Ecology and experimental biology

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KURZFASSUNG: **Ökologie und experimentelle Biologie.** Der Begriff „Ökologie" wird erörtert und die praktischen sowie theoretischen Schwierigkeiten aufgezeigt, welche einer präzisen Definition im Wege stehen. Ökologie wird als ein Forschungsgebiet aufgefaßt, das sich mit dem Studium von Systemen beschäftigt, welche aus Komponenten oder Variablen bestehen, von denen jede wieder eine Anzahl von Vektoren enthält und Vergleiche mit abiotischen Systemen anstellt. Die Bedeutung des Wortes „experimentell" wird erörtert und dessen Beziehung zu einer Serie von Transformationen an einem biologischen System diskutiert. Eingehende Überlegungen werden dem auf Grund der gegebenen Definitionen eingeschränkten Begriffsinhalt „experimentelle Ökologie" und den praktischen Problemen gewidmet, welche dieses Forschungsgebiet uns aufgibt. Die Konotation des Terminus „experimentelle Biologie" wird behandelt und die Beziehung zwischen experimenteller Biologie und experimenteller Ökologie im Hinblick auf Pflanzen- und Tiersysteme diskutiert. Die Zukunft der Ökologie – experimentell und nichtexperimentell – bedarf besonderer Aufmerksamkeit. Das ständige Anwachsen der pro Zeiteinheit produzierten neuen Informationen macht eine stärkere Integration erforderlich; Vorschläge, wie dies erreicht werden könnte, werden vorgelegt, und zwar unter besonderer Berücksichtigung meeresbiologischer Aspekte.

PREFACE

Es ist für mich eine sehr große Ehre, der erste Redner auf diesem ersten wahrhaft europäischen Symposion über Meeresbiologie zu sein. Mit dem heutigen Tag wird, so hoffe ich aufrichtig, die Reihe der deutschen Symposien durch eine neue Reihe europäischer Symposien auf diesem Gebiet abgelöst oder doch ergänzt. Dazu muß ich meinem Freund, Herrn Dr. KINNE, und seinen Kollegen herzlich gratulieren.

Wir alle wissen, daß die Naturwissenschaften keine Grenzen kennen, doch gibt es leider noch immer Grenzen, die es zu überwinden gilt. Die Bemühungen unserer deutschen Kollegen, solche „menschlichen" Grenzen zu beseitigen, sind sehr lobenswert. Nur auf diesem Weg können Fortschritte erzielt werden.

Ich habe seinerzeit verschiedenen deutschen Symposien beigewohnt. In allen Fällen handelte es sich um sehr interessante und anregende Treffen, – nun, und das trifft ja nicht immer für alle Symposien zu. Ich hoffe, daß die neue Reihe von Symposien, die heute ihren Anfang nimmt, diese Tradition fortsetzen wird.

Jetzt wird es klar, daß Deutsch zu sprechen für mich sehr schwierig ist – bei mir ist es besonders so morgens um halb neun! Auch Sie dürften dabei Schwierigkeiten haben; dasselbe gilt für den Übersetzungsdienst. Ich möchte daher um Ihr Verständnis bitten, wenn mein Symposionsbeitrag in Englisch abgefaßt ist.

INTRODUCTION

I have been asked by Professor KINNE to introduce this, the first section of the proceedings, by a general discussion of experimental ecology – with particular reference, of course, to its impact on, and relevance to, marine biology. For much of our time most of us are quite rightly immersed in the day to day details of some specific problem and even when we do think about the basis and meaning of our subject, rarely are our ideas explicitly formulated. Nevertheless, repressing our usual impatience with semantics, we should pause from time to time lest we fall prey to a rather superficial and naive realism and come to believe that, since words can only be defined in words, the philosopher – foredoomed to failure by argument in a vicious circle – is wasting his time fussing about definitions.

Yet it is true that many wise, experienced and distinguished biologists have set out their views on ecology and, as may readily be seen by reading the excellent historical introduction given by ALLEE and his co-workers in their text-book of Animal Ecology (ALLEE et al. 1949), it is not easy to say anything really startling or new; indeed, almost all that I have to say will be replete with plagiarisms, sometimes patently obvious, sometimes more or less disguised – but always less often acknowledged than not. I shall illustrate some of the problems by reference to particular investigations but such references will be by no means exhaustive and must of necessity reflect my own interests and reading. Probably the best that I can do is to try to take a brief look at the meaning and state of the subject and, shifting the emphasis from time to time, to consider how it might develop, and be developed, in relation to marine science. Perhaps such will form a not entirely irrelevant introduction to the more specialized and more immediately pertinent papers subsequently to be presented.

ECOLOGY: A RESTRICTED DEFINITION

There will be some difficulty in defining ecology in a manner which is agreeable to you all and perhaps even more in reaching an acceptable definition of "experimental". Ecology will be taken to mean the study of organisms in relation to the totality of their environment, abiotic and biotic. Since it will be assumed that there is organism-organism and organism-environment interaction one must, by this definition, study assemblages of organisms, that is, systems. For the moments the term community will be avoided – whether one adopts the completely individualistic concept of the community first stressed by workers such as GLEASON (1926) and BODENHEIMER (1938), or the organismic view of CLEMENTS (1916)[1]. Whatever views are held regarding such terms as association, consociation, biocoenosis and the like, few would argue against the existence of naturally occurring and recognizable biotic groupings or against the

[1] The individualistic view has recently found considerable favour amongst some plant ecologists (CURTIS & MCINTOSH 1951, CURTIS 1959) but more recently still, others such as WATT (1964) and POORE (1964) take an intermediate view – believing that opportunity determines the components and competition gives dynamic balance which leads to structure and pattern.

possibility of studying them irrespective of schemes of classification. Even if the components are fortuitously brought together, ecosystems are organisations, bound together by a system of communication and with a dynamics in which processes of feedback play an important part. Any system can be considered to be made up of a number of components, or variables, each of which, in theory, can at any moment be given some specific value. Furthermore, a component may be a compound entity with a number of properties to each of which appropriate numerical values may be assigned – for example, with a non-motile organism, position and size; in this case the component is made up of a number of vectors (in the cybernetic sense).

