



## Survival estimates for the Australian sea lion: Negative correlation of sea surface temperature with cohort survival to weaning

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### ABSTRACT

The Australian sea lion (*Neophoca cinerea*) population at Seal Bay Conservation Park, South Australia, is estimated to be declining at a rate of 1.14% per breeding season. To better understand the potential causes of this decline, survival rates were examined to 14 yr of age for eight cohorts marked as pups (aged 0.17 yr) between 1991 and 2002. Apparent yearly survival rates ( $\Phi$ ) varied by cohort for pups from marking to weaning at 1.5 yr ( $\Phi = 0.30$ – $0.67$ ). Postweaning juvenile survival (1.5–3 yr) was 0.89 and survival from 3 to 14 yr was constant ( $\Phi$  female: male = 0.96:0.89).  $\Phi$  of pup cohorts was negatively correlated to local sea surface temperature where the sea lions forage (SST) and was especially low for cohort 7 in 2000 (0.30). It is possible that periods of unusually warm oceanographic conditions may be limiting primary production and inhibiting maternal provisioning to pups. Pup survival to weaning is relatively low compared to other otariid species, is likely to limit recruitment, and may be contributing to the decline in pup abundance observed in the colony.

Key words: mark-recapture, *Neophoca cinerea*, otariid, threatened species.

Knowledge of several fundamental life-history parameters is required to understand population dynamics in mammals, including production, survival, fecundity, and dispersal. Age-specific survival rates are considered the best predictor of population change in pinnipeds (Cushing 1995, Pendleton *et al.* 2006). Age may affect survival rates because pups, juveniles, and adults have contrasting biological patterns, with varying physiological abilities and levels of experience determining

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foraging strategies, and varying behavioral priorities such as growth *vs.* reproduction (Caughley 1977, Wickens and York 1997). In sexually dimorphic mammals with polygynous mating systems, such as otariids (fur seals and sea lions), females frequently have higher survival rates than males, largely attributed to the costs of sexual selection and larger body size in males (Clutton-Brock 1988, Wickens and York 1997, Beauplet *et al.* 2006, Pendleton *et al.* 2006). Survival is expected to be lowest in juveniles, somewhat higher before maturity, reaching a plateau and remaining at a constant rate at maturity, and then declining with senescence (Caughley 1966, Wickens and York 1997).

Survival rates in otariids may be impacted by many natural factors including starvation, predation, and disease, and direct anthropogenic factors including habitat destruction, overexploitation, and fisheries interactions. Climate variability or anomalous environmental conditions can also affect ecological processes and population dynamics (Trillmich and Ono 1991, Stenseth *et al.* 2002, Lea *et al.* 2006). Individuals and populations may be impacted directly by climate variability through physiological confines (Arnould and Costa 2006, Costa 2008) or indirectly through shifts in food webs and predator-prey relationships (Trillmich and Ono 1991, Soto *et al.* 2006). Female otariids feed their pups on land but forage at sea. Changes in ocean climate and food abundance may have a large impact on foraging success, and subsequently on the health of individuals and the rates of birth and death in the population (Costa 2008). Higher than usual ocean temperatures have been shown to negatively affect ocean productivity and therefore prey availability for otariids, resulting in lowered levels of pup production and reduced ability for females to provision their pups and therefore lower pup survival (*e.g.*, Trillmich and Ono 1991, Guinet *et al.* 1994, Beauplet *et al.* 2005, Lea *et al.* 2006, Soto *et al.* 2006).

The Australian sea lion (*Neophoca cinerea*; ASL) was listed as “threatened” in February 2005 under the Australian *Environment Protection and Biodiversity Conservation Act* (1999) due to the small total population size, estimated at around 14,700 individuals (Goldsworthy *et al.* 2009), and the extreme philopatry identified in this species (Campbell *et al.* 2008a). Eighty percent of the total population occurs in South Australia with most colonies producing fewer than 50 pups a breeding cycle. Trends in abundance (based on pup production) are only available for the three largest colonies (Goldsworthy *et al.* 2009). These provide contrasting trends; increasing (Dangerous Reef; 709 pups), stable (The Pages; 589 pups), and declining (Seal Bay; 260 pups; Goldsworthy *et al.* 2009, Shaughnessy *et al.* 2011). Vital rates are poorly understood in this species and there are no estimates of survival rates available to improve our understanding of the trends in abundance.

The ASL colony at Seal Bay is of great conservation priority because of the identified population decline of  $-1.14\%$  per breeding season (Shaughnessy *et al.* 2006). Because female immigration into or emigration from the Seal Bay population is minimal (Campbell *et al.* 2008a), the decline at Seal Bay is likely to result from intrinsic decreases in survival and/or reproductive rates (Pendleton *et al.* 2006). The ASL is unusual in that it is the only otariid with a nonannual breeding cycle that is temporally asynchronous across its range (Gales *et al.* 1994). The ASL has a 14 mo gestation period and a 15–18 mo lactation period that are among the longest for an otariid (Higgins and Gass 1993, Gales *et al.* 1994). This nonannual breeding cycle translates into a lower lifetime reproductive potential for this species, the result of which is a high vulnerability to minor changes in survival rates due to environmental variability and anthropogenic factors (Page *et al.* 2004, Goldsworthy and Page 2007, Campbell *et al.* 2008b).

Adult female ASLs feed on the benthos (Costa and Gales 2003) and diet studies indicate they eat a wide variety of prey (Gales and Cheal 1992, McIntosh *et al.* 2006). Benthic foraging requires greater effort than epipelagic foraging and otariids that feed off the benthos regularly undertake dives that exceed their metabolic limit (Arnould and Costa 2006). Because ASLs breed during all times of the year throughout their reproductive life, it is likely they can tolerate seasonal variability in environmental conditions. However, the ASL is expected to be affected by dramatic changes in their environment that result in reduced food supplies because of their high Field Metabolic Rate (FMR; Costa and Gales 2003, Arnould and Costa 2006, Costa 2008). High FMRs are associated with working harder while at sea with either long foraging trips or high intensity foraging. At Seal Bay, the ASL has a high dive rate with almost no surface swimming and relatively short trips, staying close to shore (within 76.6 km; Costa and Gales 2003, Fowler *et al.* 2007a). Pups start to forage at 6 mo of age, supplementing their milk diet, and spending more time on deeper dives as they age (Fowler *et al.* 2006, 2007a, b). Because ASLs operate at the limit of their physiological capabilities, their ability to respond to reduced prey availability is minimal (Costa 2008). It is unknown how environmental variability affects survival. Postweaning survival rates are also largely unknown for otariids, due to the high dispersion rate in most species after weaning and their delayed return to the colony for their first attempt at reproduction (Beauplet *et al.* 2005).

That environmental variability influences ASL survival is a compelling hypothesis because the region where ASLs forage is influenced by the Bonney Upwelling. The Bonney Upwelling is the largest and most predictable upwelling in the southeastern Australian region (Butler *et al.* 2002). It is strongest during the austral summer (November–March) and carries nutrient rich cold water to the surface near the coast between Portland, Victoria to Robe, South Australia, with two upwelling zones adjacent to Kangaroo Island, one to the southeast and the other to the southwest at Cape du Couedic. The nutrient rich waters support productive fishing grounds, feeding sites for blue whales (*Balaenoptera musculus*), and large colonies of seabirds and seals (Butler *et al.* 2002). Changes in oceanographic conditions can vary the amount of primary productivity and may impact the abundance of prey species and higher order predators (Strom *et al.* 2006). Nieblas *et al.* (2009) determined that cold water plume areas were linked to primary production in the region. The Bonney Upwelling may also be influenced by the Southern Oscillation (SO; measured by the Southern Oscillation Index [SOI]), a climate phenomenon caused by shifts in air pressure between the Asian and east Pacific regions (Bureau of Meteorology 2007). Periods of sustained negative SOI (equating to El Niño periods) are thought to enhance the Bonney Upwelling (Middleton and Bye 2007, Middleton *et al.* 2007). A second significant oceanographic feature of the region is the Leeuwin Current, a warm boundary current which runs from Western Australia along the continental shelf break to Tasmania. Less is understood about the influence of this current on the region, except that the current may be weakened during significant upwelling periods (Li and Clarke 2004, Clarke and Li 2004, Middleton and Bye 2007).

