THE PARADOX OF THE PLANKTON*

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The problem that I wish to discuss in the present contribution is raised by the very paradoxical situation of the plankton, particularly the phytoplankton, of relatively large bodies of water.

We know from laboratory experiments conducted by many workers over a long period of time (summary in Provasoli and Pintner, 1960) that most members of the phytoplankton are phototrophs, able to reproduce and build up populations in inorganic media containing a source of CO_2, inorganic nitrogen, sulphur, and phosphorus compounds and a considerable number of other elements (Na, K, Mg, Ca, Si, Fe, Mn, B, Cl, Cu, Zn, Mo, Co and V) most of which are required in small concentrations and not all of which are known to be required by all groups. In addition, a number of species are known which require one or more vitamins, namely thiamin, the cobalamines (B_{12} or related compounds), or biotin.

The problem that is presented by the phytoplankton is essentially how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials. The problem is particularly acute because there is adequate evidence from enrichment experiments that natural waters, at least in the summer, present an environment of striking nutrient deficiency, so that competition is likely to be extremely severe.

According to the principle of *competitive exclusion* (Hardin, 1960) known by many names and developed over a long period of time by many investigators (see Rand, 1952; Udvardy, 1959; and Hardin, 1960, for historic reviews), we should expect that one species alone would outcompete all the others so that in a final equilibrium situation the assemblage would reduce to a population of a single species.

The principle of competitive exclusion has recently been under attack from a number of quarters. Since the principle can be deduced mathematically from a relatively simple series of postulates, which with the ordinary postulates of mathematics can be regarded as forming an axiom system, it follows that if the objections to the principle in any cases are valid, some or all the biological axioms introduced are in these cases incorrect. Most objections to the principle appear to imply the belief that equilibrium under a given set of environmental conditions is never in practice obtained. Since the deduction of the principle implies an equilibrium system, if such sys-

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tems are rarely if ever approached, the principle though analytically true, is at first sight of little empirical interest.

The mathematical procedure for demonstrating the truth of the principle involves, in the elementary theory, abstraction from time. It does, however, provide in any given case a series of possible integral paths that the populations can follow, one relative to the other, and also paths that they cannot follow under a defined set of conditions. If the conditions change the integral paths change. Mere failure to obtain equilibrium owing to external variation in the environment does not mean that the kinds of competition described mathematically in the theory of competitive exclusion are not occuring continuously in nature.

Twenty years ago in a Naturalists' Symposium, I put (Hutchinson, 1941) forward the idea that the diversity of the phytoplankton was explicable primarily by a permanent failure to achieve equilibrium as the relevant external factors changed. I later pointed out that equilibrium would never be expected in nature whenever organisms had reproductive rates of such a kind that under constant conditions virtually complete competitive replacement of one species by another occurred in a time (t_c), of the same order, as the time (t_e) taken for a significant seasonal change in the environment. Note that in any theory involving continuity, the changes are asymptotic to complete replacement. Thus ideally we may have three classes of cases:

1. $t_c \ll t_e$, competitive exclusion at equilibrium complete before the environment changes significantly.
2. $t_c \simeq t_e$, no equilibrium achieved.
3. $t_c \gg t_e$, competitive exclusion occurring in a changing environment to the full range of which individual competitors would have to be adapted to live alone.

The first case applies to laboratory animals in controlled conditions, and conceivably to fast breeding bacteria under fairly constant conditions in nature. The second case applies to most organisms with a generation time approximately measured in days or weeks, and so may be expected to occur in the plankton and in the case of populations of multivoltine insects. The third case applies to animals with a life span of several years, such as birds and mammals.

Very slow and very fast breeders thus are likely to compete under conditions in which an approach to equilibrium is possible; organisms of intermediate rates of reproduction may not do so. This point of view was made clear in an earlier paper (Hutchinson, 1953), but the distribution of that paper was somewhat limited and it seems desirable to emphasize the matter again briefly.

It is probably no accident that the great proponents of the type of theory involved in competitive exclusion have been laboratory workers on the one hand (for example, Gause, 1934, 1935; Crombie, 1947; and by implication Nicholson, 1933, 1957) and vertebrate field zoologists (for example, Grinnell, 1904; Lack, 1954) on the other. The major critics of this type of ap-

proach, notably Andrewartha and Birch (1954), have largely worked with in-
sects in the field, often under conditions considerably disturbed by human
activity.

