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The role of Steller sea lions in a large population decline of harbor seals

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ABSTRACT

We provide the first direct evidence that Steller sea lions will prey on harbor seals. Direct observations of predation on marine mammals at sea are rare, but when observed rates of predation are extrapolated, predation mortality may be found to be significant. From 1992 to 2002, harbor seals in Glacier Bay declined steeply, from 6,200 to 2,500 (~65%). After documenting that Steller sea lions were preying on seals in Glacier Bay, we investigated increased predation by sea lions as a potential explanation for the large decline. In five independent data sets spanning 21–25 yr and including 14,308 d of observations, 13 predation events were recorded. We conducted a fine-scale analysis for an intensively studied haul-out (Spider Island) and a broader analysis of all of Glacier Bay. At Spider Island, estimated predation by sea lions increased and could account for the entirety of annual pup production in 5 of 8 yr since 1995. The predation rate, however, was not proportional to the number of predators. Predation by Steller sea lions is a new source of mortality that contributed to the seal declines; however, life history modeling indicates that it is unlikely that sea lion predation is the sole factor responsible for the large declines.

Key words: *Phoca vitulina*, harbor seal, *Eumetopias jubatus*, Steller sea lion, predation, population dynamics, Leslie matrix life history model, Glacier Bay National Park, marine protected area, killer whales.

In terrestrial environments, predation on mammalian populations is more important than generally appreciated: up to 68% of the mortality within some mammal populations is due to predatory attacks (Palomares and Caro 1999). Interspecific predation among marine mammals, many of which capture, process, and consume prey underwater or far from shore, is hard to observe and difficult to quantify.

Consequently, few studies have evaluated whether top-down effects are the causes of marine mammal population declines; instead, most have focused on bottom up forces (*e.g.*, nutrient limitation) and environmental factors (Bowen 1997, National Research Council 2003). The role of predators in marine mammal population declines has recently received attention (Estes *et al.* 1998, Springer *et al.* 2003, Williams *et al.* 2004) and spurred an important dialog over the importance of top-down *vs.* bottom-up forces in shaping marine mammal populations (Heise *et al.* 2003, Whitehead and Reeves 2005, Trites *et al.* 2007, Wade *et al.* 2007, Springer *et al.* 2008).

From 1992 to 2002, the number of harbor seals (*Phoca vitulina richardii*) in Glacier Bay National Park declined by more than 65%, from 6,200 seals counted on haul-outs down to 2,550 seals (Mathews and Pendleton 2006), and this decline has continued (Womble *et al.* 2010). This local depletion of harbor seals is the second largest documented decline in Alaska, and it occurred despite National Park Service (NPS) regulations in Glacier Bay that: (1) prohibited subsistence hunting of harbor seals by Alaska Natives since 1974 (Catton 1995), (2) seasonally restricted tour boats and cruise ships from accessing key seal resting and breeding areas (CFR 1996), and (3) implemented a phasing out of commercial fishing beginning in 1999 (CFR 1999). These regulations make Glacier Bay functionally a marine protected area (MPA definition: Executive Order 13158, May 2000) for harbor seals. Increased predation is one of several potential explanations for the population decline of harbor seals in Glacier Bay. Evidence suggesting predation as a factor in the large decline includes a demographic signal consistent with predation, no increase in reported carcasses locally or regionally, and no evidence for large scale (*i.e.*, several thousand seals) redistribution of seals out of Glacier Bay (Mathews and Pendleton 2006).

Predatory attacks by Steller sea lions on harbor seals were first reported in Glacier Bay in 1995. Since then there have been a total of 13 direct observations of predation by Steller sea lions on harbor seals. Our objective in this study was to use known levels of observer effort associated with direct observations of predation to quantify predation by Steller sea lions on the seal population in Glacier Bay and to determine if this was a new source of mortality consistent with the timing of the seal decline. We estimated predation rates under assumptions ranging from most likely to more conservative scenarios. We also develop a Leslie life history model to evaluate the amount of increased mortality necessary to produce declines in harbor seals comparable to those observed in Glacier Bay and we evaluate the role of sea lion predation in those declines. We report the first direct observations of predation by Steller sea lions on harbor seals and the first evidence of Steller sea lion predation having a population-level effect on another pinniped species.

Methods

Study Sites

Glacier Bay is a large glacial fjord system with 16 active tidewater glaciers in its northern reaches (Fig. 1). In southern Alaska, from the Kenai Peninsula to southeastern Alaska including Glacier Bay, harbor seals rest and nurse their pups on two different substrates: small icebergs calved from tidewater glaciers (Fig. 1, Johns Hopkins and McBride inlets) and tidally influenced terrestrial sites on small islands, islets, and reefs (Fig. 1). During late spring and summer when harbor seals give birth, breed, and molt, roughly two-thirds of all seals in Glacier Bay haul

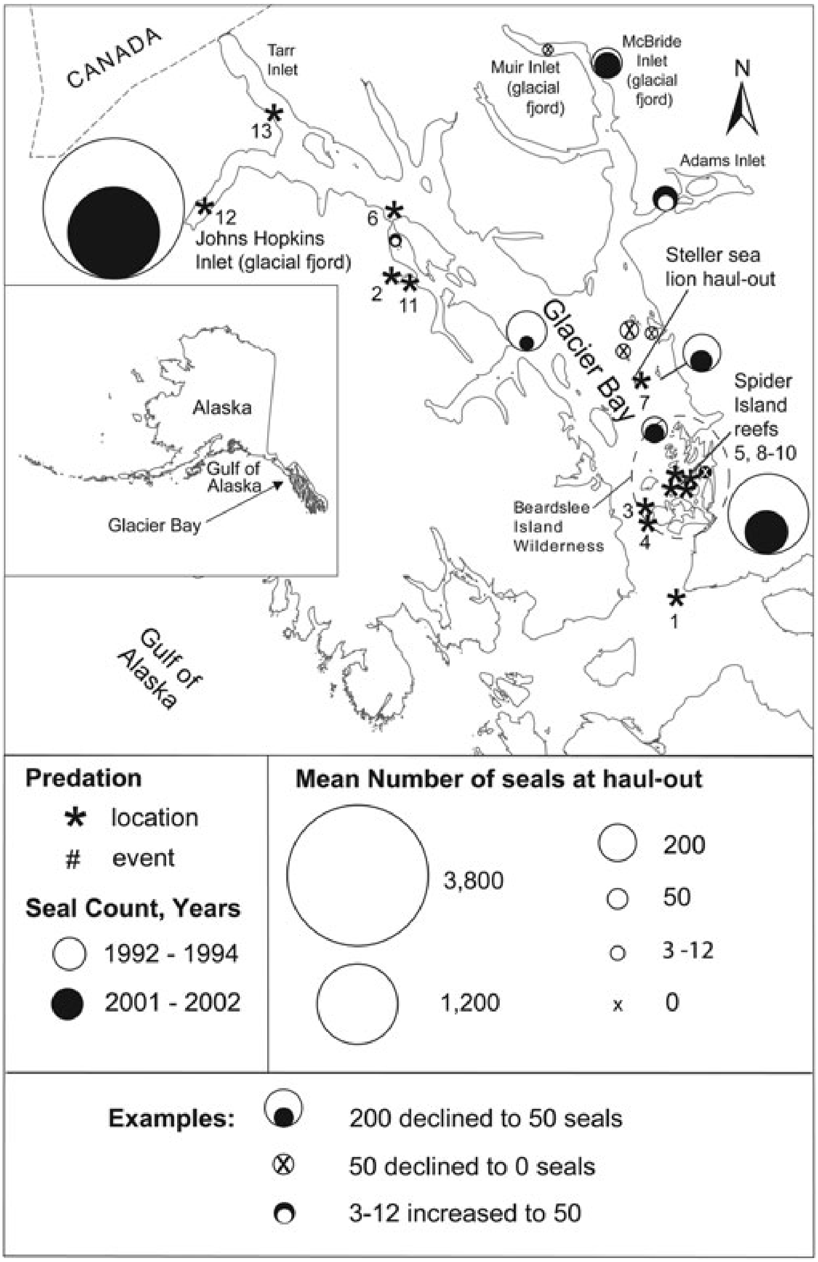

Figure 1. Map of Glacier Bay showing the 13 larger harbor seal haul-out sites (circles), including the largest terrestrial haul-out (Spider Island complex), the largest tidewater glacial haul-out (Johns Hopkins Inlet), and the only regularly used Steller sea lion haul-out in Glacier Bay. Mean counts of seals from August 1992 and 1994 (open circles) are compared to mean counts from August 2001 and 2002 (filled circles) to show relative trend in each haul-out area. Circle area is scaled to the number of seals. The locations of 13 predatory attacks by Steller sea lions on harbor seals are denoted with *'s and chronologically numbered.

out in one glacial fjord (Johns Hopkins Inlet), whereas the remaining third were found at up to about 20 tidally submerged terrestrial sites or in one other small glacial fjord (McBride Inlet) (Mathews and Pendleton 2006). Among the terrestrial resting areas, the majority of seals are found on sand bars (locally called "reefs") near Spider Island in the Beardslee Island Wilderness area (Fig. 1). We define the "Spider Island complex" as six haul-outs within about 1.9 km of Spider Island (Fig. 1). Typically, one to four of these haul-outs were occupied during summer low tide surveys. From 1992 to 2002, seal numbers at most haul-outs declined (Fig. 1).

Overview of Analytical Approach

In the sections which follow, we summarize the predatory attacks, present our two approaches for evaluating whether predation increased over the study period, and describe how we tested if predation rates were proportional to sea lion numbers. We then evaluate temporal trends in predation, describe the demography of predators and prey, and present the methods used in the fine-scale analysis of predation at the Spider Island complex. Finally, we develop a Leslie life history population model to evaluate what level of predation by sea lions would be needed to produce the observed population declines in harbor seals.

