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TROPHIC CASCADES: PREDATORS, PREY, AND THE CHANGING DYNAMICS OF NATURE



Edited by
John Terborgh and James A. Estes

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CHAPTER 3



Some Effects of Apex Predators in Higher-Latitude Coastal Oceans

James A. Estes, Charles H. Peterson, and Robert S. Steneck

There have been numerous published accounts of predation and top-down forcing from temperate-latitude coastal oceans (Connell and Gillanders 2007; McClahanan and Branch 2008). These studies include diverse predators, various methodological approaches, and a broad range of geographic regions. This literature has become so extensive that we cannot possibly review it all in the space available here. Our goal is thus to provide a sampling of the details, a more superficial survey of the better-known or more persuasive studies, and a synthesis of the principles and generalizations that are emerging from this published literature.

Our chapter centers on three case studies: sea otters in the northeast Pacific Ocean, sharks in estuaries of the central U.S. Atlantic seaboard, and cod in the Gulf of Maine. We have chosen these particular examples because each was assembled around a progression of field studies conducted over many years, the resulting evidence for direct and indirect effects of predation is diverse and compelling, and collectively we have worked in each of these systems. We will follow these detailed accounts with a series of vignettes that further chronicle the ecological roles of predators in temperate marine systems around the world.

SEA OTTERS IN THE NORTH PACIFIC OCEAN

Sea otters ranged across the North Pacific rim for several million years before anatomically modern humans peopled the region. The discovery of abundant sea otter populations by the Bering Expedition in 1740–1741 initiated the Pacific maritime fur trade, which motivated Russian colonization of northwestern North America and led to the near extinction of sea otters.

The Fur Trade: A Fortuitous Natural Experiment

Only a handful of very small sea otter populations survived the fur trade (Kenyon 1969). These occurred in Russia, southwest Alaska, and central California. Additional populations were reestablished by translocations to southeast Alaska, British Columbia, Washington, and southern California (Jameson et al. 1982). The growth of these colonies, coupled with the species' sedentary nature, created a patchy distribution of habitats with and without sea otters. The sea otter's keystone role in kelp forest ecosystems was discovered in the early 1970s through comparisons of islands in the Aleutian archipelago where the species had recovered with those where it had not (Estes and Palmisano 1974; Estes et al. 1978) and through experimental studies of competitive interactions between kelp species at Amchitka Island, where otters were numerous at the time (Dayton 1975). The results of these early studies have been substantiated by similar studies in other areas (e.g., Breen et al. 1982; Kvitek et al. 1992, 1998). Elucidating the workings of the interaction chain has relied on fortuitous "experiments" such as documenting temporal changes at unoccupied sites as they were recolonized by expanding sea otter populations (Estes and Duggins 1995) and, more recently, by documenting temporal changes in the Aleutian archipelago as sea otter numbers collapsed because of increased killer whale predation (Estes et al. 1998).

Top-Down Forcing and Trophic Cascades

Sea otter predation reduces the size and density of numerous shellfish species in soft sediment and reef systems (Wendell et al. 1986; Kvitek et al. 1992; Estes and Duggins 1995). For example, sea urchin biomass density on shallow reefs is typically 10–100 times greater at locations lacking sea otters. Because sea urchins are herbivores, sea otters, sea urchins, and kelp interact via a trophic cascade (Paine 1980; Carpenter and Kitchell 1993), thus leading to rocky reef ecosystems that are either adorned with kelps (hereafter called kelp forests) or extensively deforested (hereafter called urchin barrens), depending on the presence

or absence of sea otters. Intermediate configurations between kelp forests and urchin barrens are rarely observed, thus indicating that these states are highly unstable or transitory. Kelp forests and urchin barrens therefore are known as phase states, and the transitions between these phase states are called phase shifts (Lewontin 1969; Sutherland 1974; Done 1992; Hughes 1994).

The occurrence of kelp forests or urchin barrens is a predictable consequence of the presence or absence of sea otters in outer coast reef environments across much of the eastern North Pacific Ocean (Estes and Duggins 1995). By contrast, population and community structure varies substantially over time within these phase states, depending on invertebrate recruitment dynamics, physical disturbances, ocean temperature changes, and a host of other factors.

Complex Interactions

The sea otter's influence on reef systems extends well beyond the previously described trophic cascade (Figure 3.1). Kelp forests affect other species through increased production, the creation of three-dimensional habitat, and reductions in wave height and current velocity. These processes play out in numerous ways. For example, barnacles and mussels grow three to four times faster in otter-dominated kelp forests than in otter-free urchin barrens (Duggins et al. 1989); rock greenling (*Hexagrammos lagocephalus*, a common kelp forest fish in the Aleutian Islands) are roughly ten times more abundant in otter-dominated kelp forests than they are in otter-free urchin barrens (Reisewitz et al. 2005); the diets of glaucous winged gulls contain about 90 percent fish in otter-dominated kelp forests and about 90 percent intertidal invertebrates in otter-free urchin barrens (Irons et al. 1986); the loss of otters causes bald eagles to shift their diet from a roughly even mix of fish, marine mammals, and seabirds to one dominated by seabirds (about 80 percent by number of prey consumed; Anthony et al. 2008); sea otters compete with various benthic feeding sea ducks (eiders and scoters), thus limiting their populations (Irons, Byrd, and Estes, unpublished data); and predatory starfish are eaten by sea otters, thus reducing starfish size, abundance, and interaction strengths as predators of mussels and barnacles (Vicknair and Estes, unpublished manuscript).

