A Core Stochastic Population Projection Model
for Florida Manatees (*Trichechus manatus latirostris*)

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Abstract

A stochastic, stage-based population model was developed to describe the life history and forecast the population dynamics of the Florida manatee (*Trichechus manatus latirostris*) in four separate regions of Florida. This population model includes annual variability in survival and reproductive rates, demographic stochasticity, effects of changes in warm-water capacity, and catastrophes. Further, the model explicitly accounts for uncertainty in parameter estimates. This model is meant to serve as a flexible tool for use in assessments relevant to management decision making, and was used in the State of Florida's recent biological status review. The parameter estimates and model structure described herein reflect our understanding of manatee demography at the time that this status review was completed. In the Northwest and Upper St. Johns regions, the model predicts that the populations will increase over time until warm-water capacity is reached, at which point growth will taper off. In the Atlantic region, the model predicts a stable or slightly increasing population over the next decade or so, and then a decrease as industrial warm-water capacity is lost. In the Southwest region, the model predicts a decline over time, driven by high annual mortality in the short-term and exacerbated by loss of industrial warm-water winter refuges over the next 40 years. Statewide, the likelihood of a 50% or greater decline in three manatee generations was 12%; the likelihood of a 20% or greater decline in two generations was 56%. These declines are largely driven by the anticipated loss of warm-water capacity, especially in the Atlantic and Southwest regions. The estimates of probability of extinction within 100 years were 11.9% for the Southwest region, 0.6% for the Northwest, 0.04% for the Atlantic, and <0.02% for the Upper St. Johns. The estimated probability that the statewide population will fall below 1000 animals within 100 years was 2.3%. Thus, while the estimated probability of extinction is low, the model predicts that current and emerging threats are likely to result in a long-term decline in the statewide population and a change in the regional distribution of manatees. Analyses of sensitivity and variance contribution highlight the importance of reducing uncertainty in some life-history parameters, particularly adult survival, temporal variance of adult survival, and long-term warm-water capacity. This core biological model is expected to evolve over time, as better information becomes available about manatees and their habitat, and as new assessment needs arise. We anticipate that this core model will be customized for other state and federal assessments in the near future.

1. Introduction

The Florida manatee (*Trichechus manatus latirostris*) is a marine mammal endemic to the southeastern United States that is currently listed as endangered under the U.S. Endangered Species Act (Lefebvre et al., 2001). The primary threats to manatee populations, as identified in the current recovery plan, are collisions with watercraft, the potential loss of warm-water refuges, and ongoing coastal development (USFWS, 2001). In 2002-2003, scientists from both the Florida Fish and Wildlife Conservation Commission and US Geological Survey published population models for the Florida manatee as components of specific assessments—the 2002 Biological Status Review model (BSR; FMRI, 2002) and the Incidental Take model (IT; Runge, 2003), respectively. While these models shared many of the same parameters, the focus of each was specific to the context that generated its need. Over a series of meetings in the summer and fall of 2003, State and Federal scientists and managers expressed a desire to have a single, common modeling framework to form the basis of future assessments. The vision for this

framework included a "core biological model" to describe Florida manatee life history and generate population forecasts using the best currently-available information and including careful expression of uncertainty. This core biological model (CBM) would be used for future assessments by connecting it to "adaptive components" that are specific to those assessments. The adaptive components include model inputs that are tied to alternative management actions or scenarios in the assessment, and model outputs (response variables) that are relevant to the management objectives.

The primary function of the CBM is to forecast relative population size, growth rates, and quasi-extinction risk of manatees in the four regions (Atlantic, Southwest, Upper St. Johns and Northwest) given a set of life-history parameters and assumptions about the future state of the environment. The CBM provides a structure to integrate the current known life-history parameters of the Florida manatee particular to each region, and combines this information with assumptions about potential future threats; these threats include the frequency and magnitude of catastrophes (e.g., red tide or virulent disease), reduction in warm-water capacity due to power plant closures and spring flow reduction, changes in various anthropogenic causes of mortality, and habitat loss. The model incorporates multiple sources of variability, including uncertainty in parameter estimation, variability across the environment (environmental stochasticity) and factors that work at small population sizes (demographic stochasticity).

The modular structure of the CBM accounts for the dynamic nature of our knowledge of manatee life history, the species' environment, changes in management, and changes in population assessment metrics. All parameters are dynamically assigned when the model is run; therefore, it is easy to include new information. Additionally, different assumptions about the environment, anthropogenic effects, or management scenarios can be explicitly modeled. For example, we could change both the assumed frequency of red tide mortality events as well as assess the impact of reducing the warm-water capacity as the result of a change in power plant operation.

There have been numerous efforts to model the dynamics of Florida manatee populations, from deterministic, age-based methods (Packard, 1985; Eberhardt and O'Shea, 1995) to stochastic methods (Marmontel et al., 1997). The CBM draws upon the assumptions and components of three more recent population models: the aforementioned 2002 BSR model (FMRI, 2002) and IT model (Runge, 2003), and an analytical stage-structured matrix model (SSM; Runge et al., 2004); the core biological model extends the capabilities of each model by allowing more flexibility through a modular design. The CBM, IT model and SSM model were all written specifically to explore the population demography of the Florida manatee. These three models also explicitly addressed uncertainty in parameter estimates and model assumptions. The SSM model was developed primarily to examine the impact of parameter uncertainty on population growth rates; therefore, it did not include environmental or demographic stochasticity, catastrophic events, or density dependence. The SSM model was the basis of the stage-structured matrix formulation used in the CBM and IT models; however, unlike the other two models, the SSM model tracked only females.