Observations of Predation by Steller Sea Lions

From 1995 to 2006, 13 direct observations of predation by a Steller sea lion on a harbor seal were reported (Table 1). Four observations (Table 1: #5, 8, 9, and 10) of predation were made by seal researchers during shore-based and aerial surveys of harbor seals in the Spider Island complex. The remaining nine observations were made elsewhere in the Bay (Fig. 1) by NPS biologists, NPS Interpretive and Enforcement Rangers, and the captain of one of the seasonal tour boats. Because of the dramatic nature of the predatory attacks and the local focus on research and nature observation, it seems very likely that most, if not all, direct observations of such attacks would have been reported. We also include two indirect observations which suggest additional predatory attacks, and we describe the first observations of scavenging by Steller sea lions on recently killed harbor seals made by a local seal hunter in the Juneau area.

Has Predation by Steller Sea Lions Increased?

To test whether the rate of predation by sea lions had increased over the study period, we examined predation rates inferred from five independent observer data sets (Spider Island Shore, Spider Island Aerial, Ships, Biologists, and Rangers, described later) from Glacier Bay and for which we had data spanning 21–25 yr, 1982–2006.

Field Observations: Data Sets

1. *Spider Island complex, shore-based*: Each summer in 1991–1993 and 1996–2003, for a few days to a month, shore-based observers counted harbor seals and recorded their behaviors from a field camp located 1.5 km northwest of the Spider Island reefs (Fig. 1). Systematic counts and behavioral

Table 1. Summary of 13 direct observations of predation by Steller sea lions on harbor seals and two examples of indirect evidence for predatory attacks by sea lions on harbor seals. Minimal estimates of attack duration from six observations ([a]) were used to calculate mean handling time.

				Observations			Age/sex category			
Number	Year	Date	Time	Observer	Platform	Location	Seal	Sea lion	Other sea lions	Attack duration (min)
1	1995	Summer	~0900 h	Chad Soiseth, NPS biologist	Research vessel	Gustavus Point	Unknown	Adult		
2	1995	Summer	NA	Pavia Wald, NPS interpretive ranger	Kayak	Weird Bay	Unknown	Adult male		
3	1995	Summer	NA	Cory Heimbuch, Captain, Glacier Spirit	Tour/cruise ship	Young Island	Unknown	Adult		
4	1995	26 October	1405 h	Chris Gabrielle, Katy Teeter, NPS biologists	Research vessel	Sitakadday Narrows	pup/sm = yearling	Adult male	1	20[a]
5	1997	25 July	1600 h	Beth Mathews, Braun Lowry, biologists	Shore counts	Spider Island reefs	pup/sm	Adult male	2 juveniles	32[a]
6	1997	16 August	1200 h	Beth Mathews, marine mammalogist	NPS skiff	Skidmore Cut	pup/sm = yearling	Adult male	0	>5
7	1998	16 July	0730 h	Doug Lucchetti, NPS interpretive ranger	Tour/cruise ship	S. Marble Island	pup/sm	Adult	1	>10
8	1998	19 July	0732 h	Janene Driscoll, Lara Dzinich, seal biologists	Shore counts	Spider Island reefs	Unknown	Unknown	0	20[a]
9	2000	2 August	0914 h	Beth Mathews, marine mammalogist	Aerial survey	Spider Island reefs	Unknown	Adult	0	>5

Continued

Table 1. (Continued)

				Observations			Age/sex category			
Number	Year	Date	Time	Observer	Platform	Location	Seal	Sea lion	Other sea lions	Attack duration (min)
10	2002	13 August	1300 h	Amy Kamaranien, Janene Driscoll, seal biologists	Shore counts	Spider Island reefs	Unknown	Unknown	0	22[a]
11	2004	26 March	~1200 h	Maya Seraphin, Chuck Young, Gus Martinez, Wendy Bredow, Margaret Hazen, NPS rangers	Kayak	Weird Bay	Small adult/ subadult	Adult male (large bull)	1 medium-sized	60[a]
12	2006	29 April	1300 h	Jamie Womble, NPS marine mammalogist	Research vessel	Johns Hopkins Inlet	Subadult	Adult	0	60[a]
13	2006	1 September	1039 h	Karin Harris, NPS biologist	Tour/cruise ship	Tarr Inlet	Unknown	Adult male	0	
	Indirect observations			Observer	Specimen	Location	Seal			
1	1997	27 September	NA	Lara Dzinich, seal biologist	Beach cast strip of seal skin	S. Marble Island	Possible yearling			
2	2005	22 August	NA	K. Burek, veterinarian; necropsy	Dead seal, two puncture wounds in hindquarter	Bartlett Cove	Subadult (~2-yr-old)			

[a]Attack duration used to calculate minimal mean handling time.
NA = not available.

observations, including disturbances of seals, were conducted every 10–30 min for an average of 5 h per day during daylight when seals were on haul-outs exposed during low tide cycles (Mathews 1995). We calculated observer effort by summing the duration of all shore survey periods including the 30 min walk along the beach (facing the haul-outs) to the observation site. During this time, observers would have had a high probability of noticing a predatory attack by a Steller sea lion, because attacks were highly visible with audible stampedes of seals, as many or most abandoned the haul-out. A narrative from a field journal is provided for one of these direct observations and two others are available in Appendix S1.

Additional survey and observational data in the Spider Island area came from earlier harbor seal and wildlife surveys. During 1982, 1983, and 1984 one to six counts of harbor seals lasting approximately 45 min were made in the Spider Island area by a research team on 5–10 d each summer (Calambokidis *et al.* 1987).[1] In 1989, two NPS biologists conducted wildlife surveys from kayaks and camped in the Beardslee Island area for 39 days.[2] We conservatively estimated the total observation effort for the 1989 study as 450 min.[3]

2. *Spider Island complex, aerial*: A second independent source of observations came from aerial surveys of seals at the Spider Island complex from 1992 to 2002. During these surveys, as the plane was approaching a haul-out, the biologist scanned ahead to determine the exact location of seals and to provide information to the pilot on the best approach path. The average approach and survey time over the Spider Island haul-outs was 8 min ($n = 16$). We used data and observations from aerial surveys conducted only by seasoned seal biologists (E.A.M. and B. P. Kelly, NOAA, NMFS, Auke Bay Lab, Juneau, AK).
3. *Tour boats and cruise ships*: All tour boats and cruise ships that enter Glacier Bay National Park between 10 May and 18 September have an NPS Interpreter on board during their time in the Bay, and records of all vessel entries are maintained by NPS staff. NPS Interpreters receive extensive training on the natural history and biology in the Park and a majority are experienced observers of Glacier Bay wildlife. Effort was recorded as an "observer day" because most vessels spent most of the day touring Glacier Bay. We assumed that the potential to observe a predatory event from these platforms had not changed over the time span of our analyses.
4. *Biologists*: Observations from biologists working in the Park included those from us and made by members of our pinniped field crews, as well as NPS biologists. Effort for biologists was determined from data bases, field notes, and interviews.
5. *Rangers*: Time on the water in hours, or effort, for NPS Protection Rangers was compiled from annual logbooks maintained as part of their boat-based patrols. We also interviewed four long-term staff and Division Chiefs from

[1] Personal communication from John Calambokidis, Cascadia Research Collective, 218 1/2 W 4th Avenue, Olympia, WA 98501, 25 October 2006.

[2] Lentfer, H., and A. Maier. 1989. Wildlife and vessel observations in the Beardslee Islands in the early summer. Unpublished report, U.S. National Park Service, Glacier Bay National Park and Preserve. 10 pp.

[3] Personal communication from Hank Lentfer, Gustavus, AK , 20 Oct 2006.

this NPS program, including individuals who had worked in Glacier Bay from 1989 to 2006.

Interviews

To determine if there were any observations of predatory attacks by Steller sea lions on harbor seals reported to, or made by, NPS staff or visitors prior to 1995 or any we had overlooked, we also interviewed four long-term Glacier Bay National Park employees. These individuals had tenure spanning up to 27-yr in Glacier Bay and routinely spent time on the water or were in charge of staff who patrolled the Bay.

Statistical Analysis: Has Predation by Sea Lions Increased?

Our first question was whether predation by Steller sea lions in Glacier Bay could have been occurring before 1995, but was not detected? The five types of observations were jointly tested statistically both for equality of rates of predation before and after 1995. Units of observation effort for each data type were chosen to be long enough so that a predation event would be unlikely to span adjacent units. For shore observation effort we used 5-h units centered around low tide cycles. Spider Island aerial samples occurred in 8 min units corresponding to the average time over the haul-out. All other observation types (ships, biologists, and rangers) were categorized as a "day" of effort, which generally consisted of a 6–9 h period on the water. The likelihood was calculated assuming a binomial distribution of predation events. Under the null hypothesis, the rate of predation was assumed to be constant for all years; under the first alternative, the rate made a step increase beginning in 1995. The test statistic was the difference in the maximum log-likelihood between the competing models.

To compensate for any violation of the assumptions of the analysis (*e.g.*, nonindependence of observations, overdispersion, *etc*.), we used two bootstrap techniques to assess significance of results. We calculated the *P*-value as the fraction of 1,000 bootstrap trials where the difference in log-likelihood was greater than that observed using the true data. To account for a possible bias in the test caused by picking the year of increase in predation based on the first year predation was observed, in each bootstrap trial we searched for the shift year that gave the largest increase in likelihood compared to the constant predation rate model, subject to the constraint that the number of years before or after the shift had to be at least 5-yr long. Only bootstrap trials where the apparent shift in predation rate was consistent among the five data types (*i.e.*, where all five increased or all decreased) were counted.

The first bootstrap test consisted of creating simulated data sets by independently and randomly resampling predation/effort combinations from the 25-yr series of each type of observation. The second bootstrap test differed from the first in that we resampled all five types of observations simultaneously; that is, when we resampled a random value from the Spider Island Shore data series, we filled the other data series using the values from that same year. This preserved the within-year associations among the different types of observations.

Statistical Analysis: Is Predation Proportional to the Number of Sea Lions?