In this study, we used long-term mark-recapture data collected from eight pup cohorts between 1991 and 2006 to assess apparent survival rates of ASLs at Seal Bay. In the analysis we examined the effects of time, age, and sex on apparent survival rates. We then examined whether the aseasonal breeding cycle and the regional and local oceanographic variation affected cohort survival to weaning.

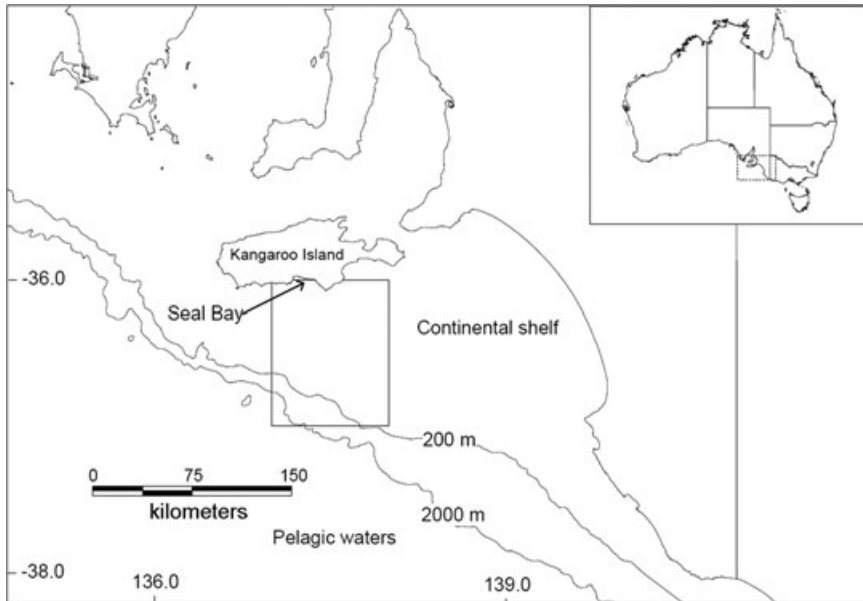


Figure 1. Map of Kangaroo Island, South Australia showing Seal Bay ( $35^{\circ}59'S$ ,  $137^{\circ}19'E$ ) showing location of the Australian sea lion breeding colony. Depth contours are in meters. Oceanographic data were obtained from the area located to the south of Seal Bay ( $36^{\circ}$ – $37^{\circ}S$  and  $137^{\circ}$ – $138^{\circ}E$ ).

## METHODS

### Study Site

Seal Bay ( $35^{\circ}59'S$ ,  $137^{\circ}19'E$ ) is located on the south coast of Kangaroo Island (Fig. 1) and is divided into four main areas: Pup Cove, the Western Prohibited Area, Main Beach, and Eastern Prohibited Area (EPA). Pup Cove is characterized by steep limestone cliffs, making it inaccessible for research. ASLs generally use this area for breeding and typically move into other parts of the colony after breeding seasons.

### Marking

Between 49 and 62 ASL pups per cohort were marked at Seal Bay over eight consecutive breeding seasons between 1991 and 2001–2002 (Table 1) using 12 mm subcutaneous Passive Integrated Transponders (PIT tags; Destron Fearing Corporation, South St. Paul, MN) by staff from the Department for Environment and Heritage (DEH), South Australia. Pups were captured at a minimum age of 0.17 yr, estimated by their size and lanugo coat. The median pupping date for the breeding season (Shaughnessy *et al.* 2006, McIntosh 2007) was used as the date of birth for individual pups.

PIT tags were inserted subcutaneously over the dorsal line, parallel to the spine and near the tail to minimize movement under the skin. To identify the PIT tag, the surveyor approached sleeping individuals using an antenna of 1.5 m length to scan

*Table 1.* Numbers of male and female Australian sea lion pups marked with microchips at Seal Bay over eight breeding seasons from 1991 to 2001–2002. Median pupping dates are from Shaughnessy *et al.* (2006) and McIntosh (2007). Maximum pup counts were obtained from monthly counts during the breeding season.

Cohort	Season of most births	Median pupping dates	Maximum pup count	Males marked	Females marked	Total marked	% Marked of maximum pup count
1	Winter	10 June 1991	128	31	27	58	45.3
2	Summer	28 November 1992 <sup>a</sup>	153	23	39	62	40.5
3	Autumn	29 May 1994	124	21	28	49	39.5
4	Spring	28 November 1995	145	21	29	50	34.5
5	Autumn	5 May 1997 <sup>a</sup>	149	31	26	57	38.3
6	Spring	29 October 1998	148	25	33	58	39.2
7	Autumn	22 April 2000	135	26	25	51	37.8
8	Spring	22 October 2001	147	31	22	53	36.1
Total				209	229		

<sup>a</sup>Median pupping date used for MARK analysis is 1 mo later (See Fig. 3) due to grouping of original data for the input models.

for the tag. In addition, fore-flipper tags, freeze branding, and scars have been used sporadically at Seal Bay to identify individual sea lions used in research programs; those marks were also used in this study. Overall, 229 female pups were marked with PIT tags including 29 that had an external mark, and 209 male pups were marked with PIT tags including 33 that had an external mark (Table 1).

### *Resighting*

Tag and scar resights were obtained during monthly counts of animals throughout the colony. These counts were conducted on foot with the aid of binoculars by up to four trained staff over 1 d. Because of site policy, access to the EPA was prohibited for PIT scanning but it is known from resights of external marks that animals moved between the EPA and other areas of the colony. PIT scanning effort varied throughout the study; before 2003, it occurred about once in 10 d. During three breeding seasons from September 2003 until July 2006, scanning surveys lasted a whole day and occurred at least four times per week to increase the resight effort.

### *Input Data*

Mark-resight histories were derived for analysis of apparent survival. Resight occasions were not rolled into years as is common for pinniped survival studies because smaller time intervals were required to examine seasonal and breeding season (1.5 yr) effects for survival and recapture rates. The data set was created by grouping resights into months and selecting months that had more than 16 resights (this made 71 capture occasions). Because effort (time spent in the colony, areas of the colony surveyed, and number of individuals scanned) were not always recorded and varied over time, and due to the large number of capture occasions, these time periods were grouped into 3 mo blocks and the median of the three largest values was selected as the time period (making 23 capture occasions). Occasions of initial marking were

included in the nearest blocks to ensure the allocation to the appropriate cohort group for analysis. Resights falling outside the selected occasions were deleted. The final data set contained resights from August 1991 to November 2006 and time points were rounded to the nearest 0.25 yr.

### *Model Assumptions and Notation*

The Cormack–Jolly–Seber (CJS) model for open populations was used to examine survival and recapture rates (Cormack 1964, Jolly 1965, Seber 1982, Lebreton *et al.* 1992). CJS models are conditional upon the animal being released alive at the first encounter, and survival and catchability refer only to these marked animals. There are four basic assumptions that need to be satisfied for the CJS model to determine survival estimates reliably: (1) every animal, marked and unmarked, must have the same probability of capture and recapture; (2) every animal must have the same probability of mortality or of leaving the sampling area for the duration of the experiment; (3) marks must not be lost and must be correctly reported; and (4) all samples are instantaneous, that is, birth, death, immigration, and emigration does not occur during the sampling process.

Subscripts in the model notation refer to factors such as constant ( $\cdot$ ), age (age), time (time), sex (sex), mark type (type), and cohort number (cohort), or combinations of factors, with (\*) showing multiplicative interactions and (+) additive interactions. The age classes in a model are represented by the numbers following the subscript (*e.g.*,  $\text{age}_{0.17,1.5,3+}$  = age classed in groups from 0.17 to 1.5, 1.5 to 3, and 3+ yr). A colon (:) shows an effect such as cohort, season of birth, sex, or SST anomaly (SSTa) on an age class.

