

CAPTURE-RECAPTURE ANALYSIS FOR ESTIMATING MANATEE REPRODUCTIVE RATES

WILLIAM L. KENDALL

USGS Patuxent Wildlife Research Center,
11510 American Holly Drive, Laurel, Maryland 20708, U.S.A.
E-mail: william_kendall@usgs.gov

CATHERINE A. LANGTIMM

CATHY A. BECK

USGS Florida Integrated Science Center, Sirenia Project,
412 NE 16th Avenue, Gainesville, Florida 32601, U.S.A.

MICHAEL C. RUNGE

USGS Patuxent Wildlife Research Center,
11510 American Holly Drive, Laurel, Maryland 20708, U.S.A.

ABSTRACT

Modeling the life history of the endangered Florida manatee (*Trichechus manatus latirostris*) is an important step toward understanding its population dynamics and predicting its response to management actions. We developed a multi-state mark-resighting model for data collected under Pollock's robust design. This model estimates breeding probability conditional on a female's breeding state in the previous year; assumes sighting probability depends on breeding state; and corrects for misclassification of a cow with first-year calf, by estimating conditional sighting probability for the calf. The model is also appropriate for estimating survival and unconditional breeding probabilities when the study area is closed to temporary emigration across years. We applied this model to photo-identification data for the Northwest and Atlantic Coast populations of manatees, for years 1982–2000. With rare exceptions, manatees do not reproduce in two consecutive years. For those without a first-year calf in the previous year, the best-fitting model included constant probabilities of producing a calf for the Northwest (0.43, SE = 0.057) and Atlantic (0.38, SE = 0.045) populations. The approach we present to adjust for misclassification of breeding state could be applicable to a large number of marine mammal populations.

Key words: breeding probability, capture-recapture, manatees, mark-resighting, misclassification, photo-identification, population modeling.

The Florida manatee (*Trichechus manatus latirostris*) is a long-lived marine mammal that inhabits the estuaries and coastal rivers of the southeastern United States, mainly Florida (Lefebvre and O'Shea 1995). This species is currently listed as endangered under the Endangered Species Act. Current and future potential threats include

collisions with an increasing fleet of watercraft in Florida waterways, the loss of warm-water *refugia* in winter, and coastal human development (USFWS 2001). To understand the dynamics of this species, and especially to predict the impacts of human development, it is important to acquire unbiased and precise estimates of the vital rates. With such information a population model can be developed to identify key life history parameters, and model predictions can provide a basis for optimizing the management of manatees (Runge *et al.* 2004).

The vital rates of many animal populations have been estimated by capturing and marking a subset of individuals, followed by recapturing or resighting them over time (Williams *et al.* 2002). Although it is practical to capture and mark some marine mammals such as pinnipeds (*e.g.*, Manske *et al.* 2002), for larger mammals such as cetaceans one must rely on natural marks or scars (*e.g.*, Barlow and Clapham 1997). Since 1978 the USGS Sirenia Project has conducted a mark-resighting study of manatees, in which individuals are identified by the pattern of scars and other marks on their skin (Beck and Reid 1995). Data from this study have been used to estimate survival rates (Langtimm *et al.* 1998, Langtimm *et al.* 2004) using open-population capture-recapture models.

Breeding probability is another important vital rate. Previous authors have used photo-identification data to estimate the probability that any given sexually mature or adult female in a given year is accompanied by a first-year calf (O'Shea and Hartley 1995, Reid *et al.* 1995, Rathbun *et al.* 1995). We call this an unconditional breeding probability. Their methods were *ad hoc*, consisting of selecting females that met the desired criteria and computing the proportion of years in which each was observed with a first-year calf. These investigations did not account for two potentially important problems. First, they did not account for sighting probabilities of <1.0 , and more specifically that there could be differences in sighting probabilities between females with and without first-year calves, which would bias their estimates. Second, they did not account for the fact that an attendant first-year calf could elude detection by the observer, even though its mother was sighted. This could be due to the angle of sight, turbidity of the water, *etc.* In this case a female with a first-year calf would be misclassified as not having produced a calf. There is a chance that this calf could be missed for an entire season, even though its mother was sighted multiple times. Barlow and Clapham (1997) used a maximum likelihood approach to estimating interbirth intervals as a function of the time since last giving birth for humpback whales (*Megaptera novaengliae*), but did not permit time variation in these parameters. Nichols *et al.* (1994) provided capture-recapture models that model transitions between breeding states as a Markov process (*i.e.*, dependent only on the year and current breeding state), and permit each state to have its own survival, detection, and transition probabilities. We generalize Nichols *et al.* (1994) and other previous methods by correcting for mis-classification of breeding states due to failure to observe a calf with its mother.

To project population dynamics, conditioning breeding probability on whether a female has bred in the previous year is more useful than relying on unconditional breeding probability (see Caswell 2001). This is especially true if there is a difference in survival rate between those with and without a first-year calf.

