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Book Review

Marine Metapopulations

Kritzer, J.P. & Sale, P.F. (Eds)

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While the title of this book 'Marine Metapopulations' is mellifluous and rolls easily off the tongue, the application of metapopulation theory to marine organisms is a less graceful match. Levins' (1969, 1970) original theory of metapopulations examines a balance between extinction and recolonization rates of local patches that are connected by dispersal. In an attempt to minimize the threat of extinction to species living within increasingly fragmented terrestrial ecosystems, many ecologists and resource managers have evoked the concepts inherent in metapopulation ecology. However, in the marine realm, it remains unclear whether habitat fragmentation is a major threat to the many ecosystems present that have evolved within the constraints of a naturally fragmented world, and how a metapopulation concept could be applied to conservation efforts. Relatively few marine taxa experience extinctions on ecological time scales, in part due to high population connectivity conferred by planktonic larvae. Thus, most authors in this volume relax the extinction requirement to better examine their own system within a metapopulation framework. The theory of marine metapopulations is nascent still, and empirical evidence of its utility is just now surfacing.

Prior to the publication of Marine Metapopulations there have been three primary texts in the field: *Metapopulation Biology: Ecology, Genetics, and Evolution*, Hanski and Gilpin (eds) (1997); Hanski's sole author text, *Metapopulation Ecology* (1999); and the most recent *Ecology, Genetics and Evolution of Metapopulations*, Hanski and Gaggiotti (eds) (2004). These books clearly establish the place of metapopulation ecology within the broader fields of ecology and evolution, and provide ample evidence, both theoretical and empirical, of the applicability of metapopulation concepts in terrestrial ecosystems. However, across all three of these texts, there is a dearth of examples from the marine environment. *Marine Metapopulations* by Jacob Kritzer and Peter Sale begins to remedy this situation by introducing metapopulation theory across a diversity of marine ecosystems and organisms.

The book contains 16 chapters from 29 contributors, including a laudatory forward by Joan Roughgarden. Following the introduction, the chapters are grouped into sections, first by taxon, with three chapters on fishes, five chapters on invertebrates, and two chapters on marine plants (seagrasses and kelp). The book ends with a 'Perspectives' section containing five synthetic chapters addressing conservation, genetic approaches, metacommunities, and the future of metapopulation science. The authors wrote about systems they knew well, and, in most chapters, provided a good reference list of previous work in that field, especially for studies done after 2000. The chapters include a wealth of compendium tables and useful conceptual diagrams that review or illustrate metapopulation principles.

The first chapter provides historical context for the development of metapopulation theory, explaining the emergence of metapopulation ideas from marine ecological studies on settlement, recruitment, dispersal and connectivity, and from conservation imperatives. Most remaining chapters start with a nod to the classic Levins definition of a metapopulation and progress rapidly to the 'contemporary' definition in which extinction is unlikely. The majority of chapters review the relationship between a particular taxon and metapopulation theory, following a similar format wherein the authors review the relevant literature, discuss their definition of a metapopulation, justify that definition based on the natural history of the organism or phylum under consideration, and present case studies illustrating or contradicting the match between metapopulation theory and their taxon.

The chapter on estuarine and diadromous fish metapopulations stands out as exceptionally well organized, well researched, and well contextualized in the theories of ecology and fisheries science. The sometimes vague concept of a metapopulation is clarified by (i) clearly defining 'population' and 'local population', (ii) describing a continuum of adherence to the definition of metapopulations for marine species, (iii) recognizing a distinction between naturally evolved and fragment-induced metapopulations, and (iv) choosing and describing appropriate methods (population genetics and tagging) to answer questions at different temporal scales (evolutionary and ecological). Undoubtedly, this clarity is assisted by the tidy fit between anadromous fish and metapopulation theory.

The two other chapters on fishes provide an interesting contrast in how the authors approach the fit of their taxon to a metapopulation framework. The chapter on coral reef fishes relies mainly on a description of the natural history and ecology of the organisms, while the rocky reef fish chapter focuses primarily on population genetics supported by a discussion of aspects of reef geology and oceanography that might influence population structure. These different approaches appear throughout the book, although the natural history approach dominates.

Several of the other 'taxon' chapters help the reader understand the usefulness of metapopulation theory in asking and answering ecological and conservation questions. The chapter on giant kelp contains one of the few quantitative examples of local patch extinction and recolonization events. Convincing arguments are made for the metapopulation structure of abalone and *Tigriopus* (an intertidal copepod) due to their limited dispersal, as well as for hydrothermal vent organisms and corals, due to their naturally patchy habitat structure. However, discussions of the endangered white abalone, classic intertidal invertebrates (such as mussels and barnacles), and specific hydrothermal vent organisms are missing from their respective chapters.

The 'Perspectives' section succeeds in providing synthesis while reflecting the broad applications of marine metapopulation theory. This section reviews the information that genetics can contribute to explanations of demographic and metapopulation dynamics, the role of metapopulation theory to marine conservation, and that of metacommunity theory to marine systems. The final chapter summarizes the usefulness of metapopulation theory in understanding population dynamics and its applicability to the management of marine species. It reexamines the similarities and differences between marine and terrestrial systems, outstanding research questions, and the potential for use of metapopulation theory in management through marine protected areas (MPAs).

One fairly consistent, recurrent theme is the dearth of empirical connectivity data available for most taxa. There is a clear consensus that theoretical development has outpaced experimental support, and that this is due to the difficulty of measuring dispersal and connectivity in marine ecosystems. This difficulty appears to be a primary barrier in applying metapopulation theory, and led authors to tailor the theory to the model system or organism. Still, many authors do an excellent job of emphasizing outstanding research questions related to larval dispersal and population connectivity.

Although this book lacks the organization and uniformity of approach to function as a textbook, a problem often unavoidable with multi-authored contributions, it offers readers a general understanding of metapopulation dynamics in the ocean and serves as a strong foundation for more detailed and focused studies. Authoritative reviews are provided by most authors, who adhered closely to their area of expertise and focused their chapters on a few specific case studies. A broad range of fishes, invertebrates, and marine plants are considered in the volume, but there are important omissions such as marine tetrapods, plankton and microbes. In general the authors view marine metapopulation applications as grounded in demersal and benthic systems, with little thought to water column/holoplankton applications, perhaps due to the lack of metapopulation research currently being pursued in those fields.

The book chapters are written at a range of levels, with some assuming advanced technical knowledge and others providing extensive background. Taken as a whole, the book is best suited to practicing marine scientists at or above a graduate student level, as a reference for specific applications of metapopulation theory.

This review reflects the opinions of 16 marine science graduate students who read the entire book and spent approximately 20 h over 2 months discussing the concepts and applications of metapopulation theory highlighted in the chapters. That we could do that much talking is a testimony either to the provocative nature of the material covered, or to the subject itself. Some ultimately felt the purpose of framing populations in a metapopulation context was unclear, perhaps because the concept is not a strong fit for some marine systems, or because marine systems are not yet ready to be critically assessed via metapopulation dynamics. Overall, however, the book convinces us that metapopulation theory is useful in identifying the continuum of connectivity levels that occurs in marine systems. It helps us define and refine questions that are, in the words of forward author Joan Roughgarden, 'the last hope for marine conservation'.

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