PHYTOPLANKTON ECOLOGY
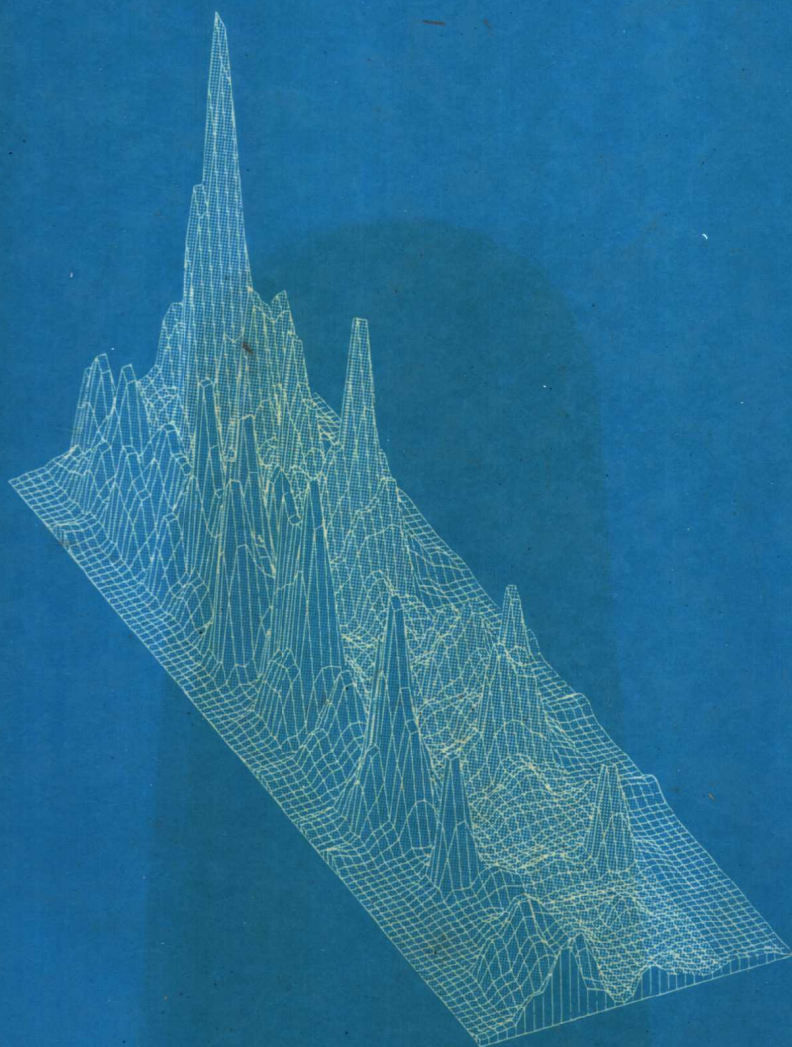
STRUCTURE, FUNCTION AND FLUCTUATION

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Phytoplankton Ecology

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To
Richard Vollenweider

who contributed so much to my education over a
number of years. Many of the ideas in this book were
first spawned at our regular Friday lunches. It always
took me some months to appreciate the value of the
ideas that Richard threw away in a moment.

Acknowledgements

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CHAPTER 1

Preamble

Many text books of limnology and oceanography begin by reminding the reader that two thirds of the surface of the Earth is covered by water. Perhaps the most striking image that drives this point home is the Apollo mission view of the Earth taken from directly over the Pacific Ocean, which shows little land and one complete third of the surface of the Earth covered with water. Phytoplankton are the 'grass' of the surface waters of lakes and the oceans, so this book is concerned with the ecology of a group of organisms which are responsible for the process of primary production over much of the surface of the Earth. This is a book about phytoplankton but it is also, I hope, a book about some general ecological principles. I believe that phytoplankton have much to teach us about the way this world works and the lessons we may learn should be as widely applied as possible. I take a certain pride in using phytoplankton as model organisms in an ecology text because phytoplankton have long been regarded as paradoxical. Most of the standard theory of ecology has not included phytoplankton. Phytoplankton do not appear to fit most of the standard explanations and examples from phytoplankton data are missing from most of the standard literature.

