THE INFLUENCE OF DAMSELFLY NAIAD PREDATION ON THE DYNAMICS OF PREY POPULATIONS

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
Dan Myron Johnson
1969

This is to certify that the

thesis entitled

THE INFLUENCE OF DAMSELFY NAIAD PREDATION ON
THE DYNAMICS OF PREY POPULATIONS

presented by

Don M. Johnson

has been accepted towards fulfillment
of the requirements for

Ph.D. **degree in** Zoology

William E. Cooper
Major professor

Date 11/11/69

O-169

S ~~MAY 14 '81~~ 7065

OCT 04 2000

P

were r

the sp

serrul

Ceriod

Orthoc

prey in

also pr

Ar

substra

easily

Sampl

day

and

pr

fo

c

ABSTRACT

THE INFLUENCE OF DAMSELFLY NAIAD PREDATION ON THE DYNAMICS OF PREY POPULATIONS

By

Dan Myron Johnson

Predacious *Ishnura verticalis* naiads (Odonata; Zygoptera) were reared in eight plastic-lined wading pools within which the species composition of prey was manipulated. *Simocephalus serrulatus* (Entomostraca; Cladocera) was present in all pools; *Ceriodaphnia reticulata* (Entomostraca; Cladocera) and *Orthocyclops modestus* (Copepoda; Cyclopoida) were alternate prey in some pools. Midge larvae (Diptera; Chironomidae) were also present.

Artificial "weeds", strips of fiberglass screening, were substrate for damselfly naiads and *Simocephalus* and provided easily sampled units consistent in surface area and volume. Samples of damselflies and their prey were obtained at four-day intervals. Naiads collected in each sample were measured and classified to instar. Randomly sampled portions of the prey were protected by predator exclosure nets during each four-day interval. These were preserved and then re-established on each sampling date. Subtracting the observed density of

each s

provic

preda

associ

these

ful in

An ind

tainec

struc

previ

ment

in m

an i

betw

grov

the

ter

each size category outside from that inside the exclosure provided an estimate of mortality attributable to damselfly predation during each four-day interval. A large bias associated with the exclosure procedure limited the value of these estimates as quantitative data, but they provided useful insights into the pattern of predator influence on prey. An independent estimate of *Simocephalus* mortality was obtained using extrapolation of a predicted density and size structure from observed population parameters four days previously and estimates of temperature dependent development rates.

Estimates of *Simocephalus* mortality fluctuated greatly in magnitude from date to date within most pools, suggesting an intermittent influence by the damselflies. Similarity between fluctuations in *Simocephalus* mortality and damselfly growth increments during each sampling interval suggested the following hypothesis to explain the sometimes intermittent nature of the predators' influence on prey:

> It is assumed that damselfly feeding rate is highest at the beginning of each instar and declines thereafter, especially when prey are very dense. A somewhat synchronous molting pattern among the naiads within a pool might then produce fluctuations in the proportion of naiads feeding most intensely, and therefore in the influence these naiads exert upon their prey.

E

made b

dates.

mortal

clusio

1.

2.

3.

The pres

influenc

occasion

average

Dan Myron Johnson

Estimates of damselfly naiad molting frequency were made by examining the shifts in instar distribution among dates. Comparison of these estimates to Simocephalus mortality estimates yielded the following tentative conclusions:

1. Synchronous molting patterns, in the presence of high prey densities, led to intermittent predator influence on prey which caused fluctuations in prey density.
2. Continuous molting patterns led to more continual influence on prey which often caused a decline in prey density.
3. Synchronous molting patterns, in the presence of low prey density did not yield fluctuations in mortality, possibly because feeding rates were continuous throughout each instar, and may have been responsible for limiting the density of Simocephalus at a low level.

The presence of alternate prey seems to have modified the influence of damselfly naiads on Simocephalus on only a few occasions. Predator influence was also larger when the naiads' average size was larger.

THE INFLUENCE OF DAMSELFLY NAIAD PREDATION ON THE DYNAMICS OF PREY POPULATIONS

By

Dan Myron Johnson

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Zoology

1969

661605

ACKNOWLEDGEMENTS

I thank Dr. William E. Cooper, chairman of my guidance committee, for his support and encouragement throughout the course of this research. Drs. R. C. Ball, D. L. Haynes, and J. A. King offered valuable advice and criticism as members of the guidance committee. Dr. D. J. Hall contributed several ideas which were incorporated into the experiment. Dr. Ivan Valiela has offered particularly useful criticism of the manuscript.

The Michigan State University River Research Laboratory provided field and laboratory facilities. Financial support was received from an NIH Pre-doctoral Fellowship, an NIH Animal Behavior Training Grant, an All-University Research Grant to Dr. Cooper, and NSF Research Grants to Drs. Hall and Cooper.

I extend loving thanks to Karol Lynn, who contributed time and talent to this endeavor as a seamstress, "weed"-maker, bug-counter, typist, bread-winner and wife.

TABLE OF CONTENTS

LIST OF TABLES

FIGURE

1. Fr
wi
pe
di
as
me

2. Da
in
sp

3. Nu
sa
me
is

4. Me
ta
po

5.1 and
la
pc
cl
st

6.1-6.8.
da
(–
<u>Or</u>
an
la

7.1-7.8.

A.
da
in
of

LIST OF FIGURES

LIST OF

FIGURE

fo
●
se
ou
sa

B.
of
te

C.
fe
li
fo
va
(S

D.
Si
pa
nc
ca
se
Pe

E.
ti
0.
le

8.1-8.8.

A.
bi
mi
Th
in
th
en
na
tr
we
vi

INTRODUCTION

Littoral weed beds are very productive zones within lakes and ponds (Straskraba _et al_., 1967; Allen, 1970) and provide refuge for important sources of fish food. The organisms inhabiting these areas have received less attention from limnologists than those in the more easily sampled pelagic community. The trophic dynamic relationships underlying secondary production, particularly the roles of invertebrate predators, are not well understood. Recent research on the productivity of experimental ponds near Ithaca, N. Y., hereafter referred to as "the Cornell ponds" (Hall, Cooper and Werner, in preparation), obtained data on the population ecology of most components of the pond ecosystem, including the inhabitants of littoral weed beds. Access to these data as background information led to an experimental study of the influence which a common weed-dwelling predator, the damselfly naiad (Odonata: Zygoptera) exerts on the dynamics of its prey populations.

Predators may exhibit behavioral responses to changes in prey density (Holling, 1965), distribution (Ivlev, 1961) and relative abundance of alternate prey (Murdock, 1969). Behavioral feeding responses could be important components

of the i
especial
rapid nu
hensive
havioral
such pre
populati
clusions
predator
unless i
prey den
pest spe
to suppo
agents us
the prey
are repre
times co
it might
on their
studies c
particula

Few
prey popu
of the in
of predat
(or in di

of the influence which predators exert on prey populations; especially when the predators do not have a capacity for rapid numerical increase. Holling (1966) presents a comprehensive model which attempts to generalize from some behavioral properties of individual predators to the role such predators might play in regulating the density of prey populations. One of the most provocative of Holling's conclusions is that the feeding behavior of typical invertebrate predators may not exert much influence on prey populations, unless in conjunction with numerical response to changes in prey density. A review of successful attempts to control pest species by introduction of predators or parasites tends to support this conclusion, since the effective control agents usually have generation times comparable to those of the prey (Huffaker and Kennett, 1969). Damselfly naiads are representative of invertebrate predators with generation times considerably longer than those of their prey; therefore, it might be predicted that they exert little or no influence on their prey populations. Such predictions, derived from studies of individual predators, require confirmation for particular interactions of predator and prey populations.

Few studies of the interaction between predator and prey populations are designed to determine the dynamic nature of the influence which predators exert upon prey. Estimates of predatory mortality during consecutive time intervals (or in different localities during the same time interval) are requ

with res

density.

during e

the rela

results

ing the

of preda

Est

enclosin

tive cag

Connell

impact o

one-year

predator

populati

Straskra

also bee

populati

Saunders

exclosur

predatio

populati

etc. whi

become c

to grow

are required. The observed effect may then be interpreted with respect to the value of other parameters (i.e., prey density, alternate prey density, and prey distribution) during each interval (or in each locality). The form of the relationship among these variables may be compared to results of behavioral studies, and inferences made concerning the importance of behavioral components in the influence of predators upon prey populations (Hassell, 1966).

Estimates of predator influence may be obtained by enclosing portions of the prey population within a protective cage which prevents predators access to the prey. Connell (1961) used predator exclosures to determine the impact of _Thais_ on barnacle populations during each of three one-year intervals. Studies of fish predation have used predator exclosures to estimate the impact of fish on prey populations (Hruska, 1961; Lellak, 1965; Kajak, 1966; Straskraba _et al._, 1967; Berglund, 1968). Exclosures have also been used extensively to protect terrestrial insect populations from predators (Hodek _et al._, 1965; Smith, 1968; Saunders and Knight, 1968). Most studies using predator exclosures have been designed to determine whether or not predation was an important mortality factor for the prey population. Initial changes in prey density, age structure, etc. which might be attributed to the predation treatment become compounded as the separate prey populations continue to grow and reproduce. As time since beginning of the

exclosure increases, the apparent effect of predation becomes confounded with intraspecific interactions among the prey (Kajak, 1966; Berglund, 1968). If predator exclosure cages were established for relatively brief time intervals, sacrificed, and then re-established using representative samples of the prey population, they might provide more meaningful estimates of the mortality attributable to predation during each of several consecutive intervals.
A series of such predator exclosures was used in the present study in an attempt to obtain direct estimates of the impact of damselfly naiad predation on experimental prey populations.

Methods have been devised for projecting the growth of animal populations into the future based on observed population parameters (i.e., density, age structure, reproductive rate) and a knowledge of temperature-dependent development times for different growth stages. Hillbricht-Ilkowska and Patalas (1967) and Cummins (1969) review the use of these models as applied to zooplankton populations. The difference between the predicted and observed densities at some point in time is an estimate of mortality during the interval over which the projection is made. Hillbricht-Ilkowska and Patalas (1967) recommend the linear extrapolation of the number in each size category devised by Winberg (Petrovich _et_ _al_., 1961; Winberg _et_ _al_., 1965). Cooper (1965) used a modification of this method to make inferences concerning the impact of perch on amphipod populations. A similar extrapolation procedure is used in the present study to obtain a second independent estimate of prey mortality during each predator exclosure interval. Independent mortality estimates using exclosures and extrapolations for each of several consecutive four-day intervals should provide data appropriate for making inferences concerning the mechanisms underlying the interactions of damselfly naiad populations with their prey.

The availability of alternate prey may modify the responses which predators make to different densities of their principle prey populations (Holling, 1959). Tinbergin (1960) described the response of birds to a new prey source as the development of a "searching image." Murdock (1969) studied the ability of a mollusk predator, Thais, to "switch" its feeding preference as the proportion of different prey species changed. Extensive training was necessary to produce "switching" casting some doubt on the importance of "switching" behavior in his particular system. However, the significance of "switching" and the modifying influence of alternate prey availability deserve further study in other predator-prey systems. An attempt was made to approach this problem in the present study by manipulating the species composition of the prey available to each experimental naiad population.

EXPERIMENTAL ORGANISMS

Damselfly naiads are often abundant predators in littoral communities (Macan, 1964) and may provide an important source of food for fish (Macan, 1966). They feed primarily on Entomostraca and aquatic larvae of Diptera (Fischer, 1964; Macan, 1966; and Lawton, 1967). The naiads are ambush predators, staying motionless until a potential prey item moves nearby. Capture is accomplished with a swift extension of the labium when contact is made with the antennae (Fischer, 1964; Corbet, 1962, p. 60; and personal observations).

Ischnura verticalis Say was the most abundant predator in the weed beds of the Cornell ponds (Hall, Cooper, and Werner, in preparation) and was selected as a typical invertebrate predator for the purposes of this study. Naiads overwinter in the late instars, emerge in the spring, and oviposit in emergent vegetation around the pond. Eggs hatch after one to two weeks and the tiny naiads begin feeding on protozoans or rotifers. They molt and soon may feed on microcrustaceans and midge larvae. Grieve (1937) describes the general biology of *I. verticalis* and diagnostic characters for each of the twelve instars. Naiads fed *ad libetum* at

23^oC complete development from hatching to adult emergence in about six weeks. During this time total body length increases from approximately 1.2mm to 11-15mm. Naiads hatching in June grow as a cohort throughout the summer, emerging in early August. Eggs laid by these adults hatch and the naiads reach late instars in September before winter diapause slows development, emergence being delayed until the following spring. Temperature and photoperiod are factors responsible for synchronizing the emergence of the damselfly _Lestes eurinus_ (Lutz, 1968) and may have a similar effect on _I. verticalis_.

Simocephalus serrulatus was the most abundant prey organism in the weed beds of the Cornell ponds, and was chosen as the principal prey in this study. It is a large cladoceran (adult female length=1.2-3mm) and is an important prey of bluegills (Hall, Cooper, and Werner, in preparation). Reproduction is typically parthenogenetic, the eggs being carried in a transparent brood sac. Ephippial eggs may be produced by sexual reproduction when the population is stressed by high densities, poor food supply, or other environmental parameters (Grosvenor and Smith, 1912; Banta, 1939). Cervical glands on the dorsal edge of the carapace are a unique adaptation to the littoral weed bed habitat. They permit _Simocephalus_ to sit motionless while continuing to feed by filtering algae and bacteria from the water with its legs. Frank (1952) comments on the role this behavior

may play in segregating *Simocephalus* from potential competitors such as *Daphnia*. One might speculate that selection for such a trait has been induced by the action of ambush predators such as damselflies.

Ceriodaphnia reticulata was the most abundant cladoceran in the open water of the Cornell ponds (Hall, Cooper and Werner, in preparation), and was chosen as an appropriate alternate prey for this study. Reproduction is usually parthenogenetic. *Ceriodaphnia* are smaller than *Simocephalus* (adult female length = 0.5-1.0mm) and swim constantly in a jerky pattern. They represent a distinct prey type from *Simocephalus*.

Orthocyclops modestus is a common littoral cyclopoid copepod. Though not present in the Cornell ponds, it was chosen as a second alternate prey because it is found among aquatic vegetation (Pennak, 1953, p. 397) and was available in laboratory cultures. Fryer (1957) describes the feeding habits of similar cyclopoids as predaceous, and I have observed adults of *Orthocyclops* feeding on *Simocephalus*. Its swimming motions are very rapid and its size intermediate between *Simocephalus* and *Ceriodaphnia* (adult female length = 0.8-1.25mm). Reproduction is sexual and eggs are carried in sacs on the abdomen of the female. They can be counted while intact, but with less reliability than for the cladocerans because they are more numerous (20-60 per sac).

Members of two midge taxa, Chironominae and Tanypodinae, although not included in the initial experimental design, became alternate prey for the damselfly naiads in this experiment. Midge larvae are common components of the littoral fauna (both of these taxa occur in the Cornell ponds) and are important food organisms for damselflies (Fischer, 1964; Macan, 1964; and Lawton, 1967). The Tanypodinae may be predaceous upon midges and the crustacean prey used in this study (Pennak, 1953, p. 650; Hamilton, 1965). The Chironominae feed on algae, detritus and microorganisms (Hamilton, 1965).

MATERIALS AND METHODS

Materials

If meaningful comparisons among samples of prey populations from within and outside of predator exclosures are to be made, it is essential that consistent replicated sampling of the prey populations be possible. Control of the species composition of the prey available is necessary if the effect of alternate prey abundance is to be studied. An artificial "weed bed" was designed which would meet these criteria and provide a reasonably realistic habitat for the animals involved.

Plastic-lined wading pools eight feet in diameter and twenty inches deep are replicable units of convenient size. Fiberglass insect screening was cut into strips ¼ x 36 inches. Twenty-five strips, folded in half lengthwise and hung from a 6 x 6 inch square of 3/8 inch galvanized wire screen, formed an artificial "weed". Forty such "weeds" were suspended from a lattice of aluminum poles above each pool. The "weeds" were spaced approximately 12 inches apart and hung to within 2 inches of the pool bottom. The total surface area of "weeds" was approximately equivalent to the area of the bottom and sides of the pool. Individual "weeds" having identical surface area and volume could be sampled by moving a net of Nitex (mesh 153 μ) directly under the "weed" and lifting it swiftly, surrounding the entire "weed" and all associated organisms. The "weed" was shaken vigorously into the net and then removed. The contents of the net were washed gently down into a 50 cc plastic tube attached to the apex. In this manner it was possible to sample both damselfly naiads and all prey species. Predator exclosure nets were constructed using Nitex (# 153) and consisted of cyclinders 9 inches in diameter and 15 inches long which have a conical net attached to the bottom. Each net encloses one "weed" and is suspended by nylon cords from the aluminum poles above the pool. Two sets of four pools were each enclosed within a tent of Saran screening (20 x 20 mesh) 20 x 20 x 6 feet to prevent contamination by unwanted insects. The tents have a flap of screening along the bottom edge which is buried in the soil and zippers which provide tightly sealed door flaps. The manufacturer estimates approximately 15% shading by the material used.

Experimental Treatments

The species composition of the prey introduced to each pool is presented in Table 1. All pools contained Simocephalus, which was considered the principal prey of damselfly naiads in this study. Orthocyclops and Ceriodaphnia are considered

Table 1. Experimental Design.

Tent	Pool	Prey Composition*
1	1	S,C,O
	2	S,O
	3	S,C
	4	S
2	5	S,C,O
	6	S,O
	7	S,C
	8	S

*S = _Simocephalus serrulatus_
C = _Ceriodaphnia reticutata_
O = _Orthocyclops modestus_

alternate prey to the Simocephalus. Each of the four prey compositions was established in two replicate pools. A set of four pools, one with each prey composition, was enclosed within each of two tents. Predator exclosures were established within each pool for each of fifteen four-day intervals while damselfly naiads were present in the pools.

Sampling Procedure

Three samples were obtained within each cell in the design during each sampling period. It was only possible to sample four pools in one day; therefore, a sampling period consisted of two adjacent dates. Pools within tent 1 were sampled on the first date and tent 2 on the second. All manipulations were performed according to a staggered schedule, so that pools had identical histories on the dates sampled. Variation introduced by differences in meteorologic conditions between days within a sampling period contribute to between-tent error, and are presumed to be small. Samples were usually taken from the pools in the same order; beginning with the simplest species composition of prey (S), followed by (SC), (SCO), a thorough washing of the net, and then (SO). This procedure minimized the possibility of transferring species among the pools in the sampling nets. Within each pool the following procedure was followed:

1. Three predator exclosures established four days previously were removed from the pool and their

contents preserved.

