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AN EXPERIMENTAL APPROACH TO THE ASSESSMENT OF THE INFORMATIONAL ASPECTS OF ENERGY TRANSFER

by

HOWARD A. RUBIN

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree 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.

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ABSTRACT

An Experimental Approach to the Assessment of the Informational Aspect of Energy Transfer

by

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The role of information processing in food web energetic transformations was experimentally tested. In these experiments, caloric value of food was normalized so that information transfer could be measured. The informational quality of food was experimentally demonstrated by 3 independent means: 1) decay of synchrony in optimally reproducing cultures; 2) switching time lags; 3) comparison of generation times on calorically normalized diets. Information utilization was measured in terms of cell cycle advancement. In monoxenic cultures, *Euplotes vannus* grew and reproduced fastest when fed a species of *Chlamydomonas* (generation time $\sim$4.0 hr), while it was longest ($\sim$7.8 hr) on a diet of *Dunaliella salina*, a very closely related alga. The generation time of *Uronema marinum* varied from a low of 2.7 hr to a high of 8 hr on various food organisms. On some mon-algal diets, $E_e \approx$ 20%, on others i /as $\sim$ 6%. The E_e of *Euplotes* varied from 2-12%. Reprodu: ion of the ciliates was often delayed when they were transferred -rom a diet of one algal species to a diet of another species. These switching time lags ($\gtrsim$ 2.5 hr) were interpreted as a consequence of adaptive enzyme formation, an information recognition response. Simple food web experiments tested whether the ciliates selected food to maximize their biotic potential. The information transfer system was modeled within the conceptual framework of automata theory. The model was successful in predicting the outcome of 80% of the mixed diet experiments. It also predicted, because of switching time lags, that a patchy environment should be more productive than a homogeneous one. Food quality and spatial distribution of predators and their prey are therefore important factors in population dynamics. A measure of informational gain in food web transformations was developed. "Cyberons", a new unit of information utilization realted to the energy saved per food organism processed, are defined and can be converted to Moles ATP or caloric equivalents.

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Introduction

Increasing public awareness of environmental impact has created a demand for ecological decision making without regard to fragility of the conceptual framework upon which modern ecosystem theory is built. Our views of ecosystems have undergone a rather rapid evolution since the introduction of the trophic dynamic concept by Lindemann (1942). Since then, concepts derived from thermodynamics (Linschitz, 1953; Morowitz, 1955, 1968), information theory (Shannon, 1948), and systems analysis (Patten, 1970) have been applied to ecosystem dynamics in attempts to give ecologists measures of system stability, function, and structure. (Conrad, 1971, 1972; Hairston, 1959, 1968; Levin, 1970; MacArthur, 1955; Margalef, 1958; Odum, E.P., 1953, 1969; Slobodkin, 1961; Smith and Slatkin, 1973).

Though dramatic advances have been made in certain subsets of ecosystems analysis, a coherent picture of ecosystem structure, function, and stability has yet to be developed. By their nature, ecosystems are extremely complicated and "noisy" (somewhat unpredictable in their behavior; Zwanzig, 1973). Contemporary analysts realize this, and most attack the problem by either extracting manageable portions of the problem or abstracting, compartmentalizing, and generally conceptualizing the system or subsystems in which they have interests.

By inference, some of the properties of the larger systems are deduced (Patten, 1970). Following rapid advances in computational methods and wider availability of computers, ecologists have been increasingly concerned with the quantitating aspects of their discipline (Margalef, 1973). This renewed emphasis on quantification has in turn generated greater awareness of the softness of our data on ecosystem properties, (Lee _et al_., in press; Mann, in press; Margalef, 1973).

Thermodynamic considerations have underlain all the general ideas of energy flow in ecosystems. The energy flow concepts is a way of describing the number and type of organisms within the system of concern and the rate by which energy is transformed, and materials circulated within and/or to adjacent systems, as the system functions. Historically (Lindemann, 1942), and even contemporarily (Margalef, 1973; Morowitz, 1968 ; Odum, E.P., 1969), energy flow is usually considered in, or translated into caloric terms. Calorific value is measured relatively easily (Paine, 1963). Many sophisticated models and simulations have been organized to describe ecosystem functions or bits of them in caloric terms (Conrad, 1972; Odum, H.T., 1957; Patten, 1970). Briefly, each species population or assemblage of "similar" species on the same trophic level is (are)

quantified in terms of calorific energy content and nodal position in a food web (Gallopin, 1972). The system is then treated as an interconnection of energy transducers, each realizing a transfer function associated with a particular compartment. The mathematical framing of these models is in the form of differential equations which readily lend themselves to computer simulation and solution.

This approach has many flaws and ignores some of the basic properties of living organisms and biological communities:

1. The uniqueness of the species, or in other terms, the fine biological distinctions between species.
2. The capacity of organisms to regulate, within bounds, their activities and life processes, including the rates at which they expend energy and accumulate it.
3. Collective attributes of communities beyond those of the subordinate populations.

Many biologists have difficulty in understanding the application of information conçepts to ecosystems and their dynamics despite pioneering papers by (Margalef, 1956; Odum, H.T., 1956; and Patten, 1959), and the current wide applications of information principles and systems optimization in molecular biology and genetics (Jacob and Monod, 1956). Initial applications of information theory to living systems were highly abstract and statistical (Johnson, 1970). Information was described in terms of increasing degree of certainty,

design, orderliness, regularity, uniqueness, and specificity, and expressed in terms of the negative of entropy (Brillouin, 1951, 1956) as:

$$I = -S = -k \ln P$$

where:

I = information; k= natural constant;
P= probability of obtaining a particular quantum orientation

Using such an approach, Dancroff and Quastler (1952), calculated the atomic orientation of a mature man as 2×10^{28} bits and Patten (1959) computed that Odum's Silver Springs community consumed 3×10^{24} bits/cm^2/yr. While theoretically interesting, even Patten's approach was too abstract for anything but a generalized application to ecosystem thermodynamics. This need not be. Classical energy flow ideas (reviewed by Morowitz, 1968) can be integrated with information theory to give a more realistic thermodynamic picture.

Partial measures of ecosystem information are in wide use today (Johnson, 1970; Ryan, 1972). Most common are various species diversity indices (Pielou, 1966; Shannon-Weaver, 1949) and stability measures (Conrad, 1971 ; MacArthur, 1955). These indices have been used to compare ecosystem development and pollution effects (Patten, 1969). System well being and stability is considered a function of the number of nexues in the food web (Hairston *et al*., 1968). The greatest drawback in utilizing informational transformation in studying ecosystem dynamics has been a general lack

of experimental methods and data which would enable one to relate information and the parallel calorific transfers in the same system.

This weakness is particularly apparent when one tries to make practical applications of species diversity indices. Diversity indices give little insight into the functional and dynamic relationships among community members beyond Lotka-Volterra (1926) kinetics (May, 1973). It is assumed that the frequency of interactions is proportional to the product of the densities of the interacting species (Hairston, 1959; Smith and Slatkin, 1973). For the first rough approximation, these assumptions are probably as good as any other we have today. We know, however, that many herbivores and predators do select their food, spend different amounts of energy capturing food (Marten, 1973; Schoener, 1971), or assimilate food species at different rates, (i.e. Dunstan, 1972, 1973; Lee _et al_; in press, Murdoch, 1969; Salt, 1968). General optimization theory would predict that other predator-prey energy conserving relationships would evolve and most hold in biological system (Cody, 1974; Marten, 1973; Rosen, 1967).

New developments in synchronization techniques (Prescott, 1967) and general acceptance of optimization theory by molecular biologists have set the theoretical and practical

stages for advancing ecosystem energetic theory. Micro-organisms, and presumably higher organisms, conserve energy by controlling their metabolic machinery to ensure orderly processing and synthesis of needed enzymes and metabolites in an efficient manner. Each specific pathway comprises a number of reactions catalyzed by specific enzymes. Regulation of metabolic activity is exerted particularly at early branching points through:

1. regulation of enzyme synthesis and
2. regulation of specific enzyme activity.

Both are mediated by compounds of low molecular weight which are either formed in the cell as intermediary metabolites, or enter it from the environment as food.

In assessing the role of genetic coding we can liken the cellular processing programs to modern computer programs. We can consider some operons analogous to subroutines and co-routines. It is logical that in the cell, as in the computer, such a sequence of routines will have multiple entry points and various branch points to allow skipping of routines that are not necessary at a particular time. If an organism receives an input compound which it must normally synthesize, it may, if it has the ability, skip over that portion of its programming that would act to synthesize it. If we view optimal processing as maximizing

potential energy utilization in order to advance the growth and reproduction of individual organisms or species, these assumptions make sense (Schroedinger, 1945). I believe that the operon concept ought logically to be extended to the organismic and community levels of interactions. There is substance to this proposition even though it is usually not recognized by most ecologists as a facet of energy flow. Most of the evidence comes from nutritional studies but the best comes from gnotobiotic studies of protozoa.

The literature is replete with examples of the effects of diet on morphogenetic changes in protozoa, (i.e. Tetrahymena vorax, Kidder, 1951; Allogramia, Lee and Pierce, 1963, 1968; Allogromia laticollaris, Lee, McEnery, Rubin, 1970). Most protozoan studies of diet effects have utilized Tetrahymena pyriformis because of its availability in axenic cultures and ease of culturing. It is assumed that other organisms, so far unstudied, will also demonstrate these effects.

In a now classical experiment, Cameron and Nachtwey (1967) synchronously grew cultures of Tetrahymena pyriformis in three different media; Protose peptone (PP); enriched defined (ED); and minimally defined (D). The cultures had been synchronized using thermal shock methods (Hotchkiss, 1954). Significant

differences in their generation time were found on each medium with a five fold slower time on the less complex media (D). This was accompanied by phase shifts in the normal cell cycle with the G_1 and S phases lasting longer and accounting for proportionately longer shares of the cycle. One can interpret these results in cybernetic terms (Patten, 1959). Unicellular herbivores, and by extension, higher forms, can be thought of as cybernetic processors of food with preprogrammed (genetically coded) processing options. The optimization principle (Rosen, 1967) dictates that it is energetically advantageous for the organism to utilize available organic compounds in its food instead of synthesizing them from simpler metabolites at the expenditure of energy. Presence of required metabolites could act in a feedback loop to advance the cell cycle and skip a portion of the processing programs. The net result of such a "program jump" would be an advancement of the cell cycle and a saving of ATP.

Cyberneticists would interpret this savings of energy as a realization of information recognition and transfer. In processing a food, a consumer destroys much existing information and encodes new forms (Hubell, 1973). Information encoded in organisms takes many forms, needed molecules, organelles, organs, and other structures and has cost the

organism energy, usually in the form of phosphorolated nucletides. Dismantling and retrieval of the basic components also requires energy. Though there is evidence that certain organelles can be directly incorporated by the consumer to yield an energy savings (Trench, 1973) the energy expended in structural synthesis is almost always lost. On the molecular level, however, greater possibilities for energy scavenging probably exist.

Lee, et al (1974) speculate that predators may have more than one type of nutritional relationship to food depending upon their ability to sweep macromolecules into their metabolic streams. Many molecules may be totally degraded and fed into general metabolic energy yielding pathways (Morowitz, 1968). Other may only be partially decoded and degraded, and some are not decoded at all because they are recognized as being essential nutrients.

The latter two categories are the crux of this study. Vitamins are well recognized examples of essential nutrients but most ecologists don't think of them in terms of either information or thermodynamic constructs. Evolution would seem to favor the development of organisms which could maximize their energy by minimizing food processing costs through superior efficiency of informational energy in their food. If this is true, then there are food web transformations

which cannot be measured calorically and it follows that this energy should be measurable in some form.

Synchronous culture techniques developed by cell biologists (Lorensen and Vankataramen, 1974; Prescott, 1974; Scherbaum and Zeuthen, 1956) offer the ecologist the best initial approach to measuring food processing modes. If all consumers are at the same metabolic and cell cycle stage and are given two foods of equal caloric value, one should be able to detect differences in information processing and utilization if it exists. One should also be able to detect and measure food switching (food recognition) times by observing lags in cell cycle advancement.

The aims of this study are therefore:

1. To measure, model, and test experimentally information flow in one step laboratory food chains.
2. To compare the informational processing abilities of two herbivorous organisms from the same habitat eating the same food.

This is being done with the hope of advancing ecological systems analysis to the next stage by incorporating information theory with energy flow concepts to yield a complete thermodynamic picture.

Materials and Methods

The following steps were involved in analysis and evaluation of information flow to the test animals in the experimental laboratory food webs:

1. selection of consumers and potential food organisms
2. measurement of respiration rates
3. measurement of food uptake rates by the consumers
4. calorific measurement
5. measurement of consumer ATP pool
6. nutritional assays
   a) generation time
   b) ecological efficiency
   c) calculation of food dependent synchrony decay rates
   d) food switching (metabolic recognition) times
   e) food preferences
7. modeling

1. Selection of consumers and potential food organism

From among the large selection of experimental organisms in the Marine Microbial Ecology Laboratory, two ciliates, *Euplotes vanus* and *Uronema marinum* were chosen as the consumers for comparison because of their extreme size differences

and feeding habits. Euplotes vanus feeds in a two dimensional space by grazing on surfaces. Uronema marinum, a hymenstone ciliate with prominent sail-like oral membranelles, feeds in three dimensional space by rotating and scooping food from the water column. Both ciliates are common inhabitants of salt marsh littoral and sublittoral and sublittoral epiphytic communities. Uronema is also often found in the pelagic community while Euplotes can sometimes be isolated in the bentho-pelagic communities.

Stocks of ciliates and potential food organisms were cultures exenically in Pyrex screw-capped test tubes (20 cm. x 125 cm) in 10 ml. of medium. Medium "S" (Appendix) was used for algal stock and "B" (Appendix) was ued for the ciliates. A variety of algae and diatoms from their natural habitat were selected as potential foods: (S8) Nitzchia acicularis, (38) Chlorococum spp (S41) Nanochloris, (S93) Chlamydomonas sp(S94) a chlorophyte (S95) Dunaliella salina, (S98) a chlorophyte (RF-8) Amphora spp, or (9) Cylinderotheca closterium (BL-27) Clyndrotheca fusiformis, (PB-6) Nitzchia frustulum (Pb-8) Nitzchia sp, (Pb-13) Nitzchia hungaria

2. Measurement of respiration rates

The respiration rates of each of the experimental organisms were measured with the aid of a Gilson differential respirometer Model GRP-14. In order to slow reproduction and avoid photosynthetic effects, the algae were removed from the light and the cultures individually wrapped in aluminum foil for 24 hours preceding respiration measurement. Experimental measures were replicated ten fold.

The potential food organism and *Uronema marinum* were enumerated in an American Optical Bright-Line hemocytometer. The volume of *Euplotes vanus* is too large to fit in a hemocytometer and therefore they were counted in a Sedgewick-Rafter counting chamber.

3. Measurement of food uptake rates by the consumers

Tracer feeding is generally regarded as one of the standard quantitative methods of determining food uptake in small animals (Lee *et al*. 1969; Lee and Muller, in press). A prerequisite to application of this technique is the ability to effectively separate the consumer from the radionuclide labeled food and effective control or evaluation of nuclide recycling. (Conover and Francis, 1973). Some experiments had previously been done in our laboratory to determine the feasibility of separating ciliates from their food by either

filtering or centrifugation. Neither method was effective with Euplotes or Uronema.

In feeding experiments, potential food organisms were inoculated into the side arms of respirometer flasks. As before, the algae were kept in the dark for 24 hours prior to the experiment. To avoid growth medium carry over, the algae were harvested by centrifugation and asceptically resuspended in minimal medium, (medium "B"). The test ciliates were placed in the main body of the flask. Experiments were done in dectuplicate.

Equilibration lasted 90 minutes; readings were recorded at 15 min. intervals for 1 hour. After 2 1/ 2 hours (90 min. ± 60 min.) the algae in the side arm was mixed with the ciliates. Respiration of the mixed system was observed at 15 min. intervals for an additional two hours. Controls included:

1. unmixed flasks containing ciliates in the main body and food in the side arm;
2. ciliates alone;
3. food alone.

The experiments were timed to minimize the effects of growth on respiration and were shorter than minimum ciliate generation time. When concentration was not a variable, food was in excess.

Decrease in total respiration after mixing was used as a measure of feeding. Feeding rate was estimated by calculating the change in respiration of the whole system using the relation:

$$\frac{dR}{dt} = -r_c R_c N_c e^{-r_c t} + -r_f R_f N_f e^{-r_f t} + - N_{fe} r_f$$

where:

R_c	is ciliate respiration per individual
R_f	is food respiration per individual
r_c, r_f	is the intrinsic rate of increase of ciliates and food
N_c, N_f	is the initial population of ciliates amd food
N_{fe}	is the number of food organisms eaten
R	is the total system respiration
t	is the time and $t << r_c$, r_f

The food saturation level was determined as the food concentration above which there was no increase in uptake. The lower threshold level was calculated as the food level below which uptake was erratic and could not be distinguished from background variations.

4. <u>Calorific measurement</u>

The calorific value of each experimental food was measured with the aid of a Parr bomb calorimeter. Organisms for

these measurements were harvested by centrifugation from batch cultures grown in 60 ml. of medium "B", washed quickly and gently in diluted saline and dried to a constant weight and pelletized. The pellet was weighed and placed in the calorimeter. Since the measurements were relatively close, only 5 replicate determinations were made.

5. Measurement of consumer ATP pool

ATP estimates were made both directly and indirectly for each ciliate. Direct measurements were made with the aid of a JRB ATP photometer. Ciliate cellular material was concentrated by filtration. The moist filter was immersed in 5 ml.of boiling TRIS buffer and frozen until analysis. For each replicate, a constant volume of 0.2 ml enzyme preparation and 0.5 ml sample was used. Indirect measures were calculated by extrapolation from respiration rates using Forest's (1971) method.

6. Nutritional assays

a) Generation Time

Cultures of the two ciliates were synchronized by application of thermal shock techniques. (Lorenzen and Vankataran, 1974, Prescott, 1964). The effectiveness of various thermal shock cycles in inducing synchrony was analyzed with the aid of a Coulter Counter model ZBI equipped with a P 64 size distribution

analyzer and plotter. The basic Coulter Counter Module recorded total count within a chosen band width while the distribution analyzer stored data on counts in individual size classes within theband for graphing on the plotter. In advance of synchronization, stock cultures of each ciliate species were grown with an unidentified chlorophyte (S93), harvested by centrifugation, and inoculated into a series of Pyrex screw-capped test tubes (20 mm. x 125 mm.) with 10 ml. of medium "B". The ciliate cultures were then incubated in the dark in a programmable environment chamber, Sherer CER-78, for 72 hours. Size distributions within the populations were plotted by the Coulter Counter for determination of the degree of synchrony. Three temperature cycles were tested:

1. 12 hours at 25° C and 12 hours at 30° C;
2. 12 hours at 22° C and 12 hours at 28° C;
3. 16 hours at 25° C and 8 hours at 28° C.

Regime 3 was most effective in inducing synchrony (see results) and therefore used in all subsequent experiments. Controls were ciliate populations incubated at 25° C.

Generation times of the synchronized consumers on different diets were measured in the presence of excess food. Food concentrations were normalized with respect to their caloric contents. The ciliates were enumerated after 12 and 24 hours. Ten replicates were made for each

ciliate/food combination. Generation times were calculated as follows:

$$G_T = t \times \log_2 \left[\frac{P_t}{P_0} \right] -1$$

where:

t is time of incubation

P_t is the ciliate population at harvest

P_0 is the initial ciliate population

b) Ecological Efficiency

The ecological efficiency of the ciliate population (conversion of ingested carbon into body tissue) was calculated from the food uptake rates and generation times. The growth of the population was calculated by:

$$P = 30\% \times D_w x f_n$$ (Lee and Muller, 1968)

where

30% = estimate of the carbon percent dry weight

D_w = dry weight of a single organism

f_n = population size

Ecological efficiency for each ciliate feeding on each species of food was calculated as

$$E_e = \frac{P}{I}$$

where

P = production (defined above)

I = ingestion

c) and d) Calculation of food dependent synchrony decay rates and food switching (metabolic recognition) times.

Food was also in excess in synchrony decay and food switching experiments. As before, food for experiments was ascepticalyharvested from growth medium by centrifugation and resuspended in minimal medium "B". Synchrony decay was calculated from ciliate size distribution data obtained by means of the Coulter Counter and accessories described above. Measurements were made at intervals which correspond to the generation times on each food. Populations were sampled for three successive generations. Rooney's method (1972) was used to calculate the degree of synchrony. Controls were unfed ciliate populations in minimal defined media.

A combinatoral experimental design was used in switching experiments. All permutations were tried. The populations of ciliates used in switching measurements were harvested by centrifugation 24 hours before beginning the experiment and resuspended in fresh media without food. Before the new food was introduced at the initiation of each experiment, the residual food, centrifuged with the ciliates, was reduced by ciliate activity to very low levels, which in most cases were below the lower feeding threshold concentration.

Cells in switching experiments remained under the synchronizing regime during both preincubation and experimental phases. Transfers from one species to the same food species served as manipulation-shock controls. Generation times were calculated for each ciliate/food switch. The new generation time values were compared with the previously calculated generation times. The period between growth on one food and the time delay before the onset of the first division was called switching-time-lag and was calculated as follows:

$$T_L = G_{T_1} - G_{T_2} \quad x \quad \log_2 \left[\frac{P_{T_1}}{P_0} \right]^{-1}$$

where:

T_L	is switching - time - lag
G_{T_1}	Generation time of synchronized culture growing continuously on the reference food
G_{T_2}	is the observed Generation time on the food after switching
P_{T_1}	is the normal expected population after time "t"
P_0	is the inoculum size at time 0

e) Food preferences

Synchronized ciliates were inoculated with two food species both at feeding saturation concentrations. Food

organisms were harvested as before. After 24 hrs. the ciliates were enumerated and generation time calculated. Controls were ciliates fed only one algal species. Experiments were replicated two times.

7. Modeling

Among the types of models of natural systems of growth and development recently formulated (Odum, H.T., 1970, Patten, 1969, Williams, 1969) models based on the theory of automata (Arbib, 1969, 1970, Apter, 1967, Pask, 1969, Rubin, 1971) seem most applicable to the type of problem being studied. Automata models realize populations as nets of finite state machines. A finite automaton is quintuple:

$M =$	$(X, Y, Q, \gamma, \lambda)$
X:	is the input set
Y:	is the output set
Q:	is the state set
$\gamma : Q x X$	is the next state function
$\lambda : Q x Y$	is the next ouput function

In the proposed model, the ciliates are treated as "black boxes" or processing machines with specific inputs and specific end products (Fig.1). Food and other environmental input factors are represented by the set X. In formal mathematical terms, X is an infinite set. However, the organism as modeled,

is not effected by every possible member of X, i.e. it has limited temperature, salinity, pH, etc., ranges and can not eat or digest every possible food. The subset of useable input is represented by X_r. Growth (G), reproduction (D), Energy storage (Ge), waste energy (L)*, respiration (R), and excretion (W) are included in the output set. When D is output, a complete copy of the automaton is produced and allowed to function independently within the system (Apter, 1967). All new automatons start in an initial state denoted by q_o. At any instant, the animal is at some life cycle and metabolic state (q_k). Q, the set of states, is actually an n-tuple of substates denoted by a single meta-state q_k. The f_i represents a food in X_r. The states q_1 through q_n are processing states for utilization of food species f_1 through f_n. To reach the final pre-reproduction processing state, the automata must proceed through a series of substate transitions corresponding to advances along metabolic pathways. Many series of transitions may be occurring simultaneously. The number of substates in particular channels and the number of active channels determine processing time. The processing (generation time) may vary as a function of the input characteristics, i.e. particular food species, mixtures of food species, external conditions, etc. The model can also account for changes which may be necessary in the program as a consequence

of changes in X_r. Some programs are constitutive, that is they are always present; other programs are adaptive, that is, they are present when needed but have a finite existence and must be reconstructed by the automaton from memory, when necessary, resulting in some measurable time delay (switching time). The model required some means of input recognition to ensure orderly and efficient processing. This is modeled by a finite state acceptor, a binary output construct, which parses input to substrings of decreasing levels of complexity until the input components can be recognized and processed along some channel. A finite state acceptor of strings with a vocabulary represented by T, is a machine whose input set 1 is from T and whose output set has two members, 0 and 1. If the output is 1, the string is accepted (recognized). A state of the recognizer which produces an output of 1 is an accepting state. (Fig.2) In our model, T corresponds to X_r which is repeatedly parsed. After each parse the substrings are each processed by the recognizer. Any string not recognized is parsed again and reprocessed. When a component is recognized by the acceptor, it is forwarded to the proper processing channel.

