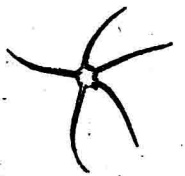
Marine Ecology

MOORE



Marine Ecology

HILARY B. MOORE

Professor of Marine Ecology
and Assistant Director Marine Laboratory
University of Miami

Research Associate
Woods Hole Oceanographic Institution

NEW YORK · JOHN WILEY & SONS, INC.
London · Chapman & Hall, Ltd.

Copyright © 1958, by John Wiley & Sons, Inc.

All rights reserved. This book or any part thereof must not be reproduced in any form without the written permission of the publisher.

Library of Congress Catalog Card Number: 58-10807

Printed in the United States of America

Preface

ECOLOGY IN RELATION TO OTHER SCIENCES

The science of ecology embraces all aspects of the interrelations of organisms and their environment, and since the organisms themselves are part of the environment, their own interrelations form part of the study. A field as broad as this of necessity makes contact with many other sciences. Within the limits of marine ecology as defined here, the ecologist is concerned with physical and chemical oceanography as well as with meteorology and marine geology in describing and explaining the physical and chemical aspects of the environment. He is concerned with physiology and animal behavior in understanding the reactions of the organisms to particular conditions. Taxonomy plays a vital role in defining the species, races, etc., with which he is dealing, and itself receives help from ecology in explaining problems of speciation and race formation. Biochemistry and biophysics similarly interlock with ecology, whereas mathematics, and particularly statistics, comprises a vital section of ecological studies. The list

might obviously be extended further, but the point is already clear that this is no compact entity, self-sufficient, but rather a meeting place of many sciences.

Ecology in general has been surveyed in various texts, perhaps the most comprehensive of which, at least from the point of view of animals, is *Principles of Animal Ecology*, by Allee et al. (1949). Unfortunately, there is no such comprehensive treatment of the special field of marine ecology, which comprises, usually, only a minor portion of most general works. This minor role is understandable, since so many general principles of ecology can be best illustrated by land or fresh-water examples, and these two habitats are more accessible to the majority of students than is the ocean. There is, nevertheless, an extremely extensive literature pertaining to marine ecology, although widely scattered in different journals. In attempting to bring this together into a coherent book, there at once arises the problem of how much to include, and decisions are the more difficult with so many sciences contributing to the wide field of ecology.

It is intended that this book shall be of use to students of marine science. Already available to them are such texts as *The Oceans* by Sverdrup et al. (1946), Harvey's *Recent Advances in the Chemistry and Biology of Sea Water* (1945), and many others, and it seems unnecessary to duplicate what is well treated in them, simply for the sake of completeness in the present volume. It is sufficient to give references that will enable the student to locate such material when needed. It must be stressed, however, that ecology is concerned not merely with the environment as it affects the organism. Ecology must equally embrace the effects of the organism on the environment. A recently published treatise on marine palaeoecology* comes closest to covering the field, and includes both authoritative articles by a number of different authors and very valuable bibliographies.

SOURCE MATERIAL IN RELATED FIELDS

Throughout subsequent chapters, references will be found to source material from which the student may follow up lines of interest in greater detail than can be given here. Where possible, these have been chosen to include good bibliographies on the subject. Also, those written in English have been chosen wherever possible, and this certainly requires justification. A general text of this type should

* J. W. Hedgepeth, (Editor) (1957). Treatise on marine ecology and palaeoecology. Vol. I. *Geol. Soc. Am., Mem. No. 67*, 1-1296.

此为试读，需要完整PDF请访问：www.ertongbook.com

be as world-wide in application as possible. The research on which it is based has been carried out in many countries and described in various languages. It will, however, be read, in all probability, by more English-speaking students than any others, and unfortunately they are notoriously poor linguists. Additional reading, based on the bibliography, will, then, undoubtedly meet the needs of the greatest numbers if it is mainly in English, at least when an alternative exists. This is a deliberate selection, and in no way reflects the value of the work of other countries. It cannot be too strongly stressed, though, that the student who reads only in his own language must realize the wide field which he is missing thereby, and the unbalanced outlook which he must inevitably have.

