Ecology of Phytoplankton

Phytoplankton communities dominate the pelagic ecosystems that cover 70% of the world's surface area. In this marvellous new book Colin Reynolds deals with the adaptations, physiology and population dynamics of the phytoplankton communities of lakes and rivers, of seas and the great oceans. The book will serve both as a text and a major work of reference, providing basic information on composition, morphology and physiology of the main phyletic groups represented in marine and freshwater systems. In addition Reynolds reviews recent advances in community ecology, developing an appreciation of assembly processes, coexistence and competition, disturbance and diversity. Aimed primarily at students of the plankton, it develops many concepts relevant to ecology in the widest sense, and as such will appeal to a wide readership among students of ecology, limnology and oceanography.

Born in London, Colin completed his formal education at Sir John Cass College, University of London. He worked briefly with the Metropolitan Water Board and as a tutor with the Field Studies Council. In 1970, he joined the staff at the Windermere Laboratory of the Freshwater Biological Association. He studied the phytoplankton of eutrophic meres, then on the renowned 'Lund Tubes', the large limnetic enclosures in Blelham Tarn, before turning his attention to the phytoplankton of rivers. During the 1990s, working with Dr Tony Irish and, later, also Dr Alex Elliott, he helped to develop a family of models based on, the dynamic responses of phytoplankton populations that are now widely used by managers. He has published two books, edited a dozen others and has published over 220 scientific papers as well as about 150 reports for clients. He has given advanced courses in UK, Germany, Argentina, Australia and Uruguay. He was the winner of the 1994 Limnetic Ecology Prize; he was awarded a coveted Naumann–Thienemann Medal of SIL and was honoured by Her Majesty the Queen as a Member of the British Empire. Colin also served on his municipal authority for 18 years and was elected mayor of Kendal in 1992–93.

ECOLOGY, BIODIVERSITY, AND CONSERVATION

The world's biological diversity faces unprecedented threats. The urgent challenge facing the concerned biologist is to understand ecological processes well enough to maintain their functioning in the face of the pressures resulting from human population growth. Those concerned with the conservation of biodiversity and with restoration also need to be acquainted with the political, social, historical, economic and legal frameworks within which ecological and conservation practice must be developed. This series will present balanced, comprehensive, up-to-date and critical reviews of selected topics within the sciences of ecology and conservation biology, both botanical and zoological, and both 'pure' and 'applied'. It is aimed at advanced (final-year undergraduates, graduate students, researchers and university teachers, as well as ecologists and conservationists in industry, government and the voluntary sectors. The series encompasses a wide range of approaches and scales (spatial, temporal, and taxonomic), including quantitative, theoretical, population, community, ecosystem, landscape, historical, experimental, behavioural and evolutionary studies. The emphasis is on science related to the real world of plants and animals, rather than on purely theoretical abstractions and mathematical models. Books in this series will, wherever possible, consider issues from a broad perspective. Some books will challenge existing paradigms and present new ecological concepts, empirical or theoretical models, and testable hypotheses. Other books will explore new approaches and present syntheses on topics of ecological importance.
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The Ecology of Phytoplankton

C. S. Reynolds

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This book is dedicated to
my wife, JEAN, to whom its writing
represented an intrusion into
domestic life, and to Charles Sinker,
John Lund and Ramón Margalef. Each is
a constant source of inspiration to me.

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Preface

This is the third book I have written on the subject of phytoplankton ecology. When I finished the first, *The Ecology of Freshwater Phytoplankton* (Reynolds, 1984a), I vowed that it would also be my last. I felt better about it once it was published but, as I recognised that science was moving on, I became increasingly frustrated about the growing datedness of its information. When an opportunity was presented to me, in the form of the 1994 Ecology Institute Prize, to write my second book on the ecology of plankton, *Vegetation Processes in the Pelagic* (Reynolds, 1997a), I was able to draw on the enormous strides that were being made towards understanding the part played by the biochemistry, physiology and population dynamics of plankton in the overall functioning of the great aquatic ecosystems. Any feeling of satisfaction that that exercise brought to me has also been overtaken by events of the last decade, which have seen new tools deployed to the greater amplification of knowledge and new facts uncovered to be threaded into the web of understanding of how the world works.

