A MULTISTATE MARK RECAPTURE ANALYSIS TO ESTIMATE REPRODUCTIVE RATE IN THE STELLER SEA LION (*EUMETOPIAS JUBATUS*), AN ENDANGERED SPECIES

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DEDICATION

To my parents, who instilled in me a love of learning.

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ABSTRACT

The Steller sea lion is an endangered species whose reproductive rate estimates need to be updated. The species is divided into two populations: the endangered western population has declined over 80% from historical levels, while the threatened eastern population has been increasing at approximately 3% for the past three decades. The statistically most compelling reproductive rate estimates for this species are based on now out of date population dynamics, and hence are not applicable to current concerns. Extensive recent branding and resighting efforts by the Alaska Department of Fish and Game in Southeast Alaska make possible an updated estimation of eastern population Steller sea lion reproductive rates. However, the complexity of these data required a different statistical approach than is typically used to estimate reproduction in marked and resighted animals. I developed a novel statistical analysis, based upon a multistate mark recapture likelihood function, specifically to analyze the Southeast Alaska Steller sea lion data. The likelihood function estimates a reproductive rate when only adult females (not pups) are marked, female sightability is correlated with reproductive status, state classification uncertainty is present and the population is open to births during many of the resighting intervals. I apply this analysis to the Southeast Alaska Steller sea lion data and estimate a reproductive rate of 0.66 (0.55, 0.77). Not only does this provide a reproductive rate estimate for the eastern population, which is important for monitoring its health, but it also provides a basis for comparison to the endangered western population. Furthermore, the Alaska Department of Fish and Game continues to have an active branding and resighting program. The methods developed here can be applied to future data collected in either population.

INTRODUCTION

The Steller sea lion is an endangered species whose three decade decline is still largely unexplained. Under the Endangered Species Act, the species is split into two Distinct Population Segments, the eastern population and the western population. The endangered western population declined by over 80% between the late 1960's and 2000, while the threatened eastern population has been increasing since the late 1970's at approximately 3% per year (NMFS 2008). Although the western population appears to be stabilizing, its status is still uncertain.

Critical to managing the sea lion populations are good estimates of their vital rates. Recent survival rate estimates exist (Pendleton et al. 2006); however reproductive rates (the number of pups born per mature cow) need to be updated. The statistically most compelling estimates of Steller sea lion reproductive rates come from the dissection of animals collected in the western population during the 1970's (Calkins and Pitcher 1982), a time for which the population trend is difficult to reconstruct, and the 1980's (Calkins and Goodwin 1988), when the population was declining. As a result, these reproductive rate estimates are not currently applicable to either the eastern or western populations.

Reproductive rate estimates from the eastern population are important for two reasons. First, although the population is considered healthy, it is listed as threatened and needs to be monitored. Second, estimated rates from a healthy population will provide a basis for comparison for estimates from the endangered western population, whose status remains uncertain.

Extensive sea lion branding and resighting by the Alaska Department of Fish and Game (ADFG) make possible an updated reproductive rate estimation for Steller sea lions in Southeast Alaska (eastern population). However, the complexity of these data required a different statistical approach than is typically used to estimate reproduction in marked and resighted animals. In the following chapters, I derive an analysis specifically for the ADFG data, and use it to estimate the Southeast Alaska Steller sea lion reproductive rate. In addition, ADFG continues to have an active branding and resighting program, and the methods developed here can be applied to future data collected from either population.

This dissertation is a melding of biology and statistics. In Chapters 2 and 3 I describe Steller sea lion biology, the Southeast Alaska study system and the methods of data collection. Next (Chapters 4 and 5), I motivate and derive a multistate mark resight likelihood function to estimate a reproductive rate when only adult cows (not pups) are marked, cow sightability is correlated with reproductive status, state classification uncertainty is present, and the population is open to births during many of the resighting intervals. Chapter 6 addresses additional confounding factors in the data. Chapter 7 gives a synthesis of the methods and the results of the reproductive rate estimation, and Chapter 8 contains recommendations for future analyses.

THE STELLER SEA LION

Taxonomy

Steller sea lions (*Eumetopias jubatus*) are the largest member of the Otariidae, a Pinniped family distinguished by external pinnae, and hind flippers that rotate to allow improved locomotion on land. They belong to the subfamily Otariinae (sea lions), which is distinguished from the Arctocephalinae (fur seals) by their relatively sparse pelage (Berta et al. 2006). Steller sea lions are the sole member of the genus *Eumetopias* (Loughlin et al. 1987).

General Description

Steller sea lion pups weigh 16 - 23 kg and are about a meter in length at birth (Loughlin et al. 1987). Females appear to reach maximum skeletal growth in about six years, and males in about eleven (Calkins and Pitcher 1982). Steller sea lions show strong sexual dimorphism: adult females can be up to 2.92 m in length and 350 kg, while males are up to 3.25 m in length and 1120 kg (Loughlin et al. 1987). The adult pelage ranges in color from blond to brown; pups are dark brown to black. Mature males have massive, muscular chests and necks, and longer hair on the chest, shoulders and back of the neck (Loughlin et al. 1987). Females collected from the wild and aged by counts of dental annuli have been as old as 30 years of age (Pitcher and Calkins 1981) and males as old as 18 (Calkins and Pitcher 1982).

Distribution and Populations

The Steller sea lion is found throughout the North Pacific Rim, from Hokkaido, Japan to the Kuril Islands and Okhotsk Sea, through the Aleutian Islands and central Bering Sea, along the southern coast of Alaska, and down the west coasts of Canada and the continental United States as far south as California (Loughlin et al. 1987).

The species is divided into two evolutionarily distinct populations: the western population includes rookeries from Prince William Sound, Alaska and westward, and the eastern population includes rookeries from Southeast Alaska to California (Bickham et al. 1996; Loughlin 1997). The western population appears to have undergone a more recent subdivision, as well, and Baker et al. (2005) suggest the existence of a third population, the Asian population, west of the Commander islands in Russia. This population includes rookeries from the Kamchatka Peninsula, Kuril Islands, and Sea of Okhotsk. Within Alaska, the western population may be further subdivided into populations that are demographically, if not evolutionarily separate. This split occurs in the Aleutian chain at Samalga Pass, where rookeries to the east lie within the continental shelf, and those to the west lie within the ocean basin (O'Corry-Crowe et al. 2006).

Two recently established rookeries in the range of the eastern population appear to have been colonized by a mix of eastern and western cows. Some neonates on Graves Rocks Rookery (in Glacier Bay National Park) and to a lesser extent, White Sisters Rookery have haplotypes heretofore found only in the western population (Gelatt et al. 2006).

Diet and foraging

Steller sea lions forage at sea and haul out on land. They are primarily pscivorous, although cephalopods are an important dietary component as well. They target densely schooled fish in near shore waters (Sinclair and Zeppelin 2002), but they are opportunists, and their prey varies by area, season and water depth (Loughlin et al. 1987; Calkins and Pitcher 1982; Sinclair and Zeppelin 2002). Fish eaten include herring (Clupeidae), salmon (Salmonidae), capelin and smelt (Osmeridae) pollock and cod (Gadidae), flatfishes (Pleuronectiformes), sculpins (Cottidae) and rockfishes (Scorpaenidae) (Calkins and Pitcher 1982; Sinclair and Zeppelin 2002). Greenlings and mackeral (Hexagrammidae) as well as sand lances (Ammodiytidae) are also eaten (Sinclair and Zeppelin 2002). Dissections have revealed stomach contents as varied as gastropods, bivalves and harbor seals (Phocidae) (Calkins and Pitcher 1982).

Predation

The major natural predator of the Steller sea lion is the transient killer whale (*Orcinus orca*) (Maniscalco et al. 2007; Heise et al. 2003). Pups appear to be preferred when an individual Orca is hunting alone or when a calf is being taught how to handle prey; whereas older ages appear to be preferred by groups of adult Orcas (Maniscalco et al. 2007). Historically, humans have been a serious predator of Steller sea lions. Commercial harvests were conducted in this country through 1972, when passage of the Marine Mammal Protection Act made shooting Steller sea lions illegal except to protect fishing gear or human safety. In 1990, a prohibition on discharge of firearms near Steller sea lions was implemented (Ferrero and Fritz 2002). A small

Native American subsistence harvest is still permitted in the United States; the only remaining commercial harvest is in Japan (NMFS 2008).

Diseases and Parasites

Bacterial disease agents of Steller sea lions include *Leptospira interrogans*, *Chlamydia psittaci* and *Brucella sp.*. Viral disease agents include canine adenoviruses, phocid herpesviruses, and marine caliciviruses such as the San Miguel sea lion virus (SMSV). Leptispirosis, Chlamydiosis, Brucellosis and SMSV are known to cause reproductive failures in other species, although they do not appear to be a major problem for Steller sea lions (Calkins and Goodwin 1988; Burek et al. 2005).

Steller sea lions are known to contract the following parasites: intestinal cestodes; intestinal and billiary trematodes; stomach, intestinal, and pleural nematodes; intestinal acanthocephalans, pleural and nasopharyngial acarian mites and an anopluran skin louse (Loughlin et al. 1987). Lice infestations are most common on pups (Thorsteinson and Lensink 1962).

Reproductive Physiology

Maturation and Senescence

Males typically become sexually mature between the ages of six and seven (Perlov 1973), although the range is between three and eight years of age (Calkins and Pitcher, 1982). Females begin to ovulate between the ages three and eight, with a mean of 4.6 and a mode of four (Calkins and Pitcher 1982). First ovulations in other studies were also within this range (Perlov 1973; Ishinazaka and Endo 1999). Three females collected between the ages of ages 21 and 30 had ovulated, but were not pregnant (Calkins and Pitcher 1982).

Annual Cycle

Mature female Steller sea lions ovulate and mate annually: most ovulate once per summer and a few ovulate twice (Calkins and Pitcher 1982; Ishinazaka and Endo 1999; Pitcher and Calkins 1981). Twinning is rare. Most copulation occurs between early June and early July (Pitcher and Calkins 1981), ten to fourteen days post parturition (Sandegren 1970). Although mating occurs during mid-summer, embryo implantation occurs in late September or October, approximately three months post copulation, resulting in an approximately nine month active gestation (Pitcher and Calkins 1981). Reproductive failure is common. Missed pregnancies (ovulation but no fertilization or failure to implant), resorption of embryo, or spontaneous abortion were found in 20 of 85 sexually mature females collected by Calkins and Pitcher (1982). Missed pregnancies were usually associated with first ovulations; but abortions occurred in multiparous females of various ages.

Reproductive Behavior

Breeding Colonies

The species is polygynous and colonial. The overwhelming majority of mating, birthing and nursing occur on traditional sites called rookeries, where harem bulls maintain summer territories. Rookeries are typically located on exposed shorelines with rock slab or cobble beach substrate (Ban and Trites 2007; Call and Loughlin 2005). Steller sea lion rookeries tend to cluster at transitions between major oceanic currents, where nutrients and therefore prey are concentrated (Call and Loughlin 2005), probably a result of the foraging needs of lactating females. Land sites used by non-reproductive Steller sea lions are called haulouts. Although some parts of some rookeries are used as haulouts as well, the sea lions disperse widely in the non-breeding season (Sease and York 2003).

Harem Bulls

Bulls maintain rookery territories (and access to cows for mating) for lengths of time as short as a few day to over sixty consecutive days (Sandegren 1970). In order to maintain a territory a bull must be continuously present on site to defend against intruding males (Thorsteinson and Lensink 1962; Sandegren 1970), and as a result, must fast. Average age of harem bulls is notably older than average age of male sexual maturity. Although harem bulls can range in age from six years old to over seventeen years old, 86% of 185 harem males collected by Thorsteinson and Lensink (1962) were between the ages of nine and thirteen, suggesting that inability to defend a breeding territory limits the reproductive activity of younger males, even though they may be sexually mature.

Cows and Pups

Site Fidelity: Female Steller sea lions display a moderately high level of natal site fidelity, and a higher level of adult breeding site fidelity. An estimated 67% of western population and 81% of eastern population females give birth to pups at their natal rookeries. The first published record of of a female known to have given birth on two different rookeries was in 2002 (Raum-Suryan et al., 2002). Despite the high level of breeding site fidelity, individuals can move long distances, especially when they are non-reproductive. Marked individuals have been observed at sites 1300 - 1700 km apart (Raum-Suryan et al. 2002, 2004; Calkins and Pitcher 1982).

Birthing: Almost all pupping, range wide, occurs between May 15 and July 15. Within this two month period, 90% of the births at an individual rookery occur within a 25 day period, and timing can differ significantly among rookeries. The earliest mean date of birth has been found at the Forrester Island Rookery Complex (FI) in Southeast Alaska, on June 4. Significant differences in birth timing can also exist among years at a single rookery. Differences in annual timing ranged from 3.2 days at FI to 10.2 days at Año Nuevo, California (Pitcher et al. 2001).

Cow Pup Interactions: Although attentive to their own pups, females are aggressive to other pups, especially during the first few post-parturition weeks. It is not uncommon for a cow to respond to neighboring female's pup by biting it or tossing it in the air (Sandegren 1970; Gentry 1970; Kaplan et al. 2008).

Female Attendance Patterns at Rookeries: Steller sea lions follow a 'foraging cycle' maternal strategy (Boness and Bowen 1996). A pregnant female arrives at her pupping site in early summer, gives birth to one pup and stays on land for (a per study average of) 5 - 11 days post-parturition (Maniscalco et al. 2006; Milette and Trites 2003; Higgins et al. 1988; Merrick 1988; Sandegren 1970) to nurse and care for her pup. After this perinatal period, the female alternates fishing at sea and caring for the pup on the rookery.

Post-perinatal summer foraging trips averaged 0.7 to 1.6 days per study, while between-trip summer rookery visits averaged 0.7 to 2.3 days per study (Maniscalco et al. 2006; Milette and Trites 2003; Hood and Ono 1997; Higgins et al. 1988; Brandon 2000, Merrick 1988; Sandegren 1970). As pups mature, mothers spend proportionally more time at sea, either because of longer trips (Maniscalco et al. 2006; Higgins et al. 1988; Merrick 1988) or both longer trips and shorter visits (Milette and Trites

2003). In either case, the post partum female's average foraging trip distance is 17 km from the rookery (Merrick and Loughlin 1997). This short distance reflects her need to return to the rookery to nurse her pup, and it makes her unlikely to frequent a haulout during the post-parturition, summer months.

Conversely, a mature female who does not give birth needs to visit a rookery only to mate, and is not tied to any particular location. Females caring only for juveniles are more likely to attend haulouts than rookeries (Pitcher and Calkins 1981). Few studies have examined the attendance patterns for females who are not caring for pups, although their onshore visits appear to be shorter than the visits of females attending pups. Merrick (1988) was able to document 238 trips and 228 visits among the 41 females with pups that he was tracking. In the same study he was able to document only 15 trips and 15 onshore visits for seven females who were hauling out on Ugamak Island Rookery, but deemed to be without pups or juveniles. These cows took trips of approximately twice the length (67 versus 29 hours) and stayed onshore for approximately half the length (31 versus 55 hours) of the females at Ugamak with pups.

Differences in the attendance of females with and without pups are also suggested by the large dichotomy in the foraging and haulout behavior of five adult females radio tracked during winter (Merrick and Loughlin 1997). Although their reproductive status could not be definitively ascertained, two maintained a foraging cycle similar to that of females caring for pups during the summer: trips averaging 18 hours that ended with the female returning to the same or a nearby haulout from which she departed. The remaining three females spent up to 24 days at sea, suggesting they were not caring for pups.

Detailed observations made possible by continual video surveillance on the Chiswell Island rookery (Maniscalco et al. 2006) reveal that some females who have regularly pupped on the island will attend the rookery during summers in which they do not have pups, although with reduced presence. However, other individuals who regularly pup on the rookery go unseen for an entire summer. It is unclear where these females are and what is their reproductive status.

I will continue to revisit the differences in behavior between post partum and non-post partum females throughout this dissertation. The following facts are worth bearing in mind.

1. A female caring for a pup is unlikely to frequent a haulout.
2. A female not caring for a pup spends less time on land than a female caring for a pup.
3. A female not caring for a pup spends less time at a rookery than a female caring for a pup.
4. Relatively little is known about the attendance patterns of females without pups.

Pup Maturation and Movements: Pups learn to swim in stages, and are landlocked for the first few weeks of age. For the first 12 to 20 days of life, they do not willingly enter the ocean. During the subsequent 10 to 18 days, they can dabble in the shallows, but they do not begin learning to swim with their mothers until 24 to 32 days of age. Swimming lessons are generally within 500 m of shore, although pups as young as 36 days have been seen following their mothers beyond this distance (Sandegren 1970). Cows and pups are highly faithful to the birthing beach for the first three weeks post-parturition (Kaplan 2005). As the season progresses, however, cows and pups are more mobile, and move among the beaches of the rookery. Pups also become more independent as they mature, and are increasingly willing to wander away from their mothers (Mathisen et al. 1962). Although some individual rookeries continue to be used at a reduced rate during the non-breeding season, many are not. By autumn, it is common for mother-pup pairs to disperse from rookeries to haulouts (Calkins and Pitcher 1982).

Pup Mortality: During the summer when pups are on the rookeries, the highest average mortality occurs during the neonatal period (Maniscalco et al. 2008). For example, Sandegren (1970) noted that of 56 pups under regular observation during the summer of 1967, seven died during the first two weeks of life, but none died during the following four to six weeks. Of the 43 pups under regular observation during the summer of 1968, six died during the first two weeks. Kaplan et al. (2008) studied pup mortality during the first three weeks of life on two of the beaches on Lowrie Island (the largest island in FI that is inhabited by breeding sea lions). The mortality rate was significantly higher on the first day of life than on any of the subsequent days, and it also differed significantly between the two beaches.

Neonatal mortality is caused by trauma (being bitten or trampled by adults), maternal abandonment and being washed off the rookery into the sea (Maniscalco et al. 2008; Kaplan 2005; Sandegren 1970). Once pups begin to swim, they are vulnerable to the predation of transient Orcas (Maniscalco et al. 2008). Notably, pup mortality on the rookeries also varies substantially from year to year, at least in part as a result of the event related nature of several of the causes (storms, stampedes and Orcas). In a seven year study on Chiswell Island, a small rookery under continual observation by multiple remotely operated video cameras, live births varied between 54 and 80 per year, while pup deaths varied from one to thirteen, giving a death rate during the first 2.5 months of life of 1% to 25%. Causes of mortality also varied greatly among years. In any given year, most pup mortality was attributable *either* to the neonatal causes or to Orcas consuming older pups (Maniscalco et al. 2008). For example, 52 pups were born alive on Chiswell Island in 2001, and 64 in 2002. In both years, 13 deaths occurred, and all were of known causes. In 2001 one neonate was washed away by surf, and 12 pups over a month in age were eaten by Orcas. Conversely, in 2002, all deaths were among neonates, and deaths were caused by surf in 11 cases; trauma in one; and abandonment in one.

The Non-breeding Season: Haulout use by mothers and their dependent young appears to be individualized: some show high site fidelity to a particular haulout during the non-breeding season, while some do not (Trites et al. 2006). Nursing females continue to alternate foraging trips and rookery visits, and pups take short trips while their mothers are away, suggesting that they are also conducting foraging trips of their own (Raum-Suryan et al. 2004; Trites et al. 2006). At least some three month olds are supplementing their diet with fish. This was evidenced by the presence of lungworm (*Filaroides sp.*) L1 larvae in pup feces, as this parasite is contracted by ingesting fish with L3 larvae encysted in the gut wall (Raum-Suryan et al. 2004). Regardless of early foraging efforts, pups continue to nurse at least into the next spring (Calkins and Pitcher 1982; Raum-Suryan et al. 2004; Trites and Porter 2002). Weaning usually occurs between April and June, (Raum-Suryan et al. 2004; Trites and Porter 2002), from late gestation (Pitcher and Calkins, 1981) to the start of the pupping season (Trites et al. 2006). Although most weaning occurs at one or two years of age (Trites et al. 2006), three (Calkins and Pitcher 1982; Sandegren 1970) and four (Trites et al. 2006) year olds have been observed nursing. A female who is nursing a subadult will sometimes give birth to a new pup, and care for both the pup and the subadult. Timing of weaning for at least a few of the subadults in these triads has occurred in autumn (Maniscalco and Parker 2009).

