A re-examination of the timing of pupping for Steller sea lions *Eumetopias jubatus* breeding on two islands in Alaska

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ABSTRACT: Steller sea lions are distributed from Japan to the California coast, USA, and population demographics vary spatially, with populations in some regions increasing while others are declining. To assess changes in population size, aerial surveys are conducted annually to quantify pup production. The timing of these surveys is critical for accurate population estimates, and survey windows were determined based on historical estimates of mean pupping date. We reassessed the timing of pupping for Steller sea lions at 2 breeding islands in the central Gulf of Alaska, USA (Marmot Island) and the eastern Aleutian Islands (Ugamak Island) for evidence of temporal shift. Using land-based counts of pups, we quantified mean pupping date and the duration of the pupping season between 2003 and 2013 and compared these data to historical mean pupping dates between 1977 and 1999. The mean pupping date of 9 June on Marmot Island was not significantly different than the mean pupping date on Ugamak Island, 8 June. On Marmot Island, mean pupping date differed by 3.7 ± 0.9 d between beaches; however, mean pupping date did not differ between beaches on Ugamak Island. On Ugamak Island, mean pupping date was significantly earlier than previously reported by 2.5 d, but this may be an artifact of the limited number of years available for comparison. On Marmot Island mean pupping date was not different from historical dates. On both islands, 94.2 ± 1.6 % of the pups were born prior to the planned start of aerial surveys in Alaska (23 June). Our results demonstrate that although mean pupping date was variable and may have shifted earlier relative to historical data at Ugamak Island, the current timing of the aerial survey is suitable for obtaining peak pup counts for Steller sea lions in these regions.

KEY WORDS: Marmot Island · Pupping date · Pup production · Reproduction · Ugamak Island

INTRODUCTION

Seasonality and synchrony in the timing of reproduction is a pattern found in numerous plant and animal species, which has been linked to increased reproductive success through a variety of mechanisms (Rutberg 1987, Ims 1990). Yet, many studies have found that both intrinsic and extrinsic factors can influence the timing of reproduction within a season. Intrinsic factors that play a role can include age, body size, and previous reproductive history (e.g. Lunn et al. 1994, Plard et al. 2014, Rotella et al. 2016). For example, Plard et al. (2014) showed that parturition date in roe deer was negatively related to adult quality (measured as median body mass) and age. Extrinsic factors such as resource availability and environmental factors may also play a role (e.g. Daan et al. 1988, Boyd 1996, Schaper et al. 2012). For South American sea lions *Otaria flavescens*, median birth dates were negatively correlated to prey availability and differed by up to 16 d over a 6 yr study period (Soto et al. 2004).

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Understanding the sources of variation in reproductive timing is critical because reproductive events, such as births, are often used as the baseline for other life-history studies (e.g. age-related survival, growth patterns) and for population assessments (Eberhardt et al. 1979, Bradshaw et al. 2000, Hastings et al. 2009). For example, for many species, counts of young are used to assess population size or track populations over time when direct counts of an entire population are unfeasible (Ling 1969, Eberhardt et al. 1979, Berkson & DeMaster 1985). In pinnipeds (seals, sea lions, and walrus), newborn pups spend a period of time on land prior to entering the water, making them an ideal population segment to census (Berkson & DeMaster 1985). If reproductive timing varies, then estimates of production can be falsely reduced or inflated, impacting measures of population size, which are vital for demographic studies and for development of successful management and conservation strategies.

Because their breeding locations are remote, distant from each other, and span a large geographic region, population counts of Steller sea lions *Eumetopias jubatus* in US waters are primarily conducted via aerial surveys and supplemented with some land- or boat-based counts (Westlake et al. 1997, Snyder & Pitcher 2001, Fritz et al. 2016). Accurate indices of population size are critical for this species because population trends vary substantially across the species' range (Johnson & Fritz 2014). Steller sea lions are widely distributed throughout the Pacific Rim from Japan to California, USA (Kenyon & Rice 1961, Loughlin et al. 1984, NMFS 2008). The population is separated into 2 distinct population segments (DPS), eastern and western, based on genetic and demographic differences between regions, which are divided at 144° W longitude (Bickham et al. 1996, Loughlin 1997).

In 1990, after large declines in Steller sea lion numbers, the species was listed as threatened range-wide under the US Endangered Species Act (ESA). Following continued population declines in the western DPS, in 1997 the listing was changed to endangered for the western DPS (National Oceanic and Atmospheric Administration 1997). The eastern DPS has increased at a rate of approximately 3% yr^{-1} since the 1970s (Pitcher et al. 2007, Fritz et al. 2016) and was removed from the list of ESA-threatened species in 2013 (NMFS 2013). The decline in the western DPS in Alaska likely ended in 2003 and between 2003 and 2015, counts of both pups and non-pups (1 yr and older) have increased in most areas (Johnson & Fritz 2014, Fritz et al. 2016). Nonetheless,

within the western DPS, sea lion numbers remain well below historic levels and regional variability in demographic trends remain significant (Johnson & Fritz 2014).

