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Inter-decadal patterns of population and dietary change in sea otters at Amchitka Island, Alaska

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Abstract After having been hunted to near-extinction in the Pacific maritime fur trade, the sea otter population at Amchitka Island, Alaska increased from very low numbers in the early 1900s to near equilibrium density by the 1940s. The population persisted at or near equilibrium through the 1980s, but declined sharply in the 1990s in apparent response to increased killer whale predation. Sea otter diet and foraging behavior were studied at Amchitka from August 1992 to March 1994 and the data compared with similar information obtained during several earlier periods. In contrast with dietary patterns in the 1960s and 1970s, when the sea otter population was at or near equilibrium density and kelp-forest fishes were the dietary mainstay, these fishes were rarely eaten in the 1990s. Benthic invertebrates, particularly sea urchins, dominated the otter's diet from early summer to midwinter, then decreased in importance during late winter and spring when numerous Pacific smooth lumpsuckers (a large and easily captured oceanic fish) were eaten. The occurrence of spawning lumpsuckers in coastal waters apparently is episodic on a scale of years to decades. The otters' recent dietary shift away from kelp-forest fishes is probably a response to the increased availability of lumpsuckers and sea urchins (both high-preference prey). Additionally, increased urchin densities have reduced kelp beds, thus further reducing the availability of kelp-forest fishes. Our findings suggest that dietary patterns reflect changes in population status and show how an ecosystem normally under top-down control and limited by coastal zone processes can be significantly perturbed by exogenous events.

Key words Kelp forest · Lumpsucker · Sea urchin · Subsidized food web

Introduction

Behavioral shifts by consumers often accompany changes in population status or resource availability (Krebs 1978). Mammalian carnivores are particularly interesting in this context because many species are food-limited, or were until recently (Estes 1996a). However, characterizing such behavioral variation for the carnivores is difficult because of their typically secretive nature and the depressed or uncertain status of nearly all populations.

Study of the sea otter (*Enhydra lutris*) is not constrained by these difficulties because their foraging behavior is easily observed and extant populations vary greatly in density and status (Rotterman and Simon-Jackson 1988). Visual measures of diet are possible because sea otters dive to hunt and captured prey are consumed on the surface where they can be identified. Variation in density and population status exists because otters were hunted to near-extinction in the Pacific maritime fur trade. Take was prohibited in 1911, at which time a dozen known colonies survived (Kenyon 1969). Because of the happenstance locations of these remnant colonies and the sea otter's limited capacity for dispersal, subsequent recovery created a fragmented distribution across a once continuously occupied range. Extreme variation in population status developed among islands of the Aleutian archipelago because deep ocean passes further inhibited dispersal, which caused established populations to become abundant and unoccupied islands to remain so.

This "historical accident" has been used as a natural experiment to evaluate the role of sea otter predation in kelp-forest ecosystems, providing one of the better-known examples of both a "keystone species" (Power et

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al. 1996) and an ecosystem under top-down control (Hunter and Price 1992). Contrasts in space and time of islands with and without sea otters also have demonstrated that otters, by consuming grazing invertebrates (principally sea urchins, *Strongylocentrotus* spp.), prevent kelp deforestation (Estes and Palmisano 1974; Duggins 1980; Breen et al. 1982; Estes and Duggins 1995). This "trophic cascade" (*sensu* Carpenter and Kitchell 1993) creates a host of indirect influences on coastal food webs (Duggins et al. 1989; Estes 1996b). Substantial differences in sea otter diet and foraging behavior also exist among recently-established (low-density) and long-established (high-density) populations (Estes et al. 1981, 1982).

Refined tagging and radio-tracking techniques have been developed since these early studies of sea otter diet and foraging behavior were conducted. We set out in the early 1990s to contrast demography, social behavior, and foraging ecology between equilibrium and growing sea otter populations. Amchitka Island, one of our study sites, had supported a near-equilibrium population for decades and was the location of several earlier studies dating from the 1930s. We resumed fieldwork at Amchitka in 1992 believing that the population was stable at or near equilibrium density, food was the limiting resource, and the coastal ecosystem was closed to significant influences from either the land or the open sea. Two unanticipated events occurred to contradict these beliefs and assumptions. First, the sea otter's diet was subsidized by a massive inshore spawning migration of oceanic fishes, thus creating strong seasonal variation in food availability and releasing the population from food resource limitation. Second, sea otter populations across the Aleutian archipelago began declining abruptly in about 1990 in apparent response to increased killer whale predation (Estes et al. 1998). We did not recognize these declines until after the fieldwork reported here had been completed.

Here we present dietary information obtained during a study of sea otters at Amchitka Island conducted between July 1992 and March 1994. Although our original goal was annulled by the above-described changes, the sea otter's response to these events proved interesting because of the long time-series of information on diet and population size at Amchitka Island. The findings illustrate the following three points of broader interest: measures of prey availability and foraging behavior may provide a more immediate indication of population change than measures of population abundance; diverse linkages across ecosystems over large temporal and spatial scales are important to ecosystem function; and long-term data often are necessary to thoroughly understand these patterns and processes.

