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Population growth and colonization of Steller sea lions in the Glacier Bay region of southeastern Alaska: 1970s–2009

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ABSTRACT

We estimated trends in numbers of Steller sea lions in the Glacier Bay region of the eastern population from the 1970s to 2009. We documented the colonization of several new haul-outs and the transition of one haul-out (Graves Rocks) to a rookery, assessed seasonal patterns in distribution, and compared counts from different observation platforms. Sea lions increased in the region by 8.2%/yr (95%CI = 6.4%–10.0%), with the most growth at South Marble Island in Glacier Bay (16.6%/yr, 1991–2009) and rapid growth in Cross Sound. Seasonal patterns in the distribution of sea lions were likely influenced by new breeding opportunities and the seasonal availability of prey. Factors that likely contributed to the exceptional growth include availability of new habitat following deglaciation, immigration, redistribution, decreases in mortality, and ecosystem-level changes. The rapid increase in sea lion numbers in this region is of particular interest in light of dramatic declines in the western population and evidence that Steller sea lions from both the eastern and western populations colonized the Graves Rocks rookery. The colonization and rookery development in this dynamic area may signal the reversal of the reproductive isolation of the two populations.

Key words: *Eumetopias jubatus*, otariid, colonization, range expansion, population trends, seasonal haul-out patterns, rookery development, dispersal.

Steller sea lions (*Eumetopias jubatus*) range along the North Pacific rim from Japan to Russia in the west, along the Aleutian Island chain into the Bering Sea and Gulf of Alaska, and south to central California (*e.g.*, Loughlin *et al.* 1987). Historically, major haul-outs and rookeries were centered in the Aleutian Islands and the Gulf of Alaska where up to 70% of the world's population was located in the 1950s and 1960s (Loughlin *et al.* 1984). In 1990, following steep declines, Steller sea lions within U.S. waters were listed as threatened under the U.S. Endangered Species Act (U.S. Federal Register 1990). Differences in mitochondrial DNA and in population trajectories of sea lions west and east of Cape Suckling in the Gulf of Alaska led to the reclassification of Steller sea lions into western and eastern populations with a boundary at Cape Suckling (144°W) (Bickham *et al.* 1996, Loughlin 1997). In 1997 the western population segment of sea lions was classified as endangered, because of continuing declines (Loughlin 1997), whereas the eastern population retained its threatened status under the ESA (U.S. Federal Register 1997). From the 1970s to 2004, the eastern population increased at an average annual rate of 3.1% and may have reached a historic peak (Pitcher *et al.* 2007).

Such growth in a population could naturally lead to colonization of new breeding sites (*e.g.*, Bradshaw *et al.* 2000), however colonization of new rookeries by Steller sea lions is not common. From at least the 1920s into the 1980s, the Forrester Island complex (54°48′10″N, 133°31′37″W) was the only Steller sea lion rookery in southeastern Alaska (Rowley 1929, Pitcher *et al*. 2007). Presently, there are five rookeries in southeastern Alaska: Hazy Islands which became a rookery around 1979, White Sisters began producing pups in the early 1990s, Graves Rocks developed into a rookery in the late 1990s, and Biali Rocks (Sitka Sound) first produced >50 pups annually in the early 2000s (Pitcher *et al*. 2007). Genetic studies indicate that the Graves Rocks and White Sisters rookeries (Fig. 1) were colonized by sea lions from both the western and eastern populations (O'Corry-Crowe *et al.* 2005, 2006; Gelatt *et al.* 2007). Resightings of branded sea lions confirm that female sea lions from both stocks have produced pups at the two rookeries (Gelatt *et al*. 2007), even though the rookeries are located 450 km (Graves Rocks) and 550 km (White Sisters) east of the current boundary between the two stocks. Prior to the recent joint colonization within the study region during the 1990s, the eastern and western stocks of Steller sea lions had been largely reproductively isolated, for possibly more than 12,000 yr (Harlin-Cognato *et al.* 2006); natal dispersal between the populations had not been documented from resightings of animals branded as pups (Raum-Suryan *et al.* 2002). Given the upper trophic level of Steller sea lions, the dramatic increases in their local density has the potential to significantly influence local food webs and the population dynamics of sympatric species directly through predation or by altering prey species composition or abundance, or indirectly by altering the behavior of prey (*e.g.*, Bundy 2001, Heithaus *et al.* 2007, Creel and Christianson 2008).

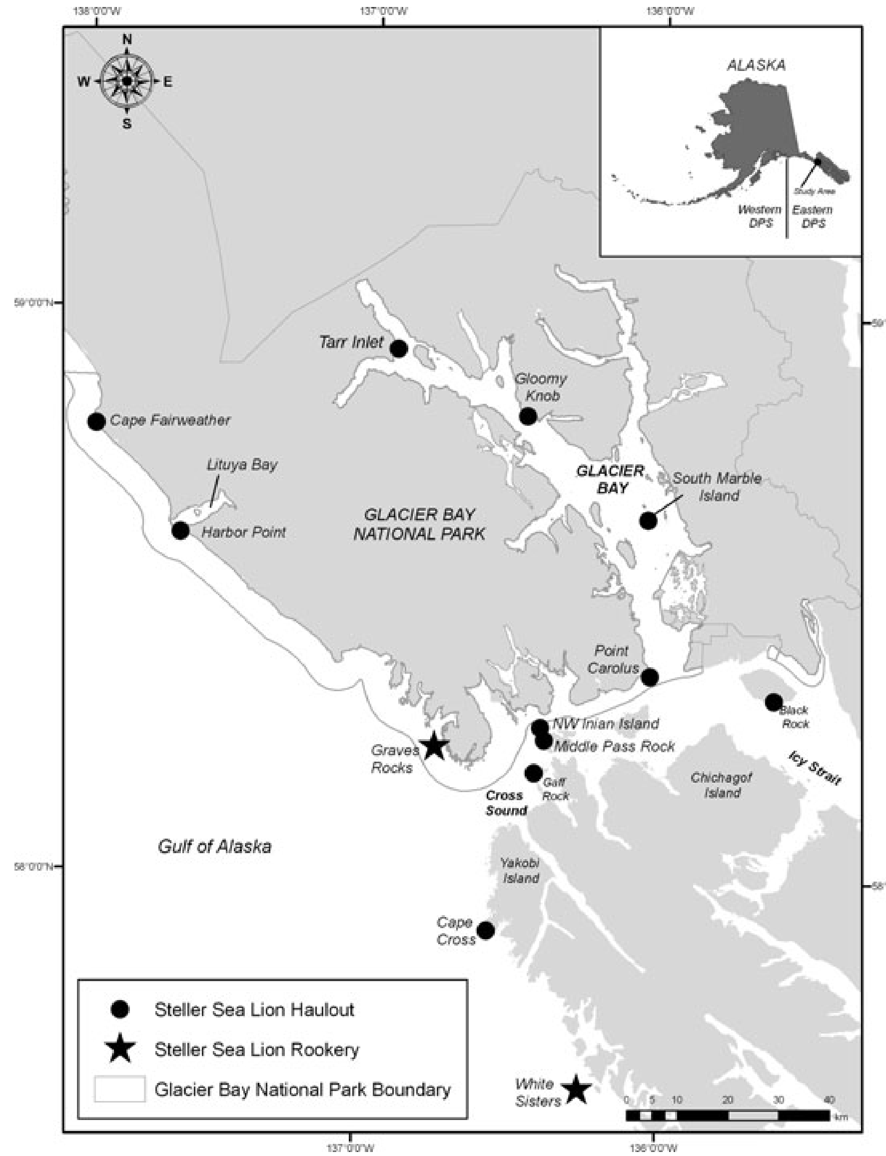

Figure 1. Map of the eight haul-outs (closed circles) and one rookery (star) included in this study (Graves Rocks), plus three very recently colonized haul-outs (Gaff Rock, Black Rock, and Gloomy Knob) in the GB/IS/CS area. The "outer coast" in this study is from Cape Cross to Cape Fairweather.

The specific objectives of our study were to (1) estimate long-term trends (1970s–2009) in the number of Steller sea lions counted in the Glacier Bay, Icy Strait, Cross Sound (GB/IS/CS) region and outer coast from Cape Cross to Cape Fairweather (Fig. 1); (2) characterize recent seasonal patterns in sea lion distribution; and (3) describe the timing of colonization of the Graves Rocks rookery and several haul-outs. We also discuss the potential factors that may have contributed to the localized growth in the number of sea lions and colonization of new sites by Steller sea lions in the northern region of the eastern population.

