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**Evidence for high natality rates among  
Steller sea lions in the Gulf of Alaska**

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# Evidence for high natality rates among Steller sea lions in the Gulf of Alaska

John M. Maniscalco, Daniel Hennen, and Pamela Parker

## **Abstract**

Steller sea lions have experienced a drastic population decline of more than 80% during the past 30 years throughout their western range. It is now widely believed that reduced female reproductive (natality) rates have contributed to those declines and are a continuing problem in the Gulf of Alaska that may be limiting their recovery, despite the fact that there have been very few attempts to directly measure natality in this species. We conducted a longitudinal study of natality among individual Steller sea lions at a rookery in the northern Gulf of Alaska. Birthing status of 185 females was recorded for up to 8 years. The annual natality rate for females that were known to be reproductively mature ( $n = 110$ ) averaged 73.8% (range: 60.6 – 83.5%) over the years 2003 – 2008. Females that were tracked for  $\geq 6$  years ( $n = 26$ ) gave birth in four out of every five years (80% natality) on average. These figures exceed estimated natality for Steller sea lions in the Gulf of Alaska prior to their decline and contradict recently published estimates based on census counts of females and pups that suggest current natality is 36% lower than in the 1970s. We present information on neonatal pup mortality and daytime female sightability to illustrate how models based on census counts and untested assumptions could misrepresent estimates of natality.

## **Introduction**

Between the early 1970s and 2000, the western distinct population segment (WDPS) of Steller sea lions (*Eumetopias jubatus*) declined by more than 80% (Sease et al. 2001) and was listed as endangered in 1997. Reduced rates of reproduction (natality) in females (Calkins and Goodwin 1988; Pitcher et al. 1998) and low juvenile survival (Holmes and York 2003; York 1994) are believed to be the proximate reasons for the population decline from the 1970s through 1980s. Since 2000, some parts of the WDPS have experienced modest increases (Eberhardt et al. 2005; Fritz et al. 2008). Statistical models based on census counts of Steller sea lions indicate that recent population increases are related to improved juvenile and adult survivorship, but that natality rates have continued to deteriorate during the 1990s and 2000s (Holmes and York 2003; Holmes et al. 2007). Natality rates in the Central Gulf of Alaska were estimated to be 67% during the 1970s, 55% in the 1980s (Pitcher et al. 1998), and 43% in the 2000s (Holmes et al. 2007).

Methodologies for determining natality rates among female Steller sea lions have changed considerably since the 1970s, making strict comparisons between time periods tenuous even with complex models (e.g., Holmes et al. 2007). Early studies of natality were conducted by collecting mature females during early and late gestation and determining the proportion that were pregnant (Calkins and Pitcher 1982; Calkins and Goodwin 1988). Sources of error in natality rate calculations using those methods would have included variation in the status of different females that were collected early and late, variation in abortion rates during the last month of gestation after late collections occurred, and potential violation of the assumption of random sample collection (e.g., bias towards collecting younger, more naïve, or bigger, more easily observed animals). Now that collection of endangered Steller sea lions is no longer acceptable or permissible, census counts of non-pups and pups, and estimates of the proportions of non-pups that are adults and juveniles, provide the primary data for determining natality rates in the WDPS (Fritz et al. 2008; Holmes and York 2003; Holmes et al. 2007).

Those data, however, may not be appropriate for an accurate assessment of natality when compared with earlier studies because they contain different sources of error. Those sources include variations in the proportion of animals hauled out during a

census, the proportion of pups that have died and/or washed away prior to a census, the number of pups that have not yet been born, and determination of which animals are reproductively mature. The effects of each of these sources of error might be mitigated by surveying many rookeries and haulouts over a broad area, but it is more probable that changes that occurred over time introduced a systematic bias over an entire region. For example, shifting oceanic regimes caused large-scale changes in prey abundance (Anderson and Piatt 1999) that likely affected foraging trip durations (e.g., Boyd 1999; Hood and Ono 1997), resulting in changes of vital rates based on censuses of adult females that were unreal across the affected region because animals are not counted when out at sea. Similarly, changes in oceanic storm activity during different regimes (Benson and Trites 2002) can cause variation in the number of neonatal pups washed out to sea (Maniscalco et al. 2008) and thereby affect apparent natality rates based on census counts alone. Therefore, it may not be possible to accurately determine changes in pinniped vital rates based on census data without a complete understanding of how environmental factors affect sightability of different age-classes throughout a region over extended periods.

A more accurate way to determine natality and survival rates in most animals is through longitudinal studies of known-age individuals (Clutton-Brock 1988). Such methodology will be more comparable with earlier studies of Steller sea lion natality that were based on actual observation of reproductive status (Calkins and Pitcher 1982; Calkins and Goodwin 1988) as opposed to “snap-shot,” cross-sectional data on estimated age-class composition that unrealistically assumes no long-term variation in female sightability and neonatal mortality. However, estimates based on the relatively small and more localized samples that typify longitudinal studies may not necessarily be extrapolated to a larger population.

In this study, we examined natality in Steller sea lions for up to 8 years using a mark-recapture study design at a small rookery within the WDPS. The results presented here are compared to recently published estimates of natality within the WDPS based on modeling of census counts (Holmes et al. 2007). We present evidence that Holmes et al. (2007) are underestimating natality in the Gulf of Alaska.

