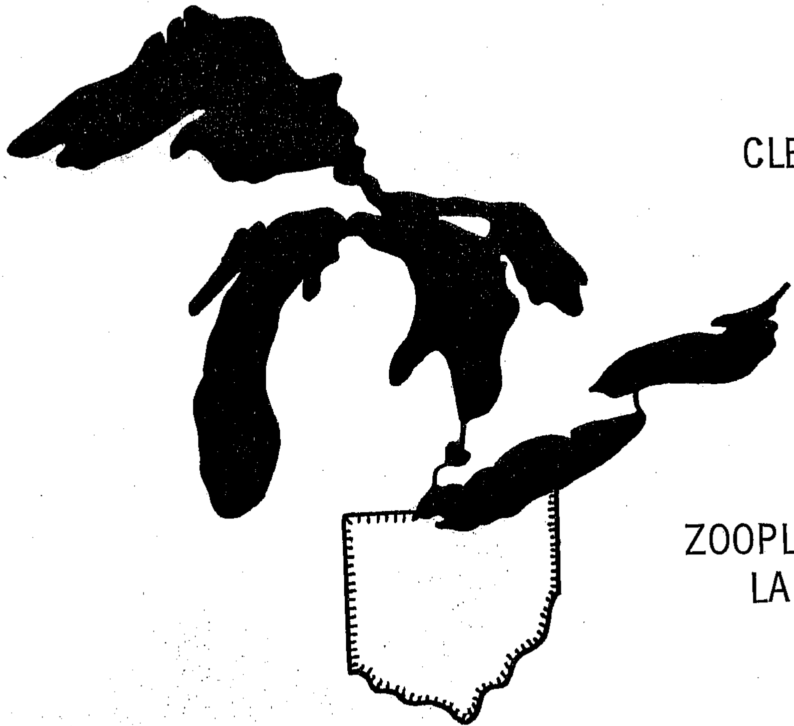

# CLEAR TECHNICAL REPORT NO. 58

# ZOOPLANKTON PRODUCTIVITY IN WESTERN LAKE ERIE AT LOCUST POINT, OHIO

Prepared by

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Prepared for:

Large Lakes Field Station
U.S. Environmental Protection Agency
and
U.S. Fish and Wildlife Service
and
Ohio Division of Wildlife

THE OHIO STATE UNIVERSITY
CENTER FOR LAKE ERIE AREA RESEARCH
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# PREFACE

The following report was prepared by William R. DeMott as partial fulfillment for an M.S. degree in the Environmental Biology Program. Research conducted for this thesis was part of a project coordinated by the Center for Lake Erie Area Research (CLEAR) at The Ohio State University and was in part sponsored by The U.S. Environmental Protection Agency (Grant No. R-802543) and The U.S. Fish and Wildlife Service and Ohio Division of Wildlife (Project F-41-R). Dr. Clarence E. Taft, Department of Botany, and Dr. David A. Culver, Department of Zoology, served as advisors. Dr. Charles E. Herdendorf served on the reading committee.

On behalf of the Center for Lake Erie Area Research, I am pleased that we are able to reproduce copies of this research effort and make it available to other scientists.

Charles E. Herdendorf
Director

# ACKNOWLEDGEMENTS

I wish to thank Dr. Clarence E. Taft and Dr. David A. Culver for their advice, understanding, and support during this study and for useful criticisms of this manuscript.

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Don Davies and Roger Toma carefully collected samples in both fair weather and foul. My brother, Peter DeMott, helped prepare the figures.

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# INTRODUCTION

The zooplankton form major trophic links between phytoplankton and fish in lake ecosystems. As primary consumers, directly utilizing primary production, herbivorous zooplankton decide to large extent the nature of energy flow in the ecosystem. In order to know how and to what extent primary production is utilized by zooplankton and ultimately by fish, it is necessary to know the production of each trophic level.

Primary productivity in the Great Lakes has been the subject of many recent reports (Vollenweider et al., 1974). Although the zooplankton of the Great Lakes have been extensively studied (see Watson, 1974), there are no published measurements of zooplankton productivity for any of the Great Lakes. The purpose of this study is to provide the first estimate of planktonic secondary productivity for Lake Erie. Plankton samples collected from April, 1975 through March, 1976 provided the data needed to estimate the magnitude of annual zooplankton production and the amplitude of seasonal variation at an inshore area in western Lake Erie. Improvements in methods and techniques which will be useful in future studies of zooplankton productivity are presented and discussed.

Numerous reports of Lake Erie zooplankton have provided estimates of zooplankton standing crop expressed as numbers of individuals or units of biomass. The results of this study allow comparisons between zooplankton numbers, biomass, and productivity.

# STUDY AREA

This study is a part of a continuing comprehensive preoperational aquatic monitoring program initiated at the Davis-Besse Nuclear Power Plant site by the Center for Lake Erie Area Research (CLEAR) in the spring of 1972. The results for 4 years of sampling at monthly intervals during spring, summer, and fall have been summarized in the 1975 progress reports prepared for the Toledo Edison Company by CLEAR (Reutter and Herdendorf, 1975a; 1976). The aquatic monitoring program includes an analysis of water quality parameters and phytoplankton, zooplankton, benthos, and fish populations from the power plant site.

The plant site is located at Locust Point, Ottawa County, Ohio (41° 35' N and 83° 05' W) on the southwestern shore of Lake Erie, 21 miles east of Toledo and 7 miles northwest of Port Clinton. Information concerning many aspects of the plant site has been compiled in the Final Environmental Statement Related to Construction of Davis-Besse Nuclear Power Station (Toledo Edison Company and Cleveland Electric Company, 1973).

Lake Erie plankton sampling stations were located along transects following the power plant intake and discharge conduits and at a right angle to the discharge conduit (Fig. 1). When the power plant becomes operational these sampling stations will be used to assess the effects of both passage through the plant's cooling system and thermal effluents on

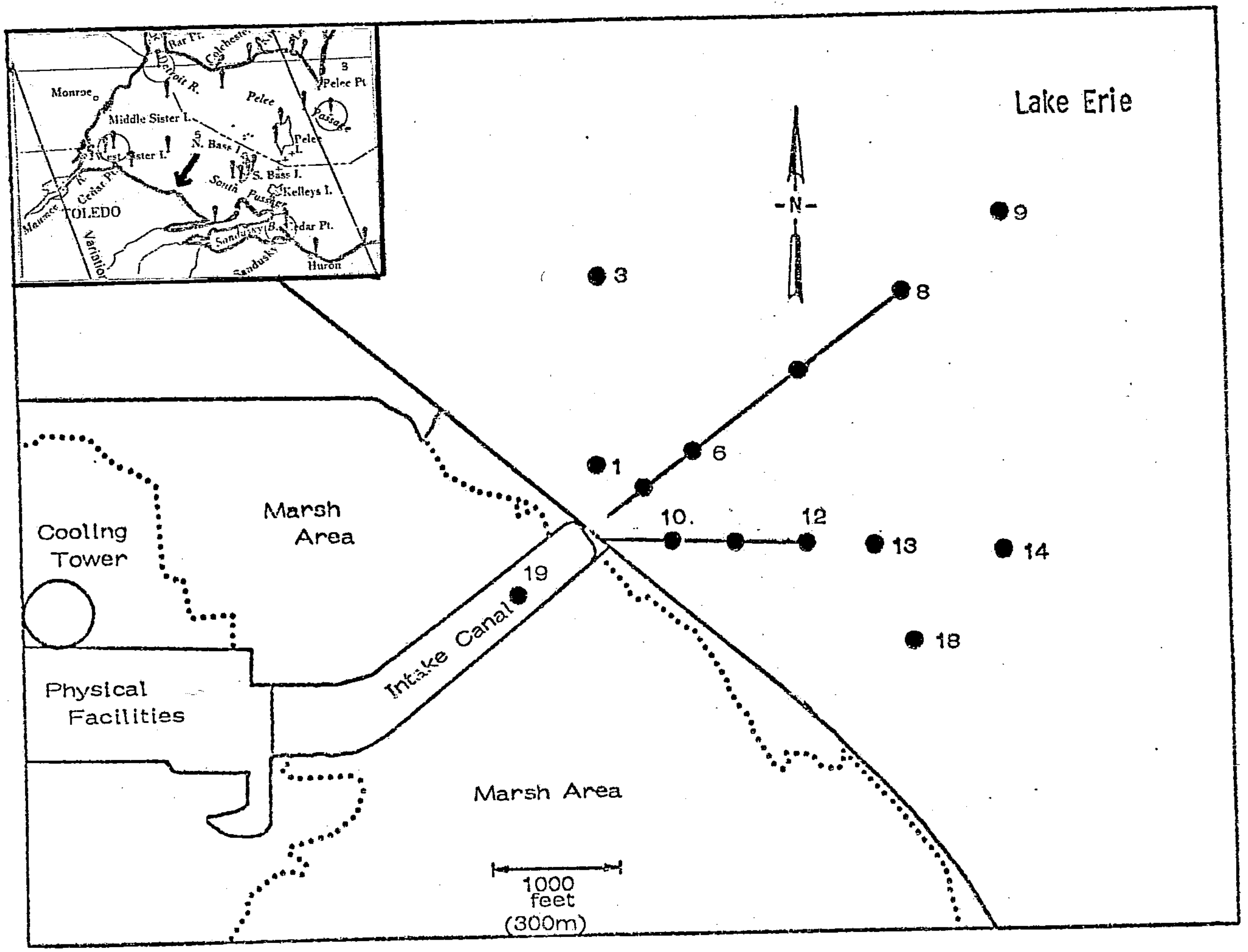

Figure 1. Lake Erie plankton sampling stations at the Davis-Besse Nuclear Power Plant, Locust Point, Ohio. Insert shows the location of Locust Point on the southern shore of western Lake Erie.

local plankton populations.

Water currents at Locust Point are variable, depending on wind direction and seiche action. During periods of calm weather the main flow is eastward along the shore (Hartley et al., 1966).

The Western Basin of Lake Erie averages only 8 meters deep. The slope of the bottom is especially gentle along the southwestern shore at the power plant site, Mean depth of the water column at station 9, 1.2 kilometers from shore, was 4.9 meters. (Table 1).

Water quality parameters from Locust Point (Table 2) have shown similar seasonal trends over the past 4 years and are generally typical of waters along the Ohio shore of the Western Basin of Lake Erie (Reutter and Herdendorf, 1975a; 1976). Because of the extreme shallowness, the waters at the plant site are well-mixed. There were only small differences between surface and bottom samples and samples collected from 3 different stations. The greatest ranges in water temperatures among the stations were 6.0°C to 8.0°C on April 22, and 20.6°C to 22.2°C on June 16. On other sampling dates the range of water temperature measurements from 3 stations was 1°C or less. The difference between surface and bottom water temperatures at a single station was never more than 1°C.

In Lake Erie, primary productivity and phytoplankton populations are typically highest in the southern half of

Table 1. Distance from shore and mean depth of water column at open lake plankton stations, Locust Point, Lake Erie.

| Station Number | Distance from Shore (m) | Mean Depth (m) |
|---|---|---|
| 1 | 100 | 2.3 |
| 3 | 450 | 4.1 |
| 6 | 300 | 2.5 |
| 8 | 900 | 4.4 |
| 9 | 1200 | 4.9 |
| 10 | 100 | 1.8 |
| 12 | 300 | 3.0 |
| 13 | 400 | 3.4 |
| 14 | 600 | 4.0 |
| 18 | 300 | 3.5 |

Table 2. Sampling dates and selected water quality parameters, Locust Point, Lake Erie, 1975. Each value represents the mean of surface and bottom samples from stations 1, 8, and 13 (data from Reutter and Herdendorf, 1975a; 1976).

| Sampling Date | 4-22 | 5-29 | 6-16 | 7-14 | 8-11 | 9-8 | 10-6 | 11-3 | 12-16 |
|---|---|---|---|---|---|---|---|---|---|
| Field Measurements | | | | | | | | | |
| Temperature ($^{o}$C) | 7.2 | 20.3 | 21.2 | 22.8 | 24.3 | 20.5 | 13.3 | 10.3 | 4.5 |
| Dissolved Oxygen (ppm) | 12.0 | 8.3 | 10.2 | 8.9 | 9.3 | 9.5 | 10.6 | 11.7 | 12.6 |
| Conductivity ($\mu$mhos$\cdot$cm$^{-1}$) | 272 | 311 | 279 | 280 | 218 | 236 | 301 | 260 | 254 |
| Secchi Disk Transparency (m) | 0.4 | 0.5 | 0.5 | 0.8 | 0.9 | 0.6 | 0.4 | 0.5 | 0.4 |
| Laboratory Determinations | | | | | | | | | |
| Total Alkalinity (mg$\cdot$l$^{-1}$) | 87 | 103 | 93 | 88 | 85 | 88 | 104 | 95 | 95 |
| Suspended Solids (mg$\cdot$l$^{-1}$) | 29 | 31 | 10 | 25 | 10 | 18 | 21 | 18 | 21 |
| Dissolved Solids (mg$\cdot$l$^{-1}$) | 164 | 232 | 167 | 128 | 159 | 139 | 178 | 174 | 145 |
| Turbidity (F. T. U.) | 21 | 21 | 16 | 3.9 | 2.0 | 13 | 24 | 33 | 47 |
| pH | 8.0 | 7.9 | 8.7 | 8.7 | 8.8 | 8.5 | 8.5 | 7.8 | 7.9 |

the Western Basin (Glooschenko et al., 1974; Munawar and Munawar, 1976). During 1975 net phytoplankton populations at Locust Point, Lake Erie were highest in April, August, and December samples (Fig. 2). The early spring and fall samples were dominated by filamentous centric diatoms, Stephanodiscus binderanus (= Melosira binderana) and Melosira varians. High midsummer net phytoplankton populations were a result of a bloom of the blue-green alga Aphanizomenon flos-aquae.

Ichthyoplankton collections in the vicinity of Locust Point during 1975 suggest that inshore waters at the power plant site serve as a nursery area for fish fry which are probably spawned on nearby offshore reefs (Reutter and Herdendorf, 1976). Yellow perch (Perca flavescens), first collected on May 12, and gizzard shad (Dorosoma cepedianum), first collected on June 2, were the numerically most important fish fry species.

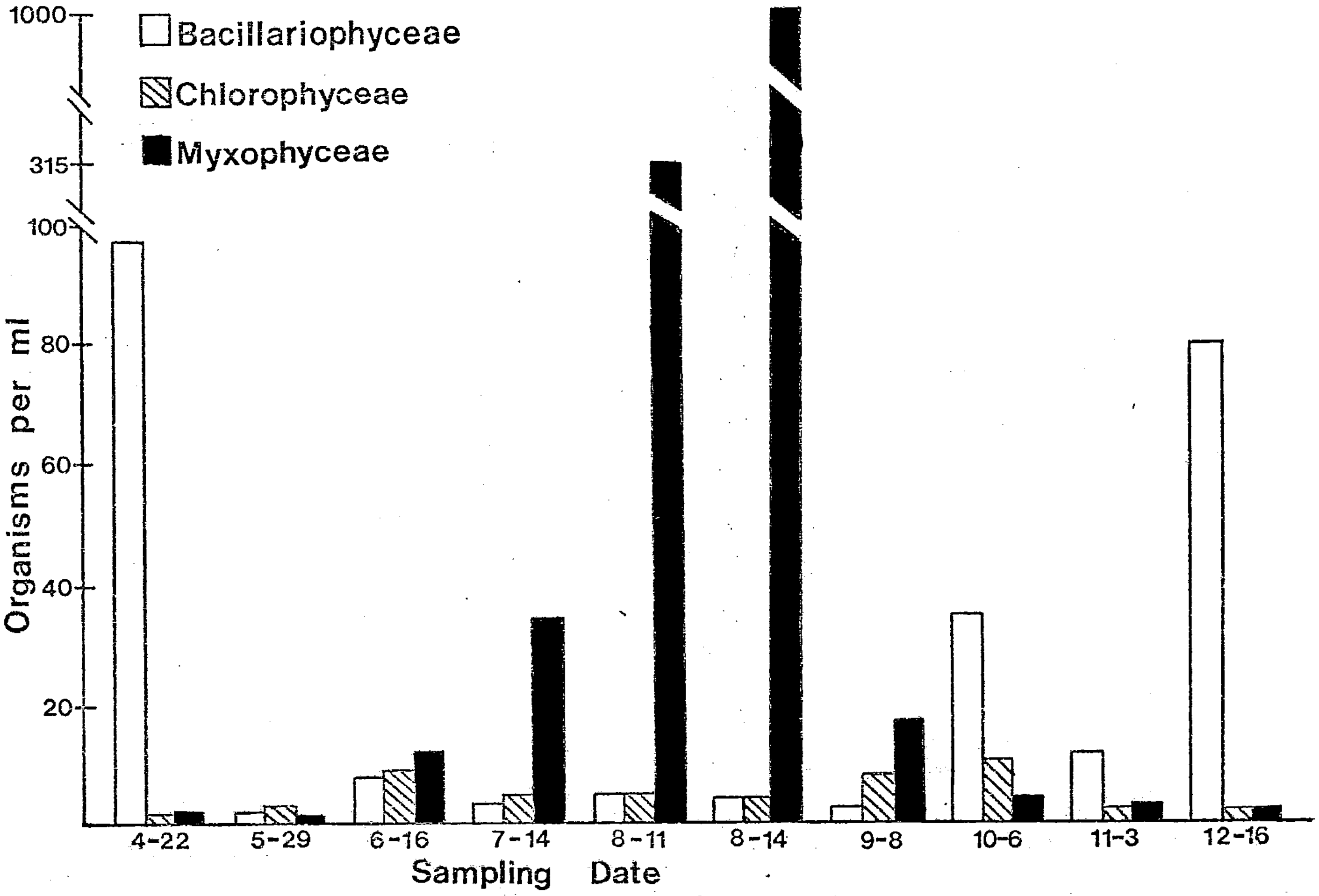

Figure 2. Populations of 3 major phytoplankton taxa: Bacillariophyceae, Chlorophyceae, and Myxophyceae, Locust Point, Lake Erie, April 22-December 16, 1975. Samples were collected at 11 stations by vertical tows with a 64 µ mesh plankton net. Additional information on methods and phytoplankton species composition has been reported by Reutter and Herdendorf (1975a; 1976).

# METHODS

Secondary production can be thought of as the formation of consumer organisms in a community. According to the definition adopted by the International Biological Programme (IBP), secondary production is the total of all growth increments of all individuals alive at the beginning of a time interval, whether or not they survive to the end of the interval, plus the growth increments of those born into the population during the interval (Winberg, 1971). For primary productivity, the rate of $CO_2$ uptake measured by the $^{14}C$ method provides a direct measure of the photosynthetic process. As no similar method for measuring the secondary production of a community exists, measurements made on individual species must be summed.

The estimation of secondary production of zooplankton requires knowledge or assumptions about four parameters: (1) population numbers, (2) population age or size frequency distribution, (3) the weights of various size classes or stages, and (4) the time spent in the particular size class or stage, the development time. In this study, production calculations were based on methods used by Patalas (1970), Weglenska (1971) and others, with minor modifications. Population numbers and size-frequency distributions were determined by counting zooplankters from field collections and measuring their lengths. Weights of individual size classes were computed using length-weight functions from the literature. Development times were taken from studies in which zooplankters were cultured in the laboratory under controlled temperature conditions.

## Field and Laboratory Techniques

During 1975, Lake Erie zooplankton was sampled from April 22 through November 3 at monthly intervals (Table 2) at each of 10 stations (Table 1). Additional collections were made at stations 8, 13, and 14 on August 14 and at stations 1, 8, and 13 on December 16 and on March 16, 1976. Duplicate vertical tows from bottom to surface were taken at each station with a Wisconsin plankton net (12 cm opening diameter; no. 25, 0.064 mm mesh). Each sample was concentrated to 50 ml and preserved in 5% formalin to which 40 grams per liter sucrose had been added to prevent "ballooning" and subsequent loss of eggs by Cladocera (Haney and Hall, 1973).

