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# Sex- and age-specific survival of harbor seals (*Phoca vitulina*) from Tugidak Island, Alaska

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We estimated sex- and age-specific apparent survival of harbor seals (*Phoca vitulina richardii*) born at Tugidak Island, Alaska, from 2000 to 2007 using mark–recapture models and photographs of ventral pelage markings to identify individuals. Estimates of annual apparent survival (1 − (mortality + emigration)) of females were from 0.05 to 0.10 higher than those of males and were 0.820 for weaning (~1 month) to 1 year, 0.865 for 1–3 years, and 0.929 at 3–7 years. Annual survival of males was 0.717, 0.782, and 0.879 for the same ages. Highest mortality occurred preweaning, with cumulative mortality to 4 weeks of age of 0.259, indicating this is the most vulnerable period for Tugidak harbor seals. Estimates of survival, not biased by misidentification, required that an individual had at least 2 good-quality, matching photographs in the photograph library. The number of photographs available for matching improved resighting probabilities from 0.43 for seals with 2 photographs to 0.69 for seals with 8 photographs, but this heterogeneity did not affect survival estimates. Survival estimates based on photograph-identification data were nearly identical to those based on resightings of flipper-tagged seals using mark–recapture models with a preliminary double-tag–loss estimate of 2.5% per year. Photograph identification of natural pelage markings provides a viable method for estimating vital rates of harbor seals even at large haul-outs (>1,000 animals) and may be useful for populations of conservation concern that require low disturbance of animals or where capturing sufficient numbers of seals for artificial marking is not feasible.

Key words: harbor seal, mark–recapture, natural markings, *Phoca vitulina*, photograph identification, survival


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Historically, Tugidak Island, ~25 km south of Kodiak Island in the northern Gulf of Alaska (56°27′N, 154°40′W; Fig. 1), had one of the largest known harbor seal (*Phoca vitulina richardii*) haul-outs in the world. Nearly 17,000 seals were counted in the Tugidak area in 1956 (Mathisen and Lopp 1963). However, from 1976 to 1988, average counts of seals during the pupping (June) and molting seasons (August–September) at the island's major haul-out area, the southwestern shore, declined by 72% and 85%, respectively (Pitcher 1990). The trend in seals ashore stabilized in the early 1990s and increased from 1994 to 2000 at 3.4% per year during the molting season and 8.3% per year during the pupping season, although numbers remained much reduced from historic numbers at 1,000–1,500 seals (Jemison et al. 2006). The decline was of particular interest because concurrent declines at other harbor seal haul-outs in Alaska (e.g., Nanvak Bay, Otter Island, and Prince William Sound), and declines of northern fur seals (*Callorhinus ursinus*) and Steller sea lions (*Eumetopias jubatus*) were observed throughout the northern Gulf of Alaska and in the Bering Sea (reviewed by Jemison and Kelly 2001). The decline of multiple species occupying similar niches suggested that wide-scale, ecosystem-level changes were affecting marine mammal populations in the North Pacific (reviewed by Jemison and Kelly 2001; Jemison et al. 2006; Pitcher 1990).

Understanding how different age classes and demographic processes influence population change provides insight into potential causes for population declines when conservation and management concerns arise (Sibly et al. 2003). Studies of Tugidak Island harbor seals have been conducted since the mid-1960s, but age-specific survival and birth rates have not been estimated for this important site, and have rarely been directly estimated for this species anywhere. In the past, demographic rates of harbor seals were estimated from the age structure of samples of dead seals (Bigg 1969; Boulva and McLaren 1979; Härkönen and Heide-Jørgensen 1990; Pitcher and Calkins 1979). More recently, identification of individuals by their unique and intricate pelage markings has been a useful

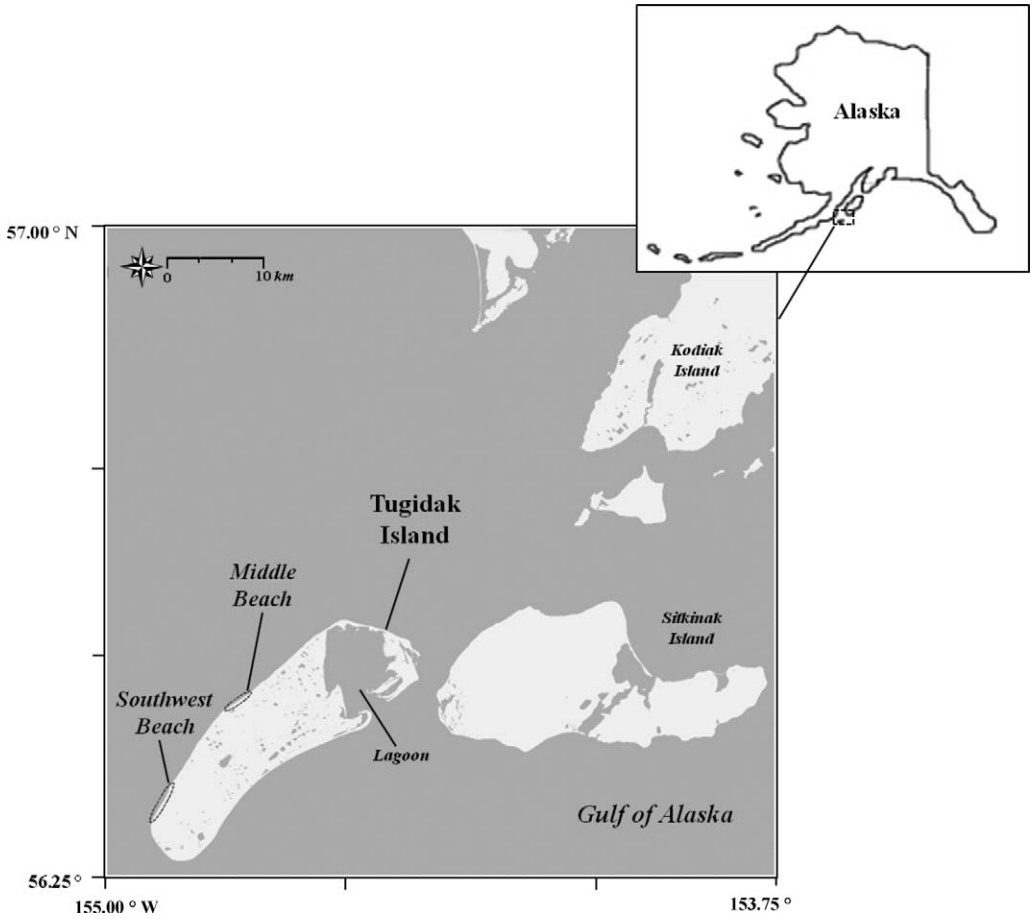


**Fig. 1.**—Map of Tugidak Island, Alaska. Harbor seals were monitored on 2 beaches: Southwest Beach and Middle Beach.

means of monitoring harbor seal populations (Cunningham 2009; Yochem et al. 1990), including estimating survival probabilities (Mackey et al. 2008) and reproductive performance (Thompson and Wheeler 2008). Although more labor-intensive than monitoring populations through artificial marks, efficiency and accuracy of this method was improved by a computer-assisted photograph-matching system (Hiby and Lovell 1990), even for very large photograph libraries from large haul-outs, such as at Tugidak Island (Hastings et al. 2008).

We used photograph identification of natural markings to follow individuals to provide a large sample of marked seals of all sex and age classes, particularly adult females, in a short time period. Capturing and artificially tagging modest numbers (20–50 per year) of seals (Pitcher and McAllister 1981), particularly pups (Small et al. 2005), has been successful at Tugidak Island. However, we wished to minimize disturbances to seals at this recovering site and low returns of seals flipper-tagged in recent years (72 pups were tagged from 1997 to 1999 with 29 [40%] seen after the birth year) suggested large numbers of tagged pups would be required to provide a sufficient sample, particularly of adults. Data from pup-only captures would require multiple years before marked adult age classes exist, and delay studies of reproductive performance and adult survival. Use of natural markings allowed animals to enter the study as adults to alleviate this delay and also provided large samples of marked animals for population monitoring. We were concerned, however, about potential bias in parameter estimates due to misidentification (particularly due to false negatives, i.e., failing to match photographs of the same seal) when relying on photographs and natural markings to identify individuals.

