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POPULATION STABILITY OF THREE SPECIES OF ZOOPLANKTON IN WESTHAMPTON LAKE,

RICHMOND, VIRGINIA

BY

JAMES CHRISTOPHER CONYERS

A THESIS SUBMITTED TO THE GRADUATE FACULTY OF THE UNIVERSITY OF RICHMOND IN CANDIDACY FOR THE DEGREE OF MASTER OF SCIENCE IN BIOLOGY

MAY 1981

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BY

JAMES CHRISTOPHER CONYERS

APPROVED:

Dr. John W. Bishop

Committee Chairman

William S. Wooleett

mad K. May
Thomas R. Platt

Committee Members

Examining Committee

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Acknowledgements

I have many people to thank for their kind assistance in the completion of this thesis. I thank Dr. Harry C. Yeatman of the University of the South for identification of Mesocyclops edax and other copepods collected in Westhampton Lake. I thank Dr. Van Bowen for assistance in statistical analysis and Dr. James Worsham for help with computer operation. I thank Ed Delany and Paul Nugyen who furnished the map and bathymetric data on Westhampton Lake and Margaret Shugart who provided updated bathymetry readings. I thank Katherine Smith for her help with the literature search. I thank Margaret Hill and Jan Mccarren who typed the manuscript. Special thanks go to Ors. Thomas R. Platt and William S. Woolcott who served on my committee and to Dr. John W. Bishop, my graduate advisor, who has worked with this thesis from conception to completion.

Abstract

Populations of zooplankton, Keratella cochlearis (Rotifera) Bosmina longirostris (Cladocera), and Mesocyclops edax (Copepoda) were sampled in Westhampton Lake from June 30 to December 22, 1978. Population densities were estimated over time and analyzed for stability relative to the occurrence of rainfall. Two aspects of stability were used for analysis and given operational definitions as follows: Resistance - a population was resistant if its density was not more variable during periods of rain compared with periods of little or no rain; Persistence - a population was persistent if its density during periods of rain was not different from its density in periods of little or no rain. In the summer, K. cochlearis showed low resistance and non-persistence; B. longirostris showed high resistance and persistence; M. edax showed high resistance and non-persistence. In the fall, all three populations showed high resistance and persistence relative to the occurrence of rainfall. Resistance of populations in summer was consistent with the opportunistic, r-selected life history strategy of the rotifer, the more K-selected strategy of the copepod and the intermediate, compromising strategy of the cladoceran. Persistence in the summer was also consistent with these strategies for the rotifer and cladoceran, but not for the copepod. In the fall, the effects of rainfall were masked by the effects of fall turnover in the lake.

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INTRODUCTION

Organisms respond in various ways to environmental disturbances, and a result of these responses is often a change in population size. Such a change is an emergent property of population size, intrinsic growth rate, competition, predation, natality, mortality, emigration and immigration.

Stability is a measure of the extent that population size changes with respect to environmental disturbance. An early definition of stability, borrowed from classical mechanics, is that a system tends to return to its equilibrium state after being perturbed (Botkin and Sobel, 1975). This definition is inadequate for biological systems as populations are likely to be continually in a transient state, i.e., never reach an equilibrium (Holling, 1973).

Definitions of stability that do not require an equilibrium state have been recently developed. These definitions focus on three aspects of stability. The first, resilience, refers to whether or not a population returns to a previous size following a disturbance (Holling, 1973). The second, resistance, is the capacity of a population to remain constant in size in the face of an environmental disturbance (Ricklefs, 1973). The third, persistence, refers to the population size remaining within specified bounds over a period of time. (Botkin and Sobel, 1975).

The concepts of resilience and resistance define a spectrum of compromises in life history strategies. One population is likely to be more resilient and less resistant than another population or vice

versa. The more resilient population will respond faster to environmental change, declining rapidly in an adverse environment and increasing rapidly in a favorable environment. The more resistant population will be less variable over a wider range of environmental conditions. Both populations, however, could be equally persistent (Harrison, 1979).

Resilience and resistance may be further explained by the concepts of r- and K-selection (MacArthur, 1972). An r-selected species has a relatively high growth potential and reproduces rapidly in favorable environmental conditions, whereas a K-selected species has a lower growth potential, but remains close to the carrying capacity of the environment and is less sensitive to environmental change. The r-selected species would be more resilient and the K-selected species would be more resistant. The concepts of r- and K-selection describe how populations of different life history strategies achieve stability.

Not only the characteristics of the species but also the nature of the environmental disturbance determines population stability. Environmental disturbances may be rhythmic, e.g., diurnal or seasonal cycles or arrhythmic, e.g., rainfall, floods, or fires. The former have been studied extensively with respect to population changes. The latter have been largely neglected. Arrhythmic events are unpredictable and, therefore, difficult to study. They are a common part of an organism's environment, however, and are likely to play an important role in determining sizes of populations and their presence or absence {Connell, 1978).

The present study examines population stability of zooplankton with respect to natural arhythmic disturbances. The organisms used in this study were Keratella cochlearis (Rotifera), Bosmina longirostris (Cladocera), and Mesocyclops edax (Copepoda) in Westhampton Lake. The environmental disturbance is rainfall occurring in the drainage basin of the lake. These species possess differing life history characteristics, but each occupies the pelagic zone of the lake (Hutchinson, 1967). Rainfall on the drainage basin may, therefore, similarly influence the environments of the three populations.

