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Graphic Representation of Niche Width and its Application to Salt Marsh Littoral Foraminifera

by

William A. Muller

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, the City University of New York.

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This manuscript has been read and accepted for the Executive Committee in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

April 27, 1972
Date

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ABSTRACT

Graphic Representation of Niche Width and its Application to Salt Marsh Littoral Foraminifera

by

William A. Muller

Advisor: Professor John J. Lee

A method for representing the Hutchinsonian niche graphically has been designed and tested. The method provides a means for comparing the niche width of 3 species of foraminifera: Allogromia laticollaris, Rosalina leei and Spiroloculina hyalina. A niche polygon is constructed for each species using 6 factors; temperature, salinity, pH, feeding, interspecific competition, and intraspecific competition. The niche is estimated by measuring and comparing the areas of the polygons. The method should have a more general application than previous single parameter niche determinations. The three species reproduce within the following ranges: temperature (10-33 C), salinity 16-46 ‰), and pH (5-10). Biotic parameters were more difficult to evaluate. An equation, based on competitive feeding experiments, was developed to reduce data to a single coefficient (≤ 1). Spiroloculina hyalina did not compete with other species for food and the interspecific competition was 0.25 compared to 0.69 for Allogromia laticollaris and 0.74 for Rosalina leei. Intraspecific competition appears to be an important factor limiting the exploitation of available community space by A. laticollaris. Crowding seems to have little effect on the other 2 species. The feeding of foraminifera is affected by the quality and quantity of food organisms. The feeding rate of the species tested increases as more food is made available within a range of 10^2-10^6 cells fed. S. hyalina is a bacterial feeder. Experimental data and graphic analysis suggests that the niches of each experimental organism is different. A. laticollaris is a rare species which may become locally abundant when dominant species are missing. S. hyalina is also a rare species which can bloom in remote places (i.e., under algal mats) where the density of bacteria is high, water currents and wave action are negligible, and other species are not competing. R. leei is a stable, conspicuous species whose moderate numbers are relatively unaffected by physical stress and competition. A test polygon of Ammonia beccarii, a cosmopolitan generalist, was constructed using Bradshaw's (1957) data and laboratory observations. The species had the largest polygon and the result illustrates the utility of the method for niche comparison.

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INTRODUCTION

The multidimensional niche concept formulated by Hutchinson (1958) is considered by many (Levins, 1962, 1963, 1968; MacArthur, 1958; MacArthur and Pianka, 1966; Maguire, 1967; McNaughton and Wolf, 1970; Schoener, 1965) to be a significant advance in conceptualization of a central ecological theme because it theoretically lends itself to precise analysis. Diverse data can potentially be educed to geometric interpretation. Since the concept was advanced, ecologists have attempted to develop the methods to measure niches based upon the theory (Maguire, 1967; McNaughton and Wolf, 1970; Preston, 1962; Whittaker, 1960). Many studies have contributed to the development and interpretation of the multidimensional niche hypothesis. Though the theory itself is simply stated, its application to real situations presents a formidable challenge. Perhaps the greatest impediment to practical application is an inability to measure, weigh, and reduce niche dimensions to precise analytical statements.

To Grinnell (1917) the niche was a spatial concept, but distribution is merely the end result of the interaction of many factors. Elton (1927) developed the idea of the trophic niche which could be identified by studying feeding habits and the resultant flow of energy. Although feeding patterns are an important niche vector, the concept is unidimensional and negates the importance of physical and other biotic factors. For Gause (1934) the exclusion of species A by species B, in mixed culture, was a clear indication that the niche of species B was wider than species A, but he was unable to quantify this decision. Park (1962) modeled competition among populations of Tribolium spp. beetles under controlled laboratory conditions and discussed the potential of mathematical theory to measure ecological phenomena. Maguire (1967) in his analysis of Cairns' (1964, 1965) field data, developed a useful method, the versatility index, for considering the tolerances of protozoa to levels of 17 chemical and 2 physical factors (phenolphthalein alkalinity, methyl orange alkalinity, Cl^-, CO_2, O_2, Fe, total hardness, Ca^{++}, Mg^{++}, NH_4^+ - N, NO_2^+ - N, NO_3^+ - N, pH, $PO_4^{\equiv}$, SiO_2, $SO_4^{\equiv}$, temperature, turbidity, and biological oxygen demand).

His method did not consider trophic dynamics, competition, or other biotic factors. Frank (1952) studied interspecific and intraspecific competition as a measure of the "niche width" of several species of Daphnia, and VanValen (1965) suggested that certain key morphological characters are indices of "niche width" in birds. All of these studies were limited because they considered only one or a few key factors, but they do demonstrate how complex and abstract niche theory has become.

In spite of considerable evidence that the Gaussian view is an oversimplification (Hairston et al., 1960; Hutchinson, 1957, 1959; MacArthur, 1958; Park, 1962) it underlies current ecological theory. Recently proposed methods for determining niche width have considered only data on species dominance and relative abundance (McNaughton and Wolf, 1970; Whittaker, 1960). The McNaughton and Wolf equation is descriptive of community structure but does not reveal much about the complex interactions that might have been important factors in the development of the experimental community.

$$W = \left[\frac{\Sigma (Y_p \times P)^2 - (\Sigma Y_p \times P)^2 / \Sigma Y}{\Sigma Y} \right]^{\frac{1}{2}}$$

The formula calculates W, the niche width of a species, P equals the position of the community in the environmental ordering; Y_p is the importance of the species in that community, and Y is the total importance of the species for all of its occurrences.

Thus, the fundamental problem remains unsolved. A method is needed which can quantify niche width is such a way that many of the previously proposed niche parameters are included. At the same time, the method should be consistent with the multidimensional niche concept. The Hutchinsonian description seems to offer the most comprehensive, albeit abstract, definition of niche. It is the sum total of an organism's abiotic and biotic requirements which can be viewed as a flexible multidimensional hypervolume. Each group of organisms seems to present different problems in this respect. There is, because of these difficulties, a feeling that

the Hutchinsonian concept can only be approached in a qualitative way.

Many of the observational and experimental difficulties are simplified when one works with microorganisms (Gause, 1934) and it seemed an opportune time to make a more precise attempt at applying the theory. Foraminifera were chosen for a laboratory investigation of niche theory because they are easily cultured in the laboratory and the gross physical aspects of their habitats are so well known (Phleger, 1960; Phleger and Bradshaw, 1968) that assemblages of foraminifera are used by oceanographers and paleoecologists as indicator organisms in biogeographic studies (Bé, 1968; Jones, 1966; Lipps, 1967; Loeblich and Tappan, 1957; Myers, 1944; Stehli, 1965). Although much is known about their distribution patterns and phylogeny, little is known about the biology of any species of foraminifera and even less about their niches - this, in spite of the fact that some habitats such as marshes and shallow lagoons may annually support the growth of 100 or more different species of foraminifera.

Most laboratory studies of foraminifera have focused on descriptions of physical tolerances, nutrition, and life cycles of littoral benthic forms. Of these, 4 physical parameters of foraminifera have been considered important: temperature, salinity, pH, and oxygen (Arnold, 1954, 1964, 1966; Bradshaw, 1955, 1961, 1968; Lee et al., 1961, 1963; Muller and Lee, 1969; Myers, 1937, 1943).

Of those foraminifera which have been cultured in the laboratory most grow best at 20-25 C (Arnold, 1954; Bradshaw, 1955; Føyn, 1936; Lee et al., 1963), which approximates the temperature range at which these forms were collected. One species, Allogromia sp (NF) reproduced best at slightly higher temperatures (25-35 C; Lee and Pierce, 1963). Since many of these organisms are tide pool inhabitants or can be exposed to the full effects of heat and desiccation at ebb tide, Bradshaw (1961) tested the upper lethal limits of those organisms he had in culture. It ranged from 38 C for Bolivina vaughni to 46 C for Ammonia beccarii.

Foraminifera survive a wide range of salinities, but good growth occurs between 20-35 ‰. Bradshaw (1961) found that Ammonia beccarii cultures were most successful when incubated at

34 ‰. Lee and Pierce (1963) reported that when other factors were not limiting, Allogromia laticollaris and Allogromia sp (NF) reproduced at salinities as low as 5 ‰ and as high as 55 ‰, although the generation time was longer at bordering levels. Murray (1963) found that Elphidium crispum did best at slightly higher salinities, with an optimum of 30-35 ‰. Muller and Lee (1969) reported that most of the species of littoral foraminifera they tested grew well between 20-40 ‰. Quinqueloculina lata reproduced optimally at salinities between 35-55 ‰ while Trochammina inflata (Freudenthal et al., 1963) reproduced fastest at 55 ‰. They interpreted the discrepancy between field observations and laboratory data as an adaptation for reproduction at ebb tide.

Although many foraminifera are known to live in the sediments (Boltovosky, 1964; Brooks, 1967; Matera and Lee, 1972) very little is known about either pH or redox tolerances. Lee and Pierce (1963) found that Allogromia sp (NF) grew very well over a wide range of pH (6.0-9.0); Allogromia laticollaris did as well (Pierce, 1965). Bradshaw (1968) and McEnery and Lee (1970) showed that calcareous forms could survive and recover from exposure to acidic conditions for short periods of time.

The influence of food, interspecific competition, and intraspecific competition seem to be the most important biotic parameters although little is known about them. In association with studies on culture, the importance of proper food sources has been frequently described. Early studies were largely qualitative (Arnold, 1954; Jepps, 1942; Lee et al., 1961, 1963; Føyn, 1936; Myers, 1936). Bradshaw (1955, 1961) was the first to study foraminiferan nutrition from a quantitative point of view. He found that larger populations of Rotaliella heterocaryotica were produced when twice the amount of food was fed, and that the reproductive rate of Ammonia beccarii increased with increased density of food organisms. Tracer feeding techniques were a significant advance in the understanding of foraminiferan nutrition, and in making studies of interspecific and intraspecific competition for food feasible. More than 50 axenic species of algae, yeasts, and bacteria were tested by Lee et al. (1966) as potential food for foraminifera. Only a few of these, mostly diatoms, chlorophytes, and a few species of bacteria, were actually eaten

by the foraminifera. Most of the yeasts, cyanophytes, dinoflagellates, chrysophytes, and bacteria were not eaten. Three additional factors were found to affect feeding: the age of the culture of the food organisms, the age or position of the foraminifera in its life cycle, and the concentration of food cells. The lower threshold for feeding was found to be $\sim 1 \times 10^3$ cells/experimental tube and feeding rate was approximately directly proportional to concentration within a range of $1 \times 10^3 - 1 \times 10^6$ organisms/tube. Lee et al., (1966) showed that interspecific competition for food could be studied by this technique but restricted their studies to 2 demonstration experiments between Allogromia laticollaris and Allogromia sp (NF). Some qualitative interspecific competition experiments between Rosalina leei and Allogromia laticollaris have been reported (Muller and Lee, 1969). Although A. laticollaris reproduces quickly in laboratory culture, it does not replace R. leei when the two are grown together. The presence of R. leei causes a premature drop in the A. laticollaris population and the normal growth of R. leei continues.

The foraminifera, A. laticollaris, R. leei, and S. hyalina, in the present study were chosen from many cultures established in continuously reproducing laboratory cultures (Muller and Lee, 1969), because at the outset they seemed to have very different niches. The gross ecology of the 3 species is understood (Lee et al., 1969 b, Muller and Lee, 1969). In a study of the standing crop of a Long Island salt marsh, Lee et al., (1969 b) showed that Allogromia laticollaris was not abundant. Further, they demonstrated that the frequency of A. laticollaris increased sharply during the second year of the study apparently due to a change in the physical environment resulting from the onset of a drought. They concluded that A. laticollaris was a rare safety valve species. The frequency of R. leei did not change during the course of the investigation. The moderate frequencies observed for this species suggested that R. leei is a conspicuous species. S. hyalina is a bloom organism that has been found in dense clusters under algal mats (Lee et al., 1969 b). Its small size apparently limits its occurrence to protected places. Muller and Lee (1969) showed that S. hyalina is basically a bacterial feeder and cultures of this species were sustained solely on bacteria.

MATERIALS AND METHODS

The experimental organisms were isolated from field collections taken at Towd Point, North Sea Harbor in Southampton, Long Island, and cultured following procedures previously described (Lee et al., 1961, 1963, 1970; Muller and Lee, 1969).

Foraminifera were separated from the detritus and sediment by spreading the crude mixture in Pyrex baking dishes (34 x 23 x 5 cm), with 2-5 cm of sea water overlay. After 24 hours the foraminifera migrated 3 cm to the sediment surface. The organisms were harvested by means of Pasteur pipettes. Appropriate species were picked and washed ~ 25 times with sterile sea water and then inoculated into sterile media with various mixtures of food organisms from available laboratory stocks. Successful agnotobiotic cultures were used to develop clone gnotobiotic cultures.

Stock cultures of the 3 species of foraminifera used in this study were grown in erdschreiber medium (Føyn, 1936). Allogromia laticollaris and Rosalina leei have been in clone culture for about 10 years in liquid erdschreiber (~ 26 ‰). In the A. laticollaris agnotobiotic cultures Phaeodactylum tricornutum (39) and Amphora sp (5) are the only algae. R. leei are grown with Nannochloris sp (41) and Amphora sp (5). Clone cultures of S. hyalina were established 6 years ago. Stocks of S. hyalina are grown on erdschreiber agar with an overlay of 5 ml Millipore (HA 0.45 μM) filtered sea water (~ 26 ‰). Amphora sp (5) and Cylindrotheca fusiformis (B1-27) were the only algae in the cultures. No attempt was made to limit bacterial stocks in these stock cultures.

Algal species used in this study were isolated from the same environment by Dr. John J. Lee. Crude collections were streaked onto a variety of artificial media being developed in our laboratory (US AEC Progress Report NYO 3995-20). In 2 to 3 weeks colonies of algae were visible and were excised from the agar with a nichrome wire needle and inoculated into sterile media. Stocks of 10 species of algae were grown axenically at 25 C on an artificial sea water medium (S) (Lee et al., 1970).

Bacteria were isolated from field samples which were collected by means of sterile forceps (Lee et al., 1970). The samples

were chilled to prevent decay and deterioration. Aliquots of the sample were then streaked onto the differential media. The 10 strains of bacteria selected for the present study were chosen because they are taxonomically representative of the bacteria from the Southampton salt marsh and because they were found by a fellow graduate student (Miss Eileen Kennedy) to be among the most dominant forms during the course of the growing season (US AEC Progress Report NYO 3995-20). Bacteria were grown axenically on an enriched artificial sea water medium (YEP-1; 1% acidicase and 1% yeast extract).

Algae and bacteria, in appropriate physiological studies, were enumerated by measuring optical density with a Gilford micro-sample spectrophotometer (Model 300 N). A nomograph for each species of algae was constructed by plotting optical density against direct cell counts. The algae were counted by means of an A.O. brightline hemocytometer. A similar relationship was obtained for the bacteria using viable cell counts.

All experiments were conducted in either plastic Falcon flasks (250 cm^2) or in Pyrex screw-capped test tubes (20 x 125 cm). Ten ml of media were added to test tube studies and 50 ml were used for flask cultures. All experiments were gnotobiotic and were incubated under controlled conditions of temperature and light in Sherer environmental chambers (model CEL 4-4). Cultures and experiments were grown in full light (200 $\mu W/cm^2$) at 25 C. Light was measured with an ISCO spectroradiometer (model SR). When pH and salinity were not variables, the media were adjusted to pH 8.0 at a salinity of 26 ‰. These variables were used as controls when each of these factors was an independent variable.

The temperature tolerance studies were conducted in Sherer environmental chambers at 5 C intervals ranging from 5 C to 40 C. One degree intervals were tested at the upper and lower limits of the range.

In salinity experiments, the medium was slowly evaporated to 80 ‰ to prevent the formation of precipitates. The salinity of the evaporated media was measured by titration with $AgNO_3$ following the high precision method of Strickland and Parsons (1968). The media

was then diluted to lower salinities by adding distilled water. Reproductive rates of the organisms were studied in media with a range of salinity from 5-80 ‰.

The pH tolerances of experimental organisms were also studied at 0.5 intervals from pH 2-10.5.

The rate of oxygen consumption by the foraminifera was measured with a Gilson differential respirometer (Gilson, 1963). In another experiment the survival of the foraminifera in an oxygen free atmosphere was studied in a Forma (model 3159) anaerobic chamber. The chamber was continuously flushed with nitrogen gas during the studies. Heavy inoculations of food organisms ($\sim 1 \times 10^7$ cells) were supplied in the absence of light.

The tolerances of experimental organisms to organic stress was determined by adding yeast extract or peptone in concentrations that ranged from 1×10^{-6} - 5×10^{-4} %.

As a control for abiotic growth experiments, the growth responses of the appropriate algae and bacteria under various conditions of temperature, salinity, pH, and organic stress were also investigated.

The carrying capacity of each species of foraminifera under standard culture conditions was measured in 100 replicate tubes of each species. They were counted weekly. The average number of individuals/tube at maximum density was the carrying capacity. The carrying capacity in flask cultures was determined using the same procedures.

Radioactive tracers were used in qualitative and quantitative feeding studies (Lee *et al.*, 1966). Foraminifera for these studies were washed 10 times with sterile media and any food adhering to the surface of the animals was removed with glass needles. Care was taken to select organisms of approximately the same size for each experiment. Except when population size was a variable in tracer feeding studies, the following test populations were used: 10 *Allogromia*, 20 *Rosalina*, and 50 *Spiroloculina*. Previous studies (Lee *et al.*, 1966; Muller and Lee, 1969) demonstrated that these were the minimum inocula for statistically meaningful data. Experiments were replicated in quadruplicate or sextuplicate.

Potential foods were inoculated into appropriate media with ^{32}P (0.5-1 μCi/ml) as a label, and incubated in strong light for 24 hours. As in previous experiments (Lee et al., 1966) the level of radionuclide was adjusted to ~ 0.1-1 count/min/cell. Labeled food cells were harvested by centrifugation and washed 5 times in sterile unlabled sea water. The population density of each food species was determined by counting an aliquot with a hemocytometer. The appropriate number of food cells was inoculated into the cultures of foraminifera and incubated for 24 hours. The foraminifera were harvested by gentle agitation with a vortex mixer, allowing the animals to settle, and removing the supernatant fluid. Autoclaved dead organisms were used as controls. The process was repeated 5 times. The foraminifera were placed in scintillation vials with a minimum amount of water carry over, dried, and 15 ml of scintillation fluid added per vial. Radioactivity was measured by means of a Beckman liquid scintillation counter.

The rate of feeding of the foraminifera on representative algae was measured for each species when grown alone and when several species were competing for the same food (s). The existence of threshold and saturation levels of food organisms was investigated using the same tracer techniques with a range of 10-10^8 cells fed.

The biomass of the algae eaten was determined by measuring the volumes of 100 individual logarithmically growing algae cells. Log phase cells were chosen for measurement since they were used in the tracer feeding studies. Previous studies (Lee et al., 1966) had shown that fewer stationary phase cells are eaten by foraminifera than cells in any other phase.

Six variables were used in mathematical considerations: temperature; salinity; pH; intraspecific competition; feeding levels; and interspecific competition. In the analysis, they were plotted as intersecting vectors. Two values for each factor were plotted - the maximum and the minimum.

The construction of the symbolic environment niche circle was not done according to any formal mathematical procedure. In one method, the variables were weighted according to certain logical premises. Zoogeographical studies (Bé, 1967; Berger and Soutar, 1967;

Cifelli, 1962; Donk and Mathieu, 1969; Lidz, 1966; Matoba, 1970; Murray, 1967; Vilks, 1969) suggest that temperature, salinity, and pH are the key factors affecting the distribution of foraminifera in all marine provinces. For these classical reasons the physical factors were given a proportionately greater area of the available environmental circle. Arbitrarily, a system was formulated in which the intersection of the parameter lines would be eccentric to the center of the environmental circle.

Because of its classical importance to foraminifera, the temperature vector (DZ) was drawn as a diameter of the circle. Next the line QR, representing the intraspecific competition, was drawn perpendicular to line DZ such that it intersected the circle at 2 points (Q, R) which are one radius (= PZ) from point Z. All other vectors were drawn to intersect at the same locus (O). The vectors representing pH, salinity, feeding rate, and the interspecific competition coefficient were constructed such that they each carved out equal arcs (DT, TM) on the circumference of the niche width circle and are equal to one-half the line DO (Fig. 1).

In a second approach bias toward physical factors was avoided by plotting the tolerances as diameters. In this way each parameter consists of an equal available area space.

It was difficult to reduce interspecific competition for food to a single vector form. The analysis required it, however, if the approach to niche width was to be consistent. That is, if each of the major factors was to receive the same relative importance. The following equation was developed to evaluate this parameter.

(I) $$\text{I.S.C.} = \frac{(\Sigma F_1) + (\Sigma F_2)}{2\ (\Sigma F_a)}$$

Equation (I): The expression of the interspecific competition coefficient

I.S.C. = the interspecific competition coefficient

F_1 = feeding rate in competition with another species

F_2 = feeding rate in competition with a second species

F_a = feeding rate when the species grows without competition

Foods which were found to be ingested in the greatest amounts were used, including representative bacteria, chlorophytes, and diatoms. Thus the total value for single species feeding represents the sum of the individual feeding rates on each potential food. For example, the total rate of feeding of R. leei is:

$$F_a = 1962 + 339 + 1007 + 517 + 320 + 300 + 275 + 375 + 90 = 6085 \text{ food cells/foraminifera/day}$$

Table 8 summarizes the calculations for each species.

In multivariate analysis the area under the curves were calculated using the least squares method of fitting a second degree polynomial to the observed values and integrating the resulting equation between the limits of the observations. Analysis and calculations were performed with the help of an IBM 360/50. The reproductive capacity (R_n) is defined mathematically.

$$(II) \qquad R_n = \int_L^u f_n(x)dx$$

Equation II: The expression of the reproductive capacity

R_n = Reproductive capacity of a species with respect to the physical variable x with a second physical variable, y, kept fixed at the value y_n.

L = The lower limit for x

U = The upper limit for x

$f_n(x)$ = The generation time with respect to the physical variable x with a second physical variable, y, kept fixed at the value y_n.

RESULTS

Abiotic Parameters

Temperature

All 3 species of foraminifera reproduce in the laboratory between 10-33 C (Table 1). Of the species tested, A. laticollaris had the shortest generation time (~ 8 days) (Fig. 2). The minimum generation time extended over a rather broad range of temperature (18-29 C); almost to the upper and lower limits of reproduction, 10-32 C. Temperature strongly influences the reproduction of S. hyalina; generation time gradually decreased from 60 days at 10 C to a minimum of 14 days at 29-30 C, which was close to the upper thermal limit for the species (Fig. 2). Temperature was less important as a factor affecting the reproduction of R. leei. At their lower and upper thermal limits (14 and 32 C), generation time was longest (~ 65 days); at 25 C the generation time was shortest (~ 48 days) (Fig. 2). Algal and bacterial growth was less affected over the same temperature range (Table 2). The growth of populations of 4 species [Phaeodactylum tricornutum (39), Amphora sp (5), Nannochloris sp (41) and Amphora sp (RF-8)] gradually increased to a maximum at 30 C. Five species [Chlamydomonas subehrenbergii (93), Chlorococcum sp (38), Nitzschia apiculata (Pb-13), Cylindrotheca fusiformis (BL-27), and Nitzschia rhombica (Pb-6)] had optima near 20 C, and the reproduction of 1 species [Nitzschia rhombica (Pb-6)] was unaffected by temperature throughout the test range (10-30 C). Most bacteria (A5-703, D5-702, C1-704) also grew well within the temperature range tested (5-35 C). Three strains (A5-6, A5-7, and D2-7 had a more restricted growth range with optima between 20-25 C; 1 (A1-711) had an optimum at 30 C and 2 others (A3-111, D2-703) at 35 C.

Salinity

Salinity does not restrict the reproduction of any of the species tested; all 3 species of foraminifera reproduce well in the laboratory between 16-46 ‰ (Table 1; Fig. 3). At the standard test temperature (25 C) the generation time of A. laticollaris decreased

from 25 days at 20 ‰ (Lower limit) to 8 days at 30 ‰. The minimum generation time (~ days) extended over a wide range (30-40 ‰). The upper limit of salinity for reproduction in this species was 45 ‰. The shortest generation time of S. hyalina occured within an even broader range (20-40 ‰), but outside these limits it increased sp sharply that no reproduction was observed at salinities above 44 ‰ or below 17 ‰. The reproductive range of R. leei is very similar to the other species tested (18-47 ‰); the minimum generation time was restricted to 30 ‰. Bacterial growth was less affected over the same salinity range but algal growth was more restricted (Table 3). Four species [Amphora sp (RF-8), Cylindrotheca fusiformis (BL-27), Nitzschia rhombica (Pb-6) and Nitzschia apiculata (Pb-13] grew well only between 30-40 ‰ and had optima of 30 ‰. The growth of six species [Nannochloris sp (41), Nitzschia acicularis (8), Chlorococcum sp (38), Chlamydomonas subehrenbergii (93), Amphora sp (5) and Phaeodactylum tricornutum (3)] was less affected by salinity. The optima for 3 of those species [Nannochloris sp (41), Nitzschia acicularis (8) and Chlorococcum sp (38) extended over a wide range (20-40 ‰). Chlamydomonas subehrengergii (93) and Amphora sp (5) had optima at 30-40 ‰; and Phaeodactylum tricornutum (39) reproduced best at ~ 30 ‰. Most bacteria grew well over a broad range. Two strains (D5-7, and D5-702) grew well within the range of 10-50 ‰; 3 others (D1-701, A5-6, A5-7) grew better at higher salinities (20-60 ‰), and 2 (A1-711, A5-703) were restricted to an optimum of ~ 30 ‰.

pH

All 3 species were tolerant to relatively wide ranges of pH and within these ranges generation times were not affected (Table 1; Fig. 4). The optimum range for A. laticollaris was pH 5.0-9.5; for S. hyalina it was more restricted (pH 6.0-8.0); and for R. leei it was pH 6.9-10.0. The range of pH in which A. laticollaris reproduced as ~ 1.3 times greater than that of R. leei and 2.2 times the range of S. hyalina. The growth of algae was less affected by pH (Table 4). Eight species [Amphora sp (RF-8), Chlorococcum sp (38), Nitzschia rhombica (Pb-6), Nitzschia apiculata (Pb-13), Cylindro-

theca fusiformis (BL-27), Nitzschia acicularis (8), Chlamydomonas subehrenbergii (93) and Amphora sp (5)] grew well over a broad range (pH 4.0-8.0). while the growth of 2 species, Phaeodactylum tricornutum (39) and Nannochloris sp (41) was good within a narrower range (pH 5.0-8.0), with optima at pH 8.0. Bacteria grew best within much narrower pH limits; the optimum for all species was ~ pH 7.0 (Table 4). Five of the strains (C1-704, A5-7, A5-6, A3-111, D1-701) grew well between pH 6.0-9.0 and the others (A5-703, D2-7, D5-702, A1-711, D2-703) had a narrower range (pH 6.0-8.0).

Oxygen

All 3 species of foraminifera consumed oxygen at similar rates (Fig. 5). They used between 0.5-4.5 µl/mg body weight/hr within the temperature range 15-31 C. A. laticollaris consumes little oxygen (0.5 µl/mg/hr) when the temperature is less than 21 C. Between 21-35 C, the rate of oxygen consumption increases sharply to 4.2 µl/mg/hr at 35 C. The rate of oxygen consumption of R. leei increases from 0.7 µl/mg/hr at 15 C to 4.5 µl/mg/hr at 25 C, and then declines to 2.8 µl/mg/hr at 35 C. The rate of oxygen consumption of S. hyalina gradually increases from 1.0 µl/mg/hr at 15 C to 4.4 µl/mg/hr at 35 C. The generation time of all 3 species increased only slightly (~ 10%) when the foraminifera were cultured without oxygen.

