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Short-term Survival Rates of Branded Steller Sea Lion Pups

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Abstract

Survival rates of western Steller sea lion (*Eumetopias jubatus*) pups (total N = 621) were estimated during 2000, 2002, and 2004 at one rookery on Marmot Island and during 2003 and 2005 at two rookeries on Ugamak Island for up to 73 days following hot-iron branding. Estimated daily apparent survival rates increased and standard errors of the estimates decreased with increasing durations of in-season monitoring. An asymptotic apparent survival rate (ϕ_a) of 0.9995 d^{-1} was estimated from sightings of marked pups on 7-30 occasions between 1 and 73 days after branding, as well as in subsequent years through 2015. Sex and pup mass at the time of branding were not strong factors affecting survival. Extrapolations of ϕ beyond the in-season period yielded 12-week and 1-year survival rates of 0.960 and 0.837, respectively. During six of the seven in-season monitoring periods, numbers of dead pups counted by observers following branding were less than those estimated to have died based on our calculated survival rate. Two more dead pups were counted than predicted at Marmot in 2000, but the actual cause(s) of any of the pup deaths are not known.

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Introduction

Permanently marking individuals and recording observations of them through time is a standard method to estimate vital rates (i.e., survival, reproduction, and dispersal) of wild animal populations (Buckland 1982, Pradel 1996, White and Burnham 1999). For Steller sea lions (*Eumetopias jubatus*), hot-iron branding has been used since at least the 1980s to mark ~1-month-old pups to estimate survival (Merrick et al. 1996; Pendleton et al. 2006; Hastings et al. 2009, 2011; Fritz et al. 2014; Maniscalco 2014; Altukhov et al. 2015; Wright et al. 2017). Steller sea lions give birth and mate during the summer at rookeries located across thousands of kilometers of the North Pacific Ocean coast and offshore islands from California north to Alaska and west to Russia. Adult females begin arriving at rookeries in late May and usually give birth shortly after arrival. Mean pup birth dates range from 4 to 21 June (Pitcher and Calkins 1981, Pitcher et al. 2001; Kuhn et al. 2017b). Adult females generally remain ashore to nurse their new-born pups and mate during a 10-14 day post-partum period.

There are two distinct population segments (or stocks) of Steller sea lions in the North Pacific divided approximately at 144°W longitude (Bickham et al. 1996, Loughlin 1997). The western stock experienced a population decline beginning in the 1970s and extending through the 1990s, whereas the eastern stock was at low levels throughout much of the early 20th century and increased at ~3% per year between the late 1970s and the early 2000s (Pitcher et al. 2007; NMFS 2013). The species was listed as threatened range-wide under the U.S. Endangered Species Act (ESA) in 1990 (55 FR 12645), and the status of the western stock was changed to endangered in 1997 once the National

Marine Fisheries Service (NMFS) recognized the two stocks (62 FR 30772). The eastern stock was removed from ESA protection in 2013 following a determination that it had reached its recovery goals (NMFS 2008, 2013; 78 FR 66139).

The Alaska Fisheries Science Center's Marine Mammal Laboratory (MML) renewed its Steller sea lion vital rates project in Alaska during 2000 at rookeries within the range of the western stock to investigate the stock's continuing decline in abundance (Fritz et al. 2014). At the time, little was known about the specific effects of branding Steller sea lion pups or the incidental effects on adult and juvenile animals present at the rookery. The MML branded 751 Steller sea lion pups in June-July 1987 and 1988 at Marmot Island, but sighting effort did not commence until November 1987 for the 1987 cohort and not until April 1989 for the 1988 cohort. MML and the Alaska Department of Fish and Game began studies of the Steller sea lion rookery on Marmot Island in 1979, stationing observers at a remote field camp to monitor pup production, count and assess behavior of sea lions by age and sex class, and to record sightings of marked animals (Chumbley et al. 1997). Occasional field camps had been deployed on Ugamak Island to conduct similar studies in the 1980s (Merrick et al. 1988). Since 2000 at Marmot and 2002 at Ugamak, field camp scientists collected sightings of recently branded pups and data on behavior and abundance to monitor and assess the impacts of the hot-branding program for approximately 1 month (Chumbley et al. 1997; Wilson et al. 2012). Here, we report estimates of short-term survival (up to 73 days) of pups branded in 2000 and 2002-2005 at Marmot and Ugamak islands based on sightings made by both observers at remote field camps and at subsequent times and locations by others.

Methods

Marking

Steller sea lion pups on Beach 4 of Marmot Island¹ and on South and North rookeries of Ugamak Island were marked at an age of approximately 1 month in late June or early July (Table 1; Fig. 1). Pups were marked by hot-branding a letter corresponding to the natal rookery ('T' on Marmot, and 'A' on Ugamak) followed by a unique 1- to 3-digit number starting on the left shoulder and extending down the left side (Fig. 2). Groups of pups were herded together after adult sea lions were driven to other parts of the rookery beach or into the water. All pups were weighed, measured (length and axillary girth), and sedated using isoflurane gas anesthesia prior to branding. The total time that an individual was handled (measuring and branding) ranged from 5 to 20 minutes. The duration that individual pups were herded into a group prior to being measured and branded ranged from 1 minute to 3 hours. After branding, pups were held in a series of 'recovery' areas away from the work stations until they were awake and to prevent them from entering the water; time spent in each recovery area was variable. The total duration that the rookery was disturbed by human presence on land ranged from 6 to 10 hours. A maximum of half of the pups present on the beach were branded and ranged from 75 to 107 (Table 1). Pups were randomly selected in that all pups within a herded group were branded except those lighter than 20 kg or with any remnant of an umbilicus still attached. Details of the branding procedure can be found in Merrick et al. (1996) and a summary of the effects of the research disturbance are described in Wilson et al. (2012).

¹ Beach 7 on Marmot Island is also a rookery beach, but pups were not branded there due largely to difficulties in observing animals on the beach from the high cliff-side location.