Reproductive Strategy

The total energy cost of lactation to Steller sea lions is extremely high (Boness and Bowen 1996), in part because of the one to two year period in which they nurse their offspring. Simultaneously lactating and maintaining a pregnancy is energetically expensive, and abortion may be a Steller sea lion reproductive strategy to deal with nutritional stress (Pitcher et al. 1998). The western population of Steller sea lions is thought to have been nutritionally stressed during the 1970's and 1980's, with the stress being greater in the latter decade. Although 97% of females collected in the Gulf of Alaska during these decades were pregnant in early getstation, only 67% were pregnant in late gestation in the 1970's, and only 55% were pregnant in late gestation in the 1980's (Pitcher et al. 1998). Aborting the fetus may be the least costly option for a stressed female, as ceasing lactation could jeoporadize an offspring in which she already has a large investment, and continuting to lactate and gestate might threaten the survival of mother, extant pup and fetus.

Although most Steller sea lion cows wean one offspring before giving birth to the next, it is not uncommon for a female to have both a pup and a juvenile. Cows with both pup and juvenile sometimes make the energetic trade-off post parturition. For example, of 17 cases on Chiswell Island where a female was seen with both a pup and subadult, nine cows nursed both pup and subadult, eight abandoned the pup in favor of the subadult, and none abandoned the subadult (Maniscalco and Parker 2009).

Population Decline and Current Status

Population Numbers

From the late 1960s through 2000, the western population declined over 80% in abundance, with steepest declines (of approximately 15% per year) occurring in the late 1980's, and slower declines (of about 5% per year) in the 1990s. The decline has been highly variable, not only temporally, but geographically as well (NMFS 2008; Loughlin 1997; Trites and Larkin 1996; Loughlin et al. 1992). Since the year 2000, the western population may have stabilized, although its status is still uncertain. Based on 2004-2005 data, the western population was composed of approximately 45,000 sea lions in Alaska and approximately 16,000 in Russia (NMFS 2008).

By contrast, the eastern population has been increasing at approximately 3% per year since the late 1970s. Once much smaller than the western population, it is now of a similar size: the 2002 estimate was between 46,000 and 58,000 animals (Pitcher et al. 2007). The eastern population is listed under the Endangered Species Act as threatened, the western population, endangered, and the regulatory population division occurs at 144° West (U. S. Federal Register 62: 24345-24355).

Potential Reasons for the Decline

The cause of decline is probably multifactorial, and no consensus exists regarding the exact combination of contributing factors. Reduced survival or natality (Pitcher et al. 1998) due to nutritional stress (Trites and Donnelly 2003; Pitcher et al. 1998; Calkins et al. 1998), either because of competition from commercial fisheries (Hennen 2004) or because of a major regime shift in the mid-1970s (Benson and Trites 2002) is likely to be at least one of the factors. Other mechanisms that have received support include direct mortality such as incidental take in fisheries, commercial harvests, illegal shooting and killer whale predation (NMFS 2008).

Life Table

The most widely referenced demographic rate estimates for Steller sea lions come from a life table constructed by York (1994). This life table is based on data from dissections of cows collected in the Gulf of Alaska between 1975 and 1978 (Calkins and Pitcher 1982). Adult survival rates were calculated from the age structure of the collected cows, and reproductive rates from the examination of their reproductive tracts. The estimated reproductive rate from the collected cows was 0.63 pups born per mature cow, thus the life table uses a fecundity of 0.315 female pups born per mature cow.

Because the cows were originally collected for reproductive studies, few juveniles were taken, and the proportion of juveniles in the sample under-represented the proportion of juveniles in the population. As a result, juvenile survival rates could not be estimated from the collections. To account for this, the life table is constructed under the assumption of population stationarity, and juvenile survival rates are back-calculated to make sure the population is neither increasing nor decreasing.

Western Population

Reproductive Rate Estimates

In 1985 and 1986, a sequel collection of Steller sea lions was conducted in the Gulf of Alaska. Examination of the cows' reproductive tracts yielded an estimated reproductive rate of 0.55. (Pitcher et al. 1998; Calkins and Goodwin 1988).

Several modeling efforts have made retrospective predictions about what changes in vital rates might have produced the observed western population decline. These models all base initial vital rates or age structure on one or both of the Gulf of Alaska collections (1975-1978, Calkins and Pitcher 1982; 1985-1986, Calkins and Goodwin 1988), and model subsequent trends in pup and non-pup counts. For example, Fay and Punt (2006) used four sources of data to model the Steller sea lion decline in the Gulf of Alaska. These included pup and non-pup counts, survival rates based on tagging programs and the age structure of the 1980's collection. Their results suggest that Gulf of Alaska Steller sea lions experienced as much as a 22% drop in fecundity during their decline, but that fecundity is no longer a limiting vital rate for this population.

Holmes and York (2003) used the York (1994) life table to represent a stationary western Steller sea lion population in the late 1970's. They allowed this matrix to change in 1983, 1988 and 1993 to allow vital rate changes one to two years before large observed changes in the population's rate of decline (York et al. 1996), and fit this model to series of pup and non-pup counts and a juvenile fraction index. According to their modeling results, declines in the 1980's were associated with low juvenile survivorship and declines in the 1990's were associated with low fecundity.

Winship and Trites (2006) estimated the number of non-pups in the western population in 1978, and under the assumption of a stationary population at carrying capacity, calculated a pre-decline set of vital rates where fecundity and juvenile survival were consistent with York (1994). They then calculated a starting age structure, and estimated vital rates for the declining population by fitting a model to time series of pup and non-pup counts at rookeries. They assumed that pup counts are an unbiased estimator for twice the number of female pups in the population, and they estimated two parameters to scale the predicted number of female non-pups in the population to the number of non-pups observed on the rookeries. The annual reproductive rates they present range from 0.1 to 0.33, depending on the region and time phase being modeled.

Holmes et al. (2007) estimated the change in central Gulf of Alaska Steller sea lion vital rates. They based pre-decline Leslie matrices on the York (1994) life table, which they updated to include reproductive senescence. They assumed that Steller sea lion population dynamics were governed by this matrix until 1983, at which point juvenile survival, adult survival and fecundity were allowed to vary independently across four time periods. This gave 12 parameters which scaled each of the three rates relative to its pre-decline level across each of the four times. The twelve scaling parameters were estimated by maximum likelihood fitting to a 1976 - 2004 time series of pup counts, non-pup counts and juvenile fraction indexes. The index of the fraction of juveniles in the population was based on measurements of Steller sea lions in aerial photos of haulout sites. The best fit model showed that fecundity declined to 64% of pre-decline levels, and it showed an increase in juvenile and adult survival nearly to pre-decline levels after a severe reduction in the early 1980s. The authors conducted sensitivity analyses using four different pre-decline matrices, nine different sets of time periods, and two different data sets (one with the juvenile fraction index, and one without). The decline in reproduction and the increase in survival was consistent across models, largely because of the decreasing ratio of pups to non-pups in the data. The analyses indicated that the declining ratio could not be accounted for by increasing survival rates alone; it required a concomitant decline in natality. Predicted 2004 fecundities from this study are 0.21 and 0.25 for females aged eight to ten, and eleven to sixteen, respectively.

The reproductive rate estimates based strictly on current data come from detailed observations of naturally marked females who attend the Chiswell Island Rookery, in the Kenai Fjords area of the Central Gulf of Alaska (Maniscalco et al. 2005b). Chiswell

Island is continually observed by multiple remotely operated cameras, so it is known whether or not a marked female gives birth on the island. However, these same individuals can rarely be tracked elsewhere, and the reproductive status of absent animals is, by necessity, based on assumption. From 2001 through 2004, the average reproductive rate was estimated to be 0.83, giving a fecundity approximately twice the estimated 2004 fecundity from the most recent of the modeling studies (Holmes et al. 2007).

Eastern Population
Reproductive Rate Estimates

Only rough calculations of eastern population reproductive rates have been made, and they are older than the western stock estimates. Pike and Maxwell (1958) counted pups and non-pups at rookeries and haulouts during the summers of 1956 and 1957. Assuming a 50:50 sex ratio among *non*-pups, they estimated the pregnancy rate for mature females in British Columbia was over 70%. Gentry (1970) estimated the size of the Año Nuevo pup population by summing the high summer pup count for areas that could be seen well and the number of pups tagged on areas that could not be seen well. Dividing this estimate by the largest count of adult females on the rookery, he obtained a 68% reproductive rate. No adjustment was made, in either estimate, for the fraction of the non-pup population that is at sea, and therefore not counted.

Need for Updated
Reproductive Rate Estimates

Of the reproductive rate estimates for the different Steller sea lion populations during various time periods, the statistically most compelling are those from the western population during the 1970's and 1980's, based on dissections of cows collected in the Gulf of Alaska (Calkins and Pitcher 1982; Calkins and Goodwin 1988). The other estimates involve more assumptions, and all but the Chiswell Island estimates are based on less direct evidence.

Regardless, it is clear that the dynamics of the western population have changed appreciably, more than once, since the collections were made. It is also clear that the dynamics of the eastern population have been different than those of the western population. More current estimates of vital rates are needed to explain the present dynamics of both populations. Survival rates have recently been updated from mark resight studies of individuals born and branded on Marmot Island (western population) in 1987-1988 and FI (eastern population) in 1994-1995 (Pendleton et al. 2006); however reproductive rates still need to be updated (NMFS 2008).

Extensive branding and resighting efforts by the Alaska Department of Fish and Game make possible an updated estimation of Steller sea lion reproductive rates in Southeast Alaska. However, the complexity of these data required a different statistical approach than is typically used to estimate reproduction in marked and resighted animals. In the following chapters, I derive an analysis specifically for the ADFG data, and use I it to estimate the Southeast Alaska Steller sea lion reproductive rate.

THE SOUTHEAST ALASKA STUDY SYSTEM

Rookery and Haulout Sites

Southeast Alaska contains five Steller sea lion rookeries (Table 1 on page 24, Figure 1 on the next page), which account for approximately half of the Eastern Stock's pup production (Pitcher et al. 2007). The rookeries are Forrester Island Rookery Complex (FI), Hazy Islands, White Sisters, Graves Rocks and Biali Rocks. Forrester Island Rookery Complex is a group of rocks and islands just north of Forrester Island (54.80° N, 133.52° W), and has grown to be the largest SSL rookery in the world (Trites and Larkin 1996). Twenty major (greater than 50 animals) Southeast Alaskan haulout sites are used during the breeding season. Several smaller sites are also used during the breeding season, as well as and numerous sites during the non-breeding season (Pitcher et al. 2007).

The Forrester Complex is notable not only for its size, but also for the fact that it is a complex of islands (Figure 2 on page 23). Although pupping site fidelity to a rookery is high, within FI, it is not uncommon for a cow to pup on different islands in different years. Furthermore, although faithful to their pupping beaches when pups are young, as the summer wears on, cows move about the complex more. Finally, although a pup would not normally swim with its mother from island to island until autumn, the islands of the Forrester Complex are close enough together that by late summer, it is not only the cows, but the cows and pups who are swimming about the complex.

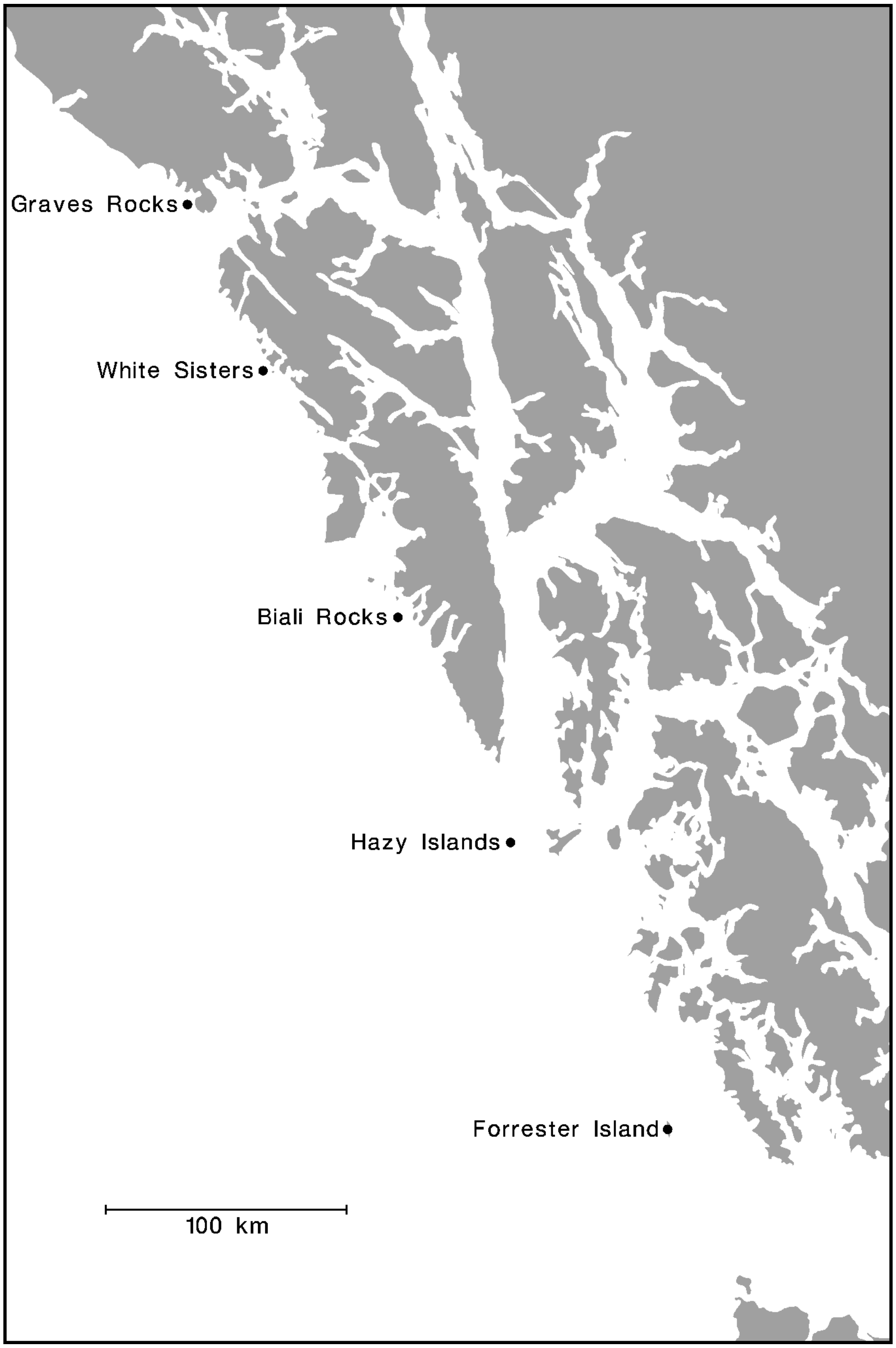


Figure 1: Steller sea lion rookeries in Southeast Alaska This map was created by Daniel Gustafson.

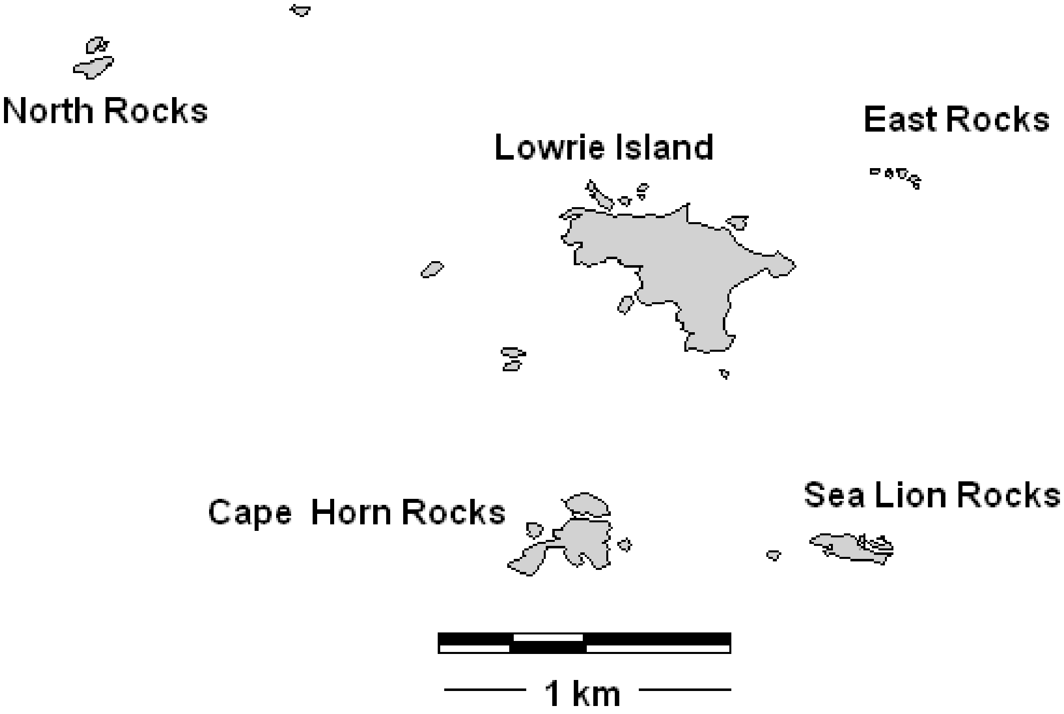


Figure 2: The Forrester Island Rookery Complex. This map was provided by Ken Pitcher at the Alaska Department of Fish and Game.

Table 1: Location in decimal degrees and size index of southeast Alaskan rookeries. Number of pups and non-pups are from the 2002 population wide survey of the eastern population (Pitcher et al. 2007)

Rookery	Island	Latitude	Longitude	# Pups	# Non-pups
Forrester				3060	3699
	Lowrie Island	54.86° N	133.54° W		
	Cape Horn Rocks	54.85° N	133.55° W		
	East Rocks	54.85° N	133.52° W		
	North Rocks	54.88° N	133.56° W		
	Sea Lion Rocks	54.84° N	133.54° W		
Hazy Islands		55.87° N	134.58° W	1257	2050
White Sisters		57.63° N	136.25° W	403	1156
Graves Rocks		58.25° N	136.76° W	98	1001
Biali Rocks		56.71° N	135.34° W	59	625

Historical Population

Beginning in 1929, there have been sporadic reports on the locations, numbers, and demographic composition of Steller sea lions in Southeast Alaska. It is worth noting the changes over time in the sites occupied and in the use of sites as rookeries or haulouts.

Forrester Island was noted to have had a breeding colony of 50-100 animals in 1929 (Rowley 1929), while in late August of 1945, pupping was not noted among the close to 350 animals observed (Imler and Sarber 1947). Substantial growth occurred by spring of 1957, when 2500 animals were seen at Forrester and Lowrie Islands (Mathisen and Lopp 1963). The 1961 aerial survey estimated almost 2400 animals, approximately a third of which were pups (Bigg 1985). Forrester Island Rookery

Complex has continued to increase in size (Table 1 on the previous page); however, the rate of increase has slowed since the late 1970's (Pitcher et al. 2007).

An estimated 350 Steller sea lions were observed at Hazy Islands in late August of 1945 (Imler and Sarber 1947) and had increased to 2500 animals by spring of 1957 (Mathisen and Lopp 1963). Pups were first observed there in 1979 (Pitcher et al. 2007). White Sisters became a rookery in the early 1990's, while Graves Rocks and Biali Rocks are currently developing rookeries (Pitcher et al. 2007).

Several factors combine to suggest that FI is approaching its carrying capacity. Southeast Alaska pup production increased by an average of 3.2% per year from 1979 through 2005, and new Southeast Alaskan rookeries are currently developing, yet pup production at FI has increased by only 0.6% per year since the late 1970's (Pitcher et al. 2007). Furthermore, cows attending pups on Lowrie Island (the largest island in FI that is inhabited by breeding sea lions) in the mid-1990's spent longer at sea and less time ashore than did their counterparts at Sugarloaf Island Rookery in the western population (Milette and Trites 2003), suggesting that finding sufficient food required more effort from the Lowrie Island cows. Likewise Lowrie Island pups in the 1990's grew at the same or slower rates as pups on four different western population rookeries that were examined during the same time period (Brandon et al. 2005). Thus, although the Forrester Complex is clearly a choice rookery, animals being recruited to the breeding population may find less competition with established females at a different site.

Data Collection

Marking and Resighting Sea Lions

The Alaska Department of Fish and Game (ADFG) branded 373 female pups on FI during the summers of 1994 and 1995 (Raum-Suryan et al. 2002; Pendleton et al. 2006). The marked individuals became reproductively mature over the course of this data set. The first pup known to be born to a branded female was born in 1998, although eight females alive in 2004 had not yet been observed with a pup.

