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SEA OTTER POPULATION DECLINES IN THE ALEUTIAN ARCHIPELAGO

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Sea otter (*Enhydra lutris*) populations were exploited to near extinction and began to recover after the cessation of commercial hunting in 1911. Remnant colonies of sea otters in the Aleutian archipelago were among the first to recover; they continued to increase through the 1980s but declined abruptly during the 1990s. We conducted an aerial survey of the Aleutian archipelago in 2000 and compared results with similar surveys conducted in 1965 and 1992. The number of sea otters counted decreased by 75% between 1965 and 2000; 88% for islands at equilibrial density in 1965. The population decline likely began in the mid-1980s and declined at a rate of 17.5%/year in the 1990s. The minimal population estimate was 8,742 sea otters in 2000. The population declined to a uniformly low density in the archipelago, suggesting a common and geographically widespread cause. These data are in general agreement with the hypothesis of increased predation on sea otters. These data chronicle one of the most widespread and precipitous population declines for a mammalian carnivore in recorded history.

Key words: aerial surveys, Aleutian Islands, *Enhydra lutris*, population declines, population trends, sea otters, skiff-based surveys

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Early European explorers reported vast numbers of sea otters (*Enhydra lutris*) in coastal waters of the Aleutian archipelago and mainland Alaska (Bancroft 1959; Lensink 1962). Extensive hunting of these animals for their valuable pelts eliminated the species from most of its historic range, which extended across the Pacific Rim from Japan to the Pacific coast of Mexico (Kenyon 1969; Lensink 1962; Riedman and Estes 1990; L. Rotterman and T. Simon-Jackson, in litt.). The International Fur Seal Treaty protected the surviving remnant colonies from further harvest beginning in 1911. These colonies subsequently increased to repopulate much of the sea otters' former range.

The earliest and most extensive recovery of sea otters after the fur trade occurred in the Aleutian archipelago. Remnant populations, located in the central Aleutian Islands, were monitored infrequently through the 1950s (Kenyon 1969; Lensink 1962; Murie 1959). Systematic aerial surveys of sea otters in the Aleutian Islands were initiated in 1957 (Kenyon 1969) in conjunction with site-specific surveys that employed a variety of techniques (Estes et al. 1978; Kenyon 1969; Lensink 1962). Collectively, these efforts chronicle a pattern of population recovery that began in the central Aleutians and gradually spread throughout the archipelago. By the 1950s, sea otter numbers apparently had recovered to precommercial harvest levels at some islands in the central Aleutians, although the majority of the archipelago was yet to be recolonized (Estes 1990; Kenyon 1969). By

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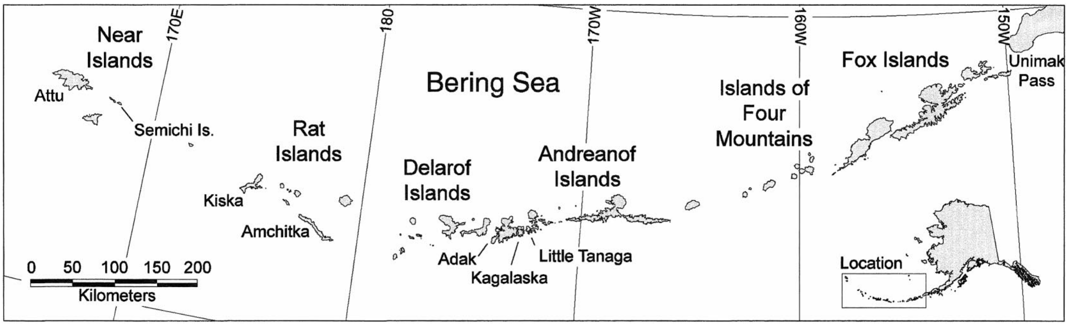

FIG. 1.—Map of the study area denoting 6 major island groups (Near, Rat, Delarof, Andreanof, Four Mountains, and Fox islands) in the Aleutian archipelago.

the 1980s, an estimated 55,000–74,000 animals inhabited the archipelago, and continued population growth was expected (D. Calkins and K. Schneider, in litt.; Estes 1990; L. Rotterman and T. Simon-Jackson, in litt.; K. Schneider, in litt.). Sea otters had spread to all island groups by 1992, but the overall count at that time had declined by approximately 50% in the central Aleutians since the 1965 survey (T. Evans et al., in litt.). Population trends from a time series of skiff-based counts documented a precipitous decline in sea otter numbers at Adak Island during the early to mid-1990s, and subsequent surveys at Little Kiska, Amchitka, and Kagalaska islands indicated similar declines (Estes et al. 1998). These findings prompted us to conduct another aerial survey of the entire Aleutian archipelago in April 2000 to assess the magnitude and geographic extent of the population decline.