The first purpose of this paper is to describe the core biological model, including the structure of the model, the origin of the core parameter estimates, methods for incorporating uncertainty, and the sensitivity of results to such uncertainty. The second purpose is to present results from the

first assessments conducted with this model, namely a status review under Florida state statute (Haubold et al., 2006) and evaluation under IUCN classification criteria. These results, however, are not meant to be exhaustive, and because the CBM will evolve as new information and new needs arise, we expect these results to be refined in the future. The parameter estimates and model structure described herein reflect our understanding of manatee demography at the time that the state's 2006 biological status review was completed (Haubold et al., 2006).

2. Model Structure

2.1. Core stage-structured model

The CBM is based on a matrix structure of manatee population dynamics (Fig. 1) that is an extension of the model developed by Runge et al. (2004). The CBM consists of 10 different stages: juveniles are classified by age and sex; adult females are classified by reproductive condition, because their survival and reproduction directly control population growth; and adult males are pooled into a single class, since manatees have a promiscuous mating system whereby a single male can inseminate multiple females (Hartman, 1979, p. 100).

First-year male and female calves (0.5-yr-old). While manatee population monitoring focuses on the winter aggregation sites, most calves 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 are collected when females with dependent nursing calves return to the winter aggregation sites in fall and winter, when calves are ca. 3-9 months old. Thus a first-year calf represents successful pregnancy, birth, and survival to ca. age 0.5. There currently are no reliable means to monitor pregnancy or births in the wild (Rathbun et al., 1995). Note that in the model (Fig. 1), first-year calves are not tracked separately, because they are fully dependent on their mothers.

Second-year male and female calves (1.5-yr-old). Data on second-year calves (denoted as age class 2) are collected the following year at the aggregation sites. 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. Weaning interval varies from one to 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, females are independent but rarely sexually mature and capable of reproducing (Marmontel, 1995; O'Shea and Hartley, 1995). Males of this age may be reproductively active (Hernandez et al., 1995).

Fourth-year female subadults (3.5-yr-old, age class 4) and *Pre-breeders* ($\geq$ 4.5-yr-old, state P). Pre-breeders are females 5+ years old 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 first appearance with a calf is age 4.5 yr (the gestation length is 12-13 months, Rathbun et al., 1995). 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 ca. 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 pre-breeder class for some time.

Fourth-year male subadults (3.5-yr-old, age class 4) *and male adults*. At four years of age males may be reproductively active (Hernandez et al., 1995). Male reproductive stages are not modeled because we assume males do not limit population growth.

Female adults with first-year calves (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 "breeder," respectively. Mature females accompanied by an unweaned second-yr calf are considered "breeders," since the attendant calf was not born during the current year.

Two types of life-history parameters describe the transitions between the classes in the model: survival rates (s) and breeding rates (γ). There is no evidence that survival rates differ between males and females (Langtimm et al., 1998), so the same survival rates are used for corresponding male and female age classes. For instance, s_1 is the probability a first-year calf (either male or female) survives to become a second-year calf. The reproductive rate γ_P is the probability that an adult female that has not yet given birth, breeds and successfully gives birth within the next year, given survival until that time. Pre-breeders that survive either give birth to a calf (with probability γ_P) or remain as pre-breeders. 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 (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 female calf (weaned or not) in the next year with probability $s_1/2$, reflecting the probability of calf survival and an even primary sex ratio. Note that litter size is assumed to be 1 calf. While twinning is possible in nature, it is 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

$$
\begin{bmatrix} N_2^F \\ N_3^F \\ N_4^F \\ N_P^F \\ N_C^F \\ N_B^F \\ N_2^M \\ N_3^M \\ N_4^M \\ N_A^M \end{bmatrix}_{t+1} =
\left[\begin{array}{cccccc|cccc}
0 & 0 & 0 & 0 & \frac{1}{2}s_1 & 0 & 0 & 0 & 0 & 0 \\
s_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & s_3 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & s_4(1-\gamma_4) & s_P(1-\gamma_P) & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & s_4\gamma_4 & s_P\gamma_P & 0 & s_A\gamma_B & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & s_A & s_A(1-\gamma_B) & 0 & 0 & 0 & 0 \\ \hline
0 & 0 & 0 & 0 & \frac{1}{2}s_1 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & s_2 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & s_3 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & s_4 & s_A
\end{array}\right]
\begin{bmatrix} N_2^F \\ N_3^F \\ N_4^F \\ N_P^F \\ N_C^F \\ N_B^F \\ N_2^M \\ N_3^M \\ N_4^M \\ N_A^M \end{bmatrix}_t
\qquad (1)
$$

where the N_i represent the number of manatees in class i at time t. In the matrix formulation, first-year calves are not counted separately, as they are assumed to be dependent on their mothers; hence, 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 population size at time t can be calculated as:

$$N_{Total} = N_2^F + N_3^F + N_4^F + N_P^F + 2N_C^F + N_B^F + N_2^M + N_3^M + N_4^M + N_A^M \qquad (2)$$

where the number of females with first-year calves is multiplied by two to include both the mothers and their calves (of either sex) in the total.