## Methods

### *Study site and observational methods*

This study was conducted using remotely-operated video cameras at the Steller sea lion rookery on Chiswell Island. The rookery is within the endangered WDPS and considered part of the eastern Gulf of Alaska population; although it is closely bordered by the central Gulf population (Figure 1). It is a relatively small (*ca.* 90 breeding animals) rookery but the pattern and magnitude of population decline there were similar to other rookeries in the central Gulf of Alaska—that is, abundance fell by more than 70% between the mid-1970s and mid-1990s and has remained comparatively stable since (Fritz et al. 2008). We used up to six remotely operated video cameras that were viewable and controllable in real-time from the Alaska SeaLife Center 65 km away and provided complete spatial coverage of the rookery. Additional details about the Chiswell Island rookery and remote video equipment can be found in Maniscalco et al. (2006).

Many adult Steller sea lions can be individually identified by unique scars, fungal patches, and/or flipper patterns and longitudinal studies have been successfully conducted on animals identified by such means (Kaplan et al. 2008; Maniscalco et al. 2006; Milette and Trites 2003). During the course of this study at Chiswell Island, female sea lions with unique markings were tracked and digital photos of those animals and their distinguishing marks were taken on a regular basis. A few breeding females were identified by flipper tags ( $n = 4$ ) or brand ( $n = 1$ ) and age was known only for those animals. Females that did not have at least two distinguishing marks and could not be reliably resighted from one year to the next were not used in analyses of natality rates. Although pictures and data for some females were collected as early as 1999, we did not consider the years 1999-2002 in the specific analysis of natality rates because of a potential bias for identifying females that gave birth over those that did not in those years. However, we do present data for some females dating back to 1999 to illustrate long-term reproductive patterns among individuals. All females with unique markings were non-preferentially (whether or not they gave birth) identified from 2003 onward. Pictures, descriptions, and resighting information for each individual were entered into a MS Access database.

Observations each year began with the arrival of the first female on the rookery in mid- to late-May and included full census counts of all sea lions by age-class on the rookery throughout the breeding season. Counts were made at approximately 1100 h and 1900 h, and hour-long scan sampling for identifiable females and their pups was done four to ten times daily from 0600 h to 2200 h; earlier and later hours were added around the summer solstice when light levels were sufficient for viewing sea lions. After 10 August, observations were recorded from approximately sunrise to sunset as diminishing daylight allowed. Events such as births and mortality-related incidents were opportunistically recorded as they occurred or within  $\pm 4$  hr of their known occurrence (Maniscalco et al. 2008). Births that happened overnight were recorded the following morning as having occurred at the half-way point of non-observation hours.

Steller sea lion mothers in the WDPS will normally remain with their newborn pups for eight to twelve days following parturition (Maniscalco et al. 2006; Merrick 1987; Milette and Trites 2003). Given the duration and detail (frequent scans and complete spatial coverage) of our rookery observations, it is unlikely that an identified female was miscategorized as with or without pup even though the actual birth may not have been observed. Identified females were considered for this analysis if they were present on the Chiswell Island rookery during the pupping and breeding season from 15 June until 15 July. Females that gave birth earlier still had a definitive presence on the rookery during that time. That time period also included females that were present to copulate and hence had a presumed intention to breed at this rookery but excluded some females that hauled out briefly on Chiswell Island before leaving to potentially pup elsewhere. Females that gave birth to a pup whether or not it was stillborn were considered productive because of the energetic investment it takes to bring a developing fetus to term and to make our data more comparable with earlier natality studies based on late-term pregnancies (Calkins and Pitcher 1982; Calkins and Goodwin 1988). Fewer than 2% of pups born at Chiswell Island were stillborn (Maniscalco et al. 2008).

#### *Analysis (Chiswell Island natality rates)*

Our method of identifying animals using natural markings may introduce a bias towards those that have higher fitness than average. This is because it takes an

unspecified amount of time (except in rare cases) for observers to locate and record identifying characteristics. Therefore, animals that are seen more often have a better chance of being identified and later recognized. Animals that are seen more often tend to be the ones participating in breeding and tend to survive from one observing period to the next. In order to account for this possible bias towards the more successful members of the population, we employed a correction factor as follows:

$$Bt_i = \frac{Bo_i}{\left(\frac{A_i}{p_i} - Be_i\right)} \quad (1)$$

where  $Bt_i$  is the true natality rate for all breeding age females that “belong” to the Chiswell population in year  $i$ ;  $Bo_i$  is the number of observed births to identified females in year  $i$ ;  $A_i$  is the total number of identified and observed adult females in year  $i$ ;  $p_i$  is the resight probability calculated as the ratio of  $A_i / (A_i + \text{identified females not seen in the sampling interval but that were seen in a later season or year, indicating that they were alive but not present in the breeding season in year } i)$ ; and  $Be_i$  is the number of identified females who “belong” to the Chiswell population but gave birth elsewhere in year  $i$  (tracked by later observation of that animal with a pup, or a yearling – indicating an unobserved birth in the previous year at a different rookery). Equation 1 has three assumptions: 1) All births to identified females were observed. 2) If an identified female was alive in a particular year, she was either observed in that year, or in a later year. Otherwise, she died or permanently emigrated. 3) Any identified female that was absent during the breeding season of a particular year and seen later, but did not have a pup or yearling, did not pup in the year in question. Confidence intervals for both estimates were based on confidence intervals around the resight probability,  $p_i$ , calculated as in Zar (1999; confidence limits for binomial parameters).

