International Council for the Exploration of the Sea

C.M.1974/L:15
Plankton Committee

PLANKTON PATCHINESS

by
John H. Steele
Marine Laboratory, Aberdeen, Scotland

The variability of an ecosystem in space and time is usually one of its most important features, influencing both practical problems of sampling and conceptual questions about its structure. Patchiness or spatial heterogeneity can occur on nearly every scale of measurement and must depend on the nature of the response of organisms to their aquatic environment.

Plankton are by definition supposed to be at the mercy of the horizontal movements of the sea. Zooplankton copepods can migrate vertically but any directed horizontal motion, except at very small scales, would appear to be impossible. The flagellates also can migrate vertically but many of the major groups, particularly the diatoms, can only sink or rise slowly by changes in buoyancy. Thus we can expect to find vertical stratification of plankton dependent on the behaviour of the organisms themselves, but horizontal variations should depend on physical factors and so might be expected to be similar in scales and patterns to parameters such as salinity or chemically important aspects like the essential nutrients.

In fact, both the microscopic plants and the small zooplankton seem to display much greater variability than the environment in which they live, although the evidence for this at a wide range of scales is still not as definite as one would wish.

Bainbridge (1957) described observations of physically distinguishable patches of phytoplankton either observed directly from ships or apparent in the counts of particular phytoplankton species along lines. These patches in the open sea have been reported at a wide range of scales from a few metres wide to areas with diameters of hundreds of kilometres. However, according to Bainbridge, there appear to be two main categories; strips a few metres wide but hundreds of metres in length; and much larger patches, roughly elliptical, with a mean diameter of, very approximately, 50 km.

Continuous measurements from a ship (Lorenzen, 1971) showed that in the sub-tropical Pacific there are large areas of open ocean with uniformly low chlorophyll values showing negligible variability. In these regions any chlorophyll changes which occurred were associated with horizontal temperature discontinuities. In nearshore waters off Peru where the chlorophyll levels were higher, these levels were also much more variable, Fig. 1. Oxygen and pH values in the water increase as a result of photosynthetic activity and so these measurements gave some indication of the "history" of the water. From these data, Lorenzen deduced that the ship's track had cut across two "parcels" of upwelled water in which phytoplankton blooms had occurred on a scale of, approximately, 20 km.

The main evidence of zooplankton patches is confined to the larger scales. Cushing (Cushing, 1955; Cushing and Tungate, 1963) has made detailed studies of phytoplankton and zooplankton patches in the North Sea. The areas surveyed were usually about 100-200 km squares containing 30-40 sampling positions. The main feature of the results, relevant here, is that normally the distributions of both phytoplankton and zooplankton species could be contoured, showing gradients (or "patches") of the same scale as the area sampled. Fig. 2 gives two examples from Cushing's work. From mid-March to early June 1954, Cushing and his colleagues followed a patch of *Calanus* which appeared to remain intact throughout this period. These very detailed studies give some idea of the time and space scales of patchiness that can occur with zooplankton.

Using a similar approach in the northern North Sea, I observed the simultaneous distributions of chlorophyll pigment in the upper layers and the zooplankton dry weight under a m^2. Fig. 3 shows the results from two surveys approximately two days apart. The distributions did not appear to be related to any physical factors such as salinity. Also it can be seen that the concentrations appear to be inversely related. A detailed analysis of these data (Steele, 1974a) suggests that this inverse relation between pairs of values for phytoplankton and zooplankton might be expected to be found during a sequence in *time*, as a zooplankton population grows and grazes down the phytoplankton. The problem raised by these data is that they occur as nearly simultaneous distributions in *space*. Further, the variation in zooplankton biomass within this small area is of the same order as that found in surveys with more widely spaced stations covering the whole of the northern North Sea.

It is apparent that many of the smaller and medium scale fluctuations in plankton abundance can be related to physical variations including Langmuir circulation but in areas where there are no obvious physical boundaries, patchiness is still observed. What will be the effect of lateral mixing in these less restricted conditions?