Observations of Marked Animals and Counts of Pups

Observation effort to identify branded pups began the day after branding on Marmot and Ugamak islands. Observers based at field camps on the islands recorded the brand (i.e., letter and number) and date on each occasion that a branded pup was observed, and whether it was alive or dead. Observations were primarily made from land-based overlooks several hundred feet above the rookeries; sea lions were unaware of observer presence. During the breeding season (before and after branding), observers also counted all sea lions on the beach each day (weather permitting), and assigned them to age-sex classes; live and dead pups were tallied separately. Details regarding information collected by field camp observers are available in Chumbley et al. (1997) and Wilson et al. (2012). At Marmot, breeding season sighting effort occurred primarily at Beach 4 (Fig. 1), but also at the other rookery (Beach 7) and haul-out beaches on the island as weather conditions permitted. At Ugamak, South rookery overlook is located at the top of a cliff that is ~250 m lower than that overlooking North rookery. Consequently, conditions permitted far more opportunities to observe sea lions on South rookery than North (Table 2). Effort by field camp observers to record sightings of branded pups lasted for 21-27 days following branding at Marmot in 2000, 2002 and 2004, and for 31-35 days following branding at Ugamak in 2003 and 2005. There was additional in-season effort at Ugamak in late August and early September 2003 (between 68 and 73 days after branding) by observers who conducted sighting effort from skiffs offshore or from land-based observation points on the rookery.

Observation effort in years following branding (through 2015) consisted of 1) vessel-based small boat surveys for approximately 1-4 weeks between May and August

in the eastern Aleutian Islands and Gulf of Alaska; 2) land-based observations on Marmot and Ugamak islands from late May through July each year; 3) land-based opportunistic observations by residents of the Pribilof Islands and scientists conducting research on northern fur seals (*Callorhinus ursinus*) and by scientists studying Pacific walrus (*Odobenus rosmarus*) based at a field camp on Round Island; 4) high-resolution aerial images taken during abundance surveys (see Fritz et al. 2016); and 5) photographs or video taken by cameras mounted above terrestrial Steller sea lion haul-out and rookery sites by the Alaska SeaLife Center (ASLC 2005; see additional description of effort in Fritz et al. 2014). Animals branded during this study were also observed in subsequent years by collaborating scientists in southeast Alaska. Observations in subsequent years were included in this analysis to improve estimates of in-season survival; only subsequent year observations from May through August were included in the analysis.

To be included in the MML sighting database, an individual branded animal must be positively and unambiguously identified. In the field, observers recorded each brand character and a code indicating the quality of the identification and of the character/digit itself on the animal:

- ‘+’ Certain of digit: brand is clear, without distortion or hair coverage, and is very good to near perfect;
- ‘0’ Certain of digit: some distortion or hair coverage, may be under- or over-branded and is not perfect;
- ‘-’ Uncertain of digit: poor brand; has hair or is distorted, blurred or smeared;
- ‘\$’ Uncertain of digit: poor view due to bad lighting, far distance, angle, glare, or blocked by a rock or another animal.

A sighting of a marked animal was confirmed if each brand character or digit was given either a '+' or '0' quality code. In addition, most marked animals were observed twice in a single effort event to verify the initial sighting; if more than one observer was present, then sightings were individually recorded prior to discussion and verification by the group. In the majority of cases, field identifications of marked animals were supported by high-resolution digital photographs (Fig. 2).

Analysis and Estimation of Survival Rates

Cormack-Jolly-Seber (CJS) open population mark-recapture models were used to estimate apparent daily survival (ϕ) and sighting (recapture) probability (p). The model estimates apparent daily survival (hereafter referred to only as 'daily survival' for conciseness) because death and permanent emigration from the study area (in which the sea lion population was surveyed for marked animals) are conflated. All analyses were conducted using the program MARK 8.0 (White and Burnham 1999). For in-season sightings, the time interval in days between effort occasions (t) was used in the analysis (Table 2). Capture histories consisted of a series of 1's (observed) and 0's (not observed) for the day of branding (observed) and each in-season effort day thereafter. For sightings in subsequent years through 2015, a single recapture was used to indicate whether it had been observed in any one year after the year in which it was branded. The subsequent year sighting was assigned a date of 1 July and the last time interval was the number of days between the last in-season effort day and 1 July of the following year. Because of differences in the number of in-season sighting days and the intervals between them, ϕ and p for each marked cohort were estimated separately in MARK. Average ϕ was

estimated for each marked cohort from the series of in-season observations, with mass (at the time of branding) included as a covariate. Sighting probability was allowed to vary for all sighting occasions, but initial runs indicated that sex was not a significant factor for p . Four models were run for each marked cohort using all combinations of sex and mass (co-variate on in-season ϕ), $p(t)$, and an identity design matrix for each model run. Models were ranked (1 through 4) based on AICc values as well as by AICc weights from MARK, and mean rank and mean AICc weight were calculated for each model type across the seven marked cohorts. The model used for ϕ had the lowest mean rank and the highest AICc weight across all cohorts.

Results

In-season p of marked pups varied considerably between days, cohorts, and islands (Figs. 3 and 4). At Marmot, in-season p was somewhat related to the number of live pups (LP) on Beach 4, which is the location where the majority of the in-season sighting effort was conducted. Pups begin to leave Beach 4 with their mothers in mid-July each year, often moving to other beaches on Marmot, particularly Beach 7 (Fig. 1; Chumbley et al. 1997, Wilson et al. 2012, Kuhn et al. 2017a). Deviations from the general p and LP relationship on Beach 4 were due to inclement weather and additional sighting effort at Beach 7. For instance, in 2000, poor visibility caused by fog and rain at Beach 4 on 5 and 9 July likely caused the drops in p (relative to LP on Beach 4) estimated for these days (Fig. 3A). On the other hand, additional sighting effort at Beach 7 on 8, 9, 16, and 17 July 2002 likely led to the higher than expected estimates of p for

these days (relative to LP on Beach 4; Fig. 3B). At both Ugamak rookeries, p was not as consistently related to LP as it was at Marmot Beach 4.

Male pups were 3.7-9.0 kg heavier than female pups (on average) at the time of branding (Table 1). For the two cohorts that had differences in mean weights of < 5.0 kg between females and males (Marmot 2004 and Ugamak North 2003), neither sex nor pup mass were significant co-variates for survival in the top-ranked models (Table 3A). For the five cohorts where male pups were ≥ 5 kg heavier than female pups, sex and pup mass were significant co-variates in three of the top-ranked models. However, the $\phi(\cdot)$ model had the lowest mean rank and the highest AICc mean weight (Table 3B) across all cohorts, suggesting that both mass and sex were weak factors affecting in-season ϕ . Consequently, the $\phi(\cdot)$, $p(t)$ model results were used for estimates of in-season ϕ for each cohort. Our results, however, did not reflect absolute differences in mass between cohorts and are relative only to individual cohorts.

