web somehow contribute to the stability of the system"; Steele's conclusion, which parallels much recent work elsewhere, is that such added complexity does not in itself enhance community stability. He next discusses the stabilizing effects of spatial heterogeneity, deeming them insufficient to explain the long-term survival of populations in the open sea. Steele finally turns to the functional form of the interactions between the grazing zooplankton and their prey, the phytoplankton, and argues that it will in general be of the "Holling Type III" (or "vertebrate") character: there is a threshold at low food densities, below which feeding is negligible and above which feeding increases rapidly, eventually leveling off to some saturation value. It is widely appreciated that such functional responses between plant and herbivore, or prey and predator, can be stabilizing over a wide range of prey densities. Looking ahead to the simulation results, Steele argues that these features of the plant-herbivore interaction are the crucial stabilizing elements in marine ecosystems.

Many insights are tossed off in passing. One concerns predator "switching," a phenomenon often appealed to as a sort of Universal Stabilizing Mechanism. Steele remarks that if a predator switches between two prey species, with each of which individually its interaction is unstable, the outcome remains unstable: the discussion crisply encompasses qualitative reasoning, analytic results, and computer simulation, within the space of two pages.

Chapters 4, 5, and 6 set out and discuss the simulations, which include the hydrodynamics of the North Sea, plant (phytoplankton) production, copepod (zooplankton) grazing and growth, and predation upon these herbivores. The model eventually contains 14 adjustable parameters, and four initial conditions. The system has a strong propensity to exhibit stable limit cycles, with (as mentioned above) the key element in the dynamics being the zooplankton grazing behavior. Among other things, the model leads to predictions about copepod respiration rates, which have been successfully tested in laboratory experiments. It is clear that fluctuations in the recruitment of common fish (whiting, haddock, plaice) are tied to variations in copepod populations; one interesting, if unhelpful, practical conclusion is that although the factors underlying these variations are undoubtedly physical, there is unlikely to be a significant correlation between fish stock size and any one or two physical parameters.

A theme which is emphasized in the introduction (chapter 1) and in the conclusion (chapter 7) is the dichotomy between marine ecosystems, where the stabilizing "control" resides at the plant-herbivore level (and where man largely harvests higher predators, usually with little effect on lower trophic levels), and terrestrial ecosystems, where control is alleged to be provided by predators (and man mainly harvests plants and herbivores). These are provocative ideas, but they rest on too uncritical an acceptance of the fact that herbivores rarely consume more than 10 percent of terrestrial vegetation as a proof that such populations must be controlled by carnivores. The argument that "herbivores would decimate their food unless controlled in a density-dependent manner by the carnivores" (p. 6) overlooks the biological warfare waged between most land plants and herbivores. (Pedantically, it may be noted that in this sentence the misuse of "decimate" to mean something in excess of the literal decimation that prevails testifies to the slack copy editing.) The strategic decisions as to investment in biochemical defenses against being eaten are likely to differ in many ways between trees and phytoplankton, and the possibility remains that the plant-herbivore interface dominates the dynamics both on land and in the sea.

A blemish in the book is its lack of contact with the recent ecological literature. In the extensive bibliography, only eight citations refer to 1971, two to 1972, and one to 1973; chapter 3, in particular, could have benefited from connection with recent work. The explanation, I believe, is that the printers were slow. It remains a pity.

Science recently ran a Research News article entitled "Theoretical ecology: beginnings of a predictive science" (**183**, 400 [1974]). This took a rather generous view of the successes to be expected in this field in the near future. For those who wish to form a closer view of such questions, Steele's excellent monograph is a readable and thoroughly professional account of efforts to marry theory and empiricism in an area of great practical importance.

ROBERT M. MAY
Department of Biology,
Princeton University,
Princeton, New Jersey

Bottom-Dwelling Faunas

Abyssal Environment and Ecology of the World Oceans. ROBERT J. MENZIES, ROBERT Y. GEORGE, and GILBERT T. ROWE. Wiley-Interscience, New York, 1973. xxiv, 488 pp., illus. $24.95.