The simulation of this model used a program written in FORTRAN IV and executed by an IBM 360/50 computer.(see appendix) The environment was represented as a cubic tesselation containing 4096 lattice points. When population size was not an initial condition, 100 ciliates of either or both species were the inoculum. Abiotic conditions were not varied in these simulations. The simulation program used direct measured experimental data, i.e.:

1. feeding rate on each,
2. generation time;
3. switching time lags;
4. reproduction rates of the various species of algae at 25° C

(Data from Drs. N. Saks and W. Muller). Variables were population sizes, distribution of food, and food quality. The following simulated microcosms were investigated:

I. <u>A single ciliate species with</u>

a) a randomly distributed food of low informational value and patches of a food of high value

b) a randomly distributed food of high informational value and patches of a food of low informational value

c) both food types randomly distributed

II. Two ciliate species

a) patches of two food species, each having a high informational value for only one of the ciliates

b) patches of a single food of high informational value to both

c) a randomly distributed single food species of high informational value to both

d) in the same environment as in "c" but with a delayed inoculum of the second species of ciliate

e) patches of five different foods - 3 foods of high informational value to only one ciliate, 1 food of high informational value to the other ciliate, 1 food of value to both.

f) with the same foods as in "e" but randomly distributed.

The results of the simulation were displayed at 10 day intervals for 365 days. Spatial distributions of all organisms, population sizes, and biomass were recorded. Each simulation was replicated ten times to take into account the stochastic nature of the model. Representative results of each class of simulation are presented.

RESULTS

Respiration

The respiration of Euplotes vanus (8.1, µl CO_2/mg dry wt/hr) is approximately half that of Uronema marinum (15.0, µl CO_2/mg dry wt/hr). Algae tested had a wide range of respiration rates (Table 1) with a maximum of 58, µl CO_2/mg dry wt/hr for the diatom Amphora sp. (RF-8) and a minimum of 3, µl CO_2/mg dry wt/hr for an as yet unidentified chlorophyte (S98).

Feeding

Feeding was easily measured by the new respirometric method (Lee and Muller, in press) employed. If the food was eaten, (i.e. Fig. 4,5) respiration of the mixed system dropped; if not, respiration was indistinguishable from unmixed cultures (i.e. Fig. 6,7). S93, Chlamydomonas sp was eaten in the greatest amount by Euplotes (2 mg/mg dry wt ciliate/hr.). Two species of Amphora (Pb-6, RF-8) were not eaten at all. Data are summarized (Table 2). Equalizing their mass on a dry weight basis, Uronema marinum, on the average, fed at approximately the same rate as Euplotes vanus (Table 3). Uronema ate the most of Amphora spp., the diatom species not consumed at all by Euplotes. As could be predicted from general theory (Lotka-Volterra), within limits, feeding was found to be a function of food density. Upper and lower threshold for feeding were identified as the points where sharp changes in slope were noted (i.e.Fig.8).

In both ciliates, feeding seems erratic, or can not be detected by the method employed, below 10^5 algal cells/ml. Saturation level was reached at about 10^7 algal cells/ml. The most meaningful concentrations of feed for each ciliate food mixture are tabulated (Tables 2,3).

Caloric Content

The algae tested had caloric values within the range 7.5 cal/g (± 5%) to 11.3 cal/g (± 5%), Table 4). At the low end of this range was S95 *Dunaliella salina*, and at the high end S98 an unidentified chorophyte It is of interest to note that 7 of the 14 species analyzed had calorific values within the narrow band 8-8.7 cal/gm.

ATP Analysis

Results of both direct and indirect measures of ATP content of the ciliates are summarized, (Table 5). The indirect measures, calculated by extrapolation from respiration rates, were almost a constant 80% of the direct readings by ATP Photometer. *Euplotes* has an ATP pool on the order of 10^2 greater than that of *Uronema*. (10^{-10} mole/g vs. 10^{-12} mole g).

ATP content was calculated as follows:

$$\text{Moles ATP} = \frac{\mu/CO_2 \text{ hr}}{22.4 \times 10^6} * \frac{36}{6}$$

where

μ/ CO_2 hr = respiration rate

22.4×10^6 = number of μ/CO_2/Mole CO_2

$\frac{36}{6}$ = ratio of ATP production to CO_2 respiration

Generation Time

Euplotes vannus grew and reproduced fastest when fed S 93, Chlamydomonas sp, GT = 4.04 hr. It took almost twice as long for Euplotes to reproduce on a diet of S95 Dunaliella salina, GT = 7.79 hr. Other values fell between these two extremes (Table 6).

Uronema marinum, in most cases, has a shorter generation time than Euplotes vannus (Table 7). Uronema reproduced most rapidly on a diet of S 94 a chlorophyte (GT = 2.7 hr). Growth and reproduction approached that of the starred controls on one of the poorest food sources S 98, another chlorophyte (GT = 8 hr). The average generation time was skewed toward the low end of the range. Several species of algae, S 93 and S 94, were eaten in rather large numbers by both ciliates and resulted in short generation time. Some algal species had differing effects on each of the ciliates. Some stimulated the

growth of one ciliate (i.e. S 95 for *Uronema*; S 98 for *Euplotes*) but not the other.

Ecological Efficiency

Uronema was the ecologically more efficient of the two species tested. When logarithmically growing and fed strains of chlorophytes S 93, S 94, and S 95, its ecological efficiency approached 20% (Table 8). However, on a diet of another chlorophyte, S 98, its efficiency dropped to only 6%. Maximum ecological efficiency of *Euplotes* was 10-12% on two of the same species of algae, S 93 and S 94 (Table 8). Of the foods eaten lowest efficiency (2%) was found on a diet of S 95. Under the experimental conditions, on the average, *Uronema's* efficiency was 12.4% (S.D.=4.1) while *Euplotes* mean efficiency was 5.8% (S.D.=2.2). In both ciliates most food was processed at less than one half maximum efficiency. In this regard both ciliate species can be considered specialists.

Synchrony decay

The Coulter Counter size distribution analyzer and Plotter was a simple and effective tool for analysis of synchrony decay. Diet strongly effected the rate of synchrony decay Figs. 9=12). Decay of synchrony, predictably, was greatest on the poorest food species, i.e. *Euplotes* when fed S 95, a chlorophyte, the food species on which it reproduced the slowest,

had the highest decay (.24/generation). The converse was also true, i.e. least decay for *Euplotes* was observed on a diet of S 93, another chlorophyte (.07/generation). All synchrony decay rates are tabulated (Table 9).

Similar results were obtained with *Uronema* (Table 10). Its best food minimally perturbed synchrony (.09/generation) and its poorest food, S 98, approached the maximum observed decay rate (.18/generation when grown on a diet of S 8).

Switching Time

Switching times were usually minimal when the switch was from an algal species associated with a high synchrony decay rate to one with a low decay rate. Minimal switching time for *Euplotes* was .3 hrs more than the controls in the switch from a diet of Pb-8 to S 93 and .2 hrs for *Uronema* in a switch between a diet of S 98 and S 93. (Table 11). At the other extreme, long switching time lags were found in diets in which both algal species were associated with high synchrony decay rates. The maximum switching lag for *Euplotes* (2.5 hr) was measured in the switch from a diet of Pb-13 to BL-25. A corresponding lag of 1.3 hrs was measured for *Uronema* grown first on a diet of BL-25 then switched to S 98. Long lags were also measured between diets in which both species were associated with slow synchrony decay rates, i.e. *Uronema* from S 98 to S 8 (1.01 hr), *Euplotes* from Pb-13 to BL 27 (2.56 hr).

Population growth on mixed diets

These simple food web experiments were designed to indirectly test whether the ciliates would select food species which would maximize their biotic potential. A model based on entropy considerations was also constructed (see Appendix). The theory embodied in the model would predict that if the two food species are present in equal number, if the species differ in information content, and if the food species are randomly distributed, then the ciliates will choose enough of the high information food (short generation time for the ciliate) to minimize the generation time of the ciliate. The model theory also predicts that it is possible for two low information content species (long generation time) to complement each other, resulting in a shorter net generation time on the mixed diet.

The basic validity of the model was supported by the experimental results. In 80% of the cases, the predicted generation time was within 5% of the observed value. The exceptions were mainly those diets in which both foods were similar in information content. Results are summarized (Table 12). When either ciliate species was grown on a diet of algae differing in information value to the ciliates, they reproduced at rates very close to thos observed when grown only on a diet of the most informational food. The generation time of *Euplotes,* for

instance, was 4.7 hr when fed S 93 (GT= 4.04 hr) and S 95 (GT= 7.97 hr). Although it was possible that two food species might contain complementary information which could result in a shorter ciliate generation time when fed together than when alone, this was not experimentally observed in any of the 90 combinations tested for either ciliate.

Modeling

Modeling was more successful in minimizing many field observations then might have been predicted at the onset of this work. If thermodynamic considerations govern the system, as in the simulation patchy distribution of ciliates and their food were more probable and more productive. Random community organizations eventually became patchy and cyclical.

Ia In the simulations in which a single ciliate species was placed in an environment containing a food of high informational value in patches and another food, randomly distributed, low informational content, the model ciliates fed selectively on the better food (Fig. 13a). Selection was realized by a rapid increase in ciliate population size when a patch of optimal food was encountered. Organisms the encountered the poorer feed continued reproduction and growth at minimal rates. The ciliates virtually ignored the poorer food at the boundaries

of the food patches. Patches of ciliates reached their maximum density after 30 days (Fig 13b). At this time, ciliate food uptake exceeded the reproduction rate of the food population. Feeding on the patches continued until the food density was below threshold level for the ciliate at which point the population started to decrease (day 50, Fig 13c). The ciliates feeding on the poorer food and reproducing much slower were not affected by this problem. With the absence of an abundant ciliate population in the depleted patch areas, the food organism population was able to regenerate to its previous level (day 100, Fig 13d). When sufficient concentrations were reached, and the new patches located by the randomly moving ciliates, ciliate patches again began forming and the whole cycle repeated (day 121, Fig. 13e). As environmental abiotic factors were not considered, the cycle repeated indefinitely (Fig. 13f).

Ib When the reverse food distribution was simulated, patches of a low informational value food and a randomly distributed better food, results were similar (Fig 14a,b,c,d). Initially the randomly distributed better food was grazed down to below the lower threshold level of detection by the ciliates. The patches of poor food were then the only area of feeding available to maintain the population. As

the poorer food was not efficiently processed, its patches remained fairly stable with a small population of ciliates feeding on them. The absence of an abundant ciliate population allowed the better food to grow without any grazing decreases. Patches were formed at which point the ciliates located the patch and exploited it by blooming (day 60). The cycle noted in the previous simulation were then initiated. (Fig. 14 e). A possible weakness in the data is indicated by the fact that all simulations involved equal food concentrations whether in patches or randomly distributed. Concentration effects have yet to be studied.

Ic When both of the foods were available in the environment in a random distribution, the ciliate population remained unproductive (biomass 2 grams) when compared with the patchy environment (200 grams at maximum) (Fig 15 a,b,c). This can be accounted for by the continual switching between foods necessitated by such an organisation. Equal coincidences of encountering either food prevented the ciliates from exploiting other one.

IIa When two species of ciliates with different information processing abilities were placed in a patchy environment of two foods, each of high value to only one ciliate, only one ciliate was able to achieve full biotic potential. Each ciliate was most abundant on the particular food it could process most efficiently with a low level of the ciliate present on the

same patch. The food patch depletion rate was dependent upon the generation time of the dominant consumer. The patches of food on which the ciliate with the shorter generation time grew, was depleted first. The population was then forced to migrate to the patches of food where the other slower reproducing ciliate was dominant. The competition for food on these patches prevented the second ciliate from achieving its full potential. However, as the depleted food patches regenerated, patches of the more efficient ciliate again developed. The system continued to cycle in this fashion. (Fig. 16)

IIb Competition for a single food of high informational value distributed in patches resulted in population distributions and population sizes that were a function of inoculum size, generation time, and a random variable. The element of chance determined which ciliate located a patch first and therefore had an exploitation advantage. Two such cases were documented (Fig 17 a ,b). In most cases the ciliate with the shorter GT was dominant after a given period of time in which it was able to counter the effects of initial coincidence. The single food was quickly overgrazed by both species and the entire population collapsed (time 70).

II c Competition for a single randomly distributed food of high information value to both ciliates resulted in a rather rapid extinction of both populations. As population centers were randomly distributed about the system and were not as spatially distinct as in the patchy systems, competition was more fierce, (Fig. 18). The system was only able to support one half the biomass (50 g) at its maximum, than the similar patchy system (100 g). The species with the shorter generation time was greatest in abundance, as it had a reproductive advantage.

II d The advantage of the species with the shorter generation time could be counteracted by decreasing its inoculum size in comparison with that of the other ciliate. If the inoculum porportions of the two species were in the ratio of their generation times, the dominance in the population could be shifted for a period of time (Fig.17B). In all cases, however, the less abundant species could catch up to the slower.

II e A natural environment for the two organisms was simulated by having five food species of different informational value present: Three of the foods were close to optimal for one ciliate, one optimal for the other, and one of high value to both. The same cyclic behavior of ciliate patch formation was observed.(Fig. 19) The generalist ciliate with 4 possible foods, was greatest in abundance,

however it patches were not as dense as those of the specialist, with only two available foods. The depletion time of the food patches was a function of the individual food uptake rate of the ciliate feeding on the patch and its generation time. The shared food species acted as a safety valve for the growth of both food organisms in the event that their primary patch feeding areas were depleted. It supported populations of both organisms at all times, but the combined population remained at a low level (50 g) compared with the biomass that could be supported when only a single species was growing on the patch (70 g).

II f When the same foods were randomly distributed, the specialist was not able to exploit its food source because of the interference in switching caused by coinsidence with other foods. (Fig. 20) It eventually was extinct and the generalist species was able to remain, using the shared food as a safety valve. Total system biomass was less than before, 40 g. because of inefficiencies generated by generalist switching lags.

Discussion

Nutritionists have long emphasized the importance of diet, but most ecologists have failed to give nutritional quality factors proper ecological perspective. The data obtained in this study clearly demonstrate that information is a part of energy flow in at least some food webs. Reproduction of the ciliates studied was neither a strict function of feeding rate nor coupled with the calorific values of the food organism themselves. Food quality was an important life cycle determinant. While it can be urged, *a priori*, and perhaps anthropocentrically, that mixed diets might be better than homogeneous diets, the data obtained in the present study do not support this view. The ciliate studied come from an extremely complicated *Aufwuchs* community where perhaps a hundred or more species are crowded into a single milliliter (Lee *et al*, 1973). Community productivity seems to be derived from a continuous series of blooms, that is rapid fluxes in the population structure, where many species are quite specialized and initially ecologically efficient (Lee and Muller, 1973). Aside from the present study which shows that the ciliates do not seem to be able to grow on every potential food organism, data on the foraminifera and nematodes from the same community reinforce this view

(Lee *et al*, 1966, 1973, 1974 in press, Tietjen et al, 1969, Tietjen and Lee, 1972, 1973). Three species of foraminifera from the community, for instance, ate significant quantities of only four or five of the more than thirty which were offered to them as food sources (Muller, 1972). Within bounds, feeding rate on the good food was proportional to concentration and followed Lotka-Volterra kinetics. Ecological growth efficiency was an inverse function of time dropping from the 10-20% range to less than 0.1% in a few weeks. We can now ask what does this food specificity and informational aspect of food quality mean in terms of our present ideas on community structure and food web dynamics?

Margalef (1973), in his recent critical review of the state of the art of ecological modeling, expressed his dismay at the paucity of fresh ideas in model formulations. He sensed little progress in the expanding literature since Volterra, Lotka, and Riley, Stommel, and Bumpus. Many of his major criticisms of contemporary modeling constructs underly the rationale for this thesis. In his colorful way, he compares most models as conceptualizations, however elegant. of ecological machines with workings of cogs, levers, wheels, etc. There are sets of inputs and a corresponding set of outputs and an almost

rigid deterministic linkage between them. Most models, according to Margalef, are closed with respect to materials, open with respect to energy, and described in the form of a set of deterministic differential equations which permit common solutions representing either a single state or a set of final states of the system. Not much is changed if stochastic considerations are introduced into the modeling behavior because as soon as probability laws are stated the model becomes for all practical purposes, deterministic.

His generalized equations have the form:

$$\frac{dN}{dt} = \sum_{j=1} a_{ij} N_i N_j + \sum_{j=1} b_{ij} R_j$$

Where the initial expression is a restatement of Lotka-Volterra kinetics and R_j represents the independent stochastic functions. Although most models are multi-dimensional, pecularly the most common missing dimension is not time but space. The importance of space and time have been discussed by both Margalef (1973) and Patten (1968) in general terms but to my knowledge their ideas have not been applied because deterministic solutions to such equations, i.e.

$$\frac{\delta^2 N_1}{\delta t \delta_z} = \sum_{j=1} f(N_i, N_j)$$

are really mathematically intractable because the function "f" is not clearly defined.

If one changes the modeling frame to automata theory, the problems of time and space can be solved because individuals can be embedded and function independently in a time-space continuum. Each automaton is deterministically constructed but its behavior in the system is stochastic. As in the real world, there are no finite solutions, only a spectrum of probable states at discrete times. It seems from the present simulations that the embedded automatons accurately mimic the spatial and temporal patterns observed in natural systems (MacArthur, 1968; Lee _et al_, 1974; Lee and Matera, 1972). Many modelers are beginning to concern themselves with spatial distribution of predators and their prey (Bulmer, 1974; Levin, 1974; Pulliam, 1974; and Salt, 1974). Unlike the modeling approach in this study, all have used deterministic constructs. Informational considerations, i.e. switching time, were neglected. Perhaps this may be a valid point of view for higher organisms. This remains to be tested. Although not incorporated into the present model because of the experimental difficulties in making the measurements, environmental grain factors (Vandermeer, 1972), a spatial consideration, can and should be part of the automata characteristics.

The ciliates in the present study are not typical of all animals because they appear to have fairly free running clocks. Their growth rate and maturation times are closely coupled. Other organisms, even protozoa like foraminifera, have more complicated life cycles which require developmental time. The present automata model can be modified to include this factor by making

the state transition functions time-variant. The outcome of some of the predator-prey interactions will be predictably different if the generation time of the predator is much greater than the prey.

Secondary productivity in our model was directly linked to temporal and spatial distribution of the various food oragnisms. Simulated environments with patchy food distribution were as much as 60 times more productive than environments which were randomly distributed with respect to equivalent food inocula. Since patchiness is a quality of many aquatic communities (Wiebe, 1969, 1970), one wonders if it is not a mechanism for lowering competition and increasing diversity of the habitat to provide more niches for highly specialized and very productive organisms. As such, the phenomenon favors exploitation of "Hi I" foods. This is logical if optimization principles (Schoener, 1971; Rosen, 1967) govern ecosystem development. This is not meant to deemphasize the importance of the converse situation which has same of the same optimal characteristics. Uniform, almost pure, montypic standing crops of some plants and their consumers are as highly productive as patchy ones and for the same reason.

In our simulations, interpatch distance (within critical bounds) directly affected secondary productivity through switching and inter- and intrapsecific competition. When patches of different species of food are too close, switching can become important. Switching,in a general sense, is a spatial phenomenon, but it usually not considered in this construct. Usually switching is considered only as a function of abundance relations

(Murdoch, 1968). The time necessary for a consumer to switch food sources is also not usually considered even though this time is now shown to be nontrivial. At the extreme, switching time can equal generation time. Because of recent advances in the molecular biology of ciliates and bacteria (Stebbing,1974; Hirsch and Engleberg,1973),it is easy to understand some of the functional bases for switching in protists, whether switching can be an important factor in metazoa is a question begging for an answer.

An important consideration in the analysis of ecological growth efficiency, a food web quality directly a function of information transfer, is the realtive amounts of energy utilized for maintenance and for biosynthesis of new cellular materials. Mammalian cells growing maximally seem to require 65% of their total energy budget for maintenance, while the comparative figure for bacteria is only 10% (Stebbing, 1974).

At the present time, it does not seem feasible to attempt to find a common measure which can be quantitatively used to evaluate the information in all food-consumer relationships. Initially we thought it unlikely that values could be obtained without performing an impractical number of experimental measures of great detail, a formidable task when one considers the microbial food web which can be in a single drop of water. But advances in our ever expanding knowledge of metabolic processing and the complexities of molecular organization given promise that we may soon parse the problem down to a more manageable level and also much more reasonable

proportions. (Stebbing, 1974). In a somewhat more limited context the data obtained do seem to lend themselves to the development of a comparative index of the relative informational value of the food organisms to the ciliates tested which can be translated into energetic terms. If some algae species used as food advance the cell cycle faster than others, even when their calorific values are the same, then food information is being processed by the ciliate to yield energetic advantage. Among other possibilities the consumer has to do less synthesis of new molecules.

The information processing abilities of the two test ciliates can readily be compared with each other on the basis of laboratory data obtained. Both grew best on the same two algal food species and perhaps we might deduce that both have similar abilities. However, the third ranked food for *Uronema marinum*, S 95, was the poorest food for *Euplotes*. The converse was observed in the case of food organism S 8, on which *Euplotes* prospered and *Uronema* reproduced slowly. There were also two foods, Pb-8 and Pb-13, on which *Euplotes* was able to reproduce and *Uronema* was not. We can either conclude that both organisms have entirely different informational processing abilities or that they have some degree of processing similarity as exhibited on the best two foods shared by both. The latter is suggested

as both ciliates overlap in time and space in their natural habitat.

In comparison with other protozoa from the community, the foraminifera, the two ciliates studied seem to have different information processing abilities. Of the foram species whose nutrition is best known, *Allogromia laticollaris*, *Allogromia* sp NF, *Rosalina leei*, *Spiroloculina hyalina*, all grow better on mixed diets containing two or three species than they do in monoxenic culture. This suggests that the forams have less synthetic abilities than the ciliates and require growth substances which are not found in a single species of prey or found in limiting quantities in any one species of prey. The forams appear to be able to combine and utilize information from many sources selectively to optimize productivity over a short period of time. The ciliates were most productive on a monotypic diet and were able to maintain their efficiency. Interestingly enough, the two species of *Allogromia* which have been studied, have extremely plastic life cycles (Arnold, 1954; Lee *et al*, 1969; Lee and McEnery, 1972). On bacteria rich diets they reproduce primarily by binary fission and on diets enriched with various species of algae, they undergo budding, cytotomy, and schizogony. This suggests another adaptive mechanism present in these species, balancing cell cycle with nutritional input, really an optimization process. Our knowledge in this area will increase as more organisms are tested within the model framework.

