

Available online at www.sciencedirect.com

SCIENCE \overrightarrow{a} direct^o

Ecological Modelling 178 (2004) 77–80

www.elsevier.com/locate/ecolmodel

Review

Review of Ecological Microcosms by Robert J. Beyers and Howard T. Odum

Joan A. Browder

Southeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, 75 Virginia Beach Drive, Miami, FL 33149, USA

"Ecological Microcosms" (Beyers and Odum, 1993, 557 pp.) is a big book about small worlds. In a review and synthesis of microcosm studies, the authors, Robert J. Beyers and Howard T. Odum, cover the literature on microcosms including everything from algal mats in clear plastic tubes to humans in "Biosphere 2," extracting ecosystem principles wherever they look. Both authors are pioneers in building microcosms and using them in research, and they have published previously together on this topic (e.g. Beyers et al., 1963; Odum et al. 1963a,b). The work of both spans freshwater and marine systems. A paper by Odum and Hoskin (1957) on a flowing water microcosm was thought to have been one of the first publications on a microcosm experiment; however, my cursory perusal of this book's bibliography suggests that the first publication about microcosms might have been that of Conger (1922).

Information in "Ecological Microcosms" was synthesized from many original papers and reviews. There have been many previous reviews of microcosm and mesocosm studies. This, however, may be the most ambitious review and synthesis because of the scope of coverage, depth of treatment, and systems ecology framework. The bibliography is 64.5 pages and contains well over 1000 papers, most of which were cited (asterisks indicate those cited in the text).

In defining the scope of their book, Beyers and Odum explain that while any assemblage of living organisms in a container might be called a microcosm they are considering only those that have the characteristics of ecosystems—food chains, hierarchies, coupling of production and consumption, mineral cycling, diversity, and animal control of plants and microorganisms. The book considers only systems in artificial containers, created by humans, not those isolated in nature, such as ponds, that are sometimes referred to as microcosms.

1. Part 1: a microcosm approach to ecosystem theory

Microcosm studies helped develop the foundation of systems ecology. They are rich in principles, most of which were encapsulated in the chapter headings of part 1: "succession and self-organization," "metabolism and homeostasis," "chemical cycles and limiting factors," "diversity and information," "hierarchy, control, and oscillation," and "stress, toxicity, and adaptation."

Microcosm studies helped Odum to develop and educate others about the "maximum power principle," a principle of self-organization first fully stated by Odum in a 1967 paper that cited Lotka (1922a,b) as the origination of the concept. According to this principle, organisms thrown together in space and

E-mail address: Joan.Browder@noaa.gov (J.A. Browder).

^{0304-3800/\$ –} see front matter © 2003 Published by Elsevier B.V. doi:10.1016/j.ecolmodel.2003.12.007

time will organize themselves into an ecosystem by developing feedback pathways that reinforce the most mutually useful processes in terms of capturing and using energy, and those species that are mutually reinforcing will become the functional dominants. The phenomenon has most effectively been induced in microcosms by introducing organisms in waves, a procedure called multiple seeding. Beyers and Odum refer to microcosm studies with multiple seeding as being some of the most successful in terms of generating complex trophic structure. The Microcosm Estuarine Research Laboratory (MERL) mesocosm studies at Narragansett, Rhode Island, are examples in which continual seeding occurs from pumped sea water. For the original work, look up the name C.A. Oviatt in the Beyers and Odum bibliography.

The MERL studies and others were used to illustrate the relationship of diversity to production, efficiency, and resiliency. This relationship, as described by Beyers and Odum, is a concept related to the maximum power principle. The authors make the point that, although diversity is costly to maintain, it is self-reinforcing because it increases the intake and efficient use of resources. Diversity is described as a balance of information inflow and extinction. The ingredients are species that may arise de nova through mutation and recombination or via immigration. Species that get there first (or were already there) have an advantage in becoming dominants, however, they can be replaced by new system entries, supposedly if the system were not yet functioning optimally under the prevailing conditions and especially if the conditions have changed. There are limits to the number of species that can be maintained in a microcosm or any other ecosystem. For example, roughly half of the new species introduced by Cairns and Yonge (1973) to protozoan communities in a microcosm experiment were successful, yet the microcosms each ended up with approximately the same number of species to which they had equilibrated initially (6–12 species per microcosm) because some of the species previously present had been displaced. At some point, as species are replaced, the ecosystem itself has been replaced by another ecosystem. The authors may not state this explicitly, but one can infer that ecosystem replacement has occurred when energy flows and other basic ecosystem characteristics have changed substantially. The simplest example would be succession from early pioneer stages to climax, yet, even here, it is easy to distinguish the end states but more difficult to identify the break point in the continuum. If succession is restarted, it will not necessary follow a pathway to the same climax, especially not if conditions or the species mix has changed. Defining an ecosystem and determining when, and under what circumstances, it is replaced by another is an issue at the heart of systems ecology as well as restoration ecology and is a reason for devising and measuring indices of ecosystem characteristics, especially emergent properties.

