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The University of Oklahoma, Ph.D., 1972
Zoology

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THE UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

ASPECTS OF THE POPULATION DYNAMICS OF THE CALANOID COPEPOD, *DIAPTOMUS CLAVIPES* SCHACHT

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

degree of

DOCTOR OF PHILOSOPHY

BY

CARL W. GEHRS

Norman, Oklahoma

1972

ASPECTS OF THE POPULATION DYNAMICS OF THE CALANOID

COPEPOD *DIAPTOMUS CLAVIPES* SCHACHT

APPROVED BY

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ASPECTS OF THE POPULATION DYNAMICS OF THE CALANOID COPEPOD, *DIAPTOMUS CLAVIPES* SCHACHT

INTRODUCTION

The Cladocera and Copepoda have long been recognized as the most important primary consumers in aquatic environments, with the former more important in fresh water, the latter, in salt water (Pennak, 1953). Little is known, however, about the population dynamics of these groups (Armitage and Davis, 1967). Several environmental parameters have been studied in an attempt to determine the more important factors affecting zooplankton populations. Temperature was found to affect population numbers in three species of cyclopoid copepods by Andrews (1953). Edmondson *et al.* (1962) found a positive relationship between the abundance of phytoplankton and the rate of reproduction in copepods, with a bloom of algae being followed closely by increased reproductive activity in the copepods. An inverse correlation between phytoplankton and zooplankton was found by Anderson *et al.* (1955) in two lakes in Washington. They suggested that this resulted from the zooplankton effectively checking the rise of the phytoplankton numbers through grazing activities. Their findings concur with those of Harvey *et al.* (1935) and Hardy (1936).

Several investigations have suggested that temperature affects the ultimate size a zooplankter attains with those animals developing in

colder waters attaining larger sizes than those animals developing in warmer waters. Coker (1934), however, reported that although temperature and a shortage of food retarded the development of three species of Cyclops; C. vernalis, C. serrulatus, and C. viridis, food had no affect on the size of the individuals of the various stages. Green (1966) found that the low numbers of eggs produced by several species of Cladocera in the summer were caused by a single dominant factor, temperature, the size of the adults being inversely correlated with the developmental temperature. Egg production in Cyclops strenuus strenuus was found to follow a similar pattern (Elgmork, 1959), while Smyly (1968, 1970) encountered similar results in Diaptomus gracilis and Acanthocyclops viridis, respectively. Ravera and Tonolli (1956) also found a correlation between body size and the number of eggs per clutch in Arctodiaptomus bacillifer and Acanthodiaptomus dentricornus. They further correlated this body size and egg relationship to the extent of water renewal in mountain lakes. The larger organisms were more fecund, and therefore their chances of successful reproduction in the lake were enhanced on a strictly arithmetic basis. An inverse correlation between temperature and body size in copepods with the decreased size resulting in fewer eggs per clutch was found in Diaptomus gracilis by Chapman (1969). McLaren (1965) studied the relationships between temperature and egg size, body size, development rate, and fecundity in Pseudocalanus. In a study of the effects of temperature on growth of zooplankton (McLaren, 1963), he concluded that although development time is a function of temperature, a shortage of food may retard the rate of development.

Although significant correlations between reproduction and temperature, food, or the size of the adult organisms were found by the previous investigators, these correlations do not, in themselves, show a cause and effect relationship. A major purpose of the current investigation was to determine if temperature does, in fact, affect the number of eggs produced by Diaptomus clavipes.

Life Table Approach to Population Dynamics

Much of the previous work in freshwater ecology has been at the community level, sampling and identifying the various organisms present and attempting to draw conclusions concerning their interactions and relationships in the community or ecosystem (e.g., Hazelwood and Parker, 1961).

Another approach, however, is to learn as much as possible about the population ecology of a single (or a few) very important species, and then, armed with this knowledge, analyze the interrelations of this (these) species to the entire community. My research utilizes this approach in a study of the dynamics of a population of the calanoid copepod, Diaptomus clavipes Schacht, in a small pond. The presentation of population data in the form of life tables (Deevey, 1947) lends itself well to this approach. In this phase of my research the duration of the various life stages was determined, thus permitting the construction and comparison of life tables and survivorship curves for the generations occurring in a population of D. clavipes during a single reproductive year. Comparisons between survivorship curves developed from field and laboratory data are made in order to determine the stages in the life cycle of the field population in which mortality rates do not parellel those obtained in the laboratory, and, therefore, deserve further investigation.

A life table summarizes the vital statistics for every stage or age interval of a population. These statistics include, for each interval, the number surviving at the onset (l_x), the number dying (d_x), the mortality rate (q_x), the mean number alive (L_x), the total life expectancy for the remaining animals (T_x), and the mean life expectancy (e_x) (Allee et al., 1949). Life tables are of further usefulness in that data from the various columns may be presented graphically to permit comparison of parameters of different populations. An example of the use of the life table approach to population studies is the report of Morris and Miller (1954), who determined the weak points of, and the environmental factors having the greatest effect upon, the life cycle of the spruce budworm.

Two basic types of life tables are recognized. A horizontal table is formed when a large cohort is followed through life, with deaths being recorded as they occur. A vertical life table is produced by determining the number of organisms of the various ages present on a given date, or in a given collection, and constructing a table from these data. For the latter type one must assume that birth and death rates remain equal and that the population is stable. In actual practice, ecological data for life tables are derived in one of three ways: (1) observation or determination of the age at death (e.g., Murie, 1944); (2) following the survival of a large cohort at fairly close intervals (e.g., Edmondson, 1945); and (3) determining the age structure in a sample and equating shrinkage between age classes at a point in time with survivorship (e.g., Kortland, 1942). Only the second derivation is considered statistically acceptable (Deevey, 1947).

Deevey (1947) has recognized three general types of curves when survival (l_x) is plotted against time on semilog paper. A diagonal curve is found when a constant mortality occurs in each stage: the probability of death being independant of age and no individual living long enough to die of old age. This type of survivorship curve is typical of adult birds and fish. A second type of survivorship curve results when there is little early mortality and most of the adult organisms die more or less simultaneously. It is referred to as a negatively skewed or physiological curve and is characteristic of many laboratory populations. The final form of survivorship curve, the positively skewed curve, results when there is heavy early mortality followed by relatively long survival of the few remaining organisms.

Pearl and Doering (1923), in a comparison of the mortality rates of various organisms to that of man, constructed a survivorship curve for the rotifer, Proales decipens, based on data published by Noyes (1922). Although Frank et al. (1957) used this approach in analyzing laboratory populations of Daphnia pulex, few subsequent investigations on zooplankton have utilized this valuable approach in the study of populations. Edmondson (1945) was able to follow the dynamics of populations of sessile rotifers through the use of different colored dyes. He determined the death rates of the various age classes by the decrease in the number of organisms of a particular color (age) in the colony. Slobodkin (1954) studied the population dynamics of Daphnia obtusa in the laboratory. By following populations grown at various food, temperature, light, and density levels, he constructed life tables for the animals' grown at the different levels of the various parameters. He concluded that the amount of food was the most important factor in determining population size.

Comita (1956) in a field study of the calanoid copepod, Limnocalanus johanseni, estimated the durations of the instars by the time intervals between peaks in abundance of successive stages. He was unable to determine egg production in this population, however, since the eggs are not carried by the female of this species but are dropped after production. With no census of egg production he was also unable to calculate the hatching success in this population. Comita and Anderson (1959) and Chapman (1969) used similar approaches to determine the durations of the various stages of copepods. Hall (1964) in his paper on Daphnia galeata mendotae integrated the laboratory and field approaches to population studies. Having determined the development times in the laboratory and the number of eggs produced in the field, he predicted the size of the field population using the exponential growth formula. Comparing the actual population size to the predicted size, he determined that predation during the summer months, rather than decreased reproduction, had caused the observed decrease in total population size.

Reproduction

A second concern of this study was an analysis of reproduction. In any population, the change in the number of organisms is the result of four factors; immigration, emigration, birth, and death. Since the pond in which this population resides is not connected to any other body of water immigration and emigration are negligible. Edmondson (1960) uses as his reproductive index the ratio of eggs to animals in a population of rotifers (crude birth rate). A similar technique was used by Elster (1964) in his study of Eudiaptomus gracilis. Since the adult of D. clavipes is

easily distinguished from the immature stages (Ewers, 1930; Kamal and Armitage, 1967), it was possible to determine the ratio of eggs to adults. The specific birth rates (m_x) (Allee et al., 1949) were calculated and compared for the various seasons, and several environmental parameters were studied in an attempt to determine the underlying controls of reproduction in this population.

Heterogeneity of Distribution

It is widely acknowledged that clumping occurs in populations of various species of zooplankton in marine and larger freshwater environments, with the extent and degree of clumping directly affecting the reliability of the data collected. Cushing and Tungate (1963) studied patchiness in Calanus in the North Sea. Hardy (1936, 1955) described the uneven distribution of oceanic plankton. Cassie, in a series of papers (1959a, 1959b, 1960, and 1963), discussed the microdistribution of marine plankton and factors causing these distributional patterns. Little effort has been expended, however, in determining whether similar phenomena occur in smaller bodies of water.

Several investigators have utilized Fisher's coefficient of dispersion ($S^2/\bar{X}$, where S^2 is the variance and $\bar{X}$ is the mean size of the population) to study heterogeneity of dispersion in a population. Any departure of this ratio from unity is a measure of dispersion. Ricker (1937) examined the variability of distribution of freshwater plankton in Cultus Lake, British Columbia and found Cyclops clumped, Daphnia uniformly distributed, and Epischura and Bosmina randomly distributed. Comita and Comita (1956) studied the vertical distribution patterns of

various stages of the calanoid copepod, Diaptomus siciloides. They found each stage except nauplius II clumped. Tash et al. (1966), in a study on the occurrence and distribution of Cladocera and Copepoda in Lewis and Clark Lake, South Dakota, found apparent differences in the relative abundance of various species between littoral and limnetic areas. Wiebe and Holland (1968) studied the effects of plankton patchiness on the catches in repeated net tows. Wiebe (1970, 1971) determined the effects of patchiness on sampling in marine systems and utilized a computer model in determining its effects on sampling error.

Gehrs (1967), in a study of the relative abundance of Cladocera and Copepoda in a Kansas pond, found that at least 50% of each of the ten species collected was obtained at one of the six stations sampled, with the different species being concentrated at different stations. In a study designed primarily to determine vertical migration patterns of the various stages of the calanoid copepod Diaptomus leptopes, Healy (1967) noted that although horizontal clumping appeared to occur, the data did not completely support such a conclusion. Parr (1967) concluded that most species of Cladocera, Copepoda, and Rotatoria occurring in Fish Lake, Utah, were typically littoral or limnetic rather than both, while Straskraba (1965), in a study of the productivity of littoral regions of pools and ponds, found increased numbers of zooplankton in littoral as compared to limnetic regions. This resulted from a concentration of copepods in these areas rather than from a concentration of cladocerans. Quade (1970) correlated the occurrence of cladoceran species, primarily chydorids, with species of rooted aquatics.

To make accurate extimates concerning population numbers it is of value to determine the distributional pattern exhibited by the population being studied. An important purpose of the present work was to determine the internal distributional pattern of the D. clavipes population and to investigate the causes of the observed pattern.

METHODS AND MATERIALS

The study pond is located in Township 9N, Range 3W, Section 11 of Cleveland County, Oklahoma. It is approximately 13.1 km SSE of Norman, Oklahoma. It is a man-made impoundment receiving runoff from the surrounding prairie at its east and southwest margins. There are no fish in the pond. The morphometry of the pond (Appendix I) was determined following procedures outlined by Welch (1948). Pennak (1957) suggested that if one wants a reliable estimate of species composition and relative abundance of each species in an aquatic environment sampling from top to bottom is imperative. The same reasoning applies when determining the absolute numbers of a given species. In the present study sampling was done by means of a semi-pliable, 6.5 cm diameter, wire-embedded polyethylene tubing, suitable calibrated for depth measurements. A rope was attached to one end of the tube. This end was lowered perpendicular to the surface until it reached the bottom of the pond. After attaching a #20 plankton net over the oppositie end of the tube, the lowered end was raised in a similar manner to that described by Pennak (1962), thereby causing a vertical column of water to be filtered through the plankton net.

Although sampling was carried out from May, 1970 until October, 1971, only data from 19 February through 29 October, 1971 are considered in this paper. These dates encompass the period of the year during which successful reproduction occurred in this population. On 19 February

almost the entire population was in the adult stage and reproductive activity had begun, as evidenced by the high number of females carrying eggs. By the termination date, 29 October, although the temperature was still well within the range necessary for successful reproduction (approximately 10° C to 30° C), successful reproduction was greatly curtailed. This was evidenced by the fact that only low numbers of immature copepodid animals were collected on the last three dates. Collections were taken every other day from 19 February to 20 April, and every two weeks from 24 April until the termination of the study. The intensive collection period was instigated to determine the duration of the instars (Comita, 1956) and to allow the development of a horizontal life table (Deevey, 1947) for the first generation.

In analyzing reproduction it was the intent of this study, not only to follow and describe the various reproductive parameters, but also to relate variations in these parameters to temperature and food. Thus, at the same time that samples of animals were collected, the vertical temperature profile of the water was determined. Temperature readings were taken at 0.5 m depth intervals from surface to bottom in the open water region with a Whitney Underwater Thermistor.

Chlorophyll _a_ concentrations were used as an index of food availability. Water for chlorophyll _a_ determinations was gathered at two week intervals at the same time animals were collected. Five hundred milliliters of water was collected from both the surface and bottom of the open water region of the pond through use of a Kemmerer water sampler. The two samples were combined, the water was returned to the laboratory, and chlorophyll _a_ determinations were made following a modification of the

procedures outlined by Small (1961). After shaking the water sample to mix it thoroughly two 200 or 300 ml subsamples were poured into separate 300 ml beakers. Which of these two amounts was used was determined by the turbidity of the water - high turbidity, a 200 ml subsample; low turbidity, a 300 ml subsample. Each of the subsamples was passed through a membrane filter apparatus using a 0.8 micron (average pore size) filter to concentrate the phytoplankton. The filter was then removed from the apparatus, placed in a 50 ml test tube, and the test tube was capped. A duplicate procedure was followed using tap water rather than pond water in order to provide a control. Ten milliliters of 90% acetone were added to each test tube. The tubes were then capped and placed in a constant temperature water bath (21° C) for 30 minutes. After 15 minutes the tubes were lightly shaken to aid mixing of the materials. When the 30 minute incubation period was over, the tubes were removed from the water bath, the dissolved materials were transferred to centrifuge tubes, and these were centrifuged at high speed for 1 minute. The supernate was then transferred to a cuvette, and, using the tap water extract to zero the spectrocolorimeter (B & L Spectronic 20), the percent absorbance of the two extracts at a wavelength of 665 millimicrons was determined. The average of two readings was recorded as a measure of the chlorophyll a present.

Field Data

To determine the dispersion pattern of the population it was necessary to obtain data appropriate for statistical testing. During the preliminary period of sampling it was apparent that most individuals of this species were located in open water rather than where rooted

aquatics were growing. For this reason the pond was divided horizontally into two regions or strata, the area where rooted aquatics came within 40 cm of the surface and the open water area. Eight samples were taken from each region on each date with the sites sampled selected by means of a random numbers table. The number of adults (copepodid VI) per liter in each sample was determined by dividing the total number of adults by the number of liters sampled.

The number of adult and copepodid V individuals of each sex, the number of females carrying eggs, and the numbers of the other copepodite stages were determined by complete census of each sample. The numbers of the various naupliar stages were determined after combining the samples from each stratum into two groups. Each pooled sample was then divided several times through use of a plankton splitter, and the nauplii in one of the resulting subsamples were counted. The mean number of eggs per clutch was determined at the same time. The number of splits necessary was determined in relation to the total number of animals counted in each region and was chosen to insure the census of at least 20 clutches. The amount of time an individual spends in naupliar stages I to III is relatively small (apparently less than 24 hours), and, for this reason these stages were uncommon in the samples, and so they were lumped for counting.

Laboratory Data

Animals were cultured in 100 ml beakers each containing 80 ml of pond water which had been filtered twice through #20 bolting cloth. The beakers were kept in a constant temperature chamber at 21° C and under a daily cycle of 12 hours of light and 12 hours of dark. The animals were fed 0.1 ml of an aqueous mixture of trout food and dried

alfalfa, twice weekly. The mixture was prepared by combining 10 g of commercial trout food, 0.5 g of dried alfalfa, and 250 ml of distilled water in a Waring blender. This was run at high speed for 5 minutes after which the material was strained through #20 bolting cloth. An additional 50 ml of water was added to the blender to wash out all material, and this wash water was then strained and added to the 250 ml of material already prepared. The filtrate was placed in a capped flask and stored in a refrigerator until used. If this food solution was not used within two weeks it was discarded and a new mixture prepared. To initiate an experiment, a single pair of adult animals (one male and one female) was added to each beaker. The animals to be used were taken from a stock culture reared at the same temperature and light as used in the experiment and consisting of individuals at least one generation removed from the field.

Two questions pertaining to the effect of rooted aquatics on D. clavipes were studied in the laboratory. The first question concerns the ability of the adults to survive when they are forced to live in an environment in which Potamogeton sp., a "narrow leafed species" (Fassett, 1957), is allowed to float free. Two sets of ten replicates each were used in this study. One set of beakers had Potamogeton sp. floating freely in the water, while the other set had no Potamogeton sp. added. To insure that the results obtained were due to the vegetation rather than to periphyton, the Potamogeton sp. was soaked for 15 minutes in tap water and then for 15 minutes in distilled water. The vegetation was then washed with fast flowing tap water for 5 minutes after which it was placed in a container of double filtered pond water until it was used. After four days, during which time the beakers were censused daily for mortality, the experiment was terminated.

