Published by the Press Syndicate of the University of Cambridge
The Pitt Building, Trumpington Street, Cambridge CB2 1RP
32 East 57th Street, New York, NY 10022, USA
10 Stamford Road, Oakleigh, Melbourne 3166, Australia

© Cambridge University Press 1985

First published 1985

Library of Congress Cataloging in Publication Data
(Revised for vol. 4)
Main entry under title:
Handbook of phycological methods.
Vol. 2-4 published by Cambridge University Press,
Cambridge, New York.
Includes bibliographies and indexes.
Contents: [1] Culture methods and growth measurements,
methods, edited by J. A. Hellebust and J. S.
edited by Mark M. Littler and Diane S. Littler.
1. Algology – Methodology – Collected works. I. Stein,
Janet R. II. Hellebust, J. A. III. Phycological
Society of America.
QK565.2.H36  589.3’028  73-79496
ISBN 0 521 20049 0 hard covers  0 521 29747 8 paperback (v. 1)
ISBN 0 521 21855 1 (v. 2)
ISBN 0 521 22466 7 (v. 9)
ISBN 0 521 24915 5 (v. 4)

Transferred to digital printing 2003
# Contents

Contributors *page* viii  Editors’ preface *page* xi

Introduction *page* 1

## I ENVIRONMENTAL SAMPLING AND MONITORING (MAJOR PARAMETERS)

1 Water motion 7  
*Mark W. Denny*

2 Light 33  
*J. Ramus*

3 Nutrients 53  
*Patricia A. Wheeler*

## II ASSESSMENTS OF POPULATIONS AND COMMUNITIES

4 Collection, handling, preservation, and logistics 67  
*Roy T. Tsuda and Isabella A. Abbott*

5 Electrophoresis 87  
*Donald P. Cheney*

6 Natural products chemistry: uses in ecology and systematics 121  
*James N. Norris and William H. Fenical*

7 Destructive (harvest) sampling 147  
*Robert E. De Wreede*

8 Nondestructive sampling 161  
*Mark M. Littler and Diane S. Littler*

9 Remote sensing and mapping 177  
*T. Belsher, L. Loubersac, and G. Belbeoch*

10 Subtidal techniques 199  
*Michael S. Foster, Thomas A. Dean, and Larry E. Deysher*
Contents

11 Equipment for conducting research in deep waters 233
   Sylvia A. Earle

12 Demography 251
   A. R. O. Chapman

13 Succession 269
   Michael S. Foster and Wayne P. Sousa

14 Biomechanics 291
   M. A. R. Koehl and Stephen A. Wainwright

15 Biogeographical analyses 315
   Louis D. Druehl and Robert G. Footit

III ECOLOGICAL ENERGETICS

16 Respirometry and manometry 329
   Clinton J. Dawes

17 Electrodes and chemicals 349
   Mark M. Littler and Keith E. Arnold

18 The carbon-14 method for measuring primary productivity 377
   Keith E. Arnold and Mark M. Littler

19 Measurement of photosynthesis by infrared gas analysis 397
   John A. Browse

20 Carbon allocation 415
   Richard G. Buggeln

21 Open-flow systems 427
   Donald W. Kinsey

22 Growth patterns and rates 461
   Boudewijn H. Brinkhuis

23 Calorimetry 479
   Thomas H. Carefoot

24 Nutrient uptake 493
   Marilyn M. Harlin and Patricia A. Wheeler

IV BIOLOGICAL INTERACTIONS

25 Competition among macroalgae 511
   E. J. Denley and P. K. Dayton

26 Herbivory 531
   Robert L. Vadas

27 Pathology 573
   John H. Andrews and Lynda J. Goff
Contents vii

V APPENDIX

List of suppliers 595

VI INDEXES

Author 601
Taxonomic 616
Introduction

Marine macroalgae are a diverse group of organisms that have evolved an astounding variety of life histories, external morphologies, internal anatomical features, biochemical constituents, and metabolic activities. Although most macroalgae are restricted to a relatively small portion of the world’s oceans, their concentrated biomass, high primary productivity, and role in coastal detrital and herbivore food webs make them important contributors to continental borderlands, deep sea benthic communities, and planktonic ecosystems. Yet despite their ecological significance and diversity, macroalgae have been largely overlooked as experimental organisms for the examination of selective forces that may not be operable or obvious in terrestrial and planktonic habitats or that may not have been considered in the predominantly animal-oriented studies of benthic marine systems. This treatment is especially timely because of recent technological advances and an increased awareness of the potentialities and amenability of macroalgal systems to innovative ecological experimentation.

