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SIMULATION OF A VERTICAL STRUCTURE IN A PLANKTON ECOSYSTEM

BY

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Introduction

The modelling of plankton ecosystems was started 25 years ago by Gordon Riley (Riley et al, 1949) who showed that simple models could simulate some of the general features of planktonic cycles although the correspondence with observation was not very good. Since then, and especially in the last few years, there has been a great increase in this form of activity but with little if any improvement in the goodness of fit of theory to observation. Essentially this arises from the great variability in the observations of phytoplankton and zooplankton concentrations. In general, these models assume that variability arises from "forcing functions" associated with the physical environment; basically changes in light, turbidity and water movement, vertical and horizontal.

An alternative approach is to consider whether this variability can arise from effects at higher trophic levels, that is from inherent biological processes rather than imposed physical factors. This paper (and the next one) will explore the possibilities of variations arising from the growth cycles and feeding behaviour of the herbivorous zooplankton. The model used here is being developed to study changes in vertical distributions of nutrients, phytoplankton and zooplankton in large plastic enclosures in Loch Ewe, Scotland, and Saanich Inlet, Vancouver Island, Canada. For brevity, only the temporal changes in surface phytoplankton and in depth integrated zooplankton populations will be considered in detail, in this context.

The Model

A 24 m water column is divided into 12 layers with variable vertical mixing between them. The mixing rates and photosynthetic rate per unit plant carbon can be input for each layer on a day-to-day basis. Here these factors are taken constant with time to provide a "smooth" physical world (Fig. 1). Nitrogen (N) is assumed to be the limiting nutrient. All biological components are assumed to have a fixed C/N ratio so that uptake of N by phytoplankton according to Michaelis-Menten kinetics is equivalent to growth. Zooplankton excrete N in proportion to their respiration. It is assumed that phytoplankton sinking is related to nutrient concentrations (Steele and Yentsch, 1960) with a maximum rate at N=0.

The zooplankton population consists of 6 cohorts. The "species" used here is taken to be Calanus with an initial weight (in carbon units) of 0.2 µgC and a final adult weight of 100 µgC. When any cohort reaches 100 µgC, the individuals remain at this weight and food taken for the next 20 days is used for production of eggs. This egg production should occur continuously over the 20 days and would spread the cohort over this time period. I have found this too complicated to handle at present and so have assumed that all reproduction over the 20-day period results in a new cohort of individual weight 0.2gC.

Grazing is related to weight as $W^{0.7}$; it depends on phytoplankton concentration P as

$$C\ (P - PO)/(D + P)$$

where C, D are constants and PO is a threshold below which feeding is zero. It is assumed that a constant fraction, 0.7, of ingested food is assimilated. Metabolism has two components, a basal rate dependent only on weight (as $W^{0.7}$) and a component proportional to the food assimilated.

Predation on the zooplankton is the most difficult factor to define. A fixed mortality on eggs is used to determine the size of the juvenile population for each cohort. In the example here the mortality of numbers (Z) in a cohort is taken to be roughly proportional to biomass W.Z. A more detailed description of the assumptions (and problems) regarding the zooplankton is given in Steele (1974).

For vertical distributions two strategies are used

(1) zooplankton spend equal time at all depths

(2) time in each layer is proportional to food concentration.

Output

Depending on mixing and sinking rates, various vertical distributions of N & P can be obtained such as midwater phytoplankton maximum, Figs. 2 and 3. These contain no surprises but require good observational and, especially, experimental data, on sinking rates, mixing rates and the carbon/chlorophyll ratio of the phytoplankton. For the run in Fig. 2, the corresponding zooplankton cohort structure, Fig. 4, developed from initial values given in Table I. Looking at the time sequence of numbers of juveniles at the start of each cohort, it can be seen that this varies by more than a factor of 10 and that the variation does not follow through any particular cohorts. The effects of this on zooplankton biomass (BIOM = ΣWZ) and on surface plant carbon concentration (Ps, taken as an index of phytoplankton in the euphotic zone) is given in Fig. 5 for three different initial values of N & P in the water column.