Materials and methods

Study area

Amchitka Island (51.5°N, 179°E) is in the Rat Island group of the western Aleutian archipelago (Fig. 1). A remnant sea otter colony containing roughly 100 animals survived the fur trade at Amchitka (Kenyon 1969). The earliest population survey of sea otters at Amchitka, conducted in 1936, provided an estimate of 3,100 animals. By 1943 the population had grown to an estimated 4,550 otters, but 6 years later it had declined to about 1,500. Food limitation and starvation caused the late-1940s decline (Raush 1953; Kenyon 1969). Subsequent surveys indicated that Amchitka supported more than 5,000 sea otters from the late 1960s through the late 1980s (Estes 1990). Numerous dead or moribund otters were found on Amchitka's beaches in late winter/early spring in studies conducted during this time period, most of which died from starvation (Kenyon 1969; Estes 1977).

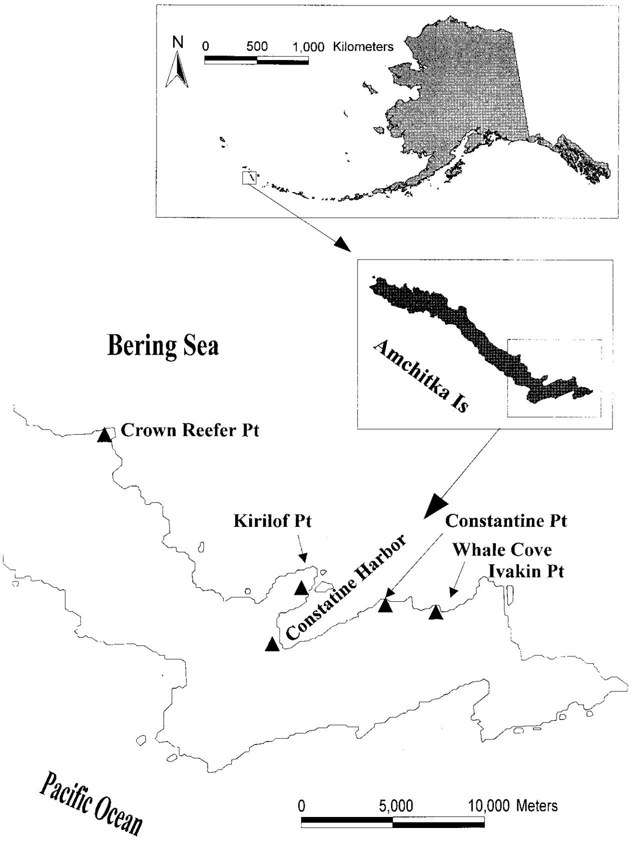

Fig. 1 The study area at Amchitka Island, Alaska. *Filled triangles* show positions of observation blinds

Work reported here (historical and recent) was conducted on the Bering Sea (north) side of Amchitka Island, mainly between Crown Reefer and Ivakin points (Fig. 1). Most of our recent observations were made from the five hides shown in Fig. 1. Sea otters segregate sexually; some adult males occupy territories within areas used by females while non-territorial males, including juveniles, occupy distinct male areas (Kenyon 1969). A male area has persisted at Crown Reefer Point for at least several decades (Kenyon 1969; Schneider 1978; authors' personal observations). The other four observation areas were utilized principally by females and territorial males.

Study animals

Using tangle nets and diver-held traps, 96 sea otters were captured in July 1992 and 18 in June 1993. The animals were weighed and those over 9 kg were immobilized with intramuscular injections of fentanyl and valium (Williams et al. 1981). An upper premolar was extracted for age estimation (Garshelis 1984). Radio transmitters (Advanced Telemetry Systems, Isanti, Minn., USA) were implanted intraperitoneally (Williams and Siniff 1983) in 80 otters (26 independent males, 43 independent females and 11 dependent pups). These otters, plus 21 near-term females, were marked with colored tags on both hind flippers for visual identification.

Feeding observations

Information on dietary variation by age and sex is not available from early studies of sea otters at Amchitka Island because these characters are difficult to determine in the field and none of the otters were tagged. Although these data are not available for comparison, we report age- and sex-related dietary patterns from recent work because they help explain the demographic effects of altered prey availability. Feeding observations were made from August 1992 to March 1994. Questar field telescopes (50 or 80× magnification) and spotting scopes (15–50× magnification) were used for tag and prey identification. Tagged animals were preferentially selected although some untagged individuals also were observed. When possible, untagged otters were identified as male or female. It was also possible, retrospectively, to categorize the tagged adult males as territorial or non-territorial animals.

Dive times and surface intervals between dives were recorded during foraging observations, prey were identified to the lowest possible taxon and foraging locations were marked on maps (U.S. Army Map Service, series Q801, 1948, 1949 and 1968).

Otters usually captured more than one prey item per successful dive (Table 1). As individual prey items were often small and handled rapidly, it was not always possible to count the number caught. Therefore, many of our analyses are based on the proportion of dives in which a particular prey type was captured. Prey mass per capture was estimated from the number and species of prey captured per dive multiplied by the average mass of a single prey item. Prey item masses were calculated from published data and our own collections. None of the unidentified prey were fish. Thus, the mass of unidentified prey was estimated as the mean for identified invertebrate prey, weighted by percent occurrence of each prey type in the otter's diet.