For Steller sea lion pup production estimates, aerial surveys in Alaska are generally conducted during a 3 wk period between late June and mid-July when most pups are ≤1 mo old (Pitcher et al. 2001, Fritz et al. 2016). The aerial survey window was determined based on historical measures of mean pupping date (Pitcher et al. 2001) with the goal of conducting counts near the peak of pupping (defined as the date of maximum pup counts) but before most pups begin entering the water (Gentry 1970, Sandegren 1970, Pitcher et al. 2001). The current timing of Steller sea lion aerial surveys in Alaska (preferred window of 23 June to 10 July) assumes that the timing of pupping has not changed since 1999 when it was last examined for Steller sea lions breeding in the USA (Pitcher et al. 2001).

The objective of this study was to reassess mean pupping date and determine if there is evidence for variability in the timing of pupping for Steller sea lions. We quantified mean pupping date at 2 breeding islands in the central Gulf of Alaska (Marmot Island) and the eastern Aleutian Islands (Ugamak Island) over 10 yr between 2003 and 2013. In addition, we assessed whether the current timing of aerial surveys occurs near the date of peak pupping, which is essential for accurate estimates of pup production.

MATERIALS AND METHODS

Data collection

Data were collected between 2003 and 2013 by land-based observers at Marmot Island (Kodiak archipelago, Alaska, USA; 58° 13.6′ N, 151° 47.8′ W) and Ugamak Island (western side of Unimak Pass, Alaska; 54° 13.5′ N, 164° 47.5′ W; Fig. 1A, Table A1 in the Appendix). In 2006, the field season was suspended for the month of June on Marmot Island and canceled on Ugamak Island because of a research injunction, which resulted in insufficient data to model mean pupping date in that year. Between May/June and August each year, counts were conducted daily, weather permitting, at Beaches 4 (MB4) and 7 (MB7) on Marmot Island (Fig. 1B) and at 'Beach South' (UBS) on Ugamak Island (Fig. 1C). A second beach on Ugamak Island, 'Beach North' (UBN, Fig. 1C), was observed intermittently with a goal of at least one visitation per week. A detailed
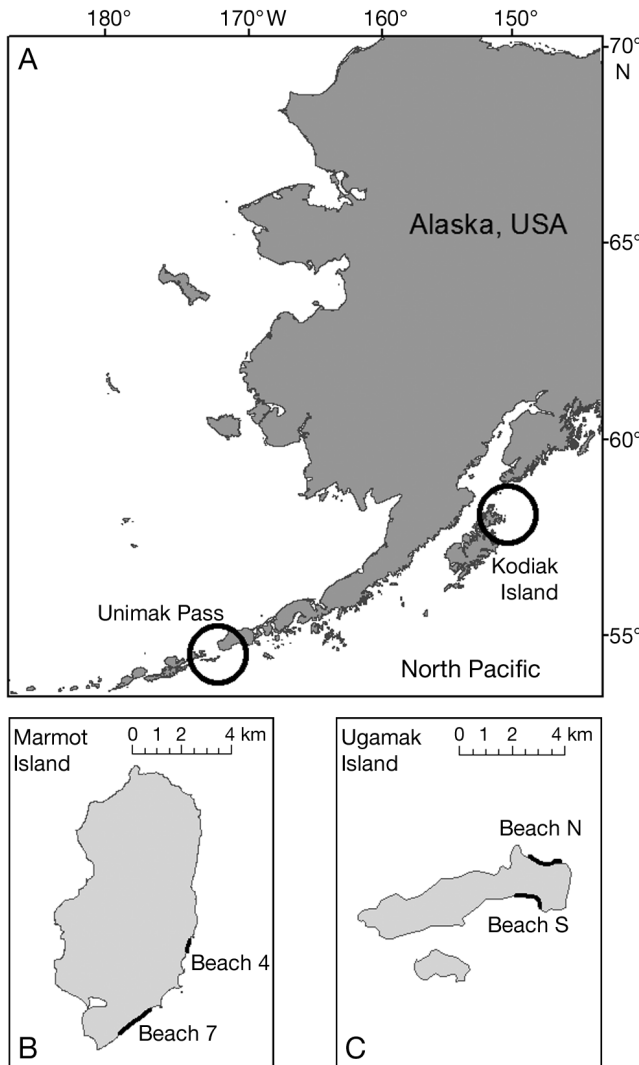
Fig. 1. (A) Steller sea lion research sites (circles) on Marmot and Ugamak islands (Alaska, USA). Marmot Island is located 45 km northeast of Kodiak Island in the Central Gulf of Alaska; Ugamak Island is on the western side of Unimak Pass in the Eastern Aleutian Islands. (B,C) Black lines show breeding beaches on each island: (B) Beach 4 (MB4) and Beach 7 (MB7) on Marmot Island; (C) Beach North (UBN) and Beach South (UBS) on Ugamak Island

description of the data collection procedures can be found in Chumbley et al. (1997) and Wilson et al. (2012).