We also conducted tests of the hypothesis that the rate of predation of Steller sea lions on harbor seals was proportional to the abundance of Steller sea lions. Steller sea lions in Glacier Bay primarily used one nonbreeding haul-out, South Marble Island (Fig. 1, Sea Lion Haul-out) during this study. The overall rate of increase in Steller sea lions at South Marble Island from 1991 to 2004 was 23%/yr (95% CI = 14%–32.5%).[4] We extrapolated the abundance estimate for 2005 using the trajectory from the 1991 to 2004 data. We examined this hypothesis using two approaches. First, we modeled predation rate as proportional to the index of Steller sea lion abundance, and second, we added an intercept term to this model. The likelihood of both models was compared to the likelihood of the null model, in which the rate of predation was assumed to remain constant, as for the tests of a step shift in predation rate.

The methodology for testing whether sea lion predation had increased relative to the abundance of sea lions in Glacier Bay was identical to that used to test for a shift in predation rates beginning in 1995. As before, likelihoods for both the null and alternative models were calculated using all five observer data sets, and *P*-values were calculated using two bootstrap resampling methodologies. However, the alternative hypothesis in this second analysis was that the rate was proportional to the index of abundance of Steller sea lions.

Temporal Trends and Demography of Predatory Interactions

Because harbor seal pups and recently weaned juveniles are presumably easier to capture for sea lions than older, more experienced seals, and harbor seals spend less time hauled out in winter than in summer (Frost *et al.* 2001), we hypothesized that there might be a tendency for more predation to occur during summer months (June–August), when seals are born and weaned and when seals spend more time aggregated densely at haul-outs, than during other months. As a first test of this hypothesis, we standardized all observer effort into units of days and compared numbers of predatory attacks and observer effort across seasons (June–August, September–November, December–January, February–April).

For each direct observation of predation where data were available, we recorded the age category of the attacking Steller sea lion (adult male/bull, adult sex unknown, juvenile) and of the attacked harbor seal (dependent pup, weaned pup, yearling, small adult/juvenile, adult, unknown). If an observer reported that the attacked seal was a pup or a very small seal, we assumed that if the date of an attack was after July, that the seal was a weaned yearling rather than a dependent pup, because the majority of pups are born by mid-June (Mathews and Pendleton 2006) and pups are weaned at 3–6 wk (Hoover-Miller 1994).

Spider Island Complex: Quantifying Observer Effort and Extrapolating Sea Lion Predation Rates

We were interested in determining if the levels of predation directly observed at the Spider Island complex could have a population-level effect. For this haul-out site, we had precise measurements of the amount of time observers were present as well as the number of predatory attacks observed, which could be combined to calculate a predation rate. Because Steller sea lion predation on a harbor seal in Glacier Bay was first reported in 1995, we divided our Spider Island data into two blocks: 1982–1994 and 1995–2003.

[4]Personal communication from Grey Pendleton, Alaska Department of Fish and Game, Douglas, AK, December 2009.

The rate of predation by Steller sea lions for 1995–2003 was the number of predatory attacks observed in this area divided by the total number of hours of observation. To estimate the annual number of seals killed by sea lions, we needed to extrapolate this rate over the fraction of time in a year to which it might apply. To do this, we made lower and upper boundary assumptions about the effects of two factors—daylight and season—on whether predation might occur and a correction factor for periods when observers were not "on effort." First, we assumed that predatory attacks might occur less often or be less successful after sunset compared to daylight hours, because lower light could make seals more difficult to locate or secure. For the lower boundary we assumed an effect of shorter day length, whereas for the corresponding upper boundary we did not limit the model by available light (Table 2). Second, we also included the assumption that predatory attacks by Steller sea lions on harbor seals during non-summer months might occur less often or be less successful than during the summer months. This seasonal assumption was based on three observations. First, as young of the year mature, their probability of successfully avoiding or escaping an attack should improve. Among mammals, it is common for the highest risk of mortality to occur early in life (Caughley 1966), but with experience and skill, survival probabilities from predatory attacks presumably improve. For the lower and upper boundaries of the predation rate for fall through spring, we chose 10% and 25% times the observed predation rate during summer (Table 2) as reasonable "best guesses" because we knew that predation by sea lions in non-summer months did not drop to zero (Table 1, observations 4, 11–13) and we reasoned that it would be lower than during summer as young of the year gained experience and grew.

Annual Pup Production and Sea Lion Predation

As one measure of the potential effects of predation by sea lions, we wanted to compare pup production at the Spider Island complex to our estimates of the number of seals killed annually by Steller sea lions at this one site. For this evaluation, we used the two (1992) or three (all other years) highest counts of seals from aerial photographic surveys to calculate the mean in peak numbers of seals ashore during the August molt from 1992 to 2002 (Mathews 1995, Mathews and Pendleton 2006). In Glacier Bay most seal pups are born by mid-June (Calambokidis *et al.* 1987, Mathews and Pendleton 2006), but by August they are difficult to distinguish from yearlings in aerial photographs. We had survey data from June (pupping) for 1997 and 1999; fewer seals were counted on haul-outs during June compared to August (Mathews, unpublished data). To estimate numbers of seals ashore during June for years in which there were not June surveys, we calculated the ratio of peak counts of seals ashore in June *vs.* August for 1997 and 1999 and applied this ratio to the other years with surveys only in August. We then used the pups and total seals counted on shore (%Pups in Count = pups/[non-pups + pups]) from 1997 and 1999 to calculate a mean percent of pups ashore. To estimate the total number of seal pups present at the Spider Island reef complex each year (=Pup Production), we also incorporated a pup correction factor of 1.18 (=1/0.85) (Huber *et al.* 2001) to account for pups that were in the water (*i.e.*, not visible) during aerial surveys (=In the Water CF). The in-the-water correction factor was developed for harbor seal pups at terrestrial haul-outs in Washington and Oregon, during surveys comparable to our June survey period. In summary, our estimate of pup production at the Spider

Table 2. Lower and upper boundaries of variables used to estimate the annual harbor seal mortality due to predation by Steller sea lions. Estimates are based on assumptions summarized in the table and in the text.

Variable	Assumptions	Lower boundary June–August	Lower boundary September–May	Lower boundary All months	Upper boundary June–August	Upper boundary September–May	Upper boundary All months	Units
(a) Daylight	Lower boundary: light is a factor in predator success. Used average hours of daylight in Juneau, Alaska. Upper boundary: Light is not a factor.	16.5 69%	11.1 46%	 **52%**	24 100%	24 100%	 **100%**	h %
(b) Season	Predation at observed level during summer; during non-summer at 10% and 25% of observed rate for lower and upper boundaries, respectively.	3	9 × 10%		3	9 × 25%		mo
	Months × days × hours	2,182	654	**2,836**	2,182	1636	**3,818**	h
(c) Observation correction	Surveys only conducted during low tide cycles, which excluded 25% of the tide cycle. Upper boundary incorporates a correction for potential predatory attacks during this time.	100%	100%	100%	133%	100%	**108%**	%
(d) Subtotal, hours available for potential predatory attack				1,471			4,136	h
(e) Observed predation rate				0.01633			0.01633	Seals/h
Estimated seal mortality per year [(d) × (e)]				24			**68**	Seals/yr

Island complex was calculated as follows:

$$\text{Pup Production} = (\text{August Count}) \times (\text{June:August ratio}) \times (\%\text{Pups in June Counts}) \times (\text{In Water CF for pups}).$$

Spider Island Complex: Observations of Killer Whales

During seal surveys at Spider Island we also recorded when killer whales (*Orcinus orca*) were in the area and if they elicited a disturbance of harbor seals. Disturbances were characterized as an increase in seal vigilance (head held up, seal looking outward) or activity (*e.g.*, seals moving up or down the haul-out) or a rapid departure of some or all of the seals from the haul-out into the water. In southeastern Alaska coastal waters, two non-interbreeding forms—or ecotypes—of killer whales are recognized: one ecotype eats fish (often called "residents") whereas the other is a marine mammal specialist (called "transients") (Ford *et al.* 1998). In most cases, we could not tell if a particular group of killer whales was composed of the mammal-eating *vs.* fish-eating ecotype.

Unlike the sea lion attacks, killer whale predation on harbor seals typically occurs under water with very little above water evidence (Deeke *et al.* 2006) that would likely be visible (or conclusively indicate predation) from our low angle shore view (Mathews, personal observation). As such, we present the observations of killer whales as an indicator of potential predatory attacks on seals. We hypothesize that the killer whales observed near the Spider Island complex would have a higher probability of being the mammal-eating ecotype for several reasons. First, the maximal size of foraging mammal-eating killer whale groups is typically eight (Baird and Dill 1996), compared to 10–25 for the fish-eating ecotype (Ford *et al.* 1998); we only observed one group in the study area with more than seven killer whales. Second, in Glacier Bay 55% of observations of killer whales from 1986 to 2005 were of the mammal-eating rather than the fish-eating ecotype. Third, harbor seals can distinguish fish-eating and mammal-eating ecotypes underwater acoustically (Deecke *et al.* 2002), and perhaps visually by group size or behavior (Baird 1994). From these observations, we suggest that the disturbances elicited by close approaches of killer whales were more likely the result of mammal-eating than fish-eating killer whales.

Population Modeling: What Is the Role of Steller Sea Lion Predation in the Harbor Seal Declines?

From 1992 to 2008, harbor seal numbers at terrestrial haul-outs in Glacier Bay declined by −12.4%/yr (95% CI = −13.7% to −11.1%) and −8.2%/yr (95% CI = −8.5% to −7.8%) in Johns Hopkins Inlet, a tidewater glacial fjord (Womble *et al*. 2010). Between the early 1990s and 2000–2001 declines occurred at 11 of the 14 larger haul-outs (Fig. 1). In 1995, the mean number of seals on terrestrial haul-outs in Glacier Bay was approximately 2,000 (Mathews and Pendleton 2006). Using the estimated trend (−12.4%), from that year to the next, approximately 248 seals would have been removed from the population of seals ashore or about twice that many (Boveng *et al.* 2003) if we account for seals in the water during aerial surveys. Is it possible that Steller sea lion predation might explain all or most of this large decline? To address this, we constructed a Leslie model (Caswell 1989) of harbor seal population dynamics using female mortality and pregnancy schedules (Table 3) from

Table 3. Survival of female harbor seals and fecundity (as female pups). Data from Pitcher and Calkins 1979.

