**DISCOVERING KEYSTONE SPECIES**

**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**

**1 YEAR AFTER REMOVAL**

**5 YEARS AFTER**

**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.

**INTERTIDAL ZONE**

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.

**REFERENCES:**


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