What these pioneers discovered was a set of ecological rules that are surprisingly analogous to the physiological rules I have described. Indeed, I deliberately introduced you first to negative and positive regulation, double-negative logic, and feedback regulation at the molecular scale. You are about to see their power on the grandest stage.

CHAPTER 6

SOME ANIMALS ARE MORE EQUAL THAN OTHERS

> You push an ecological system too far and
> suddenly all the rules change.
>
> —ROBERT PAINE

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 forty-eight 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 onto 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.

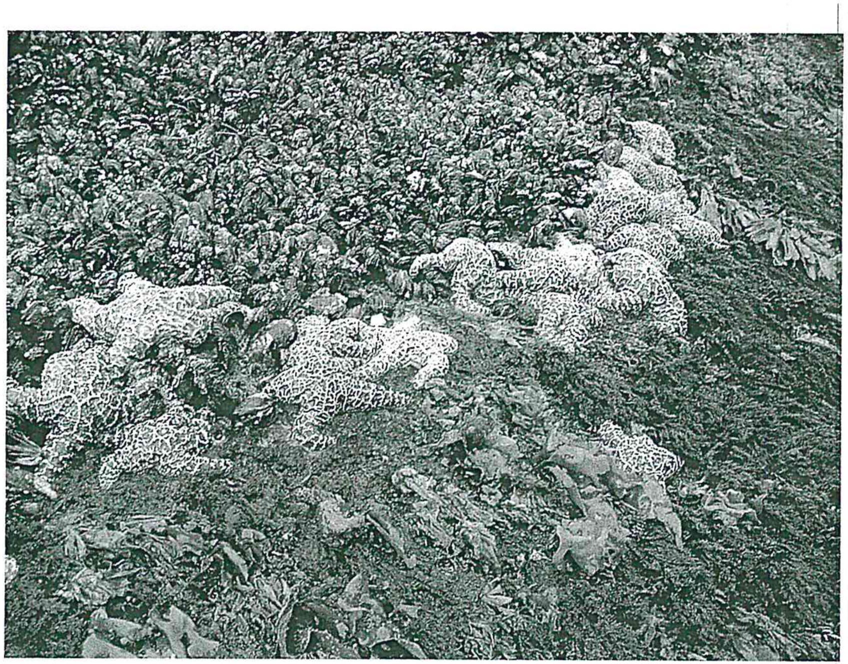

FIGURE 6.1 The ochre starfish Pisaster ochraceus in the rocky intertidal zone on the Pacific coast. The starfish prey on the mussels, which enables other species such as kelp and small animals to co-occupy the community.

Photo courtesy of David Cowles, rosario.wallawalla.edu/inverts.

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 Strait of Juan de Fuca, onto the lands of the Makah Nation, and out to the cove of Mukkaw Bay. At low tide, he scampered on to a rocky outcrop. Then, with a crowbar in hand and mustering all of the leverage he could with his six feet six 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.

WHY IS THE WORLD GREEN?

Paine's journey to Mukkaw Bay and its starfish was a circuitous one. Born and raised in Cambridge, Massachusetts, Paine was named for his ancestor Robert Treat Paine, who was a signer of the Declaration of Independence. His interests in nature were fueled by exploring the New England woods. His first love was bird-watching, with butterflies and salamanders close seconds.

Paine went on frequent bird-watching walks with a neighbor, who insisted that he make a record of all his sightings. It was good discipline, for Paine became such a sharp bird-watcher that he became the youngest member of the Nuttall Ornithological Club, an exclusive tribe of top birders.

He was also inspired by the writings of prominent naturalists, who opened his eyes to the drama of wildlife. Passages such as this from Edward Forbush's *Birds of Massachusetts* stoked his youthful imagination:

> A gang of men were startled one winter's day ago in Medfield woods by the sight of what seemed like a huge bird "with four wings" whirring past. The "bird" dropped into the snow not far away. It turned out to be a Goshawk and a Barred Owl locked in deadly clasp. Both were dead when picked up.

He was just 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 Kumoan.* Spiders, in fact, were considered "sacred objects" in the Paine household. Young Paine spent many hours admiring the orb weavers preying on houseflies he provided.

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 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.

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 eleven months he studied the range, habitat, and behavior of one species.

It was the sort of work that provided a solid foundation for a naturalist-in-training, and it would earn Paine his PhD. 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—some, such as the horse conch, more than a foot long. The mud and sawgrass of Alligator Point was not at all boring, quite the contrary—it was a battlefield.