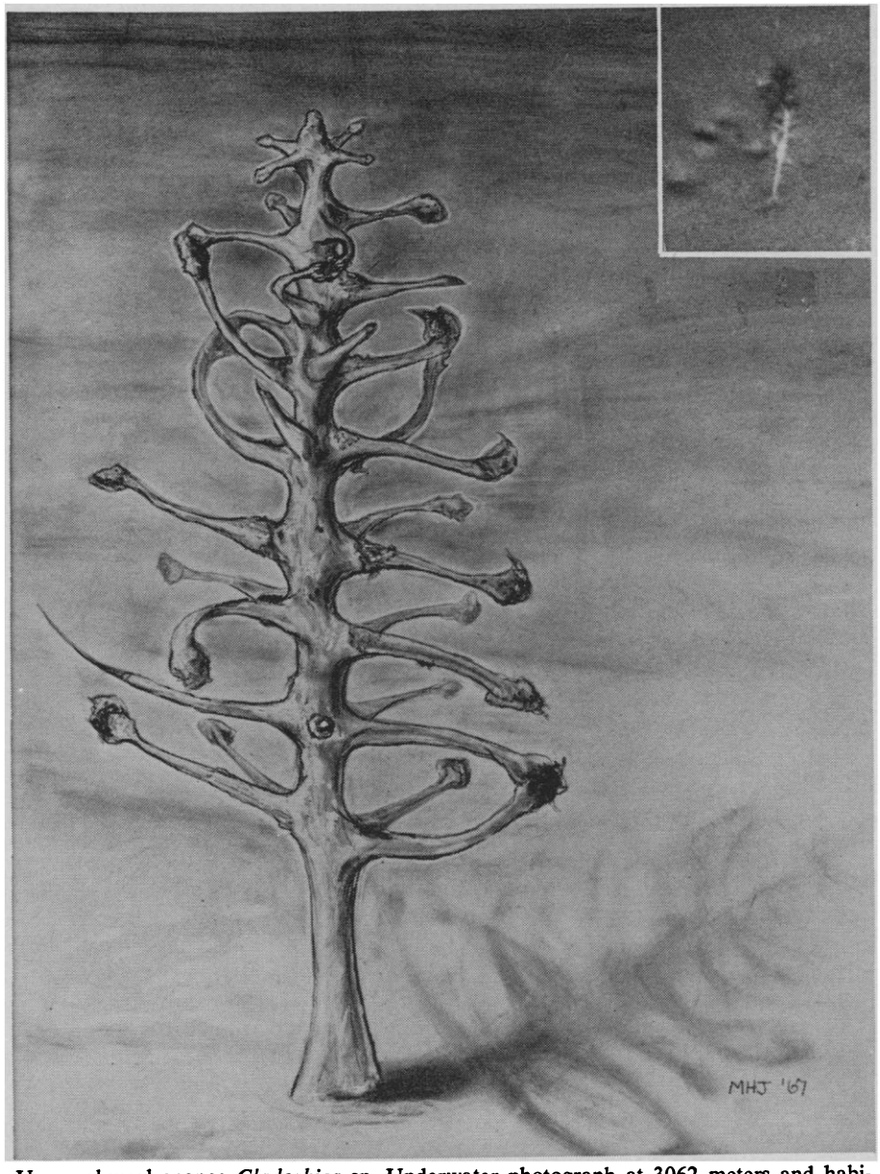
The biology of deep-sea benthic animals has not been dealt with before in a single monographic work. There is a voluminous literature on the faunistics, physical surroundings, and history of the deep-ocean biota, some of it in scarce 19th-century treatises and a significant fraction of that from the 20th century in Russian, both difficult to approach for those without easy access to the major libraries. Menzies, George, and Rowe review much of this field and present some important hypotheses about the distribution of deep-sea animals, adaptations for feeding and breeding, and the age, origin, and changes of deep-water faunas in relation to continental drift and climatic shifts since the Precambrian.

One chapter, as an introduction, deals with some aspects of the history of deep-sea biology from Edward Forbes to modern research vessels. It is followed by a description of the methods and difficulties of sampling. Next, a system of vertical faunal regions in the deep sea, based mainly on isopod Crustacea, is set up. The five chapters following are devoted to this concept: that four major faunal provinces, the intertidal, the shelf, the archibenthal zone of transition, and the abyss (with several zones), varying geographically in extent and bathymetric limits, may be distinguished by objective means, namely, an "index of distinctiveness" which expresses the percentage of genera or species not held in common by any two sampling points along a depth gradient. A chapter is devoted to trench faunas, to which some other investigators have attributed distinctive faunal composition, high endemism, and peculiar morphological features.

