COMPLEX TROPHIC INTERACTIONS IN KELP FOREST ECOSYSTEMS

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ABSTRACT

The distributions and abundances of species and populations change almost continuously. Understanding the processes responsible is perhaps ecology's most fundamental challenge. Kelp-forest ecosystems in southwest Alaska have undergone several phase shifts between alga- and herbivore-dominated states in recent decades. Overhunting and recovery of sea otters caused the earlier shifts. Studies focusing on these changes demonstrate the importance of top-down forcing processes, a variety of indirect food-web interactions associated with the otter-urchin-kelp trophic cascade, and the role of food-chain length in the coevolution of defense and resistance in plants and their herbivores. This system unexpectedly shifted back to an herbivore-dominated state during the 1990s, because of a sea-otter population collapse that apparently was driven by increased predation by killer whales. Reasons for this change remain uncertain but seem to be linked to the whole-sale collapse of marine mammals in the North Pacific Ocean and southern Bering Sea. We hypothesize that killer whales sequentially "fished down" pinniped and sea-otter populations after their earlier prey, the great whales, were decimated by commercial whaling. The dynamics of kelp forests in southwest Alaska thus appears to have been influenced by an ecological chain reaction that encompassed numerous species and large scales of space and time.

The distributions and abundances of species and populations vary through time. Although human activities contribute to this variation, they are not solely responsible for it. Hence, managers and conservationists should be less concerned with change per se than with the extent to which change is driven by human influences and the degree to which it can be managed. Before these determinations can be made, however, the underlying mechanisms of change must be understood. Unfortunately, these mechanisms are usually poorly known because observing pattern is relatively easy whereas understanding process is much more difficult.

Although the truth of this claim is evident from any number of case studies, two well-known examples suffice to make the point. First consider the early Holocene megafaunal extinctions. Beginning about 13,000 yrs ago, more than half of medium to large-sized mammalian species abruptly disappeared from the New World (Martin and Wright, 1967). The pattern is clear, but the responsible processes are still debated (Krech, 1999), despite a substantial body of evidence that hunting by early humans was the main cause (Martin, 1973; Alroy, 2001). The problem is that the Pleistocene-Recent boundary was a time of rapid climate change, which some believe indirectly caused the megafaunal extinctions and others believe must at least have interacted with human hunting in important ways. Next consider the disappearance of large dinosaurs at the Cretaceous-Tertiary boundary, again a period of rapid environmental change. Although the pattern is indisputable, the responsible processes are still debated, despite a wealth of evidence that the extinctions were caused by a large meteor crashing into the earth (Alvarez et al., 1980). Many other examples of the asymmetry in understanding between pattern and

process could easily be provided, including any number of recent or ongoing trends that are concerns for conservation and management.

Why are ecological processes so elusive, and how might we better understand them? The answer to the question of "why" seems clear enough. Recognizing pattern amounts to little more than identifying and enumerating species and individuals on proper scales of space and time, tasks the human body and mind are well equipped to handle. The processes that drive these changes are typically much more difficult to see and understand because of their dynamic nature and enormous potential for complexity.

The present paper focuses on both the nature and the understanding of process in some North Pacific kelp-forest ecosystems. Marine ecosystems in this region have undergone a number of marked changes over the past 50 yrs but with little understanding about why (National Research Council, 1996). Our perspectives are based primarily on three decades of research on sea otters and kelp forests in the Aleutian archipelago, admittedly a marginal part of the Bering Sea–North Pacific ecosystem but one about which we have developed a mechanistic understanding for some of the observed changes.

Until recently, we watched others attempt to understand the precipitous population declines of northern fur seals, harbor seals, and Steller sea lions, never imagining that the future of sea otters and kelp forests might be connected to these changes. Then, in about 1990, following nearly a century of recovery from the ravages of the Pacific maritime fur trade, sea otter populations in southwest Alaska unexpectedly plummeted (Doroff et al., 2003). We were forced to look both to the past and to the open sea for explanations and, although much remains to be learned, these retrospections have added insight to our growing view of the sea-otter–kelp-forest system. We will explain why by recounting the history of our key findings, how we have interpreted them, and how these interpretations have altered some of our views about the changeability, and hence the meaning, of food-web dynamics.

Early Perceptions

One of us (J.A.E.) began working on sea otters and their coastal ecosystems at Amchitka Island in 1970, knowing a few things about pattern but almost nothing about process. We knew, for example, that sea otters had been hunted to the brink of extinction during the period of the Pacific maritime fur trade and that recovery following the protection afforded them by international treaty in 1911 was highly asynchronous in space and time (Kenyon, 1969). We also knew something about food-web structure, in particular, that sea otters ate sea urchins and that sea urchins ate kelp and other macroalgae. However, we also held beliefs about process that later turned out to be either oversimplifications or incorrect. One of these beliefs was that populations in the kelp–sea urchin–sea otter food chain were regulated largely by bottom-up forcing mechanisms—kelps by nutrients and light, urchins by the abundance and quality of kelp and other macroalgae, and otters by the abundance and nutritional composition of sea urchins and other kelp-forest prey species. In retrospect, this view was based in part on training and in part on preconceived interpretations of the then-available evidence.