We initiated a photograph-identification study based on ventral pelage markings of seals on Tugidak Island in 2000 to provide long-term resighting histories of individuals for vital rate estimation. The main objective of this paper is to estimate age- and sex-specific apparent survival ($1 - (\text{mortality} + \text{permanent emigration})$) probabilities for harbor seals born at Tugidak Island based on seals 1st photographed as pups, and therefore of known age. We also used multistate mark–recapture models and resighting data of pups during the pupping season to estimate preweaning survival probabilities. Finally, we compare our photograph-based estimates to survival estimates based on flipper-tagged seals during the same years to verify that misidentification and other complications of photograph identification based on natural markings did not bias survival estimates.

## Materials and Methods

*Data collection, photograph matching, and photograph review*.—From 2000 to 2007, we photographed the ventrums of seals hauled out on Tugidak Island from cliffs 20–40 m above haul-outs using Nikon D1 or D1X digital cameras (Nikon Inc., Melville, New York) and Celestron C5 telescopes (Celestron LLC, Torrance, California) during the pupping (19 May–12 July) and molting (16 July–26 September) seasons. We monitored the molting season every year and the pupping season in 5 of the 8 years: 2000–2002, 2004, and 2006. We attempted to survey each of 2 beaches (Southwest Beach and Middle Beach; Fig. 1) in 2- to 3-day consecutive blocks/week, surveying the entire beach in a day, when possible. We did not survey seals hauled out in the large lagoon at the north end of the island. At this site viewing seals was difficult because of the lack of elevated and hidden land-based vantage points and the far distances to seals. Recent island-wide surveys suggest that during molting season, up to 60% of seals on Tugidak Island may be at this unmonitored site.

For each survey, we systematically photographed all seals that showed a proper ventrum view (head, hips, and both foreflippers visible and angle of body slight to moderate from the camera [Hastings et al. 2008]), and whose ventrums were not overly sandy or bleached. Bleaching of the pelage occurs in August–September for pups and from May to August for nonpups, often resulting in the complete erasure of the pattern until molting of the coat produces the clear pattern again (K. Hastings, pers. obs.). A single ventrum viewpoint was chosen to allow sex determination and to avoid complexity in modeling mark–recapture data based on multiple viewpoints. Seals showing a proper ventrum view but too sandy for photographing were ignored; those in advanced bleach stages on the ventrum were tallied by age–sex class and bleach or molt stage but not photographed.

For each seal photographed, we recorded in the field sex, age class (pup, yearling, subadult, or adult) based on relative size compared to seals nearby, and, during the breeding season, associations between mothers and pups. We recorded a subjective assessment of pup size and age in the field for each pup photographed as N (newborn: with fresh umbilicus, very thin and uncoordinated, and often wet with other indications of recent birth), X (very young pup: uncoordinated often moving flippers separately, and neck particularly skinny), Y (coordinated most often moving flippers together, neck was filled out but distinct from body, and rolls of fat create wrinkles on the body trunk), Z (older pup: neck was very fat and often indistinguishable from body, few to no winkles from rolls of fat on the body trunk, overall very fat especially at hips, belly, and neck, and mother is present), and W (weaned pup: same as Z but no mother present). Categories XY and YZ also were used when the categories could not be definitively assigned. We suspected this rough subjective measure of age and size would be useful because neonatal body growth is dramatic, with pups usually doubling in mass over the first 20 days (Bigg 1969; Boulva and McLaren 1979). Our methods of surveying and photographing harbor seals conformed to guidelines approved by the American Society of Mammalogists (Sikes et al. 2011).

For each survey day, we included the best photographs of each seal photographed in the photograph library. Photographs of the same seal were matched using the computer-assisted system described by Hastings et al. (2008) that used numerical descriptions and comparisons of standard "cells" in the fore- and hind-ventrum regions to order lists of potentially matching photographs for visual checking. This system greatly improved efficiency of photograph matching by placing, on average, 95.2% of good-quality photographs in the top 0.3% of ordered lists for visual checking (Hastings et al. 2008). A test of the system indicated that misidentification rates between any 2 good-quality photographs of 2.5–5.0% could occur with this system, with this rate dropping to nearly 0.0% with 4 or 5 good photographs of an individual seal in the library (Hastings et al. 2008).

After photograph matching, a single observer (KKH) reviewed all photographs to grade photograph quality, to subjectively categorize pelage markings, and to assign sex of the seals independently of field observations. Sex designations from photograph review were classified as "positive" or "marginal." The review was conducted without knowledge or indication of the fate or identity of animals in photographs. Photograph quality (excellent, good, fair, and poor) and pelage color phase (light [L], light-intermediate [LI], intermediate [I], dark-intermediate [DI], and dark [D]) were determined as described in Hastings et al. (2008).

We were interested in color phase to control for bias in survival estimates due to coat color changes with age or bleach stage. On Tugidak, a greater proportion of adults are I–D phase compared to pups (Hastings et al. 2008; Kelly 1981), suggesting population dynamics or haul-out patterns differ among seals of different color phases, or that a portion of seals darken with age. For example, we suspected I–DI pups may more likely morph to darker phases with age, causing negative bias in estimated survival from reduced ability to match pup photos to those taken of these same seals at older ages. Between-year photograph matching probabilities were much poorer for I–DI seals than other color phases (Hastings et al. 2008). We also hypothesized that photographs of the coat of I–DI seals might be particularly difficult to match between the bleaching phase (i.e., pupping season for nonpups) and the molting season, because of faster bleaching of the dark background and rings, with spots retained longer during bleaching and appearing much more prominent than on a newly molted coat (K. Hastings, pers. obs.). This effect could reduce estimated resighting and survival probabilities for I–DI seals if some of these seals, as nonpups, preferentially used Tugidak during the breeding season but not during the molting season. In addition to color phase, other subjective pelage-related measures for the ventrum recorded during photograph review included spot darkness for L–I seals (faint, medium darkness, and dark), and mark density for all seals (0 = none, 1 = <one-fourth ventrum cells with marks, 2 = one-fourth–one-half cells with marks, 3 = >one-half cells with marks), and

allowed evaluation of whether inclusion of poorly marked seals may cause negative bias of survival estimates.

*Mark–recapture modeling*.—In order to establish seal age, we included only animals 1st photographed as pups during the pupping season. We excluded pups that were 1st identified as pups during the molting season (0.04 of pups photographed), because yearlings and pups could not be reliably distinguished during molting. We assigned color phase as the darkest phase an animal was observed as a pup, preferably when wet. We assigned other coat pattern categories as the darkest or densest category recorded during their birth year, preferably when dry. For each pup, we also assigned a size category (LA) based on the last observation during the birth year, with 3 categories: S = newborn or small (N, X, or XY), M = medium (Y or YZ), and L = large (Z, W, or seen in molting season).

We estimated apparent survival (φ) and resighting ($p$) probabilities using the Cormack–Jolly–Seber model (Cormack 1964; Seber 2002), and programs MARK (White and Burnham 1999) and RMark (Laake and Rexstad 2010). We created capture histories from 2000 to 2007 by summarizing multiple sightings per year into a single annual resighting. Poor photograph quality may cause negative bias in survival estimates because of poor photograph matching, but photograph matching error is negligible when ≥2 good or excellent photographs are in the library (Hastings et al. 2008). To reduce this bias, individual capture histories began the year a seal had accumulated ≥2 good or excellent photographs in the library. After this initial entry, resightings based on photographs of any quality were used.

To fit sex effects, we also conditioned an animal's initial entry into the study on when the sex of the animal was 1st reliably determined. The sex of a pup was difficult to determine in the field because of small body size, thick coat, and our distance from animals. Sex was assigned in the field for only 48% of pup, compared to 92% for subadults and adults. We also suspected that field-based sex determinations for pups had high error rates. Therefore, we examined error rates in sex determinations to decide when seals could be reliably considered of known sex. Because entry into the data set was contingent on these criteria, animals entered the study at different ages although all were photographed as pups, and therefore of known age at the time of entry.