METHODS

Study Sites

The study area included GB/IS/CS, and the outer coast from Cape Cross north to Harbor Point at the mouth of Lituya Bay with less coverage out to Cape Fairweather (Fig. 1) (hereafter called "GB/IS/CS" and the "outer coast"). We characterize the "outer coast" as the area exposed to the open ocean without protection by intervening large islands; we use this term in contrast to "inside" waters which include primarily Glacier Bay and Icy Strait. We analyzed counts from eight haul-out sites (South Marble Island, Northwest Inian Island, Middle Pass Rock, Point Carolus, Tarr Inlet, Cape Cross, Cape Fairweather, and Harbor Point) and one site, Graves Rocks (Fig. 1), that transitioned from a haul-out to a rookery in the late 1990s (Pitcher *et al*. 2007). We note the recent development of three additional haul-outs at Gaff Rock, Black Rock, and Gloomy Knob (Fig. 1), but there were too few counts from these sites to include in this analysis. Haul-outs were defined as terrestrial sites where sea lions come ashore but few or no pups are born. A rookery was defined as a terrestrial site where $\geq$50 pups are born annually (Calkins and Pitcher 1982, Loughlin *et al*. 1984, Pitcher *et al*. 2007).

Data Sources

Data included systematic and opportunistic counts from the nine sites. Count data from multiple sources and various methodologies, including aerial surveys, boat surveys, and land-based counts (Table 1) were used to estimate population trends and seasonal use of sea lions at haul-outs from the 1970s to 2009. Data were compiled from multiple sources and merged into a single relational database.

Counting Methods

Aerial photographic surveys: Oblique 35 mm photography—Systematic aerial surveys of known sea lion haul-outs began in 1975 by the Alaska Department of Fish and Game (ADFG), however, coverage did not include all currently used sites because some sites had not been documented or had not yet been colonized by sea lions. Various agencies and academic institutions continued aerial surveys through 2009 (Table 1), primarily during the summer breeding season. From 2001 to 2004, as part of a larger regional study aimed at quantifying the seasonal distribution of Steller sea lions in the northern region of southeastern Alaska, systematic monthly aerial surveys were conducted at haul-out sites and one rookery in the Glacier Bay/Icy Strait study area (Womble *et al.* 2009).

During aerial surveys, oblique photographic slides or digital images of sea lions were taken using a 35 mm auto-focus camera equipped with a 70–210 mm zoom lens or an auto-focus digital camera with a 70–300 mm zoom or fixed 300 mm lens. The

Table 1. Summary of data sets used to estimate trends in Steller sea lions in the GB/IS/CS and outer coast region from 1975 to 2009.

Years	Investigator	Affiliation[a]	Platform	Method[b]	Location[c]	Frequency	Season
1975–1976, 1979, 1982, 1989–1994, 1996	ADFG	ADFG	Aerial	1	SMI, GR, NWI, PC, HP, CF, CC[d]	Annual	Summer
1998, 2000, 2004–2005	ADFG	ADFG	Aerial	2	SMI, GR, NWI, HP, CF, CC[d]	Annual	Summer
1983, 1984	Acuna and Selig, Jettmar	NPS	Boat and shore	4	HP	Annual	Summer
1988–1989	Streveler	NPS	Aerial and boat	4	SMI, GR	Opportunistic	
1985, 1987–1989, 1992–1993	NPS Interpreters	NPS	Boat (tour boat)	4	SMI	Daily	Summer
1994–1998, 2000	Mathews	UAS/NPS	Aerial	1	SMI, GR	Annual	Summer
1994–1995, 1997–1998	Mathews	UAS/NPS	Land	4	SMI	Daily	Summer
1994–1999	Mathews	UAS/NPS	Boat (tour boat)	3	SMI	Daily	Summer
1996	NMFS/NMML	NMFS-NMML	Aerial	1	SMI, GR, NWI, PC[d]	Annual	Summer
2001–2002, 2004–2005, 2009	NMFS/NMML	NMFS-NMML	Aerial	2	SMI, GR, NWI, HP, CC[d]	Annual	Summer
1999	Zador	USGS	Land	3	SMI	Opportunistic	Summer
1999–2009	Raum-Suryan, Jemison	ADFG	Boat (skiff)	4	SMI, GR, NWI, MPR	Annual	Summer
2001–2004	Womble	UAF/NMFS-ABL	Aerial	1	SMI, GR, NWI, MPR, PC, TI	Monthly	Year-round
2004–2009	Womble	NPS	Aerial	1	SMI, GR, NWI, MPR, PC, TI	Annual	Summer

[a]Affiliation: NMFS-ABL = National Marine Fisheries Service-Auke Bay Laboratory, NMFS-NMML National Marine Fisheries Service-National Marine Mammal Lab, ADFG = Alaska Department of Fish and Game, NPS = National Park Service; UAF = University of Alaska Fairbanks, UAS = University of Alaska Southeast, USGS = United States Geoglogical Survey.

[b]Method: 1 = oblique 35 mm photography, 2 = vertical 126 mm photography, 3 = real-time count with photo, 4 = real-time count without photo.

[c]Location: CC = Cape Cross, CF = Cape Fairweather, GR = Graves Rocks, HP = Harbor Point, NWI = Northwest Inian Island, PC = Point Carolus, SMI = South Marble Island, TI = Tarr Inlet, MPR = Middle Pass Rock.

[d]Not all sites were surveyed every year.

observer photographed sea lions at terrestrial sites from an altitude of 250–300 m at a speed of 183–210 km/h. Surveys were conducted between the hours of 1000 and 1600.

Overlapping photographs were taken if more than one photograph was needed to count sea lions at a site. The clearest slide images were projected onto a white paper, each sea lion was marked, and each group was counted twice by an experienced counter. Digital photographic images were downloaded to a computer. The clearest digital image of each group was imported into a geographic information system (GIS) (ArcView 3.2a, ESRI, Redlands, CA), and sea lions in each image were counted twice by an experienced counter. The total count of sea lions reported for each site included sea lions on the haul-out as well as animals visible in the water adjacent to the site.

Aerial photographic surveys: Vertical medium format aerial photography—Beginning in 1998, aerial surveys conducted by ADFG and the National Marine Fisheries Service (NMFS) used medium-format vertical photographs (Snyder *et al.* 2001, Fritz and Stinchcomb 2005) taken from altitudes of 195–240 m between 0900 and 1700. Photos were taken with a medium-format military reconnaissance camera mounted in the belly of the aircraft. Counts of medium format photographs were made using a dissecting microscope over a light table (Fritz and Stinchcomb 2005).

Boat surveys (tour boat and skiff surveys)—Beginning in 1985, National Park Service (NPS) interpretive rangers visiting South Marble Island on a daily tour boat recorded sea lion numbers. From 1995 to 1999 a crew member from the tour boat was trained to count the sea lions by one of us (EAM) and to take a series of photographs of them using a 35 mm SLR camera equipped with a 200 mm lens. Photographed sea lions were later counted from projected images (see aerial survey counting method).

Beginning in 1999, sea lions were observed from small boats by ADFG at haul-outs at GB/IS/CS sites and Cape Cross, and Graves Rock on the outer coast. Sites were approached at a slow speed and initially counted from a distance of >100 m to allow sea lions to become accustomed to the boat. Observers used binoculars (8–14×) to count sea lions. At some sites, when conditions allowed, observers went ashore and surveyed from a high point above the haul-out or rookery.

Land-based surveys (South Marble Island {SMI} only)—In 1994, 1995, and 1997–1999 during late spring and summer, sea lions on SMI were also counted from an elevated shore overlook on the northeastern side of the island. Count and behavioral data were collected every 20–30 min on 7–17 d each year by University of Alaska Southeast (UAS) and NPS biologists. Only the daily high count and counts within 10 min of the daily tour boat counts or an aerial survey were included in the analyses for SMI. During the 1990s, most sea lions were visible from the elevated shore site; however, on some days a small number of sea lions along the far north edge of the haul-out ledge could have been missed, but this would have been a small proportion of the total. After 1999, sea lions expanded their use of SMI such that shore counts from the single elevated vantage were no longer sufficient for monitoring island-wide haul-out activity.

Counts from shore were conducted using either 7 × 42 mm or 20 × 60 mm binoculars mounted on a tripod; animals on the haul-out and in the water were tallied separately. For visual, real-time counts from boats and shore, we ranked the observer's level of experience according to the following criteria: (1) experienced pinniped observer; (2) experienced observer, wildlife biologist, or designated tour boat crewmember known to provide reliable counts; (3) less experienced or unknown experience level.

Use of covariates with counting methods—We investigated the effects of covariates, including counting method, on counts at SMI. Covariates included observation platform (aerial, boat, land), observer experience (1–3 listed earlier), and count method (real-time visual count, count from photographs). South Marble Island was the only site where counting method was investigated as it was the only site where all methods were employed.

Data Analysis: Population Trends (1970–2009)

Generalized linear models (Poisson error distribution, log link function) (McCullagh and Nelder 1989) were used to estimate site-specific trends at six sites (South Marble Island, Northwest Inian Island, Graves Rocks, Middle Pass Rock, Harbor Point, and Cape Cross) (Fig. 1). Counts from June and July from 1970 to 2009 were used for these sites; however, the range of years varies among sites as there are few counts prior to 1989. To estimate site-specific trends, we used counts from June and July because this is the peak of the pupping/breeding season for Steller sea lions (Pitcher *et al.* 2001) when the distribution of the population is likely the most stable, and these months have been used for estimating Steller sea lion population change throughout its North American range (Calkins *et al.* 1999, Fritz and Stinchcomb 2005, Pitcher *et al*. 2007). Point Carolus, Cape Fairweather, and Tarr Inlet had too few non-zero June and July counts for the trend analysis. All models contained a linear (on the log scale) year predictive variable (*i.e.,* trend); the model for Cape Cross also included a quadratic year term because the pattern of counts from this site was obviously nonmonotonic.

