

THE CASE FOR THE MULTI-SPECIES ECOLOGICAL
SYSTEM, WITH SPECIAL REFERENCE TO
SUCCESSION AND STABILITY

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GPO PRICE \$ _____

CFSTI PRICE(S) \$ _____

Hard copy (HC) 3.00

Microfiche (MF) _____

653 July 65

FACILITY FORM 602	N 68-27428	
	(ACCESSION NUMBER)	(THRU)
	25	0
	(PAGES)	(CODE)
	C1-83489	05
	(NASA CR OR TMX OR AD NUMBER)	(CATEGORY)

ABSTRACT

This paper presents an evaluation of proposed life support systems based on ecological theory. The two organism life support system (i.e. algae - man) is compared with a multi-species life support system as to stability, structure, and energy flow. It is concluded that the multi-species system is ecologically more sound. This position is supported with data taken from laboratory microecosystems.

A man in a space capsule is a member of an ecosystem, consequently, will be affected by all that goes on in this ecosystem. The success of long-term space flight may well depend on our success in developing a life supported system which is stable and long-lived. It is the purpose of this paper to discuss some properties of ecosystems which promote stability and longevity, and to propose that life support systems must be developed within the conceptual framework of the mature multi-species ecosystem.

Several types of life support systems have been designed or suggested to handle the following aspects of astronaut metabolism: gas exchange, food production, waste disposal and nutrient and water regeneration. Of those proposed, only the storage system, designed for short flights, has been successfully tested. For flights of long duration, only bio-regenerative systems appear to be feasible. The two-species gas exchange and/or food production model has received much attention. These have been described as the unialgal-man gas exchanger (Myers, 1960; others) and the Hydrogenomonas - man life support system (Bongers and Kok, 1964; others). In addition, Oswald, et al. (1965) have discussed the feasibility of an algae-bacteria-mammal system. One other type of life support system has been suggested. This is the multi-species climax ecosystem as proposed by H. T. Odum (1963), and which will be the topic of this paper.

There are at least two approaches to the development of life support systems. One of these consists of the testing and later assembling of separate biological, chemical and mechanical components. The second consists of allowing groups of species known to occur together to re-assemble and reorganize in a new environment into an integrated, self-maintaining system. This system we call an ecosystem. Nature operates

by the second method. Man uses the first in constructing his machines. We submit that the first is ecologically unsound and will prove to be unsuccessful. The balance of this paper will present evidence to show that the multi-species approach will provide the greatest chance of a successful long-term life-support system.

An ecosystem is any assemblage of organisms and their abiotic environment which have the following characteristics (E. P. Odum, 1959, 1963): structural organization, interdependency of components, homeostasis and regulation (either external or internal or both), limits and thresholds, and a development toward a steady state with increasing adaptation with and control of the physical environment (succession). There are four components of an ecosystem: (1) abiotic substances (organic and inorganic), (2) producers, or autotrophs, (3) consumers or phagotrophs which feed on larger particles, and (4) decomposers or osmotrophs, which derive their support from smaller or molecular size particles. Both of these latter categories decompose organic material and release products usable by producers.

One of the most important attributes of ecosystems is the unidirectional flow of energy from green plants through food webs to consumers and decomposers. The amount of photosynthate stored in excess of daytime community respiration is termed net community photosynthesis. At night, part or all of this net storage is consumed by community respiration. A continued excess of community photosynthesis over community respiration leads to an accumulation of biomass. Eventually this accumulation of biomass stops as limits of utilization of light input are reached or nutrients becoming limiting, or some physical threshold such as space requirements is reached.

Ecosystems have structure. By this we mean biomass, stratification of both living and non-living substances, and biochemical and species diversity. Depending on age and limitations of the physical environment, structure is more or less apparent in terms of the numbers of species. An ecosystem with many species per unit number of individuals may have a very complex food web as a result of niche ("way of life") specialization by these species. Also, as the number of species increases, the number of homeostatic or regulatory mechanisms increases, and the organisms within and between the various trophic levels become more independent. There is increasing evidence to show that diverse ecosystems are also diverse biochemically (Margalef, 1963b).

The truly unique feature of ecosystems, however, is not structure or regulation, since these might be accomplished through external mechanical means, but the ability of ecosystems to develop, to come to a steady, self-maintaining, mature stage, often called a climax ecosystem. Some examples of mature systems adapted to particular physical factor regimes are temperate North American Stipa-Bouteloua perennial grassland, eastern deciduous oak-hickory forest, intertidal mangrove forest (Golley, et al. 1962), tropical rain forest and coral reef (Odum and Odum, 1959). Oriental rice culture represents an agricultural system maintained by man which is more mature and stable than, for example, shifting row crop tropical agriculture. The mature ecosystem tends to exhibit the maximum in structure and stability, within the limits imposed by the physical environment.

It is the mature ecosystem which we propose as the theoretical basis for the development of life support systems. We believe that long-term stability, which is the result of the development of many homeostatic mechanisms through succession, must be the underlying concept in the

development of a dependable life support system. In other words, a multi-species system, with its associated high stability, has a far higher probability of survival than, for example, a two-species system.

A two-species system represents what we call "young nature." It has characteristics of early developmental stages of succession. A multi-species system, the result of a long developmental period, represents what we call "old nature" or a mature developmental stage (E. P. Odum, 1962a).

