

A STAGE-BASED MODEL OF MANATEE POPULATION DYNAMICS

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ABSTRACT

A stage-structured population model for the Florida manatee (*Trichechus manatus latirostris*) was developed that explicitly incorporates uncertainty in parameter estimates. The growth rates calculated with this model reflect the status of the regional populations over the most recent 10-yr period. The Northwest and Upper St. Johns River regions have growth rates (λ) of 1.037 (95% interval, 1.016–1.056) and 1.062 (1.037–1.081), respectively. The Southwest region has a growth rate of 0.989 (0.946–1.024), suggesting this population has been declining at about 1.1% per year. The estimated growth rate in the Atlantic region is 1.010 (0.988–1.029), but there is some uncertainty about whether adult survival rates have been constant over the last 10 yr; using the mean survival rates from the most recent 5-yr period, the estimated growth rate in this region is 0.970 (0.938–0.998). Elasticity analysis indicates that the most effective management actions should seek to increase adult survival rates. Decomposition of the uncertainty in the growth rates indicates that uncertainty about population status can best be reduced through increased monitoring of adult survival rate.

Key words: stage-structured population model, Florida manatee, *Trichechus manatus latirostris*, uncertainty, elasticity, variance decomposition, recovery criteria, forecasting.

The Florida manatee (*Trichechus manatus latirostris*) is an endangered marine mammal endemic to the southeastern United States (Lefebvre *et al.* 2001). The primary threats to manatee populations are collisions with watercraft, the future of warm-water refuges, and coastal development (USFWS 2001). The recovery criteria for downlisting the Florida manatee to threatened under the Endangered Species

Act (ESA) include removal of threats to manatee habitat, establishment of adequate regulatory mechanisms for protection of manatees, and achievement of quantitative demographic criteria. These quantitative criteria are stated in terms of integrated life-history parameters (survival, recruitment, and population growth rate) rather than population size (USFWS 2001), because of concern over methodological difficulties in monitoring population size (Lefebvre *et al.* 1995). Thus, assessing whether manatees have met the demographic criteria for recovery requires a population model to integrate the life-history parameters estimated from monitoring programs. Other manatee management activities also require a population model to evaluate the potential effects of alternative actions. For instance, the determination of negligible impact of incidental take of manatees by watercraft-related activities requires a population model for evaluation (USFWS 2002). The purpose of this paper is to develop a demographic model for Florida manatee population dynamics, to use this model to integrate recent estimates of population parameters, and to suggest ways this modeling effort could be extended for other purposes.

Formal quantitative modeling has assumed a central role in assessment and management of marine mammal populations. As this body of theory and applications grows, we gain general insights about the population dynamics of large mammals and how to manage them. There are several open questions about the uses of and conclusions from population models in the management of marine mammals that are evident in the manatee work described herein. First, which life-history parameters have the greatest potential to affect population growth? The methods for answering this question (sensitivity and elasticity analysis, Caswell 2001) are well developed, and for large mammals, we also know the answer: adult survival rate is the critical determinant of population growth rate (*e.g.*, Eberhardt and Siniff 1977). This implies that adult survival rate is the most important target for management and for monitoring. Second, how does imprecision in the estimation of life-history parameters affect uncertainty about growth rate? Again, the methods for answering this question (variance decomposition, Caswell 2001) are well developed, although general conclusions are not as readily available. Because adult survival has the greatest potential impact on growth rate, it is also important to have precise measures of it, but the question of how to allocate monitoring effort for a range of life-history parameters will depend on the specific life-history as well as the status of past monitoring efforts. Third, there is increasing recognition of the importance of integrated model development and parameter estimation (*e.g.*, Brault and Caswell 1993, Fujiwara and Caswell 2002). Parameter estimation needs to reflect the modeling context in which the parameters will be used, and model construction is often constrained by which parameters can be rigorously estimated. That is, statistical estimation of parameters and population model development cannot successfully be undertaken separately. Because estimability of parameters depends heavily on how data are collected (see Kendall *et al.* 2004, Langtimm *et al.* 2004), study design also needs to be integrated with model development and parameter estimation. Fourth, how should models be used for assessment purposes? How do the assessment criteria, the models, and the field methods used to generate data relate? As models take a more central role in assessment of population status, the importance of integrating objectives, models, and monitoring emerges. Fifth, what additional structure and information is needed to build a model for use in forecasting from a model used for assessment? This paper explores these five issues in the context of the Florida manatee, but the use of population models for marine mammal assessment and management is the general backdrop.

There have been three published models for Florida manatee population dynamics (Packard 1985, Eberhardt and O'Shea 1995, Marmontel *et al.* 1997). Packard (1985) constructed a deterministic, age-structured model of manatee dynamics, and used it to obtain a preliminary understanding of potential population growth rates, as well as to identify the most important uncertainties in parameter estimates. At that time, there were few robust estimates for any life-history parameters, and Packard (1985) emphasized the need for expanded monitoring programs, particularly for adult survival rate.

Eberhardt and O'Shea (1995) constructed a simple Lotka model (Lotka 1907) for manatee population dynamics. Again, this was a deterministic age-structured model, with the age-specific information collapsed into two age-classes, greatly reducing the number of parameters required. They built models for three of the four regional subpopulations identified as management units in the Recovery Plan (Northwest, Upper St. Johns River, and Atlantic), and found growth rates (λ) that varied between 1.01 and 1.07. Analysis of their model showed that growth rate was most sensitive to adult survival rate, and that uncertainty in the adult survival rate contributed the most to uncertainty in the growth rate. Thus, increasing adult survival rate was important for recovery, and better monitoring of adult survival rate was important for improving assessment. The Eberhardt and O'Shea (1995) model was the basis for the quantitative demographic recovery criteria in the Manatee Recovery Plan (USFWS 2001).

Marmontel *et al.* (1997) constructed a stochastic, age-structured model of manatee population dynamics, relying on available software (VORTEX) for simulation and population viability analysis. Their model included environmental stochasticity, in the forms of both variation of life-history parameters and inclusion of catastrophes, but it is not clear if they included demographic stochasticity. Marmontel *et al.* (1997) dealt with model and parameter uncertainty in an *ad hoc* manner by running a number of different scenarios. The population growth rate estimates from Marmontel *et al.* (1997) are all very close to $\lambda = 1.0$, but were incorrectly derived. Marmontel *et al.* (1997) used adult survival estimates based on age-at-death data from recovered carcasses (Marmontel 1993, 1995), but the method they used requires the assumptions of a stable age-distribution and a population growth rate (λ) of 1.0. Thus, their observation of a growth rate of 1.0 is tautological. However, some specific results, like sensitivity, are not greatly affected by this error. As in the previous models, Marmontel *et al.* (1997) showed that adult survival rate has a profound effect on growth rate and other measures of population viability.

The model proposed in this paper extends past modeling efforts, while attempting to strengthen several aspects of estimation and model structure. First, the parameters of the previous models were estimated with data that increased in quality as time went by, but all three sets of authors acknowledged the deficiencies of the data sets. In this paper, the approach is most similar to that of Eberhardt and O'Shea (1995), in using parameters estimated from individual life-histories of live animals. An additional decade of data is now available to aid in this estimation. Second, all three previous models treated adult females as a homogeneous group, and used measures of fecundity that incorporated the physiological constraints on the interbirth interval implicitly, but not explicitly. In this paper, the minimum interbirth interval is built into the structure of the model. Third, Packard (1985) and Marmontel *et al.* (1997) dealt with parametric uncertainty by running several scenarios with values for parameters that bracketed the potential range of values.

The difficulty with this approach is that there are separate results for each scenario, with no guidance for how to integrate them into a single conclusion. Instead, uncertainty in parameter values can be built directly into simulations by sampling each parameter from a distribution that represents the current knowledge about that parameter. This is the approach that Eberhardt and O'Shea (1995) took to decompose the variance (uncertainty) in growth rate into contributions from uncertainty in the underlying life-history parameters. A similar approach is used in this paper, with explicit distributions provided for the uncertainty about each parameter. Fourth, all three previous models assumed a fixed age at first reproduction (sexual maturity at ~ 3.5 yr of age, first potential parturition at ~ 4.5 yr). For some life histories, age at first reproduction can strongly affect growth rates (Cole 1954), and differences in age at first reproduction have been shown to explain differences in growth rate in some species (Levin *et al.* 1996, Oli and Zinner 2001). While the effect of age at first reproduction on growth rate is typically not strong in large, long-lived mammals, it may be more important in populations that have adult survival rates depressed due to human impacts. Eberhardt and O'Shea (1995) suggested their model could be developed to allow initial reproduction to be spread over several age classes in order to reflect field observations and anatomical studies of manatees. The stage-based model described below contains a prereproductive adult class; the rate of transition out of this class serves to adjust the age at first reproduction.