The objectives of this study were to test the following hypotheses: (1) The zooplankton populations are resistant to the environmental disturbance of rainfall, (2) The zooplankton populations are resilient relative to the environmental disturbance of rainfall, {3) The zooplankton populations are persistent relative to the environmental disturbance of rainfall, {4) Stability (resistance, resilience, and persistence) of a zooplankton population varies according to life history characteristics of the species.

METHODS AND MATERIALS

The study was conducted in Westhampton Lake, a freshwater impoundment on the campus of the University of Richmond, Virginia. The surface area of the lake is 6.2 ha. (15.3 acres) with a mean depth of 2.8 m and a maximum depth of 7 m (Fig. 1). The northeastern neck of the lake is formed by the confluence of Little Westham Creek, the major tributary, and Robins Branch (new name).

The lake receives runoff from a 6.69 km² (2.58 mi²) drainage basin, covered principally by suburban development.

Rainfall data were gathered throughout the study period. A graduated cylindrical rainfall gauge located on the roof of the Gottwald Science Center, approximately 100 m from Westhampton Lake, was used to measure rainfall. A stage-rain recorder located on Robins Branch at the northern end of the lake proved to be inaccurate in measuring rainfall quantities, but it did indicate when rainfall began and subsided so that rainfall intensity could be calculated. Additional data were obtained from the National Weather Service at Byrd Field, and from the National Weather Service Three Chopt Station. The latter was located within the Little Westham Creek drainage basin approximately 1.6 km from Westhampton Lake.

Runoff volumes during rain storms on July 25 and August 4, 1978 were estimated from hydrographs generated by a stage-rain recorder located on Robins Branch. Mechanical failure of a stage recorder on Little Westham Creek prevented measurement of runoff in that stream. Efforts to directly calibrate the stage recorder were hindered by intermittent failure of the flow meter, relatively brief periods of peak flow in the stream, and the unpredictability of storms of sufficient intensity to create measurable flow.

Available information, however, made calibration of peak flow possible based on the equation $Q = CIA$ (Chow, 1964); where Q is the peak flow in cubic feet per second, C is an index of runoff according to the surface type of the drainage basin, I is the rainfall intensity in inches per hour, and A is the area of the

drainage basin in acres. The peak flow for the two graphs were different, therefore, the calculated values were used as points to define a line of stream height versus discharge.

With the points on the hydrograph calibrated, the discharge, as a function of stream height, was measured at fifteen-minute intervals and summed for the entire time of discharge, giving the runoff volume for Robins Branch. The area drained by Robins Branch is approximately 20% of the entire drainage basin of Westhampton Lake (Bishop, pers. comm.). Assuming that the surface type of the Robins Branch drainage is similar to the surface type of the remainder of the basin, the runoff for the basin was extrapolated from the calculated values.

Two sampling stations were established for routine data collection. One station (UL) was located at the bridge near the northern end of the lake midway between the east bank and the island. The second station (DL) was located at the Student Conmons Building at the front wall that extends over the lake midway between the east and west banks (Fig. 1).

A Kerrmerer bottle was used to collect samples at 1 m intervals from the surface to near bottom. Each sample was poured into a bucket, agitated to make the contents homogeneous, then a 1 1 aliquot was drawn off and poured into an 8 1 polyethylene bottle. Aliquots of samples taken at successive depths were combined to form a composite sample. A separate bottle was used for each station. Sixteen collections were made in the summer (prior to the onset of fall mixing) and 18 collections were made in the fall.

A T.N. Tronics temperature meter and probe were used to measure water temperature in Celsius degrees at 0.5 m intervals from surface to bottom. Data were recorded on days of collection and compiled to give temperature profiles of the lake throughout the study period. Other field data included site, time, air temperature and observations of atmospheric conditions, changes in turbidity, and development of blue-green algae blooms.

The abundance of algae was estimated with a Turner Model III fluorometer that irradiates a water sample with UV light and measures the fluorescence of the sample on an arbitrary scale from 0 to 100. Fluorescence is linearly proportional to the concentration of chlorophyll, therefore, the instrument reading corresponds to the abundance of algae (Lorenzen, 1966).

Each field sample was agitated and a portion was poured into a 50 ml beaker. The subsample was then agitated, poured into a cuvette, and placed into the fluorometer for measurement. The subsample was recombined with the field sample after a reading was made for each station.

The zooplankton samples were concentrated through a #20 mesh plankton bucket and placed in jars that contained 95 % ethanol. Before organisms were counted, the sample was adjusted to a known volume between 150 ml and 350 ml and poured into a 500 ml beaker. The sample was stirred with a magnetic stirrer at slow speed (approximately 150 R.P.M.) to insure homogeneous distribution of the zooplankton while the subsamples were drawn off (Wetzel and Likens, 1979).

Five 12 ml subsamples were drawn from each sample with a calibrated pipette and placed in a grid-marked petri dish for counting. Counts were made by scanning the entire subsample following the procedure of Edmondson and Winberg (1971). Zooplankton species were identified by keys in Edmondson (1959) and Pennak (1978), and counts of each species were recorded.