If females did not produce a pup in their first year or more of being sighted on Chiswell because they were reproductively immature, it would negatively bias natality rate estimates. Tracking females only from their year of first birth, however, would introduce a positive bias into natality rate estimates because it is possible that some mature animals did not give birth in the first year they were identified on Chiswell Island.

Therefore, we performed a second analysis excluding females that were never observed to give birth and also removing each female's first birth.

It might also be assumed that by examining only the Chiswell rookery, we were excluding females at haulouts that were not giving birth. However, that was not the case because a large proportion of the animals in the Chiswell population that were not giving birth on Chiswell Island in any given year were spending the summer elsewhere, presumably at haulouts. Those animals, when not observed with an offspring in a subsequent year or season were included in the natality estimates and assumed to have not given birth during the summer they were away from Chiswell Island. We considered this to be a conservative approach to our natality estimates because a small proportion of females will give birth at haulouts (Withrow 1982, ASLC unpublished data).

*Analysis (a reexamination of published estimates of natality)*

We reexamined recently published data for field estimates of natality rates during the current decade (Holmes et al. 2007) with corrections for pup mortality and daytime female sightability based on our observations. Since studies of natality prior to and during the decline of Steller sea lions were undertaken by collecting mature females during early and late pregnancy (Calkins and Pitcher 1982; Calkins and Goodwin 1988), any post-natal mortality would not have yet occurred. Holmes et al. (2007) applied a survival correction to their life history matrices for their modeling effort of 0.949 to account for neonatal mortality (it is unclear if that correction was applied to their field estimates of natality). That correction factor was based on counts of live and dead pups found on rookeries in the 1970s. However, the leading cause of mortality in young pups results from being washed away in high surf conditions (Kaplan et al. 2008; Maniscalco et al. 2008). Thus, counting dead pups on rookeries likely underestimates actual mortality to varying degrees depending on differences in storminess between years. To be directly comparable with earlier work on natality rates, studies based on ratios of adults and pups at three to four weeks after peak pupping must also account for pups that have been washed out to sea.

In addition, Steller sea lions normally forage at night (Gentry 1970; Withrow 1982); so during daylight hours, when census counts occur, sightability should be greater

than what has been reported in Alaskan field studies as average presence over 24 hr periods (Brandon 2000; Maniscalco et al. 2006; Merrick and Loughlin 1997; Milette and Trites 2003). To properly account for the presence of females during daytime, we calculated a sightability ratio from presence/absence records of individual females between 1000 h and 1800 h during the last week in June across years at Chiswell Island. Pup mortality and female sightability estimates based on our observations were used to correct estimates of natality based on field counts of pups and mature females hauled out on rookeries and haulouts using the following equation modified slightly from Holmes et al. (2007):

$$R_t = \frac{\frac{P}{P_{sr}}}{\left(\frac{AF_h}{AF_{hs}}\right) + \left(\frac{AF_r}{AF_{rs}}\right)} \quad (2)$$

where  $R_t$  is the natality rate based on census counts of age and sex classes;  $P$  is the June pup count;  $P_{sr}$  is the average survival rate to three weeks of age (not explicitly included in the Holmes et al. field estimates of natality);  $AF_h$  and  $AF_r$  are adult female count at haulouts and rookeries respectively; and  $AF_{hs}$  and  $AF_{rs}$  are adult female daytime sightability at haulouts and rookeries (in the Holmes et al. study, sightability was calculated based on a 24 h period).

## Results

A total of 185 female Steller sea lions observed during one or more pupping/breeding seasons on Chiswell Island met our criteria for being individually identifiable between 2003 and 2008 (annual mean =  $80.8 \pm 11.3$  SD; Appendix 1). Correcting for resight probability resulted in an average annual natality rate of 0.598 (Table 1a). When first births were removed to account for females that may have been immature, estimates of natality increased to 0.738 ( $n = 110$ ; Table 1b).

Five females of known age had a mean age of first pupping at 5.4 yr (range: 4 – 6 yr; Appendix 1). Those females had an average natality rate of 0.853 or 0.920 (dependant upon the status of female 4 in 2008 which was unknown) over their first three

to five years of pupping. Similarly, females whose history was known for  $\geq 6$  yr since 1999 ( $n = 26$ ) had a high average natality rate of 0.798; i.e., they gave birth in four out of every five years (Table 2). When a pup was not born, a female often continued to nurse a juvenile throughout at least the summer months (20 of 35; Table 2) and, in some cases, through multiple years.

From 2004 through 2007 we recorded presence and absence of 38 to 57 (mean = 45) lactating females from 24 June through 30 June at Chiswell Island (5854 total records). Sightability during the daytime (1000 h to 1800 h) ranged from 0.795 to 0.976 (mean = 0.878) during those years. We used those estimates of daytime sightability for females at rookeries, kept daytime sightability of females at haulouts similar to that used by Holmes et al. (2007; 40%), and used 0.896 pup survival to 3 weeks of age (Maniscalco et al. 2008) to adjust field estimates of natality based on adult female counts in 2004 and pup counts in 2005 as reported in Holmes et al. (2007). These figures resulted in an estimated natality rate of 0.562 (range 0.531 – 0.597).