Three 1 ml subsamples were taken from each sample with a wide bore pipette and placed in Sedgewick-Rafter cells. The entire cell was scanned under a compound microscope at 100x while counting and identifying zooplankters, cladoceran embryos, copepod egg sacks, and rotifer eggs. Degenerate (Brooks, 1946) and ephippial eggs were differentiated from parthenogenic cladoceran eggs. Additional aliquots were withdrawn from each sample and scanned under a dissecting microscope while counting Leptodora, ovigerous copepods, and, during periods of low zooplankton abundance, other crustacean zooplankters. When ovigerous copepods were present a minimum of 25 egg sacks from each species was dissected each month to obtain an estimate of the mean number of eggs per sack. In order to determine population length-frequency distributions, a Whipple disk was used to measure the total lengths of approximately 200 specimens of each of the common crustacean species and all of the rarer forms encountered in each month's samples. A minimum of 50 ovigerous females from each common cladoceran species was measured. Measurements from different sampling stations were pooled into a single length-frequency distribution for each of the common species collected on each sampling date.

Cladocerans, adult copepods, and rotifers were identified to species when possible. Copepodites were identified to genus and nauplii to order. The works of Edmondson (1959), Jahoda (1948), Torke (1974), Chengalath et al. (1971), and Deevey and Deevey (1971) were useful in zooplankton identification.

Numbers per liter (= number per meter$^3$ x $10^{-3}$) were calculated for each sample from percent of sample counted, assuming 100% removal of organisms from the water column, length of tow, and net opening diameter. Number per meter$^2$ were obtained by multiplying the number per meter$^3$ by the depth of the water column in meters.

## Zooplankton Development Times

There is generally good agreement between experimentally determined development times reported by different authors. Schindler (1972) incorporated egg development data from a variety of cladoceran and copepod species into a curvilinear equation ($\frac{1}{D} = 0.0426 + 0.0008T^2$, D = development time in days, T = temperature $^{o}C$) and obtained a very high regression coefficient $r^2 = 0.99$.

A comparison of egg development times for Daphnia, the best studied genus, is presented in Table 3. In each study development times were long at low temperatures and became shorter at an ever decreasing rate as temperature increased. There is need for more studies comparing development times of a single species from different populations and development times of several species of a single genus. Until such studies are undertaken, it cannot be known to what extent differences in development time data reported by various authors (Table 3, for example) reflect experimental technique or actual interspecific or interpopulation differences. In a single comparative study, Munro and White (1975) reported very small but statistically significant differences in egg development rates for Daphnia longispina from two different lakes (Table 3).

Some workers, particularly those from eastern Europe, have measured development rates at a single temperature and used a series of coefficients from the empirically derived

Table 3. A comparison of *Daphnia* egg development times (in days) compiled from reports by various authors.

| Temperature $^{o}$C | 5 | 8 | 10 | 13 | 15 | 17 | 20 | 23 | 25 |
|---|---|---|---|---|---|---|---|---|---|
| (1) Schindler (1972) | 16.0 | 10.7 | 8.2 | 5.6 | 4.5 | 3.7 | 2.8 | 2.1 | 1.8 |
| (2) Elster and Schwoerbel (1970) | 18.2 | 10.6 | 8.0 | 5.4 | 4.3 | 3.5 | 2.8 | 2.2 | |
| (3) Hall (1964) | 18.0 | 12.3 | | 6.0 | 4.5 | | 2.6 | | 2.0 |
| (4) Hillbricht-Ilkowska and Patalas (1967) | | | 5.1 | 3.8 | 3.0 | 2.4 | 1.8 | 1.4 | |
| (5) Weglenska (1971) | | | | | | 3.0 | | | |
| (6) Weglenska (1971) | | | | | | 3.0 | | | |
| (7) Munro and White (1975) | 16.8 | | 7.8 | | 4.2 | | 2.5 | | |
| (8) Munro and White (1975) | | | 8.2 | | 4.0 | | 2.3 | | |
| (9) Patalas (1970) | 8.8 | 5.9 | 4.5 | 3.3 | 2.7 | 2.2 | 1.7 | 1.3 | 1.1 |
| (10) Krogh's curve | 14.5 | 9.7 | 7.5 | 5.4 | 4.4 | 3.7 | 2.8 | 2.2 | 1.8 |

(1) From an equation based upon pooled data; (2) *Daphnia longispina*; (3) *Daphnia galeata mendotae*; (4) *Daphnia* sp.; (5) *D. cucculata*; (6) *D. longispina*; (7) and (8) *D. longispina* from two different lakes; (9) *D. cucculata*, values extrapolated from 20$^{o}$C using Krogh's curve (Winberg, 1971); (10) Extrapolated from a time of 2.8 days at 20$^{o}$C using Krogh's curve (Winberg, 1971).

Krogh's curve to extrapolate to other temperatures (Winberg, 1971). Using this method, any imprecision in the experimentally determined development time is multiplied by a series of coefficients. Patalas (1970) obtained a *Daphnia* egg development time of 1.7 days at 20°C and then used Krogh's curve to extrapolate to other temperatures. His development times are much shorter at all temperatures than those from other sources listed in Table 3. *Daphnia* egg development times calculated using a time of 2.8 days at 20°C and Krogh's curve coefficients from Winberg,(1971) show good agreement with experimentally measured development times (Table 3).

Development times were obtained for each cladoceran genus, with the exception of a single set of values for *Bosmina* and *Eubosmina*, and for each copepod order (Tables 4 and 5). Sources for the development times were selected on the basis of: (1) comparability to other literature values, (2) available temperature range, (3) a subjective evaluation of the author's technique, and (4) the species studied. Since the original Russian publications cited by Hillbricht-Ilkowska and Patalas (1967) were not available and the development times therein were somewhat shorter than those from other authors (Table 3), the development times given in Hillbricht-Ilkowska and Patalas (1967) were used only when other suitable data were unavailable.

To interpolate development times to temperatures

Table 4. Zooplankton development times (in days) used in production calculations. Literature sources and experimental species are listed in Table 5.

| Sampling Date | 4-22 | 5-29 | 6-16<br>9-8 | 7-17 | 8-11<br>8-14 | 10-6 | 11-3 | 12-16<br>3-16 |
|---|---|---|---|---|---|---|---|---|
| Temperature (°C) | 7 | 20 | 21 | 23 | 24 | 13 | 10 | 5 |
| *Bosmina* eggs* (1) | 8.2 | 1.5 | 1.5 | 1.4 | 1.3 | 4.1 | 5.5 | 10.7 |
| *Bosmina* juveniles* (1) | 17.9 | 4.2 | 3.8 | 3.1 | 2.9 | 9.0 | 12.0 | 23.3 |
| *Chydorus* eggs (1) | 7.0 | 1.7 | 1.5 | 1.2 | 1.1 | 3.6 | 4.7 | 9.1 |
| *Chydorus* juveniles (1) | 17.1 | 4.0 | 3.6 | 3.0 | 2.8 | 8.4 | 11.5 | 22.4 |
| *Daphnia* eggs (2) | 14.2 | 2.6 | 2.3 | 2.1 | 2.0 | 6.0 | 9.4 | 18.0 |
| *Daphnia* juveniles (3) | 28.7 | 5.1 | 4.7 | 4.0 | 3.7 | 11.6 | 17.0 | 41.5 |
| *Diaphanosoma* eggs (1) | 7.9 | 1.8 | 1.5 | 1.5 | 1.4 | 4.2 | 5.3 | 10.3 |
| *Diaphanosoma* juveniles (1) | 16.7 | 4.8 | 4.4 | 3.5 | 3.2 | 8.9 | 11.2 | 21.8 |
| *Leptodora* eggs (4) | 23.9 | 6.0 | 5.2 | 4.0 | 3.2 | 11.6 | 16.0 | 31.1 |
| Cyclopoida eggs (5) | 10.4 | 2.4 | 2.4 | 2.1 | 1.9 | 4.4 | 6.1 | 14.9 |
| Cyclopoida nauplii (6) | 21.3 | 6.6 | 6.6 | 5.5 | 5.0 | 10.2 | 14.3 | 27.8 |
| Cyclopoida copepodites (1) | 46.2 | 11.5 | 11.0 | 9.5 | 8.7 | 22.0 | 31.0 | 60.3 |
| Calanoida eggs (7) | 12.8 | 3.6 | 3.3 | 2.3 | 2.1 | 5.0 | 8.0 | 20.4 |
| Calanoida nauplii (8) | 35.0 | 11.0 | 10.1 | 8.6 | 7.9 | 17.0 | 25.0 | 50.0 |
| Calanoida copepodites (8) | 23.0 | 9.0 | 8.3 | 7.0 | 6.5 | 12.0 | 16.0 | 29.0 |
| *Keratella* eggs (9) | 4.0 | 1.3 | 1.1 | 0.9 | 0.8 | 2.0 | 2.7 | 5.3 |

* These values were used for both *Bosmina* and *Eubosmina*.
Numbers in parentheses are keyed to literature sources in Table 5.

Table 5. Literature sources and experimental animals for development times used in production calculations. Numbers in parentheses are keyed to Tables 4 and 6.

| Source | Experimental Species | Life Stage |
|---|---|---|
| (1) Hillbricht-Ilkowska and Patalas (1967) | *Bosmina* sp. | eggs, juveniles |
| | *Diaphanosoma* sp. | eggs, juveniles |
| | *Chydorus* sp. | eggs, juveniles |
| | *Cyclops* sp. | copepodites |
| (2) Hall (1964) | *Daphnia galeata mendotae* | eggs |
| (3) Munro and White (1975) | *Daphnia longispina* | juveniles |
| (4) Cummins et al. (1969) | *Leptodora kindtii* | eggs |
| (5) Torke (1975) | *Cyclops bicuspidatus thomasii* | eggs |
| (6) Spindler (1971) | *Cyclops vicinus* | nauplii |
| (7) Cooley (unpublished data) | *Diaptomus minutus* | eggs |
| (8) Nauwerck (1963) | *Eudiaptomus graciloides* | nauplii, copepodites |
| (9) Edmondson, (1960) | *Keratella cochlearis* | eggs |

between those measured by a given author, temperature-development time data points were fit by polynomial regression using Biomedical Program BMDO5R) to equations of the form:

$$D = a + bT + cT^2 + dT^3$$

where a, b, c, and d are constants, D = development time in days, and T is temperature in °C (Table 6). Exceptions were development times for Keratella cochlearis eggs which were calculated from the equation ($\frac{1}{D} = 0.043T - 0.060$) used by Edmondson (1960) and development times for Leptodora eggs which were read directly from a graph presented by Cummins et al. (1969).

Extrapolations to temperatures outside the temperature range examined by an author were made using Krogh's curve coefficients given by Winberg (1971). A single temperature rounded to the nearest degree was used for calculating development times for zooplankters in all samples collected on a sampling date. Since no means of extrapolating to temperatures lower than 5°C was available, development times for 5°C were used in calculating March 16, 1976 production even though the actual temperature was 1.5°C.

## Zooplankton Dry Weights

Techniques for determining the weight of micrometazoa are not standardized and as a result weights obtained by different workers often show wide discrepancies. To insure comparable results from different taxa weight measurements

Table 6. Constants for zooplankton development time equations of the form: $D = a + bT + cT^2 + dT^3$; where a, b, c, and d are constants, D is development time in days, and T is temperature in °C. Literature sources and experimental species are listed in Table 5.

| | Experimental Temperature Range °C | a | b | c | d |
|---|---|---|---|---|---|
| *Bosmina* eggs * (1) | 10-23 | 7.68189 | 0.07937 | -0.04142 | 0.00113 |
| *Bosmina* juveniles * (1) | 10-23 | 29.59940 | -2.39509 | 0.07125 | -0.00075 |
| *Chydorus* eggs (1) | 10-23 | 7.76565 | -0.18763 | -0.01770 | 0.00059 |
| *Chydorus* juveniles (1) | 10-23 | 27.29521 | -2.03096 | 0.04753 | -0.00022 |
| *Daphnia* eggs (2) | 4-25 | 31.61116 | -3.29130 | 0.12132 | -0.00148 |
| *Daphnia* juveniles (3) | 5-20 | 98.10000 | -15.51667 | 0.93800 | -0.01973 |
| *Diaphanosoma* eggs (1) | 10-23 | 3.03396 | 0.96177 | -0.09558 | 0.00221 |
| *Diaphanosoma* juveniles (1) | 10-23 | 24.02210 | -1.79436 | 0.06034 | -0.00092 |
| Cyclopoida eggs (5) | 5-23 | 31.25587 | -4.29259 | 0.22091 | -0.00389 |
| Cyclopoida nauplii (6) | 9-24 | 52.58591 | -6.42305 | 0.31213 | -0.00530 |
| Cyclopoida copepodites (1) | 10-23 | 95.23981 | -9.88021 | 0.40517 | -0.00599 |
| Calanoida eggs (7) | 4-23 | 46.61966 | -7.17236 | 0.40624 | -0.00776 |
| Calanoida nauplii (8) | 5-20 | 103.08315 | -14.29260 | 0.78524 | -0.01505 |
| Calanoida copepodites (8) | 5-20 | 54.24854 | -6.51653 | 0.32663 | -0.00569 |

* These values were used for both *Bosmina* and *Eubosmina*.
Numbers in parentheses are keyed to literature sources in Table 5.

from a single recent study (Dumont et al., 1975) were used to determine zooplankton weight increments and biomass whenever possible. Dumont et al. (1975) oven-dried samples at 110°C for 2 hours before weighing on a Mettler microbalance.

Except for Asplanchna, which has a low dry weight to wet weight (Dumont et al., 1975), the rotifer weights reported by Dumont et al. (1975) are much higher than values based on volume measurements (Table 7). Dumont et al. (1975) reported weights for the rotifer genera which are numerically important at Locust Point, Lake Erie. Weights for rotifers not weighed by Dumont et al. (1975) were estimated from the weight for that rotifer reported by another author and the ratio of weights for a common rotifer measured by both Dumont et al. (1975) and the other author. Weights for a few less common rotifer taxa not reported by any available source were estimated from the weights of rotifers of similar size and shape (Table 8).

Weights reported by Dumont et al. (1975) are comparable to values given by Burns (1969) and Duncan (1975) for Daphnia, and by Burgis (1975) and Wilson and Roff (1973) for copepods. The weights of copepodite and adult copepods, Daphnia, Bosmina, Eubosmina, and Chydorus were computed from regression equations from Dumont et al. (1975) of the form:

$$W = aL^b$$

where W is the dry weight, L is the length, and a and b are

Table 7. Comparison of rotifer weights (µg per rotifer) reported by different authors.

| | Dumont et al. (1975) (1) | Makarewicz (1974) (1) | Comita (1972) (2) | Schindler and Novén (1971) (3) | Nauwerck (1963) (3) | Sebestyen (1958) (3) |
|---|---|---|---|---|---|---|
| *Asplanchna priodonta* | 0.51 | 0.212 | 2.31 | | .24-2.3 | |
| *Brachionus calyciflorus* | 0.29 | | 0.057 | | 0.030 | |
| *Keratella cochlearis* | 0.11 | 0.070 | 0.013 | 0.035 | 0.0025 | .006-.011 |
| *Polyarthra* spp. | 0.74 | 0.060 | 0.11 | .035-.070 | 0.028 | 0.019 |
| *Synchaeta* spp. | 0.26 | | 0.12 | | 0.050 | |

(1) Direct weighing.
(2) Based upon volume measurements
(3) Calculated from volume by assuming a specific gravity of 1.0 and a dry weight to wet weight ratio of 0.05 for all rotifers except *Asplanchna* which was assumed to have a dry weight to wet weight ratio of 0.01 (after Schindler and Noven, 1971).

Table 8. Rotifer weights used in zooplankton production calculations.

| Taxa | Weight (µg) | Source |
|---|---|---|
| *Asplanchna priodonta* | 0.51 | (1) |
| *Brachionus calyciflorus* | 0.29 | (1) |
| *B. angularis* | 0.47 | (1) |
| *B. havanaensis* | 0.50 | (4) |
| *B. urceolaris* | 0.20 | (1) |
| *Chromogaster ovalis* | 0.20 | (1) and (3) |
| *Conochiloides* sp. | 0.20 | (1) and (3) |
| *Filinia terminalis* | 0.45 | (1) |
| *Kellicottia longispina* | 0.28 | (1) and (2) |
| *Keratella cochlearis* | 0.11 | (1) |
| *K. quadrata* | 0.34 | (1) |
| *Noltholca* spp. | 0.40 | (4) |
| *Pompholyx sulcata* | 0.22 | (1) and (3) |
| *Synchaeta* spp. | 0.26 | (1) |
| *Trichocerca* spp. | 0.35 | (1) |

(1) Dumont et al. (1975)
(2) Schindler and Novén (1971)
(3) Nauwerck (1963)
(4) Estimated from the weights of rotifers of similar size and shape.

constants (Table 9). The weights of Leptodora and Diaphanosoma were calculated from the weights for sizes given by Cummins et al. (1969) and Dumont et al. (1975) respectively (Table 10).

## Zooplankton Production Calculations

The formula used by Patalas (1970) for assessing the daily production of a single species of crustacean may be written in the general form:

$$P_{i.} = \sum_{j=1}^{n} \frac{N_{ij}\,\Delta W_{ij}}{T_{ij}} \qquad \text{(equation 1)}$$

$P_{i.}$ = Production of the ith species in weights units per day;

$n$ = Number of stages or size classes of the ith species;

$N_{i1}, N_{i2}, \ldots. N_{in}$ = Numbers of individuals in the various stages or size classes;

$\Delta W_{i1}, \Delta W_{i2}, \ldots. \Delta W_{in}$ = Weight increment gained per individual in the particular stage or size class; and

$T_{i1}, T_{i2}, \ldots. T_{in}$ = Developement time of individuals in the particular stage or size class in days.

Edmondson (1974) noted that the main differences between the many methods for assessing secondary production

Table 9. Equations used in calculating the weights of crustacean zooplankters.

| Taxa | Equation or weight | Units | Source |
|---|---|---|---|
| *Bosmina* and *Eubosmina* | $W = 26.6\ L^{3.13}$ | (mm, µg) | (1) |
| *Chydorus sphaericus* | $W = 89.43\ L^{3.93}$ | (mm, µg) | (1) |
| *Daphnia retrocurva* | $W = 1.5 \times 10^{-8} L^{2.84}$ | (µm, µg) | (1) |
| *D. galeata mendotae* | $W = 9.5 \times 10^{-8} L^{2.56}$ | (µm, µg) | (1) |
| Cyclopoida (copepodites, adults) | $W = 1.1 \times 10^{-5} L^{1.89}$ | (µm, µg) | (1) |
| Calanoida (copepodites, adults) | $W = 7.9 \times 10^{-7} L^{2.33}$ | (µm, µg) | (1) |
| Cyclopoida nauplii | 0.34 | (µg) | (2) |
| Calanoida nauplii | 0.40 | (µg) | (2) |
| Cyclopoida eggs | 0.06 | (µg) | (2) |
| Calanoida eggs | 0.20 | (µg) | (3) |

(1) Dumont et al. (1975)

(2) Schindler and Noven (1971)

(3) Rigler and Cooley (1974)

Table 10. Weights for *Leptodora kindtii* and *Diaphanosoma leuchtenbergianum* used in production calculations.

| *Leptodora kindtii* (from Cummins et al., 1969) | | *Diaphanosoma leuchtenbergianum* (from Dumont et al., 1975) | |
|---|---|---|---|
| Size Class (mm) | Dry Weight (µg) | Length (mm) | Dry Weight (µg) |
| eggs | 51 | 0.40 | 0.53 |
| 2 | 50 | 0.50 | 0.85 |
| 3 | 60 | 0.60 | 1.25 |
| 4 | 80 | 0.70 | 1.74 |
| 5 | 100 | 0.80 | 2.30 |
| 6 | 120 | 0.90 | 2.95 |
| 7 | 150 | 1.00 | 3.68 |
| 8 | 160 | 1.10 | 4.49 |
| 9 | 180 | 1.20 | 5.40 |
| 10 | 210 | | |
| 11 | 240 | | |
| 12 | 250 | | |

which have been presented in the literature concern the detail with which size or age classes are recognized and the method for estimating development times. The number of stages or size classes depends on the life history of the organism and the efforts of the researcher. Since copepods do not grow after reaching the adult instar, their production is summed over three major stages: eggs, nauplii, and copepodites. The number of cladoceran instars is indeterminant; therefore, production is summed for egg, juvenile, and adult stages. The more these major stages are subdivided the closer the production estimate should reflect production in the natural population.

