

## MONTE CARLO MODELLING OF PHYTOPLANKTON DYNAMICS

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### RESUM

Els models de la dinàmica del fitoplàncton basats en les equacions de creixement i competència de Lotka-Volterra no poden predir certes classes de comportament que es veuen sovint a la natura, com són les distribucions heterogènies d'escala petita i la supervivència d'un gran nombre d'espècies de requeriments nutricionals similars en aigües tropicals. Moltes hipòtesis, algunes de les quals necessiten mecanismes forçants o circumstàncies especials, han estat adduïdes per explicar aquestes distribucions. Malgrat això, si es construeix un model de Monte Carlo que impliqui l'arribada de nutrients a l'atzar en l'espai i el temps, es pot demostrar que les distribucions heterogènies són la condició normal, i que l'obtenció de distribucions més uniformes requereix alguna forma de barreja. A més, el grau d'heterogeneïtat de les distribucions de fitoplàncton hauria d'ésser una funció de l'aleatorietat de l'arribada de nutrients. En aquest tipus d'univers, no es poden predir les distribucions d'espècies que es fan competència; per això, el resultat d'una addició de nutrient a gran escala, com a resultat, per exemple, d'un episodi de barreja, és igualment impredecible. Això implica que els ecosistemes del mar obert són inherentment impredecibles, excepte en termes molt generals.

**MOTS CLAU:** *models de població, model Monte Carlo, fitoplàncton, distribució d'espècies, agrupacions irregulars.*

### SUMMARY

Models of phytoplankton dynamics based on the Lotka-Volterra growth and competition equations cannot predict some kinds of behaviours commonly seen in nature, such as the short-range patchy distributions and the survival in tropical waters of a large number of species with very similar nutritional requirements. Many hypotheses, all of them requiring forcing mechanisms or special circumstances, have been brought forth to explain these distributions. However, if a simple Monte Carlo model involving the arrival of nutrients

randomly in both time and space is constructed, it can be shown that patchy distributions should be the normal condition, and that more uniform distributions imply some form of mixing. Furthermore, the level of heterogeneity in phytoplankton distributions should be a function of the randomness of the arrival of nutrients. The distribution of competing species in such a universe cannot be predicted; therefore, the result of any large-scale addition of nutrient, as, for example, from a mixing event, is equally unpredictable. This implies that open ocean ecosystems are inherently unpredictable except in a general fashion.

KEY WORDS: *population modelling, Monte Carlo model, phytoplankton, species distribution, patchiness.*

## INTRODUCTION

For many decades now, the normal method for modelling the dynamics of most populations, and certainly of phytoplankton populations, has involved the use of the Lotka-Volterra types of equations for growth, competition, and prey-predator relationships. These equations are popular because they are easily understood, and they give rise to solutions which have features which resemble what we see in nature. True, the models do not take into account the necessary time relationships between cause and effect; but when somewhat more complex models are built, incorporating such lags, we find the diversity of population growth forms so generated provides even better fits to the populations we are examining. This being the case, we are encouraged to believe that, by extending this type of modelling, getting better numbers and even more complex relationships, we will finally arrive at a predictive model for marine populations. This is an end greatly to be desired, since it would permit us to set rational limits to the exploitation of marine populations, and to defend these limits in the face of political pressures from our own and foreign governments.

The lack of success we have had in the use of such models for prediction has often been laid to the sparseness in both time and space of our sampling grid. The distribution of plankton has long been known to be patchy, for reasons much discussed in the literature; we must know the reasons for such patchiness if we hope to

incorporate these distributions into our models. The Lotka-Volterra models give us no information about spatial distributions, only about populations size, averaged over the region examined. We cannot consider that we know the true sizes of our plankton populations until we know when our sampling is sufficient for our averaging to include the effects of patchiness. If the patchiness is caused by physical forcing, we must sample the physical parameters at close enough intervals to discover how these forcing functions are generated, and what sizes of patch they will produce. Hence the recent spate of international programs involving sampling dense in time and space. If only we sample enough, the answers will appear out of the data, and we will be able to predict.