Average in-season ϕ for the seven cohorts of branded pups at Marmot and Ugamak islands ranged between 0.9914 and 1.0000, with standard errors between $4.43\text{E-}07$ and 0.0029 (Table 4). In-season survival increased with duration of in-season monitoring (m), whereas standard errors generally decreased (Fig. 5). In-season survival was unrelated to the number of in-season effort occasions ($r^2 = 0.09$). Of the 75 pups branded in 2003 at Ugamak South, 74 were observed at least once during in-season monitoring, and the one that was not seen then, was observed during at least one subsequent year. As such, ϕ was very close to the upper bound of 1 and was difficult to estimate in MARK (Table 4). Estimates of ϕ increased non-linearly with increasing m

through approximately 35 days, then increased only slightly through 73 days. We fit a 3-parameter exponential model of the form:

$$\varphi = \varphi_{\infty} * (1 - e^{(-K*(m-m_0))})$$

to the seven pairs of φ and m data, where K and m_0 are slope and intercept constants, respectively, and φ_{∞} is an estimate of the asymptotic φ . From this model, we estimated $\varphi_{\infty} = 0.9995$ (95% confidence interval of 0.9989-1.0000), which is used as the average in-season daily φ (φ_a) for the seven cohorts of branded sea lion pups. Extrapolation of φ_a to 84 days (see Hastings et al. 2009) and 365 days yields cumulative survival estimates for Steller sea lion pups branded at Marmot and Ugamak islands of 0.960 and 0.837, respectively.

The observed and estimated cumulative number of dead pups before and after branding for Marmot Beach 4 in 2000, 2002 and 2004, and the sum of North and South beaches on Ugamak Island in 2003 and 2005 are shown in Figure 6. To estimate pup mortality after branding at each rookery, the maximum count of live and dead pups obtained by field camp observers each year (Table 5) was decayed by $1 - \varphi_a = 0.0005$ per day. The observed numbers of dead pups (Fig. 6) as well as the observed rates of pup mortality (Table 5) following branding were less than or similar to the estimates in all cases except Marmot 2000. In addition, Marmot 2000 was the only cohort for which the rate of observed pup mortality after branding was greater than before, although there were limited data obtained before branding which resulted in wide confidence bounds (Table 5). Marmot 2004 was the only cohort for which the estimated rate of pup mortality after branding (0.1 pups per day based on sightings of marked pups) exceeded the observed rate prior to branding (based on counts of dead pups; 0.05 pups per day given

the number of pups present; Table 5 and Fig. 6). This is likely due to the low number of dead pups observed before branding at Marmot in 2004 ($N = 2$), because the estimated pup survival rate after branding was high. Observed pup deaths could be lower than those estimated from mark-recapture because 1) counts of dead pups at Marmot Island only included Beach 4, and by 10-15 days after branding, adult females and their dependent pups began to move from Beach 4 to other haulouts on Marmot Island or elsewhere (Chumbley et al. 1997, Wilson et al. 2012, Kuhn et al. 2017a); and 2) poor ‘sightability’ of dead pups on the beach due to habitat complexity (e.g., dead pup hidden under a rock) or their removal from the beach (e.g., by storms, carried away or eaten by scavengers).

Discussion

Given that p varied considerably between in-season sighting days, it is not unexpected that estimates of ϕ would become more precise and increase as the duration of in-season monitoring increased. Locations where observers scan the rookeries at Marmot and Ugamak islands are located hundreds of meters above the beaches, with parts of them obscured from view, which reduces the likelihood of observing every marked pup present on the beach each day. In addition, weather (e.g., fog, rain, wind) greatly affects sighting probability and large rocks and other sea lions on the beach hide pups from view. We found that ϕ increased by 0.0005 and standard error decreased by 5% per day as m increased from 21 to 35 days. As m increased from 35 to 73 days, there were no significant differences in either ϕ or standard error, indicating that in-season monitoring durations of approximately 1 month are likely to be sufficient to accurately

estimate short-term post-branding survival rates. Differences in sighting probability between Marmot and Ugamak islands could have contributed to the observed relationship between ϕ and m , particularly given that the three shortest m periods were from Marmot. In general, in-season p -values were lowest at Marmot, highest at Ugamak South, and intermediate at Ugamak North. However, Fritz et al. (2014) found no differences in survival at age 1 between Marmot and Ugamak, which supports the proposed relationship between ϕ and m (Fig. 5).

Hastings et al. (2009) found a complex interaction between week after branding, sex, mass, capture area, and survival that resulted in a positive relationship between mass and in-season survival for male pups, but a negative relationship for female pups. Whereas the result for females was unexpected, it was apparently supported by recaptures up to age 7 years. We did not find a consistent relationship between sex, mass, and survival in our study, and the relationship appeared to be weak. Our best survival model that considered neither mass nor sex had only 2% more AICc weight than the second best model that considered both. In a longer study, Maniscalco (2014) found that birth mass was positively related to survival for juveniles weaned at age 1 year, but was unrelated to survival for those juveniles that suckled to age 2 or 3 years.

Hastings et al. (2009) provided the only other published survival estimates for Steller sea lion pups (84-day survival probability of 0.87), which was estimated for eastern Steller sea lions at Lowrie Island (part of the Forrester Island complex) in southeast Alaska (Phillips et al. 2009). Their estimate was also based on in-season (summers of 2001 and 2002) and subsequent year sightings of branded pups, and is based on pups that had a similar age interval: ~23-107 days for Hastings et al. (2009) and

~15-89 days in our study. Our 84-day survival estimate of 0.96 was obtained in similar years (2000-2005) for branded western Steller sea lion pups. It is not clear why pup mortality is greater for eastern than western pups. Maniscalco et al. (2008) and Maniscalco (2014) reviewed the issue and concluded that density-independent factors were generally more important than density-dependent factors at the small Chiswell Island (western) rookery that they studied. Density-independent factors include rookery topography and high waves from storms that wash pups off the beach either to be preyed upon or drowned at sea, while density-dependent factors include trampling (trauma) and disease. Rookery density has been cited as a cause of high pup mortality in other otariids (e.g., Antarctic fur seals *Arctocephalus gazella*; Doidge et al. 1984; Reid and Forcada 2005) and could be a contributing factor at large eastern stock rookeries. The Forrester Island complex is the largest rookery in southeast Alaska and currently the second largest Steller sea lion rookery in the world (behind Triangle Island in British Columbia, Canada; S. Majewski, Fisheries and Oceans Canada, pers. comm.). Pup counts at the Forrester Island rookery complex averaged 3,104 in 2001 and 2002, and this was similar to the mean of all pup counts between 1990 and 2017 for the complex (mean $N = 3,213$; Fritz et al. 2015; Sweeney et al. 2017). This suggests that the rookery at the Forrester Island complex was close to ‘carrying capacity’ with respect to pup production in 2001-2002, a conclusion supported by the lower survival rate of yearlings born at this rookery relative to other, newer rookeries in northern southeast Alaska (Hastings et al. 2011). By contrast, pup counts at all rookery beaches on Marmot Island during 2000 through 2004 (mean $N = 499$) and Ugamak Island during 2003 through 2005 (mean $N = 665$) were 91% and 59% lower, respectively, than counts in 1984 and 1985 (Fritz

et al. 2015), and were likely far below ‘carrying capacity’. The high survival rates of western pups reported here indicate that both density-dependent and independent mortality factors had very low impact at Marmot and Ugamak islands during the study period (2000-2005).