Success in elucidating the behaviour of a system depends very much on choosing the appropriate vectors with which to define it. We may note that many of the terms used, particularly by botanists, in attempting to assess the status of groupings – such as abundance, dominance and frequency as defined by BRAUN-BLANQUET, or the life forms of RAUNKIAER – are no more than selected vectors which are used in an attempt to define important variables. Variables which are not usually included in the system may be termed parameters; for example, light, temperature, salinity, pressure, and tidal variations are normally treated as parameters since they are considered to act on the system from "outside" it. (Botanists when confining their attention to plants often regard animals as a parameter, the biotic factor, acting on the plant components.) Since abiotic and biotic interaction has been assumed and, over a restricted space, the recognizability of systems with a certain constancy of components accepted, one is clearly directing attention to synecological and biocoenological features of the systems. One may note that there are no difficulties in this definition with regard to the concept of autecology (which, although MACFADYEN 1957, appears to give a rather more restricted meaning to the word, will be taken to include the autecology of populations) for in an autecological study one is merely concentrating attention on what happens to a single selected organism (or population of it) in a variety of systems and formally regarding all other components of those systems as parameters of that selected organism. If this communal or system nature is stressed then ecology is not entirely synonymous with either scientific natural history nor environmental biology. Since this definition seems, by general concensus of opinion, to express the essence of an ecological approach to biology as well as to embody in principle HAECKEL's original views we shall here adopt it and, accepting the severe practical and intellectual challenges it presents, try to see where it leads.

There are, however, those, particularly animal ecologists, who, while agreeing and even stressing that ecology should be defined as above, cease to maintain this position when faced with the serious practical and representational difficulties which arise; they tend, therefore, to slip into the usage of such terms as population ecology, energy ecology, and even the redundancy of community ecology where, I submit, the terms population biology and so on would be preferable. Thus, in some studies labelled as population ecology and concerned only with the numbers of a given species and their fluctuation over a period, little or no reference is made to the species as a component of a system; one might regard this as a pseudo-autecological approach in which attention is concentrated on a single vector of the given species. Such studies are valuable and interesting but only if their relation to the system is considered, and only when it is realised that important interactions are being neglected for reasons of practical or theoretical convenience can such work be considered as population ecology rather than population biology. Because when only they are considered terrestrial plants make up non-motile systems, these are more easily described and more readily studied from the truly ecological point of view and it is not surprising, therefore, that botanists were the pioneers of synecology; indeed there are those who would contend that, because of problems associated with the time scale, the purely synecological approach is virtually impossible when motile organisms are involved. To reject the definition on this account is a defeatist attitude; very often an apparent impasse arises because it is difficult to specify the necessary vectors of motile components. Thus some stress that unlike a plant community the position of a motile organism cannot be specified in fixed coordinates – but there are other equally valid measures of what may still be termed position – for example the time spent by a motile organism in any one place or activity: a return to this particular point will be made later. Again, the large numbers of species involved, the complex life-histories and often the shortness of the life-span have all been put forward by animal ecologists to explain why they seem to be more concerned with fragmentation rather than true ecology (CRAGG 1961).

I am at the same time under no delusions as to the difficulties, both practical and conceptual, in trying to maintain the apparently simple definition and the position set out above. The difficulties which complex biological systems pose are severe – the restricted competence and interest of the observer to a single field, the difficulty of defining the components and choosing measurable and significant vectors, and the conceptual difficulties in integrating the results. However, similar problems arise in all fields of biology – one only need mention the nervous system and its integrative action – but new methods of attacking such problems at the conceptual level (for example the cybernetic approach to the nervous system) are becoming available and indeed are increasingly being used and developed; I do not think we should as yet despair. An appreciation of the wide variety of biological problems now being considered in terms of models of one kind or another may readily be seen from a variety of publications of such as that of the 14th Symposium of the Society for Experimental Biology (1960). Further there is nothing *(vide supra)* in the definition to prevent us focussing attention on specific parts of the system according to our interests or inclinations, as long as it is realised that in dissecting the system in this way only partial statements about it are being made and that these statements are of restricted ecological value. Indeed, in considering any complex system some arbitrary selection of components is forced on an observer; any variable may be selected for study – as long as its relation to the system is firmly kept in view – but if one wishes to know something of the system as a whole then one must select the essential variables.

You may think that in admitting this I have sacrificed the rigidity of the original definition and am hoisted by my own petard; this is not so – for the sub-system, the essential variables, the components and their study have been set in their proper perspective in relation to ecology. To select essential variables is not always easy. Important variables may go unsuspected because of the subtle but yet no less important way in which they exert their influence. It is perhaps comforting in this respect to remember that the most precise worker in the non-biological sciences does not in fact control, or indeed take account of, all possible variables and parameters – it is considered neither desirable nor necessary. A chemist, for example, investigating the kinetics of a chemical reaction would not think of measuring the incidence of cosmic radiation nor of controlling the ambient magnetic field. He has no reason – on the basis of a vast background of evidence – to believe that they are relevant to the phenomenon he is studying; nevertheless, unless so proved, he may be making unwarranted assumptions. One can consider that there is a hierarchy of variables "likely", on the basis of past experience, to influence the behaviour of any system, biological or otherwise, and the most likely of these will naturally be first investigated. In comparison with abiotic systems, however, a good deal more caution must be exercised in setting up any such hierarchy.

