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INFORMATIONAL ENERGY FLOW AS AN ASPECT OF THE
ECOLOGICAL EFFICIENCY OF MARINE CILIATES * **

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and

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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; May, 1973; Odum, E.P., 1953, 1959; Slobodkin, 1961; Smith and Slatkin, 1973).

Thermodynamic considerations have underlain all the general ideas of energy flow in ecosystems. The energy flow concept 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 routinely (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 (Gallopín, 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 concepts to ecosystems and their dynamics despite pioneering papers (Margalef, 1956; Odum, H.T., 1956; Patten, 1959), and the current wide applications of information principles and systems optimization in molecular biology and genetics (Jacob and Monod, 1961). Initial applications of information theory to living systems were highly abstract and statistical (Johnson, 1970). Information was described in terms of increasing degrees of certainty, design, orderliness, regularity, uniqueness, and specificity, and expressed in terms of negative entropy. 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/cm²/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 nexuses 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

(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.,

Lee et al. in press; Murdoch, 1969; Salt, 1968).

General optimization theory would predict that other predator-prey energy conserving relationships would evolve and hold in many biological systems (Cody, 1974; Marten, 1973; Rosen, 1967). Since it is energetically advantageous for the organism to utilize available organic compounds in its food, if it could recognize the molecules it needs at particular times instead of synthesizing them from simpler metabolites at the expenditure of energy, the presence of required metabolites in food could act to advance the cell cycle. The net result of such a "program jump" would be 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 phosphorylated nucleotides. Dismantling and retrieval of the basic components also requires metabolic energy. Though there is evidence that certain organelles can be directly incorporated by the consumer to yield an energy savings (e.g., Trench, 1973), the energy expended in structural synthesis is almost always lost. On the molecular level, however, greater possibilities for informationally-encoded energy scavenging probably exist (Lee et al., 1974). We felt at the onset of this study that there must be some way to measure or estimate food web energetic transformations which cannot be measured by direct calorimetric methods.

Synchronous culture techniques developed by cell biologists (Lorensen and Vankataramen, 1974; Prescott, 1974; Scherbaum and Zeuthen, 1956) seemed to offer to 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 were therefore: 1) to measure, model and test experimentally information flow in one step laboratory food chains, and 2) to compare the informational processing abilities of two herbivorous organisms from the same habitat eating the same food.

Materials and Methods

Two ciliates, Euplotes vannus and Uronema marinum were chosen as the consumers for comparison because of their extreme size differences and feeding habits. Euplotes vannus feeds in a two dimensional space by grazing on surfaces. Uronema marinum, a hymenostome 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 epiphytic communities. Uronema is also often found in the pelagic community while Euplotes can sometimes be isolated in the benthopelagic communities.

Stocks of ciliates and potential food organisms were cultured axenically (Lee et al., 1971) in Pyrex screw-capped test tubes (20 cm x 125 cm) in 10 ml of medium. Medium "S" (Lee et al. 1970) was used for algal stock and "C" (Lee et al. 1971) was used for the ciliates. A variety of algae and diatoms from their natural habitat were selected as potential foods: (S8) Nitzschia acicularis, (38) Chlorococcum spp, (S41) Nannochloris sp, (S93) Chlamydomonas sp, (S94) a chlorophyte, (S95) Dunaliella salina, (S98) a chlorophyte, (RF-8) Amphora spp, or (9) Cylindrotheca closterium, (BL-27) Cylindrotheca fusiformis, (PB-6) Nitzschia frustulum, (Pb-8) Nitzschia sp, (Pb-13) Nitzschia hungarica.

Respiration rates were measured with 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. Euplotes vannus was counted in a Sedgewick-Rafter counting chamber.

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 aseptically resuspended in minimal medium (Lee et al. 1970). The test ciliates were placed in the main body of the flask. Experiments were done in dectuplicate.

After 90 min equilibration, measurements were made at 15 min intervals for 1 hour, at which time (90 min + 60 min) the algae in the side arm were 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 and food

N_{fe} is the number of food organisms eaten

R is the total system respiration

t is the time and $t \ll r_c, r_f$

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.

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.

ATP estimates were made both directly and indirectly for each ciliate. Direct measurements based on Holm-Hansen's method (1967) were made with the aid of a JRB ATP photometer. Synchronized ciliates at mid-point between divisions were 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 estimates were calculated by extrapolation from respiration rates using Forrest's (1971) method.