There is another class of phenomena which simply contradicts these types of models; that is the existence in tropical waters of many species of phytoplankton whose nutritional needs are very much the same, the so-called «paradox of the plankton» (Hutchinson, 1961). According to L-V theory, the species having even marginal advantages should have eliminated the less-favoured species. This is the well-known «Principle of Competitive Exclusion». Again, there is a large literature describing a variety of mechanisms which would bring about this co-existence. Usually, the mechanisms involve minor environmental differences conferring slight selective advantages to one or another species for some short period of time, so that the balance of competition is forever tilting one way

and then another. A similar situation is seen in the benthos, where the coexistence and patchy distribution of competing species is commonly attributed to the existence of microniches, each offering a slight advantage to one of the competing species. These hypotheses have the advantage that they cannot be disproven; if two organisms are sufficiently different so that they can be assigned to separate species, differences in nutritional, behavioral, or spatial requirements can certainly be found sufficient to account for coexistence under specific circumstances.

What is often forgotten in our attempts to explain what we see in nature is that the «Principle of Competitive Exclusion» stems not from the nature of the beasts, but from the nature of the mathematics employed in our models. The principle does not emerge from the model, it is written into the model. We can delay exclusion with the use of time lags, with the selection of birth and death rates shifting with the seasons or with temperature or salinity, but as soon as we write down the coefficients of competition, we have fixed the direction and intensity of selection. We assume that the organisms we are studying behave in accordance with the model we have chosen, but we must remember this is an unproven assumption; the literature is also full of attempts to prove or disprove this principle.

The deterministic L-V models have hidden assumptions stemming from the type of mathematics used. These include the assumption that whatever determines the carrying capacity of the environment is renewed rapidly compared to the rate of growth of the population, so that the carrying capacity remains essentially constant. This is not a necessary assumption, since a varying carrying capacity can be built into a model, although it is almost never done. The progress of the spring plankton bloom in temperate waters is a demonstration that, at least for phytoplankton, this assumption does not hold. A more important assumption is that all organisms, of every species present, have an equal chance at the available limiting factor. The

average value of the limiting factor is the global value, with no patchiness of either organisms or limiting factor.

The Lotka-Volterra approach has so permeated the ecological literature that we often forget that other kinds of models, using other assumptions, can be constructed, and that some of these models need not have their conclusions built into their mathematical expressions. I would propose that we examine one such model.

### **The Manna model**

The question I wish to consider is «What would the distribution of organisms be like if food arrived randomly in time and space?» This is a central question in oceanic regions with stable water columns, since regeneration of inorganic nutrients depends upon the distribution of bacteria and zooplankton, and is not necessarily uniform throughout the water column or even throughout any single horizontal section. It is also an important question in benthic regions, where much of the food arrives as material falling from the water column above. One could attempt to answer this question by the construction of models using probabilistic equations, but finding solutions to the large number of simultaneous equations would not be a trivial task. With the help of the modern digital computer, however, we can obtain numerical solutions using the Monte Carlo technique.

This technique, named after the casino, is designed to deal with systems composed of a large number of linked steps, each step containing a probability distribution, either normal or skewed. A number, sometimes also chosen from a probability distribution, is started through the system, and at each step is treated as the probability distribution of that step indicates; when a sufficient number of trials has occurred, the shape of the final distribution of properties can be seen (Wangersky and Wangersky, 1980, 1981, 1983).