One hardly need give any examples of possible pitfalls and of the complexities inherent in biological systems when compared with those of a purely physical or chemical nature: endogenous rhythms of a simple or complex kind may, and do, affect response to major variables like temperature and salinity; even magnetic and possibly cosmic ray fields may be of considerable importance in the metabolism and activities of some plants and animals – as seems evident from the work of BROWN and his colleagues. Constantly more and more subtle and unsuspected relations are being revealed. Perhaps two of the most notable in the marine field are those relating to the substrate preference of many sedentary animals and those concerned with algal excretory products. Our ideas on the effect of relatively specific interaction of organism and substrate are rapidly changing. It has long been known that invertebrates living in sand or mud are limited to sediments having a restricted range of particle size but MEADOWS (1964) has recently shown that the amphipod *Corophium volutator* is restricted by more subtle influences than particle size. Again it seems that in many species with planktonic larvae settlement on specific substrate is common even though the level of discrimination may be lowered if a preferred substrate is not immediately found. Substrate preference has been demonstrated in many groups: for polychaetes by WILSON (1952); for barnacles and serpulids by KNIGHT-JONES and his colleagues (KNIGHT-JONES 1951, 1953, KNIGHT-JONES & MOYSE 1961, KNIGHT-JONES & STEVENSON 1950) and for Polyzoa by RYLAND (1959, 1962). One may also point to the contrast in substrate preference between the mature larvae and the young adults of *Mytilus edulis:* the former settle on filamentous substrates but eventually migration takes place to adult mussel beds (BAYNE 1964). We may point out here that factor analysis (see p. 19) is often a useful preliminary in finding the inherent organization and in delineating the important variables.

The recognizable system is usually limited to a restricted range of abiotic factors and over wide values of the latter ecology usually passes over into biogeography; the latter subject tends, however, to stress the classification and structure of systems or merely to consider the distribution of individual species – when it ceases to be ecology as defined above. An important aspect of biogeography must nevertheless be to compare systems; identical sets of abiotic parameters do not give rise to identical systems since evolutionary and geographical factors determine the availability of the components which may live together and so come to make up the system. Under similar abiotic parameters, however, the specifically distinct components of a system will tend to have similar properties and so come to occupy similar functional relations to one another; they will occupy similar habitats.

"EXPERIMENTAL": A DEFINITION

I suggest that for our purposes we may define an experimental procedure as the activity in which a given system is observed when it is subject to a set of conditions whose values, numerical or otherwise, are selected and, ideally, controlled by the observer. Under this definition an experiment is the observation of the effect of a series of transformations, passing from one parameter to another, on the variables of the system under investigation. In the case of a fully natural ecosystem – existing, that is, only under natural conditions – rarely can an experiment, as so defined be carried out. But only if this is done and the interactions of the biotic components allowed full rein can the procedure be termed – if both the above definitions are accepted – experimental ecology. Small, physically restricted systems may sometimes be dealt with in this way; for example, it is not difficult to envisage controlling the temperature, salinity, or even nutrient status of a small pool and observing the changes on selected or essential variables. Probably the most carefully controlled and correctly analysed ecological experiments are those conducted in the field of agriculture. It is not too difficult, however, to make changes – particularly those of a substractive kind – in some of the biological components of some systems under natural conditions and to observe the results. The effect of the browsing action of limpets on the littoral by controlling their numbers has been studied by SOUTHWARD (1956) and CONNELL (1961) has investigated the part played by the predation of *Thais* on the composition of the lower littoral and particularly in the competition between *Balanus balanoides* and *Chthamalus stellatus.* Although perhaps, in a sense, the situation is unnatural, observations on the effect of an immigrant into a given ecosystem may be considered to come within the category of experimental ecology. In the case of larger natural systems the best that can usually be done in regard to abiotic variables is to observe the effect on the system of changes in the environment which are not under control but which are known to, and measured by, the observer. In this category one would include observations made when certain parameters are taken outside their normal range for any given system; extremes of temperature and salinity, sometimes catastrophic, often give excellent opportunities for such studies. HOESE (1960) has taken advantage of the sudden release from a continued drought to study the effects of marked salinity changes on the fauna of a Texas lagoon, the pre-drought and drought conditions being known from earlier work. The recent extremely cold winter of 1962/63 gave an excellent opportunity to investigate the effect of temperature on a variety of ecosystems many of which were reported at the Fourth Marine Biological Symposium, Hamburg, 1964. In most of these studies it was assumed – and with good reason – that the extremely low temperatures were directly responsible for the changes observed. A direct correlation of the changes in some common littoral barnacles and the temperature anomalies over western European shores was demonstrated by

BARNES & BARNES (1966) who were also able to examine the "recovery" of the littoral system as more normal conditions returned.

In order to include such studies in the original definition of an experiment we must allow that the conditions, although not under the observer's control are known to him and measurable: even in its amended form the definition rules from the province of experimental ecology all experimentation on organisms isolated from their total environment and freed from any interactions. The disadvantage of so widening the definition is that if the observations are properly treated almost any well founded ecological work may be regarded as at least approaching experimental. Thus can a series of observations on the changing populations of the benthos with depth be regarded as an experiment, namely, one in which the parameter, depth, – and the parameters dependent upon it – are chosen by nature and their values determined by the observer? If so, the situation then tends to become confused because rarely do natural changes take place singly and the interactions may be lost to sight; for example, in the case given above, a change in depth usually means a change in the character of the substratum as regards both its physical and chemical characters. The possibility of analysing such systems in which many variables are allowed to change simultaneously by powerful new statistical techniques – in particular factor analysis and the method of principal components – makes the distinction even more diffuse. In these methods the situation is recorded as it presents itself to the observer and the subsequent analysis isolates relations of interest, all other being disregarded and relegated to an error component. Factor analysis, in its classical form, is always so applied but an extension of the method does allow of its application to controlled situations. (There is, of course, no reason why factor analysis should not be applied to artificial systems.) Clearly in any given investigation the statistical and experimental methods are complementary and cognisance should be taken of both. Even the physicist cannot, in fact, measure precisely (the very act of measuring may change that which is being measured) and on the atomic scale he is confronted by HEISENBERG's Principle of Uncertainty. In the final analysis – as R. A. FISHER pointed out – the two methods – experimentation and observation – represent two extreme points along a continuum concerned with error variance. The two approaches are normally, however, different in their setting and – for the moment – the notions of manipulation and control will be considered to be essential to, and characteristic of, the idea of experimentation; this position will help us to make a formal distinction between experimental ecology and experimental biology and to examine the relevance of the latter to the former.

