

## DECLINES IN HARBOR SEAL (*PHOCA VITULINA*) NUMBERS IN GLACIER BAY NATIONAL PARK, ALASKA, 1992–2002

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### ABSTRACT

Glacier Bay National Park had one of the largest breeding aggregations of harbor seals in Alaska, and it is functionally the only marine reserve for harbor seals in Alaska; yet, numbers of seals in the Bay are declining rapidly. Understanding why seals in Glacier Bay are declining may clarify their minimal habitat needs. We estimated population trends using models that controlled for environmental and observer-related factors. In 1992, 6,200 seals were counted on icebergs in a tidewater glacial fjord and at terrestrial sites; by 2002 only 2,550 seals were counted at these same haul-outs. Numbers of non-pups in the glacial fjord declined by 6.6%/yr (–39%/8 yr) in June and by 9.6%/yr (–63%/11 yr) in August and at all other haul-outs by 14.5%/yr (–75%/10 yr) during August. In the glacial fjord the number of pups remained steady from 1994 to 1999 and made up an increasing proportion of seals counted (5.4%/yr), and the proportion of pups peaked at 34%–36%. The rapid declines do not appear to be due to changes in seal behavior or redistribution. The declines reinforce genetic evidence that harbor seals in Glacier Bay are demographically isolated from other populations and indicate that current management stocks need to be redefined. Changes in Glacier Bay's ecosystem and population demographic data from the glacial fjord suggest that interspecific competition and predation are likely factors in the declines.

Key words: harbor seal, *Phoca vitulina*, population monitoring, trend analysis, aerial surveys, Glacier Bay, tidewater glacial fjord, Johns Hopkins Inlet, marine reserve.

One decade ago a tidewater glacial fjord in Glacier Bay National Park (Johns Hopkins Inlet) had one of the largest breeding aggregations of harbor seals (*Phoca vitulina richardii*) in Alaska (Calambokidis *et al.* 1987, Hoover-Miller 1994, Mathews

1995), but numbers at this and all other sites in Glacier Bay have declined steeply in recent years. In contrast, harbor seal numbers in other parts of southeastern Alaska, currently classified as a single management stock (Angliss and Lodge 2004), appear to be either stable or increasing (Small *et al.* 2003). Compared to the rest of southeastern Alaska, harbor seals in Glacier Bay National Park are highly protected. Glacier Bay is the only place in Alaska where subsistence hunting of harbor seals has been prohibited by Federal regulations since 1974 (Catton 1995), and where commercial fishing is either prohibited or being phased out.<sup>1</sup> In addition, the National Park Service has seasonal quotas on the number and types of vessels and area closures to vessels and campers near breeding harbor seals.<sup>2</sup> This suite of Federal protections make the marine waters of Glacier Bay (1,312 km<sup>2</sup>) functionally the only marine protected area for harbor seals (as well as many other species) in Alaska. It is, thus, surprising that seal numbers are declining there. Pronounced declines in a marine predator within an area where human impacts are minimized indicate either underlying ecosystem changes or inadequacy of measures to protect the population from human activities throughout their life cycle (Hooker and Gerber 2004). Understanding why harbor seals in Glacier Bay National Park are declining may clarify their minimal habitat needs and improve our ability to create effective marine reserves for this and other marine mammal species.

Harbor seals in southeastern Alaska were considered to be increasing overall,<sup>3</sup> until we first reported declines in Glacier Bay for 1992–1998.<sup>4</sup> Population trends from surveys in Glacier Bay, and at two other areas within southeastern Alaska (near Ketchikan and Sitka) have been used as trend indices for this stock (Angliss and Lodge 2004). From 1983 to 2000, seal numbers along the Ketchikan trend route (~550 km south of GB) increased 5.5%/yr and numbers along the Sitka trend route (~100 km south of GB) were stable from 1984 to 2002 (Small *et al.* 2003). In 1998, seals along the three trend routes comprised, approximately, 12% (Glacier Bay),<sup>4</sup> 9% (Ketchikan), and 5% (Sitka) (Small *et al.* 2003) of the minimal population estimate (35,226) of harbor seals in the southeastern Alaska stock (Angliss and Lodge 2004).

In southeastern Alaska harbor seals haul out to rest on terrestrial sites and on drifting ice from tidewater glaciers. During summer more than two-thirds of all seals in Glacier Bay haul out to breed, rest, or nurse on drifting icebergs in tidewater glacial fjords, primarily in Johns Hopkins Inlet (Fig. 1); the remaining animals haul out at terrestrial sites elsewhere in the Bay. This general pattern of hauling out on both land and drifting glacial ice is typical of much of the region.

In this paper we report the population trends of harbor seals in Glacier Bay from 1992 to 2001 and 2002 for terrestrial haul-out and glacial ice sites, respectively. We used covariates to incorporate the effects of environmental and observer-related factors to improve the sensitivity of aerial and shore surveys to detect changes in numbers of seals. Such analyses attempt to reduce variation and the potential for spurious trend estimates resulting from factors not related to real changes in population abundance (Link and Sauer 1998, Frost *et al.* 1999, Adkison and Quinn 2003, Small *et al.* 2003).

<sup>1</sup> Omnibus Consolidated and Emergency Supplemental Appropriations Act, May 21 1999, Public Law 106–31.

<sup>2</sup> May 1996. 36 Code of Federal Regulations 13.65.

<sup>3</sup> Small, R. J. 1997. Harbor seal investigations in Alaska, Annual Report, NA57FX0367. Alaska Department of Fish and Game, Division of Wildlife Conservation, Anchorage, AK.

<sup>4</sup> Mathews, E. A., and G. W. Pendleton. 2000. Declining trends in harbor seal (*Phoca vitulina richardsi*) numbers at glacial ice and terrestrial haulouts in Glacier Bay National Park, 1992–1998 (unpublished). Available from Glacier Bay National Park. P. O. Box 140, Gustavus, AK. 99826, 24 pp.

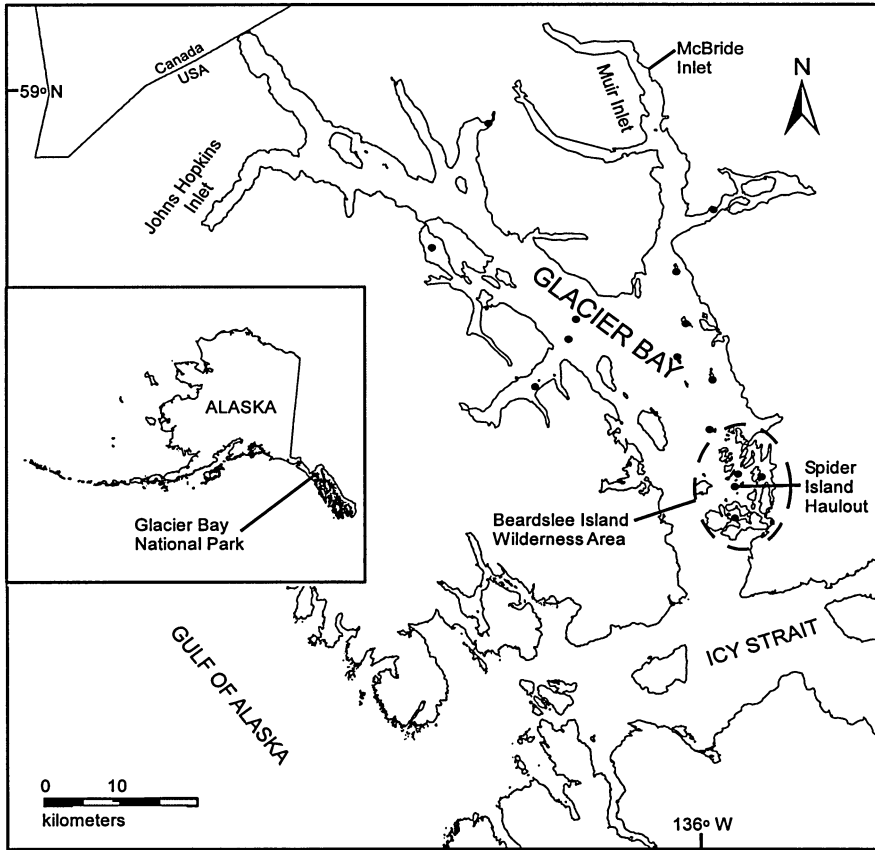


Figure 1. Map of Glacier Bay showing the main harbor seal haul-out sites, including terrestrial haul-outs (filled circles). Johns Hopkins, Muir, and McBride inlets are tidewater glacial fjords where seals congregate, or used to congregate (Muir), on drifting icebergs to breed and molt during spring and summer. All other haul-outs are terrestrial sites.

Finally, we discuss possible causes for the large declines in seal numbers in both habitats.

