ESTIMATING SURVIVAL AND CAPTURE PROBABILITY OF FUR SEAL PUPS USING MULTISTATE MARK–RECAPTURE MODELS

Corey J. A. Bradshaw,* Richard J. Barker, Robert G. Harcourt, and Lloyd S. Davis

*Department of Zoology, University of Otago, P.O. Box 56,
Dunedin, New Zealand (CJAB, LSD)
Department of Mathematics and Statistics, University of Otago, P.O. Box 56,
Dunedin, New Zealand (RJB)
Marine Mammal Research Group, Graduate School of the Environment, Macquarie University,
Sydney, New South Wales 2109, Australia (RGH)
Present address of CJAB: Antarctic Wildlife Research Unit, School of Zoology, University of
Tasmania, GPO Box 252-05, Hobart, Tasmania 7001, Australia*

We use a multistate mark–recapture model incorporating information on body mass, sex, time of capture, and natal colony to estimate the probabilities of survival, capture, and mass-state transition of New Zealand fur seal (*Arctocephalus forsteri*) pups from 3 sites (colonies) on Otago Peninsula, South Island, New Zealand. Apparent survival for a mean sampling interval of 47 days was high (≥ 0.850) after correcting for tag loss, and there was evidence that there were differences between sexes and among sites even after controlling for mass at capture. Survival did not differ among body-mass classes. Heavier pups had lower capture probabilities; however, differences in mass adequately explained any potential differences in capture probability due to sex. State-transition probabilities among mass classes also differed with time of capture, and between sexes and among sites. Although bias in estimates of survival probability is minimal when survival is high, heterogeneity in capture probabilities among different classes of individuals can bias estimates of pup growth rate and sex ratio. We recommend measuring mass of individuals and incorporating this and perhaps other pertinent information into multistate mark–recapture models when attempting to estimate survival and to determine the effect of capture probability on estimates of other life-history parameters.

Key words: *Arctocephalus forsteri*, mark–recapture, multistate model, New Zealand fur seal, pinniped, survival, transition

Estimating survival probability in young mammals has important implications for the understanding of population dynamics, especially with regard to density-dependent processes (Sinclair 1996). However, obtaining precise estimates of survival probability is often difficult because many time- and density-dependent factors, such as body mass and condition, can affect 1st-year survival. These individual covariates may also affect survival more extensively under con-

ditions of fluctuating food availability, which has important implications for life-history strategies (Hall et al. 2001). Under exceptional circumstances, mammal populations can be monitored for the presence or absence of nearly all individuals in a population (Clutton-Brock 1988; Clutton-Brock et al. 1985), thus allowing for the calculation of precise estimates of juvenile survival. For most mammals, however, this is impractical, if not impossible, and demands more intensive mark–recapture modeling. Recent developments in mark–recap-

* Correspondent: corey.bradshaw@utas.edu.au

ture modeling have allowed for the incorporation of individual covariates at the time of initial capture into the estimation of survival (Hall et al. 2001; White and Burnham 1999) and so provide a powerful tool for modeling populations of mammals.

In addition, it is important to determine if there is heterogeneity in capture rates among individuals or groups of individuals (Gehrt and Fritzell 1996) because this heterogeneity can also bias estimates of population parameters (Clobert 1995; Johnson et al. 1986; Nichols 1992; Pollock et al. 1990; Trites 1991, 1993). Capture or recovery probabilities can vary among areas and times (Cameron et al. 1999; Gehrt and Fritzell 1996; Lindenmayer et al. 1998; Pace and Afton 1999; Pradel et al. 1997); among size, condition, or age classes (Anderson 1995; Pace and Afton 1999; Pradel et al. 1997; Trites 1991, 1993); and between the sexes (Buskirk and Lindstedt 1989; Flatt et al. 1997; Gehrt and Fritzell 1996; Lindenmayer et al. 1998; Pradel et al. 1997; Prévot-Julliard et al. 1998). If the assumption of homogenous capture probabilities is violated, then estimates of survival, growth, and sex ratios may be biased.

Pinnipeds are suitable for the assessment of individual covariates on survival and capture probabilities because body mass or condition can be assessed with relative ease and large sample sizes can be obtained. This has been shown in phocid seals such as gray seals (*Halichoerus grypus*—Hall et al. 2001) and southern elephant seals (*Mirounga leonina*—McMahon et al. 2000). In these studies, survival probability increased with increasing body mass (McMahon et al. 2000) or body condition (Hall et al. 2001) at weaning. However, little quantitative assessment of these parameters has been obtained for otariid seals (fur seals and sea lions). This lack of rigorous testing may lead to bias in population models for otariid seals and may confound the many different applications of these models. Otariid seals have been the subject of extensive modeling to estimate population size, biomass,

and trends (Butterworth et al. 1987, 1995; Lander 1981; Shaughnessy and Best 1982; Smith and Polacheck 1981; Wickens et al. 1992). Models have also been used to examine the effects of commercial harvests on populations (DeMaster 1981; Eberhardt 1981; Frisman et al. 1982; Lett et al. 1981; Smith and Polacheck 1981; Trites and Larkin 1989) and to examine the effects of fur seals foraging on commercial fish stocks (Butterworth et al. 1995; Wickens et al. 1992). In addition, outputs of models used to predict population growth rates of fur seals and food consumption rates are sensitive to changes in age-related survival (Butterworth et al. 1995; Wickens and York 1997). Wickens and York (1997) demonstrated that survival to age at 1st reproduction in fur seals was 50–80% of adult survival. Because juvenile survival in this taxon is 1 of the most important parameters affecting population growth models, it is imperative to obtain precise and unbiased estimates of survival and other associated parameters.