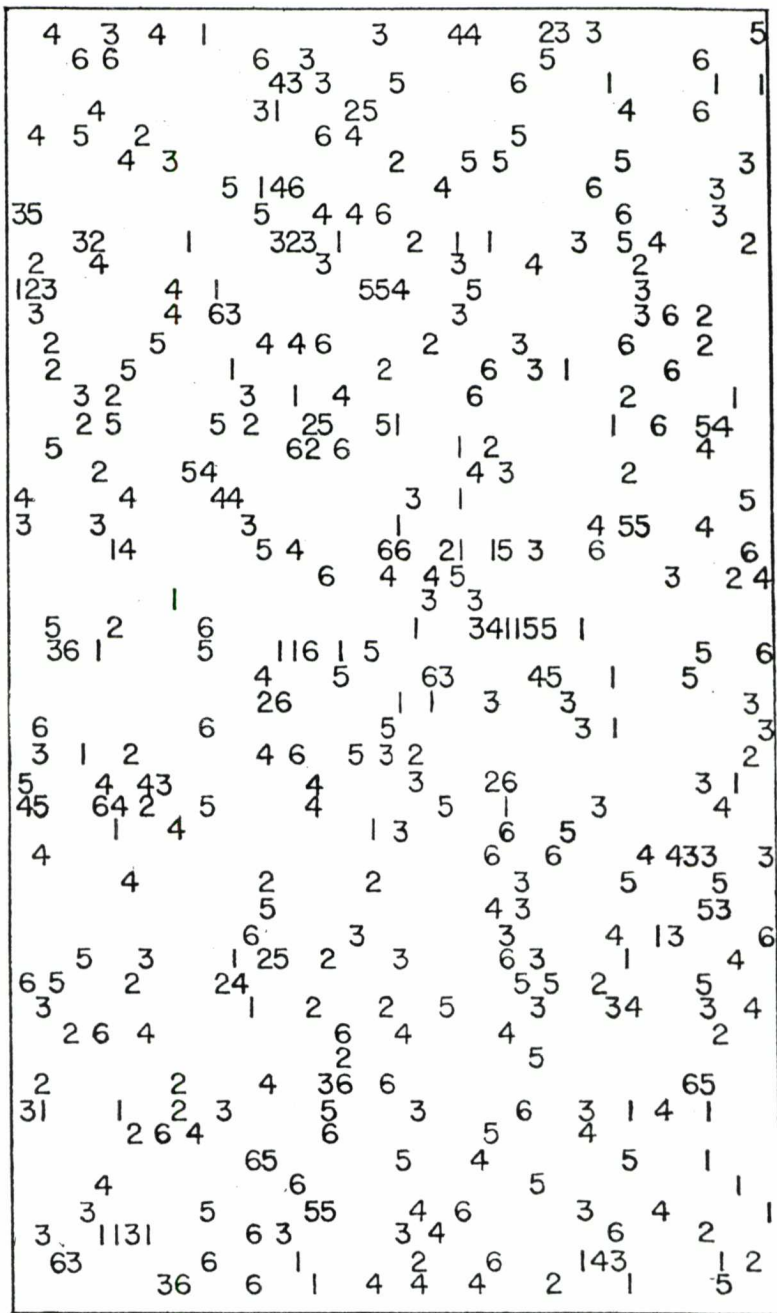


FIGURE 1. Species distribution, generation 0. From Wangersky and Wangersky, 1980; Figs. 5 and 6 from Wangersky and Wangersky, 1983.

For the example we will run, we will consider an area consisting of a grid of 50x50 points. On some of these points we will distribute, randomly, representatives of six species (fig. 1). These organisms are very simple, one might even say schematic creatures. They can take in food when it occurs in their space or the spaces immediately surrounding them. They metabolize this food at a constant rate. Any excess over metabolic needs is stored; when this stored nutrient reaches a given level, the organism divides, with the new organism being placed on the nearest empty grid point. If the stored nutrient goes to zero, the organism dies, and is removed from the grid. Thus the organism is born, it eats, metabolizes, divides, perhaps, and dies, all normal functions, although simplified for the purposes of this demonstration. In this set of models, the assumption is made that competition occurs only through the utilization of nutrients. More complex models could be constructed, perhaps one in which competition was enhanced by the release of toxins injurious to other species, but such complications are special cases, to be examined at some later time. Other forms of competitions can easily be written into these models; the limitations are the ingenuity of the modeller and the natural justification for the phenomenon modelled.

The six species may vary in the efficiency with which they perform these functions, or they may all be alike, distinguishable only by the numbers on their backs, like football players as seen from the top of the stadium. For our first runs, we will make them all alike in nutritional needs and responses. We will give each organism a store of nutrient varying randomly between 0 and the amount needed for reproduction. We will then distribute a set number of packets of nutrient randomly among the grid points. If the packets land within the search region of an individual, the food is taken up; if it is not found by the end of a cycle, it disappears, hence the name «Manna» model. When all of the grid points have been queried, a new cycle is started.

The food is thus supplied randomly in space and time.

