

Estimation of an unobservable transition: from dependence to weaning in the California sea lion
(*Zalophus californianus*)

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A thesis

submitted in partial fulfillment of the
requirements for the degree of

Master of Science

University of Washington

2016

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Program Authorized to Offer Degree:

School of Environmental and Forest Sciences

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Abstract

Estimation of an unobservable transition: from dependence to weaning in the California sea lion
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For wild mammals, weaning begins the most vulnerable life-history period. Success during this transition hinges on an individual's ability to elude predators while learning to handle and locate prey. In most mid-latitude marine ecosystems there is a strong seasonal influence on productivity and prey availability. Thus, the timing of weaning should play a critical role in a successful transition in these systems. In some wild marine mammal populations, however, weaning is largely an unobservable event and, therefore, its timing is poorly understood. Accordingly, we initiated a study in 2010 to estimate the timing of weaning using a single cohort of California sea lions (*Zalophus californianus*) on San Miguel Island, CA (SMI). We marked 244 sea lions (n = 119 males, n = 125 females) so that they were individually identifiable when less than four months of age and then conducted 19 sighting occasions for marked individuals prior to, during,

and after weaning, ending in August 2013. There were 2,179 resights collected for use in analysis, and the data were analyzed using a hidden Markov multi-state model with two levels of state uncertainty. Models included combinations of weight, sex, age, area, and time to assess the influence of these explanatory factors on the probabilities of survival, state detection, sighting, movements between resight areas, and the timing of weaning. The majority of weaning occurred abruptly during a 4-week period starting in late April. The timing of weaning was not affected by the sex or weight of pups, but survival was reduced by 30% for individuals with below-average weight. Sexual segregation occurred immediately after weaning, with males being 3.68 times more likely to disperse from the rookery island. The abrupt weaning transition in late spring revealed by this study coincides with peak upwelling in the California Current Ecosystem, illustrating the importance of prey availability to successful weaning in the California sea lion. Recently, young-of-the-year California sea lions have experienced four years of unusual and largely unexplained increases in mortality, most notably in 2013 and 2015, when record numbers of pups stranded as early as January. Our findings offer new insight into a putative driver of these mortality events – mismatch between seasonal upwelling and weaning – and suggest that pup weights and stranding rates may serve as an index of the health of the California Current Ecosystem.

INTRODUCTION

Three stages of survival rates are generally accepted for all mammals. Namely, mammals begin in a juvenile stage with a low survival rate, then enter a prime-age adult stage with a high survival rate, and end in a senescent stage characterized by a gradually decreasing survival (Pistorius & Bester 2002; Eberhardt 1985; Graeme Caughley 1966). The low survival rate of young mammals is often attributed to mortality occurring during the transition from the stage of nutritional dependence on maternal care to the stage where an individual must nourish itself (weaning) (Proffitt et al. 2008; McMahon et al. 2000; Devilliers & Roux 1992). Weaning poses a great risk to the previously-dependent offspring because the individual must develop the appropriate skills necessary to undertake efficient independent foraging in an unfamiliar environment (Verrier et al. 2011; Spence-Bailey et al. 2007; Lee 1996). Once weaned, an individual's relative body size and condition, interactions with predators, and the ability to discover, handle and consume prey dramatically influence their probability of survival (Lee 1996; Lawson & Renouf 1987). Offspring survival represents a significant contributor to population fluctuations in large mammal species, and periods of low juvenile survival can lead to population declines (Beauplet et al. 2005; Sinclair 2003). Hence, precise assessment of the factors that have the greatest impact on offspring survival during weaning is crucial for the understanding of population dynamics (Coulson *et al.* 2006; Beauplet *et al.* 2005).

In order to identify the biotic and abiotic drivers of survival during the transition to nutritional independence in mammals, the timing of weaning must first be estimated accurately. In wild populations estimating the timing of a transition such as that between weaning and post-weaning can be difficult (Coulson et al. 2006; Eberhardt 1985). Accurately estimating the timing of weaning is especially complicated in some marine mammal species due to their aquatic,

sexually dimorphic, and highly migratory lifestyles (Gulland and Hall 2007). Even for marine mammal species that spend part of their lives on land, such as pinnipeds, weaned offspring can spend a considerable amount of time at sea where they cannot be observed (Beauplet et al. 2005). Thus, in order to gain a better understanding of marine mammal population dynamics, there remains a need for techniques to estimate the timing of weaning.

Modeling state transitions of individuals and associated changes in survival has long been essential to ecologists studying population dynamics (Kendall 2004; Holgate & Caswell 1990; Crouse et al. 1987). This approach was first developed by Darroch (1958) and Arnason (1973), who extended traditional Cormack –Jolly-Seber (CJS) models of survival by allowing individuals to transition between ‘states’ (Ford et al. 2012; Leberon and Pradel 2002). Nichols et al. (1992) later modeled survival with state transitions using body mass (weight) as a covariate, and multistate models now commonly incorporate covariate data (White *et al.* 2006; Leberon & Pradel 2002; Nichols & Kendall 1995). Because many biological states are undetectable without the use of captures or other invasive sampling techniques, many transitions are not practical to estimate, especially at the population level. Kendall (2004) and Pradel (2005) addressed this challenge by using hidden Markov models that not only account for non-detections but also include “state” uncertainty of detected individuals. Today, multistate mark-recapture modeling is performed using Hidden Markov models with state uncertainty (HMM), which include a robust design to improve precision and are designed to cope with the uncertainty of knowing if an observed individual has or has not completed a transition (Kendall et al. 2012). HMMs provide a powerful new tool for researchers to not only identify the timing of transitions in wild populations, but also to determine the influence of covariates (e.g. sex and weight) on post-weaning survival. In this study an HMM allowing two levels of ‘state’ stratification (suckling

status and area of observation) was used to explore the weaning process in the California sea lion (*Zalophus californianus*). This species is well suited for the application of an HMM due to its mid-latitude distribution, high site-fidelity, and the adult female's year round dependence on a terrestrial rookery to give birth, breed, and nurse her young (Williams *et al.* 2011; Trillmich 1996; Peterson & Bartholomew 1967).

The California sea lion is the most abundant sea lion in the world, with a distribution that spans the North Pacific Coast from British Columbia, Canada to southern Mexico, including the Gulf of California (Melin *et al.* 2012; Orr *et al.* 2011; Hernandez-Camacho *et al.* 2008). The U.S. population has been increasing due to protection under the U.S. Marine Mammal Protection Act of 1972 and is currently estimated at 300,000 animals (Carretta *et al.* 2013). Pups are considered full-term if born after May 20th, with a mean pupping date of June 15th. After a 5-day perinatal period, the adult female begins an attendance cycle during which she alternates 2-4 day foraging trips at sea with 1-2 day nursing visits ashore (Heath 1989, Antonelis *et al.* 1990, Melin *et al.* 2000). The duration of foraging trips can vary considerably. The female's foraging efficiency, which is a function of prey proximity and abundance, determines the duration of her foraging trips and subsequently the fitness of her dependent offspring (Boyd 1999). Females and pups do not travel together and continue meeting at rookery beaches during the lactation period until weaning occurs, at which time the female and pup disperse to separate foraging locations (Melin *et al.* 2000). It is currently accepted that female California sea lions nurse their young for 6 to 12 months, with weaning occurring before the birth of the female's subsequent pup (Orr *et al.* 2011; Melin *et al.* 2010b; Bograd *et al.* 2009). Despite the accessibility of the California sea lion's breeding rookeries and considerable attention from researchers, the weaning process of this species has only been broadly described using small sample sizes and indirect methods, and

much uncertainty about the transition to a weaned state remains (Orr et al. 2011; Melin et al. 2010; Williams et al. 2007).

The life history of the California sea lion is tied to annual oceanographic events in the California Current Ecosystem (CCE), such as strong or weak upwelling and El Niño events that influence productivity and prey availability (Melin et al. 2012; Bjorkstedt et al. 2010; Steinfartz et al. 2007; Greig et al. 2005). Thus, knowledge of the timing of weaning is critical to understanding the environmental conditions newly weaned individuals are encountering and how these conditions will impact their survival. A better understanding of relationships between environmental conditions and sea lion survival would, in turn, provide ecologists with a tool to predict population dynamics and allow stranding networks advanced notice of what to expect during the weaning season. The objective of this study was to use a HMM to accurately estimate: 1) The timing of weaning; 2) Survival before, during, and after weaning into the juvenile stage (3rd year of life); and 3) Movements of individuals during and after the weaning process in a wild population of California sea lions.

METHODS

Study area

San Miguel Island (SMI; 34.03° N, 120.44° W) sits 52km off the California coast at the northwesterly extent of the Channel Islands. SMI represents 45% of pup production in the U.S. population of California sea lions and is the northernmost California sea lion rookery (Melin et al. 2010) (Fig. 1). California sea lions use SMI as a rookery and for hauling-out, with the majority of pup production occurring on the western shorelines of the island. Rookeries and hauling sites consist of all substrate types, from rocky coves, steep bedrock benches, cobble, and

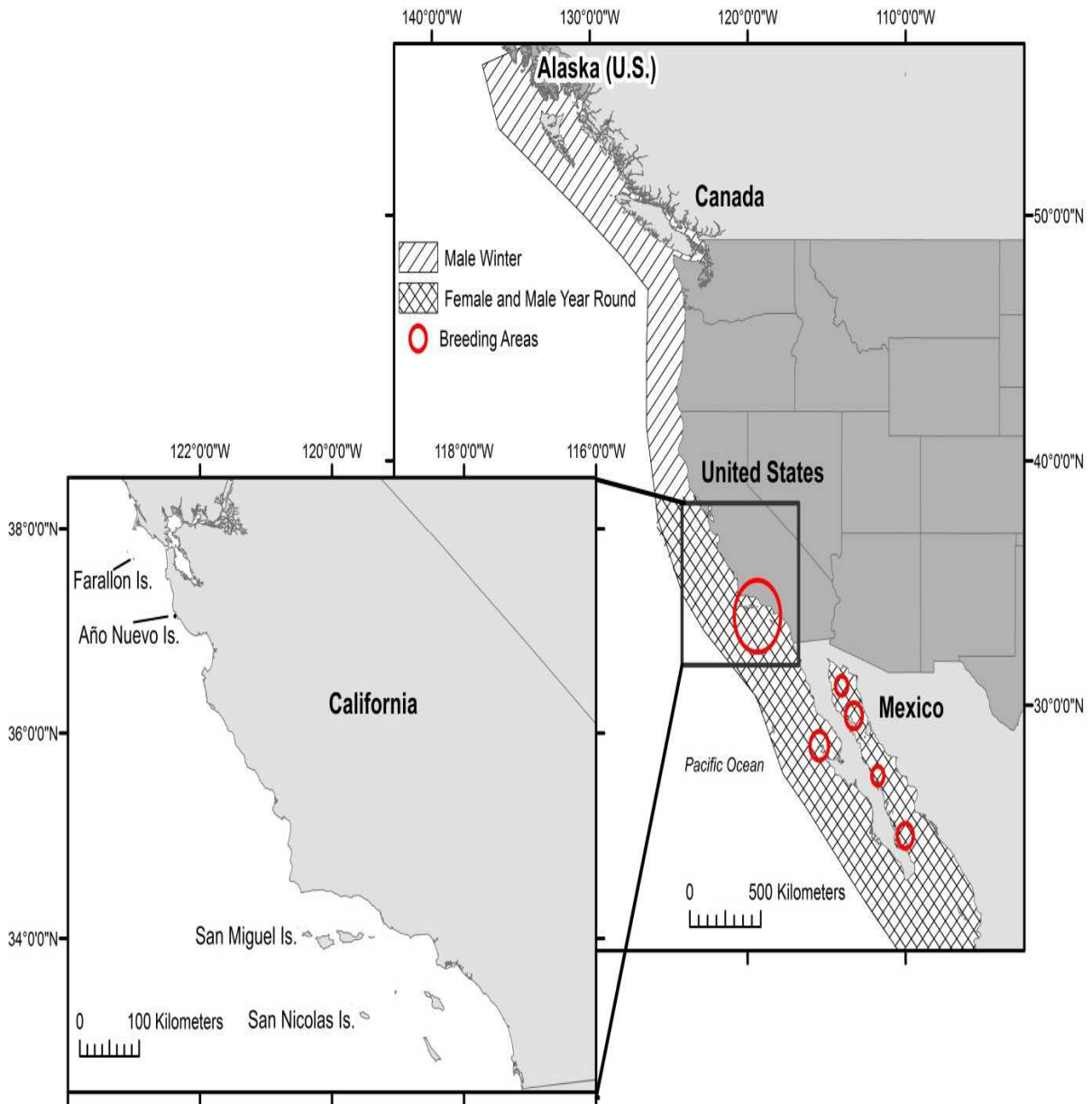


Figure 1: Range of adult California sea lions separated by sex and season. Breeding areas are circled in red. The primary locations of resight effort, San Miguel Island and Año Nuevo Island, are labeled and primary breeding rookeries are outlined.

large sandy beaches. Reproduction of California sea lions was once confined to the westernmost tip of SMI (Point Bennett), but as the population has increased the rookery has expanded to include most of the suitable beaches on the western portion of the island (Fig. 2). Non-rookery shorelines are primarily used by juvenile and non-breeding animals during the reproductive season. All age, sex, and reproductive classes of California sea lions inhabit SMI at various times throughout the year, but as on all rookery islands the greatest numbers of individuals gather between late May and early August during the reproductive season (Peterson and Bartholomew 1967; Odell 1981; Heath 1989).

Marking

Beginning in 1987, the National Marine Fisheries Service (NMFS) has been annually marking 200-500 California sea lion pups at SMI as part of a long-term demography and population monitoring study. As part of this monitoring program, 244 California sea lion pups were marked using hot iron branding and flipper tags in September 2010. At the time of marking the pups were less than four months of age and nutritionally dependent on maternal care. Large groups of adult females and pups hauled-out in Area 1 (Fig. 2) were slowly herded and moved until pups could be isolated. Pups that were obviously unhealthy were removed from the group, because increased stress could greatly reduce their chances of survival. Once separated from adult females, pups were moved and held in a large holding pen until they were processed and released. During processing each pup's sex, weight, length, and molt status were recorded. Yellow roto-tags (Dalton Ltd, London, England) with individual identifiers were placed in the fore-flippers of each animal. The tags help with sighting branded animals in large groups and serve as legible and returnable identification for animals found dead. Each pup was branded on the left shoulder with a unique letter/number combination and released. Branding techniques are

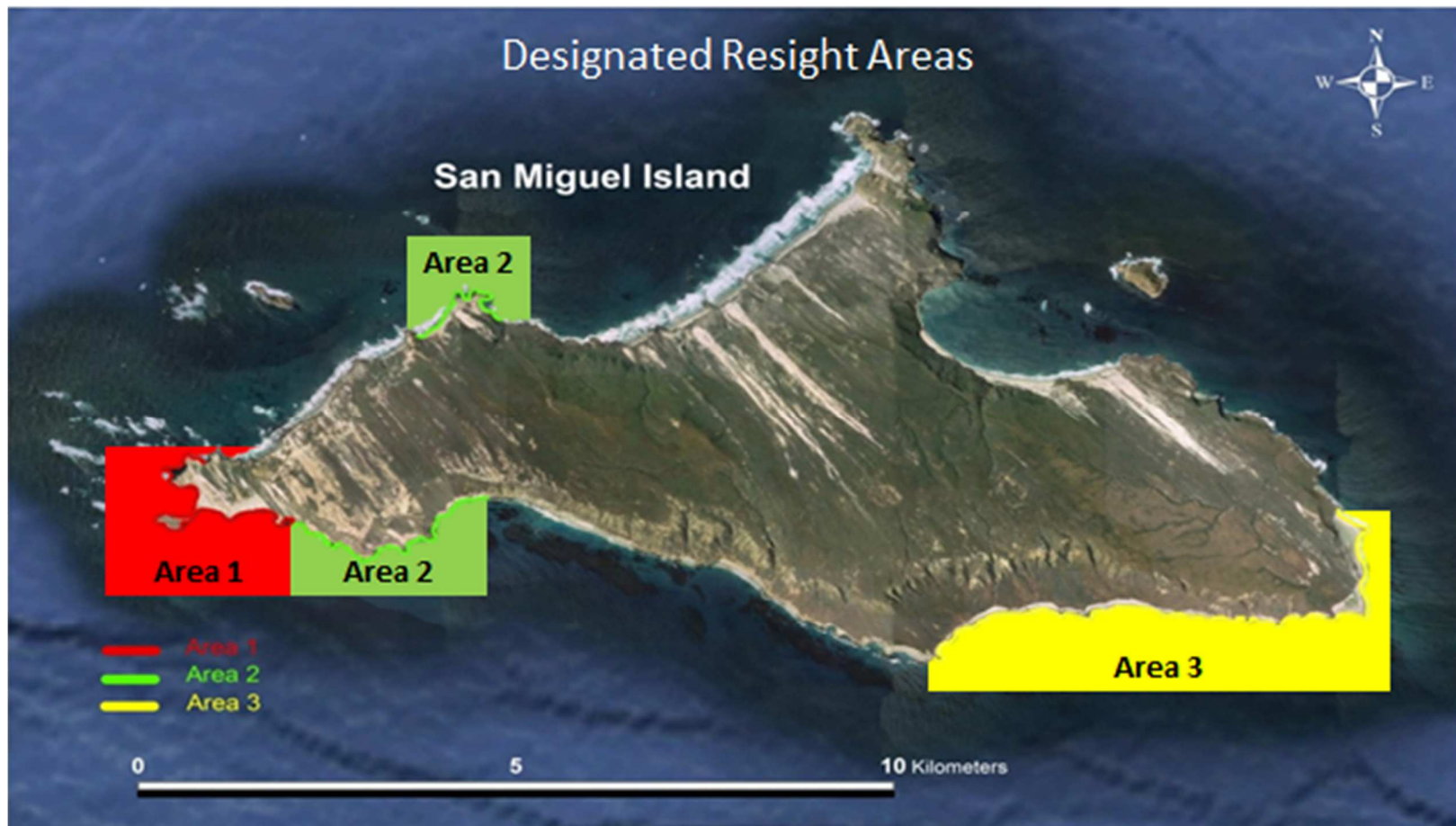


Figure 2: San Miguel Island, California. Three Observation Areas covering all main California sea lion rookery and haul out beaches on SMI are color coded. Capture, marking, and release of all sea lion pups were completed in the eastern portion of Area 1. Area 1 consists of vast sandy beaches. Area 2 features shorelines composed mainly of steep cliffs and large rocks. Area 3 is primarily a juvenile haul-out consisting of vast sandy beaches.

described in Merrick et al. (1996). The research at San Miguel Island was conducted under Marine Mammal Permit Number 782-1613-02.

Resighting

Subsequent to marking, an intensive resight effort of the 244 marked individuals was conducted. Observations were made from stationary blinds and cliffs overlooking populated beaches. Five experienced observers rotated observation areas and scanned populated beaches with binoculars, spotting scopes, and cameras until marked animals were located and identified. For biological, geographical and logistical sampling reasons, beaches on SMI were split into three defined resight areas (Fig. 2). Area 1 included Point Bennett, where all sea lion pups were captured, marked, and released. Area 1 was selected because pups could be easily observed without disturbance. Area 2 included sections of shoreline in close proximity to Area 1. Due to the topography of the shoreline, Area 2 was more challenging for observation than Area 1. Area 3 was located on the east end of SMI and was primarily used as a haul-out site by juvenile California sea lions. Pups traveled to Area 3 less frequently, and suckling behavior was difficult to observe in this area due to the sea lions' distribution on the shoreline and their distance from the observation points. A fourth area was included in the analysis that was not on SMI. Resight Area 4 was located at Año Nuevo Island, California (ANI; 37.01 N, 122.30 W) (Fig. 1), located 380km north of SMI. Resight effort was expanded to include Año Nuevo Island because juvenile California sea lions haul-out at ANI during the reproductive season and will often not return to the SMI rookery beaches. Including resight data from Area 4 in the analysis allowed for a more accurate estimate of juvenile California sea lion survival.