From cliff edges approximately 200 to 300 m above the rookeries, at least one count of sea lions by age-sex classes was conducted per day between 10:00 and 18:00 h (local time) using binoculars or spotting scopes. Pups were also counted hourly during a weekly dawn-to-dusk survey. Each count was assigned a confidence category based on the observers' assessment of completeness: 'complete' (ob-

server was confident all sea lions present were counted); 'partial' (all visible sea lions were counted but some sea lions may not have been visible from the observation site); and 'complete partial' (a special category for UBN where the entire beach area cannot be observed from the counting location, indicating that every pup in the viewable region was counted). For partial counts, observer comments were used to identify and remove counts that were incomplete (e.g. 'large proportion of pups in the surf not counted' and 'fog moved in; low confidence in total') in order to ensure anomalously low counts did not influence the model parameters. 'Estimate' counts and any other counts where observer comments signified potentially poor data were not included in data analysis. When both count types occurred within a year at a beach, they were generally distributed throughout the survey period (e.g. in 2012, as shown in Fig. 2 below). Because of pup movements into and out of visible areas (or the water), partial counts were equal to or higher than complete counts within the same day on multiple occasions. In these cases, the highest total count was used for that day.

Pup count growth model and statistical analysis

A logistic growth model (Trites 1992, Pitcher et al. 2001) was fit to daily pup counts for each of the 4 beaches separately (MB4, MB7, UBN and UBS; Fig. 2). When modeling counts at each beach, annual variation in logistic parameters was accommodated with a random effect for each year. For beach i in year j, observed cumulative pup production on day d was modeled as follows:

$$N_d = \frac{\phi_{1ij}}{1 + \exp\left\{-\dfrac{d - \phi_{2ij}}{\phi_{3ij}}\right\}} + \epsilon_{ijd}$$

where N_d is the total number of pups observed on day d, ϕ_{1ij} is the pup production asymptote, ϕ_{2ij} is the mean date of birth, ϕ_{3ij} is a scale parameter controlling birth synchrony, and ϵ_{ijd} is an error term with $N(0, \sigma_i^2)$ distribution. For the ϕ_1 and ϕ_3 parameters we used the following parameterization for $k = 1, 3$; log $\phi_{kij} = \beta_{ki} + \alpha_{kij}$, where β_{ki} is the parameter intercept and α_{kij} is a $N(0, \tau_{ki}^2)$ random effect. The ϕ_2 parameters were modeled in the same fashion without the log transformation. To account for leap years, date was based on days since 1 May (i.e. 1 May = 0 and 2 May = 1). All calendar dates presented are calculated from a common year.
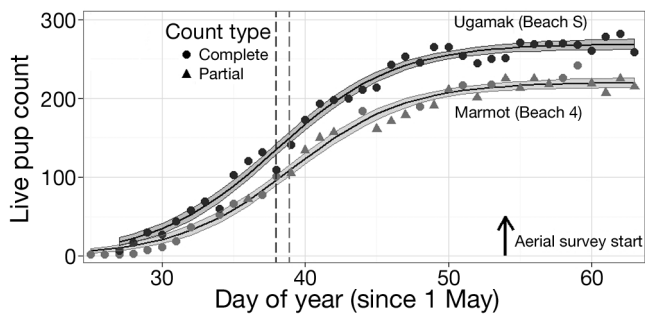
Fig. 2. Example of the results of the logistic growth model for Steller sea lion pup production, based on counts in 2012, at Beach 4, Marmot Island (light gray) and Beach S, Ugamak Island (dark gray) (Alaska, USA). Shaded areas encompass the 95% CIs; points along the curve are live pup counts. Counts are separated between 'complete' and 'partial' counts' to show the variability in count types between locations (Table A1). Vertical dashed lines denote mean pupping dates: 8 June at Beach 4 (light gray); 7 June at Beach S (dark gray). The planned start of the aerial survey, June 23 (Day 53), is marked with an arrow