## METHODS

### *Study Areas*

Johns Hopkins Inlet ( $58^{\circ}53'N$ ,  $137^{\circ}5'W$ ) is located in the northwest arm of Glacier Bay (Fig. 1). Approximately 2,000–4,400 harbor seals use the ice calved from Johns Hopkins glacier as resting substrate during pupping, breeding, and molting periods in late spring and summer. In addition, about 20 tidally influenced terrestrial resting areas are occupied during the breeding and molting seasons. Close to half of all seals on these terrestrial haul-outs are found on ledges at the Spider Island reefs in the Beardslee Island Wilderness Area (Fig. 1).

*Shore-based Counts: Seals on Glacial Ice, Johns Hopkins Inlet*

Standard aerial photographic surveys from fixed winged aircraft using a 35-mm camera (e.g., Stewart and Yochem 1984, Olesiuk *et al.* 1990), are not feasible at Johns Hopkins Inlet glacial fjord, where large numbers of seals are dispersed over a large (5–10 km<sup>2</sup>) area within the fjord. Therefore, we conducted shore-based counts of harbor seals in this region. Counts were obtained during the pupping season in June (1992–1999) and during the annual molt in August (1992–2002). At these times, seals typically spend a higher proportion of time out of the water (Stewart and Yochem 1984, Calambokidis *et al.* 1987, Thompson 1989, Jemison and Kelly 2001). Counts were made by two observers from an elevated (~35 m above sea level) site about 2.5 km from the face of Johns Hopkins glacier (Fig. 1) two or three times each day. Observers used tripod-mounted monocular spotting scopes (1992 and 1993) or 20 × 60 Ziess binoculars (1994–2002) to count seals within two or three non-overlapping parallel scans (Mathews 1995). Observers attempted to compensate for movement of ice between subareas. During the June counts, seals were categorized as non-pups or pups in all years except 1993 when only non-pups were counted. Because of lower accuracy in pup counts in the first two years due to inferior optical equipment, we used counts only from 1994 to 1999 in our pup analyses. In August, no age class distinctions were made because pups are weaned by this time and difficult to distinguish from juveniles and adults, especially at distances of ≤6 km.

Environmental and observer-related covariates were also recorded during each count. Cloud cover was categorized as clear (<25% clouds), partly cloudy (26%–75%), or overcast (>75%) during counts. Precipitation was categorized as none, light rain, or heavy rain. Air temperature at the observation site was recorded during most counts beginning in 1995. Before comparing results, each observer also recorded a subjective count quality rating from 1 (excellent) to 7 (very poor). This variable encompassed environmental conditions (e.g., visibility, lighting, shimmer from heat waves, *etc.*), as well as the observer's overall perception of count accuracy. Only counts with quality ratings ≤4 were used in the analyses. We used two different measures of observer experience, one within a season and one for multiple seasons. Observer experience within a season ranged from one to three. Beginners were categorized as level 3 for their first two counts. These counts were not used in analyses presented in this paper. Level 2 observers were in training. Level 1 observers had conducted at least four counts that produced numbers within at least 20% of an experienced observer. Long-term experience level was an ordinal variable that increased by one for every season (*i.e.*, pupping and molting surveys counted separately) that an observer counted harbor seals (range = 1–14).

Beginning in 1994, we recorded entry and departure times and vessel type (primarily tour boats, private boats, kayaks, or cruise ships; cruise ships were prohibited from entering the inlet after 1995) for each vessel that entered Johns Hopkins Inlet during August surveys. To evaluate whether vessel traffic reduced the numbers of seals on icebergs (by displacing them into the water), we tabulated the number of vessels in the inlet for 1994–2001 during the four hours before the end of each count.

*Aerial-based Counts: Seals on Terrestrial Haul-outs*

In 1992 and 1994–2001, aerial surveys of the terrestrial haul-outs in Glacier Bay were conducted in August during the annual molt. The aerial surveys also

included small glacial haul-out areas in Muir (1992) or McBride inlets (1995–2002) where <200 seals were typically found. All subsequent references to “terrestrial sites” include one of these small glacial fjords. Aerial surveys of terrestrial haul-outs were scheduled to occur during monthly low tide cycles (within two hours of low tide) and, in all except 1992, while there was a field crew in Johns Hopkins Inlet so that we could have full survey coverage of Glacier Bay. During aerial surveys we checked all known haul-outs and also searched for new haul-outs. Weather conditions occasionally prevented complete surveys of the bay. Surveys were conducted from single engine aircraft at an altitude of about 300 m, and observers scanned with binoculars for seals. Photographs were taken through an open window with a 35-mm SLR camera equipped with a motor drive and either an 80–200-mm zoom lens or a 300-mm fixed lens. All occupied haul-outs were photographed for later enumeration. We used 400 ASA slide film exposed at 1/500–1/1000 s.

For each haul-out we recorded the location, time, film frame numbers, and usually a visual estimate of the number of seals. We also noted any evidence of a recent disturbance. For known haul-outs, we noted if weather conditions prevented counting, and when weather conditions were suitable for counting, whether or not seals were present. Groups of seals at all terrestrial haul-outs were small enough to fit in one photographic field of view except at the Spider Island reefs where a series of overlapping photographs was required to include all seals. We counted seals by projecting slide images onto paper and each animal was marked and counted.

#### *Minimal Population Estimates, 1992–2001*

The minimal population estimate for harbor seals in August throughout Glacier Bay was calculated by adding the highest aerial survey count of terrestrial sites to the mean of the daily high counts in Johns Hopkins Inlet from the three days closest to the date of the maximal aerial survey; there were two to eight days between the aerial survey and high counts in Johns Hopkins Inlet. This estimate is based on the assumption that minimal movement occurs between Johns Hopkins Inlet and other haul-outs in Glacier Bay during late summer, an assumption generally supported by harbor seal tagging studies (Pitcher and McAllister 1981, Yochem *et al.* 1987, Thompson and Miller 1990, Tollit *et al.* 1998, Lowry *et al.* 2001).

#### *Trends in Seal Numbers: Covariate Analysis*

Aerial and shore-based surveys of seals at their haul-outs measure only the portion of the population that is out of the water and available to be counted. If the proportion of animals available remains constant, such surveys produce unbiased estimates of population trend. However, due to environmental and behavioral factors that influence the number of seals ashore, the proportion available is never constant across time or space. We used standardized survey methods and included covariates in the population trend analyses to reduce the variation caused by changing availability; if the covariates account for most of this variation, the resulting trend estimates will have small bias (Adkison and Quinn 2003). Covariate effects are likely to differ by resting substrate; for example seal numbers on glacial ice, unlike terrestrial sites, do not fluctuate with tide height (Calambokidis *et al.* 1987, Boveng *et al.* 2003). Because we used different survey methods and expected differences in environmental effects on seal behavior on the different substrates, we considered different sets of

environmental and observer-related covariates for surveys of seals resting on ice and those at terrestrial haul-outs.

For terrestrial sites we used the same covariates and analyses (*i.e.*, Poisson regression) as used by Small *et al.* (2003). This approach is based on within-site changes in counts. All haul-outs were treated individually except for the Spider Island reefs where, because of an apparent shift in seal distribution beginning in August 1997, we treated all seals within 1.9 km of the reefs as a single "site." The environmental covariates included date, time relative to solar noon ( $[\text{sunrise} + \text{sunset}]/2$ ), tide height, and time from low tide at the time of the survey for each site. In addition to the linear form of covariates we also included quadratic effects (e.g., date<sup>2</sup>) for date, time, tide height and time and allowed the effect of tide height to vary by site (e.g., site  $\times$  tide height interaction). The quadratic and interaction covariates were chosen because of known or suspected non-linear patterns in seal haul-out behavior with respect to these variables. Covariates included in the trend analyses for Johns Hopkins Inlet were date, time of day, sky condition, precipitation, count quality, within-season observer level, and long-term experience level. We initially included the number of boats in Johns Hopkins Inlet within four hours of the survey ("boats") as a covariate, but "boat" was strongly correlated with year (*i.e.*, there was a strong time pattern in the number of boats across years probably caused by changing ice conditions), which was our principal variable of interest. Because of this co-linearity, "boat" was dropped from the analyses. As with the aerial survey data, we also included quadratic effects for date and time, and added a quadratic effect for long-term experience to allow for a non-linear effect of this variable.

We tested models with both linear and quadratic population trajectories (*i.e.*, change in population size across years on the log scale). Population trajectories can be thought of as a smoothed version of the actual population size across years. However, trajectories were not always linear (*i.e.*, the rate of change varies through time) on the log scale, so we defined trend as the geometric mean rate of change over the interval of interest (Link and Sauer 1997, Link and Sauer 1998). Trend is therefore a single-number summary of the average change in the trajectory for a selected period of time (*i.e.*, percent change per year from 1992 to 2002).

