Using mark–recapture to estimate the numbers of a migrating stage-structured population

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Abstract: A model is presented for the joint analysis of mark–recapture data and stage- or age-structured data that allows the population abundance, birth rates, and migration rates to be estimated in situations where standard methods may be unreliable. The model assumes that birth rates follow a continuous distribution and that migration can be described by a simple Markov process. Application of the model is illustrated using mark–recapture and stage-structured data for grey seal (*Halichoerus grypus*) pup production in the Gulf of St. Lawrence and resulted in estimates of 9800 and 10 500 pups produced in 1989 and 1990, respectively.

Résumé : Un modèle est présenté pour l'analyse conjointe des données de marquage–recapture et des données structurées en fonction du stade ou de l'âge qui permettent d'estimer l'abondance de la population, les taux de natalité et les taux de migration dans les situations où les méthodes standard peuvent s'avérer peu fiables. Le modèle suppose que les taux de natalité adoptent une distribution continue et que la migration peut être décrite par un processus markovien simple. L'application du modèle est illustrée à l'aide de données de marquage–recapture et de structure des stades pour la production de petits du phoque gris (*Halichoerus grypus*) dans le golfe du Saint-Laurent et on a obtenu des valeurs estimées de 9800 et 10 500 petits produits en 1989 et 1990, respectivement.
[Traduit par la Rédaction]

Introduction

There are many species whose numbers are inherently difficult to estimate; for example, they may not be reliably detected, animals may be born or die during the survey period, or they migrate into and out of the study area. Here we develop an extension of mark–recapture models to a situation where it is extremely difficult to use standard estimation methods to obtain a reliable estimate of abundance. In particular, we develop a stage-structured, mark–recapture model that allows us to estimate the abundance of an open population that has geographical structure. Although our application is developed to estimate grey seal (*Halichoerus grypus*) pup production, the model is generally applicable. In our model, we use age-dependent stages based upon pelage type to identify the pattern of births over time and migration rates. Our model differs from recently developed models (Schwarz et al. 1993; Brownie et al. 1993; Anganuzzi 1994). We consider many mark–recapture episodes (greater than 20 in the studies examined here) and incorporate additional information on the temporal changes in the observed age-dependent developmental stages of the seal pups in the likelihood function.

We proceed as follows. First, we describe the study population and outline the problems inherent in estimating abundance of such an open population. We then develop the model and apply it to the population for 2 years of data. Finally, we conclude by comparing our estimates to independent population estimates.

The study population

Although grey seals are found throughout Atlantic Canada, only two large breeding concentrations have been identified (Mansfield and Beck 1977). The largest and most intensively studied concentration whelps on Sable Island where complete tagging of pups was carried out from 1977 to 1989 when pup production was 9712 animals (Stobo and Zwanenburg 1990). The second major pupping area is located in the southern Gulf of St. Lawrence (Fig. 1). Although in most areas grey seals give birth on land (Ward et al. 1987), in the Gulf, females whelp primarily on the drifting pack ice. Smaller whelping concentrations are found on several small islands along the eastern shore of Nova Scotia ($N < 500$; M.O. Hammill, unpublished data) and in the Gulf of St. Lawrence on Amet Island ($N < 100$), and Deadman Island ($N < 200$; M.O. Hammill, unpublished data).

Attempts to assess pup production in the Gulf of St. Lawrence are complicated by several factors. The majority of females whelp on drifting ice over a 6-week period beginning in late December. Whelping females are often found in clusters, but unlike some other pinnipeds, these clumps consist of relatively few individuals (<500 animals), are widely spaced, and in some areas, are constantly being expelled from the Gulf on the drifting ice. An aerial survey flown early in the year would be incomplete because many births have not yet occurred, whereas a survey flown late in the season will miss pups that have left the ice or drifted out of the region. Peterson mark–recapture estimates using returns from hunted animals have been used with some success to estimate pup production in this population (Stobo and Zwanenburg 1990). However, in

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the absence of a commercial hunt and the increasing difficulties associated with collection programs, this approach is no longer feasible.

Owing to the problems outlined above, a new approach to estimate pup production in the Gulf of St. Lawrence population was warranted. Here, we use a combination of new mark–recapture and traditional mark–recapture techniques to estimate pup production of grey seals in the Gulf of St. Lawrence during 1989 and 1990.