### *Goodness of Fit Testing for General Model*

Program U-CARE was used to test the goodness of fit (GOF) of the most highly parameterized (general) model for survival ( $\Phi$ ) and capture probability ( $p$ ) with time effects ( $t$ ) ( $\Phi_{(t)} p_{(t)}$ ) as outlined in Cooch and White (2010). The model fit was tested by summing the components of tests 2 and 3 (3.Sr+3.Sm+2.Ct+2.Cl; Choquet *et al.* 2005).

Because the species is sexually dimorphic, sex effects were considered likely and recapture rates were expected to vary for individuals with external marks *vs.* PIT tags only. Four groups were examined separately: males and females marked with PIT tags only, and males and females marked with PIT tags and external marks. Upon failure of the summed test, the groups (sex and tag type) were tested in relation to a two age class model ( $\Phi_{(\text{age}2*t)} p_{(t)}$ ) by summing the components of tests 3.Sm+2.Ct+2.Cl. Over-dispersion ( $\hat{c}$ ) was calculated by dividing the summed  $\chi^2$  values by the summed degrees of freedom of the individual test components from each group (White and Burnham 1999, Cooch and White 2010). When  $\hat{c} = 1$  the model fits data perfectly (Lebreton *et al.* 1992).

### *Model Selection and Inference*

Mark-resight data were modeled using Rmark (2.4.1 A Language and Environment 2006) as an interface for Program MARK (4.3; Gary C. White, Colorado State University). Akaike's Information Criterion (AIC), after adjusting for over-dispersion (AIC<sub>c</sub>), was used to select the most parsimonious and biologically meaningful model

for the data from *a priori* specified models based on the GOF results; Akaike weights and QAIC's were used for inference and model selection. Models with the highest Akaike weights and  $QAIC \leq 2$  were considered to have substantial support. Models with  $QAIC = 4-7$  were considered to have less support, but still explain some variation in the data (Burnham and Anderson 2002). Parameter counts were adjusted where appropriate to take into account those that could not be estimated (Laake and Rexstad 2010).

Numerous combinations of models for apparent survival and capture probability were possible. The following steps were performed to reduce the number of combinations: (1) based on the current understanding of the biology of the ASL, mark-recapture studies on other otariids (*e.g.*, Holmes and York 2003, Beuplet *et al.* 2005, 2006) and the GOF test results, a simple age-structure model of apparent survival was designed ( $\Phi_{(\sim\text{age}0.17,1.5,3,6,10+)}$ ) and used as a starting point to explore changes in information criteria under different capture probability models; (2) the reduced set of capture probability models was used with a wider candidate set of constant apparent survival ( $\Phi$ ) models and models with varying age structure; (3) the reduced set of age-structured  $\Phi$  models was used and additional interactions with age-structure were explored to look for other effects, for example, sex and time effects; (4) a final candidate set of  $\Phi$  models was used to test some of the capture probability models excluded originally to ensure that the original reduced set, at step (2), was the most appropriate.

#### *Capture Probability (p) Models*

The candidate set of *a priori* models included capture probability ( $p$ ) varying with four factors. (1) Time—because resighting effort varied during the study and sea lion behavior may vary over time (there was insufficient data on effort for each capture occasion to model a relationship between  $p$  and effort). (2) Type of mark, *i.e.*, PIT tag only *vs.* PIT tag plus an external mark—it was expected that individuals with only PIT tags would have a lower resight probability than those with an externally visible tag. (3) Age—pups were expected to have a higher resight probability than older age classes because of their maternal dependence and it was also expected that older age classes may have different resight probabilities. Ages were binned in increments of 1.5 yr to represent the 18 mo breeding season and major behavioral changes that occur at the time of breeding seasons (*i.e.*, weaning and parturition). (4) Sex—females were expected to have a higher resight probability than males, particularly for older age classes, because females spend more time ashore due to lactation and are likely to have higher site fidelity. Interactions between some of these terms were also expected, but data were insufficient to explore all possible interactions.

#### *Apparent Survival ( $\Phi$ ) Models*

Different age-structured models for  $\Phi$  were tested first. Because the maximum age that sea lions could reach in this study was 13.5 yr, evidence of senescence effects were not expected, given the observed longevity of 26 yr in females and 21.5 yr in males (McIntosh 2007). Based on the GOF test and results from other otariid species, it was expected that  $\Phi$  for pups would be lower than for older age classes and various combinations of age groupings were tried for individuals.

Once a starting set of age-structured  $\Phi$  models was identified, additional effects on  $\Phi$  were explored. These effects included (1) sex; (2) cohort; (3) time, where time was binned into *ca.* 1.5 yr blocks for animals older than 1.5 yr of age, *i.e.*, from breeding season to breeding season; (4) timing of breeding seasons, *i.e.*, median pupping date falling in autumn, winter, summer, or spring; and (5) ocean productivity as measured by sea surface temperature anomaly (SSTa). Beta estimates are provided as estimable slopes in the models with additional effects on  $\Phi$  and real estimates of  $\Phi$  are provided as final model results.

Because the rates provided by MARK are apparent finite annual survival rates, pup survival from marking at 0.17 yr to weaning at 1.5 yr was calculated by  $\exp[1.5 \ln(\text{apparent annual survival rate})]$ . All other statistical analyses were performed with SYSTAT 9.0 statistical software (SYSTAT, 9.0 statistics, SPSS Inc.). Unless otherwise stated, values are reported as means  $\pm$  standard deviation (SD) and statistical significance was determined at  $P < 0.05$ .

### *Oceanographic Data*

Sea surface temperature (SST) data were examined as a proxy for primary production and environmental variation (Nieblas *et al.* 2009). Although SST data represent the surface temperatures of the ocean, it acts as an important tracer of several oceanographic processes (*e.g.*, upwelling) that have a surface thermal signature (Cracknell and Hayes 1991, Nieblas *et al.* 2009). Monthly averaged SST data from Pathfinder 5.0 was used to estimate a baseline monthly SST, with a  $4 \times 4$  km resolution, for the period between January 1982 and December 2008. Night-time data were obtained because daily variations on solar radiation can affect SST. Each pixel was considered a time series and the monthly anomalies (SSTa) were found based on the long-term mean for each month (Fig. 2). Sea Surface Color (*Cchl-a*, SSC) data were only available from 1998 to 2008, covering the three cohorts (1998, 2000, and 2001), and hence the series was too short to be used. The Southern Oscillation Index (SOI), calculated using pressure differences between Tahiti and Darwin, was used to measure SO phases, with sustained negative (positive) values equating to El Niño (La Niña) periods. Monthly averaged SOI was downloaded from the Bureau of Meteorology (2007). The monthly data were used to find the SOI anomalies (SOIa) based on the mean value of all months corresponding to sustained periods of negative indices (El Niño) and sustained periods of positive indices (La Niña). The SSTa and SOIa data were cross-correlated to identify any relationship between SST and SO effects.

The monthly SSTa were then used to find the mean value for the 1 yr period after the median pupping date of each breeding season. Using 1.5 yr postmedian pupping date would have taken the data into the next breeding season and there was little difference between the two data sets (87% similar). The minimum time needed for a pup to be successfully weaned to independence is 1.25 yr (Higgins and Gass 1993). One yr after the median pupping date includes the most important period of dependence for all pups because the median pupping date occurs on average 0.25 yr after the onset of breeding (Shaughnessy *et al.* 2006). Intervals between breeding seasons were calculated from successive median pupping dates using probit analysis following Shaughnessy *et al.* (2006) and McIntosh (2007).