So how can phytoplankton, a group of microscopic photosynthetic organisms, be useful as models of general principles? In my opinion, the problems with ecological theory in the past have lain in an incorrect appreciation of scale and an unrealistic reliance on equilibrium theory. Scale is a measure of the way organisms perceive their environment. We, as human beings of a characteristic size and life span, tend to see the world in an anthropocentric way (Allen and Starr, 1982). We have trouble coming to grips with the long time scale components of what we see today, with such concepts as succession and evolution. At the same time we can easily comprehend time scales of minutes, days and seasons as these fit easily into the working span of the average ecologist and into the time span of most research grants. In scales of size the converse is true. With maps and expeditions to the far corners of the globe we may comprehend the larger scale, global distributions of organisms and ecosystems. It is at very small spatial scales that we have had problems. We have tended to see the world

in terms of cubic metres and kilometres, convenient scales for us, but entire universes for organisms such as bacteria and phytoplankton. This has been particularly true in the study of marine phytoplankton where the size of the oceans and the ships in use has led oceanographers to concentrate on scales of many kilometres and to neglect scales more relevant to the organisms (Harris, 1980a). We have regarded phytoplankton as paradoxical because we have looked at the environment of the organisms at too large a scale.

The climate of intellectual opinion keeps intruding on the world view and this sometimes encourages us to accept explanations which may be at variance with reality. There has been too much reliance on equilibrium theory in ecology with the result that while the mathematics of the theory has been simplified, the application of the theory to the real world has become more difficult. Clearly there is a great deal of spatial and temporal variability in the real world. Equilibrium theory, by its very nature, considers the results of competition and other environmental interactions at steady state. But what if this steady state is perturbed by external events? What are the consequences of such perturbations? If we consider such questions then equilibrium theory is reduced to a special limiting case of a broader theoretical framework which seems to be slowly emerging. The extremes are equilibrium and chaos: where do real world events lie?

There is one way to deal with the complexity of the real world. In a recent book, Allen and Starr (1982) interpreted ecological events in terms of hierarchy theory. They classified systems into three categories: small, middle and large number systems. Small number systems may be thought of as being akin to billiard ball physics; representable as differential equations. Large number systems are the biological equivalents of physical gas laws. Allen and Starr (1982) asserted that the real world may be thought of as complex middle number systems: systems in which the number of significant elements are too many to be treated by reductionist approaches but too few to be treated by statistical approaches. Koestler (1967) stated that biological systems may 'be regarded as a multi-level hierarchy of semi-autonomous sub-wholes, branching into sub-wholes of lower order and so on. Sub-wholes on any level of the hierarchy are referred to as holons' (Fig. 1.1). Koestler (1967) was discussing the organization of organisms but the analogy to supra-organismic (ecological) organizations had already been made by von Bertalanffy (1952) who discussed the hierarchy of parts and of processes in biological systems. Thus it is important to remember that holons may be both discrete structural units (organelles, organs, organisms) and discrete units of process which may cut across structural boundaries. The evident complexity in the behaviour of biological systems may be analysed by decomposing them into a fully, or partially, nested hierarchy of holons. This approach to biology is characteristic of von Bertalanffy's 'General Systems Theory'.

The definition of the holon contains within it a dichotomy, as the holon
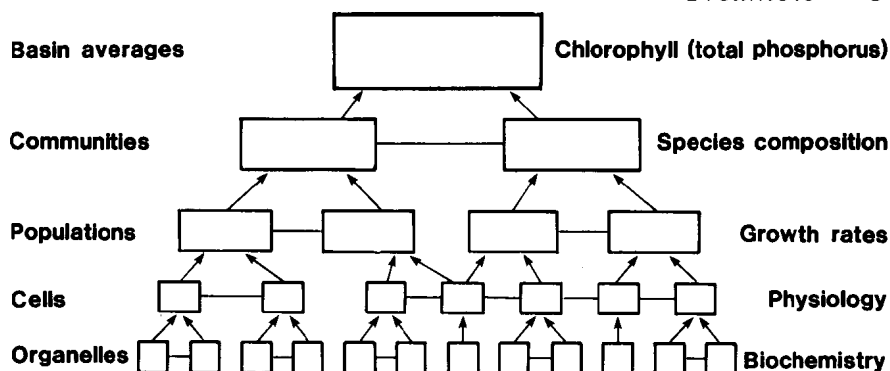
Fig. 1.1 A diagrammatic representation of the hierarchy of process and organization in phytoplankton ecology.

