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Duration of Pelage Stages of Grey Seal, *Halichoerus grypus*, Pups

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ABSTRACT

Estimates of the duration of the pelage stages of grey seals *Halichoerus grypus* pups are carried out using maximum likelihood estimates of know age pups. The estimates are critical for present methods of estimating grey seal population dynamics.

RÉSUMÉ

On examine la durée des phases du pelage du phoque gris (*Halichoerus grypus*) par des estimations de vraisemblance maximale de petits d'âge connu. Ces estimations prennent une part essentielle dans les méthodes actuelles d'étude de la dynamique des populations de phoques gris.

Introduction

Grey seals *Halichoerus grypus* inhabit waters on both sides of the North Atlantic where they interact with commercial fisheries as potential competitors and as one of the definitive host of the sealworm parasite, *Pseudoterranova decipiens* (Malouf 1986, Bowen 1990). The larvae of this parasite infect a number of commercially important fish stocks, resulting in increased production costs and reduced product value (Malouf 1986). Thus the ability to precisely estimate population size is fundamental to an understanding of grey seal-fisheries interactions.

Like most other phocid seals, it is not practically possible to estimate directly the size of a grey seal population. Instead, pup production is estimated and a population model is used to generate an estimate of total population size. Although it is possible to enumerate pup production at some colonies (Stobo and Zwanenburg 1990), more commonly one or more surveys are conducted at a time when not all pups may have been born (Ward et al. 1987). Therefore any one survey is likely to underestimate pup production. However, like several other seal species, grey seal pups pass through readily identifiable stages involving changes in pelage and body fatness over the lactation period and the first several weeks post weaning (Kovacs and Lavigne 1986). Given information on the proportion of pups in each of these developmental stages at several times and the duration of each stage, it is possible to estimate the distribution of births over the pupping season. This information can then be used to correct an aerial survey estimate of abundance for those pups that have yet to be born at the time of the survey (Bowen et al. 1987, Myers and Bowen 1989). The purpose of this paper is to estimate the duration of these stages to improve estimates of grey seal pup production and hence population size .

Methods

The study was conducted during the grey seal pupping season in January and February 1987 on Sable Island, a vegetated sand bar about 150 km off Nova Scotia, Canada. Pups (n=79) were individually marked with rototags within 24 hr of birth. The birthdate of each pup could be determined because all pups examined in the the study area each day during the pupping season. A total of 398 observations were made on marked pups from 15 January to 7 February 1987 (Table 1).

Marked pups were classified into one of the five stages at 3 day intervals until approximately 25 days of age. Observations were generally made between 1030 and 1500 hr but, to facilitate the estimation of stage durations, we assumed that all marked pups were born at noon on the day of tagging and that all resightings also took place at noon.

Description of pup stages

We recognized five pup stages for the purpose of this study. Stage 1 included newborns still wet with birth fluids and those whose pelage was stained a yellowish colour from amnionic fluid. Stage 2 pups, known as thin whites, had a well defined concave neck, a cylindrical trunk, and white fur. In fat whites or stage 3 pups, both the neck and the trunk of the animal combined to give the pup a fusiform shape. Stage 4 pups had started to moult their natal coat on the neck and/or trunk revealing the underlying spotted juvenile pelage. By stage 5 pups had fully moulted their natal pelage, although pups with isolated tufts of hair with a diameter smaller than 5 cm on the back or neck were also classified as stage 5.

Estimating the Duration of Pup Stages

A maximum likelihood method was used to estimate stage duration (Myers and Bowen 1989). Stages are denoted by the subscript j, and if an animal survives it passes from stage j to $j+1$. We specify stage duration in terms of instantaneous transition intensity functions: $\phi_j(\tau) = \lim_{\Delta\tau\to 0}$ (probability an animal passes from stage j to $j+1$ in the interval $[\tau, \tau + \Delta\tau])/\Delta\tau)$, where τ is the time spent in stage j. This specifies the force of transition into stage $j+1$ from stage j, given that the animal has spent time τ in stage j (and has survived). Note that the transition intensities depend only on the current stage and the time so far spent in that stage. The rate at which pups enter stage j at time t is denoted by $m_j(t)$.