In this study the copepodite and juvenile and adult cladoceran stages were further subdivided based upon the assumption that these organisms grow in length at a constant rate (Ingle et al., 1937; Weglenska, 1971). If, for example, Daphnia developed from neonates (newborns) 0.60 mm in length to adults 1.0 mm in length in 4 days, the development time of each 0.10 mm juvenile size class would be 1 day. Growth curves for cladocerans show that the growth rate of body length of adults is about three times slower than the growth rate of juveniles (Ingle et al., 1937; Anderson and Jenkins, 1942; Richman, 1958; and Weglenska, 1971). Thus in the example given above, the development time for each 0.1 mm adult Daphnia size class would be 3 days.

The production of copepodites, Daphnia, and

Diaphanosoma was summed over 0.1 mm size classes; the production of Bosmina, Eubosmina, and Chydorus was summed over 0.02 mm size classes. From equation 1, the daily production of each size class for a species i is $P_{ij} = \frac{N_{ij} \Delta W_{ij}}{T_{ij}}$. For example, the calculated weight of a Daphnia retrocurva 1.0 mm in length is 5.0 µg while an individual 1.1 mm in length weighs 6.5 µg. The growth increment for D. retrocurva in the 1.0 to 1.1 mm size class is 6.5 µg - 5.0 µg = 1.5 µg. If the development time of the 1.0 to 1.1 mm size class were 3 days the production per individual in the size class would be $1.5\ \mu g \cdot (3\ days)^{-1} = 0.5\ \mu g \cdot day^{-1}$. The production per individual in a size class was multiplied by the percentage of individuals in that size class and summed over the size range of the species. The result was the mean production per individual of a given species on a given sampling date.

In calculating the weight increments of crustacean zooplankters the initial weight of an egg was taken as 0.0. Copepod egg weights were based upon direct weighing. Each cladoceran egg weight was assumed to equal the calculated weight of a neonate. The weight increment added during naupliar stages was taken as the weight of a first instar copepodite (C1) less the weight of an egg. The total weight increment added during copepodite stages was the difference in weight between an adult copepod of mean length and the weight of a C1 copepodite.

The lengths of neonates and C1 copepodites were estimated from the length-frequency distributions. Variation around the modal length for C1 copepodites was often small and the modal length was therefore estimated to the nearest 0.01 mm. The length of neonates was set as the midpoint of the size interval which appeared to include the greatest number of neonates. The size at maturity of cladocerans was determined from the length-frequency distribution of ovigerous females. Since the smallest ovigerous female is clearly smaller than the average of a number of primapara, the size at maturity of cladocerans was arbitrarily defined using percentiles. The midpoint of the size interval constructed such that 10% of the ovigerous individuals were shorter than the lower limit of that size interval was set as the size at maturity of cladocerans.

For every sampling date the development times and size-frequency distributions were applied to the abundance estimates from plankton counts to estimate the production of each of the common cladoceran species, copepodite genera, and nauplii orders. Size-frequency distributions for rare forms were determined either by pooling measurements from two or more sampling dates or by utilizing measurements from the closest time period when the form was more abundant. Biomass was computed by summing the weights of the midpoints of the same intervals used in estimating production.

Rotifers are not susceptible to size classification because of their small size and meager growth after hatching. Edmondson's (1960; 1965) method for estimating the birth rate of rotifers is the basis for most methods of calculating rotifer production. His method utilizes the ratio of eggs per female to the development time of the egg:

$$B = \frac{E}{D} \qquad \text{(equation 2)}$$

where B = the finite birth rate (eggs hatched·female$^{-1}$·day$^{-1}$); E = the number of eggs per female; and D = development time of the egg. Edmondson also used an exponential model based on the instantaneous birth rate b:

$$b = \ln (1 + B) \qquad \text{(equation 3)}$$

In both models the birth rate is a measure of the recruitment of newly hatched individuals. Use of the egg ratio method to estimate the production of biomass is based upon the implicit assumption that the turnover rate (days$^{-1}$) of the number of individuals is equal to the turnover rate of biomass. Since rotifers do not grow very much after hatching and have short life spans, the egg ratio method is applicable in calculating their production.

The turnover rate of biomass for the rotifer *Keratella cochlearis* was equated with the finite birth rate B. The production of all rotifers was calculated by multiplying their biomass by the turnover rate obtained for *K. cochlearis* as was done by Patalas (1970). For example, given a weight of 0.11 µg per *K. cochlearis* and a birth rate B of 0.2 eggs·female$^{-1}$·days$^{-1}$, the production per individual female K. cochlearis would be 0.11 $\mu g \cdot 0.2$ eggs$\cdot$female$^{-1}\cdot$day$^{-1}$ = 0.022 $\mu g \cdot$female$^{-1} \cdot$day$^{-1}$.

Unlike rotifers, crustaceans may grow considerably after hatching and go through periods when production is taking place only through the growth of individuals, and not through reproduction. Although the egg ratio method has been used to estimate the production of Daphnia (Wright, 1965) and other crustacean plankters (Cummins et al., 1969), its use for assessing production is best limited to rotifers. Since juvenile development times were not available, the production of the cladoceran Leptodora kindtii was calculated using the egg ratio method and the finite birth rate B.

Production over a time interval was calculated using the formula found most approppropriate by Hillbricht-Ilkowska and Weglenska (1970):

$$P_{t1 \rightarrow t2} = \left(\frac{P_{t1} + P_{t2}}{2}\right) \times (t2 - t1) \qquad \text{(equation 4)}$$

$P_{t1 \rightarrow t2}$ = Production for the entire sampling interval;

$P_{t1}$ = Daily production in the moment t = 1;

$P_{t2}$ = Daily production in the moment t = 2;

t2 - t1 = Time in days between t1 and t2.

Since samples were collected from April 22, 1975 through March 16, 1976, annual production was calculated by assuming that production on April 22, 1976 was the same as production on April 22, 1975.

## Measures of Zooplankton Reproduction

Birth rate is a function of the eggs per adult ratio, the percentage of immature stages in the population, and the development time of eggs. If one assumes no mortality, initial population size ($N_o$) and the population size after time t ($N_t$) are related by the equation:

$$N_t = N_o e^{bt} \qquad \text{(equation 5)}$$

where b is the instantaneous birth rate (equation 3) and e is the base of natural logarithms. Potential population doubling time (PPDT) may be calculated by letting $N_t = 2N_o$ and solving for t, giving:

$$\text{PPDT} = \frac{\ln 2}{b} \qquad \text{(equation 6)}$$

where ln 2 is the natural logarithm of 2, 0.693.

# RESULTS

## Species Composition and Seasonal Occurrence

Mean numbers per liter for each zooplankton taxon collected at Locust Point, Lake Erie on each sampling date are listed in Tables 11, 12, and 13. Numbers per liter and species composition at individual stations for the same samples have been reported by Reutter and Herdendorf (1975a; 1976).

A total of 23 rotifer taxa belonging to 16 genera were identified during the study period. The three most abundant forms, Keratella cochlearis, Polyarthra spp., and Synchaeta spp. were present in each sample and accounted for 68% of the mean number of rotifers per liter found throughout the year. K. cochlearis (26% of the annual rotifer mean) was abundant from May 29 through August 11 and again in the October and December samples. A peak of 104 per liter occurred in the July 14 samples. Polyarthra spp. (23%) followed a similar pattern with a population maximum of 152 per liter on July 14 and secondary peaks in the May and December samples. Synchaeta spp. (19%) was most abundant on November 3 (71 per liter).

Chromogaster ovalis (8%), Pompholyx sulcata (5%), and Trichocerca multicrinis (5%) were all warm water species with maxima in the July and August samples. The predaceous rotifer Asplanchna priodonta (4%) was present in all but the March and June samples and was most abundant in the

Table 11. Mean number of rotifers per liter, Locust Point, Lake Erie, April 22, 1975-March 16, 1976. P- present in numbers less than 0.05 per liter.

| Sampling Date | 4-22 | 5-29 | 6-16 | 7-14 | 8-11 | 8-14 | 9-8 | 10-6 | 11-3 | 12-16 | 3-16 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Asplanchna priodonta* | 0.1 | 1.2 |  | 25.0 | 1.1 | 5.9 | 36.8 | 1.0 | 0.7 | 21.8 |  |
| *Brachionus angularis* | 0.6 | 6.5 | 17.8 | 9.1 | 0.9 | 2.3 | 2.9 | 0.4 | 0.1 | 0.1 | 0.9 |
| *B. calyciflorus* | 6.1 | 0.2 | 0.4 | 0.9 | 0.3 |  | 0.2 |  | 6.9 | 0.5 | 0.2 |
| *B. havanaensis* |  | 0.6 | 0.2 | 1.6 | 0.5 | 1.8 | 1.8 | 0.2 |  |  |  |
| *B. urceolaris* | 1.1 |  |  |  |  |  |  |  |  |  |  |
| *Chromogaster ovalis* |  |  |  | 82.7 | 77.6 | 13.6 | 2.4 |  |  |  |  |
| *Conochiloides* sp. |  | 0.1 | 38.9 | 3.8 | 0.9 | 0.8 |  |  |  |  |  |
| *Filinia terminalis* | 0.9 | 0.8 | 1.8 | 9.1 | 0.6 | 0.9 | 0.3 | 0.1 |  | 0.6 | 0.6 |
| *Hexarthra mira* |  |  |  |  |  |  | 0.2 |  |  |  |  |
| *Kellicottia longispina* | 0.6 | 0.2 | 8.4 |  | 0.1 | 0.1 |  |  | 0.1 | 2.6 | 0.1 |
| *Keratella cochlearis* | 4.6 | 77.6 | 95.0 | 104.4 | 89.3 | 13.9 | 23.7 | 58.3 | 32.7 | 68.5 | 1.1 |
| *K. quadrata* | 4.1 | 7.7 | 16.9 | P | 0.1 |  | 0.1 | 0.1 | 1.1 | 6.0 | 1.0 |
| *Lecane lunaris* |  |  |  | P |  |  |  |  |  |  |  |
| *L. luna* |  |  |  | P |  |  |  |  |  |  |  |
| *Noltholca* spp. | 34.1 | 0.1 |  |  |  |  |  |  |  | 0.1 | 0.8 |
| *Polyarthra* spp. | 16.1 | 83.3 | 25.2 | 151.5 | 22.2 | 16.9 | 42.6 | 18.6 | 37.1 | 82.6 | 6.3 |
| *Pompholyx sulcata* |  |  | 4.5 | 3.9 | 86.6 | 10.3 | 2.6 | 2.0 |  |  |  |
| *Rotaria* sp. |  |  |  |  |  |  | 0.1 |  |  |  |  |
| *Synchaeta* spp. | 36.5 | 0.9 | 32.7 | 28.3 | 124.6 | 11.0 | 27.8 | 12.9 | 71.2 | 53.2 | 16.4 |
| *Trichocerca cylindrica* |  |  |  | 0.1 |  |  | 0.1 |  |  |  |  |
| *T. multicrinis* |  | 0.9 | 0.6 | 6.5 | 17.5 | 64.0 | 15.5 | 0.4 |  |  |  |
| *Trichocerca* sp. |  |  | 0.9 | 0.3 | 3.5 |  |  |  |  |  |  |
| *Trichotria tetractis* |  |  | 0.1 | 0.3 |  |  |  |  |  |  |  |

Table 12. Mean number of copepods per liter, Locust Point, Lake Erie, April 22, 1975-March 16, 1976. P- present in numbers less than 0.05 per liter.

| Sampling Date | 4-22 | 5-29 | 6-16 | 7-14 | 8-11 | 8-14 | 9-8 | 10-6 | 11-3 | 12-16 | 3-16 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| CALANIODA | | | | | | | | | | | |
| <u>Diaptomus aslandi</u> | 0.4 | | 0.1 | | | | | | | | P |
| <u>D</u>. <u>minutus</u> | 0.1 | | | | P | | | | | 0.1 | |
| <u>D</u>. <u>oregonensis</u> | | | P | | | | | | | | P |
| <u>D</u>. <u>siciloides</u> | | 4.5 | 2.2 | 0.8 | 0.5 | 0.7 | 11.7 | 1.7 | 0.5 | 0.1 | |
| <u>D</u>. <u>sicilis</u> | 0.3 | | | | | | | | | | |
| <u>Diaptomus</u> copepodites | 0.3 | 1.2 | 2.1 | 2.5 | 1.9 | 8.2 | 24.1 | 1.9 | 2.5 | 0.3 | |
| <u>Epischura lacustris</u> | | | P | | | | | | | | |
| <u>Eurytemora affinis</u> | | 0.3 | P | | | | | P | 0.6 | 0.2 | |
| <u>E</u>. <u>affinis</u> copepodites | | P | | | | | | | 1.0 | 0.3 | |
| <u>Limnocalanus macrurus</u> | P | | | | | | | | | | |
| Calanoid nauplii | 15.9 | 15.9 | 10.4 | 7.3 | 10.8 | 14.9 | 28.6 | 6.9 | 7.6 | 1.8 | 0.1 |
| CYCLOPOIDA | | | | | | | | | | | |
| <u>Cyclops bicuspidatus</u> | 0.6 | 3.5 | 7.3 | | | | P | 0.1 | 0.5 | 0.4 | 0.1 |
| <u>C</u>. <u>vernalis</u> | P | 12.5 | 36.2 | 15.6 | 0.7 | 1.8 | 1.5 | 6.1 | 3.7 | 1.1 | P |
| <u>Cyclops</u> copepodites | 0.7 | 3.6 | 8.0 | 66.3 | 3.5 | 15.3 | 7.8 | 22.5 | 22.7 | 10.3 | 0.2 |
| <u>Mesocyclops edax</u> | | P | P | 0.8 | 0.1 | | 0.2 | | | | |
| <u>M</u>. <u>edax</u> copepodites | | | | | 0.3 | 0.1 | 0.8 | | | | |
| <u>Tropocyclops prasinus</u> | | | | | | | | 0.1 | 0.3 | 0.1 | P |
| <u>T</u>. <u>prasinus</u> copepodites | | | | | | | | 0.1 | 0.1 | P | |
| Cyclopoid nauplii | 3.3 | 286.0 | 126.1 | 78.1 | 45.9 | 25.8 | 9.1 | 34.3 | 47.5 | 37.1 | 4.1 |

Table 13. Mean number of cladocerans per liter, Locust Point, Lake Erie, April 22, 1975-March 16, 1976. P- present in numbers less than 0.05 per liter.

| Sampling Date | 4-22 | 5-29 | 6-16 | 7-14 | 8-11 | 8-14 | 9-8 | 10-6 | 11-3 | 12-16 | 3-16 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Bosmina longirostris* | 0.7 | 210.0 | 0.9 | 4.5 | 0.1 | 0.3 |  | 0.2 | 15.2 | 6.1 | P |
| *Ceriodaphnia* sp. |  |  |  | 0.1 |  |  | P | P |  |  |  |
| *Chydorus sphaericus* | P | 3.2 | 0.6 | 0.2 | 7.5 | 36.8 | 61.8 | 51.7 | 8.9 | 0.4 |  |
| *Daphnia galeata mendotae* |  | 0.1 |  | 9.1 | 0.3 | 0.6 | 0.3 | 0.9 | 0.4 | 0.1 |  |
| *D. parvula* |  |  | P |  |  |  |  |  |  |  |  |
| *D. retrocurva* | 0.3 | 121.2 | 32.7 | 150.9 | 5.6 | 15.3 | 16.5 | 54.9 | 3.7 | P | P |
| *Diaphanosoma leuchtenbergianum* |  |  | P | 1.0 | 1.1 | 4.5 | 17.2 | 0.9 | P |  |  |
| *Eubosmina coregoni* | P | 5.7 | 77.9 | 0.6 | 21.0 | 28.2 | 8.0 | 79.2 | 34.0 | 5.2 | P |
| *Leptodora kindtii* |  | 0.8 | 1.6 | 0.8 | 0.1 | 0.6 | 0.3 | 0.6 |  |  |  |

September 8 samples (37 per liter). The remaining 10% of the annual rotifer mean was divided among 15 less common taxa.

Egg-bearing rotifers were found in all samples. Males were never observed. Of the three numerically important rotifers, only *Keratella cochlearis* and *Polyarthra* spp. carry eggs externally. A large percentage of *Polyarthra* spp. eggs were detached, perhaps as a result of distortion of the rotifer's cuticle by the formalin-sucrose preservative.

*Diaptomus siciloides* accounted for 92% of the annual mean number of adults of seven species of calanoid copepods and over 99% of the total collected from June 16 through October 3. *D. siciloides* adults (11 per liter), *Diaptomus* copepodites (24 per liter), and calanoid nauplii (29 per liter) were all most abundant in the September samples. *Cyclops vernalis* and *Cyclops bicuspidatus thomasi*, both of which were most abundant in the June 16 samples, comprised 85% and 13% respectively of the annual mean per liter of four cyclopoid copepod species. *Cyclops* copepodites were most abundant in the July samples (66 per liter). The cyclopoid nauplii peak abundance of 286 per liter occurred in the May 29 samples. Although copepodites were identified only to genus and nauplii to order, it is reasonable to assume that the great majority of immature cyclopoid copepods were *Cyclops vernalis*, and nearly all immature calanoid copepods were *Diaptomus siciloides*.

Even though cyclopoid nauplii were common year around, ovigerous cyclopoid females were found only from April 22 through July 14. Diaptomus siciliodes reproduced from May 29 through November 3.

Of nine species of Cladocera, the following four species contributed 96% to the annual cladoceran mean: Daphnia retrocurva, 37%; Eubosmina coregoni, 23%; Bosmina longirostris, 22%; and Chydorus sphaericus, 15%. D. retrocurva was present in all samples but particularly abundant on May 29 (121 per liter), July 14 (151 per liter) and October 6 (55 per liter). E. coregoni was present in each set of samples and was most abundant in June (78 per liter) and October (79 per liter) samples. While B. longirostris was found each month except for September, 88% of its annual total came from a density of 210 per liter on May 29. Chydorus sphaericus was common from August 14 through October 6. Leptodora kindtii was present from May 29 through October 3 in numbers not exceeding 1.6 per liter.

With the exception of a few ovigerous Bosmina longirostris and Eubosmina coregoni found in the December samples, cladoceran reproduction was limited to May 29 through November 3. Male and ephippia-bearing Daphnia retrocurva females were present in the May, October, and November samples. B. longirostris and E. coregoni males and ephippial eggs appeared in the October, November, and December samples. The sucrose-formalin preservative was very effective in preventing egg loss from brood chambers of all cladocerans except Leptodora. Eggs of Leptodora kindtii were invariably lost from the brood chamber.