2. Three randomly selected "weeds" were sampled and their contents poured into a petri dish. Damselfly naiads were removed with a plastic spoon and placed in holding beakers for subsequent enumeration and measurement. The rest of the sample was preserved.
3. Three randomly selected "weeds" were sampled, damselflies removed as before, and the prey organisms returned to the pool within a predator exclosure.

A restriction was placed on the random selection process such that one sample and exclosure were placed in each third of the pool ("weeds" 1-13, 14-27, 28-40; see Figure 4). Samples were preserved in 50% alcohol and stored in 100 ml bottles to which a few drops of formaldehyde were added. Four pools could be sampled in this manner between 0630 and 1200 hours EST. Damselfly naiads sampled in the morning were counted during the afternoon. Three measurements were made on each naiad (total body length, head width, and rear wingpad length) using a microscope with an ocular micrometer. All naiads were then returned to the pool from which they had been taken.

A frequency distribution of damselfly naiad head widths including all pools and all dates is plotted in Figure 1. Comparison with published mean head widths for each instar of

I. verticalis (Grieve, 1937) made it possible to assign prominent modes to instars, and an arbitrary division was made at the lowest frequencies between modes. All naiads sampled were then classified to instar on the basis of their head width.

Temperature Records

Temperature records were obtained daily using a max-min thermometer suspended in Pool 1. Occasional checks of the temperature in other pools showed little variation among pools, and no evidence of vertical stratification within pools. Figure 2 shows the maximum and minimum temperatures recorded in Pool 1 during each day. Four-day averages of the median temperatures were used as estimates of the average temperature during each interval. A sharp decline in temperature on 27th August divides the experiment into two relatively distinct temperature regimes.

Procedure for Analyzing Samples

High densities of *Simocephalus* in all pools made it necessary to count subsamples from most samples. Contents of the bottle were diluted to either 100 ml or 200 ml in a beaker and stirred vigorously until all organisms were suspended in the alcohol. Five subsamples of 1, 2, or 4 ml volume were removed with a Hensen-Stemple pipette. This procedure provided a range of subsample volume from 0.5% to

Figure 1. Frequency distribution of _I_. _verticalis_ head widths for all naiads sampled during the experiment. Dashed lines represent arbitrary divisions between instars. Instar number was assigned after comparison with published means (Grieve, 1937).

Figure 2. Daily maximum and minimum temperatures recorded in Pool 1. (Dotted lines represent records spanning more than one day.)

rticalis
led during
epresent
ars.
comparison
57).

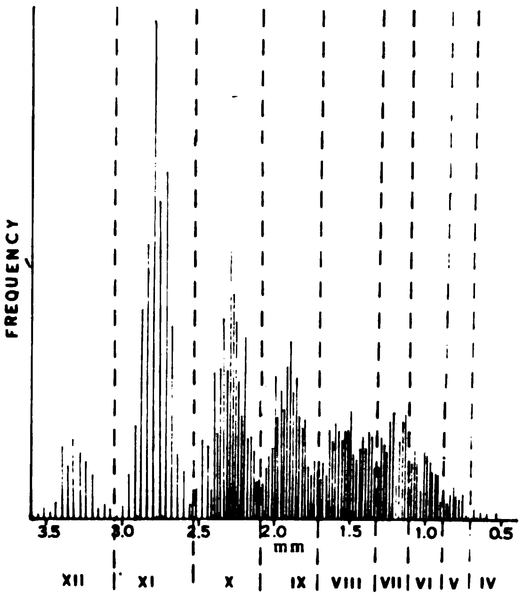


Figure 1

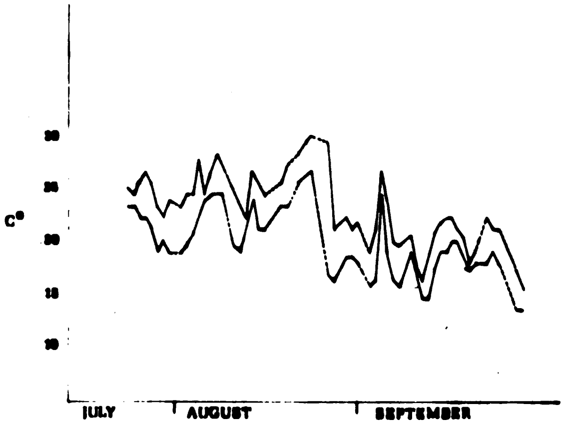


Figure 2

4% of the sample volume within which I could choose a convenient size for counting. The size chosen depended on density of the prey species and amount and texture of filamentous periphyton if present. Subsampling variance was minor compared to that among samples and was not partitioned out in subsequent analyses.

Organisms were classified into taxa, size categories, and reproductive condition when appropriate (Table 2). For each date, the density of each category from "weed" samples both subjected to and protected from damselfly predation for four days is estimated as the mean of three samples. Eggs tended to drop from brood sacs when the animals were preserved; therefore, an attempt was made to count all eggs encountered both in brood sacs and free in the sample. Because Simocephalus eggs are larger than those of Ceriodaphnia, these counts are considered more accurate for Simocephalus. Simocephalus having apparently intact broods were selected from each sample and their length and brood size recorded. A linear relationship between brood size and body length was observed. Least square linear regressions were fitted to these data for both the exclosure and observed samples within each pool on each date. These equations were used to calculate an adjusted mean brood size for a female of standard length (1.4 mm) for each of these cases. Since brood size in daphnids is known to reflect food supply (Slobodkin, 1954; Hall, 1964) these data represent an index of food supply/individual which is adjusted to be independent

Table 2. Size categories into which prey were classified during analysis; dry weight biomass estimate for each category; and the source of these estimates.

Prey size category	Biomass (μg)	
Simocephalus serrulatus		
parthenogenetic eggs*		
juveniles < 0.8 mm } ***	4.1 ± 0.4^a	8.5^c
1.2 > juveniles > 0.8 mm }	10.1 ± 1.1^a	
1.6 > small adults > 1.2 mm**	20.4 ± 0.7^a	
2.0 > large adults > 1.6 mm** } ***	28.6^b	
large adults > 2.0 mm** }		
Ceriodaphnia reticulata		
parthenogenetic eggs*		
juveniles < 0.5 mm	2.2^c	
adults > 0.5 mm**	4.2^c	
Orthocyclops modestus		
eggs		
nauplii	$1.0 \times 10^{-2\ c}$	
copepodids	3^c	
adult males	8^d	
adult females**	$18^{c'}$	
Chironominae		
0-1 mm	5^d	
0-2 mm	7^c	
2-3 mm	10^c	
3-4 mm	20^c	
4 mm	35^c	
pupae	35^d	

Tanypodinae	
0-1 mm	5^c
1-2 mm	7^c
2-3 mm	10^c
3 mm	20^c
pupae	20^d

---

[*] Eggs carried by females plus those dropped in sample when preserved.

[**] Each adult was classified as to whether it carried parthenogenetic eggs, no eggs, or ephippial eggs (for Simocephalus and Ceriodaphnia only).

[***] Categories lumped during subsequent analyses.

[a] Animals from lab culture, dried at 60°C for 15 hours. Mean ± SE of three replicates. Each replicate consisted of 10 individuals.

[b] Extrapolation from values in "a" by the regression equation: weight = 21.83 (length) - 10.66. Length of each size category was assumed to be the midpoint of that category.

[c] Hall, Cooper, and Werner, in preparation.

[c'] Estimate is for Mesocyclops edax (Hall et al., op. cit.) which is slightly larger than Orthocyclops modestus.

[d] Values assigned arbitrarily; the most reasonable estimate on the basis of the weight of other categories for the same taxon.

of the size structure of adult females. Males were not distinguished from females for Simocephalus or Ceriodaphnia, though the presence of ephippial eggs during the experiment attests to their existence in the population. Samples taken on three sampling dates (22-23, 26-27 July, and 28-29 September) were classified according to a slightly different size category breakdown. Though providing estimates of the total density of each prey species, these counts were not appropriate for use in some subsequent analyses.

Extrapolation

A mathematical model was used to predict the potential Simocephalus population density and size structure on each date from observed parameters four days previous. Estimates of the following parameters were required:

1. The number of each size category and total number of eggs observed on date t_0.
2. The average temperature during the interval t_0 to t_1.
3. The duration of each size category at that temperature.

The number of young (< 1.2 mm), small adults ($1.6 > x > 1.2$ mm), and large adults (> 1.6 mm) from each of three replicate samples was entered into the model. The average temperature was estimated as the mean of four medians between daily maximum and minimum temperatures recorded in Pool 1

(Figure 2). The development times for eggs, young, and small adults were determined by rearing individuals at 25°C and 15°C in the laboratory (Table 3). A linear interpolation between experimentally determined development times was used to estimate the duration of each stage at the average temperature observed during each interval. Distribution of age among eggs and within each size class was assumed to be uniform. This is a simplifying assumption which will introduce an error toward prediction of larger potential population if the actual distribution is skewed toward young individuals. This is probably the case during most of the study because population size structure was skewed toward young. The length of each interval was only four days, so that the absolute magnitude of such error is rather small. The model also assumes no mortality during the interval over which it is predicting. For these reasons, the extrapolations are intended to be a maximum estimate of the potential growth of the Simocephalus population. The equations used are the following:

$$N_{1j} = N_{oe} (T/D_e) + N_{oj} (1 - T/Dj)$$
$$N_{1a} = N_{oj} (T/D_j) + N_{oa} (1 - T/D_a)$$
$$N_{1a'} = N_{oa} (T/D_a) + N_{oa'}$$

where

N_o = number of individuals at the beginning of an interval

N_1 = number of individuals at the end of an interval

Table 3. Egg development time, age upon reaching each size category, and average duration of each size category of *Simocephalus serrulatus* females grown individually at constant temperatures. $\bar{x}$ ± SE (days).

	15°C			25°C		
	N	$\bar{x}$ Age ± SE	Duration	N	$\bar{x}$ Age ± SE	Duration
egg	20		5.7 ± 0.30	43		2.1 ± 0.03
juveniles		0	9.6		0	4.2
1.6 > adults > 1.2 mm	24	9.6 ± 0.70	8.7	42	4.2 ± 0.2	5.3
adult > 1.6 mm	19	18.3 ± 2.6		39	9.5 ± 0.7	

D = duration of a size category at observed temperatures

e = eggs

j = juveniles

a = adults > 1.2 mm and < 1.6 mm

a' = large adults > 1.6 mm

and T = length of the interval between samples = four days.

The notation is that of Hillbricht-Ilkowska and Patalas (1967) and the equations are essentially those of Petrovich *et al*. (1961). The terms N_{oj} $(1- T/D_j)$ and N_{oa} $(1- T/D_a)$ are appropriate whenever the interval between samples (T) is less than the duration of either stage (D_j or D_a) (Petrovich *et al*., 1961). This condition is met for almost all sample intervals considered in the present study. In three cases (23, 24, and 27th August) the interpolated values for D_j were slightly less than the 96 hour sampling interval (88,77, and 93 hours respectively). These discrepancies were considered too minor to warrant modification of the extrapolation procedure for these particular dates.

Damselfly Biomass

The average growth increment of the damselfly naiads during each four-day interval was estimated in the following way. The relationship between dry weight and body length was determined using a sample of twenty-one *I. verticalis* naiads collected from the same source as those

used in the experiment. Naiads were measured, dried at $100^{\circ}C$ for 48 hours, and weighed. The linear regression line,

$$\log (1 + \text{dry weight})\text{mg} = -0.21566 + 0.07210 \text{ mm},$$

provides a least squares fit to the observed points with a correlation coefficient, $r = 0.985$. The mean biomass per naiad was estimated from mean total body length using this equation. The error introduced by transforming means rather than individual observations is considered small because body lengths were distributed over a very narrow range within a particular pool on any given date (Figures 5.1-5.2). Growth in length is discontinuous, occurring mostly at ecdysis; while actual biomass is accumulated continually throughout an instar. Therefore, the estimates of biomass obtained using this method will appear more discontinuous than if they were measured directly.

Initiation of the Experiment

The pools and "weeds" had been used both for pilot studies and for a similar experiment conducted from 1st May to 12th July 1968. All pools were drained, cleaned thoroughly with water and sponge and allowed to dry for two days. "Weeds" were sprayed with water to remove animals and periphyton and then allowed to dry. "Weeds" were systematically redistributed among the pools in an attempt to eliminate any differences which might have resulted from different previous histories.

Pools 1-4 were filled with tap water on 15th July and pools 5-8 on 16th July 1968, and water was added to or drained from the pools whenever necessary to maintain a depth of 30 cm. Algae from laboratory cultures (*Ankistrodesmus*, *Chlorella*, and *Scenedesmus*) were introduced into each pool on 16-17th July. A total of 1200 prey organisms (30/"weed") were added to each pool on 18-19th July from cultures maintained in the laboratory for several months. This number was equally distributed among the prey species included in each pool (Table 1). Three exclosure nets were suspended in each pool and thirty of the prey organisms were placed into each exclosure. Thus each exclosure received a number of each prey species equal to the average number per/"weed" introduced to the pool. Since no damselflies were yet present, and prey placed into the exclosures had been selected and handled in a manner identical to those placed outside, the growth and survival of prey within the exclosures during the subsequent four days is assumed to be similar. The different prey species may be expected to distribute themselves differentially within the pools. *Ceriodaphnia*, a limnetic form, may be expected to utilize the entire water volume while *Simocephalus*, which usually feeds while sitting motionless on a substrate might tend to aggregate on the "weed" and pool surfaces. The nauplii and

copepodid stages of Orthocyclops are more or less limnetic, while the adults tend to cling to surfaces. The ratio of the mean number of each prey category in samples taken from "weeds" on 22-23rd July to the mean number surviving per "weed" in the three exclosure nets should provide an estimate of the proportion of each size category of each prey which is associated with the "weeds" (Table 4). Approximately 70% of the Simocephalus are estimated to be included in samples taken from "weeds" while only about 20% of the Ceriodaphnia are included. The estimate for adult Orthocyclops is about 50% while only 12.5% of the nauplii are included. No estimate is available for copepodids since they were not present during this time interval.

Exclosures were established on 22-23rd and 26-27th July with prey sampled from a randomly selected "weed" placed into each. These prey were subjected to whatever mortality may have been associated with the sampling procedure used for setting up exclosures. Prey within the exclosures were preserved after four days, and their density compared with that on "weeds" sampled outside the exclosures on the same date. Since no damselflies were present in the pools during these intervals, these comparisons provide an estimate of the overall bias associated with the exclosure technique (Table 5). The bias is substantial. Density of Simocephalus was more than twice as dense outside than inside the exclosures; young Ceriodaphnia showed an eleven-fold difference,

Table 4. Proportion of each prey category in the samplable population on 22-23rd July.

	$\overline{x}$ (sample/exclosure)± SE	n = number of pools
Simocephalus		
juveniles	0.79 ± 0.21	8
adults	0.63 ± 0.14	8
Ceriodaphnia		
juveniles	0.18 ± 0.09	3
adults	0.25 ± 0.07	3
Orthocyclops		
nauplii	0.125 ± 0.02	4
copepodids	none present	
males	0.50	1
females	0.49 ± 0.15	4

Table 5. Exclosure bias on control dates (26-27th and 30-31st July)

	$\bar{x}$ (sample/exclosure) ± SE	n = number of pools
<u>Simocephalus</u>		
juveniles < 0.8 mm	2.27 ± 0.65	16
$1.2 >$ juveniles > 0.8 mm	2.78 ± 0.75	16
$1.6 >$ small adults > 1.2 mm	2.345 ± 0.54	16
large adults > 1.6 mm	1.525 ± 0.57	8
<u>Ceriodaphnia</u>		
juveniles	11.35 ± 4.39	5
adults	1.465 ± 0.42	6
<u>Orthocyclops</u>		
nauplii	0.72 ± 0.57	3
copepodids	2.285 ± 0.46	8
adult males	1.32 ± 0.66	5
adult females	1.40 ± 0.50	7

while for adult *Orthocyclops* the bias is 1.3 to two-fold. The source of this bias is thought to be the mortality or injury imposed upon individual prey during the sampling procedure prior to their placement into the exclosure. Though care was exercised to avoid damaging prey, it appears that the sample of prey placed into the exclosures was not a representative quantitative sample of the prey populations in the pools. In addition, comparison of *Simocephalus* brood sizes inside and outside of exclosures throughout the experiment (Figures 7.1-7.8, C) shows a significant tendency for slightly smaller brood sizes within the exclosures (Paired t test: $\bar{d} = 0.316$ eggs/brood; $s_{\bar{d}} = 0.077$; $P(t_{117} \geq 4.1) < 0.0001$). This may indicate slightly lower food levels within the exclosure. The bias introduced by either of these factors is in a conservative direction relative to the objectives of this study. Any instances when exclosure densities exceed those observed in the presence of damselfly naiads (those differences which should be attributable to the action of damselfly predation), arose despite a rather formidable bias. For this reason, mortality estimates determined by the exclosure method must be considered *minimum*, and it should not be surprising if these estimates are sometimes negative (exclosure density less than observed). These facts cast considerable doubt on the usefulness of the predator exclosures for the system under study. Nevertheless, the data will be presented parallel to that obtained using the extrapolation procedure because they provide minimum estimates of mortality and an independent estimate of the pattern of predator influence.

Ishnura verticalis naiads were collected from Wintergreen Lake, W. K. Kellogg Biological Station, Kalamazoo County, Michigan on 1st August 1968. Naiads less than 5 mm long were selected from the collection and introduced into the pools on 2-3rd August. Three hundred and seventy naiads were introduced into each pool. This represents an average of ten per non-enclosed "weed", a density estimated to be comparable to those found in weed beds in the Cornell ponds. The naiads grew as a cohort increasing in size throughout the experiment (Figures 5.1-5.2). Thus predator size is confounded with temporal trends. The growth of damselfly populations has often been observed to be somewhat synchronous (Macan, 1964; and Lutz, 1968), though in the present case similarity in size was accentuated by the initial selection of naiads within a certain size range.

Exclosure samples from 3-4th August have not been included because they are not comparable to either controls or subsequent experimental samples since damselflies had only been present for one day when they were taken. On 7-8th August the first experimental samples were taken, and sampling continued at four-day intervals until 28-29th September. Four days is less than the generation time for Simocephalus at the temperatures observed, so that observed values for the exclosures are not confounded with the type of intraspecific and interspecific competition which might arise over the course of several generations (Frank, 1952). Such short-term estimates are necessary if the role of predation is to be interpreted with respect to changes in density or composition of the prey populations.

