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Causes and Extent of Natural Mortality Among Steller Sea Lion (*Eumetopias jubatus*) Pups

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Abstract

The authors studied the causes and extent of mortality in endangered Steller sea lion (*Eumetopias jubatus*) pups at a small rookery in the northern Gulf of Alaska over seven consecutive summers (2001 to 2007). Mortality among pups up to 2.5 mo post-partum ($n = 69$) averaged 15.4% (range = 3.8 to 27.8%) and was not dependent on number of pups born. The causes of mortalities varied greatly from year to year, although high surf conditions and killer whale predation accounted for more than half of all deaths. Stillbirths, traumatic injury, and maternal abandonment were individually relatively minor sources of mortality. Causes of mortality were age-dependent. Pups greater than 2 wks old were not washed away by high surf conditions or killed by traumatic injury; whereas pups less than 1 mo old were not subject to predation. The authors also summarize historical observations of pup mortality in this species to compare similarities over time and differences between regions. Current and historic evidence suggests that rates of pup mortality have been higher in the eastern/increasing population of Steller sea lions compared to the western/decreasing population. Therefore, an increase in pup mortality was probably not a major cause of the overall population decline or current lack of recovery.

Key Words: Steller sea lion, *Eumetopias jubatus*, abandonment, pup mortality, high surf, predation, stillbirths, traumatic injury

Introduction

An understanding of both the extent and causes of mortality among animals of different ages is critical for proper management of any species, especially those that are listed under the Endangered Species Act (ESA). Mortality may be related to density-independent processes (e.g., weather conditions) or to density-dependent processes (e.g., trampling or suffocation caused by overcrowding). Such general classifications can be useful in defining how mortality may affect increasing or decreasing animal populations, including pinnipeds (e.g., Reid & Forcada, 2005).

Along the coast of the North Pacific Ocean, Steller sea lions (*Eumetopias jubatus*) are divided into a western distinct population segment (DPS) that is listed as endangered and an eastern DPS listed as threatened under the ESA. Reviews of mortality in non-pup Steller sea lions indicate that the causes are varied and include direct and indirect effects of both anthropogenic and environmental changes (Loughlin & York, 2000; Atkinson et al., 2008). Yet, causes of mortality among pups in this species are likely different than for older age-classes, and a good accounting of its occurrence in this youngest age-class has heretofore been lacking.

Low survival of juvenile Steller sea lions has been thought to be at least partly responsible for their decline or lack of recovery (York, 1994; Holmes & York, 2003). A recent analysis of marked animals suggests that first-year mortality may be around 30% (Pendleton et al., 2006). Prior to the age that pups are marked for survival and movement studies (*ca* 3 wks), an additional 32% of pups may die (Kaplan et al., 2008). Those studies provide good estimates of mortality in young Steller sea lions, but much variability in the rate and type of pup mortalities between years and locations has been observed in several other pinniped species (Anderson et al., 1979; Doidge et al., 1984; DeVilliers & Roux, 1992; Majluf, 1992; Soto et al., 2004; Reid & Forcada, 2005). Therefore, long-term assessment of interannual variability in the extent and sources of pup loss is also valuable and necessary.

Steller sea lions prefer to haul out, give birth, and breed on rocky platforms that are exposed to harsh marine weather conditions (Call & Loughlin, 2005; Ban & Trites, 2007) that can wash many newborn pups away (Edie, 1977; Kaplan, 2005). However, others have found that pups are generally not lost to high surf (Sandegren, 1970; Merrick, 1987). Such contradictory findings could be the result of differences in rookery topography or weather conditions in different years, and these findings should be considered when assessing the extent of mortality for pups across their range. Rates of other sources of pup mortality caused by stillbirths, trauma, maternal abandonment, predation, and disease are generally unknown for this species.

The purpose of this study was to quantify the different sources of mortality in Steller sea lion pups over several years by direct observations and to define what ages of pups are vulnerable to different sources of mortality. The authors further summarize information on pup mortality from gray and peer-reviewed literature to look for general spatial and temporal trends throughout the range of this species.