Dives were categorized as successful if one or more prey items were brought to the surface, and unsuccessful if none were. The sequence of observations of a continuously foraging otter is referred to as a foraging bout.

Table 1 Mean (±1 SD) number of each prey type caught per dive in which that particular prey type was captured

Prey type	Number per capture	
	Mean	Range
Invertebrates		
Rock jingle	1.7±0.9	1–6
Mussel	6.8±5.2	1–26
Unidentified bivalve	3.0±2.7	1–23
Chiton	1.4±0.9	1–5
Crab	1.2±0.5	1–4
Sea cucumber	1.5±0.8	1–3
Starfish	1.1±0.2	1–2
Sea urchin	6.1±4.3	1–45
Worms	1.1±0.3	1–3
Algal holdfast	1.0±0.0	1
Fish		
Lumpsucker	1.0±0.2	1–3
Greenling	1.0±0.1	1–2
Gunnel	1.0±0.2	1–2
Sand lance	3.0±2.9	1–12

Scat analysis

Many prey were too small to identify by direct observation. Therefore, we supplemented the dietary analysis with information from 374 scats collected at Crown Reefer Point, 141 at Kiriloff Islands and 70 at Constantine Point/Whale Cove (Fig. 1). Scats were broken apart in the field, the occurrence of all prey types noted, and the contribution of each prey type to total volume estimated. Relative importance of the various prey types was determined by both frequency of occurrence and percent volume.

Urchin sampling

Sea urchins are one of the sea otter's most important prey as well as essential players in the otter-urchin-kelp trophic cascade. To document patterns in abundance and size structure of sea urchins at Amchitka through time, samples were obtained at 7 and 15 m depths from 30 randomly selected sites between Crown Reefer Point and Whale Cove. Ten 0.25-m^2 quadrats were sampled at each site/depth. Quadrats were placed on the sea floor by divers making a random number of kicks between placements. All urchins within a quadrat were collected and their test diameters measured. Samples were obtained at various times from the late 1960s to1999. All 30 sites were sampled in 1987 and 1999. Arbitrarily chosen subsets of these sites were sampled in other years.

Mortality

Kenyon (1969) reported that most sea otter mortality at Amchitka Island during the 1950s and 1960s occurred in late winter/early spring. In order to obtain comparative data for the 1990s we conducted monthly beach surveys of otter carcasses. Approximately 50 km of coastline (roughly 25% of Amchitka's perimeter) was surveyed each month. Carcasses were also found opportunistically during the course of other field work. All carcasses were counted, sex was noted, and skulls and teeth were collected for aging. Scattered bones or detached skulls were excluded from the analysis as the times of death of these partial skeletons were unknown.

Data analysis

Many of the foraging data are presented according to time of year, based on variation in mean water and air temperature at Amchitka (Armstrong 1977; O'Clair 1977) as follows: January-June (winter/spring), July-December (summer/autumn).

Between group differences (sex/status of otters, season) were tested using analysis of variance (ANOVA). Where necessary, the data were log-transformed to eliminate heterogeneity of variances between groups. Percentage values were arcsine square-root transformed prior to analysis. In multi-factor tests with differing degrees of freedom among factors, Bonferroni critical values were used to avoid inflated type 1 errors (Zar 1984; SYSTAT 1992). Tukey multiple range tests were used to identify significant differences in paired comparisons.

Results

Diet

Overall composition

A total of 11,068 successful dives were observed during our recent study. Overall, sea urchins were caught on 56.2% of these dives. Other identifiable invertebrates were taken on 10.4% of the successful dives and comprised bivalve molluscs (*Pododesmus macroschisma*, rock jingles; *Musculus discors* and *Mytilus trossulus*, mussels; and *Macoma* spp., clams), sea stars, sea cucumbers, decapod crustaceans, gastropod molluscs, *Octopus* sp. and annelids. Fish were caught on 7.8% of successful dives (although contribution by mass was much greater). The most commonly eaten fish species was the Pacific smooth lumpsucker *Aptocyclus ventricosus* (572/917 dives during which fish were captured), followed by sand lance *Ammodytes hexapterus* (on 94 dives) and rock greenling *Hexagrammos lagocephalus* (on 74 dives). Unidentified prey (generally too small to identify) were taken on 33.5% of dives. Our impression, based on handling behavior by the otters, was that most of these items were small sea urchins.

Seasonality

Smooth lumpsuckers were consumed from January until June, with a peak in April and May (Fig. 2). Because of their relatively large size, these fish made up 62% of the estimated dietary biomass in winter/spring. Lumpsuckers were not consumed in summer/autumn. Fishes other than lumpsuckers also were eaten most frequently in spring, the exception being sand lance which were eaten only in autumn. Sea urchins were the most commonly eaten prey in summer/autumn, making up 54% of observed prey captures. Urchins also were commonly eaten in winter/spring although lumpsuckers, by virtue of their large size, contributed more to dietary biomass during this period.