The Alaska Department of Fish and Game began limited resighting surveys of these branded animals in 1994 at select sites, and began conducting dedicated large-scale vessel-based annual summer brand-resighting trips in 1999-2000, covering sites throughout Southeast Alaska and northern British Columbia. Almost all branded animals were observed when they were hauled out of the water so most resighting was conducted at rookeries and haulouts during the breeding season, and at some haulouts during the non-breeding season. Resighting effort increased markedly in 2000, when photographic confirmation of sightings and stricter standards of data collection were implemented (Raum-Suryan et al. 2002; Pendleton et al. 2006). Notably, the increase in resight effort was concomitant with cohort maturation.

Cows were rarely sighted more than once a day. When a cow was seen, her brand number, location, behavior, photographic confirmation status and the initials of the observer(s) were recorded. Counts of pups and non-pups may also have been collected, and start and end time of observations might have also been recorded.

Photographic confirmation includes the following five categories; the observations retained for analyses included only those in the first two categories.

1. Confirmed = Photograph was taken during the resighting and later confirmed against a photographic library.

2. Field = Photograph from the library was printed out and used in the field to confirm the sighting.
3. Likely = Photograph is not of very good quality.
4. Poor = Photograph is of poor quality.
5. Not Applicable = No photograph exists.

Cow behavior includes the following six categories.

1. A = Alone
2. WP = With pup
3. NP = Nursing pup
4. WJ = With juvenile
5. NJ = Nursing juvenile
6. U = Unknown
7. N = Nursing pup or juvenile. This category was only used in the late winter and spring when when pups of the year and older juveniles are more difficult to distinguish.

To be categorized as with pup, the pup and cow must have been observed interacting in a manner that suggested they were together. For example, a female interacting extensively with a pup (moving around the rookery together, reuniting after separation, extensive nuzzling) was classified as with pup. Most Steller sea lion cows that have pups are aggressive to pups not their own, especially within two to three weeks after birth (Sandegren 1970; Gentry 1970; Kaplan et al. 2008).

I structured encounter histories for my analyses on a per day basis, meaning a cow could be seen once per day or not at all. I condensed the with pup and nursing pup observations into a single category that indicated the cow was with a pup. All other codes were assigned to a category that indicated the cow was not with a pup. In the handful of cases where a female was seen more than once on the same day, I recorded her as seen with a pup if at least one sighting included a pup observation.

Differences Among Sites

Within a summer, rookeries received more effort than haulouts for two reasons. First, multiple day surveys were conducted at rookeries during boat resighting trips; whereas most haulouts were visited only one time per summer. Second, there is an annual one to four month long field camp on Lowrie Island, the largest island in FI inhabited by breeding sea lions. This camp allows daily monitoring of Lowrie Island. Other islands at FI (as well as the non-FI rookeries) require boat surveys during annual summer vessel trips. Visits to non-Lowrie rookery sites for resighting, capture or branding occurred one to three times a summer, for one to three day stretches.

Table 2 on the following page contains the average number of days on which resighting effort took place at rookeries during the summers of 2002 through 2004. In addition, an average of 56 haulout sites were visited during these summers, for an average of 98 site-days. These numbers are not meant to be a definitive index of effort. For example, some observation days are more thorough than others, and effort among the haulout sites is unevenly distributed. The point is simply that coverage is much higher and more consistent on Lowrie Island than elsewhere.

Table 2: Average Number of Observation Days per rookery per summer (June - August) for the years 2002 - 2004.

Biali	Graves	Hazy	WHSI	FI Boat Trips	Lowrie Land Camp
2	3	3	4	6	72

Seasonal Differences

Sea lions vacate most rookeries at the end of summer, and disperse to numerous haulouts, resulting in fewer sea lion observations during the remainder of the year. In addition, pup survival rates are expected to change after they leave the rookeries.

Implications for the Analyses

Cow Sightability

If a branded female is not seen, it may be because she is 1) dead, 2) not present where the observers looked, or 3) present but simply not seen. Because cows with pups regularly attend rookeries, and observers are present on Lowrie Island throughout much of the summer, post partum females are more likely to be seen than females who did not give birth that year. However, the possibility that a female pupped but was not seen on a less observed rookery or a less observed island of the Forrester Complex cannot be disregarded.

It would be helpful to assign each female to rookery for her lifetime; that is, to say that if she has a pup, we know on what rookery to search for her and her pup. This is impossible for three reasons. First, the cohorts are maturing over the course of this data set, and individuals cannot be assigned to a rookery until they have been seen with a pup on that rookery. Second, although pupping site fidelity is undeniably high, it may be overestimated, as observer effort is substantially higher at FI than elsewhere in Southeast Alaska. Of the 60 females in the ADFG Steller sea lion resight database through 2004 who were seen with a pup on a rookery during two or more summers, three individuals were known to have given birth at two different rookeries. (This number considers FI to be a single site.) Finally, it is not uncommon for a cow to switch pupping islands within FI between years.

Furthermore, for observers, Lowrie island is a different site than the rest of FI, whereas for sea lions, it is not (pages 21 and 28). This means that cows who pupped on Lowrie Island, and as a result, were highly visible early in the season may become less visible later in the season as they move about the complex. Conversely, cows who pupped elsewhere in the complex and were therefore less visible early in the season, may become more visible as the season progresses if they swim to Lowrie Island.

In short, because of the high attendance at rookeries of females with pups (page 9), and because of the Lowrie Island land camp, it is easier, *on average*, to see an individual who has given birth than one who has not. That is, the sample of cows seen each summer is biased high with respect to reproductive rate. For the same reasons, the *average* number of days on which an individual is seen is higher for a cow who has given birth than one who has not. In other words, the number of observations per cow is also biased high with respect to reproductive rate. Although we know that sightability and reproductive status are correlated, the complicating factors of sea lion movement and sporadic effort at most sites, makes quantifying this correlation extremely difficult. Correcting for this bias is an important element in the analysis.

Pup Sightability

Because only cows, and not pups are marked, a cow must be seen in order for her pup to be seen and identified. Thus a pup observed by itself cannot be recorded. If a branded female is observed alone during the summer, it may be because 1) she has not given birth, 2) she gave birth but the pup died or 3) her live pup simply went unseen.

Furthermore, as the summer progresses, pups are willing to stray further from their mothers, even if the mothers are on land. Thus even when a cow is seen, the chance of seeing an existing pup decreases over the summer. This too, forms an integral part of this analysis.

MOTIVATING THE ANALYSIS

Comparison to Other Multistate Capture Mark Recapture Analyses

In this chapter, I motivate a likelihood function to estimate reproductive rate from within season encounter histories of adult female Steller sea lions who are resighted with and without pups. This likelihood function pertains to a situation where only adult females (not pups) are marked, state classification uncertainty is present (i.e. a female seen alone might or might not actually have a pup) and the population is open to births during many of the resighting intervals. This likelihood function belongs to a group of models known as Multistate Capture Mark Recapture Models (MCMR), and it is helpful to view the analysis within this framework. Capture mark recapture (CMR) analyses are used to estimate the parameters of a transition matrix when the probability of detecting an animal is less than one, and they employ a multinomial likelihood function. The multinomial likelihood function is based on the ability to put observations in groups.

Consider a CMR estimation of survival for known aged animals. Survival rate is the transition rate being estimated, but the *order* of the states is predetermined. That is, once an animal's age is determined, its age in future sampling intervals will also be known. As a result, individuals can be grouped, a priori, based on state.

The opposite is true for a multistate CMR analysis, where an animal can stay in the same state for multiple time periods or move back and forth among states (Brownie et al. 1993). The seminal MCMR models (Arnason 1972, 1973) were developed to estimate movement between populations. Even though a reproductive rate analysis has only two states (reproductive and non-reproductive) it is a multistate model because the female can stay in the same state for multiple time periods or move back and forth between states. Thus it is not the number of states, but the inability to construct a priori groups that makes a model multistate.

My analysis is different than most MCMR analyses in four ways. First, although it is not a requirement for a MCMR analysis, multistate models are often applied to transitions at an annual level, not a within season level. Conversely, I conduct a separate reproductive rate analysis for each year, and the inference is based on sightings of cows with and without pups during the summer of each year.

Second, although again not a requirement, many MCMR analyses estimate transition probabilities that are conditioned on each other. For example, many multistate models that include reproductive rate estimates will include survival in such a way that the following quantities are estimated:

- p(female survives to time t + 1 | she gave birth in time t)
- p(female survives to time t + 1 | she did not give birth in time t)
- p(female gives birth in time t + 1 | she gave birth in time t and survived to time t + 1)
- p(female gives birth in time t + 1 | she did not give birth in time t and survived to time t + 1)

The Steller sea lion data are sufficiently complicated that the above quantities are not estimable, and the goal of my analyses is simply to obtain an unbiased estimate of adult reproductive rate. In addition, Steller sea lion survival rates have already been estimated for this same group of cows (Pendleton et al. 2006).

Third, most MCMR analyses are based on the assumption that upon observation, the true state of the animal can be ascertained. Only recently have MCMR analyses addressed the alternative, which is termed misclassification bias (Kendall et al. 2003) or state classification uncertainty (Nichols et al. 2007). It is important to distinguish state classification uncertainty from the situation where a certain state is completely unobservable. Models are commonly used to estimate transition probabilities between reproductive and non-reproductive states when non-reproductive animals are completely unobservable (Kendall and Nichols 2002; Schwarz and Arnason 2000; Schwarz and Stobo 1997). The probably of misclassifying a reproductive Steller sea lion cow as non-reproductive is high, so my analysis belongs to this recent group of analyses that includes state uncertainty.

The few reproductive rate analyses that have accounted for state uncertainty tend to treat the transition from the non-reproductive state to the reproductive state as an event that occurs prior to that season's sampling (Nichols et al. 2007; Kendall et al. 2003, 2004), which means that during the season, the population can be considered closed to births. Nichols et al. (2007) accounted for the possibility that young might not be observable early in the season by allowing Spotted Owl (*Strix occidentalis*) chick detection rates to vary over the season. Kendall et al. (2003, 2004) used an extension of Pollock's robust design (Pollock 1982), where manatee (*Trichechus manatus*) reproductive state transitions occurred at the annual level, and the determination of the animal's true state occurred at the within-year level, after the cessation of births and before the commencement of weaning. Because births occur throughout much of the time during which Steller sea lions are observed by ADFG, I did not assume population closure for the ADFG data, but instead, I modeled births as time specific within season rates.

Motivating the Steller Sea Lion Likelihood Function

The notation below follows Kendall et al. (2003) in that the within season probability of seeing a cow is given by ρ, the probability of seeing a pup who has been born, given that it's mother has been seen is δ and the birth probability is α. However, the fact that α functions as a within season parameter and ρ is not conditioned on past or present reproductive status means that this model functions quite differently than the aforementioned model. I present the probability of each possible encounter history first for an observation season that has one resight interval, and second for an observation season that has two resight intervals.

For simplicity's sake in this motivation, I use the same cow sighting parameter for the probability of seeing a cow who gives birth and the probability of seeing one who does not. In the formal derivation (Chapter 5), I assign different sighting parameters to cows who give birth versus versus those who do not, and I elucidate the differences between the two models.

Parameters

α_j	p(cow gives birth at the beginning of interval $j\vert$ she has not yet given birth this season)
ρ_j	p(cow seen in interval j)
δ_j	p(pup seen in interval $j\vert$ pup has been born, mother seen in interval j)

Observables

$\vec{EH}$	An encounter history where the cow is assigned on each day: 0 if not seen, 1 if seen alone, 2 if seen with pup

Encounter History Probabilities

One Individual, One Resighting Interval: One observation day generates three encounter histories, with the following probabilities.

$\vec{EH}$	probability
0	$(\alpha_1 + (1-\alpha_1))(1-\rho_1) = (1-\rho_1)$
1	$(1-\alpha_1)\rho_1 \ + \ \alpha_1\rho_1(1-\delta_1)$
2	$\alpha_1\rho_1\delta_1$

When the cow is not seen, the pup may or may not have been born; thus no information about reproduction is available. A pup who is not seen when the cow is seen might have been born but not seen, or simply not born. The only definitive encounter history occurs when both cow and pup were seen: the pup was born, the cow was seen and the pup was seen.

One Individual, Two Resighting Intervals: Anytime a cow is seen before she has been sighted with a pup, the pup must be categorized as either born but not seen or not born. Furthermore, unless a pup is seen during the first observation period of the pupping season, is impossible to know exactly when the pup was born. This is shown below by a subset of encounter histories for a season with two observation periods, where each encounter history can be explained by either of two scenarios, depending on which time interval contained the birth. The probabilities based on either scenario are possible, so they are summed.

$\vec{EH}$	probability
$0, 2$	$\Big(\alpha_1(1-\rho_1)\Big)\rho_2\delta_2 \quad + \quad \Big((1-\alpha_1)(1-\rho_1)\Big)\alpha_2\rho_2\delta_2$
$1, 2$	$\Big(\alpha_1\rho_1(1-\delta_1)\Big)\rho_2\delta_2 \quad + \quad \Big((1-\alpha_1)\rho_1\Big)\alpha_2\rho_2\delta_2$

The model continues to build in such a fashion until the pup is first seen. Once the pup has been seen, the α parameter is no longer used, as the pup can only be born once. This is shown by another subset of the encounter histories.

$\vec{EH}$	probability
$2,0$	$\alpha_1\rho_1\delta_1\Big(1-\rho_2\Big)$
$2,1$	$\alpha_1\rho_1\delta_1\Big(\rho_2(1-\delta_2)\Big)$
$2,2$	$\alpha_1\rho_1\delta_1\Big(\rho_2\delta_2\Big)$

Finally, if a pup is never seen, the model accounts for the fact that it may or may not have been born. These are the remaining encounter histories from the season with two observation periods. Note again, that no information about reproduction is obtained when the cow is not seen, and all possible birthing scenarios are accounted for.

$\vec{EH}$	probability
$1,1$	$\Big(\alpha_1\rho_1(1-\delta_1)\Big)\Big(\rho_2(1-\delta_2)\Big) + \Big((1-\alpha_1)\rho_1\Big)\Big(\alpha_2\rho_2(1-\delta_2)\Big) + \Big((1-\alpha_1)\rho_1\Big)\Big((1-\alpha_2)\rho_2\Big)$
$1,0$	$\Big((1-\alpha_1)\rho_1\Big)\Big(1-\rho_2\Big) + \Big(\alpha_1\rho_1(1-\delta_1)\Big)\Big(1-\rho_2\Big)$
$0,1$	$\Big((1-\alpha_1)(1-\rho_1)\Big)\Big((1-\alpha_2)\rho_2\Big) + \Big((1-\alpha_1)(1-\rho_1)\Big)\Big(\alpha_2\rho_2(1-\delta_2)\Big) + \Big(\alpha_1(1-\rho_1)\Big)\Big(\rho_2(1-\delta_2)\Big)$
$0,0$	$(1-\rho_1)(1-\rho_2)$

Note on Cow Sightability

Because this model uses the same sighting parameter for post partum and non-post partum cows, each encounter history (and therefore the joint likelihood function) factors into the product of two terms. One term contains the cow sighting parameters, and the other contains the reproductive rate and pup sighting parameters. This indicates that cow sightability is independent of reproductive rate (see independent random variables, Berry and Lindgren 1996). I explore these mathematical details and their implications at length in the next chapter, but the following conclusion is important to note. In order to fit a model that assigns different sighting parameters to post partum and non-post partum cows, the relationship between cow sightability and reproductive status must be clearly defined. If this relationship cannot be defined clearly enough to permit the estimation of separate sighting parameters for cows who give birth and those who do not (page 52), then the model's estimate of reproductive rate does not depend on cow sightability. In other words, the following models give identical reproductive rate estimates.

1. The above model, where the parameters are ρ, α and δ; an entry is made in the encounter history of every cow on every day during which observers looked for sea lions; and the data are $0 =$ cow not seen, $1 =$ cow seen alone and $2 =$ cow seen with pup.

2. A model where the parameters are α and δ; an entry is made in a cow's encounter history only when she is seen; and the data are $1 =$ cow seen alone and $2 =$ cow seen with pup.

Even if there are multiple ρ parameters, perhaps specific to sites or time intervals, these will not effect the reproductive rate estimation unless they are conditioned on reproductive status. If the data cannot support a model that accurately differentiates between sightability of post partum and non-post partum cows (and therefore ρ cannot be conditioned on reproductive status) then a cow sighting is nothing more than a prerequisite for seeing a pup, and any corrections to ρ based on site, effort, or anything else will not change the estimate of reproductive rate.

DERIVING THE LIKELIHOOD FUNCTION FOR THE STELLER SEA LION DATA

Introduction

I begin this chapter by deriving the likelihood function for a data set where births occur during much of the observation season, only cows (not pups) are marked, state classification uncertainty is present (that is, a cow seen alone may or may not actually have a pup), cow sightability is correlated with reproductive status and all sites on which sea lions are located are observed numerous times during the observation season. I then reduce this model to a more flexible model that can be used for the actual Steller sea lion data, where most sites cannot be observed numerous times during the observation season.

Notably, the Steller sea lion data do not allow a standard approach to the modeling of cow sightability because, despite daily observations on the Lowrie Island part of the Forrester Island Rookery Complex, almost all other sites (including the rest of FI, the other four Southeast Alaska rookeries and the haulouts) are visited only once or twice during the summer (the season from which reproductive information is available). I discuss the combined effects on the data of sea lion and observer location in Chapter 3, beginning on page 3, and I discuss in detail the difficulty in modeling the resulting bias in Ch. 6, starting on page 6.

Nevertheless, it is important to put this analysis in the context of other mark resight studies, so I first derive the likelihood function for a more standard data set, and then show the differences between this more standard model and the more flexible model, which can be applied to the Steller sea lion data.

The Multinomial Likelihood Function in Mark Resight Analyses

The multinomial likelihood function is used to model data where the M total individuals in the database can be grouped according to a set of k mutually exclusive, exhaustive outcomes. That is, each outcome belongs to exactly one group. In mark resight analyses, the outcome is the encounter history. The probability of outcome i is given by β_i, and these probabilities must sum to one. The likelihood function is proportional to the probability of all encounter histories occurring simultaneously, therefore, it is proportional to the product of the probability of each individual's encounter history. Define the number of individuals having outcome (encounter history) i as m_i. This gives

$$\sum_{i=1}^{k} m_i = M$$

$$\sum_{i=1}^{k} \beta_i = 1$$

$$p(\vec{m}|\vec{\beta}) \;\propto\; \prod_{i=1}^{k} {\beta_i}^{m_i}.$$

If each cow has a unique encounter history, the equation becomes

$$p(\vec{m}|\vec{\beta}) \;\propto\; \prod_{i=1}^{M} \beta_i.$$

Considerations in Estimating Reproduction

Several factors confound the estimation of the Steller sea lion reproductive rate, meaning that females cannot simply be grouped into those who are seen with pups and those who are not. First, because it is the adult females who are marked, pups can only be identified when they are seen with their mothers. However, even if a female has a live pup, resighting the mother does not guarantee seeing the pup. Furthermore, because births occur during much of the observation season, the model must account for the fact that in all intervals until a pup is first seen with its mother, the pup might have been born but not seen, or it might not yet have been born. Finally, the probability of resighting the cow is correlated with her reproductive status. Three sets of parameters are necessary to sort out these issues: reproductive rate parameters (α's), cow sighting parameters (ρ's) and pup sighting parameters (δ's).

The first model I derive cannot be used for the Steller sea lion data, because of a clear violation of Assumption 7. However, I derive this full model to show my original approach to the problem, an approach which is consistent with published mark recapture studies. I then reduce this model to a more flexible form, and in the next chapter (Ch. 6) I tailor the more flexible model to the data set at hand.

Model Assumptions

1. A cow gives birth to at most one pup per season.
2. Births occur instantaneously at the beginning of each time interval.
3. A pup can only be seen during a time interval in which its mother has been seen.
4. Cows and pups survive until the end of the observation season.
5. Brands are not misread or lost.
6. If a cow is recorded as being with a pup, that is correct. However, a record of a cow *not* with a pup may or may not be correct.
7. The entire population of cows is surveyed during each time interval. This is not to say that all cows were seen during each interval, but that all *could* have been

seen. This implies that *systematic* differences in cow sightability reflect only differences in reproductive status, not differences in effort.

