Keystone Species

By: Stephen C. Wagner (*Department of Biology, Stephen F. Austin State University*) © 2012 Nature Education

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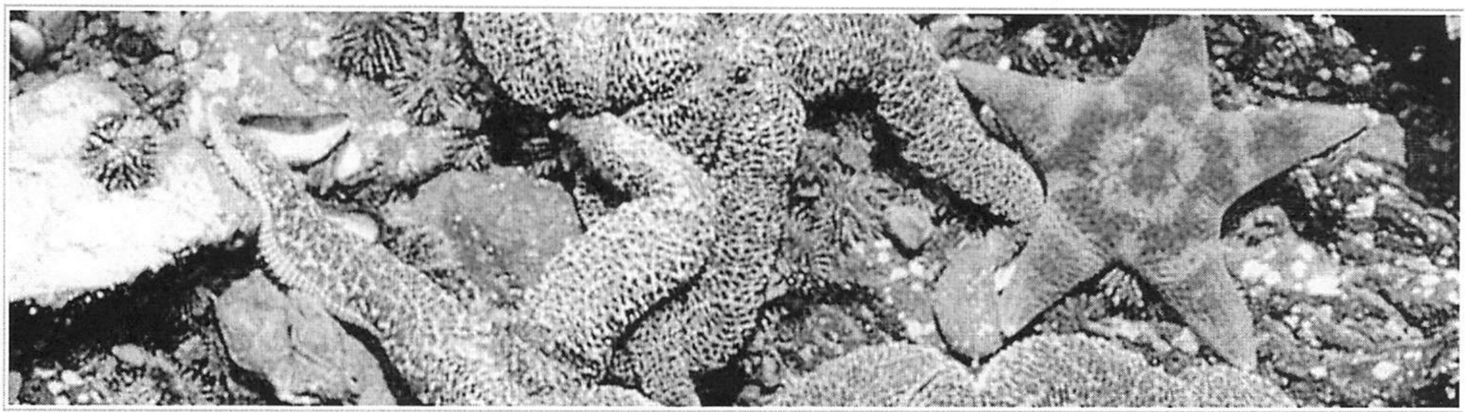
A keystone in an arch's crown secures the other stones in place. Keystone species play the same role in many ecological communities by maintaining the structure and integrity of the community.



Paine's Milestones

The term keystone species was first coined by Robert Paine (1966) after extensive studies examining the interaction strengths of food webs in rocky intertidal ecosystems in the Pacific Northwest. One of his study sites, located at Mukkaw Bay, contained a community consistently dominated by the same species of mussels, barnacles, and the starfish, *Pisaster ochraceus*, which preys upon the other species as a top predator (Figure 1).

Paine (1966) had observed that the diversity of organisms in rocky intertidal ecosystems declined as the number of predators in those ecosystems decreased. He hypothesized that some of these consumers might be playing a greater role than others in controlling the numbers of species coexisting in these communities. He tested his hypothesis in an experiment that involved selecting a "typical" piece of shoreline at Mukkaw Bay, about 8 meters long by 2 meters wide, that was kept free of starfish. This area was compared to an adjacent, undisturbed control area of equal size.