Time-series SST and SOI data were examined on regional and local scales. The regional examination ( $32^{\circ}$ – $37^{\circ}$ S and  $132^{\circ}$ – $143^{\circ}$ E) considered whether upwelling areas at Cape du Couedic to the west of Seal Bay or the Bonney Upwelling to its



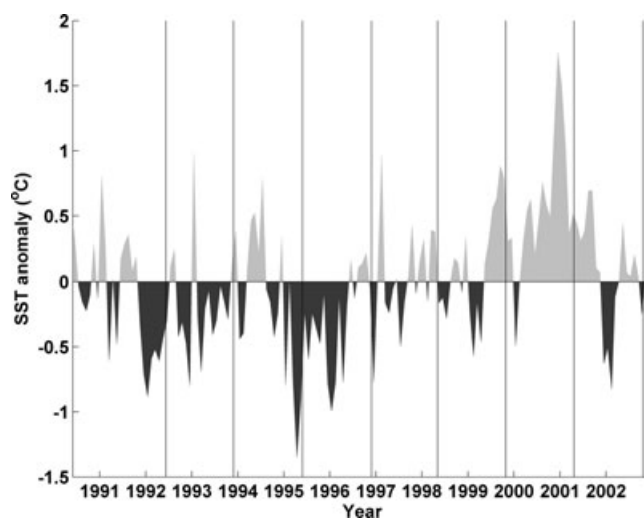


Figure 2. Monthly mean SST anomalies for the region south of Kangaroo Island ( $36^{\circ}$ – $37^{\circ}$ S and  $137^{\circ}$ – $138^{\circ}$ E). The dashed vertical lines indicate the median pupping dates for Australian sea lions at Seal Bay and the solid lines the time period of 12 mo after these dates. Gray areas above the origin (mean temperature for the local region) represent warmer temperatures, black areas below the origin represent cooler temperatures.

east were influencing local oceanographic conditions. The coordinates of the area for the local examination of oceanographic data were ( $36^{\circ}$ – $37^{\circ}$ S and  $137^{\circ}$ – $138^{\circ}$ E, Fig. 1); they were chosen to represent an area south of Seal Bay where ASL females, juveniles and pups over 1.25 yr forage (Costa and Gales 2003, Fowler *et al.* 2007a). Hydrological data required to examine the effects of the Leeuwin Current on the oceanography surrounding Kangaroo Island are unavailable.

## RESULTS

### *Model Assumptions*

Each pup cohort was marked when healthy and at a similar age and developmental stage, and therefore had similar likelihoods of capture and recapture, and the same probability of mortality or leaving the sampling area. Due to the high retention rate of PIT tags (R. R. McIntosh, unpublished data; Chilvers and MacKenzie 2010) and their individual identification, marks were not lost or incorrectly reported. Marking occurred over a relatively short time period during breeding seasons (1 wk); while some births and deaths may have occurred during the sampling process this would have been minimal. CJS models only estimate apparent survival; therefore both animals that died and animals that emigrated are modeled. In ASLs female natal site fidelity is extreme, but emigration rates are unknown for males (Campbell *et al.* 2008a). This provides a greater ability to meet the assumptions of the CJS model (at least for females and their pups) than in many other survival studies.

### Goodness of Fit (GOF) Testing

From the 438 pups marked, 194 resighted individuals with 1,129 resights made up the final data set. Using program U-CARE for the GOF analysis, basic  $\Phi(t)p(t)$  models were not supported, with the summed  $\chi^2$  value (tests 3.Sr+3.Sm+2.Ct+2.Cl) for all groups having  $P < 0.001$ . The two age-class models tested in U-CARE ( $\Phi_{(a2^+t)}p(t)$ , tests 3.Sm+2.Ct+2.Cl) appeared reasonable for females with PIT tags only ( $\chi^2 = 46.72$ ,  $df = 44$ ,  $P = 0.36$ ), males with PIT tags only ( $\chi^2 = 47.32$ ,  $df = 33$ ,  $P = 0.05$ ) and females with PIT tags and external marks ( $\chi^2 = 42.66$ ,  $df = 31$ ,  $P = 0.08$ ), but not for males with PIT tags and external marks ( $\chi^2 = 29.88$ ,  $df = 14$ ,  $P = 0.008$ ). Hence, overall an age-structured model was a good starting point for further model selection and inference with these data. The value of the over-dispersion parameter  $\hat{c}$  was 1.37, calculated by summing the  $\chi^2$  values from the four groups and dividing by the summed  $df$ ; this  $\hat{c}$  value is a conservative estimate given our data had unequal time periods which were not considered by the default models in U-Care.

### Model Selection Sequence

*Step 1:* From the ten models tested for capture probability, the model with most support included time, marking type, and age structure, with some models also including sex (Table 2). Generally models with additive effects were supported more than models with interactions, possibly due to the sparse data, but there was some evidence for a sex by age interaction (Table 2, model 2). The first three capture probability models that had a combined Akaike weight of 0.93 were used to explore models for age-structured apparent survival rates.

*Step 2:* Eight models were tested for apparent survival and those with age structure were highly supported compared with models with no age structure, *i.e.*,  $\Phi(\text{age})$  vs.  $\Phi(\cdot)$  models (Table 3), consistent with the results of the U-Care analysis. There was no strong support for any particular age-structured model over another. The clearest distinction in the age-structured models was between pup survival to 1.5 yr (at weaning) and the remainder. We used the top four models for age structure (Table 3) combined with the top three models for capture probability (Table 2) as a starting point to explore additional effects on apparent survival.

*Step 3:* The top 17 models (of 155 tested) had a combined Akaike weight of 0.98 (Table 4). The two top models indicated that apparent survival was different between pups and older animals, and there was some support that apparent survival differed between the ages of 1.5 and 3 (Table 4, model 3). For the purpose of this study, we classified individuals aged up to 1.5 yr as pups, individuals from 1.5 to 3 yr as postweaning juveniles, and individuals aged 3+ as older individuals. There was no support for models that included time variation in apparent survival for animals older than 1.5 yr. The top three models, with a combined weight of 0.62, suggest that the apparent survival of older males differed from that of older females. It must be noted, however, that the high and constant survival rate of individuals older than 3 yr may have resulted from low power to discriminate because few marked, known-age animals were alive as adults and this study was not conducted for a long time period relative to the longevity of ASLs.

*Step 4:* From the top two models (Table 4) the most appropriate capture probability model included variation with time, marking type and age structure between 0–1.5 and 1.5+ yr (the same result as Step 1, Table 2). In total, 187 models were tested.

*Table 2.* Selection table for capture probability models ( $p$ ) with an age-structured apparent survival ( $\Phi$ ) model held constant. Ages are expressed in years. Only the most supported capture probability age-structure models are shown to simplify the table. npar represents the number of model parameters; QAIC<sub>c</sub> is the quasi-likelihood Akaike's Information Criterion value adjusted for overdispersion ( $\hat{c} = 1.37$ );  $\Delta$ QAIC<sub>c</sub> is the difference between the QAIC<sub>c</sub> of the best model and that of the given model; the Akaike weight and deviance are also provided.

No.	Model	npar	QAIC <sub>c</sub>	$\Delta$ QAIC <sub>c</sub>	Weight	QDeviance
1	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{time} + \text{type} + \text{age}_{0,17,1.5+})$	27	2104.27	0.00	0.53	1110.25
2	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{time} + \text{type} + \text{age}_{0,17,1.5+} * \text{sex})$	28	2106.15	1.88	0.21	1110.02
3	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{time} + \text{type} + \text{age}_{0,17,1.5+} + \text{sex})$	28	2106.35	2.08	0.19	1110.22
4	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{time} + \text{type})$	25	2108.64	4.37	0.06	1118.84
5	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{time} + \text{type} + \text{sex})$	26	2110.73	6.47	0.02	1118.83
6	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{time} * \text{type})$	49	2138.8	34.53	0.00	1097.23
7	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{type})$	7	2268.64	164.37	0.00	1316.05
8	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{type} + \text{sex})$	8	2270.67	166.41	0.00	1316.05
9	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{type} * \text{sex})$	9	2272.24	167.97	0.00	1315.57
10	$\Phi(\sim \text{age}_{0,17,1.5,3,6,10+})/(\sim \text{time})$	27	2272.61	168.34	0.00	1278.59

Table 3. Selection table for basic age-structured apparent survival ( $\Phi$ ) models ( $\hat{c} = 1.37$ ).

