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LONG-TERM TRENDS IN HARBOR SEAL NUMBERS AT TUGIDAK ISLAND AND NANVAK BAY, ALASKA

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ABSTRACT

We conducted land-based counts of harbor seals (*Phoca vitulina richardii*) and collected related environmental data at Tugidak Island (Gulf of Alaska, 1994–2000) and Nanvak Bay (Bristol Bay, 1990–2000) to estimate population trends and identify factors influencing counts. At Tugidak Island, the seal population declined substantially during molting from 1976 through the 1980s, stabilized in the early 1990s, and increased at a moderate rate (3.4%/yr, CI: 1.0%–5.8%) from 1994 to 2000. Pups and all seals ashore during pupping increased at higher annual rates of 5.4% (CI: 2.2%–8.8%) and 8.3% (CI: 4.5%–12.3%) from 1994 to 2000 at Tugidak Island. At Nanvak Bay seals declined in abundance between 1975 and 1990 but increased during the 1990s at 9.2%/yr (CI: 7.2%–11.3%) during pupping and 2.1%/yr (CI: 0.6%–3.6%) during molting. Date and time-of-day were significant covariates in all analyses. Factors that led to declines at Tugidak Island and Nanvak Bay have seemingly abated sufficiently such that these populations are currently increasing, though still greatly reduced from the 1970s. Index sites are useful adjuncts to aerial surveys, providing survey-related information not always available from aerial counts, which is useful in survey design and data analysis.

Key words: harbor seal, *Phoca vitulina richardii,* population trend, Tugidak Island, Nanvak Bay, Bering Sea, Bristol Bay, Alaska, pupping, molting.

Populations of harbor seals (*Phoca vitulina richardii*) in the northeastern North Pacific Ocean have fluctuated during the past century as a result of natural and anthropogenic influences, although the relative contributions of these influences are somewhat unclear (*e.g.*, Fisher 1952, Lensink 1958, Olesiuk *et al.* 1990, Pitcher 1990). Throughout much of the Pacific Northwest (*e.g.*, California, Oregon, Washington, British Columbia), harbor seal populations have increased since the 1970s (Boveng 1988, Harvey *et al.* 1990, Olesiuk 1999, Jefferies *et al.* 2003). In Alaska, large population declines have occurred in some areas of the Gulf of Alaska (Tugidak Island and Prince William Sound) from the mid-1970s through at least the early to mid-1990s (Pitcher 1990, Frost *et al.* 1999). In contrast, harbor seals population counts have been stable or increasing in most of southeastern Alaska (Small *et al.* 2003), except for recent declines in Glacier Bay (Mathews and Pendleton 2006). This pattern of increasing seal populations in most of southeastern Alaska and declines in other regions of the state is of particular interest as it generally parallels spatial and temporal population trends of Steller sea lions (*Eumetopias jubatus*) (Braham *et al.* 1980, Merrick *et al.* 1987, Loughlin *et al.* 1992, Calkins *et al.* 1999). Additionally, populations of northern fur seals (*Callorhinus ursinus*) and sea otters (*Enhydra lutris*) have declined in the Bering Sea over the past two to three decades (York and Kozloff 1987, Doroff *et al.* 2003). Information on long-term harbor seal population trends contributes to a more complete picture of how pinniped populations fluctuate over time, potentially providing a better understanding of the factors that cause those fluctuations.

Knowledge of population abundance and trend is critical for conservation and management of wildlife species. Estimating these parameters for pinnipeds can be challenging as they spend only a portion of their time on shore, where they are most easily counted. Counts of pinnipeds at index sites have been used to estimate population trend and as indices of local and regional abundance (Pitcher 1990, Udevitz 1999). However, estimates not adjusted for effects of environmental and other covariates could be biased because the proportion of the population available to be counted is not constant. Additional information recorded at index sites on "covariates" (*e.g.*, date, time-of-day, tidal stage) should be incorporated into statistical analyses to account for variation in the proportion of the seal population ashore when counts are conducted (Frost *et al.* 1999, Small *et al.* 2003). Knowledge of the effects of covariates on seal counts can be used to improve the experimental design, data collection, and statistical analyses of spatially extensive population surveys (*e.g.*, aerial surveys of multiple sites) resulting in more accurate and precise estimates of regional population trend (Adkison *et al.* 2003).

In Alaska most estimates of harbor seal population abundance and trend are based on aerial counts conducted during one to two weeks during the molting period (Frost *et al.* 1999, Boveng *et al.* 2003, Small *et al.* 2003). In the mid-1970s, three large harbor seal haul-outs were selected as index sites where seals were counted throughout the pupping and molting periods. Tugidak Island, in the western Gulf of Alaska, was perhaps the largest harbor seal haul-out in the world in the 1950s and 1960s, and the site where declines were first documented in Alaska (Pitcher 1990). Nanvak Bay, the largest haul-out in northern Bristol Bay, is located near the northern extent of the harbor seal range and southern extent of the spotted seal (*Phoca larga*) range. Otter Island, in the Bering Sea, likely supported the greatest concentration of harbor seals in the Pribilof Islands and is isolated from other haul-outs. Although each of these sites is important regionally, the relative abundance of seals at each site differs. For example, maximum counts in the mid-1970s at each site were 9,300 at Tugidak

Island, 2,918 at Nanvak Bay, and 1,175 at Otter Island. The only other sites in Alaska where standardized, land-based counts were conducted over a decade or more are at Johns Hopkins Inlet and Muir Inlet in Glacier Bay National Park (Calambokidis *et al*. 1987, Mathews and Pendleton 2006).

Here we examine long time series of harbor seal counts collected over several decades at three important sites in the Bering Sea and the Gulf of Alaska using generalized mixed linear models. We adjust counts for the effects of covariates and estimate trends during the pupping and molting periods at Tugidak Island (1994–2000) and Nanvak Bay (1990–2000) during both the periods. We also update the long-term Tugidak Island population trend estimate of Pitcher (1990), based on molting period counts from 1976 to 2000. We compare count data from three summers on Otter Island, the only systematic count data available for harbor seals in the Pribilof Islands.

METHODS

Study Areas

The Alaska Department of Fish and Game and the University of Alaska Fairbanks established field camps at Tugidak Island (56°30′N, 154°40′W), Nanvak Bay (58°35′N, 161°45′W), and Otter Island (57°02′N, 170°24′W) in the mid-1970s to count harbor seals (Fig. 1). Monitoring efforts varied among sites across years, but effort declined or was nonexistent during the 1980s at all three locations. We resumed standardized daily counts during the pupping and molting periods at Tugidak Island and Nanvak Bay during the 1990s and monitored the Otter Island haul-out during the pupping period in 1995.

Harbor seals haul out on Southwest (SW) Beach and Middle Beach along the southwestern shores of Tugidak Island. These sand and gravel beaches are bordered by 15–30-m cliffs that afford excellent views of the seals. Haul-out space is available to seals during most tide stages although space is reduced during moderate high tides and not available during extreme high tides. Seals also haul out on the beaches and sandbars in and around the lagoon on the northeast end of the island; these sites are difficult to observe from land and, thus, land-based counts have not been conducted there. Nanvak Bay is 25 km southeast of Cape Newenham, the peninsula that divides Bristol and Kuskokwim bays. Harbor seals, and some spotted seals (a closely related, visually similar species), haul out on sandbars, mudflats, and a barrier spit near the mouth of the bay. The sandbars and mudflats are submerged at high tide but the haul-out site on the barrier spit is exposed during all but extreme high tides. Although the bay is shallow, all haul-outs are adjacent to a deep-water channel, allowing direct access to the bay and the outer coast. Harbor seals haul out along the cobble beaches of Otter Island.