The first phase of any ecological enquiry must be to describe the system – so that the components and vectors and their relation one to another may be known. This is purely descriptive – and no conclusions need be drawn. Some may then wish to classify such systems. The second phase, in which experimental ecology is concerned, is still essentially descriptive; the behaviour of the system is studied when the parameters are changed; the system is described in a set of states. The results of such studies may then be used to interpret the behaviour of systems under natural conditions as the parameters change with time or place. It is not necessary to know the reason for any effect in order to know the behaviour of the system for this can be determined from observations on it under the appropriate conditions. One does not ask how the changes take place – one is not interested in mechanisms at this point – although quite clearly one can argue about the properties and mechanisms acting within the system from its observed behaviour. For example, if a certain organism is reduced in numbers when the temperature of a given system is raised it may be considered reasonable to assume that the organism is temperature sensitive and that high temperatures are deleterious. This may not, however, be the case; higher temperatures may be without effect on the organism *per se;* the effect may be produced by a beneficial effect of temperature on a competing organism.

EXPERIMENTAL BIOLOGY

If one substitutes the word organism, tissue, or cell for ecosystem in the above definition of an experiment, then we have a definition of experimental biology – the performance of experiments, as defined above, on these entities. In this, since the organism is isolated from others, the complications of biotic interactions are eliminated and the properties of the organism *per se* more easily investigated. A knowledge of the behaviour of the component organisms as determined in experimental zoology enables us to ask questions as to how the observed behaviour of systems is brought about, and to decide what are the essential vectors of the components. The approach of the experimental biologist is essentially analytical and one may refer here to the Helgoland Symposium on the Quantitative Biology of Metabolism for some excellent examples of this approach. Even in studying the isolated organism one is still dealing with a system and unless the behaviour of the whole organism is studied "integrative" problems will still arise. The analysis may take various directions and be conducted at various levels of organization – behavioural, physiological or biochemical, and an interpretation of the whole organism attempted in terms of the results. It is the attempt to answer questions regarding mechanisms – to ask how the observed changes take place and what "properties" of the biotic components determine these changes that motivates many so-called experimental ecologists whose activities at the practical level are, in truth, purely experimental biology. It is important to remember that care must be taken in the application of all experimental studies to systems with interaction. To give a trivial example: we may investigate the temperature tolerance of a motile organism of a given littoral ecosystem experimentally and find, say, that 20° C is lethal. On examining an ecosystem containing the organism and subject to an ambient air temperature of 20° C it may well be found that all the individuals of the given species do not die; they may retreat to such parts of the ecosystem where, because say of evaporative processes, the temperature is sub-lethal. From the point of view of the system-information, the experiment was ill-designed although giving perfectly valid information about the species.

The ecologist, pursuing experimental biology for ecological reasons, is, in both a theoretical and practical way, in a somewhat different position from that of the purely experimental biologist. The latter is, as we have seen, interested in the properties of the organism, tissue or cell *per se* – or often in some process – respiration, photosynthesis, and the like – divorced from any particular organism. He can, therefore, choose an organism which is particularly suited to his interests – indeed his success as an experimental zoologist may often be determined by his choice. Thus one thinks immediately of the importance of some large unicellular algae in the study of active transport in plant cells, of large insects used in the study of flight mechanisms and insect biochemistry, and, of course, of the part that studies of the giant axon of the squid have played in nerve physiology. In contrast, the ecologist comes to his problems in experimental ecology in a different – and much more prescribed – way; he starts with the ecosystem and its components which he must first define and describe as accurately as possible – so that his organisms are in this sense chosen for, and not, by him. In his search for mechanisms he soon finds himself up against considerable practical difficulties – organisms that are difficult to keep, and even more so to culture, and organisms that make the well tried methods of experimentation difficult or impossible. Even the small size of the animals of planktonic ecosystems precludes most of the common methods of experimental zoology. These difficulties merely present a challenge either to adapt the classical methods or develop new ones; I believe, for example, that anyone who would apply modern histochemical methods to planktonic copepods would reap a rich harvest. But it is as well that the purely experimental zoologist should appreciate these difficulties before he accuses the ecologist of a lack of sophistication in his experimental approach.

I suppose it is pertinent to ask at what point does the ecologist end his analytical approach in terms of experimental work; for example, having shown, say, a differential response to changes in salinity of two major components in an ecosystem which allows him to explain the changes observed in that system, does he go no further – or does he then investigate the mechanisms – at the organ and cellular level – by which the salinity tolerances are mediated? Clearly in the latter case he is moving further from the ecological problem. It is difficult to answer this question. To some extent the choice is determined by individual preference, by personal temperament, and not infrequently by the available facilities. It is generally true that a given individual gets more and more interested in a given species, or group of organisms, and with increasing experience more competent in dealing with its, or their, vagaries. The temptation for many is to continue with one such group and to become more and more inclined to autecology and experimental biology: there is a wide range of problems within any single group – all of which are of great intellectual interest and relevant to the ecosystems in which it is found. Of course an eventual limit is set by the point at which a worker no longer feels competent to pursue the problems of, say biochemistry and physiology increasingly involved. Even so, far too rarely is the ecologist brave enough to stop – and decide to consider another species of a given ecosystem at a less analytical level, although the relevance of such is evident from both his knowledge of the system and the results of his work on the first chosen component organism of that system. *Peccavi* – would seem an appropriate confession at this point! It would, nevertheless, be a refreshing sight to see more people make this change with respect to a given ecosystem than is currently the case.

THE FUTURE OF ECOLOGY, EXPERIMENTAL AND OTHERWISE

We may perhaps now turn to the future of ecology and examine the problems – experimental and otherwise – which are presented. Clearly if we wish to know more about mechanisms a great expansion of experimental biology as it relates to ecological systems is required; too often are our judgements on ecological systems based on inadequate experimental data. How is this to be brought about? Any information provided by experimental biologists is to be welcomed and is likely to prove important – even if only by analogy and by suggestion. Ecologists must keep abreast of the relevant literature. Our real problem, however, is to get more ecologically orientated experimental zoology. Of course, a greater effort should be made to attract experimental biologists into the marine field – and better still into marine laboratories where they would then at least be available for advice; but even so they may never, if left to themselves, direct their activities to ecological work and after all why should they? I feel ecologists will more and more have to tackle their own experimental work – whether biological or ecological – and this leads to problems of ways and means of a different kind.