Age	0–3	4	5	6	7
Survival	0.26	0.895[a]			
Fecundity	0	0.085	0.315	0.44	0.46[a]

[a]Applies to all older animals.

intensive sampling of seals in the Gulf of Alaska (Pitcher and Calkins 1979). Pitcher and Calkins reported (p. 277) a cumulative female mortality of 74.2% between ages 0 and 4, and 11.4% per annum thereafter. To get production rates of female pups only, we halved pregnancy rates given in their table 6 for each age up until age 6; for older individuals (age classes where ovulation rates were 100%) we summed the number pregnant and divided by the number sampled, then divided again by two. These schedules resulted in a slight annual decline; we increased the survival rate of seals age 4 and older (4+) from 88.6% to 89.5% per year to produce a stable population, which we used as a baseline for our analyses.

To examine the effect of additional mortality due to predation, we reduced all fecundities (equivalent to reducing juvenile survival) or the survival rate of age 4+ females by a fraction ranging from zero to one, and calculated the resultant annual rate of decrease of the population. We looked specifically for the fractional reduction that would produce an annual decline of 12.4% per year, similar to what has been observed at the terrestrial haul-out sites in Glacier Bay over the period 1992–2008 (Womble *et al*. 2010).

Results

Observations of Predation by Steller Sea Lions

We compiled more than 14,000 effort days from the five observer categories used in our analyses (Table 4). The first reported observations of a Steller sea lion attacking a harbor seal in Glacier Bay were made in summer 1995 when four different NPS employees each observed a different instance of a Steller sea lion preying on a harbor seal (Table 1). Since 1995 a total of 13 observations of predation by a Steller sea lion in Glacier Bay have been reported, including five observations made by researchers studying harbor seals with three by one of us. One description of Steller sea lion predation on a harbor seal is summarized later and two others are included in Appendix S1.

Field Observation of Predation at Spider Island (EAM)

On 25 July 1997 (Table 1, observation 5), my field assistant, Brawn Lowry, and I were conducting surveys of harbor seals from a field camp on a small island ~0.8 km west of the Spider Island reefs to document haul-out patterns, behaviors, and disturbances. Using 20 × 60 Leica binoculars mounted on tripods, we counted seals and recorded their behavioral states every 15–30 min. On 25 July we began surveys at 0715 h. It was a sunny, calm day with excellent viewing conditions. At 1100 h there were 577 seals hauled out and 5 in the water nearby; this was

Table 4. Summary of units of effort and years of coverage from five categories of observers in Glacier Bay National Park.

			Years			Observer effort			
Observer category	Platform	Location	Range	Span	*n*	Total	<1995	≥1995	Units
Biologists	Shore	Spider Island complex	1982–2003	22	15	81.8	35	47	Days[a]
Biologists	Aircraft	Spider Island complex	1992–2002	11	11	82	13	69	Surveys
Interpretive rangers	Ships	Glacier Bay	1984–2006	23	23	10,492	4,337	6155	Days[b]
Biologists	Boats	Glacier Bay	1985–2005	21	21	1,345	525	820	Days[b]
Rangers	Boats	Glacier Bay	1985–2006	22	22	2,119	618	1,501	Days[b]
		Subtotals =		25		14,038[c]	5,515[c]	8,523[c]	Days

[a]Shore survey "days" were defined in 5-h blocks constrained by low tide cycles.
[b]Time on the water was typically 6–9 h.
[c]Subtotals do not include aerial survey effort due to different units.

our high count for the day. The following is a summary from my field notes of an attack we witnessed. We were approximately 400–700 m from the predation event.

> Around 1540 h the tide was rising and 204 seals were bunched tightly together on the remaining two strips of exposed haul-out; 13 were visible in the water nearby. At 1559 h, all seals on the haul-out stampeded into the water. A large, adult male Steller sea lion was then observed with a small harbor seal in its mouth close to the edge of the seal haul-out. The sea lion bit onto the head of the seal and began slinging it from side to side. At 1615 h, a subadult Steller sea lion approached the bull, which had continued to fling the small seal from side to side. By 1616 h the seal was clearly dead after rigorous shaking and thrashing during which blood and tissues were flung widely. At this time the smaller sea lion moved in to within a meter of the bull, which had just resurfaced with the seal remains in his mouth. By 1620 h approximately 20 gulls were clustered near and above the scene and some were swooping down to the water, apparently consuming pieces of harbor seal tissue. The bull surfaced, chewing and breathing hard (we could easily hear it huffing from our observation site). Brawn saw the inner abdominal cavity of the seal and possibly the pelvic bones during one of the bouts of flinging. At 1623 h, a third Steller sea lion, another subadult, approached the site and the two smaller sea lions moved to within a couple of meters of the bull. Their attention was clearly directed toward the bull and they may have consumed some scraps of tissue. At 1628 h, the bull was still thrashing and flinging the seal remains over his head, and the two smaller sea lions were close to one another, but about 30 m from the bull. At 1632 h, the adult male sea lion swam steadily away from the attack site heading to the south . . . and out of the Beardslee Island area. Moments earlier, the other two sea lions had departed approximately in the same direction. At 1640 h, I saw two sea lions, possibly the two smaller ones again. By this time no harbor seals were on the haul-outs.

Predatory Behavior: Overview

Accounts of the predatory attacks had many similarities with the preceding description and with one another. The observer's attention was typically drawn to the activity by splashing from what was most often described as an "adult" or "a large" or "a bull" Steller sea lion. With the exception of the October 1995 event (Table 1), the attacking sea lion's behaviors included biting and flinging of the seal from side to side. Observers noted a lot of red blood in the water and exposed red or "dark red" tissue visible on or near the attacked seal. In most cases, chewing and swallowing was noted specifically and several observers commented that the seal's head was grabbed by the sea lion during some of the flinging bouts or that the seal appeared to be eviscerated. Minimal prey handling times ranged from 20 to 60 min (mean = 36 min, SD = 19, $n = 6$) (Table 1); handling times were considered minimal because observers did not always see the beginning of an attack.

Indirect Evidence for Predatory Attacks

In addition to the 13 direct observations of predation, two observations suggest additional predatory attacks by Steller sea lions. On 27 September 1997, a longitudinal strip of skin and fur from a harbor seal pelt was found on the beach at South Marble Island, immediately adjacent to the only regularly used Steller sea lion haul-out in Glacier Bay at that time. The second indirect evidence for a predatory attack on a small (37kg) harbor seal by a sea lion came from the necropsy of a ∼2-yr-old harbor seal which was found on 22 August 2005 on a beach in Bartlett Cove, south of the Beardslee Island Wilderness area in Glacier Bay (Fig. 1). The necropsy revealed that the seal had paired puncture wounds spaced 6 cm apart in the hind quarters and associated with a broken tibia.[5] The puncture wound spacing was consistent with that of an adult Steller sea lion's (or brown bear's) canines. The seal "died of either blood loss and shock (most likely) or there could have been an element of drowning as indicated by the fluid in the lungs and the emphysema indicating forced respirations." No other source of injury or disease was evident and the veterinarian concluded that the injuries were most consistent with a seal that had escaped a predatory attack by a Steller sea lion or possibly a bear.

Has Predation by Steller Sea Lions Increased? Interviews with Long-Term NPS Staff

None of the NPS employees or biologists who had worked in Glacier Bay in the decades prior to 1995 had witnessed or heard reports of Steller sea lions attacking harbor seals before 1995. Bruce Paige,[6] Glacier Bay National Park's Chief of Interpretation from 1968 to 1994, had never heard of a Steller sea lion attacking a harbor seal, and he noted that those "kinds of observations would have been discussed immediately" among his staff and "would certainly have been relayed" to him. Paige also noted that during his tenure as the head of the Interpretive Division "Steller sea lions were not a major component of the fauna." Similarly, Rose Salazar,[7] a seasonal Interpretive Ranger at Glacier Bay National Park from 1986 to 1995 and the Supervisory Interpretive Ranger from 1996 to 2007, had not heard of any predatory attacks prior to 1995. We also interviewed the head of the NPS Enforcement Ranger Division (Randy King 1990–2000) and a long-term Enforcement Ranger (Mike Sharp, 1988–1993, 1997–2005); neither individual had ever witnessed nor heard of a Steller sea lion attacking a harbor seal before 1995. Biologists who had surveyed harbor seals in Glacier Bay during the 1980s also reported that they had never witnessed a Steller sea lion attacking a harbor seal.[3,8]

[5]Burek, K. A. 2006. Pinniped necropsy report for a harbor seal from Glacier Bay (ID# GBNP-PV-22AUG05). Alaska Veterinary Pathology Services, P. O. Box 773072, Eagle River, AK 99577. 4 pp.

[6]Personal communication from Bruce Paige, retired Chief of Interpretation, Glacier Bay National Park. Gustavus, AK, 22 June 2006.

[7]Personal communication from Rosemary Salazar, Interpretive Ranger and Assistant Chief of Interpretation, Glacier Bay National Park, P. O. Box 140, Gustavus, AK, June 2006.

[8]Personal communications from John Calambokidis and Gretchen Steiger, Cascadia Research, Olympia, WA, 25 October 2006; Greg Streveler and Hank Lentfer, Gustavus, AK, June 2006.

Statistical Analysis: 1995 Increase in Predation Rate

All analyses of the five independent observer data sets supported the hypothesis that the rate of predation of Steller sea lions on harbor seals in Glacier Bay was higher after 1994 compared to the study years before (Fig. 2). When comparing a model where the predation rate changed in 1995 to a model with a constant predation rate, the log-likelihood increased by 5.83. Creating a null distribution for the change in log-likelihood by independent bootstrap draws from each of the five data series resulted in a P-value of 0.013. Creating a null distribution by bootstrapping entire years (*i.e.*, keeping the correlation among data sets) gave a P-value of 0.029. Both analyses indicate that it is highly improbable that a similar rate of predation by sea lions was occurring prior to 1995.

Statistical Analysis: Is Predation Proportional to the Number of Sea Lions?