For this analysis we calculated the net informational gain from processing a particular food species as a ratio of the consumer's energy expenditure to the informational and calorific content as follows:

$$I = \frac{(1-k) \quad x \quad GT_i \quad x \quad R_i}{GT_i \; x \quad F_i \; x \quad C_i}$$

where

I	is the net informational gain
GT_i	is the generation time of the consumer when when food i
R_i	is the respiration rate of the consumer growing on a diet of food i
F_i	is the ciliate feeding rate on food i
C_i	is the calorific value of a food organism of type i
k	is the percent of the consumer's respiration used for maintenance (Stebbing, 1974)

The numerator of the ratio represents the consumer's energy expenditure in processing the energetic and informational components of the food roganism required to advance its life cycle to the next generation. The denominator is the potential energy yield available from the food source. The food organism with the lowest I value which would still support continuous growth and reproduction of the ciliate species was chosen as a base to which all other food species could be compared (Tables 13 & 14). The difference between the energetic cost of growth on the lowest "I" food and other foods can therefore be expressed in terms of energy saved per food organism processed per consumer generation. Our units of energy saved are expressed as cyberons. This new unit of the informational gain in food web transformations

can be translated to other energy units through fundamental respiration relations following the reasoning of Forrest (1971). In order to readily interconvert ATP saved per generation to cyberons we have set the cyberon value equal to a high energy phosphate bond (= 15k cal.). Cyberons are practically calculated as follows:

$$\text{Cyberon content} = Cyb_{base} - \frac{(1-k) x GT_i x R_i x 36.0}{GT_i x F_i C_i x 22.4 x 10^6}$$

where

k, GT_i, R_i, F_i, C_i are defined as before

Cyb_{base} the I value of the food choosen as a base converted to ATP

From the experimental and simulation results there are obviously many questions remaining to be answered and new areas for exploration. The model and laboratory observations should be expanded to make them more realistic. Feeding and behavior patterns need to be considered as aspects of environmental grain. Abiotic and seasonal factors will help make the model more accurate. Coincidence data on appearance and abundance of organisms in field observations (some of these relationships are suggested in a paper now in press) could be used as a starting point. Laboratory tests of the effects of conditioning time on switching time lags could take many directions. Additional organisms on the same trophic level also should be tested so that

more realistic tests of the informational aspects of competition can be evaluated. Many experiments on the critical size and distance between food patches are suggested. The replica plating technique of Lederberg seems like a handy tool for doing this. Metazoans and other protozoa need be evaluated in the sample experimental framework. We already have such organisms available and preliminary work along these lines has been done (Lee *et al*., 1969). And finally, one would hope that nutritional and molecular biology studies will eventually advance to a point so that it will no longer be necessary to test every possible food web relationship. The general informational processing abilities of the consumer will be known and potential food organisms can be evaluated on the basis of their ability to provide this information.

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Identification Key

Species	Organism
8	Nitzchia acicularis
38	Chlorodocum sp
41	Nanochloris sp
93	Chlamydomons sp
94	unidentified chlorophyte
95	Dunaliella salina
98	unidentified chlorophyte
RF-8	Amphora sp
Bl-25	Cylindrotheca closterium
Bl-27	Cylinderotheca fusiformis
Pb-6	Nitzchia frustulum
Pb-8	Nitzchia sp
Pb-13	Nitzchia hungarica

TABLE 1

Respiration rates of the various organisms used in this study

Organisms	Respiration** (μl CO_2/mg dry wt/hr)
Euplotes	8.1
Uronema	15.0
S8	37.2
S38	20.0
S41	52.0
S93	43.0
S94	23.0
S95	10.0
S98	3.0
Pb6	20.0
Pb8	21.0
Pb13	18.0
BL25	3.0
BL27	2.0
RF8	58.0

*See key for identification

**All values ± 5%

TABLE 2

Feeding rates of Euplotes vannus* on various marine algae

Food** Organism	Food Count (X10^{6})	Change in*** Respiration After Mixing (ul/hr)	Food Uptake*** (X10^{-1} mg/mg dry wt/hr)
S41	2.5	- .6	6.25
S41	5.0	- .62	6.73
S41	7.0	- .63	6.71
S41	.5	- .45	4.79
S94	60.0	-1.	7.5
S94	30.0	-1.	7.1
S94	80.0	- .9	7.2
S94	.6	- .5	2.5
S95	.5	- .2	2.0
S95	2.5	- .15	1.5
S95	.5	.0	-
S95	10.0	- .4	2.0
S93	40.0	- .5	20.0
S93	20.0	- .4	17.0
S93	80.0	- .39	20.0
S93	.4	- .4	12.0
S8	.2	- .2	6.2
S8	.2	- .8	2.1
S8	20.0	0	0
RF8	.6	0	0
RF8	.3	0	0
RF8	60.0	0	0
RF8	10.0	0	0
BL25	2.5	0	0
BL25	5.0	- .2	2.6
BL25	25.0	0	0
BL25	1.1	0	0
BL27	2.2	- .2	4.3
BL27	1.12	- .9	2.1
BL27	.2	0	0
BL27	22.0	- .3	5.8
S38	2.2	- .9	5.5
S38	1.1	- .1	.6
S38	4.4	-1.7	9
S98	40.0	- .2	5.2
S98	20.0	- .3	8.2
S98	80.0	- .2	5.2
S98	4.0	0	0
Pb6	3.0	0	0
Pb6	1.5	0	0
Pb6	6.0	0	0
Pb8	5.0	- .2	3.
Pb8	2.5	- .2	3.

TABLE 2 (continued)

Food** Organism	Food Count ($X10^6$)	Change in*** Respiration After Mixing (ul/hr)	Food Uptake*** ($X10^{-1}$ mg/mg dry wt/hr)
Pb8	.5	0	0
Pb8	10.0	0	0
Pb13	4.5	- .2	.3
Pb13	.45	0	
Pb13	2.5	- .2	.3
Pb13	45.0	0	0

*Inoculum of $1X10^3$ cells/ml
**See key for identification
***Average of 10 replicates
****Values ±5%

TABLE 3

Feeding rates of Uronema marinum * on various marine algae

Food** Organism	Food Count($X10^6$)	Change in Respiration*** After Mixing (ul/hr)	Food Uptake**** ($X10^{-1}$mg/mg dry wt/hr)
S41	2.5	- .2	.83
S41	5.0	- .2	.83
S41	7.0	- .21	.875
S41	.5	- .1	.4
S94	60.0	- .25	5.45
S94	30.0	- .25	5.45
S94	80.0	- .15	4.09
S94	6.0	1.5	4.09
S95	5.0	.1	.34
S95	.5	0	0
S95	10.0	- .2	.6
S93	40.0	- .2	3.4
S93	20.0	- .1	1.7
S93	80.0	- .1	1.7
S93	4.0	- .15	2.5
RF8	6.0	- .2	9.8
RF8	3.0	- .17	7.3
RF8	60.0	0	0
BL25	2.5	- .15	.96
BL25	5.0	- .15	.96
BL25	25.0	0	0
BL25	1.1	0	0
S38	2.2	- .3	.66
S38	1.1	0	0
S38	4.4	- .7	4.4
BL27	2.25	- .1	.86
BL27	1.12	- .05	.43
BL27	2.25	0	0
BL27	2.25	.1	.86
S98	40.0	- .3	.41
S98	20.0	- .7	.92
S98	80.0	0	0
S98	40.0	0	0
Pb8	5.0	- .7	1.5
Pb8	2.5	- .6	1.3
Pb8	.5	0	0
Pb8	10.0	0	0
Pb6	3.0	0	0
Pb6	1.5	0	0
Pb6	6.0	0	0
Pb13	4.5	0	0
Pb13	.45	0	0

TABLE 3 (continued)

Food** Organism	Food Count($X10^6$)	Change in Respiration*** After Mixing (ul/hr)	Food Uptake**** ($X10^{-1}$ mg/mg dry wt/hr)
Pb13	2.5	0	0
Pb13	45.0	0	0
S8	2.0	- .6	.66
S8	1.0	- .8	.88
S8	.2	- .2	.22
S8	20.0	0	0

*Inoculum of $1X10^4$ cells/ml
**See key for identification
***Average of 5 replicates
****Values ±5%

TABLE 4

CALORIC CONTENT OF FOOD ORGANISMS

Algae*	Cel/gm**
S94	8.0
S93	8.0
S95	7.5
S38	8.1
S41	9.0
RF8	9.3
BL27	8.4
BL25	8.7
S8	7.7
S98	8.0
Pb6	9.0
Pb8	8.7
Pb13	7.2
S98	11.3

*See key for species identification

**Calculated following the methods of Paine (1953)

TABLE 5

ATP Content of Euplotes and Uronema

Ciliate*	JRB ATP Photometer** (Moles/mg)	Indirect *** (Moles/mg)
Euplotes	5.7×10^{-10}	4.9×10^{-10}
Uronema	2.3×10^{-12mg}	1.74×10^{-12mg}

*Measured during midpoint between divisions in synchronized cultures. Measurements represent average of 5 measurements.

**Calculated following the methods of Holm-Hansen (1967)

***Calculated following the method of Forest (1969)

TABLE 6

Generation time of Euplotes on various algae*

Food Organisms**	Euplotes Harvest***	Generation Time (hrs)****
Stark Media	660	10.00
S41	2300	5.6
S94	6000	4.06
S95	800	7.97
S93	6100	4.04
RF8	-	-
BL27	4700	4.32
S38	5300	4.13
BL25	890	7.74
S98	1200	6.4
Pb8	3200	4.9
Pb6	-	-
Pb13	1300	6.6
S8	2200	5.45

*Inoculum 100 synchronized Euplotes

**For species identification see key

***Harvest after 24 hr incubation. Average of 5 replicates

****Formula:

$$G_{\tau} = t * [\log_2 \frac{P_t}{Po}]^{-1}$$

where G_{τ} = generation time

t = time of experiment

P_t = population at time t

Po = initial population

TABLE 7

Generation time of Uronema on various algae

Food** Organisms	Uronema Harvest ($X10^4$)	Generation Time (hrs)
Stark Media	16	8.00
S41	12.6	3.01
S94	14.9	2.7
S95	14.3	2.81
S93	15.	2.75
RF8	10	3.44
BL27	8	4.00
S38	13.2	2.93
BL25	6	5.04
S98	4.5	7.9
Pb8	-	-
Pb6	-	-
Pb13	-	-
S8	5.5	5.98

*Inoculum of 10000 synchronized Uronema
**For species identification see key
***Harvest after 24 hr incubation. Average of 5 replicates
****Formula:

$$G_\tau = t * [\log_2 \frac{P_t}{Po}]^{-1}$$

where G_τ = generation time
t = time of experiment
P_t = population at time t
Po = initial population

TABLE 8

Ecological Efficiencies of Euplotes vannus and Uronema marinum When Fed on Different Diets.

Food* Organism	Ee** Euplotes	Ee** Uronema
S8	4%	7%
S38	6%	12%
S41	4%	11%
S93	12%	21%
S94	10%	21%
S95	2%	19%
S98	4%	6%
Pb6	-	-
Pb8	6%	-
Pb13	-	-
BL25	2%	7%
BL27	6%	9%
RF8		19%

*See **key** for specific identification

**Calculated as:

$$Ee = \frac{P}{I}$$

where P = production

I = ingestion

TABLE 9

Decay of Synchrony in *Euplotes* Populations Fed Different Diets

Food* Organism	Generation	Euplotes Count**	Synchrony Index***	Mean Decay Rate/Generation
Pb8	0	100	.93	
	1	195	.72	.18
	2	357	.43	
	3	722	.39	
S38	0	100	.93	
	1	212	.57	.17
	2	367	.43	
	3	745	.41	
BL25	0	100	.91	
	1	150	.52	.21
	2	335	.39	
	3	495	.28	
BL27	0	100	.87	
	1	152	.66	.17
	2	279	.42	
	3	549	.37	
S41	0	100	.92	
	1	215	.63	.20
	2	387	.42	
	3	762	.32	
S8	0	100	.93	
	5	221	.61	.20
	10	406	.52	
	24	2000	.32	
S95	0	100	.95	
	1	255	.52	.24
	2	573	.38	
	3	926	.21	
S94	0	100	.96	
	1	150	.87	.09
	2	420	.80	
	3	874	.69	
S93	0	100	.93	
	1	225	.87	.07
	2	401	.85	
	3	971	.72	
S98	0	100	.94	
	1	137	.65	.20
	2	392	.42	
	3	921	.33	
Pb13	0	100	.95	
	1	197	.59	.21
	2	340	.42	
	3	822	.31	

*See

**Average of 2 replicates

***Calculated as (Rooney, 1970)

TABLE 10

Food* Organism	Generation	Uronema** Count(X10^4)	Synchrony Index***	Mean Decay Rate/Generation
S38	0	2	.91	
	1	3.7	.86	.06
	2	7.6	.77	
	3	13.3	.73	
BL25	0	2	.92	
	1	4.2	.73	.15
	2	7.8	.51	
	3	12.7	.47	
BL27	0	2	.91	
	1	4.1	.75	.16
	2	8.0	.53	
	3	15.2	.46	
S41	0	2	.91	
	1	3.6	.85	.10
	2	7.5	.74	
	3	14.4	.61	
S95	0	2	.92	
	1	4.1	.87	.06
	2	8.0	.82	
	3	14.1	.74	
S94	0	2	.93	
	1	3.8	.87	.05
	2	7.7	.81	
	3	14.7	.78	
S93	0	2.0	.92	
	1	4.1	.88	.05
	2	7.8	.83	
	3	15.1	.77	
S98	0	2.0	.92	
	1	4.0	.78	
	2	7.6	.59	
	3	14.9	.41	
RF8	0	2.0	.91	
	1	3.9	.81	.13
	2	8.1	.67	
	3	15.6	.52	
S8	0	2.0	.91	
	1	3.7	.61	.18
	2	7.2	.50	
	3	14.0	.37	

*See

**Average of 2 replicates

***Calculated as (Rooney, 1970)

TABLE 11

Food Organism* From	To		Euplotes*** Switching Time/hrs	Uronema*** Switching Time
S98	S41		1.71	.56
S98	S94		0.30	.32
S98	S95		0.59	.34
S98	S93		0.30	.31
S98	BL27		1.39	.97
S98	S38		1.35	.41
S98	BL25		2.56	1.01
S98	S98	Control**	0.50	.2
S98	Pb8		1.17	-
S98	Pb13		2.09	-
S98	S8		1.73	1.11
S8	S41		1.71	.4
S8	S94		0.30	.37
S8	S95		0.59	.43
S8	S93		0.30	.31
S8	BL27		1.39	.86
S8	S38		1.35	.50
S8	BL25		2.56	.91
S8	S98		2.16	1.2
S8	Pb8		1.17	-
S8	Pb13		2.09	-
S8	S8	Control**	0.40	.23
Pb13	S41		1.71	-
Pb13	S94		0.30	-
Pb13	S95		0.59	-
Pb13	S93		0.30	-
Pb13	BL17		1.39	-
Pb13	S38		1.35	-
Pb13	BL25		2.56	-
Pb13	S98		2.16	-
Pb13	Pb8		1.17	-
Pb13	Pb13	Control*	0.48	-
Pb13	S8		1.73	-
Pb8	S41		1.17	-
Pb8	S94		0.30	-
Pb8	S95		0.59	-
Pb8	S93		0.30	-
Pb8	BL27		1.39	-
Pb8	BL25		2.56	-
Pb8	S98		2.16	-
Pb8	Pb8		0.27	-
Pb8	Pb13		2.09	-
Pb8	S8		1.73	-

*See key for identification

**Manipulation shock controls (see text)

***Average of 5 experiments per switch

TABLE 11 (continued)

Food Organism* From	To	Euplotes*** Switching Time/hrs	Uronema*** Switching Time
BL25	S41	1.71	.7
BL25	S94	0.30	.61
BL25	S95	0.59	.58
BL25	S93	0.30	.41
BL25	BL27	1.39	1.2
BL25	S38	1.35	.39
BL25	BL25 Control**	0.59	.27
BL25	S98	2.16	1.31
BL25	Pb8	1.17	-
BL25	Pb13	2.09	-
BL25	S8	1.73	.83
S38	S41	1.17	.56
S38	S94	0.30	.71
S38	S95	0.59	.82
S38	S93	0.30	.41
S38	BL27	1.39	.92
S38	S38 Control**	0.31	.23
S38	BL25	2.56	1.2
S38	S98	2.16	1.01
S38	Pb8	1.17	-
S38	Pb13	2.09	-
S38	S8	1.73	.86
BL27	S41	1.17	.71
BL27	S94	0.30	.4
BL27	S95	0.59	.47
BL27	S93	0.30	.39
BL27	BL27 Control**	0.32	.21
BL27	S38	1.35	.5
BL27	BL25	2.56	1.11
BL27	S98	2.16	.98
BL27	Pb8	1.17	-
BL27	Pb13	2.09	-
BL27	S8	1.73	.8
S93	S41	1.24	.7
S93	S94	0.62	.8
S93	S95	1.22	.71
S93	S93 Control**	0.30	.2
S93	BL27	1.01	.91
S93	S38	0.98	.72
S93	BL25	1.86	1.01
S93	S98	1.57	.77
S93	Pb8	0.85	-
S93	Pb13	1.52	-
S93	S8	1.26	1.3

TABLE 11 (continued)

Food Organism* From	To		Euplotes*** Switching Time/hrs	Uronema*** Switching Time
S95	S41		1.24	.62
S95	S94		0.62	.71
S95	S95	Control**	0.59	.27
S95	S93		0.62	.18
S95	BL27		1.01	1.01
S95	S38		0.98	.92
S95	BL25		1.86	1.21
S95	S98		1.57	1.01
S95	Pb8		0.85	-
S95	Pb13		1.52	-
S95	S8		1.26	.97
S94	S41		1.24	.8
S94	S94	Control**	0.30	.21
S94	S95		1.22	.5
S94	S93		0.62	.4
S94	BL27		1.01	1.2
S94	S38		0.98	.87
S94	BL25		1.86	1.31
S94	S98		1.57	.82
S94	Pb8		0.85	-
S94	Pb13		1.52	-
S94	S8		1.26	.89
S41	S41	Control**	0.39	.26
S41	S94		0.30	.63
S41	S95		0.59	.67
S41	S93		0.30	.52
S41	BL27		1.39	1.2
S41	S38		1.35	.53
S41	BL25		2.56	.87
S41	S98		2.16	.73
S41	Pb8		1.17	-
S41	Pb13		2.09	-
S41	S8		1.73	.69
RF8	S41		-	.5
RF8	S94		-	.46
RF8	S95		-	.43
RF8	S93		-	.42
RF8	BL27		-	.8
RF8	S38		-	.51
RF8	BL25		-	.79
RF8	S98		-	1.1
RF8	S8		-	.76
RF8	RF8	Control**	-	.71

TABLE 12

Food Combination	F_1*	F_2**	Euplotes Generation Time Observed	Euplotes Generation Time Predicted	F_1*	F_2**	Uronema Generation Time Observed	Uronema Generation Time Predicted
S8, S41	5.45	5.6	5.5	5.5	5.98	3.01	3.7	4.5
S8, S93	5.45	4.04	4.11	4.2	5.98	2.75	2.8	2.9
S8, S94	5.45	4.06	4.13	4.25	5.98	2.7	2.8	2.95
S8, S95	5.45	7.9	6.10	6.8	5.98	2.81	2.92	3.1
S8, S98	5.45	6.4	5.6	6.0	5.98	7.9	7.5	7.0
S8, Pb6	5.45	0	-	-	5.98	-	-	-
S8, Pb8	5.45	4.9	5.42	5.2	5.98	-	-	-
S8, Pb13	5.45	6.6	6.2	6.0	5.98	-	-	-
S8, BL25	5.45	7.7	5.7	6.5	5.98	5.04	6.1	5.5
S8, BL27	5.45	4.32	4.9	4.8	5.98	9.04	5.7	5.1
S8, RF8	5.45	0	-	-	5.98	3.44	4.1	4.6
S38, S41	4.13	5.6	4.3	5.0	2.93	3.01	3.1	2.93
S38, S93	4.13	4.04	4.06	4.1	2.93	2.75	2.9	2.94
S38, S94	4.13	4.06	4.1	4.15	2.93	2.7	2.81	2.91
S38, S95	4.13	7.9	4.22	4.54	2.93	2.81	2.8	2.86
S38, S98	4.13	6.4	5.1	5.0	2.93	7.9	3.1	3.2
S38, Pb6	4.13	0	-	-	2.93	-	-	-
S38, Pb8	4.13	4.9	4.5	4.4	2.93	-	-	-
S38, Pb13	4.13	6.6	5.1	5.0	2.93	-	-	-
S38, BL25	4.13	7.7	5.02	5.6	2.93	5.04	4.1	3.9
S38, BL27	4.13	4.32	4.20	4.25	2.93	4.0	3.2	3.5
S38, RF8	4.13	0	-	-	2.93	3.49	3.11	3.2
S41, S93	5.6	4.04	4.16	4.2	8.00	2.75	2.8	2.8
S41, S94	5.6	4.06	4.6	4.32	8.00	2.7	2.75	2.8
S41, S95	5.6	7.9	5.9	6.8	8.00	2.81	2.92	2.9
S41, S98	5.6	6.4	5.7	5.8	8.00	7.9	3.13	3.3
S41, Pb6	5.6	0	-	-	8.00	-	-	-
S41, Pb8	5.6	4.9	5.0	5.1	8.00	-	-	-
S41, Pb13	5.6	6.6	5.8	6.2	8.00	-	-	-
S41, B125	5.6	7.7	6.9	6.6	8.00	5.09	4.03	4
S41, BL27	5.6	4.32	5.4	4.7	8.00	4.00	3.11	3.5
S41, RF8	5.6	0	-	-	8.00	3.44	3.2	3.3
S93, S97	4.04	4.06	4.05	4.05	2.75	2.7	2.77	2.71
S93, S95	4.04	7.9	4.7	4.24	2.75	2.81	2.79	2.76
S93, S98	4.04	6.4	5.0	4.23	2.75	7.9	2.8	2.79
S93, Pb6	4.04	0	-	-	2.75	-	-	-
S93, Pb8	4.04	4.9	4.1	4.6	2.75	-	-	-
S93, Pb13	4.04	6.6	4.7	4.68	2.75	-	-	-
S93, BL25	4.04	7.7	5.1	4.62	2.75	5.09	3.1	3.3
S93, BL27	4.04	4.32	4.1	4.5	2.75	4.0	3.01	3.26
S93, RF8	4.04	0	-	-	2.75	3.99	2.9	2.8
S94, S95	4.06	7.9	5.2	4.22	2.75	2.81	2.78	2.75
S94, S98	4.06	6.4	4.2	4.23	2.75	7.9	3.12	3.1
S94, Pb6	4.06	0	-	-	2.75	-	-	-

* generation time of F_1 alone
** generation time on F_2 alone

TABLE 12 (continued)

Food Combination	Euplotes Generation Time				Uronema Generation Time			
	F_1*	F_2**	Actual	Predicted	F_1*	F_2**	Actual	Predicted
S94, Pb8	4.06	4.9	4.2	4.3	2.7	-	-	-
S94, Pb13	4.06	6.6	4.7	4.31	2.7	-	-	-
S94, BL25	4.06	4.3	4.8	4.2	2.7	5.04	2.92	3.0
S94, BL27	4.06	4.32	4.2	4.6	2.7	4.0	3.0	2.8
S94, RF8	4.06	0	-	-	2.7	3.44	2.8	2.9
S95, S98	4.06	6.4	6.6	6.0	2.7	-	-	-
S95, Pb6	7.97	0	-	-	2.81	7.9	-	-
S95, Pb8	7.97	4.9	5.2	5.3	2.81	-	-	-
S95, Pb13	7.97	6.6	6.1	6.8	2.81	-	-	-
S95, BL25	7.97	7.7	7.8	6.6	2.81	5.04	4.1	3.0
S95, BL27	7.97	4.32	4.6	4.9	2.81	9.0	3.61	3.5
S95, RF8	7.97	0	-	-	2.81	3.44	3.2	3.3
S98, Pb6	7.97	0	-	-	7.9	-	-	-
S98, Pb8	6.4	4.9	5.6	5.3	7.9	-	-	-
S98, Pb13	6.4	6.6	6.5	6.7	7.9	-	-	-
S98, BL25	6.4	7.7	7.0	7.2	7.9	5.04	6.2	6.5
S98, BL27	6.4	4.32	4.41	4.6	7.9	4.0	4.8	6.2
S98, RF8	6.4	0	-	-	7.9	3.44	4.3	3.96
Pb6, Pb8	6.4	4.9	-	-	7.9	-	-	-
Pb6, Pb13	6.4	6.6	-	-	7.9	-	-	-
Pb6, BL25	6.4	7.7	-	-	7.9	-	-	-
Pb6, BL27	6.4	4.32	-	-	7.9	-	-	-
Pb6, RF8	6.4	0	-	-	7.9	-	-	-
Pb8, Pb13	4.9	6.6	5.1	5.3	7.9	-	-	-
Pb8, BL25	4.9	7.7	5.2	6.7	7.9	-	-	-
Pb8, BL27	4.9	4.32	4.2	4.9	7.9	-	-	-
Pb8, RF8	4.9	0	-	-	7.9	-	-	-
Pb13, BL25	6.6	7.7	6.8	7.0	7.9	-	-	-
Pb13, BL27	6.6	6.6	4.5	4.7	7.9	-	-	-
Pb13, RF8	6.6	0	-	-	5.04	-	-	-
BL25, BL27	6.6	6.6	4.8	5.8	5.04	4.0	4.3	4.3
BL25, RF8	7.7	0	-	-	5.04	3.44	6.0	4.2