Multivariate studies

As anticipated, the generation times of the 3 species tested were more strongly affected by varying several abiotic factors simultaneously. The least affected species was R. leei, with the only significant negative synergistic interaction occurring between temperature and pH (Fig. 6). At 10 C the reproduction of R. leei was only 1% of its biotic potential at 30 C and reproduction was restricted to a very narrow range around pH 8.0. At intermediate temperatures (20-25 C) reproductive capacity was 40.6% and 72% of those grown at 30 C.

Although A. laticollaris has wide tolerances to individual abiotic environmental variables, its reproductive capacity is severely

restricted at the periphery of several variables when tested simultaneously. The reproductive capacity of this organism at pH 5.5 was only 12% of the biotic potential measured at pH 7.5-9.5 when tested against salinity (Fig. 7). A similar pattern was noted when temperature was tested against salinity (Fig. 8) or against pH (Fig. 9). The reproductive capacity of A. laticollaris at 10 and 15 C was only 16% of the biotic potential measured at 25-30 C and reproduction was restricted to ~ 25%. At 20 C the reproductive capacity was much higher (~ 60%) than that found at 25 and 30 C. The biotic potential of A. laticollaris was reached over a wide range of pH at optimum temperature (25-30 C). At 10 C reproduction was restricted to pH 8.0 and was only 20% of the potential.

S. hyalina was affected by multiple abiotic variables only at the fringes of its niche. Full biotic potential was reached throughout a pH range of 5.5-9.5 from 20-40 ‰ salinity (Fig. 10). At pH 4.0-4.4 and 10.0 the reproductive capcity was only 60% of maximum. When temperature and salinity were the variables, biotic potential was expressed from 15-30 ‰ at 20-30 C (Fig. 11). At lower temperatures (10-20 C) the reproductive capacity was 68% of maximum over the same salinity range. Very little negative synergistic effects were found when pH and temperature were the variables. At higher temperatures the range for reproduction was reduced to 80% of maximum.

Organics

The 3 species of foraminifera tested vary in their ability to tolerate the effects of organic enrichment (Table 5). When small amounts (10^{-5}%) of peptone were added to cultures of A. laticollaris, growth was better (126%) than control tubes, but at slightly higher levels (10^{-4}%) growth was only 25-42% of control tubes. Almost no growth was observed in tubes containing 10^{-3}-10^{-2}% peptone. The growth of R. leei was less than 1% of controls when as little as 10^{-5}% peptone was added to the cultures. No reproduction was observed in tubes containing more than this amount of peptone. The responses of S. hyalina to organics were similar to A. laticollaris. Growth was 90% of controls when small amounts of peptone (10^{-5}%) were used, but declined to 1% when 10^{-4}% peptone was added.

The peptone itself at 0.01% did not effect pseudopodial activity of the 3 species tested when they were exposed for several hours. Death was gradual over a period of days suggesting that inhibition was through effects on cultural associates. Most of the algal strains tested, Nitzschia apiculata (Pb-13), Cylindrotheca fusiformis (B1-27), Nitzschia acicularis (8), Phaeodactylum tricornutum (39), Amphora sp (5), Amphora sp (RF-8) and Nitzschia rhombica (Pb-6) grew best in minimal media enriched with 10^{-5}% peptone but were inhibited by greater amounts (Table 6). Three chlorophytes and all the bacteria tested grew best when peptone was ~ 10^{-4}% (Table 6).

Biotic Factors

Under optimum laboratory conditions the reproductive rate of A. laticollaris is rapid (Generation Time = 8 days; Fig. 13), and after 1 month the carrying capacity is reached. The carrying capacity for A. laticollaris is large and sometimes exceeds 2600 organisms per 10 ml of media. Although the carrying capacity changes, depending upon the parental inoculum, the intrinsic rate of increase (r) during the logarithmic phase is the same. The value of r (2.533 org/day) is the largest of the foraminifera tested. The sizes of individual populations varied greatly during the logarithmic growth phase reflecting the various asexual reproductive pathways which can occur during the life cycle of this organism (Lee et al., 1969 a). The carrying capacity of R. leei in optimum laboratory conditions is 1350 organisms per 10 ml, but almost 2 years (540 days) are required to reach this population (Fig. 14). The intrinsic rate of increase is correspondingly smaller (0.272 org/day). Under optimum conditions the carrying capacity (3600/org/day) of S. hyalina cultures is reached in about 50 days (Fig. 15). The intrinsic rate of increase is equal to 1.472 org/day which is intermediate to those of A. laticollaris and R. leei. The large range in the sizes of individual populations probably can be best explained as dampening oscillations of the mean carrying capacity.

Feeding

Foraminifera are selective feeders. Of the 28 species of

diatoms and chlorphytes tested only 4-5 were consumed in significant quantities (40-150 x 10^{-5} mg/foram/day) by the foraminifera (Table 1). Two species of algae, Phaeodactylum tricornutum (39) and Amphora sp (5) were eaten in large amounts by all the foraminifera. In synxenic culture A. laticollaris ate almost 5 times more Amphora sp (5) (1.5 x 10^{-3}/animal/day) than most of the other species tested (Fig. 16). Four other species, Phaeodactylum tricornutum (39), Amphora sp (RF-8) Nannochloris sp (41) and Nitzschia rhombica (Pb-6) were also eaten in large amounts (5.6-8.0 x 10^{-4} mg/animal/day). Although great numbers of bacteria were eaten (Table 7), their biomass (0.1-8.3 x 10^{-6} mg/animal/day) was negligible when compared to the algae.

Two of the algal species, Amphora sp (RF-8), and Nannochloris sp (41), which were eaten by Allogromia in large amounts were not eaten by the other foraminifera. R. leei ate 2 species of algae, Chlamydomonas subehrenbergii (93) and Nitzschia apiculata (Pb-13) that the other foraminifera did not consume in large amounts. Nitzschia apiculata (Pb-13) was eaten in the greatest amounts (6.4 x 10^{-4} mg/foram/day), followed by Amphora sp (5) and Chlamydomonas subehrenbergii (93). In terms of total biomass the other algae were eaten in less significant amounts (range 1-35 x 10^{-5} mg/foram/day; Fig. 17).

The feeding of S. hyalina on algae was unusual; only 1 species of alga, Amphora sp (5), was an important food source (1.2 x 10^{-4} mg) (Fig. 18). The biomass of most of the others was < 20% of the number of Amphora sp (5) eaten. The biomass (0.2-1.0 x 10^{-6} mg/animal/day) of bacteria consumed were similar to that of R. leei and were not significant.

Tracer experiments confirmed the relationship between available food and feeding rate. The lower threshold for feeding is ~ 10^2 algal cells fed; feeding is directly proportional to the concentration of food organisms from 10^2-10^6 cells at which time saturation is reached (Figs. 19-21). When bacteria are tested as potential foods, feeding begins when 10^4-10^6 cells are fed and the rate increased until 10^8 bacterial cells are fed (Figs. 22-24).

Intraspecific competition

Crowding strongly affects the feeding and reproduction of A. laticollaris. Inoculum size for this species must be small if it is to reach full reproductive capacity (Fig. 25). A clone culture produced 400 % more animals than an inoculum of 10. When the inoculum size was increased to 33, reproduction was ~ 7% of a clone. Tracer feeding experiments suggested that there is a great competition for food or interference with feeding even in moderately crowded cultures (100 animals). In such cultures the feeding rate on Nitzschia acicularis (8) and Phaeodactylum tricornutum (39) was less than 1/3 of the rate of single animals (Table 8).

R. leei and S. hyalina were affected less by crowding. It is difficult to establish reliable cultures of these species with small inocula (1-15). Inocula of 50-200 animals produced only 50% as many R. leei as did inocula of < 50 in the same time (Fig. 26). Reproduction was even more sharply reduced when the inocula were increased to 300 animals. In tracer feeding experiments individual animals in moderately large inocula (20-50 animals) ate twice as many algae as did fewer animals (5) fed the same amount of algae (Table 8). Feeding was not affected in the same way in S. hyalina even though reproduction was inhibited by large inocula (> 50; Fig. 27). Crowded animals (50-100) ate less than half the food eaten by uncrowded animals (Table 8).

An inoculum of 50 S. hyalina produce ~ 10% more cells than inocula of 10-25 and 20% more animals than when the inoculum is greater than 50 cells. Tracer feeding studies suggest that small populations of R. leei and S. hyalina have difficulty finding or collecting food cells. The rate of feeding in moderately crowded cultures (20-100 animals) was up to 100% greater than in uncrowded cultures (1-20 animals).

Interspecific competition

The growth of populations of each of the animals tested is affected differently by interspecific competition. The rate of

increase of A. laticollaris populations (r) is not changed by the presence of other foraminifera species but the final population size may be as little as 20% of controls (Fig. 28). The effect of competition of R. leei is different from that of S. hyalina. A. laticollaris populations in the former reach the levels of controls and then decline while in the latter populations are only half the level of monospecific controls. Tournament tracer feeding experiments help to explain these results (Table 8). R. leei strongly affected the feeding rate of A. laticollaris. The feeding rate of A. laticollaris on its most important foods, Amphora sp (5), Amphora sp (RF-8), Phaeodactylum tricornutum (39), and Nannochloris sp (41) dropped to 39%, 23%, 71%, and 86% respectively. A. laticollaris ate less algae and more bacteria in the presence of S. hyalina. Reproduction of R. leei is delayed in the presence of A. laticollaris (Fig. 29). At the same time that the populations of A. laticollaris declined the rate of reproduction of R. leei became exponential. Maximum populations of R. leei in the presence of A. laticollaris is only 10% of controls. The presence of S. hyalina in R. leei cultures did not greatly affect its reproduction (Fig. 30). Tournament tracer feeding experiments also help to explain the results of population growth experiments (Table 8). Feeding by R. leei on its 2 most important food organisms, Amphora sp (5) and Chlamydomonas subehrenbergii (93), in the presence of optimum feeding populations of A. laticollaris was only 36-40% of controls whereas in the presence of S. hyalina it was 2.5-3.5 times that of controls. S. hyalina can not compete with either foraminifera in liquid culture (Fig. 30). Reproduction was observed only on agar slopes. (The agar was used to stimulate bacterial populations). On agar, reproduction was delayed. In tracer experiments feeding on Amphora sp (5), the only alga eaten in significant amounts by S. hyalina, was reduced to only 39% of controls in the presence of A. laticollaris populations and ~ 22% with R. leei. Feeding on bacteria was also strongly inhibited.

DISCUSSION

Many studies (Connell, 1961; Gause and Witt, 1935; MacArthur, 1958; Park, 1962) have demonstrated that minute differences in one or a few niche parameters, of closely related species, is sufficient to separate their niches.

Of the 6 biotic and abiotic factors considered by Monod (1949) as key limiting growth factors for microorganisms, the abiotic factors seem least important for the growth of the organisms under study. The results support the suggestion made by many workers (Bradshaw, 1961; Lee et al., 1966; Muller and Lee, 1969) that the niches of foraminifera are separated by small differences in the biotic rather than the physical niche. Many students have reported that most species of foraminifera survive and reproduce within wide ranges of temperature, salinity, and pH (Arnold, 1964,1966; Bradshaw, 1957, 1961; Lee et al., 1963,1970; Muller and Lee, 1969; Murray, 1963; Myers, 1937, 1943). Bradshaw (1957) reported that Ammonia beccarii, perhaps the most commonly studied and widely distributed species, survives temperatures of 10-35 C and salinities of 7-67 ‰. The 3 species of foraminifera used in the present study also survive within similar ranges of these abiotic factors, no doubt an adaptation to the littoral and sublittoral habitat in which they naturally occur. This is not meant to exclude the importance of the physical factors. They delineate which of the thousands of the species of foraminifera can potentially grow in the marsh. The biotic factors, including adaptation to the random colonization and succession within patches of food organisms of the littoral community (Lee et al, 1972), seem to more strongly influence niche dimensions.

Unlike the physical factors which are easily evaluated by means of their effects on generation time (Phleger, 1960) or on population growth (Arnold, 1954, 1964, 1966; Bradshaw, 1955, 1957, 1961; Lee et al., 1961, 1963; Lee and Pierce, 1963; Muller and Lee, 1969) the biotic factors must be evaluated by more sophisticated procedures. As an example, the data from tracer feeding experiments in the present study had to be summarized in a form which could be mathematically manipulated. The interspecific competition coefficient

was devised as a means for evaluating feeding competition. The coefficient has potential for wider application. The calculation includes the rate of feeding by a single species as well as the effects of competition from other species. Although we know very little of the feeding patterns of foraminifera it is likely that there are unknown complexities similar to those found in other meiofauna (Provasoli et al., 1959; Tietjen et al., 1970). The foraminifera which have been studied gnotobiotically grow better on mixed algal and bacterial diets than they do on more restricted diets (Lee and McEnery, 1970; Lee et al., 1966, 1969 a, 1970; Muller and Lee, 1969; Pierce, 1965). Some bacteria in the diet seems essential for the growth and reproduction of all of the species studied so far. The effect of peptone on the growth and survival of the 3 species of foraminifera used in the present study suggests still another dimension of niche and offers a possible explanation for the recent disappearance of these organisms from many coastal regions. All 3 species eat some bacteria but are inhibited by exposure to large numbers of bacteria or their growth products. R. leei is primarily an algal feeder and was inhibited the most by growth in peptone enriched media. Both A. laticollaris and S. hyalina eat considerable numbers of bacteria so it is understandable that the low concentrations of peptone which favor the growth of the bacteria which they eat would also enhance or at least not inhibit their growth. With an enrichment of 0.01 mg% peptone the growth and reproduction of A. laticollaris was 125% of growth obtained in unenriched media (Table 5). Reproduction of S. hyalina was slightly inhibited (90%) at the same concentration. Although not tested, it seems possible that at lower concentrations of peptone growth of S. hyalina would also be enhanced. The equation makes provision for the inclusion of such subtleties and, in fact, its accuracy of expression is improved with their addition.

With these considerations in mind, one can estimate the niche width of specific species of foraminifera and compare these estimates to those which could be gleaned from field studies alone (Bradshaw, 1968; Buzas, 1969; Lee et al., 1969 b; Matera and Lee, 1972; Redfield, 1959). Although some observations from the Towd Point

marsh are available, the physical field data from these studies is not as extensive as would be desirable for niche width estimations. For example, the water temperature at Towd Point varies in the summer from ~ 17-30 C (Lee et al., 1969 b; Matera and Lee, 1972). Systematic measurements at other seasons have not been made but the water temperature generally drops 10 C or less from late November through March. Ice usually forms on the surface of the marsh during December, January, and February. Salinity varies greatly depending upon the weather and tidal cycle. The general range of salinity at Towd Point in a normal summer is ~ 13-30 ‰ (Lee et al., 1969 b; Matera and Lee, 1972), although the salinity may exceed 50 ‰ in isolated tide pools on hot sunny days. With the same reservations, it seems fair to assume that for analytical purposes the data from other comparable marshes, shallow bays, and rivers can also be used for general extrapolation (Bradshaw, 1968; Buzas, 1969; Redfield, 1959). The daily dynamic ranges of environmental variables are considerable. Bradshaw (1968) in his study of the Mission Bay, California marsh, one which is rich in foraminiferan fauna, has drawn attention to the daily and annual stresses to which salt marsh foraminifera are subjected. The pH fluctuated from 6.8 at night to 8.5 during the day. In this marsh the pH was < 7.6 for more than half the day. At pH 7.6 or less $CaCO_3$ tends to dissolve so that the foraminifera must be expending considerable energy to build or maintain their tests. Temperature ranged annually from 12.7 - 24.1 C and salinity from 25-50 ‰ in the same marsh. Buzas (1969) studied the relationship of environmental variables to the distribution of several common littoral foraminifera in the Choptank River, part of the Chesapeake Bay estuarine system. For 1 station that was located in the bay temperatures ranged from a minimum of 1.02 C to a maximum of 26.2 C, salinity varied from 12.02 - 16.52 ‰, and oxygen levels were as low as 4.3 mg/1 in June and July and as high as 15.5 mg/1 in January. Values for pH changes were not tested. The 3 species of foraminifera used in this study were able to reproduce in the laboratory within wider ranges of these abiotic factors than in any of the previously described estuaries (Figs. 2 and 3; Table 1). Allogromia laticollaris

reproduced at temperatures of 10-33 C, salinities of 19-45 ‰, and a wide pH range (pH 5.0-9.5). The other 2 species tested seemed to have similar tolerances. R. leei reproduced at temperatures as low as 14 C and as high as 32 C, and at salinities from 18-50 ‰. R. leei can reproduce at pH 6.5 in spite of the fact that they must use energy to maintain their test. Reproduction of S. hyalina is most affected by pH. The lower limit of reproduction is pH 6.0 and the upper limit is pH 8.0. The tolerance of low pH suggests that it could reproduce in sediments where pH can be reduced by bacterial activities. Thus each species of foraminifera tested in the present study can reproduce within a sufficiently wide range of each abiotic factor so that the opportunity for reproduction is available during much of the growing season.

Historically, data pertaining to abiotic tolerances of foraminifera have been used to qualitatively describe the ecology of the organisms. Bradshaw (1957, 1961) showed that unfavorable physical conditions delay reproduction in foraminifera but growth continues. Bradshaw (1957) concluded that when conditions were unfavorable for reproduction of Ammonia beccarii the organisms would continue to grow, adding more chambers than those which grew under more favorable physical conditions. Nicoll (1944) came to similar conclusions for Elphidium spp and stated that temperature may be the most important ecological factor. The evidence from Murray's (1963) experiments are derived from biotic, as well as abiotic studies. He concluded that foraminifera reproduce fastest when the physical environment is optimum, but explained that a shortage of food and calcium may limit their size and reproduction. The method devised in this study provides an alternative to these qualitative discussions and to the unidimensional treatment offered in previous niche descriptions (Gause, 1934; Gause and Witt, 1935; Levins, 1968; Maguire, 1967; McNaughton and Wolf, 1970; Whittaker, 1960) by employing those factors, physical and biological, which are thought to be most important (Bradshaw, 1957, 1961; Lee et al., 1963, 1966; Muller and Lee, 1969) and representing them graphically. The polygonal method makes it easy to compare the niches of species. This

type of multidimensional analysis is consistent with the Hutchinsonian (1958) conceptualization of niche theory. The method of computation is generalized enough to be useful in the characterization of the niche of any species at any trophic level because the representation permits the simultaneous evaluation of many niche factors. In this respect, the procedure goes beyond the single parameter mathematics suggested by many (Levins, 1968; McNaughton and Wolf, 1970; Whittaker, 1960). A most recent attempt (Green, 1971) compares several factors but uses only 2 of these in any given analysis. Green's model is difficult to understand because he does not offer a single graphic summary of the niches of his organisms, although his method provides us with considerable ecological data. In the method presented here, the primary niche dimensions for each experimental organism are plotted so that a meaningful polygonal graphic representation of the niche is formed.

The relationships between the areas of the niche polygons for each foraminifer used in the present study are similar regardless of whether the eccentric or central model is used (Table 9). In both systems the area of the A. laticollaris polygon is almost as large as the R. leei polygon. For example, using the central model the area of the A. laticollaris polygon is 32.48% total theoretical niche area, while the area of the R. leei polygon is 32.32% total niche area. The areas of both polygons are remarkably similar to that which was estimated for the cosmopolitan generalist Ammonia beccarii (37.2% total theoretical niche area). However, the A. laticollaris polygon is not as evenly distributed about the niche epicenter as are those of R. leei and A. beccarii (Figs. 31 and 31 a). The A. laticollaris polygon is skewed by high tolerances to physical factors and a relatively low competitive ability. Reproduction is inhibited by crowding (Fig. 25) and in spite of the fact that the interspecific competition coefficient is large (0.69), studies show that populations of A. laticollaris decline in competition with other species of foraminifera (Fig. 28). Since A. laticollaris grows best on mixtures of foods, including algae and bacteria (Lee et al., 1966; Lee and McEnery, 1970; Muller and Lee, 1969), but

competes poorly, the organism would be at a disadvantage in a crowded complex epiphytic community.

The regularity of the R. leei polygon reflects its competitive ability (Figs. 32 and 32 a). This species is relatively unaffected by crowding (Fig. 26) and in competition with other species of foraminifera feeding is sometimes enhanced (Table 8). This results in an increase in the reproduction of R. leei and a decline in the numbers of competing species (Fig. 29).

The conspicuous irregularities of the S. hyalina polygon suggest that the organism has a very specialized niche and does not compete well, physically or biologically, with the other salt marsh foraminifera (Figs. 33 and 33 a). The irregularities are principally the result of the low interspecific competition coefficient (0.25) which was the lowest of all the species tested (Table 1). The interspecific competition coefficient falls so far to the left of the niche epicenter that the niche polygon is divided into 2 sections. Thus, the S. hyalina polygon has the smallest area (19.38% total theoretcial niche area) of the species tested (Table 9). Competition experiments provide additional evidence that S. hyalina can not compete with other species of foraminifera. In the presence of other species of foraminifera reproduction is strongly inhibited, and in some cases, the populations of S. hyalina are completely replaced (Fig. 30). The growth and reproduction of S. hyalina are probably dependent upon the very specialized conditions which might inhibit the growth of other species of foraminifera. The species is small (10-50 μ) and it can live in and under debris and in the sediments where localized blooms have been observed by the author. The likelihood of abundant unicellular algae in such places is small since there is little light available. The nutritional requirements of S. hyalina are different from the other species tested. Although small amounts of algae are eaten the species can be cultured synxenically with bacteria only (Muller and Lee, 1969). The inability of this species to compete for algal food with the other 2 species tested is still another line of evidence suggesting trophic aspects of niche separation (Table 8).

None of the 3 species is dominant in the field (Lee et al., 1969 b; Matera and Lee, 1972). Small numbers of R. leei and S. hyalina were found during the 3 summer seasons which were surveyed. R. leei was approximately 43 times more abundant than S. hyalina. Blooms of A. laticollaris were found following a prolonged drought suggesting that A. laticollaris is a rare safety valve species which can multiply rapidly and fill the niches that are vacated by the declining populations of dominant forms. In the Towd Point marsh their reproduction is probably inhibited by competing species while in gnotobiotic laboratory culture, their large biotic potential can produce abundant populations in a short period of time (Fig. 13). The results of this study support available untested hypotheses concerning the niches of these 3 species of foraminifera (Lee et al., 1969 b; Matera and Lee, 1972). Since A. laticollaris has broad physical tolerances its large biotic potential was realized when competition was minimized by environmental stress. S. hyalina occurs with the same frequency as A. laticollaris under normal conditions but is rare at other times too. The present study suggests that S. hyalina is also a rare safety valve species, unable to compete with other foraminifera, but not inhibited by its own dense populations. Laboratory data can be used to interpret field observations on R. leei. At Towd Point R. leei occurs in moderate numbers. This species has the highest interspecific competition coefficient of the 3 species of foraminifera tested, and is not inhibited by crowding. It has a small biotic potential (Fig. 14) because of slow growth. Because of this large blooms of this species probably do not occur in the field. Field and laboratory data on Ammonia beccarii are comparable. It is the most widely distributed of all of the species studied. It has been observed as a littoral and sublittoral species in the temperate zones throughout the world (Phleger, 1960) though it has been suspected that physiological races of this species may occur (Bradshaw, 1957; Brooks, 1967; Buzas, 1969; Matera and Lee, 1972) the species, in general, is tolerant of a wide range of abiotic variables. Using Bradshaw's (1957) data on physical parameters and the present data on trophic dynamics (Fig. 34) the niche width of this species can also be

estimated (Figs. 35 and 35 a). It has the largest niche of any of the foraminifera tested and provides substantiating evidence for the validity of the polygon system for niche width determination.

The present study has obvious limitations. No attempt was made to study the interaction of the individual species of foraminifera with a large variety of foraminifera or with other organisms on the same trophic level such as amoeba, ciliates, rotifers, or nematodes. If this is done the characterization of the Hutchinsonian niche will be even more precise and it should be possible to interpret natural phenomena more closely and design predictive laboratory experiments. One can envision the day, in the not too distant future, when the niche parameters of organisms may be so precisely understood and measured that several dozen dimensions will be used in niche analysis. Rotating the polygon 360 degrees will provide the flexibility and space for manipulating 20 or 30 dimensions in an analysis of niche width.