Covariates known to affect sea lion counts were included in the models: time relative to solar noon (hereafter "time"), and tide height (Withrow 1982, Kucey 2005). These covariates affect the proportion of sea lions out of the water and available to be counted, rather than the actual population. The model for South Marble Island also included survey platform/count method (airplane, land, boat-visual, boat-photo) as covariates. All four types of counts were used in the trend and moving-average seasonal analyses, although only aerial counts were used in the trend analyses for years after 1999 when regular aerial surveys commenced. Initial models for each site contained all trend and covariate terms; we eliminated unimportant predictors sequentially based on Wald F-statistics ($P > 0.05$).

To estimate a regional trend, we used a weighted average of the six site-specific estimates from counts in June and July using an established procedure (Calkins *et al*. 1999). This procedure uses empirical Bayes shrinkage to account for the varying precision of the individual site-specific estimates and an abundance weight to account for the widely varying proportions of the regional sea lion population at each site. We used the predicted June 2003 count to calculate the abundance weights. Using a predicted count for the weights better reflects all of the data for a site relative to individual observed counts. Because sites had different trends, relative abundance among sites varied continually making the choice of month for calculating weights somewhat arbitrary. We chose June 2003 for calculating weights because it reflected relative abundance in the latter half of the survey data for all sites, better representing recent years; using 2003 for abundance also allowed the trend from the rapidly growing Middle Pass Rock site to be included. For this combined regional estimate, we estimated the trend from Cape Cross without the quadratic year predictor used in the base model for that site.

Seasonal Patterns in Sea Lion Distribution (2001–2004)

We used generalized linear models to describe seasonal patterns in the counts at four sites (Graves Rocks, Northwest Inian Island, Point Carolus, and South Marble Island) (Fig. 1) that were surveyed using aerial photography between March 2001 and May 2004. In addition, for South Marble Island, we used daily counts from May to September from 1985 to 1999 to examine possible systematic changes in haul-out patterns during summer. We did not fit seasonal pattern models to the other five sites because they had too few nonzero counts. Because "month" is a circular predictor variable (*i.e.*, months 1 and 12 are adjacent), we transformed month into two variables, sin(M) and cos(M), where M is the month in radians (Fisher 1993). Both of those variables were always included together in the models. Because this transformation allows only a single peak within a year, we used a two-part model for South Marble Island, where there were two seasonal peaks, with the two segments defined as January–July and July–December. We allowed abundance to vary among years, and we allowed the seasonal pattern to vary among years (*i.e.,* sin(M)*year and cos(M)*year interaction terms). We also included the covariates time, time^2, and tide height. As with the trend models, we began by including all variables in the model and eliminated unimportant variables sequentially. To describe an overall regional pattern, we fit a similar model (without covariates) to the monthly sum of the counts from the four sites.

Early History of Study Area Use, Colonization of New Haul-Outs, and Rookery Development

To provide a general overview of the early history of use of the study area we consulted anthropological and archaeological reports. We used our survey data and reviewed unpublished reports and narratives to describe the relatively recent temporal and spatial patterns of colonization of haul-outs and the transition of Graves Rocks to a rookery. We also conducted interviews with biologists, former Glacier Bay NPS rangers, commercial fisherman, and hunting/fishing guides regarding their observations of sea lions in the study area.

Results

Population Trends (1976–2009)

The number of nonpup Steller sea lions counted in the Glacier Bay/Icy Strait/Cross Sound region increased by 8.2%/yr from 1970 to 2009 (Table 2, Fig. 2). The most growth occurred at South Marble Island in Glacier Bay (16.6%/yr, 1991–2009) (Fig. 2b) with rapid growth in use of haul-outs in Cross Sound/Icy Strait at Middle Pass Rock (24.4%/yr, 2001–2009) and the Northwest Inian Island (13.9%/yr, 1989–2009) (Table 2, Fig. 2d, e). Steep increases in June and July counts began around 1997 at South Marble Island and around 2002 at the Northwest Inian Island haul-out. Graves Rocks, the only site that transitioned from a haul-out to a rookery during the study period, had a positive trend (3.8%/yr) (Table 2, Fig. 2h); because of its larger June 2003 predicted count, Graves Rocks was most heavily weighted in the composite estimate. Harbor Point, where we had counts for the longest interval (1970–2005), increased at a low rate (3.1%/yr) (Table 2, Fig. 2g). Cape Cross had

Table 2. Steller sea lion trend estimates, cumulative change in numbers, and predicted counts for June 2003 at six sites in the GB/IS/CS and outer coast region.

Site	Area	Years	June 2003	Trend%/year	SE	95% CI	Cumulative change (%)
Cape Cross	Outer coast	1975–2009	1	−6.1	3.21	−12.2, −0.4	−88
Graves Rocks	Outer coast	1989–2009	942	3.8	0.8	2.2, 5.3	210
NW Inian Island	Cross Sound	1989–2009	161	13.9	4.06	6.2, 22.1	1,352
Middle Pass Rock	Cross Sound	2001–2009	163	24.4	11.86	3.2, 50.0	575
Harbor Point	Outer coast	1970–2009	218	3.1	1.13	0.9, 5.3	328
S Marble Island	Glacier Bay	1991–2009	419	16.6	2.3	12.2, 21.2	1,588
Composite (overall)				8.2	0.93	6.4, 10.0	

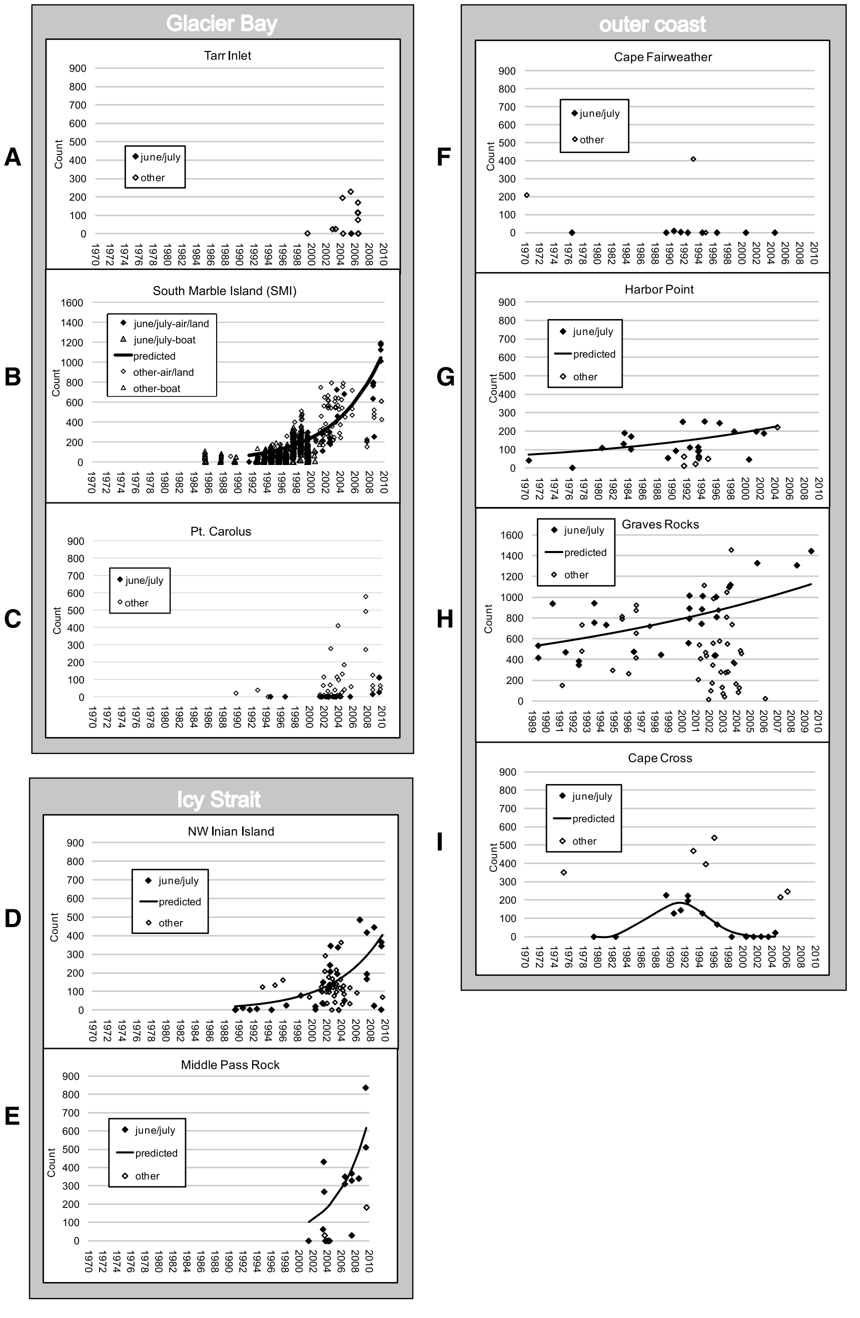

Figure 2. Counts of Steller sea lions at eight haul-outs and one rookery (2a–i) in the Glacier Bay/Cross Sound, Icy Strait, and outer coast region and trends in numbers (lines) of sea lions at six of these sites where there were enough nonzero counts to calculate a trend (2b, d, e, g–i). Within the three broad areas (Glacier Bay, Cross Sound/Icy Strait, and the outer coast), sites are organized north to south (top to bottom).

a distinctly nonmonotonic pattern of counts over time with no sea lions observed during summer in 1979 and 1982, followed by higher counts in the early 1990s, and low counts again after 1998 (Fig. 2i). The linear trend estimate for Cape Cross was negative overall (Table 2). Count data were too sparse to estimate trends in sea lions at Tarr Inlet, Point Carolus, or Cape Fairweather (Fig. 2a, c, f).