We present general patterns of population change for sea otters in the Aleutian Islands through compilation of aerial survey data from the late 1950s to 2000. We evaluated the hypothesis that otter densities varied among island groups over time. We analyze trends in sea otter abundance by comparing the number of animals counted over time and by computing proportional changes between time periods. We evaluated the null hypothesis that there was no difference between observed and expected distributions. The more detailed results of skiff-based surveys conducted at several islands during the 1990s are used to define decline trajectories more precisely and provide a minimal estimate of bias in the aerial counts.

MATERIALS AND METHODS

The Aleutian archipelago extends westward from Unimak Pass to Attu Island (Fig. 1). The islands are volcanic in origin, forming a boundary between the Bering Sea and the North Pacific Ocean. There are 6 major island groups (Near, Rat, Delarof, Andreanof, Four Mountains, and Fox) that collectively contain 78 major islands with >5,000 km of coastline.

Aerial surveys.—We conducted aerial surveys from 1–30 April 1992 and 11–29 April 2000. Viewing conditions were good to excellent during both surveys with approximately 90% of sightings made in average wind speeds of ≤19 km/h. We surveyed all major islands and offshore rocks of the Aleutian archipelago except for Chagulak Island in the Islands of Four Mountains, which was omitted because of the high risk associated with flying near its large seabird colony.

In 1992, the survey aircraft was a deHavilland turbine Twin Otter, and in 2000 the survey aircraft was a turbine Aero Commander 690A. Both aircraft were equipped with large bubble windows and long-range fuel tanks. The survey crew consisted of a pilot, copilot, 2 observers, and 1 data recorder. Observers sat aft of the pilots on each side of the plane. The aircrafts were flown approximately 0.23 km from the shoreline at an altitude of 91 m and an average airspeed of 185 km/h during the surveys, sampling an area from shoreline to approximately 0.7 km offshore (T. Evans et al., in litt.). Location, altitude, weather, visibility, and observer identification were recorded directly into an onboard computer interfaced with a global positioning system.

We surveyed the shoreline of each island in its entirety. We sampled offshore habitat by surveying line transects that were perpendicular to the shoreline and extended to the 50-fathom (91.4 m) isobath (Burnham et al. 1980; T. Evans et al., in litt.). Transects were digitized for the entire archipelago and of these, 61 were randomly sampled in 1992. In 2000, we resurveyed 35 transects in the western and central Aleutians. Mean encounter rates (otters/km) for the shoreline and transects were compared between 1992 and 2000 surveys.

Skiff-based surveys.—Skiff-based surveys were conducted several times during the 1990s at Adak, Kagalaska, Kiska, Little Kiska, Amchitka, Shemya (Semichi Islands), and Attu islands (Fig. 1) when viewing conditions were good to excellent (Beaufort sea state of 1–2, and >1 km of clear visibility at sea level). Two or more observers counted sea otters from a 5.2-m skiff as it was run parallel to shore along the outer margins of kelp (*Alaria fistulosa*) beds at 15–22 km/h. We counted sea otters with the unaided eye, using binoculars to confirm sightings or to count animals in large groups. The shoreline of each island was divided into contiguous segments, each 3–10 km in length and separated by distinctive topographic features (e.g., prominent points of land). Counts were recorded separately for each section. Cloud cover, Beaufort sea state, wind speed, and visibility conditions were recorded at the beginning of each segment.

Analytical methods.—We established early trends of sea otter abundance and distribution in the Aleutian archipelago from historical records provided by Kenyon (1969). When combined with aerial survey data from 1965, 1992, and 2000, these records are sufficient to chronicle broad patterns of population change across the 6 main island groups.

Encounter rates of sea otters for each island were obtained by dividing the uncorrected counts by the length of shoreline surveyed (hereafter these measures are referred to as densities). Otter densities were log-transformed before statistical analyses. We tested the hypothesis that otter densities varied among island groups with a 1-way analysis of variance, using island groups as treatments and islands as replicates. This analysis was done separately for aerial survey data from 1965, 1992, and 2000.