Data Collection

We used spotting scopes (20×–60×) and binoculars (10 × 42) from elevated vantage points to conduct daily counts of seals during May and June and from mid-July to mid-September in 1994–2000 at Tugidak Island and from mid-May through September or October in 1990–2000 at Nanvak Bay. These dates encompassed the pupping and molting periods, which we identified based on visual observations of seal behavior and pelage condition. In 2000 additional counts were made at Nanvak Bay during 15 d centered around both the peak pupping and molting periods. During

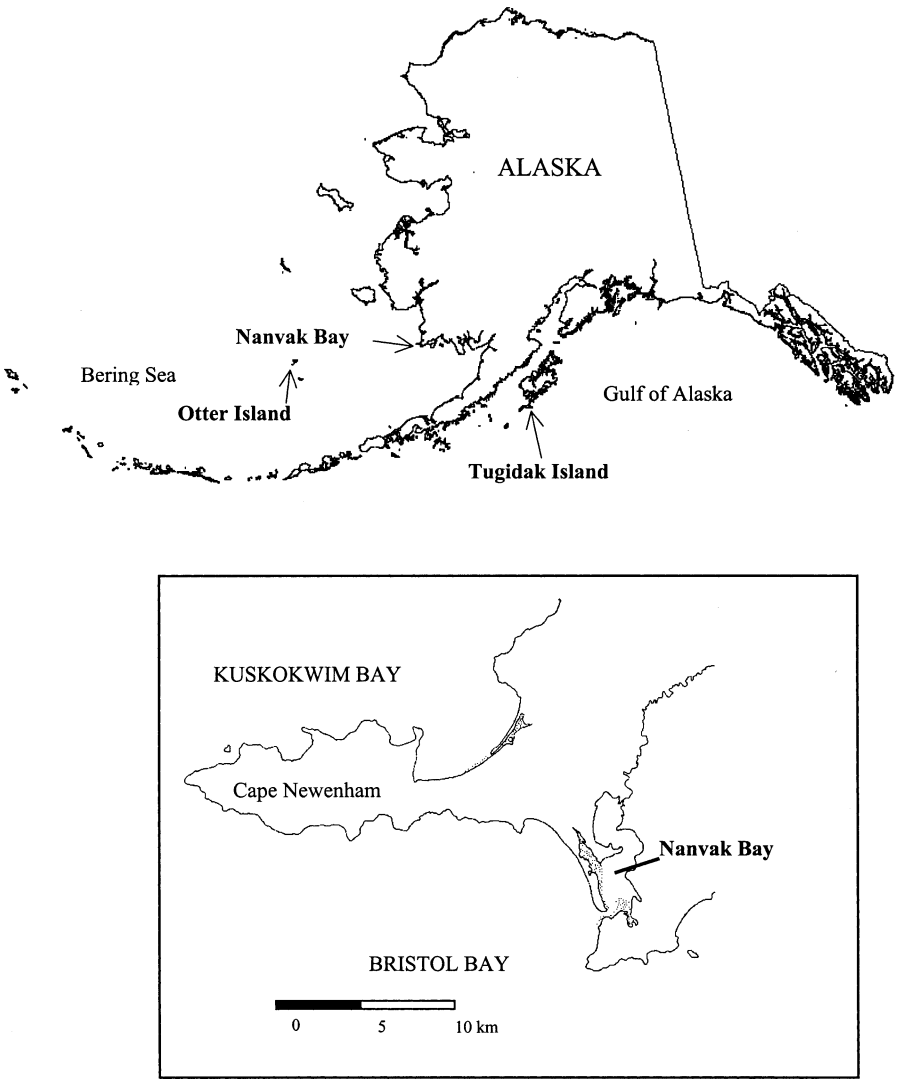

Figure 1. Location of harbor seal population monitoring sites at Tugidak Island, Otter Island, and Nanvak Bay (in northern Bristol Bay), Alaska.

those periods, seals were counted every 3–5 h between 0600 and 2100. Counts at Otter Island were conducted daily or every other day throughout July, the main pupping period, in 1974, 1978,[1] and 1995.

At Tugidak Island during 1994–2000, similar numbers of seals used SW and Middle beaches during the pupping period. Seals primarily used SW Beach during the molting period although Middle Beach generally was used through mid-August and then abandoned. We combined counts from SW and Middle beaches for analyses until

[1] Unpublished data provided by Brendan P. Kelly, University of Alaska Southeast, 11120 Glacier Highway, Juneau, Alaska, 99801, April 2000.

Middle Beach was abandoned, then we used only SW Beach counts. We additionally used counts collected from SW Beach during the molting period from 1976 to 1992 (from Pitcher 1990 and ADF&G, unpublished). Counts from Middle Beach during this earlier period were not included because only small numbers of seals (<50; a small fraction of the total number) hauled out there sporadically and they were not monitored regularly. At Nanvak Bay on most days, we counted seals from either of two points: North Spit Dune (NSD) or Watch Point Dune (WPD). NSD provided a closer and better view of seals hauled out on the mudflats and was our preferred observation point. At WPD, a 4-m tower atop the dune provided extra elevation to view seals. WPD was used when rough water made channel crossing risky or when seals were present on the barrier spit.

We counted the total number of seals ashore at Tugidak Island and Nanvak Bay, and the number of pups at Tugidak Island only. At Nanvak Bay we assigned a quality rating to our count (high, moderate, low) based on seal haul-out location and the observation site. We recorded six weather parameters: cloud cover (none, partial, complete), precipitation (Tugidak Island: none, mist/light rain, heavy rain; Nanvak Bay: absent, present), air temperature (°C), average March sea-surface temperature for each year (Tugidak Island: an index of oceanic conditions), wind speed (km/h), and wind direction based on predominant weather patterns (Tugidak Island: N–NE, E, S–SE, SW, W–NW, calm or variable; and Nanvak Bay: N–NE, E–SE–S, SW, W–NW, calm or variable). Tide height and timing were computed from published tide tables for Tugidak Island. Tides in Nanvak Bay are unusual in that they do not follow predicted cycles in published tide tables, so we recorded tidal stage as a categorical variable (high, low, rising, falling) based on direct observations during each count. During daylight hours, all but one low tide observation ($n = 64$) occurred after solar noon and 56 of 72 high tides occurred in the morning (Fig. 2). Usually, we counted seals during the afternoon or evening when the one obvious daily low tide regularly occurred, except in 2000 when additional counts were made throughout the day.

Analyses

For Tugidak Island, we used counts from 25 May through 20 June for the pupping period and from 24 July through 31 August for the molting period. For Nanvak Bay, we used counts from 8 June to 10 July for the pupping period and 1 August to 15 September for the molting period. We did not use counts conducted in 1999 at Nanvak Bay due to inconsistencies in data collection. Multiple counts were made on some days; all counts were included in the analyses.

We evaluated the influence of the following covariates on counts: date, time-of-day (time relative to solar noon), time in relation to low tide (Tugidak Island), tide height (Tugidak Island) or tidal stage (Nanvak Bay), count quality (Nanvak Bay), and weather conditions. We included a variable that allowed the effect of wind speed to vary by wind direction (*i.e.*, wind speed × wind direction interaction). We evaluated quadratic terms for the covariates date, time-of-day, time relative to low tide, tide height (Tugidak Island), and wind speed (by direction). Analysis of Tugidak Island molting period counts from 1976 to 2000 included date, tide, and diurnal effects, but not weather covariates, except for March sea-surface temperature. A quadratic year effect was included for the 1976–2000 Tugidak Island analysis and all Nanvak Bay analyses because of the longer time spans. We use the 1994–2000 Tugidak Island analyses to discuss the effects of covariates because the long-term analysis (1976–2000) was not based on the complete suite of covariates and relatively few counts (10 or less per year) were available in five of the earlier years (1977, 1982–1988).