The simplest case is the growth of phytoplankton on its own. The original treatment of this problem (Kierstead and Slobodkin, 1953) dealt with red tides where this is a reasonable, or at the least, a possible assumption. Also, at the beginning of a spring outburst, when plant growth begins but herbivore grazing will be at a low level, this can be taken as a first approximation. Kierstead and Slobodkin considered the problem of a circular patch of diameter, l, with a growth rate, a. They showed that if l is small the patch will leak away due to the effects of mixing. However, if l is large enough then the growth within the patch will more than counteract the effects of dispersion, and the concentration of phytoplankton within the patch will increase. They calculated the critical diameter l_c above which this increase would occur as

$$l_c = 4.8 \sqrt{k/a} \qquad (1)$$

For any plant growth rate this defines a relation between l_c and the diffusion coefficient k. For two division rates of 1.0 and 0.1 per day (or doubling times of 1.0 and 10 days) these relations are shown in Fig. 4.

Using the solid line as an average for the observed relation between l and k, the minimum critical size of a patch would go from 2 km to 50 km as the division rate goes from a high to a low value. This is one general conclusion about patch size that can be taken from this relation. The other main conclusion, evident from Fig. 4, is that, although these lines represent the average conditions, there are likely to be large variations from the average. This is due to the small angle of the intersections of the dashed lines with the solid line and the relatively large scatter of the observations of diffusion coefficients.

These theoretical considerations appear to support the general observations described earlier, that plankton patches in the open sea occur at scales the order of 10 km-100 km but this theory considers only the growth of phytoplankton and not the interactions of plants and herbivores. It implies that patchiness will develop in the absence of zooplankton grazers. Theoretically, this can be explained from equation (1). In this a was the growth rate of phytoplankton and the critical diameter l_c increases as a decreases. If grazers are present, we can take a to represent the net growth expressed as the difference between actual production and loss due to grazing. Then in any circumstance where grazing is not negligible a will be smaller and so l_c larger than the value deduced from phytoplankton only. If, again theoretically, we think of summer conditions as approximating to a steady state, then on average $a = 0$ and no patchiness would be possible. Yet, as illustrated by the observations in the North Sea (Fig. 2 and 3), patches occur when large zooplankton populations are present. For these reasons, although simple combinations of diffusion rates and phytoplankton growth can illuminate some types of patchiness, they do not fully explain the more general features.

One question concerns this idea of a "steady state". Simple models of the interactions of phytoplankton and zooplankton (e.g. Steele, 1958) treat the latter as "biomass" with a growth rate, rather like the phytoplankton growth rate. Such "pictures of reality" produce those steady states after the spring outburst. Zooplankton, however, go through life cycles and may do so in cohorts. Thus *Calanus* has about three generations in the North Sea (Marshall and Orr, 1955) from spring to autumn. If this cohort structure is simulated in a model, then cycles of phytoplankton and zooplankton result, Fig. 5 (Steele, 1974a). When these cycles are compared with the observations in Fig. 2, they show the same type of variation (Steele, 1974a). The difficulty is that the theoretical cycles occur as changes with time while the observations are distributions in space at about the same time. Can such temporal fluctuations, which arise from zooplankton growth cycles, be the cause of variations in space?

Theoretically, the problem is that we are now dealing with changes in space and time of both phytoplankton (P) and zooplankton (Z). These changes are connected by grazing which depends on both P and Z, thus

$$\text{change in } P = \text{growth } (P) - \text{grazing } (P.Z) + \text{diffusion } (P)$$

$$\text{change in } Z = \text{grazing } (PZ) - \text{predation } (Z) + \text{diffusion } (Z)$$

These are similar to the Lotka-Volterra equations (Pielou, 1969) with diffusion added, although the grazing term may be more complicated than the simple Lotka-Volterra form.

The addition of terms multiplying P and Z not merely makes the equation more complicated than the simple form used for phytoplankton only, it alters the whole character of the solutions. For the simple form (Kierstead and Slobodkin, 1953) any perturbation at one time with a wavelength, l, would remain at that wavelength and decrease or increase in amplitude depending on whether $l < l_c$ or $l > l_c$. The so-called "non-linearity" of the equations for P and Z means that a perturbation at one wavelength can propagate changes at other wavelengths. In particular, perturbations at short wavelengths, less than l_c can alter the mean values of P and Z (Steele, 1974b). Thus, small-scale variations of P and Z which, considered separately, would be damped out by diffusion, in conjunction could lead to changes at larger scales beyond the critical value of l_c. There are, mathematically, certain conditions on these perturbations. It is necessary that they be correlated (Steele, 1974c) but this is a probable feature of such fluctuations, as shown by the model of cohort structure.

