9,610	70,803	204,750	10,760	26,513	3,428	5,556
4 Mar	13,030	171,590	74,053	8,289	73,721	22,874	9,133
1 Apr	14,010	163,570	140,980	1,092	50,057	4,952	2,282
22 Apr	25,370	60,650	122,580	4,014	7,387	24,354	72
6 May	8,835	41,936	48,211	1,145	1,614	9,705	-----
20 May	13,870	30,659	94,393	1,750	2,389	1,231	50
3 Jun	7,896	46,628	49,519	6,160	6,790	753	-----
16 Jun	4,881	47,208	73,602	12,290	6,637	-----	176
1 Jul	8,932	31,426	33,599	15,940	5,077	1,321	-----
15 Jul	8,837	29,447	18,671	6,440	2,805	63	-----
3 Aug	7,885	11,038	18,987	1,227	3,156	879	-----
11 Aug	3,612	5,179	27,836	5,706	3,876	-----	-----

Table 2 - continued

	Cyclopoid (2 sp.)	Diaptomus floridanus	Larval Copepods	Bosmina coregoni	Daphnia ambigua	Diaphanosoma brachyurum	Holopedium amazonicum
26 Aug	33,013	22,484	74,147	18,050	761	-----	-----
5 Oct	32,260	34,420	69,990	49,670	15,710	693	-----
12 Oct	16,110	29,110	18,250	18,710	17,090	462	-----
19 Oct	47,100	10,700	69,500	11,100	231	-----	-----
26 Oct	123,400	66,800	83,600	58,000	48,000	980	-----
2 Nov	74,350	57,650	71,930	34,750	85,670	1,347	-----
18 Nov	35,843	40,409	56,630	7,762	24,428	685	-----
25 Nov	40,866	53,880	64,152	19,862	51,824	1,598	-----
1 Dec	40,181	31,962	65,070	20,547	36,528	228	-----
13 Dec	23,286	55,480	45,203	6,392	84,928	913	-----

Table 3

Population Densities (No./m^2) of Zooplankton -- Rotifera of Anderson-Cue, 1967

	Conochiloides sp.	Conochilus sp.	Keratella americana	Keratella taurocephala	Lecane sp.	Pedalia sp.	Polyarthra sp.	Trichocerca sp.
7 Jan	-----	21,900	36	-----	50	-----	-----	---
21 Jan	-----	404,600	825	-----	---	-----	-----	---
4 Feb	1,125	337,100	771	-----	130	-----	-----	---
18 Feb	19,675	60,600	14,702	-----	75	-----	-----	---
4 Mar	1,150	71	672	-----	---	-----	-----	---
1 Apr	5,452	787	16,344	-----	17	-----	-----	110
22 Apr	1,333	353	15,153	-----	93	-----	-----	137
6 May	-----	-------	12,105	-----	108	-----	-----	66
20 May	1,286	485	151,800	-----	29	-----	-----	---
3 Jun	256	5,390	68,820	-----	131	-----	-----	986
16 Jun	302	14,700	156,700	-----	74	-----	-----	494
1 Jul	-----	-------	56,356	1,068	192	583	129	433
15 Jul	29	-------	7,861	-----	198	1,086	1,436	155
3 Aug	-----	-------	9,922	-----	---	699	116	71
11 Aug	7,776	-------	9,065	-----	58	403	6,560	58

Table 3 - continued

	Conochiloides sp.	Conochilus sp.	Keratella americana	Keratella taurocephala	Lecane sp.	Pedalia sp.	Polyarthra sp.	Trichocerca sp.
26 Aug	4,589	-------	26,699	-----	185	437	5,178	208
5 Oct	231	-------	2,310	-----	---	-----	-----	---
12 Oct	-----	-------	3,470	-----	---	-----	-----	---
19 Oct	-----	-------	10,900	-----	---	-----	462	---
26 Oct	-----	-------	8,230	-----	196	-----	196	196
2 Nov	-----	-------	2,649	-----	---	-----	-----	---
18 Nov	457	-------	2,511	-----	---	-----	-----	228
25 Nov	4,109	228	6,392	-----	---	-----	-----	228
1 Dec	5,936	457	3,653	-----	228	-----	-----	685
13 Dec	-----	-------	913	-----	---	-----	-----	457

Table 4

Population Densities (No./m^2) of Zooplankton -- Microcrustacea of Anderson-Cue, 1968

	Mesocyclops edax	Tropocyclops prasinus	Diaptomus floridanus	Larval Copepods	Bosmina coregoni	Daphnia ambigua	Diaphanosoma brachyurum	Holopedium amazonicum
5 Jan	5,936	32,190	39,496	86,980	7,306	31,551	457	---
11 Jan	6,849	18,949	38,354	52,737	10,730	62,326	---	---
20 Jan	2,968	10,274	46,117	45,888	13,926	59,815	913	---
27 Jan	4,566	28,081	27,624	44,747	20,547	50,226	---	---
2 Feb	3,425	15,752	24,200	37,670	27,853	29,907	228	---
17 Feb	685	17,122	42,920	25,341	67,577	36,071	---	---
24 Feb	5,479	29,222	22,145	37,441	59,130	19,177	---	---
29 Feb	5,936	30,136	31,048	47,030	53,422	24,656	---	---
8 Mar	4,566	2,283	20,547	22,830	66,207	27,396	---	---
16 Mar	4,794	18,721	23,743	46,573	70,545	17,579	---	---
27 Mar	9,589	38,126	32,190	126,707	42,236	58,445	---	---
5 Apr	17,807	41,779	40,181	133,100	5,251	47,030	---	---
11 Apr	24,885	55,249	39,268	214,145	4,338	45,203	---	---
17 Apr	13,241	61,641	41,322	197,023	3,653	59,358	913	---

Table 4 - continued

	Mesocyclops edax	Tropocyclops prasinus	Diaptomus floridanus	Larval Copepods	Bosmina coregoni	Daphnia ambigua	Diaphanosoma brachyurum	Holopedium amazonicum
25 Apr	17,579	49,769	51,596	176,019	3,881	62,326	---	---
2 May	27,624	35,615	156,522	85,613	------	74,654	4,566	---
14 May	6,849	5,479	24,428	86,526	2,740	33,332	228	---
24 May	6,392	20,775	13,470	168,942	10,730	13,241	---	---
30 May	5,479	12,557	10,958	95,658	11,643	23,287	---	---
10 Jun	1,370	4,566	28,309	119,858	2,511	913	228	---
18 Jun	4,566	7,534	91,092	205,242	228	1,370	---	---
26 Jun	10,502	13,926	122,579	228,575	228	3,653	---	---
4 Jul	456	5,479	20,547	111,182	685	228	---	---
13 Jul	4,338	7,534	55,477	156,386	456	228	---	---
22 Jul	5,936	15,524	14,840	99,539	------	------	---	---
29 Jul	2,740	10,274	26,711	129,446	------	------	---	---
12 Aug	7,991	24,200	144,514	192,000	1,142	228	---	---
19 Aug	16,666	39,496	92,690	90,635	685	228	228	---
26 Aug	44,385	43,847	291,058	194,756	7,801	807	4,035	---

Table 4 - continued

	Mesocyclops edax	Tropocyclops prasinus	Diaptomus floridanus	Larval Copepods	Bosmina coregoni	Daphnia ambigua	Diaphanosoma brachyurum	Holopedium amazonicum
9 Sep	32,812	51,379	75,051	68,326	52,724	2,152	10,760	---
16 Sep	40,350	56,607	113,787	69,940	69,402	10,760	19,099	---
28 Sep	39,543	66,712	68,864	142,301	46,537	4,304	31,204	---
14 Oct	52,724	62,946	210,627	186,955	94,419	7,532	181,037	---
21 Oct	15,064	49,765	60,794	221,925	90,653	6,456	71,016	---
25 Oct	17,754	49,765	105,986	193,680	54,338	8,339	119,167	---
1 Nov	23,134	62,139	142,839	203,633	51,648	22,327	154,944	---
9 Nov	25,017	59,180	105,179	167,856	45,461	5,918	61,601	---
22 Nov	18,830	41,426	29,321	114,056	8,608	6,994	59,449	---
1 Dec	19,099	21,789	93,074	105,986	7,263	13,719	76,934	---
6 Dec	15,064	17,216	115,670	79,893	7,801	9,953	52,455	---
12 Dec	12,105	22,865	104,103	114,056	15,333	18,292	38,736	---
30 Dec	11,836	16,140	99,530	80,162	34,970	22,058	64,560	---

Table 5

Population Densities (No./m^2) of Zooplankton -- Rotifera of Anderson-Cue, 1968

	Conochiloides sp.	Conochilus sp.	Keratella americana	Keratella taurocephala	Lecane sp.	Pedalia sp.	Polyarthra sp.	Trichocerca sp.
5 Jan	-------	------	1,826	---	---	----	------	---
11 Jan	-------	------	1,598	---	---	----	------	---
20 Jan	1,370	------	913	---	---	----	------	---
27 Jan	685	457	228	---	---	----	------	---
2 Feb	------	------	457	---	---	----	------	---
17 Feb	------	------	2,283	---	---	----	------	228
24 Feb	------	------	2,283	228	---	----	------	---
29 Feb	------	------	3,653	---	---	----	------	---
8 Mar	------	------	15,981	---	---	----	------	---
16 Mar	------	------	10,502	---	---	----	------	228
27 Mar	------	9,132	5,479	---	---	----	------	---
5 Apr	------	5,479	2,511	---	---	----	------	---
11 Apr	------	1,142	------	---	---	----	------	---
17 Apr	------	------	1,142	228	---	----	------	---