Effects of Covariates and Survey Method

Covariates generally were not important when estimating trends. No covariates were retained in the models for Graves Rocks, Harbor Point, or Northwest Inian Island. At Cape Cross, time was retained when only the linear year effect was used, but was not retained in the quadratic year model. At South Marble Island, survey platform was important with higher predicted counts from aircraft and the elevated land overlook and lower counts of sea lions from boats. For the South Marble analyses, predicted counts also were affected by tide height, but the effect of tide on predicted counts varied with survey platform. Aerial counts were negatively associated with tide height, which has been documented previously for Steller sea lions (Kastelein and Weltz 1990, Kucey 2005). However, counts from boats and land had a positive association with tide height; this could be a function of improved views at high tide from small boats or changes in sea lion behavior. This pattern justifies our decision to exclude from our trend analyses boat and land-based counts at South Marble Island after 1999 when the number of sea lions hauled out became too large and the area covered too extensive for us to be confident that boat and land-based counts always were accurate. Our estimates of population change (*i.e.,* trend) should be interpreted as approximations. Although we included covariates to help account for variation in counts not due to changes in the population, it is still possible that the source of some of the changes we observed were the result of factors that affected the availability of sea lions to be counted.

Seasonal Patterns

Seasonal counts of sea lions at the four main sites in the Glacier Bay/Icy Strait region (South Marble Island, Graves Rocks, Northwest Inian Island, and Point Carolus) in recent years (2001–2004) were generally lowest during winter months (December–February) with notable differences among years in peaks in abundance (Fig. 3a). The seasonal patterns in 2001–2002 were similar with overall low winter abundance and higher abundance in spring (March–May) and fall (September–November). Peak numbers of sea lions ashore in 2003 occurred in July and August, driven largely by Graves Rocks and the higher summer (June–August) counts at South Marble Island. Counts from 2003 also brought the composite peak (Fig. 3a) more in phase with the 2001–2004 summer peak at Graves Rocks (Fig. 3f).

In contrast to the Graves Rocks rookery, seasonal peaks at South Marble Island occurred in spring and fall, with more pronounced bimodal peaks and a mid-summer decline evident in recent compared to earlier years (Fig. 3b, c). From 1985 to 1996, sea lions were observed on South Marble Island in late May/early June and again in August with a notable drop in July including most (1985–1989) to many (1992–1996) days in July and August with no sea lions hauled out (Fig. 3b). Beginning in 1997, the pronounced drop in July began to diminish and a late summer/fall peak became more apparent. During the 1997–1999 period about 100 more sea

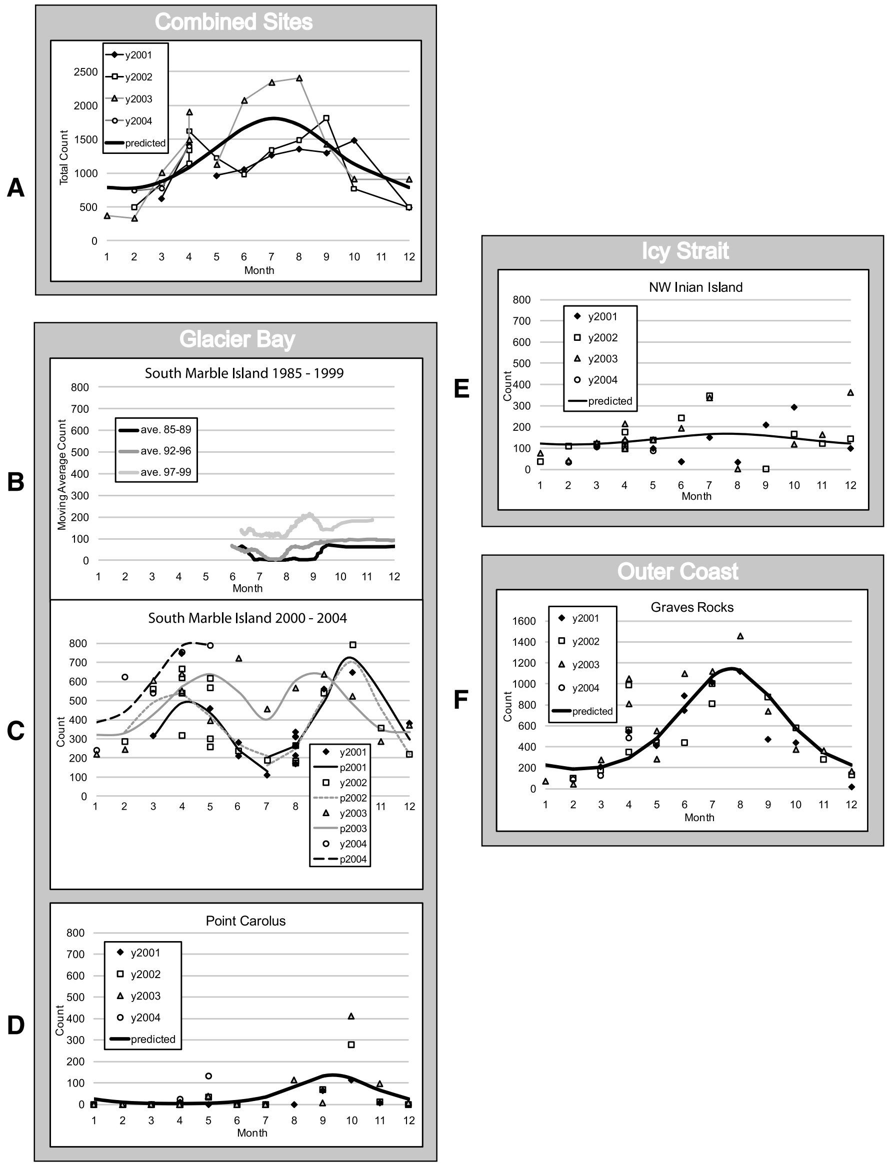

Figure 3. Predicted seasonal abundance curves of all sites combined (a) and observed counts at individual sites (b–f) in the Glacier Bay, Icy Strait/Cross Sound and outer coast areas.

lions, on average, occupied the site from spring to fall, more than doubling usage observed from 1985 to 1989 (Fig. 3b, c). In more recent years (2001–2004) with year-round survey effort, South Marble Island was occupied throughout the year and was much more heavily used in the spring and fall (Fig. 3c). However, there was a less pronounced drop in numbers during mid-summer in 2003 (Fig. 3c).

Only a single equation was needed to describe the seasonal pattern at Graves Rocks with high counts in summer corresponding to the pupping and breeding season, and lower, more variable counts at other times of year (Fig. 3f). A relatively consistent (across years) spike occurred in the April counts (Fig. 3f). The seasonal peak at Graves Rocks (summer) was out of phase with the two peaks at South Marble Island (spring and fall), especially in recent years (Fig. 3b, c, f). There was only a subtle seasonal pattern at the Northwest Inian haul-out with a slight increase around July and August (Fig. 3e). Point Carolus was used primarily in late summer and fall, with high counts of 413 in October 2003 and 578 in August 2009 (Fig. 3d). The few nonsummer counts ($n = 6$) at Cape Cross (Fig. 2i), including those in more recent years, have been higher than the June–July counts indicating that this site is an important winter haul-out. Cape Fairweather had only two nonzero counts in June or July, both fewer than 10 animals (Fig. 2f). Two hundred and seven sea lions were seen there in spring of 1970 and 409 were counted in March of 1993, but because of the small number of nonsummer counts, it is unclear whether this site was regularly used in late winter or spring, or was a transient, atypically used haul-out. During the early 1970s NPS Rangers noted that in spring there were more sea lions at Cape Fairweather than at Harbor Point off Lituya Bay (Table 3a).

As with the trend analyses, covariates in the seasonal pattern analyses were generally not important; three covariates (time, time^2, and tide height) were retained only for the first half of the year at South Marble Island.