The prediction that the predation rate would be proportional to the index of sea lion numbers in Glacier Bay was not supported (Fig. 3). The model where the predation rate was proportional to the index of Steller sea lion abundance gave an even lower likelihood than assuming that the predation rate did not vary among years. Adding an intercept term to this sea lion index model resulted in an insignificant improvement in the likelihood. The crux of the lack of significance between the index of sea lion abundance and the rate of predatory attacks is in the timing of the observed predation events. Although predation did not occur when the sea lion index was low, the number of predation events was the same (or even higher) when sea lions were at index values of 77–147, from 1995 to 1998, as compared to when the sea lion index was many times higher later on (Fig. 3). This pattern is very unlikely if the predation rate is proportional to the number of sea lions.

Temporal Trends and Demography of Predatory Interactions

Contrary to our prediction of higher predation rates during summer, our results suggest that the predation rate is proportional to observer effort and that there was not much of a seasonal effect (Fig. 4). Sixty-four percent (9/13) of the observed predatory kills of harbor seals were observed during summer; however, 67% percent of the observer effort also occurred in summer months (June–August). The low coverage during winter (93 of 13,720 d or 0.7% of observer effort), however, precludes a conclusive assessment of the frequency of predation during this season.

The age-category of the attacking sea lion was reported in 11 of the 13 direct observations of predation. Of these 11, all were reported as adults and six observers (55%) indicated that the attacking Steller sea lion was an adult male or a “bull sea lion” (Table 1). The age category of the attacked harbor seal was reported in six of the 13 observations. Four of these six (66%) noted that the seal was small or a pup; we categorized these animals as pups/yearlings (Table 1). Two experienced seal observers, who had handled harbor seals during temporary research captures, classified the attacked seal as a subadult (33%).

Spider Island Complex: Annual Pup Production and Sea Lion Predation

From 1992 to 2002, mean counts of harbor seals hauled out throughout Glacier Bay declined steeply, from a total of 6,200 down to 2,500 (~65%) (Mathews and

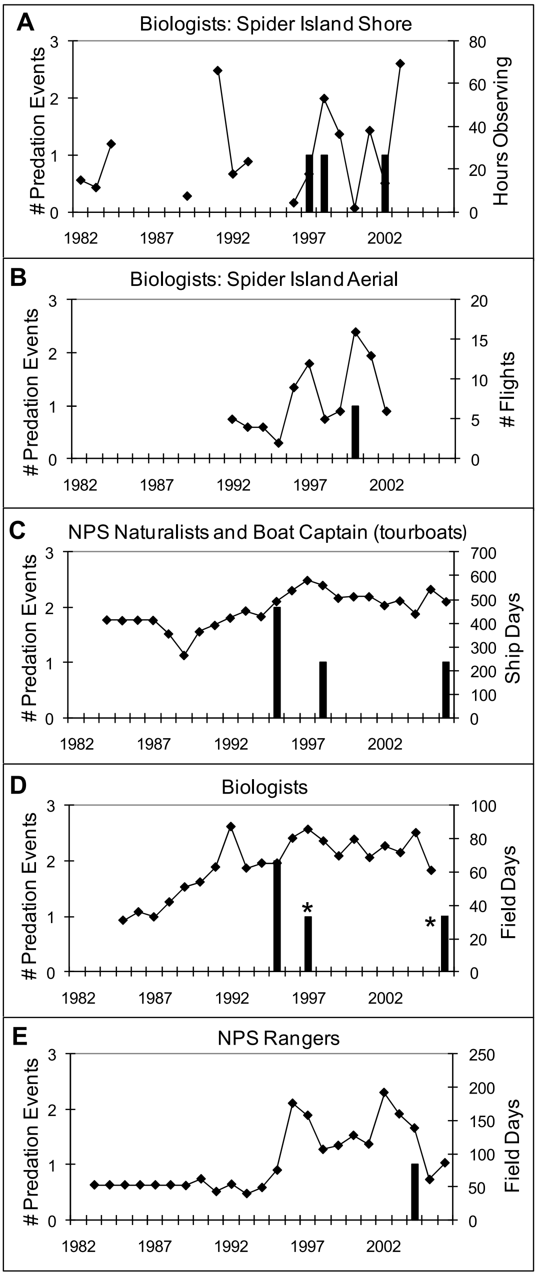

Figure 2. Summary of 13 direct observations of predation by Steller sea lions on harbor seals (solid bars, left axis) and observer effort (lines, right axis) for five independent categories of observers in Glacier Bay National Park (A–E). (D) One observation of predation (Biologists 2006) could not be used in this analysis, because we did not have corresponding observer data from earlier in the study. *'s denote indirect observations that suggest two additional predatory attacks by sea lions. The likelihood that predation by Steller sea lions on seals was occurring before 1995, but went undetected, was statistically very low in three different analyses ($P \leq 0.04$).

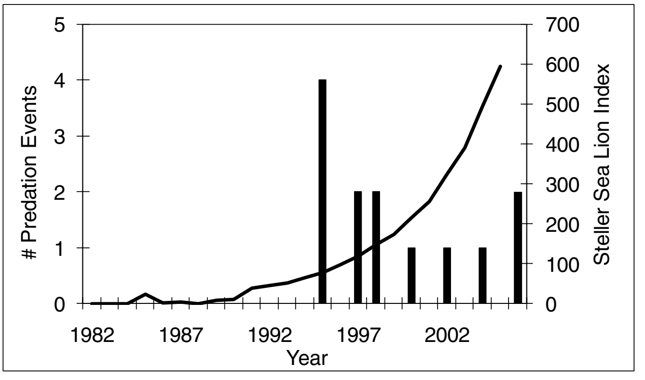

Figure 3. Index of Steller sea lion numbers (line) at the only regularly used haul-out within Glacier Bay compared to 13 observations of predation (solid bars) used in this analysis. The hypothesis that predation rate was proportional to the sea lion index was not supported.

Pendleton 2006). In a more recent analysis (Womble *et al.* 2010) counts at the terrestrial haul-outs—a subset of the overall survey area—seal numbers declined by 12.4%/yr (1992–2008: 95% CI = −13.7 to −11.1). Similarly, plots of the mean of peak counts of harbor seals ashore at the Spider Island reefs declined from 1992 to 2002 (Fig. 4A). Early in the study (1992–1994) the estimated number of pups born at the Spider Island reefs annually ranged from 135 to 179 (Fig. 4B). In contrast, we estimated that there were only 27–62 pups born at the Spider Island complex from 2000 to 2002 (Fig. 4B). Although predation by Steller sea lions does occur on non-pup seals, for illustrative purposes we note that our lower estimates of mortality from sea lion predation exceeded 33% of the pups produced at this haul-out in 5 of the 8 yr since 1994 (1997, 1998, 2000–2002) and averaged 57% from 2000 to 2002 (Fig. 4C). The upper boundary estimate of mortality exceeded 100% of annual pup production in 5 of the 8 yr since 1994, suggesting that subadults and/or adults were most likely taken in addition to younger animals (Fig. 4C).

Quantifying Observer Effort and Extrapolating Sea Lion Predation Rates

The predation rate calculated from four direct observations of predation by Steller sea lions on harbor seals at the Spider Island complex between 1996 and 2003 was 0.01633 kills/h (=4/245 h) (Table 2; Fig. 5A). The annual mortality of harbor seals due to predation by sea lions derived from our lower and upper boundary assumptions ranged from 24 to 68 seals per year (Table 2; Fig. 4B,C).

Spider Island Complex: Observations of Killer Whales

During surveys of the Spider Island complex, we observed a total of 13 groups of killer whales ranging in size from 2 to 15 whales. We excluded four off-effort observations of killer whales in groups of 3–6 from the 1995 to 2003 data set. As mentioned, we also excluded the one group of 15 whales from consideration as potential predators because most foraging mammal-eating groups have 8 or fewer whales (Baird and Dill 1996). The size of the remaining eight groups of killer whales

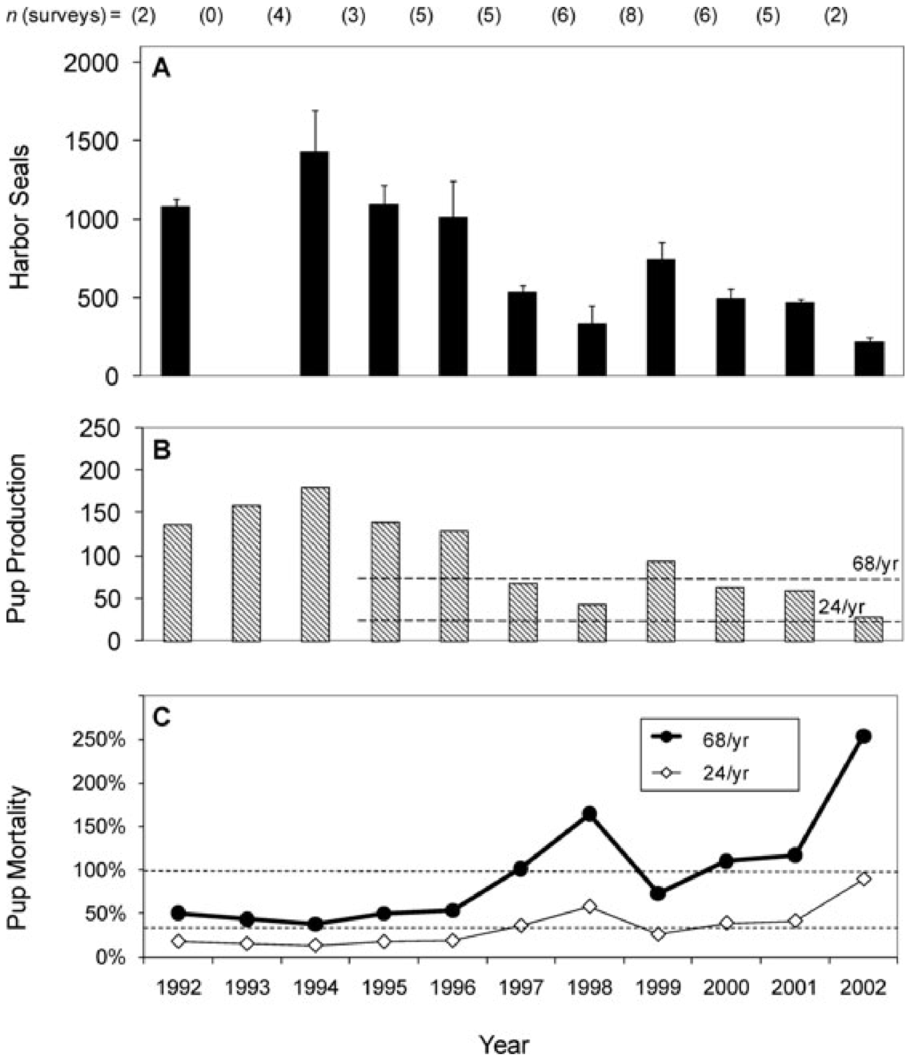

Figure 4. (A) Mean number of harbor seals counted on haul-outs in the Spider Island complex during aerial photographic surveys in August (no survey in 1993). (B) Estimate of pup production (1993 = mean of 1992 and 1994) with lower and upper estimates of mortality from predation by Steller sea lions. (C) Percent of pups or weaned juveniles potentially preyed upon by Steller sea lions under our lower and upper range assumptions (Table 2).