No.	Model	npar	QAICc	DQAICc	Weight	QDeviance
1	$\Phi(\sim \text{age}_{0,17,1,5+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+})$	26	2104.94	0.00	0.21	1113.03
2	$\Phi(\sim \text{age}_{0,17,1,5,3+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+})$	27	2105.21	0.28	0.19	1111.2
3	$\Phi(\sim \text{age}_{0,1,5,3,4,5+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+})$	28	2106.48	1.54	0.10	1110.34
4	$\Phi(\sim \text{age}_{0,17,1,5,3,6+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+})$	28	2106.81	1.87	0.08	1110.67
5	$\Phi(\sim \text{age}_{0,17,1,5+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	27	2106.97	2.03	0.08	1112.95
6	$\Phi(\sim \text{age}_{0,17,1,5,3+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	28	2107.27	2.34	0.07	1111.14
7	$\Phi(\sim \text{age}_{0,17,1,5,3,6,10+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+})$	29	2108.5	3.57	0.04	1110.25
8	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	29	2108.54	3.60	0.04	1110.28
9	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5,6+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	29	2108.59	3.66	0.03	1110.34
10	$\Phi(\sim \text{age}_{0,17,1,5+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} * \text{sex})$	28	2108.85	3.91	0.03	1112.72
11	$\Phi(\sim \text{age}_{0,17,1,5,3,6+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	29	2108.87	3.94	0.03	1110.62
12	$\Phi(\sim \text{age}_{0,17,1,5,3+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} * \text{sex})$	29	2109.18	4.24	0.03	1110.93
13	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5,6,10+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+})$	30	2110.39	5.46	0.01	1110.02
14	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} * \text{sex})$	30	2110.44	5.51	0.01	1110.07
15	$\Phi(\sim \text{age}_{0,17,1,5,3,6,10+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	30	2110.59	5.96	0.01	1110.22
16	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5,6+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	30	2110.66	5.72	0.01	1110.28
17	$\Phi(\sim \text{age}_{0,17,1,5,3,6+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} * \text{sex})$	30	2110.78	5.85	0.01	1110.41
18	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5,6,10+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	31	2112.49	7.56	0.00	1109.99
19	$\Phi(\sim \text{age}_{0,17,1,5,3,6,10+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} * \text{sex})$	31	2112.52	7.59	0.00	1110.02
20	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5,6+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} * \text{sex})$	31	2112.57	7.63	0.00	1110.06
21	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5,9,10+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} * \text{sex})$	32	2114.42	9.49	0.00	1109.79
22	$\Phi(\sim \text{age}_{0,17,1,5,3,4,5,6,10+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	25	2161.48	59.55	0.00	1171.68
23	$\Phi(\sim \text{age}_{0,17,1,5+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} + \text{sex})$	26	2163.11	58.17	0.00	1171.2
24	$\Phi(\sim \text{age}_{0,17,1,5+})\beta(\sim \text{time} + \text{type} + \text{age}_{0,17,1,5+} * \text{sex})$	27	2164.76	59.83	0.00	1170.75

Table 4. Selection table for more detailed age-structured apparent survival ( $\Phi$ ) models showing a subset ( $QAIC_c < 2,105$ ) of the 155 models tested. Model weight is based on the entire set ( $\hat{c} = 1.37$ ).

No.	Model	npar	QAICc	DOAICc	Weight	QDewiance
1	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	28	2089.31	0.00	0.39	1093.18
2	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	29	2091.55	2.99	0.14	1095.1
3	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	29	2092.3	2.54	0.09	1094.05
4	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	27	2092.78	3.47	0.07	1098.76
5	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	30	2093.47	4.16	0.05	1093.1
6	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	28	2093.82	4.51	0.04	1097.69
7	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	30	2094.38	5.07	0.03	1094.01
8	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	28	2094.87	5.55	0.02	1098.75
9	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{Season} + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	31	2094.89	5.57	0.02	1092.38
10	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	29	2094.92	5.61	0.02	1096.67
11	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	29	2095.47	6.16	0.02	1097.22
12	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	29	2095.92	6.61	0.01	1097.67
13	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	31	2096.49	7.17	0.01	1093.98
14	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	29	2096.82	7.51	0.01	1098.57
15	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{Season} + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	32	2096.94	7.65	0.01	1092.3
16	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	30	2097.02	7.71	0.01	1096.65
17	$\Phi(\sim \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	30	2097.58	8.26	0.01	1097.2
18	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{Season} + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	32	2097.84	8.52	0.01	1093.2
19	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{Season} + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	30	2097.89	8.58	0.01	1097.51
20	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	29	2098.62	9.31	0.00	1100.37
21	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	34	2098.98	9.67	0.00	1090.07
22	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	31	2098.99	9.68	0.00	1096.49
23	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{Season} + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	33	2099.07	9.76	0.00	1092.3
24	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	31	2099.55	10.24	0.00	1097.05
25	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{Season} + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	33	2099.93	10.62	0.00	1093.16
26	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	35	2101.04	11.73	0.00	1089.98
27	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{Season} + \text{age}_{0.17+1.5} \text{SSTa} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	34	2102.05	12.74	0.00	1093.14
28	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	35	2102.24	12.95	0.00	1091.18
29	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	33	2102.29	12.97	0.00	1095.51
30	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	36	2103.10	13.78	0.00	1089.89
31	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	28	2103.13	13.81	0.00	1106.99
32	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	36	2103.19	13.88	0.00	1089.98
33	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	34	2103.51	14.20	0.00	1094.6
34	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	36	2104.55	15.04	0.00	1091.14
35	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	34	2104.72	15.08	0.00	1095.48
36	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+} + \text{sex})$	35	2104.73	15.11	0.00	1093.57
37	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{ty})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	36	2104.48	15.17	0.00	1091.27
38	$\Phi(\sim 1 + \text{age}_{0.17+1.5} \text{cohort} + \text{age}_{1.5+} \text{sex})/(\sim \text{time} + \text{ty} + \text{age}_{0.17+1.5+})$	26	2104.94	15.62	0.00	1113.03

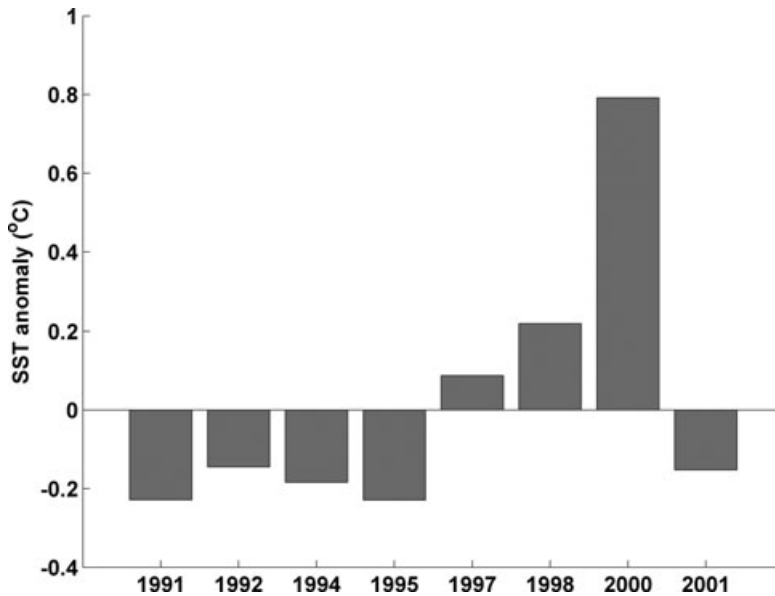


Figure 3. Mean SST anomalies for the 12 mo following each median pupping date for eight cohorts of Australian sea lions for the region south of Kangaroo Island ( $36^{\circ}$ – $37^{\circ}$ S and  $137^{\circ}$ – $138^{\circ}$ E). Years on the x-axis indicate the median pupping dates and the origin represents the mean SST for the local area.