The second question studied in the laboratory concerns the effect of higher aquatics on reproduction. The female of D. clavipes generally carries her eggs in a sac on the underside of the last body region, or urosome, until they hatch into nauplii. Hardin (1972) found that temperature affects the length of time the eggs are carried by the female of this species. My experiment was designed to determine if rooted aquatics affect the length of time eggs are carried by females and whether any effect found is physical or chemical. Five sets of ten replicates each were used in the study. One set of beakers had pieces of Potamogeton sp. restricted to a small region with nylon netting (weed restricted) while in a second set only nylon netting was added. A third group of containers had fifteen pieces of polyethylene tubing of approximately the same cross-sectional diameter as the Potamogeton sp. suspended vertically and randomly in each container. Suspension of the polyethylene tubing in the containers was accomplished by fastening a section of nylon netting over the top of the beaker to act as a guide for the sections of tubing. The polyethylene tubing was soaked in distilled water for 96 hours prior to the onset of the experiment. A fourth set of beakers also included polyethylene tubing, but it was restricted to the perimeter of the beaker. The final set of beakers, the controls, had nothing added.

In an attempt to keep conditions constant, animals were transferred to a clean beaker containing fresh water weekly. At this time young were removed and discarded. The beakers were checked at 24 hr intervals for animals carrying eggs and for nauplii. Checking for nauplii was necessary to insure that a clutch was not produced and hatched during the preceeding 24 hr period.

RESULTS AND DISCUSSION

Heterogeneity of Distribution

Field Data

At the onset of the study the concentrations of adults in the two regions showed only minor differences, with higher concentrations of adults in open water on one date and in the region of rooted aquatics on the next (Figure 1). Starting with 6 April, however, a definite pattern, with higher concentrations of adults in the open water region than in the region of rooted aquatics, began (Figure 2). This pattern prevailed until 21 October. The concentrations of adults ranged from 0.00 per liter in the area of rooted aquatics on 25 June to approximately 18 per liter in the open water region on 23 July.

To determine whether a significant difference in the concentrations of adults in the two regions existed on the different dates, the Student's 't' test was employed. A detectable difference was found on only five of twenty-three dates, 23 February, 9, 17, and 25 March, and 2 April, prior to 6 April (Figure 1) but from 6 April until 20 August, a significant difference ($P = 0.05$) between means was found on all but three of twenty-four dates (Figure 2). This onset of relatively continuous stratification coincides with two observations, an increased rate of growth of rooted aquatics and an addition to the population of new

Figure 1. Mean numbers of adults per liter in the two regions of the pond from 19 February to 4 April, 1971. Enlarged arabic numerals show those dates when there were detectable differences (P = 0.05) between concentrations of adults in the two regions

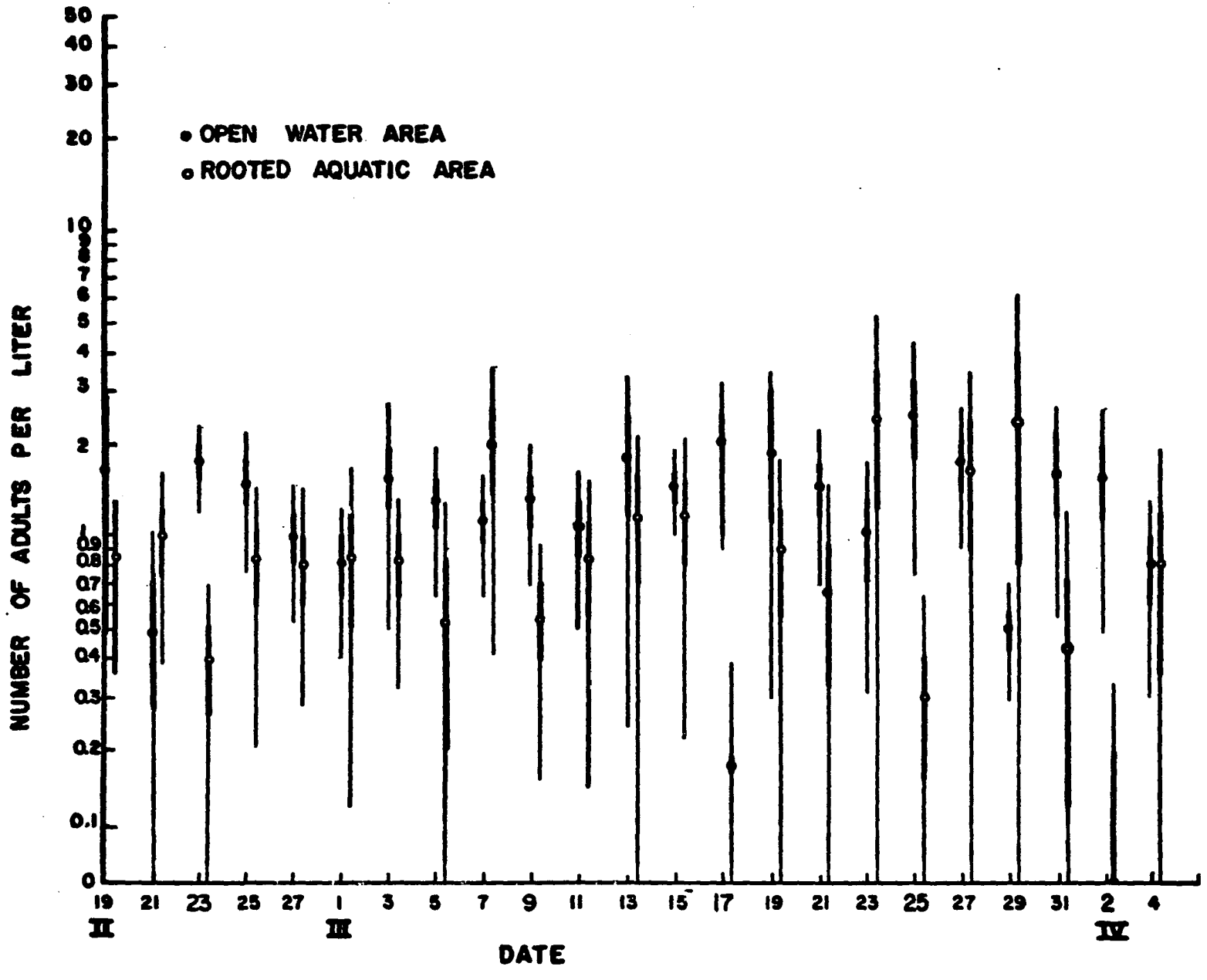
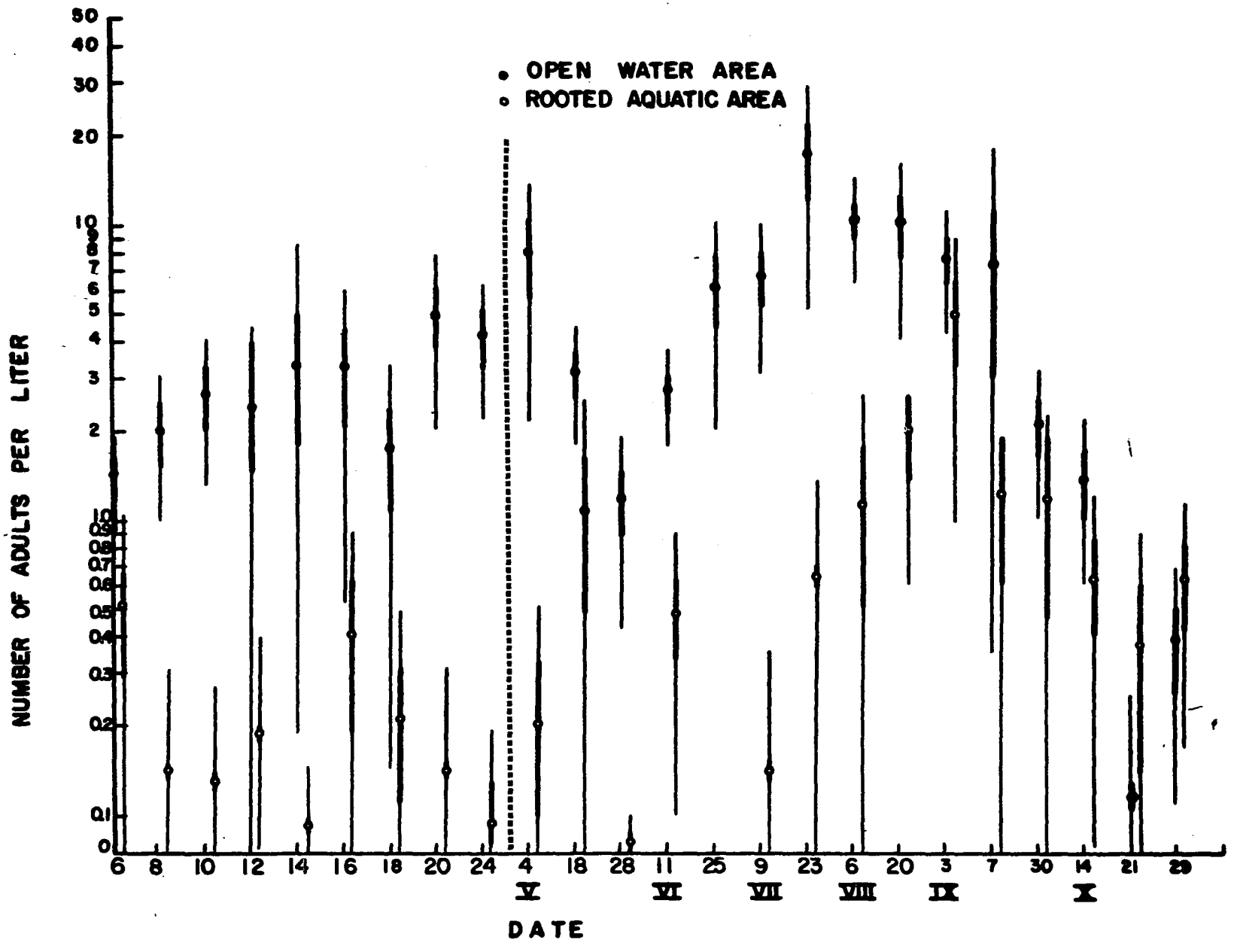

• OPEN WATER AREA
o ROOTED AQUATIC AREA
NUMBER OF ADULTS PER LITER
50
40
30
20
10
9
8
7
6
5
4
3
2
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
19 21 23 25 27 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 2 4
II
III
IV
DATE

Figure 2. Mean numbers of adults per liter in the two regions of the pond from 6 April to 29 October, 1971. Enlarged arabic numerals show those dates when there were detectable differences ($P = 0.05$) between concentrations of adults in the two regions. The vertical dotted line between 18 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.

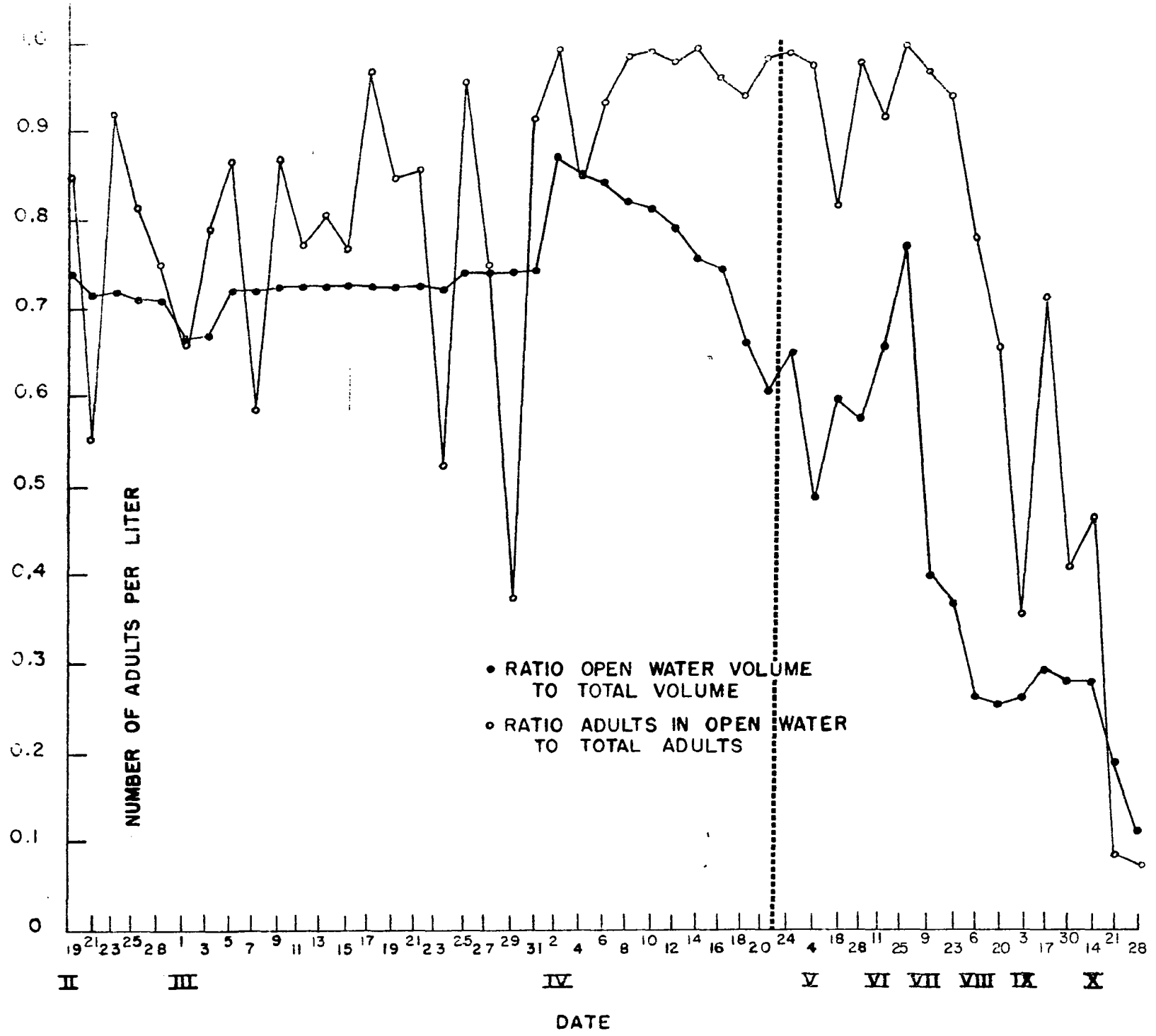

• OPEN WATER AREA
○ ROOTED AQUATIC AREA
NUMBER OF ADULTS PER LITER
50
40
30
20
10
0
6 8 10 12 14 16 18 20 24 4 18 28 11 25 9 23 6 20 3 7 30 14 21 29
V VI VII VIII IX X
DATE

adults which developed from the current year's reproductive activity (see RESULTS AND DISCUSSION: Life Table Approach to Population Dynamics, page 32).

More evidence of differential distribution between the two areas of the pond was obtained when the proportion of the total water volume in the open water region and the fraction of animals collected in open water are both graphed against time (Figure 3). If the animals are not concentrating in one of the areas of the pond, the probability of one proportion being larger than the other on any given date is 0.5. However, if the animals are concentrating in one of the areas, one of the proportions will be consistently larger than the other. The data were placed into two of three groups on the basis of the time of year they were gathered. The groupings include total sampling period (19 February to 29 October), early spring (19 February to 4 April), and spring-summer (6 April to 29 October). The early April date was chosen as the dividing time because of the increased rate of growth observed in the rooted aquatics from that date on and the addition of new adults to the population beginning then. In approximately 75% of the collections during early spring and 88% of the collections during the spring-summer period the proportion of the total adult population located in the open water region was greater than the proportion of the total water volume located in this region. These values are quite different from expected and are further evidence that the adult population is not evenly distributed between the two regions.

Although the Student's 't' test showed a detectable difference in the concentrations of adults in the two regions of the pond during most of the spring-summer period, it did not show a similar pattern during

Figure 3. Proportion of total water volume of the pond which was in the open water area and proportion of the total number of adults which were collected in the open water region on each collecting date. The vertical dotted line between 20 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
NUMBER OF ADULTS PER LITER
• RATIO OPEN WATER VOLUME TO TOTAL VOLUME
∘ RATIO ADULTS IN OPEN WATER TO TOTAL ADULTS
19 21 23 25 28 1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 2 4 6 8 10 12 14 16 18 20 24 4 18 28 11 25 9 23 6 20 3 17 30 14 21 28
II III IV V VI VII VIII IX X
DATE

the early spring period. One method of testing the data obtained during this period is to run an 'F' test on the two groups, the mean number of adults per liter in the open water region as compared to the mean number of adults per liter in the area in which rooted aquatics were found (Table 1). The F_s value is significant at the 0.05 level and indicates that a difference in the concentrations of adults also prevailed in the early spring period. These data plus the difference between means (Figures 1 and 2), show significant variation in the concentrations of adults in the two regions of the pond throughout the collecting period. In the early spring it is demonstrated for the entire period while in the spring-summer period it is shown by the degree of difference between the means on specific sampling dates. It appears, therefore, that a significant, somewhat continuous, stratification of the population is found during the period of active growth of the rooted aquatics. During the remainder of the year, although stratification can be detected, it is periodic and not to the same degree as in the summer.

Laboratory Data

Field data revealed heterogeneity of distribution prevailing throughout the collecting period and appearing to be correlated with the growth of higher aquatics. Laboratory experiment showed that these differences in concentrations were, in fact, a result of the rooted aquatics.

In the experiment 18 of 20 animals, forced to live in environments in which Potamogeton sp. was allowed to float free, died within 96 hours; whereas of 20 control animals 1 died in a comparable interval.

Table 1. Anova table on the difference between the mean number of adults per liter in the open water region and the region in which rooted aquatics were found during the early spring (19 February to 4 April, 1971).

Source of variation	df	DD	MS	F_s
Among regions	1	2.2751	2.2751	7.1454*
Within regions	44	14.0138	0.3184	
Total	45	16.2889		

* P = 0.05.

These data clearly demonstrate that adult D. clavipes are unable to survive when forced to live in proximity to Potamogeton sp..