A work such as this is largely a compilation of the work of others, and adequate acknowledgment should cover all those whose names appear in the bibliography. Even this would be inadequate, since so much selection has been necessary and so much important work has had to be omitted. I am deeply indebted to Dr. J. A. Kitching without whose collection of references and abstracts the work would hardly have been possible. Dr. Gunner Thorson and Dr. D. P. Wilson have read the manuscript and offered a wealth of suggestions. Dr. W. R. Taylor not only helped with suggestions but also provided the classification of the algae in the appendix. Among the many others who have helped with suggestions and criticism, particular mention should be made of Dr. G. L. Clarke, Dr. C. P. Idyll, Mr. R. M. Ingle, Dr. B. H. Ketchum, Dr. A. C. Redfield, Dr. F. G. W. Smith, and a succession of students at the Marine Laboratory of the University of Miami. To all these, as well as to those authors and publishers who have given permission for the reproduction of text figures, I wish to express my great indebtedness.

HILARY B. MOORE

June 1958

Contents

1

Introduction

LITERATURE

In the opening section of Allee et al., *Principles of Animal Ecology* (1949), two chapters are devoted to the history of animal ecology. Although much of this material is non-marine, it also includes many marine works and covers the subject so fully that there seems little call to repeat it here. This work, incidentally, has 71 pages of bibliography which will prove invaluable to the student in search of further information on animal ecology. Gislén (1930) in his Epibioses of the Gullmer Fjord gives a very comprehensive bibliography of work on marine ecology up to that date, and Fischer-Piette (1940) has brought this further up to date for the intertidal region. Hesse's *Tiergeographie auf oekologischer grundlage* (1924), Hesse Allee, and Schmidt's *Ecological Animal Geography* (1951), and Ekman's *Zoogeography of the Sea* (1953) contain a wealth of additional material. A treatise on marine ecology and palaeoecology, to be published by the Geological Society of America, is now being prepared.

Flattely and Walton's *The Biology of the Sea Shore* (1922) is a work which, in its field, has not yet been superseded. In the field of marine biology, more recent works which will be invaluable to the student include Russell and Yonge's *The Seas* (1936) and Yonge's *The Sea Shore* (1949), Wilson's *Life of the Shore and Shallow Sea* (1951) and *They Live in the Sea* (1947), MacGinitie and MacGinitie's *Natural History of Marine Animals* (1949), and Buchsbaum's *Animals without Backbones* (1938). In all these, though, the more accessible shores have received the most attention, with progressively smaller space devoted to the less accessible ocean waters. For these the student must turn to sections of more general works such as Murray and Hjort's *The Depths of the Ocean* (1912) and Sverdrup et al. *The Oceans* (1946). For deeper water, two excellent books are Hardy's *The Open Ocean* (1956) and Marshall's *Aspects of Deep Sea Biology* (1954). Even with all these to draw on, we have no comprehensive work to turn to for the biological side of marine ecology, and the student will be forced to track down his facts laboriously through an extensive literature of more specialized and limited works.

Most books on marine biology are based mainly on the fauna and flora of a relatively small area. This can be very discouraging for the occupant of a region which shares few species in common with that of the book. It is true that a large proportion of the earlier work in this field has centered around the Naples laboratory and the various northern European laboratories, and later the laboratories on the northeast coast of the United States and on the California coast. More recently, though, much ecological work has been done in South America, South Africa, Japan, Australia, and elsewhere, and it seems proper to choose illustrations from as wide a field as possible, if a general point of view is to be obtained. This introduces the difficulty that most of the names of plants and animals referred to will be strange to all but the specialist. To meet this difficulty, a partial classification of the plant and animal kingdoms is given in an appendix; here all genera referred to in the text can be located.

Although some ecological research can make use of gross analyses of the total quantity of animal or plant material present in a region or being produced in it, still most of the work calls for a detailed knowledge of the species concerned. It is perhaps in this aspect, more than in any other, that ecology has lagged behind other sciences in mechanization. Modern oceanography has accelerated its routine by using such time-saving devices as the bathythermograph, the geomagnetic electrokinetograph, the echo sounder, and the salinity-tem-

此为试读,需要完整PDF请访问: www.ertongbook.com

perature-depth recorder, to mention only a few. All have reduced enormously the time needed to make certain field observations and to interpret them in the desired form. Biochemistry, biophysics, and physiology have likewise accelerated many of their methods. Yet ecologists are still faced, in so many cases, with laborious sorting and identification of individual specimens. In the laboratory, they may be able to work with unispecific cultures and estimate their changing population density photometrically. In the field, such simplification is rarely possible.