Population Stability

Questions about diffusion and patchiness are related to questions about the factors determining the stability of populations of phytoplankton and zooplankton. The term stability, as used here, means the ability of plankton populations to absorb fluctuations imposed by "external" factors. These could be either the physical environment or predators such as shoals of herring moving through an area. Nearly all theoretical studies of this problem consider the distributions or organisms to be uniform in space and deal with changes in time (May, 1973). For plankton this approach (Steele, 1974a) leads to the idea that the zooplankton must be prudent grazers and have low feeding rates when phytoplankton is below some threshold concentration. It would seem possible that the dispersing effects of diffusion might provide an alternative method of eliminating any perturbations.

Considering the simple relation between growth and diffusion, the critical wavelength l_c for patchiness would also be critical for stability since any perturbation on a smaller scale would be dispersed. On the other hand, perturbations on a larger scale could be unstable. Such large-scale perturbations can occur, typically, when the seasonal thermocline is formed in the spring over large areas of the North Sea or North Atlantic and the spring outburst of phytoplankton begins, followed by the growth of zooplankton.

If this remained as a smooth process with, at any one time, the same concentrations of P and Z everywhere, then the need for "clever" zooplankton would remain. If, at the other extreme, instability tended to appear as local perturbations then, using the simple concepts, diffusion would tend to smooth these out. Further, as the zooplankton populations developed, the net rate of increase of phytoplankton, taken as the balance of growth and grazing, would become much lower and the critical patch size much larger leading again to a relatively "smooth" world. If, however, larger-scale patchiness can be continually produced by smaller-scale interactions, then these perturbations at all wavelengths up to the average values (i.e. zero frequency) of P and Z would produce instabilities unless counteracted by some general behavioural adaptations such as threshold feeding levels. In other words, some of the conditions presumed by theories which ignore spatial heterogeneity would still be necessary in a patchy world.

Patchiness and Fish

Many pelagic fish species may migrate long distances to areas of generally high food concentration. Yet within these general areas variations in food concentration may be equally important. For adult fish, the patches may provide a source of food which can be consumed at a rate much greater than would be the case if only the average concentration were available. In turn, this predation may be another source of patchiness in the plankton and illustrates the simplifications of the previous discussion where plankton was considered as a relatively closed system.

For larval fish, patchiness may be even more important. Jones (1973) has shown that larval fish may require relatively high concentrations of the smaller stages of zooplankton if they are not to starve to death during their early stages. Also, they need these above-average concentrations for periods of one or two weeks. Such conditions would occur in large patches since the larger the patch the slower is exchange of water through its circumference.

On this basis, for fish or fish larvae, patchiness may not be merely a random variation in their environment, but an essential requirement for obtaining adequate concentrations of food. The variance of plankton distributions (i.e. the maximum possible food concentrations) may be more important than the average. If this is so, then a relatively constant variance is needed or, in other words, patchiness must be a regular and normal feature of planktonic environment. Further, any differences in variance that did occur from year to year at the time of larval development could be of greater significance to larval survival than differences in average zooplankton populations.

Summary

The evidence from observations of spatial heterogeneity is rather scant but suggests that, although variability occurs at all scales, there may be patches with, typically, dimensions of 10-100 km. Many of these features can be explained by a combination of accumulation due to phytoplankton growth and dispersion due to turbulent diffusion. However, combined phytoplankton and zooplankton patches are less easy to explain. It is possible that small-scale perturbations resulting from cohort structure or predation can generate large-scale patches, but these perturbing effects are balanced by functional responses of the zooplankton to changes in their food. This balance could lead to a relatively regular structure of patchiness which is utilised by higher trophic levels.

References

Bainbridge, R. 1957 The size, shape and density of marine phytoplankton concentrations. Biol. Rev. 32, 91-116.