2.2. *Environmental stochasticity*

Manatees are subject to several sources of environmental stochasticity including (but not limited to) periodic red tide events (O'Shea et al., 1991; Bossart et al., 1998), severe cold events (Buergelt et al., 1984), and hurricanes (Langtimm and Beck, 2003). Two types of environmental stochasticity are often distinguished: "normal" variation, which causes the life-history parameters to fluctuate on an annual basis; and catastrophes, which are rarer events that have strong negative effects. In this model, the effects of red tide and virulent, infectious disease are treated as catastrophes because of their infrequency and potentially substantial effects, while the effects of cold, hurricanes, and other factors are treated as "normal" variation because of their presumed frequency and highly variable effects. In the remainder of this paper, "environmental stochasticity" refers to the "normal" variation, while catastrophes are identified specifically.

The time series of observations used to estimate survival and reproduction include "normal" variation, and so the estimated life-history parameters integrate stochasticity from the corresponding sources for each particular region. For events such as hurricanes, which occur sporadically in the time series used to estimate survival rates, the demographic rates in years with these events will be tempered or "averaged" with those in years when these events do not occur. All environmental effects are assumed to be short-term, affecting manatee survival or reproduction only in the current year.

In this model, environmental stochasticity is represented by probability distributions for the annual values of the life-history parameters. All model parameters are probabilities (survival probabilities, s; breeding probabilities, γ) and thus must be in the interval [0,1]. Because of this, variation in these parameters is modeled with logit-normal distributions, which ensure biologically-permissible values. The logit transformation is

$$x = \ln\left(\frac{p}{1-p}\right) \qquad (3)$$

and if x is normally distributed, then p is said to follow a logit-normal distribution. Specification of a logit-normal distribution requires a mean (μ) and variance (σ^2) for the transformed variable (i.e., x).

The year-specific values for each life-history parameter are sampled from the appropriate logit-normal distribution. Thus, the first-year calf survival rate in year t is distributed according to

$$\ln\left(\frac{s_{1,t}}{1-s_{1,t}}\right) \sim Normal\left(\mu_{s_1}, \sigma^2_{s_1}\right). \tag{4}$$

The survival rates are assumed to vary together, since the same environmental factors will likely affect juvenile survival rates in similar ways as adult survival rates, albeit to varying degrees. To model this, the same standard normal deviate is used to generate each of the survival rates for a given year. This simulation method produces perfect temporal correlation among the survival rates across age classes.

The breeding probabilities, γ, are also assumed to vary together. This implies that the same set of environmental factors affects all three breeding probabilities (γ_4, γ_P, and γ_B).

Survival rates and breeding probabilities are not assumed to vary together, but may be correlated. The correlation between the two sets of life-history parameters is given by a correlation coefficient, r. In general, we assume the correlation is positive (years that are better for survival are also better for reproduction), but the model can accommodate negative values for this parameter as well. The default value for r is 0.5.

2.3.   Catastrophes

Two types of catastrophes were considered, following the structure of the population viability analysis conducted by the state of Florida in its 2002 status review (FMRI, 2002): the emergence of a virulent, infectious disease (Type 1); and severe red tide (Type 2). Large-scale mortality events caused by disease or toxins occur occasionally in marine mammals and have the potential to greatly reduce population size (Harwood and Hall, 1990)—the Type 1 catastrophes describe this occurrence. Type 1 catastrophes were assumed to occur in all regions whereas Type 2 catastrophes (red tide mortality) were assumed to occur only in two of the four regions (Northwest and Southwest). The probabilities of occurrence and magnitudes of effects are drawn from the population viability analysis developed by the state of Florida (FMRI, 2002). In the core biological model, the frequency and the magnitude of effects on survival and reproduction can vary by region.

2.4.   Demographic stochasticity

Demographic stochasticity is variation in population growth driven by chance variation in fates of individuals within a year. 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 because there is no evidence of a skewed primary sex ratio nor of different 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 first-year calves. The number of female first-year calves is sampled from a binomial distribution with success probability 0.50; the number of male calves is then found by subtraction. Several other instances of demographic stochasticity are included in the model, and are described in Appendix A ("Outline of the modeled annual cycle").

2.5.   Density-dependence

The model shown in equation (1) is an exponential population model, which can include stochastic effects. No real population can follow exponential growth indefinitely—at some point, some resource becomes limiting, thereby reducing survival and/or reproductive rates.

Density effects on life-history parameters in manatees have not yet been documented or estimated in the literature. Four possible reasons for this are: (1) manatee densities may be too low to have shown any strong density-dependent effects; (2) since robust monitoring programs have been in place, manatee densities may not have varied over a wide enough range to allow detection of density-dependent effects; (3) appropriate monitoring programs specifically designed to detect density-dependent effects have not been developed; and (4) the relevant limiting factors may be unknown and/or may change over time and space, making detection of the effects of limitation difficult.

One of the major limiting factors for manatee population growth is presumed to be the availability of warm-water refugia (USFWS, 2001). As the older power plants that currently provide warm water are phased out of use, it is probable that manatee populations, particularly in the Atlantic and Southwest regions, will experience a reduction in available warm water. In addition, reduction of aquifer capacity from increased human use is decreasing the availability of warm water at natural springs. Whether these factors affect long-term recovery of manatees will depend on the extent to which this loss of warm water can be mitigated by other management measures.