<div align="center">DISTRIBUTION OF SPECIES AND INDIVIDUALS</div>

MacArthur (1957, 1960) has shown that by making certain reasonable as-
sumptions as to the nature of niche diversification in homogeneously diver-
sified[1] biotopes of large extent, the distribution of species at equilibrium
follows a law such that the rth rarest species in a population of S_s species
and N_s individuals may be expected to be

$$\frac{N_s}{S_s} \sum_{i=1}^{r} \frac{1}{S_s - i + 1} \ .$$

This distribution, which is conveniently designated as type I, holds remark-
ably well for birds in homogeneously diverse biotopes (MacArthur, 1957,
1960), for molluscs of the genus Conus (Kohn, 1959, 1960) and for at least
one mammal population (J. Armstrong, personal communication). It does not
hold for bird faunas in heterogeneously diverse biotopes, nor for diatoms
settling on slides (Patrick in MacArthur, 1960) nor for the arthropods of soil
(Hairston, 1959). Using Foged's (1954) data for the occurrence of plank-
tonic diatoms in Braendegård Sø on the Danish island of Funen, it is also
apparent (figure 1) that the type I distribution does not hold for such assem-
blages of diatom populations under quite natural conditions either.

MacArthur (1957, 1960) has deduced two other types of distribution (type
II and type III) corresponding to different kinds of biological hypotheses.
These distributions, unlike type I, do not imply competitive exclusion. So far
in nature only type I distributions and a kind of empirical distribution which
I shall designate type IV are known. The type IV distribution given by dia-
toms on slides, in the plankton and in the littoral of Braendegård Sø, as well
as by soil arthropods, differs from the type I in having its commonest species
commoner and all other species rarer. It could be explained as due to het-
erogeneous diversity, for if the biotope consisted of patches in each one of
which the ratio of species to individuals differed, then the sum of the as-
semblages gives such a curve. This is essentially the same as Hairston's
(1959) idea of a more structured community in the case of soil arthropods
than in that of birds. It could probably arise if the environment changed in
favoring temporarily a particular species at the expense of other species be-
fore equilibrium is achieved. This is, in fact, a sort of temporal analogue to

[1]A biotope is said to be *homogeneously diverse* relative to a group of organisms
if the elements of the environmental mosaic relevant to the organism are small com-
pared to the mean range of the organisms. A *heterogeneously diverse biotope* is
divided into elements at least some of which are large compared to the ranges of
the organisms. An area of woodland is homogeneously diverse relative to most
birds, a large tract of stands of woodland in open country is heterogeneously di-
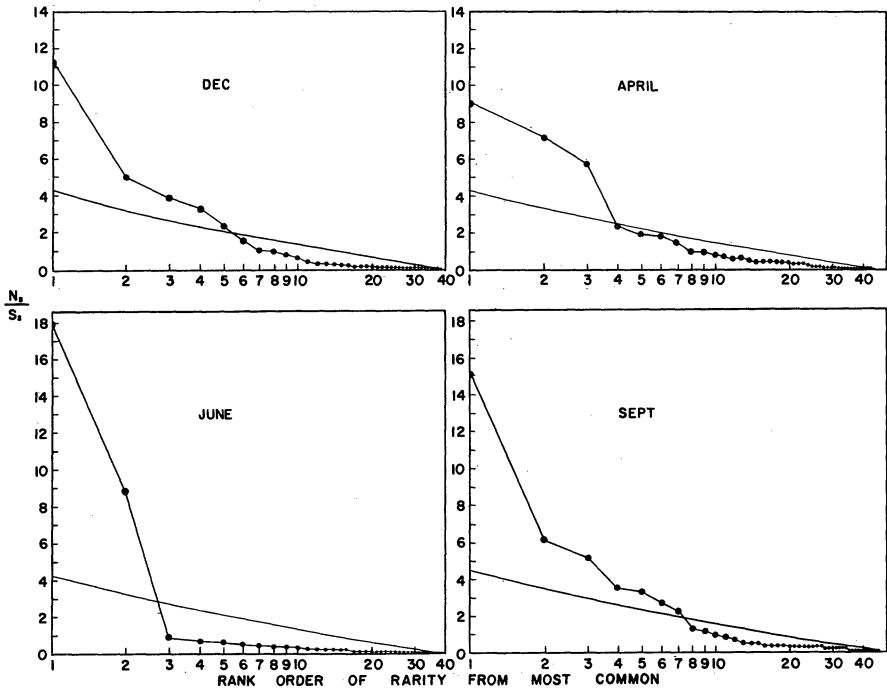verse (Hutchinson, 1957, 1959).