The objectives of this paper are to present a stage-based population model structure that describes the critical elements of manatee life-history, to analyze the resulting region-specific models, with particular emphasis on decomposing uncertainty in the growth rate into contributions from uncertainty in the underlying parameters, and to explore the consequences of this analysis for management and monitoring of manatee populations. Although we estimate the current growth rates of the manatee populations in four regions of Florida, this is *not* an attempt to forecast growth rates. Population viability analysis is often used to calculate the probabilities of different fates of a population by forecasting its future growth. To do this requires incorporating reasonable forecasts of the forces that affect the population. The model presented herein can be used as the central structure of a model for such forecasting, and is described in enough detail to allow the necessary extensions to be implemented easily.

Model Structure

The model (Fig. 1) is a stage-based description of female manatee population dynamics on an annual cycle from winter to winter. The model centers on females because their survival and reproduction directly control population growth. Manatees have a promiscuous mating system. A single male can inseminate multiple females (Hartman 1979); therefore males do not directly limit population growth. The manatee population is broken into seven classes of females.

First-year calves (0.5-yr-old)—Manatee population monitoring focuses on the winter aggregation sites. Calves, however, are born during the spring and summer (Marmontel 1995, Rathbun *et al.* 1995, O'Shea and Hartley 1995, Reid *et al.* 1995). The first reliable data on reproduction is collected when a female with a dependent nursing calf returns to the winter aggregations in fall and winter. Calves are ca. 3–9 mo old at this time. Thus a first-year calf represents successful

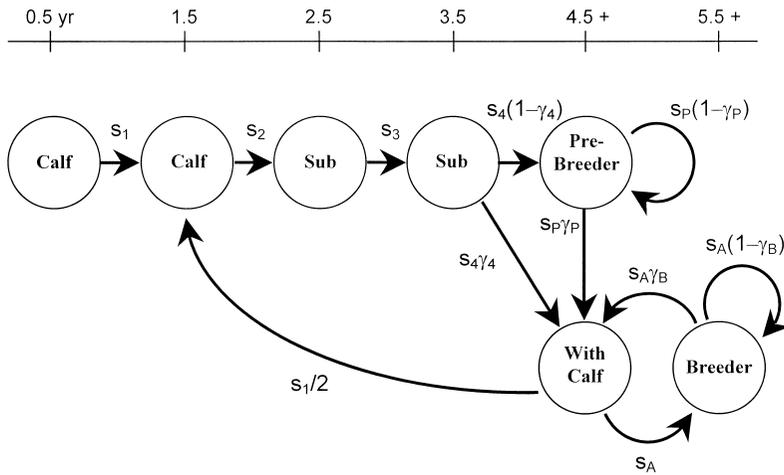


Figure 1. Life-history diagram for the stage-based model. The arrows govern transitions between the classes as a result of survival and reproductive events. In the matrix formulation, first-year calves are not tracked separately, but are inferred from the number of females with calves.

pregnancy, birth, and survival to about age 0.5. There currently are no reliable means to monitor pregnancy or births in the wild (Rathbun *et al.* 1995).

Second-year calves (1.5-yr-old)—Data on second-year calves (denoted as age-class 2) are collected the following year at the aggregation site. Second year calves are primarily identified by size—they are larger than first-year calves, but smaller than subadults. They may or may not be weaned and independent of their mothers. There is considerable variation among individuals as to whether a calf will nurse for one or two years (Rathbun *et al.* 1995, O’Shea and Hartley 1995, Reid *et al.* 1995).

Third-year subadults (2.5-yr-old, age class 3)—At three years of age, individuals are independent but only rarely sexually mature and capable of reproducing (Marmontel 1995, O’Shea and Hartley 1995).

Fourth-year subadults (3.5-yr-old, age class 4) and prebreeders (≥ 4.5 -yr-old, state P)—Prebreeders are individuals 4.5 yr old or older that have not yet successfully reproduced. This model assumes that the earliest a female can breed is in her fourth year (at age ~ 3.5 yr), thus, the earliest possible first appearance with a calf is at age 4.5 yr. Based on winter observations, the earliest that a female manatee has been observed with a dependent calf is four winters after she herself was observed as a new calf, that is, at about 4.5 yr (Rathbun *et al.* 1995, O’Shea and Hartley 1995). However there is considerable individual variation in the age of first successful reproduction (Marmontel 1995, O’Shea and Hartley 1995); this is reflected in females that remain in the prebreeder class for some time.

Adults with first-year calves (denoted as state C) and breeders (state B)—Sexually mature females that are accompanied by a dependent first-year calf, or that have previously produced a calf are classified as “with a 1st-yr calf” or as a “breeder,” respectively. Mature females accompanied by a not-yet-weaned second-yr calf are considered “breeders,” since the attendant calf was not born during the current year. It would be possible to extend this model to include additional classes of “resting” breeders in order to accommodate the effect of time since last birth on breeding

probability (Barlow and Clapham 1997), but in the interests of parsimony and parameter estimation, we have not yet pursued that extension.

It is uncertain if senescence occurs in manatees, due to the small sample of old animals observed (Marmontel 1995). Previous modeling efforts have truncated population dynamics at 40–50 yr, reflecting the assumption that manatees either become reproductively inactive or have higher mortality rates beyond that age (Packard 1985, Eberhardt and O’Shea 1995, Marmontel *et al.* 1997). However, in analyses not included here, we have demonstrated that the effects of such truncation on the dynamics of this model are minuscule, because such a small fraction of the population reaches the truncation point. Thus, for purposes of conciseness, we have neither truncated the population dynamics nor included a postreproductive class in the model.

Two types of life-history parameters describe the transitions between the classes in the model: survival rates (s) and breeding rates (γ). For instance, s_1 is the probability a first-year calf survives to become a second-year calf; γ_P is the probability that an adult female that has not yet given birth to a calf, breeds and successfully gives birth within the next year, given survival until that time. Prebreeders that survive either give birth to a calf (with probability γ_P) or remain as prebreeders. Females with a first-year calf that survive become breeders the next year (with probability = 1.0), regardless of whether they wean the calf after the first year. That is, the model does not allow females to have calves two years in a row—this constraint reflects the physiological limitations imposed by the length of pregnancy (12–13 mo, Rathbun *et al.* 1995, O’Shea and Hartley 1995, Reid *et al.* 1995) and early dependence of the calf. Breeders (without calves) that survive to the next year either give birth to a calf (with probability γ_B) or remain as breeders. A female with a first-year calf gives rise to a second-year calf (weaned or not weaned) in the next year with probability $s_1/2$, reflecting the probability of calf survival and an even primary sex ratio (recall this is a model for the female segment of the population, and only half the calves are expected to be female). The litter size is assumed to be one calf. While twinning is possible in nature, it is negligibly rare (Marmontel 1995, Rathbun *et al.* 1995, O’Shea and Hartley 1995).

This life history diagram (Fig. 1) can be expressed in matrix form as:

$$\begin{bmatrix} N_2 \\ N_3 \\ N_4 \\ N_P \\ N_C \\ N_B \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & 0 & 0 & 0 & \frac{1}{2}s_1 & 0 \\ s_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & s_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & s_4(1 - \gamma_A) & s_P(1 - \gamma_P) & 0 & 0 \\ 0 & 0 & s_4\gamma_A & s_P\gamma_P & 0 & s_A\gamma_B \\ 0 & 0 & 0 & 0 & s_A & s_A(1 - \gamma_B) \end{bmatrix} \begin{bmatrix} N_2 \\ N_3 \\ N_4 \\ N_P \\ N_C \\ N_B \end{bmatrix}_t \quad (1)$$

where the N_i represent the number of manatees in class i at a given point in time. In the matrix formulation, first-year calves are not counted separately, as they are assumed to be dependent on their mothers, although their numbers can be inferred from the number of females with calves (N_C). New births first appear in the population model as second-year calves. The total female population size at time t can be calculated as:

$$N_{Total} = N_2 + N_3 + N_4 + N_P + 1.5N_C + N_B \quad (2)$$

where the number of females with first-year calves is multiplied by 1.5 to include both the mothers and their *female* calves in the total.

