8

From Causes to Consequences: Considering the Weight of Evidence

Scientists sometimes publish papers with intriguing titles. One of my favorites is "Epidemiology and the Web of Causation: Has Anyone Seen the Spider?" by Nancy Krieger. Epidemiology includes the study of epidemics, or the spread of diseases in populations, but has much broader scope as the scientific foundation of public health. Epidemiology is closely related to biology and medicine but also has strong ties to social sciences like psychology and sociology. For example, epidemiologists studied the recent outbreaks of measles described in Chapter 6 as well as the relationships between lead exposure and crime described in Chapter 5.

Krieger was near the beginning of her scientific career when she published her groundbreaking paper in 1994. She argued that epidemiologists use the "web of causation" as a metaphor for the idea that diseases result from a complex network of multiple interacting causes. This parallels my discussion of gene–environment interactions in the last chapter. Just as it's too simplistic to think that some traits are strictly determined by genes and others are strictly determined by the environment; it's too simplistic to consider only microbes as causes of infectious disease—spread of these diseases also depends on cleanliness of food and water, nutrition and general health of susceptible people, and the social, economic, and political factors that influence these things. Krieger didn't deny that diseases have multiple complex causes but argued that epidemiologists should focus on the *root* causes of webs of causation, that is, "spiders." For Krieger, spiders represent the socioeconomic factors that make different populations susceptible to different diseases.

Neither Nancy Krieger nor I would argue that we should give up trying to understand webs of causation just because they involve many factors interacting in complex

ways. Webs of causation have important consequences for us as individuals and as members of communities. We may wish to break some webs and reinforce others to enhance individual and community well-being. To do so, we need to learn what links are most important and how to alter these links without inducing unintended consequences.

Hurricane Katrina, New Orleans, and the Web of Causation

Hurricane Katrina hit New Orleans on August 29, 2005, causing more than 1,800 deaths and at least $80 billion in property damage. It seems straightforward to designate the hurricane as the cause of this massive toll of death and destruction, but a closer look shows a more complex situation (Figure 8.1). Had the levees designed to protect New Orleans from storm surges not failed, damage in the city would have been much less. Perhaps the Corps of Engineers, which designed and built the levees, did a poor job, either because of incompetence or lack of funding. Development of the vast wetlands of the Mississippi Delta for housing and industry also contributed to the damage because these wetlands in their natural state would have absorbed much of the water brought ashore by the hurricane.

Politics played a role as well, as exemplified by poor planning and slow response of the Federal Emergency Management Agency (FEMA) as well as missteps by state and local governments. The tradition of presidents appointing political supporters to leadership positions in government agencies contributed to these problems. President George W. Bush appointed Michael D. Brown as head of FEMA in January 2003. Brown was a lawyer who had no prior experience in emergency services or management; before joining the Bush administration, he worked for the International Arabian Horse Association for 13 years. Although Bush congratulated Brown in early September 2005 for his management of the federal response to Katrina (Figure 8.1), Brown resigned on September 12 in reaction to widespread criticism of FEMA's performance.

Hurricane Katrina was the most obvious direct cause of damage to New Orleans in 2005, some of which remains eight years later. We can't eliminate or control hurricanes, however, so situating the hurricane in the web of interacting factors that influenced the extent of damage (levees, development of wetlands) and the recovery process (actions of governmental agencies) can help us figure out how to manipulate similar webs to reduce damage from future storms. But we must consider one additional component of the Katrina web if we hope to manage future storms more effectively. This is climate change, which has consequences for hurricanes and other severe weather events in the future and which requires more than single, specific actions to disrupt the web, like building stronger levees or appointing professionals to head FEMA (Figure 8.1).

At the time of Katrina, climatologists speculated that climate change might increase the frequency or intensity of hurricanes, but there was little direct evidence to test this idea. Since then, several researchers have shown that average intensity
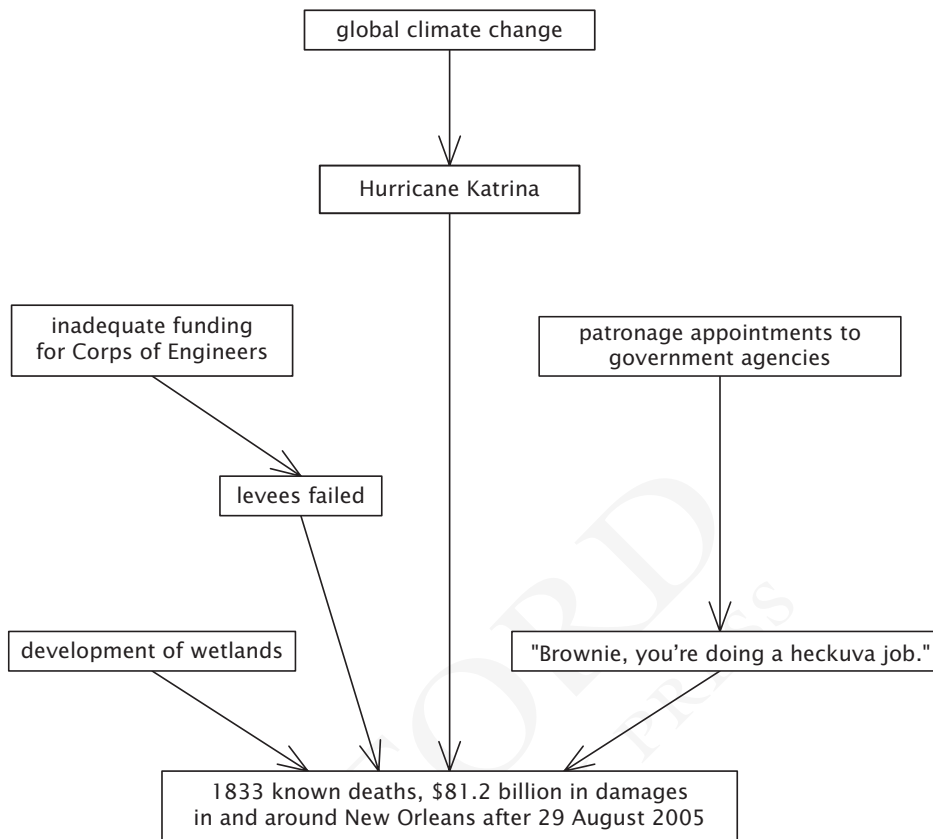
FIGURE 8.1 Web of causation for damage in and around New Orleans attributed to Hurricane Katrina. We could build a much more elaborate web by including additional direct and indirect causes and interactions between causes.

of hurricanes has increased as global temperatures have increased in recent decades, although there is no corresponding pattern of change in number of hurricanes. Hurricane intensity is measured on a scale from 1 to 5 based on wind speed, with speeds greater than 157 miles per hour for category 5. There were eight category 5 hurricanes in the Atlantic Ocean north of the equator between 2000 and 2010, including Katrina. This was an average of slightly less than one category 5 hurricane per year, compared to one every four years from 1970 to 2000. Climatologists have known for quite a while that warmer surface water in the ocean contributes to the energy of hurricanes by increasing evaporation, which ultimately increases wind speed as well as amount of rainfall. Since global climate change encompasses temperature increases in oceans as well as on land, climatologists were not surprised by recent analyses showing a correlation between temperature and average intensity of hurricanes in the past century. Combining these analyses with models of global climate change (Appendix 4), Aslak Grinsted and two colleagues predicted that hurricanes with storm surges as

great as those of Katrina would occur at least twice as often in the twenty-first century as in the twentieth century.

Including climate change in the web of causes of large-scale death and damage in New Orleans following Hurricane Katrina (Figure 8.1) illustrates one important complexity of causation beyond simply the fact that events usually have multiple interacting causes, as shown by the web itself. Some of these causes of things are deterministic. If a person is bitten by a rabid dog and infected with the rabies virus, the virus will travel to the person's brain and cause acute encephalitis and death. Many infectious diseases are similar in that the disease invariably follows infection with a causal microorganism, although not all infectious diseases end in death. But other causes are probabilistic rather than deterministic. This means that a causal factor increases the likelihood of a particular result but doesn't invariably produce the result. The relationship of smoking to lung cancer is a good example—a long history of smoking increases the chance that a person will get lung cancer but doesn't make lung cancer a certainty. Global climate change has a parallel influence on hurricane intensity. Climate change increases the probability that any hurricane that forms will be stronger—category 4 or 5—but doesn't guarantee this result. With climate change, there will still be relatively weak hurricanes in categories 1 to 3 but a greater percentage will be in categories 4 and 5 than in the past. In addition, when Hurricane Alice first forms in the Atlantic in August 2018, climatologists can't say, "Because of climate change, we know this will be a category 5 storm." As Alice or any hurricane develops and moves toward land, climatologists can begin to predict its intensity, not based on general knowledge of climate change but on observations of the hurricane itself.

Challenges in Dissecting Webs of Causation

I've used several examples in previous chapters to show how and why scientists seek to understand causation, but you've also seen that this is a challenging problem. The challenges come from two main sources. One is the complexity of causation, illustrated by the web of causes associated with damage from Hurricane Katrina (Figure 8.1) and by the fact that many causal factors in this web are indirect and probabilistic rather than direct and deterministic. The second major challenge in understanding causation is limitation of our methods. Experiments offer the best opportunity for a clear test of an hypothesis about the cause of some phenomenon, but experiments aren't always possible. Even when experiments are possible, they can go astray for a host of reasons such as faulty design, unjustified assumptions, or inadequate sample sizes. In addition, experiments work best where potential causes are few and straightforward. This is one reason why microbiologists of the nineteenth century like Louis Pasteur were so successful in finding causes of diseases like anthrax, cholera, and rabies (another reason is that they were brilliantly creative scientists).