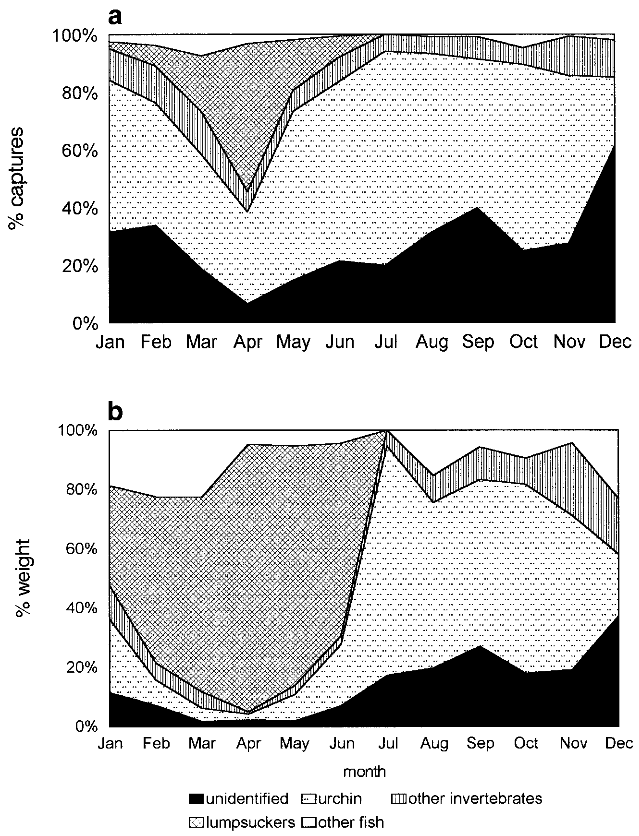

Fig. 2a,b Temporal variation in occurrence of major prey species in sea otter diet over the 20 months study. Data are **a** percent frequency of occurrence by number of prey captures and **b** percent biomass in diet

Table 2 Occurrence of main prey categories by season and otter status (mean percent of successful dives ±1 SEM)

	Urchin	Other invertebrate	Lumpsucker	Other fish	Unknown	Bouts (*n*)
January–March						
Territorial male	34.0±6.1	3.2±3.3	31.5±6.7	18.8±4.6	17.4±5.6	36
Non-territorial male	9.6±4.7	5.5±2.5	57.6±5.1	14.4±3.5	14.7±4.3	62
Female	36.3±2.2	8.4±1.2	20.9±2.4	9.0±1.6	28.5±2.0	293
April–June						
Territorial male	20.1±9.3	2.0±3.5	60.9±9.6	3.2±1.7	15.1±6.5	19
Non-territorial male	15.0±8.4	3.8±3.2	36.1±8.7	1.4±1.5	45.7±5.9	23
Female	46.1±3.7	6.6±1.4	35.3±3.8	1.7±0.7	11.3±2.6	122
July–September						
Territorial male	78.8±7.4	2.9±1.3	0.0	1.5±1.1	22.6±7.0	18
Non-territorial male	54.6±11.8	14.3±4.7	0.0	0.0	41.5±11.6	7
Female	70.5±3.4	6.9±1.4	0.0	4±2.3	28.4±3.4	83
October–December						
Territorial male	82.5±10.3	0.5±5.1	0.0	0.2±4.1	18.0±8.7	14
Non-territorial male	48.8±15.7	6.3±7.7	0.0	4.0±6.3	45.3±13.2	6
Female	50.2±3.2	10.9±1.6	0.0	4.8±1.3	39.1±2.7	145

2-Way ANOVA (% of prey by status and season)

	Otter status	Season	Otter status×season
Urchins	$F_{2,816}=4.4$, $P=0.011$	$F_{3,816}=23.7$, $P<0.001$	$F_{6,816}=3.7$, $P<0.01$
Other invertebrates	$F_{2,816}=5.4$, $P=0.005$	$F_{3,816}=1.26$, $P=0.287$	$F_{6,816}=0.50$, $P=0.795$
Lumpsuckers	$F_{2,816}=3.4$, $P<0.03$	$F_{3,816}=29.9$, $P<0.001$	$F_{6,816}=4.9$, $P<0.001$
Other fish	$F_{2,816}=0.20$, $P=0.795$	$F_{3,816}=9.6$, $P<0.001$	$F_{6,816}=1.2$, $P=0.32$
Unidentified	$F_{2,816}=4.1$, $P=0.017$	$F_{3,816}=2.9$, $P=0.035$	$F_{6,816}=6.1$, $P<0.01$

Table 3 Percent of foraging bouts in each half of year during which fish were the only prey captured, invertebrates were the only prey captured, or both fish and invertebrates were captured, with total number of bouts

Season	Fish only (%)	Invertebrates only (%)	Fish and invertebrates (%)	Bouts (*n*)
Winter/spring				
Territorial male	38.9	33.3	27.8	54
Non-territorial male	54.8	28.6	16.7	84
Female	25.4	53.9	20.8	414
Summer/autumn				
Territorial male	0.0	87.9	12.1	33
Non-territorial male	0.0	84.6	15.4	13
Female	0.0	85.5	14.5	224

Table 4 Average diving success (% dives in which prey were captured) during bouts when otters caught fish and bouts when otters caught only invertebrate prey, by period and otter status. *Figures in parentheses* refer to number of foraging bouts observed. Bonferroni adjusted critical values were used to decide significance of effects