* generation time on F_1 alone
**generation time on F_2 alone

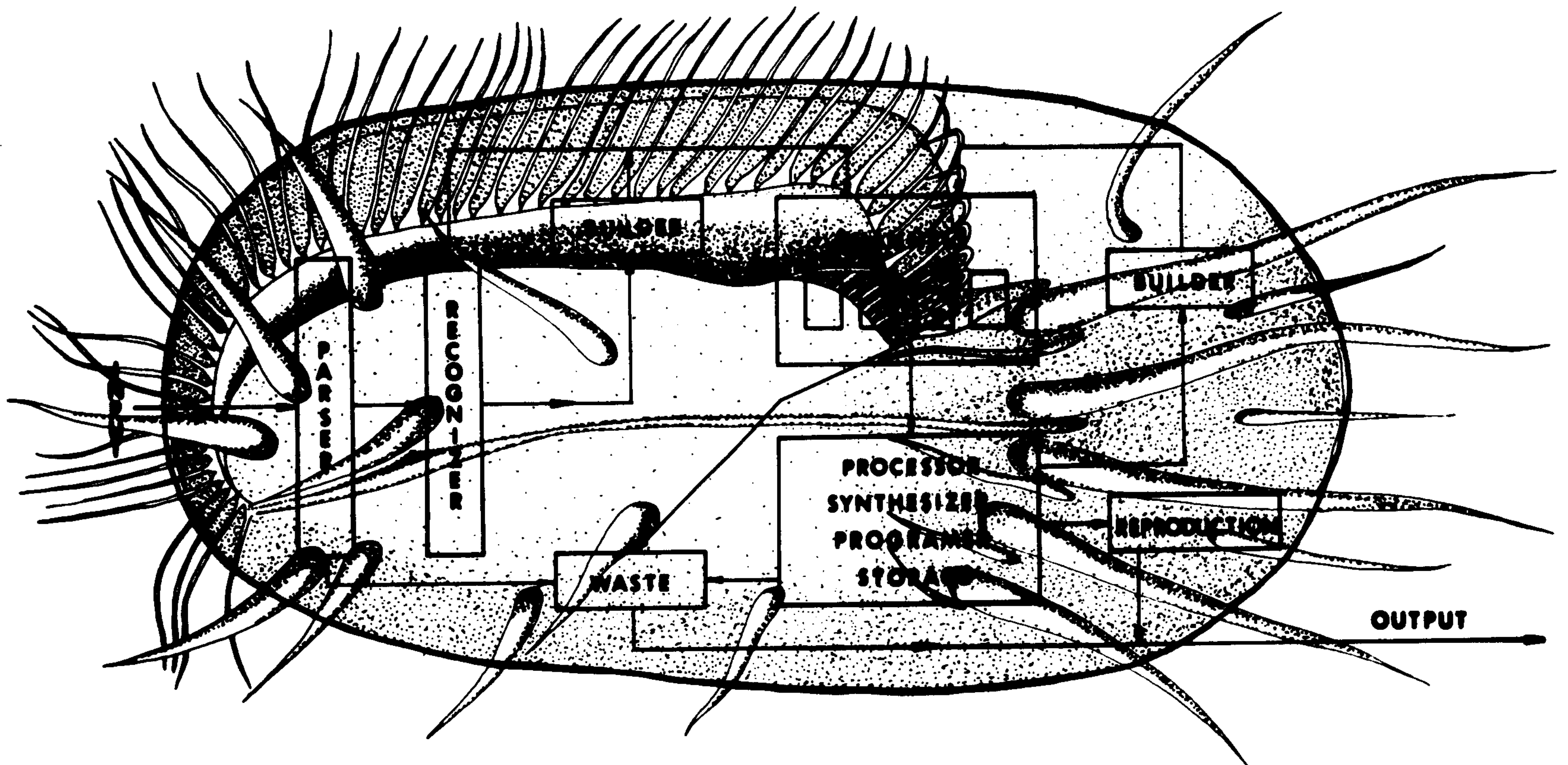
TABLE 13

Food	G.T.	Rank with Euplotes	CAL/gm	Decay Rate	Cyberons	Ee
S93	4.04	1	8.0	.07	.48	12%
S94	4.06	2	8.0	.08	.40	10%
S38	4.13	3	8.1	.17	.36	16%
BL27	4.32	4	8.1	.18	.34	9%
Pb8	4.90	5	8.7	.17	.23	6%
S8	5.45	6	7.7	.20	.36	4%
S41	5.60	7	9.0	.20	.35	4%
S98	6.40	8	10.3	.20	.35	4%
BL25	6.60	9	8.7	.21	.26	2%
Pb13	7.74	10	7.2	.20	.09	2%
S95	7.97	11	7.5	.24	.00	2%

TABLE 14

Food	G.T.	G.T. Rank with Uronema	CAL/gm	Synchrony Decay Rate	Cyberons	Ee
S94	2.70	1	8.0	.05	4.03	21%
S93	2.75	2	8.0	.05	3.82	21%
S95	2.81	3	7.5	.06	3.30	19%
S38	2.93	4	8.1	.10	3.21	12%
S41	3.01	5	9.0	.13	2.49	11%
RF8	3.44	6	9.3	.16	2.58	19%
BL27	4.00	7	8.4	.15	.93	9%
BL25	5.04	8	8.7	.18	.45	7%
S8	5.98	9	7.7	.18	.92	7%
S98	7.9	10	10.3	.17	0.0	6%

Figure 1	The ciliate automaton (overlay)
Figure 2	*Euplotes vannus*



THE CILIATE AUTOMATON

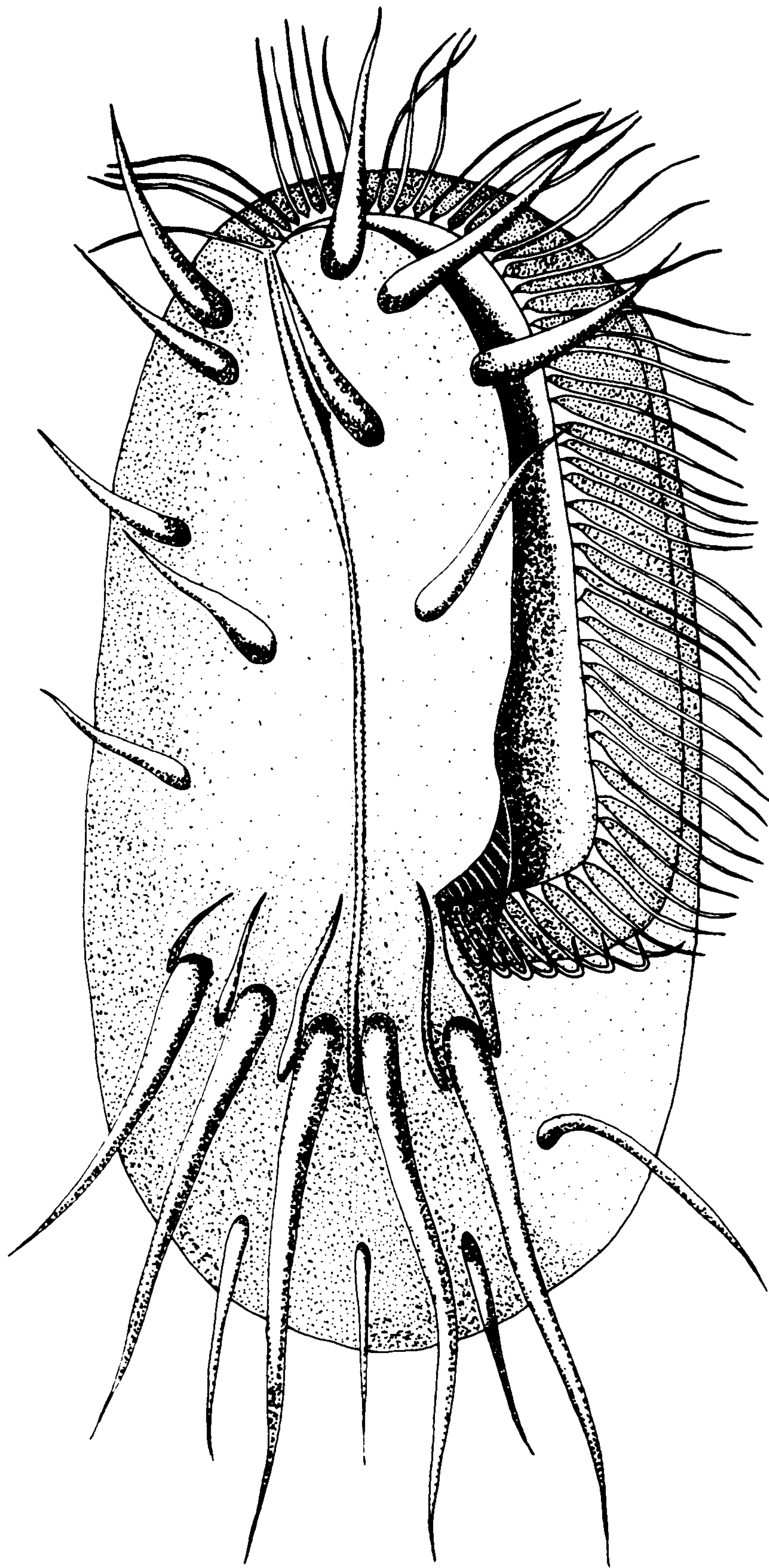
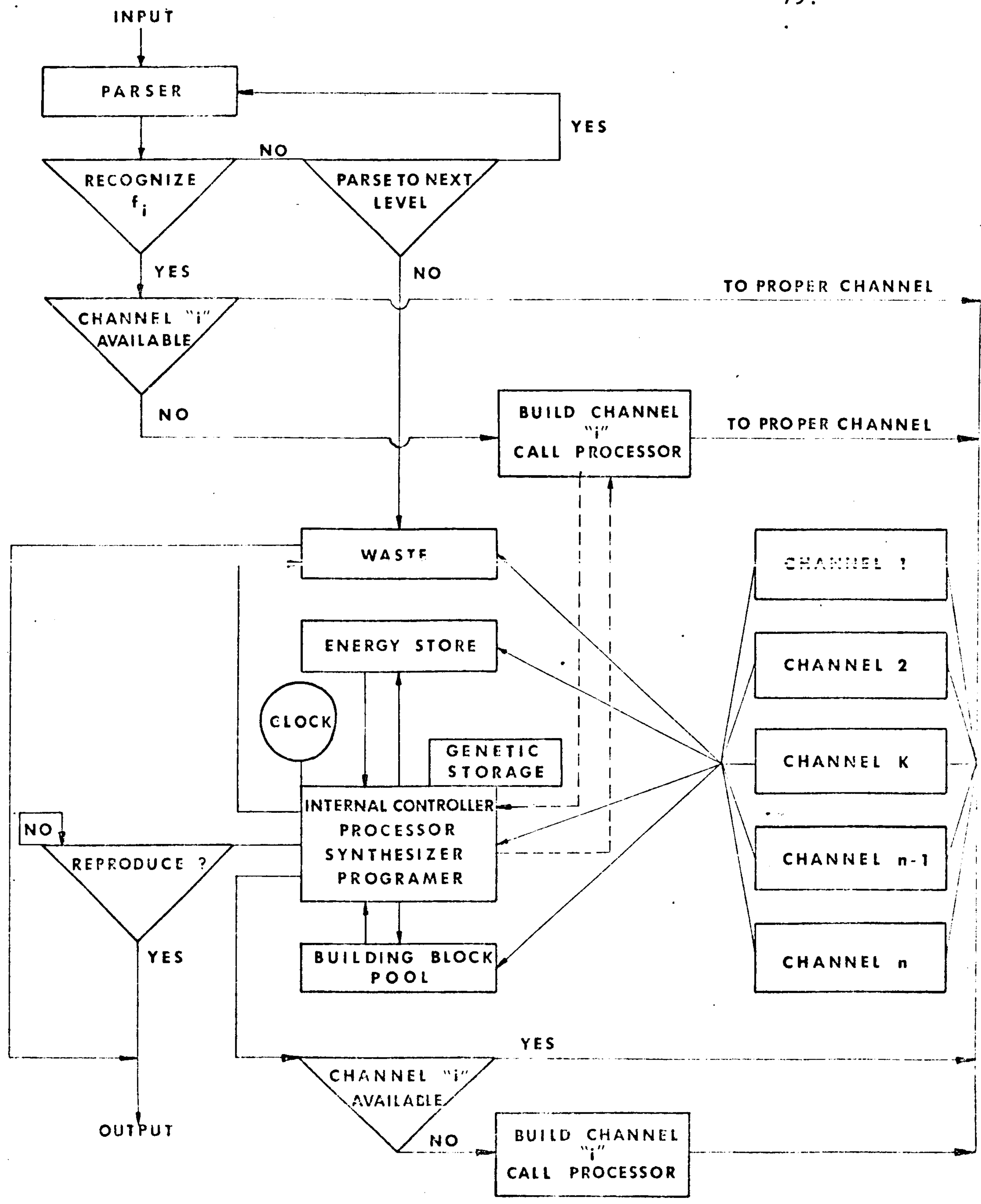


Figure 3 A flowchart of the automaton functions



INPUT
PARSER
YES
NO
RECOGNIZE f_i
PARSE TO NEXT LEVEL
YES
NO
TO PROPER CHANNEL
CHANNEL "i" AVAILABLE
NO
BUILD CHANNEL "i" CALL PROCESSOR
TO PROPER CHANNEL
WASTE
CHANNEL 1
ENERGY STORE
CHANNEL 2
CLOCK
GENETIC STORAGE
CHANNEL K
INTERNAL CONTROLLER PROCESSOR SYNTHESIZER PROGRAMER
NO
REPRODUCE ?
CHANNEL n-1
YES
BUILDING BLOCK POOL
CHANNEL n
YES
CHANNEL "i" AVAILABLE
OUTPUT
NO
BUILD CHANNEL "i" CALL PROCESSOR

Figure 4 - Respiration rates of mixed and unmixed cultures of *Euplotes vannus* and S 41, *Nanochloris* sp

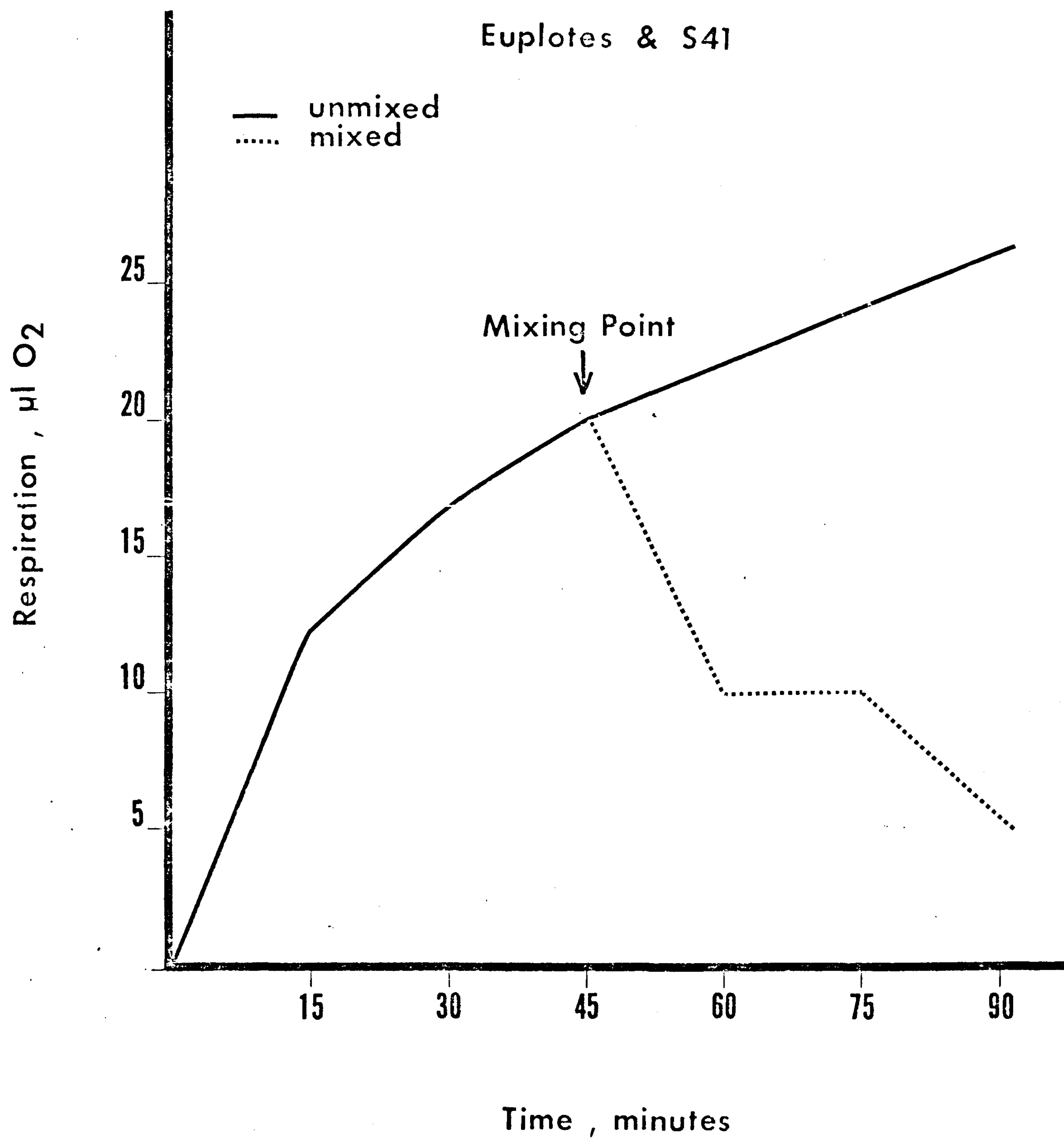


Figure 4
Euplotes & S41
unmixed
mixed
Mixing Point
Respiration , µl O2
25
20
15
10
5
15
30
45
60
75
90
Time , minutes

Figure 5 - Respiration rates of mixed and unmixed cultures of *Euplotes vannus* and S 8, *Nitzchia acicularis*

Figure 5

Euplotes & S8

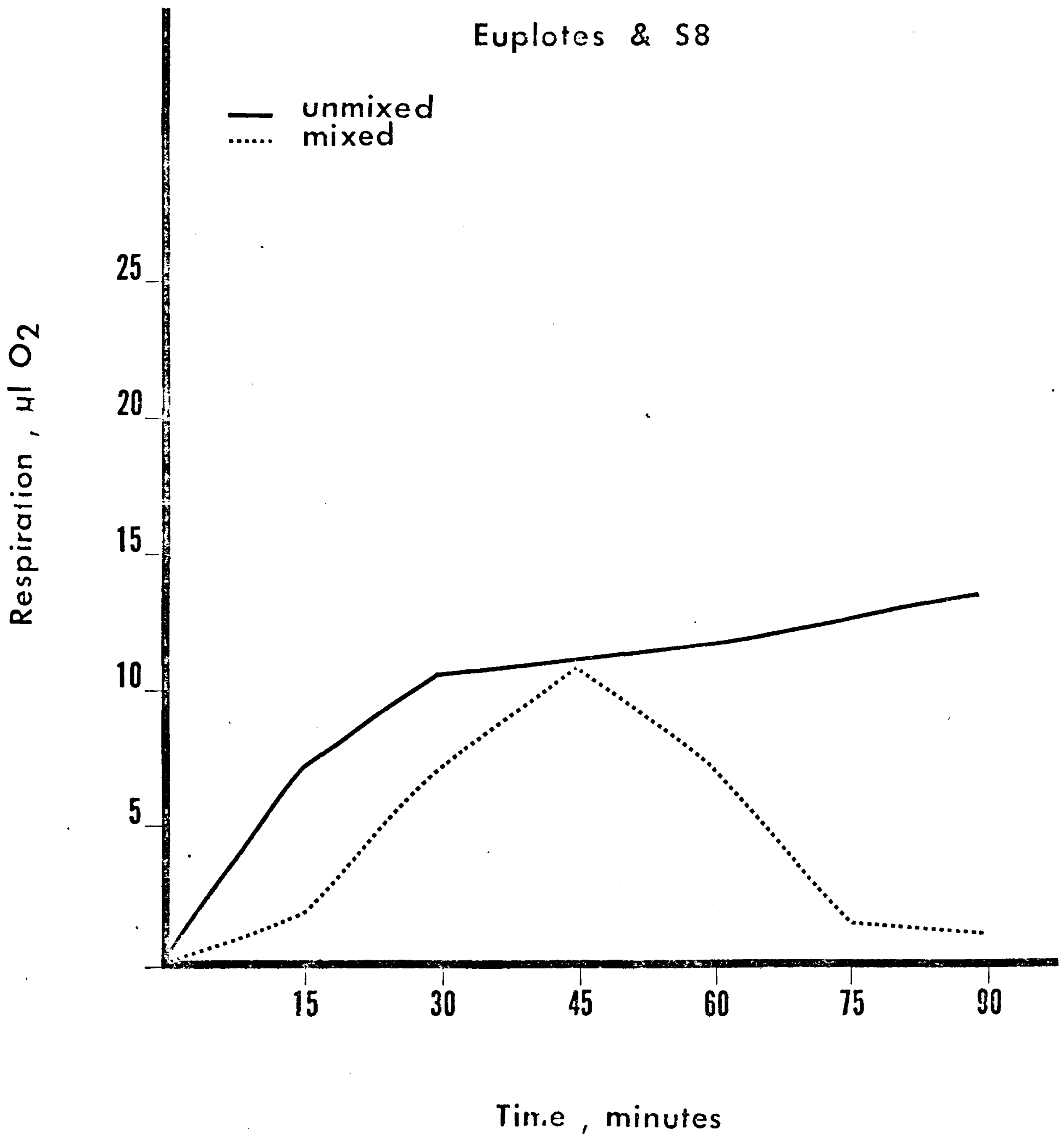


Figure 6 - Respiration rates of mixed and unmixed cultures of *Euplotes vannus* and Pb-6, *Nitzchia frustulum*

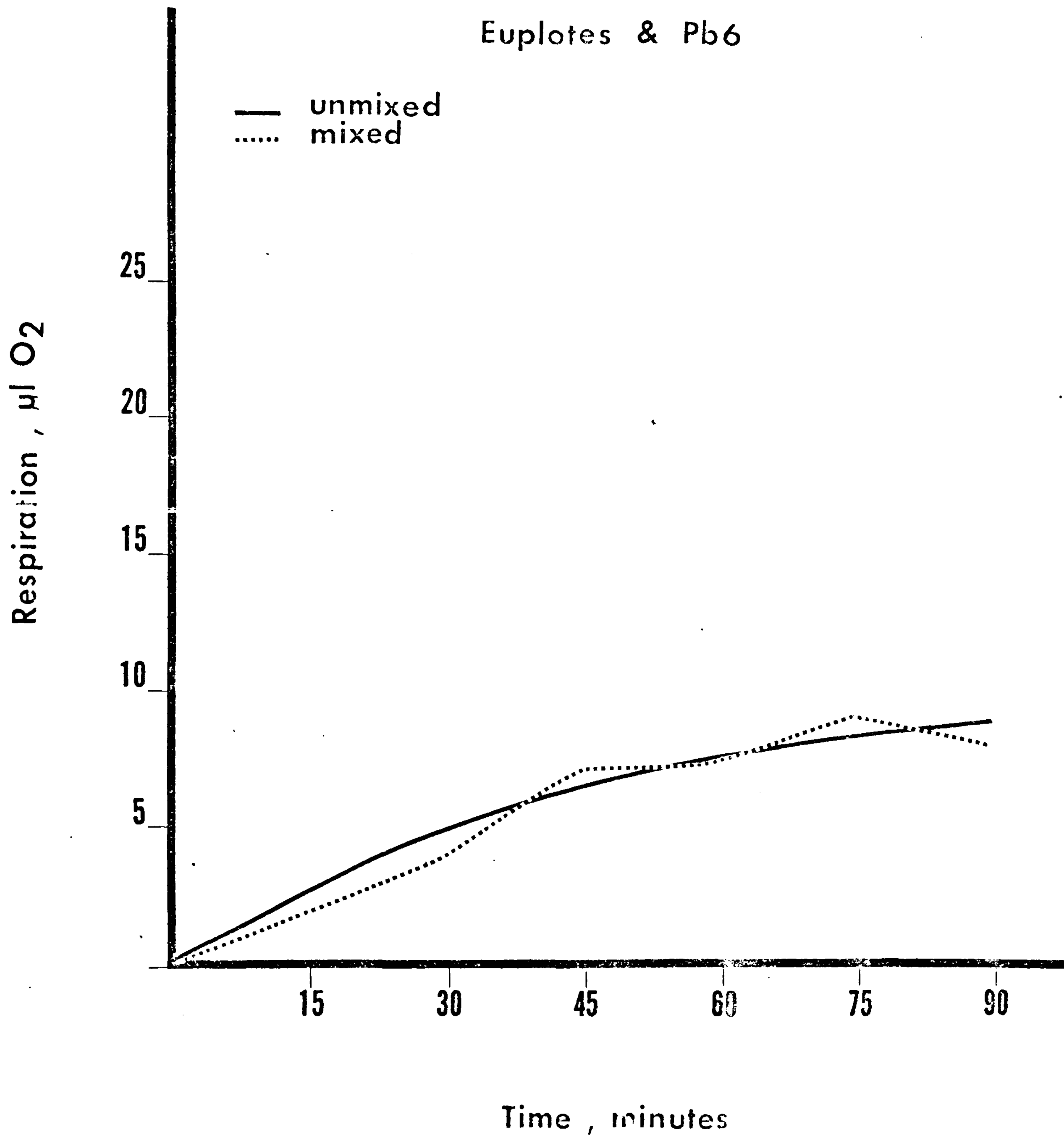


Figure 6
Euplotes & Pb6
unmixed
mixed
Respiration , µl O2
25
20
15
10
5
15
30
45
60
75
90
Time , minutes