For each analysis, we fit models with all combinations of covariates and trajectories (*i.e.*, linear and quadratic). Final trend estimates and standard errors were obtained as a weighted average of estimates from the individual models with weights based on corrected Akaike's Information Criteria (AICc; Hurvich and Tsai 1989, Burnham *et al.* 1995). This model-averaging procedure (Burnham and Anderson 1998) incorporates the uncertainty about which model is most appropriate into the trend estimate and its variance. We also calculated an importance index for each covariate (Burnham and Anderson 1998:140–141). This index ranges from 0 (unimportant) to 1 (very important). Based on similar analyses for seal count data from a number of locations, covariates with importance indices  $<0.85$  rarely have substantial influence on estimated trends (G. W. Pendleton, unpublished).

#### *Pup Proportions, Johns Hopkins Inlet*

In Johns Hopkins Inlet seal pups at a distance can be obscured by their mothers or pieces of ice. Consequently, our overall counts of seals during June underestimated pups. To address this, we estimated pup proportions from counts of 100 nearby seals every 2–3 h from 0700 to 2200. We used logistic regression (Hosmer and Lemeshow

2000) to examine the relationship between the proportion of pups in samples counted near the observation site and potential predictor variables. Predictors we used were year (*i.e.*, trend), date, time relative to solar noon, sky condition, precipitation (raining or not), temperature, observer experience (number of survey seasons), and observer level (1 or 2). In addition, we included quadratic terms for date, time-to-midday, and observer experience because we suspected that these relationships were non-linear. All predictor variables were included in the initial model with variables eliminated one at a time based on Wald chi-square statistics until all remaining variables were deemed important (Wald *P*-value <0.05).

## RESULTS

### *Minimal Population Estimates*

The minimal population estimate for seals on shore during August surveys in Glacier Bay declined from 6,189 to 2,551 seals during 1992–2001 despite increased survey effort (Table 1). The means of the three high counts from Johns Hopkins Inlet follow the same general pattern of decline, as did the three counts closest to the peak aerial survey date. Because some proportion of seals is in the water during surveys, the minimal population estimate for each year is a conservative (*i.e.*, minimal) estimate of the number of seals in Glacier Bay. On average, 72% (range = 62%–80%, *n* = 9 yr) of all seals in Glacier Bay from 1992 to 2001 were found in tidewater glacial fjords (Johns Hopkins Inlet + Muir Inlet + McBride Inlet).

### *Trends in Seal Numbers*

We analyzed 176 counts of seals in Johns Hopkins Inlet from 60 d in June and 383 counts from 131 d in August, and aerial surveys of terrestrial haul-outs from 45 different days. Trend estimates were negative for non-pup counts from Johns Hopkins Inlet during June, and for all seals in Johns Hopkins Inlet and at terrestrial sites during August (Table 2, Fig. 2). Annual declines in Johns Hopkins Inlet during August were greater than those during June (–9.56% vs. –6.55%), but not as large as at terrestrial sites in August (–14.46%) (Table 2). In contrast to the declines in non-pup numbers, there was no significant trend in numbers of harbor seal pups in Johns Hopkins Inlet in June (*i.e.*, the 95% confidence interval includes 0) (Table 2).

### *Influential Covariates*

In Johns Hopkins Inlet with all years combined, we estimated when peak counts would occur during the June and August survey periods (Fig. 3a–c). Pup numbers showed a more pronounced peak than non-pups but the predicted peaks were within one day of one another (16 June for non-pups; 15 June for pups) (Fig. 3a, b). The predicted peak count of seals in Johns Hopkins Inlet during molt surveys is 18 August (Fig. 3c). By contrast, seal numbers at terrestrial sites peaked at or before the start of the August survey period (Fig. 3d). Rain tended to reduce all counts at Johns Hopkins Inlet (Table 2); heavy rain had a greater effect than light rain in August, whereas the opposite was true in June. Sky condition was also an important covariate during the June counts (Table 2), with more pups predicted under overcast

*Table 1.* Survey of harbor seals in Glacier Bay in August 1992–2002, (a) mean of high counts in Johns Hopkins Inlet on the three days closest to the maximal aerial survey date ( $n = 3-6$  of the usable paired counts), (b) maximal aerial survey counts of seals on all terrestrial sites and one small glacial haul-out site, and (c) the minimal population estimate (MPE) is the sum of the mean counts from Johns Hopkins Inlet and the high count from all sites surveyed from aircraft. Survey effort is the total number of days over which surveys were conducted. No aerial surveys were flown in 1993 and weather conditions precluded aerial surveys during optimal times in 2002.

Year	(a) Johns Hopkins Inlet (glacial fjord)						(b) Aerial surveys				
	Dates	Mean	CV	$n$ (counts)	Survey effort (d)	Max survey date	Terrestrial	Glacial	Survey effort (d)	(c) MPE	
1992	21	4,378	0.22	5	4	28	1,734	77 <sup>a</sup>	2	6,189	
1993	23	3,361	0.31	3	3				0		
1994	10	3,742	0.11	5	9	8	2,507	0	4	6,249	
1995	9	2,730	0.15	6	13	1	2,451	6	3	5,187	
1996	13	3,719	0.15	6	13	11	1,832	NA	5	5,551	
1997	18	3,143	0.20	6	9	19	1,093	132	6	4,368	
1998	13	2,808	0.12	6	14	11	1,231	143	6	4,182	
1999	14	2,187	0.10	6	21	15	1,459	172	8	3,818	
2000	14	1,886	0.08	6	18	17	900	75	6	2,861	
2001	19	1,648	0.24	6	10	21	747	156	5	2,551	
2002	15	1,740	0.11	6	17						

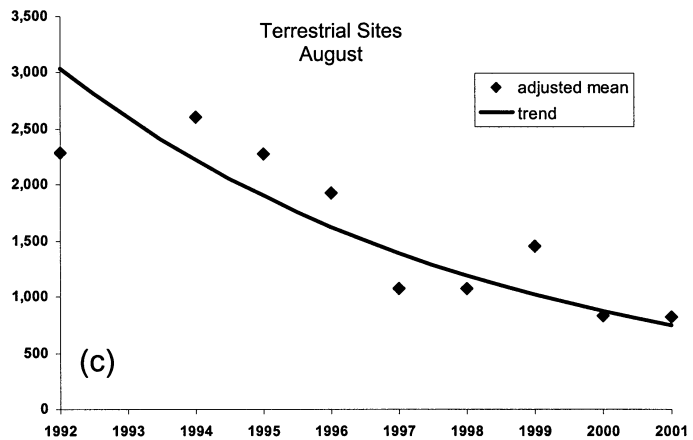
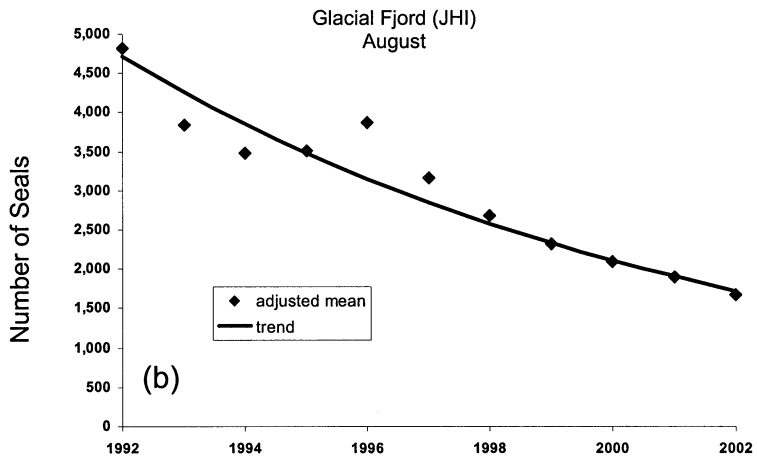
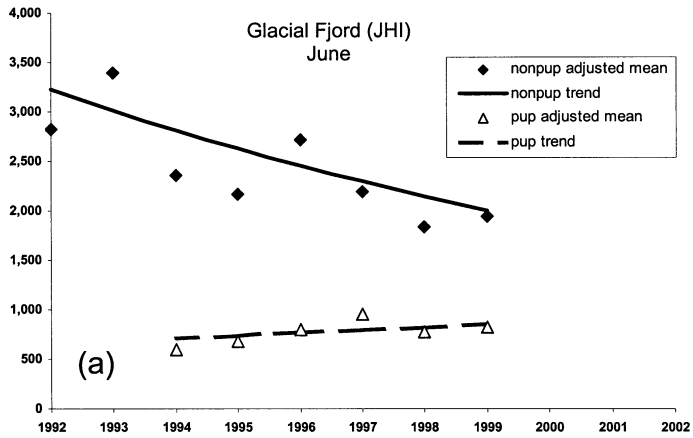
<sup>a</sup>Muir Inlet was occupied by harbor seals in 1992; in all remaining years aerial counts of seals on glacial ice are from McBride Inlet.



