

This Week's Citation Classic

Hall D J, Cooper W E & Werner E E. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.* **15**:839-928, 1970.

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Utilizing a set of 20 identical ponds, we performed a three-year field experiment demonstrating the impact of nutrients and predation on zooplankton and benthos community structure. Fish had a much greater size-selective effect on prey populations than did invertebrate predators. [The SC[®] indicates that this paper has been cited over 130 times since 1970.]

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"Upon my arrival at Cornell University in the mid-1960s, I was offered the use of a large number of newly built experimental ponds. Shortly thereafter, Bill Cooper paid me a visit and, as former graduate students (along with Bob Paine, Dick Root, Tom Poulsen, and Conrad Istock) who had studied under the stimulating triumvirate of Smith, Hairston, and Slobodkin at the University of Michigan, our eyes glowed with anticipation as we contemplated the prospects of a well-controlled, replicated field experiment. Indeed, the ecological ferment of that decade emanating largely from the niche concept, systems analysis and the diversity-stability controversy saw community ecology rapidly ascend to lofty if not premature heights of popularity.

"The ponds, which were excellent ecological 'test tubes,' provided us an opportunity to explore experimentally some of the structural dynamics of aquatic invertebrate communities. Quite idealistically, we hoped that by inducing changes in the community structure we could begin to tease apart the set of interacting population parameters

critical to the construction of a general theory of community organization. Our ecological biases suggested that nutrients and predation were the most likely parameters to create meaningful changes in these communities. Here also was an opportunity to apply what every graduate student had been led to believe is a crucial ingredient of good science, namely, experimental design and statistical analysis. Consequently, we laid out a replicated, cross-classified randomized block design and over the next three years we invested a prodigious physical effort in manipulating densities of invertebrate predators, nutrient levels, and sampling populations in 20 ponds. And this was only the beginning!

"At this juncture Earl Werner joined the effort and we all spent the remainder of the decade (about two years) analyzing enormous amounts of data and writing a monograph length manuscript which finally appeared as the longest paper ever published in *Limnology and Oceanography*. (This was the first and apparently last attempt by the editor, Yvette Edmondson, to devote virtually an entire journal issue to a single study.)

"In spite of its great length (86 pages) our study has been widely cited primarily because of the 'keystone' predator effect of the fish on the nature and extent of interactions among a constellation of other species, in much the same manner as Paine's intertidal study.¹ However, we feel that the major impact of this study was that it revealed (certainly to us) the many problems and shortcomings of such a 'broad brush' approach to community-level phenomena. Indeed, this study helped convince us that 'pulling-off a fundamentally important field experiment is more likely when you are guided by a substantive conceptual framework. Our more recent experimental studies of competition and niche relations in fish communities seem to support this contention."²

1. **Paine R T.** Food web complexity and species diversity. *Amer. Naturalist* **100**:65-75, 1966. [Citation Classic. *Current Contents/Agriculture, Biology & Environmental Sciences* **10**(49): 12, 3 December 1979.]

2. **Werner E E & Hall D J.** Foraging efficiency and habitat switching in competing sunfishes. *Ecology* **60**:256-64, 1979.