For a given number of pups marked at time 0 and the transition intensities ϕ_j's, we would like to calculate the $m_j(t)$'s for $j \geq 1$. Thus, $m_1(t)$ is 1 for time 0, and 0 for other times. If mortality can be ignored, the rate that a pup enters successive stages is given by the recurrence relationship:

$$m_j(t) = \int_0^\infty m_{j-1}(t-\tau)\phi_{j-1}(\tau)\ \mathrm{d}\tau. \tag{1}$$

Although pre-weaning mortality is often in the range of 10%, this mortality generally occurs near birth or is the result of starvation caused by abandonment (Stobo and Zwanenburg 1990). The sample of pups used in our study was not affected by either of these sources of mortality, i.e. no mortality occurred in the marked group of pups. If there is no mortality, the total number of pups in stage j that can be observed at time t, $n_j(t)$, is the integral of the rate pups entered stage j time τ ago times the probability that those pups have not entered stage $j+1$, i.e.

$$n_j(t) = \int_0^\infty m_j(t-\tau)\left(1 - \int_0^\tau \phi_j(s)\ \mathrm{d}s\right)\ \mathrm{d}\tau \tag{2}$$

Equations (1) and (2) adequately describe stages 1-5. The transition intensity, ϕ_j, of stages 1, 2, 3, and 4 was assumed to follow a gamma density. That is, $\phi_j(t) = \rho_j(\rho_j t)^{\kappa_j - 1}e^{-\rho_j t}/\Gamma(\kappa_j)$ where κ_j is the shape parameter, ρ_j is the scale parameter, and $\Gamma()$ is the gamma function. Let the predicted proportion of the known-age population in stage j, i days after birth be q_{ij}. For any particular parameter values of the gamma distribution, the proportion, q_{ij}, can be calculated by setting m_1 to 1 at time zero (and zero elsewhere) and iterating equation (1), calculating $n_j(t)$ from (2), and then calculating the resulting predicted proportion at each day. The log-likelihood of any combination of parameters is proportional to:

$$\sum_i \sum_j N_{ij} \ln(q_{ij}) \tag{3}$$

where N_{ij} is the observed number of known-age pups in stage j, i days after birth. Confidence intervals are determined by standard likelihood methods (Cox and Hinkley 1974:207-249).

The maximization of expression (3) requires an iterative maximization algorithm. At each iteration, the calculations of the integrals in equations (1) and (2) are performed numerically. The program that we have implemented uses the Broyden-Fletcher-Goldfarb-Shanno positive definite secant update algorithm (Dennis and Schnabel 1983). Details of the implementation and program listings can be obtained from RAM.

Results

An 8-parameter model, separate κ_j and ρ_j for each stage, was initially fit to the data. However, it did not fit the data significantly better (likelihood ratio test, Cox and Hinkley 1974:279-363), than a simpler 5-parameter model in which the the shape parameter, κ, was the same for these stages, but the scale parameter,

ρ_j, was different for each stage (Fig. 1).. The use of alternative density functions, e.g. the Weibull, did not produce a better fit to the data.

The mean and variance of the stage durations can be calculated from the estimated parameters of the gamma distribution (Table 2). The mean duration of each stage is κ divided by ρ_j; the variance is κ/ρ_j^2. The parameters estimates have relative small standard errors, and the correlation among the parameters were acceptable, i.e. the absolute values of the correlations were less than 0.4. Pups spend an average of 2.9 and 3.7 d in stages 1 and 2, respectively. Stages 3 and 4 are nearly 4 times as long as these early two stages (Table 2) and are considerably more variable (Fig. 2).

Discussion

We have estimated the duration of grey seal pup stages 1 through 4 on Sable Island. The duration of stage 5, i.e. fully moulted pups, cannot be estimated from available data, and in any case is not required for the estimation of the distribution of births over time. Our estimates of stage duration differ from those of Radford et al. (1978). They fit normal distributions to data collected in a similar manner to that used in our study, and estimated the durations of stages 1-4 at 4, 7, 6, and 6 days, respectively. Some of the difference might be accounted for by slight differences in the definition of stages. However, the description of stages given by Radford et al. appear to differ little from those used in our study. It is also possible that there are real differences between the population on Sable Island and the British colony studied by Radford et al. (1978).

Our estimates of the mean age of pups the newborn/yellow, thin white, and fat white stages (Stage 1-3, Table 2) are similar to those obtained by Kovacs and Lavigne (1986) for grey seals on North Rona, England. However, our estimate to the duration of moulting stage (24 days; the the duraton of stages in Table 2 must be summed to obtain this number) is considerably longer than the 16 days given by Kovacs and Lavigne (1986). Much of this difference is likely explained by the difference in the method of estimation used in the two studies. Our estimates of stage duration are based on a dynamic model which is relatively insensitive to sampling times. On the other hand, the Kovacs and Lavigne (1986) estimates are simply mean values of the ages of pups sampled. Since older pups in stage 4 become more difficult to find, the sample statistic calculated by Kovacs and Lavigne underestimates the population parameter.