Table 5 - continued

	Conochiloides sp.	*Conochilus* sp.	*Keratella americana*	*Keratella taurocephala*	*Lecane* sp.	*Pedalia* sp.	*Polyarthra* sp.	*Trichocerca* sp.
25 Apr	------	1,142	------	228	---	----	------	---
2 May	------	1,370	228	---	---	----	------	---
14 May	1,142	------	------	228	---	----	------	---
24 May	228	------	456	---	---	----	------	---
30 May	------	------	228	---	---	----	------	228
10 Jun	2,055	------	5,936	---	---	----	------	1,142
18 Jun	2,055	228	76,024	456	---	----	1,142	228
26 Jun	29,679	51,596	183,782	228	---	----	228	---
4 Jul	32,419	1,142	437,879	---	---	----	456	685
13 Jul	15,981	------	506,826	228	---	----	456	3,881
22 Jul	7,991	------	263,458	456	---	2,968	40,409	2,283
29 Jul	1,142	------	271,905	---	---	4,794	8,219	1,142
12 Aug	913	------	58,901	---	---	4,109	228	---
19 Aug	913	------	42,464	---	---	15,981	228	456
26 Aug	1,345	------	538	---	---	----	------	---
9 Sep	18,292	------	3,497	---	---	538	------	---

Table 5 - continued

	Conochiloides sp.	*Conochilus* sp.	*Keratella americana*	*Keratella taurocephala*	*Lecane* sp.	*Pedalia* sp.	*Polyarthra* sp.	*Trichocerca* sp.
16 Sep	1,076	------	2,152	---	---	1,883	------	---
28 Sep	4,304	------	2,959	---	---	-----	------	269
14 Oct	3,766	------	269	---	---	-----	------	---
21 Oct	3,228	------	269	---	---	-----	------	269
25 Oct	269	------	269	---	---	-----	------	269
1 Nov	------	------	269	---	---	-----	------	538
9 Nov	------	------	------	---	538	-----	------	269
22 Nov	------	------	------	---	---	-----	------	---
1 Dec	------	------	------	---	---	-----	------	---
6 Dec	------	------	------	---	---	-----	------	---
12 Dec	------	------	------	---	---	-----	------	---
30 Dec	------	------	------	---	---	-----	------	---

Table 6

Population Densities (No./m^2) of Zooplankton -- Microcrustacea of McCloud, 1967

	Cyclopoid (2 sp.)	*Diaptomus floridanus*	Larval Copepods	*Bosmina coregoni*	*Daphnia ambigua*	*Diaphanosoma brachyurum*	*Holopedium amazonicum*
20 May	2,718	11,470	32,020	2,826	1,986	---	500
3 Jun	5,224	5,805	59,710	4,721	431	79	1,184
16 Jun	3,272	2,905	26,010	2,791	447	---	26
1 Jul	3,528	8,334	56,010	2,201	351	---	-----
15 Jul	6,010	7,905	56,450	4,103	129	132	-----
3 Aug	9,406	9,628	36,030	6,503	105	---	-----
11 Aug	8,982	9,713	47,800	10,540	79	26	-----
5 Oct	34,400	24,300	126,000	16,900	6,470	---	924
12 Oct	40,200	17,800	98,600	19,400	7,390	231	1,390
19 Oct	35,800	32,100	84,100	19,900	8,320	---	462
26 Oct	42,710	30,760	83,060	21,160	13,710	392	1,959
2 Nov	38,605	47,121	51,322	5,205	16,181	251	1,941
18 Nov	58,445	31,734	98,854	4,794	21,460	---	913
25 Nov	34,930	47,715	72,371	4,566	23,058	---	913
13 Dec	25,798	45,432	74,882	10,045	18,492	228	3,196

Table 7

Population Densities (No./m^2) of Zooplankton -- Rotifera of McCloud, 1967

	Conochiloides sp.	Conochilus sp.	Keratella americana	Keratella taurocephala	Lecane sp.	Pedalia sp.	Polyarthra sp.	Trichocerca sp.
20 May	5,093	-------	5,551	600	50	-----	103	76
3 Jun	1,389	-------	5,183	5,939	315	-----	3,922	58
16 Jun	313	1,292	31,350	6,953	53	-----	3,031	76
1 Jul	260	78	84,830	5,359	55	807	2,143	403
15 Jul	139	158	76,870	6,207	189	3,729	4,511	851
3 Aug	129	-------	41,370	1,259	53	5,252	1,877	29
11 Aug	4,434	348	66,190	555	155	3,367	6,580	903
5 Oct	1,160	-------	7,850	231	---	-----	231	924
12 Oct	1,620	924	15,200	693	231	-----	1,390	462
19 Oct	2,080	231	6,930	231	---	-----	-----	---
26 Oct	3,526	2,547	2,547	-----	---	-----	-----	784
2 Nov	-----	51,436	3,835	46	46	-----	69	388
18 Nov	-----	365,052	2,968	-----	---	-----	-----	1,142
25 Nov	-----	127,391	10,045	228	---	-----	-----	457
13 Dec	-----	63,011	10,730	-----	228	-----	-----	685

Table 8

Population Densities (No./m^2) of Zooplankton -- Microcrustacea of McCloud, 1968

	Mesocyclops edax	*Tropocyclops prasinus*	*Diaptomus floridanus*	Larval Copepods	*Bosmina coregoni*	*Daphnia ambigua*	*Diaphanosoma brachyurum*	*Holopedium amazonicum*
5 Jan	19,634	41,551	78,764	87,896	17,579	13,241	1,142	3,881
11 Jan	15,068	18,264	60,728	80,590	23,058	15,753	457	9,360
20 Jan	7,077	7,762	36,300	30,364	28,309	11,643	457	2,511
27 Jan	6,392	16,209	27,168	40,637	37,441	9,817	685	2,055
2 Feb	3,653	8,447	44,975	71,458	5,936	7,077	685	8,447
17 Feb	3,425	13,470	80,590	108,443	10,958	6,849	-----	1,142
24 Feb	2,968	8,219	45,888	76,937	1,598	8,675	457	228
29 Feb	3,881	5,936	33,104	127,163	2,511	5,936	228	685
8 Mar	5,023	7,991	80,818	110,726	1,598	6,164	228	685
16 Mar	2,740	1,598	57,532	54,792	1,598	4,566	457	913
5 Apr	4,338	7,306	105,931	65,522	3,653	10,958	1,142	913
11 Apr	5,251	13,013	84,014	65,979	4,566	5,251	228	228
17 Apr	7,306	9,360	113,693	76,709	39,724	28,766	2,968	457
25 Apr	5,023	17,123	106,844	78,992	115,063	35,153	7,534	228

Table 8 - continued

	Mesocyclops edax	*Tropocyclops prasinus*	*Diaptomus floridanus*	Larval Copepods	*Bosmina coregni*	*Daphnia ambigua*	*Diaphanosoma brachyurum*	*Holopedium amazonicum*
2 May	8,447	9,132	96,343	106,160	67,120	30,592	9,589	228
14 May	4,566	22,830	71,915	123,282	4,566	31,962	20,547	-----
24 May	8,904	7,762	40,866	69,403	4,566	2,740	22,373	-----
30 May	9,132	5,023	35,158	74,882	2,740	456	2,968	228
10 Jun	6,392	4,794	20,319	93,831	13,470	228	-----	685
18 Jun	5,708	10,274	42,007	179,444	53,442	3,196	-----	2,511
26 Jun	21,689	47,030	56,847	288,800	78,307	15,981	1,142	5,251
4 Jul	7,762	10,502	8,447	193,827	17,351	4,109	685	456
13 Jul	8,904	18,264	32,419	156,157	17,123	4,109	456	-----
22 Jul	4,338	10,730	14,611	101,365	16,438	228	2,055	-----
29 Jul	7,762	21,689	11,872	118,716	7,991	228	456	228
12 Aug	11,187	36,528	25,570	86,982	27,168	1,142	12,785	228
19 Aug	19,405	23,743	34,702	101,137	24,656	------	20,775	-----
26 Aug	28,514	27,976	91,998	80,162	112,980	------	35,625	-----
9 Sep	22,596	88,232	67,519	215,200	40,888	1,076	1,345	-----
16 Sep	82,045	65,905	93,612	111,097	32,549	6,725	538	-----

Table 8 - continued

	Mesocyclops edax	*Tropocyclops prasinus*	*Diaptomus floridanus*	Larval Copepods	*Bosmina coregoni*	*Daphnia ambigua*	*Diaphanocoma brachyurum*	*Holopedium amazonicum*
28 Sep	49,227	61,063	70,209	96,571	18,561	8,070	-----	-----
14 Oct	12,912	57,566	52,186	171,084	28,245	39,812	807	-----
21 Oct	9,953	77,472	41,426	161,669	538	19,099	807	-----
25 Oct	13,719	106,255	60,794	204,709	------	59,449	1,345	-----
1 Nov	13,719	120,781	55,952	172,160	------	71,554	1,345	-----
9 Nov	13,450	103,565	48,689	114,325	807	50,841	269	-----
22 Nov	28,514	76,396	52,993	118,360	1,345	33,087	538	-----
1 Dec	16,409	40,619	26,362	91,729	2,959	18,023	-----	-----
6 Dec	19,099	35,777	58,104	143,915	9,415	24,210	807	-----
12 Dec	12,643	54,876	72,361	192,335	16,140	15,333	538	-----
30 Dec	7,532	30,397	101,144	182,113	12,912	12,374	538	269