It is obvious that initial N & P have some effect on Ps and BIOM over the first 100 days but it is also apparent that large amplitude variations in Ps and BIOM occur later which are similar for the three different initial conditions. These result from the initial structure of the zooplankton cohorts and from the predation pattern imposed on them.

One way to illustrate this is to let a run go on for a very long period of time, Fig. 6. Any portion of this run could be considered as a separate shorter run from different initial conditions. Thus a portion towards the end has very low amplitude variation with a short cycling time of 30 days. This figure also shows that the period of initial large amplitude fluctuations is about 150 days which is approximately twice the life cycle of the copepods.

Conclusions

The purpose of these calculations is to demonstrate the scale of variation which can be imposed by the life cycles inherent in the zooplankton populations. These large amplitude changes with time depend on the initial conditions of the zooplankton cohort structure. In practice, these conditions could arise from a particular pattern of egg laying by over-wintering copepods during very early stages of the spring outburst when transient thermoclines can produce sporadic bursts of production. Such a particular pattern, which is difficult to observe except by a special survey, could then determine some features of events in the rest of the productive season.

Of course the details of the subsequent events shown in these examples also depend on details in the construction of the model. Especially the simulation of reproduction used here will be a major determining factor, and other forms of simulation might vary the pattern. Thus the aim is not to suggest that the details of reproduction or of growth and metabolism modelled here are the correct ones; but that, without good information on these aspects, a major source of environmental variability would be omitted.

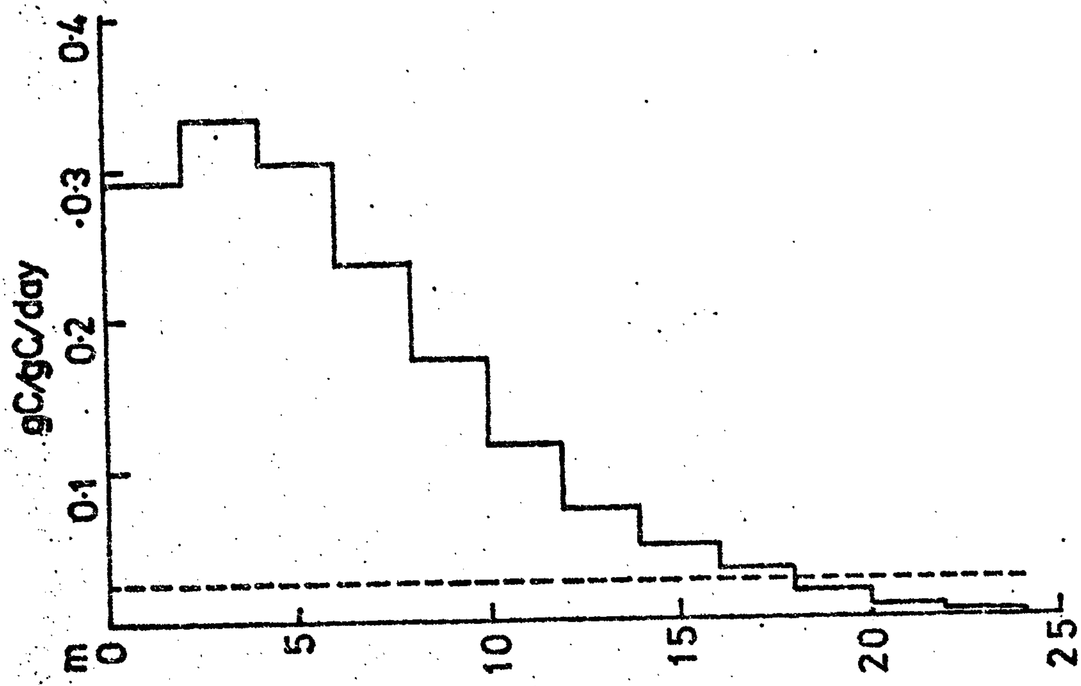
References

Riley, G. A., Stommel, H. and Bumpus, D. F.	1949	Quantitative ecology of the plankton of the western North Atlantic. Bull. Bingham Oceano. Coll., 12, Art. 3.
Steele, J. H. and Yentsch, C. S.	1960	Vertical Distribution of Chlorophyll. J.mar.biol.Ass. U.K. 39 (2), 217-226.
Steele, J. H.	1974	The Structure of Marine Ecosystems. Harvard Univ. Press, Cambridge, Mass. 128 pp.

