A PROBABILISTIC APPROACH TO THE DYNAMICS OF NATURAL POPULATIONS OF THE CHYDORIDAE (CLADOCERA, CRUSTACEA)

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ABSTRACT

A PROBABILISTIC APPROACH TO THE DYNAMICS OF NATURAL POPULATIONS OF THE CHYDORIDAE (CLADOCERA, CRUSTACEA)

By

Robert E. Keen

This study had three objectives: (1) description of annual changes in abundance and reproductive structure of natural chydorid populations; (2) use of laboratory data to estimate rates of natural population processes; (3) probabilistic analysis of the changes from the basis of a simple birth model.

I. DESCRIPTIVE APPROACH. Chydorid populations were sampled in the littoral of Lawrence Lake, Barry Co., Michigan. The chydorids were counted and classified in six reproductive categories. Four species dominated: *Chydorus sphaericus*, *Acroperus harpae*, *Camptocercus* cf. *rectirostris*, and *Graptoleberis testudinaria*. Populations of *Acroperus*, *Camptocercus*, and *Graptoleberis* appeared in April, stayed low through the summer, peaked in August, September, or October, and then dropped rapidly, disappearing in December. Populations of *Chydorus* peaked in March

or April, dropped sharply to a low summer level, rose during the fall, and remained high through the winter. Ephippial females and males dominated the populations of *Camptocercus*, *Acroperus* and *Graptoleberis* before their winter disappearance. Males and ephippial females of *Chydorus* appeared briefly in small numbers during early December.

II. ANALYTICAL APPROACH. Simple analytical population models can give insight into processes of change. The familiar egg-ratio method is such a model that is well adapted for studies of natural chydorid populations. Its use requires knowing water temperatures in the lake and development times of chydorid eggs at these temperatures. Littoral temperatures were monitored continuously with a recording thermistor. Egg development times for the four species were found in the laboratory at eight temperatures between 27 and 4 C. The rates of birth, observed change, and population loss were calculated with a modification of the usual procedure.

Predicted birth rates for the four species were relatively stable, rising during the spring to a midsummer plateau, and declining during the fall. For *Chydorus* the observed rates of change were relatively stable and low from November through April, with negative values as the populations declined in May and October. For the other three species, and for *Chydorus* during the summer months, the values of the observed rate of change fluctuated violently from (+) to (-).

III. PROBABILISTIC APPROACH. Given the size and reproductive potential of a population, two important probabilistic questions may be asked: what is the most probable population size at some later time, and what is the probability of the size actually observed at that later time. The egg-ratio method in fact calculates the most expected population size. To answer the second question, a method was developed to find the probability of the observed increase from a binomial probability distribution based on the chance of hatching of a given egg through the time interval.

For the populations of Chydorus, the probabilities of observed increase were relatively large from late fall to early spring, and during the summer were mostly zero because of insufficient increase or decrease in population size. For the populations of the other three species, the probabilities of the observed increases were mostly zero with a few positive values randomly scattered through the year.

Testing the probabilities of observed increase for Chydorus showed that most differed significantly from the probabilities of expected increase. Very few of the observed increases could be explained on the basis of birth potential alone, as predicted by the egg-ratio method. The egg-ratio method will inadequately explain the observed

increases when the population is losing individuals. Emigration and "natural" mortality were excluded as important factors of loss, so that predation appears as the major probable cause of population loss.

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Respectfully, I wish to dedicate this thesis to my parents.

TABLE OF CONTENTS

LIST OF FIGURES

I. INTRODUCTION

Man's curiosity and concern about the abundance of animals is ancient (e.g. frogs, lice, locusts: Exodus 8-10). Darwin (1859) based his theory of evolution on some observations of populations, one being that their sizes tend to constancy despite a capacity for geometrical increase. Formalizing the study of the abundance of organisms is the concern of population ecology.

The present work describes some populations of chydorids, small crustaceans living principally in the littoral of lakes. The rationale for this study is best considered from the dual viewpoints of chydorid biology and the study of populations. Interests in the chydorids and in population ecology were developed simultaneously.

The Chydoridae are a family of the Cladocera with several quite intriguing biological characteristics. They reproduce parthenogenetically and continuously during most of the year, and have at most two eggs in the brood pouch (except the genus Eurycercus, not considered here). Something is known of their general and population biology (Fryer 1968; Shan 1969; Smirnov 1963a, 1963b, 1964), but

comparatively little is known of natural populations. There are no quantitatively adequate descriptions of both seasonal abundance and reproductive structure of their populations.

In the context of population biology, this study is one of a series analytically investigating natural populations of small aquatic invertebrates. There has been similar work on copepods (Elster 1954, 1955), rotifers (Edmondson 1960), *Daphnia* (Stross, Neess and Hasler 1961; Hall 1964), and amphipods (Cooper 1965). Other workers, of course, have used the methods of population analysis developed in these papers. This study was prompted by a desire to apply rigorously the methods of the earlier papers and to extend these methods with a probabilistic approach.

II. DESCRIPTIVE APPROACH

A. Introduction

To understand natural population processes, one must describe abundance in the natural habitat. Formulating and considering population theory without attention to natural situations serves only heuristic purposes. Laboratory and field experiments of population processes will be relatively sterile unless one knows the seasonal dynamics of natural populations. This study of natural chydorid populations in therefore based upon as thorough a seasonal description as possible.

B. Materials and Methods

The site of the study, Lawrence Lake, is a small (4.9 ha) marl lake in Barry County of southwestern Michigan. The two reasons for chosing Lawrence Lake were its physical suitability and the large amount of background data available. Wetzel *et al* (1971) have extensively studied the chemistry and productivity of the lake. There is additional work on the lake's biological history (Rich 1970a), on the productivity of the algae attached to the vascular plants (Allen 1969), and on the importance of the macrophytes in the general lake metabolism (Rich 1970b).

Lawrence Lake was suited for this research primarily because of its shallow, homogeneous beds of the submerged rush, Scirpus subterminalis Torr. Two dense and lawn-like stands of this plant, which formed ideal habitat for chydorids, were selected for sampling. These two extensive beds of S. subterminalis were located in 0.5 m of water on the east and west shores of the lake, and were isolated from other plant beds by bare marl-covered bottom (Rich, Wetzel and Thuy 1971). The plant stems were coated with marl ($CaCO_3$) deposits through most of the year.

It is difficult to take replicable, quantitative samples of animals in the littoral regions of lakes. Then it is usually tedious to separate the animals from the bits of vegetation, organic detritus, and other particles also collected. Unworkable sampling techniques included two different types of water substrate column samplers. Unsuitable and unreliable techniques for separation of chydorids from the particulate matter of Lawrence Lake included sugar floatation, light avoidance, electro-migration, benzene separation, and centrifugation through sugar. The sampling and separation techniques for this study were purposely kept simple, to avoid complications that usually result in infrequent sampling.

The sampling platform was a small boat tied to stakes in the middle of the plant beds. A one-liter enamel beaker was pushed mouth downward into the water and plants.

The beaker was righted, raised, and the water was poured through a small net (Nytex, mesh opening 153 μm); the method is similar to Straskraba's (1965). Each liter was collected successively from near the surface, near the bottom, and at mid-depth; the process was repeated until 40 liters had been collected. The concentrate from 40 liters represented a sample. Three such samples were taken from each plant bed, one from each seat in the boat, about one meter apart. In the winter, three half-meter holes through the ice over each plant bed permitted sampling. The concentrated samples were taken to the laboratory in half-liter jars.

The samples with their concentrated marl particles, organic debris, and animals were poured into beakers and allowed to settle for a few minutes. When the beaker bottom was gently heated with a small alcohol lamp, the chydorids and other small invertebrates left the bottom material and swam freely in the upper water. Then the water and animals were quickly decanted from the beaker. The beaker was refilled with water and the settling, heating, and decanting process was repeated three or more times. The decanted samples were finally concentrated with a net to about 10 ml in a 50 ml vial. The vial was filled forcibly and rapidly with 95% ethanol from a narrow-tipped wash bottle. This procedure killed and preserved the chydorids with no detectable loss of eggs.

Chydorids were never sufficiently abundant in the samples to allow reliable subsampling, so each sample was completely inspected. Small parts of a sample were examined in a ruled 35 mm Petri dish. Species counts and individual reproductive states were recorded. The six reproductive categories were juveniles, mature females, females with one egg, females with two eggs, ephippial females, and males. Although the heat separation technique removed most of the interfering particles, enough remained to slow the sorting to 2.5 hours per sample.

Sampling began 1 October 1968 and ended 30 September 1969. Some considerations discussed below dictated sampling frequency, which depended upon the temperature of the littoral water. Sampling intervals varied from two days in July and August to seven days during the period of ice cover. The chydorids were sampled on 89 days during the year. Sampling was usually at about 1600 hours, and through the ice at 1200 hours. To check the efficiency of the technique of heat separation, six times during the year all the material left after separation of a sample was preserved and sorted. An average of 6% (std. error 0.6%) of the total chydorids were not removed with the technique. Probably more than 90% of the chydorids collected were consistently removed with the heat technique.

C. Results

Four species of chydorids dominated the samples: *Acroperus harpae* Baird, *Graptoleberis testudinaria* (Fischer), *Chydorus sphaericus* (O.F.M.), and *Camptocercus* cf. *rectirostris* Schødler. Through the entire year, they represented at least 75%, and usually more, of the chydorid numbers in each sample. Work beyond preliminary identification of some fifteen other species has been deferred.

Figure 1a-h shows the results of counting and categorizing the four dominant species. The population size is given as number per 40-liter sample. The populations of *Chydorus* (Figure 1a-b) peaked in March or April, dropped sharply to a low summer level, rose during the fall and remained high through the winter. Populations of *Acroperus* (Figure 1c-d) appeared in late March with a small peak, stayed low in abundance during the summer, peaked in October and then dropped rapidly, disappearing from the shallow *S. subterminalis* beds in January. The populations of *Graptoleberis* (Figure 1e-f) and *Camptocercus* (Figure 1g-h) appeared in April without even a small peak and stayed very low during the summer. *Graptoleberis* rose through August to a peak in September, while *Camptocercus* rose to a small peak in August and dropped during September.

The match of population sizes at the beginning of the sampling and at the ending one year later is remarkable in most of the populations. This suggests that the populations may follow a relatively strict pattern of seasonal abundance.

The population size of the chydorids during the year was undoubtedly linked to the annual cycle of the *S. subterminalis*. In the shallows the plants began to grow in early June and in about two weeks apparently obtained maximum density. Almost immediately settling particles and growths of algae began to cover the plants. By the beginning of July marl lightly encrusted the stems and progressively thickened on the plants and in the samples through the year. The plants were present with both living and dead stems during the winter under the ice. After ice-out in the first week of April, the plants began to break up and to mat on the bottom as a result of wave action. By mid-May, most disappeared or were on the bottom and decomposing.

The precipitous decline in the *Chydorus* populations for the spring are probably related to the disappearance of the plants. The smallness and brevity of the spring peaks in *Acroperus* are probably similarly related to the plant cycle. *Graptoleberis* and *Camptocercus* appeared shortly before the plants disappeared, and did not develop abundant populations that could noticeably be affected by the plants' spring disappearance.

The abundance curves of each species on opposite shores are generally similar. The patterns are not so alike, however, that the populations can be considered as one. Perhaps part of the differences are due to the annual cycle of *S. subterminalis*, with the plants of the west shore disappearing about a week later and starting to grow about a week earlier than those on the east shore. This might be related to the heavier wave action on the east shore of the lake.

The percentage graphs of reproductive structure (Figure 1a-h) describe the relative abundance of the six categories through the year. For any species, when the mean population size was greater than 20, the standard error of each category was less than one-tenth of the mean percent plotted.

Parthenogenetic reproduction occurred through the spring and summer for *Camptocercus*, *Graptoleberis*, and *Acroperus* (Figure 1c-h), and gave way to increasing gamogenetic reproduction of resting eggs through the fall and early winter. *Chydorus* (Figure 1a-b) overwintered as parthenogenetic individuals with very little production of resting eggs and males in the fall. No females of *Chydorus* or *Acroperus* carrying only one egg were discovered in the samples.

The populations of *Camptocercus*, *Acroperus*, and *Graptoleberis* were clearly established by the hatching of

ephippia in the spring. The percentage patterns then show the populations as 100% juveniles. In Acroperus (Figure 1c-d) one also sees a generation effect with two distinct peaks in the percentage of young. The young of the first peak hatched from ephippia and matured to a predominantly adult population, which reproduced to give the second peak of young animals. The population numbers are too low to validate a similar interpretation in Camptocercus and Graptoleberis.

The percent composition curves during the summer are erratic because of the low numbers of animals. For example, the west shore population of Camptocercus (Figure 1h) shows no juveniles on a sampling date in June. This is likely an artifact of low sample size. If only three or four animals are collected per sample for a series of dates, eventually the random sampling error will yield three samples on one date with no juveniles in any of the samples. On several occasions for other species during the period with low numbers, other categories were not represented for probably the same reason.

The occurrence of the low numbers during the summer well illustrates a problem of establishing a sampling program at the wrong time of the year. The sample size of 40 liters was set in the fall of 1968 just before sampling began. This size was initially adequate, but during much of the rest of the year was too small. However, increasing

sample size would have made extreme the detritus and marl problems, and sorting would have become almost impossible. Increasing the sample size by a factor of, say, ten to obtain adequate numbers of animals would have made field work likewise impractical. The problems of quantitative work in the littoral zone are not easily circumvented, even with the careful selection and restrictions of the present study.