The model

The model estimates the total number of pups using information on the number of marked animals recaptured in different geographical strata (Fig. 1) and the age composition (days) of pups in each of these regions. It describes the distribution of births of seal pups over time, the migration between regions, the progression of pups through their stages, and the entry of late stage (older) pups into the water where they cannot be observed.

The distributions of whelping over time were assumed to follow a beta density function with time limits A_i to B_i. The starting date of whelping, A_i, was the first date on which ice suitable for whelping was observed in a region, and the final date, B_i, was chosen to correspond to the last birth observed in a region. The parameters of the beta distribution in region 1 are a_1 and b_1. Similar notation is used for region 2, i.e., a_2 and b_2.

The probability density of a pup being born at time t in region i is

$$(1) \qquad \frac{1}{B(a_i,b_i)} \frac{(t-A_i)^{a_i-1}(B_i-t)^{b_i-1}}{(B_i-A_i)^{a_i+b_i-1}}$$

where $B(a_i, b_i)$ is the beta function and $A_i \le t \le B_i$. In general, we expect that whelping will be unimodal, which implies that $1 \le a_i$, and $1 \le b_i$. The number of seals born in region i on day s, $m_{i,s}$, is eq. 1 integrated over the day, times the total number of pups born in the region, N_i.

Movement of pups is assumed only to occur between adjacent regions. In our analysis, migration occurs in only one direction. The proportion of pups that remain in region i and do not migrate to region $i + 1$ each day is $T_{i,i+1}$.

Let $n_{i,s,j,t}$ be the number of pups born in region i on day s that are in region j on day t. The numbers of pups born in region i, for $i = 1$ or 2, that remain in the region is described by

$$(2) \qquad n_{i,s,i,t} = T_{i,i+1}^{t-s} m_{i,s}$$

For example, the change in the numbers of pups in region 2 that were born in region 1 on day s is described by

$$(3) \qquad n_{1,s,2,t} - n_{1,s,2,t-1} = (1 - T_{1,2})\, n_{1,s,1,t-1} - (1 - T_{2,3}) n_{1,s,2,t-1}$$

Similar equations can be written for the other regions.

The above equations describe the dynamics of pups that are born in each region; however, we do not usually know where a pup was born because of drifting of the ice. We thus define $n^*_{i,s,j,t}$ to be the number of pups in region i on day s that are in region j on day t, i.e., it is the sum of $n_{i,s,j,t}$ over all regions where pups are born.

The second part of the model uses data on age-dependent stages of seal pups; this part of the model is identical to that described by Myers and Bowen (1989) and will not be repeated in detail here. The pups are assumed to pass through a series of identifiable stages from which the age distribution of the pups can be inferred. The stage durations for grey seals are estimated in Myers et al. (1997).

A final complication is that not all stage-5 pups are on the ice. When pups are in the water between ice flows they are much less likely to be observed or recaptured. We estimate the proportion of stage-5 pups on the ice and visible, which we will call δ.

Estimation

The model parameters are the number of seals born in region 1, N_1, and region 2, N_2; the parameters of the beta distributions, a_i and b_i; the transition probabilities, $T_{1,2}$ and $T_{2,3}$; and δ. The first and last days of whelping are estimated independently from observations on ice conditions and reconnaissance surveys.

We use the sum of the log-likelihood from the mark–recapture plus the likelihood from the stage composition to estimate pup production. The log-likelihood for the stage composition is identical to that used by Myers and Bowen (1989) and will not be discussed in more detail here. The log-likelihood for the mark–recapture is the standard binomial model used in mark–recapture studies of large populations. The model predicts the proportion of animals marked in one region that will be observed at a subsequent time in any of the regions.

Let the number of pups marked in region i on day t be $M_{i,t}$. Let the number of recaptures in region j on day t of pups marked in region i on day s be $R_{i,s,j,t}$. Let the number of pups examined for marks in region j on day t be $S_{j,t}$.

To examine the probability of a marked seal being recaptured we need the number of pups in region j on day t, which we define as $n^*_{\cdot,\cdot,j,t}$ where the "dot" notation is the sum over all regions or days.