Top-Down Forcing and Trophic Cascades

There was little precedent for thinking about top-down forcing processes in 1970. Hairston et al.'s (1960) now classic paper set the stage conceptually and was followed

by early empirical evidence provided by Brooks and Dodson (1965) for lakes and by Connell (1961) and Paine (1966) for rocky shores. Paine and Vadas (1969) had just demonstrated the limiting effects of sea urchin grazing on kelp assemblages. Knowing that sea otters ate sea urchins, we explored this theme further by contrasting islands in the Aleutian archipelago with and without sea otters. These contrasts (Estes and Palmisano, 1974), and subsequent time series from other sites as they were repopulated by otters during the late 1970s and 1980s (Estes and Duggins, 1995), revealed a consistent pattern: where otters were common, sea urchins were rare and kelps abundant; where otters were rare or absent, sea urchins were common and kelps rare or absent. These and other findings have led to the view that top-down forcing processes (Hunter and Price, 1992) and trophic cascades (Paine, 1980; Carpenter and Kitchell, 1993) are important regulatory processes in kelp-forest ecosystems.

INDIRECT EFFECTS

The aforementioned discoveries also led us to search more widely for indirect effects of the otter-urchin-kelp trophic cascade. Such effects were anticipated because kelps and sea urchins are dominant structural components of the coastal ecosystem and kelps contribute considerably to organic carbon fixation and energy flux by virtue of their high biomass and productivity (Mann, 1973, 1982; Duggins et al., 1989). Although trophic cascades are known or suspected in a diversity of ecosystems (Pace et al., 1999), the indirect effects of trophic cascades have not been so extensively studied. Said differently, relatively little work has been designed to discover how a simple, linear trophic cascade can generate far-reaching chains of effects that more broadly influence community composition and dynamics. Here again, our general approach was to contrast otherwise similar islands in the Aleutian archipelago with and without sea otters, looking for differences in population densities, behaviors, and interaction strengths. We have restricted these investigations to several of the more conspicuous species (i.e., kelps, sessile invertebrates, fishes, marine birds) and a few likely processes (i.e., altered habitat and food availability). For the most part we have not looked for indirect effects that were separated by more than one or two trophic links from the otter-urchin-kelp cascade. Interisland differences in species diversity were never considered, although the physical environment appears to be largely invariant across this region and, except for the distribution and abundance of sea otters, all of the key species occur at all islands.

Known or suspected indirect effects of predation by sea otters include increases in total production and the proportion of kelp-derived organic carbon in a variety of coastal consumers (Duggins et al., 1989), altered abundance and diet of kelp-forest fishes (Reisewitz, 2002), reduced interaction strengths between predatory sea stars and several of their sessile invertebrate prey (Vicknair, 1996), altered diet and foraging behavior of glaucous-winged gulls (Irons et al., 1986), increased competitive interactions among the common kelp species (Dayton, 1975), reduced populations of benthic-feeding sea ducks (D. B. Irons, G. V. Byrd, and J. A. Estes, unpubl. data), and altered diet of bald eagles (R. G. Anthony, unpubl. data). Although numerous other indirect effects undoubtedly occur, these examples are sufficient to demonstrate that the influences of sea otter predation on the coastal ecosystem are diverse, powerful, and far-reaching.

EVOLUTIONARY EFFECTS

Another line of inquiry has centered on the potential evolutionary consequences of predation by sea otters. We have focused on plant-herbivore interactions because the species are relatively easy to work with in both the field and the laboratory; interaction strengths between plants and herbivores vary considerably with the presence or absence of sea otters; and a substantial literature from work done in both terrestrial and marine systems exists on defense and resistance in plant-herbivore interactions. Our general approach was to contrast the North Pacific region (the sea otter's range from the Pleistocene to the Recent) with other temperate regions that contained similar functional groups of plants and herbivores but that seemingly lacked benthic-feeding predators of influence comparable to that of the sea otter. Mostly, these contrasts have been between the eastern North Pacific (a three-tiered food chain) and temperate Australasia (a two-tiered food chain). We have focused on the prevalence and function of algal secondary metabolites (specifically phlorotannins) because prior studies had shown secondary compounds to mediate marine plant-herbivore interactions (Hay and Fenical, 1988) and phlorotannins appeared to be the principal mode of defense against herbivory in kelps and other brown algae.

While such studies are fraught with potential confounding influences, our findings are at least consistent with the expectation that sea-otter predation has helped shape the life histories of marine plants and the character of marine plant-herbivore interactions in the North Pacific Ocean. Phlorotannin concentrations are an order of magnitude greater in Australasian than in North Pacific macroalgae (Steinberg, 1989; although see Van Alstyne et al. 2001). In addition, comparable concentrations of phlorotannins deter herbivory by common echinoderms and gastropods much more strongly in North Pacific than in Australasian species, regardless of whether these compounds come from Australasian or North Pacific algae (Steinberg and Van Altena, 1992; Steinberg et al., 1995). We interpreted these patterns to mean that Australasian and North Pacific plant-herbivore systems have evolved in fundamentally different ways, in large measure because of the importance of top-down forcing processes and differences in food-chain length between the two regions (Fig. 1). That is, herbivores are the apex predators in Australasian kelp forests and the resulting high levels of damage inflicted on marine plants caused an evolutionary arms race between defense in the plants and resistance in the herbivores. This scenario would explain why secondary-metabolite concentrations are so high in Australasian algae and why Australasian herbivores are relatively undeterred by these compounds. Predators (sea otters and their recent ancestors) add a third trophic level to North Pacific food chains, causing herbivore populations to be strongly limited by predation and in turn decoupling the coevolution of defense and resistance in North Pacific plants and their herbivores. It would also explain why North Pacific algae have such low concentrations of secondary metabolites, why North Pacific herbivores are so strongly deterred by phlorotannins, and why Northern Hemisphere kelp forests have been so extensively damaged by overgrazing after the loss of sea otters and other key predators (Harrold and Pearse, 1987; Steneck et al., 2003).