Table 9

Population Densities (No./m^2) of Zooplankton -- Rotifera of McCloud, 1968

	Conochiloides sp.	Conochilus sp.	Keratella americana	Keratella taurocephala	Lecane sp.	Pedalia sp.	Polyarthra sp.	Trichocerca sp.
5 Jan	------	74,654	4,338	-----	---	---	---	457
11 Jan	------	58,445	3,653	-----	---	---	---	---
20 Jan	------	8,675	228	-----	---	---	---	---
27 Jan	------	1,142	1,370	-----	---	---	---	228
2 Feb	------	228	228	-----	---	---	---	---
17 Feb	------	685	1,370	-----	---	---	---	---
24 Feb	------	------	1,598	-----	---	---	---	---
29 Feb	------	228	1,142	-----	---	---	---	---
8 Mar	------	------	913	-----	---	---	---	---
16 Mar	------	228	913	-----	---	---	---	---
5 Apr	------	46,753	4,109	228	228	---	---	---
11 Apr	-------	92,005	4,338	-----	---	---	---	---
17 Apr	4,109	9,589	11,872	1,142	---	---	---	---
25 Apr	2,511	913	23,743	2,055	---	---	---	456

Table 9 - continued

	Conochiloides sp.	Conochilus sp.	Keratella americana	Keratella taurocephala	Lecane sp.	Pedalia sp.	Polyarthra sp.	Trichocerca sp.
2 May	1,370	------	10,730	685	456	456	---	228
14 May	18,264	------	2,283	-----	---	---	---	---
24 May	10,274	456	4,338	-----	---	---	---	---
30 May	2,055	------	5,936	228	---	685	---	---
10 Jun	56,618	1,826	17,123	-----	---	1,826	---	---
18 Jun	35,387	456	50,683	228	---	228	---	685
26 Jun	11,186	------	69,175	228	---	1,142	---	1,142
4 Jul	7,306	228	73,056	456	---	456	228	228
13 Jul	3,653	------	37,441	-----	456	913	---	228
22 Jul	42,236	------	43,149	-----	---	2,283	1,593	913
29 Jul	19,177	------	20,775	-----	---	7,077	456	3,196
12 Aug	------	------	2,511	-----	---	2,968	---	---
19 Aug	------	------	1,826	-----	228	1,826	---	228
26 Aug	269	------	------	-----	---	---	---	---
9 Sep	25,824	------	269	-----	269	269	---	---
16 Sep	40,350	------	3,766	-----	---	---	---	807

Table 9 - continued

	Conochiloides sp.	*Conochilus* sp.	*Keratella americana*	*Keratella taurocephala*	*Lecane* sp.	*Pedalia* sp.	*Polyarthra* sp.	*Trichocerca* sp.
28 Sep	807	------	1,614	-----	---	---	---	538
14 Oct	59,718	------	6,725	-----	---	---	---	3,228
21 Oct	58,911	------	4,304	-----	---	---	---	4,842
25 Oct	4,304	------	1,076	-----	---	---	---	9,415
1 Nov	538	------	538	-----	---	---	---	9,415
9 Nov	1,076	------	1,614	-----	---	---	---	538
22 Nov	1,345	------	538	-----	---	---	---	---
1 Dec	807	------	538	-----	---	---	---	---
6 Dec	------	------	538	-----	---	---	---	---
12 Dec	538	------	1,614	-----	---	---	---	---
30 Dec	269	------	2,421	-----	807	---	---	---

Table 10

Dry Weight of Zooplankton

Organism	Number of Weighings	Number per Weighing	Number Weighed	Range (µg)	Mean Individual Weight (µg)
Bosmina coregoni	5	20	97	0.730 - 1.38	1.182 ± 0.321
Daphnia ambigua	7	10	70	1.49 - 5.77	3.922 ± 1.334
Diaphanosoma brachyurum	6	20	110	0.870 - 1.82	1.423 ± 0.338
Holopedium amazonicum	2	10	18	4.50 - 6.60	5.549
Diaptomus floridanus	10	10	100	3.11 - 4.53	3.603 ± 0.345
Mesocyclops edax	10	10	95	4.81 -10.8	8,470 ± 1.367
Tropocyclops prasinus	5	50	125	0.371 - 0.608	0.503 ± 0.117
Larval Copepods	5	100	225	0.145 - 0.148	0.137 ± 0.0083
Keratella americana	5	200	320	0.035 - 0.053	0.0417± 0.0115

Changes in Lake Anderson-Cue

Enrichment of a lake may cause changes in the species present, with some dropping out perhaps being replaced by new species. The tendency for a species to become more or less common should be reflected in changes in the fraction of samples in which it was found. To test the significance of changes in frequency, the fraction of samples was treated as a binomial variable "p" and the difference between p_{1967} and p_{1968} was tested using a "z" test and pooled estimate of variance, where $z = \frac{p_1 - p_2}{p_1 + p_2}$ and $\sigma_{p_1 + p_2}$ is estimated by

$$\sqrt{\frac{p^*(1 - p^*)}{n_1} + \frac{p^*(1 - p^*)}{n_2}} \qquad \text{(Dunn, 1964)}$$

p^* is the best estimate of p over both periods, i.e., the combined estimate of both. Table 11 shows the values of p and the associated z for species falling in the range $0.2 < p < 1.0$. Rarer species ($p < 0.2$) were excluded since the test used could not show significant differences with the number of samples available.

D. brachyurum, H. amazonicum, and K. americana were found in a significantly different fraction of the samples from Anderson-Cue in 1967 and 1968, Anderson-Cue, 1968, and McCloud, 1968, but not from Anderson-Cue, 1967, and McCloud, 1968. Conochilus sp. was found in a different fraction of the samples in Anderson-Cue, 1967, and 1968, but not in other lake-year combinations.

Table 11

Frequency of Rarer Species as Related to Eutrophication

Organism	Observed "p"			"Z"		
	A-Q 1967	A-Q 1968	McC 1968	A-Q 1967 + A-Q 1968	A-Q 1968 + McC 1968	A-Q 1967 + McC 1968
B. coregoni	1.00	0.928	0.952	1.38	0.459	1.109
D. ambigua	1.00	0.952	0.952	1.114	0.000	1.109
D. brachyurum	0.800	0.523	0.879	2.267*	3.524*	0.856
H. amazonicum	0.360	0.000	0.537	4.180*	5.542*	0.986
Conochiloides sp.	0.6	0.476	0.634	0.982	1.448	0.277
Conochilus sp.	0.480	0.214	0.390	2.268*	1.747	0.716
K. americana	1.00	0.786	0.976	2.487*	2,656*	0.786

*Significant at the 0.05 level.

The mean biomass (and 95 percent confidence interval) for each species in different lake-years is shown in Table 12. These means were tested for each combination of lake-years. Most species did not differ significantly between lakes or years. The mean biomass of D. brachyurum differed significantly in Anderson-Cue between 1967 and 1968, and between Anderson-Cue, 1968, and McCloud, 1968, but not between Anderson-Cue, 1967, and McCloud, 1968. The mean biomass of B. coregoni differed between 1967 and 1968 in Anderson-Cue, but neither year in Anderson-Cue differed from McCloud, 1968. The apparent increase in mean total biomass from 1967 to 1968 in Anderson-Cue is not statistically significant at the 0.05 level, nor is the value for McCloud, 1968, statistically different from either year in Anderson-Cue.

General Population Dynamics

Climatic factors affecting zooplankton populations would be expected to act on both lakes in the same manner. To determine the extent to which species in both lakes varied in the same fashion, correlation coefficients between lakes were calculated for the biomass of each species and group of zooplankton in 1968 (Table 13). The results show total biomass to be strongly correlated between lakes. The correlation coefficient for the total biomass in the two lakes for the period of May to December, 1967, was found to be 0.749, showing that the tendency toward similarity in the two lakes was approximately equal in both years.

All group correlations between the two lakes are significant, usually being much better than correlations for component species.

Table 12

Mean Biomass of Zooplankton (mg/m^2)

Organism	Anderson-Cue 1967	Anderson-Cue 1968	McCloud 1968
M. edax	73.66 ± 32.2	120.4 ± 33.3	112.9 ± 36.9
T. prasinus		15.26 ± 3.01	16.58 ± 4.88
D. floridanus	215.7 ± 77.6	252.1 ± 64.8	205.7 ± 30.8
Larval Copepods	9.502 ± 2.15	16.38 ± 2.61	16.17 ± 2.27
B. coregoni	15.40 ± 6.84	30.24 ± 10.3	26.12 ± 10.1
D. ambigua	101.3 ± 42.2	87.04 ± 25.8	59.74 ± 20.4
D. brachyurum	4.506 ± 4.53	34.35 ± 19.1	5.380 ± 3.36
H. amazonicum	5.552 ± 10.9	0.00	5.525 ± 3.62
K. americana	0.982 ± 0.695	1.894 ± 1.50	0.432 ± 0.233
Other Rotifers	1.854 ± 1.84	0.341 ± 0.213	0.789 ± 0.320
TOTAL	428.5 ± 118.9	557.9 ± 105.9	449.3 ± 66.0

Table 13

Relative Stability of Populations

	Coefficient of Variation		
	A-Q	McC	r Value
Total Zooplankton	62.0	48.0	0.686*
Copepoda	75.7	51.4	0.552*
Cladocera	69.7	77.0	0.523*
Rotifera			0.413*
M. edax	90.5	106.9	0.605*
T. prasinus	64.4	96.0	0.605*
D. floridanus	84.0	49.0	0.252
Larval Copepods	52.1	45.9	0.346
B. coregoni	111.4	126.6	-0.262
D. ambigua	96.7	111.7	0.101
D. brachyurum	181.5	204.3	-0.366
H. amazonicum	---	210.2	---
K. americana	257.9	176.3	0.764*
Other Rotifers	204.2	132.7	0.029

*Significant at the 0.05 level.

The only species showing a better correlation than its group or the total was K. americana; this correlation is probably explained by its seasonal nature.

