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The Ecologist Who Threw Starfish

Robert Paine showed us the surprising importance of predators.

BY SEAN B. CARROLL
ILLUSTRATION BY AAD GOUDAPPEL
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Even in 1963, one had to go pretty far to find places in the United States that were not disturbed by people. After a good deal of searching, Robert Paine, a newly appointed assistant professor of zoology at the University of Washington in Seattle, found a great prospect at the far northwestern corner of the lower 48 states.

On a field trip with students to the Pacific Coast, Paine wound up at Mukkaw Bay, at the tip of the Olympic Peninsula. The curved bay's sand and gravel beach faced west into the open ocean, and was dotted with large outcrops. Among the rocks, Paine discovered a thriving community. The tide pools were full of colorful creatures—green anemones, purple sea urchins, pink seaweed, bright red Pacific blood starfish, as well as sponges, limpets, and chitons. Along the rock faces, the low tide exposed bands of small acorn barnacles, and large, stalked goose barnacles, beds of black California mussels, and some very large, purple and orange starfish, called *Pisaster ochraceus*.

"Wow, this is what I have been looking for," he thought.

STAR HURLER: Robert Paine at Mukkaw Bay, on the Olympic Peninsula in Washington, in 1974, and again recently. To understand the role of predatory starfish he hurled them from an area and later returned to assess the sea life without them.

Left: Bob Paine / Alamy.com ; Right: Kevin Schafer / Alamy Stock Photo

The next month, June 1963, he made the four-hour journey back to Mukkaw from Seattle, first crossing Puget Sound by ferry, then driving along the coastline of the Straits of Juan de Fuca, then onto the lands of the Makah Nation, and out to the cove of Mukkaw Bay. At low tide, he scampered onto a rocky outcrop.

With a crowbar in hand and mustering all of the leverage he could with his 6-foot, 6-inch frame, he pried loose every purple or orange starfish on the slab, grabbed them, and hurled them as far as he could out into the bay.

So began one of the most important experiments in the history of ecology.

The 1960s were a time of revolution, but it was not all just sex, drugs, and rock and roll. Inside laboratories across the world, scientists were plumbing the depths of the gene to decipher the genetic code and the molecular rules of life, sparking a revolution that would gather dozens of Nobel Prizes and ultimately transform medicine.

But largely outside of this spotlight, a few other biologists had started asking some simple, seemingly naïve questions about the wider world: Why is the planet green? Why don't the animals eat all of the food? And what happens when certain animals are removed from a place? These questions led to the discovery that, just as there are molecular rules that regulate the numbers of different kinds of molecules and cells in the body, there are ecological rules that regulate the numbers and kinds of animals and plants in a given place. And these rules may have as much or more to do with our future welfare than all the molecular rules we may ever discover.

Why Is the Planet Green?

Paine's journey to Mukkaw Bay and its starfish was a circuitous one. Born and raised in Cambridge, Massachusetts, Paine's interests in nature were fueled by exploring the New England woods. His first love was bird-watching, with butterflies and salamanders close seconds. Paine was inspired by the writings of prominent naturalists, who opened his eyes to the drama of wildlife. He was as enthralled by intimate accounts of spider behavior as by Jim Corbett's hair-raising tales of tracking down tigers and leopards in rural India, in *Man-Eaters of Kumaon*.

After enrolling at Harvard, and inspired by several famous paleontologists on the faculty, Paine developed an intense new interest in animal fossils. He was so fascinated by the marine animals that lived in the seas more than 400 million years ago that he decided to study geology and paleontology in graduate school at the University of Michigan.

The course requirements entailed rather dry surveys of various animal "ologies"—ichthyology (fishes), herpetology (reptiles and amphibians), and so forth that Paine found very boring. One exception was a course on the natural history of freshwater invertebrates taught by ecologist Fred Smith. Paine appreciated how the professor provoked his students to think.

He pried loose every purple or orange starfish on the slab, grabbed them, and hurled them as far as he could.

One memorable spring day, the sort of day when professors don't feel like teaching and students don't want to be inside, Smith told the class, "We are going to stay in this room." He looked outside at a tree that was just getting its leaves.

