Age- and sex-specific survival estimates incorporating tag loss for New Zealand sea lions, *Phocarctos hookeri*

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The estimation of life-history parameters for a threatened species is important for understanding its biology and helping to determine management options. This research investigates age- and sex-related survival estimates incorporating tag loss for New Zealand (NZ) sea lions (*Phocarctos hookeri*) from Sandy Bay, Enderby Island, Auckland Islands, New Zealand, using multistate mark–recapture data from known-age individuals over 8 years (1997–1998 to 2005–2006). Survival estimates and tag loss rates differed significantly by sex and age class, with adult males having the lowest tag retention of any age or sex class and females ≥ 3 years old having lower survival estimates than their male counterparts. The variability and lower female survival relative to males is a critical problem for NZ sea lions, because even small changes in adult female survival significantly affect population trends for such large, long-lived mammals. DOI: 10.1644/09-MAMM-A-285.1.

Demographic information that can be obtained only through long-term studies of the life histories of individuals is essential for understanding the dynamics of populations. However, few long-lived species have had sufficient long-term study to enable their demographics to be well defined. For managers, lack of demographic data can result in considerable uncertainty and unsustainable decisions (i.e., setting of bycatch or harvest limits) in species management or conservation. In particular, age-related variation in survival affects the size and dynamics of a population and, therefore, its status and trend (McCallum 2000; Stearns 1992). For long-lived, slow-breeding marine mammals survivorship among younger age classes is generally recognized as significantly different from adult survival; however, high adult survival is critical for population stability or growth (Caughley 1966; Mills 2006; Pendleton et al. 2006).

The New Zealand sea lion (NZ sea lion, *Phocarctos hookeri*) is one of the rarest and most highly localized pinnipeds. It has been classified as ''Vulnerable'' and in decline by the International Union for the Conservation of Nature (2008) and ''Threatened'' under the New Zealand threat classification system (Hitchmough et al. 2007). NZ sea lions breed only on New Zealand's subantarctic islands between the latitudes 48°S and 53°S (Chilvers et al. 2007; Gales and Mattlin 1997). Their population size is one of the smallest reported for an otariid, with <10,000 individuals

recorded during the 2008–2009 breeding season (Geschke and Chilvers 2009). Eighty-six percent of pup births occur on the Auckland Islands (50°30′S, 166°E; Fig. 1—Chilvers et al. 2007). Pup production of this species has declined >50% in the last 10 years. This decline is thought to have been driven by a decline in the number of breeding adult females (Chilvers 2008; Chilvers et al. 2007; Wilkinson et al. 2006).

Over the past decade the interaction between NZ sea lions and the arrow squid (*Nototodarus sloanii*) trawl fishery, which operates on the Auckland Islands shelf between February and May each year, has been investigated (Chilvers 2008; Chilvers et al. 2005, 2006; Costa and Gales 2000; Gales 1995; Gales and Mattlin 1997; Uozumi 1998, Wilkinson et al. 2003). Estimates of incidental captures and killings of NZ sea lions in squid trawl nets have varied between 32 and 150 sea lions per year since 1992 (Baird 1996, 1999, 2005a, 2005b; Baird and Doonan 2005; Smith and Baird 2005;Wilkinson et al. 2003). The impact of this fisheries-related mortality on the NZ sea lion population remains unclear (Breen et al. 2003; Doonan and Cawthorn 1984; Woodley and Lavigne 1993), with limited information available on population parameters for NZ sea lions and limited availability of verified fisheries bycatch data. Estimates of survival for all age classes of NZ
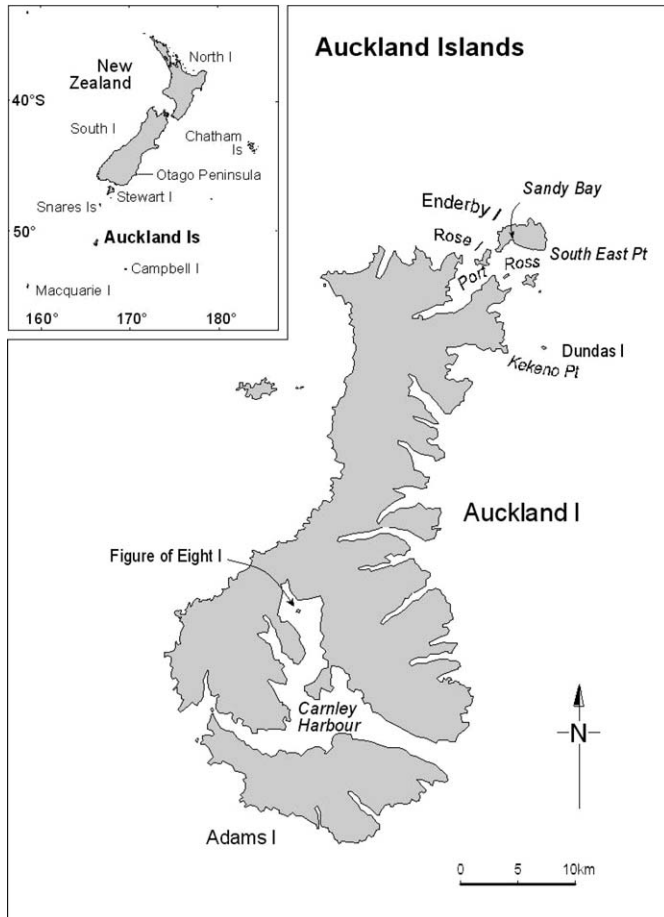
FIG. 1.—Sandy Bay breeding colony, Enderby Island, Auckland Islands (50°30′S, 166°17′E).

sea lions are needed for both ongoing species research and conservation purposes.