Materials and Methods

This study was conducted at a small (*ca* 90 breeding animals) Steller sea lion rookery on Chiswell Island, located in the northern Gulf of Alaska and within the western DPS. The pupping area on Chiswell Island faces northwest and consists of solid granite/slab with some cracks. Up to six remotely operated video cameras were used that were viewable and controllable in real-time from the Alaska SeaLife Center 65 km away and provided complete spatial coverage of the rookery. (See Maniscalco et al., 2006, for more details about the Chiswell Island rookery and remote video equipment.)

The duration of this study extended from 2001 through 2007, beginning with the arrival of the first female on the rookery in mid- to late-May each year. Observations included full census counts of all sea lions by age-class on the rookery at approximately 1100 h and 1900 h and hour-long scan sampling for identifiable females and their pups 4 to 10 times daily from 0600 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, aggressive interactions, and mortality-related incidents were also recorded as they occurred. Births and mortalities that happened overnight were recorded the following morning as having occurred at the halfway point of non-observation hours. Dedicated observations for this study were conducted until the end of August when pups were about 2.5 mo old. By the end of August, mother/pup pairs began leaving Chiswell Island for other haulout sites, making it more difficult to assess specific mortality events.

There were four ways by which the authors accounted for pup mortalities: (1) twice-daily census counts of pups on the rookery, (2) actual observations of pup deaths, (3) tracking of pups via maternal association, and (4) tracking of pups via unique markings. Those latter two methods are explained in more detail here. During the perinatal period subsequent to parturition, females at Chiswell Island spend an average of 10.7 d on shore with their pups before returning to an alternating cycle of foraging at sea and resting/nursing on shore (Maniscalco et al., 2006); other studies indicate that Steller sea lion pups are dependent on their mothers for at least 1 y (Raum-Suryan et al., 2004; Trites et al., 2006). Therefore, females that were consistently observed without pups had either not given birth or had given birth and their pup died. By recording all births and identifying a substantial portion of females that gave birth, individually identifiable females were used as a proxy for identifying pups and often their fate. Through the remote video system at Chiswell Island, the authors kept track of all female sea lions with distinguishable scars; fungal patches; other unique, natural markings; and brands or tags. An average of 78 ± 14.6% females that gave birth each year were identifiable by their marks. Video recordings and digital photographs of these animals and their distinguishing marks were taken on a regular basis. In 2001 and 2005, white plastic cattle "ear" tags were applied to the trailing edge of the foreflippers of 17 and 13 pups, respectively. Pups were also hot branded (Merrick et al., 1996) in 2005 ($n = 26$) and 2007 ($n = 51$) with unique 3- or 4-digit codes. Those permanent markings aided in the identification of dead or missing pups of about 3 wks of age and older. With complete spatial coverage of the rookery, twice-daily census counts, and continuous tracking of identifiable females and their pups, it was possible to determine the minimum extent and often the source of pup mortalities whether a pup died on the rookery or disappeared from the rookery. Some females begin moving off the rookery in mid- to late-August (Maniscalco et al., 2006), however, and those that did were assumed to have taken their pups with them. Most females with pups continued to use Chiswell Island through the month of August, and those seen consistently without their pup for > 2 wks were presumed to have lost them to some mortality event.

The sources of mortality as presented in this study are synonymous with the distal (ultimate) causes of mortality, not proximate (mechanistic) causes. Proximate causes of death such as drowning, hemorrhaging, or starvation may, distally, be the result of being washed away in high surf, traumatic injury, or maternal abandonment, respectively. The authors could not specifically identify the proximate causes of death in most cases (only one dead pup was collected and necropsied). Through observations, however, the sources of mortality could be determined in most cases, and these were useful for assessing the effects of density-independent processes (e.g., predation, weather conditions, or food availability) vs density-dependent processes (e.g., traumatic injuries or disease transmission).

Sources of mortality were assigned as follows:

- *Stillbirth*—A pup that was born during the pupping season (late-May through early-July) and was never observed to move or take a breath. This does not include premature births or aborted fetuses that may occur prior to late-May.
- *High surf conditions*—A pup that was washed away into the ocean when combined surf and tide conditions were greater than average and, to help distinguish this event from abandonment, the mother was generally in close proximity to, attentive to, and had nursed her pup within 24 h prior to the loss. These pups were presumed to have drowned, but if they were able to haul out in another location, it is unlikely they would have survived for long as their mothers remained at Chiswell Island for > 2 wks.
- *Abandonment*—A pup whose mother departed the rookery and never returned or, whether or not the pup entered the water and was washed away, it was defined as abandonment rather than high surf conditions if the mother also continued to nurse a yearling, was inattentive to the pup for > 24 h prior to the loss (or ignored the pup immediately from birth), and surf conditions were mild.
- *Trauma*—The pup died on the rookery within 12 h after it was observed to be involved in a traumatic event such as trampling by an adult bull or, in one case, was necropsied to determine the distal cause as traumatic injury.
- *Predation*—The pup was observed being preyed upon by a killer whale (*Orcinus orca*) or went missing from the rookery during times of killer whale presence as per Maniscalco et al. (2007a).
- *Unexplained*—The pup died on the rookery or disappeared from the rookery and the cause could not be definitively attributed to any of the sources listed above.

To compare wave intensity with pup loss, historical wave height information was obtained from the National Data Buoy Center (www.ndbc.noaa.gov) for a northern Gulf of Alaska site (Station 46001, 200 nm south of Chiswell Island) with consistent data during the course of this study. Significant changes in wave height at that buoy are reflected along exposed areas of the north gulf coast such as Chiswell Island as judged by regional marine forecasts. A multiple comparison of perinatal periods (the time from when a female gives birth to her next foraging trip to sea) was conducted as per Maniscalco et al. (2006) to determine if there was any difference among years when abandonment was prevalent or not. Results are presented with descriptive statistics ± SD, and p values of < 0.05 were considered significant.

Historical accounts of pup mortalities were also gathered from gray and peer-reviewed literature dating back to 1921. However, many of the early studies were *ad hoc* assessments at rookeries and lacked a strict methodology. The means to obtain those estimates of mortalities varied from 1- to 2-d counts of live and dead pups to detailed studies lasting several months. Therefore, the data summarized here are only meant to show general trends in rates of pup mortality and its various sources. This puts the present work into a broader perspective and pulls together much isolated information on pup mortality from across the range of this species.

Results

Mortality, including stillbirths, during the first 2.5 mo of life averaged 9.9 pups (15.4%, range = 3.8 to 27.8%) of those born (mean = 66.6, range = 54 to 80) over the years 2001 to 2007 at Chiswell Island (Table 1). The annual mortality rate was not significantly correlated with number of pups born ($r^2 = 0.297$, $p = 0.205$), and the sources of mortalities varied widely among years with SD exceeding the mean for all except stillbirths (Table 1). Survival to 3 wks of age, the approximate time when pups are permanently marked for long-term studies, was 89.6 ± 6.0%.

High surf conditions caused more mortalities (31.9%) than any other source over all years combined. Three major storms, two in June 2002 and one in June 2006, caused the loss of 15 of 22 (68%) pups that were washed away in high surf. Wave heights were significantly greater on those days (M = 3.35 m) compared to all other days during the month of June for all years combined (M = 1.46 m; Mann-Whitney test, $p < 0.001$). The seven additional pups that were lost to high surf conditions were solitary events.

Killer whale predation on pups was only known to occur during 2001 and 2003 (Table 1) and accounted for 24.6% of all mortalities. Predation was attributed to a small group of killer whales. No other sea lion predators were observed at Chiswell Island.

Table 1. The number and proportion of pups ≤ 2.5 mo of age that died each year from different causes with mean proportion ± SD for each category in the bottom row

Year (births)	Stillbirths	Surf	Trauma	Abandoned	Preyed upon	Unexplained	% died per year
2001 (54)	2	1	0	0	12	0	27.8
2002 (65)	1	11	1	1	0	0	21.5
2003 (71)	0	0	0	1	5	7	18.3
2004 (80)	2	1	0	0	0	0	3.8
2005 (54)	2	3	0	2	0	1	14.8
2006 (62)	0	4	0	0	0	1	8.1
2007 (80)	1	2	1	6	0	1	13.8
Total (466)	8	22	2	10	17	10	15.4
Mean % mortalities	1.8 ± 1.6	4.9 ± 5.8	0.4 ± 0.7	2.0 ± 2.8	4.2 ± 8.4	2.1 ± 3.5	

Other sources of mortality were relatively minor, with maternal abandonment, stillbirths, and trauma-related deaths accounting for 14.5%, 11.6%, and 2.9% of all pup deaths, respectively. One of the two pups that died from traumatic injury was collected and necropsied in 2002. It died from apparent sepsis caused by a puncture wound; the cause of that wound was never determined. The other trauma-related death was assumed from observations of an adult bull trampling on a 2.5-d-old pup. The pup was not observed to move normally after that and died within the following 6 h.

