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TREATISE ON
MARINE ECOLOGY AND PALEOECOLOGY

Volume 1

ECOLOGY

Joel W. Hedgpeth, *Editor*
University of California, Scripps Institution of Oceanography
La Jolla, Calif.

Prepared under the direction of a Committee of the Division of Earth Sciences
National Research Council, National Academy of Sciences
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Dedicated to
Thomas Wayland Vaughan
who organized the group responsible for this Treatise
and who served as a member until a few months before his death.

Foreword

The late Dr. T. Wayland Vaughan, who had long been interested in marine ecology and paleoecology, in 1940 planned and organized a Subcommittee on the Ecology of Marine Organisms as a part of the Committee on Geologic Research (Norman L. Bowen, Chairman) in the Division of Geology and Geography of the National Research Council of the National Academy of Sciences. The members of this Subcommittee were: C. H. Edmondson, Remington Kellogg, Harry S. Ladd (Chairman), Kenneth E. Lohman, Roger Revelle, F. W. Rolshausen, H. C. Stetson, T. Wayland Vaughan. The first annual report, which attempted to summarize current activities in marine ecology and paleoecology, was issued in 1941. In this report the possibility of preparing an ecological treatise was mentioned. In 1942 the Subcommittee was made a full Committee and its title was changed to Committee on Marine Ecology As Related to Paleontology to emphasize the paleontological nature of its interests. With the encouragement and assistance of Walter H. Bucher, Chairman of the Division of Geology and Geography, the Committee in its second report, issued at the close of 1942, briefly listed its aims. There were six of these, the last of which read: "Possibly, at a later date, to prepare a special treatise on ecology that would stress geological interpretation." World War II greatly curtailed most activities in marine ecology and also curtailed the activities of the Committee. Serious consideration was given to the possibility of recessing the work, but the members felt that it might be difficult to revive the program if work was stopped. Interest in the *Treatise* continued at a low level until the war was over, but in 1946 in its sixth annual report the Committee published a tentative outline for the *Treatise* and invited criticism. In this same year Kenneth E. Lohman was made Vice-Chairman of the Committee.

During the first 5 years of its existence the group that formed the original Subcommittee continued to serve. Gordon Gunter was added as a member in 1942 and Earl H. Myers in 1944. In 1946, the sixth year, H. C. Stetson resigned because of the pressure of other duties, and three new members were added: K. O. Emery, of California, A. W. B. Powell, of New Zealand, and H. G. Schenck, then stationed in Japan. In 1947 four more members were added: R. H. Fleming, Julia Gardner, J. B. Reeside, Jr., and Waldo L. Schmitt. At a two-day meeting held in March 1947, Gordon Gunter was named Vice-Chairman for Biology, Kenneth E. Lohman Vice-Chairman for Geology, and Roger Revelle Vice-Chairman for Oceanography; and concrete plans for the completion of the *Treatise* were formulated. In 1948 Frank C. Whitmore was made a member, and in the following year Roland W. Brown and Joel W. Hedgpeth were added and assumed editorial duties. These additions brought the total membership of the Committee to 19. In 1951 Doctor Vaughan asked that his name be dropped from the Committee because of his failing eyesight. The Committee accepted his resignation reluctantly, and John W. Wells was appointed to fill the vacancy.

Most of the members of the Committee have prepared one or more units of the text or the accompanying bibliographies, but the Committee alone could not have produced the *Treatise* in its present form. To obtain as nearly complete coverage as possible the aid of nearly 100 specialists was enlisted, each of whom prepared one or more units in his particular field. To this large group the Committee extends its deepest thanks. Formal titles of the contributors are not given but the field of interest of each is indicated, together with his address at the time of going to press.