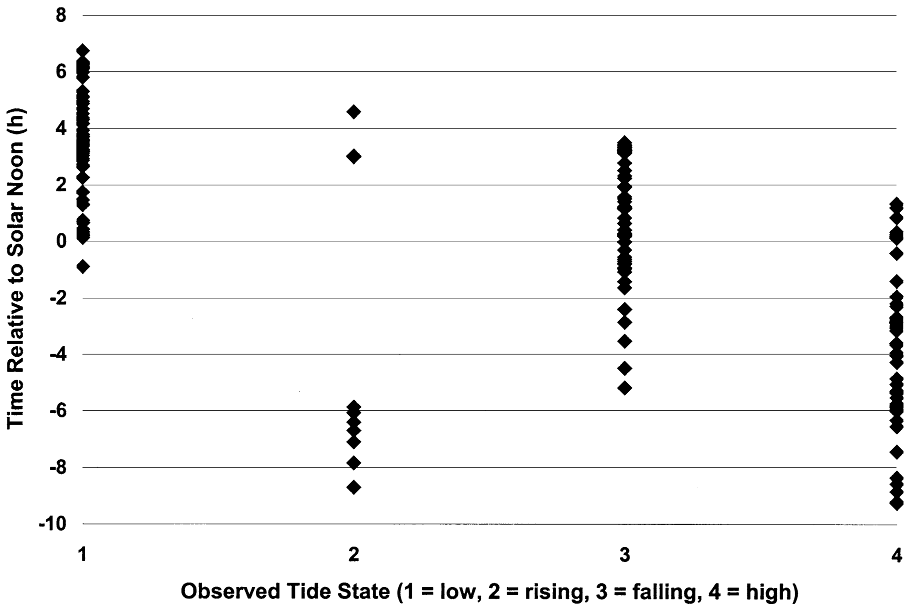

Figure 2. Observed tide state relative to time-of-day (0 = solar noon) at Nanvak Bay in 2000. All but one low tide observation was after solar noon and most high tide observations were before solar noon.

Many studies have shown that numbers of harbor seals hauled out vary significantly with date, generally increasing to a peak then declining within both the pupping and molting periods (Schneider and Payne 1983, Allen *et al.* 1988, Grellier *et al.* 1996, Mathews and Kelly 1996, Thompson *et al.* 1997, Frost *et al.* 1999, Small *et al.* 2003, Ver Hoef and Frost 2003). There are several analytical approaches to account for this pattern. One approach is to fit a single curve for all years of survey data (Small *et al.* 2003), which assumes that the shape and peak date of the curve are the same for all years. With this approach, nondirectional variation among years in the actual timing of peak abundance does not bias estimates of trend but potentially reduces precision (Adkison *et al.* 2003); directional variation in date of peak counts could be confounded with population change over time. If sufficient data are available (*i.e.*, enough counts throughout the pupping or molting period), another strategy is to align the peaks of the counts across years prior to analysis. This method assumes that only the shapes of the curves, and not the peak dates, are the same among years and allows us to better estimate trend and the effects of other covariates with fewer parameters than modeling date separately for each year. We used this latter method for the 1994–2000 Tugidak Island pupping period analyses (both pups and all seals) and all of the Nanvak Bay analyses, because we had long series of counts within all years to determine the date of peak abundance. Within each year, we subtracted the date of the maximum count from each date to center the data. Therefore, the date covariate represents the decrease in counts relative to the within-year peak. For both the 1994–2000 and 1976–2000 Tugidak Island molting period analyses, sufficient counts were not available to estimate the date of peak abundance for each year, and thus we fit a single curve for all years.

We estimated trends and adjusted counts for the effects of covariates using generalized mixed linear models (Poisson errors and log link) (Littell *et al.* 1996). We accounted for temporal autocorrelation among counts within years by using a spatial correlation structure with distance based on the time elapsed between counts (Littell *et al.* 1996). When final models did not fit the Poisson assumptions (*e.g.*, variance > mean), we used quasilikelihood methods (McCullagh and Nelder 1989) to inflate the estimated standard errors. We began with the full model including all of the covariates and quadratic terms and eliminated terms from the model one at a time based on the Wald F statistics ($P > 0.05$). We also used a small sample version of Akaike's Information Criteria (AICc) to help assess which variables to retain in the final model (Hurvich and Tsai 1989). In order to estimate trend, the year effect was retained in all models regardless of the Wald statistic. To evaluate the relative effect of the covariates on the final trend estimate, we omitted individual covariates and estimated the trend using the remaining covariates that were significant in the final model. We then calculated the percent change in trend by comparing the model with the covariate omitted to the final model.

Results

Trends

Based on counts of all seals during the molting period from 1976 to 2000, the population of harbor seals on Tugidak Island declined dramatically through the early 1980s, declined at a slower rate through the late 1980s, stabilized in the early 1990s, and then increased beginning in the mid-1990s (Fig. 3). The overall annual trend across this 25-yr period was −3.3% (95% CI: −4.4%–−2.3%; Table 1). During 1994–2000, the number of all seals increased at a moderate rate of 3.4%/yr (95% CI: 1.0%–5.8%; Table 1, Fig. 4A) during the molting period, while the number of pups and all seals during the pupping period increased at higher annual rates of 5.4%/yr (95% CI: 2.2%–8.8%) and 8.3%/yr (95% CI: 4.5%–12.3%), respectively (Fig. 4B, C, Table 1). For the 11-yr period from 1990 to 2000, land-based counts of harbor seals at Nanvak Bay increased 9.2%/yr (95% CI: 7.2%–11.3%) during the pupping period and 2.1%/yr (95% CI: 0.6%–3.6%) during the molting period (Fig. 5A, B, Table 2).

Covariates

Date and time-of-day were significant covariates in all analyses (Table 1, 2, Appendix I). The model predicted that the highest counts during the molting period at Tugidak Island would occur between late July and early August; the maximum counts in 1976–1979 occurred 19 August–3 September, 2–4 wk later than in the 1990s. Generally, maximum counts observed at Nanvak Bay occurred in late August or very early September. Predicted counts in all analyses were highest after midday. At Nanvak Bay, tidal stage and count quality also were significant covariates during both pupping and molting periods. Counts were negatively related to high and rising tides during molting and negatively related to high tides during pupping (Table 3). High-quality counts were 33%–39% higher than moderate-quality counts, and were 30%–40% higher than low-quality counts during both periods. Tide height and time-to-low-tide were not significant covariates in the Tugidak Island analyses.

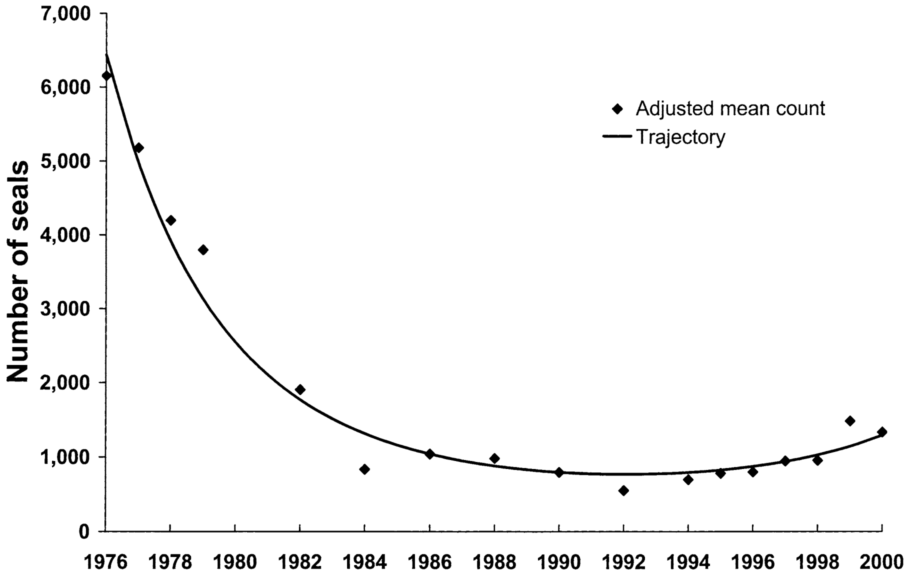

Figure 3. Estimated population change of harbor seals at Tugidak Island, Alaska, 1976–2000, based on counts of all seals during the molting period. Note the steep decline in the late 1970s and early 1980s and modest increase in the late 1990s. The trajectory is calculated from the linear and quadratic year terms from the final generalized mixed linear model, scaled to the yearly mean counts; yearly mean counts are adjusted for other covariates in the final model (see Table 1).