The proportion of pups in region j on day t that were in region i on day s is

$$(4) \qquad \frac{n^*_{i,s,j,t}}{n^*_{\cdot,\cdot,j,t}}$$

The proportion of pups in region i on day s that were marked is

$$(5) \qquad \frac{M_{i,s}}{n^*_{\cdot,\cdot,i,s}}$$

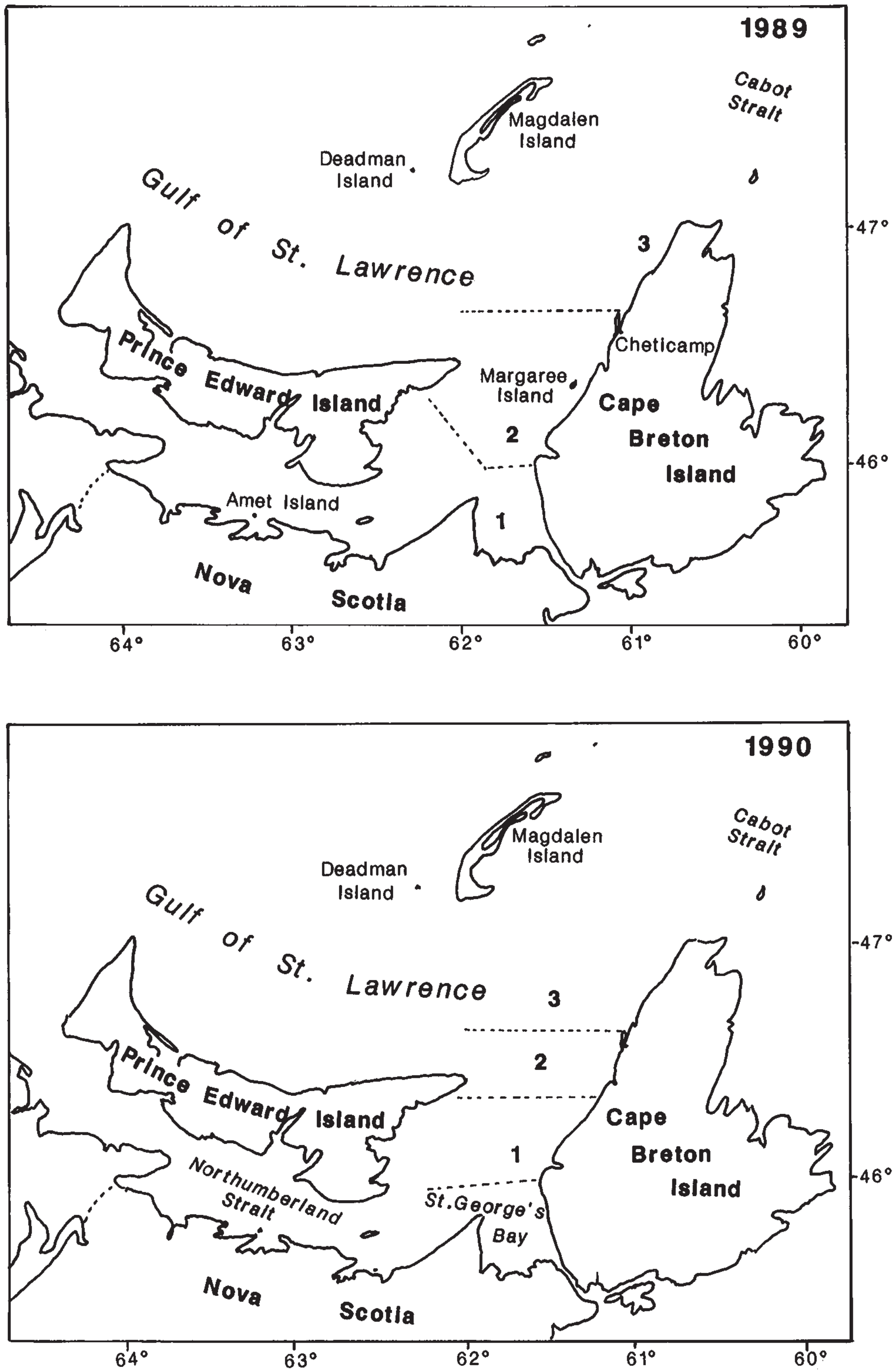
The proportion of pups in region j on day t that were marked in region i on day s is

$$(6) \qquad \frac{M_{i,s} n^*_{i,s,j,t}}{n^*_{\cdot,\cdot,i,s} n^*_{\cdot,\cdot,j,t}}$$

The likelihood of observing $R_{i,s,j,t}$ marked seals out of $S_{j,t}$ is the binomial likelihood with the probability given by eq. 6.