RESULTS

Damselfly Naiad Density and Growth

Damselfly density was estimated by the mean of six samples taken from each pool on each sampling date (Figure 3). Ten naiads per "weed" were initially introduced to each pool, and no adults emerged from the pools. There is considerable variation in the density estimate within each pool from date to date, but five naiads per "weed" is a good approximation to the average density in the samples from all pools over all dates. After the experiment was completed a count was made of all naiads surviving in each pool (Table 6). These data demonstrate approximately 50% survival of the damselflies introduced to the pools. The distribution of this mortality over the course of the study is not known.

The naiads were not uniformly distributed among the forty "weeds" in each pool (Figure 4). Naiads tended to aggregate around the edges of the pool, especially along the southern edge ("weeds" 36-40). These were the positions shaded by the side of the pools during the morning hours when sampling was done. Naiad distribution at other times of day was not determined. Since two samples were randomly selected from

Table 6. Survival of damselfly naiads 2-3rd August to 12-13th October.

Pool Number	Introduced 2-3rd August	Final census 12-13th October	Percent survival
1	370	139	37.6
2	370	156	42.2
3	370	180	48.6
4	370	185	50.0
5	370	159	43.0
6	370	194	52.4
7	370	202	54.6
8	370	177	47.8
			$\bar{x}$=47.0

Figure 3. Number of damselfly naiads per sample on each sampling date in Pools 1-8. Each point is the mean of six samples. Mean of all eight pools is presented on the top line.

Figure 4. Mean number of damselfly naiads per sample taken from each "weed" position within all pools over all dates.

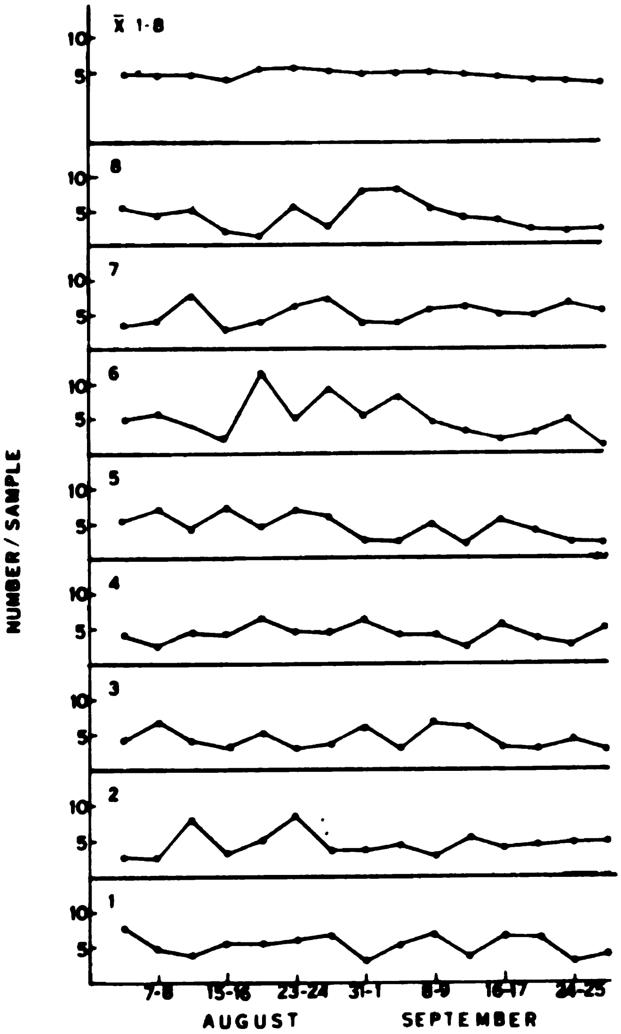


Figure 3

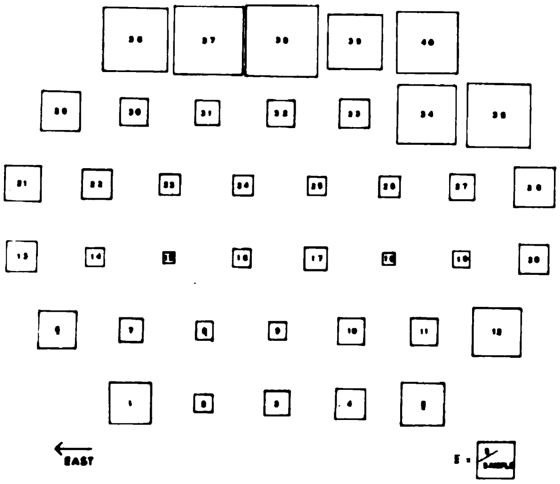


Figure 4

each third of the pool ("weeds" 1-13, 14-27, 28-40) samples from high and low density areas were usually included in the estimate of each mean.

The percent composition, by instar, of the damselfly population on each date is presented in Figures 8.1-8.8 (C). The naiads within each pool show a somewhat synchronous growth pattern. A majority of the naiads are often in the same instar, and the mode of the instar distribution often shifts dramatically during one or two sampling intervals (i.e., Pool 1, 23-27 August, 4-12 September; Pool 2, 19-23 August, 4-8, 12-16 September; Pool 3, 4-12 September). The average growth increment of the naiad population fluctuates dramatically from date to date, reflecting this somewhat synchronous molting pattern (Figures 8.1-8.8 (A)).

The average size of damselfly naiads increased throughout the study within each pool (Figures 5.1-5.2). Naiads in Pool 2 were consistently smaller than those in other pools after 11 August, while those in Pools 1 and 5 tend to be largest. The means of total body lengths presented in Figures 5.1 and 5.2 were ranked from smallest to largest on each date and assigned ranks 1-8. The ranks for each pool were summed over all dates and a Friedman two-way analysis of variance (Siegle, 1956) used to test the hypothesis that the eight average ranks were drawn from the same population (Table 7). This hypothesis was rejected ($P(X^2_7 \geq 451) << 0.001$). It may be concluded that there was a significant tendency for

Figure 5.1 and 5.2. Mean total body length (excluding caudal lamellae) for all naiads sampled within each pool on each sampling date. Parentheses enclose a line equal in length to the average standard error for all means in each figure.

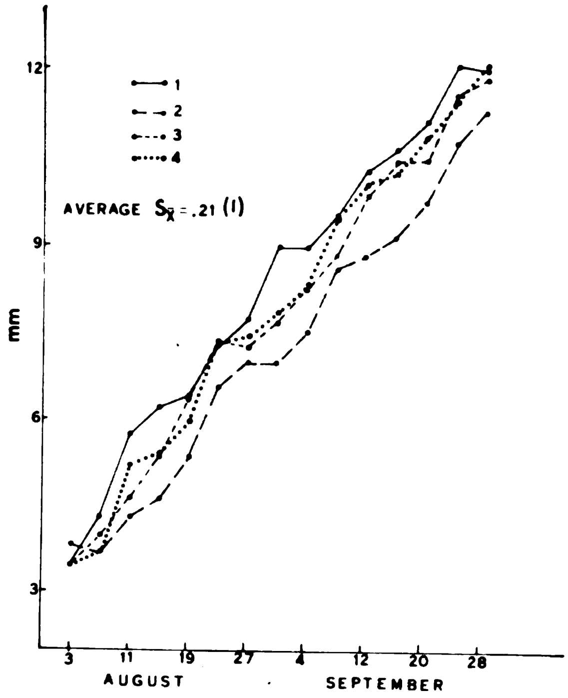


Figure 5.1

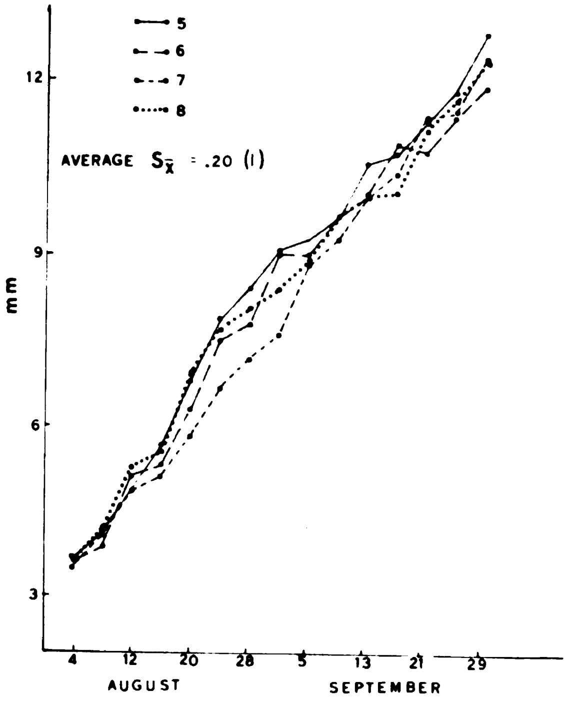


Figure 5.2

Table 7. Average rank over all dates of the mean total body length of damselfly naiads in each pool. Means from Figures 5.1 and 5.2 for each date were ordered from smallest to largest and assigned ranks 1-8.

Pool	Average rank over fifteen consecutive sampling periods
5	6.97
8	6.03
1	5.77
6	4.93
4	3.83
7	3.73
3	3.27
2	1.47

Friedman two-way analysis of variance (Siegel 1956):

$X_r^2 = 12/Nk(k + 1)\ \Sigma(R_j)^2 - 3N(k + 1)$

N = number of dates = 15

k = number of pools = 8

R_j = rank (1, 2...8) assigned to the mean total body length for each pool on each date.

$P(X_7^2 \geq 451) << 0.001$

the naiads to grow slightly larger in some pools than in others, and that this tendency was somewhat consistent over the course of the study.

Prey Densities

The densities of prey species observed among the "weeds" within each pool are presented in Figures 6.1-6.8. Prey species compositions established in each pool at the beginning of the study (Table 1) were maintained with two exceptions: *Orthocyclops* contaminated Pool 3 after 8 September, and midge larvae contaminated all pools during the second half of the study. *Simocephalus* became the most abundant prey species in all pools, being surpassed by midges toward the end of the study in Pools 1-4. Densities of *Ceriodaphnia* remained very low in Pool 1 throughout the study, as did those of *Orthocyclops* in Pool 2. Only in Pools 5 and 7 did these alternate prey reach densities which seem significant relative to those of *Simocephalus*.

Simocephalus Population Dynamics

Information needed for the interpretation of changes in the *Simocephalus* population within each pool is presented in Figures 7.1-7.8. The observed changes in density throughout the study (A) may be compared to the mean brood size for females of a standard length (C), the reproductive status of

Figures 6.1-6.8. Number of each prey taxon per sample on each date within each of eight pools. Solid line (——) = *Simochephalus*; dotted line (•••) = *Orthocyclops*; dashed line (---) = *Ceriodaphnia*; and alternate dots and dashes (•-•-•-•) = midge larvae.

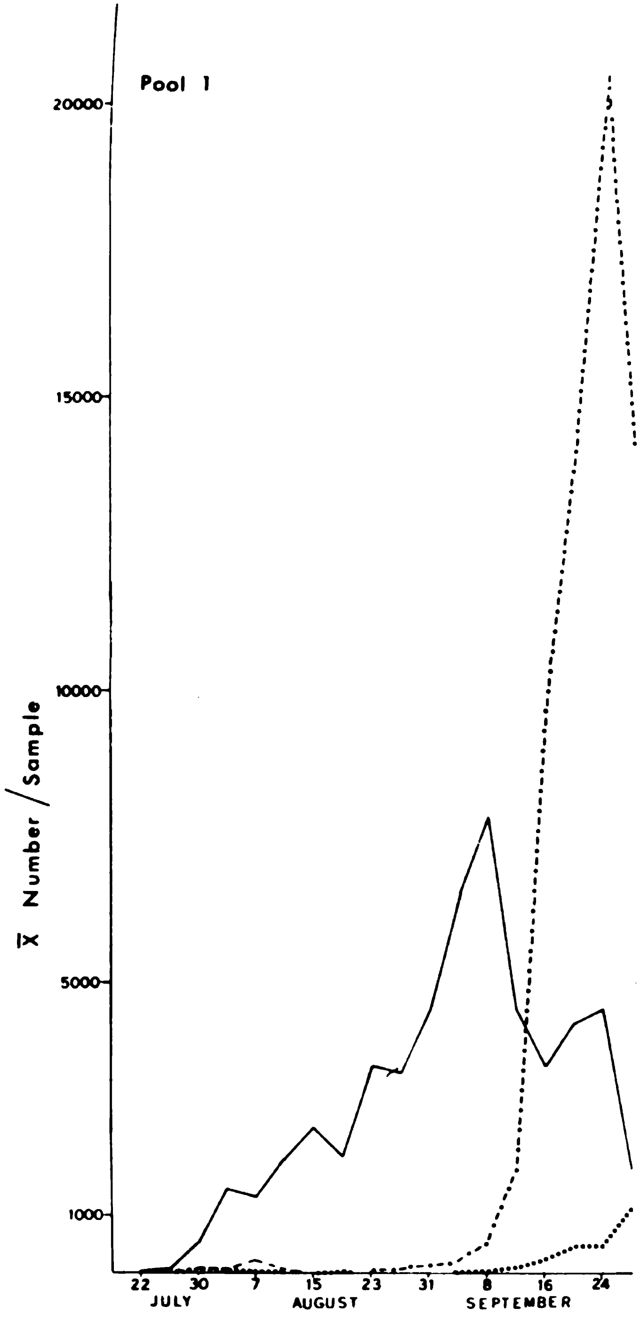


Figure 6.1

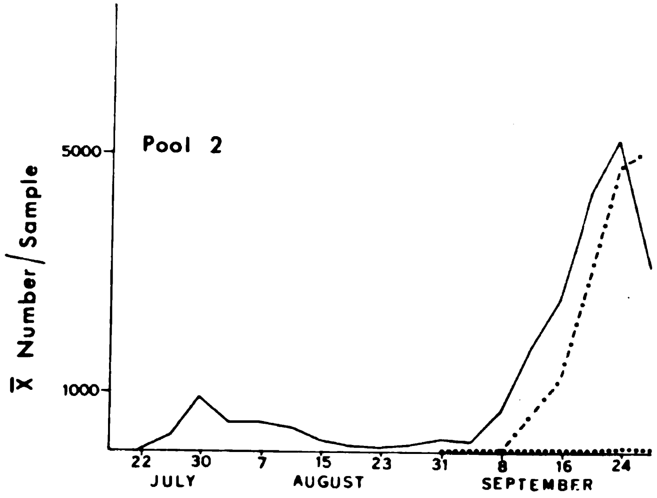


Figure 6.2

Figures 6.1-6.8. Number of each prey taxon per sample on each date within each of eight pools. Solid line (——) = *Simochephalus*; dotted line (···) = *Orthocyclops*; dashed line (---) = *Ceriodaphnia*; and alternate dots and dashes (·-·-·-·) = midge larvae.