One of the authors of this paper (E. P. Odum) has prepared a tabular model of succession (table 1) with which we can compare the characteristics of old and young nature. Using some of the concepts of this model, we intend to compare two-species life support systems and multi-species systems. We will show in greater detail some properties of ecosystems which demonstrate why we believe that a system with the characteristics of a mature ecosystem must be the basis of future life support systems.

Not all of the ecosystem attributes of the model shown in table 1 are applicable, at present, to life support systems. For example, no one envisions the possibility of man completing a life cycle in space. Other attributes are not well documented and need further research. Our remarks here will be confined primarily to attributes of ecosystem energetics and structure.

Many of the data which we will use during this paper to demonstrate the functional and structural events during succession has been obtained from the study of laboratory microcosms. These microecosystems are at least partially physically isolated from other ecosystems and in this respect are unnatural, since there is no export or import, other than light and gas exchange with the atmosphere. However, the data obtained from these systems has particular applicability to the topic in question here, since a space capsule is a microecosystem.

Table 1. A tabular model of ecological succession.* Trends to be expected in the development of ecosystems.

	Ecosystem Attributes	Developmental Stages	Mature Stages
Community	1. gross production/ community respiration	P/R ratio or one	approaches one
	2. gross production/ standing crop biomass	P/B ratio high	low
Energetics	3. net community production (yield)	high	low
	4. food chains	linear, predom- inately grazing	web-like, predom- inately detritus
Community	5. standing crop biomass & organic matter	small	large
	6. Species diversity	low	high
Structure	7. biochemical diversity	low	high
	8. stratification	undeveloped	well developed
Life	9. niche specialization	broad	narrow
	10. size of organism	small	large
History	11. life cycles	short, simple	long, complex
	12. free inorganic nutrients	large	small
Nutrient	13. mineral cycles	open	closed
	14. nutrient exchange rate, organisms-environment	rapid	slow
Cycling	15. role animals in nutrient regeneration	unimportant	important
	16. internal symbiosis (interdependence of organisms)	low	high
Overall	17. Nutrient conservation	poor	good
	18. stability (resist external perturbation)	poor	good
Homeostasis	19. Entropy	high	low
	20. Information	low	high

The microcosm method has been described by Beyers (1963a, 1964). Briefly, materials from a natural ecosystem are brought into the laboratory and divided equally among a group of containers. Cross-seeding minimizes any possibility of divergence between microcosms. The systems are then placed on the desired regime of physico-chemical variables. Metabolism is measured by recording diurnal pH changes and these data are translated into total CO_2 changes through the use of a graph depicting the relationship between microcosm pH and CO_2 changes. Microcosm biomass is determined by pouring an ecosystem into a tared weighing dish or through a tared Millipore filter. The materials are then dried and weighed. Similarly, total ecosystem chlorophyll is measured by filtering all or part of the system, reading the acetone extract at the appropriate wave lengths for the various pigments, and calculating the amount of chlorophyll according to Strickland and Parsons (1965). These and other measurements are made at intervals during development or succession of the microcosm, and from these data, we have been able to show the course of some of the events of metabolic and structural succession.

In comparing the structure and function of old and young nature, we intend to emphasize these main points. (1) The two-species system represents young nature and has the advantage of a high rate of productivity per unit biomass, but has low stability. The multi-species system has a low ratio of photosynthesis to biomass and thus must be large to support an astronaut, but has the distinct advantage of multi-channel stability. (2) The astronaut is part of a microecosystem, whether we are considering a two-species or a multi-species system, and is therefore part of the structure and function of the system. Depending on system stability, he will be more or less influenced by perturbations in its structure and function.

In Figure 1, and 2 some data on succession in laboratory microcosms are plotted. In these experiments succession was initiated by innoculating material from a mature system into new medium. In young communities the rate of day-time photosynthesis exceeds that of night respiration and biomass accumulates. Total or gross photosynthesis is high in the early stages. After about 70 days of succession, the ratio of day-time photosynthesis to night respiration approaches one, and biomass reaches a stable value. At this point, the efficiency of the system is maximum, under a given set of environmental conditions, in that the highest level of biomass is maintained per unit of gross photosynthesis. Notice also that the rates of respiration and photosynthesis are steady.

In our comparison of young and old nature, we are actually comparing two types of efficiency (Figure 2). In early developmental stages such as the two-species life support system, the ratio of gross photosynthesis to biomass is very high--a small amount of structure is maintaining a high rate of photosynthesis. This is one type of efficiency, and is that which has been emphasized by proponents of the two-species system. If succession is allowed to proceed, whether by design or accident, the ratio drops. The trend in succession is to develop as large and diverse a structure, per unit of energy flow, as possible. Thus in early stages, the ratio biomass/photosynthesis is low; in a mature stage the ratio is high. At climax a more complex structure, with a reduced waste of energy, allows the maintenance of the same biomass with a lower expenditure of energy or cost to the system (Margalef, 1963). The more stable the system, both externally and internally, the less energy needed to maintain this biomass (Connell and Orias, 1964). In other words, as the system ages and develops structure, it becomes more

efficient at maintaining that structure. This is the other type of efficiency, and is that which we propose to be the basis of a stable life support system.