Environmental stochasticity—Variation in life-history parameters (survival and reproductive rates) due to uncontrolled factors in the environment is called environmental stochasticity. Manatees experience environmental stochasticity due to a number of factors, for example, red tide (O’Shea *et al.* 1991, Bossart *et al.* 1998), severe cold (Buergelt *et al.* 1984), and hurricanes (Langtimm and Beck 2003). Although the results in this paper do not incorporate environmental stochasticity, the model presented above can be extended to include it, by allowing the life-history parameters to vary. One way to do this is to use an aggregate measure of variation for each life-history parameter, rather than treating specific sources of variation separately. With such an approach, catastrophes are not distinguished from “normal” variation. The advantage is that parameter estimation is easier—the time series of observations used to estimate survival and reproduction include years when these factors were operating, and so the estimated life-history parameters integrate stochasticity from all sources.

Environmental stochasticity can be represented by probability distributions for the annual values for the life-history parameters. All of the parameters in the model are probabilities (survival probabilities, s ; breeding probabilities, γ) and thus must be in the interval $[0,1]$. Given this restriction, the beta distribution is a natural choice for modeling variation in these parameters.

Specification of the beta distribution for each life-history parameter requires a mean value, μ , and a concentration parameter, θ . The concentration parameter reflects how “tight” the distribution is—a larger value of θ results in narrower probability distribution, hence a smaller variance (the variance of the beta distribution is given by $\mu(1 - \mu)/(\theta + 1)$). The year-specific values for each life-history parameter would then be sampled from the appropriate beta distribution. Thus, the first-year calf survival rate in year t would have the distribution

$$s_{1,t} \sim \text{beta}(\mu_{s_1}, \theta_{s_1}). \quad (3)$$

When the model described above is extended to include environmental stochasticity, it will be important to consider the temporal correlation among the life-history parameters, as this correlation can strongly affect the model dynamics (Tuljapurkar 1982). Unfortunately, no analysis of manatee life-history parameters has yet examined such correlations. One useful way to start would be to assume that the survival rates are all driven by the same environmental factors and are perfectly correlated. Strong positive correlation is a conservative assumption, as it will tend to increase the variance in the growth rate, and decrease its mean. Likewise, it would be conservative to assume the breeding probabilities are perfectly correlated with each other. Some thought will need to be given to how to handle the correlation between the group of survival rates and the group of breeding probabilities.

Demographic stochasticity—An additional form of variation, demographic stochasticity, arises because each individual animal experiences its fate independently. That is, while an expected value for a survival or breeding rate applies to a group of animals, the realized rate depends on the random outcomes experienced by the individuals, and may differ from the expected rate. The model used to generate the results in this paper does not include demographic stochasticity, but could be easily extended to do so. Since all the life-history parameters in the model are probabilities with binary outcomes (survive *vs.* not-survive, breed *vs.* not-breed), an appropriate distribution for the demographic

stochasticity is the binomial distribution. Thus, for each class in the population model, the number that survives or breeds is drawn from a binomial distribution with success probability equal to the year-specific value for the appropriate life-history parameter. Because demographic stochasticity represents the application of life-history parameters to individuals, it is calculated independently for each class in the model (this is equivalent to calculating it independently for each individual in the population).

The sex ratio in the first-year calves is assumed to be 0.50. There is no evidence of a skewed primary sex ratio or differential neonatal survival by sex (O'Shea and Hartley 1995, Reid *et al.* 1995). The number of first-year calves is determined by the number of females with calves. To include demographic stochasticity, the number of *female* first-year calves can be sampled from a binomial distribution with success probability 0.50.

Uncertainty—Confidence intervals express uncertainty about the true values for each life-history parameter. The point estimates and confidence intervals for each parameter were used to find independent logit-normal distributions to characterize the uncertainty. That is, the logit of each parameter,

$$\ln\left(\frac{p_i}{1-p_i}\right) \quad (4)$$

was normally distributed with a mean and variance chosen to match the appropriate point estimate and approximate confidence interval.

METHODS

Parameter Estimation

For a deterministic analysis, the model described above requires estimates for nine parameters: six survival rates ($s_1, s_2, s_3, s_4, s_B,$ and s_A , where s_A applies to both breeders and females with calves, *i.e.*, stages B and C); and three breeding probabilities ($\gamma_A, \gamma_B,$ and γ_C). To incorporate uncertainty associated with parameter estimation, a confidence interval for each of those parameter estimates is also needed. To incorporate environmental stochasticity (with uncertainty), estimates and confidence intervals are also needed for the nine θ 's (the concentration parameters for the nine life-history rates). No additional parameters are required to describe demographic stochasticity. As previously noted, environmental and demographic stochasticity are not included in the analyses described below. Thus, estimates for the concentration parameters are not required. Estimates, with confidence intervals reflecting sampling variation, were obtained for the nine parameters in each of the four regions. Where possible, parameters estimates were taken from analyses that separated temporal and sampling variation, and the confidence intervals expressed only the latter.

Direct estimates of adult survival (s_A and s_P) for all four regions were taken from Langtimm *et al.* (2004). These estimates were derived from maximum likelihood mark-recapture analyses of photo-ID data, accounting for temporal variance, with the mean survival rate found for a recent 10-yr period. Direct estimates of survival of younger age classes (s_1, s_2, s_3, s_4) were available for the Upper St. Johns River region, based on analysis of capture histories of known-age animals (Langtimm *et al.* 2004). The estimation by Langtimm *et al.* (2004) was undertaken in coordination with the development of this population model, thus the parameters were estimated in the appropriate context for use in the model.

Direct estimates were not available for the remaining survival rates (of younger age classes in the Northwest, Southwest, and Atlantic regions). To obtain indirect estimates for those rates, the following assumptions were used: (1) subadult survival rates (s_3 and s_4) are identical to adult survival rates in the same region, based on evidence in the Upper St. Johns River region (O'Shea and Hartley 1995, Langtimm *et al.* 2004); (2) calf survival rates (s_1 and s_2) are lower than adult survival rates in the same proportion in all regions (this same assumption was used by Eberhardt and O'Shea [1995] and FMRI [2002]); (3) the confidence intervals for the subadult survival rates are the same as those for the adult survival rates in the same region; and (4) the confidence intervals for the calf survival rates in the other regions are 50% larger than the confidence intervals for the calf survival rates in the Upper St. Johns River region (as measured by the standard deviation on the logit scale), to reflect uncertainty about the ratio of calf to adult survival rate.

Direct estimates of adult breeding probability (γ_B) were obtained for the Northwest and Atlantic regions using the maximum likelihood methods of Kendall *et al.* (2004). These are direct estimates of the transition probability from "breeder" to "with calf," taking into account both detection probability and misclassification of reproductive state. The transition structure for breeders used by Kendall *et al.* (2004) was motivated by the population model presented herein, thus, adult breeding probability was estimated in exactly the same context in which it was used in the model.

For the Northwest region, the remaining two breeding probabilities (γ_4 and γ_P) were estimated from observations of the reproductive status of known-age females,¹ using methods for calculating the estimate and exact confidence interval for a binomial proportion from the numbers of successes and trials. The same method was used for all three breeding probabilities in the Upper St. Johns River region, based on observations of known-age females.²

Direct estimates of two of the breeding probabilities (γ_P and γ_B) for the Southwest region were based on a reexamination of the reproductive histories of marked animals in Sarasota Bay (Koelsch 2001). As above, the breeding rates were treated as binomial proportions, and estimated as such.

No direct estimates were available for three of the breeding probabilities (γ_4 in the Southwest region; γ_4 and γ_P in the Atlantic region). Estimates and confidence intervals were inferred by comparison with the rates in other regions (see Results).

