Book Reviews

Food Webs

Food Webs. STUART L. PIMM. Chapman and Hall, London, 1982 (U.S. distributor, Methuen, New York). xii, 220 pp., illus. Cloth, $35; paper, $16.95. Population and Community Biology.

A food web is a schematic diagram showing the relationships among species in a community of plants and animals. Part of the received wisdom of ecology's early days—still to be found in many introductory texts—was that complex food webs, with many species interconnected by a tangled maze of strong interactions, tended to be more stable (less affected by natural or man-made disturbances) than simple webs. In the late 1960's and early 1970's, the empirical basis for this generalization began to be questioned (for example by Watt). This questioning was sharpened by studies of mathematical models for "randomly constructed" food webs. Such studies showed that as complexity increased, in the sense of there being more species, or more connections, or stronger interactions, stability usually decreased, in the sense that the system was less likely to recover from disturbance. In demonstrating that stability does not automatically follow from complexity, these early studies of model ecosystems served mainly to set the agenda for a second generation of investigations: do real food webs show any systematic patterns, and, if so, how may these patterns be explained?

Pimm's book is a well-organized and nicely written survey of a decade of progress on this agenda. He begins with a taxonomy of the mathematical models that are used to explore the dynamical properties of various kinds of food webs; the two main types of models are the so-called Lotka-Volterra differential equations and systems of differential equations with donor control (in which prey/donor abundance affects predator/recipient dynamics, but not the converse). There is also a lucid catalogue of the variety of ways in which "stability" can be defined, with comments on the biological and mathematical virtues of each definition. The mathematics here, as elsewhere throughout the book, should be within the reach of anyone who has done introductory calculus.

With this groundwork laid, Pimm goes on to summarize and tabulate information about the structural properties of real food webs. These data come from a variety of sources and extend earlier compilations such as Cohen's *Food Webs and Niche Space* (Princeton University Press, 1978). Pimm then discusses a diversity of theoretical investigations in the light of these data.

Pimm shows that different kinds of mathematical models lead to different general conclusions about the relation between stability and complexity. In particular, perturbation of a community by removal of a predator species will tend to lead to further losses of species when Lotka-Volterra models are used but has no such further effects when donor control models are used. The evidence available from field studies in which predator species are experimentally removed from communities is that further species losses nearly always occur. Pimm uses this fact to justify confining his attention mainly to Lotka-Volterra models in what follows.

He also surveys evidence showing that as the number of species, S, increases, the average connectance in the web (C, the number of actual links between species as a ratio to the number of topologically possible links) decreases; the product SC is very roughly constant, at around 4 to 5, for essentially all food webs. Although this empirical observation accords with early suggestions that food web stability may depend on the product SC, a simpler explanation is that species tend to interact directly only with a handful, $n \simeq 4$ to 5, of other species, regardless of the size of the community (whence, for large S, $C \sim nS/S^2$ and $SC \sim n$). But even this simpler explanation leaves the problem of understanding *why* each species, on average, interacts with such a relatively small and constant number of other species.

By tracing food chains from primary producers, through successive levels of consumers, to top predators, it can be shown that most food webs comprise only three or four trophic levels. The conventional explanation for the relative constancy and relative shortness of food chains is that at most 10 percent or so of available energy can be transferred from one level to the next and that this rapid attenuation forbids long chains. But, as Pimm and Lawton first emphasized, such an explanation carries the implication that food chains should tend to be longer in highly productive environments (with a larger energy base) and in communities of cold- rather than warm-blooded species (where the efficiency of energy transfer between trophic levels is significantly higher). Neither of these tendencies appears to be exhibited by real ecosystems. Pimm expounds the alternative explanation that dynamical considerations shape food web structure: in simulated webs with Lotka-Volterra interactions among species, long food chains lead to severe population fluctuations that are inconsistent with long-term persistence. DeAngelis *et al.* have observed, however, that such dynamical arguments are keyed to the characteristic doubling times of the slowest-changing populations, so that a tenfold speeding of metabolic rates throughout the ecosystem may—other things being equal—enable food chains to lengthen while the overall dynamical stability remains unchanged; I would have liked to see more discussion of this point.

Another pattern adduced by Pimm is that the number of omnivores—animals consuming prey from two or more different trophic levels—in real food webs tends to be significantly lower than would be found if the connections within the web were made at random. This pattern is predicted by numerical studies of the dynamical stability of model webs with Lotka-Volterra interactions. More specific theoretical predictions are that: (i) there is typically only one omnivore per food chain; (ii) omnivores rarely exploit prey not at adjacent trophic levels; (iii) systems dominated by insects and their parasitoids permit greater complexity of patterns of omnivory than do vertebrates.

Later chapters discuss a variety of other possible patterns, including ratios between numbers of predator species and their prey species, the possible organization of apparently complicated food webs into loosely coupled subunits, and Cohen's finding that food webs can be represented in a one-dimensional niche space far more often than would be expected by chance alone (food webs are usually "interval graphs").