There is a potential source of bias in the above estimation procedure if pups in the older stages disperse from the whelping patch. However, this is not a problem here because independent observations indicate that few if any seals leave the island within the first 25 days after birth, i.e. after 25 days pups in known locations could not always be resighted and were assumed to have entered the water. If the pups do move away from the main survey areas, this movement is probably age and not stage dependent. In this case, stages would be equally censored at age and no bias in the estimates would occur.

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Table 1. Resighting data from 79 grey seal pus from Sable Island used to fit the stage duration.

Age(days)	Stage				
	1	2	3	4	5
1	2	0	0	0	0
2	21	6	0	0	0
3	10	22	0	0	0
4	5	14	0	0	0
5	0	2	0	0	0
6	1	6	15	1	0
7	0	6	3	0	0
8	0	0	1	0	0
9	0	2	18	1	0
10	0	1	8	0	0
11	0	0	2	0	0
12	0	0	17	1	0
13	0	0	10	1	0
14	0	0	8	0	0
15	0	0	22	2	0
16	0	0	20	3	0
17	0	0	21	13	2
18	0	0	0	3	0
19	0	0	12	23	1
20	0	0	1	11	0
21	0	0	0	1	0
22	0	0	1	13	3
23	0	0	1	15	3
25	0	0	0	26	12
26	0	0	0	1	2

Table 2. Fit of stage duration. Units are in days, except for the gamma distribution parameter ρ_j. A common shape parameter, κ was fit. $\hat{\kappa} = 9.41$ with a standard error of 0.02. The absolute value of the correlation between the estimates of the parameters was less than 0.4 in all cases.

Stage Number	Stage Name	ρ_j	Standard Error	Mean Duration	Variance of Duration	Mean Age
1	newborn	2.47	0.07	2.9	1.2	1.69
2	thin white	1.93	0.07	3.7	1.9	5.02
3	fat while	0.65	0.03	11.2	17.4	12.95
4	moulting	0.66	0.05	10.9	16.4	41.65