Only pup counts prior to 4 July (MB4, MB7, and UBS) were used for analysis due to potential dispersal of females with pups and reduced sightability of pups as they mature and begin swimming (Raum-Suryan et al. 2004, Marine Mammal Laboratory unpubl. data). A longer survey period was required at MB4 in 2004 (until 8 July) due to a late season sampling gap and at UBN in all years (until 9 July) due to the reduced sampling effort and greater time gaps between samples. Mean pupping date (MPD) was defined as the date when pup count estimates reached one-half of the maximum pup count in the model (i.e. the asymptote). As in previous analyses for Steller sea lions (Pitcher et al. 2001), no adjustments were made for pup mortality, which resulted in MPD estimates being negatively biased (Trites 1992). For example, for northern fur seals *Callorhinus ursinus*, MPD was biased between 0.1 and 2.0 d earlier when pup mortality was not taken into account (Trites 1992, Kunisch 2011). To determine if the timing of pupping has changed since 1999, estimates of MPD were compared to those from Pitcher et al. (2001) for Marmot and Ugamak islands. The date by which 90% of the pups were born was a derived parameter from the model which was determined by calculating 90% of the asymptote pup count and identifying the date this value was reached. Similarly, the proportion of pups born prior to the start of the planned aerial survey (23 June) was a derived model parameter determined by calculating the number of pups born on 22 June and dividing that value by the maximum pup count from the model.

Statistical analysis was conducted using R (R Core Team 2015). Parameters and random effects were estimated using Markov chain Monte Carlo (MCMC) via the 'rstan' package (Stan Development Team 2015). The MCMC was run for 30 000 iterations following a burn-in of 10 000 iterations which were discarded. The posterior mean and 95% credible intervals (CIs) were calculated for all parameters and derived parameters (e.g. island averages or differences between island parameters). Island MPD was calculated by averaging MPD for beaches at each island. No weighting factor was used because maximum pup count values were similar between beaches within an island.

To compare current MPD with historical data from Pitcher et al. (2001), we assumed a normal posterior distribution around the published MPD values and sampled 20 000 values in order to make comparisons between current and historical posterior distributions. The resulting yearly historical values were averaged for each island and compared to the current posterior distribution for MPD by island. Historical MPD at each island was considered significantly different from current MPD if the resulting 95% CIs of the posterior differences did not include zero. Summary data for MPD, date of 90% pupping, and proportion of pups born by the planned start of the aerial survey are reported as means ± posterior standard deviations (SD).

RESULTS

Data collection

The earliest start date for pup count surveys was 24 May in 2013 and the latest end date was 1 August in 2007 and 2011 (Table A1). The total number of daily pup counts used in the model and the proportion of complete counts varied among years, islands, and beaches (Table A1). At MB7, a late start in 2005 (first count on Day 41) and too few counts in 2003 and 2004 resulted in a poor model fit. At UBN, insufficient sampling, late starts, or large time gaps (up to 8 d) resulted in poor model fits for 2003, 2004, 2007, 2008, and 2013. As a result, these years were removed from the analysis.

Mean pupping date

MPD was not significantly different between Marmot (9 June) and Ugamak (8 June) islands when all

years were averaged (Table 1; difference 1.3 d, CI −0.3 to 3.1 d). Differences among yearly estimates of MPD ranged between −0.4 and 2.6 d later at Marmot Island, with MPDs at Marmot Island significantly later than those at Ugamak Island in only 3 years (2009, 2010 and 2011). When beaches were examined separately, MPD was 3.7 ± 0.9 d later at MB7 than MB4 (Table 1; CI −5.5 to −2.1 d), but there were no differences between beaches on Ugamak Island. On Marmot Island, annual estimates of MPD were

Table 1. Model estimates for timing of pupping of Steller sea lions on 4 beaches in Alaska (MB4 and MB7 on Marmot Island, and UBS and UBN on Ugamak Island; see Fig. 1) between 2003 and 2013: mean pupping date (MPD), date of 90 % pup production, the proportion of pups born by the planned start of the aerial survey on 23 June (Day 53), and maximum pup production estimated from the model (asymptotes). Estimates are shown as mean ± posterior SD. Dates are shown as number of days since 1 May in each year, with corresponding calendar dates determined based on a common year. Beach and island averages were calculated for all years pooled. *Significant difference between beaches within a year or, for pooled data, between beach averages on an island