## **Discussion**

We initially calculated natality rates by including all recognizable females that had a presence on Chiswell Island during the pupping/breeding season. This calculation resulted in natality rates of 60% when resight probabilities were accounted for (eq. 1). This estimate is substantially higher than predicted for the broader Gulf of Alaska in the current decade (*ca.* 43%; Holmes et al. 2007) but still less than observed in Steller sea lions prior to the decline. Our initially calculated rate did not, however, account for females that may have been reproductively immature.

Female Steller sea lions reach sexual maturity with their first ovulation at an average age of 4.6 yr (Pitcher and Calkins 1981) and nearly all mature Steller sea lion females become pregnant in any given year (Pitcher et al. 1998). At Chiswell, known-age females ( $n = 5$ ) produced their first pups at an average age of 5.4 yr indicating they were ovulating at 4.4 yr, although we cannot necessarily assume that was their first ovulation. Two of the known-age females were observed on Chiswell during the breeding season the year preceding their first birth. Those females were considered mature during that year even though they may have been pre-reproductive. In any given

year an unknown fraction of the observed adult animals are pre-reproductive and therefore should not be counted as adults for the purpose of assessing natality rates. Including those animals would tend to bias the observed natality rate downwards. To account for this bias we removed all the instances of each female being observed through the year in which its first observed birth took place. Doing this increased our estimated natality rate to 74% (Table 1b), indicating that our dataset included several pre-reproductive animals. This rate is higher than estimated pre-decline levels but may still be conservative because of the possible inclusion of older, post-reproductive animals. There is some evidence that Steller sea lions become reproductively senescent at more than 20 years of age (Pitcher and Calkins 1981) and previously calculated reproductive rates for the 1970s did not include elderly, non-pregnant females because of potential biases (Pitcher et al. 1998). Female 21 (Appendix 1, Table 2) is one example of an individual that may be post-reproductive since she had not given birth in the six most recent years of this study. Future studies of known-age individuals should help to clarify the extent of senescence in this species.

The five females of known-age in our study were young (4 – 8 yr old) but had natality rates exceeding 85%, much higher than the greater Chiswell Island population combined. Those rates could potentially increase further since female Steller sea lions may reach peak fecundity at 11 to 16 years of age (Holmes et al. 2007, Appendix C). The natality rates of 26 identifiable Chiswell Island females tracked for  $\geq 6$  yr were also more than 5% lower than the five young females, providing suggestive evidence that natality is reduced by older, senescent or nearly senescent animals at this location. The upper potential for natality in Steller sea lions might be close to 85% but this small subset of data could be biased by the selective inclusion of young females that spent more time on the rookery compared to those that spent more time at haulouts.

We have no reason to suspect the natality rates of sea lions at Chiswell Island are unusually high compared to sea lions elsewhere in the Gulf of Alaska. Measurements of maternal care at Chiswell have been excellent, suggesting that sufficient food resources are readily available (Maniscalco et al. 2006) and are similar to measures at other rookeries in the central Gulf of Alaska (Brandon 2000; Milette and Trites 2003). The Chiswell rookery is relatively small and un-crowded which could limit competition for

food and/or suitable pupping space (Parker et al. 2008), yet the degree of crowding at neighboring rookeries should also be reduced as most sea lion rookeries in the WDPS have experienced the same dramatic population decline. There was also a highly unusual case of twins born in 2007 (Female 70, Appendix 1; Maniscalco and Parker 2009) but the detail of our observations allows us to witness such extremely rare events that may go unnoticed at other locations.

Our reanalysis of the Holmes et al. (2007) field estimates based on adjustments for pup mortality and daytime female sightability increased the natality rate estimate from 43% to 56% in the 2000s. Still, this rate is much lower than our average rate estimates from longitudinal tracking of individual females and more similar to rates during the height of the decline (Pitcher et al. 1998). One explanation for this disparity is that natality in 2005, the year Holmes et al. (2007) used as a representative example for the late 1990s through 2004, was considerably below average among the general population of Steller sea lions at Chiswell Island (45%, Table 1a) as it may have been throughout the eastern and central Gulf of Alaska. We have not yet discovered any unusual environmental conditions in that year that could explain the low production we observed, although during winter 2005 at a local haulout, we observed five abortions (more than in any other year) and one pup that apparently starved to death. Aborting a developing fetus is thought to be a typical reproductive strategy for Steller sea lions during periods of low food availability (Pitcher et al. 1998). Interpreting abortion rates is problematic however, as observations of abortions were infrequent and opportunistic rather than systematic. Abortions can occur at any one of the haulouts we monitor, at a location we do not monitor, or potentially at sea, and may be attributable to transiting animals not part of the Chiswell population. Drawing inference on the relative frequency of observed abortions in different years is therefore probably not warranted and we mention it only as a potential contributor to lowered natality rates. It is also possible that recruitment into the breeding population was low in 2005 due to heavy killer whale predation on pups in 2000 and 2001 (Maniscalco et al. 2007). Regardless of the reason why 2005 was a poor year for natality, it should be clear that one year of pup counts is not necessarily representative of an entire decade.