Cultures of the two ciliates were synchronized by thermal shock (Lorenzen and Vankataraman 1974; Prescott, 1964). Synchrony was analyzed with the aid of a Coulter Counter model ZBI equipped with a P 64 size distribution analyzer and plotter. In advance of synchronization, stock cultures of each ciliate species were grown with an unidentified species of 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 environmental chamber, Sherer CER-78, for 72 hours. 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 was 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

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:

$$P = 30\% \times D_w \times f_n \quad (\text{Lee and Muller, 1968})$$

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

Food was also in excess in synchrony decay and food switching

experiments. As before, food for experiments was aseptically harvested from growth medium by centrifugation and resuspended in minimal medium "B". Synchrony decay was calculated from ciliate size distribution data. Measurements were made at intervals which corresponded 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 combinatorial 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 those previously calculated. 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:

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

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

Synchronized ciliates were inoculated with two food species both at feeding saturation concentrations. Food organisms were harvested as before. After 24 hours the ciliates were enumerated and generation time calculated. Controls were ciliates fed only one algal species. Experiments were done in replicate.

RESULTS

The respiration of Euplotes vannus ($8.1 \mu\text{l CO}_2/\text{mg dry wt/hr}$) is approximately half that of Uronema marinum ($15.0 \mu\text{l CO}_2/\text{mg dry wt/hr}$). Algae tested had a wide range of respiration rates (Table 1) with a maximum of $58 \mu\text{l CO}_2/\text{mg dry wt/hr}$ for the diatom Amphora sp (RF-8) and a minimum of $3 \mu\text{l CO}_2/\text{mg dry wt/hr}$ for an as yet unidentified chlorophyte (S98).

Feeding was easily measured by the new respirometric method employed (Lee and Muller, in press). If the food was eaten (Fig. 1) respiration of the mixed system dropped; if not, respiration was indistinguishable from unmixed cultures (Fig. 2). S93, Chlamydomonas sp, was eaten in the greatest amount by Euplotes ($2 \text{ mg/mg dry wt ciliate/hr}$). 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 vannus (Table 3). Uronema ate Amphora sp, 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 thresholds for feeding were identified as the points where sharp changes in slope were noted (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 food for each ciliate food mixture are tabulated (Tables 2, 3).

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

Using Holm-Hansen's method (1967) Euplotes has an ATP pool on the order to 10^2 greater than that of Uronema ($5.7 \times 10^{-10} \text{ mole/g}$ vs $2.3 \times 10^{-12} \text{ mole/g}$). ATP values calculated by Forest's method (1969) were slightly lower (80%) but within the same order of magnitude.

Euplotes vannus grew and reproduced fastest when fed S93, 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, had a shorter generation time than Euplotes vannus (Table 7). Uronema reproduced most rapidly on a diet of S94, a chlorophyte (GT = 2.7 hr); on one of the poorest food sources S98 growth and reproduction approached that of starved controls (GT = 8 hr). The average generation time was skewed toward the low end of the range. Two species of algae, S93 and S94 were good food sources for both ciliates but many stimulated the growth of one ciliate (i.e., S95 for Uronema; S98 for Euplotes) but not the other.

Uronema was the ecologically more efficient of the two species tested. When logarithmically growing and fed strains of chlorophytes S93, S94 and S95, its ecological efficiency approached 20% (Table 8). However, on a diet of another chlorophyte, S98, its efficiency dropped to only 6%. Maximum ecological efficiency of Euplotes was 10-12% on two of the same species of algae, S93 and S94 (Table 8). Of the foods eaten, lowest efficiency (2%) was found on a diet of S95. 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.

Diet strongly effected the rate of synchrony decay. Decay of synchrony, predictably, was greatest on the poorest food species, i.e. Euplotes when fed S95, 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 S93, 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, S98, approached the maximum observed decay rate (.18/generation when grown on a diet of S8).

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. The shortest switching time for Euplotes was .3 hours more than the controls in the switch from a diet of Pb-8 to S93 and .2 hours for Uronema in a switch between a diet of S98 and S93 (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 longest 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 S98. Long lags were also measured between diets in which both species were associated with slow synchrony decay rates, i.e. Uronema from S98 to S8 (1.01 hr), Euplotes from Pb-13 to BL 27 (2.56 hr).

DISCUSSION

Nutritionists, particularly those working with gnotobiotic cultures of protozoa and micrometazoa (e.g. Cameron and Nachtwey, 1967; Hall, 1953; Lee et al., 1970; Provasoli, 1968; Shiraishi and Provasoli, 1959) have long emphasized the importance of diet, but most ecologists have failed to give nutritional quality factors (molecular information) 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 strictly coupled with the calorific values of the food organism themselves. Food quality was important as a life cycle determinant. None of the small herbivores we have studied from the community is able to grow and reproduce on a diet of every potential food organism it might encounter (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. 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 (Muller and Lee, 1969; Lee and Pierce, 1963). 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

McEnergy, 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 that another adaptive mechanism present in these species, balancing cell cycle with nutritional input, is really an optimization process. The ciliates 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). Ecological growth efficiency of foraminifera 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.