All matching photographs of an animal were retained in the library for matching to future observations. We were concerned about among-animal heterogeneity in $p$ resulting from the number of photographs available for matching to future photos. Photograph matching success improved with the number of good photographs, but particularly with the number of photographs of any quality (Hastings et al. 2008). Therefore, to model $p$, we included an individual, time-varying covariate (np) whose value at each time was based on the cumulative number of photographs available up to that time (8 individual covariates, 1 fit for each year, 2000–2007). Therefore, the value of np an individual had was ≥2 at entry into the study and could either remain the same or increase at later ages, depending on whether additional photographs were acquired and matched. We hypothesized $p$ would increase with the number of photographs in the library, and therefore cause negative bias in parameter estimates for animals with few photographs or for transient animals. Similarly, we were concerned that heterogeneity in $p$ caused by this effect could bias survival. The positive and asymptotic relationship between numbers of photographs in the library and probability of matching photographs (Hastings et al. 2008) suggested $p$ would be positively related to np only to a certain point (e.g., if its effect was similar given at least 4 photographs were in the library). As a preliminary step to determine a reasonable cutoff point for pooling, we fit models that differed in the pooling structure of the individual covariates, based on either good photographs or all photographs, from all separate (i.e., no truncation of the maximum number of photographs) to pooling after 4 (np5+), 5, 6, 7, 8, and 9 (np10+) photographs in the library (e.g., for np5+: np takes on 4 values, 2–5; for np6+: np takes on 5 values, 2–6, etc.). We then used the best (based on minimum Akaike's information criterion corrected for small sample size [$AIC_c$—Burnham and Anderson 2002]) pooling structure for np in the remainder of our models.

To model $p$, we included the variables time (modeled in 2 ways), age (modeled in 5 ways), birth beach (bb, 2 beaches: Southwest and Middle), sex, age*sex, time*sex, and np. Time effects were fit with either each year having a separate estimate or with 2 groupings: 2003, 2005, and 2007 versus other years (time2). We photographed seals only during the molting season in these years, possibly resulting in lower $p$. Age effects on $p$ were modeled as: 1) 7 separate age parameters, "a"; 2) linear change with age, "Age"; 3) quadratic change with age, "$Age^2$"; 4) 2 age classes "agePB": prebreeding age 0–4 years versus ≥5 years; and 5) 2 age classes "agePB2": prebreeding age 0–3 years versus ≥4 years. We chose the dividing points of 3 or 4 years because, in other studies, mean age of 1st ovulation ranged from 3 to 5 years, and therefore potential age of 1st primiparity, from 4 to 6 years (Bigg 1969; Boulva and McLaren 1979; Härkönen and Heide-Jørgensen 1990; Pitcher and Calkins 1979). We expected that resighting rate would increase with age and especially after maturity. The youngest nonpups had a much shorter window of opportunity to be photographed compared to older animals, because of their bleached coats from May to July, and their scarcity on beaches after molting by mid- to late August. Females with pups in the pupping season likely had high resighting rates, because of their attendance patterns and our emphasis on these individuals during photograph surveys.

Variables used to model φ were age (modeled in 4 ways), sex, age*sex, bb, and last age and size observed in the birth year (LA). The age effect was modeled with: 1) 2 age classes, "age2": 0–1, 1+; 2) 3 age classes, "age3A": 0–1, 1–2, 2+; 3) 3 age classes, "age3B": 0–1, 1–3, 3+; and 4) 4 age classes, "age4": 0–1, 1–2, 2–3, 3+. We 1st fit LA affecting only 1st-year survival because we expected it would most reflect preweaning survival or effects of body size at weaning influencing survival in the 1st year postweaning. However, we also included models with a common effect for all ages to

consider a delayed life-history effect of body size at weaning. We included models where survival differed between L and S–M pups (LAL), but also included models with the 3 class grouping (LA) or the alternative 2 class grouping (LAS: S versus M–L) to determine which grouping provided a better fit to the data.

We 1st simplified *p* by fitting all *p* models (290 models) and the most complex φ model (age4*sex + bb + LAL_year1), and then simplified φ (51 models) using the best *p* model. We simplified models based on $AIC_c$. Goodness of fit of the most complex model to the data was evaluated using the median $\hat{c}$ procedure in MARK (Cooch and White 2011). To verify that poorly marked animals and intermediate color-phase animals (LI–DI) were not causing negative bias in survival estimates due to low matching success or coat changes with age, we fit the best model to data from the best marked seals (judged in their birth year with mark density categories of 2 or 3, and as L with medium to dark spots or D). Finally, we fit a series of models based on all pup data regardless of quality to assess the degree of bias in survival that would be caused by not adequately considering photograph matching error due to photograph quality. We fit the same series of models for *p* and φ for data pooled over sexes and included best photograph quality in the pup year (3 categories based on the "best" as at least 1 excellent, at least 1 good photo, and neither of these) as a covariate affecting 1st-year survival.

*Comparison to a tagged seal sample*.—From 1997 to 1999 and from 2000 to 2001, 72 and 107 pups, respectively, were captured in late June on Tugidak Island and double-tagged in their hind flippers with unique tag number and color combinations of Dalton Rototags (Dalton Rototags, Henley-on-Thames, United Kingdom). We used Cormack–Jolly–Seber models to analyze tag resightings for the 2000–2001 cohorts from 2000 to 2007 to compare with our estimates based on photograph identification. However, because of small sample size, we did not fit effects of birth beach and we fit only additive effects of sex. We also used only the "age3B" age-structure in φ models.

Survival estimates based on tagged seal resightings are biased low by double-tag loss (Caughley 1977). Because of our distant resightings of tags on seals, observing single-tag loss was rare and observing double-tag loss was not possible, so estimating tag loss probabilities by examining proportions of animals observed with a single or both tags lost was not feasible. To estimate double-tag loss directly, without the assumption of independent tag loss, we created a data set of any of the 179 tagged animals seen during our matching of 2006–2007 photographs (seals known to have survived to 2006), and resightings of any tag (left or right) from 2000 to 2006. The capture histories began at the age the animal 1st entered the photograph-identification study and also were identified by at least 1 tag, and were truncated at 2006, which allowed tag rather than animal survival to be estimated. Because of small sample size ($n = 43$), we fit only the constant *p* and *S* models, where *S* reflected true rather than apparent survival of the tag (i.e., true tag retention not confounded with seal survival). Therefore, parameter estimates were for the flipper tags rather than seals in this analysis. Point estimates from the tagging data were corrected for tag loss as the uncorrected estimate divided by the tag retention probability (i.e., 1 − probability of losing both tags) to compare with the estimates based on photograph-identification data.

*Preweaning mortality*.—To further explore the effect of pup size on φ when LA was included in the best Cormack–Jolly–Seber models, we used a multistate model to separate the effects of preweaning mortality and pup size on postweaning survival. For the multistate modeling, we divided the pupping season into 6, approximately week-long, pup resight "occasions": 19–31 May, 1–7 June, 8–14 June, 15–21 June, 22–28 June, and 29 June–12 July. The 1st and last resight occasions were extended due to small sample sizes of pups in the 1st and last weeks. Capture histories were based on these 6 pup resight occasions, plus, 3 nonpup ages (1–3 years of age) to account for dispersal of pups after weaning (9 occasions total, with time intervals of 1 between pup resight occasions and 52 between nonpup resight occasions). The 2000–2002 and 2004 cohorts were included, but the 2006 cohort was not because only sightings at 1 year of age were available for this cohort.

For pup resight occasions, we used the pooled categories (S, M, and L) and summarized data as the maximum age observed during each occasion. We considered the 1st sightings of pups during pup resight occasions to be the 1st time pups had photographs with fore- and hind-ventrum cells both graded as at least "good"; we used subsequent resightings of any quality. We increased sample size by including resightings of mothers with sample pups when the mothers were observed with the pup but photographs of the pup were either not taken or not matched due to viewpoint or quality issues. Pup sightings provided through the marked mother were only included as resightings and not 1st marking events.

Age effects were included as 4 "strata" related to size and age class (S, M, and L reflecting size class during preweaning, and NP reflecting true age as nonpups at 1–3 years). Because age was reflected in strata, many parameters were fixed to zero; for example, all pups transitioned to state NP for the 1st nonpup occasion, and all animals remained in state NP for nonpup resight occasions. Using the most complex *p* and *S* models, we 1st simplified transition probabilities (Ψ) by fitting 3 models. Our most complex model allowed the probability of moving from size classes S to M, S to L, and M to L during pup resight occasions to differ during the 1st and 2nd half of the preweaning period (first 2 intervals versus the last 3 intervals). The final 2 Ψ models fit only transition probabilities from S to M, S to L, and M to L for pup resight occasions (not differing with time), and constant Ψ.