displays the dependent properties of a part as well as the autonomous properties of a whole. Koestler (1967) called this dichotomy the Janus effect. Allen and Starr (1982) define the holon as

> The representation of an entity as a two-way window through which the environment influences the parts, through which the parts communicate as a unit to the rest of the universe. Holons have characteristic rates for their behaviour, and this places particular holons at certain levels in a hierarchy of holons.

The Janus effect is a reference to the passage of information through the two-way window – the holon boundary. Allen and Starr assumed that the world may be thought of as an hierarchy of holons with small, fast holons at the base and large, slow holons at the apex. They did not assume that the world really was such a system, it may merely be conveniently thought of in this way. This is no place for a deep discussion of Marxist dialectics. The hierarchy of holons is nearly decomposable if the holons exhibit apparent disjunctions when viewed in the appropriate way. Allen and Starr assumed that the hierarchy of spatial and temporal processes in nature was continuous and that the relative intensities of the interactions between levels could be used to decompose the continuum into more or less discrete holons. The nested hierarchy of holons is a particular type of hierarchy in which the upper level holons actually contain the lower levels. This need not always be the case.

The hierarchical approach will be used throughout this book as a means of classifying ecological, physical and chemical processes. From the smallest scales of nutrient uptake and cellular physiology to the largest scales of interannual variability there are a number of important interactions between physics and biology. At each level I will attempt to describe the physical and chemical processes in operation and their effects on biological processes.

The view of Allen and Starr is a radical change from the usual ecological

approach, where reductionism is rampant and questions about emergent properties have become the purview of metaphysics. The analytical and summative approach of much biological research was criticised by von Bertalanffy (1952) who showed that such methods could not account for the properties of organized wholes. His approach stressed the organized properties of living systems and stressed the role of information exchange in maintaining the organization. He allowed that supra-organismic levels of organization are much less well coordinated than those at the organismic level but the same principles apply. Different properties are expected to emerge as the level in the hierarchy alters; whether the emergent properties are a simple, additive function of the lower holons will depend on the completeness of the data sets, the point of view of the observer and the presence of properties which are not, in themselves, derivable from the behaviour of the components. This world view also obviates all discussion about the difference between equilibrium and non-equilibrium ecology, about the effects of endogenous and exogenous factors and about the discreteness, or otherwise, of ecological communities.

We are thus faced with the problem of classifying temporal and spatial scales of variability in terms of the organisms of interest. What is small and fast for one organism may be large and slow for another. We must also be consistent in our treatment of variability; it is not correct to combine processes which operate at different scales in one discussion. This is as true for biological processes as it is for environmental variables such as fluctuations in light and nutrient availability. Thus we have to contend with a hierarchy of spatial and temporal variance in a number of relevant ecological parameters. What is really interesting about a correct classification and treatment of the hierarchy of variance in ecosystems is the fact that 'noise' at one level may contribute to the predictable behaviour of ensemble averages at higher levels. Thus there are statistical properties of the cascade of variance in ecosystems.

I believe that this cascade of variance in ecologically relevant parameters from large and slow processes to small and fast processes is a vitally important factor in determining what we see. The diversity of life on Earth depends on it. The variability we observe is not just something that we can average out and equilibrium solutions to ecological problems only apply for some organisms in some cases. I shall review the basic tenets of equilibrium theory in order to show that these cannot apply in many instances.