We designed the resight effort to collect data prior to, during, and after the transition to a weaned state. Because California sea lions occupy most of the beaches on SMI, all areas could

not be surveyed daily. Rather, we conducted a total of 19 separate resighting surveys (sighting occasions), including the initial mark-release occasion, between September 2010 and August 2013 (Table 1). Monthly resight surveys focused on estimating the 2010 California sea lion cohort's transition to a weaned state were conducted on SMI from October 26, 2010 until August 18, 2011 (occasions 1-14). Resight surveys during this period were pooled into sighting occasions that were either a trip (7 days) or two half-trips (3.5 days) in length. Each 7 day resight survey was blocked as a single sighting occasion, with the exception of March and April, during which designated resight areas were surveyed twice in consecutive 3.5 day occasions to satisfy the requirements of a robust design (Kendall et al. 2012). Sighting occasions after May 1, 2012 (occasions 15-19) were focused on juvenile survival and were conducted during the reproductive seasons of 2012 and 2013 (Table 1). During the reproductive season (May – August) the California sea lion's range contracts to the breeding islands of California, allowing a more geographically focused resight effort and maximizing the number of marked individuals resighted (Melin et al. 2012a). The resight effort during the breeding season of 2011 was blocked into 5 separate occasions (occasions 10-14) for analysis to better capture the movements of sea lion pups as they weaned and dispersed from Area 1 to the other observation areas. The 2012 and 2013 breeding season sighting occasions (occasions 15 – 17 and 18 – 19, respectively) were blocked in extended intervals with the intention of estimating survival of the 2010 cohort (Table. 1).

Upon resighting a marked sea lion, the date, area of observation, brand number and suckling state were recorded. If an individual was resighted multiple times during a sighting occasion, the observation supplying the most data about the suckling status of the individual was used. When an individual was seen in more than one observation area, the observation closest to

the median date of the observation period was used if the information about sucking was identical. Opportunistic resights were included in the analysis if a photograph was supplied.

Occasion	Midpoint	Begin	End	Comment
1	9/26/2010			Release date
2	10/26/2010	10/24/2010	10/29/2010	First trip
3	12/2/2010	11/30/2010	12/5/2010	Second trip
4	1/21/2011	1/18/2011	1/24/2011	Third trip
5	2/25/2011	2/22/2011	2/28/2011	Fourth trip
6	3/16/2011	3/15/2011	3/18/2011	Fifth trip - first half
7	3/20/2011	3/19/2011	3/22/2011	Fifth trip - second half
8	4/17/2011	4/16/2011	4/18/2011	Sixth trip - first half
9	4/20/2011	4/19/2011	4/21/2011	Sixth trip - second half
10	6/3/2011	5/24/2011	6/12/2011	Summer 2011 - occasion 1
11	6/16/2011	6/13/2011	6/19/2011	Summer 2011 - occasion 2
12	6/22/2011	6/20/2011	6/24/2011	Summer 2011 - occasion 3
13	7/1/2011	6/25/2011	7/9/2011	Summer 2011 - occasion 4
14	7/29/2011	7/10/2011	8/17/2011	Summer 2011 - occasion 5
15	6/10/2012	5/1/2012	6/30/2012	Summer 2012 - occasion 1
16	7/20/2012	7/1/2012	8/9/2012	Summer 2012 - occasion 2
17	9/27/2012	9/18/2012	10/7/2012	Summer 2012 - occasion 3
18	6/7/2013	5/15/2013	6/30/2013	Summer 2013 - occasion 1
19	7/23/2013	7/1/2013	8/15/2013	Summer 2013 - occasion 2

Table 1: Dates of California sea lion resight surveys, split into designated sighting occasions. Resights of individuals were pooled into 19 sighting occasions that were either a trip or half-trip from Fall 2010 to Spring 2011 (9 occasions), and sighting occasions were then defined based on breaks in effort during summer 2011 (5 occasions from 24 May - 17 Aug) and based on timing of field study activities in 2012 (3 occasions), and summer 2013 (2 occasions).

Model building and data analysis

A hidden Markov model with state uncertainty (HMM) can be used to cope with resighting data where a marked individual's state is unclassifiable at the time of observation. When a sea lion pup is resighted suckling, the state of the individual is known, but when a pup is resighted and not seen suckling its state is unclassifiable. Thus, the only observable state is suckling and all other observations of the marked sea lion are unknown. The observable state-dependent sequence $\{X_t : t=1,2, \dots,T\}$ is an HMM that is derived from an unobserved sequence $\{C_t : t=1,2, \dots,T\}$ that satisfies the Markov property, $\Pr(C_t | C_{t-1}, \dots, C_1) = \Pr(C_t | C_{t-1})$ (Laake 2013; Zucchini and MacDonald 2009). When observed, a sea lion that was seen suckling was recorded in state "S" for the occasion. If a pup was seen, but not observed suckling, it was recorded as "U". If the pup was not seen, a "0" was recorded. Prior to occasion 15 the model was allowed to estimate the suckling state of a pup; subsequently all pups were considered weaned and classified as "W" (Table 1). By occasion 15 all pups are weaned ($W=1$). Forcing the model to account for this fact made it more precise by removing unnecessary parameters associated with estimating the transition to a weaned state. Though likely weaned when resighted away from resight Areas-1, 2 and 3, pups were not recorded as such, thereby allowing the model to estimate the suckling state of the individual until the 14th sighting occasion. During each sighting occasion the suckling state of each individual was assessed, creating a single level capture history for each of the 244 California sea lions. An example of a single level capture history for the suckling state of a sea lion pup is as follows: S,U,0,0,0,U,S,U,U,U,U,0,0,0,W. The example capture history reads from left to right and indicates the state of the individual during each sighting occasion. On the first occasion the sea lion pup was seen suckling (S), on the

second occasion the individual was seen, but not seen suckling, and classified as “U”. During the third, fourth and fifth occasions the individual was not seen, and recorded as a “0” for each of those occasions, and so on. The HMM provides the basis for predicting the true state for occasions when the animal is not observed (0), or the animal is observed but the state is unknown (U). In the example sequence above, the state of the individual was uncertain (U or 0) for occasions 2-6, but when the sea lion was observed on the 7th occasion suckling it was clearly not weaned during occasions 2-5. This observation sequence provided the information to estimate *delta* (δ_s), the parameter for state classification. Likewise, on occasions 3 and 4, when the individual was not seen, but then observed during occasion 5, it was clearly still alive, which provided information about *p*, the sighting probability. To take advantage of a robust design, in March and April 2010 we split the 7-day sighting occasion into two 3.5-day occasions. During each 3.5-day occasion the entire island was surveyed. We assumed that there was no mortality during each of the two 3.5-day sighting occasions and that pups did not wean. The robust design improves the accuracy of the estimate for the parameter *delta* by increasing the sample size of sighting occasions used in the calculation. *Delta* is estimated with observation sequences such as S, U, S, where an individual is not seen (U) during a sighting occasion followed by an observation of the true observed suckling state (S), which allows a probability to be calculated for the unknown suckling status (U). By increasing the number of sighting occasions we increased the accuracy of our estimate for *delta*, which in turn increased the accuracy of our estimate for *psi*, the transition to a weaned state.

The robust design model of Kendall et al. (2012) is model RDMSMisClass in the mark-recapture analysis software MARK (White and Burnham 1999). The RDMSMisClass model only allows a single stratification level of states with a single unknown state “U”. During data

collection, it became apparent that there was a reduced likelihood of observing suckling outside of Area 1 due to the sight fidelity of California sea lions. To accommodate for this variability, it was important to include two levels of state stratification (Area and Weaning status). Each resight was classified based on the observation area (Area 1, 2, 3, 4) in which the pup was seen and the weaning state (S,U,0). Thus, there could be 12 different observations for a capture history occasion: 1S, 1W, 1U, 2S, 2W, 2U, 3S, 3W, 3U, 4S, 4W, 4U and 0 when an individual was not observed, allowing state uncertainty (the probability of observing suckling for a non-weaned pup) to differ for the 4 observation areas. Because the area for each observation was known, only the weaning state was uncertain. When constructed as a 2-level capture history, the above capture history example would now be: 1S,3U,0,0,0,3U,1S,1U,1U,1U,1U,0,0,0,4W. The pup was released in Area 1 in the suckling state “S”. It was observed in Area 3 on occasions 2 and 6 but was not observed suckling. It was seen in Area 1 on occasions 7, 8, 9, and 10 but was only seen suckling in occasion 7. The pup was then seen in Area 4 during occasion 15 and was considered to be in a weaned state (W). In this example capture history, we knew that the pup was not weaned when it was seen at Area 3 because it was observed suckling in a subsequent sighting occasion. By creating a model with 2-levels of state stratification, any variation in state uncertainty due to area of observation was accounted for, leading to a more precise estimate of the timing of weaning. The RDMSMisClass model cannot handle a structure with more than one uncertain state (e.g., 1U, 2U, 3U, 4U). Thus, specialized software was included in the R package marked (Laake et al. 2013), creating the model HMMU2IMSCJS.

As described by Kendall et al. (2012), use of an HMM model necessitates making the following assumptions: 1) For individuals in a given state, and for given covariate values, all individuals are equally likely to survive, transition to another state, be detected, and to have their

current state accurately identified; 2) Marks placed on the animal do not affect survival or transitions, are not lost, and are recorded correctly; 3) Each individual acts independently with respect to survival, transitioning to another state, detection, and state assignment.

The following 5 parameters were used with the HMMU2IMSCJS model, and their relevance to the analysis is described below.

1) Sighting probability (p), or the probability of resighting a live sea lion (p_{ist}) that is in Area- i in either state “S” (suckling) or “W” (weaned) on resight occasion t .

2) Survival probability (phi (ϕ)), or the probability that a sea lion survives the time interval from one sighting occasion to the next, was set at an annual rate that was adjusted for the length of the time interval between sighting occasions.

3) State identification probability ($delta$ (δ_s)), or the probability of accurately identifying the state (suckling/weaned) of a sea lion pup that is observed (unknown states are recoded as “U” in the data), was estimated until August 2011 (occasion 14) due to the weaned state being unobservable. After that time (occasions 15-19), $delta$ was set to zero ($\delta_s = 0$ and $\delta_W = 1$), and all sea lions were considered weaned.

4) Transition probability (psi (ψ_{SW})), or the probability that a live sea lion transitions from suckling to weaned during the interval between sighting occasions ($\psi_{SS} = 1 - \psi_{SW}$, $\psi_{WS} = 0$ and $\psi_{WW} = 1$).

5) Movement probability ($alpha$ (α)), is the probability of moving from Area- i to Area- j (i.e., α_{ij}) during the interval between sighting occasions. Transitioning from one state-area to another is the product of the appropriate psi (ψ) and $alpha$ (α) parameters.

These 5 parameters (p , ϕ , δ , ψ and α) were used to form the state transition matrix (Γ) and the observation probability matrix (D) for the hidden Markov model (Laake 2013) (Table 2). The state transition matrix for the 3 possible states (“S”, “W”, or “0”) in combination with the 4 possible observation areas (1-4) is the product of the suckling state transition matrix (Table 3) and the movement transition matrix (Table 4) because the model assumes these processes are independent. Weaning is an absorbing state; individuals were not allowed to transition from weaned to suckling, so transition from “W” to “S” is set to zero. Between the two 3.5 day occasions in March and April and during each 7 day sighting occasion, we assumed the population was closed in that all pups survived and did not wean, but they were allowed to move between areas. The observation probability matrix (Table 5) describes the probability of each type of observation for the state, which is a function of p and δ . For occasions 1 to 14, the weaning state $\delta_w = 0$ because the weaned state cannot be known and the suckling state S (δ_s) is estimated. After occasion 14, we assumed all pups were weaned so any observation was coded as W, which meant that $\delta_w = 1$ and $\delta_s = 0$. The HMMU2IMSCJS model differs from the Kendall et al. (2012) model in three important ways: 1) We created a second level hidden Markov multi-state model allowing for two levels of state uncertainty (Observation area and Weaning state), allowing for variation in behavior between observation areas; 2) All animals are released in a known state and observation area; and 3) There were no new entrants to the population through the course of the study, negating the need to include π (π) and ω (Ω), which are parameters used by Kendall et al. (2012). The mixture parameter π would have been used only if this were a multi-year study and more than one cohort was included in the analysis. The parameter ω (Ω) does not need to be included in the model because it can be

derived from the ψ (ψ) and ϕ (ϕ) parameters given there are no new entrants during the course of the study.

Sub-model specification

Using the model HMMU2IMSCJS, we explored a total of 18 sub-models. For each of the 5 parameters (p , δ , ϕ , α , and ψ), we identified a set of variables and their interactions that might have the most influence on the parameter (Appendix 1). One such variable, weight, was expected to play a critical role in the timing of weaning. We calculated it from the residual of the sex-specific mean in order to create a weight factor distinguishing between below average ($< -1.5\text{kg}$), normal (-1.5kg to $+1.5\text{kg}$), and above average ($>1.5\text{kg}$) pups. This approach defined three categories for each sex: Females (Small $< 15.2\text{kg}$, $15.2\text{kg} \leq \text{Normal} \leq 18.2\text{kg}$, Large $< 18.2\text{kg}$); Males (Small $< 17.6\text{kg}$, $17.6\text{kg} \leq \text{Normal} \leq 20.6\text{kg}$, and Large $< 20.6\text{kg}$). Using this variable set, a limited number of formulas (sub-models) were defined for each parameter (p (n=3), δ (n=2), ϕ (n=6), α (n=3), and ψ (n=4)). Because there was uncertainty in

(AREA) (STATE)	1S	1W	2S	2W	3S	3W	4S	4W	Dead
1S	$\alpha_{11}(1 - \psi_{SW})\phi$	$\alpha_{11}\psi_{SW}\phi$	$\alpha_{12}(1 - \psi_{SW})\phi$	$\alpha_{12}\psi_{SW}\phi$	$\alpha_{13}(1 - \psi_{SW})\phi$	$\alpha_{13}\psi_{SW}\phi$	$\alpha_{14}(1 - \psi_{SW})\phi$	$\alpha_{14}\psi_{SW}\phi$	$1 - \phi$
1W	0	$\alpha_{11}\phi$	0	$\alpha_{12}\phi$	0	$\alpha_{13}\phi$	0	$\alpha_{14}\phi$	$1 - \phi$
2S	$\alpha_{21}(1 - \psi_{SW})\phi$	$\alpha_{21}\psi_{SW}\phi$	$\alpha_{22}(1 - \psi_{SW})\phi$	$\alpha_{22}\psi_{SW}\phi$	$\alpha_{23}(1 - \psi_{SW})\phi$	$\alpha_{23}\psi_{SW}\phi$	$\alpha_{24}(1 - \psi_{SW})\phi$	$\alpha_{24}\psi_{SW}\phi$	$1 - \phi$
2W	0	$\alpha_{21}\phi$	0	$\alpha_{22}\phi$	0	$\alpha_{23}\phi$	0	$\alpha_{24}\phi$	$1 - \phi$
3S	$\alpha_{31}(1 - \psi_{SW})\phi$	$\alpha_{31}\psi_{SW}\phi$	$\alpha_{32}(1 - \psi_{SW})\phi$	$\alpha_{32}\psi_{SW}\phi$	$\alpha_{33}(1 - \psi_{SW})\phi$	$\alpha_{33}\psi_{SW}\phi$	$\alpha_{34}(1 - \psi_{SW})\phi$	$\alpha_{34}\psi_{SW}\phi$	$1 - \phi$
3W	0	$\alpha_{31}\phi$	0	$\alpha_{32}\phi$	0	$\alpha_{33}\phi$	0	$\alpha_{34}\phi$	$1 - \phi$
4S	$\alpha_{41}(1 - \psi_{SW})\phi$	$\alpha_{41}\psi_{SW}\phi$	$\alpha_{42}(1 - \psi_{SW})\phi$	$\alpha_{42}\psi_{SW}\phi$	$\alpha_{43}(1 - \psi_{SW})\phi$	$\alpha_{43}\psi_{SW}\phi$	$\alpha_{44}(1 - \psi_{SW})\phi$	$\alpha_{44}\psi_{SW}\phi$	$1 - \phi$
4W	0	$\alpha_{41}\phi$	0	$\alpha_{42}\phi$	0	$\alpha_{43}\phi$	0	$\alpha_{44}\phi$	$1 - \phi$
Dead	0	0	0	0	0	0	0	0	1

Table 2: Full independence state transition matrix (Γ) for the possible 9 states with four Areas (1-4), two suckling states (suckling (S) and weaned (W)), and death ($1 - \phi$). The parameters combined in the matrices are the area transition probability *alpha* (α), the state transition probability *psi* (ψ), and survival probability *phi* (ϕ).

State	S	W
S	$(1 - \psi_{sw})$	ψ_{sw}
W	0	1

Table 3: Weaning state transition matrix for the two suckling states (suckling (S) and weaned (W)). The weaned state is absorbing, meaning once an individual is considered weaned it cannot return to a suckling state. The values of each state transition probability *psi* (ψ) are calculated and used in the full independence state transition matrix (Γ).

Area	1	2	3	4
1	α_{11}	α_{12}	α_{13}	α_{14}
2	α_{21}	α_{22}	α_{23}	α_{24}
3	α_{31}	α_{32}	α_{33}	α_{34}
4	α_{41}	α_{42}	α_{43}	α_{44}

Table 4: Area transition matrix of the 4 resight areas (1-4). All possible combinations of an individual's movement between sighting occasions are estimated using this matrix. The value of each possible area transition probability (*alpha* (α)) is calculated separately and used in the full independence state transition matrix (Γ). By definition, $\sum_j \alpha_{ij} = 1$.

(AREA) (STATE)	1S	1W	2S	2W	3S	3W	4S	4W	Dead
0	$1 - p_{1S}$	$1 - p_{1W}$	$1 - p_{2S}$	$1 - p_{2W}$	$1 - p_{3S}$	$1 - p_{3W}$	$1 - p_{4S}$	$1 - p_{4W}$	1
1S	$\delta_S p_{1S}$	0	0	0	0	0	0	0	0
1W	0	$\delta_W p_{1W}$	0	0	0	0	0	0	0
1U	$(1 - \delta_S)p_{1S}$	$(1 - \delta_W)p_{1W}$	0	0	0	0	0	0	0
2S	0	0	$\delta_S p_{2S}$	0	0	0	0	0	0
2W	0	0	0	$\delta_W p_{2W}$	0	0	0	0	0
2U	0	0	$(1 - \delta_S)p_{2S}$	$(1 - \delta_W)p_{2W}$	0	0	0	0	0
3S	0	0	0	0	$\delta_S p_{3S}$	0	0	0	0
3W	0	0	0	0	0	$\delta_W p_{3W}$	0	0	0
3U	0	0	0	0	$(1 - \delta_S)p_{3S}$	$(1 - \delta_W)p_{3W}$	0	0	0
4S	0	0	0	0	0	0	$\delta_S p_{4S}$	0	0
4W	0	0	0	0	0	0	0	$\delta_W p_{4W}$	0
4U	0	0	0	0	0	0	$(1 - \delta_S)p_{4S}$	$(1 - \delta_W)p_{4W}$	0

Table 5. Observation probability matrix (D); each equation in the matrix is created by the product of the 9 possible states with the 13 possible observation area scenarios. Indices for the sighting probability (p) are limited to state and area but can also vary by time depending on the model. Many of the equations are not possible, which result in the value 0 (e.g., cannot be observed as Area 1 when in Area 2).

which set of sub-models would best fit the data, all combinations of each parameters sub-models were fitted to the data to select the top model.