FAILED EXPECTATIONS

What we have learned about sea otters and kelp forests was founded on an appreciation of the importance of history and a belief in the importance of top-down forcing
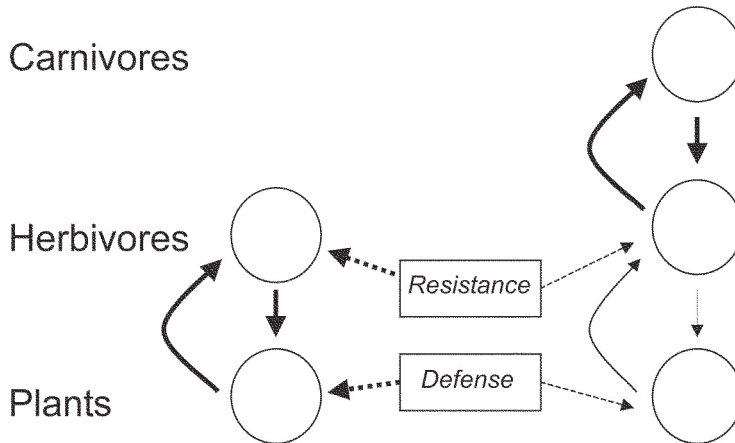
Figure 1. Hypothesized evolutionary consequences of food-chain length in systems under top-down control. Strong plant-herbivore interactions occur in systems with two (or any even number of) trophic levels. The result is strong (indicated by heavy lines) selection for the coevolution of plant defenses against herbivory and herbivore resistance to those defenses. Addition of a third trophic level (or any odd number of trophic levels) weakens (indicated by lighter lines) the influence of herbivores on plants, thus reducing selection for the coevolution of defense and resistance (after Fretwell, 1987, and Steinberg et al., 1995).

processes. Scientists have known for some time that offshore areas serve as nursery grounds and transportation corridors for dispersive life stages of many coastal plants, invertebrates, and fishes (Caley et al., 1996), and our own studies at Amchitka Island during the early 1990s showed that episodic spawning migrations of smooth lumpsuckers (*Apocyclus ventricosus*) affected the foraging behavior and survival of sea otters (Watt et al., 2000). Nonetheless, we assumed that kelp forest ecosystems were functionally closed to the influences of offshore fisheries, ocean regime shifts, and other changes to the nearby oceanic realm. This, in retrospect, was a significant misperception that led to failed expectations (sea-otter population regulation by resource depletion at some islands; the continued recovery of sea otters at others) as well as the failure even to recognize changing trends until they were well along.

SEA OTTER POPULATION DECLINES

By the late 1980s, sea-otter populations had recovered to near maximum levels throughout much of southwest Alaska, and we expected this trend to continue. In 1992 the U.S. Fish and Wildlife Service conducted an aerial survey of sea otters throughout the Aleutian archipelago, the first since 1965. Although the 1992 counts were lower at nearly all islands believed to be at or near carrying capacity in 1965, this result was not taken as strong evidence for a decline because of possible methodological inconsistencies and the expectation that otter numbers should have been stable or increasing. The failure of sea otters to recover at the expected rate in the Semichi Islands in the early to mid 1990s also was discounted initially as being extraordinary, the presumption being that the missing animals had moved elsewhere (Konar, 2000). About 4200 sea otters were counted in a 1994 shore-based survey of Amchitka Island, and although this number was lower than estimates from the early 1970s (Estes, 1977), here again we did not take the count as a strong signal of population decline, despite what in retrospect were
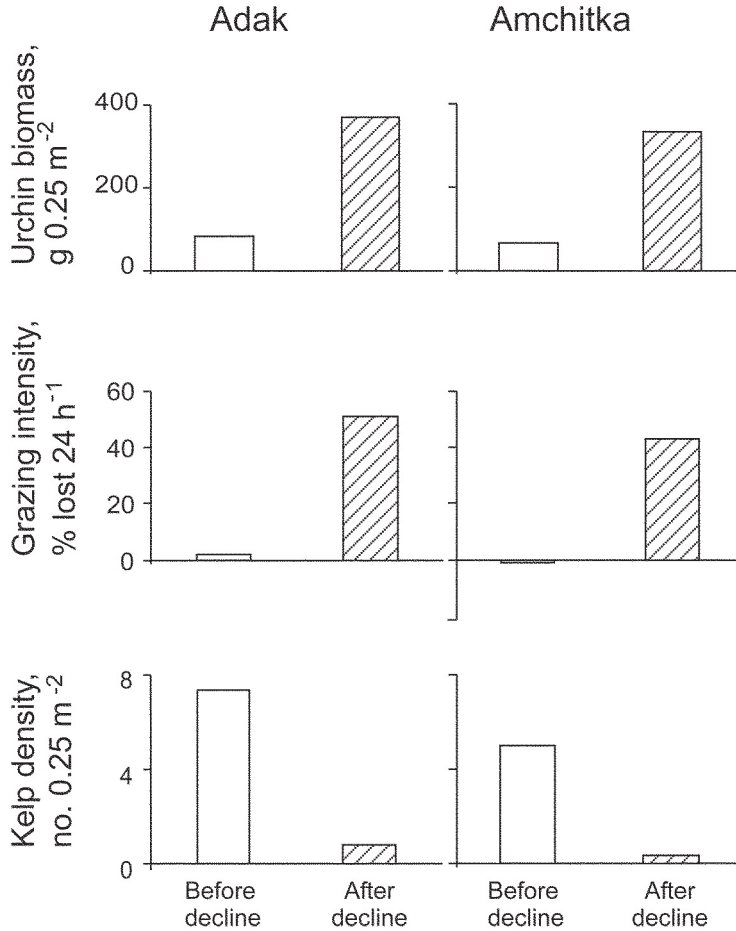
Figure 2. Changes in sea-urchin biomass, herbivore grazing intensity, and kelp density at kelp-forest monitoring sites at Adak and Amchitka islands following the decline of sea-otter populations. Sites and sampling methods are described in Estes and Duggins (1995) and Steinberg et al. (1995).

a number of behavioral and ecological indicators of change (Monson et al., 2000; Watt, 2000; Gelatt et al., 2002).