As noted above (under Model Structure), the uncertainty for each parameter was assumed to follow a logit-normal distribution. The parameters of this distribution (mean and standard deviation on the logit scale) were estimated from the desired mean and standard deviation on the nominal scale, using the first-order estimates in equations (18) and (19) of Runge and Moen (1998).

Matrix Analysis and Simulation

Distributions for the uncertainty in the growth rate (λ) of the population in each region were found through Monte Carlo simulation. For each of 10,000 replicates, independent values for seven parameters were generated using the logit-normal

¹ Personal communication to CAL from C. A. Beck, U.S. Geological Survey Sirenia Project, Florida, 7 March 2002.

² Personal communication to CAL from W. C. Hartley, Florida Department of Environmental Protection, 21 March 2002.

distribution (s_3 and s_4 were constrained to be equal; s_P and s_A were also constrained to be equal). These parameters were inserted into equation 1, and the dominant eigenvalue (λ) of the transition matrix was found (Caswell 2001). The distribution of the 10,000 estimates of λ was used to characterize the uncertainty in the growth rate for each region.

The variance in λ was decomposed into contributions from the variances in the parameters by using a random-design life-table response experiment (Caswell 2001). The realized values of λ and the values of the parameters from the simulations described above were used as the sources of information for this variance decomposition.

Stable stage-distributions (left eigenvectors), eigenvalue sensitivities, and eigenvalue elasticities (Caswell 2001) were found by analyzing the region-specific transition matrices formed from the point estimates of the parameters. A contour plot of λ , as a function of adult survival (s_A) and breeding probability (γ_B), was formed by systematically varying those two parameters and finding the dominant eigenvalue, while holding the other parameters constant. All simulations and analyses were performed with MATLAB.

RESULTS

Parameter Estimates

All of the survival rate estimates come from combined analyses of male and female manatees, but previous studies have shown that survival rates do not differ by sex (Langtimm *et al.* 1998). Adult survival rates were highest in the Upper St. Johns River and Northwest regions and lowest in the Southwest region (Table 1). In the Atlantic region, Langtimm *et al.* (2004) found some equivocal evidence for a declining trend in survival over the past 10 yr; thus, both the 10-yr and 5-yr mean survival rates are reported (Table 1). In the Upper St. Johns River region, subadult survival rates (s_3 and s_4) do not differ from adult survival rates (s_A) (O'Shea and Hartley 1995, Langtimm *et al.* 2004). Presumably, the prebreeder survival rate (s_P) also does not differ from the adult survival rate. These patterns have been applied to the estimates in Table 1. Direct estimates of calf survival rates (s_1 and s_2) are available only from the Upper St. Johns River region. The pattern in calf survival rate among regions is assumed to follow the pattern of adult survival rates.

In the Northwest region, reproductive histories were available for 16 females of known-age (1977–2000),¹ but not every female was observed every year, so care has to be taken to infer breeding rates. Of 11 females observed at age 4.5 yr, none were with a dependent calf. This suggests an estimate for γ_4 of 0.0 (exact 95% binomial confidence interval, 0.0–0.29). In 13 nulliparous older females (≥ 5.5 yr), 8 calves were produced in 21 yearly observations, leading to an estimate for γ_P of 0.381 (exact 95% binomial confidence interval, 0.18–0.62). The estimate for γ_B was obtained from Kendall *et al.* (2004).

In the Upper St. Johns River region, reproductive histories were available for 35 females of known age (1980–2000),² but again, not every female was observed every year. Of 24 females observed at age 4.5 yr, five were with a dependent calf (their first), thus, γ_4 is estimated to be 0.208 (95% CI, 0.071–0.422). For older females, of 26 observations of females who were known not to have had a calf previously, 17 produced a calf (thus, $\hat{\gamma}_P = 0.654$, 95% CI, 0.443–0.828). There was no effect of age on this breeding rate ($\chi^2 = 1.495$, $df = 2$, $P = 0.47$). There were 69 observations

Table 1. Life-history parameter estimates for Florida manatees in the four regions. Values in bold are direct estimates of the appropriate parameter from published studies or recent analyses. Values in roman type are inferred. The "uncertainty" column represents a range of potential values for each parameter; in general, this is the 95% confidence interval for the parameter estimate.

Parameter	Northwest		Upper St. Johns		Southwest		Atlantic ^a	
	Estimate	Uncertainty	Estimate	Uncertainty	Estimate	Uncertainty	Estimate	Uncertainty
s_1	0.81	(0.67, 0.90)	0.81	(0.73, 0.87)	0.77	(0.62, 0.87)	0.79	(0.65, 0.89)
s_2	0.91	(0.75, 0.97)	0.92	(0.83, 0.96)	0.86	(0.65, 0.96)	0.89	(0.71, 0.97)
s_3	0.96	(0.94, 0.97)	0.96	(0.92, 0.98)	0.91	(0.87, 0.94)	0.94	(0.92, 0.95)
s_4	0.96	(0.94, 0.97)	0.96	(0.92, 0.98)	0.91	(0.87, 0.94)	0.94	(0.92, 0.95)
s_P	0.96	(0.94, 0.97)	0.96	(0.94, 0.98)	0.91	(0.87, 0.94)	0.94	(0.92, 0.95)
s_A	0.96	(0.94, 0.97)	0.96	(0.94, 0.98)	0.91	(0.87, 0.94)	0.94	(0.92, 0.95)
γ_4	0.00	(0.00, 0.29)	0.21	(0.07, 0.42)	0.0	(0.0, 0.3)	0.0	(0.0, 0.3)
γ_P	0.38	(0.18, 0.62)	0.61	(0.51, 0.71)	0.30	(0.13, 0.53)	0.30	(0.13, 0.53)
γ_B	0.43	(0.22, 0.54)	0.61	(0.51, 0.71)	0.60	(0.42, 0.75)	0.38	(0.29, 0.47)

^a The survival rates shown are based on the mean for 1990–1999. The corresponding survival rates for a 5-yr mean (1995–1999) in the Atlantic region are: $s_1 = 0.76$ (0.61–0.87); $s_2 = 0.86$ (0.64–0.95); $s_3 = s_4 = s_P = 0.90$ (0.87–0.93).

Table 2. Logit-normal distributions used to represent uncertainty in the simulations. The parameters given are the mean (and standard deviation) on the logit-scale. Normal random variables were generated on this scale, and then back-transformed to the nominal scale. These values were chosen to closely match the means and confidence intervals shown in Table 1.

Parameter	Northwest	Upper St. Johns	Southwest	Atlantic ^a
s_1	1.43 (0.36)	1.45 (0.24)	1.18 (0.36)	1.33 (0.36)
s_2	2.33 (0.62)	2.38 (0.42)	1.85 (0.62)	2.12 (0.62)
$s_3 = s_4$	3.07 (0.16)	3.17 (0.29)	2.26 (0.23)	2.69 (0.13)
$s_A = s_P$	3.07 (0.16)	3.17 (0.29)	2.26 (0.23)	2.69 (0.13)
γ_4	-6.91 (3.06)	-1.34 (0.50)	-6.91 (3.06)	-6.91 (3.06)
γ_P	-0.49 (0.45)	0.45 (0.21)	-0.83 (0.45)	-0.83 (0.45)
γ_B	-0.29 (0.23)	0.45 (0.21)	0.39 (0.34)	-0.49 (0.19)

^a The corresponding values for the 5-yr mean scenario for the Atlantic region are: s_1 , 1.15 (0.36); s_2 , 1.80 (0.62); $s_3 = s_4$, $s_A = s_P$, 2.20 (0.16). The reproductive rates are the same under both scenarios.

of females that had previously produced a calf but not in the preceding year; of these, 41 had first-year calves in the current year (thus, $\hat{\gamma}_B = 0.594$, 95% CI, 0.469–0.711). This rate (γ_B), however, was not statistically significantly different than the rate for mature females who had not previously bred (γ_B , $\chi^2 = 0.283$, $df = 1$, $P = 0.595$). The combined estimate for these two breeding rates is 0.611 (58 calves from 95 opportunities, 95% CI, 0.505–0.709).