Known Constants

N	# of time intervals during which observations were conducted
N_p	# of time intervals during which pups can be born
M	# of branded female sea lions known alive throughout the season

Unknown Parameters

α_t	p(cow gives birth during time interval t | she has not yet given birth this season)
δ_s	p(pup seen $\geq$ 1x in time interval s | pup has been born, mother seen $\geq$ 1x in interval s)
ρ_{1u}	p(a cow who gives birth this season is seen $\geq$ 1x during time interval u, which is before the pup is born)
ρ_{2w}	p(a cow who gives birth this season is seen $\geq$ 1x during time interval w, which is after pup is born)
ρ_{0z}	p(a cow who does not give birth this season is seen $\geq$ 1x during time interval z)

Observables for Each Cow

$\vec{EH}$	An encounter history of length N where the cow is assigned in each interval: 0 if not seen, 1 if seen alone, 2 if seen with pup
f	Either the time interval the cow was first seen with a pup or N, if the cow was never seen with a pup

Encounter History Probability for N Time Intervals

The Reproductive Probability: Each encounter history probability can be written in terms of three groups of probabilities: reproductive (α's), cow sighting (ρ's) and pup sighting (δ's). I derive the probability of an encounter history below, by dealing first with the reproductive probability, then the cow sighting probability and then the pup sighting probability. At some steps in this process, the resulting equation is not useful; however, the probability of the entire encounter history is the foundation of the likelihood function. My goal here is to build the probability of the encounter history in a stepwise fashion.

The reproductive probability accounts for the fact that if a cow is seen with a pup, she might have given birth to the pup at any time from the beginning of the observation season ($t_b = 1$) to the time the pup was first seen with the cow ($t_b = f$). A cow who is never seen with a pup may have given birth at any time until the end of the pupping season ($t_b = 1$ to $f = N_p$) or not at all. Thus,

p(cow_i gave birth during interval t_b) =

$$A_{t_b} = \alpha_{t_b} \prod_{t=1}^{t_b-1} (1 - \alpha_t), \tag{1}$$

and p(cow_i gave birth by time interval f) =

$$\sum_{t_b=1}^{f} A_{t_b} = \sum_{t_b=1}^{f} \left(\alpha_{t_b} \prod_{t=1}^{t_b-1} (1 - \alpha_t) \right). \tag{2}$$

If (and only if) a pup was never seen during the season, the next step in building the encounter history probability is to add to this summation the probability that the pup was not born at all.

p(cow_i did not give birth during the season) =

$$\prod_{t=1}^{N_p}(1-\alpha_t). \tag{3}$$

To indicate whether or not this term needs to be included in the encounter history probability, we define the following indicator function.

$$I = \begin{cases} 0 & \text{if a pup was seen sometime during the season} \\ 1 & \text{if a pup was not seen at all during the season} \end{cases} \tag{4}$$

The data that relate directly to the reproductive probability are contained in I (the indicator of whether or not a pup was ever seen with the cow) and f (which is the date on which a pup was first seen, or N_p if a pup is never seen). The complete reproductive probability (which forms the skeleton of the encounter history probability) is given by

$$\begin{aligned} & \sum_{t_b=1}^{f}\left(\alpha_{t_b}\prod_{t=1}^{t_b-1}(1-\alpha_t)\right) \;+\; I\prod_{t=1}^{N_p}(1-\alpha_t) \\ = & \sum_{t_b=1}^{f} A_{t_b} \;+\; I\prod_{t=1}^{N_p}(1-\alpha_t) \end{aligned} \tag{5}$$

By itself, this skeleton is not helpful; however, it provides a framework on which to build the entire encounter history probability.

The Cow Sighting Probability: Because all possible birthing scenarios have been modeled, the probability of resighting a cow in any given interval of any given scenario can be conditioned on her reproductive status. It is important to distinguish between the sightability of post partum and non-post partum cows, because it is easier to see cows who have pups than those who do not. Notably, a cow can be non-post partum in two ways, by being pre-partum or by not giving birth at all that year. The biggest concern for the Steller sea lion data is that cows who do not give birth in a particular year are more difficult to see than those who do, meaning that the estimated reproductive rate will be biased high, unless a correction can be made for the different sighting rates of post partum and non-post partum cows. Let

$$P_u = \begin{cases} \rho_{1_u} & \text{if cow seen} \geq \text{1x in interval } u\text{, which is before} \\ & \text{she gives birth} \\ (1-\rho_{1_u}) & \text{if cow not seen in interval } u\text{, which is before} \\ & \text{she gives birth} \end{cases} \tag{6}$$

$$P_w = \begin{cases} \rho_{2_w} & \text{if cow seen} \geq \text{1x in interval } w\text{, which is after} \\ & \text{she gives birth} \\ (1-\rho_{2_w}) & \text{if cow not seen in interval } w\text{, which is after} \\ & \text{she gives birth} \end{cases} \tag{7}$$

$$P_z = \begin{cases} \rho_{0_z} & \text{if cow who does not give birth this season is} \\ & \text{seen} \geq \text{1x in interval } z \\ (1-\rho_{0_z}) & \text{if cow who does not give birth this season is not} \\ & \text{seen in interval } z \end{cases} \tag{8}$$

The skeleton encounter history probability (Eqn. 5) has been updated below, with the reproductive probability in black and the cow sighting probabilities in blue.

$$\sum_{t_b=1}^{f} \left\{ A_{t_b} \left(\prod_{u=1}^{t_b-1} P_u \right) \left(\prod_{w=t_b}^{N} P_w \right) \right\} + I \left(\prod_{t=1}^{N_p} (1-\alpha_t) \right) \left(\prod_{w=1}^{N} P_z \right) \tag{9}$$

The Pup Sighting Probability: The reproductive probability has already modeled the probabilities of whether or not (and when) a pup was born. Furthermore, an extant pup can be identified only when its mother is seen. Therefore, the pup sighting probability is conditioned on the pup having already been born and its mother having been seen in that time interval. Let

$$\Delta_s = \begin{cases} \delta_s & \text{if pup (and cow) seen} \geq \text{1x in interval } s,\ s \geq t_b \\ (1-\delta_s) & \text{if cow seen} \geq \text{1x in interval } s\ (s \geq t_b), \\ & \text{but never with a pup in that interval} \\ 1 & \text{if cow (and pup) not seen in interval } s\ (s \geq t_b) \\ & \text{this is simply a placeholder, as seeing} \\ & \text{the pup is conditioned on seeing the cow} \end{cases} \tag{10}$$

Recalling that $f = N_p$ if a pup is never seen, the probability of the encounter history for cow_i is given below, with the reproductive and cow sighting probabilities in black, and the pup sighting probability in blue.

$$\sum_{t_b=1}^{f} \left\{ A_{t_b} \left(\prod_{s=t_b}^{N} \Delta_s \right) \left(\prod_{u=1}^{t_b-1} P_u \right) \left(\prod_{w=t_b}^{N} P_w \right) \right\} + I \left(\prod_{t=1}^{N_p} (1-\alpha_t) \right) \left(\prod_{z=1}^{N} P_z \right) \tag{11}$$

Closer Examination of the Cow Sighting Probability

The Steller sea lion data set cannot be analyzed using this model, because it violates the assumption (Assumption # 7) that the entire population of cows is surveyed during each time interval, and systematic differences in cow sightability reflect *only* differences in reproductive status, not differences in effort (page 52). Suppose, however, that cows could be assigned to groups based on the number of times they were seen during the season and the locations at which they were seen, and that these groups were expected to have different reproductive rates (page 54). For this model, the parameter list is as follows.

$\alpha_{j,t}$	p(cow in $group_j$ gives birth during time interval t | she has not yet given birth this season)
δ_s	p(pup seen $\geq$ 1x in time interval s | pup has been born, mother seen $\geq$ 1x in interval s)
$\rho_{1_{j,u}}$	p(a cow in $group_j$ who gives birth this season is seen $\geq$ 1x during time interval u, which is before the pup is born)
$\rho_{2_{j,w}}$	p(a cow in $group_j$ who gives birth this season is seen $\geq$ 1x during time interval w, which is after pup is born)
$\rho_{0_{j,z}}$	p(a cow in $group_j$ who does not give birth this season is seen $\geq$ 1x during time interval z)

The following equation gives the probability of the encounter history for cow_i, who is a member of $group_j$. Note that birthing probabilities and cow sighting probabilities depend on the group to which the cow is assigned; however, the probability of seeing a pup, given that it has been born and its mom was seen in that interval remains constant across cows, regardless of group.

$$\sum_{t_b=1}^{f}\left\{A_{j,t_b}\left(\prod_{s=t_b}^{N}\Delta_s\right)\left(\prod_{u=1}^{t_b-1}P_{j,u}\right)\left(\prod_{w=t_b}^{N}P_{j,w}\right)\right\} + I\left(\prod_{t=1}^{N_p}(1-\alpha_{j,t})\right)\left(\prod_{z=1}^{N}P_{j,z}\right) \tag{12}$$

By assuming that cow sightability depends on reproductive status only through the group to which the cow belongs, we can set equal $P_{j,u}$, $P_{j,w}$ and $P_{j,z}$. The resulting encounter history probability is

$$\begin{aligned}&\sum_{t_b=1}^{f}\left\{A_{j,t_b}\left(\prod_{s=t_b}^{N}\Delta_s\right)\left(\prod_{u=1}^{N}P_u\right)\right\} + I\left(\prod_{t=1}^{N_p}(1-\alpha_{j,t})\right)\left(\prod_{u=1}^{N}P_u\right)\\ &= \left\{\sum_{t_b=1}^{f}A_{j,t_b}\left(\prod_{s=t_b}^{N}\Delta_s\right) + I\left(\prod_{t=1}^{N_p}(1-\alpha_{j,t})\right)\right\}\left(\prod_{u=1}^{N}P_u\right)\end{aligned} \tag{13}$$

This model can be factored into the product of two terms, the second of which contains only the cow sighting probability. This indicates that the joint likelihood function can likewise be factored, and the cow sighting probability is independent of the term containing both the reproductive and pup sighting probabilities (see independent random variables, Berry and Lindgren 1996). In effect, each cow sighting is simply an opportunity to observe (or not observe) a pup, in the same way that a time interval is an opportunity to observe (or not observe) a cow. Consequently, for reproductive rate estimation, the probability of this encounter history is proportional to

$$\sum_{t_b=1}^{f} A_{j,t_b}\left(\prod_{s=t_b}^{N}\Delta_s\right)\ +\ I\left(\prod_{t=1}^{N}(1-\alpha_{j,t})\right). \tag{14}$$

ADDRESSING THE ADDITIONAL CONFOUNDING FACTORS

Introduction

In the previous four chapters, I have reviewed Steller sea lion biology, described the study system and data collection, and motivated and derived a likelihood function for a population open to births, where only the adults are marked, where cow sightability is correlated with reproductive status and where state classification uncertainty is present. In this chapter, I describe important methodological details that are specific to the Steller sea lion analysis. In the next chapter, I will present the actual analyses.

Filtering the Observations by Time of Year

Reproductive rate was estimated from encounter histories of females resighted with and without pups. Juvenile sightings were not included in the estimation for two reasons. First, juveniles were not commonly sighted with the marked cows, in part, because cows with juveniles tend to occupy haulouts (page 9) which are less observed than rookeries (page 28). Furthermore, the highly variable age of weaning (page 13) and the inability to determine age of resighted juveniles made it impossible to obtain birth years from these sightings.

The overwhelming majority of cow and pup observations are made during the summer, the time when cows who give birth are using the rookeries, and mature cows who do not pup that summer return, at least briefly, to the rookeries to mate. Observers were present at the Lowrie Island land camp between the following dates: May 23 to September 17, 2002; May 14 to August 30, 2003; and June 2 to September 6, 2004. All visits to other rookeries occurred within these dates. The sparse information about pups that could be obtained during the remainder of the year would have been outweighed by the highly unrealistic assumptions needed to distinguish between pup sightability and pup mortality after cows and pups departed the rookeries. As a result, the encounter histories used to estimate reproductive rate included all observations (whether on rookeries or haulouts) taken during the summer rookery observation season, and I did not include data from other times of year.

Addressing the Bias in the Observations

Returning to the Kendall et al. (2003, 2004) estimation of manatee reproductive rates; different cow sighting parameters were assigned to cows who gave birth that year versus cows who did not, and the likelihood function was able to adjust the reproductive rate estimate for the different sightability of the two sets of cows. However, a stated assumption of their model is that the entire population of adult cows was surveyed during each interval. This is not to say that all cows were seen in each interval; however it does mean that all cows *could* have been seen in each interval, and that systematic differences in cow sightability reflected only differences in reproductive status, not differences in effort. This allows the model to correctly differentiate between sightability of cows who did or did not give birth, because the effect of resighting effort on cow sightability is constant across both classes of cows.

In this Steller sea lion analysis, not only was it impossible to devise resight intervals in which the entire population was surveyed; it was impossible to devise intervals during which the surveyed population could be considered a reproductively representative sample of the marked animals. Because of the difficulty in resighting cows who did not give birth during the summer, even considering an entire summer as a single resight interval would not have made equal the probability of seeing at least once a cow who did give birth that summer and a cow who did not. At the same time, differences in sightability could not be assumed to be based strictly on reproductive status, because effort was so high at the Lowrie Island part of the Forrester Island Rookery Complex, and not at other islands in the complex or at the other four Southeast Alaska rookeries (page 28). Simply fitting separate cow sighting parameters for post partum and non-post partum cows would imply that the uneven effort introduced no bias into the sightings.

Cow sightability in these data is an unknown function of sea lion biology and observer effort. The presence of a cow on any given island is some function of her reproductive status, philopatry, adult pupping site fidelity and attendance cycle; however, it is not a function of observer effort. The probability of seeing a cow given that she is present on a site is a function of observer effort and qualities of the site, but it is not a function of the cow's reproductive status. If site use by sea lion cows depended on their reproductive status, and resight effort varied by site, but was consistent enough that it occurred on the large majority of sites in the large majority of resight intervals, then the resighting bias could be modeled. However, the sporadic nature of resight effort at all sites but Lowrie Island prevents the site based modeling of the bias introduced by the combination of sea lion behavior and observer effort. In particular, the rookery sites visited by boat are (in the years analyzed) usually visited for resighting, capture or branding purposes for one to three consecutive days in June, and again for one to three consecutive days in August. In other words, even if data were to be pooled by week (which would require the assumption that pups can be born only once a week), rookery sites other than Lowrie Island would have been visited during only two of the summer resight intervals, and most haulouts would have been visited during only one.

Other approaches to different sightability of reproductive and non-reproductive cows, though appropriate for the situations in which they have been used, are not applicable to the Steller sea lion data. Often these studies are conducted in systems where it can be assumed that one of the states (reproductive or non-reproductive) is either completely observable or completely unobservable, age class can be used as a surrogate for reproductive status when modeling sightability, or pupping site fidelity can be assumed complete and it is known to which site a cow should be assigned (Kendall and Nichols 2002; Hadley et al. 2006; Schwarz and Arnason 2000; Schwarz and Stobo 1997, Melin 2002). In all of these cases, the sighting bias is not due to an unknown mixture of animal behavior (different site use by post partum and non-post partum cows) and observer behavior (lack of observations at most sites in most intervals).

Because it was not possible to fit a model where cow sightability could be considered a function only of reproductive status, the model used in my analyses is based on the more flexible model shown in Equations 13 on page 49 and 14 on page 50. This is an extension of the model that was motivated on page 35, Chapter 4, and it is able to account for the relationship between cow sightability and reproductive status because cows are grouped based on how many times and where they were seen, and separate reproductive rates are estimated for each of the groups.

Grouping the Cows Used in the Likelihood Function

Because it is easier to resight cows who have pups than those who do not, the number of per cow observations is, on average, greater for cows with pups than those without. I addressed this observational bias by assigning each cow *in each summer* to one of three groups, based on how many times she was seen and whether or not she was seen on a haulout in June or July. Within the likelihood function, I assigned different reproductive parameters to each group, but used a common pup sighting parameter for all groups. The reproductive rate estimated by the mark-resight analysis is a weighted average of the reproductive rate of each of these groups, where the weights are the numbers of individuals within each group. Each group was expected to have a different reproductive rate from the other groups for the following reasons.

Group 1 is comprised of cows seen on a haulout during June or July of the summer being analyzed. No other restrictions were put on this group: they may or may not have been seen on rookeries as well. Due to the high attendance of post partum cows at rookeries (page 9) and the timing of births (page 8), it is unlikely that cows seen on haulouts in June and July are caring for pups.

Group 3 contains cows seen a total of eight or more times during the summer, but not seen on a haulout during June or July of that year. It would be difficult to see a cow this many times if she were not in high attendance at Lowrie Island, and high attendance at a rookery suggests she has a pup.

Group 2 is an intermediate group. It contains cows seen a total of one to seven times during the summer, but not on a haulout during June or July that year. It is not possible to make an a priori prediction regarding the reason for the relative lack of sightings of these cows. It could be because these cows were without pups, and therefore not in high attendance at rookeries, or it could be they chose to pup at a site that could not be routinely observed.

Grouping the cows in this manner served two functions. First, within each group, the cows are relatively homogeneous with respect to reproductive rate. Second, because the cows observed many times were assigned to a single group, they were not able to unduly influence the reproductive rate estimation by their sometimes overwhelming number of observations. Table 3 on the next page and Figure 3 on page 57 display the discrepancy in reproductive rate expected for these groups. It should be noted that I placed no constraints on any of the group reproductive rates; I simply placed the cows in groups. Each group's reproductive rate was allowed to vary freely between zero and one.

Table 3: Grouping Cows

2002

Group	Seen on Haulout	# Times Seen Median	# Times Seen Range	Proportion Seen With Pup	# of Cows
1	Yes	2	1 to 11	0.15	13
2	No	2	1 to 7	0.30	53
3	No	14	9 to 26	1.00	11

2003

Group	Seen on Haulout	# Times Seen Median	# Times Seen Range	Proportion Seen With Pup	# of Cows
1	Yes	3	1 to 6	0.09	11
2	No	2	1 to 7	0.48	60
3	No	12	8 to 40	0.94	16

2004

Group	Seen on Haulout	# Times Seen Median	# Times Seen Range	Proportion Seen With Pup	# of Cows
1	Yes	3	1 to 5	0.00	12
2	No	3	1 to 7	0.51	57
3	No	15	8 to 28	1.00	17

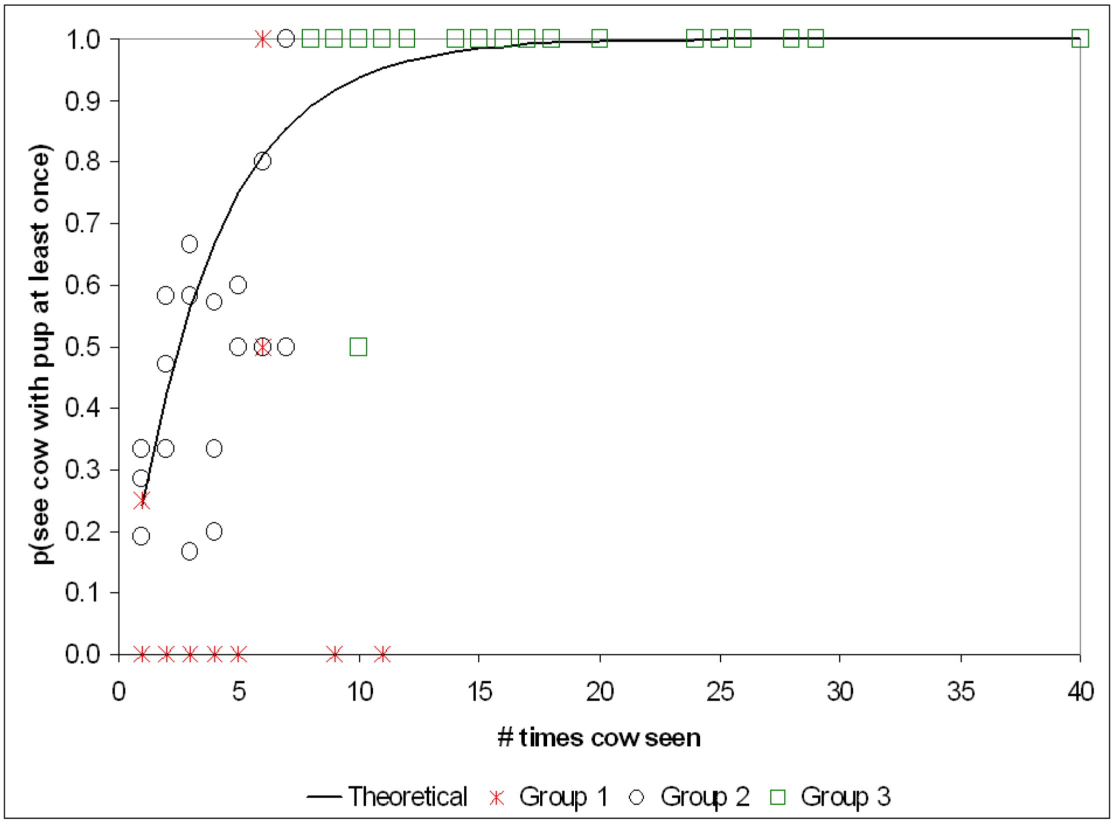


Figure 3: Probability of seeing a cow with a pup at least once versus number of times cow is seen during the summer. For each point, the X coordinate is the number of cows seen X times during a summer (either 2002, 2003 or 2004), and the Y coordinate is the proportion of cows seen at least one time with a pup during that summer. Group 1 is comprised of cows seen on a haulout during June or July of the summer in question. No other restrictions are put on this group: they may or may not have been seen on rookeries as well. Group 2 contains cows seen a total of 1 - 7 times during the summer, but not on a haulout during June or July that year. Group 3 contains cows seen a total of 8 or more times during the summer, but not seen on a haulout during June or July of that year. The line shows the expected relationship if the the three groups had the same average reproductive rate. Sample sizes for some points are small. Each of the three red stars that are not at Y = 0 and the one green square that is not at Y = 1 are outliers due to one individual.