Figure 7 - Respiration rates of mixed and unmixed cultures of *Euplotes vannus* and RF-8, *Amphora* sp

Figure 7

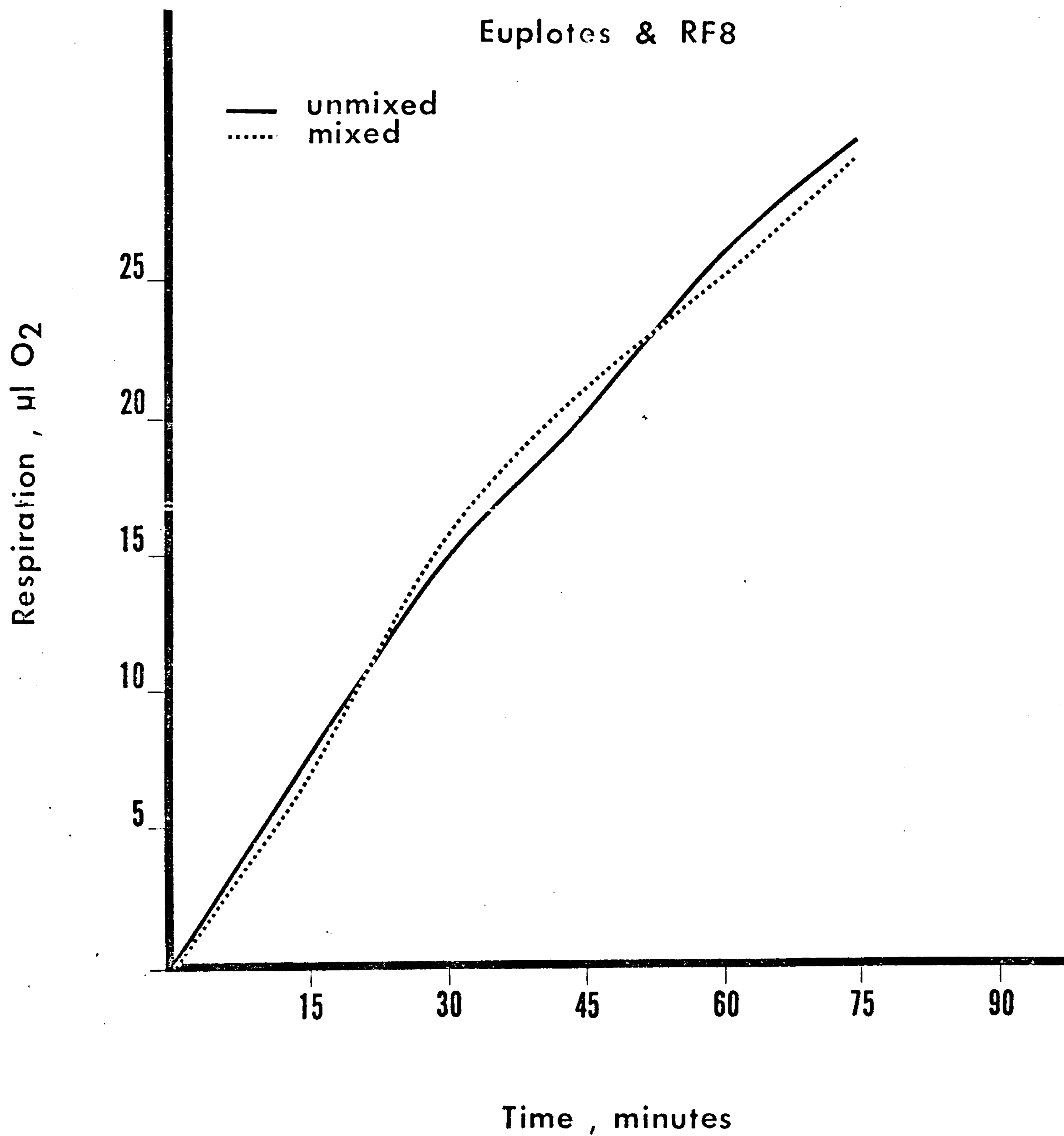


Figure 8 - Uptake threshold levels of <u>Euplotes vannus</u> and S 95, <u>Dunaliella salina</u>

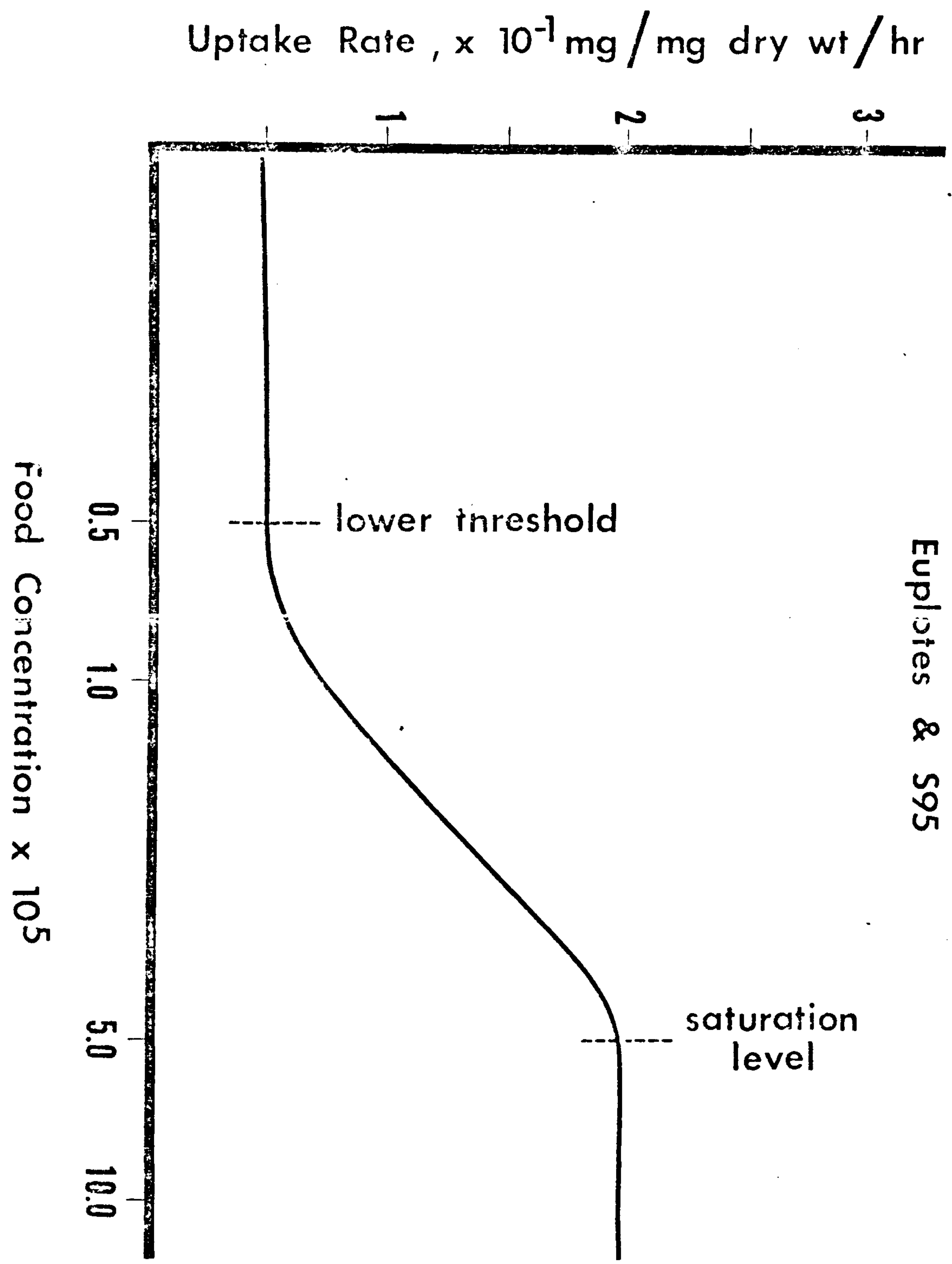


Figure 8
Euplotes & S95

Figure 9 - Synchrony decay of *Euplotes vannus* populations on a diet of Bl-27, *Cylindrotheca fusiformis*

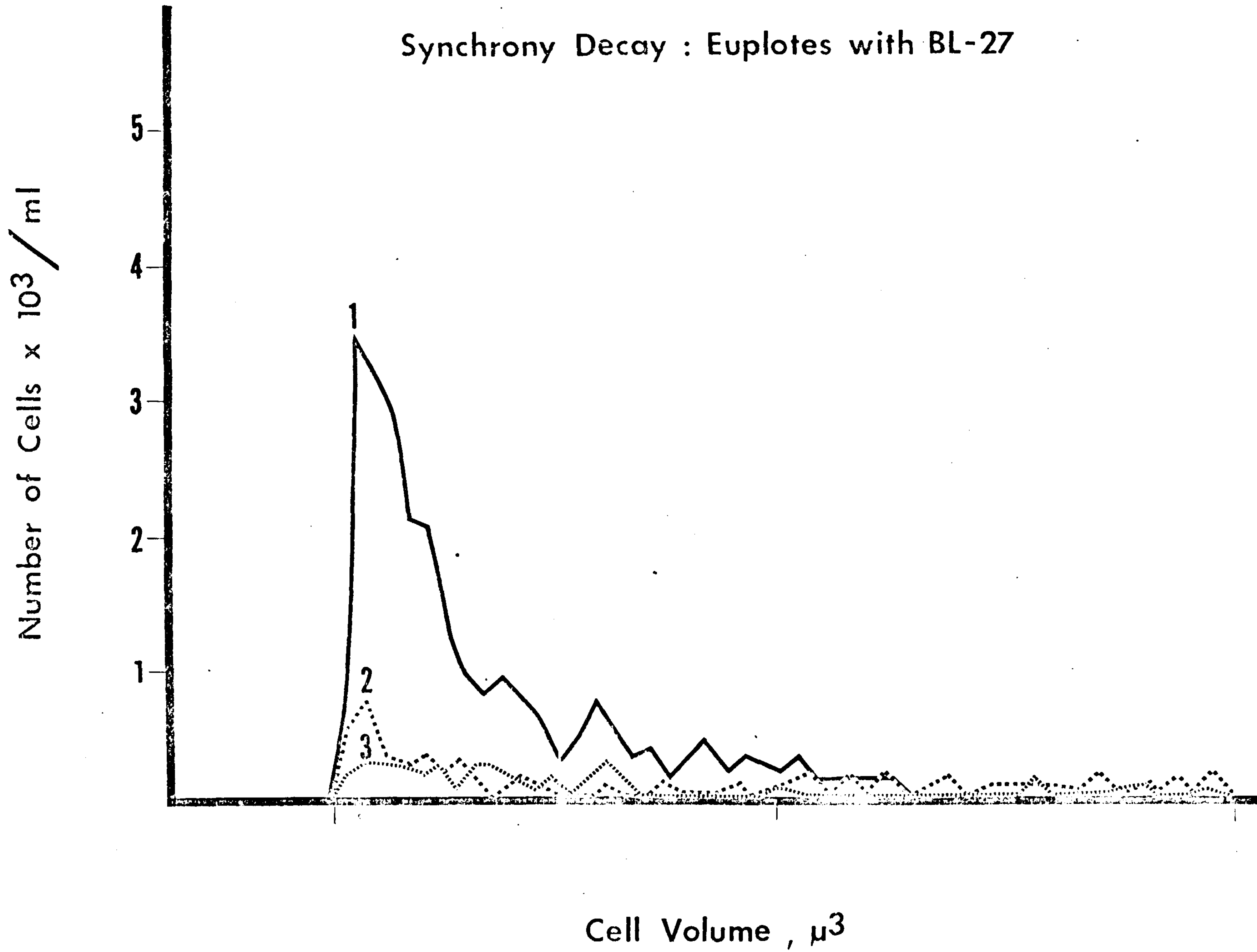


Figure 9

Synchrony Decay : Euplotes with BL-27

Figure 10- Synchrony deacy of *Euplotes vannus* populations on a diet of Pb-8, *Nitzchia* sp

Figure 10

Synchrony Decay : Euplotes with PB-8

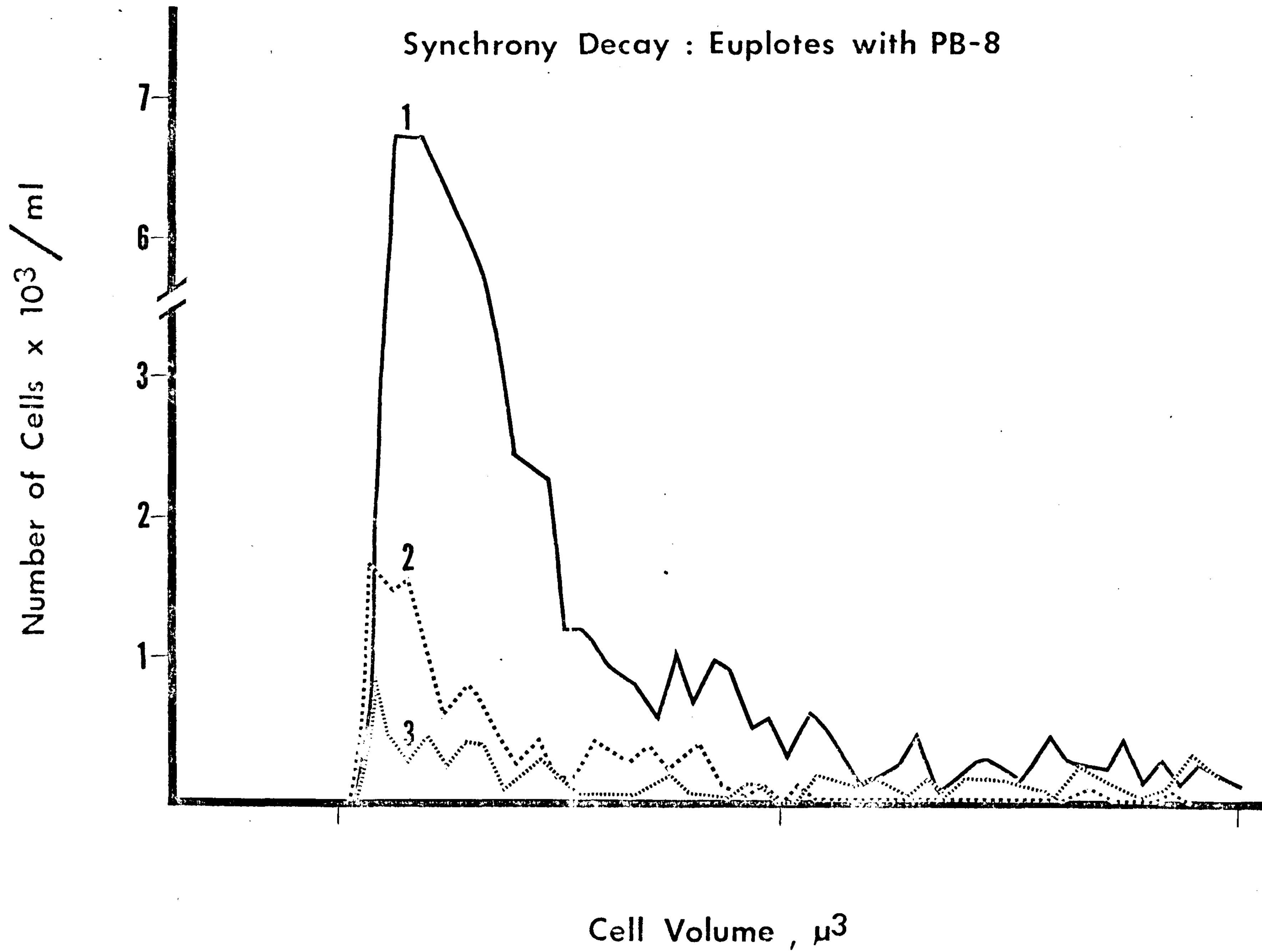


Figure 11 - Synchrony decay of *Uronema marinum* populations on a diet of S 95, *Dunaliella salina*

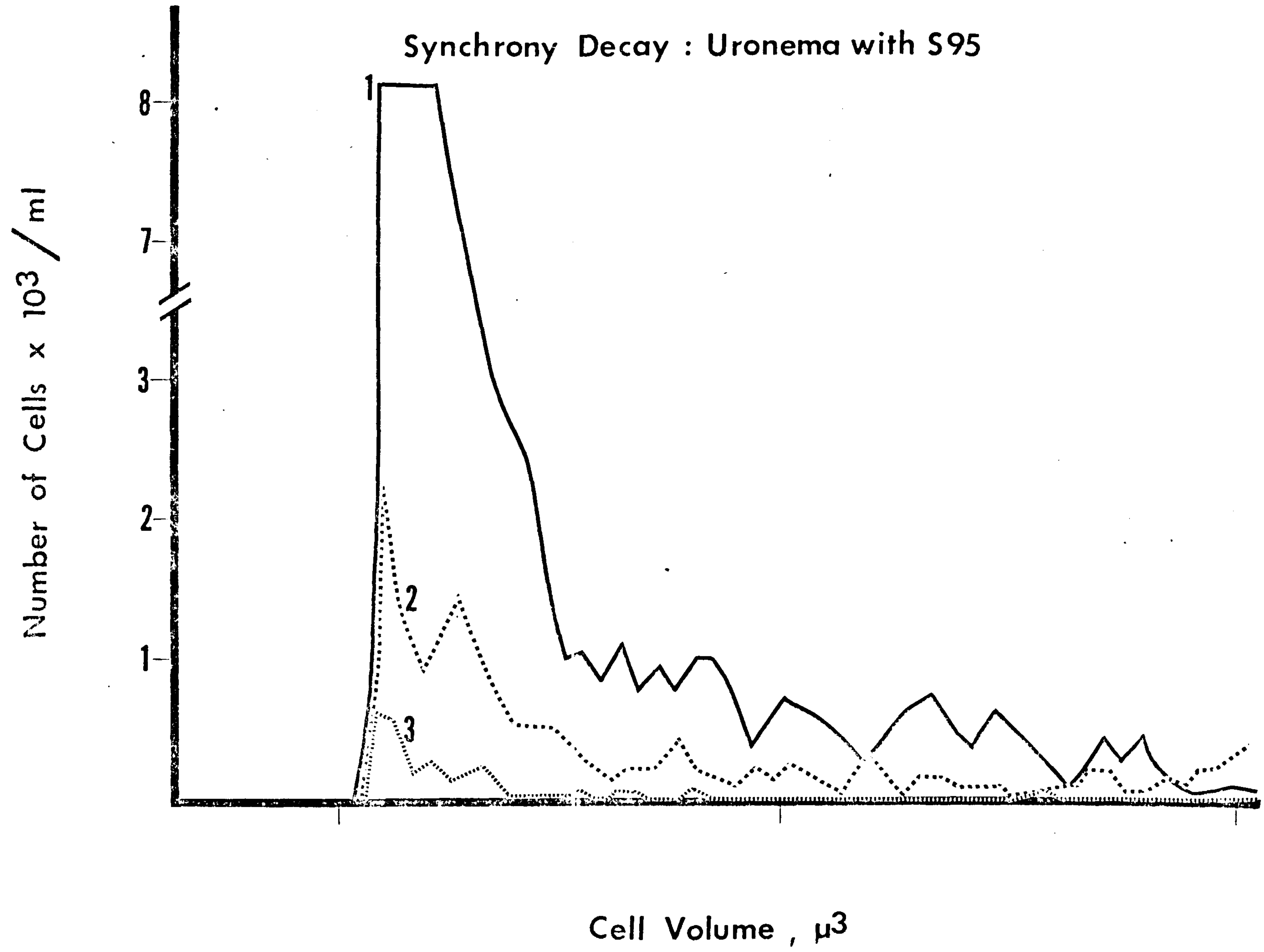


Figure 11

Synchrony Decay : Uronema with S95

Figure 12 - Synchrony decay of *Uronema marinum* populations on diet of Bl-25, *Cylindrotheca closterium*

Figure 12

Synchrony Decay : Uronema with BL-27

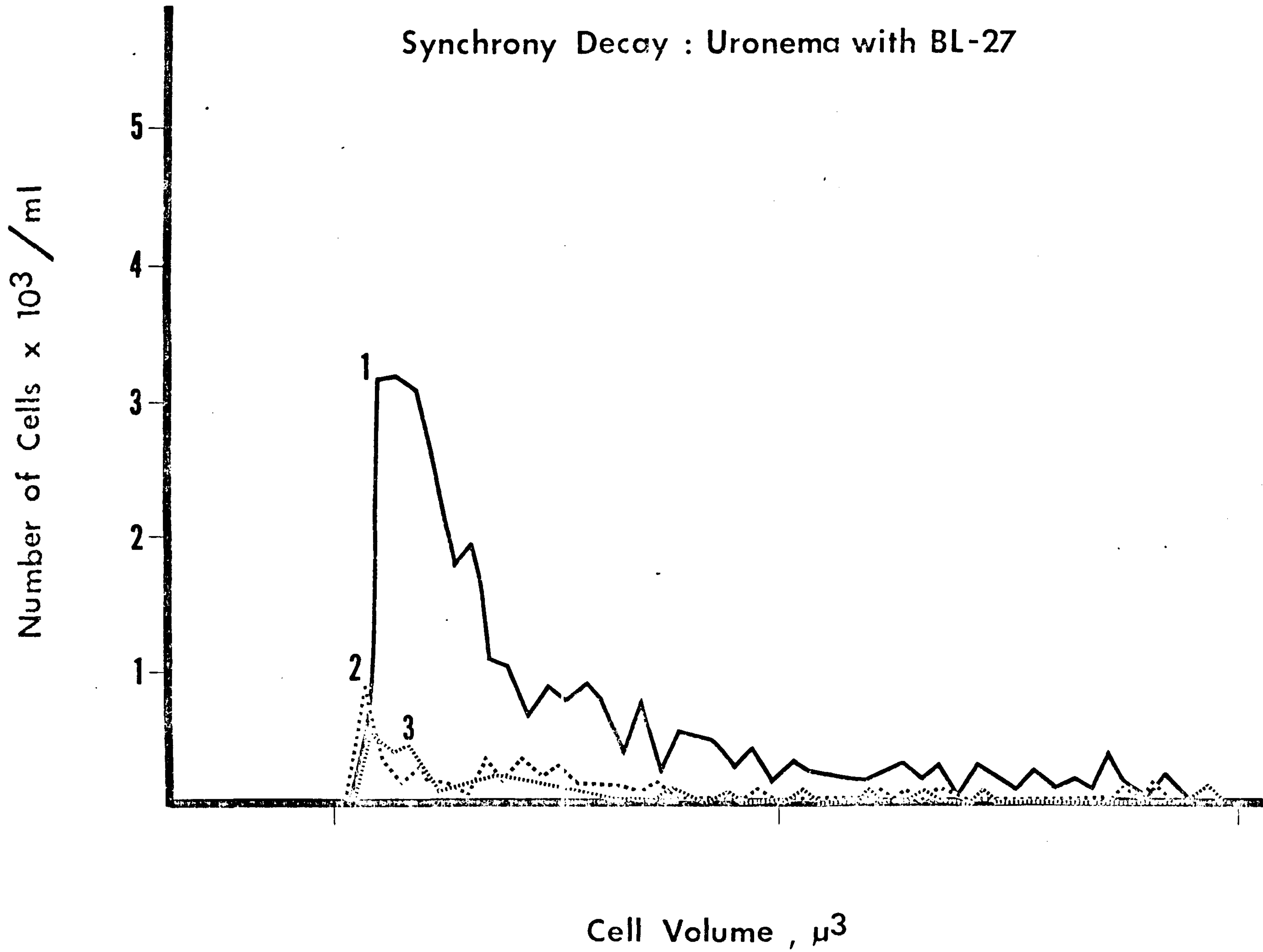


Figure 13- Single ciliate simulation _Ia_ - patchy "Hi I" food, random "Low I" food