Effects of Survey Method on Counts at South Marble Island

Although there were few near-simultaneous counts made from aerial photographs and other methods for comparison, aerial photo-based counts were higher than visual counts from boats as expected, given the more vertical viewing angle compared to other platforms. Counts from aerial photographs are clearly the most accurate of the four methods and provide a permanent record of sea lion distribution and numbers. In some circumstances, surveys from vessels or elevated shore sites may provide counts useful for trend assessments depending upon the number and distribution of sea lions as well as the topography of the site.

In our comparison of visual and photo-based counts of sea lions from boats at South Marble Island, these two methods generally tracked one another well, but there was some variation. Visual, real-time counts averaged 6.9 sea lions more than the corresponding counts from oblique photographs taken from boats (Fig. 4). Highly experienced observers had a residual standard error of 44.4 (due to a small sample size), compared with 22.7 for moderately experienced observers and 35.2 for novice observers (Fig. 4). Visual, land-based counts from the elevated site were very similar to visual counts from boats and slightly higher than photo-based counts from boats. Due to the small sample sizes from simultaneous counts from different platforms, especially airplanes, conclusions about the comparability of counts from differing sources should be viewed cautiously and may be site specific.

Early History of Use, Colonization of New Haul-Outs, and Rookery Development

Early history of use: Southeastern Alaska—Fossils of Steller sea lions in southeastern Alaska date to 20,800 B.P., before the last glacial maximum (Heaton and Grady 2003), and an ethno-historic account from investigations in the 1880s and 1890s

Table 3. Summary of individuals interviewed about their observations of Steller sea lions or commercial fisheries in the study area. NPS refers to Glacier Bay NPS.

Ref.	Personal communication	Position at time of observation	Current location	Interviewer	Interview dates	Years in study area
a.	Bruce Paige	NPS Outer Coast Ranger	Gustavus, AK	EAM	November 2007	1969–1994
b.	Wayne Howell	NPS Cultural Resource Specialist	Gustavus, AK	LAJ and JNW	January 2007	1989–present
c.	Julia (Richards) Pinnix	NPS Interpretive Ranger	Arizona	EAM	May 1999	1992–2001
d.	Walter Baldwin	Commercial Fisherman	Sitka, AK	JNW, EAM	November 2007, January 2010	1969–2007
e.	Roger Gross	Commercial Fisherman	Sequim, WA	LAJ	November 2007	1974–2000
f.	Bruce Smith	Commercial Fisherman	Gustavus, AK	LAJ	November 2007	1974–present
g.	Paul Johnson	Commercial Fisherman	Gull Cove and Juneau, AK	LAJ	November 2006	1970–present
h.	Dennis McAllister	ADFG Wildlife Technician	Sitka, AK	LAJ	November 2006	1989–1996
i.	Clarence Summers	NPS Outer Coast Ranger	Eagle River, AK	EAM	November 2007	1972–1980
j.	Karen Jettmar	NPS Outer Coast Ranger	Anchorage, AK	EAM	May 2001, September 2009	1979, 1984
k.	Greg P. Streveler	NPS Outer Coast Ranger	Gustavus, AK	EAM	November 2007	1968–present
l.	Kevin Apgar	NPS Chief of Concessions	Anchorage, AK	EAM	November 2007	1983–1996
m.	Jim de la Bruere	Charter Fisherman	Juneau, AK	LAJ and JNW	November 2009	1984–1994
n.	Greg Howe	Commercial Fisherman	Hobbit Hole, Inian Islands, AK	LAJ	November 2006	mid-1970s–present
o.	Jack Anderson	Commercial Fisherman	Sitka, AK	EAM	March 2010	1946–present
p.	Kevin Monagle	ADFG Commercial Fisheries Biologist	Juneau, AK	LAJ	2007	(not applicable)
q.	David Harris	ADFG Division of Commercial Fisheries	Juneau AK	LAJ	January 2011	(not applicable)

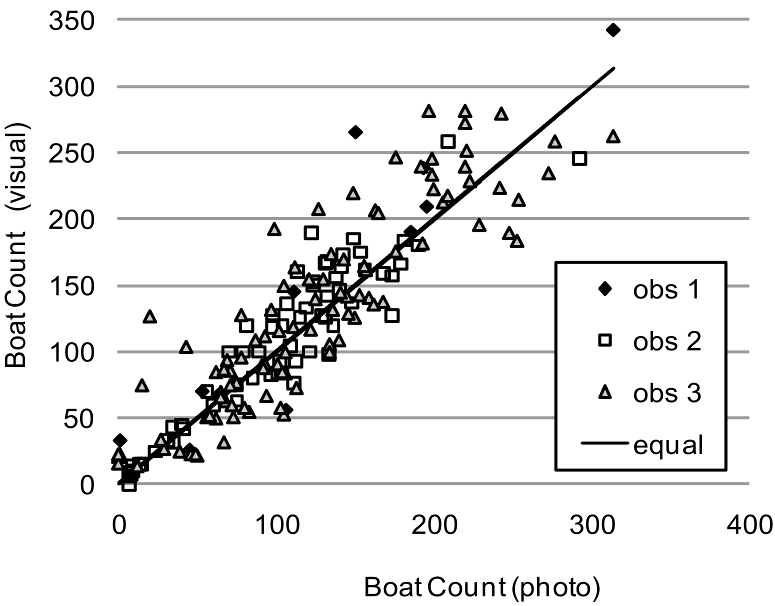

Figure 4. Comparison of real-time visual counts made from boats to counts from photographs taken just before or after the corresponding real-time count at the South Marble Island haul-out in Glacier Bay. Level 1 observers (Obs 1) were the most experienced, whereas level 3 observers (Obs 3) had the least or unknown levels of experience counting pinnipeds.

notes that the "sea lion . . . was found on the outer rocks and islands, and . . . hunted industriously in the spring," (p. 122) by the Tlingit in southeastern Alaska (Emmons 1991). Yet, the earliest recorded counts of Steller sea lions on specific haul-outs that we found for the study area were from the 1960s and 1970s. Compared to sites in inside waters, the outer coast haul-outs tend to have a longer history of documented use by sea lions (Table 4). The first record of a specific count from a haul-out in the study area of which we are aware is from 1962 when average counts of 150 sea lions were noted at the Harbor Point site, immediately south of Lituya Bay (Jettmar 1984) (Fig. 1). In 1963, during an anthropological exploration of the area, a sea lion skull with a bullet hole in it was found on the mainland, to the east of the mouth of the Carolus River, near Point Carolus (Fig. 1). The skull was associated with Tlingit artifacts at a salmon smoke house used in the 1950s or early 1960s.[1] Sea lions on the outer coast were reported on haul-outs at Cape Fairweather and Cape Cross in the early and mid-1970s, respectively (Table 4). In the summer of 1974, R. Patten conducted surveys of the outer coast for marine mammals on 35 days from Torch Bay (the next bay north of Graves Harbor), north to Palma Bay (Patten 1975). She recorded small numbers of sea lions hauling out at Torch Bay (3 sea lions), Sugarloaf Island south of Dixon Harbor (11), Dixon Harbor (3), and Boussole Head (3), but none of these sites were regularly occupied during surveys in recent decades.

[1]Personal communication from R. E. Ackerman, Anthropologist, Washington State University, Pullman, WA, February 2010. The sea lion skull is currently archived at the University of Alaska Fairbanks Museum.

Table 4. Earliest documented dates of occupation of Steller sea lions at each haul-out and first year when 50 or more pups were observed at Graves Rocks.

Site	Region	Type	Colonization year or earliest estimate	Earliest count	Source, Colonization	Highest count	Date of highest count	Source, High count
Cape Fairweather	Outer coast	Haul-out	<1970	207	NPS, G. Streveler, B. Paige	409	13 March 1993	ADFG
Harbor Point (Lituya Bay)	Outer coast	Haul-out	<1962	150[b]	NPS, K. Jettmar	264	25 June 2009	NMML, Fritz
Graves Rocks	Outer coast	Haul-out	≤1969	~100	W. Baldwin	923	24 August 1996	UAS/NPS, Mathews
Cape Cross	Outer coast	Haul-out	<1975	350	ADFG, D. McAllister	540	1 February 1996	ADFG, McAllister
S Marble Island	Glacier Bay	Haul-out	1985	50	NPS, Devaney	1190	24 June 2009	NPS, Womble
Point Carolus	Glacier Bay	Haul-out	*ca.* 1989	2	NPS, R. Perkins	578	16 August 2007	NPS, Womble
Tarr Inlet	Glacier Bay	Haul-out	1999	1	NPS, J. (Richards) Pinnex	230	8 May 2005	NPS, Womble
NW Inian Island	Icy Strait/Cross Sound	Haul-out	≤1969	20–30	W. Baldwin	905	24 July 2006	ADFG, Jemison
Middle Pass Rock	Icy Strait/Cross Sound	Haul-out	2003	2–3	NPS, W. Howell	835	26 June 2009	NPS, Womble
Graves Rocks[a]	Outer coast	Rookery	1999		ADFG, K. Pitcher	1455	18 August 2003	UAF, Womble
						440[c]	25 June 2009	NMML, Fritz

[a]Transition from haul-out to rookery characterized as when more than ~50 pups were born at the site.
[b]Average
[c]Maximum pup count, Graves Rocks