Since 1998 all NZ sea lion pups born on Enderby Island, Auckland Islands, have been double-tagged (1 tag in each fore flipper) to enable individual identification and thus facilitate the estimation of life history parameters for the species. In addition, between 1998 and 2002 all pups were tagged with passive integrated transponders (PITs). In 2000, 297 pups and 134 adult female NZ sea lions also were hot-iron branded, and all brands have remained legible to date (B. L. Chilvers, pers. obs.). The combination of these marking strategies allows identification of individuals that have lost both flipper tags. This is important because one of the key assumptions when estimating population demographics from mark–recapture data is that identifying markers are not lost (Seber 2002). Animals that lose markers or tags (or other unique markings) no longer can be identified and, hence, are effectively removed from the pool of marked individuals in the population able to be recaptured. From the perspective of the data this removal is indistinguishable from mortality, so loss of marks or tags results in underestimation of population parameters such as survival probability (Pollock et al. 1990).

Research on pinnipeds often relies on use of flipper tags to mark animals (Beauplet et al. 2005; Bradshaw et al. 2000; Cameron and Siniff 2004). Survival estimates for flipper-

tagged pinnipeds (when permanent emigration is 0 or accounted for) can be represented as $\phi = \theta \times S$, where ϕ represents apparent survival rate, θ is the probability of an animal retaining a tag, and S is the probability of survival. However, pinnipeds are known to lose flipper tags, and double-tagging of individuals is a common approach for combating the effects of tag loss. Two main benefits result from double-tagging: the animal will be identifiable provided at least 1 tag is retained (so that proportionally fewer animals will be removed from the pool of marked individuals than with single-tagging); and the fraction of animals recaptured with only 1 tag can be used to estimate the probability of losing 1 tag (τ). By assuming tags are lost independently, the probability of tag retention (i.e., at least 1 tag retained) is $\theta = 1 - \tau^2$, which can be used to adjust the apparent survival rate.

The objectives of this research were to use multistate mark–recapture data from known-age individuals to estimate survival of NZ sea lions, taking into consideration tag loss relative to age and sex. The accurate estimation of survival in all age classes is important for investigating overall population viability, management, and conservation of the species.

MATERIALS AND METHODS

Study site and tagging.—This research was conducted at Sandy Bay, Enderby Island, in the northeast of the Auckland Islands group (50°30′S, 166°17′E; Fig. 1) during the summers of 1997–1998 to 2005–2006. The Sandy Bay breeding area is the 2nd largest for NZ sea lions, with approximately 400 pups per year born there (Chilvers et al. 2007). Tagging has been intermittent, and the numbers of animals tagged annually have varied from 0 to >500 since 1979–1980. Between 1979–1980 and 1992–1993 the flipper tags used were uniquely numbered Alflex laser-marked button tags (Alflex NZ Ltd., Palmerston North, New Zealand), attached to the right pectoral flipper only. Since 1997–1998 all NZ sea lion pups born at Sandy Bay have been tagged at 1 month of age as part of a long-term population demographics study. In the 1997–1998 and 1998–1999 seasons the same Alflex tags were used as previously, but animals were tagged on both pectoral flippers. Since 1999–2000 uniquely numbered Dalton DAL 008 Jumbotags coffin-shaped tags (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) have been used to tag animals on both pectoral flippers. Between 1998–1999 and 2002–2003 all animals that were flipper-tagged also were injected with PITs (Trovan, Ltd., Douglas, United Kingdom). During the 1999–2000 season 297 pups and 135 adult females from Sandy Bay were hot-iron branded, with adults also being tagged (if untagged at the time of branding) or retagged if they had been tagged as pups (I. S. Wilkinson, Department of Environment and Conservation, Australia, pers. comm.) All research on live animals followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and was approved by the Department of Conservations Animal Ethics Committee (86 and 158).

Resighting of tagged animals.—Details on presence at the breeding area and number of tags were collected opportunistically from marked animals before the 1998–1999 breeding season. Subsequently, daily tag resightings and records of presence of a PIT or brand were conducted on Enderby Island between 1 December and 20 February each season (1998–1999 to 2005–2006). Sightings from other breeding areas and haul-out sites (including on the New Zealand mainland) also were recorded at least once a year during this time (Chilvers and Wilkinson 2008). The resighting data presented here are from the 1998–1999 to 2005–2006 seasons.

Resightings of animals were accepted only for inclusion in this analysis if the tag number or brand had been recorded twice in 1 breeding season (December–February); twice within 1 year on the New Zealand mainland; or was a single sighting confirmed by photograph, presence of a PIT, or identification by 2 independent observers simultaneously. These procedures were designed to minimize the potential bias resulting from the misreading of tags during resightings. Although tagging has occurred since 1979–1980, this study involved only animals tagged since 1989–1990, and used resightings data only since 1998–1999, because field effort was inconsistent prior to the 1998–1999 season. Note that for animals tagged before 1998–1999, the period between tagging and their 1st resighting was not included in the analysis, because this can bias estimated survival probabilities.