Abandonment was more prevalent in 2007 compared to other years, and 80% of all mothers who abandoned their pups continued to nurse a yearling or, in one case, the second pup from a set of twins (Maniscalco & Parker, in press). Females that abandoned their pups at a young age were usually not tracked for analysis of attendance patterns but, of all other females that were tracked, those in 2007 had shorter perinatal periods (M = 9.9 d, $n = 49$) than in those from 2002 (M = 12.2 d, $n = 29$) and 2003 (M = 11.5 d, $n = 36$; Dunn's multiple comparison, $p < 0.05$), but not other years (M [range] = 9.8 to 11.0 d, n [range] = 27 to 47).

Ten additional mortalities resulted from undetermined factors. Most (seven) of those pups died on the rookery in 2003 when many sea lions on Chiswell Island, including some of these mortalities, had visible lesions and blisters on their flippers and lips. Those lesions and blisters might have been caused by an infectious disease and were rarely seen on sea lions at this rookery in other years. Unfortunately, the authors were unable to collect any of the dead pups in 2003 for necropsy. The three other mortalities were categorized as unexplained because, although their mothers remained at the rookery, the pups disappeared from (two cases) or died on the rock (one case) with no obvious explanation.

The sources of some pup mortalities were dependent on age (Fisher exact test, $p < 0.001$). All that died from high surf conditions or trauma were ≤ 2 wks of age, and predation by killer whales occurred only with pups > 1 mo old (Figure 1). Death because of maternal abandonment was not observed in pups between 1 and 2.5 mo old. Pups that were abandoned at young ages were typically washed away in the surf (eight of 10 cases) instead of starving to death on the rookery. However, after the 2.5 month-per-year term of this core study, the authors did opportunistically observe at least three pups that apparently starved to death after several weeks of no maternal association. In one of those cases, the mother was a known female with a 7-y history on Chiswell Island. In 2007, she gave birth to a male pup on 7 June that was given a permanent identification mark (E62) on 3 July. The mother was last seen on the rookery and nursing E62 on 21 September. Over the subsequent weeks, the pup got noticeably thinner and weaker and died on the rookery 26 d later on 17 October. Observations on the other two starving pups lasted about 3 wks before they died.

A summary of Steller sea lion pup mortality dating back to the early 1900s shows differences between regions (Table 2). Rates of mortalities in the western DPS were generally low (3 to 15%), notwithstanding a large mortality event at Seal Rocks (Prince William Sound) in 1976 and at the Cape St. Elias haulout where few pups were born. Those mortalities were assigned to a wide variety of sources but generally included trampling/traumatic injury, abandonment, and high surf. Pup mortality rates within the eastern DPS were often higher (10 to 83%) than the western DPS and frequently attributed to high surf conditions. Data from the Russian Far East are more limited with 1 to 2 d censuses between 1989 and 1996 indicating low pup mortality but work in the first half of

