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Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago

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Abstract Although trophic cascades—the effect of apex predators on progressively lower trophic level species through top-down forcing—have been demonstrated in diverse ecosystems, the broader potential influences of trophic cascades on other species and ecosystem processes are not well studied. We used the overexploitation, recovery and subsequent collapse of sea otter (*Enhydra lutris*) populations in the Aleutian archipelago to explore if and how the abundance and diet of kelp forest fishes are influenced by a trophic cascade linking sea otters with sea urchins and fleshy macroalgae. We measured the abundance of sea urchins (biomass density), kelp (numerical density) and fish (Catch per unit effort) at four islands in the mid-1980s (when otters were abundant at two of the islands and rare at the two others) and in 2000 (after otters had become rare at all four islands). Our fish studies focused on rock greenling (*Hexagrammos lagocephalus*), the numerically dominant species in this region. In the mid-1980s, the two islands with high-density otter populations supported dense kelp forests, relatively few urchins, and abundant rock greenling whereas the opposite pattern (abundant urchins, sparse kelp forests, and relatively few rock greenling) occurred at islands where otters were rare. In the 2000, the abundances of urchins, kelp and greenling were grossly unchanged at islands where otters were initially rare but had shifted to the characteristic pattern

of otter-free systems at islands where otters were initially abundant. Significant changes in greenling diet occurred between the mid-1980s and the 2000 although the reasons for these changes were difficult to assess because of strong island-specific effects. Whereas urchin-dominated communities supported more diverse fish assemblages than kelp-dominated communities, this was not a simple effect of the otter-induced trophic cascade because all islands supported more diverse fish assemblages in 2000 than in the mid-1980s.

Keywords Kelp · Rock greenling · Sea urchins · Trophic cascades

Introduction

The effects of apex predators on ecosystem structure and function are well known, especially in certain aquatic systems (Paine 1966; Estes et al. 2001; Soulé et al. 2003). Trophic cascades (sensu Paine 1980)—the progressive downward-reaching influences of high trophic status consumers on lower trophic level species through consumer–prey interactions—have been particularly well chronicled (Carpenter et al. 1985; Power 1990; Pace et al. 1999). Trophic cascades often have strong effects on plant communities, as predicted by the “green world” hypothesis of Hairston et al. 1960). However, trophic cascades represent only one of numerous potential pathways linking species and ecosystems (e.g., see Jones et al. 1998; Roemer et al. 2002) and thus probably do not define the full range of predator-induced effects on species or ecosystem processes. In particular, changes in biotic habitats resulting from trophic cascades may influence species utilizing these habitats. A small number of studies have chronicled indirect effects of this kind (Estes 1996; Berger et al. 2001; Levin et al. 2001), although in general they are poorly known.

Sea otters (*Enhydra lutris*) initiate a trophic cascade in southwest Alaskan kelp forest ecosystems by consuming herbivorous sea urchins (*Strongylocentrotus*

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polyacanthus), thus releasing kelps and other fleshy algae from limitation by herbivory (Estes and Palmisano 1974; Estes et al. 1978). The kelp-rich benthic communities in sea otter-dominated coastal ecosystems are strikingly different from the urchin-dominated state of these communities in systems lacking sea otters (Estes and Duggins 1995), with known or suspected indirect effects on various other species (Irons et al. 1986; Duggins et al. 1989; Estes 1996). Although there has been a large amount of work on sea otter–sea urchin–macroalgal relationships, our study focuses on the indirect effects of this trophic cascade on kelp forest fishes. Simenstad et al. (1977a) identified several interaction web pathways by which sea otters might influence the behavior and population biology of kelp forest fishes, including direct predation by sea otters, the provisioning of 3-dimensional habitat (the kelp forest), and nutritional fueling by the highly productive kelps. While these pathways could easily lead to dietary and population level effects on various fish species (Simenstad et al. 1977a; Estes 1996), such effects have not been rigorously demonstrated to date.