Although our studies at Amchitka Island ended in 1994, we continued working at nearby Adak Island where, over the next several years, sea-otter numbers declined precipitously. This decline prompted several questions: what was causing sea otters to decline at Adak; had similar declines occurred elsewhere, and if so how widespread were they; and what were the consequences to the kelp-forest ecosystem? This latter question was easy to answer because we had been monitoring numerous kelp-forest sites at Amchitka Island since the early 1970s and at Adak Island since 1987. Dense kelp and sparse sea-urchin populations characterized both islands through the 1980s (Estes and Duggins, 1995). We resurveyed Adak in 1997 and Amchitka in 1999 and found that both locations had been extensively stripped of kelps and other fleshy macroalgae by sea-urchin grazing (Fig. 2), almost certainly because of the reduced number of sea otters. Because sea urchins are one of the sea otter's most highly sought-after prey, these findings also indicate that food limitation did not cause the sea-otter decline.
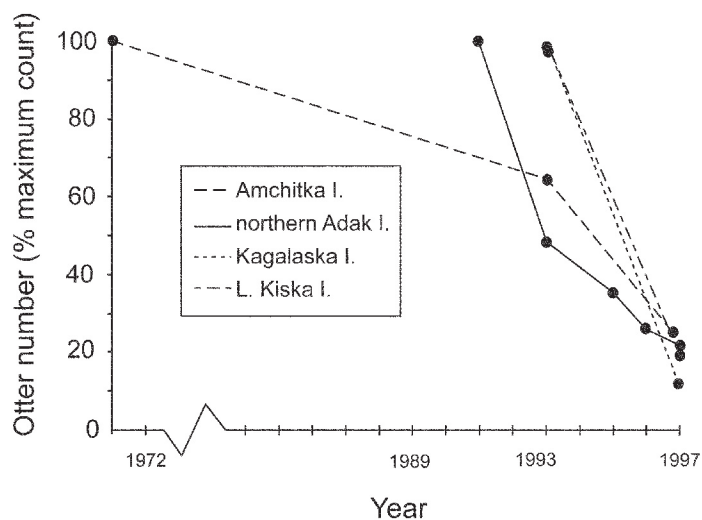
Figure 3. Sea-otter population trends at Amchitka, northern Adak, Kagalaska, and Little Kiska islands. Data are plotted as percentages of maximum counts for each island. Survey methods described by Estes (1990) and Doroff et al. (2003). Data are from Estes et al. (1998).

The geographical extent of the sea otter decline was also easy to determine because a variety of earlier survey data existed for coastal Alaska and the Commander Islands. A resurvey of sea otter numbers along the southeast coast of Amchitka Island in May of 1998 indicated a decline comparable to that at Adak Island, as did counts later that summer of Little Kiska and Kagalaska islands (Fig. 3) and counts from the Semichi Islands done in 1994, 1995, and 1997 (Konar, 2000). In 2000, the U.S. Fish and Wildlife Service conducted another aerial survey of the Aleutian Islands, and in 2001 they surveyed coastal waters of the Alaska peninsula eastward through the Kodiak archipelago. These surveys show that sea-otter densities have declined to a common low value (5–10% of the estimated equilibrium density; Fig. 4) throughout the Aleutian archipelago (Doroff et al., 2003) and that significant population declines have occurred eastward to at least the Kodiak archipelago (A. Doroff, unpubl. data).

Why did sea-otter numbers decline so suddenly and synchronously? Population surveys and tagging and telemetry studies at Adak and Amchitka islands established the general cause to be elevated mortality, as opposed to reproductive failure or redistribution. Starvation, disease, toxins, and direct human take (either purposeful or incidental) were also excluded as likely causes (Table 1). Killer whales, not known to prey on sea otters, were rarely seen in coastal waters of the Aleutian Islands during the 1970s and 1980s, but they were seen much more often in the early 1990s. Many appeared to be hunting, and attacks on sea otters were observed on several occasions (Hatfield et al., 1998). These observations, and the pattern of sea-otter population declines around Adak Island (i.e., absence of otherwise ubiquitous declines in several shallow lagoons that were inaccessible to killer whales), led us to suspect that killer whales were responsible for the decline (Estes et al., 1998). Nonetheless, it seemed that more attacks should have been observed if killer whales truly were responsible for so many losses. We tested this supposition by computing the expected number of observed deaths between Kiska and Seguam islands (the area within which our field studies had been conducted) for the 1991–1997 period as $n(p_t))(p_a)$, where $n = 40{,}728$ sea otters (the total number of ad-
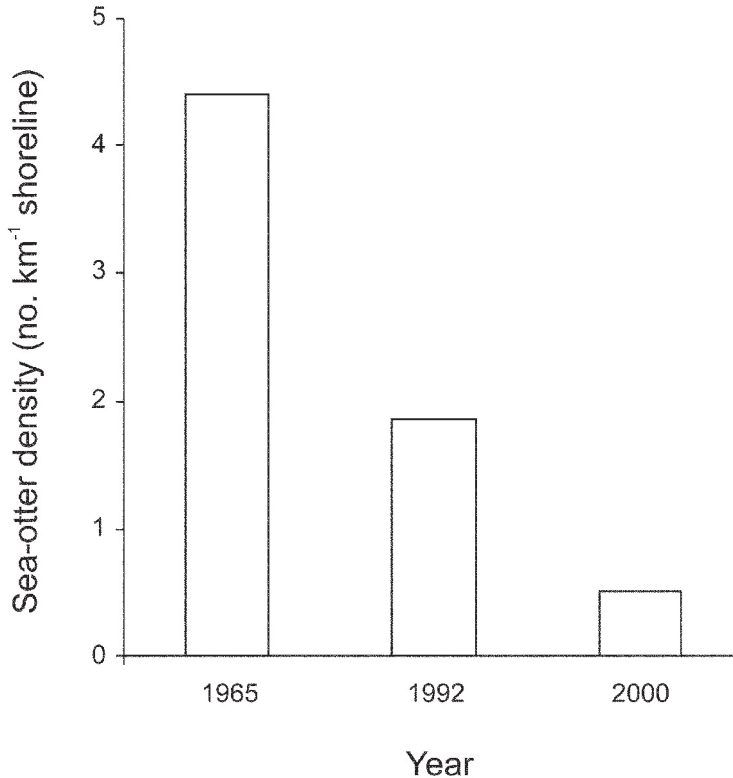
Figure 4. Sea otter densities (no. km^{-1} of shoreline) as determined by aerial surveys of Rat, Delarof, and western Andreanof islands (Aleutian archipelago) in 1965, 1992, and 2000. Data are from Adak, Amatignak, Amchitka, Buldir, Gareloi, Great Sitkin, Kagalaska, Kanaga, Kavalga, Khvostov, Kiska, Little Sitkin, Little Tanaga, Oliuga-Skagul, Rat, Segula, Semisopochnoi, Tanaga, Ulak, Umak, and Unalga islands, all islands judged by Kenyon (1969) to have reached equilibrium density by 1965. Densities were computed from counts and shoreline distances, totaled across all islands.