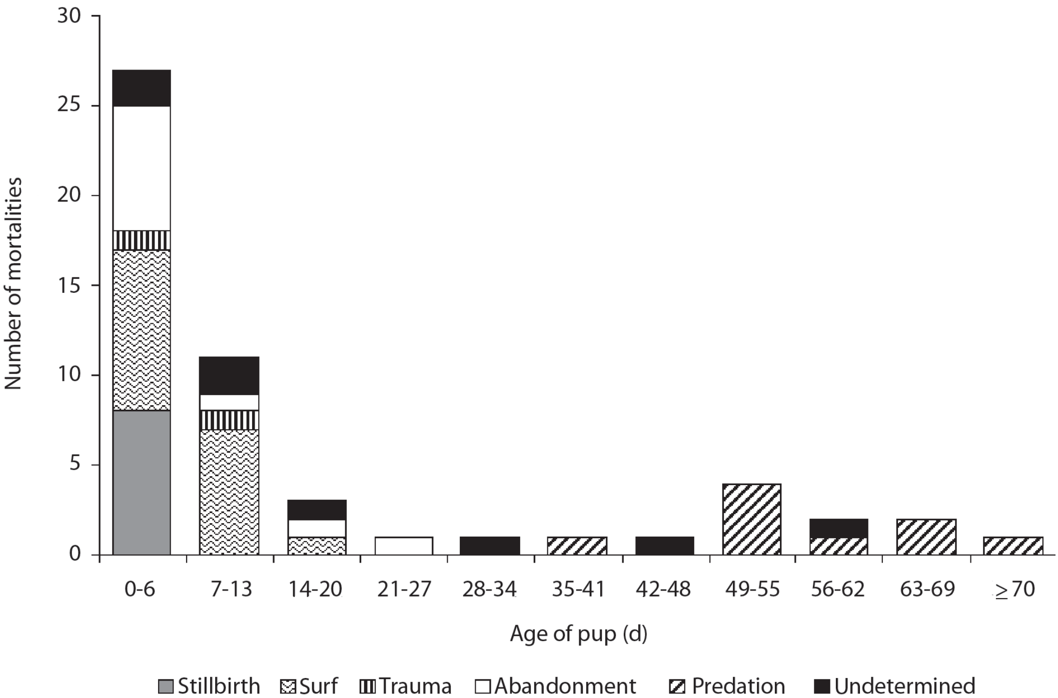

Figure 1. The source of mortalities is presented in relation to age of pups. These data represent only pups of known age (± 12 h) at time of death, not all pup mortalities.

the 20th century indicating that some pups were lost to high surf (Table 2).

Discussion

Causes and Extent of Mortality

Rates of pup mortality were slightly higher at Chiswell Island between 2001 and 2007 (mean = 15.4%) compared to most other recorded locations within the western DPS from 1959 through the mid-1980s, with pups being washed away in high surf conditions as the most common cause. These findings at Chiswell Island are more closely related to eastern DPS rookeries and are discussed below in "Regional and Historic Comparisons." It should be apparent, however, that 1- or 2-d counts of live and dead pups on rookeries, as was performed in many of the studies listed in Table 2, would not be able to account for pups that were washed away in high surf. Yet, some studies lasting for many weeks after the peak of pupping have found low rates of mortality (e.g., Gentry, 1970; Merrick et al., 1988) compared to some single-day counts such as seen at Seal Rocks in 1976 (Calkins & Pitcher, 1982). There would also be bias toward lower mortality if, by chance, a particular study was conducted during a year(s) of mild surf conditions. Half of all surf-related mortalities that we observed from Chiswell Island occurred in just one of the seven years of the present study—2002—exemplifying the importance of long-term data sets for a true assessment of mortality in a stochastic environment.

Most other sources of mortality were also highly variable among years. Predation by killer whales on pups was observed in only two of seven years, although it was a major contributor to overall mortality at Chiswell Island. This was attributed to the activity of a small group of killer whales focusing their efforts on Steller sea lions in the northern Gulf of Alaska and only circumstantially on pups (Maniscalco et al., 2007a). Predation on older age-classes of sea lions is somewhat common and has not been reported for Steller sea lion pups at other rookeries, although Heise et al. (2003) report that several flipper tags from young sea lions were found in a necropsied killer whale. Predation on pups can be difficult to detect, and most Steller sea lion rookery studies end prior to August, the month when the most predatory activity has been observed (Maniscalco et al., 2007a).

Maternal abandonment of pups was a smaller source of mortality but greater in 2007 than any other year of our study. In other pinnipeds, abandonment of pups was found to be common when females spend a greater amount of time searching for food and less time nursing pups on shore (Costa et al., 1989; Soto et al., 2004; Reid &

Table 2. Summary of Steller sea lion pup mortality in the eastern (threatened) DPS, western (endangered) DPS, and Russian Far East; sources of mortality are listed as "ultimate" causes and a "?" indicates the cause was speculated, although it was not always clear if causes were positively determined or speculated.