*Table 2.* Covariate trend analysis of harbor seal numbers at glacial and terrestrial sites in Glacier Bay. The most influential covariates are those with an importance index  $\geq 0.85$  (Burnham and Anderson 1998) and they are listed in order of decreasing influence. No covariates met the importance threshold for the terrestrial sites.

Years	Site	Month	Seals	Annual trend	SE	95% conf int	Cumulative change	Trend period (yr)	Most influential covariates <sup>a</sup>
1992–1999	JHI glacial fjord	June	non-pups	-6.55	0.97	-8.45 to -4.65	39%	8	date <sup>2</sup> , sky, precipitation
1994–1999	JHI glacial fjord	June	pups	3.56	2.32	-0.98 to 8.10	19%	6	date <sup>2</sup> , date, sky, precipitation
1992–2002	JHI glacial fjord	August	all	-9.56	0.39	-10.33 to -8.78	-63%	11	precipitation, date <sup>2</sup> , trm
1992–2001	Terrestrial sites	August	all	-14.46	1.33	-17.07 to -11.85	-75%	10	(none)

<sup>a</sup>trm = time relative to midday (solar noon), longterm exper = number of observer survey seasons.



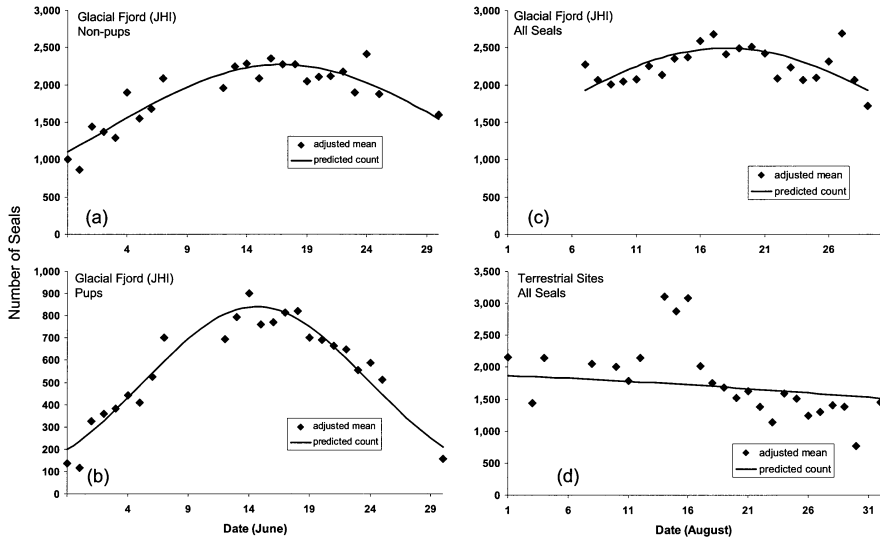


Figure 3. Effects of date on counts of harbor seals in Johns Hopkins Inlet during surveys from 29 May through 30 June from (a) 1992 to 1999 for non-pups and (b) 1994 to 1999 for pups. Effects of date on counts of all seals on haul-outs during August molt surveys (c) in Johns Hopkins Inlet (glacial fjord) from 1992 to 2002 and (d) at terrestrial haul-outs in Glacier Bay from 1992 to 2001. Symbols are adjusted mean counts which incorporate the effects of influential covariates; lines are the estimated population trajectories.

skies than other conditions. Time relative to solar noon was important in August counts at Johns Hopkins Inlet (Table 2), with slightly higher seal counts between one and four hours after solar noon. The number of vessels in Johns Hopkins Inlet in August declined over the eight-year period along with the seal counts. Because of the co-linearity between vessels and our main predictor (year) and seal counts, we excluded the number of vessels from subsequent analyses.

At terrestrial haul-outs no covariates had importance values  $>0.85$ . This result should be interpreted cautiously because survey protocols were designed to reduce the effect of some factors (*e.g.*, tide, date). For example, tide height had the largest importance value of 0.68, but all surveys were conducted close to the low tide; if surveys were conducted across the range of potential tide heights, it is likely that the importance of this variable would be substantially higher.

←

Figure 2. Population trajectories (lines) and adjusted mean counts (symbols) for harbor seals in Johns Hopkins Inlet, a tidewater glacial fjord (a) for non-pups (diamonds) and pups (triangles) during June 1994–1999. Non-pups in June declined by 6.55%/yr (solid line), while there was no significant trend for pups (dashed line). (b) Seals declined by 9.56%/yr during August counts of all seals on icebergs in Johns Hopkins Inlet from August 1992–2002. (c) The population trend (line) was negative (−14.5%/yr) at terrestrial sites during August surveys from an aircraft. Adjusted mean counts are the mean seal count after accounting for all predictors in the model other than the one being graphed.

### *Pup Proportions, Johns Hopkins Inlet*

We analyzed 323 counts of 100 non-pups and pups (mean count = 102, SD = 6.4) conducted in Johns Hopkins Inlet on 54 d during 1994–1999. Pup proportions increased at 5.4% per year (Fig. 4a) and peaked at 34%–36% from 13 to 18 June (= Julian date 164–169, Fig. 4b). The proportion of seals on icebergs that were pups declined slightly over the course of the day (Fig. 4c). The average proportion of pups counted by experienced observers was slightly higher than that counted by less experienced observers (35.6% *vs.* 33.4%). Four explanatory variables (along with year) were retained ( $P \leq 0.05$ ) in the model for trend in pup proportions (Table 3).

## DISCUSSION

Between 1992 and 2002 the number of harbor seals counted during surveys in Glacier Bay declined at annual rates and magnitudes exceeding any documented harbor seal decline in Alaska with the exception of that at Tugidak Island. Mean counts on Tugidak dropped from approximately 7,000 to 1,000 seals (Pitcher 1990), and the causes of these declines, as well as the declines in Steller sea lion numbers in Alaska, are poorly understood (Jemison and Kelly 2001, National Research Council 2003). The declines in harbor seals in Glacier Bay are in contrast to the two other harbor seal trend sites within southeastern Alaska, where numbers are stable or increasing (Small *et al.* 2003). The 14.5%/yr decline in seals at terrestrial haul-outs from 1992 to 2001 (Table 2) exceeds the maximum observed annual reproductive rate for harbor seals (12.5%; Olesiuk *et al.* 1990), indicating that mortality or emigration of more than just young of the year is occurring in Glacier Bay. Furthermore, the lack of a decline in seal pups counted in Johns Hopkins Inlet (Fig. 2a), reinforced by the increase in the proportion of pups (Fig. 4a), indicates that the decline in this glacial fjord is not due to reproductive failure. Such rapid declines in a discrete subarea of the southeastern stock reinforce recent population genetic data<sup>5</sup> indicating that seals in Glacier Bay are a demographically isolated population or subpopulation (Dizon *et al.* 1991).

In the sections that follow we first discuss the effects of covariates on our analyses and we follow with a discussion of possible causes of the declines.

### *Effects of Covariates on Population Trend*

High counts of molting seals in Johns Hopkins Inlet occurred at least 17 d later than at terrestrial haul-outs in Glacier Bay (Fig. 3c, d). Such habitat differences could be due to difference in the age and sex composition of seals ashore during the molt. At Tugidak Island, peak counts varied by age class with yearlings molting first, followed by subadults, adult females and then males (Daniel *et al.* 2003). A similar pattern was found for harbor seals in Orkney, Scotland, but at this site adult females molted a few days before subadult males (Thompson and Rothery 1987). If the differences in the timing of molt within Glacier Bay follow those at Tugidak Island, then the

<sup>5</sup> O'Corry-Crowe, G. M., K. K. Martien and B. L. Taylor. 2003. The analysis of population genetic structure in Alaskan harbor seals, *Phoca vitulina*, as a framework for the identification of management stocks. Administrative Report LJ-03–08, Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92037. 54 pp.