The Committee wishes to express its thanks to the Office of Naval Research, whose support made it possible for Vice-Chairman Gunter to make an extended stay at the University of California, Scripps Institution of Oceanography and a short visit to the Woods Hole Oceanographic Institution in 1948–1949. Later, through a similar co-operative arrangement between the Scripps Institution of Oceanography and the Office of Naval Research, Joel W. Hedgpeth was able to spend several years at Scripps assembling and organizing the materials for volume I and writing certain of the units. During the summer of 1953, again with the support of the Scripps Institution and the Office of Naval Research, he was able to travel in Europe and consult with many of the contributors to the *Treatise*. The Committee also desires to express its appreciation to the United States Geological Survey for encouragement and support; six members of the Committee and many of the other contributors to the *Treatise* are on the staff of the Geological Survey. Many members of the staff of the Geological Survey, the Scripps Institution, the National Museum and of other organizations have assisted the Committee in the critical review of manuscripts; this help is gratefully acknowledged. We also wish to thank Karl P. Schmidt for translating Chapter 25, which was submitted in German.

Messrs. Walter H. Bucher, W. W. Rubey, Arthur Bevan, Ernst Cloos, and Francis Birch, who have successively served as Chairman of the Division of Geology and Geography—now known as the Division of Earth Sciences—since the formation of the Committee have encouraged and supported the work in every way possible. The Committee desires to express its special thanks to Miss Margaret L. Johnson, Secretary to the Division, for great assistance particularly in assembling and duplicating of the Annual Reports, and to Mr. G. D. Meid, Business Manager of the National Academy of Sciences, National Research Council, for aid in making publication arrangements for the *Treatise*.

From the start the *Treatise* has been planned as an appraisal of accomplishments in the fields of marine ecology and paleoecology, particularly those ecological investigations related directly or indirectly to paleontology. In attempting to obtain broad coverage the Committee and its collaborators discovered several blank areas in the paleoecological field and thus initiated several investigations that otherwise might not have been started until some time later. These developments were gratifying and have served to bridge the gap between past and present work in the field. Paleoecology, though it deals with the past, is a comparatively youthful but active branch of paleontology.

With these thoughts in mind it was decided to supplement the appraisals of past work with some sort of prophetic look into the future. In what direction is paleoecology going, how far may it hope to go, and what sorts of tools may be used in the future? Some of the new techniques developed in recent years in borderline fields such as biochemistry, biophysics, and geochemistry exhibit great promise and may be successfully applied to paleoecological investigations. These prospects are discussed in a concluding chapter in Volume 2.

COMMITTEE ON MARINE ECOLOGY AND PALEOECOLOGY

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Chapter 1

Introduction*

JOEL W. HEDGPETH

*Biologist, University of California, Scripps Institution of Oceanography, La Jolla, Calif.***

Ecology has no aim, but ecologists have. The problems of the ecologist are not fundamentally different from those of any other kind of naturalist. The superficial differences in aim are due to the different points of view, or methods of approach, rather than to any essential difference in the character of the problems.

—Charles C. Adams, *Guide to the Study of Animal Ecology*, 1913

Since the early history of ecology has been discussed in some detail by Allee *et al.* (1949), among others, there is no need to repeat it here. Our concern is with the development of marine ecology in general, especially as it may be related to paleoecology. Gislén (1930) traced the study of "marine sociology," in particular of intertidal zonation, as far back as 1812, although Wahlenberg's pioneer effort to describe zonation was overlooked until 1917. The early work of d'Orbigny (1820) was also for the most part neglected, and it is not until the decades 1830–1840 that we find the unmistakable beginnings of modern marine ecology. In France it was the work of Audouin and Milne Edwards (1832), whose scheme of zonation of the life of the shore and shallow sea persisted for 50 years. In England, it was the influence of the Manxman Edward Forbes that gave marine ecology its start. In Norway Michael Sars, in Sweden Sven Lovén, and in Germany Johannes Müller turned their attention to the animals of the sea. Dredging for bottom animals was the fashion of the day, and in 1839 the British Association appropriated £60 to defray the expenses of "researches with the dredge, with a view to the investigation of the marine zoology of Great Britain, the illustration of the geographical distribution of marine animals, and the more accurate determination of the fossils of the pleistocene period." Forbes was the leading spirit on this dredging committee, and gave its activities a strong ecological cast.

In Ireland an army surgeon, J. Vaughan Thompson, studied a number of strange creatures that had usually been considered adult animals; he demonstrated that they were really larval stages. These included the zoea of crabs and the nauplius and cypris of barnacles. While Johannes Müller is usually credited with "inventing" the plankton net in the 1840's, Thompson was using such a net as early as 1828 (Hardy, 1953). Although Thompson published very little, his work was of the highest quality: "It has been said of him that 'no great naturalist has written so little and that so good.' " (Singer, 1950).