The pup survival estimates reported by Hastings et al. (2009) and in this study are for pups that were marked at ~1 month of age. As such, early pup mortality is not reflected in either survival rate. For six of the seven cohorts we analyzed, pup mortality rates (as measured by field camp observations of dead pups) were greater before branding than after, a trend that is also evident by comparing survival rates computed from birth with those that commenced weeks later (both Hastings et al. (2009) and the present study). Early pup mortality must be accounted for when attempting to estimate natality from time series of counts of ~1-month-old pups and survival estimates based on sightings of marked animals (see also Holmes and York 2003; Holmes et al. 2007).

Our 1-year extrapolation (both sexes and both islands combined) is within the range of first-year male and female survival estimates (0.779-0.873) reported by Fritz et al. (2014) for Steller sea lion pups branded at rookeries in the eastern Aleutian Islands (Ugamak Island) and central Gulf of Alaska (Marmot and Sugarloaf islands). This suggests that mortality rates of 1- to 3-month-old pups are similar to rates experienced during the remainder of their first year of life which, for Steller sea lions, is spent under close maternal supervision (Pitcher and Calkins 1981, Maniscalco 2014).

We estimated short-term survival of branded Steller sea lion pups only, and we have no complementary survival estimates for control pups that were not subjected to handling and branding (Scordino 2006, Hastings et al. 2009). However, the high rates of

survival of branded pups that we observed strongly suggests that there was little, if any, mortality associated with the handling and branding of sea lion pups or the disturbance caused by the branding process during at least six of the seven occasions discussed here. The one exception may be at Marmot Beach 4 in 2000, when the rate of observed pup mortality was greater after branding than before, and the observed number of dead pups exceeded the estimate by two pups at the end of in-season monitoring.

Wilson et al. (2012) qualitatively ranked the magnitude of research disturbance on each of the cohorts based on the duration of researcher presence on the beach and whether any adult and juvenile sea lions remained on the beach during branding. For Marmot Beach 4, the highest research disturbance occurred in 2000, the lowest in 2004, and intermediate in 2002. In 2000, all adult and juvenile animals were removed from Beach 4 during branding operations, which lasted 9 hours (the longest of any of the cohorts analyzed here). This resulted in significantly fewer adult territorial males with females during the post-disturbance period (Wilson et al. 2012). Estimated ϕ 's for Marmot 2002 and 2004 were not significantly different from each other, but were greater than for Marmot 2000. Wilson et al. (2012) qualitatively ranked the research disturbance in 2005 as greater than that in 2003 at Ugamak Island yet there was no significant difference in estimated ϕ between the four cohorts. If the Marmot 2000 estimate of ϕ is dropped, ϕ_{∞} decreases to 0.9992, which is within the 95% confidence bounds of ϕ_{∞} when all data are included.

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Table 1. -- Number (N) and mass (mean, minimum (min), and maximum (max) in kg) of Steller sea lion pups permanently and individually marked by sex, rookery and year between 2000 and 2005 at Marmot and Ugamak islands used in the analysis of short-term survival.

Rookery	Year	Females				Males			
		Mean	Min	Max	N	Mean	Min	Max	N
Marmot	2000	28.1	16.4	36.8	49	33.3	23.4	42.0	58
Marmot	2002	29.2	21.0	37.0	50	38.2	25.6	46.0	39
Marmot	2004	29.8	20.4	41.0	37	34.4	22.6	44.0	38
Ugamak South	2003	28.7	19.8	43.2	32	34.3	25.2	44.2	43
Ugamak South	2005	28.1	20.0	38.6	41	34.4	26.0	49.4	59
Ugamak North	2003	28.9	18.0	44.2	38	32.6	24.6	44.0	37
Ugamak North	2005	27.3	21.2	36.4	50	32.3	25.0	41.6	50

Table 2. -- Dates of in-season sighting effort for each cohort of Steller sea lion pups branded at Marmot and Ugamak island rookeries in 2000 and 2002 through 2005. D = number of days after branding.

Rookery Year	Marmot 2000		Marmot 2002		Ugamak South 2003		Ugamak North 2003		Marmot 2004		Ugamak South 2005		Ugamak North 2005	
	Date	D	Date	D	Date	D	Date	D	Date	D	Date	D	Date	D
Branding date	2-Jul		4-Jul		24-Jun		25-Jun		4-Jul		24-Jun		23-Jun	
	3-Jul	1	5-Jul	1	25-Jun	1	26-Jun	1	5-Jul	1	25-Jun	1	25-Jun	2
	5-Jul	3	6-Jul	2	26-Jun	2	5-Jul	10	7-Jul	3	26-Jun	2	27-Jun	4
	7-Jul	5	7-Jul	3	27-Jun	3	8-Jul	13	8-Jul	4	27-Jun	3	1-Jul	8
	8-Jul	6	8-Jul	4	28-Jun	4	26-Jul	31	9-Jul	5	28-Jun	4	5-Jul	12
	9-Jul	7	9-Jul	5	30-Jun	6	1-Sep	68	10-Jul	6	29-Jun	5	6-Jul	13
	10-Jul	8	10-Jul	6	1-Jul	7	4-Sep	71	11-Jul	7	30-Jun	6	7-Jul	14
	11-Jul	9	11-Jul	7	2-Jul	8	6-Sep	73	12-Jul	8	1-Jul	7	8-Jul	15
	13-Jul	11	12-Jul	8	3-Jul	9			14-Jul	10	2-Jul	8	13-Jul	20
	17-Jul	15	13-Jul	9	4-Jul	10			16-Jul	12	3-Jul	9	14-Jul	21
	18-Jul	16	15-Jul	11	5-Jul	11			18-Jul	14	5-Jul	11	15-Jul	22
	19-Jul	17	16-Jul	12	6-Jul	12			19-Jul	15	6-Jul	12	16-Jul	23
	20-Jul	18	17-Jul	13	7-Jul	13			20-Jul	16	7-Jul	13	18-Jul	25
	21-Jul	19	20-Jul	16	8-Jul	14			23-Jul	19	8-Jul	14	21-Jul	28
	23-Jul	21	24-Jul	20	9-Jul	15			24-Jul	20	9-Jul	15	22-Jul	29
			25-Jul	21	11-Jul	17			25-Jul	21	12-Jul	18	26-Jul	33
			26-Jul	22	12-Jul	18			26-Jul	22	13-Jul	19		
			27-Jul	23	14-Jul	20			27-Jul	23	14-Jul	20		
			31-Jul	27	17-Jul	23			28-Jul	24	15-Jul	21		
					18-Jul	24					16-Jul	22		
					19-Jul	25					18-Jul	24		
					20-Jul	26					19-Jul	25		
					21-Jul	27					20-Jul	26		
					22-Jul	28					21-Jul	27		
					26-Jul	32					22-Jul	28		
					1-Sep	69					23-Jul	29		
					4-Sep	72					24-Jul	30		
											25-Jul	31		
											26-Jul	32		
											28-Jul	34		
											29-Jul	35		