Comparison of the mean clutch carrying times for females in the simulated weed and weed-free environments revealed that those animals in simulated weeds carried their eggs almost twice as long as did the animals in weed-free environments, 4.00 days and 2.22 days, respectively (Table 2). As a check on these results, the environments of the animals were reversed; with those animals previously in simulated weed environments now in weed-free environments and those animals previously in weed-free environments now in simulated weed environments. After the environments were switched, the mean clutch carrying times were 3.71 days in the simulated weed environment and 1.86 days in the weed-free environment (Table 3), again almost twice as long in the simulated weed as in the weed-free environments. In both cases the results were highly significant ($P \leq 0.01$) when the Student's 't' test was employed. Comparison of the mean clutch carrying times for females in the weed-free environments and the environments having polyethylene tubing around the perimeter of the beakers (Table 2) showed little difference between the two. This indicates that the difference between the average clutch carrying time for animals in simulated weed environments and that for animals in weed-free environments is not due to some chemical found in the polyethylene tubing. These data show that simulated weeds increase the length of time eggs are carried by the females. The cause or causes of this developmental retardation and the pathway by which it is implemented are not known and deserve further investigation.

Table 2. Means ($\bar{Y}$) and standard errors ($S_{\bar{Y}}$) for the times eggs were carried by females in simulated weed environments, weed-free environments, and environments in which the simulated weed was relegated to the perimeter of the beaker.

Environment	n	$\bar{Y}$ (in days)	$S_{\bar{Y}}$	P
Simulated weed	18	4.00	0.52	≤ 0.01
Weed free	18	2.22	0.22	
Simulated weed relegated to the perimeter of the beaker	18	2.01	0.25	

Table 3. Means ($\bar{Y}$) and standard errors ($S_{\bar{Y}}$) for the times eggs were carried by females in simulated weed environments and weed free environments after the environments of the animals were reversed.

Environment	n	$\bar{Y}$ (in days)	$S_{\bar{Y}}$	P
Simulated weed	7	3.71	0.42	$\leq$0.01
Weed free	7	1.86	0.14	

A comparison of the mean clutch carrying times for animals kept in restricted Potamogeton sp. environments and nylon netting environments (Table 4) revealed no detectable difference.

Field data revealed a heterogeneous distribution of D. clavipes during the entire study period apparently related to the occurrence of rooted vegetation. Laboratory data showed that the effect of rooted aquatics, in cases where the vegetation is not so thick that the organisms are simply killed, retardation of development and hence a decrease in reproductive rate occurred. Apparently the rooted aquatics are an effective factor in determining the regions of a body of water in which this species can live and reproduce.

In the past, investigations of zooplankton in small bodies of water commonly utilized one or two tows of a plankton net to determine species composition and abundance. To accept such data as accurate, one must assume either that the pond is a homogeneous environment with all species randomly or uniformly distributed or that the sampling method adequately cuts across all the habitats present in the pond. The data from the current study demonstrate that the first assumption is not necessarily correct, at least if macrophytes are present near the surface.

If one is to obtain meaningful data, even in relative terms, an adequate method of sampling must be undertaken. If one wishes to obtain data on the species composition in small bodies of water having areas of rooted aquatics and areas of open water, without undertaking a detailed sampling procedure, sampling should be during periods when rooted aquatics are at a minimum.

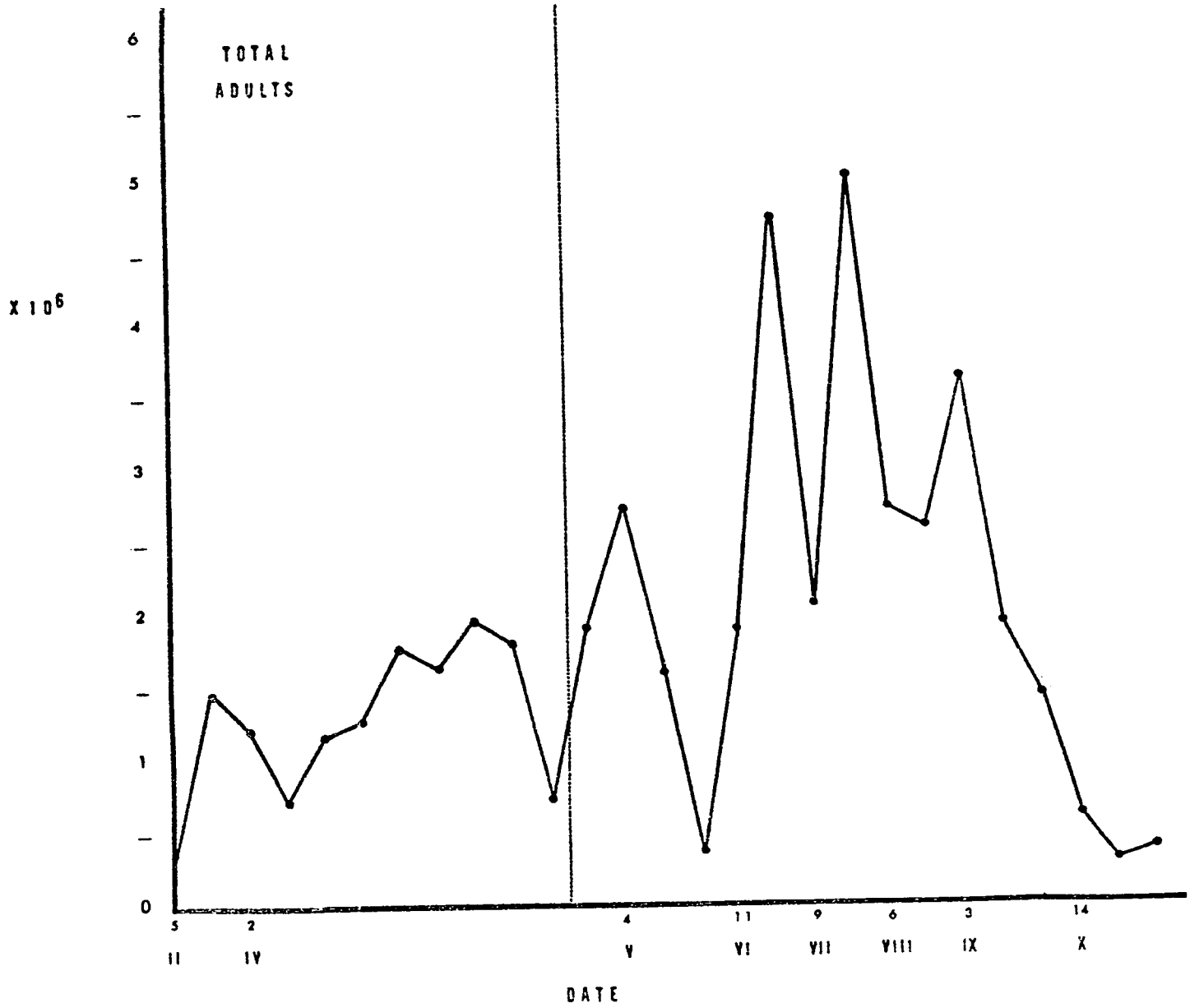
Table 4. Means ($\bar{Y}$) and standard errors ($S_{\bar{Y}}$) for the times eggs were carried by females in environments in which Potamogeton sp. was restricted to a small region by nylon netting and in nylon netting environments.

Environment	n	$\bar{Y}$ (in days)	$S_{\bar{Y}}$	P
Weed restricted	6	2.66	1.09	≤ 0.90
Nylon netting	6	3.00	0.45	

Life Table Approach to Population Dynamics

During February and early March, 1971, 'false starts' in the population development occurred during periods of relatively warm weather (surface water temperature between 6° and 9° C). The eggs hatched and the nauplii developed until nauplius IV where development ceased and the individuals eventually died. Data from these individuals were not used in determining the durations of the various instars. Since only adults and a few early nauplii were found at the start of this investigation the durations of the various instars were determined by taking the length of time between the first observation of successive instars in the population. This procedure could not be used in estimating the duration of the adult instar, however, since at no time were adults absent from the population. Instead, the duration of the copepodid VI stage was determined by measuring the length of time between low numbers of adults in the population. These lower inflection points in adult numbers were assumed to follow large mortality in this instar group. A low point in the number of adults occurred on 18 April, 1971, with a similar low point occurring on 28 May, 1971 (Figure 4). The period of time between these two dates, 40 days, was taken as an estimate of the duration of CVI. This compares closely with that of 38.65 days for the same species in the laboratory at 21° C (Hardin, 1972). The mean water temperature in the field during this period was approximately 15° C. The value of the mean temperature in this context is debateable, however, since vertical migration of the organisms and the diurnal temperature patterns at the various water depths would enable the organisms to live in a variety of temperature situations. The exact correlation of instar durations with temperature

Figure 4. Size of the adult population on each collecting date. The vertical dotted line between 18 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.


TOTAL
ADULTS
X 10⁶
6
5
4
3
2
1
0
5
II
2
IV
4
V
11
VI
9
VII
6
VIII
3
IX
14
X
DATE

is further complicated by food, since both quantity and quality of food apparently affect the developmental rates of copepods (Coker, 1934; Smyly, 1970).

Table 5 shows the durations of the various instars as determined in the field and also as computed from a composite of laboratory data. The laboratory data for this species were from Samples (1972) and were obtained at a temperature range of approximately 20° C to 25° C. Several studies have shown an inverse relationship between temperature and the developmental time of the various instars, for example McLaren (1965) found a longer developmental time in the Arctic calanoid Pseudocalanus at lower than at higher temperatures. A comparison of the field durations (obtained at lower temperatures) to the laboratory durations shows similar results in D. clavipes with a total developmental time to CVI of 28 days in the field and 21.46 days in the laboratory.

Life tables were constructed for the first generation (g_1) (Table 6), total year (Table 7), and laboratory animals (Table 9). Because of the ability of the animals to migrate vertically, the depth and diurnal differences in pond temperature, and the relatively similar developmental times at temperatures similar to those found in the pond, the durations of the various instars computed from a composite of the laboratory data were used for all generations except g_1. Since the field durations were determined from the first generation, these same durations were used for developing the life table of the first generation.

The number of individuals entering each of the various stages for the g_1 and laboratory study were determined by following the survival of a cohort of individuals at close intervals. This was accomplished by

Table 5. Durations of the various instars as determined in the field and computed from a composite of the laboratory data (approximately 20° to 25° C; Samples, 1972).

Stage	Duration		
	First Occurrence	Laboratory	
Egg-NIII	2	1.81	
NIV	2	1.39	
NV	2	1.20	
NVI	2	1.24	
CI	2	1.47	
CII	2	1.89	
CIII	6	3.46	
CIV	6	4.35	
CV	4	4.65	
Composite through CV	28	21.46	
CVI	40	40.00	(used field duration after comparison with Hardin, 1972)
Total life cycle	68 days	61.46 days	

computing the loss of individuals between the various stages at two day intervals. In g_1 the number of individuals reaching CVI was estimated by multiplying the ratio of new adults to total adults by the total adult population on 31 March, the first date new adults were observed in the population. The g_1 adults were distinguished from older animals by their more opaque appearance and slightly smaller size. Prior to 31 March none of the adults collected were opaque. This opaque appearance was thought to result from their new carapace (following the molt from CV to CVI) not yet having hardened, not yet having become covered with debris, or for some other undetermined reason. The total number of individuals entering each instar during the different generations or periods was determined by using the following formula:

$$\sum_{x=j}^{k} \frac{l_{i,x} + l_{i,x+1}}{2} \frac{W_x}{D_i} = N_i$$

where: l refers to the number of individuals alive;

i refers to the instar designation;

x refers to the collection designation;

j refers to the first collection prior to the appearance of instar i;

k refers to the collection following the last collection in which instar i appears;

D_i refers to the duration of instar i;

W_i refers to the interval in days between collection x and collection x + 1;

N_i refers to the number of individuals of instar i produced in the interval x to x + 1; and it also refers to the number of individuals of instar i produced in a particular generation.

Table 6 shows the life table for g_1. The l_x and d_x columns of this life table reveal over 80% mortality from egg to NIV with 836.62 out of every 1000 individuals entering, dying during this interval. Except for the adult instar which, of course, has a mortality rate (q_x) per 1000 entering this stage of 1000, the egg to NIV interval has the highest mortality rate. The second highest mortality rate occurs between stages NVI and CI with 613.87 out of every 1000 individuals entering, dying during this interval. The CIII to CIV interval has a mortality rate of 422.73 per 1000 (third highest). The apparent negative mortality rate found between stages CV and CVI reveals the limitation of this technique. It (negative mortality) resulted from either an overestimate of the numbers of CVI or an underestimate of the numbers of CV in this generation. The negative mortality rate does suggest, however, that little mortality occurred between stages CV and CVI.

The shortest life expectancy for g_1 is in the egg to NIII stage, with the remainder of the naupliar stages also having lower e_x values than any of the copepodite stages (Table 6). The longest life expectancy in this generation (32.36 days) is found in the CIV, although in all copepodite stages except CII (e_x of 18.45 days) the life expectancy is greater than 20 days. The life expectancies of the six copepodid stages contrast with those of 3.12 days, 11.97 days, and 9.14 days for egg, NIV, and NVI, respectively.

Survivorship, mortality, and longevity rates for the complete study (Table 7) revealed similar trends as those of g_1. The highest mortality rate, 881.40 per 1000 individuals entering dying during the interval, occurred in the egg to NIII stage. This was followed by a

Table 6. Life table for the first generation using the first occurrence to determine the durations of the various stages.

Stage	Number living at beginning of age interval	Number dying in interval	Mortality rate per 1000 alive at beginning of age interval	Mean number alive	Total life expectancy	Mean life-time remaining for those attaining age interval
	l_x	d_x	q_x	L_x	T_x	e_x
Egg-NIII	1000.00	836.62	836.62	581.69	3119.02	3.12
NIV	163.38	17.22	105.39	154.77	1955.64	11.97
NV	UNABLE TO DETERMINE FROM DATA.					
NVI	146.16	89.73	613.87	101.30	1336.56	9.14
CI	56.44	1.05	18.61	55.92	1133.96	20.09
CII	55.39	15.79	285.07	47.49	1022.12	18.45
CIII	39.60	16.74	422.73	31.58	927.14	23.41
CIV	22.86	0.57	24.93	22.58	739.76	32.36
CV	22.29	-3.16	-141.63	23.87	604.28	27.11
CVI	25.44	25.44	1000.00	12.72	508.80	20.00

Original l_x equals 10.454×10^6.

Table 7. Life table for the complete year study using the composite laboratory data to determine the durations of the various stages.

Stage	Number living at beginning of age interval	Number dying in interval	Mortality rate per 1000 alive at beginning of age interval	Mean number alive	Total life expectancy	Mean life-time remaining for those attaining age interval
	l_x	d_x	q_x	L_x	T_x	e_x
Egg-NIII	1000.00	881.40	881.40	559.30	1691.90	1.69
NIV	118.60	50.62	426.79	93.29	679.57	5.73
NV	67.98	15.24	224.15	60.36	549.89	8.09
NVI	52.74	24.76	469.42	40.36	477.46	9.05
CI	27.98	1.22	43.54	27.38	427.41	15.28
CII	26.77	11.09	414.21	21.22	387.17	14.46
CIII	15.68	0.85	53.93	15.26	347.06	22.13
CIV	14.83	0.18	11.80	14.75	294.26	19.84
CV	14.66	5.88	401.01	11.72	230.10	15.70
CVI	8.78	8.78	1000.00	4.39	175.60	20.00

mortality rate of 469.42 per 1000 for the NVI to CI interval. The greatest life expectancy (22.13 days) was found in the CIII stage. Although life expectancies for the various stages of the complete year's data were not as long as those for the first generation, they followed a similar trend with all the copepodite stages having longer life expectancies than naupliar stages. The lowest life expectancy was again in the egg to NIII stage, 1.69 days, while NIV, NV, and NVI had life expectancies of 5.73 days, 8.09 days, and 9.05 days, respectively. The lowest life expectancy for copepodite stages was found in CII (14.46 days) with each of the other copepodite instars having life expectancies of greater than 15 days.

The life table from the full year furnishes further evidence that the duration determined for the adult stage was relatively accurate. A successful population having an annual reproductive period, with no emigration and immigration, and whose numbers are in part determined by the cycle of available food, should have approximately the same number of organisms alive at the beginning of the reproductive period in one year as the next, provided that the available environment remains the same. The intrinsic rate of natural increase (Birch, 1948), or 'r', for such a population would be expected to approach 0 for the complete year. When 'r' was calculated from the full year's data using a 40 day duration for the adult stage and the average m_x (number of eggs/adult/day) values for the year (Figure 8), it came out to be -0.03 (Table 8), surprisingly close to 0 in view of the limitations of the method employed.

Morris and Miller (1954) chose the stages in the life cycle of the spruce budworm when it could most easily be destroyed by determining

Table 8. Calculation of the intrinsic rate of natural increase (r) using the adult survivorship from the full year study, a 40 day duration for the adult stage, and the average m_x value for the year.

Stage	Duration	l_x	m_x	$l_x m_x$	$x l_x m_x$
Egg	0-1.81	1.00000	00.00		
CV	21.46				
CVI	25.46	0.00878	2.78339	0.02443	0.62980
"	29.46	"	"	"	0.71970
"	33.46	"	"	"	0.81742
"	37.46	"	"	"	0.91514
"	41.46	"	"	"	1.01286
"	45.46	"	"	"	1.11058
"	49.46	"	"	"	1.20830
"	53.46	"	"	"	1.30602
"	57.46	"	"	"	1.40374
"	61.46	"	"	"	1.50146
		Total		0.24430	10.61720

T (generation time) = 39.45968

R_o (net reproductive rate) = 0.24430; ln = -1.4094

r = - 0.03572

the stages where the greatest mortality rates occurred. In a comparison of the life tables developed from the field data (g_1 and full year; Tables 6 and 7) two stages have similarly high mortality rates. The highest mortality rate is found in the egg to NIII stage with greater than 80% of the animals dying in this interval in each group. A second high mortality rate, almost 47%, although much less than in the egg to NIII stage, occurs in NVI. This is not unexpected in view of the drastic morphological changes occurring in the individual between this stage and CI. In contrast to survival of approximately 11% in eggs, once CI is attained the probability of surviving to maturity approaches 50%. This difference in survivorship between the egg, naupliar, and copepodite stages is further demonstrated by the life expectancies of the various instars, the copepodite stages having larger e_x values than any of the younger stages.