ditional deaths needed to drive the observed decline in this region), p_t = the proportion of the 6-yr time interval that was sampled by field observers, and p_a = the proportion of the sample area seen by an observer at any instant. n was determined from the estimated predecline population size and an age-structured population model, which we initially parameterized with age-specific fertility and mortality estimates (summarized in Monson et al., 2000) to create a stable population. We then added increased mortality evenly to each age class (on the basis of results of our field studies at Amchitka and Adak) so as to achieve the observed rate and magnitude of population decline. p_t was estimated as 0.412 (21,677 person-hrs in the field divided by 6 yrs; 52,560 h) and p_a as 0.0003 (1 km, the maximum distance for observing an attack, divided by 3,327 km, the coastal length of the study area). Given that predation by killer whales was entirely responsible for the sea otter decline, the expected number of observed kills (40,728 × 0.412 × 0.0003 = 5.03) is remarkably close to six, the observed number of kills (Estes et al., 1998).

Table 1. Common hypotheses (excluding predation) for elevated sea-otter mortality in the Aleutian archipelago, and the reasons for their acceptance or exclusion.

Hypothesis	Rationale for acceptance or exclusion
Starvation	1. Increased size and abundance of sea urchins, the sea otters preferred prey species.
	2. Absence of stranded carcasses. Food limitation typically results in large numbers of emaciated beach-cast animals (Kenyon, 1969).
	3. Increased age-specific mass/length ratio (Monson et al., 2000); indicative of increased prey availability.
Disease	1. Absence of stranded carcasses. Large numbers of sea otters that die from infectious disease in central California appear as beach-cast carcasses.
	2. Absence of any known sign of disease in 66 living sea otters captured in Aleutian Islands in 1997 and examined by wildlife veterinarians (D. Jessup, Senior Wildlife Veterinarian, California Department of Fish and Game, pers. comm.)
Toxins	1. Low concentrations of common organic and inorganic human-caused contaminants in blue mussels (*Mytilus trossulus*) from 39 sites across the Aleutian archipelago. (S. L. Reese, W. M. Jarman, and J. A. Estes, unpubl. data).
	2. Low blood-contaminant levels in Aleutian Islands sea otters compared with those in stable or increasing populations elsewhere (W. M. Jarman and J. A. Estes, unpubl. data).
	3. Absence of stranded carcasses.
Human take	1. Absence of reported human kills, even near human settlements.
	2. Remote region; small number of human visitors.
	3. No known human motivation for exploitation in Aleutian Islands.
	4. Absence of sea otter products in world market.

Ultimate Causality?

Although killer-whale predation seems to have driven the sea-otter declines, why it did so is less clear. Nonetheless, the most likely scenarios must be identified if we are to evaluate properly the weight of evidence, because different explanations have vastly different implications for conservation and management policy. Furthermore, similar degrees of uncertainty about causal processes characterize many other well-described population- and ecosystem-level changes, so this particular case is of broader general interest. The following, although necessarily speculative, is a brief synopsis of our current thinking. Our approach is to address specific questions that logically arise in a retrospective overview of the system. The analyses were done for the Aleutian archipelago, from Unimak Island in the east to Attu Island in the west (Table 2).

WHY WOULD KILLER WHALES BEGIN EATING SEA OTTERS?—Individual killer whales (or more properly, matrilineal groups) tend to forage either on fish or on marine mammals (Matkin, 1994; Baird and Dill, 1996). The two common species of pinnipeds in the Aleutian Islands (harbor seals and Steller sea lions) declined drastically during the 1970s and 1980s, so the sea-otter collapse may have resulted from dietary switching by mammal-eating killer whales. Such a dietary shift by as few as six killer whales (if these fed exclusively on sea otters) could account for the Aleutian-wide sea-otter decline (Table 2; Williams et al., in press).