Sighting probability (p)

Three sub-models for sighting probability (p) were examined. Sub-model 1 ($\sim W + \text{area}$) included an additive model with the suckling state (W), which is a binomial variable ($W=1$ if a pup is weaned, and $W=0$ if a pup is not). Suckling state was combined with area of observation (area), which is a factor variable that includes the 4 possible resight areas (Area 1,2,3,4) in which an individual pup could be seen. In sub-model 1 we allowed variation in p due to the possibility that once a pup weaned individuals were likely to move away from their natal beach. Sub-model 2 ($\sim W + \text{time} + \text{area}$) included “area” and “W”, but added a time variable (time). The variable “time” was a factor variable that allowed p to be estimated for each sighting occasion (2-19). Sub-model 3 ($\sim -1 + W + \text{time}:\text{area}$) included an interaction effect between “time” and “area” with an additive effect for “W”, which allowed the model to assess variation in p due to an individual’s movement in time by area and also for differences between pups and non-pups.

Suckling detection probability (δ)

The parameter δ , the probability of correctly classifying the suckling state of a pup, was explored with two sub-models. Suckling was never observed in Area 3 and Area 4 and was more difficult to observe in Area 2 than in Area 1. We therefore assumed area should be included in both sub-models for δ . The period in this study where δ was estimated was from occasions 2-14 (October 2010 to August 2011), after which δ was forced to 1 because all pups were considered weaned. Sub-model 1 ($\sim t1 + \text{area}$) included variation in the estimate during the first sighting occasion where suckling behavior was not recorded ($t1$); by adding the

factor variable “t1” the time periods where delta was and was not recorded (occasion 2) were separated. An additive effect for the factor variable “area” was included in sub-model 1 to allow variation between Area 1 and Area 2. We expected differences in *delta* between Area 1 and Area 2 given that all individuals were marked in Area 1 and because Area 2 consisted of more challenging terrain for observation. Sub-model 2 (~ timebin + area) included an additive effect with “area” and variation in *delta* across three time periods (timebin) during sighting occasions 2-13. The factor variable “timebin” estimates *delta* in three blocked time periods (occasion 2, occasions 3-9 and occasions 10-14) and was selected due to variation in the number of suckling observations between them. These three time periods were chosen for the “timebin” variable because the majority of suckling observations occurred during occasions 3-9.

Survival probability (phi)

There were 6 sub-models selected for the survival parameter (*phi*). The first sub-model for *phi* (~ ageclass) allowed for variation by age class (i.e., split *phi* by time), estimating sea lion survival approximately annually. The variable “ageclass” is a factor variable that separates pups into 3 age categories: (1) Pup, 2) Yearling, and 3) 2 Year old. Pup is defined by occasion 1-13, Yearling is defined from occasion 14-17, and 2-year old is defined by occasions 18-19. Sub-model 2 (~ ageclass + sex) allowed for variation with age class but also included an additive effect of “sex”. The variable sex is a binomial variable (Male = 1, Female=0), letting survival rates differ between males and females. Sub-model 3 (~ pup:Wt) allowed for variation in *phi* between pups and non-pups by including the variable “pup”, a binomial variable (Pup=1, non-pup=0) defined by the age of the animal; individuals were considered pups during occasions 1-13 and non-pups from occasions 14-19. The factor variable interacting with “pup” in sub-model 3 was weight category (Wt), which consisted of three levels assigned to an individual at the time of

marking. Pups were designated as non-pups (juveniles) after the 13th sighting occasion, using 1 July as their first birthday. Sub-model 4 (\sim pup:Wt + ANI) only differed from sub-model 3 through the inclusion of an additive effect allowing pups observed in Area 4 (ANI) to have different survival rates than those that were not. “ANI” is a dummy variable (0/1) that allowed separate survival probabilities for individuals that moved to Ano Nuevo Island (Area 4). Individuals traveling to Area 4 were assigned ANI=1, and individuals that did not were assigned ANI=0. ANI was only included in the model if ANI=1. Sub-model 4 explores the possibility of decreased survival associated with greater movements. Sub-model 5 (\sim pup:Wt + pup:W) included the interaction with “pup” and “ageclass” and an additive interaction with “pup” and a weaned effect (W), which is a binomial variable (W=1 if a pup is weaned, and W=0 if a pup is not). Sub-model 5 explores variation in survival rates due to age class and weight class before and after weaning. Sub-model 6 (\sim -1 + pup:Wt + nonpup:sex) removes the intercept, keeping the interaction with “pup” and “Wt”, and adds the interaction of non-pups with “sex”, where “non-pup” is a dummy variable (“nonpup”=0 if an individual is still a pup and equal to 1 if an individual is not). Sub-model 6 allowed the survival probability to vary between pups and non-pups as well as between males and females.

Movement probability (alpha)

There were 3 sub-models considered for movement transition probability (*alpha*). The *alpha* parameter was specified by a multinomial logit model due to the multiple movement possibilities between the 4 observation areas. For each area, movement could occur to the other 3 areas and the probability of staying in the same area was computed by subtracting from 1, the sum of the probabilities of moving to one of the other 3 areas. *Alpha* was set to zero for sighting occasions 1-4 for Area 3, under the assumption that pups were not large enough to travel this

distance from their natal beach. Likewise, *alpha* was set to zero for sighting occasions 1-9 for Area 4. Sub-model 1 ($\sim -1 + \text{male:to4} + \text{area:toarea}$) allowed variation in movement between sexes, the interaction between male pups (male) moving to Area 4 (to4), where “male” was a binomial variable (Male=1 and Female=0) and “to4” a dummy variable (0/1) set to 1 for movement to Area 4 and 0 for any other observation area. The variable “to4” allowed differential movement to Area 3 for some sea lions. Sub-model 1 also includes an additive interaction allowing movements of all age classes between all resight areas (area:toarea). The factor variable “area” includes the 4 possible resight areas (Area 1, 2, 3, and 4) and the factor variable “toarea”, which allowed movement to Area 1, 2, 3, and 4. When an interaction of “area” and “toarea” is included, allowing the model to differentiate transition probabilities for all possible movements between the four areas of observation. (e.g. Area 1 to 2, 3, 4; Area 2 to 1, 3, 4. . . etc.). Sub-model 2 ($\sim -1 + \text{area:toarea} + \text{nonpup:from3} + \text{nonpup:to3} + \text{nonpup:from4} + \text{nonpup:to4}$) removes the male interaction with Area 4 but allowed for variation between age classes (nonpup) and movement to Area 3 and 4 (nonpup:to3 and nonpup:to4) as well as from Area 3 and 4 between sighting occasions. The dummy (0/1) variables “to3” and “to4” allowed the model to differentiate movement probabilities between observation Areas 3 and 4, where the dummy variables “from3” and “from4” allowed differentiation between movements away from observation Areas-3 and 4. The “to” and “from” variables are only added to the model if an individual makes the transition either to or from the specified observation area. Sub-model 3 ($\sim -1 + \text{area:toarea} + \text{nonpup:from3} + \text{nonpup:to3} + \text{nonpup:from4} + \text{nonpup:to4} + \text{male:to4}$) for *alpha* is the same as sub-model 2, where the movements of non-pups were considered separately between observation Areas-3 and 4, but includes an interaction allowing variation in movement

of males to resight Area 4 (male:to4). Sub-model 3 accounts for variation due to increased dispersal of male pups to resight Area 4.

Suckling transition probability (ψ)

The probability of a suckling pup transitioning to a weaned state (ψ) was assessed using 4 sub-models. Sub-model 1 ($= \sim \text{Time}$) allowed for variation in time fitting a linear model to the estimated timing of the transition to a weaned state. The variable “Time” is a numeric time field that increases or decreases continuously as time progresses. Sub-model 2 ($\text{Time} + \text{Wt}$) also uses “Time”, but adds a variable for a pups weight class (Wt). The factor variable “Wt” is the same as that used in sub-models for ϕ . By including “Wt”, the timing of the transition was allowed to vary between the three weight classes. Sub-model 3 ($= \sim \text{timebin}$) allows for variation in ψ by binning (timebin) sighting occasions. The factor variable “timebin” separates estimates for ψ into 3 periods spanning sighting occasions 2-13 (occasion 2-8, occasion 9, occasions 10-14), allowing ψ to vary before during and after the peak transition period of April 2011. By including “timebin” we allowed a non-linear and more dramatic trend in the timing of weaning to be evaluated by the model. Sub-model 4 ($\sim \text{timebin} + \text{Wt}$) also uses “timebin” but adds “Wt” to the model to assess variability in ψ due to a pups weight class.

Model selection and prediction

In total, 432 models were fitted to the data using all combinations of the 18 sub-models for the 5 parameters (p , δ , ϕ , α , and ψ). For each model, the probabilities for the set of observed capture histories were derived from (Γ) and (D) with the HMM framework (Laake 2013) and the set of parameter values that produced the maximum likelihood (ML) was found using numerical optimization. The best-fit models were identified using the Akaike Information

Criterion (AIC). Model averaged parameter estimates and standard errors were computed using models within 4 units of Δ AIC. Global decoding (Zucchini and MacDonald 2009) was used for the best model to predict the most likely values of the hidden states (“Area” and “Suckling Status”). Hidden states in this application were occasions in which an individual sea lion was observed but its suckling state was not classifiable, resulting in a “U” in the capture history, or an individual was not seen during an occasion, resulting in a “0” in the capture history. Global decoding provides an estimated complete capture history from the incomplete observed capture history by replacing the “0” and “U” observations with the most likely state from the fitted model; for predicted “area” and “weaning state” of each individual during designated sighting occasion, see Appendix 2. Estimates of precision and confidence intervals were obtained using a non-parametric bootstrap by re-sampling the pups with replacement. For estimates of precision with the best model, 100 bootstrap replicates were performed and for model averaged estimates 200 bootstrap replicates were performed. The number of replicates was doubled with model-averaged estimates due to the increased uncertainty while incorporating multiple models. The number of replicates was considered sufficient for the precision estimates because results were changing insignificantly with increased replicates.

RESULTS

In late Sept 2010, 244 sea lion pups were marked and released. The mean pup weight at time of marking was 16.7kg (12kg to 22.6kg) and 19.1kg (12kg to 27.6kg) for females and males, respectively. Animals below 12kg were handled but not included as part of the study due to permit restrictions. The three weight categories – below average (n=75), average (n=85) and above average (n=84) – were distributed as evenly as possible about the mean weight of the cohort. The mean weight of the 2010 cohort was equivalent to the 41 year mean (females=17.0kg

and males=19.0 kg), and their estimated growth rate was above the long-term average (Melin et al. 2012).

During the three-year study 2,179 observations of sea lions were recorded and used for analysis. Some of these observations were of the same animal within an occasion and were therefore collapsed to yield 1,261 resightings for analysis. Eighteen pups were never seen after the initial release, and 150 individuals were resighted subsequent to reaching one year of age. All pups were captured and released in observation Area 1 while still dependent on maternal care. Consequently, the majority of the resightings were in Area 1 (60.1%) and the fewest in Area 4 (8.7%) (Fig. 3).

Suckling behavior was observed at least once for 62.4% of the 226 pups that were resighted. However, suckling behavior was only observed in Area 1 (76.9%) and Area 2 (23.1%) (Fig. 3). Sighting occasions 2-14 (10/2010 to 8/2011) were designed to estimate a pup's transition to a weaned state, so they needed to take place before, during, and after the transition. During these occasions, 1858 observations were recorded and of these only 392 (21.1%) were classified as suckling. The suckling observations were equal between males (n=196) and females (n=196). Only five individuals were observed suckling after 24 May, 2011 (Fig. 4), which indicates the majority of the 2010 cohort weaned abruptly during a four week period between sighting occasions 9 and 10 (4/21/2011 to 5/24/2011).

Initially (occasions 2 - 9), most resightings occurred in Area 1, where all pups were marked and released (Fig. 5). However, by the time the pups reached age 1(occasion 11), less than 10% of males and 30% of females remained in Area 1 where the majority of suckling behavior was observed and all pups were marked. Area 1 consists of Point Bennett and has the

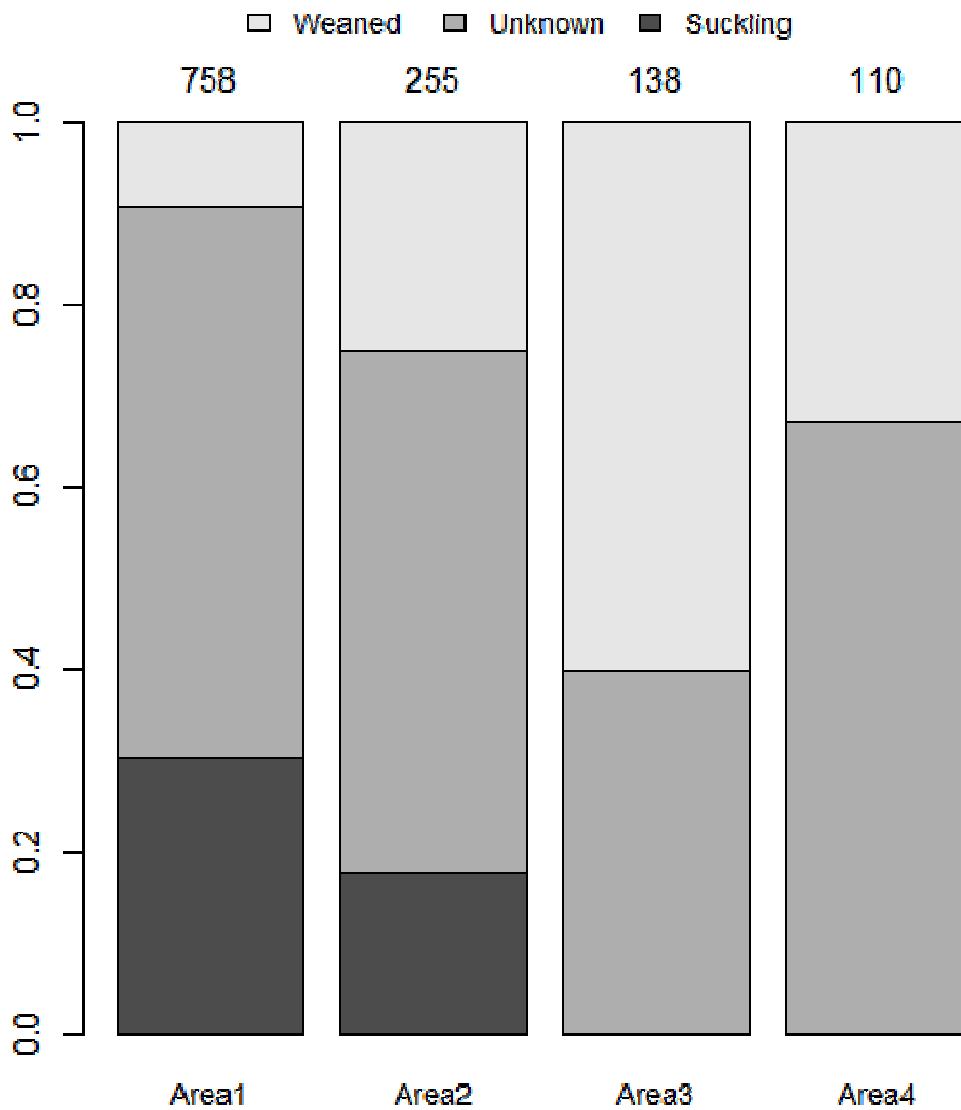


Figure 3. Cumulative number of California sea lion pups observed in each designated resight area (Area 1-4). Within each area, are the proportions of the observed individuals’ suckling states (“Suckling”, “Weaned” [only those in 2012-2013] and “Unknown”) at the time of observation. Designated resight area is given on the y-axis. Suckling was only observed in Area 1 and Area 2.

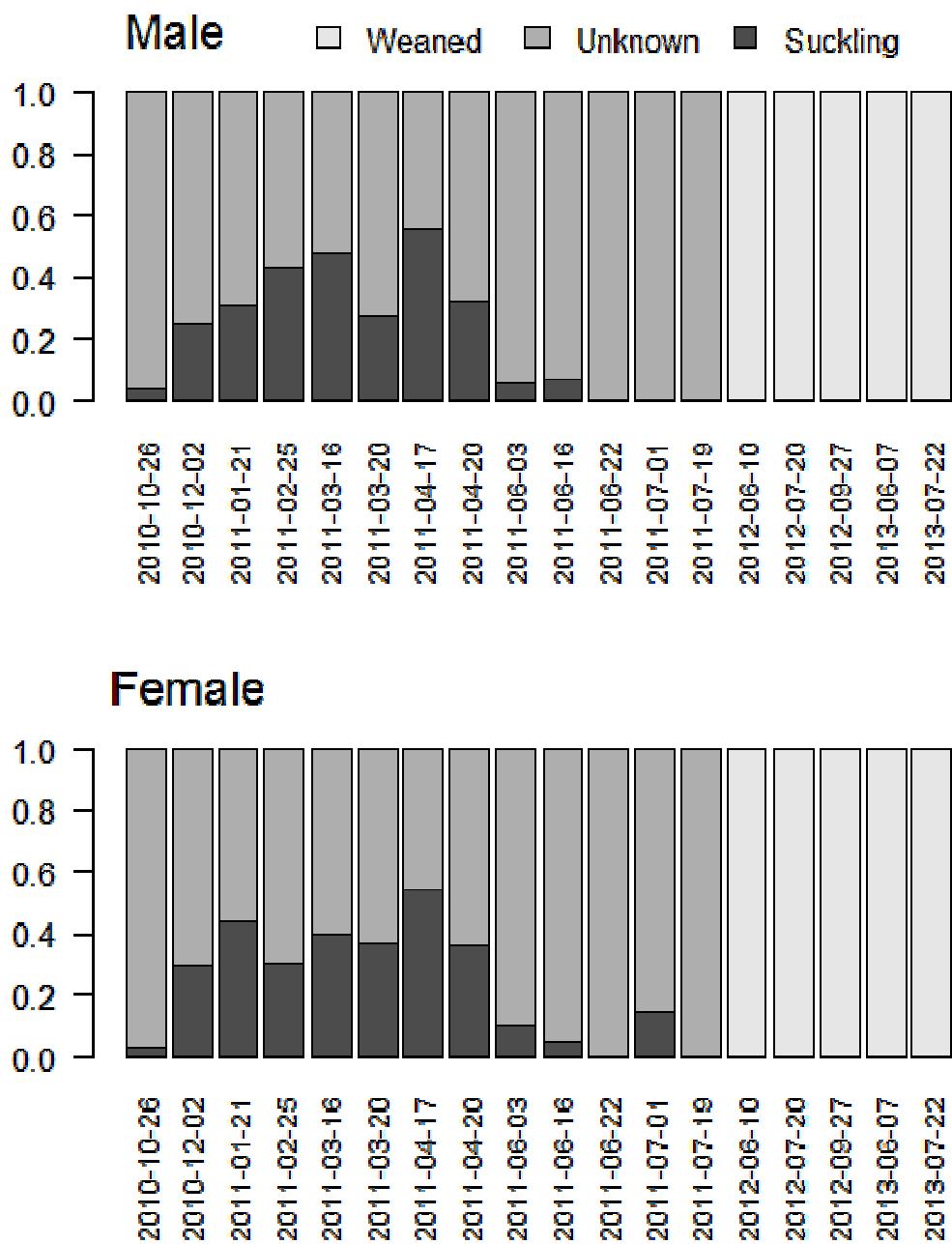


Figure 4. The proportion of the 2010 California sea lion cohort observed in a specific suckling state (Weaned [only those in 2012-2013], Unknown or Suckling), during each designated sighting occasion. Dates given represent the mid-point of each sighting occasion; survey start and stop dates are available in Table 1. All California sea lion pups were considered weaned after sighting occasion 14 (07-19-2011).