Location	Year	MPD	MPD (d mo)	90 % pupping date	90 % pupping (d mo)	Proportion born prior to survey	Asymptote estimate
MB4	2003	37.7 ± 0.4	7 June	49.6 ± 1.0	19 June	0.944 ± 0.01	177.2 ± 2.8
MB4	2004	38.2 ± 0.5	8 June	49.3 ± 1.1	19 June	0.949 ± 0.01	216.1 ± 5.7
MB4	2005	38.1 ± 0.4	8 June	48.0 ± 0.8	18 June	0.965 ± 0.01	151.0 ± 2.5
MB4	2007	38.7 ± 0.2*	8 June	48.1 ± 0.5	18 June	0.966 ± 0.01	185.1 ± 1.7
MB4	2008	37.3 ± 0.3*	7 June	47.4 ± 0.8*	17 June	0.968 ± 0.01*	202.9 ± 3.2
MB4	2009	38.5 ± 0.2*	8 June	49.4 ± 0.5*	19 June	0.949 ± 0.01*	235.5 ± 2.0
MB4	2010	37.9 ± 0.4*	7 June	48.4 ± 0.9*	18 June	0.958 ± 0.01*	250.6 ± 5.1
MB4	2011	38.0 ± 0.3*	8 June	48.1 ± 0.7*	18 June	0.962 ± 0.01*	258.0 ± 3.5
MB4	2012	38.9 ± 0.3	8 June	48.0 ± 0.7	18 June	0.967 ± 0.01	220.5 ± 3.2
MB4	2013	37.2 ± 0.2*	7 June	46.6 ± 0.4*	16 June	0.975 ± 0.003	281.8 ± 2.4
MB7	2003	41.8 ± 2.2	11 June	52.8 ± 4.9	22 June	0.900 ± 0.07	244.4 ± 20.0
MB7	2004	41.9 ± 2.3	11 June	52.9 ± 4.8	22 June	0.897 ± 0.07	245.0 ± 20.5
MB7	2005	41.8 ± 2.3	11 June	52.8 ± 4.6	22 June	0.900 ± 0.07	245.1 ± 20.8
MB7	2007	42.2 ± 0.4*	12 June	50.3 ± 1.1	20 June	0.948 ± 0.02	242.2 ± 5.8
MB7	2008	42.2 ± 0.4*	12 June	51.7 ± 0.9*	21 June	0.924 ± 0.02*	239.0 ± 5.2
MB7	2009	42.6 ± 0.5*	12 June	54.4 ± 1.5*	24 June	0.873 ± 0.03*	237.1 ± 6.4
MB7	2010	43.0 ± 0.7*	13 June	55.1 ± 1.5*	25 June	0.860 ± 0.03*	247.0 ± 8.5
MB7	2011	42.9 ± 0.9*	12 June	57.6 ± 2.0*	27 June	0.820 ± 0.04*	227.2 ± 9.4
MB7	2012	39.3 ± 0.3	9 June	49.5 ± 0.7	19 June	0.951 ± 0.01	263.0 ± 3.8
MB7	2013	40.2 ± 0.3*	10 June	48.7 ± 0.7*	18 June	0.964 ± 0.01	255.3 ±4.3
MB4	Average	38.0 ± 0.3*	8 June	48.2 ± 0.5*	18 June	0.962 ± 0.01	217.9 ± 3.2
MB7	Average	41.8 ± 0.8*	11 June	52.3 ± 1.6*	22 June	0.912 ± 0.03	244.5 ± 10.5
UBN	2003	38.8 ± 3.9	8 June	52.0 ± 13.2	22 June	0.907 ± 0.09	301.3 ± 68.7
UBN	2004	39.0 ± 4.0	9 June	52.0 ± 7.7	22 June	0.905 ± 0.09	301.4 ± 66.4
UBN	2005	37.4 ± 0.8	7 June	50.8 ± 2.2	20 June	0.928 ± 0.03	300.0 ± 8.6
UBN	2007	39.0 ± 4.8	9 June	52.1 ± 8.5	22 June	0.905 ± 0.09	301.2 ± 55.8
UBN	2008	39.0 ± 3.9	9 June	52.3 ± 10.6	22 June	0.904 ± 0.10	302.4 ± 79.3
UBN	2009	37.5 ± 1.0	7 June	48.1 ± 2.7	18 June	0.958 ± 0.03	284.1 ± 10.9
UBN	2010	39.5 ± 1.0	9 June	51.1 ± 3.1	21 June	0.925 ± 0.04	269.8 ± 11.9
UBN	2011	39.0 ± 0.6	9 June	51.6 ± 1.7	21 June	0.919 ± 0.02*	298.7 ± 7.9
UBN	2012	40.1 ± 1.2*	10 June	54.8 ± 2.5*	24 June	0.870 ± 0.04*	332.0 ± 16.2
UBN	2013	38.8 ± 3.8	8 June	52.4 ± 16.1	22 June	0.906 ± 0.08	302.3 ± 61.4
UBS	2003	37.4 ± 0.5	7 June	46.6 ± 0.9	16 June	0.976 ± 0.01	299.6 ± 6.7
UBS	2004	38.1 ± 0.3	8 June	48.5 ± 0.8	18 June	0.958 ± 0.01	244.7 ± 3.4
UBS	2005	38.9 ± 0.4	8 June	47.9 ± 0.9	17 June	0.968 ± 0.01	263.0 ± 6.5
UBS	2007	38.8 ± 0.3	8 June	47.9 ± 0.6	17 June	0.970 ± 0.01	302.2 ± 3.8
UBS	2008	38.1 ± 0.4	8 June	47.1 ± 0.8	17 June	0.973 ± 0.01	312.1 ± 5.9
UBS	2009	38.5 ± 0.4	8 June	47.1 ±0.8	17 June	0.976 ± 0.01	306.0 ± 6.1
UBS	2010	38.5 ± 0.3	8 June	48.0 ± 0.8	18 June	0.966 ± 0.01	293.8 ± 4.7
UBS	2011	39.0 ± 0.3	9 June	47.8 ± 0.6	17 June	0.970 ± 0.01*	321.9 ± 4.9
UBS	2012	38.0 ± 0.2*	8 June	47.2 ±0.5*	17 June	0.972 ± 0.01*	270.0 ± 3.2
UBS	2013	37.7 ± 0.3	7 June	46.6 ± 0.6	16 June	0.977 ± 0.01	266.7 ± 3.7
UBN	Average	38.8 ± 1.4	8 June	51.2 ± 2.9	21 June	0.923 ± 0.04	299.3 ± 38.7
UBS	Average	38.3 ± 0.3	8 June	47.5 ± 0.5	17 June	0.971 ± 0.004	288.0 ± 4.9
Marmot Island	Average	39.9 ± 0.4	9 June	50.3 ± 0.9	20 June	0.936 ± 0.01	−
Ugamak Island	Average	38.6 ± 0.7	8 June	49.3 ± 1.5	19 June	0.947 ± 0.02	−