If we appreciate the true scale of interaction in phytoplankton populations they become extremely useful model organisms. There are a number of reasons for this. Phytoplankton are small and they grow very rapidly so that many generations may pass during a year. We may therefore observe the seasonal succession of species which is, in many respects, analogous to that in forest successions. Instead of taking hundreds of years the seasonal

succession of phytoplankton may be complete in one hundred days and is thus more amenable to study. In the terminology of holons, we may study more levels and more holons than in most other ecological disciplines as we may study holons which span the range from nutrient uptake kinetics, through physiology, population dynamics and communities to biomass and we may average over minutes and centimetres or whole basins and years. I shall go to some length to show that many phytoplankton populations are, in fact, nowhere near equilibrium, but that there are statistical properties of assemblages of species that allow high level, averaged properties to be discerned. Such high level, statistical properties of ecological systems are akin to physical gas laws as they are characteristic of large number systems. I believe that the study of phytoplankton can reveal such statistical properties more easily than most other systems as the small size and rapid growth of the organisms allows properties to be averaged at a very high level. Allen and Starr point out that changing the scale of observation often reveals important aspects of the functioning of ecological systems. I shall show that this is, indeed, the case.

Another feature of the ecology of phytoplankton which makes them useful model organisms lies in the enormous range of different sized waters which they inhabit. Phytoplankton may be found in water bodies ranging in size from rain water puddles to the oceans. This provides the ecologist with a wide ranging set of environments and it is possible to study the response of the organisms to physical and chemical processes operating at a wide range of spatial and temporal scales. Many textbooks deal with the marine and freshwater environments separately but I recognize no such distinction here. The differences between freshwater and marine environments are essentially only those of scale as Margalef (1978b) has demonstrated. The oceans, because of their size, are dominated by large scale horizontal motions (ocean currents) but in many respects the physics of the surface mixed layer of lakes and the oceans is very similar. One respect in which lakes and the oceans differ is in the fact that lakes are bounded systems which may be treated as wholes for statistical purposes. This makes the study of populations within lakes much easier (Weatherley 1972) and means that the properties of different lakes may be compared by calculating average properties for each lake.

This will not be a compendium of information on phytoplankton: no-one could hope to better the work of Hutchinson (1967). This book is not so much descriptive as process oriented. I wish to make some specific points about the ecology of the organisms and to show how the study of the organisms relates to ecology in general. There is a reason for attempting to do this at this time as in recent years the study of phytoplankton has undergone something of a 'revolution' ('sensu Kuhn') as ecologists and physiologists realized that the standard theory and methodology was not

always applicable to the real world. We failed to appreciate that ecologically significant events were occurring at very small temporal and spatial scales; scales which were not fully resolved by traditional methods. In short it has become apparent of late that our knowledge of the ecology of planktonic ecosystems requires reinterpretation. A more dynamic approach has recently emerged (Legendre and Demers, 1984). There will be some general themes in this book that will discuss the relationship between theory and practice in aquatic ecology and the problems of the interpretation of field and experimental data.

Phytoplankton have, in the past, been regarded as paradoxical by virtue of the fact that small samples of water contain many coexisting species. Phytoplankton are very small organisms and they are not to be thought of merely as small flowering plants: in many respects they behave as microorganisms. For example, one of the major debates at present concerns the growth rates of phytoplankton in the central ocean areas where nutrients are apparently lacking. For years it has been assumed that no nutrients meant no growth, as a simple curvilinear relationship between nutrient concentration and growth rate could be demonstrated in laboratory cultures. Now we have begun to realize that an apparent lack of nutrients may not lead to a suppression of growth in the field. There may be rapid uptake of nutrients and rapid growth by the phytoplankton if the uptake and growth rates are balanced by equally rapid grazing and regeneration of the nutrients. Thus it is not the concentration of nutrient in the water which is the important parameter but the flux rates between the various compartments in the system. For this explanation to be valid we must invoke rapid nutrient uptake and storage by the phytoplankton from small patches of regenerated nutrient in the water. The interpretation of data from laboratory cultures and experiments requires a knowledge of the limitations of the methods used, and the interpretation of data from similar methods in the field requires a knowledge of the temporal and spatial scales of the processes in operation. The scales of observation and natural process must be understood and correctly matched (Harris, 1980b).