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TABLE 1

Summary of niche parameters

	Allogromia		Rosalina		Spiroloculina	
	reproductive range	optimum	reproductive range	optimum	reproductive range	optimum
Temperature (°C)	10-33	21.5	14-32	23	12-33	22.5
Salinity (‰)	19-45	32	18-50	34	12-45	26
pH	5.0-9.5	7.25	6.5-10	8.25	6.0-8.0	7.00
Feeding rate (# cells/f/day)	$10-10^7$	$50x10^5$	$5x10^2-10^7$	$\sim 5x10^6$	$5x10^2-10^7$	$\sim 5x10^6$
Inoculum size (before crowding)	1-75	38	25-150	87.5	25-150	87.5
Intraspecific Competition Coefficient	0-0.69	0.345	0-0.74	0.370	0-0.25	0.120

TABLE 2

The effect of temperature on the growth of axenic food cells

Algal Strain #	Maximum Growth (100%)	TEMPERATURE (°C) 5	10	15	20	25	30	35
39	2×10^6	<1	15	35	45	75	100	1
5	2×10^6	1	15	35	45	75	100	1
41	2×10^6	1	15	35	45	75	100	1
RF-8	2×10^6	1	15	35	45	75	100	1
93	6×10^5	10	66	90	100	80	60	1
38	6×10^5	10	66	90	100	80	60	1
8	9×10^5	0	<1	3	22	77	1	0
Pb-13	2×10^5	1	35	90	100	40	1	0
BL-27	2×10^5	1	35	90	100	40	1	0
Pb-6	3×10^4	1	100	100	100	100	100	1
Bacteria Strain #								
A5-6	3×10^8	7	10	80	100	100	80	8
A5-7	3×10^8	7	10	80	100	100	80	8
D1-701	3×10^8	7	10	80	100	100	80	8
A5-703	3×10^7	66	100	100	100	100	100	80
D5-702	3×10^7	66	100	100	100	100	100	80
D2-7	3×10^7	66	100	100	100	100	100	80
C1-704	3×10^7	66	100	100	100	100	100	80
A1-711	5×10^7	5	10	50	75	90	100	20
A3-111	9×10^7	0	0	<1	<1	2	30	100
D2-703	9×10^7	0	0	<1	<1	2	30	100

TABLE 3

The effect of salinity on the growth of axenic food cells

Algal Strain #	Maximum growth (100%)	Salinity (‰) and % Maximum Growth							
		0	10	20	30	40	50	60	70
41	1×10^7	0	50	100	100	100	60	1	0
8	1×10^7	0	50	100	100	100	60	1	0
38	1×10^7	0	50	100	100	100	60	1	0
93	5×10^5	0	60	75	100	100	75	1	0
5	5×10^5	0	60	75	100	100	75	1	0
RF-8	1×10^6	0	10	<1	100	40	1	0	0
BL-27	1×10^6	0	10	<1	100	40	1	0	0
Pb-6	1×10^6	0	10	<1	100	40	1	0	0
Pb-13	1×10^6	0	10	<1	100	40	1	0	0
39	5×10^4	1	40	75	90	50	30	10	0
Bacteria Strain #									
D1-701	4×10^8	0	60	100	100	100	100	100	10
A5-6	4×10^8	0	60	100	100	100	100	100	10
A5-7	4×10^8	0	60	100	100	100	100	100	10
A5-703	3×10^8	0	2	16	90	80	50	10	0
A1-711	3×10^8	0	2	16	90	80	50	10	0
D2-703	9×10^7	0	50	100	100	100	50	10	0
C1-704	9×10^7	0	50	100	100	100	50	10	0
A3-111	9×10^7	0	50	100	100	100	50	10	0
D2-7	4×10^7	1	100	100	100	100	100	10	0
D5-702	4×10^7	1	100	100	100	100	100	10	0

TABLE 4

The effect of pH on the growth of food cells

Algal Strain #	Maximum growth (100%)	pH and % Maximum Growth 2	3	4	5	6	7	8	9	10
39	3×10^7	0	1	2	33	100	100	100	1	0
RF-8	3×10^6	0	1	90	100	100	100	100	10	1
39	3×10^6	0	1	90	100	100	100	100	10	1
Pb-6	3×10^6	0	1	90	100	100	100	100	10	1
Pb-13	3×10^6	0	1	90	100	100	100	100	10	1
BL-27	3×10^6	0	1	90	100	100	100	100	10	1
8	3×10^6	0	1	90	100	100	100	100	10	1
41	6×10^6	0	<1	3	13	33	83	95	1	0
93	2×10^5	0	<1	40	100	100	100	100	1	0
5	2×10^5	0	<1	40	100	100	100	100	1	0
Bacteria Strain #										
C1-704	5×10^8	0	0	<1	10	80	100	90	50	10
A5-7	5×10^8	0	0	<1	10	80	100	90	50	10
A5-6	5×10^8	0	0	<1	10	80	100	90	50	10
A3-111	5×10^8	0	0	<1	10	80	100	90	50	10
D1-701	2×10^8	0	0	10	20	100	100	95	60	10
A5-703	8×10^7	0	0	10	20	75	100	75	10	0
D2-7	8×10^7	0	0	10	20	75	100	75	10	0
D5-702	5×10^8	0	0	<1	10	70	100	70	10	0
A1-711	5×10^8	0	0	<1	10	70	100	70	10	0
D2-703	5×10^8	0	0	<1	10	70	100	70	10	0

TABLE 5

The effect of organics on the growth of foraminifera

mg Peptone	% of control		
	A. laticollaris	R. leei	S. hyalina
control	2600	1300	3700
0.01	126 %	<1 %	90 %
0.02	35	0	41
0.03	42	0	29
0.04	40	0	35
0.05	40	0	38
0.06	25	0	12
0.07	34	0	10
0.08	39	0	20
0.09	19	0	5
0.10	20	0	1
0.20	25	0	0
0.30	1	0	0
0.40	1	0	0
0.50	0	0	0
0.60	0	0	0
0.70	0	0	0
0.80	0	0	0
0.90	0	0	0
1.0	0	0	0
2.0	0	0	0

TABLE 6

The effect of organics on the growth of axenic food organisms*

Algal Strain #	Maximum Growth (100%)	% Peptone (W/V) 1×10^{-6}	1×10^{-5}	1×10^{-4}	1×10^{-3}
93	7×10^6	1	10	100	1
41	7×10^6	1	10	100	1
38	7×10^6	1	10	100	1
Pb-13	9×10^6	10	100	10	0
B1-27	9×10^6	10	100	10	0
8	9×10^6	10	100	10	0
39	9×10^6	10	100	10	0
5	9×10^6	10	100	10	0
RF-8	8×10^5	70	100	10	0
Pb-6	8×10^5	70	100	10	0
Bacteria Strain #					
A5-6	3×10^8	<1	1	90	1
A5-7	3×10^8	<1	1	90	1
D1-701	3×10^8	<1	1	90	1
C1-704	3×10^8	<1	1	90	1
A1-711	3×10^8	<1	1	90	1
D2-703	3×10^8	<1	1	90	1
A5-703	2×10^6	10	10	100	<1
D2-7	2×10^6	10	10	100	<1
A3-111	2×10^6	10	10	100	<1
D5-702	2×10^6	10	10	100	<1

* % Maximum growth

TABLE 7

The feeding rate of three species of foraminifera on selected species of bacteria (1×10^{-6} mg)

Bacteria	A. laticollaris	R. leei	S. hyalina
D1-701	3.4	0.6	0.5
D5-702	0.9	0.1	0.4
A5-7	1.6	0.3	0.9
A5-6	1.0	0.2	0.4
D2-7	1.4	0.3	0.2
A1-711	2.1	0.7	1.0
A5-703	8.7	0.2	0.5
D5-703	0.5	0.2	0.3
C1-704	1.8	0.2	0.3
A3-111	0.8	0.2	0.5

Table 8

The effect of interspecific competition on the feeding of three species of foraminifera

	Allogromia laticollaris			Rosalina leei			Spiroloculina hyalina		
Algae	# cells eaten /A. laticollaris/ day	% control in competition w/ R. leei	% control in competition w/ S. hyalina	# cells eaten /R. leei/day	% control in competition w/ A. laticollaris	% control in competition w/ S. hyalina	# cells eaten /S. hyalina/day	% control in competition w/ A. laticollaris	% control in competition w/ R. leei
RF-8	750	23	67	320	47	16	250	10	4
39	1400	71	44	300	33	250	600	33	18
5	2600	39	24	275	36	367	510	39	22
41	990	86	51	375	40	261	650	23	39
9	700	21	44	90	220	50	75	27	11
93	990	86	51	375	40	261	650	23	39
Bacteria									
D1-701	11440	55	87	1962	36	71	1615	37	26
D5-702	3153	32	68	339	65	89	1308	12	17
A5-7	5361	69	187	1007	40	159	3106	29	42
A5-6	3358	07	155	517	87	135	1334	11	38

TABLE 9

The calculation of niche width using the eccentric and central model graphic

Foram species	Eccentric model OA/TA = N.W.*	Niche width (%)	Central model OA/TA = N.W.	Niche width(%)
A. laticollaris	21.16/50.24	42.16	16/32/50.24	32.48
R. leei	20.34/50.24	40.48	16.24/50.24	32.32
S. hyalina	13.41/50.24	26.69	9.74/50.24	19.38
A. beccarii	22.13/50.24	44.05	18.69/50.24	37.20

* OA = observed area
TA = total theoretical niche area
NW = niche width

Table 10

Species of algae used in feeding experiments

Name	Strain number
Diatoms	
Amphora sp	RF-8
Amphora sp	5
Amphora sp	B1-45
Amphora ovalis var. *affinis*	B1-20
Nitzschia acicularis	8
Nitzschia rhombica	Pb-6
Nitzschia apiculata	Pb-13
Nitzschia sp (f) new species	123
Cylindrotheca closterium	9, B1-35
Cylindrotheca fusiformis	B1-27
Phaeodactylum tricornutum	39
Chlorophytes	
Dunaliella parva	14, 96
Dunaliella salina	13
Dunaliella quartolecta	50
Nannochloris sp	41
Chlorococcum sp	38
Chlamydomonas subehrenbergii	93

Figure 1 Six-dimension eccentric model of a potential niche

p = center of the circle

o = intersection of parameter lines

DZ = diameter

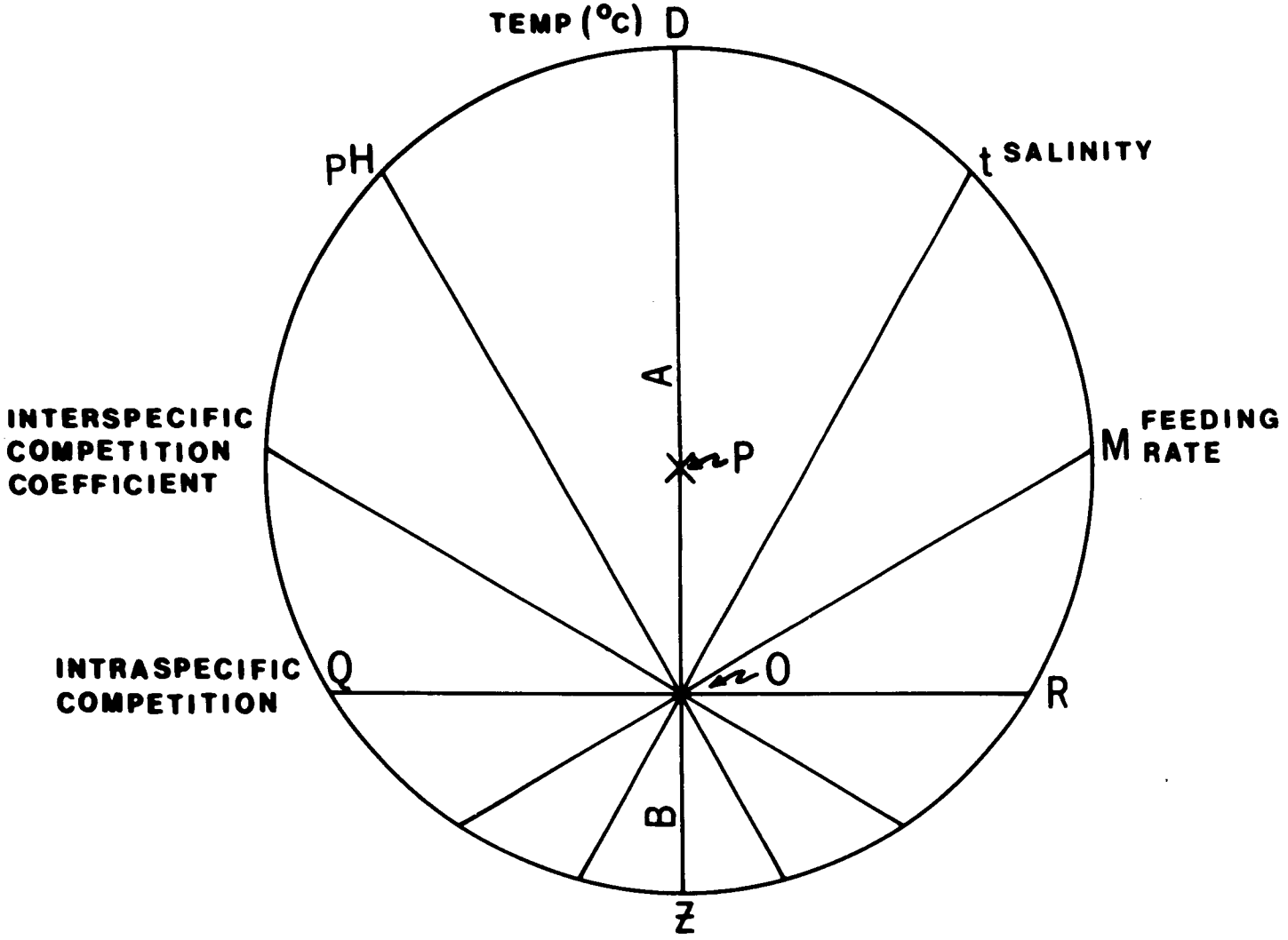

TEMP (°C) D
pH
t SALINITY
INTERSPECIFIC COMPETITION COEFFICIENT
A
P
M FEEDING RATE
INTRASPECIFIC COMPETITION
Q
O
R
B
N

Figure 1 a Six-dimension model of a potential niche

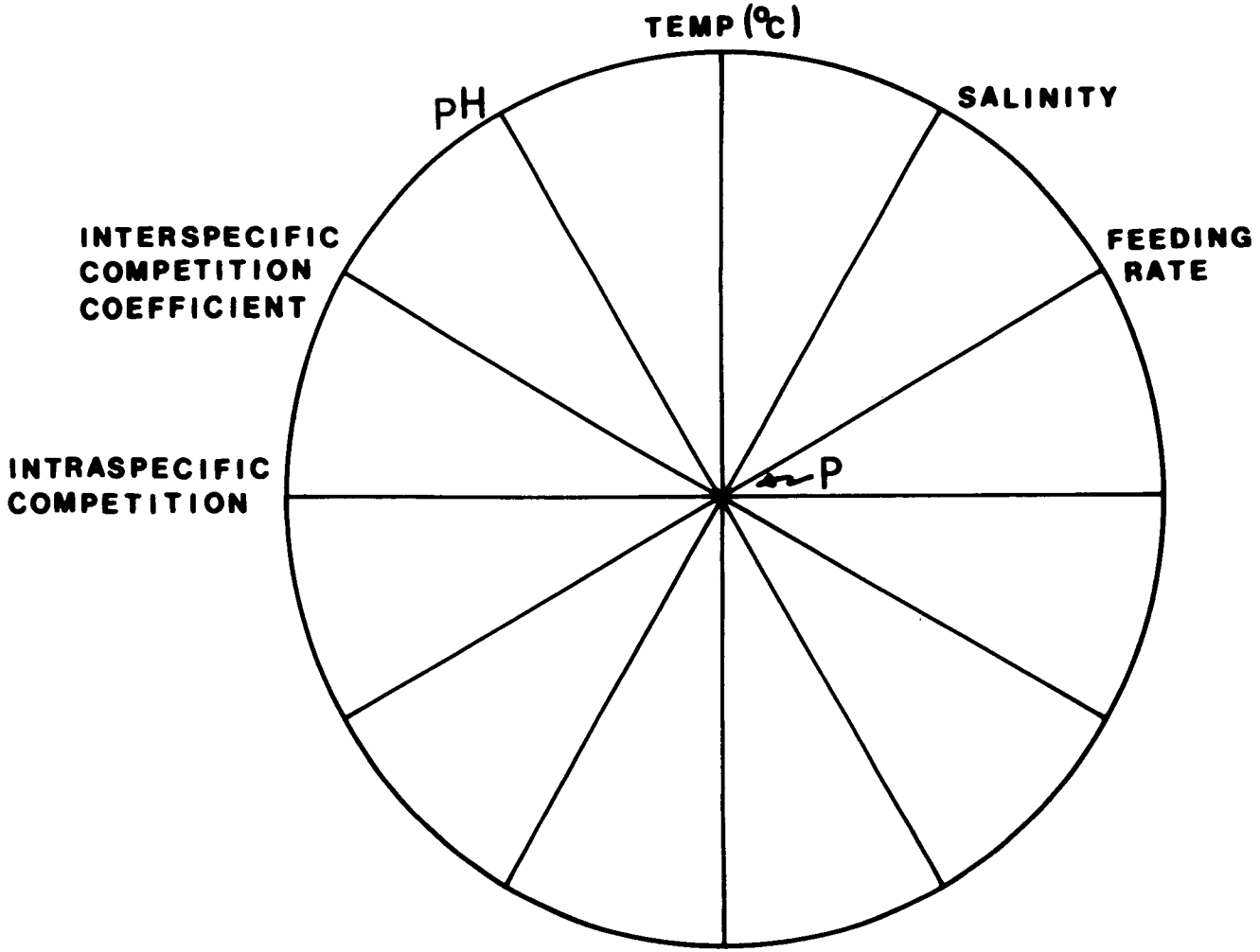

TEMP (°C)
SALINITY
FEEDING RATE
P
INTRASPECIFIC COMPETITION
INTERSPECIFIC COMPETITION COEFFICIENT
pH

Figure 2 The effect of temperature on the reproduction of 3 species of foraminifera

1 Spiroloculina hyalina

2 Allogromia laticollaris

3 Rosalina leei

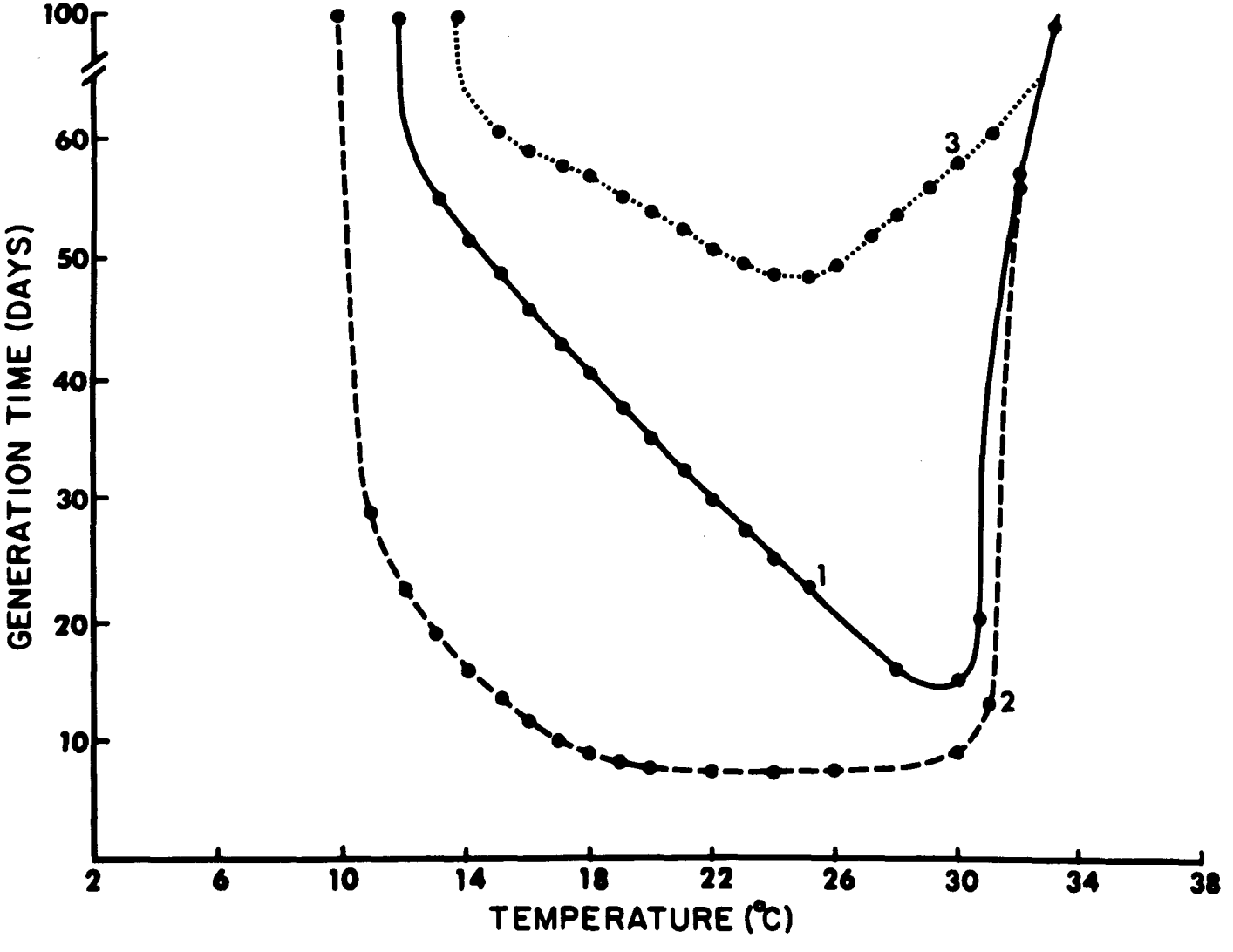

GENERATION TIME (DAYS)
100
60
50
40
30
20
10
2
6
10
14
18
22
26
30
34
38
TEMPERATURE (°C)
1
2
3

Figure 3 The effect of salinity on the reproduction of 3 species of foraminifera

1 Spiroloculina hyalina

2 Allogromia laticollaris

3 Rosalina leei

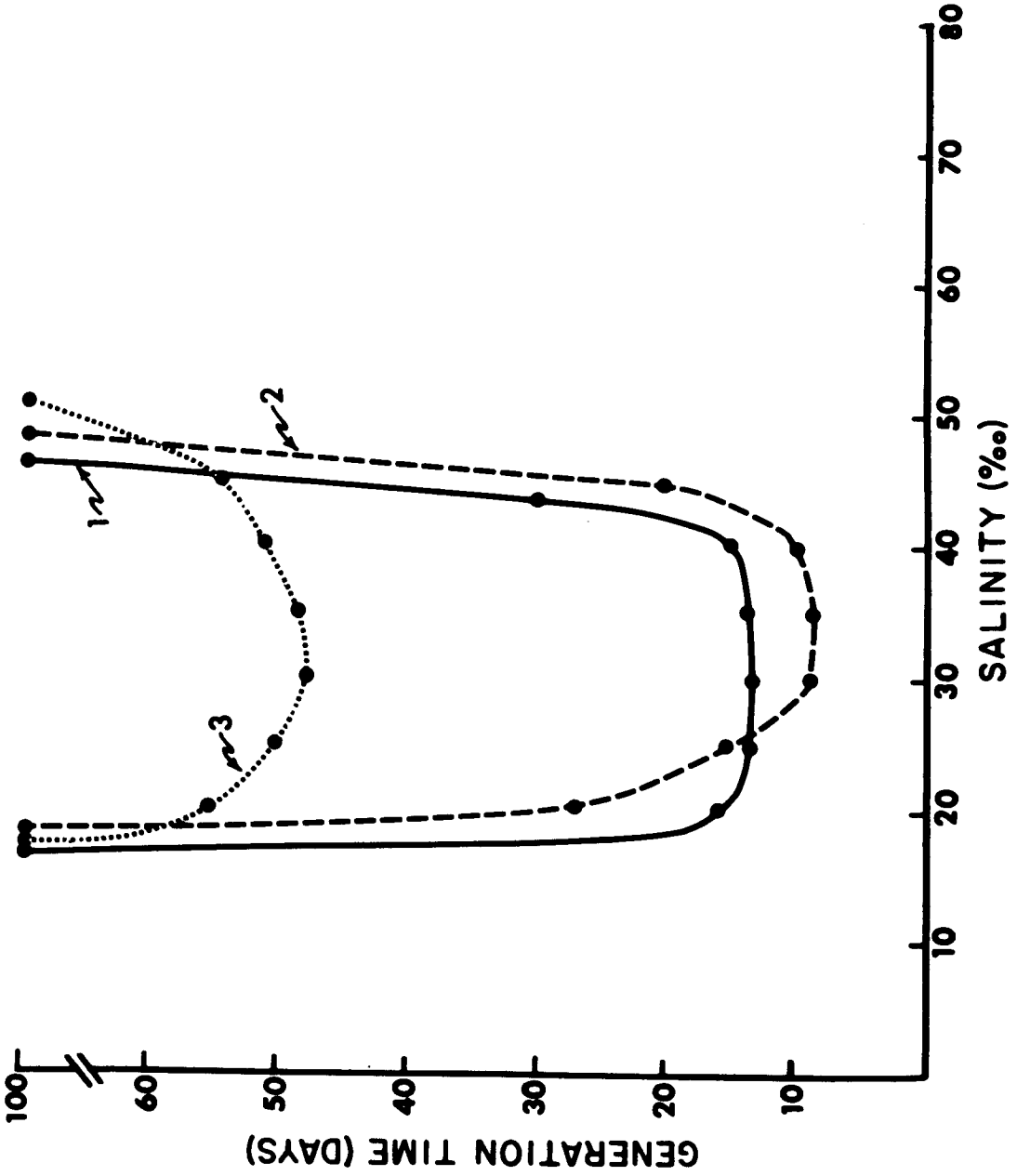

GENERATION TIME (DAYS)
100
60
50
40
30
20
10
SALINITY (‰)
10
20
30
40
50
60
70
80
1
2
3

Figure 4 The effect of pH on the reproduction of 3 species of foraminifera

1 Spiroloculina hyalina

2 Allogromia laticollaris

3 Rosalina leei

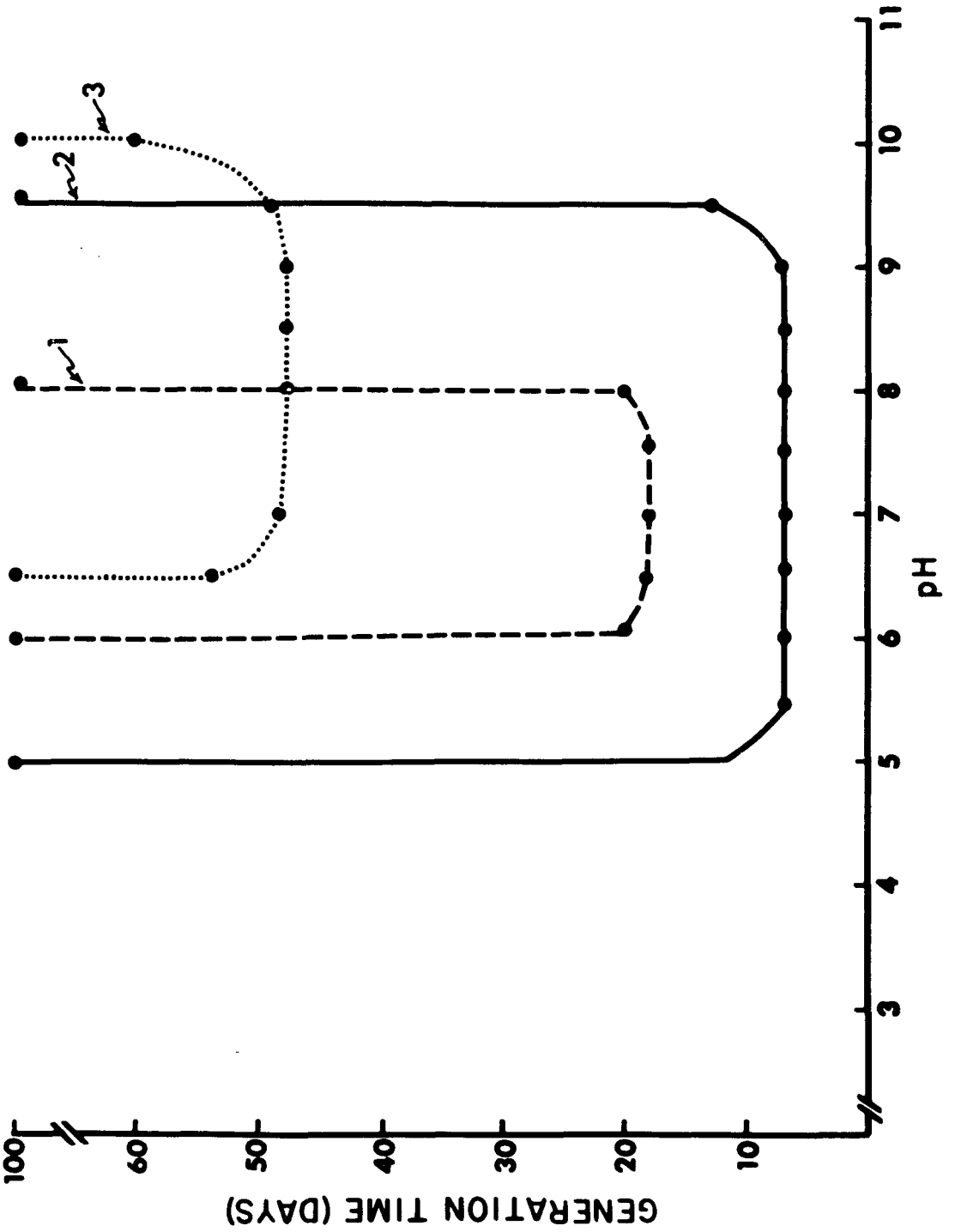

GENERATION TIME (DAYS)
100
60
50
40
30
20
10
3
4
5
6
7
8
9
10
11
pH
1
2
3

Figure 5 Oxygen consumption of 3 species of foraminifera as a function of temperature

1 Spiroloculina hyalina

2 Allogromia laticollaris

3 Rosalina leei

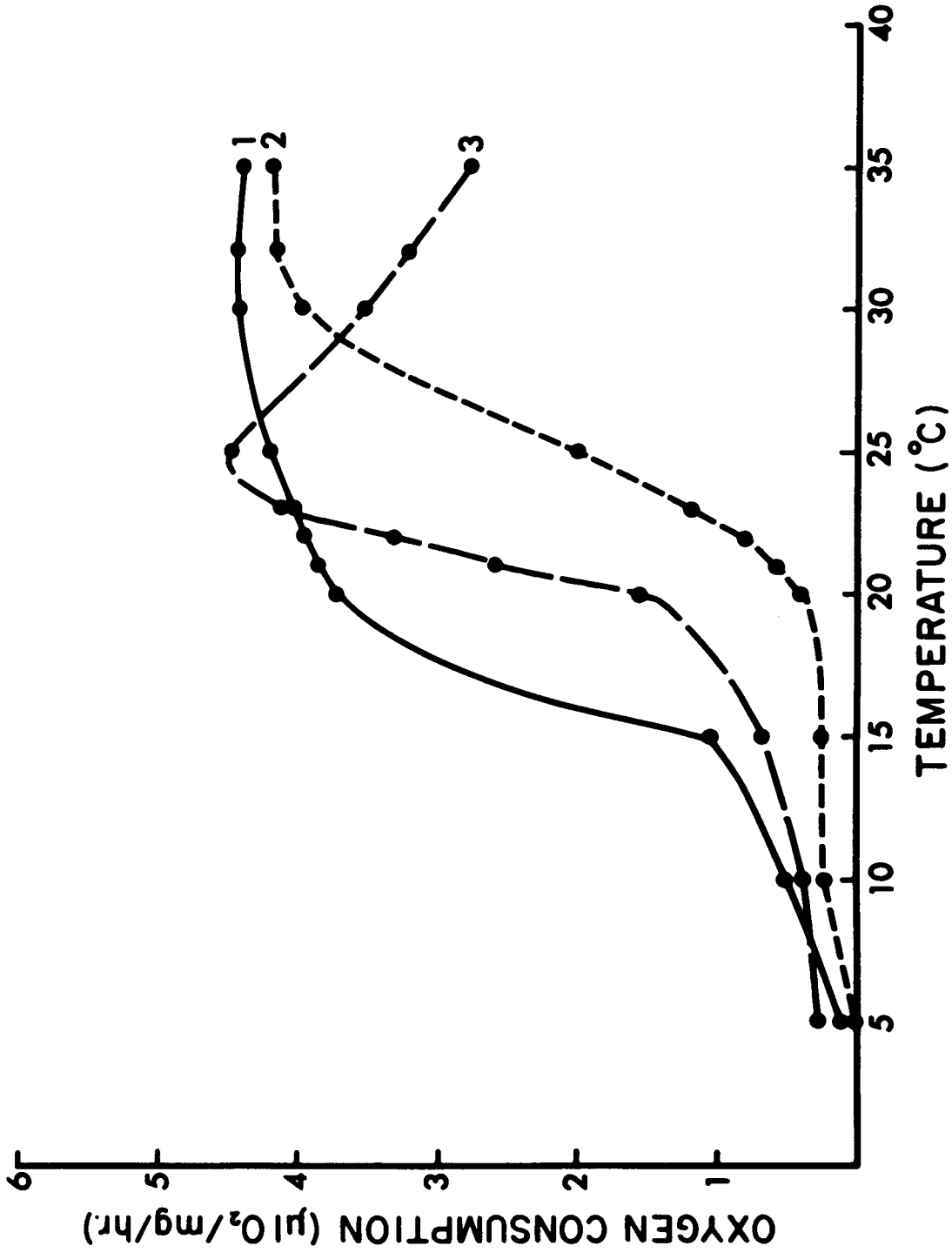

OXYGEN CONSUMPTION ($\mu l O_2$/mg/hr.)
1
2
3
4
5
6
TEMPERATURE (°C)
5
10
15
20
25
30
35
40
1
2
3

Figure 6 The effect of temperature and pH on the reproduction of Rosalina leei.