#### Oceanographic Data Analysis

Although there was no significant correlation (all  $r^2$  values  $< 0.25$ ) between the SOIa and SSTa, the average SSTa for all months with positive and negative SOI suggest that during negative periods of SOI (El Niño years) the SST is  $0.25^{\circ}\text{C}$  colder than average and during positive periods of SOI (La Niña years) the SST is  $0.15^{\circ}\text{C}$  warmer over the region. Maps (not shown) were created for the region  $32^{\circ}$ – $37^{\circ}$ S and  $132^{\circ}$ – $143^{\circ}$ E allowing a regional analysis of the data that included the upwelling sites of the Bonney Coast and Cape du Couedic. In general, the region presented spatially homogeneous SST anomalies with exception of the 12 mo period after the median pupping date for the 1997–2000 cohorts. The 1997 and 1998 periods presented positive anomalies around Kangaroo Island and deep regions off the continental shelf, with negative anomalies in the coastal region. The highest positive SST anomalies occurred over the entire region after the median pupping date for the 2000 cohort, cooling again in the 2001 period.

The SSTa for the local scale ( $36^{\circ}$ – $37^{\circ}$ S and  $137^{\circ}$ – $138^{\circ}$ E) were binned to create a time series of anomalies (Fig. 3) that showed warmer than average SSTs between 1997 and 2000. The local area of interest included the western edge of the Bonney Upwelling zone, the area of interest was also shifted slightly east to include the upwelling region of Cape du Couedic, but there were no differences in the results and we retained the original coordinates for the cohort survival models. Because there were no differences between the regional and local scale analyses, the local scale results were used for the survival analysis to utilize the area where ASLs are known to forage.

### *Inferences from the Parameter Estimates in the Final Selected Models*

*Capture probability*— The presence of external marks in addition to PIT tags increased the odds of resight by *ca.* 6.6 times (log-odds coefficient ( $\beta$ ) = 1.90, SE = 0.19). The odds of resighting a live animal older than 1.5 yr were *ca.* 50% the odds of resighting a live pup ( $\beta$  = -0.70, SE = 0.21). From model 2 (Table 2), the odds of resighting a live male were *ca.* 1.05 times the odds of resighting a live female ( $\beta$  = 0.047, SE = 0.1). With time effects added, the modeled probability of resighting a live pup with only a PIT tag ranged from 0.02 to 0.6, the probability of resighting a live pup with external marks ranged from 0.10 to 0.91, the probability of resighting a live animal older than 1.5 yr of age with only a PIT tag ranged from 0.01 to 0.42, and the probability of resighting a live animal older than 1.5 yr of age with external marks ranged from 0.05 to 0.83.

*Apparent survival*— Table 5 shows the results of the first three models from Table 4. The first two models ( $\Delta\text{QAIC} \leq 2$ ) have the same  $\Phi$  probability model, with survival varying between pups (0.17–1.5 yr) and the sex-specific older individuals (1.5+ yr), but the second model has a sex effect in the capture probability. The third model separates  $\Phi$  for pups (0.17–1.5 yr), postweaned juveniles (1.5–3 yr), and sex-specific older individuals (3+ yr). Results for model 3 are provided because this model has some support ( $\Delta\text{QAIC} < 4$ ) and has biological relevance because it provides a survival estimate for postweaning juvenile survival.

Apparent annual cohort  $\Phi$  was between 0.50 yr<sup>-1</sup> and 0.67 yr<sup>-1</sup> for all cohorts except cohort 7, where  $\Phi$  was particularly low (0.30 yr<sup>-1</sup>; model 1, Table 5). Survival rates from 0.17 yr to weaning at 1.5 yr ranged from 0.16 yr<sup>-1.5</sup> to 0.55 yr<sup>-1.5</sup> (model 1, Table 5). For older individuals (1.5+ yr)  $\Phi$  was higher for females (0.95 yr<sup>-1</sup>) than for males (0.88 yr<sup>-1</sup>; model 1, Table 5). From model 3 (Table 5) postweaning juveniles (1.5–3 yr) and males aged 3+ yr had the same  $\Phi$  (0.89 yr<sup>-1</sup>) and both had lower  $\Phi$  than females aged 3+ yr (0.96 yr<sup>-1</sup>).

Figure 4 shows the effect of the average SSTa in the 12 mo following the median pupping date on  $\Phi$  of pups (model 1 from Table 4). There was a negative relationship between apparent pup survival and average SSTa. Median pupping dates occurred in all seasons, summer ( $n = 1$ ), autumn ( $n = 3$ ), winter ( $n = 1$ ), and spring ( $n = 3$ ) (Table 1). No effect of season on  $\Phi$  was apparent for pup survival to weaning (Table 4, models 9, 15, 18, 23, 25, and 27). Apparent annual survival was lowest for cohorts 6 (0.50 yr<sup>-1</sup>) and 7 (0.30 yr<sup>-1</sup>), for which the median pupping dates were October (spring) 1998 and April (autumn) 2000.

## DISCUSSION

The most parsimonious models in this study indicated that survival of pups differs with SSTa and that survival of older individuals differs by sex (Models 1 and 2  $\Delta\text{QAIC} \leq 2$ , Tables 4 and 5). There is some evidence that the survival rates vary for postweaning juveniles (1.5–3 yr) (Model 3  $\Delta\text{QAIC} < 4$ , Tables 4 and 5). The survival rates for postweaning juveniles and older individuals must be interpreted with caution because few pups were marked in each cohort (49–62), resulting in few individuals being available for recapture as adults. While the number of marked individuals was low, at the time of marking it was 34%–45% of the maximum count of live pups obtained from monthly counts each breeding season of this study (Table 1). Despite the low sample size, clear effects on pup survival to weaning are detected in the models.

Table 5. Estimate values from models 1, 2, and 3 (from Table 4) showing the Beta and Real survival estimates for the Australian sea lion at Seal Bay. Standard errors (SE) and lower and upper 95% confidence levels (LCL and UCL) are also provided. Cohorts 1–8 include pups from 0.17 to 1.5 yr of age. Survival to weaning ( $\Phi_{yr^{-1.5}}$ ) was calculated from Real values ( $\Phi_{yr^{-1}}$ ) using the equation  $\Phi_{yr^{-1.5}} = \exp(1.5 \ln(\Phi_{yr^{-1}}))$ .

Model	Beta				Real				
	Estimate	SE	LCL	UCL	$\Phi_{yr^{-1}}$	SE	LCL	UCL	$\Phi_{yr^{-1.5}}$
1	Intercept	0.55	0.11	0.13	0.58	0.67	0.60	0.73	0.55
	age 0.17–1.5: SSTa	-1.53	0.36	-2.23	-0.83	0.64	0.58	0.70	0.51
	age 1.5+: F	2.65	0.38	1.90	3.40	0.65	0.59	0.71	0.52
	age 1.5+: M	1.68	0.29	1.10	2.26	0.67	0.60	0.73	0.55
						0.55	0.50	0.61	0.41
						0.50	0.44	0.57	0.35
						0.30	0.06	0.19	0.16
						0.64	0.03	0.58	0.51
2	Intercept	0.55	0.11	0.12	0.57	0.67	0.60	0.73	0.55
	age 0.17–1.5: SSTa	-1.53	0.36	-2.23	-0.83	0.64	0.58	0.69	0.51
	age 1.5+: F	2.67	0.39	1.90	3.43	0.65	0.60	0.71	0.52
	age 1.5+: M	1.67	0.29	1.10	2.25	0.67	0.60	0.73	0.55
						0.55	0.03	0.61	0.41
						0.50	0.03	0.44	0.35
						0.30	0.06	0.19	0.16
						0.64	0.03	0.58	0.51
3	Intercept	0.59	0.13	0.14	0.64	0.68	0.61	0.74	0.56
	age 0.17–1.5: SSTa	-1.55	0.36	-2.26	-0.84	0.65	0.58	0.71	0.52
	age 1.5–3	1.70	0.49	0.74	2.66	0.66	0.60	0.72	0.54
	age 3+: F	2.80	0.48	1.87	3.74	0.68	0.61	0.74	0.56
	age 3+: M	1.73	0.36	1.02	2.43	0.56	0.50	0.62	0.42
						0.51	0.04	0.58	0.36
						0.30	0.06	0.19	0.16
						0.65	0.03	0.59	0.52
					0.89	0.04	0.78	0.84	
					0.96	0.02	0.91	0.94	
					0.89	0.03	0.82	0.84	



