Chapter 5

ECOSYSTEM EFFECTS OF SEA OTTERS

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The interplay between sea otters (*Enhydra lutris*) and coastal marine ecosystems is a key point of interest and concern surrounding the possible repatriation of sea otters in Oregon. This interplay has two distinct dimensions: (1) effects of the ecosystem on otters and (2) effects of otters on the ecosystem. These classes of effects intersect broadly with the science of ecology, a discipline that is complex and often opaque to nonspecialists. We thus begin this chapter with a short primer about ecology's central concepts, goals, methods, and challenges (see the primer in the upcoming callout box). The remainder of this chapter will consider the effects of sea otters on ecosystems. The effects of ecosystems on sea otters will be addressed elsewhere in this study (Chapter 6 on habitat suitability considerations and Chapter 10 on health and welfare considerations).

How do ecologists determine a species' effects on its associated ecosystem? The most compelling approach is contrasting otherwise similar habitats in which the species is present and absent. For some species, an analysis can be accomplished experimentally, but for many others (like sea otters), purposeful experiments are difficult or impossible to do. In these latter cases, the ecological effects of species have been inferred through what is often referred to as *natural experiments*, wherein the contrasts are made opportunistically in space (i.e., between otherwise similar habitats with and without the species) or time (i.e., at some location wherein the species appears, disappears, or undergoes significant changes in abundance over time). Both the spatial and temporal approaches have been applied repeatedly to sea otters and their coastal marine ecosystems in various parts of the North Pacific Rim, thereby providing what is arguably the most extensively studied and best-known example of ecological influence by any large-bodied predator in all of ecology. The strength of this case results in large measure from six attributes of sea otters and their associated ecosystems.

The first of these attributes is historical. Sea otters were exploited to near extinction during the Pacific maritime fur trade, after which populations recovered in several areas with surviving remnant colonies but remained absent in nearby areas where they had been hunted to extinction. Half a century later, after many surviving remnant colonies had recovered from the fur trade, translocations were used to establish additional colonies. The ecological influences of sea otters were thus identified simply by comparing nearby areas in which the species was present or absent and by observing changes at specific locations as otter populations waxed or waned through time.

The second important attribute of sea otters and coastal ecosystems is replication. The historical patterns have played out repeatedly across the sea otter's natural range, from the northern Japanese archipelago, across the Pacific Rim, to the central Pacific coast of Baja California, Mexico.

The third important attribute of sea otters and coastal ecosystems is the tendency of individual otters to live their entire lives in relatively small areas. This feature of the species' natural history, which is unusual for large predators, prevented large-

scale diffusion and mixing with population recovery from the fur trade, thereby maintaining high levels of spatial granularity in nearshore ecosystems with and without sea otters.

Fourth is the ease with which other key elements of the interaction web (e.g., macroalgae, benthic macroinvertebrates, reef fish, etc.) can be observed and measured. This is due in large part to the sessile nature and spatially constrained distribution of these species (i.e., the narrow coastal zone defined by the intertidal and shallow subtidal depths).

A fifth is the capacity of these species to recover quickly following pulse perturbations (i.e., the addition or removal of sea otters).

A sixth and final attribute of the system is the sea otter's high rate of food consumption (Williams and Yeates 2004, Yeates et al. 2007).

Our discussion of the significance of these attributes presupposes a familiarity with fundamental concepts in ecology. Therefore, we have provided a brief introductory review of key ecological concepts in the following callout box. Readers already familiar with ecological concepts and terminology can skip this primer and go directly to the next section.

A PRIMER OF ECOLOGY

This primer provides interested or unfamiliar readers with further background on those dimensions of the science of ecology that intersect intimately with our current understanding of the influences of sea otters on their associated ecosystems. Although we have tried to make this treatment understandable to nonspecialists, the subject is admittedly complex and often nuanced. Therefore, we refer readers to the referenced literature if they wish to obtain a more detailed or additional understanding.

The central goals of ecology are to understand, manage, and conserve the distribution and abundance of species (Krebs 1972). *Understanding* is the province of basic ecology, whereas *conservation* and *management* are the provinces of applied ecology. Successful conservation and management usually rest on a foundation of science, which in the case of ecology, has two dimensions: (1) the *description of pattern* (i.e., which species occur where and in what numbers) and (2) the *determination of causal process* (i.e., knowing why the distribution and abundance of species are what they are). The description of pattern, while frequently tedious, is otherwise a relatively straightforward endeavor, attainable simply via "boots on the ground" observations and measurements. However, understanding the processes that underlay these patterns is more challenging because, in contrast with descriptions of pattern, processes are more complex and much more difficult to observe and measure.

This challenge, while daunting, can be brought into focus by recognizing that the multitude of processes that determine the distribution and abundance of any species is divisible into three broad categories—those stemming from (1) biogeography and evolution (i.e., history), (2) the current abiotic environment (i.e., physical and chemical), and (3) the current biotic environment (i.e., species interactions). These categories of processes create a further dichotomy of perspective in describing and understanding the distribution of species: where any particular species **can live** (the species' so-called *fundamental niche*) versus where it actually **does live** (the species' so-called *realized niche*). The abiotic environment and species interactions largely determine a species' fundamental niche; the historical influences of biogeography further determine its realized niche.

