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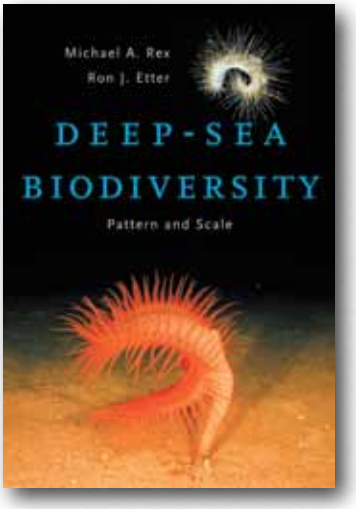
Deep-Sea Biodiversity: Pattern and Scale



By Michael A. Rex and Ron J. Etter, Harvard University Press, 2010, 354 pages, ISBN 978-0-674-03607-9, Hardcover, $55 US

REVIEWED BY NICHOLAS J. BAX

It was a pleasure to read *Deep-Sea Biodiversity: Pattern and Scale*. The book provides a detailed synthesis of patterns in bathyl and abyssal diversity, accounting for the vagaries of sampling, analysis, and the existing history of hypothesis definition and testing. Of course, the authors' detailed review of the literature—more than 800 references occupy 60 pages—comes at a price. The wealth of material in the book makes it a challenging read, but fortunately the authors provide good concluding sections for each chapter and a summary chapter that pulls together the major points and suggests future research. The book will remain an excellent reference for deep-sea biodiversity researchers for many years. The illuminating juxtaposition of quotations going back over 150 years is an indication of how our understanding of the creatures that inhabit the deep sea has changed over that period.

The authors work through the various aspects of diversity in a straightforward sequence. Chapter 1 addresses the patterns of benthic standing stock, starting with the organic carbon flux from the surface. They point out that particulate organic carbon (POC) declines exponentially with depth, so only 1% remains at the depth of the abyssal plain, making it an extremely energy-poor system. Only a few opportunistic species can take advantage of seasonal flux in POC, or local phytodetritus accumulations; most abyssal species appear to show little variation in abundance over time. Good evidence is provided for an exponential decline of biomass with depth and a movement toward smaller-sized organisms so that by the time the abyssal plain is reached, bacteria, foraminiferans, and minute metazoans dominate. Standing stocks are higher in areas where food supply is increased, further reinforcing the link between surface production and benthic standing stock.

Chapter 2 describes local species diversity (i.e., within a range of centimeters to tens or possibly hundreds of meters at bathyl depths). It is one of the more difficult chapters, given the diversity of sampling devices and survey designs used over the years, and in different areas, complicating the authors' synthesis task. Rarefaction curves are used extensively, although the authors later acknowledge their tendency to conflate species richness and evenness. This seems especially relevant, as bathyl communities are reported to show generally higher evenness and more rare species than those on the shelf. High local bathyl diversity is considered to arise from multiple factors operating over a range of spatial and temporal scales: the authors list sinking phytodetritus, dead falls, foraging activity, bioturbation, pits, mounds, minute biogenic structures, and periodic disturbance. The smaller size of bathyl species is seen as important, causing these species to experience environmental heterogeneity at smaller scales, potentially increasing the importance of smaller physical properties such as sediment grain-size diversity. The authors conclude that more precise sampling, including experimental work, is necessary to explain local high bathyl diversity. Recent technological and statistical advances mean that this is now possible; improved understanding of larger scale evolutionary and ecological patterns provide the context for their interpretation.

Chapter 3 discusses regional patterns of alpha species diversity within deep-sea basins or around large topographic features of basins, covering scales of tens to hundreds of kilometers. A major focus is on regional-scale depth gradients, and the authors synthesize information on mega-, macro-, and meiofauna, but concentrate on North Atlantic macrofauna where there are more examples to show a general unimodal trend of diversity with depth. Overall diversity is lower in the Norwegian and Mediterranean seas, in the core of oxygen minimum zones, and in areas of heavy nutrient loading. An interesting discussion of alternative statistical and ecological causes (productivity, particle size, disturbance) for these patterns follows, with

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the authors proposing patterns in food supply mediated through their effects on population density and growth as the main contributing factor. The authors conclude that "all circumstances of high nutrient loading in the deep sea, irrespective of depth, result in high population density and depressed diversity compared to neighboring habitats." Higher and more variable productivity is used to explain the lower diversity in shallow waters. Alpha diversity peaks at a shallower depth in less-productive systems, until it finally disappears in the impoverished Mediterranean, leading to the observed monotonic decline with depth. The authors present and discuss clear exceptions to these general trends—foraminiferans, isopods, and holothurians—and illustrate the need to also consider ecological release, adaptation, and evolutionary radiation. Source-sink dynamics may maintain many abyssal populations, and even bathyl populations in the Mediterranean.