ranged from 2 to 8 (mean = 4.0). After 1995, we observed groups of killer whales about twice as often as in the earlier part of the study (1991–1995) (Fig. 5B). Seven of the eight observations occurred after 1995, as did all four of the disturbances of seals by killer whales on the Spider Island haul-outs (Fig. 5B). During one observation, a group of six whales surfaced twice close together in front of the occupied haul-out. All of the ~103 seals suddenly became vigilant and began moving up the haul-out,

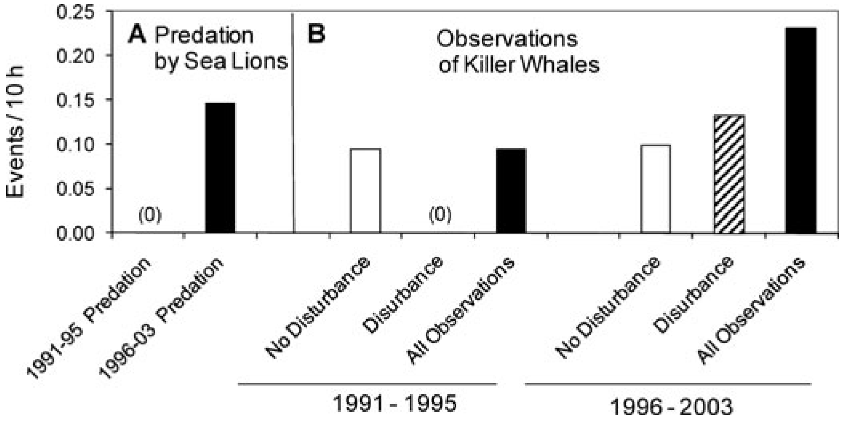

Figure 5. Frequencies (events per 10 h) during 245 h of observations near the Spider Island complex of (A) predatory attacks by Steller sea lions on harbor seals and (B) killer whales observed. Some Killer whales initiated disturbances of harbor seals (increased vigilance, activity, or stampedes into the water); others did not (No Disturbance). Only groups of killer whales with seven or fewer individuals were included.

away from the water. A minute later, the observer (L. B. Dzinch) noted a "huge explosion" of water in the vicinity of the killer whales, which were adjacent to the haul-out.

Population Modeling: What Is the Role of Steller Sea Lion Predation in the Harbor Seal Decline?

Leslie matrix analyses showed that the growth rate of the harbor seal population was much more sensitive to a reduction in age 4+ survival (Fig. 6B) than to a reduction in fecundity/juvenile survival (Fig. 6A). To achieve a 12.4% rate of population decline, annual survival of adults would have to be reduced by 0.20, from 0.895 (Table 3) to 0.715. Juvenile survival alone could not explain the observed 12.4% annual rate of decline; that is, reducing juvenile survival to zero resulted in an annual decline of only 10.5% (Fig. 6A).

Discussion

We provide the first direct evidence that Steller sea lions will prey on harbor seals. Is this a rare, insignificant phenomenon, or a behavior that can affect the targeted population? Observations of predation by top-level carnivores on other mammals are often rare, leaving researchers to assume that their occurrence is also rare. Consequently, the potential for a population-level effect from predators is often underrated until predation rates are quantified. In Alaska high levels of predation on moose calves (*Alces alces*) by black bears (*Ursus americanus*) were first suggested in 1950 (Chatelain 1950). Predation by black and brown (*Ursus arctos*) bears on moose was not confirmed, however, as a primary source of mortality in moose populations until three decades later, following the advent of radio-collars with mortality switches (Ballard *et al.* 1979, Franzmann *et al.* 1980).

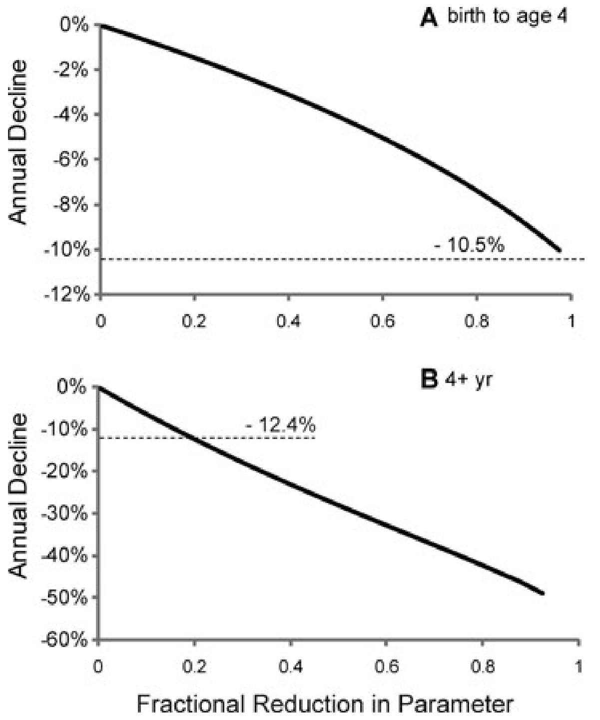

Figure 6. Annual percentage decline in a simulated harbor seal population as a function of the fractional reduction in survival from birth to age 4 (A) or in annual survival of females age 4 and older (B).

Previously Unidentified Predation Can Shape Populations

Two long-term field studies demonstrate that predation can have large effects on marine mammal populations as well. In the Seal Islands Archipelago, off Antarctica, the abundance and reproduction of two adjacent Antarctic fur seal (*Arctocephalus gazella*) breeding colonies were monitored from 1987 to 1995 (Boveng *et al.* 1998). The two colonies had similar densities and environmental conditions. Leopard seals were frequently observed killing and consuming fur seal pups at one of the colonies, but predation was never observed at the other. Pup mortality at the site without predation was 16%–29% compared to 51%–66% at the site with leopard seal predation. Annual counts of fur seal pups and estimates of total births declined steadily at the site with predation, indicating that the sustained high pup mortality resulted in low recruitment to the reproductive population. Several lines of evidence were consistent with a hypothesis that leopard seal predators limited fur seal population growth not just in the small colonies that were observed, but in the broader region of the South Shetland Islands.

The second long-term study demonstrating the potential for large effects of a marine mammal predator on another marine mammal species involves killer whales and sea otters (*Enhydra lutris*) in the North Pacific. During the 1990s, sea otter population throughout western Alaska declined at 25%/yr (Estes *et al.* 1998). By

1997 sea otter numbers in the Aleutian Islands had declined by 80% compared to the early 1970s. After ruling out reduced fertility, disease, and redistribution of otters to other areas, predation by killer whales was considered (Estes *et al*. 1998). Predatory attacks on sea otters by killer whales were virtually unknown prior to detection by this very long-term study. During six recent years, however, 10 predatory attacks by killer whales on sea otters were directly observed (Estes *et al*. 1998, Hatfield *et al.* 1998). Despite the small sample size, rates of predation could be estimated because the number of days of researcher effort was known for each year of the study. Estes *et al*. (1998) concluded that predatory attacks by killer whales had increased and that predation by killer whales could have been responsible for the large decline in the sea otter population.

In each of these three studies, the authors initially underestimated the effects of a predator (black bears, brown bears, leopard seals, and killer whales) on a well-studied prey population. Clearly, quantifying known predation is a logical step toward understanding—or ruling out—factors contributing to population declines.

The Onset of Predation by Sea Lions Is Consistent with the Timing of the Seal Declines

Harbor seal numbers in Glacier Bay were stable at terrestrial sites and increasing slightly in glacial fjords until the mid-1990s (Mathews and Pendleton 1997); declines became evident after the mid-1990s and have been steep since then (Mathews and Pendleton 2006, Womble *et al*. 2010). The timing of this decline is correlated with the apparent onset of predation by Steller sea lions. Predation by Steller sea lions was first reported in Glacier Bay in 1995, but never in the 12 previous years, despite a high level of both quantifiable observer effort from 1982 to 2006 (14,038 observer days across 25-yr), and unquantified effort by scientists, Park staff, fishermen, local residents, and Park visitors.

The correlation in the timing between the onset of predatory attacks and the decline in seals in Glacier Bay supports the hypothesis that sea lion predation may have played a role in the decline of seals, but this alone is of course inadequate to demonstrate causation. Our next step was to evaluate the level of predation to determine if it might have a population-level effect on harbor seals.

