AN ABSTRACT OF THE THESIS OF

Erin H. Kunisch for the degree of Master of Science in Wildlife Science presented on March 2, 2011.

Title: Northern Fur Seal Reproductive Rates and Early Maternal Care

Abstract approved: ______________________________________________

Markus Horning

The majority of the world’s breeding population of northern fur seals (Callorhinus ursinus) is found on the Pribilof Islands (St. Paul and St. George) in the Bering Sea, Alaska. Pup production on these islands experienced an irregular but overall decline since the early 1970’s. Between 1998 and 2010, pup production declined precipitously at an annual rate of 4.9% on the Pribilof Islands, and 5.5% on St. Paul Island. Specific reasons for this decline remain unknown, and contemporary estimates for many vital rate parameters including reproductive rates are unavailable.

This study determined a contemporary estimate of natality and fertility rates, as well as reproductive timing on the Polovina Cliffs rookery of St. Paul Island during the 2008 (30 June–31 August) and 2009 (1 July–25 August) breeding seasons. Natality rate (defined as the number of pups born divided by the number of reproductively mature females) was determined from visual
observations of parturition or associated maternal behavior in 208 and 217 individually marked females (via flipper tags) in 2008 and 2009, respectively. Data yielded observed natality estimates of 0.79 in 2008 and 0.88 in 2009. The fertility rate (defined as the number of pups born divided by the total number of females present, irrespective of reproductive maturity/age) was determined for the 2008 breeding season only. This ratio of total pup to female counts was derived from adjusted daily cross-sectional counts conducted through the breeding season. Maximum pup and female counts were derived as asymptotes of sigmoid growth models fitted to corrected daily counts. Live pup counts were corrected for mortalities by estimates of cumulative pup mortalities. Daily counts of females present in the rookery were corrected for reduced detection probabilities resulting from increased maternal foraging trip durations through the season, typical of attendance patterns associated with colonial, income breeders. Daily detection probabilities for individually marked females were generated from Cormack-Jolly-Seber (CJS) open population models using maximum likelihood estimators (MLE) in Program MARK. Multiple a priori models accounting for the effects of possible covariates on detection probabilities were evaluated in an information-theoretic approach using Akaike’s Information Criterion (AIC) and AICc model weights. Data yielded a minimum fertility rate estimate of 0.60 in 2008. Detection probabilities derived from the top CJS model for dual flipper-tagged females only were used to adjust the daily cross-section counts of all (marked and unmarked) females. Therefore, the actual fertility rate is probably higher
than the estimate presented here, which should be regarded as the lowest likely value for 2008. However, AICc model weights also demonstrated the absence of density effects on detection probability estimates. This supports the applicability of marked female–based detection probabilities for correcting cross-sectional counts of all females and further suggests that the actual fertility estimate likely does not differ much from the presented estimate. Median dates of birth were calculated as the date closest to 50% of modeled corrected pup count asymptotes, yielding median dates of 17 July in 2008 and 15 July in 2009. Pregnant females are highly consistent in their arrival dates, with parturition occurring approximately 1 day after arrival. Median observed dates of arrival from individually marked females resulted in dates of 16 July in 2008 and 15 July in 2009. These dates occurred 5 to 13 days later than historic reports from 1951 through 1995. With median arrival dates 1 day prior to parturition, the observed match between birth dates derived from pup counts and from observed arrival dates of marked females supports the finding of a contemporary delay in the timing of parturition. Median arrival derived as the date closest to 50% of the asymptote from corrected and modeled female counts yielded 13 July in 2008. This earlier data is likely an effect of the inclusion of immature and nulli–parous females.

In a subset of 62 females with pregnancy confirmed through a trans–rectal ultrasonography procedure in November 2007 and 29 females in 2008, the return rate for the following reproductive season was 0.92 and 0.76, respectively. In 2008, the return and natality rate was measured by radiotelemetry data, detected
from females outfitted with VHF-radio transmitter. In 2009 both rates were determined by observational data. Observed natality rates for returned females of a known pregnancy status were 0.95 in 2008 and 0.96 in 2009. Radiotelemetry data from 76 females was analyzed for early maternal attendance patterns (duration and ratio of presences and absences) in 2008. The mean date of detected return was 18 July. The mean duration of the perinatal period was 7.5 days (+/− 1.3 SD). Excluding the perinatal period, the mean duration of presence on shore for the first five visits was 1.47 days (+/− 0.21 SD). The mean duration of absence at sea for the first five trips was 7.07 days (+/− 0.42 SD). Results presented from this study do not provide any direct evidence of a contemporary reduction in natality or fertility rates in northern fur seals. Since observed rates were comparably high and consistent between 2008 and 2009, it is unlikely that reduced natality rates are contributing to the current population trajectory. Attendance patterns do not provide any evidence of increased maternal foraging effort or secondarily, reduced prey availability. Interestingly, median pupping dates were found to occur significantly later than historical estimates. Potential reasons for this shift could be an increase in younger females within the reproductive female population at this rookery, or a shift in the timing of ocean climate conditions and peak prey availability during the breeding season.
Northern Fur Seal Reproductive Rates and Early Maternal Care

by

Erin H. Kunisch

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APPROVED:

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Major Professor, representing Wildlife Science

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Head of the Department of Fisheries and Wildlife

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

________________________________________________________________________
Erin H. Kunisch, Author
ACKNOWLEDGEMENTS

First and foremost I want to express my utmost gratitude to my advisor, Dr. Markus Horning, for his support and guidance. His patience and enthusiasm throughout this process has been much appreciated and won’t soon be forgotten. Thank you for helping me become a better scientist! I want to acknowledge the rest of my graduate committee: Dr. Katie Dugger for her advice throughout the Program MARK analysis (without her help I would still be running models today), Dr. Chuck Estill, and Dr. Tom Gelatt who provided the much needed logistical support for this project.

The Pribilof Islands are about as remote as you can possibly get in Alaska, but truly a unique and unforgettable place. I am fortunate to have worked and lived on this tiny island in the Bering Sea. I want to thank my project collaborators: Dr. J. Ward Testa whose assistance made this project possible; in addition to Dr. Testa, Dr. Gregg Adams and Dr. Don Bergfelt who provided the ultrasound data included in this study. I am indebted to my field crews: Athena Merculief, Louise Taylor, Stephen Meck, Brett Miller, and Sam Zacharof. Thank you for your endless hours of sitting outside on exposed sea cliffs in the middle of the Bering Sea getting blasted in the face with wind and rain reading tags while safely avoiding curious (and sometimes aggressive) subadult male fur seals. I want to thank the Alaska Ecosystem Program at the National Marine Mammal
Laboratory (NMML) especially: Dr. John Bengston, Bob Caruso, Dr. Rolf Ream, Rod Towell, and Dr. Carey Kuhn. Thank you to Tom Bloxton with the U.S. Forest Service in Olympia, W.A. as well as everyone in the Polar Ecosystems Program (at NMML) for lending me much needed telemetry field equipment. I also want to acknowledge Dr. Brad Page, Dr. Paddy Pomeroy, Dr. Terry Spraker, Juan Leon Gurrero, Mike Williams, Dr. Brian Batallie, and Jane Lee for their much appreciated assistance and laughter in the field. Thank you to the Saint Paul Island Aleut community and the Tribal Government Ecosystem Conservation Office for their hospitality and for helping me find student volunteers for this project.

My time at Oregon State University has been a great and memorable experience. Thanks to the grad students both in the Fisheries and Wildlife Department and at the university for your friendship, laughter, and support. Thank you to the Marine Mammal Institute and the Pinniped Ecology Applied Research Lab, especially my labmate Jamie Womble. I want to express my sincere gratitude to Dr. David Roundy at the OSU Physics Department with last minute \LaTeX{} assistance. Thank you to Brooke Penaluna, Matt Gray, Art Bass, Dr. Tracey Johnson, Katie Gillespie, Dr. Ivan Arismendi, Heather Ziel, Erin Moreland, Nick Nosko, Angela Sokolowski, and Becky Latanich for their much needed emotional support—you all are rock stars! Thanks to my surfing buddies in Newport and Corvallis for introducing me to such a humbling and invigorating sport that resulted in a newfound appreciation of the ocean, and always provided mental clarity during the times I needed it the most. Finally thanks to my family,
especially my parents for their love and guidance.

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DEDICATION

This thesis is dedicated to my Dad, William J. Kunisch (1–9–1947 – 10–5–2005), who would have been absolutely thrilled to know I graduated from his alma mater. Dad, I did it!
Northern Fur Seal Reproductive Rates and Early Maternal Care
Chapter 1 – General Introduction

“The story of [northern] fur seal management reflect in many ways the strengths and weaknesses of men.” –Alton Roppel and Stuart Davey, 1965
1.1 Northern Fur Seal Range

Northern fur seals (*Callorhinus ursinus*, Linnaeus 1758) are a sub-polar species distributed in the North Pacific Ocean, Bering Sea, the Sea of Okhotsk, and the Sea of Japan; roughly from 35° to 60° north. Breeding colonies (or rookeries) are found on the Pribilof Islands (located in the Southeast Bering Sea), three Russian islands, Bogoslof Island (located in the Aleutian Island chain), and San Miguel Island (part of the Channel Islands, California; see Figure 1.1). The majority of the world’s breeding population of northern fur seals can be found in the Pribilof Island Archipelago, primarily Saint Paul Island and Saint George Island (Figure 1.3 and Figure 1.4).

![Figure 1.1: Northern fur seal distribution with major breeding islands (in boxes) and general winter range (shaded area) denoted. Figure from NMFS (2007).](image)
1.2 History of the Pribilof Island Northern Fur Seal Population

Like other fur seal species of the world, northern fur seals were intensely hunted for their pelts during the 18th, 19th, and 20th centuries (Wickens and York, 1997). The extensive history of northern fur seal exploitation began in 1786 when their main breeding grounds, the Pribilof Islands, were discovered by Russian explorers. The Pribilof Island population was hunted almost out of existence several times throughout history, first by Russia and subsequently by the United States after the Alaska Purchase in 1867. Soon after the Alaska Purchase, pelagic sealing followed as a monumental commercial enterprise in 1868 and lasted until 1911 when the Pribilof Island herd faced near extirpation (Roppel and Davey, 1965). This resulted in the first international treaty to collaboratively abstain from pelagic sealing, signed by the United States, Great Britain (for Canada), Japan, and Russia (Roppel and Davey, 1965). Better known as the North Pacific Fur Seal Convention of 1911, it was one of the first treaties that addressed wildlife conservation. The convention called for an immediate moratorium on fur seal harvests, and land–based commercial harvests did not resume until 1917 (Roppel and Davey, 1965). The Pribilof Island population grew rapidly after the cessation of pelagic sealing until 1940 (Roppel and Davey, 1965; York and Hartley, 1981). In 1940, Japan abrogated the international treaty of 1911. The seal harvest increased again in 1941, in part due to Japan’s claim that fur seals were negatively impacting off-shore fishing operations (Roppel and Davey, 1965). A new convention among the same nations was established in 1957 (Roppel and Davey, 1965).
Because of the increase in the Pribilof Island population, a period of extensive female reduction from this population occurred from 1956 to 1968, and annually removed more than 300,000 females (York and Hartley, 1981; Towell, 2007). This reduction program was initiated based on the thought that a smaller population would result in maximum productivity and an eventual increase in pregnancy and survival rates (York and Hartley, 1981). At the time, this was a widely accepted idea and the methodology supported by other wildlife studies although this harvest did not achieve the intended results. The Pribilof population declined once more, due to the massive removal of females with the greatest reproductive potential (York and Hartley, 1981; Lander, 1982). Additionally, females were pelagically harvested for research purposes from 1958–1974 (York and Hartley, 1981). Commercial harvests on the Pribilof Islands ended by 1985, and the populations experienced a brief increase after the end of female harvests, but general declines from 1980–1998 (Testa, 2008). This species was designated as “depleted” under the Marine Mammal Protection Act in 1988 (Loughlin et al., 1992). Declines have continued since 1998, but since hunting has ended, the cause of this recent decline is unknown.

Northern fur seal abundance on the Pribilof Islands is determined by estimates of pup production (the total number of pups born) in a breeding season. Pup production in the Pribilof Island population declined at an estimated rate of 4.9% per year between 1998 and 2010 (see Figure 1.2; Towell et al. (2010)). Between 1998 and 2010, pup production on Saint Paul Island has declined at an annual rate of 5.5% per year (Towell et al., 2010).
Figure 1.2: Northern fur seal pups born on Saint Paul and Saint George Islands, 1975–2010. Vertical bars represent 95% confidence intervals. Figure from Towell et al. (2010).
Figure 1.3: Location of the three northern fur seal breeding areas within Alaskan waters. The majority of the northern fur seal population breeds on the Pribilof Islands, Saint Paul and Saint George. Figure from Testa (2008).
Figure 1.4: Location of northern fur seal rookeries on Saint Paul Island, Alaska. Polvina Cliffs is located on the northeast side of the island. Figure from Testa (2008).
1.3 General Otariid Biology

Otariids are long–lived animals with a low annual reproductive rate, usually giving birth to one offspring (or pup) per year. Generally, age at sexual maturity for Otariid females is anywhere from 3–6 years (Atkinson, 1997). Unlike most members of the Phocid family, Otariids are known as income breeders, meaning females have to continue to feed to meet the energetic requirements of lactation. Otariids alternate between spending time onshore nursing their offspring and departing for foraging bouts at sea. This results in Otariid pups growing at a slower rate than Phocid pups (Oftedal et al., 1987). Because of the energetic demands of this reproductive strategy, Otariids have strong ties to land masses adjacent to productive marine areas (Gentry, 1998). Otariids are colonial breeders, and confined to a central place for breeding and raising offspring (Orians and Pearson, 1979). As part of this type of breeding behavior, Otariids have evolved into sexually dimorphic, polygynous breeders (Bartholomew and Hoel, 1953; Gentry, 1998). Similar to many members of the Otariid family, the reproductive cycle of the northern fur seal operates on a 12–month cycle (Boyd, 1991). This cycle, further described in detail below, is also displayed in Figure 1.5.

1.4 Timing of Reproductive Events in the Northern Fur Seal

Northern fur seals exhibit a high degree of annual reproductive synchrony. Males arrive first on the breeding colonies, during the months of May and early June in order to pick favorable sites and establish their territories (Gentry, 1998). Females
exhibit breeding philopatry or site fidelity, with repeated returns to their natal colonies throughout their reproductive lifetime. Arrival at the colony is highly consistent for females, as parturition occurs approximately 1–2 days after their arrival (Peterson, 1965; Gentry, 1998). Following arrival, females also exhibit synchronous timing of estrus post parturition (Atkinson, 1997).

Before returning to the breeding colonies each year, females will acquire adequate energy stores before their first haulout. Hauling out is a typical behavior of Otariids (and Phocids), referring to the temporary stays on land between periods of foraging activities at sea. The first haulout, better known as the perinatal period, lasts an average of 7 to 8 days. The perinatal period consists of a series of sequential events: parturition, the onset of lactation, estrus (approximately 5–7 days), and mating (Gentry, 1998; Boyd, 1991). The perinatal period also provides the mother and pup adequate time to bond by calling to one another and for the mother to determine her pup’s scent based on olfactory cues.

An important part of fur seal reproductive biology is the annual employment of an embryonic diapause. If ovum fertilization is accomplished during mating, the blastocyst undergoes a period of diapause of approximately 4 months (Craig, 1964). Embryonic diapause ends approximately in mid– to late–November when lactation ends (Craig, 1964). After embryonic diapause, the blastocyst implants into the uterine wall. Females then enter active gestation and fetal development continues for the next eight months until their return back to the rookery the following year (Craig, 1964). It has been suggested that photoperiod may regulate when diapause ends, thereby influencing synchronous reproductive timing (Temte, 1985).
However, reproductive timing has also been found to be affected by environmental conditions, individual age or body condition (Lunn and Boyd, 1993; Boyd, 1996; York and Scheffer, 1997; Guinet et al., 1998).

Soon after the perinatal period, females will alternate time on land suckling their pup and foraging at sea to maintain the energy stores needed for lactation (Ofstedal et al., 1987). This is better known as the maternal attendance pattern or foraging cycle strategy (Gentry and Kooyman, 1986). Pups are precocial and form tight aggregations onshore soon after birth as their mothers begin to depart on foraging trips. As pups grow, the majority of them can be found learning to swim in the surf zone (Baker and Donohue, 2000), although they are all still bound to the rookery during the suckling period. While northern fur seals are gregarious in nature, they are not social. Mothers are usually aggressive towards pups that are not their own and display confrontational behavior like open mouth threats, growling, or grabbing pups with their mouths and tossing them aside if hungry pups try to suckle (Bartholomew and Hoel, 1953). Thus, regular absences by mothers results in the pups regularly adapting to fasting periods during the lactation period. For northern fur seals, the lactation period lasts approximately 4 months and weaning is initiated by the offspring.