The effect of weather variables on counts of seals was not consistent between sites or between pupping and molting periods. At Nanvak Bay, pupping period counts were unaffected by weather variables. At Tugidak Island during the pupping period, pup counts also were unaffected by weather covariates but mean counts of all seals were 19% lower on clear days than on days with partial or complete cloud cover (Table 4). Mean counts of all seals at Tugidak Island during pupping were also lower during onshore (west) winds and during periods of precipitation (Table 4).

Molting period counts were affected by wind speed at both sites, wind direction at Tugidak Island, and precipitation at Nanvak Bay. At Nanvak Bay, the number of seals decreased with wind speeds >40 km/h, and at Tugidak Island, during west/northwest (onshore) winds (Table 4). Nanvak Bay counts were lower when there was precipitation (Table 3). March sea-surface temperature was a significant covariate in the 1976–2000 Tugidak Island molting period analysis only, with more seals counted in years with higher temperatures. Air temperature was not significant in any analysis.

Trend estimates during pupping and molting for both sites were substantially influenced by covariates included in the models (Table 5, 6). When all covariates were omitted from the Tugidak Island models, the estimated trend in pups (−1.7%/yr) and in all seals (5.2%/yr) during the pupping period represented changes of −132% and −37%, respectively, from the final covariate model (Table 5). The molting period estimate without covariates (6.0%/yr) corresponds to an 80% change from the final covariate model. The Nanvak Bay pupping period trend, estimated without covariates, was 5.5%/yr, a −41% change from the final covariate model estimate

Table 1. Annual trend estimates for harbor seals on Tugidak Island, Alaska, during the pupping and molting periods, and covariates that significantly ($P < 0.05$) influenced the number of seals hauled out. A "+" indicates a positive relationship between count and covariate, a "−" indicates a negative relationship, and a "*" indicates significance for categorical covariates.

				Covariates									
Years	Season	Trend (%/yr)	95% CI	Date	Date^2	Time-of-day	Time-of-day^2	Wind speed	Wind speed^2	Wind direction	Sea-surface temperature	Cloud cover	Precipitation
1976–2000[a]	Molting (all seals)	−3.3%	−4.4%–2.3%	+	−	+	−				+		
1994–2000	Molting (all seals)	3.4%	1.0%–5.8%	−	−	+	−	+	−	*[b]			
1994–2000	Pupping (all seals)	8.3%	4.5%–12.3%	+	−	+	−			*[c]		*[d]	*
1994–2000	Pupping (pups)	5.4%	2.2%–8.8%	+	−	+							

[a] Year^2 included in the model but cloud cover, precipitation, temperature, and wind variables were not available to be included.
[b] Wind direction reduced to two categories: west/northwest and other.
[c] Wind direction reduced to two categories: east and west.
[d] Cloud cover reduced to two categories: clear and partial/complete.

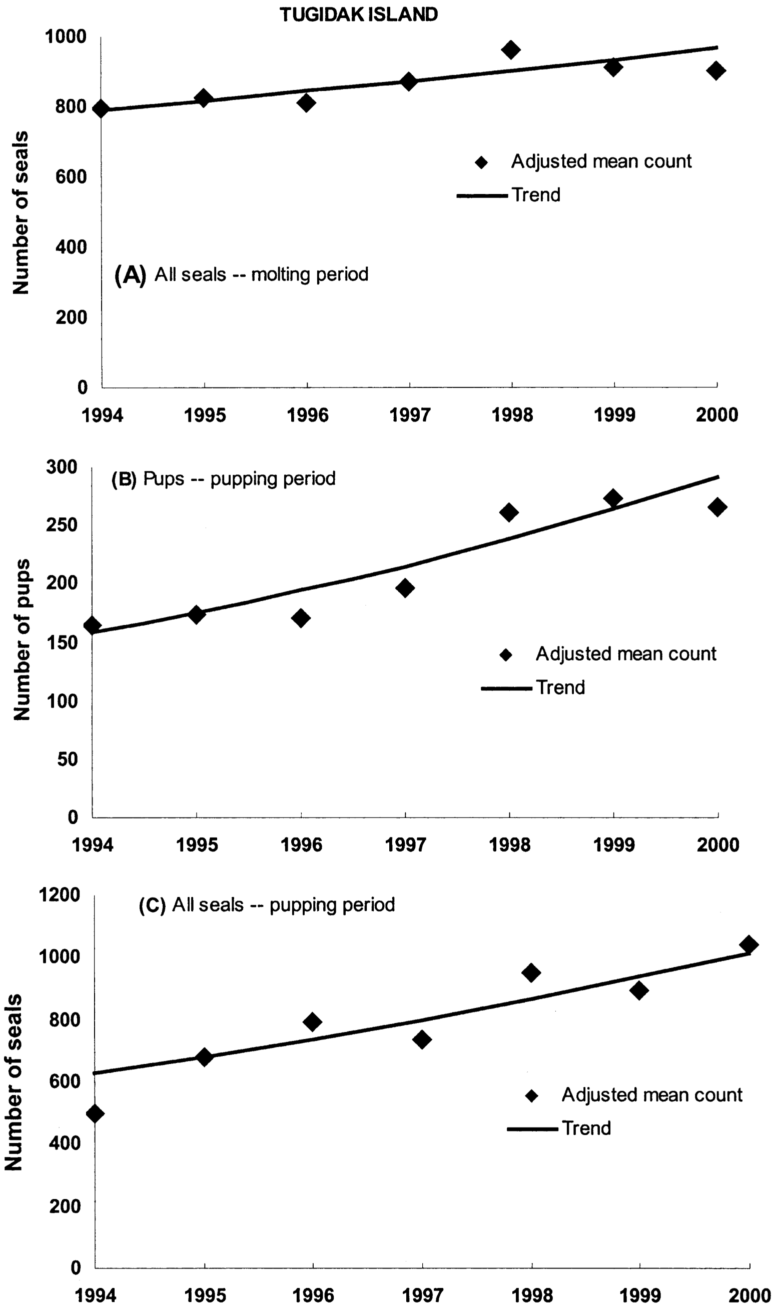

Figure 4. Estimated population change of harbor seals at Tugidak Island, Alaska, 1994–2000, based on counts of (A) all seals during the molting period, (B) pups during the pupping period, and (C) all seals during the pupping period. The trend is calculated from the linear year term from the final generalized mixed linear model, scaled to the yearly mean counts; yearly mean counts are adjusted for other covariates in the final model (see Table 1).