Species interactions can be thought of most simply as how two species that co-occur in nature influence the respective distributions and abundances of one another. Such interactions play out in several ways, the most important of which are *competition* (i.e., the influence of each species on the other species is negative), *mutualism* (i.e., the influence of each species on the other species is positive), and *consumer-prey interactions* (i.e., the influence of the prey on the consumer is positive whereas the influence of the consumer on the prey is negative). All three categories of interactions occur widely in nature, although consumer-prey interactions are critical because it would be impossible for any species to exist anywhere without them (other than photosynthesizing plants and a few chemosynthetic autotrophs). The network of *trophic linkages* (interactions between consumers and prey) is known as a *food web* (Pimm 1982, Ch. 1), and the scientific enterprise of understanding how this network of linkages influences species distribution and abundance is the province of *food web dynamics*.

The simple fact that consumers depend on the species that nourish them had a dominating impact on ecology through the 1950s. Until about that time, the distribution and abundance of species were believed to be determined by what is known as *bottom-up forcing processes* (Hunter and Price 1992). Via these processes, the distribution and abundance of species are dictated by three essential resources—energy (sunlight/temperature), water, and nutrients—and the efficiencies by which these resources are extracted from the environment and transferred from prey (lower in the food web) to consumers (higher in the food web; hence the term "bottom-up forcing"). Further variation in the distribution and abundance of species at any one trophic level was attributed mainly to competition for these limiting resources.

Ecology's conceptual mindset broadened in the 1960s with Hairston et al.'s (1960) *Green World Hypothesis.* Hairston et al. (1960) argued that the distribution and abundance of species can also be limited by their consumers and that most of our planet's terrestrial realm, when viewed from a distance, appears green because autotrophs are green and predators limit their herbivores, thus causing green plants to be more abundant than they otherwise would be. By this view, species distribution and abundance are influenced by what has become known as *top-down forcing processes.* The networks of consumer-prey interactions—from apex predators at the top of the food web to plants at the bottom—are known as *trophic cascades* (Paine 1980, Terborgh and Estes 2013, Ripple et al. 2016). See Figure 5.1. The *trophic level* of a species within a trophic cascade simply refers to the number of consumer-prey interactions between that species and the bottom of the food chain (thus, primary producers are Trophic Level 1, herbivores are Trophic Level 2, consumers of herbivores are Trophic Level 3, and so on).

In this top-down view of the ecological process, relatively rare species (e.g., apex predators) can have disproportionately strong influences on the distribution and abundance of other species. These comparatively rare but otherwise ecologically important species are known as keystones or, more precisely, *keystone species* (Paine 1969, Power et al. 1996). Keystone species are often apex predators within their food webs. The processes that cause these predators to have such strong and wide-ranging effects on their ecosystems also are diverse and somewhat complex. Therefore, before reviewing the effects of sea otters on coastal ecosystems, we describe some of these general processes.

A more general construct for thinking about the functional dynamics of ecosystems is that of an *interaction web*[1] (Menge and Sutherland 1987). The more widely known concept of a food web—a sort of road map to who is eaten by whom (Paine 1988)—is embedded in this more encompassing notion of the interaction web. We have chosen to frame our discussion of sea otters' ecological influences in the context of interaction webs rather than food webs because some of the important ecological effects of sea otters are not exclusively trophic (although most are), and species interactions initiated by sea otters can feed back to influence the abiotic environment. We next discuss some of the more important structural features and properties of interaction webs.

Direct Versus Indirect Species Interactions

Linkages between any two species in a species interaction can be either direct (no intervening species) or indirect (one or more intervening species). If species A eats species B, and species B eats species C, then A-B and B-C are direct interactions, while A-C is an indirect interaction. It is important to understand that the number of potential indirect interactions is vastly greater than the number of potential direct interactions in all but the simplest interaction webs (Estes et al. 2013). Moreover, indirect interactions can link up across numerous species to create long chain reactions across complex ecological pathways.