Analysis.—The tag-resight data were analyzed using multistate mark–recapture models, where the number of flipper tags was used to define states (i.e., 2, 1, or 0). In a multistate mark–recapture model, where individuals can transition from 1 state to another in successive years, the probability of survival from year t to $t + 1$ can depend upon the individual's state in year t, and probability of recapture (or resighting) also can vary between states. In this application the probability of transitioning from 1 state to another, therefore, represents the tag loss rates, which can be estimated with the transition probability matrix (TPM):

$$\text{TPM} = \begin{bmatrix} \psi_A^{2,2} & \psi_A^{2,1} & \psi_A^{2,0} \\ 0 & \psi_A^{1,1} & \psi_A^{1,0} \\ 0 & 0 & 1 \end{bmatrix},$$

where $\psi_A^{r,s}$ is the probability of the animal having r tags in year t and s tags in year $t + 1$, where the tags are of age A in year t (rows indicate state in year t and columns state in $t + 1$). The only constraint on the TPM is that each row must sum to 1, hence here the probability of retaining the same number of tags during the year (i.e., the elements on the main diagonal, $\psi_A^{r,r}$) was obtained by subtraction. We assumed that the number of tags did not influence survival, so survival was made to be equal for all 3 states, although resighting probability was allowed to vary by the number of tags.

The exact method of analysis varied slightly for male and female NZ sea lions. Males were tagged only as pups so that 3 groups of males exist: flipper-tagged only as pups; flipper- and PIT-tagged as pups; and flipper- and PIT-tagged and branded as pups. These groupings are necessary to account for

potential heterogeneity in the resighting probabilities. Female NZ sea lions were tagged (or retagged) occasionally as adults, so that 5 groups were recognized: the same 3 as males; plus flipper- and PIT-tagged as adults; and flipper- and PIT-tagged and branded as adults. If a female was retagged, in the year of retagging she would be regarded 1st as a loss on capture for her current group, but released as a member of the new group.

For both males and females tag loss rates in the 1st year following tagging were allowed to be different from those in later years; and for females tag loss rates for females tagged as pups were allowed to be different from those tagged as adults. For both sexers survival rates were estimated as:

$$\text{logit}(S_{t,a}) = \beta_t \qquad\qquad a \geq 4$$
$$= (a-4)\beta_{\text{juv}} + \beta_t \qquad 0 < a < 4,$$

where a is the age of the animal, implying that once animals were 4 years old they were considered to be adults, and that between the ages of 0 and 3, survival changed (expectation is that it will increase) at a constant rate. β_{juv} is the rate at which logit-survival is expected to change each year, and β_t is logit-survival in year t. The use of the logit-link here ensures that the survival probability will be between 0 and 1, and it is analogous to performing logistic regression on the survival probabilities (if they were directly observable). A slightly different model for survival also was considered, where the survival probability for juveniles was assumed to be constant between the ages of 0 and 3; that is, $\text{logit}(S_{t,a}) = \beta_{\text{juv}}^* + \beta_t$. Resighting probabilities also were modeled using the logit-link, with the intention of allowing for general year effects that were the same for all groups of animals regardless of the number of tags; differences between groups and the number of flipper tags (e.g., resighting probabilities could be different for NZ sea lions with only 1 flipper tag compared with those with brands and 2 flipper tags); and that younger animals are less likely to return to the breeding colonies and therefore will have a lower resighting probability than older animals (Chilvers and Wilkinson 2008). Specifically, resighting probability was modeled as:

$$\text{logit}(p_{t,a,g \times s}) = \gamma_t + \gamma_{g \times s} \qquad\qquad a \geq x$$
$$= (a-x)\gamma_{\text{juv}} + \gamma_t + \gamma_{g \times s} \qquad 1 < a < x,$$

where γ_t is the year effect, $\gamma_{g \times s}$ is the effect on resighting probability for a NZ sea lion in group g with s flipper tags, and γ_{juv} is the rate at which resighting probabilities change (expectation is that they will increase) for juvenile animals up to age x, at which point they are considered to have the same resighting probability as adults. For male NZ sea lions, $x = 3$, and for females, $x = 4$. In addition, the biological reality is that if an animal is not PIT-tagged or branded, once it has lost both flipper tags it has 0 probability of being resighted. This constraint was applied in our analysis.

The data were analyzed using program MARK (MARK 5.1, Colorado State University, Fort Collins, Colorado). The structure for the resighting probability component of the model was maintained in the general form described above, with

TABLE 1.—Model selection summary for male New Zealand sea lions. ΔAIC_c is the relative difference in Akaike's information criterion corrected for small samples (AIC_c) values, w is the AIC_c model weight, K is the number of parameters estimated, and *Dev.* is the model deviance. The terms in parentheses denote which factors are included for each parameter in the respective model, with ''·'' indicating that a constant value has been estimated. Juv.con denotes a model where the survival rate of juveniles is constant with ages, and Juv denotes the more general model where survival is changing by a constant rate as the animal gets older. All models had the same structure for resighting probabilities. Yr = annual variation was included in model; Age = tag loss varied by age of the tag was included in model.