Northern fur seals are highly migratory, with adults and juveniles of both sexes departing the breeding grounds during October–November for approximately eight months. From this time, seals remain entirely pelagic until the following breeding season. Adult males have been found to remain at high latitudes in the waters surrounding Alaska and Russia (Bigg, 1990). Females and younger age classes
of both sexes migrate as far south as California, and can be found along the continental shelf and in the North Pacific Ocean during the winter (Bigg, 1990; Ream et al., 2005; Lea et al., 2009). Sexually mature seals return back to their natal breeding colonies in the spring and summer (Bigg, 1986), to begin this reproductive cycle anew.

Reproductive success, defined as the production of offspring living to a reproductive age and breeding (Clutton-Brock, 1988), is difficult to quantify for northern fur seals. Pups are pelagic for the first two, if not three, years of their life. The average age of primiparity in females is 5–6 years (York and Hartley, 1981), although females can come into estrus and begin breeding at the age of 3 (Craig, 1964; Yoshida, 1982). While males of the same age could also theoretically begin breeding, they are not socially or physically mature enough to hold harems until they reach an age of approximately 8–10 years. Juvenile males are found hauled out in non–reproductive groups adjacent to rookeries where they are able to spar with males of similar age and size. Subadult males will start to appear in rookeries as the territorial harem structures break down in early August (Gentry, 1998), as adult males will begin to depart the rookery as mating ceases.

1.5 Current Research

The Pribilof Islands are home to the majority of the world’s breeding population of northern fur seals, currently estimated at 55% (Testa, 2008). The populations on the Pribilof Islands expanded after the 1911 Convention called for the suspension of
Figure 1.5: Reproductive schedule of northern fur seals in the Pribilof Islands. Dashed lines represent median dates of parturition and weaning based on previously published dates in the literature. Female captures and field observations are also denoted, refer to Sections 2.2.2 and 2.2.3 for further details.
intense pelagic and land harvests until the late 1940’s (Roppel and Davey, 1965). The populations experienced brief increases after the end of female (1968) and commercial (1985) harvests, but since 1998 has declined 4.9% annually (Towell et al., 2010). Declines since 1998 are not related to hunting and the cause of the current decline is unknown. Current population estimates are extrapolated from the number of pups produced within a given breeding season (Towell et al., 2006). For a complete description of these methods please refer to Testa (2008) and Towell et al. (2006). While this provides the best estimate of pups produced in a given breeding season, no extant study has established the reproductive rates (in this thesis, a general term referring to either fertility or natality) of females.

Interestingly, there have been similar population declines in sympatric pinniped species like the Steller sea lion (*Eumetopias jubatus*) and the harbor seal (*Phoca vitulina*), as well as the sea otter (*Enhydra lutris*). In addition, population declines in black-legged and red-legged kittiwakes (*Rissa tridactyla* and *Rissa brevirostris*), and common and thick-billed murres (*Uria aalge* and *Uria lomvia*) have concomitantly occurred on the Pribilof Islands (Byrd et al., 2008). Current studies are investigating whether top-down or bottom-up forcing mechanisms exist that may potentially affect top predators in the North Pacific Ocean and Bering Sea. The Sequential Megafaunal Collapse Hypothesis postulated by Springer et al. (2003) suggested that the decimation of great whales in the Bering Sea caused the region’s apex predator, the killer whale (*Orcinus orca*), to shift prey preferences to pinnipeds and sea otters. Horning and Mellish (2009) recently showed that a proportion of juvenile Steller sea lions tagged in their study suffered mortalities
due to predation, and most likely by killer whales in the Gulf of Alaska.

An alternative hypothesis is based on the 1976–77 climatic regime shift in the North Pacific Ocean that impacted prey assemblages throughout the region (Anderson and Piatt, 1999). The Oscillating Control Hypothesis suggests that this regime shift caused nutritionally poorer quality prey to be more available in the eastern Bering Sea, resulting in deleterious impacts to the northern fur seal population on the Pribilof Islands (Hunt Jr. et al., 2002; Mantua and Hare, 2002). Another example of a bottom–up forcing mechanism is the interaction with commercial fisheries, as current Alaskan pollock (*Theragra chalcogramma*) landings are the largest of any single species in the United States (National Research Council, 2003).

Reproductive rates are essential for any effective modeling of population dynamics. Testa et al. (2010) recently determined an early term pregnancy rate for northern fur seals to vary from 0.85 to 0.92. In this study, direct estimates of the subsequent return and natality rates of the same females sampled in Testa et al. (2010) are presented, as well as a contemporary estimate of reproductive rates. In addition, the current timing of reproduction maternal attendance patterns were investigated and compared to historical estimates.
Chapter 2 – Reproductive Rates and the Timing of Births in a Northern Fur Seal Rookery

2.1 Introduction

Vital rates, such as natality and survival, are key demographic parameters in the study of population dynamics (Caughley, 1980). Life history theory posits that organisms will trade-off reproduction and survival in order to maximize their individual fitness (Stearns, 1992). There are natural physiological trade-offs made by reproductive females, because lactating females can be at a higher risk of mortality and subject to poorer body condition which may also decrease survival when compared to non-reproductive females (Clutton-Brock et al., 1982; Stearns, 1992). Since mammalian reproduction is an energy-depleting process, suboptimal environmental conditions may also result in changes in reproductive success (Bronson, 1985; Stearns, 1992). Colonial breeding and reproductive synchrony for mid– to high–latitude species occurs during the most favorable environmental conditions, thus ensuring peak food availability when nutritional requirements are at their greatest (Bronson, 1988; Boyd, 1991; Frederiksen et al., 2004). Current studies are investigating whether top–down or bottom–up forcing mechanisms may potentially affect apex predators in the North Pacific Ocean and Bering Sea (Anderson and Piatt, 1999; Mantua and Hare, 2002; Springer et al., 2003; Mueter and Litzow,
Monitoring vital rates can provide more immediate information on the potential effects of current ecological conditions as well as any age- or stage-related effects (Promislow and Harvey, 1990).

Otariids (fur seals and sea lions) are long-lived colonial breeding marine mammals, with low annual reproductive rates (or birth rates) and strong ties to land masses for reproductive purposes. Many Otariids exhibit a high degree of annual reproductive synchrony, with the timing of estrus synchronous to parturition (Atkinson, 1997). The peak of parturition for many fur seal species occurs early in the summer, partly due to favorable environmental conditions and the peak availability of prey that maximizes offspring survival (Boyd, 1991; Trites, 1992). If fertilization is accomplished following mating, the blastocyst undergoes a period of embryonic diapause of approximately 4 months (Craig, 1964). It has been suggested that photoperiod may regulate when diapause ends, therefore influencing synchronous reproductive timing (Temte, 1985). However, there has also been evidence that, similar to parturition, reproductive timing can also be affected by environmental conditions and individual age (Lunn and Boyd, 1993; Boyd, 1996; York and Scheffer, 1997).

Like other fur seal species of the world, northern fur seals (Callorhinus ursinus, Linnaeus 1758) were intensely hunted for pelts during the 19th and 20th centuries (Wickens and York, 1997). The exploitation of northern fur seals began in 1786, after the discovery of the Pribilof Islands by Russian explorers (Roppel and Davey, 1965; Towell, 2007). An extensive island and pelagic female harvest occurred from 1956 to 1968 with the thought that a smaller population would result
in maximum productivity and an increase in pregnancy and survival rates (York and Hartley, 1981; Towell, 2007). Although commercial harvests of northern fur seals ended in 1985, a small proportion of sub-adult males are still harvested annually for native subsistence purposes (Testa, 2008). Northern fur seals are a high latitude species with most breeding colonies located in the sub-polar region of the northern hemisphere. The two main islands of the Pribilof Island archipelago, Saint Paul and Saint George, are home to approximately 55% of the world’s population of northern fur seals (Testa, 2008). Current population estimates are extrapolated from the number of pups produced within a given breeding season (Towell et al., 2006, 2010). Since 1998, the Pribilof Island population has declined 4.9% annually (Towell et al., 2010). The cause of the most recent decline in northern fur seals is unknown.

Past Otariid studies have estimated natality rates (the number of young produced per reproductive females) from pregnant, harvested females (York and Hartley, 1981; Guinet et al., 1998; Pitcher et al., 1998). Recent studies measured serum progesterone concentrations during active gestation to determine pregnancy rates (McKenzie et al., 2005; Gibbens et al., 2010). Gibbens et al. (2010) reported pregnancy rates (the potential reproductive output, measured during gestation) of Australian fur seals (Arctocephalus pusillus doriferus) to be 0.84, and McKenzie et al. (2005) reported an early pregnancy rate (determined in the first 2–3 months of gestation) in New Zealand fur seals (Arctocephalus forsteri) to be 0.86. Although these reported pregnancy rates are relatively high, substituting pregnancy rate information for reproductive rates (or birth rates, a general term referring to
either fertility or natality) does not necessarily reflect the number of pups born.

Although a contemporary early term pregnancy rate on Saint Paul Island was found to be high and varied from 0.85 to 0.92 (Testa et al., 2010), a current estimate of natality (the number of young produced per reproductive female) is unknown in northern fur seal populations. Existing natality estimates were inferred from harvested females from the Pribilof Island population. York and Hartley (1981) estimated pup production (the annual number of female pups not born because of female harvests) to be highest for harvested females aged 2–8 years during 1958–1979 using age-specific survival and pregnancy tables (Lander, 1982). Natality rates were determined for a breeding colony in the Russian Commander Islands incorporating direct observational data on marked individuals of a known age. Vladimirov (1987) reported a natality rate of 0.82 during 1977–1981 for a northern fur seal breeding colony on the Russian Commander Islands, and determined pregnancy rate (the percentage of postpartum females in each age class during June and July) was highest for females aged 4–5 years.

Determining accurate reproductive rates in pinniped populations can be quite challenging. Loss of individual identification (i.e., tags or pelage markings), accuracy of classifying reproductive females, and low detection rates all increase the difficulty of estimating reproductive rates (Testa, 1987). Longitudinal studies of marked individuals provide the most comprehensive information on an individual’s lifetime reproductive contribution to a population, as well as the ability to compare total fitness between cohorts (Testa, 1987; Clutton-Brock, 1988; Lunn et al., 1994). However, reporting a cross-sectional natality rate can immediately evaluate
the possible effects of short-term variation in behavior or phenotype regardless of cohort (Clutton-Brock, 1988).

Direct counts of pinniped pups and adults, if conducted systematically, can provide information on population abundance and trends (Berkson and DeMaster, 1985; Calkins et al., 1999), as well as natality rates (Vladimirov, 1987). Uncorrected direct counts can underestimate population size because of the assumption that individuals are always detected if present, or that detection probability is always = 1. Detection probabilities of females can be influenced by reproductive status (with or without pups) (Testa, 1987), as well as the attendance patterns (or temporary emigration) of females suckling pups during the breeding season. Recent studies have begun to incorporate mark–recapture estimates in order to achieve better inferences on population size (Eberhardt, 2002; Watson et al., 2009). Mark–recapture estimates can provide researchers with a better understanding of detection probability, and allows for the incorporation of individual covariates to provide additional information that may improve the probability of detection (White, 2005).

In this study, the cross-sectional rate is defined as the fertility rate (total number of pups born divided by total number of females present), a rate based on all females present in the rookery (regardless of age) and all pups produced within a given year. Natality rates are based on all females present that are capable of reproducing (that have reached the age of reproductive maturity) and on all pups produced by these females within a given year. Reproductive rates are a more general term, including both natality and fertility rates as previously defined.
Additional reproductive parameters are defined within the text once introduced, but are also listed in Appendix A.

Reproductive rates are essential for any effective modeling of population dynamics, and can provide information on underlying causes in population trends (Eberhardt and Siniff, 1977). Contributing a contemporary reproductive rate in conjunction with estimates of early term pregnancy rates presented by Testa et al. (2010) will provide more detailed knowledge of the reproductive biology of this species, and will contribute further insight on the present demography of this declining population and establish a baseline dataset for future studies. The current timing of reproduction is important within the context of the current age structure of the population, as Vladimirov (1987) found that younger females arrived and bred later than females aged 7 years and older. Thus, the objectives of this study were to: (1) determine reproductive timing of breeding females and evaluate consistency through time, and (2) determine the reproductive rates for 2008 and 2009 and compare to existing pinniped reproductive rates.

2.2 Methods

2.2.1 Study Site

Saint Paul Island (57°06.54’N, 170°17.5’W), part of the Pribilof Island archipelago in Alaska, is located in the southeast Bering Sea continental shelf (see Figure 1.3. The archipelago is of volcanic origin and is part of the arctic tundra ecosystem.
There are 14 breeding colonies (rookeries) of northern fur seals dispersed around Saint Paul Island (see Figure 1.4). Animal captures and field observations were conducted in the last demarcated section of one rookery, Polovina Cliffs (see Figure 1.4). Polovina Cliffs is located on the eastern side of the island, and has been demarcated into sections for ease of scientific data collection and research (pup production estimates and male counts). The northernmost section of this breeding colony, section 7, is approximately 230 meters in length. The topography at section 7 is variable. The southern part of the section begins with a deep, sandy ravine that opens onto a wide boulder beach. As an observer walks northward, the topography changes. The beach narrows and starts to break into 8 successive coves. These coves result in high sea cliffs above the colony, such that an observer can be anywhere from 3 to 35 meters above the breeding colony depending on his/her location within this section. In addition to the boulder-like substrate, there are many caves and tall, rocky ledges on this beach.

2.2.2 Late Autumn Capture Methods

The National Marine Mammal Laboratory (NMML) is responsible for the management and monitoring of the northern fur seal population, and there have been numerous tagging studies for research purposes. In 2007, a female tagging program was initiated to better understand the population demographics of this breeding colony. Captures occurred between 6 and 16 November 2007 and between 15 and 22 November 2008, based on the median date (14 November) of blastocyst im-
plantation (or when the implantation chamber forms) determined from a prior study (York and Scheffer, 1997). Animals were captured using a noose pole and then held in a restraint board (Gentry and Holt, 1982) to be weighed, aged, and marked with individual alphanumeric plastic or monel flipper tags. Seals were permanently marked with individually numbered tags attached to the inter–digital connective tissue on the trailing edge of both fore flippers. In 2007, female seals (n = 135) were tagged with one small Allflex (AllFlex USA, Inc.) tag and one Monel (National Band and Tag Company, USA) tag; and in 2008, female seals (n = 66) were tagged with two Dalton (Dalton ID Systems, USA) Superflexitags.

Additionally in 2007 and 2008, females underwent a transrectal ultrasound imaging examination to determine pregnancy (Adams et al., 2007). In 2007, these females were marked with one large Allflex tag and a VHF-radio transmitter (n = 95, Advanced Telemetry Systems, Isanti, MN, USA) or two large Allflex tags (n = 1). In 2008, these females were marked with one Dalton Superflexitags and a VHF-radio transmitter (n = 38) or two Dalton Superflexitags (n = 2). The radio transmitters assisted in determining return rates the following breeding season in addition to quantifying whether or not a female gave birth to a pup based on her maternal attendance patterns.

Flipper-tagged females from older studies (prior to 2007) were also still using this rookery for breeding purposes. These females were all double-tagged with large Allflex tags (n = 25) or small Allflex tags (n = 1) during their respective captures. The reproductive status of these females were also included in order to improve the observed estimates of colony natality.
2.2.2.1 Age Determination

Age data was collected, analyzed and provided by the National Marine Mammal Laboratory, and the details of collection are provided here in the methods. A subsample of 50 females in 2008 were sedated using gas anesthesia (0.5–5% Isoflurane) administered with oxygen using a portable vaporizer. Once sedated, females were given a small dose of local anesthetic (0.7 ml lignocaine hydrochloride) next to the 1st postcanine tooth to reduce potential postoperative pain. The tooth was then extracted using a dental elevator. Details on the methodology of tooth removal is described in McKenzie (2006). Preparation of teeth and counting of growth layers were similar to the methods presented in McKenzie (2006) and Childerhouse et al. (2004). Age estimation was inferred from incremental growth layers counted in the cementum annuli of thin, stained sections of teeth. Analysis and age estimation was conducted by two separate laboratories: Matson’s Laboratory (Milltown, MT, USA) and the National Marine Mammal Laboratory. Results of this analysis were made available via the National Marine Mammal Laboratory.