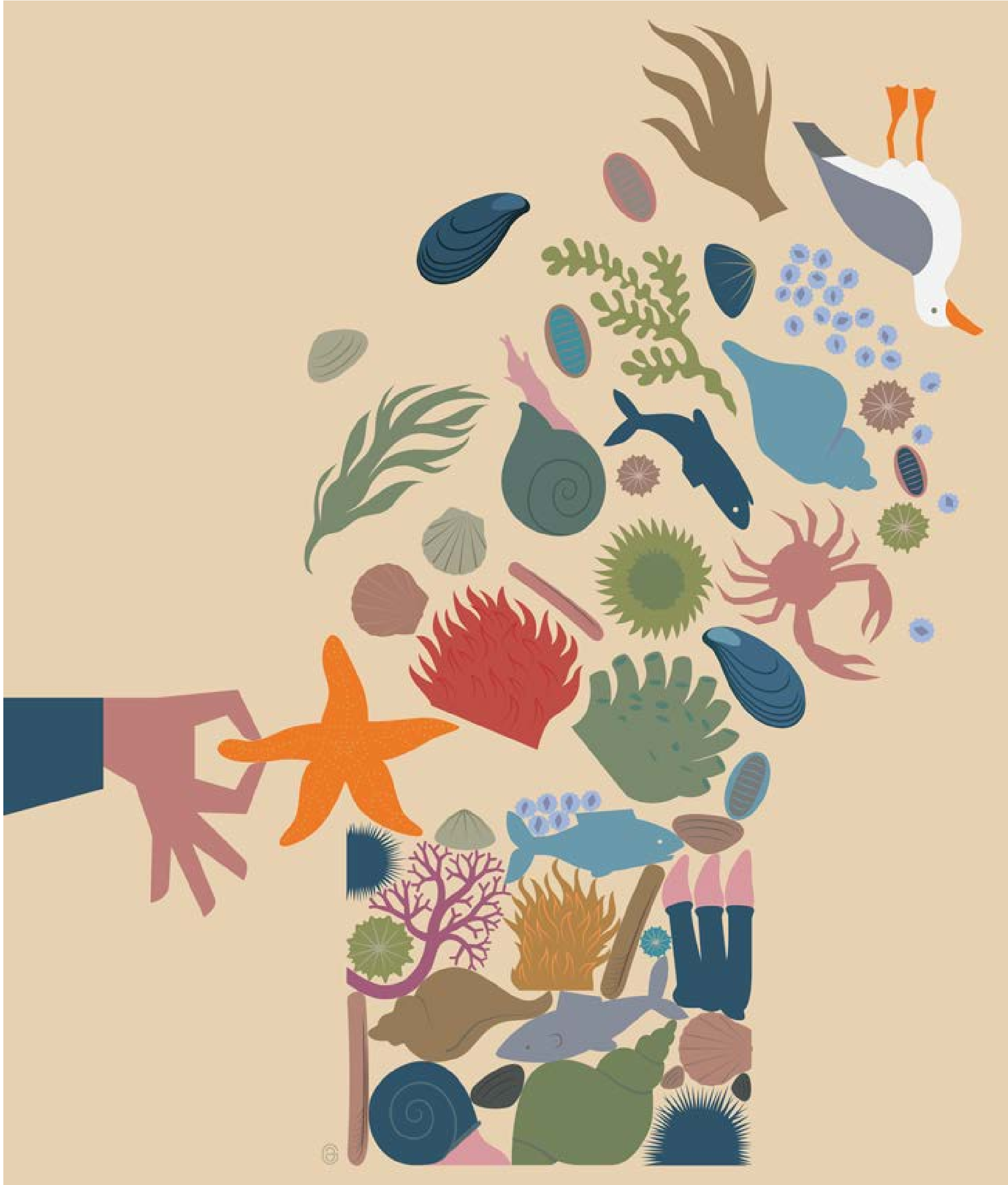
"Why is that tree green?" Smith asked, looking out the window.

"Chlorophyll," a student replied, correctly naming the leaf pigment, but Smith was heading down a different path.

"Why isn't all of its greenery eaten?" Smith continued. It was such a simple question, but Smith showed how even such basic things were not known. "There is a host of insects out there. Maybe something is controlling them?" he mused.

At the end of his first year, Smith sensed Paine's unhappiness with geology, and suggested that he consider ecology instead. "Why don't you be my student?" he asked.

It was a major change in direction, and there was a catch. Paine proposed to study some fossil animals from the Devonian period in nearby rocks. Smith said, "No way." Paine had to study living, not extinct creatures. Paine agreed, and Smith became his adviser.