The important point is that stability in these rates and ratios has been developed and will be maintained without external controls at maturity, while in young stages, stability must be constantly maintained through external controls. Mature microecosystems in the laboratory of Beyers have maintained themselves for years.

Another development during succession is the shift from an early planktonic-open water system to a detritus system in later stages. Recent studies (Engelmann, 1961; MacFayden, 1961; Odum, 1963b) have shown that up to 90% or more of the metabolism of natural mature systems is in the detritus layer. The consequence of this in the use of a mature multi-species life support system is that the astronaut must become a detritus-feeder, or a consumer of detritus-feeding organisms. This may, in fact, prove to be far more palatable than bacteria or algae since a great variety of vertebrates and invertebrates are detritus-feeders.

As communities develop, there is an increase in species diversity and this has been assumed to contribute to stability (Connell and Orias, 1964). In a young ecosystem, there are a large number of unexploited ways of life, or niches. During succession, organisms from other ecosystems invade such structurally simple communities or organisms which have been dormant or rare in the early stages become active and numerous. With time, the number of species per unit number of individuals, which we may call a species/number diversity index, increases. It is assumed on incomplete evidence that an increase in the diversity index favors the establishment of homeostasis in terms of checks and balances. During the early stages of succession there

may be "blooms" of the invader populations, often at the expense of one or more established species. Such "blooms" create perturbations that may seriously upset the balance within systems as does a "cancer" growth in individuals. For instance, in the development of unialgal life support systems Miller and Ward (1966) have remarked on the difficulty of preventing the establishment of large populations of grazing zooplankton in their cultures. In a mature ecosystem, with most or all niches filled, the probability of blooms, or even the successful invasion by a new species, is very low (Elton, 1958). That is, the system now possesses stability. For example, the probability of invasion by extra-terrestrial species or a bloom of a mutated form of some component species in a climax system would be much less than in an unsaturated system.

To summarize, the presence of many species not only means a diversity of energy pathways, but also the presence of a great many regulatory and symbiotic relationships. We cannot envision a two-species mechanical-bioregenerative system with this sophistication of control.

Another important trend from young to mature ecosystems, which is a direct result of increasing diversity, is the increase in complexity of food webs. In young stages, the number of species is small and, therefore, the number of pathways of energy transfer between producers and consumers is limited. In the two-species life support system this pathway is linear. In older stages, a great many species have had an opportunity to become established and the food web becomes more complex -- so complex, in fact, that few have been completely described for any large natural area. Figures 3 and 4, based on the data of Paine (1966), illustrates food webs of a simple and a complex ecosystem. The importance of food web complexity to ecosystem stability is very apparent here. The top consumer in the more

nature food web has the choice of ten prey and most of these prey also have several food chains from which to graze, whereas in the less mature system, the number of interactions is much lower. This is analogous to the back-up systems built into the circuitry of space vehicles. In the microecosystem, the investigator has some choice about the number of species in the system, at least initially. During succession, several of the original groups of species may become extinct. For example, truly planktonic species do not survive succession to the climax stage.

Several examples will illustrate our point about the stability of climax ecosystems. In a climax forest, the outbreak of a pest is rare (Nixon, 1958), but in a corn field (an ecosystem much like the two-species life support system) large numbers of pests are common. In the forest a system of checks and balances exists such that an increase in insect population density is automatically followed by an increase in predator density. No such system exists in the corn field and the farmer has to resort to pesticides or mechanical devices. With increasing insecticide resistance, he must resort to more and more potent chemicals. In practice, a combination of biological and physical control is usually optimum from man's standpoint. Our point is that we should fully utilize all possible self-regulation in order not to have to create unnecessary artificial substitutes.

Beyers (1962) has shown that the metabolism of a complex climax ecosystem is considerably more independent of temperature than the metabolism of a simpler sewage community or a single organism. He postulated that the closer a living system approaches the integration of a balanced ecosystem, the less it is affected by temperature. This hypothesis may be expanded to state that the more complex the ecosystem, the less it

will be affected by temperature extremes, adding stability to the system as a whole.

A mature ecosystem is also stable metabolically. Golueke and Oswald (1964) have pointed out that the CO_2/O_2 exchange ratio of the plant used in setting up a biological gas exchanger must match that of the crew, since a very slight mismatch between human RQ and plant AQ would lead to the accumulation or loss of a certain fraction of the human oxygen demand and carbon dioxide output per day. In the multi-species system, the RQ 's of several kinds of heterotrophs would balance the AQ 's of the several autotrophs so that a temporary imbalance with one species would be compensated for by other species.

Additional evidence for the increased stability for a multi-species system is shown by the data presented in Figure 4. A climax microecosystem was irradiated with 10^6 R in an acute dose. With the exception of the loss of one species (an ostracod) there was no visible effect on the system. However, when the system was used to initiate a new autotrophic succession, the results of radiation became apparent. As can be seen in Figure 4, the rate of growth of the system was decreased in comparison to the non-irradiated controls. However, this effect decreased with time, indicating the system's capacity for self repair. The curve for each inoculation, made at weekly intervals after irradiation, shows progressive recovery. The greater the time after irradiation, the closer the curve approaches that of the controls. The principal primary producer and the organism accounting for the maximum biomass in this microcosm was a Chlorella. It is interesting to note that Posner and Sparrow (1964) found that 90% of their pure culture Chlorella died after a dose of 23,000 R. Our Chlorella showed no effects of radiation until they were

irradiated at 2,000,000 R and then took 40 days to die. These results may indicate that the system confers some radiation protection to its member organisms.

