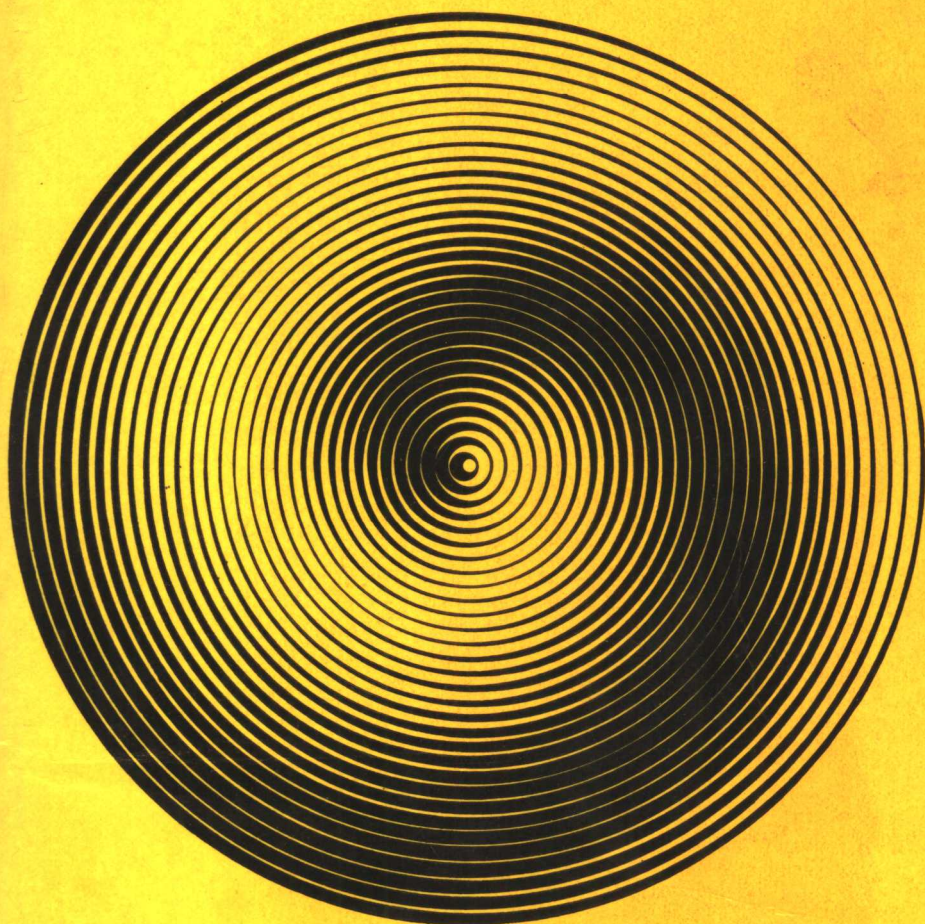


International Biological Programme **22**

# **The functioning of freshwater ecosystems**

Edited by E. D. Le Cren &  
R.H.Lowe-McConnell



INTERNATIONAL BIOLOGICAL PROGRAMME 22

# **The functioning of freshwater ecosystems**

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# Preface

The first two chapters of this volume – by Professor Tonolli and Dr Rzóška – between them provide a good introduction to the work of the IBP/PF Section that is summarized in the rest of the book. This preface will therefore concentrate on some comments and explanations essential for those who wish to understand fully what follows.

The final discussion meetings for the preparation of this volume took place in 1974 and drafts of some of the chapters had been completed by then. Why then has the publication taken so long? In part this has been the result of the nature of some of the chapters which required a great deal of collation, editing and cross-checking by the Chapter editors. Some chapters thus took a long time to complete and had to be the spare-time work of people busy on other new projects. Largely, however, the delay has been the result of the first editor taking on a new and demanding professional post and thus having all too little time and energy for editing. He must therefore apologize sincerely to readers who have had to wait, and especially to colleagues in the IBP/PF who completed their share of the work on time. Fortunately the second editor has been able to pick up the large number of loose ends and unpolished MSS and draw them together into a published volume.