Of course, this is the way of science. There is no scientific text that can be closed with a sigh, 'So that's it, then'. There are always more questions. I actually have rather more now than I had at the same stage of finishing the 1984 volume. No, the best that can be expected, or even hoped for, is a periodic stocktake: 'This is what we have learned, this is how we think we can explain things and this is where it fits into what we thought we knew already; this will stand until we learn something else.' This is truly the way of science. Taking observations, verifying them by experimentation, moving from hypothesis to fact, we are able to formulate progressively closer approximations to the truth.

In fact, the second violation of my 1984 vow has a more powerful and less high-principled driver. It is just that the progress in plankton ecology since 1984 has been astounding, turning almost each one of the first book's basic assumptions on its head. Besides widening the scope of the present volume to address more overtly the marine phytoplankton, I have set out to construct a new perspective on the expanded knowledge base. I have to say at once that the omission of 'freshwater' from the new title does not imply that the book covers the ecology of marine plankton in equivalent detail. It does, however, signify a genuine attempt to bridge the deep but wholly artificial chasm that exists between marine and freshwater science, which political organisation and science funding have perpetuated.

At a personal level, this wider view is a satisfying thing to develop, being almost a plea for absolution – 'I am sorry for getting it wrong before, this is what I should have said!' At a wider level, I am conscious that many people still use and frequently cite my 1984 book; I would like them to know that I no longer believe everything, or even very much, of what I wrote then. As if to emphasise this, I have adopted a very similar approach to the subject, again using eight chapters (albeit with altered titles). These are developed according to a similar sequence of topics, through morphology, suspension, ecophysiology and dynamics to the structuring of communities and their functions within ecosystems. This arrangement allows me to contrast directly the new knowledge and the understanding it has rendered redundant.

So just what are these mould-breaking findings? In truth, they impinge upon the subject matter in each of the chapters. Advances in microscopy have allowed ultrastructural details of planktic organisms to be revealed for the first time. The advances in molecular biology, in particular the introduction of techniques for isolating chromosomes and ribosomes, fragmenting them by restriction enzymes and reading genetic sequences, have totally altered perceptions about phyletic relationships among planktic taxa and suppositions about their evolution. The classification of organisms is undergoing change of revolutionary proportions, while morphological variation among (supposedly) homogeneous genotypes questions the very concept of putting names to individual organisms. At the scale of cells, the whole concept of how they are moved in the water has been addressed mathematically. It is now appreciated that planktic cells experience critical physical forces that are very different from those affecting (say) fish: viscosity and small-scale turbulence determine the immediate environment of microorganisms; surface tension is a lethal and inescapable spectre; while shear forces dominate dispersion and the spatial distributions of populations. These discoveries flow from the giant leaps in quantification and measurements made by physical limnologists and oceanographers since the early 1980s. These have also impinged on the revision of how sinking and settlement of phytoplankton are viewed and they have helped to consolidate a robust theory of filter-feeding by zooplankton.

The way in which nutrients are sequestered from dilute and dispersed sources in the water and then deployed in the assembly and replication of new generations of phytoplankton has been intensively investigated by physiologists. Recent findings have greatly modified perceptions about what is meant by 'limiting nutrients' and what happens when one or other is in short supply. As Sommer (1996) commented, past suppositions about the repercussions on community structure have had to be revised, both through the direct implications for interspecific competition for resources and, indirectly, through the effects of variable nutritional value of potential foods to the web of dependent consumers.

Arguably, the greatest shift in understanding concerns the way in which the pelagic ecosystem works. Although the abundance of planktic bacteria and the relatively vast reserve of dissolved organic carbon (DOC) had long been recognised, the microorganismic turnover of carbon has only been investigated intensively during the last two decades. It was soon recognised that the metazoan food web of the open oceans is linked to the producer network via the turnover of the microbes and that this statement applies to many larger freshwater systems as well. The metabolism of the variety of substances embraced by 'DOC' varies with source and chain length but a labile fraction originates from phytoplankton photosynthesis that is leaked or actively discharged into the water. Far from holding to the traditional view of the pelagic food chain – algae, zooplankton, fish – plankton ecologists now have to acknowledge that marine food webs are regulated 'by a sea of microbes' (Karl, 1999), through the muliple interactions of organic and inorganic resources and by the lock of protistan predators and acellular pathogens (Smetacek, 2002). Even in lakes, where the case for the top–down control of phytoplankton by herbivorous grazers is championed, the otherwise dominant microbially mediated supply of resources to higher trophic levels is demonstrably subsidised by components from the littoral (Schindler *et al*., 1996; Vadeboncoeur *et al*., 2002).