The overall log-likelihood for the mark–recapture is the sum of the above binomial log-likelihood over all markings and subsequent resightings. The resulting log-likelihood is a constant plus

Fig. 1. Map of the Gulf of St. Lawrence showing regions used in the 1989 and 1990 surveys.



$$(7)\quad \sum_{i,s,j,t} (S_{j,t} - R_{i,s,j,t}) \log\left(1 - \frac{M_{i,s} n^*_{i,s,j,t}}{n^*_{i,\cdot,i,s} n^*_{\cdot,\cdot,j,t}}\right) + R_{i,s,j,t} \log\left(\frac{M_{i,s} n^*_{i,s,j,t}}{n^*_{i,\cdot,i,s} n^*_{\cdot,\cdot,j,t}}\right)$$

The predicted numbers of pups of each category, e.g., $n_{i,s,j,t}$, is calculated using the parameters that are estimated in the model, e.g., the total number of pups born in region 1, N_1. We have not included information on multiple recaptures of the same individual, because there were relatively few of these.

The above log-likelihood is added to the log-likelihood for the stage composition. For any region, i, and day of observation, t, the number of pups in each stage, k, is assumed to

Table 1. Resightings of tagged grey seals in the Gulf of St. Lawrence, 1989.

Day of the year	No. tagged	No. examined	Area	Day and area of resighting of previously tagged seals																			
				23	24	26	27	31	32		33	36		37	38	39	40	41		44		45	46
				2	1	1	1	2	2	3	1	1	2	1	1	1	1	1	2	2	3	1	1
14	57		1																				
16	22	26	2																				
17	13	15	2																				
18	103	103	1				11							6				3					30
19	250	253	1	1	69			1			19					9		6			1	4	
20	185	185	1			58										6		1				1	
22	59	59	1		2	13		16															
23	79	83	2					9	8	2										1			
24	204	275	1						3							16		4					
26	173	248	1								24	18											2
27	104	118	1									6		1				2					
31	111	138	2																	10			
32	70	82	2										5										
	30	32	3																				
33	103	148	1									3											
36	37	64	1																			2	
	14	19	2																				
37	111	117	1															11					
38	191	192	1																			49	
39	143	175	1															1					
40	128	128	1																				
41	42	70	1																				
	1	1	2																				
44	6	21	2																				
	7	8	3																				
45	11	69	1																				
46	51	83	1																				

Note: No tagged seals were resighted between day 14 and day 22 during tagging operations.

follow a multinomial distribution with the predicted proportion of pups as $q_{i,t,k}$. For any particular parameter values for the model, the proportion, $q_{i,t,k}$, can be calculated. The log-likelihood of any combination of parameters is the sum of the above multinomial log-likelihood over all regions and stages for which there are observations. That is, the log-likelihood is a constant plus

$$(8) \qquad \sum_i \sum_t \sum_k N_{i,t,k} \ln(q_{i,t,k})$$

where $N_{i,t,k}$ is the observed number of pups. The stage transitions follow the formula presented in Myers and Bowen (1989) and will not be given here. The important point is that they allow the approximate age composition to be estimated for each day observations are made.

The maximization of log-likelihood, was performed numerically using the Broyden–Fletcher–Goldfarb–Shanno positive definite, secant update algorithm (Dennis and Schnabel 1983).

Application of the model

Study region

In the southern Gulf of St. Lawrence, large concentrations of grey seals breed on the pack ice in eastern Northumberland Strait, St. George's Bay, and along the western coast of Cape Breton Island (Fig. 1) (Mansfield 1966; Mansfield and Beck 1977). Ice formation begins during the middle of December along the New Brunswick coast and in Northumberland Strait, which drifts towards the east (Markham 1980). Depending on a combination of prevailing winds and local currents, the ice moves into St. George's Bay, or moves across the mouth of St. George's Bay, north along the Cape Breton coast, and out Cabot Strait to the Atlantic Ocean.