Here we provide estimates of conditional manatee breeding probability for two of the four regions in Florida designated as management units in the Florida Manatee Recovery Plan (USFWS 2001)—the Northwest and Atlantic Coast. The two regions differ in manatee population characteristics, human population and development, implementation of conservation and management actions, habitat characteristics,

habitat quality, and factors affecting carrying capacity (see Langtimm *et al.* 2004 for a full discussion). The Atlantic Coast presents higher mortality risks to manatees not only in the magnitude of human interactions, particularly with watercraft (O'Shea *et al.* 1985, Ackerman *et al.* 1995), but also in the frequency of natural events such as cold stress (Buergelt *et al.* 1984). Habitat suitability for manatees is considered lower on the Atlantic Coast compared to the Northwest, suggesting that manatee breeding probabilities may differ between the two populations. Our analysis is based on photo-identification data in the USGS Manatee Individual Photo-identification System (MIPS) and rectifies previous methodological problems. Specifically, we estimate the probability that in a given year an adult female manatee produces a calf which survives to the winter sighting period, conditional on whether that female produced a calf that survived to the winter sighting period in the preceding year. To put the sampling process in the proper probabilistic framework for estimation, we use multi-state (*i.e.*, two breeding states: with a first-year calf and without) capture-recapture statistical models (Arnason 1972, 1973; Nichols *et al.* 1994), adjusted for the probability that breeding state is misclassified due to observers missing calves (Kendall *et al.* 2003). Runge *et al.* (2004) have incorporated the results of this analysis into a stage-based projection matrix model of population dynamics.

METHODS

Field Methods and Data Selection

The study populations occur along the north Gulf Coast (Northwest population or NW) and the Atlantic Coast (Atlantic population or AC) of Florida. In winter (November–February) individuals in the NW converge on two artesian-spring, warm-water refuges—the Crystal and Homosassa rivers. Individuals from the AC tend to congregate at a series of warm-water effluents from power plants up and down the coast. These assemblages are conducive to photographing individuals, allowing them to be uniquely identified by scars or other marks (see Beck and Reid 1995, Langtimm *et al.* 2004). Observers survey these winter *refugia* each year, visiting each site multiple times within a season. Depending on conditions, observers either enter the water to photograph animals or photograph them from boats or shore.

Since 1978, the USGS Sirenia Project has annually photographed and documented sightings of known individuals at these winter aggregation sites. The identification of individuals by scar pattern acquired from boat strikes, the determination of their sex and reproductive status, and maintaining individual identities as they continue to accumulate new scars, is a complex process. Briefly, inclusion in the photo database requires full documentation of the dorsal and lateral parts of the body and tail, and positive matches require agreement by at least two experienced personnel, one being the database manager. Only healed scars or other unique permanent features are used for identification. Nearly all individuals in the catalog have multiple scar patterns distributed over >1 area of their body, providing redundant information for identification. High fidelity to monitored sites makes it easier to document the accumulation of scars over time. See Beck and Reid (1995) and Langtimm *et al.* (2004) for more detailed discussion of identification.

Mating generally is observed from February to July. Most births occur from May to September and only rarely in winter, after a gestation of about 11–13 mo (Lefebvre and O'Shea 1995). Litter size is usually one, with calf dependency from 1 to 2 yr. During the winter sighting period observers noted whether an adult female was

accompanied by a calf. The timing of sighting effort relative to when calves were born and the size of the calf usually permitted observers and the database manager to determine if the calf was born in the preceding 12 mo. Site fidelity to the winter refuges is high among observed individuals (Rathbun *et al.* 1995, Deutsch *et al.* 2003).

We constructed adult female sighting histories based only on sightings after an individual was identified and known to be adult (>5 yr), following conservative criteria defined by O'Shea and Langtimm (1995, see also Langtimm *et al.* 1998). These criteria were based on at least one of the following: known age, body length, accompaniment by calf, or time since initial identification. The 90-d sighting period was 15 November through 12 February, when females were most easily photographed, births are rare, and the likelihood of weaning low. A sighting history was constructed for each adult female, consisting of its non-sighting (0) during each sampling period or its sighting with (C) or without (N) a first-year calf, for each year of the study. Great effort was expended to age calves and match them with the mother. However, if reasonable doubt remained about age or association, a female was assigned to state N. Although sightings began in 1978, effort was more regular beginning in the fall of 1982. Therefore our analysis is restricted to the winters of 1982–1983 to 2000–2001 for both the NW and AC.

