MARINE ZOOGEOGRAPHY

John C Briggs

McGraw-Hill Series in Population Biology

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McGRAW-HILL BOOK COMPANY

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1234567890 MAMM 7987654

This book was set in Helvetica Light by Black Dot, Inc.
The editors were William J. Willey, Renée E. Beach, and Richard S. Laufer;
the designer was J. Paul Kirouac;
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The drawings were done by John Cordes, J & R Technical Services, Inc.
The Maple Press Company was printer and binder.

Library of Congress Cataloging in Publication Data

Briggs, John C
Marine zoogeography.

(McGraw-Hill series in population biology)
1. Marine fauna—Geographical distribution.
I. Title.
QL121.B77 591.9'2 73-14502
ISBN 0-07-007800-9

Preface

I was fortunate to be raised near the sea and to become familiar at a young age with the California beaches and rocky headlands. Later, I had the privilege of attending two coastal universities, Oregon State as an undergraduate and Stanford as a graduate student. At Stanford, I was exposed to an exceptional faculty and a stimulating group of fellow graduate students. My research interests were most strongly influenced by the courses taught and the personal examples set by two of my Stanford professors, George S. Myers and Rolf L. Bolin.

Following my student days, I was able to continue my research in marine biology—with an emphasis on fishes—first at Stanford on a postdoctoral appointment and then as a faculty member at the University of Florida, University of British Columbia, University of Texas, and now at the University of South Florida.

The research for this book started in 1962 when I was on the staff of the Marine Science Institute of the University of Texas at Port Aransas. My move to the University of South Florida, a new state university, in 1964 involved the assumption of considerable administrative responsibility. Consequently, there was less time available for research, and progress on the book became discouragingly slow. Now, after almost 10 years, I can with great relief add the preface and send it off to the publisher.

The greater part of this volume is devoted to the various marine life zones and to the delineation and characterization of the many zoogeographic regions and provinces that are found within them. This had not not previously been done in a detailed manner, so it was a necessary task. In the last chapter, it was possible to trace the history of a few of the faunas to some extent and to examine certain aspects of the relationship between zoogeography and evolution.

Zoogeographic conclusions, if they are to have lasting value, must be based on dependable systematic work. Consequently, I have attempted to be selective about the works I have utilized for analysis. The reader will find that I have placed considerable emphasis on the fishes. There are two reasons for this. First, I am primarily an ichthyologist and am therefore better able to evaluate systematic works on this group. Second, in many parts of the world the fishes happen to be better known than the major groups of invertebrates. Among the phyla of marine animals, the general distributional patterns seem to coincide remarkably well so that good data for one group are likely to have significance for the rest.

In the introduction to his valuable little volume, *The Natural History of European Seas*, published in 1859, Edward Forbes remarked, "In this age of volumes, a man needs to offer a good excuse before adding a new book, even though it be a small one, to the heap already accumulated." If Forbes were alive today, what would he have thought about the need of adding one more volume to an annual world production of something on the order of 100,000 titles?

I would like to think that I am offering this book in the same spirit that Jean Baptiste Lamarck did his *Zoological Philosophy* in 1809. In the introduction to that monumental work he said, "In publishing these observations, together with the conclusions that I have drawn from them, my purpose is to invite enlightened men who love the study of nature to follow them out, verify them, and draw from them on their side whatever conclusions they think justified."

JOHN C. BRIGGS

Acknowledgments

Since a fair amount of the material in this book has been dealt with in a series of my published papers or has been presented as talks at seminars and scientific meetings, I have had the benefit of criticisms and suggestions from a large number of colleagues. I hope I will be forgiven for not attempting to thank each person at this time. To do so would not only result in a long list of names but, since this process went on for about 10 years, I'm afraid I might leave someone out. Let me say only that I am grateful for all the help that I have received.