Other methods for learning about causation such as the comparative and correlational studies of cell phone use as a potential cause of brain cancer discussed in Chapter 5 may be better suited than experiments for phenomena that have multiple interacting causes. However, comparative and correlational studies usually don't generate results that are as definitive as those from experimental studies.

Crime stories, whether true or fictional, sometimes involve a "smoking gun" that leads to conviction of the person holding the gun. Stories in science are occasionally resolved by definitive evidence that constitutes a smoking gun. For example, the combination of Watson and Crick's model of DNA, Rosalind Franklin's X-rays, and Erwin Chargaff's discovery of consistent patterns in amounts of the four bases in different samples of DNA was a smoking gun that convinced everyone that DNA was a double helix (Chapter 6). Much more often, however, there is no smoking gun in scientific research and scientists must answer questions based on the weight of evidence for and against various hypotheses. This is especially true in ecology, where complex webs of causation are as pervasive as they are in epidemiology. It's also true for questions that impact decisions about policies that managers, legislators, and voters must make.

Wolves were extirpated from much of the contiguous United States during the nineteenth and twentieth centuries, even in national parks like Yellowstone. Wolves were protected under the US Endangered Species Act in 1973 and reintroduced in Yellowstone National Park in 1995 after an absence of 60 years. The population in Yellowstone grew rapidly and spread beyond the park borders, and wolves in other parts of the country have expanded their range as well. In June 2013 the US Fish and Wildlife Service proposed to remove wolves in the contiguous United States from protection under the Endangered Species Act, leaving it up to individual states to manage wolf populations and, if they wished, set hunting seasons for wolves. In response, 16 leading wolf researchers wrote a letter to the Secretary of the Interior outlining four major objections to this proposal. How can we evaluate the proposal of the US Fish and Wildlife Service to remove wolves from the endangered species list? Our evaluation won't be based solely on science but will involve economic and ethical considerations too. Even disregarding these added complexities, the scientific arguments for and against the proposal are complex enough. The only way to fairly evaluate the scientific foundation of policy proposals like these is to consider all the evidence, pro and con, and decide whether the weight of evidence favors one path or another. Our final decision may rest on economic or ethical arguments but should be consistent with scientific evidence. For example, if you were a rancher in Idaho who raised sheep and thought wolves should be killed to protect your income, the persuasiveness of your argument would depend on evidence about wolf predation on sheep. Is it incidental or pervasive? How does it depend on the distribution and abundance of wolves? Are there other methods for protecting sheep that are more effective or less expensive than killing wolves (see Question 1)? We'll return to the wolf story at the end of this chapter, but first I'll describe some other examples of ecological questions that can only be answered by thinking about weight of evidence rather than hoping for a smoking gun.

Keystone Species in Food Webs—Analyzing Complex Causation in Ecology

Ecologists study many features of the natural world, but many of us focus on interactions between individuals and populations that live together in ecological communities. Just as a sociologist might study the human community in the Haight-Ashbury District of San Francisco, an ecologist would study the plants and animals in a mountain meadow. This ecological community contains various species of grasses, sedges, forbs (non-woody flowering plants, commonly known as wildflowers), and shrubs. There are also grasshoppers, butterflies, ants, mice, snakes, ground squirrels, gophers, rabbits, foxes, and songbirds. Coyotes wander through from time to time, and hawks fly overhead. The mountain meadow community also includes invertebrates and microorganisms that live in the soil.

You've already seen examples of the fundamental ecological interactions of competition, predation, and mutualism. When two species use the same resources and these resources are in limited supply, the species are in competition. Each has a negative effect on the other, ultimately by suppressing its population size although this can happen through several different mechanisms. Yampah is a plant with delicate white flowers and a large starchy root that occurs in our mountain meadow. If a gopher traveling through its burrow under the meadow encounters a yampah root, it will probably eat it, killing the plant and making it unavailable to a ground squirrel that would have eaten the leaves and flowers. Predation is an interaction in which one species benefits at the expense of the other. If a coyote catches and kills a rabbit in our meadow, the coyote gets a meal that helps keep it alive and may contribute to its ability to reproduce, while the cost to the individual rabbit as well as the population of rabbits is obvious. The interaction between the gopher and the yampah plant or a ground squirrel and another yampah plant is like predation in that one party benefits at the expense of the other, although predation on plants is given the special name of herbivory. Mutualism is an interaction in which both species benefit, like the pollination of flowers by bees discussed in Appendix 3.

Feeding interactions in ecological communities are often illustrated by food webs, as in Figure 8.2 for a site called Wytham Woods that has been an environmental research site for Oxford University since 1942. Like other food webs, this one includes green plants such as oak trees, other trees, shrubs, and herbs; herbivorous insects, mammals, and birds; predators such as spiders and weasels; parasites; and parasites of parasites, or hyperparasites. It also includes organisms that live in the soil and feed on dead organic matter such as the leaves of plants that drop in fall and become part of the litter layer on the surface of the soil. This is an incomplete depiction of the food web at Wytham Woods because it doesn't show all individual species that live in the community. Except for very simple communities, it's difficult to draw complete food webs.

This discussion of basic ecological interactions and food webs sets the stage for our first example of an important question in ecology—are there certain species that have especially important roles in ecological communities—so important that if they weren't
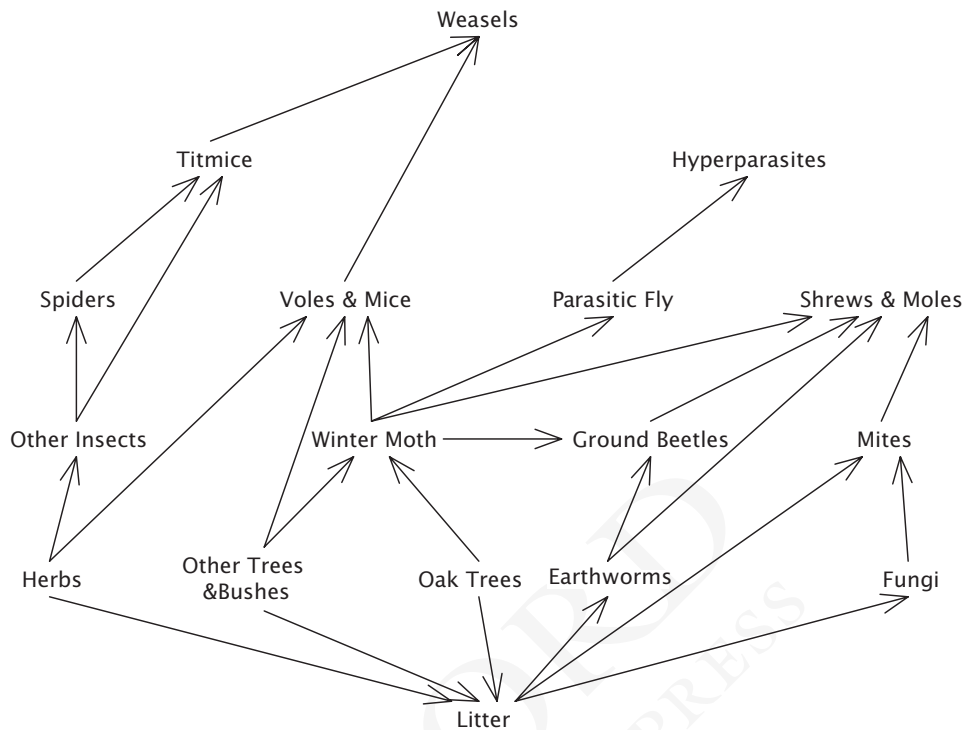
FIGURE 8.2 Food web for Wytham Woods, near Oxford in the United Kingdom. Like most diagrams of food webs, this is incomplete. For example, herbs, other insects, and spiders each comprise many different species.

present the structure and function of the community would be much different? The structure of a community is its species composition and general appearance; for example, an oak woodland looks quite different from a pine forest. The function of a community includes the flow of energy from the sun to green plants to herbivores to predators and the cycling of nutrients between plants, animals, and the soil. Suppose the food chains in one community include at most three species—a plant, an herbivore that eats the plant, and a carnivore that eats the herbivore—while some food chains in another community include as many as five species. This would be a functional difference between the communities (see Question 2).

Species that have especially important roles in their communities are called *keystone species*. More specifically, Mary Power and several colleagues defined a keystone species as "one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance." These researchers offered their definition in a 1996 paper entitled "Challenges in the Quest for Keystones," indicating that the identities of keystone species in various communities aren't obvious. In some cases, ecologists disagree about whether any species should be singled out as a keystone.