One possibility would be to set up a central Institute of Marine Ecology staffed by ecologists equipped in a wide variety of disciplines and furnished with the necessary technical facilities; this has of course been done in atomic physics. Apart from financial difficulties this poses other problems – where for example should such an Institute be sited? The problems in many other disciplines are not peculiar to any particular region but ecology refers to a particular place and since each system poses its own problems a central institute in the north-boreal could not investigate the problems of tropical ecology. Of course with the appropriate financial support a relatively small number of Institutes could serve the major climatic regions of the world. Even so it is desirable that ecological work should continue to expand in all centres of marine research and we shall have to progress by – if necessary – re-education, by a willingness to learn new techniques, and by more mutual cooperation.

Perhaps a word about cooperation may not be entirely misplaced. To some it invariably means the formation of team and without doubt this may be essential in an efficient approach to some ecological problems. Although at present popular, teams are not always the answer, for in an ultimate analysis science is very much a personal activity, requiring for success an almost romantic passion for knowledge and the intense energy and devotion to seek it. I may remind you of NEWTON's reply when asked how he made his most important discoveries "By always thinking into them. I keep the subject constantly before me and wait till the first dawnings open little by little into the full light" and as HINCHELWOOD (1965), a great scholar and scientist, in citing this statement, says – "No committee structure however logical and tidy will replace the devotion of which Newton speaks". While some overall planning is of course desirable, it cannot in detail be a purely logical process; inspiration is rare, discreet and unplanned. It is impossible to predict ideas. I think we should put immediate pressure in two directions: first for increased facilities in such laboratories – and there are many – that still need them and, secondly, for increased possibilities of cooperation.

On both these questions one can only base one's comments on personal experience and observations. The availability of sophisticated equipment is very variable but in the first instance one need only stress the necessity to have access to even simpler equipment which is basic to much experimental ecology or ecologically orientated experimental biology. For example, many people are still frustated by a lack of adequate facilities for conducting experiments in temperature controlled rooms. Some of us are more fortunate than others but how many laboratories have say half a dozen walk-in rooms all temperature controlled at intervals from say 0^0 to 30^0 C and with water of variable salinity available in them? Such equipment is not expensive by modern standards and can often be set up in a simple auxiliary building. The local butcher is often better equipped! Secondly we should establish that cooperation is essential and that finances should more readily be available for any well constructed case based on the point reached by the individual worker. This kind of cooperation can take many forms from simple requests for local observations to the most intimate mutual practical work. One must stress, however, that the ecologist cannot – and indeed most would not – wish merely to farm out his problems to someone else. He must, for true cooperation at a technical level, be at least prepared to make himself sufficiently well acquainted with the subject on which he seeks help as to be able to present his problem as having an intrinsic interest in the field of the worker whose help is sought.

We may now turn to more scientific aspects of future ecology. One would like to see many more relatively simple "artificial" systems set up in the laboratory and studied experimentally. In this way one can attempt to define the essential variables of more complex systems under controlled values of the major parameters.

I would like to see more emphasis placed on the behavioural aspects of marine ecological studies. That the structure of many populations – birds, for example, – is markedly under the influence of behavioural characters is well known. Some attention has been given to behavioural problems in the marine field, but so far these studies have been restricted to a few groups or even species and their relevance to ecosystems has been little pursued. For example, SMITH & NEWELL (1955) in their work on the littoral distribution of *Littorina littorea* have stressed that the stimuli and situations to which the snails respond are, in part at least, age specific and that although the movement of the adults are directed to survival, "token" stimuli may be most important to the juveniles.

I would like to see more work on the genetical aspects of populations related directly to given ecosystems. Evolution is no longer considered as a specific lineage but rather as a change in the genetical structure of populations; some forms of polymorphism, particularly chemical, are now known to be widespread. Since the population is moulded by – and interacts with – the environment, much more attention should be given to this field. In comparing the behaviour of ecosystems with common components over a range of environments or in autecological studies it is usually assumed – for evidence has rarely been sought to the contrary – that the responses of any common component is mediated only by its reactions to the environment, often as modified by acclimation. It is evident from many other fields that clinal situations are common and that over a wide range there may be sufficient genetic variability to modify the "properties" of the morphologically defined species. We have very little information in the marine field on clinal situations as they affect ecosystems. Such studies as exist have been largely limited to the examination of minor morphological characters and while these are of considerable interest to the genetisist they are of less importance to the ecologist; this would not be the case, of course, if it could be shown that such minor morphological changes are correlated with changes in properties of ecological significance. Even in a genus such as *Drosophila*, only recently has the relation between species and certain ecological requirements been studied. We may refer to the work of ROYES & ROBERTSON (1964) who studied the nutrition and growth patterns in sibbing species of the *obscura* group, *subobscura*, *obscura* and *anilirgua*, and in *immigrans* and *funebris*. Differences in a variety of nutritional requirements – as regards vitamins, cholesterol and protein – were demonstrated, as were differences in response to suboptimal diets, the latter being reflected in variations of growth pattern. These differences were related to the range of habitats exploited. CRISP (1964) has shown that the rate of development of *Balanus balanoides* embryos from widely separated localities is different and that this difference is maintained in transplants; and this has lead him to suggest sub-speciation. That there may exist a clinal situation in this species as evidence from a biometrical study of the valves is indicated by the work of BARNES & HEALY (1965).

In systems where both plants and animals are present, both must be considered together – even though for some purposes one aspect is stressed at the expense of the other; it is only for convenience that the botanist regards animals as parameters of the fauna and the zoologist regards plants as merely something on which animals feed.