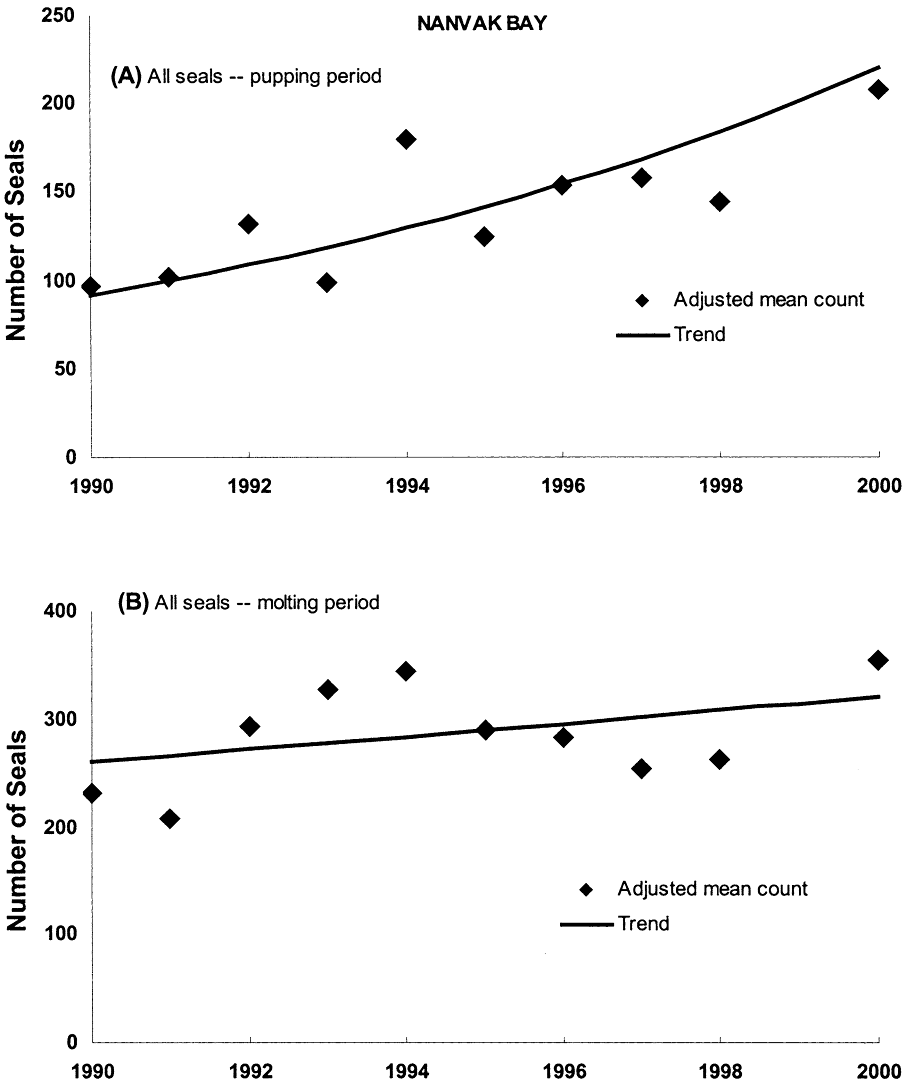

Figure 5. Estimated population change of harbor seals at Nanvak Bay, Alaska, 1990–2000, based on counts of all seals during (A) the pupping period, and (B) the molting period. The trend is calculated from the linear year term from the final generalized mixed linear model, scaled to the yearly mean counts; yearly mean counts are adjusted for other covariates in the final model (see Table 2).

(Table 6). During the molting period, the estimated trend without covariates in the Nanvak Bay model was 0.7%/yr, a change of −66% from the final covariate model. In all Tugidak Island analyses, trend estimates were most sensitive to date. Nanvak Bay trend estimates were most sensitive to tidal stage and count quality during the pupping period, and time-of-day and precipitation during the molting period.

Table 2. Annual trend estimates for harbor seals at Nanvak Bay, Alaska, during the pupping and molting periods from 1990 to 2000 (excluding 1999), and covariates that significantly ($P < 0.05$) influenced the number of seals hauled out. A "+" indicates a positive relationship between count and covariate, a "−" indicates a negative relationship, and a "*" indicates significance for categorical covariates.

			Covariates							
Season	Trend (%/yr)	95% CI	$Date^2$	Time-of-day	Time-of-day^2	Tidal stage	Count quality	Precipi-tation	Wind speed	Wind $speed^2$
Pupping period	9.2%	7.2%–11.3%	−	+	−	*	*			
Molting period	2.1%	0.6%–3.6%	−	+	−	*	*	*	−	−

Table 3. Least-squares mean harbor seal counts (and percent change from the maximum) at Nanvak Bay for levels of categorical variables adjusted for other variables in the models.

Variable	Level	Mean total count (pupping period)	Mean total count (molting period)
Precipitation	none		199
	rain		178 (−10%)
Tide	falling	132	219
	low	132	215 (−2%)
	rising	126 (−4%)	193 (−12%)
	high	44 (−67%)	138 (−37%)
Count quality	low	89 (−30%)	159 (−40%)
	moderate	86 (−33%)	160 (−39%)
	high	127	263

Table 4. Least-squares mean harbor seal counts from 1994 to 2000 (and percent change from the maximum) at Tugidak Island for levels of categorical weather variables adjusted for other variables in the models.

Variable	Level	Mean total count (pupping period)	Mean total count (molting period)
Precipitation	None	739	
	Light	642 (−13%)	
	Heavy	581 (−21%)	
Cloud cover	None	588 (−19%)	
	Partial/complete	723	
Wind direction	Other		929
	West/northwest		827 (−11%)
	East	709	
	West	597 (−16%)	

Otter Island Counts

Based on daily pupping period counts of harbor seals at Otter Island in the Pribilof Islands, maximum counts (data not available to calculate means) of all seals declined 40% (from 1,175 to 707) and maximum counts of pups declined 50% (from 228 to 114) between 1974 and 1978[1] (Johnson 1976). Between 1978 and 1995, further declines in all seals (71%; from 707 to 202) and in pups (63%; from 114 to 42) were documented.

Discussion

Population Trends

The positive population trend estimates of harbor seals on Tugidak Island during 1994–2000 document an important change in status at one of the largest terrestrial haul-outs in the Gulf of Alaska. Pitcher (1990) estimated molting period declines at Tugidak Island of −17%/yr from 1976 to 1988 and suggested the decline was steeper from 1976 to 1979 (−21%/yr) and less catastrophic from 1982 to 1988 (−7%/yr). We estimated a −3.3%/yr decline during the molting period for the entire

Table 5. Sensitivity of harbor seal trend estimates during the pupping and molting periods at Tugidak Island, Alaska, 1994–2000, to exclusion of covariates. Seal counts are influenced by all of these factors; those that cause only a small change in the trend estimates (*i.e.*, low sensitivity) were largely controlled through survey design, whereas it is more important to include variables with large sensitivities in the trend estimation model. Sensitivity of trend estimates to the use of covariates can change with differing conditions and survey design.

	Pupping period				Molting period	
	All seals		Pups		All seals	
Covariate omitted	Trend	Percent change	Trend	Percent change	Trend	Percent change
None	8.32		5.4		3.35	
Date and date^2	3.76	−54.8	−0.83	−115.3	6.91	+106.3
Time-of-day and time-of-day^2	8.93	+7.4	5.61	+3.7	3.61	+7.8
Cloud cover	9.31	+11.9				
Precipitation	8.22	−1.2				
Wind speed and wind speed^2					3.53	+5.4
Wind direction	9.37	+12.6			1.15	−65.7
All covariates omitted	5.22[a]	−37.3	−1.72[b]	−131.7	6.03[c]	+80.0

[a] 95% confidence interval = (0.02, 10.68).
[b] 95% confidence interval = (−25.46, 29.60).
[c] 95% confidence interval = (3.34, 8.79).

1976–2000 interval. This long-term estimate is an average change over the entire time interval and incorporates the large declines described by Pitcher (1990) along with the population increases during the 1990s. The substantial negative average change over this long interval places the current increase in perspective by highlighting that the population in 2000 remained reduced by approximately 80% from 1970s levels.

From 1990 to 2000, the number of seals ashore at Nanvak Bay increased significantly. These are the first covariate-adjusted trend estimates from the Bering Sea based on counts collected during both the pupping and molting periods. We believe that Nanvak Bay is an important site to monitor, being the largest haul-out in northern Bristol Bay and located near the northern extent of the harbor seal range and southern extent of the spotted seal range in Alaska. At Nanvak Bay, maximum pupping period (157) and molting period (470) counts were approximately 2.5× and 6× lower, respectively, when we began surveys in 1990 than they were in 1975 (maximum pupping period count: 375, maximum molting period count: 2,918) (Johnson 1976). The maximum molting period count in 1975 was greater than any count since that time. To put this number in perspective, the highest count of seals at all northern Bristol Bay haul-outs combined (from Cape Constantine to Cape Newenham, but excluding Nanvak Bay), based on six aerial surveys flown during the molting period in both 1991 and 1995, was less than 800 animals.[2] These data suggest that the decline in seal numbers at Nanvak Bay cannot simply be explained by seals moving to nearby haul-outs. In 2000 the maximum pupping period count (477) was greater than in 1975, whereas the maximum molting period count (575) was still 5× lower

[2] Personal communication from Dave E. Withrow, National Marine Mammal Lab, National Marine Fisheries Service, NOAA, Seattle, Washington, December 2003.

Table 6. Sensitivity of harbor seal trend estimates during the pupping and molting periods at Nanvak Bay, Alaska, 1990–2000, to exclusion of covariates. Seal counts are influenced by all of these factors; those that cause only a small change in the trend estimates (*i.e.*, low sensitivity) have largely been controlled through survey design while it is more important to include variables with large sensitivities in the trend estimation model. Sensitivity of trend estimates to the use of covariates can change with differing conditions and survey design.