Year(s)	Location	Mortality rate	Major source(s)	Reference
Eastern DPS				
1920	Año Nuevo Is.	~50%[1]	High surf, traumatic injury	Evermann, 1921
1927-1928	California[2]	"very high"	High surf, traumatic injury, starvation	Bonnot, 1929
1956	British Columbia[2]	"slight"	Undetermined[3]	Pike & Maxwell, 1958
1961-1964	Año Nuevo Is.	"high"	High surf, traumatic injury	Orr & Poulter, 1967
1967-1969	Año Nuevo Is.	< 10%	High surf, abandonment	Gentry, 1970
1969-1971	Orford Reef	22-36%	High surf	Mate, 1973
1969-1971	Simpson Reef	43-83%[4]	High surf	Mate, 1973
1972	Cape St. James	"heavy"	High surf	Fisher, 1981
1973	Cape St. James	30-50%	High surf	Edie, 1977
1982	Rogue Reef	12%	Various?	Merrick, 1987
2003	Lowrie Is.	32%	High surf & tide	Kaplan et al., 2008
Western DPS				
1959	Ugamak Is.	10%	Abandonment? traumatic injury?	Thorsteinsen & Lensink, 1962
1967, 1968	Fish Is.	13%, 14%	Abandonment? traumatic injury?	Sandegren, 1970
1969	Ugamak Is.	No estimate	Traumatic injury, high surf	Fiscus, 1970
1976	Seal Rocks	> 20%[1, 5]	Traumatic injuries caused by overcrowding?	Calkins & Pitcher, 1982
1977, 1978	Cape St. Elias	27%, 90%[4]	High surf, traumatic injury?	Cunningham & Stanford, 1978
1977, 1978	Ugamak Is.	10%, 12%[6]	High surf	Withrow, 1982
1978	Sugarloaf Is.	4.6%[1]	Undetermined	Johnson & Smith, 1978
1979	Marmot Is.	6.3%[1]	Undetermined	Aumiller & Orth, 1979
1983	Marmot Is.	11%	Abandonment?	Merrick, 1987
1985, 1986	Ugamak Is.	3.4%, 4.5%	Abandonment?	Merrick et al., 1988
2001-2007	Chiswell Is.	15.4%	High surf, predation	This study
Russian Far East				
1939, 1941, 1947, 1949	Kuril Is.[2]	No estimate	High surf	Sleptsov, 1950
1989	Kuril Is.[2]	1.6-3.4%[1]	Undetermined	Merrick et al., 1990
1995-1996	Kuril Is.[2]	2.6-7.1%[1]	Undetermined	Pavlov & Isono, 1999

Notes
[1]Mortality estimates were based on 1- to 2-d counts of live and dead pups on the rookery.
[2]A general survey was performed of several rookeries and haulouts.
[3]It is speculated that high surf/storms could cause major mortality in some years.
[4]Location would be considered as a haulout since < 40 pups were born during the study years.
[5]Mortality was not listed for several other rookeries visited but was especially high at this location and worth noting.
[6]These were peripheral rookeries where the few pups that were born had much higher mortality rates.

Forcada, 2005), or when an older offspring outcompetes the newborn (Trillmich & Wolf, 2008). Pups that were abandoned in the present study were left at a very young age and usually in favor of an older offspring. No deaths due to abandonment in pups between 4 wks and 2.5 mo old were observed. Abandonment at a very young age might be reflected in a mother's perinatal period which is shorter in females that nurse both a pup and a yearling (Maniscalco & Parker, in press) but would not necessarily be reflected in later foraging cycles after the pup is given up. The present data indicate somewhat shorter perinatal periods in 2007 but not significantly so from most other years, suggesting that sibling competition may have also played a role in the cases of abandonment in this study.

There have been no prior assessments of the cause and extent of full-term stillbirths in Steller sea lions except that Sandegren (1970) noted that no stillbirths were observed at Fish Island in the late 1960s. At Chiswell Island, only 1.8% of pups were stillborn between 2001 and 2007. Steller sea lions will commonly have premature births or abort fetuses prior to the pupping season (Gentry, 1970; Pitcher & Calkins, 1981; Huber et al., 1984), and such losses may be related to poor caloric intake among several other possibilities (Pitcher et al., 1998). However, the high energetic investment required for a full-term pregnancy suggests that other factors may be causing stillbirths during the pupping season. Unfortunately, the authors were unable to necropsy any stillborn pups from Chiswell Island. Rates of stillbirths have also been found to be very low among other pinnipeds, and causes have been conjectured to be related to viral infections or unknown factors (Mattlin, 1978; Anderson et al., 1979; Kovacs et al., 1985). Infections that have been identified in Steller sea lions such as chlamydia (*Chlamydophila* spp.), caliciviruses, and certain bacteria (Calkins & Goodwin, 1988; Burek et al., 2005a) are known to cause premature births in this species (Spraker & Calkins, unpub. data) as well as in other pinnipeds and may have played a role in the full-term stillbirths documented here.