The life table prepared from laboratory data (Table 9) shows that the mortality rates of the egg to NIII stage and the NVI stage are almost identical, with 281.51 and 284.58 deaths per 1000 individuals, respectively. The mortality rates of the egg to NIII stage and all naupliar stages are higher than for any copepodite stage except CV. The mean life expectancies for the different copepodite stages are higher than those for either the egg to NIII or any of the naupliar stages, with values ranging from 20.00 days for the CVI instar to 24.19 days for CI and 24.58 days for CIII. The life expectancies for the naupliar stages and the egg to NIII stage ranged from a low of 12.92 days for the egg to NIII stage to 18.37 days for the NVI instar.

Table 9. Life table for laboratory animals using complete data from all animals at all temperatures.

Stage	Number living at beginning of age interval	Number dying in interval	Mortality rate per 1000 alive at beginning of age interval	Mean number alive	Total life expectancy	Mean life-time remaining for those attaining age interval
	l_x	d_x	q_x	L_x	T_x	e_x
Egg-NIII	1000.00	281.51	281.51	859.29	12917.72	12.92
NIV	718.49	115.55	160.82	660.71	11362.49	15.81
NV	602.94	71.43	118.47	567.23	10444.11	17.32
NVI	531.51	151.26	284.58	455.88	9763.43	18.37
CI	380.25	18.91	49.72	370.80	9198.14	24.19
CII	361.34	35.71	98.84	343.49	8653.06	23.95
CIII	325.63	27.31	83.87	311.97	8003.87	24.58
CIV	298.32	18.91	63.38	288.87	6924.45	23.21
CV	279.41	54.62	195.49	252.10	5667.87	20.29
CVI	224.79	224.79	1000.00	112.39	4495.60	20.00

Original l_x equals 1.302×10^3.

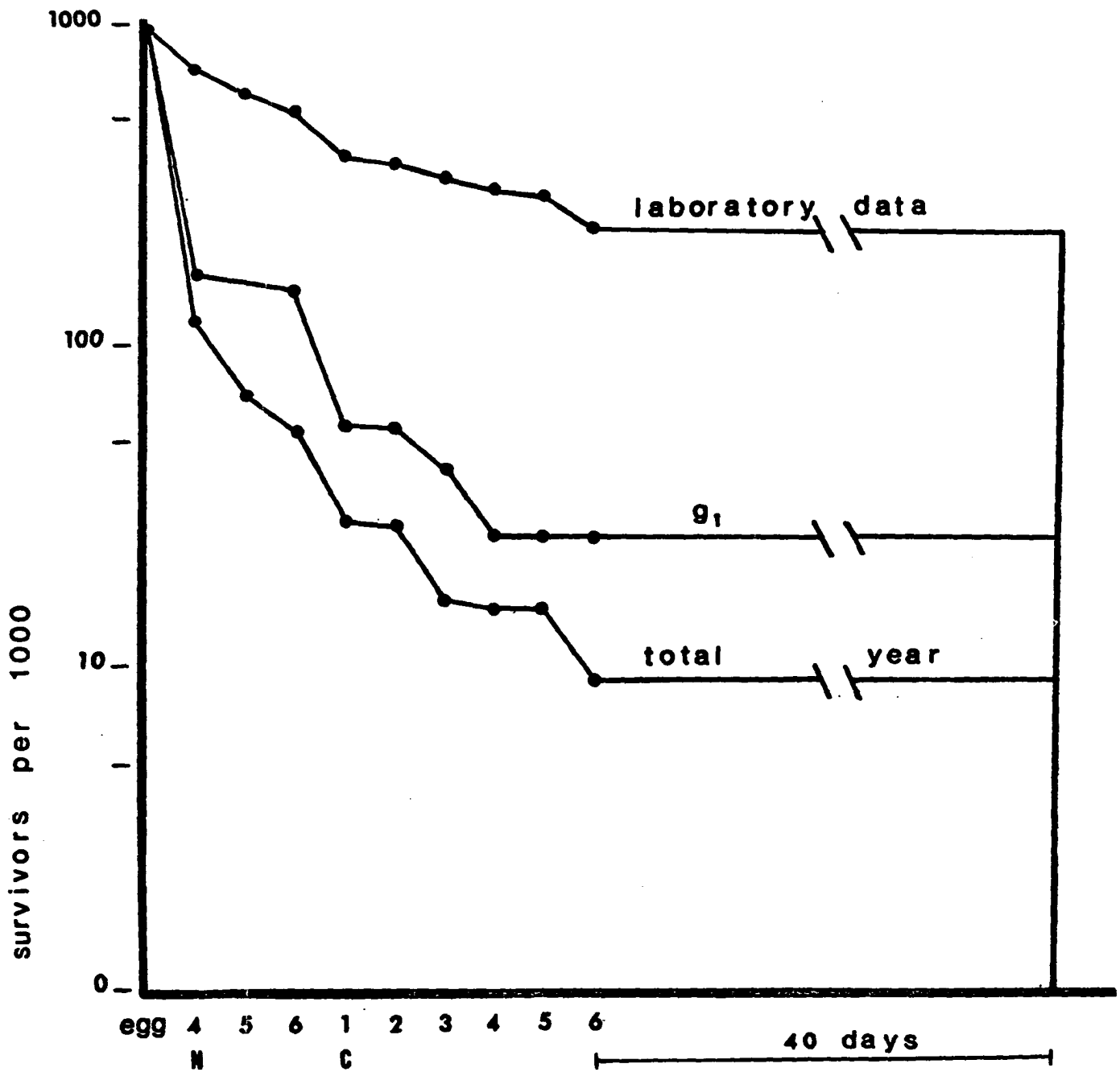
Comparison of the three life tables reveals several interesting points. Although a similar trend in the mortality rates of animals is seen in the three tables with egg to NIII and NVI having the highest mortalities, the table derived from laboratory data reveals almost the same mortality rates in the egg to NIII and NVI stages; whereas, in the field derived tables, mortality is far greater in the egg to NIII stage than in the NVI stage.

Another difference between laboratory and field derived mortality is in degree. Approximately 28% of the eggs perished in the laboratory while over 84% of all the eggs produced in the field and almost 84% of the eggs produced by the overwintering females failed to develop to NVI.

Plots of l_x curves for the first generation, laboratory population, and complete year's data allows visual comparison of survivorship for the three groups (Figure 5). A definite similarity in form exists among the three curves with the greatest survival occurring in the laboratory population. If the survivorship curve of the laboratory population is considered to show the survival for the various stages without the effects of a natural environment, then the differences between this curve and the two field derived curves can be considered as rough indications of the effects of environmental factors.

The forms of the three survivorship curves range from a near diagonal curve for the immature stages of the laboratory animals (death occurring independant of age) to the positively skewed curve for the instars of the two field populations (high early mortality). It appears that a negatively skewed curve characterizes the adult stage of each

Figure 5. Survivorship curves for the first generation (g_1), laboratory population, and complete year's study.

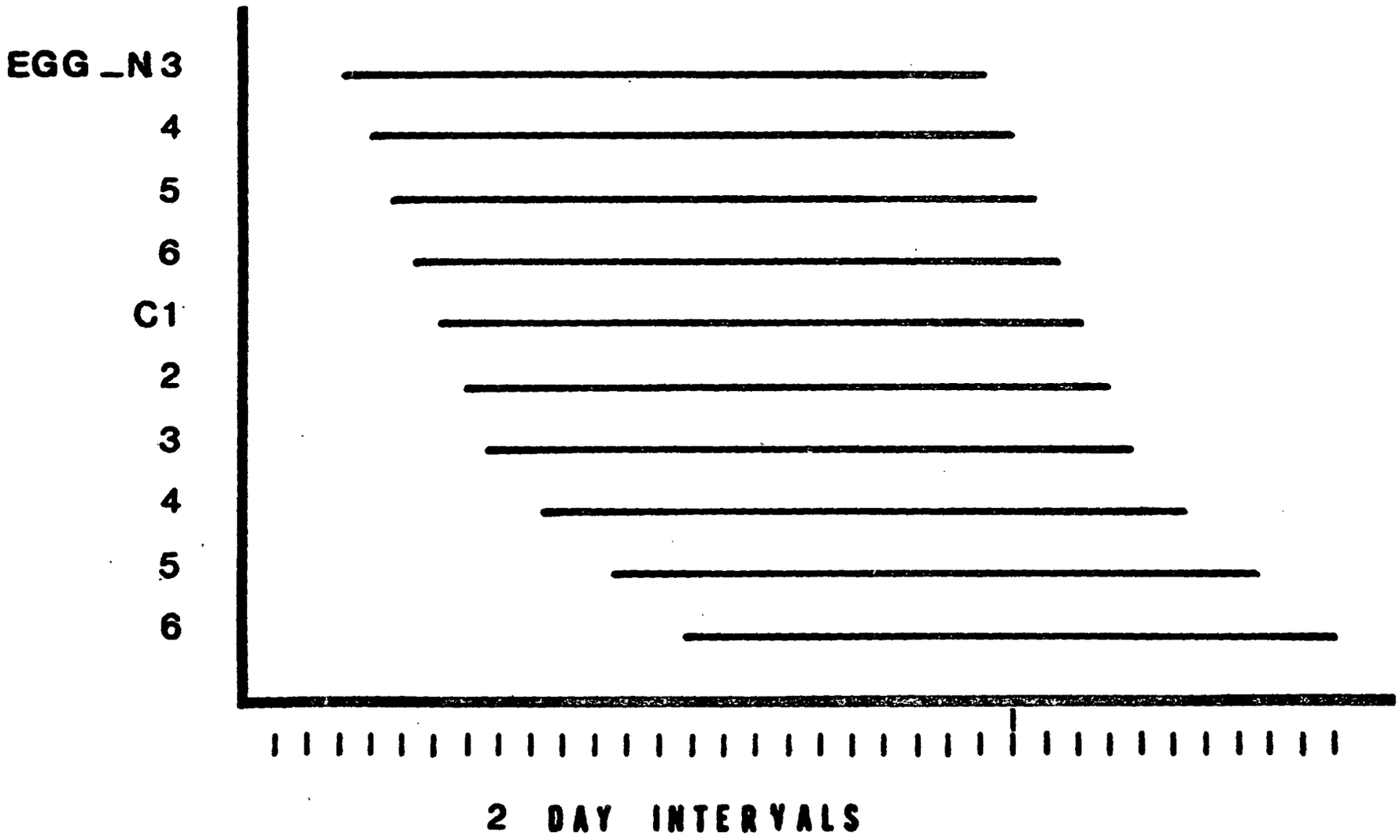

1000
100
10
0
survivors per 1000
laboratory data
g_1
total
year
egg 4 5 6 1 2 3 4 5 6
N
C
40 days

group with those animals reaching adulthood surviving until they die of old age. This follows when:

1) it is assumed that the sharp declines in adult population on 18 April and 28 May resulted from a more or less synchronous death of a large segment of the adult population;
2) it is recalled that the 'r' value for the entire year was close to the expected 0 for a 40 day duration of adult instar (Table 9);
3) the close agreement with laboratory data for the same species (Hardin, 1972) is considered.

A summation of the duration periods of the various stages gives the length of time that a particular generation survived. Assuming that the decline of adults on 28 May indicates the midpoint of the CVI duration for the second generation (it would also be the last day of occurrence for g_1), it was possible to determine the dates during which the g_2 adults were living. Subtracting the developmental time from egg to CVI from the total generation time provided the date when the first g_2 eggs were produced. A similar calculation determined the last possible date an egg could be produced and still develop into what would be considered a g_2 adult. This procedure is illustrated in Figure 6. A summation of the eggs produced in this period was taken as an estimate of the number of eggs entering g_2. Estimates of the numbers of the various instars were determined in like manner (using formula on page 36). Using the final dates of the various stages for a particular generation as starting points, subsequent generations could be followed.

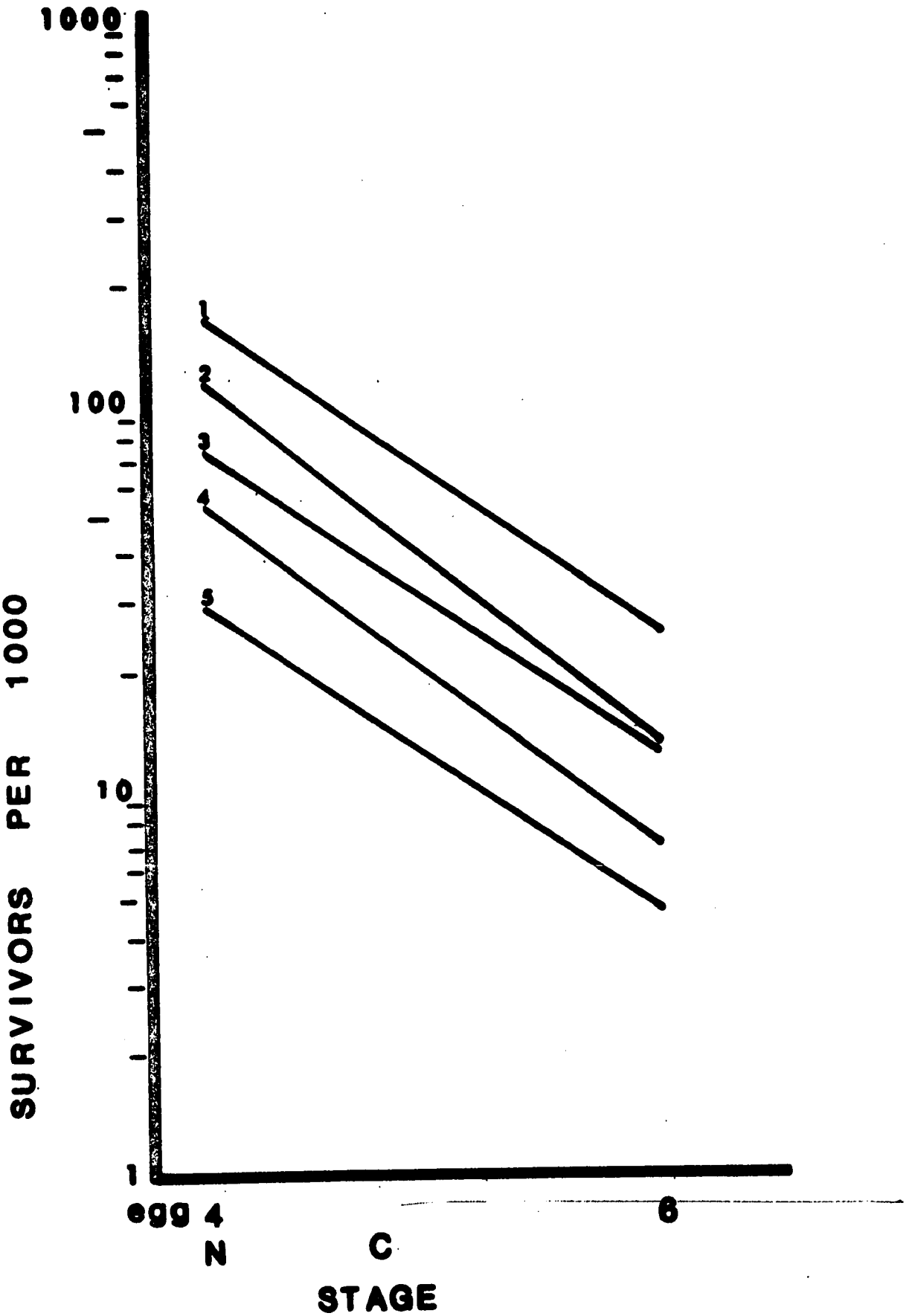
Figure 6. Graphical model of the method used in determining the first and last dates that an animal could enter each of the various stages (egg to CV) and still mature in time to be considered a member of the second generation (g_2).


EGG _N 3
4
5
6
C1
2
3
4
5
6
2 DAY INTERVALS

The numbers of the different instars of four successive generations (g_2 through g_5) were calculated accordingly. Because of the increased possibility of error resulting from sampling at fourteen day intervals the life tables for generations two through five are not presented here but are included in Appendix II. Of interest, however, is the fact that when the rate of survival from egg to NIV and CVI for the five generations are plotted on semilog paper (Figure 7) similar slopes are found in all cases with a decreasing rate of survival from g_1 to g_5. It appears that a somewhat constant mortality rate is found in all generations once the NIV stage has been attained.

Life tables and certain curves that can be constructed from them are valuable aids in determining general characteristics of animal populations. They also aid the investigator in determining those stages of the life cycle which have the highest mortality rates. This is of value to the individual studying pest species in that he can, through use of this approach, determine the weak points of the life cycle; and he can concentrate on increasing the mortality rates in these stages. If one is interested in studying the population dynamics or productivity of a species of animal, the use of l_x curves gives the information necessary in determining where to concentrate and what to study. In D. clavipes it is apparent that the cause of mortality (what) is of importance primarily during the egg to NIII interval (where) with the possible incusion of the metamorphosis from NVI to CI. Mortality is of little consequence in the adult instar since apparently a physiological l_x curve is found in this stage. Consequently attention should be focused on those factors which may affect the reproductive rate.

Figure 7. Rate of survival from egg to NIV and CVI for the five generations encountered in the 1971 reproductive year.