Evolutionary Effects

The preceding summary outlines strong interactions between sea otters and numerous other species through direct and indirect food web linkages. How might these interactions have played out over evolutionary time scales? One intriguing possibility is that sea otters and their ancestors thwarted an evolutionary arms

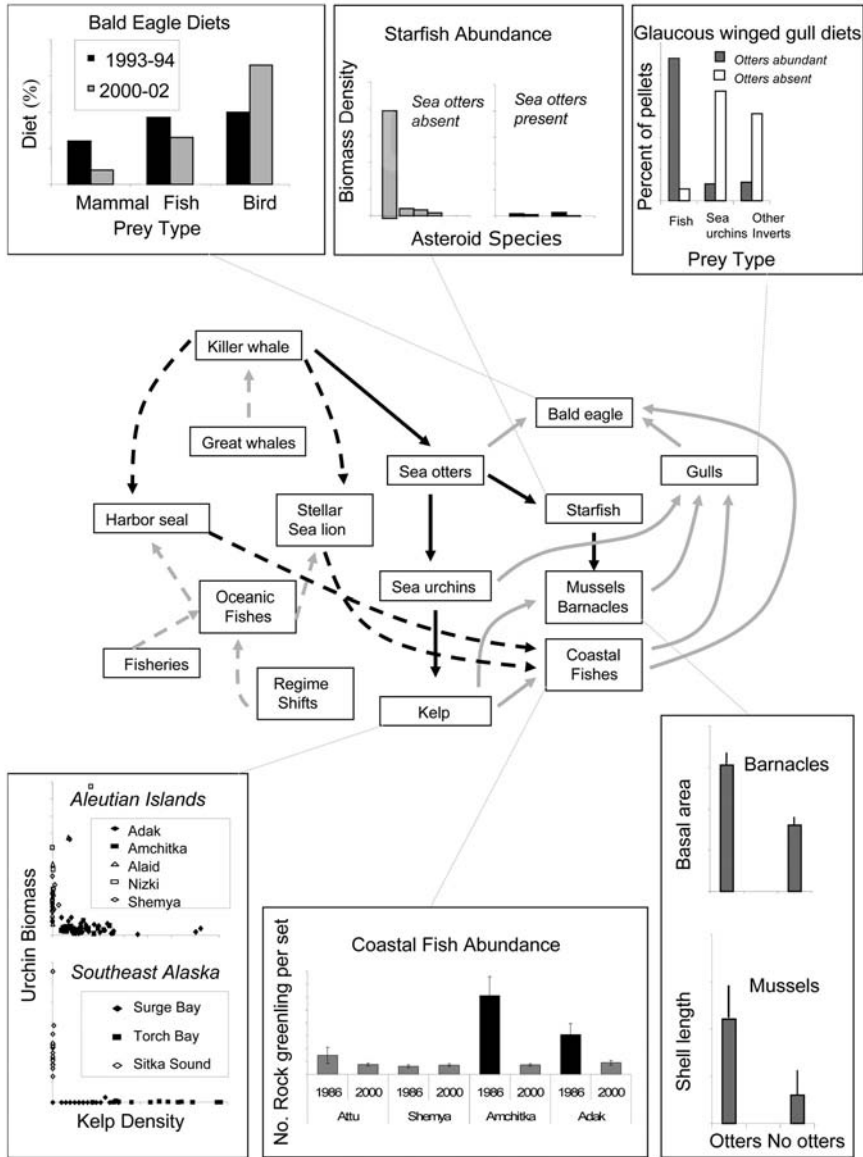


Figure 3.1. Selected food web showing key elements of North Pacific kelp forest system. Top-down forcing processes are indicated in black, bottom-up forcing processes in gray. Solid lines between species indicate linkages for which the evidence of a strong interaction is strong; dashed lines are linkages for which the evidence of a strong interaction is more speculative. The surrounding panels connected to particular species by dotted lines show the effects of sea otter predation on the indicated parameters.

race for defense and resistance between the kelps and their herbivores. Although predatory fishes and lobsters also drive trophic cascades in southern hemisphere kelp forests (Babcock et al. 1999), these do not appear to be as powerful or pervasive as the sea otter-induced trophic cascade in the North Pacific Ocean. A comparison of plant chemical defenses (tissue phlorotannin concentrations) and the resistance of herbivores to these putative defenses between western North America and Australasia (where the plants and herbivores evolved without sea otters or their ancestors) supports the arms race hypothesis. On average, phlorotannin concentrations in Australasian kelps and rockweeds are ten times higher than they are in northeast Pacific species, whereas Australasian sea urchins and gastropods are less deterred by these compounds (Steinberg et al. 1995). This coevolutionary model might explain why northern hemisphere kelp forests collapse so spectacularly in response to sea urchin population outbreaks, why the world's largest abalones (species for which growth rate is reduced by phlorotannins; Winter and Estes 1992) evolved in the North Pacific Ocean (Estes et al. 2005), and why the kelp-eating hydrodamalid sirenians (Steller sea cows and their ancestors) radiated from a pantropically distributed ancestor into the North Pacific Ocean but not elsewhere.