It is difficult to see what is popularly termed a break-through in ecology. Ecology has shown a steady development with varying emphasis and this will clearly continue; here as in other fields the future is an extension of the present as the present is a reflection of the past. The earlier ecologists, although perhaps laying stress on, and often bitterly divided over, aspects that are now of little concern, were competent workers and the foundations laid by people such as WARMING, SCHIMPER, CLEMENTS, TANSLEY, DU RIEZ, ELTON, and others have stood the test of time. (One may add that except perhaps for the work of SHELFORD the earlier attitudes which are now outdated, such as the concern with terminology and succession, never really affected marine ecology.)

The increased activity called for in any or all of these fields will give more and more data on the structure and functioning of a wider and wider variety of ecosystems and will present an even greater challenge to our powers of synthesis and integration. I believe that it is this field of integration which presents the greatest problems and in which the greatest advances will be made, and perhaps I may be forgiven for considering this aspect of the development of ecology in a little more detail. We shall have to set up models and these may be of various kinds – but probably most usefully – electrical analogues and mathematical symbolism. We shall have to deal in these models with multi-component-multivector systems and instead of considering the relations between two or three vectors on paper or in the solid, we shall have to deal with n-vectors in n-dimensional space. A useful model – which has essentially the same conceptual status as a theory, a hypothesis, or a law – is positive in that it should help us to understand the system of which it is a model; in this sense it stands in contrast to a description which, in spite of its obvious primary importance, is negative or, perhaps one should say, neutral.

A preliminary warning is not out of place. We must in all this kind of work remember that a model will rarely be isomorphic with a biological system (see, however, p. 20), isomorphism implying that the relations between the parts of system and model are identical – even though expressed differently in mechanical, electrical or mathematical terms (the canonical representations of two systems are isomorphic if a one-to-one transformation of the states of one machine into those of the other can convert one representation into the other). Rather they will be homomorphic in which a many-to-one transformation gives a system isomorphic with the other. In addition it must be remembered that it is commonly the case that only some aspect of the model is related to the biological system – not its whole; certain non-relevant aspects of the model-system relation are neglected. Further, in applying any mathematical techniques, no matter how powerful, we should always remember that mathematics is only a form of symbolic logic; a mathematician is in no way concerned with experience nor of necessity, with physical reality. He does not, in the real world, create or discover and unless the premises are correct the conclusions will be false. As LINDEMANN has pointed out, although material is neither added nor substracted, what comes out of the mathematical sausage machine is very different from the quadruped that was put into it. I would draw two inferences; first, that we do not become so enamoured of the sausage machine itself and so delighted with the taste of the produce that we forget what went into it; secondly we know as much as possible of the primary material.

A variety of mathematical techniques have already been applied to ecosystems. One line of approach is to consider the distribution of the individuals of an ecosystem and to set up mathematical models with known properties by which they may be represented. The pioneers in this approach have been the terrestrial botanists but no one working with the benthos should be unfamiliar with this approach, nor should he be unaware of the pitfalls which have already been uncovered; for example, it is well known to botanists that the distribution (statistical) of an organism is related to population and sample size and many kinds of non-random distribution when randomly sampled (either by area or volume) will appear random with very large or very small samples i. e. when whole clusters are being sampled or when samples are taken within a cluster. In spite of this, in studies of bottom fauna every effort is often made to standardize the sample size, so that the results – and by this is usually meant the number and kind of animals present – are comparable from one area to another; this procedure, adequate for some porposes, can lead to quite unwarranted conclusions regarding so-called communities. Whether for any given species such a sample shows randomness or not depends on its population density, and the benthos worker would do well to look at the various tests by which randomness has been tested, for the tests vary in their sensitivity to various kinds of departure from a Poisson distribution.

The fitting of a given distribution to a set of data should not, however, be an end in itself – but should serve as a guide to the factors underlying such distributions. Two mechanisms are usually suggested giving aggregation (variance : mean) namely a variation in the Poisson parameters, λ, and a constant λ but the dependence of one observation or another. It was this that was termed "contagion" by POLYA. Both mechanisms probably apply in natural conditions and it is impossible to distinguish between the two causes merely by examining the overall frequency distribution. By fitting certain distributions in which assumptions are made about the size of the clusters the latter may be estimated. An approach of this kind, with an effort to correlate the observed distribution patterns with some abiotic parameters of the environment was made by BARNES & MARSHALL (1951) who took a large number of small replicate plankton samples and this work has been extended by CASSIE (for a review of this kind of work, see CASSIE 1963); COMITA & COMITA (1957) have investigated the distribution patterns of the freshwater *Diaptomus siciloides* by similar techniques.

The plant ecologists have also given considerable attention to the measures and description of association between species occurring together, and of the correlation with habitat factors. Correlation analysis of a given community in an effort to show assemblages which are responding in a similar manner to influencing factors is essentially the same as that used to classify communities by species groupings. χ^2 tests on presence or absence, correlation coefficients between abundance values, and rank correlation coefficients can all be used. (The results are again dependent upon sample size.) Animal ecologists have been more interested in the degree of association rather than in the significance of association tests and the value of the correlation coefficient has been used for this purpose.

These methods, which have been used by WIESER (1960) and SANDERS (1960) in their studies of the benthos, will be largely superceded by more sophisticated forms of multivariate analysis. Multivariate techniques are always appropriate when observations of several variables are taken under several different sets of conditions; and this is commonly the case in ecological work. In the simplest case multiple regression relations may be calculated or multiple and partial regression coefficients, and these may be used to indicate the extent of any association. In the method of principal component analysis one finds a series of functions of the observations which have decreasing variances, each successive function being independent of the previous one; some of the components will account for little of the variability and each component which accounts for a negligible proportion of the total variance indicates the existence of equivalence amongst the measurements; it may be shown, for example, that virtually all of the information contained in a number of measurements is present in, say, two principal components.