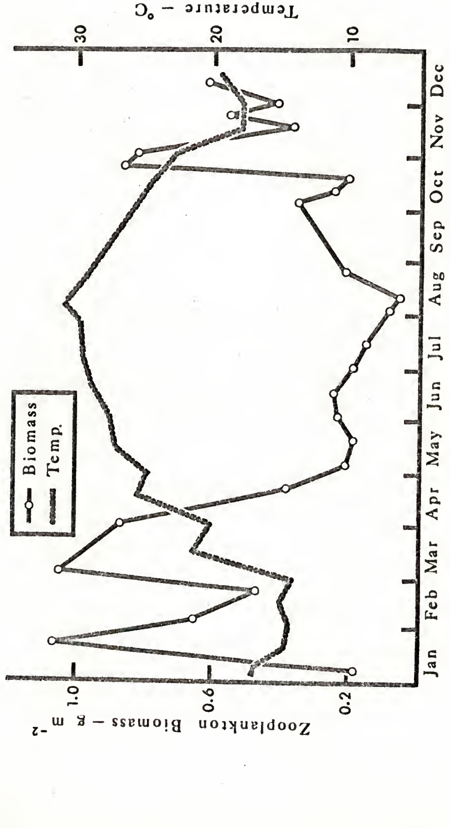
Coefficients of variation for major species and groups in the two lakes are also shown in Table 13. The coefficient of variation is defined as $\frac{\text{standard deviation X 100}}{\text{mean}}$. In general, the individual species are much more variable than the total. The Cladocera and Rotifera, particularly, are less variable as a group than as individual species. Larval copepods are less variable than adults of any species and less variable than the adults grouped together.

Relationship of Temperature to Zooplankton

Variations in surface temperature and total zooplankton biomass in the two lakes are shown in Figures 2-4. The biomass curves for Anderson-Cue and McCloud in 1968 follow the temperature curve closely until about May when biomass falls. Biomass remains low (with some oscillations) until late August or early September, then climbs rapidly to its highest level from which it tends to decline following the fall temperature decrease. To check the apparent relationship of temperature and biomass, correlation coefficients were calculated (Table 14) using only data from that section of the year in which biomass appeared to follow temperature, i.e., all dates except the period of 6 May through 26 August in A-Q 1967, 14 May through 19 August in A-Q 1968, and 2 May through 9 September in McC 1968.

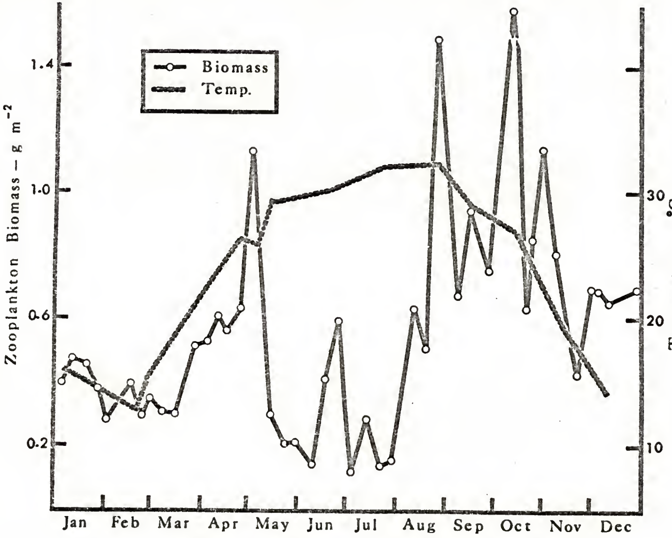
Total zooplankton biomass and copepod biomass were significantly correlated with temperature during the nonsummer months in both Anderson-Cue and McCloud in 1968. Rotifer biomass (including the summer

Figure 2. Seasonal changes in temperature and zooplankton biomass in the experimental lake in 1967.



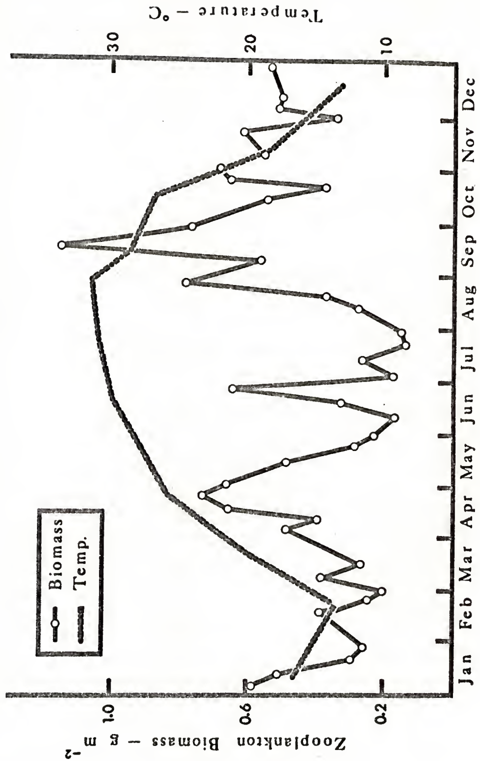
LAKE ANDERSON-CUE 1967

Figure 3. Seasonal changes in temperature and zooplankton biomass in the experimental lake in 1968.



LAKE ANDERSON-CUE 1968

Figure 4. Seasonal changes in temperature and zooplankton biomass in the control lake in 1968.



LAKE McCLOUD 1968

Table 14

Relationship between Temperature and Zooplankton Biomass
(r values)

Group	Anderson-Cue 1967	Anderson-Cue 1968	McCloud 1968
Total Zooplankton	-0.349	0.683*	0.674*
Copepods	-0.330	0.703*	0.609*
Cladocera	-0.237	0.003	0.332
Rotifers	0.409	0.461*	0.437*

*Significantly different from zero at the 0.05 level.

data, as rotifers did not show a summer decline--Figure 7) was significantly correlated with temperature in 1968 in both lakes. No biomass to temperature correlations were significant for Anderson-Cue, 1967.

The phenomenon of a summer decline was confined to the copepods and cladocera (Figures 5-7). The rotifers, by contrast, reached their maximum biomass during the general summer decline. To determine the nature of the summer decline, the difference between mean biomass in summer and nonsummer months was tested for total as well as individual species using a t test (Table 15). <u>M. edax</u>, <u>D. floridanus</u>, and <u>D. ambigua</u> declined during the summer in both lakes, significantly so in at least one. Rotifers in general increased, <u>K. americana</u> markedly so. Other species were ambiguous on their summer response, showing either no significant change or changes in different directions in the two lakes.

Some of the rarer species appeared to be more common during the summer months when total zooplankton biomass was low. To check this, data from all lake-years were pooled with samples divided into two groups: those taken when the water temperature was greater than 25°C, and those taken at less than 25°C. The value of 25°C was arbitrarily chosen because approximately half of the samples were taken at lower temperatures and half at higher temperatures. The frequency of occurrence (fraction of samples in which a species was seen) was treated as a binomial variable with probability "p" and the observed occurrence at warm temperatures was compared with occurrence at cold temperatures (Table 16). Several of the rarer rotifers were seen in a statistically greater fraction of the samples taken when water temperature was above 25°C. None were statistically more common at low temperatures.

Food Limitation

The food of zooplankton is mostly algae (Gauld, 1950, 1951; Gibor, 1956; Davis, 1958). As algal biomass was not measured directly in this study, the concentration of chlorophyll in the water (Figure 8) was assumed to indicate the algal standing crop. Biomasses of different groups of zooplankton were compared with chlorophyll concentrations at the sample dates and at several points prior to the sample dates. The correlation coefficients obtained are shown in Table 17. Rotifer biomass showed no significant correlation with chlorophyll concentration. The best correlation between cladocera and chlorophyll occurred when a six day lag was included. However, this correlation, while significantly different from zero at the 0.05 level, would

Figure 5. Seasonal distribution of copepod biomass in the experimental and control lakes.

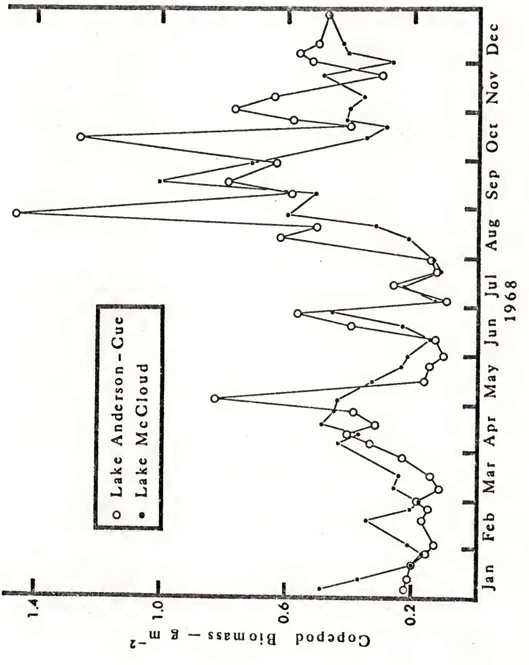

Lake Anderson-Cue
Lake McCloud
Copepod Biomass — g m^{-2}
0.2
0.6
1.0
1.4
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
1968

Figure 6. Seasonal distribution of cladocera biomass in the experimental and control lakes.

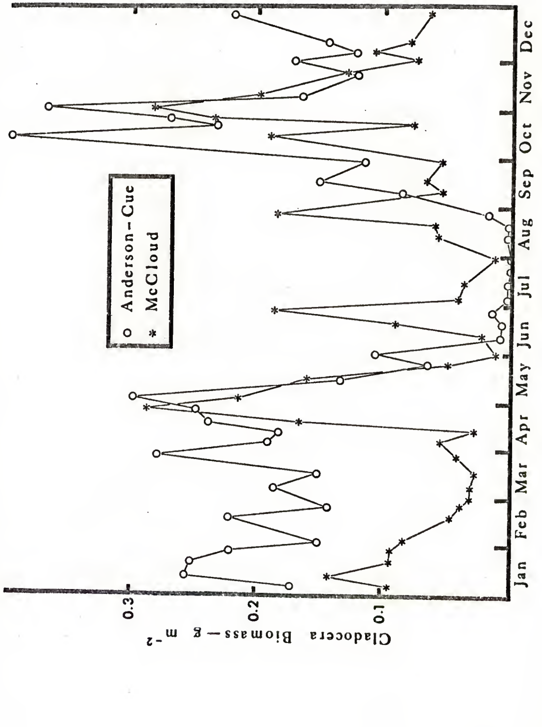

Cladocera Biomass — g m^{-2}
0.3
0.2
0.1
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
1968
○ Anderson-Cue
* McCloud

Figure 7. Seasonal distribution of rotifer biomass in the experimental and control lakes.