### **Patchiness**

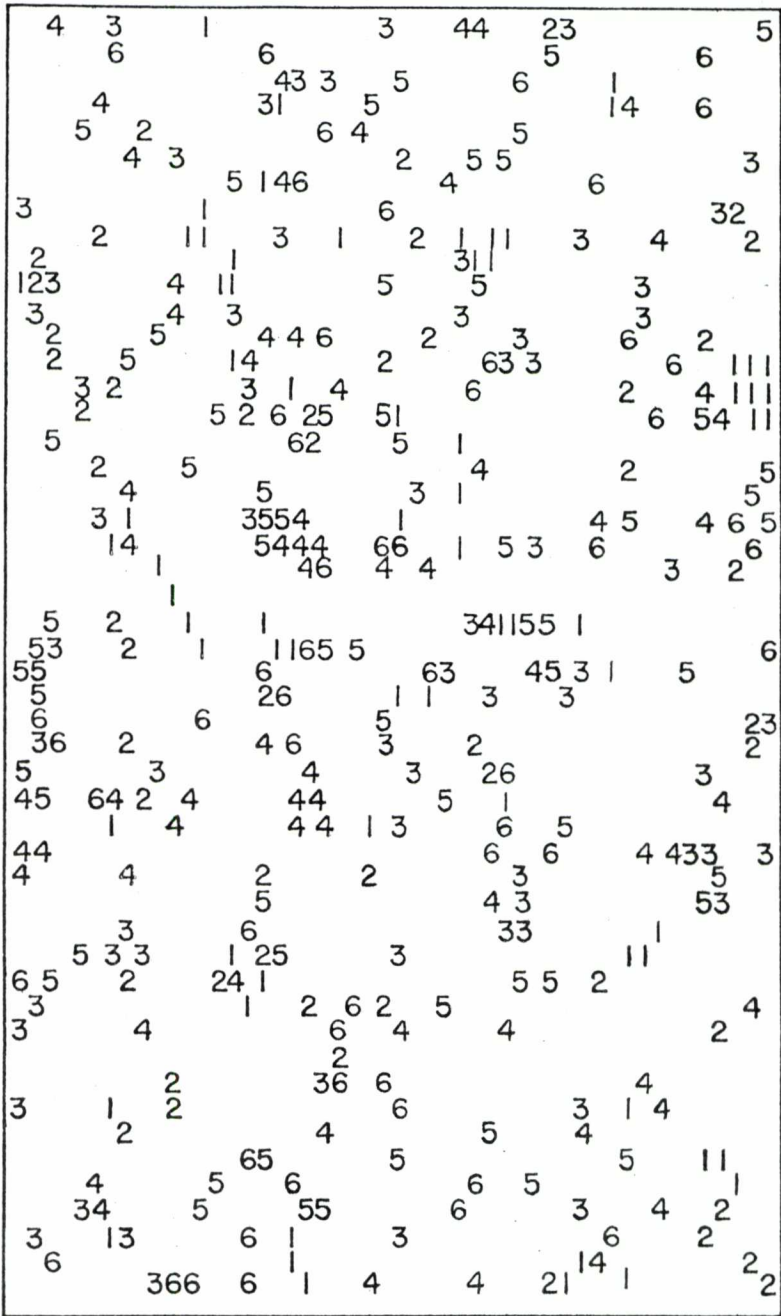
When we run this model, we find that, within three cycles (fig. 2), there are evidences of patchiness of organisms, which are further increased by the sixth cycle (fig. 3). By nine cycles (fig. 4), the organisms are found in patches consisting of one or two species, and they maintain this distribution for as long as you care to run the model. We have run such models for thousands of cycles, and with grids of  $130 \times 130$  points and 36 species, always with the same result. Our conclusions, based on this model, are that if food arrives randomly in space and time, whether through regeneration of nutrients or food falls, the natural distribution of species will be patchy. If the distribution is even, one must look for a forcing mechanism which mixes the patches or distributes the food evenly.

Further, in the case of the benthic organisms, the hypothesis of the existence of microniches is unnecessary to explain the patchy distribution of species or organisms on an apparently featureless plain. The randomness of the foodfalls will ensure that the populations are patchy.

If the food which is not found is allowed to accumulate, eventually some organism will find it, and a bloom will ensue, dying out as the accumulated food disappears. The resultant series of blooms and crashes cannot be distinguished from a cycling phenomenon interrupted by random occurrences (fig. 5).