The recent history of sea otter populations in the Aleutian archipelago provided a unique opportunity to explore some of the potential interactions among sea otters, kelp forests, and kelp forest fishes. The near extinction of sea otters in the Pacific maritime fur trade and their subsequent recovery following the cessation of harvest serendipitously caused sea otters to be abundant at some islands and absent from others by the mid to late twentieth century (Kenyon 1969). The shallow reef ecosystems at islands supporting abundant otter populations supported lush kelp forests whereas those at islands lacking otters were largely devoid of kelps due to intense sea urchin grazing (Estes and Duggins 1995). Then, following nearly a century of range expansion and population growth, in about 1990 sea otter numbers began to decline rapidly and synchronously across the Aleutian archipelago (Doroff et al. 2003), probably because of increased killer whale (*Orcinus orca*) predation (Estes et al. 1998). This decline caused a rapid ecosystem phase shift from the kelp-dominated to the urchin-dominated state at islands where otters had previously been abundant (Estes et al. 1998, 2004). Consequently, the Aleutian archipelago was a heterogeneous mix of kelp-dominated and urchin-dominated islands prior to the sea otter decline whereas the inter-island community structure following the decline had homogenized to the urchin-dominated state. Here we report associated patterns of kelp forest fish abundance, assemblage structure, and diet at four islands in the Aleutian archipelago before and after the sea otter decline.

Methods

Our study is based on data obtained at (west to east) Attu, Shemya, Amchitka, and Adak islands at various times during the past 35 years. Sea otters have been

counted at each island during this period (Estes 1977; 1990; Doroff et al. 2003; J. A. Estes, unpublished data), and thus the recent status and trends of the otter populations are well established. Surveys of kelp, sea urchins, and fishes were conducted in the summers of 1986 and 1987 (referred to hereafter as mid-1980s), and in 1998, 1999, and 2000 (referred to hereafter as 2000). In the mid-1980s, sea otters were absent from Shemya (Estes et al. 1999; Konar 2000), were well below equilibrium density but increasing at Attu (Estes 1990), and were at or near maximum density at Amchitka and Adak (Estes 1990; Doroff et al. 2003). Benthic communities at that time were urchin-dominated at Attu and Shemya and kelp-dominated at Amchitka and Adak (Estes and Duggins 1995). Since about 1990, sea otter numbers have decreased sharply across the Aleutian archipelago so that by 2000 all four islands supported similar but low population densities, estimated to be about one order of magnitude below the environmental carrying capacity (Doroff et al. 2003). The shallow subtidal habitats at Amchitka and Adak had become urchin-dominated by 1997 (Estes et al. 1998; 2004).

These spatio-temporal patterns in the sea otter density and kelp forest community structure allowed us to test several hypotheses concerning the nature of interaction web linkages (*sensu* Menge 1995) among otters, urchins, macroalgae, and fish. Information on the kelp forest community structure at each island was obtained in the mid-1980s and again in 2000. Data on sea urchin biomass and kelp density from the mid-1980s are from Estes and Duggins (1995). Data on rock greenling (*Hexagrammos lagocephalus*) abundance, diet, and fish species diversity were obtained in the mid-1980s from each of the four islands as part of an earlier coastal marine food web study (Duggins et al. 1989; Simenstad et al. 1993). We made similar measures of the coastal fish assemblage at these same sites in 2000. All of the sites were wave exposed rocky shorelines and fish samples were all obtained from 5 to 15 m depth. The reported data were obtained during summer periods between late June and early September.

Our fish studies focused on rock greenling, the most conspicuous and abundant shallow reef fish species in the central/western Aleutian archipelago (Simenstad et al. 1977a). Rock greenling feed on a wide array of invertebrates and small fishes although they do not consume sea urchins (Simenstad 1971). We compared rock greenling abundance, prey composition, and fish species diversity among islands within the sampling periods, expecting a priori to observe greater inter-island variation in the mid-1980s (when otter densities varied among islands) than in 2000 (when otter densities were uniformly low across islands). We subsequently refer to comparisons of this kind as spatial contrasts. Additionally, we compared these same metrics at each island between sampling periods, expecting a priori to find greater changes at those islands (Adak and Amchitka) where the sea otters had declined from previously high levels and the kelp forests had collapsed than at islands

where otters had continuously been rare. At these former islands we specifically expected to find decreases in rock greenling abundance, changes in fish community composition, and changes in rock greenling dietary composition, including decreases in kelp-associated and kelp detritus-associated prey items such as mysids and amphipods and increases in benthic invertebrates such as crabs and molluscs. At islands where sea otter populations remained low between sampling periods (Shemya and Attu), we expected to find fewer changes in fish abundance, species composition, and diet. We subsequently refer to comparisons between sampling periods as temporal contrasts.