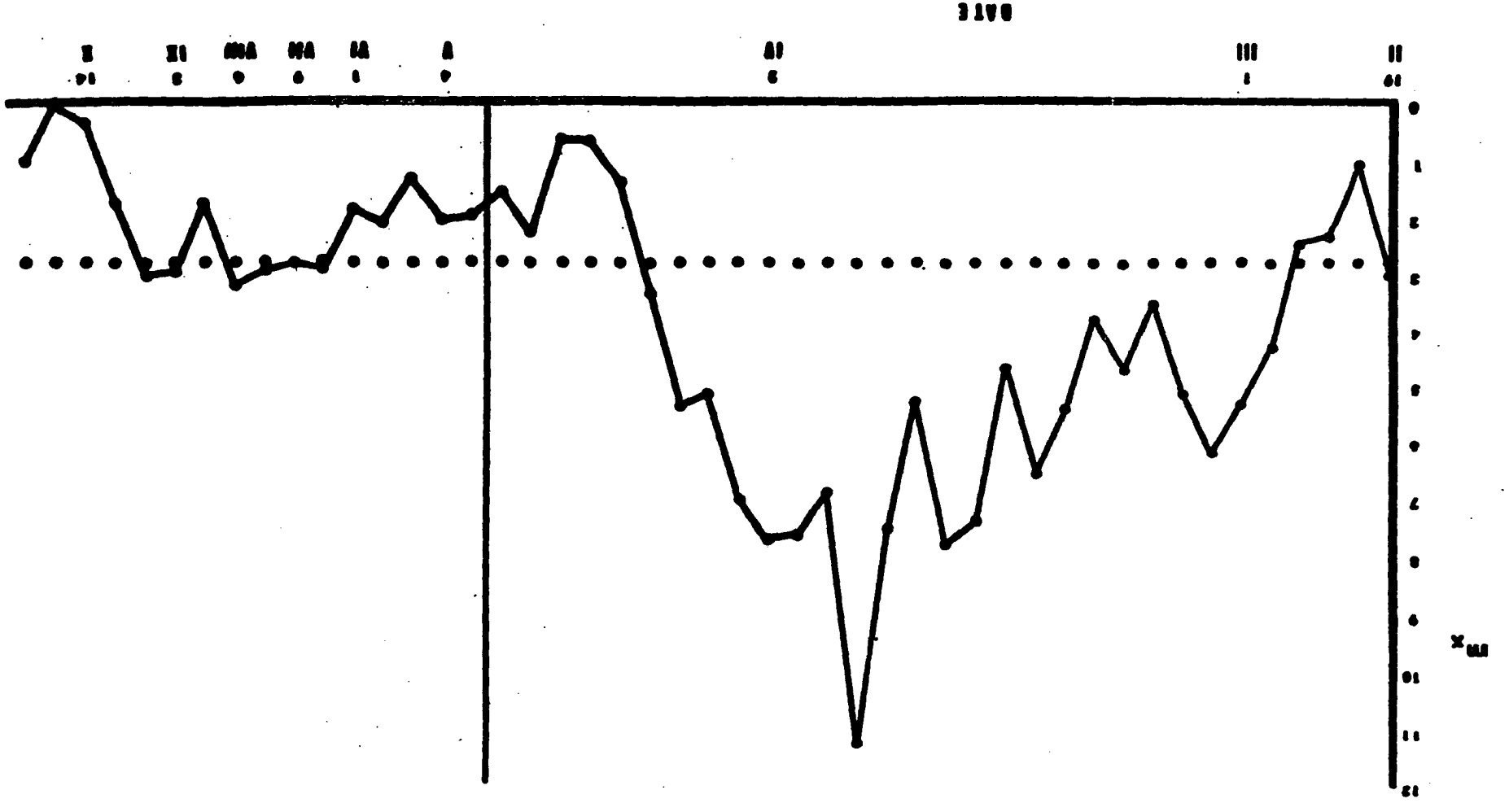

1000
100
10
1
SURVIVORS PER 1000
1
2
3
4
5
egg
4
6
N
C
STAGE

Reproduction

Analysis of the survivorship curves revealed three points of the life cycle requiring further consideration, egg production, the survivorship of the egg to NIII, and survivorship from NVI to the CI stage. Edmondson (1960) used as his reproductive index the ratio of eggs to animals in the population (crude birth rate). Since the eggs are carried by the female and the adults are easily distinguished from the immature copepodite stages (Kamal and Armitage, 1967) in this species, it was possible to determine the ratio of eggs to adults. In the previous section the development time from egg to NIII was shown. Because the development time varies only slightly with temperature (Hardin, 1972) except near the lower limit for reproduction, a two day duration for the egg stage has been used to compute the specific birth rates. By dividing the total number of eggs by the product of the total adult population and the duration of the egg stage, a specific birth rate, or m_x value, can be calculated for any date.

An average of 2.78 eggs per adult per day was produced during the entire study period (Figure 8). During the first three collecting dates, when the temperature was well below the lower limits for reproductive activity, as determined in the laboratory, the m_x values were below the yearly weighted mean. Starting with 27 February and continuing until 27 March, the m_x values rose, peaking at 9.35. After this date the m_x values steadily decreased but remained above the mean until 10 April. From this date until the culmination of the study, the m_x values rose above the mean only during the period of 9 July to 6 August, 1971.

Figure 8. Specific birth rates (m_x) as calculated for each collecting date and the weighted mean m_x value (2.78) for the entire reproductive year. The vertical dotted line between 18 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.



Although the mean water temperature (Figure 12) rose during the period from 27 March until 3 September, reaching the optimum temperature for reproduction of this species of 21° C (Hardin, 1972) on 28 May, the m_x values did not follow a similar pattern (Figure 8).

To determine whether the apparent differences in m_x values during the various periods of the year were statistically different, the data were divided into four groups by season. These seasons are the periods of the year when the reproducing animals reached adulthood. The first season of this study is called winter and includes data from the onset of the study, 19 February, until 31 March, when the first new individuals reached maturity. The spring group of organisms are those collected between 31 March and 28 May. This latter date was previously described as the final die-off date for the first generation. Summer season is 28 May until 30 September while the fall season runs from 30 September until 29 October. The fall season was characterized by decreasing temperatures, although they were well above the lower limit for reproduction.

Analysis of variance of the four groups (Table 10) showed a significant difference among means of the various seasons. To determine which pairs of seasons were significantly different, a Student-Newman-Keuls test (SNK) was used. The SNK test is an a posteriori test in which the means are ranked from smallest to largest. Testing begins by comparinge the most extreme pairs and proceeds step-wise to the most similar pairs so long as a detectable difference between each pair is found. The lowest mean m_x value was that for the fall season followed in increasing order by the summer, spring, and then winter means (Table 11).

Table 10. Anova table on the difference between the m_x values of the various seasons.

Source of variation	df	SS	MS	F_s
Among seasons	3	109.6651	36.5534	8.7624*
Within seasons	42	175.3545	4.1701	
Total	45	285.0196		

* $P < 0.01$

Table 11. A posteriori comparison of the seasonal m_x values using the Student-Newman-Keuls test.

			Fall	Summer	Spring	Winter
$\bar{Y}$			0.4472	2.5779	3.03.6	5.3306
n			3	9	14	21
S^2			0.2583	2.7774	5.3713	5.3967
	$\bar{Y}$	n				
F	0.4472	3	—			
Su	2.5779	9	2.1307*	—		
Sp	3.0316	14	2.5844*	0.4537	—	
W	5.3306	21	4.8834*	2.7527*	2.2990*	—

* P = 0.05

Figure 9. Proportion of adult females carrying eggs on each collecting date. The vertical dotted line between 18 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.

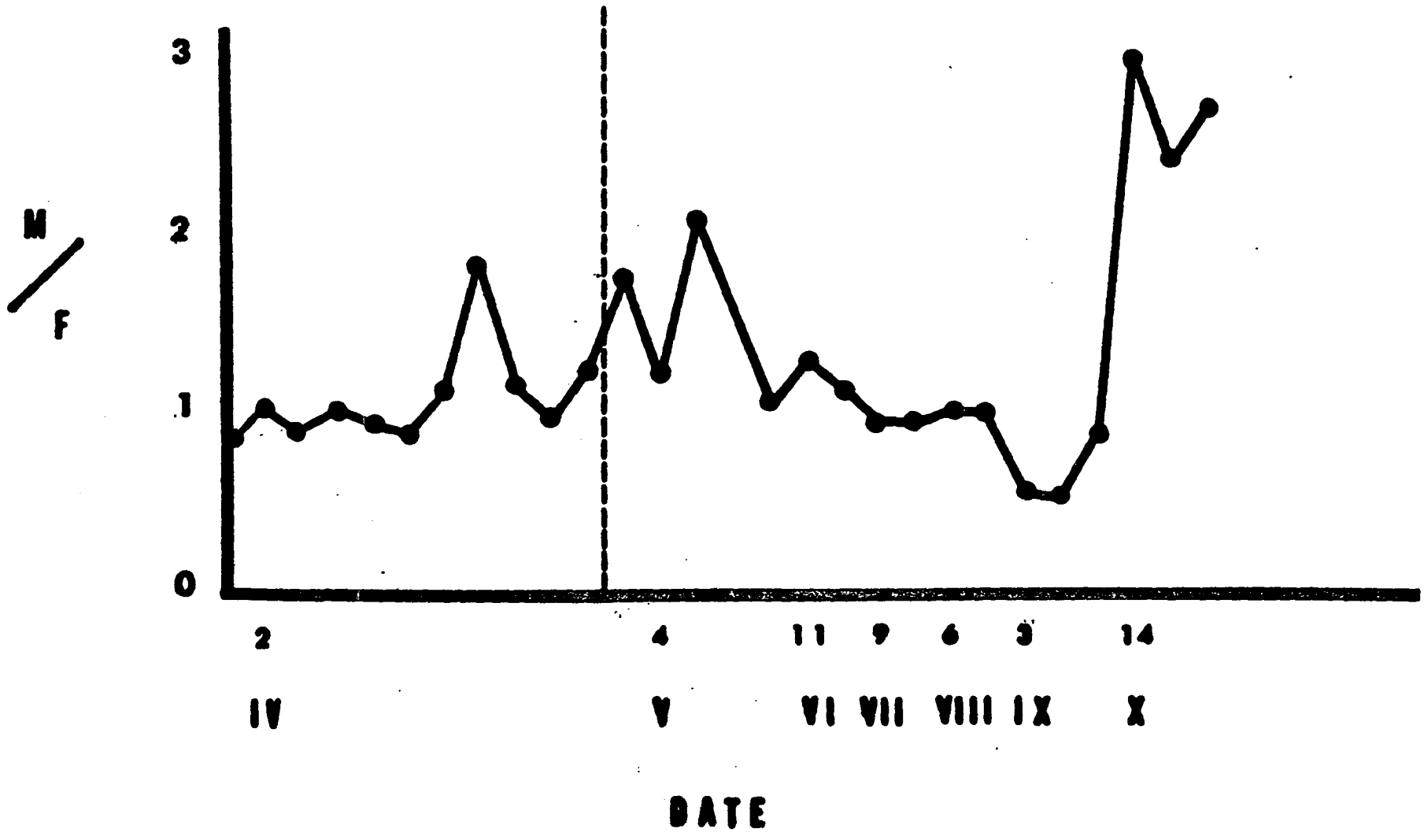
PROPORTION OF FEMALES CARRYING EGGS
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
DATE
II 6
III 1
IV 2
V 4
VI 11
VII 9
VIII 6
IX 3
X 14

Table 12. Anova table on the difference between the percentage of females carrying eggs during the various seasons.

Source of variation	df	SS	MS	F_s
Among seasons	3	74.1164	24.7054	2.3181*
Within seasons	43	458.2621	10.6572	
Total	45	532.3785		

* $P < 0.10$

Figure 10. Ratio of males to females in the adult population on each collecting date. The vertical dotted line between 18 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.


3
2
1
0
M
F
2
4
11
9
6
3
14
IV
V
VI
VII
VIII
IX
X
DATE

low (Figure 4) the ratio of males to females was significantly above the yearly average of 1.28 (tested by a modification of the Student's 't' test designed to test the difference between a single observation and the mean of a group; Sokal and Rohlf, 1969). Previously it was indicated that these dates were taken as the die-off dates for the previous generations (winter and g_1, respectively).

An analysis of variance performed on the values for the ratios of males to females during the four seasons (Table 13) revealed a significant difference among seasons. However, when an SNK test was run on on these data (Table 14), the only seasonal differences detectable were between the fall mean and those for each of the remaining three seasons. Since the ratio of males to females in the fall would have no bearing on the m_x values obtained during the preceding reproductive year, the ratio of males to females was assumed to be unimportant in determining the m_x values obtained in this study.

The final factor studied was the mean number of eggs per clutch (Figure 11). Analysis of variance showed a significant difference among means of the four seasons (Table 15). The lowest mean number of eggs per clutch (15.25) occurred in the summer period and was followed in ascending order by the means for fall, spring, and winter (Table 16). The mean value for winter was twice that of summer with 30.53 eggs per clutch occurring. A detectable difference occurred between the pairs of means for all seasons except summer and fall (Table 16). The mean number of eggs per clutch appears to be the most important of the three factors studied in determining the m_x values.

Table 13. Anova table on the difference between the ratio of males to females during the various seasons.

Source of variation	df	SS	MS	F_s
Among seasons	3	8.2784	2.7594	28.8037*
Within seasons	42	4.0268	0.0958	
Total	45	12.3052		

* $P < 0.01$

Figure 11. Mean number of eggs per clutch on each collecting date. The vertical dotted line between 18 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.

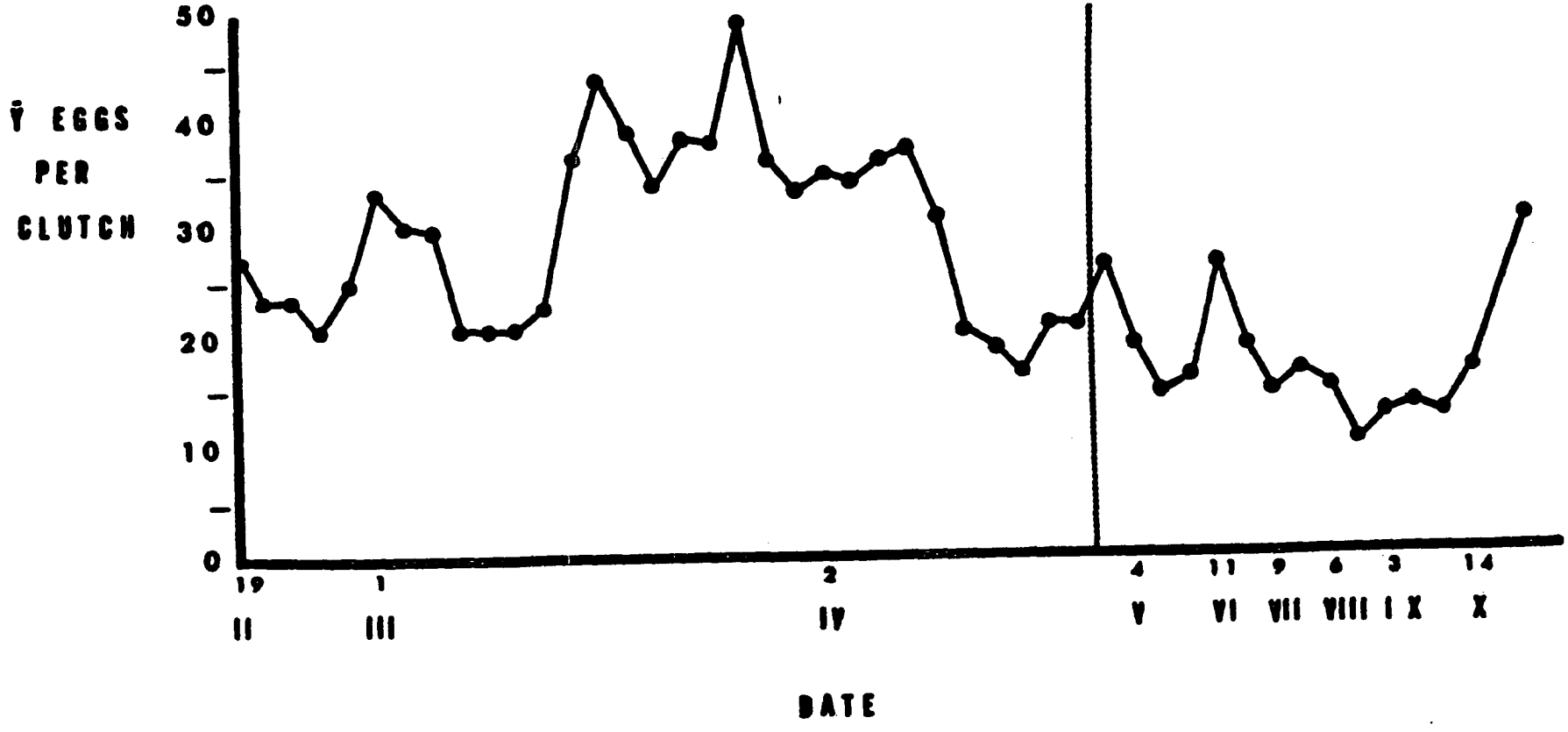

Ŷ EGGS PER CLUTCH
50
40
30
20
10
0
19
II
1
III
2
IV
4
V
11
VI
9
VII
6
VIII
3
I X
14
X
DATE

Table 14. A posteriori comparison of the seasonal means of the ratios of males to females using the Student-Newman-Keuls test.

			Summer	Winter	Spring	Fall
$\bar{Y}$			0.9278	0.9938	1.2436	2.7367
n			9	21	14	3
S^2			0.0654	0.0779	0.1489	0.0901
	$\bar{Y}$	n				
Su	0.9278	9	—			
W	0.9938	21	0.2515	—		
Sp	1.2436	14	0.3248	0.2178	—	
F	2.7367	3	0.5583*	0.4692*	0.4016*	—

* P = 0.05

Table 15. Anova table on the difference between the mean number of eggs per clutch during the various seasons.

Source of variation	df	SS	MS	F_s
Among seasons	3	1779.9860	593.3286	8.7990
Within seasons	43	2899.5354	67.4310	
Total	46	4679.5214		

* $P < 0.01$

Table 16. A posteriori comparison of the seasonal mean number of eggs per clutch using the Student-Newman-Keuls test.