Statistical Modeling

The estimation of reproductive rates of manatees using sighting data is best considered within the context of multistate capture-recapture models (Nichols *et al.* 1994). In this case an adult female can occupy one of two states in a given winter: accompanied by a calf that was born in the previous 12 months (state C), implying that she reproduced in the previous year; or accompanied by no calf or a second-year calf (state N), implying that she did not reproduce or the calf did not survive to the winter sighting period. We assume that an adult female that survives from winter i to winter $i + 1$ (with probability S_i^C for those with first-year calf in year i or S_i^N for those without first-year calf in year i) will make a transition from one of these states to the other with some probability that is dependent on her current state (*i.e.*, ψ_i^{CC} , ψ_i^{NC} are the probabilities she produces a calf in year $i + 1$ that survives to winter, given that she produced or did not produce, respectively, a calf that survived to winter in year i). The estimation of these parameters is complicated by the fact that not all adult females in the population are sighted in any given year. Therefore to produce unbiased estimates of survival and productivity one must also estimate detection probability for those with and without first-year calves.

An additional complication arises with manatees, as well as other species, where state is assigned based on field observation. In some cases a female with a first-year calf can be misclassified due to the calf being missed, because of the difficulty of determining cow/calf associations in an aggregation of animals, difficult viewing conditions, or in some cases a large calf being misclassified as a second-year calf. The detection probability of a calf is <1.0, even when the mother is sighted. Therefore, we have two sets of states: true states and observed states. If a female is observed with a calf that is clearly <12 mo old, then we assign her to state C and assume we do that without error (*i.e.*, her observed state matches her true state). If she is observed without a calf that is clearly <12 mo old, we are not sure if indeed she might have one that was missed. Therefore we call this observed state “apparently without first-year calf” (state N'). This potential misclassification would tend to produce

underestimates of breeding probabilities using traditional multistate models (Nichols *et al.* 1994) or *ad hoc* methods (O'Shea and Hartley 1995, Reid *et al.* 1995, Rathbun *et al.* 1995), and could also hide differences in survival for those that have or have not bred in a given year.

Here we use an extension of a maximum likelihood statistical method developed by Kendall *et al.* (2003), which estimates and adjusts for the probability of misclassifying breeders as non-breeders using multinomial models. Briefly, we consider the sighting effort within each winter in terms of Pollock's robust design (Pollock 1982), dividing the season into two sampling periods where we assume the entire population is sampled in each of the two periods. We assume the population of adult females and their calves is closed to additions (births or immigration) and deletions (deaths or weaning) for the duration of the two sampling periods. We can partially relax this assumption to permit entry of adults or exit or death of the adult or calf between sampling periods, assuming each adult female or each calf is subject to the same probability of exit (Kendall 1999). Essentially misclassification is dealt with by modeling the sighting history of a calf and its mother together.

Before illustrating this method, we first define p_{ij}^C, p_{ij}^N as the probabilities that an adult female that is or is not, respectively, accompanied by a first-year calf, is sighted in sampling period j of winter i ; δ_{ij}^C is the probability that a first-year calf is sighted in sampling period j of winter i , given that its mother has been sighted; and α_i is the probability that an adult female in the study area in winter i has a first-year calf.

We illustrate the idea with the following sighting histories for two adult females over a two-year period: CN 0N; NN CC. The first history implies that a female was sighted in year 1, sampling period 1 with a first-year calf, but then in sampling period 2 she was sighted but the calf was not. The fact that the calf was not seen with her in both sampling periods implies that its detection probability is <1.0 . If it can be missed in one period it could be missed in both, thereby causing its mother to be misclassified with regard to breeding state. In year 2 the female was sighted only in the second sampling period, but no first-year calf was sighted with her. The female with the second sighting history was seen in both sampling periods of both years. In year 1 no first-year calf was seen with her in either sampling period, but in year 2 a first-year calf was seen with her in both sampling periods. We first describe the probability structure for the within-year part of the model, conditioning on the fact the female was sighted at all in a given year, repeating the capture history followed by the probability associated with it (Table 1). If a first-year calf is seen with its mother in either of the two sampling periods then we assume that she is in state C for that year. Calves were examined as closely as possible to determine age. When there was residual doubt we called it a second-year calf, thus effectively making δ_i^C the probability a first-year calf is detected and correctly identified as first-year. If a first-year calf is not seen with an adult female, then she could be in either state. All of these parameters can be estimated from these within-season sighting histories.

Survival and breeding probabilities are computed from between-year information. For this part of the model the above sighting histories can be pooled, based on whether or not an individual adult female was seen in a given year, and if she was seen whether a first-year calf was seen with her at all (*i.e.*, history CN 0N is pooled into history C N, and history NN CC is pooled into history N C). In Table 2 we describe the probability associated with these histories, conditional on their sighting in year 1. For the second animal the state of "release" is not certain. Each term within the brackets for capture history N C is a product of two probabilities: (1) the probability an animal released in apparent state N' was actually released in state N (π_1) or state

Table 1. Conditional (on being sighted in a given year) probability structures for example within-year sighting histories in a 2-yr study of adult female manatees and their calves.