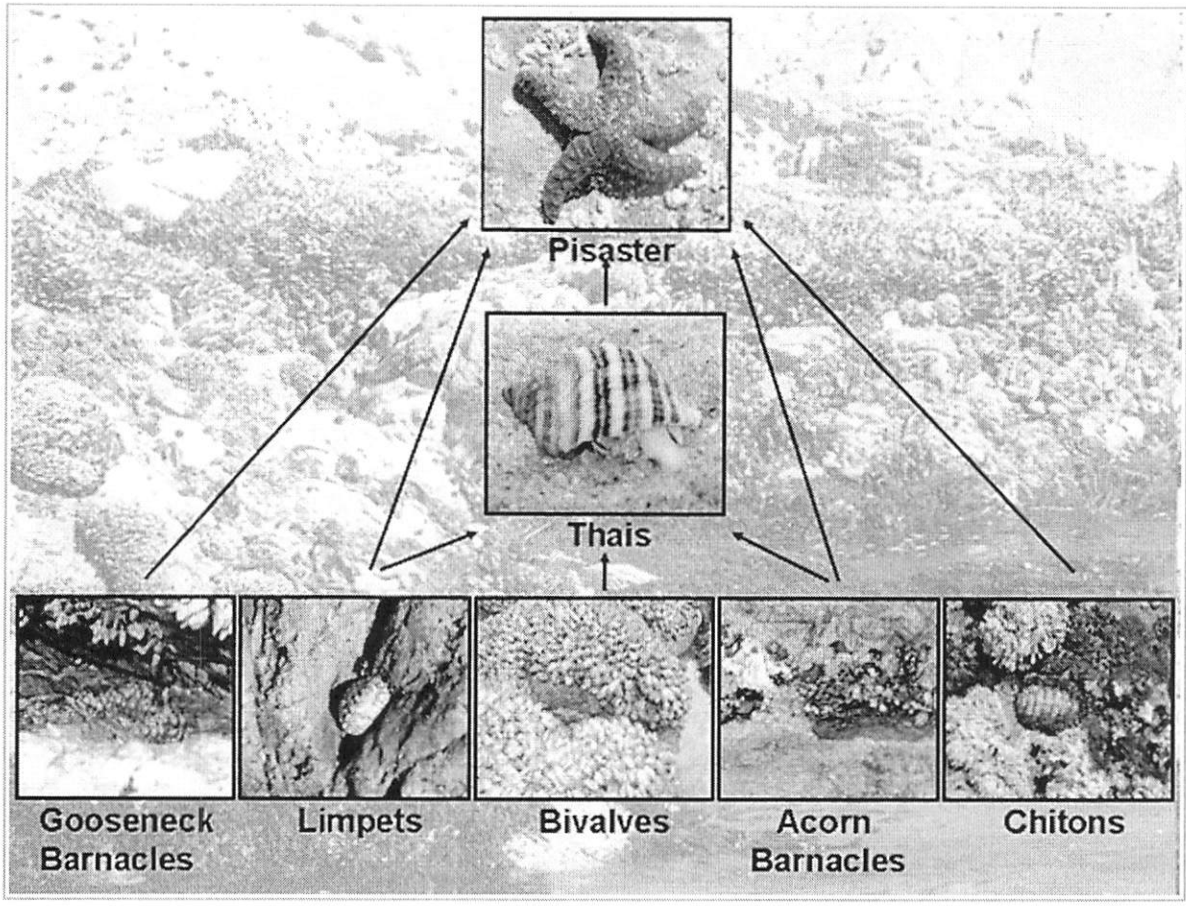


Figure 1: Food web of species present in temperate intertidal ecosystem

Paine observed dramatic changes in the temperate intertidal ecosystem after *Pisaster* was artificially removed compared with the control area that remained unchanged in its species number and distribution. The intertidal area where *Pisaster* had been removed was characterized by many changes. Remaining members of the ecosystem's food web immediately began to compete with each other to occupy limited space and resources. Within three months of the *Pisaster* removal, the barnacle, *Balanus glandula*, occupied 60 to 80% of the available space within the study area. Nine months later, *Blanus glandula* had been replaced by rapidly growing populations of another barnacle *Mitella* and the mussel *Mytilus*. This phenomenon continued until fewer and fewer species occupied the area and it was dominated by *Mytilus* and a few adult *Mitella* species. Eventually the succession of species wiped out populations of benthic algae. This caused some species, such as the limpet, to emigrate from the ecosystem because of lack of food and/or space. Within a year of the starfish's removal, species diversity significantly decreased in the study area from fifteen to eight species (Figure 2).