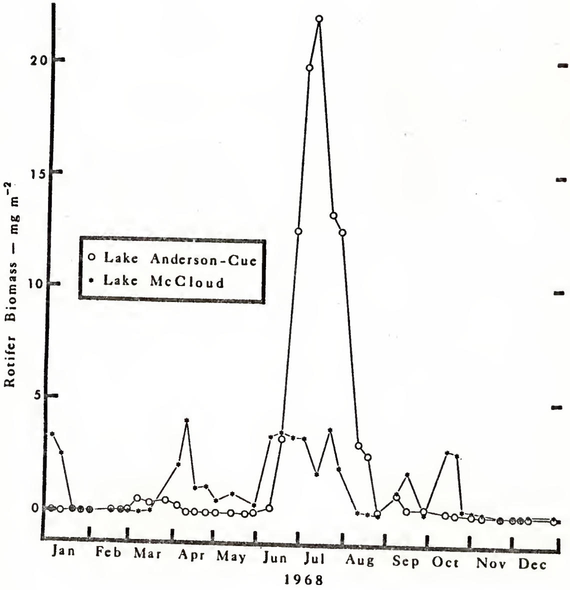

Rotifer Biomass — mg m^{-2}
20
15
10
5
0
o Lake Anderson-Cue
• Lake McCloud
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
1968

Table 15

Summer Changes in Zooplankton

	Mean Biomass (mg/m^2)			
	Anderson-Cue 1968		McCloud 1968	
	Nonsummer	Summer	Nonsummer	Summer
Total biomass	653.4	307.4*	497.2	366.4*
M. edax	147.8	51.70*	120.9	98.99
T. prasinus	18.55	26.14*	19.48	11.55
D. floridanus	275.4	193.9	234.2	156.3*
Larval Copepods	15.22	19.28	14.99	18.22
B. coregoni	42.53	26.49*	20.46	38.52
D. ambigua	111.8	25.07*	79.71	28.98*
D. brachyurum			1.497	14.32*
K. americana	0.112	7.005*	0.136	1.011*
Other Rotifers	0.142	0.958*	0.878	0.752

*Significant at the 0.05 level.

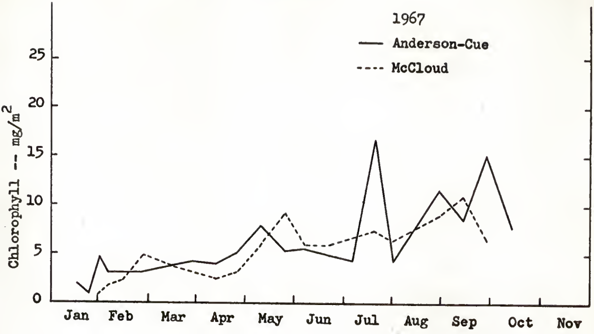
Table 16

Frequency of Rarer Species as Related to Temperature

Organism	Observed p Below 25°C	 Above 25°C	Z
D. brachyurum	0.726	0.672	-0.649
H. amazonicum	0.419	0.279	-1.636
Conochiloides sp.	0.323	0.852	+5.690*
Conochilus sp.	0.468	0.311	-1.777
Pedalia sp.	0.000	0.459	+6.070*
Polyarthra sp.	0.064	0.393	+4.279*
Trichocerca sp.	0.355	0.656	+3.337*

*Significant at the 0.05 level.

Figure 8. Annual variation of chlorophyll a
in Anderson-Cue and McCloud lakes.


1967
Anderson-Cue
McCloud
Chlorophyll -- mg/m^2
0
5
10
15
20
25
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

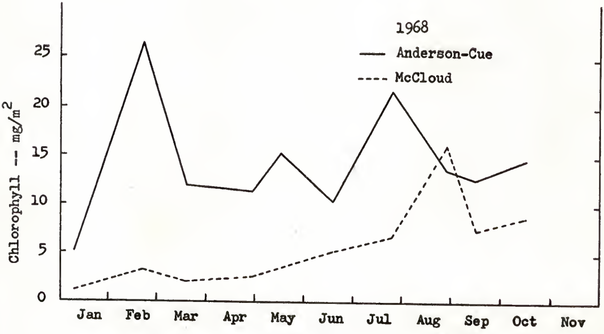

1968
Anderson-Cue
McCloud
Chlorophyll -- mg/m^2
0
5
10
15
20
25
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov

Table 17

Relationship between Zooplankton and Chlorophyll

Lag Period	Rotifer Biomass	Cladoceran Biomass	Copepod Biomass
0 days	0.172	0.207	0.065
6 days	0.129	0.280*	0.099
15 days	0.072	0.126	0.160
21 days	0.067	0.102	0.580*
30 days	0.076	0.131	0.313*
40 days	0.086	0.187	0.327*

*Significantly different from zero at the 0.05 level.
Values are correlation coefficients based on pooled data from both lakes over both years.

explain only about 8 percent of the variation in cladocera in terms of variations in chlorophyll. Copepod biomass, on the other hand, is more strongly related to chlorophyll, but only after a lag period of 21 days or more.

Primary productivity (Figure 9) may give a better estimate of potential zooplankton food than does chlorophyll concentration. The correlations between zooplankton biomass and primary productivity are shown in Table 18. Mean monthly values of each were correlated to smooth out the extreme variations which occurred and to partly include variable lag periods which might be associated. Since zooplankton biomass declined in the summer and primary productivity did not, correlations were also calculated omitting the summer months. Considered for

Figure 9. Annual variation of primary productivity in Anderson-Cue and McCloud lakes.

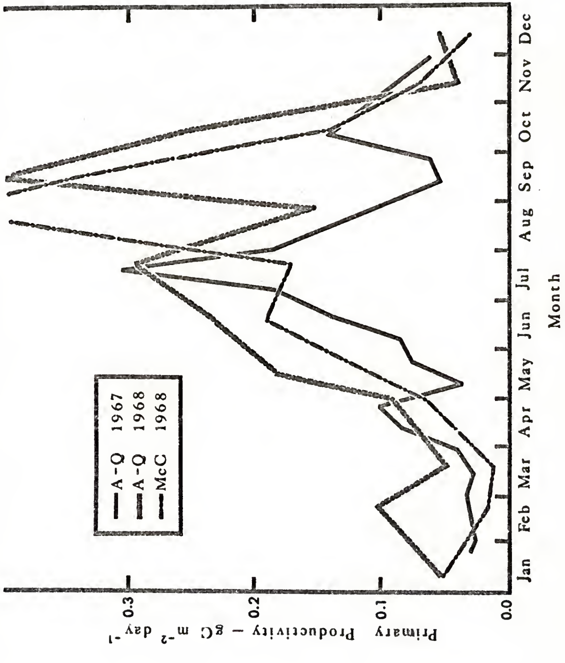

A-Q 1967
A-Q 1968
McC 1968
Primary Productivity – gC m^{-2} day^{-1}
0.0
0.1
0.2
0.3
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Table 18

Correlation of Zooplankton Biomass to Primary Productivity

	Anderson-Cue, 1967		Anderson-Cue, 1967		McCloud, 1968	
	Whole Year	Summer Omitted	Whole Year	Summer Omitted	Whole Year	Summer Omitted
Total Zooplankton	-0.691*	-0.485	0.196	0.722*	0.262	0.757*
Rotifera	-0.361	-0.552	0.547	0.364	0.387	0.586
Cladocera	-0.600*	-0.353	-0.559	-0.016	-0.046	0.155
Copepoda	-0.677*	-0.469	0.372	0.747*	0.319	0.737*

*Significant at the 0.05 level.

the whole year, zooplankton biomass was apparently unrelated to primary productivity except in Anderson-Cue, 1967, where a negative correlation existed. When the summer data were excluded, a strong positive correlation between zooplankton biomass and primary productivity was found in each case (except Anderson-Cue, 1967, where no significant correlation existed). However, when the zooplankton were broken up into groups only the copepods showed a strong relationship to primary productivity.

Primary productivity and temperature are strongly related (Table 19), with variations in temperature accounting for 57-75 percent of the variation in primary productivity.

Table 19

Relationship between Temperature and Primary Productivity

lake-year	r value
Anderson-Cue, 1967	0.757
Anderson-Cue, 1968	0.865
McCloud, 1968	0.860

Since photoperiod could influence primary productivty and zooplankton reproduction, correlation coefficients for photoperiod compared to primary productivity and zooplankton biomass were calcuated (Table 20). The correlation of primary productivity with photoperiod was not as good as the correlation with temperature. Zooplankton biomass is unrelated to photoperiod.

Table 20

Correlation Coefficients for Photoperiod Compared to Primary Productivity and Zooplankton Biomass

	Anderson-Cue 1967	Anderson-Cue 1968	McCloud 1968
Primary Productivity	0.612*	0.623*	0.525
Zooplankton Biomass (Summers omitted)	0.036	0.040	0.323

*Significant at the 0.05 level.