Table 3. -- Results of MARK model runs to estimate apparent daily short-term survival of Steller sea lion pup cohorts branded at Marmot and Ugamak island rookeries.

A. Results for each cohort. # Par = number of parameters. Dev = Deviance. B. Mean rank and AICc weight of each model.

A. Rookery (Year)	Model	Rank	AICc	Delta AICc	AICc weights	Model likelihood	# Par	Dev
Marmot (2000)	$\varphi(\text{mass}), p(t)$	1	1474.77		0.45	1.00	17	1439.70
	$\varphi(\text{sex}), p(t)$	2	1476.10	1.33	0.23	0.51	18	1438.90
	$\varphi(\cdot), p(t)$	3	1476.18	1.41	0.22	0.49	16	1443.23
	$\varphi(\text{mass*sex}), p(t)$	4	1477.88	3.10	0.10	0.21	20	1436.40
Marmot (2002)	$\varphi(\text{mass*sex}), p(t)$	1	1775.27		0.60	1.00	22	1729.83
	$\varphi(\text{sex}), p(t)$	2	1777.30	2.03	0.22	0.36	21	1733.99
	$\varphi(\text{mass}), p(t)$	3	1778.43	3.16	0.12	0.21	21	1735.12
	$\varphi(\cdot), p(t)$	4	1779.81	4.54	0.06	0.10	20	1738.62
Marmot (2004)	$\varphi(\cdot), p(t)$	1	1416.87		0.45	1.00	20	1375.34
	$\varphi(\text{mass}), p(t)$	2	1417.37	0.50	0.35	0.78	21	1373.68
	$\varphi(\text{mass*sex}), p(t)$	3	1419.26	2.39	0.14	0.30	23	1371.24
	$\varphi(\text{sex}), p(t)$	4	1420.83	3.96	0.06	0.14	22	1374.98
Ugamak South (2003)	$\varphi(\text{mass}), p(t)$	1	2354.84		0.41	1.00	27	2299.47
	$\varphi(\cdot), p(t)$	1	2354.84		0.41	1.00	27	2299.47
	$\varphi(\text{mass*sex}), p(t)$	3	2357.42	2.58	0.11	0.28	30	2295.73
	$\varphi(\text{sex}), p(t)$	4	2358.39	3.55	0.07	0.17	29	2298.81
Ugamak North (2003)	$\varphi(\cdot), p(t)$	1	704.91		0.51	1.00	9	686.22
	$\varphi(\text{mass}), p(t)$	2	706.41	1.50	0.24	0.47	10	685.57
	$\varphi(\text{sex}), p(t)$	3	706.70	1.80	0.21	0.41	11	683.69
	$\varphi(\text{mass*sex}), p(t)$	4	709.50	4.59	0.05	0.10	13	682.10
Ugamak South (2005)	$\varphi(\text{mass*sex}), p(t)$	1	3661.54		0.35	1.00	36	3588.18
	$\varphi(\text{sex}), p(t)$	2	3661.96	0.42	0.29	0.81	34	3592.74
	$\varphi(\cdot), p(t)$	3	3662.42	0.88	0.23	0.64	32	3597.34
	$\varphi(\text{mass}), p(t)$	4	3663.51	1.97	0.13	0.37	33	3596.36
Ugamak North (2005)	$\varphi(\text{mass*sex}), p(t)$	1	1963.06		0.61	1.00	21	1920.14
	$\varphi(\cdot), p(t)$	2	1965.33	2.27	0.20	0.32	17	1930.72
	$\varphi(\text{mass}), p(t)$	3	1965.73	2.68	0.16	0.26	18	1929.06
	$\varphi(\text{sex}), p(t)$	4	1968.91	5.85	0.03	0.05	19	1930.15

Table 3. -- Cont.

B.

Model	Mean Rank	Mean AICc Weight
$\varphi(\cdot), p(t)$	2.14	0.30
$\varphi(\text{mass}*\text{sex}), p(t)$	2.43	0.28
$\varphi(\text{mass}), p(t)$	2.29	0.27
$\varphi(\text{sex}), p(t)$	3.00	0.16

Table 4. -- Mean daily apparent in-season survival (ϕ , standard error (SE), and lower/upper bounds of 95% confidence interval) of Steller sea lion pup cohorts branded at Marmot and Ugamak island rookeries, listed in order of duration of in-season monitoring (m in days). Estimates of 84-day cumulative survival (84-day S) are provided for comparison with data reported in Hastings et al. (2009).

Rookery	Year	m	Daily ϕ				84-d S
			Mean	SE	Lower	Upper	
Marmot	2000	21	0.9914	0.0029	0.9833	0.9956	0.4846
Marmot	2004	24	0.9974	0.0017	0.9907	0.9993	0.8046
Marmot	2002	27	0.9977	0.0019	0.9886	0.9995	0.8218
Ugamak North	2005	33	0.9989	0.0007	0.9965	0.9996	0.9097
Ugamak South	2005	35	0.9988	0.0007	0.9961	0.9996	0.9049
Ugamak South	2003	72	1.0000	<0.0001	1.0000	1.0000	1.0000
Ugamak North	2003	73	0.9989	0.0005	0.9971	0.9996	0.9132
Asymptote			0.9995		0.9989	1.0000	0.9599

Table 5. -- Observed rate of pup mortality (dead pups per day per 100 live and dead pups counted; 95% confidence interval) before and after branding. Max Pup = maximum count of live and dead pups on Beach 4 at Marmot Island, and for North and South rookeries combined on Ugamak Island each year.