Smith had long been interested in brachiopods or “lamp shells,” marine animals with an upper and lower shell, joined at a hinge. Paine knew about the animals because they were abundant in the fossil record, but their present-day ecology was not well known. Paine’s first task was to find living forms. Lacking a nearby ocean, Paine made scouting trips to Florida in 1957 and 1958, and found some promising locations. With Smith’s approval, he began what he called his “graduate-student sabbatical.” In June 1959, he drove back to Florida and began living out of his Volkswagen van. For 11 months he studied the range, habitat, and behavior of one species.

It was the sort of work that provided a solid foundation to a naturalist-in-training, and it would earn Paine his Ph.D. But the filter-feeding brachiopods were not the most dynamic animals. And sifting large amounts of sand for the less than quarter-inch-long creatures was, well, just not very exciting.

As Paine shoveled his way along the Gulf Coast, it was not Florida’s brachiopods that captured his imagination. On the Florida panhandle, Paine discovered the Alligator Harbor Marine Laboratory, and was given permission to stay there. At the tip of nearby Alligator Point, he noticed that for a few days each month, the low tide exposed an enormous gathering of large predatory snails, such as the horse conch, some more than a foot long. The mud and sawgrass of Alligator Point was not at all boring, quite the contrary—it was a battlefield.

> *"The most dramatic moment of learning in my life happened in less than a second. And that was sticking my head in the water."*

On top of his thesis work on brachiopods, Paine made a careful study of the snails. He counted eight abundant snail species, and took detailed notes on who ate whom. In this "gastropod eats gastropod" arena, Paine saw that without exception it was always a larger snail devouring a smaller one, but not everything that was smaller. The 11-pound horse conch, for example, dined almost exclusively on other snails, and paid little attention to smaller prey such as the clams that were the main fare for the smaller snails.

While Paine was in Florida watching predators up close, his advisor Smith had kept thinking about those green trees and the roles of predators in nature. Smith was keenly interested in not just the structure of communities, but in the processes that shaped them. He often had bag lunches with two colleagues, Nelson Hairston Sr. and Lawrence Slobodkin, during which they had friendly arguments about major ideas in ecology. All three scientists were interested in the processes that control animal populations, and they debated explanations circulating at the time. One major school of thought was that population size was controlled by physical conditions such as the weather. Smith, Hairston, and Slobodkin (hereafter dubbed "HSS") all doubted this idea because, if true, it meant that population sizes fluctuated randomly with the weather. Instead, the trio was convinced that biological processes must control the abundance of species in nature, at least to some degree.

HSS pictured the food chain as subdivided into different levels according to the food each consumed (known as trophic levels). At the bottom were the decomposers that degrade organic debris; above them were the producers, the plants that relied on sunlight, rain, and soil nutrients; the next level were the consumers, the herbivores that ate plants; and above them the predators that ate the herbivores.

The ecological community generally accepted that each level limited the next higher level; that is, populations were positively regulated from the "bottom up." But Smith and his lunch buddies pondered the observation that seemed at odds with this view: The terrestrial world is green. They knew that herbivores generally do not completely consume all of the vegetation available. Indeed, most plant leaves only show signs of being partially eaten. To HSS, that meant that herbivores were not food-limited, and that something else was limiting herbivore populations. That something, they believed, were predators, negatively regulating herbivore populations from the "top-down" in the food chain. While predator-prey relationships had long been studied by ecologists, it was generally thought that the availability of prey regulated predator numbers and not vice-versa. The proposal that predators as a whole acted to regulate prey populations was a radical twist.

To bolster their case, HSS noted instances where herbivore populations had exploded after the removal of predators, such as the Kaibab deer population in Northern Arizona that increased after decimation of local wolf and coyote populations. They assembled their observations and arguments in a paper entitled "Community Structure, Population Control, and Competition" and submitted it to the journal *Ecology* in May 1959.

It was rejected. The article did not see the light of day until the year-end issue of the *American Naturalist* in 1960.

The proposal that predators regulate herbivore populations is now widely known as the "HSS hypothesis" or "Green World Hypothesis." While HSS declared, "The logic used is not easily refuted," their ideas, like most that challenge the status quo, drew a lot of criticism. One legitimate critique was their claims needed testing and more evidence. And that was just what Smith's former student set out to do on Mukkaw Bay in 1963.