Year	Sighting history	Probability structure ^a
1	CN	$\alpha_1 p_{11}^C \delta_{11}^C p_{12}^C (1 - \delta_{12}^C) / [\alpha_1 p_{11}^C + (1 - \alpha_1) p_{11}^N]$
	NN	$[\alpha_1 p_{11}^C (1 - \delta_{11}^C) p_{12}^C (1 - \delta_{12}^C) + (1 - \alpha_1) p_{11}^N p_{12}^N] / [\alpha_1 p_{11}^C + (1 - \alpha_1) p_{11}^N]$
2	ON	$[\alpha_2 (1 - p_{21}^C) p_{22}^C (1 - \delta_{22}^C) + (1 - \alpha_2) (1 - p_{21}^N) p_{22}^N] / [\alpha_2 p_2^C + (1 - \alpha_2) p_2^N]$
	CC	$\alpha_2 p_{21}^C \delta_{21}^C p_{22}^C \delta_{22}^C / [\alpha_2 p_2^C + (1 - \alpha_2) p_2^N]$

^a $p_i^C = 1 - \prod_{j=1}^2 (1 - p_{ij}^C)$ and $p_i^N = 1 - \prod_{j=1}^2 (1 - p_{ij}^N)$ are probabilities that an adult female with or without, respectively, a first-year calf in year i is sighted at least once in winter i .

$C(1 - \pi_1)$; and (2) the probability of the observed sighting history, conditional on the actual state of the animal at release.

Besides the assumption of population closure within a winter season, this model also assumes that adult female detection probabilities, survival probabilities, and transition probabilities depend only on the animal's breeding state and either the sampling period (for detection probability) or year. We assume no heterogeneity among individuals in these probabilities. The same assumptions apply to calf detection probability. These are similar assumptions to other multistate capture-recapture models (Brownie *et al.* 1993).

The model structure and assumptions above affected our structuring of sampling periods within each winter season. The goal is to design the study so that, for each sampling period, detection probabilities are approximately equal for each individual. We also assume the entire population of adult females is surveyed in each sampling period. Finally, although not necessary it is advantageous with respect to precision to have $p_{i1}^C \approx p_{i2}^C$, $p_{i1}^N \approx p_{i2}^N$ for each year i . Because we assumed population closure within the winter period, we post-stratified sampling periods in each year for each population to include about the same number of sightings in each sampling period. For the NW this entailed selecting a potentially different date for the entire population in each year. The AC sighting effort was more spread out geographically. Therefore we sorted the data by locality (Brevard County, Port Everglades, Miami, Riviera Beach) and then divided the sighting interval for each locality into the best split for comparable number of sightings between the two sampling periods.

Our global model that accounts for misclassification of adult females is $\{S(b, T), \psi(b, T), p(b, T, t), \delta(T, t), \alpha(T)\}$, which indicates that survival rate and conditional breeding probability of adult females can vary by breeding state (b) and year (T); unconditional breeding probability α can vary by year; detection probabilities for adult females can vary by breeding state, year, and sampling occasion within year (t); and conditional detection probabilities for calves can vary by year and sampling occasion within year. For the NW population we fixed $\psi_i^{CN} = 1$, due to gestation, breeding behavior, and the fact that breeding in two consecutive years has not been observed. Because there were two apparent cases of breeding in consecutive years for the AC population, for this population we estimated ψ_i^{CN} . We ran various restricted

Table 2. Conditional (on being first sighted in year 1) probability structures for example between-year sighting histories in a 2-yr study of adult female manatees and their calves.

Sighting history	Probability structure ^a
CN	$S_1^C(\psi_1^{CC} p_2^{C(1-\delta)} + \psi_1^{CN} p_2^N)$
NC	$[\pi_1 S_1^N \psi_1^{NC} + (1 - \pi_1) S_1^C \psi_1^{CC}] p_2^{C\delta}$

^a $p_i^{C\delta} = 1 - \prod_{j=1}^2 (1 - p_{ij}^C \delta_{ij}^C)$ is probability that adult female is sighted with her first-year calf in year i ; $p_i^{C(1-\delta)} = \prod_{j=1}^2 (1 - p_{ij}^C \delta_{ij}^C) - \prod_{j=1}^2 (1 - p_{ij}^C)$ is probability adult female in state C is sighted in year i , but her calf is not; $\pi_i = (1 - \alpha_i) p_i^N / [\alpha_i p_i^{C(1-\delta)} + (1 - \alpha_i) p_i^N]$ is probability adult female seen apparently without a first-year calf in year i actually had no first-year calf with her.

versions of this model (*i.e.*, constraining parameters to be equal across time, both within and between years, and breeding state), using program MSSURVIVmis (J. Hines, www.mbr-pwrc.usgs.gov/software).

Goodness of fit was assessed using a Pearson Chi-square test after pooling cells whose expected frequencies were < 2 (White 1983). Issues of relative bias and precision across models were balanced based on small-sample Akaike Information Criterion values, adjusted for lack of fit of the most general model (QAICc, Burnham and Anderson 1998). Lack of fit is measured by the goodness of fit test statistic divided by the degrees of freedom, which also provides a factor for inflating estimated variances from the model. We then used QAICc values for each model as weights to average parameter estimates across models (Buckland *et al.* 1997, Burnham and Anderson 1998).