In factor analysis[2] it is assumed that the observed variables are largely determined by a small number of factors although "errors" in each measurement affect the results. The factors which together determine the measurements are sought and their minimum number which adequately summarize the correlations determined. A start has been made in marine biological studies. WILLIAMSON (1961, 1963) has used correlation methods in his investigation of plankton assemblages. In the first instance the

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[2] Factor analysis differs from partial correlation in that it holds whole factors constant while the latter holds variables constant; an inherent weakness in partial correlation methods is that a variable may be held constant which is part of the same functional unity as the dependent variable. Factor analysis differs from mutiple correlation in that the variables are first grouped into independent functional entities before giving a weighted composite.

variations in abundance of several zooplankton animals were examined by means of correlation matrices and WILLIAMSON was able to show that some groups of species showed common patterns of annual variation which were related to hydrographical parameters; COLEBROOK has been able to show distinct patterns of annual fluctuations in the area of his surveys and discussed the possible factors responsible for these patterns. COLEBROOK & ROBINSON (1964) have extended this method to examine the relations between zooplankton and certain species of diatoms. Both the correlation between the abundance of a given species in different areas over a series of years and that between the different species in a single area were examined. They were able to show that for most of the species the patterns were in accordance with the geographical disposition of the areas; some species, however, showed correlations which were area-independent so suggesting large scale factors acting over the whole area. COLEBROOK (1964) has extended this type of approach using principal component analysis; he selected variables which were linear functions of the geographical distribution of all the species and found that the first three of his components provided a satisfactory representation of the distribution of the species; and of these the first was identified with salinity, the second with a complex function involving temperature during the summer months and the range of seasonal temperature variations, while the third component was provisionally identified with the distribution of mixed oceanic and coastal waters. The applications of multivariate analysis leads to a much more sophisticated appreciation of the structure of a system at any given time and, of the relations of that structure to some of the important parameters.

Systems undergo change and except by comparing the structures in each state the multivariate analysis does not direct by deal with these changes. The cybernetic approach – which as regards marine ecosystems has been pioneered by MARGALEF (1961) – seems to be one of the most promising ways in which the gap between the structure of systems and their energetics may be bridged; indeed, PATTEN (1961) has shown that a comparison of statistical and thermodynamical entropies, with the translation of an energy budget into an information budget, leads to an isomorphic model of negentropy flux in planktonic communities. The initial structure of a system can be considered as a message with its biotic diversity as a measure (after coding) of its entropy expressed in terms of information.

Communication theory is concerned with what happens to this coded information when it flows along a channel from which it can be recovered and decoded, the amount of recoverable information deteriorating as the noise of the channel increases. The biotic diversity is a measure of the channel capacity, that is, the maximum information that can be transmitted. Although the channel width can change with time because of changes in the numbers of kinds of species present, its relative constancy – which is expressed in the recognizability of the system – must be maintained, and this conservation is effected by negative feedback and is related to the niche structure of the system. The amount of noise – disturbance – is extremely important in regard to the information to be transmitted and QUASTLER (1959) has discussed the degree of integration in ecosystems which is equivalent to the reduction of noise, and the "feature" sampling by organisms. In general, complex environments are more stable (SOLOMON 1949). "Primitive" environments are noisy and are associated with high reproductive rates, high power outputs and low efficiency. The species respond more directly to the parameters of the system and do not resort to information storage and effective sampling of new features. When reproductive rate is low, mean life span long, and fluctuations buffered, the systems correspond to a channel with a lower noise level and their behaviour is more predictable.

We have already referred to the problems associated with the mobility of animals (p. 9) which has been invoked by some to regard our definition of ecology as of little practical significance; it was stressed that alternative measures other than specific coordinates – for example, the time spent in a given place – can be used to define position. ASHBY (1956) points out that one may consider that every individual of a motile population present at a given point has definite probabilities of being found in other places and that a matrix of transition probabilities, the average steady state-distribution, and the noise can be constructed for such an assemblage. If the individuals remain fixed or change in a completely determinate way no information is lost; with completely random movements the information recovered is only the number of species and number of individuals; organisation is absent. All the properties of the system which increase its organizational properties – its interactions – decrease noise and increase the information transmitted.

The efficiency of coding is related to ideas previously expressed concerning the essential variables and their hierarchy, and MARGALEF has pointed out that changes in the diversity at the specific level are often strikingly analogous to these at other, say, biochemical levels. In MARGALEF's model described above the different individuals were considered as identical and interchangeable; the information was coded with this restriction and in so doing only part of the information or organization was encompassed. Further we may note that while increase in the number of niches[3] (and negative feedback) increases the channel capacity, this falls as the possible existence of more than one species in a niche increases, that is with increasing competition. This loss of information–carrying capacity is restricted to that information provided by the code and information may be transferred to a level outside the code at which it is no longer evident in the model. Coding at any given level always results in information below that level being lost. In MARGALEF's coding much information of a finer quality was, as he fully realized, neglected and considerable advances must come as our coding includes greater amounts of information more accurately modelling the structure of the systems involved. In this connexion it may be noted that recently LLOYD & GHELARDI (1964) have pointed out how desirable it is to have a measure of both aspects of species diversity, namely, number of species and number of individuals; the one may depend much on the availability of diverse habitats, the other more on the stability of physical conditions. They derive an expression for the "equitability" (numbers) from the SHANNON – WIENER function which does not distinguish between the two kinds of diversity, used by MARGALEF and others to express species diversity (information per individual), and MACARTHUR's (1957) model for apportioning indi-

[3] The term is here used in the sense of a specialized habitat; the term niche has been variously used. For a discussion, see UDVARDY (1951), ROSS (1957, 1958) and PARKER & TURNER (1961).

viduals among the species and they have discussed the meaning of the derived function in relation to some problems associated with sampling.