FIGURE 1. Abundance of individual species plotted against rank order for the planktonic diatoms of Braendegård Sø, for the four seasons, from Foged's data, showing type IV distributions. The unmarked line gives the type I distribution for a like number of species and individuals. The unit of population for each species is the ratio of total number of individuals (N_S) to total number of species (S_S).

heterogeneous diversity. Existence of the type IV distribution does not necessarily imply non-equilibrium, but if we assume niches are separated out of the niche-hyperspace with any boundary as probable as any other, we may conclude that either non-equilibrium in time or unexpected diversity in space are likely to underlie this type of distribution.

APPLICATION TO THE PLANKTON

Before proceeding to inquire how far plankton associations are either never in equilibrium in time or approach heterogeneous diversity in space in a rather subtle way, it is desirable to inquire how far ordinary homogeneous niche diversification may be involved. The presence of a light gradient in all epigean waters by day does imply a certain diversification, but in the epilimnia of lakes the chances of any organism remaining permanently in a particular narrow range of intensities is small in turbulent water. By day the stability of the epilimnion may well never be zero, but since what has to be explained is the presence of many species of competitors in a small volume of water, the role of small vertical variations is probably insignificant. A few organisms may be favored by peculiar chemical conditions at the surface film, but again this hardly seems an adequate ex-

planation. The Langmuir spirals in the wind drift might also separate motile from non-motile forms or organisms of different densities to some extent but again the effect is likely to be small and transitory. It is hard to believe that in turbulent open water many physical opportunities for niche diversification exist.

SYMBIOSIS AND COMMENSALISM

The mathematical theory of competition permits the treatment of commensal and symbiotic relations by a simple change in sign of one or both of the competition functions. It can be shown (Gause and Witt, 1935) that under some conditions commensal or symbiotic species can occupy the same niche. There is a little evidence that occasionally water in which one alga has been growing may be stimulatory to another species (Lefèvre, Jacob and Nisbet, 1952; see also Hartman, 1960) though it is far more likely to be inhibitory. Since some phytoplankters require vitamins and others do not, a more generally efficient species, requiring vitamins produced in excess by an otherwise less efficient species not requiring such compounds, can produce a mixed equilibrium population. It is reasonably certain that this type of situation occurs in the phytoplankton. It is interesting to note that many vitamin-requiring algae are small and that the groups characteristically needing them (Euglenophyta, Crytophyceae, Chrysophyceae, and Dinophyceae) tend to be motile. The motility would give such organisms an advantage in meeting rare nutrient molecules, inorganic or organic. This type of advantage can be obtained by non-motile forms only by sinking in a turbulent medium (Munk and Riley, 1952) which is much more dangerous than even random swimming.

ROLE OF PREDATION

It can be shown theoretically, as Dr. MacArthur and I have developed in conversation, that if one of two competing species is limited by a predator, while the other is either not so limited or is fed on by a different predator, co-existence of the two prey species may in some cases be possible. This should permit some diversification of both prey and predator in a homogeneous habit.

RESULTS OF NON-EQUILIBRIUM CONDITIONS

The possibility of synergistic phenomena on the one hand and of specific predation on the other would probably permit the development of a somewhat diversified equilibrium plankton even in an environment that was essentially boundaryless and isotropic. It may, however, be doubted that such phenomena would ever permit assemblages of the order of magnitude of tens of species to co-occur. At least in homogeneous water in the open ocean there would seem to be no other alternative to a non-equilibrium, or as MacArthur (1960) would term it, an opportunistic community.

The great difficulty inherent in the opportunistic hypothesis is that since, if many species are present in a really variable environment which is con-

trolling their competition, chance extinction is likely to be an important aspect of the process.[2] That this is not an important aspect of the problem, at least in some cases, is shown by the continual presence of certain dominant species of planktonic diatoms as microfossils in sediments laid down under fairly uniform conditions over periods of centuries or millenia. This is, for instance, clear from Patrick's (1943) study of the diatoms of Linsley Pond, in which locality *Stephanodiscus astrea*, *Melosira ambigua* and certain species of Cyclotella must have co-occurred commonly for long periods of time. It is always possible to suppose that the persistent species were continually reintroduced from outside whenever they became extinct locally, but this does not seem a reasonable explanation of the observed regularity.

IS THE PHYTOPLANKTON A VALID CONCEPT?