While many of the investigations of this period were concerned with zoology *per se*,

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** Present address: *Pacific Marine Station, College of the Pacific, Dillon Beach, Marin County, Calif.*

those of Edward Forbes produced some of the first ecological generalizations to receive wide notice in science. The most famous of these was his recognition of distribution by bathymetric zones: (1) littoral ("The tract between tidemarks"); (2) the laminarian zones; (3) the coralline zones ("to some thirty fathoms or more"); (4) the deep-sea coral zone ("toward an abyss where life is either extinguished, or exhibits but a few sparks to mark its lingering presence.") (Forbes and Godwin-Austen, 1859). In earlier papers, notably his lecture before the Geological Society in 1844, Forbes suggested that there was a "probable zero of life" at 300 fathoms. It was this mistake that did so much to stimulate the investigation of the depths of the ocean, and Forbes was in a real sense the instigator of the events that led to the CHALLENGER Expedition.

Forbes was also one of the earliest systematic biogeographers and recognized a series of provinces in the European seas—*viz.*, Arctic, Boreal, Celtic, Lusitanian, Mediterranean, and Black Sea. Although he considered these provinces to have originated as the result of dispersal of species complexes from "centers of creation," he had a lively appreciation of the ecological factors governing such dispersion, and we may consider his *Natural History of the European Seas* (completed after his untimely death by Robert Godwin-Austen) the first treatise on marine ecology. Most of his important ideas, however, were expressed in papers presented at meetings, and it was apparently in the discussions that followed them that his influence was most felt. It would be interesting to have a record of the discussion which followed his report on the invertebrates of the Aegean Sea to the 1843 meeting of the British Association. In this report he presented his findings as to distribution by depth, accompanied by the first recognition of population dynamics (as pointed out by Allee *et al.*):

> As each region shallows or deepens, its animal inhabitants must vary in specific associations, for the depression which may cause one species to dwindle away and die will cause another to multiply. The animals, themselves, too, by their over-multiplication, appear to be the cause of their own specific destruction. As the influence of the nature of sea bottom determines in a great measure the species present on that bottom, the multiplication of individuals dependent on the rapid reproduction of successive generations of Mollusca will of itself change the ground and render it unfit for the continuation of life in that locality until a new layer of sedimentary matter, uncharged with living organic contents, deposited on the bed formed by the exuviae of exhausted species, forms a fresh soil for similar or other animals to thrive, attain their maximum, and from the same cause die off.

Forbes then goes on to describe the probable fossil record which might be expected if the Aegean Sea were to be elevated or filled with sediment (1844, pp. 176–178); in doing this he outlined for the first time the methodology of paleoecology. There was in all Forbes' work and thought a strong geological cast, and he is in a real sense the founder of paleoecology:

> To Forbes is due the credit of having been the first to treat these questions in a broad philosophical sense, and to point out that the only means of acquiring a true knowledge of the *rationale* of the distribution of the present fauna, is to make ourselves acquainted with its history, to connect the present with the past . . . Forbes, as a pioneer in this line of research, was scarcely in a position to appreciate the full value of his work. (Wyville Thomson, 1873, p. 6).

A recent appraisal of Forbes' contribution, with an account of his field methods, is given by Ritchie (1956).