			Summer	Fall	Spring	Winter
$\bar{Y}$			15.25	15.33	24.43	30.53
n			9	3	14	21
S^2			23.68	225.33	69.30	67.93
	$\bar{Y}$	n				
Su	15.25	9	—			
F	15.33	3	7.5610	—		
Sp	24.43	14	5.8300*	7.2155*	—	
W	30.53	21	5.9875*	8.4225*	3.9130*	—

* P = 0.05

Correlation coefficients were calculated between the mean number of eggs per clutch and each of three factors: chlorophyll a content of the algae; temperature of the water; and density of adults (Table 17). Chlorophyll content has been taken as a quantitative measure of the total food available for grazing in several studies (e.g., Hall, 1964). In a predator-prey (D. clavipes-algae) food relation an inverse correlation would be expected when the density of the predator increased to the level where the prey were harvested faster than they could reproduce. On the other hand, a positive correlation would be expected when the prey was not limited by the predator, but rather the reproductive intensity of the predator was determined by the amount of prey available. Although an insignificant correlation was found between the mean number of eggs per clutch and chlorophyll content during the full study period, analysis of data during the early spring season (19 February to 31 March) showed a highly significant positive correlation while a similar analysis for the data from the remainder of the year revealed a significant inverse correlation. Apparently, quantity of food was not a limiting factor during the early spring season, whereas it may have been during the remainder of the year.

Food quality (e.g., species of algae) present would be important in determining the value of chlorophyll as an indicator of available food. In the spring of the year filamentous Spirogyra and colonial Volvox were the dominant species numerically, while in the summer Ankestrodesmus and Scenedesmus were the dominant algal genera. If the filamentous and colonial algae were of such size that the filter-feeding diaptomids could not ingest them, they would be of no food value to these animals---even though the quantity of food (chlorophyll content) would be high.

Table 17. Correlation coefficients existing between the mean number of eggs per clutch and chlorophyll content, temperature, and density of adults during the study year.

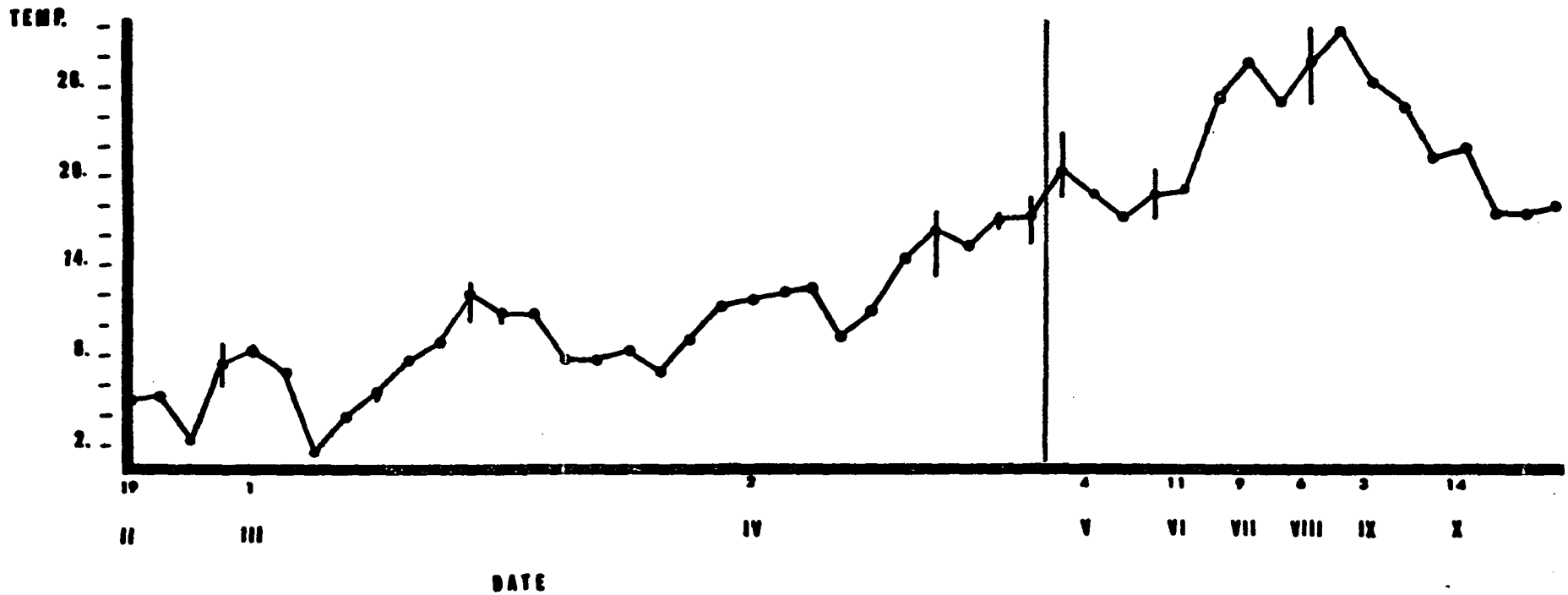
Parameter	n	Correlation Coefficient	P
Chlorophyll	18	-0.3650	nonsignif.
Temperature	47	-0.6003	< 0.01
Adult densities	47	-0.4176	< 0.01

A second problem relating to food was suggested by the laboratory study where it appeared that materials such as detritus and protists might be sources of food. Since the actual food source of D. clavipes is not known, placing too great a value on chlorophyll content alone is tenuous.

Several investigators, including Comita and Anderson (1959) and Chapman (1969) have suggested that the mean number of eggs per clutch in copepods is correlated to the size of the female. They further state that, since the size a female attains is inversely correlated to the temperature at which she develops, temperature is an important factor in determining the mean number of eggs per clutch. In the current study a significant correlation between temperature and mean number of eggs per clutch was also found.

Figure 12 shows the mean temperatures and the ranges on the various dates of this study. At the onset of the study the temperature was below the lower limit for successful reproduction as determined in the laboratory (Hardin, 1972). The temperature steadily increased, however, until 18 August when the yearly maximum of 27° C was reached. After this date the temperature steadily decreased until the termination of the study. When analysis of variance was run on the seasonally grouped date, a significant difference among the seasonal means was found (Table 18). The lowest temperatures were found during the winter season with a mean value of 7.02° C; while the summer period had a mean of 24.91° C, the highest seasonal average (Table 19). A significant difference between the pairs of means for all seasons except spring and fall was found. Although the relationship observed between temperature and mean number of eggs per clutch agrees with the findings of Chapman (1969) and Comita and Anderson (1959), the

Figure 12. Mean temperature and range on each collecting date. The vertical dotted line between 18 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.


TEMP.
26.
20.
14.
8.
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II
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VII
VIII
IX
X
DATE

Table 18. Anova table on the difference between the temperatures of the various seasons.

Source of variation	df	SS	MS	F_s
Among seasons	3	2144.3380	714.7793	73.2738*
Within seasons	43	419.4612	9.7549	
Total	46	2563.7992		

* $P < 0.01$

Table 19. A posteriori comparison of the mean temperatures of the different seasons using the Student-Newman-Keuls test.

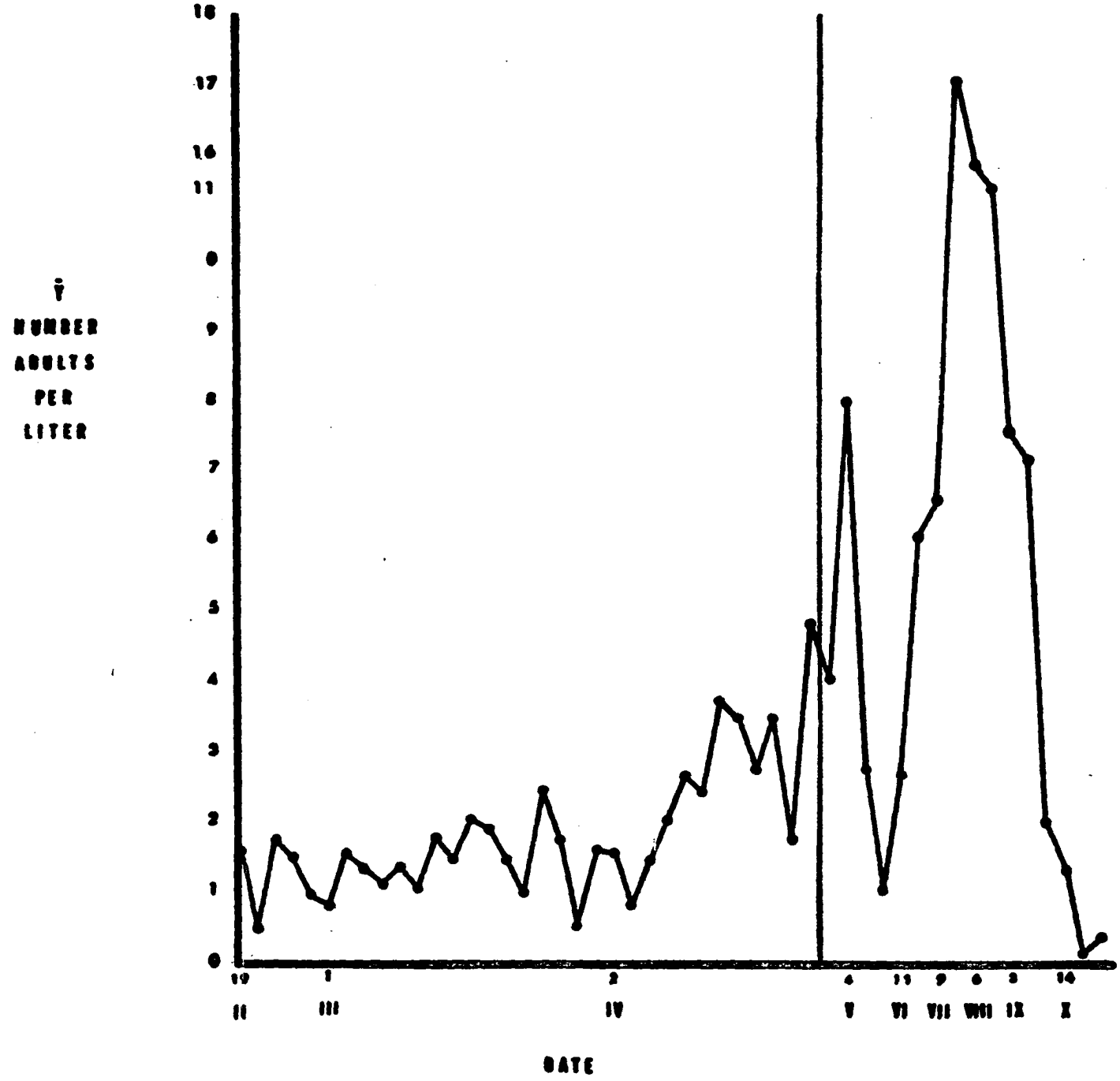
		Winter	Spring	Fall	Summer
$\bar{Y}$		7.02	15.42	17.17	24.91
n		21	14	3	9
S^2		7.79	15.78	0.04	7.30
	$\bar{Y}$ n				
W	7.02 21	—			
Sp	15.42 14	3.0544*	—		
F	17.17 3	6.5830*	5.6324	—	
Su	24.91 9	4.6882*	4.5567*	5.9002*	—

* P = 0.05

data do not, in themselves, show a cause and effect relationship. Hardin (1972), in a study on the relationship between temperature and the mean number of eggs per clutch in D. clavipes in the laboratory found the degree of difference between the developmental temperature and the incubation temperature to be more important in determining the mean number of eggs per clutch than was the incubation temperature alone. The temperatures he used were 14° C, 21° C, 27° C, and 31° C. He found the highest mean number of eggs per clutch produced by animals incubated at the same temperature at which they were reared, with the exception of 31° C, near the maximum thermal limit for reproduction. When he compared the mean number of eggs per clutch at the various temperatures, using only data from animals incubated at the same temperature at which they developed, no significant difference was found among the means for the various temperatures, except, again, at 31° C where the mean number of eggs per clutch was lower. His findings suggest that some factor other than temperature alone is controlling the number of eggs per clutch in the field.

The final factor studied in relation to egg production was adult density (Figure 13). Only the densities in the open water were considered. Concentrations of adults ranged from less than 0.5 to greater than 17 adults per liter during the reproductive year, the higher values later in the year. A decrease in concentrations present on the last three collecting dates coincided with a major die-off in total adults (Figure 4). Although the concentration of adults had a 30-fold range during the study period, the total number of adults did not fluctuate to this extent. The greater variation in concentration than in population resulted primarily from the decrease in open water volume due to the encroachment of rooted aquatics.

Figure 13. Mean number of adults per liter in the open water region on each collecting date. The vertical dotted line between 18 April and 24 April shows a change in scale from two day to approximately fourteen day intervals.


18
17
16
11
0
9
8
7
4
5
4
3
2
1
0
$\hat{Y}$
NUMBER
ADULTS
PER
LITER
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III
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IV
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VII
6
VIII
3
IX
14
X
DATE

As with temperature an inverse correlation was found between density and the mean number of eggs per clutch. Results of analysis of variance (Table 20) revealed a significant difference among the mean densities of adults of the various seasons. Seasonal mean densities ranged from 0.64 adults per liter in fall to 7.98 adults per liter during the summer period with 1.40 adults per liter and 2.90 adults per liter in the winter and spring seasons, respectively (Table 21). The only significant differences between seasonal mean densities occurred between summer and each of the remaining seasons (Table 21).

In a laboratory investigation we were unable to generate self-sustaining cultures at concentrations greater than 10 to 15 adults per liter. Although concentrations slightly exceeding this were found in the pond, they also were of short duration.

The plot of clutch size and density (Figure 14) shows a wide range of clutch sizes when densities were below 3 adults per liter, thereby indicating little effect of densities at these levels. When the density is greater than 3 adults per liter, however, it appears that an inverse relationship between the mean number of eggs per clutch and the adult density prevails.

In Table 22 the seasonal m_x values, mean numbers of eggs per clutch, mean densities of adults, and mean temperatures are ranked from lowest to highest. When these data were plotted from lowest to highest (Figure 15), the rankings of m_x values and mean eggs per clutch were the same, showing again the relationship between the two. Although at first it appears that density and the mean number of eggs per clutch do not fluctuate together, closer interpretation reveals a very close

Table 20. Anova table on the difference between the mean densities of adults during the various seasons.

Source of variation	df	SS	MS	F_s
Among seasons	3	293.5048	97.8349	18.3266*
Within seasons	42	224.2141	5.3384	
Total	45	517.7189		

* $P < 0.01$

Table 20. Anova table on the difference between the mean densities of adults during the various seasons.

Source of variation	df	SS	MS	F_s
Among seasons	3	293.5048	97.8349	18.3266*
Within seasons	42	224.2141	5.3384	
Total	45	517.7189		

* $P < 0.01$

Table 21. A posteriori comparison of the densities of adults during the different season using the Student-Newman-Keuls test.

			Fall	Winter	Spring	Summer
$\bar{Y}$			0.64	1.40	2.90	7.98
n			3	21	14	9
S^2			0.43	0.24	3.67	21.50
	$\bar{Y}$	n				
F	0.64	3	—			
W	1.40	21	2.4911	—		
Sp	2.90	14	3.0896	1.3925	—	
Su	7.98	9	3.5657*	1.9347*	1.7243*	

* P = 0.05

Figure 14. Mean clutch size plotted against density of adults.

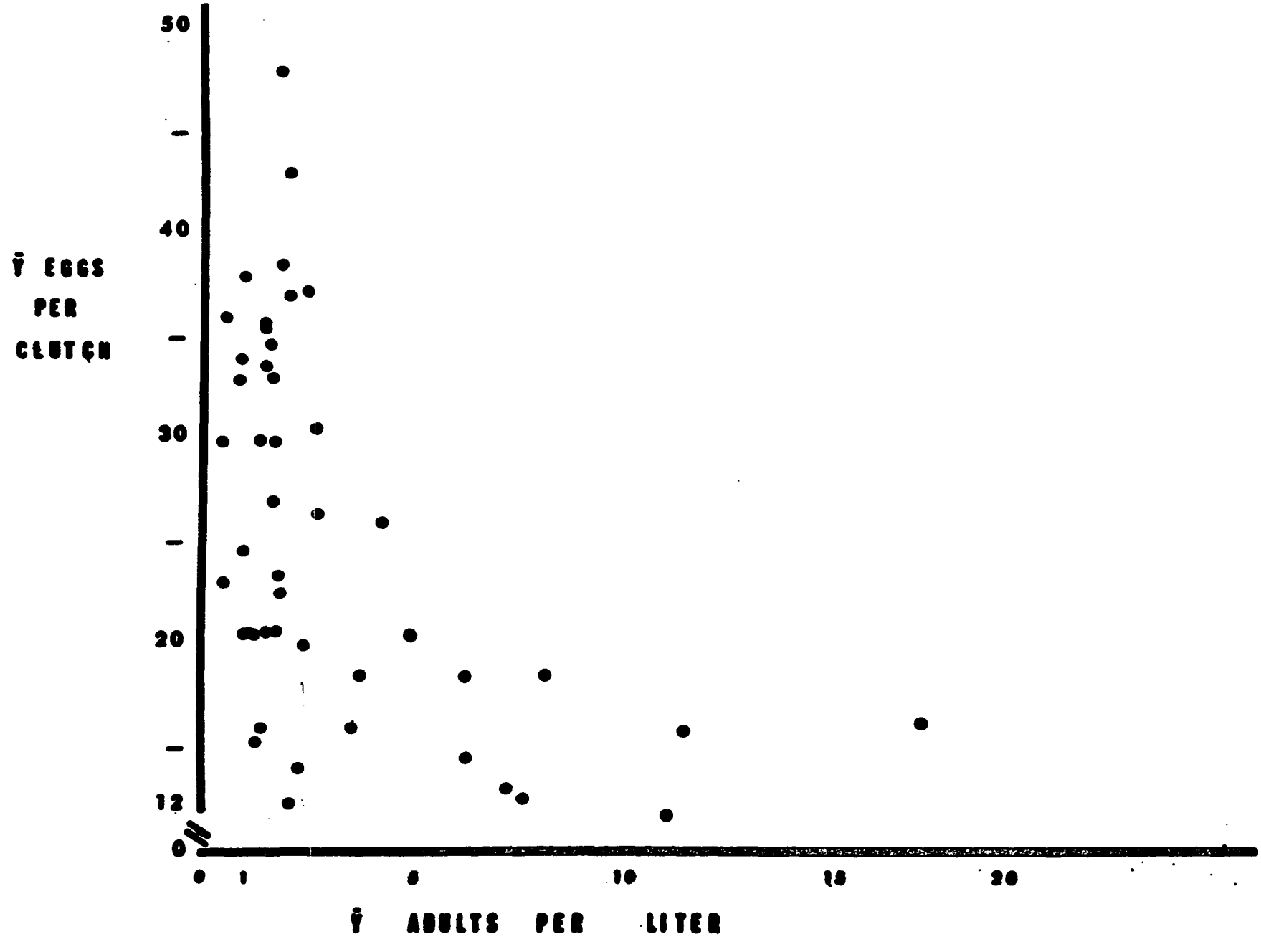
50
40
30
20
12
0
Ŷ EGGS PER CLUTCH
0
1
6
10
18
20
Ŷ ADULTS PER LITER

Figure 15. Rankings of the seasonal m_x values, mean number of eggs per clutch, mean density of adults, and mean temperature plotted by season.