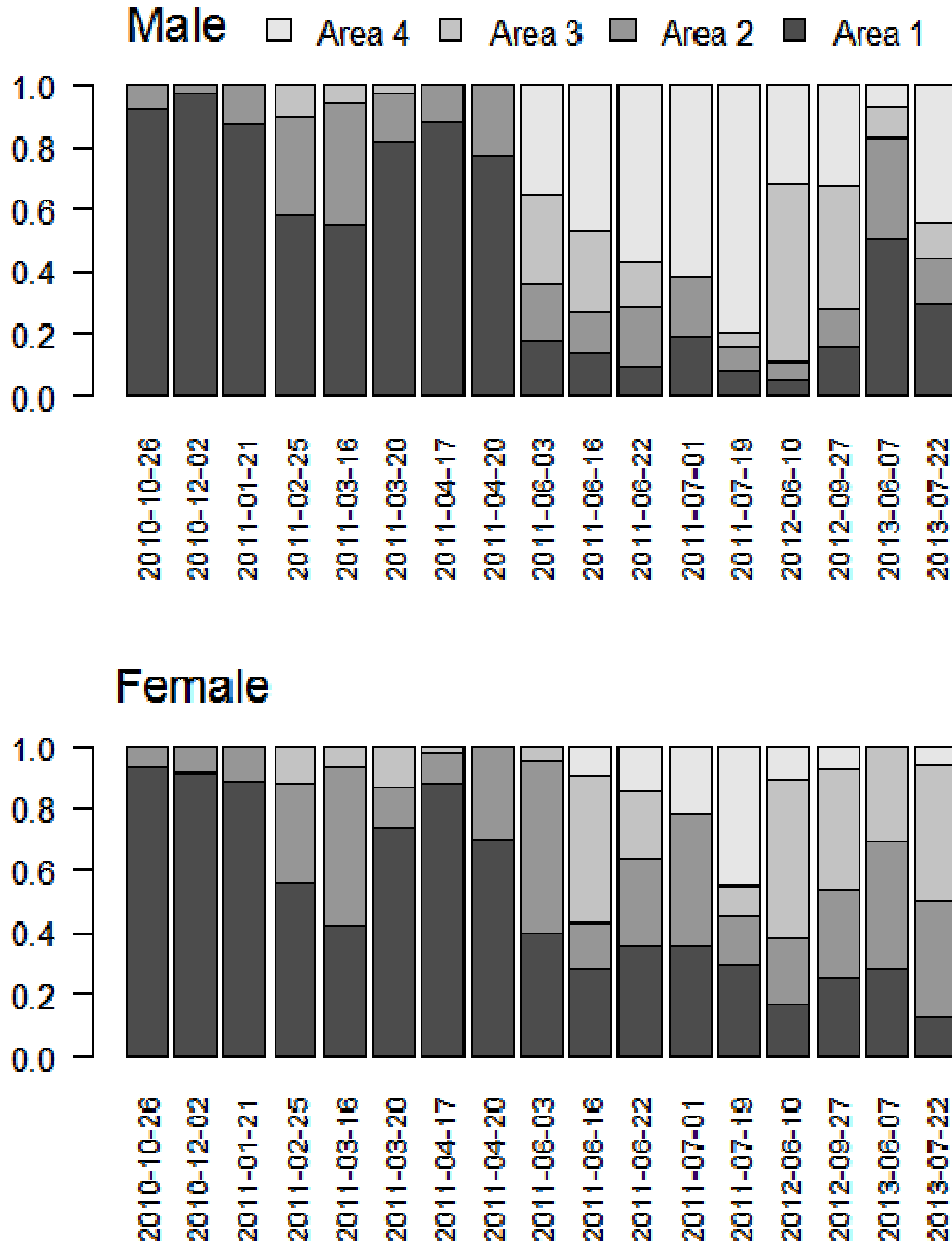


Figure 5. Separated by sex, the proportion of the 2010 California sea lion pup cohort resighted in each Area(1-4) during each designated resight occasion. Dates given represent the mid-point of each resight occasion. The beginning and end dates of each survey are available in Table 1.

highest densities of breeding animals on SMI from May to August (occasions 10 - 14). During these five occasions, females moved to Area 2 and Area 3 whereas males were 3.68 times more likely to move to Area 4 than females (Fig. 5).

Model selection

Of the 432 models tested, 16 accounted for 97% of the model weight. Thus, model averaging and bootstrapped confidence intervals were restricted to these 16 top models (Table 6). The variation across models was due to uncertainty about the best sub-model for survival (ϕ), weaning transition probability (ψ), and state identification probability (δ). All sixteen models had the same sub-model for sighting probability (p) and movement probability (α), which indicates that sub-model 3 best fit the data for these parameters. Different sub-models for α and p were not supported; the closest models that included variation in these two parameters had a DeltaAIC value of 17.6 and 165.5, respectively. The top model included variables for each parameter as follows: sighting probability (-1+W+time:Area); survival probability (pup:Wt); state identification probability (timebin+Area); movement probability (-1+Area:toArea + Nonpup:from3 + Nonpup:to3 + Nonpup:from4 + Nonpup:to4 + male:to4); transition probability, ψ (timebin).

Sighting probability (p)

Sighting probability varied across sighting occasions and observation areas. Generally, it was highest in Area 1 for non-weaned pups (Fig. 6). Sighting probability remained fairly constant throughout resight occasions 2-14 in Area 1 and Area 2 and was more variable in Area 3 and Area 4. Sighting probability estimates for non-weaned pups after occasion 10 were

Suckling pups

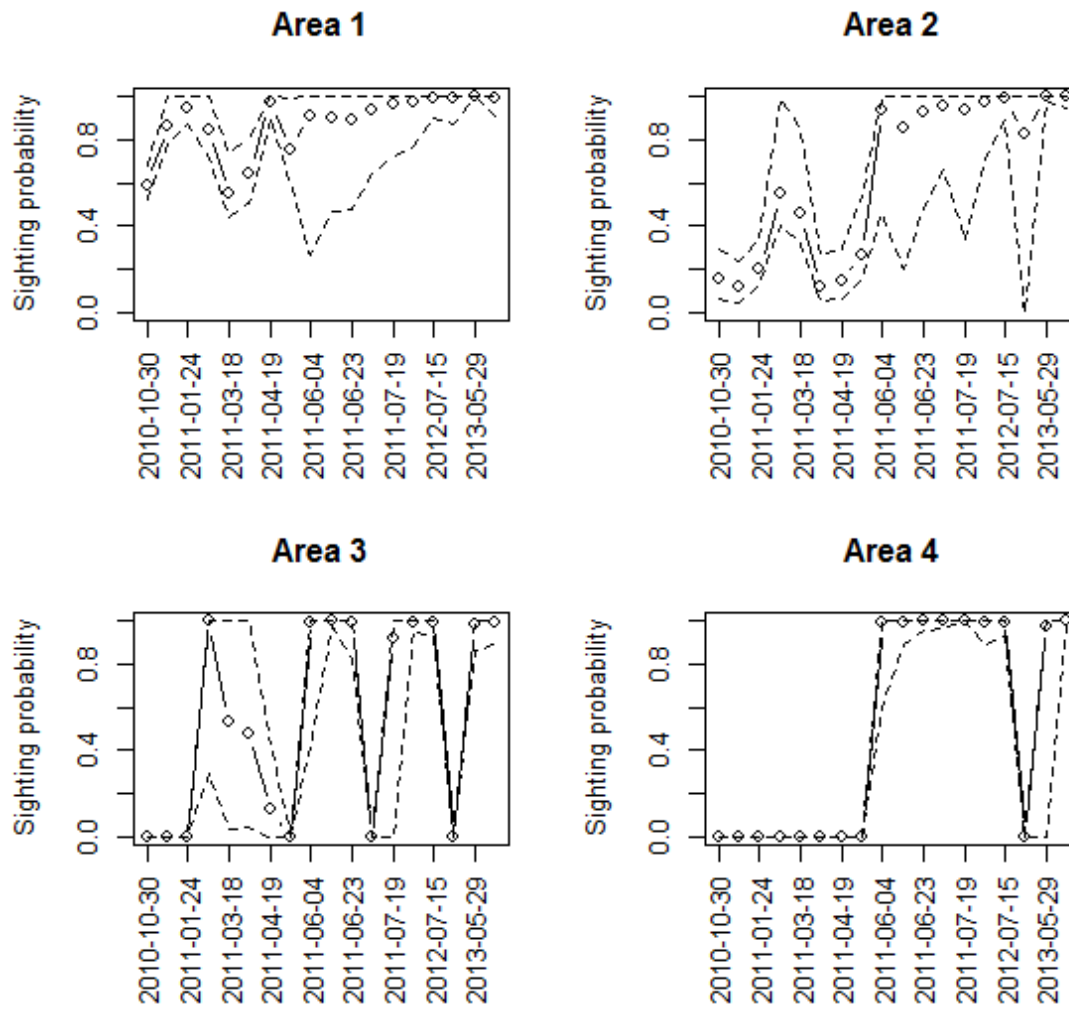


Figure 6. Sighting probability (p) for non-weaned pups in each of the four areas. For occasions with no sighting effort in an area, $p=0$.

unimportant in fitting the model to estimate the transition to a weaned state because most, or possibly all, of the pups were weaned by this occasion. There were 512 resights of 148 individuals during occasions 15 to 19; because of this low sample size estimates of p were imprecise during these occasions. Weaned pups had a reduced sighting probability due to increased dispersion after weaning (Fig. 7). The sighting probabilities were less precise for observation Area 3 and 4 because they had fewer observations. Also, the estimates became more variable through time because the number of live pups decreased through time. Sighting probability increased during occasions 18-19 for Area 1 and Area 2. By the time of these occasions, the 2010 cohort had matured to 3 years of age and begun returning to their natal rookery.

State identification (delta)

During sighting occasion 2 (October 2010), most suckling behavior was errantly ignored, the value for the estimate of δ during this occasion was greatly reduced and had to be accounted for in the modeling (Fig. 8). Beyond October 2010, δ was either kept constant across time or allowed to differ during the summer breeding seasons. δ was allowed to vary during the breeding season following weaning (occasions 10-14) because there were other field duties being conducted simultaneously, and our probability of observing suckling behavior might have differed from that of occasions 2 – 9, when suckling behavior was the focus of work. Unlike sub-models of p and α , there was no definitive best model for δ (Table. 6). The estimate was less precise during the summer period because very few pups were still suckling. There were only 4 individuals observed suckling after occasion 9. δ during occasions 3-9 differed between Area 1 (0.40, 95% CI, 0.45 – 0.35) and Area 2 (0.30, 95% CI, 0.23 – 0.34) (Fig. 8). However, the primary difference in δ was the values of 0 for Area 3 and Area 4, where

Weaned pups

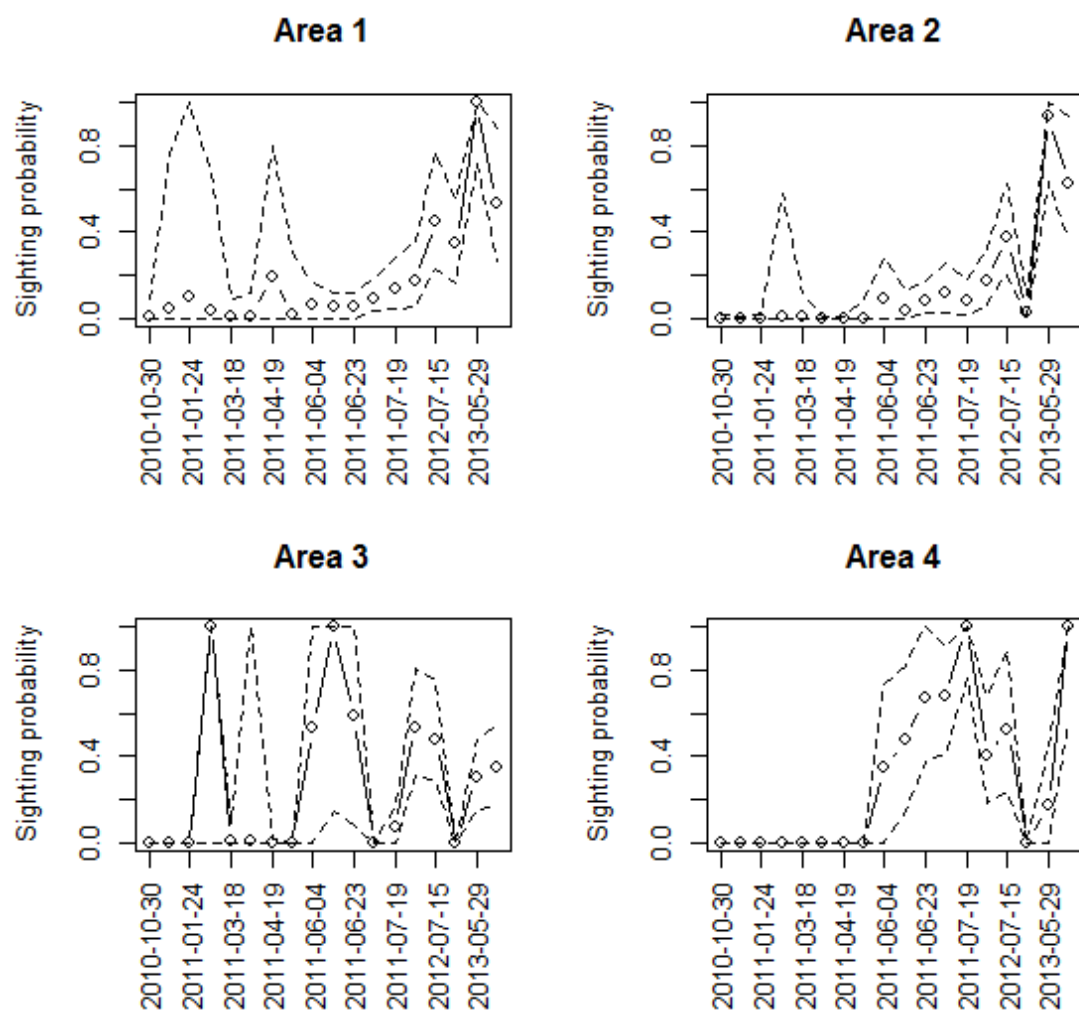


Figure 7. Sighting probability (p) for weaned pups in each of the four areas. For occasions with no sighting effort in an area, $p=0$.

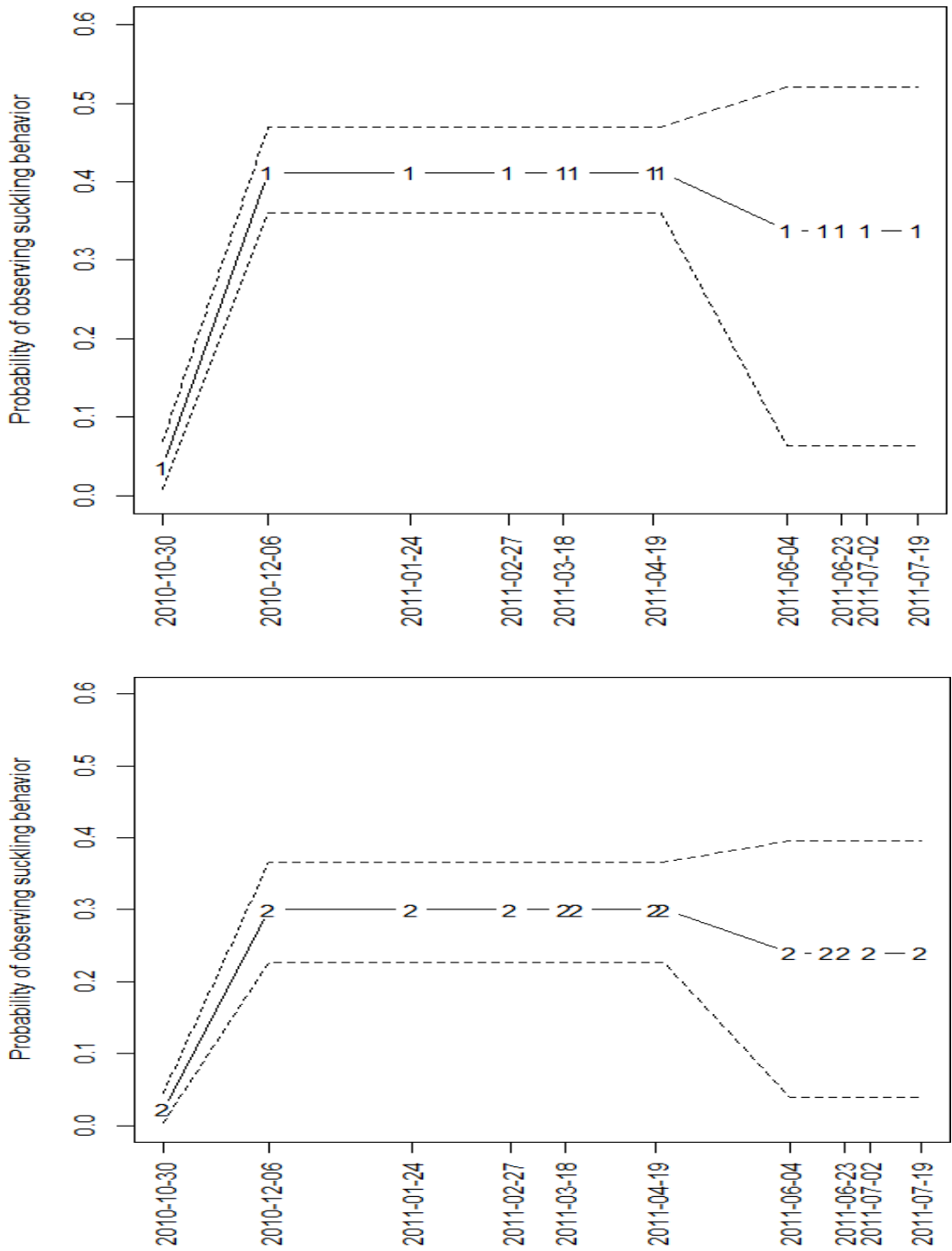


Figure 8. Model averaged estimates of the probability that an observed pup that is still dependant on its' mother for nutrients will be observed suckling in Area 1(1) and Area 2(2) through the first year. 95% bootstrap confidence intervals are shown with dashed lines.

<i>phi</i>	<i>psi</i>	<i>delta</i>	#par	AIC	DeltaAIC	Weight
3	3	2	90	6957.33	0.00	0.16
3	3	1	89	6957.57	0.24	0.15
4	3	2	91	6958.54	1.21	0.09
4	3	1	90	6958.75	1.42	0.08
5	3	2	91	6958.76	1.42	0.08
5	3	1	90	6959.00	1.66	0.07
6	3	2	91	6959.33	2.00	0.06
3	3	2	92	6959.55	2.22	0.05
6	3	1	90	6959.56	2.23	0.05
3	4	1	91	6959.70	2.36	0.05
4	4	2	93	6960.75	3.41	0.03
4	4	1	92	6960.87	3.54	0.03
5	4	2	93	6960.98	3.65	0.03
5	4	1	92	6961.13	3.80	0.02
6	4	2	93	6961.36	4.03	0.02
6	4	1	92	6961.44	4.11	0.02

Table 6. Model selection table for the top sixteen models fitted to weaning data, which represent 97% of the model weights for all of the models tested. Each model used sub-model 3 for p and $alpha$. The numbers specified in the phi , psi and $delta$ columns correspond to the sub-model selected for each parameter in the model. The following columns represent the number of parameters (#par), Akaike Information Criterion (AIC), Delta AIC (difference from the best model) and the model weight using only these sixteen models.

suckling was never observed even though pups were observed in those areas when they were not weaned.