Filtering the Sample of Cows by Those Known to be Alive

Estimating separate reproductive rates for the three groups of cows accounts for the reproductive bias in the number of per cow observations during the summer; however, it does not account for the fact that cows who did not pup that summer are more likely to go *completely* unseen than those who did pup. To account for this bias in the sample of individuals seen during the summer, I used survival beyond the summer to filter the data and obtain a subset of cows that was relatively unbiased with respect to reproductive status during the summer being analyzed. I defined a cow as 'known to be alive' during a given summer if she was seen *subsequent* to that summer, and I used data from all times of year to determine whether or not she was alive.

Although the data for this dissertation included full encounter histories only through the end of 2004, a list of cows seen in 2005 was provided, as was a list of cows seen from 2005 through 2009. Beginning in 2002, females could be categorized as follows: those who never went unsighted for more than a year, and those who were never seen again. Due to the substantial annual increase in effort, there is no reason to expect that more resighting years will produce observations of these individuals who have now been missing for four to six years (Figure 4 on page 62). I assumed that the individuals never seen again either died or permanently emigrated from the population.

Because a one year absence was not unusual, it is difficult to infer, for example, whether or not the eight individuals last seen in 2002 were still part of the population during 2003 (Table 6 on page 60). If they were part of the population, the fact that they were not sighted suggests they probably did not have pups. However because they were never resighted again, they no longer contributed to the reproductive rate estimation. This illustrates the observational bias toward seeing cows who have pupped. In order to reduce that bias, I discarded from each year's analysis any females not seen *subsequent* to that summer, whether or not they were seen during the summer being analyzed.

By filtering for the females who were known to have survived beyond the breeding season, I may have introduced some bias because reproduction can negatively effect Pinniped survival (Hadley et al. 2007; Boyd et al. 1995). For example, in the Antarctic fur seal (*Arctocephalus gazella*, another Otariid) the reproductive rate among females who survived the year was 71%, but 73% among both survivors and non-survivors (Boyd et al. 1995). However, considering the known, substantial association in the Steller sea lion data between sightability and reproduction, I believe the least bias was introduced by filtering the data as described. Furthermore, I confined my analyses to 2002, 2003 and 2004, because these were the years for which the females ever seen again went missing for no more than a year. Because of this, my filtering mechanism was consistent among years, and any downward bias in the reproductive rate that may have been introduced due to the survival cost of reproduction would only amount to the cost of one year.

<ins>Females Known Alive and Seen in Summer</ins>: Although 99, 92 and 89 cows were known to be alive in the summers of 2002, 2003 and 2004, respectively, it is the females known alive *and* observed during the summer at hand that are assigned to groups and used in the mark-resight analysis to estimate reproductive rate. Sample sizes of females known alive and observed during the summer are 77, 87 and 86 for each of the three years in order.

Table 4: Cow Survival

Filtering Categories for 2002 Analysis

	Known Alive in 2001 and Seen in 2002	Known Alive in 2001 but Not Seen in 2002	Total	
Known Alive After 2002	**77**	**22**	**99**	**Used**
Not Seen After 2002	8	?		Discarded
Total	85			

Filtering Categories for 2003 Analysis

	Known Alive in 2002 and Seen in 2003	Known Alive in 2002 but Not Seen in 2003	Total	
Known Alive After 2003	**87**	**5**	**92**	**Used**
Not Seen After 2003	7	8	15	Discarded
Total	94	13	107	

Filtering Categories for 2004 Analysis

	Known Alive in 2003 and Seen in 2004	Known Alive in 2003 but Not Seen in 2004	Total	
Known Alive After 2004	**86**	**3**	**89**	**Used**
Not Seen After 2004	3	7	10	Discarded
Total	89	10	99	

Females Known Alive but Not Seen all Summer: Each year, I had to account for the individuals known to be alive, but not seen during the summer. Because reproductive information comes from summer observations of cows with and without pups, it was not possible to estimate reproductive rate for the unseen cows, who numbered 22, 5 and 3, for 2002, 2003 and 2004, respectively. For each year, I allowed the reproductive rate of the known alive but unseen group of cows to vary between zero and the mean reproductive rate estimated from the cows who were known alive and seen during the summer. I then calculated an overall reproductive rate as a function of the reproductive rate for the unseen cows. This allowed me to explore how sensitive the overall reproductive rate estimates were to assumptions regarding the reproductive rate of the unseen cows.

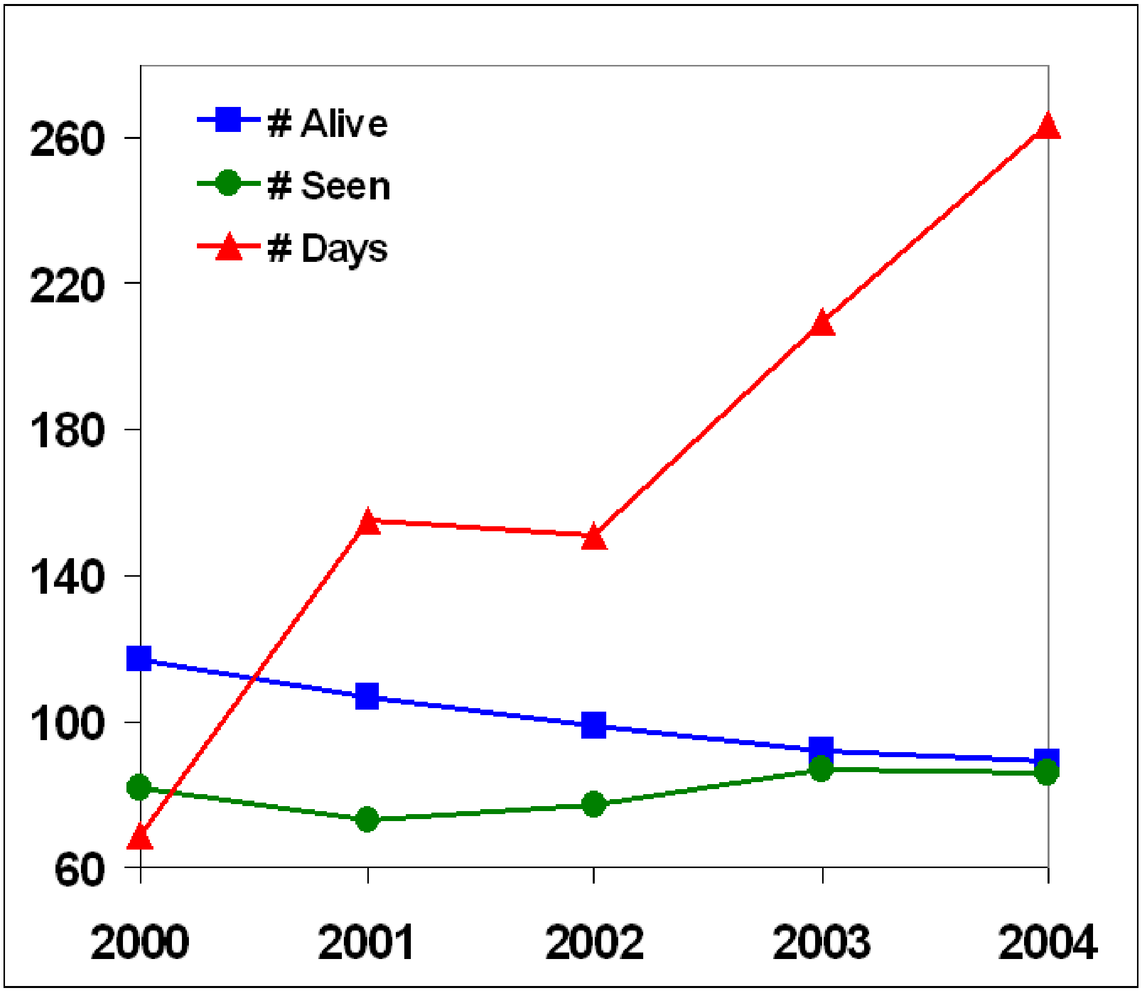


Figure 4: Annual number of days on which resight effort was expended, number of cows known alive and number of cows known alive and seen that year. The proportion of cows known alive who are resighted in a given year increases dramatically over time. This is a function of two factors: the dramatic annual increase in resighting effort and the increasing maturity of the cows, which results in them being concentrated at rookeries where they are more easily observed.

Specifications Relating to Pups

Timing of Births

I specified that pups could be born daily and that births start on May 14 each year. The earliest rookery observation in the analyses occurred on May 14, and almost all births at Steller sea lion rookeries range wide occur between May 15 and July 15 (Pitcher et al. 2001).

Because the the Forrester Complex is the only rookery observed consistently throughout the summer, it contributes the most information to the estimation of pup sightability (δ) over time, which is confounded with the time specific birth probabilities (A_{t_b}). Therefore, it is most important for birth timing in the model to be consistent with the Forrester Complex. Although almost all pups at rookeries range wide are born by July 15, the Forrester Complex has the earliest mean date of birth, June 4 (Pitcher et al. 2001). Furthermore, the last 2003 birth on Lowrie Island, Area 5, took place on July 5, and very few births were observed there in late June and early July (Kaplan 2005). Therefore I specified that births in the model cease after July 1. Because 90% of births at a given rookery occur within a 25 day period (Pitcher et al. 2001), I allowed the daily birth rate to vary by week, without constraint.

In order to determine the effect of the birth timing specifications, I also conducted the analyses under two other sets of specifications, one less restrictive and one more restrictive. The first differed only in that pups could be born through July 8, instead of July 1. The second specified that 90% of births occurred from May 14 through June 10, and the remaining 10% of the births occurred from June 11 through July 1.

Pup Sightability as a Function of Time

Due to sample size constraints, it was not possible to allow rates other than birth rates to vary freely by week. However, it was important to account for the known decrease in pup sightability over time. Pups become increasingly comfortable wandering away from their mothers as the summer progresses, and as a result, it becomes harder over time to see an extant pup, even when the mother is resighted. As a *preliminary* method of quantifying this relationship, I conducted a logistic regression of p(see pup|pup alive, mom seen) versus Julian date, which was first centered.

To obtain data for this regression, I filtered the data set for cows who were seen at least three times during the summer. In the first and last observations, the cow had to be seen with a pup. No requirements were placed on any aspect of the intermediate observations. I used only the intermediate observations in this preliminary regression analysis, and therefore was assured that the regression included only observations of cows who were known to have a live pup.

These regressions confirmed that pup sightability declines over the course of the summer. Because of this, in the main analysis, I included pup sightability as a logistic function of centered Julian date. That is, date is used as a covariate, and the logistic regression coefficients are estimated within the multinomial likelihood function.

Pup Survival

It was not possible to include pup survival as a parameter in the analysis, due to sample size and lack of specific information on pup mortality. Pup mortality (page 12) is spatially and temporally variable, and often related to events such as storms or presence of killer whales near the rookery (Kaplan 2005; Maniscalco et al. 2008). Furthermore, it can be vastly underestimated by counting dead pups on the rookery from a distance that will not disturb the sea lions (Kaplan 2005). Sample size did not permit the inclusion of pup mortality as a rate that varies freely by week, and I lacked the specific temporal and spatial information that would allow me to construct a justifiable (yet parsimonious) relationship between pup mortality, time and location. As a result, the analyses are conducted under the assumption that pups survived the summer rookery observation season. Especially because neonatal mortality is highest on the first day (Kaplan et al. 2008), it is possible for a pup to be born, but then die before it is seen, biasing low the estimated reproductive rate. As a result, the reproductive rate I estimated should be considered the product of the reproductive rate and the neonatal survival rate, rather than a true reproductive rate.

An additional concern is that a pup might be born and seen, but die sometime later during the summer. This could bias low the estimate of pup sightability, which could in turn bias high the estimated reproductive rate. In particular, a late summer event leading to substantial pup deaths could change the slope of the regression line of pup sightability versus time. Alternatively, a mid-summer mortality event or more diffuse mortality over time could change the intercept of the regression line. To evaluate these potential effects, I compared the regression coefficients estimated from within the multinomial likelihood function to the coefficients obtained from the stand alone regressions, where the data filtering assured that the pups were alive (page 64).

SOUTHEAST ALASKA STELLER SEA LION REPRODUCTIVE RATE

Introduction

The Steller sea lion is an endangered species whose reproductive rate estimates need to be updated. Reproductive rate estimates for this species are either rough (eastern population), from a time during which population dynamics were probably quite different from today (western population) or contradictory (western population). Extensive branding and resighting efforts by the Alaska Department of Fish and Game make possible an updated estimation of eastern population Steller sea lion reproductive rates.

Updated reproductive rate estimates from the eastern population are important for two reasons. First, although the population is considered healthy, it is listed as threatened and needs to be monitored. Second, estimated rates from a healthy population will provide a basis for comparison for estimates from the endangered western population, whose status remains uncertain. Furthermore, the Alaska Department of Fish and Game continues to have an active branding and resighting program: the methods developed here can be applied to future data collected in either population. In this chapter, I estimate the Southeast Alaska Steller sea lion reproductive rate in the years 2002 through 2004, using the ADFG data.

Methods

I conducted a Bayesian mark resight reproductive rate estimation. The analyses are based on 99 Steller sea lion cows who were branded as neonates on the Forrester Island Rookery Complex in 1994 and 1995; they are now old enough to have their own pups. The following methodologies are relevant to the analyses. In the list below, assumptions are identified as such. Items not identified as assumptions are either known aspects of Steller sea lion biology or known qualities of the data.

Facts and Assumptions

1. Birthing
    (a) A Steller sea lion cow can give birth up to one time per year, and litter size is almost always one (page 7). Therefore, I assumed that each year, a cow either gives birth to one pup or does not give birth at all.
    (b) I assumed that births can occur daily during the pupping season, but they happen at night, when observations are not being made.
    (c) Three different analyses were conducted in each year, under different assumptions regarding the length of the pupping season and the timing of parturition within the pupping season (page 73).
2. Survival
    (a) In order to obtain a relatively unbiased sample of individual cows (item 2c) and to minimize the effect of the assumption regarding pup survival (item 2b), I limited my analyses to the years 2002, 2003 and 2004. I estimated reproductive rate separately for each year, and each year's encounter histories included only observations taken during the summer.
    (b) It was not possible to model pup mortality (pages 12 and 64) so I assumed that pups survived until the end of the encounter history used in each analysis. To minimize the effect of this assumption, I included in each year's reproductive rate analysis only those observations that were taken

during the summer rookery observation season. Haulout observations were included as long as they occurred during the same time period in which the rookeries were being observed.

(c) In order to obtain a sample of individuals for each summer's reproductive rate estimation that was relatively unbiased with respect to reproductive rate, I filtered the data to include only cows known to have survived beyond the summer being analyzed (page 52). Because of this filtering, I completely satisfied the assumption that cows survived until the end of the summer, and I did not include cow survival rate as a parameter in the analyses. The cows known to have survived the summer were split into two groups.

    i. The cows who were also seen during that summer provided the data used in the likelihood function.

    ii. Cows known to be alive, but not seen during the summer at hand, were included in the analysis in the following manner. For each year, I allowed the reproductive rate of the known alive but unseen group of cows to vary between zero and the mean reproductive rate from the mark resight estimation. I then calculated an overall reproductive rate as a function of the reproductive rate for the unseen cows (pages 59 and 117).

3. Sightability

    (a) Cows in this data set are branded; their pups are not. Therefore, in order to be recorded as seen, the pup must be seen with its mother.

(b) I assumed that on any single day, a cow can either be seen once or not at all. It was rare for cows in this data set to be seen more than once a day. In these few cases, I collapsed the within day observations into one, and recorded the cow as with a pup provided she was seen at least once that day with a pup.

(c) When a cow is seen, she is assumed to take on one of two states: with a pup or not definitively with a pup. In other words, it is assumed that a record of a cow with a pup is correct (page 26). However, a cow seen without a pup may or may not actually have a pup.

(d) It is not physically possible for a cow to lose a brand, so the typical mark resight assumption of marks not being lost is satisfied. I also assumed that brands were not misread. To help meet this assumption, I used a cow sighting in the analyses only if it was confirmed in one of the following manners.

    i. A photograph was taken during the resighting and later confirmed against a photographic library.
    ii. A photograph from the library was printed out and used in the field to confirm the sighting.

(e) I assumed that a cow's sightability and reproductive status are related only through the group to which the cow was assigned (page 54). Any single cow sighting is simply an opportunity to observe (or not observe) a pup, in the same way that a resight day is an opportunity to observe (or not observe) a cow (page 38). The groups are as follows.

   - i. Cows seen on a haulout during June or July of the summer being analyzed. No other restrictions are put on this group: they may or may not have been seen on rookeries as well.
   - ii. Cows seen a total of one to seven times during the summer, but not on a haulout during June or July that year.
   - iii. Cows seen a total of eight or more times during the summer, but not seen on a haulout during June or July of that year.

(f) I estimated a separate reproductive rate for each of these groups and calculated the reproductive rate of the cows known to be alive and seen during the summer as a weighted average (page 117) of the reproductive rates of these three groups, where the weights are given by the number of individuals in each group.

(g) I assume that the probability of seeing a pup given that it has been born and its mother was seen on that day varies only as a function of date; it is constant across cows. I assume that the relationship between the logits of the pup sighting probability and centered Julian date is linear.

The Likelihood Function

Known Constants

M	# of branded female sea lions who were seen at least once during and at least once after the summer
$\vec{N}$	# of summer days on which each cow was observed
N_p	the last date of the pupping season; either July 1 or July 8, depending on the analysis

Unknown Parameters

$\alpha_{j,t}$ p(a cow in Group j gives birth on date t | she has not yet given birth this summer)

δ_s p(pup seen on date s | pup has been born, mother was seen on date s)

Observables for Cow_i

$\vec{EH}$ An encounter history of length N_i where each cow sighting is assigned a 2 if she was definitely with a pup, and a 1 otherwise.

$\vec{DH}$ a Julian date history of length N_i giving the date of each sighting in $\vec{EH}$. May 14 = Julian date 1.

f Either the Julian date the cow was first seen with a pup, or N_p, if the cow was never seen with a pup

Encounter History Probability for Cow_i

The probability that cow_i gave birth to a pup by Julian date f is given by the following equation.

$$\sum_{t_b=1}^{f} A_{t_b} = \sum_{t_b=1}^{f} \left(\alpha_{j,t_b} \prod_{t=1}^{t_b-1} (1 - \alpha_{j,t}) \right). \tag{15}$$

To know whether or not to include the possibility that cow_i did not give birth that summer, define the following indicator function.

$$I = \begin{cases} 0 & \text{if a pup was seen sometime during the summer} \\ 1 & \text{if a pup was never seen} \end{cases} \tag{16}$$

Define the pup sightability function as follows.

$$\Delta_s = \begin{cases} \delta_s & \text{if pup seen on sighting } s\text{, for } cow_i, \\ & \text{which occurred on } DH_{i,s} \text{ which is } \geq t_b \\ 1-\delta_s & \text{if pup not seen on sighting } s \text{ for } cow_i, \\ & \text{which occurred on } DH_{i,s} \text{ which is } \geq t_b \\ 1 & \text{if } DH_{i,s} < t_b \end{cases} \tag{17}$$

and,

$$\ln\left(\frac{\delta_s}{1-\delta_s}\right) = \beta_0 + \beta_1 \left(DH_{i,s} - \frac{\sum_{i=1}^{M}\sum_{s=1}^{N_i} DH_{i,s}}{\sum_{i=1}^{M} N_i} \right) \tag{18}$$

The probability of the encounter history for cow_i is proportional to

$$\sum_{t_b=1}^{f} A_{t_b} \left(\prod_{s=1}^{N_i} \Delta_s \right) \; + \; I \left(\prod_{t=1}^{N_p} (1-\alpha_{j,t}) \right). \tag{19}$$

and the likelihood function is proportional to the product of the encounter histories for the M cows.