Ecosystem Collapse

After nearly a century of recovery from the ravages of the Pacific maritime fur trade, sea otter numbers in southwest Alaska began a precipitous decline in about 1990 (Estes et al. 1998; Doroff et al. 2003). Not surprisingly, the kelp forest ecosystem quickly followed suit by shifting to the urchin-dominated phase state (Estes et al. 2004). The sea otter collapse appears to have been caused by killer whale predation (Estes et al. 1998), and similar but somewhat earlier population declines by harbor seals and Steller sea lions may have been driven by this same process (Williams et al. 2004). The mystifying question is why killer whales changed their feeding habits. Springer et al. (2003) proposed an explanation that again involves anthropogenic disturbances to predator-prey interactions, in this case one initiated by post-World War II industrial whaling. Springer and colleagues proposed that the depletion of whale populations reduced prey availability for transient (marine mammal-eating) killer whales, thus causing these megapredators to expand their diets to include increased numbers of pinnipeds and sea otters, thereby driving their populations rapidly downward. Although this proposal remains hypothetical, it suggests an even more extensive and complex role for predation and top-down forcing in higher-latitude ocean ecosystems (Figure 3.1).

SHARKS AND EAST COAST ESTUARIES

Dating from the approximate advent of industrialized fishing by highly mechanized and efficient fleets, and in some cases much earlier (Rosenberg et al. 2005; Roberts 2007), abundances of large predatory fishes have declined dramatically throughout much of the world's oceans (Myers and Worm 2003). This influence, which includes reductions in apex predatory sharks in both open ocean and coastal seas (Musick 1993; Baum et al. 2003), is reflected in the reduction in average trophic level in fishery landings (Pauly et al. 1998). The great sharks represent a particular conservation challenge to fishery managers because their generally low fecundity and slow maturation rates deprive them of the demographic resilience to respond readily to exploitation.

Consequences to Estuarine Ecosystems of Trophic Cascades Following Losses of Apex Sharks

A test of the hypothesis that removal of apex predatory sharks by overfishing can have important indirect impacts on estuarine ecosystems was conducted by Myers et al. (2007) along the Atlantic seaboard. These authors analyzed survey data on the great sharks and the smaller elasmobranchs that formed their prey. All eleven great sharks in this guild exhibited significant population declines over the past 35 years, ranging from 87 percent in sandbar sharks to 99 percent or more for bull, dusky, and smooth hammerhead sharks (Figure 3.2). The average sizes of blacktip, bull, dusky, sandbar, and tiger sharks declined by 17–47 percent, consistent with intensified exploitation.

Over this same 35-year period, meta-analyses of survey data on the mesopredatory elasmobranch prey of these great sharks revealed that twelve of the fourteen species analyzed increased significantly in abundance (Myers et al. 2007). Among the largest of these population increases was an approximately twenty-fold increase in cownose ray (*Rhinoptera bonasus*) abundance (Figure 3.2). The eastern seaboard population of this species spends summers in the shallow waters of Raritan Bay, Delaware Bay, Chesapeake Bay, and Pamlico Sound. Myers et al. (2007) computed that the Chesapeake Bay population of cownose rays now totals more than 40 million.

Cownose rays consume shellfish of commercial and recreational value, including soft-shell clams (*Mya arenaria*), oysters (*Crassostrea virginica*), hard clams (*Mercenaria mercenaria*), and bay scallops (*Argopecten irradians*), as well as other clams not taken in fisheries, such as *Macoma balthica*. The projected consumption of bivalves by the current population of cownose rays over the 100 days of