New Zealand fur seals (*Arctocephalus forsteri*) occur around New Zealand, southern Australia, and the Australasian temperate and subantarctic islands (Bradshaw et al. 2000b; Crawley 1990; Shaughnessy et al. 1994). In the New Zealand region, breeding colonies were once widespread around the coasts of all New Zealand islands, but subsistence and commercial hunting by humans reduced the population to remnant pockets on remote islands by 1830 (Lalas and Bradshaw 2001; Mattlin 1987). However, in recent years the numbers of *A. forsteri* in New Zealand have increased, and much of their previous range has been recolonized (Bradshaw et al. 2000c; Lalas and Murphy 1998; Taylor et al. 1995).

New Zealand fur seals come ashore on rocky coastlines to breed colonially from mid-November through early January, with mean pupping in mid- to late December (Lalas and Harcourt 1995; Mattlin 1987). Mothers give birth to a single pup and re-

main with it for a mean of 9 days before going to sea to feed for the 1st time since parturition (Crawley 1990; Mattlin 1987). Mothers alternate between foraging trips at sea and time ashore to suckle pups until weaning occurs approximately 10 months later (Mattlin 1987). Early foraging trips last 2–7 days, though subsequent trips are progressively longer as pups grow older (Harcourt et al. 2002). Thus, pups have progressively longer bouts of fasting while mothers are foraging, and solitary pups often band together during these times. During the fasting period pups may be exposed to adverse weather. There are no large land predators in New Zealand; however, occasional predation by New Zealand sea lions (*Phocarctos hookeri*) has been recorded (Bradshaw et al. 1998).

Despite nearly 30 years of research on the population dynamics and behavior of *A. forsteri* in New Zealand, the recent substantial increase in population size and the potential importance of this species as a competitor with commercial fisheries (Harcourt et al. 2002; Lalas and Bradshaw 2001), there are still no regionally replicated, precise estimates of pup survival for *A. forsteri*. Without reliable estimates of pup survival, models attempting to assess the longer-term trends and potential impacts of this species on the local ecosystem can be inadequate.

We use a multistate, mark–recapture model (Nichols et al. 1992; Schwarz et al. 1993) to estimate survival of *A. forsteri* pups from immediately after the breeding season up to approximately 155 days of age. This type of model controls for individual characteristics such as estimated body mass, which may influence the probability of recapture as shown in northern fur seals, *Callorhinus ursinus* (Trites 1993). The model structure also allows a covariate such as body mass to be transformed into a discrete input for each capture session, thus maximizing the data available. We also provide a correction to survival estimates for tags lost during the period of the study and
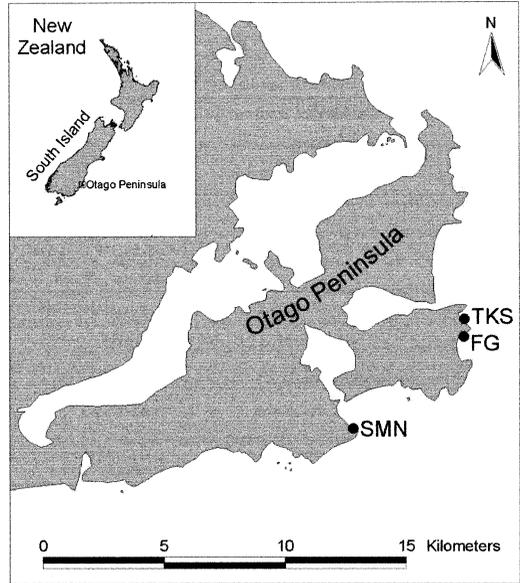

Fig. 1.—Study areas of New Zealand fur seal pups at Otago Peninsula, South Island, New Zealand, showing the 3 colonies sampled: Fuchsia Gully (FG), Sandymount North (SMN), and Titikoraki South (TKS).

investigate the effect of differential capture probabilities on estimates of survival. We test whether multistate mark–recapture models provide insights into survival and growth rate models that may be missed when data on mass change in growing individuals are not incorporated.

MATERIALS AND METHODS

Study sites, capture, and tagging.—We studied New Zealand fur seals on Otago Peninsula, South Island, New Zealand in 1997 and 1998. In 1997 we captured pups from Fuchsia Gully (Ohinepuha; 45°50′S, 170°45′E; Fig. 1). In 1998 we sampled Fuchsia Gully, Sandymount North (45°53′S, 170°41′E), and Titikoraki South (45°51′S, 170°44′E; Fig. 1). Fuchsia Gully is a 2,596-m² site characterized by rocks 0.6–5.0 m in diameter on a mostly flat surface. Some scrub vegetation populates the base of a 20-m cliff overlooking the colony. Sandymount North is a 1,493-m² site made up of rocks 1.3–5.0 m in diameter and is relatively flat. There are 2 main sections of the site separated by an area of small pebbles that appears to be used only by non-

breeding fur seals. Titikoraki South is a smaller, 907-m^2 site just to the north of Fuchsia Gully, backed by a 70-m cliff. The site is characterized by a narrow, rocky region above high tide (approximately 7 m) with rocks 1.3–2.5 m in diameter. The colony is split into several sections by large rock embankments that pups do not appear to traverse easily until closer to the weaning period (Bradshaw 1999; Bradshaw et al. 1999).

The 3 sites were chosen for their proximity to each other to control for potentially confounding effects due to characteristics of the terrestrial and marine habitats, and population demographics (Bradshaw et al. 1999, 2000b). Using principal components derived from terrestrial characteristics of each site (Bradshaw et al. 1999), we determined that the 3 target colonies, Fuchsia Gully, Sandymount North, and Titikoraki South, were similar in their breeding terrain relative to 23 other breeding colonies around South Island, New Zealand. However, Sandymount North had slightly smaller rocks and lower rock density than did Fuchsia Gully and Titikoraki South (Bradshaw et al. 1999). All sites were within 10-km swimming distance from each other. We assume that lactating females from each colony had approximately the same foraging habitat conditions (Bradshaw et al. 2000b, 2002) because it is known that they can travel >100 km from the colony when foraging (Harcourt et al. 2002). All 3 sites demonstrated similar pup densities (pups/100 m^2) and condition (observed mass/predicted mass—Bradshaw et al. 2000b) at the end of the breeding season (early January) in both 1997 and 1998 (Fig. 2). Although colonies had similar pup densities in both years, mean pup condition was significantly lower in 1998 for all colonies (Fig. 2; Bradshaw et al. 2000b). Breeding colonies have occupied all sites since at least the early 1990s and have been increasing annually since their inception (Bradshaw et al. 2000c; C. Lalas, pers. comm.).