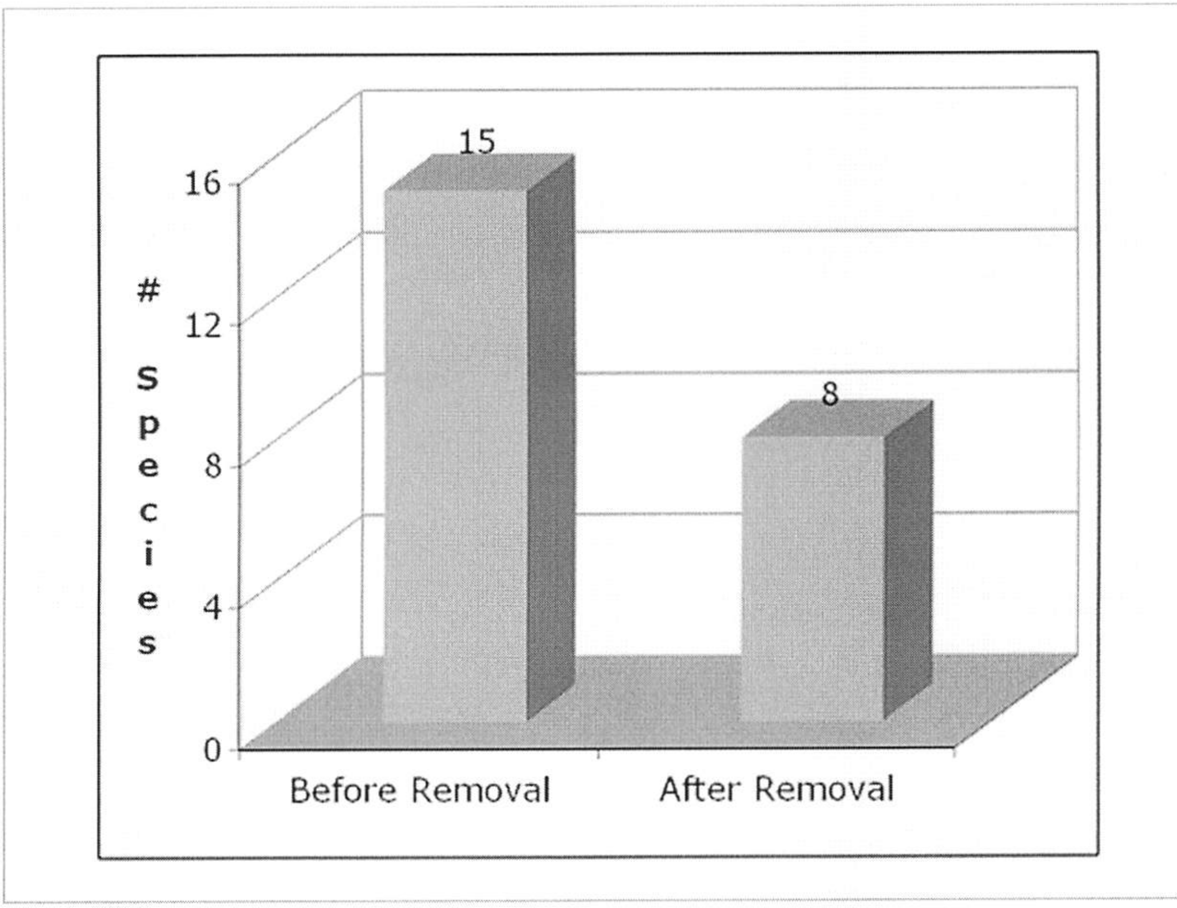


Figure 2: Effect of removal of top predator on total species number in intertidal ecosystem

In his seminal paper that followed this work, Paine (1969) derived the term keystone species to describe the starfish in these intertidal ecosystems. Of these species he commented: "The species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time."

Paine went on to describe the criteria for a keystone species. A keystone species exerts top-down influence on lower trophic levels and prevents species at lower trophic levels from monopolizing critical resources, such as competition for space or key producer food sources. This paper represented a watershed in the description of ecological relationships between species. In the twenty years that followed its publication, it was cited in over ninety publications. Additionally, the original paper describing the intertidal areas was cited in over 850 papers during the same time period (Mills *et al.* 1993).