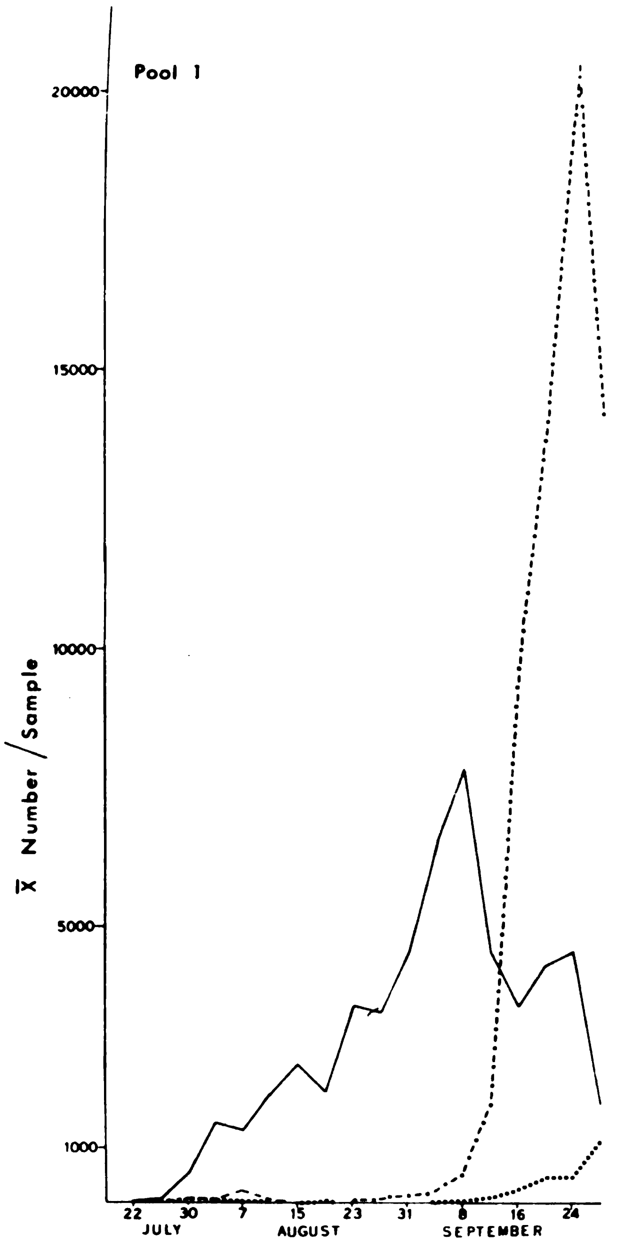


Figure 6.1

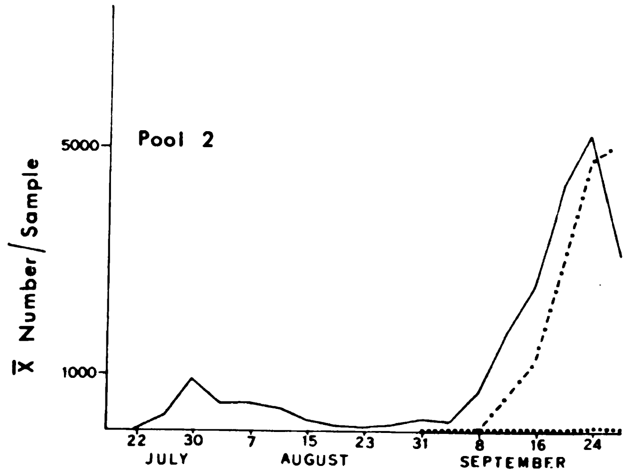


Figure 6.2

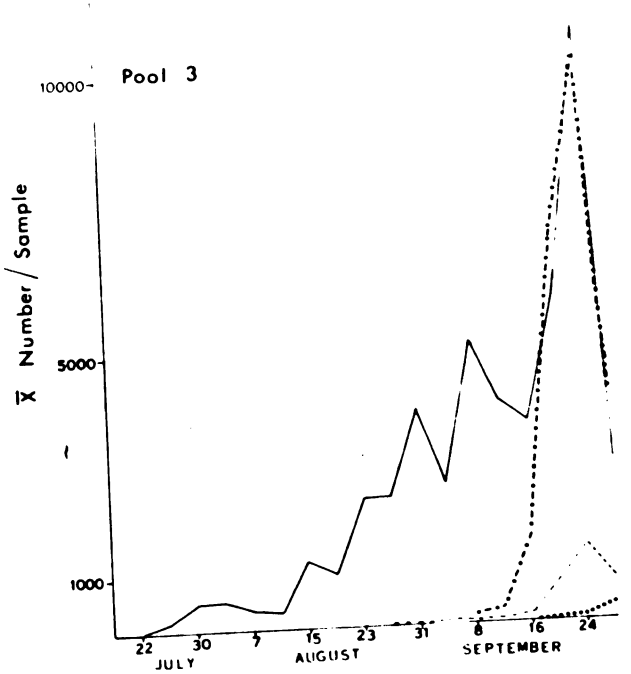


Figure 6.3

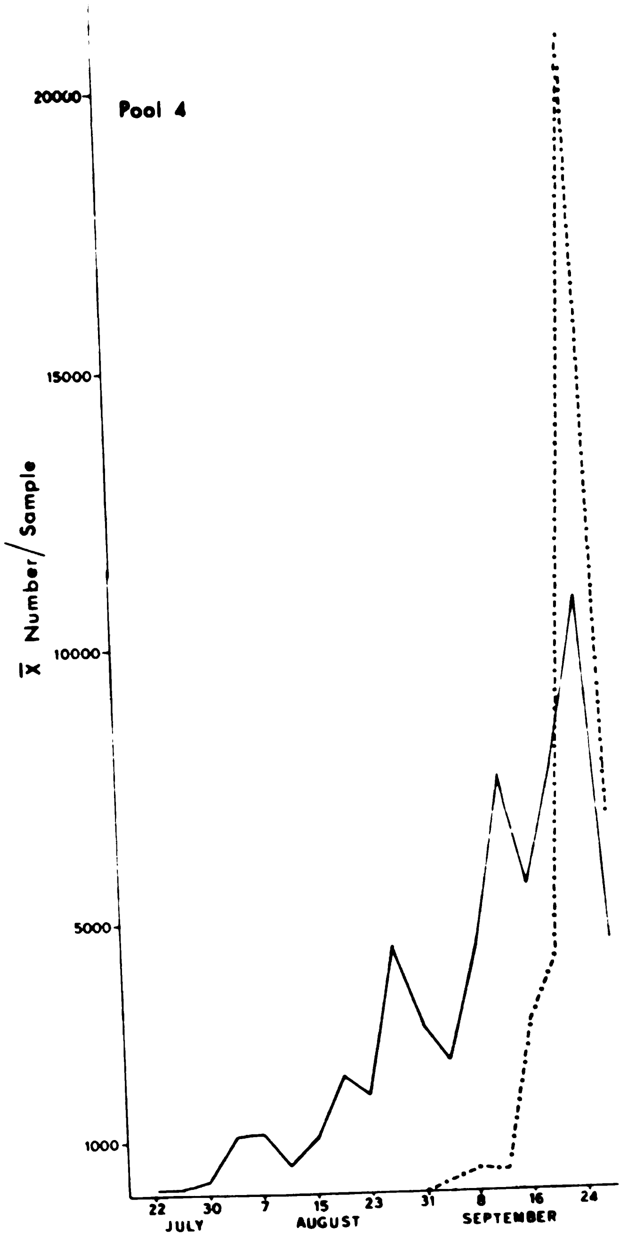


Figure 6.4

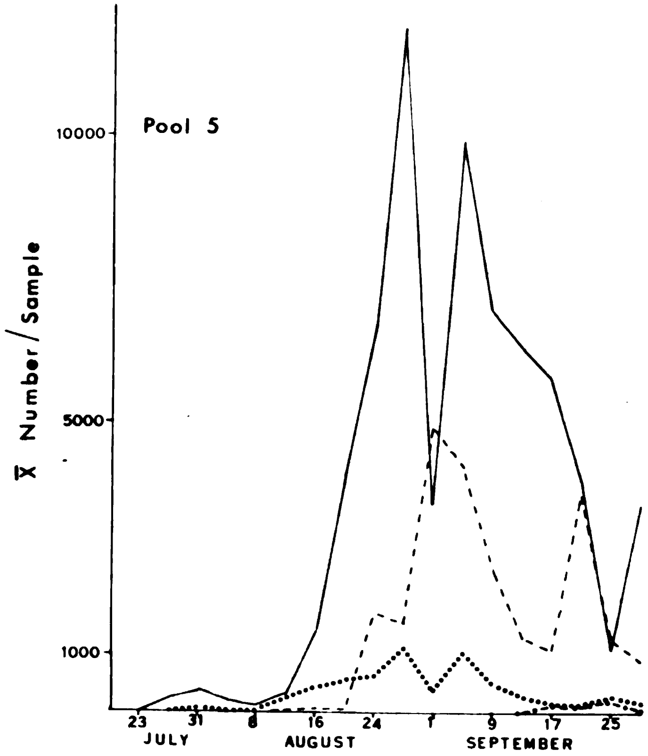


Figure 6.5

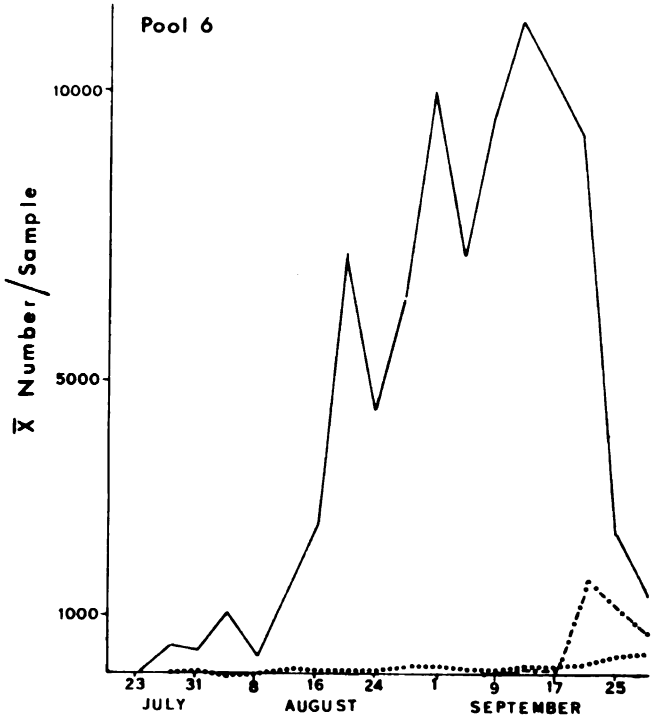


Figure 6.6

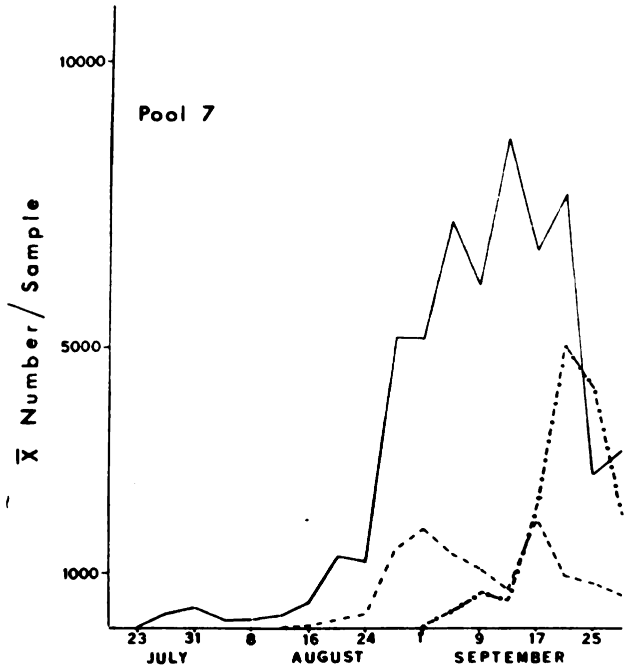


Figure 6.7

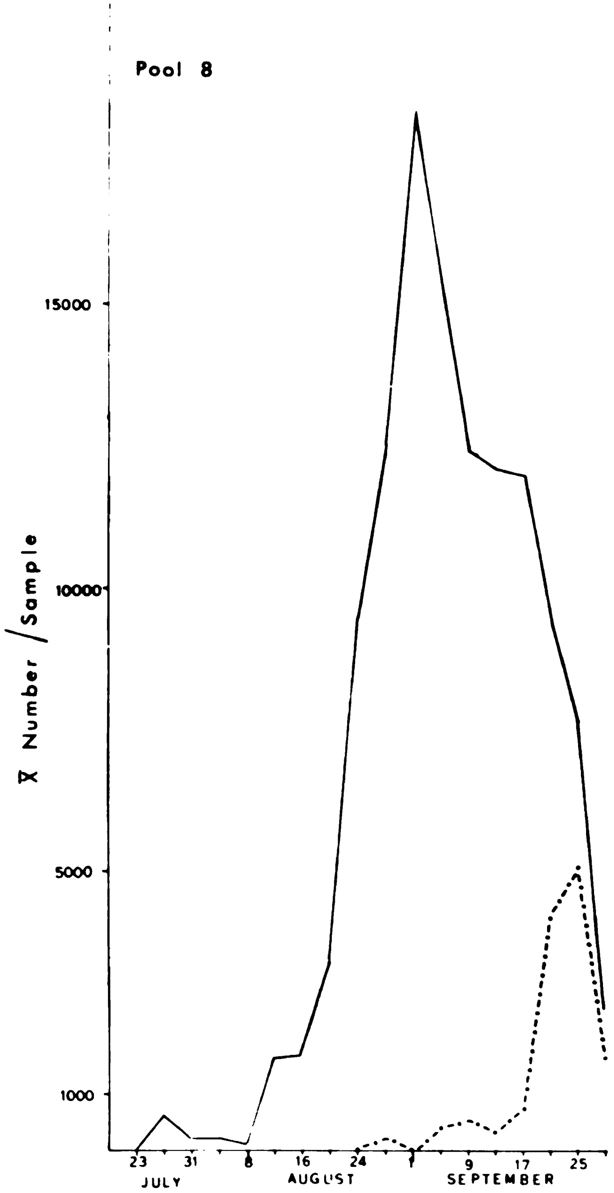


Figure 6.8

Figures 7.1-7.8. Simocephalus population dynamics.

A. Number of Simocephalus per sample on each date within each pool: ▲ = observed population in the presence of damselfly naiads; ■ = portion of population protected from naiad predation for four days within a predator exclosure net; ● = predicted population extrapolated from observed population parameters four days previously. Each point is the mean of three samples (see text for further details).

B. Diamonds denote differences between pairs of means judged to significant at $\alpha = 0.05$ (see text for criterion used).

C. Adjusted mean brood size for Simocephalus female of standard length (1.4 mm). Solid line connects values observed in the pool at four day intervals. Open squares represent values observed within predator exclosure nets (see text for further explanation).

D. Reproductive status of small adult Simocephalus ($\geq$ 1.2 mm). Percentage with parthenogenetic eggs, sexual ephippal eggs, or no eggs in brood sac. Preservation technique caused many with eggs to drop them, so that observed percentages are biased toward "no eggs". Percent with ephippia is shaded.

E. Size structure of the Simocephalus population. Percentage of all Simocephalus less than 0.8 mm, 1.2 mm and 1.6 mm, respectively. Those less than 1.2 mm are juveniles.

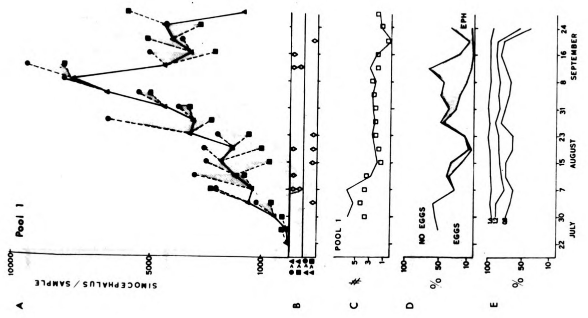


Figure 7.1

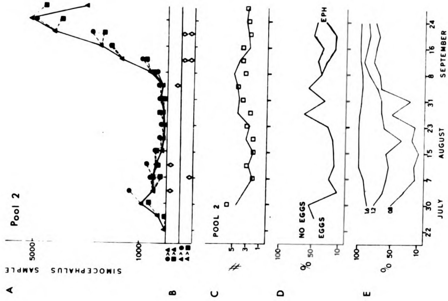


Figure 7.2

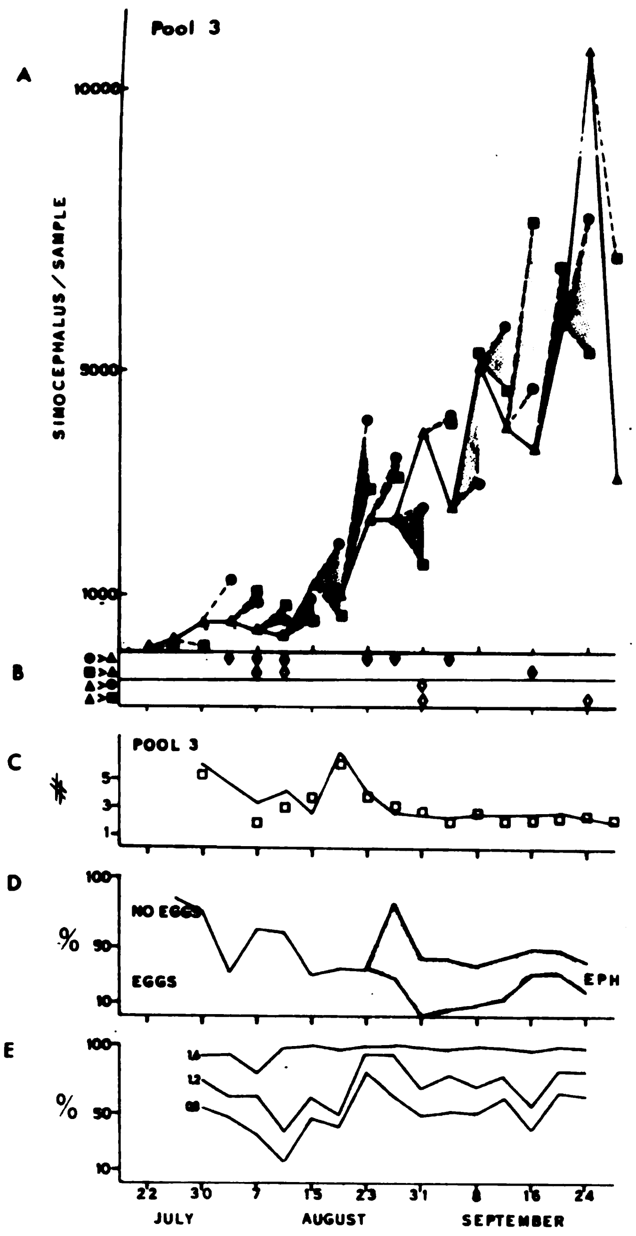


Figure 7.3

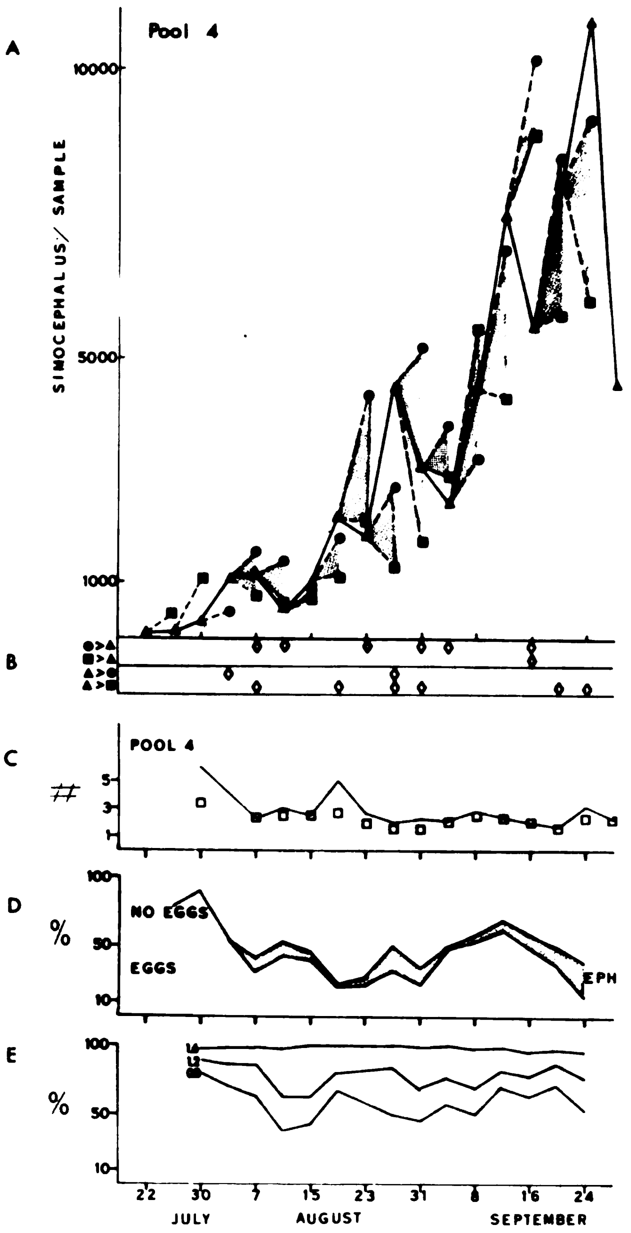
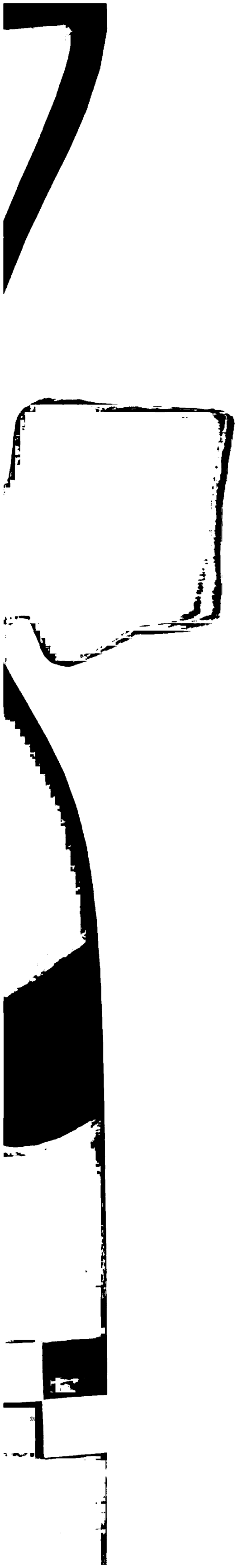