WHY DID THE PINNIPEDS DECLINE?—Here both the logic and the evidence are more equivocal. Initially, nutritional limitation was thought to be responsible for the pinniped declines (Anonymous, 1993), for the following reasons. Bottom-up forcing provided the conceptual framework for thinking about process in oceanic ecosystems, so that is where scientists looked. With this apparent predilection, it was easy to imagine how

Table 2. Essential data and calculations used to compute the minimum number of killer whales needed to eat enough sea otters or Steller sea lions to drive the observed population declines. All analyses conducted for region of the Aleutian archipelago. Data from Williams et al. (in press).

Parameter	Species	
	Sea otter	Steller sea lion
Initial abundance (year)	77,435 (1990)	70,412 (1979)
Final abundance (year)	17,036 (1997)	10,340 (2000)
Population model	Leslie matrix	Leslie matrix
Model parameters for stable age distribution	Monson et al. (2000)	York (1994)
Added mortality function	Time constant, fit to create decline function based on skiff counts from Adak Island, 1991–1997	Time-varying logit fit to NMFS census data for Aleutian archipelago, 1975–2000
Estimated total deaths	69,874	60,465
Maximum per-year mortality	9,982	11,575
Per-individiual caloric value	41,630 (adult females); 61,450 (adult males)	104,400 (pups); 586,858 (adult female blubber and muscle)
Minimum number of killer whales needed to consume maximum per-year mortality[a]	6	26

[a]At field metabolic rate of 2.5–2.9 W k^{-1} and 82% assimilation rate.

commercial fishing and an oceanic regime shift, both of which had occurred, could have led to nutritional limitation. Human fishers and sea lions take many of the same prey, so competition for a common resource was a reasonable supposition. Apparent decreases in fertility and body condition in Steller sea lions from the 1970s to the 1980s seemed to support this view (Calkins et al., 1998; Pitcher et al., 2000), but the current weight of evidence does not support nutritional limitation or bottom-up forcing. In brief, (1) fish stock assessments indicate that sea-lion prey availability has remained constant or increased over much of the region in which sea lions have declined (Anonymous, 2000), and (2) a variety of data on the physiology (e.g., body condition, field metabolic rate) and behavior (foraging range, depth of dive, time spent feeding) of sea lions indicate that food is relatively more abundant in the western Gulf of Alaska and Aleutian Islands (where sea lions are declining) than it is in southeast Alaska (where sea lions are increasing; Anonymous, 2001; National Research Council, 2003).

The available information now seems more consistent with top-down forcing processes, of which the most likely possibilities are predation, incidental losses in fisheries, purposeful killing (illegal shooting and native subsistence), and disease. Toxins have also been identified as a possible cause of the decline. A weight-of-evidence analysis helps to clarify the likelihood of these various possibilities. The native subsistence take cannot account for the decline by any reasonable extrapolation of available records. Similarly, no evidence supports the hypothesis that diseases or toxins are affecting sea lions. Incidental losses were considerable at times in the past, especially during the period of the joint-venture fishery (National Research Council, 2003), but it is difficult for us to reconcile the geography (and very high rate of decline in the mid 1980s) with the areas in which most incidental losses would have occurred (the western Gulf of Alaska

and eastern Bering Sea) and the abruptness of changes in fishing practices required to explain the period of rapid decline. Many sea lions probably were killed by illegal shooting during the 1980s and earlier, but again most shooting would have occurred in the western Gulf of Alaska and eastern Bering Sea; it is unclear why shooting deaths would have increased so markedly in the mid 1980s; and shooting losses are presently thought to be very low (National Research Council, 2003). Losses to subsistence hunters, entrapment in fishing gear, and purposeful illegal killing must have contributed to the sea lion decline, especially in some areas, but they do not explain the magnitude or range of the earlier declines, and are probably not responsible for the continuing decline.

Only predators remain. Because killer whales were presumed to have caused the sea otter declines, we began to wonder if they might also have eaten the pinnipeds. Although records of killer-whale foraging behavior from the 1970s and 1980s—those periods when pinniped losses would have been highest—are lacking, we believe the weight of indirect evidence lines up more consistently with killer-whale predation than it does with the other hypothesized causes. Energetic and demographic models (similar to those used in the sea-otter analyses described above, Estes et al., 1998; Williams et al., in press) have shown that the sea-lion declines in the Aleutian archipelago can also be accounted for by small changes in killer-whale foraging behavior (Table 2). For example, as few as 26 killer whales feeding exclusively on sea lions, a 1% change in diet by the entire population, or a 10% dietary change by the mammal-eating population would account for the decline. Of course, similar results could be obtained from any number of more realistic interpolations between these extreme-case scenarios. Predation would also account for the near-absence of beach-cast carcasses during the period of decline as well as the sequential nature of the harbor seal, sea lion, and sea otter collapses (Springer et al., 2003) if killer whales "fished down" (sensu Pauly et al., 1998) coastal marine mammals in this ecosystem.