In addition to the neonatal mortality and sighting biases discussed above, Holmes et al. (2007) used a size differential to remove juvenile animals from estimates of the number of females present on rookeries. The size cut off they employed (animals <50% of the length of the largest male in the photograph) was conservative with respect to misclassifying adults as juveniles, but therefore, was more likely to classify the largest juveniles as adult females. In each case, the techniques used in Holmes et al. (2007) would tend to produce lower estimates of natality.

There is little or no direct evidence of a biological mechanism that might continue driving natality rates lower since the late 1980s. Population losses during the 1980s may have been at least partially caused by nutritional stress (Rosen and Trites 2000; Donnelly et al. 2003; Trites and Donnelly 2003), although some researchers disagree (e.g., Springer et al. 2003; Fritz and Hinckley 2005; Atkinson et al. 2008). Nevertheless, it is plausible that decreased natality in the 1980s was caused by nutritional limitation during that period and may explain some of the population losses (Pitcher et al. 1998; Trites and Donnelly 2003). In more recent years, studies of juvenile health and maternal care provide no evidence of nutritional limitation in this species (DeMaster and Atkinson 2002; Maniscalco et al. 2006; Milette and Trites 2003; Rea et al. 1998). Disease, parasitism, and contaminants could adversely affect reproduction (Calkins and Goodwin 1988), but existing research has been unable to show significant trends over time or major problems in the current decade (e.g., Burek et al. 2005; Myers et al. 2008). Other explanations for population losses such as predation and fisheries related mortalities could play a major role in adult and juvenile survivability but probably have less of an effect on natality rates; although exposure to predation risk does increase levels of stress in female Steller sea lions (Mashburn and Atkinson 2007) and can decrease natality in some mammals (Creel et al. 2007).

The lack of a convincing mechanistic explanation for the purported decrease in natality should be weighed against the modeling exercise of Holmes et al. (2007) which shows a downward trend in natality through the mid-2000s. The model itself is logical, elegant, and the authors of the study were creative and thorough in using the existing population census data to provide insight into the difficult process of estimating natality in a remotely located wild pinniped population. The persuasiveness of the model results,

however, are weak without a proper accounting of neonatal mortality and daytime female sightability, and variability in those parameters between years and over longer intervals. There is currently little empirical evidence for long-term changes in neonatal mortality but a proper assessment of storm-wave intensity during the peak pupping period over the past 30 years may provide new insights (Maniscalco et al. 2008).

A logical hypothesis that may explain the *appearance* of long-term variation in natality based on age-class census counts is that female sightability in the Gulf of Alaska has changed systematically between oceanographic regimes in recent decades. For example, if critical prey availability was reduced during the 1980s (Anderson and Piatt 1999; Rosen and Trites 2000; Trites and Donnelly 2003), then females would spend more time foraging away from rookies (Boyd 1999; Hood and Ono 1997), lowering their sightability and thereby increasing the apparent natality rate (i.e., adult females spending more time foraging would reduce the number counted in an aerial census but the number of pups counted would be unaffected). As sea lion populations continued to decline and additional regime shift(s) occurred (Hare and Mantua 2000), food availability may have recovered, effectively reducing foraging durations and thus increasing sightability. The effect would be to cause a further decline in *apparent* natality rates based on ratios of adults and pups hauled out.

The aforementioned hypotheses explaining how declining natality rates between the mid-1980s and mid-2000s could be illusory do not specifically address why the Holmes et al. (2007) model matched the change in natality between the 1970s and 1980s observed by Pitcher et al. (1998). We posit that natality may have appeared higher earlier in the decline era due to reduced sightability of females. The results of Calkins and Goodwin (1988) do not superficially appear to support this hypothesis because the natality rates in that sample were lower than the natality rates seen in the sample collected in the 1970s (Calkins and Pitcher 1982). Collections of Steller sea lions in the 1980s however, were focused on mature females that were hauled out compared to collections in the 1970s that were often killed in the water with no preferential selection for age or sex (Calkins and Goodwin 1988). Therefore, biases were introduced that might have preferentially selected pregnant females in the 1980s, which suggests that overall natality was probably lower than the 55% estimated. This would also mean that

the Holmes et al. (2007) model overestimated natality during that period, which agrees (in terms of the downward trend in natality rates being illusory) with our hypothesis based on changing sightability of females.

The only field estimates of natality from the 1970s (Calkins and Pitcher 1982) and 1980s (Calkins and Goodwin 1988) were based on the direct examination of animals collected in the Gulf of Alaska. Those data are all that exists regarding sea lion age structure, natality and body condition in the western stock during the early part of the decline. The basis for the Holmes et al. (2007) model was an analysis by York (1994), who produced a life table that was *designed* to fit the data collected by Calkins and Pitcher (1982) and Calkins and Goodwin (1988). Holmes et al. (2007) modified the life table used by York (1994) slightly, by incorporating reproductive senescence and some additional age structure into the fecundity schedule. When the model results using the Holmes et al. (2007) life table are compared to the York (1994) life table, for the time period covering the sample collection in Calkins and Goodwin (1988), resulting estimates of natality differ by less than 1% (see Holmes et al. 2007, Appendix D). Holmes et al. (2007) have suggested that the agreement between their model results and these field estimates of natality lend support to their model. We argue, however, that these estimates are related and therefore, agreement between the Holmes et al. (2007) estimates of natality and the findings of Calkins and Goodwin (1988) should have been expected.