Model	ΔAIC_c	w	K	*Dev.*
$S(\text{Juv} + \text{Yr})\psi(\cdot)$	0.00	0.35	27	881.25
$S(\text{Juv} + \text{Yr})\psi(\text{Age})$	1.19	0.19	29	878.30
$S(\text{Juv})\psi(\cdot)$	1.24	0.19	21	894.85
$S(\text{Juv} + 2002)\psi(\cdot)$	2.32	0.11	22	893.87
$S(\text{Juv})\psi(\text{Age})$	2.64	0.09	23	892.14
$S(\text{Juv} + 2002)\psi(\text{Age})$	3.65	0.06	24	891.09
$S(\text{Juv.con} + \text{Yr})\psi(\cdot)$	86.93	0.00	27	968.18
$S(\text{Yr})\psi(\cdot)$	110.68	0.00	26	993.99

modeling efforts being focused on the structure of the tag loss and survival components. Loss of flipper tags was assumed to be constant in all years, although models that allowed tag loss to be higher in the 1st year after tagging were used and, for female NZ sea lions, whether tag loss was higher for animals tagged as adults compared with those tagged as pups. Because all animals were double-tagged, it was possible to have a tag-age effect only for the $\psi_A^{2,1}$ and $\psi_A^{2,0}$ probabilities (i.e., if an animal only has 1 flipper tag, then that tag must already be more than 1 year old [with the other tag having been lost in a previous year]). For survival rates we focused on whether evidence of annual variation and differential survival between adult and juvenile animals existed. A submodel of the degree of annual variation in survival addressed whether survival was different in 2002 but equal in the other years. This was motivated by a mass mortality event that occurred in 2002. The combination of these different hypotheses about factors that can influence loss of flipper tags and animal survival rates defined our candidate model set. Models were fitted to the data and compared for parsimony using Akaike's information criterion corrected for small samples (AIC_c). AIC_c model weights were used to indicate the level of support for different models, hence, different hypotheses (Burnham and Anderson 2002). Model-averaged estimates of flipper-tag loss and animal survival rates have been reported so that model uncertainty can be accounted for (i.e., models with different structures and parameter estimates can be ranked similarly—Burnham and Anderson 2002).

RESULTS

Resighting of tagged animals.—Between 1998–1999 and 2005–2006, on average, 1,690 individuals (range 1,431–1,924 individuals) were resighted each year from an average of 5,665 sightings recorded a year. Of these individuals
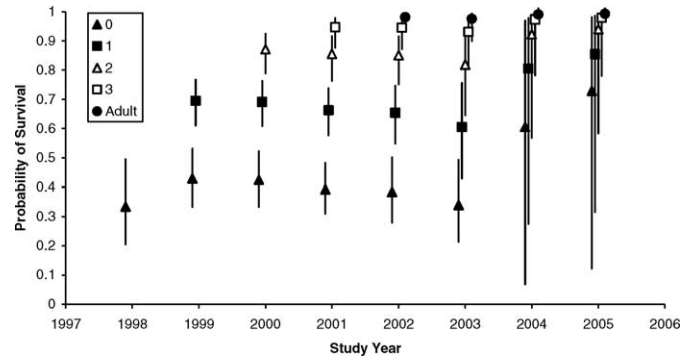

FIG. 2.—Model-averaged estimates of survival from 1998 to 2005 for 0-, 1-, 2-, and 3-year-old and adult male New Zealand sea lions. Vertical lines represent 95% *CI*s.

approximately equal numbers of individuals were identified only from brands or a PIT, an average of 104 individuals per year were recorded as being sighted by brands only (range 91–119 individuals), and an average of 84 individuals per year by a PIT only (range 44–159 individuals). Eighty-six percent of all sightings each year were from Enderby Island, 13% from around the Auckland Islands, and only 1% from other places. Those sightings away from Enderby Island were mainly males, particularly juveniles (Chilvers and Wilkinson 2008).

Males.—As indicated by model weights, models allowing juvenile survival to change gradually each year until age 4 have the highest degree of support (Table 1). Otherwise, the models provide little conclusive information about the factors influencing tag loss and animal survival rates for males. Models that assume tag loss is the same in the 1st year after tagging as in later years consistently ranked higher, but only slightly so. Models with annual variation in survival had the most support, but models with no variation, or a difference in 2002, also had substantial support.

Survival rates in 2004 and 2005 are poorly estimated (as evidenced by wide confidence intervals [*CI*s]), reflecting the small sample sizes (Fig. 2). Potential confounding with resighting probabilities may exist in some of the models when both components have year effects. Focusing on the earlier years, survival rates are estimated to increase with age, from approximately 0.4 for pups to >0.95 for adults.

For males the probability of losing both tags in a single year is surprisingly close to the probability of losing a single tag, which suggests that flipper tags may not be lost independently (Table 2). When animals are double-tagged it is slightly more difficult to deduce potential tag loss bias on survival estimates, because it depends on what fraction of animals still have 2, or only 1, tag. If we assume that a cohort of animals are all double-tagged, we can project forward to determine what proportion of animals that are still alive in subsequent years have 1 or 2 tags (Fig. 3). The retention probability is then the ratio of the fraction of animals with at least 1 tag in consecutive years; that is, the probability that an animal with at least 1 tag in year t still has at least 1 tag in year $t + 1$ (Fig. 3). This suggests that without accounting for flipper-tag loss, and with no other way of identifying individuals, the

TABLE 2.—The model-averaged probability of having *r* flipper tags in year *t* and *s* tags in the next year for male New Zealand sea lions. *SE*s are given in parentheses.

$r \rightarrow s$	First year	Later years
$2 \rightarrow 1$	0.16 (0.04)	0.13 (0.02)
$2 \rightarrow 0$	0.09 (0.03)	0.09 (0.02)
$1 \rightarrow 0$	0.14 (0.03)	0.14 (0.03)

apparent estimate of adult male survival would be between 86% and 90% of the true value on an annual basis. Furthermore, if these estimates of tag loss apply long term, by age 10 approximately 30% of the male NZ sea lions tagged as pups that are still alive will have at least 1 tag but only 10% will have 1 tag by age 20.