Outer coast: Rookery development at Graves Rocks—We do not know exactly when Graves Rocks (Fig. 1) were first colonized by sea lions as a haul-out. The first report of Steller sea lions using the site is from summer 1969 with an estimated 100 animals present (Table 3d). One fisherman with a 60 yr history of fishing the outer coast beginning in 1946 did not observe sea lions at Graves Rocks during the early 1960s when he frequently anchored within the Graves Rocks complex during late spring and summer (Table 3o). There are few quantitative data available for sea lion use of Graves Rocks during the 1970s and 1980s. Based on NPS reports (Patten 1975, Streveler 1977, Acuna and Selig 1983, Jettmar 1984), interviews with NPS biologists and rangers, and with fishermen who fished in the area beginning in the late 1960s through the 1970s, sea lions were using the area throughout these two decades, possibly at a low level, and not continuously (Table 3a, d–g, i–k, m). Use might have been seasonal with the site apparently more likely occupied from late summer through winter and less likely to be occupied in the spring and early summer. By 1989, however, Graves Rocks was a regularly used summer haul-out (Fig. 2h). That summer, more than 500 sea lions were present during an aerial survey by ADFG, but no pups were observed during a concerted effort to look for them (Table 3h). By 1996 a few harem-like clusters were visible in aerial photographs (Mathews and Dzinich 2001), a structure that has also been observed at haul-outs (LAJ, JMM, and JNW, personal observations). In 1999 and 2000 more than 50 newborn pups were documented at Graves Rocks (Pitcher *et al*. 2007); in July 2000 Ken Pitcher (ADFG) confirmed that females were whelping on site, rather than arriving with their pups from another rookery (personal communication from K. Pitcher in Mathews and Dzinich 2001). From 1989 to 2009 Graves Rocks had increasing nonpup summer counts (3.8%/yr, Table 2).

Colonization and use of inside waters: Glacier Bay, Cross Sound, and Icy Strait—In the inside waters, we have strong evidence that South Marble Island, Tarr Inlet, and Middle Pass Rock were colonized by Steller sea lions in the 1980s, 1990s, and 2000s, respectively (Table 4). The oldest, well-documented colonization in the study area is of South Marble Island in Glacier Bay (Fig. 1) where sea lions began hauling out consistently around 1985.[2] That year, 40–105 animals were recorded from 31 May to 11 June followed by sightings of a single animal on two days during July and 10 or fewer during August (NPS Interpretive Division tour boat log books). Counts at South Marble Island were relatively stable from 1985 to about 1993 or 1994; June/July numbers have increased steeply since then (Fig. 2b). In recent years, peaks in late April and October were more pronounced (Fig. 3c).

During the 1960s sea lions were observed swimming in Glacier Bay primarily during the nonbreeding season; an early record of Steller sea lions hauling out in Glacier Bay is from around 1968 when sea lions were observed (uncharacteristically) on an iceberg in Muir Inlet.[2] During the summers of 1971 and 1972, a small number of immature Steller sea lions were observed at North Marble Island in Glacier Bay, 3 km north of South Marble Island (Patten 1974). Since then, there have been no records of sea lions using North Marble Island.

Use of Point Carolus, a sandy reef on the western side of the mouth of Glacier Bay and adjacent to Icy Strait (Fig. 1), as a haul-out by sea lions was first documented in 1989 (Table 4; Fig. 2h). In recent years the Point Carolus haul-out has typically been occupied by sea lions between April and November with higher numbers between

[2]Streveler, G. 1989. Steller sea lion haul-out use history along Glacier Bay. Internal memorandum. October 1989. 1 pp.

August and October (Fig. 3d). Compared to South Marble Island, Tarr Inlet, and Middle Pass Rock, we are less certain of the first usage at Pt. Carolus because it was not monitored regularly before 2001 (Table 4).

In Glacier Bay's northwest arm along Tarr Inlet (Fig. 1), a lone Steller sea lion was first observed hauled out in 1999 in mid-May.[3] This area was passed nearly every day by NPS rangers on tour boats from late spring through summer from the early 1990s through the present, so regular use during those seasons would not have been overlooked. Because our highest counts of sea lions for Tarr Inlet were from spring, between March and May with up to 230 observed (Fig. 2a), it is thus possible that use of this site in nonsummer months before 1999 could have been overlooked. With only two fall/winter counts for Tarr Inlet, fall and winter use of this site is currently not well known.

Haul-out use by sea lions in Cross Sound (Fig. 1) has also increased in recent years. The Northwest Inian Island haul-out in Cross Sound, used by a few sea lions during summer from at least 1969 until the late 1990s (Table 3b, d, h, m), experienced increasing use beginning around 2002 and had a 13.9%/yr trend from 1989 to 2009 (Table 2, Fig. 2d). Counts in other months from 1993 to 2009 at this site remained relatively consistent across time, possibly with a slight increase between 2001 and 2003 (Fig. 2d). Use of Middle Pass Rock, near Northwest Inian Island, increased rapidly between 2001 and 2009 (24.4%/yr). Local residents noted that the Middle Pass site was first used by sea lions in the early 2000s (Table 3b, g) and systematic aerial surveys were started in 2003 (Womble *et al*. 2009). Alaska Natives visited Middle Pass Rock to collect gull eggs in 2001, 2002, and 2003 and first observed a few sea lions hauled out on 10 June 2003. Since 2003, sea lions have consistently used Middle Pass Rock with a steep increase in numbers, primarily between June and August.

Discussion

Regional Trends

In the last three decades, the number of haul-outs, rookeries, and Steller sea lions counted have increased in the GB/IS/CS area, in the northern region of the eastern population. The growth in our study area (8.2%/yr) is a substantial component of the overall growth in the eastern stock of sea lions (3.1%/yr) (Pitcher *et al*. 2007). In southeastern Alaska, long-established rookeries have followed patterns of relative stability (Forrester Island) or slight growth (Hazy Island), with much faster growth at newly established rookeries (Calkins *et al*. 1999, Pitcher *et al*. 2007), including Graves Rocks (Fig. 2h). The rapid growth in the number of sea lions at White Sisters (Pitcher *et al*. 2007) and Graves Rocks (Pitcher *et al*. 2007; current analysis) since they became rookeries, has likely contributed to the overall 8.2% growth in the GB/IS/CS region, but rates of growth from 1976 to 2009 were not evenly distributed. The number of sea lions at South Marble Island, Middle Pass Rock, and Northwest Inian Island increased much more rapidly than other sites in the eastern population and other sites in our study area (Fig. 2, Table 2). The largest cumulative increase (1,588%/18 yr) occurred at South Marble Island in Glacier Bay (Table 2).

[3]Personal communication from Julia (Richards) Pinnex, Interpretive Ranger, 1992–2001. Glacier Bay National Park Service, May 1999.

Potential Factors Influencing Population Growth and Redistribution

Potential factors that may have contributed to the increase in sea lions in the Glacier Bay/Icy Strait/Cross Sound region that we discuss include (1) recent deglaciation and subsequent ecosystem development and prey species colonization, (2) immigration and redistribution of sea lions, and (3) decreases in sea lion harassment and mortality.

Recent Deglaciation and Colonization of Prey Species in Glacier Bay

New haul-outs may be colonized if suitable habitat becomes available, such as following periods of glacial retreat or if prey resources become more abundant in new areas. The genetic divisions among populations of Steller sea lions are thought to be rooted in glacial advances and retreats that occurred 60,000–180,000 yr ago (Bickham *et al*. 1996, Harlin-Cognato *et al.* 2006). These authors suggest that glacial advances during cooling periods left refugia where isolated groups of Steller sea lions diverged genetically. Glacier Bay is a "complex fiord tributary to Icy Strait" that has undergone a rapid deglaciation of over 100 km in the last 230 yr (Cooper 1937). On Vancouver's voyage in 1794, the ice sheet that covered Glacier Bay was only about 10 km in from the mouth of the Bay (Cooper 1923). Very little marine or terrestrial habitat would have been available to sea lions within the Bay at that time with no islands yet uncovered. During the rapid ice retreat from about 1750 to 1950, over 2,600 km^3 of glacial ice melted within Glacier Bay (Larsen *et al.* 2003). The ice has retreated 110 km, exposing $\sim$1,322 km^2 of new marine habitat, which has become a very productive marine ecosystem (Etherington *et al*. 2007) fed by 5 tidewater glaciers (JNW, personal observation).

South Marble Island (Fig. 1), currently the largest sea lion haul-out in Glacier Bay, was covered by a glacier until the mid-1800s (Cooper 1923). In his extensive travels (1879–1899) and writings on Glacier Bay, John Muir did not mention Steller sea lions, although he did mention harbor seals *(Phoca vitulina)* and their importance to Native hunters (Muir 1915).