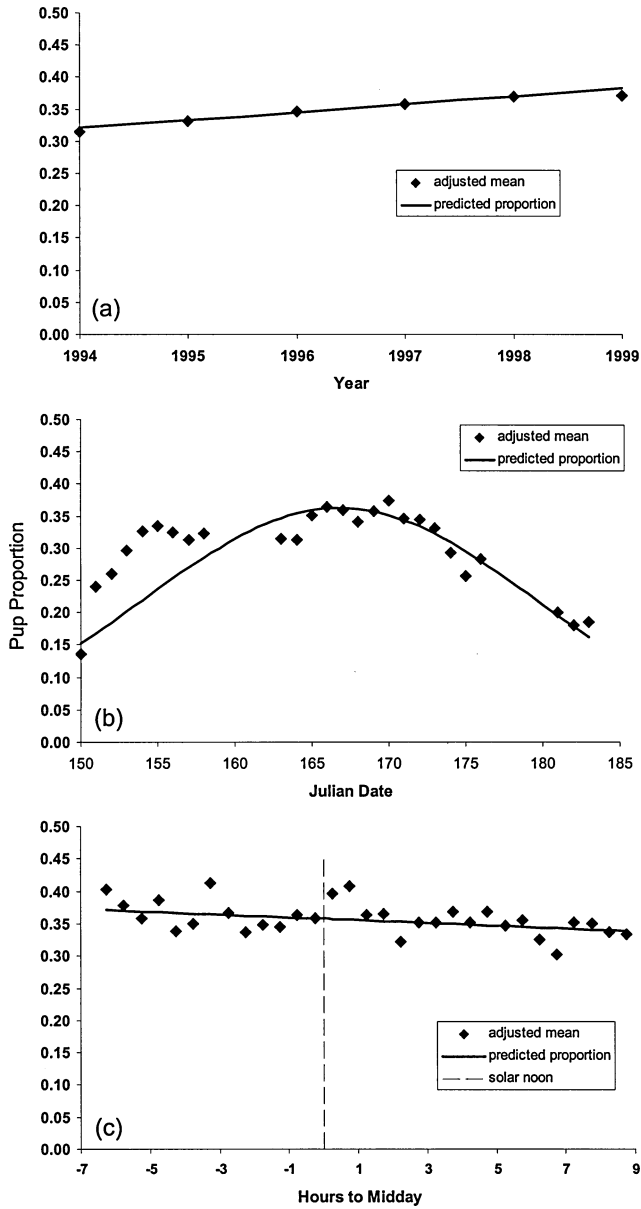


Figure 4. The proportion of harbor seal pups in Johns Hopkins Inlet counted in nearby subsections of 100 seals by (a) year (= trend), (b) date (Julian Date 165 = June 14), and (c) hours from solar noon. The proportion of pups increased significantly by 5.4% per year (Table 3); peak pup counts occurred around 15 June, and there was a slight tendency for the number of pups counted to decrease from morning to evening.

*Table 3.* Effects of covariates on the proportion of harbor seal pups observed in subsets of 100 seals in Johns Hopkins Inlet glacial fjord from 1994 to 1999. Covariates in bold were retained in the final model.

Variable	Estimate	95% CI	<i>P</i>
<b>Year</b>	0.0539	0.0394,0.0683	<0.001
<b>Date</b>	-0.0226	-0.0267,-0.0184	<0.001
<b>Date</b> <sup>2</sup>	-0.003	-0.0034,-0.0027	<0.001
<b>Time</b>	-0.00092	-0.0148,-0.0035	0.001
Time <sup>2</sup>	0.0002	-0.0013,0.0017	0.865
Sky <sup>a</sup>	*	*	0.234
Precipitation <sup>a</sup>	*	*	0.631
Temperature	-0.0039	-0.0087,0.0009	0.145
Long-term observer experience	-0.0103	-0.0208,0.0001	0.053
Long-term observer experience <sup>2</sup>	-0.0018	-0.0042,0.0005	0.1167
<b>Observer level</b>	0.0977	0.0309,0.1644	0.001

<sup>a</sup>Two categorical parameters in the effect; *P*-values given are the minimum values.

later peak in molting in Hopkins is consistent with higher proportions of yearlings and subadults at terrestrial compared to glacial sites. If proportionally more adults breed and tend to remain in Johns Hopkins Inlet to molt after breeding, then we would expect peak molt counts to be later at this site than at terrestrial sites. Peak numbers during the molt at terrestrial sites in Glacier Bay occurred on or before 1 August, at least three weeks earlier than at terrestrial sites in the Ketchikan area (~550 km south of GB), but more similar to the Sitka area (~100 km south of GB) where estimated molting peaks are before 14 August (Small *et al.* 2003).

Except at locations where seals are disturbed by humans (Allen *et al.* 1984, Calambokidis *et al.* 1987, Suryan and Harvey 1998) or affected by tides (Olesiuk *et al.* 1990), harbor seals often show a strong diel pattern in number hauled out. Most commonly, peak seal counts are near solar noon or near mid-afternoon (Stewart 1984, Yochem *et al.* 1987, Thompson *et al.* 1989, Boveng *et al.* 2003, Small *et al.* 2003). However, some sites with morning peaks also have been documented (Boulva and McLaren 1979, Calambokidis *et al.* 1987, Olesiuk *et al.* 1990, Frost *et al.* 1999), and a late afternoon through early evening (~1900) peak in seals ashore occurred at Tugidak Island (Moran 2003) and Sable Island (Bowen *et al.* 2003) during August and September. Counts at glacial ice sites or large terrestrial sites that have beach available at all tide stages are most likely to have consistent diel patterns. In Glacier Bay we found only a weak indication of higher molt (August) counts in Johns Hopkins Inlet from one to four hours after solar noon; neither June counts of non-pups and pups in Johns Hopkins Inlet nor August counts at terrestrial sites varied significantly with respect to time-of-day. This lack of pattern could be because of a broad peak in abundance lasting most of the day as has been reported for seals on ice in Aialik Bay, Alaska (Hoover 1983), or because most of our counts in Johns Hopkins Inlet were conducted two hours before and two to three hours after solar noon, reducing the ability of the model to detect a pattern more than if we had counted seals over a wider range of times. Similarly, the lack of influence of tide height and time relative to tide in our trend model for terrestrial sites is most likely due to the design of our aerial surveys, which were scheduled to begin one to two hours before low tides

during maximal low tide periods. Tide does influence harbor seal haul-out patterns at terrestrial sites in Glacier Bay; the Spider Island reefs, for example, are completely awash and unoccupied by seals during monthly high tides in August (Mathews, unpublished data).

A number of weather variables (*e.g.*, precipitation, wind) affect the number of harbor seals hauled out, but the effects of these variables were not consistent among studies (L. A. Jemison, ADF&G, unpublished data). In Johns Hopkins Inlet rain tended to lower the number of seals on icebergs, a result similar to that found at primarily terrestrial sites in the Gulf of Alaska and Bristol Bay (Boveng *et al.* 2003; L. A. Jemison, ADF&G, unpublished data) and at Bering Glacier (Savarese 2004), where seals also rest on icebergs. However, non-pups at Johns Hopkins Inlet favored clear days, while more seals were seen at Tugidak Island on overcast days with no precipitation (L. A. Jemison, ADF&G, unpublished data). The effects of the weather covariates in Johns Hopkins Inlet were also similar to those at Aialik Bay, another tidewater glacial fjord, but at this site high winds had the greatest effect on numbers of seals hauled out (Hoover 1983). In contrast, weather covariates did not influence counts for terrestrial sites in Glacier Bay (Table 2), most likely because of the narrow range of weather conditions available in our database.

#### *Pup Proportions and Timing of Pupping*

From 1994 to 1999 we observed 34%–36% pups in mid-June in Johns Hopkins Inlet (Fig. 4b). Calambokidis *et al.* (1987) reported 37% pups in Johns Hopkins Inlet on 11 June, 1984 and 40% pups for Muir Inlet during pupping (1982–1984). The proportion of pups in glacial fjords in Glacier Bay is notably higher than the 14.2%–23.8% reported for harbor seals at five terrestrial sites ranging from the north Atlantic to Oregon and Washington (summarized in Olesiuk *et al.* 1990) and the 20.4% calculated from life tables for British Columbia, Canada (Bigg 1969). It is also substantially higher than the 10% reported for terrestrial sites in Glacier Bay from 1982 to 1984 (Calambokidis *et al.* 1987). Lower levels of predation have been suggested as a factor making ice habitat more favorable to breeding harbor seals and other pagophilic pinnipeds (Fay 1974, Calambokidis *et al.* 1987). Observations of higher numbers and proportions of pups in Johns Hopkins Inlet compared to terrestrial sites in Glacier Bay suggest that, relative to other age and sex classes, pregnant females select glacial ice over terrestrial habitat. Higher proportions of pups in Johns Hopkins Inlet were not due to higher numbers of unaccompanied pups on icebergs (Mathews, unpublished data); they could, however, be caused by adult males or juveniles spending more time in the water rather than fewer seals of these age/sex categories.

The timing of pupping by harbor seals varies both among sites (Temte *et al.* 1991) and among years within a site (Jemison and Kelly 2001, Bowen *et al.* 2003), possibly associated with differing photoperiods and food availability, respectively. Our estimate of peak pupping at Johns Hopkins Inlet (15 June) was similar to, or perhaps slightly later than, the timing provided by Streveler (1979)<sup>6</sup> who indicated that pupping in Johns Hopkins Inlet in 1975 to 1979 began in mid-May and that “by

<sup>6</sup> Streveler, G. P. 1979. Distribution, population ecology, and impact susceptibility of the harbor seal in Glacier Bay, Alaska (unpublished). Available from Glacier Bay National Park, P. O. Box 140, Gustavus, AK 99826. 49 pp.