Females.—As indicated by AIC$_c$ model weights for female NZ sea lions, the models allowing juvenile survival to gradually change each year until age 4 have the highest degree of support (Table 3). Also, loss rates of flipper tags for females tagged as adults differ from those tagged as pups. Unlike for male NZ sea lions, the 2 top-ranked models for females have essentially all of the AIC$_c$ model weight. Both models have a very similar structure, where tag loss in the 1st year is different for animals tagged as pups and those tagged as adults, but is equal in later years, and juvenile survival gradually increases to the level of adult survival by age 4. The only difference between the 2 models is whether survival in 2002 was different from all other years or whether the difference simply represents annual variation.

As was also the case for males, estimates of survival for females for 2004 and 2005 have poor precision (as evidenced by the width of *CI*s), reflecting the small sample sizes and, possibly, some confounding (Fig. 4). Focusing on the earlier years, survival rates are estimated to increase with age, from approximately 0.55 for pups to 0.95 for prime-age adults (4–15 years).

For females tagged as pups the probability of losing 1 of 2 tags in the 1st year is slightly higher than for males, and
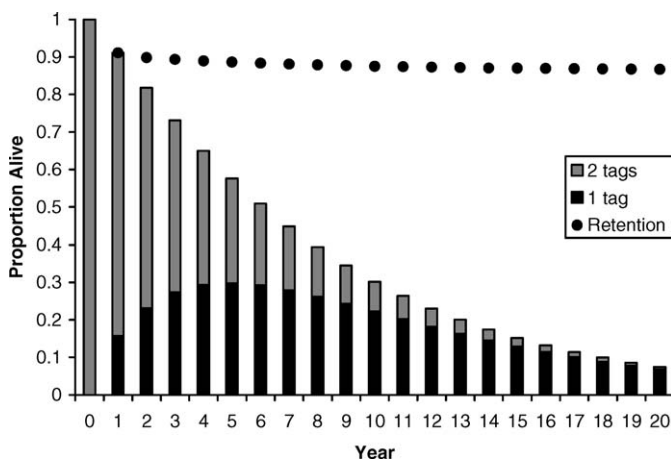
TABLE 3.—Model selection summary for female New Zealand sea lions. ΔAIC$_c$ is the relative difference in Akaike's information criterion corrected for small samples (AIC$_c$) values, *w* is the AIC$_c$ model weight, *K* is the number of parameters estimated, and *Dev.* is the model deviance. The terms in parentheses denote which factors are included for each parameter in the respective model, with ''·'' indicating that a constant value has been estimated. Juv.con denotes a model where the survival rate of juveniles is constant with ages, and Juv denotes the more general model where survival is changing by a constant rate as the animal gets older. Ad indicates that tag loss rates are different for females tagged as adults versus pups. All models had the same structure for resighting probabilities. Yr = annual variation was included in model.

Model	ΔAIC$_c$	*w*	*K*	*Dev.*
S(Juv + 2002)ψ(1st × Ad + later)	0.00	0.87	32	1,377.34
S(Juv + Yr)ψ(1st × Ad + later)	3.99	0.12	38	1,369.01
S(Juv + Yr)ψ(Age × Ad)	9.72	0.01	41	1,368.55
S(Juv + 2002)ψ(Age × Ad)	11.04	0.00	35	1,382.23
S(Juv)ψ(1st × Ad + later)	15.31	0.00	31	1,394.70
S(Juv)ψ(Age × Ad)	21.04	0.00	34	1,394.28
S(Juv.con + Yr)ψ(1st × Ad + later)	62.04	0.00	37	1,429.12
S(Juv.con + Yr)ψ(Age × Ad)	67.73	0.00	40	1,428.63
S(Juv + Yr)ψ(Age)	73.15	0.00	36	1,442.28
S(Yr)ψ(1st × Ad + later)	233.77	0.00	37	1,600.85
S(Juv + Yr)ψ(·)	237.30	0.00	34	1,610.55

tags may not be lost independently (Table 4). Flipper-tag loss in the 1st year for females tagged as adults is even higher. Long-term retention rates of tags for female NZ sea lions with 1 and 2 tags that were initially tagged as pups with 2 tags were higher (Fig. 5) than for females tagged as adults (Fig. 6). Proportionally more females tagged as pups had at least 1 tag after the same period of time than females tagged as adults (10 years: 50% versus 30%, respectively; 20 years: 17% versus 9%, respectively). This suggests that without accounting for flipper-tag loss, and with no other way of identifying individuals, the apparent estimate of female adult survival would be between 90% and 96% of the true value.
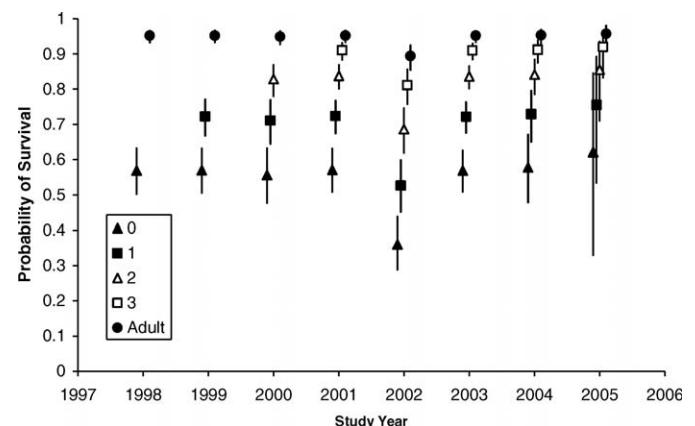

FIG. 3.—Proportion of male New Zealand sea lions alive with 1 or 2 tags (stacked columns) and retention probability of at least 1 tag.