Knowledge of natality rates is crucial in any population projection, but we believe that natality rates for the current decade found in Holmes et al. (2007) are underestimated for the reasons discussed herein. We further believe that the assumption of static long-term sightability of females used by Holmes et al. (2007) is tenuous if changes in the ecosystem over this time are as important to the abundance of forage species as has been claimed. There is likely a complex suite of factors, more than identified here, that would affect apparent natality rates based on census counts in ways that are difficult to predict even with highly elaborate models. Taken together, these issues weaken the credibility of the conclusion that sea lion natality has been in prolonged decline for the past 30 years. Given the ecological and economic importance of management decisions regarding Steller sea lions, and the dynamic nature of natality with respect to time and space, we believe that additional long-term monitoring is critically important.

## **Conclusions**

We measured Steller sea lion natality rates among individual females at the Chiswell Island rookery in a number of different ways, and in each case we found rates to be higher than those indicated by the analysis of Holmes et al. (2007) in the 2000s. There is no reason to believe that the animals at Chiswell Island are more fecund than those at other rookeries in the eastern and central Gulf of Alaska. Our calculated rates are based primarily on direct, longitudinal observation of individual animals rather than model estimation based on cross-sectional snapshot counts of different age and sex classes and suspect assumptions. Observational examples from other rookeries are currently unavailable or unpublished. Holmes et al. (2007) state that their analysis of long-term declines in natality assumes static female sightability and neonatal mortality. We believe there may have been a systematic shift in female sightability between the 1980s and 2000s, and the potential for a systematic change in pup mortality due to storm-wave intensity during the month of June should also be investigated. Their system for estimating the fraction of juvenile animals at each rookery and haulout was conservative in that it was unlikely that an adult would be misclassified as a juvenile but therefore, more likely that some juveniles were misclassified as adults. The number of pups born on rookeries was probably also biased low because a low pup mortality rate was used and the method of counting pups (either through aerial photographs or ground counts) was far more likely to miss pups than to overestimate them. Finally, for the 2000s, the year used to estimate natality (2005) in the Central GOA was a very poor year for pup production at Chiswell Island, and it is possible that it was a poor year at the rookeries used in the Holmes et al. (2007) analysis as well. Each of these factors would tend to bias natality estimates downwards. Individually, these factors may have little effect on the results found in Holmes et al. (2007), but together they could be important. Tracking individual animals and their birthing status over a significant portion of their life is a more accurate means to assess natality than estimating age and sex classes from infrequent census counts. We suggest that more research on longitudinal estimates of vital rates is needed before specific regulatory or management decisions are made based on trends in Steller sea lion demographic parameters.

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## Tables and Figures

Table 1. Steller sea lion natality rates at Chiswell Island by year, and averaged over all years. Observed births are births that occurred from recognizable females. True natality rate is adjusted based on resight probability for each year. a) Natality rates based from first year presence on Chiswell Island regardless of birthing status. b) Natality rates based on first births of all females removed in order to adjust for females that may have been immature.

Year	2003	2004	2005	2006	2007	2008	Average
a)							
Observed births ( $Bo_i$ )	47	56	42	48	70	63	
Observed adults ( $A_i$ )	63	80	78	78	95	91	
Resight prob. ( $p_i$ )	0.926	0.889	0.823	0.842	0.883	0.858	
Births elsewhere ( $Be_i$ )	1	3	1	2	1	2	
True natality rate ( $Bt_i$ )	<b>0.701</b>	<b>0.644</b>	<b>0.448</b>	<b>0.530</b>	<b>0.657</b>	<b>0.606</b>	<b>0.598</b>
Lower C.I.	0.633	0.581	0.398	0.472	0.601	0.548	0.539
Upper C.I.	0.739	0.686	0.487	0.573	0.697	0.649	0.638
b)							
Observed births ( $Bo_i$ )	33	36	29	26	47	44	
Observed adults ( $A_i$ )	37	42	35	34	49	48	
Resight prob. ( $p_i$ )	0.894	0.889	0.778	0.793	0.855	0.816	
Births elsewhere ( $Be_i$ )	1	0	0	0	1	1	
True natality rate ( $Bt_i$ )	<b>0.817</b>	<b>0.762</b>	<b>0.644</b>	<b>0.606</b>	<b>0.835</b>	<b>0.761</b>	<b>0.738</b>
Lower C.I.	0.700	0.663	0.543	0.510	0.730	0.661	0.635
Upper C.I.	0.883	0.821	0.723	0.679	0.908	0.836	0.809

Table 2. – A detailed history of 26 Steller sea lion females whose status was known for  $\geq 6$  yr since 1999. P indicates a pup was born, P\* indicates the pup died within a few months of birth, N indicates no pup was born, and Y indicates a yearling or juvenile continued to nurse through at least the summer months. Natality rates in this table were calculated simply by dividing the number of pups that were born to each female by the number of years they were tracked. Female numbers correspond to same females listed in Appendix 1.