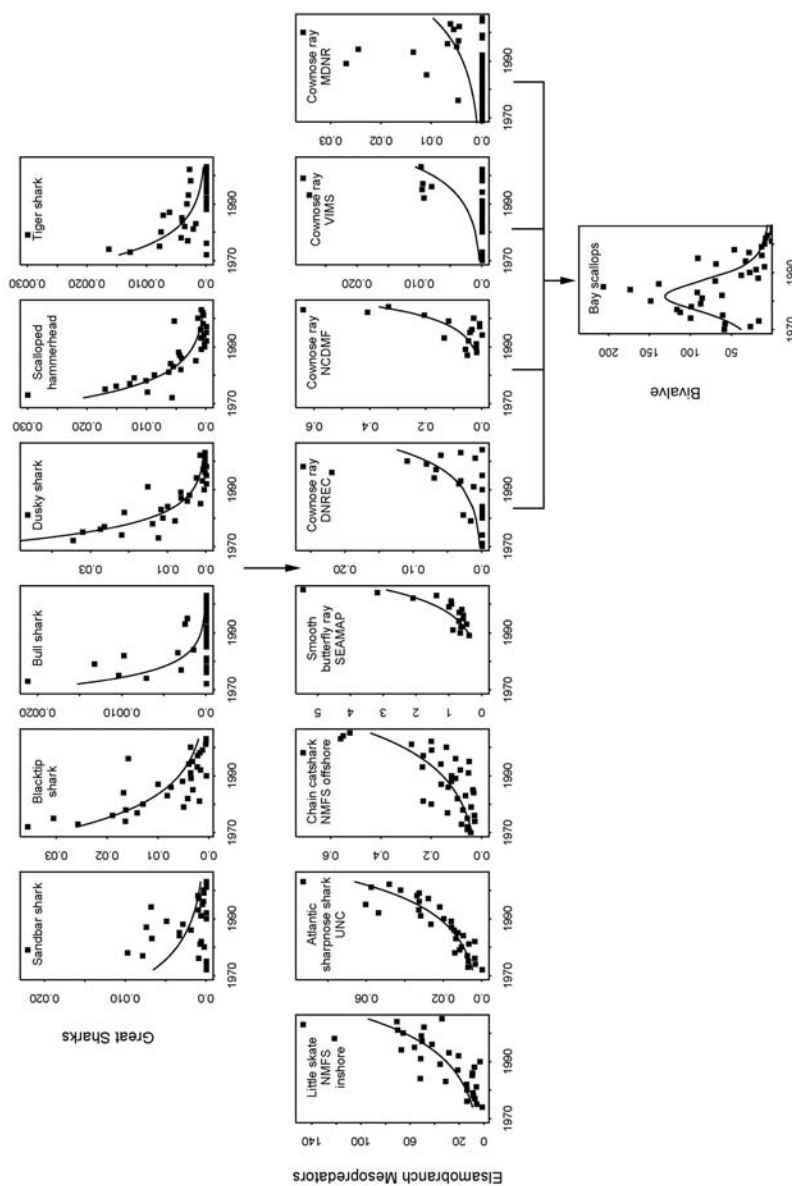


Figure 3.2. Patterns of temporal covariation among the declines of great sharks, the rise of small elasmobranchs, and the declines of bay scallops in East Coast estuaries and coastal oceans (from Myers et al. 2007). DNREC = Delaware Department of Natural Resources and Environmental Control, Division of Fish & Wildlife; MDNR = Maryland Department of Natural Resources, Fisheries Service; NCDMF = North Carolina Department of Environment and Natural Resources, Division of Marine Fisheries; NMFS = National Marine Fisheries Service; SEAMAP = Southeast Area Monitoring and Assessment Program, South Atlantic; UNC = University of North Carolina Institute of Marine Sciences longline shark monitoring survey; VIMS = Virginia Institute of Marine Science.

summer occupation of Chesapeake Bay totals 840,000 metric tons. In contrast, the total harvest of bivalves in Virginia and Maryland in 2003 was only 300 metric tons (Myers et al. 2007). Such intense demand for bivalves by an exploding population of rays suggests a potential for extending the impact of the losses of great sharks down another trophic level in a trophic cascade.

Peterson and colleagues (e.g., Peterson et al. 1989, 2001) had been studying the impacts of cownose ray feeding on bay scallops in North Carolina sounds during the late summer southward migration for nearly two decades. This work provides observational and experimental evidence that the impacts of cownose ray predation on bay scallops have grown along with ray abundances. Field sampling of bay scallops in several scalloping grounds immediately before and after the late summer migration of cownose rays showed no detectable change in scallop abundances in 1983 or in 1984, whereas repetition of the observations in 2002–2004 showed that bay scallops were virtually eliminated from all important scalloping grounds (Figure 3.2). Use of stockades constructed of closely spaced vertical poles that excluded rays demonstrated experimentally that bay scallop mortality during these recent years could be attributed to predation by the cownose rays. Thus, the loss of great sharks at the top of the food web led to a trophic cascade that indirectly eliminated a century-old shellfishery.

The further implications of the exploding cownose ray population after release from control by great sharks are profound but as yet untested. After cownose rays have consumed the visibly detectable epifaunal bivalves such as scallops and oysters, they may turn to the abundant bivalves in seagrass habitats (Orth 1975). Bivalves are much denser inside seagrass beds than on unvegetated bottom because the roots and rhizomes provide protection from typical predatory invertebrates such as crabs and whelks (Peterson 1982; Summerson and Peterson 1984). Seagrass habitat provides an important nursery for juvenile fishes and crustaceans (Heck et al. 2003), so the destruction of seagrass beds by foraging cownose rays implies a possible extension of the shark–ray cascade to additional species.

Another hypothesized effect of hyperabundant cownose rays on estuarine habitat involves their consumption of oysters. Oysters influence habitat type and quality in two important ways (Grabowski and Peterson 2007; Coen et al. 2007): by filtering enough particulates from the water column to reduce turbidity and enhance light penetration (Newell and Koch 2004) and by forming biogenic reefs that provide habitat for various other species (Lenihan et al. 2001). The explosion of cownose rays may well have contributed to the multi-decade decline in oysters and is certainly inhibiting restoration efforts (National Research Council 2004).