RULER OF THE TIDAL ZONE: Starfish are opportunistic gourmands that eat barnacles, limpets, snails, and mussels. In this rocky intertidal zone on the Pacific coast, the starfish prey on mussels, which enables other species such as kelp and small animals to occupy the community.

David Cowles, rosario.wallawalla.edu/inverts

Kick It and See

The HSS hypothesis was essentially a description of the natural world based on observation. Indeed, virtually all of ecology up to the 1960s had been based upon observation. The limitation of such observational biology was that it left itself open to alternative explanations and hypotheses. Paine realized that if he wanted to understand how nature worked—the rules that regulated animal populations—he would have to find situations where he could intervene and break them. In the specific case of the roles of predators, he needed a setting where he could remove predators and see what happened—what would later be described as "kick it and see" ecology. Hence, the starfish-hurling.

Twice a month every spring and summer, and once a month in the winter, Paine kept returning to Mukkaw to repeat his starfish-throwing ritual. On a 25-feet long, 6-feet tall stretch of rock, he removed all of the starfish. On an adjacent stretch, he let nature take her course. On each plot, he counted the number and calculated the density of the inhabitants, tracking 15 species in all.

To understand the structure of the Mukkaw food web, Paine paid close attention to what the predators were eating. The starfish has the neat trick of everting its stomach to consume prey. To see what they were feasting upon, Paine turned more than 1,000 starfish over and examined the animals held against their stomachs. He discovered that the starfish was an opportunistic gourmand that ate barnacles, chitons, limpets, snails, and mussels. While the small barnacles were the most numerous prey—the starfish was able to scarf up dozens of the little crustaceans at a time—they were not its primary source of calories. Mussels and chitons were the most important contributors to the starfish diet.

By September, just three months after he began removing the starfish, Paine could already see that the community was changing. The acorn barnacles had spread out to occupy 60 to 80 percent of the available space. But by June of 1964, a year into the experiment, the acorn barnacles were in turn being crowded out by small, but rapidly growing goose barnacles and mussels. Moreover, four species of algae had largely disappeared, and the two limpet and two chiton species had abandoned the plot. While not preyed upon by the starfish, the anemone and sponges populations had also decreased. However, the population of one small predatory snail, *Thais emarginata*, increased 10- to 20-fold.

Altogether, the removal of the predatory starfish had quickly reduced the diversity of the intertidal community from the original 15 species to eight.

The results of this simple experiment were astonishing. They showed that one predator could control the composition of species in a community through its prey—affecting both animals it ate as well as animals and plants that it did not eat.

As Paine continued the experiment over the next five years, the line of mussels advanced down the rock face by an average of almost 3 feet toward the low tide mark, monopolizing most of the available space and pushing all other species out completely. Paine realized that the starfish exerted their strong effects primarily by keeping the mussels in check. For the animals and algae of the intertidal zone, the important resource was real estate—space on the rocks. The mussels were very strong competitors for that space, and without the starfish, they took over and forced other species out. The predator stabilized the community by *negatively regulating* the population of the competitively dominant species.

Paine's starfish-tossing was strong confirmation of the HSS hypothesis that predators exerted control from the top down. But this was just one experiment with one predator in one spot on the Pacific Coast. If Paine was going to draw any generalities, it was important to test other sites and other predators. The dramatic results of the Mukkaw Bay experiments inspired a flurry of kick-it-and-see experiments.

Today, of course, one predator has more influence than any other. And humans will be the ultimate losers if the rules are not understood.

Paine discovered uninhabited Tatoosh Island when he was out on a salmon-fishing trip. On this small, storm-battered island, several miles up the coast from Mukkaw Bay and about half a mile offshore, Paine found many of the same species clinging to the rocks, including large *Pisaster* starfish. With the permission of the Makah tribe, Paine started tossing them back in the water. Within a few months, the mussels started spreading across the predator-free rocks.

While on sabbatical in New Zealand, Paine investigated another intertidal community at the north end of a beach near Auckland. There, he found a different starfish species called *Stichaster australis* that preyed on the New Zealand green-lipped mussel, the same species exported to restaurants around the world. Over a period of nine months Paine removed all of the starfish from one 400-square-foot area, and left an adjacent, similar plot alone. He saw immediate and striking effects. The treated area quickly began to be dominated by mussels. Six of 20 other species initially present vanished in just eight months; within 15 months the majority of space was occupied solely by the mussels.