	Pupping period		Molting period	
Covariate omitted	Trend	Percent change	Trend	Percent change
None	9.22		2.08	
Date^2	9.66	+4.7	1.99	−4.3
Time-of-day and time-of-day^2	8.59	−6.9	2.49	+19.6
Precipitation			2.53	+21.3
Tidal stage	7.91	−14.1	1.96	−5.8
Count quality	10.68	+15.8	2.22	+6.3
Wind speed and wind speed^2			1.88	−10.0
All covariates omitted	5.47[a]	−40.7	0.70[b]	−66.3

[a] 95% confidence interval = (3.28, 7.70).
[b] 95% confidence interval = (−1.24, 2.68).

than in 1975. Although the Nanvak Bay data are from a single site, they indicate a substantial decline in harbor seal numbers between 1975 and 1990, which cannot be explained by local movements. Unfortunately, except for 1975 no other comparable surveys were conducted at Nanvak Bay in the 1970s or 1980s. Accounting for the effects of covariates, Small *et al.* (2003) reported a stable trend estimate for harbor seals in southern Bristol Bay from 1998 to 2001, based on counts from molting period surveys.

Spotted seals apparently make up a small proportion of seals on shore at Nanvak Bay,[3] (Johnson 1976), and so fluctuations in spotted seal numbers could contribute to changes in seal counts at that site; however, we have no data to evaluate whether there has been a change in proportions.

During the 1970s, Otter Island likely supported the largest concentration of harbor seals in the Pribilof Islands. Comparisons of maximum counts of seals in 1974 and 1978 on Otter Island suggest large declines in pups and in all seals onshore during pupping. The population declined even further by 1995. Given Otter Island's remote location and the difficulty of accessing the island, it is unlikely that human activity played a direct role in the large reduction in seal numbers. Northern fur seals, which began using Otter Island in the early 1980s (Hansen 1982) and were abundant by 1995 (L. Jemison, unpublished data), might have been a factor in the later stages of the decline. Examination of four dead pups on Otter Island in 1995 suggested that their death might have been due to trampling, presumably by fur seals (L. Jemison, unpublished data).

Harbor seal population trend estimates at Tugidak Island and Nanvak Bay are similar in several respects: (1) harbor seal counts in the mid-1970s were much higher than counts in the early to mid-1990s; (2) population trend estimates were positive during the 1990s through 2000, with trend estimates based on pupping period counts substantially higher than those estimated using molting period counts; and

[3] Personal communication from John J. Burns, Living Resources Inc., Fairbanks, Alaska, May 1990.

(3) despite steady population increases during the 1990s, molting period counts in 2000 were still much reduced from 1970s levels.

The cause of the different pupping and molting period trend estimates is unknown and would be difficult to determine without permanently marked seals. We suggest that age and sex differences in behavior between these periods have contributed to the different magnitude of the trends. The pupping period trend estimate is more likely influenced by the behavior of reproductive females and pups. During the pupping period, nursing females have higher site fidelity than at other times of the year, and have a higher degree of site fidelity than males or females without pups (Godsell 1988). The molting period trend estimate is likely influenced by differing behaviors of all age–sex classes associated with molting. Daniel *et al*. (2003) demonstrated that the timing of the annual molt differed among age–sex classes and that the maximum numbers hauled out in each age–sex class were positively related to the molt. In Sweden, sighting frequency of branded harbor seals varied by age and sex throughout the summer (Härkönen *et al*. 1999). We have evidence that fewer pups (by a factor of 10 or more) are hauled out during the molting period relative to the pupping period, based on composition and count data collected from 1997 to 2000 (L. Jemison, unpublished data). Barring immigration during pupping, we suspect that the strong pupping period trend estimates are driven by high adult female survival and strong recruitment of young animals into the population.

Alternatively, the differing pupping and molting period trends could be explained by an increase in pup production that is offset by low pup survival, resulting in a lower molting period trend. We have no evidence to suggest that pup survival is low. Based on sightings of tagged pups at Tugidak Island, minimum estimates of pup survival to one year of age range from 65% to 90% from 1997 to 2000[4] suggesting that pup survival was high during the late 1990s–2000.

Identifying the causes of the harbor seal declines in southwestern Alaska, and possibly related decreases in Steller sea lion and northern fur seal populations, remains highly controversial (*e.g.*, Trites 1992, Merrick *et al*. 1997, Calkins *et al*. 1998, Pitcher *et al*. 1998, Jemison and Kelly 2001, Springer *et al*. 2003, Fritz and Hinckley 2005). However, factors that led to the harbor seal decline in some parts of Alaska (*e.g.*, Tugidak Island, Kodiak Island, Nanvak Bay) seemingly have abated sufficiently such that populations are currently increasing.

Covariate Effects

In addition to changes in population abundance, other factors influence the number of seals on shore. At Tugidak Island and Nanvak Bay, date was an important covariate during both pupping and molting. At Tugidak Island, Moran (2003) determined that the local population declined during their August–September study period, but the proportion of the local population that was hauling out did not change over time. He projected peak local abundance in early August, which is consistent with our findings and those of Small *et al*. (2003) for the Kodiak area and Boveng *et al*. (2003) for the Gulf of Alaska. This suggests that the within-season declines in counts were a function of seals leaving the count area, perhaps when they completed molting (Daniel *et al*. 2003).

[4] Personal communication from Kelly Hastings, Alaska Department of Fish and Game, 525 W. 67th Ave. Anchorage, Alaska, December 2003.

At Nanvak Bay, we adjusted (*i.e.*, centered) the date variable by subtracting the date of the largest count. This removes the variation that occurs when peak dates shift among years, either at random or directionally, resulting in improved estimates of trend, but does not yield predicted dates of peak counts. Our model predicted counts declining evenly away from the central peak date. Based on one year (2000) of haul-out behavior from radio-tagged seals, Simpkins *et al*. (2003) found a complex association between date and the proportion of seals hauled out at Nanvak Bay, with the estimated peak proportion in mid-September. However, Simpkins *et al*. (2003) did not begin monitoring seals until 16 August, one day after our maximum (unadjusted) count. Our observed maximum counts over multiple years (including 2000) ranged from 13 August to 3 September, with the exception of 1993, which had two peak counts, 17 August and 22 September. In a separate analysis of 2000 count data from Nanvak Bay, using a wider date range than in our other analyses (1 August–3 October; G. Pendleton, unpublished data), we found a weak decline in predicted counts with respect to date for linear, quadratic, and cubic date functions, rather than complex fluctuations.

Other variables such as time-of-day and tide can affect the number of seals hauled out. At both sites, during pupping and molting, covariate models predicted highest counts in the afternoon, from about 1–3 h after midday at Tugidak Island and from about midday to 6 h after midday at Nanvak Bay. Similar results were found at Tugidak Island by Moran (2003), and at Nanvak Bay by Simpkins *et al*. (2003). In studies at sites where haul-out substrate is available only at low or moderate tides, maximum counts of seals have been reported during morning low tides (Olesiuk *et al*. 1990, Frost *et al*. 1999) or, more frequently, during afternoon low tides (Allen *et al*. 1984, Pauli and Terhune 1987, Thompson *et al*. 1989, Kovacs *et al*. 1990, Watts 1996, Small *et al*. 2003). In studies at sites where haul-out space is available during all tidal stages, diurnal patterns are dominant over tidal cycles with seal numbers peaking in the afternoon (Stewart 1984, Godsell 1988). At Tugidak Island, where haul-out substrate is reduced but still available during high tides, we found strong diurnal effects, but no relationship between tide height or timing and seal counts. Moran (2003) found tide height to be an important covariate at Tugidak Island. However the relationship between counts and tide height was nonlinear, with few seals hauled out at very high or very low tides, but a larger number of seals on the beach at other tide levels. This is consistent with our lack of a tide effect because we rarely counted seals during extreme high tides, due to the difficulty of observing seals pushed by the tide high up onto the beach, directly below the bluffs. At Nanvak Bay, haul-out space is limited during high tides as all haul-outs are submerged except the barrier spit; we found a negative relationship between high tide and counts of seals. The effect was greater during pupping (−67%) than during molting (−37%), probably because seals do not haul out on the barrier spit during the pupping season. At Nanvak Bay, tide stage and time-of-day could be confounded (Fig. 2), as high tides during daylight hours almost always occurred in the morning, and low tides occurred in the afternoon and evening. Simpkins *et al*. (2003) found that seal counts were related to tidal conditions with time relative to low tide a good predictor, but tide height a much poorer predictor. They predicted that the largest proportion of seals would be hauled out >2 h after low tide (considered a rising tide in our categorical grouping) whereas we predicted highest counts occurred during low and falling tides. We believe the tide prediction by Simpkins *et al*. (2003) could be spurious because they used published predictions of tide height and timing from a site 39 km away, which we found to be only weakly related to our field observations of tide stage (G. Pendleton, unpublished data). The unusual tides at Nanvak Bay highlight the advantage of collecting detailed data at index sites, allowing a more complete understanding of covariate effects than is sometimes possible with other types of studies.