We next simplified *p* (6 additional models) using the best Ψ model. We included models in which *p* varied among the 4 size and age stratum, among pups versus nonpups (with *p* of pups constant for all pup resight occasions or differing between the 1st and 2nd half of pup resight occasions), and among 3 strata groupings: *p* of small and medium pups equal and differing

from that of large pups and of nonpups. Preliminary modeling of data demonstrated that time was an important factor in resighting rates of nonpups. Because our capture histories were based on week of pupping season and on age rather than the more common time parameterization, we including time effects in nonpup resight occasions by allowing $p$ of nonpups to vary by age and cohort, thus allowing a full age*time effect to be fit for nonpups.

Finally, we modeled $S$ (8 additional models) using the best $p$ and $\Psi$ models, for a total of 17 models fit. We allowed $S$ to vary based on several poolings of size and age classes: all separate (4 groups: S, M, L, and NP), pooling groups S and M (3 groups), and pooling groups S, M, and L (2 groups). We allowed $S$ of all pups to vary among the 1st and 2nd half of the pupping season ($pup_2$), to be estimated separately for all 5 pup resight intervals ($pup_t$) and to be equal among the 5 pup intervals. We also allowed $S$ over the pup to nonpup interval (1st-year survival) to differ from other nonpup intervals (>1 year of age), especially for S–M pups. We proceeded with model fitting and evaluation as described for Cormack–Jolly–Seber modeling.

## Results

*Sex misclassification*.—Conditioning initial entry into the study on at least 2 good or excellent photographs removed the 2006 cohort from the data (with only 1 year of resighting possible, 2007), and greatly reduced sample size of animals from the 2000–2002 and 2004 cohorts from 1,067 to 353. To evaluate criteria for known-sex seals, we examined 1,561 observations of 303 animals whose sex was determined >1 time as nonpups, and found 2.5% were errors (i.e., the sex assigned to the same animal on different dates did not match). The probability of misclassifying sex for nonpups increased with darkness and complexity of coat, with estimates of 1%, 2%, 6%, and 10% for L, LI, I, and D/DI seals, respectively. Because sex misclassification of nonpups was low (assuming independence among separate sighting: ≤1% for 2 sightings), we assigned sexes to animals based on 2 corroborating sightings as nonpups in order to estimate misclassification probability of pups. The sex misclassification probability for a single observation was 10% for field data and for marginal photograph review data, and 3% for a positive photograph review. Therefore, we accepted a sex misclassification probability ≤3% by considering pups of known sex if sex was assigned consistently ≥2 times by field or marginal photograph data or 1 time from a positive photograph, and by including all nonpup sightings in which sex was determined in the field. These criteria reduced the data set by only 6 animals resulting in 347 animals in the data set, 166 females and 181 males, 146 seals from Middle Beach and 201 from Southwest Beach, and 58 seals last seen in their birth year as small, 123 last seen as medium, and 166 last seen as large or in the molting season of their birth year. In this assigned-sex data set, 30%, 28%, 26%, 8%, 7%, and 2% of animals were initially released at age 0, 1, 2, 3, 4, and 5 years, respectively. Using the assigned-sex criteria shifted the ages at which animals entered the data set slightly later with 6% fewer at age 0 and 1% more from 1 to 5 years of age compared to the data set requiring ≥2 good or better photographs in the library.

*Cormack–Jolly–Seber model*.—The goodness-of-fit test indicated adequate fit ($\hat{c} = 1.003$, $SE = 0.006$) of the most complex model without np (individual covariate): φ (age4*sex + bb + LAL_year1) $p$ (age*sex + time*sex + bb). Of the 14 models we considered with differing np structure, the best model included np8+ for total photographs. However, 5 models had $AIC_c$ values within 2 of the best model (np6+, np7+, np9+, and np10+ for total photographs and np5+ for good photographs). Models truncating np were preferred, as was the use of the total number of photographs rather than good photographs only, providing 5 of the lowest 6 AIC values. Subsequent modeling used np8+ total photographs, which had the lowest AIC value; similar results were found by Hastings et al. (2008). The best $p$ model ($Age^2$ + time + np) had 2.4 times the support than the next best model ($Age^2$ + time + bb + np; Table 1a). Resighting probability averaged 0.556 among ages and years, was lowest for yearlings (0.431) and 7-year-olds (0.368), compared to 2–5-year-olds (0.600), and ranged from 0.385 to 0.623 among years. Resighting probability increased from 0.429 for seals with 2 photographs to 0.687 for seals with 8+ photographs; all of the top 5 models included this effect (Table 1a).

The best φ model (age3B + sex + LAL_year1) had an $AIC_c$ weight nearly twice that of the next best model (age3A + sex + LAL_year1; Table 1b). First-year apparent survival of seals last seen as S or M averaged 0.29 lower (absolute value) than seals last seen in their birth year as L (Table 2a), indicating significant preweaning mortality or body-size effects on postweaning apparent survival. Estimated apparent annual survival of males was 0.12 lower than that of females for the 1st year, and 0.05 lower for ages 3–7 (Table 2a). These differences would result in 46% of weaned females versus 26% of weaned males recruited to the population by 7 years of age.

Despite the strong effect of np on $p$, inclusion or exclusion of the variable in the $p$ model had little effect on point estimates or precision of φ estimates, with its exclusion resulting in changes of only –0.004 to –0.016 in φ point estimates. Using the same model but with poorly marked seals removed yielded nearly identical estimates, except for an unexpectedly lower apparent 1st-year survival of well-marked seals last seen in the birth year as S or M (Table 2b). However, confidence intervals largely overlapped and precision of these estimates were poor.

The analysis of data for all pups (i.e., not conditioning an individuals' entry into the study on when ≥2 good or better photographs had been matched, hereafter termed "unconditioned analysis"), 1st-year survival estimates for pups with at least 1 excellent photograph in the birth year (0.75) were identical to those from our "conditioned analysis" (compare with Table 2d). However, 1st-year survival estimates were biased low by an absolute value of –0.10 for seals with best birth-year photographs of only ≥1 good photo in the library, and by –0.31 for seals with only poor photos in the birth year.

**Table 1.**—Model selection results from Cormack–Jolly–Seber models used to estimate age- and sex-specific survival probabilities of harbor seals from Tugidak Island, 2000–2007. Photograph-identification data were used for models in subtables a and b and models using tagging data are in subtable c. Top models are shown. a) 290 models fit, b) 51 models fit, and c) 72 models fit. Notation: $p$ = probability of resighting; φ = apparent survival probability (1 − (mortality + emigration)); Npar = number of parameters in the model; $AIC_c$ = Akaike's information criterion corrected for small sample size; $QAIC_c$ = $AIC_c$ corrected for overdispersion; Weight = weight of the model based on $AIC_c$ or $QAIC_c$; Age = linear change with age; $Age^2$ = quadratic change with age, age groupings: age2 (0–1, 1+), age3A (0–1, 1–2, 2+), age3B (0–1, 1–3, 3+), age4 (0–1, 1–2, 2–3, 3+), agePB (0–4, 5+); s = sex; bb = birth beach; np = number of total photographs of a seal in the library (an individual time-varying covariate); LAL_year1 = effect of last size class seen in the birth year on 1st-year survival (contrasting pups last seen as large versus pups last seen as small–medium); t = calendar year; t2 = 2 year groupings: 2003, 2005, 2007 versus other years.

| Top models | Npar | $AIC_c$ | Weight |
|---|---|---|---|
| a) Photograph-identification data: $p$ model (φ (age4*s + bb + LAL_year1)) | | | |
| $p$ ($Age^2$ + t + np) | 20 | 1,510.70 | 0.26 |
| $p$ ($Age^2$ + t + bb + np) | 21 | 1,512.41 | 0.11 |
| $p$ ($Age^2$ + t + s + np) | 21 | 1,512.82 | 0.09 |
| $p$ ($Age^2$ * s + t + np) | 23 | 1,512.96 | 0.08 |
| $p$ ($Age^2$ + t + bb + s + np) | 22 | 1,514.52 | 0.04 |
| b) Photograph-identification data: φ model ($p$ ($Age^2$ + t + np)) | | | |
| φ (age3B + s + LAL_year1) | 15 | 1,503.42 | 0.18 |
| φ (age3A + s + LAL_year1) | 15 | 1,504.50 | 0.10 |
| φ (age2 + s + LAL_year1) | 14 | 1,504.80 | 0.09 |
| φ (age4 + s + LAL_year1) | 16 | 1,505.19 | 0.07 |
| φ (age3B + s + LAL_year1 + bb) | 16 | 1,505.50 | 0.06 |
| φ (age2 * s + LAL_year1) | 15 | 1,505.95 | 0.05 |
| c) Tagged seal data | | $QAIC_c$ | |
| φ (age3B) $p$ (agePB + t2) | 6 | 539.47 | 0.14 |
| φ (age3B) $p$ (t2) | 5 | 539.80 | 0.12 |
| φ (age3B) $p$ (t2 + s) | 6 | 540.32 | 0.09 |
| φ (age3B) $p$ (agePB + t2 + s) | 7 | 540.39 | 0.09 |
| φ (age3B) $p$ (Age + t2) | 6 | 540.95 | 0.07 |
| φ (age3B) $p$ (agePB2 + t2) | 6 | 541.10 | 0.06 |
| φ (age3B + s) $p$ (agePB + t2) | 7 | 541.42 | 0.05 |
| φ (age3B) $p$ (Age + t2 + s) | 7 | 541.73 | 0.04 |
| φ (age3B + s) $p$ (t2) | 6 | 541.73 | 0.04 |
| φ (age3B) $p$ (agePB2 + t2 + s) | 7 | 541.82 | 0.04 |