	(January–June)		(July–December)	
	Non-fishing bouts	Fishing bouts	Non-fishing bouts	Fishing bouts
Territorial male	86.9 (17)	42.3 (30)	90.3 (30)	85.2 (4)
Non-territorial male	85.5 (23)	57.4 (50)	90.5 (11)	100.0 (2)
Female	85.7 (222)	51.4 (159)	92.8 (195)	86.7 (32)

3-way ANOVA (bout type×season×status)

Source	SS	*df*	MS	*F*-ratio	*P* (*F*>observed)
Bout type	1.33	1	1.33	10.61	<0.001
Period	1.85	1	1.85	14.73	<0.001
Status	0.26	2	0.13	1.03	NS
Bout type×period	1.19	1	1.19	9.48	<0.05
Bout type×status	0.25	2	0.12	0.98	NS
Period×status	0.06	2	0.03	0.24	NS
Bout type×period×status	0.12	2	0.06	0.47	NS

Although seasonal dietary shifts were broadly similar for both sexes and both territorial and non-territorial males (Table 2), there were significant differences among these classes in the proportions of urchins, lumpsuckers and unidentified prey consumed (2-way ANOVA, $F_{2,816}=4.4$, $P<0.01$). In particular, males ate more lumpsuckers than did females. At almost any time during spring, many of the non-territorial males at Crown Reefer Point could be seen consuming these fish.

The presence of large numbers of lumpsuckers in winter and spring was associated with a change in otter foraging behavior. During winter and spring, fish were the only prey captured in 31% of the foraging bouts (Table 3) suggesting that otters frequently specialized on capturing fish in this period. During summer and autumn however, fish were never the only prey captured in a foraging bout, otters apparently taking fish opportunistically while also consuming invertebrates. Diving success was significantly lower during foraging bouts when otters specialized on fish than during bouts when mixed fish and invertebrate prey or invertebrate prey only were taken (Table 4).

Scat analysis

Dietary patterns determined from the scat analyses were similar to those made by direct observations (Table 5). Lumpsuckers only occurred in scats collected during winter and spring. They occurred in 24–28% of the scats from female areas and in 52% of scats from the male area at Crown Reefer Point during this period, thus confirming that non-territorial males consumed relatively more of these fish. There was no clear seasonal pattern in the consumption of other fish species.

Sea urchin remains predominated in scats from all areas at all times of year, both by frequency of occurrence and estimated volume. The preponderance of urchin remains in scats supported our impression that most small, unidentified prey were sea urchins. Urchins occurred in 94% of summer/autumn scats at Crown Reefer Point and made up 93% of the total scat volume, thus indicating a reliance on urchins during months when lumpsuckers were not consumed. Urchins occurred in 96% of scats from Kiriloff Point but contributed slightly less to total scat volume.

The contribution of other invertebrate taxa, even those with robust exoskeletons, to total scat volume was low. Large bivalves, such as rock jingles, were easily identified during foraging observations but were rarely found in scats as only the soft parts of these species normally are eaten.

Prey capture rates

The estimated prey mass captured per hour during foraging bouts (Fig. 3) varied among age/sex classes with

Table 5 Composition of sea otter scats, collected during winter/spring and summer/autumn, from three locations within the study area

	Winter/spring						Summer/autumn			
	Kiriloff (*n*=54)		Crown Reefer (*n*=68)		Constantine (*n*=87)		Kiriloff (*n*=306)		Crown Reefer (*n*=70)	
	Freq. (%)	Volume (%)	Freq. (%)	Volume (%)	Freq (%)	Volume (%)	Freq. (%)	Volume (%)	Freq. (%)	Volume (%)
Limpets Archaeogastropoda	13.8	0.4	0.7	0.0	11.4	1.0	9.3	0.3	0.0	0.0
Snails Meso/Neogastropoda	26.4	0.9	8.5	1.0	7.1	1.5	27.8	0.8	1.5	0.1
Mussels *Musculus*/*Mytilus*	14.9	1.6	2.3	0.4	12.9	0.7	44.4	2.6	2.9	0.1
Other bivalves Bivalvia	11.5	1.1	3.9	0.2	1.4	0.1	13.0	0.4	10.3	3.2
Chitons Polyplacophora	9.2	0.3	9.5	0.7	7.1	0.6	11.1	0.3	1.5	0.1
Unidentified Molluscs	9.2	0.6	0.0	0.0	5.7	0.2	5.6	0.2	0.0	0.0
Total Mollusca	**59.8**	**4.9**	**20.3**	**2.3**	**37.1**	**4.1**	**66.7**	**4.6**	**14.7**	**3.5**
Decapods Decapoda	42.5	2.7	18.6	4.1	35.7	1.2	57.4	6.8	8.8	1.5
Other arthropods	8.0	0.4	6.2	1.1	1.4	0.5	4.4	0.2	0.0	0.0
Total Arthropoda	**49.4**	**3.1**	**24.8**	**5.5**	**37.1**	**1.7**	**61.1**	**7.0**	**8.8**	**1.5**
Urchins Echinoidea	**89.7**	**76.4**	**52.6**	**51.8**	**80.0**	**71.1**	**96.3**	**82.4**	**94.1**	**93.4**
Lumpsuckers *Aptocyclus ventricosus*	28.7	12.1	52.3	36.5	24.3	17.2	0.0	0.0	0.0	0.0
Other fish Pisces	18.4	3.5	8.2	1.9	15.7	4.7	16.7	4.1	11.8	4.5
Total fish	**46.0**	**15.6**	**60.5**	**38.4**	**40.0**	**21.9**	**16.7**	**4.1**	**11.8**	**4.5**
Other and unidentified	0.0	0.0	4.6	2.1	1.4	1.2	7.4	0.5	1.5	0.1