Generality of Shark-Topped Trophic Cascades in Estuarine and Coastal Systems

Various evidence suggests that the great shark–ray–benthic mollusk trophic cascade is geographically widespread. First, the review by Libralto et al. (2006) indicates that great sharks are often keystone predators. Second, analyses of reef systems in the Hawaiian archipelago (Parrish and Boland 2004) and the Caribbean (Bascompte et al. 2005) further indicate that apex sharks initiate strong predatory interactions with their prey species. Third, rays, skates, and smaller sharks are rarely eaten by predators other than great sharks, implying little functional redundancy beyond members of the great shark guild. Fourth, many rays are well known worldwide as consumers of bivalves and other benthic mollusks. For example, the recent explosion of longheaded eagle rays has eliminated valuable wild shellfish and cultured shellfish stocks in Ariake Sound, Japan (Yamaguchi et al. 2005), probably a consequence of overfishing of great sharks. Fifth, although Bascompte et al. (2005) show that omnivory can reduce the likelihood and strength of trophic cascades, great sharks are piscivorous and rarely if ever include clams and benthic mollusks in their diets.

COD AND LOBSTERS IN THE GULF OF MAINE

Vast numbers of cod (*Gadus morhua*) that occasionally exceeded 90 kilograms in body mass once populated the North Atlantic Ocean (Steneck 1997). Archaeological evidence suggests this large-bodied, large-mouthed trophic generalist may have been the most important apex predator in shallow coastal ecosystems of the North Atlantic (Steneck et al. 2004). Like large predatory fishes elsewhere (Myers and Worm 2003), the abundance and size of cod were reduced greatly by fishing. Intensive cod fishing occurred during prehistoric periods (4,500 to 500 years before present) but expanded with European colonization and the establishment of small coastal fishing villages in the early 1600s. Coastal fish stocks first showed signs of localized nearshore depletion as early as 2,000 years ago (Bourque et al. 2007). Shore-based fishing continued into the eighteenth and nineteenth centuries but at ever-increasing distances from home ports (O’Leary 1996; Rosenberg et al. 2005). With expanded takes, body size and abundance have declined such that no cod exceeding 90 kilograms has been reported from the North Atlantic Ocean since the late 1800s (Collette and Klein-MacPhee 2002). Beginning in the 1930s, expanding zones of depletion radiated from coastal ports as industrial-scale fisheries and associated technology escalated. The most recent and most publicized collapses occurred on

offshore banks in the United States and Canada since the 1990s (Steneck 1997).

Cod have remarkably local distributional affinities (Ames 2003). Tagging and genetic studies show that inshore stocks are demographically distinct from those offshore (Ruzzante et al. 1996), and these stocks consist of subpopulations with specific spawning, feeding, and nursery grounds. This spatial structure may explain the overall protracted and geographically asynchronous nature of the cod decline and explain why the final collapse of the fishery in the late 1980s and early 1990s was so abrupt.

Consequences of Overfishing

The depletion of cod and other predatory fishes has strongly affected the structure and function of coastal ecosystems in the northwest Atlantic Ocean. The key evidence comes from spatial contrasts detected in the 1980s between coastal areas where predatory fishes were ecologically extinct, and less intensively fished offshore seamounts. The offshore habitats supported fewer lobsters, crabs, and herbivorous sea urchins, had more abundant kelp (Vadas and Steneck 1995), and were characterized by higher predator attack rates on adults of all three invertebrate groups (Witman and Sebens 1992; Vadas and Steneck 1995; Steneck 1997).

The abundant lobster and sea urchin populations that developed in the coastal zone after the cod depletions became the primary target of local fisheries (Figure 3.3). By 1993, the value of sea urchins in Maine was second only to that of lobsters. As sea urchin populations were reduced in the fishery, so too was the rate of herbivory (Steneck 1997). In less than a decade, sea urchins became so rare that they could no longer be found over large areas of the coast (Andrew et al. 2002; Steneck et al. 2004) and as a result, kelp forests came to dominate the coastal ecosystem once again (Figure 3.3). This recent kelp forest recovery in the Gulf of Maine superficially resembles the initial phase state, although the present system is devoid of large vertebrate predators. Not surprisingly, the regulatory processes that maintain the kelp forest are now quite different from those in the earlier predator-dominated system. The combination of abundant algae and a lack of large predatory fishes has favored Jonah crabs (*Cancer borealis*), which have de facto assumed the role of apex predator. This was well illustrated when 36,000 adult urchins were relocated over a 2-year period to six widely spaced patches in an area that had been an urchin barren a decade earlier, only to be eaten by the now abundant Jonah crabs (Leland 2002).

