

The ecology of freshwater phytoplankton

C. S. REYNOLDS

Freshwater Biological Association





> Published by the Press Syndicate of the University of Cambridge The Pitt Building, Trumpington Street, Cambridge CB2 1RP 40 West 20th Street, New York, NY 10011-4211, USA 10 Stamford Road, Oakleigh, Melbourne 3166, Australia

© Cambridge University Press 1984

First Published 1984 Reprinted 1986, 1990, 1993

Library of Congress catalogue card number: 83-7211

British Library Cataloguing in Publication Data Reynolds, C. S. The ecology of freshwater phytoplankton – (Cambridge studies in ecology) 1. Freshwater phytoplankton – Ecology I. Title 589.4'0916 QK035

ISBN 0 521 23782 3 hardback ISBN 0 521 28222 5 paperback

Transferred to digital printing 1999



This book is dedicated to

MY WIFE, to whom its writing
represented an intrusion
into domestic life,
to Dr JOHN LUND and Mr CHARLES SINKER
who taught me so much



Contents

	Preface	Page ix
1	What is phytoplankton?	1
	Terminology	1
	Planktonic organisms	4
	Planktonic 'algae'	8
	General features of planktonic 'algae'	8
	The composition of planktonic 'algae'	28
2	Mechanisms of suspension	40
	The problem of suspension	40
	The nature of water movements	41
	Particle behaviour in turbulent columns	48
	Phytoplankton settling velocities	50
	Adaptive mechanisms for depressing v'	52
	Vital regulation of sinking rate	7
	Conclusions	81
3	Spatial and temporal distribution of phytoplankton	83
	Distribution patterns: the problem of scale	83
	Vertical distribution	87
	Horizontal distribution	105
	Temporal variations in abundance and composition of	
	phytoplankton	112
	Intra-assemblage structure and competition	120
4	Photosynthetic activity of phytoplankton	123
	General features of planktonic photosynthesis	123
	Photosynthetic behaviour in isolated samples of natural	
	phytoplankton	126
	Photosynthetic behaviour in non-isolated natural communities	131



viii

5	Nutrients	157
	Nutrient requirements of phytoplankton	157
	Phosphorus	162
	Nitrogen	164
	Silicon	168
	Other nutrients	173
	Nutrient interactions	178
	Eutrophication	183
6	Growth and survival	192
	Optimal growth rates	193
	Increase in natural waters	202
	Perennation	217
	Growth and survival strategies	22
7	Loss processes	22:
	What is a loss process?	225
	Hydraulic washout	228
	Sedimentation losses	233
	Death and decomposition	245
	Grazing	253
	Loss processes and phytoplankton composition	274
8	Periodicity and change in phytoplankton composition	277
	Seasonal periodicity of phytoplankton	279
	Longer-term floristic changes	32
	Glossary of symbols	329
	References	333
	Index to lakes and rivers	36
	Index to genera/species	369
	General index	374



Preface

The importance of phytoplankton is beyond question. Planktonic primary production provides the base upon which the aquatic food chains culminating in the natural fish populations exploited by man are founded, at the same time generating some 70% of the world's atmospheric oxygen supply. Excessive algal production in lakes and reservoirs presents expensive problems in the water industries, whilst deleterious effects upon fisheries and water-based recreation are fairly attributed to overabundance of phytoplankton. There is, therefore, a powerful economic and social need for as complete as practicable an understanding of the factors which regulate the spatial and temporal variations in the distribution and productivity of phytoplankton – or, in short, its ecology.

The volume of scientific literature devoted to phytoplankton biology is daunting and often bewildering. Many more titles are added each year. Fortunately, for both the beginner and the more seasoned student, there is a number of excellent general books and review papers describing fundamental features of plankton biology but there is a constant need for updating and revision as new principles and hypotheses become established.

I shall make no further attempt to justify the addition of yet another book to those already available. This volume is concerned mainly with the factors which determine the wax and wane of specific phytoplankton populations in standing freshwaters (lakes and reservoirs), though reference is made to marine plankton which is, generally, subject to similar controls. It is primarily intended for use by students, and I have therefore tended to oversimplify some of the more complex aspects of the subject, for the sake of ready comprehension, but further reading is recommended wherever suitable or relevant texts are available. I hope that I have adequately resisted the temptation to be unnecessarily encyclopaedic in referencing literature: there are many significant contributions that have not been cited.

Ecology is a complex science. There are probably almost as many definitions of 'ecology' as there are books on the subject. In framing this

ix



x Preface

text, I have adopted the phrase to which I was introduced as a would-be ecology student: 'What lives where – and why'. Specifically, I have endeavoured to develop this theme through an overview of the structure of planktonic communities in which the functional adaptations of pelagic life are emphasised, building up to the dynamic aspects of production and seasonal periodicity. Biochemical aspects of phytoplankton are not specifically covered and I have included no more physiological information than I have found necessary. Again, appropriate further reading is referenced.

The text could not have been prepared without the considerable help of a great many friends and colleagues. I am grateful for advice on the presentation and discussion of subject matter (often outside my primary interests) freely contributed by Dr G. Fryer, F.R.S., Mr T. I. Furnass, Dr D. G. George, Dr G. H. Hall, Dr S. I. Heaney, Dr J. Hilton, Mr J. E. M. Horne, Mr G. H. M. Jaworski, Dr J. G. Jones, Dr J. W. G. Lund, F.R.S., Dr J. F. Talling, F.R.S. and Dr L. G. Willoughby. The excellence of the Freshwater Biological Association's comprehensive library facilities proved to be extremely beneficial to my background reading and literature searches; it is a pleasure to express my appreciation to the Council, Director and Library staff of the Association.

I should like to thank especially: Dr Hilda Canter-Lund F.R.P.S., not only for the selection of her excellent collection of algal photomicrographs but also for the enthusiastic and time-consuming trouble she took over their presentation; Sheila Wiseman, whose collaboration and support during the preparation of the book has been invaluable, and whose illustrative talents contributed most of the text figures herein; and Elisabeth Evans, upon whom fell the almost impossible task of turning my handwritten pages into a legible typescript.

Finally, special acknowledgements are also accorded to Mr Charles Sinker, O.B.E., M.A., and to Dr John W. G. Lund, C.B.E., F.R.S., both of whom deeply influenced my appreciation of ecology in general and of phytoplankton in particular, during my formative years. The most that I could wish for is that, through the pages of this text, I may in turn pass on the benefit of their teaching to others.

The Ferry House, Ambleside, Cumbria January 1983

C. S. REYNOLDS