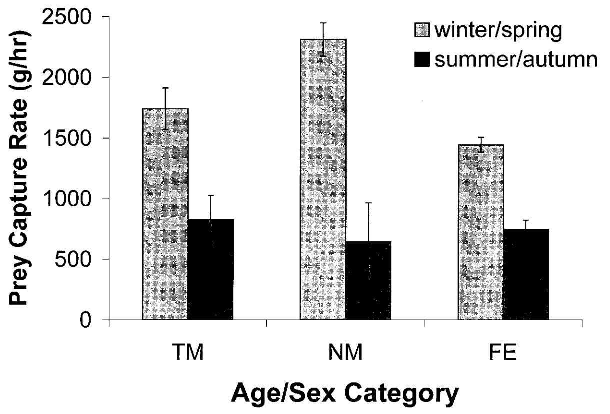

Fig. 3 Estimated rates of prey capture (g h^{-1}) for each age/sex class during winter/spring and summer/autumn (*TM* territorial male, *NM* non-territorial male, *FE* female). *Error bars* represent ±1 SE

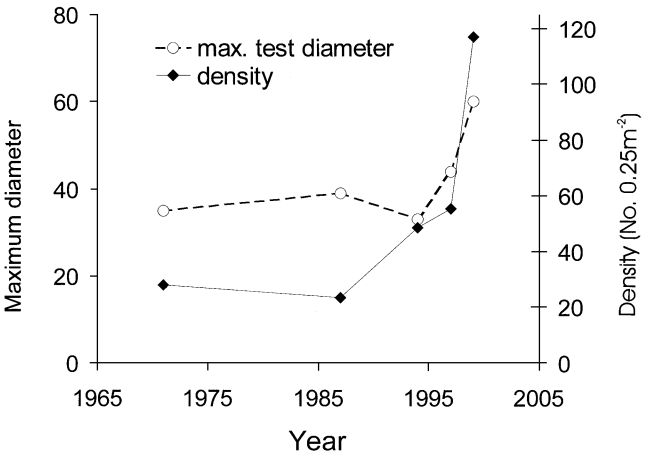

Fig. 4 Trends of sea urchin density and size at Amchitka Island, Alaska, 1970–1999. Data from 1997 and 1999 are included to show that the changes first noted in 1992–1994 have continued up to the present

females tending to capture less prey mass per hour than males (2-way ANOVA, factor status, $F_{2,769}$=3.94, P=0.02). There was also significant between-season variation (2-way ANOVA, factor season, $F_{1,769}$=42.89, P<0.001). Estimated prey capture rates were higher during winter/spring than summer/autumn. This mainly resulted from different capture rates between fishing bouts ($\bar{x}$=1833 g h^{-1}±75.4 SEM) which mainly occurred in winter/spring, and non fishing bouts ($\bar{x}$=737 g h^{-1}± 129.5 SEM) which were commoner during summer/autumn. Highest prey capture rates were observed among the non-territorial males at Crown Reefer Point during winter and spring when lumpsuckers dominated their diet.

Sea urchin densities

Average density and size of sea urchins have increased over the past 3 decades in a manner consistent with observed sea otter population declines (Fig. 4). Density and maximum test diameter of sea urchins remained largely unchanged from 1970 through 1987. By 1994 urchin density had nearly doubled, and by 1999 both density and maximum test diameter had increased dramatically.

Otter mortality

The number of dead otters found during each 3-month period is shown in Table 6. Highest numbers of recently

Table 6 Number of otter carcasses of each sex found during beach surveys of Amchitka in each season

	Jul–Sept 1992	Oct–Dec 1992	Jan–Mar 1993	Apr–Jun 1993	Jul–Sep 1993	Oct–Dec 1993	Jan-Mar 1994	Total
Male	1	3	4	0	1	0	1	10
Female	1	0	3	2	0	1	2	9
Unknown	0	0	0	4	0	1	2	7
Total	2	3	7	6	1	2	5	26

dead otters were found during winter and spring although the total number of beached carcasses found never exceded seven in any season (approximately two per month). Of the 26 carcasses found 7 were sufficiently decomposed and disarticulated to make sexing impossible. In the remaining 19 sex ratios were approximately equal.

Discussion

Although the sea otter population at Amchitka Island was probably food-limited from the mid-1940s through the 1980s, and was numerically stable during the 1970s and 1980s, the 1990s have been a period of rapid decline. Amchitka supported an estimated 6,432 otters in 1972 (5226–7638, 95% confidence intervals, Estes 1977), and while there was no indication of substantial change through the mid to late 1980s (Estes 1990), in 1993 we counted only 3,577 independent otters in an island-wide census conducted under nearly perfect viewing conditions. In 1997 the number counted in our core study area (Fig. 1) had further declined by 65%. The decline, likely caused by increased killer whale predation (Estes et al. 1998), was well underway during this study (1992–1994). Sea otter diet and food resource availability also changed substantially during the early 1990s. Three major dietary patterns occurred: decreased consumption of kelp-forest fish, increased consumption of sea urchins, and a marked seasonal exploitation of smooth lumpsuckers. The former two changes appear, in retrospect, to be predictable consequences of the declining otter population while the last was largely unpredictable.