In all scientific research, and perhaps especially in ecology, the processes of collecting field data, conducting experiments and analysing the data are only the early stages of completing the whole project. Preliminary analyses and results need checking and polishing, their statistical variabilities estimating, and then their meanings interpreted in relation to other results. No more is this so than in the interpretation of data collected over a wide range of habitats in international cooperative ventures. Some of such difficulties that arose in the IBP/PF are discussed by Tonolli in Chapter 1. The synthesis of the results of such broad projects is a continuing process, in some ways an iteration of successive analyses and syntheses each incorporating some new or better-analysed data or different ways of looking at the results. It must be remembered that not all the results on which this volume is based have yet been published. Ideally any attempt to make a synthesis should await the primary publication of all the component investigations, but this ideal is an impossible one and a compromise is essential. This must result in a volume that is more a collection of interpretations using different approaches, or based on data in different stages of analysis, than a synthesis valid at the moment it is published. It is important for the reader to realize this.

A particular example arises in Chapter 9 by Brylinsky. This chapter is based on an analysis commissioned by the IBP/PF Executive to provide a preliminary statistical analysis of the results from a wide range of lakes. This analysis was carried out in 1972, two or more years before the final 'data

reports' were written, during which time significant revisions were made to some of these data. Thus, some of the conclusions reached in this chapter may no longer be valid and this may be the reason for disagreements between this chapter and some of the others.

*The form of the volume.* Early on, the IBP/PF Executive Committee agreed that one large synthesis volume should be produced, rather than a series of volumes each dealing with a different aspect of freshwater production-ecology. The volume thus consists of a series of groups of chapters with different approaches.

✓ Chapters 1 and 2 provide an introductory background of the ideas behind IBP/PF, its planning, organization and its history. Livia Tonolli was the Convener of the IBP/PF Committee during its later years and had been in touch with the centre of its activities from the start. Rzóska was its Scientific Coordinator from 1965 onwards and more than any other person was responsible for its central planning and execution; he must therefore be given credit for much of its achievement as a cooperative venture.

✓ The next five chapters deal with the 'meat' of the scientific findings of IBP and synthesize the results in the respective fields of physics, chemistry, primary production, secondary production, and decomposition and microbial production. Straškraba's Chapter 3 adopts a theoretical, mathematical and modelling approach to the physical environmental features of lakes though it draws on a large number of data obtained during the IBP. It provides a basis for the prediction of much of the ecological character of lakes from relatively simple physical variables.

Golterman and Kouwe have analysed the basic chemical data provided by the data reports and provided a brief general account of the chemical environment of lakes with special reference to nutrient pathways and chemical limitations to productivity.

Chapter 5 on primary production has been synthesized and edited by Westlake, but is the work of a large number of co-authors. In the PF programme more attention was paid to primary production and its measurement, than to any other aspect of lake ecology. There were thus a large number of new data to be analysed, interpreted and synthesized. The estimation of primary production and the interpretation of the experimental data obtained are not easy. So this chapter is not just a straight presentation of results, but a series of comparisons and discussions of different aspects of primary production, the processes involved and the factors that may control them.

Chapter 6 on secondary production is also a team effort; the work of synthesis and editing being organized and led by Morgan. The estimation of secondary production is difficult and the consumers in most water bodies are organized in a complex food-web so the analyses are open to different interpretations. The results from some situations where sampling was difficult



had to be treated with reservation. The main sections of this chapter deal with zooplankton, zoobenthos and fish.

Chapter 7 deals with the important but difficult and under-researched area of the roles of organic matter, detritus feeders and decomposers.

Chapter 8 adopts a different approach and reviews some aspects of the trophic relationships in the freshwater ecosystem that are not discussed fully in the other chapters and some experiments. This chapter is concerned with physiological and ecological efficiencies and the dynamics of trophic relationships.