The interdependency of components in a climax microecosystem was clearly illustrated in a recent investigation in our laboratory by Mr. Robert Gorden. Gorden has shown that a bacterium also present in the climax is an important source of thiamine, a requirement for the growth of the Chlorella. Close symbiosis between pairs of taxonomically unrelated species is an outstanding characteristic of the most successful natural communities, for example, lichen growths in the arctic or coral reefs in the tropics.

Although little information is presently available, it appears that during succession, both the variety and amount of biochemicals increase (Margalef, 1963b). Many of these extra-metabolites apparently have the properties of inhibitors or of growth promoters (Saunders, 1957). These substances then are environmental hormones and act as regulators (Margalef, 1963b). Another biochemical change during succession is the increase in the quantity of accessory photosynthetic pigments, thus affording the ecosystem with more complete utilization of light as well as a complement of more stable pigments. The increased ability of mature systems to regulate themselves by internal chemical feedback means that less outside energy need be applied by man to achieve stability.

Boyers (1963a, 1965) has shown that there is a general pattern in the metabolism of aquatic ecosystems correlated with the onset of light and dark. The maximum metabolism occurs in the first half of the day or night period. The implications of this pattern for multi-species life

support systems have been discussed elsewhere (Beyers, 1963b). It must be admitted that there is the possibility of deleterious effects on an astronaut by this periodic reduction of photosynthesis and respiration. However, it does seem that the intensity of this phenomena decreases as the species diversity increases (Beyers, 1963a), adding another bit of evidence for the use of complex systems to support man in space.

Our main point in this discussion of ecosystem structure and function is high diversity and high stability in mature systems, low diversity and low stability in early stages. The more mature system has a built-in set of checks and balances which prevent internal disturbances and buffer the system against most external disturbances. Of course, no system is immune to severe perturbations, and, in fact, the limits of ecosystem stability are strongly related to the stability of the physical environment (Dunbar, 1960).

There are certain distinct advantages to young nature, when viewed as life support systems. These advantages are primarily energetic. That is, young ecosystems have high productivity rates per unit biomass which means that they are more efficient gas exchangers in terms of O_2 produced or CO_2 absorbed per unit of biomass. As we have pointed out, however, there are serious disadvantages to young systems as well. It should now be apparent that in the development of a life support ecosystem for man, we must first select for system stability and longevity and then turn to the development of maximum productivity per unit biomass consonant with this stability. We cannot, as has been suggested by Miller and Ward (1966), simply select organisms as needed on the basis of certain desirable functional characteristics and hope successfully to integrate them into a system. This attitude implies that the addition of new species will have no effect

on resident species and this, of course, is ecologically unsound. It should also be apparent that homeostatic mechanisms of ecosystems are far more sophisticated and reliable than their mechanical counterparts. As H. T. Odum (1963) has pointed out, man has yet to develop the miniaturization of circuitry that is found in ecosystems.

The area of a multi-species life support ecosystem capable of supporting an astronaut has been estimated at two acres (H. T. Odum, 1963). This estimate is based on an expenditure of all but about 2% of the photosynthetic production on respiratory requirements of other components of the system. Obviously, practicality dictates some compromise between two-species mechanical systems and the multi-species system which depends on natural self-regulation.

To date, the major emphasis in the development of life support systems has been on single components. These data are valuable and such work should be supported in the future. However, we believe, based on our knowledge of the properties of ecosystems, that future work must stress the development of a multi-species system.

Since such a system will necessarily be larger than proposed two-species systems, we need to determine which processes can be satisfactorily supplemented or replaced by mechanical or chemical devices. For example, the reduction of fecal material to small particles might best be handled by some mechanical method, thus eliminating the need for populations of consumers which ordinarily would fill this role. In other words, we may be able to reduce the predicted size of a multi-species life support ecosystem without reducing the built-in stability of the system.

Finally, it is clear that a great deal of work must be directed towards an analysis of properties of ecosystems before we attempt to advise a multi-species life support system. Part of the controversy regarding the simple vs. complex system may be resolved by a set of experiments. Laboratory microecosystems ranging in complexity from a single alga and consumer to a highly complex system containing several representatives of each trophic level could be cultured under identical conditions. The climax systems and successional stages could be tested for metabolic and species stability under various stresses. Such stresses could include thermal manipulations, ionizing radiation, invasion by foreign species, and mechanical and photoperiodic stresses. We propose to perform such experiments in the future.