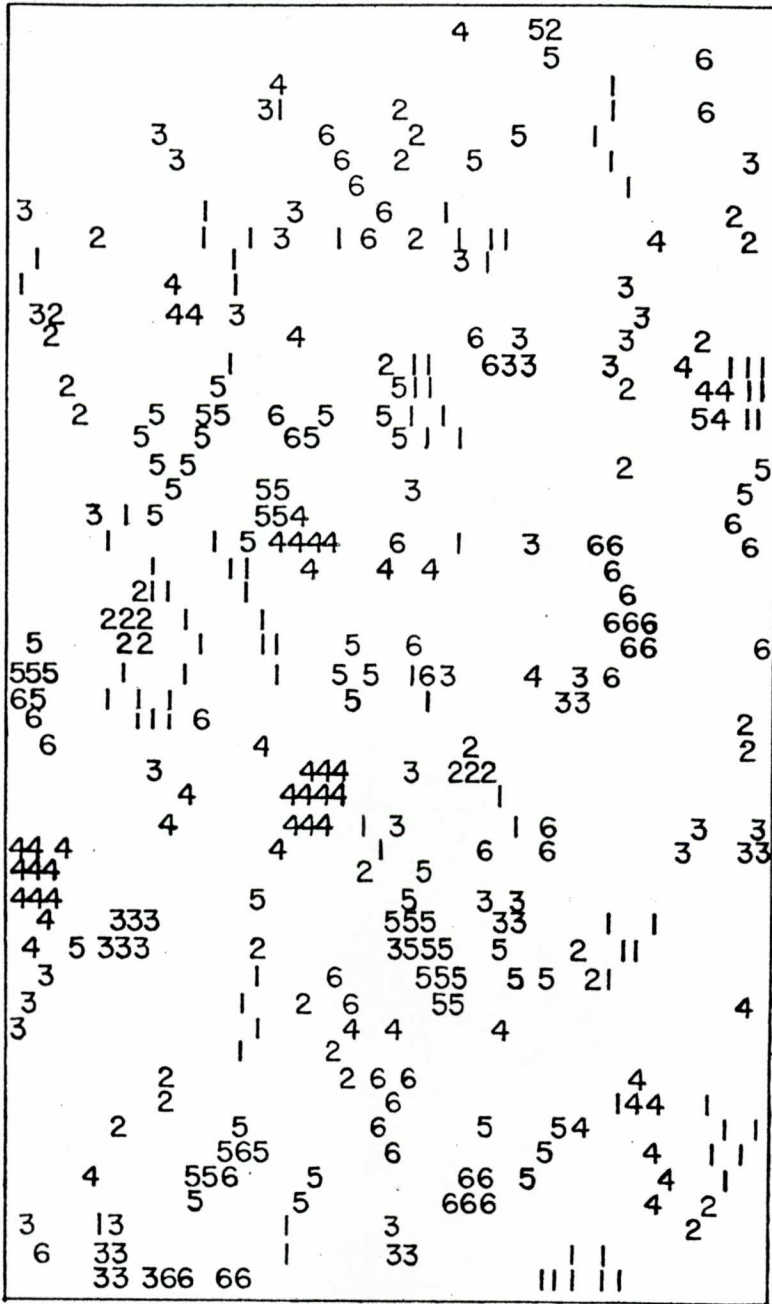
### **Selective advantage**

Let us now look at the effect of varying efficiencies on such distributions. We have run the models with as much as a 30% difference in efficiency between the least and the most