Other Keystone Species

There are a number of other well-described examples where keystone species act as determinate predators. Sea otters (i) regulate sea urchin populations, which in turn feed upon kelp and other macroalgae (Duggins 1980). The otters keep the sea urchin populations in check, thus allowing enough kelp forests to remain as a habitat for a variety of other species. As a result, the entire ecosystem is kept in balance. In terrestrial environments, fire ants function as keystone predators by suppressing the numbers of individuals and species of arthropods that could be harmful to agriculture.

Keystone species also play important roles in many other ecosystems (Mills *et al.* 1993). For example, hummingbirds are sometimes referred to as keystone mutualists because they influence the persistence of several plant species through pollination. On the other hand, keystone modifiers, such as the North American beaver (*Casor candensis*), determine the prevalence and activities of many other species by dramatically altering the environment (Figure 3). Species like the Saguaro cactus (*Carnegiea gigantea*) in desert environments and palm and fig trees in tropical forests are called keystone hosts because they provide habitat for a variety of other species. Keystone prey are species that can maintain their numbers despite being preyed upon, therefore controlling the density of a predator.

Figure 3: A dam built by beavers as keystone modifiers

Gray Wolves: A Case Study of Keystone Species Removal and Restoration

Gray wolves (*Canis lupus*, Figure 4) once roamed the western portions of North America from Alaska to Mexico. During the latter part of the nineteenth century, most of the important prey for wolves — bison, deer, elk, and moose — were severely depleted by human settlers. The wolves soon became the enemies of the ranchers and farmers when they turned to preying upon sheep and other livestock (Grooms 1993, Breck & Meier 2004, Outland 2010).

Figure 4: The gray wolf (*Canis lupus*), a keystone species in Yellowstone National Park

When the federal government set aside the Greater Yellowstone Ecosystem (GYE) as a national park in 1872, about three to four hundred wolves were present, preying mostly upon large hooved ungulates such as elk (*Cervus canadensis*, Figure 5) and bison (Yellowstone Association 1996). Fearing the wolves' impact on elk and bison herds as well as livestock owned by area ranchers, the federal government began eradicating the wolf population. Bounty programs that continued until 1965 offered as much as $50 per wolf. Wolves were trapped, shot, dug from their dens, hunted with dogs, and poisoned. In Yellowstone National Park, park rangers killed the last two remaining pups in 1924. By the 1930s wolves had been effectively eliminated from the contiguous 48 States and Mexico and only remained in high numbers in Alaska.

Figure 5: The elk (*Cervus canadensis*), principal prey of gray wolves (*Canis lupus*)

With their primary predator eliminated, elk populations exploded, leading to the overgrazing of plants, especially those found in riparian zones (Laliberte & Ripple 2004). Significant declines in the populations of many plant species (e.g., aspen, willow) resulted, which in turn influenced other wildlife, such as beaver and songbird populations (Ripple & Breschetta 2004, Hallofsky & Ripple 2008). Intensive browsing of aspen (*Populus tremuloides*) stands, for example, led to a rapid decline in the number of seedlings and root sprouts growing into saplings and trees. For many stands of these trees, only large diameter trees (i.e., those that had matured before the wolves were eradicated) remained.

Disappearance of these and other plant species not only caused the loss of habitat for many other animals but also influenced other ecological factors (Smith *et al.* 2009), including stream bank stability, the deposition of organic matter and fine sediment in riparian zones, water temperature regulation via shading, and nutrient cycling. The removal of wolves thus led to the instability of riparian and other environmentally sensitive areas.