I am indebted particularly to Joseph L. Simon for taking the time to read the entire finished manuscript. Also, four people were kind enough to read complete chapters for me: Margaret M. Smith provided useful comments on Chapter 6 (Southern Hemisphere Warm-Temperate Regions), Thomas L. Hopkins and Ronald C. Baird on Chapter 10 (The Pelagic Realm), and Daniel M. Cohen on Chapter 11 (The Deep Benthic Realm). I was fortunate to have the services of two fine artists, Henry W. Compton and Nancy Smith. Mr. Compton executed the beautiful colored drawing of *Hemanthias leptus*. Finally, I am indebted to the National Science Foundation for their support of the research that led to this book in the form of two grants, GB 2866 and GB 4330.

The reader will find that some of the material in Chapter 5 (Relationships of the Tropical Shelf Regions) has been taken, almost verbatim, from two of my papers on the subject: Dispersal of tropical marine shore animals: coriolis parameters or competition? (1967, *Nature*, 216(5113):350) and Tropical shelf zoogeography (1970, *Proc. Calif. Acad. Sci.*, 38(7):131–138). Part I of Chapter 12, on the history of marine life, contains material from my article, A faunal history of the North Atlantic Ocean (1970, *Syst. Zool.*, 19(1):19–34); and part II of Chapter 12, on Worldwide patterns, includes material from my article, Zoogeography and evolution (1966, *Evolution*, 20(3):282–289). I am indebted to the editors of the indicated journals for their permission to utilize these publications.

JOHN C. BRIGGS

Contents

Introduction

The design of a book is the pattern of a reality controlled and shaped by the mind of the writer. This is completely understood about poetry or fiction, but it is too seldom realized about books of fact. And yet the impulse which drives a man to poetry will send another man into the tide pools and force him to try to report what he finds there.

John Steinbeck in Sea of Cortez, *1941*

Our Water Planet

As viewed from outer space, the planet we inhabit is a beautiful, blue and white sphere. The blue is reflected from the oceans which cover 71 percent of the surface, and the white comes from the clouds which float above both oceans and land. In our solar system, only earth has liquid water. The other planets are either too hot or too cold. Our total volume of water has been estimated at 1,500 million cu km, about 97 percent of it forming the oceans. Most of the rest exists in the form of ice. If all the water were liquid and the surface of the earth perfectly smooth, our planet would be covered by a layer of water about 3,000 meters deep (Penman 1970). In the words of Ray (1970), "Earth is different from the other planets. Earth is unique. Earth has water."

Life on earth is confined to the globe's fluid envelope, or covering. This envelope is divided in two parts—a gaseous portion called the atmosphere and a liquid portion called the hydrosphere. The atmosphere is so thin that very few living things have been able to achieve a purely aerial existence. Almost all atmospheric organisms are obliged to depend on the physical support of the substrate that forms the lower boundary of the atmosphere. So, from the standpoint of their overall distribution, we can see that such organisms occupy a thin, two-dimensional layer on the earth's surface.

In contrast, the liquid of the hydrosphere is viscous enough to provide physical support and contains sufficient nutrients in suspension so that almost all its volume is continually occupied by a vast array of living things. Here, we find that life exists on a truly three-dimensional scale with its vertical component extending from the surface to the greatest depths—almost 11,000 meters. If we call that portion of the earth inhabited by life the biosphere, it is clear that the oceans comprise by far the greatest part of it. Thorson (1971:20) estimated that the total oceanic living space is roughly 300 times larger than that available for life on land.

The Marine Fauna

Although the number of species of animals described from the terrestrial environment greatly exceeds that reported from the sea or from fresh water, such superior terrestrial diversity is due mainly to the enormous number of species of arthropods, especially arachnids and insects. However, if one considers diversity at the level of the phylum or class, a much different picture results. No less than 34 of the 37 phyla of living animals are found in the sea, while only 17 occur in fresh water, and 15 occur on land; at the class level, 73 occur in the seas, 35 in fresh water, and 33 on land (Nicol 1971).