**Table 2.**—Age- and sex-specific apparent survival estimates (φ) of harbor seals from Tugidak Island, 2000–2007, based on photograph-identification and tagging data. Subtables a and b are from the best model in Table 1b; subtable c is from the best model in Table 1c. Estimates in subtable d are from the comparable model to that in subtable c, but using model φ (age3B + LAL_year1) and $p$ ($Age^2$ + t + np), which combined sexes. *SE* = standard error; 95% *CI* = 95% confidence interval.

| Age | φ | *SE* | 95% *CI* |
|---|---|---|---|
| a) Photograph-identifiation data: all seals ($n$ = 347) | | | |
| Females ($n$ = 166) | | | |
| 0–1 (last seen small–medium) | 0.549 | 0.093 | 0.369–0.717 |
| 0–1 (last seen large) | 0.820 | 0.069 | 0.646–0.919 |
| 1–3 | 0.865 | 0.027 | 0.803–0.910 |
| 3+ | 0.929 | 0.026 | 0.858–0.966 |
| Males ($n$ = 181) | | | |
| 0–1 (last seen small–medium) | 0.405 | 0.089 | 0.248–0.584 |
| 0–1 (last seen large) | 0.717 | 0.088 | 0.520–0.856 |
| 1–3 | 0.782 | 0.035 | 0.706–0.842 |
| 3+ | 0.879 | 0.038 | 0.784–0.936 |
| b) Photograph-identification data: light–dark well-marked seals only ($n$ = 166) | | | |
| Females ($n$ = 74) | | | |
| 0–1 (last seen small–medium) | 0.424 | 0.127 | 0.210–0.672 |
| 0–1 (last seen large) | 0.796 | 0.098 | 0.545–0.927 |
| 1–3 | 0.858 | 0.038 | 0.766–0.918 |
| 3+ | 0.920 | 0.037 | 0.812–0.968 |
| Males ($n$ = 92) | | | |
| 0–1 (last seen small–medium) | 0.293 | 0.109 | 0.128–0.539 |
| 0–1 (last seen large) | 0.686 | 0.121 | 0.421–0.868 |
| 1–3 | 0.773 | 0.051 | 0.659–0.857 |
| 3+ | 0.866 | 0.050 | 0.735–0.938 |
| c) Tagged seal data: not corrected for tag loss, 2000–2001 ($n$ = 107) | | | |
| Both sexes | | | |
| 0–1 (last seen large) | 0.743 | 0.048 | 0.639–0.825 |
| 1–3 | 0.835 | 0.036 | 0.753–0.894 |
| 3+ | 0.874 | 0.036 | 0.784–0.930 |
| d) Photograph-identification data: comparable model, both sexes combined | | | |
| Both sexes | | | |
| 0–1 (last seen large) | 0.750 | 0.078 | 0.570–0.872 |
| 1–3 | 0.824 | 0.026 | 0.766–0.870 |
| 3+ | 0.905 | 0.030 | 0.829–0.950 |

Estimated survival probabilities for older ages were not affected. The "unconditioned analysis" improved precision of 1st-year survival for the combined sexes for seals released with ≥1 excellent photo (0.75, 95% confidence interval [95% *CI*]: 0.64–0.83) but not estimates for other age classes, with estimates for the 2nd and 3rd age classes of 0.82 (0.77–0.86) and 0.91 (0.84–0.95; compare with Table 2d). We consider this "unconditioned" analysis less ideal than our "conditioned" analysis for dealing with photograph matching error because it does not explicitly address the error in the model or through data selection, but instead relies on estimating and then ignoring the biased 1st-year survival estimates.

*Comparison to a tagged seal sample*.—The double-tag retention rate estimated from photograph-identified tagged seals alive in 2006–2007 was 0.975 (0.924–0.992), with annual resighting probability of either tag of 0.852 (0.781–0.903), yielding an annual double-tag loss probability of 0.025. Goodness-of-fit testing of the Cormack–Jolly–Seber model fit to the tag resighting data indicated only slight lack of fit for the most general model we considered ($\hat{c}$ = 1.176, *SE* = 0.006). We adjusted results and parameter estimates by this $\hat{c}$ ($QAIC_c$—Burnham and Anderson 2002). The best model for the tag resighting data was φ (age3B) $p$ (agePB + time2) (Table 1c). For years when both pupping and molting seasons were monitored, estimates of $p$ were 0.90 for prebreeding-aged (1–4 years) and 0.84 for older (5+ years) seals. Resighting probability was reduced for years when only molting season was monitored with $p$ of 0.77 and 0.65 for the 2 age classes. Post hoc correction of estimates of φ (Table 2c) for a double-

**Table 3.**—Model selection results for the multistate model to estimate preweaning mortality and time to weaning for harbor seals from Tugidak Island, Alaska, 2000–2007. Npar = number of parameters in the model, $AIC_c$ = Akaike's information criterion corrected for small sample size; Weight = support of the model relative to other models fit based on $AIC_c$; $\Psi$ = transition probability between age and size classes (stratum); $p$ = resighting probability; $S$ = survival probability. Notation for models: AC = age and size class (S, M, L, NP) as stratum; $pup_t$ = time-specific for all pup resight occasions (5 occasions); pup = constant across pup resight occasions; $pup_2$ = separate for 1st and 2nd half of pup resight occasions; year1 = 1st-year survival (post–pup surveys) separate from other nonpup intervals ($S$ only); NP, age = age-specific nonpup resight occasions (or * cohort for full time dependence in nonpup resight occasions; $P$ only); S, M, L, NP = strata based on pup size preweaning (small, medium, large) or age (NP = nonpup); $S_g$ = (S–M) * $pup_2$ + (S–M) * year1 + L + NP (global model); $p_g$ = (S–M) * $pup_t$ + NP, age * cohort (global model). Models with (.) set parameters constant across all groups and time.

| Model | Npar | $AIC_c$ | Weight |
|---|---|---|---|
| a) $\Psi$ model ($S = S_g$, $p = p_g$) | | | |
| $\Psi$ (.) | 24 | 38,423.66 | 0.46 |
| $\Psi$ (AC * $pup_2$) best | 27 | 38,423.89 | 0.41 |
| $\Psi$ (AC) | 26 | 38,426.27 | 0.13 |
| b) $p$ model ($S = S_g$, $\Psi$ = best) | | | |
| $p$ (S + M + L + NP, age * cohort) best | 25 | 38,419.18 | 0.74 |
| $p$ (SM + L + NP, age * cohort) | 24 | 38,421.88 | 0.19 |
| $p_g$ = (S–M) * $pup_t$ + NP, age * cohort | 27 | 38,423.89 | 0.07 |
| $p$ (AC) | 14 | 38,434.75 | 0.00 |
| $p$ ($pup_2$ + NP, age * cohort) | 24 | 38,442.54 | 0.00 |
| $p$ (pup + NP, age * cohort) | 23 | 38,456.36 | 0.00 |
| $p$ (.) | 11 | 38,556.05 | 0.00 |
| c) $S$ model ($p$ = best, $\Psi$ = best) | | | |
| $S$ (SM + L + NP) | 22 | 38,416.10 | 0.78 |
| $S_g$ = (S–M) * $pup_2$ + (S–M) * yr1 + L + NP | 25 | 38,419.18 | 0.17 |
| $S$ (S–M) * pup + (S–M) * yr1 + L + NP) | 23 | 38,422.69 | 0.03 |
| $S$ (AC) | 23 | 38,423.76 | 0.02 |
| $S$ ($pup_2$ + yr1 + NP) | 23 | 38,426.10 | 0.01 |
| $S$ (.) | 20 | 38,427.48 | 0.00 |
| $S$ (pup + yr1 + NP) | 22 | 38,427.68 | 0.00 |
| $S$ ($pup_t$ + NP) | 26 | 38,431.24 | 0.00 |
| $S$ (SML + NP) | 21 | 38,433.87 | 0.00 |

tag loss rate of 2.5% per year produced corrected estimates of 0.762, 0.856, and 0.896 for the respective age classes. These estimates were nearly identical to those from the comparable Cormack–Jolly–Seber model for the photograph-identification data, φ (age3B + LAL_year1) with no sex effects (Table 2d).