In the Southwest region, Koelsch (2001) gathered partial reproductive histories for 54 females between 1993 and 1997. These were not known-age females, so γ_4 could not be estimated. Since these were partial histories of unknown-age females, it was not possible to reliably identify prebreeders (since they could have bred before Koelsch first observed them). There were 23 observations of adult females not known to have previously produced a calf; of these, seven had a first-year dependent calf in the year of observation. This produces an estimate for γ_P of 0.304 (95% CI, 0.132–0.529), which might be biased high if some of those females had actually bred previously. Of the 37 observations of females that were known to have bred previously, but not in the preceding year, 22 were with a first-year calf ($\hat{\gamma}_B = 0.595$, 95% CI, 0.421–0.752). These two breeding rates are significantly different ($\chi^2 = 4.785$, $df = 1$, $P = 0.029$). The reproductive rate of four-year-old subadults (γ_4) was assumed to be 0, since there was no evidence of reproduction at that age even in the Northwest region, which is relatively more protected than the Southwest. The confidence interval for this rate, however, is wide enough to admit the possibility that it could be as high as the observed subadult reproductive rate in the Upper St. Johns River region.

In the Atlantic region, γ_B was estimated using the methods of Kendall *et al.* (2004). No data are available at this time to estimate γ_4 or γ_P for this region. Values for these parameters were taken from the Southwest region, because these are the most conservative estimates available, and because the Southwest and Atlantic regions are more similar than the other two regions, with regard to the threats manatees face.

The parameters for the logit-normal distributions expressing uncertainty in the life-history parameters are shown in Table 2. Because the logit transform is not defined for $p_i = 0$, a small value of γ_4 (0.001) was chosen as the desired mean for the three relevant regions.

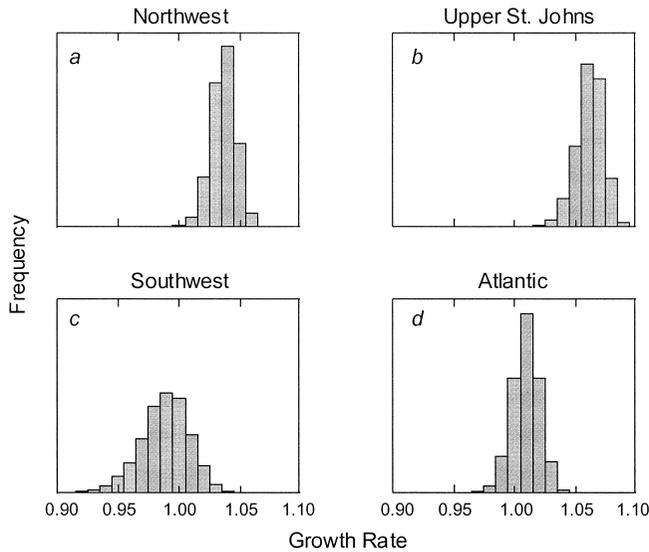


Figure 2. Growth rates from the population model for the four regional populations. The histograms of growth rate reflect uncertainty in the growth rate due to uncertainty in the underlying life-history parameters. For the Atlantic region, the scenario using the 10-yr mean survival rates is shown.

Matrix Analysis and Simulation

For the Northwest region, the mean growth rate (λ) was 1.037 ± 0.010 (SD), with a simulated 95% prediction interval of (1.016, 1.056). That is, our best estimate of the growth rate in the Northwest is 3.7% per year. The distribution of the simulated values for growth rate was narrow, and largely above 1.0 (Fig. 2a). Only 0.04% of the simulated values were less than 1.0.

In the Upper St. Johns River region, the mean growth rate was 1.062 ± 0.011 , with a simulated 95% prediction interval of (1.037, 1.081). None of the simulated values of λ were less than 1.0 ($n = 10,000$); the minimum value was 1.001. Again, the distribution reflecting uncertainty in λ for this region is narrow (Fig. 2b).

The mean growth rate for the Southwest region was 0.989 ± 0.020 , with a 95% prediction interval of (0.946, 1.024). Many (70.8%) of the simulated values were less than 1.0. The uncertainty in the growth rate is greater in this region than the previous two, as reflected in a wider distribution (Fig. 2c).

The estimated growth rate in the Atlantic region depended heavily on the survival rate used in the matrix analysis. Using the survival rates from the most recent 10-yr period available, the mean growth rate was 1.010 ± 0.011 , with a 95% prediction interval of (0.988, 1.029). Only 18.1% of these simulated values were less than 1.0 (Fig. 2d). Using the survival rates from the most recent 5-yr period available, however, the mean growth rate was 0.970 ± 0.015 , with a 95% prediction interval of (0.938, 0.998). Nearly all (98.3%) of the simulated values were less than 1.0 (histogram not shown).

Stable stage distributions were derived from the left eigenvectors of the projection matrices for each region, using the point values of all parameter estimates. The fraction of female first-year calves (N_1) was calculated as half the

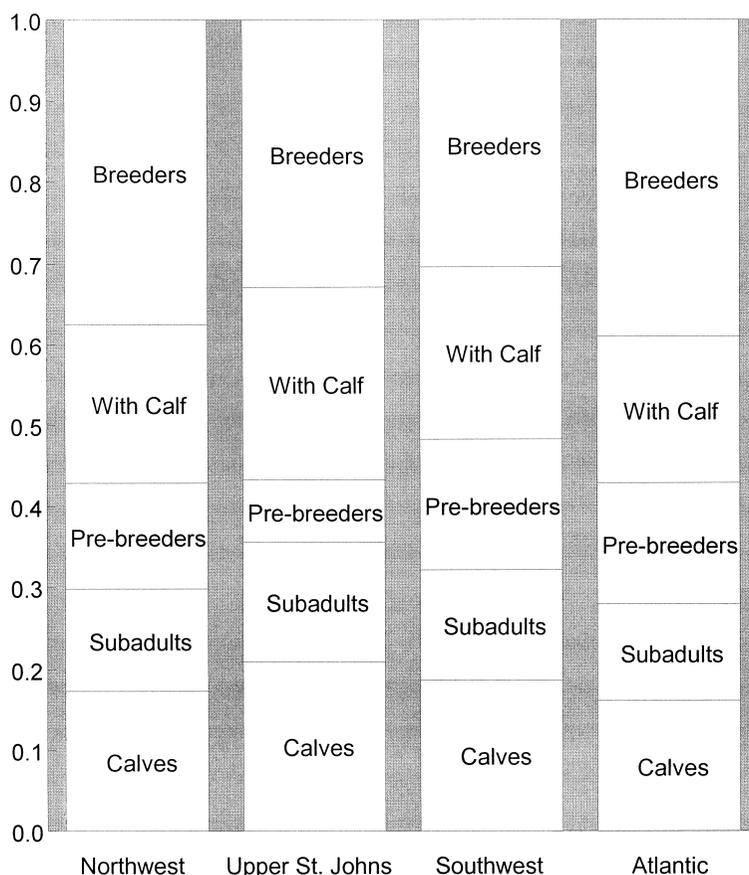


Figure 3. Stable-stage distributions for the four regional populations. The y-axis indicates the cumulative proportion of the population found in each class. These results were based on an eigenvector analysis of the matrix formed from the mean estimates of the life-history parameters.

fraction of females with calves (N_C), and the total in equation 2 was used to adjust the stage distributions so that the sum of them was 1. The stage distributions did not differ much among regions (Fig. 3). For the Northwest region, the stable stage distribution was 17% calves, 13% subadults, 13% prebreeders, 19% females with first-year calves, and 38% breeders without first-year calves. The other regions were similar, with the Upper St. Johns River and Southwest regions having slightly higher fractions of calves, reflecting the higher reproductive rates. We are not aware of any direct, empirical estimates of the stage distribution to which to compare these model results.

The stable stage distributions can be used to look at various ratios that serve as measures of reproductive rate (Table 3), and that have been estimated from empirical observations. The ratios of first-year calves (of either sex) to adult females (including prebreeders but not subadults) were 0.28, 0.37, 0.31, and 0.25 for the Northwest, Upper St. Johns River, Southwest, and Atlantic regions, respectively.