A keystone species is analogous to the keystone in an arched, stone bridge (Figure 8.3). The keystone in a bridge is just a single stone under the highest point at the center of the
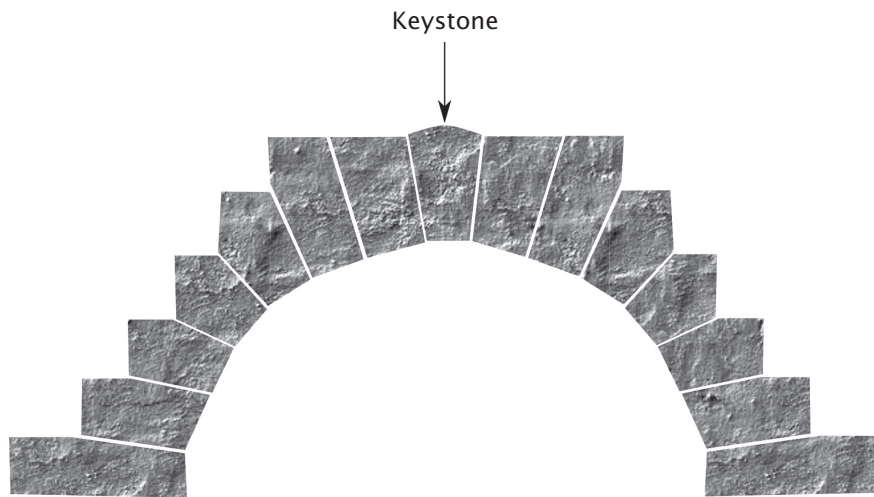
Keystone

FIGURE 8.3 An arch made of wedge-shaped blocks. The structural integrity of the arch depends on the keystone block.

bridge. It holds the least weight of all the stones, but the bridge collapses without the keystone. This analogy to keystones in bridges illustrates why Power's group defined a keystone species as one with a *disproportionate* influence on its community. For example, distemper is caused by a virus that infects dogs, cats, and their wild relatives. The Serengeti is a savannah ecosystem in east Africa with huge populations of large mammals such as wildebeest, zebras, gazelles, lions, cheetahs, wild dogs, hyenas, and many other species (Plate 1d). If distemper became established in the lion population of the Serengeti and killed a substantial number of lions, there would be ramifying effects on the prey species that lions eat, on the other predators that compete with lions, on the vegetation, and even on things like termites and songbirds. As a tiny virus, the biomass of distemper would be minuscule, but its impact could be huge, so we would consider it a keystone species.

In introducing keystone species, I suggested that removal of a keystone would cause major changes in the structure and function of a community. This definition complements that of Power and her colleagues, but it also implies that we can identify keystones by doing experiments. To test whether or not a particular species is a keystone in its community, remove it and see what happens. If there are unexpectedly big changes relative to the abundance of the species, it is considered a keystone.

Robert Paine introduced the concept of keystone species in 1969 to describe the results of such an experiment that he did at Mukkaw Bay on the coast of Washington state. He worked on a rocky ledge in the intertidal zone, which is covered by water at high tide and exposed to the air at low tide. The intertidal community includes organisms like barnacles, mussels, sponges, and anemones that attach themselves to the rocks and filter nutrients from the water as the tide rises. There are also seaweeds and various mobile herbivores that feed on seaweeds such as snails, limpets, and chitons. The food web at Mukkaw Bay included two main predators, whelks that drill holes in the shells of barnacles and mussels

and extract the meat within and starfish that feed on chitons and limpets but also can detach barnacles and mussels from the rock and turn them over to access the edible parts of these animals. Not counting microscopic organisms called plankton in the water that covered the intertidal at high tide, there were 15 species in the food web at Mukkaw Bay.

Paine marked out two large plots on the rocks in July 1963. He visited his study site once or twice a month and removed all of the starfish from one of the plots, throwing them into the ocean. At the end of one year, the food web on the removal plot was much simpler, with only eight species, while the food web on the control plot still had the original 15 species. The removal plot was now dominated by mussels, which apparently had outcompeted many of the other species of herbivores. Starfish eat most of the species attached to rocks in this intertidal community but prefer mussels (Plate 13a), keeping the population of mussels low enough under natural conditions that other herbivores can coexist with them. When mussels were released from control by predators, their population grew rapidly at the expense of other herbivores.

Paine continued removing starfish from his experimental plot through 1968 and monitored the study site periodically until 1973. At that time, the control plot still had 15 species but the experimental plot had just two, mussels and starfish. As top predators, starfish weren't especially abundant, but their presence had a noticeable effect on the species composition of the rocky intertidal community at Mukkaw Bay, so Paine coined the term keystone species to describe the role of starfish in this community (see Question 3).

Some researchers argue that experiments are the only way to test whether a species is a keystone. For some species in some communities, however, manipulative experiments aren't feasible, so we have to rely on observations, comparisons, correlations, and what we might call natural experiments (Chapter 6). Sea otters are one of the most famous examples of an animal considered by many researchers to be a keystone species, but this is based on the weight of various kinds of evidence, most of which is from observational and comparative studies rather than manipulative experiments. Therefore I'll tell the story of sea otters as a keystone species to introduce how we can evaluate hypotheses by considering the weight of evidence both for and against the hypotheses.

Is the Sea Otter a Keystone Species? What Does the Weight of Evidence Suggest?

Sea otters (Plate 13b) are the second smallest marine mammals and spend their entire lives close to shore, unlike seals, sea lions, dolphins, and whales. Sea otters have extremely thick and dense fur, with up to 1 million individual hairs per square inch, so they were highly sought by fur traders. Before exploitation by humans, sea otters were widely distributed along coasts in the North Pacific Ocean from Japan to the Aleutian Islands to Baja California. Rough estimates of their total number ranged from 150,000 to 300,000, but by 1900 there were only about 2,000 left in widely scattered populations in Russia, Alaska, and California. The International Fur Seal Treaty signed in 1911 banned hunting of sea otters and the US.

Marine Mammal Protection Act of 1972 provided further protection. As a result of these actions and because their habitat was largely intact, sea otters recolonized much of their original range and the population rebounded to about 106,000 in 2007, although the species is still classified as endangered by the International Union for Conservation of Nature.

Sea otters eat a wide variety of foods, including fish and various marine invertebrates, but they especially favor sea urchins, which are mobile grazers that feed on large seaweeds called kelp. In the coastal habitats where they live, sea otters dive 20 to 50 meters to the ocean floor to collect sea urchins, abalones, and other invertebrate prey. For a prey item with a thick hard shell like a mussel, a sea otter may bring a rock to the surface of the water, roll over on its back, set the rock on its chest, and pound the mussel against the rock to break the shell. When this use of tools was first studied by Hall and Schaller in 1964, it was thought to be the only example of tool use in a mammal outside the primates (although a handful of other examples have been reported since).

Jim Estes was a graduate student at the University of Arizona in 1970 when the Atomic Energy Commission was planning underground nuclear tests on Amchitka Island, in the middle of the Aleutian Chain between the Alaska Peninsula and the Kamchatka Peninsula of Russia. The Atomic Energy Commission wanted to fund research on sea otters, and Estes was hired to work on the project. In his first summer, he mostly got oriented to the study site—tagging the otters, observing their behavior from shore, and scuba diving to get a closer look at the sea floor where they foraged. In 1971, his coworker John Palmisano suggested that Estes visit Amchitka when Robert Paine was going to be on the island. By this time, Estes knew that an important food chain went from kelp to sea urchins to sea otters, and he started to wonder how the abundance of kelp might influence the population of otters, thinking that more kelp would support more sea urchins and therefore a higher population of otters since sea urchins were a preferred food for otters. This was a "bottom–up" hypothesis about the control of an ecological community—traditional thinking was that green plants produce the food that all the animals in a food web rely on directly (herbivores like sea urchins) or indirectly (carnivores like sea otters). But Paine told Estes about his experiments with starfish at Mukkaw Bay and suggested that Estes give some thought to top–down effects instead.

If Estes and Palmisano wanted to study the effects of sea otters on nearshore ecological communities in the ocean, they needed a study site where otters were absent to compare to Amchitka Island where they had survived through the fur-harvesting period of the 1800s and early 1900s. Russians were the main hunters of sea otters in the western Aleutians, and a few otters survived at Amchitka because it was relatively far from Russia and from the eastern Aleutians where Americans hunted. Shemya Island is much farther west in the Aleutians, thus closer to Russia, and otters had been completely eliminated at Shemya and were still absent in the 1970s. Therefore Estes and Palmisano decided to compare the abundance of kelp and sea urchins at Amchitka and Shemya.

Their basic methods were straightforward although "their data did not come cheaply" (Stolzenburg 2008). Palmisano drove the boat; Estes dove. They worked

in summer when the water averaged 45ºF and winter when it was 35ºF. Stolzenburg reported,

> Estes would dive in the morning for an hour, collecting samples of kelp and urchins, staring into square meter quadrates, filling data sheets with names and numbers. He would write underwater on slates until his chilled hands were shaking too violently to continue. After a hot shower to thaw the blood, he would head out again in the afternoon for another hour, until he was too numb to write anything more. The next day he would repeat the process.
>
> (STOLZENBURG 2008:60)

Estes and another researcher named David Duggins extended this research to three more sites in the Aleutians and three in southeast Alaska in 1987 and 1988. Sea otters had been eliminated by hunting throughout southeast Alaska in the nineteenth and early twentieth centuries but were reestablished at Surge Bay and Torch Bay by 1970. They were still absent at Sitka Sound, however. Figure 8.4 shows the quantitative results. In both
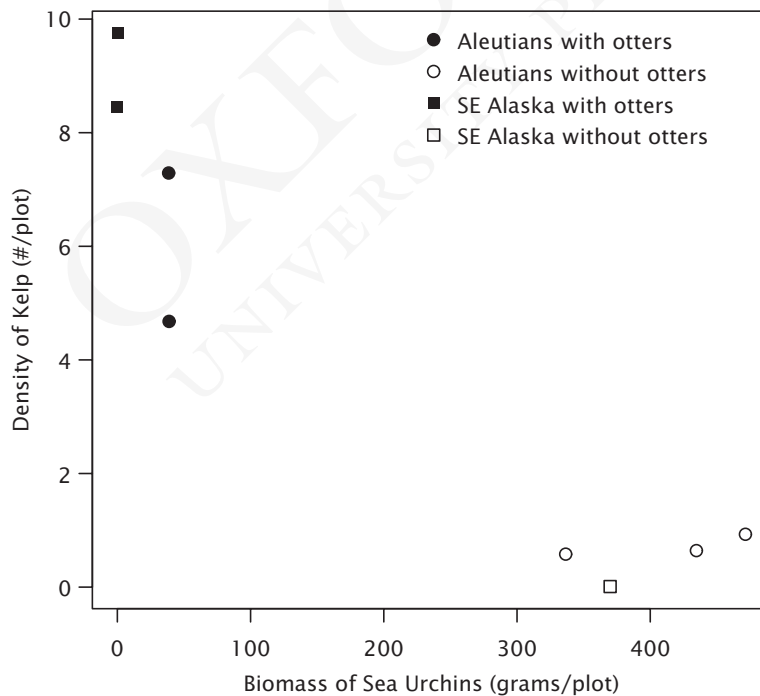

FIGURE 8.4 Average density of kelp and average biomass of sea urchins in 0.25 m² plots on the ocean floor at five sites in the Aleutian Islands and three sites in southeast Alaska. Density of kelp is the average number of individual plants in each plot; biomass (total weight) of sea urchins is an estimate based on counts of individuals and their estimated sizes. Each site is shown by a different symbol: filled symbols for sites with sea otters present and open symbols for sites lacking sea otters.

regions, sites with sea otters were dominated by kelp while sites without sea otters were dominated by sea urchins. Plate 14 illustrates these differences visually.