Figure 7.4



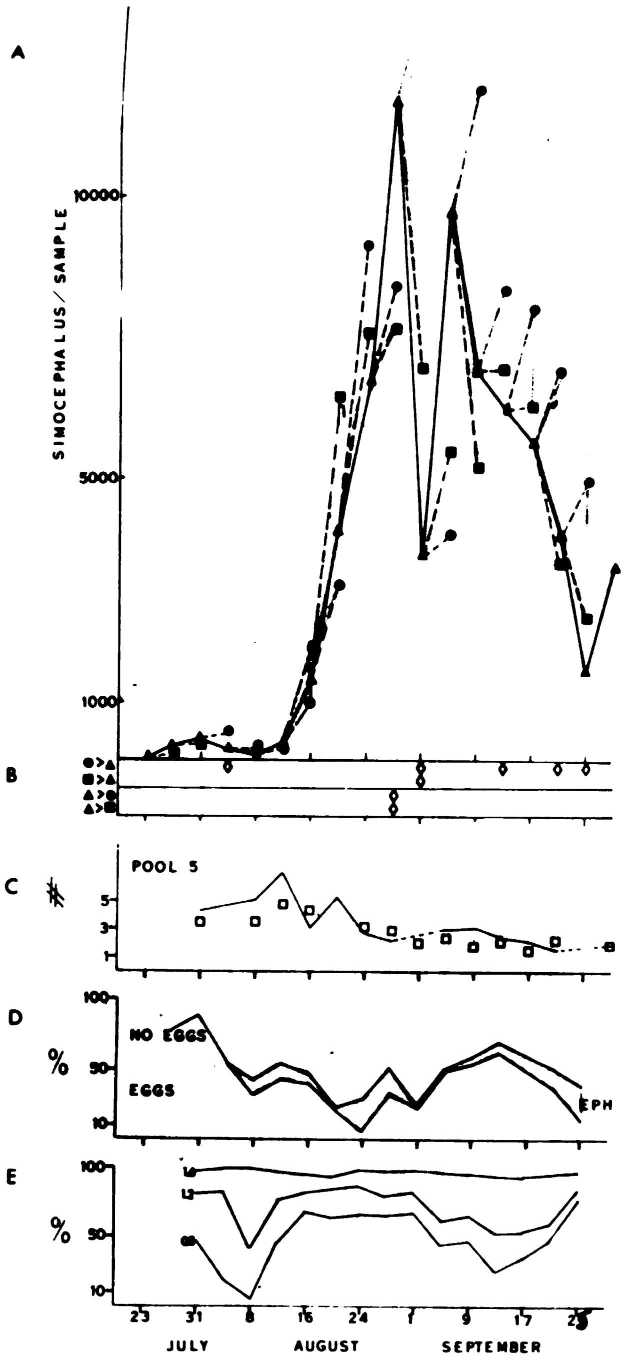


Figure 7.5

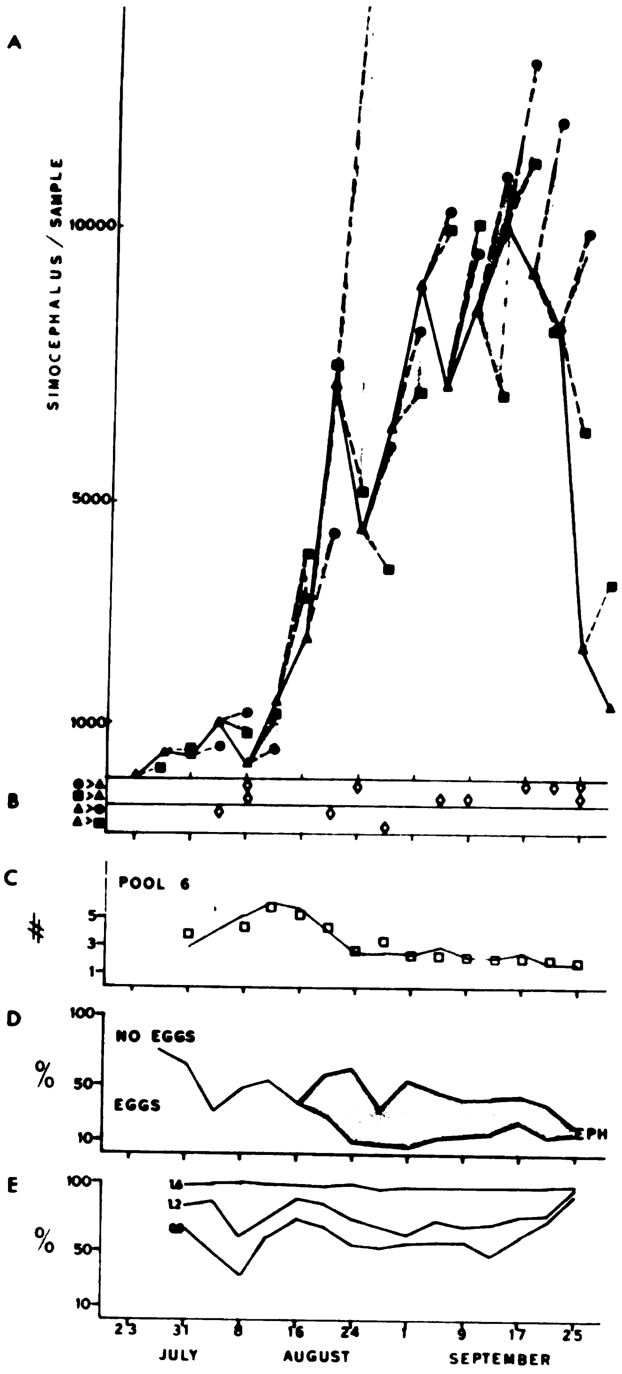
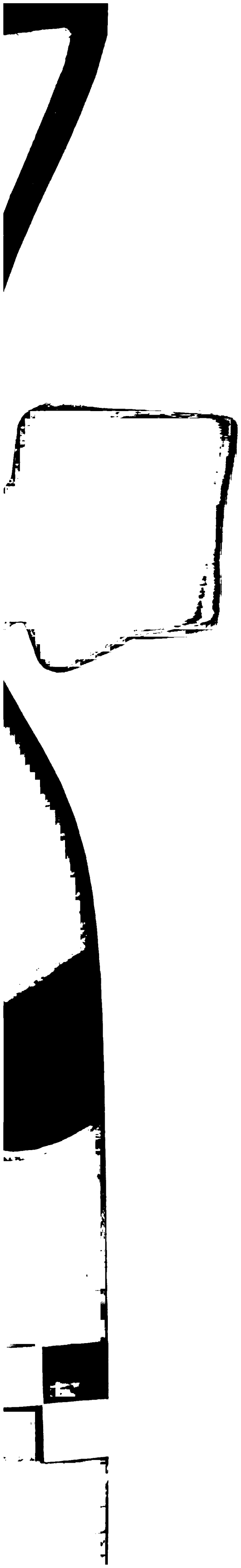


Figure 7.6



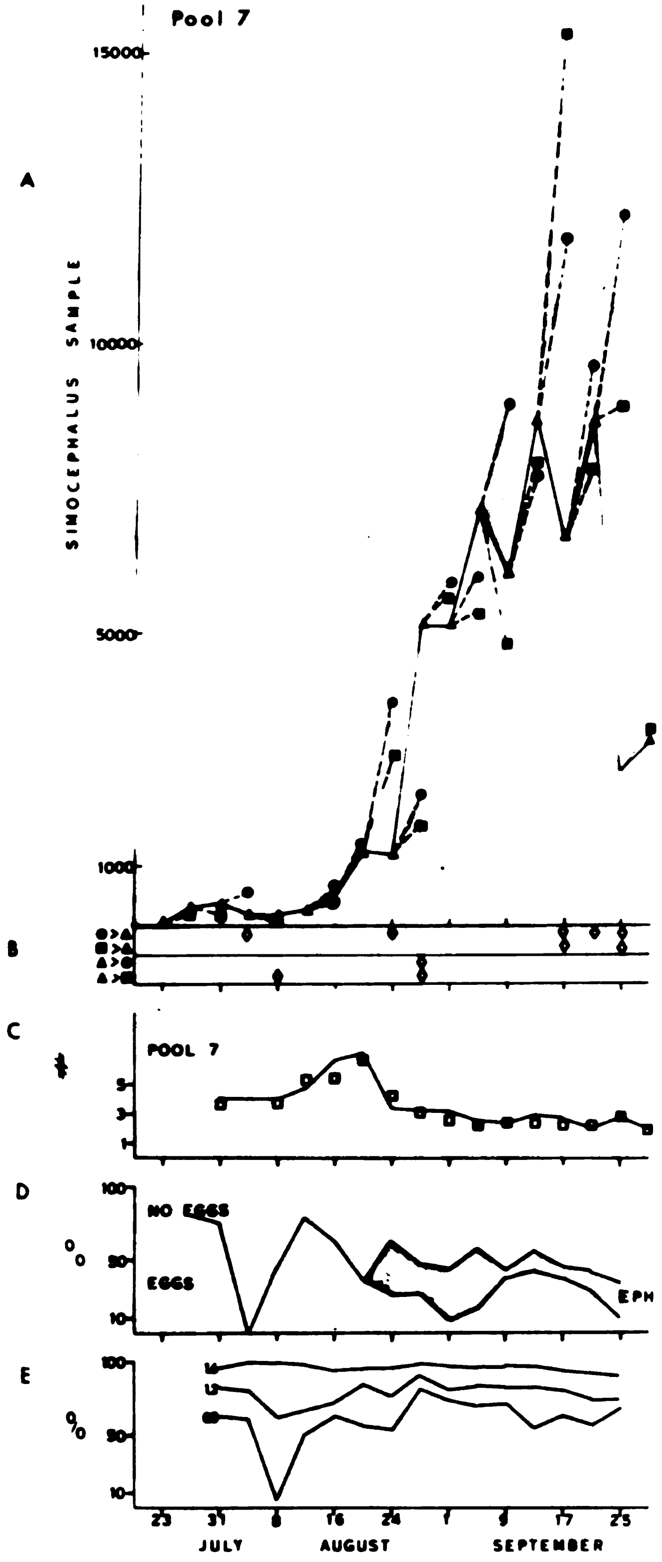


Figure 7.7

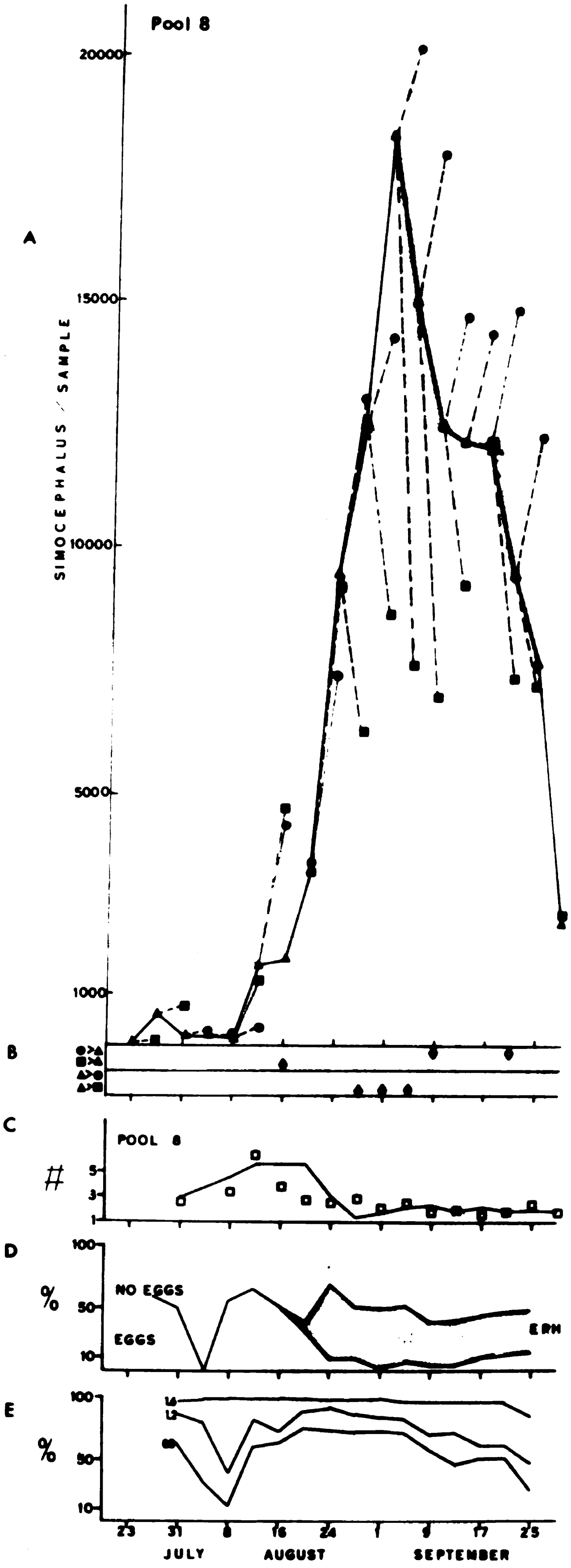


Figure 7.8

small adults (D), and the size structure of the population (E). Brood size (C) is considered a reflection of food supply per individual and tends to decline as populations become more dense. The production of ephippial eggs (D) is a response to environmental stress, probably a complex interaction of temperature, food supply, and density. A size structure skewed toward small (young) individuals is indicative of either a rapidly expanding population, or of a population subjected to intense mortality (i.e., predation).

The potential growth of the Simocephalus population during each four-day interval, estimated by the use of predator exclosure nets and mathematical extrapolations, is presented in Figures 7.1-7.8 (A). The density attained within an exclosure is considered a minimum estimate of the population's potential density because of the large bias associated with establishing the exclosure (Table 5). Consequently, these estimates are often less than the density reached in the presence of predators. Extrapolations based on observed population parameters at the beginning of each interval are considered maximum estimates, though the fact that they are occasionally exceeded indicates that they fail to be so on occasions.

Estimates based on exclosures and extrapolations are subject to variance associated with the three samples from which they were established or calculated respectively. A strong relationship between means and variances made it necessary to perform a fourth root transformation ($x' = x^{-\frac{1}{4}}$) on the data before statistical inferences were made concerning the significance of differences among means. If the difference between two means of transformed data is greater than twice the average of their standard errors, they are considered significantly different (Student t test, $n = 3$, $\alpha = 0.05$). Mean densities of exclosures or extrapolations judged to be significantly different from the observed mean using this criterion are denoted in Figures 7.1-7.8 (B).

The differences between exclosure or extrapolated densities and those observed in the presence of damselflies provide mortality estimates for each size category of the _Simocephalus_ population during each four-day interval. These estimates were converted to biomass using the values in Table 2, and the sums over all size categories are presented in Figures 8.1-8.8 (A). The magnitude of these mortality estimates fluctuates dramatically during the course of the study in most pools.

Alternate Prey Mortality

Estimates of alternate prey mortality, based on the difference between the density of each size category inside and outside the exclosure were converted to biomass using Table 2 and presented in Figures 8.1-8.8 (B). Exclosure estimates for _Ceriodaphnia_ and _Orthocyclops_ are subject to a converva-tive bias associated with the sampling procedure (Table 5).

Figures 8.1-8.8. Predator influence and growth pattern.

A. ● = Extrapolated means minus observed mean biomass of Simocephalus. ■ = Exclosure mean minus observed mean biomass of Simocephalus. The area between these estimates is shaded to indicate that one is considered a maximum and the other a minimum estimate of predator influence.

▲ = Growth increment of the damselfly naiads during each interval (based on data transformed from total body length to dry weight biomass; see text). Increment per individual x 100.

B. Predator influence on alternate prey species (exclosure mean minus observed mean biomass). Dotted lines (····) = Orthocyclops; dashed lines (----) = Ceriodaphnia; alternate dots and dashes (·-·-) = midge larvae.

C. Percent distribution by instar of the damselfly naiads on each date. The width from one date's base to the next's is equal to 100%.