The decade 1840–1850 was marked by an active interest in marine biology on the continent as well as in England. In the United States, interest during this period was more in the physical aspects of the sea, and the pre-eminent marine scientist was Matthew Fontaine Maury, whose *Physical Geography of the Seas* (1855) marked the beginning of physical oceanography. Diving as a method of ecological investigation was introduced by H. Milne Edwards and A. de Quatrefages about 1844 off the coast of Sicily, but it has only come into serious use since the invention of free-diving apparatus (Drach, 1952). The first seaside summer station was instituted by P. J. van Beneden at Ostend in 1843, and summer classes in marine zoology appear to have been the innovation of Carl Vogt in 1844. It was not until 1859 that the first permanent marine station, at Concarneau, was founded (Kofoid, 1910).[1] During this period the lively interest of literate laymen provided a market for such semi-popular works as Vogt's *Ozean und Mittelmeer* (1848), Quatrefage's *Souvenirs d'un Naturaliste* (1854, translated into English, 1857), and the various superbly illustrated volumes by Philip Henry Gosse, including *A Naturalist's Rambles on the Devonshire Coast* (1853) and *Tenby* (1856). The fever of seashore study reached strange heights in Victorian England, when a well-ordered holiday was incomplete without exercises in the identification of seaweeds and zoophytes, and Gosse conducted classes at the seaside for "a party of ladies and gentlemen . . . and very novel and agreeable the amusement was unanimously voted." (E. Gosse, 1890).[2] It appears that this fad may have been received by some in a spirit of desperate resignation, if we are to judge from the amusing account by Marsden (1947).

The lines of investigation suggested by the work of Forbes and Milne Edwards were carried further by J. R. Lorenz in a remarkable and neglected work, *Physicalische Verhältnisse und Vertheilung der Organismen im Quarnerischen Golfe* (Vienna, 1863). This author discussed in detail the temperature regime, with curves for the entire year at surface and various depths to 30 fathoms, the tidal levels and currents, wave action, prevailing winds, geological formations and salinity in relation to the distribution of plants and animals in the Gulf of Quarnero. He recognized various communities, indicating the characteristic species of the facies, and provided graphs for his physical data (which are absent from many modern papers in this field). It is in all respects a master work, but is still ignored although his usages of the terms supra- and sublittoral are now in general use.[3] Gislén (1930) attributes part of this neglect to the author's early death, which occurred before Lorenz could distribute his book. Whatever the cause for this neglect, it must be said that his achievement was years ahead of its time and indeed is still beyond many later efforts.

The next great decade in the history of marine biology, and of marine ecology in particular, is that of 1870–1880, the time of the CHALLENGER Expedition. It is the decade which saw the beginning of applied ecology under government auspices. The United States Fish Commission, with Spencer F. Baird as secretary, and the Commission zur Wissenschaftlichen Untersuchungen der Deutschen Meere, including

[1] For an excellent summary of this subject, see C. M. Yonge, "Development of marine biological laboratories" Science Progress, no. 173, pp. 1–15, Jan. 1956.

[2] "Since the British mind was all alive and trembling with that zoological fervor excited by the appearance of the hippopotamus in Regent's Park, no animal has touched it to such fine issues and such exuberant enthusiasm as the lovely Sea-Anemone." G. H. Lewes, *Seaside studies* . . . (1858, p. 115).

[3] Lorenz spelled these "Supra-litoral" and "sub-litoral"; the single "t" is etymologically correct, but the spelling "littoral" is now so widely used that it would be tilting at windmills to attempt to restore the older spelling.

Karl Möbius and V. Hensen, both began their activities in 1871. A year later Dohrn founded the Zoological Station at Naples, but in all its long history it has been devoted primarily to embryological and physiological researches.

While the United Stated and Germany started their investigations of fisheries problems in the same year, the groundwork of the German commission had been laid by Karl Möbius several years before, with his *Fauna der Kieler Bucht* (Meyer and Möbius, 1865). This work is viewed by Nordenskiold (1928, p. 559) as the start of "the modern system and methodics of oecology." Möbius and Victor Hensen, the founder of plankton research, were both members of the Commission. In the first report of the work of the Commission, Möbius (1873, p. 139) introduced three terms which are now universally used in ecology: eurythermal, stenothermal, and euryhaline. The early reports of the German commission inaugurated such lines of research as the distribution of organisms in relation to salinity and quantitative analysis of the plankton, which are still being carried out at Kiel. While the problem of assaying the quantities of plankton in a given volume of water is still unsolved, the methods introduced by Hensen in his monograph (1887), especially the vertical haul with standardized net, are still widely used. It was in this monograph, incidentally, that the term plankton was first used. Hensen continued his work with a special expedition in the Atlantic Ocean devoted exclusively to the investigation of plankton, the famous "Plankton-Expedition" of 1889. Haeckel, who had been introduced to the plankton by Johannes Müller, attacked Hensen's conclusions, but his criticism was vitiated by reliance on "general impressions" and by his idea of zoorema or animal streams, and Hensen (1891) ably defended himself.[4] Kofoid's (1897) criticisms were somewhat beside the point, and it remained for Lohmann, another "Kiel Planktologist" (Johnstone, 1908), to make the next great advance in plankton study with the use of the centrifuge.