Drivers Versus Recipients

Many interactions among species and between species and the elements of their abiotic environments are asymmetrical, which means that one member of the interacting pair is the *driver* (i.e., its abundance is the primary determinant of pairwise dynamics) and the other the *recipient*. Adding or losing driver species from food webs affects ecosystem dynamics more strongly than adding or losing recipients.
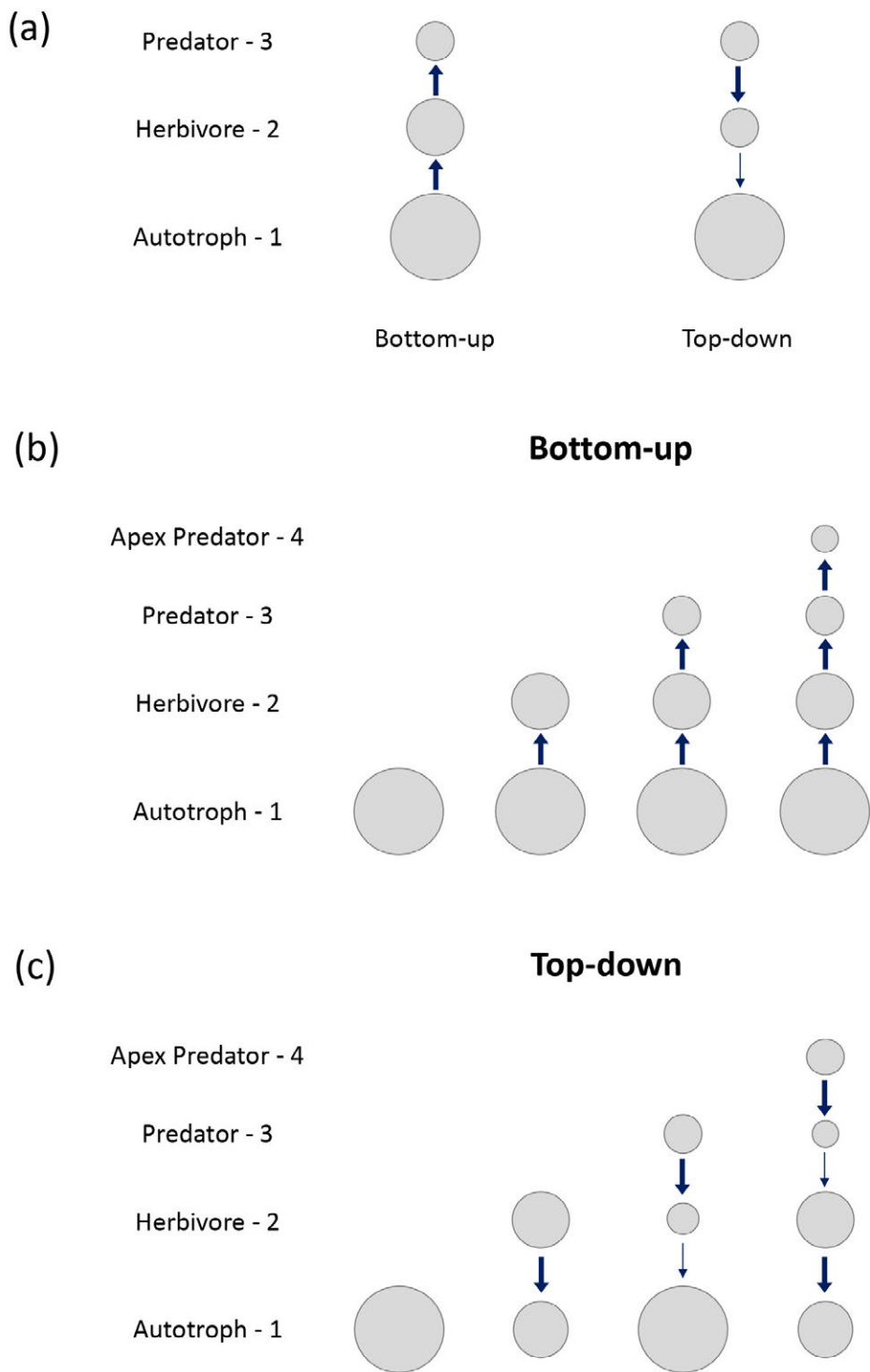
Interaction Strength

The functional importance of a driver (*D*) in its interaction with any other species depends on the *interaction strength* (Berlow et al. 1999), commonly defined as the difference in abundance of the recipient species (*R*) when the driver is present (R_{dp})

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1   An interaction web is the network of linkages (interactions) among species and between species and their physical environment.

Figure 5.1. How bottom-up and top-down forcing differ and why it matters to species distribution and abundance.

(a)

Predator - 3

Herbivore - 2

Autotroph - 1

Bottom-up   Top-down

(b)   **Bottom-up**

Apex Predator - 4

Predator - 3

Herbivore - 2

Autotroph - 1

(c)   **Top-down**

Apex Predator - 4

Predator - 3

Herbivore - 2

Autotroph - 1

Note. Panel (a) depicts how bottom-up and top-down forcing differ. See (b) and (c) for illustrations of why the differences matter to the distribution and abundance of species. In all panels, the trophic-level descriptors and numbers are indicated at left, the circles represent species in each trophic level, circle size indicates relative abundance, lines with arrows represent species interactions, arrows indicate the direction of forcing, and the arrow or line weight indicates interaction strength (thin [weak] vs. heavy [strong]). Differences in interaction strengths and abundances are shown between odd- and even-numbered food chains under (b) bottom-up and (c) top-down forcing.

versus when the driver is absent (R_{da}). Interaction strength is often calculated per capita: (R_{dp} - R_{da})/D, where D is driver abundance. When (R_{dp} - R_{da}) and D are both large, the driver is referred to as an *ecological dominant*. When (R_{dp} - R_{da}) is large and D is small, the driver is referred to as a *keystone species* (Power et al. 1996). A keystone species is thus one that exerts inordinately large impacts on food web structure and dynamics relative to its abundance.

Bottom-Up Versus Top-Down Forcing

Trophic interactions, which necessarily define much of an interaction web's structure and function (as explained above), vary fundamentally depending on which member of the consumer-prey pair is the main driver and which is the main recipient. When prey are the main drivers of the distribution and abundance of their consumers (through maintenance, growth, and reproduction), the interaction web is said to operate through *bottom-up control*. This operation implies that *net primary production* (NPP—defined as the amount of carbon fixed by autotrophs per area per time) and the efficiency of energy and material transport upward across trophic levels primarily control the distribution and abundance of species. Conversely, when consumers are the main drivers, the interaction web is said to operate through *top-down control*, meaning that either mortality or behavioral effects imposed by the consumer on its prey are the most important controlling influences on the distribution and abundance of species. It is important to understand that all interaction webs operate, to a greater or lesser degree, through both bottom-up and top-down control.

Size-Selective Predation

All consumers must choose what to eat from an array of possibilities. The economics of consumer choice are driven by decisions that maximize consumer fitness. These decisions include where to feed, what prey species to eat, and which sizes of the chosen prey to eat. Prey size matters a great deal in a consumer's behavioral calculus because of both benefit and risk effects. As a result, prey species typically are consumed in a strongly size-selective manner. In some cases, small prey are avoided because they are not sufficiently valuable, while in other cases, large prey are avoided because they are too energetically costly or too risky to pursue, capture, and consume. The scientific literature is full of examples of these kinds of consumer choices; one that is especially pertinent to this assessment is the tendency of sea otters to avoid the consumption of smaller individuals for many of their prey species.