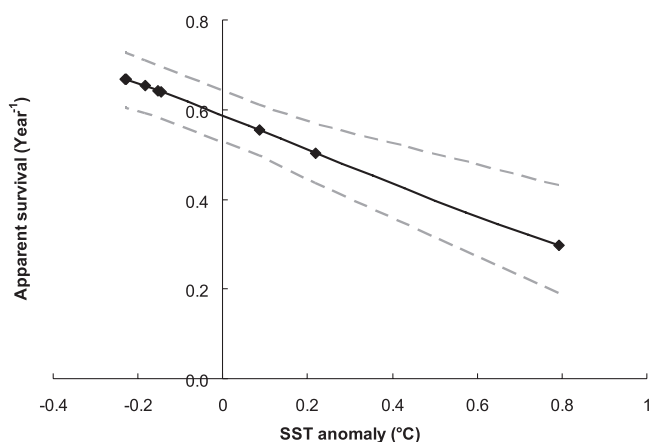


Figure 4. Relationship between apparent finite yearly survival of pups and the Sea Surface Temperature anomaly (SSTa) occurring after the median pupping dates for Australian sea lions at Seal Bay in breeding seasons from 1991 to 2002. Solid line shows the model predicted rate and points are the Real estimates of yearly pup cohort survival (model 1, Table 4). 95% upper and lower confidence levels are shown by the dashed lines. The model is  $\text{logodds}(\text{apparent survival}) = 0.351 - 1.67 * \text{SSTa}$ , where the standard error (adjusted for  $\hat{\epsilon} = 1.37$ ) was 0.11 for the intercept and 0.38 for the slope.

#### Pup Cohort Survival and SST

Survival rates of ASL pups from marking (0.17 yr) to weaning (1.5 yr) at Seal Bay over the eight cohorts were variable with cohort 7 having particularly low survival ( $0.16 \text{ yr}^{-1.5}$ ), with survival before weaning of the other cohorts ranging from  $0.41 \text{ yr}^{-1.5}$  to  $0.55 \text{ yr}^{-1.5}$ . Despite the variability, pup survival estimates were typically lower than those observed for other otariid species to weaning (0.53–0.99; Payne 1977, Wickens and York 1997, McKenzie 2006, Pendleton *et al.* 2006). In this study we were unable to estimate the survival rate of pups from birth to marking (0.17 yr). However, based on results from five breeding seasons at Seal Bay following this study (2002–2009), survival from birth to marking ranges from 0.66 to 0.80 (R. McIntosh, unpublished data); therefore actual survival from birth to weaning at 1.5 yr  $\{(\Phi_{\text{birth to marking}}) * (\Phi \text{ yr}^{-1.5})\}$  identified in this study may range from as little as  $0.11 \text{ yr}^{-1.5}$ – $0.44 \text{ yr}^{-1.5}$  in this population.

California sea lions (*Zalophus californianus*) in Gulf of Mexico have declined by 20% in the past 20 yr. Pup survival in this population was higher than for ASL pups, although the five pup cohorts studied (1981–1984) also showed wide temporal variation in survival rates (0.556–0.998; Hernández-Camacho *et al.* 2008). Annual variability in environmental conditions and genetic variation were suggested to be potential factors causing that variation. From 1997 to 2006, New Zealand sea lions (*Phocarctos hookeri*, NZSLs) had relatively low levels of pup survival to 1 yr of age during bacterial epizootics (0.35–0.55; Chilvers and MacKenzie 2010). Pup production of NZSLs has declined 50% in the last 10 yr, largely due to the interaction between NZSLs and the arrow squid (*Nototodarus sloanii*) trawl fishery. This decline is thought to have been driven by a decline in the number of breeding adult females and exacerbated by pup mortality from bacterial epizootics (Wilkinson

*et al.* 2006, Chilvers *et al.* 2007, Chilvers 2008). Since pup survival is lower in the ASL than other species with declining populations, it is possible that the high pup mortality in the ASL from birth to weaning is hindering recovery of the population at Seal Bay. Pinniped survival rates are typically lower in a decreasing population than in increasing or stable populations of the same species (Pendleton *et al.* 2006), but we have no data to make such comparisons between Seal Bay which is declining, and other colonies such as The Pages Islands (stable) or Dangerous Reef (increasing).

Known anthropogenic factors may be contributing to the low survival rates of pups at Seal Bay. The rate of entanglement in fishing debris recorded at Seal Bay is the highest recorded for any species (1.3% in 2002). Pups were the most frequently entangled age class (54%) with monofilament gill net from the demersal gill net sector of the Gillnet Hook and Trap (GHAT) fishery the predominant entanglement (Page *et al.* 2004). Incidental mortality through fisheries bycatch is identified as a major threat to many pinniped species (De Master *et al.* 2001) and is a reported form of mortality for the ASL. Models by Campbell *et al.* (2008*b*) and Goldsworthy and Page (2007) indicated that low rates of additional female mortality increase the risk of extinction for many ASL populations.

A significant correlation was identified between apparent annual pup cohort survival and SST anomaly. Pup survival was higher when SST anomalies were low both regionally and locally where the sea lions forage. The lowest survival rates were for cohorts 6 and 7 when SST anomalies were high. It is possible that these warm SSTs affected ocean productivity in the Kangaroo Island region and the ASL mothers' ability to provision food to pups. Nieblas *et al.* (2009) showed that SST could be used to predict primary production (using chlorophyll *a*) along the Bonney coast, South Australia, with lower productivity in warmer periods.

SST was also correlated to pup production between 1997 and 2007 in the Australian fur seal (AFS, *A. pusillus doriferus*) in Bass Strait, which also feeds predominantly off the benthos. In that study, pup production was positively correlated to cool winter SSTs and negatively correlated to warm SSTs in the previous summer (Gibbens and Arnould 2009). In the AFS warm SSTs were correlated to a negative impact in maternal success. We propose that the causality between warmer SST and low ASL pup survival to weaning is due to nutritional effects on mothers as a consequence of reduced prey availability and nutritional flow-on effects to the pups, because average SST was calculated after the median pupping date.

Maternal provisioning can be disrupted by oceanographic aberrations and reductions in food supply. South American sea lions (*Otaria byronia*) in Peru showed that acute prey shortage during the warmer conditions of the 1997–1998 El Niño resulted in females increasing the length of their foraging trips and decreasing the time they spent onshore with their pups, which led to an increase in pup mortality from 13% up to 100% during times of low prey availability (Soto *et al.* 2006). Pup mortality remained high following this event due to the punctuated short-term effects it had on population dynamics and subsequent maternal behaviour (Soto *et al.* 2004). Responses to anomalous oceanographic conditions can be instantaneous or ongoing when food supplies are affected.