Survival (phi)

Pup survival differed across weight groups, with the largest difference being reduced survival for the below-average weight class (Fig. 9). Annual survival for average and above-average pups was similar in both pre-weaning and juvenile survival (Fig. 9). Other than weight class standing out as the most important predictor of survival in the top two models, it was difficult to differentiate between the next 14 top models with respect to the sub-models with the greatest influence on survival (Table. 6). Sub-model 4 was selected in 4 of the top 16 best fit models, suggesting there may have been slight variation in survival for pups that transition to ANI (Area 4) (Table. 7). There was very little difference in the model-averaged survival estimates between the sub-model that included weaned pups (sub-model 5) and one that included a sex difference for non-pups (sub-model 6) (Table. 6). It was clear that survival was most influenced by weight at the time of marking. The state predictions from the top model of survival to age 1, 2, and 3 years for the pups with below-average weight were 50.7% (se=5.8), 34.7% (se=5.5%), and 30.7% (se=5.3%), respectively. For pups of average weight, the same values were 74.1% (se= 4.8%), 56.5% (se= 5.4%), and 48.2% (se= 5.4%), and for the pups with above-average mass the values were 72.6% (se=4.9%), 60.7% (se=5.3%), and 51.2% (se=5.5%) (Fig.

9). Movement (alpha)

Movement probability (*alpha*) between areas increased as pups aged; however, sea lion pups during this study were most likely to be resighted where they had last been observed (Table 8).

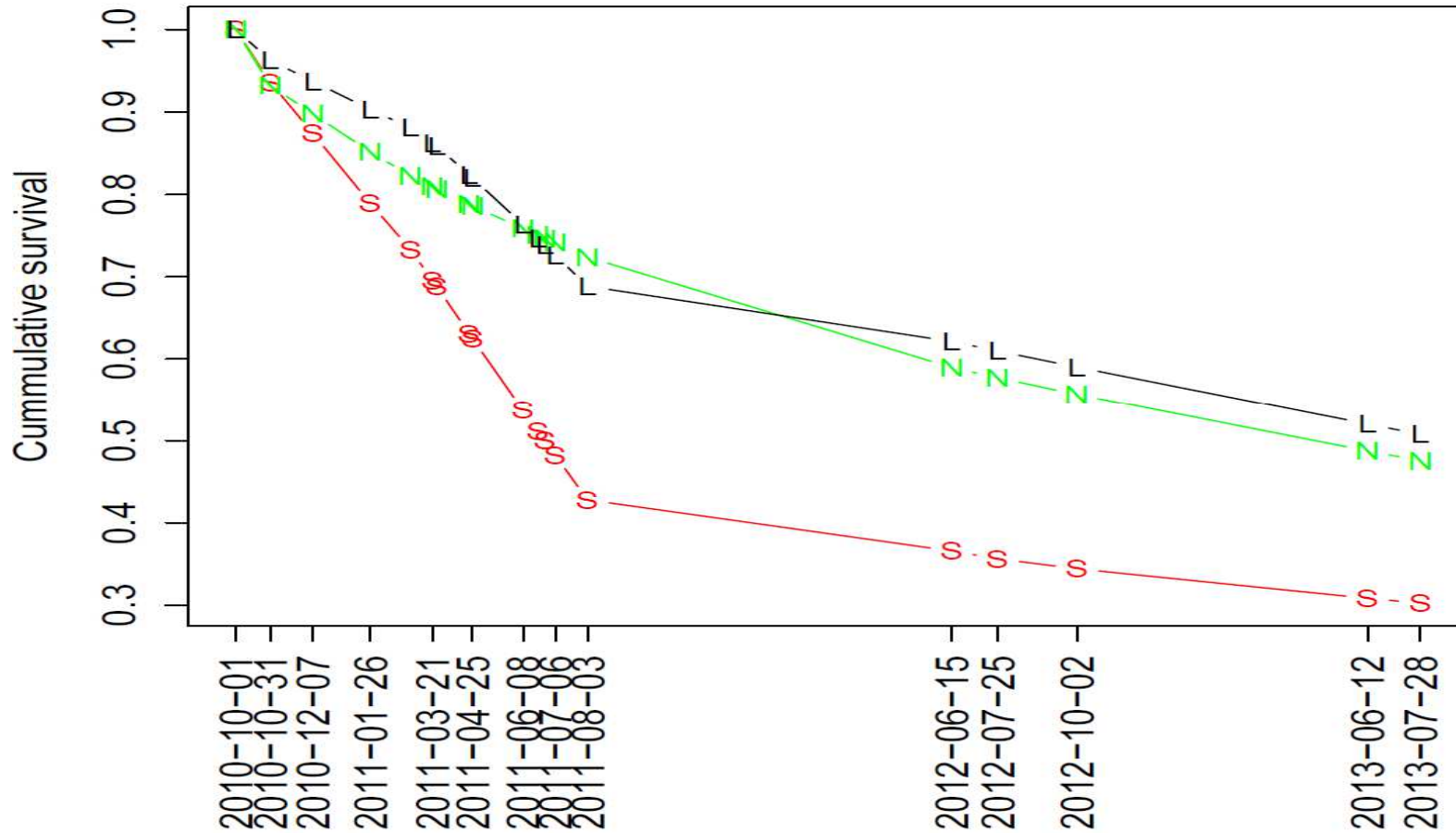


Figure 9. Cumulative survival for sea lions in below-average (S), average (N), and above-average (L) pup weight classes computed from state predictions with the top model. Not all sighting occasions occasions are included on the x-axis.

Age	Weight	State	Area	Estimate	95% confidence interval		
Pup	Low (< -1.5kg)	Suckling	SMI	0.53	0.39	1.00	
		Weaned	SMI	0.55	0.04	1.00	
		Weaned	ANI	0.52	0.04	1.00	
	Avg (-1.5 to 1.5 Kg)	Suckling	SMI	0.75	0.60	1.00	
		Weaned	SMI	0.76	0.24	1.00	
		Weaned	ANI	0.74	0.23	1.00	
	Above Avg (>1.5 kg)	Suckling	SMI	0.81	0.69	1.00	
		Weaned	SMI	0.82	0.23	1.00	
		Weaned	ANI	0.79	0.22	1.00	
	Non-pup		Weaned	SMI	0.78	0.72	0.92
			Weaned	ANI	0.76	0.54	0.91

Table 7. Model-averaged estimates of survival as an annual rate for pups and non-pups in the suckling and weaned states on San Miguel and Año Nuevo islands. Pups were categorized based on their weight anomaly from the sex-specific mean. The Low (below-average) category is 1.5kg or more below the mean. Avg. (Average) is 1.5kg about the cohort mean. Above Avg (above-average) are pups that weighed 1.5kg and greater than the cohort mean.

		Female				Male			
	Area	1	2	3	4	1	2	3	4
Pup Oct-Dec	1	0.797	0.203	0.000	0.000	0.797	0.203	0.000	0.000
Pup Oct-Dec	2	0.177	0.823	0.000	0.000	0.177	0.823	0.000	0.000
Pup Oct-Dec	3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pup Oct-Dec	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pup Jan-Feb	1	0.744	0.189	0.067	0.000	0.744	0.189	0.067	0.000
Pup Jan-Feb	2	0.165	0.766	0.070	0.000	0.165	0.766	0.070	0.000
Pup Jan-Feb	3	0.560	0.440	0.000	0.000	0.560	0.440	0.000	0.000
Pup Jan-Feb	4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pup Mar-June	1	0.736	0.187	0.066	0.011	0.715	0.182	0.065	0.039
Pup Mar-June	2	0.163	0.757	0.069	0.012	0.158	0.733	0.067	0.042
Pup Mar-June	3	0.560	0.440	0.000	0.000	0.560	0.440	0.000	0.000
Pup Mar-June	4	0.021	0.045	0.000	0.934	0.021	0.045	0.000	0.934
Non-pup	1	0.583	0.148	0.233	0.037	0.529	0.134	0.211	0.126
Non-pup	2	0.128	0.594	0.239	0.040	0.115	0.535	0.215	0.134
Non-pup	3	0.121	0.095	0.784	0.000	0.121	0.095	0.784	0.000
Non-pup	4	0.097	0.206	0.000	0.697	0.097	0.206	0.000	0.697

Table 8. Movement transition probabilities between Areas-1, 2, 3 and 4 are shown for female and male pups and non-pups through time. The transition is from an area (row) to the same or different area (column). Movement to area was set to 0 for area 3 prior to January and for area 4 prior to March based on the swimming abilities of pups.

Until weaning, movements of male and female pups were similar. Subsequent to weaning, male pups were 3.68 (95% CI 1.97-10.07) times more likely to transition to Area 4 (Fig. 10). Male pups dispersed away from rookery areas earlier than female pups. The highest proportion of females observed in Area 4 was during resight occasion 14 (36%) (10-July 2011 to 17- August 2011). Unlike males, females did not return to resight Area 4 as juveniles during their 2nd and 3rd years. During occasions 15-19 juvenile males continued to be observed at ANI 3.52 (95% CI, 1.90-9.24) times more than juvenile females. Following weaning the 2010 cohort moved away from Area 1 and Area 2 during the pupping and breeding season. As juveniles the proportion of individuals observed in Area 1 and Area 2 remained low until the spring of 2013 (occasion 18); at this point 50% of the surviving pups were estimated to have transitioned back to rookery beaches.

Weaning (ψ and ω)

The 2010 cohort transitioned to a weaned state abruptly during a one-month period from the end of April to the end of May (between sighting occasions 9 and 10). The model with a linear trend in the transition to a weaned state was not supported (Delta AIC = 22.9). Model-averaged estimates for ψ were below 0.10 (95% CI, 0.01 - 0.15) up to the 8th occasion, and there was then an abrupt increase in the estimate of ψ , which reached approximately 0.85 (95% CI, 0.47- 0.95) during occasion 9 (Fig. 11). Following the 10th resight occasion, estimates of ψ dropped and were less precise because there were so few pups estimated to still be suckling (n=11). Surprisingly, there was little support for a difference in the timing of weaning due to a pup's initial weight or sex. In combination with the survival probability (ϕ), ψ is used to

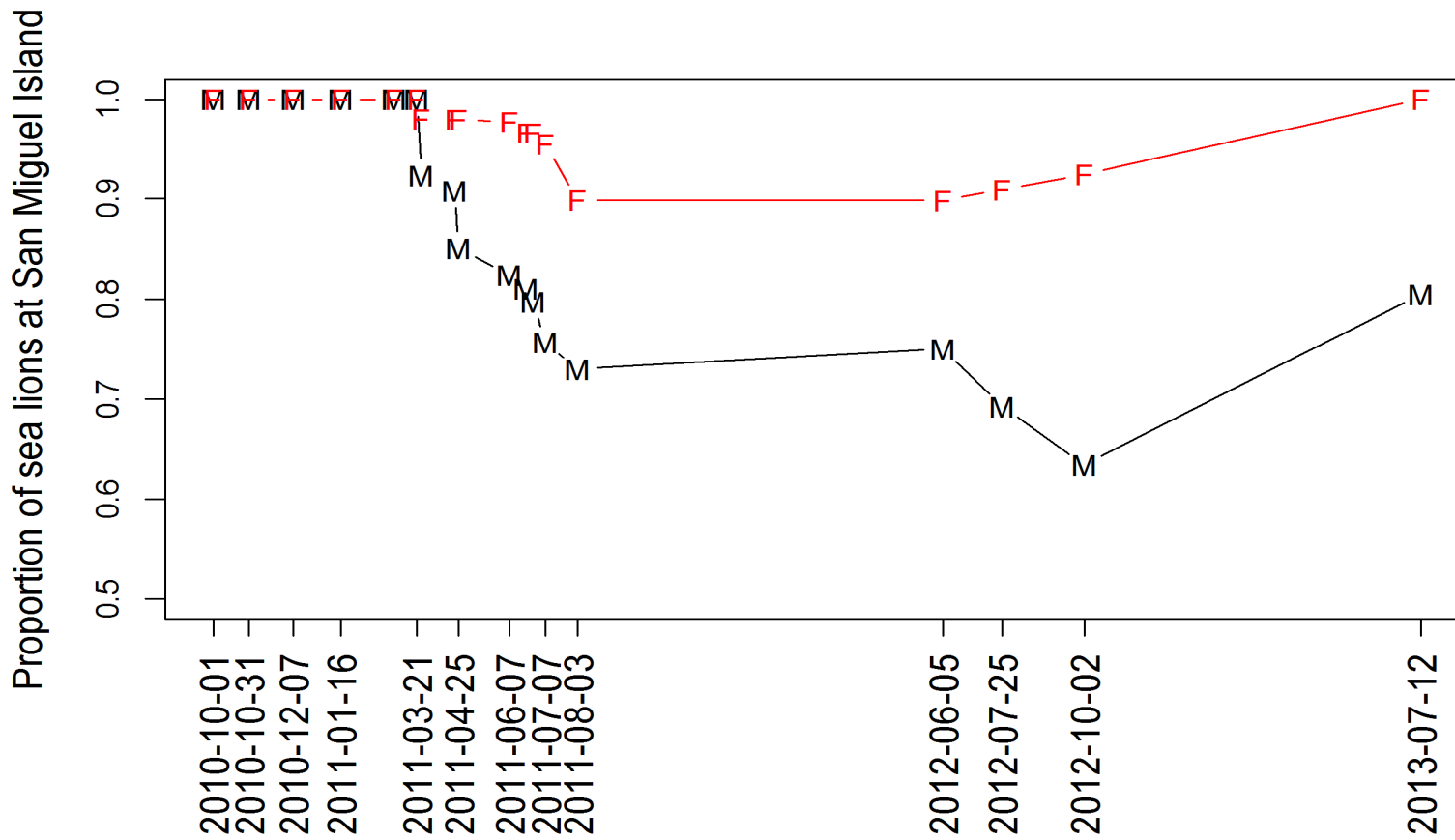


Figure 10. The proportion of females (F) and males (M) at San Miguel island (Areas 1-3) through time computed from state predictions using the top model.

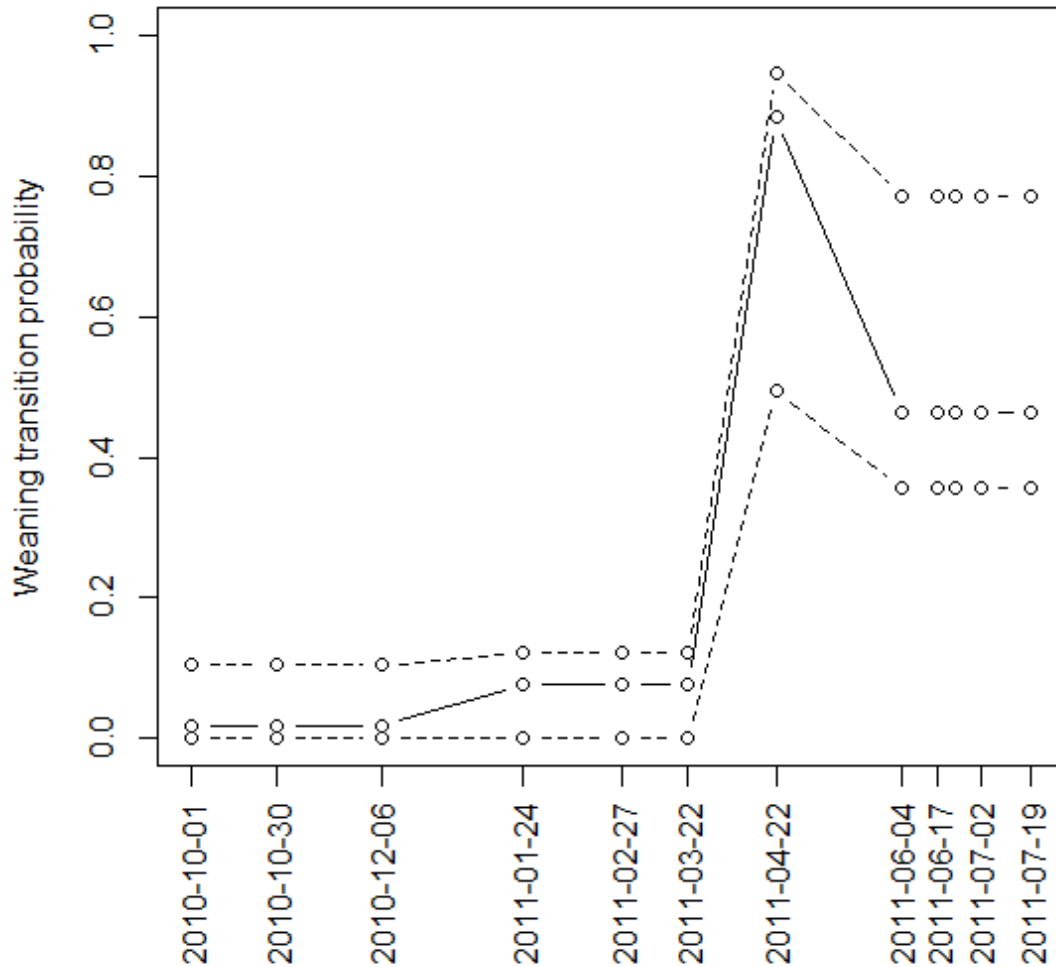


Figure 11. Model-averaged estimates of the probability of a California sea lion pup transitioning from suckling to a weaned state (psi) during the first year (occasions 1-14). 95% bootstrapped confidence intervals are shown with dashed lines.

derive the true parameter of interest in this study, *omega*. The parameter *omega* represents the estimated proportion of living pups that were suckling during each resight occasion (Fig. 12). The percentage weaned prior to late April (occasion 9) was 25.3% (95% CI, 12.4% - 47.3%), and by early June (occasion 10) 91.3% of pups had weaned (48.3% - 96.9%, 95% CI) (Table 9; Fig. 12).

DISCUSSION

Like other marine mammal species, California sea lions exhibit a life-history strategy that challenges assessment of state transitions such as weaning (Gulland and Hall 2007). Specifically, due to this species' extended lactation period, variable foraging trip duration, and pattern of pup dispersal post-weaning, determining if a pup is dependent on maternal care is difficult. This study is the first to estimate the timing of weaning in a wild California sea lion population by combining direct observation and analysis using hidden Markov modeling with state uncertainty (HMM). The 2010 cohort that we used as the basis for our study is the only cohort during the past 7 years (2009 – 2015) with a mean weight equal to the 41 year mean for the population (females = 17.0 kg and males = 19.0 kg) (NMML, unpublished data). Our analysis revealed approximately 25% of the cohort weaning gradually from February to April and then an abrupt four-week weaning period at the end of April to the end of May. During this latter interval, 70% of the cohort was estimated to complete the transition to nutritional independence from maternal care (Fig.12). Following this transition, the cohort experienced a four-month period of enhanced mortality that was especially evident among individuals that were in poorer body condition. We also documented significantly greater post-weaning dispersal in male relative to female pups, revealing a driver of sexual segregation in this sexually dimorphic species. Our results underscore the utility of HMMs for exploring cryptic state transitions in marine mammals, shed

Date	Proportion suckling	95% confidence interval	
10/26/2010	0.98	0.89	1.00
12/02/2010	0.96	0.79	1.00
01/21/2011	0.95	0.71	1.00
02/25/2011	0.87	0.66	0.94
03/16/2011	0.81	0.60	0.91
04/17/2011	0.75	0.54	0.87
06/03/2011	0.09	0.03	0.28
06/16/2011	0.05	0.01	0.13
06/22/2011	0.03	0.01	0.06
07/01/2011	0.01	0.00	0.03
07/29/2011	0.01	0.00	0.02

Table 9. Model-averaged estimates and bootstrapped 95% confidence intervals of the proportion of pups suckling from late October 2010 to late July 2011.