After the United States Congress passed the original Endangered Species Preservation Act in 1966, the gray wolf made the original Endangered Species List. The subsequent Endangered Species Act of 1973 called for their restoration. Consequently, the National Park Service changed their policy to restore natural conditions within Yellowstone National Park, including the reintroduction of the gray wolf (Smith & Bangs 2009). In 1995, the federal government began reintroducing gray wolves into the GYE. Initially, fourteen wolves were captured in Canada and relocated to one-acre acclimation pens where they were held for ten weeks before being released into the GYE. This process was repeated in 1996 and 1997 with an additional seventeen wolves from Canada and ten pups from Montana (Smith *et al.* 2009). For the most part, wolf populations have continued to grow at a rapid rate, averaging 17% per year (Smith & Bangs 2009). At the end of 2009, there were between 96 and 98 wolves in Yellowstone, with 14 packs, 1 non-pack grouping, and 2 loners (Figure 6). Park staff recorded 365 prey animals killed by wolves, most of which were elk (302).

Despite some setbacks (e.g., disease outbreaks within the fledgling wolf packs), recovery efforts in the GYE have greatly surpassed expectations. Since their reintroduction, wolves have overwhelmingly targeted elk over other prey. This has coincided with an increase in willow heights in several areas. This may indicate that a wolf-elk-willow trophic cascade has been reestablished within the GYE. Furthermore, investigators believe that restoration of willow populations has led to a ten-fold increase in beaver populations (Smith 2004) as well as a significant songbird rebound (Baril & Hansen 2007).

Halofsky & Ripple (2008) found that aspen browsing by elk had ceased in areas burned during the historic 1988 fires but continued in unburned areas. These results were attributed to the increased risk of wolf predation in burned areas. The authors proposed that a recoupling of fire with increased predation risk from wolves may help improve aspen restoration. The results also suggest that much more research needs to be conducted to determine the effects of wolf reintroduction into the GYE.

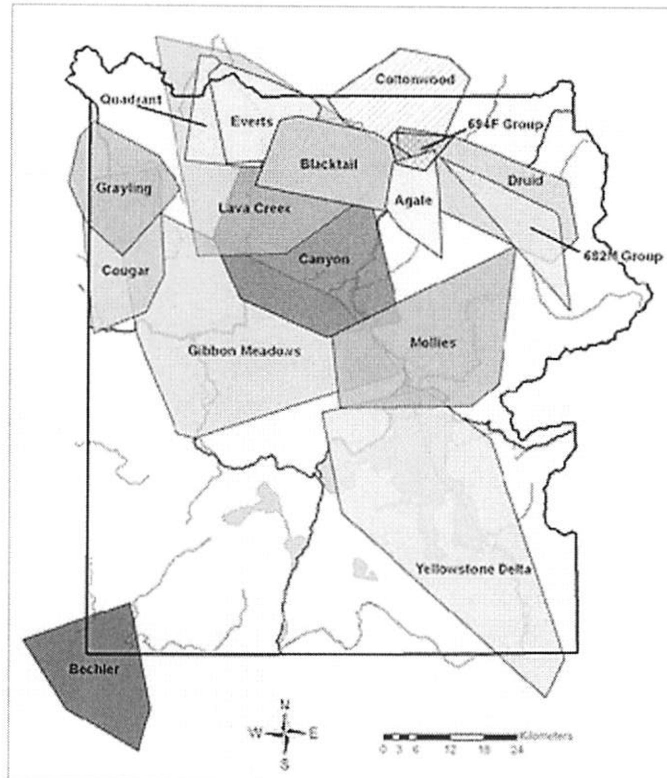


Figure 6: Map of wolf pack territories in Yellowstone National Park in 2009
Public Domain National Park Service.

Summary

The concept of keystone species was first proposed and demonstrated in the 1960s by the dominance of top-predator starfish in intertidal ecosystems. Keystone species are species that play a disproportionately large role in the prevalence and population levels of other species within their ecosystem or community. The recovery of the gray wolf after its eradication from Yellowstone National Park, almost ninety years ago, demonstrates how crucial keystone species are to the long-term sustainability of the ecosystems they inhabit. Most importantly, the preservation and restoration of keystone species is essential for maintaining and/or reestablishing the historic structure and function of the ecosystems they inhabit.

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