The examination of oceanwide variation in alpha species diversity in Chapter 4 is confined to the Atlantic Ocean due to a lack of comparative information outside of this area. The authors first note that the deep-sea environment is not as constant as once assumed. A major pattern (once depth and evenness have been accounted for) is a decline in diversity with latitude, at least where a trend can be detected. Evolutionarily isolated regions like the Norwegian Sea require special consideration due to their reduced diversity. Meiofauna (or at least foraminifera) again show a clearer signal of ecological interactions, with an increasing proportion of opportunistic phytodetritus consumers at higher latitudes. The authors suggest that the general decline in diversity with latitude results from higher, seasonally pulsed production at higher latitudes, but they caution that our knowledge of basin and global patterns in biodiversity is still in its infancy. The deep sea is not immune from outside influence as shown by the diversity of foraminifera and ostracods that has varied on orbital, millennial, centennial, and decadal time scales. The authors conclude that understanding deep-sea biodiversity patterns and their contribution to global biodiversity requires us to consider both current and historical processes.

Chapter 5 describes beta diversity along depth gradients. The difficulty of comparing different studies using different gear and strategies is compounded by the variety of ordination methods used to describe the results. And the authors note that only rarely are distinct zones observed in the deep sea; the rate of species replacement corresponds roughly to the rate of change in depth, with abrupt changes only occurring at topographic barriers and environmental boundaries—oxygen minimum zones, nutrient depocenters, water mass boundaries, and high-energy currents. They note that beta diversity cannot be considered independently from abundance and alpha diversity; low alpha diversity in the abyss precludes high similarity in multivariate analyses with adjacent bathyl areas. The decreased food supply leads to a disproportionate decrease in the abundance of larger animals (mega- and macrofauna) and an increase in prevalence of smaller deposit feeders. Holothurians and isopods, which show high abyssal diversity including abyssal

endemics, are presented as exceptions to the general trend.

In their final discrete chapter, the authors consider the role of evolutionary processes in generating deep-sea diversity. Or, where did all the species come from, given the comparative lack of physical barriers to drive allopatric speciation, the frequently high dispersal potential of deep sea fauna, and a presumed lack of diversity in many deep-sea species' diets—detritus? Noting that horizontal variability is higher on the shelf and bathyl areas, a prevailing view is that deep-sea fauna and their diversity originate from coastal fauna, punctuated by periods of anoxia, extinction, and further invasions of the deep sea possibly enabled by the resulting increase in organic carbon flux. However, the authors report that invasion has not been all one way, with some groups originating in the deep sea and invading shallower communities.

They consider potential barriers to dispersal—distance, currents, topography, oxygen levels, vicariance, and depth-related (hydrostatic) pressure—which lead them to conclude that the greater spatial and temporal variability at bathyl depths plus the extraordinarily low food supply to the abyss indicate that deep-sea diversity originates at bathyl depths. Thus, to understand the processes that shape macroecological patterns in the deep sea requires an understanding of the geographic, bathymetric, and temporal patterns that generate new species.

A final summary chapter provides a good review of the earlier chapters and suggests where further research is required to improve our understanding of deep-sea diversity.

Deep-Sea Biodiversity: Pattern and Scale provides an interesting snapshot in time and space. As the authors mention, much has happened in the last two decades to warrant this book. That much of this activity has happened close to the most established research institutes leads to a high reliance on data from the North Atlantic. At the same time, much is happening now that will expand on the subject of the book, which focuses on the soft sediments of the deep sea (i.e., the habitat that can be successfully sampled with more established sampling methods). Over the last two decades, as navigational, positional, and sampling capabilities have increased (for industry and researchers), there has been increasing interest and focus on the hard grounds of the deep sea—seamounts and vents being key examples. Through international collaborations such as the Census of Marine Life, which reported results of its 10-year census of the world's ocean in October 2010, information on hard-ground communities of the deep sea (especially bathyl depths) is becoming available. For example, new hypotheses to explain the biodiversity of deep seamount communities are being proposed and refuted at a rapid rate (Rowden et al., 2010). Coincidentally, as the authors allude to in their final chapters, new genetic technologies are changing the way in which we look at wide-spread "species" as increased structuring is being found over horizontal distance and depth.

This increased knowledge of deep-sea communities comes at an important time in the international management of the deep sea, as international organizations such as the Global Ocean Biodiversity Initiative, the Convention on Biological Diversity, and the Fisheries and Agricultural Organization of the United Nations consider how to identify and manage ecologically and biologically significant areas, or vulnerable marine ecosystems. This book provides an important scientific contribution to those international initiatives. The authors end the first chapter with a plea for a greater consistency in sampling gear and sample processing protocols, together with the suggestion that scientists make raw data available at the same time that papers are published. Based on this substantial synthesis and coincident international initiatives, it is clear that furthering our knowledge in the deep sea will be best advanced through international collaboration, consistent sampling protocols, and sharing our data.

I would recommend *Deep-Sea Biodiversity* as a reference book and a good read for graduate students, researchers, advocates, and managers interested in understanding and managing the 60% of our planet that is the deep sea.

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