Acknowledgements

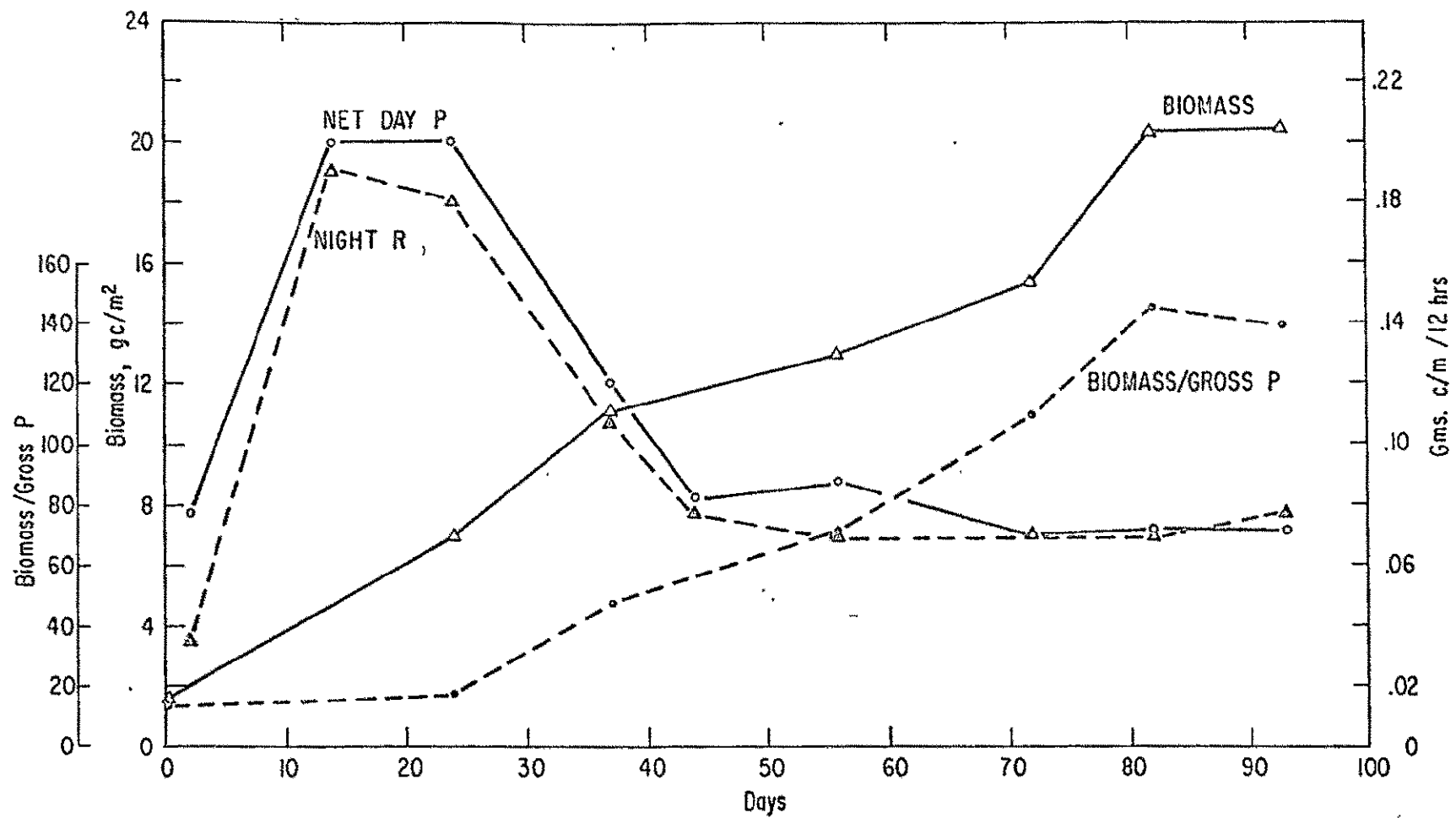
Preparation of this manuscript was supported by a United States Public Health Service (Division of Water Supply and Pollution Control) Post-doctoral Fellowship, contract AT(38-1)-310 between the U. S. Atomic Energy Commission and the University of Georgia, and grant NSF-706/11-003-001 from the U. S. National Aeronautics and Space Administration to the University of Georgia. The authors wish to express their appreciation to Drs. Frank B. Colley, Richard G. Wiegert, and Mr. Peter C. Fraleigh for their criticisms and comments. Figures were prepared by Mr. M. E. Chavis.