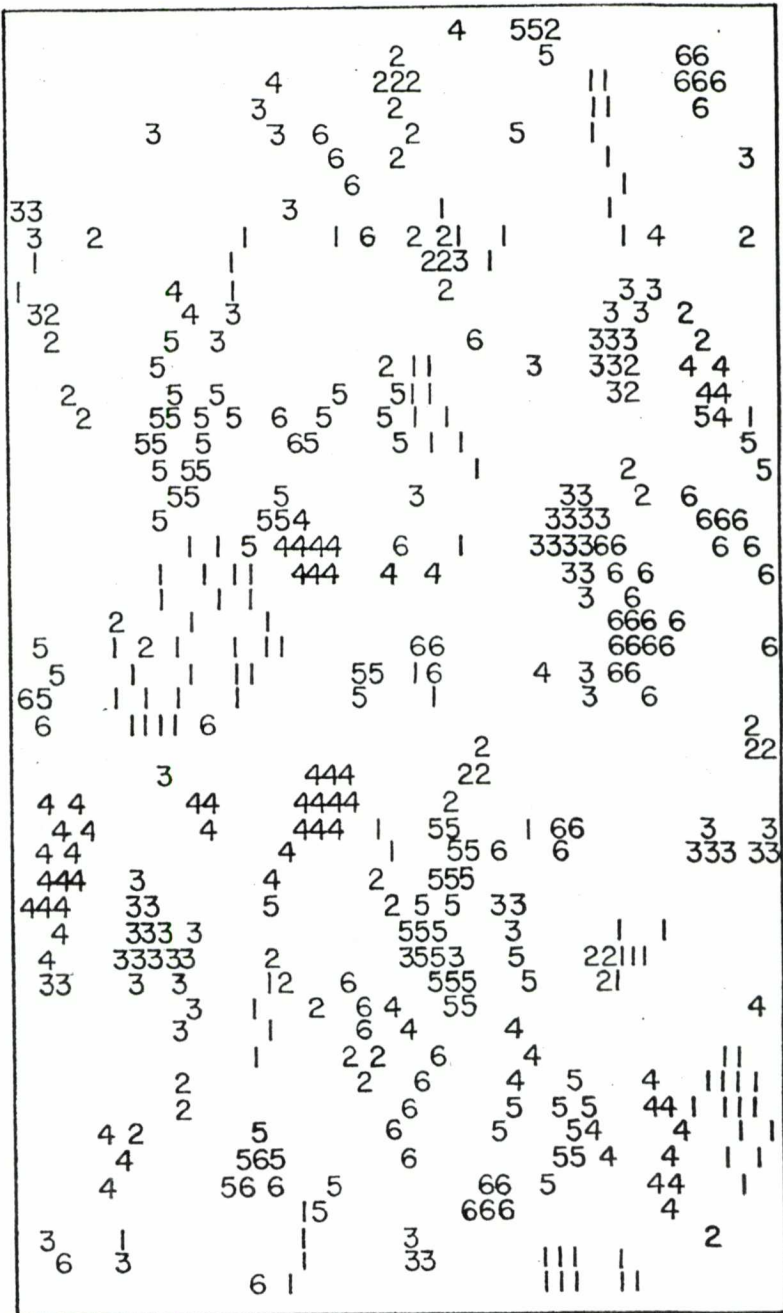
GENERATION 3

FIGURE 2. Species distribution, generation 3. From Wangersky and Wangersky, 1980; Figs. 5 and 6 from Wangersky and Wangersky, 1983.



GENERATION 6

FIGURE 3. Species distribution, generation 6. From Wangersky and Wangersky, 1980; Figs. 5 and 6 from Wangersky and Wangersky, 1983.



GENERATION 9

FIGURE 4. Species distribution, generation 9. From Wangersky and Wangersky, 1980; Figs. 5 and 6 from Wangersky and Wangersky, 1983.



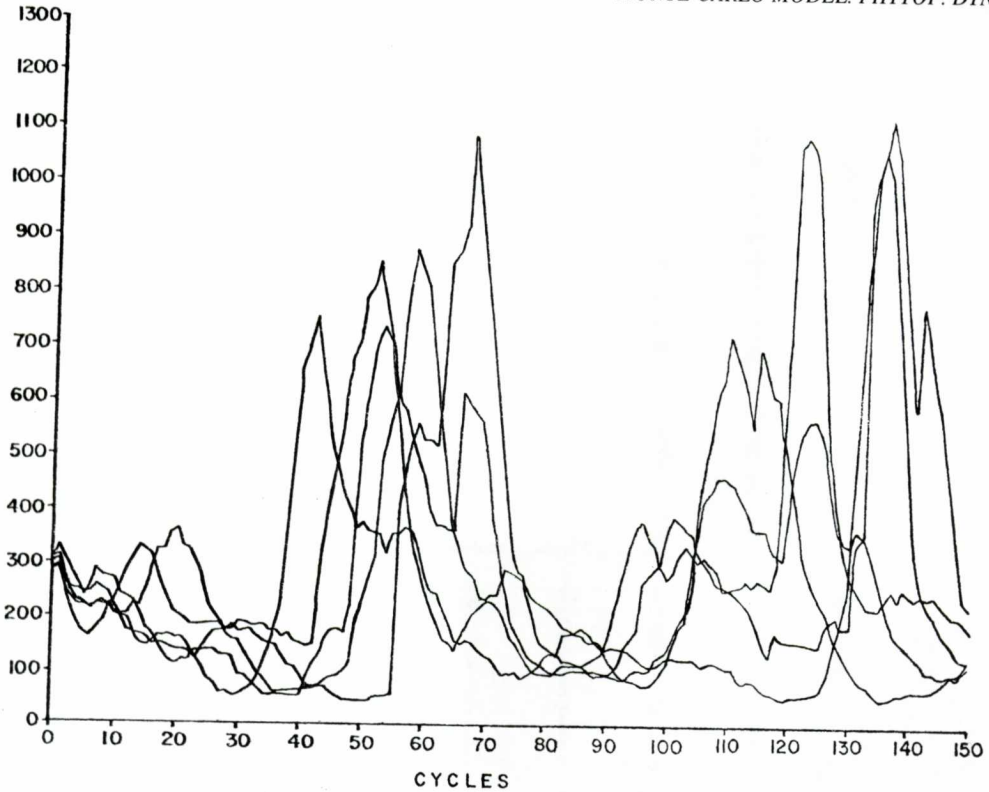


FIGURE 5. Plot of 5 populations, low food supply, with food not found in the current cycle remaining until found.