WHY MIGHT THE INTENSITY OF KILLER-WHALE PREDATION ON PINNIPEDS HAVE INCREASED?—Possibilities include fortuitous behavioral innovations, increased killer-whale numbers, and dietary shifts in response to changing prey fields. The last of these seems most likely because the intrinsic capacity for population growth in killer whales is very low, dietary shifts by consumers commonly follow changes in the abundance and quality of their prey (Murdoch, 1969), and various killer-whale prey species in the North Pacific region—both fishes and other marine mammals—have undergone radical changes in abundance over the past half-century. If indeed a behavioral barrier separates the marine-mammal-eating and fish-eating ecotypes (the so-called transients and residents), as many people now believe (Matkin, 1994; Ford et al., 1998), then one might expect population declines in some other of the killer whale's marine-mammal prey just prior to the onset of the earliest pinniped declines. The great whales are obvious candidates. Although depletions by whaling in the North Pacific region begin much earlier, only after World War II were the area's most abundant species—sperm and fin whales—harvested in large numbers. This fishery grew rapidly (Fig. 5A), spreading eastward from Asia (Fig. 5B), harvesting some half a million whales (Springer et al., 2003), and reducing the estimated whale biomass by roughly an order of magnitude—from 30 to 3 million mt (Pfister and DeMaster, in press). Judging from International Whaling Commission harvest records, most of these reductions had occurred by the late 1960s or early 1970s. Killer whales are known to prey on all of the great whale species (Matkin, 1994). If a substantial number of killer whales derived significant nutritional resources from the great whales when they were abundant, then these killer whales would either have
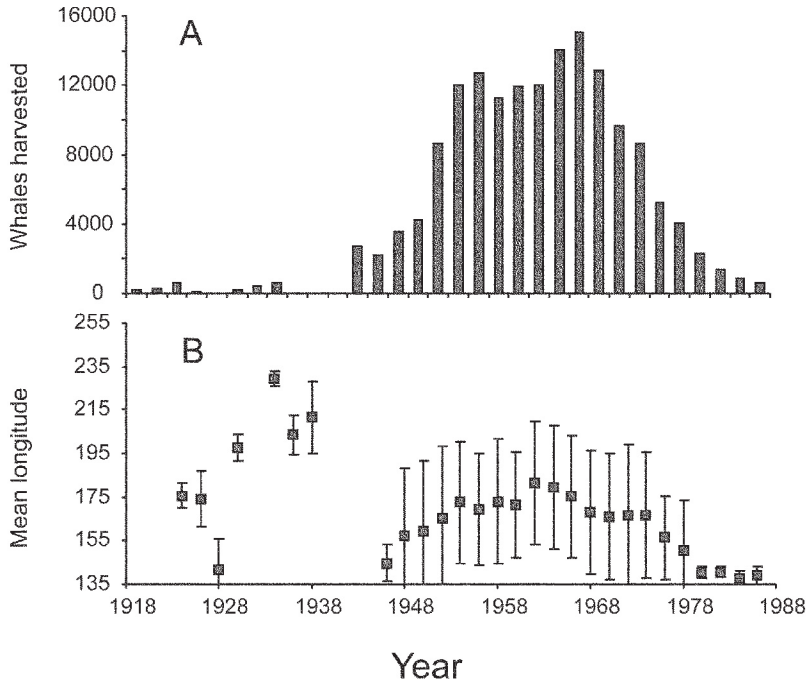
Figure 5. Summary of catch statistics for fin and sperm whales for the North Pacific Ocean and southern Bering Sea. These two species comprised the majority of this region's landed whales. Only data from Japanese catcher vessels were used in this analysis. Panel A. Number of landed whales per 2-yr time interval. These data show that, although some fin and sperm whales were taken as early as the 1920s, the fishery did not grow to obviously harmful levels until after World War II. Panel B. Mean longitude (error bar is 1 SD) of the landings reported in Panel A for the same time intervals. This analysis demonstrates that the small number of prewar landings was broadly distributed across the North Pacific region. After World War II, the landings were concentrated close to Japan (Tokyo is at 139° east), but rapidly spread eastward and dispersed (greater error bars) over the next several decades. Toward the end of the industrial whaling era, as stocks were depleted and the whale fishery came under increasingly stringent regulations, the landings again were concentrated closer to Japan.

starved to death, left the area, or turned elsewhere for sustenance after the great whales became rare. As explained above, such a dietary shift could easily have driven the subsequent population collapses of pinnipeds and sea otters.

Many of the uncertainties about process in this system result from a poor understanding of the natural history and ecology of killer whales. This problem arises in part because killer whales are difficult to study in nature, but also in no small part because ocean ecologists seem to have viewed these animals as little more than spectacular curiosities in the functioning of ocean ecosystems. Much more might be known about killer whales had there been a real sense of need.

EMERGENT PRINCIPLES AND PROBLEMS

What lessons can we take from this experience for the general understanding of process in ecology and conservation? All species are components of interaction webs. Any hope for an empirical understanding of process must rest with the assumption that population dynamics are driven by one or several dominant interaction-web pathways. If this

assumption is correct, then measures of change in a species' distribution, abundance, and population structure following certain kinds of perturbations can clarify the location, strength, and direction of those pathways. For example, imagine a simple three-species food chain consisting of an autotroph, a primary consumer, and an apex predator. One might wonder whether these populations are regulated more strongly by bottom-up or by top-down forcing functions. Answering that question would be difficult in the absence of change. Now imagine that we impart a change to the food chain by removing the apex predator. If the dominant forcing processes were bottom-up in nature, then dramatic effects of this removal on the biomass of autotrophs and primary consumers would not be expected. In contrast, if the dominant forcing processes were top-down in nature, the primary consumers should increase in abundance and the autotrophs should decline. Fortuitous changes in some component of the food web could even be used to make these inferences. For example, imagine that a storm, or disease, or human exploitation reduced the number of primary consumers. If bottom-up forcing processes were the principal drivers of population size, one would expect to see a decline in the abundance of apex predators and no change in the abundance of autotrophs. In contrast, one might expect to see an increase in the abundance of autotrophs and little or no change in the apex predators if the system were under top-down control.

Although this approach to understanding food web process is logical in concept, it might provide incomplete or even misleading results for a number of reasons:

First is the potential for unpredictable influences from indirect interactions, which is large even in simple systems and increases exponentially with food-web complexity (Fig. 6). In other words, the sheer number of possible indirect effects means that even if most are quite weak, indirect effects as a whole are likely to have strong influences on community dynamics.