The two chapters that follow adopt two different mathematical approaches to the data gained in the IBP/PF projects. As already mentioned, Brylinsky's Chapter 9 reports on a statistical analysis of the preliminary data from several lakes. It is based on correlation analyses of estimations of primary and secondary production in relation to various physical and chemical variables and to each other. Chapter 10 by Walters *et al.* discusses the modelling of lake ecosystems and presents the results of some of the attempts at such modelling carried out during the IBP/PF.

The last chapter, no. 11, is again different from the others. At the start of the IBP, the idea of lakes as trophic-dynamic systems and the measurement of freshwater biological production had advanced further in Russia than in any other country. The Russian PF programme was thus quicker off the mark in its systematic planning than most others. Its results have been extensively published in Russian, but, as this language is not easily read in the West, these publications are not as widely known as they should be. Winberg has therefore prepared an English summary of the results of the Soviet IBP/PF studies for publication in this volume.

The chapters of this book thus present a series of different approaches to the main results of the IBP/PF programme and the study of the functioning of freshwater ecosystems. Many readers will have particular interests and will wish to go straight to the relevant chapter or chapters. They should find that most chapters can be read and comprehended on their own. We have attempted to include cross-references where important information is presented in a different chapter. The chapters have however been arranged in the order that we believe to be the most logical for those who wish to read the whole book and get an overview of all aspects of the IBP/PF.

*The IBP/PF in the context of other research.* In writing their sections or chapters authors were asked to base their accounts as far as possible on IBP results and to present the main findings of these, but to do so in the context of the large amount of non-IBP research, both past and present. Thus this volume is not just a summary of IBP/PF, but draws strongly on other research as well, though it looks at such research from the IBP viewpoint and primarily as the context in which the results from IBP research must be interpreted.



Readers should find in this volume a fairly comprehensive account of the state of knowledge about production ecology in fresh waters in the 1970s and a great deal that is relevant to limnology and freshwater biology in general, but some areas of these wider disciplines are covered only superficially or from a limited viewpoint. As the chapters were not all completed at the same time, they also vary in the extent to which they are up to date.

The list of references at the end of this volume is a long one and should serve as an excellent introduction to the literature in freshwater biology, especially if supplemented by the references given in one of the larger textbooks or treatises in the subject (e.g. Hutchinson 1957, 1967, 1975).

*The management of freshwater ecosystems.* The subject of the IBP was defined as: 'the biological basis of productivity and human welfare'; how may the IBP/PF results contribute to human welfare?

The production of biological material in fresh waters usually terminates in the form of fish, many of which can be harvested as human food or provide recreation through angling. Fish are the result of primary production and secondary production and are thus a product of the system and processes discussed in this book. Parts of Chapters 6 and 8 specifically deal with fish production and its relationships to the rest of the freshwater ecosystem.

In general it is the wish of the fisherman and fish farmer to *increase* biological productivity, but in recent years there has been much concern over the *overproduction* of algae in many lakes – the so-called problem of 'eutrophication'. Problems caused by excessive crops of phytoplankton are clearly related to productivity and primary production and there is a great deal of information in this book about such topics. The physical features of lakes relevant to their productivity are discussed in Chapter 3 and the models presented there should help a planner to predict the probable productivity of any new man-made lake. The nutrient cycles in lakes and their role in algal production are discussed in Chapters 4 and 5.

This volume is not a practical guide to the ecological management of fresh waters; its approach is essentially the scientific interpretation of basic and strategic research. But such research provides the understanding fundamental to the control and manipulation of biological production in fresh waters, so its findings are essential to the wise management of inland waters for human welfare.

*The Data Reports.* As described above and in Chapters 1 and 2, many of the basic data collected by the PF teams working on each lake or river were summarized in a specified format as a 'data report'. These data reports are listed in Appendix I, with a minimum of information about each site. Analyses of some of these data are used in this book, other analyses have been published by the authors working on the sites. The original data reports are now stored

in the library of the Freshwater Biological Association at The Ferry House, Ambleside, Cumbria, England, where they may be consulted. The IBP has given an undertaking to the authors of the data reports that the actual data will not be published without their permission and access for consultation will be granted on this understanding.