Cushing, D. H. 1955 Production and a pelagic fishery. Fish. Invest., Lond., ser. 2, 18, No.7, 104 pp.

Cushing, D. H. and Tungate, D. S. 1963 Studies on a Calanus patch. I. The identification of a Calanus patch. J.mar.biol. Ass.U.K., 43, 327-337.

Jones, R. 1973 Density dependent regulation of the numbers of cod and haddock. Rapp. p.-v. Reun. Cons. perm. int. Explor. Mer, 164, 156-173.

Kierstead, H. and Slobodkin, L. B. 1953 The size of water masses containing plankton blooms. J. mar. Res., 12, 141-147.

Lorenzen, C. J. 1971 Continuity in the distribution of surface chlorophyll. J. Cons. int. Explor. Mer, 34, 18-23.

Marshall, S. M. and Orr, A. P. 1955 The biology of a marine copepod. Oliver and Boyd, Edinburgh, 195 pp.

May, R. M. 1973 Stability and Complexity in Model Ecosystems. Princeton Univ. Press. 235 pp.

Pielou, E. C. 1969 An introduction to mathematical ecology. Wiley-Interscience, London, 286 pp.

Steele, J. H. 1958 Plant production in the northern North Sea. Mar. Res. No. 7, 36 pp.

Steele, J. H. 1974a The structure of marine ecosystems. Harvard Univ. Press, Cambridge, Mass. 128 pp.

Steele, J. H. 1974b Spatial heterogeneity and population stability. Nature, 248, 83.

Steele, J. H. 1974c The stability of plankton ecosystems. (eds.) Usher, M. B. and Williamson, M. H. In Ecological Stability. Chapman and Hall, London, 179-194.