Ecosystem release from predation played out differently elsewhere in the northwest Atlantic Ocean. Hyperabundant sea urchins in Nova Scotia proved vulnerable to a thermally triggered waterborne disease, leading to sea urchin mass mortality and kelp reforestation. Nova Scotian coastal reefs have fluctuated

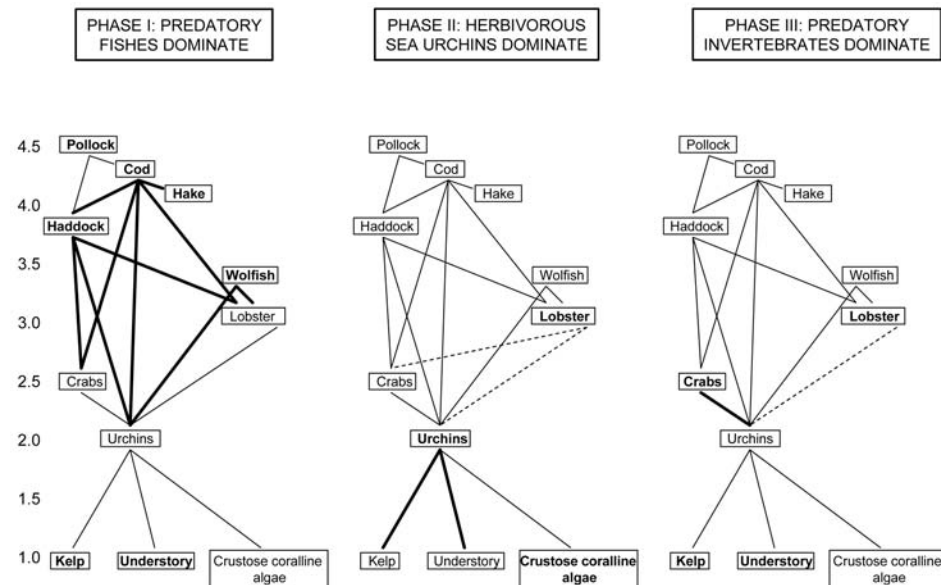


Figure 3.3. A schematic showing the progression of change in the structure and function of kelp forests in the Gulf of Maine. Bold lines and species names indicate comparatively great interaction strengths or great abundances, respectively (redrawn from Bourque et al. 2007).

between kelp forests and urchin barrens three times since 1965 (Steneck et al. 2002).

Overall, the loss of large predatory fishes from coastal zones of the western North Atlantic has caused a shift from strongly top-down to more bottom-up control. Today, larval settlement and available nursery habitat control the demography of lobsters (Steneck and Wilson 2001), crabs (Palma et al. 1999), and sea urchins (Vavrinec 2003). For all three species, nursery habitats have become the limiting resource (i.e., bottom-up) as opposed to predation on adults (top-down) that regulated abundances in the past.

Fishing as the Prime Ecosystem Driver

Although climate and physical oceanographic change have been invoked by some as an explanation for the extirpation of groundfish in the western North Atlantic, we think this unlikely. Evidence of asynchronous declines argues against such large-scale drivers. For example, the prehistoric cod decline at North Haven Island in Maine (Bourque et al. 2007) was not observed in other coastal midden sites (Lotze et al. 2006). Much better documentation of small-scale fishing operations in Maine in the 1600s reveals locally increased fishing efforts followed by local depletions that were not noted at other fishing stations

elsewhere along the coast. Similarly, the coastal decline of cod in Maine in the 1930s was not evident at Georges Bank. Asynchronous cod declines in the Gulf of St. Lawrence, Scotian Shelf, Grand Banks, and Georges Bank all show patterns of decline related to fishing effort and do not accord with hypotheses based on a climate-driven event.

The loss of apex predators corresponds with increased abundances of mesopredators such as lobsters, shrimp, smaller fish, and herbivores. Again, these changes are synchronous with predator declines but are not regionally correlated. For example, increases in lobsters along the coast of Maine correspond with the extirpation of coastal cod stocks in the 1930s. More recent offshore declines of predators correspond to more recent increases in crabs (Frank et al. 2005) and shrimp (Worm and Myers 2003) off Canada's Scotian Shelf. Greene and Pershing (2007) have suggested that that physical oceanographic changes in polar regions since 1990 may have contributed to changes in the abundance of mesopredatory fishes and crabs reported by Frank et al. (2005). Although the changes described by Frank and colleagues for the 1990s do generally correspond to the timing of the regime shift described by Green and Pershing (2007) for the Scotian Shelf, there is no evidence that similarly "unique conditions" occurred at other locations where shrimp or crabs had increased in abundance earlier.

Ecological and Economic Simplification

Fishing down food webs in the Gulf of Maine has resulted in hundreds of kilometers of coast with low biological and economic diversity. Bloodworms used for bait are worth more to Maine's economy than cod. The trophic level dysfunction (sensu Steneck et al. 2004) of both apex predators and herbivores leaves a coastal zone suited for crabs and especially lobsters, the latter attaining population densities that exceed one per square meter along much of the coast of Maine (Steneck and Wilson 2001). Although the economic value of lobsters is high, this one species accounts for more than 80 percent of the total value of Maine's fisheries (the remaining 20 percent is contributed by forty-two harvested species). Thus, if a disease such as the one that decimated Rhode Island's lobster stocks (Castro and Angell 2000) were to infect lobsters in the Gulf of Maine, the result would be a socioeconomic disaster.