Beyers and Odum consider stress an agent of change. They define stress as "some factor for which species are not adapted to profit." The Random House College Dictionary's (1975) applicable definition is similar: "any stimulus, as fear or pain, that disturbs or interferes with the normal physiological equilibrium of an organism." Applied at the ecosystem level, Beyers and Odum consider stress as a temporary condition because the arrival or generation of new species and the self-organization that ensues in response to new conditions result in a system adapted to the new conditions, no longer stressed. With the right set of species, an ecosystem can adapt to almost any stress (although it is not necessarily the same ecosystem that it was when it started out, or one that we as humans would want). This is especially true if the stress is applied steadily or at least with somewhat predictable frequency.

The question of whether stress has a positive or negative effect on diversity is discussed without conclusion. Hutchinson's (1961) "paradox of the plankton" concept is evoked by Beyers and Odum to suggest that a general stress such as physical turbulence and dispersal could increase diversity by preventing any one species from becoming dominant. If so, they say, then this is another case of energy (the energy of the turbulence) maintaining diversity. On the other hand, Margalef (1958), found that turbulent waters contained low diversity. Species that are adapted to a stress have an advantage over those that are not, which they may out-compete, resulting in an ecosystem with lower diversity. Certainly this applies to brine systems and thermal systems, made up of a very few highly adapted species.

Larger species tend to be more sensitive to stress than smaller ones. Several reasons are given for this. One is the greater accumulation of toxins within the greater mass of body fat that tends to characterize larger organisms. Another is, the cumulative effect of ionizing radiation, which causes genetic damage, in larger animals, which have greater exposure. Another reason that larger species are discriminated against in stressful environments is their longer time for maturity, reproduction, and recruitment. Continual or intermittent stress tends to favor those species that can regenerate quickly; therefore, in general, stress favors "*r*" type rather than "*k*" type species. There are cases, however, when longer lived species can ride over or benefit from the effects of predictable repetitive stress as, for example, both wading birds and cypress trees tolerate and take advantage of the alternating wet and dry seasons and wet and dry years in South Florida.

Many microcosm experiments have been conducted by environmental protection agencies to test the ecosystem-level effects of toxins (for example, look up the name F.B. Taub in the Beyers and Odum bibliography). Some have indicated that ecosystems can become adapted even to toxins. Undesirable changes in the system may have occurred, however, and we might wonder whether, at some point, an ecosystem has died, so to speak, and another taken its place. It follows from examples given by Beyers and Odum that toxins in an ecosystem can result in decreased diversity, compressed food webs, and reduced resiliency to other stresses. As another example the authors gave results of their work with irradiation in microcosms, an area that both authors have considerable experience with. In almost all cases presented, time was an important consideration. For example, the length of time that irradiated organisms were held before placement together in a microcosm affected the microcosm ecosystem that developed. The authors offered the explanation that DNA repair took place that improved the ability of the species to maintain themselves in a competitive environment.

According to Beyers and Odum, there are implications of the effect of stressors on energy flow because energy must be diverted from production to enable adaptation. The authors suggest that, in future analyses of the effect of stress, it should be expressed in energy terms so that energy flows and stresses can be studied in relation to each other. They suggest a way that the conversion of stress to energy terms might be accomplished.

2. Part 2: practical information on microcosms

This book is not just for theorists but contains much practical material. Part 2 describes the types of microcosms: aquaria, streams, terraria and soil, ponds and pools, reefs and benthic, plankton water column, thermal, and brine. The latter two, experiencing the most extreme conditions, are especially fascinating. Microcosms can be further classified into "open" and "closed," as defined by Beyers and Odum.