III. EXPERIMENTAL APPROACH

A. Introduction

Population descriptions are the basis for studying population dynamics, but they can yield little understanding of underlying processes. After inspecting the age structure of a population, one can at most say that "it looks as if the population should be growing" (e.g. Gerking 1962).

Experimentation and correlation are the two prevalent approaches to investigation population events under natural conditions. Experimentation demonstrates causal relationships more positively than correlation (King 1967). The experimental approach in ecology (Hall 1964; Gray 1968) ordinarily uses laboratory experiments to interpret the results of field work by intensively analyzing the effects of environmental variables.

The "egg-ratio method" (Edmondson 1968) is an experimental approach that attempts measurement of rate processes in natural populations of certain small aquatic invertebrates. Its basic aim is to census a population and determine the reproductive potential in order to

predict a population birth rate. The actual rate of change is estimated by censusing the population at a later time. The population loss rate is the difference between the predicted birth rate and the observed rate of change.

The reproductive potential of a censused population will depend most immediately upon temperature. The effect of temperature on reproduction is mediated through the duration of egg development, which must be experimentally determined.

B. Materials and Methods

The egg-ratio method uses the development times of the eggs carried by the females in the natural populations. In chydorids, as in most Cladocera with open brood pouches, the development time of eggs is apparently dependent only upon temperature (Hutchinson 1967). Therefore one must know the temperature of the water during the intervals between sampling, and the development times of the eggs at those temperatures.

To determine water temperature, a continuously-recording thermistor was set up on the east shore of Lawrence Lake with the probe anchored about 15 cm from the bottom in the middle of the S. subterminalis bed. The recorder operated with a paper speed of one inch (2.54 cm) per hour, so that littoral temperature changes were monitored in detail. At every sampling period the temperatures of both east and west plant beds were taken with another thermistor (Whitney Inst. Co.). The temperatures of the two sampling areas never differed more than 1.0 C and were usually within 0.1 C of each other.

Egg development times for the four dominant species were determined in the laboratory at eight temperatures between 4 and 27 C. The chydorids for this work were collected in Lawrence Lake at temperatures ± 5 C of that at which development times were determined. Animals from the field were isolated in individual culture dishes and put into constant temperature chambers (± 0.5 C) at the required temperatures under continuous, low fluorescent illumination.

Well water was aerated at least three weeks over a substrate of Lawrence Lake littoral mud before use in culture work. Food was from a "detritus culture" of aerated detrital material from some local lake shores. The food particles were scattered over the bottom of each culture dish to provide a superabundance of food for the single animals. Food and water in the dishes were changed daily. Further culturing details are in Keen (1967).

The reproductive condition of each isolated animal was observed at intervals of four hours for 21, 24, and 27 C, six hours for 14 and 18 C, and eight hours for 4, 6, and 10 C. Development times were recorded as extending from the midpoint of the observational interval when the eggs appeared, to the midpoint of the interval when the young were released from the brood pouch.

The numbers of development time determinations for each species were from twelve to sixteen above 20 C; eight for 14 and 18 C; six for *Chydorus* and *Acroperus* and four for *Graptoleberis* and *Camptocercus* at 10 C; four for *Acroperus* and five for *Chydorus* at 6 C; and two for *Chydorus* at 4 C. No more than two determinations were taken from any individual animal. Two or more animals of each species were used at each temperature.

C. Results

Figure 2 shows the results of the constant monitoring of temperature. Figure 3 shows mean development times for the four species of chydorids. The variability of the development time for a species at a given temperature was quite low. All the time determinations for any particular species at one temperature were ± one interval around the median interval.

The interspecific consistency of the development times of the eggs over the range of temperatures is remarkable. Always *Chydorus*' eggs developed most rapidly and *Graptoleberis*' most slowly. The causes of this difference are not attributable to any obvious factor, such as size. *Chydorus* and *Graptoleberis* are the smallest of the four species.

In the calculations explained below, temperature through the year was taken as mean temperature to the

nearest whole degree over eight-hour intervals (0000-0800, 0800-1600, 1600-2400 hours). Thus, 1095 temperature observations were available. Development times for each degree of the temperature range 3-30 C were interpolated from the semi-log plot of development times (Figure 3).

D. Calculations

Population numbers increase approximately exponentially in a constant, unlimited environment. This type of increase is conveneiently expressed in the common formula for exponential growth:

$$dN/dt = rN \tag{1}$$

For populations, N is population size at time t, with r a growth constant of units N/N/t. Because populations usually grow in discrete units, this continuous formula is inexact, and difference or differential-difference equations would be more appropriate (Watt 1969). However, (1) is the usual equation and just here exactness is not important. Integrating (1) gives:

$$N_t = N_o e^{rt} \tag{1a}$$

and solving for r:

$$r = (\ln N_t - \ln N_o)/t \tag{1b}$$

The term r, expressing instantaneous rate of change, has been variously used in population ecology, and the discussion of Mertz (1970) on this subject is quite lucid.

For a population growing with a stable age distribution in an environment with negligible feedback from population size to individual reproduction, r is a constant through time. If the logarithm of population size is plotted with time, r will be the slope of the line described by such a population. However, for any population under any conditions, r may be calculated for any time interval with (1b), to give the slope of the line connecting two points on a semi-log plot of numbers vs. time. Then r will represent the observed rate of population change. There is no intention of describing the rates of population change beyond the two points, or at intermediate points in time. Through the rest of this study, r will be used as this instantaneous rate of observed change.

If immigration and emigration do not occur, r is the sum of two instantaneous rates, birth (positive) and death (negative):

$$r = b-d \tag{2}$$

The principal aim of the egg-ratio method is to estimate the instantaneous birth rate for the interval over which the population is observed. Finding a suitable way to calculate the rate, b, has been a problem. Edmondson's (1960) initial formulation was

$$b = \ln (1+B) \tag{3}$$

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where B is the "finite birth rate" obtained from

$$B = E/D \tag{4}$$

with E the average number of eggs per female in the population and D the egg development time. F. E. Smith (unpub. ms.) has pointed out that (3 and 4) will give biased estimates if D is not unity, by underestimating b if D is less than one, and by overestimating b if D is greater than one.

Edmondson (1968) gives an alternative formula for b, probably taken from Smith (unpub. ms.):

$$b = [\ln (N_o + Y) - \ln N_o]/D \tag{5}$$

with Y the number of eggs in the population of size N_o. Edmondson (1968) incorrectly states that (5) uses D as the time unit; the time units are those associated with measurement of D. Hughes (1962) discusses the correct use of time units based on development times.

The following method for finding instantaneous predicted birth rate was used in this study. If a population (of chydorids) contains a number of eggs, E (=Y), with a development time of D, the number of eggs hatching, K, over a period of time t will be

$$K = Et/D \tag{6}$$

This assumes a uniform distribution of egg ages and no egg mortality through death of females with eggs. The relationship will hold for intervals of t longer than D if every egg is replaced after hatching, and if E does not increase with recruitment of brooding females from initially immature females. The instantaneous predicted rate of birth can then be expressed with

$$b = [\ln (N_o + K) - \ln N_o]/t \qquad (7)$$

Formulas (3 and 4) and (5) calculate b independently of the time between observations. In the method of (6 and 7), the value of b is quite time-dependent. The basic formula (1b) for instantaneous rates is likewise time influenced. As used in the egg-ratio method, (1b) finds rates only for the interval t, indicating nothing about rates over longer or shorter intervals. This is true also for (6 and 7). The other formulas provide birth rates unvarying with t; the method of (6 and 7) is probably a more realistic approach. Thus it avoids the assumptions of exponential growth in (3 and 4) with bothered Elster and Schwoerbel (1970). The predicted increases are first calculated and then the rate is expressed in the convenient exponential terms. The assumptions made with these formulas are not unreasonable, and are probably better met by the data of this study than in most egg-ratio work. The assumption of no mortality in the egg-bearing females is unimportant because the method works toward estimating mortality in the population. It is difficult to insure meeting the assumption of a uniform distribution of egg ages. Theoretically the age distribution of the eggs should shift towards younger eggs in an expanding population and towards older eggs in a declining population. Smith (Cooper 1965) and Leigh (Edmondson (1968) present compensating formulas. However, a check of several chydorid samples during periods of rapid population change showed no striking differences in the numbers of the various stages of embryos in the four species.

The sampling schedule was purposely designed to meet the assumption of no increase in egg numbers. Sampling intervals were kept short enough so that no female initially classed as immature could mature and produce young. The longest sampling interval in terms of development time was two-D long for Chydorus, in June. Normally the sampling interval was less, averaging about 1.3 D in the summer and 0.5 D in the winter.

The instantaneous rate of observed change was calculated for the eight chydorid populations with (1b). N_t and N_o were the final and initial mean population sizes over the period t.

The expected increase K during the period t is found with (6). However, in field studies development time D varies through t because of varying temperature. K was therefore calculated over eight-hour intervals from the development times determined by the mean temperature of the eight-hour interval. The series of K values was summed to find total increase over the sampling interval t. E was the mean number of eggs in the initial sample, excluding ephippial eggs. The instantaneous predicted rate of birth was then calculated with (7).

Calculating K over eight-hour intervals gives results differing from the usual procedure of working with an average temperature. Trial calculations made with the average temperature of the entire sampling interval often predicted increases 10% or more different than the increase calculated over eight-hour intervals. The differences would have been greater if "average" temperature were taken from the usual one or two observations.

The estimated mortality rate was the difference of birth and change rates given by (2).

E. Results of Calculations

The computed values of rates of change, birth, and mortality are plotted in Figure 4a-h for the eight populations. Points are at the midpoints of the sampling intervals.

For each population the values of b are relatively stable and peak in mid-summer. The zero b values at the beginning and end of the plots for Camptocercus, Graptoleberis, and Acroperus (Figure 4c-h) are caused by the populations beginning with only young animals hatched from ephippia, and ending with only ephippial females and males.

In *Chydorus* (Figure 4a-b) the values of r were relatively stable and low from November through April, with negative values as the populations declined in May and November. During the summer, r fluctuated violently. In the three other species there was little stability in r, with a resulting instability in d, throughout the year.

Theoretically, values of b should always exceed or equal the corresponding values of r, i.e. d should never be negative. A population should not be able to increase faster than the birth rate predicts. A negative value of d can be produced several ways. Immigration can cause the observed increase to exceed the expected, with negative values of d resulting. If the estimate of development time is too high, so that b is low, d can be negative. Sampling variance can cause this also, if the initial estimates of population size or egg number are too low, or the final estimate of population size is too high.

Each population shows several negative d values, most occurring in the summer period of violent r fluctuations. These can probably be attributed to sampling variance associated with low population numbers. The negative d values at the spring beginnings of the *Acroperus*, *Camptocercus*, and *Graptoleberis* populations (Figure 4c-h) are caused by the hatching of ephippia, which will affect the calculation of d like immigration.

The factors contributing to population loss rates, d, could be emigration or death. Emigration could be a factor in this study because sampling was not designed or intended to characterize more than the chydorids of the specific S. subterminalis beds. However, these beds were isolated from adjacent plant beds by several meters of bare marl bottom. No chydorids occurred in several samples taken through the year over this bare substrate. Two sampling programs by other workers for two years just preceding this study showed chydorids completely absent from the limnetic region of Lawrence Lake at least from April to September. The lake does not develop the blue-green algae blooms that usually accompany appearance of chydorids in the plankton (Hutchinson 1967).

A series of samples in September 1968 taken in the west bed showed no statistically significant difference in the number of chydorids collected at noon and midnight. This probably indicates no nocturnal increase in activity. Night sampling at that time over the bare marl substrate also yielded no chydorids. All available information seems to indicate that emigration from these plant beds was probably minimal.

Death from "old age" can probably be neglected as a significant contributor to mortality. In the laboratory, Shan (1969), Keen (1967) and Smirnov (1965) found that chydorids had fairly long life spans, varying with temperature but usually on the order of weeks. Deaths from old age could therefore not occur rapidly enough to account for the high mortality rates observed in the field.

With "natural" mortality and emigration negligible, predation would appear to be the probable major contributor to population losses. Assuming that predation is the dominant mortality factor, the general pattern for the four species is fairly clear. Mortality rates are low in the late fall and winter when predation pressure is presumably low. When predation should be most intense, in the spring and summer, the mortality rates are higher, though erratic. The low summer population levels are maintained by balancing the high predicted birth rates with high rates of mortality.

Preliminary investigations of possible predators point to smaller fish and odonate larvae. About 15 small fish (less than 4 cm) and 25 odonate larvae were collected from the S. subterminalis beds during the spring and summer, and dissected. Chydorids appeared in about three-fourths of the fishes' guts and in about half of the odonate's. Schools of these small fish were always observed swimming and feeding in the plant beds during the summer sampling.

IV. PROBABILISTIC APPROACH

A. Introduction

Given the size and reproductive potential of a population at some initial time, two probabilistic questions are of interest: (1) what is the most probable population size at some future time, and (2) what is the probability of the population size actually observed at that future time? These questions are typically asked with stochastic models of population growth (Peliou 1969). When the research was initiated, using a stochastic analog of the egg-ratio method seemed the next obvious step in work with field populations. The chydorids with two young per brood as a reproductive limit appeared particularly suited for this approach. However, as given, the chydorid data will not fit a truly stochastic model of population processes.

The stochastic forms of the homogeneous birth processes (Bailey 1964, chapter 8) do not fit the chydorids. These models would require newly-hatched animals to have the reproductive potential of a fully-developed adult.