Table 3. Measures of reproduction. Several different ratios of calves to adult females are shown, with comparison to previously published values from field observations. The values calculated from the matrix model are based on the stable stage distribution. “Calves” are of either sex; “adults” are females of reproductive age (including prebreeders); “reproductive” females are females that have previously bred (*i.e.*, females with calves and breeders).

Measure		Northwest	USJ	Southwest	Atlantic
1 st -yr calves: adult females	Model	0.28	0.37	0.31	0.25
	Field	0.36 ^a	0.30 ^b	–	0.39 ^c
1 st -yr calves: reproductive females	Model	0.34	0.42	0.41	0.32
	Field	–	–	–	–
1 st - and 2 nd -yr calves: adult females	Model	0.49	0.65	0.55	0.45
	Field	0.42 ^a	0.41 ^b	–	0.42 ^c

^a Derived from Rathbun *et al.* (1995).

^b O’Shea and Hartley (1995).

^c Reid *et al.* (1995).

The ratios of first-year calves to “reproductive” females (not including prebreeders) were 0.34, 0.42, 0.41, and 0.32 for the four regions. The ratios of first-year *and* second-year calves (of either sex) to adult females were 0.49, 0.53, 0.46, and 0.38 for the four regions. Note that this latter ratio includes all second-year calves, not just the proportion that might still be nursing. All of these model-based results appear to compare favorably to observed field-based ratios, with no evidence of consistent bias (Table 3).

The elasticities of the growth rate (λ) to changes in the life-history parameters (rather than the matrix elements themselves) indicate that adult survival rate has the greatest potential to affect growth rate, with subadult survival rate having the next highest potential, and the remaining life-history parameters having only very minor effects (Fig. 4a). This pattern is similar for all four regions. The pattern in the less important parameters does differ, to some extent, depending on whether the comparison is of sensitivities, elasticities (using survival rates, as in Fig. 4a), elasticities (using mortality rate), or variance-stabilized sensitivities (Link and Doherty 2002), but in all cases adult survival rate has the greatest effect on λ .

We decomposed the variance (*i.e.*, uncertainty) in growth rate into contributions from variance (uncertainty) in each of the life-history parameters (Fig 4b–e). In the Northwest region, the greatest relative contribution was from the adult survival rate (s_P and s_A combined, 0.31), but uncertainty in the two calf survival rates (s_1 , 0.20; and s_2 , 0.17) and the mature breeding rate (γ_B , 0.21) also made significant contributions to uncertainty in growth rate. In the other three regions, the relative contribution made by uncertainty in the adult survival rate (range, 0.65–0.72) was nearly an order of magnitude larger than contributions made by any other life-history parameter.

The contour plot of growth rate as a function of both adult survival rate and mature breeding probability (Fig. 5) shows that the growth rate is much more sensitive to changes in the adult survival rate than to changes in the breeding probability. When approximate confidence ellipses for the four regions (including both Atlantic scenarios) are overlain on the contour plot, the current estimates of growth rate and the contributions to their uncertainty are evident. For instance, since

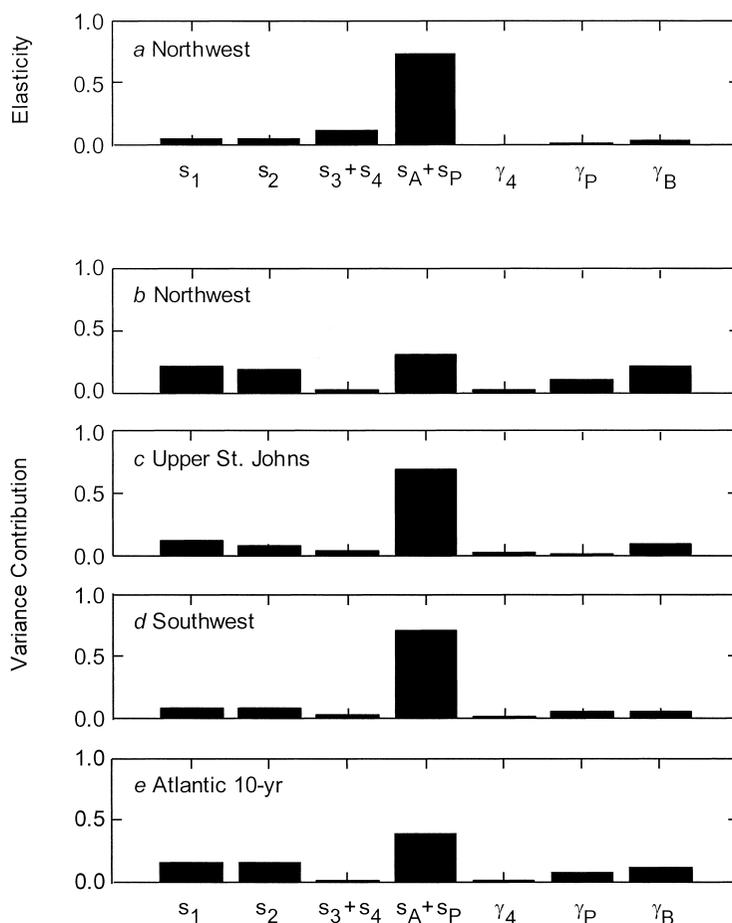


Figure 4. Effects of the life-history parameters on the growth rate: elasticity and variance decomposition. In the graphs, the third and fourth bars refer to the combined effects of s_3 and s_4 , and s_A and s_P , respectively. (a) Elasticity of growth rate to changes in the underlying life-history parameters, calculated from the mean matrix for the Northwest region. (b–e) Relative contributions to uncertainty in growth rate (λ) from uncertainty in the life-history parameters.

the estimates of the survival and breeding rates in the Northwest region are the most precise, the rough confidence ellipse for growth rate in this region is smallest.

DISCUSSION

Status of Regional Populations

The growth rates calculated in this paper are based on life-history parameters estimated for the most recent ten-year periods. As such, the growth rates can be interpreted as integrated measures of the status of these populations over this time frame. Thus, these are retrospective, or at best, current, statements about status.

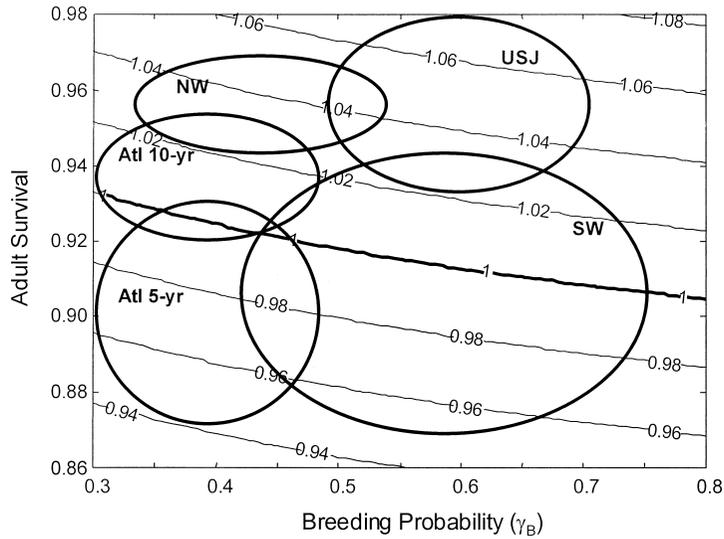


Figure 5. Contour plot of growth rate (λ) as a function of adult survival rate and mature breeding probability. The four subadult and adult survival rates (s_3 , s_4 , s_B and s_A) are assumed to be equal and are all expressed by the value of the y-axis. The calf survival rates are assumed to be proportional to the adult survival rate, with the same proportion as observed in the Upper St. Johns River region. The four-year-old breeding rate is assumed to be 0, and the prebreeder breeding rate is assumed to be 0.304. The ellipses show the approximate confidence intervals for the two parameter estimates, and enclose the approximate confidence regions for the growth rate.