In three chapters the authors discuss the distribution of biomass in the oceans, the dispersion of animals and species diversity, morphological adaptations to life in the deep ocean, hypotheses about the distribution of feeding methods, evidence for reproductive periodicity, and the incidence of eyes in deep-water benthic isopods. Two concluding chapters deal with biogeography, first in terms of tolerance to temperature, salinity, and depth, then in terms of the geographical distribution

and origin of abyssal species and faunas. Appendices list "Scientific publications of the great men in deep-sea ecology," results of some major expeditions, and marine research laboratories of the U.S.S.R.

The scope of this work is broad, and it has some strikingly interesting and useful sections, particularly those on sampling, on trench faunas as now known (that is, imperfectly), and on the origin and evolution of the deep-sea fauna related to temperature change in the abyss. The very broadness, though, leads to uneven treatment, and there are some idiosyncrasies. For example, the appendix of publications of "the great men in deep-sea ecology" lists only works by Edward Forbes, Alexander Agassiz, and L. A. Zenkevitch. Are there no others? There are more surprising omissions. For example, there is no discussion of Rowe's own important work showing the relation between primary production at the surface, depth, and the biomass of abyssal animals. The bibliography seems to have been completed in 1969 (although a few of the authors' own publications to 1972 are included), just too soon, apparently, to include mention of Riley's (1970) monograph on particulate organic matter, Dell's (1966, 1972) papers on Antarctic faunas, Koblentz-Mishke's (1970) paper on primary production of the world oceans, Jannasch and co-workers' (1971) studies on bacterial metabolism in deep water, and Heezen and Hollister's (1971) beautiful book based on photographs of the deep-ocean environment. Of course because of the time needed for production it is too much to expect a large, complex book to be completely up to date. However, the total effect of the absence of recent work and of selective coverage is to make this book representative of knowledge of deep-sea animals several years ago, rather than now. Useful and sometimes entirely new information has become available on the metabolism of deep-ocean bacteria and animals, the abundance and significance of predators on the deep-sea floor, the location and extent of areas where Antarctic deep water forms, the late-Tertiary isolation of the Mediterranean and the breakup of Tethys, surface temperatures during the Tertiary, and high diversity in the oligotrophic "red clay" areas of the oceans.



Upper abyssal sponge *Cladorhiza* sp. Underwater photograph at 3062 meters and habitat sketch (artist, Marcia Johnson) at 1940 meters. Height of specimen, 20 centimeters. [From *Abyssal Environment and Ecology of the World Oceans*]

Nearly half the book is devoted to schemes of faunal zonation with depth based mostly on the authors' close knowledge of the distribution of isopod genera and species. Will work on other groups of animals, such as the polychaete worms (which are very abundant in the abyss) substantiate this zonation, or will we eventually have a picture of faunas changing in gradual fashion, as a series of overlapping distributions with depth? A hint of the latter appears in the authors' own tables of species distribution, which, viewed broadly, show a sweeping panorama of change, dissected into zones by percentages which often are of dubious statistical validity. Thorson's concept of parallel communities, developed first for shallow-water faunas, is applied by Menzies, George, and Rowe to a hypothetical reconstruction of deep-sea communities since the Cretaceous. Since species dominance breaks down in the deep ocean (as well as in tropical shallow waters) this, I believe, is an unfortunate way of approaching the faunal changes associated with different kinds of sedimentation in the deep ocean. We know so little about the functional meaning of parallel communities (where they exist) that to apply their names as representative of deep-sea assemblages seems unsound.

A picture emerges from the last two

chapters of a deep ocean that has changed sufficiently in temperature and extent since the Precambrian that major faunal changes must have occurred also. The authors believe that the high species diversity known from great depths cannot be related to constancy of environment, as most of the recent discussions have suggested, because of significant changes in bottom temperature since the mid-Mesozoic. Here they seem to have set up a straw man. I know of no deep-sea biologist today who does not believe that the deep-ocean environment has changed since the Mesozoic because of both continental drift and changes in the amount of deep water being formed at high latitudes. The difference between the deep sea and shallower depths is relative; the deep ocean, at least in the last 160 million years, although changing, has undergone changes at a slower rate than high-latitude shallow water or terrestrial environments, and today has by far the least amplitude of change of any biotic environment. In this lies the *relative* stability that seems to be at the heart of the species diversity problem.