Complex Emergent Properties of Food Webs

In ecosystems dominated by bottom-up control, the distribution and abundance of species are essentially predictable from two processes: primary production and material–energy transfer efficiency across trophic levels. Under this condition, the qualitative relationship between consumers and prey is always the same, regardless of trophic status or food chain length. That is, prey are always the drivers, and consumers are always the recipients, so the nature of interactions upward across trophic levels has a neutral effect on the prey and a positive effect on the consumer. Variation in primary production thus has a uniform enhancing or reducing effect on all species, irrespective of trophic status or position in the interaction web.

In contrast, for ecosystems dominated by top-down control, there are qualitative differences in species interactions depending on food chain length. For example, increasing food chain length by one trophic level via the addition of a new apex predator alters the nature of direct consumer-prey interactions throughout the food web, thus shifting the strength (from weak to strong or vice versa) of all direct trophic interactions and the sign (from negative to positive or vice versa) of all indirect trophic interactions (Figure 5.1). Top-down influences by a species of a high trophic level downward through a food web is known as a *trophic cascade* (Paine 1980), which can also be thought of as the propagation of indirect effects of higher trophic-level consumers downward through a food web. Bottom-up forcing can also modulate the relative abundance of multiple prey species of a common predator through apparent competition (Holt 1977), whereby one prey species may be eliminated (or its abundance reduced) by a predator that is attracted to an alternative prey species that is also able to persist in the presence of the shared predator. Additional variation in food web structure based on indirect effects and the directionality of the forcing is discussed in greater detail by Schoener (1993) and Estes et al. (2013).

Scale

To observe and document the ecological influences of most large-bodied predators, one must measure dynamics at the spatial and temporal scales over which the important controlling processes operate. Large marine predators often are highly mobile animals, and even weakly motile or sedentary species of marine autotrophs and invertebrates that comprise coastal food webs often have dispersive life stages (Palumbi 1994). The size of the spatial area within which the predator's effects should be measured therefore depends on the individual mobility and home-range size of the predator itself, as well as the scale at which its limiting resources (prey populations) vary in time and space. Failing to properly account for scale can lead to a misunderstanding of predator-prey interactions and predator effects.

Consumptive Versus Risk Effects

Consumers can influence their prey in two ways: via direct predation (also called *consumptive effects*) and via risk effects (also called *trait-mediated* or *nonconsumptive effects*; Werner and Peacor 2003, Creel and Christianson 2008). Consumptive effects obviously reduce prey numbers; however, the risk of predation can influence prey population sizes by inducing costly physiological or behavioral changes that affect access to food resources: This is a trait-mediated effect. The risk effects of consumers on prey behavior and the *knock-on effects*[2] of these influences on the larger interaction web have together become known as the *ecology of fear* (Brown et al. 1999). Importantly, trait-mediated effects may be strong even for prey species rarely successfully captured by a predator. Therefore, a particular predator does not have to be a primary mortality source for a given prey species, and that prey does not have to be common in the predator's diet for strong top-down effects to occur in nature (Creel and Christianson 2008, Heithaus et al. 2008).

Functional Relationships

As ecological drivers, predators can affect their ecosystems in ways that might vary linearly or nonlinearly with predator population size. Nonlinear relationships, which growing evidence indicates are common in nature, occur when the magnitude of the ecological impacts of a per capita change in predator abundance differs depending on how abundant the predator is. Nonlinear interactions can cause abrupt *phase shifts* (a rapid shift between states of an ecosystem) and demonstrate *hysteresis* (the condition by which a functional relationship differs depending on whether the predator is increasing or decreasing). Nonlinear interactions can also lead to the existence of *alternative stable states* in the composition of communities (Scheffer et al. 2001).

Generality and Variation

Although many of the above-described patterns and processes are recurrent among species, habitats, and ecosystems, nothing in ecology is invariant across these entities. This fundamental truth must be kept in mind when considering what can be reasonably predicted about the ecological, social, and economic consequences of repatriating Oregon's coastal ecosystem with sea otters.

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2   Ripple et al. (2016) define the knock-on effects of trophic cascades as indirect interactions that spin off the trophic cascade via qualitatively different sorts of species interactions (e.g., competition, mutualisms, or bottom-up forced consumer prey interactions).

Ecological Effects

The ecological influences of sea otters on coastal ecosystems are probably the best documented and among the most widely known of those for any predator species. These influences have been determined using the two-step procedure explained in the preceding primer—that is, by first describing the interaction web linkages leading outward from sea otters through coastal ecosystems and then observing how the various species and physical and chemical environmental entities that define this network change as sea otter populations increase or decline in abundance. In all cases, the linkage pathways begin with the limiting effects of otters on the abundance, size, and/or behavior of their macroinvertebrate prey. Although the magnitudes of these limiting influences by sea otter predation (i.e., their interaction strengths) vary somewhat with the environment and prey type, they are often large—in the realm of one to two orders of magnitude for sessile or weakly motile prey, like sea urchins and abalone, that live on the exposed seafloor in rocky reef systems. The resulting direct and indirect effects of sea otter predation have been chronicled in three main ecosystem types—rocky reefs, soft sediments, and estuaries.

Sea otters commonly select the largest available individuals of a given prey species (Estes and Duggins 1995, Tinker et al. 2008), so in most areas, it is the smaller individual prey that survive predation. Cracks and crevices in rocky substrate can also provide important refuges from sea otter predation for certain species, such as abalone and sea urchins (Lowry and Pearse 1973, Hines and Pearse 1982, Raimondi et al. 2015, Lee et al. 2016). The limiting effects of otters on more mobile species, like lobsters and crabs, appear to be somewhat less, although these effects have not been as well-quantified.