significantly later at MB7 than MB4 in 6 years with the largest differences occurring in 2010 (5.1 ± 0.8 d later; Table 1). On Ugamak Island, the only annual difference in MPD between beaches occurred in 2012 when female sea lions pupped significantly later at UBN (3.0 d, CI 0.7 to 5.3 d; Table 1). When beaches were averaged, MPD on Marmot Island was not different from the historical data (1979 to 1998: 9 June) (Pitcher et al. 2001). However, on Ugamak Island, MPD was 2.5 d earlier than historical data (1977 to 1999: 11 June; CI −4.1 to −0.8 d) (Pitcher et al. 2001).

Pupping season and aerial survey schedule

In all years, 90% of the pups were born by Day 49.8 ± 1.2 (19 June). This date was not significantly different between islands (Table 1; difference 0.9 d, CI −2.3 to 4.1 d) or between beaches on Ugamak Island (Table 1; difference 3.8 d, CI −1.6 to 9.2 d). The date of 90% pupping was significantly later at MB7 than at MB4 (Table 1; difference −4.1 d, CI −7.4 to −0.8 d), which is a reflection of the differences in MPD at these beaches. On Ugamak Island, annual estimates of the 90% pupping date differed only in 2012, the year when MPD at UBN was also later (Table 1).

Prior to the planned start of the aerial survey (23 June), the proportion of pups born at both islands was 0.942 ± 0.02, and this did not vary between island (Table 1; difference −0.01, CI −0.06 to 0.04). When beaches were considered separately, the proportion of pups born prior to the survey did not differ (Marmot difference 0.05, CI −0.003 to 0.10; Ugamak difference −0.05, CI: −0.12 to 0.02). For both islands, the proportion of pups born prior to the start of the survey ranged from 0.89 ± 0.02 (Marmot 2010) to 0.97 ± 0.005 (Marmot 2013) among years.

DISCUSSION

By conducting extensive observational research over a 10 yr period, data collected during this study were used to examine the timing of reproduction in a pinniped species that breeds in remote, hard-to-access locations. The land-based counts of pups born at Marmot and Ugamak islands should be considered an index of pup production at these locations and not a census of total pup production (Merrick et al. 1988, Chumbley et al. 1997, Kirkwood et al. 2005). Factors that impact the visibility (e.g. fog, rain, heat haze) and the ability to sight pups (e.g. observation height,

topography) vary significantly at each beach (Merrick et al. 1988, Chumbley et al. 1997), which likely explains the differing ratios of complete to partial counts (Table A1). Nevertheless, for this study it was not necessary to get complete counts of the pups born at each beach, only consistent counts of pups within the sampled regions to detect changes in pup numbers over the reproductive period.