*Preweaning survival.*—Multistate modeling marginally supported a model with $\Psi$ differing for the 1st and 2nd halves of the pupping season (Table 3a). Between weeks, 0.62 and 0.67 of S pups became M in the 1st and 2nd halves of the pupping season, respectively, whereas 0.18 of S pups became L, and 0.75 of M pups became L. The estimated weekly resighting probability varied by time for nonpup resight occasions and by age (Table 3b) and declined with pup size class from 0.43, 0.37, to 0.13 for S, M, and L pups, respectively. Finally, a single best $S$ model was strongly supported (weight = 0.78; Table 3c), with weekly $S$ increasing from 0.882 (0.811–0.928, 95% *CI*) for S–M pups to 0.994 (0.990–0.996) for L pups. Using these estimates of $S$ and $\Psi$, we calculated the proportion of pups in size class L by week after approximate birth (i.e., week since 1st seen as size class S) and cumulative mortality probability to ~8 weeks of age (Fig. 2). By weeks 2 and 3, 0.70 and 0.91 of pups had moved to size class L, respectively, indicating that most pups were of approximate weaning size by 3–5 weeks of age. Mortality was concentrated during the period when pups were youngest and smallest. Of the mortality occurring during the first 8 weeks of life, 55% and 76% occurred during the 1st week and first 2 weeks, respectively (Fig. 2). We estimated cumulative mortality probability to 4 and 8 weeks of 0.259 and 0.276, respectively, which was similar to 0.291 from our Cormack–Jolly–Seber model (the difference between 1st-year survival of pups last seen as S–M versus those last seen as L). This result suggested the variable LA may have largely captured effects of preweaning mortality (i.e., age) on 1st-year survival, rather than effects of body size on postweaning survival in the 1st year.

## Discussion

Our estimates of apparent survival from birth to 4 years were 0.38 for females and 0.22 for males. Comparisons with other published estimates for harbor seals are necessarily qualitative because few estimates include estimates of precision. Methodology also differs, with most studies relying on age structure of dead animals or modeling of counts to examine age-specific survival. Therefore, we report if our estimates differ from other published estimates by ≥0.10 in absolute value, to provide a rough comparison to other studies and populations. Our estimate for males was similar to that reported for males from the Gulf of Alaska in the 1970s (0.21—Pitcher and Calkins

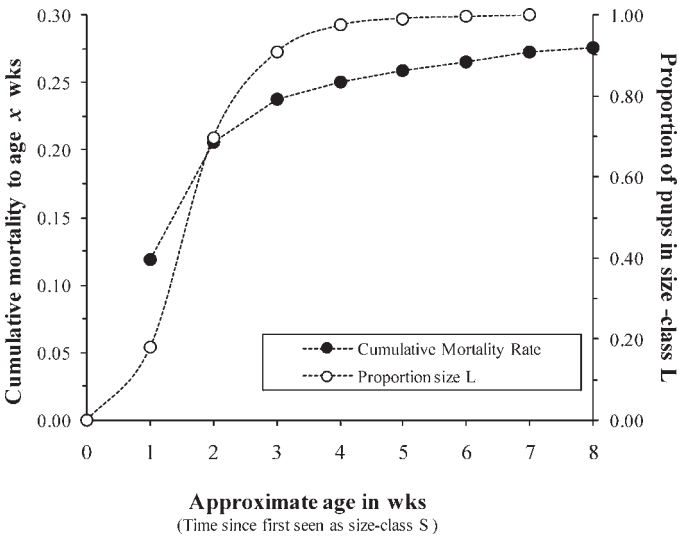


**Fig. 2.**—Preweaning mortality and time to weaning for harbor seal pups from Tugidak Island, 2000–2002 and 2004. Values were calculated from survival and transition probabilities from the top model in Table 3c.

1979). However, we estimated higher survival to maturity for Tugidak females than for females in the Gulf of Alaska in the 1970s (0.26—Pitcher and Calkins 1979), a time of rapid population decline in the few areas of the Gulf of Alaska and Bering Sea that were monitored (reviewed by Jemison et al. 2006; Pitcher 1990; Small et al. 2003). Our estimates are lower than survival to maturity (0–4 years) estimated for females in the Kattegat–Skagerrak during a period of rapid population growth of 12% per year (>0.48—Heide-Jørgensen and Härkönen 1988). Our estimate for males was lower than that of males in British Columbia (0.40 for both sexes—Bigg 1969).

Our 1st-year survival estimate was similar to a mark–recapture estimate of 1st-winter survival (pups released approximately October–November and resighted May–September the following year, ~9 months [Härkönen et al. 1999]) for branded pups from the Skagerrak (Harding et al. 2005). They estimated an ~9-month survival of ~0.80–0.85 for seals with a mean mass of 24 kg (Harding et al. 2005). Adjusting for a 12-month interval by assuming constant survival over the period, yielded a rough estimate of 0.74–0.81, similar to our estimate of postweaning 1st-year survival for the pooled sexes of 0.75 (Table 2d).

For adults, our point estimate for annual survival for the combined sexes at 3+ years of 0.91 (Table 2d) was just below the lower bound of the 95% confidence interval for the estimate for 2+-year-olds from the Moray Firth, Scotland, using identical methodology (0.97, 95% *CI* = 0.92–0.99—Mackey et al. 2008). Our estimates were similar to those of Boulva and McLaren (1979), who reported annual survival of 1+-year seals at 0.83, similar to our 0.86 estimate calculated by averaging the estimates of males and females for the last 2 age classes (1+ years). An estimate of 0.86 also is comparable to the estimate of 0.88 for combined sexes at 1+ years from the Wadden Sea during a period of moderate population growth (9% per year) and the 0.93 estimate from the Wadden Sea study during particularly high population growth (14% per year—Ries et al. 1999).

Compared with published sex-specific adult survival estimates, our estimates for males (0.88) were similar to (0.91 [Härkönen and Heide-Jørgensen 1990] and 0.87 [Pitcher and Calkins 1979]) or higher than others (0.71—Bigg 1969). Our estimate for females (0.93) was similar to others (0.85 [Bigg 1969] and 0.85 [Heide-Jørgensen and Härkönen 1988]), including the estimate for adult females in the Gulf of Alaska in the 1970s (0.89—Pitcher and Calkins 1979), when using our cutoff of 0.10 difference for comparisons. This limited comparison between the 1970s and our results since 2000 suggests that the survival of juvenile Alaskan harbor seal females (as indicated by higher survival to maturity) may have increased in concert with the stabilization or reversal of population declines in the Kodiak region in the 1980s and 1990s (Jemison et al. 2006; Small et al. 2003). Similarly, survival of Steller sea lion females, but not males, was compromised in the Kodiak area during the late 1980s, a period of rapid population decline for that species (Pendleton et al. 2006).

Our age-specific survival estimates for females are reasonable given the recent population trend on Tugidak. Using our age-specific survival estimates for females (preweaning survival of 0.74 over 4 weeks × postweaning survival of large female pups of 0.82 = 0.61 1st-year survival) in a Leslie matrix model with maximum age of 30 and average birth rates based on age-specific pregnancy rates (divided by 2 for female offspring—Pitcher and Calkins 1979:Table 6), resulted in an estimated population growth rate ($r$) of 5.8% per year. Birth rates were likely less than pregnancy rates. If pregnancy rates are reduced by 10% for all ages, we estimated an $r$ of 4.9% per year. These values are intermediate between the estimated trends in all seals hauled out during molting (3.4% per year) and pupping (8.3% per year) from the previous decade, 1994–2000 (Jemison et al. 2006).