Sea Lion Predation Partly Explains the Decline in Harbor Seals

Our results indicate that sea lion predation is an important factor in the recent precipitous decline in harbor seals in Glacier Bay for several reasons. First, both the interviews with long-term NPS employees and our statistical analyses (Fig. 2) indicate that it was a *new* source of mortality in Glacier Bay that coincided with the timing of the harbor seal decline. Second, predatory attacks have occurred throughout most of the Park (Fig. 1). Third, in five of the years from 1995 to 2002, predation by Steller sea lions could have removed from 33% up to more than the entirety of pup production at the site where we had fine-scale data (Fig. 4C). It does not seem likely, however, that the addition of predation by Steller sea lions alone could fully explain the 12.4%/yr rate of decline in harbor seals from 1992 to 2008 at terrestrial sites in Glacier Bay and declines in Johns Hopkins Inlet of −8.2%/yr (95% CI = −8.5, −7.8) (Womble *et al*. 2010). Leslie matrix analyses suggest that even if sea lions eliminated all young of the year from terrestrial sites throughout Glacier Bay, it would be difficult to reach the observed 12.4% annual decline rate (Fig. 6A). Our life

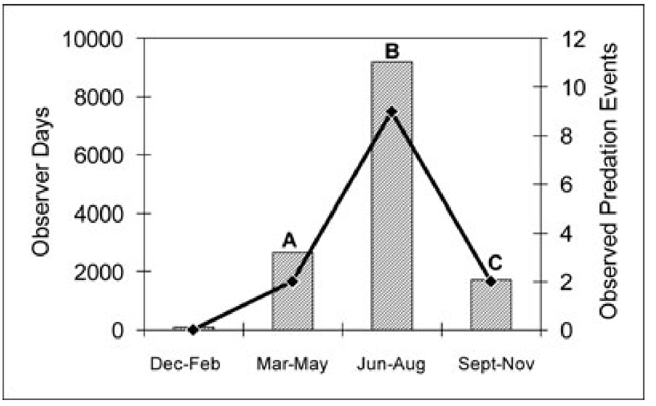

Figure 7. Observations of predation by Steller sea lions on harbor seals (lines) with effort (bars) for all five observer categories by season. We found no strong evidence for a seasonal effect, although observer coverage in winter (December–February) was too low to evaluate that season.

history model suggests that such a decline could occur if 20% of the adult population were removed (Fig. 6B). Our Leslie model results suggesting greater sensitivity to adult mortality are similar to life history analyses for a population of harbor seals in the northeast Atlantic (Härkönen and Heide-Jørgensen 1990). Although our estimate of sea lion predation at Spider Island was comparable to the total number of pups at that well-studied location and that subadults and adults were most likely also subject to increased mortality, we believe that it is unlikely that predation on harbor seals elsewhere in the Park is as large as observed at the Spider Island complex, particularly in the areas of glacier-derived ice flows where the majority of pupping occurs. Harbor seals in glacial fjords in Glacier Bay experience lower predation rates by Steller sea lions (Mathews, unpublished data) and presumably by killer whales as well (Calambokidis *et al.* 1987, Mathews, unpublished data), most likely due to the increased difficulties for predators to maneuver in, and to locate seals resting on, drifting ice bergs within silt-laden, acoustically challenging waters.

The Leslie matrix model indicates that the harbor seal population is more vulnerable to mortality of adult seals than to mortality of pups and juveniles; Steller sea lions would have to take nearly a fifth of the adults each year to produce the observed decline rate of 12.4% (Fig 7B). The population of seals in Glacier Bay in the early 1990s, when the harbor seal decline began, numbered several thousands of animals, making this level of predation by Steller sea lions alone also seems unlikely, particularly given how few sea lions were present at that time.

Are There Other Factors That May Be Contributing to the Declines in Harbor Seals in Glacier Bay?

If harbor seals in Glacier Bay have responded to Steller sea lion predation by learning new antipredator behaviors or spending more time avoiding sea lions, as we would expect (Ives and Dobson 1987, Lima and Dill 1990), the harbor seal population could also incur costs reflected at the population level beyond those due to direct mortality alone (*e.g.*, reduced foraging efficiency) (Linnell and Strand 2000). Such a "trait-mediated indirect interaction" (Abrams 1995) could have a greater effect on the population of harbor seals than that from direct mortalities through effects such as reduced fitness from higher costs of foraging or increased energetic costs from avoidance of previously preferred foraging sites (Herreman *et al.* 2008). Prey avoidance behaviors resulting in reduced access to resources following the introduction of a new predator, as well as changes in prey demographics, have been well documented in other food webs (*e.g.*, Werner *et al.* 1983). Herreman *et al.* (2008) evaluated seal diet over time and suggest that an increase in competition and predation may have caused harbor seals in Glacier Bay to begin feeding on prey with lower fat content during summer. Such a shift in diet and energy intake, particularly during the breeding season, could reduce the overall fitness of seals. Other indirect effects resulting in population declines have also been inferred for harbor seals in a behavioral model in which harbor seals were exposed to both predation by sleeper sharks or killer whales and limitations in prey resources (Frid *et al.* 2006). By increasing foraging time, seals could individually maintain body condition, despite declines in prey resources. The increased exposure, however, resulted in increased predation levels for the simulated seal population, even when predator populations were held constant.

Unlike Steller sea lions, killer whales are known predators throughout the harbor seals' range (Hoover-Miller 1994, Ford *et al*. 1998) and this has presumably been the case for millennia. Harbor seals appear to have developed antipredator behaviors toward mammal-eating killer whales (Barrett-Lennard *et al.* 1996, Deecke *et al*. 2002). In June 2004, the behavior of an adult female harbor seal equipped with a head-mounted VHF transmitter and a time-depth recorder was monitored during an interaction with three mammal-eating killer whales in Glacier Bay within about 3 km of the Spider Island reef haul-out (Womble *et al.* 2006). The seal's dive times increased when the killer whales approached and the seal moved away from the killer whales, suggesting detection and evasion.

Other factors that may be contributing to the declines in harbor seals in Glacier Bay include predation by and/or competition with Pacific sleeper sharks (*Somniosus pacficus*) (Taggart *et al.* 2005, Mathews and Pendleton 2006) and competition for food with Steller sea lions and humpback whales (Mathews and Pendleton 2006, Herreman *et al*. 2008).

Predation by Steller Sea Lions on Harbor Seals Is Rare

Direct observations of predation by Steller sea lions on harbor seals have not been previously reported, although three indirect observations indicate that this rare behavior is not completely new. As early as 1755, Steller sea lions were reported to "live on fish and *possibly* on seals . . ." (emphasis is ours) in the *Description of the Land of Kamchatka* (Krasheninnikov, S. P. 1755, p. 149), but the species of seal in this historic account—indeed if a phocid or otariid—is not clarified. In 1956, one of four adult male Steller sea lions examined had the remains of a white-coat (neonate) ringed seal in its stomach (Tikhomirov 1959). Evidence for predation by Steller sea lions specifically on harbor seals was first reported in 1982 (Pitcher and Fay 1982). Among 250 Steller sea lion stomachs collected from 1975 to 1978 and examined for prey, two contained the remains of harbor seals. An 11-yr-old male sea lion had consumed at least two harbor seals (one a yearling or younger and the other an adult seal) and a 6-yr-old female sea lion's stomach contained the remains of one fetal or newborn harbor seal (Pitcher and Fay 1982). From 1945 to 1986, six other studies sampled the stomach contents of 753 (230 with food) Steller sea lions, but no remains of harbor seals were identified (Imler and Sarber 1947, Wilke and Kenyon 1952, Mathisen *et al.* 1962, Thorsteinson and Lensink 1962, Fiscus and Baines 1966, Calkins and Goodwin 1988). Samples from these studies were collected from the eastern Aleutian Islands (159°32′W) through the Gulf of Alaska and southeastern Alaska and south to California. The wide geographic range of these prey studies with a time span of more than 40-yr provide further evidence that consuming harbor seals is a spatially and temporally restricted behavior.

Is Steller Sea Lion Predation More Common Elsewhere but Undetected Due to Lower Observer Effort?

We wondered if it was possible that predation by Steller sea lions on harbor seals was more widespread, but underreported due to lower observer coverage elsewhere. One area in Alaska where field observations of harbor seals exceed those in Glacier Bay is Tugidak Island off Kodiak Island in the Gulf of Alaska. Over periods of 4–5 mo from April to September each year in 1964, 1976–1979, 1994–1999 (Jemison and Kelly 2001, Daniel *et al.* 2003) and August–September 2000 (Moran 2003), researchers surveyed harbor seals from elevated cliffs with excellent views of seal resting beaches occupied by 3,000–8,000 harbor seals in the 1960s and 1970s and 1,000–2,000 seals in more recent years. In 1978, Dennis McAllister (Alaska Department of Fish and Game) observed stalking and "probable predatory behavior" by a Steller sea lion toward harbor seals on two occasions at Tugidak Island, but no actual attacks (personal communication in Pitcher and Fay 1982). During 11-yr of extensive seal surveys and behavioral observations at Tugidak Island from 1964 to 2000, no other predatory behavior by Steller sea lions was observed;[9] observations of Steller sea lions near Tugidak Island in general were rare.

Evidence that the predatory behavior has existed at extremely low levels or in restricted areas comes from Alaska Native Elders from Hoonah, the Native village nearest to Glacier Bay. Elders were aware of predation by Steller sea lions on harbor seals, but had not witnessed it themselves.[10] In addition, contemporary hunters from Hoonah and Juneau had not observed scavenging on freshly killed harbor seals prior to 2006, and they never observed predatory attacks.[11]

Two recent observations from a long-term Alaskan Native hunter reinforce that Steller sea lion consumption of harbor seals is a recent phenomena in southeastern Alaska. In December 2006, Steller sea lions appropriated eight harbors seals immediately after they had been shot by Les Jensen, a Native subsistence hunter currently based in Juneau, Alaska.[11] When Mr. Jensen and his two hunting partners first arrived at a small island where he had hunted seals before, he noticed that the seals were not in their normal haul-out spot, but around the corner and "penned up" on a rock by a group of about seven Steller sea lions, including one large bull. After Mr. Jensen shot a seal from his position on rocks overlooking the haul-out, he expected

[9] Personal communications from R. G. Daniel, Ocean Conservancy, Washington, DC; L. A. Jemison, ADF&G, Juneau, AK; J. R. Moran, National Marine Fisheries Service, Juneau, AK, September 2007; and B. P. Kelly, University of Alaska Southeast, September 2007 and October 2008.

[10] Personal communication from Mike See, Alaska Native hunter, Hoonah, AK, 22 January 2007.