Cohort	1	2	3	4	5	6
Weight (µg/C)	0.2	4	20	50	100	100
No. ($10^{-3}/m^2$)	20	10	5	2	1	0.2
Maturity (days)	-	-	-	-	0	10

Table I. Initial conditions for the six cohorts. Maturity refers to the number of days the cohorts have spent as adults.

Figure 1. Photosynthetic rate (PH) as a function of depth (dashed line represents respiration).



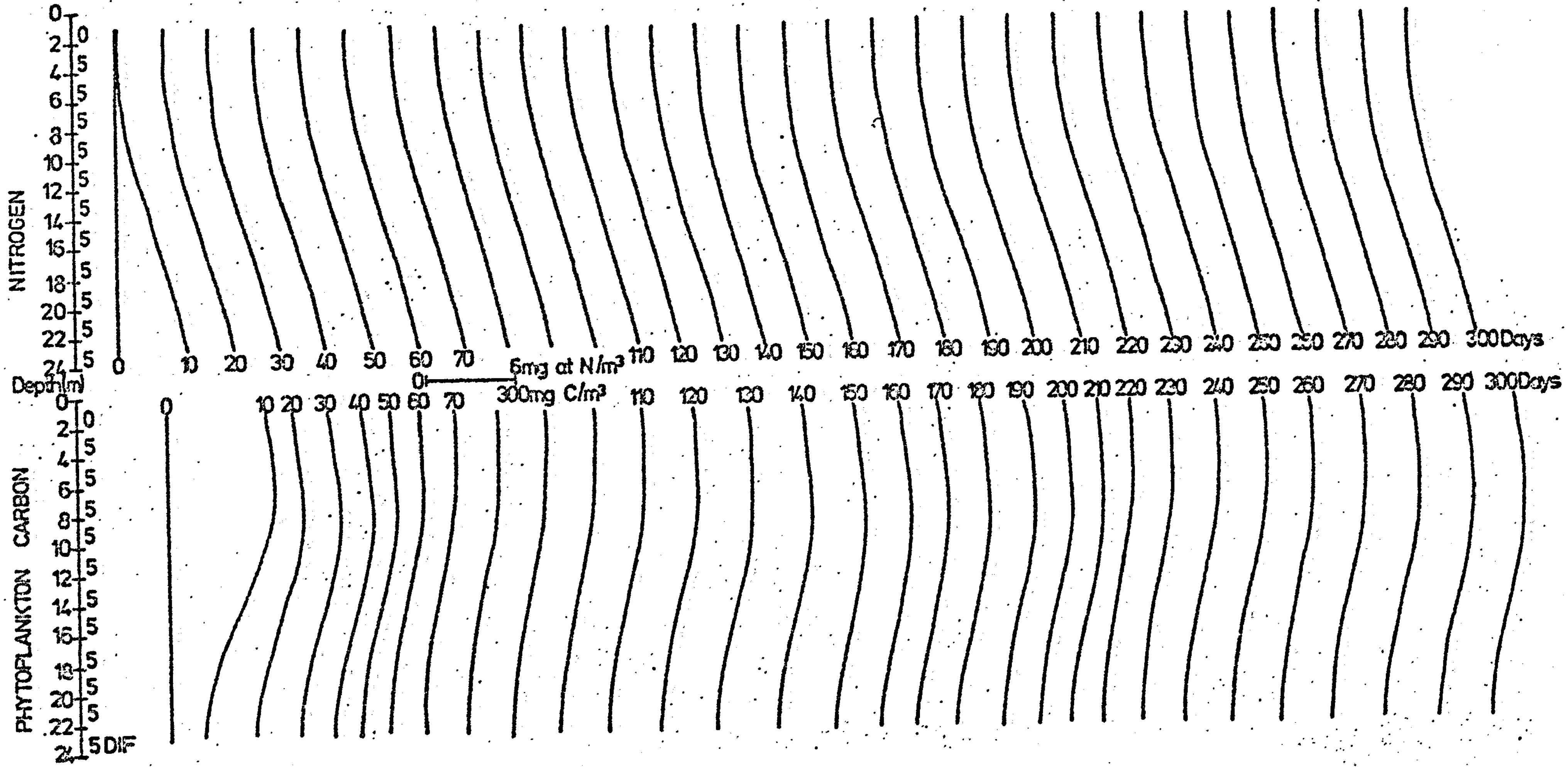


Figure 2. Depth distribution of nitrogen and phytoplankton carbon with mixing rate constant with depth.