2.2.3 Summer Field Methods

For 2008 and 2009, pup status was determined by the daily observations of marked females. In 2008, the association of females with pups was classified into the following categories: unknown, with pup, nursing. In 2009, the sampling protocol was modified and behavioral codes were expanded to better quantify the observed association of females with pups. The female behavioral codes were defined as
follows: 0–completely unknown, 1–apparently alone (no contact or interaction with any pup), 2–passive association with a pup (non–interactive but lying together as a distinct pair), 3–active association with a pup followed by positive interaction (nose–nose or nose–body contact), 4–nursing, 5–parturition (actual observation of a marked female giving birth).

In 2008, observations were conducted once per day between the hours of 0900 and 2100 (Alaska Time Zone), between 30 June and 31 August. In 2009, observations were conducted twice per day: first between the hours of 0700 and 1700 and second between the hours of 1800 and 2400 between 1 July and 25 August. The additional observational period in 2009 was included not only to increase the number of direct observations, but to extend observations into hours during which females when they would be more active. Females typically depart the colony on a crepuscular pattern (Loughlin et al., 1987).

Individual resight records were collected by observers walking above the colony using binoculars and/or spotting scopes to record a marked female’s presence in the colony and note her daily reproductive status. The daily frequency of observational visits allowed us to estimate i) when parturition occurred and ii) the attendance patterns of marked females throughout the breeding season. Observations spanned the time when the majority of pregnant females return to their natal colony to give birth, breed, and wean their pup (Table 2.1). On some days, observations were impossible to conduct because of inclement weather. Female attendance patterns meant that on any given day a female may be absent from the colony. In addition, because of the beach substrate and the topography surrounding this colony it is
possible that some of the marked individuals were noted as absent when in fact they were present. Thus, resighting rates of marked individuals are a composite of the probability the female was present in the rookery, the detection rate, and the probability a marked female was seen if she was present in the rookery.

Table 2.1: Observation dates during the breeding seasons in 2008 and 2009.

<table>
<thead>
<tr>
<th>Year</th>
<th>Period</th>
<th>Days of Observation</th>
<th>Missed Observation</th>
<th>Days</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>30 June-31 August</td>
<td>63</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>2009</td>
<td>1 July-25 August</td>
<td>56</td>
<td>4</td>
<td></td>
</tr>
</tbody>
</table>

In 2008 only, the 24-hour presence or absence of females instrumented with a VHF-radio transmitter was monitored using a stationary, remote data-logging system placed at the southernmost part of Section 7. This system consisted of a VHF receiver (Model R4000, Advanced Telemetry Systems Inc., Isanti, Minnesota) linked to a Data Collection Computer (DCC; Model DC5041, Advanced Telemetry Systems Inc., Isanti, Minnesota) powered by a rechargeable 12v battery hooked up to a solar panel. The VHF receiver was also connected to one 2-element antenna that pointed northward and directly into the colony. The DCC sequentially scanned each programmed frequency for 10 seconds before moving onto the next programmed frequency. Pulse data and median pulse rate was collected for each detectable frequency from 6 July to 26 August 2008. The 24-hour monitoring for these transmitters allowed the determination of the presence for those females outfitted with VHF transmitters during the previous fall season. Daily counts of females and pups (2008, 23 June through 25 August) and pups only (2009, 1 though 31 July) were conducted. Counting was conducted during female resight
observations using a tally counter and binoculars. In 2008, there were thirteen
days where pups were not counted (26 June; 14, 20, 27, and 30 July; 3, 8, 11,
13, 14, 20, 22, and 24 August). In 2009, pups were counted twice a day during
each visit to the breeding colony and the highest count from both visits was used.
Dead pups were separately counted during both breeding seasons. In 2008, dead
pup counts were conducted from 5 July through 30 August (dead pups were not
counted on 8, 12, and 13 July). In 2009, dead pup counts were conducted from 14
July through 29 July (dead pups were not counted on 16, 18, and 20 July), and
additionally on 1 and 16 August.

2.2.4 Timing of Reproductive Events

Mean and median date of birth were determined from sigmoid growth models fitted
to the corrected, cumulative pup counts. These dates were estimated as the date
corresponding to one-half of the maximum count reached in a sigmoid growth
model following Trites (1992). Because this type of growth curve is symmetrical,
the mean and median are equivalent to one another. Estimating mean dates of
birth can provide estimates on the mean age of pups as well as provide information
on the timing of implantation the previous year (Trites, 1992). Trites (1992)
estimated mean and median dates of birth from historical pup count data on Saint
Paul Island. Since these dates were calculated using similar sigmoid growth models,
a secondary objective was to test the prediction that the 2008 and 2009 mean and
median dates of birth were similar to historical estimates. Data presented as
means are $\pm$ 1 SE and statistical differences are considered significant at $p < 0.05$. Statistical analyses were conducted using S–PLUS (version 8.0, TIBCO Software, Inc.).

The 2008 and 2009 pup counts were corrected for pup mortality. Because some carcasses will disappear, the dead pup count will fluctuate between days and not increase in a linear fashion throughout the breeding season. When the daily count decreased during the season (i.e., if the day 2 count was less than the day 1 count) it was assumed that the difference was caused by carcasses disappearing. Any dead pup increments between successive counts were summed throughout the season. Cumulative pup counts were estimated from a sigmoid growth model (displayed in Appendix C) to account for the inability to access the breeding colony to remove dead pups. The daily estimates from the sigmoid equation were added to the daily count estimates of the uncorrected live pup counts, and the sigmoid growth models corrected for pup mortality are presented.

Cumulative pup count data were fit to the following sigmoid function (Tsoularis and Wallace, 2002) that estimates the total number of pups produced within the breeding season can be described as:

$$P_t = a + \frac{b}{1 + \exp\left(\frac{-(x-c)}{d}\right)}$$

Where: $a =$ minimum asymptote, $b =$ maximum asymptote, $c =$ inflection point, and $d =$ slope factor. Parameter estimates for $a$, $b$, $c$, and $d$ were obtained by fitting the sigmoid growth model in TableCurve 2D (Sigma Plot, 2010).
2.2.5 Detection Rate Model Estimations

Tagged females can be present or absent from the rookery during daily counts because of variation in individual attendance patterns and reproductive status. In addition, if present, tags can remain undetected (or detected and unread) during direct observations because of the beach substrate and topography surrounding this colony as well as the resting behavior of females onshore. For these reasons, detection rates of marked females were < 1 and some measure of detection rates was needed in order to reduce the bias in daily counts of females. In this study, resighting rates of marked individuals comprised of 1) the probability the female was present in the rookery and 2) the probability a marked female was seen if she was present in the rookery.

The probability of detecting a marked female if she was present on the colony was calculated using a Cormack-Jolly-Seber (CJS) open population model (Lebreton et al., 1992). Models were parameterized and maximum likelihood estimates, standard errors, and confidence limits were generated using Program MARK (White and Burnham, 1999). Variable attendance patterns of lactating females means that for any given survey, only part of the population is available for resighting. As pups get older, females spend more time at sea and less time on the colony (Gentry and Kooyman, 1986). Thus, data analysis was initially confined to the two weeks surrounding the median pupping date because females spend the most time on the colony during the first 7-10 days postpartum, and this should be the time when peak numbers of females are present in the rookery. This approach
was used to increase the proportion of the females with pups that were present onshore during direct observations. However, it has been documented that older females give birth earlier than younger females (Boltnov and York, 2001). Because of this staggered age effect in returning to the breeding colony, an additional analysis was conducted for the entire season to determine how detection rates changed throughout the season. In this case, resighting probability estimates incorporate effects on detections when a female was present on the colony and effects resulting from temporary emigration associated with attendance patterns as females were not always present and available for sampling.

The primary purpose of this modeling effort was to estimate detection probabilities and the factors that may influence the detection of females. Because the reported annual survival of reproductive-aged females is relatively high (>0.80; (York and Hartley, 1981; Lander, 1982)), I predicted daily survival rates would be constant. This prediction was tested by comparing a $\Phi(t)p(t)$ model to a $\Phi(.)p(t)$ model. The outcome of this comparison was then considered the most general structure for survival and used for all further detection rate modeling. Separate candidate models were fit for 2008 and 2009. Daily detection rate estimates, $p$, from the best model were used to correct the daily female count data collected in 2008 to determine the total number of females using the breeding site on any given day regardless of their reproductive status (i.e., with pup, without pup, or undetermined).
2.2.5.1 *A priori* models for hypothesized effects on detection rates

I considered the effects of the following covariates: general time effects/full time variation (t), three possible time trends, linear (T), logarithmic (lnT), and quadratic, tag status (one tag or two), and density of females (Table 2.2). The daily counts of females (the density covariate) were included in the 2008 models because of the tight aggregation of females and harem social structures during the peak of the breeding season, which could affect detection probabilities. All of these covariates were considered as additive effects as I did not hypothesize *a priori* any relevant interactions.

Table 2.2: Covariates estimated for their effects on marked female detection probabilities.

<table>
<thead>
<tr>
<th>Covariate</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>General time effect</td>
<td>detection rates allowed to vary by survey period <em>(i.e. daily)</em></td>
</tr>
<tr>
<td>Time trend</td>
<td>linear (T), logarithmic (ln(T)), quadratic</td>
</tr>
<tr>
<td>Tag status</td>
<td>1 or 2 tags</td>
</tr>
<tr>
<td>Density</td>
<td>density of animals at the site</td>
</tr>
</tbody>
</table>

I followed an information-theoretic approach and selected the best model based on the lowest Akaike’s information criterion (AIC) value, and AICc model weights (Burnham and Anderson, 2002). I interpreted the strength and direction of effects using the 95% confidence limits on slope coefficients (β) in the best models. Those effects with coefficient confidence limits that did not include zero were considered to have more support. A candidate model set was constructed to test the *a priori* hypotheses about the factors that would most affect the probability of a female being detected if she was present in the breeding colony.
Table 2.3: Candidate model set for 2008 and 2009.

<table>
<thead>
<tr>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Phi(t)p(t)$</td>
</tr>
<tr>
<td>$\Phi(.p(t)$</td>
</tr>
<tr>
<td>$\Phi(t)p(.)$</td>
</tr>
<tr>
<td>$\Phi(.)p(.)$</td>
</tr>
<tr>
<td>$\Phi(.)p(T)$</td>
</tr>
<tr>
<td>$\Phi(.)p(ln(T))$</td>
</tr>
<tr>
<td>$\Phi(.)p(\text{quadratic})$</td>
</tr>
<tr>
<td>$\Phi(.)p(\text{density}), \text{2008 only}$</td>
</tr>
<tr>
<td>$\Phi(.)p(\text{tag status})$</td>
</tr>
<tr>
<td>$\Phi(.)p(\text{best time+density}), \text{2008 only}$</td>
</tr>
<tr>
<td>$\Phi(.)p(\text{best time+tag status})$</td>
</tr>
<tr>
<td>$\Phi(.)p(\text{best time+tag status+density}), \text{2008 only}$</td>
</tr>
</tbody>
</table>

*Time effects*—A decrease in detection rates, $p$, was predicted over the course of breeding season, although the specific structure (linear, quadratic, etc.) was unknown. As pups get older, females will spend less time at the breeding colony and more time at sea foraging. Over the course of the season, a proportion of pups will die and the mothers of these pups do not need to return back to the colony.

*Females with 2 tags will have higher detection rates than females with 1 tag*—Females caring for pups have a predictable pattern of behavior. After returning to the colony, mothers spend some time actively searching for their pup. Once they find their pups, mothers will begin to suckle their pups and rest. The normal resting pattern for a female onshore is to tuck both foreflippers under her body, which can make tags hard to see. If one of her tags was missing, I hypothesized that she would have an overall lower detection rate throughout the breeding season, despite the time of the season or animal density.
Decreased detection rates at increased densities of animals—During the height of the breeding season, many females and males will be on land for reproductive purposes. Males fiercely guard their harems against other males and often patrol the perimeter of the harem boundary. Females tend to form tight aggregations during this time period. I predicted that females would have decreased detection rates during the peak of the breeding season because it will be harder to see tags and distinguish individuals when densities are high.

2.2.6 Observed Reproductive Rate Estimates

Reproductive rate was calculated in two different ways. First, observed estimates of natality based on repeated behavioral observations for two consecutive breeding seasons are presented for all marked females in 2008 and 2009 and for females marked and outfitted with a VHF–radio transmitter in 2007 (and subsequently monitored in 2008). During the autumn capture season in 2008, a subsample of females were marked and outfitted with a VHF–radio transmitter. During the 2009 breeding season, a similar monitoring system was constructed at the same location at Polovina Cliffs to monitor females outfitted with VHF–radio transmitters. There were considerable mechanical complications and logistical constraints with the data logging system in 2009, thus only the telemetry data from 2008 is presented.

A female was considered as having a pup in the year of observation if she was 1) observed nursing at least one time, 2) observed or detected via VHF radio telemetry for 1–3 sequential days on ≥ 2 separate occasions during the main breeding season
(suggesting repeated returns to the colony to care for an offspring), or 3) observed or detected via VHF radio telemetry for 4 sequential days upon first sighting or radio detection (indicating a perinatal period). A female was considered to be with pup if she met at least one of these established criteria and considered ‘undetermined’ if she failed to meet at least one of these established criteria. The different methods of detection (direct observations of marked individuals versus detection of VHF–radio transmitters) were compared, and the observed estimates of natality for these two related groups are presented.

Directly observed estimates of natality were calculated as the number of marked females determined with a pup/total number of marked females. This calculation is based on the assumption that all marked females were of reproductive age at the time of their marking (for the majority of the females in this study, the time of marking was the previous November). Females assigned to the undetermined category were likely without a pup because of their irregular behavior and infrequent visits to the breeding colony. Females with pups have predictable behavior as they have to continually return to the colony to suckle their pups.

Second, the cumulative counts of females were compared to the cumulative counts of pups to generate a fertility estimate in 2008. Female count data was corrected by the daily detection rate estimates (\( \hat{P}_t \)) generated in program MARK (raw count/detection rate = corrected count). This adjustment was made in order to determine the daily number of females frequenting the rookery regardless of having marks, their reproductive status, or whether present in the rookery or absent on a foraging trip. Daily counts throughout the breeding season will result
in multiple counts of the same females because of maternal attendance patterns of females suckling pups. To adjust for this behavior, only female counts up to the date inclusive of 98% of pup births (determined from sigmoid cumulative pup count models) were used. I assumed the calendar date closest to this calculated percentage was the closest to when the majority of females would be on land. The curve fitting routine was similar to the methods described in Section 2.2.4. The ratio of the values at the asymptotes from the corrected pup and female sigmoid curves is presented as the fertility estimate in 2008. Because daily female counts were not conducted in 2009, a fertility estimate cannot be estimated for that year.

2.3 Results

2.3.1 Timing of Reproductive Events

The corrected estimates from the sigmoid growth models with their 95% confidence intervals are presented for 2008 and 2009 in Figure 2.1 and Figure 2.2. In 2008, the mean and median date of parturition was 17 July, with the following parameter values: \( a = -60.21, b = 1567.13, c = 24.48, d = 5.57, \) Table 2.4. In 2009, the mean and median date of parturition was 15 July, with the following parameter values: \( a = -279.11, b = 1829.87, c = 13.14, d = 7.30, \) Table 2.4. The uncorrected estimates from the sigmoid growth models are presented in Appendix B. Pup mortality estimates from the sigmoid growth models are presented in Appendix C.

The results from a 2–tailed, heteroscedastic Student’s t-test indicated that the
median dates of parturition from this study significantly differed \((p = 0.0098)\) from the historical median dates of parturition (Table 2.4) calculated using similar methods (Trites, 1992). Under the central limit theorem (Rice, 1995), I am assuming normal distribution of the means under the assumption that the type of distribution of the cumulative pup birthing model does not change over time. Based on the sample sizes of \(> 200\) (1983) and \(> 700\) (all other years) in Trites (1992), this suggests that sigmoid curves accurately model the arrival of pups. Thus the assumptions of comparable distributions is based on all cumulative pup counts being explained by the same type of sigmoid growth curve.