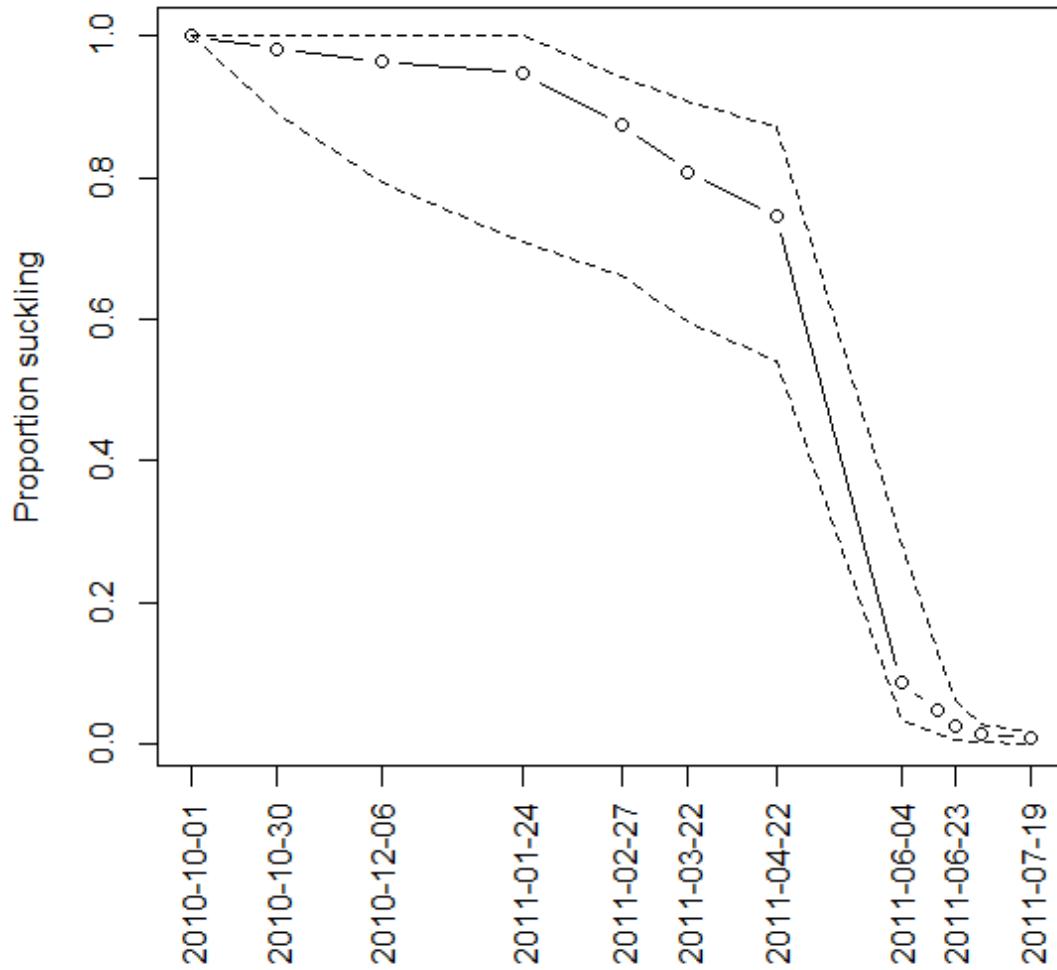


Figure 12. Model-averaged estimates of the proportion of pups that were not weaned through the first year. Values were calculated from survival (ϕ) and state transition probabilities (ψ). 95% bootstrapped confidence intervals are shown with dashed lines.

new light on the weaning process of the California sea lion, and help to explain record mass stranding/mortality events of weaned pups that have occurred recently with the 2011 and subsequent cohorts of California sea lions.

Prior work estimating the timing of weaning in California sea lions and other otariids has largely relied on indirect methods such as stable isotope analysis (Orr et al. 2012), telemetry (Melin et al. 2000), captive studies (Williams et al. 2011; Greig et al. 2007; Hanggi and Schusterman 1990), and food habits analysis (Orr et al. 2011; García-rodríguez and Auriolles-gamboa 1997). These indirect methods have limitations in describing a transition like the timing of weaning in wild pinniped populations, most notably the large sample sizes and/or repeated disturbance to the rookery required for longitudinal data collection. Moreover, telemetry can be expensive, and longitudinal sampling where individual animals must be handled on multiple occasions causes disturbance of unknown levels to both individuals and the colony. In contrast, using an HMM allows for a large sample size and generates an accurate estimate of an unobservable transition with only a single handling event (Laake 2013). After the initial marking event, all subsequent recaptures can be done without disturbing any animals, thereby minimizing the possibility of altering an individual's behavior during data collection. The HMMU2IMSCJS model we employed allowed us to not only estimate the timing of weaning in a wild California sea lion population but also to assess the influence of biological variables on this transition, subsequent survival, and movements between areas. The methods and analysis used in this study describe an efficient way to estimate the timing of an unobservable transition such as weaning (Laake 2013). These modeling methods provide a framework that could be applied to other marine mammal species or any taxa where mark-recapture is appropriate, allowing not only a better understanding of the transition but its impact on the life history of the study species.

Weaning

The results of our modeling exercise offer an appropriate baseline for understanding the weaning process of the California sea lion. In accord with previous studies in wild and captive individuals, we found that weaning in the California sea lion occurs during a window of 6 to 11 months after birth (Williams et al. 2011; Weise et al. 2006; Melin et al. 2000). Our study, however, also provides new insights into the California sea lions' weaning process. First and foremost, we were able to describe the temporal link between weaning and environmental conditions in this species. Namely, successful weaning in the California sea lion overlaps with increased seasonal upwelling in the California Current Ecosystem (Bograd et al. 2009). The overlap of increased productivity in the costal marine ecosystem with the timing of weaning is biologically relevant, but to date it has been difficult to describe statistically. The California sea lion's adaptation to the seasonality of the California Current Ecosystem allows both the adult female and the weaned pup the best opportunity for success. Lactation is energetically expensive, so adult female California sea lions with dependent pups are unable to allocate large amounts of additional energy to fetal growth until the third trimester, when weaning occurs. At this point, the female is no longer a central place forager and is able to allocate all excess energy to gestation without having to maintain lactation or the return to the rookery in regimented intervals (Williams et al. 2011). With 70% of weaning occurring in late April, the majority of females are able to exploit abundant prey over approximately eight weeks during the peak upwelling period for prenatal development before the median pupping date of June 15th. Similarly, the inexperienced pup benefits from weaning in late April by getting to develop foraging skills during peak productivity when prey abundance is increased.

Second, multistate mark-recapture modeling allowed us to assess the importance of individual covariates, and in doing so we learned that in a year where growth rates were normal there was no significant difference in the timing of weaning between males and females as well as between weight classes. Our *a priori* expectation was that weight would play an important role in the weaning process, with adult females prolonging their attendance to pups that were relatively small and less likely to survive. Previous work suggests that there may be two modes of weaning in California sea lions, one where the pup weans itself and one where the female initiates weaning of her dependent pup (Melin et al. 2000). Yet, because there was no difference in the timing of weaning between weight classes, we surmise that weaning during the peak period is not initiated by the dependent pup. Rather, the adult female likely weans her pup once she receives either hormonal or metabolic cues that have evolved in order to allow her to support gestation. We estimated that 20% of weaning occurred prior to the 8th sighting occasion (April 16, 2011). Prior to occasion 8, lactating females should not be constrained by energetic demands due to gestation and would have no reason energetically to wean their pup. Thus, weaning occurring prior to the time period where adult females are entering their third trimester (February and March) is likely initiated by the pup (self-weaning). Self-weaning would be advantageous a pup had developed adequate foraging abilities and prey was abundant. This scenario is supported by a slight increase in the proportion of pups observed suckling just before weaning (occasions 8 – 9) (Fig. 4). During occasions 8 and 9, pups were capable swimmers likely spending more time exploring their environment and less on rookery beaches, returning only to intercept the adult female and suckle (Orr et al. 2011). Given the gregarious nature of the species, California sea lion pups likely interact with and learn from older individuals while exploring their environment (Ono et al. 1987). Such social learning could facilitate self-weaning by enabling individuals to

become efficient enough foragers to support themselves. If so, then we would expect the number of pups that wean early to vary greatly between years because the ability to self-wean would be directly linked to prey availability.

Survival

Weaning poses great risk to a California sea lion pup because successfully completing the transition hinges on an individual's ability to learn how to handle and locate prey efficiently enough to maintain body mass (Lee 1996). The naive pup must at the same time recognize and elude novel predators. Our data show that the period approximately four months after weaning is the most vulnerable period in this species' life history. All three weight classes experienced increased rates of mortality during occasions 8-14 (April to July), and the cumulative rate of mortality for the cohort was approximately 15% during this short period. The mortality rate of the below-average weight class was greatest during occasions 8-14, accounting for more than 50% of the cumulative mortality during this period (Fig. 9). Weight at time of marking was the most influential predictor of the likelihood that pups would survive weaning. As with other pinniped species, weight as a proxy for body condition is incredibly important for survival (Donohue et al. 2002; Lee 1996; Reiter et al. 1978). Sea lion pups of above average body condition have an increased thermal capacity as well as diving ability (Costa and Sinervo 2004; Reiter et al. 1978), both of which confer an energetic and physiological advantage.

We used weight at capture (occasion 1) as a surrogate for weight at the timing of weaning because previous survival modeling of cohorts marked in previous years has shown weight at time of marking is a significant contributor to survival and lifetime reproductive output (Melin et al. 2008). Yet, the majority of weaning occurred when pups were at approximately 10 - 11

months of age. Thus, a second capture effort conducted prior to weaning may have facilitated a better understanding of the impact of weight on survival during the weaning process. Indeed, a small sample (47 individuals) of marked pups were reweighed as part of a concurrent study in January 2011, and 6 (12.7%) of the recaptured pups had undergone an extreme weight change, all but one moving from the below average weight class to the above average weight class. The second weighing of the 2010 cohort also revealed that, for individuals, weight and growth are often non-linear (Bradshaw et al. 2003). The second weighing occasion of the 2010 cohort highlights the growth fluctuation that is possible during an extended lactation period, where females can have pups above the mean weight in one period and below the mean in a subsequent period. Such non-linearity might be expected in a seasonally changing environment such as the California Current Ecosystem, where the abundance and proximity to the rookery of prey species targeted by lactating females is dynamic in time and space. The adult female is a generalist predator relying on a variety of prey species during the lactation period, and the condition of her pup is a reflection of her ability to locate various prey species during all four seasons (Orr et al. 2011; Lowry and Carretta 1999). Furthermore, studies conducted on other otariid species have shown that growth rate is a better predictor of post weaning survival than pup mass (Beauplet et al. 2005). Including growth rate in the HMMU2IMSCJS model would involve adding weight class as an unknown state, allowing it to shift in the sighting occasion where the recapture took place.

Three to four months after weaning, the survival rates between all three weight classes equalized (Fig. 9). This result emphasizes the impact the weaning process has on mortality; once an individual makes it through the critical survival period after weaning (occasion 14) it has successfully reached a level of foraging efficiency where its' survival is no longer impacted by

pre-weaning its' weight. After the critical survival period following weaning the more gradual decline in survival of the 2010 cohort is somewhat surprising given that in 2012 record numbers of yearlings and juveniles stranded on the California coast. If the survival of the 2010 cohort was impacted during these major stranding events we would have expected to see increased mortality rates between the 2nd and 3rd year (2012-2013) in comparison to the 1st to the 2nd year (2011-2012). We were not able to detect a significant change in the rate of mortality after pups had reached their 1st year (Fig. 9). This result could indicate that the majority of juvenile sea lions stranding during 2012 were not from the SMI colony, and that juveniles from other colonies that historically forage farther south in the California Bight were impacted more heavily during this event. The un-impacted survival rates could also indicate that yearling juveniles were affected more heavily than two-year-olds and that the juveniles coming ashore were primarily members of the younger age class that were less capable foragers. It is also possible that our estimated rate of survival after weaning actually reflects the stranding event, meaning that juveniles in the 2010 cohort experienced a decreased rate of survival after weaning from the 1st to 3rd year of life (2011-2013 and the conditions they were facing were consistent throughout this period.

Movements

This study describes sexual segregation occurring immediately after weaning and the sexes continuing to exhibit variation in movement patterns into their third year. Though weaning occurred simultaneously for male and female pups, male post-weaning dispersal from the rookery beaches of SMI occurred earlier and they traveled farther than female pups. Males were approximately four times more likely to travel to Año Nuevo Island (Area 4) than females. Sexual segregation is a well-known part of the California sea lion's life history (Leung et al. 2012; Wolf et al. 2005), but this is the first quantitative description of segregation occurring

immediately after weaning. Once breeding is finished the majority of adult and sub-adult males travel to the northern end of the California Current Ecosystem, targeting the rich prey resources that exist in these waters (Weise et al. 2006). Increased dispersal of males minimizes resource competition with lactating females that are bound to rookery islands by their dependent pup. Females of the 2010 cohort traveled the greatest distances away from rookery beaches during their first year of independence. After their first year, juvenile females were infrequently observed in Area 4 and were primarily resighted on juvenile haul-out beaches at SMI. Similar findings of sexual segregation were suggested in the Antarctic fur seal and the New Zealand sea lion where males and females were exploiting different foraging locations as well as dispersing greater distances (Leung et al. 2012; Page et al. 2005; Bradshaw et al. 2003).

Our top models suggest the possibility of a reduction in survival due to increased dispersal in males. Effects of sex (sub-model 6) and movement to Año Nuevo Island (Area 4) (sub-model 3) on survival were included in 8 of the top 16 models, indicating that traveling greater distances to take advantage of rich prey resources exposes an individual to greater risk. Along with the greater use of energy to physically travel these distances, the probability of encountering predators during greater dispersal is also increased (Klimley et al. 1992).

Males did return to SMI in the early summer of both 2012 and 2013 during occasions 15 and 17, respectively, and during these occasions they were observed primarily in the juvenile haul-out areas of Areas 2 and 3. Juvenile females were using the same haul-out sites concurrently. It is likely that both males and females did not return to take part in the breeding season but rather to exploit the ephemeral prey aggregations that were first encountered after weaning. Indeed, each spring and early summer, large numbers of juvenile sea lions arrive at SMI (especially in Area 3) that are not participating in breeding. Rather, these juveniles appear

to be targeting squid spawning events and other prey aggregations around the islands. In general, California sea lions are known to identify and utilize ephemeral prey aggregations such as spawning Chinook salmon (*Oncorhynchus tshawytscha*) and Eulachon (*Thaleichthys pacificus*) in the Columbia River and spawning Pacific herring (*Clupea pallasii*) in San Francisco Bay. These ephemeral prey aggregations are targeted annually by individuals and the densities of prey available during these events are likely a major contributor to the success of the individuals that rely on them (Willson and Womble 2006). Likewise, juvenile sea lions that return to SMI are likely utilizing the annual prey aggregations found during their first years of life and may continue to do so until an alternate prey source is discovered.

Stranding events and weaning

In recent years (2009 – 2015) prey availability in the California current has been highly variable and all prey species have declined substantially in biomass (Heine and McClatchie 2013). At the same time, young-of-the-year California sea lions have experienced four years of unusual and largely unexplained increases in mortality and stranding events. Most of this mortality has been attributed to anomalous oceanographic conditions resulting in a reduction of forage fishes available to lactating female California sea lions (Melin et al. 2012). The overall lack of prey available to the lactating female results in increased foraging trip duration and inadequate milk production, which in turn lead to malnourishment of her dependent pup. Interestingly, stranding events of young-of-the-year sea lions have been occurring much earlier than the estimated timing of weaning found in this study. Our results describe weaning in a “normal year”, and thereby allow for a better understanding of what underlies the recent periods of increased mortality and mass stranding events. The most severe stranding events for the California sea lion were recorded in 2013 and 2015, with the peak stranding period occurring

from January to April (NOAA Fisheries, 2013-2015 California Sea Lion Unusual Mortality Event in California). Along with near record-low pup weights (at 4 months of age) recorded for both of these cohorts, these stranded sea lions were weaning up to 3 months early (Appendix 3). This pattern supports the idea that individuals that wean early are self-weaning, and that once a pup has matured to 7 months of age it is capable of making the decision to leave the rookery. It is likely that with the prolonged duration of foraging trips by adult females, self-weaning is an emaciated pup's last resort in an attempt for survival. From our results we can infer that if a malnourished pup decides to self-wean 1-3 months early it has almost no chance of survival. It is possible that the increased mortality rates of the below-average weight class in our results are a reflection of malnourished individuals self-weaning. If pup weights continue to be low at the time of weaning, the survival estimates indicated by this study suggest there will be a major decrease in the number of juvenile sea lions recruiting into the breeding population. As a mesopredator limited to a specific geographic foraging range, the lactating California sea lion is an excellent indicator for the health of the southern CCE (Melin et al. 2012). Accordingly, the below-average pup weights during six of last seven years along with record numbers of pups stranding during the winter and early spring of 2013 (n = 1192) and 2015 (n = 3300) should raise concern about the health of the California Current Ecosystem and warrant more exploration of the relationship between prey availability, pup condition, and lactating California sea lion foraging strategies.

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APPENDICES

Appendix 1.

Sub-model descriptions and variables

Sighting probability (p):

$p.1 = \text{list}(\text{formula} = \sim W + \text{area})$
 $p.2 = \text{list}(\text{formula} = \sim W + \text{time} + \text{area})$
 $p.3 = \text{list}(\text{formula} = \sim -1 + W + \text{time} : \text{area})$

Variables in the sighting probability sub-models were defined as:

W: Binomial variable where $W=1$, if weaned and $W=0$, if suckling, describing the suckling status of a pup.

area: Factor variable which includes the 4 possible resight areas (Area 1,2,3,4) in which an individual pup could be seen.

time: Factor variable with a level for each of the sighting occasions 2-19. time values are the median date of each sighting occasions.

Suckling detection probability (δ):

$\delta.1 = \text{list}(\text{formula} = \sim t1 + \text{area})$
 $\delta.2 = \text{list}(\text{formula} = \sim \text{timebin} + \text{area})$

Variables in the probability of identifying the suckling state (δ) sub-models are defined as:

t1: Factor variable for time that allows for variation in δ during the first observation period.

area: Factor variable which includes only Area 1 and Area 2 as possible resight areas where a suckling pup could be seen.

timebin: Factor variable that separates estimates for δ into 3 periods during sighting occasions 1-14 (occasion 2, occasions 3-9, occasions 10-14).

Survival probability (ϕ):

$\phi.1 = \text{list}(\text{formula} = \sim \text{ageclass})$
 $\phi.2 = \text{list}(\text{formula} = \sim \text{ageclass} + \text{sex})$
 $\phi.3 = \text{list}(\text{formula} = \sim \text{pup} : Wt)$
 $\phi.4 = \text{list}(\text{formula} = \sim \text{pup} : Wt + ANI)$
 $\phi.5 = \text{list}(\text{formula} = \sim \text{pup} : Wt + \text{pup} : W)$
 $\phi.6 = \text{list}(\text{formula} = \sim -1 + \text{pup} : Wt + \text{nonpup} : \text{sex})$

Variables in the sighting probability sub-models are defined as:

ageclass: Factor variable that separates sea lions into 3 categories (1) Pup, 2) Yearling, 3) 2 Year old) according to age. Pup is defined by occasion 1 – 13, Yearling is defined from occasion 14-17, and 2-year old is defined by occasions 18-19.

sex: Sex is a binomial variable where male = 1 and female=0

pup: Binomial variable where a Pup=1 and a non-pup=0 is defined by the age of the animal which is considered a pup during occasions 1-13 and non-pup from occasions 14-19

Wt: a factor variable with three levels assigned to an individual at the time of marking. Below average (< -1.5kg), normal (-1.5kg to +1.5kg), above average (>1.5kg).