Misperceptions of spatial scale can also lead one astray in the quest for understanding process, because the spatial boundaries of interaction webs, though known to be vast in some instances (Scott et al., 1999), are almost always unclear, and evidence is mounting for important linkages across ecosystems (Polis et al., 1997).

Yet another under-appreciated dimension to process is that of time. The past is the pathway to the present, and many important interactions from the recent past are now extinct or greatly altered (Janzen and Martin, 1982; Jackson et al., 2001).

Finally, our work has illustrated the uncertainties that can be introduced into predictions of community dynamics by behavioral flexibility. The usual assumption of community ecologists is that observed diet breadth and prey preferences will remain unchanged or only slightly perturbed. More realistically, the majority of predator and consumer species have evolved over time spans that ensure selection for flexible responses to changing environmental conditions, including the ability to alter foraging methods and food sources dramatically.

All these problems bear on our initial question: why has community ecology, with several notable exceptions where experimental tests were possible, had a relatively poor record of understanding the processes responsible for observed changes in the distributions and abundances of species and populations? In essence, our answer is that the scope of possible explanations for the patterns we see is considerably larger than we usually recognize, making the task of understanding and prediction much more fraught with uncertainties than we are usually willing to admit.
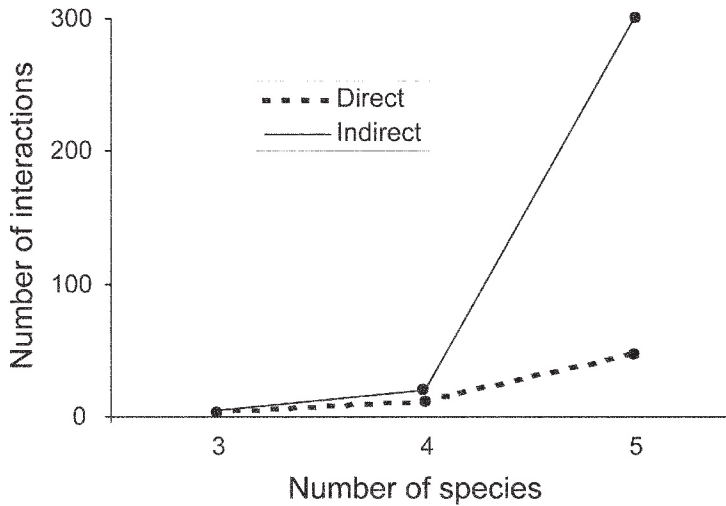
Figure 6. Potential numbers of direct (no intermediary species between initiator and recipient) and indirect (one or more intermediary species) interaction pathways as species number in a food web increases. Direct pathway number was computed as P_2^n, where n = species number. The potential number of indirect pathways was computed as $\Sigma\,P_i^n\,(2 < i \leq n)$. The relative number of indirect pathways increases rapidly with species number. For example, a six-species food web has 30 possible direct linkage pathways and 1920 possible indirect linkage pathways, whereas a 10-species food web has 90 possible direct linkage pathways and 9,864,000 indirect linkage pathways.

CONCLUDING REMARKS

Temperate reef ecosystems throughout much of the world undergo distinct phase shifts between kelp-dominated and sea-urchin–dominated states (Steneck et al., 2003). Population changes in apex predators commonly drive these shifts through top-down forcing processes. Shallow reef habitats in southwest Alaska have undergone two such phase shifts during the 20th century. The first of these (from the urchin- to the kelp-dominated state) occurred gradually and in a spatially asynchronous manner as sea-otter populations recovered from the fur trade (Estes and Duggins, 1995; Konar and Estes, 2003). What successes we have realized in understanding this phase shift were set up by two assumptions, which in retrospect seem to have been largely correct. One assumption was that top-down forcing processes are important drivers of change. Our appreciation of the urchin-algal linkages, which had been defined by earlier experimental studies (Paine and Vadas, 1969), was particularly important. The other assumption was that historical human-caused effects on the distribution and abundance of sea otters could be used as a window into these processes.

The second phase shift (from the kelp- to the urchin-dominated state) occurred relatively rapidly and synchronously across the Aleutian archipelago in the mid 1990s. This event has been more difficult to understand because the chain of causal processes is more complicated and the search was founded on three incorrect assumptions. First, we assumed that the coastal ecosystem was closed to significant interconnections with events in the open sea. Even as sea-otter populations were declining in the early 1990s, we were slow to recognize the declines because all else in the coastal ecosystem appeared normal. Second, those people working on the pinniped declines assumed that significant

forcing processes in open-ocean ecosystems were largely bottom-up in nature. Even af-
ter the importance of onshore-offshore linkages became apparent, nutritional limitation
imposed by competition with fisheries or oceanic regime shifts was thought to be the
ultimate driver of the pinniped declines. Although these bottom-up forcing processes
may have played some role, it now appears that the most important forcing processes
were top-down in nature (Anonymous, 2001; National Research Council, 2003). Third,
scientists and managers had failed to look far enough back in time for the answers. Most
of the search focused on the period from the late 1970s onward, by which time the ulti-
mate cause may have come and gone.

Despite these uncertainties, it is clear that kelp-forest phase shifts have complex and
often unexpected explanations and consequences. This complexity involves linkages
across multiple species, large areas, and long periods of time. The uncertainties may
never be entirely resolved, in which case policy and management decisions will depend
on a fair assessment of the weight of available evidence. However this assessment is
eventually done, the implications of this complexity for conservation and management
of living marine resources are obvious and profound.

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