We captured pups on 4 occasions between January and June during both years (Appendix I). We placed individually numbered plastic tags (Allflex® ''Mini'' tags, 52 by 17 mm, Palmerston North, New Zealand) in the connective tissue on the trailing edge of both foreflippers on all pups captured. All pups received the same type of tag, and the tagging procedure did not vary among colonies (Bradshaw et al. 2000a). Pups were also weighed to the nearest 0.1 kg (Bradshaw et al. 2000b) using a 20-kg balance
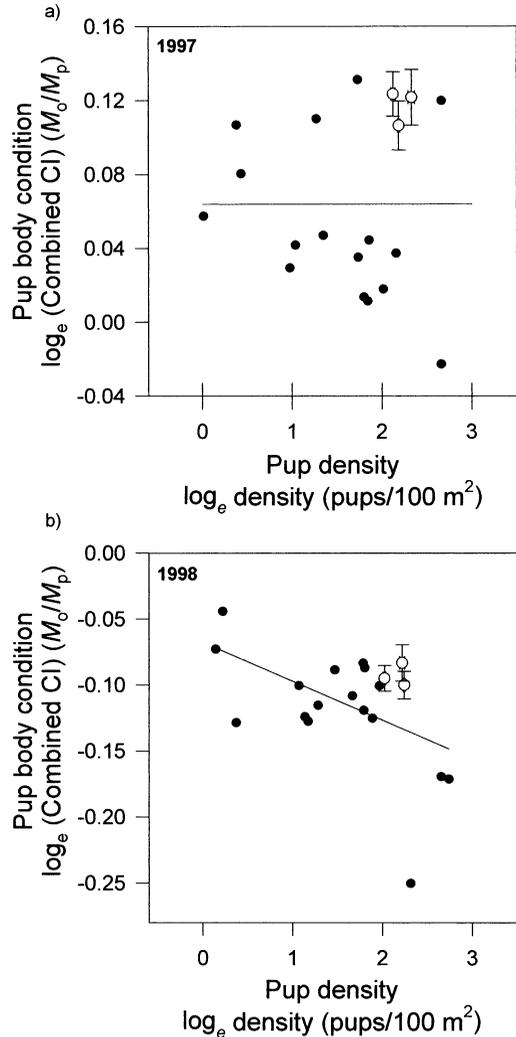

FIG. 2.—Relationship between body condition (log$_e$[combined condition index]) of pups of New Zealand fur seals and pup density (log$_e$[pups/100 m^2]) for colonies of New Zealand fur seals in summer at Otago Peninsula, New Zealand, in a) 1997 and b) 1998 (data from Bradshaw et al. 2000b). Straight line in a) represents mean condition among colonies, and line in b) represents negative relationship between condition and density in that year ($r^2 = 0.25$—Bradshaw et al. 2000b). The 3 target colonies (Fuchsia Gully [FG], Sandymount North [SMN], and Titikoraki South [TKS]) are shown in both graphs (mean ± *SE*) as open circles, demonstrating that pup density was similar among colonies and between years. Note difference in y-axis scale in a) and b). Mean pup condition was significantly lower in 1998 (Bradshaw et al. 2000b); however, the condition was similar among the 3 target colonies within a particular year.

(Pesola®, Baar, Switzerland). During each session we started at 1 end of the colony and captured as many pups as possible while moving to the other end of the colony. We attempted to keep human disturbance to a minimum during the capture and tagging procedures. We applied tags once to all captured pups, and for each recapture session thereafter, we noted the status of previously tagged animals (i.e., tags present or missing). Lost tags left a small notch in the connective tissue of the flipper; in this way we were able to distinguish pups that had never been captured from those that had lost both tags (Bradshaw et al. 2000a). To standardize capture effort and procedures, one of us (CJAB) was present during all capture sessions and weighed all pups.

Previous tagging of *A. forsteri* pups using metal tags demonstrated 77% incomplete healing; however, no difference in mortality was observed between tagged and untagged pups (Mattlin 1978), nor was handling by humans a significant factor affecting pup growth in that study (Mattlin 1978). Researchers have attempted to assess these effects for other species of pinnipeds. Some have suggested an increase in pup mortality due to the application of metal tags (Chapman and Johnson 1968), whereas others have suggested that differences (mass, growth rate) between tagged and untagged pups can be explained by differences in capture probability (Trites 1991).

Each population of pups was assumed to be geographically "closed" (i.e., no emigration or immigration of pups to or from neighboring colonies). Ninety-two percent of 75 mark–recapture estimates around South Island indicated geographic closure, and for those that were considered to be "open," the magnitude of the bias was only 1.9% on average (Bradshaw et al. 2000b). The realistic assumption of population closure to births, deaths, and immigration permits a more accurate estimation of the probability of survival because mark–recapture models can only provide estimates of apparent survival (the number of individuals available for recapture). Although emigration is unlikely for suckling pups, animals that emigrate from the population appear, in the model, to have died, hence underestimating the true probability of survival (Cormack 1972; White and Burnham 1999). All animal treatment procedures were approved by the University of Otago Committee on Ethics in the Care and Use of Laboratory Animals (No.

83-95) and a New Zealand Department of Conservation Permit to Take Marine Mammals.