Neither can the population growth be modeled as a stochastic Poisson process (Chiang 1968, chapter 3). A chydorid has some chance of hatching an egg during a small time interval Δt, which appears to make egg hatching a Poisson process. But the chydorid egg must hatch after a certain lapse of time. In a truly Poisson process, the chance of occurrence of an event approaches unity as time passes. With the chydorid egg the chance of the occurrence (hatching) equals unity after the lapse of a given time period (development time).

However, by making the same assumptions that are made in using the egg-ratio calculations it is possible to formulate a probabilistic statement for growth of chydorid populations. With this approach one can quantify inferences drawn from the plots of population rates. One can state the accuracy of conclusions that under certain conditions the "birth model alone is an adequate expression of population growth" (Hall 1964). The formulation of the statement is mathematically uninteresting, if not trivial.

One knows from the data the time between samplings, t; the average time of egg development during that interval, D; the number of eggs in the population at the initial observation, E; and the increase in the population over the interval, X. If t is short so that no initially immature female will reproduce during the interval and if one assumes that E is constant during t (no mortality or adult recruitment), then when t equals D, X should equal E. If one also assumes a random, uniform distribution of egg ages, then t/D is the chance that a given egg will hatch at time t, with t less than D. The probability of finding X out of E eggs hatched at t out of D time can be found with the standard binomial distribution formula (Feller 1968):

$$P(X;\ E,\ t/D) = \binom{E}{X} (t/D)^{X} (1 - t/D)^{E-X} \quad . \qquad (8)$$

When the sampling interval exceeds one, but is less than two development time periods, X must be reformulated. The model assumes that E eggs will have hatched after D time. The number of eggs E is subtracted from the total observed increase to find X for times longer than D. The chance of an egg hatching (t/D) must similarly be recalculated when t is greater than D. When $2 > (t/D) > 1$, the chance of hatching is $(t-D)/D$.

The observed population increase occurs with zero probability in three circumstances. If the population decreases, then the observed increase is negative and the probability is zero. If the population increase in one development time is more than the number of eggs in the population, then the probability is also zero, because more eggs cannot hatch than are available for hatching. A third zero probability case is if, in intervals greater than one development time, the population increase is

less than the number of eggs present. After one development period has passed, population increase must equal at least the number of eggs, and any lesser increase has a probability of zero.

This probabilistic approach is really an extension of the egg-ratio technique. Unless the usual egg-ratio calculations are made, information about the population change rates will be lost. The zero probability cases can show little about these processes, except that attempts to explain population changes with birth alone are impossible. The probabilistic formulation states precisely how well the birth rate model explains the observed population changes. Often when the egg-ratio will show an impossible negative death rate, the probabilistic model will indicate a positive probability of the increase; it is possible for more than the most probable number of eggs to have hatched after the given interval.

B. Results

The probabilities of the increases observed in the eight chydorid populations were computed with equation (7). Figure 5a-b shows only the results for the *Chydorus* populations. The other populations were plagued by problems of small sample size, with most of the observations showing either population decrease or too little increase. Less than 10% of the observations of these six populations were

of non-zero probability, and the positive points were randomly scattered through the year. For *Chydorus* the probabilities of the observed increases were relatively large from late fall to early spring. During the summer they were mostly zero because of decrease or insufficient increase.

The "b-r-d plots" for *Chydorus* (Figure 4a-b) show birth rate and change rate very similar during the late fall, winter, and early spring, with mortality as a result close to zero. One might say for the period November-April that a birth rate model was a fairly good predictor of population chnage in *Chydorus*. Examining the probability plots of the same populations (Figure 5a-b) could lead to a similar conclusion, since most positive points occur during the November-April period.

Figure 5, however, gives the probabilities of exactly the observed number of eggs hatching. The probabilities shown are therefore dependent on E, the number of eggs in the population, and are thus not comparable through the year. (With an unbiased coin 50 heads in 100 flips has a much lower probability of occurring than 5 heads in 10 flips.) A test of significance is required to discover whether the probabilities are so low as to indicate the impossibility of the observed number of eggs hatching.

The probability of the observed number hatching should be compared with the probability of the expected number hatching, based on the chance (t/D) of any given egg hatching. An appropriate test would be the chi-square (Snedecor and Cochran 1967). The test used here instead is the likelihood ratio test with the G-statistic, which was easier to calculate for these data (Sokal and Rohlf 1969; Feinberg 1970). The test uses the ratio of the probability of the observed number of eggs hatching based on the chance of hatching that was observed, to the same probability based on the chance of hatching that was expected.

The circled values in Figure 5-b are those occurring with a probability greater than 0.05. It appears that birth alone can account reliably for few of the observed changes in population size. Certainly the instances are far fewer than one would expect from scrutiny of the plots in Figure 4a-b.

V. DISCUSSION

A. Population Description

Most studies of the littoral chydorids (e.g. Reinsch 1925; Ponyi 1957; Pennak 1966; Lindstrom 1957; Quade 1969; Hirai 1970) have concerned the association of various species with substrate type. These works have little bearing on a study of population dynamics of chydorids in a single kind of plant bed.

From observations in the few other quantitative investigations of chydorid populations, the seasonal patterns of abundance observed for the four species in the *S. subterminalis* beds were typical. Straskraba (1965) observed *C. sphaericus* with a single April population peak in one of the plant beds he studied, and with twin peaks in June and October in another bed. He also found *Acroperus harpae* peaking once, in June. The picture of the populations of Straskraba's study lacks detail because of a one-month sampling interval, with no winter samples.

Smyly (1952, 1955, 1957, 1958) investigated the littoral fauna of some English lakes and ponds near Windermere. In Weise Een Tarn *C. sphaericus* populations peaked in April-May, and were almost absent through the rest of the year, with no winter occurrence. In Hodson and Scale tarns *C. sphaericus* was abundant during the spring and numerous in the winter, but scarce at other times.

C. sphaericus overwintered in Lawrence Lake as a parthenogenetic population, in contrast to the winter disappearance of the other three dominant species. Borecky (1956) and Lilljeborg (1900) both found *C. sphaericus* under ice in winter, although Borecky's animals were more limnetic than littoral. Nordquist (1921) found chydorids abundant in the summer, but absent under the winter ice of the littoral in Swedish ponds. Sebestyen (1948) did not find *C. sphaericus* during January and February in Lake Balaton, Hungary.

The sexual cycles observed for the four species in Lawrence Lake were not unusual. The patterns of *Graptoleberis* and *Camptocercus* were almost identical with Flossner's (1964) findings, although in his study these species had an additional brief gamogenetic period in early summer. *Acroperus harpae* in his study overwintered as purely parthenogenetic individuals after a fall period of mixed gamo- and parthenogenesis, and *C. sphaericus* overwintered parthenogenetically, with some gamogenesis in the early spring.

The occurrence of one or two eggs in the brood pouch is an interesting phenomenon. Neither *Chydorus* nor *Acroperus* were observed with one egg during the entire year. Yet Nauwerck (1963) observed limnetic individuals of *C. sphaericus* carrying one egg, and attributed it to low food conditions. Older individuals of *Chydorus* often produce one egg (Keen 1967). Apparently the populations of *Chydorus* and *Acroperus* were feeding well during the year. The story is not as clear with *Graptoleberis* and *Camptocercus*. When their populations were growing to the maximum levels in the fall (Figure 1e-h), the percentages of one-egged adults were increasing and causing a drop in the predicted rate of birth (Figure 4e-h).

B. Population Dynamics

The picture of chydorid mortality is probably the most striking feature of this study. Investigations of mortality would certainly be the most obvious next step in looking at chydorid populations.

The sharp drops in the populations of *Chydorus* in the spring (Figure 1a-b) are probably related to the disappearance of *S. subterminalis*. For this period it is impossible to distinguish between losses of predation or emigration. These spring decreases in population size were not precipitated by great increases in the mortality rates (Figure 4a-b).

The violent, rapid fluctuations of r and d during the summer period characterize all the populations (Figure 4a-h). One could ascribe this to sampling variance of small population size. Random sampling errors have a marked effect on r when population sizes are very small. Nevertheless, the fluctuations may partly indicate real population events. Synchrony of reproduction, for example, could cause such fluctuations, though there was no evidence for the clumped egg age distribution which must accompany synchronous reproduction.

The birth rate b is also sensitive to sampling variance and should fluctuate as much as r or d when numbers are low. But b is more stable than r or d during the low summer populations. Fluctuations in r and d in excess of that in b could be attributed to real changes in population growth rates.

Similar fluctuations of r and d are also found in other egg-ratio studies with sampling at frequent intervals. Cummins *et al*. (1969 and unpublished) with very frequent sampling found fluctuations in rates of change and of mortality for several species of zooplankton in Pymatuning Reservoir, Pennsylvania. These fluctuations would not be attributed to sampling variance coupled with low population numbers, because sampling variance was low and the numbers were large. Possibly natural population rates do change radically from day to day, but only frequent sampling can discover these changes.

C. Analytical Approach

Peliou (1969) classified ecological modelers into two groups: those studying simple models and those using elaborate models. Levins (1966) makes three classes based on attempts at acheiving balance among realism, precision, and generality in models. The approach of this study and of similar studies of field populations is more pragmatic. The complexity of the mathematics is irrelevant; the model will be as complex as necessary to answer the questions of population processes. Usually there is no striving for any particular combination of realism, precision or generality. The criterion for judging models in the context of work on natural populations is one of usefulness in giving insights into population processes.

The mathematics of the egg-ratio model and of its probabilistic extension are quite simple. There is no attempt to balance aspects of generality, realism or precision; the two former are almost completely sacrificed to the latter.

The egg-ratio method and its probabilistic extension are perhaps better classed with those demographic models that Hajnal (1957) has called "analytical." These models are formulated primarily for their utility and are concerned with questions that relate to brief time spans of about generation length. Their assumptions may be quite unrealistic. Their usefulness lies in pointing to the operation of some factor specifically excluded in the basic assumptions. They exploit simple common-sense relationships with suitably chosen auxiliary assumptions (Hajnal 1957). Opposed to analytical models are "ambitious" models which try to establish relationships that at least approximate the real world. This latter category of models is that discussed and subdivided by Peliou (1969) and Levins (1966). It is quite possible for a given mathematical formula to be used both ambitiously and analytically.

The egg-ratio method is not really intended to be predictive or accurate in forecasting. It is not even a true model in Bartlett's (1960) sense of explaining the complexities of population growth in idealistic, simplified terms. It is an analytical model elucidating factors influencing population growth in nature.

The formulation of the egg-ratio method and the probabilistic approach developed here may be useful in other studies if data are carefully collected to meet the assumptions involved. Organisms that carry a fixed number of eggs, such as rotifers and chydorids, are probably best adapted to this approach.

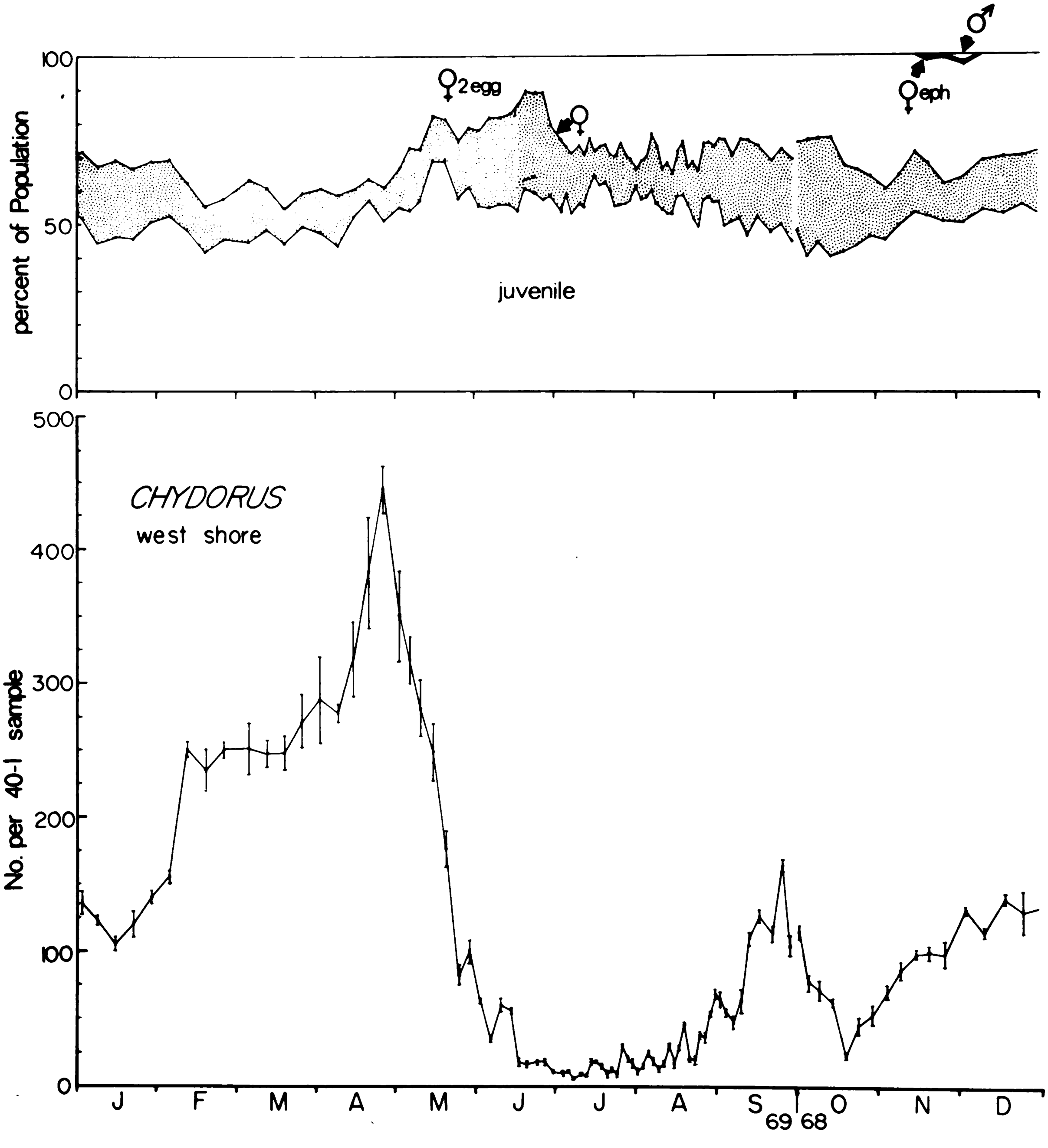
It is perhaps unfortunate that the egg-ratio method which relies so heavily on precision has been traditionally coupled with field work, which is usually characterized by large sampling variances. A critical and basic assumption made with analytical models is that those data entering the analysis are reliable. The validity of the assumptions associated with the model, or the operation of excluded factors, cannot be detected if the predictions are subject to doubt. The non-homogeneity of the littoral environment seems to assure that relatively large sampling variance will always be associated with studies of populations there, and particularly of organisms living on or among the macrophytes. Various strategies may be adopted to avoid some of the inherent variability, for example using artificial substrates, or carefully choosing homogeneous areas, as attempted in this study.

