Ecological Studies

Analysis and Synthesis

Edited by

Volume 38

The salt marshes of Sapelo Island, with the Duplin River in the foreground.

The Ecology of a Salt Marsh

Edited by
L.R. Pomeroy and R.G. Wiegert

With 57 Figures

Springer-Verlag
New York Heidelberg Berlin

Lawrence R. Pomeroy
Richard G. Wiegert
University of Georgia
Department of Zoology
Institute of Ecology
Athens, Georgia 30602
U.S.A.

Library of Congress Cataloging in Publication Data
The Ecology of a Salt Marsh

(Ecological studies; v. 38)
Bibliography: p.
Includes index.
1. Tidemarsh ecology. I. Pomeroy, Lawrence R., 1925-
II. Wiegert, Richard G. III. Series.
QH541.5.S24E26 574.5'2636 80-29676 AACR1

ISBN-13: 978-1-4612-5895-7 e-ISBN-13: 978-1-4612-5893-3
DOI: 10.1007/978-1-4612-5893-3

Softcover reprint of the hardcover 1st edition 1981

9 8 7 6 5 4 3 2 1

Foreword

Ecologists have two long-standing ways to study large ecosystems such as lakes, forests, and salt-marsh estuaries. In the first, which G. E. Hutchinson has called the *holological* approach, the whole ecosystem is first studied as a "black box," and its components are investigated as needed. In the second, which Hutchinson has called the *merological* approach, the parts of the system are studied first, and an attempt is then made to build up the whole from them. For long-term studies, the holological approach has special advantages, since the general patterns and tentative hypotheses that are first worked out help direct attention to the components of the system which need to be studied in greater detail. In this approach, teams of investigators focus on major functions and hypotheses and thereby coordinate their independent study efforts. Thus, although there have been waves, as it were, of investigators and graduate students working on different aspects of the Georgia salt-marsh estuaries (personnel at the Marine Institute on Sapelo Island changes every few years), the emphasis on the holological approach has resulted in a highly differentiated and well-coordinated long-term study.

Very briefly, the history of the salt-marsh studies can be outlined as follows. First, the general patterns of food chains and other energy flows in the marshes and creeks were worked out, and the nature of imports and exports to and from the system and its subsystems were delimited. Next, a number of general hypotheses were formulated and subsequently tested by detailed studies of key components, studies designed to prove or disprove the general hypotheses. This approach lent itself naturally to experiments and modeling, and efforts along these lines dominated studies for the next decade or so. Finally, the group of investigators who were most active in the study in recent years got together to prepare a composite analysis of the salt-marsh estuary as an ecosystem and of the major populations that are most vital to its function. This volume is the result of that synthesis.

When Sidney Lanier sat under the oak tree on the edge of the Georgia marsh at Brunswick, in Glynn County, and wrote his well-known poem, "The Marshes of

Glynn," he was obviously very much impressed with the marsh grasses;

In a league and a league of marsh grass, waist high, broad in the blade,
Green, and all of a height, and unflecked with a light or a shade,
Stretch leisurely off, in a pleasant plain,
To the terminal blue of the main.
Oh, what is abroad in the marsh and the terminal sea?
Somehow my soul seems suddenly free
From the weighing of fate and sad discussion of sin,
By the length and the breadth and the sweep of the marshes of Glynn.

If Lanier had walked out into the marsh, as he may very well have done, he would have been impressed with two other major aspects of the marshes of Glynn—the powerful ebb and flow of brown tidal waters and the vast banks and flats of mud, which at low tide glisten golden in the sun due to the myriad diatoms and other living organisms which populate these sediments. These three major components, the marsh grass, the ever-moving water masses, and the soils and sediments, are bound together as a functional input-output ecosystem by the energy of the sun and the tides. It has taken the scientists at Sapelo Island some 30 years to partially answer Lanier's question, "What is abroad in the marsh?" and, we might add, the effect of the marsh on the "terminal sea" is even today not fully understood.