In discussing the early history of the German and American commissions, it should not be forgotten that the British may claim priority with the Royal Commission to Investigate Fisheries Problems, which met in 1863. This commission, which included T. H. Huxley, was not a permanent research organization, however, and did little more than offer recommendations in its report in 1866.

The United States Fish Commission began its activities under the guidance of Spencer Fullerton Baird, whose broad interests and appreciation of the complexity of fisheries problems rivaled those of Möbius, although they seem to have begun their careers as applied ecologists independently. In drawing up the program for the Fish Commission, Baird wrote:

> The inquiry, therefore, ultimately resolved itself into an investigation of the chemical and physical character of the water, and of the natural history of its inhabitants, whether animal or vegetable. It was considered expedient to omit nothing, however trivial or obscure, that might tend to throw light on the subject of inquiry . . . (Baird, 1873, p. xiii).

The first annual report of the United States Fish Commission (1873) is a bulky volume in which is embedded, under the authorship of A. E. Verrill, the classic work

[4] It was in this critique of Hensen that Haeckel (1890, transl., 1893) was at his best (or worst) as a fabricator of terms. A few of the many introduced in this paper have survived, notably benthos, nekton, and neritic.

in American marine ecology, the *Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region.* Allee *et al.* express the opinion that this elaborate report, written in collaboration with S. I. Smith and others, and discussing the occurrences of animals in assemblages and according to substrates, "did not receive the recognition or have the influence among ecologists that it merited." Because it was not the fashion in those days to make detailed acknowledgment of other researches, especially when not directly quoted, it is hard to support or to deny this statement. We do know that Möbius read Verrill's work since he mentions it in his famous monograph on the oyster, and the later work of Möbius was frequently called to the attention of American workers through the publication of translations in the Reports and Bulletins of the Commission. Verrill came closer than Forbes to grasping the idea of the community, but it is Möbius who defined it in unmistakable terms and gave it the name biocoenosis in his book, *Die Auster und die Austernwirthschaft* (1877), which was translated and published in the Report of the U. S. Fish Commission for 1880 (1883).

What we must remember in assessing the comparative influence of these men is that in the United States, where the marine fauna was still incompletely known, Verrill's influence as a teacher was directed to training systematists, and that this phase was followed almost immediately by the era of cell-lineage studies, during which the only proper subject for a doctorate was a study of the early cleavage stages of some invertebrate. In Germany, at least under such men as Möbius and Hensen, students were introduced to the problems of economic zoology in the sea, and from the early work of Möbius in the Gulf of Kiel and on the Helgoland oyster banks there is a direct line of research to C. G. J. Peterson. It is true that in the United States the first seaside studies were inaugurated by Louis Agassiz at Penikese in 1873. This forerunner of the Woods Hole Laboratory was originally the idea of Nathaniel Southgate Shaler, the Harvard geologist and paleontologist, but his part in its history seems to have been forgotten.[5] With the establishment of the Woods Hole Marine Biological Laboratory in 1886 and the building of the permanent station of the Fish Commission in 1885, Woods Hole became a center for seaside studies and soon established a tradition which did little to foster ecological studies. It is true that Verrill's work was supplemented by the faunal survey of Sumner, Osburn, Cole, and Davis (1913), but actually little was added, other than a detailed catalogue, to Verrill's original presentation. The arrival of men like Allee and Shelford on the scene in the early 1920's revived to some extent the original ecological approach of Verrill, but it was not until 1952 that a formal course in ecology was established at Woods Hole.