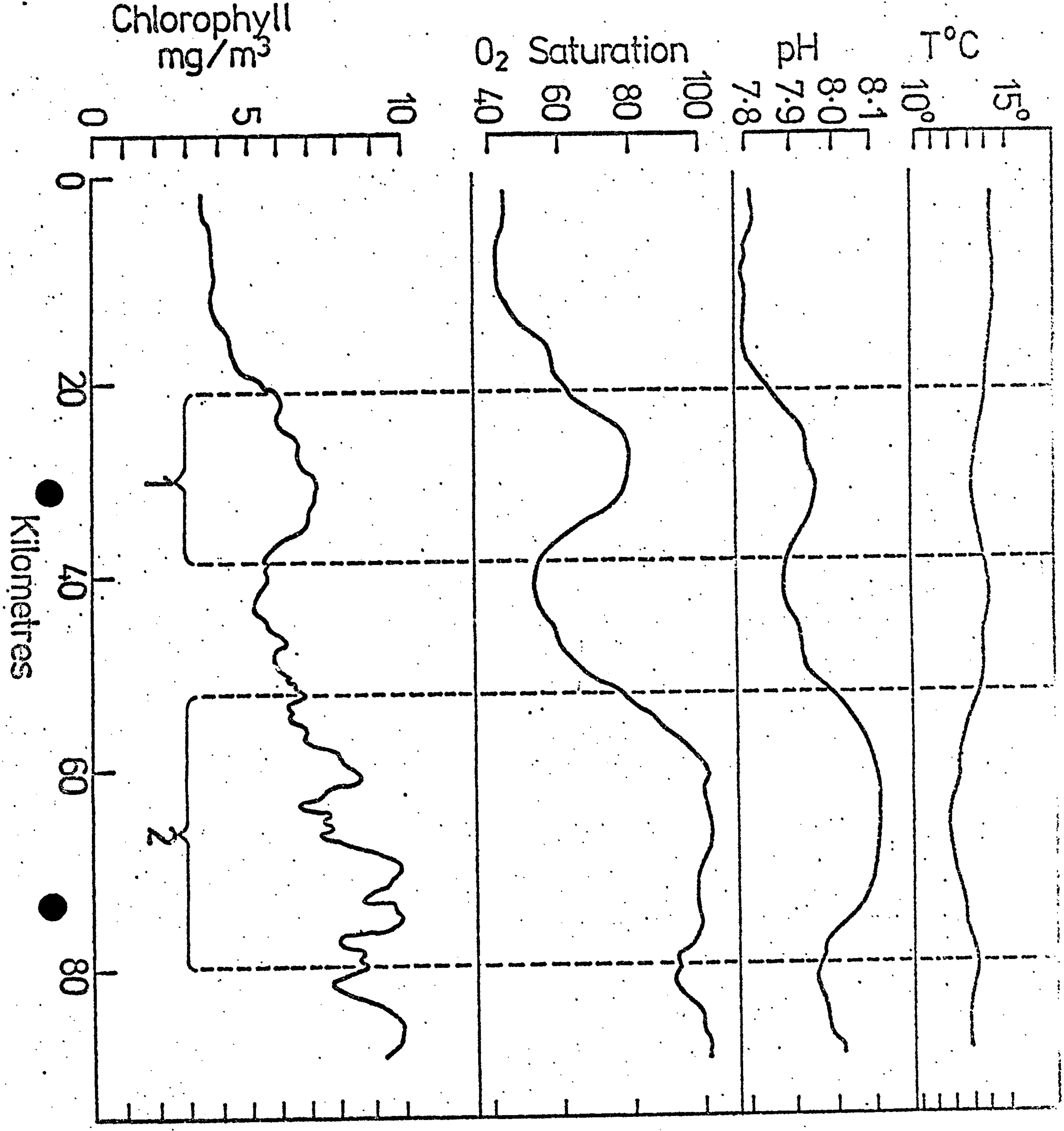

Fig. 1 Variations in properties encountered nearshore in the Peruvian upwelling area (Lorenzen, 1971)