Table 2.4: The 2008 and 2009 estimates of the mean and median dates of parturition presented along with previous estimates of this date on Saint Paul Island. Trites (1992) presented estimates from models corrected for pup mortality, these estimates are displayed here.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Corrected</td>
<td>10 July</td>
<td>4 July</td>
<td>5 July</td>
<td>10 July</td>
<td>17 July</td>
<td>15 July</td>
</tr>
</tbody>
</table>

2.3.2 Detection Rate Model Results, 2008

Out of the four general time variant \(\Phi\) and \(p\) models, the \(\Phi(.), p(t)\) model had the lowest AICc, as shown in Table 2.5. This result supported the preliminary hypothesis that the survival parameter, \(\Phi\), should be held constant (and not equal to zero) during the breeding season. Resighting probability \((p)\) was best modeled with general time variation, and none of the time trend structures were supported
Figure 2.1: 2008 sigmoid curve fit to pup count data with 95% confidence intervals. The dashed line represents the mean and median date of parturition. The presented model is corrected for pup mortality (mean and median date 17 July; D.F. adjusted $r^2 = 0.99$, S.E. fit = 47.69). 23 June = 1, 2 July = 10. For details on equation, see text in Section 2.3.1.
Figure 2.2: 2009 sigmoid curve fit to pup count data with 95% confidence intervals. The dashed line represents the mean and median date of parturition. The presented model is corrected for pup mortality (mean and median date 15 July; D.F. adjusted $r^2 = 0.98$, S.E. fit = 62.53). 1 July = 1, 5 July = 5. For details on equation, see text in Section 2.3.1.
(shown in Table 2.6). As anticipated, resighting probability continually declined as the season progressed (Figure 2.4), though early season (2 through 10 July) detection rates varied from 0.32 to 0.85 with high standard errors (Figure 2.4). This suggests that female attendance patterns resulting in progressive absences throughout the breeding season are a major driver of resighting probabilities.

After retaining the best time structure on detection rates I added the additional covariates of interest (Tag Status and Density) and the two models were equally competitive, with identical deviance, AICc, and AICc weights (Table 2.7). Both included the effect of Tag Status, and one of these models also included Density (Table 2.7). The effect of tag status was positive as females with 2 tags had higher detection rates than those with only one tag and this was a strong effect ($\beta = 0.87; 95\% \text{ CI: } 0.54 \text{ to } 1.21$; Figure 2.3). The effect of female density was also positive, but the 95% confidence limits associated with the slope coefficient for this effect strongly overlapped zero. Given that Density added so little to explain variation in detection rates ($\beta = 0.002; 95\% \text{ CI: } -0.050 \text{ to } 0.054$), and did not improve the model at all when included, I opted to use the competitive model that excluded this covariate. I corrected the daily female counts in 2008 using detection rates generated for double–tagged females from $\Phi(.)p(TS+t)$ (Figure 2.3). I chose to use the probability derived for double–tagged females to correct female counts because density explained only a small portion of variation in detection rates.

Detection probability of unmarked females is probably higher than the probability of seeing flipper tags, since only bodies need to be seen for counts. Thus, daily detection probabilities for females with two tags were used to correct fe-
male counts in order to provide the best estimates of females using the rookery. Nevertheless, the corrected female count may be an overestimate, and secondarily derived fertility an underestimate, or minimum value.

Table 2.5: 2008 general time variant models of \( \Phi \) and \( p \).

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>( \Delta )AIC</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th>Number of Parameters</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Phi(\cdot)p(t) )</td>
<td>5972.60</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>50</td>
<td>5868.81</td>
</tr>
<tr>
<td>( \Phi(t)p(t) )</td>
<td>6064.80</td>
<td>92.20</td>
<td>0</td>
<td>0</td>
<td>97</td>
<td>5856.15</td>
</tr>
<tr>
<td>( \Phi(\cdot)p(\cdot) )</td>
<td>6291.70</td>
<td>319.11</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>6287.70</td>
</tr>
<tr>
<td>( \Phi(t)p(\cdot) )</td>
<td>6306.34</td>
<td>333.74</td>
<td>0</td>
<td>0</td>
<td>50</td>
<td>6202.54</td>
</tr>
</tbody>
</table>

Table 2.6: 2008 models testing various time effects on \( \Phi(.) \) and \( p \).

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>( \Delta )AIC</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th>Number of Parameters</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Phi(\cdot)p(t) )</td>
<td>5972.60</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>50</td>
<td>5868.81</td>
</tr>
<tr>
<td>( \Phi(.)p(\text{quadratic}) )</td>
<td>6026.52</td>
<td>53.93</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>6018.49</td>
</tr>
<tr>
<td>( \Phi(.)p(\text{T}) )</td>
<td>6029.74</td>
<td>57.14</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>6023.72</td>
</tr>
<tr>
<td>( \Phi(.)p(\text{lnT}) )</td>
<td>6031.27</td>
<td>58.68</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>6025.26</td>
</tr>
</tbody>
</table>

Table 2.7: 2008 models of apparent daily resight probability.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>( \Delta )AIC</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th>Number of Parameters</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \Phi(.)p(\text{Density+TS+t}) )</td>
<td>5942.25</td>
<td>0</td>
<td>0.5</td>
<td>1</td>
<td>52</td>
<td>5838.46</td>
</tr>
<tr>
<td>( \Phi(.)p(\text{TS+t}) )</td>
<td>5972.60</td>
<td>28.2</td>
<td>0</td>
<td>0</td>
<td>51</td>
<td>5868.81</td>
</tr>
<tr>
<td>( \Phi(.)p(\text{Density+t}) )</td>
<td>5970.45</td>
<td>30.35</td>
<td>0</td>
<td>0</td>
<td>50</td>
<td>5868.81</td>
</tr>
<tr>
<td>( \Phi(.)p(\text{Density}) )</td>
<td>625.26</td>
<td>323.01</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>6259.24</td>
</tr>
<tr>
<td>( \Phi(.)p(\text{TS}) )</td>
<td>6271.29</td>
<td>329.05</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>6265.28</td>
</tr>
</tbody>
</table>
Figure 2.3: Detection probability estimates based on tag status from model $\Phi(.)p(TS+t)$ in 2008. Daily resight probabilities throughout the observed breeding season for marked females with 2 tags and females with 1 tag are presented.
2.3.3 Detection Rate Model Results, 2009

Out of the four general time variant $\Phi$ and $p$ models, the $\Phi(.)p(t)$ model had the lowest AICc, as shown in Table 2.8. This result supports the preliminary hypothesis that the survival parameter, $\Phi$, should be held constant (and not equal to zero) during the breeding season.

Various time effects were investigated to determine how resighting probability, $p$, was best modeled throughout the breeding season. Similar to the results in 2008, the general time variant model performed the best, as shown in Table 2.9.

After retaining the best time structure on detection rates I added the additional
Table 2.8: 2009 general time variant models of $\Phi$ and $p$.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$AIC</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th>Number of Parameters</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Phi(.)p(t)$</td>
<td>7505.26</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>52</td>
<td>7398.15</td>
</tr>
<tr>
<td>$\Phi(t)p(t)$</td>
<td>7599.25</td>
<td>93.99</td>
<td>0</td>
<td>0</td>
<td>102</td>
<td>7383.05</td>
</tr>
<tr>
<td>$\Phi(.)p(.)$</td>
<td>7978.42</td>
<td>473.16</td>
<td>0</td>
<td>0</td>
<td>2</td>
<td>7974.41</td>
</tr>
<tr>
<td>$\Phi(t)p(.)$</td>
<td>8030.89</td>
<td>525.63</td>
<td>0</td>
<td>0</td>
<td>52</td>
<td>7923.78</td>
</tr>
</tbody>
</table>

Table 2.9: 2009 models testing various time effects on $\Phi(.)$ and $p$.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$AIC</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th>Number of Parameters</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Phi(.)p(t)$</td>
<td>7505.26</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>52</td>
<td>7398.15</td>
</tr>
<tr>
<td>$\Phi(.)p$(quadratic)</td>
<td>7530.69</td>
<td>25.43</td>
<td>0</td>
<td>0</td>
<td>4</td>
<td>7522.67</td>
</tr>
<tr>
<td>$\Phi(.)p$(lnT)</td>
<td>7553.58</td>
<td>48.32</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>7547.57</td>
</tr>
<tr>
<td>$\Phi(.)p$(T)</td>
<td>7584.41</td>
<td>79.15</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>7578.40</td>
</tr>
</tbody>
</table>

Table 2.10: 2009 models of apparent daily resight probability.

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>$\Delta$AIC</th>
<th>AICc Weights</th>
<th>Model Likelihood</th>
<th>Number of Parameters</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\Phi(.)p(TS+t)$</td>
<td>7492.80</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>53</td>
<td>7383.57</td>
</tr>
<tr>
<td>$\Phi(.)p(t)$</td>
<td>7505.26</td>
<td>12.46</td>
<td>0</td>
<td>0</td>
<td>52</td>
<td>7398.15</td>
</tr>
</tbody>
</table>
covariate of interest (Tag Status); the top models are presented in Table 2.10. The Tag Status covariate had a similar effect on resighting rates as it did in 2008, although the magnitude of the effect was not as strong ($\beta = 0.41$; 95% CI: 0.19 to 0.62; Figure 2.5), compared to 0.87 in 2008. However, there was evidence that females with two tags had an overall higher detection probability than females with only 1 tag (Figure 2.5). This supports the preliminary hypothesis that tag status should have an effect on detection probability throughout the observed breeding season, after accounting for the effects of maternal attendance patterns.

Early in the season, from 3 to 11 July, detection rates varied from as low as 0.38 to as high as 0.87. Standard errors were high from 3 to 7 July, but became smaller for the remainder of this early part of the season (Figure 2.6). As anticipated, overall resighting probabilities dropped considerably after 11 July and this low detectability trend continued throughout the remaining breeding season (Figure 2.6).

### 2.3.4 Observed Reproductive Rate Estimates

Of the 208 marked females observed at the rookery in 2008, 58% ($N = 121$) were observed nursing, though it often took more than 5 observations to determine reproductive status (Table 2.11). Post hoc criteria (shown in Table 2.12) were applied to the observation data to assign a reproductive status to marked females. The most inclusive set of criteria resulted in an observed natality rate of 0.79 (Table 2.11, Table 2.13). Based on these criteria, the reproductive status of 43 females
Figure 2.5: Detection estimates based on tag status from model $\Phi(.) p(TS+t)$ in 2009. Daily resight values throughout the observed breeding season for marked females with 2 tags and females with 1 tag are presented.
remained undetermined. Of the 217 marked females observed at the rookery in 2009, 79% were observed nursing. The application of the *post hoc* criteria (Table 2.12) resulted in an observed natality rate of 0.88 (Table 2.11, Table 2.13). Based on these criteria, the reproductive status of 26 females was remained undetermined. Compared to 2008, more females were determined with a pup in 2009 by the direct observation of a female nursing her pup, displayed in Figure 2.7.

Two different methods were compared for the females that were tagged with one Allflex tag and one VHF-radio transmitter in 2007. In 2008, 77 females were observed returning to the colony, and reproductive status was confirmed from observations for 61 of these females. This resulted in an observed reproductive rate of 0.79 (Table 2.11). Conversely, 85 females were detected with the stationary data
logger. Two of the afore mentioned criteria were applied to this subset of females: if the female was detected for four consecutive days, or if she was detected for 1–3 sequential days on $\geq 2$ times throughout the breeding season via the VHF data logging system (Table 2.12. Similar to the direct observations, these patterns were assumed to be indicative of maternal attendance behavior. Out of the 85 detected females, 81 were assumed to have given birth to a pup based on the established criteria, resulting in an observed natality rate of 0.95 (Table 2.11).

The timing of parturition can also be estimated based on the observed arrival of the marked females. Out of the 165 females that were determined with a pup in 2008, the mean and median date of return was 16 July, with a range of 1 July through 25 August. Out of the 191 females that were determined with a pup in 2009, the mean and median date of return was 14 July with range of 1 July through 23 August. From this, one can assume that the subsequent peak of parturition occurred from 17–18 July in 2008 and 15–16 July in 2009.

2.3.5 Age Distribution

Cementum annuli from the post canine teeth were counted by two separate laboratories: Matson’s Laboratory (Milltown, MT, USA) and the National Marine Mammal Laboratory. A correlation matrix was constructed for the two estimations of the aged females. Age estimations from both labs were correlated at 0.99, and the estimations from the National Marine Mammal Laboratory are presented. As shown in Figure 2.8, the majority of the females sampled were of the ages 5,
Table 2.11: Number of observations necessary to link marked females with pups at Polovina Cliffs in 2008 and 2009. The observations on females that were outfitted with VHF–radio transmitters are compared to their VHF attendance patterns, and their reproductive rates are also presented. For definitions of the listed numerical criteria, see Table 2.12.

<table>
<thead>
<tr>
<th>Year</th>
<th>Criteria</th>
<th>(N^1)</th>
<th>No Pup</th>
<th>Pupped</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4–5</th>
<th>&gt;5</th>
<th>Observed Natality</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>1,2,3</td>
<td>208</td>
<td>43</td>
<td>165</td>
<td>16</td>
<td>22</td>
<td>18</td>
<td>36</td>
<td>73</td>
<td>0.79</td>
</tr>
<tr>
<td>2008</td>
<td>1</td>
<td>208</td>
<td>87</td>
<td>121</td>
<td>16</td>
<td>22</td>
<td>18</td>
<td>26</td>
<td>39</td>
<td>0.58</td>
</tr>
<tr>
<td>2008</td>
<td>1,2,3</td>
<td>77</td>
<td>16</td>
<td>61</td>
<td>10</td>
<td>10</td>
<td>6</td>
<td>10</td>
<td>25</td>
<td>0.79</td>
</tr>
<tr>
<td>2008</td>
<td>4 and 5</td>
<td>85</td>
<td>4</td>
<td>81</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>81</td>
<td>0.95</td>
</tr>
<tr>
<td>2009</td>
<td>1,2,3</td>
<td>217</td>
<td>26</td>
<td>191</td>
<td>24</td>
<td>46</td>
<td>35</td>
<td>43</td>
<td>43</td>
<td>0.88</td>
</tr>
<tr>
<td>2009</td>
<td>1</td>
<td>217</td>
<td>45</td>
<td>172</td>
<td>24</td>
<td>46</td>
<td>35</td>
<td>35</td>
<td>32</td>
<td>0.79</td>
</tr>
</tbody>
</table>

\(^1\)The total number of marked females observed or detected.

\(^2\)Natality rate for 77 females outfitted with a VHF–transmitter that were observed at least once during the season in the colony.

\(^3\)Natality rate for 85 females outfitted with a VHF–transmitter and detected through direct observation in the colony (\(n = 77\)), plus those by the VHF receiver only (\(n = 8\)).

Table 2.12: *Post hoc* criteria established for the inclusion of different female behaviors in order to achieve the best estimate of a natality rate at Polovina Cliffs. Criteria used for natality estimates are shown in Table 2.11.

<table>
<thead>
<tr>
<th>Criterion</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Nursing</td>
</tr>
<tr>
<td>2</td>
<td>Observed Perinatal Period</td>
</tr>
<tr>
<td>3</td>
<td>Observed Attendance Pattern</td>
</tr>
<tr>
<td>4</td>
<td>VHF–determined Perinatal Period</td>
</tr>
<tr>
<td>5</td>
<td>VHF–determined Attendance Pattern</td>
</tr>
</tbody>
</table>
Table 2.13: Observed Natality Rates in 2008 and 2009, displayed for the different criteria that were established post hoc, as per Table 2.12.

<table>
<thead>
<tr>
<th>Year</th>
<th>N&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Observed Rate</th>
<th>N&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Observed Rate</th>
<th>N&lt;sup&gt;3&lt;/sup&gt;</th>
<th>Observed Rate</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>121</td>
<td>0.58</td>
<td>131</td>
<td>0.63</td>
<td>165</td>
<td>0.79</td>
</tr>
<tr>
<td>2009</td>
<td>172</td>
<td>0.79</td>
<td>180</td>
<td>0.83</td>
<td>191</td>
<td>0.88</td>
</tr>
</tbody>
</table>

<sup>1</sup>The total number of females identified as nursing, criterion 1.
<sup>2</sup>The total number of females identified as nursing plus identified as having a 4 consecutive day-presence onshore, criteria 1 and 2.
<sup>3</sup>The total number of females identified as nursing plus identified as having a 4 consecutive day-presence onshore plus 2 onshore visits during the breeding season, criteria 1, 2, and 3.

Figure 2.7: Comparison of behavioral observation methods in two years. Pup categories as per Table 2.12.
6, and 7 (thus pupping at ages 6, 7, and 8), which was to be expected because of the late November sampling periods in both years and since these age groups have the greatest reproductive potential and may still be present in the rookery in November weaning pups (York and Hartley, 1981).

Figure 2.8: Age–frequency distribution of sampled females (n=50) at Polovina Cliffs in 2008. Females that returned and pupped the following year (n=32) and females that returned whose pup status was not determined (n=3) are also presented.