We further evaluated trends in sea otter abundance by comparing the number of animals counted by island, island group, and across the archipelago, and by computing proportional changes between time periods (N_{t2}/N_{t1}). To avoid spurious results, we arbitrarily restricted the latter analyses to islands where 20 or more otters were counted during at least 1 aerial survey. Proportional changes were then plotted as frequency distributions and contrasted with expected distributions for stable populations, assuming sampling variation but with no prevailing tendency toward increase or decline. Expected distributions were computed from a lognormal density function with a mean of 1 and the observed variance. The null hypothesis of no difference between observed and expected distributions was evaluated using a 1-sample K-S test. To avoid the unknown and potentially confounding effects of range expansion and population growth between 1965 and 1992, we repeated the analysis for those islands that Kenyon (1969) assumed to be at or near equilibrial density in 1965 (defined here as that which occurred when populations ceased growing because of resource limitation). The latter analysis included all the Rat and Delarof islands, and the Andreanof Islands from Great Sitkin westward ($n = 23$ islands; Table 1) in which ≥20 otters were counted in at least 1 survey period.

We computed independent rates of population change from skiff-based counts conducted in the western and central Aleutian Islands. Two or more surveys were conducted in separate years at each of these islands during the 1990s. The annual percentage of decline in population density was calculated for skiff-based and aerial surveys as $100(1 - \lambda)$, where λ is the annual rate of population growth ($\lambda = e^r$, $r = [\ln(D_{t+dt}) - \ln(D_t)]/dt$, where D_t = density at year t and dt = number of years between surveys). We arbitrarily restricted this comparison to islands at which ≥20 otters were counted during at least 1 of the surveys, to avoid spurious results. Differences in aerial and skiff-based population trends were evaluated using a paired *t*-test. We also compared the distribution of annual rates of decline for the 6 islands surveyed by skiff with that for the entire archipelago, based on 1992 and 2000 aerial surveys.

Because sea otter counts obtained from aerial

TABLE 1.—Aerial survey counts of sea otters in the Aleutian Islands, Alaska. Islands in italics are considered to have been at or near equilibrium density in 1965.

		Year					
Island group	Island[a]	1959[b]	1960[b]	1962[b]	1965[b]	1992[c]	2000[d]
Near Islands	Attu	0			13	636	282
	Agattu	0			4	216	46
	Adlaid and Nizki	0			0	54	22
	Shemya	0			10	49	18
	Subtotal	0			27	955	368
Rat Islands	*Buldir*				15	11	1
	Kiska and Little Kiska	1,127			1,229	456	60
	Segula	47			56	19	1
	Khvostov and Davidof	33			39	41	7
	Little Sitkin	50			135	38	0
	Rat	270			326	79	11
	Amchitka	1,560			1,144	755	112
	Semisopochnoi	393			203	62	0
	Subtotal	3,480			3,147	1,461	192
Delarof Islands	*Amatignak*	102			70	16	4
	Ulak	352			107	36	7
	Unalga	51			16	6	17
	Kavalga	275			155	95	20
	Oliuga and Skagul	393			190	123	12
	Ilak	183			32	40	2
	Gareloi	41			83	19	2
	Tanaga	902		898	1,059	317	187
	Bobrof	57			32	10	2
	Kanaga	1,822		846	1,054	333	90
	Subtotal	4,178			2,798	995	343
Andreanof Islands	*Adak*	1,718		2,260	1,336	1,045	470
	Kagalaska	1		251	298	157	18
	Little Tanaga	0		214	509	38	19
	Umak	0		94	392	38	6
	Anagaksik	0		14	0	1	0
	Great Sitkin	0		325	710	170	18
	Igitkin				7	36	4
	Chugul				5	23	0
	Tagalak				7	19	1
	Ikiginak				0	0	0
	Oglodak				6	3	0
	Kasatochi	0			0	5	0
	Koniuji	0		0	0	0	0
	Atka	33		50	228	1,137	171
	Amlia	83		91	159	425	119
	Seguam	14		23	28	10	21
	Subtotal	1,889		3,322	3,685	3,107	847
Islands of Four Mountains	Amukta		0			1	7
	Yunaska		0			6	5
	Herbert		0			13	12
	Chuginadak		0			33	16
	Carlisle		0			11	6
	Kagamil		0			7	3
	Uliaga		0			1	3
	Subtotal		0			72	52

TABLE 1.—Continued.