The density (no./liter) of each species at each station was calculated by taking the average number from the subsamples then solving the following equation:

No./liter =
$$
\frac{xss (Vcs/Vss)}{Vs}
$$
 (1)

Where Xss = average number of individuals of a species counted in the subsamples, Vcs = volumes of the concentrated sample, Vss = volume of one subsample, Vs = volume of the original sample.

The validity of combining data from the two stations was ascertained through correlation analysis. Correlations were calculated on an IBM 360 computer with an Interactive Data Analysis Program. The formula used was as follows:

$$
r = \frac{\sum xy}{\sqrt{\sum x^2 \sum y^2}}
$$
 (2)

where r is the correlation coefficient, x is the value at station UL, and y is the value at station DL. The resultant was compared to r value tables for the test of significance (Steel and Torrie, 1960). Further analysis for the same reason, was done by a three-way analysis of variance with treatments of station, season, and precipitation regimes (Steel and Torrie, 1960).

The two tailed Student's t-test was used to test significance of differences in means of fluorescence measurements between the rainy and dry periods. The following formula was used:

$$
t = \frac{\overline{x}_1 - \overline{x}_2}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_1}}}
$$
 (3)

where t is the Student's t value, \bar{x}_1 and \bar{x}_2 are the means of values from the rainy and dry periods, respectively, S_1^2 and S_2^2 are the variances of values from the respective periods and n_1 and n_2 are the number of observations from the respective periods (Steel and Torrie, 1960).

Statistical analyses were used to test population stability. Resistance was given the operational definition that a population was resistant if its size was not more variable during periods of rain compared with periods of little or no rain. Significant differences were tested by homogeneity of variances given by the following formula:

$$
F = S_1^2 / S_2^2 \tag{4}
$$

where F is the resultant F value from the ratio of the two variances, S_1 is the variance of population densities in the rainy period and S_2 is that of the dry period. Variance was calculated by the previously mentioned computer program using the formula:

$$
s = \Sigma x^2 - (\Sigma x)^2 / n \tag{5}
$$

where s is the variance, x is the population density value, and n is the number of observations. A population was defined as resilient if its size after the rainfall event returned to the same level as that before the event. This could _be tested by using the Student's t test for comparing measurments before and after the rainfall event. This was not carried out in this study as peroids of rainfall were long relative to generation times of the zooplankton, and other physical conditions, i.e., temperature, were different before and after the rainy periods. Persistence was given the operational definition that a population was persistent if its size during periods of rain was not different from its size in periods of little or no rain. Significnace was tested by the analysis of variance with treatments of season and precipitation regime. Calculation was carried out as given in Steel and Torrie (1960). Further analysis of means was carried out by use of Duncan's New Multiple Range Test as given in Steel and Torrie (1960). All values for these tests were transformed to log $_{10}$ (X+1) to satisfy the assumption that variances of compared data sets were similar.

RESULTS

Physical factors

According to the National Weather Service, Byrd Field, Richmond, Virginia, total rainfall during the study was less than the forty year average for a comparable time of year (Table 1). Rainfall in the Westhampton drainage basin was less than at Byrd Field.

Rain in the drainage basin occurred as clustered events during the study. Several weeks of rain were separated by longer periods of little or no rain (Table 2}. Most rainfall occurred during two periods, July 14 to August 13, 1978 and November 15 to December 9, 1978. Of the 408 mm total rainfall, 202 mm, or 49.5 % of the total, occurred in the first period and 141 mm, or 34.6 % of the total, occurred in the second period (Table 3).

Estimates of runoff into the lake following rain on July 25 and August 4, 1978,taken from hydrographs of Robins Branch {Figure 2) were $100,278$ m³ and $56,407$ m³, respectively. Assuming equal rainfall over the 6.69 km2 of the drainage basin, the 45 mm rain on the former date equalled $301,050$ m³ of water and the 27 mm rain on the latter date equalled 180,630 m³ of water falling on the drainage basin. Runoff, therefore, was 33 % and 31 % of the total rainfall on those dates, respectively. These percentages are within the range of expected runoff from a moderately sloping suburban area (Chow, 1964), such as that of the Westhampton drainage basin.

The lake was thermally stratified from the beginning of the study in late June into late September. During summer stratification, the surface temperature ranged from 30 C to 33 C and the bottom temperature gradually rose from 7 C to 12 C. The thermocline, layer of steepest temperature gradient, ranged in depth from 2.5 to 3.5 m (Fig. 3). Fall turnover began in late September and proceeded until the lake was isothermal at 7 C by mid-December. ·The increased flushing rate following rainfall did not result in a measurable change in thermal stratification.

Phytoplankton

Phytoplankton density had a bimodal distribution with peaks in late July to early August and in late November to early December (Fig. 4). A correlation coefficient of 0.90 for fluorescence at stations UL and DL was statistically significant at the 95 % confidence level. Data from the two stations, therefore, were combined in further computations. Average fluorescence was significantly higher in rainy periods than in dry periods in the summer and the fall (Table 4).

Zooplankton Populations

All populations constantly fluctuated throughout the study period. Keratella cochlearis and Bosmina longirostris populations had bimodal distributions. Both populations peaked in late July and in late October to early November (Figs. 5 and 6). The copepod population had one peak in early September and disappeared from samples by early December (Fig. 7).