As new habitat became available, improving prey resources may also have played a role in increased use of Glacier Bay by sea lions. Colonization by Pacific salmon (*Oncorhynchus* spp.) in Glacier Bay has occurred many times from *ca*. 1890 in the Berg Bay river, near the mouth of the Bay where the ice first retreated, to recent decades including two well studied streams colonized in 1985 and 1989 in upper Glacier Bay (Milner and Bailey 1989, Milner 1994). Multiple source populations of salmon in Glacier Bay at different times are also evident from salmon genetics (Kondzela and Gharrett 2007). Since 1989 high numbers of salmon have returned to the northeastern arm of Glacier Bay (Muir Inlet and Wachusett Inlet) (Fig. 1) with estimates of $>$20,000 pink salmon in odd years.[4]

Salmon are seasonally important in the diet of Steller sea lions in southeastern Alaska and the seasonal availability of salmon influences the distribution of sea lions (Womble and Sigler 2006, Gelatt *et al*. 2007, Trites *et al.* 2007). In southeastern Alaska the frequency of occurrence of salmon in sea lion scat samples is typically highest in summer (June–August) and autumn (September–November) (Womble and Sigler 2006, Trites *et al*. 2007, Sigler *et al.* 2009) and varies depending upon the geographic region and the timing of salmon runs in the area. In the Glacier Bay

[4]Personal communication from Alexander Milner, University of Birmingham, Edgbaston, Birmingham, U.K., February 2008.

region, sites such as Middle Pass Rock, Northwest Inian Island, Graves Rocks, and Point Carolus, are located in the Cross Sound and Icy Strait area (Fig. 1), one of the major migratory corridors for salmon as they return to their spawning streams in the inside waters of southeastern Alaska from the Gulf of Alaska (Vaughan 1947, Elling and Macy 1955). The seasonal use of Middle Pass Rock between June and August corresponds to the return of salmon to this area and sea lions have often been observed foraging on salmon around Middle Pass Rock (Womble *et al*. 2009) (Table 3g, n).

Improvements in salmon fisheries management in Alaska during the early 1970s, such as the salmon Limited Entry Act in 1973 (Marine Advisory Program 2003) and, specifically, elimination of purse seine net fisheries in the Cross corridor area with restrictions on seine net fishing in Icy Strait (Table 3g, p, q) in 1974 (Mackovjak 2010), are likely to have benefitted sea lions in the study area as well as commercial fishermen. In 1999, sections of Glacier Bay were closed to commercial fishing with a complete closure to commercial (but not sport) fishing planned; commercial permits will not be reissued as current permit holders retire (U.S. Department of the Interior 1999).

In addition to salmon, other sea lion prey species common during surveys in Glacier Bay included walleye pollock (*Thereagra chalcogramma*), capelin (*Mallotus villosus*), sand lance *(Ammodytes hexapterus)*, and Pacific herring *(Clupea pallasi)*; these small schooling fish surveys identified more than 50 species of fish (Robards *et al.* 2003, Arimitsu *et al.* 2008). Given that sea lions are central-place foragers, if foraging conditions and prey availability have improved in recent decades in the Glacier Bay region, then establishing or using sites that are closer to prey resources would reduce overall travel costs for sea lions (Womble *et al*. 2009).

The population trajectories of two other, large vertebrate species also suggest local, recent ecosystem changes in Glacier Bay from the 1990s to the current decade. From 1994 to 2009, the number of humpback whales (*Megaptera novaeangliae*) identified in Glacier Bay and Icy Strait during the feeding season increased from 60 to 176 whales (Neilson and Gabriele 2009), an increase of 7%–8% per year.[5] In contrast to sea lions and humpback whales, harbor seal numbers in Glacier Bay declined by more than 75% from 1992 to 2008 (Mathews and Pendleton 2006, Womble *et al.* 2010). Harbor seals, Steller sea lions, and humpback whales all consume similar prey species. Factors in the harbor seal decline that involve Steller sea lions include potential competition from overlap in prey and competitive exclusion (Mathews and Pendleton 2006, Herreman *et al.* 2008), as well as direct predation by Steller sea lions, a previously unknown source of significant mortality (Mathews and Adkison 2010). An ecosystem model also suggests that the population dynamics of Steller sea lions in southeastern Alaska from the early 1960s to 2002 were influenced by multiple factors (Guénette *et al.* 2006).

Immigration and Shifts in Distribution of Sea Lions

From the 1970s to 2002, the eastern population of Steller sea lions grew at 3.1%/yr (Pitcher *et al*. 2007). Multiple factors may be needed to explain the more rapid growth at South Marble Island in Glacier Bay (16.6%/yr; 2001–2009), Northwest Inian Island (13.9%/yr; 1989–2009) and Middle Pass Rock (24.4%/yr; 2001–2009), both at the junction of Cross Sound and Icy Strait (Table 2, Fig. 1). During the 1980s

[5]Personal communication from Chris M. Gabriele, Glacier Bay National Park, Gustavus, AK, November 2010.

the number of Steller sea lions in southeastern Alaska was increasing at more than 5.9%/yr (Calkins *et al*. 1999), explaining some of the observed increases in our study area during that decade, but not the especially large growth in use of Glacier Bay and Icy Strait. The maximum theoretical net productivity rate for pinnipeds, including Steller sea lions, is estimated at 12%/yr (Wade and Angliss 1997). The observed high rates of increase within our study area indicate that localized redistributions favoring these areas must have occurred.

Immigration and temporary seasonal movements from the western population into the GB/IS/CS area, while not necessary to explain high localized growth rates, are demonstrated by population genetic data indicating that female sea lions from both the eastern and western stocks colonized Graves Rocks and White Sisters as they became rookeries (O'Corry-Crowe *et al*. 2005, 2006; Gelatt *et al*. 2007). Evidence of continued colonization of this region from both stocks is provided by females that were branded after 1999 as pups at rookeries in the eastern and western stocks and observed as breeding adults at Graves Rocks as recently as 2010 (ADFG, unpublished data). Thus, the notion of "population" is not completely clear for this region. Equally problematic in defining and managing the two populations is temporary immigration. Marked juvenile and adult sea lions from as far away as northern California (eastern stock) and Kodiak Island, Alaska (western stock) have been observed in the GB/IS/CS region during both summer and winter, principally at Graves Rocks, Middle Pass Rock, Northwest Inian Island, and South Marble Island (Raum-Suryan *et al*. 2002; ADFG, unpublished data). Some proportion of the increase in the June/July counts of sea lions used for trend analysis could be due to an increase in animals that may be temporarily visiting the Glacier Bay region.

Natal site fidelity, or philopatry, is a widespread, evolutionary strategy for pinnipeds that forage widely at sea, but seasonally aggregate at predator-free terrestrial sites to give birth, locate a mate, and raise a pup (Stirling 1983). In otariids, natal site fidelity can be extreme. Northern fur seal *(Callorhinus ursinus)*, Antarctic fur seal *(Arctocephalus gazella)*, and Australian sea lion *(Neophoca cinerea)* females return to their natal rookery—some to within meters of their own birth location—year after year to give birth and mate (Gentry 1980, Lunn and Boyd 1991, Baker *et al.* 1995, Campbell 2003, Wolf and Trillmich 2007). Female-mediated philopatry operating at local scales is evident from population genetic studies of Steller sea lions as well (O'Corry-Crowe *et al*. 2006). Compared to documenting site fidelity, however, detecting dispersal in pinnipeds typically requires broader and longer resight or resampling coverage. We are consequently less likely to document or quantify dispersal than natal site fidelity. Colonization of a new rookery is unequivocal evidence for dispersal.

Given the high degree of site fidelity in otariids, what circumstances or factors may favor dispersal? There is evidence from other island-breeding pinnipeds that new rookeries may form when females leave established breeding areas that have become crowded (Bradshaw *et al*. 2000, Gaggiotti *et al.* 2002). Limited breeding space may have been a factor for eastern population Steller sea lion females. Graves Rocks was a nonbreeding haul-out for close to three decades before females from the increasing eastern population (and the declining western population) started breeding there.

Rookery crowding, however, was an unlikely factor for females that emigrated from the declining western to the eastern population. The period of transition of White Sisters and Graves Rocks into rookeries (1990s) coincides with some of the largest declines and low juvenile survival in the western population (York 1994, Holmes *et al.* 2007). This raises the possibility that ecosystem changes or density-dependent processes in the western population may have favored dispersal over site fidelity.

A population's potential for dispersal is also influenced by its evolutionary history. For species or populations that occupy habitat subject to large-scale disruptions, such as the periodic advance and retreat of glacial ice sheets that cover and later uncover suitable breeding habitat, or decadal fluctuations in ocean and prey conditions, we would predict a greater retention of the genetic potential to colonize new habitat, compared to populations that have not experienced such long-duration fluctuations in breeding habitat availability and suitability. Eight North Pacific pink salmon populations, which currently breed in streams that were covered by glaciers during the last glacial advance, exhibited a much higher tendency to disperse (or stray), compared to one pink salmon stock (Little Susitna River) that exhibited no genetic evidence of straying from a stream that had persisted in an ice-free refuge through the last ice advance (Churikov and Gharrett 2002). The glacial history of the Pacific Northwest has also influenced the dispersal of Steller sea lions (Harlin-Cognato *et al.* 2006).