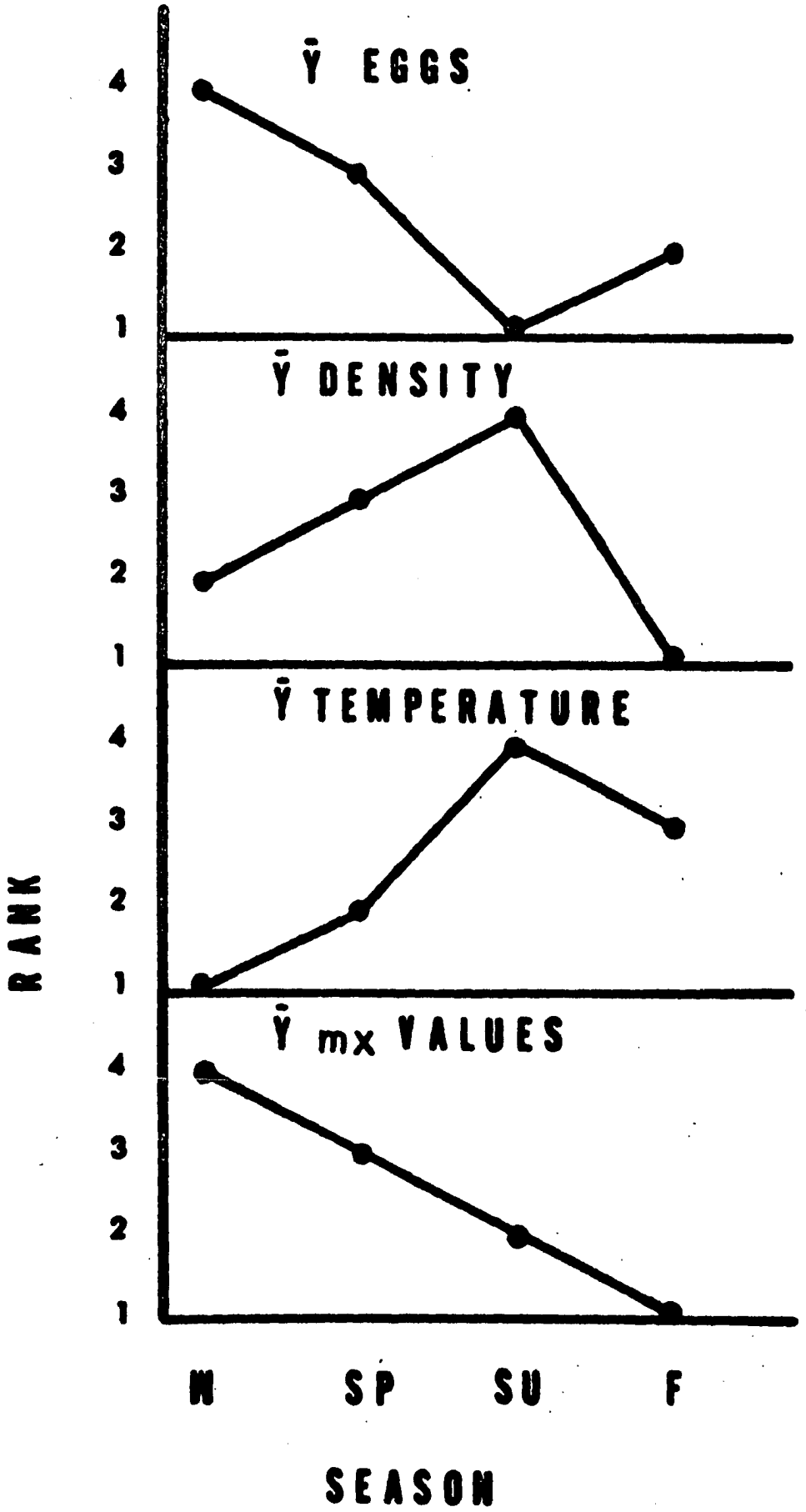
Ȳ EGGS
Ȳ DENSITY
Ȳ TEMPERATURE
Ȳ mx VALUES
RANK
4
3
2
1
W
SP
SU
F
SEASON

Table 22. Ranking of the various parameters from smallest to largest.

Parameter	Rank 1	2	3	4
$\bar{Y}$ eggs per clutch	Fall	Summer	Spring	Winter
$\bar{Y}$ density of adults	Fall	Winter	Spring	Summer
$\bar{Y}$ temperature	Winter	Spring	Fall	Summer
$\bar{Y}$ m_x values	Fall	Summer	Spring	Winter

relationship. In this study the density at which an organism developed would be that of the preceding season. Using this approach and utilizing the adult density of the fall of 1970, an exact inverse relationship between densities and mean eggs per clutch is seen.

In this study it was found that the major factor affecting the reproductive rate was the mean number of eggs per clutch during the various seasons. Several investigators have correlated the number of eggs per clutch with the size of the female; the size being inversely correlated with water temperature during development. Other investigators have found a correlation between the number of eggs per clutch and food. Similar correlations existed between both temperature and food and the mean number of eggs per clutch in this population. The use of the laboratory data of Hardin (1972) demonstrates that the occurrence of a significant correlation does not necessarily indicate a cause and effect relationship. Interpretation of these data suggest, however, that the density of adults may be the regulating mechanism for determining the number of eggs per clutch produced by the females. Selection for a self-regulating mechanism would be expected in a species whose environment is limited and whose individual members are unable to migrate.

SUMMARY

The dynamics of a population of Diaptomus clavipes Schacht were analyzed by constructing life tables for the various generations. Collections were taken every other day from 19 February until 20 April, and every fourteen days from 24 April until 29 October, 1971. This period of time included one complete reproductive year. The pond was divided into two horizontal regions, on the basis of the occurrence of rooted aquatics, and eight samples were taken from each region on each collecting date.

The adult population was found to be unevenly distributed in the pond with greater concentrations occurring in the open water regions than in areas in which rooted aquatics grew close to the surface. Analysis of laboratory data revealed that when rooted aquatics were dense the adult animals were unable to survive. Simulated weeds caused a retardation in the developmental rate of the egg to the naupliar III stage and hence a decrease in reproduction.

Durations of the various instar stages was determined through data obtained during an intensive collection period and through analysis of laboratory data. Life tables and survivorship curves constructed for the various generations revealed the highest mortality rates for each generation occurred in the egg to NIII stage. The second highest mortality rate was found in the NVI to CI stage. The greatest survival occurred

in the laboratory population. A physiological survivorship curve characterized the adults of each generation in the field population and the laboratory population.

Reproduction in the population was analyzed by determining the specific birth rates for adults in the various seasons. Analysis of three factors; male to female ratio, percent of females carrying eggs, and the mean number of eggs per clutch, revealed that the mean number of eggs per clutch was the most important factor in determining the specific birth rates.

Chlorophyll a (food), temperature, and adult densities were studied to evaluate their effects on clutch size. Although significant correlations between the mean number of eggs per clutch, and both temperature and adult densities, existed, analysis of field and laboratory data suggests that density may be the regulating factor in controlling clutch size, and hence reproduction, as long as the temperature is within the range necessary for reproduction in this population.

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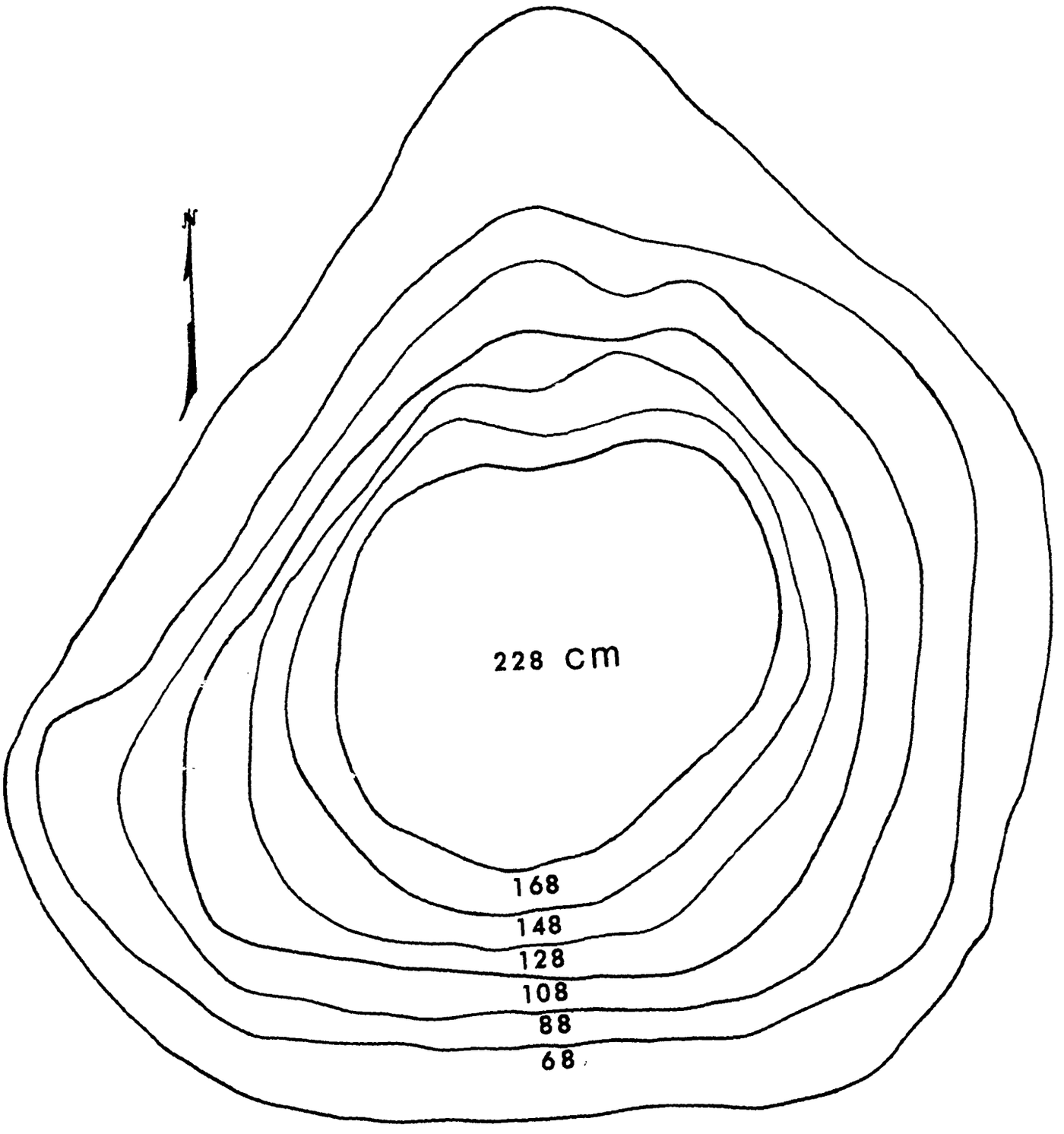
APPENDICES

APPENDIX I

All measurements pertaining to the morphometry of the pond were determined following procedures outlined by Welch (1948). These include construction of the morphometric map (Appendix I-1), determination of the surface area and volume for each depth stratum (Appendix I-2), and the determination of surface area (Appendix I-3) and volume (Appendix I-4) of each region of the pond on each collecting date. The two regions of the pond are described in METHODS AND MATERIALS. On each collecting date the depth of the pond and the depth of the water at the junction of the open water region and the area of rooted aquatics was measured. By subtracting the depth of the water at the junction of the two regions from the total depth of the pond the appropriate dimensions of the open water area could be calculated.

Appendix I-1. Morphometric map of the pond showing depth contours in centimeters. The scale of the map is 1:200.


N
228 cm
168
148
128
108
88
68

Appendix I-2. Surface area and volume of the various depth strata of the pond.

Depth stratum (cm)	Surface area (cm^2)	Volume (l)
0- 68	9,536,250	981,996
- 88	7,247,250	413,116
-108	5,689,500	284,058
-128	3,898,000	188,746
-148	2,827,750	121,774
-168	2,162,000	72,025
-228	1,683,500	33,670

Appendix I-3. Number of quadrats in each region of the pond and in the total pond on each collecting date. The surface area can be computed by multiplying the number of quadrats by 45.54 cm^2.

Date	Open water region	Rooted aquatic region	Total pond
II-1971			
19	86,965	86,965	173,931
21	92,508	92,508	185,016
23	91,769	91,769	183,538
25	94,355	94,355	188,711
27	94,355	94,355	188,711
III-1971			
1	93,247	93,247	186,494
3	93,247	93,247	186,494
5	90,660	90,660	181,321
7	90,660	90,660	181,321
9	89,921	89,921	179,843
11	89,921	89,921	179,843
13	89,921	89,921	179,843
15	89,182	89,182	179,364
17	89,182	89,182	179,364
19	89,182	89,182	179,364
21	88,813	88,813	177,626
23	87,867	87,867	175,734
25	86,962	86,962	173,925
27	86,585	86,585	173,171
29	86,208	86,208	172,417
31	85,857	85,857	171,714
IV-1971			
2	115,099	55,107	170,206
4	109,198	59,551	168,749
6	99,363	67,878	167,241
8	95,429	71,108	166,538
10	91,495	73,534	165,030
12	81,409	81,409	162,819
14	73,746	86,862	160,608
16	70,092	90,516	160,608
18	55,973	104,634	160,608
20	54,088	109,494	163,573
24	55,728	105,633	161,362
V-1971			
4	45,234	119,042	164,277
18	48,936	111,671	160,608
28	47,474	113,133	160,608
VI-1971			
11	79,719	105,261	184,981

Appendix I-3. Number of quadrats in each region of the pond and in the total pond on each collecting date. The surface area can be computed by multiplying the number of quadrats by 45.54 cm^2 (continued).

Date	Open water region	Rooted aquatic region	Total pond
VI-1971			
25	106,575	84,335	190,910
VII-1971			
9	39,594	141,718	181,312
23	30,806	141,211	172,417
VIII-1971			
6	18,483	150,265	168,749
20	16,019	146,700	162,819
IX-1971			
3	16,019	145,343	161,362
17	18,360	143,002	161,362
30	18,360	144,459	162,819
X-1971			
14	18,360	144,459	162,819
21	12,800	157,406	170,206
29	7,344	162,862	170,206

Appendix I-4. Volume in liters of each region of the pond and in the total pond on each collecting date.

Date	Open water region	Rooted aquatic region	Total pond
II-1971			
19	429,690	150,739	580,429
21	504,605	201,313	705,919
23	496,246	192,942	689,188
25	532,242	215,506	747,748
27	532,242	215,506	747,748
III-1971			
1	485,087	237,562	722,649
3	485,087	237,562	722,649
5	477,640	186,448	664,089
7	477,640	186,448	664,089
9	469,500	177,857	647,358
11	469,500	177,857	647,358
13	469,500	177,857	647,358
15	457,366	173,261	630,627
17	457,366	173,261	630,627
19	457,366	173,261	630,627
21	451,349	170,910	622,259
23	438,341	167,187	605,528
25	429,676	150,753	580,429
27	423,790	148,277	572,067
29	417,938	145,760	563,699
31	412,247	143,089	555,336
IV-1971			
2	469,895	68,705	538,600
4	444,849	77,020	521,869
6	425,731	79,407	505,138
8	408,138	88,632	496,770
10	390,545	89,494	480,039
12	358,480	96,459	454,940
14	332,976	105,233	438,209
16	320,128	109,718	429,847
18	284,478	145,369	499,847
20	281,736	181,572	463,308
24	285,380	152,829	438,209
V-1971			
4	230,704	240,972	471,677
18	257,514	172,332	429,847
28	247,147	182,699	429,847
VI-1971			
11	462,438	243,481	705,919
25	593,881	178,966	772,847

Appendix I-4. Volume in liters of each region of the pond and in the total pond on each collecting date (continued).

Date	Open water region	Rooted aquatic region	Total pond
VII-1971			
9	266,846	397,243	664,089
23	207,631	356,067	563,699
VIII-1971			
6	137,205	384,664	521,869
20	115,993	338,947	454,940
IX-1971			
3	114,534	323.675	438,209
17	127,927	310,282	438,209
30	129,599	325,341	454,940
X-1971			
14	129,599	325,341	454,940
21	102,011	436,589	538,600
29	61,873	476,726	538,600

APPENDIX II

Life tables for generations two through five.

Appendix II-1. Life table for the second generation using the composite laboratory data to determine the various stage durations.

Stage	Number living at beginning of age interval	Number dying in interval	Mortality rate per 1000 alive at beginning of age interval
	l_x	d_x	q_x
Egg-NIII	1000.00	887.29	887.29
NIV	112.71	10.22	90.68
NV	102.49	15.08	147.14
NVI	87.41	14.95	171.03
CI	72.46	5.37	74.11
CII	67.09	29.91	445.82
CIII	37.18	-8.23	-221.36
CIV	45.41	1.90	41.84
CV	43.51	30.92	710.64
CVI	12.59	12.59	1000.00

Appendix II-2. Life table for the third generation using the composite laboratory data to determine the various stage durations.