Island group	Island[a]	Year 1959[b]	1960[b]	1962[b]	1965[b]	1992[c]	2000[d]
Fox Islands	Umnak and Samalga		6	10	9	517	123
	Unalaska and Sedanka				0	554	374
	Egg and Unalga					11	23
	Akutan			1	0	59	20
	Akun				0	298	73
	Rootok				0	0	3
	Avatanak				2	11	9
	Tigalda		11		32	6	14
	Ugamak				0	2	1
	Aiktak					0	0
	Subtotal		17	11	43	1,458	640
Aleutian Islands	Total	9,507	17	5,077	9,700	8,048	2,442

[a] Kiska and Little Kiska include Pyramid Island; Great Sitkin includes Ulak, Aziak, Tanaklak, Kanu, Asuksak, and Tagadak islands; Atka includes Segchudak, Sadatanak, Amtagis, and Salt islands; Umnak and Samalga include Bogoslof, Vsevidof, Ogchul, Kigul, and Adugak islands.
[b] Kenyon (1969).
[c] T. Evans et al., in litt. (1997).
[d] This survey.

surveys are biased low (Bodkin and Udevitz 1999; Kenyon 1969; Lensink 1962), we estimated a minimal correction factor for the 2000 aerial survey by computing the mean ratio of the skiff : aerial counts for the 6 islands surveyed in 2000. The mean ratio was then multiplied by the aerial count to obtain a minimal estimate of current population abundance.

All statistical tests were considered to be significant when $P < 0.05$. All statistics are reported ± 1 *SE,* unless otherwise indicated. Nonsignificant results are accompanied by a report of statistical power $(1 - \beta)$, where β is the probability of making a type-II error. For power analyses we set $\alpha = 0.1$, standard deviation equal to that observed and calculated the power to detect a medium effect size (sensu Cohen 1988), given existing sample sizes.

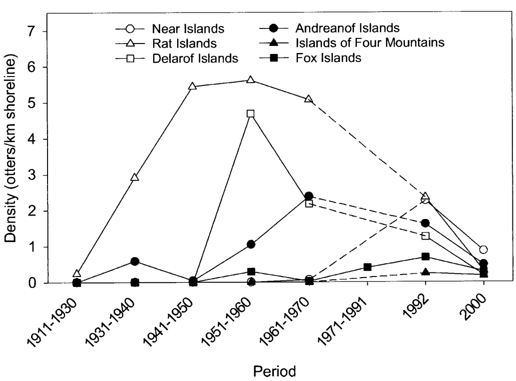

FIG. 2.—Temporal changes in density of sea otters for major island groups, 1911–2000. Representative densities for each period were based on maximal counts by aircraft for each island divided by the length of shoreline surveyed for each group. Dashed lines indicate when no data were available.

RESULTS

Population trends.—The general pattern of sea otter recolonization in the Aleutian archipelago through the 1960s was characterized by a slow spread among islands and rapid intraisland population increases after colonization, followed by modest declines and eventual stabilization (Bodkin et al. 2000; Kenyon 1969). By 1992, sea otters had repopulated all major island groups, although the status of populations varied among islands. By 2000, sea otter densities had declined to a uniformly low level throughout the archipelago (Fig. 2). Population densities differed significantly among island groups in 1965 ($F = 9.50$, $P < 0.001$) and 1992 ($F = 7.44$, $P < 0.001$) but not in 2000 ($F = 1.79$, $P = 0.138$, $1 - \beta = 0.76$).