The ecologist must, then, be able first to identify his material with certainty and then, having established the species with which he is concerned, to sort it with the least possible consumption of time. Where primary identification is concerned, he may usually submit material to specialists in that particular field, although these, even when available, usually have a heavy accumulation of similar material already awaiting their attention. Even with a named set of material available, the ecologist still requires good taxonomic training to be sure that his own later identifications are correct. To many non-taxonomists, the specialist often appears unjustifiably concerned with the erection of new subspecies and races. There is a purpose in this, however, which has very real significance to the ecologist. What today are considered as two subspecies may one day be more properly separated into distinct species. Ecologically, these may prove to be widely different. If this happens, earlier ecological work may prove valueless if it has not been made clear at the time with precisely what form the work was done. An example at the time of writing can be seen in the copepod *Calanus*. Prior to a few years ago, much classical work was done on *C. finmarchicus*. It now appears that this must be distinguished from *C. helgolandicus*, and it has not always been possible to refer back to preserved material to see which species was included in the earlier work (Russell, 1951).

To attempt to indicate available taxonomic literature is out of the question. For workers in the older marine laboratories there are usually available extensive fauna and flora lists such as the *Plymouth Marine Fauna* (Marine Biological Association, 1931), "A Biological Survey Of The Waters Of Woods Hole and Vicinity" (*Bull. U.S. Bur. Fisheries*, 1913), and "Manx Algae" (Knight and Parke, 1931). The bibliographies quoted in these usually afford an excellent starting point. For a few groups there are world-wide monographs (e.g. Mortensen's *A Monograph of the Echinoidea*, 1928–1950) or ones of wide application (e.g. the journal *Johnsonia* for east coast American molluscs), and the *Fiches d'Identification du Zooplankton* published

by the International Council in Copenhagen. All too few groups have, however, been treated in this way, and for many parts of the oceans neither species lists nor comprehensive works exist. Descriptions of oceanic plankton and nekton, in particular, are largely confined to the various expedition reports concerned. Unfortunately, complete sets of these reports are not always readily accessible. The ecologist who must be able to recognize a wide array of species, particularly if he is to work in a region remote from a long-established marine laboratory, is faced with a difficult taxonomic problem. A long time delay may be involved before all his species have been identified, and early work may be invalidated by delay in distinguishing various species present. Nevertheless, the success with which the problems can be met may be seen in the teamwork of the members of the Great Barrier Reef expedition or of Stephenson and his coworkers in South Africa.

The embryology and life history of the organisms studied is a field in which even less information is available to the student. There are excellent textbooks of invertebrate embryology, such as *Textbook of Embryology* by MacBride (1914) and Dawydoff's *Traité d'embryologie comparée des invertébrés* (1928), and algal life histories are covered in such general texts as Smith's *Manual of Phycology* (1951) and Fritsch's *The Structure and Reproduction of the Algae* (1935, 1945). Nearly all the examples included, though, are selected types, usually from a limited region of the ocean. Even for such classical areas as Naples, Plymouth, or Woods Hole, the life history of only a small percentage of the local species is known. For most of the fauna and flora of the oceans, information on life histories is negligible. As with general marine biology, few comprehensive works exist. Probably for no other area is there a review as comprehensive as Thorson's "Reproduction and Larval Development of Danish Marine Bottom Invertebrates" (1946a). The latter work, incidentally, provides a valuable starting point in tracing further literature on particular forms, as well as containing a very extensive survey of the ecology of the larvae. A few comprehensive works on particular groups are available, such as Gurney's "Larvae of Decapod Crustacea" (1942) and Mortensen's "Contributions to the Study of the Development and Larval Forms of Echinoderms" (1931–1938), but these are the exception and the available literature is in general widely scattered. For most marine organisms, the life histories are still unknown.