Because of space constraints, the individual chapters are not intended to be comprehensive. References to more technical and specialized methods have been provided by all authors. The diverse audience for whom this volume is intended includes novice as well as seasoned researchers. In general, each section is concerned primarily with the method itself rather than its theoretical or historical development. Modern ecological research represents a quantitative discipline designed to produce statistically sound data bases, which are beyond the capabilities of subjective visual surveys, arbitrary scales, and other anecdotal procedures. Consequently, such approaches are not included in this handbook. The procedures presented here, although state of the art, usually are quite project specific and should be utilized as a guide and modified according to the questions being asked, resources available, and systems used. All have room for further development and improvement depending on the individual need, local circumstances, and backgrounds of those using the techniques.

An attempt has been made to present the methods in a reasonably consistent fashion; however, because the subject matter is not uni-
form, natural variations in content and format are to be expected. Inconsistencies occur among authors in controversial nuances of technique (e.g., optimal temperatures for obtaining dry weights), and some redundancies have been retained to avoid cumbersome cross-referencing. In most cases, the authors have described the limitations of the various techniques and have included references and discussions of how procedures may be adapted to suit various habitats, different algal systems, or other conditions.

Creativity and originality are essential to the experimental field ecologist. Consequently, we thought that a constraining format structure requiring either a "how to" viewpoint, literature survey approach, or theoretical/philosophical perspective, for example, might unnecessarily restrict the potential quality of the authors' contributions. Therefore, to the benefit of all concerned, a spectrum of appropriate tactics was encouraged to various degrees. The content ranges from stepwise descriptions of routine and standardly applied techniques to pioneering methods that are still in a rapid state of conceptual or technological development. Most of the procedures are readily adaptable for general use by the majority of scientists, whereas others require considerable sophistication, are still prohibitively expensive in their application, or have significant future potential.

In recent years there has been a dramatic advance in benthic algal ecology owing largely to the synthesis of traditional and empirical (i.e., observational and correlative) approaches and mechanistic or causative (i.e., experimental) studies, although vital, descriptive studies dominated previous research on algal ecology. Philosophically, this is an important point, because the products of such studies are usually empirical correlations based on habitat- or organism-oriented descriptions that are too often repeated from one algal system to another. We do not hesitate to emphasize that no good substitutes exist for thorough understanding of natural history based on careful field observations. The importance of preceding and supplementing experimental work with a generous amount of descriptive information and common sense should be underscored. Furthermore, ecological research frequently requires time spans of more than one cycle of seasons so that unusual macro- and microclimatic fluctuations will not exert a disproportionate influence on the outcome or interpretations.

However, properly controlled, experimental, hypothesis-testing approaches that lead to predictive understandings of causal phenomena generally have been relatively few, although the number of such studies on biological interactions is increasing rapidly. Manipulative investigations are leading to improved theory at the physiological,
populational, and community levels. Many significant advances, concerning algal growth, productivity, distribution, succession, and especially algal–algal and algal–animal interactions, have been forthcoming from experiments and controlled perturbations performed under natural field conditions.

Another reasonable approach, which recently has garnered renewed attention, involves searching for convergent evolutionary patterns within macroalgal systems by indirect means, taking advantage of natural experiments, successional events, or developmental sequences. This technique has been designated "postdictive," rather than predictive, since the focus is on attempting to decipher the events of the past leading to present results. However, this viewpoint does contain a strong element of prediction, because hypotheses are generally of the form, "If selection has acted in the following way over evolutionary time, then we would expect nature to have the following structure."

In addition, important methodological developments have resulted in the acquisition of new information, greater standardization, and improved consistency. The recognition of the importance of both physiological stress and physical disturbance has led to major advances in our ability to understand the effects of natural and anthropogenic factors on seaweed community function, stability, and diversity. General ecological theory is becoming increasingly influenced and revitalized by studies of macroalgal ecology, and a broader awareness of the amenability and advantages of seaweeds as experimental systems for the elucidation of ecological and evolutionary mechanisms promises exciting prospects for the future. The methodology included herein contains considerable potential for developing approaches that will shed new light on ecological and evolutionary processes that may be quite widespread throughout the vast oceanic realm of the biological world. Recognition of the great importance of macroalgae as ecological research tools and their roles in marine ecosystems is long overdue.