Effects of exceeding warm-water capacity. In the event that the population in a particular region exceeds its warm-water capacity, what are the consequences? Presumably, animals outside the warm-water refugia would face greater mortality due to cold stress, but the consequences are likely to be different depending on the age of the animal and the severity of the winter. Calves and subadults may be more vulnerable than adults to the effects of cold because of metabolic and behavioral vulnerabilities: calves have a high surface area to volume ratio (hence, greater heat loss) and subadults lack experience finding suitable wintering sites (O'Shea et al., 1985), but the metabolic vulnerability of dependent calves may be offset by the mother's behavioral experience. This model considers two levels of severity in winter, "normal" and "cold", where "cold" winters occur at some rate (20% by default), and are determined from the standard normal deviate that governs environmental stochasticity in survival rates (that is, cold winters and "bad" years for survival are assumed to coincide). A cold winter is one in which there are multiple, prolonged cold spells. The effect of exceeding the warm-water capacity and/or enduring a cold winter can be expressed as an additional source of mortality. If the population size is less than

the warm-water capacity, all animals are presumed to have access to warm-water refugia. If the population size is greater than the warm-water capacity, the difference constitutes animals that face additional mortality from being excluded from refugia. Four cold-related mortality parameters are included for animals that are outside refugia: the additional mortality of adults (including subadults) in normal winters, calves (both first- and second-year) in normal winters, adults in cold winters, and calves in cold winters. The core biological model has the capacity to apply additional mortality to both adults and calves presumed to be "inside refugia", but currently those values default to 0. Note that since the core biological model is a winter-to-winter model, the cold stress mortality is applied first. Those animals that survive are then subject to the annual class-specific survival rates, as described above.

Effects of approaching warm-water capacity. In addition to the sharp effect of exceeding warm-water capacity during cold years, the model includes a more gradual density-dependent component. As the population approaches warm-water capacity, reproductive rates (the breeding probabilities, γ) are reduced, due to presumed crowding and displacement from prime habitat. In the CBM, the reproductive rate as a function of population size in a region is described by

$$\gamma(N) = \gamma_0 \left(1 - \alpha \left(\frac{N}{K} \right)^\beta \right),$$
(5)

where N is the population size in a region, K is the warm-water capacity for that region, α is the fraction by which reproduction is reduced when the population is at its warm-water capacity, β controls how close the population size has to be to K before the density-dependent effects are felt, and γ_0 is the reproductive rate at low population density (i.e., maximum rate).

Future trends in warm-water capacity. In the absence of specific intervention, warm-water capacity for manatees is expected to decrease in all regions over time (USFWS, 2001). In the Atlantic and Southwest regions, the primary warm-water refuges are industrial effluents. These power plants were all built before the Clean Water Act was enacted in 1972 and make use of "once-through cooling" technology. These aging plants are expected to be retired over the next 20-40 years; their replacements will not produce warm-water effluent. In the Northwest and Upper St. Johns regions, the primary warm-water refuges are first-order springs. As the aquifers in Florida are drawn down for human use, flows at many springs have decreased. As flow decreases, the size of the warm-water plume produced by the springs may shrink, reducing the capacity of the springs to support manatees during cold weather. Models for these trends, described below, were developed in consultation with an expert panel (the Warm Water Task Force and its advisors).

For the Northwest and Upper St. Johns regions, change in warm-water capacity is described by an exponential decay model, on the assumption that reduction in flow will occur gradually and will stabilize at some proportion of the current flow. The warm-water capacity in year t is described by

$$K_t = k_1 \left[k_0 + (1 - k_0) e^{-mt} \right]$$
(6)

where k_1 is the current warm-water capacity in a region (at $t = 0$), k_0 is the long-term warm-water capacity for that region, and $m = (\ln 2)/t_{1/2}$ is a rate parameter related to the half-life of the reduction.

For the Atlantic region, the loss of warm-water is described by a logistic function, on the assumption that warm-water capacity will drop from current levels to a lower level once all the power plants have gone offline, but the drop may be fairly gradual, given the number of plants. The warm-water capacity in year t is described by

$$K_t = k_0 + \frac{(k_1 - k_0)}{1 + e^{m(t-c)}} \tag{7}$$

where k_1 is the current warm-water capacity in the Atlantic region, k_0 is the long-term warm-water capacity, c is the time at which half the vulnerable capacity will be lost, and m governs the rate of loss.

For the Southwest region, a more mechanistic model was used, because the warm-water capacity is primarily at two industrial sites, Tampa Electric Big Bend and Florida Power & Light Ft. Myers. When those plants are retired, there will be an instantaneous drop in capacity. The warm-water capacity in year t is described by

$$K_t = k_0 + k_M I_{t<cM} + k_T I_{t<cT} + k_X e^{-mt} \tag{8}$$

where k_0 is the long-term warm-water capacity, k_M and k_T are the warm-water capacities at the Ft. Myers and Tampa power plants, respectively, c_M and c_T are the respective years when those plants are retired, k_X is other capacity in the region (smaller industrial sites as well as spring sites) that will eventually be lost, and m is the rate parameter that governs the loss of that extra capacity. Note that the current warm-water capacity is not a parameter in this model, but can be calculated as the sum of k_0, k_M, k_T, and k_X. The indicator variables take the value 1 if the corresponding inequality is true, 0 if it is false (thus, if $t < c_M$, $I_{t<cM} = 1$, meaning the Ft. Myers plant is still operating at time t).