Female	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	Rate
6		P	P	P	P*	P	P	N/Y			0.857
21			N	P*	N	N	N	N	N	N	0.125
30			P	P*	P	P	P/Y	N/Y	P	P	0.875
31			P	P	P	P	N/Y	N/Y	N/Y	N/Y	0.500
37	P	P	P	N/Y	P*	P	P	P			0.875
44				P	P	P	N/Y	N/Y	P		0.667
50			P	P	P	P	P	P	P	P	1.000
55			P	P	P	N/Y	P*	P/Y	P*/Y	P	0.875
58			P*	P	P*	P	P	P	P	P	1.000
59				P*	P	N/Y	N/Y	N/Y	P	P	0.571
63				P	P	P	P	P	P	P	1.000
66			P	P	N/Y	P	P	P	P	P	0.875
79					P	N/Y	N/Y	P	P	P	0.667
81					P	P	P	P	P	P*	1.000
84			P*	P	P/Y	P	P	N/Y	P		0.857
86			P	P	P	P	P	P	P	N	0.875
108	P		P*	N	N	N	P	N/Y	P*		0.500
119				P	P*	P	N	P	P		0.833
123			P	P	P	P	N/Y	P	P	P	0.875
132				P	P	P	P*/Y	P	P	P	1.000
147					N	P	P	P	P	P	0.833
152			P	N	N	N	P	N/Y	N	P	0.375
161			P*	P	P*/Y	P	P	P	P	P	1.000
162			P	P	P/Y	P	P	P	P	P	1.000
169			P	P*	P	P	N	P	P	P	0.875
182					P	P	P	P	N/Y	P*	0.833
Average natality rate =											0.798

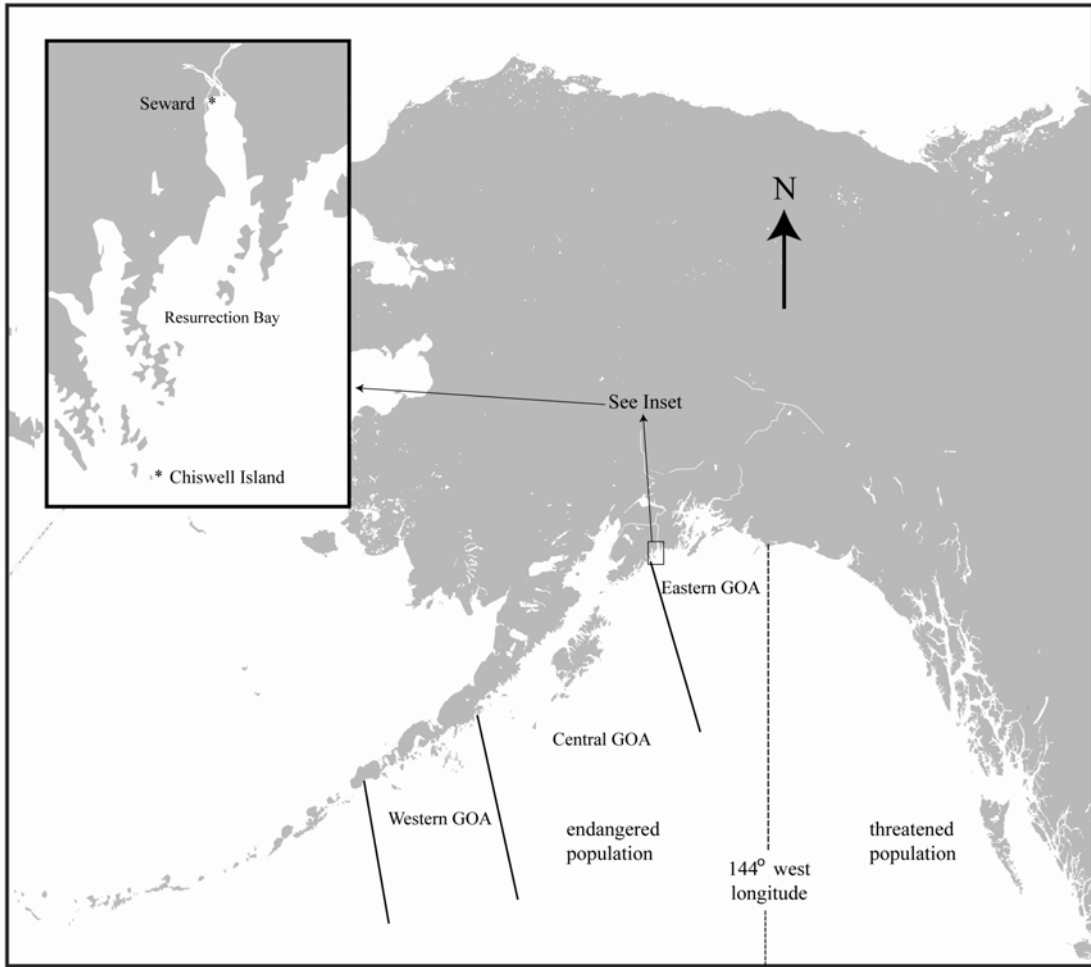


Figure 1. Location of Chiswell Island (inset) within the Eastern Gulf of Alaska (GOA) sub-population of endangered Steller sea lions.

