DISCOVERING KEYSTONE SPECIES

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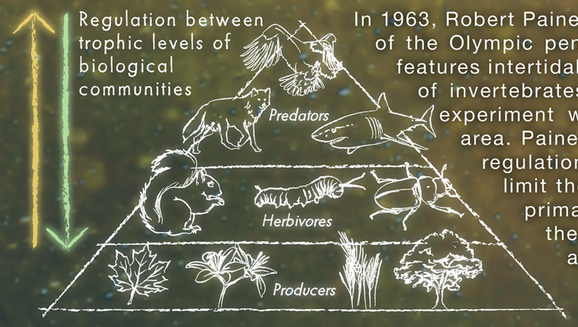
EXPERIMENT



In 1963, Robert Paine embarked on a landmark experiment at the tip of the Olympic peninsula in Washington's Mukkaw Bay. The bay features intertidal zones where members of a diverse community of invertebrates compete for resources. The concept of the experiment was simple: remove all the starfish from one area. Paine was testing the **top-down** view of community regulation, in which predators at the top of the pyramid limit the herbivores below them and indirectly control primary producers at the base. This was contrary to the then-popular **bottom-up** view, in which the availability of producers at the bottom controls the numbers of herbivores, which in turn regulates predators at the top.

KEYSTONE SPECIES

This experiment demonstrated the importance of **top-down control** by the predatory starfish *Pisaster ochraceus* on the structure and composition of the community. When starfish were removed, the diversity of the community plummeted. Because of its large effect relative to its population size, Paine coined the term **keystone species** to describe species that, like the starfish, have large disproportionate impacts on their communities.

Removal of the starfish revealed their role in controlling species that they prey upon, which in turn had an impact on species the next level down in the food web. Paine named these strong but indirect top-down effects **trophic cascades.**

BEFORE STARFISH REMOVAL

The intertidal zone is the area that is submerged at high tide and exposed at low tide. In an 8-meter-by-2-meter patch of the intertidal zone, Paine removed all of the starfish as a predator exclusion treatment. He left a similar area untouched as a control. He maintained the starfish exclusion for five years and noted changes in species diversity and abundance.

FOOD WEB The food webs at the top of each panel illustrate the community as the experiment progressed. The arrows in the food webs point from the prey to the species consuming it. Starfish are predators that eat a variety of species including barnacles, chitons, limpets, and mussels, with mussels being their most important food. Organisms not directly eaten by starfish also occupied the plots: different species of algae, and a species of anemone, a sponge, and a sea slug. At the beginning of the experiment, the experimental and control plots each had 15 species.

MUSSEL BOUNDARY The dashed line indicates how far down the rock face the mussel beds reached as the experiment continued.

1 YEAR AFTER REMOVAL

FOOD WEB In the absence of starfish predation, mussel populations exploded and outcompeted the other species. The algae, chitons, and limpets disappeared, reducing the species richness from 15 species to 8.

MUSSEL BOUNDARY Mussels advanced down the rock face 67 cm from their original zone toward the low tide line.

5 YEARS AFTER

FOOD WEB The mussels crowded out almost all other species. Eventually, only the mussels remained, and the community simplified from 15 species to 1.

MUSSEL BOUNDARY The maximum distance mussel beds advanced was 85 cm below their original zone. Paine ended the starfish exclusion after 5 years. In the following years, the line of mussels retreated a bit, but the community remained essentially a monoculture of mussels.

REFERENCES: 1. Paine, R. T. "Food web complexity and species diversity." *American Naturalist* 100 (1966): 65-75., 2. Paine, R. T. "Intertidal community structure." *Oecologia* 15 (1974): 93-120.