In view of the paradoxical nature of the phytoplankton, perhaps it is justifiable to inquire to what extent the concept itself has validity. In the ocean it is reasonably certain that the community is a self-perpetuating one, but in lakes it has long been regarded as largely an evolutionary derivative of the littoral benthos (for example, Wesenberg-Lund, 1908, pp. 323–325) and in recent years much evidence has accumulated to suggest that the derivation in some cases is not an evolutionary process in the ordinary sense of the word, but a process occurring annually, some individuals of a benthic flora moving at times into plankton. The remarkable work of Lund (1954, 1955) on Melosira indicates that the planktonic species of this genus become benthic, though probably in a non-reproductive condition, when turbulence is inadequate to keep them afloat. Brook (1959) believes that some of the supposed planktonic varieties of littoral-benthic desmids are non-genetic modifications exhibited by populations annually derived from the littoral. If most of the phytoplankton consisted of species with well-defined, if somewhat restricted, benthic littoral niches, from which at times large cultures in the open water were developed but perhaps left no descendants, much of our paradox would disappear. In the sea we should still apparently have to rely on synergism, predation and opportunism or failure to achieve equilibrium, but in fresh waters we might get still more diversity from transitory invasions of species which in the benthos probably occupy a heterogeneously diverse biotope like the soil fauna studied by Hairston (1959).

[2]The chance of extinction is always finite even in the absence of competition, but for the kind of population under consideration the arguments adduced, for instance, by Cole (1960) appear to the writer to be unrealistic. In a lake of area 1 km^2 or 10^6 m^2, in a layer of water only one meter deep, any organism present at a concentration of one individual per litre, which would be almost undetectibly rare to the planktologist using ordinary methods, would have a population N_0 of 10^9 individuals. If the individuals divided and the two fission products had equal chances of death or reproduction, so that in the expected case the population remained stable, the probability of random extinction (Skellam, 1955) is given by $p_e = [t/(1 + t)]^{N_0}$ where t is measured in generations. For large values of N_0 and t we may approximate by $t = -N_0/\ln p_e$. In the lake in question p_e would reach a value of 0.01 in 2.2×10^8 generations which for most phytoplankters would be a period of over a million years. Less than half a dozen lakes are as old as this, and all these are vastly larger than the hypothetical lake of area 1 km^2.

The available data appear to indicate that in a given lake district there is no correlation between the area of a lake and the number of species comprising its phytoplankton. This is apparent from Järnefelt's (1956) monumental study of the lakes of Finland, and also from Ruttner's (1952) fifteen Indonesian lakes. In the latter case, the correlation coefficient of the logarithm of the numbers of phytoplankton species on the logarithm of the area (the appropriate quantities to use in such a case), is −0.019, obviously not significantly different from zero.

It is obvious that something is happening in such cases that is quite different from the phenomena of species distribution of terrestrial animals on small islands, so illuminatingly discussed by Dr. E. O. Wilson in another contribution to this symposium. At first sight the apparent independence indicated in the limnological data also may appear not to be in accord with the position taken in the present contribution. If, however, we may suppose that the influence of the littoral on the species composition decreases as the area of the lake increases, while the diversity of the littoral flora that might appear in the plankton increases as the length of the littoral, and so its chances of diversification, increases, then we might expect much less effect of area than would initially appear reasonable. The lack of an observed relationship is, therefore, not at all inconsistent with the point of view here developed.

CONCLUSION

Apart from providing a few thoughts on what is to me a fascinating, if somewhat specialized subject, my main purpose has been to show how a certain theory, namely, that of competitive exclusion, can be used to examine a situation where its main conclusions seem to be empirically false. Just because the theory is analytically true and in a certain sense tautological, we can trust it in the work of trying to find out what has happened to cause its empirical falsification. It is, of course, possible that some people with greater insight might have seen further into the problem of the plankton without the theory that I have with it, but for the moment I am content that its use has demonstrated possible ways of looking at the problem and, I hope, of presenting that problem to you.

LITERATURE CITED

Andrewartha, H. G., and L. C. Birch, 1954, The distribution and abundance of animals. XV. 782 pp. Univ. of Chicago Press, Chicago, Ill.

Brook, A. H., 1959, The status of desmids in the plankton and the determination of phytoplankton quotients. J. Ecol. 47: 429–445.

Cole, L. C., 1960, Competitive exclusion. Science 132: 348.

Crombie, A. C., 1947, Interspecific competition. J. Animal Ecol. 16: 44–73.

Feller, W., 1939, Die Grundlagen der Volterraschen Theorie des Kampfes von Dasein in Wahrscheirlichkeitstheoretischer Behandlung. Acta Biotheoret. 5: 11–40.