Appendix 1. Birthing status of 185 Chiswell Island Steller sea lion females used in the analysis of natality rates (numbers assigned 1-185 for simplicity). 1 indicates that the female gave birth, 0 indicates she did not give birth but was observed on Chiswell during the pupping/breeding season, and the \* superscript indicates she was not on Chiswell Island during the breeding season but was observed later with or without a pup. Females 1 – 5 are of known age and believed to have a complete reproductive history to date; notwithstanding the status of #4 in 2008.

<b>Fem.#</b>	<b>2003</b>	<b>2004</b>	<b>2005</b>	<b>2006</b>	<b>2007</b>	<b>2008</b>	<b>Notes</b>
1				1	1	1	
2			0	1	1	1	
3		1	0	1	1	0*	
4			0	1	1		
5				1	1	1	
6	1	1	1	0			
7	1						
8						1	
9				1	0*	0*	
10	1	1	0*				
11	1*	0	0	0	0		
12					1	0	
13				0			
14					1		
15	1	1					
16				0	1	0*	
17						1	
18		1	1	1	1	1	
19		0					
20		1*	0				
21	0	0	0	0	0	0*	
22		1					
23		0	0*				
24	0						
25				1	1*		
26	0*	0*					gave birth on Chiswell in '01
27					0	1	
28			1				stillbirth in '05
29	1	1	0				
30	1	1	1	0*	1	1	
31	1	1	0*	0*	0*	0*	
32				0			
33	1	0					
34						1	
35	1						
36		0*	0*	1	1	1	
37	1	1	1	1			

Fem.#	2003	2004	2005	2006	2007	2008	Notes
38	1	1	1				
39	1	1					
40		1					
41				1			
42			0	1	1	1	
43					0	1	
44	1	1	0*	0*	1		
45	1						
46		1	1	0*	1		
47		1	1	1	0*	1	
48			1	1	1	1	
49					1	1	
50	1	1	1	1	1	1	
51				1*	1	0*	
52	0	0	0*				
53					1	1	
54			1*	0*	1	0	
55	1	0	1	1	1	1	
56						1	
57				1	1	0*	
58	1	1	1	1	1	1	
59	1	0*	0*	0*	1	1	
60						1	
61				0			
62					1		
63	1	1	1	1	1	1	
64	0	1	1				stillbirth in '04
65				0	1	1	
66	0	1	1	1	1	1	
67	1	1					
68			0	1*	0*	1*	
69		1	0*	0	1		
70			1	1	2		gave birth to twins in '07 <sup>1</sup>
71		0					
72		1					
73					1	1	
74		1	0*	0*			
75					1	0*	
76	1	0*	1				
77		0					
78					0*	1	
79	1	0*	0*	1	1	1	
80	0	1					
81	1	1	1	1	1	1	stillbirth in '08
82		0					
83		1*	0*	1	0		
84	1	1	1	0*	1		

Fem.#	2003	2004	2005	2006	2007	2008	Notes
85		0					
86	1	1	1	1	1	0	
87				1	1	1	
88		1					
89	0						
90				0			
91		1*	0				
92			0	1	0*	1	
93			0*	1	1	1	
94	0	1					
95					0	1	
96	1	1	0*	0*			
97	1	1	1				
98				0			copulated in '06
99	1						
100						0	
101		0	1				stillbirth in '05
102	0*	1					
103	0*	1					stillbirth in '04
104			1	1	0*	1	
105					1		
106			0				
107		1	1	0	1	1	
108	0	0	1	0	1		
109				1	0*		
110					1	1	
111			0	1	1	1	
112			0				
113			1	0*	1	1	
114						0	
115			1				
116					1	1	
117						1	
118				1	1	1*	
119	1	1	0*	1	1		
120	1	0*					
121	1	1	0	1	1		
122			1	0*	1	0*	
123	1	1	0*	1	1	1	
124					0	1	
125					1	1	
126					1	0	
127	1	1	0				
128					1	0	
129				1	0*	1	
130					0	0	
131	1						

Fem.#	2003	2004	2005	2006	2007	2008	Notes
132	1	1	1	1	1	1	
133	1	1					
134				0			
135				1			
136		0	0				
137				0	0		copulated in '06
138					1		
139						0	
140			1				
141	1						
142					1	1	
143						1	
144					0	1	
145			0				
146	0	0					
147	0	1	1	1	1	1	
148			0				
149			1	0*	1	1	
150				0	1	0*	
151					1	1	
152	0*	0*	1	0*	0*	1	
153						0	
154						0	
155			1	1	0*		
156					1	0*	
157						1	
158						0	
159	0	0					
160		0					
161	1	1	1	1	1	1	
162	1	1	1	1	1	1	
163				1	0*		
164				1	1	0*	
165					0	0	
166		1					
167			0				
168		1	1				
169	1	1	0*	1	1	1	
170					1		
171						0	
172					0		
173						1	
174						0	
175	1						
176		1	1	0	1	0*	
177	1	1	1				
178	1	1					

<b>Fem.#</b>	<b>2003</b>	<b>2004</b>	<b>2005</b>	<b>2006</b>	<b>2007</b>	<b>2008</b>	<b>Notes</b>
179						1	
180	1	1	1				
181					0	1	
182	1	1	1	1	0	1	
183					1		
184	1						
185						1	

<sup>†</sup>Maniscalco and Parker (2009)