2.3.5.1 2008 Fertility Estimate

The top two CJS models in 2008 were equally competitive, with identical deviance, AICc, and AICc weights (Table 2.7). This resulted in both models having identical daily estimates of detection probability (p) and standard errors. Additionally, there was no significant difference between mean detection estimates derived from the top
two CJS models for the entire season ($p = 0.99$). The top two models were equally competitive, though density added very little to explain the variation in detection rates. Because of this reason, I chose the more parsimonious model, $\Phi(.) p(TS+t)$. The effect of tag status was positive, as females with 2 tags always had higher detection rates than those with only one tag (Figure 2.3). The 2008 female counts were corrected using daily detection rates generated for double-tagged females from the model $\Phi(.) p(TS+t)$.

This correction resulted in one outlier, based on a low daily detection probability with large standard error. The mean of the corrected count the day before and the day after was calculated; this value was used to replace the outlier that was omitted from the sigmoid growth model fitting. The calendar date closest to 98% of the pup asymptote was 8 August. I assumed that the majority of the females would be on land for reproductive purposes up to 8 August. After fitting a model to the count data, two further outliers outside of the 95% confidence intervals were deleted. The sigmoid curve fit to the corrected female count data is shown in Figure 2.9, with the following parameter values: $a = 93.34$, $b = 2428.74$, $c = 20.89$, $d = 3.18$.

The asymptote of the corrected female count curve was 2522. The asymptote of the corrected pup count curve was 1507. Thus, the ratio between these two asymptotes results in 0.60, the 2008 fertility estimate.
2.4 Discussion

2.4.1 Detection Rate Model Estimations

As shown in Figures 2.4 and 2.6, there was a high degree of variability in the early resighting rates, when most females that have arrived would presumably be observed during their perinatal period. However, with a median arrival date of July 15 and 17 in the two years, respectively (see Section 2.4.2), the sample size early in the season is small. Subsequently, as the sample size (female count) increases, earlier arrivals are initiating foraging trips. The initial prevalence of perinatal periods, combined with a small initial sample size thus explains the high resight probabilities combined with large variance early in the season. The subsequent onset of foraging trips combined with an increasing female count then explains the progressively reduced resight probabilities and variance, respectively.
In both years, resighting rates sharply declined by the third week of the observed breeding season, but had much smaller standard errors as the season progressed (Figures 2.4 and 2.6. These results partially support the preliminary hypothesis that there would be a decrease in detection rates over time. Additionally, there are marked behavioral changes in both females and males after the peak of parturition. After estrus and mating, only a proportion of lactating females will be onshore as the rest will be at sea foraging. These attendance patterns explain much of the overall decline in resighting rates during the observed breeding season and suggest that females with surviving pups exhibit similar attendance patterns over time during lactation and weaning. In addition, many harem–holding males begin departing the colony soon after breeding, and their absence allows females more freedom to move about the colony. The probability of resighting marked individuals early in the season was higher in 2009 than in 2008, most likely due to the additional sampling period and the time of day direct observations were conducted.

Females with two tags had higher detection probabilities throughout the season compared to females with one tag, in support of my preliminary hypothesis. There was little support for the effect of female density on detection rates, thus I concluded that increased densities of animals onshore did not lead to an overall decrease in detection rates.
2.4.2 Observed Estimates of Natality

When I compared observation–based estimates of natality of marked females versus those classified as with a pup via VHF–telemetry data in 2008, substantial differences were noted (0.79 direct observations vs. 0.95 VHF–determined attendance patterns). Additionally, the 2008 observed natality rate for the subset of females outfitted with a radio transmitter was identical to the rate observed for all marked females (0.79 direct observations). There are a number of potential explanations for these differences. Observations were only conducted once per day in 2008, and female behavior classifications were limited to three categories (as opposed to 6 categories in 2009). The stationary logging system recorded the attendance patterns of females outfitted with a VHF–radio transmitter more or less continuously (details are further described in Chapter 4) throughout the observed breeding season. Because of the continual operation of this station, I was able to derive the reproductive status for more females that were outfitted with radio transmitters than for females that only had flipper tags. Reproductive status was determined via attendance patterns for some females that were never observed during the breeding season. Reproductive status was assumed based on criteria applied post hoc to the attendance data (Table 2.12). These reasons may partially explain the differences in observed natality for 2008. Thus, these rates should be treated as minimum (0.79) and maximum (0.95) natality rates for this year.

Additionally, for the subsample of females outfitted with a VHF–radio transmitter and an alphanumeric plastic tag, there was evidence of females that were
detected as having returned to the colony but were never observed. As shown in Table 2.11, 85 females were detected while 77 were observed returning to Polovina Cliffs in 2008. This difference in return rates suggests that the observed return rate for marked females without a radio transmitter may be negatively biased, which may inflate the overall observed natality rate in 2008.

The additional sampling period and coded behavioral scales in 2009 may be partially responsible for the higher observed natality rate, as it allowed observers more opportunities to determine reproductive status of females and accurately classify female behavior. Females assigned to the undetermined category were either observed less than 5 times or had low pup-association values (0, 1, or 2) as per the female–pup association codes determined during field observations. Based on sporadic observations and little behavioral information on reproductive status, data on these females could not be determined by the criteria listed in Table 2.12. While it is possible to misclassify females who may have had pups in the undetermined category, a large proportion of undetermined females were likely without a pup as females that fail to give birth have irregular and infrequent visits to the breeding colony (Vladimirov, 1987).

Although sampling methodology was modified between years, the similar results suggest that the natality of marked females in 2008 and 2009 was relatively stable. Observed natality rates for marked individuals were $\geq 0.79$ for both 2008 and 2009, and similar to the rates of 0.83 observed on the Commander Islands in 1977–1982 (Vladimirov, 1987).
2.4.3 Observed Estimate of Fertility

Since count data was used to determine reproductive timing and the cross-sectional fertility estimate, it is important to recognize the biases commonly associated with this type of data. In a perfect field situation, dead pups should be removed from the breeding colony and live pups marked to avoid double counting. Northern fur seal pups are precocial and form tight aggregations onshore soon after birth as their mothers begin to depart on foraging trips. As pups grow, the majority of them can be found learning to swim in the surf zone (Baker and Donohue, 2000). Female numbers can be underestimated because of their maternal attendance patterns throughout the breeding season. I attempted to minimize errors commonly associated with this type of data by conducting daily counts and incorporating post hoc model fitting techniques.

The age distribution of both rookery males and females changes as the breeding season progresses. Harem bulls leave their territories in early August, and the social structure quickly deteriorates, allowing nonterritorial and subadult males the opportunity to move into rookeries (Bigg, 1986). Juvenile females (not yet of reproductive age) arrive later in the breeding season than older females (Bigg, 1986). Thus, daily counts may also include females that returned and failed to pup in 2008, and females from other colonies that were temporarily resting at this rookery. Females suckling pups will sometimes use a different rookery as a haul out before returning to their natal rookeries to care for their pups (Gentry, 1998).

Female count data was also corrected by the daily detection probabilities de-
rived from the double–tagged females. The density covariate had a low effect when modeling detection probability, suggesting that the decline in detection probability throughout the season is mostly driven by attendance patterns. I assumed that the detection rates of double–tagged females were comparable to the detection rates of unmarked females. Detection probability of unmarked females is probably higher than the detection probability of marked females since sighting any portion of the body is sufficient to count, versus having to see and read a flipper tag. Therefore, the highest rates of detection probability, derived from double–tagged females, were used to correct the overall counts. The final calculated estimate should be regarded as the minimum estimate of fertility for this year. The fertility rate for 2008 (0.60) was lower than the observed natality rate for the marked females. This is consistent with the likely inclusion of nulli–parous females and older females not carrying their pregnancies to term in the overall count and thus the fertility rate estimate.

2.4.4 Reproductive Synchrony

Ideally, females give birth during the most favorable environmental conditions, in order to maximize their fitness and offspring survival (Bronson, 1988; Clutton-Brock, 1988; Boyd, 1991; Trites and Antonelis, 1994). For pinniped species that breed in subpolar environments, the occurrence of annual optimal conditions is notably predictable but brief (Boyd, 1991; Lunn and Boyd, 1993). Similar to other Otariid species, the timing of colony arrival and parturition is highly synchronous
in northern fur seals. Further, the synchronous nature of the timing of arrival has historically remained consistent; even during harvest pressures and extreme weather events, like the 1982–1983 El Niño and the 1979 climatic regime shift in the Bering Sea (Gentry, 1998).

Female arrival and subsequent parturition is also highly synchronous, with parturition occurring approximately 1–2 days after arrival (Peterson, 1965; Gentry, 1998). During a 14-year study on the Pribilof Islands, median arrival date was consistent and remained between 7 and 14 July with parturition occurring 1.3 days after arrival (Gentry, 1998). Additionally, Goebel (2002) presented an observed mean date of parturition of 12 July in 1995 on Saint Paul Island. This results in 50% of pups being born during the first two weeks of July (Peterson, 1965; Trites, 1992). From daily pup count data, Peterson (1965) reported mean dates of birth to be 7 and 8 July in 1962 and 1963, respectively. In addition to the 1962 and 1963 pup count data collected from Peterson (1965), Trites (1992) fit 1951 and 1983 count data to sigmoid growth models and derived estimates for the median (and mean) dates of parturition, after correcting for pup mortality (shown in Table 2.4). Based on his calculations, the median (and mean) dates of parturition fluctuated between 3 and 10 July (Trites, 1992).

The 2008 and 2009 median and mean parturition dates at Polovina Cliffs were compared to previous studies that determined this parameter on Saint Paul Island (see Table 2.4). As shown in Figure 1.4 in Chapter 1, breeding colonies occur on the northeastern, eastern, and southern parts of the island. Comparing reproductive timing to other colonies and past years can help elucidate information if there
has been any shift between years or colonies. Because Gentry (1998) and Goebel (2002) did not calculate mean pupping dates from count data, their estimates were not included in my retrospective comparison. Results from a parametric test indicated that the mean/median dates of parturition significantly differed, though results from a less sensitive nonparametric test just failed to indicate any significant difference in the mean/median dates. A larger sample size may indicate a significant difference in the mean/median dates of birth on Saint Paul Island.

The peak of parturition determined in this study occurs during the third week of July, later than previously reported dates. Interestingly, these dates are similar to the dates presented in Section 2.3.4, where the peak of parturition was calculated by observational data. This consistency supports the accuracy of the observed estimate of parturition in the marked female sample. The estimates hardly differed between 2008 and 2009. This lack of interannual variation can be partially explained by the hypothesis that the timing of parturition is being regulated by external cues like a latitudinal effect or a decrease in photoperiod that induces implantation (Temte, 1985). However, the timing of implantation can also be regulated by hormonal control (Craig, 1964). Embryonic diapause is obligate for northern fur seals, allowing for some flexibility in when implantation occurs (Boyd, 1991; Atkinson, 1997); though active gestation for this species is considered more or less fixed (Boyd, 1991; Gentry, 1998).

Both age and body condition can play a role in the timing of parturition. In short-lactating northern and Antarctic fur seals (*Arctocephalus gazella*), younger females pup later in the breeding season and give birth to lighter pups, which may
influence pup survival to weaning (Doidge and Croxall, 1989; Lunn and Boyd, 1993; Boltnev and York, 2001). Therefore, the observed change in the timing of parturition compared to historic data might suggest a change in the age structure of this population. Additionally, implantation is thought to occur earlier in older northern fur seal females (York and Scheffer, 1997). It has been shown in grey seals (Halichoerus grypus) that implantation occurs earlier in females that are in better body condition (Boyd, 1984). Guinet et al. (1998) suggested that body condition may be more influential during implantation and gestation of fur seal females, as they demonstrated that South African fur seal (Arctocephalus pusillus) females in better body condition were more likely to be pregnant during the gestation phase of the breeding cycle. Thus, the date of parturition can partially be determined by the date of implantation, and a potential shift in the peak of parturition could be a result of a shift in the timing of implantation.

The sample of known–aged females presented in this study may be biased and not truly representative of the current population. As shown in Figure 2.8, the majority of the females sampled were 5, 6, and 7, which have been shown to have the greatest reproductive success (York and Hartley, 1981). While the October–November capture seasons allow for the ease of female captures because large, harem–holding males are absent, we may only be targeting females that are of reproductive age and are still suckling their pup. Young females, females that failed to pup, and mothers that lost their pups may no longer be at the colony late in the breeding season. Larger samples of females and sampling earlier in the breeding season should occur before making any further conclusions if the overall
ages of breeding females are contributing to shift in reproductive synchrony.

In other pinniped species, there is evidence that prey availability may influence the timing of reproduction (Doidge and Croxall, 1989; Boyd, 1996; Pitcher et al., 2001; Soto et al., 2004; Gibbens and Arnould, 2009). Timing of reproduction was also found to coincide with prey availability in the American mink (*Neovison vison*), another species that employs embryonic diapause as part of their reproductive strategy (Ben-David et al., 1997).

Northern fur seals, as opposed to fur seal species that breed in low latitudes, have a comparatively short nursing period of approximately four months (Gentry and Kooyman, 1986). The end of the nursing period seems more or less fixed, as the surrounding environment drastically changes and the onset of winter storms impact the timing of pup departure (Goebel, 2002; Lea et al., 2009). Because of the possibility of a shorter birth to weaning period, any shift in the timing of arrival could have either a beneficial or detrimental effect on the amount of resources transferred to pups.

Northern fur seal females, juveniles, and pups from the Pribilof Islands are highly migratory during the winter months, traveling to the North Pacific transition zone and as far south as southern California during the winter (Gentry, 1998; Ream et al., 2005; Lea et al., 2009). While the timing of reproduction has apparently shifted, as reported in this study, the estimated minimum natality rate is relatively high. If prey conditions were poor during active gestation in the winter months, we would expect to see some evidence of reproductive failure shown either in the failure to return to the colony and/or pup the following year. Females are
epipelagic predators and have been found to forage on similar prey items as the piscivorous seabirds that also breed on the Pribilof Islands (Sinclair et al., 2008). Interestingly, population declines in black-legged and red-legged kittiwakes (Rissa tridactyla and Rissa brevirostris), and common and thick-billed murres (Uria aalge and Uria lomvia) have concomitantly occurred on the Pribilof Islands (Byrd et al., 2008).

High natality rates of 0.69 were also recently reported for the Steller sea lion (Eumetopias jubatus), a sympatric Otariid that has recently experienced a dramatic population decline (Maniscalco et al., 2010)). Several hypotheses attempt to explain the Alaskan pinniped population decline by exploring top–down and bottom–up forcing mechanisms. The Oscillating Control Hypothesis suggests that poorer quality prey not only is now more abundant in the Bering Sea, but that climatic shifts in the Bering Sea were the cause of this poor prey abundance evident in pinniped diets (Hunt Jr. et al., 2002). Conversely, recent findings suggest high predation rates of juvenile Steller sea lions by killer whales ((Orcinus orca); Horning and Mellish (2009)).

Future studies should investigate emigration and juvenile survival rates, and the contribution of sexually (and socially) mature males, as McKenzie et al. (2007) suggested a delay in the age of reproductive maturity for New Zealand fur seal males until they reached a definitive size. Juvenile survival rates are difficult to quantify because young seals are pelagic for the first 2–5 years of their life, with staggered rates of return to the colony (Gentry, 1998). This life history stage needs additional research to determine how juvenile survival is contributing to the
current decline. On the Commander Islands, there was a slight correlation between the number of 8 year–old northern fur seal males and the number of pups born the following year (Vladimirov, 1987). The current contribution of males in these breeding colonies is unknown, and an exploration of male ages and reproductive contributions will provide additional information on the Pribilof Island population.