Curve	Temperature (°C)	$\int_L^{\mu_1} f_\mu \, d\,pH = \%\int_L^{\mu_1} f_{\mu+1} \, d\,pH$
f_1	30	100
f_2	25	72
f_3	20	41
f_4	10, 15	1

GENERATION TIME (DAYS)
10
20
30
40
50
60
70
80
100
pH
2
3
4
5
6
7
8
9
10
11
f_{4-m}
f_{3-m}
f_{2-m}
f_1

59.

Figure 7 The effect of pH and salinity on the reproduction of Allogromia laticollaris.

Curve	pH	$\int_{L}^{pH} f_{\mu}\, d\,pH = \%\int_{L}^{pH} f_{\mu+1}\, d\,pH$
f_1	7.5-9.5	100
f_2	6.0-7.0	85
f_3	5.5	12

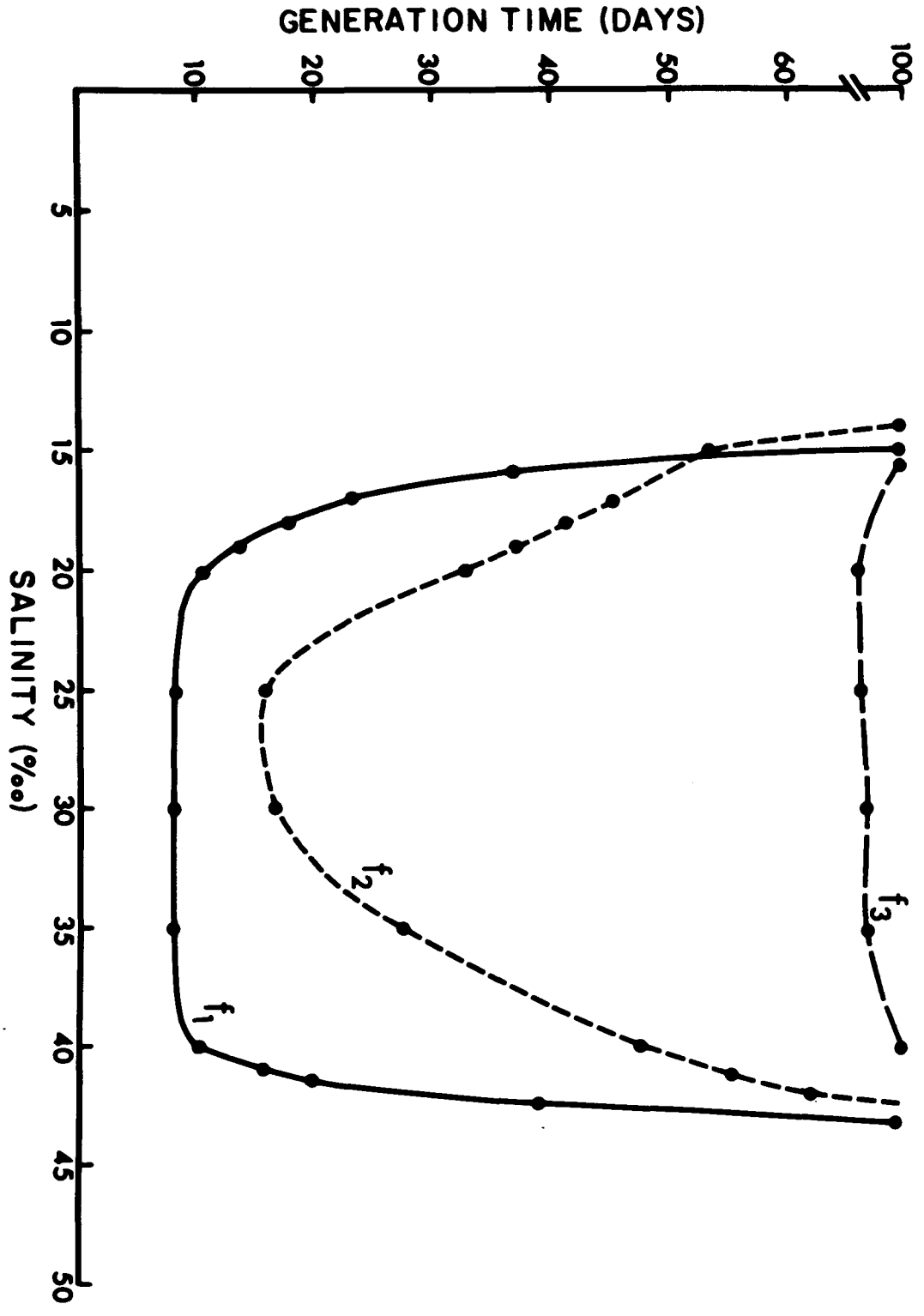

GENERATION TIME (DAYS)
10
20
30
40
50
60
100
SALINITY (‰)
5
10
15
20
25
30
35
40
45
50
f1
f2
f3

Figure 8 The effect of temperature and salinity on the reproduction of Allogromia laticollaris.

Curve	Temperature (°C)	$\int_{L}^{\mu_1} f_{\mu}\, d\,‰ = \%\int_{L}^{\mu_1} f_{\mu+1}\, d\,‰$
f_1	25	100
f_2	20	61
f_3	10	16

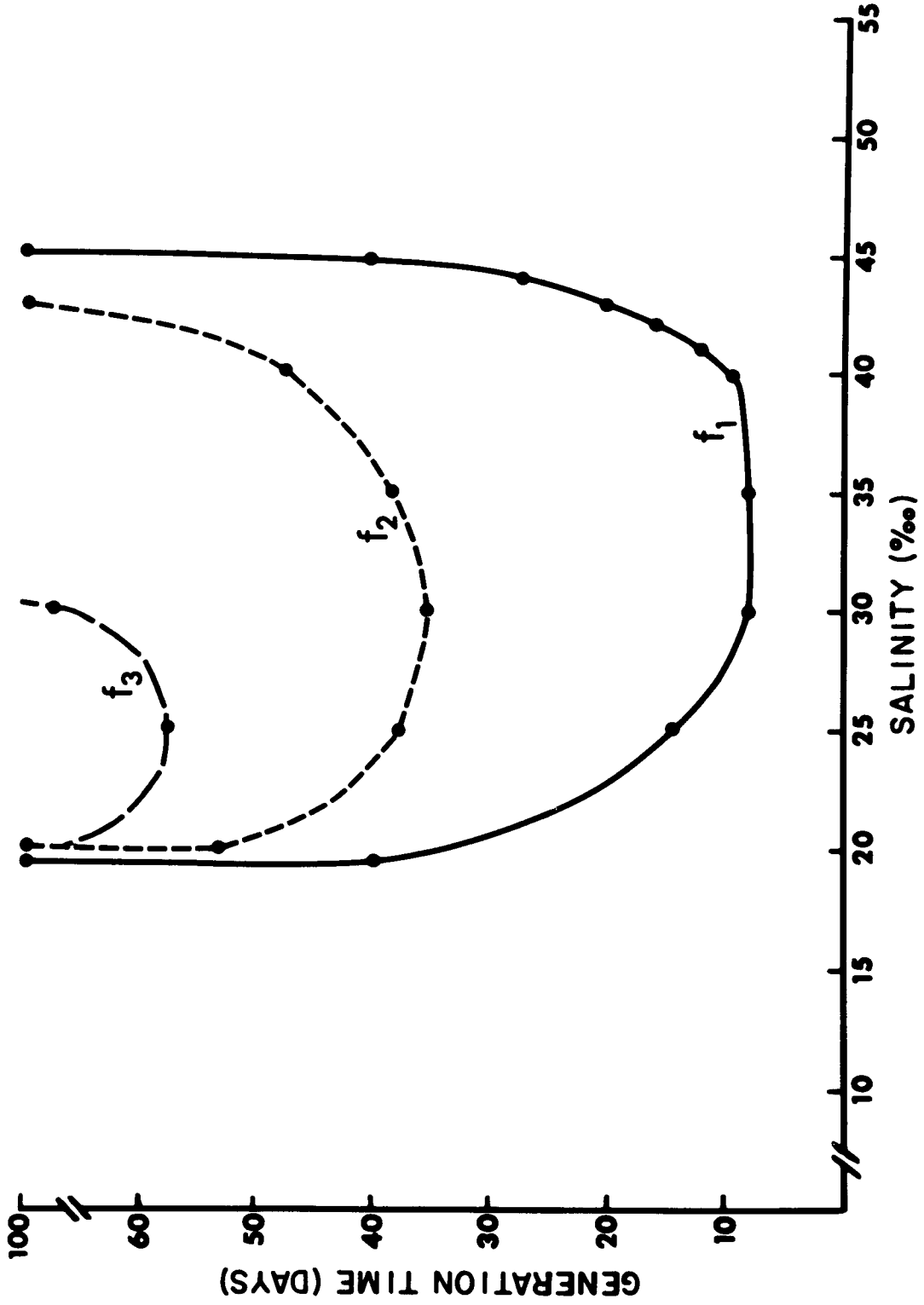

GENERATION TIME (DAYS)
100
60
50
40
30
20
10
SALINITY (‰)
10
15
20
25
30
35
40
45
50
55
f_1
f_2
f_3

Figure 9 The effect of temperature and pH on the reproduction of Allogromia laticollaris.

Curve	Temperature (°C)	$\int_{L}^{\mu_1} f_{\mu}\, d\,pH = \%\int_{L}^{\mu_1} f_{\mu+1}\, d\,pH$
f_1	25	100
f_2	30	
f_3	15,20	79
f_4	10	20

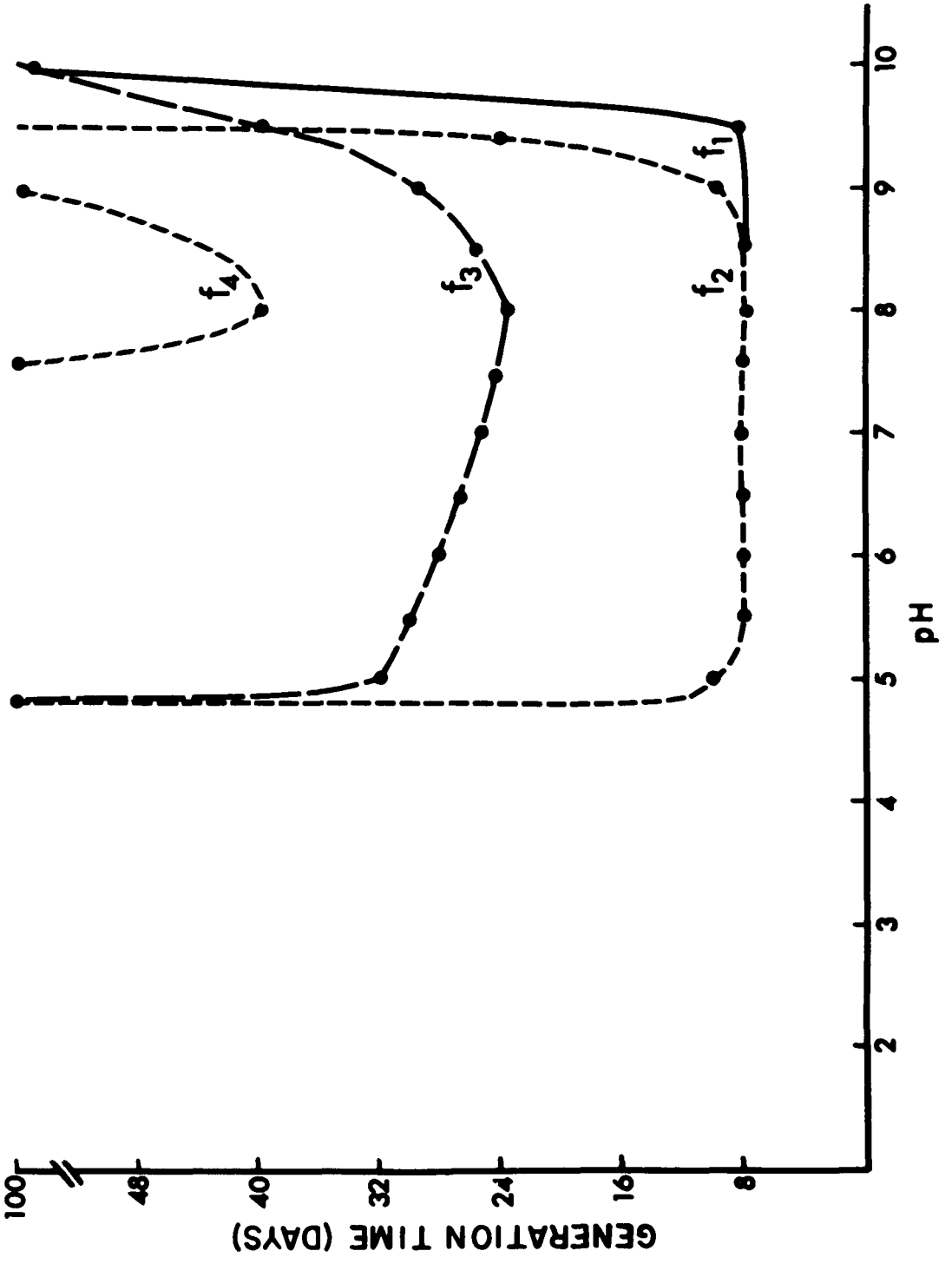

GENERATION TIME (DAYS)
100
48
40
32
24
16
8
2
3
4
5
6
7
8
9
10
pH
f_1
f_2
f_3
f_4

Figure 10 The effect of pH and salinity on the reproduction of Spiroloculina hyalina.

Curve	pH	$\int_{L}^{41} f_{\mu}\ d\ ‰ = \int_{L}^{41} f_{\mu+1}\ d\ ‰$
f_1	5.5-9.5	100
f_2	4.0-5.0, 10.0	69

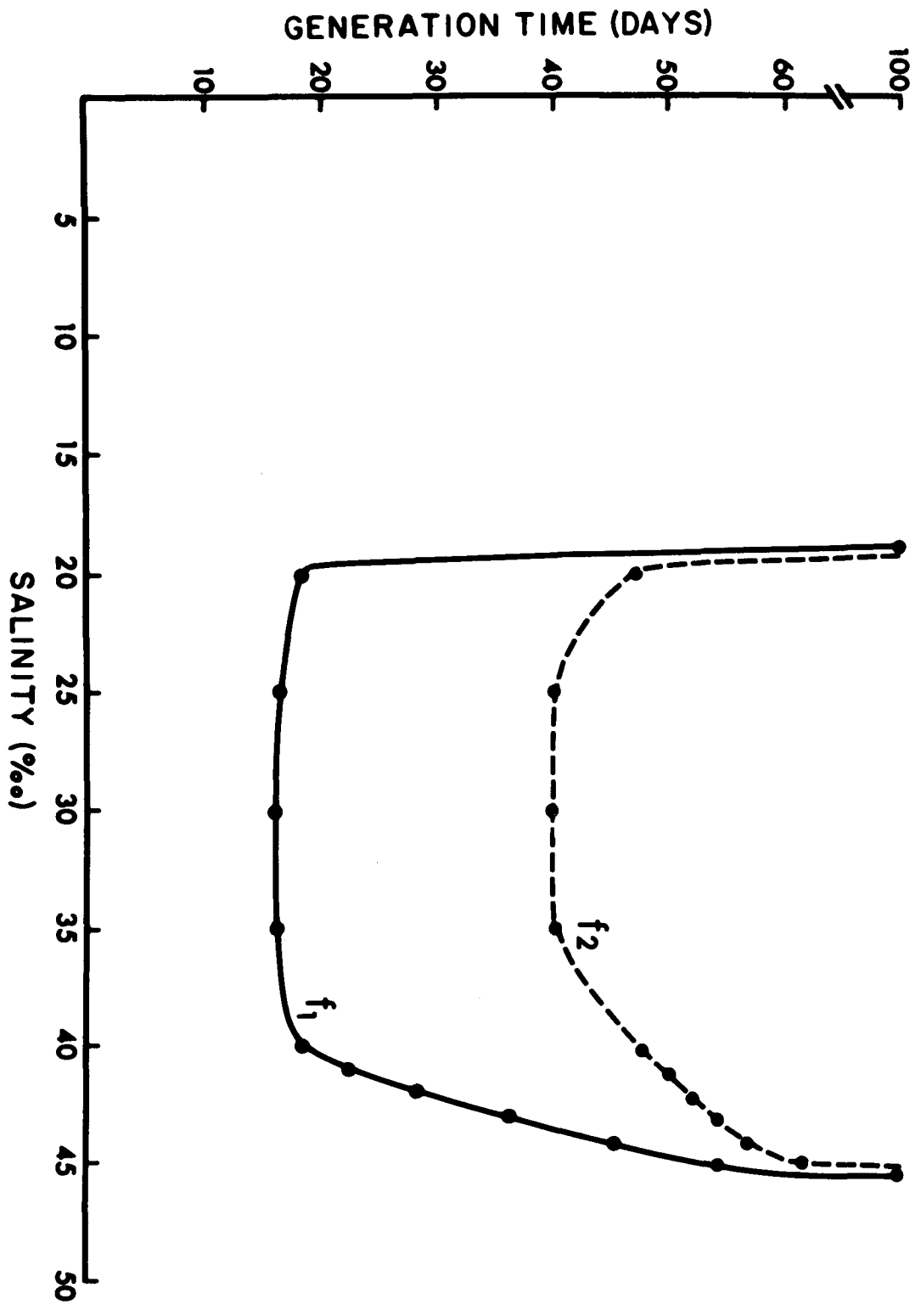

GENERATION TIME (DAYS)
10
20
30
40
50
60
100
SALINITY (‰)
5
10
15
20
25
30
35
40
45
50
f_1
f_2

Figure 11 The effect of temperature and salinity on the reproduction of Spiroloculina hyalina.

Curve	Temperature (°C)	$\int_L^{\mu} f_{\mu}\, d\,‰ = \%\int_L^{u} f_{\mu+1}\, d\,‰$
f_1	20, 25, 30	100
f_2	10,15	68

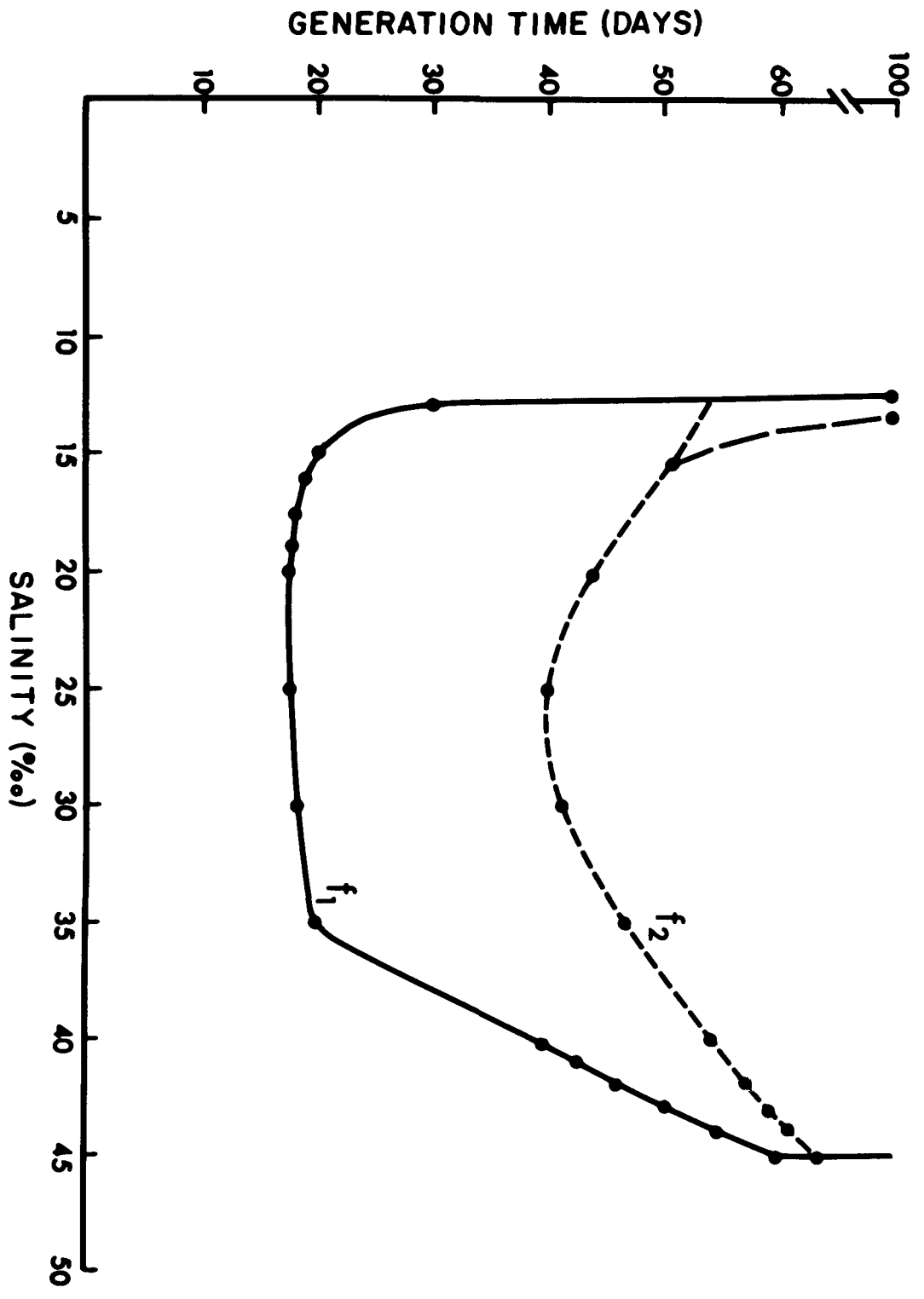

GENERATION TIME (DAYS)
10
20
30
40
50
60
100
SALINITY (‰)
5
10
15
20
25
30
35
40
45
50
f_1
f_2

Figure 12 The effect of temperature and pH on the reproduction of Spiroloculina hyalina.

Curve	Temperature	$\int_{L}^{u} f_{\mu}\, d\,pH = \%\int_{L}^{u} f_{\mu+1}\, d\,pH$
f_1	25, 30	100
f_2	10, 15, 20	80

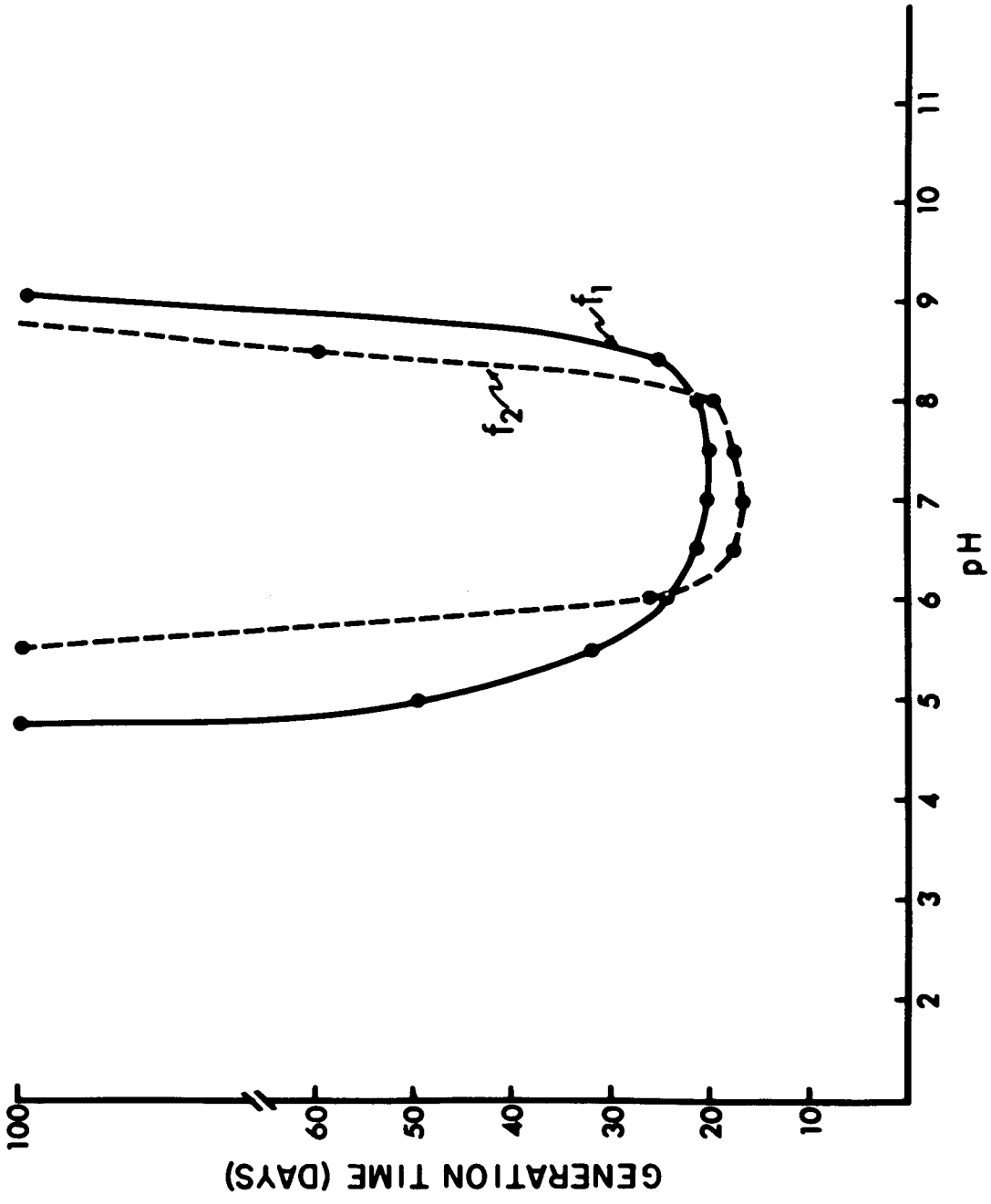

GENERATION TIME (DAYS)
100
60
50
40
30
20
10
2
3
4
5
6
7
8
9
10
11
pH
f_1
f_2

Figure 13 The intrinsic rate of increase of Allogromia laticollaris populations in synxenic laboratory culture.