Data analysis, estimation, and model selection procedures.—We used 4 generalized linear models for each capture session to test for the effects of sex, site, and the interaction between sex and site (sex × site) on mass at capture. We log_e-transformed the mass data to homogenize variances among groups. All differences were considered significant at a rejection probability $(P) <0.05$.

To assess the effects of sex, site, time, and mass class at each capture session on apparent pup survival (ϕ), capture probability (p), and probability of transition of pups from 1 mass class (state) to another between capture sessions (ψ), we fitted a series of mark–recapture models with different restrictions on model parameters. Due to the large number of potential models (a total of 6,877 possible models if all combinations of sex, time of capture, mass at capture, and colony of capture on ϕ, p, and ψ were tested), we examined only those models that tested explicit hypotheses regarding the biology of *A. forsteri* pups and the sampling technique used.

Given that terrain features and pup density were similar among sites, we hypothesized that survival could depend on sex (DeVilliers and Roux 1992; Oosthuizen 1991) as well as on mass (Hall et al. 2001) and sampling time. We hypothesized that capture probability would vary according to pup mass but that any differences due to sex would be explained adequately by mass. We also expected to find a significant effect due to site, even though the colonies did not differ markedly in the composition of the terrain (Bradshaw et al. 1999). Therefore, we treated all sites and the extra year (1997) at Fuchsia Gully as separate levels of the same factor. Capture probability was also investigated for time effects in addition to the variation described by pup mass. We expected nontrivial differences in the probability of mass-state transition over time because the pups were growing. Because all sites were <10 km from each other (Fig. 1), we assumed that differences in growth trends among sites would be insignificant. However, because food resources can vary markedly from year to year and have been hypothesized to affect pup condition and possibly growth rates (Bradshaw et al. 2000b), we expected that differences between years at Fuchsia Gully would be nontrivial.

We used program MARK (White and Burnham 1999) to construct reduced-parameter versions of a multistate mark–recapture model (Nichols et al. 1992; Schwarz et al. 1993). This model incorporated the effect of body mass on survival by categorizing mass into 3 classes for all capture sessions: light ($0 < \text{mass} \leq 6.8$ kg), medium ($6.8 < \text{mass} \leq 9.0$ kg), and heavy ($\text{mass} > 9.0$ kg). The mass classes were chosen so that an approximately equal proportion of pups occurred in each mass class at 1st capture.

Changes in mass class between sampling occasions were modeled using a Markov chain in which the probability of moving from one mass class to another (ψ) depends on the mass class occupied at the previous sampling occasion. The use of mass classes in a multistate mark–recapture model allows the effect of time-varying body mass on survival to be modeled despite mass not being observed at every sampling occasion due to pups evading capture.

Categorizing mass results in a loss of information, and the fewer the mass classes, the greater is this loss of information. However, because each transition matrix in the model requires $s(s - 1)$ parameters, where s is the number of mass classes, the number of transition probabilities grows rapidly with an increasing number of mass classes. Three classes were chosen to compromise between having too few classes (to capture the effect of mass meaningfully) and too many (which would result in many poorly estimated parameters and a reduced ability to detect effects of body mass).

We allowed parameters to differ for the 2 years at Fuchsia Gully, the only site sampled for 2 years. We did this by treating Fuchsia Gully in 1997 as a separate colony because the condition of pups throughout South Island was much higher in 1997 than in 1998 (Fig. 2; Bradshaw et al. 2000b). We denoted the combined effect of year and colony as yr/site. In addition, we allowed parameters to depend on capture time (t), mass (m), and sex (sex). To indicate the year effect on transition probabilities, which applied only to Fuchsia Gully, we used the notation yr(FG). The symbol $\times$ between a pair of variables indicates that the effect of one parameter is different at all levels of the other. For example, sex $\times$ t indicates that the parameter concerned varies from sample to sample, is different for male and female pups, and also varies from sampling time to sampling time.

Thus, the parameters denoting apparent survival (ϕ) or capture (p) were described as the probability of a pup surviving or being caught, respectively, from time i to $i + 1$ for pups at site j ($j = 1, \ldots, 4$ sites) and of sex k (male or female) in body-mass state a (light, medium, or heavy). The probability of mass-state transition (ψ) was described as the probability that a pup at site j and of sex k alive at time i in body-mass state a and alive at time $i + 1$ is in body-mass state b at time $i + 1$. We incorporated the term $\psi(\text{yr(FG)} \times m \times \text{sex} \times t)$ in all the models tested because intersite differences in the growth rate of pups were assumed to be trivial.

Model selection was based on a small-sample version of quasi-likelihood adjusted Akaike's information criterion for overdispersion, c (QAICc—Burnham and Anderson 1998). We used a 2-stage model-selection procedure in which we first fitted a sequence of 16 models that incorporated all possible combinations of the effects of yr/site, m, sex, and t on survival probabilities. These models all included an effect of yr/site, m, and t on capture probabilities and of yr(FG), m, sex, and t on transition probabilities. We denoted the most general model in this sequence as $\phi(\text{yr/site} \times \text{sex} \times m \times t)p(\text{yr/site} \times m \times t)\psi(\text{yr(FG)} \times m \times \text{sex} \times t)$.

At the 2nd stage of model selection, we constructed another sequence of 8 models that began with the best-fitting model from the 1st stage of selection and that considered restrictions on the effects of yr/site, m, and t on capture probabilities.

To compare models we adopted the selection strategy recommended by Burnham and Anderson (1998) for selecting the best-approximating model from a set of candidate models. Here, models within 2 QAICc units (i.e., $\Delta\text{QAICc} \leq 2$) of the model minimizing QAICc are considered to have substantial support and should be used for making inferences. Models with ΔQAICc of 4–7 have considerably less support, and models with $\Delta\text{QAICc} > 10$ have nearly no support. QAICc weights and deviance scores (-2 log-likelihood[current model] $- 2$ log-likelihood[saturated model]) are reported for each model fitted (McCullagh and Nelder 1989). QAICc weights are normalized to sum to 1 to provide the relative weight of evidence in favor of a particular model being the best from a larger set of models (Burnham and Anderson 1998).