Stability

. The study period was partitioned into four segments for the purposes of assessing the impact of rain and season on zooplankton populations. The criteria for partitioning were amount of rain and temperature profile of the lake. The segments were summer rainy, summer dry, fall rainy, and fall dry. The summer rainy period was July 14 to August 13, 1978. The summer dry period was June 30 to July 13, 1978 and August 14 to September 20, 1978. The fall rainy

period was November 15 to December 9, 1978. The fall dry period was September 21 to November 14, 1978 and December 10 to December 22, 1978 (Table 3).

The coefficient of correlation for population densities at stations UL and DL were significant for the rotifer and cladoceran, but the statistic was not significant for the copepod (Table 5). A three-way analysis of variance was calculated for population densities transformed to log 10 {X+l) {Steel and Torrie, 1960). Densities at the two stations were not significantly different for the three populations (Table 6). Graphic analysis also reveals similarities at both stations for density changes of the three populations (Figs. 5, 6, and 7). Population data for stations UL and DL, therefore, were pooled for stability analysis.

Of the three aspects of stability that were to be examined, resilience, resistance, and persistence, only the latter two have been analyzed. In order to have analyzed population responses for resilience, a relatively brief period of high intensity rainfall preceded and succeeded by relatively long, dry periods would have had to occur. As these events did not occur during the study, the tendency of each population to return, following the rainfall event to its initial density before the event, could not be tested.

Resistance was analyzed by comparison of variances of population densities in dry and rainy periods. A significantly higher variance in the rainy period, compared to the dry period, would indicate a low resistance relative to factors associated with rain. Persistence was analyzed by comparison of mean population

densities in the rainy period with that of the dry period. A significant difference in population density, either higher or lower, in the rainy period, compared to the dry period, would indicate that the population density was not persistent.

Kerate11a cochlearis had a significantly higher variance in population density in the rainy period than in the dry period during the summer (Table 7). The reverse was found for this species in the fall; the variance was significantly lower in the rainy period than in the dry period. Bosmina longirostris, similarly, had a higher variance of population density in the rainy period than in the dry period during the summer and a lower variance in the rainy period than the dry period during the fall. The difference in variances, however, were not statistically significant in either season. Mesocyclops edax had a lower variance in population density in the rainy period compared to the dry period in both summer and fall. The variances were significantly different in the summer but not in the fall.

The two-way analysis of variance was used to determine the differences in population means in rainy and dry periods for the two seasons. Further analysis of the statistical interaction of season and precipitation was accomplished by use of Duncan's multiple range test. Significant differences in population densities in different precipitation regimes were emphasized within each season and differences in population densities between seasons were not considered.

Two-way analysis of variance indicated no significant

difference in population density related to season or precipitation for K. cochlearis (Table 8). The interaction term for season and precipitation, however, was significant. The multiple range test revealed a significant difference in means between the rainy and dry periods in the summer for K. cochlearis, but showed no significant difference for the precipitation regimes in the fall (Table 9).

Mean population densities were not significantly different for season, precipitation, or interaction of the two treatments by the two-way analysis of variance for B . longirostris (Table 10). The multiple range test similarly revealed no significant difference between means for the four season-precipitation regimes (Table 11).

The two-way analysis of variance revealed significance in all treatments of population density means for M. edax (Table 12). The multiple range test showed a significant difference in precipitation regimes in the summer only and not in the fall for that population $(Table 13)$.

DISCUSSION

Much attention has been given to the influence of rhythmic environmental changes, e.g., seasonal cycles, on planktonic populations (Hutchinson, 1967; Porter, 1977). Population changes related to rhythmic environmental changes are cued by changes in photoperiod and temperature {Hutchinson, 1967).

Less information has been gathered on the influence of arrhythmic disturbances. The unpredictability of arrhythmic events presents problems in experimental design and in interpretation of data gathered relative to such events. In this study, for example,

data were partitioned into rainy and dry periods. Rain occurred, however, during the dry periods, and during the rainy periods, there were days that no rain occurred. Study of arrhythmic events is also complicated by unknown mechanisms of response by planktonic organisms.

Rainfall often results in physical, chemical, and biological changes in lakes. The flushing rate increases with runoff from the drainage basin following rainfall. Increased runoff may also result in changes of thermal stratification in lakes (Wetzel, 1975). Increased concentrations of nutrients, such as nitrates and phosphates, may occur following increased runoff. If nitrates and phosphates are limiting factors in algal growth, blooms of algae, or dramatic increases in their density, may occur following the influx of these nutrients (Odum, 1959).

Numerous changes in biotic and abiotic factors in Westhampton lake occur following rainfall. Runoff and flushing rate has been shown to increase after rainfall in this and other unpublished studies (Bishop, pers. comm.). Models have been successfully tested showing increases in turbidity, nitrate and phosphate following rainfall in Westhampton Lake (Bishop and Moore, 1975; Bishop, 1977). Phytoplankton production has also been shown to increase after rainfall (Bishop, 1971).