Death from traumatic injuries was the least important source of overall mortality at Chiswell Island. Some researchers have speculated that trauma-related deaths were the most prominent cause of mortality in young Steller sea lion pups (Table 2), but Gentry (1970) and Merrick (1987) found such mortality to be rare. Based on the data collected in this study, the authors concur. Young pups have often been bitten and tossed about violently by females other than their mothers at Chiswell Island (Maniscalco et al., 2007b), yet none of those observed traumatic events resulted in a pup's death. Traumatic injuries resulting in death have not been found to be a significant source of mortality during anthropogenically caused stampedes either (Lewis, 1987). One might expect trauma to be a more prominent cause of mortality at densely populated rookeries as has been noted in Antarctic fur seals (Doidge et al., 1984; Reid & Forcada, 2005) and may well have occurred at Steller sea lion rookeries where 5,000 to 10,000 pups were born in the past. Such may also be the case during some years at Seal Rocks where the pupping beach is constrained between rocky outcrops, and space becomes very limited during high spring tides and high surf conditions (Calkins & Pitcher, 1982), but there has been little evidence for this at other rookeries throughout the range of Steller sea lions.

Most of the unexplained mortalities in 2003 were probably not related to traumatic injuries since adult aggression did not appear to contribute to such mortalities in other years and no major trampling events were observed during that year. It is more likely that a disease or infection was afflicting the sea lions more prevalently that summer. The lesions and blisters observed on their flippers and lips were consistent with a poxvirus infection found in Steller sea lions in nearby Prince William Sound in recent years (Burek et al., 2005b) or possibly a calicivirus (Calkins & Goodwin, 1988). The extent to which diseases such as this have contributed to the Steller sea lion decline or lack of recovery is uncertain (Burek et al., 2005a), although its occurrence was relatively low in pups at Chiswell Island even if all unexplained mortalities were attributed to infectious diseases.

Age-Related Differences

It was not surprising to find that the sources of most mortality were dependent on age as mortality rates generally decrease with age from birth in many pinnipeds (Doidge et al., 1984; DeVilliers & Roux, 1992; Kaplan, 2005). In addition to early mortalities due to abandonment discussed previously, the present data suggest that by 2 wks of age, Steller sea lion pups are physically capable of hauling out of the water if washed in and that they can probably move about well enough to avoid trampling by adult males (Orr & Poulter, 1967; Lewis, 1987). Pups engage in activities on shore that may help to develop swimming skills, but they do not voluntarily enter the ocean until 2 to 3 wks of age (Sandegren, 1970). By the end of July, most pups at Chiswell Island are swimming often. As they are just developing swimming skills at that point, they are potentially easy targets for interested killer whales; whereas, being shore-bound previously, they were virtually unavailable.

After the end of August, death because of starvation and predation were the only sources of mortality observed among pups. Similarly, those were the only two types of mortality that continued to affect New Zealand fur seal (*Arctocephalus forsteri*) pups greater than 2 mo old (Mattlin, 1978). In Alaska, killer whales are the only known predator of Steller sea lions of any age, and younger ones may be preferred by individuals or small groups (Ford et al., 1998; Heise et al., 2003; Maniscalco et al., 2007a). Therefore, it is expected that predation will continue to be a threat through at least the first few years of a sea lion's life.

Starvation at more than 2.5 mo of age likely results from mother/pup separation or death of the mother. The mother/pup bond should be well-established at an early age (Sandegren, 1970), but pups probably do not develop sufficient foraging skills and continue to rely on their mother's milk throughout their first fall and winter (Pitcher & Calkins, 1981; Trites et al., 2006). During the fall and winter, they also tend to travel broadly and haul out in distant places (Loughlin et al., 2003; Raum-Suryan et al., 2004), potentially increasing the likelihood of mother/pup separation. That could be the reason additional cases of starving pups during the fall months were observed when none were observed in pups 1 to 2.5 mo old. Observations of E62 provided a unique natural experiment of starvation to the point of death that would not otherwise be possible in this endangered species. Data collected on that pup and other starvelings indicate that a 4-mo-old Steller sea lion may only survive less than 1 mo without its mother's milk.