There have been a number of recent papers and books about the relationships between physiology, methodology, and the interpretation of productivity and growth rate measurements, many of which serve to illustrate the need for the revision of some basic ideas in the field. Little has been written about the effects of a revised paradigm on our understanding of population dynamics and community structure. Inevitably, any discussion of population dynamics must include a discussion of growth rates and in order to measure growth rates we must make kinetic measurements. Thus I will need to discuss the relationship between theory, kinetic measurements, observed growth rates and population studies

In lakes, the seasonal succession of communities in surface waters may be

managed by virtue of the fact that the physical and chemical environment may be manipulated. Thus we may consider both the intellectual implications of our results as well as the practical implications for human intervention and mangement. Phytoplankton are relatively easy to grow in culture so the field data may be supported by experimental data. This is of some considerable importance when it is remembered that the great variability in the real world makes it very difficult to perform controlled experiments with natural populations and ecosystems. The resources required by phytoplankton may also be studied in culture and, while it is not always easy to extrapolate from the constant conditions of culture to the real world, many useful insights have been obtained. Competition between phytoplankton has been studied in culture and such studies have contributed significantly to the development of equilibrium theory. As we shall see, there is good reason to question the role which competition plays in the formation of natural communities in a fluctuating environment. If competition is less important in the real world than in culture this will have considerable implications for our ability to predict the biological responses to changed environmental conditions.

1.1   A brief introduction to the organisms

The term plankton refers to the group of organisms which float in the surface waters of rivers, lakes and the oceans. The term plankton has its roots in the Ancient Greek adjective meaning wanderer. The modern adjective normally used is planktonic but there is some debate as to the correct form. Planktic may be etymologically correct (Rodhe, 1974), whereas planktonic may be preferred for reasons of euphony and common usage (Hutchinson, 1974). As the term implies, planktonic organisms float freely in the water and live at the mercy of water movements. Many phytoplankton are curious and beautiful organisms and microscopic examination of water samples reveals a great diversity of forms (Fig. 1.2). While many planktonic organisms are themselves immobile others have a limited capacity to swim through the water and hence have the ability to change their position in the water column. There is a range of swimming ability depending largely on the size of the organism.

The term phytoplankton is used for the large group of planktonic plants that live in surface waters. There is always some debate as to exactly which organisms to include in this group as, among the single-celled and simple multicellular forms, there is uncertainty about the best form of classification and it is sometimes difficult to distinguish between animals and plants. The vast majority of phytoplankton are algae and belong to a diverse group of lower, non-flowering plants. Some phytoplankton may strictly be described as bacteria as they are prokaryotes while others, by virtue of their mobility
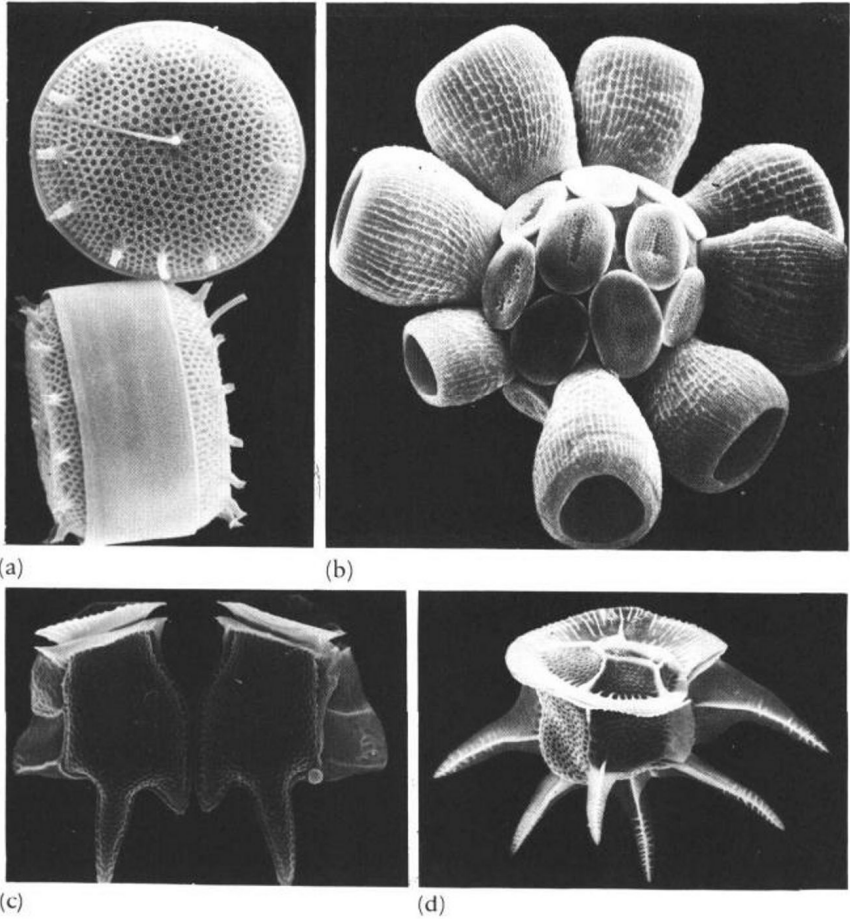
Fig. 1.2 Scanning electron micrographs of some marine phytoplankton. I am indebted to Gustaff Hallegraeff for the original of this figure.
(a) *Thalassiosira allenii*, a chain forming diatom.
(b) *Scyphosphaera apsteinii*, a coccolithophorid.
(c) *Dinophysis tripos*, a dinoflagellate, dividing pair.
(d) *Ceratocorys horrida*, a tropical dinoflagellate.