When the late R. J. Reynolds, Jr. invited the University of Georgia to begin studies at Sapelo Island in 1954, he set up a foundation to support these studies. There were sufficient funds at that time to hire three young PhD.s to form the core of a resident staff. It was only natural that we looked for persons with interest and expertise in each of the three major components of the ecosystem. Thus, we hired a zoologist-ecologist to study the food chains and related aspects of the marshes, a hydrologist-limnologist to investigate the water masses, and a microbiologist to study the golden mud. As it turned out, the early microbiological efforts were premature, since effective methods of studying microbial activities in such a complex and difficult situation as the marshes had not yet been developed. The conventional techniques that involve isolating organisms and culturing them in the laboratory are not by themselves sufficient for the study of natural ecosystems. Not until a dozen or so years later were techniques developed to study microorganisms *in situ* by measuring and assessing their products and their activities, rather than by counting or isolating the organisms themselves. It became evident in the early stages of the work that the microbial transformations of the primary production of grasses and algae are the key to the function of the Sapelo Island salt-marsh ecosystem, a system that is, in large measure, a detritus-based system, rather than the better understood grazing-based. If I were asked to single out the major contributions which our long-term studies at Sapelo Island have made to the general field of ecology, I would certainly rate the work in microbial ecology as being of a breakthrough variety.

It is with great personal pleasure and satisfaction that I introduce to you this synthesis of some 25 years of study on the marshes of Sapelo Island.

Eugene P. Odum

Preface

The organization of this volume and the research it synthesizes is testimony to our long-standing belief that the study of either macroorganisms or microorganisms in isolation from each other cannot yield a true synthesis of the structure and function of any ecosystem. Our goal is not only to conduct a balanced analysis of the roles of both the macrocommunity and the microbial community, but to understand how these communities interact. Because of the prominence of the detritus food web in salt marshes, that aspect of the interaction is quite evident. However, we find other, perhaps equally pivotal, interactions in the relationship of algae to their grazers and in the effects of both higher plants and higher animals on microbial communities of marsh soils. Therefore, we intend not to stress any single aspect of the salt marsh ecosystem for its own sake, or to only redress former oversights, but to present, in so far as possible, a balanced view of the system and how it works.

Through the use of a model of the flux of carbon through the salt marsh we achieved an efficient research plan and brought together the investigators who carried out the necessary interdisciplinary work. The choice of carbon was arbitrary. We could have worked with another element or in energy units. The choice of the kind of model, however, was important. Building the ecosystem model together, we became participants in the quest for missing pieces of the system as we perceived it. Throughout the process, the model continuously told us unexpected things about how the system might operate, and served both as a unifying force in our work and as an arbiter of balance in our approach. We studied not whatever struck the fancy of any one of us, but rather what modeling showed us to be potentially significant. The word *potentially* must be emphasized because the modeling process did not tell us how the system worked. We could only discover that by studying the real-world salt marsh, thereby validating, or invalidating the results of our modeling exercise. We proceeded in this way over six years, years which began and ended with modeling, but which were spanned by continuing interaction between simulated experiments and experiments in the real salt marsh.

The importance of good, basic, descriptive science to the success of an interdisciplinary study such as this can hardly be overstated. We began with the secure feeling that we were building upon an established description of the structure and function of the marshes and estuaries of Sapelo Island. Yet, the early results of our modeling almost immediately began to challenge our current beliefs. As a result, we repeated some measurements of such basic processes as photosynthesis, with results which did indeed alter our view of how the salt marsh operates.

