

## Book Review

*Predation, Direct and Indirect Impacts on Aquatic Communities.* Edited by W. Charles Kerfoot and Andrew Sih, 1987, University Press of New England, Hanover and London. 386 pp.

The goals of the symposium were to clarify the kinds of indirect 'effects' exerted by predators and to determine their importance in community dynamics. The decision to publish led to expansion of coverage and inclusion of more authors but the primary value of the book remains in the indirect, not the direct aspects of predation.

The publisher boasts of a "volume on marine and freshwater predators" but those with parochial interests in things marine will be disappointed: Only two contributions are exclusively marine and most make only brief mention of marine communities. However, concentration on freshwater systems certainly simplifies satisfying the goals of the symposium and makes for a more coherent group of offerings.

Researchers from outside of the field such as myself will learn a great deal from the generally review-oriented contributions. The breadth of coverage of indirect effects should also provide the specialist with new ideas and at least some source materials. Some papers present a good deal of new information and data that is not cited as appearing elsewhere.

Contributions were solicited in three areas: "(1) direct and indirect influences of top predators on food web dynamics, (2) chemically mediated interactions between predators and prey, and (3) research on the variety of ways that predators modify prey behavior, life-styles, and morphology." Actual organization of the book follows a more logical separation into description of aspects of direct and indirect effects, food web dynamics, and behavioral and morphological responses to these effects. For me, the final chapter on paleoecology adds little to the central theme of the book.

I felt mixed enthusiasm for the initial chapters describing types and properties of direct and indirect interactions. O'Brien gives a very useful review of physical and biological factors of importance to planktivory in freshwater fish-zooplankton systems. One could use this chapter to start into the literature on various topics from evolution of zooplankton pigmentation to visual acuity in zooplanktivorous fishes. Murdoch and Bence use extensive work on mosquitofish and others as the basis for a useful discussion of the relative instability of freshwater prey populations as compared with terrestrial systems. Miller and Kerfoot propose a "new" organization and terminology to define indirect associations as having either trophic linkages, behavioral or chemical responses. Little new thought and few suggestions for research emerge from their exercise. Abrams concludes the section with a well written and informative review of the various ways in which changes in one prey

population can effect the instantaneous growth of another. I was greatly appreciative of his word descriptions for the various formulations that enable the less mathematically inclined such as me to grasp how prey can have all possible combinations +, 0 and - indirect effects on one another.

Food web dynamics are introduced by Kerfoot with a summarization of theory and experimental results that begin to apply real (or almost real) world results to the hypotheses of the preceding chapters. Facilitative and inhibitory effects are presented with an easily followed discussion. If Lyapunov criteria, Taylor series, and the "method of Hurwitz" are your bed-fellows (they are not mine), then Levitan's experimental and formal mathematical analysis of stability in the same lake community will be of great interest.

"Trophic cascade" or "top-down" indirect effects are modeled by Adams and DeAngelis who conclude that population growth of their bass predator is more sensitive to changes in the timing of reproduction of its shad prey *relative* to its own than it is to length of growing season or growth efficiency. This is a useful exercise to help guide field studies so long as we realize that "sensitivity" is measured relative to a 10% change in each parameter of the model and we do not know how changes of this magnitude compare to changes that are possible or probable in the field. Mills, Forney and Wagner synthesize a large amount of data on the Oneida Lake community from the level of the Discovorous walleye perch to phytoplankton. You can easily develop a grasp of the nature of the cascade effect without their actual creation of a formal model of the community. Kitchell and Carpenter present a formal model for pheophytin (a decomposition product of chlorophyll *a*) deposition and test its application to cores from Lake Michigan with a well known history around 1960. Their results indicate the cascade effect of the well documented "alewife crash" and are encouraging for paleolimnological applications of this tool as an indicator of phytoplankton grazers.

Vanni leads off the section on experimental analysis of indirect facilitation by showing that selective predation on large size classes of a zooplankter can enhance its population growth rates by releasing smaller size classes from intraspecific competition. Threlkeld suggests caution in interpreting such facilitation effects as due to "trophic cascade" as opposed to direct nutrient enrichment by the fish zooplanktivore. His experimental results are convincing for oligotrophic but not eutrophic waters. Morin's experimental communities resulted in somewhat less convincing evidence of indirect facilitation of microcrustaceans by salamander predators: The correlations are clear but there is only circumstantial evidence of the suggested mechanism of predatory release from interspecific competition. Dungan ends the section with a welcome shift to the marine intertidal and a summary of his 2.5 year experiment that indicated an indirect mutualism between a grazer and a predator whose "prey" are in "space pre-emption" competition.

Sih introduces the section on behavioral and morphological responses with a very useful review of behavioral and life history adaptations that prey use to avoid predation. It is loaded with references (almost 5 pages), some original data and largely avoids repetition of material already covered by O'Brien (see above).

The subsection on responses mediated by chemicals is unfortunately named. The title adequately describes only the first contribution by

Scrimshaw and Kerfoot who provide what they believe to be the first review of chemical defenses in aquatic beetles and bugs. They give extensive coverage and references and suggest that the lack of chemical defenses in larval arthropods is a mystery worthy of study. Stemberger and Gilbert's review of the defense mechanisms of rotifers is much broader than its placement in a section on "Evolutionary Responses Mediated by Chemicals" would suggest and provides useful source material for researchers dealing with communities that include rotifers. Havel's review of predator induced defenses includes both defenses and induction mechanisms that are *non-chemical*. He includes a detailed review of freshwater zooplankton, and comparison with terrestrial plants and two organisms from the near-shore marine environment. He draws attention to an induced size reduction in *Daphnia pulex* that could easily be mistaken as a result of size-specific predation.

The section on ecological adjustments in time and space is more aptly named. Hairston reviews published results and includes some new data to form a convincing argument that the timing of diapause in some *Daphnia* spp. is an evolutionary adaptation to catastrophic predation pressure. Lampert reviews and synthesizes laboratory, field and modeling studies and gives a convincing argument for indirect enhancement of phytoplankton by fish predators due to their direct selection for vertical zooplankton migrations. Folt presents mostly new (I think) data for the benefits (through reduced predation) and costs (through reduced foraging) of mixed species aggregations of freshwater zooplankton. I found it difficult to absorb the complexities of both the analysis and the multifaceted relationships described in only a few pages. Mittelbach and Chesson review evidence for indirect effects of predation when the prey fishes have distinct bluegill and pumpkinseed sunfish. They explain a simplified model with words and graphs and leave added complexities for the more stout of heart in the appendices. Power closes the section with a mixture of review and unpublished data on the distribution of grazing fishes and benthic algae within pools and streams. The chapter lacks a clear and interpretive discussion of the conclusion that this distribution results from the avoidance of predators.

Paleoecology is revisited in the final section. Aronson and Sues use an extant ophiuroid-dominated community in an isolated saltwater lake as evidence that such dense aggregations in the fossil record indicate a lack of predation. Kerfoot and Lynch end the book with evidence from the fossil record and suggest that the increase in efficiency of fish predation during the Mesozoic led to massive extinctions of branchiopods and restriction of survivors to predator-free refugia.

George Losey  
University of Hawaii