An overdispersion factor was estimated to ac-

TABLE 1.—Probabilities of survival for New Zealand fur seal pups at Otago Peninsula, New Zealand, as indicated by ϕ, apparent 47-day probability of survival up to about 5 months of age (Appendix I) under the multistate model, and $\hat{S}$, estimates of survival probability corrected for tag loss (using estimates of τ, probability of retaining at least 1 tag—Bradshaw et al. 2000a). The multistate model is $\phi((yr/site) \times sex)$, $p(m)$, $\psi(yr(FG) \times m \times sex \times t)$.

Site	Apparent survival (uncorrected)		Probability of retaining at least 1 tag		Apparent survival (corrected for tag loss)	
	$\hat{\phi}$	SE	$\hat{\tau}$	SE	$\hat{S}$	SE
Fuchsia Gully						
1997						
Female	0.918	0.039	0.988	0.012	0.929	0.041
Male	0.999	0.017	0.988[a]	0.012	1.000	0.021
1998						
Female	0.904	0.035	0.917	0.030	0.986	0.050
Male	0.917	0.035	0.917	0.030	1.000	0.050
Sandymount North						
1998						
Female	0.910	0.041	0.897	0.049	1.000	0.072
Male	0.831	0.049	0.897	0.049	0.926	0.074
Titikoraki South						
1998						
Female	0.788	0.051	0.923	0.037	0.853	0.065
Male	0.869	0.048	0.923	0.037	0.941	0.064

[a] No sex-specific $\hat{\tau}$ calculated (Bradshaw et al. 2000a).

count for the unexplained variation in the data. This factor was estimated by comparing the most general model considered in model selection with a model in which survival and capture probabilities were fully sex-, time-, site-, and mass-specific, and transition probabilities were site-, time-, and sex-specific ($\phi((yr/site) \times sex \times m \times t)$, $p((yr/site) \times sex \times m \times t)$, $\psi((yr/site) \times m \times sex \times t)$). The ratio of the chi-square goodness-of-fit statistic to its degrees of freedom was used to estimate the overdispersion factor c (c = 1.0 indicates no overdispersion). For our most general model, the estimated factor indicated some overdispersion ($\hat{c} = 1.50$; $\chi^2 = 86.99$, $d.f. = 58$, $P = 0.008$). Thus, we calculated the estimates of sampling variance by multiplying the theoretical (model-based) variances by $\hat{c}$ (Finney 1971).

Estimates of survival probability are confounded with the probability that a pup loses both tags (Bradshaw et al. 2000a). Arnason and Mills (1981) demonstrated that the estimated true survival rate ($\hat{S}$) after correcting for tag loss is

$$\hat{S} = \frac{\hat{\phi}}{\hat{\tau}}$$

where $\hat{\tau}$ is the estimated probability of retaining at least 1 tag (i.e., $1 -$ the probability of losing both tags—Bradshaw et al. 2000a). The variance of $\hat{S}$ is estimated as

$$\text{Var}(\hat{S}) = \hat{S}^2 \left\{ \left(\frac{\text{Var}(\hat{\phi})}{\hat{\phi}^2} \right) + \left(\frac{\text{Var}(\hat{\tau})}{\hat{\tau}^2} \right) \right\}$$

(Seber 1982). Although tag loss varied among sites, the Allflex ''Mini'' tags used provided $\hat{\tau} \geq 0.90$ during the course of the study (Bradshaw et al. 2000a). Nonetheless, we used separate, colony-specific values of τ to correct the survival probabilities estimated for each site.

RESULTS

We tagged 719 individual pups and obtained 1,650 masses of pups (including reweighings; Appendix I). Males were heavier than females at all capture times, but there was considerable variation in mean mass between years at Fuchsia Gully (Fig. 3). There was a significant effect of sex on capture mass in each capture session (males were heavier than females; all rejection
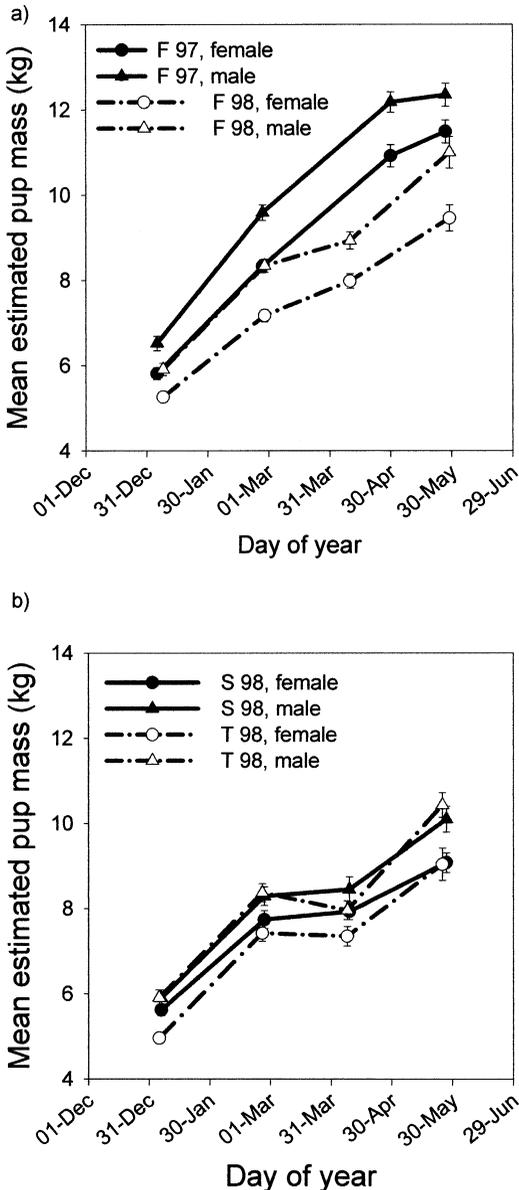
F<small>IG</small>. 3.—Mass of male and female New Zealand fur seal pups at Otago Peninsula, New Zealand, for a) Fuchsia Gully (F) in 1997 and 1998 and b) Sandymount North (S) and Titikoraki South (T) in 1998. Symbols indicate means and error bars, 1 *SE.*

0.109). In none of the 4 capture sessions were the sex $\times$ site interactions significant (all rejection probabilities $\geq$ 0.146).