With the departure of the CHALLENGER from Portsmouth on December 21, 1872, on her four-year cruise around the world, the modern science of oceanography was begun. As a science it was a "possibility" to be fully realized within the short span of two generations (Merriman, 1948); little of the CHALLENGER's results, however,

[5] Shaler's name is not even mentioned in Lillie's (1944) history of the W.H.M.B.L.; however, he does cite the New York Tribune for July 9, 1873. At the end of the account of the opening day at Penikese this statement is found: . . . "Prof. N. S. Shaler of Harvard, who was the first proposer of this scheme, and who is at present in Europe . . . "

was what might be considered ecology, although much of the basic data secured advanced our understanding of the oceans as an environment for life. From the viewpoint of the history of ecology, the most significant result of the CHALLENGER Expedition was the training of John Murray, whose influence on all phases of marine research prevailed throughout a long and active scientific career. This career was capped by the publication of *The Depths of the Ocean* (Murray and Hjort, 1912) which remains, after 40 years, one of the most essential references on the ecology of the seas. The CHALLENGER Expedition inspired a host of imitators, and much of the effort of governments and universities in the field of marine biology in the decades 1880–1890 was expended in sending out oceanographic expeditions and in writing reports on the collections. Yet as early as 1883 a young student in Denmark, who began his investigations with a conventional catalogue of the booty of a collecting cruise, displayed a sharp interest in the ecological factors governing the distribution of bottom animals.

This was, of course, C. G. J. Petersen, who in 1889 became the first director of the Danish Biological Station and conducted the investigations into the valuation of the sea which were published in a series of papers from 1911 to 1918. Before the publication of Petersen's first report (with Boysen-Jensen) in 1911, a few preliminary efforts at quantitative estimating of the productivity of the sea were made, notably by that remarkable self-made oceanographer James Johnstone (1908) and Fr. Dahl (1893). Nevertheless, it was Petersen who perfected the method, invented the instruments (notably the famous "Petersen grab"), and placed quantitative marine ecology on a sound footing. He also introduced fish tagging as a method of estimating populations. It was generally held, up to the time of the publication of *The Valuation of the Sea*, that plankton constituted the principal food of bottom animals, but Petersen advanced the hypothesis that detritus, especially the organic remains of *Zostera*, made up the principal food resource for the bottom fauna in the shallow Danish waters (Blegvad, 1945, 1951). This contradiction of the older view and the detailed work on the assemblages of bottom organisms, with its recognition of characteristic communities, was a sensation at the time and stimulated similar work in many other

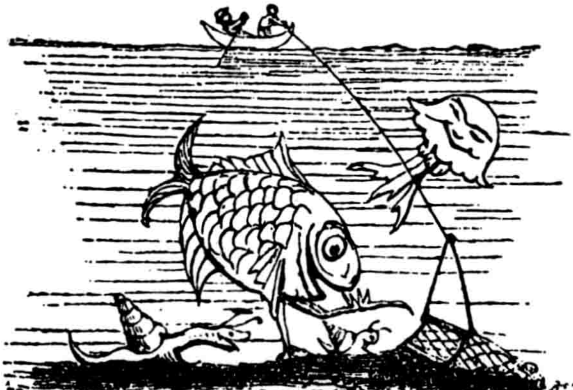

FIGURE 1.—*Edward Forbes' criticism of the dredge, as quoted by Petersen in* Valuation of the Sea

parts of the world. Petersen himself considered his method an extension of Hensen's investigations.[6]

Although Petersen was the first to designate bottom communities on the basis of the most characteristic or abundant organisms present on a given type of bottom, his debt to the Danish plant ecologist Warming is obvious. The plant ecologists have always been ahead of the animal ecologists in their methods of recognizing and delineating communities for the obvious reason that plants will not move away and thus lend themselves more satisfactorily to statistical treatment of this sort. Sedentary marine animals are equally satisfactory in this respect; hence, it is inevitable that most of the work with communities in the sea has been done with plants and the fixed animals on hard substrates or with the relatively sedentary bottom forms.