efficient. While the most efficient species usually did better than those of lesser efficiency, this was not always the case. Even the «fittest» species could be reduced to a few individuals by an unlucky series of food falls. Survival of the species then depends on chance happenings during periods of low population.

Fig 6b illustrates a 150-cycle competition between 6 species of varying efficiency. The efficiency decreases from left to right, with about a 30% difference between the extreme species. As one would expect from competition theory, both the population sizes and the probability of extinction vary as the efficiency of food utilization. However, it must be remembered that, unlike the Lotka-Volterra equations, there is no explicit competition term in this model; what we observe is simply the

result of the combined efficiency of food capture and utilization.

Fig. 6a appears to offer the same story, but in reverse order, left to right. However, in this series, the species were all exactly the same in every parameter except their names. If this were a field experiment in competition, the experimentalist would certainly feel justified in assigning competition coefficients to what is really a random process with historical effects.

In fig. 6c, as in fig. 6b, the efficiency of utilization decreases from left to right, and in the same amount. In this series, after a good start the most efficient species had an unfortunate series of foodfalls and was eliminated from the competition. It should also be noticed that the ranking of the other species depends very much on which cycle you choose to make the

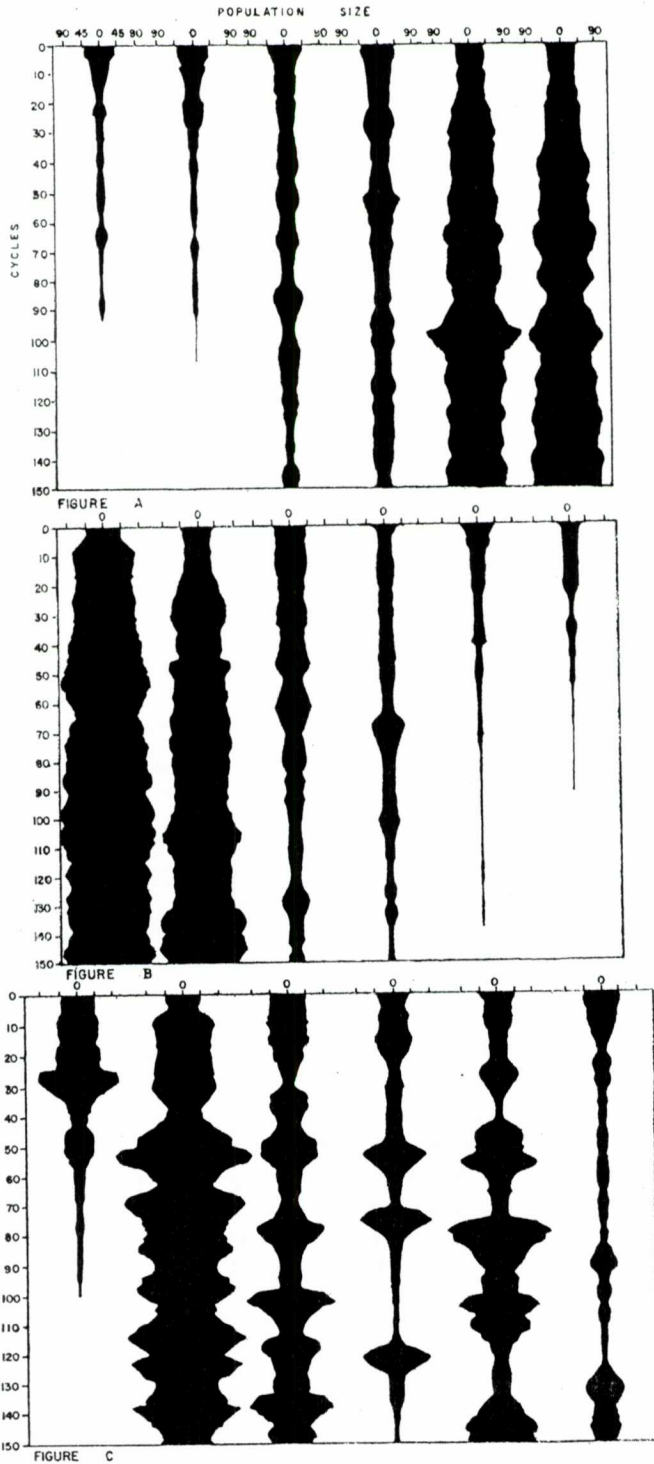


FIGURE 6. Fluctuations in competing populations. *a*, Efficiencies of populations equal. *b* and *c*, Efficiencies decreasing from left to right.

measurement. It is not at all clear that even the «average» population level would be a reliable guide; species 4, although more efficient, is obviously less successful than species 5 if average population size is the criterion.

Many such series were run, with a wide variety of food supplies. Only in a narrow band of food supply was efficiency of utilization of any great importance to the survival of the species. At high food supplies, all species survived, in spite of differences in efficiency which should have resulted in competitive exclusion. This was the case even when we ran such competitions for more than 2000 cycles. On the very long runs with high food supply, we would occasionally lose a species. However, the species lost could as well be the most efficient. This part of the study suggested that, if competitive exclusion works in systems with sufficient food, it works over very long time spans. At low food supplies, luck was more important than efficiency of utilization. Even in the narrow band of food supplies where efficiencies were most important, the more efficient species were often eliminated by a series of unfortunate foodfalls. One is forced to the conclusion that, while it is good to be skillful at what you do, it is even better to be lucky. I am not suggesting that evolution through competition does not work. I am suggesting that the process is slow, and that many false steps are taken along the pathway.