Both copepods and cladocerans were most abundant during late spring and early summer, and had population minima in August and during the months of cold water temperatures (Fig. 3). Rotifers were particularly abundant in the July 14 and August 11 samples, and then again on December 16.

## Measures of Zooplankton Reproduction

Seasonal changes in the mean number of eggs per ovigerous female showed two patterns. Cyclops vernalis and C. bicuspidatus thomasi clutch sizes decreased from May 29 until ovigerous females were no longer collected (Table 14). Each remaining taxon had June 16 maxima and only modest changes in mean clutch size prior to the cessation of reproduction in late fall.

The mean number of eggs per adult includes the numbers of ovigerous and nonovigerous females and the numbers of males in the denominator. Male cladocerans were rare and usually smaller than the size of maturity for female Cladocera. Cyclops vernalis declined sharply from a May 29 peak to 0.0 eggs per adult on August 11 (Fig. 4). The remaining taxa, all considered herbivores, had low eggs per adult ratios on May 29 and maxima on June 16. Diaptomus siciloides eggs per adult declined steadily throughout the summer and

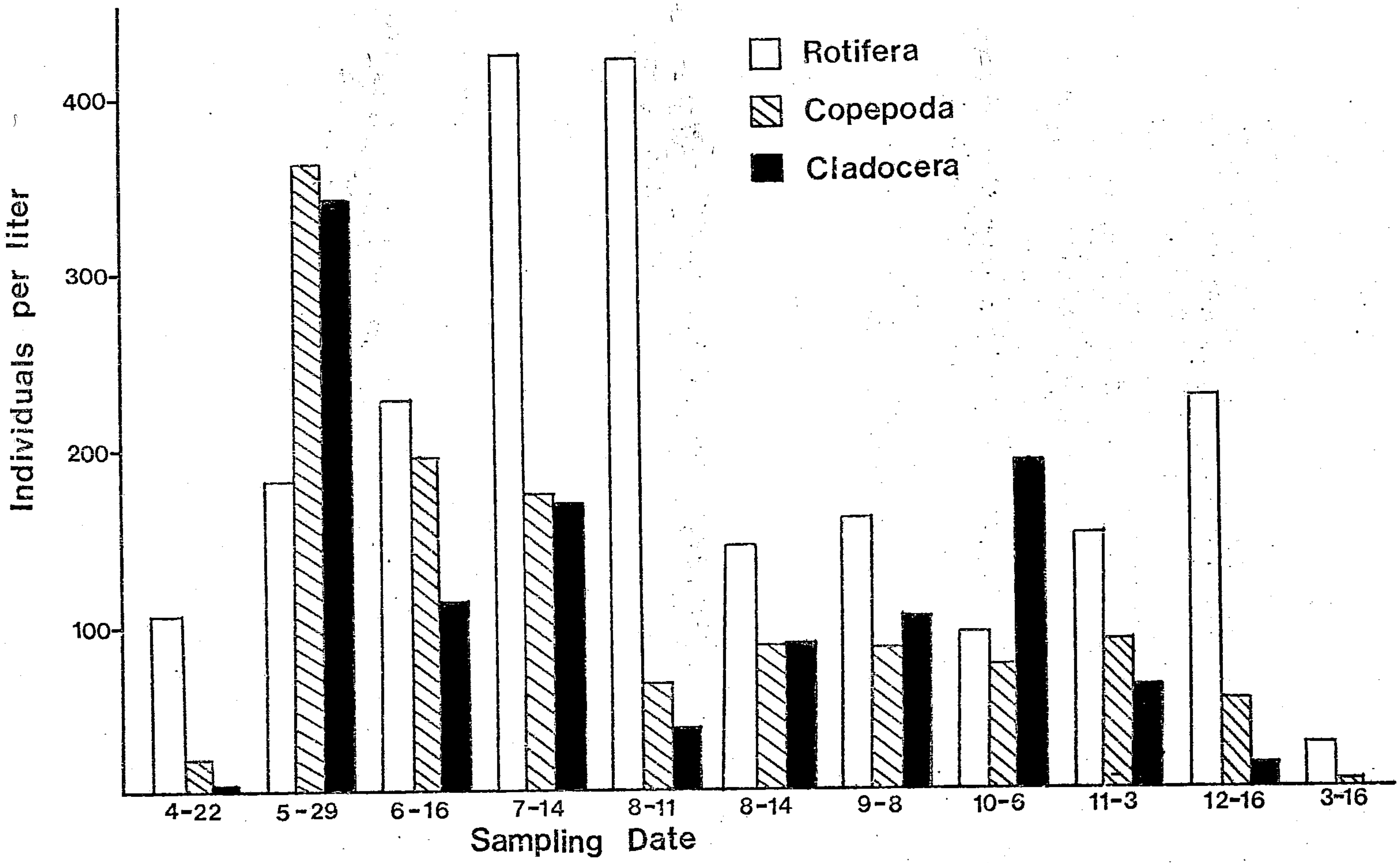

Figure 3. Mean number of rotifers, copepods (including nauplii), and cladocerans, Locust Point, Lake Erie, April 22, 1975-March 16, 1976.

Table 14. Mean clutch size (eggs per ovigerous female) for five crustacean zooplankters, Locust Point, Lake Erie, May 29-November 3, 1975. Each mean was computed from at least 25 ovigerous copepods or at least 50 ovigerous cladocerans.

| Sampling Date | 5-29 | 6-16 | 7-14 | 8-11 | 8-14 | 9-8 | 10-6 | 11-3 |
|---|---|---|---|---|---|---|---|---|
| *Cyclops bicuspidatus thomasii* | 70 | 29 | | | | | | |
| *C. vernalis* | 94 | 85 | 48 | | | | | |
| *Diaptomus siciloides* | 15.6 | 26.0 | 21.6 | 21.8 | | 14.3 | 15.8 | |
| *Daphnia retrocurva* | 3.0 | 7.4 | 2.1 | 2.2 | 2.4 | 2.4 | 2.1 | |
| *Eubosmina coregoni* | 2.0 | 3.6 | 1.4 | 1.5 | 2.0 | 1.7 | 2.4 | 1.8 |

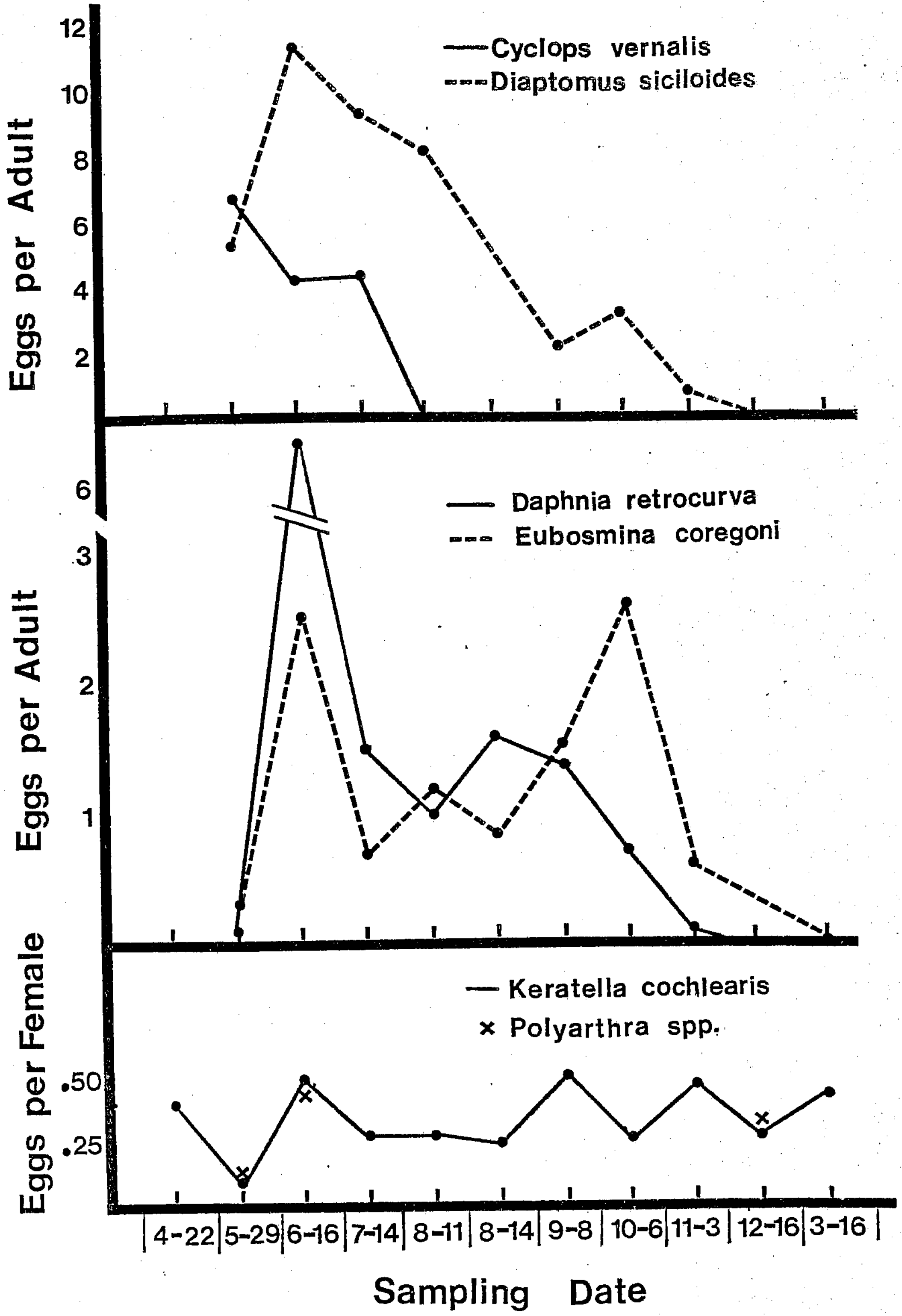

Figure 4. Eggs per adult crustacean zooplankter and eggs per female rotifer, Locust Point, Lake Erie, April 22, 1975-March 16, 1976.

autumn.

Since immature and adult rotifers could not be differentiated, the rotifer egg ratio is expressed as "eggs per female" rather than "eggs per adult." Unlike crustaceans, rotifer reproduction continued year around. When both loose and attached Polyarthra spp. eggs were counted the Keratella cochlearis and Polyarthra spp. egg ratios were nearly identical (Fig. 4).

Potential population doubling times were calculated according to equation 6. All calanoid nauplii and Diaptomus copepodites were counted as Diaptomus siciloides. Potential population doubling time (in days) was shortest on June 16 for all 5 zooplankton taxa (Table 15). Potential population doubling times for Keratella cochlearis, Daphnia retrocurva, and Eubosmina coregoni remained very short throughout the summer and increased in late autumn.

Brood sizes appeared to show a simple linear relationship to body length in Cladocera and copepods. Both the intercept and slope of linear regressions of egg numbers versus body length for ovigerous Daphnia retrocurva varied over time (Fig. 5). Body length and clutch size were most closely correlated when increases in length resulted in relatively large increases in clutch size (Table 16).

Generally, different measures of reproduction showed similar patterns. With the exception of cyclopoid copepods, reproduction was depressed on May 29, very high on June 16,

Table 15. Potential population doubling times (PPDT) in days for five zooplankters, Locust Point, Lake Erie, April 22, 1975-March 16, 1976. Calculated from equation 6:

$$\mathrm{PPDT} = \frac{0.693}{b}$$

where b is the instaneous birth rate from equation 3.

| Water Temperature °C | 7 | 20 | 21 | 23 | 24 | 24 | 21 | 13 | 10 | 5 | 5 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Sampling Date | 4-22 | 5-29 | 6-16 | 7-14 | 8-11 | 8-14 | 9-8 | 10-6 | 11-3 | 12-16 | 3-16 |
| *Cyclops* spp. | 14.2 | 5.2 | 1.7 | 3.4 | | | | | | | |
| *Diaptomus siciloides* | | 2.7 | 1.3 | 2.3 | 4.7 | | 6.7 | 138.6 | | | |
| *Daphnia retrocurva* | | 90.1 | 1.1 | 3.6 | 2.2 | 2.4 | 2.0 | 9.9 | 46.5 | | |
| *Eubosmina coregoni* | | 7.4 | 0.9 | 1.9 | 1.8 | 2.3 | 1.4 | 1.9 | 11.2 | 30.0 | |
| *Keratella cochlearis* | 7.5 | 8.2 | 1.5 | 2.3 | 2.0 | 2.2 | 1.5 | 5.0 | 11.0 | 13.6 | 9.0 |

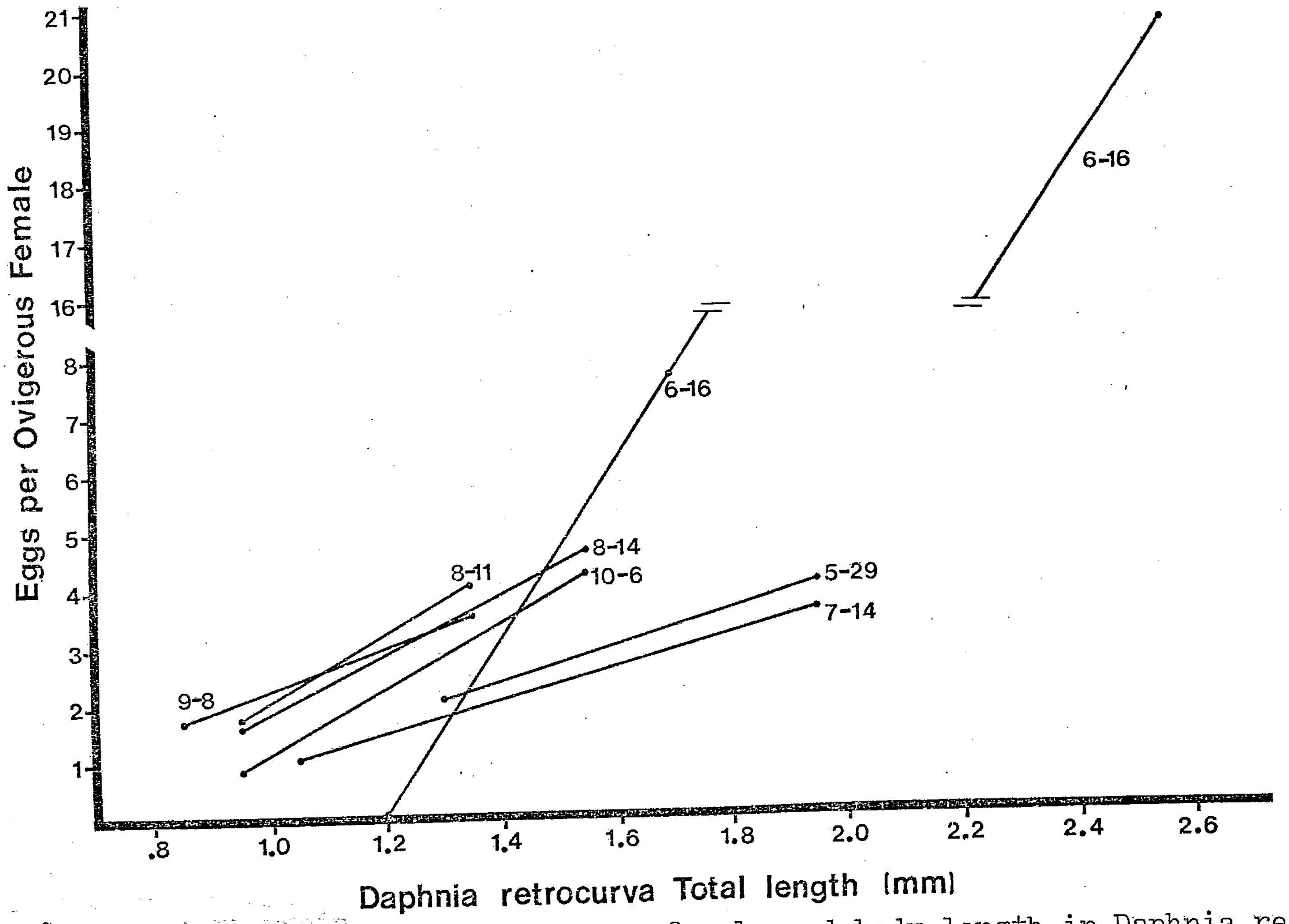

Figure 5. Relationship between eggs per female and body length in *Daphnia retrocurva*, Locust Point, Lake Erie, May 29-October 6, 1975. Linear regression equations (Table 16) were plotted over size range of ovigerous females for each sampling date.

Table 16. Eggs per female versus body length linear regression equations for *Daphnia retrocurva*, Locust Point, Lake Erie, May 29-October 6, 1975. Y = mx + b, where Y is eggs per female, x is body length in mm, m is slope, and b is the Y intercept.

| Sampling Date | Number Measured | Slope m | Intercept b | Correlation Coefficient r | Mean Clutch Size | Mean Length (mm) |
|---|---|---|---|---|---|---|
| 6-16 | 52 | 15.28 | -18.33 | 0.87 | 7.4 | 1.69 |
| 8-11 | 50 | 6.19 | -4.30 | 0.65 | 2.2 | 1.05 |
| 10-6 | 100 | 5.65 | -4.50 | 0.69 | 2.1 | 1.16 |
| 8-14 | 50 | 5.06 | -3.16 | 0.62 | 2.4 | 1.10 |
| 9-8 | 67 | 3.58 | -1.30 | 0.50 | 2.4 | 1.04 |
| 5-29 | 50 | 2.99 | -1.67 | 0.39 | 3.0 | 1.56 |
| 7-14 | 47 | 2.81 | -1.84 | 0.49 | 2.1 | 1.40 |

and intermediate during the summer and early autumn.

## Crustacean Zooplankton Size-Frequency Distributions

The size-frequency distribution of a population depends on both the growth rate of individuals and the population age structure. The *Daphnia retrocurva* in spring and early summer samples were much larger than those collected later in the year at the same water temperatures (Fig. 6). In the May, June, and July samples *D. retrocurva* neonates were 0.65 mm long (midpoint of the 0.60 to 0.70 mm size interval) and primaparous adults were 1.35 mm, 1.35 mm, and 1.25 mm in length respectively (Table 17). From August through November 0.55 mm neonates matured at 0.95 mm in length. Other cladocerans exhibited only small changes in the lengths of neonates and primapara (Table 17).