To Paine, the predatory starfish of Washington and New Zealand were "keystones" in the structure of intertidal communities. Just as the stone at the apex of an arch is necessary for the stability of the structure, these apex predators at the top of the food web are critical to the diversity of an ecosystem. Dislodge them, and as Paine showed, the community falls apart. Paine's pioneering experiments, and his coining of the term "keystone species" prompted the search for keystones in other communities, and would lead him to another seminal idea.

Sea Otters and the Cascading Effect

Paine's kick-it-and-see experiments were not limited to manipulating predators. He was interested in understanding the rules that determined the overall make-up of coastal communities. Other prominent inhabitants of the tide pools and shallow waters included a great variety of algae, such as the large brown seaweed known as kelp. But their distribution was patchy—abundant and diverse in some places, nearly absent from others. One of the most prevalent grazers on the algae were sea urchins. Paine and zoologist Robert Vadas set out to find out what effect the urchins had on algal diversity.

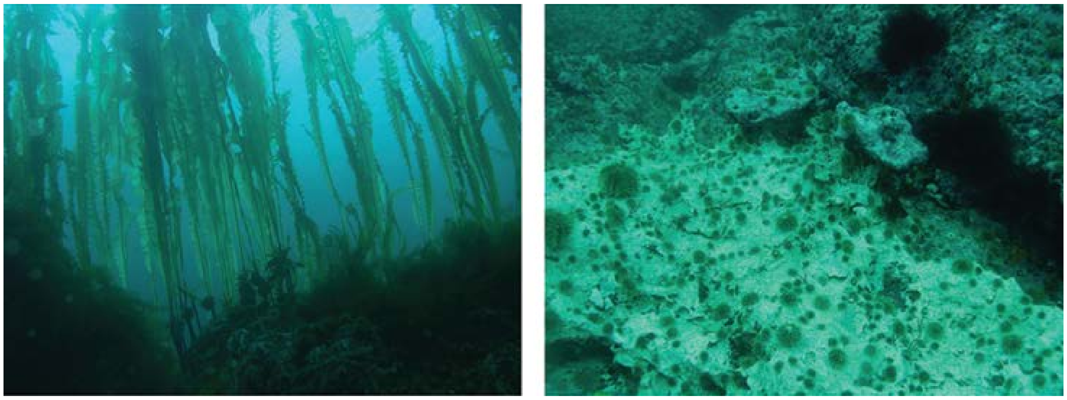
To do so, they removed all of the urchins by hand from some pools around Mukkaw Bay, or barred them from areas within Friday Harbor (near Bellingham) with wire cages. They left nearby pools and areas untouched as controls for their experiment. They observed dramatic effects of removing the sea urchins—several species of algae burst forth in the urchin-free zones. The control areas with large urchin populations contained very few algae.

Paine also noticed that such urchin-dominated "barrens" were common in pools around Tatoosh Island. At first glance, the urchin barrens seemed to violate a key assertion of the HSS hypothesis that herbivores tended not to consume all of the vegetation available. But the explanation for why there were such barrens in Pacific waters would soon become clear—in the surprising discovery of another keystone species, an animal that had been removed from Washington's coast long before Paine started tinkering with nature.

Sea otters once ranged from Northern Japan to the Aleutian Islands and along the North American Pacific Coast as far south as Baja California. Coveted for their luxurious fur, the densest of all marine mammals, the animals were hunted so intensively in the 18th and 19th centuries that by the early 1900s only 2,000 or so animals remained of an original population of 150,000 to 300,000, and the species had disappeared from most of its range, including Washington state. The species gained protected status in 1911 under the terms of an international treaty. After their near-extermination from the Aleutian Islands, the animals rebounded to high densities in some locations.

In 1971, Paine was offered a trip to one of those places—Amchitka Island, a treeless island in the western part of the Aleutians. Some students were working on the kelp communities there and Paine flew out to offer his advice. Jim Estes, a student from the University of Arizona, met with Paine and described his research plans. Estes was interested in sea otters, but he was not an ecologist. He explained to Paine that he was thinking about studying how the kelp forests supported the thriving sea otter populations.

"Jim, you are asking the wrong questions," Paine told him. "You want to look at the three trophic levels: sea otters eat urchins, sea urchins eat kelp."



