

# This Week's Citation Classic

CC/NUMBER 49  
DECEMBER 3, 1979

**Paine R T.** Food web complexity and species diversity. *Amer. Naturalist* 100:65-75, 1966. [Department of Zoology, University of Washington, Seattle, WA]

**The paper proposed that predation, especially that which prevented spatial monopolization by a competitively dominant species, maintained or enhanced local species diversity. The viewpoint was supported by a controlled field experiment involving starfish removal, and observed subsequent decline in community species richness. [The *SCI*<sup>®</sup> indicates that this paper has been cited over 275 times since 1966.]**

R.T. Paine  
Department of Zoology  
University of Washington  
Seattle, WA 98105

August 10, 1979

"The most general explanation for the paper's popularity was that the time was ripe. Ecologists were looking with increased interest at the phenomenon of diversity gradients, and G.E. Hutchinson had recently called attention to biological mechanisms that might enhance coexistence.<sup>1</sup> Probably of equal importance was my own mind set. I'd recently finished both my dissertation research, during which I had become convinced that marine invertebrate carnivores were easily observed, and a post-doc at Scripps Institution of Oceanography where Bill Fager had inspired me to think about controlled field manipulation. These experiences suggested that predators could determine the structure of natural assemblages, but the usual explanation for coexistence involved some form of competition-based interaction. This contrast was strongly focused by continued debate with my ecologically-oriented colleagues and a gaggle of excellent graduate students at the University of Washington, which I'd joined in 1962.

"Further, one would have had to be blind not to see the impact of the starfish *Pisaster ochraceus* on the local intertidal biota. On my second trip to the outer coast I selected a study site with an appropriate adjacent control and began hurling starfish off. There was no pretense of elegance, but dramatic differences developed by June, 1964, and the experimental site, in contrast to the control, was well on the road to monopolization of the limiting resource by the competitive dominant. Performance of the work generated more than its quota of adventure and misery, as could be anticipated from working at an exposed coastal site in winter at dusk.

"The paper itself did little more than demonstrate that removal of a predator in nature reduced local diversity substantially, and suggest that diverse communities have a higher proportion of predators. I regret now not being more specific about defining the terms 'space' and 'diversity,' and especially in not presenting more of the data. I also should have ordered more reprints.

"Perhaps the most surprising aspect of the paper was its immediate influence, since most ecological truths seem to be relatively simple and self-evident. Ecologists were obviously prepared for a field demonstration of species coexistence mediated by a predator, having forgotten Darwin (as I embarrassingly had).<sup>2</sup> I derive satisfaction that the results have been repeated and extended by others, and that qualitatively similar patterns seem to be obtained in plankton communities. One of the terms (keystone species) derived from a second generation of studies seems well on its way to becoming jargon.<sup>3</sup> In sum, the paper's primary significance was that it provided an example and stimulus for theoretician and field biologist alike to include the role of predation in considerations of community structure."

1. **Hutchinson G E.** Homage to Santa Rosalia or why are there so many kinds of animals?

*Amer. Naturalist* 93:145-59, 1959.

2. **Darwin C.** *The origin of species*. New York: Modern Library. 1859. 563 p.

3. **Paine R T.** A note on trophic complexity and community stability. *Amer. Naturalist* 103:91-3, 1969.