There is no adequate textbook of physiology of marine invertebrates. Perhaps the most useful is *Comparative Animal Physiology* by Prosser

et al. (1950), which has a particularly good bibliography. For the physiology and ecology of marine algae, there are sections in Smith's *Manual of Phycology* (1951) and Chapman's *An Introduction to the Study of Algae* (1941). With a few exceptions, marine organisms have been used by physiologists as convenient material for studying particular reactions rather than for the purpose of understanding the particular organism itself. This is of course true, though probably to a lesser extent, of other aspects of ecology. From the ecologist's point of view, though, it has had the unfortunate result of yielding an unbalanced picture. There is a tremendous wealth of knowledge concerning the physiology of the sea urchin egg, for example, but little is known about the adult sea urchin. Certain aspects of physiology have received more widespread treatment, of course. Examples may be found in Yonge's work on invertebrate digestion, that on respiratory pigments, done by various workers, etc. Again particular animals of economic importance, such as oysters, *C. finmarchicus,* etc., have been studied from many points of view. Once again, though, the ecologist is faced with the fact that if information is sought on the physiology of a particular species, the chances are very high that nothing is known about it.

The behavior of marine organisms has received some study, and the results are, on the whole, more immediately applicable ecologically than those of other fields so far discussed. The diurnal migration of zooplankton has yielded excellent material for the study of phototropic and geotropic reactions. The complex conditions in the intertidal zone have led to the examination of similar reactions in its inhabitants as well as of their reactions to desiccation, etc. Fish have been studied with regard to their schooling behavior, their ability to "learn," and their sensitivity to different stimuli. Although, again, no one book summarizes such information, reference may be made to Fraenkel and Gunn's *The Orientation of Animals* (1940), and "Physiological Mechanism in Animal Behaviour" (Society for Experimental Biology, 1950).

Turning from the organisms themselves, to the environment in which they live, we find a more encouraging series of texts available. Murray and Hjort's *The Depths of the Ocean* (1912) represents a landmark in the history of our knowledge of both the chemistry and physics of sea water. *The Oceans,* by Sverdrup et al. (1946) surveys the knowledge 60 years later. Three books by Harvey, *Biological Chemistry and Physics of Sea Water* (1928), *Recent Advances in the Chemistry and Biology of Sea Water* (1945), and *The Chemistry and Fertility of Sea Water* (1955) are also invaluable. Day (1951) gives

an extensive discussion and bibliography of estuarine conditions. In most of these, oceanic waters tend to be more adequately covered than inshore ones, particularly those bathing the intertidal zone and those in estuaries. For these, reference must be made to individual papers. Tides, which comprise an important ecological factor near shore, are covered by Darwin (1898) and more recently by Russell and MacMillan (1952).

Meteorology impinges somewhat less on marine ecology, at least less directly. Sverdrup's *Oceanography for Meteorologists* (1943) contains some useful data not given in Sverdrup et al. (1946). On the whole, the ecologist most often finds his contact with meteorology limited to a study of weather records which are available in various government publications of different countries.

The influence of the organism on the environment has perhaps received more attention in geology than in any of the other sciences bordering on ecology, although it is true that, in a large proportion of cases, the organisms are most important geologically after they are dead. This is true of those sedimentary rocks formed largely from a rain of dead plankton, as well as for the oil content of some such deposits believed to have a similar origin. It is as true for rocks formed from ancient coral reefs, or dominated by fossil crinoids. On the other hand, much of both the cementation and the breakdown of intertidal and shallow water rocks may be due to the activities of living plants and animals, and both the consolidation of sediments into coarser fecal masses and their attrition may be due to passage through animal guts.