Rookery	Year	Max pup	Before			After		
			Rate	-95% CI	+95% CI	Rate	-95% CI	+95% CI
Marmot	2000	240	0.05	-0.01	0.11	0.09	0.07	0.11
	2002	180	0.08	0.07	0.09	0.03	0.02	0.04
	2004	214	0.02	0.02	0.03	0.00	0.00	0.00
Ugamak	2003	641	0.14	0.07	0.22	0.02	0.01	0.03
	2005	724	0.08	0.05	0.12	0.02	0.01	0.04

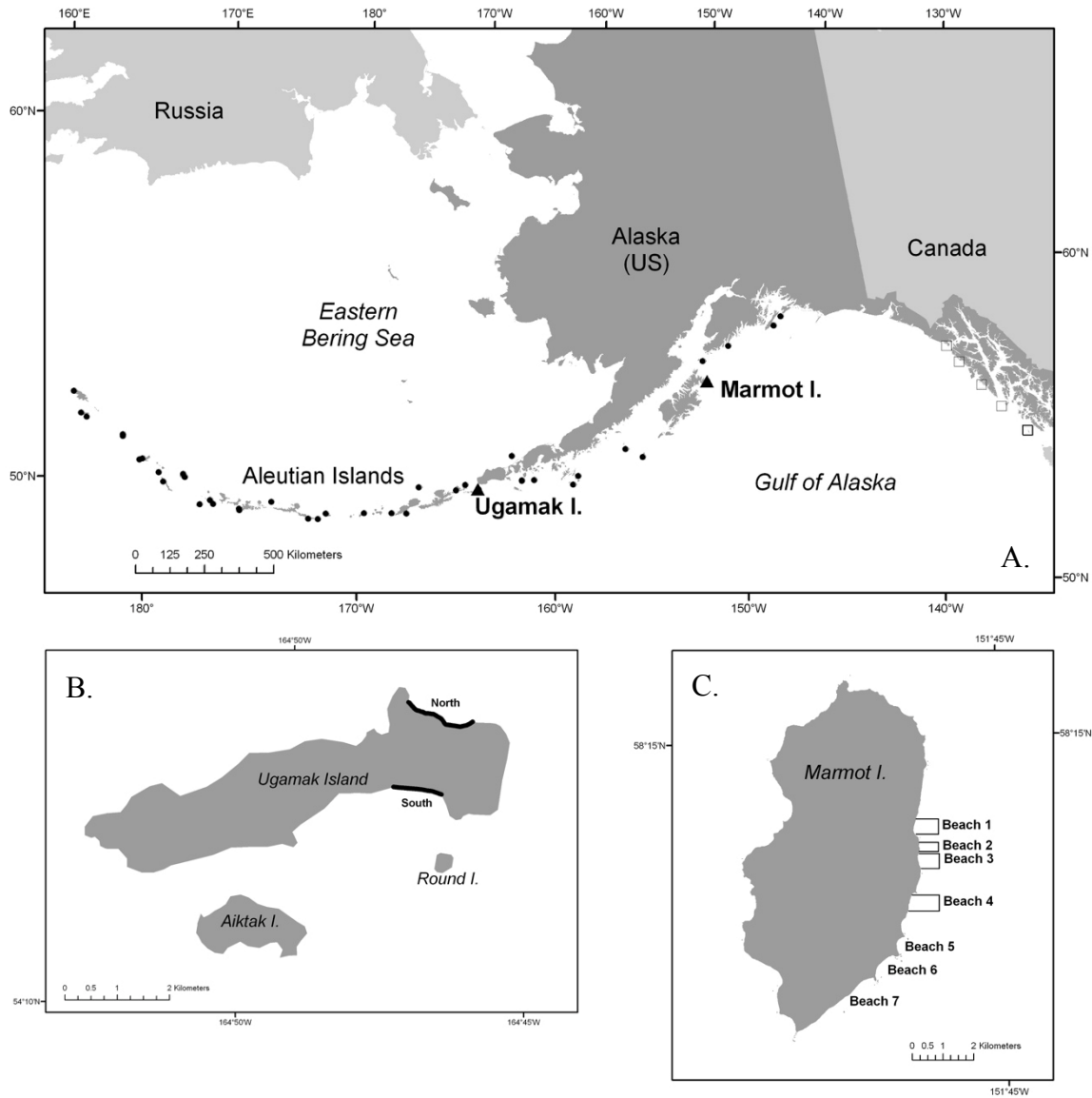


Figure 1. -- A. Map of the northeastern Pacific Ocean and coastal Alaska showing location of Marmot and Ugamak islands (\blacktriangle), other Steller sea lion rookeries in the western stock (\bullet), and rookeries in southeast Alaska in the eastern stock (\square). B and C. Details of Ugamak (B) and Marmot (C) islands showing locations of the Steller sea lion rookery and haul-out beaches.

A.



B.



C.

D.

Figure 2. -- Photographs of a branded male Steller sea lion pup (A189) moments after branding on 24 June 2003 on Ugamak South (A), on 27 June 2003 on Ugamak South (B), and on 4 September 2003 on Ugamak North (C). A189 was also observed at 1 year of age on 11 June 2004 on Ugamak South (D).