3. Parameter Estimates and Uncertainty

The parameters used in the model are shown in Tables 1-5 and in Appendix B. These parameter estimates come from several sources: published peer-reviewed literature, recent unpublished analyses, and consensus views of expert panels. In the latter two cases, the methods for deriving the parameter estimates are described in some detail below. Appendix B describes in detail all the parameters in the model, their values, and the sources of the estimates. The parameter estimates presented here reflect our understanding of manatee demography at the time that the state's 2006 biological status review was completed (Haubold et al., 2006).

3.1. Uncertainty

A concerted effort is made throughout to explicitly characterize the uncertainty associated with parameter estimates. This uncertainty is integrated into the simulations so that the results

appropriately reflect the state of current knowledge. There are two primary ways that uncertainty was characterized. First, in the case of parameters that could be estimated through formal statistical analyses, uncertainty is expressed as the sampling distribution for the estimate (e.g., the credible interval for a survival rate appropriately expresses the uncertainty in the mean value for that rate). Second, in the case of parameters that were elicited from expert panels, low, median, and high values were derived by consensus. The uncertainty in the corresponding parameter was expressed as a two-phase uniform distribution having the specified low, median, and high values (Fig. 2). In the sections that follow, the uncertainty in the parameter values is discussed along with the point estimates.

3.2.   Survival and reproductive rates

The mean annual survival rates and breeding probabilities are shown in Table 1, along with confidence intervals that express the uncertainty in those values. The survival rates were derived from analysis of mark-recapture photo-identification data (Langtimm et al., 2004). Direct estimates of adult survival rates were available for all four regions. Direct estimates of survival rates for the younger age classes were only available for the Upper St. Johns region (Langtimm et al., 2004); the ratios of younger to adult survival rates in the other regions were assumed to be the same as in the Upper St. Johns region (Runge et al., 2004). The breeding probabilities for females that have previously bred (γ_B) were derived from the reproductive histories of known females. In the Atlantic and Northwest regions, formal mark-recapture analysis was used to estimate these breeding probabilities (Kendall et al., 2003; Kendall et al., 2004). In the other regions, and for the other breeding probabilities (γ_P and γ_4), estimates were obtained by calculating binomial proportions from the observed stage transitions of known, marked females (Runge et al., 2004). In the Southwest, this involved a reexamination of reproductive histories of marked animals in Sarasota Bay (Koelsch, 2001).

The uncertainty in the mean survival rates and breeding probabilities 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). The four-year-old reproductive rate (γ_4) was constrained to be less than γ_P; otherwise, the uncertainty among mean parameters was assumed to be independent.

3.3.   Temporal variance

The temporal variance for the adult survival rates (Table 2) was estimated from the year-specific estimates of survival over the years 1990-1999 (Langtimm et al., 2004), using the variance components estimation method of Burnham et al. (1987, pp. 260-266). The distribution of the estimate for the variance ($\hat{\sigma}^2$) is such that

$$\frac{SSQ}{\hat{\sigma}^2 + \hat{\text{var}}} \sim \chi^2_{n-1} \tag{9}$$

where *SSQ* and $\hat{\text{var}}$ are derived from the data as described in equations (4.9) and (4.10) of Burnham et al. (1987, p. 265). This distribution was used to characterize the uncertainty in the

variance, negative values were truncated to 0, and the square root was calculated. The 95% confidence interval for the standard deviation, as generated by this distribution, is shown in Table 2. The subadult survival rates were assumed to have the same variance as the adult survival rates.

Direct empirical estimates of temporal variance were not available for the two calf survival rates in each region. Instead, based on our own expert judgment, we set the coefficient of variation to be roughly twice that in the adult survival rates. For adult survival rates in each region, the means (and 95% confidence intervals) for the coefficient of variation were: Atlantic, 1.26% (0 – 5.6%); Upper St. Johns, 0% (0 – 0%) (there is no empirical evidence for temporal variance in this region); Northwest, 1.35% (0 – 5.6%); Southwest, 0% (0 – 10.3%). Assuming that calves are approximately twice as vulnerable to environmental variation as adults, the desired coefficients of variation for calf survival rates were: Atlantic, 2.5% (0 – 10%); Upper St. Johns, 0% (0 – 5%) (we wanted to include the possibility that calves might experience some temporal variance in survival in this region, even though adults do not appear to); Northwest, 2.5% (0 – 10%); Southwest, 0% (0 – 20%). These coefficients of variation were converted to values for standard deviation on the logit-scale (Table 2). The point estimate and range were treated as the median, low and high of a two-phase uniform distribution, in order to characterize uncertainty in the temporal variance of calf survival rates.