Prior Probability Distributions

The prior probability distributions on the pup sighting regression parameters were improper uniform, both for the regression within the multinomial likelihood function, and for the stand alone regression (page 64). The prior probability distribution on each year's annual reproductive rate for each group of cows was a uniform (0,1) distribution. In all analyses, pups were allowed to be born daily, and the probability that a pup was born on day t_b was A_{t_b}. In order to avoid having 49 - 56 time specific birth rates for each of the three groups, the same rate was used for each day in week; however the rate was allowed to vary among weeks. Depending on the analysis, this gave seven to eight time specific birth rates for each of the three groups.

One analysis specified that all births occur between May 14 and July 1. In this case, the seven time specific priors were all identically distributed. In the analysis that specified that births occur between May 14 and July 8, the eight time specific priors were identically distributed. In the analysis where 90% of births occur between May 14 and June 10 and the remaining 10% occur between June 11 and July 1, the time specific rates in the first four weeks were identically distributed, and the time specific rates in the subsequent three weeks were identically distributed. Having a uniform annual birth rate prior and identical distributions for the time specific birth rate priors means that the the time specific priors are right skewed.

Simulating Population Trend from Estimated Demographic Rates

To determine whether estimated demographic rates would produce a similar rate of population growth to the rate estimated by trends in pup counts, I combined my estimated reproductive rates from the 2004 posterior distribution on the 86 cows used in the likelihood function, the Cormack-Jolly-Seber (CJS) survival rate estimates from Pendleton et al. (2006) and an age of first birth of 5.9 (age of first pregnancy plus one, Pitcher and Calkins 1981) via a simplified form of the Euler-Lotka equation (Eberhardt and Siniff 1977). This equation (Eqn. 20) calculates population growth rate (λ) given the following four quantities: average age of first reproduction (a), survival from birth to average age of first reproduction (S_0), annual survival rate for reproductively mature animals (S_1) and fecundity (F), which is the number of female pups born per mature female per year. Implicit in this equation are the assumptions that 1) all individuals commence reproduction at the average age, 2) the reproductive rate is constant across all mature age classes and 3) the annual survival rate is constant across all mature age classes. The largest real root to the following equation gives the simulated λ.

$$1 = \lambda^{-a} S_0 F (1 - S_1 \lambda^{-1})^{-1} \tag{20}$$

Further Statistical Details

Further details regarding the prior distributions, the weighted average, the simulation of population growth rate, MCMC methods and assessment of convergence are given in the appendices. These are important details in that they must be correct; however, they lend no further biological meaning to the analyses.

Results

Reproductive Rates

Estimated mean reproductive rates for cows known to be alive and seen during the summer were 0.53 (0.41, 0.66), 0.70 (0.57, 0.83) and 0.66 (0.55, 0.77) for 2002, 2003 and 2004 respectively (Table 5 on page 77, Figure 5 on page 78). When I calculated the overall reproductive rate as a function of the reproductive rate of the known alive but unseen cows, the following results were obtained. In 2002, the *mean* reproductive rate for all cows known to be alive that year was between 0.42 and 0.54; for 2003, it was between 0.65 and 0.70, and for 2004, it was between 0.63 and 0.66 (Tables 6 on page 80, 7 on page 81, 8 on page 82 and Figure 6 on page 79). The 95% credibility intervals showed substantial overlap among years, meaning there is no detectable difference in reproductive rate among years.

Population Growth Simulations

The population growth rate predicted by my 2004 reproductive rate estimate, survival rates (Pendleton et al. 2006) and the age of first birth (Pitcher and Calkins 1981) had a mean of 1.031 and a 95% credibility interval of (1.003, 1.073). The mean rate is comparable to the 3.2% annual increase in Southeast Alaska pup counts, but high for the 0.6% rate for the Forrester Island Rookery Complex. The credibility interval includes populations which vary from stationary to vigorously increasing.

Sensitivity to Different Reproductive Rate Priors

The effect of prior assumptions on birth rates had little effect on the posterior distributions. Differences in mean annual birth rates from the most restrictive prior to the least restrictive prior varied from 2% to 4% depending on year (Table 9 on page 83, Figure 7 on page 84). These same estimates have credibility intervals where the difference between the estimated reproductive rate at the 0.975 tail and the 0.025 tail is 22 - 26%. This indicates that the variation as a result of prior assumptions was minimal compared to the overall variation. Unless otherwise stated, the rates I present use the intermediate prior, where births occured daily from May 14 to July 1, and birth rates were allowed to vary by week, without constraint.

Pup Sightability

The assumption that pups survive the summer does not appear to have substantively influenced the reproductive rate estimation. The slope of the regression line from within the multinomial likelihood function estimated the change over time of the probability of seeing a pup given that *it had been born* and its mother had been seen that day; whereas the slope of the stand alone regression line estimated the change over time of the probability of seeing a pup given that *it was alive* and its mother had been seen that day. The posterior distributions from the stand alone regressions were wider than the corresponding distributions from the main analyses, which is to be expected with the smaller sample size created by the filtering in the stand alone regressions (6). The supports of main analysis posteriors were completely contained within the supports of the stand alone posteriors, suggesting that pups who may have died in late summer did not have a large influence on the change in pup sightability over time (Table 10 on page 85).

Similarly, for the intercept term, the supports of the posterior distributions from the two analyses were almost completely overlaid on each other, indicating that a potential mid-summer mortality event or more diffuse mortality across the summer probably did not have a large influence on the pup sightability estimation, and therefore probably did not have a large influence on the estimation reproductive rate either.

Table 5: Posterior reproductive rate estimates given by group: Group 1 = cows seen at least once on a haulout during June or July, Group 2 = cows not seen on a haulout during June or July and seen a total of 1 - 7 times during the summer, Group 3 = cows not seen on a haulout during June or July and seen a total of 8 or more times during the summer. The average rate is an average of the three groups, weighted by the number of cows in each group. It gives the average reproductive rate for all cows seen during and known to have lived beyond the summer.

2002

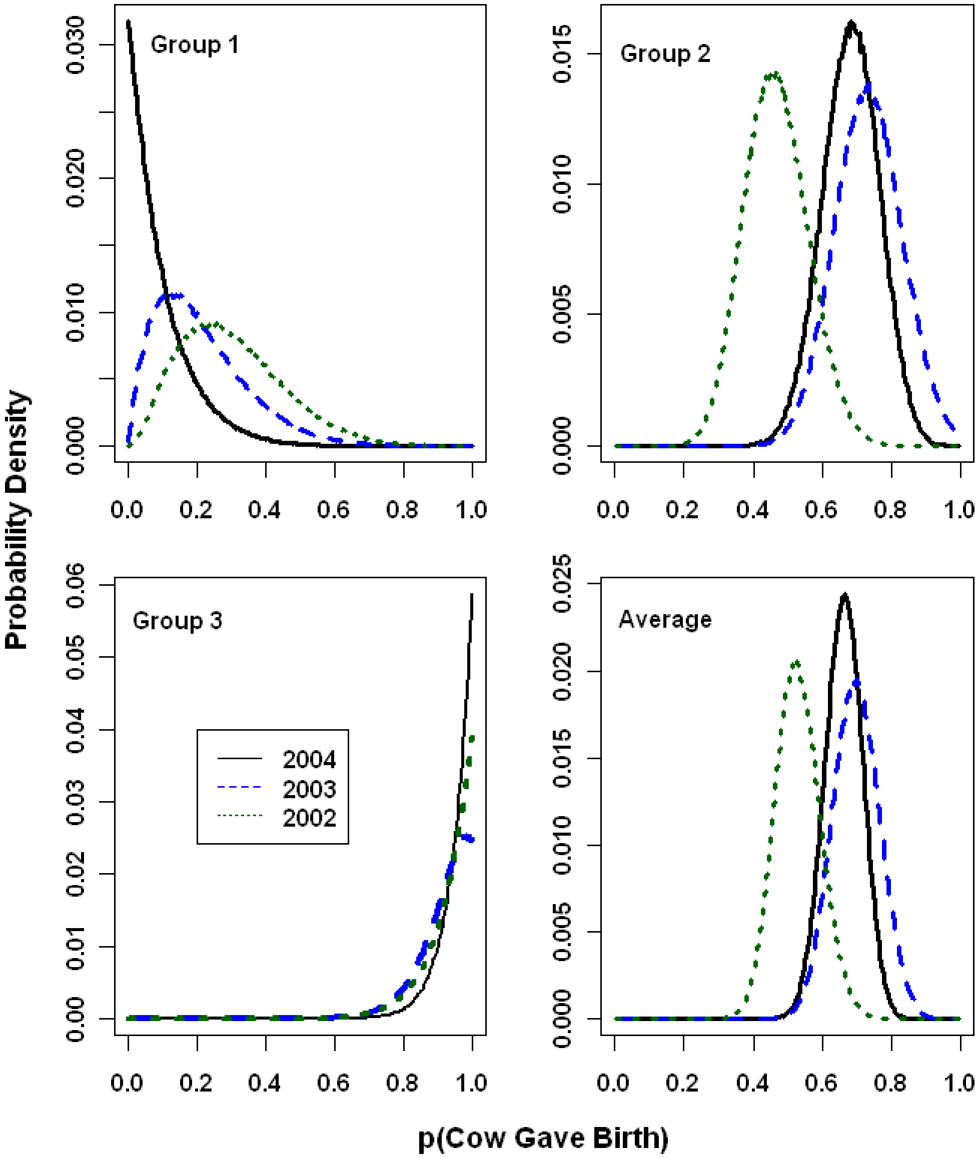
Birth Rate	Mean	95% CI	SE
Group 1	0.3013	(0.0700, 0.6367)	0.1484
Group 2	0.4668	(0.2933, 0.6567)	0.0925
Group 3	0.9236	(0.7367, 1.0000)	0.0706
Average	0.5300	(0.4067, 0.6633)	0.0650

2003

Birth Rate	Mean	95% CI	SE
Group 1	0.2106	(0.0267, 0.5300)	0.1322
Group 2	0.7341	(0.5467, 0.9267)	0.0964
Group 3	0.9127	(0.7367, 0.9967)	0.0701
Average	0.6988	(0.5667, 0.8333)	0.0677

2004

Birth Rate	Mean	95% CI	SE
Group 1	0.0964	(0.0000, 0.3400)	0.0903
Group 2	0.6834	(0.5167, 0.8400)	0.0819
Group 3	0.9475	(0.8133, 1.0000)	0.0498
Average	0.6629	(0.5533, 0.7700)	0.0544



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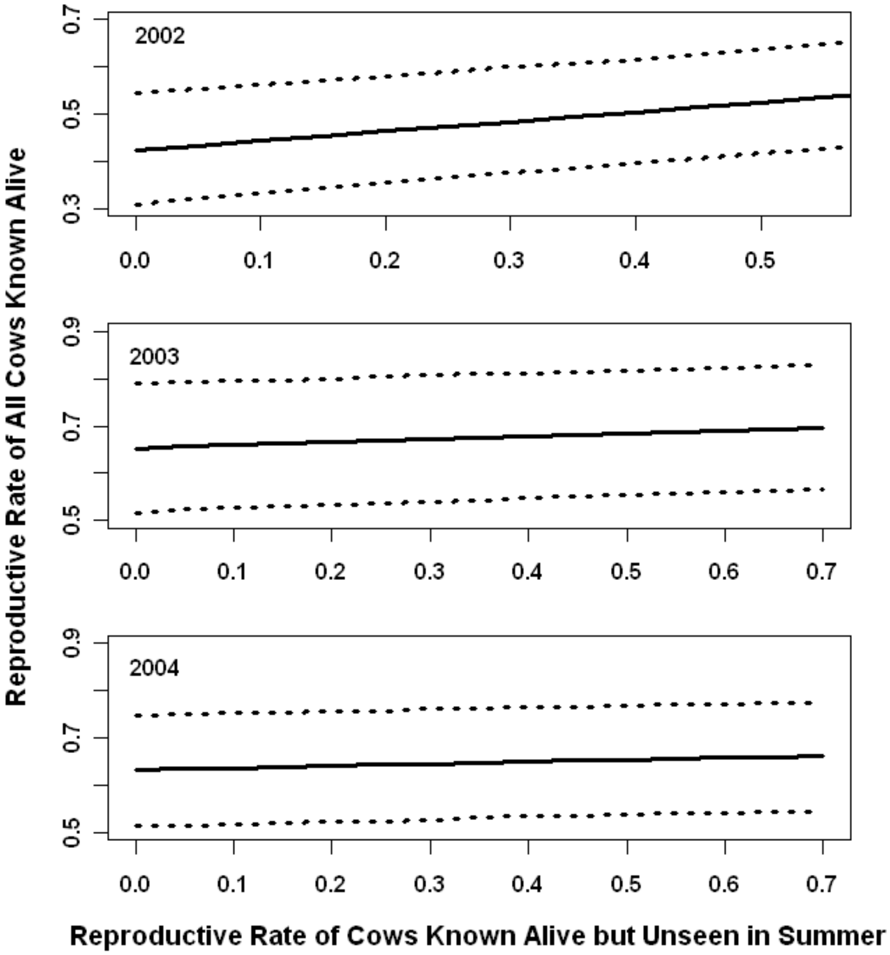

Figure 6: Reproductive rates of all cows known to have survived the summer as a function of cows known alive but unseen during the summer. The reproductive rates of the unseen cows were allowed to vary, by steps of 0.05, from a low of 0.0 to a high of the estimated reproductive rate of the cows who were seen during that summer, and known to have survived it as well.

Table 6: 2002 reproductive rate as a function of the point reproductive rate for cows known alive but unseen during the summer. Reproductive rate of the unseen cows was allowed to vary, by steps of 0.05, from a low of 0.0 to a high of the estimated reproductive rate of the cows who were seen during the summer of 2002, and known to have survived it as well.

Point Value	Mean	95% CI	SE
0.0000	0.4229	(0.3100, 0.5433)	0.0590
0.0500	0.4331	(0.3233, 0.5533)	0.0583
0.1000	0.4433	(0.3333, 0.5633)	0.0577
0.1500	0.4535	(0.3433, 0.5700)	0.0571
0.2000	0.4637	(0.3567, 0.5800)	0.0566
0.2500	0.4739	(0.3667, 0.5900)	0.0562
0.3000	0.4841	(0.3767, 0.6000)	0.0559
0.3500	0.4943	(0.3867, 0.6067)	0.0556
0.4000	0.5045	(0.3967, 0.6167)	0.0553
0.4500	0.5147	(0.4067, 0.6267)	0.0552
0.5000	0.5248	(0.4167, 0.6367)	0.0551
0.5500	0.5350	(0.4267, 0.6467)	0.0551

Table 7: 2003 reproductive rate as a function of the point reproductive rate for cows known alive but unseen during the summer. Reproductive rate of the unseen cows was allowed to vary, by steps of 0.05, from a low of 0.0 to a high of the estimated reproductive rate of the cows who were seen during the summer of 2003, and known to have survived it as well.

Point Value	Mean	95% CI	SE
0.0000	0.6527	(0.5167, 0.7900)	0.0687
0.0500	0.6558	(0.5233, 0.7933)	0.0684
0.1000	0.6589	(0.5267, 0.7967)	0.0682
0.1500	0.6620	(0.5300, 0.7967)	0.0679
0.2000	0.6652	(0.5333, 0.8000)	0.0677
0.2500	0.6683	(0.5367, 0.8033)	0.0675
0.3000	0.6714	(0.5400, 0.8067)	0.0673
0.3500	0.6745	(0.5433, 0.8100)	0.0671
0.4000	0.6777	(0.5467, 0.8100)	0.0670
0.4500	0.6808	(0.5500, 0.8133)	0.0669
0.5000	0.6839	(0.5533, 0.8167)	0.0668
0.5500	0.6870	(0.5567, 0.8200)	0.0667
0.6000	0.6902	(0.5600, 0.8233)	0.0666
0.6500	0.6933	(0.5633, 0.8267)	0.0666
0.7000	0.6964	(0.5667, 0.8300)	0.0666

Table 8: 2004 reproductive rate as a function of the point reproductive rate for cows known alive but unseen during the summer. Reproductive rate of the unseen cows was allowed to vary, by steps of 0.05, from a low of 0.0 to a high of the estimated reproductive rate of the cows who were seen during the summer of 2004, and known to have survived it as well.

Point Value	Mean	95% CI	SE
0.0000	0.6316	(0.5133, 0.7467)	0.0595
0.0500	0.6337	(0.5133, 0.7500)	0.0593
0.1000	0.6359	(0.5167, 0.7533)	0.0591
0.1500	0.6380	(0.5200, 0.7533)	0.0589
0.2000	0.6402	(0.5233, 0.7567)	0.0587
0.2500	0.6423	(0.5233, 0.7567)	0.0585
0.3000	0.6445	(0.5267, 0.7600)	0.0584
0.3500	0.6466	(0.5300, 0.7600)	0.0583
0.4000	0.6488	(0.5333, 0.7633)	0.0582
0.4500	0.6509	(0.5333, 0.7633)	0.0581
0.5000	0.6531	(0.5367, 0.7667)	0.0580
0.5500	0.6552	(0.5400, 0.7700)	0.0580
0.6000	0.6574	(0.5400, 0.7700)	0.0579
0.6500	0.6595	(0.5433, 0.7733)	0.0579
0.7000	0.6617	(0.5433, 0.7733)	0.0579

Table 9: Prior influence on reproductive rate estimates. Summary statistics for the 2002, 2003 and 2004 posterior distributions of the reproductive rate for all cows seen during and known to have lived beyond the summer. Priors are 1) most restrictive: 90% of pups born from May 14 - June 10 and 10% born from June 11 - July 1, 2) intermediate: pups born from May 14 - July 1; and 3) most liberal: pups born from May 14 - July 8.

2002

Restrictiveness of Prior	Posterior Birth Rate Mean	95% CI	SE
Most	0.5147	(0.3967, 0.6433)	0.0621
Intermediate	0.5300	(0.4067, 0.6633)	0.0650
Least	0.5373	(0.4133, 0.6733)	0.0661

2003

Restrictiveness of Prior	Posterior Birth Rate Mean	95% CI	SE
Most	0.6651	(0.5433, 0.7867)	0.0615
Intermediate	0.6988	(0.5667, 0.8333)	0.0677
Least	0.7158	(0.5800, 0.8500)	0.0692

2004

Restrictiveness of Prior	Posterior Birth Rate Mean	95% CI	SE
Most	0.6545	(0.5467, 0.7567)	0.0530
Intermediate	0.6629	(0.5533, 0.7700)	0.0544
Least	0.6717	(0.5600, 0.7800)	0.0557

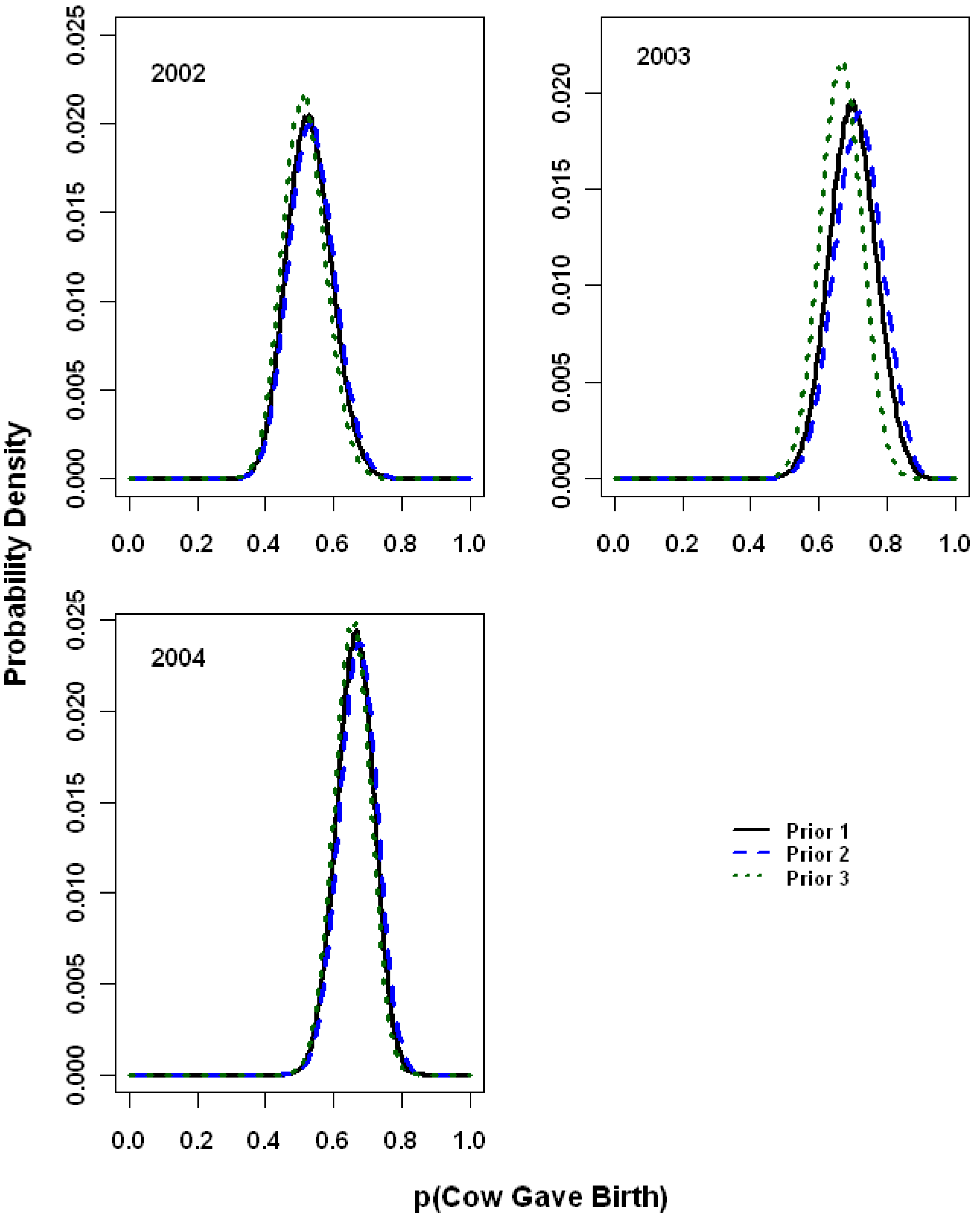

Figure 7: Posterior distributions for the 2002, 2003 and 2004 estimates of the reproductive rate for all cows seen during and known to have lived beyond the summer. Priors are 1) most restrictive: 90% of pups born from May 14 - June 10 and 10% born from June 11 - July 1, 2) intermediate: pups born from May 14 - July 1; and 3) most liberal: pups born from May 14 - July 8.