Although these studies by Estes and his colleagues gave very clear results, they weren't true experiments because sites were not randomly selected to have sea otters present or absent. Amchitka and Adak Islands in the Aleutians had otters because they were a long distance from the home base of the Russians who hunted them to extinction at Shemya and other islands closer to Russia. Without random assignment of treatments (presence or absence of sea otters) to sites, we can't exclude the possibility that other differences between sites might have accounted for the results. For example, the weather might be even harsher at islands like Shemya lacking otters than at islands closer to the Alaskan mainland with otters, and this might explain the low density of kelp at islands lacking otters. In southeast Alaska, the Department of Fish and Game didn't select random sites to release otters but used other criteria—perhaps where they thought the otters might be most successful, most accessible to tourists for observation, or in least conflict with anglers, or simply for convenience. This makes these studies a natural experiment rather than a true experiment. As we discussed in Chapter 6, the possibility of confounding factors makes the interpretation of natural experiments shaky.

Estes and his colleagues did their work in the far north. What about California? Sea otters were almost completely eliminated from California by 1900, although the population increased from about 50 in 1938 to 2,800 in 2012. Michael Foster and David Schiel reviewed survey data for 224 sites lacking sea otters along the California coast to examine the relationship between sea urchins and kelp in the absence of otters. They found some sites with 100% kelp cover and no large sea urchins, like those shown by the filled symbols in Figure 8.4, and some sites with no kelp but abundant sea urchins, like those shown by the open symbols in Figure 8.4. But these sites were only a small percentage of the total number that they considered, while 89% of the sites had both sea urchins and moderate cover of kelp. Foster and Schiel used this result to argue that sea otters are not a keystone species, at least in the southern part of their range in California.

The last remaining population of sea otters in California after hunting was prohibited in 1911 lived at Big Sur, about 150 miles south of San Francisco. As the population increased, animals dispersed north and south along the coast, so that the current range extends from Half Moon Bay, just south of San Francisco, to Point Conception, near Santa Barbara, a distance of 300 miles. Glenn VanBlaricom compared the amount of kelp along two stretches of coastline before and after the reestablishment of sea otters. There were no otters and little kelp south of Point Lobos in 1911–1912 but abundant otters and widely distributed kelp in 1983. There were no otters and only scattered kelp north of Point Estero as late as 1973, but otters had colonized this area by 1983 and kelp was now widely distributed (Figure 8.5).

These are three independent lines of evidence about the potential role of sea otters as a keystone species. In the Aleutian Islands and southeastern Alaska, Estes's team measured the abundance of sea urchins and kelp at sites with and without otters. In California, VanBlaricom plotted the distribution of kelp before and after the arrival of otters. Foster
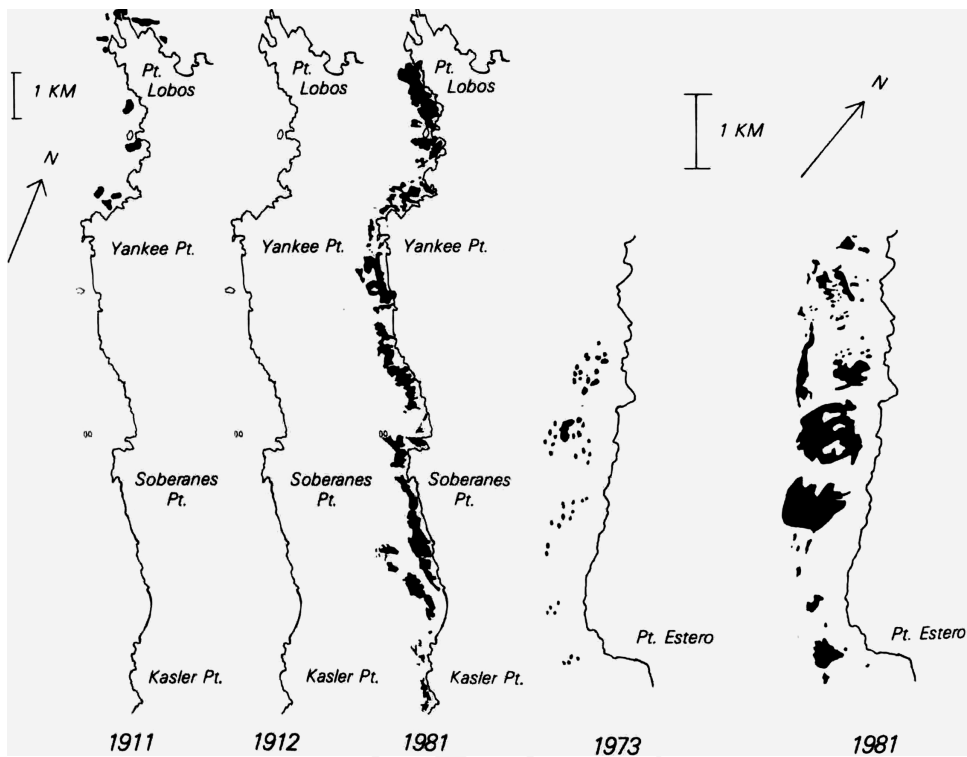
FIGURE 8.5 Distribution of kelp along the California coast south of Point Lobos (left three maps) and north of Point Estero (right two maps) before and after recolonization by sea otters. Sea otters were absent from the area south of Point Lobos in 1911–1912 but present in 1981. Sea otters were absent from the area north of Point Estero as late as 1973 but present in 1981.

and Schiel examined sites without otters in California but found that most such sites contained both kelp and sea urchins. At these sites, however, they only found sea urchins living in small patches or in crevices, suggesting that something other than otters limited the abundance of sea urchins at these sites. They didn't speculate about what this might be, but damage by strong waves or currents might be a possibility. What are the strengths and limitations of these three lines of evidence? How relevant are the observations of Foster and Schiel, since they didn't examine any sites *with* sea otters? The research by Estes and his colleagues in the Aleutians and southeastern Alaska produced clear and dramatic quantitative results (Figure 8.4), but since this was only a natural experiment, it may be that other differences between sites besides presence or absence of otters might have accounted for the results. The research by VanBlaricom in California showed increases in kelp distribution after colonization by sea otters, but he didn't provide quantitative data on the abundance of kelp because he did broad-scale surveys rather than intensive sampling. However, these two studies by Estes's group and VanBlaricom provide complementary evidence consistent with the keystone species hypothesis for sea otters (see Question 4).

Keystone species have large effects on the structure and function of their communities even though they aren't the most abundant members of these communities. The

starfish studied by Robert Paine and the sea otters studied by Jim Estes meet the second qualification because they are top predators and not as abundant as the plants and herbivores in their communities. This characteristic of food webs occurs because top predators depend on herbivores for energy, herbivores depend on plants, and less energy is available at each higher level in the web (see Chapter 3). Paine showed that starfish had a big effect on the composition of a rocky intertidal community because the number of species of animals was much higher when starfish were present than when they were absent. By influencing the abundance of sea urchins and kelp, sea otters can change the appearance of a nearshore oceanic community from a site covered with sea urchins (Plate 14a) to a kelp forest (Plate 14b). This change has effects that ramify through the community. In their initial work in the Aleutians, Estes and Palmisano found more kelp at Amchitka Island, where otters were present, than at Shemya, where otters were absent. Kelp provides cover for fish, and there were more rock greenling and other fish at Amchitka than at Shemya. Harbor seals and bald eagles prey on fish, and these two predators were also more abundant at Amchitka. So there is evidence that sea otters influence several different species in nearshore environments in addition to sea urchins and kelp. The appearance and species composition of a community are aspects of its structure, but sea otters also influence community function, as described in Box 8.1.

BOX 8.1 Sea Otters, Kelp, and Climate Change

In 2013, Christopher Wilmers, Jim Estes, and three colleagues extended their analysis of nearshore communities to ask a functional question. Their ultimate goal was to estimate the potential contribution of kelp forests to ameliorating climate change. Since green plants use carbon in photosynthesis, plants that are large and long-lived may sequester substantial amounts of carbon in their tissues. Individual kelp plants don't live for centuries, like some trees, but when kelp dies and sinks to the bottom of the ocean, it is removed from an environment in which it would decompose and release its stored carbon to the atmosphere. Since predation by sea otters on sea urchins favors the development and maintenance of kelp forests, Wilmers's group wondered if sea otters might help ameliorate climate change.