FIG. 4.—Model-averaged estimates of survival from 1998 to 2005 for 0-, 1-, 2-, and 3-year-old and adult female New Zealand sea lions. Vertical lines represent 95% *CI*s.

TABLE 4.—The model-averaged probability of having *r* flipper tags in 1 year and *s* tags in the next year for female New Zealand sea lions. *SE*s are given in parentheses.

	Tagged as pup		Tagged as adult	
$r \rightarrow s$	First year	Later years	First year	Later years
$2 \rightarrow 1$	0.21 (0.05)	0.13 (0.02)	0.54 (0.04)	0.13 (0.02)
$2 \rightarrow 0$	0.10 (0.04)	0.01 (0.01)	0.25 (0.03)	0.01 (0.01)
$1 \rightarrow 0$	0.13 (0.02)	0.13 (0.02)	0.13 (0.02)	0.13 (0.02)

DISCUSSION

These are the 1st age- and sex-specific survival estimates for NZ sea lions that incorporate tag loss. Overall, survival estimates and tag loss rates differed significantly by sex and age class, with adult males having the lowest tag retention and females of 3 years of age and older having lower survival estimates than their male counterparts. This research was undertaken (1998–1999 to 2005–2006) while the NZ sea lion population in the Auckland Islands (determined from yearly pup production estimates) has been in decline (Chilvers et al. 2007), and even greater declines have occurred since (Chilvers 2009).

The estimated loss rate of flipper tags for NZ sea lions is equal to or relatively low compared with rates estimated for other otariid species. For example, annual probabilities of losing individual tags were 0.09 for adult female antarctic fur seals (*Arctocephalus gazella*—Boyd et al. 1995), and for African fur seals (*A. pusillus*) the probability of losing an individual tag was 0.15 in the first 5–9 months (Shaughnessy 1994). The probability of losing both tags within the first 6 months ranged from 0.04 to 0.34 depending on tag type for NZ fur seal (*A. forsteri*) pups (Bradshaw et al. 2000). Annual juvenile tag loss rate for subantarctic fur seals (*A. tropicalis*) was constant at 0.217 (Beauplet et al. 2005).

The highest tag loss rate estimated was for females tagged as adults in the 1st year after tagging. This loss rate is thought
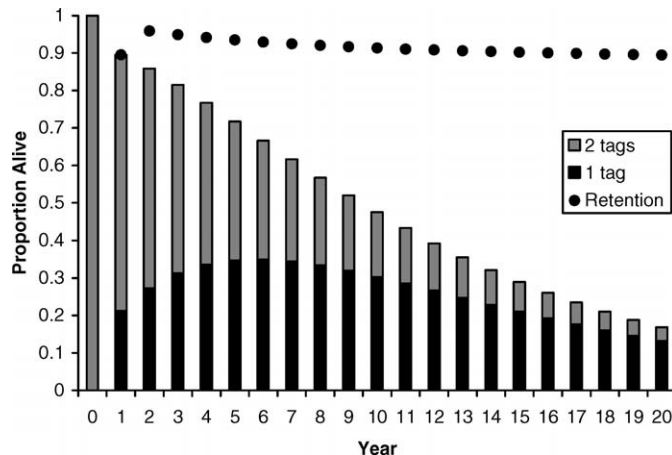

FIG. 5.—Proportion of female New Zealand sea lions tagged as pups alive with 1 or 2 tags (stacked columns) and retention probability of at least 1 tag.
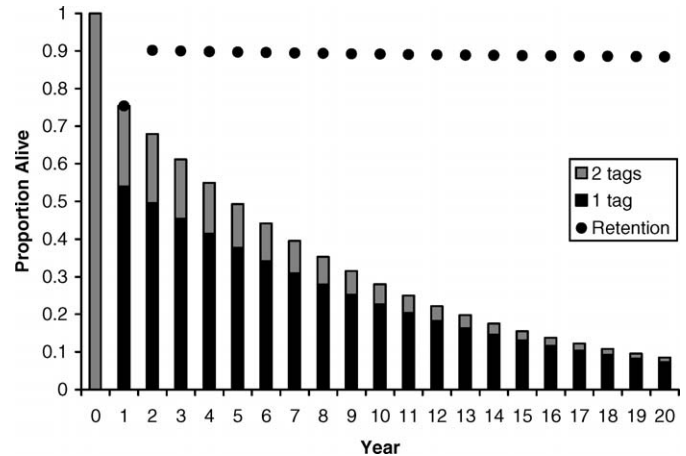

FIG. 6.—Proportion of female New Zealand sea lions tagged as adults alive with 1 or 2 tags (stacked columns) and retention probability of at least 1 tag.

to relate to the application method used to retag adult females. Females that were tagged previously (either as pups or adults) had their old tags removed, and to avoid creating additional scar tissue, the new tags were placed in the same hole (for 62 of 134 or 46% of all females animals tagged as adults). This application method appears to have resulted in a higher rate of tag loss. Despite losing their tags, these animals still contributed to the survival estimates, because they also were branded and had PITs.