A few words should be said at this point concerning the relation of such studies, as those of Petersen and his colleagues, to systematic zoology. Without a good knowledge of the flora and fauna of the region, it is impossible to make a detailed study of the populations. Steuer (1926) suggested that the work in Denmark could not have been done at Naples because the fauna of the Mediterranean is so much richer and still incompletely known. He might also have pointed out that the splended tradition of systematic zoology at the University of Copenhagen aided these researches (as Petersen himself implies in his introduction to his initial paper, 1911), and that without a staff of systematists it is impossible to study even an impoverished fauna. This seems to be one of the principal reasons why such studies as Petersen's have not yet been attempted in North America.[7] However impractical they may seem to some fisheries biologists and even to some ecologists, studies in systematic zoology and botany are a necessary preliminary to critical work in ecology. Many of the great students of ecology have also been highly competent systematic zoologists, including Forbes, Milne Edwards, Verrill, Möbius, and Herdman, and many others, including Petersen, were trained as systematic zoologists.

At about the same time that Petersen became director of the Danish Marine Station, the Marine Biological Association of the United Kingdom, which was organized in 1884, opened its laboratory at Plymouth. Although the laboratory began, at its outset, investigations of fisheries problems, its research program has been guided by individuals and universities, with the result that problems of marine ecology and physiology have received attention. Indeed, it would be possible to compile a satisfactory textbook of marine ecology from the back issues of the Journal of the Marine Biological Association alone. The Marine Biological Association was inspired in part by the example of the Zoological Station at Naples and in part by the United States exhibit at the International Fisheries Exhibition in London in 1883. T. H. Huxley

[6] While the importance of detritus in the economy of the sea has never been seriously questioned since Petersen's work, the idea that the breakdown of *Zostera* was necessarily the principal food resource in the shallow waters of Denmark has been upset by the eel-grass disease epidemic of the 1930's which removed the eel grass, at least as a serious component of the economy, without affecting the organic production of the waters as a whole (Poulsen, 1951; *see also* Burkenroad, 1951, p. 196 [note] in which this is discussed on theoretical grounds).

[7] It is also in part because the United States Bureau of Fisheries was too often placed in the hands of politicians and fish culturists and was never able to carry out the example set in the golden seventies by Verrill and Möbius. A more fundamental reason is that the Fish Commission clung to Baird's original idea that fluctuations in fish populations were the result of fishing pressure, and conducted its investigations accordingly. Is there any connection, incidentally, between the publication of a translation of Haeckel's Plankton Studies in 1893 and the failure of the Bureau of Fisheries to conduct any serious plankton work until Bigelow's investigations in the Gulf of Maine in 1912?

presided at the original meeting in 1884. It was Sir E. Ray Lankester, however, who, as the first secretary, did most to start the Association and guide it through its formative stages. Early in its career, the Plymouth Laboratory became associated with practical fisheries investigations, when the Association was asked by H. M. Treasury to undertake the English share of the work of the International Council for the Exploration of the Sea.[8]

At the present time the program of the Plymouth Laboratory is concerned with the problems posed by these questions:

> The first is how much living matter can the sea produce, what are the variations and causes of variation in productivity, and how do the organisms obtain the materials necessary for life? The second is how do marine animals in general live, how do they fit their various individual environments, and what alterations in the conditions of their environment can they appreciate? (Russell, 1948).

It would be difficult to find a better summary of the aims of modern marine ecology than these questions, although a more explicit statement as to the interactions of the organisms themselves might be added.

A sketch of the historical development of fisheries research, even as brief as this, would be incomplete without some mention of the active school of fisheries researchers at Liverpool under the direction of W. A. Herdman, the intellectual heir of Edward Forbes, and the phenomenally long career of W. C. McIntosh at St. Andrews. Herdman founded the laboratory at Port Erin, Isle of Man, and compiled the first history of oceanography (1923). Many fisheries researchers in Britain acknowledge their indebtedness to his inspiration. Not the least of these was James Johnstone, whose *Conditions of Life in the Sea* (1908) was the text for many prominent English fisheries biologists of the present generation. McIntosh is best remembered as director of the station at St. Andrew's and as a discerning and sometimes disconcerting critic of fisheries research and theories. In Russia marine ecological investigations were placed on a sound basis by S. A. Zernov, whose *Contribution to the Knowledge of the Life of the Black Sea* (1913) was prepared with a thorough knowledge of the work of Petersen, Johnstone, and McIntosh, among others. Zernov later wrote an excellent textbook, *General Hydrobiology* (1931), which was reissued in a revised, posthumous edition (1949). The quantitative methods introduced by Petersen have been extensively used in Russia by Zenkevich, whose "*Fauna and Biological Productivity of the Seas*" (1947) is a summary of this work.[9] Significant work with bottom communities has also been conducted by Vatova in the upper Adriatic, especially in the Lagoon of Venice.