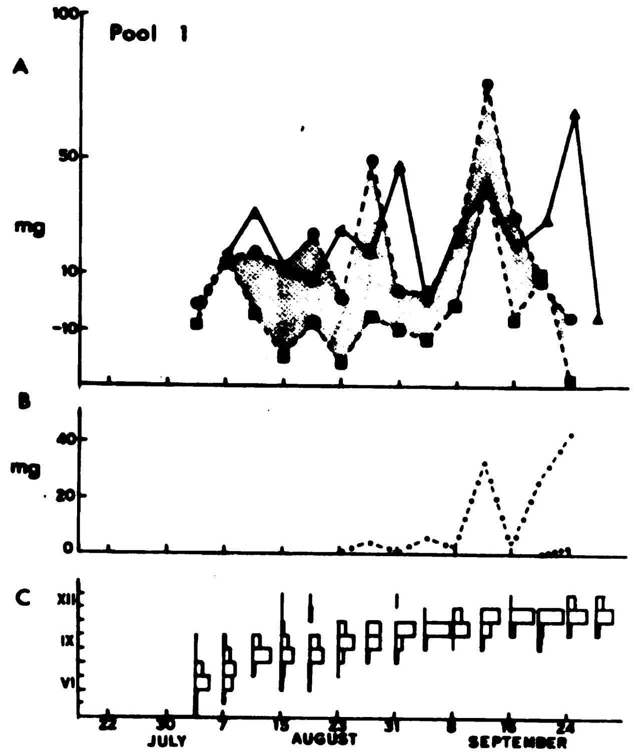


Figure 8.1

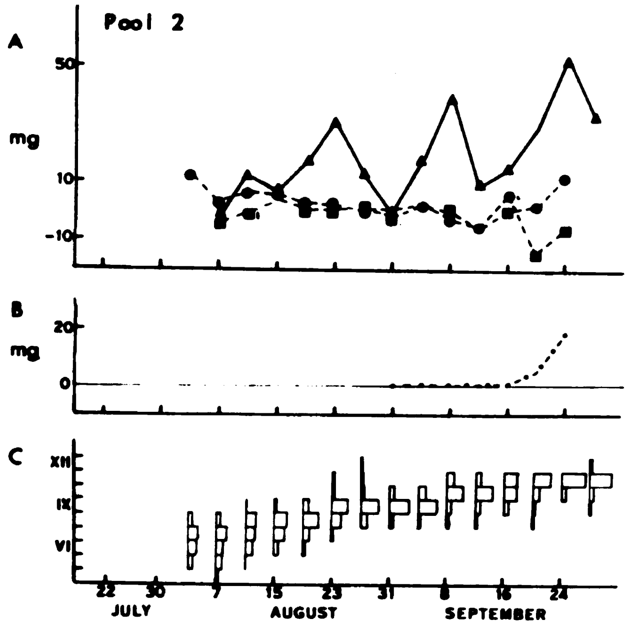


Figure 8.2

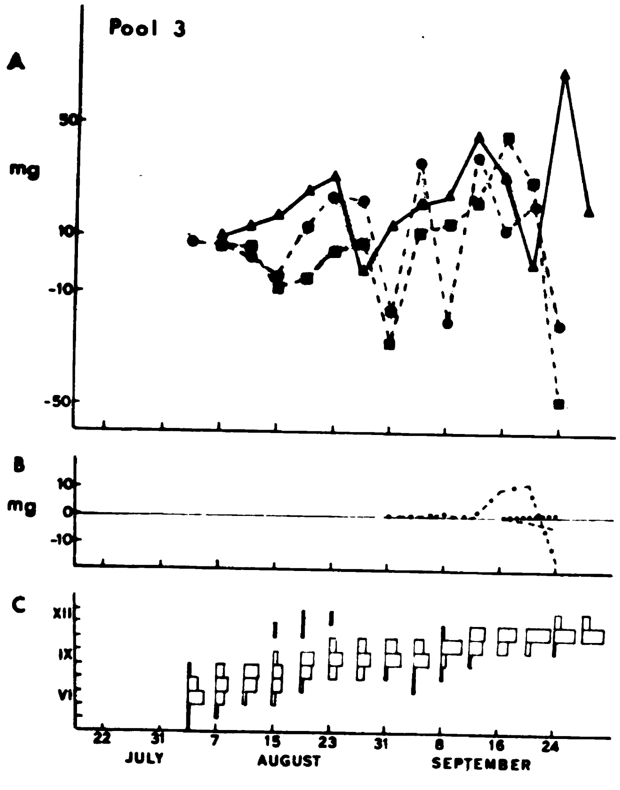


Figure 8.3

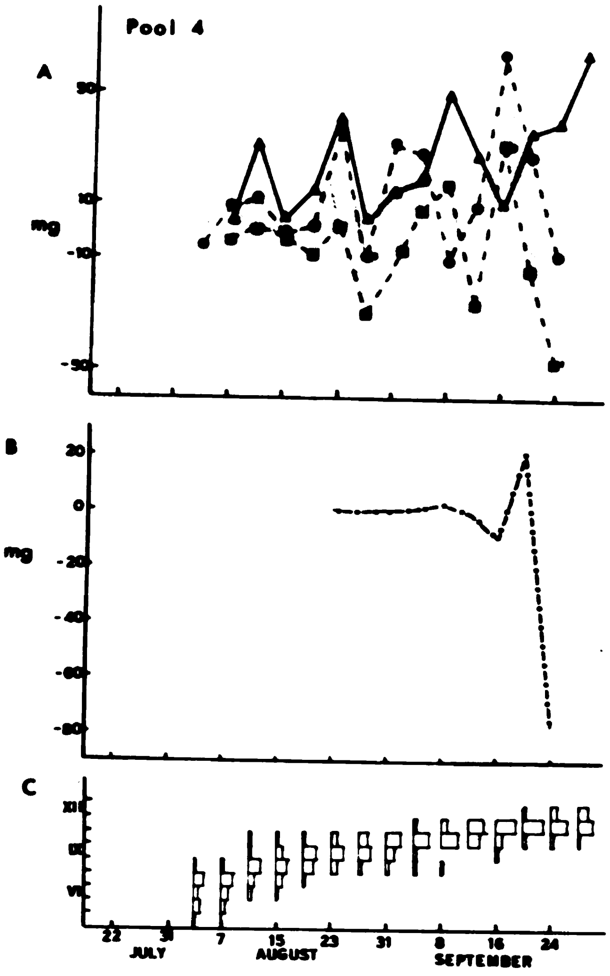


Figure 8.4

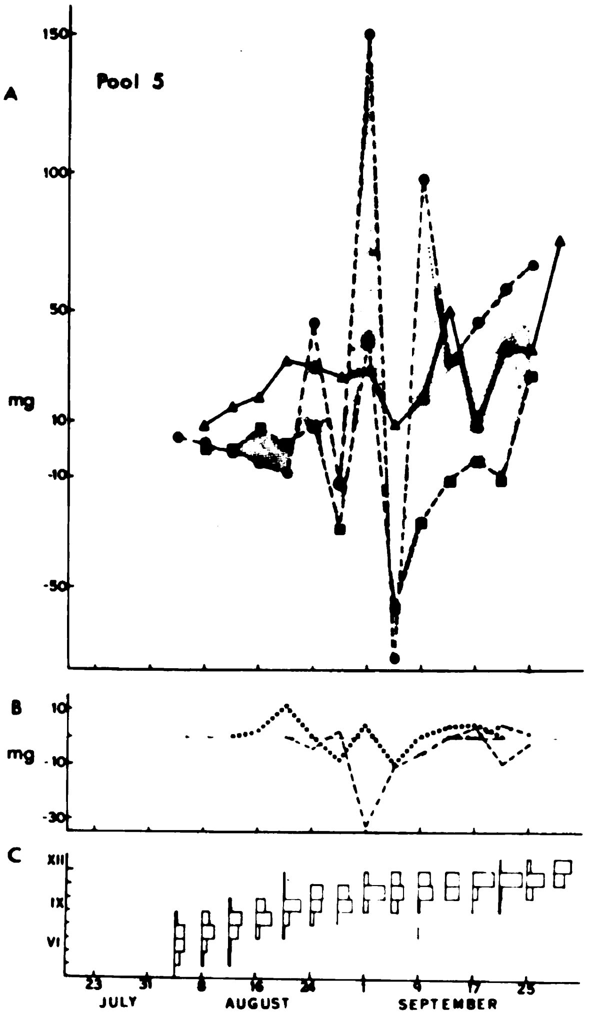


Figure 8.5

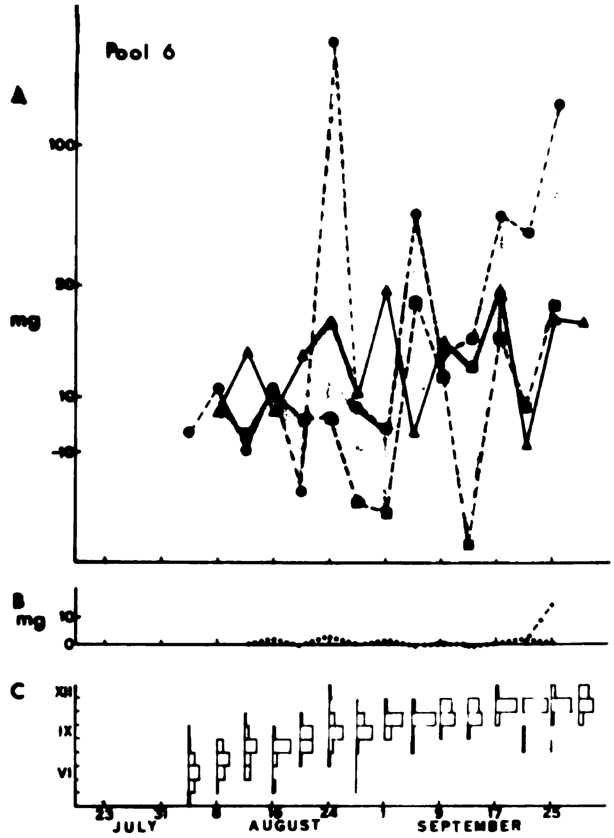


Figure 8.6

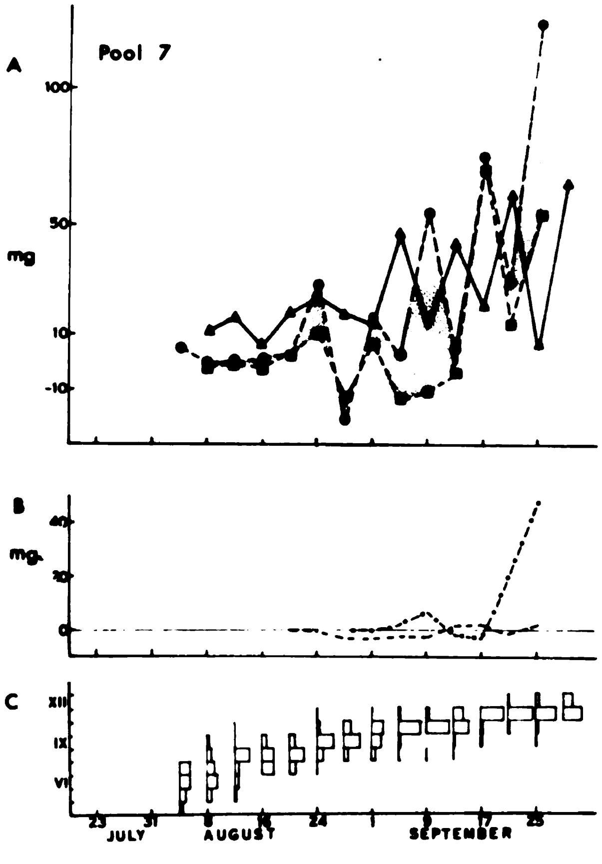


Figure 8.7

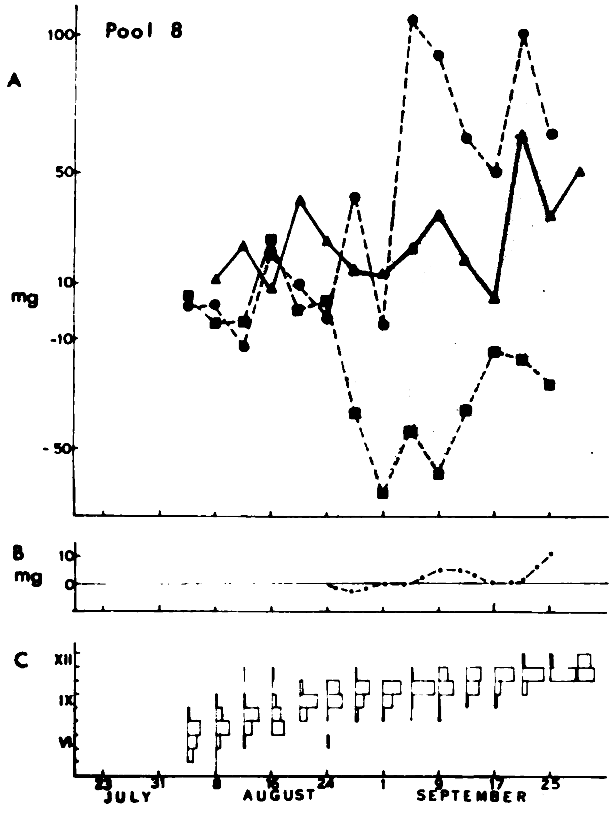


Figure 8.8

Estimates for midge larvae are probably less biased because the larvae are less easily damaged by the sampling procedure.

DISCUSSION

Damselfly Density

Estimates of damselfly naiad density show little change in the number of naiads living among the "weeds" throughout the study (Figure 3). This number, about five per sample, is half of the total number added to the pool. A final census two weeks after the last sample was taken indicated approximately 50% survival of the naiads introduced to the pools (Table 6). These data are consistent with any of three interpretations concerning damselfly naiad mortality during the experiment:

1. Half of the naiads died within a few days of introduction; almost all were living among the "weeds"; and little mortality occurred during the rest of the study.
2. Half of the naiads were living among the "weeds" (the others dispersed over the surface area of the pool); most of those among the "weeds" survived through 28-29 September when the last sample was taken; and 50% mortality occurred either among those not living in "weeds" or during the two week period before the final census was made.

3. Half of the naiads were initially living among the "weeds"; mortality was distributed over the entire period of the experiment with those dying among the "weeds" being replaced from a reservoir of naiads living on other surfaces.

The last interpretation is consistent with the hypothesis of Macan (1966) that intraspecific competition for "feeding sites" among damselfly naiads leads to a group of naiads in "good" sites which are replaced when they emerge or die by individuals forced to live in "poorer" sites. Regardless of which interpretation is correct, it is concluded that an average density of five naiads per weed is a reasonable estimate of the number of naiads feeding in the sampled portion of each pool throughout the study. Since all subsequent discussion is based on the data obtained from this sampled portion, naiad density is considered a constant.

The tendency for naiads to aggregate in certain parts of the pool (Figure 4) suggests that predation pressure may have been distributed non-uniformly among the "weeds". However, it is possible that naiads moved around the pool in response to changing light conditions during the course of each day. There is no evidence to suggest that damselflies were aggregating in these areas in response to higher prey densities.

Simocephalus Population Dynamics

The observed densities of Simocephalus in each pool (Figures 7.1-7.8, A) may be compared to the mean brood size for females of standard length (C) and the reproductive status of small adults (D) to make inferences concerning some factors modifying the potential growth of the population during each sampling interval. Brood sizes were initially high (4-6 eggs) in most pools, but declined to 2-3 eggs as population density increased. Having declined to this level, they remained nearly constant for the remainder of the study in most pools. The decline in brood size with increasing density was often accompanied by formation of ephippial eggs (D) which may represent a response to lowered food supply or physiological stress at this time. In four pools (3, 6, 7 and 8) brood size declined and ephippial eggs were formed during a period when temperatures were very high (Figure 2), suggesting that a complex interaction of food supply, density, and temperature may have been involved. The percentage of small adults carrying parthenogenetic eggs declines to a low level during this same period in some pools (1, 3, 5, 6, 8). Pool 2 (Figure 7.2) represents a unique case among the eight pools. Simocephalus density failed to increase until much later than in any other pool (A). Brood sizes (C) and percentage producing parthenogenetic eggs (D) were initially lower than in other pools, and ephippial formation (D) was delayed until much later. The size structure (E) reflected less recruitment into the population than in other pools. The failure of this population to increase rapidly once brood sizes and percentage producing parthenogenetic eggs increased (about 27th August) may be attributable to the cooler temperatures, and thus longer development times, prevailing after this date. Since the production of parthenogenetic eggs is the means by which population recruitment and growth is achieved, it may be concluded that the potential rate of increase of the Simocephalus population was sometimes limited by low brood sizes and/or physiological stress usually associated with high densities.

The observed growth of Simocephalus populations within some pools was interrupted by intervals during which little growth or a sharp decline in density occurred (i.e., Figure 7.1 (A), 3-7, 15-19, 23-27 August, 8-12, 12-16 September; Figure 7.5 (A), 28 August-1 September; Figure 7.7 (A), 20-24 August, 28 August-1 September). Periods of density decline sometimes alternate with periods of increase producing apparent fluctuations (i.e., Figure 7.3 (A), 27 August-24 September; Figure 7.4 (A), 23 August-24 September; Figure 7.6 (A), 20 August-13 September; Figure 7.7 (A), 1-21 September). In Pools 5 and 8 Simocephalus density reaches a peak about 5th September and declines continually thereafter (Figures 7.5 and 7.8 A). Few of these observed trends can be wholly accounted for by changes in mean brood size (C), reproductive status of small adults (D) or size structure (E). The fluctuations in density observed in Pools 3 and 4 occur while brood size remains virtually constant, and the percentage producing ephippia, though larger in 3 than 4, is nearly constant from date to date within each pool (Figures 7.3 and 7.4, A, C, D). The size structure of both populations is approximately 75% juveniles throughout the period, indicating a continual recruitment into the population (E). The fluctuations observed in Pools 6 and 7 are similarly not correlated with dramatic changes in these indices (Figures 7.6 and 7.7). The continual decline of Simocephalus density in Pool 5 began when the percentage of small adults producing parthenogenetic eggs was near its peak (Figure 7.5 A, D). Only about 50% of the population was composed of juveniles as density began to drop, but this shifted toward about 75% juveniles on 25th September even though density continued to decline. Examination of Figures 7.1-7.8 reveals other instances when observed changes in population density are not attributable to changes in the population parameters presented. The implication of these observations is that an independent source of mortality (i.e., predation) is responsible for the irregularities observed in the growth curve.

Independent estimates of the potential growth rate of the Simocephalus population during each four-day interval show that during thirty-seven of one hundred four intervals studied between 3rd August and 24th September (35.6%) one or both estimates of potential density exceed the observed density by a significant amount (Figures 7.1-7.8 A, B). Extrapolation means significantly exceed the observed means in thirty-two cases (30.8%) while exclosure means, despite the large bias against them, are significantly larger in fifteen cases (14.4%). Mortality estimates based on these data account for many of the irregularities in the growth curves discussed above. In several other cases one or both of the estimated means was larger than the observed mean, but could not be judged as significantly larger because of the size of the variances associated with the means. However, it is important to note that in the majority of intervals studied (64.4%) mortality attributable to damselfly predation is not statistically significant. It must be concluded that though damselfly predation may have been an important mortality source on some occasions, it was certainly not on many occasions.

Careful examination of Figures 7.1-7.8 (A) reveals a fluctuating pattern of mortality presumed to be attributable to predation in most pools. When these data are converted to mortality estimates and transformed into biomass these patterns are more obvious (Figures 8.1-8.8, A). Negative estimates are usually attributable to exclosure bias or sampling error (see Figures 7.1-7.8, B). Comparison of mortality estimates with the growth increment of damselfly

naiads during each interval (Figures 8.1-8.8, A) reveals a superficial similarity which may provide a clue to the factor responsible for the apparent intermittent effect of predation. It will now be suggested that the somewhat synchronous development of the cohort of damselfly naiads within each pool (Figures 8.1-8.8, C) which is reflected in fluctuating growth increments (A) also resulted in intermittent feeding activity and therefore intermittent influence on Simocephalus.

Studies of the feeding rate of arthropod predators in the presence of surplus prey have shown a tendency to feed intensively for short periods of time until the predator is satiated, after which feeding rates decline to a lower level. Holling (1966) found that a model including hunger as one component described this feeding pattern for mantids. Haynes and Sisojevic (1966) found that feeding rates of female spiders were very high immediately following ecdysis, declining after a few days to a much lower level. Lawton (1967) studying damselfly naiads, Pyrrhosoma nymphula, found that feeding rates following a period of starvation, low prey supply, or ecdysis were initially very high, but declined to a lower "maximum sustainable feeding rate". Such a pattern is likely to have occurred within each instar among naiads feeding on very dense Simocephalus populations in the present study. If it did, then the somewhat synchronous growth pattern observed for the damselfly population (Figures 8.1-8.8, A and C) could have caused similar fluctuations in the number of naiads feeding intensively on different dates. These may explain the observed intermittent pattern of predator influence.