During the molting period, we found a decline in counts associated with wind at both sites, and a relatively weak negative relationship between counts and precipitation at Nanvak Bay. At Nanvak Bay, our findings generally agree with Simpkins *et al.* (2003). Weather factors had a greater influence during the pupping period at Tugidak Island where mean counts of all seals showed changes of up to 21% in relation to precipitation, cloud cover, and wind direction, though pup counts were unaffected by weather. Boveng *et al.* (2003) also noted reduced numbers of seals hauled out during high wind and rain.

Utility of Land-Based Index Sites

At Tugidak Island and Nanvak Bay, we estimated trends in abundance and determined the effects of covariates on counts collected over long time intervals within and across years. We believe that index sites such as these are useful adjuncts to, not replacements of, aerial trend surveys. Telemetry-based studies of haul-out patterns (*e.g.*, Simpkins *et al.* (2003).) are intermediate between land-based counts and aerial surveys, providing more detailed information over longer time spans than is possible with aerial surveys, but with less intensity than land-based studies. Regional trend estimates often are of more utility for management decisions at larger spatial scales than site-specific trends, which might differ from the regional pattern. However, land-based counts at single sites do provide survey-related information not readily available from aerial counts. Index site data can be collected on many variables, providing information on which variables should be considered in aerial survey design and analysis of the resulting data. Covariates that affect counts relatively consistently at a regional scale (*e.g.*, date, time-of-day), and bounds on minimal survey conditions (*e.g.*, wind, precipitation) can more easily be studied at an index site because of the broader range of the covariates typically obtained there. Adkison *et al.* (2003) evaluated the current design of aerial trend routes and the analyses used to estimate harbor seal trends in Alaska and found the current methods to be robust to most of the potential confounding factors. The one source of bias that could affect population trend estimates is a directional change in a covariate (Adkison *et al.* 2003) that is unknown or cannot be adjusted for. Index site data are likely better than aerial survey data for detecting relationships between covariates and counts and potentially for detecting directional change in a covariate. Land-based counts at Tugidak Island documented a 2–4-wk shift in dates of peak counts during the molting period, a pattern that may not have been evident with aerial survey data. Other valuable data that can be collected at index sites, such as productivity indices (*e.g.*, accurate counts of pups and mother-pup pairs), pupping and molting phenology, food habits, body condition, and survival rates can be helpful when interpreting population trend information.

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Literature Cited

Adkison, M. D., T. J. Quinn II and R. J. Small. 2003. Evaluation of the Alaska harbor seal (*Phoca vitulina)* population survey: A simulation study. Marine Mammal Science 19:764–790.

Allen, S. G., D. G. Ainley, G. W. Page and C. A. Ribic. 1984. The effect of disturbance on harbor seal haulout patterns at Bolinas Lagoon, California. Fishery Bulletin 82:493–500.

Allen, S. G., C. A. Ribic and J. E. Kjelmyr. 1988. Herd segregation in harbor seals at Point Reyes, California. California Fish and Game 74:55–59.

Boveng, P. 1988. Status of the Pacific harbor seal population on the U. S. west coast. National Marine Fisheries Service Administrative Report LJ-88–07. 43 pp. (unpublished). Available from National Marine Mammal Lab, 7600 Sand Point Way, NE, Seattle, WA 98115.

Boveng, P. L., J. L. Bengston, D. E. Withrow, J. C. Cesarone, M. A. Simpkins, K. J. Frost and J. J. Burns. 2003. The abundance of harbor seals in the Gulf of Alaska. Marine Mammal Science 19:111–127.

Braham, H. W., R. D. Everitt and D. J. Rugh. 1980. Northern sea lion population decline in the Eastern Aleutian Islands. Journal of Wildlife Management 44:25–33.

Calambokidis, J., B. Taylor, S. Carter, G. Steiger, P. Dawson and L. Antrim. 1987. Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. Canadian Journal of Zoology 65:1391–1396.

Calkins, D. G., E. F. Becker and K. W. Pitcher. 1998. Reduced body size of female Steller sea lions from a declining population in the Gulf of Alaska. Marine Mammal Science 14:232–244.

Calkins, D., D. C. McAllister, K. W. Pitcher and G. W. Pendleton. 1999. Steller sea lion status and trend in Southeast Alaska: 1979–1997. Marine Mammal Science 15:462–477.

Daniel, R. G., L. A. Jemison, G. W. Pendleton and S. M. Crowley. 2003. Molting phenology of harbor seals on Tugidak Island, Alaska. Marine Mammal Science 19:128–140.

Doroff, A. M., J. A. Estes, M. T. Tinker, D. M. Burns and T. J. Evans. 2003. Sea otter population declines in the Aleutian Archipelago. Journal of Mammalogy 84:55–64.

Fisher, H. D. 1952. The status of the harbour seal in British Columbia, with particular reference to the Skeena River. Bulletin of Fisheries Resources Board of Canada No. 93. 58 pp.

Fritz, L. W., and S. Hinckley. 2005. A critical review of the regime shift—"junk food"—nutritional stress hypothesis for the decline of the western stock of Steller sea lion. Marine Mammal Science 21:476–518.

Frost, K. J., L. F. Lowry and J. M. Ver Hoef. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. Marine Mammal Science 15:494–506.

GODSELL, J. 1988. Herd formation and haul-out behaviour in harbour seals (*Phoca vitulina*). Journal of Zoology, London 215:83–98.

GRELLIER, K., P. M. THOMPSON AND H. M. CORPE. 1996. The effect of weather conditions on harbour seal *(Phoca vitulina)* haulout behaviour in the Moray Firth, northeast Scotland. Canadian Journal of Zoology 74:1806–1811.

HANSEN, C. 1982. Report on a census of the pinniped population on Otter Island, June 26, 1981. National Marine Fisheries Service. 12 pp. (unpublished). Available from National Marine Mammal Lab, 7600 Sand Point Way, NE, Seattle, WA 98115.

HÄRKÖNEN, T., K. C. HÅRDING AND S. G. LUNNERYD. 1999. Age and sex specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. Journal of Applied Ecology 36:825–841.

HARVEY, J. T., R. F. BROWN AND B. R. MATE. 1990. Abundance and distribution of harbor seals *(Phoca vitulina)* in Oregon, 1975–1983. Northwest Naturalist 71:65–71.

HURVICH, C. M., AND C.-L. TSAI. 1989. Regression and time series model selection in small samples. Biometrika 76:297–307.

JEFFERIES, S., H. HUBER, J. CALAMBOKIDIS AND J. LAAKE. 2003. Trend and status of harbor seals in Washington State: 1978–1999. Journal of Wildlife Management 67:207–218.

JEMISON, L. A., AND B. P. KELLY. 2001. Pupping phenology and demography of harbor seals on Tugidak Island, Alaska. Marine Mammal Science 17:585–600.