Part 2 provides many examples regarding the construction of microcosms. One topic is "microcosm apparatus for working with dangerous chemicals." This is another topic with which both Beyers and Odum have had first-hand experience, and one major use of microcosms has been for testing the effect of toxic materials.

Included also are detailed illustrations of stream microcosms, including the flowing water microcosm built by Odum and Hoskin at Duke University. The discussion of stream microcosms is especially rich and touches on many of the roles of flowing water in an ecosystem. Many aspects of the chapter on stream microcosms have application to ecosystem restoration projects in the Everglades, the Louisiana coastal wetlands, and elsewhere (see article in this volume by Mitsch and Day.)

3. Part 3: the use of microcosms by society

Part 3 explains the use of microcosms and mesocosms by society, including food producing and waste processing micro- and mesocosms. There is even a discussion of microcosms as it relates to humans in space. Finally, in appendices A and B, the authors provide details on how to build, maintain, and monitor "classroom" microcosms. Appendix C, authored by Abigail Alling and others at Space Biospheres Ventures and Robert Frye of the University of Arizona, describes the experiments on the Biosphere 2 Test Module, a closed ecological system "designed both as a test of physical structure and engineering components for Biosphere 2 and as a test bed for developing ecological systems." Odum was deeply interested in that effort and followed it closely.

Models, when available from the original work, were presented along with energy-flow mini-model translations, often with equations. Where models were missing from the original papers and needed to illustrate structure and make points, Beyers and Odum created them anew. The diagrams are used throughout this book to clarify concepts, relate mechanisms, show patterns of organization and temporal trends, and reveal and explore emergent properties of ecosystems. The use of system diagrams and simulations to organize and synthesize microcosm research gives this book a special significance. In this book, Beyers and Odum present aggregated model diagrams that depict the structure and function of whole systems with a relatively small number of compartments and connections that are easy for the reader and viewer to follow. With these, he synchronizes the flows of energy, materials, and information. For modelers, the examples and equations for simulating a number of ecosystem processes are a less obvious value of this book—an added bonus, probably unexpected by most who might first open it.

I originally purchased this book because I shared the authors' interest in algal mats and wanted to model the ones in the Everglades. I found that the book is a good overview of systems ecology, microcosms, and mini-models. It is rich in ideas and practical information. Both in its size and in its content, the book was even more than I expected. Reading it, I realized that this one book encapsulates in an unselfconscious way the entire spectrum of H.T. Odum's dynamic and diverse professional life, from its roots in basic ecology to the application of emergy to world-scale social and environmental problems. This makes it a special jewel to those of us who knew him.

References

- Beyers, R.J., Odum, H.T., 1993. Ecological Microcosms. Springer-Verlag, New York, 557 pp.
- Beyers, R.J., Larimer, J.L., Odum, H.T., Parker, R.B., Armstrong, N.E., 1963. Directions for the determination of changes in carbon dioxide concentrations from changes in pH. Publ. Inst. Mar. Sci. Texas 9, 454–489.
- Cairns Jr., J., Yonge Jr., W.H., 1973. The effect of an influx of new species on the diversity of protozoan communities. Rev. Biologia 8 (1–4), 1187–1206.
- Conger, G.P., 1922. Theories of Macrocosms and Microcosms in the History of Philosophy. Columbia University Press, New York.
- Hutchinson, G.E., 1961. The paradox of the plankton. Am. Nat. 95, 135–146.
- Margalef, R., 1958. Temporal succession and spatial heterogeneity in phytoplankton. In: Perspectives in Marine Biology. University of California Press, Berkeley, California, pp. 323–349.
- Odum, H.T., Hoskin, C.M., 1957. Metabolism of a laboratory stream microcosm. Publ. Inst. Mar. Sci. Texas 4, 116– 133.
- Odum, H.T., Beyers, R.J., Armstrong, N.E., 1963a. Consequences of small storage capacity in nannoplankton pertinent to measurement of primary production in tropical waters. J. Mar. Res. 21, 191–198.
- Odum, H.T., Siler, W.L., Beyers, R.J., Armstrong, N., 1963b. Experiments with engineering of marine ecosystems. Publ. Inst. Mari. Sci. Texas 9, 373–403.