All this is equivalent to producing more hypotheses. In spite of NEWTON's dictum "I frame no hypotheses" and the fact that his works constantly urge the "abhorence" of such, I think that, armed with some of the newer techniques suggested above we shall benefit from such developments. NEWTON's extreme position was, of course, adopted because he became involved in a whole series of quarrels regarding the nature and validity of his doctrines and laws; in the Opticks, even he could not avoid some speculation. To try by constructive imagination to infer and predict on the basis of sound experiments or observations is surely part of the scientific discipline; there is a good deal of evidence to show that only those who have thought deeply and long about a subject produce hypotheses which are subsequently verified. I would, however, add a rider, namely, that there is an obligation upon the proposer of the hypothesis to do something regarding the testing of its validity. With this proviso and the obligation to consider all the evidence carefully – imagination tempered by facts and experience – we may be spared the trivial and superficial, masquerading under the guise of brilliant intuition.

Finally, I would like to say a work about the status of ecology. Snobbery – if that is the appropriate word – seems for the time being to be inerradicable from many human activities – whether it be intellectual, financial, social, national or political. Variability there should be – but tolerance too. Although the terms should be mutually exclusive, scientific snobbery most surely exists – and in scientific work, as in other human activities, it is often allied to what is most fashionable; we are often made aware that in some circles ecology is not high in the peck-order. I would like to draw a moral from another field – systematics. With the rise of some modern disciplines the systematist became almost a depressed – and even in some quarters – a despised class; by and large I think their reaction to this situation was unfortunate – consisting as it did of merely sniping at their accusers by retorting that *they* were working with animals whose names they could not even spell properly. This attitude did them little good; only relatively recently – and not completely – have systematists asserted the importance of their own subject, particularly by seizing upon the relevance of newer developments, mathematical and otherwise, in the fields of genetics. We should not make the same mistake by merely replying to those who accuse ecologists of naivety and the subject of intellectual and technical simplicity, that it is in fact *the* most complex subject and that it is the accusers who are in reality being naive in thinking that, because they apply more sophisticated techniques to so-called simpler systems they are superior beings. There may be some truth in this counter-accusation but by itself it is a totally inadequate reply. We are not second rate citizens of the scientific world but must clearly demonstrate this fact if we are to attract good recruits into the field. Too often discussion amongst ecologists and accounts of ecological work are dull and do lack sophistication in their approach, but if we really advance along some of the broad lines that have already been indicated there will be no danger of taking any but an honourable place in the scientific community.

SUMMARY

1. The definition of the word "ecology" is considered and the difficulties – both practical and theoretical – associated with a precise formulation outlined.
2. Ecology as the study of systems consisting of components, or variables, each made up of a number of vectors is discussed.
3. A comparison of the difficulties inherent in the definition with those – less apparent – in abiotic systems is made.
4. The meaning of the word "experimental" is considered and its relation to a series of transformations on a biological system discussed.
5. The meaning – in the restricted sense determined by the definitions given – of experimental ecology and the practical problems it poses are dealt with in some detail.
6. The meaning of "experimental biology" and its relation to experimental ecology, as defined above, is discussed in relation to plant and animal systems.
7. The future of ecology – experimental and otherwise is discussed.
8. The increase in information will call for a greater integrative approach and the possible ways by which this can be achieved are outlined, particularly as they relate to the marine biological sciences.

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Discussion following the paper by BARNES

KINNE: I am still fascinated by your very interesting introductory paper. You certainly are to be commended for an exciting and thorough consideration of the fundamentals and complexities of the fields of ecology and experimental biology. I wholeheartedly agree with most of your statements and conclusions. There are, however, two points which I would like to bring up for discussion here: (1) In your definition of the term "ecology", you have added the word "totality" to the generally accepted meaning of this term ("study of organisms in relation to the totality of their environment, abiotic and biotic"); this leads you – and rightly so – to stress the need for studying assemblages of organisms and whole systems. But then you seem to conclude that experimental ecology is in practive exclusively concerned with systems as a whole, which is where I can no longer follow you. Here are my reasons: (a) The boundaries of an ecosystem are frequently difficult to define; the system itself is not easy to get "into grip" and to work with experimentally. (b) In most natural situations the total environment, abiotic and biotic, is extraordinarily complex; several factors cannot yet be measured appropriately; others may still be unknown. The possibilities seem infinite unless the experimental ecologist restricts himself to the study of ecological "master" factors or the role of "key" organisms. (c) In addition to working with the whole system, we must study and experiment with suitable parts (e. g. subsystems, groups of representatives from key species of the food chain, multi-species cultures containing representatives from 2, 3, 4, etc. species, mono-species cultures *sensu lato,* axenic cultures) hoping that the information obtained at these different levels will help us to understand how the whole system works. (d) We can hardly expect that the "pure" physiologist or experimental biologist will do this job for us, at least not by producing that kind of data which we urgently need. (2) Your definitions of "ecology" and "experimental" lead you to conclude that "all experimentation on organisms isolated from their total environment and freed from any interactions" are ruled from the province of experimental ecology. I am afraid that such a statement would make most of us – including you and me – anything but experimental ecologists; imagine how sad that would be!

BARNES: Thank you for your comments. I intended to be provocative! – and to take two fairly widely accepted definitions of – in the one case "ecology" and the other "experimental" – and see where they would lead. That it has led us to the point at which one has to say that many who regard themselves as experimental ecologists are in reality experimental biologists is no reflection on either; it should merely invite them to review their experimental work in the light of the ecological situations to which they are supposedly related. I tried to relate experimental biology to ecological situations, for the former is absolutely necessary if we are to understand the mechanisms involved, that is, if we are not willing merely to observe the behaviour of the system as a whole, when it is subjected to a series of constraints. Both are legitimate approaches to this and many other fields of science. Your comments regarding the complexity of ecosystems and the severe difficulties are true, but surely your "master" factors and "key" organisms are only what I have called the essential variables and your subsystems are mine too. One should perhaps stress that in choosing "master" or "key" factors in complex systems, there is a vicious circle element; such factors are chosen on the basis of current knowledge, and as this increases, we may have to change our views on what *are* "master" or "key" factors. Indeed there is some danger in this view, for a system is completely integrated; altering any one factor will change the system, even though some alterations produce less obvious effects than others. The truly "master" or "key" factors at any given moment in time may be completely unknown and only revealed as a result of subsequent work.