A direct estimate of temporal variance of γ_B using year-specific estimates from a mark-recapture analysis of photo-identification data could only be obtained for the Northwest and Atlantic regions (Kendall et al., 2004), using the methods of Burnham et al. (1987), as described above. The uncertainty was characterized using Eq. (9). In the Upper St. Johns region, γ_B was assumed not to vary, based on the very low estimate of variance in the Atlantic region, and the protected nature of the Upper St. Johns region. In the absence of information for the Southwest region, the temporal variance in γ_B was assumed to be the same as for the Northwest region. The temporal variance of the breeding probability of the pre-breeders (γ_P) was assumed to have the same distribution on the nominal scale as that of the breeders (γ_B). The breeding probability of four-year-olds (γ_4) was assumed not to vary temporally.

3.4. Catastrophes

The probabilities of Type 1 and Type 2 catastrophes and the magnitude of the corresponding effects on survival and reproduction are summarized in Table 3. These estimates match those used by the state of Florida in their 2002 Status Review (FMRI, 2002).

3.5. Warm-water capacity

Warm-water capacity for the core biological model is interpreted as the number of manatees that can fit into suitable warm-water habitat during prolonged cold periods, and so escape injury or death due to cold stress. The estimates used in this model were derived from discussions with the Warm Water Task Force, a multi-agency, multi-stakeholder group of experts formed under the auspices of the Manatee Recovery Team to address the issues associated with manatees and warm water (Runge, 2003). Elicitation of the parameters for Eqs. (6)-(8) from this expert panel took place through discussion guided by model results. That is, in the first round of discussions,

preliminary model forms and parameters were elicited. These parameters were then used to generate results (in the form of distributions of warm-water capacity over time). In the second and subsequent rounds of discussion, the panel was shown the results and asked whether they conformed to their intuition; any tension motivated further discussion and refining of parameters. In all discussions, deliberate attention was given to characterizing uncertainty: instead of being asked to provide only a point estimate for any parameter, the panel was asked to consider the range of plausible values.

The projected warm-water capacity for manatees is shown in Fig. 3, with explicit characterization of uncertainty. The details of the parameter estimates are given in Appendix B. In the Northwest region, current warm-water capacity was estimated to be 1200 animals (range of uncertainty, 750-3000); long-term capacity was estimated to be 70% of that (40-85%), and the half-life of loss was estimated as 20 yr (10-40). In the Upper St. Johns region, the estimate for current capacity was 325 (150-500), the estimate for long-term capacity was 71% of that (33-89%), and the estimate of half-life of loss was 20 yr (15-30). In the Southwest region, the estimates for long-term capacity, Ft. Myers capacity, Tampa capacity, and "extra" capacity were 850 (500-1100), 450 (400-500), 540 (480-600), and 600 (200-800), respectively, giving a derived estimate of current capacity of 2440 (1580-3000). In the Atlantic region, current capacity was estimated to be 2000 animals (1200-5000), long-term capacity was estimated to be 750 (600-2000), the mid-point of the drop was expected to occur 15 yr (10-20) in the future, and there was considerable uncertainty about the rate at which the drop would occur.

3.6. *Effects of approaching or exceeding warm-water capacity*

The potential effects of exceeding warm-water capacity during severely cold years were discussed by an expert panel convened to provide input to the State's population viability analysis, August 16, 2002 at the Florida Marine Research Institute. The estimated mortality rates associated with cold-stress are shown in Table 4. Where a range is provided to express uncertainty, the three values are used as the median, low, and high values in a two-phase uniform distribution (Fig. 2). The parameters associated with the density-dependent decline in reproductive rates (Eq. (5)) have not been measured in wild manatee populations. Point estimates were postulated that produced biologically reasonable patterns (e.g., smooth, rather than chaotic, approach to equilibrium), then bounded by large ranges to capture uncertainty. The median value for α was 0.25 (range 0.15-0.50). The median value for β was 2 (range 1-4).

Direct estimates of the reproductive rates at low density, γ_0, are not available; instead, estimates of the realized reproductive rates are available (Section 3.2), but the associated population sizes (relative to warm-water capacity) are not known. To estimate γ_0 for any particular replicate of the simulation, we extrapolated Eq. (5) back to low density, using the initial population size and the sampled estimate of the current warm-water capacity. That is,

$$\gamma_0 = \frac{\hat{\gamma}}{1 - \alpha \left(\frac{N_0}{K_0} \right)^{\beta}} . \tag{10}$$

3.7. Generation length

Some of our desired summary metrics required us to estimate the generation length for manatees. We interpreted generation length as the mean age of the parents of offspring produced by a population at the stable age distribution (Caughley, 1977, p. 124; Caswell, 2001, p. 129). This can be calculated from the entries of a life table as

$$\bar{T} = \frac{\sum_x x\lambda^{-x}l_x m_x}{\sum_x \lambda^{-x}l_x m_x} \; . \qquad (11)$$

This measure of generation length is influenced positively by survival rates, negatively by age at first-breeding, and negatively by growth rate (because the faster a population is growing, the more the standing age-distribution is skewed toward young animals, including younger breeders). We used the life-history parameters from Runge et al. (2004) and focused on the Atlantic and Northwest regions because the high growth rate in the Upper St. Johns region biases the generation length low, and because the low growth rate in the Southwest region biases the generation length high (these trends are counter to the intuition based on survival rates alone, but it's important to consider the other factors as well). Using the same parametric uncertainty as Runge et al. (2004), we estimated the generation length for manatees to be between 16.8 and 22.6 yr.

4. Simulation

All simulations described in this paper were based on projecting the population 150 yr into the future, and completing 5,000 replicates. A detailed outline describing how the simulations were carried out can be found in Appendix C.