Benthic community structure

To confirm previously reported effects of sea otter predation on local sea urchins and kelp populations (Estes and Duggins 1995), we analyzed data from a benthic monitoring program that were collected in 1987 (all four islands), 1997 (Shemya), and 2000 (Attu, Amchitka and Adak). Data on epibenthic kelp and urchin densities were collected by divers using the sampling methods of Estes and Duggins (1995). In brief, varying numbers of randomly located sites (25–40) were chosen at each island and 20 randomly located 0.25 m² quadrats were placed on the sea floor at each site. Within each quadrat, the kelps were counted and identified to species and the urchins were counted and their test diameters measured. We calculated urchin biomass using a test diameter-biomass regression function from Estes et al. (1978), and calculated sea urchin standing stocks from urchin densities and size distributions at each site. Our estimates of kelp abundance excluded the surface canopy-forming *Alaria fistulosa* because rock greenling tend to utilize understory kelps for hiding, foraging, and egg laying (Simenstad 1971).

Rock greenling abundance and fish assemblage structure

To determine changes in the relative abundance of rock greenling and other similarly sized fishes, we resampled the fish assemblage in 2000 at the same sites and using the same methods as Simenstad et al. (1993) in 1986 and 1987. At each site, we set one–three trammel nets (45.8-m long by 1.8-m deep, with two outer panels of 50.8-cm and an inner panel of 5.1-cm nylon stretch mesh) in depths of 10–15 m, for approximately 2 h each. Only fish of a size range that could be caught by the net (from approximately 0.08 to 5 kg) were thus included in the analysis. Because total catch was unrelated to soak time ($r^2 = 0.002$, 48 nets set in similar habitats for 1–5 h—this study combined with data from Simenstad 1977b, 1978a), we define “effort” in catch per unit effort (CPUE) as a single set (as in Jardas et al. 1998, Johnson et al. 1999), and use the number of fish caught per set as a relative measure of fish abundance. For each set, we

recorded the species, total length and weight of each fish, and sacrificed approximately five rock greenling for stomach content analyses.

While diver-swum census data were available from 1986 (R. K. Cowen, unpublished data) and 2000 (Reisewitz, unpublished data), we chose not to use these data in our analyses. We observed extreme diver-averse behavior by greenling during the underwater censuses and therefore believe the greenlings’ ability to hide in the algal understory may bias fish counts between kelp-dominated and urchin-dominated habitats.

We characterized the net-caught fish assemblage using the Shannon-Wiener index (H') of relative diversity, a measure that incorporates both species richness and evenness. In addition to looking for inter-island and time period differences in fish diversity, we compared kelp-dominated (Amchitka 1986, and Adak 1986 and 1987) and urchin-dominated (Attu 1986 and 2000, Shemya 1986 and 2000, Amchitka 2000, and Adak 2000) environments.

Rock greenling prey composition

To determine if the diet of rock greenling varied between kelp forests and urchin barrens, we compared the stomach contents of fish collected from each of the four islands in the mid-1980s and 2000. The effects of time period and island were accounted for as covariates in this comparison. Each stomach was processed under a dissecting microscope by counting, weighing (damp weight) and identifying its contents to the lowest possible taxon. We divided prey into the following groups: epibenthic crustaceans (gammarid amphipods, caprellid amphipods, isopods, and leptostracans), benthic molluscs (chitons and other gastropods), decapods (anomuran and brachyuran crabs), polychaetes, other benthic invertebrates (hydroids, poriferans, and echinoderms), mysids, fishes, fish eggs, rocks and sand, and algae. We enumerated and weighed each taxonomic group from each stomach (method reviewed in Hypslop 1980), and calculated the percent gravimetric composition (W%) of each prey group at each island and time period. This value is assumed to represent nutritional value to the fishes (Liao et al. 2001).