In the 1st stage of model selection, the best-approximating model of the 16 models considered was $\phi((\text{yr/site}) \times \text{sex})p((\text{yr/site}) \times m \times t)\psi(\text{year(FG)} \times m \times \text{sex} \times t)$; QAICc = 2,645.17, K = 95, deviance = 434.20. Under this model there are survival probabilities estimated for male and female pups at each yr/site combination (Table 1). This model had a QAICc weight >0.999, so no subsequent models were considered in the 1st stage of selection.

The top model of the 8 models considered in the 2nd stage of model selection was $\phi((\text{yr/site}) \times \text{sex})p(m)\psi(\text{yr(FG)} \times m \times \text{sex} \times t)$; QAICc = 2,645.17, K = 72, deviance = 447.79. This model had a QAICc weight of 0.974; therefore, no subsequent models were considered. The model includes a yr/site and sex effect on the probability of survival. Correcting for tag loss, the true estimated survival ($\hat{S}$) probabilities for the 47 days (average) between sampling intervals from postpupping to approximately 155 days (about 5 months) for each yr/site combination were $\geq$0.850 (Table 1).

There was strong evidence of a mass effect on the probability of capture. Here, the heaviest mass class had the lowest capture probability ($\hat{p}$ = 0.540 $\pm$ 0.026 *SE*), followed by the medium class ($\hat{p}$ = 0.664 $\pm$ 0.042) and the light class ($\hat{p}$ = 0.873 $\pm$ 0.081). The lack of a significant sex effect on capture probability can be explained by the relative difference in mass between males and females. Because males weighed more at each capture time than did females (Fig. 3), any difference in capture probability between the sexes would have been due to differences in mass alone.

Transition probabilities ranged widely under the model term $\psi(\text{yr(FG)} \times m \times \text{sex} \times t)$. Transitions from lower to higher states represent a gain in mass between captures i and $i + 1$. Transitions from higher to lower states represent loss of mass. Mean transition probabilities revealed a higher prob-

probabilities $\leq$ 0.021) and a significant effect of site in all capture sessions (all rejection probabilities $\leq$ 0.021) except the initial capture (F = 5.029, *d.f.* = 3, 493, *P* =

ability of mass gain for males than for fe-
males (Fig. 4a). However, males demon-
strated a higher capacity to lose mass once
they attained the heavier mass classes (Fig.
4b).

DISCUSSION

Pup survival from shortly after birth to
age of approximately 155 days was high
during the period of our study (0.88 ± 0.05;
Table 2). Expressed as a standardized, 50-
day survival probability, our estimates
(mean $\hat{S}_{50} = 0.952 \pm 0.02$) fall within the
upper range of pup survival estimated for
other otariid seals (Wickens and York 1997;
Table 2). There is some suggestion that the
probability of surviving from immediately
after the breeding season to weaning in
otariids is higher than that from weaning to
the end of the 1st year (DeVilliers and Roux
1992; Mattlin 1978). However, there are no
convincing empirical estimates of post-
weaning survival of juveniles for New Zea-
land fur seals. If survival during this period
is lower for *A. forsteri* in New Zealand,
then our survival estimates would overes-
timate the survival of 1st-year pups. Anoth-
er reason for overestimating apparent sur-
vival is that we did not take into account
any mortality that occurred before the ini-
tial capture session (Lalas and Harcourt
1995). Mortality during this period cannot
be dismissed as negligible or unimportant
because in some populations early pup mor-
tality (during the 1st month of life) can be
as high as 50% (DeVilliers and Roux 1992;
Harcourt 1992; Majluf 1992).

The significance of the yr/site term on
$\hat{\phi}$ is more likely to reflect the higher sur-
vival probabilities observed for pups from
Fuchsia Gully in 1997 relative to the colo-
nies sampled in 1998 (Table 1). Given that
pups at the Fuchsia Gully colony in 1997
were in much better physical condition than
were pups sampled from all 3 colonies in
1998 (Fig. 2), and all colonies had essen-
tially identical terrain and density charac-
teristics (Bradshaw et al. 1999), we suggest
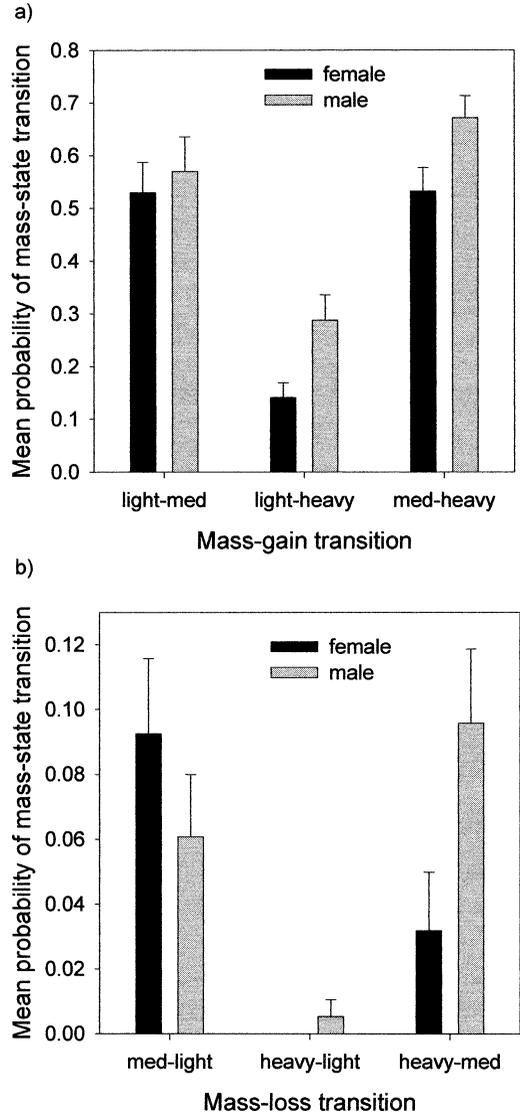that the year difference in apparent survival