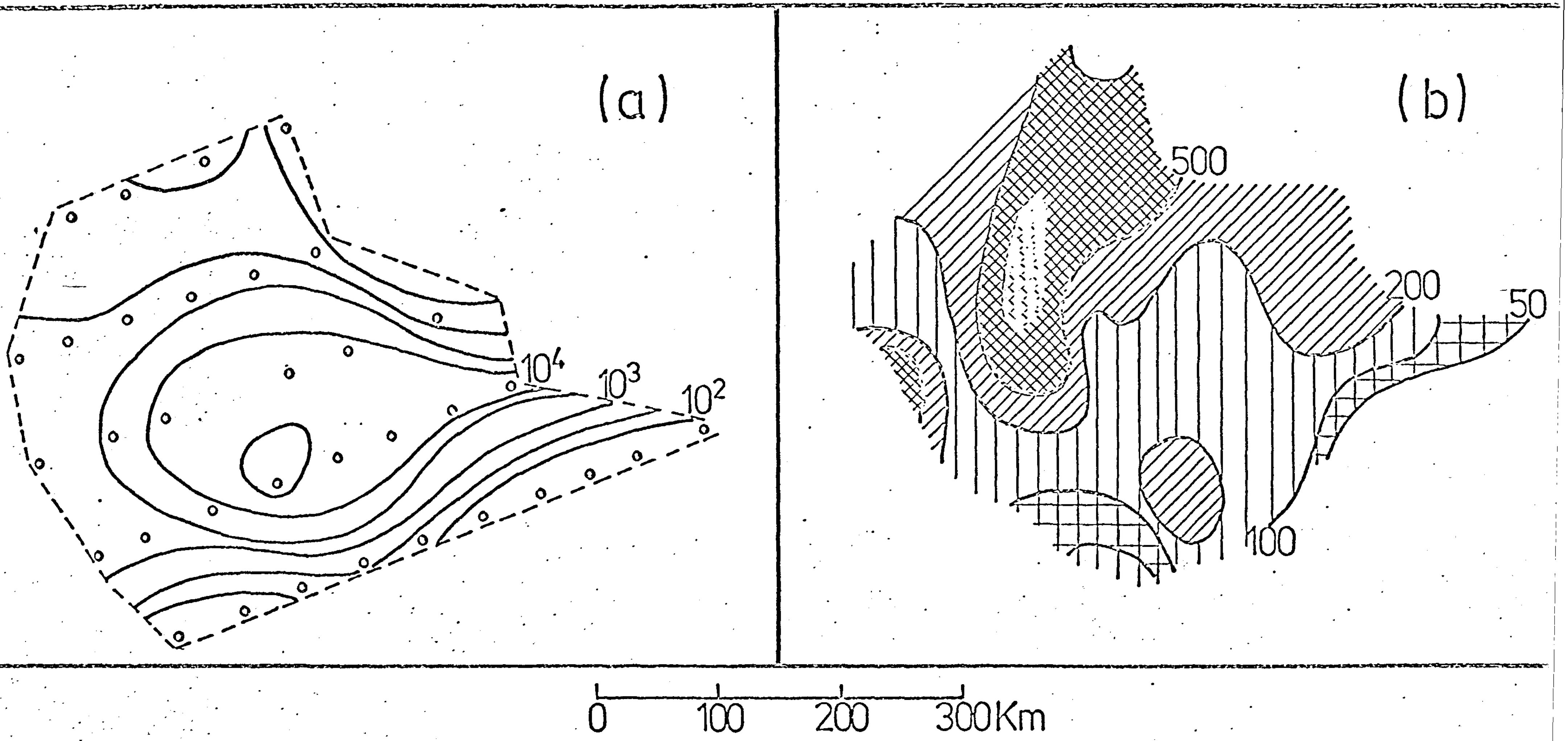

Fig. 2 Distribution of (a) a diatom Thalassiosira gravida and (b) a copepod Calanus Stage V in the southern North Sea (Cushing 1955), numbers of organisms per m^2.

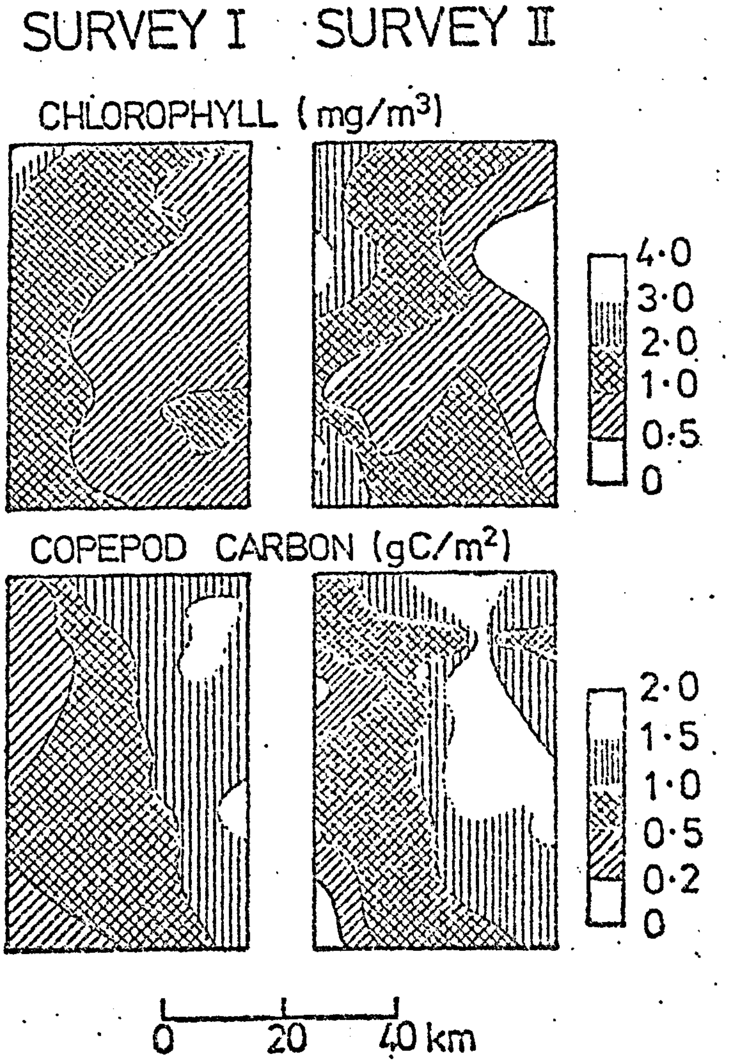

Fig. 3 Distribution of chlorophyll a and copepod carbon on two surveys in the northern North Sea, two days apart (Steele, 1974a).