On top of his thesis work on brachiopods, Paine made a careful, Eltonian 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 eleven-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. The junior scientist interpreted his data in Eltonian terms:

> Elton (1927) suggested that size relationships were the chief reason for the existence of food chains since what is too large, or too small, to be consumed by one organism can be eaten by another. In this way, small items after passing through one or more intermediate steps become indirectly available to larger predators.

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 not just in the structure of communities, but also 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.

Like Elton's pyramid, 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; at the next level were the consumers, the herbivores that ate plants; and above them the predators that ate the herbivores. [Figure 6.2]

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 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 titled "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 *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. I need not recount all of it here. One legitimate critique was that 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.

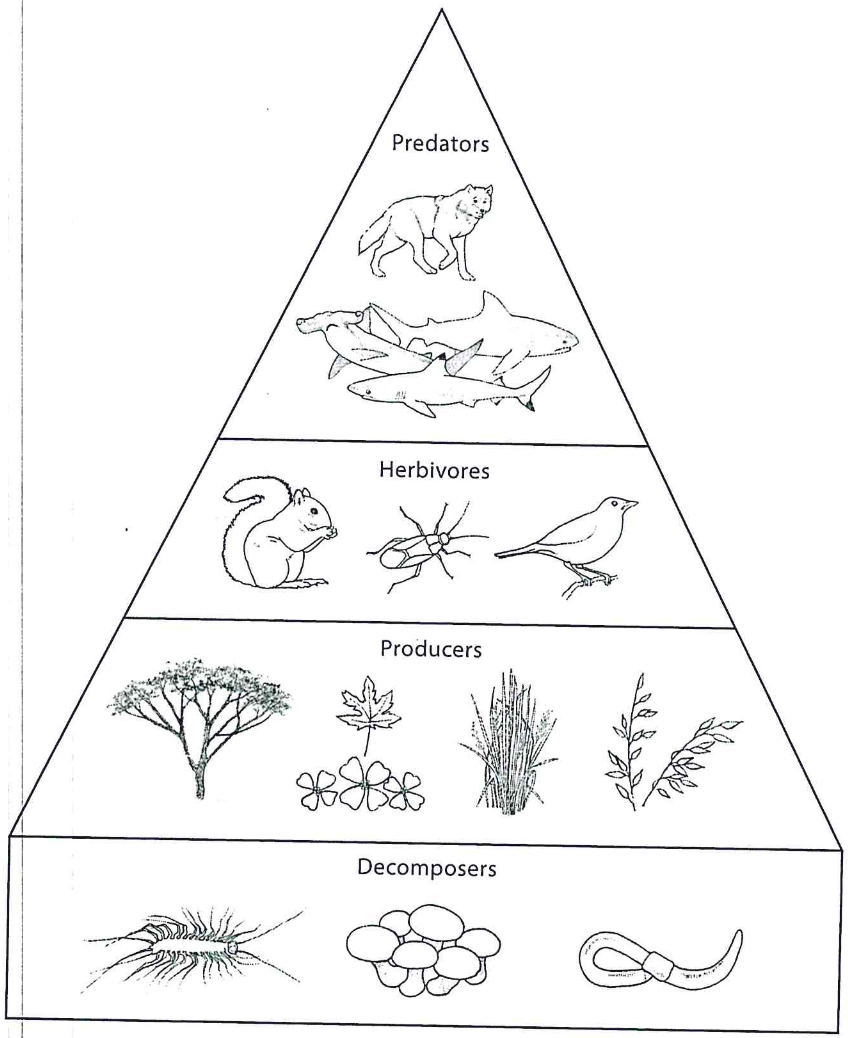

FIGURE 6.2 The trophic levels of biological communities. According to the Hairston, Smith and Slobodkin (HSS) green world hypothesis, organisms belong to one of four trophic levels: decomposers (fungi and worms), producers (plants and algae), herbivores, and carnivores.

Illustration by Leanne Olds.