VI. CONCLUSION

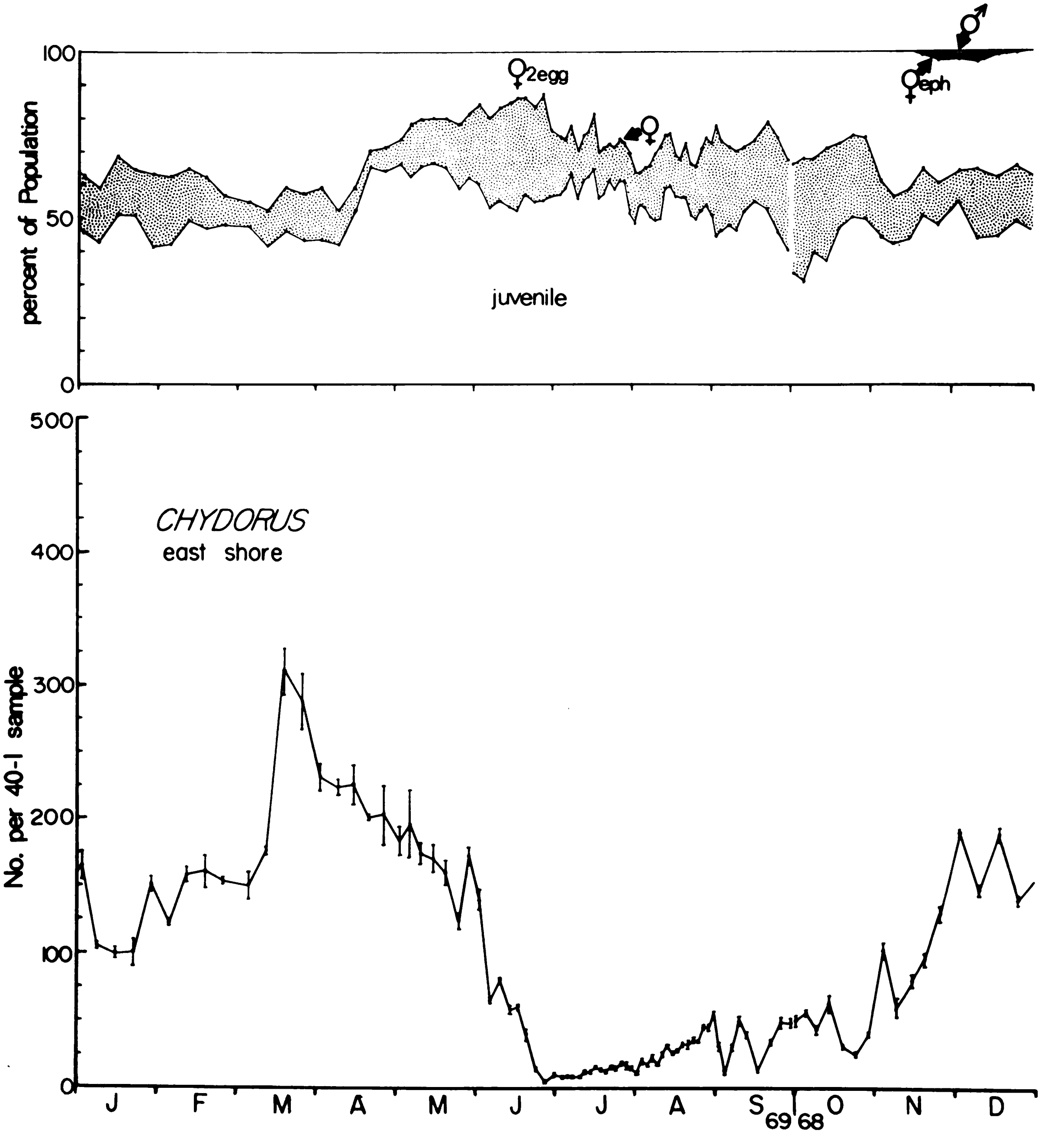
This study was initiated with three objectives: (1) description of annual changes in abundance and reproductive structure of natural chydorid populations; (2) application of laboratory data to estimate rates of natural population processes; (3) probabilistic analysis of population changes from a simple birth model as an extension of analytical laboratory-field approach.

The investigations carried out on Lawrence Lake described the dynamics of eight populations of four species of chydorids. With supporting data on egg development and temperature, the egg-ratio method showed the annual patterns of mortality in the populations. Predation was the probable major cause of mortality. A probabilistic approach quantified the failure of birth rate to explain the population changes.

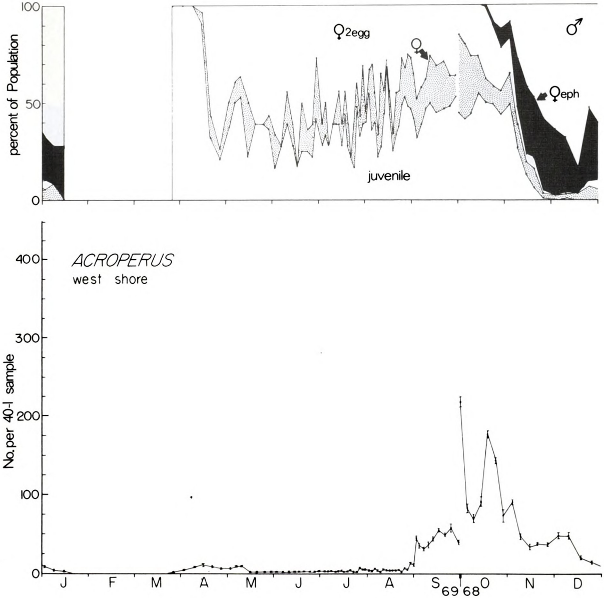
Figure 1. Annual abundance and percent composition of four species of Chydoridae on two sides of Lawrence Lake. (Vertical bars represent standard error.)



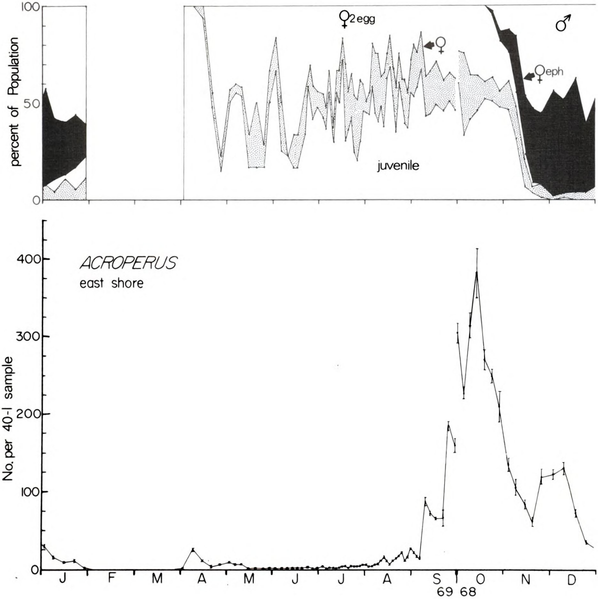
1a. Chydorus sphaericus: west shore



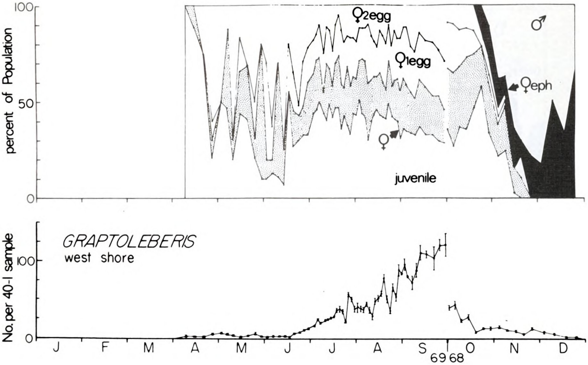
1b. <u>Chydorus sphaericus</u>: east shore