Figure 13

Single Species Simulation Ia

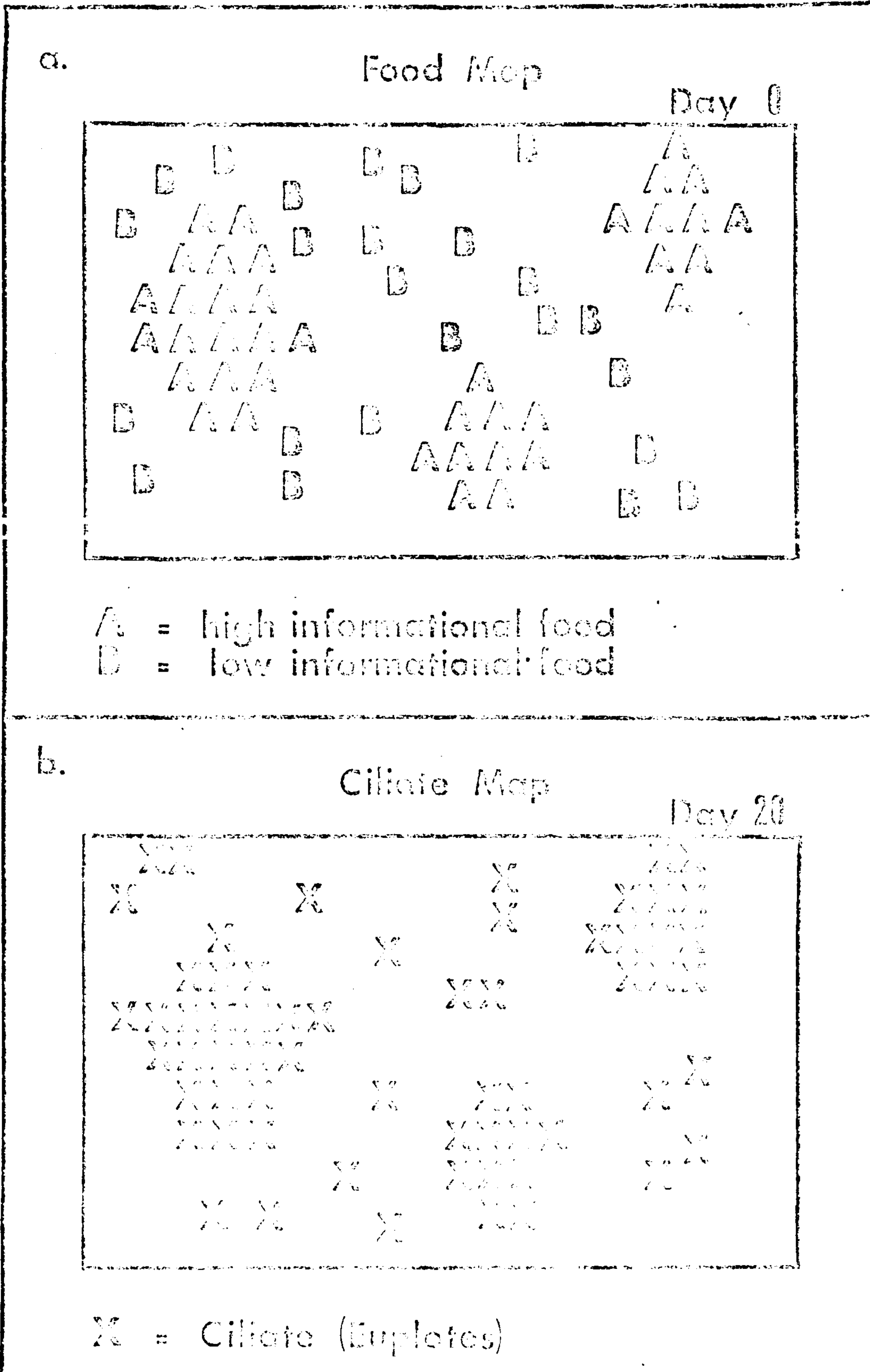
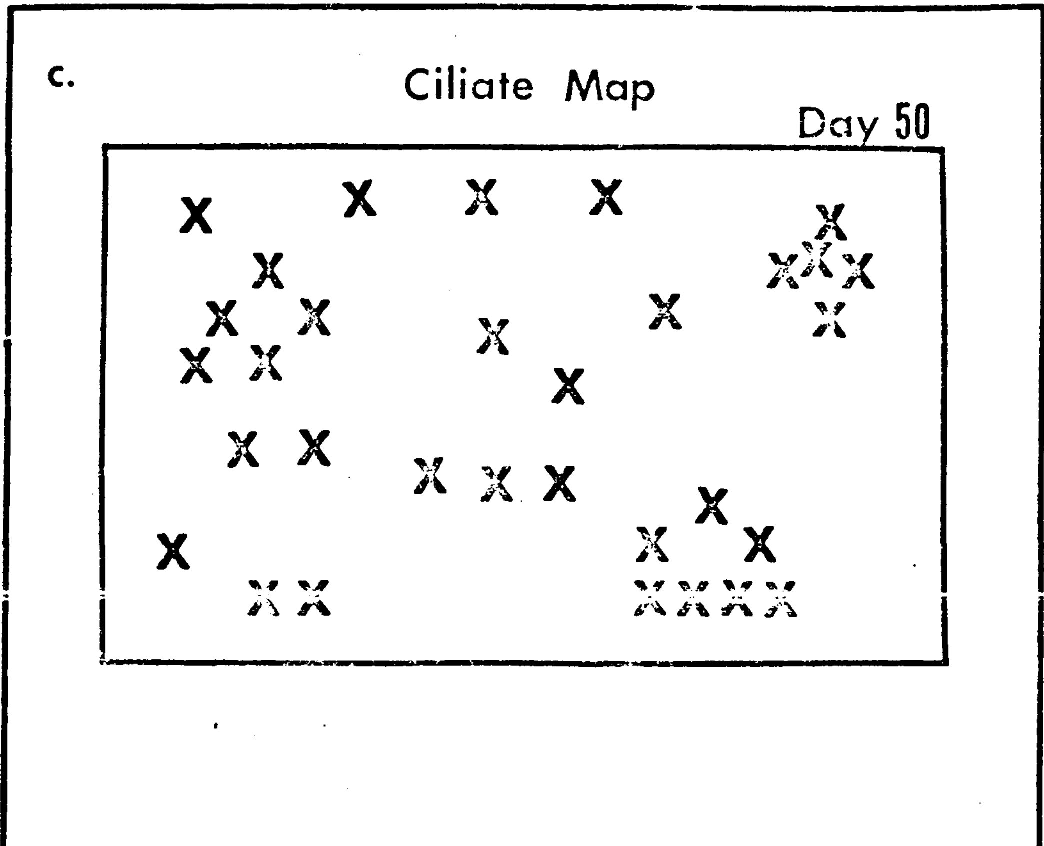


Figure 13, cont'd



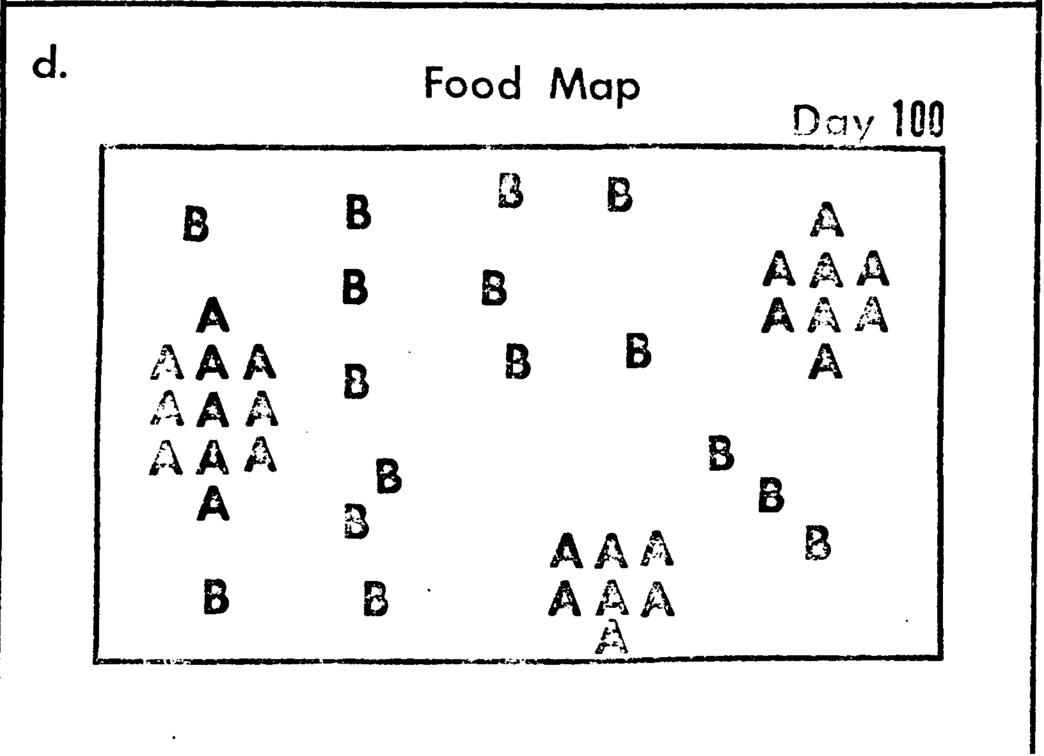
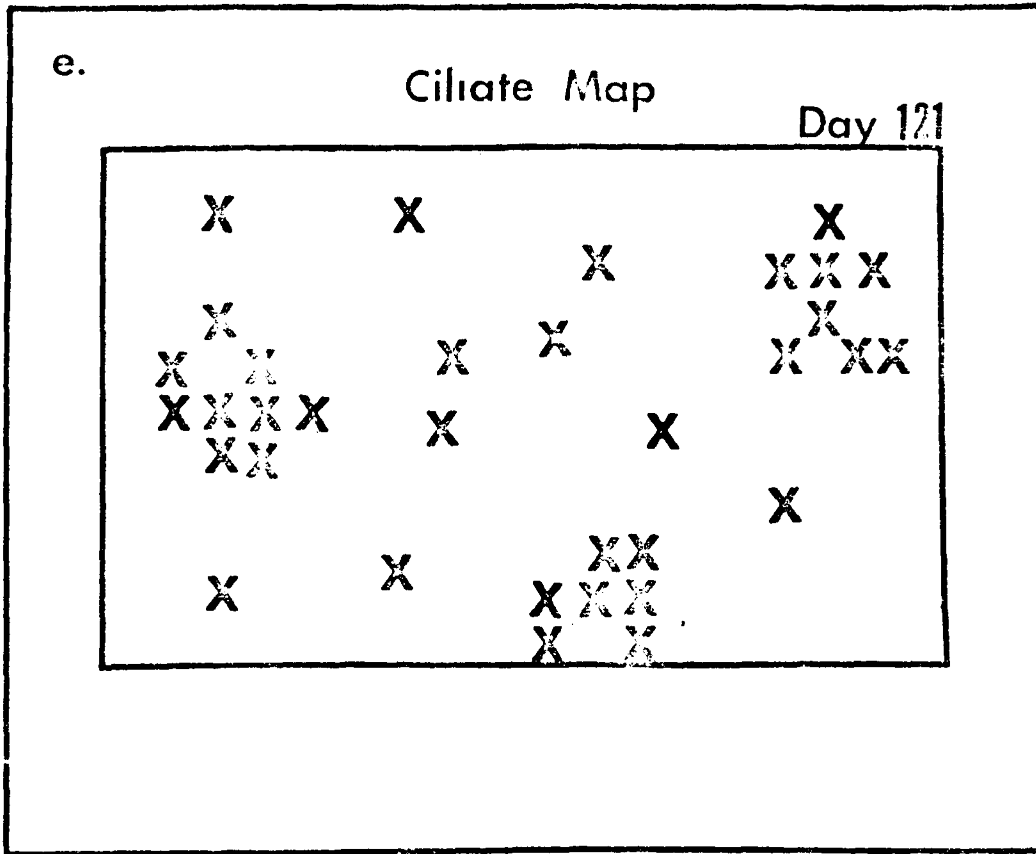


Figure 13, cont'd



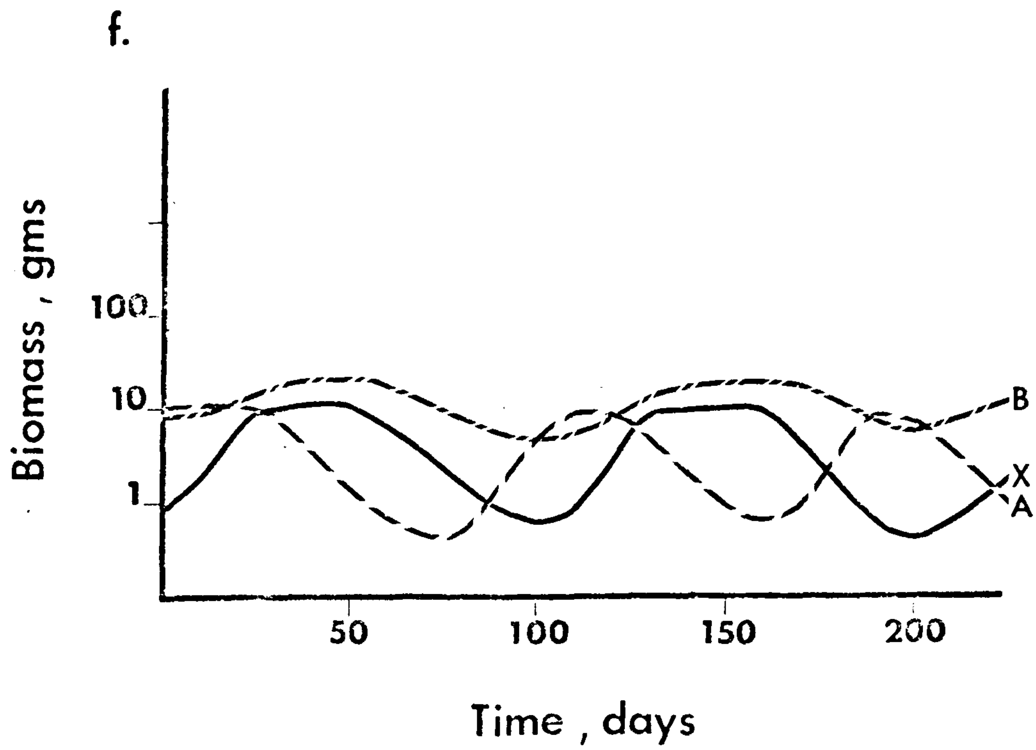


Figure 14 - Single ciliate species simulation I b - patchy Low I food, random Hi I food

Figure 14

Single Species Simulation Ib

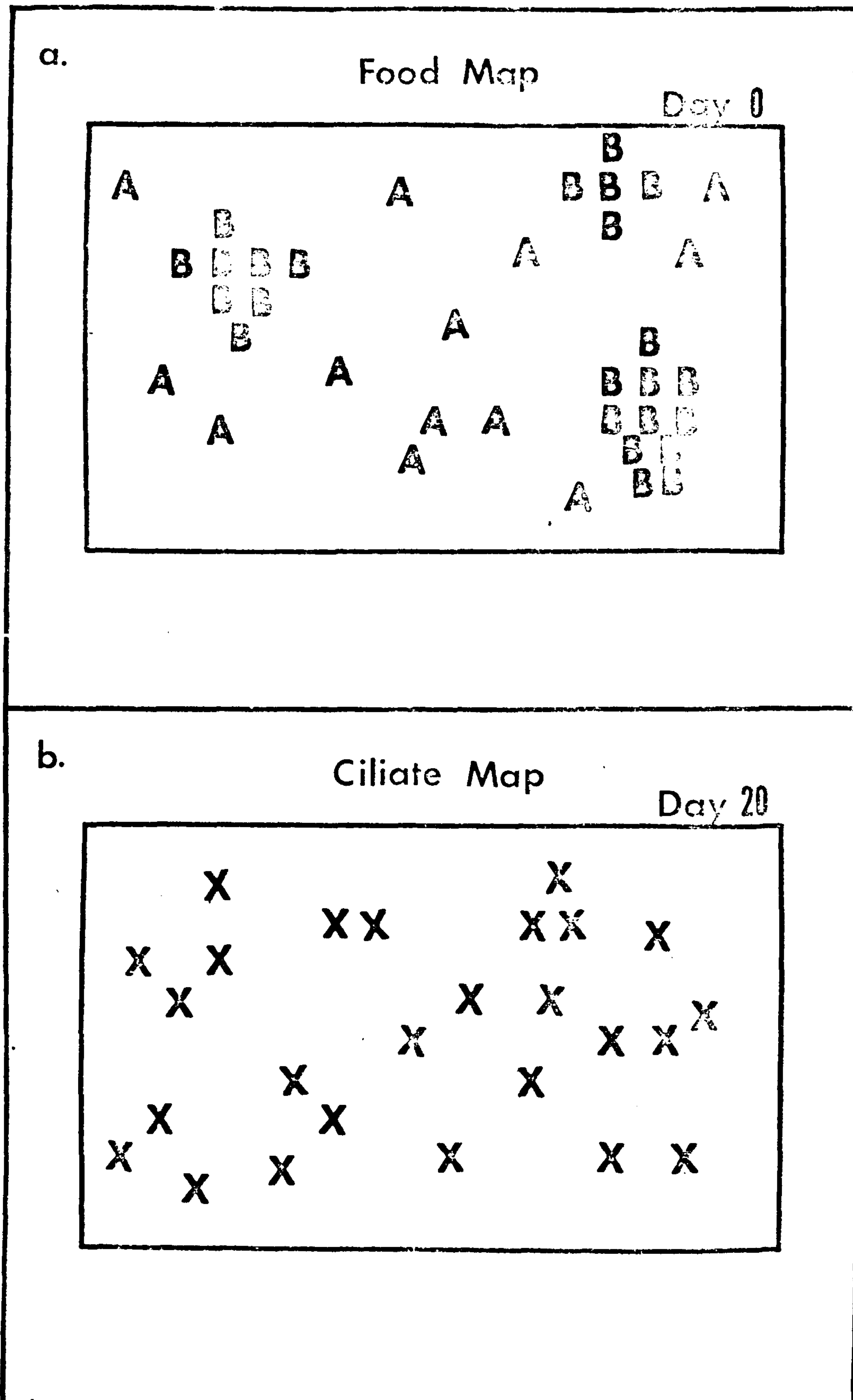


Figure 14, cont'd

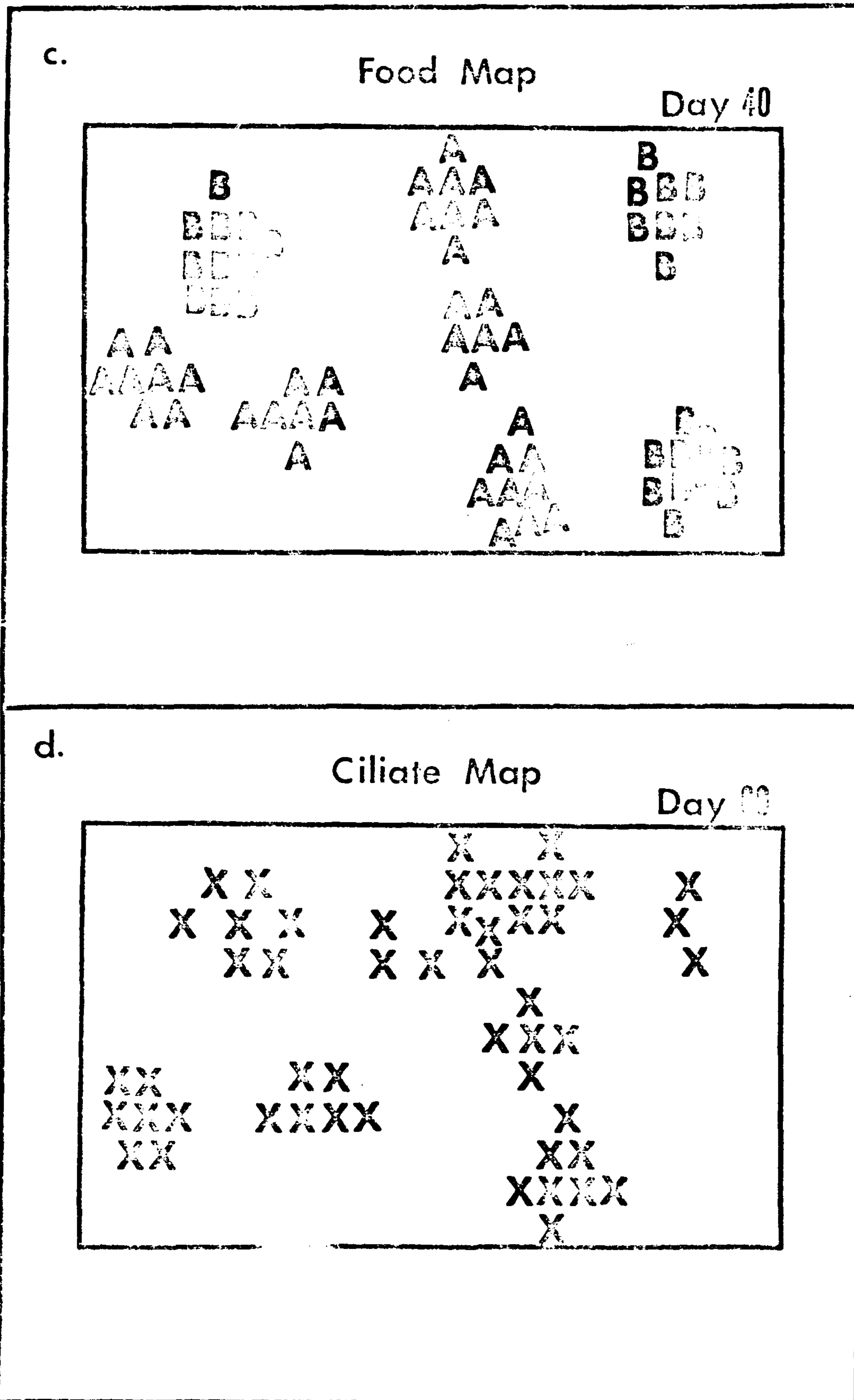


Figure 14, cont'd

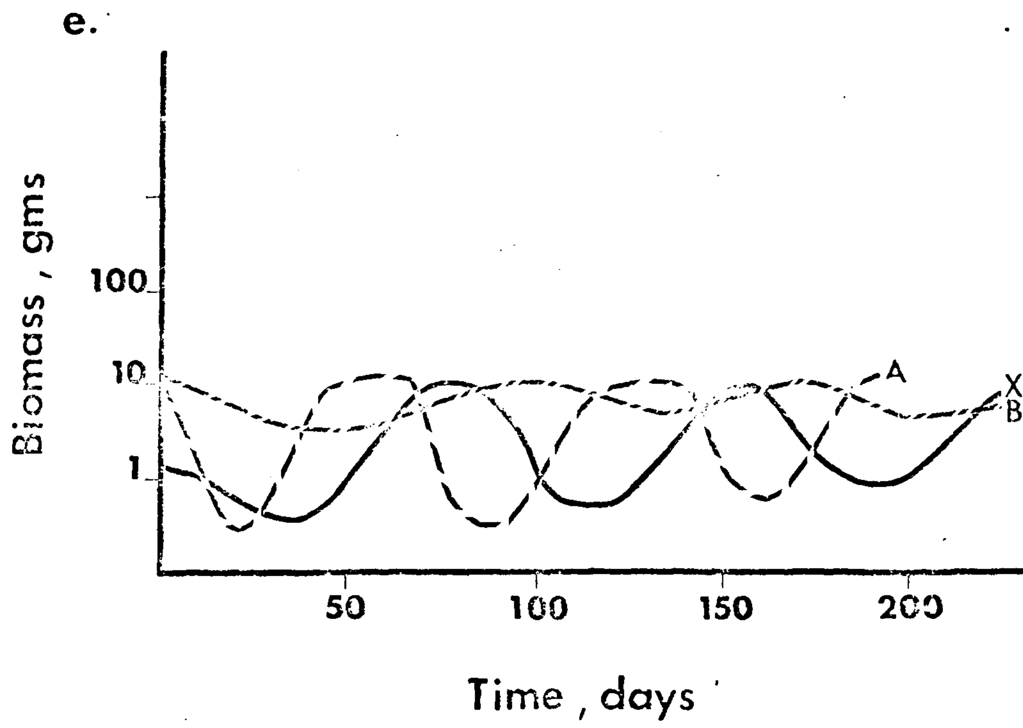


Figure 15 - Single ciliate simulation <u>I c</u> - random "Hi I" food, random "Low I" food

Figure 15

Single Species Simulation Ic

a.