The study of "self conscious ecology" (to use the phrase of Allee *et al.*) developed in the meanwhile in the rather specialized field of zonation on the shore. Many studies of individual behavior and relationships of animals were made, most of which might be more properly considered natural history or autecology, rather than the compre-

[8] The International Council for the Exploration of the Sea was organized in 1899 as a co-operative effort of the governments of northern Europe and the British Isles. Among the moving spirits responsible for this organization may be named Sir John Murray, Johan Hjort, and C. J. G. Petersen. While it has restricted its investigations primarily to the North Sea and the northern Atlantic between Scandanavia and Greenland, it is nevertheless the outstanding research organization concerned with problems of pure and applied oceanography and fisheries problems.

[9] Unfortunately we have not been as enterprising as the Russians in translation; there are Russian editions of Johnstone, Murray's *The Ocean*, and Russell and Yonge's *The Seas*, but no standard Russian work in hydrobiology has been translated into any other language.

hensive synecology characteristic of most of the fisheries research. Such studies of the "environmental physiology" of individual organisms are an essential part of the work of ecologists and are especially needed in application to paleoecology, however little they may contribute to our understanding of populations. Among the noteworthy contributions in this field of environmental physiology we may mention Krogh's *Osmotic regulation in aquatic animals* (1939), Pelseneer's *Essai d'éthologie zoologique d'après l'étude des Mollusques* (1935), a summary of the life-long studies of a master malacologist, and the MacGinities' (1949) account of their natural history researches. It might be mentioned that many studies of "marine sociology" or "bionomics" have been as drily descriptive as a report on the anatomy of some animal and are of little more than academic interest.

An exception to this judgment is the detailed work of Gislén (1929; 1930), who studied the rocky subtidal environment of the Gullmar Fjord. With the use of diving gear and counting frames, Gislén catalogued the various hard-bottom associations and computed their biomasses and production of organic matter. In doing this he combined the methods of Petersen and of the students of intertidal zonation with the most intensive use of diving gear up to that time. His work, with its detailed attention to hydrographic as well as ecological factors, provides a model for future studies with the self-contained diving equipment now coming into wide use.

Up to the 1930's studies of shore populations, intertidal zonation, or littoral bionomics were the particular favorite of French investigators, following the venerable tradition of Audouin and Milne Edwards. The leading workers in this field have been P. M. de Beauchamp, E. Fischer-Piette, and Th. Monod, among zoologists, and the algalogist J. Feldmann. Around 1930, however, investigators on almost every temperate coast in the world turned their attention to the seashore, and the result has been a veritable deluge of papers on the general subject of intertidal zonation or seashore bionomics. The most important contributors to this literature have been T. A. and Anne Stephenson and their colleagues, who conducted a 10-year survey (1931-1941) of the South African intertidal (Stephenson, 1947), and have since turned their attention to North America. Recent studies in this field, too numerous to mention here, are reviewed in Chapter 18.

Another approach to the study of communities of hard substrates has been through the experimental device of test squares or blocks, first used by Fr. Dahl (1893) in the lower Elbe. Much of this work, concerned with the time and rate of settling of fouling organisms, or the settling of oyster larvae, has had an economic motivation, but some studies of this nature have been carried out over a period of several years and have yielded valuable information about the development of communities and the variations of populations. Among the most noteworthy of these is the study by Coe (1932; Coe and Allen, 1937) from 1926 to 1935 at the Scripps Institution of Oceanography at La Jolla.

It was about the same time that studies in intertidal zonation became so popular that the original lines of inquiry followed by Edward Forbes were taken up again, and paleoecology began to be developed primarily as a branch of paleontology. The leaders in this movement were T. Wayland Vaughan, who became interested in the interpretation of past environments through his work on corals, and the German