RESULTS

Sparseness in data can make it difficult to fit complex models. In these cases fitting simpler models first is easier, and parameter estimates from these models can provide starting values for fitting more complex models. Despite this approach, the global model identified above was very difficult to fit. Although in theory all parameters in the global model can be estimated, the poor performance of the more general models we did fit (Table 3) indicated the global model would not fare well, so we abandoned that effort.

Normally a goodness of fit test is performed on the global model, providing a basis for model comparison using QAICc and an inflation factor for variances (Burnham and Anderson 1998). Because a more general model should always fit better than a more restrictive one, we based goodness of fit on the best-fitting model. In this case fit was reasonably good even under this conservative approach, with variance inflation factors of 1.90 (NW) and 2.02 (AC).

Figure 1 contains plots of ψ_t under model 15 (Table 3), the most general model we fit. However, the annual variation indicated is not statistically significant based on QAICc. With few exceptions the ranking of models with respect to fit was identical for the Northwest and Atlantic Coast populations. Only models 1–3 received non-negligible weight. For each of these models most parameters were equal over time, with the most glaring exception being detection probabilities for adult females.

Table 3. Comparison of fit for models that account for misclassification of adult female manatees with first-year calves, for the Northwest (NW) and Atlantic Coast (AC) populations, 1982/83–2000/01.

Model #	Model ^c	# Parameters		ΔQAICc^a		Akaike Weight ^b	
		NW	AC	NW	AC	NW	AC
1	$S(\cdot, \cdot), \psi(b, \cdot), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(\cdot)$	23	24	0	0	0.529	0.529
2	$S(b, \cdot), \psi(b, \cdot), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(\cdot)$	24	25	1.42	1.36	0.260	0.268
3	$S(\cdot, \cdot), \psi(b, \cdot), p(\cdot, T, \cdot), \delta(\cdot, t), \alpha(\cdot)$	24	25	1.85	2.03	0.210	0.202
4	$S(\cdot, \cdot), \psi(b, \cdot), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(T)$	41	42	14.6	58.9	<0.001	<0.001
5	$S(\cdot, T), \psi(b, \cdot), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(\cdot)$	40	41	18.4	13.3	<0.001	<0.001
6	$S(\cdot, \cdot), \psi(b, T), p(b, T, \cdot), \delta(\cdot, \cdot), \alpha(\cdot)$	42	43	20.4	22.6	<0.001	<0.001
7	$S(\cdot, \cdot), \psi(b, T), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(\cdot)$	40	41	20.6	23.9	<0.001	<0.001
8	$S(\cdot, \cdot), \psi(b, \cdot), p(b, T, \cdot), \delta(\cdot, t), \alpha(\cdot)$	43	44	22.3	24.6	<0.001	<0.001
9	$S(\cdot, \cdot), \psi(b, \cdot), p(\cdot, T, t), \delta(\cdot, \cdot), \alpha(\cdot)$	42	43	22.5	66.9	<0.001	<0.001
10	$S(\cdot, T), \psi(b, \cdot), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(T)$	58	59	44.6	38.8	<0.001	<0.001
11	$S(\cdot, \cdot), \psi(b, T), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(T)$	58	59	46.2	49.6	<0.001	<0.001
12	$S(b, T), \psi(b, \cdot), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(T)$	58	59	48.6	44.1	<0.001	<0.001
13	$S(\cdot, T), \psi(b, \cdot), p(\cdot, T, t), \delta(\cdot, \cdot), \alpha(\cdot)$	59	60	51.5	46.8	<0.001	<0.001
14	$S(\cdot, \cdot), \psi(b, \cdot), p(b, T, \cdot), \delta(\cdot, t), \alpha(T)$	61	62	53.8	49.4	<0.001	<0.001
15	$S(\cdot, T), \psi(b, T), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(T)$	75	76	67.4	64.6	<0.001	<0.001

^a Based on the following sample sizes (NW: 1250, AC: 2193 releases) and variance inflation factors (NW: 1.9, AC: 2.02).

^b See Buckland *et al.* (1997) and Burnham and Anderson (1998).

^c A “.” in any model indicates a particular effect that was removed by setting parameters equal over time or breeding state (*e.g.*, model $\{S(\cdot, T), \psi(b, T), p(\cdot, T, \cdot), \delta(\cdot, t), \alpha(T)\}$ assumes survival probabilities (S) vary by year (T) but not breeding state (b), conditional breeding probabilities (ψ) vary by breeding state and year, detection probabilities (p) vary by year but not within year (t) or breeding state, and conditional detection probabilities for first-year calves (δ) vary within year but not among years.