Although this was only a two–year study, the majority of marked females did return to the colony (see Chapter 3) and successfully gave birth to pups. The sampling period for these females occurred late in the season, thus we were able to mark females that were 1) of reproductive age and 2) still suckling their pup. Due to the late sampling of the female population, one can conclude that this study provides the closest estimate of a current natality rate. These findings, concomitant with the high pregnancy rates recently determined by Testa et al. (2010), suggest that natality rates are not currently contributing to the population decline. Extant projects on the Pribilof Islands will continue to build on the information presented in this study. These ongoing studies will provide more detailed information on individual age at primiparity, age–specific natality rates, and whether a female produces a pup every year. Northern elephant seals (Mirounga angustirostris) that delayed age at primiparity had higher overall natality and weaning success (Huber, 1987). Pomeroy et al. (1999) found a high degree of variation in pupping success on an individual level for grey seals. Long–term studies will provide a better understanding of vital rates, on both an individual–based and colony–wide level. Future studies will be able to incorporate the findings presented here in order to better understand the Pribilof Island population decline.
In conclusion, estimates of the minimum natality rates for marked individuals were high and $\geq 0.79$ in 2008 and 2009. These findings suggest that natality is not currently contributing to the population decline, and that other life history stages in northern fur seals should be further explored. The minimum fertility rate was estimated to be 0.60. Juvenile females, visiting females, and females without a pup are all contributing to this fertility rate, which reflects an overall population level reproductive rate for females. Further investigation is needed to determine how much these different afore mentioned groups could be driving this rate. Reproductive timing, while highly consistent between 2008 and 2009, has shifted later in the breeding season to the third week of July. For a species that has historically been highly synchronous in the timing of arrival and subsequent parturition, it is intriguing that this shift has occurred. Further investigation is needed to determine how this shift may affect weaning success and juvenile survival.
Chapter 3 – Return and Parturition Rates for Females of a Known Early Pregnancy Status

3.1 Introduction

Natality (the number of young produced per reproductive age female) is an essential vital rate for any demography study or population dynamics model. Historical studies on northern fur seals (*Callorhinus ursinus*) determined pregnancy rates from harvested females (determined from the examination of reproductive tracts from pelagically harvested females) to be $\geq 0.86$ for 6–8 year olds (Trites and York, 1993), and proximate reproductive rates (the annual number of pups produced per number of females) have been inferred from these calculated pregnancy rates, as it was assumed that all pregnant females would subsequently give birth to pups. Though pregnancy rates represent a suitable proxy for reproductive rates, recent fur seal studies suggest the use of such a proxy does not necessarily reflect the number of pups born (McKenzie et al., 2005; Gibbens et al., 2010). Testa et al. (2010) recently estimated early term pregnancy rates for northern fur seals to vary from 0.85 to 0.92. In this study, direct estimates of the subsequent return and natality rates of the same females sampled in Testa et al. (2010) are presented. The objectives of this study were: (1) to estimate how many early term pregnant females carried a pup to term, (2) to present a corrected natality rate based on the
afore mentioned pregnancy rates, and (3) to test the hypothesis that embryonic vesicle size predicted the dates of pregnant female return to the rookery.

Saint Paul and Saint George Islands (part of the Alaskan Pribilof Island Archipelago) are home to the majority of the world’s breeding population of northern fur seals (see Figure 1.3). This population experienced many fluctuations since its discovery, primarily due to commercial exploitation (Roppel and Davey, 1965; Towell et al., 2010). Although commercial harvests ceased by 1985, this species was designated as depleted under the Marine Mammal Protection Act in 1988 (Loughlin et al., 1992). Beginning in 1998, the Pribilof Island population has steadily declined at approximately 4.9% (SE = 0.36) per year (Towell et al., 2010). The cause of this recent decline is unknown, although changes in reproductive rates could be contributing to the current decline.

3.2 Methods

In a separate study, diagnostic, B–mode ultrasonography was used to determine early pregnancy status and provide an in situ description of the uterus and ovaries in northern fur seal females (Adams et al., 2007; Testa et al., 2010). Ultrasound examinations were conducted using a portable field unit with a side–fire transducer (7.5 MHz), and transrectal images of the reproductive tract were recorded using digital video (Adams et al., 2007). Pregnancy was inferred from the presence or absence of embryonic vesicles (EV) in the uterus and corpora lutea in the ovaries of female seals (Adams et al., 2007). For a complete description of the field proce-
dures and ultrasound images, refer to Adams et al. (2007) and Testa et al. (2010). Late autumn captures occurred around the peak of the published blastocyst implantation period, 14 November (York and Scheffer, 1997). In 2007 and 2008, females were captured between 11 and 16 November (surrounding the known peak of implantation) and 18 and 22 November (after the known peak of implantation), respectively. Captures were conducted at the northernmost demarcated section of Polovina Cliffs rookery, located on the northeast side of Saint Paul Island (see Figures 1.3 and 1.4).

In 2007, 62 females determined pregnant by transrectal ultrasonography were marked with one large Allflex tag (AllFlex USA, Inc.) and one VHF–radio transmitter (40 pulses per minute, 164 to 165 MHz, Advance Telemetry Systems [ATS], Insanti, MN, USA) in the interdigital connective tissue on the trailing edge of both fore flippers. In 2008, 29 females determined pregnant by transrectal ultrasonography were marked with one Dalton (Dalton ID Systems, USA) Superflexitag and one VHF–radio transmitter. There were considerable mechanical complications and logistical constraints with the data logging system in 2009, thus only the telemetry data from 2008 is presented. The VHF–radio transmitters assisted in determining return rates the following season in addition to quantifying parturition based on maternal attendance patterns. Transmitters were duty–cycled and programmed to activate just before the following breeding seasons.

In 2008, the 24–hour presence and absence of VHF–tagged females was monitored using a stationary remote data logging system placed above the southernmost part of the rookery. The system consisted of a VHF–radio receiver (Model R4000,
ATS) linked to a data collection computer (DCC; Model DC5041, ATS) powered by a rechargeable 12v battery hooked up to a solar panel. The receiver was connected to one 2–element H type antenna that pointed northward and directly into the rookery. The DCC was programmed to sequentially scan each programmed frequency for 10 seconds before advancing to the next programmed frequency. A reference transmitter was placed approximately 15 meters away from the logging system, and its regular occurrence in the data file ensured that the system was working properly. Pulse counts (a count of the number of incoming pulses detected for each frequency during a sequential scan) and median pulse rate for each detectable frequency was collected continuously from 6 July to 26 August 2008. Telemetry data was first filtered by median pulse rate, then by pulse data. Data points were accepted if the median pulse rate was equal to 38, 39, or 40 and if the pulse count was between 4 and 19 per scan. Data points that fell outside of these ranges were considered noise and dropped from further analysis. Visual observations of marked females were also conducted once a day throughout the breeding season. Refer to Section 2.2.3 for a complete description on how these observations were conducted. Similar to the methods described in Section 2.2.6, a female was considered with a pup in 2008 if she was 1) detected for 1–3 sequential days on ≥ 2 separate occasions during the main breeding season (suggesting repeated returns to the colony to care for an offspring), or 2) detected for 4 sequential days upon first sighting (indicating a perinatal period). If any female outfitted with a VHF–radio transmitter did not meet either of these two detection criteria, observational data from 2008 was incorporated to additionally determine if she was observed nursing
at least one time. A female was considered to be with pup if she met at least one of these established criteria and was considered as ‘undetermined’ if she failed to meet at least one of these established criteria.

In 2009, a similar monitoring system was constructed at the same location at Polvina Cliffs. Additionally, a second data logging system was placed at the northernmost part of the rookery with one 3–element Yagi antenna that pointed southward and directly into the rookery. The 2009 VHF scanning data from these two stations was apparently subject to a combination of false positives (the telemetry data denoted a female was present when in fact she was absent), and false negatives (a female was actually present when it was denoted by telemetry that she was absent), as confirmed by scanning the same frequencies using a portable VHF receiver. These inconsistencies were likely caused by disrupted power supplies and the use of a duty-cycled, only intermittently operating reference transmitter. As a result, telemetry data from this year is not presented, because there is no clear way of determining maternal behavior based on erratic telemetry data alone. In 2009, an additional visual observation period was added to increase the direct observations of marked females. Visual observations were conducted twice daily between the hours of 0700 and 1700, and 1800 and 2400. For 2009, only the observational data is presented to determine how many females of a known pregnancy status subsequently returned to Polovina Cliffs and gave birth. Similar to the methods described in Section 2.2.6, a female was considered with a pup in 2009 if she was 1) observed nursing at least one time, 2) observed for 1–3 sequential days on ≥ 2 separate occasions during the main breeding season (suggesting repeated returns
to the colony to care for an offspring), or 3) observed for 4 sequential days upon first sighting (indicating a perinatal period). A female was considered to be with pup if she met at least one of these established criteria and was considered to be 'undetermined' if she failed to meet at least one of these established criteria. Return dates of females were determined by the first time a radio tagged female was detected by the stationary data logging system.

3.3 Results

Of the 62 females determined pregnant in 2007, 57 females were detected as having returned to the rookery in 2008. Of these, 54 gave birth to a pup. This number resulted in a natality rate of 0.95 (Table 3.1). Interestingly, if compared to the observational data from the same year, 43 females were observed as having returned to the rookery. Of these, 37 were determined as giving birth to a pup using observational data only. This results in an observed return rate of 0.69 and an observed natality rate of 0.60 in 2008.

Of the 29 females determined pregnant in 2008, 22 females were observed as having returned to the rookery in 2009. Of these, 21 gave birth to a pup. This number, derived from daily observational data only, resulted in a natality rate of 0.96 (Table 3.1).

As defined in Chapter 2, natality rates were calculated as the total number of pups born divided by the total number of females of reproductive age in the rookery each year. Natality was calculated from any returned female, regardless
of a known early pregnancy status and old enough to reproduce. As shown in Table 3.1, the natality rate of *returned* females took into account the females of a known pregnancy status that 1) returned and 2) were confirmed to have given birth to a pup.

The detected mean date of return in 2008 was 16 July (range: 6 July to 28 July, SD = 5.41). The observed mean date of return in 2009 was 20 July (range: 4 July to 23 August, SD = 10.21).

3.4 Discussion

Maternal attendance data derived from the VHF–radio transmitters in 2008 resulted in higher estimates of return and natality when compared to the rates derived from repeated observations of the same female during the observed breeding season (*i.e.* $0.95 > 0.60$). The detected (via VHF) natality rate of returned females outfitted with a VHF–radio transmitter in 2008 was 0.95. The observed natality rate for the same females outfitted with a VHF–radio transmitter in 2008 was 0.60. In 2008, the stationary logging system recorded the attendance patterns of females outfitted with a VHF–radio transmitter more or less continuously (details are further described in Chapter 4) throughout the observed breeding season. This difference suggests that the VHF–radio transmitters resulted in a higher daily detection probability for determining animal presence in rookeries than visual observations, where topography may play a factor in lowered observed detection probabilities. Similar to Section 2.4.2 in Chapter 2, this difference in return rates
Table 3.1: Observed return rates and subsequent natality rates for pregnant females. Differing field methods used to calculate the rates are denoted and combined rates are also presented. Natality rates of returned females represent the proportion of pregnant females that returned and gave birth.

<table>
<thead>
<tr>
<th>Year</th>
<th>Method</th>
<th>Pregnant</th>
<th>Returned</th>
<th>Pupped</th>
<th>Return Rate</th>
<th>Natality Rate of Returned Females</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>VHF–Detected</td>
<td>62</td>
<td>57</td>
<td>54</td>
<td>0.92</td>
<td>0.95</td>
</tr>
<tr>
<td>2009</td>
<td>Visually Observed</td>
<td>29</td>
<td>22</td>
<td>21</td>
<td>0.76</td>
<td>0.96</td>
</tr>
<tr>
<td>Combined</td>
<td></td>
<td>91</td>
<td>79</td>
<td>75</td>
<td>0.87</td>
<td>0.95</td>
</tr>
</tbody>
</table>
supports the finding that the observed return rate for this subsample of females is an underestimate, because the VHF–detected return > observed return (0.92 > 0.69).

Although the methods to calculate return and natality differed for the years sampled, all rates presented were higher than 0.70. Return rates were ≥ 0.76. Natality rates of returned females were ≥ 0.95, and the mean rate for both study years was 0.95. Mean natality rates of females of a known pregnancy status for both study years was 0.82. This rate for pregnant females should be considered a minimum estimate as it does not adjust for females that may have returned and pupped, but were not VHF–detected or visually observed in 2008 and 2009.

The 2008 capture season occurred in mid–to late–November, well after the departure of territorial bulls. After the peak of breeding, the harem structure quickly breaks down, allowing females to freely move within the rookery. As pups grow older, they develop ontogenetic shifts in their swimming and diving skills prior to weaning (Baker and Donohue, 2000). Because of these reasons, females have more freedom to move about their natal rookery and adjacent rookeries. Philopatric females generally give birth at or near the same location in the rookery each year (Peterson, 1965). Because of the late sampling period, there is the potential that females from adjacent breeding rookeries were captured and marked at Polovina Cliffs.

Testa et al. (2010) present three different estimates of early term pregnancy: 0.92 (SE = 0.04, 2007), 0.85 (SE = 0.05, 2008), and 0.88 (SE = 0.05). The 0.88 estimate was calculated for the combined 2007 and 2008 data sets from a Bayesian
hierarchical model that accounted for possible false negatives and EV detection probability (Testa et al., 2010). The 0.88 combined estimate derived from Testa et al. (2010) factored by the combined natality rate of pregnant females (0.82 for 2008 and 2009) equals 0.72, or an overall minimum natality estimate for 2008 and 2009. This is lower than what is presented in Table 2.11 in Chapter 2. This is expected, as the natality rates presented in Chapter 2 are for returned females only. However, 0.72 is higher than the fertility rate (0.60), as the latter includes immature females. Based on these results, there is little support that reproductive rates are contributing to the current decline.

Minimum natality rates in this study are similar, or higher than reproductive rates (the proportion of reproductively mature females giving birth to pups) of stable or increasing populations of fur seals. Lunn et al. (1994) reported an age-specific reproductive rate of 0.75 between 6–11 year old female Antarctic fur seals (*Arctocephalus gazella*), with a peak of 0.80 for females in their reproductive prime (7–9 year olds). In female New Zealand fur seals (*Arctocephalus forsteri*), McKenzie et al. (2005) reported a reproductive rate between 0.56 and 0.64. Interestingly, the minimum natality rates are higher when compared to similar rates in declining populations. Dabin et al. (2004) determined an overall reproductive rate in subantarctic fur seal females (*Arctocephalus tropicalis*) to be 0.48 for females older than 5 years. However, a reproductive rate of 0.69 was reported for Steller sea lion females (*Eumetopias jubatus*), a sympatric Otariid that has recently experienced a dramatic population decline (Maniscalco et al., 2010).

One possible cause of a positively biased natality rate may be that the major
proportion of females are captured at their reproductive peak (Bigg, 1984; Boyd, 1984). Age–specific reproductive rates in northern fur seals rapidly increase until a reproductive peak at the ages of 5, 6, and 7 then subsequently decrease with increasing age (York and Hartley, 1981). Field captures occurred around the known weaning period for this species, which may exclude females not yet of reproductive age and senescent females. From a random sample of 171 females sampled in 2005, 2007, and 2008, only 13 were determined as young and likely immature (either nulliparous or of uncertain parity) (Testa et al., 2010). Older northern fur females have been shown to pup earlier and implant earlier than younger females (York and Scheffer, 1997; Boltnev and York, 2001). The late timing of female captures may also exclude females that failed to pup or lost their pup to neonatal mortality as these females would no longer be present in the rookery. Additionally, the minimum natality rates presented here are similar to reproductive rates of other Arctic mammals of prime reproductive age (Gaillard et al., 2000).

It has been shown that there can be a high degree of individual variation in reproduction between years in other pinniped species. Pomeroy et al. (1999) and Testa (1987) both demonstrated that female Phocids have the ability to forego reproduction in order to maximize their individual fitness in grey seals (Halichoerus grypus) and Weddell seals (Leptonychotes weddellii), respectively. Lunn et al. (1994) demonstrated that female age, reproductive experience, and prey availability influenced reproductive success during a 10–year study on Antarctic fur seals. In other mammalian species, the individual quality of females can affect the likelihood of succeeding in all aspects of reproduction (i.e. breeding, gestation,
birth, weaning) (Hamel et al., 2009). Longitudinal sampling on this population will provide the most accurate information on periodicity of reproduction and lifetime reproductive success.

Estimates of the Pribilof Island population are derived from pup production estimates (Towell et al., 2006). As shown in Figure 1.2, pup production on Saint Paul Island declined dramatically beginning in 1998, well after the cessation of an experimental female harvest (1968) and pelagic sampling (1974) (Towell et al., 2006). The results from this study, coupled with the high pregnancy rates reported by Testa et al. (2010), suggest that most females at this rookery are returned and gave birth to pups in 2008 and 2009.

Although the sample sizes are small and this was only a two-year study, the consistency of the calculated rates between years and methods suggest that natality is fairly high and consistent for marked females of reproductive age. These results also suggest that future studies should fully explore other life stages, like juvenile survival or age at primiparity, in order to determine how these factors may currently be contributing to the Pribilof Island population decline.
Chapter 4 – Attendance Patterns of Female Northern Fur Seals in 2008

4.1 Introduction

Colonial breeders can utilize cues from the surrounding environment in order to maximize their reproductive success (Danchin et al., 1998). Because colonial breeders are usually confined to a central place to raise dependent offspring, organisms benefit most by maximizing on their net energy gain rate while foraging (Orians and Pearson, 1979). Colonial breeders raising offspring will continually return to the central place to transfer this gained energy to their offspring in order to ensure neonate survival (Orians and Pearson, 1979). Like other marine vertebrate species found on the Alaskan Pribilof Islands, northern fur seals (*Callorhinus ursinus*) depend on the predictable and seasonal abundance of prey resources in the Bering Sea ecosystem. The Pribilof Islands are currently home to an estimated 55% of the world’s breeding population of northern fur seals (Testa, 2008). Recent population estimates report that pup production has declined at an annual rate of 4.9% from 1998 to 2010 (Towell et al., 2010). During a time when reasons for the recent population decline remain unknown, assessing foraging trip duration and maternal presence onshore will result in a more complete understanding of this aspect of maternal behavior when pups are nutritionally dependedent on their mothers.
Low prey abundance can lead to longer foraging trips, which may result in higher pup mortality (Duck, 1990).