*Cyclops* adults and C1 copepodites decreased in length during the spring and summer and increased in length during the fall. The decrease in mean length reflected, in part, changes in the sex ratio favoring the smaller-sized males. The percentage of females in the May 29 population, 44%, was not significantly different from the expected value of 50% (chi square test, p  0.30). The percentage of females decreased to 30% on June 16, 20% on July 14, and 13% on August 11, all significantly different from 50% (chi square test, p  0.01). *Diaptomus siciloides* exhibited only small seasonal changes in the lengths of adults, spring and fall adults

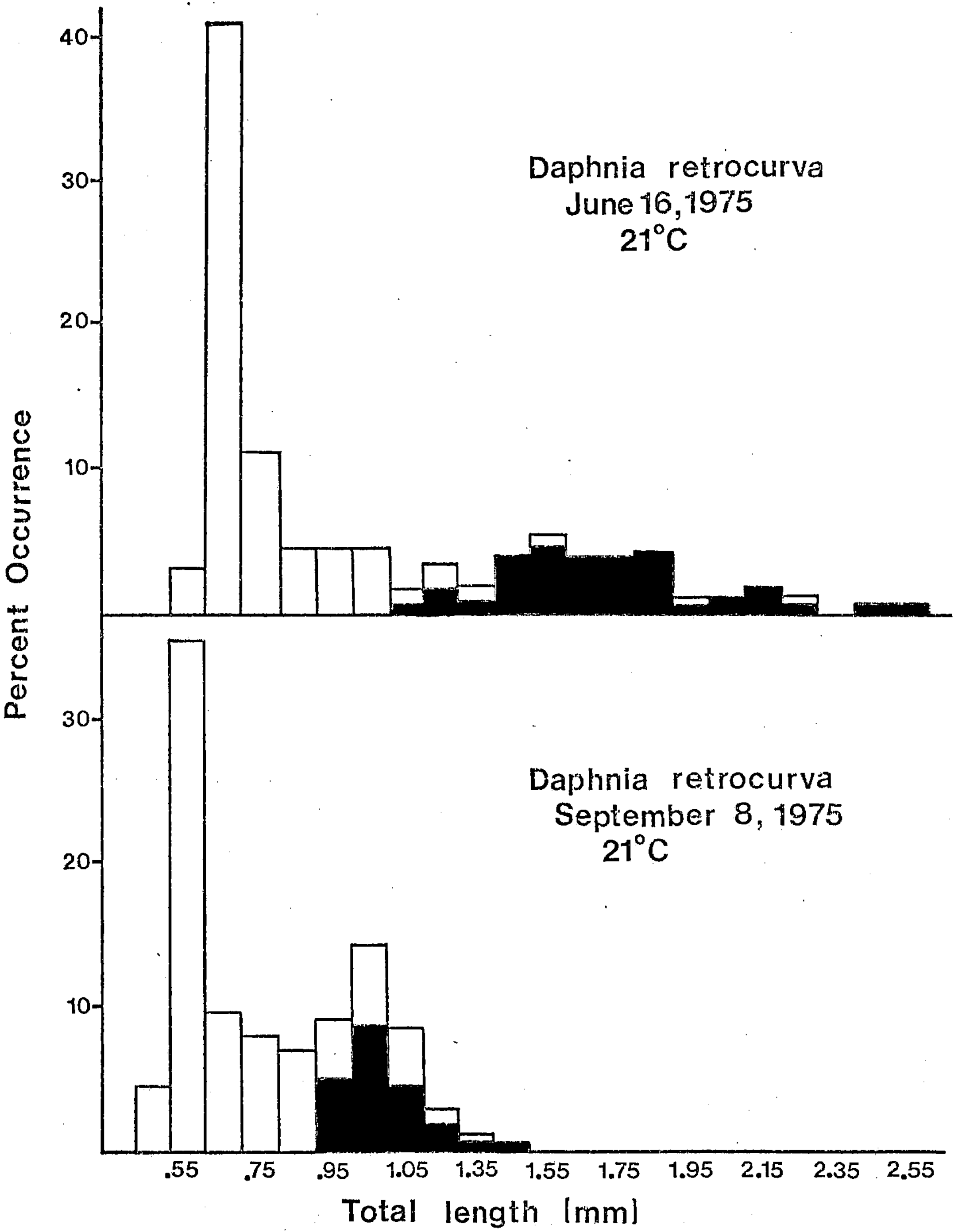

Figure 6. Population length-frequency distributions of *Daphnia retrocurva* from 21°C water on June 16 and September 8, 1975, Locust Point, Lake Erie. Lengths are interval midpoints in mm. Shaded areas indicate ovigerous females.

Table 17. Growth increments of juvenile cladocerans and copepodite copepods, Locust Point, Lake Erie, April 22-November 3, 1975. The first number is the length (mm) of neonate cladocerans or C1 copepodites. The second number is the length (mm) of primaparous cladocerans or copepod adults.

| Sampling Date | *Daphnia retrocurva* | *Eubosmina coregoni* | *Bosmina longirostris* | *Chydorus sphaericus* | *Diaptomus siciloides* | *Cyclops* spp. |
|---|---|---|---|---|---|---|
| 4-22 | .45- | | | | | .38-.97 |
| 5-29 | .65-1.35 | .275-.385 | .225-.305 | .225-.285 | .40-1.08 | .35-.97 |
| 6-16 | .65-1.35 | .305-.425 | .245-.345 | .225-.285 | .40-1.08 | .35-.97 |
| 7-14 | .65-1.25 | | .225-.305 | | .40-1.04 | .33-.77 |
| 8-11 | .55-0.95 | .285-.385 | | .205-.265 | .40-1.04 | .33-.74 |
| 8-14 | .55-0.95 | .285-.385 | | .205-.265 | | |
| 9-8 | .55-0.95 | .285-.365 | | .205-265 | .40-1.03 | .35-.82 |
| 10-6 | .55-0.95 | .285-.365 | .245-.345 | .205-.285 | .40-1.10 | .37-.87 |
| 11-3 | .55-0.95 | .285-.365 | .245-.345 | | .40-1.11 | .38-.88 |

were slightly larger than those from summer generations.

As size intervals were used to determine length, it was not possible to calculate confidence intervals for the lengths of C1 copepodites, and neonate and primaparous cladocerans. The 95% confidence interval for the mean lengths of adult copepods was always ± 0.04 mm or less.

Since weight of zooplankters increases exponentially with length (Table 9), a change in length results in a relatively larger change in weight. The mean weight per Daphnia retrocurva ranged from 1.1 µg in the April 22 samples to 15.2 µg in the June 16 samples (Table 18). D. retrocurva from the April 22 samples consisted entirely of individuals between 0.40 and 0.80 mm in length. The absence of adults and the presence of developing ephippia suggest that these smallest Daphnia of the year had just hatched from resting eggs. The May 29 D. retrocurva population was also atypical in that only 10% of the population were adults. During the remainder of the year the percentage of adult D. retrocurva ranged from 29% in the June 16 samples to 62% on October 6. The mean weights for other Cladocera and Cyclops spp. also varied considerably throughout the year. (Table 18).

Generally, the weights of crustaceans tended to be high on June 16 due to the presence of large individuals and low during the summer when the maximum size was smaller. Mean weights increased during the fall when decreasing reproductive rates resulted in an increase in the percentage of

Table 18. Mean dry weight (µg) per crustacean zooplankter, Locust Point, Lake Erie, April 22-December 16, 1975. Calculations were based on length-frequency distributions for each taxon on each sampling date and the equations in Table 9. The mean dry weights for Cladocera and adult copepods include the weight of eggs.

| Sampling Date | *Bosmina longirostris* | *Chydorus sphaericus* | *Daphnia retrocurva* | *Eubosmina coregoni* | *Cyclops* spp. |  | *Diaptomus* spp. |  |
|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | copepodites | adults | copepodites | adults |
| 4-22 | 0.94 |  | 1.1 |  | 1.8 | 5.1 | 2.0 | 9.3 |
| 5-29 | 0.57 | 0.87 | 4.6 | 1.2 | 1.9 | 5.3 | 2.9 | 9.5 |
| 6-16 | 0.96 | 0.90 | 15.2 | 2.5 | 2.5 | 5.1 | 3.3 | 10.8 |
| 7-14 | 0.76 |  | 8.6 |  | 1.8 | 3.4 | 2.0 | 9.8 |
| 8-11 |  | 0.49 | 4.7 | 1.5 | 1.3 | 2.9 | 2.2 | 9.5 |
| 8-14 |  | 0.56 | 3.6 | 1.7 | 1.3 | 2.9 | 2.2 | 9.5 |
| 9-8 |  | 0.79 | 3.4 | 1.6 | 1.5 | 3.5 | 2.6 | 7.9 |
| 10-6 |  | 0.65 | 5.6 | 2.2 | 1.8 | 4.0 | 3.2 | 9.4 |
| 11-3 | 1.17 |  | 6.5 | 1.6 | 1.3 | 4.1 | 2.3 | 9.0 |
| 12-16 |  |  |  |  | 1.8 | 4.7 | 2.3 |  |

mature individuals and the mean size per adult also increased.

## Zooplankton Production

Total annual zooplankton production at Locust Point, Lake Erie was 29.6 $g \cdot m^{-3}$ or 99.4 $g \cdot m^{-2}$. Converting to units of energy (1 g dry weight = 5.5 kcal, after Winberg et al., 1972), annual zooplankton production was about 160 $kcal \cdot m^{-3}$ or 550 $kcal \cdot m^{-2}$. Of total annual production, 77% occurred between April 22 and August 11, 1975, and only 8% from November 3, 1975 through April 22, 1976. Production during the "vegetative period" from April 22 through November 3, 1975 was 506 $kcal \cdot m^{-2}$.

Zooplankton daily production estimates ranged from 0.67 $mg \cdot m^{-3} \cdot day^{-1}$ (2.47 $mg \cdot m^{-2} \cdot day^{-1}$) on March 16, 1976 to 383 $mg \cdot m^{-3} \cdot day^{-1}$ (1202 $mg \cdot m^{-2} \cdot day^{-1}$) on July 14, 1975 (Table 19). The sum of the coefficients of variation based on production at each station on each sampling date was slightly lower for the production estimates per $meter^2$ than for the estimates calculated per $meter^3$.

The between station variation in zooplankton production is illustrated through a comparison of mean production at the two inshore stations, the two offshore stations, and the mean of all ten stations. On May 29, production per $meter^2$ was over three times higher at the offshore stations than at the inshore stations (Fig. 7). On July 14, the opposite

Table 19. Mean zooplankton production, 95% confidence intervals of the mean and coefficients of variation, all computed from production estimates for each station, Locust Point, Lake Erie, April 22, 1975-March 16, 1976.

| Sampling Date | Number of Stations | Mean Production $mg \cdot m^{-2} \cdot day^{-1}$ | 95% C.I. of Mean ± | Coefficient of Variation | Mean Production $mg \cdot m^{-2} \cdot day^{-1}$ | 95% C.I. of Mean ± | Coefficient of Variation |
|---|---|---|---|---|---|---|---|
| 4-22 | 10 | 4.80 | 1.04 | 0.10 | 15.11 | 2.62 | 0.08 |
| 5-29 | 10 | 256.6 | 63.3 | 0.11 | 887.5 | 337.5 | 0.17 |
| 6-16 | 10 | 201.4 | 66.7 | 0.15 | 661.7 | 124.0 | 0.08 |
| 7-14 | 10 | 382.6 | 127.6 | 0.15 | 1202.4 | 257.9 | 0.09 |
| 8-11 | 10 | 60.5 | 10.9 | 0.08 | 206.6 | 30.8 | 0.07 |
| 8-14 | 3 | 68.1 | 23.7 | 0.08 | 290.5 | 31.8 | 0.03 |
| 9-8 | 10 | 89.0 | 16.5 | 0.08 | 297.0 | 55.6 | 0.08 |
| 10-6 | 10 | 52.6 | 10.4 | 0.09 | 174.9 | 29.9 | 0.08 |
| 11-3 | 10 | 21.0 | 4.3 | 0.09 | 66.1 | 3.5 | 0.02 |
| 12-16 | 3 | 7.02 | 3.8 | 0.13 | 21.3 | 18.1 | 0.20 |
| 3-16 | 3 | 0.67 | 0.13 | 0.04 | 2.47 | 1.42 | 0.13 |
|  |  |  |  | 1.10 |  |  | 0.93 |

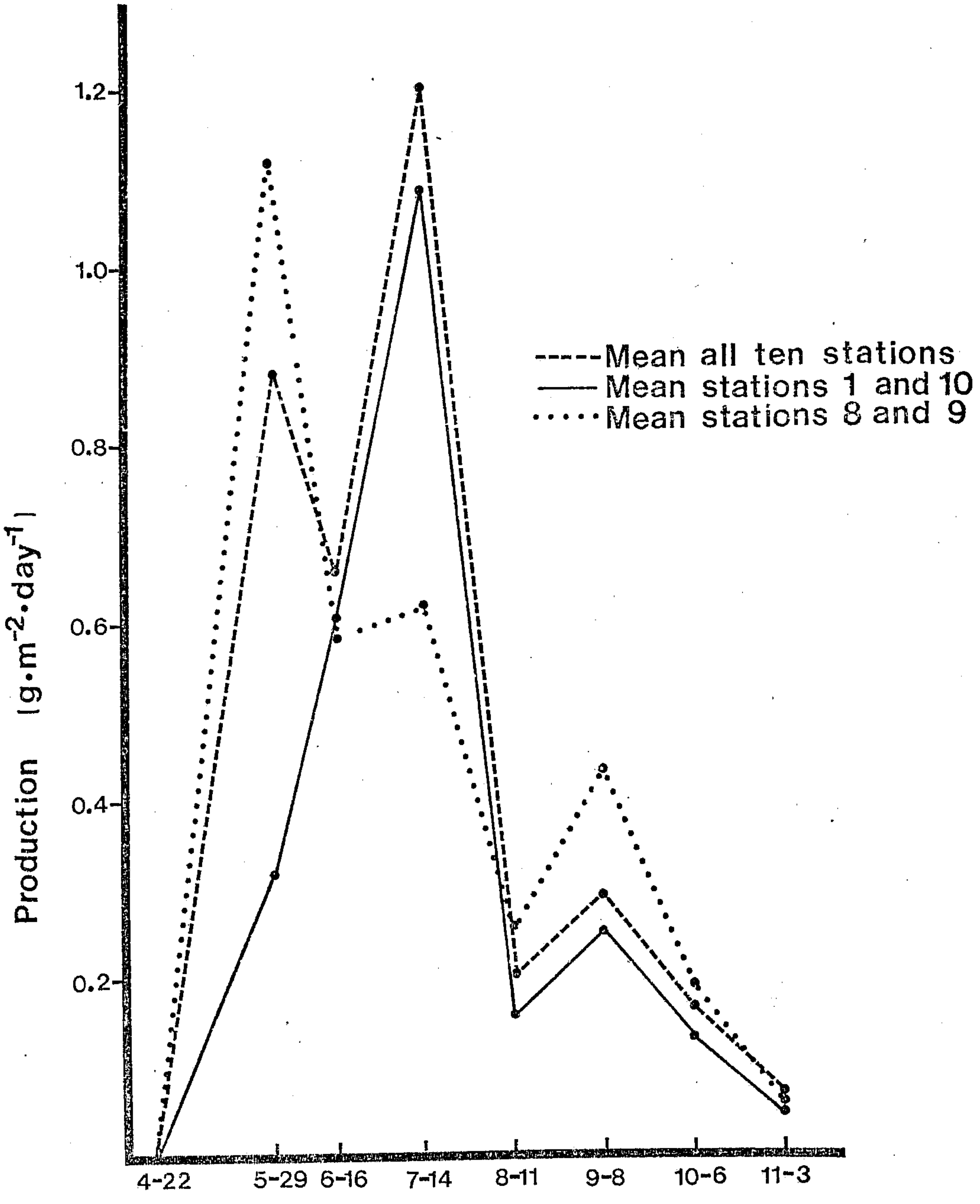

Figure 7. Comparison of zooplankton productivity per $m^2$ at inshore stations 1 and 10 (mean depth 2.1 m), offshore stations 8 and 9 (mean depth 4.7 m), and the mean of all ten stations (mean depth 3.4 m), Locust Point, Lake Erie, April 22-November 3, 1975.

occurred; overall mean production was highest and inshore production was about twice that of offshore waters. On other sampling dates the differences between inshore and offshore zooplankton productivity per meter$^2$ were much less.

Crustacean species composition, relative abundance, and length-frequency distributions showed little variation between stations. Typically, samples from stations with high zooplankton productivity contained greater numbers of each common species than samples from stations with low zooplankton productivity. The relative abundance of rotifers was more variable. Single rotifer species often showed a patchy distribution, usually with greater relative abundance at the inshore stations.

Daphnia retrocurva was the major producer during the spring-summer period of high zooplankton productivity (Fig. 8). The greatest relative change in zooplankton community production between two sampling dates occurred between April 22, and May 29, 1975, when water temperature rose from 7°C to 20°C and zooplankton productivity increased 50 fold. D. retrocurva accounted for 68% of the total zooplankton production on May 29 (Fig. 8). A decline in D. retrocurva production from 263 $mg \cdot m^{-3} \cdot day^{-1}$ to 5.5 $mg \cdot m^{-3} \cdot day^{-1}$ accounted for 80% of the precipitous decline in zooplankton production between July 14 and August 11, 1975. During the autumn, other Cladocera, and especially Eubosmina coregoni were important as producers. Rotifers

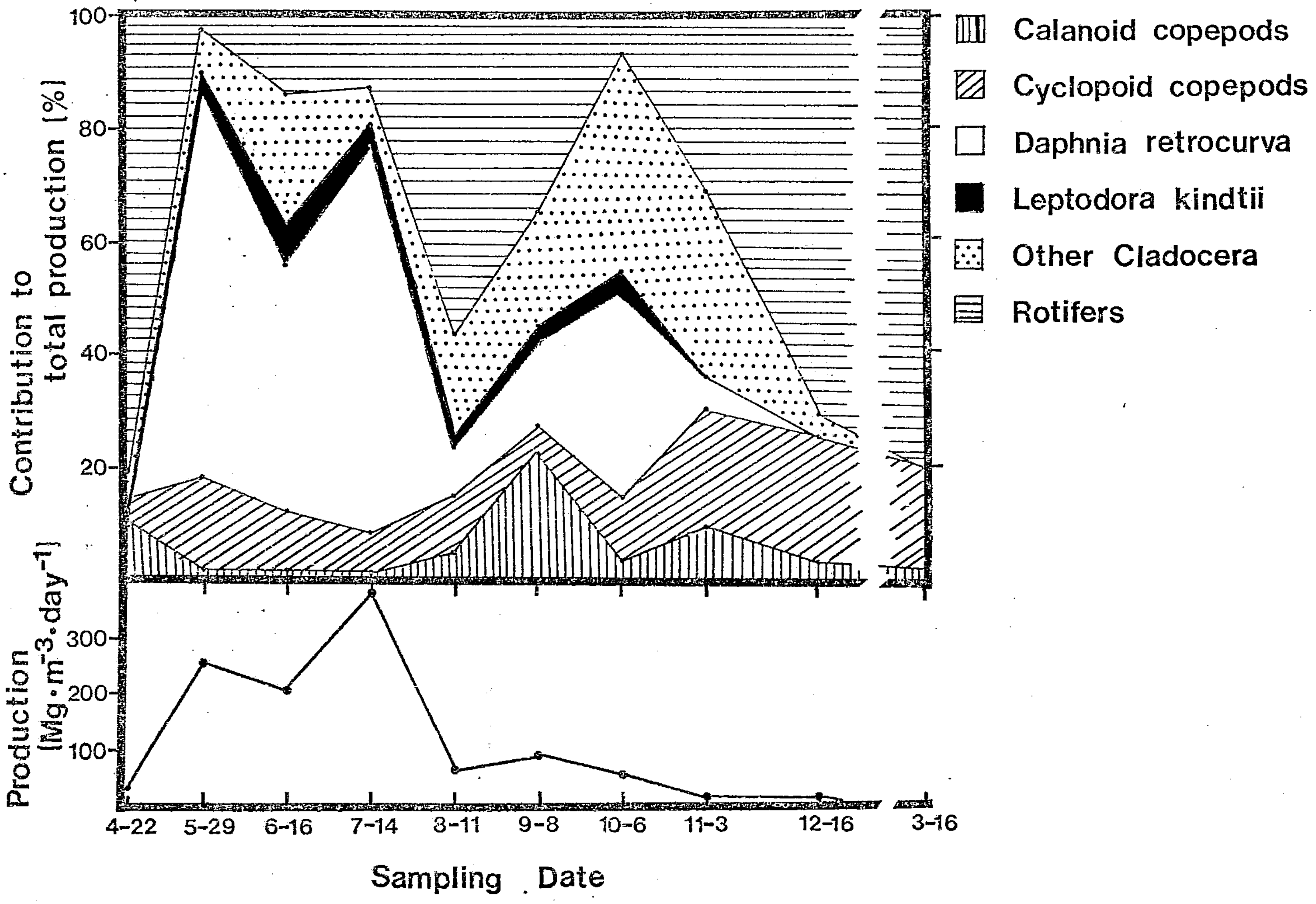

Figure 8. Relative contribution of each taxon to zooplankton production, Locust Point, Lake Erie, April 22, 1975- March 16, 1976.

contributed over 50% to total zooplankton production during the midsummer and winter periods of low zooplankton production. Rotifer production reached an annual maximum on July 14 but only amounted to 14% of zooplankton production on that date.

