Light and Photosynthesis in Aquatic Ecosystems

Third edition

Beginning systematically with the fundamentals, the fully updated third edition of this popular graduate textbook provides an understanding of all the essential elements of marine optics. It explains the key role of light as a major factor in determining the operation and biological composition of aquatic ecosystems, and its scope ranges from the physics of light transmission within water, through the biochemistry and physiology of aquatic photosynthesis, to the ecological relationships that depend on the underwater light climate. This book also provides a valuable introduction to the remote sensing of the ocean from space, which is now recognized to be of great environmental significance due to its direct relevance to global warming.

An important resource for graduate courses on marine optics, aquatic photosynthesis, or ocean remote sensing; and for aquatic scientists, both oceanographers and limnologists.

JOHN T.O. KIRK began his research into ocean optics in the early 1970s in the Division of Plant Industry of the Commonwealth Scientific & Industrial Research Organization (CSIRO), Canberra, Australia, where he was a chief research scientist, and continued it from 1997 in Kirk Marine Optics. He was awarded the Australian Society for Limnology Medal (1981), and besides the two successful previous editions of this book, has also co-authored *The Plastids: Their Chemistry, Structure, Growth and Inheritance* (Elsevier, 1978), which became the standard text in its field.

Beyond his own scientific research interests, he has always been interested in the broader implications of science for human existence, and has published a book on this and other issues, *Science and Certainty* (CSIRO Publishing, 2007).

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Preface to the third edition

Four things are required for plant growth: energy in the form of solar radiation; inorganic carbon in the form of carbon dioxide or bicarbonate ions; mineral nutrients; and water. Those plants which, in the course of evolution, have remained in, or have returned to, the aquatic environment have one major advantage over their terrestrial counterparts: namely, that water – lack of which so often limits productivity in the terrestrial biosphere – is for them present in abundance; but for this a price must be paid. The medium – air – in which terrestrial plants carry out photosynthesis offers, within the sort of depth that plant canopies occupy, no significant obstacle to the penetration of light. The medium – water – in which aquatic plants occur, in contrast, both absorbs and scatters light. For the phytoplankton and the macrophytes in lakes and rivers, coastal and oceanic waters, both the intensity and spectral quality of the light vary markedly with depth. In all but the shallowest waters, light availability is a limiting factor for primary production by the aquatic ecosystem. The aquatic plants must compete for solar radiation not only with each other (as terrestrial plants must also do), but also with all the other light-absorbing components of the aquatic medium. This has led, in the course of evolution, to the acquisition by each of the major groups of algae of characteristic arrays of light-harvesting pigments that are of great biochemical interest, and also of major significance for an understanding both of the adaptation of the algae to their ecological niche and of the phylogeny and taxonomy of the different algal groups. Nevertheless, in spite of the evolution of specialized light-harvesting systems, the aquatic medium removes so much of the incident light that aquatic ecosystems are, broadly speaking, less productive than terrestrial ones.

Thus, the nature of the light climate is a major difference between the terrestrial and the aquatic regions of the biosphere. Within the underwater environment, light availability is of major importance in determining how much plant growth there is, which kinds of plant predominate and, indeed, which kinds of plants have evolved. It is not the whole story – biotic factors, availability of inorganic carbon and mineral nutrients, and temperature, all make their contribution – but it is a large part of that story. This book is a study of light in the underwater environment from the point of view of photosynthesis. It sets out to bring together the physics of light transmission through the medium and capture by the plants, the biochemistry of photosynthetic light-harvesting systems, the physiology of the photosynthetic response of aquatic plants to different kinds of light field, and the ecological relationships that depend on the light climate. The book does not attempt to provide as complete an account of the physical aspects of underwater light as the major works by Jerlov (1976), Preisendorfer (1976) and Mobley (1994); it is aimed at the limnologist and marine biologist rather than the physicist, although physical oceanographers should find it of interest. Its intention is to communicate a broad understanding of the significance of light as a major factor determining the operation and biological composition of aquatic ecosystems. It is hoped that it will be of value to practising aquatic scientists, to university teachers who give courses in limnology or marine science, and to postgraduate and honours students in these and related disciplines.