Results

Benthic community structure

The magnitude of the sea otter population decline from the mid-1980s to 2000 varied considerably among the four islands because of differing population densities at the onset of the decline (Fig. 1; also see Doroff et al. 2003). The declines were most severe at Adak and Amchitka (otter populations at high levels prior to the decline), less severe at Attu (otter populations at mid-recovery level prior to the decline), and minimal at

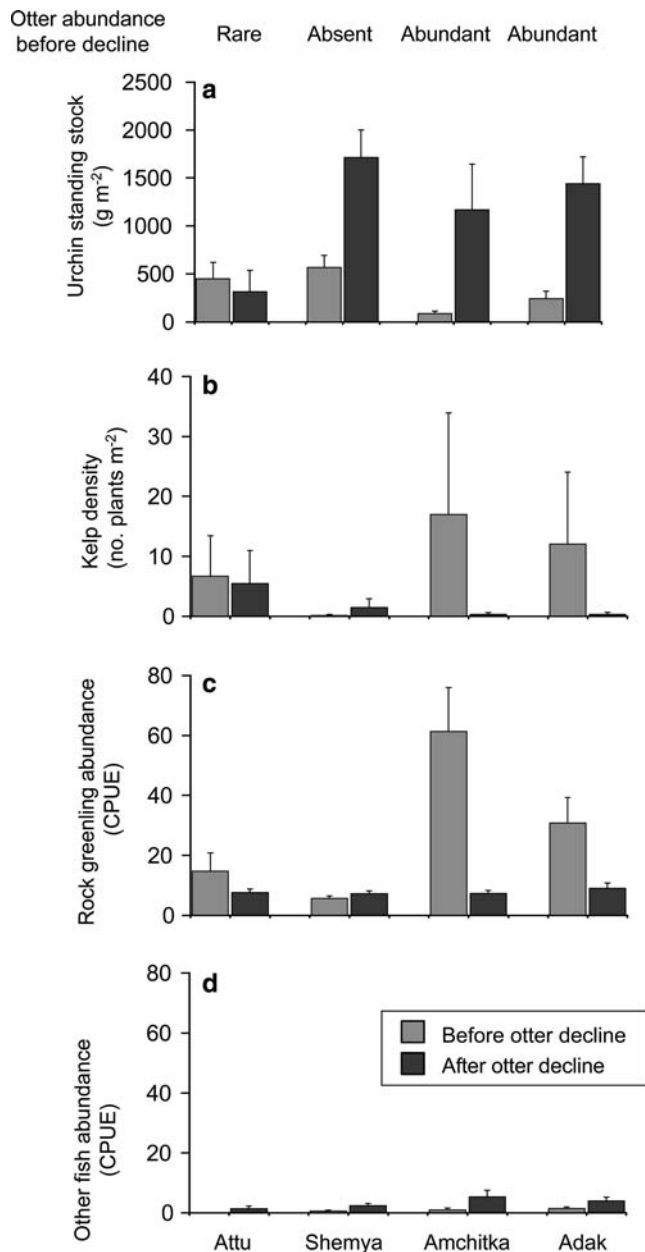


Fig. 1 Estimated **a** sea urchin standing stock, **b** understory kelp density, **c** rock greenling abundance, and **d** other fish abundance at the four islands (west to east) Attu, Shemya, Amchitka, and Adak in the mid-1980s, before (*lighter bars*) and in 2000, after (*darker bars*) sea otter population decline. Sea otters were rare throughout the archipelago by 2000. CPUE represents the number of rock greenling or other fishes caught per net. Error bars represent +1 SEM

Shemya (otter numbers low prior to the decline, due to their recent colonization of this island). Post-decline otter densities were similar at all four islands (Doroff et al. 2003).

Predictable changes in sea urchin and kelp populations were associated with these various sea otter population levels and trends. In the mid-1980s sampling period, urchin biomass density was much lower at

Amchitka and Adak than it was at Shemya and Attu (Fig. 1). By 2000, the urchin biomass density had increased substantially at Amchitka and Adak while remaining relatively unchanged at Attu and Shemya when averaged across both islands (Table 1, Fig. 1). Although urchin biomass increased significantly at Shemya, the epibenthic community was urchin-dominated at both time periods (Estes and Duggins 1995; Estes et al. 2004). Variance in the urchin biomass density among islands was significant in both time periods (mid-1980s: $F_{3,73} = 16.95$, $P < 0.001$; 2000: $F_{3,65} = 7.139$, $P < 0.001$); however, both the significant island \times time interaction effect (Table 1) and the differing F -ratios indicate a greater among-island variance in the mid-1980s (Table 2). The statistically significant among-island variance in 2000 is largely due to Attu's relatively low urchin biomass density in the latter sampling period [apparently due to a recruitment failure of sea urchins near the Attu study sites—Estes and Duggins (1995), J. A. Estes unpublished data]. When the Attu data were removed from the analysis, the variance among islands was highly significant during the mid-1980s ($F_{2,70} = 25.09$, $P < 0.001$) but insignificant during the late 1990s/2000 ($F_{2,71} = 1.757$, $P = 0.183$).