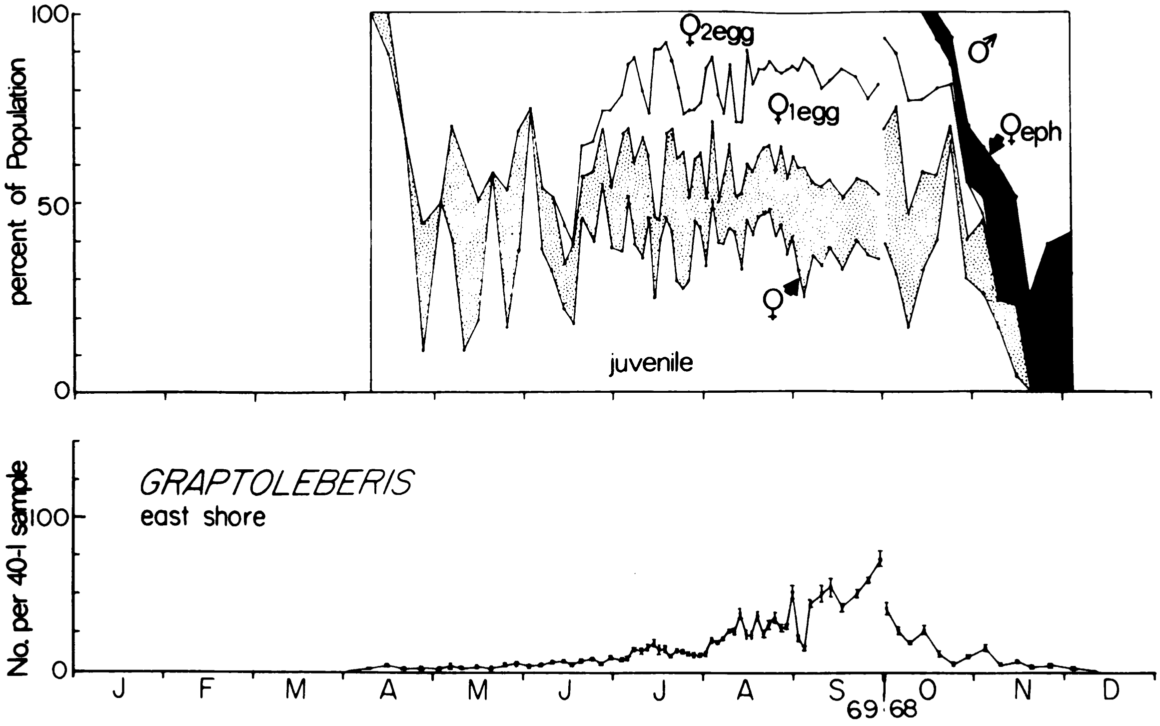
1c. Acroperus harpae: west shore



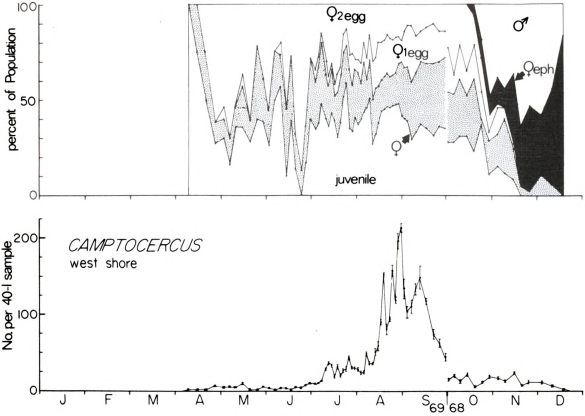
1d. Acroperus harpae: east shore



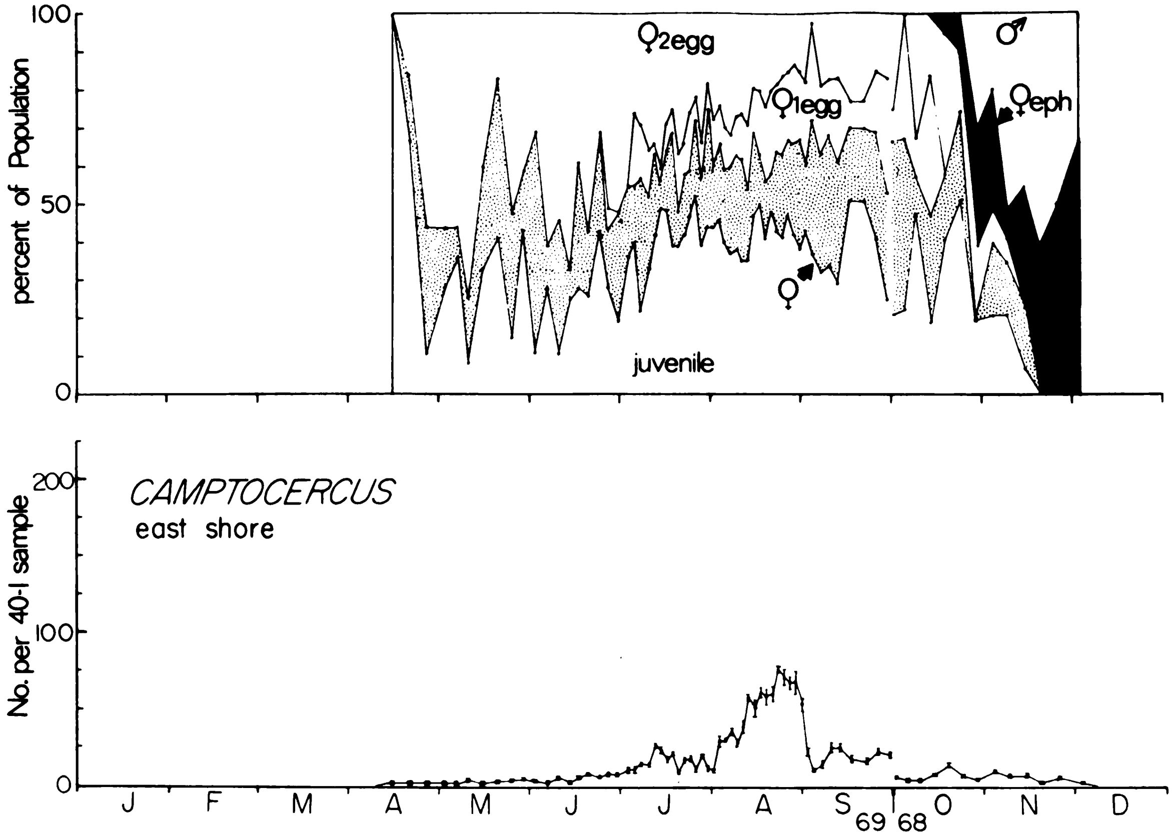
1e. Graptoleberis testudinaria: west shore



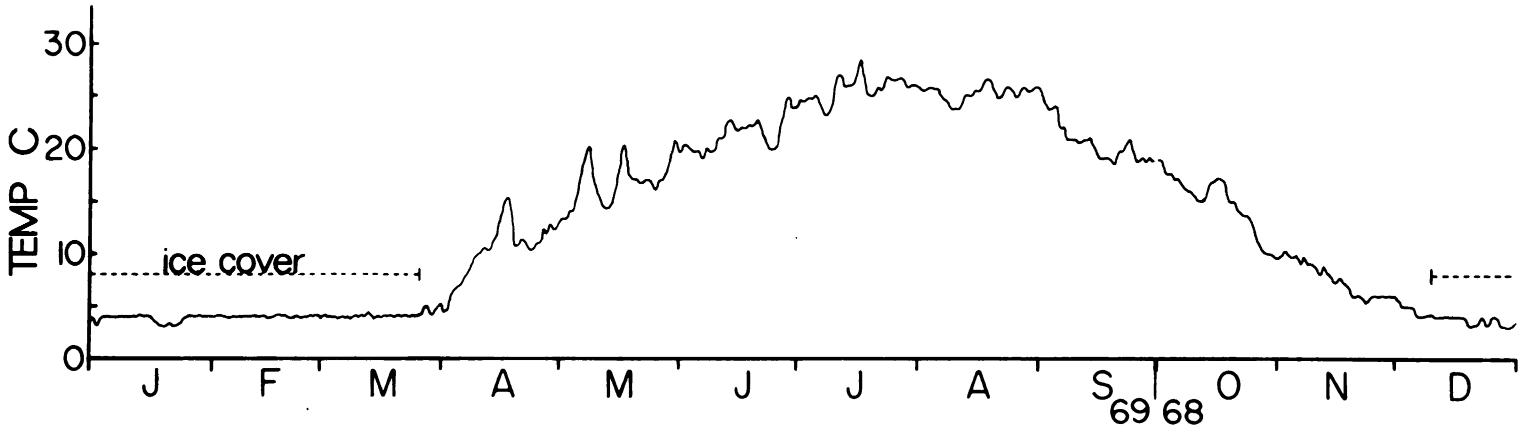
1f. Graptoleberis testudinaria: east shore



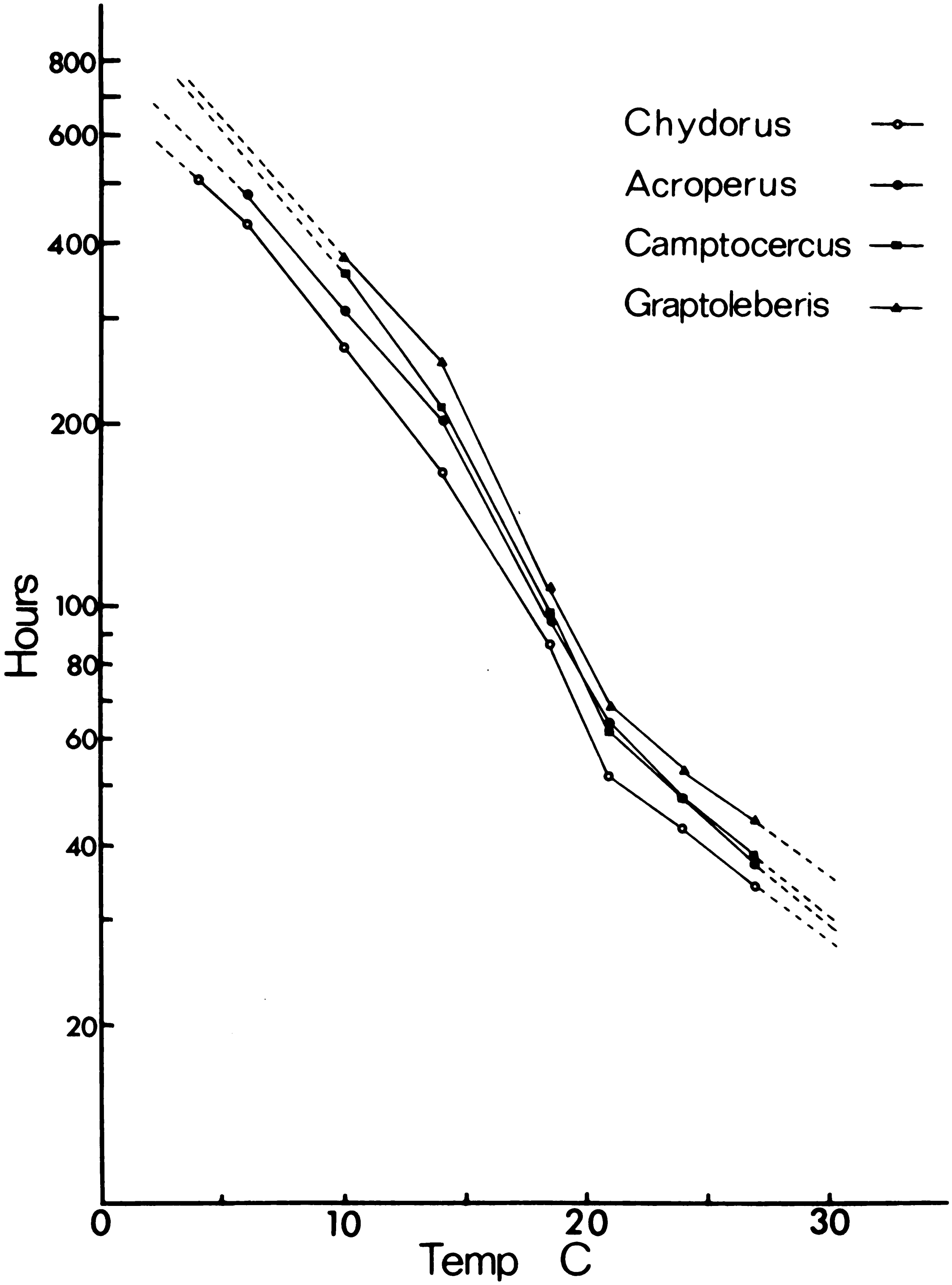
1g. Camptocercus cf. rectirostris: west shore