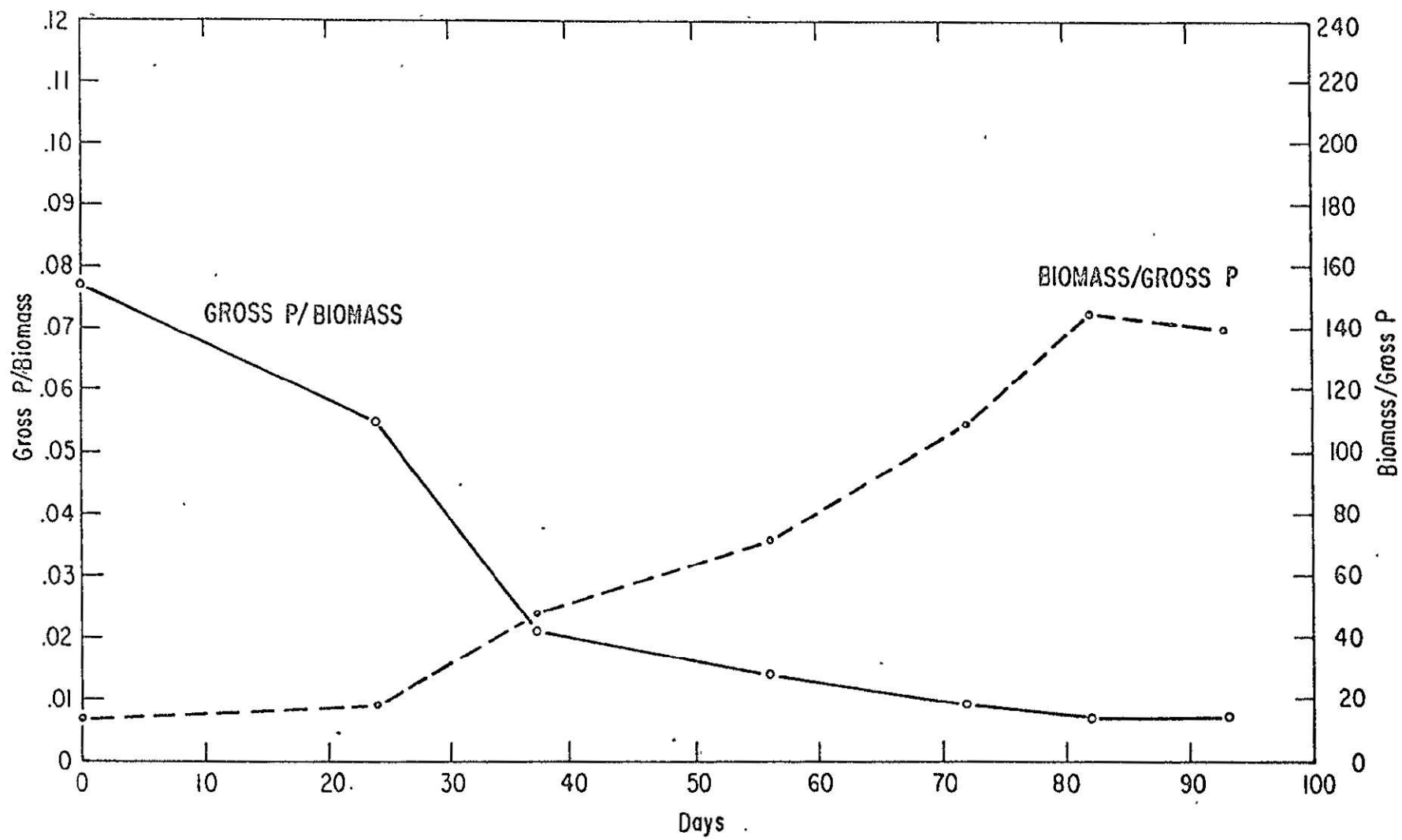
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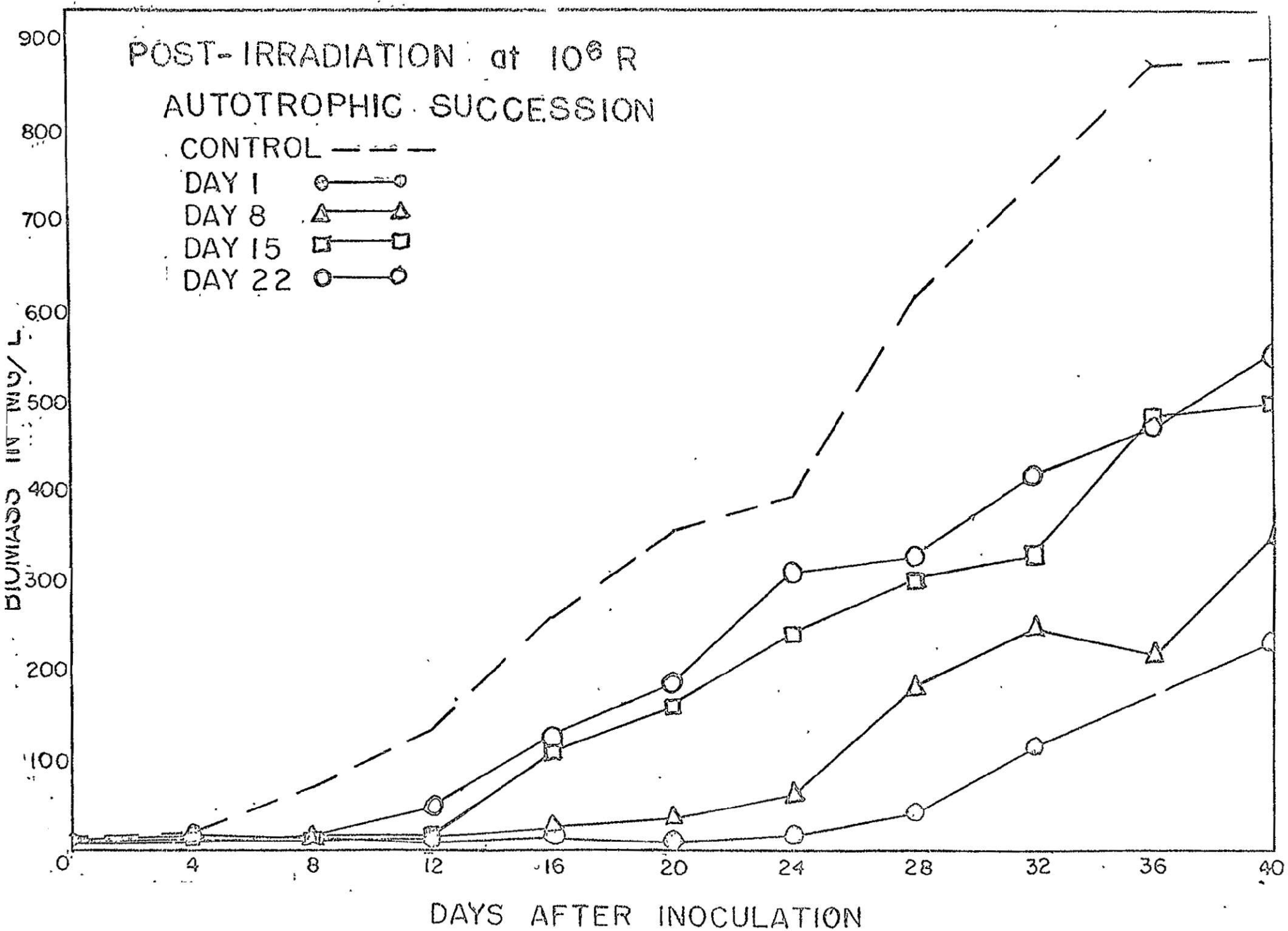
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PISASTER