Stage	Number living at beginning of age interval	Number dying in interval	Mortality rate per 1000 alive at beginning of age interval
	l_x	d_x	q_x
Egg-NIII	1000.00	925.13	925.13
NIV	74.87	0.86	11.49
NV	74.01	44.60	602.62
NVI	29.41	-3.65	-124.11
CI	33.06	2.60	78.64
CII	30.46	8.26	271.18
CIII	22.20	0.26	11.71
CIV	21.94	2.39	108.93
CV	19.55	7.38	377.49
CVI	12.17	12.17	1000.00

Appendix II-3. Life table for the fourth generation using the composite laboratory data to determine the various stage durations.

Stage	Number living at beginning of age interval	Number dying in interval	Mortality rate per 1000 alive at beginning of age interval
	l_x	d_x	q_x
Egg-NIII	1000.00	945.70	945.70
NIV	54.30	9.42	173.48
NV	44.88	13.90	309.71
NVI	30.98	25.06	808.91
CI	5.92	1.28	216.22
CII	4.64	1.36	293.10
CIII	3.28	0.49	149.39
CIV	2.79	-2.41	-863.80
CV	5.20	-2.07	-398.08
CVI	7.27	7.27	1000.00

Appendix II-4. Life table for the fifth generation using the composite laboratory data to determine the various stage durations.

Stage	Number living at beginning of age interval	Number dying in interval	Mortality rate per 1000 alive at beginning of age interval
	l_x	d_x	q_x
Egg-NIII	1000.00	970.23	970.23
NIV	29.77	1.26	42.32
NV	28.51	10.48	367.59
NVI	18.03	11.58	642.26
CI	6.45	-6.15	-953.49
CII	12.60	6.28	498.41
CIII	6.32	2.61	412.97
CIV	3.71	-0.94	-253.37
CV	4.65	-0.19	-40.86
CVI	4.84	4.84	1000.00

APPENDIX III

Numbers of each of the various instars on each collecting date.

Appendix III-1. Total number of adults (CVI) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of adults per quadrat in each region by the total number of quadrats in that region and summing the products for each date.

Date	Open water region	Rooted aquatics region	Total pond
II-1971			
19	1,052,454	263,113	1,315,568
21	300,651	346,905	647,556
23	1,295,112	127,198	1,422,556
25	1,086,969	312,214	1,399,183
27	778,387	247,668	1,026,056
III-1971			
1	648,656	342,018	990,675
3	1,130,623	256,430	1,387,053
5	1,002,468	554,306	1,556,775
7	813,768	754,800	1,568,568
9	1,002,860	146,122	1,168,982
11	809,295	281,005	1,090,301
13	1,067,820	438,368	1,506,189
15	1,047,897	379,026	1,426,924
17	1,696,500	70,687	1,767,187
19	1,189,906	294,531	1,484,437
21	1,121,267	199,829	1,321,096
23	735,888	801,789	1,537,678
25	1,521,848	76,092	1,597,940
27	1,114,793	454,575	1,569,369
29	366,308	1,009,878	1,376,264
31	1,083,947	139,517	1,223,465
IV-1971			
2	1,251,705	13,887	1,265,593
4	668,839	89,326	758,166
6	1,068,160	161,210	1,229,371
8	1,526,877	26,665	1,553,543
10	1,749,859	32,682	1,782,542
12	1,641,783	54,006	1,695,789
14	1,908,190	21,715	1,929,906
16	1,690,980	101,830	1,792,811
18	643,697	104,634	748,332
20	1,886,343	41,056	1,927,399
24	1,497,714	26,408	1,524,122
V-1971			
4	2,572,700	178,565	2,751,264
18	911,433	781,697	1,693,130
28	344,186	14,141	358,327

Appendix III-1. Total number of adults (CVI) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of adults per quadrat in each region by the total number of quadrats in that region and summing the products for each date. (continued).

Date	Open water region	Rooted aquatics region	Total pond
VI-1971			
11	1,813,607	118,418	1,932,025
25	4,782,553	0	4,782,553
VII-1971			
9	1,994,547	106,288	2,100,835
23	4,181,914	388,330	4,570,244
VIII-1971			
6	1,827,506	957,939	2,785,445
20	1,521,805	1,173,600	2,695,405
IX-1971			
3	1,085,287	2,579,838	3,665,125
17	940,950	858,012	1,798,962
30	348,840	1,137,614	1,486,454
X-1971			
14	218,025	415,319	633,344
21	17,600	255,784	273,384
29	25,704	346,081	371,785

Appendix III-2. Total number of copepodite five (CV) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of 'CV' per quadrat in each region by the total number of quadrats in that region and summing the products for each date.

Date	Open water region	Rooted aquatics region	Total pond
II-1971			
19	0	0	0
21	0	0	0
23	0	0	0
25	0	0	0
27	0	0	0
III-1971			
1	0	0	0
3	0	0	0
5	0	0	0
7	0	0	0
9	0	0	0
11	0	0	0
13	0	0	0
15	0	0	0
17	0	0	0
21	0	0	0
23	0	0	0
25	0	0	0
27	0	0	0
29	21,552	49,262	70,814
31	233,041	71,547	304,588
IV-1971			
2	776,921	41,331	818,251
4	286,646	126,546	413,192
6	633,444	263,028	894,472
8	966,227	8,889	975,116
10	972,144	9,192	981,336
12	1,037,973	30,529	1,068,502
14	719,028	0	719,028
16	718,448	33,944	752,391
18	279,868	13,079	292,948
20	635,542	0	635,542
V-1971			
4	327,948	89,282	417,230
18	183,512	125,630	309,143
28	89,015	0	89,015
VI-1971			
11	1,863,449	26,315	1,889,764
25	1,372,163	21,083	1,393,247

Appendix III-2. Total number of copepodite five (CV) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CV per quadrat in each region by the total number of quadrats in that region and summing the products for each date. (continued).

Date	Open water region	Rooted aquatics region	Total pond
VII-1971			
9	148,478	0	148,478
23	396,630	40,345	436,976
VIII-1971			
6	221,805	93,916	315,721
20	104,125	55,012	159,137
IX-1971			
3	68,081	218,014	286,096
17	119,341	53,625	172,967
30	6,845	144,459	151,344
X-1971			
14	44,589	72,229	116,818
21	8,000	196,758	204,758
29	11,934	81,431	93,365

Appendix III-3. Total number of copepodite four (CIV) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CIV per quadrat in each region by the total number of quadrats in that region and summing the products for each date.

Date	Open water region	Rooted aquatics region	Total pond
II-1971			
19	0	0	0
21	0	0	0
23	0	0	0
25	0	0	0
27	0	0	0
III-1971			
1	0	0	0
3	0	0	0
5	0	0	0
7	0	0	0
9	0	0	0
11	0	0	0
13	0	0	0
15	0	0	0
17	0	0	0
19	0	0	0
21	0	0	0
23	0	21,967	21,967
25	239,148	0	239,148
27	507,146	284,496	791,642
29	290,955	2,142,909	2,433,864
31	723,654	85,857	809,511
IV-1971			
2			
4	327,596	141,434	469,029
6	621,023	398,784	1,019,808
8	858,869	8,889	867,757
10	823,463	0	823,463
12	783,568	10,176	793,744
14	516,226	0	516,226
16	464,363	0	464,363
18	118,944	26,159	145,103
20	610,429	13,686	624,115
V-1971			
4	197,900	74,401	272,301
18	336,439	348,974	685,414
28	41,540	0	41,540
VI-1971			
11	2,072,713	78,946	2,151,659
25	785,996	0	785,996

Appendix III-3. Total number of copepodite four (CIV) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CIV per quadrat in each region by the total number of quadrats in that region and summing the products for each date. (continued).

Date	Open water region	Rooted aquatics region	Total pond
VII-1971			
9	287,058	17,714	304,773
23	134,777	0	134,777
VIII-1971			
6	95,499	56,349	151,848
20	50,060	48,899	98,959
IX-1971			
3	40,048	124,579	164,627
17	58,140	115,285	173,426
30	0	41,273	41,273
X-1971			
14	34,425	126,402	160,827
21	5,485	118,054	123,540
29	4,590	61,073	65,663

Appendix III-4. Total number of copepodite three (CIII) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CIII per quadrat in each region by the total number of quadrats in that region and summing the products for each date.

Date	Open water region	Rooted aquatics region	Total pond
II-1971			
19	0	0	0
21	0	0	0
23	0	0	0
25	0	0	0
27	0	0	0
III-1971			
1	0	0	0
3	0	0	0
5	0	0	0
7	0	0	0
9	0	0	0
11	0	0	0
13	0	0	0
15	0	0	0
17	44,591	11,148	55,739
19	66,887	11,148	78,035
21	388,558	25,375	413,933
23	285,572	329,502	615,074
25	793,535	32,611	826,146
27	655,578	556,623	1,212,201
29	420,269	1,490,183	1,910,452
31	1,018,021	157,405	1,175,426
IV-1971			
2			
4	368,545	37,219	405,764
6	285,671	93,333	379,003
8	846,940	8,889	855,828
10	651,909	0	651,909
12	651,909	0	651,909
14	221,240	0	221,240
16	245,324	0	245,324
18	174,918	39,238	214,156
20	517,706	0	517,706
V-1971			
4	175,282	59,521	234,804
18	220,214	348,974	569,189
28	47,474	28,283	75,758
VI-1971			
11	1,265,551	39,473	1,305,024
25	586,167	0	586,167

Appendix III-4. Total number of copepodite three (CIII) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CIII per quadrat in each region by the total number of quadrats in that region and summing the products for each date. (continued).

Date	Open water region	Rooted aquatics region	Total pond
VII-1971			
9	296,957	0	296,957
23	84,717	20,172	104,889
VIII-1971			
6	33,886	0	33,886
20	40,048	146,700	186,748
IX-1971			
3	26,031	207,632	233,634
17	67,320	35,750	103,071
30	24,480	168,535	193,015
X-1971			
14	36,720	180,574	217,294
21	7,314	0	7,314
29	7,344	61,073	68,417

Appendix III-5. Total number of copepodite two (II) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CII per quadrat in each region by the total number of quadrats in that region and summing the products for each date.

Date	Open water region	Rooted aquatics region	Total pond
II-1971			
19	0	0	0
21	0	0	0
23	0	0	0
25	0	0	0
27	0	0	0
III-1971			
1	0	0	0
3	0	0	0
5	0	0	0
7	0	0	0
9	0	0	0
11	0	0	0
13	0	0	0
15	38,221	0	38,221
17	568,540	11,148	579,688
19	925,271	78,035	1,003,306
21	810,421	253,752	1,064,173
23	263,602	219,668	483,270
25	293,499	43,481	336,981
27	606,101	272,126	878,228
29	495,702	886,721	1,382,422
31	331,163	85,857	417,021
IV-1971			
2	1,107,831	158,434	1,266,265
4	709,790	44,663	754,454
6	335,353	25,454	360,807
8	477,149	8,889	486,038
10	194,429	9,192	203,621
12	325,639	10,176	335,815
14	73,747	0	73,747
16	330,434	12,930	343,366
18	188,911	254,113	443,024
20	664,518	13,686	678,204
V-1971			
4	378,837	0	378,837
18	250,800	265,220	516,021
28	23,737	0	23,737
VI-1971			
11	1,145,971	78,946	1,224,917
25	306,405	10,541	316,947

Appendix III-5. Total number of copepodite two (II) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CII per quadrat in each region by the total number of quadrats in that region and summing the products for each date. (continued).

Date	Open water region	Rooted aquatics region	Total pond
VII-1971			
9	113,833	0	113,833
23	83,616	0	83,616
VIII-1971			
6	43,128	0	43,128
20	64,077	122,249	186,326
IX-1971			
3	12,114	62,289	74,304
17	39,780	71,501	111,281
30	104,041	385,224	489,265
X-1971			
14	32,130	18,057	50,187
21	3,657	59,027	62,684
29	1,836	0	1,836

Appendix III-6. Total number of copepodite one (I) in each region of the pond and in the toal pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CI per quadrat in each region by the total number of quadrats in that region and summing the products for each date.

Date	Open water region	Rooted aquatics region	Total pond
II-1971			
19	0	0	0
21	0	0	0
23	0	0	0
25	0	0	0
27	0	0	0
III-1971			
1	0	0	0
3	0	0	0
5	0	0	0
7	0	0	0
9	0	0	0
11	0	0	0
13	67,441	11,240	78,682
15	535,097	55,739	590,836
17	624,279	78,035	702,314
19	590,836	122,626	713,462
21	588,388	177,626	766,014
23	637,038	208,685	845,723
25	271,759	10,870	282,629
27	284,496	86,586	371,082
29	775,881	812,827	1,588,708
31	760,449	57,238	817,687
IV-1971			
2	776,921	110,215	887,136
4	696,141	7,444	703,584
6	273,250	25,454	298,705
8	262,432	17,777	280,209
10	194,429	0	194,429
12	437,577	10,176	447,753
14	92,183	10,858	103,041
16	480,634	38,793	519,426
18	118,944	134,530	253,474
20	494,525	0	494,525
V-1971			
4	390,145	0	390,145
18	220,214	181,466	401,681
28	41,540	0	41,540
VI-1971			
11	966,601	26,315	992,917
25	213,151	0	213,151

Appendix III-6. Total number of copepodite one (I) in each region of the pond and in the total pond on each collecting date. The total number was determined by multiplying the $\bar{Y}$ (mean) number of CI per quadrat in each region by the total number of quadrats in that region and summing the products for each date. (continued).

Date	Open water region	Rooted aquatics region	Total pond
VII-1971			
9	79,188	0	79,188
23	88,017	0	88,017
VIII-1971			
6	80,096	18,783	98,879
20	74,089	48,899	122,988
IX-1971			
3	30,036	0	30,036
17	30,600	17,875	48,475
30	146,882	24,075	170,957
X-1971			
14	16,065	0	16,065
21	3,657	19,675	23,332
29	0	0	0

Appendix III-7. Total numbers of naupliar six (NVI), naupliar five (NV), naupliar four (NIV), and naupliar one through three (NI-NIII) on each collecting date.

Date	NVI	NV	NIV	NI-NIII
II-1971				
19	0	86,965	347,862	1,739,310
21	0	1,017,589	740,065	1,942,671
23	367,076	367,076	367,076	458,845
25	0	94,355	471,778	1,604,046
27	0	377,422	1,037,912	3,868,582
III-1971				
1	0	466,236	932,473	2,237,935
3	93,247	93,247	279,741	2,331,182
5	0	0	45,330	158,656
7	0	0	45,330	1,613,761
9	44,960	112,402	629,452	1,528,670
11	449,609	359,687	1,079,061	4,586,009
13	1,528,669	809,295	1,618,592	5,754,992
15	989,139	899,217	2,967,418	6,834,053
17	1,978,278	1,348,826	1,618,591	4,316,244
19	1,162,982	629,452	989,139	3,417,026
21	1,592,451	921,945	2,346,770	3,687,782
23	615,071	527,203	1,581,611	3,778,294
25	869,627	347,851	1,304,441	2,608,883
27	346,343	865,858	1,125,616	2,510,990
29	862,089	1,206,925	1,120,716	2,327,642
31	772,713	858,570	772,713	2,232,282
IV-1971				
2	680,827	1,191,447	1,872,275	2,638,206
4	506,248	590,623	928,122	2,278,118
6	83,620	250,862	668,967	2,675,871
8	416,346	333,076	416,346	1,332,307
10	330,061	330,061	247,546	1,072,700
12	407,049	569,869	488,459	2,605,115
14	240,912	562,130	401,521	1,124,260
16	0	160,608	562,130	562,130
18	401,521	240,912	240,912	481,825
20	490,720	245,360	81,786	817,867
V-1971				
4	523,302	320,205	465,211	887,493
18	321,217	160,608	321,217	883,347
28	0	0	80,304	160,608
VI-1971				
11	647,433	1,109,886	1,387,358	1,757,320
25	190,910	0	95,455	286,366

Appendix III-7. Total numbers of naupliar six (NVI), naupliar five (NV), naupliar four (NIV), and naupliar one through three (NI-NIII) on each collecting date. (continued)

Date	NVI	NV	NIV	NI-NIII
VII-1971				
9	0	362,625	271,968	815,906
23	517,253	258,626	603,462	2,069,015
VIII-1971				
6	421,873	337,499	590,623	1,181,246
20	569,869	651,278	895,508	3,419,214
IX-1971				
3	242,043	161,362	80,695	806,812
17	0	0	0	0
X-1971				
14	0	81,409	162,819	407,049
21	0	0	0	170,206
29	0	0	85,103	0

Appendix III-8. Total number of eggs in the pond on each collecting date. The total number of eggs was determined by multiplying the $\bar{Y}$ (mean) number of eggs per adult by the total number of adults in the population on each date.

Date	Number of eggs (X 10^3)	Date	Number of eggs (X 10^3)
II-1971		VI-1971	
19	7,631	11	7,162
21	1,359	25	27,339
23	6,561	VII-1971	
25	6,955	9	11,845
27	9,892	23	29,489
III-1971		VIII-1971	
1	10,385	6	17,844
3	17,134	20	9,560
5	15,646	IX-1971	
7	10,454	3	21,832
9	11,060	17	11,689
11	8,295	30	5,310
13	16,186	X-1971	
15	18,687	14	433
17	15,644	21	0
19	19,048	29	744
21	20,557		
23	16,277		
25	23,890		
27	35,243		
29	18,793		
31	18,602		
IV-1971			
2	19,444		
4	10,565		
6	12,650		
8	16,674		
10	11,849		
12	4,753		
14	2,570		
16	2,229		
18	3,416		
20	5,905		
24	6,028		
V-1971			
4	11,220		
18	4,505		
28	1,511		