The researchers collected all the kelp rooted in 10 quadrats at each of four sites in the Aleutian Islands, two with and two without otters. They dried these samples and then used an elemental analyzer to measure the percentage of carbon in the samples. In previous work, Estes, Duggins, and others had counted kelp rooted in quadrats at other sites with and without otters (Figure 8.4) but had not collected samples to measure carbon content. To extend the scope of their analysis, Wilmers's team used these earlier data as well. This introduced potential error because they had to estimate carbon storage from counts of individual plants, but the authors described their approach as conservative, that is, minimizing estimates of potential

(Continued)

BOX 8.1 Continued

effects of sea otters on carbon storage. By including the earlier data, the authors added 3,215 quadrats at 153 sites in six regions from Vancouver Island to the western end of the Aleutian Chain.

Box Figure 8.1 summarizes the results of Wilmers and colleagues. The figure shows estimates of rates of transfer of carbon to and from the nearshore ecological community and amounts of carbon stored in kelp—the kelp carbon pool. Note that each of these estimates is a range of values, not a single value, because the researchers collected multiple samples and there was variation in the biomass and carbon content of kelp in these samples. Despite this variation, areas with sea otters and abundant kelp had much more carbon stored in the kelp and greater potential for transfer of this carbon to the ocean depths than areas without otters and with little kelp.

What are the broader implications of these results? Suppose sea otters recolonized their original range in the North Pacific, either on their own or with human help.
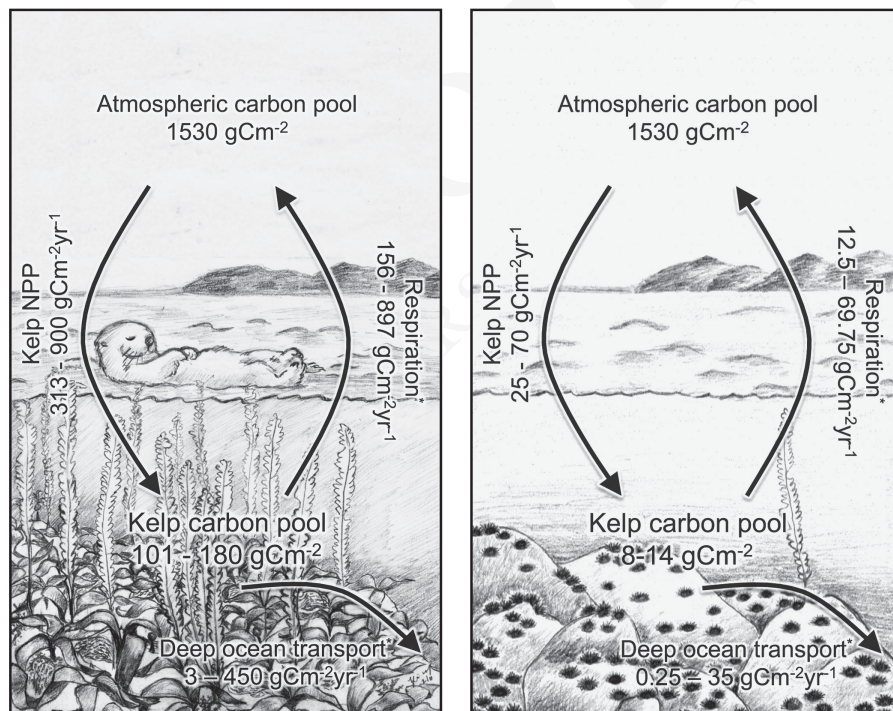
BOX FIGURE 8.1 Estimated effects of sea otters on carbon transport and storage in nearshore environments of the North Pacific. The left panel illustrates a site with sea otters and a healthy population of kelp; the right panel shows a site without sea otters and with little kelp. C. C. Wilmers and colleagues reported amounts of carbon in the atmosphere and in the kelp (pools) in grams of carbon per square meter. The arrows represent transfer of carbon from the atmosphere to kelp in photosynthesis (NPP = net primary production), from the biological community to the atmosphere in respiration, and to the bottom of the ocean when kelp die and sink. The units for these transfers are grams of carbon per square meter per year.

(*Continued*)

BOX 8.1 Continued

Wilmers's group extrapolated from the kelp carbon pool shown in Box Figure 8.1a to the area from the western Aleutians to British Columbia to estimate that 4.4 trillion to 8.7 trillion grams of carbon could be stored in the kelp that might exist along these rocky coasts if otters were present to control sea urchins that would otherwise eat the kelp. This is 21% to 42% of the total amount of carbon our burning of fossil fuels has added to the atmosphere above the sea otter's potential range in the North Pacific since the start of the Industrial Revolution. Since this range is only 0.01% of the Earth's surface, restoring otters won't have a measurable effect on total carbon in the atmosphere of Earth as a whole. The next step will be to extend this analysis to other ecosystems, especially on land, with different top predators that may increase plant production by keeping herbivores under control, thereby contributing to additional carbon sequestration.

The Plot Thickens for Sea Otters

Following protection of sea otters from hunting in the early 1900s, the population increased rapidly, especially in the Aleutian Islands, where it reached a peak of about 74,000 between 1965 and 1990. In the 1990s, however, the population in the Aleutians dropped sharply to fewer than 10,000, and in 2005 the US Fish and Wildlife Service classified sea otters in the Aleutians as threatened based on the Endangered Species Act. Just as for testing the idea that sea otters are a keystone species, searching for the cause of this dramatic decline of their population involved weighing various kinds of evidence, much of which was circumstantial and none that could be considered a smoking gun. This detective story also illustrates the benefits of long-term, intensive research. The Aleutian Islands are a difficult place to do biological research, especially on sea otters. The archipelago is remote, some of the islands are widely separated from each other, the weather is often harsh, and the subjects live in and under the water, although they generally can be observed from shore. But Estes began working in the Aleutians in 1970 and has continued studies of sea otters in this area with colleagues and students to the present. Consequently the researchers accumulated a substantial amount of data in the 1970s and 1980s that provided context for understanding the dramatic changes that occurred in the 1990s.

Estes's team was working intensively on Adak Island in the 1990s when they noticed fewer and fewer sea otters each year. They soon saw similar patterns at Little Kiska, Amchitka, and Kagalaska Islands, so that by 1997 the numbers of otters on all four islands were at most 10% of what they had been in the early 1990s. Since changes in population size are determined by the relative values of birth rate, death rate, and migration rate, Estes's team knew that declines of the magnitude that they saw had to be

due either to an increase in death rate, a decrease in birth rate, or large-scale emigration of the otters—or some combination of these factors. They discounted emigration as a cause for two reasons. First, the decline occurred over a large geographic area—most of the length of the Aleutian Chain. Second, they radio-tagged sea otters on Amchitka and Adak Islands in the central Aleutians but never found them in aerial surveys of other islands. They also found that radio-tagged females on Amchitka and Adak were just as likely to have pups during the population decline of the 1990s as were females before the beginning of the decline, suggesting that a change in birth rate wasn't responsible for the decline.

These observations led Estes's team to consider possible reasons for increased mortality. Perhaps their food supply had declined for some reason, causing starvation of otters; the population had been hit by infectious disease; or a new pollutant in the Aleutians had killed animals. In the past, when they found occasional animals who died from starvation or disease or pollution, the animals came ashore to die, but in the 1990s die-off they found virtually no carcasses as they walked along the shores of various islands.

There is one more possible source of increased mortality of sea otters in the 1990s: predation. In a summary of the biology of sea otters published by the American Society of Mammalogists in 1980, Jim Estes reported observations of bald eagles preying on young otters at Amchitka Island and observations by earlier researchers of predation by sharks in California. Otherwise, the main predators are humans, and there was no evidence of otter pelts showing up in the black market, indicating increased poaching of otters in the 1990s. The mystery deepens, but before describing a possible solution let me generalize from the last three paragraphs.

Estes's approach to solving the mystery of missing sea otters illustrates an important element of reasoning in science—it's helpful to consider a wide range of alternative explanations for something that you are trying to explain. If you can marshal evidence to eliminate most of the alternatives, that gets you closer to a solution by limiting your search. By taking this approach, Estes and his coworkers were able to discount migration, decreased birth rates, and several possible sources of increased mortality as explanations for the decline of sea otters in the Aleutians. The only remaining possibility seemed to be an increase in predation. In this example, it was relatively straightforward to identify a complete set of potential hypotheses to explain a phenomenon, although this isn't always the case.

Because of their intensive studies, the researchers had a handful of observations supporting the predation hypothesis—for a new predator of sea otters. During their two decades of work prior to 1990, they sometimes saw killer whales (Plate 13c) in the same general areas as sea otters, but the frequency of sightings of these predators increased substantially in the 1990s. In addition, their first observation of an attack by a killer whale on an otter occurred in 1991 and they saw five more attacks in the next five years.

These observations showed that killer whales attacked and sometimes killed sea otters but certainly didn't prove that killer whales were responsible for the steep decline

in number of otters in the Aleutians in the 1990s. The researchers estimated that the population of otters in the west-central Aleutians dropped from about 53,000 in 1991 to 12,000 in 1997. If predation by killer whales accounted for all of this loss of 41,000 animals, you might think that many more attacks would have been seen. Despite intensive sampling, however, the study area is very large, and it was impossible to watch more than a handful of the otters at any one time. The group estimated the chance of seeing an attack based on the number of person-hours that they spent in the field and the distance that they could observe with binoculars or spotting scopes relative to the total length of the coast of the islands in the study area. Although they spent a total of 21,677 person-hours observing and could see an average distance of 1 kilometer, this distance was a tiny fraction of the total coastline of 3,327 kilometers. These numbers implied that the proportion of attacks that they might have seen if killer whales were entirely responsible for the decline of sea otters was 0.0001, which translates to 5 of the 41,000 otters that died. This is similar to the six attacks that they actually saw. In short, even if killer whales were responsible for most of the estimated mortality of otters in the Aleutians in the 1990s, we wouldn't expect Estes's team to see very many of the attacks in this huge area.