The location of large concentrations of grey seals is dictated largely by the availability of 40–80 cm thick ice, distributed as medium-sized floes 20–50 m in diameter. Larger floes and solid land-fast ice appear to be avoided, possibly because these areas provide only limited access to the water, and they are accessible by surface predators. Small floes (<20 m) are also avoided presumably because they are too unstable. Females whelping early in the season tend to haul out on the ice in eastern Northumberland Strait, which depending on wind conditions drifts as previously described. The pups suckle for approximately 15 days (Iverson et al. 1993; Baker et al. 1995), after which they are weaned abruptly. After weaning the pups may remain with the ice for another 2–3 weeks, although this is affected by the pattern of ice movement; pups may move ashore where the ice jams against the coast or be forced into the water as the ice breaks up during storms or drifts into the Atlantic.

Pup tagging and stage determination

During January and February of 1989 and 1990, flights to locate whelping patches were flown daily using a Bell 206B helicopter on fixed floats. When seals were located, the aircraft landed and the animals were tagged or examined for the presence of tags. Pups were marked by attaching a tag to the webbing of the hind flipper using uniquely numbered, coloured tags (Stobo and Zwanenburg 1990). Once animals in the patch had been tagged, the helicopter continued to search throughout the region for other patches. After a region had been searched, the helicopter moved to another region and continued searching for patches until the whole study area had been examined. The position of patches was determined using a Loran C navigation system, and this information was used to monitor ice drift. The number of pups tagged and resighted for 1989 is shown in Table 1.

We recognized five pup stages for the purpose of this study (Myers et al. 1997). 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.

Pups were assigned to one of the five age-related developmental categories. (Table 2). The change in the proportion of pups in different stages obtained during the tagging experiment conducted throughout the whelping season was used to model the distribution of births throughout time. This birthing distribution was then used to correct the within-season mark–recapture data for pups not yet born or pups that had entered the water.

Table 2. Numbers of grey seal pups in age-dependent stages observe in the gulf of St. Lawrence, 1989.

Day of the year	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total observed
Area 1[a]						
14	11	39	9	0	0	59
18	64	39	0	0	0	103
19	22	67	158	5	0	252
20	10	79	135	2	0	227
22	3	45	11	0	0	59
24	10	30	182	50	3	275
26	0	30	185	20	0	235
27	3	26	89	0	0	118
33	0	5	99	38	6	148
36	0	6	47	10	1	64
37	0	12	87	17	1	117
38	0	6	135	48	1	190
39	2	3	91	53	26	175
40	0	6	88	31	3	128
41	0	1	32	27	11	71
45	0	1	14	37	17	69
46	0	0	12	54	11	87
Area 2[a]						
16	7	19	0	0	0	26
17	2	13	0	0	0	15
23	0	13	69	1	0	83
31	1	11	106	19	1	138
32	3	6	56	16	1	82
36	0	1	17	1	0	19
41	0	0	0	0	1	1
44	0	0	1	11	9	21
Area 3[a]						
32	4	10	16	2	0	33
44	0	2	2	1	3	8

[a]Area 1, St. George's Bay to Port Hood Island; area 2, Port Hood Island to the north end of Cheticamp Island; area 3, north of Cheticamp Island.

Results

The whelping area was divided into three regions (Fig. 1), defined using information gathered in the field on ice drift and ice stability. In 1989, region 1 corresponded to St. George's Bay (south of 46°01′N), region 2 is St. George's Bay to Cheticamp (46°39′N), and region 3 is from Cheticamp to Cape North (north of 46°39′N) (Fig. 1).

The proportion of pups that remain in region 1 and do not migrate to region 2 each day is $T_{1,2}$. Similarly, pups are assumed to migrate from region 2 to region 3. We assume that no seals migrate from region 2 or 3 to region 1. The proportion that remain in region 2 each day is $T_{2,3}$. The assumption that the pups do not migrate from region 2 to 1, or from region 3 to 2 is consistent with all resighting of seals and the observed patterns of ice drift (Table 1).