Throughout this volume there are references to those data reports made, for example, in the form: 'DR 96'; the numbers refer to the list in Appendix I.

*The IBP/PF Publications.* Appendix II lists all the Handbooks and other publications that were published directly by the PF section. Their provenance is discussed in Chapters 1 and 2.

*The List of References.* All the citations to literature made throughout the volume have been gathered into one reference list on pages 517 to 570. This list includes many of the hundreds of papers arising directly from IBP/PF research on the sites listed in the Data Reports. There are also many citations to the general limnological literature. The authors and editors have tried to make this list full enough to support all the statements made in the text, but have not attempted to make it comprehensive or a 'bibliography' in the true sense. Nor will all the papers arising from the PF programme have been listed.

*Conventions.* Several of the conventions followed in this volume are those laid down by the Publications Committee of SCIBP. We have attempted to follow the *Système International* in the matter of quantities, units and symbols and outside the specifications of SI, we have used the guide given by SCIBP booklet '*Quantities, Units and Symbols. Recommendations for use in IBP synthesis*' published in 1974. We commend this guide to other authors and editors publishing in this field. (The special symbols used in Chapter 3 are listed in table 3.1.)

*Epilogue.* In this Preface we have attempted to provide a guide to this volume for the prospective reader; to tell him a little of what this book is about and also, so as to avoid his disappointment, to warn him a little of what it is not. Perhaps a few final words from the Editors, as the first readers of the whole book, may be appropriate.

One of us has given a brief review elsewhere of his personal assessment of the successes, limitations and failures of the IBP/PF programme (Le Cren, 1976). It may be a surprise to some that biologists were attempting to measure aquatic production and model aquatic biological systems over fifty years ago. The ideas behind the IBP were not new ones, but by 1960 they were ripe for further development with the aid of new techniques for field work, analysis and modelling. As Tonolli points out in Chapter 1, the development and standardization of PF methodology took place simultaneously with its use in

the field. Some data produced thus lacked comparability and rigour. The time, effort and resources needed for the analysis, interpretation and publication of the results after the end of the period of data collection were also underestimated. With hindsight, it is possible now to see that those planning the PF programme were too optimistic over the possibilities of international coordination without the stimulus and control of central funding, and too optimistic of solving the extremely complex problems posed by the freshwater ecosystem without a much larger and more experimental programme. The ideas that were to be explored and tested were too simplistic and too imprecisely defined to be testable hypotheses.

It is always easy to look back and criticize after the event. We believe that this volume, and also the many papers derived from the PF programme, will be a tribute to the energy and enthusiasm of those that started IBP/PF and overcame the scepticism of many of their colleagues in the national and international scientific Establishments. As a result of the IBP, the science of limnology will never be the same. Above all, a great many young and enthusiastic researchers have become limnologists, had experience of international cooperation and made lasting friendships with one another.

E.D. LE CREN  
R.H. LOWE-McCONNELL

*March 1979*

# Acknowledgements

A volume like this involves the work of a great many people to all of whom we are grateful.

Professor Livia Tonolli's wise guidance and warm generosity did much towards bringing the PF programme through its final stages to this synthesis. This volume is the result of hard work put in by authors and especially by the chapter coordinators. The IBP Scientific Director, Dr E.B. Worthington, and Gina Douglas and Sue Darell-Brown of the IBP Publications Office have done much to help and keep us at our task. We are grateful to Peter Hargreaves for his careful checking of the references. The FBA Library Staff and our colleagues in the Freshwater Biological Association and at the British Museum (Natural History) have helped us with many detailed problems. Cambridge University Press staff, especially Peter Silver, gave great assistance over many editorial matters and with finding places where the Editors' attention had lapsed.

We are grateful to our very many friends who took part with us in the IBP/PF programme; we hope that we will still be friends after they have read this volume. Finally, we are deeply indebted to the Scientific Coordinator of the IBP/PF, Julian Rzóška; if the PF and this volume belong to any one person, it is to him.

E.D. LE CREN  
R.H. LOWE-McCONNELL

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