KICK IT AND SEE

The HSS hypothesis was essentially a description of the natural world based on observation. So, too, were Elton's work and ideas, and Paine's own studies to date on brachiopods and predatory snails (as were Darwin's, for that matter). Indeed, virtually all of ecology up to the 1960s had been based on observation. The limitation of such observational biology was that it left itself open to alternative explanations and hypotheses. Paine, like the pantheon of molecular biologists I have described, 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 one twenty-five-foot-long by six-foot-tall stretch of rock, he removed all the starfish. On an adjacent stretch, he let nature take its course. On each plot, he counted the number and calculated the density of the inhabitants, tracking fifteen 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, so to see what it was feasting on, 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 60–80 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 on by the starfish, the anemone and sponges populations had also decreased. However, the population of one small predatory snail, *Thais emarginata*, increased ten- to twentyfold. Altogether, the removal of the predatory starfish had quickly reduced the diversity of the intertidal community from the original fifteen 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 three 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 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. Schematically, the plots with and without starfish looked like:

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.

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 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, which extended their range by about 40 percent down toward the low tide mark. Six of twenty other species initially present vanished in just eight months; within fifteen months the majority of space was occupied solely by the mussels. Interestingly, this expansion occurred despite the abundance of another large mussel predator (a sea snail).

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.

CASCADING EFFECTS AND DOUBLE-NEGATIVE LOGIC IN FOOD CHAINS

Paine's kick-it-and-see experiments were not limited to manipulating predators. He was interested in understanding the rules that determined the overall makeup 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 Robert Vadas set out to find out what effect the urchins had on algal diversity.

To do so, they removed all 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 face value, the urchin barrens seemed to violate a key assertion of the HSS hypothesis that herbivores tended not to consume all 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 eighteenth and nineteenth centuries that by the early 1900s, only 2,000 or so animals remained of an original population of 150,000–300,000, 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."

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 six-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—and saw that the bottom was carpeted with large sea urchins and had no kelp. He saw other striking differences between the two communities around each island: colorful rock greenling, harbor seals, and bald eagles were abundant around Amchitka but not around otter-less Shemya.

Estes and Palmisano 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's 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 recolonized 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. Schematically, the rules of sea urchin and kelp regulation looked like:

Otters
⊥
Sea urchins
⊥
Kelp

Double-negative logic once again. 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 strong support for the HSS hypothesis and for Paine's keystone species concept. [Figure 6.3]

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 when species were removed or reintroduced: he called these effects *trophic cascades*.

The discovery of trophic cascades was very 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 trophic cascades might be general features of ecosystems—rules of regulation that governed the numbers and kinds of creatures in a community.

Indeed, many trophic cascades have been discovered in all sorts of habitats. Just a few examples will suffice.

In a freshwater stream in Oklahoma, a predator-herbivore-algae trophic cascade regulates the abundance of minnows and plants. In pools in Brier Creek, Mary Power and colleagues noticed an inverse relationship between the number of bass and the number of minnows: the two animals co-occurred in just two of fourteen pools, and only then after a large flood. Moreover, pools that contained bass were green with filamentous algae, while those lacking bass but with minnows were barren. These distributions suggested the possibility that bass, like sea otters, kept the herbivorous minnow population in check, which in turn enabled algae to grow.

To test this, Power removed bass from a green pool and made a fence down the middle. She added the minnows to one side and left the other as a control. The minnows chomped the algae down to the barren state. She then added three largemouth bass to a minnow pool. Within just three hours, the minnows moved to the shallow