An estimate of the proportion of damselfly naiads which molted into a new instar during each four-day interval and, therefore, are presumed to have been feeding most intensively was obtained using the instar distribution data presented in Figures 8.1-8.8 (C). A hypothetical cohort of 100 naiads was set up with the instar distribution observed on the first sampling date. For each successive date, a number of naiads were moved into later instars so that their distribution matched that observed. Minor discrepancies were introduced by the fact that instar distributions were determined from samples in which those instars with lowest frequencies were not always represented. However, this procedure provided an estimate of the proportion of naiads which must have molted during each interval (Figures 9.1-9.8, B). The variation in the estimates of this proportion from date to date within each pool reflects the extent to which the molting pattern of the naiads was synchronous. The naiads in Pool 2 were most highly synchronized, more than 75% of them molting during the same interval on four occasions (Figure 9.2, B). Those in Pools 6 and 7 also exhibited regular fluctuations in molting frequency, 50% or more often molting during the same interval. The other pools fail to show such regular patterns, but peaks of molting frequency are discernable on

Figures 9.1-9.8. Comparison of estimated damselfly molting frequency to estimates of _Simocephalus_ mortality.

A. Estimates of _Simocephalus_ mortality based on mathematical extrapolations (see legend for Figures 8.1-8.8, A).

B. Percentage of damselfly naiads estimated to have molted during each interval.

C. Percentage of the damselfly naiads estimated to have entered each instar within each interval (distance between base lines = 100%).

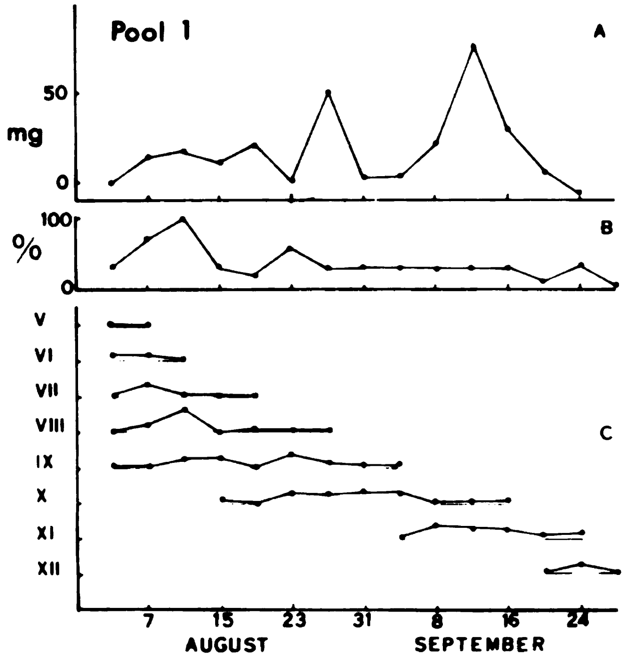


Figure 9.1

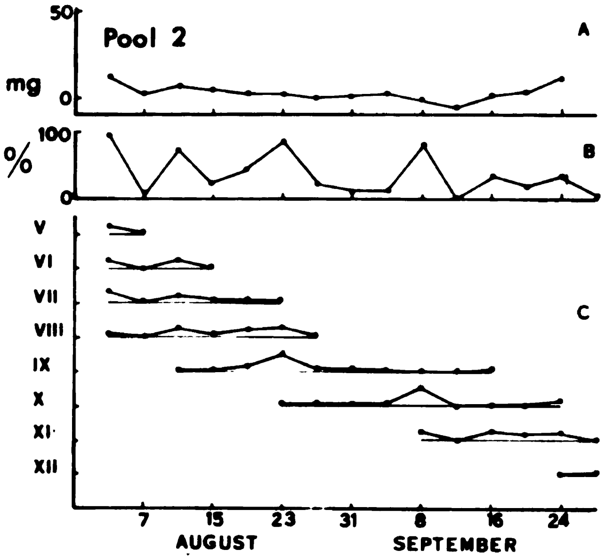


Figure 9.2

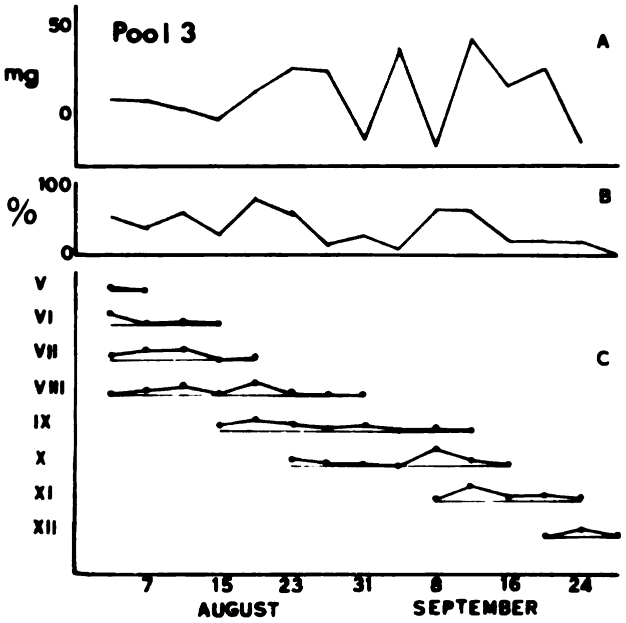


Figure 9.3

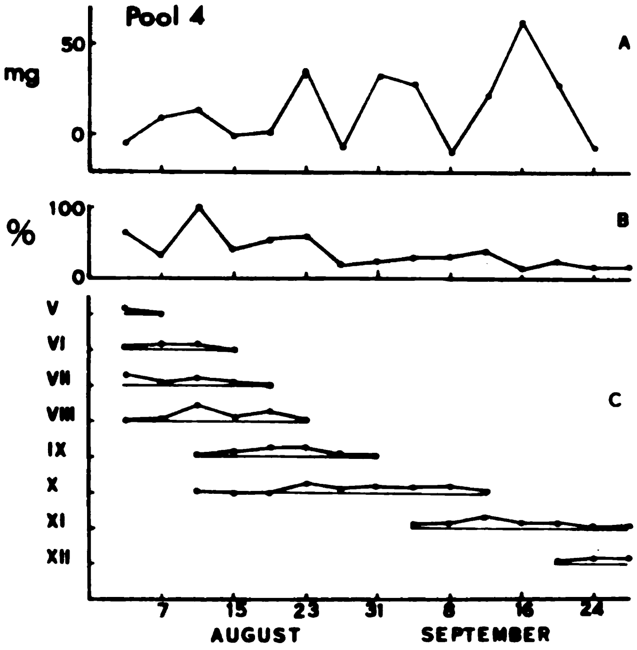


Figure 9.4

Figures 9.1-9.8. Comparison of estimated damselfly molting frequency to estimates of Simocephalus mortality.

A. Estimates of Simocephalus mortality based on mathematical extrapolations (see legend for Figures 8.1-8.8, A).

B. Percentage of damselfly naiads estimated to have molted during each interval.

C. Percentage of the damselfly naiads estimated to have entered each instar within each interval (distance between base lines = 100%).

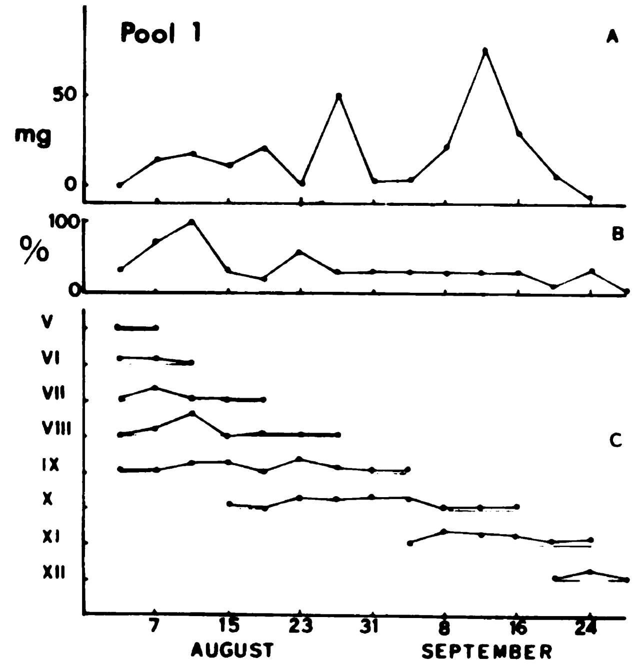


Figure 9.1

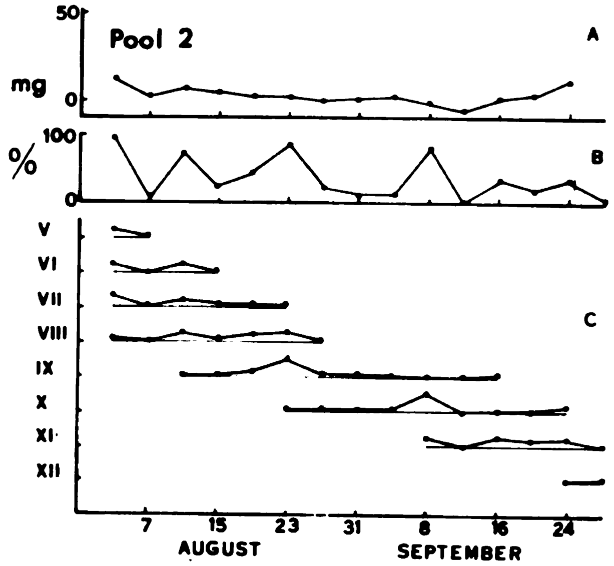


Figure 9.2

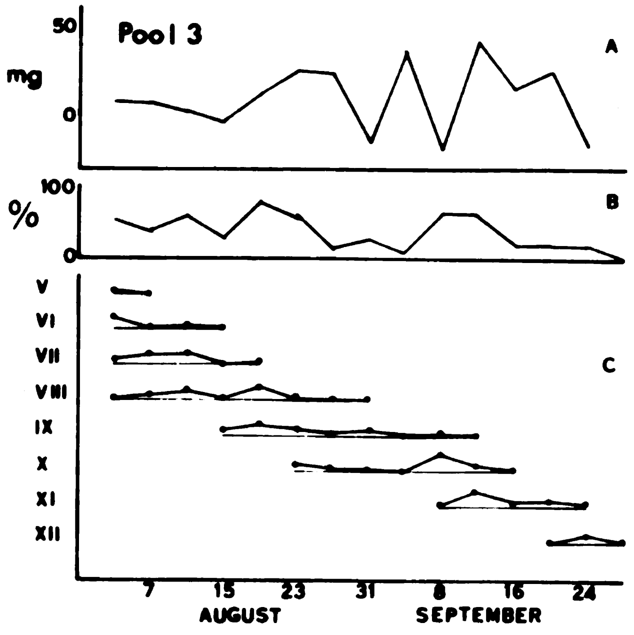


Figure 9.3

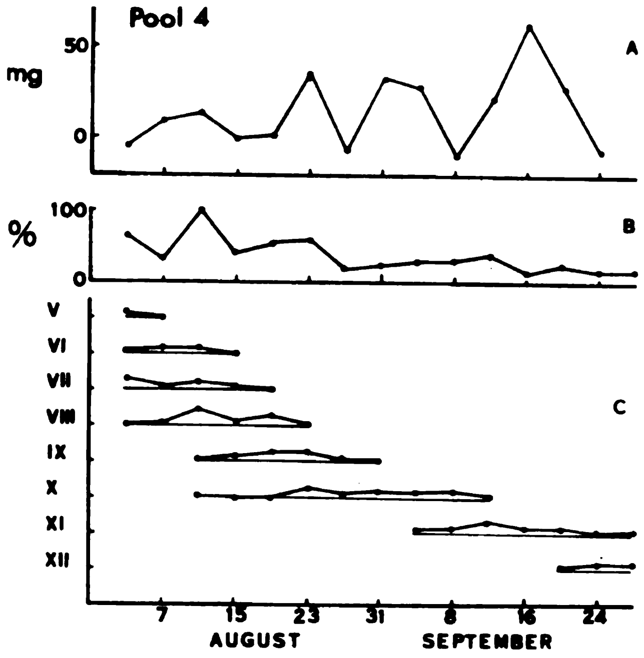


Figure 9.4

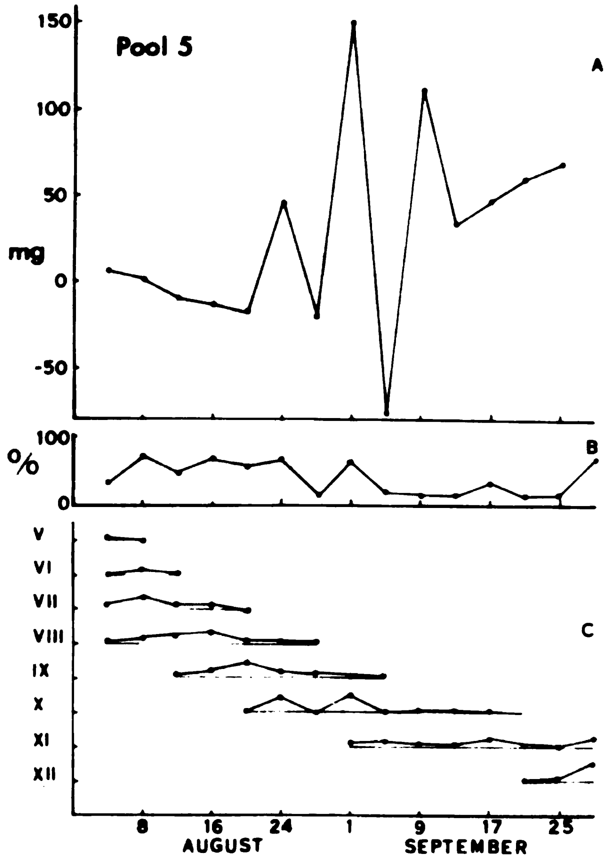


Figure 9.5

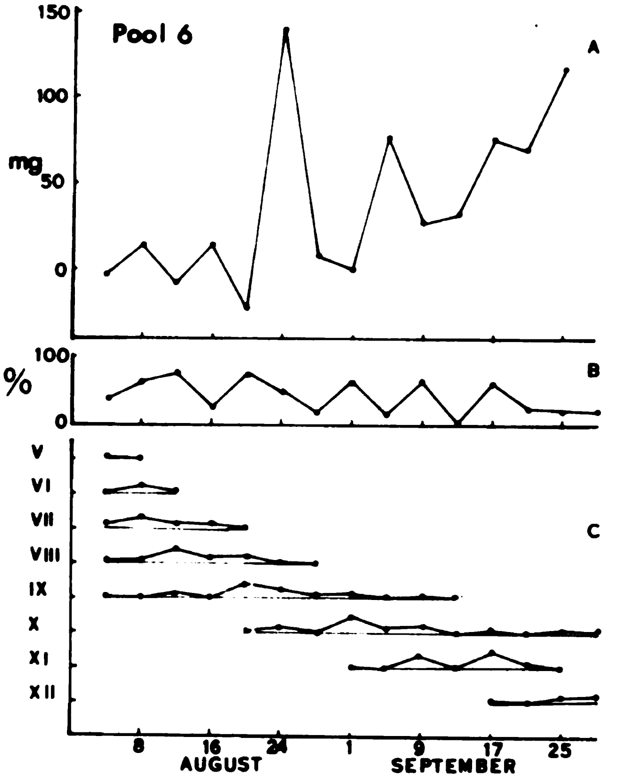


Figure 9.6

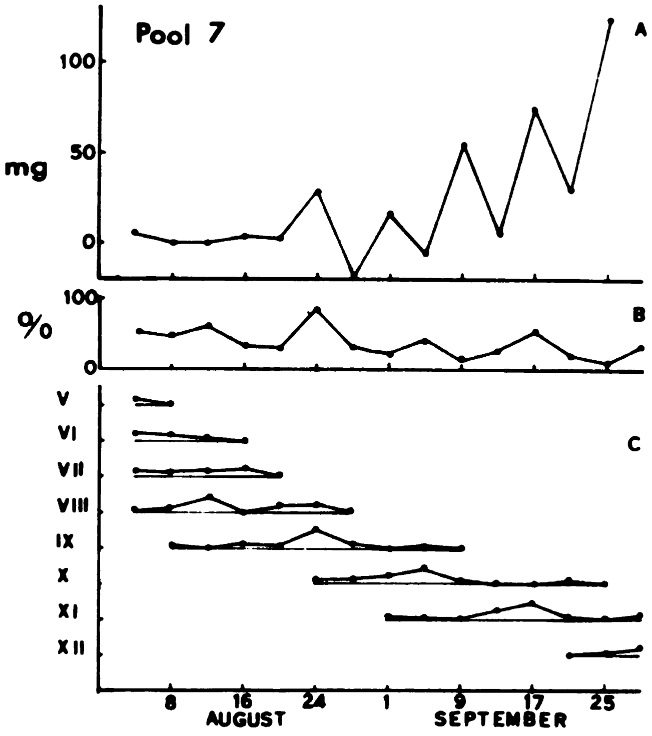


Figure 9.7

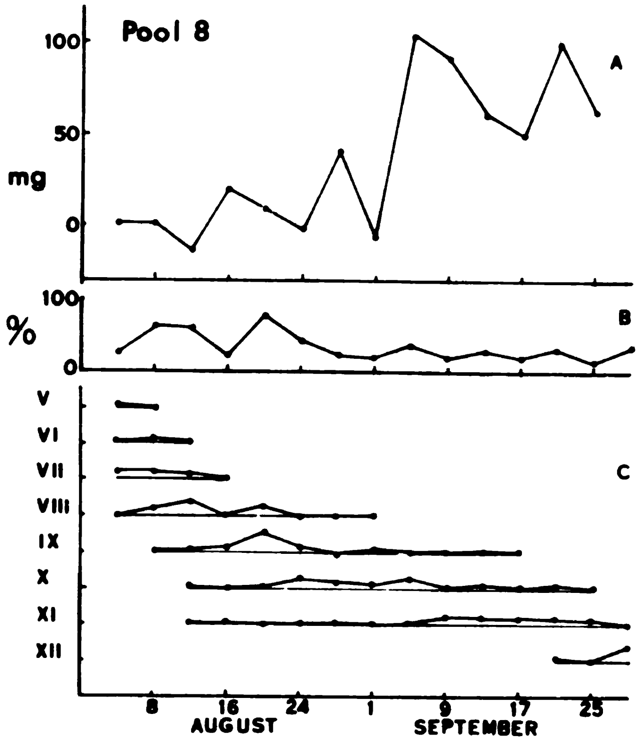


Figure 9.8

some occasions. In Pool 5, the naiads were growing so rapidly during the first half of the study that 50% or more molted during each of five consecutive intervals.