In this study, many factors could have been monitored to indicate changes in environmental factors in Westhampton Lake associated with rainfall. Runoff volume and phytoplankton production were chosen, however, because both have been previously

shown to vary immediately following rainfall and they could be important factors in regulating or limiting zooplankton population densities.

Hall (1964) found that the factors regulating population density of the cladoceran Daphnia galeata mendotae in Baseline Lake were food (principally phytoplankton), temperature, predator pressure, and flushing rate. The latter was not found to be of great importance in his study because emigration was offset by irmnigration from lakes upstream from Baseline Lake. This was not the case with Westhampton Lake, as there were no lentic habitats upstream. Therefore, food for the herbivorous zooplankters K . cochlearis and B. longirostris and flushing rates were estimated relative to the occurrence of rainfall. Food sources of the carnivorous M. edax were not measured. Variation in density of the herbivorous zooplankton with respect to rainfa11,however, may give an indication of variation in food sources for this species.

The results of this study showed that rainfall could have a biologically significant effect on Westhampton Lake with regard to zooplankton populations. Phytoplankton production was significantly higher during rainy periods than dry periods in both sunmer and fall. The amount of runoff measured on July 25 and August 4, 1978 displaced 58% and 33% of the total lake volume, respectively. As Hall (1964) found the density of *Q.* galeata mendotae in outlet water of Baseline Lake to be approximately equal to the population density of the lake, these displacements could export a large percentage of standing crops.

Zooplankton population density data were partitioned between the summer and fall seasons for analysis. This was done because of changes that occur in the limnetic environment as lakes pass from summer stratification into fall mixing. Typically, changes in zooplankton densities are associated with this event. Additionally, changes in zooplankton physiology associated with the decrease in temperature and change in photoperiod occur during the transition period (Hutchinson, 1967). These events in the fall may mask differences in rainy and dry periods between seasons.

The results of the test for resistance (homogeneity of variance) in summer showed that variance of population densities for K· cochlearis significantly increased from the dry to rainy period. The statistic showed no significant difference for the B. longirostris population and a significant decrease for the M. edax population. The K. cochlearis population, therefore, showed low resistance and the population of B. longirostris and M. edax showed high resistance relative to the occurrence of rainfall in summer.

In the fall, the K. cochlearis population densities significantly decreased in variance from the dry to rainy period, and the population densities of B. longirostris and M. edax showed no significant difference in variance during that period. All three populations, therefore, revealed high resistance relative to the occurrence of rainfall in the fall.

The tests for persistence (two-way ANOVA. and multiple range test) in summer showed that means of population densities for K· cochlearis were significantly higher in the rainy period than in the

dry period. Population densities for B. longirostris were not significantly different in the two precipitation regimes, and M . edax population densities were significantly lower in the rainy period than in the dry period. The K. cochlearis and M. edax population were, therefore, not persistent, and the B. longirostris population was persistent in summer relative to the occurrence of rainfall.

In the fall, mean population densities for all three populations showed no significant difference between the rainy and dry periods. The three populations were, therefore, persistent relative to the occurrence of rainfall in the fall.

In order to compare these results with other studies, data from collections made in 1969 from Westhampton Lake (Bishop, 1971) were analyzed in the same manner. In that study, data were taken in the summer only and all species of rotifers, cladocerans, and copepods were combined in their respective groups. Partitioning rainfall data into a dry period (July 1 to July 18, 1969) and a rainy period (July 30 to August 12, 1969) gives a mean rainfall per day of 1.56 mm/day and 5.57 mm/day, respectively. Zooplankton data were also partitioned between the two periods for analysis.

Homogeneity of variance of data from the three groups gave the same results as in this study (Table 14). Variances were significantly different for rotifers but not for cladocerans and copepods. The former group, therefore, showed low resistance and the latter two groups showed high resistance with respect to the occurrence of rainfall.

A one-way analysis of variance was used to analyze zooplankton data as the additional treatment of season could not be included in analysis. Rotifer mean densities were significantly different between the dry and rainy periods, and the mean densities for cladocerans and copepods were not significantly different (Table 15). The rotifers were, therefore, not presistent, and the cladocerans and copepods were persistent. The results for the rotifers and cladocerans were consistent with the study, but the result for the copepods was not. The latter may be due to the lumping of all copepods in the counts by Bishop (1971). Mesocyclops edax departs from the life history characteristics of most other copepods in Westhampton Lake in some significant ways. It is larger and likely slower in development than most other copepods and it is carnivorous, rather than herbivorous. The latter characteristic may impose a greater lag time in which the species could not take advantage of immediate increases in phytoplankton.

In sumnarizing the results of this study, each population had a different combination of low or high resistance and persistence or non-persistence in the sunmer. The three populations in the fall, however, were the same with high resistance and persistence relative to the occurrence of rainfall. These results may be a consequence of differences and similarities in life histories of these organisms.

The life histories of rotifers, cladocerans, and copepods exhibit a continuum of compromises in the potential for rapid population increases, predator avoidance, and competitive ability

(Allan, 1976). The three major groups, ranked with respect to opportunism, would be rotifers greater than cladocerans greater than copepods. In favorable circumstances, such as abundance of food sources and/or relatively low predator pressure, populations of more opportunistic species would increase more rapidly. In adverse circumstances, however, the less opportunistic populations would be influenced less and the more opportunistic species would decline more rapidly.