JOHNSON, B. 1976. Studies of the northernmost colonies of Pacific harbor seals, *Phoca vitulina richardsi*, in the eastern Bering Sea. 67 pp. (unpublished). Available from Alaska Department of Fish and Game, Division of Wildlife Conservation, 525 W. 67th Avenue, Anchorage, AK 99518.

KOVACS, K., K. JONAS AND S. WELKE. 1990. Sex and age segregation by *Phoca vitulina concolor* at haul-out sites during the breeding season in the Passamaquoddy Bay Region, New Brunswick. Marine Mammal Science 6:204–214.

LENSINK, C. J. 1958. Predator investigation and control. Alaska Department of Fish and Game Annual Report No. 10. Juneau, Alaska. pp. 91–104. (unpublished). Available from Alaska Department of Fish and Game, Division of Wildlife Conservation, 525 W. 67th Avenue, Anchorage, AK 99518.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Cary, NC.

LOUGHLIN, T. R., A. S. PERLOV AND V. A. VLADIMIROV. 1992. Range-wide survey and estimation of total number of Steller sea lions in 1989. Marine Mammal Science 8:220–239.

MATHEWS, E. A., AND B. P. KELLY. 1996. Extreme temporal variation in harbor seal (*Phoca vitulina richardsi*) numbers in Glacier Bay, a glacial fjord in Southeast Alaska. Marine Mammal Science 12:483–489.

MATHEWS, E. A., AND G. W. PENDLETON. 2006. Declines in harbor seal (*Phoca vitulina*) numbers in Glacier Bay National Park, Alaska, 1992–2002. Marine Mammal Science 22:170–191.

MCCULLAGH, P., AND J. A. NELDER. 1989. Generalized linear models. 2nd edition. Chapman and Hall, New York, NY.

MERRICK, R. L., M. K. CHUMBLEY AND G. V. BYRD. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. Canadian Journal of Fisheries and Aquatic Science 54:1342–1348.

MERRICK, R. L., T. R. LOUGHLIN AND D. G. CALKINS. 1987. Decline in abundance of northern sea lions, *Eumetopias jubatus*, in Alaska, 1956–86. Fishery Bulletin 85:351–365.

MORAN, J. R. 2003. Counting seals; estimating the unseen fraction using a covariate and capture-recapture model. M.S. thesis, University of Alaska, Fairbanks. 49 pp.

OLESIUK, P. F. 1999. An assessment of the status of harbour seals (*Phoca vitulina*) in British Columbia. Canadian Stock Assessment Secretariat Research Document 99/33, Department of Fisheries and Oceans Canada, Ottawa, Canada. 130 pp.

OLESIUK, P., M. BIGG AND G. ELLIS. 1990. Recent trends in the abundance of harbour seals, *Phoca vitulina,* in British Columbia. Canadian Journal of Fisheries and Aquatic Science 47:992–1003.

PAULI, B. P., AND J. M. TERHUNE. 1987. Tidal and temporal interactions on harbour seal haul-out patterns. Aquatic Mammals 13:93–95.

PITCHER, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. Marine Mammal Science 6:121–134.

PITCHER, K. W., D. C. CALKINS AND G. W. PENDLETON. 1998. Reproductive performances of female Steller sea lions: An energetics-based reproductive strategy? Canadian Journal of Zoology 76:2075–2083.

SCHNEIDER, C. C., AND P. M. PAYNE. 1983. Factors affecting haul-out of harbor seals at a site in southeastern Massachusetts. Journal of Mammalogy 64:518–520.

SIMPKINS, M. A., D. E. WITHROW, J. C. CESARONE AND P. L. BOVENG. 2003. Stability in the proportion of harbor seals hauled out under locally ideal conditions. Marine Mammal Science 19:791–805.

SMALL, R. J., G. W. PENDLETON AND K. W. PITCHER. 2003. Trends in abundance of Alaska harbor seals, 1983–2001. Marine Mammal Science 19:344–362.

SPRINGER, A. M., J. A. ESTES, G. B. VAN VLIET, T. M. WILLIAMS, D. F. DOAK, E. M. DANNER, K. A. FORNEY AND B. PFISTER. 2003. Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? Proceedings of the National Academy of Sciences of the U.S.A. 100:12223–12228.

STEWART, B. S. 1984. Diurnal hauling patterns of harbor seals at San Miguel Island, California. Journal of Wildlife Management 48:1459–1461.

THOMPSON, P. M., M. A. FEDAK, B. J. MCCONNELL AND K. S. NICHOLAS. 1989. Seasonal and sex-related variation in the activity patterns of common seals (*Phoca vitulina*). Journal of Applied Ecology 26:521–535.

THOMPSON, P. M., D. J. TOLLIT, D. WOOD, H. CORPE, P. HAMMOND AND A. MACKAY. 1997. Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. Journal of Applied Ecology 34:43–52.

TRITES, A. W. 1992. Northern fur seals: Why have they declined? Aquatic Mammals 18:3–18.

UDEVITZ, M. S. 1999. Modeling variability in replicated surveys at aggregation sites. Pages 167–177 *in* G. W. GARNER, S. C. AMSTRUP, J. L. LAAKE, B. F. J. MANLY, L. L. MC-DONALD and D. G. ROBERTSON, eds. Marine mammal survey and assessment methods. A. A. Balkema, Rotterdam, Netherlands.

VER HOEF, J. M., AND K. J. FROST. 2003. A Bayesian hierarchical model for monitoring harbor seal changes in Prince William Sound. Environmental and Ecological Statistics 10:201–219.

WATTS, P. 1996. The diel hauling-out cycle of harbour seals in an open marine environment: Correlates and constraints. Journal of Zoology, London 240:1–26.

YORK, A. E., AND P. KOZLOFF. 1987. On the estimation of numbers of northern fur seal, *Callorhinus ursinus*, pups born on St. Paul Island, 1980–86. Fishery Bulletin 85:367–375.

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Appendix. Coefficients for final regression models predicting the natural log of harbor seal counts at Tugidak Island and Nanvak Bay. Blank cells indicate variables that were omitted from the final model; "×" cells indicate variables that were not in the initial model for that data set. Levels of categorical variables are indicated.

Effect[a]	Tugidak pups 1994–2000	Tugidak pupping; all seals 1994–2000	Tugidak molting 1994–2000	Tugidak molting 1976–2000
Intercept	5.3856	6.4371	6.4808	6.2727
Year (trend)	0.1018	0.0799	0.0330	−0.0340
Year^2	×	×	×	0.0082
March sea temperature				0.1070
JDC	0.0545	0.0162	×	×
JDC^2	−0.0034	−0.0011	×	×
JD	×	×	−0.0056	0.0232
JD^2	×	×	−0.0003	−0.0007
TRM	0.0149	0.1177	−0.0087	0.0122
TRM^2		−0.0212		−0.0023
Tide height				
Cloud (none)		−0.2097		×
(partial/complete)		0		
Precipitation (none)		0.2399		×
(light)		0.0990		
(heavy)		0		
Temperature (°C)				×
Winds (km)			0.0161	×
Winds^2			−0.0003	×
Wind direction		(E) 0.1720	(other) 0.1167	×
		(W) 0	(W NW) 0	

Effect[a]	Nanvak pupping; all seals 1990–2000	Nanvak molting 1990–2000
Intercept	3.9820	5.0190
Year	0.0882	0.0206
JDC		
JDC^2	−0.0006	−0.0003
TRM	0.0795	0.0531
TRM^2	−0.0125	−0.0120
Tide (low)	1.1064	0.4470
(falling)	1.0699	0.3418
(rising)	1.1069	0.4660
(high)	0	0
Precipitation (none)		0.1108
(rain)		0
Count quality (low)	−0.3939	−0.4981
(moderate)	−0.3547	−0.5048
(high)	0	0
Winds (km)		0.0211
Winds^2		−0.0005
Wind direction (E SE S)		0.2124
(N NE)		0.1911
(SW)		0.1966
(W NW)		0.1601
(var)		0

[a] JDC = centered Julian date (*i.e.*, Julian date minus the median Julian date of all surveys), JD = Julian date, TRM = time in minutes from solar noon, Winds = wind speed, Windd = wind direction.