Food Map

Day 0

b.

Ciliate Map

Steady State

Figure 15, cont'd

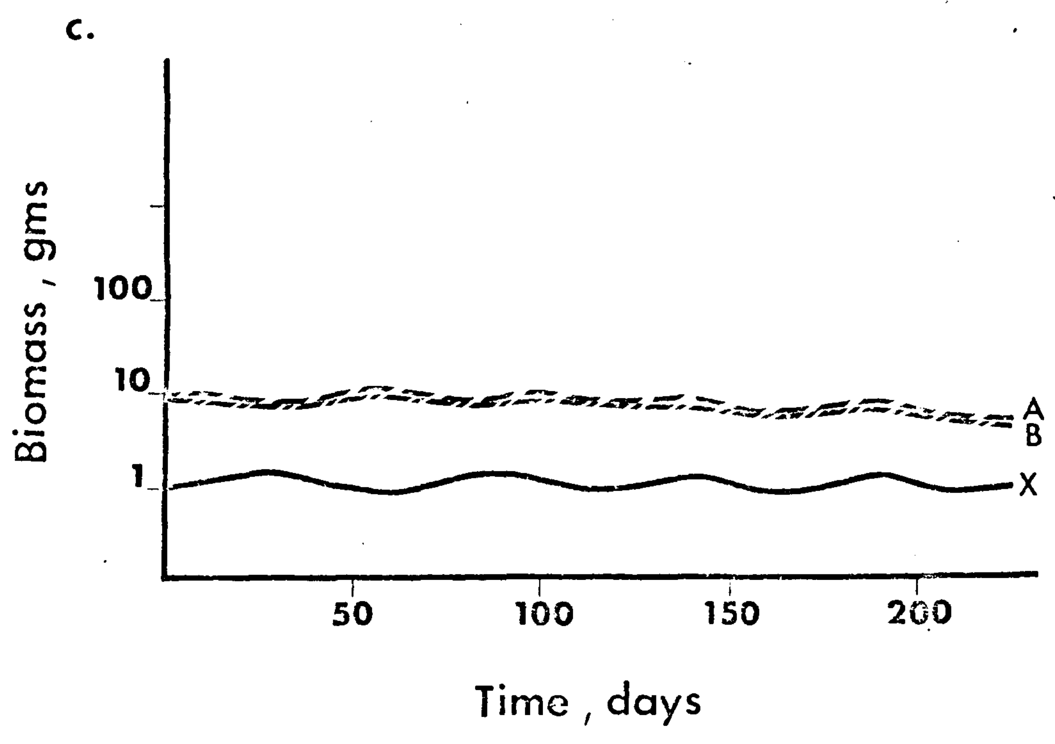


Figure 16 - Two species simulation II a - two patchy foods each "Hi I" for one ciliate

Figure 16

Two Species Simulation IIa

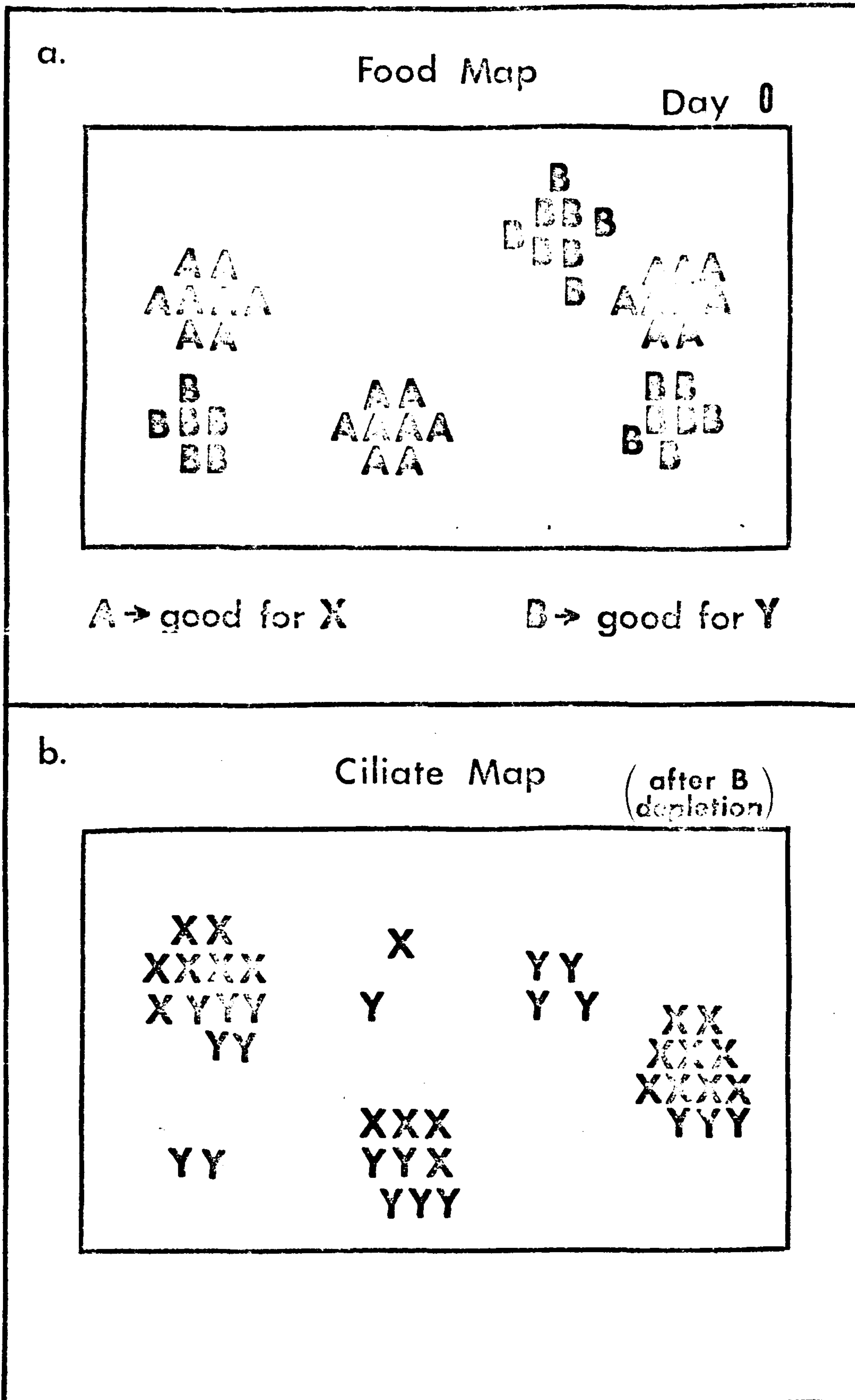


Figure 16, cont'd

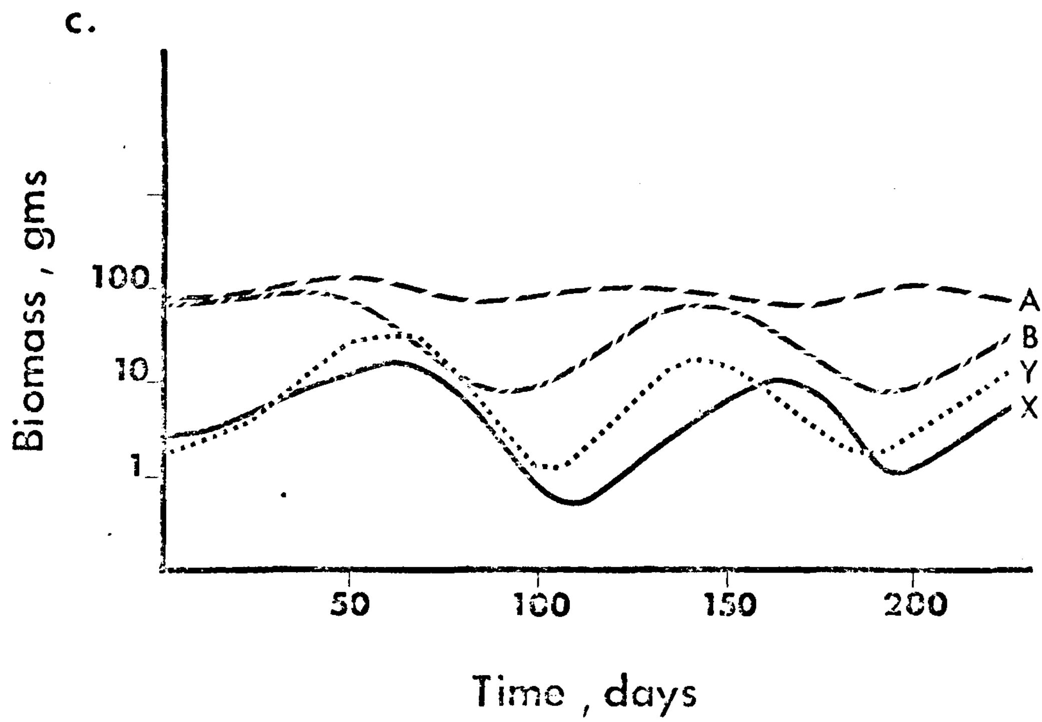


Figure 17 - Two species simulation II b - generation time, encounter time, concentration effects on a single "Hi I" food

Figure 17

Two Species Simulation IIb

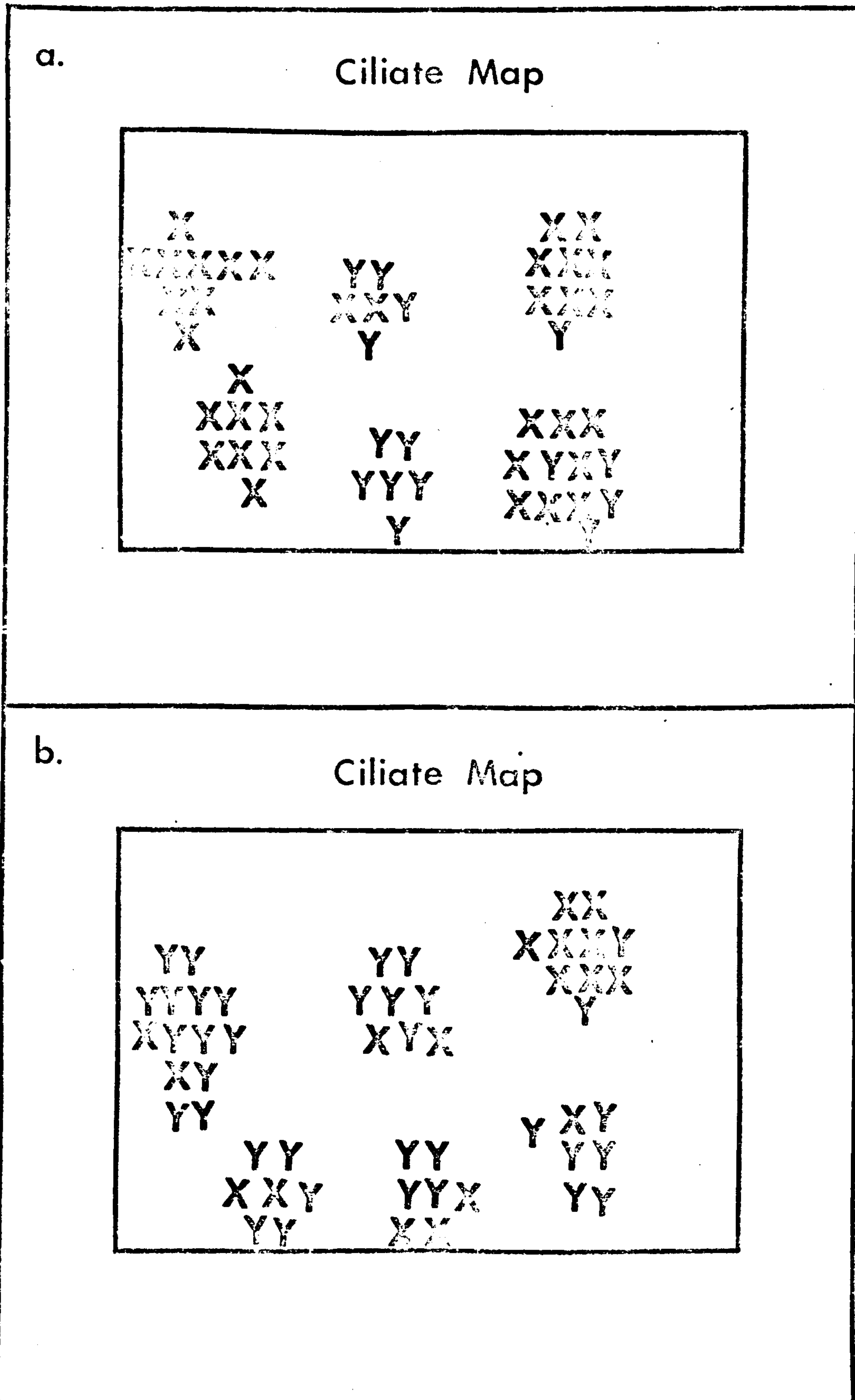


Figure 18 - Two species simulation II c - competition for a randomly distributed "Hi I" food

Figure 18

Two Species Simulation IIc

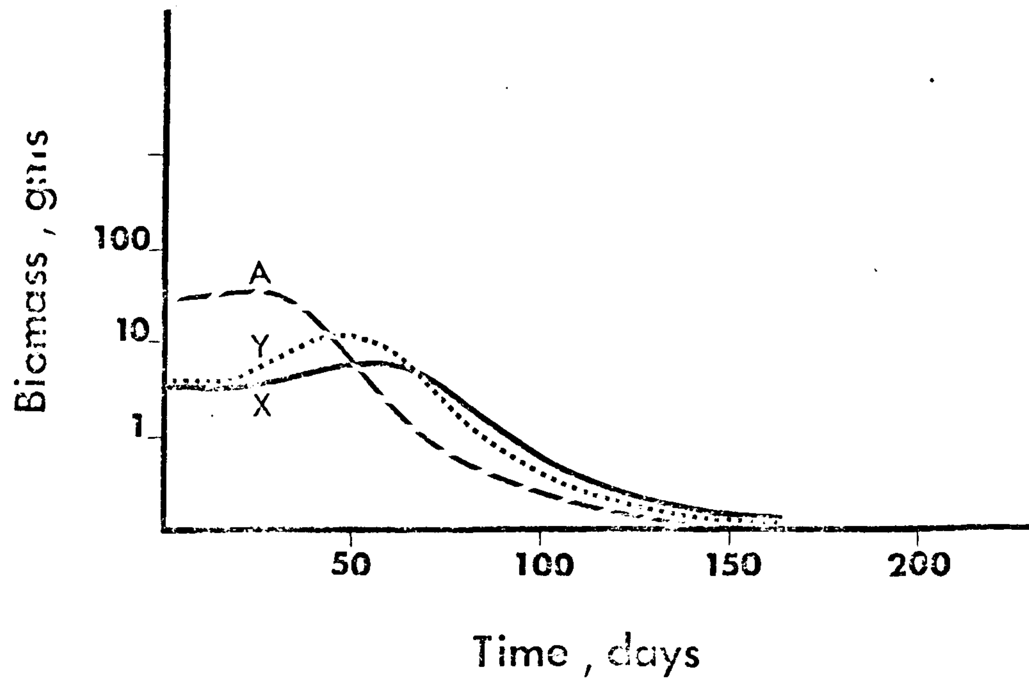


Figure 19 - Two species simulation II d - five patchy foods, three "Hi I" for one ciliate, one "Hi I" for the other ciliate, one "Hi I" for both

Figure 19

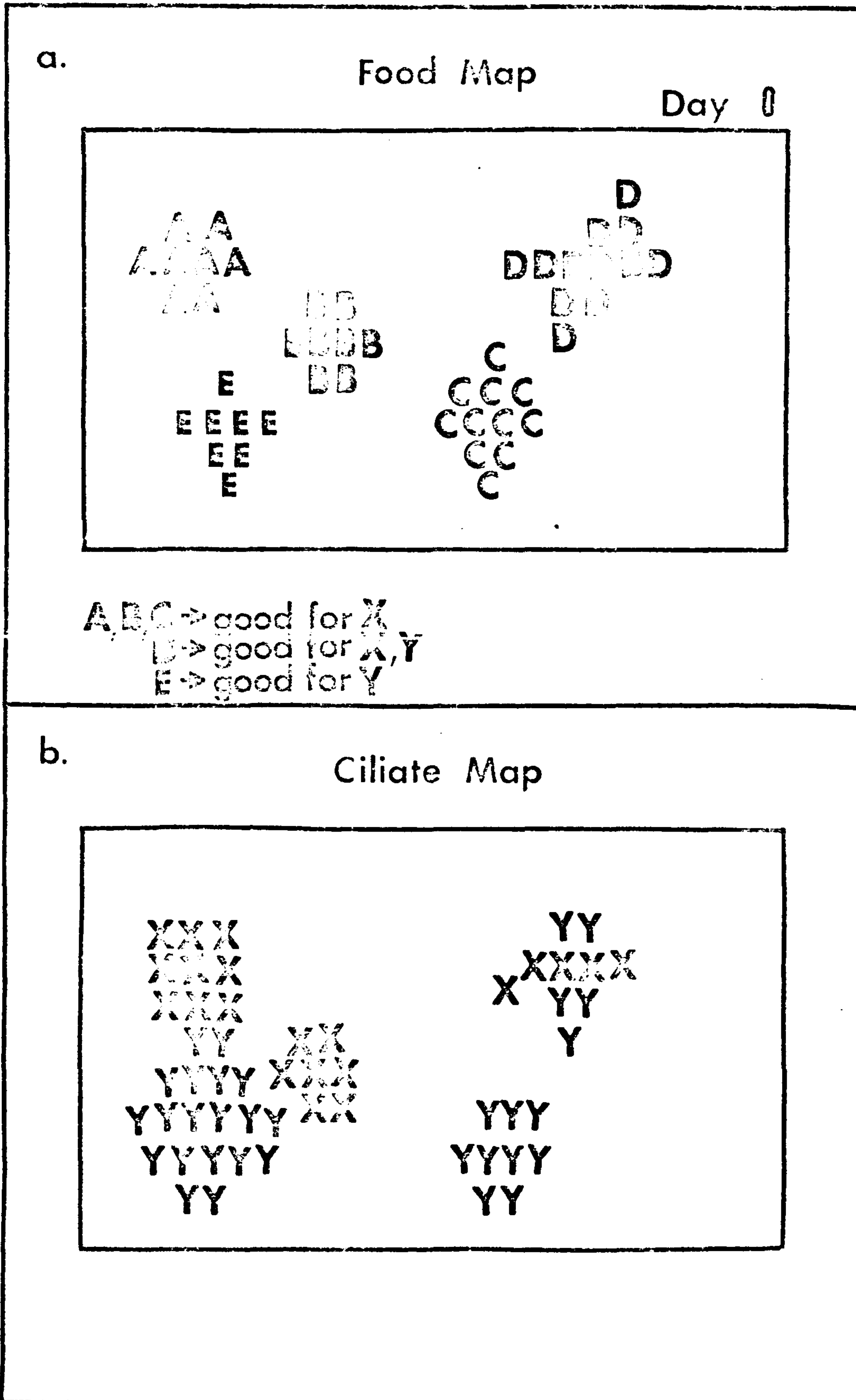


Figure 19, cont'd

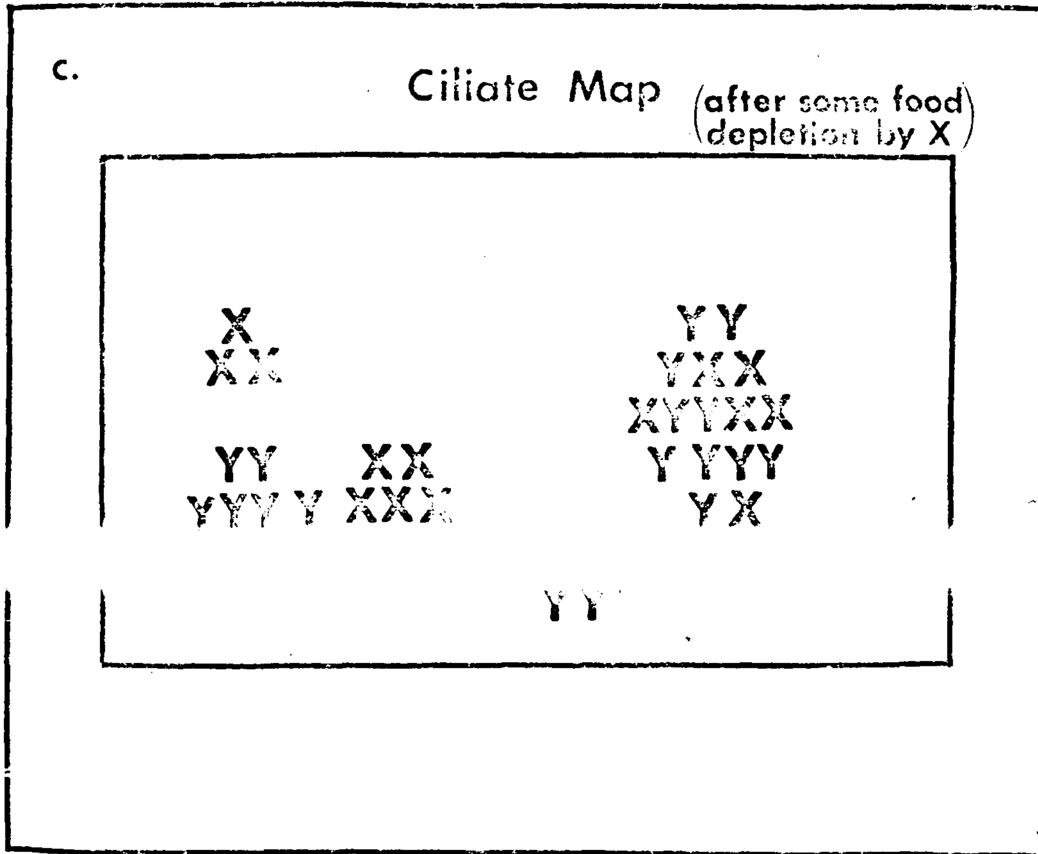
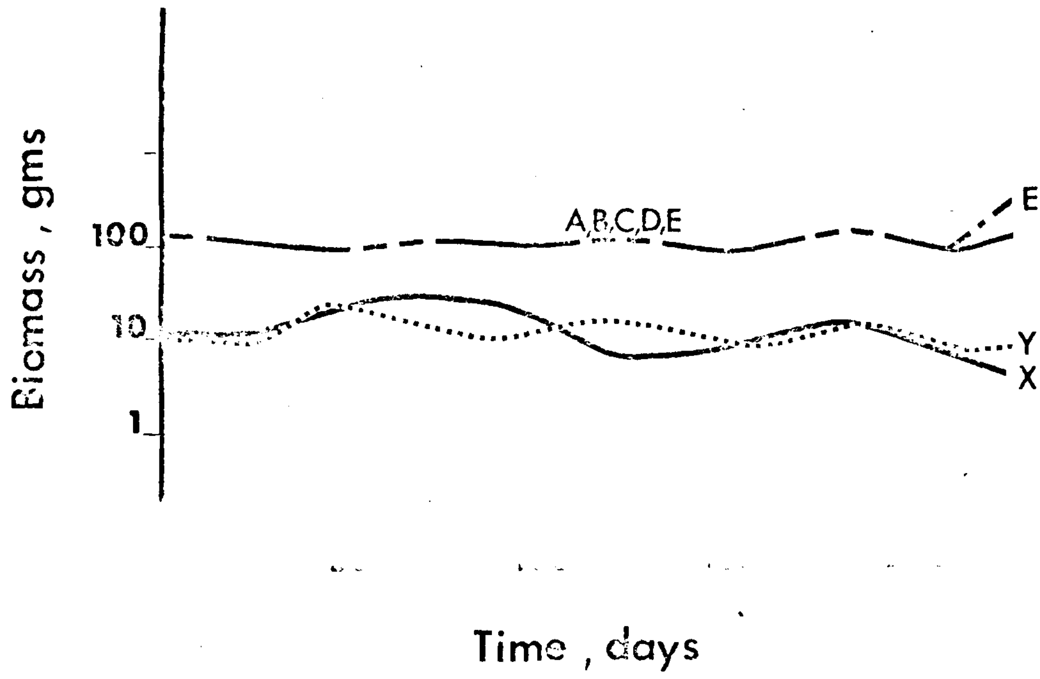


Figure 20 - Biomass vs. time for organisms in simulation
<u>II d</u>

Figure 20



Medium S

Components	g/l
NaCl*	25.0
$MgSO_4 \cdot 7H_2O$	9.0
KCL*	0.7
Ca (as Cl^-)	0.3
NH_4NO_3*	0.25
Na glycerol$\cdot PO_4$*	0.1
$Na_2SiO_3 \cdot 9H_2O$***	0.07
P II metals **	30.0 ml/l
tris*	1.0
vitamin B_{12}*	10.0 ug
NTA*	0.007
NaH_2CO_3*	0.1
aspartic acid*	0.66
glycine*	0.037
glutamic acid*	0.073
alanine*	0.044
glucose*	0.090

* Dry mix components; mixed in 100 l batches, then mixed in a porcelin mill, preweighed in 5 l amounts in freezer bags and stored in a freezer.