Killer whales are fascinating animals and quintessential predators. Unlike the filter-feeding baleen whales discussed in Chapter 3, killer whales have teeth like dolphins and porpoises. Killer whales are much larger than dolphins and porpoises but smaller than many of the baleen whales as well as the largest toothed whale, the sperm whale, made famous by Herman Melville in *Moby Dick*. Killer whales have incredibly diverse diets, with some populations eating other marine mammals and others eating exclusively fish. Like wolves, killer whales often hunt cooperatively and kill prey much larger than themselves, including blue whales and sperm whales. They are extremely intelligent and use complex acoustic communication to mediate social behavior within and between groups. Numerous observers have reported cases of killer whales inventing new methods to capture prey. For example, William Stolzenburg describes how a young killer whale at Marineland in Canada learned to catch seagulls by eating its daily meal of fish and then spitting out one of the fish and sinking out of sight below water. When a nearby gull landed to scavenge the bait, the whale lunged to the surface and caught the gull. The whale's brother soon imitated this tactic, then his mother, and finally the whole group of killer whales at Marineland.

Despite the diverse diets of killer whales, there are very few reports of them eating sea otters. A Russian biologist reported one case in 1965. Karl Kenyon studied sea otters in the Aleutians before Estes and saw killer whales swimming near otters but never saw an attack. Estes's team saw six attacks in the 1990s, but it's not clear how many of these resulted in death of the otter. Yet killer whales readily learn to exploit new foods, so it's conceivable that a group of killer whales started feeding on sea otters in the 1990s if other food sources had become scarce. Even granting this possibility, it may strain credibility to think that killer whales could account for the death of 41,000 otters in six years.

We can get a sense of the plausibility of this scenario by comparing the energy requirements of killer whales to the energy content of sea otters, as Terrie Williams, Jim Estes, Dan Doak, and Alan Springer did in 2004. Box 8.2 summarizes their calculations, which implied that only four killer whales could account for 41,000 deaths of sea otters in six years. Is this a surprising result? These calculations don't mean that killer whales that started eating otters in the Aleutians relied exclusively on otters, nor that four killer whales killed all 41,000 otters. The calculations do suggest that a relatively small number of killer whales might have been responsible for the dramatic decline in the number of sea otters in the Aleutians during the 1990s. Sea otters are much smaller than other mammalian prey of killer whales like seals, sea lions, and other whales, so killer whales would have to eat many more otters to meet their energy requirements. In fact, otters have been likened to popcorn for killer whales (Figure 8.6).

The most concrete evidence of the influence of killer whales on sea otters in this region in the 1990s came from a natural experiment at Adak Island. Otters lived in Clam Lagoon and Kuluk Bay at Adak. Clam Lagoon had a shallow entrance that prevented access by killer whales, while Kuluk Bay was freely accessible to killer whales.

BOX 8.2 Energetic Calculations for Killer Whales and Sea Otters

Williams and her colleagues compared the energy requirements of killer whales to the energy content of sea otters to estimate how many sea otters a killer whale would need to eat to stay alive if sea otters were its only source of food. Male killer whales weigh more than females, but the average of the two sexes is 4,500 kilograms. Individuals require 55 kilocalories (kcal) of energy per kilogram per day to sustain activity, for a total of 247,500 kcal/day (1 kcal = 1,000 Calories = 1 Calorie in human nutrition; we use 2,000 to 3,000 Calories [2,000 to 3,000 kcal] per day). Sea otters weigh 28.5 kilograms, with an energy content of 1,810 kcal per kilogram, for a total of 51,585 kcal. Dividing 247,500 by 51,585 gives 4.8, which is the number of sea otters a killer whale would need to eat daily if it ate nothing else. There are 2,190 days in six years, so a single killer whale feeding only on sea otters would need to eat 10,512 to survive for six years. Since the sea otter population in the Aleutians declined by about 41,000 from 1991 to 1997, four killer whales could have accounted for the entire decline. Although not as complex as the models discussed in Chapter 6, these calculations are a simple model of the interaction between killer whales and sea otters. The results of the model don't prove that killer whales accounted for the crash of the sea otter population. Instead, they support the plausibility of the hypothesis and imply that it shouldn't be rejected out of hand (see Question 5).

FIGURE 8.6 A sea otter (interior skull) is like a piece of popcorn for a killer whale (exterior skull).
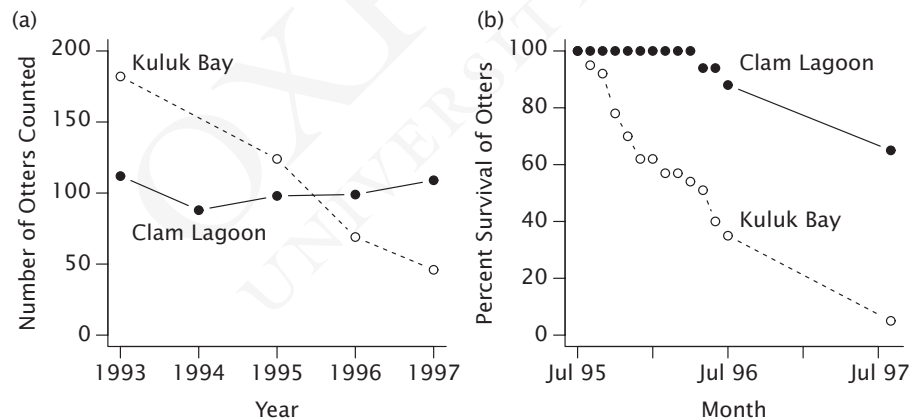

FIGURE 8.7 Estimated population sizes of sea otters between 1993 and 1997 at Clam Lagoon and Kuluk Bay on Adak Island in the Aleutians (a); survival of marked sea otters from July 1995 to August 1997 at Clam Lagoon and Kuluk Bay (b).

Estes's team of researchers counted the number of otters in these two sites every year from 1993 to 1997 and found a marked decline at Kuluk Bay but a relatively constant number at Clam Lagoon (Figure 8.7a). In 1995, they marked 37 sea otters at Kuluk Bay and 17 at Clam Lagoon with flipper tags and radio transmitters and then monitored the survival of these individuals for two years. Sixty-five percent

of the marked animals at Clam Lagoon survived, but only 5% of those at Kuluk Bay survived (Figure 8.7b).

As you know from other examples of natural experiments discussed in this book, it's always possible to imagine an alternative explanation for the results. Two researchers at the Cetacean Research Lab of the Vancouver Aquarium Marine Science Center used this approach to challenge Estes's interpretation of the results at Adak Island. Specifically, Katie Kuker and Lance Barrett-Leonard noted the existence of extensive military activity with attendant pollution on several islands in the Aleutians, including Adak. Levels of polychlorinated biphenyl (PCB) and other pollutants were higher in blue mussels and bald eagles at Kuluk Bay than elsewhere, and in 1989 the military discharged 2 million liters of JP-5 jet fuel into Kuluk Bay. Kuker and Barrett-Leonard argue that one or more of these pollutants may have killed sea otters in Kuluk Bay, while exposure of sea otters in Clam Lagoon was much less.

As noted by Kuker and Barrett-Leonard in their 2010 article, this story of killer whales and sea otters has become a "textbook case of top-down predator control," commonly known as a *trophic cascade*. However, Kuker and Barrett-Leonard went on to criticize the argument implicating killer whales on several grounds, including the possibility that differential pollution in Kuluk Bay and Clam Lagoon rather than differential access to killer whales may have been responsible for differences in survival of otters in the two sites. Estes and nine other researchers wrote a rebuttal of Kuker and Barrett-Leonard's article that hadn't been published as of June 2014 (in a footnote, these 10 authors state that they "are all scientists who believe their data or analyses have been misrepresented by Kuker and Barrett-Leonard"). Estes's group defended their interpretation of the Kuluk Bay–Clam Lagoon comparison in several ways, most notably by pointing out that "the sea otter decline was not limited to Kuluk Bay but rather occurred broadly across the Aleutian archipelago and western Alaskan peninsula and included areas far removed from established military bases or other human settlements [where otters might be exposed to pollutants]." They also reported that pollutant levels in blood samples of sea otters in the Aleutians were less than those in central California, even though the California population was increasing in size unlike the Aleutian population. Finally, they suggested that "it is difficult to reconcile how contaminants could have led to widespread decline across the Aleutians while leaving animals unaffected in Clam Lagoon, which is subject to constant flushing and tidal exchange with Kuluk Bay."

The main theme of the critique by Kuker and Barrett-Leonard is that Estes's team didn't provide definitive evidence against alternative hypotheses for the sea otter decline. One more example will give the flavor of Kuker and Barrett-Leonard's approach. They thought predation by sharks rather than killer whales might have caused the otter decline, based on the fact that white sharks are known predators of otters in California. White sharks are uncommon in the Aleutians, although Pacific sleeper sharks occur there. Sleeper sharks swim in deep water during the day but shallower water at night where they

might encounter resting sea otters. No one has ever seen a Pacific sleeper shark attack a sea otter, but Kuker and Barrett-Leonard argued that people wouldn't be observing otters at night, so there might be no recorded attacks even if these sharks prey on otters at night. This all seems pretty hypothetical, but the main thrust of the argument by Kuker and Barrett-Leonard was that the number of sleeper sharks increased in the North Pacific in the 1990s, so they may have been just as likely as killer whales to start attacking sea otters and even less likely to have been seen doing so. The 10 defenders of the killer whale hypothesis pointed out, however, that the region in which shark populations increased was mainly south and east of the region where sea otters declined (see Appendix 6).