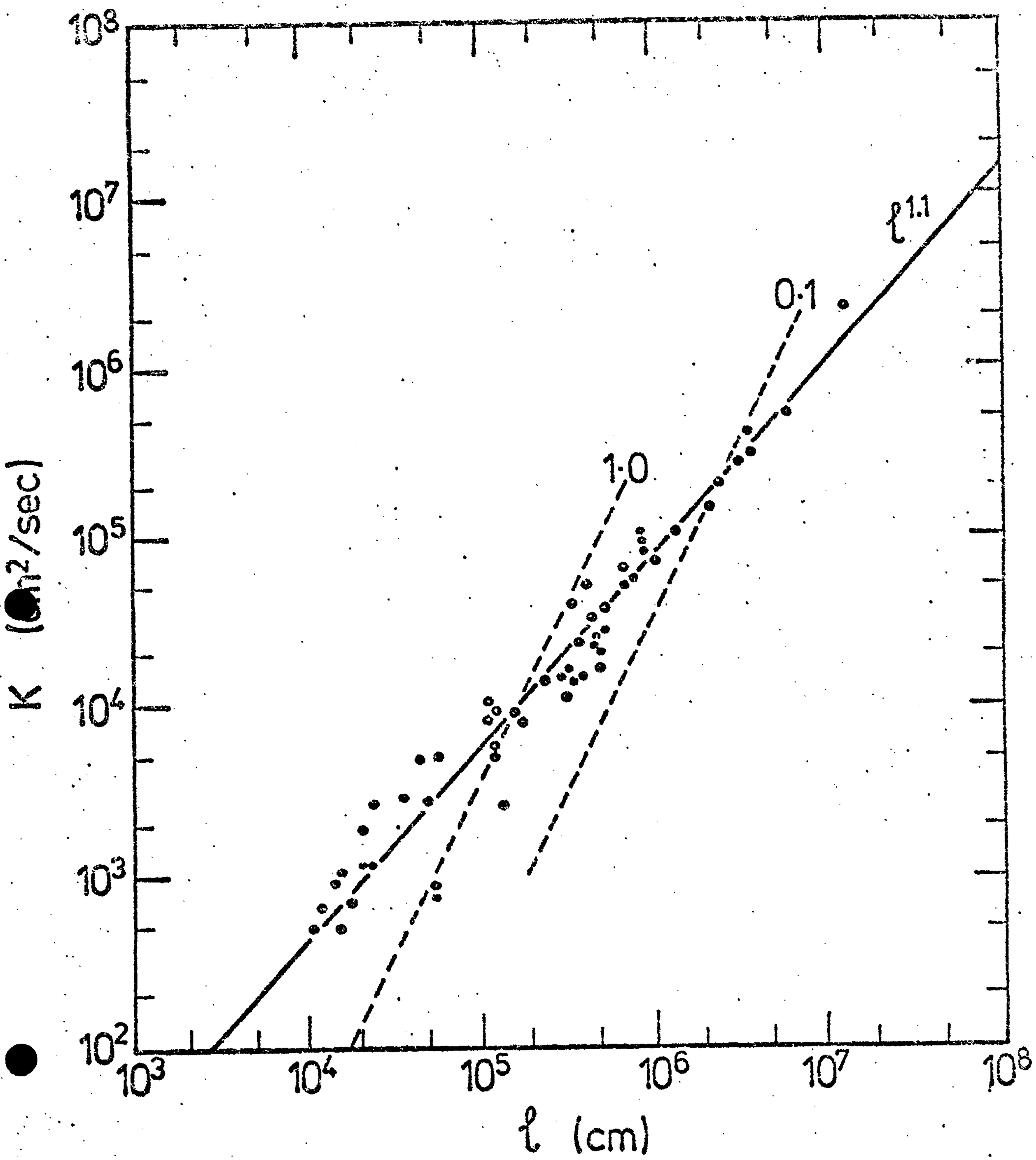

Fig. 4 Observations of diffusion coefficient k in relation to scale l (Okubo, 1972). The dashed lines indicate the relation of critical length, l_c to k for two division rates.