Our study estimated apparent survival probabilities, with the potential for confounding of survival with permanent emigration. Underestimates of survival would result if some seals had a significant probability of not returning to the 2 beaches on Tugidak Island from 2001 to 2007 (Fig. 1). More information is needed concerning probability of permanent emigration for seals using Tugidak Island to definitively judge how our results reflect survival rather than dispersal. However, we believe permanent emigration likely resulted in minimal underestimates of survival probabilities of Tugidak-born seals, particularly for females. Short-term movements of harbor seals can be extensive, particularly for pups and juveniles that may travel 300–500 km from tagging sites (reviewed by Small et al. 2005). However, examination of tag-recovery, brand-resighting, and genetic data suggests that the larger short-term movements of seals observed during tracking studies may not adequately reflect the high fidelity to summer breeding sites (reviewed by Härkönen and Harding 2001; Ries et al. 1999; Small et al. 2005). Tugidak pups instrumented with satellite tags from 1997 to 1999 also made extensive round-trips from Tugidak up to 350 km, but 1-way movements were rare and 6 of the 7 seals followed for more than 360 days returned to Tugidak by the end of the 1st year of deployment (Small et al. 2005). Similarly, the only published multiyear study of distribution of individually marked harbor seals suggests very high natal site fidelity for adult females (100% within 7 km of branding site), with reduced fidelity to natal site with age for males (Härkönen and Harding 2001). Of 1 and 2 year olds observed, a minimum of 40% and 70% were in the natal area, although the proportion of these age classes that actually used the natal site at these ages was not estimated (Härkönen and Harding 2001). However, source–sink population dynamics have been suggested for seals in the Wadden Sea (Ries et al. 1999), indicating that natal dispersal may be common in areas of high human population density and disturbance. As is common in mammals (Greenwood 1980), lower apparent survival of males at all ages may be due to a greater tendency for males to permanently emigrate than for females, especially at older ages in male harbor seals, where males may use their

natal sites less and less as they age (Härkönen and Harding 2001).

The most likely cause for underestimates in our 1st-year survival estimates by permanent emigration would be due to seals returning to Tugidak as nonpups but also having high fidelity to unmonitored portions of the island (i.e., the lagoon and surrounding tidal flats). Seals at the lagoon have rarely been monitored such that more study is needed to test whether this behavior occurs to a degree that would bias survival of seals born at Middle and Southwest beaches. Examination of data suggests high site fidelity of nonpups, high natal site fidelity, and that seals born at all areas may prefer Southwest Beach over Middle Beach, such that Southwest Beach includes a mix of animals from throughout Tugidak. Females with pups may show particularly high fidelity to specific beaches during the pupping season (such as preferring either Southwest Beach or Middle Beach, see below). A simple comparison of numbers of individuals observed moving between our 2 study beaches during molting seasons suggests the likelihood that this highly localized fidelity may apply to other demographic groups and outside the pupping season. However, a simple comparison is complicated by higher effort and higher numbers of seals at Southwest Beach than Middle Beach, with often 2–3 times as many seals at Southwest Beach than Middle Beach. To reduce bias due to unequal effort we randomly selected dates in which Southwest Beach and Middle Beach were surveyed on sequential days during molting, so that total survey days was standardized. For seals seen with $\geq$100 days between sightings (i.e., in different years), 47% of seals seen at Middle Beach were seen at Southwest Beach on their last sighting versus 9% of seals seen at Southwest Beach seen at Middle Beach on their previous sighting ($n = 2{,}312$ observations). This suggests, as does the seal distribution, that Southwest Beach is the preferred site of the 2 beaches for many seals during molting, but that seals using Middle Beach commonly moved between the 2 beaches during molting seasons.

The lagoon is more distant from either of these beaches than they are to each other (Fig. 1). However, 4 of 20 pups with radiotags were observed at both Southwest Beach and the lagoon after weaning within 1–2 months of their tagging in 1997. High fidelity to the natal site is suggested by tagging studies. For example, of 19 pups tagged at the lagoon, 63% were never seen as nonpups in contrast to ~30% of pups tagged at Middle Beach or Southwest Beach. We suspect this reduced return rate may be due to high natal site fidelity, although poorer survival of the lagoon animals cannot be discounted. The 7 lagoon animals seen as nonpups were seen at Southwest Beach or both beaches. More seals born at Middle Beach were observed there as nonpups than seals born at Southwest Beach. Of 40 tagged seals born at Middle Beach and seen again as nonpups, 83% were observed there at least once as nonpups versus 52% of 71 Southwest Beach pups observed at Middle Beach as nonpups.

We estimated a much higher rate of mortality during preweaning than postweaning in the 1st year with preweaning survival at 0.74 (over ~1 month) versus postweaning survival at 0.72–0.82 for large or weaned pups (over ~11 months). The preweaning period is therefore the most vulnerable period for Tugidak seals. Most (75%) preweaning mortality occurred for the smallest pups or in the first 2 weeks of life. Because young pups could not be distinguished from pups in poor condition (i.e., small), age effects are likely exaggerated. Our preweaning survival estimate would be biased low if mothers moved with pups outside our study beaches (i.e., the lagoon) before weaning and those that moved had lower survival or higher permanent emigration probabilities from 1 to 3 years of age. However, of individual pups seen with their mothers on 2 days that spanned a $\geq$14-day period ($n = 95$), only 5% were at different beaches on the 2 days. Even among mothers seen with pups in >1 year ($n = 251$), only 10% were observed with pups at different beaches in different years. Therefore, movements of mother–pup pairs to different beaches were rare during preweaning, and breeding beach fidelity of reproductive-age females also was high. This suggests that movements of mothers and pups to areas outside the survey beaches (such as to the lagoon or off-island) during preweaning were unlikely.

Our estimate of preweaning survival was similar to recent estimates for pups at Sable Island (0.63–0.77—Bowen et al. 2001; Coltman et al. 1998), which were lower than estimates at that site in the 1970s (0.78–0.88—Boulva and McLaren 1979). An index of 6-week survival in the Wadden Sea was 0.66 (Reijnders et al. 1997). Abandonment by the mother and predation are likely causes for high mortality during the preweaning period (Lucas and Stobo 2000). Starving and abandoned lone pups are commonly seen on the pupping beaches at Tugidak (Bishop 1967; Jemison and Kelly 2001).

Our study demonstrates successful application of photograph identification to a large harbor seal haul-out (>1,000 seals). The method was robust to potential biases due to misidentification caused by reliance on natural marks and photograph identification to determine resighting histories. Critical to the method was the reduction or elimination of misidentification by conditioning the initial entry into the study until animals had $\geq$2 good or excellent photographs in the library, or the additional time at which sex was observed (for sex-specific estimates). Beyond the criteria of having $\geq$2 good or better matching photos in the library, the degree of pelage marking did not bias survival estimates. Resighting probability increased from 0.42 for seals with 2 good photos to 0.65 for seals with 8 photographs, and this mild heterogeneity did not affect survival estimates. Our average $p$ was similar to another photograph-identification study (0.62—Mackey et al. 2008), and adequately high for precise annual survival estimates. As expected, average annual $p$ was lower using the photograph-identification method at 0.56 compared to tagged animal resightings (ranging from 0.64 to 0.90 depending on the season and age).

Our survival estimates from the photograph-identification study were corroborated with nearly identical survival estimates for the same cohorts for seals that were artificially tagged. Our rough estimate of tag loss indicated potentially very low double-tag loss rates (2.5% per year) for harbor seals

at this site. If tag loss was not independent and was high at early ages, our double-tag loss estimate may possibly be biased low by including only seals that had entered the photograph-identification study with tags, where ~25% of seals 1st entered at each age 0, 1, 2, and 3+. Therefore, 50% of animals entered the study only if at least 1 tag was retained to age 2 years. However, of the 10 animals released with photos and tags at age 0, 9 had been seen with at least 1 tag in 2006, suggesting a high retention rate. Therefore, our initial low return rates of tagged seals in the late 1990s were due most to mortality rather than tag loss. Our study shows that only 20–40% of males and females, respectively, are alive at 4 years of age such that a small artificially tagged sample would be very small by adulthood. Consistent tagging of a small sample over multiple years may alleviate this problem given annual variation in survival is not too great.

