Ecological Studies, Vol. 129

Analysis and Synthesis

Edited by

Ecological Studies

Volumes published since 1992 are listed at the end of this book.

Springer-Verlag Berlin Heidelberg GmbH

Tom Andersen

Pelagic Nutrient Cycles

Herbivores as Sources and Sinks

With 90 Figures and 16 Tables

Springer

Dr. Tom Andersen
Department of Biology
University of Oslo
P.O. Box 1069
Blindern
0316 Oslo, Norway

ISSN 0070-8356

Library of Congress Cataloging-in-Publication Data
Andersen, Tom, 1955-
Pelagic nutrient cycles : herbivores as sources and sinks / Tom
Andersen.
p. cm. - (Ecological studies, ISSN 070-8356 ; v. 129)
Includes bibliograhical references (p.) and index.

1. Nutrient cycles. 2. Food chains (Ecology) 3. Herbivores–
Food. I. Title. II. Series.
QH344.A53 1997
577.7 ´16–dc21 96-49478

ISBN 978-3-642-08279-5 ISBN 978-3-662-03418-7 (eBook)
DOI 10.1007/978-3-662-03418-7

Originally published by Springer-Verlag Berlin Heidelberg New York in 1997.
Softcover reprint of the hardcover 1st edition 1997

Cover Design: D & P Heidelberg
Typesetting: Camera ready by Dr. Kurt Darms, Bevern
SPIN 10533576 31/3137 5 4 3 2 1 0 - Printed on acid free paper -

Foreword

While ecology is one of the scientific disiplines that most clearly belongs to "basic research", it also strives to serve as a predictive tool for management. Outstanding examples of predictive ecology are Vollenweider's models on the relationship between phosphorus load and water renewal time of lakes, and the resulting algal biomass. The needed few and easily accessible input parameters to very simple models provided a direct link from basic ecology to management, and today these models are key tools for managers worldwide to control lake eutrophication and algal blooms.

The baseline of this success is the general relation between phosphorus concentration and phytoplankton biomass that is observed for most lakes. While these relationships are most frequently presented in log-log diagrams, the aquatic ecologist who replots these a linear scale may ask himself why, in spite of the overall correlation, there is still such a variability. It is possible to predict levels of algal biomass that may be synthesized at a given phosphorus load. Some lakes apparently offer optimal conditions for their phytoplankton communities, while others may support less than half the biomass at the same phosphorus load. There are limits to growth, however, and the predictive outcome of phosphorus load decreases as the load increases. This holds in particular for the higher trophic levels like zooplankton and fish. With increased enrichment there are signs of decreased efficiency of energy transfer between foodweb compartments. Moreover, system stability tends to decrease with increased load, and beyond some undefined, probably highly site-specific limits, further enrichment may cause decreased productivity at higher trophic levels. This "paradox of enrichment", as Rosenzweig (1971) labelled it, is a central theme of this book. To resolve these matters, we need to go beyond large-scale predictive models, and examine in more detail foodweb dynamics and its relationship to nutrient cycling and ecosystem stability. First of all, we need to know some of the basic, ecological features of the organisms in question. Predictive modelling without reliable inputs would be like constructing a city plan without knowing the basic demands of the people.

Daphnia is the highly appreciated key component in freshwater ecosystems. This tiny crustacean water flea is instrumental for grazing, nutrient recycling and transfer of energy to higher trophic levels. It is the obvious choice for modelling purposes, not only because it is a good mediator of high trophic efficiency, but also because there is a long tradition of ecophysiological studies on these organisms that provide reliable input parameters. In logical model development, the foundation in terms of the basic lifeand death parameters for the central actors, *Daphnia*, algae, and bacteria, is set before the first act is played. The main theme is then elaborated further through increasing model complexity in the subsequent acts.

The play metaphor is in the spirit of A. J. Lotka, who in his pioneering work from 1925, first attempted to merge nutrient cycling and stoichiometric arguments into basic ecology. Actors and the scene as well are made of the same stuff that recycle over and over again in the great theatre of life. This early attempt was largely neglected, due partly to purely practical reasons. It this book, however, the author pays an enlightening revisit to Lotka's ideas by incorporating stoichiometric concepts in his models, clearly demonstrating how vital they are to productivity and foodweb structure. Recent models incorporating stoichiometric considerations in food-web studies show that the transfer of energy in terms of carbon from autotrophs to higher trophic levels may be governed by food quality in terms of element ratios. When food is high in C relative to other essential elements like nitrogen and phosphorus, excess C simply "goes to waste". The application of the Liebig minimum principle, also for the heterotrophs, is a new way of predicting "trophic efficiency" in food webs. In a prey-predator scheme, these stoichiometric applications, when isocline analysis is carried out, show a new, paradoxically stable state with zero predator (grazer) biomass at high algal biomass, when the algae are too P-deprived to support zooplankton growth. Such qualitative predator defences should attract attention from all those working with prey-predator systems.