The synoptic survey count of January 5-6, 2001 was used to set the initial population size for three of the four regions (Table 5, for description of the surveys see Ackerman, 1995). For the Upper St. Johns region, following the 2002 BSR model, the initial population size was based on the number of individuals identified over the winter of 2000 – 2001 (141), rather than the synoptic survey count (112). For each replicate, the expected initial population structure (the fraction of the population in each sex/stage class) was found by calculating the stable stage distribution (dominant eigenvector) of the CBM projection matrix (Eq. (1)) using the sampled values for each life-history parameter. The expected stage distribution does not include first-year calves because Eq. (1) does not have a separate category for first-year calves. The initial population structure was drawn randomly from a multinomial distribution defined by the stable stage distribution, with the total given by the values in Table 5. Because the total population size includes first-year calves, the number of first-year calves (equivalent to the number of mothers with calves) was added to the total of the other classes (as in Eq. (2)). Thus, the starting population size was larger by the number of first-year calves than the totals in Table 5, and varied slightly among replicates. The initial population structure also varied between replicates to reflect uncertainty about the actual structure of the population in 2001.

Uncertainty and stochasticity were handled quite differently in the simulations. The distributions that characterized parametric uncertainty (sampling error) were sampled at the beginning of each

replicate; the values sampled were held constant through the multiple years of that replicate. In contrast, the distributions that characterized stochasticity (temporal variance) were sampled independently for each year of each replicate.

Simulation outputs were replicate trajectories over time of the population size and structure, the variation in those trajectories reflecting the integrated effects of uncertainty and stochasticity. A variety of common measures were calculated, such as the population size over time, the realized growth rates of the population over 1 or more years, the probability of extinction or quasi-extinction, and the probability of declines of various magnitudes. To calculate the change in population size over a number of generations, the length of a generation was sampled from a uniform distribution between 16.8 and 22.6 yr, to reflect uncertainty about the length of a manatee generation.

A comprehensive sensitivity analysis was conducted to explore the impacts of the variability of each parameter on model behavior and predictions. In general, each parameter in Appendix B was varied across a range defined either by the minimum and maximum values or the 95% confidence interval. For each value of the parameter being investigated, 500 replicates of a 100-yr trajectory were run. Sensitivity runs included sampling the uncertainty distributions for all parameters other than the parameter under study. All sensitivity analyses were run without demographic stochasticity to reduce computation time and to discern small effects.

The sensitivity of a response variable (e.g., growth rate) to a parameter (e.g., adult survival) is the ratio of the induced change in the response variable to the change in the particular parameter (Caswell, 2001); we calculated this from the simulation results by finding the slope of the response variable with respect to the parameter. The elasticity of a response variable to a parameter is similar, except it is the ratio of proportional, not absolute, changes (Caswell, 2001); we calculated this by finding the slope of the log(response variable) with respect to the log(parameter). Variance decomposition explores the contribution of uncertainty in parameters to uncertainty in a response metric, and is influenced both by the respective sensitivity and the range of uncertainty in the parameter (Caswell, 2001). We calculated variance contributions for each combination of response variable and parameter, by finding the difference between the values of the response variable at the maximum and minimum values of the parameter in question.

Sensitivity, elasticity, and variance contribution were calculated for all parameters, and for the following response variables: first-year population growth rate, population size (log-scale) and standard deviation of population size at 100 years, and the probability of quasi-extinction over 100 years. For this purpose, quasi-extinction was defined as less than 50 animals (including first-year calves) within a region; this is sufficiently close to outright extinction that it should be sensitive to the same variables, but the sensitivity can be examined with fewer replicates. For each response variable, the most important parameters (either for sensitivity, elasticity, or variance contribution) were identified by selecting the top four contributors from each region.

In performing the sensitivity analyses, there were several parameters that required special treatment. (1) Currently, an uncertainty range is not specified for the catastrophe parameters (Table 3). Work is needed to characterize the uncertainty in both the frequency and the effects of

catastrophes. For the sensitivity analyses, we explored the range for the probabilities of catastrophe from 0 to 4 times the specified value. For the decrease in survival as a result of Type I catastrophe, we explored a range of 10-50%, based on the suggestion by Harwood and Hall (1990) that virulent disease mortality could be as high as 50%. For the decrease in survival as a result of Type II catastrophe (red-tide), we explored a range of 5-35%. Impacts on reproduction from either red-tide or virulent disease are not well-documented. We explored values for the decline in reproduction between 0% and 20%. (2) For the mortality rate of adults outside warm-water refugia in normal winters, we explored the range 0 to 20%.

5. Results

The Core Biological Model projects statewide population dynamics over time, given that the parameters and assumptions remain valid over the forecasting period. Specifically, these results assume that the survival and breeding rates, watercraft-related mortality, and other anthropogenic effects remain the same in the indefinite future as in the recent past (5-20 years depending on region) and that the warm-water capacity follows the forecast trends.