Both tagging and photograph-based methods provided sufficient precision for survival estimation at least until 7 years of age, with estimates of 1st-year survival most problematic for the photograph-based study (Table 2). Precision of 1st-year survival estimates was improved in our tagged data set, perhaps due to higher resighting rates. However, the sample size was insufficient to detect important variation in parameters, such as caused by sex differences, in the tagged data set. Precision of nonpup survival estimates was improved in our photograph-identified data set with a sample size of 347 pups released over 4 years (average of 87 per year) compared to our tagged data set (107 released over 2 years, or 54 per year). These results suggest that a modest sample of tagged pups over multiple years (perhaps 85–90 per year over 4 years; to match our photograph-based sample) would likely provide better monitoring of 1st-year survival and comparable monitoring of survival of older ages, as that possible with a photograph-based study. However, larger releases of tagged pups would be especially required to match sample sizes of marked adult females possible through the photograph-identification method, such as for monitoring reproduction. For example, given survival rates of females and tag loss rates we observed in this study, 90 female pups (50% of maximum count of female pups on the southwestern-shore beaches per year) would need to be tagged to provide 25 tagged females at 10 years of age for studies of reproductive performance. In summary, photograph-identification methods are effective in estimating age- and sex-specific survival at haul-outs with large numbers of harbor seals where it is preferable to avoid disturbance to seals (such as areas of conservation concern) or where it is impossible to physically capture sufficient numbers of harbor seals for study goals.

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## Literature Cited

Bigg, M. A. 1969. The harbour seal in British Columbia. Fisheries Research Board of Canada Bulletin 172:1–33.

Bishop, R. H. 1967. Reproduction, age determination, and behavior of the harbor seal, *Phoca vitulina L.*, in the Gulf of Alaska. M.S. thesis, University of Alaska, Fairbanks.

Boulva, J., and I. A. McLaren. 1979. Biology of the harbor seal, *Phoca vitulina*, in eastern Canada. Fisheries Research Board of Canada Bulletin 200:1–24.

Bowen, W. D., S. J. Iverson, D. J. Boness, and O. T. Oftedal. 2001. Foraging effort, food intake and lactation performance depend on maternal mass in a small phocid seal. Functional Ecology 15:325–334.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Caughley, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, London, United Kingdom.

Coltman, D. W., W. D. Bowen, and J. M. Wright. 1998. Birth weight and neonatal survival of harbour seal pups are positively correlated with genetic variation measured by microsatellites. Proceedings of the Royal Society of London, B. Biological Sciences 265:803–809.

Cooch, E., and G. White. 2011. Program MARK: a gentle introduction. 9th ed. www.phidot.org/software/mark/docs/book/. Accessed 4 May 2011.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51:429–438.

Cunningham, L. 2009. Using computer-assisted photo-identification and capture–recapture techniques to monitor the conservation status of harbour seals (*Phoca vitulina*). Aquatic Mammals 35:319–329.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Harding, K. C., M. Fujiwara, Y. Axberg, and T. Härkönen. 2005. Mass-dependent energetics and survival in harbour seal pups. Functional Ecology 19:129–135.

Härkönen, T., and K. C. Harding. 2001. Spatial structure of harbour seal populations and the implications thereof. Canadian Journal of Zoology 79:2115–2127.

Härkönen, T., K. C. Harding, and S. G. Lunneryd. 1999. Age- and sex-specific behaviour in harbour seals *Phoca vitulina* leads to biased estimates of vital population parameters. Journal of Applied Ecology 36:825–841.

HÄRKÖNEN, T., AND M.-P. HEIDE-JØRGENSEN. 1990. Comparative life histories of East Atlantic and other harbour seal populations. Ophelia 32:211–235.

HASTINGS, K. K., L. A. HIBY, AND R. J. SMALL. 2008. Evaluation of a computer-assisted photograph-matching system to monitor naturally marked harbor seals at Tugidak Island, Alaska. Journal of Mammalogy 89:1201–1211.

HEIDE-JØRGENSEN, M.-P., AND T. J. HÄRKÖNEN. 1988. Rebuilding seal stocks in the Kattegat-Skagerrak. Marine Mammal Science 4:23l–246.

HIBY, L., AND P. LOVELL. 1990. Computer aided matching of natural markings: a prototype system for grey seals. Reports of the International Whaling Commission, Special Issue 12:57–61.

JEMISON, L. A., AND B. P. KELLY. 2001. Pupping phenology and demography of harbor seals (*Phoca vitulina richardsi*) on Tugidak Island, Alaska. Marine Mammal Science 17:585–600.

JEMISON, L. A., G. W. PENDLETON, C. A. WILSON, AND R. J. SMALL. 2006. Long-term trends in harbor seal numbers at Tugidak Island and Nanvak Bay, Alaska. Marine Mammal Science 22:339–360.

KELLY, B. P. 1981. Pelage polymorphism in Pacific harbor seals. Canadian Journal of Zoology 59:1212–1219.

LAAKE, J., AND E. REXSTAD. 2010. RMark—an alternative approach to building linear models in MARK. Appendix C in program MARK: a gentle introduction (E. Cooch and G. White, eds.). 9th ed. www.phidot.org/software/mark/docs/book. Accessed 4 May 2011.

LUCAS, Z., AND W. T. STOBO. 2000. Shark-inflicted mortality on a population of harbour seals (*Phoca vitulina*) at Sable Island, Nova Scotia. Journal of Zoology (London) 252:405–414.

MACKEY, B. L., J. W. DURBAN, S. J. MIDDLEMAS, AND P. M. THOMPSON. 2008. A Bayesian estimate of harbour seal survival using sparse photo-identification data. Journal of Zoology (London) 274:18–27.

MATHISEN, O. A., AND R. J. LOPP. 1963. Photographic census of the Steller sea lion herds in Alaska, 1956–58. United States Fish and Wildlife Service, Special Scientific Report of Fisheries 424:1–20.

PENDLETON, G. W., ET AL. 2006. Survival of Steller sea lions in Alaska: a comparison of increasing and decreasing populations. Canadian Journal of Zoology 84:1163–1172.

PITCHER, K. W. 1990. Major decline in number of harbor seals, *Phoca vitulina richardsi*, on Tugidak Island, Gulf of Alaska. Marine Mammal Science 6:121–134.

PITCHER, K. W., AND D. G. CALKINS. 1979. Biology of the harbor seal, *Phoca vitulina richardsi,* in the Gulf of Alaska. Alaska Department of Fish and Game, Outer Continental Shelf Environmental Assessment Program, RU 229, Contract 03-5-002-69:1–72.

PITCHER, K. W., AND D. C. MCALLISTER. 1981. Movements and haulout behavior of radio-tagged harbor seals, *Phoca vitulina*. Canadian Field-Naturalist 95:292–297.

REIJNDERS, P. J. H., ET AL. 1997. Population development of harbour seals *Phoca vitulina* in the Wadden Sea after the 1988 virus epizootic. Journal of Sea Research 38:161–168.

RIES, E. H., I. M. TRAUT, A. G. BRINKMAN, AND P. J. H. REIJNDERS. 1999. Net dispersal of harbour seals within the Wadden Sea before and after the 1988 epizootic. Journal of Sea Research 41:233–244.

SEBER, G. A. F. 2002. The estimation of animal abundance and related parameters. 2nd ed. Blackburn Press, Caldwell, New Jersey.

SIBLY, R. M., J. HONE, AND T. H. CLUTTON-BROCK. 2003. Wildlife population growth rates. Cambridge University Press, Cambridge, United Kingdom.

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

SMALL, R. J., L. F. LOWRY, J. M. VER HOEF, K. J. FROST, R. A. DELONG, AND M. J. REHBERG. 2005. Differential movements by harbor seal pups in contrasting Alaska environments. Marine Mammal Science 21:671–694.

SMALL, R. J., G. W. PENDLETON, AND K. W. PITCHER. 2003. Trends in abundance of Alaska harbor seals, 1983–2001. Marine Mammal Science 19:344–362.

THOMPSON, P. M., AND H. WHEELER. 2008. Photo-ID–based estimates of reproductive patterns in female harbor seals. Marine Mammal Science 24:138–146.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, supplement:120–138.

YOCHEM, P. K., B. S. STEWART, M. MINA, A. ZORIN, V. SADOVOV, AND A. YABLOKOV. 1990. Non-metrical analyses of pelage patterns in demographic studies of harbor seals. Reports of the International Whaling Commission Special Issue 12:87–90.

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