Perhaps the killer whale–sea otter story deserves its iconic status as an example of top–down predator control of an ecological community, at least until more substantive objections to the evidence favoring this hypothesis are proposed. In fact, there was one other interesting result of the studies by Estes's group at Adak Island. Estes and Duggins had surveyed the sea floor for kelp and sea urchins in 1987, before the beginning of the sea otter decline. Estes, Tinker, Williams, and Doak repeated these surveys in 1997, when the otter population had dropped by 80%. In that 10-year interval, the abundance of sea urchins increased by 800% while kelp density decreased by 92% (Figure 8.8). These results have two implications. First, one of the alternatives to the killer whale hypothesis that the
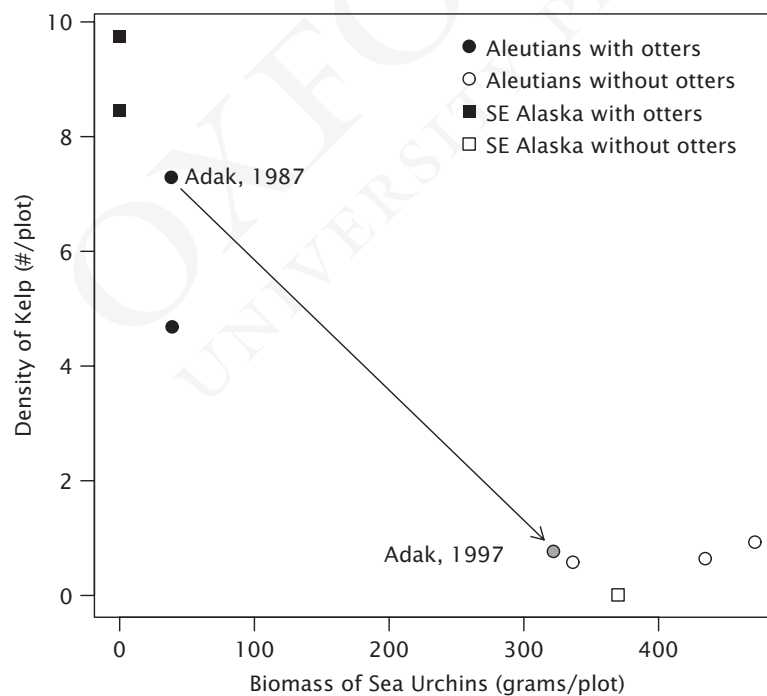

FIGURE 8.8 Average density of kelp and average biomass of sea urchins in 0.25 m² plots on the ocean floor at five sites in the Aleutian Islands and three sites in southeast Alaska. This is the same as Figure 8.4 except that data for Adak Island in the Aleutians are shown for both 1987, as in Figure 8.4, and 1997, when the population size of sea otters had declined by about 80% from its peak, indicated by the gray shading of the symbol for Adak in 1997.

researchers considered and rejected was a shortage of food leading to starvation of otters. Kuker and Barrett-Leonard thought this food-shortage hypothesis was still viable. However, sea urchins are a favorite food of otters, and urchins were abundant by the mid-1990s, making this alternative seem highly unlikely. Second, the results shown in Figure 8.8 illustrate another test of the keystone species hypothesis for sea otters. The decline of the sea otter population was followed by an increase in sea urchins and a decrease in kelp, just as the keystone species hypothesis predicts. These results contribute to the weight of evidence that sea otters are a keystone species in nearshore marine environments.

The Stage Expands for Killer Whales

I've left one big question unanswered in telling this story about killer whales and sea otters—why did killer whales start preying on otters in the 1990s? Researchers don't know the answer to this question, but they do know that sea otters weren't the only marine mammal whose population crashed in the Aleutian Islands. For example, Steller sea lions (Plate 13d) lost 80% of their population in Alaskan waters between 1970 and 2000, and the population west of the Gulf of Alaska was classified as endangered by the National Marine Fisheries Service in 1997. Although the decline of Steller sea lions started in about 1970, it was especially steep between 1985 and 1990, just before sea otters started to decline.

Steller sea lions are much larger than sea otters but much smaller than killer whales. Sea lions and their relatives among the pinnipeds (fin-footed carnivores, including seals, the walrus, and sea lions) mate and give birth on land but spend most of their lives at sea and range much farther from shore than sea otters. Steller sea lions eat fish, and the first hypothesis proposed for their population crash was a decline in the quantity or quality of their food. This, in turn, might have been due to overharvesting by humans in commercial fishing operations or climate change causing changes in the abundance or distribution of fish eaten by Steller sea lions.

The Endangered Species Act requires that species classified as endangered be protected from human activities that would further depress their populations. If the population of Steller sea lions crashed because of lack of food due to overfishing by humans, then managers would be legally justified, indeed obligated, to limit fishing in the North Pacific where sea lions live. In fact, the National Marine Fisheries Service has instituted such limits.

When Jim Estes and his colleagues were documenting the decline of sea otters in the Aleutians in the 1990s, they didn't connect it to the earlier decline of Steller sea lions and they had no clear ideas about why killer whales might have started hunting sea otters. In 2003, however, they published an hypothesis in a paper entitled "Sequential Megafaunal Collapse in the North Pacific Ocean: An Ongoing Legacy of Industrial Whaling?" The researchers suggested that killer whales in this region initially fed on other whales, some much larger than themselves. These great whales were depleted by industrial whaling after World War II, causing killer whales to switch to smaller prey: first harbor seals, then fur seals, then sea lions, and finally sea otters. According to these researchers, the killer

whales caused marked population declines of each of these species in sequence (as illustrated in Figure 8.9), hence the name of their hypothesis.

The sequential megafaunal collapse hypothesis offers an explanation for why killer whales began feeding on sea otters in the 1990s, but it also entails an alternative hypothesis for the decline of Steller sea lions and other pinnipeds before the 1990s. These declines had been attributed to depletion of their food supply, a bottom–up process, but the new hypothesis illustrated in Figure 8.9 suggested that the declines were caused by predation, a top–down process. This new hypothesis about why killer whales started hunting sea otters was much more contentious than the basic idea that killer whales caused sea otters to decline (see Chapter 9). There were three critical articles and two rebuttals totaling 99 pages in the journal *Marine Mammal Science*, plus exchanges in other journals. The critical articles and rebuttals addressed scientific issues, such as the question of whether killer whales even attack great whales, but one reason why the argument was so ferocious may have been the implications for conservation and management. For example, during this time Ted Stevens was a US senator from Alaska who strongly supported commercial fishing in Alaskan waters. Shortly after Springer's group published their idea of sequential
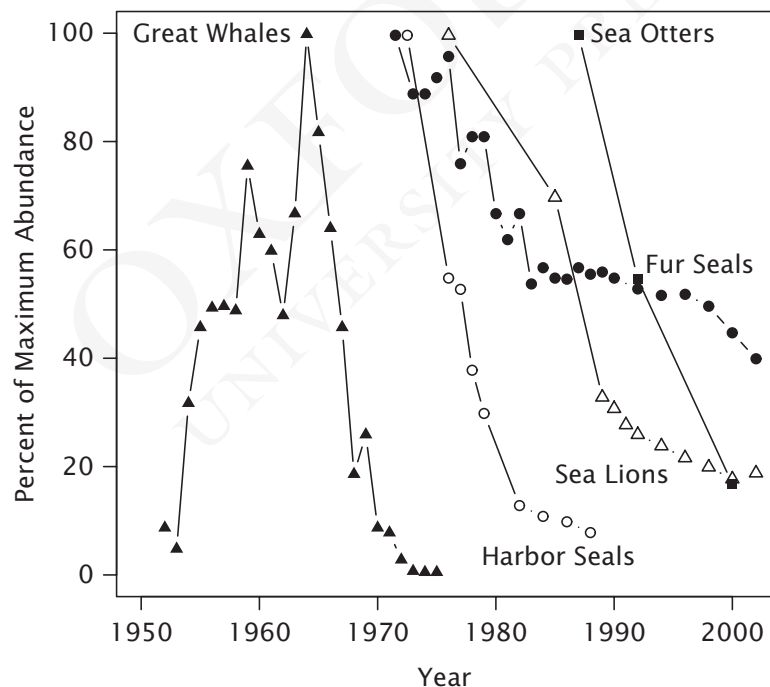

FIGURE 8.9 Population estimates for great whales, harbor seals, sea lions, fur seals, and sea otters in the North Pacific Ocean and southern Bering Sea (just north of the Aleutian Islands) from 1952 to 2002. The great whales include 12 species of baleen whales (see Chapter 3) plus the sperm whale; these are large species that are primary targets of industrial whaling. Estimates are shown as percentages of maximum abundance. For whales, the index of abundance was harvests for the region reported by the International Whaling Commission; for the other species, abundance was indexed by counts or population estimates for intensively studied sites within the region.

megafaunal collapse due to killer whales, Stevens suggested that "the government begin looking into this new evidence 'that rogue packs of killer whales' were to blame for the North Pacific's endangered sea lion" (Stolzenburg 2008:75–76). At the same time, killer whale biologists worried that Alaskans would use the report by Springer's group as a justification for attacking killer whales.