Kelp Forest Ecosystems

In kelp forest systems, the influences of trophic interactions between sea otters and their prey spread through the interaction web via several pathways. The most widely studied and well-known pathway is from sea otters to herbivorous macroinvertebrates (primarily urchins) to kelp and other macroalgae (Estes and Palmisano 1974, Duggins 1980, Breen et al. 1982, Estes and Duggins 1995, Watson and Estes 2011, Burt et al. 2018). Other pathways are less well-documented but can also be important, such as a pathway from sea otters to predatory sea stars to the sea stars' invertebrate prey, such as mussels and barnacles (Vicknair and Estes 2012).

The *otter-urchin-kelp pathway* (a trophic cascade) occurs with varying sea otter density as an abrupt phase shift between lush algal forests and deforested barrens in many parts of Alaska and British Columbia (Steneck et al. 2002, Estes et al. 2010, Selkoe et al. 2015), whereas the response function may be more graded in California (Kenner and Tinker 2018, Smith et al. 2021). The population density of sea otters at which the phase shift occurs also differs among areas (from the Aleutian Islands through Southeast [SE] Alaska and British Columbia) and with the direction of change. For example, rocky reef ecosystems in the Aleutian Islands remain in the urchin-dominated state after the repatriation of sea otters until otter population density nears carrying capacity. In contrast, kelp-dominated systems containing high-density otter populations that are in decline remain kelp-dominated until the sea otter population has reached about one-half carrying capacity (Estes et al. 2010). This dynamic ecosystem behavior—in which the functional relationship between a system and its driver differs with the directionality of change in driver intensity—is an example of hysteresis (see the previous primer).

Reef systems in SE Alaska and British Columbia also switch between kelp- and urchin-dominated states, although in this region, the sea otter population densities at which these shifts occur are lower than they are in the Aleutian Islands (Estes and Duggins 1995). In California's more complex coastal food webs, other urchin predators may act to mitigate the strength or biphasic nature of the otter-urchin-kelp cascade (Foster and Schiel 1988). Indeed, adding sea otters to a southern California kelp forest at San Nicolas Island has shown that factors other than sea otter predation can drive community state transitions. Still, despite this complexity, sea otter predation at San Nicolas has shifted the subtidal community to a previously unobserved state featuring abundant kelp canopy, understory algae, and persistent low

densities of urchins (Kenner and Tinker 2018). The relative abundance of other "complementary" predators, especially sunflower sea stars (*Pycnopodia helianthoides*), mediates the strength and functional shape of the sea otter trophic cascade in British Columbia and central California (Burt et al. 2018, Smith et al. 2021).

Whether a reef ecosystem occurs in the forested or deforested state has numerous knock-on effects on other species and ecological processes. Perhaps the most important of these is the magnitude of biological production. Kelps and other macroalgae grow rapidly. So, the abundance of kelp, as influenced by the abundance of otters, has an important influence on net primary production (NPP), which is elevated severalfold where or when sea otters are sufficiently abundant to force coastal ecosystems into the kelp-dominated state (Duggins et al. 1989). This elevated NPP, in turn, fuels elevated secondary production via bottom-up forcing. Duggins et al. (1989) demonstrated this effect by out-planting newly recruited mussels and barnacles from a common population source in the San Juan Islands, Washington, to islands in the western and central Aleutian archipelago with and without sea otters. Growth rates of the out-planted mussels and barnacles were two- to three-fold greater in the otter-dominated (forested) areas compared with the otter-free (deforested) ecosystems. Isotopic analyses confirmed that inorganic carbon fixed via photosynthesis by kelp and other macroalgae contributed importantly to overall production in otter-dominated ecosystems (Simenstad et al. 1993). Kelp-based production has been shown elsewhere to propagate upwards through coastal food webs, affecting higher-level consumers such as nearshore rockfish (Markel and Shurin 2015, von Biela et al. 2015, von Biela et al. 2016).

Kelp affects coastal marine ecosystems via three other known pathways: (1) structurally, by serving as habitat for other species; (2) by attenuating waves and currents; and (3) by absorbing carbon dioxide (CO_2) from the surrounding seawater and overlying atmosphere (i.e., part of the supply side for increased NPP). In turn, these processes have a range of essential effects on both physical and biotic elements of the ecosystem. For example, microbes (bacteria) cycle energy and materials, decompose detritus, and remineralize organic matter—processes especially important in marine ecosystems. Clasen and Shurin (2015) found that bacteria grew faster, were more abundant, and contributed more strongly to zooplankton grazing in areas where kelp forests had increased because of the otter-urchin-kelp trophic cascade.

Abundant kelp populations in ecosystems with sea otters draw down CO_2 from the overlying atmosphere, thus potentially influencing carbon sequestration (depending on the rate of organic carbon remineralization from kelp detritus and the extent to which kelp detritus is transported into the deep sea). Also, this drawdown potentially influences the CO_2–bicarbonate balance and pH in the surrounding seawater. Wilmers et al. (2012) assessed information on the areal extent of rocky reef habitat in the eastern North Pacific Ocean, kelp forest NPP, carbon concentration in living kelps, and kelp biomass density between coastlines with and without sea otters. From this data, they estimated a sea otter effect of 4.4 to 8.7 teragrams of carbon storage, a value that might be even larger depending on the rates of remineralization and transport into the deep sea.