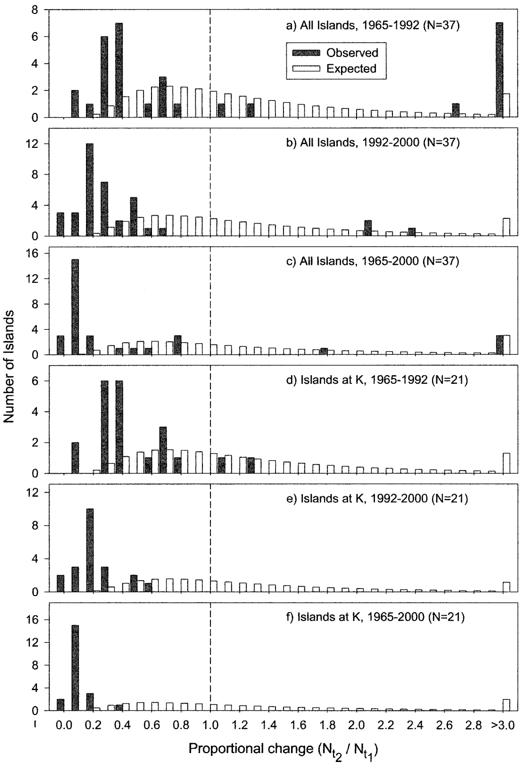

FIG. 3.—Frequency distributions of proportional changes in abundance (N_{t2}/N_{t1}) of sea otters among islands in the Aleutian archipelago. a–c) All islands surveyed during both years for which ≥20 otters were counted during at least 1 survey and d–f) only for those islands which were at or near K (defined as the population status when growth ceased because of resource limitation) in 1965.

Observed and expected distributions of proportional change in abundance between selected surveys differed significantly ($P < 0.001$ in all cases). These differences demonstrate population declines between 1965 and 1992 and between 1992 and 2000, for all of the islands in the Aleutian archipelago (Figs. 3a–c) and for those islands that were at or near equilibrial density (noted as K in Figs. 3d–f) in 1965. The frequency distributions of the first 3 contrasts (Figs. 3a–c) were distinctly bimodal, indicating that, although otter numbers at most islands were in decline during this period, they increased markedly at others. All of these increases occurred at islands with small otter populations in 1965. When we limited the analysis to islands at or near equilibrial density in 1965 (Figs. 3d–f), the resulting distributions became unimodal and were displaced strongly to the left, indicating an overall decline of 88% (±4.6; $n = 21$) between 1965 and 2000 (Fig. 3f).

Estimated rates of population decline during the 1990s based on skiff-based and aerial surveys of 6 islands in the western and central Aleutians were 17.7% (±2.98) and 17.5% (±2.29), respectively (Table 2). These estimates did not differ significantly ($t = 0.06$, $P > 0.1$, $1 - \beta = 0.41$), although the small sample size provided limited statistical power. We also compared mean annual rates of decline as estimated by skiff-

TABLE 2.—Comparison of sea otter population trends based on aerial and skiff-based surveys conducted during the 1990s at 6 islands in the Aleutian archipelago. Mean annual rates of decline were not significantly different ($t = 0.06$, $P > 0.05$).

		Aerial survey				Skiff survey			
			Density (otters/km)				Density (otters/km)		
Island	Section	Period	Start	End	Decline/year (%)	Period	Start	End	Decline/year (%)
Adak	North side	1992–2000	3.67	1.72	9.05	1992–2000	9.74	2.96	13.82
Amchitka	Partial	1992–2000	7.41	0.76	24.78	1993–2000	16.20	5.19	15.01
Attu	All	1992–2000	2.34	1.04	9.67	1994–2000	9.92	2.22	22.06
Kagalaska	All	1992–2000	1.77	0.20	23.72	1994–2000	2.56	0.61	21.28
Little Kiska	All	1992–2000	4.27	0.50	23.53	1994–2000	10.88	2.89	23.31
Semichi Islands	North side	1992–2000	2.07	0.55	15.23	1994–2000	4.68	2.62	9.24
$\bar{X}$					17.66				17.45
(±*SE*)					(±2.98)				(±2.29)

based and aerial surveys of all islands (15.0%/year (±1.74; $n = 29$)) but did not detect a difference ($t = 0.857$, $P > 0.1$, $1 - \beta = 0.47$).

Encounter rates of otters (per km) along transects differed significantly ($t = 2.32$, $P = 0.02$) between 1992 (0.04 ± 0.016) and 2000 (0.01 ± 0.004). Sample sizes are small, but the difference in encounter rates between years is similar to that observed for nearshore aerial surveys.