Table 4 contains estimates of vital rates after variances were inflated based on lack of fit, and models were averaged based on QAICc weights. Breeding probability was not significantly different for the two populations (*i.e.*, standard error of the difference was 0.07), but the direction of the difference was consistent with our prediction based on differences in habitat quality. Although manatees rarely produce young in two consecutive years, we acknowledged two apparent cases in the AC population by estimating ψ_i^{CC} . Model 2, which includes state-specific survival probabilities ($\hat{S}^C = 0.98$, $\hat{S}^N = 0.95$ for NW; $\hat{S}^C = 0.94$, $\hat{S}^N = 0.95$ for AC) received substantial weight, but differences between states were opposite in sign for each population and were reduced through averaging (Table 4).

Estimates of sighting probability were similar across the three models with non-negligible weight (Fig. 2). The average of these values was 0.41 for NW and 0.34 for AC. Given that an adult female with calf was detected in a given sighting session within season, the estimated probability that its calf was also sighted was $\hat{\delta}_{\cdot\cdot}^C = 0.73$ (SE = 0.06) for NW and $\hat{\delta}_{\cdot\cdot}^C = 0.73$ (SE = 0.06) for AC. This translates into an average probability that a first-year calf is not sighted in an entire season, given that its mother is sighted at least once, of 0.22 (SE = 0.06) for NW and 0.23 (SE = 0.05) for AC, *e.g.*,

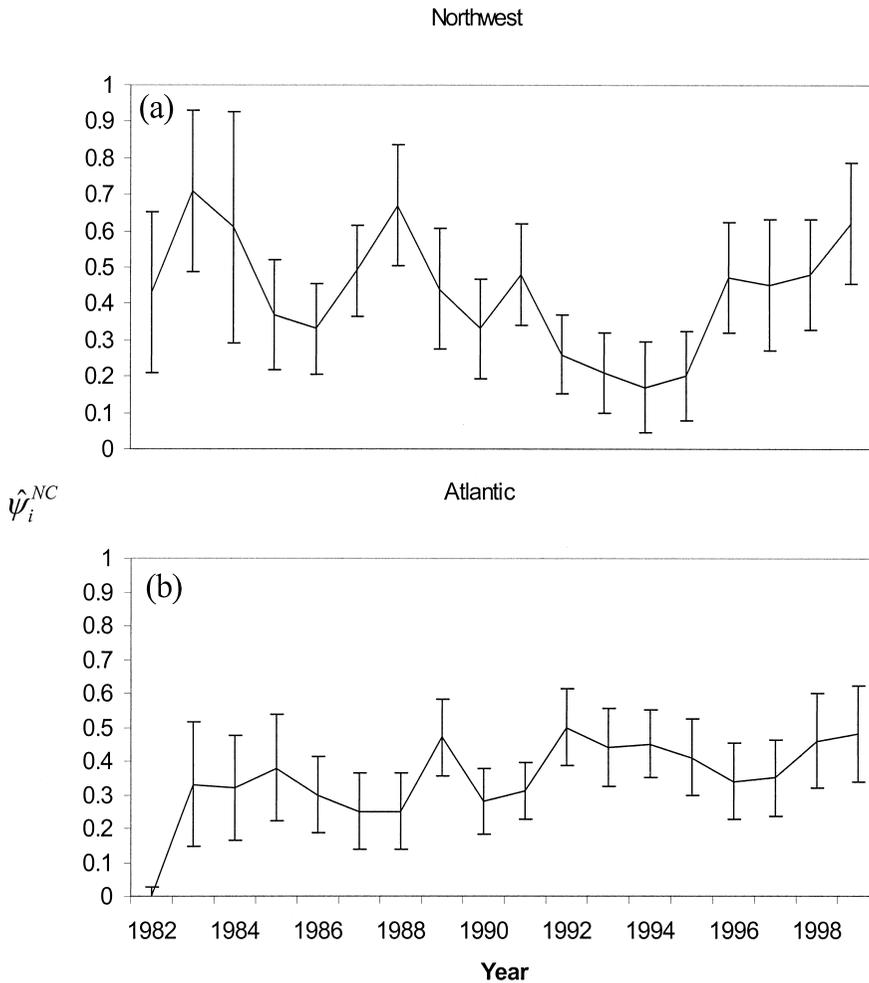


Figure 1. Plots of estimated conditional breeding probabilities ($\psi_i^{NC} \pm 1$ SE) for the Northwest (a) and Atlantic (b) populations of the Florida manatee, 1982–1999, based on model $\{S(\cdot, T), \psi(b, T), p(\cdot, T, \cdot), \delta(\cdot, \cdot), \alpha(T)\}$. Standard errors are inflated based on lack of fit.

$$\frac{p_{i1}(1 - \hat{\delta}_{i1}^C)p_{i2}(1 - \hat{\delta}_{i2}^C) + p_{i1}(1 - \hat{\delta}_{i1}^C)(1 - p_{i2}) + (1 - p_{i1})p_{i2}(1 - \hat{\delta}_{i2}^C)}{1 - (1 - p_{i1})(1 - p_{i2})}$$

$$= \frac{0.41 * 0.27 * 0.41 * 0.27 + 0.41 * 0.27 * 0.59 + 0.59 * 0.41 * 0.27}{(1 - 0.41 * 0.41)}$$

$$= 0.22,$$

with standard error based on the delta method.