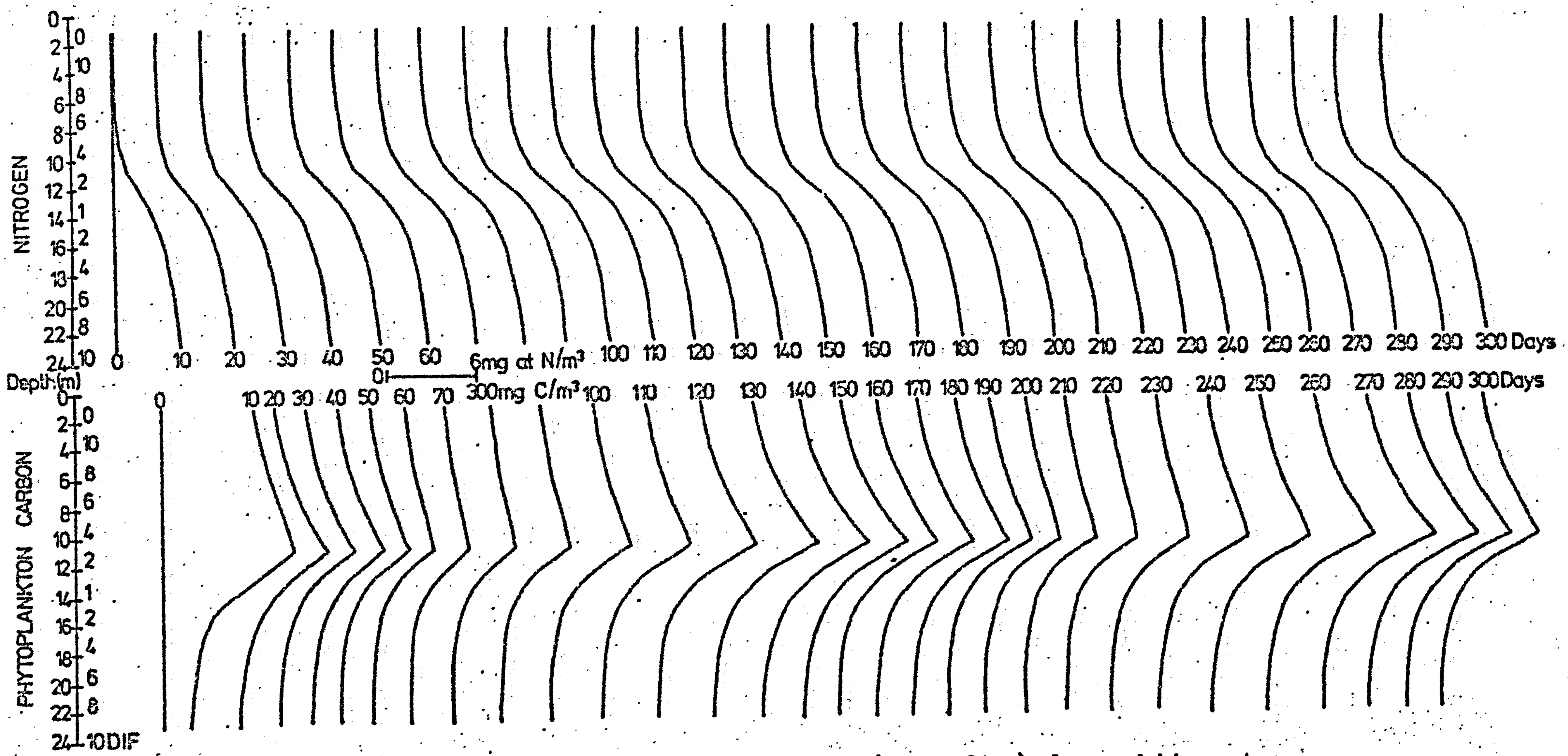


Figure 3. Effect of a low midwater mixing rate (thermocline) plus a sinking rate dependent on N.