The manatee populations in the Northwest and Upper St. Johns River regions are growing at annual rates of 3.7% and 6.2%, respectively. Although we recognize uncertainty about the exact values of these growth rates, we can be confident that both populations are growing because the prediction intervals for the respective growth rates are convincingly above 1 (only 0.04% and <0.01% of the simulated growth rates fell below 1), provided our parameter estimates are not biased (see below). These results are not surprising, as Eberhardt and O'Shea (1995) found the same results a decade ago, calculating growth rates of 7.4% and 5.7% for the Northwest and Upper St. Johns River regions. The growth rate calculated herein for the Northwest is lower than that of Eberhardt and O'Shea because of a slightly lower adult survival rate (0.956 *vs.* 0.965) and a lower equivalent reproductive rate (see Kendall *et al.* 2004, and below for a discussion of bias in reproductive rates). This difference in growth rate could be due to better estimation techniques for the life-history parameters, a longer data set, and/or a change in life-history rates over the last 10 yr, perhaps due to density-dependence. Nevertheless, the Northwest population is still clearly growing.

The status of the Atlantic population is harder to discern, because of uncertainty about the recent trend in adult survival rates (Langtimm *et al.* 2004). If we take an optimistic view, assume that the apparent trend in survival rates is not real, and use the mean survival rates for the most recent 10-yr period, then the estimated annual growth rate for the Atlantic population is 1.0%. This suggests a slowly growing population, although this conclusion is tempered by the observation that 18.1% of

the simulated growth rates indicated a declining population. If, on the other hand, we take a pessimistic view, assume the survival rates have been declining, and use the mean survival rates for the most recent 5-yr period available, then the estimated annual growth rate for the Atlantic population is -3.0% , with 98.3% of the simulated growth rates indicating a declining population. One way to interpret this is that the Atlantic population was growing at a healthy rate between 1990 and 1995, but a decrease in the survival rate caused the population to decline at about 3% annually from 1995 to 2000, with an overall positive growth rate of 1% for the decade. If that is the case, then the *current* status of the Atlantic population is poor. However, we believe the apparent decline in the survival rate is an artifact of temporary emigration on the mark-recapture estimates (Langtimm *et al.* 2004); increased photo-identification efforts at sites on the Atlantic coast by USGS personnel and colder weather driving manatees to the monitoring sites in the winter of 2002–2003 should help us evaluate this issue in the next few years. At this point, we believe the 10-yr mean estimate ($\lambda = 1.010$) is the best statement of the current status of this population.

The recent survival estimates by Langtimm *et al.* (2004) and the estimates of reproductive rate from the Sarasota Bay data of Koelsch (2001) provide the opportunity to make the first assessment of population growth rate in the Southwest region. This estimate (-1.1%) has a wider prediction interval than the growth rates in the other regions, because of greater uncertainty about the underlying life-history parameters. Nevertheless, most (70.8%) of the simulated values for the growth rate indicated a declining population.

These growth rate estimates are more robust than any previously published estimates, because they use better estimation methods, incorporate more biological realism in the population model, and formally address uncertainty in the underlying parameters. However, there are two primary sources of potential bias. First, survival rates are potentially negatively biased, due to permanent (or to a lesser extent, temporary) emigration. Animals that permanently leave a population are considered to have “died.” If there is such bias, then the estimated survival rates, and hence the growth rates, are too low. However, manatees show high fidelity to wintering sites (Reid *et al.* 1991, O’Shea and Hartley 1995, Rathbun *et al.* 1995, Deutsch *et al.* 2003), suggesting that the magnitude of permanent emigration is low. Further, on the Atlantic coast, the major aggregation sites along the known migratory routes are monitored, and we do not believe there is anywhere else to which manatees can emigrate. The larger concern is on the west coast (Langtimm *et al.* 2004). The Northwest and Southwest photo-ID databases are periodically checked for common individuals, but the two databases are not yet integrated and there is not yet a regularly implemented, coordinated protocol to check for migrants between the regions. Sighting histories used to estimate survival for these models only included sightings within a given region (Langtimm *et al.* 2004). Thus, an animal that emigrates from one region to the other might appear to have died, as far as the first region is concerned. Further, within the Southwest, there are areas that are not monitored regularly (especially in the Ten Thousand Islands and the Everglades, because of logistical constraints and difficult photography conditions), where animals could emigrate. Movement among regions needs to be looked at more closely, and special attention needs to be focused on the Southwest, because the estimated growth rate is so low there, because the time series of data is shortest there, and because the size and heterogeneity of the region increases the possibility of bias in the survival estimates. On the whole, we do not

believe that the growth rates reported herein for the Atlantic, Upper St. Johns River, or Northwest regions are significantly biased because of permanent emigration; we are less sure about the growth rates in the Southwest region.

The second source of potential bias is in the breeding rates, particularly the mature breeding rate (γ_B). This parameter was estimated in two different ways in this paper. For the Northwest and Atlantic regions, the methods of Kendall *et al.* (this volume) were used to estimate breeding rate. This modification of capture-recapture methods properly accounts for detection and misclassification probabilities. Further, it does not rely on a large group of known breeders. For the Southwest and Upper St. Johns River regions, we used a simpler method that requires more assumptions—we calculated the breeding rates from reproductive histories of known females, looking at the naïve probabilities of transition between “without calf” and “with first-year calf” status. The data for such calculations are composed primarily of observations of females with high site fidelity. If these females are also ones with higher individual reproductive rates, then the sample is biased toward “good” breeders. See Kendall *et al.* (2004) for a more detailed discussion of this bias. The breeding rates used in this paper suggest this bias may be operating (Table 1). The estimates for γ_B for the Upper St. Johns River and Southwest regions are considerably higher than those for the Northwest and Atlantic regions. It is particularly surprising that the breeding probability would be higher in the Southwest region than the Northwest region, since the Northwest region (especially Crystal River) is very protected and has higher survival rates. Further, Sarasota Bay, where Koelsch (2001) did her work, is a protected bay that appears to serve as a nursing colony; it may not provide an estimate of breeding rate that is representative of the entire Southwest region. It is more believable that the breeding rate in the Upper St. Johns River region is high, given how protected that region is (particularly Blue Spring State Park). If this type of bias does exist, then the growth rates calculated herein for the Upper St. Johns River and Southwest regions may be too high. However, this bias is not likely to change our assessment of the current status of these populations: while the population in the Upper St. Johns River region might not be growing quite as fast as we have estimated, it is very likely that it is growing; in the Southwest region, this bias would only make our assessment of the status more bleak.

Elasticity and Management Potential

The elasticities of growth rate to changes in the life-history parameters are the proportional changes in growth rate expected from proportional changes in the underlying survival and breeding rates (Fig. 4a). By far, the greatest elasticity is associated with the adult survival rate. However, different life-history parameters are not likely to be equally plastic with regard to potential management actions. Thus, there may be a parameter with a lower elasticity that is easier to change than some other parameter with a higher elasticity. In the case of manatees, the calf and subadult survival rates are probably more plastic than adult survival rates, as younger animals are often considered to be more vulnerable to threats, but it is also likely that management actions designed to reduce adult mortality would also reduce calf and subadult mortality. The combined elasticity of the survival rates accounts for nearly all of the influence of life-history parameters on growth rate. Because there are biological limits to the variation in breeding rates, and the elasticity associated with them is low, management directed at increasing manatee

breeding rates will not have as large an impact as management directed at survival rates. This conclusion is expected from previous work with other large mammals (*e.g.*, Eberhardt and Siniff 1977).

Uncertainty and Monitoring Needs

The variance in the estimated growth rates reflects uncertainty in the growth rates due to uncertainty about the underlying survival and breeding rates. In three of the four regions (Upper St. Johns River, Southwest, and Atlantic Coast), by far the major contribution to uncertainty about λ comes from uncertainty about adult survival rate (Fig. 4c–e). Thus, to reduce uncertainty in growth rate most effectively, increased monitoring efforts should be targeted at better estimating adult survival rates, through increased effort in photo-identification. This is especially true in the Southwest and Atlantic regions. In the Southwest region, with only 8 yr of data and possible geographic variation (Langtimm *et al.* 2004), the confidence interval for adult survival rate is large. In the Atlantic region, the two scenarios described above (5-yr and 10-yr means) produce profound differences in the adult survival rate, and hence, the estimated growth rates (Fig. 5).