In the normally stable, somewhat oligotrophic waters of the tropics, the governing factor in survival of a phytoplankton organism, or patch of organisms, will be the local variability in the supply of nutrients. Where the local variability is high, increased efficiency of utilization is no guarantee of increased survival. If there is a cost to be paid for increased fitness, in this kind of environment the cost may not result in selective advantage; we would therefore expect that, in a universe where nutrients are scarce and supplied randomly in time and space, either by local regeneration or by foodfalls, many species with approximately the same nutritional requirements

will co-exist. There is no profit to the species in being more competitive in an environment governed by chance occurrences. The paradox of the plankton is therefore not really a paradox, but rather a natural result of the manner in which nutrients are supplied in tropical surface waters.

### **Predictability**

These models must lead to the conclusion that in stable water columns, with regeneration the principle mechanism of nutrient supply, prediction is possible in only the most general fashion. In regions or times when the available nutrients are more evenly distributed, we would expect the deterministic models to hold somewhat more closely; however, we must keep in mind that the oceans are never strictly this or strictly that. Even in the midst of the spring plankton bloom, local regeneration is supplying some of the available nutrients. Even in midsummer, when the surface waters are stable and the nutrient supply is predominantly through regeneration, mixing events such as windstorms can cause short-term blooms of one or a few species, a temporary reversion to the determinism of the homogeneous, high nutrient systems.

While we can predict that a mixing event injecting new nutrient into the surface waters will be followed by a bloom as the water column stabilizes, we can predict which species will predominate only in a most general fashion; in this case, history is the villain. In order for a species to compete successfully for the extra nutrients supplied by a mixing event, the species must be present in sufficient numbers at the time of the event. If, in the previous period, it has been eliminated or greatly reduced by misfortune, some other, perhaps less well adapted species will bloom in its place. Thus, while the start of the spring bloom in Long Island Sound could be predicted with fair accuracy by a knowledge of day length and cloud cover, the bloom species composition was unpredictable, even after twenty years of observation.

## Future directions

The Manna type of model has certain advantages over the Lotka-Volterra models. It is obviously a tool for examining possibilities, and one not easily converted into a model for prediction; we start with the knowledge that we can predict only in the most general terms. It should be noted that the growth curves for individual species and for the total number of individuals in those systems with a high rate of nutrient supply are a good approximation to the logistic growth curve. It can give us information on the probable causes of spatial distributions. With proper instructions, it can examine the effects of mixing events of various strengths on the more general case of the stable water column. While we have at this time examined only those cases where the offspring remained close to the parent form, the model can be adapted to examine larval forms which are dispersed, as in the case of planktonic larvae of benthic organisms. The limitations are primarily the imagination of the investigator.

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