The implication of missing calves can be seen by analyzing the same data while ignoring the misclassification problem. Using sightings pooled within year, we used the traditional multistate model in program MARK (Nichols *et al.* 1994, White and Burnham 1999) to produce the following estimates: $\hat{\psi}^{NC} = 0.31$

Table 4. Estimates of conditional breeding probabilities for those without (ψ^{NC}) and with (ψ^{CC}) calf, unconditional breeding probability (α), and survival probability (S) for manatees in the Northwest (NW) and Atlantic Coast (AC) populations, 1982/1983–2000/2001.

Parameter	NW		AC	
	Estimate	SE	Estimate	SE
ψ^{NC}	0.43	0.057	0.38	0.045
ψ^{CC}	0.0 ^a		0.016	0.015
α	0.30	0.032	0.29	0.026
S^C	0.96	0.025	0.94	0.015
S^N	0.95	0.018	0.95	0.012

^a This value fixed due to no data supporting breeding in consecutive years.

(SE = 0.04) for NW and $\hat{\psi}^{NC} = 0.27$ (SE = 0.03) for AC. These estimates are 28% lower than when we accounted for misclassification.

DISCUSSION

Our use of Pollock's robust design (*i.e.*, multiple samples from the entire population within a given winter season) enabled us to account for misclassification rates and their variances. Fujiwara and Caswell (2002) used data from an independent source to account for misclassification in right whales (*Eubalaena glacialis*), which is a valid approach but produces overly precise estimates because it ignores uncertainty in these estimates.

Multistate capture-recapture models include Markovian transitions between states, and therefore lend themselves most naturally to the estimation of conditional breeding probabilities (Nichols *et al.* 1994), as opposed to unconditional breeding probabilities or intercalving intervals (O'Shea and Hartley 1995, Reid *et al.* 1995, Rathbun *et al.* 1995). We would argue that this is the preferable metric in most cases for marine mammals, because it is these transition probabilities that are needed for stage-based projection models (Runge *et al.* 2004). Nevertheless, the use of the robust design also permits the estimation of unconditional breeding probability (α_i), if the entire population of interest is in the study area during the season of sampling, or those with and without calves are equally likely to be absent. The ability to estimate conditional and unconditional breeding probability concurrently could be used to evaluate hypotheses about the relationship between these two parameters (*e.g.*, is the probability a female without a calf this year produces a calf next year dependent on the proportion of the population that produced calves this year?).

Our model estimates survival and breeding probabilities concurrently. If survival probability were dependent on breeding state, misclassification would make this model the most appropriate for inference about survival as well as breeding probability, with the following exception. Kendall *et al.* (1997) found that Markovian temporary emigration from the study area tends to bias survival estimates from traditional capture-recapture models, especially those toward the end of a study. Incorporating Pollock's robust design adjusts for this bias when the emigration process is modeled, but exacerbates the problem if this movement is not modeled. Temporary emigration from the study area has been documented in mark-resighting