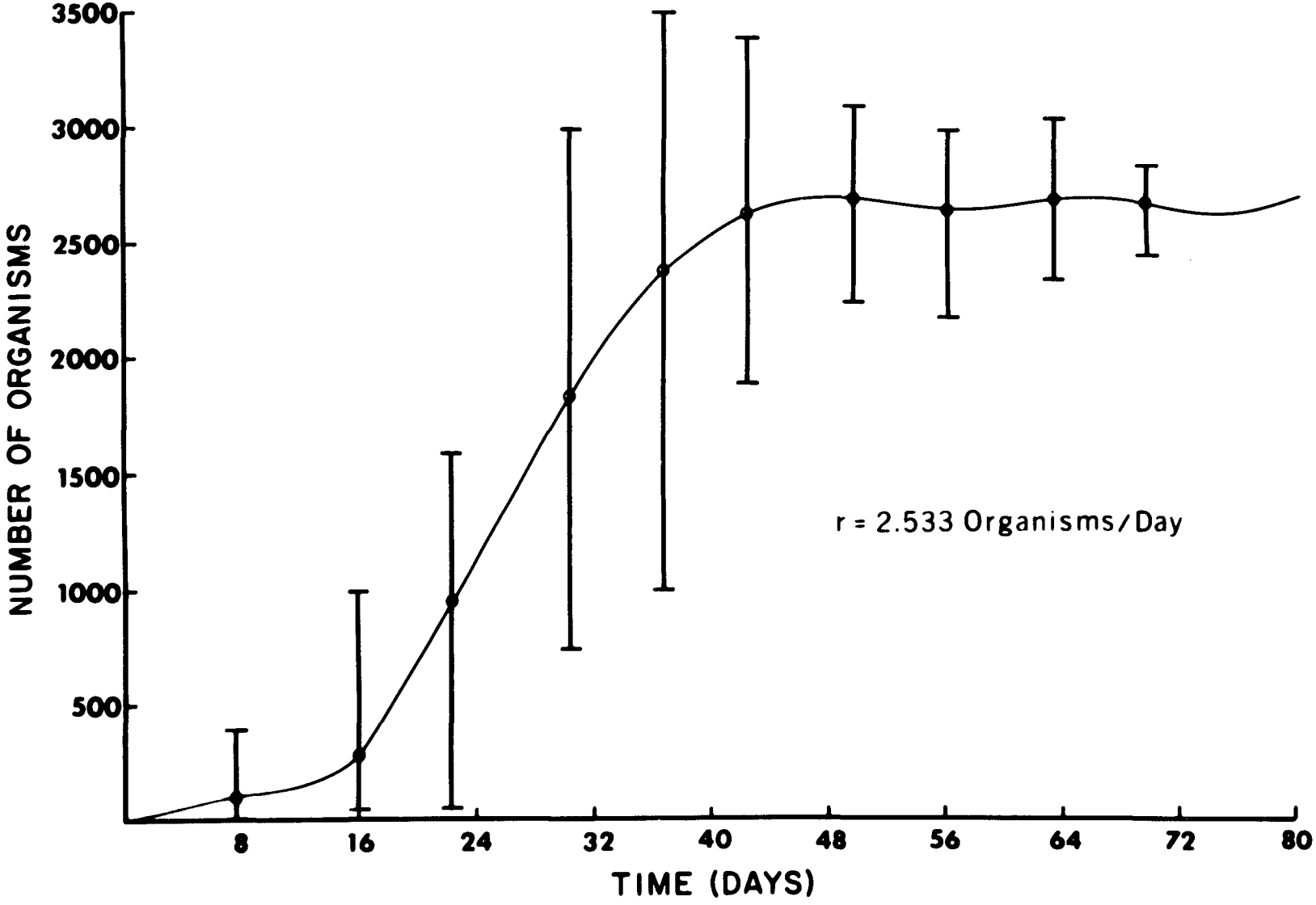

3500
3000
2500
2000
1500
1000
500
NUMBER OF ORGANISMS
r = 2.533 Organisms/Day
8
16
24
32
40
48
56
64
72
80
TIME (DAYS)

Figure 14 The intrinsic rate of increase of Rosalina leei populations in synxenic laboratory culture.

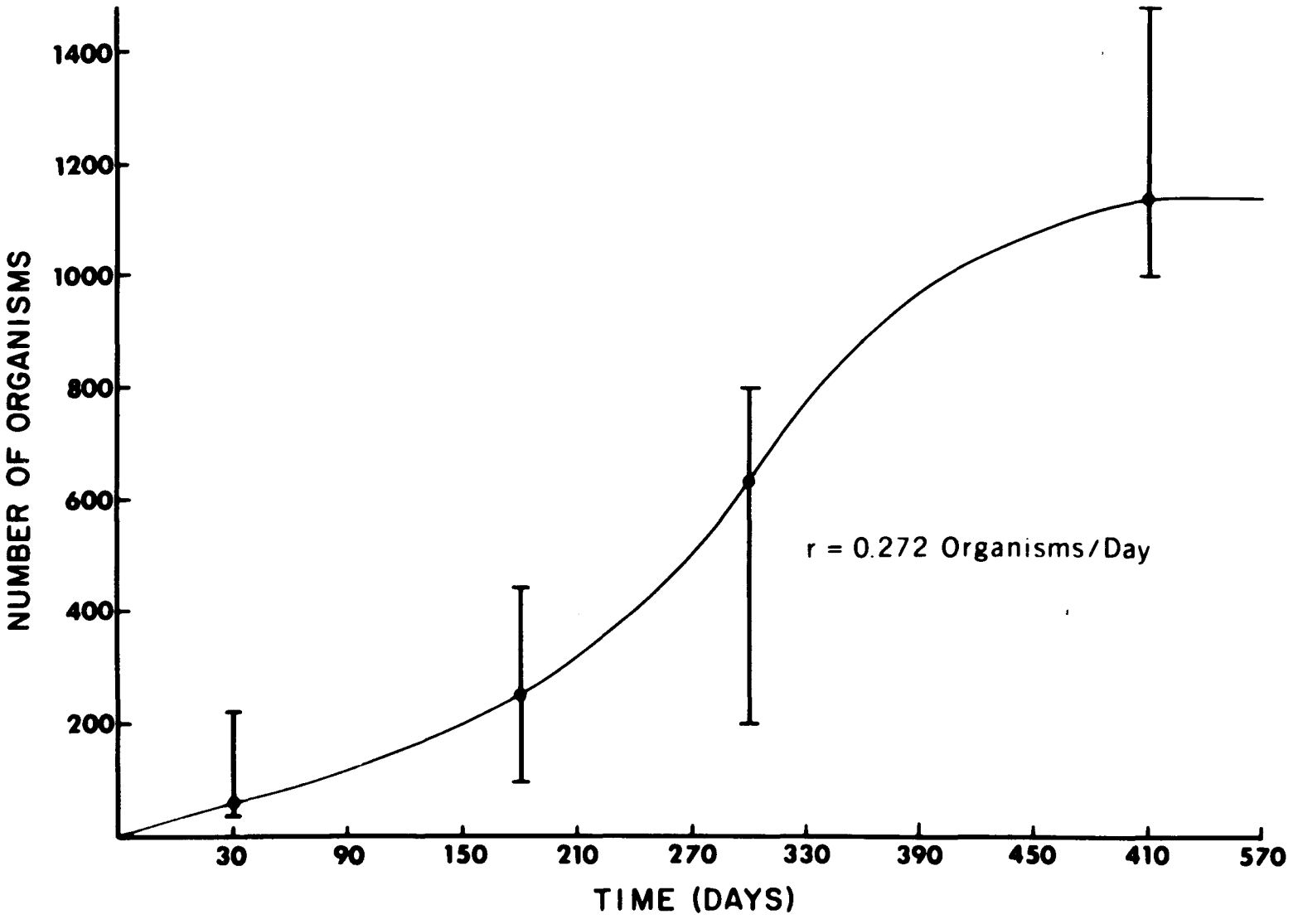

NUMBER OF ORGANISMS
1400
1200
1000
800
600
400
200
30
90
150
210
270
330
390
450
410
570
TIME (DAYS)
r = 0.272 Organisms/Day

Figure 15 The intrinsic rate of increase of Spiroloculina hyalina populations in synxenic laboratory culture.

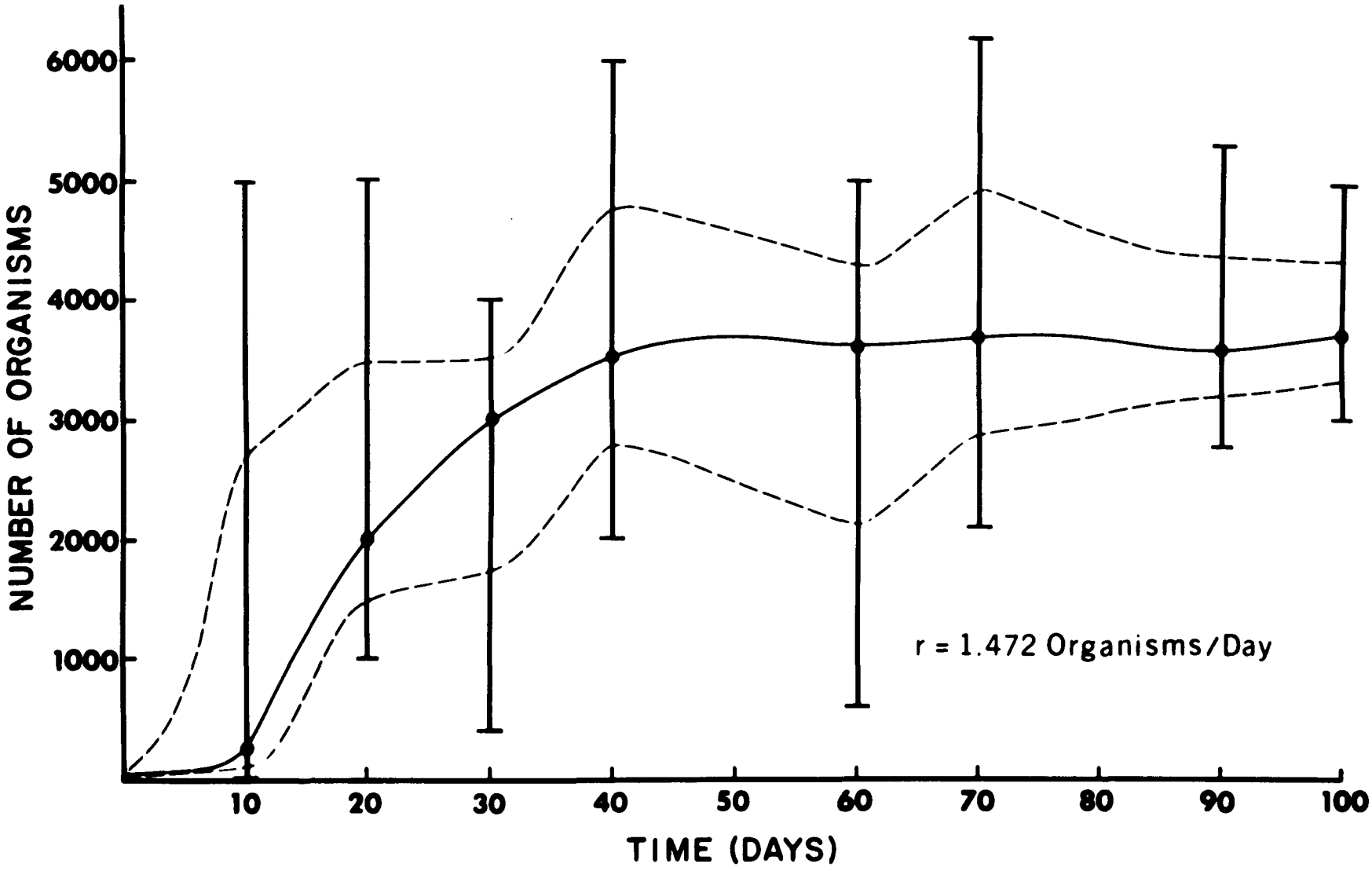

NUMBER OF ORGANISMS
6000
5000
4000
3000
2000
1000
10
20
30
40
50
60
70
80
90
100
TIME (DAYS)
r = 1.472 Organisms/Day

Figure 16 Feeding rate of *Allogromia laticollaris* on selected species of algae and bacteria.

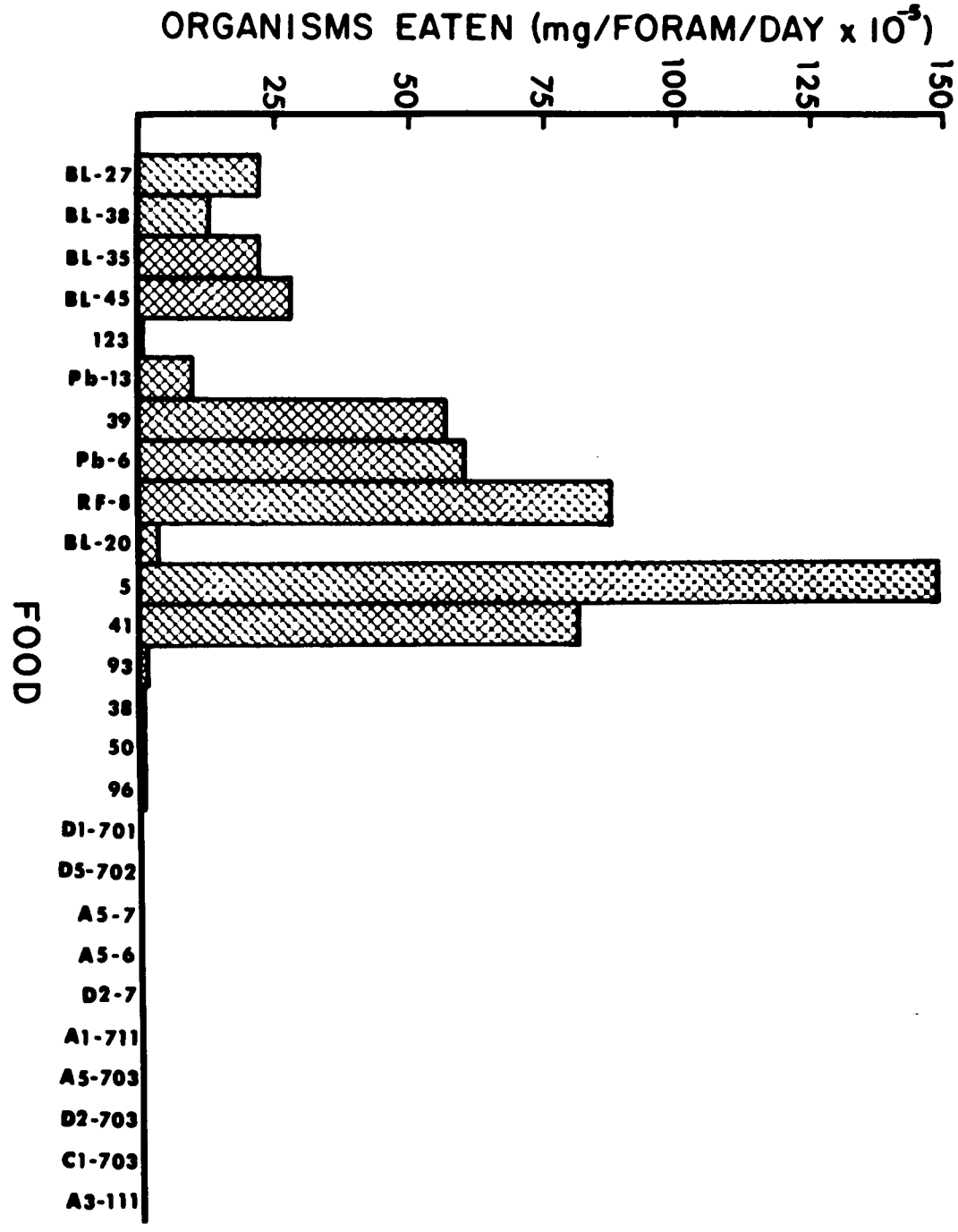

ORGANISMS EATEN (mg/FORAM/DAY x 10^{-5})
25
50
75
100
125
150
FOOD
BL-27
BL-38
BL-35
BL-45
123
Pb-13
39
Pb-6
RF-8
BL-20
5
41
93
38
50
96
D1-701
D5-702
A5-7
A5-6
D2-7
A1-711
A5-703
D2-703
C1-703
A3-111

Figure 17 Feeding rate of Rosalina leei on selected species of algae and bacteria.

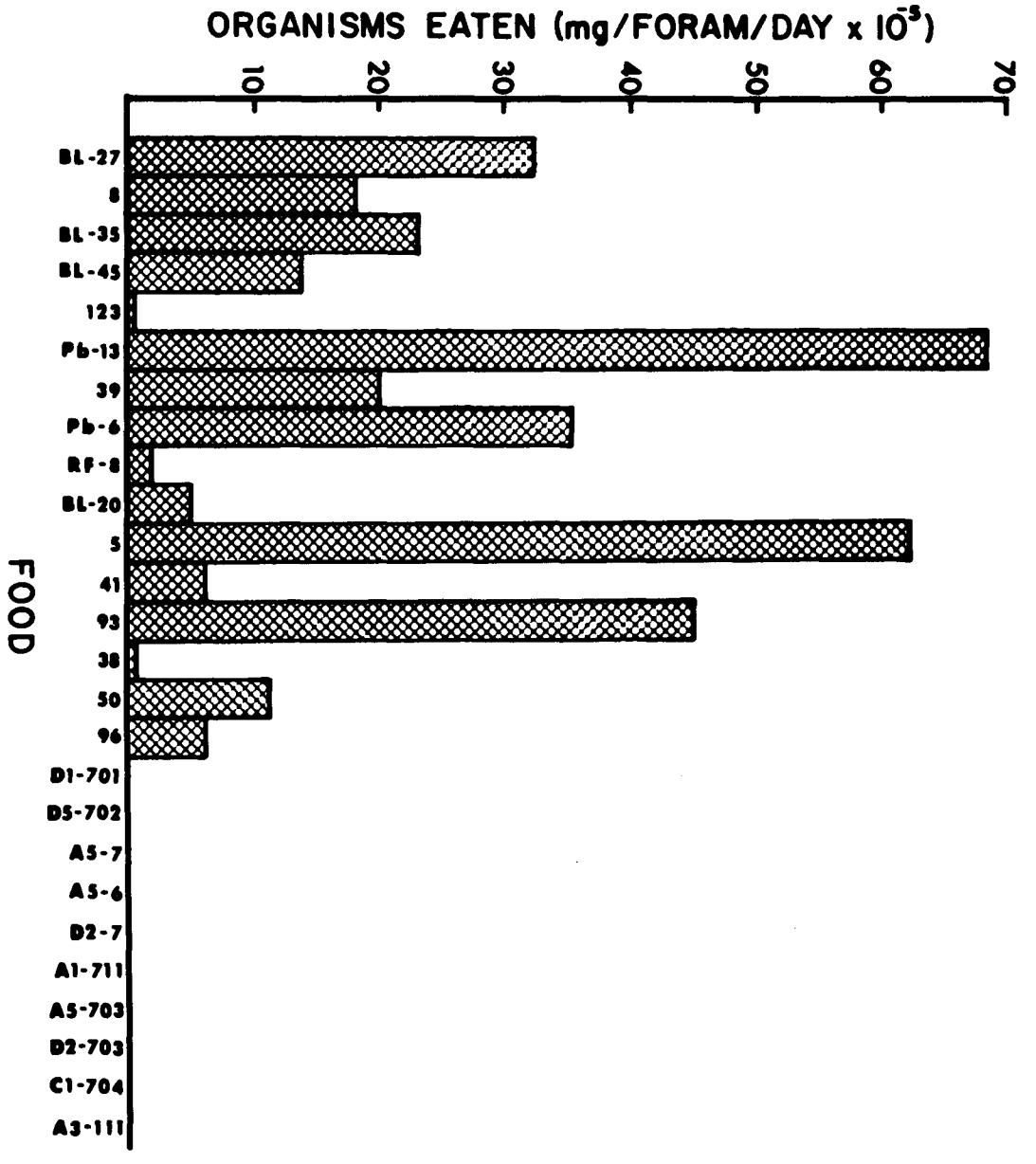

ORGANISMS EATEN (mg/FORAM/DAY x 10^{-5})
10
20
30
40
50
60
70
FOOD
BL-27
8
BL-35
BL-45
123
Pb-13
39
Pb-6
RF-8
BL-20
5
41
93
38
50
96
D1-701
D5-702
A5-7
A5-6
D2-7
A1-711
A5-703
D2-703
C1-704
A3-111

Figure 18 Feeding rate of Spiroloculina hyalina on selected species of algae and bacteria.

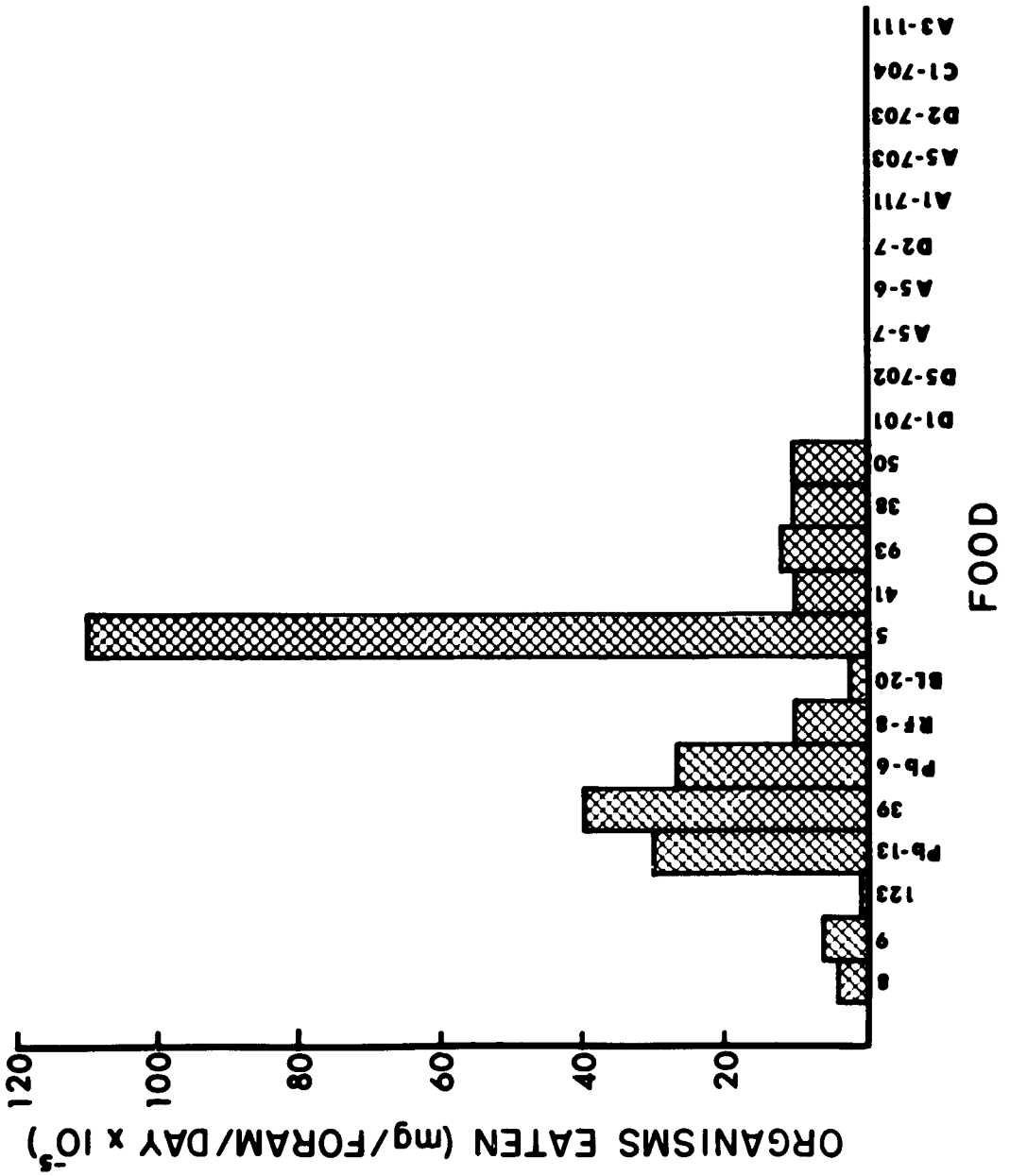

ORGANISMS EATEN (mg/FORAM/DAY x 10^{-5})
120
100
80
60
40
20
FOOD
8
9
123
Pb-13
39
Pb-6
RF-8
BL-20
5
41
93
38
50
D1-701
D5-702
A5-7
A5-6
D2-7
A1-711
A5-703
D2-703
C1-704
A3-111

Figure 19 The effect of intraspecific competition on feeding of *Allogromia laticollaris* on *Nitzschia acicularis* and *Phaeodactylum tricornutum*.

Curve number	inoculum size of *Allogromia*
1	1
2	10
3	50
4	100

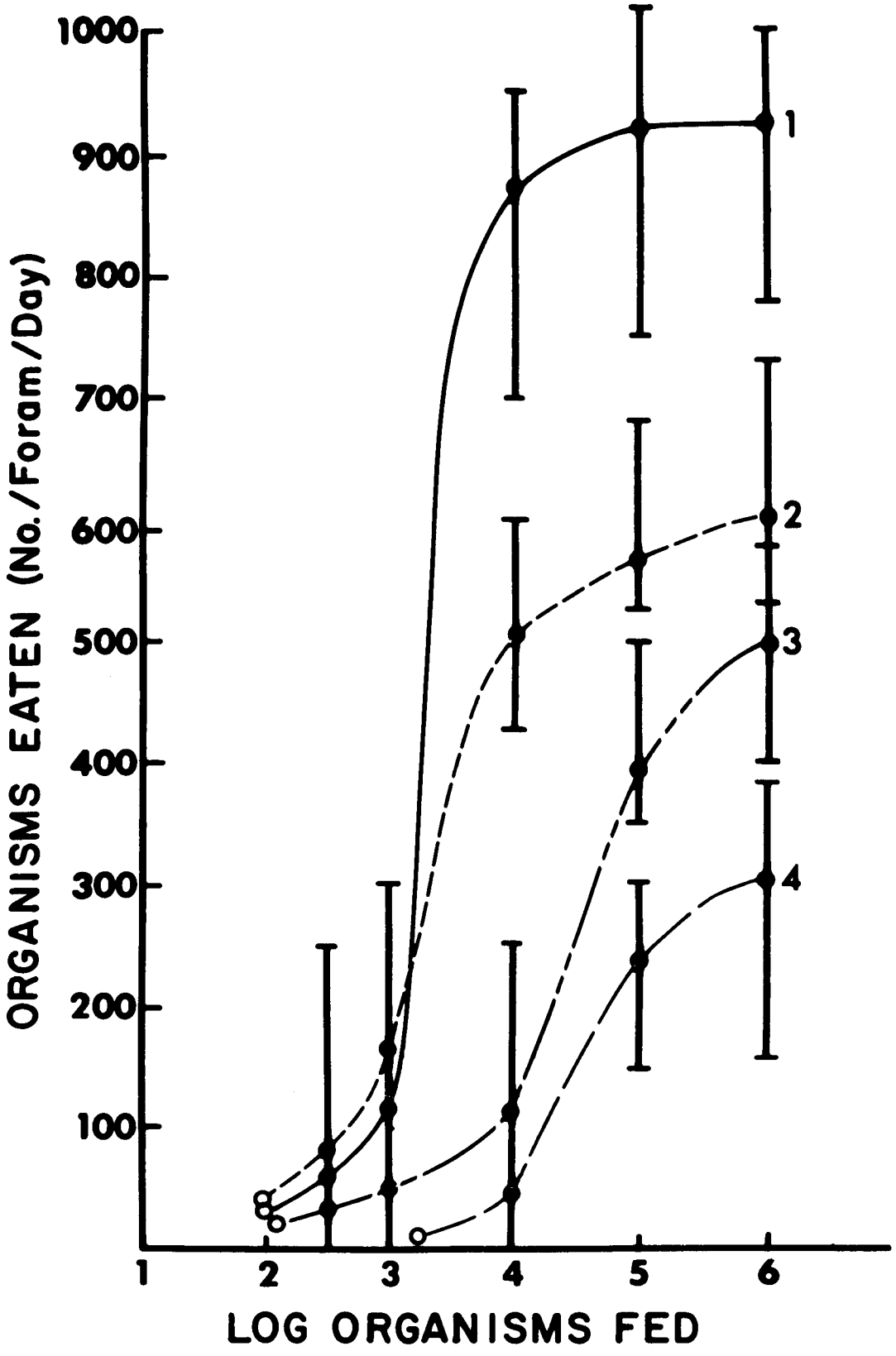

1000
900
800
700
600
500
400
300
200
100
ORGANISMS EATEN (No./Foram/Day)
1
2
3
4
5
6
LOG ORGANISMS FED
1
2
3
4

Figure 20 The effect of intraspecific competition on feeding of *Rosalina leei* on *Amphora* sp and *Phaeodactylum tricornutum*.