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 some of the same optimal characteristics. Uniform, almost pure, monotypic standing crops of some plants and their consumers are as highly productive as patchy ones and for the same reason.

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 is 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 relative 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).

Initially we thought it unlikely that we could find a common measure which could be quantitatively used to evaluate the information in all food-consumer relationships which could be obtained without performing an impractical number of experimental measures - a formidable task when one considers the microbial food web which can be found in a single drop of water (Lee et al. 1973). But advances in knowledge of metabolic processing and the complexities of molecular organization gave promise that the problem could be parsed to more manageable proportions (Stebbing, 1974). The data obtained seemed to lend themselves to the development of a comparative index of the relative informational value of the food organisms to the ciliates tested which could be translated into energetic terms. If some algal species advance the cell cycle faster than others, even when their calorific values are the same, then food information is being processed by the ciliates to yield energetic advantages (Tables 8 and 9). In the simplest situation one might expect that the two ciliates have identical information recognition and processing mechanisms. Both grew best on the same two algal food species, suggesting they might have similar abilities. However, the third ranked food for Uronema marinum, S95, was the poorest food for Euplotes. The converse was observed in the case of food organism S8, 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 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.

For analytical purposes, 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:

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

where:

I is the net informational gain

GT_i is the generation time of the consumer when fed 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 organism 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 8 and 9). 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 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:

$$\text{Cyberon content} = \text{Cyb}_{\text{base}} - \frac{(1-k) \times \text{GT}_i \times \text{R}_i \times 36.0}{\text{GT}_i \times \text{F}_i \times \text{C}_i \times 22.4 \times 10^6}$$

where

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

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

The data obtained in this study have many theoretical implications for resource distribution and utilization functions, particularly at the nano, micro, and meio- levels of marine communities. We have found particular application in modeling considerations of the productivity of spatially inhomogeneously organized communities - a topic we have chosen to model and discuss separately (Rubin and Lee, ms in preparation).

TABLE 1

Respiration rates and caloric value of the various organisms used in this study.

Organism	Respiration * (μlCO_2 /mg dry wt/hr)	Caloric content ** Cel/gm
<u>Euplotes vannus</u>	8.1	
<u>Uronema marinum</u>	15.0	
<u>Nitzschia acicularis</u> (S 8)	37.2	7.7
<u>Chlorococcum</u> sp (S 38)	20.0	8.1
<u>Nannochloris</u> sp (S 41)	52.0	9.0
<u>Chlamydomonas</u> sp (S 93)	43.0	8.0
unidentified chlorophyte (S 94)	23.0	8.0
<u>Dunaliella salina</u> (S 95)	10.0	7.5
unidentified chlorophyte (S 98)	3.0	11.13
<u>Nitzschia frustulum</u> (Pb 6)	20.0	9.0
<u>Nitzschia</u> sp (Pb 8)	21.0	8.7
<u>Nitzschia hungarica</u> (Pb 13)	18.0	7.2
<u>Cylindrotheca closterium</u> (BL 25)	3.0	8.7
<u>Cylindrotheca fusiformis</u> (BL 27)	2.0	8.4
<u>Amphora</u> sp (RF 8)	58.0	9.3

* All values $\pm$ 5%

** Calculated following the methods of Paine (1953)

TABLE 2

Feeding rates of Euplotes vannus* on various marine algae.

Food Organism**	Food Concentration ($\times 10^6$)	Food Uptake*** ($\times 10^{-1}$ mg/mg dry wt/hr)
S 41	2.5	6.25
"	5.0	6.73
"	7.0	6.71
"	.5	4.79
S 94	60.0	7.5
"	30.0	7.1
"	80.0	7.2
"	.6	2.5
S 95	.5	2.0
"	2.5	1.5
"	.5	---
"	10.0	2.0
S 93	40.0	20.0
"	20.0	17.0
"	80.0	20.0
"	.4	12.0
S 8	.2	6.2
"	.2	2.1
"	20.0	0
RF 8	.6	0
"	.3	0
"	60.0	0
"	10.0	0
BL 25	2.5	0
"	5.0	2.6
"	25.0	0
"	1.1	0
BL 27	2.2	4.3
"	1.12	2.1
"	.2	0
"	22.0	5.8
S 38	2.2	5.5
"	1.1	.6
"	4.4	.9

TABLE 2 (continued)