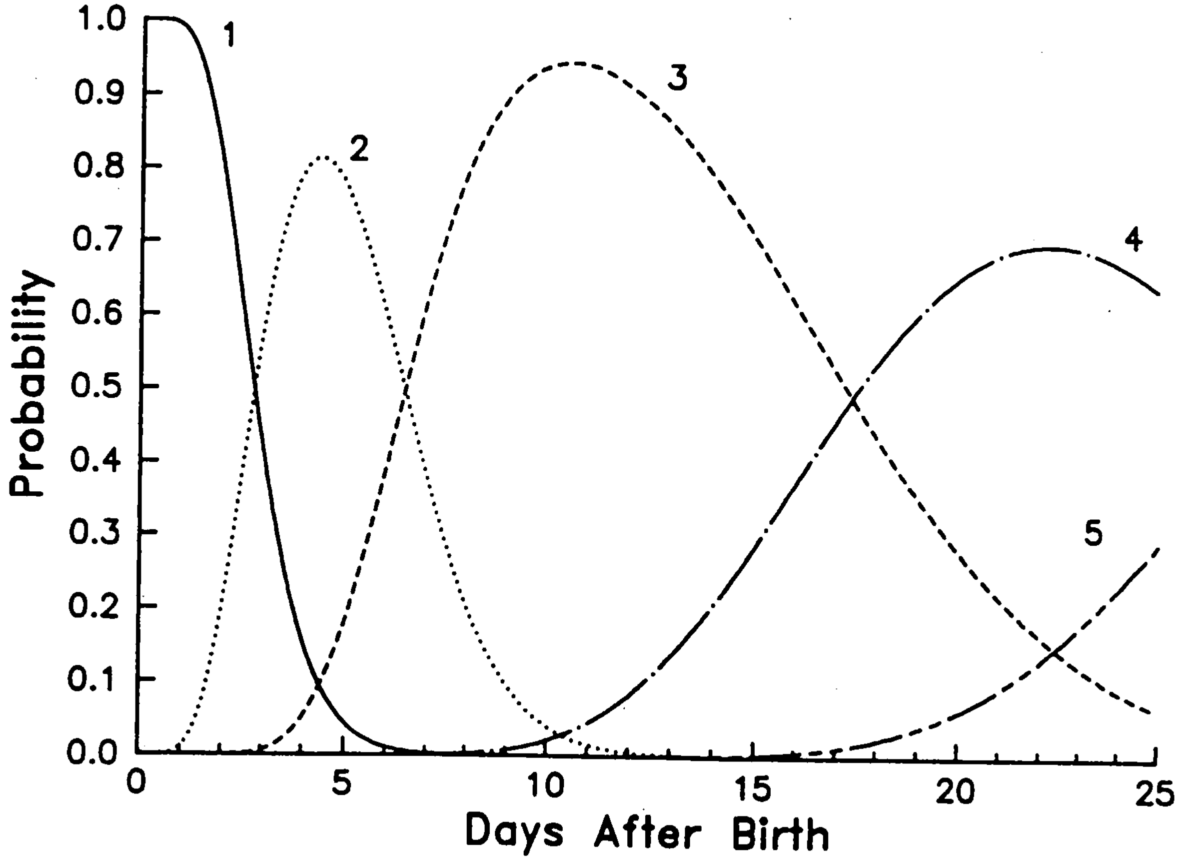

Fig. 1. Probabilities of observing grey seal pups in different stages as a function of pup age (days). The model results are based on the data in Table 1 (stage 1, newborn [-], stage 2, thin white [· · ·], stage 3, fat white [- - -], stage 4, molting [— · —], stage 5, molted [— - - —]).

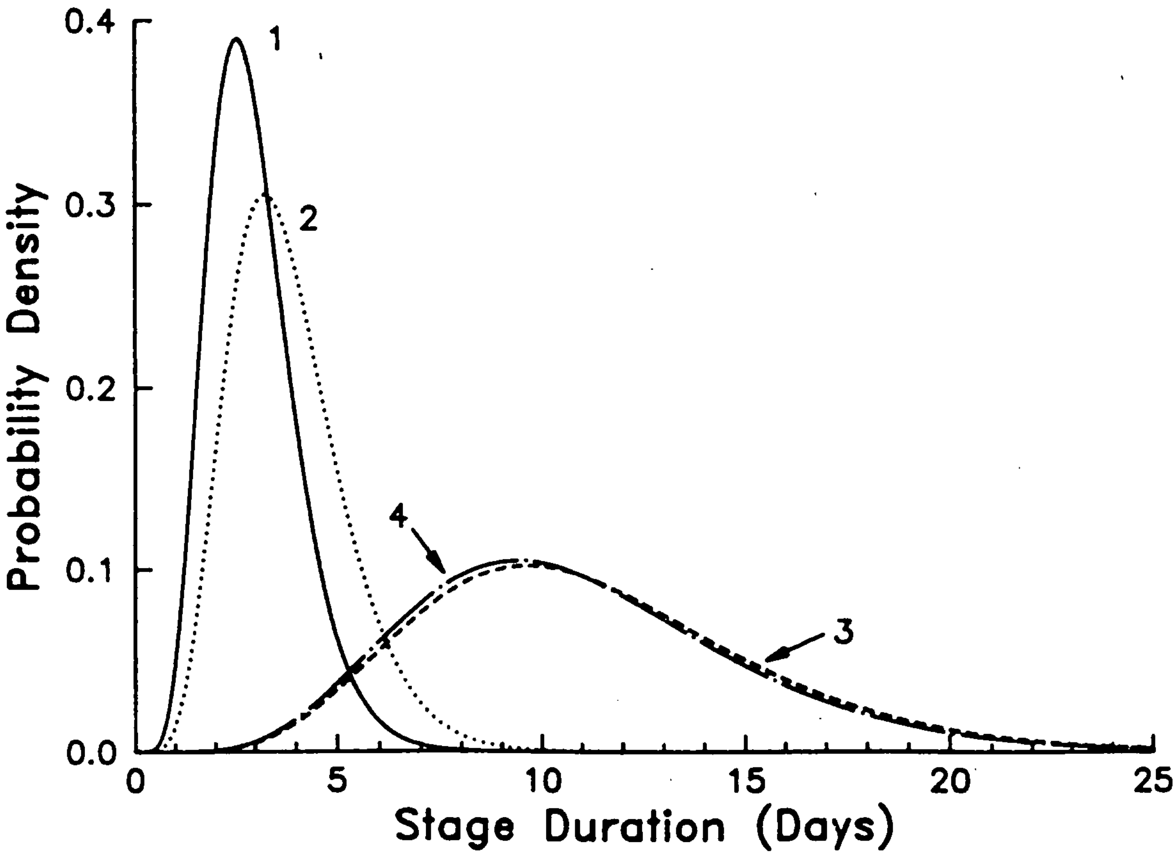

Fig. 2. Estimated probability density for the duration of the newborn (stage 1), thin white (stage 2), fat white (stage 3), and molting (stage 4) stages.