Springer, Estes, and their colleagues ended their main rebuttal of the scientific criticisms of their hypothesis by acknowledging the difficulty of definitively showing that killer whales were sequentially responsible for crashes of harbor seals, fur seals, sea lions, and sea otters after depletion of their primary food source by industrial whaling after World War II. The main source of difficulty is that their hypothesis attempts to explain historical events that weren't tracked in detail at the time that they happened. No one did systematic studies of the foraging behavior of killer whales before, during, or after the industrial whaling that occurred between 1949 and 1969. Population estimates for pinnipeds in the North Pacific were also imprecise. There's no way to recreate these key data retrospectively. The researchers suggested, however, that future events may bring an opportunity for an indirect test of the hypothesis. Great whales are now protected by the International Whaling Convention and the Convention on International Trade in Endangered Species of Wild Fauna and Flora. If these regulations are effective, populations of great whales should recover, albeit slowly because their reproductive rates are low. The sequential megafaunal collapse hypothesis predicts that killer whales may eventually switch back to feeding on great whales, allowing recovery of alternate prey such as Steller sea lions. In other words, this will be a natural experiment that can provide evidence bearing on the hypothesis—*if* the behavior and population dynamics of great whales, killer whales, and pinnipeds are closely monitored.

It may also be possible to test the alternative bottom–up hypothesis for the decline of Steller sea lions by a carefully designed manipulative experiment, even at the large scale of the North Pacific range of these animals. Steller sea lions come ashore to mate and give birth at numerous rookeries scattered throughout the Aleutians. This region could be divided into several sampling areas, each centered on a rookery. Some of these areas could be selected at random and opened to commercial fishing, while other areas are closed to fishing. If sea lions increase in the protected areas but not in the fished areas, this supports the bottom–up hypothesis that food abundance drives sea lion numbers, at least in part.

Wolves and Elk in Yellowstone—Another Trophic Cascade?

Ecological processes like interactions between kelp, sea urchins, sea otters, killer whales, and other plants and animals of the North Pacific are complex scientifically because they occur over large areas and long spans of time, because they can't be studied with manipulative experiments, and because much of the evidence about their causes and consequences is circumstantial. They are also complex because they don't happen in a realm

of nature that is isolated from human society. The bottom–up and top–down hypotheses for the decline of Steller sea lions have very different implications for commercial fishing in Alaskan waters, so anglers, owners of fishing companies, politicians, conservationists, and the general public have deep but diverse interests in the resolution of the scientific issues. As we saw earlier, the reintroduction of wolves to Yellowstone National Park has similar complexity involving science, economics, and ethics.

When I gave a brief history of wolves in the Yellowstone region on page 180, I focused on the dilemmas that arose when wolves spread beyond the boundaries of the national park after being reintroduced in the park in 1995. Wolves outside the park are killed during hunting seasons established by the states of Wyoming, Montana, and Idaho and outside hunting seasons if they prey on livestock; while wolves within the park are protected, along with all other animals and plants. Wolf biologists and other researchers have been fascinated by ecological changes in the park since 1995. Wolves eat a variety of prey species, but their main food source in Yellowstone has been elk. As the wolf population increased to about 100 between 2003 and 2007, elk declined from about 20,000 to fewer than 10,000. Elk feed heavily on aspen and willow, two deciduous woody plants that are especially abundant in riparian habitats along streams. With a large population of elk in the decades before wolf reintroduction in 1995, Yellowstone had little regeneration of aspen and willow because elk favored tender, young shoots of these plants. After 1995, as the elk population declined researchers began to see the first evidence of regeneration of aspen and willow stands (Plate 15). William Ripple and Robert Beschta documented these changes, which show the same pattern as the effect of sea otters on kelp in the ocean. Just as sea otters eat sea urchins, allowing kelp to flourish, wolves eat elk, benefitting willow and aspen.

This is another example of a top–down effect, or trophic cascade. Like the sea otter story, there were apparently ramifying effects of the return of wolves to Yellowstone. With the resulting growth of aspen and willow, the abundance of beavers and bison increased. Also like the sea otter story, there is disagreement among researchers about what's happening. In the case of wolves and elk, Ripple and Beschta proposed that two mechanisms are at work—a reduction in population size of elk due to predation by wolves and a change in the behavior of elk to avoid wolves. They suggested that elk are more vulnerable in riparian areas because these don't have expanses of open ground where the elk can outrun wolves. Therefore, with wolves present, elk avoid riparian areas, allowing even more regeneration of aspen and willow. This "behaviorally mediated trophic cascade" has been more controversial than direct predation by wolves on elk as a cause of increased regeneration of aspen and willow. As with sea otters, most of the scientific controversy has been due to the lack of evidence from rigorous manipulative experiments and reliance instead on observations, comparisons, and correlations associated with the natural experiment of reintroducing wolves to Yellowstone. This is a system in which manipulative experiments certainly are possible, although their relevance may be questionable. For example, researchers could use fencing to build a

set of exclosures to prevent elk from foraging in certain plots and compare regeneration of aspen and willow in these plots with regeneration in unfenced control plots. These would be small-scale experiments, so one question would be whether the results would be meaningful at the scale of many square miles that constitute the home ranges of elk. These experiments also don't manipulate wolves, so don't directly assess the top–down effects of wolves on the system.

Aldo Leopold was an influential early conservation biologist, best known for his book *A Sand County Almanac* published in 1949. He began his career as a US Forest Service employee in Arizona and New Mexico in 1909 where he trapped and shot mountain lions and wolves to favor deer and elk populations, consistent with Forest Service policy at that time. By 1949, he reflected on this part of his early career with some regret: "I was young then, and full of trigger-itch; I thought that because fewer wolves meant more deer, that no wolves would mean hunter's paradise. But after seeing the green fire die, I sensed that neither the wolf nor the mountain agreed with such a view" (Leopold 1968:130). With this poetic language, Leopold foreshadowed current scientific interest in the top–down effects of predators on ecosystems.

Conclusions

The title of this chapter is "From Causes to Consequences: Considering the Weight of Evidence." The two main examples focused on sea otters, first as a keystone species and second as part of a trophic cascade from killer whales through sea otters, sea urchins, and eventually kelp. We discussed various kinds of evidence about keystone species and trophic cascades, but most was indirect or circumstantial. Therefore we couldn't rely on a critical observation or experiment—a smoking gun—to evaluate the hypotheses that sea otters are a keystone species in nearshore marine environments and that killer whales caused a crash in the population of sea otters in the Aleutian Islands in the 1990s. Instead, we had to make our decisions based on the weight of evidence for and against these hypotheses. Furthermore, these decisions have consequences beyond science; for instance, they will impact how commercial fisheries are managed in Alaskan waters. This process of considering the weight of evidence to evaluate scientific hypotheses about causation that have practical consequences applies to many decisions that we make as individuals and as members of society. Going through this process doesn't mean considering only scientific evidence and ignoring factors like economics and ethics in making our decisions. But it does mean evaluating the science fully and carefully, as we'll discuss further in Chapter 10.

Has anyone seen the spider? This is what Nancy Krieger asked in thinking about complex webs of causation in her field of epidemiology. Ecologists ask the same question when they think about the control of complex food webs. For many years, ecologists focused on bottom–up control of food webs—through photosynthesis, plants are the source of energy for everything in food webs, starting with herbivores and ending

with top predators. But we've learned from the work of Bob Paine, Jim Estes, and many others that keystone predators (including actual spiders in some habitats) can exert control on both the structure and function of food webs from the top down. In other words, killer whales and sea otters, and perhaps wolves in Yellowstone, are metaphorical spiders in complex webs of causation.

Questions to Ponder

1. What if you were a conservationist or animal rights advocate? What scientific issues would you be obligated to consider in thinking about wolf management (see page 180)?

2. The food web for Wytham Woods shown in Figure 8.2 includes several different food chains. How many can you identify that include three species? Four? How about five?

3. Although Paine's experiment that led to the keystone species concept was certainly planned and is considered a classic field experiment by ecologists, it had some basic deficiencies in experimental design. What were some of these deficiencies? You might want to review Chapter 4 in thinking about your answer to this question.

4. Only one manipulative experiment has been published that is directly relevant to the keystone species hypothesis for sea otters. David Duggins did this experiment from 1976 to 1978 at Torch Bay in southeast Alaska. No sea otters occurred in Torch Bay at this time, although they had recolonized this site by 1985 (Figure 8.4). Duggins laid out five underwater plots at Torch Bay, each about 50 meters square. He removed all sea urchins from in and near three of these plots and used the other two plots as controls; he repeated his removals of sea urchins from experimental plots every two months. Various species of kelp colonized the experimental plots, resulting in an average density of 150 individuals per square meter after two years. By contrast, there were no kelp in the control plots at any time during the experiment.

   Compare this experiment to the three lines of evidence about the keystone species hypothesis for sea otters discussed in the text. How is the experiment similar to and different from each of these lines of evidence? Based on these comparisons, what are the strengths and limitations of this experiment as evidence relating to the hypothesis?

5. Some killer whales rely exclusively on fish. How is this possible, considering that fish are much smaller than sea otters?

6. Estes and colleagues argued that killer whales were responsible for the dramatic decline in the population of sea otters in the Aleutian Islands in the 1990s. Plate 22 summarizes some of the evidence consistent with this hypothesis in the form of an argument map (see Appendix 6). Which line of evidence related to the killer whale predation hypothesis is not included in Plate 22? Can you extend the argument map to include this additional line of evidence?

Resources for Further Exploration

1. Tim van Gelder started Austhink Software and has written valuable articles about critical thinking as described in Appendix 6. He has an interesting blog called "Bringing Visual Clarity to Complex Issues" at http://timvangelder.com/.

2. Parks Collins of Mitchell Community College has developed a case study about the reintroduction of wolves to Yellowstone National Park. It is available at the National Center for Case Study Teaching in Science: The Return of Canis Lupus? (http://sciencecases.lib.buffalo.edu/cs/collection/detail.asp?case_id=691&id=691).