Species Interactions

Among fresh-water zooplankton, at any given time, one member of a group will tend to be dominant in the group (Pennak, 1957). In this study the strength of dominance among cladocera was tested both in terms of numerical dominance and biomass dominance (Tables 21-23). Dominance is expressed as the percent of the total cladoceran numbers (or biomass) which is made up by that species having the greatest numbers (or biomass). No one cladoceran was dominant at all times but usually the dominant species tended to remain dominant for several weeks.

It was usual to find three or four cladoceran species in a sample. Samples containing only two species comprised just 20 percent of the total observations and under two species were found in only two samples (in which no cladocera were found). The mean percents comprised by the dominant when different numbers of species were present (Table 21) show a tendency for one species, the dominant, to be much more common than would be expected by chance. If there were no dominance, one would

Table 21

Numerical Dominance of Cladocera When Different Numbers of Species Were Present

Number of Species Present	2	3	4
Mean % Comprised by Dominant	81	72	65
% of Total Samples	19.5	52.2	28.3

Table 22

Numerical Dominance of Cladoceran Species

	D. ambigua	B. coregoni	D. brachyurum	H. amazonicum
% of Cladoceran Numbers when Dominant	74	71	67	--
% of Time Dominant	40	46	13	0
% of Time Above 25°C Dominant	20*	64*	12	0

*Significantly different from above figure (0.05 level).

Table 23

Biomass Dominance of Cladoceran Species

	D. ambigua	B. coregoni	D. brachyurum	H. amazonicum
% of Cladoceran Biomass when Dominant	75	67	58	52
% of Time Dominant	64	22	10	4
% of Time Above 25°C Dominant	45*	39*	11	0

*Significantly different from above figure (0.05 level).

expect that, when two species were present, each would make up about 50 percent of the total; three, 33 percent; four, 25 percent.

Dominance may also be considered in terms of different species and different seasons (Tables 22,23). D. ambigua and B. coregoni were most likely to be dominant, being numerically dominant in about an equal number of samples. Biomass dominance does not correspond exactly to numerical dominance; in terms of mass, larger species tend to be dominant a greater proportion of the time than in terms of numbers. In terms of biomass, D. ambigua was the species most likely to be dominant at any time.

Whether considered in terms of numbers or biomass, B. coregoni was more likely to be dominant at warmer temperatures than at colder temperatures, while D. ambigua was more likely to be dominant at colder temperatures. To check the nature of this shift in dominance, all data were pooled and the mean biomasses of D. ambigua and B. coregoni below and above 25°C were calculated (Table 24). The change in dominance is due to a significant decrease in D. ambigua, while B. coregoni is unaffected.

Table 24

Relationship of Temperature to Daphnia and Bosmina Biomass

	Mean Biomass (mg/m^2) Below 25°C	Mean Biomass (mg/m^2) Above 25°C
D. ambigua	108.5	38.9
B. coregoni	21.8	25.1

Table 25

Correlation Coefficients between Species in Lake Anderson-Cue

1967

	Cyclopoid	D. floridanus	Larval Copepods	B. coregoni	D. ambigua	D. brachyurum	H. amazonicum	K. americana
D. floridanus	-0.120							
Larval Copepods	0.065	0.381						
B. coregoni	0.798**	-0.175	-0.010					
D. ambigua	0.374	0.531*	0.170	0.252				
D. brachyurum	-0.149	0.273	0.264	-0.249	0.106			
H. amazonicum	-0.107	0.553	0.132	0.312	0.791*	0.255		
K. americana	-0.217	-0.179	0.067	-0.145	-0.361	-0.113	-0.469	
Other Rotifers	-0.303	0.580*	0.160	-0.272	0.107	-0.150	0.044	-0.187

1968

	M. edax	T. prasinus	D. floridanus	Larval Copepods	B. coregoni	D. ambigua	D. brachyurum	H. amazonicum	K. americana
T. prasinus	0.782**								
D. floridanus	0.709**	0.395*							
Larval Copepods	0.344	0.419	0.429						
B. coregoni	0.333*	0.365*	0.113	-0.398*					
D. ambigua	-0.198	0.029	-0.310	-0.278	-0.150				
D. brachyurum	0.372*	0.419*	0.372*	0.556**	0.617**	-0.314			
H. amazonicum	-	-	-	-	-	-			
K. americana	-0.299	-0.445	-0.158	0.164	-0.363*	-0.348*	-0.583*	-	
Other Rotifers	-0.185	-0.340*	-0.0003	0.145	-0.296	-0.370*	-0.314	-	0.623**

---

*Significant at the 0.05 level.

**Significant at the 0.001 level.

Table 26

Correlation Coefficients between Species in Lake McCloud

1967

	Cyclopoid	D. floridanus	Larval Copepods	B. coregoni	D. ambigua	D. brachyurum	H. amazonicum	K. americana
D. floridanus	0.748*							
Larval Copepods	0.754*	0.441						
B. coregoni	0.527*	0.252	0.655*					
D. ambigua	0.819**	0.926**	0.477	0.152				
D. brachyurum	0.591	0.434	0.195	0.424	0.203			
H. amazonicum	0.283	0.575	0.205	0.212	0.489	0.329		
K. americana	-0.615*	-0.578*	-0.399	-0.344	-0.528*	-0.448	-0.340	
Other Rotifers	0.579*	0.401	0.297	-0.261	0.660*	-0.021	-0.002	-0.247

1968

	M. edax	T. prasinus	D. floridanus	Larval Copepods	B. coregoni	D. ambigua -	D. brachyurum	H. amazonicum	K. americana
T. prasinus	0.488*								
D. floridanus	0.219	-0.127							
Larval Copepods	0.344*	0.203	-0.042						
B. coregoni	0.172	-0.115	0.356*	0.083					
D. ambigua	-0.005	0.659**	0.249	0.257	-0.050				
D. brachyurum	0.047	-0.142	0.129	-0.196	0.431*	0.016			
H. amazonicum	-0.088	-0.211	-0.045	-0.063	0.056	0.062	-0.183		
K. americana	0.114	-0.208	0.045	0.474*	0.322	-0.179	-0.138	0.123	
Other Rotifers	0.004	0.024	0.049	-0.007	-0.081	-0.071	-0.202	0.174	0.070

*Significant at the 0.05 level.

** Significant at the 0.001 level.

Table 27

Over-all Relationship between Species

	Cyclopoid							
D. floridanus	5*	*D. floridanus*						
Larval Copepods	7*	3	Larval Copepods					
B. coregoni	8*	3	0	*B. coregoni*				
D. ambigua	2	4	2	0	*D. ambigua*			
D. brachyurum	3	5*	4	5*	2	*D. brachyurum*		
H. amazonicum	-1	1	0	3	4*	1	H. *amazonicum*	
K. americana	-3	-1	3	-3	-6*	-5*	-1	*K. americana*
Other Rotifers	1	-2	2	-4	0	-4	1	2

*Indicates a significant relationship.

If two species were strong competitors over a period of time during which environmental conditions were gradually changing--first favoring one, then the other--one would expect to find a negative correlation between them. On the other hand, if two species were not competing and were favored by similar environmental conditions such as temperature, one would expect them to be positively correlated. To test for such relationships, correlation coefficients were calculated for every combination of major zooplankton species in the lakes (Tables 25, 26). The resulting data were difficult to analyze since two species which were significantly correlated in one lake-year might be unrelated in other lake-years. To simplify the results, they were scored as follows:

> Any positive but not significant correlation received a score of plus one.
>
> A positive correlation significant to the 0.05 level received plus two.
>
> A positive correlation significant to the 0.001 level received plus three.
>
> Negative correlations were scored the same way except that minus values were awarded.

The scores from all lake-years were then added algebraically (Table 27). In interpreting the results a score of $> +4$ or < -4 was considered to show a significant relationship since ± 4 could be achieved by chance (probability of ± 4 equals 0.07). Analyzed in this way, the zooplankton seem to fall into three groups:

I	II	III
D. floridanus	*D. ambigua*	Rotifers
M. edax	*H. amazonicum*	
T. prasinus		
B. coregoni		
D. brachyurum		

Groups I and II seem to be independent while group III tends to be negatively correlated with both of the other two groups.

Correlation coefficients were also calculated between taxonomic groups (Table 28). Copepod biomass shows a significant positive correlation to cladoceran biomass in all lake-years, but no relationship to rotifer biomass. Cladocera and rotifers gave a significant, but low, negative correlation in Anderson-Cue, 1968, being unrelated in other lake-years.

Table 28

Correlations between Biomass of Taxonomic Groups

	Copepoda to Cladocera	Copepoda to Rotifera	Cladocera to Rotifera
Anderson-Cue, 1967	0.698**	0.342	-0.066
McCloud, 1967	0.965**	0.339	0.334
Anderson-Cue, 1968	0.320*	-0.190	-0.492*
McCloud, 1968	0.313*	-0.092	-0.088

*Significantly different from zero at the 0.05 level.

**Significantly different from zero at the 0.001 level.

Production

The calculated yearly production by each species is shown in Table 29. Estimates of yearly primary production as determined by the Environmental Engineering staff along with the "best estimate" of secondary production and secondary efficiency are shown in Table 30. For conversion of gC to g dry weight organic matter, dry organic matter was assumed to be 50 percent carbon. Secondary production includes production by all species of zooplankton except Mesocyclops edax which, being carnivorous, belongs to the next trophic level.

Predation

The population of Labidesthes sicculus in Lake Anderson-Cue was estimated in late fall of 1967. On 25 and 26 November a total of 901 L. sicculus were captured, fin clipped,and released in the lake. On 1 December, 2,018 L. sicculus were captured, 13 of which were recaptures, From these data the population of L. sicculus was calculated (using formulas from Ricker, 1958) to be 130,000 with a 95 percent confidence interval of 86,000 to 260,000.