June 15 the peak of pupping had passed.” However our estimated peak was at least nine days earlier than at Tracy Arm, a glacial fjord approximately 350 km through the water and 1° of latitude south of Johns Hopkins Inlet where peak pupping was on or after 24 June in 2001 (Mathews, Pendleton and K. Blejwas, unpublished data). Peak pupping in Johns Hopkins Inlet was similar to the peak on 11–12 June at Tugidak Island in the Gulf of Alaska in 1964 and the mid-1990s (Jemison and Kelly 2001) and consistent with the 17 June mean pupping date determined for 8 terrestrial colonies between northern British Columbia and Alaska (Temte *et al.* 1991). In contrast to observations on Tugidak Island in 1964 and in the 1990s, peak pupping was 9–14 d later from 1976 to 1979, the period when seal numbers were declining. Jemison and Kelly (2001) suggest that the shift in the timing of pupping at Tugidak may have been due to changes in prey availability, quality, or quantity, with better conditions hypothesized for the mid-1960s and 1990s when pupping was earlier.

#### *Evidence for a Population Decline*

From our covariate analysis it is clear that the number of seals hauled out has declined dramatically. The covariate analysis, however, cannot correct for a change in the percentage of time that seals are hauled out. Thus a key question is whether the declines in the counts of seals out of the water in Glacier Bay are due to a dramatic population decline, or whether seals have become less observable because they are spending more time in the water (Green *et al.* 1995). If harbor seals in Glacier Bay were spending more time foraging in recent years compared to earlier years, we would expect numbers of seals observed in the water to increase. Although we do not have longitudinal data on the behavior of individual seals for a definitive test of this possibility, surveys of seals in the water in Glacier Bay do not support this hypothesis. Between 1996 and 2002, the number of harbor seals counted in the water in Glacier Bay during National Park Service surveys for humpback whales (*Megaptera novaeangliae*) declined by more than half, from 54 to 17 seals/100 h.<sup>7</sup> In addition, the number of harbor seals observed during systematic nearshore transects conducted by the U.S. Geological Survey (USGS) within Glacier Bay also declined by more than half between 1991 and two recent survey years (1999, 2000) from 3.86 to 0.89 and 1.48 seals per km<sup>2</sup>, respectively.<sup>8</sup> Human disturbance might also have changed seal behavior. Private and commercial vessels likely have multiple impacts on seals, but the most visible effect of disturbance is to cause seals to escape into the water from haul-outs. The overall number of cruise ships allowed in Glacier Bay increased in 1996<sup>2</sup> from average annual counts of 161 (SD = 6) for 1990–1995 to 210 ships (SD = 6) for 1996–2002 (D. Nemeth, Glacier Bay NPS, unpublished data), although a daily quota of two per day was maintained. However, cruise ships have not been allowed in Johns Hopkins Inlet during May and June since 1988, and after 1996 they have been prohibited from entering the Inlet from May through August.<sup>2</sup> Furthermore, these enormous vessels do not approach terrestrial haul-outs due to their deep draft. Although numbers of kayaks and motorized vessels entering the

<sup>7</sup> Personal communication with C. M. Gabriele, Humpback Whale Biologist, Glacier Bay NPS, P. O. Box 140, Gustavus, AK 99826, September 2004.

<sup>8</sup> Robards, M., G. Drew, J. F. Piatt, J. M. Anson, A. Abookire, J. L. Bodkin, P. Hooge and S. Speckman. 2003. Ecology of selected marine communities in Glacier Bay: Zooplankton, forage fish, seabirds and marine mammals. Available from U.S. Geological Survey, Alaska Science Center, 1101 E. Tudor Road, Anchorage, AK 99503. 156 pp.



Bay did not increase during 1990–2002 (D. Nemeth, Glacier Bay NPS, unpublished data), these smaller vessels do cause seals to stampede into the water in Glacier Bay, particularly at terrestrial sites. Vessels smaller than cruise ships, including kayakers, may be changing the haul-out behavior and distribution of seals in Glacier Bay (Mathews, unpublished data), but it is unlikely that vessel disturbance could explain the observed declines.

#### *Have Seals Moved out of Glacier Bay?*

The declines in Glacier Bay could be the result of seals emigrating. Hoover-Miller *et al.* (2001) have argued that the harbor seal declines immediately after the Exxon Valdez oil spill in Prince William Sound (Frost *et al.* 1994) were more likely due to redistribution of seals to other haul-outs within Prince William Sound, rather than increased mortality. Tagging studies demonstrate that most seals remain within 50 km of their capture sites (Brown and Mate 1983, Thompson and Miller 1990, Tollit *et al.* 1998, Lowry *et al.* 2001), and genetic (Goodman 1998, Schaeff *et al.* 1999)<sup>5</sup> and branding studies (Härkönen and Harding 2001) support strong adult female site fidelity for breeding areas. If seals had moved out of Glacier Bay, we would expect a comparable increase in numbers nearby. Aerial surveys of harbor seals in Icy Strait (Fig. 1) during August have been conducted in 1996,<sup>9</sup> 1997 (Withrow and Cesarone 1998), and 2002 (D. Withrow, NMFS, Seattle, WA, unpublished data). Although the interval between surveys and the minimal number of years limits the sensitivity of area-wide surveys to detect change, it would be hard to miss an increase of more than 3,600 harbor seals (Table 1), particularly since the high count in Icy Strait for all survey years was approximately 1,600 seals. A preliminary comparison of counts from 1996, 1997, and 2002 indicates that seal numbers did not increase within approximately 70–80 km of Glacier Bay between 1996 and 2002.

#### *Have There Been Changes in Reproduction?*

In Johns Hopkins Inlet we could not measure birth rate (pups/adult female) directly, but the number of pups counted from 1994 to 1999 did not decline (Fig. 2a) and the proportion of pups increased (Fig. 4a). A long-term study of harbor seals on Sable Island, Nova Scotia, Canada, demonstrated that differential mortality by age class produced demographic changes similar to those documented in Glacier Bay. Although the number of pups on Sable Island declined from 1991 to 1998 due to increasing shark predation (Lucas and Stobo 2000) and possibly competition from an increasing population of gray seals (*Halichoerus grypus*) (Bowen *et al.* 2003), the number of pups was stable from 1992 to 1994 and the proportion of pups increased during that three-year period (Bowen *et al.* 2003, fig 2). This short-term pattern is similar to what we observed from 1994 to 1999 in Glacier Bay (Fig. 2a, 4a). At Sable Island, where the age/sex classes of all seals were known because all pups were tagged, the increase in the proportion of pups was due to a rapid decline in the number of adult males and juveniles that preceded declines in reproductive females

<sup>9</sup> Mathews, E. A., and J. N. Womble. 1997. Abundance and distribution of harbor seals from Icy Bay to Icy Strait, southeast Alaska during August 1996, with recommendations for a population trend route. Pages 33–56 in Harbor seal investigations in Alaska. Alaska Department of Fish and Game, Division of Wildlife Conservation, 333 Raspberry Road, Anchorage, AK 99518.

and pups. These similarities suggest that both populations could be responding to similar impacts (predation and competition).

#### *Has Mortality of Seals in Glacier Bay Increased?*

Known sources of mortality for harbor seals in Glacier Bay include subsistence hunting by Alaskan natives and predation. Although Glacier Bay National Park is the only place in Alaska where subsistence hunting of harbor seals is not authorized, this protection may not be fully effective because some seals that breed in Glacier Bay presumably leave the bay during fall and winter (Mathews and Kelly 1996), when most subsistence hunting occurs. Estimates of the number of seals taken by hunters from Hoonah, the Alaskan native community closest to Glacier Bay, declined from 375 and 360 seals in 1992 and 1993 to 157 and 102 seals in 2001 and 2002, respectively,<sup>10</sup> suggesting that hunting is not the driving force behind the seal declines. Marine predators of harbor seals in Glacier Bay include transient (marine mammal eating) killer whales (*Orcinus orca*), Steller sea lions (*Eumetopias jubatus*), and possibly Pacific sleeper sharks (*Somniosus pacificus*) (Taggart *et al.* 2005). In the north Pacific, harbor seals are the most common prey of transient killer whales (Ford *et al.* 1998), and large-scale effects on marine mammal populations by transient killer whales have been proposed through shifts in their diet (Estes *et al.* 1998, Springer *et al.* 2003). We have observed predation on harbor seals by killer whales and Steller sea lions in Glacier Bay, but further analysis is needed to determine if rates of predation have increased sufficiently to be significant contributors to the observed seal declines.