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NUMBERS—CALORIES

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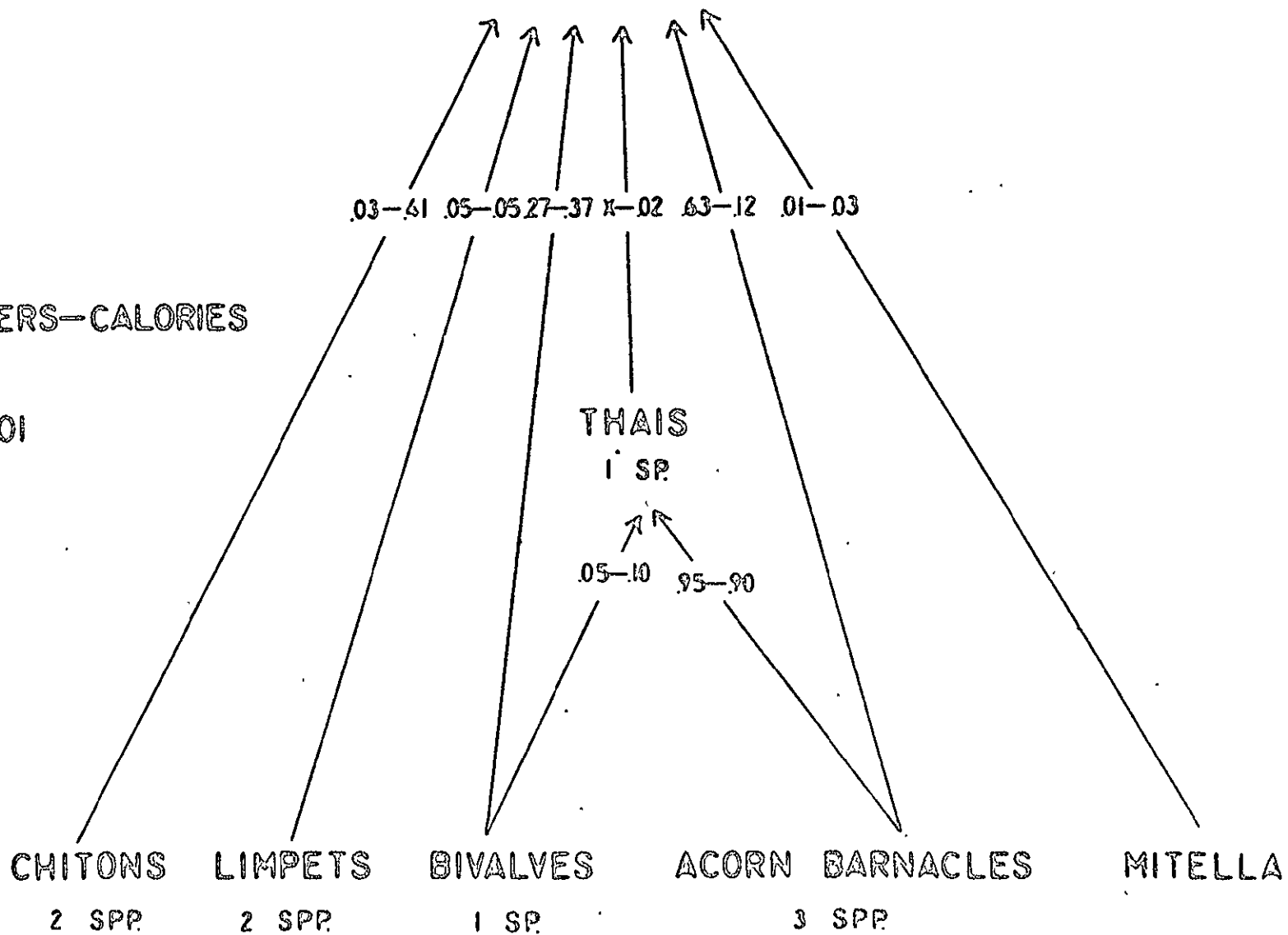
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1 SP.