Curve number	Inoculum size of *Rosalina*
1	20
2	50
3	5
	with *Nannochloris* sp as food organism
4	5

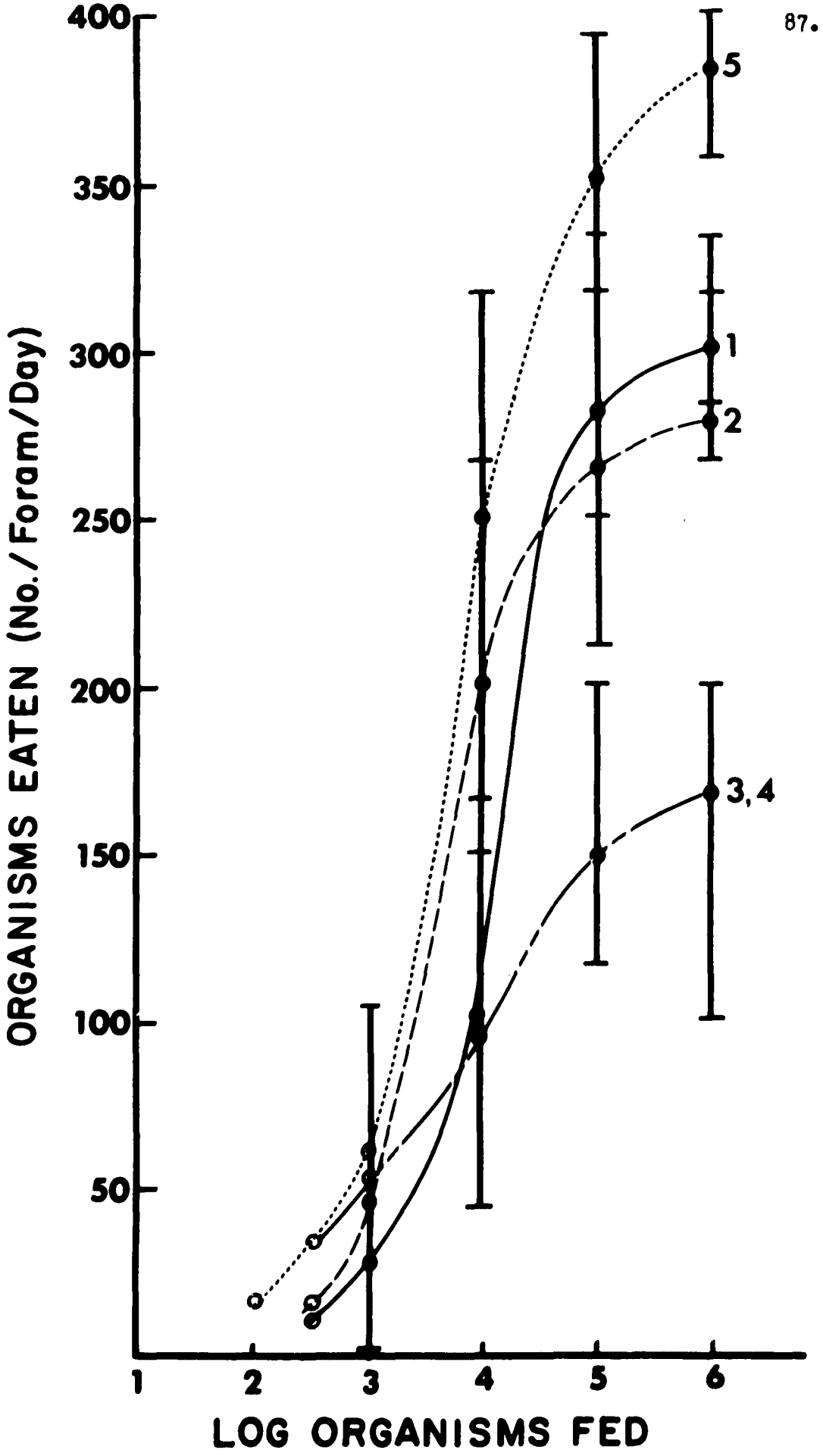

400
350
300
250
200
150
100
50
ORGANISMS EATEN (No./Foram/Day)
1
2
3
4
5
6
LOG ORGANISMS FED
5
1
2
3,4

Figure 21 The effect of intraspecific competition on feeding of Spiroloculina hyalina on Amphora sp and Phaeodactylum tricornutum.

Curve number	Inoculum size of Spiroloculina
1	10
2	50
3	100
	with Nannochloris sp as food organism
4	
5	

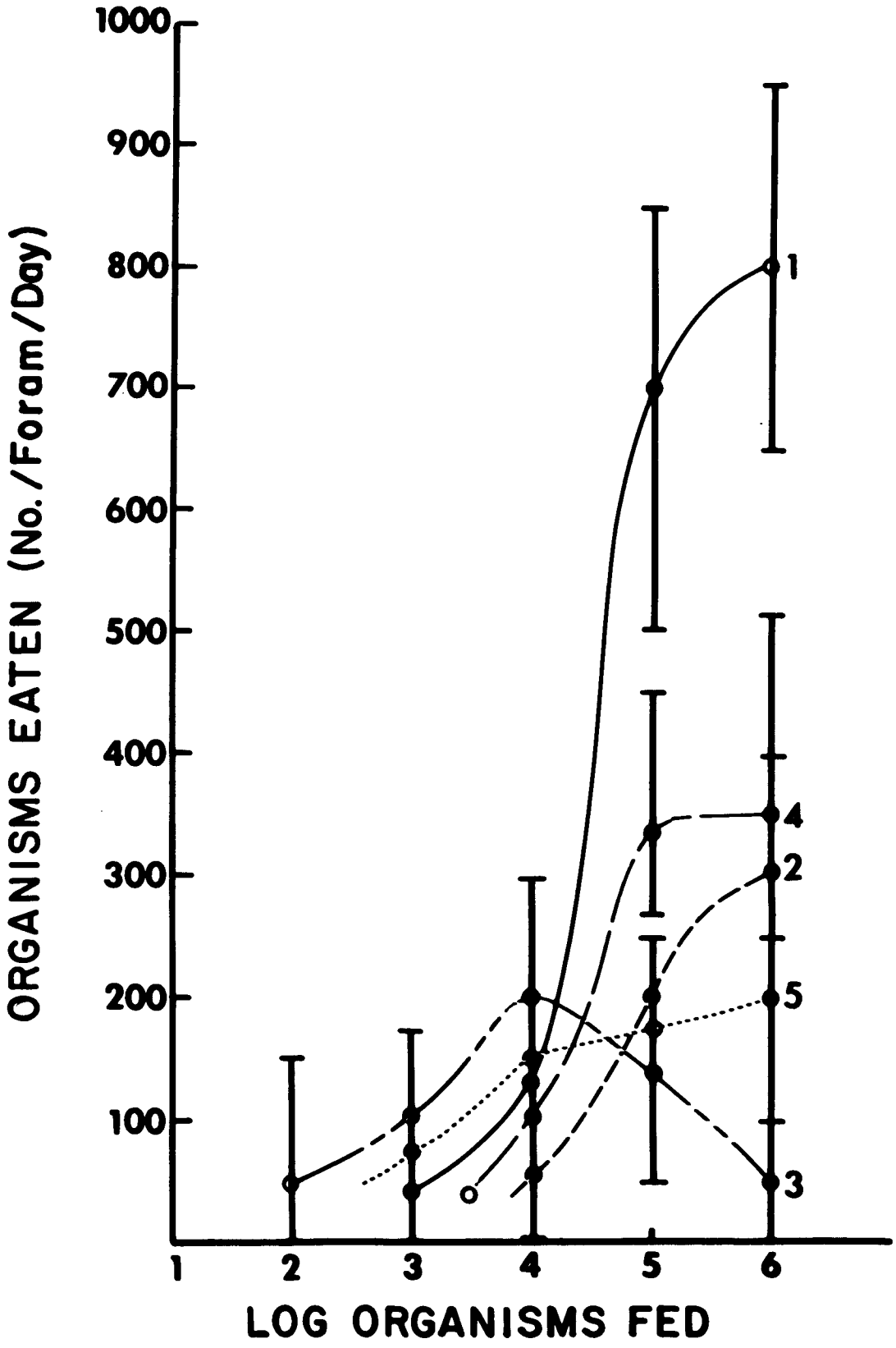

ORGANISMS EATEN (No./Foram/Day)
1000
900
800
700
600
500
400
300
200
100
1
2
3
4
5
6
LOG ORGANISMS FED
1
4
2
5
3

Figure 22 The feeding rate of *Allogromia laticollaris* on bacteria.

Curve number	Bacterial strain
1	A5-703
2	D1-701
3	D2-7, A5-6, D5-702, D2-703, A3-111
4	A1-711, A5-7, C1-704

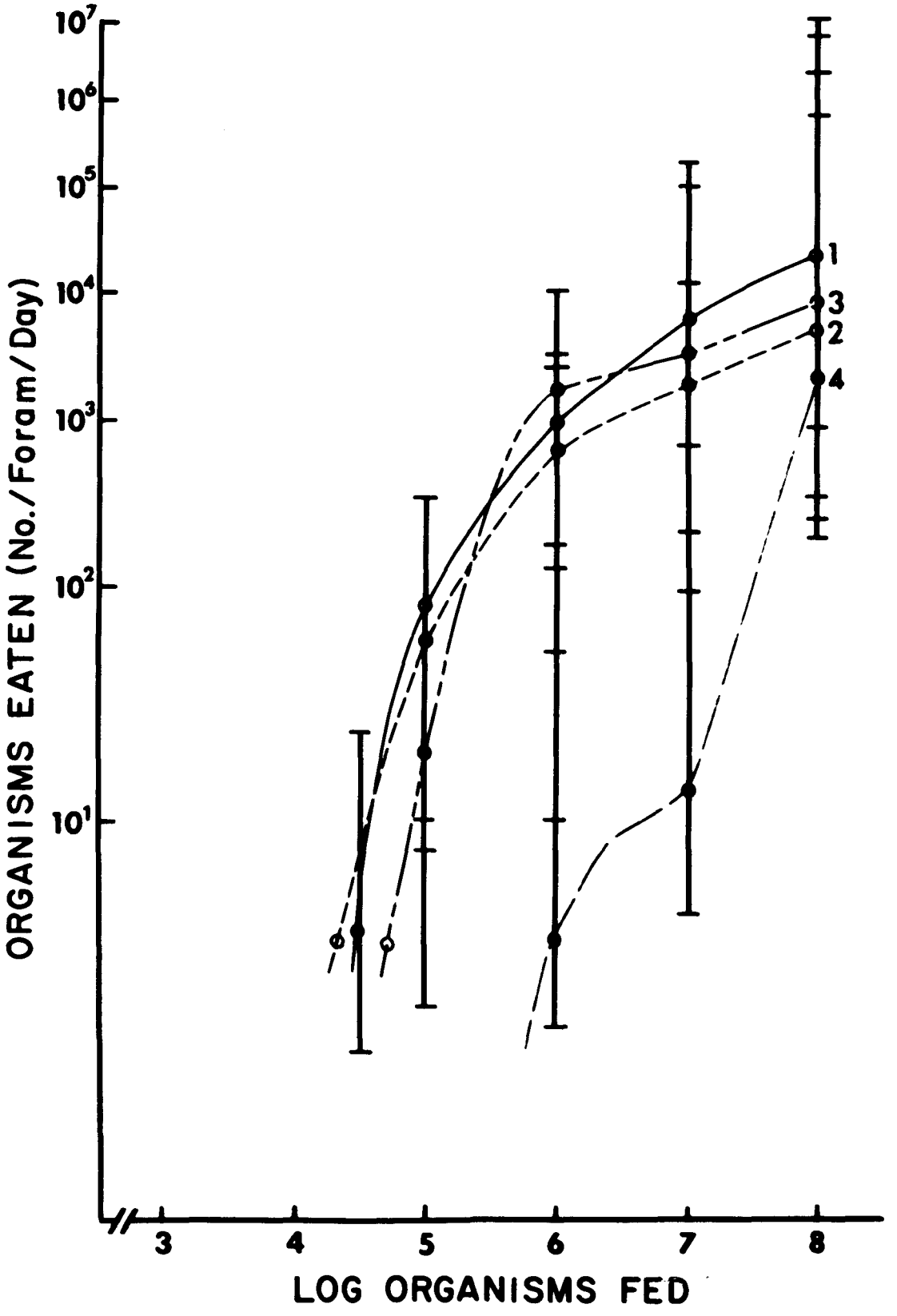

ORGANISMS EATEN (No./Foram/Day)
10^7
10^6
10^5
10^4
10^3
10^2
10^1
1
3
2
4
3
4
5
6
7
8
LOG ORGANISMS FED

Figure 23 The feeding rate of Rosalina leei on bacteria.

Curve number	Bacterial strain
1	D1-7, A5-6, D5-702, A5-7 A5-703, D2-703, C1-704, A3-111
2	A1-711, D1-701

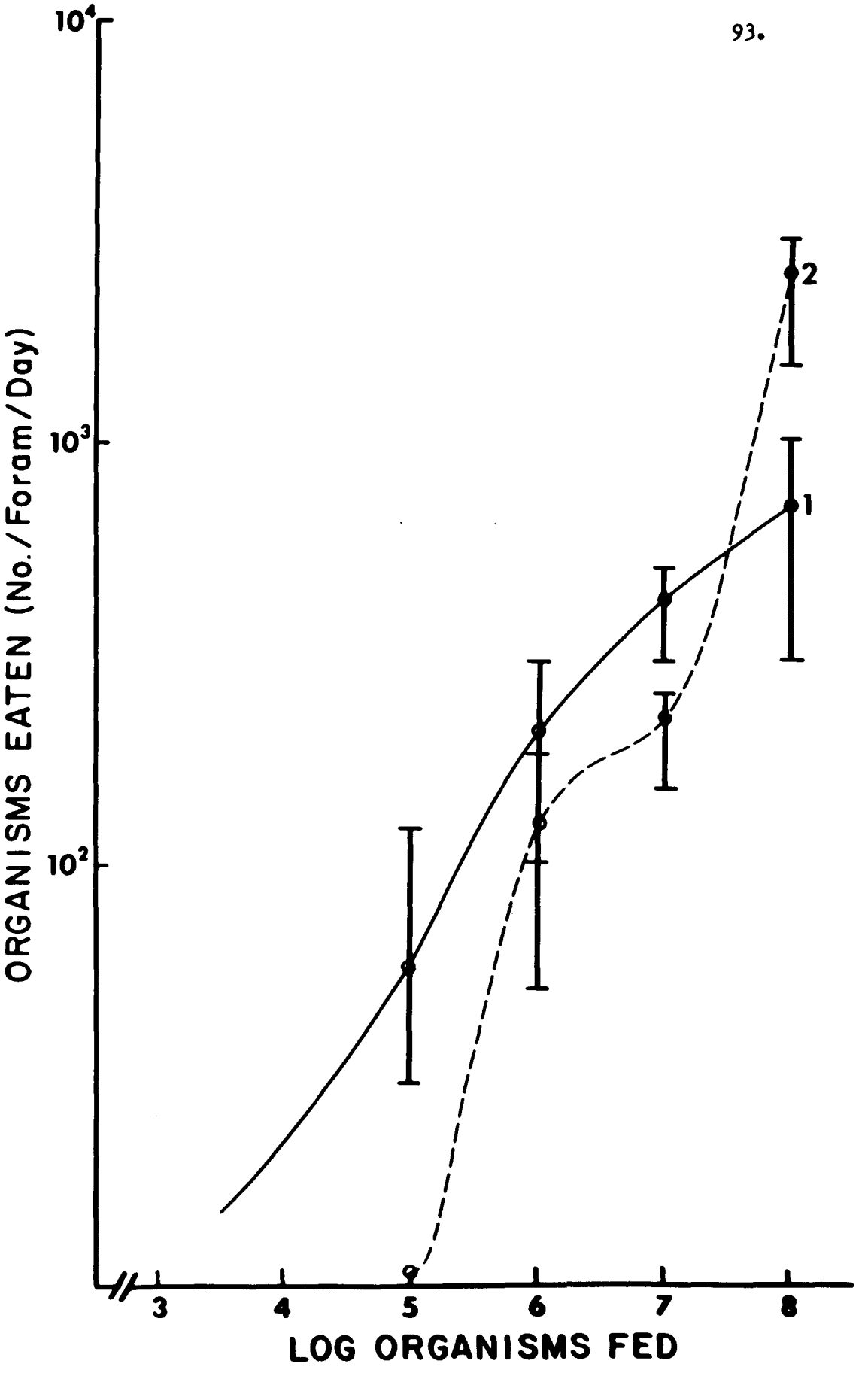

10^4
10^3
10^2
ORGANISMS EATEN (No./Foram/Day)
1
2
3
4
5
6
7
8
LOG ORGANISMS FED

Figure 24 The feeding rate of Spiroloculina hyalina on bacteria.

Curve number	Bacterial strain
1	A5-703
2	A5-6, D5-702, D2-703, C1-704, D1-701, A3-111
3	D2-7
4	A1-711, A5-7

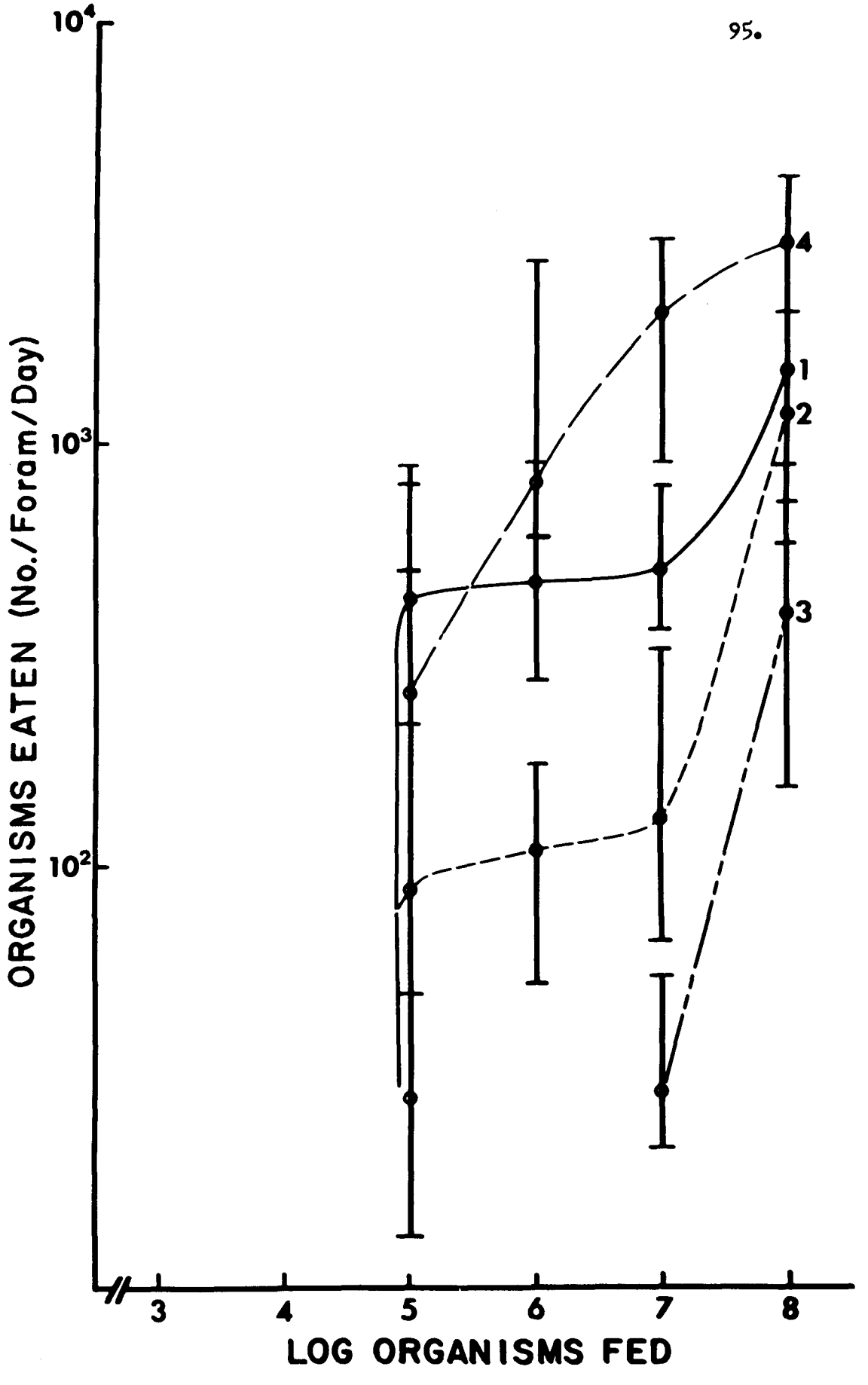

10^4
10^3
10^2
ORGANISMS EATEN (No./Foram/Day)
1
2
3
4
3
4
5
6
7
8
LOG ORGANISMS FED

Figure 25 The effect of crowding on the reproduction of Allogromia laticollaris. Incubation time = 100 days.

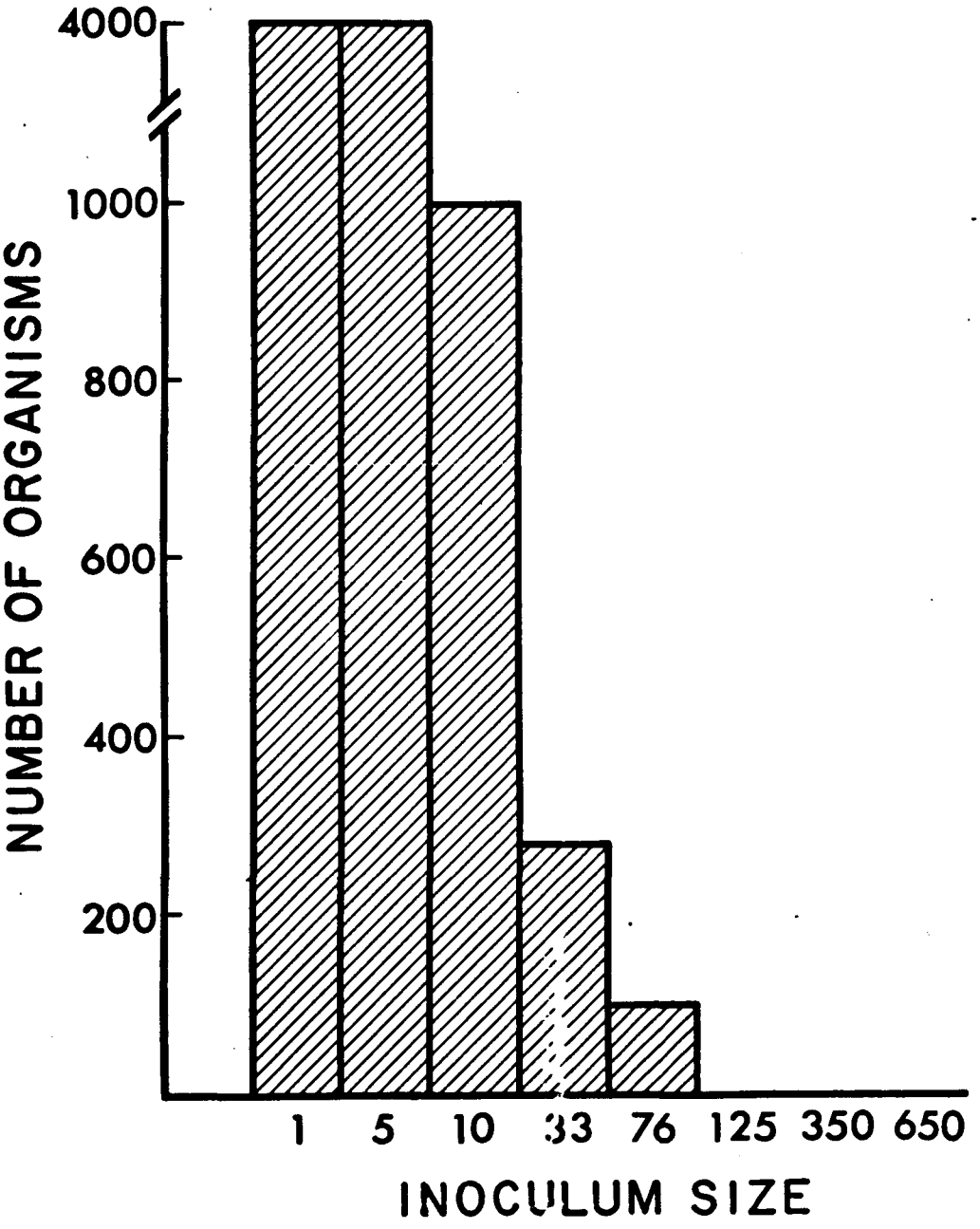

4000
1000
800
600
400
200
NUMBER OF ORGANISMS
1
5
10
33
76
125
350
650
INOCULUM SIZE

Figure 26 The effect of crowding on the reproduction of Rosalina leei. Incubation time = 100 days.