On an annual basis, Daphnia retrocurva accounted for slightly more than one half of total zooplankton production. The remaining 49% came from: other Cladocera, 18.1%; rotifers, 16.2%; cyclopoid copepods, 10.8%, and calanoid copepods, 3.9% (Table 20). The production of carnivores, that is: cyclopoid copepods (excluding nauplii), Leptodora kindtii, and Asplanchna priodonta, was 9.1% of the annual zooplankton total.

The relationship between zooplankton biomass and production is depicted graphically in Figure 9. The ratio of daily production to biomass (P/B) is a measure of the biomass turnover rate (days$^{-1}$). The inverse, B/P, is the biomass turnover time in days. P/B ratios for the entire zooplankton biomass ranged from 0.05 (turnover time 19.5 days) on March 16, 1976, time of coldest water temperature, to 0.29 (turnover time 3.5 days) on August 11, time of the warmest water temperature. The annual P/B (annual production/ mean daily biomass per meter$^3$) was 54.2. For the "vegetative period" of 196 days from April 22 through November 3, 1975, the P/B was 34.7.

During the period from May 29 through September 8 when

Table 20. The relative contribution of each taxon to annual zooplankton production at Locust Point, Lake Erie, based on sampling from April 22, 1975-March 16, 1976.

| | Annual Production mg.m-3 | % of Annual Total |
|---|---|---|
| COPEPODA | 4347 | 14.7 |
| Calanoid copepods | 1161 | 3.9 |
| Cyclopoid copepods | 3186 | 10.8 |
| CLADOCERA | 20418 | 69.1 |
| *Bosmina longirostris* | 673 | 2.3 |
| *Chydorus sphaericus* | 411 | 1.4 |
| *Daphnia galeata mendotae* | 663 | 2.2 |
| *D. retrocurva* | 15080 | 51.0 |
| *Diaphanosoma leuchtenbergianum* | 288 | 1.0 |
| *Eubosmina coregoni* | 2317 | 7.8 |
| *Leptodora kindtii* | 986 | 3.3 |
| ROTIFERA | 4795 | 16.2 |
| *Asplanchna priodonta* | 395 | 1.3 |
| *Keratella cochlearis* | 388 | 1.3 |
| *Polyarthra* spp. | 2287 | 7.7 |
| *Synchaeta* spp. | 644 | 2.2 |
| Other rotifers | 1081 | 3.7 |
| TOTAL | 29560 | 100.0 |

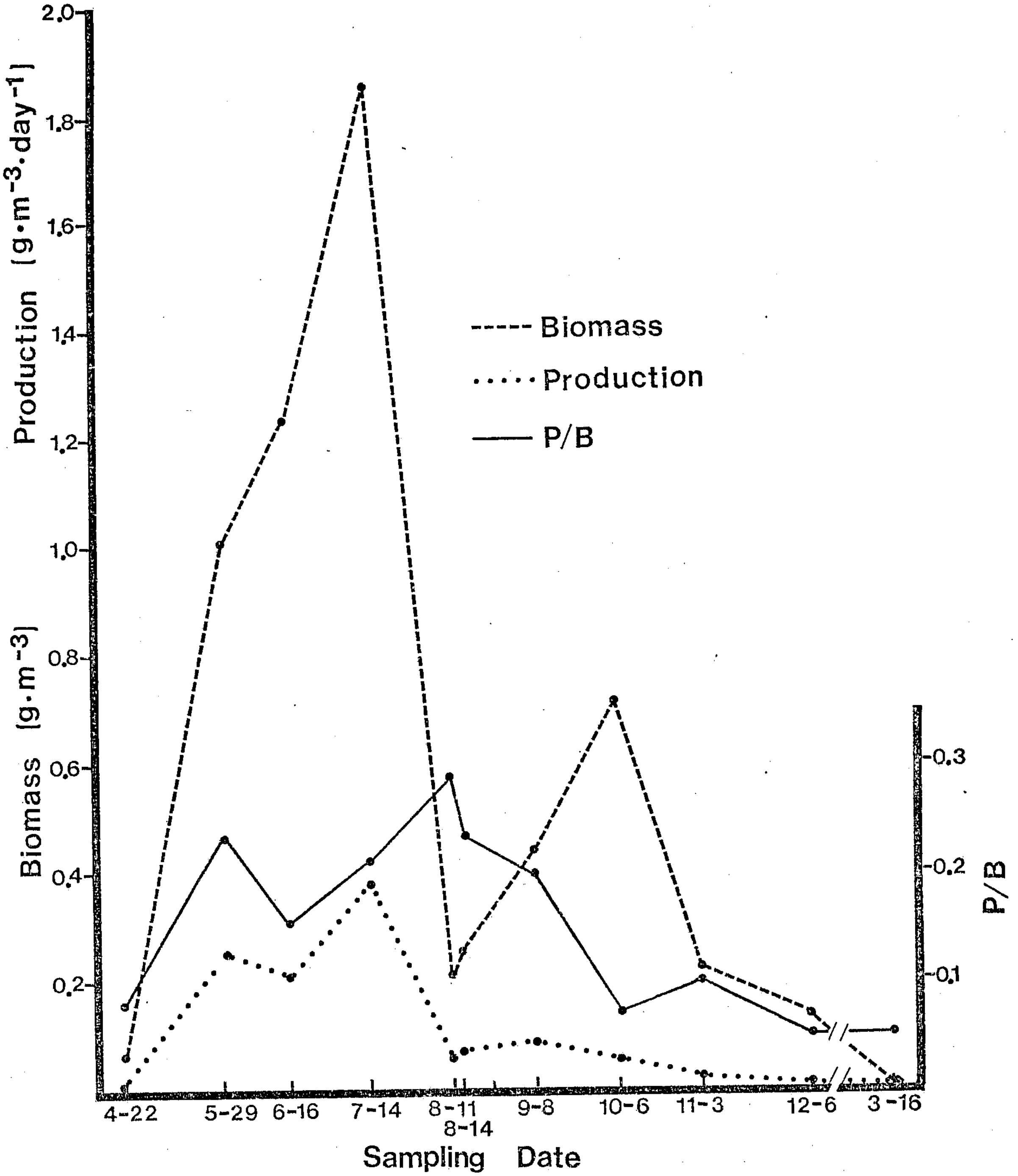

Figure 9. Zooplankton biomass, production, and daily P/B ratios, Locust Point, Lake Erie, April 22, 1975-March 16, 1976.

the water temperature varied only from 20°C to 24°C, the daily P/B ratio for the entire zooplankton biomass ranged from 0.16 on June 16 to 0.29 on August 11. Changes in species relative abundance had a direct effect on the zooplankton community P/B ratio. The June 16 biomass consisted primarily of large *Daphnia*, *Eubosmina*, *Leptodora*, and *Cyclops*, while rapidly reproducing rotifers comprised about one half of the biomass on August 11, helping to generate the high P/B ratio on that date.

Mean P/B ratios were calculated for May 29 through September 8 based on mean daily biomass and mean daily production for each taxon (Table 21). The turnover rate was highest for rotifers, intermediate for Cladocera with the exception of *Leptodora*, and lowest for copepods and *Leptodora*. Despite their short developement times (Table 4), *Chydorus sphaericus* and *Bosmina longirostris* had longer turnover times than *Daphnia retrocurva*.

Extremes in length-frequency distributions had major effects on the P/B ratios for *Daphnia retrocurva*. On May 29, when 90% of the *D. retrocurva* population were juveniles and the average weight per individual was only 4.6 µg (Table 18), the P/B ratio was 0.31. On June 16, when very large individuals comprised most of the biomass (mean weight 15.2 µg), the *D. retrocurva* P/B was 0.15. The growth increment of a large adult is a much smaller percentage of the body weight than the growth increment of a

Table 21. Mean daily production, biomass, and P/B ratios for each zooplankton taxon, Locust Point, Lake Erie, May 29-September 8, 1975. Since the birth rate B of a single rotifer, *Keratella cochlearis*, was used to calculate the turnover rate of all rotifers, only a single set of values are reported for rotifers in this table.

| | Mean Daily Production (P) $mg \cdot m^{-3} \cdot day^{-1}$ | Mean Daily Biomass (B) $mg \cdot m^{-3}$ | P/B $days^{-1}$ | B/P days |
|---|---|---|---|---|
| COPEPODA | 25.1 | 197.0 | 0.13 | 7.8 |
| Calanoid copepods | 6.4 | 44.2 | 0.14 | 6.9 |
| Cyclopoid copepods | 18.7 | 152.8 | 0.12 | 8.2 |
| CLADOCERA | 145.0 | 707.9 | 0.20 | 4.9 |
| *Bosmina longirostris* | 2.3 | 11.7 | 0.19 | 5.2 |
| *Chydorus sphaericus* | 1.9 | 9.8 | 0.19 | 5.3 |
| *Daphnia galeata mendotae* | 6.3 | 26.7 | 0.23 | 4.3 |
| *D. retrocurva* | 109.2 | 532.4 | 0.21 | 4.9 |
| *Diaphanosoma leuchtenbergianum* | 1.6 | 6.2 | 0.26 | 3.9 |
| *Eubosmina coregoni* | 16.0 | 57.2 | 0.28 | 3.6 |
| *Leptodora kindtii* | 7.7 | 63.9 | 0.12 | 8.3 |
| ROTIFERA | 32.5 | 98.7 | 0.33 | 3.0 |
| TOTAL | 202.6 | 1004.1 | 0.20 | 5.0 |

juvenile.

The number of crustacean zooplankters, exclusive of nauplii, has frequently been used in Great Lake studies as a measure of zooplankton standing crop. The May 29 peak in crustacean numbers was largely due to the small cladoceran *Bosmina longirostris* (Fig. 10). On June 16 crustacean numbers were less than one half those on May 29, however, zooplankton biomass was higher on June 16, primarily due to the high mean weight of *Daphnia retrocurva* on that date (Table 18). Numbers of crustaceans were almost equal in the July 14 and October 6 samples, however, zooplankton biomass and production were, respectively, 2.6 and 7.3 times higher on July 14.

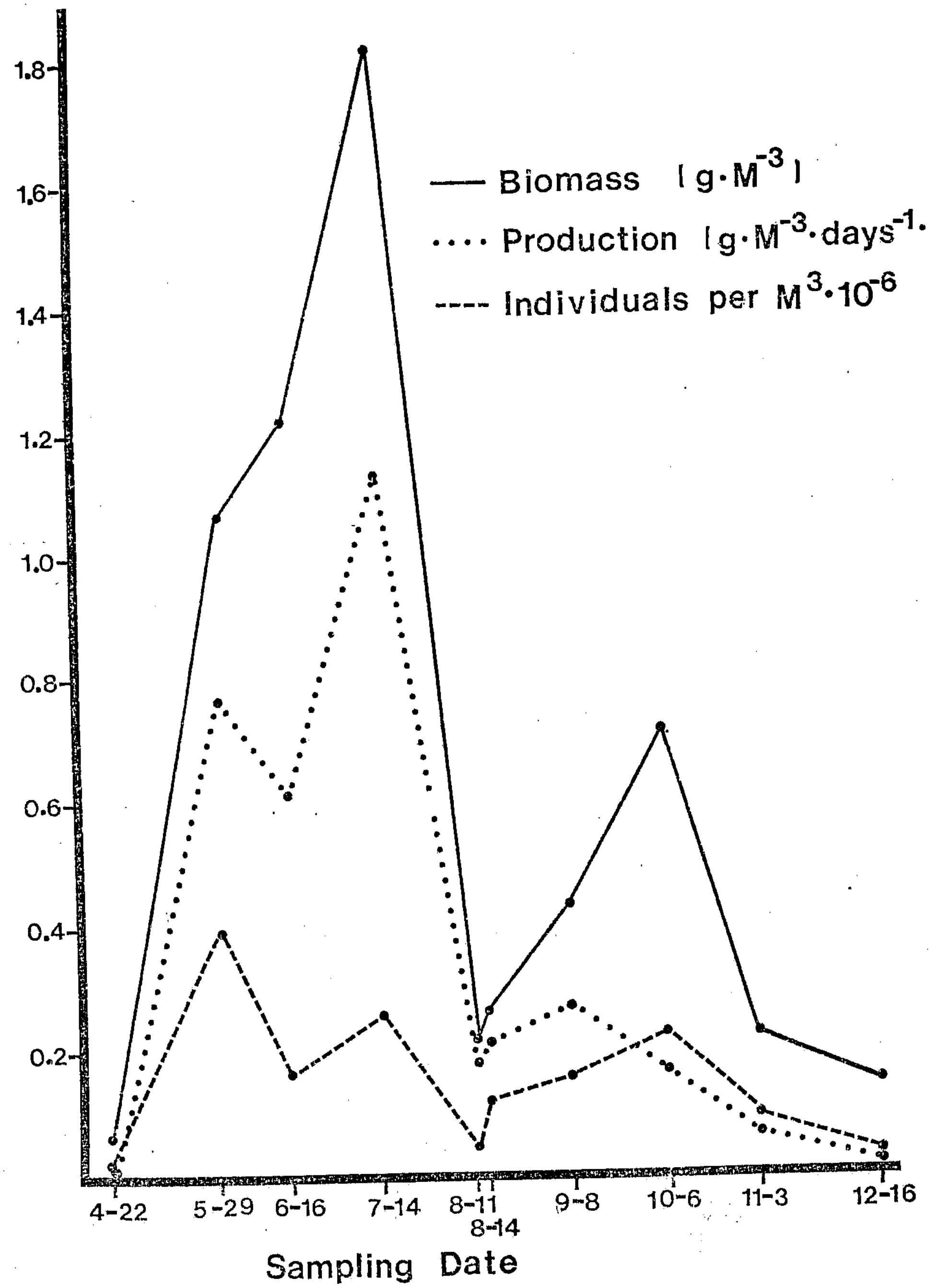

Figure 10. Comparison of zooplankton biomass, zooplankton production, and crustacean numbers exclusive of nauplii, Locust Point, Lake Erie, April 22-December 16, 1975. Values for March 16, 1976 were too low to be differentiated from 0 on a graph of this size and scale.

# DISCUSSION

Temperature and food are the major factors governing the magnitude of zooplankton productivity. Temperature directly affects the rate of hatching and molting (Table 4). Food has a marked affect on female fertility (Ingle et al., 1937; Richman, 1958; Hall, 1964; Edmondson et al., 1962). Although predation by fish (Brooks and Dodson, 1965) and invertebrates (Dodson, 1970; Sprules, 1972) has a major influence on zooplankton species composition and population dynamics, field experiments suggest that predation has little direct effect on total zooplankton community productivity (Hall et al., 1970; Hillbricht-Ilkowska and Welenska, 1973).

One way of describing the magnitude of zooplankton community production at Locust Point, Lake Erie is through comparisons with other lakes with similar or different trophic conditions and annual temperature regimes. Until recently there had been few attempts to measure zooplankton community production. This was due primarily to a lack of methods and techniques for analyzing zooplankton production and the difficulty in obtaining the necessary parameters to estimate the production of a large number of species. The International Biological Program (IBP) encouraged the development of methods for estimating secondary productivity in freshwater ecosystems (Edmondson and Winberg, 1971; Winberg, 1971) and stimulated many studies on the production of one or more trophic levels in lakes. Each study listed in Table 22 used similar methods of calculating zooplankton production. Even major errors due to sampling or weight measurements would not change the basic pattern relating water temperature and trophic state to zooplankton productivity.

Zooplankton production at Locust Point, Lake Erie from April 22 through November 3, 1975 was very high, but only about one half that of a Polish Pond, Lake Warniak, during a comparable period of time. Lake Batorin, Lake Mikolajskie, and the Western Basin of Lake Erie have all been described as "eutrophic," largely on the basis of blue-green algae blooms during the summer months. Zooplankton production in Lake Erie at Locust Point was an order of magnitude higher than in cooler Lake Batorin, but not much different from zooplankton production in Lake Mikolajskie. The zooplankton production of Lake Batorin was only a little more than twice that of nearby mesotrophic Lake Norock.

Brylinsky and Mann (1973) analyzed factors governing the productivity of lakes using data compiled from IBP projects throughout the world. They found a linear relationship between herbivorous zooplankton production during a "growing season" and phytoplankton production during the same period. In 20 lakes "growing season" energy transfer efficiency from gross primary production to zooplankton herbivore production (zooplankton herbivore production/gross

Table 22. Comparison of zooplankton production in various lakes.

| Lake | Source | Mean Depth (m) | Maximum Water Temperature °C | Zooplankton Production $kcal \cdot m^{-2}$ | Time Period | Time Period P/B |
|---|---|---|---|---|---|---|
| Char Lake | (1) | 10.2 | 4 | 1.45 | Whole Year | - |
| Mirror Lake | (2) | - | 18 | 23.8 | "ice-free" | 10.1 |
| Lake Noroch | (3) | 9.0 | 15 | 19.5 | May 1-Oct.31 | 18.4 |
| Lake Myastro | (3) | 5.4 | 15 | 44.6 | May 1-Oct.31 | 16.2 |
| Lake Batorin | (3) | 3.0 | 15 | 53.8 | May 1-Oct.31 | 19.1 |
| Lake Mikolajskie | (4) | 11.0 | - | 465 | May 1-Oct.31 | 18.9 |
| Locust Pt., Lake Erie | (5) | 3.2 | 24 | 506 | April 22-Nov.3 | 34.7 |
| Lake Warniak | (6) | 1.5 | - | 971 | May 1-Oct.31 | 36.1 |

(1) Oligotrophic arctic lake, IBP project (Rigler and MacCallum, 1974).
(2) Oligotrophic lake in New Hampshire, USA (Makarewicz, 1974).
(3) Three interconnected lakes of different trophic conditions north of Kiev, Russia, IBP project (Winberg et al., 1972).
(4) Eutrophic lake in Poland, IBP project (Kajak et al., 1972).
(5) Present study, Western Basin, Lake Erie, Ohio, USA.
(6) Stocked fish pond in Poland (Hillbricht-Ilkowska and Weglenska, 1973).

It was assumed that 1 g wet weight = 0.1 g dry weight and 1 g dry weight = 5.5 kcal (after Winberg et al., 1972).

primary production) ranged from 2.6% to 21.2% with a mean of 13.7%. Unfortunately only a limited number of primary productivity measurements have been made at Locust Point, so it is not yet possible to compare seasonal zooplankton productivity with primary productivity at Locust Point.

Glooschenko et al. (1974) reported that primary production for the Western Basin of Lake Erie from April through December, 1970 was 310 $gC \cdot m^{-2}$. Assuming that 1 gC is equivalent to 9.4 kcal and gross primary productivity is 125% of $^{14}C$ uptake (Brylinsky and Mann, 1973), gross primary production for the Western Basin of Lake Erie from April through December, 1970 was about 3640 $kcal \cdot m^{-2}$. During nearly the same period of time in 1975 zooplankton herbivore production at Locust Point, Lake Erie was 460 $kcal \cdot m^{-2}$. The calculated energy transfer efficiency is 12.6%, very close to the mean of 13.7% reported by Brylinsky and Mann (1973). The results of these calculations should not be interpreted to indicate actual phytoplankton to zooplankton energy transfer efficiencies. The Western Basin primary production estimate and the Locust Point zooplankton production estimates were based on monthly sampling during different years and from different parts of the Western Basin. The results do indicate that the annual zooplankton production estimate for Locust Point is within the range which should be expected for the Western Basin of Lake Erie.