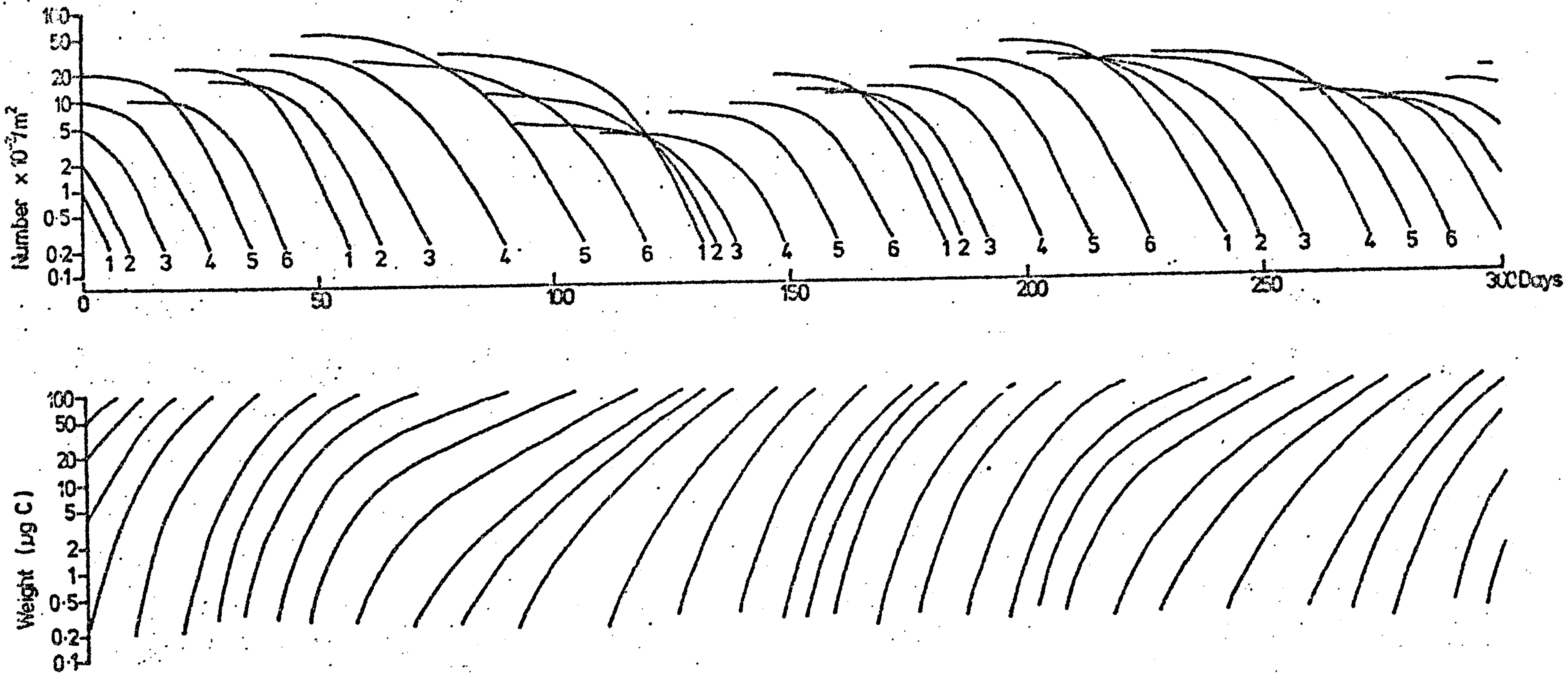


Figure 4. Numbers and weights of copepods in the six cohorts with predation approximately proportional to biomass. For changes in biomass see Figure 5(b).