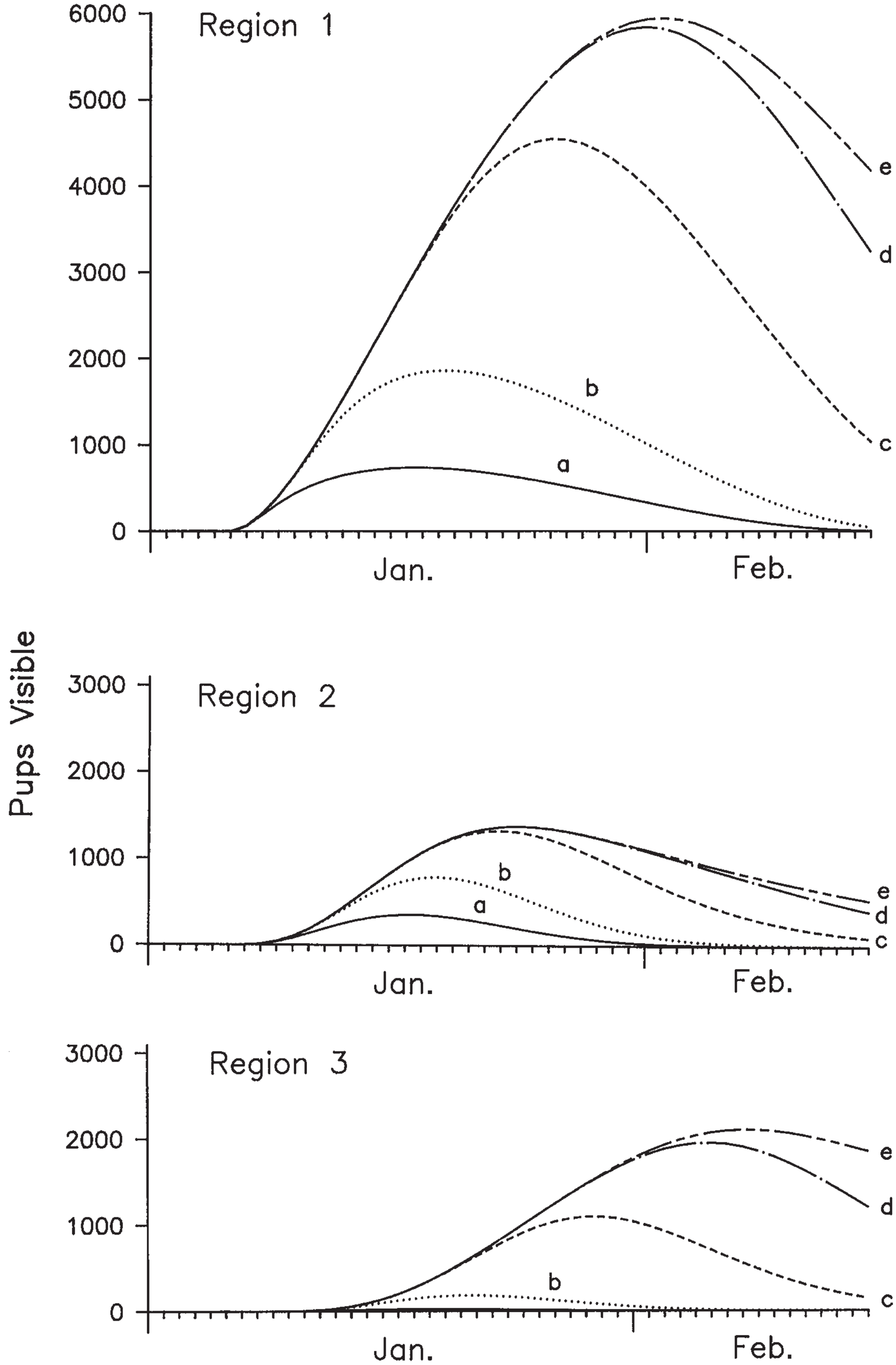
We assumed that no births occurred north of Cheticamp (area 3). We believe this assumption is reasonable because this area consisted of unstable, dispersed ice that does not appear to be favored by female grey seals. Although a few females may have given birth in this area, the number is likely small, and only a few newborns were located in this area.

Pupping on the ice begins in early January when suitable ice formed. We initially assumed that the first date of pupping (A_1 and A_2) was January 6. The season of births is prolonged with newborn pups still appearing on the ice in early February. The last date of pupping (B_1 and B_2) was assumed to be February 9. The buildup in number of births on the ice occurs rapidly with 63% of the births occurring by January 23 (Fig. 2). However, the season of births is prolonged with newborn pups still appearing on the ice in early February.