After adult females the next highest tag loss rate was for female pups in the 1st year after tagging. Tag loss differences between year of application and subsequent years are expected because of tagging-associated effects such as failure of the wound to heal or manufacturer's faults in the tags (Diefenbach and Alt 1998; Pistorius et al. 2000).

Total tag loss within a population should increase progressively with time because impacts on tags accumulate with time. For example, sea lion pups are small when tagged but become much larger (pups are tagged at an average weight of 11 kg but reach 112 kg as adult females and 300–450 kg as adult males). Tags suffer wear and tear from salt water, sun (ultraviolet rays), and habitat (sand, rocks, grass, and forest) so that a certain number of tags will fail with age. For animals tagged as pups, males have a significantly higher probability than females of losing both tags in the years after tagging (0.09 versus 0.01). This difference is likely due to sexual dimorphism between adult male and female NZ sea lions, particularly flipper thickness. The flippers of adult males reach 3–5 cm thick at the front of their fore flipper, tapering to approximately 1.5 cm thick in the area where the tags are placed (B. L. Chilvers, pers. obs.). Because the tag shaft is 1.5 cm long, wear and tear is going to affect the tags on males more than those on females, whose flippers are significantly thinner (approximately 2 cm thick at the front of the fore flipper, tapering to approximately 0.8 cm thick in the area where the tag is placed—B. L. Chilvers, pers. obs.).

Many of the NZ sea lions that we monitored could be identified, even with the loss of both flipper tags, because of

the presence of a PIT and or a brand. No brands have been lost as identifiable marks, and only 4 losses of PITs have been confirmed in NZ sea lions (B. L. Chilvers, pers. obs.). The rate of PIT loss is difficult to determine, because it is not known whether it is loss of the PIT or difficulty in reading the tags that has caused this inability to identify animals from their PIT. That these 2 alternative marking methods have lower loss rates than flipper tags suggests that alternative marking methods that permit animals with no flipper tags to be identified would be beneficial, subject to affordability and compliance with animal ethics standards. Ongoing tag loss means that fewer older animals are identifiable solely from flipper tags, which could hamper our ability to estimate population parameters such as survival or senescence reliably in older animals.

Estimated adult survival rates were 0.98 for male NZ sea lions aged 4–15 years and between 0.89 and 0.95 for similarly aged female NZ sea lions. High survival rates are to be expected for prime breeding-age animals in a species such as the NZ sea lion that is long lived and slow breeding. However, it is unlikely that such high survival rates persist given that the majority of animals in this study were <15 years old (Chilvers et al., in press). In many of the sex and age classes in the study animals the lowest survival estimates coincided with bacterial epizootics that occurred in 1998 and 2002 (Wilkinson et al. 2006).

Our study provides the 1st survival rate estimate for adult male NZ sea lions. These survival rates are high compared with those obtained for other adult male otariids. For example, Pendleton et al. (2006) estimated adult survival rates for adult male Steller sea lions (*Eumetopias jubatus*) at 88.4% (±2.3% *SE*) from branded animals from Forrester Island, Alaska, for the period 1994–2003. Hernandez-Camacho et al. (2008) estimated survival rates for branded adult male California sea lions (*Zalophus californianus*) in Mexico to be 90% (±2.9% *SE*) for animals between 5 and 9 years and dropping to 74.6% (±4.4% *SE*) for animals 10 years and older. Our estimates relate more closely with estimates of Hernandez-Camacho et al. (2008) for animals 5–9 years, because the majority of male NZ sea lions used in this analysis are <15 years of age. In the entire sighting database only 41 males have ever been confirmed to be alive past the age of 12, and this number drops to only 9 individuals 15 years and older.

For female NZ sea lions, Chilvers et al. (in press) obtained similar survival rates for prime breeding-age females using only branded adult females as the data set, with estimates between 90% and 95% for animals up to 10–15 years old; however, this dropped quickly to <80% by age 20. The range of adult female survival rates in this study was slightly higher than those previously reported for NZ sea lions at the Auckland Islands; however, these earlier estimates did not take into account tag loss, and also covered a larger range of ages (82%, *CI* = 76–86% [Gales and Fletcher 1999] and 87%, *SD* = 0.02% [Lalas and Bradshaw 2003]). Our results are similar to those observed for other female otariid species; for example, antarctic fur seals (Boyd et al. 1990, 1995; Wickens

and York 1997), subantarctic fur seals (Beauplet et al. 2006), Australian fur seals (Wickens and York 1997), northern fur seals (*Callorhinus ursinus*—Chapman 1964; Wickens and York 1997), California sea lions (Hernandez-Camacho et al. 2008), and Steller sea lions (Boyd 1992; Pendleton et al. 2006; York 1994).

It is unusual for adult female otariids to have lower survival estimates than their male counterparts in the age ranges of this research. For both California and Steller sea lions adult females are reported to have higher survival rates than adult males (Hernandez-Camacho et al. 2008; Pendleton et al. 2006). Sexual selection on males in polygamous-breeding species such as otariids favors morphological traits and behaviors that award short-term reproductive advantages (Mills 2006; Selander 1964). However, these exaggerated reproductive investments in males negatively impact long-term survival (Clinton and Le Boeuf 1993; Mills 2006).