FIG. 4.—Probability of moving from 1 mass
state (light, medium, large) to another during the
study period (mean state-transition probabilities,
ψ) among all sites, years, and capture times for
a) mass gain and b) mass loss ($+1$ *SE*).

was attributable to the body condition of
pups alone.

We found evidence that survival proba-
bilities between male and female pups dif-
fered even after controlling for body mass.
However, the difference was small (mean
47-day interval $\hat{S}_{female} = 0.942 \pm 0.033$,
$\hat{S}_{male} = 0.967 \pm 0.019$). In all sites and

TABLE 2.—Mean survival (proportion of pups born that survive or probability of survival) reported for pups of species of the genus *Arctocephalus* (see also Wickens and York 1997) during specific intervals. For comparison with this study and for ease of interpretation, all probabilities have also been standardized to a 50-day interval, $S_{50} = S_{int}^{(50/int)}$, where int = interval.

Species	Years	Interval (days)	Interval survival	50-day survival	n^a	Source
A. gazella	1978–1982[b]	~0–40	0.95	0.938	1,218	Doidge et al. (1984)—Schlieper Bay
	1979–1982[c]	~0–40	0.77	0.721	2,002	Doidge et al. (1984)—Bird Island
A. galapagoensis	1979–1981	0–30	0.91	0.855	202	Trillmich (1987)
A. tropicalis	1982	0–84	0.85	0.908	10,898	Hes and Roux (1983)—Amsterdam Island
	1987–1988	0–77	0.96	0.974	248	Shaughnessy and Goldsworthy (1990)—Heard Island
	1996	0–30	0.97	0.951	443	Georges and Guinet (2000)—Amsterdam Island
	1997	0–15	0.91	0.730	331	Georges and Guinet (2000)—Amsterdam Island
A. australis	1984–1989	0–41	0.64	0.580	8,309	Majluf (1992)
	1987–1988	0–55	0.60	0.629	3,959	Harcourt (1992)
A. pusillus pusillus	1987–1990	0–30	0.80 ± 0.03[d]	0.689	560	DeVilliers and Roux (1992)—Atlas Bay
	1988–1990	0–30	0.65 ± 0.01[d]	0.488	735	DeVilliers and Roux (1992)—Wolf Bay
A. forsteri	1988–1993	~0–39	0.99	0.987	5,792[e]	Shaughnessy et al. (1995)—Kangaroo Island
	1990–1993	~0–39	0.98	0.974	2,869[e]	Shaughnessy et al. (1995)—North Casuarina
	1993–1994	~0–55	0.92	0.927	142[f]	Lalas and Harcourt (1995)
	1997–1998	~12–155	0.88 ± 0.05[g]	0.952 ± 0.02	719[h], 1,650[i]	This study

[a] Total number of pups counted or estimated over all years of study.
[b] Excluding 1979.
[c] Excluding 1980.
[d] Mean among years.
[e] Estimated from mark–recapture techniques.
[f] Maximum daily count.
[g] Mean among sites and years calculated as mean sampling interval ($\bar{X}$ = 47 days) $\hat{S}$ to the power of 3 (3 sampling intervals) ± year-site *SE*.
[h] Number of individual pups tagged.
[i] Number of pups caught (includes recaptures).

years except Sandymount North, where all females survived, the probability of surviving was lower for female pups (Table 1). Although some studies have found significant differences in survival between the sexes in otariid seals (DeVilliers and Roux 1992; Oosthuizen 1991), others have not (Boltnev et al. 1998; Georges and Guinet 2000). When differences in survival between the sexes have been found in polygynous mammal species, juvenile males are usually reported as the sex with the lowest probability of survival (Hall et al. 2001; Ralls et al. 1980). It has been suggested that this is due to the faster-growing sex (usually males) suffering additional mortality due to nutritional stress (Clutton-Brock 1991; Clutton-Brock et al. 1994; Stewart 1997). Clearly, this was not the case in this study. However, there is evidence to suggest that male-dominated sex ratios are present in populations of mammals that are not regulated by population density (Kruuk et al. 1999). Assuming that higher densities reflect lower per capita food availability, male offspring are expected to show a relatively lower probability of survival (Kruuk et al. 1999). Bradshaw et al. (2000b) found a negative effect of density on the condition of fur seal pups at colonies around New Zealand but only during years when food resources were purported to be reduced. The higher average survival probability of males in 1998 (a year when pup condition was below a 3-year average—Bradshaw et al. 2000b) suggests that population density at these colonies had not yet reached the level required to elicit regulation (Kruuk et al. 1999). This is consistent with the observation that colonies on the eastern coast of South Island are still increasing in number and are probably below carrying capacity (Bradshaw et al. 2000c).

We did not find any effect of mass at time of capture on subsequent survival probability. Boltnev et al. (1998) demonstrated that pup survival of *C. ursinus* correlates positively with mass at birth, Calambokidis and Gentry (1985) reported that dead *C. ursinus* pups were lighter at birth than were the total marked population, and Majluf (1992) found that pups of the South American fur seal (*A. australis*) that died were lighter at birth than were those that survived. Continual monitoring of pup survival at our study sites will be necessary to determine if this relationship appears during years when survival is lower.