Not only did life apparently originate in the sea, but as far as fundamental structure is concerned, it exists in far greater variety there today. Most of the basic differentiation in the animal kingdom took place in the early Paleozoic era, and many of these marine groups have never developed the ability to invade fresh water or land. Of the large phyla that have entered the latter two environments, the phylogeny of most reflect a long history of life in the sea. For example, of the seven living classes of mollusks, all live in the sea, only two have also invaded fresh water, and only one of the latter (the gastropods) is also found on land.

Vertebrate and invertebrate zoology, and to a considerable extent ecology, can be taught best at the edge of the sea where one may gain a measure of appreciation for the vast complex of animal life in our world. Here, students can collect and study fresh or living examples of a wide variety of interesting creatures instead of concentrating upon pickled specimens of a few so-called "representative types." A number of years ago, Wheeler (1923) spoke in disparaging terms about the "present depauperate glacial fauna of the Laboratory," a condition that is unfortunately still with us.

Historical Marine Zoogeography

Most of our knowledge about the distribution of animals within the oceanic part of the biosphere is recent and, compared to what is known about the terrestrial environment, still very fragmentary. People have been interested in marine animals for a long time, but the enormous size of the world ocean, the three-dimensional pattern of life within it, and the difficulty of making adequate observations in a habitat relatively hostile to man have prevented the accumulation of needed data. For example, the limits of the terrestrial zoogeographic regions were essentially established by Sclater in 1858, but only now can we attempt to do the same thing for the continental shelves. Distributional patterns in the deep sea and the open sea are still relatively poorly known, and it will be many years before they are thoroughly worked out.

Marine zoogeography got its start with the work of a young man who was later to become a world-famous geologist. James D. Dana, who participated in the United States Exploring Expedition, 1838 to 1842, made observations on the distribution of corals and crustaceans that led him to some important conclusions. He was able to divide the surface waters of the world into several different zones based on temperature and used isocrymes (lines of mean minimum temperature) to separate them. His plan was published as a brief paper in the *American Journal of Science* in 1853.

In 1856, Edward Forbes published his "Map of the Distribution of Marine Life," together with a descriptive text, in Alexander K. Johnston's *The Physical Atlas of Natural Phenomena.* In this, the first comprehensive work on marine zoogeography, the world was divided into 25 provinces which were located within a series of 9 horizontal, "homoizoic belts." A series of five depth zones was also recognized. In the same year, Samuel P. Woodward, the famous malacologist, published part three of his *Manual of the Mollusca*, which dealt with the worldwide distribution of this group.

Three years later, in 1859, Forbes' small but skillfully written volume, *The Natural History of European Seas*, was published posthumously by Robert Godwin-Austen. This work constitutes an important contribution to both marine zoogeography and marine ecology. Also in 1859, Charles Darwin in his *On the Origin of Species* devoted two chapters to geographic distribution. He pointed out the interesting relationship between distributional and evolutionary patterns and gave some examples from the marine environment. In 1880, Albert Günther included in his book, *An Introduction to the Study of Fishes*, an analysis of shore fish distribution. In 1896, Arnold Ortmann published his *Grundzüge der Marinen Tiergeographie* based on the distribution of the decapod crustaceans. The following year, in 1897, Philip L. Sclater published a paper in the *Proceedings of the Zoological Society of London* on the general distribution of marine mammals. In 1901, David Starr Jordan, in an article in the journal *Science*, provided an improvement to Günther's scheme for the distribution of fishes.

The publication of the physical *Atlas of Zoogeography* (Bartholomew et al.) in 1911 was a significant event. It presented a compendium of knowledge about the distribution of 700 families of animals, both marine and terrestrial, on beautifully executed, color-plate maps. In 1935, Sven Ekman, a professor at the University of Upsala in Sweden, completed the huge task of analyzing all of the pertinent literature on marine animal distribution and published his results in a book entitled *Tiergeographie des Meeres.* This well-documented presentation immediately became the definitive work on the subject. In 1953, a second edition was published in English. Regrettably, the 1953 edition was not brought entirely up to date so that much of it was only a translation of the 1935 work.