The effect of sea otters on kelp extends to other coastal marine species. For example, reef fish population densities are elevated by up to an order of magnitude by the otter-urchin-kelp trophic cascade (Reisewitz et al. 2006, Markel and Shurin 2015), an indirect effect of sea otters that probably occurs because of increased production and habitat complexity. This interaction influences various species of piscivores (fish eaters) by the knock-on effect of bottom-up forcing. Irons et al. (1986), for example, demonstrated that glaucous-winged gulls (*Larus glaucescens*) in the Aleutian Islands switch from feeding on fish to invertebrates when sea otters are lost from coastal ecosystems. Anthony et al. (2008) reported similar dietary shifts by bald eagles (*Haliaeetus leucocephalus*)—in this case, from a roughly even mix of marine mammals, fish, and seabirds where otters were abundant to a diet dominated by seabirds where otters were absent.

Sea otters' indirect effects on coastal ecosystems can also follow interaction web pathways other than the otter-urchin-kelp trophic cascade. For example, using a time series of information associated with the repatriation and growth of sea otters at Attu Island, in the western Aleutian archipelago, Vicknair and Estes (2012) found that sea otters preyed on

Figure 5.2. Some known or suspected linkages between sea otters and coastal marine ecosystems.

(a)

(b)
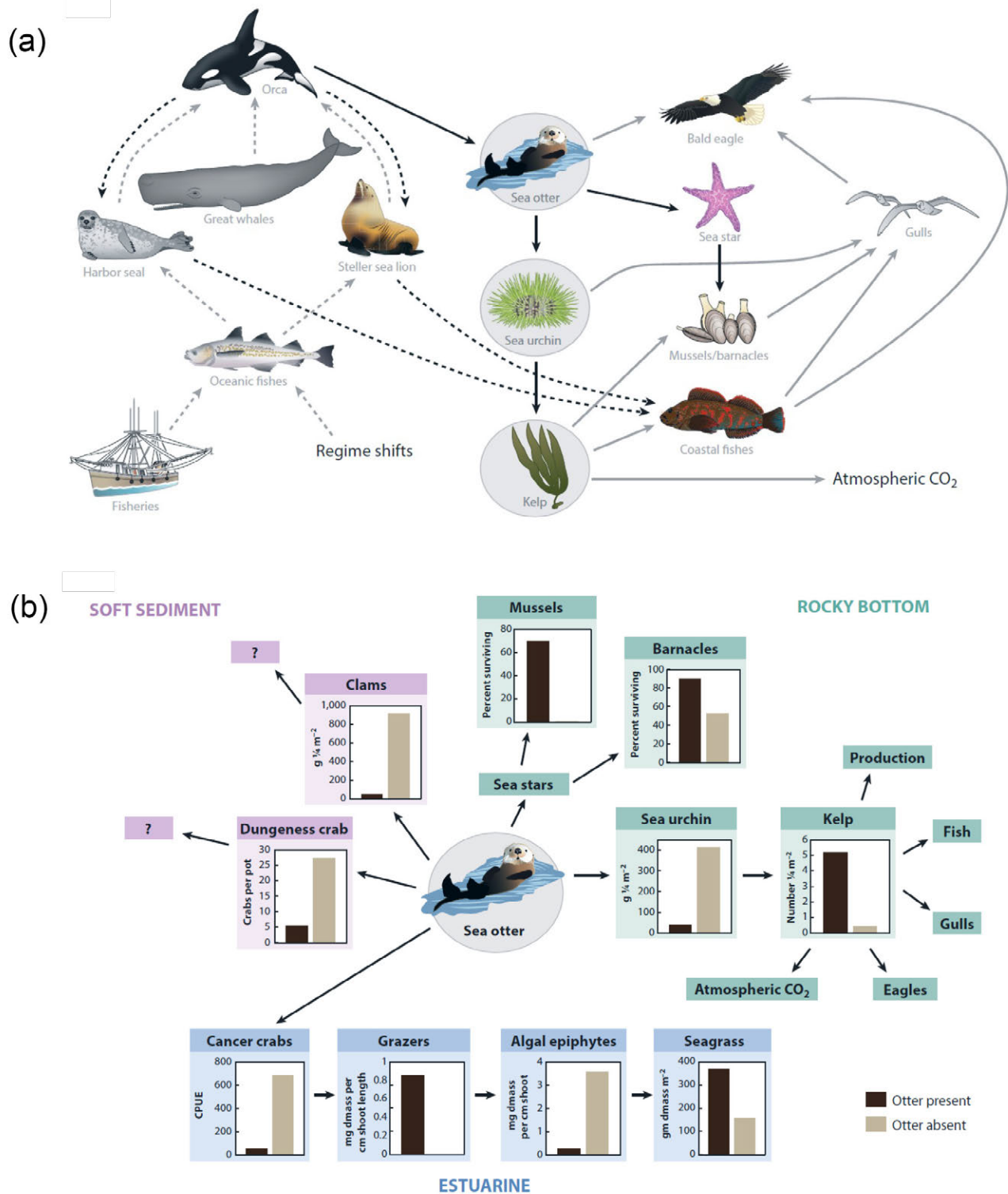
Note. Panel (a) depicts key interactions between sea otters and other species or components of coastal and oceanic ecosystems of the North Pacific. Arrows with black lines represent top-down forcing, arrows with gray lines represent bottom-up forcing, solid lines represent interactions whose effects have been confirmed based on experiments or field studies, and dashed lines represent interactions that are suspected to be important based on indirect evidence. Panel (b) depicts statistical comparisons of the relative abundance of various species in systems with and without sea otters present, with the differences representing a measure of the direct and indirect food web effects of sea otters. Comparisons are shown for three types of coastal habitats: rocky bottom reef systems, soft sediment systems on the outer coast, and estuarine systems. See the original source (Estes et al. 2016b) for further explanation and detail.

predatory sea stars, thereby reducing sea star populations and associated mortality rates from sea star predation on filter-feeding mussels and barnacles.