Food Organism**	Food Concentration ($\times 10^6$)	Food Uptake*** ($\times 10^{-1}$ mg/mg dry wt/hr)
S 98	40.0	5.2
"	20.0	8.2
"	80.0	5.2
"	4.0	0
Pb 6	3.0	0
"	1.5	0
"	6.0	0
Pb 8	5.0	3.0
"	2.5	3.0
"	.5	0
"	10.0	0
Pb 13	4.5	.3
"	.45	
"	2.5	.3
"	45.0	0

* Inoculum of 1×10^3 cells/ml

** See key for identification

*** Values $\pm$ 5%

TABLE 3

Feeding rates of Uronema marinum* on various
marine algae

Food Organism**	Food concentration ($\times 10^6$)	Food Uptake*** ($\times 10^{-1}$ mg/mg dry wt/hr)
S 41	2.5	.83
"	5.0	.83
"	7.0	.875
"	.5	.4
S 94	60.0	5.45
"	30.0	5.45
"	80.0	4.09
"	6.0	4.09
S 95	5.0	.34
"	.5	0
"	10.0	.6
S 93	40.0	3.4
"	20.0	1.7
"	80.0	1.7
"	4.0	2.5
RF 8	6.0	9.8
"	3.0	7.3
"	60.0	0
BL 25	2.5	.96
"	5.0	.96
"	25.0	0
"	1.1	0
S 38	2.2	.66
"	1.1	0
"	4.4	4.4
BL 27	2.25	.86
"	1.12	.43
"	2.25	0
"	2.25	.86
S 98	40.0	.41
"	20.0	.92
"	80.0	0
"	40.0	0
Pb 8	5.0	1.5
"	2.5	1.3
"	.5	0
"	10.0	0

TABLE 3 (continued)

<u>Food Organism</u>	<u>Food Concentration</u> ($\times 10^6$)	<u>Food Uptake</u> ($\times 10^{-1}$ mg/mg dry wt/hr)
Pb 6	3.0	0
"	1.5	0
"	6.0	0
Pb 13	4.5	0
"	.45	0
"	2.5	0
"	45.0	0
S 8	2.0	.66
"	1.0	.88
"	.2	.22
"	20.0	0

* Inoculum of 1×10^4 cells/ml

** See key for identification

*** Average of 5 replicates; values $\pm$ 5%

TABLE 4.

Generation time of two ciliates grown on various algae.*

Food Organisms**	<u>Euplotes*</u>		<u>Uronema*</u>	
	Harvest***	Generation Time (hrs)****	Harvest***	Generation Time (hrs)****
Stark Media	660	10.00	16	8.00
S 41	2300	5.6	12.6	3.01
S 94	6000	4.06	14.9	2.7
S 95	800	7.97	14.3	2.81
S 93	6100	4.04	15.0	2.75
RF 8	-	--	10	3.44
BL 27	4700	4.32	8	4.00
S 38	5300	4.13	13.2	2.93
BL 25	890	7.74	6.0	5.04
S 98	1200	6.4	4.5	7.9
Pb 8	3200	4.9	--	--
Pb 6	--	--	--	--
Pb 13	1300	6.6	--	--
S 8	2200	5.45	5.5	5.98

* Inoculum 100 synchronized Euplotes; 1×10^4 synchronized Uronema

** For species identification, see key

*** Harvest after 24 hr incubation. Average of 5 replicates.
Uronema harvest 1×10^4

**** Formula:

$$G_t = t * \left[\log_2 \frac{P_t}{P_o} \right]^{-1}$$

where:

G_t = generation time

t = time of experiment

P_t = population at time t

P_o = initial population

TABLE 5

Ecological efficiencies of Euplotes vannus and Uronema marinum when fed on different diets.

<u>Food Organism*</u>	<u>E_e Euplotes**</u>	<u>E_e Uronema**</u>
S 8	4 %	7 %
S 38	6 %	12 %
S 41	4 %	11 %
S 93	12 %	21 %
S 94	10 %	21 %
S 95	2 %	19 %
S 98	4 %	6 %
Pb 6	--	--
Pb 8	6 %	--
Pb 13	--	--
BL 25	2 %	7 %
BL 27	6 %	9 %
RF 8		19 %

* See key for specific identification

** Calculated as:

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

where

P = production

I = ingestion

TABLE 6

Decay of synchrony in Euplotes populations fed different diets.