Regional and Historical Comparisons

Eastern DPS rookeries generally had higher reported rates of pup mortality than the western DPS. While mortality due to maternal abandonment, trauma-related injuries, and most other sources were consistently low across the range of Steller sea lions, the major differences between regions appear to be related to weather conditions and/or rookery topography that caused pups to be washed away in high surf. Overcrowding at some rookeries could exacerbate pup losses, however, by forcing excess females to give birth in peripheral areas that are more exposed to sea conditions (Kaplan, 2005).

Pup mortality due to high surf and tide conditions at specific sites in the eastern DPS rookeries have contributed losses of 30% or more during certain years (Edie, 1977; Kaplan et al., 2008), with few comparisons among the western DPS rookeries studied. Within Alaska, exposure and oceanic characteristics around rookeries are similar between the eastern and western DPS regions (Ban & Trites, 2007), but major changes in marine weather conditions do occur over time and do not necessarily affect each region concurrently or in the same manner (Benson & Trites, 2002). Yet, there were no major changes in the sources of mortality over the long time span of pup mortality studies listed in Table 2 either.

Another consideration for storm-related losses is that the terrain of some rookeries might be more conducive to hauling out because of substrate type or gentler slopes (Sandegren, 1970; Lewis, 1987; Merrick, 1987). Young pups that are swept out to sea are able to swim and stay afloat but have difficulty hauling out on steep slopes in rough weather conditions. All western DPS rookeries where pup mortality has been studied for longer than 1 to 2 d (Table 2), with the exception of Chiswell Island and Fish Island, have a substrate topography consisting of sandy or cobble beach (Call & Loughlin, 2005). Chiswell Island, Fish Island, and most eastern DPS rookeries consist of boulder beach, rock/slab, or offshore rock. Those places, with more similar substrate type to each other than sandy or cobble beaches (Call & Loughlin, 2005), generally had the highest surf-related mortalities. The authors have often seen very young pups attempting to haul out on Chiswell Island but being washed back into the sea by the next wave or slipping right back off the rookery's steep slope with little in which to wedge their flippers. A sandy substrate or even large cobble with a shallow slope would offer more to push against when climbing out of the surf compared to a steep, solid granite surface with few cracks such as is the case on Chiswell Island. Many other rookeries within the western DPS do consist of boulder beach, rock/slab, or offshore rock (Call & Loughlin, 2005), but they have not been studied specifically for pup mortality other than 1- or 2-d counts of live and dead pups. Still, the western DPS sea lion decline has affected every rookery in that region regardless of substrate type.

Rates of pup mortality have been reported to be higher (22 to 68%) in other otariids with increasing populations (Aurioles & Sinsel, 1988; Majluf, 1992; Reid & Forcada, 2005). Similarly, the eastern DPS of Steller sea lions appears to have greater pup mortality than the western DPS and has experienced increased population growth during the past 25 y or more (Pitcher et al., 2007). Therefore, it is unlikely that pup mortality would have been a major contributor to the western DPS Steller sea lion decline. Nevertheless, a detailed analysis is needed to determine how pup mortality is affected by rookery substrate and changing weather conditions over time and between eastern and western Steller sea lion populations.

Although the effect of pup mortality is unknown prior to 2000, it does not currently appear to be affecting the western DPS of Steller sea lions. At Chiswell Island, the population of animals age 1+ has increased at an average annual rate of 2.5% between 1999 and 2007 (Alaska SeaLife Center, unpub. data), with rates of pup mortality around 15%. Observations of mortality among pups from other Steller sea lion rookeries in this region are generally lower than that, although it was not possible to have a strict comparison with most other studies because of different sampling schemes.

Ultimately, the causes of Steller sea lion pup mortalities were dominated by density-independent processes, mostly weather conditions. Those processes affected eastern DPS rookeries and/or offshore rookeries with rock/slab substrates to a greater extent than the western DPS rookeries with shallower beach habitat. Mortality can increase at high animal densities (Doidge et al., 1984; Kaplan, 2005), but intrinsic and density-dependent factors that may have been responsible for stillbirths, disease, abandonment, or trauma-related deaths were relatively minor causes of mortality in Steller sea lion pups.

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