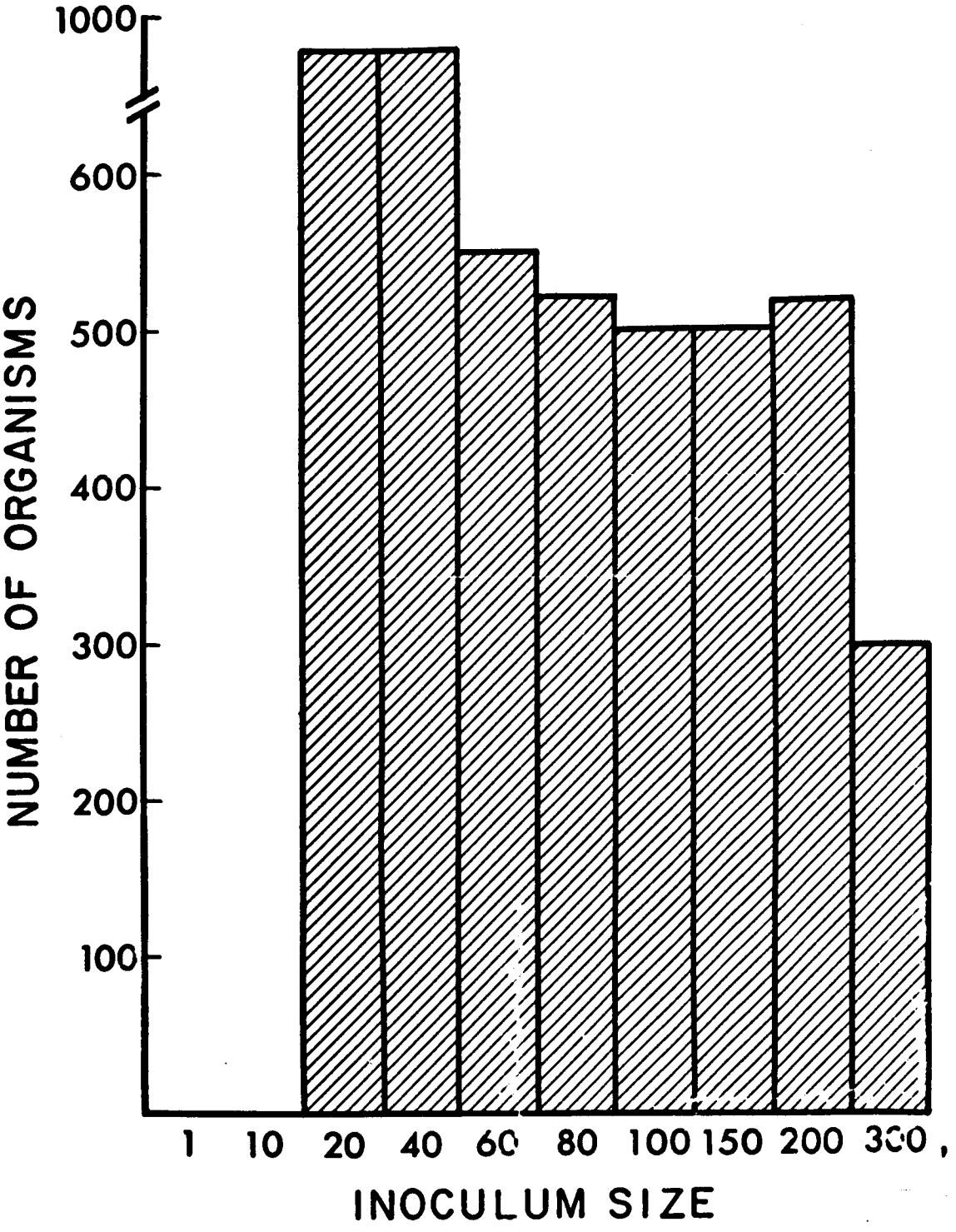

1000
600
500
400
300
200
100
NUMBER OF ORGANISMS
1
10
20
40
60
80
100
150
200
300
INOCULUM SIZE

Figure 27 The effect of crowding on the reproduction of Spiroloculina hyalina. Incubation time = 100 days.

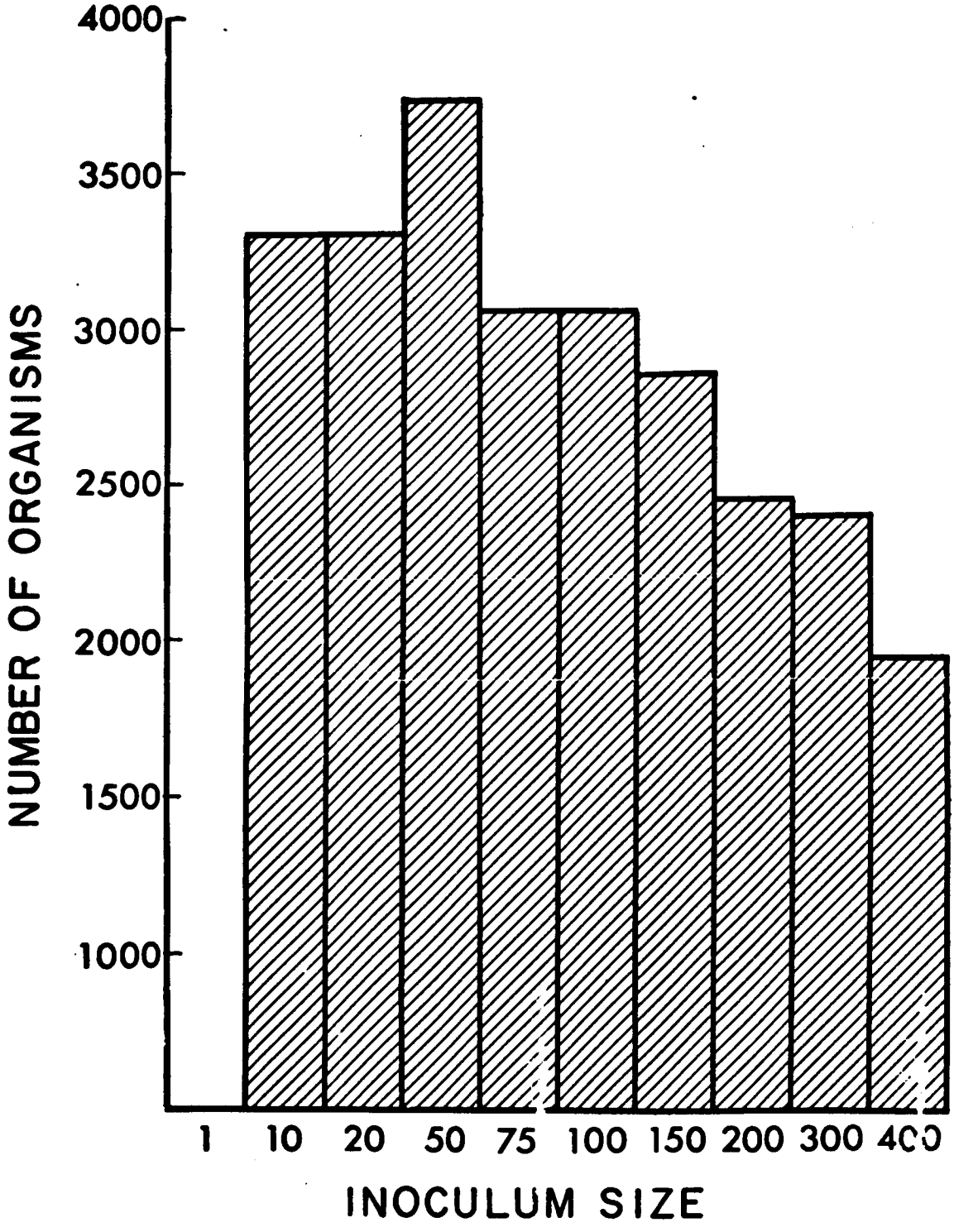

4000
3500
3000
2500
2000
1500
1000
NUMBER OF ORGANISMS
1
10
20
50
75
100
150
200
300
400
INOCULUM SIZE

Figure 28 The effect of interspecific competition on the reproduction of *Allogromia laticollaris*.

Curve number	*Allogromia*	*Rosalina*	*Spiroloculina*
1	1		
2	1		50
3	1	20	

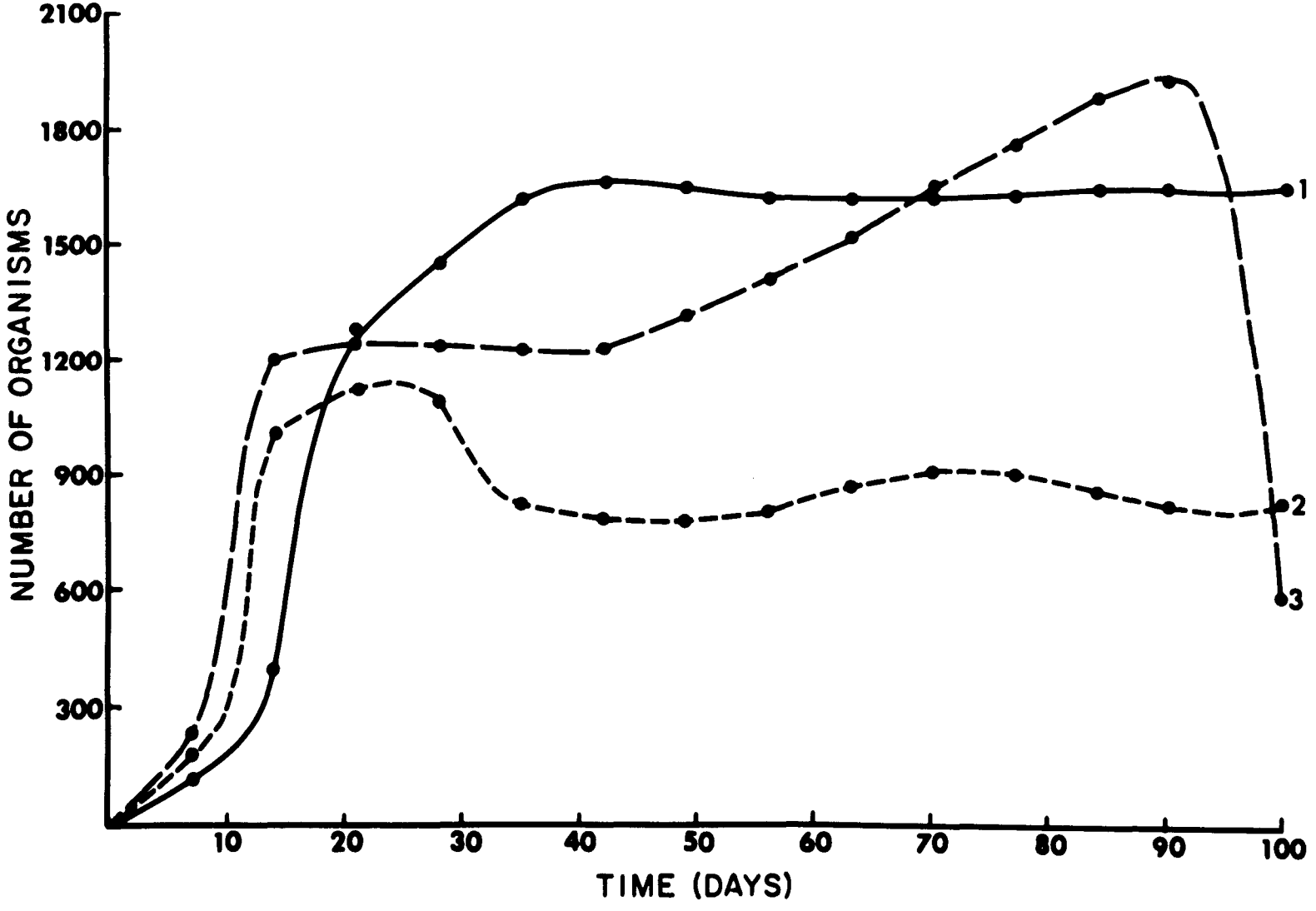

2100
1800
1500
1200
900
600
300
NUMBER OF ORGANISMS
10
20
30
40
50
60
70
80
90
100
TIME (DAYS)
1
2
3

Figure 29 The effect of interspecific competition on the reproduction of *Rosalina leei*.

Curve number	*Allogromia*	*Rosalina*	*Spiroloculina*
1		20	
3	1	20	
4		20	50

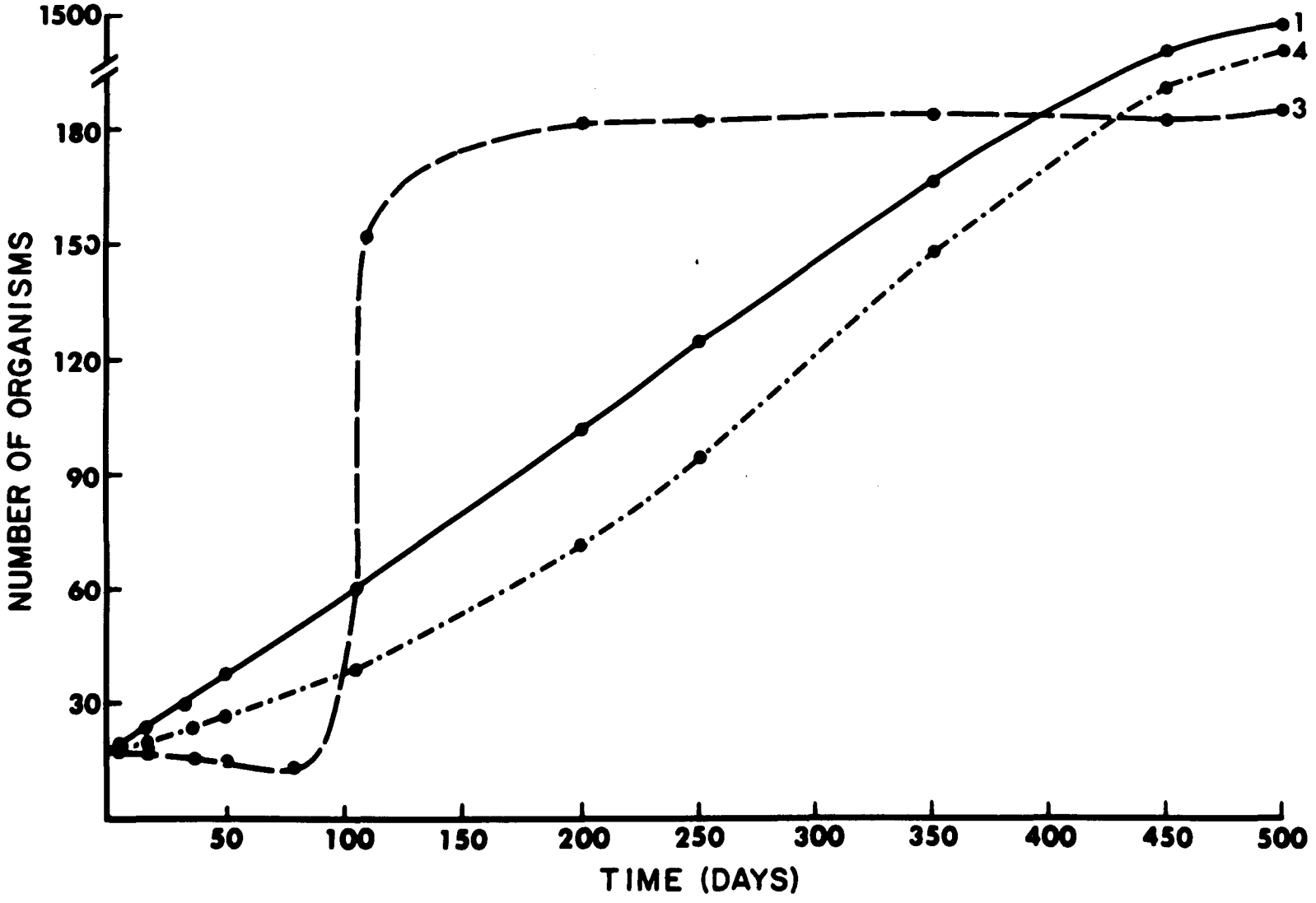

1500
180
150
120
90
60
30
NUMBER OF ORGANISMS
50
100
150
200
250
300
350
400
450
500
TIME (DAYS)
1
4
3

Figure 30 The effect of interspecific competition on the reproduction of *Spiroloculina hyalina*.

Curve number	*Allogromia*	*Rosalina*	*Spiroloculina*
1			50
2	5		50
4		20	50
5 (agar surface)	5		50
6 (agar surface)		20	50

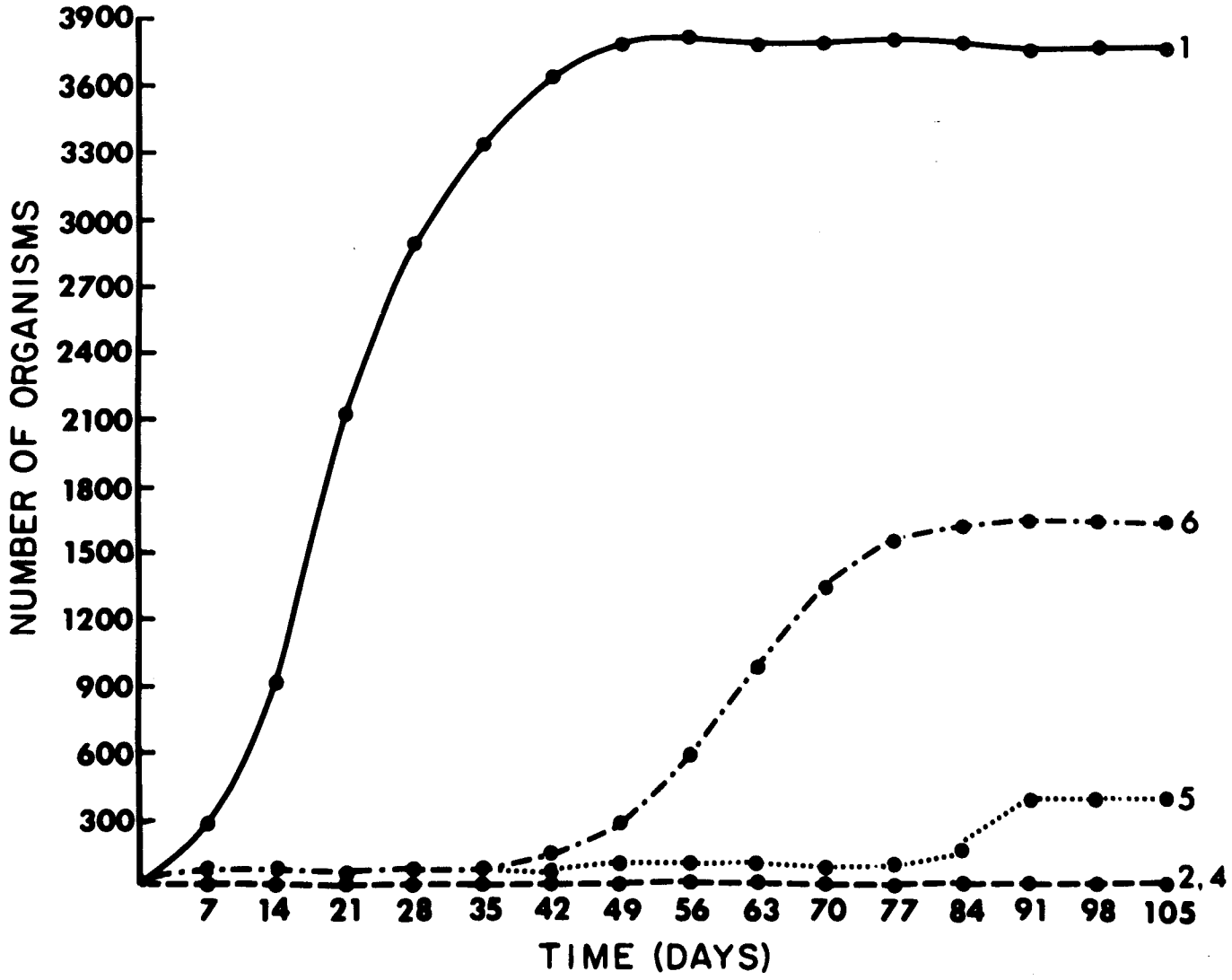
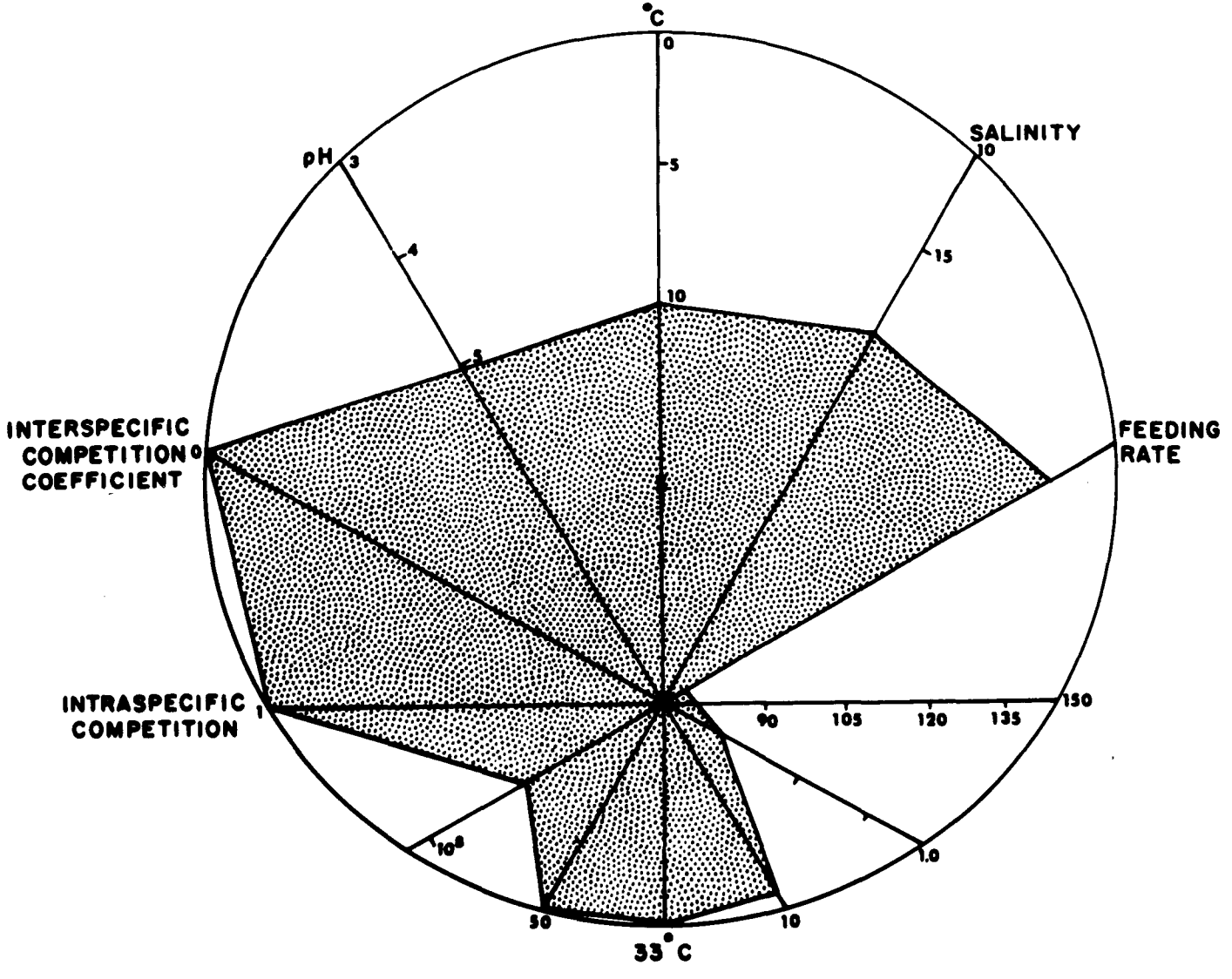

NUMBER OF ORGANISMS
3900
3600
3300
3000
2700
2400
2100
1800
1500
1200
900
600
300
7
14
21
28
35
42
49
56
63
70
77
84
91
98
105
TIME (DAYS)
1
6
5
2, 4

Figure 31 Six-dimension eccentric model of the niche of Allogromia laticollaris.

Figure 31 a Six-dimension centric model of the niche of Allogromia laticollaris.


°C
0
5
10
SALINITY
10
15
pH
3
4
5
INTERSPECIFIC
COMPETITION
COEFFICIENT
0
FEEDING
RATE
INTRASPECIFIC
COMPETITION
1
90
105
120
135
150
10^8
1.0
50
10
33°C

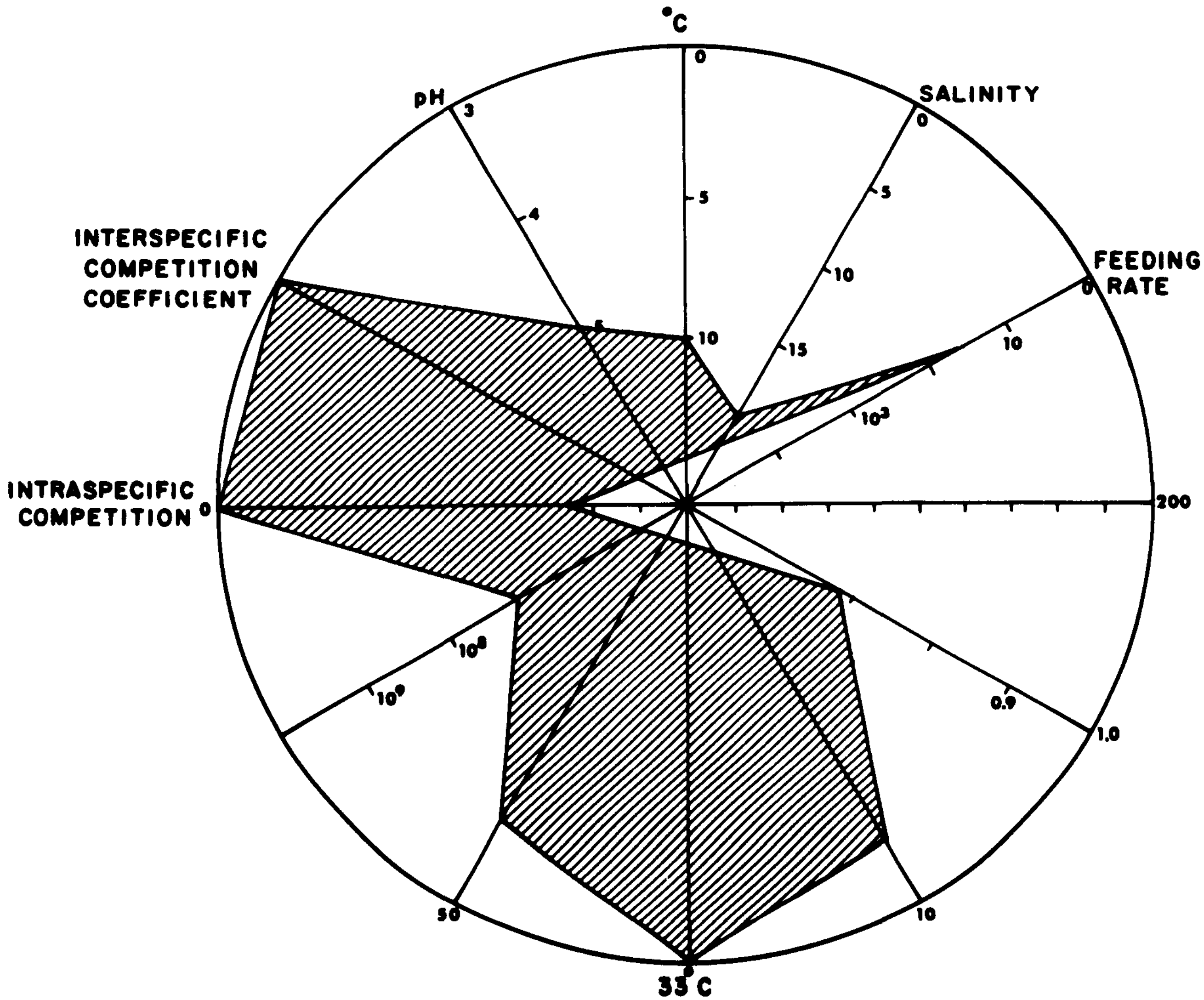
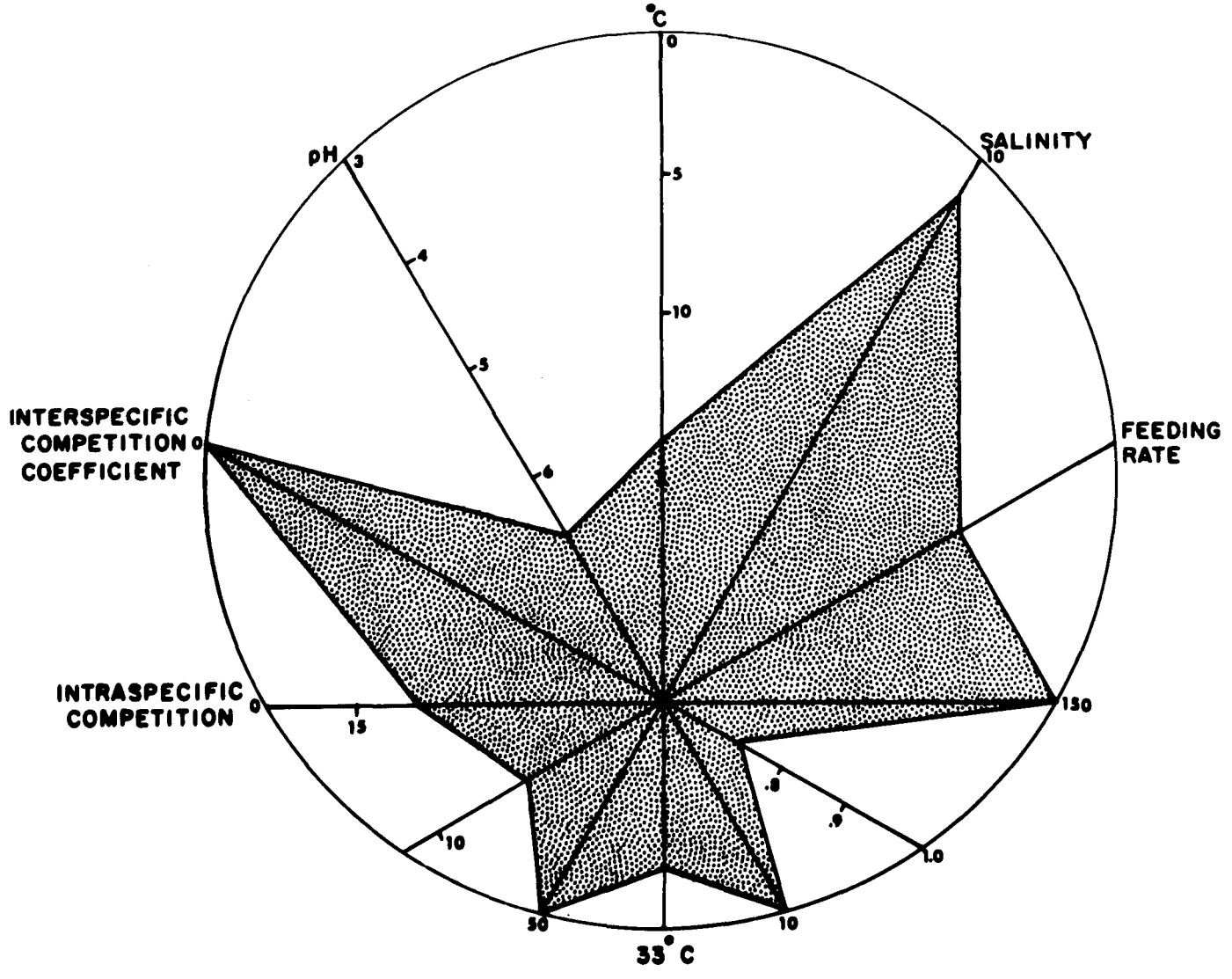

°C
0
5
10
SALINITY
0
5
10
15
FEEDING RATE
0
10
10³
200
pH
3
4
5
INTERSPECIFIC COMPETITION COEFFICIENT
INTRASPECIFIC COMPETITION
0
10⁸
10⁹
50
33 C
10
0.9
1.0

Figure 32 Six-dimension eccentric model of the niche of Rosalina leei.