There are potentially many reasons why pups of a certain size class would have lower or higher capture probabilities. We found that large pups are less likely to be recaptured, possibly due to the increased mobility of healthy pups (a pup in good condition would be more likely to avoid capture than would a smaller, weaker pup). Heterogeneity in the spatial distribution of pups of different size classes may also occur, although we endeavoured to search as much of each colony as possible. As pups age, specific size classes may become more or less likely to be captured relative to the rest of the population. This warrants further investigation.

It has been shown previously that heterogeneity in capture probabilities can lead to bias in estimates of survival (Clobert 1995; Nichols 1992) and growth (Trites 1991, 1993). This potential influence of heterogeneity, together with the results reported here, highlights the importance of measuring individual mass at time of each capture. If the assumption of homogenous capture probabilities is violated (Carothers 1973; Lebreton et al. 1992), then bias can become problematic (Buckland 1982; Prévot-Julliard et al. 1998), especially if recapture rates are low. This usually results in underestimating survival probabilities (Prévot-Julliard et al. 1998).

When capture probability depends on mass at capture, estimates of sex ratio also will be biased. For large-bodied mammals, we suggest that researchers endeavour to weigh individuals at each capture session in addition to marking to account for this potential bias. For instance, in the present study the estimated true (adjusted) number

of individuals of a particular sex (n_{adj}) becomes the observed number of individuals of a particular sex (n_{obs}) in mass class a divided by the corresponding mass-specific capture probability (p_a) and the sex-specific survival probability (S_{sex}) during the sampling interval. As an example, the sex ratio of the last capture sample (27 May 1997) at Fuchsia Gully in 1997 was 51 females to 59 males (0.86; Table 1). Adjusting for differential capture probability among mass classes and sex-specific survival probability, the true sex ratio without differential mortality and capture rates becomes 116 females to 108 males (1.07).

The mean transition probabilities between mass states varied significantly with capture time and colony; however, caution must be observed in the interpretation of these results because specific hypotheses relating to the probabilities of transition between mass classes were not tested explicitly. Nonetheless, overall means indicated that male pups are more likely to gain mass than are females, and they also are more likely to lose mass once they have reached the heavier mass classes (Fig. 4). The higher transition probabilities for males versus females from lower to higher mass states (Fig. 4) suggest that males grew faster than females. Varying capture probabilities may help to explain the conflicting evidence for differential pup growth rates between the sexes for species of the genus *Arctocephalus* (Arnould et al. 1996; Georges and Guinet 2001). Sex differences in growth patterns in terms of tissue deposition (i.e., deposition of relatively more fatty or lean tissue—Arnould et al. 1996; Georges and Guinet 2001) should also be investigated to help interpret differences in survival and growth under conditions of varying food availability.

There was an apparently different growth pattern in Fuchsia Gully in 1997 relative to the colonies measured in 1998 (Fig. 3). However, it should be noted that the sampling time for the 3rd capture session was later in 1997 (late April) than in 1998 (early April; see Table 1). Although it is impossible to determine, the different growth pattern observed may have been an artifact of this different sampling regime.

The multistate model highlighted effects that would have otherwise been missed. The implications for the calculation of individual growth rate and sex ratios are obvious: if more individuals of a specific body mass class are caught relative to others, then the number of individuals within a particular grouping (sex or mass class) will be biased. Because heavier pups had lower capture probabilities, transitions to higher mass states would be underrepresented from random pup captures. This has been found for *C. ursinus* pups by Trites (1993). It is known that cross-sectional sampling can bias estimates of growth rate (Anderson and Fedak 1987; Baptista et al. 2000; Lunn et al. 1993), thus modifying conclusions about sex differences (Doidge and Croxall 1989; Lunn et al. 1993). However, even longitudinal sampling of individuals from free-ranging populations for estimation of growth rates can be biased when capture probabilities are heterogenous among mass classes. Different probabilities of recapturing individuals within different mass classes result in mean growth rates that are biased in the direction of the most commonly recaptured class. For example, the present study has demonstrated that random samples of fur seal pups would have underestimated growth rate because individuals that have demonstrated maximal growth are less likely to be recaptured in the final capture session. For other mammals, researchers should endeavour to measure mass and other parameters thought to contribute to capture probability for all recapture sessions.

Transition probabilities provide information on the growth process, and size-dependent capture probabilities can be used to correct estimates of growth rate. The estimated true number of individuals within each mass class can be adjusted by applying the corresponding probabilities of capture. This accounts for biases attributed to sam-

pling individuals from different mass classes and provides a more realistic parameter estimation for models estimating population size, sex ratio, colonization processes, and food consumption rates.

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APPENDIX I

Capture dates, number of New Zealand fur seal pups captured, and total number of pups newly tagged per colony and per capture session at Otago Peninsula (South Island, New Zealand) colonies.

Capture details	Fuchsia gully		Sandymount north	Titikoraki south
	1997	1998	1998	1998
1st capture				
Date	5 January	5 January	8 January	6 January
Number of females	76	81	52	53
Number of males	68	69	55	47
Total caught	144	150	107	100
Newly tagged	144	150	107	100
2nd capture				
Date	26 February	25 February	27 February	26 February
Number of females	70	66	38	51
Number of males	56	58	46	46
Total caught	126	124	84	97
Newly tagged	45	32	40	21
3rd capture				
Date	30 April	8 April	10 April	9 April
Number of females	52	68	41	42
Number of males	61	55	35	44
Total caught	113	123	76	86
Newly tagged	26	19	19	16
4th capture				
Date	27 May	25 May	29 May	27 May
Number of females	51	45	31	27
Number of males	59	51	28	28
Total caught	110	96	59	55
Newly tagged	0	0	0	0
Grand total caught	493	493	326	338
Grand total tagged	215	201	166	137