Table 10: β_1 Estimates. β_1 is the slope of the logistic regression of p(see pup|pup *born*, mom seen) versus time from the main analyses, and it is the slope of the stand alone logistic regression of p(see pup|pup *alive*, mom seen). Main analyses refer to the logistic regression that is conducted within the multinomial likelihood function.

2002			
From Main Analysis	Mean	95% CI	SE
Yes	-0.0079	(-0.0185, 0.0024)	0.0052
No	-0.0097	(-0.0246, 0.0041)	0.0073

2003			
From Main Analysis	Mean	95% CI	SE
Yes	-0.0417	(-0.0555, -0.0291)	0.0065
No	-0.0389	(-0.0565, -0.0224)	0.0086

2004			
From Main Analysis	Mean	95% CI	SE
Yes	-0.0180	(-0.0266, -0.0097)	0.0042
No	-0.0167	(-0.0301, -0.0037)	0.0068

Table 11: β_0 Estimates. β_0 is the intercept of the logistic regression of p(see pup|pup *born*, mom seen) versus time from the main analyses, and it is the intercept of the stand alone logistic regression of p(see pup|pup *alive*, mom seen). Main analyses refer to the logistic regression that is conducted within the multinomial likelihood function. In the main analysis in each year, date was centered before being included as a covariate by subtracting from each observation the mean date. The mean dates for each year are within a week of each other, so the intercepts are for similar, although not identical dates. The stand alone regression for each year was centered by subtracting from each observation the mean observation date *from the main analysis from that same year*. As a result, each year, the intercept estimates from the two analyses are directly comparable.

2002

From Main Analysis	Mean	95% CI	SE
Yes	-0.1155	(-0.4000, 0.1600)	0.1406
No	-0.0817	(-0.4250, 0.2650)	0.1728

2003

From Main Analysis	Mean	95% CI	SE
Yes	-0.0464	(-0.3100, 0.2200)	0.1346
No	-0.0478	(-0.3650 ,0.2650)	0.1620

2004

From Main Analysis	Mean	95% CI	SE
Yes	-0.2992	(-0.5300, -0.0700)	0.1143
No	-0.2191	(-0.5250, 0.0850)	0.1558

Table 12: Pup sightability by date. Pup sightability on the first, mean and last days (of the summer observation seasons) on which branded cows were observed. Pup sightability is the probability of seeing a pup given that it has been born and its mother was seen on that day. The means and credibility intervals for this table were obtained by calculating the regression line at each of the 995,000 sets of retained values in the joint posterior distribution from each year's mark resight analysis.

2002

Date	Mean	95% CI	SE
First	0.58	(0.42, 0.79)	0.080
Mean	0.47	(0.40, 0.57)	0.035
Last	0.36	(0.22, 0.58)	0.075

2003

Date	Mean	95% CI	SE
First	0.91	(0.83, 0.97)	0.034
Mean	0.49	(0.42, 0.58)	0.033
Last	0.11	(0.06, 0.23)	0.033

2004

Date	Mean	95% CI	SE
First	0.62	(0.52, 0.74)	0.048
Mean	0.43	(0.37, 0.51)	0.028
Last	0.22	(0.15, 0.37)	0.044

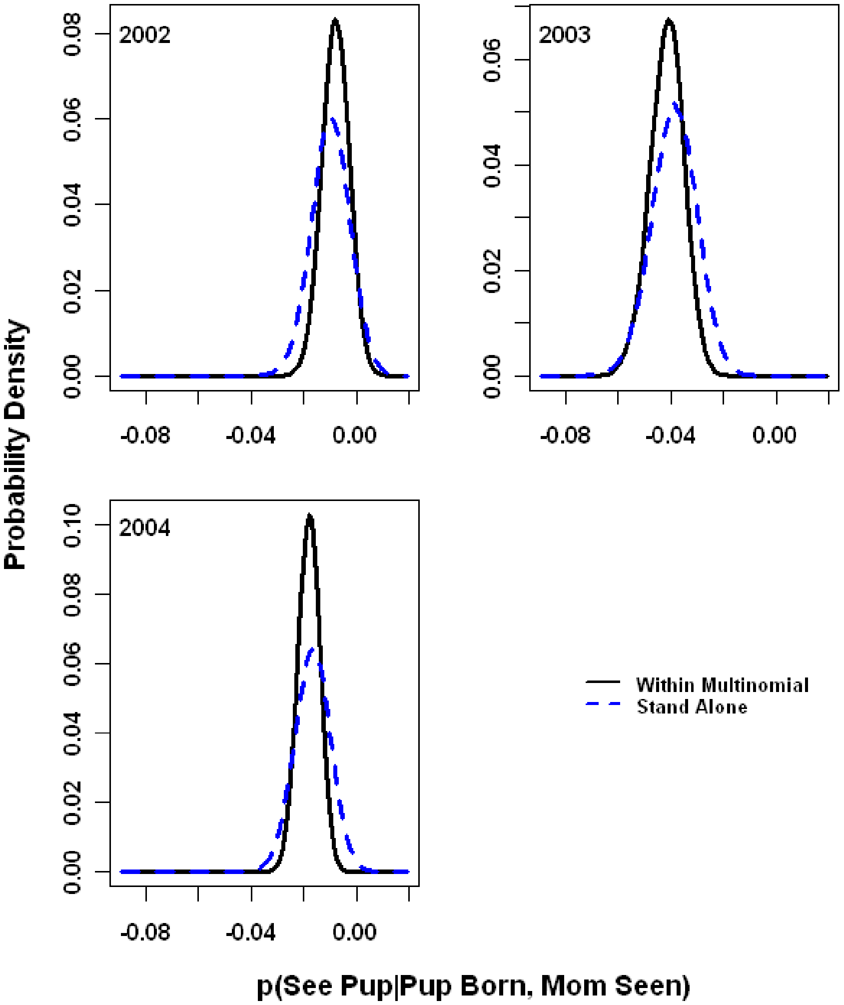

Figure 8: Posterior probabilities of the regression line slope, β_1. Within the multinomial likelihood function, logit(p(pup seen|pup *born*, mom seen) was regressed on date, which was first centered. For comparison only, a stand alone regression of logit(p(pup seen—pup *alive*, mom seen) was regressed on date, which was first centered. Because the supports of the posterior distributions of β_1 from within the multinomial likelihood functions are fully contained within the supports from the corresponding stand alone regressions, our assumption of complete pup survival does not appear to have been problematic for the reproductive rate estimation.

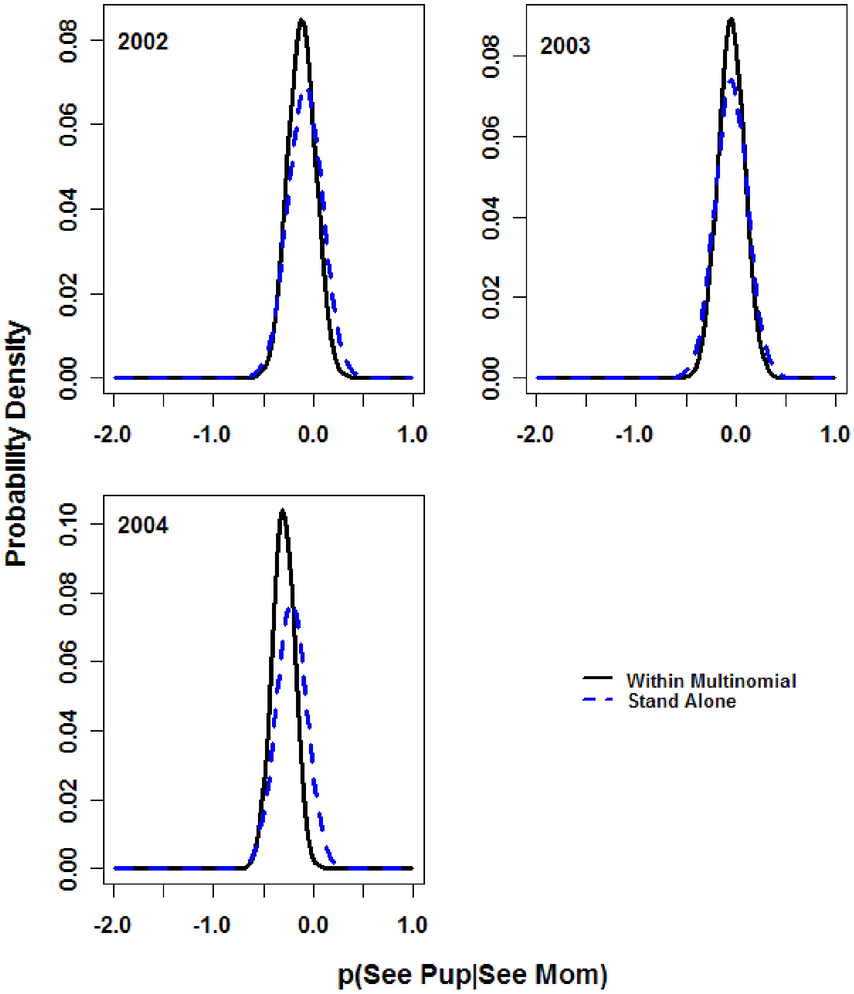

Figure 9: Posterior probabilities of the regression line intercept, β_0. Within the multinomial likelihood function, logit(p(pup seen|pup *born*, mom seen) was regressed on date, which was first centered. For comparison only, a stand alone regression of logit(p(pup seen|pup *alive*, mom seen) was regressed on date, which was first centered. Because of the almost complete overlay of the supports of posterior distributions from each of the pairs of analyses, our assumption of complete pup survival does not appear to have been problematic for the reproductive rate estimation.

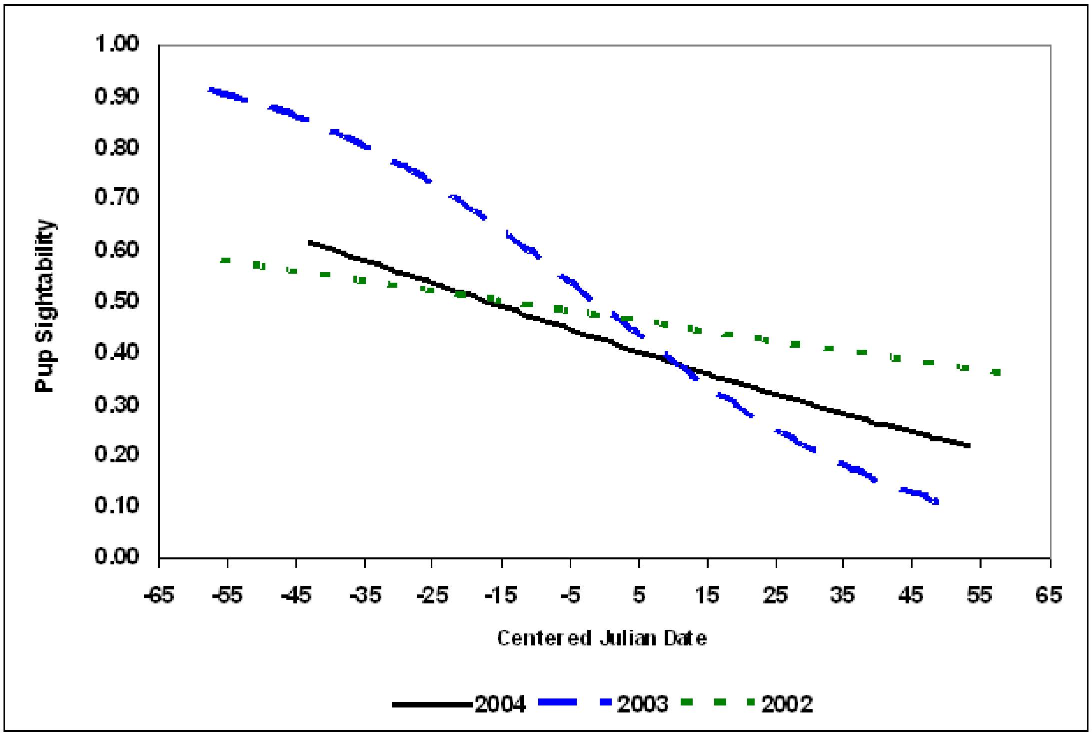

Figure 10: Regression lines of Pup Sightability versus time for three years. Pup sightability is the probability of seeing a pup given that it has been born and its mother was seen on that day. The lines were calculated using the mean estimates for slope and intercept that were estimated by logistic regression within the multinomial likelihood function. Slopes differed significantly only between 2002 and 2003. Intercepts did not differ significantly among years.

Discussion

Aspects of the Reproductive Rate Estimation

Estimated Rates: My estimates of Southeast Alaska Steller sea lion reproductive rates span three years. The best estimates come from 2004, in part due to reproductive maturation of the cohorts, and in part due to high resighting rates. Although most Steller sea lion cows have ovulated by age four or five, first ovulations as late as eight years of age have been noted in the literature (Calkins and Pitcher 1982). The females in my analyses were aged nine to ten in 2004, making them reproductively mature. Furthermore, the highest and most systematic resight effort used to obtain these data occurred in 2004. Only three individuals known to have survived the summer went unseen during the summer of 2004, compared to five in 2003 and 22 in 2002. The average 2004 reproductive rate estimate is between 0.63 and 0.66, depending on the assumption made regarding the reproductive rate of the three missing individuals.

The 95% credibility intervals surrounding the estimated annual reproductive rates for the cows known alive and seen during the summer are wide. In each year, the difference between the estimated reproductive rate at the 0.975 tail and the 0.025 tail was 22 - 26%. Because of these wide credibility intervals, comparison among years revealed no detectible differences in the mean reproductive rates, although the amount of overlap between the 95% intervals in 2003 and 2004 with the intervals in 2002 is minimal if the 22 cows missing in 2002 are assumed to have a very low reproductive rate.

The wide credibility intervals are a reflection of three things. First, the sample size of cows still alive in the cohorts, a decade after they were branded as pups, is small. Of the 373 female pups branded in 1994-1995 (Pendleton et al. 2006), 99 were known to have survived the summer of 2002. By 2004, that number dropped to 89. To examine the potential effect of the sample size of cows on the precision of the parameter estimates, I repeated the 2004 analysis under the assumption that effort was identical, but the sample size of cows had doubled. That is, I used the exact same data in the likelihood function, except the probability of each encounter history was squared. I chose 2004 because current ADFG resight effort is most similar to the level of effort in 2004. The difference between the estimated reproductive rate at the 0.975 tail and the 0.025% of the credibility interval was 19% in the new analysis, only 3% less than the 22% interval width in the original analysis. Although sample size is always important, reasons other than the small sample of cows are responsible for much of the uncertainty in the reproductive rate estimates.

The second reason for the wide credibility intervals is that a substantial number of cows were only sighted a few times during each summer. In each year, 80 - 86% of cows were assigned to Groups 1 and 2, and in each year the median number of per cow sightings in each of these groups was two to three. Although this number of sightings would be sufficient to correct for state classification uncertainty under the assumption of population closure (to pup births and deaths), when combined with an open population, it provides relatively few opportunities to determine if a cow has a pup.

Finally, the reason most responsible for the wide credibility intervals is that births occur throughout a large portion of the summer observation season. Therefore, unless and until a female is first seen with a pup, a sighting of that female without a pup could be due either to the pup not having been born or the pup having been born, but not seen. Accounting for both of these possibilities is an essential element of the analysis, and it contributes substantially to the high (but realistic) level of uncertainty in the estimate of pup sightability over time. Because it is the estimation of pup sightability that corrects reproductive rate estimation for state classification uncertainty, the additional variability in the estimate of pup sightability translates into additional variability in the estimated reproductive rate.

Pup Mortality: The temporal and spatial variation in pup mortality, its event-related nature and sample size considerations prevented the inclusion of pup survival parameters in the current model. Some pups would certainly have died before they could be observed at all, and there was no way to evaluate how many pups this might include. On Lowrie Island, some neonates probably died before being observed, especially because neonatal mortality is higher on the first day than on subsequent days (Kaplan et al. 2008). The probability of pups dying prior to being observed is even higher for sites other than Lowrie Island, because they are visited much less often. On those sites, more neonatal mortality would have gone undetected. As a result, the reproductive rate estimates herein should be considered estimates of the reproductive rate multiplied by the neonatal survival rate.

More troubling was the need to assume that pups did not die after being seen. To evaluate the effect of this assumption on the analyses, I compared the regression parameter estimates from the main analyses to estimates from a stand alone regression of pup sightability versus time, where the pups were known to be alive. The overlaying posterior distributions of the regression parameters from the main analyses and the stand alone regressions suggest that the estimation of pup sightability (and therefore the estimation of reproductive rate) was not substantially affected by mortality of pups after they were first seen.

The apparently small effect of this assumption on the reproductive rate estimation is probably due, in large part, to the high level of uncertainty already present in the estimate of pup sightability, the parameter that adjusts the reproductive rate for unseen pups. The probability of seeing a pup, given that it had been born and its mother was seen that day had wide credibility intervals. For any *single* date and year, the estimated sighting rate at the 0.975 interval tail was 14% to 37% higher than the rate at the 0.025% tail, depending on which date and year were chosen. The width of the credibility intervals was due, in large part, to the modeling of births as within season rates. Had I assumed that cows transitioned from a non-reproductive to a reproductive state at an annual level, my estimate of pup sightability would have been much more precise, although artificially so, and the analysis would have been much more sensitive to the assumption that pups do not die after first being seen.

Pup mortality can be included in the model developed here, if its relationship with time and space can be specified in a parsimonious manner. Further pup mortality studies are needed, and could make a large contribution to the estimation of reproductive rate.

Prior Assumptions: Different prior assumptions about the timing of births had little impact on the reproductive rate estimates. The minimal effects of birth timing assumptions reflect the model's design to determine how many pups were born, not when they were born. In fact, when the birth rates were allowed to vary freely by week, each week's rate had a right skewed posterior distribution that was identical to the rate for every other week during which pups could be born. These week specific birth rates varied in concert with each other such that certain annual birth rates were more likely than others, but no particular combination of week specific birth rates was favored over another that produced the same annual birth rate.

Implications for an Updated Life Table

It is worth noting that resightings of the same marked cows used in my reproductive rate analyses have been used to update age specific survival rate estimates for Steller sea lions in Southeast Alaska (Pendleton et al. 2006). Because these individuals were branded at approximately three weeks of age, first year survival estimates do not include the neonatal mortality that occurs before branding (Pendleton et al. 2006). If these survival rate estimates and my reproductive rate estimates are to be included in the same life table, I recommend not making any post hoc adjustments to the first year survival rate to account for neonatal mortality, as my reproductive rate estimates are really an estimate of the reproductive rate multiplied by the neonatal survival rate.