Figure 32 a Six-dimension centric model of the niche of Rosalina leei.


°C
0
5
10
SALINITY
10
FEEDING
RATE
150
1.0
.9
.8
10
35°C
50
10
INTRASPECIFIC
COMPETITION
0
15
INTERSPECIFIC
COMPETITION
COEFFICIENT
0
pH
3
4
5
6

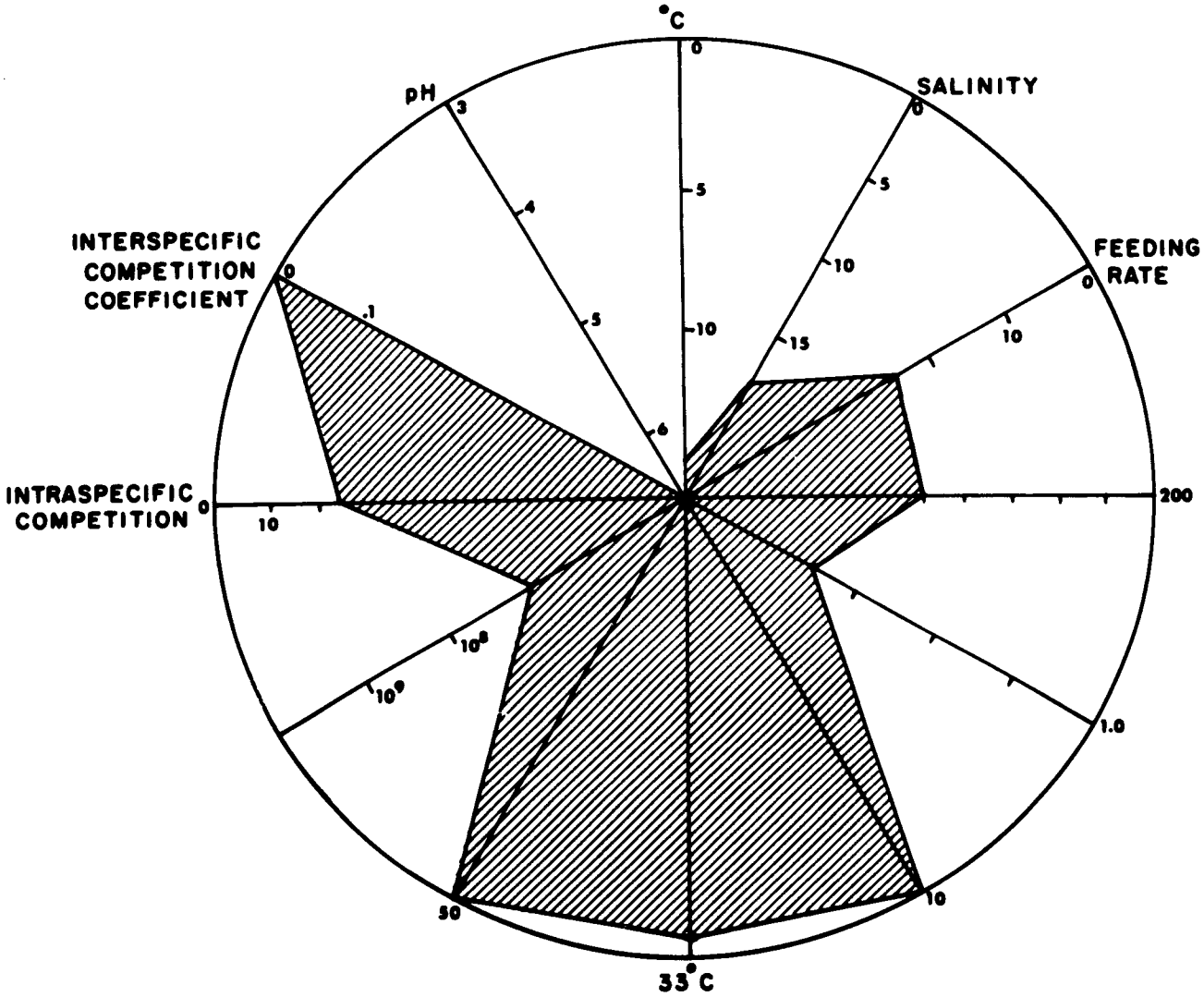
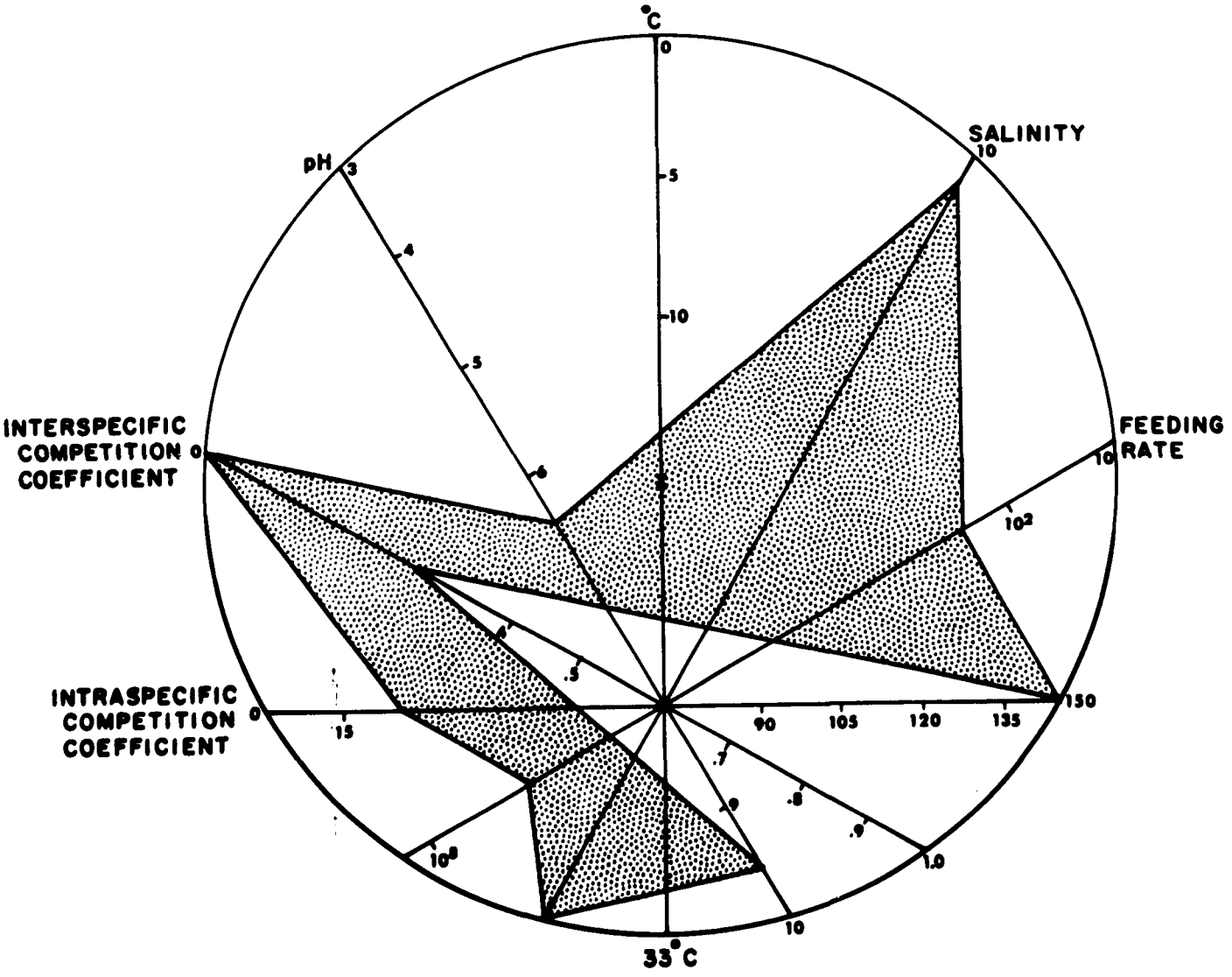

°C
0
5
10
SALINITY
0
5
10
15
FEEDING
RATE
0
10
200
1.0
10
33°C
50
10⁸
10⁹
INTRASPECIFIC
COMPETITION
0
10
INTERSPECIFIC
COMPETITION
COEFFICIENT
0
.1
pH
3
4
5
6

Figure 33 Six-dimension eccentric model of the niche of Spiroloculina hyalina.

Figure 33 a Six-dimenaion centric model of the niche of Spiroloculina hyalina.


°C
0
5
10
SALINITY
10
pH
3
4
5
6
INTERSPECIFIC
COMPETITION
COEFFICIENT
0
FEEDING
RATE
10
10^2
.4
.5
INTRASPECIFIC
COMPETITION
COEFFICIENT
0
15
90
105
120
135
150
.7
.8
.9
1.0
10^8
10
33°C

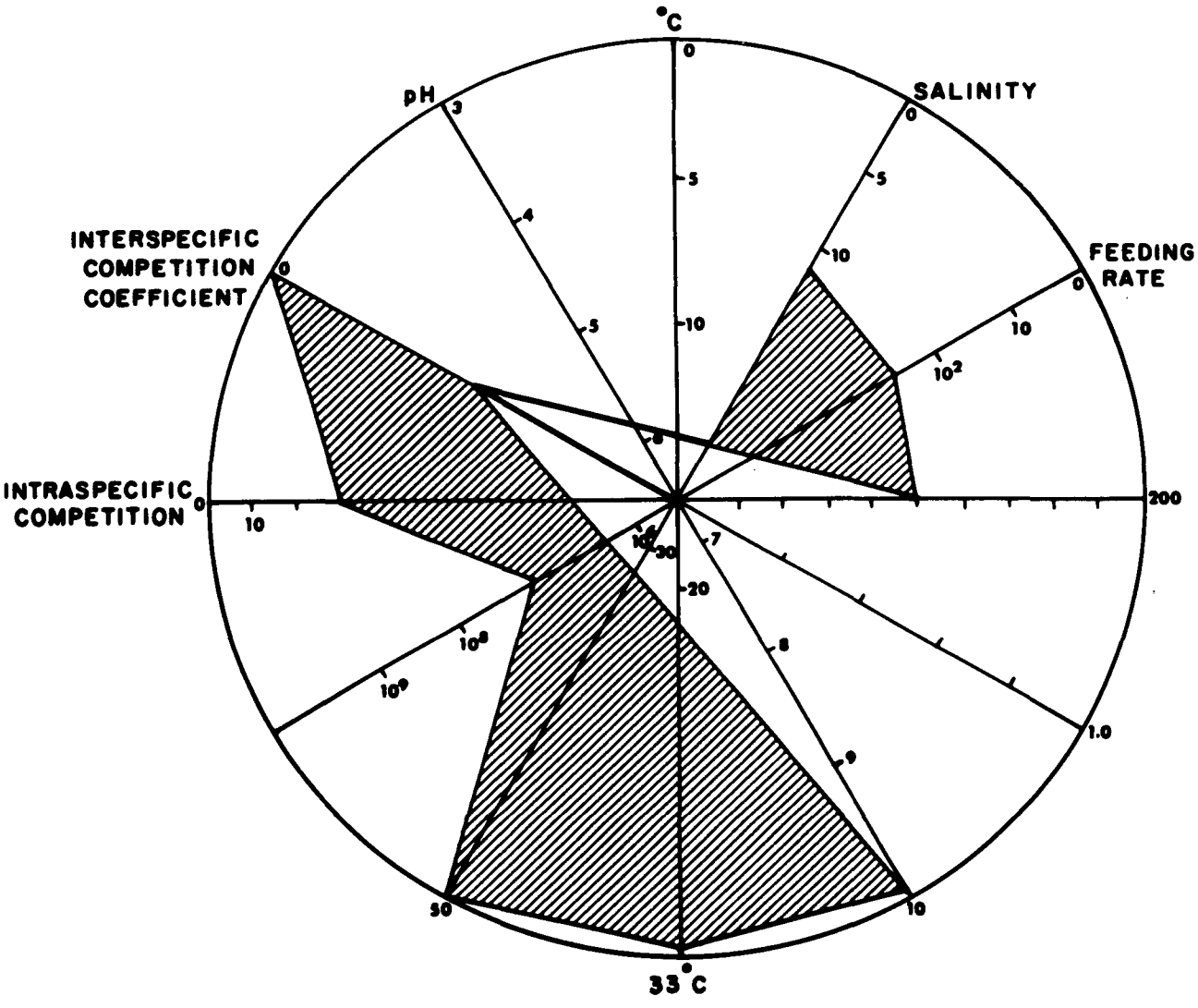

°C
0
5
10
SALINITY
0
5
10
FEEDING
RATE
0
10
10²
200
1.0
9
8
7
6
5
4
3
pH
INTERSPECIFIC
COMPETITION
COEFFICIENT
0
INTRASPECIFIC
COMPETITION
0
10
10⁸
10⁹
30
20
10
33 °C

Figure 34 The feeding rate of *Ammonia beccarii* on selected species of algae.

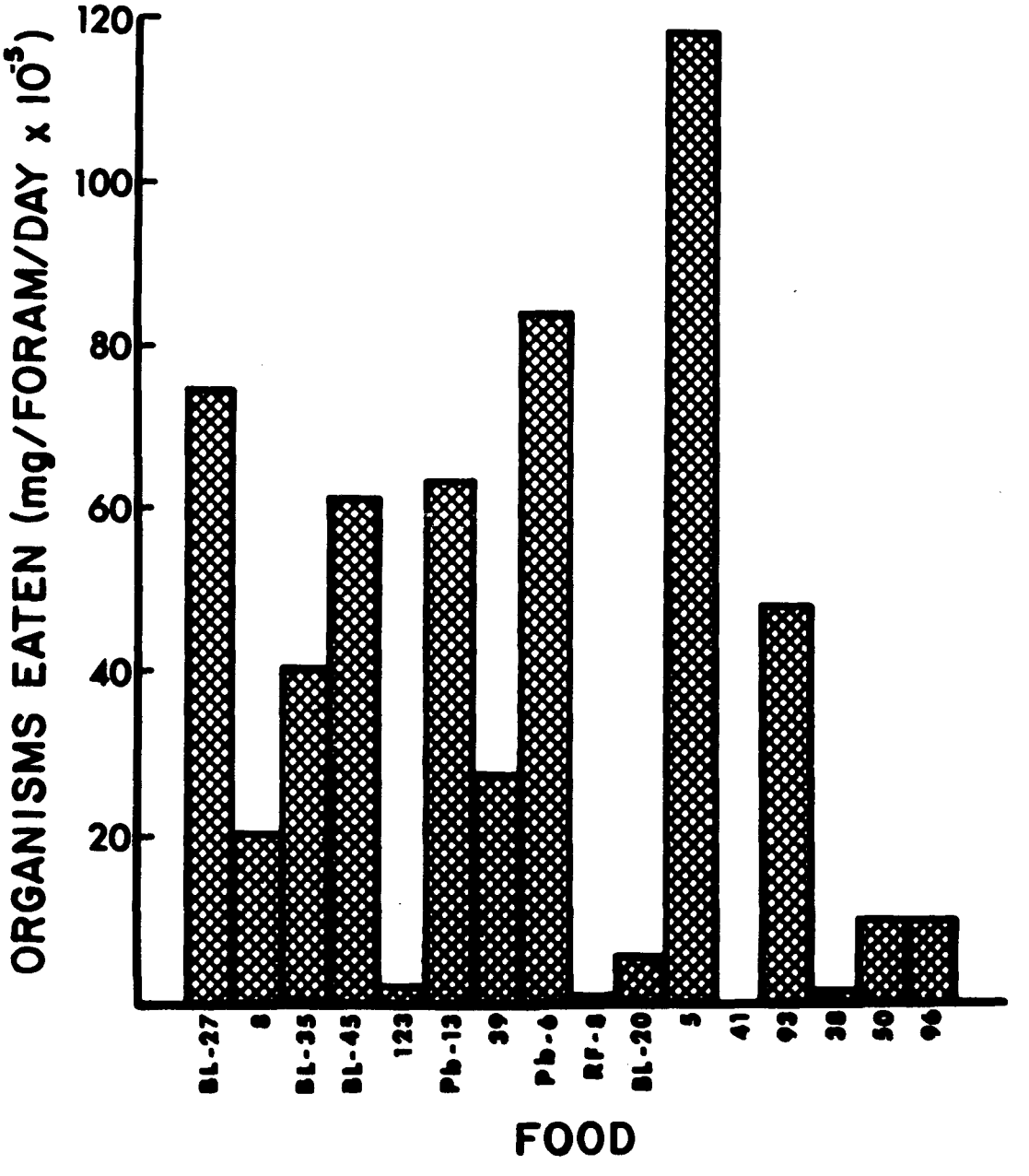

ORGANISMS EATEN (mg/FORAM/DAY x 10^{-3})
120
100
80
60
40
20
BL-27
0
BL-35
BL-45
123
Pb-13
39
Pb-9
RF-8
BL-20
5
41
49
38
50
96
FOOD

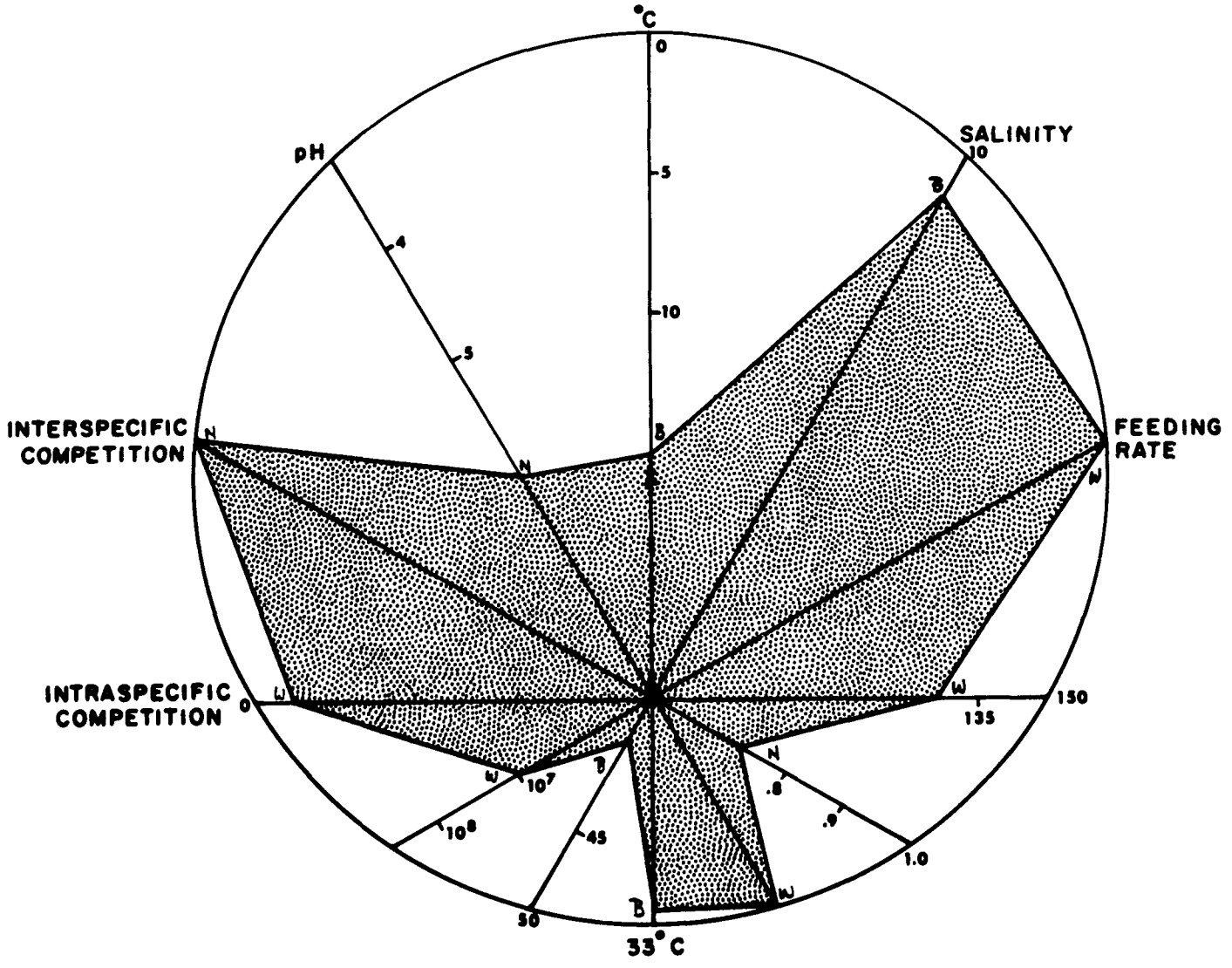
Figure 35 Six-dimension eccentric model of the niche of Ammonia beccarii.

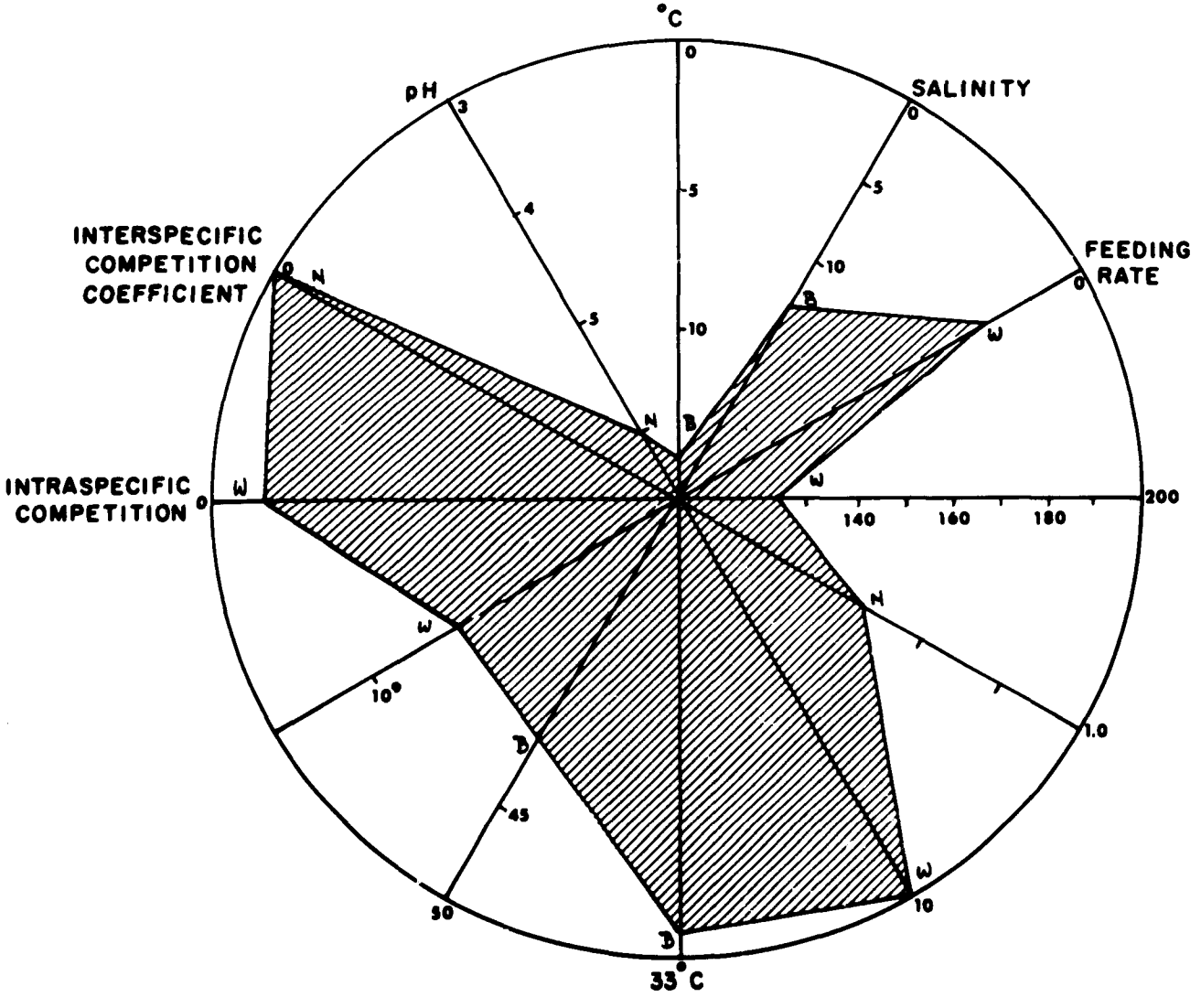
Figure 35 a Six-dimension centric model of the niche of Ammonia beccarii.

B = Bradshaw's (1957) data

W = Observed data

N = No data available


°C
0
5
10
SALINITY
10
B
pH
4
5
INTERSPECIFIC
COMPETITION
N
N
B
FEEDING
RATE
W
INTRASPECIFIC
COMPETITION
0
W
W
150
135
W
10^7
B
N
.8
.9
10^8
45
1.0
50
B
W
B
33° C


°C
0
5
10
SALINITY
0
5
10
FEEDING RATE
0
140
160
180
200
1.0
33°C
30
45
10°
INTRASPECIFIC COMPETITION
0
INTERSPECIFIC COMPETITION COEFFICIENT
0
pH
3
4
5
N
W
B