In 1957, the ecology volume of the comprehensive *Treatise on Marine Ecology and Paleoecology* was published by the Geological Society of America. A chapter in this volume, written by Joel W. Hedgpeth, was devoted to marine biogeography. Although many other books, dealing with marine zoogeography to some extent, were published and hundreds of smaller contributions appeared, I believe those mentioned have advanced our knowledge the most.

Modern Marine Zoogeography

The need for an up-to-date treatment of marine zoogeography along the lines of Ekman's original 1935 book has existed for a long time. In the past 20 years, especially, an enormous amount of useful work has been accomplished. Ekman felt that the ultimate aim of zoogeography (and zoogeographers) was not only the understanding of the present regional system but the revealing of the history which led to its establishment, the history of the faunas.

So far, it can be said that two goals of zoogeographic research have been generally recognized: (1) the delineation and characterization of each distinct faunal area and (2) the attempt to trace the history of the faunas. A third goal needs to be added: the use of zoogeographic data to augment our knowledge about the course of evolution. Several people who have had the privilege of doing systematic work on groups of marine animals that are widespread have found a close relationship between distributional and evolutionary patterns. This means that the accumulation of detailed knowledge about the distribution of species and higher categories can often be very useful in reconstructing the path of evolutionary change within a given group.

Although many ecologists are prone to consider zoogeography a segment of their discipline, there are important differences between the two fields. Ecological research is devoted primarily to community or ecosystem structure including trophic relationships, energy flow, succession, and the characteristics of ecological niches. If distribution is studied at all, it is done so on a local scale with regard to the relationship of species to their immediate physical, chemical, or biological surroundings. Important as such investigations are, they are not zoogeography. Zoogeographers are interested in the various faunal areas of the world and in the distributional patterns of individual animal groups. Studies along these lines are rewarding, since they lead to a better understanding of the faunal areas, their history, and—perhaps most important of all—the phylogeny of certain widespread groups of animals.

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Life on the Continental Shelves

The Tropical Ocean

Chapter
1

The Indo-West Pacific Region

. . . many fish range from the Pacific into the Indian Ocean, and many shells are common to the eastern islands of the Pacific and the eastern shores of Africa, on almost exactly opposite meridians of longitude.

Charles Darwin in On the Origin of Species, *1859*

Tropical Diversity

The tropical seas, as well as the better-known terrestrial environment of the tropics, support an astonishing variety of animal life. Why is this so? Ecologists have recognized for a long time that animal populations existing in the temperate parts of the world may be profoundly affected by seasonal variations in the weather. Of course, weather affects animals directly, but often more important, it also can control such vital necessities as food and shelter. Consequently, it has been suggested (Dobzhansky 1950) that natural selection in the temperate zones operates mainly in response to the exigencies of the physical environment, but in the tropics, where weather is relatively stable, natural selection appears to be closely affected by the competition among organisms; that is, it responds mainly to the biological rather than the physical environment.

We should also recognize, as Sanders (1968) did in his thoughtful study of marine benthic diversity, that in order for biological competition to have evolutionary effects, it must be able to operate under conditions of long-term physical stability. Thus, increased diversity appears to represent the slow but inevitable response of living organisms, via the mechanism of natural selection, to increased climatic stability. Since the equatorial regions are the only parts of the world that have over the ages remained relatively unaffected by climatic change, we might expect to find a greater number of species per unit area than in regions with less stable histories.

Because evolution in the tropics has apparently been controlled mainly by biological competition, the species have tended to become highly specialized, and many have developed intricate interdependencies. This tendency is nicely illustrated by a study of the latitudinal differences in the feeding habits of shallow-water marine animals (Bakus 1969). As a result, there are in the tropics numerous niches being exploited that are simply unoccupied or inefficiently utilized in temperate latitudes.

The Effect of Area

There is, in addition to climatic stability, a second factor that appears to have a profound effect upon species diversity. This is the geographic size of the habitable area. Some biologists who have approached the problem of diversity from the standpoint of community structure (Sanders 1968; Johnson 1970) apparently did not consider the possibility of an area effect. Yet, it is true that in small isolated places, such as