In the mid-1980s sampling period, understory kelp densities were higher at Adak and Amchitka than they were at Shemya or Attu (Fig. 1). By 2000, kelp densities were unchanged at Attu and Shemya, but had declined significantly at Amchitka and Adak where they had converged on the values for Attu and Shemya (Table 1B, Fig. 1). Among-island variance in understory kelp density, while significant in both time periods, was greater in the earlier sampling period than the latter period (Table 2).

Rock greenling abundance and fish assemblage structure

In the mid-1980s sampling period, rock greenling CPUE was higher at Adak and Amchitka than at Shemya and Attu. In 2000 rock greenling abundance had decreased significantly at Adak and Amchitka but was largely unchanged at Shemya and Attu (Fig. 2, Table 1b). The 2000 CPUE values for rock greenling were similar at all islands (Fig. 1). Among-island variance in rock greenling CPUE was greater in the earlier sampling period than the latter period (Table 2).

Fish diversity increased from the mid-1980s to 2000, as measured both by H' (Fig. 2) and by CPUE for the aggregate of species other than rock greenling (mid-1980s: 1.00 ± 0.26 fish per net; 2000: 3.69 ± 0.83 fish per net; Table 1a). However, no significant island or island by time period interaction effects could be demonstrated. The increased fish diversity between the mid-1980s and 2000 thus appears to be more strongly related to time period than habitat type. Even when kelp-dominated habitats were excluded from the analysis, fish diversity was greater in 2000 (all islands) than in the

Table 1 Tests for significance of variation among islands (Attu, Shemya, Amchitka, and Adak) and over time (1986 vs 2000) in sea urchin standing stock, understory kelp density, and kelp forest fish abundance (rock greenling and other fishes), diversity and diet (prey assemblage structure)

Metric	Independent variable	df	F-ratio	P-value
(A) Results of two-way ANOVAs				
Sea urchin standing stock (biomass × density)	Time period	1, 144	13.33	<0.001
	Island	3, 144	8.56	<0.001
	Island × time	3, 144	9.37	<0.001
Understory kelp density	Time period	1, 184	6.29	<0.001
	Island	3, 184	7.69	0.006
	Island × time	3, 184	5.12	<0.002
CPUE (rock greenling)	Time period	1, 40	440.29	<0.001
	Island	3, 40	14.03	<0.001
	Island × time	3, 40	13.74	<0.001
CPUE (other fish species)	Time period	1, 40	4.97	0.032
	Island	3, 40	0.93	NS
	Island × time	3, 40	0.29	NS
Fish diversity (H')	Time period	1, 40	12.08	0.001
	Island	3, 40	1.05	NS
	Island × time	3, 40	0.04	NS
Prey assemblage structure ^a	Time period	10, 211	4.20	<0.001
	Island	20, 424	3.66	<0.001
	Island × time	20, 424	2.80	<0.001

(B) Bonferonni-corrected post-hoc tests for significant changes in each metric at each island between 1986 and 2000. By 2000, sea otter populations were rare at all four islands

Island	Attu	Shemya	Amchitka	Adak
Sea otter abundance–1986	Rare	Absent	Abundant	Abundant
Metric				
Sea urchin biomass	0.052	0.044	0.006	<0.001
Understory kelp density	NS	NS	0.027	<0.001
CPUE (rock greenling)	NS	NS	<0.001	<0.001
CPUE (other fish species)	NS	NS	NS	NS
Fish diversity (H')	NS	NS	NS	NS
Prey assemblage structure ^b		0.025	<0.001	<0.001

^aPrey assemblage structure was analyzed using a MANOVA. The results presented are F-ratios and P-values of a Pillai Trace statistic