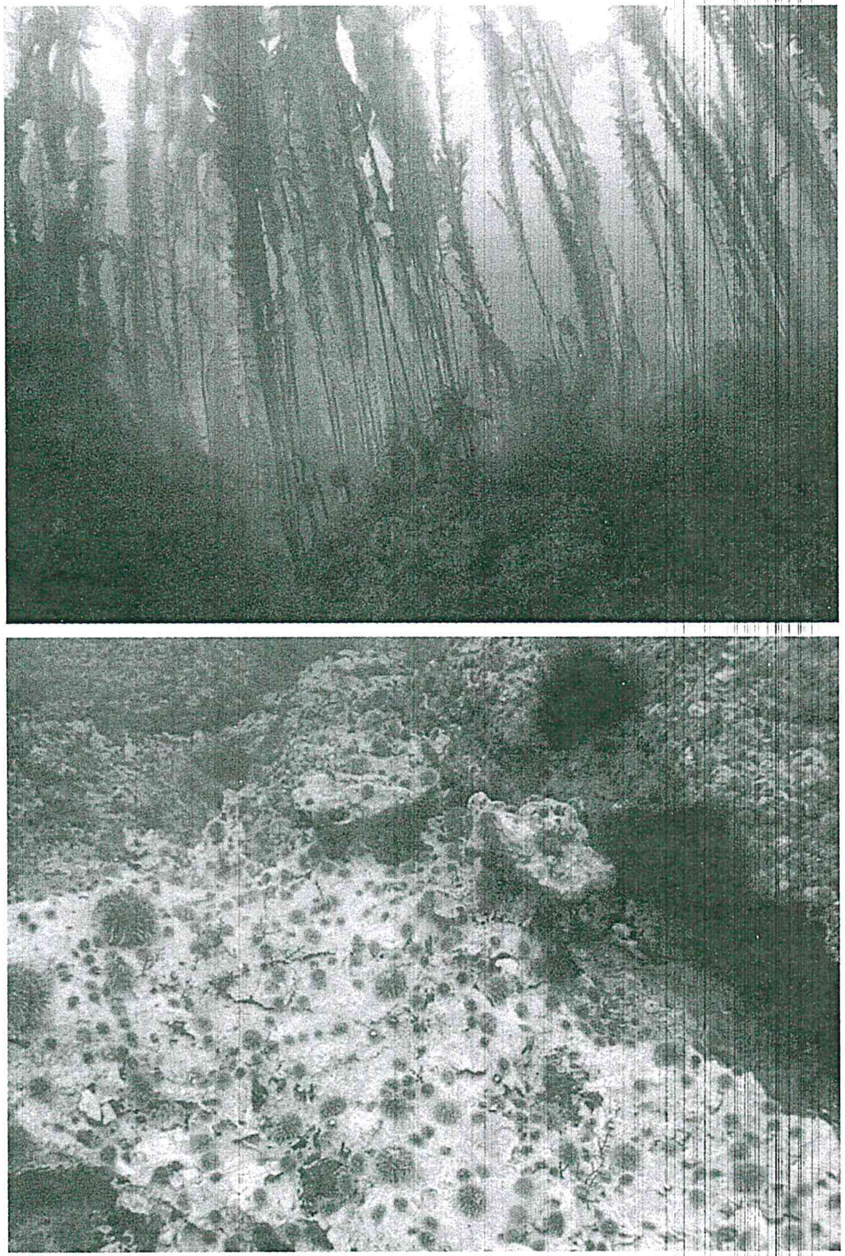

FIGURE 6.3 The influence of sea otters on sea urchins and kelp forests. (Top) In the presence of sea otters, sea urchin populations are controlled, which allows for kelp forests to grow. (Bottom) In the absence of sea otters, urchins proliferate, forming "barrens" that lack kelp.

Photos courtesy of Bob Steneck.

end of the pool where the bass could not get to them; with a few weeks, the pool was green. These results not only demonstrated the existence of a bass-minnow-algae cascade, but they also showed that predator avoidance could have a similar impact as predation itself.

Similar predator-herbivore-plant trophic cascades as the bass-minnow-algae and otter-urchin-kelp trios have been described on land. Isle Royale in Lake Superior, Michigan, was recolonized by moose and wolves in the first half of the twentieth century. Long-term studies have revealed that wolves positively influence fir tree growth by controlling the density of the moose, which feed extensively on the firs. And in Venezuela, trophic cascades were revealed when numerous predator-free islands were created in Lago Guri by the flooding of a tropical forest. For instance, the elimination of the normal army ant and armadillo predators of leaf-cutter ants unleashed a leaf-cutter population boom that decimated tree growth. By indirectly affecting tree growth, these predators also influence the habitat available for many other creatures.

The logic of these freshwater and terrestrial cascades looks like:

Predator	**Bass**	**Wolves**	**Army Ants, Armadilloes**
	⊥	⊥	⊥
Herbivore	Minnows	Moose	Leaf-cutter ants
	⊥	⊥	⊥
Producer	**Algae**	**Fir trees**	**Trees**

I have drawn these cascades in a way that emphasizes the top-down negative regulatory interactions between organisms at different trophic levels. But I must underscore that these are oversimplifications in two respects. First, most organisms are not in simple linear food chains, but as Elton knew well, are parts of food webs with more members and interactions. And second, all ecosystems are positively regulated to some degree from the bottom up. Without sunlight, there would be no plants; without plants, there would be no food for the herbivores; without herbivores, there would be no prey for the predators. That being said, the conceptual advance spurred by HHS and Paine was to flip traditional thinking upside down and to reveal strong indirect effects of predators on producers.