Certain features of the organization of the book merit comment. Although in some cases authors and dates are referred to explicitly, to minimize interruptions to the text, references to published work are in most cases indicated by the corresponding numbers in the complete alphabetical reference list at the end of the book. Accompanying each entry in the reference list is (are) the page number(s) where that paper or book is referred to in the text. Although coverage of the field is, I believe, representative, it is not intended to be encyclopaedic. The papers referred to have been selected, not only on the grounds of their scientific importance, but in large part on the basis of their usefulness as illustrative examples for particular points that need to be made. Inevitably, therefore, many equally important and relevant papers have had to be omitted from consideration, especially in the very broad field of aquatic ecology. I have therefore, where necessary, referred the reader to more specialized works in which more comprehensive treatments of particular topics can be found. Because its contribution to total aquatic primary production is usually small I have not attempted to deal with bacterial photosynthesis, complex and fascinating though it is.

The behaviour of sunlight in water, and the role that light plays in controlling the productivity, and influencing the biological composition, of aquatic ecosystems have been important areas of scientific study for more than a century, and it was to meet the perceived need for a text bringing together the physical and biological aspects of the subject, that the first, and then second, editions of *Light and Photosynthesis in Aquatic Ecosystems* were written. The book was well received, and is in use not only by research workers but also in university courses. In the 27 years since the first edition, interest in the topic has become even greater than it was before. This may be partly attributed to concern about global warming, and the realization that to understand the important role the ocean plays in the global carbon cycle, we need to improve both our understanding and our quantitative assessment of marine primary production.

An additional, but related, reason is the great interest that has been aroused in the feasibility of remote sensing of oceanic primary productivity from space. The potentialities were just becoming apparent with the early Coastal Zone Color Scanner (CZCS) pictures when the first edition was written. The continuing stream of further remote sensing information in the ensuing years, as space agencies around the world have put new and improved ocean scanners into orbit, enormously enlarging our understanding of oceanic phytoplankton distribution, have made this a particularly active and exciting field within oceanography. But the light flux that is received from the ocean by the satellite-borne radiometers, and which carries with it information about the composition of the water, originates in fact as a part of the upwelling light flux within the ocean, which has escaped through the surface into the atmosphere. To interpret the data we therefore need to understand the underwater light field, and how its characteristics are controlled by what is present within the aquatic medium.

In consequence of this sustained, even intensified, interest in underwater light, there is a continued need for a suitable text, not only for researchers, but also for use in university teaching. It is for this reason, the first and second editions being out of print, that I have prepared a completely revised version. Since marine bio-optics has been such an active field, a vast amount of literature had to be digested, but as in the earlier editions, I have tended to select specific papers mainly on the basis of their usefulness as illustrative examples, and many other equally valuable papers have had to be omitted from consideration.

In the 16 years since the second edition of this book appeared, interest in this subject has, if anything, increased. While there has been an acceleration, rather than a slackening in the rate of publication of new research it must be said that this has been much more evident in certain areas than in others. Remote sensing of ocean colour, and its use to arrive at inferences about the composition and optical properties of, and primary production going on within, ocean waters has been the standout example of a very active field. A variety of new instruments for measuring the optical properties of the water, and the underwater light field, have been developed, and a number of these are described. So far as photosynthesis itself is concerned, the most notable change has been the development of instrumentation, together with the necessary accompanying theoretical understanding, for *in situ* measurement of photosynthetic rate, using chlorophyll *a* fluorescence. A great deal more is also now known about carbon concentrating mechanisms in aquatic plants, and these topics are discussed. The presumptive role of iron as a limiting factor for primary production in large areas of the ocean has received a great deal of attention in recent years, and current understanding is summarized. Nevertheless, quite apart from these specific areas, there has been across-the-board progress in all parts of the subject, no chapter remains unchanged, and the reference list has increased in length by about 50%.

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Canberra
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