Population Growth Rates

I used these updated survival rates (Pendleton et al. 2006), my estimate of adult reproductive rate and the age of first birth (Pitcher and Calkins 1981) to simulate population growth rate. The mean simulated growth rate (3.1% per year) is comparable to the 3.2% annual increase in Southeast Alaska pup counts, but high for the 0.6% rate for the annual increase in pup counts at the Forrester Island Rookery Complex. The credibility interval includes populations which vary from essentially stationary (0.3% annual growth rate) to increasing at a rate that would be unusually high for a Pinniped (7.3% per year). This simulated population growth rate reflects conditions both on FI and in Southeast Alaska in general. Annual survival rates are more generalizable to Southeast Alaska than are reproductive rates, because juveniles disperse widely, and mature cows who have pups at FI are based at the rookery only for about a quarter of the year. The estimated reproductive rate, however, is most reflective of FI. Since the marked individuals used in these analyses were born on the Forrester Complex, most have returned there to give birth to their own pups. Furthermore, by far the highest resighting effort in Southeast Alaska occurs on Lowrie Island, the largest FI island that is inhabited by breeding sea lions.

Although the Southeast Alaska Steller sea lion population has been increasing at 3.2% per year for several decades, during the same time frame, the Forrester Complex has been increasing at 0.6% (Pitcher et al. 2007). Furthermore, cows attending pups on Lowrie Island in the mid-1990's spent longer at sea and less time ashore than did their counterparts at Sugarloaf Island Rookery in the western population (Milette and Trites 2003), suggesting that finding sufficient food required more effort from the Lowrie Island cows. Likewise Lowrie Island pups in the 1990's grew at the same or slower rates as pups on four different western population rookeries that were examined during the same time period (Brandon et al. 2005). This combination of observations suggest that FI is nearing carrying capacity. As a result, I consider my estimates of reproductive rate applicable to a healthy population nearing carrying capacity, that is, one that is slowly increasing.

The number of sea lions in the western population is dramatically reduced compared to historical levels. While the eastern population has been increasing, the western population has declined by over 80% during the last four decades. Furthermore, the higher pup growth rates and shorter foraging trips of nursing females in parts of the western population compared to FI suggest that food limitation for adult females attending pups may not currently be limiting the western population. As a result, western population reproductive rates would not be expected to be limited as a result of nutritional stress. Disease and pollutants are also known to reduce reproductive rates, but these are not thought to have a large influence on Steller sea lion population dynamics. If carrying capacity in the western portion of Steller sea lion range has been reduced such that the western population is now near a new carrying capacity, their reproductive rates may be similar to that estimated for the largely FI-based females used in the Southeast Alaska reproductive rate estimation.

Comparison to Other Reproductive Rate Estimates

Previous estimates of Steller sea lion reproductive rate have been highly variable, in part because of the different times and locations where data were collected, and in part, because of the different analytical methods employed. Table 13 gives a comparison of different Steller sea lion reproductive rate estimates.

Table 13: Comparative Steller sea lion reproductive rates. Populations noted as stationary are thought or assumed to be stationary. Sources are: 1) Calkins and Pitcher 1982 and 2) Calkins and Goodwin 1988, both obtain reproductive rate from late term pregnancy rates (of physiologically mature, collected cows) adjusted by monthly abortion rate; 3) Holmes et al. 2007, reproductive rate based on demographic rates from (1), updated over time by trends in pup and non-pup counts, see below; 4) Maniscalco et al. 2005b, reproductive rate from cows observed with and without pups on Chiswell Island, mostly mature, but ages unknown, see below; 5) This analysis, an estimate of reproductive rate multiplied by neonatal survival rate.

Mean Birth Rate	Age	Population Status	Population	Years	Source
63%	3-30	Stationary ?	Western	1975-1978	1
55%	4-20	Declining	Western	1985-1986	2
42%	8-10	Stationary ?	Western	2004	3
83%	?	Increasing	Western	2001-2004	4
66%	9-10	Slowly Increasing	Eastern	2004	5

The highest and lowest rates were both estimated for the Central Gulf of Alaska (western population) in the 2000's: 42% by Holmes et al. (2007) versus 83% by Maniscalco et al. (2005b). This discrepancy is due to at least two reasons. First, the lower estimate pertains to the Central Gulf of Alaska in general, whereas the high estimate pertains to the Chiswell Island Rookery, a specific site within the Central Gulf of Alaska. Chiswell Island has recently be re-established as a rookery, and it is is currently uncrowded and growing (Maniscalco et al. 2005a,b).

Second, the two rates are estimated by vastly different methods. The rates estimated by Holmes et al. come from models of population trend over multiple decades. An underlying assumption of these models is that the Gulf of Alaska Steller sea lion population was stationary in the 1970's, a time for which the population trend is difficult to reconstruct. The primary goal of these models was to retrospectively predict what vital rate changes might have caused the western population decline. A component of their estimation of vital rate changes was to predict current rates; however, this is an indirect way to obtain an update.

In contrast to large scale modeling, the field based estimates from the Chiswell Island rookery are based solely on current observations of naturally marked cows, who are seen either alone or with pups on the rookery. Because of the small size of the rookery and the presence of multiple remotely controlled video cameras, cows are followed in great detail when they are present on the island, and the assignment of a reproductive status to an individual in regular attendance is done with an extremely high degree of certainty. However, these same individuals can rarely be tracked elsewhere, and the reproductive status of absent animals is, by necessity, based on assumption. Furthermore, it is unknown if the acquisition of natural markings is related to age or other factors, so it is not clear to what population the reproductive rate estimate refers.

Table 14 on the next page provides reproductive rate estimates for other Otariid species from stable to increasing populations. The other species include California sea lions (CASL, *Zalophus californianus*), subantarctic fur seals (SAFS, *Arctocephalus tropicalis*), and Antarctic fur seals (ANFS, *Arctocephalus gazella*). Notably, the one population believed to be reaching carrying capacity, had an estimated reproductive rate of 0.63, much like the 0.66 rate estimated herein.

Table 14: Comparative Otariid reproductive rates. Sources are 1) Hernández-Camacho et al. 2008, 2) Melin, SR 2002, 3) Lunn et al. 1994, 4) Dabin et al. 2004; Chambellant et al. 2003.

Species	Ages	Population Status	Mean Birth Rate	Source
CASL	10-12	increasing	0.80	1
CASL	6-12	increasing	0.77	2
ANFS	6-11	increasing	0.75-0.80	3
SAFS	8-13	slightly increasing	0.63	4

Although much remains unresolved regarding the western population of Steller sea lions, current reproductive rate estimates from the healthy, eastern population provide a needed basis for comparison. In addition, the Alaska Department of Fish and Game is currently analyzing the post 2004 data, and maintains active branding and resighting programs. The methods developed here can be applied to current and future data collected from either population. The continuation of both the branding and resighting programs is imperative, both to increase sample size for vital rate estimation, and to monitor changes in those rates.

FUTURE WORK AND RECOMMENDATIONS

Challenges in Sighting Steller Sea Lions

It is important to note that the high resight rates in 2003 and 2004 are what made this reproductive rate estimation possible. The importance of these efforts can not be overstated. Furthermore, a number of aspects of Steller sea lion biology make them difficult to resight in a manner that satisfies statistical assumptions. These reasons include the following:

1. Multiple rookeries and (at least for cows not yet seen with a pup) an inability to assign them to rookeries
2. Greater mobility of sea lions than observers at the Forrester Island Rookery Complex
3. Tighter association of cows with their pups early in the season when births are still occurring, but greater difficulty resighting them together after the population is closed to births
4. Spatial and temporal variation in pup mortality

Meeting the Assumption of Population Closure

It may be impossible to satisfy the desirable statistical assumptions that would allow for an estimate of reproductive rate that is more precise, without being more biased. Nevertheless, the ideal method to correct for state classification uncertainty is the use of Pollock's robust design (Kendall et al. 2003, 2004; Pollock 1982), which requires resightings at a time when the population is closed both to both pup births and deaths. In order to satisfy the closure assumption, extensive resightings would have to be conducted after births had ceased for the year, in a short enough period of time that it could be assumed that pups don't die during the resight intervals. Pup mortality during the pupping season itself would have been missed, so the estimated reproductive rate would be the reproductive rate multiplied by the pup survival rate during the pupping season.

Alternatives to the Assumption of Population Closure

Although not as statistically helpful as satisfying the assumption of population closure, it would be helpful to increase the number of times a cow is sighted during the summer. Early and late season sightings are *both* extremely important. Early season sightings are important because it is easiest for pups to be seen with their mothers when they are young. However, the mathematical correction for incomplete pup sightability comes from observations taken after births have ceased for the summer. Although an increase in late season observations would make the correction more precise (as desired), this would, in turn, make the correction more sensitive to assumptions about pup survival. Pup survival rates could certainly be added to the model developed here; however, there presently are not enough data to allow the pup survival rate to vary freely over space or time. Collecting additional information regarding pup mortality that would allow it to be modeled in a parsimonious manner will be very important if increased observations after the end of the pupping season are used to increase the precision of the reproductive rate estimates.

Even Rookery Effort

Increased effort at the non-Lowrie Island rookery sites would also improve the reproductive rate estimation. In an ideal situation where resight effort was high enough and consistent enough at all rookery sites throughout the summer, it could be assumed that if a cow is alive and has a pup, she will be seen at least once during the summer (either with a pup or alone). If this assumption were justified, it would alleviate the need restrict the inference to cows who survived the summer at hand. This in turn, would increase the sample size of cows in each summer's analysis, eliminate any bias that may have been introduced by discarding cows who did not live beyond the summer, and make the estimated reproductive rate more generalizable beyond the sample of branded cows.

Under the stated assumption, an unbiased reproductive rate estimate could be obtained in the following two step fashion. First, a between year CJS analysis would estimate the probability that a cow who is alive is seen at least once during the summer. Second, a within year analysis (based on the likelihood function developed here) would estimate the probability that a cow seen during the summer had a pup. The product of these two estimates would give the estimated annual reproductive rate, which would have been adjusted for cow sightability and survival within the likelihood function.

With an increase in effort at the Forrester Complex, alone, this same analysis could still be used, with the additional assumption that a female who previously pupped on FI is completely faithful to the complex. Such an assumption cannot be made for Lowrie Island, where current effort highest and most consistent throughout the summer. The mixing of sea lions throughout the complex and the restriction of observers to Lowrie Island leaves hanging the question of whether an unseen female simply has a pup elsewhere on the complex. However, with comprehensive coverage of FI throughout the summer, this improved reproductive rate estimation would be possible.

Continued Evaluation of Grouping Cows in the Analyses

Finally, it is worth noting that in the analyses I conducted, the cows seen only on rookeries in June and July of a given summer are split into two groups based on the number of per cow sightings. For the years analyzed, cows seen eight or more times were much more likely to have a pup than those seen one to seven times (Figure 3 on page 57). The different sighting rates in these two groups are due to a mixture of reasons, both biological and effort related. Analyses of future data will require a re-evaluation of this group demarcation, as it will likely change with changes in effort.

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APPENDICES

APPENDIX A

NUMERICAL TECHNIQUES

The Main Analyses

Sampling the Joint Posterior Distribution

The joint posterior distributions were sampled using the Metropolis-Hastings Algorithm in program MTG (Goodman 2009). This is a random walk algorithm where the residence time at each point is proportional to the posterior probability density at that point. At each step in the random walk, the posterior density is calculated, and compared to the posterior density at the previous step. If the density at the new point is greater than the density at the old point, the new point is accepted. If the density at the new point is less than that at the old point, the new point is accepted with probability equal to the ratio of the new density to the old density.

Assessing Posterior Convergence

Each analysis was conducted three times, using different seeds and starting parameter values. I used Monte Carlo sample sizes of ten million and thinned the results to retain a joint posterior distribution sample size of one million. I then discarded the first 5,000 of the 1,000,000 retained values in order to remove any burn in effect. Histograms using the 995,000 retained points revealed that results were invariant to different starting points and seeds.

To further assess convergence, I thinned the 995,000 points to 497,500 in order to obtain a sample size small enough for program R (R Development Core Team 2008), and used it to calculate Gelman-Rubin convergence statistics, also denoted by R. R is the the ratio of the pooled variance (from the three runs) to the within run variance. Convergence is achieved when the statistic is close to 1.0. For most applications a value < 1.1 is acceptable, although sometimes better convergence is required (Gelman et al. 2004). I considered values of < 1.01 to be acceptable. The R statistic is also known as the potential scale reduction factor, because if the simulations were to be run for more iterations, the Bayesian credibility interval could potentially shrink by this factor.

Obtaining Time Specific Birth Rates

The prior distribution on the annual birth rate was Uniform (0,1). In the analyses where the daily birth rate was allowed to vary by week without constraint, a broken stick algorithm was used to ensure that A_{t_b}, the probability a pup was born on any given day, was identically distributed for all days, t_b, and that $\sum_{t_b=1}^{N_P} A_{t_b}$ was equal to the prior annual birth rate obtained from that step of the random walk. Given that N_W equals the number of weeks during which pups can be born and W_{t_b} is the week in which the pup is born, the algorithm

1. generates $N_W - 1$ uniform random variates to break the (0,1) line,
2. sorts the uniform random variates in ascending order,
3. subtracts one break point from the next to get the probability of a cow giving birth in W_{t_b} given she gave birth that year, and
4. obtains the unconditional probability a cow gave birth during interval W_{t_b} by multiplying each conditional probability from Step 3 by the probability that the cow gave birth that year.

Each of the weekly rates is then divided by seven to obtain the daily rates, and the α_t parameters used in the likelihood function are back calculated using the definition of A_{t_b}.

When the priors required that 90% of births occur during the first four weeks of the summer and 10% occur during the next three weeks, the above method was used twice to get the time specific priors, once for rates summing to 90% of the annual birth rate, and once for rates summing to 10% of the annual birth rate.

Reproductive Rate Averaging

Reproductive Rate for Cows Known Alive and Seen During the Summer

The average reproductive rate for cows seen during a given summer and known to have survived that summer was calculated as a weighted average, where the weights were the number of cows in each group. For example, in 2002, Group 1 contained 13 cows; Group 2, 53; and Group 3, 11. Denote the value of the reproductive rate for each Group j at each retained point i in the joint posterior distribution as $R_{i,j}$. The weighted average was calculated as

$$\frac{\sum_{i=1}^{995000}\left(\frac{13}{77}R_{i,1} + \frac{53}{77}R_{i,2} + \frac{11}{77}R_{i,3}\right)}{995000}. \tag{21}$$

Reproductive Rate Including the Known Alive but Unseen Cows

I also calculated an average reproductive rate as a function of the reproductive rate for the alive but unseen cows. I allowed the rate for this group to range (by steps of 0.05) from zero up to the average reproductive rate estimated for the cows who were seen that summer and known to have survived it. Furthermore, the weighted average was computed within a Bayesian inference on the number of cows in each group. The idea behind this method is that the number of cows in each group is subject to sampling variation, and the inference accounts for this. For example, if the field crew had visited haulouts a day or a week later than they did, the number of cows recorded at haulouts that summer could have been different. Note that this inference does nothing to correct for bias; it simply adds sampling variation to the averaged reproductive rate.

The inference was conducted as follows. Let p_j denote the probability that a cow belongs to group j, let n_j denote the number of cows in group j, and let N be the sum of the n_j's. To use 2002 as an example, recall that Group 4 (the alive but unseen cows) contained 22 individuals, and the estimated mean reproductive rate for the cows seen during the summer was approximately 0.55. Therefore, I calculated twelve weighted averages, one for each of the following mean reproductive rates for the unseen cows: 0.00, 0.05, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, 0.45, 0.50, 0.55.

I obtained the number of individuals in each of the four groups, using a Multinomial (13, 53, 11, 22, p_1, p_2, p_3, p_4) likelihood function and a Dirichlet (p_1, p_2, p_3, p_4, 1, 1, 1, 1) prior distribution. I used this particular Dirichlet distribution because it assigns a Uniform (0,1) marginal prior distribution to each p_j. The resulting posterior distribution is a Dirichlet (n_1, n_2, n_3, n_4, 14, 54, 12, 23).

For each of the twelve reproductive rates specified for the alive but unseen cows, I calculated the distribution of the average reproductive rate by sampling 1000 draws from the posterior Dirichlet distribution, and for each draw I calculated the weighted average as:

$$\frac{\sum_{i=1}^{995000} \left(\frac{n_1}{N} R_{i,1} \; + \; \frac{n_2}{N} R_{i,2} \; + \; \frac{n_3}{N} R_{i,3} \; + \; \frac{n_4}{N} R_4 \right)}{995000}. \tag{22}$$

Stand Alone Regression of Pup Sightability versus Date

The stand alone regression used to examine the effect of the pup survival assumption on the estimation of pup sightability was conducted using weighted likelihood sampling in program SWL (Goodman 2009), with a sample size of ten million. In weighted likelihood sampling, each sample is drawn from the joint prior distribution, and the joint likelihood function is calculated at those prior values. This probability density constitutes the weight, which is then binned for the parameter values drawn from the joint prior.

Simulation of Population Growth Rate

I used the following specific steps to obtain a distribution on population growth rate, λ, using Equation 20. I cycled through each of the 995,000 retained values from the weighted reproductive rate average for cows known alive and seen during the summer of 2004 (page 117). To obtain fecundity (F, number of female pups born per mature cow) from reproductive rate (number of pups born per mature cow) I divided each of the 995,000 weighted averages by two. For each of these fecundities, I drew five independent random variates from Beta distributions having means and standard errors equal to the following CJS survival estimates (Pendleton et al. 2006).

1. S_1 = survival from age 0 - 1
2. S_2 = survival from age 1 - 2
3. S_3 = survival from age 2 - 3
4. S_4 = survival from age 3 - 4

5. S_5 = annual survival for subsequent ages

Using 5.9 as the average age of first birth (age of first pregnancy plus one, Pitcher and Calkins 1981), this left λ as the only free parameter in Eberhardt and Siniff's (1977) form of the Euler-Lotka Equation (Eqn. 20) which can be rewritten as

$$1 = \lambda^{-5.9} S_1 S_2 S_3 S_4 S_5^{1.9} F (1 - S_5 \lambda^{-1})^{-1} \tag{23}$$

I solved this equation for λ using Brent's iteration of bisection and inverse quadratic interpolation in program SIM (Goodman 2009). I repeated the above process five times, and obtained the distribution of λ from the resulting 4,975,000 calculations.

APPENDIX B

RESULTS OF OTHER STATISTICAL EXPLORATIONS

Pup Sightability as a Function of Factors Other than Date

Sample size prohibited me from using observation time (which was not always recorded) or effort type as additional covariates in the analyses; nevertheless, I was interested in exploring the relationship between these variables and the probability of seeing a pup given it was alive and its mother had been seen on that day. In order to conduct these explorations, I filtered the data set in the following manner. Observations were taken from cows who were seen at least three times during the summer, and seen with a pup in the first and last observations. No requirements were placed on any aspect of the intermediate observations. I used only the intermediate observations for the explorations, and therefore was assured that the sighting probability pertained to live pups.

Pup sightability versus the amount of observation time that produced the cow sighting showed high variability and no trend. This is consistent with observers who, when a cow is sighted, take the necessary time to determine whether or not she is with a pup. Explorations of the effect of effort type (e.g. boat versus land based observations) on pup sightability were inconclusive, due to small sample sizes.

Cow Sightability as a Function of Site

I spent an extensive amount of time trying to construct models that conditioned the cow sighting parameters on reproductive status and adjusted for the site specific effort. Collecting data to fit these models would be prohibitive; however, in case the lessons I learned from these attempts might be helpful to others, I will summarize them here.

To condition cow sightability both on the cow's reproductive status and the site specific effort, I separated the probability of seeing a cow into its two component rates, as follows. The probability of seeing a cow on a site is the product of the probability of her being present on site and the probability of seeing her given that she is present. If this product could be partitioned into the component probabilities, adjustments could be made to sightability based both on site specific effort and the cow's reproductive status. This is because the cow's presence on site depends on the her reproductive status, but not observer effort, and the probability of seeing her given that she is present depends on observer effort, but not the animal's reproductive status.

However, any model that requires the probability of seeing a cow to be split into its component probabilities would require the following. First, the very large majority of sites at which the cows could be located would have to be observed in the very large majority of intervals. Second, observers would need to be able to operate at the same spatial and temporal scale as the cows and pups. Specifically, the intervals would have to be simultaneously long enough that observers could cover the entire site, and short enough that cows could be assumed to move among sites only between intervals.