There have been many other revolutions. One more to mention here is the progress in ecosystem ecology, or more particularly, the bridge between the organismic and population ecology and the behaviour of entire systems. How ecosystems behave, how their structure is maintained and what is critical to that maintenance, what the biogeochemical consequences might be and how they respond to human exploitation and management, have all become quantifiable. The linking threads are based upon thermodynamic rules of energy capture, exergy storage and structural emergence, applied through to the systems level (Link, 2002; Odum, 2002).

In the later chapters in this volume, I attempt to apply these concepts to phytoplankton-based systems, where the opportunity is again taken to emphasise the value to the science of ecology of studying the dynamics of microorganisms in the pursuit of high-order pattern and assembly rules (Reynolds, 1997, 2002b). The dual challenge remains, to convince students of forests and other terrestrial ecosystems that microbial systems do conform to analogous rules, albeit at very truncated real-time scales, and to persuade microbiologists to look up from the microscope for long enough to see how their knowledge might be applied to ecological issues.

I am proud to acknowledge the many people who have influenced or contributed to the subject matter of this book. I thank Charles Sinker for inspiring a deep appreciation of ecology and its mechanisms. I am grateful to John Lund, CBE,

FRS for the opportunity to work on phytoplankton as a postgraduate and for the constant inspiration and access to his knowledge that he has given me. Of the many practising theoretical ecologists whose works I have read, I have felt the greatest affinity to the ideas and logic of Ramón Margalef; I greatly enjoyed the opportunities to discuss these with him and regret that there will be no more of them.

I gratefully acknowledge the various scientists whose work has profoundly influenced particular parts of this book and my thinking generally. They include (in alphabetical order) Sallie Chisholm, Paul Falkowski, Maciej Gliwicz, Phil Grime, Alan Hildrew, G. E. Hutchinson, Jörg Imberger, Petur Jónasson, Sven-Erik Jørgensen, Dave Karl, Winfried Lampert, John Lawton, John Raven, Marten Scheffer, Ted Smayda, Milan Straškraba, Reinhold Tüxen, Anthony Walsby and Thomas Weisse. I have also been most fortunate in having been able, at various times, to work with and discuss many ideas with colleagues who include Keith Beven, Sylvia Bonilla, Odécio Cáceres, Paul Carling, Jean-Pierre Descy, Mónica Diaz, Graham Harris, Vera Huszar, Dieter Imboden, Kana Ishikawa, Medina Kadiri, Susan Kilham, Michio Kumagai, Bill Li, Vivian Montecino, Mohi Munawar, Masami Nakanishi, Shin-Ichi Nakano, Luigi Naselli-Flores, Pat Neale, Søren Nielsen, Judit Padisák, Fernando Pedrozo, Victor Smetaček, Ulrich Sommer, José Tundisi and Peter Tyler. I am especially grateful to Catherine Legrand who generously allowed me to use and interpret her experimental data on *Alexandrium*. Nearer to home, I have similarly benefited from long and helpful discussions with such erstwhile Windermere colleagues as Hilda Canter-Lund, Bill Davison, Malcolm Elliott, Bland Finlay, Glen George, Ivan Heaney, Stephen Maberly, Jack Talling and Ed Tipping.

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A special word is due to the doctoral students whom I have supervised. The thirst for knowledge and understanding of a good pupil generally provide a foil and focus in the other direction. I owe much to the diligent curiosity of Chris van Vlymen, Helena Cmiech, Karen Saxby (now Rouen), Siân Davies, Alex Elliott, Carla Kruk and Phil Davis.

My final word of appreciation is reserved for acknowledgement of the tolerance and forbearance of my wife and family. I cheered through many juvenile football matches and dutifully attended a host of ballet and choir performances and, yes, it was quite fun to relive three more school curricula. Nevertheless, my children had less of my time than they were entitled to expect. Jean has generously shared with my science the full focus of my attention. Yet, in 35 years of marriage, she has never once complained, nor done less than encourage the pursuit of my work. I am proud to dedicate this book to her.

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