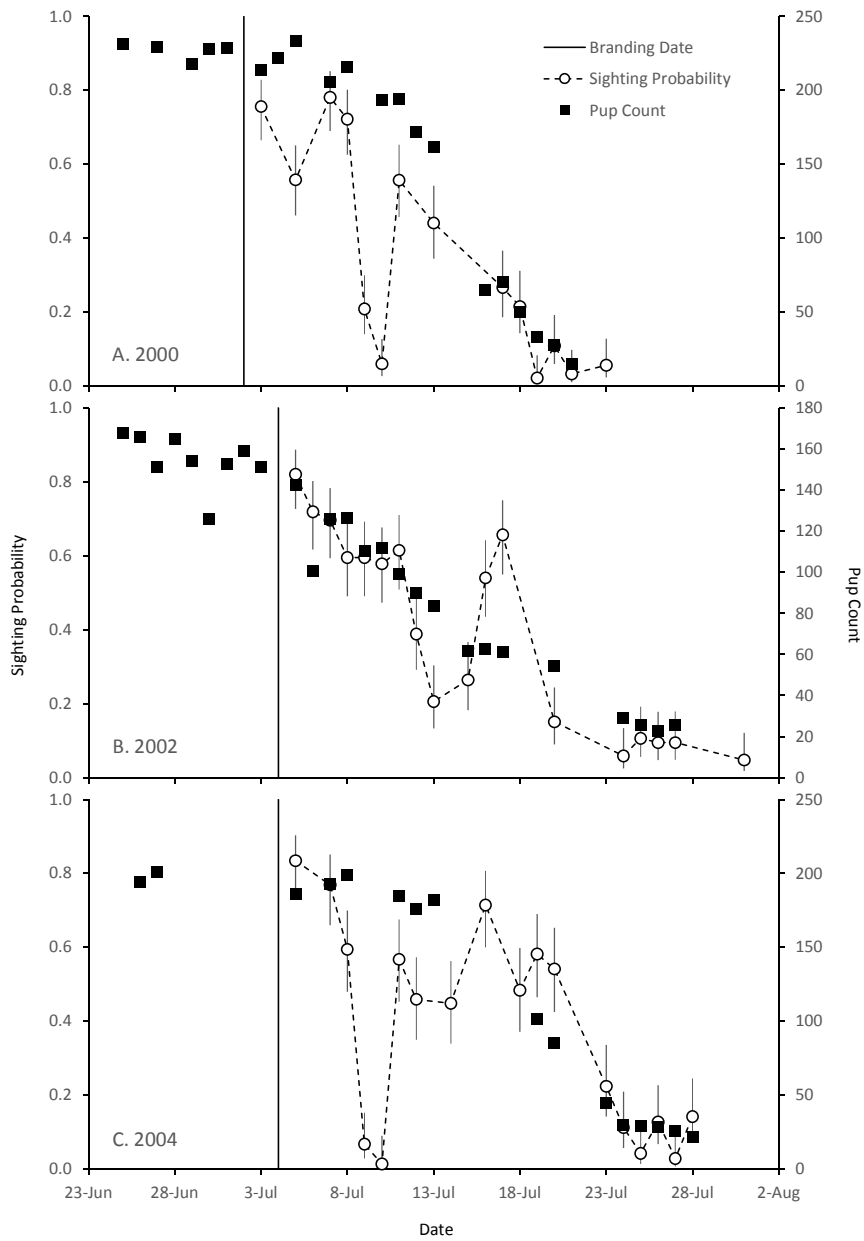


Figure 3. -- Estimated sighting probabilities ($p \pm 95\%$ confidence interval) of marked Steller sea lion pups in June and July each year from the 2000 (A), 2002 (B), and 2004 (C) cohorts on Marmot Island, along with counts of all live pups on Marmot Island Beach 4. Legend in A applies to all. Sighting probabilities are from the $\varphi(\cdot), p(t)$ model for each cohort.

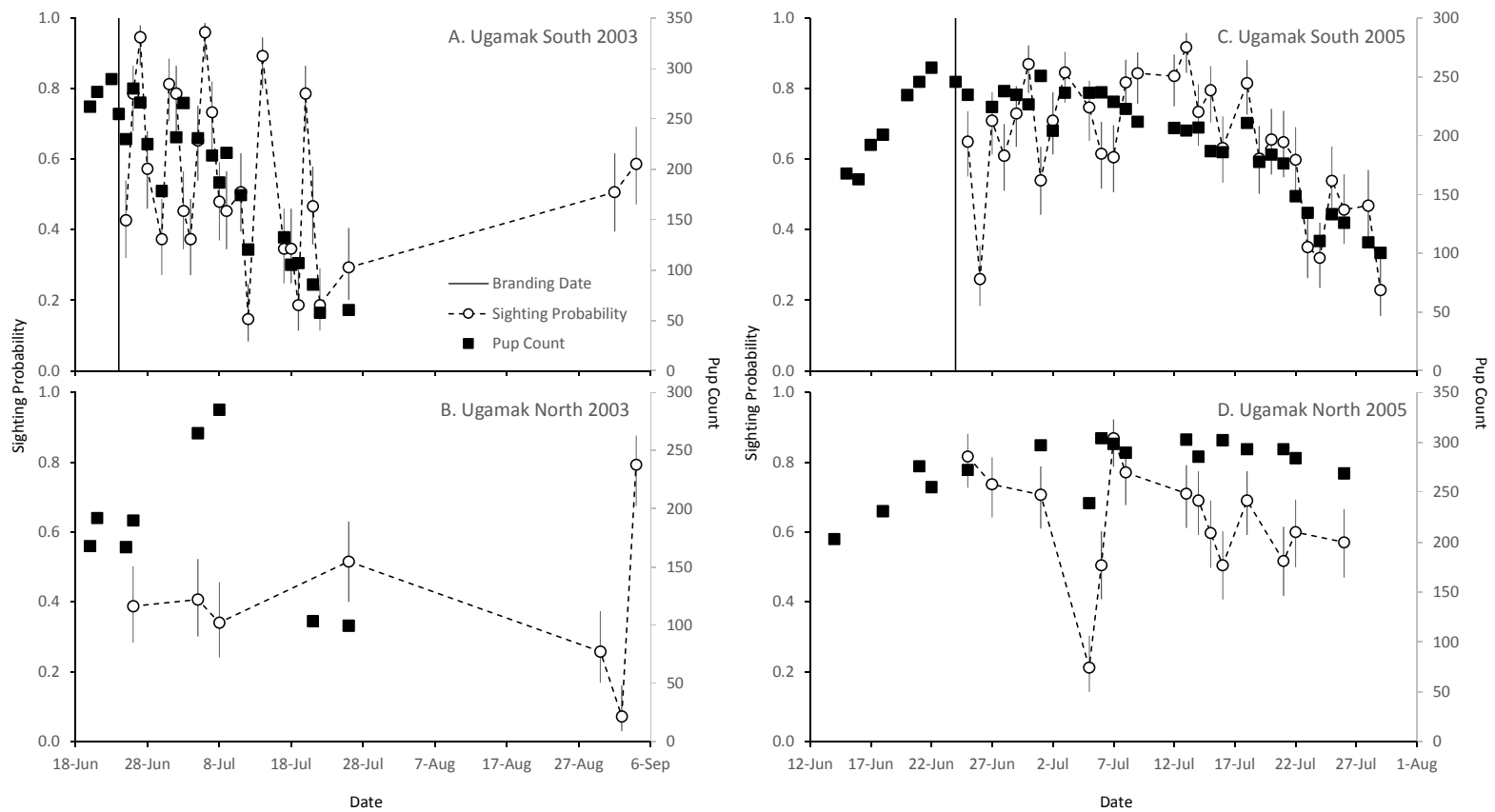


Figure 4. -- Estimated sighting probabilities ($p \pm 95\%$ confidence interval) of marked Steller sea lion pups and counts of all live pups at Ugamak South and North in June through early September 2003 (A and B, respectively), and in June and July 2005 (C and D, respectively). Legend in A applies to all. Sighting probabilities are from the $\phi(\cdot), p(t)$ model for each cohort.