THE IMPORTANCE OF BEING A SEA OTTER: In the presence of sea otters, sea urchin populations are controlled, which allows for kelp forests to grow (left). In the absence of sea otters, urchins proliferate, forming "barrens" that lack kelp (right).

Bob Steneck

Estes had only seen Amchitka with its abundant otters and kelp forests. He quickly realized the opportunity to compare islands with and without otters. With fellow student John Palmisano, Estes traveled to Shemya Island, a 6-square-mile chunk of rock 200 miles to the west without otters. Their first hint that something was very different was when they walked down to the beach and saw huge sea urchin carcasses. But the real shock came when Estes dove under the water for the first time.

"The most dramatic moment of learning in my life happened in less than a second. And that was sticking my head in the water at Shemya Island," Estes recalled. "We were in this sea of just sea urchins. And there was no kelp anywhere. Any fool would have been able to figure out what was going on."

Estes and Palmisano saw other striking differences between the two communities around each island: Colorful rockfish, harbor seals, and bald eagles were abundant around Amchitka, but not around otter-less Shemya. They proposed that the vast differences between the two communities were driven by sea otters, which were voracious predators of sea urchins. They suggested that sea otters were keystone species whose negative regulation of sea urchin populations was key to the structure and diversity of the coastal marine community.

Estes' and Palmisano's observations suggested that the reintroduction of sea otters would lead to a dramatic restructuring of coastal ecosystems. Shortly after their pioneering study, the opportunity arose to test the impact of sea otters as they spread along the Alaskan coast and re-colonized various communities. In 1975, sea otters were absent from Deer Harbor in southeast Alaska. But by 1978, the animals had established themselves there, sea urchins were small and scarce, the sea bottom was littered with their remains, and tall, dense stands of kelp had sprung up.

The presence of the otters had suppressed the urchins, which had otherwise suppressed the growth of kelp. This kind of double negative logic is widespread in biology. In this instance, otters "induce" the growth of kelp by repressing the population of sea urchins. The discovery of the regulation of kelp forest by sea otter predation on herbivorous urchins was very strong support for the HSS hypothesis and for Paine's keystone species concept.

In ecological terms, the predatory sea otters have a cascading effect on multiple trophic levels below them. Paine coined a new term to describe the strong, top-down effects that he and others had discovered upon the removal or reintroduction of species: He called them trophic cascades.

The discovery of trophic cascades was exciting. The many indirect effects caused by the presence or absence of predators (starfish, sea otters) were surprising because they revealed previously unsuspected, indeed unimagined, connections among creatures. Who would have thought that the growth of kelp forests depended on the presence of sea otters? These dramatic and unexpected effects raised the possibility that, unbeknownst to biologists, trophic cascades were operating elsewhere to shape other kinds of communities. And if they were, then keystone species and trophic cascades might be general features of ecosystems—rules of regulation that governed the numbers and kinds of creatures in a community.

Indeed, trophic cascades have been discovered across the globe, where keystone predators such as wolves, lions, sharks, coyotes, starfish, and spiders shape communities. And because of their newly appreciated regulatory roles, the loss of large predators over the past century has Estes, Paine, and many other biologists deeply concerned.

Today, of course, one predator has more influence than any other. We have created the extraordinary ecological situation where we are the top predator and the top consumer in all habitats. "Humans are certainly the overdominant keystones and will be the ultimate losers if the rules are not understood and global ecosystems continue to deteriorate," Paine says. The only species that can regulate us is us.

Sean B. Carroll is a professor of molecular biology and genetics at the University of Wisconsin-Madison and Vice President for Science Education at the Howard Hughes Medical institute. His new book is The Serengeti Rules: The Quest to Discover How Life Works and Why It Matters.

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D Hayes • 4 months ago

I don't know, mosquitoes don't do a bad job of human regulation, in some parts of the globe...

Great article, I hadn't know the experimental and theoretical history of the trophic cascade hypothesis - especially not with star fish!

(Just to be a stickler, I think *effect would be the more correct term in the line "Paine and zoologist Robert Vadas set out to find out what affect the urchins had on algal diversity.")

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Nautilus Magazine Moderator → D Hayes • 4 months ago

Good catch! We should indeed have used "effect." We've corrected that in the story above. Thanks for being a reader!