ACORN BARNACLES

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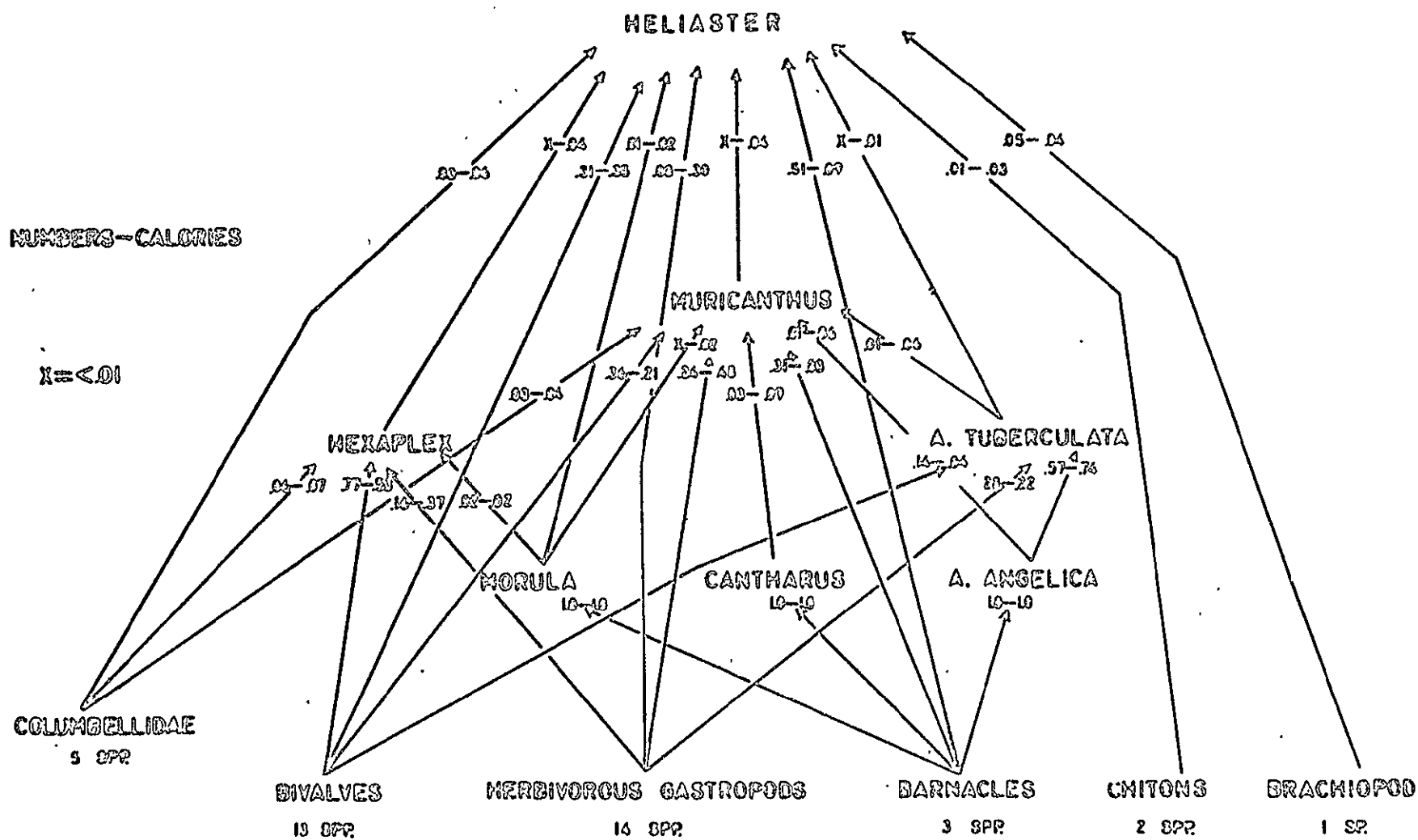


Figure Legends

Figure 1. Plots of net daytime photosynthesis, nighttime respiration, biomass and the ratio between biomass and gross or total photosynthesis against time in a microecosystem undergoing autotrophic succession. All data has been reduced to aerial dimensions.

Figure 2. Plots of the ratios of gross or total photosynthesis to biomass and vice versa against time in a microecosystem undergoing autotrophic succession. This figure illustrates the two types of efficiency outlined in the text.

Figure 3. The feeding relationships by numbers and calories of the Piaster dominated food web at Mukkaw Bay, Washington. Piaster, $N = 1049$, Thais = 287 where N is the number of food items observed eaten by the predators. The specific composition of each predator's diet is given as a pair of fractions: numbers on the left, calories on the right. (From Paine, 1966).

Figure 4. The feeding relationships by numbers and calories of the Heliaster dominated food web in the northern Gulf of California. Heliaster, $N = 2245$; Muricanthus, $N = 113$; Hexaplex, $N = 62$; A. tuberculata, $N = 14$; A. angelica, $N = 432$; Morula, $N = 39$; Cantharus, $N = 8$. See Figure 3 for further explanation (from Paine, 1966).

Figure 5. Course of biomass increase with time in an autotrophic succession in a laboratory microecosystem irradiated at 10^6 Rads. Successions were initiated by inoculating samples of the irradiated mature microecosystem at 1, 8, 15, and 22 days after irradiation. Control curve is from non-irradiated microecosystems.