The movement of pups out of region 1 is estimated to be approximately 1% a day, while a much higher migration rate, approximately 9% a day, is estimated for region 2. This higher rate is consistent with the high rate of ice movement out of this region. We estimate that only 34% of the stage-5 pups are visible. The shapes of the stage composition and birthing distribution show a later whelping in region 2 (Table 2, Fig. 2). In all cases, correlations among the parameters estimates were reasonable, i.e., less than 0.5. This indicates that the model parameters are well determined from the data. The estimate of pup production is 7491 ± 434 (mean ± SE) in St. George's Bay (region 1) and 2336 ± 941 in region 2, which results in a total of 9827 ± 1049 (Table 3, trial 1).

We assess model robustness by examining modifications of the models assumptions. We first modified the start date,

Fig. 2. The distribution of seal pup stages over time in each of the three regions in 1989 using trial 1. The lines are labelled as follows: (*a*) number of newborn pups; (*b*) number of newborn plus thin white pups; (*c*) number of newborn, thin, and fat white pups; (*d*) number of newborn, white, and molting pups; and (*e*) total number of pups.



which was originally assumed to be January 6; however, reasonable variations in the assumed value of the date that pupping started, A_1 and A_2, have little effect on the estimates. For example, moving the start date to January 9 had little effect on the estimates (Table 2, trial 2). Similar results were obtained by modifying the last dates of pupping. Constraining region 1 and 2 to have the same distribution of births in trial 3 (Table 2) reduced the estimated number of pups by about 10%. However, the hypothesis that the birthing distributions are the same can be rejected (likelihood ratio test, $p < 0.001$). We also tested the robustness of our estimates to incorrect estimates of stage duration. We found that reasonable modifications of the stage

Table 3. Results for the 1989 and 1990 mark–recapture estimates.

Year	Trial	A_1	$\hat{T}_{1,2}$	$\hat{T}_{2,3}$	$\hat{\hat{\delta}}$	$\hat{N}_1$	$\hat{N}_2$	$\hat{a}_1$	$\hat{b}_1$	$\hat{a}_2$	$\hat{b}_2$	–Log likelihood
1989	1	6	0.991	0.913	0.34	7491	2336	1.75	3.19	3.44	8.287	4657.4
SE			0.001	0.026	0.09	434	941	0.08	0.18	0.56	1.448	
1989	2	9	0.990	0.915	0.35	7556	2184	1.09	2.47	2.11	6.577	4664.6
SE			0.001	0.030	0.09	440	990	0.05	0.16	0.41	1.416	
1989	3	6	0.991	0.94	0.34	7502	1314	1.86	3.46	1.86†	3.46†	4665.2
SE			0.001	0.011	0.09	429	277	0.08	0.18			
1989	4	6	0.987	0.883	1*	7041	3389	1.91	3.11	3.46	9.189	4704.4
SE			0.001	0.034		437	1627	0.08	0.19	0.57	1.370	
1990	1	6	0.991	0.913	0.34	7491	2313	1.80	3.20	3.4	8.40	4657.4
SE			0.001	0.025	0.10	452	947	0.10	0.20	0.6	1.40	
1990	2	6	0.991	0.940	0.34	7505	1311	1.80	3.50	1.80†	3.50†	4665.2
SE			0.001	0.011	0.09	430	289	0.10	0.2			

Note: Standard errors are given below the estimates. Trial 1 is the base case; in trial 2 the assumed minimum starting date of whelping is modified; in trial 3 the two regions are constrained to have the same birthing distributions; and in trial 4 all stage-5 pups are assumed to be visible. A_1 is the start date of birthing in January in region 1, which is assumed to be the same as the start date in region 2.

*Parameter $\hat{\hat{\delta}}$ is constrained to be 1.

†Parameter for region 2 is constrained to be the same as region 1.

duration, e.g., 10%, resulted in only small changes in the estimates, e.g., less than 5%.These results are consistent with those of Stenson and Myers (1988) for hooded seals (*Cystophora cristata*) using a similar model.