1h. Camptocercus cf. rectirostris: east shore

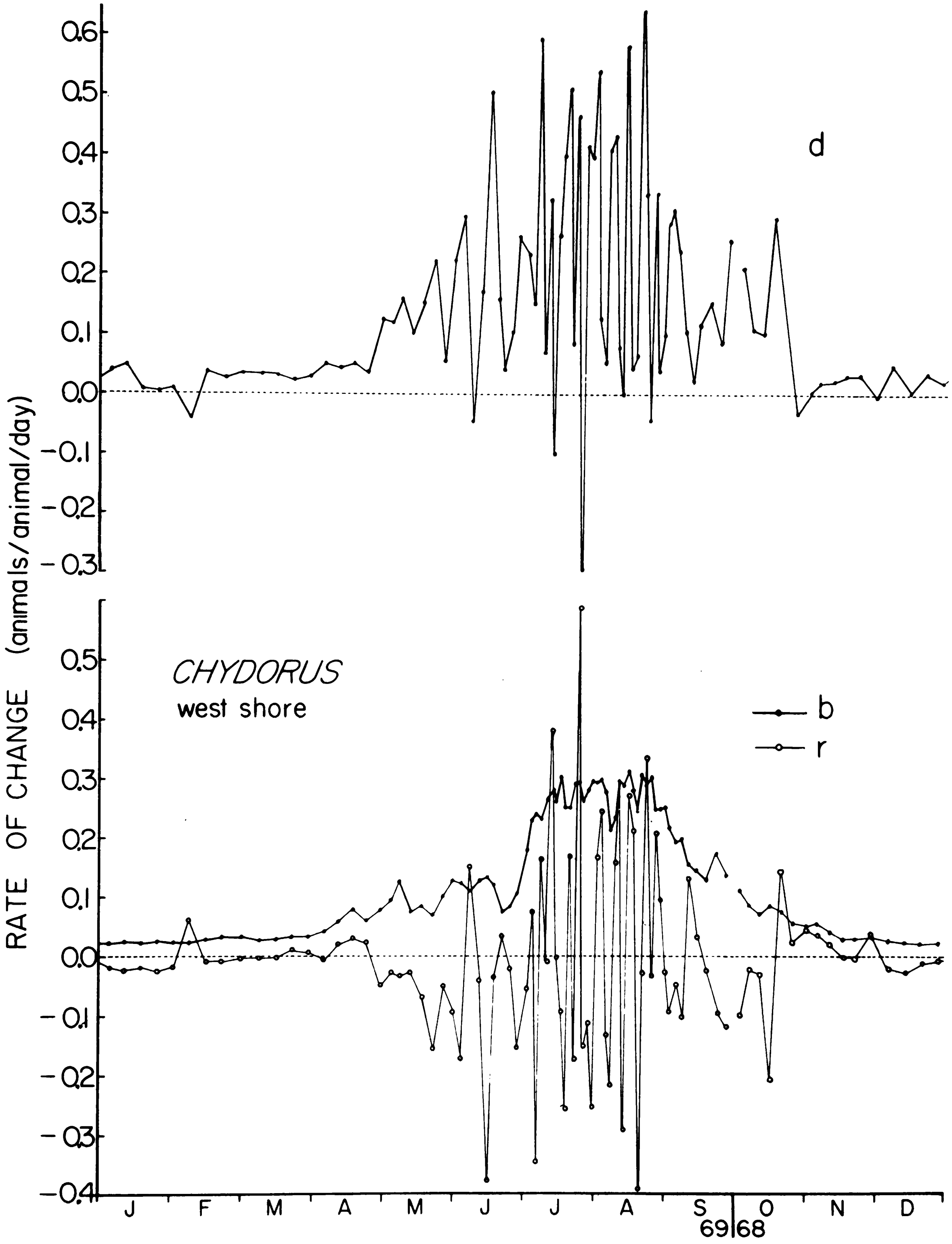


2. Temperature of <u>Scirpus subterminalis</u> plant bed, east shore, Lawrence Lake

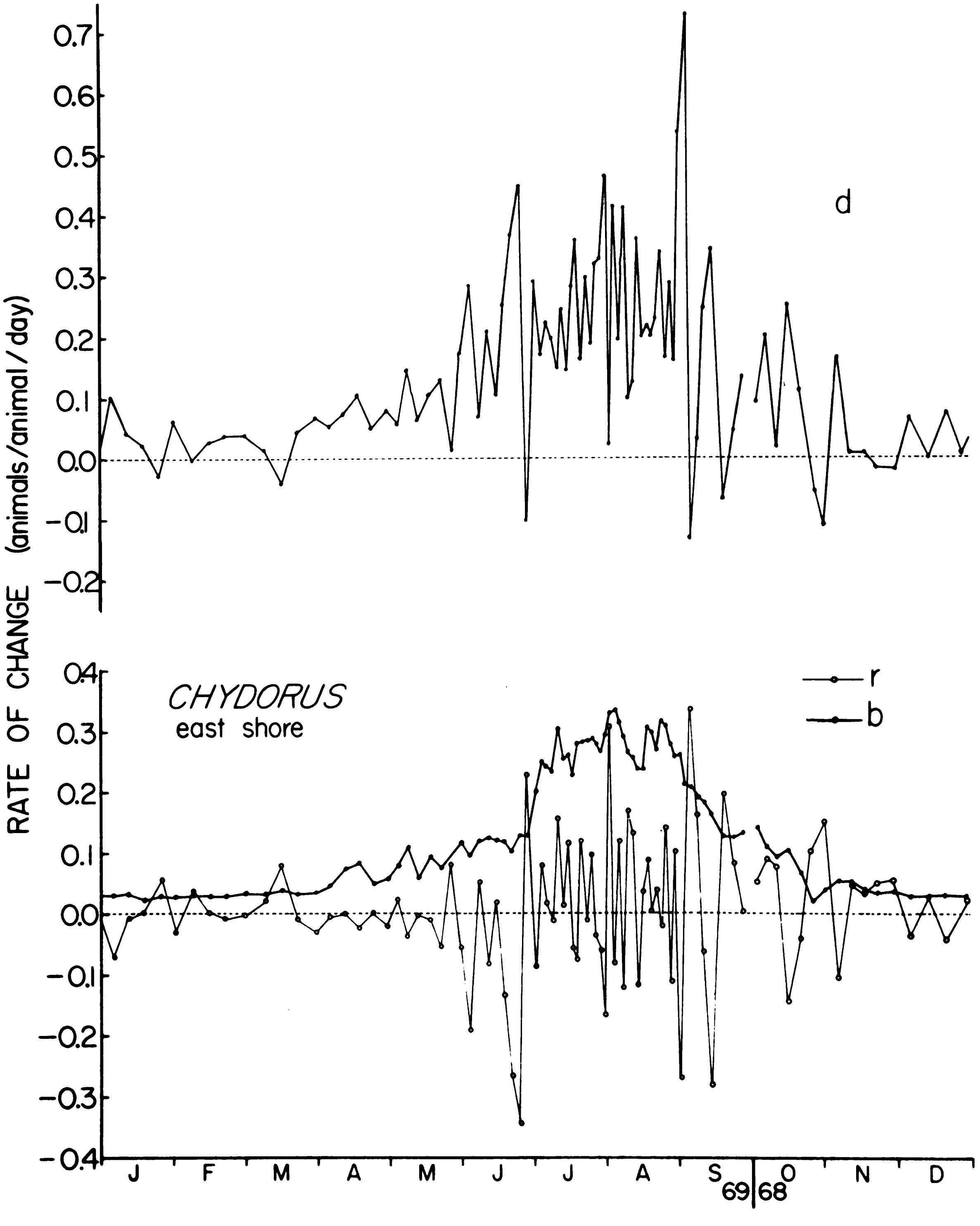


3. Egg development times for four species of Chydoridae from Lawrence Lake

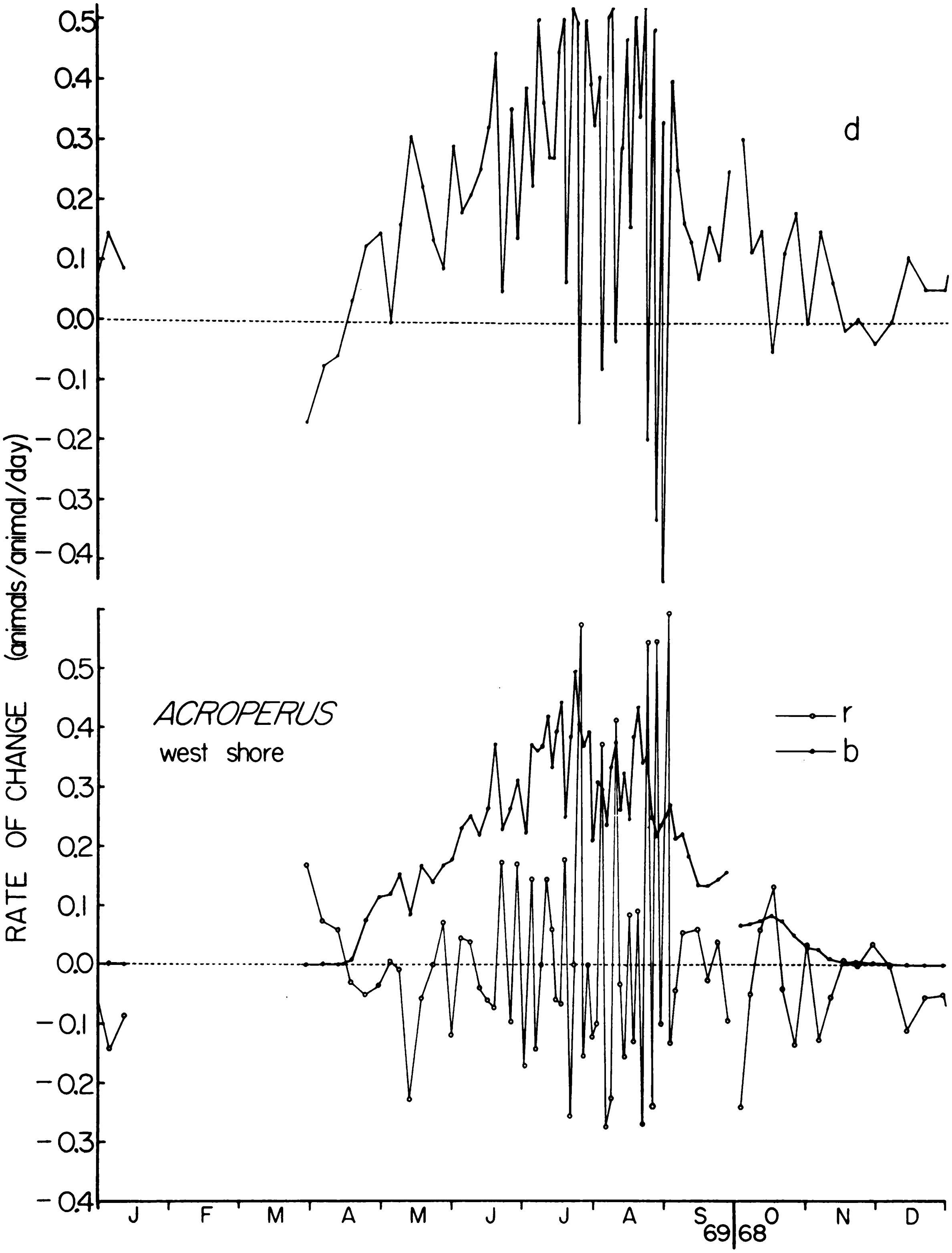
Figure 4. Instantaneous rates of observed change (r), predicted birth (b), and estimated loss (d), for populations of four species of Chydoridae on two sides of Lawrence Lake.