For the Auckland Islands NZ sea lion population direct and indirect impacts from the local squid trawl fishery on females and juveniles do not affect adult males. No adult male NZ sea lions have ever been recorded being killed in this trawl fishery, whereas up to 82% of animals killed each year are adult females (Chilvers 2008). Also, few adult males are present in the Auckland Islands area during the main fishing period (February–May each year), because they disperse to the New Zealand mainland and other subantarctic islands such as Campbell, Macquarie, and Snares islands soon after breeding finishes in late January (Geschke and Chilvers 2009; Robertson et al. 2006). This also means that they are not impacted by any possible reduced food availability or habitat disturbance due to fisheries activities. In contrast, adult females experience their highest energy demands, due to lactation, when fishing occurs and are more likely to be impacted because they are central-place foragers restricted in their foraging time and distance traveled because of their need to return regularly to feed their pups on land (Chilvers 2008; Orians and Pearson 1979). Another impact on all NZ sea lions has been the bacterial epizootics that occurred in 1998 and 2002. These appear to have affected the survival of adult females and juveniles of both sexes more than adult males (Wilkinson et al. 2006).

Small changes in the probability of adult female survival significantly affect population stability and trend for large, long-lived mammals (Caughley 1966; Mills 2006; Pendleton et al. 2006). Pup production in NZ sea lions dropped by 30% during the period of this research (1998–1999 to 2005–2006—Chilvers et al. 2007), and the reduction in numbers of females present at breeding areas has been linked to this drop (Chilvers et al. 2007; Wilkinson et al. 2006). Since 2005–2006 an additional 25% reduction in pup production and breeding females present at breeding beaches has occurred (Chilvers 2009). This indicates that survival rates for the years following this research could be lower for females, and research should be undertaken to investigate this.

Estimated survival rates for juvenile NZ sea lions, both male and female, were much lower than for adults, from

<35% for both male and female pups in certain years, to between 50% and 70% for 1-year-old females and 70% and 80% for 2- and 3-year-old females. Estimated survival rates for 2- and 3-year-old males were higher than for females, with survival between 60% and 70% for 2 year olds and 80% and 90% for 3 year olds. Lower juvenile survival relative to adult survival is reported commonly for sea lion species and other large mammals (Caughley 1966; Gaillard et al. 1997; Hernandez-Camacho et al. 2008; Pendleton et al. 2006). In a study of branded Steller sea lions from Forrester Island, Alaska, from 1994 to 2003, Pendleton et al. (2006) estimated survival rates for juveniles (pup to 1 year old) to be 53.6% (±7.1% SE) for males and 67.3% (±6.2% SE) for females. Similarly, their estimated survival rates for older juvenile females (2 and 3 year olds) were 79.1% (±7.5% SE) and 87.1 (±3.3% SE), respectively. Survival rates for juvenile males were 68% (±9.8% SE) for 2 year olds and 79.1% (±4.8% SE) for 3 year olds. For branded California sea lions in Mexico, Hernandez-Camacho et al. (2008) estimated survival rates for juvenile males and females (1–4 years old) to be 90% (±2.5% SE) and 90.4% (±2.3% SE), respectively.

The lower survival rates for ≥3-year-old female NZ sea lions compared with their male counterparts is unusual for sexually dimorphic polygamous mammals. It is particularly unusual for juveniles because juvenile dispersal, seen mainly in males (Chilvers and Wilkinson 2008), should contribute to lower male survival rates. This is because permanent emigration and mortality are indistinguishable in mark-recapture techniques such as those used in this and other studies. Juvenile male NZ sea lions also are known to disperse beyond the Auckland Islands area and are less affected by bycatch and potential resource reduction than juvenile females, which are known to be based in the Auckland Islands area and return to breeding areas earlier than males (Chilvers 2008; Chilvers and Wilkinson 2008). The bacterial epizootics recorded in 1998 and 2002 have been shown to affect both male and female juveniles similarly (Castinel et al. 2007) and are less likely to be an influence in the differences in survival between the 2 sexes.

In a management context, for a threatened species that has a low population number and a restricted breeding area in which pup production is in decline (Chilvers 2008; Chilvers et al. 2007), estimates of age- and sex-specific survival rates are important for understanding population dynamics and making management decisions that halt population declines. Survival of NZ sea lion juveniles, when compared with the accumulative survival curves of Steller sea lions in increasing and declining colonies from Forrester and Marmot islands, respectively (Pendleton et al. 2006), place NZ sea lion males at age 4 at a similar survival level to the increasing colony for Forrester Island (NZ sea lion 0.21; Steller sea lion 0.23). In contrast, 4-year-old females are well below the Forrester Island estimate (Steller sea lion 0.40; NZ sea lion 0.29) and more similar to Steller sea lions from the declining Marmot Island colony (0.21—Pendleton et al. 2006).

The current decline in pup production may not be linked to any single natural or anthropogenic factor. However, under-standing the high variability in juvenile survival, and that survival for females is lower than for males in all nonpup age classes, indicates that the Auckland Islands area, where juveniles and females are restricted to live, is leading to a decline in their survival. The variability of adult female survival rate is a critical problem for NZ sea lions, because even small changes in adult female survival significantly affect population trends for large, long-lived mammals such as NZ sea lions (Caughley 1966; Mills 2006). The significant decline in pup production, directly linked to decreasing numbers of adult females, makes the NZ sea lion vulnerable to extinction, particularly when considering the additional anthropogenic deaths caused by trawl fishing in the area when those deaths primarily affect breeding females that have dependent pups ashore and that potentially are pregnant with next season's pups as well.

ACKNOWLEDGMENTS

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