^bPillai trace probabilities for each island

Table 2 Comparisons of among-island variation in sea urchin biomass and density, kelp density, and kelp forest fish abundance (rock greenling and other fish species) and fish diversity between mid-1980s and 2000

Metric	Mid-1980s sampling period			2000 sampling period		
	df	F-ratio	P-value	df	F-ratio	P-value
Urchin biomass density (g 0.25 m ⁻²)	3,73	16.95	<0.001	3,65	7.139	<0.001
Kelp density (no. 0.25 m ⁻²)	3,109	6.970	<0.001	3,75	3.912	0.012
Rock greenling (CPUE)	3,15	9.489	0.001	3,25	0.351	0.789
Other fish species (CPUE)	3,15	2.010	0.156	3,25	0.996	0.411
Fish diversity (H')	3,15	0.888	0.470	3,25	0.448	0.721

Sea otters were abundant at some islands and rare or absent at others in the mid-1980s and rare at all islands in 2000. F-statistics from one-way ANOVAs with islands as the independent variable

mid-1980s (Attu and Shemya islands only; $t_{34}=2.02$, $P=0.05$). Finally, sea urchin-dominated communities in both time periods (Attu and Shemya in the mid-1980s, all islands in 2000) supported significantly more diverse fish assemblages than did kelp-dominated communities (Adak and Amchitka in the mid-1980s; pooled variance t-test: $t_{43}=2.38$, $P=0.02$), but fish diversity did not differ between Adak/Amchitka and Attu/Shemya in the mid-1980s ($t_{17}=0.07$, $P=0.94$; Fig. 2). Fish species richness

did not change significantly between sample periods or among islands (two-way ANOVA: $F_{\text{time}}=2.00$, $P=0.20$; $F_{\text{islands}}=1.65$, $P=0.17$).

Rock Greenling Prey Composition

The major prey of rock greenling included gammarid amphipods, chitons, polychaetes, and anomuran and

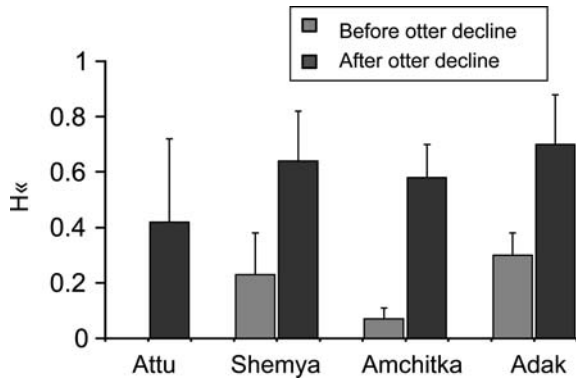


Fig. 2 Shannon-Wiener fish diversity indices (H') at Attu, Shemya, Amchitka, and Adak islands *before* (during the mid 1980s) and *after* the sea otter population decline (in 2000). Error bars represent $+1$ SEM. Note that rock greenling was the only fish species captured from the Attu site in the mid-1980s (Fig. 1), thus the diversity index of zero

brachyuran crabs. Stomach contents of secondary importance included caprellid amphipods, fish, fish eggs, shrimps, mysids, isopods, gastropods, hydroids, sponges, echinoderms (mostly ophiuroids), algae, and small rocks or sand.

A variety of dietary changes between time periods are indicated by the stomach content data, including a decline in the importance of epibenthic crustaceans, mysids and benthic molluscs, and an increase in the importance of crabs and shrimps, other benthic invertebrates (hydroids, sponges and echinoderms), fish eggs, and rocks/sand (Table 3). The greatest dietary change occurred at Attu and the smallest occurred at Shemya. The gravimetric composition of stomach contents varied significantly between time periods, among islands and for the island by time period interactions (MANOVA: Table 1a).

Despite these overall dietary changes between time periods, certain aspects of both diet and dietary change were unique to each island (Table 3). At Shemya, benthic molluscs and epibenthic crustaceans decreased while polychaetes, rocks and sand increased. At Amchitka, mysids and epibenthic crustaceans decreased while benthic molluscs, other benthic invertebrates, and algae

increased. At Adak, benthic molluscs decreased while fish eggs and other benthic invertebrates increased. At Attu, fishes increased by 47% and epibenthic crustaceans decreased by 68%. This latter increase in fishes and decrease in epibenthic crustaceans was so great compared to other islands that we excluded Attu in the statistical analyses.