ANI: Dummy variable (0/1) that allows separate survival probabilities for individuals that went to Ano Nuevo Island (Area 4). If an individual went to Area 4, ANI=1 and =0 if an individual did not. ANI is only included in the model if ANI=1.

nonpup: Dummy variable (0/1) which was 1 when an individual is a pup than nonpup= 0 and if the individual is no longer a pup “nonpup” = 1.

Movement probability (*alpha*):

alpha.1=list(formula=~-1+male:to4+area:toarea)

alpha.2=list(formula=~-1+area:toarea + nonpup:from3 + nonpup:to3 + nonpup:from4 + nonpup:to4)

alpha.3=list(formula=~-1+ area:toarea + nonpup:from3 + nonpup:to3 + nonpup:from4 + nonpup:to4 + male:to4)

Variables in the movement probability sub-models are defined as:

Male: Binomial variable where Male=1 and Female=0.

to4: Dummy variable (0/1) which is 1 for movement to Area 4 and 0 for any other area. This allowed differential movement to Area 3 for some sea lions.

from4: Dummy variable (0/1) which was 1 if the sea lion was in Area 4 and 0 if in the other areas. It allowed differential movement away from Area 4.

area: Factor variable which includes the 4 possible resight areas (Area 1,2,3, and 4)

toarea: Factor variable for movement to Area 1, 2, 3, and 4. area:toarea provided different transition probabilities for each area to each of the other areas (e.g 1 to 2,3,4; 2 to 1,2,3 etc).

nonpup: Dummy variable (0/1) which is 1 when the sea lion was no longer a pup and 0 when it was a pup. Allows for age class separation in movements because older sea lions were more likely to move and move farther distances.

to3: Dummy variable (0/1) which is 1 for movement to Area 3 and 0 for any other area. This allowed differential movement to Area 3 for some sea lions.

from3: Dummy variable (0/1) which allows movement away from Area 3. If an individual moves away from Area 3 than “from3”=1 and =0 the animal does not move away from Area 3. The variable is only added to the model if “from3”=1.

Suckling transition probability (*psi*):

psi.1=list(formula=~Time)
psi.2=list(formula=~Time+Wt)
psi.3=list(formula=~timebin)
psi.4=list(formula=~timebin+Wt)

Variables in the suckling transition probability sub-models are defined as:

Time: Numeric time field a continuous variable that will that will increase or decrease as time progresses forming a linear trend.

Wt: Factor variable with three levels assigned to an individual at the time of marking. Below average (< -1.5kg), normal (-1.5kg to +1.5kg), above average (>1.5kg).

timebin: Factor variable that separates estimates for *psi* into 3 periods during sighting occasions 1-14. (occasion 1-8, occasion 9, occasions 10-14).

Appendix 2.

State prediction table constructed from the top model in the model selection table. “Brand” represents the individual ID of each branded sea lion pup (V1 - V245). The predicted state for each sighting occasion is estimated by the model and gives the most likely state for an individual when a 0 is recorded during the sighting occasion. “Observed sighting data” is the actual data that was recorded during each sighting occasion.

ID#	SIGHTING OCCASION																			OBSERVED SIGHTING DATA
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	
V1	1S	1S	1S	1S	1S	1S	1S	1S	4S	4W	4W	4W	4W	4W	4W	4W	4W	1W	4W	1S,1U,1U,1U,1S,1U,1U,1S,0,4U,4U,4U,4U,0,4W,0,1W,4W
V2	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,1U,1U,1S,1U,1S,1U,0,0,0,0,0,0,3W,0,0,0,0
V3	1S	1S	1S	1S	3S	2S	1S	2S	1S	2W	2W	2W	2W	2W	2W	2W	2W	2W	2W	1S,0,1U,1S,3U,0,0,0,1S,0,0,0,0,0,0,2W,0,2W,2W
V4	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	3W	3W	3W	3W	1S,0,0,0,0,2U,0,2S,0,0,0,0,0,0,3W,3W,0,0,0
V5	1S	2S	2S	2S	3S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	3W	3W	3W	3W	1S,0,0,0,3U,0,0,0,0,0,0,2U,0,0,0,3W,0,0,0
V6	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	4W	4W	4W	4W	1W	4W	1S,1U,1U,1S,1S,1U,1U,1U,0,0,1U,4U,0,4W,0,1W,4W
V7	1S	1S	1S	1S	1S	1S	1S	1S	4S	4W	4W	4W	4W	2W	D	D	D	D	D	1S,0,1S,0,1S,0,0,1U,0,4U,0,4U,4U,0,0,0,0,0,0
V8	1S	1S	1S	1S	1S	1S	1S	1S	4S	4W	4W	4W	4W	4W	D	D	D	D	D	1S,1U,0,1S,1U,1S,1S,1U,0,0,0,0,4U,4U,0,0,0,0,0
V9	1S	1S	1S	1S	1S	1S	1S	2S	2S	2W	2W	2W	2W	2W	2W	2W	4W	4W	4W	1S,1U,1U,1U,0,0,1S,0,0,0,0,0,0,2W,0,0,0,4W
V10	1S	1S	1S	1S	1W	1W	1S	1W	1W	1W	1W	1W	1W	1W	D	D	D	D	D	1S,1U,1S,1S,0,0,0,0,0,0,1U,0,0,0,0,0,0,0
V11	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V12	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V13	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	3W	3W	3W	3W	1S,1U,0,1U,2U,0,0,0,0,0,0,0,0,0,0,0,0,0,3W,0
V14	1S	2S	2S	2S	3S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	3W	3W	3W	2W	1S,0,0,0,3U,0,0,0,0,0,0,0,0,0,0,0,0,0,2W
V15	1S	2S	2S	2S	2S	2S	1S	1S	1S	1W	1W	1W	1W	1W	D	D	D	D	D	1S,0,2U,0,2S,2U,0,1S,1S,0,0,0,0,1U,0,0,0,0,0
V16	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V17	1S	1S	1S	1S	3S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1W	1W	1W	1W	1S,1U,1U,1S,3U,1U,1S,1S,0,1U,1U,0,0,0,1W,1W,0,1W,1W
V18	1S	2S	2S	2S	2S	2S	1S	2S	2S	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,0,0,0,0,2U,0,0,0,0,0,0,0,0,0,0,0
V19	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,0,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V20	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1W	1W	1W	1W	1W	1W	1S,1U,1U,1S,1S,1U,1U,1S,0,0,0,0,0,0,0,0,1W,0
V21	1S	1S	2S	2S	2S	2S	1S	2S	2S	D	D	D	D	D	D	D	D	D	D	1S,1U,2U,0,2U,2U,0,2S,0,0,0,0,0,0,0,0,0,0,0

V22	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	4W	4W	2W	2W	2W	2W	2W	1S,0,0,0,2U,2S,0,0,0,0,0,0,0,4U,4U,0,0,0,2W,0
V23	1S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,0,1S,1S,1U,0,0,0,0,0,0,0,0,0,0,0,0
V24	1S	2S	2S	2S	2S	2S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,0,2S,0,1U,0,0,0,0,0,0,0,0,0,0,0,0
V25	1S	1S	1S	1S	2S	2S	1S	2S	1S	1W	1W	1W	1W	1W	1W	4W	4W	1W	1W	1S,0,1S,1U,2U,0,0,0,1U,0,0,0,0,0,0,0,4W,0,1W,1W
V26	1S	2S	2S	2S	1S	1S	1S	1S	2S	2W	2W	2W	2W	2W	2W	2W	3W	3W	3W	1S,2U,0,0,1U,0,0,1U,0,0,0,0,0,0,0,0,2W,0,0,3W
V27	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	3W	3W	3W	3W	3W	3W	1S,1U,1U,1U,1S,1S,1U,1S,1U,1U,1S,1U,1U,0,3W,0,0,0,0
V28	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V29	1S	1S	1S	2S	2S	2S	1S	1S	2S	2S	2W	2W	2W	2W	1W	4W	4W	4W	1W	1S,0,1S,0,0,0,0,1S,0,2S,0,0,0,0,1W,0,0,4W,1W
V30	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V31	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V32	1S	1S	1S	1S	1S	1S	1S	1S	1S	2W	2W	2W	2W	1W	1W	1W	1W	D	D	1S,1U,0,1U,1S,0,1S,1S,1U,0,0,0,2U,1U,0,1W,0,0,0
V33	1S	2S	2S	2S	1S	1S	1S	2S	2S	3W	1W	1W	1W	3W	3W	3W	3W	1W	1W	1S,0,0,0,1S,0,1U,0,0,3U,0,0,0,0,3W,0,0,1W,0
V34	1S	1S	1S	1S	1W	1W	1S	1W	1W	1W	1W	1W	1W	1W	1W	1W	1W	D	D	1S,0,1U,1S,0,0,0,0,0,0,0,0,0,0,0,0,1W,0,0,0
V35	1S	2S	2S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	1S,0,2U,1U,1S,1U,0,1U,1S,0,0,0,0,0,0,0,0,0,0,0
V36	1S	2S	2S	2S	3S	1S	1S	1S	1S	1W	1W	1W	1W	4W	4W	4W	4W	2W	4W	1S,0,0,0,3U,0,1U,1U,0,0,0,0,0,4U,0,0,0,2W,4W
V37	1S	1S	1S	1S	2S	2S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,0,1S,1U,2U,0,1U,1S,1U,0,0,0,0,0,3W,3W,0,3W,0
V38	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V39	1S	1S	1S	2S	2S	2S	1S	2S	2S	3W	1W	1W	1W	1W	D	D	D	D	D	1S,0,1U,2S,2S,0,0,2U,0,3U,0,0,0,0,0,0,0,0,0,0
V40	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1W	4W	4W	4W	1W	2W	1S,1U,1U,1U,1S,1U,1U,1S,0,0,0,0,0,1U,4W,4W,0,1W,2W
V41	1S	2S	2S	2S	1S	2S	1S	2S	2S	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,1S,0,0,0,2U,0,0,0,0,0,0,0,0,0,0,0,0
V42	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	3W	3W	3W	3W	1S,0,0,1S,0,2U,0,0,0,0,0,0,0,0,0,0,0,0,3W,0
V43	1S	1W	1W	1W	1W	1W	1S	1W	1W	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,0,0,0,0,0,0,1U,0,0,0,0,0,0,3W,3W,0,0,3W
V44	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	2W	1W	D	D	1S,0,0,0,0,0,0,0,2U,0,0,0,0,0,3W,2W,1W,0,0
V45	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V46	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V47	1S	1S	1S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,1U,1U,0,3U,1U,0,0,0,0,0,0,0,0,0,0,0,0
V48	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	4W	4W	4W	4W	4W	4W	4W	D	D	1S,1U,1U,1U,1U,0,0,1S,1U,0,4U,0,4U,4U,4W,0,0,0,0
V49	1S	1S	1S	2S	2S	2S	1S	2S	2S	D	D	D	D	D	D	D	D	D	D	1S,0,1U,0,0,0,0,0,2U,0,0,0,0,0,0,0,0,0,0,0
V50	1S	2S	2S	2S	2S	2S	1S	2S	1S	1W	1W	1W	4W	4W	D	D	D	D	D	1S,0,0,2U,2U,0,0,0,1S,0,0,0,4U,4U,0,0,0,0,0
V51	1S	1S	1S	1S	1S	3S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,0,1U,1U,1S,3U,1S,1S,1S,0,0,0,0,0,3W,0,0,3W,0

V52	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,1U,1U,1U,1S,1U,1U,1U,1U,0,0,0,0,0,0,0,3W,3W
V53	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V54	1S	1S	1S	1S	1S	1S	1S	1S	1S	2W	2W	2W	2W	2W	2W	2W	2W	2W	2W	2W	1S,1U,0,1S,0,0,0,1U,1U,0,0,0,0,0,0,0,0,2W,0
V55	1S	1S	1S	1S	2S	2S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,1S,0,2U,0,0,0,0,0,0,0,0,0,0,0,0,0
V56	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1W	1W	1W	1W	1W	1W	1W	1S,1U,0,1U,1U,0,0,1U,1U,0,1U,0,0,0,0,0,0,1W,1W
V57	1S	1S	1S	1S	1W	1W	1S	1W	1W	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	3W	1S,0,1S,1U,0,0,0,0,0,1U,0,0,0,0,3W,0,0,0,3W
V58	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V59	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V60	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	3W	3W	3W	2W	2W	1S,2U,0,2U,0,0,0,0,0,0,0,0,2U,0,0,0,0,0,0,2W
V61	1S	1S	1S	1S	1S	2S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,0,1U,1U,2U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V62	1S	1S	1S	1S	1W	1W	1S	1W	1W	1W	3W	1W	1W	1W	D	D	D	D	D	D	1S,0,1S,1U,0,0,0,0,0,0,3U,0,0,0,0,0,0,0,0,0
V63	1S	1S	1S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	1W	1W	1W	1W	1W	1W	1S,1U,1U,0,0,0,0,0,2U,0,0,0,0,0,1W,0,0,1W,0
V64	1S	1S	1S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	1S,1U,0,1U,1U,0,0,1S,1U,0,0,0,0,0,0,0,0,0,0,0
V65	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V66	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V67	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V68	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	3W	3W	3W	2W	2W	1S,2U,2U,0,2S,0,0,0,0,2U,0,2U,0,0,0,3W,0,3W,2W
V69	1S	1S	1S	1S	1W	1W	1S	1W	1W	1W	1W	3W	1W	1W	1W	1W	1W	D	D	D	1S,1U,1U,1S,0,0,0,0,0,0,0,3U,0,0,0,1W,1W,0,0
V70	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	4W	2W	D	D	D	D	D	D	1S,0,0,0,0,0,0,0,0,0,0,0,0,0,4U,0,0,0,0,0,0
V71	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V72	1S	1S	1S	1S	3S	1S	1S	1S	2S	2W	2W	2W	2W	2W	2W	2W	2W	2W	2W	2W	1S,0,1U,1U,3U,0,0,1S,0,0,0,0,0,0,0,0,0,2W,0
V73	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	4W	4W	4W	D	D	D	1S,0,0,0,0,0,0,0,0,0,2U,0,0,0,4W,0,0,0,0
V74	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V75	1S	1S	1S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1S,1S,1S,1S,0,1U,1S,0,0,0,0,0,0,0,0,0,0,0
V76	1S	2S	2S	2S	1S	3S	1S	1S	1S	1W	4W	4W	4W	2W	2W	3W	3W	3W	3W	3W	1S,0,0,0,1U,3U,0,1U,1U,0,4U,4U,4U,0,0,0,0,3W,0
V77	1S	1S	1S	1S	1W	1W	1S	4W	4W	4W	4W	4W	4W	4W	4W	4W	4W	4W	4W	4W	1S,1U,1U,1U,0,0,0,0,0,0,0,4U,0,4U,4W,4W,0,0,4W
V78	1S	1S	1S	1S	1S	1S	1S	1S	1S	3W	1W	1W	1W	3W	3W	3W	3W	3W	3W	3W	1S,1U,1S,1S,1S,1S,1U,1S,0,3U,0,1U,0,0,3W,3W,0,0,0
V79	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	3W	D	D	D	D	D	D	1S,0,0,1U,1S,1U,0,1S,1U,0,0,0,0,3U,0,0,0,0,0
V80	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	3S	1S	1W	2W	2W	2W	2W	2W	2W	2W	1S,1U,0,1S,1U,1S,1U,1S,1S,1U,3U,1U,0,0,0,0,0,2W,0
V81	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1S,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0

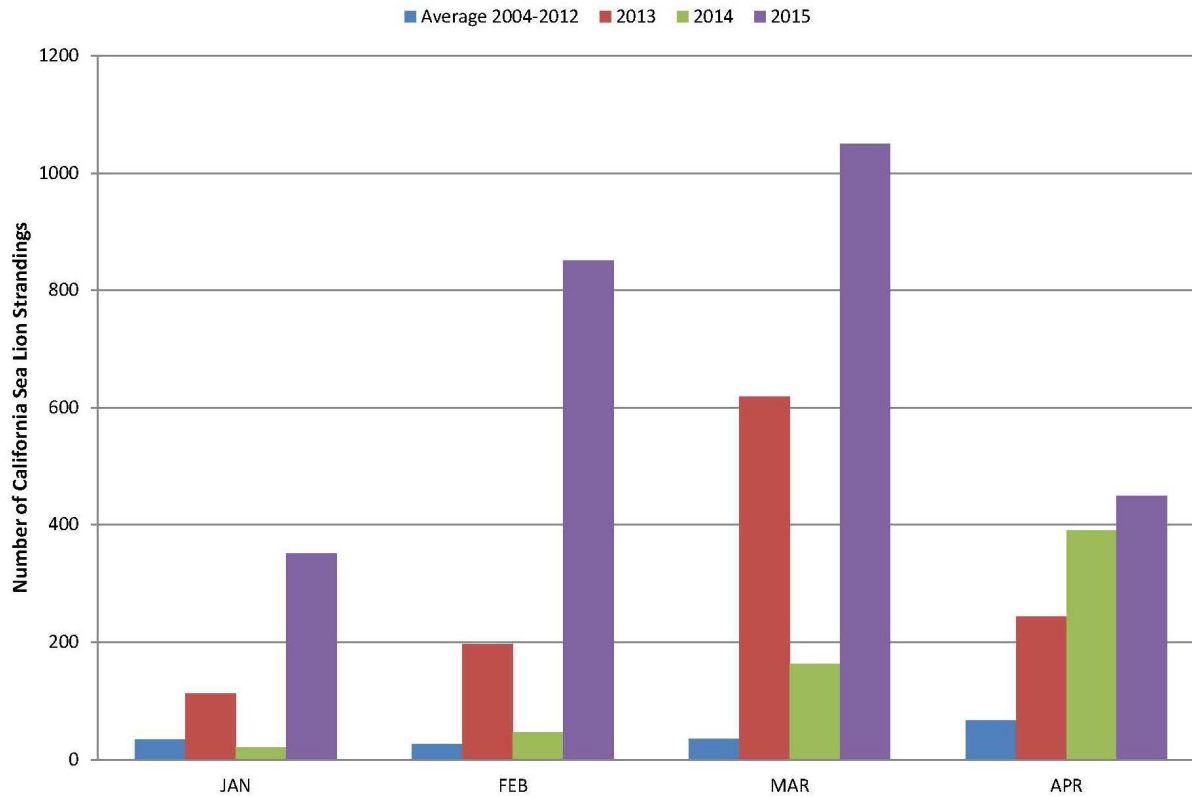
V82	1S	1S	1S	1S	1S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	3W	3W	1W	1W	1S,0,0,1U,1U,0,0,0,0,0,0,0,0,0,0,2W,3W,0,1W,0
V83	1S	1S	1S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	1S,1S,1S,1S,0,0,1S,1S,0,0,0,0,0,0,0,0,0,0,0
V84	1S	1S	1S	1S	2S	2S	1S	1S	1S	2W	2W	2W	2W	4W	D	D	D	D	D	1S,0,0,1S,2U,2U,0,1U,1U,2U,0,0,0,4U,0,0,0,0,0
V85	1S	1S	2S	2S	3S	1S	1S	1S	1S	1W	1W	1W	1W	3W	D	D	D	D	D	1S,1U,0,2U,3U,0,0,1S,1U,0,0,0,0,3U,0,0,0,0,0
V86	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V87	1S	1S	1S	1S	1S	1S	1S	3S	1S	1W	1W	1W	1W	1W	1W	1W	1W	1W	1W	1S,1U,1S,1U,1S,0,1S,0,1U,0,0,0,0,0,0,0,0,0,1W,1W
V88	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,0,1U,1U,0,1U,1U,1U,1S,0,0,0,0,0,3W,0,0,0,0
V89	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	3W	3W	3W	3W	1S,0,2U,2U,2U,2U,0,0,0,0,0,0,0,0,0,0,0,0,3W,3W
V90	1S	2S	2S	2S	2S	2S	1S	4S	4S	4W	4W	4W	2W	4W	D	D	D	D	D	1S,0,0,0,0,0,0,0,0,0,4U,4U,2U,4U,0,0,0,0,0
V91	1S	1S	1S	1S	1S	2S	1S	2S	1S	1W	1W	3W	1W	1W	D	D	D	D	D	1S,1U,1U,1U,1S,2U,0,0,1U,0,0,3U,0,0,0,0,0,0,0
V92	1S	1S	1S	2S	2S	1S	1S	4S	4S	4W	4W	4W	4W	4W	4W	4W	4W	2W	2W	1S,1U,1S,2U,2U,1U,0,0,0,4U,0,0,4U,4U,0,0,0,2W,2W
V94	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	3W	1W	1W	1W	D	D	D	D	D	1S,1U,1U,1S,1U,0,0,1U,0,0,3U,0,0,0,0,0,0,0,0
V95	1S	1S	1S	1S	1S	1S	1S	4S	4S	4W	4W	4W	4W	4W	D	D	D	D	D	1S,1U,1U,1U,1S,0,0,0,0,0,4U,4U,4U,4U,0,0,0,0,0
V96	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V97	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	3W	1W	1W	1W	1W	1W	1W	1W	1W	1S,1U,0,1U,2U,0,1U,0,0,0,3U,0,0,0,0,0,0,1W,0
V98	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	3W	1W	1W	D	D	D	D	D	1S,0,0,0,0,2S,0,2S,0,0,0,3U,0,0,0,0,0,0,0
V99	1S	1S	1S	2S	3S	1S	1S	1W	1W	1W	1W	1W	1W	1W	1W	3W	3W	2W	2W	1S,0,1U,0,3U,0,1U,0,0,0,0,0,0,1U,0,3W,0,2W,0
V100	1S	2S	2S	2S	1S	1S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	1W	2W	1S,0,0,0,1U,0,3U,1U,1U,0,0,0,0,0,0,3W,0,1W,2W
V101	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1W	1W	1S,1U,1U,1U,1U,1U,0,1U,1U,1S,1S,1U,1S,0,1W,1W,0,1W,1W
V102	1S	1S	1S	1S	1S	1S	1S	1S	1S	2W	2W	2W	2W	3W	3W	1W	4W	4W	4W	1S,0,1U,1U,1S,0,1S,1S,1S,0,0,0,2U,0,3W,0,0,0,4W
V103	1S	1S	1S	1S	3S	2S	1S	3S	1S	1W	1W	1W	1W	1W	1W	1W	1W	1W	1W	1S,1U,1U,1S,3U,2U,1U,3U,0,0,0,0,0,0,1W,0,1W,0
V104	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V105	1S	2S	2S	2S	2S	2S	1S	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,2U,2S,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V106	1S	2S	2S	2S	2S	2S	1S	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,0,0,1U,0,0,0,0,0,0,0,0,0,0,0,0
V107	1S	1S	1S	1S	1S	1S	1S	2S	2S	3W	1W	1W	1W	1W	D	D	D	D	D	1S,0,1U,1S,1S,1U,0,0,0,3U,0,0,0,0,0,0,0,0,0
V108	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1W	3W	3W	1W	1W	2W	1S,1U,1U,1S,1S,1S,0,1U,1S,0,0,0,1U,1U,3W,0,1W,1W,2W
V109	1S	1S	1S	1S	2S	1S	1S	1S	1S	1W	1W	1W	4W	4W	4W	4W	4W	2W	1W	1S,1S,1S,1U,2S,1S,1U,1S,1U,0,0,0,4U,4U,0,0,0,2W,1W
V110	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,1U,0,1U,1S,1U,1S,1U,1S,0,0,0,0,0,0,0,0,0,3W
V111	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	2W	2W	D	D	1S,0,0,0,2S,0,0,2S,2U,0,0,0,0,0,0,2W,0,0,0
V112	1S	2S	2S	2S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0