Onset of decline.—To estimate when population declines began in the Aleutian Islands, we first computed trajectories in counts at those islands where ≥3 skiff-based surveys were conducted in the 1990s (Adak, Amchitka, and Kagalaska islands). These trajectories were then hindcast to when they intersected predecline estimates of abundance. Predecline abundance was estimated from aerial counts conducted in the late 1950s and early 1960s when populations at the islands were presumed to be at equilibrial density (Kenyon 1969), and a correction factor of 3.58 (±0.77) was applied to the counts to adjust for sightability and detection (varying this correction factor between 2 and 4 did not change the results substantively). We fitted decline trajectories to the survey data using least squares, assuming an exponential function of the form $N_t = N_0e^{rt}$. There were no clear patterns to the distributions of the residual values, indicating that the exponential decay function was appropriate for describing the observed trends. Estimated annual rates of decline at the 3 islands averaged 19.4% (±0.94) during the 1990s; hindcasting provided estimates for the start of the decline as 1988 for Adak, 1991 for Amchitka, and 1986 for Kagalska (Fig. 3). To quantify uncertainty for these estimates, we computed 95% confidence interval (*CI*) for both predecline abundance and trend lines for decline, then calculated intersection points for both trajectories and confidence limits. At Adak Island (the only site with sufficient data for the analysis) the earliest intersection point suggested that population decline began in 1978; however, 7 of the 9 intersection points occurred after 1985. This analysis is based on limited data and depends on a variety of simplifying assumptions (most importantly, that the initiation of the decline was instantaneous and that the rate of decline was constant over time). However, it suggests that the population decline began some time after the mid-1980s.

Current population size.—We counted 2,442 sea otters in the aerial survey of spring 2000. Multiplying this value by the skiff : aerial correction factor (3.58 ± 0.77; $n = 6$) provides a population estimate of 8,742 (95% *CI* = 3,924–13,580) sea otters for the Aleutian Islands in 2000. This is a minimal estimate of abundance because some unknown proportion of the population is not detected in skiff-based surveys (Udevitz et al. 1995).

DISCUSSION

Aerial surveys have many limitations but provide the only practical means of rapid and complete coverage of sea otter habitat over a vast and remote region. The indicated trend for any given island may be unreliable due to a small sample size (3 survey periods) and inherent variation in the detection of otters within counts. Emergent trends, however, become more certain when similar counts are summed over multiple islands. Thus, the 3 surveys (1965, 1992, and 2000) provide a reasonable assessment of gross change in distribution and relative abundance of sea otters in the Aleutian archipelago over a 35-year period (Fig. 2; Table 1).

This assessment assumes that data gathered in the 3 aerial surveys are directly comparable. Survey methods in 1992 and 2000 were similar with respect to air speed, altitude, distance from shore, and personnel. In contrast, the 1965 survey was conducted from a DC-3 aircraft flying at 222 km/h and 61–122 m in altitude, which likely reduced the probability of detecting sea otters (Kenyon 1969). Therefore our esti-

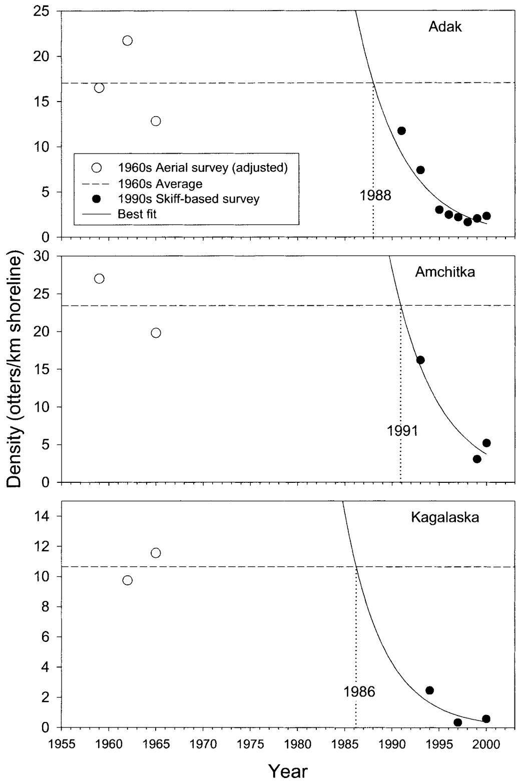

FIG. 4.—Estimated dates for the onset of population declines of sea otters at Adak, Amchitka, and Kagalaska islands.

mate of the magnitude of the decline is conservative.