A striking feature of this book is the large number of bottom photographs and artist's reconstructions of abyssal animals on the ocean floor. Many of the other illustrations and the tables are less successful. The captions for figures and tables are often not very helpful, and many figures contain symbols or designations that either are not necessary or are not explained anywhere. Several whole-page figures of virtually limbless isopods seem redundant; surely one or two would have been sufficient to illustrate the range of species and morphology.

Criticisms aside, I am not wholly displeased with this book. It puts forward an individual view of the biology of the deep ocean, often with considerable charm. Its survey of the older literature is good, and its attempt to deal with the deep-sea benthic system as a whole, changing in space and time, is commendable. It serves to mark the shift from descriptive work on deep-water benthos to experimental work on the deep-sea floor which will help to answer the many difficult problems remaining.

ERIC L. MILLS
Department of Oceanography,
Dalhousie University,
Halifax, Nova Scotia, Canada

Faunal Distribution Patterns and Affinities

The Dispersal Centres of Terrestrial Vertebrates in the Neotropical Realm. A Study in the Evolution of the Neotropical Biota and Its Native Landscapes. PAUL MÜLLER. Junk, The Hague, 1973. vi, 244 pp., illus. Dfl. 65. Biogeographica, vol. 2.

The art and science of biogeography remain among the most intriguing and frustrating of enterprises in an intellectual world that seems nowadays to limit the biologist to laboratory experiments or to detailed quantitative analyses of populations in the field. Good biogeographers are able to discern recurring patterns among the multitudinous facts of species distributions, to chart the probable ecological and historical (geodynamic and evolutionary) forces contributing to the patterning, and to provide theories to explain the relationships between co-occurring species and their past dispersal. Some biogeographers are content with the descriptive approach, but not Paul Müller, who has attempted the first explanatory review of the distribution patterns of neotropical amphibians, reptiles, birds, and mammals.

The opening portions of this work are taken up with identifying and characterizing 40 major common distribution patterns (dispersal centers) for tropical Middle America and South America. Seventeen of the centers occur in tropical or subtropical latitudes dominated by broad-leaf evergreen forest, one is a cool temperate center, 19 are found under relatively dry conditions ranging from deciduous dry-seasonal forest to desert, and three are high montane centers located above timberline, including paramo and puna zones together with the tundra (permafrost) portions. While it is clear that the more complete evidence from birds and mammals biases this section and different results are possible if amphibians and reptiles are considered separately, it provides a major source of data on distributions and patterns, unencumbered by the usual attempts to draw boundaries between areas, since only the nuclear areas of overlapping distributions (the centers) are used for discussion and evaluation. A second section reviews the affinities of the centers to one another.

The most important segment of the book is the discussion (pp. 182–204) of the many stimulating ideas generated by the previous section. The following five conclusions are of particular importance:

1) The centers of dispersal are centers of origin for many present-day species and subspecies populations.

2) During the Pleistocene and to the present, significant glacial-related fluctuations in lowland tropical climates caused the expansion of humid evergreen forests and regression of the subhumid-to-xeric areas, alternating with dry periods when evergreen forest centers regressed and became widely separated by expanding subhumid-to-xeric areas; the most recent dry segment of the cycle was between 5000 and 2300 years ago.

3) Present distribution patterns support the concept of a displacement of montane (1500 meters and up) groups downward during glacial maxima (25,000 years ago) to areas now occupied by lowland forest.

4) The most significant factor controlling speciation in the neotropics was the postglacial fluctuations with reduction and expansion of distribution refuges (centers) responsible for isolation and differentiation.

5) The fauna of the pampas of Argentina and the Parana pine (*Araucaria*) campo and campo cerrado of Brazil lends support to their long-term distinctiveness as natural units, rather than as disturbance zones of human occupation.

Conclusions 1 and 2 seem especially well documented by bird and mammal data. Conclusion 3 implies downward displacement of montane communities to such an extent that all of the lowland evergreen forests of Central America would have been eliminated. No evidence suggests that the current forests of that region or their distinctive animal associates have invaded this area during the last 11,000 years from northern South America. Such an invasion would have had to originate in the Choco forests, which might also have been eliminated by the temperature depression required by Müller. Factors other than maximum temperature displacement are therefore required to explain the similarities between several of these now isolated montane centers.

Conclusion 4 is also suspect. Many of the components of the dispersal centers doubtlessly have long Tertiary histories in the region. For example, the