Overall, we found that MPD did not differ between islands during the study period; however, there was some interannual variability. During 3 consecutive years of this study (2009 to 2011), sea lions at Marmot Island showed a pattern of slightly later pupping by 1.4 ± 0.7 d to 2.6 ± 0.6 d (95% CI: 1.4 to 3.8, 0.09 to 2.8 and 0.2 to 2.5 in 2009, 2010 and 2011 respectively). Breeding synchrony is the general pattern for many pinnipeds, though for species with wide-spread distributions, geographic or latitudinal variation has been found in the timing of reproduction (Boyd 1991, Wickens & York 1997). Marmot and Ugamak islands are near the center of the Steller sea lions large geographic range and are separated by less than 1000 km (Fig. 1), making geographic or latitudinal variation in MPD unlikely. Historically, a difference in MPD was not found between Marmot and Ugamak islands (Pitcher et al. 2001). The cause of the interannual variation between islands in this study is unknown; however, for many pinniped species, including Antarctic fur seals *Arctocephalus gazella* and South American sea lions, a strong relationship has been found between annual pupping date and prey availability (Boyd 1996, Soto et al. 2004).

In contrast to the inter-island comparisons for MPD, when all years were combined there was a significant difference between beaches for MPD on Marmot Island. This difference was greater than 3 d, yet no difference was found between beaches on Ugamak Island. A similar pattern of later pupping by sea lions at MB7 was also described by Chumbley et al. (1997), but statistical comparisons were not made. At such a small geographic scale (<5 km), it is unlikely that the later pupping date on MB7 could result from dissimilarities in prey availability. However, other factors that may influence pupping beach selection could play a role in the variation in pupping dates. For some pinniped species, older or prime-aged females give birth earlier in the season than younger females (Lunn & Boyd 1993, Gentry 1998, Boltnev & York 2001, Maniscalco et al. 2006, Hastings & Jemison 2015). This was reported for Steller sea lions that breed on Chiswell Island, Alaska, and the Forrester Island Complex, Alaska (Maniscalco et al. 2006, Hastings & Jemison 2015). For Antarctic fur seals it

was suggested that, by returning earlier, older females could select the most suitable pupping sites (Lunn & Boyd 1993). If beach MB4 on Marmot Island is the most suitable site for pupping, it could potentially be occupied first by prime-aged females, leaving MB7 for young sea lions that pup at a later date.

Movements of mother–pup pairs between beaches could also impact our calculation of MPD leading to differences between beaches at Marmot Island. Steller sea lion pups can enter the water as early as 2 wk of age and disperse from a breeding beach with their mothers at 2 mo of age (Sandegren 1970, Merrick et al. 1988, Raum-Suryan et al. 2004). On Marmot Island, observations of permanently marked sea lions suggest that as the reproductive season progresses some sea lions move from MB4 to MB7 (Chumbley et al. 1997, Marine Mammal Laboratory unpubl. data). In addition, Chumbley et al. (1997) described movement of mother–pup pairs away from MB4 starting in mid-July and, in 1991, a late season survey (July 31) found that MB4 was almost completely abandoned, whereas MB7 counts remained unchanged (Chumbley et al. 1997). If female sea lions from MB4 or other beaches moved their pup to MB7 during the count period, this would result in an increase in daily pup counts unrelated to births at that beach, which would push the estimated MPD later. Similar small-scale movements by mother-pup sea lions pairs during the breeding season have been described for Steller sea lions at the Forrester Island Complex, Alaska (Hastings & Jemison 2015).

Based on comparisons with historical data (1977 to 1999), it appears that there has been no change for MPD at Marmot Island but a potential shift to earlier pupping at Ugamak Island, i.e. 3 d earlier than recorded by Pitcher et al. (2001). Unfortunately, only 3 yr of data were available for comparison from Ugamak Island (Pitcher et al. 2001). Given the interannual variability in MPD at Ugamak Island, which ranged over 1.5 d between 2003 and 2013, it is difficult to discern if there has been an actual shift in mean pupping over time or if our results are an artifact of the small historical sample size (3 yr) used for comparison. If a change in pupping date has occurred, with sea lions on Ugamak Island pupping earlier, it is important to consider whether this small shift is biologically important. The pupping season for Steller sea lions generally occurs over a 2 mo period (mid-May through mid-July) (Calkins & Pitcher 1982, Merrick et al. 1988) and Merrick et al. (1988) estimated that at least 90% of pups are born by the last week of June. This pattern is reflected in our data as pups were counted on the earliest obser-

vation date (24 May 2013), and in all cases the date by which 90% of the pups were born occurred prior to the end of June (i.e. Day 60, Table 1). Therefore, although variability may exist in MPD between beaches, occasionally between islands, and even between our study and historical MPDs, there does not appear to be a significant shift in the overall pupping season for Steller sea lions at these 2 islands.