Northern fur seals are highly migratory, with adults and juveniles of both sexes departing the breeding grounds during October–November for approximately eight months. During this time, seals are entirely pelagic until the following breeding season. Adult males have been found to remain at high latitudes in the waters surrounding Alaska and Russia (Bigg, 1990). Females and younger age classes of both sexes migrate as far south as California, and can be found along the continental shelf and in the North Pacific Ocean during the winter (Bigg, 1990; Ream et al., 2005; Lea et al., 2009). Sexually mature seals return back to their natal breeding colonies in the spring and summer (Bigg, 1986).

Parturition occurs soon after the female’s first haulout on land. The first haulout, better known as the perinatal period, lasts an average of 7 to 8 days. The perinatal period consists of a series of sequential events: parturition, the onset of lactation, estrus (approximately 5–7 days), and mating (Gentry, 1998; Boyd, 1991). The perinatal period also provides the mother and pup adequate time to bond by calling to one another and for the mother to determine her pup’s scent based on olfactory cues. After the perinatal period, females begin a series of alternating foraging trips at sea with visits on land to suckle their pups (Bartholomew and Hoel, 1953; Peterson, 1965). While the females are away at sea, pups remain onshore fasting until their mothers return. This behavior, known as the maternal attendance or foraging cycle strategy, has been extensively documented for northern fur seals as well as for many Otariid species (Gentry and Kooyman, 1986;
Determining the attendance pattern during lactation can provide indirect information about the abundance and distribution of prey (Gentry and Kooyman, 1986; Oftedal et al., 1987). Generally, with all factors being equal, foraging trip duration displays an inverse relationship to prey abundance (Gentry and Kooyman, 1986; Boyd et al., 1997; Merrick and Loughlin, 1997). In the past, attendance patterns for northern fur seals on the Pribilof Islands have primarily been determined by daily observations (Bartholomew and Hoel, 1953; Peterson, 1965; Gentry and Kooyman, 1986), or radiotelemetry (Loughlin et al., 1987; Goebel, 2002). Unlike females outfitted with dorsal satellite or GPS tags, the females presented in this study were outfitted with a VHF–radio transmitter attached to the flipper and not glued to the dorsal fur which can be shed during the annual molt. Because radiotelemetry was used before the advent of archival tags or satellite transmitters, the data from this study can be more easily compared to older studies. The purpose of this paper is to present attendance data derived from radiotelemetry on females equipped with a VHF–radio transmitter in 2008.

4.2 Methods

In 2007, 94 females were captured between 11 and 16 November. Seal captures and subsequent observations occurred at the last demarcated section of Polovina Cliffs rookery, located on the northeast side of Saint Paul Island. For study site details and rookery location see Section 2.2.1 and Figures 1.3 and 1.4. Animals
were captured using a noose pole then held in a restraint board (Gentry and Holt, 1982) to be weighed, aged, and marked. Females (n = 94) were marked with one large Allflex tag (AllFlex USA, Inc.) and one 23g VHF–radio transmitter (Temple Tag model MM420, 164 to 165 MHz, Advance Telemetry Systems [ATS], Insanti, MN, USA) in the interdigital connective tissue on the trailing edge of both fore flippers. Pulse period on the radio transmitters were programmed at 40 pulses per minute (ppm) and duty–cycled to activate the following breeding season.

In 2008, the 24–hour presence and absence of females was monitored using a stationary remote data logging system placed above the southernmost part of the section. This system consisted of a VHF–radio receiver (Model R4000, ATS) linked to a data collection computer (DCC; Model DC5041, ATS) powered by a 12v battery that was charged by solar panel. The receiver was connected to one 2–element H type antenna that pointed northward and directly into the rookery. If an incoming signal was detected, the DCC was programmed to scan each frequency for 10 seconds. The DCC was also programmed to quit logging after 6 seconds on a frequency if no incoming signals were detected. The DCC scanned and logged data continuously throughout the observed breeding season. A reference transmitter was placed approximately 15 meters away from the logging system, and its regular occurrence in the data file ensured that the system was working properly.

Transmitters emit pulses at a constant rate of 40 ppm, resulting in 6 or 7 pulses received per monitoring interval. The DCC’s store data on pulse counts received for each monitoring interval, as well as median pulse rate. Data points were accepted first if median pulse rate was equal to 38, 39, or 40 (an acceptable
range for a 40 ppm transmitter) and second if pulse count was between 4 and 19 (what was considered an acceptable range of pulse data). Data points that fell outside of either of these ranges were considered noise and dropped from further analysis.

Pulse data and median pulse rate for each detectable frequency were collected from 6 July to 26 August 2008. Females that were not present onshore were assumed to be at sea and not hauled out at another rookery. Attendance patterns determined by previous radiotelemetry studies indicate mean visit length (after the initial perinatal visit) to be between 1–3 days (Goebel, 2002; Loughlin et al., 1987). Based on this information, I assumed that if the DCC recorded an animal as being present only once (1 positive scanned result) during a 24-hour period and absent for the rest of this period, the data point was noise and deleted. A female was determined as present if at least two consecutive positive scans were received.

DCC’s that experienced interruptions in continuous scanning were normally discovered and replaced with a backup DCC within 12 hours. If interruptions like this occurred in the data file during an animal’s presence (i.e. if she was detected before and after an interruption) she was assumed to have been present during the interruptions. The same assumption applied to those animals that were absent during DCC interruptions. If a female was present before a DCC interruption and absent afterwards, or vice versa, the transition was assumed at one-half the time of interruption.

Although telemetry data from this study was collected as pulses per minute, presence and absence determined from telemetry data are presented to the reso-
ution of one hour. The individual was given a value of 1 for every hour she was
determined present and a value of 0 for every hour she was determined absent.
Attendance history was summed by binary presence/absence throughout the moni-
tored breeding season, and presented in days (i.e., 24 hours = 1 day, 12 hours =
0.5 day). Presence and absence durations were used to infer visit times onshore
and foraging trip durations, respectively. Presented attendance data includes the
first 3–5 trips. Data presented as means are ± 1 SE and statistical differences
are considered significant at $p < 0.05$. Statistical analyses were conducted using
S–PLUS (version 8.0, TIBCO Software, Inc.).

4.3 Results

females that returned, I determined the detected date of return for 84 females. The
detected date of return was not included for one female because she was observed
before the stationary data logging system was constructed. She was observed in
the rookery on 30 June and 21 August (both days without a pup), and detected in
the rookery on 20, 21, and 22 August. There was insufficient data on this female
to determine if she had a pup; she was not included in Figure 4.1 because the
detected date of her return was not determined by radio telemetry. The median
date of detected return for 84 females with VHF–radio transmitters was 18 July
(range: 6 July to 22 August, SD = 7.07; Figure 4.1). Three females were detected
on 6 July, when the stationary data logging system was constructed. It is unlikely
that these females arrived before 6 July, as none of them were observed the week prior to 6 July (as field observations began 30 June).

Figure 4.1: Date of first VHF–based detection in 2008.

Of the returned females, 81 females were determined with a pup while 4 females were determined without a pup because they did not exhibit a detected perinatal period or a consistent attendance pattern (See Table 2.11 in Chapter 2). Irregular attendance patterns are defined in this context as extended or brief presences (i.e. visits) after the perinatal period. Extended visits were defined as any presence longer than 6 days, as northern fur seals are known to have repeated, but brief, visits to land after the perinatal period usually lasting 2 to 3 days (Gentry and Kooyman, 1986). Brief visits were defined as any presence on the order of a few hours. These types of patterns do not reflect what is known about attendance patterns of females suckling pups. Females exhibiting “irregular” patterns, either due to reproductive status or telemetry data outside of the acceptable ranges of pulse data and minimum pulse rate were not included in this analysis of mater-
nal attendance patterns. One female exhibited a normal attendance pattern but irregular data during her perinatal period. Her location in the rookery could have changed after her first foraging trip, possibly because her pup might have moved to another location; allowing for better detection of her transmitter. In this case, only visits after her undetermined perinatal period are presented.

Of the 84 females detected as returning, the perinatal period was not determined for 8 females because of irregular data during the perinatal period. Six of these 8 females had an attendance pattern and were determined as with a pup. Thus, the perinatal period was determined for 76 females. The mean duration of the perinatal period was 7.5 days ($SD = 1.3$, Table 4.1). Over half of the females ($n = 49$) had perinatal periods that were 7–8 days in duration (Figure 4.2).

Excluding the perinatal period, the mean duration of presence onshore was 1.47 days ($n = 198$). I was able to determine the first 3 visits for the majority of
the females that returned and exhibited a maternal attendance pattern, and the first 5 visits for 4 females. The first five visits following the perinatal period were all similar in duration and did not significantly differ from one another during the observed breeding period (Kruskal–Wallis $\chi^2 = 3.71$, $p = 0.45$). Total mean visit durations for the first five visits were significantly shorter in 2008 (1.47 days, see Table 4.1) when compared to Loughlin et al. (1987), (1.92 days, Student’s t-test, $p = 0.001$, $T = 2.37$).

The mean duration of all calculated absences during the observed breeding period was 7.07 days ($n = 207$). The first five trips were all similar in duration and did not differ from one another, and varied from 6.62 to 7.52 days in length (Table 4.2; Kruskal–Wallis $\chi^2 = 7.62$, $p = 0.11$). I was able to determine the first 3 foraging trips for the majority of the females that returned and exhibited a maternal attendance pattern, and the first 5 foraging trips for 6 females. The mean of the first 3 trips ranged from 7.02–7.52 days, although one female was recorded taking a trip as long as 21.46 days (Table 4.2). This female also had a detected perinatal period of 12.83 days, and she was observed 9 of those days although never visually confirmed as having a pup. She was detected as returning back to Polovina Cliffs for 1.67 days and observed on 1 day (without a pup). Although this female may have given birth to a pup, she was never detected or observed returning after her first visit of 1.67 days. Because it would be difficult for a newborn pup to survive 22 days without suckling, I assume that she was no longer a nursing female after her visit back to the rookery. Although mean trip duration for the first five trips was around 6–7 days in this study, two females took longer trips
(11–22* days, Table 4.2). Because data collection did not span the entire length of this pup dependency period, there is no foraging trip data beyond trip 5 for any females outfitted with a radio transmitter in 2008.

Foraging trip duration was compared to foraging trip duration in (Loughlin et al., 1987). Total mean foraging trip durations for the first 5 trips did not significantly differ between the 2008 sample (7.07, see Table 4.2) and the 1984 sample (5.94, Student’s t-test, \( p = 0.20, \ T = 2.78 \)).

Table 4.1: Duration of presences to shore (in days) for radio tagged females at Polovina Cliffs in 2008.

<table>
<thead>
<tr>
<th>Visits</th>
<th>( N )</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perinatal Period</td>
<td>76</td>
<td>7.5</td>
<td>4.75</td>
<td>12.83</td>
<td>1.3</td>
</tr>
<tr>
<td>Visit 1</td>
<td>67</td>
<td>1.59</td>
<td>0.79</td>
<td>4.96</td>
<td>0.68</td>
</tr>
<tr>
<td>Visit 2</td>
<td>60</td>
<td>1.49</td>
<td>0.71</td>
<td>2.91</td>
<td>0.41</td>
</tr>
<tr>
<td>Visit 3</td>
<td>47</td>
<td>1.57</td>
<td>0.92</td>
<td>3.04</td>
<td>0.48</td>
</tr>
<tr>
<td>Visit 4</td>
<td>20</td>
<td>1.51</td>
<td>0.79</td>
<td>3.33</td>
<td>0.58</td>
</tr>
<tr>
<td>Visit 5</td>
<td>4</td>
<td>1.20</td>
<td>1.04</td>
<td>1.33</td>
<td>0.12</td>
</tr>
<tr>
<td><strong>Mean Visits</strong></td>
<td>198</td>
<td>1.47</td>
<td>0.71</td>
<td>4.96</td>
<td>0.21</td>
</tr>
</tbody>
</table>

Table 4.2: Duration of absences (in days) for radio tagged females at Polovina Cliffs in 2008.

<table>
<thead>
<tr>
<th>Trips</th>
<th>( N )</th>
<th>Mean</th>
<th>Min</th>
<th>Max</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trip 1</td>
<td>68</td>
<td>7.02</td>
<td>3.96</td>
<td>21.46</td>
<td>2.51</td>
</tr>
<tr>
<td>Trip 2</td>
<td>62</td>
<td>7.52</td>
<td>3.63</td>
<td>15.08</td>
<td>1.75</td>
</tr>
<tr>
<td>Trip 3</td>
<td>50</td>
<td>7.45</td>
<td>4</td>
<td>11.17</td>
<td>1.60</td>
</tr>
<tr>
<td>Trip 4</td>
<td>21</td>
<td>6.77</td>
<td>4.13</td>
<td>9.54</td>
<td>1.53</td>
</tr>
<tr>
<td>Trip 5</td>
<td>6</td>
<td>6.62</td>
<td>3.75</td>
<td>8.88</td>
<td>2.16</td>
</tr>
<tr>
<td><strong>Mean Trips</strong></td>
<td>207</td>
<td>7.07</td>
<td>3.63</td>
<td>21.46</td>
<td>0.42</td>
</tr>
</tbody>
</table>
4.4 Discussion

The median date of VHF–detected return was 18 July in 2008. This date is one day after the calculated median date of birth for pups in 2008, 17 July (described in Section 2.3.1 in Chapter 2), and two days after the observed arrival of all females, 16 July (see Table 5.2). The detected date of return was one day after the calculated median date of birth, and this difference can be explained by the two different methods used to determine these dates. Although the presented dates were determined by different methods, these dates all lie between 16 and 18 July in 2008.

Gentry (1998) reported a 12–year mean perinatal period of approximately 7.8 days (1974–1986), before the recent population decline. The mean duration of the perinatal period in 2008 was 7.5 days. Although the mean duration presented in this study was derived from a smaller proportion of the population, the duration of the observed perinatal period in this study is similar to historical records.

While the attendance data is presented for only one year and for approximately half of the weaning period, foraging trip duration for 2008 did not differ from historical estimates provided in Loughlin et al. (1987). Although inter–annual variability in foraging trip duration has been shown for this population (Loughlin et al., 1987; Goebel, 2002), 2008 trip duration in this study (7 days) is similar to trip durations presented in previous studies: 6 days (Bartholomew and Hoel, 1953; Peterson, 1965; Loughlin et al., 1987), 8 days (Gentry and Kooyman, 1986), and 7 days (Goebel, 2002). If prey availability is less than optimal for females, it
can cause females to take longer trips at sea and result in less time spent onshore suckling pups (Duck, 1990). Because less time is spent onshore, pups can grow slower and even starve when food conditions are poor (Trillmich, 1990). Inversely, females take shorter trips if prey availability is high, resulting in shorter foraging cycles and more time spent onshore (Baker, 1991). The similarity in the length of trip durations from this study and historical records suggest that prey availability was comparably high, though not as high as in 1953, 1965 and 1987.

While foraging trip duration can give some indication on prey availability during the breeding season, it does not provide information on individual foraging characteristics and how seals may be searching for prey. The advancement of TDRs (Time Depth Recorders) and satellite tracking of females at sea can collect more detailed information on rookery–specific foraging domains, distance traveled, and dive–depth and frequency (Robson et al., 2004; Sterling, 2009; Kuhn et al., 2010).

There was a significant difference for maternal visits onshore, as females in 2008 spent less time onshore than those presented in Loughlin et al. (1987). Results from this study should be compared to other historical estimates of this parameter, to determine the extent of variability in maternal attendance patterns. Nursing duration data was not collected during maternal presences, thus I can only assume that females were using the majority of their attendance visits to nurse their pups. Macy (1982) reported pup suckling duration times of 8.5 minutes in northern fur seals, although it is not clear if other behaviors are included during this time. For example, pups of different pinniped species do not use the entire suckling bout for
suckling only, as they may occasionally break contact and switch teats (Oftedal et al., 1987). As heavier pups at the end of weaning have been shown to have higher survival rates (Baker and Fowler, 1992), further exploration of nursing events may better the understanding of maternal behavior during each rookery visit.