Foged, N., 1954, On the diatom flora of some Funen Lakes. Folia Limnol. Scand. 5: 1–75.

Gause, G. F., 1934, The struggle for existence. IX. 163 pp. Williams and Wilkins, Baltimore, Md.

1935, Vérifications expérimentales de la théorie mathematique de la lutte pour la vie. Actual. scient. indust. 277: 1–62.

Gause, G. F., and A. A. Witt, 1935, Behavior of mixed populations and the problem of natural selections. Amer. Nat. 69: 596–609.

Grinnell, J., 1904, The origin and distribution of the chestnut-backed Chickadee. Auk 21: 364–382.

Hairston, N. G., 1959, Species abundance and community organization. Ecology 40: 404–416.

Hardin, G., 1960, The competitive exclusion principle. Science 131: 1292–1298.

Hartman, R. T., 1960, Algae and metabolites of natural waters. *In* The Pymatuning symposia in ecology: the ecology of algae. Pymatuning Laboratory of Field Biology, Univ. Pittsburgh Special Publ. No. 2: 38–55.

Hutchinson, G. E., 1941, Ecological aspects of succession in natural populations. Amer. Nat. 75: 406–418.

1953, The concept of pattern in ecology. Proc. Acad. Nat. Sci. Phila. 105: 1–12.

1957, Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22: 415–427.

1959, Il concetto moderno di nicchia ecologica. Mem. Ist. Ital. Idrobiol. 11: 9–22.

Järnefelt, H., 1956, Zur Limnologie einiger Gewässer Finnlands. XVI. Mit besonderer Berücksichtigung des Planktons. Ann. Zool. Soc. "Vancimo" 17(1): 1–201.

Kohn, A. J., 1959, The ecology of *Conus* in Hawaii. Ecol. Monogr. 29: 47–90.

1960, Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. Ann. Mag. Nat. Hist. 13(2): 309–320.

Lack, D., 1954, The natural regulation of animal numbers. VIII. 343 pp. Clarendon Press, Oxford, England.

Lefèvre, M., H. Jakob and M. Nisbet, 1952, Auto- et heteroantagonisme chez les algues d'eau dounce. Ann. Stat. Centr. Hydrobiol. Appl. 4: 5–197.

Lund, J. W. G., 1954, The seasonal cycle of the plankton diatom, *Melosira italica* (Ehr.) Kütz. subsp. *subarctica* O. Müll. J. Ecol. 42: 151–179.

1955, Further observations on the seasonal cycle of *Melosira italica* (Ehr.) Kütz. subsp. *subarctica* O. Müll. J. Ecol. 43: 90–102.

MacArthur, R. H., 1957, On the relative abundance of bird species. Proc. Natl. Acad. Sci. 45: 293–295.

1960, On the relative abundance of species. Amer. Nat. 94: 25–36.

Munk, W. H., and G. A. Riley, 1952, Absorption of nutrients by aquatic plants. J. Mar. Research 11: 215–240.

Nicholson, A. J., 1933, The balance of animal populations. J. Animal Ecol. 2(suppl.): 132–178.

1957, The self-adjustment of populations to change. Cold Spring Harbor Symp. Quant. Biol. 22: 153–173.

Patrick, R., 1943, The diatoms of Linsley Pond, Connecticut. Proc. Acad. Nat. Sci. Phila. 95: 53–110.

Provasoli, L., and I. J. Pintner, 1960, Artificial media for fresh-water algae: problems and suggestions. *In* The Pymatuning symposia in ecology: the ecology of algae. Pymatuning Laboratory of Field Biology, Univ. Pittsburgh Special Publ. No. 2: 84–96.

Rand, A. L., 1952, Secondary sexual characters and ecological competition. Fieldiana Zool. 34: 65–70.

Ruttner, F., 1952, Plankton studien der Deutschen Limnologischen Sunda-Expedition. Arch. Hydrobiol. Suppl. 21: 1–274.

Skellam, J. G., 1955, The mathematical approach to population dynamics. *In* The numbers of man and animals, ed. by J. G. Cragg and N. W. Pirie. Pp. 31–46. Oliver and Boyd (for the Institute of Biology), Edinburgh, Scotland.

Udvardy, M. F. D., 1959, Notes on the ecological concepts of habitat, biotope and niche. Ecology 40: 725–728.

Wesenberg-Lund, C., 1908, Plankton investigations of the Danish lakes. General part: the Baltic freshwater plankton, its origin and variation. 389 pp. Gyldendalske Boghandel, Copenhagen, Denmark.