** McLaughlin and Zahl (1959)

*** Sodium-meta-silicate should be added first and be allowed to dissolve completely before anything else is added. Each addition should be dissolved completely before the next addition. The medium should be continuously stirred while the additions are being made.

Medium B

NaCl	2.50%
$MgSO_4 \cdot 7H_2O$	0.9
KCl	0.07
Ca (as Cl^-)	0.03
$NaNO_3$	0.005
$Na_2glycerol \cdot PO_4$	0.002
$Na_2SiO_3 \cdot 9H_2O$	0.007
P II metals	3 ml/100
Tris	0.1
B_{12}	0.1 ug
NTA	0.007
$NaHCO_3$	0.01

Definition of variables used in the simulation program.

Name	Use
NODE	Array containing food information
IAUTO	Array containing state information for each automata
EXPER	Array of each automatons life history
NUMAUT	Defines number of automatons in system
IREPLV	Energy level for reproduction
NODEFD	Energy contained in food organisms
NTRIAL	Number of cycles
FDREG	Food threshold level
EAT	Subroutine for feeding calculations
MOVE	Subroutine for random movement
GAINEX	Change experience factors
FDINC	Subroutine for environmental food calculations
AGE	Subroutine for maturation effects (not used)
OUTPUT	Subroutine for printing at selected time intervals
COPY	Subroutine to temporarily hold between move information
SFIELD	Subroutine for food sensing (not used)
AVEROC	Subroutine for carrying capacity
ORDOCC	Subroutine for feeding order
DELETE	Subroutine to delete dead organisms
REPRO	Subroutine for reproduction
GARBCO	Subroutine to garbage collect dead organisms
MAKMOV	Subroutine to perform move calculated by MOVE
RANNYU	Random number generator function

```
0001            COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOPAR
               1ISFLD(9),K
0002            COMMON/B/IOCC,IAVOCC
0003            REAL ISINC
0004            COMMON/C/IZ,IZAUTO,IFDINC,LIFE,ISV,ISINC
0005            COMMON/D/JX,JY
0006            COMMON/E/IREPLV,IREPPS
0007            COMMON/F/NUMAUT,NTRIAL,IFROUT
0008            COMMON/G/AVOCC(256)
0009            READ 100,IREPLV,IREPPS,IC,ILIM,FDREG,NTRIAL,IFROUT,IF,
               1ISINC
0010            Z=RANNYU(0,IF)
0011            READ(5,100)NODEFD,NUMAUT
0012            PRINT 1
0013            PRINT 2,IREPLV,NTRIAL
0014            PRINT13,IREPPS,IF
0015             PRINT 4,FDREG,NODEFD
0016            PRINT15,IC,NUMAUT
0017              PRINT 6,ILIM,LIFE
0018            PRINT 9,ISV,ISINC
0019            DO110 I=1,256
0020            NODE(I,1)=NODEFD
0021            NODE(I,2)=0
0022            NODE(I,3)=0
0023            AVOCC(I)=0.0
0024            IAUTO(I,1)=0
0025        110 CONTINUE
0026            DO120 I=257,600
0027            IAUTO(I,1)=0
0028        120 CONTINUE
0029             PRINT 7
0030            DO 40 I=1,NUMAUT
0031            READ 1100,ILOC,ISTMFD,IA,IT
0032             PRINT 8,ILOC,ISTMFD,IA,IT
0033            IAUTO(I,1)=1
0034            IAUTO(I,2)=ILOC
0035            IAUTO(I,3)=IA
0036            IAUTO(I,4)=ISTMFD
0037            IAUTO(I,5)=0
0038            IAUTO(I,7)=ISTMFD
0039            IAUTO(I,8)=IT
0040            BIAS=1./9.
0041            DO130 J=1,9
0042            EXPER(I,J)=BIAS
0043        130 CONTINUE
0044            NDOCC=NODE(ILOC,2)+1
0045            NODE(ILOC,2)=NDOCC
0046            NODE(ILOC,NDOCC+3)=I
0047         40 CONTINUE
0048      35    READ(5,1100,END=36) J1,J2,IF
0049            IF(J2.EQ.0) GO TO 351
0050            DO 361 II=J1,J2
0051      361   NODE(II,1)=IF
0052            GO TO 35
0053      351   CONTINUE
0054            NODE(J1,1)=IF
0055            GO TO 35
0056      36    CONTINUE
```

```
0057              N=0
0058              CALL OUTPUT(N,IA)
0059       1100    FORMAT(4I5)
0060            3 N=N+1
0061              IF(N.GT.NTRIAL)CALL EXIT
0062              CALL COPY
0063              K=1
0064            5 CALL SFIELD
0065              CALL AVEROC
0066              CALL FDINC(IC,ILIM)
0067              IF(NODE(K,2).LE.0)GO TO 30
0068              CALL ORDOCC
0069              IZ=0
0070           10 IZ=IZ+1
0071              IF(IZ.EQ.(IOCC+1)) GO TO 30
0072              IZAUTO=NODE(K,3+IZ)
0073              CALL AGE
0074              IF(IAUTO(IZAUTO,4).GT.0)GO TO 20
0075              CALL DELETE
0076              GO TO 10
0077           20 CALL EAT(FDREG)
0078              CALL GAINEX
0079              CALL MOVE
0080              IF(IAUTO(IZAUTO,4).LE.IREPLV)GO TO 10
0081              CALL REPRO
0082              GO TO 10
0083           30 K=K+1
0084              IF(K.LE.256)GO TO 5
0085              CALL MAKMOV
0086              CALL OUTPUT(N,IA)
0087              IF(IA.NE.0) GO TO 3
0088              PRINT 99
0089         99   FORMAT('1***POPULATION IS EXTINCT*********')
0090              STOP 99
0091        100   FORMAT(4I5,F5.2,5I5,F5.2)
0092          1   FORMAT('1',55X,'INITIAL   CONDITIONS'/' ',55X,20(1H-))
0093          2   FORMAT('0'/'0',T25,'FOOD LEVEL FOR REPRODUCTION',T55,'=
                 1T65,'NUMBER OF SIMULATION CYCLES',T95,'=',I5)
0094         13   FORMAT('0',T25,'FOOD AT BIRTH',T55,'=',I5,
                 1T65,'RANDOMIZING SEED',T95,'=',I5)
0095          4   FORMAT('0',T25,'FOOD INTAKE EFFICIENCY',T55,'=',F5.2,
                 1T65,'INITIAL NODE FOOD',T95,'=',I5)
0096         15   FORMAT('0',T25,'FOOD INPUT/TIME',T55,'=',I5,
                 1T65,'INITIAL POPULATION SIZE',T95,'=',I5)
0097          6   FORMAT('0',T25,'FOOD LIMIT AT NODE',T55,'=',I5,
                 1T65,'LIFE SPAN',T95,'=',I5              )
0098          7   FORMAT('0'/'0',T37,'LOCATION',T56,'STOMACH FOOD',T78,'A
                 1T91,'TYPE'/' ',T37,57(1H-)/'0')
0099          8   FORMAT(' ',T40,I3,T60,I3,T78,I3,T92,I1)
0100          9   FORMAT('0',T25,'RESPIRATION LOSS',T55,'=',I5,
                 1T65,'AGE RESPIRATION  INCREMENT',T95,'=',F5.2)
0101              END
```

```
0001        SUBROUTINE FDINC(IC,ILIM)
0002        COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOPA
           1ISFLD(9),K
0003        COMMON/B/IOCC,IAVOCC
0004        IFOOD=NODE(K,1)
0005        FACT=FLOAT(ILIM-IFOOD)/ILIM
0006        IFOOD=IFOOD+IC*FACT
0007        NODE(K,1)=IFOOD
0008        RETURN
0009        END
```

```
0001          SUBROUTINE AGE
0002          COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOPA(
             1ISFLD(9),K
0003          REAL ISINC
0004          COMMON/C/IZ,IZAUTO,IFDINC,LIFE,ISV,ISINC
0005          NEWAGE=IAUTO(IZAUTO,3)+1
0006          IAUTO(IZAUTO,3)=NEWAGE
0007          IF(NEWAGE.NE.LIFE) GO TO 10
0008          IAUTO(IZAUTO,4)=0
0009          RETURN
0010    10    IFDDEC=ISV+ISINC*NEWAGE*ISV
0011       60 IAUTO(IZAUTO,4)=IAUTO(IZAUTO,4)-IFDDEC
0012          RETURN
0013          END
```

```
0001               SUBROUTINE OUTPUT(N,IA)
0002               COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOPAI
                  1ISFLD(9),K
0003               COMMON/F/NUMAUT,NTRIAL,IFROUT
0004               IF(((N/IFROUT)*IFROUT).NE.N)RETURN
0005                PRINT 1,N
0006               IA=0
0007               DO 10 I=1,NUMAUT
0008          10   IF(IAUTO(I,1).EQ.1) IA=IA+1
0009               PRINT 2,IA
0010               DO 20 I=1,16
0011         20    PRINT 3,(NODE(I+L-1,2),L=1,241,16)
0012               PRINT 4
0013               DO 30 I=1,16
0014         30    PRINT 5,(NODE(I+L-1,1),L=1,241,16)
0015          1    FORMAT('1',58X,'TRIAL NUMBER',I5/' ',58X,17(1H-))
0016         2     FORMAT(' ','POPULATION SIZE = ',I5/'0',59X,'POPULATIO
                  1' ' ,59X,14(1H-)/'0')
0017         3     FORMAT(' ',42X,16I3)
0018         4     FORMAT('0'/'0',59X,'FOOD LEVEL MAP'/' ',59X,14(1H-)/'(
0019         5     FORMAT(' ',35X,16I4)
0020               RETURN
0021               END
```

```
0001              SUBROUTINE COPY
0002              COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOPA
                 1ISFLD(9),K
0003              DO 10 I=1,256
0004              ICOPAR(I)=NODE(I,1)
0005           10 CONTINUE
0006              RETURN
0007              END
```

```
0001          SUBROUTINE SFIELD
0002          COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICC
             1ISFLD(9),K
0003          COMMON/D/JX,JY
0004          DIMENSION JCOPAR(16,16)
0005          EQUIVALENCE (ICOPAR(1),JCOPAR(1,1))
0006          JX=K-((K-1)/16)*16
0007          JY=(K-1)/16+1
0008          ISFLD(1)=JCOPAR(JX,JY)
0009          IF(JX.EQ.1.OR.JY.EQ.16)GO TO 10
0010          ISFLD(2)=JCOPAR(JX-1,JY+1)
0011          GO TO 15
0012       10 ISFLD(2)=-1
0013       15 IF(JY.EQ.16)GO TO 20
0014          ISFLD(3)=JCOPAR(JX,JY+1)
0015          GO TO 25
0016       20 ISFLD(3)=-1
0017       25 IF(JX.EQ.16.OR.JY.EQ.16)GO TO 30
0018          ISFLD(4)=JCOPAR(JX+1,JY+1)
0019          GO TO 35
0020       30 ISFLD(4)=-1
0021       35 IF(JX.EQ.16)GO TO 40
0022          ISFLD(5)=JCOPAR(JX+1,JY)
0023          GO TO 45
0024       40 ISFLD(5)=-1
0025       45 IF(JX.EQ.16.OR.JY.EQ.1)GO TO 50
0026          ISFLD(6)=JCOPAR(JX+1,JY-1)
0027          GO TO 55
0028       50 ISFLD(6)=-1
0029       55 IF(JY.EQ.1)GO TO 60
0030          ISFLD(7)=JCOPAR(JX,JY-1)
0031          GO TO 65
0032       60 ISFLD(7)=-1
0033       65 IF(JX.EQ.1.OR.JY.EQ.1)GO TO 70
0034          ISFLD(8)=JCOPAR(JX-1,JY-1)
0035          GO TO 75
0036       70 ISFLD(8)=-1
0037       75 IF(JX.EQ.1)GO TO 80
0038          ISFLD(9)=JCOPAR(JX-1,JY)
0039          RETURN
0040       80 ISFLD(9)=-1
0041          RETURN
0042          END
```

```
0001      SUBROUTINE AVEROC
0002      COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICUP,
         1ISFLD(9),K
0003      COMMON/B/IOCC,IAVOCC
0004      COMMON/G/AVOCC(256)
0005      IOCC=NODE(K,2)
0006      TAVOCC=AVOCC(K)
0007      TAVOCC=.875*TAVOCC+.125*FLOAT(IOCC)
0008      AVOCC(K)=TAVOCC
0009      IAVOCC=IFIX(TAVOCC)
0010      RETURN
0011      END
```

```
0001                SUBROUTINE ORDOCC
0002                COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),I
                   1ISFLD(9),K
0003                COMMON/B/IOCC,IAVOCC
0004                IF(IOCC.EQ.1)RETURN
0005                DO 40 I=2,IOCC
0006                NIM1=NODE(K,2+I)
0007                NI=NODE(K,3+I)
0008                IF(IAUTO(NIM1,4).GE.IAUTO(NI,4))GO TO 40
0009                NS=NI
0010                NODE(K,3+I)=NIM1
0011                J=I-2
0012             10 IF(J.LT.1)GO TO 20
0013                NJ=NODE(K,3+J)
0014                IF(IAUTO(NS,4).GT.IAUTO(NJ,4))GO TO 30
0015             20 NODE(K,4+J)=NS
0016                GO TO 40
0017             30 NODE(K,4+J)=NODE(K,3+J)
0018                J=J-1
0019                GO TO 10
0020             40 CONTINUE
0021                RETURN
0022                END
```

```
0001          SUBROUTINE DELETE
0002          COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOPAI
             1ISFLD(9),K
0003          COMMON/B/IOCC,IAVOCC
0004          COMMON/C/IZ,IZAUTO,IFDINC
0005          IAUTO(IZAUTO,1)=0
0006          M=IOCC-IZ
0007          IF(M.LE.0)GO TO 20
0008          DO 10 I=1,M
0009          NODE(K,2+IZ+I)=NODE(K,3+IZ+I)
0010       10 CONTINUE
0011       20 IOCC=IOCC-1
0012          NODE(K,2)=IOCC
0013          IZ=IZ-1
0014          RETURN
0015          END
```

```
0001            SUBROUTINE EAT(FDREG)
0002            COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOPAR
               1ISFLD(9),K
0003            COMMON/C/IZ,IZAUTO,IFDINC
0004            IF(NODE(K,1).GT.IAUTO(IZAUTO,4))GO TO 10
0005            IFDINC=0
0006            RETURN
0007         10 IFDINC=FDREG*FLOAT(NODE(K,1)-IAUTO(IZAUTO,4))
0008            IAUTO(IZAUTO,4)=IAUTO(IZAUTO,4)+IFDINC
0009            NODE(K,1)=NODE(K,1)-IFDINC
0010            RETURN
0011            END
```

```
0001            SUBROUTINE GAINEX
0002            COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICO(
               1ISFLD(9),K
0003            COMMON/C/IZ,IZAUTO,IFDINC
0004            IF(IFDINC.EQ.0)RETURN
0005            IPRDIR=IAUTO(IZAUTO,5)
0006            TOTFD=FLOAT(IAUTO(IZAUTO,7))
0007            TOTFDN=TOTFD+IFDINC
0008            IF(IPRDIR.EQ.0)GO TO 40
0009            DO 30 I=1,9
0010            GVAL=EXPER(IZAUTO,I)
0011            IF(I.NE.IPRDIR)GO TO 10
0012            GVAL=(GVAL*TOTFD+FLOAT(IFDINC))/(TOTFDN)
0013            GO TO 20
0014         10 GVAL=(GVAL*TOTFD)/TOTFDN
0015         20 EXPER(IZAUTO,I)=GVAL
0016         30 CONTINUE
0017         40 IAUTO(IZAUTO,7)=TOTFDN
0018            RETURN
0019            END
```

```
0001                 SUBROUTINE MOVE
0002                 COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),I(
                    1ISFLD(9),K
0003                 COMMON/C/IZ,IZAUTO,IFDINC
0004                 COMMON/D/JX,JY
0005                 DIMENSION MAXSET(9),SFLD(9)
0006                 DO 10 I=1,9
0007                 IF(ISFLD(I).LT.0)GO TO 5
0008                 SFLD(I)=EXPER(IZAUTO,I)*FLOAT(ISFLD(I))
0009                 GO TO 10
0010               5 SFLD(I)=-1.0
0011              10 CONTINUE
0012                 ITEMP=1
0013                 NUMMAX=1
0014                 MAXSET(1)=1
0015                 DO 70 I=2,9
0016                 IF(SFLD(ITEMP)-SFLD(I))50,60,70
0017              50 NUMMAX=1
0018                 ITEMP=I
0019                 MAXSET(1)=I
0020                 GO TO 70
0021              60 NUMMAX=NUMMAX+1
0022                 MAXSET(NUMMAX)=I
0023              70 CONTINUE
0024                 IF(NUMMAX.EQ.1)GO TO 80
0025                  NUMB=RANNYU(0,0)*NUMMAX+1.
0026                 GO TO 90
0027              80 NUMB=1
0028              90 MOVDIR=MAXSET(NUMB)
0029                 IAUTO(IZAUTO,5)=MOVDIR
0030                 GO TO (110,120,130,140,150,160,170,180,190),MOVDIR
0031             110 MX=JX
0032                 MY=JY
0033                 GO TO 200
0034             120 MX=JX-1
0035                 MY=JY+1
0036                 GO TO 200
0037             130 MX=JX
0038                 MY=JY+1
0039                 GO TO 200
0040             140 MX=JX+1
0041                 MY=JY+1
0042                 GO TO 200
0043             150 MX=JX+1
0044                 MY=JY
0045                 GO TO 200
0046             160 MX=JX+1
0047                 MY=JY-1
0048                 GO TO 200
0049             170 MX=JX
0050                 MY=JY-1
0051                 GO TO 200
0052             180 MX=JX-1
0053                 MY=JY-1
0054                 GO TO 200
0055             190 MX=JX-1
0056                 MY=JY
0057             200 IAUTO(IZAUTO,6)=MX+16*(MY-1)
```

```
0001            SUBROUTINE REPRO
0002            COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOP(
               1ISFLD(9),K
0003            COMMON/B/IOCC,IAVOCC
0004            COMMON/C/IZ,IZAUTO,IFDINC
0005            COMMON/E/IREPLV,IREPPS
0006            IZM1=IZ-1
0007            IF(IZM1.EQ.0)GO TO 20
0008            DO 10 I=1,IZM1
0009            JZAUTO=NODE(K,3+I)
0010            IF(IAUTO(JZAUTO,4).GT.IREPLV.AND.IAUTO(JZAUTO,8).NE.I
               1)) GO TO 30
0011         10 CONTINUE
0012         20 IF(IZ.EQ.IOCC)RETURN
0013            JZAUTO=NODE(K,IZ+4)
0014            IF(IAUTO(JZAUTO,4).LE.IREPLV)RETURN
0015         30 IAUTO(IZAUTO,4)=IAUTO(IZAUTO,4)-IREPPS
0016            IAUTO(JZAUTO,4)=IAUTO(JZAUTO,4)-IREPPS
0017            CALL GARBCO(NEWAUT)
0018            IAUTO(NEWAUT,1)=1
0019            IAUTO(NEWAUT,2)=0
0020            IAUTO(NEWAUT,3)=0
0021            IAUTO(NEWAUT,4)=2*IREPPS
0022            IAUTO(NEWAUT,5)=0
0023            IAUTO(NEWAUT,6)=K
0024            IAUTO(NEWAUT,7)=2*IREPPS
0025            IT=RANNYU(0.0)+0.5
0026            IAUTO(NEWAUT,8)=IT
0027            DO 40 I=1,9
0028            EXPER(NEWAUT,I)=.5*EXPER(IZAUTO,I)+.5*EXPER(JZAUTO,I)
0029         40 CONTINUE
0030            RETURN
0031            END
```

```
0001         SUBROUTINE GARBCO(NEWAUT)
0002         COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9),ICOP
            1ISFLD(9),K
0003         COMMON/F/NUMAUT,NTRIAL,IFROUT
0004         IF(NUMAUT.GE.600)GO TO 10
0005         NUMAUT=NUMAUT+1
0006         NEWAUT=NUMAUT
0007         RETURN
0008      10 DO 20 I=1,300
0009         IF(IAUTO(I,1).NE.0)GO TO 20
0010         NEWAUT=I
0011         RETURN
0012      20 CONTINUE
0013         WRITE(6,100)
0014         CALL EXIT
0015     100 FORMAT(//10X,'PROGRAM TERMINATION--NO SPACE')
0016         END
```

```
0001              SUBROUTINE MAKMOV
0002              COMMON/A/NODE(256,50),IAUTO(600,8),EXPER(600,9)
                 1ISFLD(9),K
0003              DO 10 I=1,256
0004              NODE(I,2)=0
0005           10 CONTINUE
0006              DO 20 I=1,600
0007              IF(IAUTO(I,1).EQ.0)GO TO 20
0008              NEWLOC=IAUTO(I,6)
0009              IAUTO(I,2)=NEWLOC
0010              NDOCC=NODE(NEWLOC,2)+1
0011              NODE(NEWLOC,2)=NDOCC
0012              NODE(NEWLOC,NDOCC+3)=I
0013           20 CONTINUE
0014              RETURN
0015              END
```

```
0001              FUNCTION RANNYU(I,IF)
0002             DATA FST/0.0/
0003             IF(FST    ) 20,20,30
0004       20      IX1=IF
0005             FST=1.0
0006             RETURN
0007        30   CONTINUE
0008              CALL RANDU(IX1,IY,Y)
0009             IX1=IY
0010             RANNYU=Y
0011             RETURN
0012             END
```