Sea otters in the Aleutian archipelago have declined substantially in number. Both skiff-based and aerial and counts indicate an annual decline rate of 17% in the west-central archipelago between 1992 and 2000. Refinement of these trends is limited by a paucity of information for the 27 years that passed between the 1965 and 1992 aerial surveys (Estes 1990; Estes et al. 1978; L. Rotterman and T. Simon-Jackson, in litt.). Nonetheless, the population decline appears to have been relatively recent (Figs. 2–4) but well underway by 1992 (Table 1; Figs. 2 and 3). The sea otter population was at equilibrial density for several islands in the Rat, Delarof, and western Andreanof islands by 1965 (Kenyon 1969), but numbers declined by 88% by 2000. Population estimates for Amchitka Island in the early 1970s provide no suggestion of a decline (Estes et al. 1978), although the data are difficult to interpret because of differing survey methods. Skiff-based surveys at Attu Island (Fig. 1) suggest an increasing population from 1975 to 1994 (Estes 1990; United States Fish and Wildlife Service, in litt.); it is unclear whether equilibrial density had been reached before the onset of the decline. These data, together with the uniformly low density for the entire Aleutian archipelago in 2000, suggest that the overall population is currently about 10% of the area's potential carrying capacity.

The geographic extent of the sea otter population decline is unknown. Data from the 2000 aerial survey indicate that numbers have declined across the entire Aleutian archipelago. However, recent surveys of sea otters in the Commander Islands, Russia (approximately 300 km west of Attu Island) suggest a stable population there since 1992 (Bodkin et al. 2000; A. M. Burdin, pers. comm.). Hence, the westward extent of the decline appears to be Attu Island. The eastward extent of the decline is less clear. Population surveys in 2000 and 2001 of the Alaska Peninsula and Kodiak archipelago indicate significant declines in those areas (United States Fish and Wildlife Service, in litt.). Current status of populations in Lower Cook Inlet and the Kenai Peninsula is unknown; however, annual surveys in Prince William Sound show no indication of a decline, despite extensive impacts from the Exxon Valdez oil spill (Ballachey et al. 1994; J. Bodkin et al., in litt.). Hence, the eastward extent of the decline apparently occurs somewhere between the Kodiak archipelago and Prince William Sound.

The uniformly low density to which sea otter populations have declined across the Aleutian archipelago suggests that factors contributing to the population decline may be density-dependent. Adak Island in the central Aleutians was studied extensively in the 1990s during the population decline (Estes et al. 1998). Elevated adult mortality was found to be the primary cause of the population decline, and predation by killer whales (*Orcinus orca*) is thought to be the principal reason for this mortality (Estes et al. 1998; Hatfield et al. 1998). Killer whales presumably shifted their diet to include sea otters after populations of their preferred prey, harbor seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*), declined. Our findings are consistent with this hypothesis, given the broad geographic extent of pinniped declines across the western Gulf of Alaska and the Aleutian Islands (D. Withrow et al., in litt.; York 1994). It is interesting to note that neither sea otter nor pinniped populations in the Commander Islands, Russia have declined to the degree that they have in the Aleutian archipelago (Bodkin et al. 2000; E. Mamaev, pers. comm.; V. Nikulin pers. comm.).

Many questions about the geographic extent and ultimate cause of the sea otter decline in southwestern Alaska remain, but our findings demonstrate that once-abundant populations have collapsed across the entire Aleutian archipelago. The information presented in this article chronicles one of the most widespread and precipitous population declines for a mammalian carnivore in recorded history. Many other carnivorous mammals have been lost from large segments of their historical range, but in nearly all instances the populations dwindled more gradually because of direct human exploitation, predator control, poaching, and habitat destruction. This is arguably the case for all large terrestrial carnivores (Diamond 1984), including various species of wolves, bears, and large cats throughout the world, although in most cases the declines are poorly chronicled. The sea otter declines, which appear to differ from their terrestrial counterparts in both pattern and apparent cause, are remarkable because they occurred immediately after abrupt population declines in 3 broadly sympatric species of pinniped (northern fur seals *Callhorinus ursinus*, Steller sea lion *E. jubatus*, and harbor seals *P. vitulina*—National Research Council 1996). We suspect that these various declines are causally linked, and thus the key to understanding the sea otter decline lies with the understanding of why pinnipeds have declined. Diverse hypotheses have been advanced to explain the pinniped declines, but their cause (or causes) remains uncertain (National Research Council 1996).

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