Although the data presented here can give some indication of early maternal care, there is no way of knowing how many pups were successfully weaned in 2008. It has been shown that the winter migration of pups is more of an abrupt event instead of a continual process (Baker, 2007). Additionally, pup survival to a reproductive age is even more challenging to quantify in fur seals, as pups are completely pelagic for their first 2–3 years of life.
Chapter 5 – General Conclusion

Monitoring vital rates, like survival and natality, can provide information on the potential effects of current ecological conditions as well as any age– or stage–related effects (Promislow and Harvey, 1990). For Otariid species, survival can be a difficult parameter to quantify, as species are highly migratory and spend the majority of their life at sea. However, natality may be quantified readily because Otariids are still tied to land masses for reproductive purposes. Natality was defined in this study as a population level parameter and calculated as the total number of pups born divided by the total number of females of reproductive age in the rookery each year. Natality rates were estimated for 2008 and 2009 by two different methods: direct visual observations (observed) and maternal attendance patterns derived from VHF–radio telemetry data (detected). These rates are presented in Table 5.1.

In 2008, a substantial difference was observed in natality rates: 0.79 as estimated from direct observations versus 0.95 as estimated from VHF–based attendance patterns. There are a number of possible explanations for this difference. The methods of data collection differed between direct observations and telemetry data. The stationary logging system collected data continuously on the subset of females outfitted with a VHF–radio transmitter, opposed to visual observations in 2008 that occurred only once per day during daylight hours. As a result, re-
productive status was determined via attendance patterns for some females that were never observed during the breeding season. As shown in Table 2.11, 85 females were detected while 77 were observed returning to Polovina Cliffs in 2008. This difference in return rates suggests that the observed return rate for marked females without a radio transmitter may be negatively biased, which may inflate the overall observed natality rate in 2008. Thus, these rates should be treated as minimum (0.79) and maximum (0.95) natality rates for 2008 (Table 5.1).

Table 5.1: Summary of fertility rate (2008) and natality rates (2008 and 2009) from Chapter 2.

<table>
<thead>
<tr>
<th>Year</th>
<th>Method</th>
<th>Rates</th>
</tr>
</thead>
<tbody>
<tr>
<td>2008</td>
<td>Natality Rate based on visual observations</td>
<td>0.79</td>
</tr>
<tr>
<td>2008</td>
<td>VHF-detected Natality Rate</td>
<td>0.95</td>
</tr>
<tr>
<td>2008</td>
<td>Fertility Rate calculated by count data</td>
<td>0.60</td>
</tr>
<tr>
<td>2009</td>
<td>Natality Rate based on visual observations</td>
<td>0.88</td>
</tr>
</tbody>
</table>

There was also a difference between the observed natality rate between years: 0.79 in 2008 versus 0.88 in 2009. Field sampling methods were modified between study years. Observations were only conducted once per day in 2008, opposed to twice per day in 2009. Female behavior classifications were limited to three categories in 2008, as opposed to six categories in 2009. The additional sampling period and coded behavioral scales in 2009 may be partially responsible for the higher observed natality rate, as it allowed observers more opportunities to determine reproductive status of females and accurately classify female behavior.

Although sampling methodology was modified between years, the similar results suggest that the natality of marked females in 2008 and 2009 were relatively stable.
There is no apparent indication that this rate is low, as the observed natality rates for marked individuals were $\geq 0.79$ for both 2008 and 2009. This suggests that the majority of reproductively mature females returned to Polovina Cliffs rookery and gave birth in 2008 and 2009.

Natality estimates from this study may also be biased because it represents the proportion of reproductively mature females that give birth within a given breeding season. Females that fail to give birth have irregular and infrequent visits to the rookery (Vladimirov, 1987). It can be difficult to accurately determine the reason a reproductively mature female did not return to the rookery within a given breeding season as the female could have lost her identifying marks (tags or pelage marks), failed to give birth, emigrated to another colony, or died. Longitudinal studies of marked individuals can provide the most comprehensive information on the periodicity of reproduction (Testa, 1987; Lunn et al., 1994).

Because of the potential biases associated with the presented natality estimates, a fertility rate was also determined. Fertility was defined in this study as a population level parameter calculated by the total number of pups born divided by the total number of females present (irrespective of female age). By this definition, the fertility rate will always be lower than the natality rate because it includes females not yet of reproductive age.

The fertility rate was determined from count data of females and pups in 2008. Common errors associated with count data were minimized by conducting daily counts and incorporating post hoc model fitting techniques. Uncorrected direct counts can underestimate population size because of the assumption that individ-
uals are always detected if present, or that detection probability is always $= 1$. Detection probabilities of females can be influenced by reproductive status (with or without pups), as well as the attendance patterns (or temporary emigration) of females suckling pups during the breeding season. Recent studies have begun to incorporate mark–recapture estimates in order to achieve better inferences on population size (Eberhardt, 2002; Watson et al., 2009). Mark–recapture estimates can provide researchers with a better understanding of detection probability, and allows for the incorporation of individual covariates to provide additional information that may improve the probability of detection (White, 2005).

Thus, female count data was corrected by the daily detection probabilities derived from double–tagged females (see Figure 2.3), and pup counts were corrected for pup mortality. The fertility rate for 2008 (0.60, Table 5.1) was lower than the observed natality rate for the marked females. This is consistent with the likely inclusion of nulli–parous females and older females not carrying their pregnancies to term in the overall count and therefore the minimum estimate of a fertility rate for 2008.

It is important to point out that the natality rate estimates I present here are based on a sub–sample of adult females of reproductive age: those that are present in, or have returned to the rookery. Multiplying early term pregnancy rates of 0.88 (a combined rate from Testa et al. (2010)) with natality rates in pregnant females (0.82) yields an overall natality estimate of 0.72. This rate lies between estimates provided for the sub–sample of females present in the rookery, and the cross–sectional count based fertility estimate of 0.60 (Table 5.1). The fertility
estimate likely includes immature females, and the value of 0.72 is probably the closest value to true natality of all estimates I report here.

The timing of reproduction was also determined in 2008 and 2009. The median dates of birth were determined from sigmoid growth models fitted to the corrected, cumulative pup counts. These dates were estimated as the date corresponding to one-half of the maximum count reached in a sigmoid growth model following the methods in Trites (1992). The median date of birth was 17 July in 2008 and 15 July in 2009. Interestingly, these dates are one day after the observed median arrival of marked females determined with pups (Table 5.2, and Section 2.3.4). This consistency supports the accuracy of the observed estimate of parturition in the marked female sample.

Table 5.2: Summary of dates from Chapter 2. Calculated median arrival of marked and unmarked females is derived from female count data (2008), calculated median dates of birth are derived from pup count data (2008 and 2009). Observed and detected median arrival are for two groups: All marked and returned females, and all marked and returned females determined with a pup (2008 and 2009).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Group</th>
<th>Date</th>
<th>Year</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calculated Median Arrival</td>
<td>Marked and Unmarked Females</td>
<td>13 July</td>
<td>2008</td>
</tr>
<tr>
<td>Detected Median Arrival</td>
<td>VHF Females</td>
<td>18 July</td>
<td>2008</td>
</tr>
<tr>
<td>Observed Median Arrival</td>
<td>All Marked Females</td>
<td>16 July</td>
<td>2008</td>
</tr>
<tr>
<td>Observed Median Arrival</td>
<td>Marked Females (with pups)</td>
<td>16 July</td>
<td>2008</td>
</tr>
<tr>
<td>Calculated Median Date of Birth</td>
<td>Pups</td>
<td>17 July</td>
<td>2008</td>
</tr>
<tr>
<td>Observed Median Arrival</td>
<td>All Marked Females</td>
<td>15 July</td>
<td>2009</td>
</tr>
<tr>
<td>Observed Median Arrival</td>
<td>Marked Females (with pups)</td>
<td>14 July</td>
<td>2009</td>
</tr>
<tr>
<td>Calculated Median Date of Birth</td>
<td>Pups</td>
<td>15 July</td>
<td>2009</td>
</tr>
</tbody>
</table>

There are numerous factors that can influence the timing of births. A delay in arrival, breeding, or a later date of implantation in females could result in a
delay in the date of parturition the following year. Additionally, age or body condition may affect the timing of parturition. Pitcher et al. (2001) determined significant temporal (and spatial) variation in the timing of Steller sea lion (*Eumetopias jubatus*) births also using the sigmoid method presented in Trites (1992).

On a population level, Pitcher et al. (2001) hypothesized that prey availability or a change in the age structure of reproductively mature females could cause a temporal shift in reproduction. Northern fur seals, as opposed to fur seal species that breed in low latitudes, have a comparatively short nursing period of approximately four months (Gentry and Kooyman, 1986). Because of the possibility of a shorter birth to weaning period, any shift in the timing of arrival could have either a beneficial or detrimental effect on the amount of resources transferred to pups.

Determining maternal attendance patterns during lactation can provide indirect information about the abundance and distribution of prey (Gentry and Kooyman, 1986). Generally, with all other factors being equal, foraging trip duration displays an inverse relationship to prey abundance (Gentry and Kooyman, 1986; Boyd et al., 1997; Merrick and Loughlin, 1997). The mean duration of the perinatal period was 7.5 days (Table 5.3). Although the mean duration presented in this study was derived from a smaller proportion of the population, the duration of the observed perinatal period in this study is similar to historical records. The overall mean of the first five onshore visits was 1.47 days (Table 5.3).

The overall mean of the first five foraging trips was 7.07 days (Table 5.3). Although inter–annual variability in foraging trip duration has been shown for this population (Loughlin et al., 1987; Goebel, 2002), 2008 trip duration in this study (7
Table 5.3: Summary of maternal attendance patterns from Chapter 4.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>N</th>
<th>Mean Duration (Days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Perinatal Period</td>
<td>76</td>
<td>7.5</td>
</tr>
<tr>
<td>Duration of First Five Visits</td>
<td>198</td>
<td>1.47</td>
</tr>
<tr>
<td>Duration of First Five Trips</td>
<td>207</td>
<td>7.07</td>
</tr>
</tbody>
</table>

days) is similar to trip durations presented in previous studies: 6 days (Bartholomew and Hoel, 1953; Peterson, 1965; Loughlin et al., 1987), 8 days (Gentry and Kooyman, 1986), and 7 days (Goebel, 2002). The similarity in the length of trip durations from this study and historical records suggest that prey availability was comparably high, though not as high as in 1953, 1965 and 1987. While trip duration can give some indication on prey availability during the breeding season, it does not provide information on individual foraging characteristics. Females may alter dive frequency and depth, as well as consume different prey species without changing trip duration (Gentry and Kooyman, 1986).

Natality rates determined from this study are similar, if not higher, to reproductive rates of stable or increasing populations of fur seals (Lunn et al., 1994; McKenzie et al., 2005). Natality estimates from this study may be biased because it represents the proportion of reproductively mature females that give birth within a given breeding season. Additionally, the majority of females captured may be at their reproductive peak or in better body condition (Bigg, 1984; Boyd, 1984). Age–specific reproductive rates in northern fur seals rapidly increases until their reproductive peak, during ages 5, 6, and 7, and subsequently decreases with increasing age (York and Hartley, 1981). The natality rates presented here are
also similar to rates of Arctic ungulates of prime reproductive age (Gaillard et al., 2000). Field captures occurred around the known weaning period for this species, thus may exclude females not yet of reproductive age and senescent females. The late timing of female captures may also exclude females that failed to pup or lost their pup to neonatal mortality as these females would no longer be present in the rookery.

The fertility rate in 2008 was lower than the natality rates for both years. This is to be expected as it may include nulli–parous females and females present at Polovina Cliffs but without a pup. This estimate should be regarded as the minimum estimate of fertility. Additional years can provide further insight into this estimate, and how the fertility estimate compares to natality estimates derived from the same breeding season.

The results from this study, coupled with the high pregnancy rates reported by Testa et al. (2010), suggest that most females at this rookery returned and gave birth to pups in 2008 and 2009. Additional study years will provide more information on the periodicity in reproduction, as mammalian females may forego giving birth in order to maximize their individual fitness (Testa, 1987; Lunn et al., 1994; Gaillard et al., 2000). Like many mark–recapture studies, longitudinal sampling on this population will provide the most accurate information on the periodicity of reproduction and lifetime reproductive success. Regardless, results from this study can provide baseline information for this declining population.

Reproductive timing, while highly consistent between 2008 and 2009, was determined to occur later in the breeding season during the third week of July. For a
species that has historically been highly synchronous in the timing of arrival and subsequent parturition, it is intriguing that this shift has occurred. This could be a result of individual factors, like the timing of implantation or the length of active gestation, as well as the effects of individual age and body condition (Boyd, 1984; York and Scheffer, 1997; Guinet et al., 1998). A delay in the timing of parturition may also be related to prey availability. This link has been shown in other species that annually employ an embryonic diapause (Ben-David et al., 1997; Pitcher et al., 2001; Soto et al., 2004). Further investigation is needed to determine if this occurs annually as 2008 and 2009 were considered cold years in the Bering Sea, which had extensive sea ice cover in the spring of both years of this study (Overland et al., 2009). In conclusion, the consistency of natality rates between years and methods suggest that natality is fairly high and consistent for marked females of reproductive age, but the timing of reproduction occurred later than historical estimates. These results suggest that future studies should fully explore other life stages, like juvenile survival, in order to determine how these factors may currently be contributing to the Pribilof Island population decline.
APPENDICES
Appendix A – Definition of Terms

Natality: A population level parameter calculated as the total number of pups born divided by the total number of females of reproductive age in the rookery each year.

Fertility rate: A population level parameter calculated by the total number of pups born divided by total number of females present (irrespective of female age). By definition, the fertility rate will always be lower than estimates of natality rate because it includes females not yet of reproductive age.

Reproductive rate (Birth rate): Generic term referring to either fertility or natality.

Pregnancy rate: Number of females with detectable embryo or corpus luteum divided by number of females observed.

Pup: Common term for fur seal neonatal offspring prior to weaning.

To pup: To give birth.

Pregnancy: Refers to any process relating to gestation until actual birth, and the potential reproductive output usually measured during the gestational period.

Parturition: Birth.

Ovulation: The period when the first embryonic attachment (or implantation) occurs (Craig, 1964). In northern fur seal females, ovulation occurs spontaneously 3–5 days after parturition (Craig, 1964).
Estrus: The period in which female mammals are ready to receive a male and mate. Fur seals are monestrous, only entering heat once during the breeding season.

Embryonic diapause: A reproductive strategy for many pinniped species in which the embryo (blastocyst) does not immediately implant in the uterine wall, but remains free until approximately mid–November, when implantation occurs. This strategy allows pinnipeds to time birth for a period when environmental conditions are most favorable.

Active Gestation: The time period after mid–November when it is assumed that embryonic implantation has occurred, until the pup is born. For northern fur seals, active gestation is approximately 8 months.

Haul out: Terrestrial ground where seals come to rest. Sub–adult males and juveniles are typically found in haul outs.

Rookery: Breeding grounds, breeding colony. Rookeries are terrestrial grounds where breeding and weaning typically occur.

Nursery: Common used term for pup aggregations during weaning when only a proportion of females will be onshore as the remainder of them will be foraging at sea.
Appendix B – Sigmoid Growth Model Estimates and Graphs for Uncorrected Pup Counts

Figure B.1: 2008 sigmoid curve fit to pup count data with 95% confidence intervals. The dashed line represents the mean and median date of parturition. The presented model is uncorrected for pup mortality (median date 15 July, \(a = -31.71\), \(b = 1333.99\), \(c = 23.33\), \(d = 4.65\)).
Figure B.2: 2009 sigmoid curve fit to pup count data with 95% confidence intervals. The dashed line represents the mean and median date of parturition. The presented model is uncorrected for pup mortality (median date 15 July, $a = -237.80$, $b = 1711.57$, $c = 12.88$, $d = 6.79$).
Appendix C – Sigmoid Growth Model Estimates and Graphs for Dead Pup Counts

Figure C.1: 2008 sigmoid curve fit to dead pup count data with 95% confidence intervals. Parameter estimates: $a = 0.87$, $b = 113.61$, $c = 30.13$, $d = 5.48$). 1 = 23 June, 60 = 21 August.
Figure C.2: 2009 sigmoid curve fit to dead pup count data with 95% confidence intervals. Parameter estimates: $a = -0.22$, $b = 102.76$, $c = 32.59$, $d = 5.37$). 15 = 15 July, 50 = 19 August.
Bibliography