OTHER CASE STUDIES

Strong direct and indirect effects from top-down forcing and trophic cascades are known for various other temperate ecosystems around the world (Table 3.1).

Table 3.1. Synopsis of case study accounts of trophic cascades in temperate latitude coastal marine ecosystems.

| Location | Species | Effects | Density or Trait | Source |
|---------------------------|--|--|-----------------------------|-------------------------------------|
| Aleutian Islands | Sea otters Sea urchins Kelp | Trophic cascade; indirect influ- ences on other species and food web processes; coevolutionary impacts | Density | Estes and Palmi- sano (1974) |
| Eastern U.S. estuaries | Great sharks Small elasmobranchs Filter-feeding bivalves | Trophic cascade | Density | Myers et al. (2007) |
| Gulf of Maine | Cod Sea urchins; lobsters Kelp | Trophic cascade | Density | Steneck (1997) |
| Southern California | Sheephead Black sea urchins | Urchin diel behavior | Trait | Nelson and Vance (1979) |
| Southern California | Sheephead Red sea urchins | Sea urchin population | Density and trait | Cowen (1983) |
| Southern California | Spiny lobsters Purple sea urchins | Urchin disease outbreaks Urchin wasting disease | Density | Lafferty (2004) |
| New Zealand | Lobsters and fishes Sea urchins Kelp | Trophic cascade | Density | Babcock et al. (1999) |
| Southeast Alaska | Sunflower stars Red and purple urchins Kelp | Trophic cascade | Trait | Duggins (1983) |
| Southern California | Planktivorous fishes Mesograzers Kelp | Trophic cascade | Density | Davenport and Anderson (2006) |
| South Africa | Lobsters Whelks Mussels Kelp | Predator-prey role reversal | Density | Barkai and McQuaid (1988) |

The most detailed and numerous accounts are from the kelp forest ecosystems of southern California and northern Mexico, which support or once supported a diverse array of large-bodied consumers, including sea otters, lobsters, and various fish species. All of these consumers and many of their prey have been depleted or eliminated by human exploitation (Dayton et al. 1998; Jackson et al. 2001). A variety of experimental, comparative, and historical evidence indicates that these systems are or once were strongly influenced by top-down control.

Nelson and Vance (1979) provided some of the earliest evidence for top-down forcing effects by sheephead, *Semicociphus pulcher*, a benthic feeding labrid fish in the warm temperate eastern North Pacific Ocean. These authors noted that sea urchins at Catalina Island retreated into cryptic habitats (substrate cracks and crevices) during the day when sheephead were active but moved onto the open reef to forage at night when sheephead were inactive. Sea urchins that were moved from cryptic to exposed habitats during the day had a high probability of being attacked and killed by sheephead. Cowen (1983) subsequently removed sheephead from an isolated reef at San Nicolas Island. Red urchin population density increased at 26 percent per year, in contrast with control sites that showed no change. More recently, Lafferty (2004) analyzed a 20-year data set that included information on predators, sea urchins, and sea urchin disease outbreaks from sixteen sites in the Channel Islands National Park that had been subjected to various fishing intensities. The protected sites contained higher predator (mostly lobster) densities, lower urchin densities, and reduced frequencies of disease outbreaks in the local sea urchin populations, presumably because disease transmission was impeded by the lower host (urchin) densities.

A trophic cascade involving predatory lobsters and fish, sea urchins, and kelp has been demonstrated in New Zealand by comparison of marine reserves with nearby unprotected areas (Babcock et al. 1999). The reserve sites contained larger and more abundant lobsters and fish, fewer urchins, and more kelp than the unprotected areas. However, the trophic cascade's influence on the distribution and abundance of kelp appears to be less in New Zealand than it is in the northeast Pacific. This may be because fishes and lobsters are less effective predators than sea otters, thus having led to a stronger coevolution of plant defenses, herbivore resistance to those defenses, and lower interaction strengths between New Zealand plants and their herbivores (Steinberg et al. 1995).

Predatory starfish also initiate trophic cascades. Kelp forests and sea urchin barrens co-occur as patchwork mosaics in parts of southeast Alaska where sea otters are absent. Duggins (1983) showed that this pattern is a trait-mediated effect (Werner and Peacor 2003) of predation by the starfish *Pycnopodia heli-anthoides*. *Pycnopodia* consumes sea urchins, but at low rates. Sea urchins none-

theless flee from nearby *Pycnopodia*, thus creating urchin-free patches into which kelps and other macroalgae can recruit. Algal detritus produced by the kelp patches probably provides adequate food for the remaining sea urchins (as shown by Harrold and Reed 1985 and Konar 2000), thus preventing them from attacking the living algae and helping to maintain the mosaic structure of the system.