## Seasonal Changes in Zooplankton Production

The seasonal extremes in zooplankton production at Locust Point, Lake Erie appear to be typical of productive temperate zone lakes. Only 8% of annual zooplankton production for Locust Point, Lake Erie occurred between November 3 and April 22. In Mikolajskie Lake, Poland, about 10% of annual zooplankton production occurred between October 31 and May 1 (Kajak et al., 1972). The winter zooplankton production at Locust Point may have been overestimated since development times for 5°C rather than the actual temperature of 1.5°C were used in calculating zooplankton production for March 16, 1976.

Except for a period of low zooplankton production during August and September, changes in zooplankton community production at Locust Point were well correlated with water temperature (Fig. 9). Since primary productivity in Lake Erie is also highest at high water temperatures during the summer (Glooschenko et al., 1974), little can be said about the relative importance of food and temperature in governing zooplankton productivity. Patalas (1972) reported that crustacean zooplankton numbers in Lake Erie and Lake Ontario were positively correlated with water temperature except for August when crustacean zooplankton numbers in the Western Basin of Lake Erie fell despite an increase in temperature and high chlorophyll *a* concentrations. A sharp decline in crustacean zooplankton numbers and biomass in August at Locust Point, Lake Erie resulted in a sharp decrease in zooplankton production (Fig. 10).

Zooplankton populations at Locust Point, Lake Erie, had the potential for doubling in 1 to 3 days during the summer (Table 15). A study based on monthly sampling can add little to our knowledge of the interactions which affect zooplankton population dynamics and growth increments, thereby controlling the relative contribution of different taxa to total zooplankton production. Research efforts at Locust Point should focus on the population dynamics of Daphnia retrocurva, the dominant zooplankton producer.

A species of the genus Daphnia is often the dominant zooplankton producer in lakes. The results of zooplankton productivity studies are supported by zooplankton grazing experiments. In an in situ examination of grazing in a eutrophic Canadian lake, Haney (1973) found that zooplankton filtered the entire water column in less than 24 hours during periods of high grazing activity in May and June. During those periods Daphnia rosea accounted for 80% of the total zooplankton grazing pressure.

The possibility that predation by fish is a major factor regulating the abundance and size-frequency distributions of Daphnia retrocurva at Locust Point deserves further investigation (Gailbraith, 1967; Pycha and Smith, 1954; Hall, 1971). Wong and Ward (1972) noted that early summer yellow perch fry were unable to swallow the largest Daphnia in a Canadian lake, but that during the late summer the largest Daphnia were the preferred food. Archibald (1975) reported that the size of Daphnia pulex primapara was 1.65 mm in a fishless enclosure and 1.05 mm in the same lake in an enclosure subject to high predation by fish.

## Zooplankton Population Numbers, Biomass, and Productivity

If our goal is to understand the role of zooplankton in food chains we should measure zooplankton grazing, production and mortality rates. Zooplankton standing crop estimates are useful to the extent to which they can be related to the rates of these processes. The production of consumer populations can be divided into three components: population numbers, growth increments, and the time required to complete a growth increment, the development time (equation 1). Measures of standing crop fail to account for the major effect of water temperature on zooplankton metabolism and growth. Estimates of standing crop expressed as numbers of individuals ignore not only the effect of temperature on development times, but also the very large differences in the size of growth increments between different species and between populations of a single species on different dates (Table 18). For example, Glooshenko et al. (1974) attempted to evaluate zooplankton grazing in Lake Erie by relating zooplankton standing crop in numbers of individuals per meter$^3$ to chlorophyll a and pheopigment concentrations. The comparison presented in Figure 10 demonstrates that zooplankton total numbers are a poor estimator of biomass. The mean weight per crustacean zooplankter (excluding nauplii) was about 2 to 3 times greater during June and July than during late summer and autumn. Even if Glooshenko et al. (1974) had accurately assessed zooplankton biomass, they would still have ignored the effect of temperature on zooplankton filtering rates (Burns, 1969) and productivity.

The ratio of production to biomass (P/B) is a measure of the turnover rate of biomass. For a population with a stable age structure, the P/B ratio is theoretically constant under constant environmental conditions. If the P/B ratio for a species or a community were constant, production could be calculated simply by multiplying the biomass by P/B (B x P/B = P). Juday (1943) surmised that the annual "number of turnovers" for zooplankton in Lake Mendotae was 52 and was therefore able to estimate annual zooplankton production by multiplying mean daily biomass by 52. By chance, the annual zooplankton P/B for Locust Point, Lake Erie was 54, very close to Juday's (1943) guess.

The effect of temperature on development times explains the seasonal extremes in the daily P/B ratio at Locust Point, from 0.05 (turnover time 19.5 days) on March 16, 1976 to 0.29 (turnover time 3.5 days) on August 11, 1975. Since development times for 5°C rather than the actual water temperature of 1.5°C were used in calculating zooplankton production for March 16, 1976, the actual turnover time for that date may have been much longer than 20 days.

While the influence of temperature on P/B ratios can be predicted from development times, the range in P/B ratios of 0.16 to 0.29 during the period of relatively constant temperature from May 29 through August 11 (Fig. 9) was unexpected. Changes in species relative abundance, size-frequency distributions, and temperature all affect the P/B ratio. Since the P/B ratio was not constant, even during periods of relatively constant temperature, it should not be used to estimate zooplankton production at Locust Point.

The P/B ratio for zooplankton in a thermally polluted lake was twice as high as in a similar one, not thermally polluted, even though summer water temperatures were only about 6 degrees higher. (Patalas, 1970). The zooplankton P/B ratio of the unheated lake (21.7°C average water temperature) was 0.13, while the heated lake (27°C) had a P/B ratio of 0.26. Since the biomass of each lake was about the same, zooplankton productivity was twice as high in the heated lake. The difference in zooplankton turnover rates between the two lakes was due not only to the direct effect of temperature on development rates, but also to species relative abundance. Copepods, which tend to have low P/B ratios (Patalas, 1970; also see Table 17) accounted for 51% of total zooplankton production in Patalas' unheated lake.

Even though the biomass of copepods was slightly higher in the heated lake, they contributed only 29% to total zooplankton production because of an increase in the relative abundance of fast-growing Daphnia, Diaphanosoma, and Chydorus. From May 29 through September 8, when the mean water temperature at Locust Point was 22.3°C and the mean P/B ratio 0.20, cladoceran accounted for 71% of the zooplankton biomass. The differences in P/B ratios between the unheated lake and Locust Point probably reflect both differences in species relative abundance and the length-weight equations and development times used in the production calculations.

The seasonal or annual P/B ratio may be used to compare lakes of differing trophic conditions and temperature regimes (Table 22). Since eutrophic lakes tend to be warm and shallow, and oligotrphic lakes cold and deep, it is difficult to separate the effects of temperature and trophic conditions on the seasonal P/B ratio. Experimental nutrient enrichment studies, utilizing ponds or artificial enclosures, should reveal the relative importance of temperature and food in determining zooplankton community P/B ratios.

## Evaluation of Methods

A major problem in the assessment of zooplankton production is the reliability of basic parameters such as numbers of individuals, fecundity, and size-frequency estimated from field collections. Samples should: (1) be representative of the entire zooplankton community, (2) take into account variability with time and in space, and (3) be comparable, one to another.

Vertical tows with a plankton net is a simple, widely used method for sampling the water column. In this study the net was assumed to be 100% efficient in straining the water column. In fact, because of the resistance of the net, the efficiency is always less than 100%. The effective value of filtration depends upon such factors as mesh size, filtering surface to mouth area ratio, towing speed, and clogging by algae and other suspended particles. Net clogging is an especially acute problem with deep tows in productive lakes. In their study of Daphnia in Lake Constance Elster and Schwoerbel (1970) compared the results of 30 meter vertical plankton net tows with pump samples. The efficiency of the net varied from 5% to 36% with a mean of 18% in the Untersee. McNaught et al. (1975) electronically monitored net meters during vertical tows in Lake Ontario. A 64 μ mesh net, the mesh size used in this study, started at 65% to 70% efficiency but ended a 25 meter vertical tow with a filtering efficiency of only 15%. A rapid decline in filtration rate took place in the phytoplankton-rich epilimnion.

The degree of net clogging which occurred during 1 to

4 meter vertical tows at Locust Point, Lake Erie was not measured. Birge (1897) noted that seasonal changes in net filtration during 18 meter vertical hauls were correlated with phytoplankton abundance in Lake Mendotae. He stated, however, that 3 meter vertical tows were too short for significant net clogging to occur. Based upon the observations of McNaught et al. (1975) and Birge (1897) zooplankton numbers and production at Locust Point were probably understimated by about 35% due to net efficiency and perhaps by more during the August _Aphanizomenon_ bloom and the cold water periods of high diatom abundance. Serious errors might arise in comparing the numbers of zooplankters collected by vertical tows in deeper parts of Lake Erie with the numbers found at shallow stations such as at Locust Point.

_Leptodora_ _Kindtii_ is an important food source for Lake Erie fishes (Price, 1963). The population dynamics and production of the large, strong swimming cladoceran are of particular interest for a second reason; _Daphnia_ mortality rates have been closely correlated with the abundance of _Leptodora_ (Hall, 1964; Wright, 1965; Cummins et al., 1969). Plankton tows taken at night often result in much larger catches of _Leptodora_ than daytime tows (Andrews, 1948; personal observations). Schindler (1969) demonstrated that a 28 liter transparent plankton trap caught 2 to 3 times more _Leptodora_ than a metered plankton net 20 cm in diameter. It is likely that the numbers of Leptodora caught at Locust Point, and especially the numbers of large, ovigerous females, underestimated natural population densities.

Likens and Gilbert (1970) tested filtration through 35 µ, 48 µ, and 75 µ mesh nets and allowing the total sample to settle (0 µ, no filtration) as methods for catching rotifers. There was no statistical difference at the 5% level between numbers of rotifers from samples filtered through 0 µ, 35 µ, or 48 µ screening. The 75 µ mesh caught only 38% as many Polyarthra as 48 µ mesh. Eggs per female ratios were much higher in samples concentrated with 75 µ mesh netting, presumably due to the loss of small, nonovigerous individuals through the mesh. In this study, the effect on the production estimate of losing rotifers through the mesh would depend on the relative increase in the Keratella cochlearis egg ratio compared to the loss of other rotifers.

Despite the extra effort involved in taking samples at several depths, I recommend the use of a Schindler (1969) trap for sampling zooplankton in the shallow Western Basin of Lake Erie. Unlike plankton nets, a Schindler trap filters a constant, known volume of water and can collect representative samples of both large, strong swimming crustaceans and small rotifers.

The sampling area for this study was a very small part of western Lake Erie. Coefficients of variation for mean zooplankton production calculated from 10 sampling stations were small for a field study, less than 0.1 on the average (Table 19). These coefficients of variation are measures of the variance of zooplankton production estimates due to interstation variability in population numbers and species composition. When the Davis-Besse Nuclear Power Plant goes into operation greater differences in species composition and population numbers between stations can be expected. Studies of horizontal variation in zooplankton distribution in a small area such as the power plant site should include measurements of water currents (Ragotskie and Bryson, 1953; Small, 1963; Stavn, 1971).

The variation which may have arisen from subsampling is insignificant compared to other sources of sampling error in the zooplankton production estimates. Kutkechn (1958) found that whole cell Sedgwick-Rafter zooplankton counts were randomly distributed.

Since crustacean sooplankton numbers varied by over two orders of magnitude throughout the year (Fig. 3), the procedure of counting three Sedgwick-Rafter cells from a 50 ml concentrate year around resulted in an over-worked plankton counter during months of high plankton numbers and relatively poor estimates of population numbers when zooplankton was sparse. The poor estimates during months of low population numbers were compensated for by counting additional aliquots. An optimal counting procedure would allow for adjustments in: (1) the number of cells counted, (2) the concentration of the samples, and (3) the number of organisms of different taxonomic groups enumerated.

The great seasonal variation in zooplankton numbers, growth, and reproduction makes questionable the results of zooplankton production calculations based on samples taken at long time intervals. The zooplankton biomass at Locust Point, Lake Erie had a mean turnover time of 5 days during the summer (Table 21). Hillbricht-Ilkowska and Patalas (1967) recommended a sampling interval not exceeding 4 to 5 days during the spring and summer. The effect of sampling frequency on the reliability of zooplankton production estimates has been examined by Hillbricht-Ilkowska and Weglenska (1970).

Some indication of the reliability of monthly zooplankton samples may be obtained by comparing numbers of zooplankters collected at Locust Point using the same techniques, and on about the same dates during different years. During each of four years general seasonal trends in species composition and abundance of crustacean zooplankters at Locust Point, Lake Erie were similar (Reutter and Herdendorf, 1976). Daphnia, other Cladocera, and copepods were most abundant in the May, June, and July samples. The greatest differences between the 1975 samples and samples from previous years occurred in May. The timing of the period of rapid zooplankton population growth in the spring appears to be related to water temperature. Chandler (1940), in a limnological study of western Lake Erie, found that *Daphnia* populations increased more than 10 fold during the last week of May and the first week in June, attaining an annual maximum of 9 per liter on June 5 at a water temperature of 20°C. On May 29, 1975 the water temperature was 20°C and the *Daphnia* population density at Locust Point was 121 per liter (Table 13). On May 25, 1973, when the water temperature was 14°C, 3.4 *Daphnia* per liter were found at Locust Point, Lake Erie (Reutter and Herdendorf, 1974a). The water temperature was 15°C when the *Daphnia* was 11 per liter on May 22, 1974 (Reutter and Herdendorf, 1974b). Each year *Daphnia* populations at Locust Point have sharply declined during late July and early August (Figure 11).

Rotifers tend to show sporadic changes in population density with time (Edmondson, 1946; Halbach, 1970). On different years rotifers were particularly abundant at Locust Point in May, July, August, November, and December samples (Reutter and Herdendorf, 1976). During 1975, the greatest change in total rotifer numbers occurred between the August 11 (426 per liter) and August 14 (142 per liter) samples (Fig. 3). Monthly samples are inadequate for assessing the contribution of rotifers to total zooplankton production.

The magnitude of error in the annual zooplankton

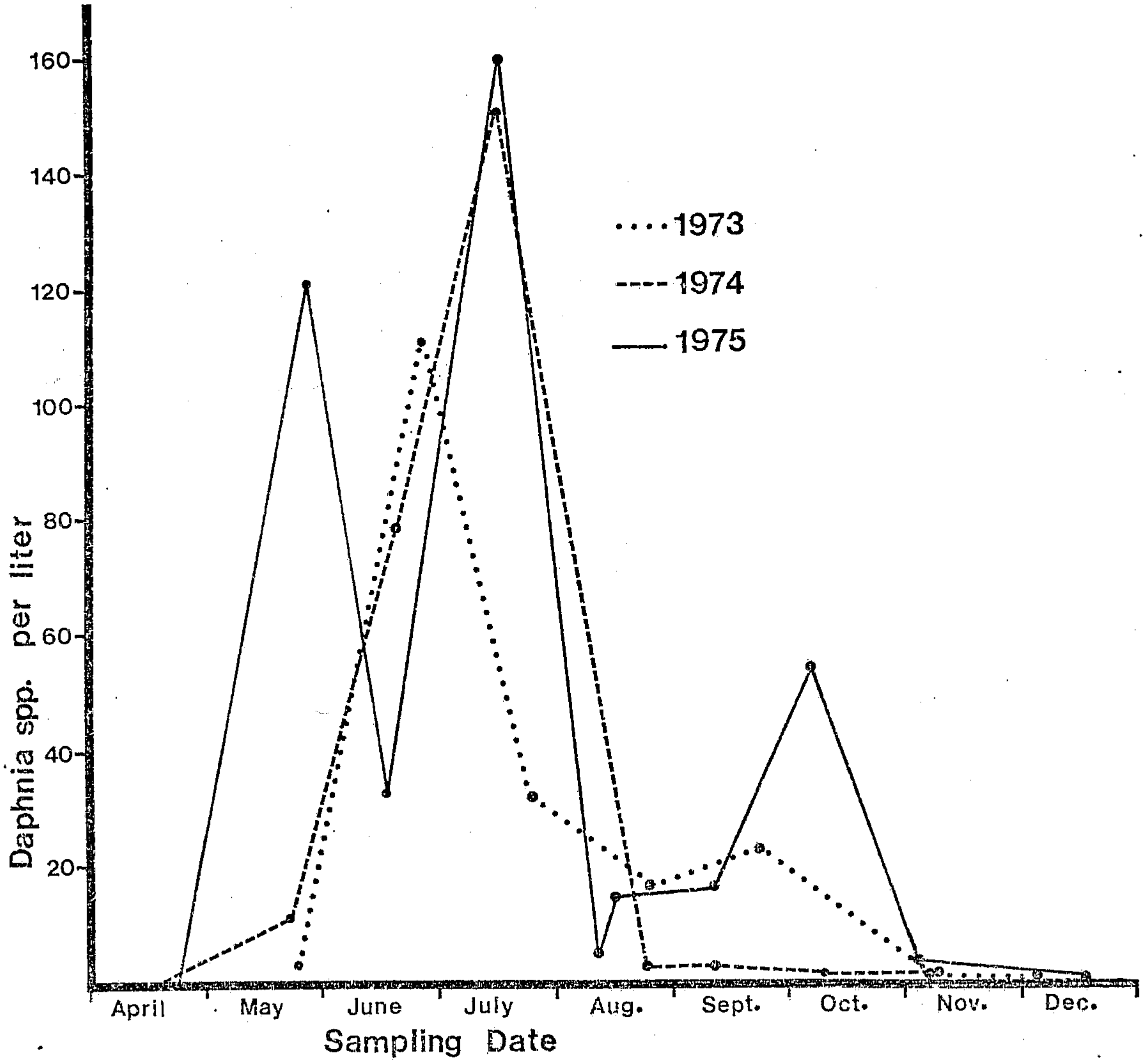

Figure 11. Daphnia spp. populations (numbers per liter), Locust Point, Lake Erie, for 1973 (Reutter and Herdendorf, 1974a), 1974 (Reutter and Herdendorf, 1974b; 1975b), and 1975 (Table 13).

production estimate which resulted from monthly sampling with a plankton net can not be measured. The zooplankton production estimates presented in this study should be regarded as a first approximation of annual production and indicative of general seasonal trends.

An accurate assessment of population numbers is the basis of every method for calculating secondary production. The relative importance of the methods for estimating growth increments and development times, and the assumptions used in determining these parameters is less well understood. Since different parameters and assumptions are involved in calculating the production of different life history stages it is useful to know which life history stages make major contributions to total production. Growth by both juveniles and adults and the production of eggs were all important components of Daphnia retrocurva production (Table 23). Since Bosmina, Eubosmina, and Chydorus grow less after hatching than Daphnia (Table 17), the production of eggs is an even greater part of their total production.