The life history of rotiferan subclass Monogononta and that of the cladoceran are very similar even though it is not closely related (Hutchinson, 1967). Most species of these groups are herbivorous, feeding primarily on phytoplankton although detritus, bacteria, and dissolved organic matter may be supplementary sources of nutrition (Saunders, 1969). Copepods have much more divergent characteristics in reproduction and nutrition.

An investigation of niche hypervolume in Mirror Lake revealed a separation of these three species by mode of feeding (carnivorous versus herbivorous), food size selectivity, depth, and timing of production maxima {Makarewicz and Likens, 1975) The monthly production values were found to reflect the gradient of greater-to-lesser opportunism with K. cochlearis production ranging between 10 to 40 micrograms/liter/month, B. longirostris ranging between 2 to 8 micrograms/liter/month, and M. edax ranging between 2 to 4 micrograms/liter/month.

The life cycle of K. cochlearis is monocyclic, i.e., sexual reproduction occurs once within an annual life cycle of otherwise

parthenogenetic reproduction (Hutchinson, 1967). Individuals overwinter as mictic resting eggs. These eggs hatch to produce amictic females with rising temperature in the spring. Reproduction is parthenogenetic through the summer; each reproducing female carries a single subitaneous egg. During the fall, the population reaches its maximum density and mictic females are then produced. Males arise from the eggs of the mictic females and sexual reproduction occurs in the late fall. The fertilized eggs develop the hard outer layer of the mictic resting eggs. During the parthenogenetic reproduction of the sunmer, generation time (egg-to-egg) is from 40 to 70 hours at 20 C (Lindstrom and Pejler, 1975), and generation time is influenced predominantly by variation in available food and temperature (Edmondson, 1965). Feeding by this species is accomplished by sweeping particles into the mouth by the action of coronal cilia. Food particles are usually less than 12 microns (Hutchinson, 1967).

Mature specimens of K. cochlearis are from 135 to 220 microns long (Edmondson, 1959). Variation in length is due primarily to development of anterior and posterior processes by cyclomorphosis.

The monocyclic life cycle of B. longirostris is very similar to K. cochlearis (Hutchinson, 1967). In the spring, females hatch from overwintering ephippial eggs. Successive generations are then produced by parthenogenetic reproduction through the sunmer. In the fall, males are produced and sexual reproduction occurs, followed by development of the ephippia. The principle difference in reproduction of the two species is that males of B. longirostris are

fully developed and diploid, whereas males of K. cochlearis are greatly simplified morphologically and are haploid (Hutchinson, 1967).

Bosmina longirostris is one of the smallest cladocerans in North America. Mature specimens range in length from 330 to 380 microns (Hutchinson, 1967). Its small size serves as an advantage in that fish prey more heavily on the larger cladocerans, such as Bosmina coregoni and species of Daphnia (Zaret and Kerfoot, 1975; Stenson, 1976). B. longirostris has been found to be more abundant in lakes stocked with bluegill (Lepomis macrochirus) and less abundant in the absence of the fish, indicating a competitive disadvantage relative to larger cladocerans (Lynch, 1979). Predation on this species occurs more commonly with invertebrate predators such as Chaoborus and Cyclops vernalis (Stenson, 1976; Kerfoot, 1978). Ingested particles by B. longirostris broadly overlaps the particle size range of macro and microconsumers. It feeds most intensely, however, in the range of 1 to 3 microns, the same as rotifers (Makarewicz and Likens, 1975). Generation time from egg to egg for B. longirostis is 5 to 7 days (Zaika, 1973). Embryonic development is 2 to 3 days and sexual maturation is 3 to 4 days at 11 to 19 C.

The life history of M. edax differs from K. cochlearis and B. longirostris in many aspects. It is much larger than the rotifer or cladoceran, reaching an adult length of 960 to 1,130 microns. It is bisexual and reproduces by obligate sexuality. Eggs are carried by the female in two egg sacs attached to either side of the genital

segment. Development of the copepod is holometabolous with six nauplier and five copepodite stages (Hutchinson, 1967). Overwintering diapause is accomplished by copepodites buried in the bottom sediment (Hutchinson, 1967). The generation time of many copepods for which data are available averages 8 days (Allan, 1976). The generation time of M. edax ,although not available, would be longer than this considering its relatively large size (Zaika, 1973). The generation time of M. edax would, therefore, be one or more days longer than B. longirostris and 5 or more days longer than K. cochlearis . The adult of the species is a strict carnivore, feeding principally on copepodites and secondarily on small cladocerans and rotifers (Confer, 1971). The copepodites are also carnivorous, but the nauplii are filter feeders (Macarewicz and Likens, 1975).

From the life history characteristics presented, K. cochlearis is the most opportunistic or r-selected species, M. edax is the least opportunistic or K-selected, and B. longirostris is intermediate in opportunism. In theory, therefore, the rotifer should exhibit the least resistance and the cladoceran and copepod should be more resistant. Persistence, in the operational definition, would also be dependent on this factor in the same way.