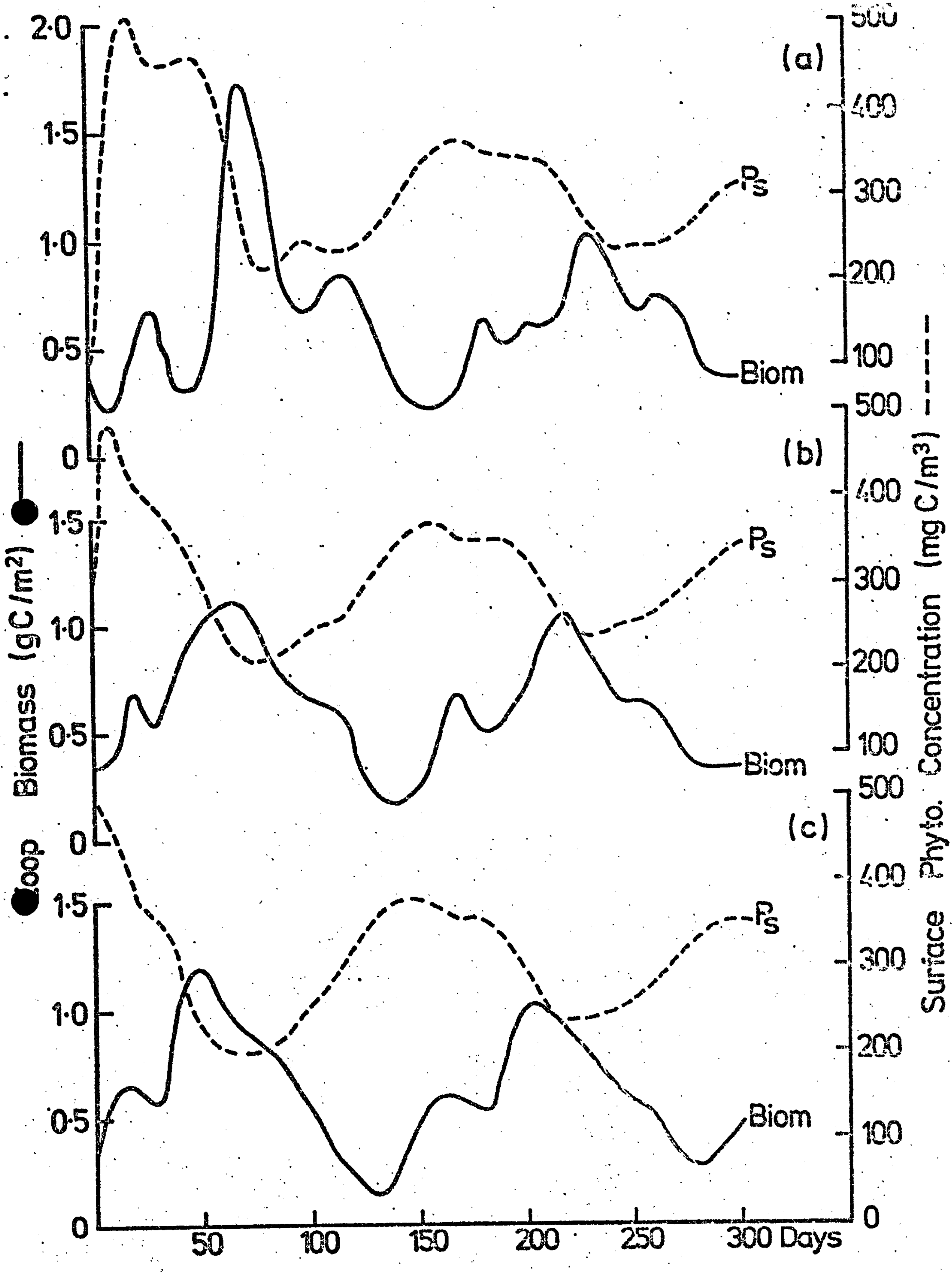


Figure 5. Simulation runs for 300 days of surface phytoplankton carbon and zooplankton biomass with different initial values of N and P (constant with depth). (a) N = 5 µg at/l. P = 100 mgC/m^3, (b) N = 3. P = 300. (c) N = 1, P = 500.

Figure 6. Simulation run for 1,500 days. First 300 days correspond to values in Figure 5(b).