#### *Evidence for Ecosystem Changes in Glacier Bay*

Large changes in the abundance of several marine vertebrates in Glacier Bay indicate that the underlying food web dynamics have changed during the period of seal declines. Steller sea lion numbers at the only haul-out in Glacier Bay increased by 32.2%/yr (95% CI = 15.9%–50.8%) between 1992 and 1998 (June and July), from seasonal high counts of 135 (1992) to 509 (1998) sea lions (Mathews, Pendleton and J. M. Maniscalco, unpublished data) and up to 791 sea lions in 2002 (Womble *et al.* 2005). Steller sea lions could affect the harbor seal population directly through predation and indirectly as competitors for food. Sea otters also increased from approximately five in 1995 to 1,200 in 2002 at rates exceeding theoretical and observed reproductive rates.<sup>11</sup> In addition, the mean number of humpback whales in Glacier Bay and Icy Strait during summer increased from 42 (SD = 4.8) for 1992–1995 to 65 whales (SD = 7.2) for 1999–2002,<sup>12</sup> indicating a shift in distribution and suggesting that prey resources in Glacier Bay improved between the early 1990s and 1999–2002. Alternatively, humpback whales (Johnson and Wolman 1984) and

<sup>10</sup> Wolfe, R., J. A. Fall and R. T. Stanek. 2003. The subsistence harvest of harbor seals and sea lions by Alaska Natives in 2002. Alaska Department of Fish and Game, Division of Subsistence, P. O. Box 240020, Juneau, AK. 90 pp.

<sup>11</sup> Bodkin, J. L., K. A. Kloeker, G. G. Esslinger, D. H. Monson, H. Coletti and J. L. Doherty. 2002. Sea otter studies in Glacier Bay National Park and Preserve: Annual Report (unpublished). Available from U.S. Geological Survey, 1101 E. Tudor Road, Anchorage, AK 99503. 82 pp.

<sup>12</sup> Doherty, J. L., and C. M. Gabriele. 2002. Population characteristics of humpback whales in Glacier Bay and adjacent waters: 2002 (unpublished). 32 pp. Available from Glacier Bay National Park, P. O. Box 140, Gustavus, AK 99826.

harbor seals (Pitcher 1980) both feed on small schooling fish, such as herring (*Clupea harengus pallasi*), capelin (*Mallotus villosus*), sand lance (*Ammodytes hexapterus*), and walleye pollock (*Theragra chalcogramma*), and they may consequently compete for prey. Using the daily energy requirements for humpback whales (Lockyer 1981) and for harbor seals (Hoover-Miller 1994), one humpback whale in one day could consume the prey required by more than 90 harbor seals, assuming 50% overlap in diet. During approximately the same time as the seal declines (1991–2000), the number of Kittlitz's (*Brachyramphus brevirostris*) and Marbled (*B. marmoratus*) murrelets in Glacier Bay also declined;<sup>8</sup> both these alcids use glacial fjords during breeding and feed on some of the same small schooling fish species as harbor seals. Information on Glacier Bay's marine ecosystem alone, however, may not be adequate for determining the cause or causes of the declines in harbor seals. Numbers of seals on haul-outs in Glacier Bay drop sharply in early fall and it is very likely that seals leave Glacier Bay to forage elsewhere (Mathews and Kelly 1996). Determining the movements and foraging behavior during fall and winter of seals that breed in Glacier Bay will be necessary for identifying factors outside of Glacier Bay that may be contributing to the declines.

The rapid declines in harbor seal numbers in Glacier Bay do not appear to be due to changes in behavior or redistribution. Dietary overlap, coupled with the rapid increases in Steller sea lion and humpback whale abundance, suggest that interspecific competition could be involved in the harbor seal declines. Competitive interactions with an increasing population of gray seals have been proposed as a co-factor (with shark predation) in the rapid decline of harbor seals on Sable Island (Bowen *et al.* 2003). Harbor seals that breed in Glacier Bay National Park are more protected from human threats than any other seals in Alaska, yet they are declining. The causes of the declines are not known, but changes in Glacier Bay's ecosystem and the population demographic data from Johns Hopkins Inlet suggest that competitive interactions and predation are likely factors.

Recent population genetic analysis indicates that harbor seals in Alaska (Westlake and O'Corry-Crowe 2002),<sup>5</sup> as well as other parts of their range (Goodman 1998), are structured on a finer scale than expected. In Alaska three management stocks of harbor seals are currently recognized by the National Marine Fisheries Service: southeastern Alaska, the Gulf of Alaska, and the Bering Sea (Angliss and Lodge 2004). However, population genetic analysis using mitochondrial DNA, as well as movement studies, indicate that there are at least five demographically and genetically separate subpopulations of harbor seals in southeastern Alaska, one of which is centered in Glacier Bay.<sup>5</sup> The declines reinforce genetic evidence that seals in Glacier Bay are demographically isolated from other seals in Alaska: dispersal from neighboring groups is clearly not offsetting the declines. These results have profound implications for the management of harbor seals, particularly in Alaska where harbor seals are an important resource for Alaskan natives who hunt seals for subsistence uses. Sixty-four percent (1,007/1,585) of the seals taken during subsistence hunts in Alaska are from the southeastern stock of seals<sup>10</sup> which comprises 46% (35,226 of 76,791) of the minimal estimate of harbor seals in Alaska based on the most recent (1998) NMFS stock assessments (Angliss and Lodge 2004). If seals are harvested or natural mortality is disproportionately from a subpopulation within a larger area currently identified as a management stock, local depletion of that subpopulation could occur. In addition, because Alaskan natives rely on harbor seals as an important source of food, local depletions could have large impacts on traditional native uses of this marine mammal.

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## LITERATURE CITED

- ADKISON, M. D., AND T. J. I. QUINN. 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 haul out patterns at Bolinas Lagoon, California. *Fishery Bulletin* 82:493-499.
- ANGLISS, R. P., AND K. L. LODGE. 2004. Harbor seal (*Phoca vitulina richardsi*): Southeast Alaska stock. Pages 23-29 in *Alaska Marine Mammal Stock Assessment, 2003*. Available from U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Seattle, WA.
- BIGG, M. A. 1969. The harbour seal in British Columbia. *Fisheries Research Board of Canada* 172:1-33.
- BOULVA, J., AND I. A. McLAREN. 1979. Biology of the harbor seal, *Phoca vitulina*, in eastern Canada. *Bulletin of the Fisheries Research Board of Canada* 200:1-24.
- 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.
- BOWEN, W. D., S. L. ELLIS, S. J. IVERSON AND D. J. BONESS. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: Implications for explaining the decline of harbour seals, *Phoca vitulina*, on Sable Island. *Journal of Zoology, London* 26:155-163.
- BROWN, R. F., AND B. R. MATE. 1983. Abundance, movements, and feeding habits of harbor seals (*Phoca vitulina*) at Netarts and Tillamook Bays, Oregon. *Fishery Bulletin* 81:291-301.
- BURNHAM, K. P., AND D. R. ANDERSON. 1998. *Model selection and inference: An information theoretic approach*. Springer-Verlag, Berlin, Germany.
- BURNHAM, K. P., G. C. WHITE AND D. R. ANDERSON. 1995. Model selection strategy in the analysis of capture-recapture data. *Biometrics* 51:888-898.
- CALAMBOKIDIS, J., B. L. TAYLOR, S. D. CARTER, G. H. STEIGER, P. K. DAWSON AND L. D. ANTRIM. 1987. Distribution and haul-out behavior of harbor seals in Glacier Bay, Alaska. *Canadian Journal of Zoology* 65:1391-1396.
- CATTON, T. 1995. *Land reborn: A history of administration and visitor use in Glacier Bay National Park and Preserve*. University of Washington, Seattle, WA. 517 pp.