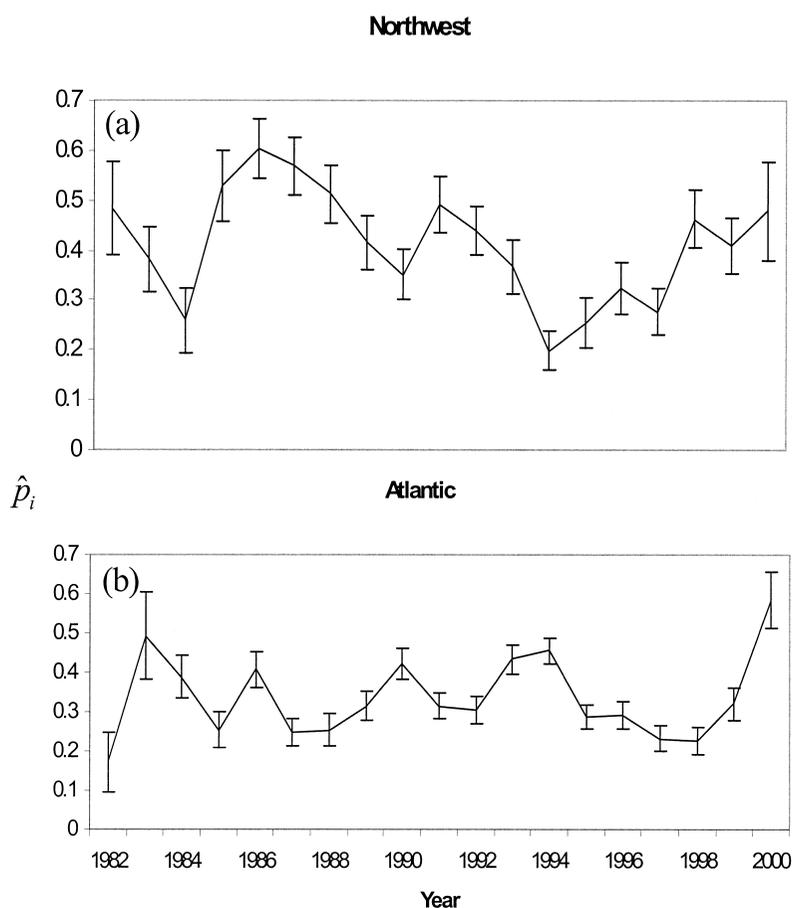


Figure 2. Plots of estimated sighting probability for each sampling period within year i ($\hat{p}_i \pm 1$ SE) for the Northwest (a) and Atlantic (b) populations of the Florida manatee, 1982–2000. These estimates and standard errors are averaged across the first three models in Table 1, weighted by the model weights indicated there. Standard errors are inflated based on lack of fit.

studies of manatees, particularly in warmer winters when cold may not drive individuals into the aggregation sites for “capture” by photographers (Langtimm *et al.* 2004). Because the method we present here does not model temporary emigration, and because we did not find significant differences between states in survival probability, the results in Langtimm *et al.* (2004) should be considered more reliable for estimating annual variation in survival probability. However, we found through simulation that the estimator for breeding probability presented here is robust to temporary emigration.

The estimation model presented in Kendall *et al.* (2003) was also designed for the manatee case. The difference in the models is that their method relies not only on females known to have a first-year calf, but also those observed without a first-year calf that are known to be without a first-year calf (*i.e.*, those that had a first-year calf in the previous year). Our method does not rely on cohorts of those known to have no calf. One would expect that the two methods should produce similar point estimates for

conditional breeding probability, perhaps with different precision. However, when our methods were applied to the data set analyzed in Kendall *et al.* (2003), our estimate of ψ^{NC} was considerably lower than theirs (0.42 *vs.* 0.61, SE = 0.06 *vs.* 0.09). A possible explanation for this discrepancy is that some female manatees are more successful breeders than others. In this case those that had just bred in year $i - 1$ would have a higher than average probability of breeding in year $i + 1$. Currently we do not have the ability to test this hypothesis directly. However, our intent here was to develop parameter estimates for the stage-based model of Runge *et al.* (2004), which treats each female manatee in a given life stage identically. The model used here is more consistent with that approach than the model presented in Kendall *et al.* (2003).

Figure 1 suggests variation in breeding probability over time for both populations, but models including time variation in this parameter got virtually no weight. Our estimate of constant ψ_i^{NC} is useful to building a stage-based population projection matrix (Runge *et al.* 2004), but the large standard errors for ψ_i^{NC} indicates that this result might be due to low statistical power. Others have posed hypotheses for what drives reproduction in manatees, including cold stress (Bossart *et al.* 2002), hurricanes (Langtimm and Beck 2003), and habitat features (O'Shea and Hartley 1995, O'Shea and Langtimm 1995). Given differences between the two regions in the frequency or magnitude of these factors, we might expect different patterns of variability for each regional population. Future model development will permit analyses that consider the effects of these covariates.

In fact the only parameter that varied significantly over time was sighting probability. Variation in detection probability over time is not a surprising result in wildlife studies, and reinforces the importance of collecting data in such a way that such parameters can be estimated (*i.e.*, it is risky to rely on the assumption that detection probability is constant, or even randomly varying, over time or space).

The specific results of our analysis could provide a benchmark for studies of other sirenian populations, although we know of no attempts to estimate breeding probability for other sirenian subspecies or species. We anticipate the specific model developed here or a similar approach could be used to estimate vital rates for other marine mammals. Breeding status for cetaceans is often assigned by association with first-year calves (*e.g.*, Barlow and Clapham 1997), with likely similar risk of non-detection of the calf. A variation on our approach could be useful in the study of assemblages of pinnipeds, to study the vital rates of pups too young to be marked and therefore identified through association with their marked mothers.

Although the population growth rate of long-lived animals is less sensitive to breeding probability than to adult survival rate, bias in the estimates of any parameter can undermine the ability to understand and predict this growth rate. This is especially true if estimates of several less sensitive parameters are biased, and these biases are compounded. Therefore studies should be designed to produce estimates of parameters that are as accurate as possible. These studies should include the use of marked animals, to permit the estimation of breeding probabilities in the face of imperfect detection of adult females, and the robust design (multiple sampling periods per year so that each adult female is exposed to sighting effort at least twice within a season), to permit adjustment for misclassification of breeding state.

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