and their ability to live on complex organic substrates in the dark, have some distinctly animal-like characteristics. The organisms exist as single cells or simple multicellular forms and are, by the standards of human experience, small. Within the phytoplankton there is a large range of cell size and growth rates. The species range in size from small prokaryotic and eukaryotic cells equivalent in size to bacteria to the largest dinoflagellates which are visible to the naked eye. Thus there is a size (volume) range of at least five orders of magnitude (Malone, 1980a). Their range in growth rates is somewhat less, ranging from a few doublings per day for the fastest

growing species, to one doubling every week or ten days for the slowest species (Eppley, 1972). What the range in size and growth rates really means is that we are dealing with a group of organisms that are very small and which (by normal ecological standards) grow very rapidly. In many respects the ecology of phytoplankton is similar to the ecology of bacteria, only the bacteria show comparable sizes, growth rates and metabolic flexibility. We cannot regard phytoplankton as small 'higher' plants (Allen, 1977), and the time scale of important processes is much more rapid than that exhibited by higher plants (Harris, 1980a).

The strict definition of phytoplankton is further confused by the presence of species which normally live on the sediment surface and which become suspended in the water by turbulence (Hutchinson, 1967). Thus some of the species present in the water column are not truly part of the planktonic community. In some species the life cycle includes an encysted or resting phase which settles on the bottom and remains there for a period of months or years, so only a part of the life cycle is planktonic. Such species are obviously more common in shallow waters: in the deep waters of the oceans such a life cycle is clearly impossible as the resting stage would never be resuspended. Thus it is not easy to produce a strict definition of the organisms to be discussed in this book. For the purposes of these arguments it will be sufficient to restrict the discussion to those algae which commonly occur in surface waters and/or those which complete a significant portion of their life cycles in such waters.

Most of the major algal groups have planktonic representatives (Table 1.1). It is evident that planktonic forms of the diatoms and chrysophytes, green algae, crytophytes and dinoflagellates are common but there are very few planktonic red algae and no planktonic brown algae or charophytes (Bold and Wynne, 1978; Sournia, 1982). There is some debate over the best means of classification of the algae and the classification of Bold and Wynne (1978) is but one of many. This classification treats the blue-green algae as algae, even though they are prokaryotes and thus structurally similar to bacteria. The justification for their inclusion here is that they are a very important group of phytoplankton which play a significant role in water quality problems in lakes. As can be seen from the table the comparative lack of morphological characters (many phytoplankton are referred to as 'little round green things' or LRGTs) has led taxonomists to use a wide range of structural, biochemical and other cellular characters as a means of classifying these organisms. The evolutionary relationships between the major groups can be clearly seen in the structure of the flagellae (if present), in the pigment composition, the structure of the chloroplast and the relationship between the chloroplast and the nuclear envelope (Coombs and Greenwood, 1976).

There are significant differences between the dominant groups of phytoplankton in marine and freshwater systems in that, while dinoflagellates are