The largest change in the estimated numbers occurs if it was assumed that all stage-5 seals are visible to be recaptured (Table 2, trial 4). However, stage-5 seals enter the water where they cannot be "recaptured" because the tag numbers cannot be read. If all pups were assumed to be visible, the maximum log-likelihood greatly decreased, and this hypothesis can be rejected with very high probability (likelihood ratio test, $p < 0.001$).

In 1990, early ice formation created heavy ice conditions in St. George's Bay resulting in no migration of pups out of the bay. Therefore, pup production in this area was estimated to be 666 ± 46 animals assuming no movement out of the region. In 1990, we defined region 1 to lie between St. George's Bay (46°01′N) and Margaree Island (46°22′N) and estimated pup production of 7491 ± 452. Region 2, which lay between Margaree Island and Cheticamp, had a pup production of 2313 ± 947, for a total pup production of 10 470 ± 1050 including St. George's Bay. Changes in the model assumptions led to similar changes for the 1989 estimates, i.e., they produced small changes in the estimates (Table 3). It is encouraging that the 1990 estimates are close to the 1989 estimates (Table 3). (The raw data for 1990 can be obtained from the authors.)

Discussion

A key feature of this model is the use of stage-specific information, which is age dependent, in the model along with mark–recapture information. The stage-specific information allows for a more precise model than would have been possible by using mark–recapture only and eliminates much of the confounding between population size and demographic rates that plague traditional methods of analyzing open populations. In our example, there simply is not sufficient information to obtain population estimates from the tagging unless the stage information is included, or a random sampling is obtained at some later date (see below). Vogt and Morton (1991) found that, by incorporating age data to estimate survival and age-dependent trapability, they were able to improve the reliability of their estimates of population size in a mark–recapture model. Although Vogt and Morton's model is very different from the one used here, the general principle of using age or stage data within a mark–recapture model is the same and shows that estimates can be greatly improved. We suggest that such information be generally incorporated into mark–recapture models when possible.

We have demonstrated that it is possible to carry out mark–recapture estimation for a population under situations when most of the usual assumptions are violated: the majority of the animals are born during the survey period, large-scale movements take place, and animals leave the survey area. The method proposed here has produced comparable estimates of Gulf of St. Lawrence grey seal pup production in 1989 (9800) and 1990 (10 500).

These estimates are also consistent with estimates obtained from a Peterson mark–recapture estimates in which the same tagged animals marked in this study were recaptured on Sable Island 3–4 months later or Anticosti Island 2–3 years later. The Sable Island recaptures resulted in estimates of 8800 ± 850 and 8100 ± 850 for 1989 and 1990, respectively; the Anticosti Island recaptures resulted in estimates of 10 400 ± 3100 and 9200 ± 2600 for 1989 and 1990, respectively.

Although pup production of grey seals in the Gulf of St. Lawrence was previously estimated using simple Peterson mark–recapture (Stobo and Zwanenburg 1990; Hammill et al. 1992*b*), these earlier studies used samples from large-scale scientific collections or live captures on Sable Island for returns and required complete tagging on Sable Island. It is unlikely that these methods can be used in the future because tagging of pups from the Sable area has been discontinued and large-scale scientific collections are unlikely to take place in the future. There are no other sources of tag return information, since there is currently no commercial hunt for grey seals and returns from the bounty hunt, which has been discontinued, are considered to be unreliable (Zwanenburg and Bowen 1990).

Therefore, pup production in the Gulf must be estimated from data obtained during the whelping season itself. Hammill et al. (1992*a*) attempted to estimate pup production using aerial surveys but were hampered by the dispersed nature of pupping in grey seals, migration of pups out of the study area, and the poor weather conditions that are common during the whelping period. Using the mark–recapture technique used in this study circumvents many of these problems.

One of the key assumptions of the model is that rate of movement of pups between strata was constant. The validity of this assumption is questionable because ice movement varies with changes in local currents and wind. In spite of these local changes there is a persistent long-term mean current and ice drift pattern in the region that makes this assumption reasonable. However, the assumption of independence is not met, i.e., that the fate of each tagged seal is independent of the fate of other tagged seals. This assumption is violated because tagged seals are resighted in groups (Table 1). Violations of this assumption will not bias the estimates but will result in an underestimate of the standard errors (Pollock et al. 1991).

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