However, intriguing they may be to a theoretical ecologist, we should, as always, ask whether these models have any bearing on predictions at the ecosystem level. They have indeed. In this book, these aspects are explored, not merely as a performance of single actors, but as an examination of the play in a more complete context. With a stepwise logical argumentation for parameter inputs, the author creates a toolbox of submodels, allowing him to judge Rosenzweig's axiom on less subjective grounds than most other people. The data do indeed provide evidence for reduced grazer (*Daphnia*) success, instability and chaotic ecosystem behaviour beyond a certain enrichment threshold; enrichment thus decreases predictability. There is a lesson to be learned from these exercises, not only for aquatic ecologists but for all those dealing with herbivore impact on ecosystems, and the impact of enrichment. Through a clear line of reasoning, we are guided on a very visible path all the way from large-scale processes such as phosphorus loading, lake hydrology and dilution rate, via species' physiology, to cellular processes and back to a better understanding of other large-scale processes like foodweb "efficiency" and ecosystem stability.

Oslo, January 1997 Dag O. Hessen

Preface

How can the tangled bank, in all its glorious, muddy complexity, be reduced to a set of antiseptic differential equations? To be fair, it isn't certain that it can; but to presume that we cannot hope to find general rules for the way nature works is to reduce every ecological interaction to a special case, to be marvelled at and then added to the vast rummage box of wonderful anecdotes and special cases.

John Lawton

Public concern about problems related to the eutrophication of inland waters reached a peak level in Norway in 1976, following the nuisance bloom of *Oscillatoria* in lake Mjøsa. Following the massive effort toward nutrient load abatement in this lake, an increasing need was felt for having better tools to determine what levels of nutrient input a given lake could tolerate without showing negative effects of eutrophication. Recent research at that time had indicated that much of the variability between lakes receiving similar nutrient loadings could be attributed to properties of pelagic food webs (Shapiro et al. 1975). Consequently, in order to increase the understanding of biological mechanisms involved in the eutrophication process, and to assess the potential for using biological control to improve water quality and increase the yield of harvestable production, the Royal Norwegian Council for Scientific and Industrial Research initiated a research programme on the eutrophication of inland waters. The Eutrophication Programme lasted for 10 years (from 1978 to 1988), involving more than 30 different researchers, resulting in more than 100 scientific papers, and 9 doctoral dissertations.

I had the good fortune of being engaged in the Eutrophication Programme for 2 years (from 1986 to 1988), together with some of the most creative and productive scientists in a new generation of European limnologists. The principal ideas that were conceived in this period are probably still among the major research topics of most of the scientists that were involved. The Eutrophicaton Programme was a scene of active cross-fertilization between the population-oriented approach of classical zooplankton ecology and the system-oriented approach of classical limnology. One of the main concepts resulting from merging these two fields was that the biomass of herbivores, as well as higher trophic levels, must be recognized as significant components of the pelagic nutrient budget. This means that the nutrient household of lakes cannot be considered independently of the trophic structure of the pelagic community, and also that pelagic foodweb structure is closely connected with nutrient supply.

Another key idea developed under the Eutrophication Programme was that nutrient regeneration is an elementary mass balance governed by the differences in element compositions between the grazer and the food it consumes. Although this mass balance approach was introduced and developed in several practically oriented publications (Olsen and Østgaard 1985; Olsen et al. 1986b; Andersen and Hessen 1991), it was felt that there was also an important theoretical potential of this simple and powerful concept. This book has grown out of the difficulties encountered with trying to fully release this potential within the space constraints of scientific journals.

While this book is written in terms of the antiseptic differential equations of theoretical ecology, it is still hoped that it may strike a balance so that it may serve a dual purpose of introducing some of the powerful techniques of mathematical biology to the field ecologist, and some of the contemporary problems in aquatic ecology to the theorist. Although simple models are emphasized throughout this work, some readers might still find the notation to be quite complex at times. As a help and reference to the reader, every chapter therefore contains a list of all symbols used in the presentation, together with definitions and relevant units. Some of the arguments used in this work are based on concepts that might be unfamiliar to the less mathematically inclined. In order to make the presentation more accessible to the general reader, some of the more technical parts have been placed in separate appendices that can be omitted in a casual reading, hopefully without the main ideas being lost.

Many of the ideas presented here resulted from collaborations with other scientists involved in the Eutrophication Programme. I am especially grateful for the continual inspiration and encouragement given by my good friends and coworkers, Dag Hessen, Anne Lyche, Yngvar Olsen and Olav Vadstein. I would also like to thank Arne Jensen, Eystein Paasche and Helge Reinertsen for the ways in which they must have influenced the course of events at times most critical to the completion of this work. Dag Hessen, Anne Lyche, Yngvar Olsen, Eystein Paasche and Tron Frede Thingstad, as well as the series editor, Ulrich Sommer, kindly provided constructive criticism and helpful suggestions on earlier drafts.

The writing of this book was supported by scholarships from the University of Oslo, the Royal Norwegian Council for Scientific and Industrial Research and the Norwegian Research Council. I dedicate it to my wife, Karin, and our children, Katrine and Tone, who patiently endured the intrusion into domestic life represented by the writing of this book.

Oslo, January 1997 Tom Andersen

Contents