Comparison of these data with the Simocephalus mortality estimates based on extrapolation procedures (Figures 9.1-9.8, A) reveals that many of the large mortality estimates either coincide with or lag four days behind a peak of molting frequency. This trend is particularly clear in Figures 9.6 and 9.7 where both molting frequency and mortality estimates undergo regular fluctuations. In Pool 3 two successive intervals during which more than 50% of the naiads molted are twice followed by broad peaks of Simocephalus mortality (Figure 9.3, 19-27 August, 8-20 September). More continuous molting patterns after 5th September in both Pools 5 and 8 compare well with less variable estimates of Simocephalus mortality. Reference to Figures 7.5 and 7.8 (A) reveals that Simocephalus density was declining throughout this period in both pools. Relatively continuous molting in Pool 4 is also reflected in large mortality estimates after 31st August. The low estimate of mortality on 8th September may be erroneous, since an independent estimate from predator exclosures provides a larger estimate (Figure 8.4, A). The declining estimates of Simocephalus mortality on 20 and 24th September coincide with a period of rapidly increasing midge density (Figure 6.4) which may have diverted the feeding pressure from Simocephalus (see also the midge mortality estimate on 20th September Figure 8.4 (B)). The data for Pool 1 after 16th September suggest a similar situation (Figures 6.1, 8.1, 9.1). Alternate prey availability may also explain why the continuous high molting rate observed during August in Pool 5 is not associated with high Simocephalus mortality. Both Orthocyclops and Ceriodaphnia were relatively abundant during this period (Figure 6.5), and predator exclosures, despite their associated bias, estimated some mortality for both species.

Comparison of estimated molting frequency with mortality estimates for prey suggests a plausible explanation for the sometimes intermittent nature of the damselfly naiads' influence on prey populations. Pool 2 once again provides a unique case. The molting pattern of the naiads was more synchronous than in any other pool, yet estimates of Simocephalus mortality were consistently low and do not fluctuate in magnitude. This may suggest that the feeding rate of naiads was more continuous throughout the course of an instar when faced with lower prey densities (Figure 7.2, A) so that changes in the proportion having recently molted had little affect on the mortality imposed upon prey.

The size of damselfly naiads was larger during each successive sampling interval within each pool (Figures 5.1 and 5.2). It might be expected that feeding rate, and therefore the impact of naiad predation on prey, would increase with predator size. There is a tendency for peak mortality

estimates to be larger toward the end of the experiment. Large estimates of Simocephalus mortality are coincident with naiads' attaining the ninth and tenth instars in several pools (Figures 8.1-8.8, A, C; Figures 9.1-9.8, A, C). This mortality, along with reduced brood sizes, seems to have been sufficient to halt population increase in Pools 5, 6, and 7. Attainment of the eleventh instar was followed by a large impact on Simocephalus and/or midge larvae in all pools; and often this was followed by a continual decline in Simocephalus density (Figures 7.1, 7.5-7.8, A).

Smaller naiads, feeding on less dense prey populations early in the study may have occassionally inflicted significent mortality upon the Simocephalus populations; however, this was not sufficiently large or continuous to prevent population increase in most pools. Larger naiads, feeding on more dense populations of Simocephalus which may have been approaching the "carrying capacity" of the pools (smaller brood sizes, ephippial egg formation) seem to have inflicted mortality sufficient to cause sharp declines in Simocephalus density. When the naiad molting pattern was continuous, this mortality led to continual decline of prey density (Pools 1, 5, 8); but when it was somewhat synchronous, intermittent relaxation of predation pressure seems to have led to fluctuations in prey density (Pools 3, 6, 7). In Pool 2, brood sizes were smaller at the beginning of the experiment and mortality estimates were small and continuous, perhaps reflecting more continuous feeding by predators at low prey densities. The coincidence of the eventual *Simocephalus* increase with the influx of midge larvae (Figure 6.2) and increasing estimates of midge mortality (Figure 8.2) suggests that the "escape" of the *Simocephalus* might be attributable to a "switch" in feeding preference by the damselflies.

Comparison of the total body lengths of the damselflies within each pool (Figures 5.1 and 5.2, and Table 7) reveals a remarkable similarity between the grouping of pools according to overall pattern of predator influence (above) and that according to average rank of the total body lengths over all dates. Pools 1, 5, and 8 showed more continuous growth by the damselflies, which reached larger sizes sooner than in other pools, and more continual decline of the *Simocephalus* population density. Pools 1 and 5 were those which contained all three species of crustacean prey (Table 1) and Pool 8 was the pool in which *Simocephalus* reached its highest density before declining (Figure 7.8, A). Pools 3, 6, and 7 showed more synchronous damselfly molting patterns and fluctuating densities of *Simocephalus*; they also fall into an intermediate range of ranked total body lengths over the course of the study. Pool 4 had more continuous molting patterns than 3, 6, and 7 but exhibited striking fluctuations in *Simocephalus* density; it also falls into the intermediate range of ranked total body lengths. Pool 2 exhibited the most synchronous molting pattern of all; *Simocephalus* population increase was delayed until much later than in any other pool; and the size of the naiads was distinctly smaller on any given date than those in other pools.

The relationship among the magnitude of *significant* predator influence (Figures 7.1-7.8, B), *Simocephalus* density, and predator size is presented in Figure 10. The entire surface cannot be described because predator size and prey density tended to increase together through time, and predator influence was often non-significant. The projection of these points onto the Predator Influence-*Simocephalus* Density plane may be considered roughly comparable to a "functional response curve" (Holling, 1965), though several components other than feeding rate *per se* are undoubtedly involved. This curve seems to have an increasing slope over the intermediate density range, similar to the Type 3 curve described by Holling (1966). This is probably a reflection of increased feeding rate, related to the naiads' growing larger rather than to behavioral response to increasing prey density. Nevertheless, for the *Simocephalus* populations in this experiment, damselfly naiad predation may have been a source of mortality, which increased its impact as density increased.

Studies of the functional response of invertebrate predators to different prey densities have been conducted with standardized predators under carefully controlled conditions (i.e., Holling, 1965). Feeding rate is usually

Figure 10. The relationship among significant predator influences during an interval, Simocephalus density at the beginning of that interval (from Figure 7.1-7.8, A and B), and predator size at the end of the interval (from Figures 5.1 and 5.2). ● = estimates based on extrapolations; ■ = estimates based on enclosures.

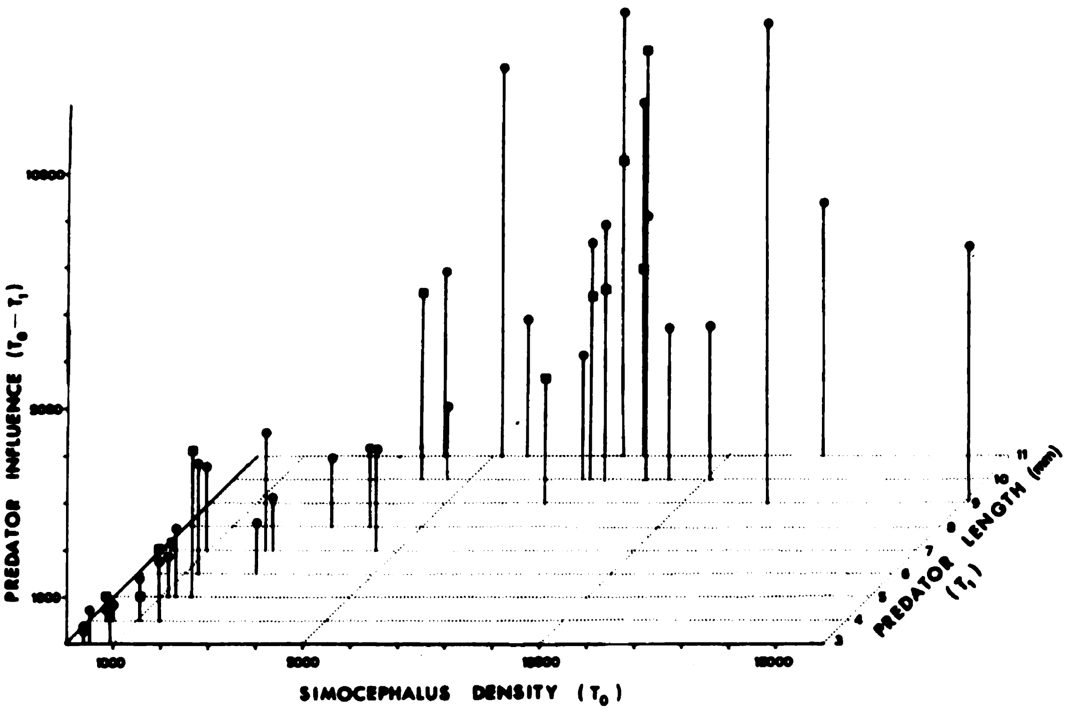

PREDATOR INFLUENCE $(T_0 - T_1)$
10000
5000
1000
1000
5000
10000
15000
SIMOCEPHALUS DENSITY (T_0)
3
4
5
6
7
8
9
10
11
PREDATOR LENGTH (mm)
(T_1)

Figure 10

determined at <u>one</u> of several densities, but results are interpreted as indicative of the response of predators to changes in prey density. Holling (1965) suggests that invertebrate predators should not be expected to impose a potentially regulatory mortality on prey populations unless they are capable of increasing their own density (through reproduction or aggregation) in response to changes in prey density. The results of the present study suggest that some invertebrate predator populations may impose significant mortality on their prey during periods of intense feeding; and that these periods may be alternated with periods of relaxed influence during which the prey often recover. Growth in size by the predators simultaneous with increasing density of the prey may increase the feeding in such a manner as to inflict increasing proportions of mortality upon the prey. The magnitude and periodicity of such influence seems to have been dependent upon the size of the predators and the extent to which their molting pattern is synchronous. Manipulation of the instar distribution of arthropod predator populations, generating different size structures and degrees of synchrony in feeding activity should influence the dynamics of their prey populations in a predictable manner, if the hypothesis presented here is correct.

The extent to which fluctuating patterns of predator influence occur under natural conditions, is not known. Certainly many invertebrate predator populations form rather

discrete cohorts with little overlap between generations. Their feeding activity and growth patterns have not been determined for consecutive short time intervals which would permit detection of fluctuating patterns, if they exist.

SUMMARY

The influence of damselfly naiad predation on experimental *Simocephalus* populations was studied in eight replicate habitats, within which the species composition of alternate prey was manipulated. Samples of predator and prey populations were taken at four-day intervals. Predator exclosures protected randomly selected portions of the prey population for the duration of the intervals between samples. Though there was a serious bias associated with the exclosure procedure, these data provide what is considered a minimum estimate of prey mortality during each interval. An independent estimate of *Simocephalus* mortality was obtained by comparing observed density and size structure on each date with those predicted by an extrapolation procedure based on samples at the beginning of each interval.

Both mortality estimates revealed a fluctuating or intermittent pattern in most pools. Comparison of this pattern to that for the observed growth increment of the damselfly naiads suggested a hypothesis which may partially explain the intermittent nature of apparent predator influence on *Simocephalus*. It is proposed that naiads feeding upon very dense prey populations fed intensely at the beginning of each

instar and then at a lower rate as they became satiated. Somewhat synchronous molting patterns among the naiads could result in different proportions feeding intensely during each interval, thus imposing differential mortality on prey populations.

Examination of the instar distribution of naiads on each sampling date provided an estimate of the proportion molting during each interval. Comparison of these estimates with Simocephalus mortality estimates led to the conclusion that the extent to which damselfly molting patterns were synchronous was an important component of their influence on prey populations. When damselfly molting frequency was somewhat synchronized, alternate periods of intense and relaxed predation pressure seem to have permitted fluctuations in Simocephalus density, the prey recovering from the impact of predators. However, when predation pressure was more continuous, Simocephalus density underwent a continual decline.

Other factors which seem to have modified the influence of damselflies on Simocephalus were the size of the naiads, the reduction of Simocephalus reproductive potential at high densities, and, infrequently, the abundance of alternate prey species.

LIST OF REFERENCES

LIST OF REFERENCES

Allen, H. L. 1970. Primary productivity, heterotrophy, and nutritional interactions of epiphytic algae and bacteria of aquatic macrophytes. Ph.D. Thesis, Michigan State University (in preparation).

Banta, A. M. 1936. Studies on the physiology, genetics, and evolution of some cladocera. Carnegie Inst. Washington, Pub. 513. Paper No. 39.

Berglund, T. 1968. The influence of predation by Brown Trout on Asellus in a pond. Inst. of Fresh Water Res. Drottningholm. Report No. 48.

Connell, J. H. 1961. Effects of competition, predation by Thais lapillus, and other factors on natural populations of the barnacle Balanus balanoides. Ecol. Monogr. 31: 61-104.

Cooper, W. E. 1965. Dynamics and productivity of a natural population of fresh-water amphipod, Hyalella azteca. Ecol. Monogr. 35: 377-394.

Corbet, P. S. 1962. A biology of dragonflies. London. H. F. and G. Witherby Ltd. 206 pp.

Cummins, K. W. 1969. The calculation of biomass (caloric) production in zooplankton populations. Unpublished MS.

Fischer, Z. 1964. Some observations concerning the food consumption of the dragonfly larvae of Erythromma najas Hans and Coenagrion hastulatum Charp. Pol. Arch. Hydrobiol. 12: 253-264. (Polish; Eng. summary.)

Frank, P. W. 1952. A laboratory study of intraspecific and interspecific competition in Daphnia pulicaria (Forbes) and Simocephalus vetulus O. F. Muller. Physiol. Zool. 25: 178-204.

Fryer, G. 1957. The food of some freshwater cyclopoid copepods and its ecological significance. J. Anim. Ecol. 26: 263-286.

Grieve, E. G. 1937. Studies on the biology of the damselfly *Ischnura verticalis* Say, with notes on certain parasites. Ent. Amer. 17: 121-151.

Grosvenor, G. H. and G. Smith. 1913. The life cycle of *Moina rectirostris*. Q. J. Microsc. Sci. 58: 511-522.

Hall, D. J. 1964. An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae*. Ecol. 45: 94-112.

Hamilton, A. L. 1965. An analysis of freshwater benthic community with a special reference to the Chironomidae. Ph. D. Thesis. University of British Columbia.

Hassell, M. R. 1966. Evaluation of parasite or predator responses. J. Anim. Ecol. 35: 65-75.

Haynes, D. L. and P. Sisojevic. 1966. Predatory behavior of *Philodromus rufus* Walckenaer (Areaneae: Thomisidae). Can. Ent. 98: 113-133.

Hillbricht-Ilkowska, A. and K. Patalas. 1967. Methods of estimating production and biomass and some problems of quantitative calculation methods of zooplankton. Ekol. Polska. Ser. B. 13(2): 139-172. (Polish; Eng. summary.) English translation presented at IBP Conference on Secondary Production. Prague. 1967.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European Pine Sawfly. Can. Ent. 91: 293-320.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Memoirs Ent. Soc. Canada. No. 45.

Holling, C. S. 1966. The functional response of invertebrate predators to prey density. Memoirs Ent. Soc. Canada. No. 48.

Hodek, I., K. Novak, V. Skuhravy, and J. Holman. 1965. The predation of *Coccimella septempunctata* L. on *Aphis fabae* Scop. on sugar beet. Acta. Ent. Bohemoslov. 62: 241-253.

Hruska, V. 1961. An attempt at a direct investigation of the influence of the carp stock on the bottom fauna of two ponds. Verh. Internat. Verein. Limnol. 14: 732-736. (Original not read; reviewed by Lellak, 1965.)

Huffaker, C. B. and C. E. Kennett. 1969. Some aspects of assessing efficiency of natural enemies. Can. Ent. 101: 425-447.

Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Trans. D. Scott. Yale University Press, New Haven, Conn.

Kajak, Z. 1966. Field experiment in studies on benthos density of some Mazurian lakes. Gewasser und Abwasser. 41-42: 150-158.

Lawton, J. H. 1967. A study of the feeding rates of Zygopteran nymphs. (Unpublished MS.)

Lellak, J. 1965. The food supply as a factor regulating the population dynamics of bottom animals. Mitt. Internat. Verein. Limnol. 13: 128-138.

Lutz, P. E. 1968. Effects of temperature and photoperiod on larval development in Lestes eurinus (Odonata: Lestidae). Ecol. 49: 637-644.

Macan, T. T. 1964. The Odonata of a moorland fishpond. Int. Rev. Hydrobiol. 49(2): 325-360.

Macan, T. T. 1966. The influence of predation on the fauna of a moorland fishpond. Arch. Hydrobiol. 61(4): 432-452.

Murdock, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol. Monogr. (in press).

Pennak, R. W. 1953. Freshwater invertebrates of the United States. Ronald Press Co., New York. 740 pp.

Petrovich, P. G., E. A. Shushkina, and G. A. Pechen. 1961. Calculation of production of zooplankton. Dolk. AH CCCP 139: 1235-1238.

Sanders, C. J. and F. B. Knight. 1968. Natural regulation of the aphid Pterocomma populifoliae on Bigtooth Aspen in Northern Lower Michigan. Ecol. 49: 234-244.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York. 310 pp.

Slobodkin, L. B. 1954. Population dynamics of Daphnia obtusa Kurz. Ecol. Monogr. 24: 69-88.

Smith, B. D. 1966. Effects of parasites and predators on a natural population of the aphid *Acyrthosiphon spartii* (Koch) on broom (*Sarothamnus scoparius* L.). J. Anim. Ecol. 35: 255-267.

Straskraba, M., J. Korinkova, and M. Postolkova. 1967. Contributions to the productivity of the littoral region of ponds and pools. Academia-Praha. 55 pp.

Tinbergen, L. 1960. The natural control of insects in pineweeds. I. Factors influencing the intensity of predation by songbirds. Archives Neerlandaises de Zoologie. 13: 259-379.

Winberg, G. G., G. A. Pechen, and E. A. Shushkina. 1965. Production of plankton crustaceans in three lakes of different types. Zool. Zh. 44: 676-687. (Russian; Eng. summary.)