V113	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1S,1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V114	1S	1S	1S	1S	3S	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1S,0,1S,1S,3U,1U,0,1U,0,1U,1U,1U,1U,0,1W,0,1W,1W
V115	1S	1S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	D	D	D	D	1S,1U,0,0,0,0,0,0,0,0,0,2U,0,0,0,0,0,0,0,0
V116	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	3W	3W	3W	1S,0,0,0,2U,0,0,0,0,0,0,0,0,2U,0,0,0,0,3W,0
V117	1S	2S	1S	1S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	2W	4W	4W	1S,2U,1U,1S,2U,2U,2S,2S,0,0,2U,0,0,2U,0,2W,0,0,4W
V118	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	3W	D	D	D	D	1S,0,1U,0,1S,1S,1U,1S,1U,0,0,0,0,0,3U,0,0,0,0,0
V119	1S	2S	2S	2S	1S	2S	1S	2S	1S	D	D	D	D	D	D	D	D	D	1S,0,0,0,1U,0,0,0,1U,0,0,0,0,0,0,0,0,0,0,0
V120	1S	1S	1S	1S	1S	1S	1S	2S	2S	2W	2W	1W	1W	1W	D	D	D	D	1S,0,1U,1S,1S,0,3U,0,0,0,0,0,0,1U,0,0,0,0,0,0
V121	1S	1S	1S	2S	2S	2S	1S	1S	2S	2W	2W	1W	1W	3W	3W	2W	1W	2W	1S,0,1U,0,2S,2U,1U,1S,2U,0,0,0,1U,0,3W,2W,1W,2W,2W
V122	1S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	1S,0,0,1U,1S,1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0
V123	1S	1S	2S	2S	2S	1S	1S	1S	2S	2W	2W	2W	2W	2W	2W	3W	3W	3W	1S,1U,0,0,0,1U,0,1S,2U,0,0,0,0,0,0,0,3W,0,3W,2W
V124	1S	2S	2S	2S	2S	2S	1S	4S	4S	4W	4W	4W	4W	4W	D	D	D	D	1S,0,0,0,0,2U,0,0,0,0,0,0,4U,0,4U,0,0,0,0,0
V125	1S	1S	1S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	1S,1S,1S,1S,1S,1S,1S,1U,0,0,0,0,0,0,0,0,0,0,0,0
V126	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	2W	2W	2W	1S,0,0,0,2U,0,2U,2S,0,0,0,0,0,0,0,0,0,2W,2W
V127	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V128	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	4W	4W	2W	3W	3W	3W	1S,0,0,0,0,0,0,0,0,0,0,2U,4U,4U,0,0,0,0,3W
V129	1S	1S	1S	1S	2S	2S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	3W	1S,0,1S,1S,0,2S,1U,1S,0,0,0,0,0,0,0,3W,0,0,0
V130	1S	1S	1S	2S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,2U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V131	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	4W	D	D	D	D	1S,0,0,1U,0,0,0,1S,1U,0,0,0,0,0,4U,0,0,0,0,0
V132	1S	1S	1S	1S	1S	3S	1S	1S	1S	1W	1W	1W	1W	4W	4W	4W	4W	2W	1S,1U,1U,1U,1U,3U,0,1S,0,0,0,0,0,4U,0,4W,0,2W,4W
V133	1S	1S	1S	1S	1S	1S	1S	2S	2S	2W	2W	2W	2W	2W	2W	2W	2W	2W	1S,1U,1U,1U,1S,1U,0,0,0,0,0,0,0,0,0,0,0,2W,0
V134	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	3W	3W	3W	1S,0,0,0,2U,2S,0,0,0,0,0,0,0,0,0,0,0,3W,0
V135	1S	1S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	3W	3W	3W	1S,1U,0,0,0,0,0,0,2U,0,0,0,0,0,0,3W,0,0,3W,3W
V136	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	3W	1W	1W	3W	3W	3W	3W	3W	1S,1U,1S,1U,0,2S,0,0,2U,0,3U,0,0,0,0,0,3W,0,0,0
V137	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V138	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V139	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V140	1S	1S	1S	2S	2S	2S	1S	2S	2S	2W	3W	2W	2W	2W	D	D	D	D	1S,0,1S,0,0,2U,2S,0,0,0,3U,0,0,2U,0,0,0,0,0
V141	1S	2S	2S	2S	2S	2S	1S	2S	2S	3W	1W	1W	1W	3W	3W	3W	3W	3W	1S,0,0,0,0,0,0,0,2U,3U,0,0,0,0,0,0,0,0,3W
V142	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	3W	1W	1W	1W	D	D	D	D	1S,1U,1U,1S,0,0,0,0,2U,0,3U,0,0,1U,0,0,0,0,0

V173	1S	2S	2S	1S	2S	2S	1S	2S	2S	2W	3W	1W	1W	3W	3W	3W	3W	3W	3W	1S,0,2U,1U,2U,0,0,0,0,0,3U,0,0,0,0,0,0,3W,0
V174	1S	1S	1S	1S	1S	1S	1S	4S	4S	4W	4W	4W	4W	4W	2W	2W	2W	2W	2W	1S,0,1U,1U,1U,0,0,0,0,0,0,4U,4U,4U,0,0,2W,2W,0
V175	1S	1S	1S	1S	2S	2S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	1S,1U,1S,1U,2U,2U,0,1U,1S,0,0,0,0,0,0,0,0,0,0
V176	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	2W	2W	2W	2W	1S,0,0,0,2U,2S,0,0,2U,0,0,0,0,0,0,0,0,2W,2W
V177	1S	1S	1S	1S	1S	1S	1S	2S	2S	2W	2W	2W	2W	3W	3W	3W	3W	3W	3W	1S,0,1U,1S,1S,0,1U,0,0,0,0,0,0,0,0,3W,0,3W,0
V178	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0
V179	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,0,0,1S,1S,1U,1U,1S,1U,0,0,0,0,0,0,3W,0,3W,0
V180	1S	1S	1S	1S	2S	1S	1S	3S	1S	D	D	D	D	D	D	D	D	D	D	1S,0,1S,1S,2U,1S,1S,0,1S,0,0,0,0,0,0,0,0,0
V181	1S	2S	1S	1S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1W	1W	1W	1W	1W	1W	1S,2U,1U,1S,0,1S,0,1U,1S,1U,0,0,0,0,0,0,1W,1W
V182	1S	2S	2S	2S	1S	1S	1S	1S	1S	1W	1W	1W	1W	1W	1W	1W	1W	D	D	1S,0,0,0,1U,1S,0,1U,0,0,0,0,0,0,0,1W,0,0,0
V183	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	2W	1W	D	D	1S,0,0,0,0,2S,0,0,0,0,2U,0,0,0,2W,2W,1W,0,0
V184	1S	1S	1S	1S	1S	2S	1S	1S	1S	1W	3W	1W	1W	1W	D	D	D	D	D	1S,0,1S,1S,1U,2S,0,1U,0,1U,3U,0,0,0,0,0,0,0
V185	1S	1S	1S	2S	1S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	3W	3W	3W	3W	1S,1U,1U,2U,1U,0,0,0,0,0,0,0,0,3W,3W,0,0,0
V186	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V187	1S	2S	2S	2S	2S	2S	1S	4S	4S	4W	4W	4W	4W	2W	D	D	D	D	D	1S,0,0,0,0,2U,0,0,0,4U,4U,0,0,0,0,0,0,0
V188	1S	2S	2S	1S	1S	1S	1S	2S	2S	2W	2W	2W	2W	3W	3W	2W	2W	1W	1W	1S,0,2U,1U,1S,0,1U,0,0,2U,0,0,2U,0,3W,2W,0,1W,1W
V189	1S	1S	1S	1S	2S	2S	1S	2S	2S	2S	1S	1W	1W	2W	2W	2W	2W	2W	2W	1S,1U,0,1S,2S,2S,0,0,2U,2U,1U,0,0,0,2W,0,2W,2W
V190	1S	1S	2S	2S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,0,2S,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V191	1S	1S	1S	1S	2S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,1U,1S,1S,2U,0,0,0,0,0,0,0,0,0,0,0,0,0
V192	1S	2S	1S	1S	1S	1S	1S	2S	2S	2W	2W	2W	2W	2W	2W	1W	1W	1W	2W	1S,2U,1U,1U,1U,1U,0,0,0,2U,0,0,0,2W,1W,0,1W,2W
V193	1S	2S	2S	2S	2S	2S	1S	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,0,3U,0,0,0,0,0,0,0,0,0,0,0,0
V194	1S	1S	1S	1S	2S	2S	1S	1S	1S	1W	3W	1W	1W	3W	3W	1W	3W	3W	3W	1S,0,1U,1U,2U,0,0,1S,1S,0,3U,1U,0,0,3W,1W,0,0,3W
V195	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	1W	1W	D	D	1S,2U,0,0,0,2S,0,0,0,2U,0,0,0,0,1W,0,0,0
V196	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V197	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	3W	1W	1W	1W	D	D	D	D	D	1S,0,0,0,0,0,0,0,0,3U,0,0,0,0,0,0,0,0
V198	1S	1S	1S	1S	1S	2S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	1S,1U,1U,1U,1U,2U,1U,1S,1U,0,0,0,0,0,0,0,0
V199	1S	1S	1S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	4W	4W	2W	2W	1S,0,1S,0,0,0,0,0,0,0,0,0,0,0,0,4W,0,2W,0
V200	1S	2S	2S	2S	1S	2S	1S	2S	2S	2W	2W	3W	2W	2W	2W	2W	2W	D	D	1S,0,0,2S,1U,2U,0,0,0,0,3U,0,0,0,2W,0,0,0
V201	1S	2S	2S	2S	2S	2S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	1S,0,0,0,2U,0,0,1S,0,0,0,0,0,0,0,0,0,0
V202	1S	1S	1S	2S	3S	2S	1S	2S	2S	2W	3W	2W	2W	2W	2W	3W	3W	2W	2W	1S,1U,1U,2U,3U,0,0,0,0,3U,0,0,0,2W,3W,0,2W,0

V203	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V204	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	2W	2W	2W	4W	4W	2W	2W	2W	2W	1S,1U,1S,1U,2U,2U,0,0,0,0,0,0,0,0,0,4U,4W,2W,0,2W,2W
V205	1S	1S	1S	1S	1S	1S	1S	3S	1S	1W	1W	1W	1W	2W	2W	2W	2W	2W	2W	1S,1U,1U,1S,1S,1S,1U,0,1U,0,1U,0,0,0,0,0,0,0,2W,0
V206	1S	1S	1S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	4W	D	D	D	D	D	1S,1U,1U,2U,2U,2U,2U,0,0,0,0,0,0,0,4U,0,0,0,0,0
V207	1S	1S	1S	1S	2S	2S	1S	1S	1S	1W	1W	1W	1W	1W	1W	4W	4W	4W	4W	1S,1U,1U,1U,2U,0,0,1U,1S,0,0,0,0,0,0,0,0,0,4W
V208	1S	1S	1S	1S	2S	2S	1S	2S	1S	1W	1W	1W	1W	1W	D	D	D	D	D	1S,1U,1U,1S,2S,0,0,0,1U,0,0,0,0,1U,0,0,0,0,0,0
V209	1S	1S	1S	1S	1S	1S	1S	1S	1S	1W	4W	4W	4W	2W	D	D	D	D	D	1S,0,1S,1U,1S,1S,1U,1S,1U,0,4U,4U,4U,0,0,0,0,0,0,0
V210	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V211	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V212	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0
V213	1S	1S	1S	1S	1S	1S	1S	1S	2S	2W	2W	2W	2W	3W	3W	3W	3W	2W	2W	1S,1U,1U,1S,0,0,0,1S,0,0,0,0,2U,0,0,3W,0,2W,0
V214	1S	1S	1S	2S	2S	2S	1S	4S	4S	4W	4W	4W	4W	4W	4W	4W	4W	4W	4W	1S,1U,1U,0,0,0,0,0,0,4U,4U,4U,0,4U,4W,4W,0,4W,4W
V215	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V216	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	2W	4W	2W	3W	3W	1S,0,0,0,2U,0,0,0,0,0,0,0,0,0,0,4W,0,0,3W
V217	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	1W	1W	D	D	1S,0,1U,1U,0,0,0,0,2S,0,0,0,0,0,3W,1W,0,0,0
V218	1S	1S	1S	1S	1W	1W	1S	1W	1W	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,1U,1U,1U,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3W
V219	1S	2S	2S	2S	3S	2S	1S	2S	2S	2W	2W	2W	2W	4W	4W	4W	4W	2W	4W	1S,0,0,2U,3U,0,0,0,0,0,0,0,0,4U,0,0,0,2W,4W
V220	1S	2S	2S	2S	1S	2S	1S	2S	2S	2S	2S	2S	2W	2W	2W	2W	2W	D	D	1S,0,0,0,1U,0,0,0,0,2U,2U,2U,0,2U,2W,0,0,0,0
V221	1S	1S	1S	1S	1W	1W	1S	1W	1W	1W	1W	1W	1W	3W	3W	3W	3W	3W	3W	1S,0,1S,1U,0,0,0,0,0,0,0,0,0,0,0,0,3W,3W,0,0,0
V222	1S	1S	1S	1S	1S	1S	1S	D	D	D	D	D	D	D	D	D	D	D	D	1S,0,1U,1U,1U,1S,0,0,0,0,0,0,0,0,0,0,0,0,0,0
V223	1S	1S	1S	1S	1W	1W	1S	1W	2W	2W	2W	2W	2W	2W	D	D	D	D	D	1S,0,1U,1U,0,0,0,1U,0,0,0,2U,0,0,0,0,0,0,0
V224	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	2W	3W	1W	1W	1W	1W	1W	1W	1W	1S,0,1U,1U,2U,0,0,0,0,0,0,3U,0,0,0,0,0,1W,0
V225	1S	1S	1S	1S	3S	1S	1S	2S	2S	2W	3W	1W	1W	3W	3W	3W	1W	3W	3W	1S,1U,1U,1S,3U,0,3U,0,0,2U,3U,0,0,0,0,3W,1W,0,3W
V226	1S	1S	1S	1S	2S	2S	1S	2S	2S	2W	2W	2W	2W	2W	D	D	D	D	D	1S,1U,0,1U,0,0,0,0,0,0,0,2U,2U,0,0,0,0,0,0
V227	1S	2S	2S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	3W	3W	3W	3W	1S,0,0,0,2U,0,0,0,0,0,0,0,0,0,0,3W,3W,0,0,0
V228	1S	1S	1S	2S	2S	2S	1S	2S	2S	2W	2W	2W	2W	3W	3W	3W	3W	3W	3W	1S,0,1S,0,2U,0,0,2S,0,0,0,0,0,0,3W,0,0,0,0
V229	1S	1S	1S	1S	1S	3S	1S	1S	1S	1W	1W	4W	4W	4W	4W	4W	4W	4W	4W	1S,1U,1U,0,1S,3U,1S,1S,1U,0,0,4U,4U,4W,4W,0,4W
V230	1S	1S	1S	1S	1S	1W	1S	1W	1W	1W	1W	1W	1W	1W	1W	3W	1W	1W	1W	1S,0,1S,1S,1U,0,0,0,0,0,0,0,1U,0,3W,1W,1W,0
V231	1S	1S	1S	2S	3S	1S	1S	1S	2S	D	D	D	D	D	D	D	D	D	D	1S,0,1S,0,3U,0,1U,1S,2S,0,0,0,0,0,0,0,0,0,0
V232	1S	1S	1S	1S	1S	2S	1S	1S	1S	3W	1W	1W	1W	1W	1W	4W	4W	4W	4W	1S,1U,1U,1U,1U,2U,1U,1S,1S,3U,0,0,1U,0,0,0,0,4W

California Sea Lion Pup and Yearling Strandings
Updated through April 20, 2015



Appendix 3. A comparison of monthly strandings for California sea lion pups and yearlings in 2013 (2012 Cohort) and 2015 (2014 cohort) versus the average rate for years 2004 – 2012. Source: Nation Marine Fisheries Service Stranding Network press release. (<http://www.nmfs.noaa.gov/pr/health/mmume/californiasealions2013.htm>)