There are many examples, in a variety of marine species across trophic levels, which link diet shifts, reduced breeding success or reduced abundance with ocean warming. In 2000–2001 there was a lowered abundance of redbait fish (*Emmelichthys nitidus*) in the diet of the largely pelagic New Zealand Fur Seals (NZFSs, *Arctophoca australis*

*forsteri*) on Kangaroo Island (Page *et al.* 2005) and the females had significantly lower pregnancy and reproductive rates (McKenzie *et al.* 2005). Pup weights were also lower than those from preceding breeding seasons (Shaughnessy and Dennis 2002). There was a diet shift in AFS in Bass Strait with less redbait eaten in the warmer SST periods of 1998 and 2002 (Kirkwood *et al.* 2008). These examples coincided with the two periods of low pup survival in ASL cohorts identified in this study. In eastern Tasmania, reduced abundance of schooling redbait and jack mackerel (*Trachurus declivis*) has been associated with periods of lower than normal primary productivity caused by ocean warming (Young *et al.* 1993). It is difficult to determine time intervals between an individual's behavioral and physiological response to changes in its environment and to directly link anomalous conditions to negative impacts on a population. However, anomalously warm ocean conditions in southern Australia can affect marine food webs, and such changes may indirectly affect the vital rates (production and survival) of predators.

Including season of median pupping date (summer, autumn, winter, or spring) as a model covariate (models 9, 15, and 18; Table 4) improved the results compared to models without a covariate (model 21, Table 4), however, the relationship between pup survival and SST anomaly without a seasonal effect was stronger. The seasonal analysis had low power, with winter and summer seasons represented once each in the data set (Table 1). SOI did not correlate to SST anomaly despite the potential link between coldwater upwelling along the Bonney Coast and negative phases of SOI (Middleton and Bye 2007, Middleton *et al.* 2007). Longer time-series data may be required to examine how seasonal, annual and quasi-decadal climate cycles affect life-history traits and to examine potential lag-effects associated with key physical drivers such as SOI, sea temperature and upwelling on survival rates.

### Postweaning Survival

As observed in other otariid species (Trites 1989, Beauplet *et al.* 2005, Hernández-Camacho *et al.* 2008, Chilvers and MacKenzie 2010), it was expected that postweaning juvenile ASLs would have lower survival rates than older age classes because they are typically naïve at the cessation of maternal dependence and because weaned juveniles have not physiologically developed the diving capabilities of adults (Fowler *et al.* 2007b). Survival rates identified in this study provided evidence that postweaned juvenile survival was higher in the ASL ( $0.89 \text{ yr}^{-1}$ ) than in many other otariid species (0.20–0.72; Payne 1977, Trites 1989, Wickens and York 1997). Weaned subantarctic fur seal (*Arctophoca tropicalis*) pups have a higher survival rate than sympatric Antarctic (*A. gazella*) fur seal pups. This is associated with their longer lactation period (11 mo compared to 4 mo) that likely prepares weaned individuals better for environmental perturbations (Guinet *et al.* 1994). Studies by Fowler *et al.* (2006, 2007a, b) suggest that the long lactation period in the ASL (1.5 yr) enables pups to become highly proficient foragers (based on their diving aptitude) by the time they wean. It is most likely that this foraging ability enables the ASL to survive better after weaning than species that have a shorter lactation period and less time to develop such abilities. However, the cost of this long lactation period is a reduced reproductive capacity. For example, an ASL female may have up to 13 pups in a lifetime (reproductive to 24 yr of age) (McIntosh 2007), while NZFS that also breed on Kangaroo Island may have up to 20 pups in a lifetime (McKenzie 2006). Benthic

foraging may also constrain reproductive potential, for example, AFSs, NZSLs and Steller sea lions (*Eumetopias jubatus*), also have lower reproductive rates (average 61.7%) when compared to epipelagic otariids (average 79.1%) (Arnould and Costa 2006). The interesting question is whether the potentially higher survival rate of postweaning juveniles balances the reduced reproductive potential of the ASL. A life history analysis to examine this in ASLs cannot yet be performed with surety because fecundity rates are unknown for this species.

For subantarctic fur seals, juvenile survival to the first return to the colony at 3–6 yr (0.964) was negatively related to SST anomaly of the first 6 mo following the weaning process (Beauplet *et al.* 2005). The most supported models in our study only detected variable cohort survival in pups, and survival for other age groups was constant. Further studies including a more intensive marking program might detect other patterns.

Our estimates of postweaning juvenile survival ( $0.89 \text{ yr}^{-1}$ ) were similar to survival rates in the declining population of NZSLs at Enderby Island aged 2 and 3 yr (male, female  $\Phi$ : 0.60–0.90, 0.70–0.80; Chilvers and MacKenzie 2010) and the increasing population of Steller sea lions aged 2 and 3 yr, respectively at Forrester Island, Alaska (male, female  $\Phi$ : 0.68, and 0.79, 0.68, and 0.87; Pendleton *et al.* 2006). Juvenile California sea lions in a declining population in the Gulf of Mexico displayed higher postweaning (1–4 yr) survival rates of 0.90 (Hernández-Camacho *et al.* 2008), however, this was based on a small sample of marked pups (96 male, 94 female over five cohorts). The population trend of a colony does not seem indicative of the rate of juvenile survival, because NZSLs and the California sea lions are declining populations while the Steller sea lion population is an increasing population. These survival rates are likely comparable or higher than ASL postweaning survival rates because they include individuals aged 2 and 3 yr, which includes up to 2 yr of experience postweaning, whereas the ASL postweaning juveniles in this study have only 1.5 yr of experience postweaning when they are 3 yr of age.

Survival rates for females older than 3 yr in the ASL ( $0.96 \text{ yr}^{-1}$ ) were similar to adult female survival rates seen in other otariid species (0.85–0.98), while survival rates of males older than 3 yr ( $0.89 \text{ yr}^{-1}$ ) were higher than adult male survival rates in many otariids (0.50–0.70; Payne 1977, Wickens and York 1997, Beauplet *et al.* 2006, McKenzie 2006). The high survival rate in ASLs was similar to those seen in the increasing population of Steller sea lions at Forrester Island (male, female  $\Phi$ : 0.88, 0.93; Pendleton *et al.* 2006), in 4–15 yr old New Zealand sea lions at Enderby Island (which is declining) (male, female  $\Phi$ : 0.98, 0.89–0.95; Chilvers and McKenzie 2010), and in California sea lions in Mexico (also declining) (male, female 5–9 yr  $\Phi$ : 0.90, 0.97 male, female 10+ yr  $\Phi$ : 0.75, 0.91; Hernández-Camacho *et al.* 2008). However, sample sizes for older age classes were also small in the California sea lion study and must be interpreted with caution.

### Conclusion

ASL pup survival from birth to weaning was low when compared to other otariid species and lower than that at the declining NZSL population at Enderby Island (Chilvers and McKenzie 2010). Pup abundance also declined at Seal Bay at a rate of 1.14% per breeding season between 1985 and 2003 (Shaughnessy *et al.* 2006). The low pup survival identified in this study is likely to be limiting recruitment and population recovery. Two consecutive pup cohorts in particular had low survival

to weaning (1998 and 2000). Many factors may contribute to low pup survival. In this study, periods of anomalously warm SST correlated negatively with pup survival from marking at 0.17 yr to weaning at 1.5 yr. Warm SSTs were used as a proxy for a lowering of ocean productivity in the area and we suggest that during periods of unusual oceanographic warming, maternal provisioning to pups may be inhibited, resulting in a reduction in pup survival.

Once pups were weaned, the probability of survival was high. There is much variability between species when comparing survival rates in declining and increasing populations, and the high survival rates of individuals older than pups are not necessarily indicative of the population trend. The high survival of weaned individuals may be attributed to the 1.5 yr period of lactation that enables pups to wean gradually and with less naivety than in other species, perhaps balancing the cost of the species' lower reproductive rate.

While these results are specific to the Seal Bay population of the ASL, and are not directly applicable to other colonies, Seal Bay is likely to remain the only population where such a marking program is undertaken due to the difficulty in accessing other colonies. Seal Bay can be visited daily because it is on a large populated island with infrastructure support and staff onsite. Consequently, research at Seal Bay is likely to provide the only survival estimates for the species and their use for the whole species is unavoidable. Despite potential variation of survival rates at colonies with differing population trends and environmental conditions, survival rates from Seal Bay are more appropriate than extrapolating survival data from other species as done previously.

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