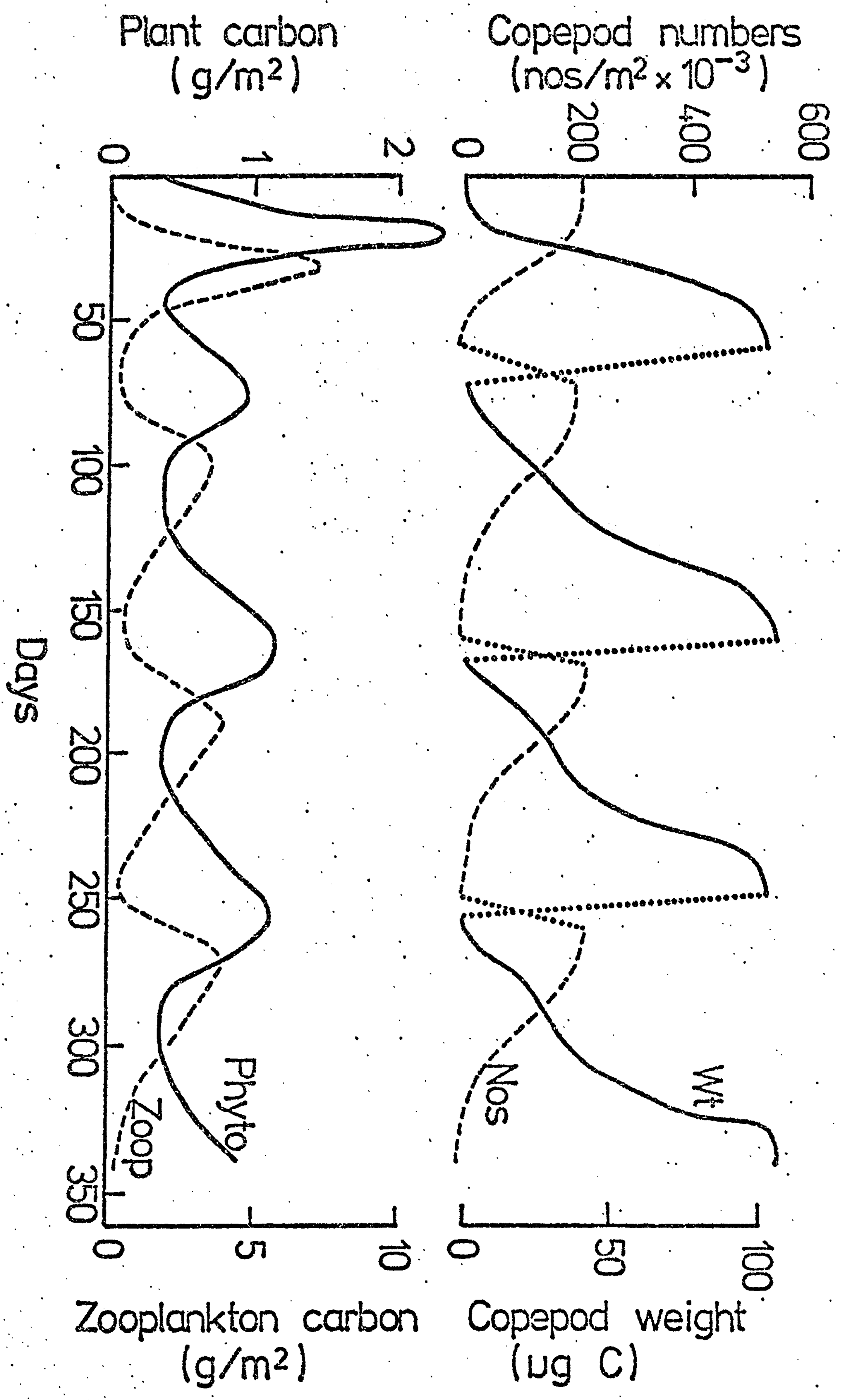

Fig. 5 The results of a simulation model showing the limit cycle produced by a zooplankton population consisting of a simple cohort (Steele, 1974a).