Although the preceding narrative summarizes a diverse array of indirect ecological influences from the otter-urchin-kelp trophic cascade (Figure 5.2), the majority of such effects are unstudied and thus are either uncertain or unknown. Some of these unknown interactions may have significant influences on human welfare. One such potential case involves Pacific herring (*Clupea pallasii*), which spawn on kelp, draw nourishment from coastal marine ecosystems, and thus are probably influenced by the otter-urchin-kelp trophic cascade. This interaction is potentially important because herring are prey (as forage fish) for numerous marine species (e.g., fish [including salmon], seabirds, pinnipeds, and cetaceans).

Soft-Sediment Coastal Ecosystems

Sea otters' effects in soft-sediment habitats along outer coasts result from their consumption of numerous prey species. The two prey groups most well studied in soft-sediment systems are infaunal bivalve mollusks (clams) and decapod crustaceans (crabs). Kvitek et al. (1992) reported reductions of one to two orders of magnitude in clam biomass density by sea otter predation in Alaska's Kodiak archipelago, and Garshelis et al. (1986) reported similarly strong limiting influences by sea otters on Dungeness crabs (*Metacarcinus magister*) in eastern Prince William Sound. Similar limiting effects of sea otter predation on various clam species have been reported elsewhere (Miller et al. 1975, Kvitek and Oliver 1988, Groesbeck et al. 2014). The indirect knock-on effects on other species and processes in these soft-sediment systems, though probably important, are largely unstudied and thus unknown. Still, they may include such factors as modifying substrate complexity and sediment turnover, facilitating clam recruitment rates on shell debris, modifying the accessibility of clams for other predators, and mediating bivalve filtration rates.

Where sea otter impacts on commercial crab species have been documented, the effects are highly variable. For example (as mentioned above), the expansion of a growing sea otter population into eastern Prince William Sound, Alaska, in the 1980s resulted in a substantial reduction in catch/effort and the collapse of the commercial Dungeness crab fishery (Garshelis et al. 1986). In contrast, recreational and commercial Dungeness crab fisheries have persisted and even increased at the northern end of the sea otters' range in central California (Grimes et al. 2020, Boustany et al. 2021). This difference between Prince William Sound and central California may be the result of comparatively fewer otters in California (although sea otters have been present at high densities in commercial crab fishery areas for many decades).

Another possible explanation for the difference is bathymetry, with the much deeper nearshore water at the edge of California's continental shelf potentially providing a depth refuge for adult crabs from sea otter predation. Although dive depths of up to 100 m by male sea otters have been documented, the cost of deep diving probably results in reduced foraging efficiency, and the vast majority of foraging dives in this species are in less than 30 m of water (Bodkin et al. 2004, Tinker et al. 2007, Thometz et al. 2016, Tinker et al. 2017).

Yet another possible reason for differences between Prince William Sound and central California is variation in the strength and frequency of the larval supply. Dungeness crab populations in Alaska's inner waters appear to be locally recruiting or self-recruiting, whereas populations in northern California probably draw more extensively from vast larval pools in the offshore California Current ecosystem (A. Shanks, pers comm).

The situation for commercial crab fisheries in Oregon is more similar to that in California, although recreational crab fisheries in Oregon's extensive coastal estuaries may respond to sea otter predation more similarly to those in coastal Alaska. As a rule of thumb, the negative influences of sea otter predation on Oregon's Dungeness crab fisheries are expected to be strong in shallow-water environments and weak to nonexistent in deeper-water habitats.

Estuarine/Seagrass Ecosystems

As with soft-sediment habitats on outer coasts, sea otters in estuaries have been shown to reduce the abundances of clams and crabs (Hughes et al. 2013, Grimes et al. 2020). Sea otters influence seagrass-dominated estuarine systems in various other ways, some of which have important conservation implications for these valuable but threatened ecosystems. For example, anthropogenic nitrogen inputs from agriculture and residential activities have enhanced the spread of epiphytic algae in many estuaries, leading to algal overgrowth and ultimately reducing estuarine seagrass beds. In one nutrient-impaired estuary in central California (Elkhorn Slough), this pattern of seagrass loss was reversed by returning sea otters to the system. This unexpected positive effect resulted from a previously undescribed trophic cascade involving top-down effects from sea otters consuming predatory decapods (crabs), which, in turn, feed on algivorous isopods and opisthobranch mollusks (sea hares), which graze epiphytic algae. The reestablishment of sea otters into Elkhorn Slough has substantially reduced the size and density of larger crabs (mostly *Cancer productus* and *Romaleon antennarium*), thereby releasing algivorous isopods and sea hares from limitation by crab predation, consequently increasing the removal rates of epiphytic algal overgrowth from seagrass blades, and ultimately facilitating seagrass bed recovery (Hughes et al. 2013).

Oregon's large coastal estuaries are likely areas for both staging sea otter reintroductions and the habitats that reestablished populations will later occupy. Because of their shallow nature, the likelihood is high that estuarine crab populations and their associated fisheries will be negatively impacted—much as in Alaska (Garshelis et al. 1986) and Elkhorn Slough in central California (Hughes et al. 2013).