<u>Food *</u> <u>Organism</u>	<u>Generation</u>	<u>Euplotes</u> <u>Count **</u>	<u>Synchrony</u> <u>Index ***</u>	<u>Mean Decay</u> <u>Rate/Generation</u>
Pb 8	0	100	.93	.18
	1	195	.72	
	2	357	.43	
	3	722	.39	
S 38	0	100	.93	.17
	1	212	.57	
	2	367	.43	
	3	745	.41	
BL 25	0	100	.91	.21
	1	150	.52	
	2	335	.39	
	3	495	.28	
BL 27	0	100	.87	.17
	1	152	.66	
	2	279	.42	
	3	549	.37	
S 41	0	100	.92	.20
	1	215	.63	
	2	387	.42	
	3	762	.32	
S 8	0	100	.93	.20
	5	221	.61	
	10	406	.52	
	24	2000	.32	
S 95	0	100	.95	.24
	1	255	.52	
	2	573	.38	
	3	926	.21	
S 94	0	100	.96	.09
	1	150	.87	
	2	420	.80	
	3	874	.69	
S 93	0	100	.93	.07
	1	225	.87	
	2	401	.85	
	3	971	.72	

TABLE 6 (continued)

<u>Food *</u> <u>Organism</u>	<u>Generation</u>	<u>Euplotes</u> <u>Count **</u>	<u>Synchrony</u> <u>Index ***</u>	<u>Mean Decay</u> <u>Rate/Generation</u>
S 98	0	100	.94	.20
	1	137	.65	
	2	392	.42	
	3	921	.33	
Pb 13	0	100	.95	.21
	1	197	.59	
	2	340	.42	
	3	822	.31	

* See key

** Average of 2 replicates

*** Calculated following the method of Rooney, 1970

TABLE 7

Decay of synchrony in Uronema populations fed different diets.

Food * Organism	Generation	Uronema ** Count ($\times 10^4$)	Synchrony Index ***	Mean Decay Rate/Generation
S 38	0	2	.91	.06
	1	3.7	.86	
	2	7.6	.77	
	3	13.3	.73	
BL 25	0	2	.92	.15
	1	4.2	.73	
	2	7.8	.51	
	3	12.7	.47	
BL 27	0	2	.91	.16
	1	4.1	.75	
	2	8.0	.53	
	3	15.2	.46	
S 41	0	2	.91	.10
	1	3.6	.85	
	2	7.5	.74	
	3	14.4	.61	
S 95	0	2	.92	.06
	1	4.1	.87	
	2	8.0	.82	
	3	14.1	.74	
S 94	0	2	.93	.05
	1	3.8	.87	
	2	7.7	.81	
	3	14.7	.78	
S 93	0	2.0	.92	.05
	1	4.1	.88	
	2	7.8	.83	
	3	15.1	.77	
S 98	0	2.0	.92	
	1	4.0	.78	
	2	7.6	.59	
	3	14.9	.41	
RF 8	0	2.0	.91	.13
	1	3.9	.81	
	2	8.1	.67	
	3	15.6	.52	

TABLE 7 (continued)

<u>Food *</u> <u>Organism</u>	<u>Generation</u>	<u>Uronema **</u> <u>Count (x 10⁴)</u>	<u>Synchrony</u> <u>Index ***</u>	<u>Mean Decay</u> <u>Rate/Generation</u>
S 8	0	2.0	.91	.18
	1	3.7	.61	
	2	7.2	.50	
	3	14.0	.37	

* See key for identification

** Average of 2 replicates

*** Calculated following the method of Rooney, 1972

TABLE 8

The effect of diet change on the reproduction
of two marine ciliates.

Food Organism*		Euplotes***	Uronema***
From	To	Switching Time/hrs	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	S8	2.16	1.2
S8	Pb8	1.17	--
S8	Pb13	2.09	--
S8	S8 Control **	0.40	2.3
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 Control **	0.27	--
Pb8	Pb13	2.09	--
Pb8	S8	1.73	--

TABLE 8 (continued)

Food Organism*		Euplotes***	Uronema***
From	To	Switching Time/hrs	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 8 (continued)

Food Organism*		Euplotes***	Uronema***
From	To	Switching Time/hrs	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 **	0.30	.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

* See key for identification

** Manipulation shock controls (see text)

*** Average of 5 experiments per switch

TABLE 9

The effect of the informational component of diet on the ecological efficiency of Euplotes vannus.

<u>Food</u>	<u>G.T.</u>	<u>Rank with Euplotes</u>	<u>CAL/gm</u>	<u>Decay Rate</u>	<u>Cyberons</u>	<u>E_e</u>
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 10

The effect of the informational component of diet on the ecological efficiency of Uronema marinum.

<u>Food</u>	<u>G.T.</u>	<u>Rank with Uronema</u>	<u>CAL/gm</u>	<u>Decay Rate</u>	<u>Cyberons</u>	<u>E_e</u>
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%

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