- 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.
- DIZON, A. E., C. LOCKYER, W. F. PERRIN, D. P. DEMASTER AND J. SISSON. 1991. Rethinking the stock concept: A phylogeographic approach. *Conservation Biology* 6:24–36.
- ESTES, J. A., M. T. TINKER, T. M. WILLIAMS AND D. F. DOAK. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–475.
- FAY, F. H. 1974. The role of ice in the ecology of marine mammals of the Bering Sea. Pages 383–399 in D. W. Hood and E. J. Kelley, eds. *Ice and marine mammals*. University of Alaska Fairbanks, Fairbanks, AK.
- FORD, J. K. B., G. M. ELLIS, L. G. BARRETT-LENNARD, A. B. MORTON, R. S. PALM AND K. C. BALCOMB, III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Canadian Journal of Zoology* 76:1456–1471.
- FROST, K. J., L. F. LOWRY, E. H. SINCLAIR, J. VER HOEF AND D. C. MCALLISTER. 1994. Impacts on distribution, abundance, and productivity of harbor seals. Pages 97–118 in T. R. Loughlin, ed. *Marine Mammals and the Exxon Valdez*. Academic Press, Inc., San Diego, CA.
- 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.
- GOODMAN, S. J. 1998. Patterns of extensive genetic differentiation and variation among European harbor seals (*Phoca vitulina vitulina*) revealed using microsatellite DNA polymorphisms. *Molecular Biology and Evolution* 15:104–118.
- GREEN, K., H. R. BURTON, V. WONG, R. A. MCFARLANE, A. A. FLAHERTY, B. C. PAHL AND S. A. HAIGH. 1995. Difficulties in assessing population status of ice seals. *Wildlife Research* 22:193–199.
- HÄRKÖNEN, T., AND K. C. HARDING. 2001. Spatial structure of harbour seal populations and the implications thereof. *Canadian Journal of Zoology* 79:2115–2127.
- HOOVER, S. K., AND L. R. GERBER. 2004. Marine reserves as a tool for ecosystem-based management: The potential importance of megafauna. *BioScience* 54:27–39.
- HOOVER, A. A. 1983. Behavior and ecology of harbor seals (*Phoca vitulina richardsi*) inhabiting glacial ice in Aialik Bay, Alaska. M.Sc. thesis, University of Alaska, Fairbanks, AK. 132 pp.
- HOOVER-MILLER, A. A. 1994. Harbor seal (*Phoca vitulina*) biology and management in Alaska. Marine Mammal Commission. Contract #T75134749. Washington, DC. 45 pp.
- HOOVER-MILLER, A., K. R. PARKER AND J. J. BURNS. 2001. A reassessment of the impact of the *Exxon Valdez* oil spill on harbor seals (*Phoca vitulina richardsi*) in Prince William Sound, Alaska. *Marine Mammal Science* 17:111–135.
- HOSMER, D. W., AND S. LEMESHOW. 2000. *Applied logistic regression*. Second edition. John Wiley and Sons, Inc., New York, NY.
- HURVICH, C. M., AND C. TSAI. 1989. Regression and time series model selection in small samples. *Biometrika* 76:297–307.
- JEMISON, L. A., AND B. P. KELLY. 2001. Pupping phenology and demography of harbor seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. *Marine Mammal Science* 17:585–600.
- JOHNSON, J. H., AND A. A. WOLMAN. 1984. The humpback whale, *Megaptera novaeangliae*. *Marine Fisheries Review* 46:30–37.
- LINK, W. A., AND J. R. SAUER. 1997. Estimation of population trajectories from count data. *Biometrics* 53:488–497.
- LINK, W. A., AND J. R. SAUER. 1998. Estimating population change from count data: Application to the North American breeding bird survey. *Ecological Applications* 8:258–268.
- LOCKYER, C. H. 1981. Growth and energy budgets of large baleen whales from the southern hemisphere. Pages 379–489. *Mammals in the seas*. Volume. III. Food and Agriculture Organization of the United Nations, Rome, Italy.

- LOWRY, L. F., K. J. FROST, J. VER HOEF AND R. A. DELONG. 2001. Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska. *Marine Mammal Science* 17:835–861.
- LUCAS, Z., AND W. T. STOBO. 2000. Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. *Journal of Zoology*, London 252:405–414.
- MATHEWS, E. A. 1995. Longterm trends in abundance of harbor seals (*Phoca vitulina richardsi*) and development of monitoring methods in Glacier Bay National Park, Southeast Alaska. Pages 254–263 in D. R. Engstrom, ed. *Proceedings of the Third Glacier Bay Science Symposium*. U.S. National Park Service, Glacier Bay National Park & Preserve, P. O. Box 140, Gustavus, AK.
- 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* 12:483–488.
- MORAN, J. R. 2003. Counting seals: Estimating the unseen fraction using a covariate and capture-recapture model. M.Sc. thesis, University of Alaska, Fairbanks, AK. 49 pp.
- NATIONAL RESEARCH COUNCIL. 2003. *Decline of the Steller sea lion in Alaskan waters: Untangling food webs and fishing nets*. National Academies Press, Washington, DC.
- OLESIUK, P. F., M. A. BIGG AND G. M. ELLIS. 1990. Recent trends in the abundance of harbor seals, *Phoca vitulina*, in British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 47:992–1003.
- PITCHER, K. W. 1980. Stomach contents and feces as indicators of harbor seal (*Phoca vitulina*) foods in the Gulf of Alaska. *Fishery Bulletin*, U.S. 78:797–798.
- PITCHER, K. W. 1990. Major decline in the number of harbor seals (*Phoca vitulina*) on Tugidak Island, Gulf of Alaska. *Marine Mammal Science* 6:121–134.
- PITCHER, K. W., AND D. C. MCALLISTER. 1981. Movements and haulout behavior of radio-tagged harbor seals, *Phoca vitulina*. *Canadian Field-Naturalist* 95:292–297.
- SAVARESE, D. M. 2004. Seasonal trends in harbor seal abundance at the terminus of the Bering Glacier in southcentral Alaska. M.Sc. thesis, University of Alaska Anchorage, Anchorage, AK. 70 pp.
- SCHAEFF, C. M., D. J. BONESS AND W. D. BOWEN. 1999. Female distribution, genetic relatedness, and fostering behaviour in harbour seals, *Phoca vitulina*. *Animal Behaviour* 57:427–434.
- SMALL, R. J., G. W. PENDLETON AND K. W. PITCHER. 2003. Trends in abundance of Alaska harbor seals, 1983–2002. *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 megafunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling. *Proceedings of the National Academy of Sciences* 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.
- STEWART, B. S., AND P. K. YOCHER. 1984. Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980–1982. *Bulletin of the Southern California Academic Sciences* 83:121–132.
- SURYAN, R. M., AND J. T. HARVEY. 1998. Variability in reactions of Pacific harbor seals, *Phoca vitulina richardsi*, to disturbance. *Fisheries Bulletin* 97:332–339.
- TAGGART, S. J., A. G. ANDREWS, J. MONDRAGON AND E. A. MATHEWS. 2005. Co-occurrence of Pacific sleeper sharks *Somniosus pacificus* and harbor seals *Phoca vitulina* in Glacier Bay. *Alaska Fishery Research Bulletin* 11.
- TEMTE, J. L., M. A. BIGG AND O. WIIG. 1991. Clines revisited: The timing of pupping in the harbour seal (*Phoca vitulina*). *Journal of Zoology*, London 224:617–632.
- THOMPSON, P. M. 1989. Seasonal changes in the distribution and composition of common seal (*Phoca vitulina*) haul-out groups. *Journal of the Zoological Society of London* 217:281–294.

- THOMPSON, P. M., AND D. MILLER. 1990. Summer foraging activity and movements of radio-tagged common seals (*Phoca vitulina*. L.) in the Moray Firth, Scotland. *Journal of Applied Ecology* 27:492–501.
- THOMPSON, P., AND P. ROTHERY. 1987. Age and sex differences in the timing of moult in the common seal (*Phoca vitulina*). *Journal of the Zoological Society of London* 212:597–603.
- 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.
- TOLLIT, D. J., A. D. BLACK, P. M. THOMPSON, A. MACKAY, H. M. CORPE, B. WILSON AND S. M. VAN PARIJS. 1998. Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *Journal of Zoology, London* 244:209–222.
- WESTLAKE, R. L., AND G. M. O’CORRY-CROWE. 2002. Macrogeographic structure and patterns of genetic diversity in harbor seals from Alaska to Japan. *Journal of Mammalogy* 83:1111–1126.
- WITHROW, D. E., AND J. C. CESARONE. 1998. Abundance and distribution of harbor seals (*Phoca vitulina richardsi*) for northern southeast Alaska from Kayak Island to Frederick Sound in 1997. Pages 116–123 in *MMPA and ESA Implementation Program 1997*. AFSC Processed Report 98–10. Annual report to the Office of Protected Resources, NMFS, NOAA, 1335 East-West Highway, Silver Spring, MD 20910. National Marine Mammal Laboratory, Seattle, WA.
- WOMBLE, J. N., M. F. WILLSON, M. F. SIGLER, B. P. KELLY AND G. R. VANBLARICOM. 2005. Distribution of Steller sea lions *Eumetopias jubatus* in relation to spring-spawning fish species in southeastern Alaska. *Marine Ecology Progress Series* 294:271–282.
- YOCHER, P. K., B. S. STEWART, R. L. DELONG AND D. P. DEMASTER. 1987. Diel haul-out patterns and site fidelity of harbor seals (*Phoca vitulina richardsi*) on San Miguel Island, California, in autumn. *Marine Mammal Science* 3:323–332.

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