The gut contents of 47 L. sicculus are reported in Table 31. During December, when the population was estimated, nearly all L. sicculus were over 25 mm long. The mean zooplankton consumption for fish above 25 mm was 267 μg. On this basis 130,000 fish would consume 34.7 g of zooplankton per unit time, where the time unit involved is that time necessary for an ingested plankter to digest beyond a recognizable state (i.e., clearance time). Unfortunately no determinations of clearance time were made in this study. To get an idea of predation pressure a minimum clearance time was needed. Bokova (1940) gave a value of 10

Table 29

Zooplankton Production

g m^{-2} $year^{-1}$

	Anderson-Cue, 1967			Anderson-Cue, 1968			McCloud, 1968		
	Maximum	Minimum	Best	Maximum	Minimum	Best	Maximum	Minimum	Best
M. edax	3,461	0.527	1.717	13.696	1.098	2.326	7,693	1.253	4.229
T. prasinus				1.446	0.101	0.227	1.148	0.136	0.353
D. floridanus	21.742	1.567	3.924	15,065	3,588	8.448	12,922	1.627	4.754
B. coregoni	1.182	0.162	0.500	3.753	0.278	0.481	3.689	0.414	1.308
D. ambigua	24,773	1.085	3.199	7.085	0.659	1.542	6.921	0.616	1.762
D. brachyurum	0.268	0.068	0.187	4.928	0.448	0.837	0.902	0.091	0.210
H. amazonicum	0.148	0.049	0.105	-	-	-	0.470	0.101	0.303
K. americana	0.079	0.012	0.045	0.234	0.022	0.031	0.056	0.0047	0.0072
Other Rotifers	0.144	0.011	0.077	0.042	0.009	0.026	0.098	0.014	0.056
TOTAL	51.801	3.490	9.754	46.249	6.203	13,918	33.968	4.257	12.801

Table 30

Production and Efficiency

	Anderson-Cue, 1967	Anderson-Cue, 1968	McCloud, 1968
Primary Production $gC\ m^{-2}\ year^{-1}$	30.4	55.8	52.2
Secondary Production $gC\ m^{-2}\ year^{-1}$	4.0	5.8	4.3
Secondary Efficiency	13.0%	10.4%	8.2%

Note:

$$\text{Secondary Efficiency} = \frac{\text{Secondary Production X 100}}{\text{Primary Production}}$$

hours for clearance time at 20-26°C for the roach, *Rutilus rutilus*. Assuming a maximum temperature of 30-35°C and a Q_{10} of 3.0 a minimum clearance time of ca. 3 hours is obtained. Since *L. sicculus* feeds only during daylight this minimum clearance rate is approximately one-fifth of a feeding day. Maximum daily consumption would then be five times the observed gut contents, or 174 g of zooplankton for the entire population. This value can be compared to the mean biomass of zooplankton in Anderson-Cue over the two years, 493 mg/m^2. Since the surface area of the lake is ca. 7.85 hectares, there would be 38.7 kg of zooplankton in the lake. Thus the *L. sicculus* population would be able to consume ca. 0.4 percent of the standing crop of zooplankton in one day. The yearly zooplankton production in Anderson-Cue was 929 kg. At the rate calculated above, *L. sicculus* would consume 63 kg/year or ca 7 percent of the zooplankton production.

Table 31

Gut Contents of *L. sicculus*

Length Range (mm)	Zooplankton Consumed (μg)	Number in Sample
25	15.01 ± 2.01	11
25 - 35	190.3 ± 85.6	6
35 - 45	282.9 ± 193.0	4
45 - 55	209.6 ± 67.2	10
55 - 65	359.8 ± 88.0	7
65	292.8 ± 80.9	9

DISCUSSION

Population Dynamics

In Florida's mild climate, reasonably shallow oligotrophic lakes such as those studied furnish a remarkably stable physical environment for plankton. The maximum yearly temperature fluctuation in Anderson-Cue and McCloud was 20°C (from 12-32°C). The maximum observed temperature difference between surface and bottom was 3°C, but it was usually less than 1°C. The water is continually mixed by wind action so that stratification of nutrients cannot occur. Sunlight typically penetrates to the bottom. In general, the physical environment varies only gradually with seasonal temperature and photoperiod changes.

By direct contrast the biological community is not at all stable; primary productivity, chlorophyll concentration, and zooplankton biomass vary by more than an order of magnitude; while species populations of both algae and zooplankton may vary by five or more orders of magnitude. Populations in natural ecosystems have traditionally been considered as being in equilibrium with their environment and changing only in response to some environmental change. Quite obviously the biotic community in these lakes is not in equilibrium with the physical environment.

Slobodkin (1954) demonstrated that a fairly long time period, on the order of 40 days, is required for a single cladoceran species, *Daphnia obtusa*, to reach an equilibrium population in a constant laboratory environment and has suggested that natural populations may never reach equilibrium before further environmental changes occur. In the light of the present study several additions may be made to Slobodkin's hypothesis. First, in a mixed culture or natural community the environment of any one species includes all of the other species as well as the physical parameters. If some environmental change occurs, all populations will tend to adjust to the new conditions. The adjustment is not instantaneous but requires a time period of at least one and probably several generations. As any one species population changes in adjustment to the environment it will automatically alter the environments of all other species. Thus the time required for a community to equilibrate is greatly extended. If other changes should occur before equilibrium is reached, the community will be in perpetual nonequilibrium. Forces will always be present pushing the populations toward equilibrium, but equilibrium can never be attained, since the equilibrial size of any population will be constantly changing.

Demonstration of cause-effect relationships between environmental variables and population size or group biomass is difficult because of the nonequilibrial nature of the relationship, as well as the lag response described by Slobodkin (1954) and Edmondson (1965). The lag period necessary for any species population to adjust to an environmental change is dependent on the generation time for that species, which in turn is dependent upon temperature and food (Ingle, et al., 1937; Hazelwood and Parker, 1961; Elbourne, 1966). Accordingly, no two species can be expected to have the same lag time, and lag time for any one species will not be constant. Even if variations in a single environmental factor are responsible for changes in zooplankton biomass, correlation of biomass with the particular factor may be poor. Comparison of taxonomic groups, or even separate species, with environmental factors should give truer correlations but even these will be blurred by variations in time lag with environmental changes.

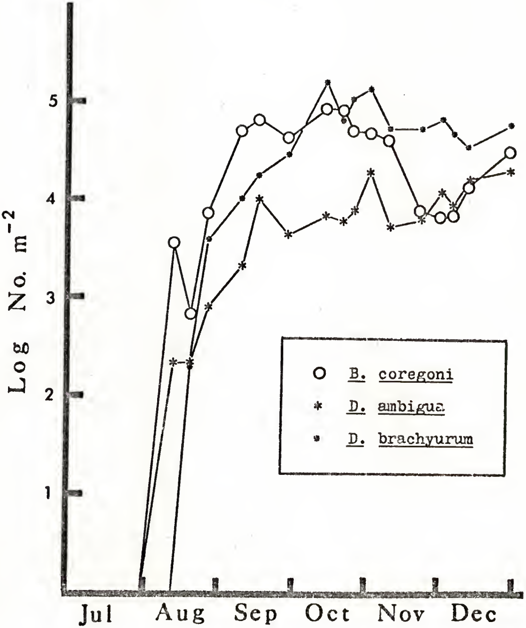
As previously mentioned, the niche diversity for zooplankton in lakes like those studied must be very low. The lack of thermal stratification permits no diversity on that basis. Cover and substrate are uniform throughout the water column. The available foods--algae and bacteria--range somewhat in size, permitting three possible divisions with considerable overlap: large raptoral feeders, small raptoral feeders, and filter feeders. The possibility of further dividing these could admit perhaps six niches in the zooplankton. Why, if the competitive exclusion principle (Hardin, 1960) holds, are there more than six species of zooplankton in a lake at one time?

To begin with, there are relatively few species of open-water zooplankton. These same lakes contain ca. 25 species of littoral cladocera but only four species are found in the open water. Still the question remains, why should there be even four? All the limnetic cladocera in these lakes are filter feeders (Hutchinson, 1967); all are about the same size--from one to five micrograms--and all were found together in the plankton about 28 percent of the time. At least three cladoceran species were found in 80 percent of the samples taken. Are they competing and, if so, why are not all but one eliminated? Different genera of cladocera and even cladocera and copepods have been shown to be unable to coexist in laboratory cultures (Frank, 1952, 1957; Parker, 1960, 1961).

The correlation coefficients between populations of the different cladocera showed no tendency for any species to decline while any other species was increasing. On the contrary, some showed positive correlations (D. ambigua to H. amazonicum; B. coregoni to D. brachyurum). The pattern of dominance in cladocera, however, showed that a given set of environmental conditions might be distinctly more favorable to one species than to another. Even though two species were positively correlated, dominance of one over the other at a given time was almost certain. In the summer of 1968 in Anderson-Cue, all cladocera disappeared from the lake for a short time. As they began to come back, three species were seen (Figure 10). B. coregoni and D. ambigua appeared together, with both populations increasing rapidly but Bosmina increased more rapidly than Daphnia, exceeding it in numbers by an order of magnitude as both populations began to level off. D. brachyurum appeared about two weeks later than the other two but multiplied at a rate nearly equivalent to Bosmina's initial rate and soon achieved a population roughly equal to Bosmina. The Bosmina population then decreased by about an order of magnitude while Diaphanosoma decreased only slightly, thus acquiring dominance.

The above example shows two things. First, competition probably exists between these species. Second, the effects of competition can be obscured by changes in the environment. When cladocera started to come back into the system all three were favored, just as populations of two or more species inoculated into a new medium would increase initially before competition became important. After the populations reached a "normal" level a distinct tendency for one to dominate was displayed.

Figure 10. Population fluctuations of cladocera in Lake Anderson-Cue following their summer disappearance in 1968.