In summer, K. cochlearis exhibited low resistance relative to the occurrence of rainfall, and B. longirostris and M. edax exhibited high resistance. This result is consistent with the expected results, based on life history characteristics. In regard to persistence, however, the results were not consistent with what

was expected from life history characteristics. The rotifer and copepod were not persistent, but the cladoceran was persistent. In the fall, all three populations exhibited a high resistance and persistence with respect to the occurrence of rainfall.

Several conclusions and observations can be presented from the results of this study. Considering the summer season, the rotifer, K. cochlearis, population shows low resistance and non-persistence relative to the occurrence of rainfall, as would be expected for an opportunistic species.

The copepod, M. edax, shows resistance and non-persistence in the summer. It should be noted that these conclusions result from a very low density of zero measured during the rainy period. It is possible that the species probably was present in the lake during that time as it immediately reappeared in samples in the subsequent dry period. Its density during the rainy period probably was too low to be detected by the methods used. The high resistance of the population appears to give an unsatisfying result relative to population stability in this case. Extinction of a species would also be interpreted from this analysis as being resistant as variance (zero) would likely be less after extinction than before. This case points clearly to the conclusion that a single definition of stability may not be appropriate for biological systems.

The B. longirostris population, intermediate between the latter two relative to opportunism, was resistant and persistent. This result suggests that compromise in population growth rate, competitive and predator avoidance abilities may increase population

stability over a variety of environmental changes.

Allan (1974) discussed a theory relating body size to predation and competition. He concluded that the smaller body size among cladocerans, e.g., B. longirostris, may compromise these factors such that an adaptive peak would occur. If increased stability could be assumed to reveal greater adaptation, these conclusions would support this theory.

In the fall, all three populations showed high resistance and presistence. This appears to indicate that population stability is related to environmental changes, as well as life history characteristics. A number of physical, chemical, and biological changes occur in the fall (Hutchinson, 1967; Wetzel, 1975). Fall mixing of lakes occurs with a decline in temperature, oxygenation of the hypolimnion, release of nutrients from the bottom layer and annual density peaks of phytoplankton and zooplankton. With these changes in the fall, the environmental impact of rainfall could have been masked.

Several questions, which could be the basis of future investigations, have been raised by this study. Resilience of zooplankton populations could be determined if sampling could be done around a brief and intensive storm to study the population responses. The question of why phytoplankton increases following rainfall has not been answered. One possible avenue of investigation would be to determine the changes in grazing pressure following a rainfall event. As zooplankton are likely exported in large numbers with increased flushing rate, a brief period of

decreased grazing may give a lag time before grazing rate catches up with phytoplankton production. Lastly, it is possible that some planktonic species exist in Westhampton Lake only because of the periodic occurrence of environmental disturbance caused by rainfall, and species, which would otherwise be competitively eliminated, may exist in the lake only because of an ability to take advantage of these episodes through rapid population growth.

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TABLE 1: Monthly rainfall quantities from July to December 1978 measured in the Westhampton Lake drainage basin and monthly rainfall quantities for the same period measured by the National Weather Service, Byrd Field, Richmond, Virginia - Mean monthly rainfall quantities for July to December are from the records of the National Weather Service, Richmond, Virginia, from 1938 to 1977. Quantities are given in mm.

*Data gathered from National Weather Service Three-Chopt Station, located within the Little Westham Creek drainage basin approximately 1.6 km from Westhampton Lake.

TABLE 3. Total rainfall quantities in mm and average rainfall per day in mm/day for rainy and dry periods in summer and fall of 1978 (T = trace of rainfall, less than l mm).

Season	Precipitation Condition	Dates	Total Rainfall (mm)	Average Rainfall (mm/day)
Summer	Rainy Dry	Jul 14-Aug 13 Jun 30-Jul 13 Aug 14-Sep 20	202 22	6.5 0.6
Fall	Rainy Dry	Nov 5 -Dec 9 Sep 21-Nov 14 Dec 10-Dec 22	141 38 5	5.6 0.7 0.4

TABLE 4. Mean phytoplankton, in units of fluorescence, in dry and rainy periods, during the summer and fall 1978. N is the number of observations within each period, t is the two-tailed student's t-test of independent means.

*Significantly correlated with P = .05.

TABLE 6. Three-way analysis of variance of population densities for K. cochlearis, B. longirostris, and M. edax. Treatment sum of squares is calculated partitioning data according
to season (summer/fall), precipitation regime (rainy/dry), and stations (UL/DL). Treatment for station only was calculated to determine significance. N.S. = not significant.

TABLE 7. Variance of population densities in periods designated summer-rainy, summer-dry, fall-rainy, and fall-dry.
Values are the pooled variances from the two stations. F value is the ratio of variances in the rainy
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* Significant at 95% level for two-tailed F test.

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TABLE 8. Two-way analysis of variance with replication of population density measurements for Keratella cochlearis. Treatments are partitioned into season (summer/fall) and precipitation regime (rainy/dry). See text for definition of season and precipitation regimes. Values are transformed to log₁₀ (X+1).

Source	df	S.S.	M.S.	F
Treatment	3	5.89	1.96	$3.92*$
Summer/Fall		0.57	0.57	1.14
Rainy/Dry	1	0.41	0.41	0.82
Interaction	1	4.91	4.91	$9.82*$
Error	58	28.86	0.50	
TOTAL	61	34.75	0.57	

*Signficant at 95% level.