Discussion

Because trophic cascades typically alter the structure of plant communities, strong effects of this biogenic habitat change on other species and ecosystem processes are expected and indeed have been shown in prior studies. For example, Berger et al. (2001) demonstrated that a trophic cascade linking grizzly bears (*Ursus arctos*) and gray wolves (*Canis lupus*) to moose (*Alces alces*) and riparian vegetation influenced species richness and nesting density of neo-tropical migrant birds in riparian habitats. Similarly, Irons et al. (1986) found that the sea otter–urchin–kelp trophic cascade influenced diet and the foraging behavior of Glaucous winged gulls (*Larus glaucescens*) in coastal marine ecosystems. However, relatively few studies have explored the influences of trophic cascades on associated species, in part because such effects are difficult to demonstrate and in part because ecologists seem to have paid little attention to them.

The rapid decline of sea otters across the Aleutian archipelago during the 1990s provided a fortuitous opportunity to study the indirect effects of trophic cascades on other species. Our assessments were based on comparisons of the abundance, species composition, and diet of kelp forest fishes before and after otter populations declined. The reduced rock greenling CPUE at Amchitka and Adak islands together with the lack of change in the rock greenling CPUE at Attu and Shemya islands indicate that the abundance of this species is linked to the otter–urchin–kelp trophic cascade. The greater among-island variance in rock greenling abundance when sea otters were abundant at some islands and rare or absent at others provides added evidence for an interaction web linkage between

Table 3 Changes in gravimetric composition (%W) of each taxonomic group in stomach contents of rock greenling caught at Attu, Shemya, Amchitka, and Adak islands between the mid-1980s and 2000

	All Islands (excluding Attu)	Attu	Shemya	Amchitka	Adak
Epibenthic crustaceans	-10	-68	-16	-11	+1
Benthic molluscs	-5	+4	-14	+11	-24
Decapods	+6	+14	+10	-1	+7
Polychaetes	+2	-5	+10	+5	-6
Other benthic invertebrates	+6	0	+3	+7	+8
Mysids	-8	0	0	-15	-3
Fishes	-1	+47	-4	-1	+2
Fish eggs	+7	+1	-1	+1	+15
Rocks and sand	+3	+1	+10	+1	+2
Algae	+3	+6	+2	+4	+2

kelp forest fishes and the otter–urchin–kelp trophic cascade. Related patterns of change in the abundance of sea otters, sea urchins, and kelp support this interpretation, as do earlier reports that rock greenling avoid kelp-free sites and utilize kelp for feeding, shelter and egg laying (Simenstad 1971; Simenstad et al. 1977a, b; Gomelyuk 2000). Our interpretations also are in keeping with reports of strong associations between reef fish and kelp abundance from studies done elsewhere (Bodkin 1988; Laur et al. 1988; Holbrook et al. 1990).

While the abundance of rock greenling appears related to the presence or absence of kelps, further studies would be required to determine the mechanisms by which this relationship occurs. At least three potential mechanisms are possible, perhaps in additive or interactive ways—the provisioning of 3-dimensional habitat; the provisioning of food through secondary production; and changes to the physical environment through altered flow and light penetration. However, since little is known about the interrelationships between kelp forests and coastal fishes in the Aleutian Islands, we focused on general patterns rather than mechanisms in this study.

Decadal-scale dietary changes reported for sea otters at the Amchitka Island provide further evidence for interaction web linkages between fishes and the sea otter–urchin–kelp trophic cascade (Watt et al. 2000). In the 1960s and 1970s, kelp forest fishes were a chief prey item of sea otters at Amchitka Island (Estes et al. 1982), but by the 1990s, as the shallow subtidal ecosystem surrounding Amchitka became more urchin-dominated, greenling and other kelp-associated fishes were less common in the sea otter’s diet (Watt et al. 2000). Watt et al. (2000) believed that this reduced consumption of greenling by sea otters was caused by the increased availability of sea urchins and an episodic inshore spawning migration of smooth lumpfishes (*Aptocyclus ventricosus*), a highly nutritious and easily captured oceanic fish. Our findings suggest that rock greenling population declines resulting from the otter declines and the associated kelp forest collapse also contributed to the reduced numbers of kelp forest fishes in the otters’ diet.