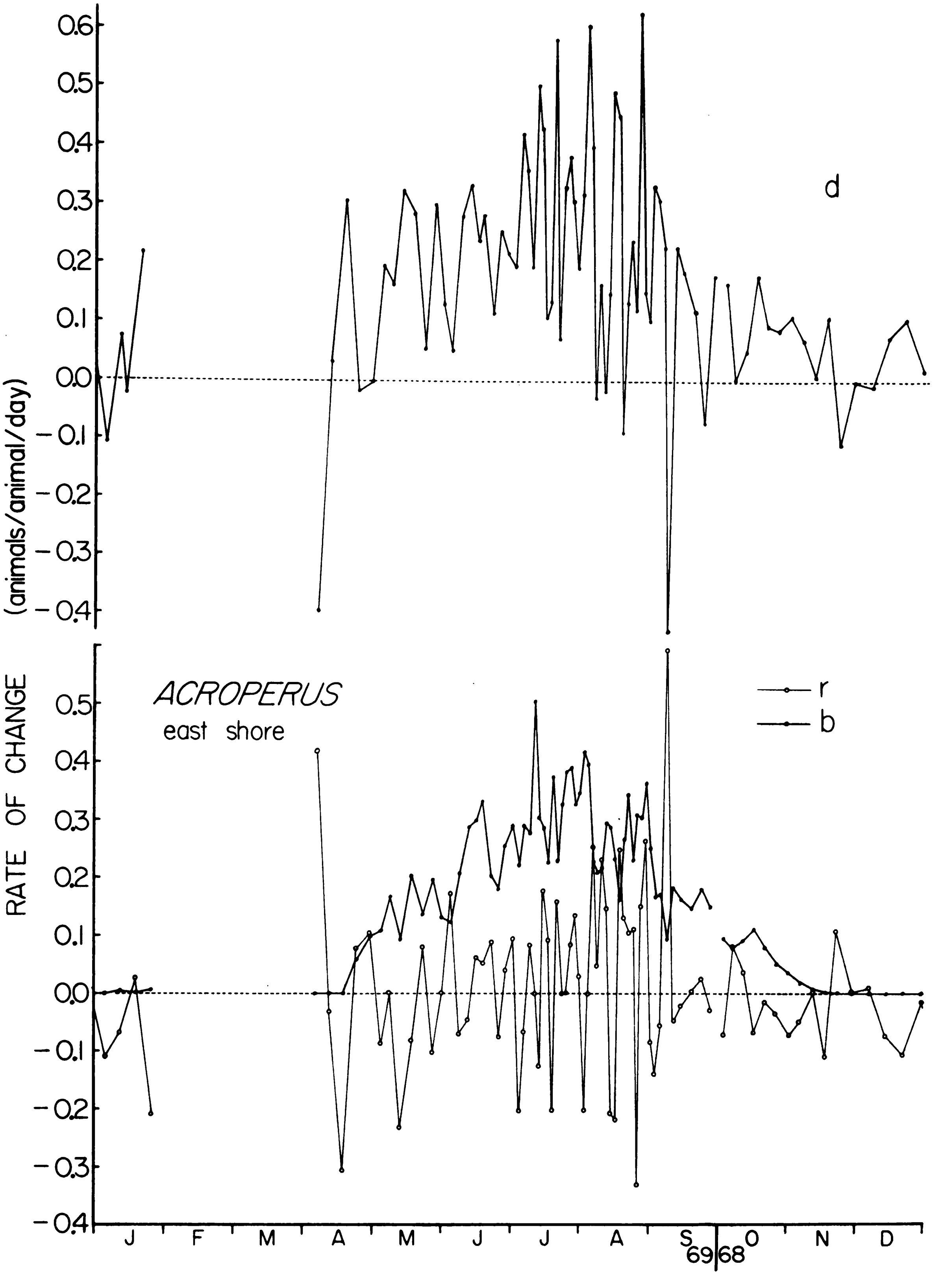
4a. Chydorus sphaericus: west shore



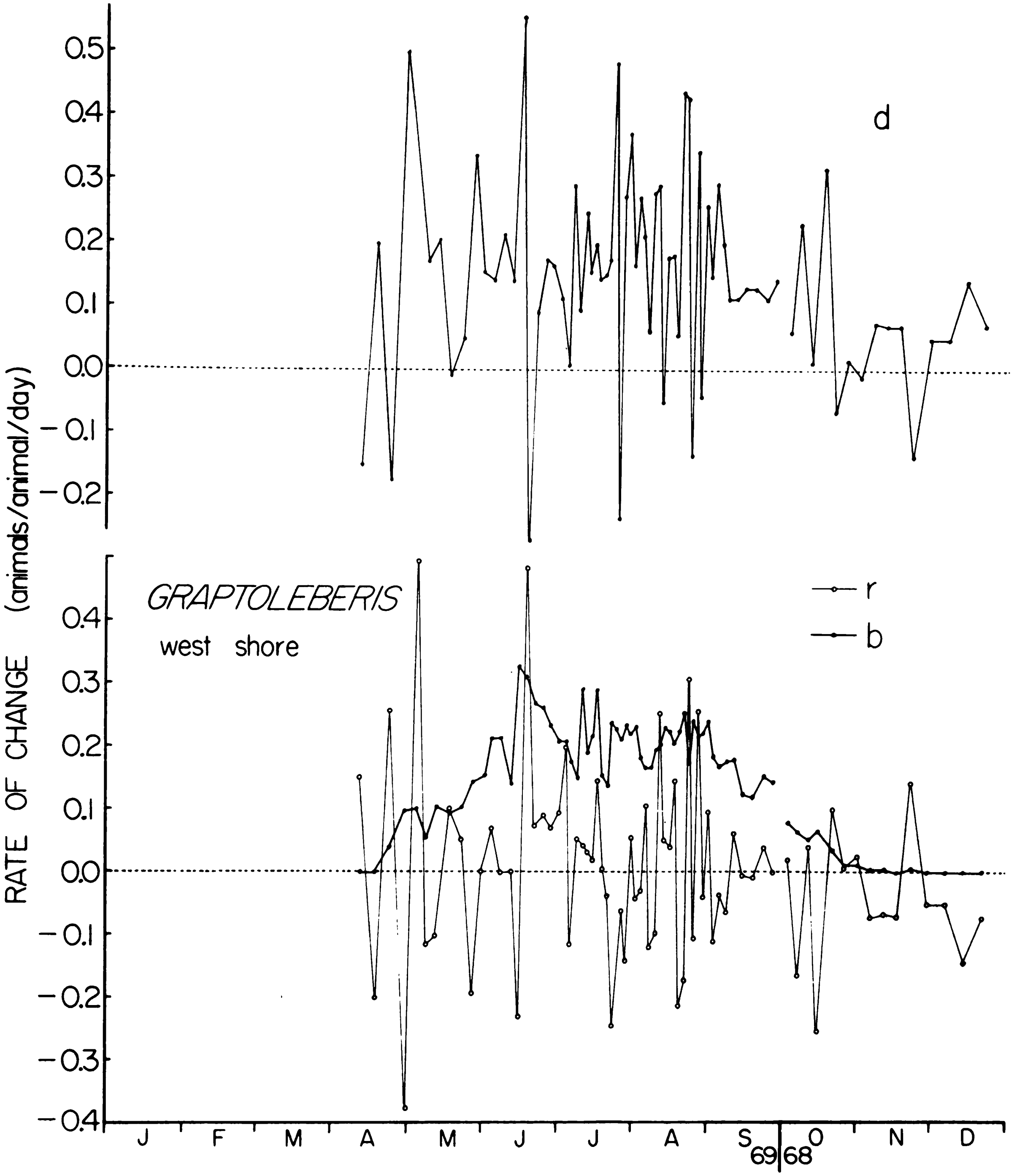
4b. Chydorus sphaericus: east shore



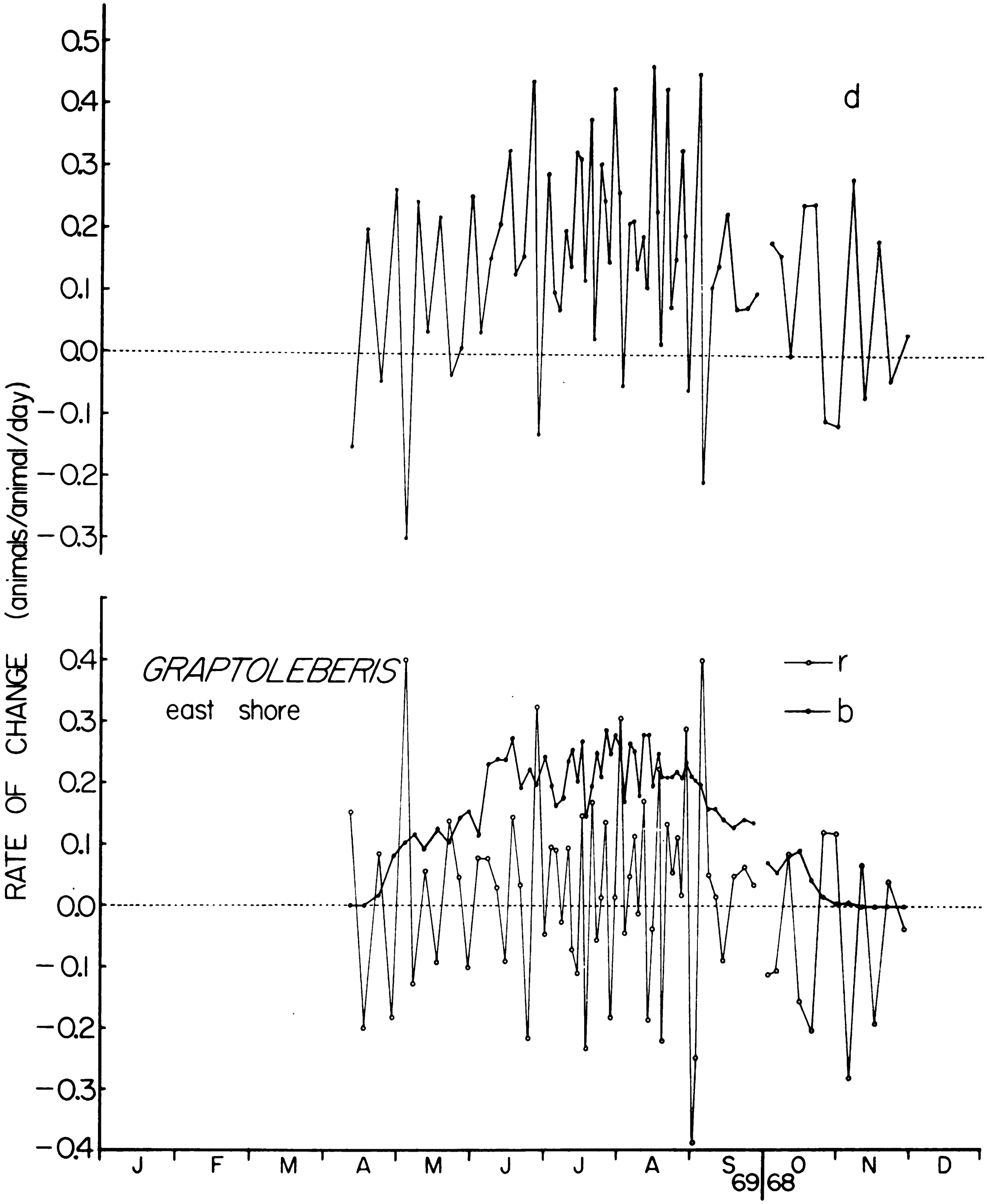
4c. Acroperus harpae: west shore



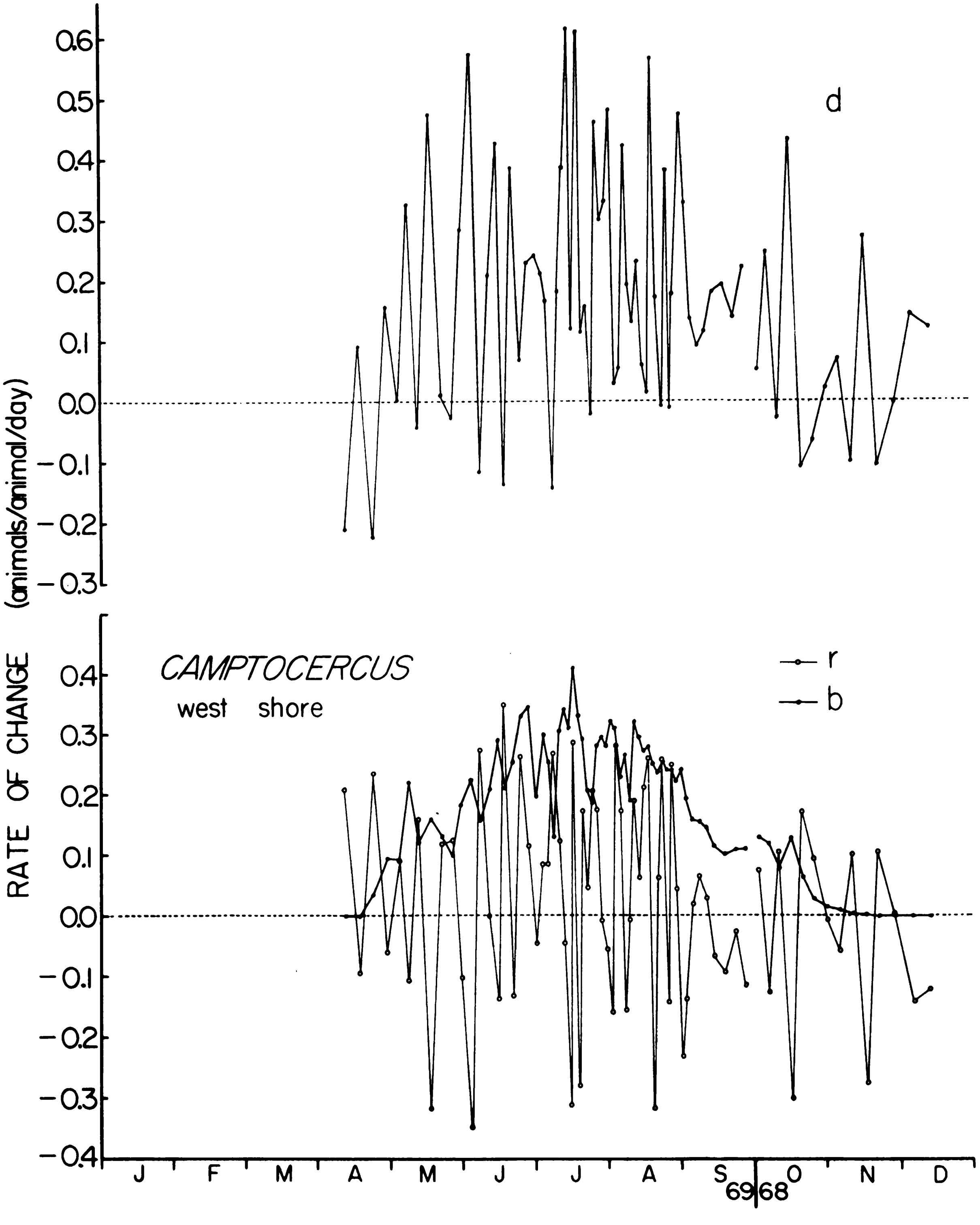
4d. Acroperus harpae: east shore



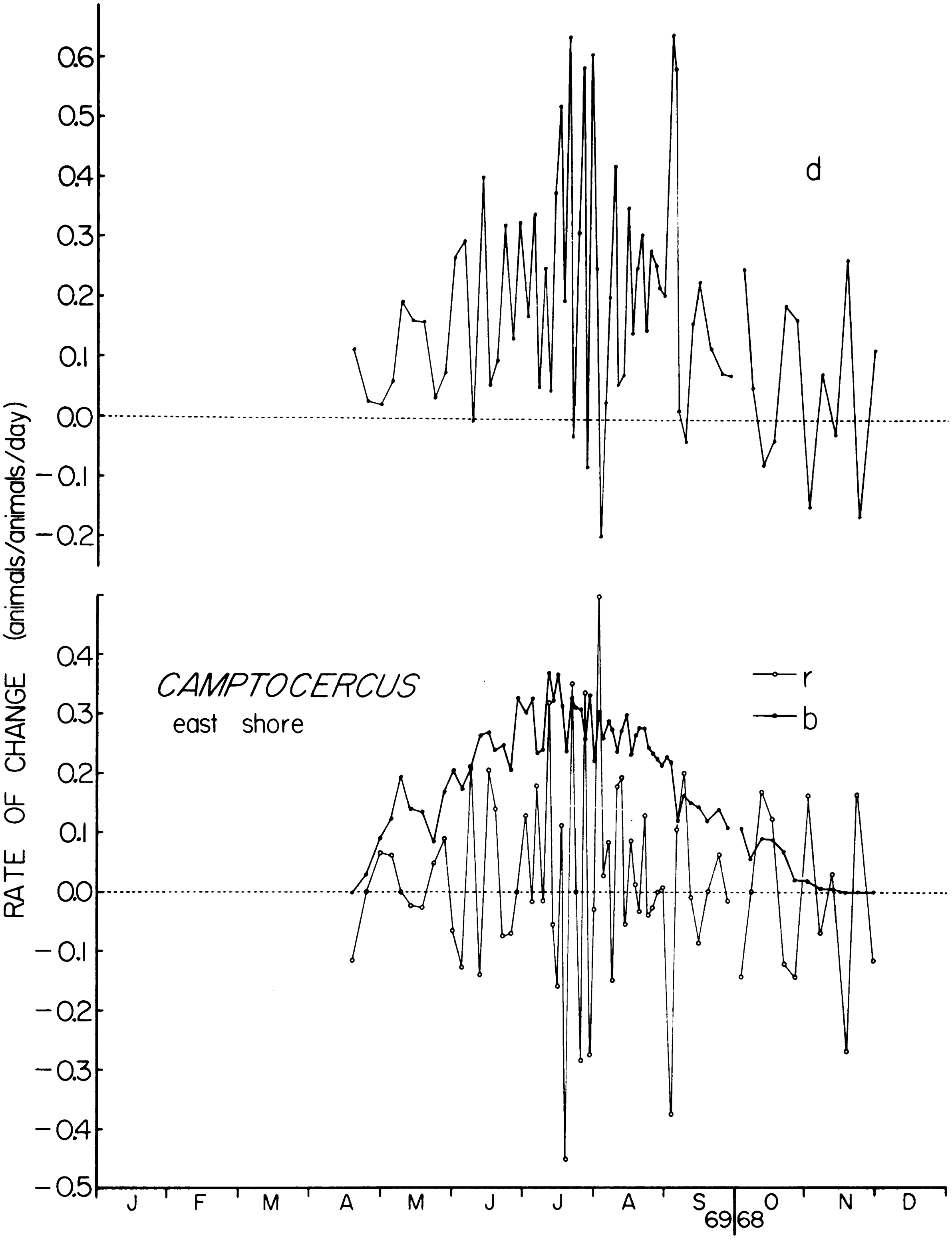
4e. Graptoleberis testudinaria: west shore