The existing variability we found in MPD, both temporal and spatial, could have an influence on estimates of population trends determined via aerial surveys (Calkins & Pitcher 1982, Fritz et al. 2008, 2013). However, when all beaches were combined, 94% of pups were born prior to the survey start (23 June) and this did not differ between islands or beaches within an island. Based on the beach maximum count estimates (asymptote values, Table 1), this results in the potential for on average only 13 to 18 pups to be born at each beach after the survey starts. In addition, the survey takes several weeks to complete, which would result in an even higher proportion of pups born as the survey progresses (Fritz et al. 2008, 2016). Because the aerial surveys are scheduled to balance the trade-off between waiting for pups to be born and the increase in time pups spend in the water as they age, our results suggest that aerial surveys are still suitably timed to ensure the majority of pups are born when surveys are conducted.

CONCLUSIONS AND CONSERVATION IMPLICATIONS

Monitoring changes in the timing of reproduction is critical for population assessment and management of Steller sea lion stocks. We found that MPD is consistent between the 2 study islands, with some interannual variability. In addition, there may have been a slight shift to an earlier MPD from historical data at Ugamak Island but this is based on only 3 historical years for comparison. As a result, the current timing of the aerial survey is suitable to monitor changes in Steller sea lion pup production in these regions. It may be necessary to examine the timing of Steller sea lion births in other parts of Alaska (e.g. Central and Western Aleutian islands) to ensure that aerial surveys are properly timed in these regions. However, given that Pitcher et al. (2001) also reported a MPD of 9 June on Medny Island (Commander Islands, Russia), we do not expect the timing of births in the rest of the Aleutian Islands between Ugamak and Medny islands to be significantly different.

The counts of Steller sea lions obtained during aerial surveys are considered a vital part of the continuing research guided by the Steller sea lion recovery plan (NMFS 2008). In addition, the recovery plan calls for focused research on sea lion population growth and reproduction to assess the relative impacts of threats to Steller sea lion population recovery (NMFS 2008). By identifying population level, multi-year patterns in MPD, researchers can now start to examine factors related to interannual and individual variation in this vital rate, such as impacts of environmental change, prey availability, maternal age, and reproductive history (e.g. Lunn et al. 1994, Bowen et al. 2003, Soto et al. 2004). An understanding of these relationships may help reduce the 'substantial uncertainty' that affects the ability to understand population-level threats responsible for the lack of recovery and, in some cases, continued regional declines within this population (NMFS 2008).

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APPENDIX

Table A1. Field season length and pup count effort on Marmot and Ugamak islands (Alaska, USA) between 2003 and 2013. Pup count days are the total number of days per season that at least 1 pup count was conducted. Different beaches divided by slashes, i.e. Marmot Island: Beach 4 [MB4]/Beach 7 [MB7]; Ugamak Island: Beach N [UBN]/Beach S [UBS]. Counts used for model are the filtered daily counts and only include counts prior to 4 July (Day 64) for all beaches, except UBN in all years (9 July, Day 69) and MB4 in 2004 (8 July, Day 68). The proportion of complete counts indicates the ratio of counts listed as complete counts or complete partial counts (at UBN) in relation to partial counts. NA: beaches with insufficient data to model or poor model fits due to time gaps or late starts

Island	Year	Start date (mm.dd)	End date (mm.dd)	Pup count days	Counts used for model	Proportion complete counts
Marmot	2003	05.29	07.31	53/18	35/NA	0.77/NA
	2004	05.28	07.28	51/9	31/NA	0.74/NA
	2005	06.06	07.27	49/34	26/NA	0.65/NA
	2007	05.27	08.01	55/45	32/25	0.78/0.36
	2008	05.29	07.27	46/41	27/27	0.15/1.0
	2009	05.28	07.26	51/37	33/24	0.52/0.54
	2010	05.28	07.28	58/39	36/25	0.31/0.28
	2011	05.26	07.25	52/48	31/26	0.26/0.73
	2012	05.25	07.25	57/42	37/29	0.49/0.52
	2013	05.24	07.24	52/39	35/22	0.51/0.41
Ugamak	2003	06.04	07.26	11/41	NA/21	NA/1.0
	2004	05.29	07.29	23/56	NA/30	NA/1.0
	2005	06.02	07.29	20/55	12/25	0/0.96
	2007	05.29	07.27	9/57	NA/35	NA/0.86
	2008	06.02	07.31	9/57	NA/31	NA/0.10
	2009	06.04	07.30	19/49	11/24	0.09/0.58
	2010	06.01	07.31	30/62	19/31	0/0.03
	2011	06.02	08.01	32/56	21/30	0.95/0.10
	2012	05.28	07.31	43/65	30/37	1.0/1.0
	2013	05.28	07.31	23/64	NA/35	NA/1.0