[11] Personal communications from Alaska Native hunters: Les Jensen, Juneau, Alaska, 23 March 2007; Lyle Owens, Juneau, AK, 29 August 2007; Mike See, Hoonah, AK, 22 January 2007; Nathan Sobolef, Juneau, AK, 22 March 2007.

it to be retrieved from the water by his hunting partners who were waiting in a skiff nearby. Instead, the seal disappeared. Jensen noted blood appearing under the water's surface, "like a streak of red ink," as a "sea lion dragged the seal underwater away from and to the west of the island." Later, the hunters witnessed the sea lion tearing the seal apart and throwing it about "like it was a large salmon." After shooting and losing a fifth seal to the sea lions in a similar manner the hunters gave up for the day. The next day Mr. Jensen and his partners tried a different location, about 32 km away from the previous site and in the mouth of creek, where they had shot harbor seals in previous winters. This time there were about three Steller sea lions present, including "one large animal, probably an adult male." After again seeing the sea lions "tear up" two seals that they had shot, Jensen and his friends gave up hunting for the day. Jensen, who has hunted in southeastern Alaska for 40-yr, remarked that he "had never heard of a Steller sea lion eating [harbor] seals," and that his hunting partners had never witnessed such behavior. The experience of these hunters represent more than 110 hunting seasons with the earliest beginning in 1967. These observations were made within about 140 km of Glacier Bay, within the normal range of winter movements for Steller sea lions in Alaska (Raum-Suryan *et al.* 2002).

Steller Sea Lion Predation on Other Pinniped Species

Records do exist of Steller sea lion predation on young of two different otariid species: northern fur seals (Gentry and Johnson 1981) and one California sea lion, *Zalophus californianus* (Byrnes and Hood 1994). In the study of northern fur seals off of St. George Island, 74 direct observations of Steller sea lions killing fur seals were made in 1974 during 112 h of observation and 89 kills during 243 h in 1975 (Gentry and Johnson 1981). From these observations and known effort it was estimated that from 2,708 to 5,416 fur seal young were killed by sea lions annually. As was observed with harbor seals in Glacier Bay, Steller sea lions attacking neonate fur seals typically grabbed the seal and shook or flung it violently from side to side, stripping off skin or other tissue and, often, eviscerated the seal. The mean prey handling time for harbor seals in Glacier Bay (36 min, SD $= 19$, $n = 6$) was higher than for predatory attacks on northern fur seal neonates (20 min, SD $= 9.5$, $n = 19$) (two-tailed t-test, $P = 0.01$), perhaps because some of the attacked harbor seals were subadults which can weigh 47–55 kg (Hoover-Miller 1994) compared to neonate fur seals which weigh from 5 to 20 kg (Boltnev *et al.* 1998). Predation on northern fur seal neonates was also spatially restricted, occurring extensively in waters near St. George Island but never observed off St. Paul, only 65 km away (Gentry and Johnson 1981).

Although the behaviors of Steller sea lions attacking and consuming harbor seals and northern fur seal neonates were generally similar, three differences in the predation on the two species stand out. First, only juvenile male Steller sea lions were involved in the killing of neonate fur seals off St. George Island (Gentry and Johnson 1981). In contrast, all of the kills witnessed in Glacier Bay in which the attacking sea lion's age category was identified (11 of 13) were categorized as adults, and 6 of these 11 were further classified as adult males or bulls. Both of the Steller sea lions found to have the remains of harbor seals in their stomachs by Pitcher and Fay (1982) were also not juveniles (an 11-yr-old male and a 6-yr-old female).

Second, the 163 northern fur seals taken by Steller sea lions at St. George Island were exclusively neonates (<5 mo), whereas predated harbor seals have included neonates (<1 mo), yearlings, and subadults (our study + Pitcher and Fay (1982) = 8 seals or 89%), and one known adult (11%) (Pitcher and Fay 1982). The largest northern fur seal neonates are males, which average 20 kg just before weaning (Boltnev *et al*. 1998). At birth harbor seals weigh 11–12 kg and near weaning about 20–25 kg (Pitcher and Calkins 1979), or about the same as the older fur seal neonates. A subadult harbor seal weighs approximately 30–60 kg (Pitcher and Calkins 1979). Compared to adults, younger fur seals and harbor seals are presumably easier or more efficient to capture because they are more aggregated during summer, and they are smaller and more naïve than adults, improving the probability of prey capture. In the Antarctic, leopard seals also targeted recently weaned (Siniff and Stone 1985) as well as yearling (Siniff and Bengston 1977) crabeater seals (*Lobodon carcinophagus*). Because the age category of the attacked harbor seals was not known for 7 of the 13 (54%) reported attacks from Glacier Bay, whether younger harbor seals are preferentially targeted by predatory Steller sea lions remains to be determined.

A third difference in the attacks on northern fur seals off St. George Island is that these were highly seasonal, from mid-August to mid-November when fur seal pups first venture into the water to when they leave the nearshore environment (Gentry and Johnson 1981). In Glacier Bay, the majority of direct observations of predation by Steller sea lions on harbor seals were from summer, but observations occurred in all seasons and were generally correlated with observer effort (Fig. 7), suggesting that there is not a seasonal peak in predation of harbor seals.

Predation Is Not Correlated with Numbers of Sea Lions

As noted, predatory behavior of Steller sea lions toward harbor seals in Glacier Bay was first reported in the mid-1990s, but the rates of predation we documented from the five independent observer categories were not correlated with the steep increase in the numbers of sea lions in Glacier Bay that occurred around this time (Fig. 3). This suggests that a small number of individual sea lions exhibiting atypical predatory behavior could be responsible for most of the sea lion predation on harbor seals in Glacier Bay. Elsewhere, population-level effects on two species of fur seals from a single predatory Hooker's sea lion (*Phocarctos hookeri*) have been suggested (Robinson *et al.* 1999). At Macquarie Island, in the Southern Ocean between Australia and the Antarctic continent, predation by a single, naturally and uniquely marked subadult male Hooker's sea lion was estimated to be responsible for 43% (54) of the annual production of 130 pups of Antarctic and subantarctic fur seals (*Arctocephalus gazella* and *A. tropicalis*, respectively).

Is Predation by Killer Whales Also a Factor in the Harbor Seal Declines?

Members of the West Coast population of mammal-eating killer whales, which range from central California to southeastern Alaska, are frequently observed during June and July in Glacier Bay where harbor seals are their most common prey (40% of 43 observed kills) (Matkin *et al*. 2007). As with Steller sea lions, we were interested in whether predation by killer whales had increased during the period when harbor seal numbers in the Park declined. The increase in observations of, and disturbances by, killer whales suggests increased predation or predatory attempts by killer whales after 1995; however, because of the cryptic nature of predation by the mammal-eating ecotype, and low angle our shore-site observation post, we could not directly document predation events by killer whales during this study. Although we observed more killer whales in the latter part of the study (1996–2003), whether killer whale predation on harbor seals in Glacier Bay has increased since the mid-1990s, and whether it is also a factor in the harbor seal declines, remain to be addressed.

Why Might Steller Sea Lions Have Started Preying on Harbor Seals?

We do not know why some Steller sea lions in Glacier Bay began feeding on harbor seals in the mid-1990s. One hypothesis is that the rapid expansion of Steller sea lions into Glacier Bay during the 1990s (Fig. 4), when harbor seals were near peak numbers, resulted in increased spatial overlap between the two species and this increased the probability for atypical predator–prey interactions, particularly given the high degree of overlap in the prey species of these two pinnipeds. Steller sea lions first colonized a haul-out in Glacier Bay at South Marble Island in the mid 1980s (Streveler, Glacier Bay National Park, NPS 1989 memorandum). From 1991 to 2004 sea lion numbers at South Marble Island grew rapidly (23%/yr, 95% CI = 14%–32.5%),[4] at rates exceeding the theoretical maximum reproductive rate for otariids (12%) (Wade and Angliss 1997).

Predation has previously been observed among two different species of marine mammals experiencing increased densities in overlapping populations. Pacific walruses (*Odobenus rosmarus rosmarus*) typically feed on benthic invertebrates, but predation by Pacific walruses on phocid seals (spotted seals, *Phoca largha*; ringed seals; and bearded seals, *Erignathus barbaratus*)—considered highly atypical for walruses—grew by a factor of 10 to 100 in the Chuckchi and Bering Seas during the 1970s and 1980s compared to the previous 30-yr (Lowry and Fay 1984). Lowry and Fay (1984) speculated that an increase in the walrus population coupled with reduced spring ice caused an unusual increase in overlap in the distributions of walruses and certain phocid seal species, and may have resulted in more predatory attacks on seals. Predation on harbor seals first occurred 10-yr after Steller sea lions colonized the first sea lion haul-out in Glacier Bay and during a period of rapid growth in numbers of sea lions in Glacier Bay (Fig. 3). What we may be observing—and one possible reason why observations of Steller sea lion predation on harbor seals are rare throughout their range—is the short-term process of spatial exclusion that may occur only during periods of initial colonization by sea lions into areas already occupied by harbor seals. If the predation in Glacier Bay is the result of relatively recent increased spatial overlap between the two pinniped species then we predict that sea lion predation will be a temporary phenomenon that will diminish if the harbor seal population in Glacier Bay stabilizes at a lower level or if the distribution of favored seal haul-outs or foraging areas shifts away from concentrations of sea lions. Indeed, the elimination of three harbor seal haul-outs close to the one Steller sea lion haul-out (Fig. 1) in the decade since the early 1990s suggests that this process may be occurring.

Conclusion

We conclude that a small number of Steller sea lions exhibiting unusual predatory behaviors could partly explain the decrease in abundance of harbor seals in Glacier Bay and that this is a *new* source of mortality, which began in the mid-1990s. The large scale of the declines in harbor seals in Glacier Bay—including seals from the glacial ice fjords where there is some protection from predation during breeding—plus results from our Leslie life history model suggest that other factors are contributing to the ongoing declines. Increased occurrences of and disturbances by killer whales near the

Spider Island complex after 1995 compared to the earlier half of the study suggest that predation by killer whales may also be a factor in the seal declines, but this hypothesis remains to be tested. This work demonstrates that top-down structuring may arise where it has not been present and that, without long-term monitoring and specific quantification, the effects of predation can remain undetected or be underestimated.

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Supporting Information

The following supporting information is available for this article online:

Appendix S1. Two additional observations of Steller sea lion predation on a harbor seal in Glacier Bay National Park.