Long-term dietary patterns of otters at Amchitka Island have tracked numerical and demographic changes. Lensink (1962) reported that urchins were the otters' dietary staple during the 1930s and early 1940s when the population was still recovering from over-exploitation. In contrast, Kenyon (1969) and Burgner and Nakatani (1972) found that fish made up 50–60% of the stomach volume of otters harvested from Amchitka in the 1960s and early 1970s, and Estes et al. (1981) reported that kelp-forest fishes were the single most important prey of otters at Amchitka in the early 1970s. The otter population had attained its highest reported density during this latter period (Estes 1977). Based mainly on these covarying dietary and population patterns, piscivory by sea otters was proposed to have reset their equilibrium density above the level that could be maintained on a diet of invertebrates alone (Estes 1990). These changes probably occurred because sea otter predation drove the size and abundance of sea urchins downward to a point where they could no longer support the growing number of otters, the kelp stands expanded in response to reduced herbivory, and kelp-forest fishes consequently were enhanced. This scenario implies that most fish eaten by the otters are inshore, kelp-associated species, which at Amchitka include greenlings, rockfishes, gunnels, pricklebacks, and sculpins. However, these species, while eaten in large numbers during the 1960s and 1970s at Amchitka, were infrequently eaten by sea otters during this study, especially in summer/autumn. The absence of kelp-forest fishes from the otters' diet is reminiscent of the recovery phase earlier in this century, when food also was not a limiting resource.

The lack of kelp-forest fish in otter diets at Amchitka in 1992–1994 coincided with an increase in sea urchin consumption by otters, especially during summer and autumn. This increase reflected an increase in the density of sea urchins around Amchitka. In the early 1970s sea urchins at Amchitka occurred at a density and size well below those at nearby islands where otters were absent (Estes et al. 1978). Data from Barr (1971) and Estes and Duggins (1995) demonstrate further that density and maximum size of sea urchins at Amchitka remained unchanged from the late 1960s through at least 1987. By 1993, however, sea urchin population density had doubled. This increase is consistent with similar measures of urchin density and size obtained at Adak Island (roughly a five-fold increase in urchin density from 1987 to 1997, Estes et al. 1998). While sea urchin density is known to vary for many reasons (e.g., recruitment variation, disease, predation), reduced otter numbers in the 1990s almost certainly caused urchin populations to increase at Amchitka, in turn causing the kelp forests and their associated fish populations to collapse. Our data demonstrate that these shifts in environment and prey availability – caused by declines in otter numbers – were in turn reflected in sea otter diet and foraging behavior.

We did not realize in 1993–1994 that the sea otter population at Amchitka Island was declining, in part because the decline had only recently begun, in part because wildlife population trends are inherently difficult to detect, and in part because we began the study knowing that a high-density population had persisted at Amchitka for decades and thus expecting that state of affairs to continue. In retrospect, changes in both sea otter diet and prey availability – particularly sea urchin density – provided the first clear signal of the otter population decline. Such co-varying shifts in diet and foraging behavior with changes in population status occur broadly in nature. Indeed, the central ideas of foraging theory and the economics of consumer choice are founded on this very notion (Krebs 1978). Examples exist for a diversity of taxa and systems, including the behavioral shift in sea urchins from a sit-and-wait to an active foraging strategy when populations increase to the point of deforesting kelp beds (Ebeling et al. 1985; Harrold and Reed 1985); dietary changes in reindeer following their introduction, growth, and population crash at St. Mathew Island, Alaska (Klein 1968); and dietary shifts by voles with increasing population density (Cockburn and Lidicker 1983). While similar case studies are lacking for mammalian carnivores, the recent review by Berger (1998) demonstrates both the importance and pliability of consumer-prey relationships across this group. In view of the cascading interactions resulting from otter predation on sea urchins, the reported changes in otter diet and prey availability seen at Amchitka in 1992–1994 are predictable consequences of declining otter numbers.

The third major change in sea otter diet was the occurrence of large numbers of smooth lumpsuckers in 1993 and 1994. Lumpsuckers were abundant in fish collections from Amchitka Island during the 1950s (Simenstad et al. 1977) and Kenyon (1969) reported that they were the commonest fish species in the stomachs of otters collected at Amchitka during spring of 1962 and 1963. However, extensive fish sampling at Amchitka Island in the late 1960s and early 1970s produced only occasional juvenile lumpsuckers (Simenstad et al. 1977). While otters commonly ate fish during this period, these fishes were not lumpsuckers but rather kelp-forest species (Estes et al. 1981). Lumpsuckers also were not observed by A.M. Johnson (personal communication), who resided at Amchitka from October 1989 to March 1990 and made numerous observations of otter foraging. Nor were lumpsuckers seen in the otter’s diet in April 1992, immediately prior to our study (D.B. Siniff and J. Bodkin, unpublished work) yet in late winter and spring of 1993 and 1994 they were being consumed in large numbers. In May and June 1993 we encountered numerous lumpsuckers while diving and exploring the shoreline at Adak and Amchitka islands, and during that same period we found their remains in otter scats throughout the central and western Aleutian archipelago. Lumpsuckers thus appear to abound in coastal habitats of the west/central Aleutian archipelago for periods of several years; longer periods (possibly decades) separate episodes of high lumpsucker abundance; and the spatial scale of these episodic events is very large. The main population of smooth lumpsuckers in the Aleutian and Commander basins undergoes year-to-year east-west redistribution in response to oceanographic conditions (Yoshida and Yamaguchi 1985; Il’inskii and Radchenko 1992), perhaps thereby explaining their episodic appearance during our study in coastal regions and in the sea otter’s diet.