Trophic cascades are dynamic—not static—features of ecosystems. Indeed, trophic cascades have also been observed to flip even without direct human intervention. By the 1970s, it was estimated that sea otter populations along the southeastern Alaskan coast had rebounded to about 100,000 animals. But the populations of sea otters has subsequently dropped dramatically from Castle Cape (south Alaska Peninsula) to Attu Island (Aleutian Island chain). While various possible culprits have been considered, Jim Estes and his colleagues have implicated killer whales as the main suspect. They suggest that the orcas recently turned to preying on sea otters when their preferred prey (sea lions and whales) became scarce. In so doing, the killer whales have turned a three-level cascade (left) into a four-level cascade (right), and the populations at lower levels have inverted—the coastal habitats are again carpeted with sea urchins and deforested of kelp.

$$\begin{array}{ccc} & & \textbf{Killer whales} \\ & & \perp \\ \textbf{Otters} & & \text{Otters} \\ \perp & \Rightarrow & \perp \\ \text{Sea urchins} & & \textbf{Sea urchins} \\ \perp & & \perp \\ \textbf{Kelp} & & \text{Kelp} \end{array}$$

NOT ALL ANIMALS ARE CREATED EQUAL

What began with the tossing of starfish has led to two fundamental insights about how nature works—two rules about the regulation of populations, our first two Serengeti Rules:

SERENGETI RULE 1

Keystones: Not all species are equal

Some species exert effects on the stability and diversity of their communities that are disproportionate to their numbers or biomass. The importance of keystone species is the magnitude of their influence, not their rung in the food chain.

It is important to stress that not all predators are keystones, and that not all keystones are predators. Nor do all ecosystems necessarily have keystones. But we will meet a couple more keystone species in Chapter 7.

SERENGETI RULE 2

Some species mediate strong indirect effects through trophic cascades

Some members of food webs have disproportionately strong (top-down) effects that ripple through communities and indirectly affect species at lower trophic levels.

Such cascades may exist wherever multiple pairs of strong regulatory interactions link trophic levels. These can be predator-predator, predator-herbivore, or herbivore-producer pairings.

It is important to emphasize that most species in a community do not exhibit strong interactions. In another colossal effort spanning several years, Paine investigated the strength of herbivore-producer interactions on Tatoosh Island. He found that most species interacted weakly or negligibly. Paine summed up that hard-earned knowledge in a quote from George Orwell's *Animal Farm*: "Some animals are more equal than others." I would add, some naturalists are also more equal than others. [Figure 6.4]

Just as the discovery of oncogenes and tumor suppressors revealed how not all genes are equal in the regulation of cell number, the discovery of keystone species and trophic cascades has revealed that in a community of organisms, not all animals are equal with respect to the regulation of populations. And just as focusing on those genes simplifies and defines the task for the oncologist, focusing on keystone species and trophic cascades simplifies the task for the ecologist in understanding the structure and regulation of an ecosystem.

So now, with new eyes, let's go back to where I started this book, and where our ancestors started—the magnificent Serengeti.

FIGURE 6.4 Robert Paine at Mukkaw Bay.

Photo courtesy of Kevin Schafer/Alamy.

CHAPTER 7

SERENGETI LOGIC

> Africa is the continent most remarkable for the number and variety of its large mammals. . . . Many have marveled at this abundance of large life . . . but why is it so?
>
> —JULIAN HUXLEY

The verandah outside Southern Highlands boarding school in Sao Hill, Tanzania, was popular with visitors. At night, the lights drew huge dung beetles, for which eight-year-old Tony Sinclair snuck out of his dormitory to collect and keep as pets. One night, the youngster was stalking the bugs when he found himself face-to-face with a leopard that was doing the same. The two hunters backed away from one another very slowly.

Sinclair has been fascinated with animals for as long as he can remember. It did not matter what sorts of creatures—beetles, birds, chameleons—so long as they moved. Although born in Zambia (formerly Northern Rhodesia), and raised in Dar es Salaam (Tanzania, formerly Tanganyika), his first eyeful of large African mammals in the wild came on a stopover in Kenya when he was eleven years old. Game parks were still a new concept in Africa in 1955, when Sinclair visited a reserve outside Nairobi. He was awestruck by the great beasts.

After attending boarding school in England, Sinclair enrolled at Oxford to study biology. On his second day on campus, he heard that