TABLE 9. Duncan's multiple range test of population density means for Keratella cochlearis in different seasons and pre- cipitation regimes. Lines below population density means group values that are not significantly different at the 95% level. Values are transfonned to 10910 (X+l).

TABLE 10. Two-way analysis of variance with replication of population density measurements for Bosmina longirostris. Treatments are partitioned into season (summer/fall) and precipitation regime (rainy/day). See text for definition of season and precipitation regimes. Values are transformed to 10910 (X+l).

TABLE 11. Duncan's multiple range test of population density means for Bosmina longirostris in different seasons and precipitation regimes. Lines below population density means group values that are not significantly different at the 95% level. Values are transformed to log $_{10}$ (X+1).

TABLE 12. Two-way analysis of variance with replication of population density measurements for Mesocyclops edax. Treatments are partitioned into season (summer/fall) and precipitation regine (rainy/dry). See text for definition of season and precipitation regimes. Values are transformed to \log_{10} (X+1).

*Significant at 95% level.

TABLE 13. Duncan's multiple range test of population density means for Mesocycl ops edax in different seasons and precipitation regimes. Lines below population density means group values that are not significantly different at the 95% level. Values are transformed to 10910 (*X+* 1).

Fig. 1. Bathymetric map of Westhampton Lake with the location of sampling stations indicated. Contour lines are in one meter intervals, and data is updated to April 1979. SR indicates the location of the stage rain recorder on Robins' Branch near the confluence of Little Westham Creek.

Fig. 2. Hydrographs during rainfall on July 25, 1978 (a) and August 4, 1978 (b) generated by a stage-rain recorder on Robins' Branch. Data represents calibrated flow in m3/sec versus time in hours.

Fig. 3. Isothermal lines of the temperature gradient of Westhampton Lake from June 30 to December 22, 1978. "D" is dry period; "R" is rainy period; "SU" is the period of summer stratification, and "FA" is the period of fall turnover.

Fig. 4. Phytoplankton abundance measured by fluorescence in Westhampton Lake from June 30 to December 22, 1978. "D" is dry period; "R" is rainy period; "SU" is the period of summer stratification, and "FA" is the period of fall turnover.

Fig. 5. Population density in numbers/l of Keratella cochlearis (Rotifera) from station UL (solid line) and station DL (dashed line) from June 30 to December 22, 1978. "D" is dry period; "R" is rainy period; "SU" is the period of summer stratification, and "FA" is the period of fall turnover.

Fig. 6. Population density in numbers/1 of Bosmina longirostris (Cladocera) from station UL (solid line) and station DL (dashed line) from June 30 to December 22, 1978 , ."D" is dry period; "R" is rainy period; "SU" is the period of summer stratification, and "FA" is the period of fall turnover.

Fig. 7. Population density in numbers/l of Mesocyclops edax (Copepoda) from station UL (solid line) and station DL (dashed line) from June 30 December 22, 1978. "D" is dry period; "R" is rainy period; "SU" is the period of summer stratification, and "FA" is the period of fall turnover.

Appendix A

Population density of zooplankton in Westhampton Lake at stations UL and DL in collection, June 30 to December 22, 1978. Units of measure were No./l.

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Appendix B. Temperature profile readings in degrees celsius from June 30, 1978 to December 22, 1978 in Westhampton Lake. Depth is in meters and all readings are from station D. L. at the front wall of the Student Commons Building.

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Appendix C. Data were gathered on ten species of zooplankton in the course of this study. This list may assist others who collect and need to identify zooplankton in Westhampton Lake in future studies. Please note that identification of copipods were confirmed by Dr. Harry C. Yeatman.

Rotifera

Conochilus unicornis Keratella cochlearis Kellicottia bostoniensis Polyarthra sp. Asplanchna sp.

Cladocera

Bosmina longirostris Daphnia longispina

Copepoda

Mesocyclops edax Tropocyclops prasinus mexicanus Cyclops vernalis

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Appendix D. Fluorescence measurements from stations UL and DL in Westhampton Lake from June 30 to December 22, 1978. Measurements were made with a Turner Model III fluorometer using an arbitrary scale from zero to 100.

Vita

I was born on August 24, 1947, and grew up in and around Atlanta, Georgia. I attended the University of Georgia and graduated in 1970 with a Bachelor of Science degree in Zoology. For six months, immediately following undergraduate school, I worked as a research assistant at the University of Georgia Marine Institute, Sapelo Island, Georgia. In 1971, I moved to Richmond, Virginia and worked as a research associate at the Virginia Institute for Scientific Research (V.I.S.R.). In both positions, I researched the effects of industrial pollution on aquatic ecosystems. During my employment at V.I.S.R., I attended graduate school as a part-time student at the University of Richmond. In 1974, my position at V.I.S.R. was terminated as research funds were not available, and I discontinued the Master Degree program. I worked as a manager of a pl asmapheresis: center for the following three and one-half years. In 1978, I returned to the University of Richmond to finish the requirements for a Master of Science degree, and, in 1979, worked at the Virginia State Water Control Board.

Presently, I am living in Alexandria, Virginia and working for Potomac Electric Power Company as a biologist. My research there involves the evaluation of environmental impact of electric generating stations on fresh water and estuarine rivers.