Our study of the salt marsh developed in directions quite different from those taken by most other studies of highly stressed ecotones, such as rocky intertidal zones. Like the rocky intertidal, the salt marsh is hospitable to a limited set of species populations that clearly interact and coexist. Rather than focus solely on these interactions, however, we also looked at the salt marsh through the other end of the telescope, viewing the geological and physical setting and observing the chemical, biochemical, and biological processes within that setting. Viewed on this level, what we have seen is a system controlled to a great degree by its physical and chemical properties. Indeed, some of the most interesting and intricate population interactions proved to be the biochemical ones of the anaerobic microorganisms in the salt-marsh soil. Primary and secondary production are the biological processes which drive the system. We believe that a study of the salt marsh from this perspective produced a more complete and balanced analysis than would have been possible with a less extensive approach. We hope that this account may be of interest not only to salt-marsh ecologists but to others whose favorite ecosystem contains, albeit in different structural configurations, comparable controls and interactions.

Acknowledgments. The 20 years of research at Sapelo Island which laid the foundation for this work would not have been possible without the support of the late R. J. Reynolds, Jr., who not only provided financial aid but also accepted us as permanent guests on his plantation. The present work has enjoyed the continuing support of the Sapelo Island Research Foundation. The National Science Foundation supported the major portion of the work synthesized in this volume through the following grants:

DES72-01605 to L. R. Pomeroy and Dirk Frankenberg,
OCE75-20842 to L. R. Pomeroy and R. G. Wiegert,
GA-41189, OCE74-00148, and OCE77-26920 to W. M. Darley and D. M. Whitney.

Drawings and drafting were prepared by Rainer Krell.

Martha Hoak helped prepare the Index.

Finally, we wish to dedicate this volume to the permanent residents of Sapelo Island, who have been loyal friends and who have contributed in many ways to the success of this undertaking.

August 1980 L. R. Pomeroy
Sapelo Island, Georgia R. G. Wiegert

Contents

Contributors

BUNKER, S. M.	Chesapeake Bay Laboratory, Solomons, Maryland, U.S.A.
CHALMERS, ALICE G.	University of Georgia Marine Institute, Sapelo Island, Georgia, U.S.A.
CHRISTIAN, ROBERT R.	Drexel University, Philadelphia, Pennsylvania, U.S.A.
DARLEY, W. MARSHALL	Department of Botany, University of Georgia, Athens, Georgia, U.S.A.
DUNN, E. LLOYD	Division of Biology, Georgia Institute of Technology, Atlanta, Georgia, U.S.A.
GALLAGHER, JOHN L.	University of Delaware College of Marine Studies, Lewes, Delaware, U.S.A.
HAINES, EVELYN B.	University of Georgia Marine Institute, Sapelo Island, Georgia, U.S.A.
HALL, JOHN R.	U.S. Department of Commerce, NOAA, NMFS, Washington, D.C., U.S.A.
HANSEN, JUDITH A.	CSIRO Division of Fisheries and Oceanography, North Beach, Western Australia
HANSON, ROGER B.	Skidaway Institute of Oceanography, Savannah, Georgia, U.S.A.

IMBERGER, JÖRG	Department of Civil Engineering, University of Western Australia, Nedlands, Western Australia
KING, GARY M.	Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan, U.S.A.
MONTAGUE, CLAY L.	Department of Environmental Engineering Sciences, University of Florida, Gainesville, Florida, U.S.A.
PACE, MICHAEL L.	Department of Zoology, University of Georgia, Athens, Georgia, U.S.A.
PFEIFFER, WILLIAM J.	Department of Zoology, University of Georgia, Athens, Georgia, U.S.A.
SHERR, BARRY D.	Kinneret Limnological Laboratory, Tiberias, Israel
SKYRING, GRAHAM	Baas-Becking Geobiological Laboratory, Canberra, Australia
WETZEL, RICHARD L.	Virginia Institute of Marine Sciences, Gloucester Point, Virginia, U.S.A.
WHITNEY, DAVID M.	University of Georgia Marine Institute, Sapelo Island, Georgia, U.S.A.
WIEBE, WILLIAM J.	Department of Microbiology, University of Georgia, Athens, Georgia, U.S.A.