Log No. m^{-2}
1
2
3
4
5
Jul
Aug
Sep
Oct
Nov
Dec
O B. coregoni
* D. ambigua
• D. brachyurum

The presence of competition but not competitive exclusion is explained by the nonequilibrium nature of the ecosystem. If an equilibrium is reached, the outcompeted species will be eliminated, but environmental changes effectively give the losing species a new start. If the environment is sufficiently transitory, species which would compete strongly in a laboratory culture may show a distinctly positive correlation. In the event that biological equilibrium should be reached, causing exclusion of some species, nearly all fresh-water plankters have some sort of resting stage which allows them to develop a new population at a later time (Hutchinson, 1967).

The smaller coefficients of variation for groups as compared to species and the better interlake correlation of total and group biomass as compared to species biomass (Table 15) indicate that factors acting to control the populations are acting on the whole trophic level rather than on individual species. The good correlation ($r = 0.686$) between zooplankton biomass in the two lakes indicates that climatic factors (i. e., factors which would affect both lakes) play a large part in regulating zooplankton populations, but the mechanism for action of climate on zooplankton is not intuitively obvious.

While the summer decline was statistically significant in both lakes, the reason it occurred is less easily demonstrated. When the summer data were ignored the zooplankton biomass followed the temperature curve. A possible explanation for the summer drop would be that temperature had passed the optimum for species present. However, zooplankton biomass returned to normal and, indeed, to its highest value while temperature was still above the level of the initial drop. Also the recovery from the summer low began while temperature was at maximum. The summer low could not be due to lack of food because both primary productivity and chlorophyll concentration were higher during the summer.

A study of the reactions of individual species to the summer discontinuity provides an insight into its cause. Only the larger zooplankters showed a significant decline during the summer. Intermediate species showed essentially no response, while very small species such as the rotifers increased significantly. Also, rarer species of rotifers were much more likely to be seen during the summer biomass low. A further clue is provided by the fact that larval copepods did not decline: they even increased slightly. Evidently conditions were favorable for copepod reproduction since fewer adults were able to produce as many or more young. Accordingly the decline in adults must have been due to an increased death rate. This in turn points to an increased predation rate in summer with apparent selection for the larger forms producing results similar to those described by Brooks and Dodson (1965).

An explanation for increased predation during summer is readily available: Labidesthes sicculus and Lepomis macrochirus are spawning and the young of both are much more dependent upon zooplankton than are the adults. Hubbs (1921) and Werner (1969) have discussed the migration of fry of these species into the limnetic zone where they feed upon zooplankton, particularly microcrustacea. McLane (1955) reported that in Florida L. sicculus spawns throughout the summer while L. macrochirus spawns from May to October with most intensive spawning in June. Since the bluegill fry spend ca. 1.5 months in the limnetic zone (Werner, 1969), their period of heaviest predation falls exactly during the summer zooplankton low. The briefer summer decline in Anderson-Cue, 1968, as opposed to 1967 or McCloud, 1968, also supports the predation mechanism; the L. sicculus population in Anderson-Cue, 1968, for some unknown reason, was very much reduced by comparison with the 1967 population or the McCloud population.

When the period of summer decline is ignored, total zooplankton biomass is closely correlated with both temperature and primary productivity. Since temperature and primary productivity are strongly correlated throughout the year, it seems reasonable that the influence of climate on zooplankton biomass, as evidenced by the close correlation between lakes, is due to two principal factors, neither of which acts directly on the zooplankton. 1. Temperature limits primary production (given a reasonably constant nutrient supply), thus limiting the food available to zooplankton and, accordingly, the zooplankton during most of the year. 2. The onset of fish reproduction, with its concomitant predation surge, is determined by climatic factors, such as temperature and photoperiod, and thus is synchronized in both lakes.

In these lakes zooplankton as a group is food-limited during most of the year. During that period competition for food should be important. In the summer, however, when zooplankton biomass is at its lowest and primary productivity is at its highest, no competition for food should exist. Thus the summer is the period when the rotifers, relatively predation immune due to their small size, develop their largest populations. Also several rarer species of rotifers are much more common during the summer. Their apparent relationship to temperature (Table 18) merely reflects their reaction to the decreased competition during the summer. The same general explanation pertains to the change in frequency of Daphnia and Bosmina dominance with warm temperatures. Temperature is not directly involved; Daphnia, being larger, receives greater predation pressure than Bosmina.

Secondary Production

The estimations of secondary production and efficiency are, admittedly, very rough. The range from minimum to maximum estimate covers about an order of magnitude. However the ranges for the 1968 values are reduced from that for 1967, probably reflecting the greater accuracy obtained with more frequent sampling. The range of efficiencies determined includes from a reasonably low efficiency to one impossibly high (Table 29). The efficiencies associated with the "best estimate" (Table 30) are in line with the general ecology efficiency of 8-12 percent (Slobodkin, 1968).

An advantage of this method of estimating zooplankton production is that contributions made by each species or higher taxonomic group can be assessed. Thus in both Anderson-Cue and McCloud, 1968, copepods accounted for ca. 75 percent of the production, cladocera contributed ca. 24 percent, and rotifers only ca. 0.5 percent. The relatively small size of rotifer species present coupled with their sporadic occurrence accounted for their low contribution to production.

There have been a few previous determinations of aquatic secondary production. As pointed out in the introduction, most of these were only rough estimates. The most important studies are summarized in Table 32. For comparative purposes all values are listed as originally reported and then as converted to kcal m^{-2} $year^{-1}$. Of the previous workers

Table 32

Some Representative Rates of Secondary Production in Aquatic Ecosystems

Investigator	Organisms	Ecosystem	Reported Rate	Converted to kcal $m^{-2}year^{-1}$
Odum and Young (1954)	most herbivores	Silver Springs, Florida	240 g $m^{-2}year^{-1}$	1200
Stross, *et al*. (1961)	crustacean zooplankton	bog lake	8 g $m^{-2}year^{-1}$	40
Straškraba (1963)	littoral zooplankton	fishpond	1.7 g N $m^{-2}year^{-1}$	53
Ilkowska, *et al*. (1966)	limnetic zooplankton	two eutrophic lakes	27 and 40 g $m^{-2}year^{-1}$	135 and 200
McAllister (1969)	marine zooplankton	fertile area Pacific	1.5-23.2 g C $m^{-2}year^{-1}$	15-232
Present study	limnetic zooplankton	oligotrophic lakes	4-52 g $m^{-2}year^{-1}$	20-260

only McAllister reported any boundaries to production. The range of values from the present study is quite similar to that reported by McAllister and includes all of the other values for standing fresh waters. The "best estimate" of mean annual zooplankton production in Lakes Anderson-Cue and McCloud is ca. 50 kcal m^{-2}. As one would expect for oligotrophic lakes, this value lies toward the low side of the range for standing waters.

Eutrophication Effects

The effects of eutrophication on the zooplankton have been gradual and usually indirect, but some have been noticeable enough to record. One of these is the apparent change in frequency of occurrence of rarer species (Table 11). No differences in frequency were found between Anderson-Cue, 1967, and McCloud, 1968, which suggests that Lake McCloud in 1968 was essentially the same as Anderson-Cue (and presumably McCloud) in 1967 before the effects of fertilization became noticeable. In every case where a significant difference occurred between lakes in 1968, a significant difference also occurred between 1967 and 1968 in Anderson-Cue. These changes in Anderson-Cue between 1967 and 1968 may be presumed to be due to the addition of nutrients.

With the exception of D. brachyurum, whose biomass increased significantly from 1967 to 1968 in Anderson-Cue, the normal variation in biomass was great enough to prevent minor changes in mean biomass from being significant. Nonsignificant changes did occur in Anderson-Cue, almost all of which were positive (Table 12). Zooplankton production also increased slightly as reported for fertilization experiments by Glonti and Tskhomelidze (1963). This trend toward increasing secondary biomass and secondary production will probably continue, at least for a time, as the lake becomes more eutrophic. One cannot make this conclusion from the insignificant increases observed but the community structure lends additional support. Considering the general link of zooplankton biomass to primary productivity and primary productivity to nutrients, an increase in nutrients should result in an increase in secondary production as long as the community undergoes no major structural changes.

SUMMARY

In this study an attempt was made to evaluate the interrelationships of zooplankton populations with environmental factors in two Florida sandhills lakes. The most important conclusions are:

1. Natural zooplankton populations are not in equilibrium with their environment.

2. Competition probably occurs between similar species of zooplankton living in the same lake, but this competition is masked by the transient nature of the environment.

3. In these lakes zooplankton is food-limited during most of the year but predator-limited during summer.

4. Climatic factors such as temperature and light regulate primary productivity and the onset of fish reproduction, thus indirectly regulating zooplankton biomass by way of food supply and predation.

5. The mean estimate for secondary production in these lakes, 50 kcal $m^{-2}year^{-1}$, lies toward

the low end of the range for standing waters as one would expect for oligotrophic lakes.

6. During the two years of this study the effects of eutrophication on the zooplankton have been slight.

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BIOGRAPHICAL SKETCH

Paul E. Maslin was born April 5, 1943, in Newcastle, Pennsylvania. He was graduated from Bushnell High School in May, 1961. In the following September he entered the University of Florida, from which he received the degree of Bachelor of Science with a major in Biology. In May, 1965, he began graduate work in the Department of Zoology at the University of Florida. He worked as a teaching and research assistant for a year, then received a traineeship grant through the Department of Environmental Engineering. From May, 1967, when he was granted permission to bypass the master's degree, until the present time, he has pursued his work toward the degree of Doctor of Philosophy.

Mr. Maslin is married to the former Karolyn Regina Johnston. He is a member of Phi Sigma, The American Society of Limnology and Oceanography, and The American Association for the Advancement of Science.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of that committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council, and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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