Although the link between rock greenling abundance and the sea otter-induced trophic cascade is reasonably clear, the potential influences of these interactions on other kelp forest fish species are less clear. We expected to find particularly strong changes in reef fish assemblage structure at Adak and Amchitka islands as they transitioned between kelp-dominated and deforested habitats from the mid-1980s to 2000. However, measures of diversity increased at all islands over this period, including those at which otter numbers and the associated rocky reef ecosystem remained largely unchanged. Elevated numbers of dusky rockfish account for some of the overall change although this cannot be the sole explanation because the pattern of increased fish diversity remained when rockfish were removed from the analysis.

A number of factors may underlie the temporal increase in fish species diversity. Some fish species apparently prefer urchin-dominated over kelp-dominated habitats. The fact that many adult fishes are more weakly tied to kelp forests than juvenile conspecifics may add to the more diverse fish assemblages in urchin-dominated habitats (Choat and Ayling 1987; Carr 1989). However, since fish diversity did not differ between kelp and urchin-dominated habitats in the mid-1980s, the increase in diversity in 2000 appears to have resulted from some wider ranging process that occurred across all islands. A decline in the other species of mammalian piscivores may have contributed the increase. Like sea otters, harbor seal (*Phoca vitulina*) and Steller sea lion (*Eumetopias jubata*) populations have declined substantially in the Aleutian Islands and western Gulf of Alaska over the past several decades (National Research Council 2003). Because of their large size, high metabolic rates, and previously great abundances, these mammalian piscivores have large potential impacts on their prey communities (Williams et al. 2004). Further support for the possibility that changes in the nearshore fish assemblage were influenced by the pinniped declines is provided by the observation that many kelp forest fishes in the Aleutian Islands are both diver-averse and known prey of sea otters (Simenstad and Nakatani 1977b; Watt et al. 2000), Steller sea lions (Merrick et al. 1997), and harbor seals (J. A. Estes, unpublished observations). Finally, oceanographic changes may have occurred over the period of our study (Hare and Mantua 2000; National Research Council 2003), thus perhaps contributing in some way to the large-scale patterns of reef fish diversity.

The patterns of variation in rock greenling diet in space and time are complex, thus belying our a priori hypothesis or any simple explanation of dietary change for that matter. Potential contributors to the observed dietary variation include kelp forest phase shifts, localized changes in greenling feeding behavior, and release of benthic macroinvertebrates from predation by sea otters. The overall decline in epibenthic crustaceans and mysids in the greenlings’ diets across islands may have occurred because of the wide-ranging reduction in kelp detritus. Likewise, the increased consumption of decapods may have resulted from an increase in crab recruitment after adult crabs were released from sea otter predation pressure. Changes in greenling feeding behavior following habitat shifts from kelp forests to sea urchin barrens may explain increases in other benthic invertebrates and polychaetes, as greenling became more dependent on benthic foraging in urchin-dominated environments. However, we have no explanation for other changes, such as the dramatic increase in fish consumption over time by greenling at Attu.

Our findings point to two important, but largely unstudied, aspects of food web dynamics. One is the diversity of processes by which apex predators can influence other species and ecosystem processes. To date, most thinking about predator effects has focused

on top-down forcing and trophic cascades. Our findings indicate that these interactions, while strong and highly significant, can influence other species through long and complex interaction web pathways. For instance, if killer whale predation was largely responsible for the sea otter declines in southwest Alaska, then our data suggest serpentine linkages across at least six species or species groups (killer whales, to sea otters, to sea urchins, to macroalgae, to rock greenling, to rock greenling prey). Our findings further demonstrate or imply that these food web linkages occur across large spatial and temporal scales. Although many uncertainties remain about the ultimate reasons for the sea otter decline, it now seems almost certain that the cause is rooted in the open ocean, not in the coastal zone. The key events likely have a long and complex history. Appreciating and understanding these spatial and temporal dimensions to interaction web dynamics are of considerable relevance to conservation and management, especially in systems where top-down forcing processes have important influences on community structure and apex predator populations are declining because of exploitation, habitat loss or other long-term ecosystem changes.

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