Oregon's extensive estuarine oyster farms are another potential concern. Otter reintroduction may conflict with the shellfishery, although in this case, there is little known evidence for negative interactions between sea otters and oyster farming in areas of Alaska and British Columbia, where the two co-occur. Nonetheless, oyster farming procedures differ somewhat between these regions, so the possibility of conflicts should not be ignored. Indirect positive effects of sea otters on Oregon's estuarine ecosystems, as shown by Hughes et al. (2013) in Elkhorn Slough, are also possible, although the nature of any such effects is presently largely unstudied and therefore uncertain.

Generality and Variation

It is important to understand that all the above-described patterns and processes can vary among locations and at any given location through time. This is not to say that little or nothing can be predicted about how the reestablishment of sea otters will influence Oregon's diverse coastal ecosystems. For example, a reduction in sea urchins and the resulting expansion of kelp forests are likely consequences, based largely on the recurrent nature of this trophic cascade across Alaska, British Columbia, and Washington State. However, the precise details of these effects are unpredictable and wholesale surprises (Doak et al. 2008) are almost inevitable.

Some of this variation is no doubt caused by spatial and temporal variation in the physical environment. However, several other features of sea otters and their ecosystems contribute to this variation, some of which have already been alluded to. They include (a) learned behavioral differences among individual sea otters, especially as they relate to dietary preferences; (b) variation in water depth; (c) variation in the regularity and strength of recruitment by species like fish, invertebrates, and macroalgae commonly characterized by complex life histories with spores or larvae; and (d) the presence or absence of other species of predators.

Evolutionary Effects

The preceding synopsis shows many of the direct and indirect ecological influences of sea otters to be strong and diverse. This finding inevitably leads to questions of evolutionary consequence. Although describing and understanding the evolutionary consequences of sea otter predation have been less thoroughly studied than their ecological counterparts, there are nonetheless several suggestions of sea otters' important evolutionary influence in kelp forest and seagrass ecosystems.

The oldest and most well-known of these evolutionary studies is Steinberg et al.'s (1995) proposal for sea otters' influences on the coevolution of kelp and herbivores via the otter-urchin-kelp trophic cascade. Steinberg et al.'s (1995) work was founded on two well-known processes—the decoupling effect of sea otters on the interaction strength between sea urchins and kelp and the coevolution of defenses (by plants) and resistance to those defenses (by herbivores) when the intensity of herbivory is strong. Steinberg et al. (1995) reasoned that an evolutionary history of weak herbivore-plant interactions in the North Pacific, stemming from the sea otter-urchin-kelp trophic cascade, should have led to a poorly defended kelp flora and weakly resistant herbivores. They reasoned that the weaknesses would have been caused by a lack of necessity on the one hand and an otherwise high evolutionary cost of defense/resistance on the other.

They tested this hypothesis via comparative and experimental studies of North Pacific and Australasian kelp forests. They discovered that (a) Australasian kelps and their analogs were well defended by secondary metabolites, whereas their North Pacific counterparts were not; (b) North Pacific herbivores were strongly deterred by these metabolites, whereas their Australasian counterparts were not; and (c) kelps and herbivores lived in close association in Australasian kelp forests, whereas in North Pacific rocky reef systems, they did not. These findings led Steinberg et al. (1995) to conclude that the lack of an effective predator on Australasian herbivores led to the coevolution of defense and resistance in Australasian kelp forests. In contrast, the presence of sea otters and their recent ancestors in the North Pacific reduced that potential. This evolutionary scenario is thought to have further promoted the radiation of Steller's sea cows (*Hydrodamalis gigas*; a kelp-eating mammal) in the North Pacific (Estes et al. 2016a) and the evolution of the unusually large body size in North Pacific abalones (Estes et al. 2005).

A final example of sea otters' evolutionary influence comes from recent work by Foster et al. (2021) on the disturbance, reproduction, and genetics in eelgrass (*Zostera marina*) meadows of British Columbia. Eelgrass has two distinct life-history variants—a long-lived form that propagates asexually via a rhizoidal root system and a shorter-lived form that propagates via flowering, sexual reproduction, and seed set. The asexual form, which is genetically impoverished, is most successful in undisturbed habitats (lacking sea otters) because the resulting dense colonies compete strongly for space and inhibit successful seed set. The repatriation of sea otters (following reintroductions in the late 1960s—see Chapter 2 of this study) has resulted in sea otters digging for prey in these dense, asexually clonal eelgrass stands as populations have increased and spread, creating patches of open space on the seafloor for successful seed set and, in turn, increasing eelgrass genetic diversity. The positive effect of sea otter recovery on eelgrass genetic diversity appears to be substantial, greater than effects associated with more typical factors, such as the depth and size of eelgrass beds.

Conclusions

The influence of sea otters on coastal ecosystems is one of the most well-known and well-documented examples of a trophic cascade (the complex network of consumer-prey interactions, from apex predators at the top of the food web to plants at the bottom). The top-down effects of sea otters on coastal ecosystems result mostly from the direct limiting influences of sea otters on their macroinvertebrate prey (including many shellfish species). Also, other species and ecological processes feel the effects indirectly through knock-on effects. The most extensively studied and well-known knock-on effect of sea otters occurs through their limiting influence on herbivorous sea urchins and the resulting enhancing effect on kelps and other groups of macroalgae. In turn, the macroalgae affect numerous other species and ecological processes (a phenomenon that has earned sea otters the reputation of being what ecologists refer to as a keystone species).

In this chapter, we have summarized these known direct and indirect ecological effects and their likely evolutionary consequences, drawing particular attention to many others that are either less well studied or entirely unknown. Although many of the patterns and processes we describe are well documented, the details can vary substantially from place to place and through time. The sea otter's powerful and diverse ecological influences result in both costs and benefits to human societies, a topic that is taken up further in Chapter 7.

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