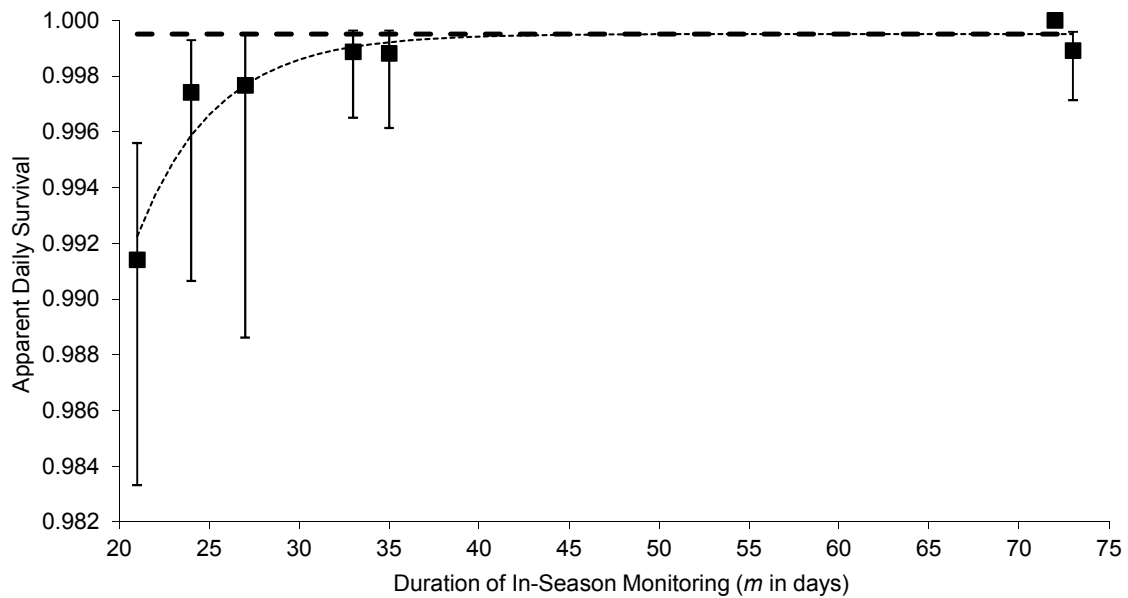


Figure 5. -- Estimated daily apparent survival ($\phi \pm 95\%$ confidence interval) of marked Steller sea lion pups at Marmot Island in June-July 2000, 2002, and 2004, and at Ugamak Island in June through early September 2003 and June-July 2005 plotted against duration of monitoring (m in days). Dotted line is a 3-parameter exponential equation fit to the data. Thick dashed line is asymptotic value of ϕ .

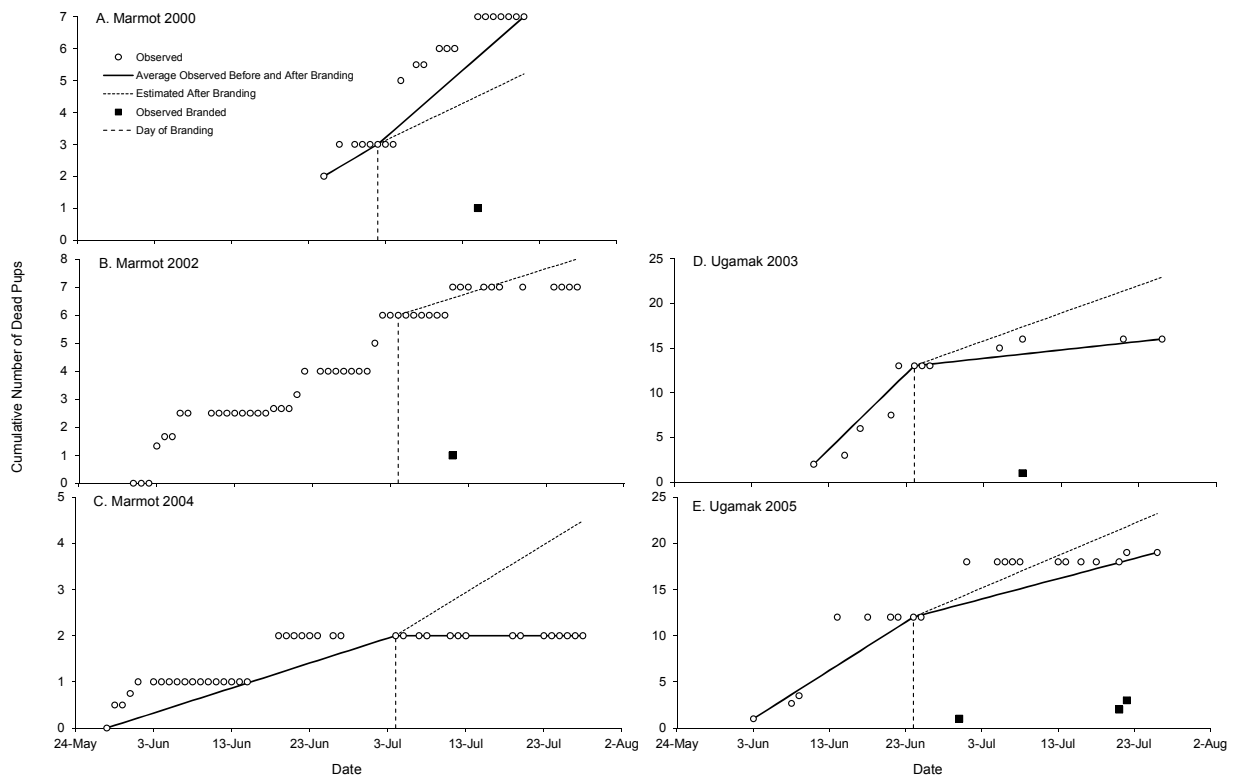


Figure 6. -- Observed and estimated numbers of dead pups on Beach 4 of Marmot Island in 2000 (A), 2002 (B), and 2004 (C), and on both North and South rookeries of Ugamak Island in 2003 (D) and 2005 (E). Observed numbers of dead pups (open circles) and average rates of pup death (solid line) before and after branding occurred (vertical dashed line) on each rookery beach are based on counts by scientists at field camps. Dotted line is the estimated number of dead pups after branding at an estimated daily mortality rate of $(1 - \phi_a) = 0.0005$. A branding date of 24 June was used for both Ugamak rookery beaches in 2003 and 2005. Filled squares indicate total number of dead branded pups that were observed (included in the count represented by the open circle).

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