Decreases in Mortality

In recent decades, Steller sea lions in the eastern population have experienced reduced lethal interactions with humans. From 1912 to 1966, approximately 55,000 Steller sea lions were killed for fisheries management and commercial harvest in British Columbia (BC), Canada (Canadian Science Advisory Secretariat 2008). From the 1970s to 2002, after the culling program ended, there was significant habitat expansion and an increase in the number of major sea lion haul-outs in BC from 18 to 24 (Pitcher *et al.* 2007). In Alaska, although there was a predator control bounty for harbor seals from 1927 to 1972 managed by the territorial or state government in an effort to improve salmon runs, there was apparently no corresponding bounty for Steller sea lions (Paige 1993). Between 1963 and 1972, more than 45,000 Steller sea lion pups were harvested at rookeries in the western population (Merrick *et al.* 1987); we did not find evidence for management-directed killing of pups on this scale in the eastern population. A small (206 animals) commercial sea lion harvest in southeastern Alaska in 1960[6] presumably had little impact compared to the large culling program in Canada. The end of the predator control program and commercial harvests is thought to be the main source of the recent (1970s–2004) increase (3.1%/yr) in sea lions in the eastern population (Pitcher *et al.* 2007).

Prior to the passage of the Marine Mammal Protection Act (MMPA) in 1972, shooting sea lions was legal in U.S. waters. From 1972 to 1990 fishermen could apply for permits that allowed legal shooting of sea lions that were destroying fishing gear or a threat to human safety (Loughlin and York 2000). In the U.S., shooting Steller sea lions became illegal in 1990 (50 Code of Federal Regulations 227.12(a) 1).

Specific reductions in human related mortalities from our study area are also likely, but not quantified. During the 1970s and into the mid-1980s, Murphy Cove, the anchorage at the head of Graves Harbor 9 km northeast of Graves Rocks (Fig. 1), was heavily used by commercial fishermen. More than 100 fishing vessels occasionally

[6]James W. Brooks, Director of Game, Department of Fish and Game, State of Alaska, Memorandum to the Commissioner on 28 November 1960.

used the region (Streveler and Worley 1975) and were supported by up to three fish-buyers in anchored barges in Murphy Cove where close to 200 people lived temporarily during summer months (Table 3i, j, l). Steller sea lions were shot by fishermen (Table 3d, g, i, o) and a few dead sea lions were found on Graves Rocks (Table 3i). In addition, salmon trollers anchored in Deer Harbor commonly shot "as many sea lions as they could" (Baldwin, Table 3d) at the Cape Cross haul-out (Fig. 1) in years before there were prohibitions against such shooting. The heightened regulatory attention on Steller sea lions, ESA listings of both populations (US Federal Register 1997) and subsequent potential for fines, a sharp drop in value of pink salmon in the early 1980s (Table 3d, o),[7] reduction in commercial fishing activities centered in Murphy Cove in the 1980s, and broad changes in sea lion management philosophy, strongly suggest that illegal shooting in the region would have become less common after the early 1990s.

During colonization in the mid-1980s, shooting of sea lions at South Marble Island would have been less likely compared to the more remote haul-outs. The island is within the main Bay where firearm use is prohibited (36 Code of Federal Regulations 2.4(a)(2)(ii) and 13.30), where NPS Rangers patrol the waters more regularly, and where commercial and private tour boats approach South Marble Island for sea bird and sea lion viewing throughout late spring and summer. The combination of being a refuge from shooting during the early years of use, and access to improving prey resources, may explain some of the early attraction of the South Marble Island haul-out, in addition to the absence of terrestrial predators.

Mortalities from indirect interactions between fisheries and sea lions also occur, but are thought to be a small factor ($<2\%$) in estimated Steller sea lion mortalities as a percent above replacement (Loughlin and York 2000). Reports of indirect interactions between Steller sea lions and sport and commercial fisheries in northern southeastern Alaska have increased in recent years. From 2000 through 2009, nearly 250 Steller sea lions were documented with ingested fishing gear (primarily salmon fishery trolling gear) in southeastern Alaska and northern British Columbia (Raum-Suryan *et al.* 2009; ADFG, unpublished data).

Factors That May Influence Seasonal Distribution

At South Marble Island, both from the 1990s (Fig. 3b) and more recent years (Fig. 3c), we observed a seasonal decline in counts of sea lions during June or July followed by a second notable increase in numbers beginning in August. The reason for the declines in sea lions using this haul-out in mid-summer is not known, however, we comment on two possible explanations, which may have been contributing factors. Sea lions may leave South Marble Island during July to search and forage elsewhere on seasonal aggregations of prey and rest at other haul-outs closer to prey concentrations. Counts of sea lions at Northwest Inian Island (Fig. 3e) (at the Icy Strait-Cross Sound junction) and South Marble Island (Fig. 3c) were out of phase with one another, and thus support the hypothesis of sea lions moving from South Marble Island to areas where seasonal salmon aggregations occur. During the 1990s, records of sea lions entangled in salmon trolling gear at South Marble Island began in late June and were most common in July and August (EAM, unpublished data), indicating that these

[7] Alaska commercial pink salmon catches and value 1878–2008, Alaska Department of Fish and Game, Division of Commercial Fisheries. Available at http://www.cf.adfg.state.ak.us/geninfo/finfish/salmon/catchval/history/pink1878.php (accessed 5 March 2010).

sea lions forage where trolling for salmon occurs. Very little commercial trolling for salmon occurs within Glacier Bay proper during summer.[8]

The seasonal haul-out pattern of sea lions at South Marble Island was also out of phase with numbers of sea lions ashore at Graves Rocks after it became a rookery in the late 1990s (Fig. 3c, f). A second possible explanation for the drop in use of the South Marble Island haul-out beginning in May (Fig. 3c) is that breeding age sea lions may depart from South Marble Island to go to rookeries. Similarly, increased use of South Marble Island beginning in August could be the result of breeding animals moving away from rookeries once the breeding season is completed. In Alaska, Steller sea lion breeding territories are established in early May and most matings have occurred by the second week in July (Pitcher and Calkins 1981). Most of the sea lions at South Marble Island in summer before 1999 were males (EAM, unpublished data); in later years, both sexes and all age classes occupied South Marble Island during summer, including a small number of pups (<5) in some years, which were very likely born at that site (LAJ and JNW, personal observations). Recent surveys suggest that the mid-summer dip in numbers at this haul-out may no longer be occurring (JNW, personal observation).

Sea lions use haul-outs at Point Carolus and Middle Pass Rock primarily during June–November (Fig. 3d) when salmon are migrating through the Cross Sound/Icy Strait region (Womble *et al*. 2009). The channel constrictions around Middle Pass and the Inian Islands concentrate prey species and appear to facilitate foraging by sea lions (Womble *et al*. 2009). The ephemeral use of Tarr Inlet (Fig. 2a) by sea lions appears to be associated with aggregations of small schooling fish. Groups of sea lions have been observed actively foraging in the upper reaches of Tarr Inlet (JNW, personal observation), a pattern also documented in other areas of Glacier Bay and southeastern Alaska (Womble *et al.* 2005). For example, eulachon *(Thaleichthys pacificus)* are high-energy, small schooling fish that aggregate during spring for spawning and attract large aggregations of Steller sea lions (Sigler *et al.* 2004, Womble *et al*. 2005). In addition to the seasonal availability of prey, other factors may influence the seasonal distribution of sea lions including physical attributes of terrestrial sites (Ban and Trites 2007), the availability of potential mating opportunities, the risk of predation, and localized depletions of prey.

Conclusion

The recent growth in Steller sea lion numbers in the Glacier Bay/Icy Strait/Cross Sound area is the highest recorded for this species and indicates that conditions for population expansion, immigration, and colonization are particularly favorable relative to other areas within their range. Our results confirm those of others (*e.g.,* Pitcher *et al*. 2007) who have documented that local changes in abundance can deviate substantially from stock or range-wide patterns. We document the colonization and development of important prey species such as salmon in Glacier Bay and evidence for reduced direct human interactions (*i.e.,* shooting) during the period of population growth in the GB/IS/CS and outer coast region. The longest-used haul-outs in our study area were on the outer coast while haul-outs in inside waters were colonized more recently (Table 4). Graves Rocks was colonized as a haul-out before or by 1969, and transitioned to a rookery by 2000. Questions that remain

[8]Personal communication with Chad Soiseth, Biologist, Glacier Bay National Park Service, October 2009.

are whether the recent growth in Steller sea lions in the GB/IS/CS area has been driven primarily by increasingly favorable local factors and redistribution within the eastern population or through negative factors in the western population and immigration into the eastern population, or combinations of both. Understanding the factors involved in, and potential for, population expansion and colonization of new habitat by Steller sea lions is important for their effective management and conservation. The recent colonization of new haul-outs, development of two new rookeries—each colonized by individuals from both populations—are perhaps late-stage consequences of the removal of ice barriers and liberation of the intervening habitat. Research and monitoring of Steller sea lions in the GB/CS/IS region will provide a rare opportunity to document evolutionary processes at the convergence of two populations experiencing opposite trajectories and the apparent reversal of their reproductive isolation.

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