The Northwest region differs from the other regions with respect to contributions to the uncertainty in growth rate. The estimate of adult survival rate is quite precise in this region, and makes a much smaller relative contribution to uncertainty in λ . Because of this, uncertainties in several other parameters (the two calf survival rates and the mature breeding rate) make nearly equivalent contributions (Fig. 4b). This implies that decreased uncertainty about growth rate can be achieved through increased monitoring of a number of parameters. Recognizing that calf survival rate has only been directly estimated for the Upper St. Johns River region, consideration should be given to improving methods and increasing effort to estimate calf survival in the Northwest region.

Great uncertainty in some of the lesser-known parameters does not make a sizeable contribution to uncertainty in the growth rate. For instance, while the data available to estimate γ_4 and γ_P are scant, uncertainty in these two parameters makes almost no contribution to uncertainty in λ ; likewise for calf survival rates in three of the regions. To make accurate estimates of growth rate, we need to be most concerned that our estimates of adult survival rate are precise and unbiased.

These results offer some generality for monitoring priorities in large mammals. It is critical to have precise estimates of adult survival rate, so this should be the first goal of a monitoring program that is designed to assess growth rate. In many cases, adult survival is one of the easiest parameters to estimate for large mammals, especially if capture-recapture methods are readily applied, so suitable precision may be relatively easy to attain. Further, several other parameters, such as survival rates of younger classes, may end up being estimated along with adult survival. In some cases, however, the initial precision in estimating growth rate may not be satisfactory. At that point, variance decomposition techniques can help identify monitoring priorities.

Recovery Criteria

The Florida Manatee Recovery Plan, Third Revision (USFWS 2001) describes quantitative demographic criteria to serve as benchmarks for recovery. For the purpose of downlisting to threatened status, these benchmarks are statistical confidence of 95% over the most recent 10-yr period that (1) the mean adult

survival rate is ≥ 0.90 , (2) the average fraction of adult females accompanied by first- or second-year calves is ≥ 0.40 , and (3) the mean growth rate (λ) is ≥ 1.0 . Two of these criteria are straightforward to interpret in the context of the model described in this paper, but the criterion regarding reproduction is not. While this criterion can be estimated from field data, it is actually difficult to interpret what it means from a modeling standpoint, because it is not clear what an “adult” is, and it requires knowledge of an additional parameter—the fraction of second-yr calves that are still dependent on their mothers. We suggest that a better measure of reproduction would be the fraction of adult females with first-year calves, that is,

$$\frac{2N_1}{N_p + N_C + N_B} = \frac{N_C}{N_p + N_C + N_B}, \quad (5)$$

where “adult” can be specifically interpreted as females ≥ 4.5 yr, regardless of past breeding history. Using the stable stage distributions, the calculated values for this ratio are lower than observed values for the Northwest and Atlantic regions but higher than the observed value in the Upper St. Johns River region (Table 3, 1st row), where the observed values have been calculated from reproductive histories of known females (Rathbun *et al.* 1995, O’Shea and Hartley 1995, Reid *et al.* 1995). Alternatively, using γ_B , the probability that an adult female without a calf produces a calf in the next year, would directly relate recovery criteria to population dynamics. Kendall *et al.* (this volume) provide a method to estimate both of these measures directly, while properly accounting for potentially different sighting probabilities for mother and calf.

The three demographic recovery criteria are almost redundant. Together, the survival rate and the reproductive rate almost completely determine the growth rate, so probably not all three measures are needed. The intent of the recovery criteria seems to be to guarantee that all four populations are growing. Certainly, that is precisely what the third criterion requires; and the first two criteria seem intended to be indirect measures that would assure the third. We recommend that if growth of the population is the primary demographic measure of recovery then the other criteria should be dropped, since they do not add additional information. This does not mean they no longer need to be measured, indeed the precision with which they are measured determines the precision with which growth rate is estimated. If we consider just the third criterion (growth rate), then the manatee populations in the Northwest and Upper St. Johns River regions meet the recovery criterion, whereas the populations in the Southwest and Atlantic regions do not.

There is a more fundamental concern to be raised about the current recovery criteria, however. No population can grow at a fixed rate indefinitely. There will come a point when scarce resources limit a growing population, density-dependence emerges, and the growth rate (λ) drops to 1. At this point, it seems reasonable to think that the populations would be recovered, yet the recovery criteria will not be met (the confidence interval for λ will overlap 1.0). That is, recovery criteria based only on growth rates fail to consider density-dependent forces and the long-range equilibrium population size. We believe the current recovery criteria, while useful for setting short-term goals, need to be revisited as long-term criteria with regard to the concerns described above.

The broader lesson is that assessment criteria, the population models used to evaluate them, and the field methods used to estimate the necessary metrics need to be finely tuned, not just for manatees or marine mammals generally, but for any

managed species. First, the assessment criteria need to be tied to metrics that are estimable from field data in a statistically rigorous manner. Second, population models should be designed and used to understand the implications of the assessment criteria, and the assessment criteria should make sense in the context of the population models. Third, population models, the estimation methods used to supply parameters to the models, and the field methods that generate the data for use in parameter estimation all need to be seamlessly integrated.

Population Viability Analysis and Adaptive Management

The challenge of forecasting, a critical step in population viability analysis and adaptive management, is anticipating the magnitude of variability and the probability of trends in the life-history parameters. For any marine mammal, developing a prospective model useful for forecasting requires several additional components not found in deterministic, stage-based models, among them environmental stochasticity, density-dependence, incidental take, indirect effects of trends in human population growth, and the effects of management actions. For projecting future growth of the Florida manatee population, the model presented in this paper can provide the framework, but several components would have to be developed. First, the parameters governing environmental stochasticity would have to be estimated and incorporated in the simulations. This could be done in one of two ways, either by estimating the concentration parameters (θ 's) described under "Model Structure," which would constitute a phenomenological model of stochasticity; or by taking a more mechanistic approach and linking variation in the life-history parameters to variation in environmental driving factors (*e.g.*, Runge and Moen 1998). Second, density-dependence would have to be incorporated, since manatee populations cannot grow indefinitely. The challenges with modeling density-dependence are determining what factors are likely to limit growth of manatee populations, estimating at what population size these factors will begin to operate, and quantifying the ways in which life-history parameters would be affected. Third, the effects of human-caused manatee mortality, including potential trends, need to be incorporated. The survival estimates used in this paper incorporate the actual effects of such mortality since they measure annual survival directly, so for the purposes of this paper, it was not necessary to decompose mortality by cause. A forecast will need to do that, in order to incorporate potential trends in the various components. Fourth, thought would have to be given to the effects on manatee population dynamics of continued human population growth in Florida. Fifth, future manatee population trends are conditional on management actions, so a defensible forecasting model would need to articulate its assumptions about likely future management actions and their effects on manatee life-history parameters. Sixth, and finally, the uncertainty associated with all of the elements of the future forecast would need to be articulated. Further, those uncertainties that are specifically tied to the effects of management should be examined with an appropriate monitoring system, and adaptive management (Walters 1986) should be used to make periodic adjustments to the management actions as this uncertainty is reduced.

ACKNOWLEDGMENTS

This modeling work was possible because of the excellent monitoring programs being conducted by scientists in federal and state agencies. We are grateful to all the dedicated

field personnel and analysts who have contributed to this body of data, among them Cathy Beck, Bob Bonde, Kit Curtin, Wayne Hartley, Jim Reid, Jessica Koelsch, Sheri Barton, Susan Tarr, Kari Higgs, and scientists at the Florida Marine Research Institute and the Mote Marine Laboratory. The 1992 Technical Workshop on Manatee Population Biology and the associated proceedings (O'Shea *et al.* 1995) provided the technical foundation for our modeling efforts. Our work was enhanced by critical discussions with Cathy Beck, Hal Caswell, Chip Deutsch, Christine Hunter, Lynn Lefebvre, and Brad Stith; as well as the panel of advisors for the April 2002 Manatee Population Ecology and Management Workshop: Solange Brault, Daniel Goodman, Aleta Hohn, Fred Johnson, Gil McRae, Helene Marsh, Jim Nichols, and Ken Pollock. Specific comments from Jim Nichols, Jay Barlow, and Don Bowen enhanced the quality of the manuscript, and Hal Caswell provided the idea for constructing Figure 5.

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Received: 21 January 2003

Accepted: 9 February 2004