Such geological aspects of ecology are treated in many geological textbooks. The more limited subject of marine geology has been well surveyed in Kuenen's *Marine Geology* (1950), and Shepard's *Submarine Geology* (1948), and from them such special aspects as coral reef formation may be traced. Because of the economic importance of oil, the sediments in which it occurs have received very intensive study, as have the conditions under which such sediments accumulate. For an introduction to the field, Landes (1951) and Cloud (1952) may be mentioned of many others. Yet another aspect is found in paleoecology and in the attempt to deduce the nature of extinct environments from the known present-day requirements of the fauna and flora, or of their nearest living relations. Where recent species occur in the deposits, fairly valid conclusion about climate may be drawn, but when all the species have changed, such deductions must be made more cautiously; however, plants can hardly have grown, at any time, at a much greater depth than they do today, and the same is probably

true of the reef corals, with their contained zooxanthellae. In this and similar ways, a comparatively accurate picture may be drawn of environmental conditions in previous eras. These are likely to be very greatly reinforced by the techniques now being developed, for the radioactive determination of both the age of fossils and the temperature at which some of their constituents must have been layed down (Urie, 1948; Urie et al., 1951).

This brief survey has been intended to point the way to additional sources of information for those who wish to explore particular fields in greater detail than is possible here. The bibliographies contained in the various works referred to should provide sufficient guides for these fields. Finally, the student is recommended to consult the ecology section, and particularly its oceanography subdivision, in *Biological Abstracts*, and the bibliography in *Journal du Conseil*. Further information may be found in the succeeding reference to ecological methods.

AUTECOLOGY AND SYNECOLOGY

During its evolution, ecology has tended to concentrate on two approaches to its problems. On the one hand there has been the study of the species as a unit, with an endeavor to arrive at as complete an understanding as possible of the internal and external relationships of one kind of animal or plant. This has come to be known as autecology. Rather sharply differentiated from this approach is synecology in which the unit studied is more complex. There we are concerned with communities, usually embracing many species of both animals and plants but characterized by the predominance of certain particular species. Unfortunately a rift has developed between the two schools of thought, and the protagonists of one sometimes fail to appreciate the true value of the other. It is manifest that either may be carried to extremes, and it is suggested that the proponents of both aut- and synecology should consider these as part of a three-way attack on the full understanding of ecology. The third facet is one that has so far been attempted only rarely but will certainly develop as our knowledge progresses: it might be termed integral ecology. The three parts form a circle, with synecology surveying the broad field, autecology differentiating this into its components, and integral ecology recombining these into the original whole.

Suppose we face the problem of understanding the interrelation of the animals and plants of a particular area. This may be the Dogger

Bank, with its economically important fishes, and the bottom-living and planktonic forms on which they prey. It may be an abyssal fauna, living too deep for living plants to exist; or it may be an intertidal rock pool, limited in size, but harboring its own peculiar forms of life and undergoing the rapid and drastic environmental changes characteristic of its location. In any of these, the first step is surely to define what life is present and what are the physical and chemical conditions under which it lives. From the biological aspect, the synecologists have devised descriptive terms covering various more or less homogeneous parts of the population. To these terms they have added estimation of the quantitative proportion of the major components, either numerically or by weight or volume. At the same time, environmental conditions are defined, and frequently a correlation becomes apparent between some of these and the dominance of particular species. The communities, or certain species in them, may be so sensitive to environmental conditions that they can be used as an index of those conditions—sometimes an easier or better index than can be obtained by a study of the conditions themselves. Furthermore, if the age of the older members of the community is known, we have evidence that environmental conditions did not vary beyond certain limits during that period. This fact could perhaps not be proved by direct methods. A classic example of such study of communities will be referred to later in describing some of Petersen's work in Danish waters. It is of interest to remember that this work was inspired by the need for an understanding of the biological productivity of these waters, particularly with reference to their fishing potential.

Now the environment in itself is sufficiently complex. In addition, no two species, or even two ages of the same species, react in quite the same way to the conditions they encounter. In unraveling the complicated network of interactions that exist in the community, it seems logical to examine it piecemeal. It may or may not be true that the whole, in such a case, is equal to the sum of the constituents. Perhaps they behave differently when isolated. Nevertheless, we cannot fail to benefit by their examination when isolated, and the possible errors which this method may introduce can be considered later.

It is this study of individual species that constitutes autecology. Study of the communities should have shown which are the most important species. These should now be examined separately. Unfortunately, there is a tendency to consider the communities in terms of their larger and more obvious members, omitting mention perhaps of much more significant but less apparent ones. An example of this

此为试读,需要完整PDF请访问: www.ertongbook.com