Compared to cladoceran eggs, copepod eggs are very small and as a result contributed little to copepod production (Table 23). In most samples nauplii were the mos important component of cyclopoid copepod production (Table 23). Considering the small size of nauplii, their role as producers is surprising. Assuming no mortality, continuous reproduction, and using the May 29 size increments and

Table 23. The percent contribution of each life stage to *Daphnia retrocurva* and cyclopoid copepod productivity, Locust Point, Lake Erie, April 22, 1975-March 16, 1976.

| Sampling Date | % of *Daphnia retrocurva* Production | | | % of Cyclopoid Copepod Production | | |
|---|---|---|---|---|---|---|
| | eggs | juveniles | adults | eggs | nauplii | copepodites |
| 4-22 | 0.0 | 100.0 | 0.0 | 5.6 | 66.7 | 27.8 |
| 5-29 | 0.7 | 90.4 | 8.9 | 5.8 | 64.5 | 29.3 |
| 6-16 | 39.2 | 37.4 | 23.4 | 21.2 | 64.0 | 14.8 |
| 7-14 | 16.1 | 50.0 | 33.9 | 6.4 | 26.0 | 67.6 |
| 8-11 | 29.9 | 40.6 | 30.3 | 0.0 | 85.2 | 14.8 |
| 8-14 | 31.3 | 45.1 | 23.6 | 0.0 | 44.6 | 55.4 |
| 9-8 | 38.3 | 40.7 | 21.0 | 0.0 | 24.3 | 75.7 |
| 10-6 | 21.0 | 36.2 | 42.8 | 0.0 | 42.6 | 57.4 |
| 11-3 | 9.0 | 45.5 | 45.5 | 0.0 | 59.1 | 40.9 |
| 12-16 | | | | 0.0 | 63.2 | 36.8 |
| 3-16 | | | | 0.0 | 89.9 | 10.1 |

development times, expected relative cyclopoid copepod production is: eggs, 3%; nauplii, 37%; and copepodites, 60%. Both assumptions are undoubtedly violated. In a study of the copepod Diaptomus oregonensis, Rigler and Cooley (1974) showed that the relative production of different life stages varied from one generation to the next. In the first generation, because there was little mortality, most production was due to later copepodite stages. During the third and final generation of the year the mortality rates of nauplii and copepodites were very high and most production took place in the naupliar stages. Since late stage cyclopoid copepodites and adults have been shown to consume a number of nauplii, copepodites, and small cladocerans about equal their body weight each day (Anderson, 1970; McQueen, 1969; Zdenek and Fernando, 1975), high nauplii and copepodite mortality should be expected.

To examine the relative effect of development time, growth increment, and length-frequency distribution on production estimates, the production per individual juvenile Daphnia retrocurva and cyclopoid copepodite was calculated as described in the methods section (variant 1) and according to two other variants, 2 and 3 (Tables 24 and 25). Variants 1 and 2 were computed using the 0.1 mm length-frequency distributions. The development time of variant 1 was the development time for the water temperature on the sampling date, while the development time for

Table 24. The production per juvenile *Daphnia retrocurva* calculated according to three variants. Samples were collected from Locust Point, Lake Erie, April 22- November 3, 1975.

| Sampling Date | Temperature °C | Growth increment mm | Production per Individual µg·day$^{-1}$, 0.1 mm Intervals Variant 1 | Production per Individual µg·day$^{-1}$, 0.1 mm Intervals, 20°C, Variant 2 | Production per Individual µg·day$^{-1}$, single size class, 20°C Variant 3 |
|---|---|---|---|---|---|
| 4-22 | 7 | .45-1.35 | 0.34 | 1.91 | 2.18 |
| 5-29 | 20 | .65-1.35 | 1.45 | 1.45 | 2.00 |
| 6-16 | 21 | .65-1.35 | 1.26 | 1.16 | 2.00 |
| 7-14 | 23 | .65-1.25 | 1.52 | 1.19 | 1.55 |
| 8-11 | 24 | .55-0.95 | 0.91 | 0.66 | 0.66 |
| 8-14 | 24 | .55-0.95 | 0.61 | 0.43 | 0.66 |
| 9-8 | 21 | .55-0.95 | 0.52 | 0.46 | 0.66 |
| 10-6 | 13 | .55-0.95 | 0.29 | 0.66 | 0.66 |
| 11-3 | 10 | .55-0.95 | 0.30 | 1.00 | 0.66 |

Table 25. Production per cyclopoid copepodite calculated according to three variants. Samples were collected from Locust Point, Lake Erie, April 22, 1975-March 16, 1976.

| Sampling Date | Temperature °C | Growth increment mm | Production per Individual μg·day$^{-1}$, 0.1 mm Intervals Variant 1 | Production per Individual μg·day$^{-1}$, 0.1 mm Intervals, 20°C, Variant 2 | Production per Individual μg·day$^{-1}$, single size class, 20°C, Variant 3 |
|---|---|---|---|---|---|
| 4-22 | 7 | .38-.97 | 0.073 | 0.29 | 0.35 |
| 5-29 | 20 | .35-.97 | 0.35 | 0.35 | 0.36 |
| 6-14 | 21 | .35-.97 | 0.38 | 0.36 | 0.36 |
| 7-14 | 23 | .33-.77 | 0.32 | 0.26 | 0.22 |
| 8-11 | 24 | .33-.74 | 0.23 | 0.17 | 0.20 |
| 9-8 | 21 | .35-.82 | 0.22 | 0.21 | 0.25 |
| 10-6 | 13 | .36-.87 | 0.080 | 0.15 | 0.28 |
| 11-3 | 10 | .38-.88 | 0.055 | 0.15 | 0.28 |

20°C was used for each length-frequency distribution in variant 2. The ratio of variants 1 and 2 reflects the effect of development time on productivity per individual. For example, the production per individual juvenile *Daphnia retrocurva* on November 3 at 10°C (variant 1) was 33% of the production which would have been expected at 20°C.

The often unstated assumption in using size intervals is that individuals are evenly distributed throughout each size interval or that size intervals are small enough that uneven distribution of individuals within them has little effect on the results of calculations. Variant 3 was calculated using the development time for 20°C and no subdivision of the growth increment. The difference between variants 2 and 3 indicates the degree to which the length-frequency distribution on each sampling date departed from an even distribution. *Daphnia retrocurva* juvenile production summed over 0.1 mm intervals, variant 2, was often much less than production summed over a single size class, variant 3, (Table 24). Daphnia length-frequency distributions tended to be skewed toward small individuals. The single notable exception was the November 3 sample which contained very few neonates due to the very low birth rate at that time (Table 15, Fig. 4). Cyclopoid copepodite length-frequency distributions also tended to be skewed toward small individuals, although to a lesser degree than those of *Daphnia retrocurva* (Table 25).

Skewed length-frequency distributions could be the result of pulses in the reproductive rate or mortality. Mortality is probably a major factor since length-frequency distributions resulting from mortality would, as was noted in Locust Point, Lake Erie samples, be consistently skewed toward small individuals. Length-frequency distributions reflecting pulses in reproduction should tend to balance out, at different times favoring both small and large individuals. The use of single naupliar, copepodite, and juvenile cladoceran size classes, as has been done by Patalas (1970), Weglenska (1971) and others (see Winberg, 1971) would give an unbiased estimate of zooplankton production only if no mortality occurred during those stages. The results of this study indicates that nauplii, copepodite, and juvenile cladoceran life history stages should be further subdivided when calculating zooplankton production or biomass.

Comparisons of variant 3 from different sampling dates show the effect of changing growth increments on production estimates. Juvenile _Daphnia_ _retrocurva_ growing from 0.65 mm to 1.35 mm in 5.1 days (development time for 20°C) increase in weight almost three times as fast as _Daphnia_ growing from 0.55 mm to 0.95 mm in the same amount of time (Table 24, variant 3). The equation for computing the length-weight relationship is a critical factor. According to the equation $W = 1.5 \times 10^{-8} L^{2.84}$ (Table 9), a _Daphnia_

0.95 mm in length weighs 4.3 $\mu g$ while a 1.35 mm *Daphnia* weighs 11.7 $\mu g$. Cyclopoid copepodites growing from 0.35 mm to 0.97 mm in length gain weight about 1.8 times faster than individuals growing from 0.33 mm to 0.74 mm in the same amount of time (Table 25, variant 3). In both *Daphnia retrocurva* and cyclopoid copepods decreases in development times at high water pemperatures were, in part, offset by decreases in the sizes of growth increments.

Since a change in the length of primaparous *Daphnia retrocurva* by a single 0.1 mm size interval from 1.35 mm to 1.25 mm results in a 32% decline in production per juvenile *Daphnia* and a similar decline in production per adult *Daphnia* (Table 24, variant 3), efforts should be made to precisely determine the lengths of *Daphnia primapara*. During periods of low egg production the size of Cladocera at maturity might be determined by examining ovary development (Kerfoot, 1974). *Daphnia retrocurva* undergo an increase in helmet length during the summer (Brooks, 1946). Since helmets add very little to total body weight, the measurements of total length used in this study overestimated the weight and production of *D. retrocurva* found from July 14 through October 6, the period when *D. retrocurva* with long helmets were present in samples from Locust Point. *D. retrocurva* weight increments should be determined from regression equations based on the relationship between body weight and the length from the posterior end of the carapace to the eye (Burns, 1969). The use of Burns' (1969) regression equations would have resulted in even greater differences between spring *Daphnia retrocurva* and those found later in the year than are shown in Table 24, variant 3.

The weight of cladoceran eggs was equated with the weight of neonates. Since a 0.55 mm *Daphnia retrocurva* weighs 0.91 µg while a 0.65 mm neonate weighs 1.46 µg, the lengths of *Daphnia* neonates should be determined using size intervals smaller than 0.1 mm. Measuring volumes is an alternative method of determining the weight of cladoceran eggs (Green, 1956).

Using the finite birth rate method of calculation, the production of rotifers is directly proportional to the population size and eggs per female ratio, and inversely proportional to the development time of eggs. Eggs per female ratios for *Keratella cochlearis* ranged from 0.51 to 0.11 (Fig. 4) while egg development times from 5°C to 24°C ranged from 5.3 days to 0.8 days (Table 4). The production per individual for *K. cochlearis* on May 29 when the water temperature was 20°C and the eggs per female ratio was 0.11 was equal to production per *K. cochlearis* when the water temperature was to be 5°C on March 16 and the egg ratio was relatively high, 0.41 (Table 26). Results from using the finite birth rate B (equation 2) and the instantaneous birt birth rate b (equation 3) to calculate rotifer production have been compared by Hillbricht-Ilkowska and Weglenska

Table 26. Production per *Keratella cochlearis* calculated using egg development times for the water temperature on the sampling date (variant 1) and egg development times for 20°C (variant 2). Samples were collected from Locust Point, Lake Erie, April 22, 1975-March 16, 1976.

| Sampling Date | Temperature °C | Eggs per female | Production per Individual $\mu g \cdot day^{-1}$ Variant 1 | Production per Individual $\mu g \cdot day^{-1}$, 20°C Variant 2 |
|---|---|---|---|---|
| 4-22 | 7 | 0.39 | 0.011 | 0.033 |
| 5-29 | 20 | 0.11 | 0.009 | 0.009 |
| 6-14 | 21 | 0.50 | 0.050 | 0.042 |
| 7-14 | 23 | 0.27 | 0.024 | 0.023 |
| 8-11 | 24 | 0.28 | 0.039 | 0.024 |
| 8-14 | 24 | 0.25 | 0.034 | 0.021 |
| 9-8 | 21 | 0.51 | 0.051 | 0.043 |
| 10-6 | 13 | 0.28 | 0.015 | 0.024 |
| 11-3 | 10 | 0.47 | 0.019 | 0.040 |
| 12-16 | 5 | 0.27 | 0.006 | 0.023 |
| 3-16 | 5 | 0.41 | 0.008 | 0.035 |

(1970).

Development times from zooplankton cultured in the laboratory at constant temperature and with ample food were applied in calculating the production of natural populations. The assumption in this and many other studies of zooplankton (see Winberg, 1971) is that most of the time food quantity and quality have not significant effect on zooplankton development times. This assumption is based on laboratory studies which have shown that food has a much greater effect on fecundity than on development times. For example, Ingle et al. (1937) compared growth and reproduction in well-fed and semistarved Daphnia longispina cultured in the laboratory. Semistarved Daphnia took about 14% more time to complete the 4 juvenile instars and were about 80% as long as well-fed individuals when maturity was attained. Well-fed Daphnia averaged 21.5 young per brood while their semistarved sisters on the average produced 5.5 young per brood.

Measuring the availability of food for zooplankton growing under natural conditions presents severe problems. Burns (1968) showed that the maximum diameter of particles ingested by Cladocera is a linear function of carapace length. According to her equation, large Bosmina feed on particles up to about 25 µ in diameter while Daphnia 1.5 mm in length may ingest particles up to about 50 µ in diameter. Some gelatinous green algae, such as Sphaerocystis, may pass through the gut of Daphnia undigested (Porter, 1973). In general, blue-green algae are a poor source of food for Daphnia (Arnold, 1973; Schindler, 1968). While detritus with associated bacteria is often ingested by zooplankton, it varies considerably in nutritive content, usually having much lower caloric values than algae (Schindler, 1968).

Weglenska (1971) measured the growth and development rates of 5 species of filter feeding zooplankton using food concentrations in the same range as found in nearby eutrophic Mikolajskie Lake. Although her use of the wet weight of nannoplankton and bacteria concentrated from Mikolajskie Lake as a measure of zooplankton food may be criticised, Weglenska's (1971) study is the best attempt to relate the growth and development of freshwater zooplankton to concentrations of natural food. Weglenska (1971) reported that the egg development times for 4 species of Cladocera and 1 species of calanoid copepods were essentially independent of the available food supply both before formation of the egg and during egg development. The number of cladoceran eggs produced increased 6 to 8 times from the lowest to the highest concentration of food. Ephippial and degenerate eggs were frequently observed at the lowest food concentration.

At food concentrations from 2.5 mg·liter$^{-1}$, the average food concentration in Mikolajskie Lake, to

10 mg·liter$^{-1}$ juvenile Daphnia longispina development times were independent of food food concentration (Weglenska, 1971) (Table 27). At lower food concentrations development rates became longer at an increasing rate. The juvenile development of other Cladocera showed similar trends. The development times of Eudiaptomus graciloides copepodites were somewhat more dependent on food concentration than the development times of cladoceran juveniles (Table 27).

From July 22 through August 30 food concentrations in Mikolajskie Lake ranged from 4.0 mg·liter$^{-1}$ in early August to 1.6 mg·liter$^{-1}$ in mid-August and slightly over 3 mg·liter$^{-1}$ in late August. During the periods of relatively high food concentrations there were only 5% to 6% differences between zooplankton production estimates taking into consideration the effect of both food and temperature on development rates and estimates based on the the effect of temperature alone on zooplankton development times. During the mid-August period of low food concentration, failure to consider the effect of food concentration on zooplankton development rates resulted in a 34% overestimation of zooplankton production (Weglenska, 1971).

Weglenska's (1971) study shows that food occasionally affects zooplankton development times in eutrophic lakes. Culture studies have demonstrated that egg production is a sensitive indicator of food supply. Measures of egg production should be used as indirect measures of zooplankton

Table 27. Comparison of juvenile *Daphnia longispina* and copepodite *Eudiaptomus graciloides* development times (in days) at different temperatures and concentrations of food. Food was bacteria and nannoplankton (mg wet weight) concentrated from lake water samples (data from Weglenska, 1971).

| Food concentration mg·liter$^{-1}$ | 17°C | 22°C |
|---|---|---|
| | *Daphnia longispina* | |
| 0.5 | 9.9 | 7.2 |
| 1.0 | 7.6 | 5.0 |
| 2.5 | 6.0 | 3.4 |
| 10.0 | 6.0 | 3.4 |
| | *Eudiaptomus graciloides* | |
| 0.72 | 20 | 15 |
| 2.0 | 16 | 11 |
| 3.0 | 14 | 9.5 |
| 5.0 | 12 | 7 |

food supply and the effect of food on zooplankton development rates. Clutch size alone is a poor measure of egg production because neither the percentage of adults bearing eggs nor the size of adult females is considered. Laboratory studies should attempt to establish quantitative relationships between female body size, egg production, and juvenile development times over a range of food concentrations.

The measures of reproduction determined in this study may be applied in a general, qualitative way to evaluate the probable effect of food on development times of zooplankton collected on different sampling dates at Locust Point, Lake Erie. The low eggs per adult crustacean and eggs per rotifer ratios on May 29, 1975 (Fig. 4) are probably indicative of poor food supply and retarded development on that date. The presence of male Daphnia retrocurva and ephippial eggs at a water temperature of 20°C is further evidence of a low food supply on May 29 (Berg, 1934). Eggs per adult crustacean ratios were never as low again until late fall, while rotifer egg ratios remained relatively high throughout the remainder of the year (Fig. 4). The decline in cladoceran eggs per adult ratios in the autumn may have been related to water teperature as well as food, and therefore should not be considered evidence for retarded growth and development rates (Green, 1956). More frequent sampling will be needed to determine how often and to what extent food has a significant effect on zooplankton development times in highly productive waters such as western Lake Erie.

# SUMMARY AND CONCLUSIONS

1. A study of zooplankton production at an inshore area in western Lake Erie was undertaken from April, 1975 through March, 1976. Production estimates were based on the numbers and length-frequency distributions of zooplankters in monthly field samples and the effect of water temperature on zooplankton development rates.

2. Sources of error in the production estimates and improvements in sampling techniques and the methods for calculating zooplankton production were discussed. Zooplankton populations respond rapidly to changes in environmental conditions and population numbers may double under ideal conditions in one or two days. Monthly samples therefore give only a first order approximation of annual zooplankton production and the range of seasonal variation. Apart from sampling, the literature values and equations used to estimate zooplankton weights represent a major source of possible error. In particular, the weights of rotifers reported by different authors vary up to ten fold. The rotifer weights used in this study were among the highest.

3. Daily zooplankton production estimates ranged from 0.67 $mg \cdot m^{-3} \cdot day^{-1}$ on March 16, 1976 to 383 $mg \cdot m^{-3} \cdot day^{-1}$ on July 14, 1975. Annual zooplankton production (160 $kcal \cdot m^{-3}$ or 550 $kcal \cdot m^{-2}$) was within the range reported for

eutrophic temperate zone lakes by other authors. Of total annual production, 77% occurred between April 22 and August 11, and only 8% from November 3 through April 22.

4. *Daphnia retrocurva* contributed 51% to annual zooplankton production, other Cladocera, 18.1%; rotifers, 16.2%; cyclopoid cpepods, 10.8%, and calanoid copepods, 3.9%. The production of carnivorous plankters was 9.1% of the annual zooplankton total. The relative contribution of each taxonomic group to zooplankton production showed great seasonal variation. During the spring-summer period of high zooplankton productivity, *D. retrocurva* was the dominant producer, while during the late summer and winter periods of low crustacean abundance rotifers contributed over 50% to total zooplankton production.

5. Zooplankton reproduction was measured using clutch size, eggs per adult crustacean, eggs per female rotifer, potential population doubling time, and the relationship between body length and clutch size. Reproductive rates may be used as an indirect measure of the suitability of environmental conditions, and especially food supply, for zooplankton growth and development.

6. The sizes of *Daphnia retrocurva* primara and cyclopoid copepod adults showed large seasonal variation. Both *D. retrocurva* and cyclopoid copepods were largest during the spring and smallest during the summer.

7. The skewed length-frequency distributions of

juvenile <u>Daphnia</u> <u>retrocurva</u> and the relatively large numbers and production of cyclpoid nauplii compared to copepodites suggested high mortality rates among these immature crustacean zooplankters.

8. Water temperature, growth increments, and population length-frequency distributions were all shown to have major effects on the calculated production per individual <u>Daphnia</u> <u>retrocurva</u> and cyclopoid copepodite.

9. Production/biomass (P/B) ratios for the zooplankton community ranged from 0.05 on March 16, 1976 to 0.29 on August 11, 1975. Although water temperature was the major factor influencing seasonal changes in the P/B ratio, species composition, growth increments, and length-frequency distributions were also important factors affecting the zooplankton community P/B ratio.

10. Due to changes in both species composition and the length-frequency distributions of individual species, total number of zooplankters did not accurately indicate zooplankton biomass. Since water temperature, growth increments, and length-frequency distributions all affect the P/B ratio, there is no simple way of relating zooplankton production and biomass.

11. A zooplankton study based on monthly sampling adds but little to our understanding of the factors governing the production dynamics of zooplankton. This study does indicate that relatively few zooplankton species are

important as producers but that population numbers, water temperature, length-frequency distributions, and growth inc increments all must be considered to quantify the production of these few species.

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