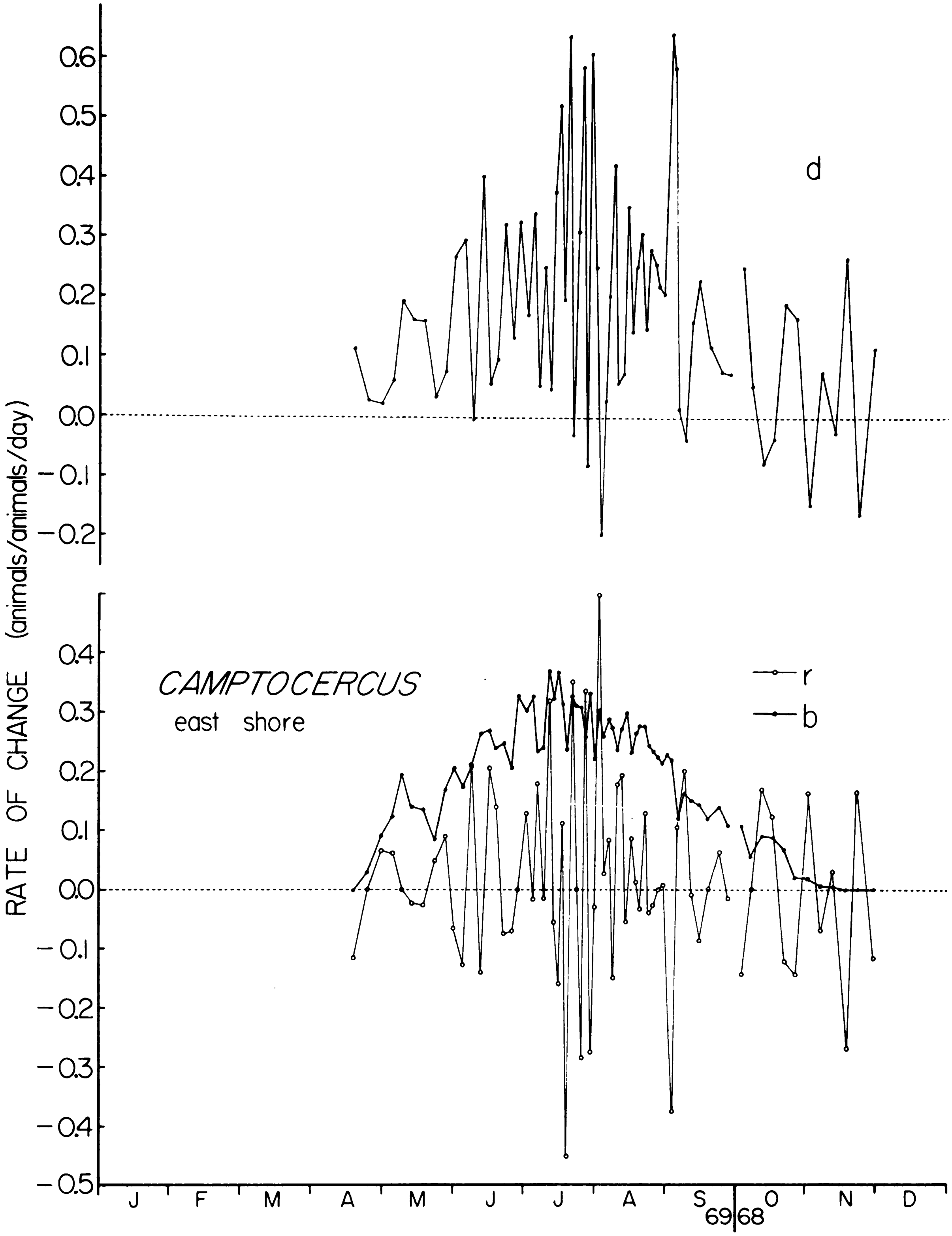
4f. Graptoleberis testudinaria: east shore



4g. Camptocercus cf. rectirostris: west shore

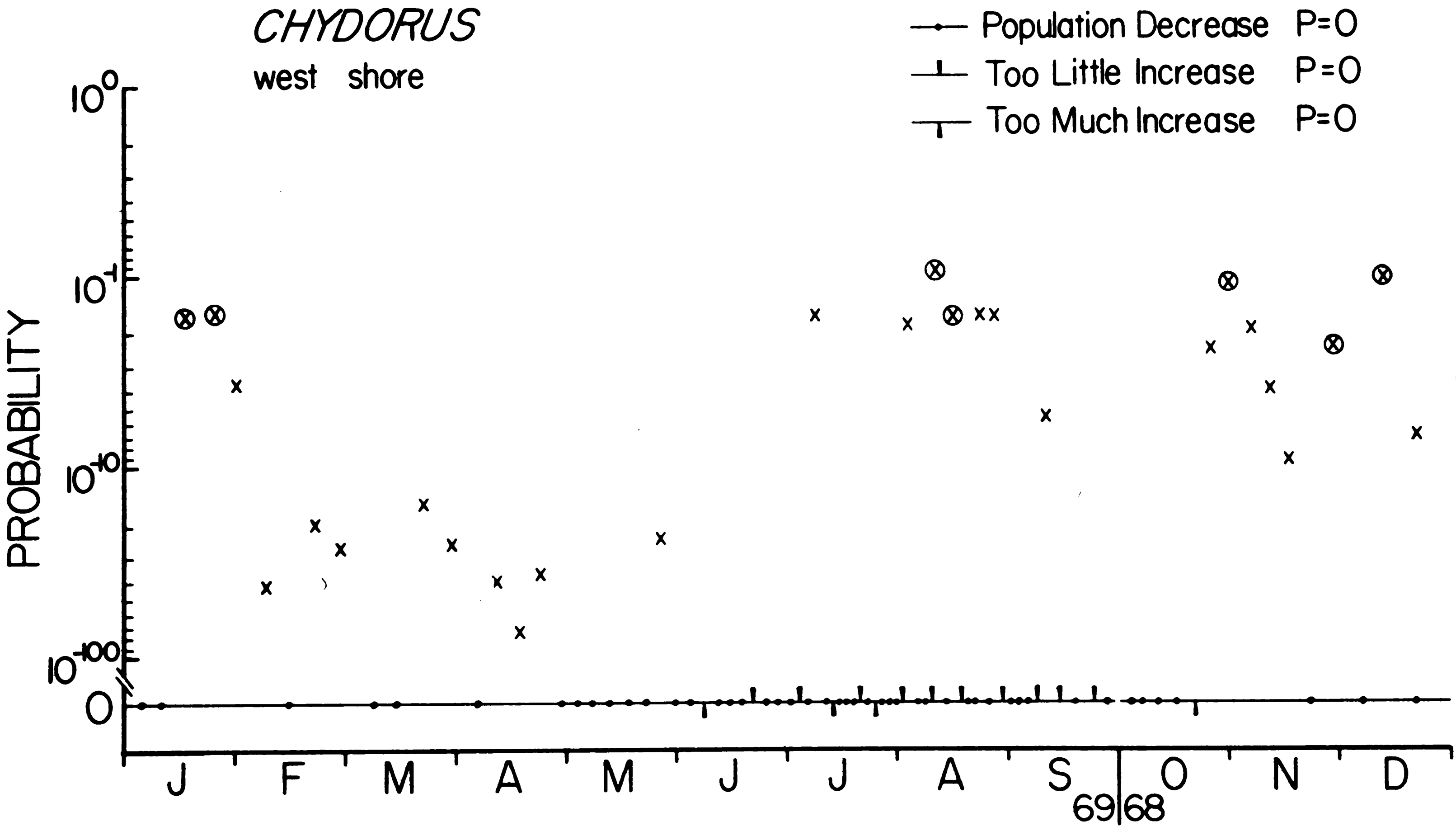


4h. Camptocercus cf. rectirostris: east shore

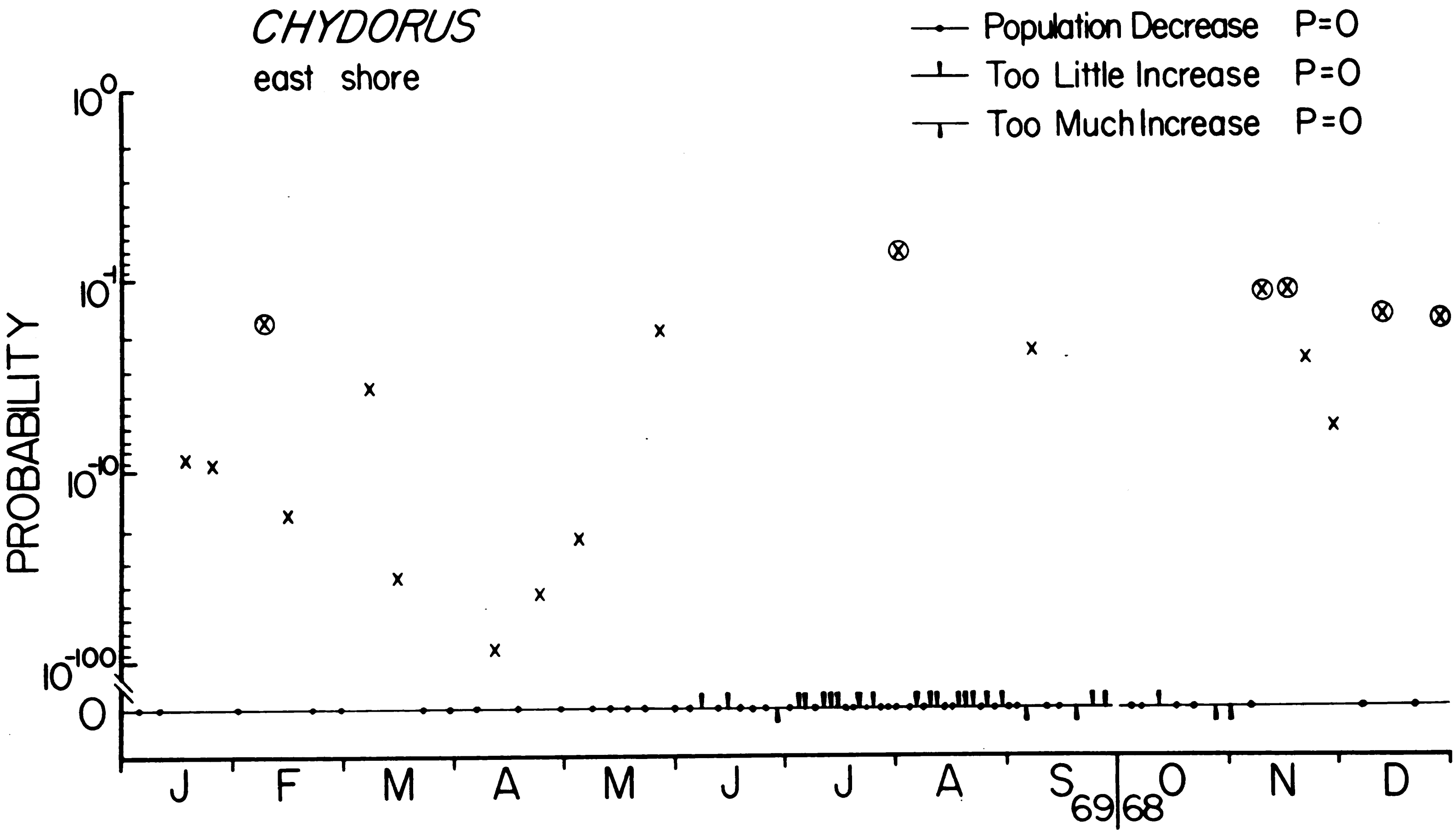


4h. Camptocercus cf. rectirostris: east shore

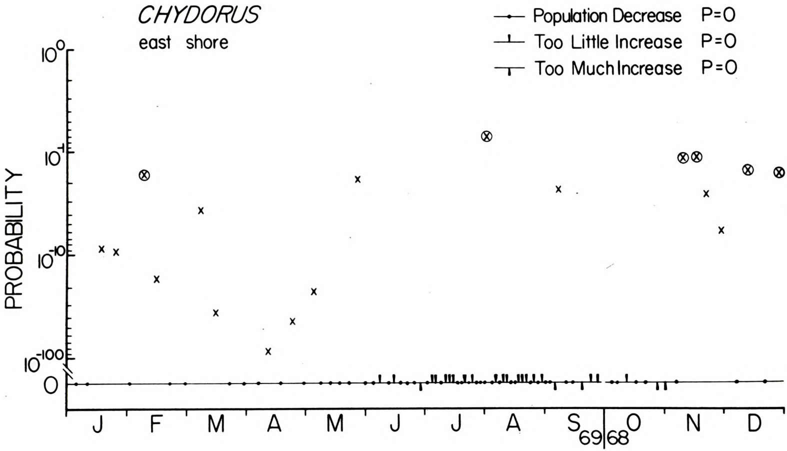
Figure 5. Probabilities of observed increases in population size of Chydorus sphaericus on two sides of Lawrence Lake.



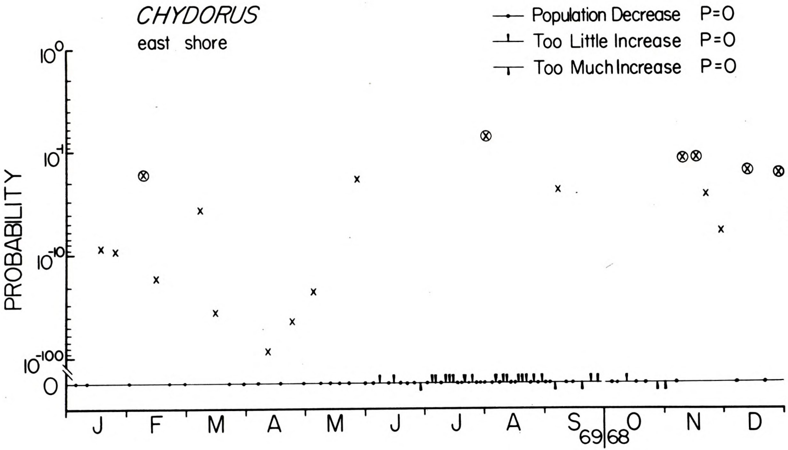
5a. West shore



5b. East shore



5b. East shore



5b. East shore

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