Interest in this general subject continues to expand rapidly. One consequence is that many significant developments have taken place since this book (which has many 1980 references and a few 1981 ones) went to press. For example, Briand has provided an excellent catalogue of 40 food webs (and a later study of 62 webs is circulating among the Invisible College); Yodzis has argued that food chain lengths can indeed be explained on energetic rather than dynamical grounds; it has been shown by Nunney and by Abrams and Allison that extensions of the simple Lotka-Volterra models to include realistic refinements (such as time lags or nonlinearities in the functional and numerical responses of predators to prey densities) can significantly modify the dynamical properties; and so on. These developments were well covered at a recent conference, the proceedings of which are available as an Oak Ridge Technical Report (D. L. DeAngelis, W. M. Post, G. Sugihara, Eds., *Current Trends in Food Web Theory*, ORNL/TM-8643 [1983]; for an overview of the issues covered in this report, see R. M. May, *Nature* **301**, 566 [1983]). None of this, however, diminishes the value of Pimm's book as the best introduction to the subject that is currently available.

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Limulus

Physiology and Biology of Horseshoe Crabs. Studies on Normal and Environmentally Stressed Animals. JOSEPH BONAVENTURA, CELIA BONAVENTURA, and SHIRLEY TESH, Eds. Liss, New York, 1982. xviii, 316 pp., illus. $48. Progress in Clinical and Biological Research, vol. 81.

In the summer of 1980 a *Limulus* expedition was organized, not aboard the *Alpha Helix* but at Duke University's Marine Biomedical Center. The editors of the resulting volume indicate that the spirit of the intellectual expedition cannot be adequately reflected in the published papers. The book is nevertheless an enthusiastic example of a multidisciplinary account of a non-mammalian species.

The 18 papers, a somewhat haphazard collection of reviews and research reports, vary greatly in length and purpose. A grand review of the natural history of horseshoe crabs and a substantial description of their developmental stages with figures and diagrams form the two opening papers. These are followed by a set of brief notes and longer research reports on osmotic, respiratory, and circulatory physiology, including a concise review of the anatomy and physiology of the *Limulus* heart and blood circulation. This set leads via a paper on coxal gland function—a paper that mixes primary data with a review and a comparison with other crustaceans—to a set of papers on blood physiology and biochemistry. The focus of these papers is on the structure and function of hemocyanin, of which they provide a state-of-the-art review.

The current surge of interest in *Limulus* blood for medical and pharmaceutical purposes is only a peripheral issue here (the subject is covered in *Biomedical Applications of the Horseshoe Crab*, E. Cohen, Ed., Liss, 1979), although it is mentioned in the context of invertebrate disease studies in a short paper by the late Frederik Bang, to whose memory the book is dedicated, and Betsy Bang. These authors emphasize the importance of invertebrate studies to human health problems, a fact not generally recognized by the public or in funding policies. In a brief note, Anne Rudloe makes a plea for environmental health and laws protecting *Limulus* from human plunder. The final paper, by Sidney Galler and Bernard Zahuranec, deals with biological policy matters in general. The authors advocate stronger representation of biologists in national policy decisions and urge biologists to take an active role rather than staying at the bench or the beach exclusively. One wonders why such pleas are hidden in the tail section of a book on *Limulus*. The message of these papers deserves attention.

Conferences—or expeditions—focusing on one or a few related species serve eminently the function of disseminating diverse facts and theoretical models among different scientific disciplines. They also serve to remind us that we deal, even in the laboratory, with animals that evolve as physiological entities both in harmony and in competition with their environments; in turn, these animals are part and parcel of our own environment. Thus I applaud the multidisciplinary principle upon which the present book is founded. However, I regret that more of the outstanding *Limulus* physiologists—for instance in photoreception and vision—were not included. The book's title promises more than is actually included. May other expeditions follow!

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Tempestites

Cyclic and Event Stratification. Papers from a workshop, Tübingen, Germany, April 1980. G. EINSELE and A. SEILACHER, Eds. Springer-Verlag, New York, 1982. xiv, 536 pp., illus. Paper, $29.50.

Sedimentologists have commonly been subdivided into catastrophists and non-catastrophists, depending upon the importance they attach to rare catastrophic events in molding sedimentary sequences. The early 1960's were dominated by proponents of non-catastrophic or cyclic sedimentation—the explanation that repetitive alternations or sequences of sedimentary layers represent periodic, gradual changes in the paleoenvironment. In the mid-1960's, cyclicity enthusiasts received a setback, as many modern and ancient basins were finally recognized to be filled with turbidites, centimeter- to meter-thick packages of sediment that episodically swept in as gravity-driven turbidity currents. A second setback occurred in the late 1960's, as many finely laminated limestone and dolomite sequences were reinterpreted to be not quiet-water basinal deposits but algal-influenced storm deposits of tidal flats. A rather quiescent decade followed.

Now, here come the tempestites.

Tempestites, a vivid term for sedimentary stratification produced by episodic storm events, have gained wide recognition in European rocks and are gradually taking hold in America. This book's greatest excitement (and bulk) lies in the presentation by Seilacher and colleagues of the concepts of and evidence for sedimentation by "rare episodic events" (the term "catastrophic" has fallen into disfavor).

Most pleasing is the rigorous evidence provided by many of the authors that layering in the sediment sequences documented is indeed of storm origin. Evidence for storm stratification is drawn from an intriguing, but logical, integration of sedimentological characteristics, early diagenetic fabrics, paleoecological attributes, and post-event biological responses.

Tempestites are documented from ancient shallow marine, shelf, and epeiric sea settings, as well as from areas slightly below wave base, where storm-generated bottom flow is thought to carry sediments seaward for some distance. Twenty papers and one abstract focus on tempestites and four papers on turbidites.

Cyclic and Event Stratification, however, attempts to cover more than event stratification. There are also sections on