The aforementioned examples all revolve around sea urchins and their well-known ability to denude reef ecosystems of various macrophytes. Temperate reefs support other potentially important herbivores, including fishes, gastropods, and various mesograzers (e.g., amphipods and mysids). Because mesograzers are consumed by a variety of microcarnivorous fishes, this predator-prey assemblage provides another potential top-down connection with autotrophs. Mesograzers are both at risk of predation and capable of damaging host plants (Hay et al. 1990). By experimentally excluding microcarnivorous fishes from small areas at Catalina Island off southern California, Davenport and Anderson (2007) demonstrated an increase in their mesograzer prey that in turn exerted a negative indirect effect on kelps. This trophic cascade may also be important in maintaining robust kelp forests. Massive mesograzer damage to giant kelp plants in southern California following an unusually large wave event that reduced the microcarnivorous fish populations supports this view (Tegner and Dayton 1991).

Our final vignette involves a predator-prey role reversal between lobsters and whelks at neighboring Marcus and Malgas islands (within 4 kilometers of each other) in South Africa (Barkai and McQuaid 1988). The shallow subtidal reefs at Malgas Island supported dense kelp forests and abundant lobsters, whereas at Marcus Island lobsters were absent, kelps were rare, extensive mussel beds covered the substrate, and whelks were comparatively abundant. The dearth of lobsters from Marcus Island was thought to have resulted from a localized anoxic event, although lobsters have been depleted elsewhere by fishing. In the absence of lobster predation, the mussel beds expanded (thus displacing kelps) and whelk numbers increased. The extraordinary feature of this example is the course of events that followed. After nine month-long caging studies conducted to ascertain that lobsters could indeed survive at Marcus Island, 1,000 lobsters were reintroduced. All of the lobsters were attacked and quickly killed (many within 15 minutes) by the now superabundant whelks, which attached themselves to and began consuming the lobsters whenever they settled to the seafloor. These various observations suggest that an alternate stable community developed with the loss of top-down forcing from lobster predation through prey population explosions and a predator-prey role reversal.

CONCLUSIONS

The depletion of apex predators is now almost ubiquitous. Nowhere is this more apparent than in the sea, where both the direct and unintended effects of whaling, sealing, and fishing have selectively stripped apex predators away from ocean food webs. And nowhere are the consequences of these losses more evident than in the higher-latitude coastal oceans, where the absence of species such as sea otters, sharks, cod, and lobsters have led to sweeping ecological changes.

Trophic cascades are the process by which apex predators commonly extend their influence to species other than their prey. Yet even trophic cascades are a gross oversimplification of the ways in which the influence of apex predators can penetrate food web structure and regulate food web dynamics. The kelp forest food web is so intimately interconnected that the loss of species such as cod and sea otters arguably extends in one way or another to all species. Similarly, the loss of great sharks may have provoked a range of nonintuitive ecosystem effects, including reduced water clarity and lowered production of benthic macrophytes, increased nutrient loading, the loss of biogenic reefs and nursery habitats for other fishes and invertebrates, and the rise or fall of various microorganisms. These highly serpentine interaction web effects of predators are not widely appreciated, in part because most ecologists haven't looked for them and in part because they are difficult to demonstrate.

One of the more intriguing indirect effects of predators is their potential link with disease. Predator reductions commonly lead to elevated prey densities. Not only might elevated prey density promote disease transmission between individuals, but prey species that historically lived at low densities would be more likely to lack resistance to parasites and pathogens for which the likelihood of infection is density dependent. These density-dependent processes could easily explain such events as the recent emergence of urchin diseases in various places around the world and abalone wasting disease in southern California. Unusually high host population densities coupled with high vulnerabilities to disease could lead in turn to the lack of ecosystem stability and extreme cyclic variation in population and community structure that has been observed recently in several kelp forest systems (Steneck et al. 2002).

If predators have strong influences on other species through direct and indirect interactions, it is not unreasonable to expect that these influences would appear as species-level characteristics when played out over evolutionary time scales. Predator-induced variation in the coevolution of plant defense and herbivore resistance may help explain why the northern and southern hemisphere

kelp forests behave so differently, implying similar as yet unstudied processes as key factors in understanding the responses of other systems to the loss of apex predators. Geerat Vermeij (1977, 1987) invoked the rise of predators as the primary drivers of wholesale faunal changes in what he called the Mesozoic Marine Revolution. Very little imagination is needed to envision the deconstruction of these powerful and diverse forces with the selective loss of marine predators 150 million years later.

The implications of top-down forcing and trophic cascades for the management and conservation of temperate latitude coastal marine ecosystems are profound. Although most of the key predators in these ecosystems have been depleted, very few are globally extinct. Restoration is thus achievable through proper conservation and management. Many large apex marine predators are highly mobile, thus implying that the spatial scales of management must be large. For instance, even if the underlying reasons that killer whales began attacking sea otter populations in southwest Alaska were understood, the restoration of sea otters and coastal ecosystems in this region probably will necessitate actions that are broadly directed at the Bering Sea and North Pacific Ocean. Finally, the cascading effects of predators influence human welfare in numerous ways. These effects include impacts on regional economies, the maintenance or loss of entire industries and associated lifestyles, recreational opportunities, and even human health. Predators in the coastal oceans truly matter, but we are just now beginning to understand why and how much.