The seasonal appearance of lumpsuckers improved the foraging profitability of otters at Amchitka during winter/spring compared with summer/autumn (Fig. 4). This seasonal oceanic food subsidy caused changes to otter foraging strategy and mortality rate. During periods of high lumpsucker abundance, sea otters increasingly specialized on large, high-value items, frequently consuming only fish during a foraging bout (Table 3). In the absence of lumpsuckers, fish were apparently taken opportunistically by otters foraging mainly on invertebrates. Low diving success due to increased selectivity was more than offset by the large size of lumpsuckers and other fish compared to the small invertebrate prey available on Amchitka.

A late winter peak in starvation-induced mortality has long occurred at Amchitka (Kenyon 1969; Estes 1977), driven by limiting food resources, seasonal rigors (storms and cold temperatures), and the post-spawning nutritional decline in sea urchins. By surveying Amchitka’s beaches during the 1950s and early 1960s, Kenyon located between 30 and 40 carcasses and moribund otters per month during March and April. Despite intensive surveys of even larger beach stretches in winter and spring 1993 and 1994 we located only two or three carcasses a month (Table 6) and no moribund otters, suggesting that the appearance of lumpsuckers greatly reduced winter/spring mortality in sea otters by making this a time of relative plenty. The typically high mortality rate of juvenile (non-territorial) males in food-limited populations (Kenyon 1969; Estes 1977) led us to hypothesize a priori that these animals were displaced to inferior habitats by territory holders, thus being more vulnerable to starvation during winter/spring. The similar foraging profitabilities of territorial and non-territorial males in winter/spring 1992–1994 was therefore unexpected and was reflected in our carcass surveys, which found no bias towards males. It would appear therefore, that the magnitude and demographic focus of winter mortality in sea otters varies among years because of changes in food availability.

Most prior work has implicitly assumed that dynamics of the sea otter/kelp forest system is driven by in situ processes. This study and that of Estes et al. (1998) demonstrate that those dynamics are linked with events in the open sea. Otter mortality dramatically increased in the late 1980s or early 1990s when killer whales apparently redirected their foraging efforts to the nearshore ecosystem. Over-fishing and/or a temperature regime shift in the North Pacific Ocean/Bering Sea ecosystems probably caused this change (National Research Council 1996). Furthermore, the inshore spawning migration of lumpsuckers delivered a rich nutritional supplement from the open sea to the coastal zone, thereby reducing starvation-induced mortality, particularly of young males, during the early 1990s. Collectively, these inter-system linkages released sea otter populations from food limitation during a period that included our 1992–1994 field study.

Intersystem linkages are known in many other systems (Polis et al. 1997). Examples include the effects of marine detritus on terrestrial food web dynamics in coastal systems (Polis and Hurd 1996; Anderson and Polis 1998), nutrient provisioning by anadramous salmonids on coniferous forest ecosystems (Willson et al. 1998), and the maintenance of extraordinarily high population densities of intertidal limpets by food input from subtidal kelp stands (Bustamante et al. 1995). These various findings are now changing our view of the sea otter-kelp forest system from one that is temporally stable, sustained largely by coastal production, and organized largely around top-down forces, to one that varies considerably through time, is perturbed episodically by oceanic subsidies, and during these perturbations is strongly influenced by bottom-up forces. Despite these episodic influences of bottom-up forces on sea otter diet and starvation-induced mortality, the abundance of otters, sea urchins and kelps remains under strong top-down control.

The reported long-term changes in sea otter populations and kelp-forest communities at Amchitka Island reinforce a growing realization by ecologists that interdecadal variation in structuring factors is common in nature (Francis and Hare 1994; Jackson 1997; Dayton et al. 1998; OEUVRE, 1998, Ocean ecology: understanding and vision for research. National Science Foundation, Division of Ocean Science, Final Report, http://www.joss.ucar.edu/joss_psq/project/oce_workshop/oeuvre/report/). Other examples include fluctuations in rocky intertidal community structure (Barry et al. 1995; Denny and Paine 1998); orders-of-magnitude change in sardine abundance related to ocean temperature regime shifts (Baumgartner et al. 1992; Francis and Hare 1994); long-term shifts in Antarctic benthic communities (Dayton 1989); multi-year fluctuations in oak masting that in turn regulates the incidence of lyme disease (Jones et al. 1998); and shifts in the interaction strengths among wolves, moose, and balsaam fir (McLaren and Petersen 1994), to list a few. Some of these changes are no doubt related to growing human influences while others are intrinsic characters of natural ecosystems. All require a sufficiently long time series of information for proper detection and understanding.

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