5.1.   *Population growth rates*

The population growth rates incorporate not only the survival rates, breeding rates, and transition rates, but also the effects of demographic stochasticity, environmental stochasticity, probability of virulent disease or red tide, and density dependence. For the Upper St. Johns Region and the Northwest Region, the model predicted an increase in the population over time until reaching warm-water capacity (Fig. 4). The one-year population growth rate was 1.053 ± 0.049 for the Upper St. Johns Region and 1.024 ± 0.064 for the Northwest Region. The mean 10-year population growth rate was 1.050 ± 0.018 (SD) for the Upper St. Johns Region and 1.022 ± 0.025 (SD) for the Northwest Region. The mean 100-year population growth rate was 1.006 ± 0.005 (SD) for the Upper St. Johns Region and 0.996 ± 0.105 (SD) for the Northwest Region. In the Southwest region the model predicted a population decline over time (Fig. 4). The one-year population growth rate was 0.959 ± 0.071 (SD), the mean 10-yr population growth rate was 0.963 ± 0.035 (SD), and the mean 100-yr population growth rate (for those populations that did not become extinct in that period) was 0.969 ± 0.016 (SD). In the Atlantic region, the model predicted an increase over the next ca. 10 yr, then a decrease as warm-water capacity is lost (Fig. 4). The one-year growth rate was 0.993 ± 0.039 (SD), the mean 10-yr growth rate was 0.999 ± 0.015 (SD), and the mean 100-yr growth rate was 0.989 ± 0.049 (SD). The statewide trend (found by summing the four regions) was predicted to be a slow decline over the next decade (driven by the predicted decline in the Southwest), followed by a faster decline as warm-water capacity is lost, finally stabilizing at a lower equilibrium point in the long run (Fig. 5a).

5.2.   *Probabilities of extinction and quasi-extinction*

The probabilities of outright extinction over 3 and 5 generations and 100 yr were calculated for each region, under the assumption that the regions are independent (i.e., that there is no movement among them). The probability of extinction for the Atlantic region was 0.04% over both 5 generations and 100 yr (the probability was <0.02% for 3 generations; that is, no extinctions occurred in 5000 replicates). In the Upper St. Johns region, the probability of

extinction was <0.02% over all time frames investigated. In the Northwest region, the probability of extinction was 0.18% over 3 generations, 0.56% over 5 generations, and 0.62% over 100 yr. In the Southwest region, the probability of extinction was 1.72% over 3 generations, 11.54% over 5 generations, and 11.94% over 100 yr.

The probability of quasi-extinction, defined as the probability of falling below a particular fraction of the initial population size at any point within a time period, was calculated for each region, for quasi-extinction thresholds between 0 and 50% of the original size, and for 50, 100, and 150-yr periods (Fig. 6). In the Northwest and Upper St. Johns regions, the probability of quasi-extinction never exceeded 10%, even for a 50% threshold over 150 yr. In the Southwest and Atlantic regions, the probability of quasi-extinction was considerably higher; for instance, the model predicted it highly likely that the Southwest population will decrease to less than half its current size over the next 50-100 yr. Statewide, the probability the population will drop from a current size near 3700 (including first-year calves) to below 1000 individuals was around 5% over 150 yr, and 2.3% over 100 yr (Fig. 5b).

5.3.   IUCN metrics

The International Union for Conservation of Nature and Natural Resources (IUCN, 2001) uses a diverse set of criteria to classify organisms as critically endangered, endangered, or vulnerable. Several of these metrics involve the predicted change in the population size over 1, 2, 3, or 5 generations. The CBM predicted a decline in the statewide manatee population over all of these time periods, ranging from an estimated 8.0% decline in 1 manatee generation to a 30.0% decline in 5 generations (Fig. 7). Specific combinations of generation length and predicted decline are used by the IUCN to classify the degree of endangerment; for instance, a population is considered endangered if it is projected to decrease by more than 50% over 3 generations. The probabilities of these various declines are listed in Table 6, for each region and for the statewide population. Based on the results from the model, it is quite possible (46.5%) that the statewide population will decline by 30% over three generations (i.e., vulnerable), conceivable (12.1%) that it will decrease by 50% (i.e., endangered), but very unlikely (<0.02%) it will decrease by 80% (i.e., critically endangered).

5.4.   Sensitivity analyses

For all regions, first year population growth rate was most sensitive to adult survival rate (Fig. 8). For all regions except the Upper St. Johns region, the magnitude of temporal variance in adult survival rates and the probability of a virulent disease ranked second and third, although their relative rankings varied across regions. In the Upper St. Johns region, the probability of virulent disease ranked second and the subadult survival rate ranked third. Again for all regions, the population size 100 yr from present was most sensitive to adult survival rate (Fig. 9), with temporal variance in adult survival and the probability of catastrophic disease ranking second and third in all regions except the Upper St. Johns, where the long-term warm-water capacity played a role. For the three regions where population size dropped to 50 animals with any measurable likelihood (i.e., Northwest, Southwest, Atlantic), the probability of quasi-extinction was most sensitive to adult survival, environmental stochasticity of adult survival and the

probability of virulent disease (Fig. 10). Parameters not shown on these figures were ranked fifth or greater in all regions, and thus were viewed as being of lesser influence.

5.5. Elasticity analyses

The results from the elasticity analysis were similar to those from the sensitivity analysis (results not shown). For all regions and all response variables investigated, the elasticity was highest for adult survival rate. In all regions except the Upper St. Johns, sub-adult survival and second-year calf survival had the second and third largest elasticities. For the Upper St. Johns region, population size 100 yr from present was influenced by current and long-term warm-water capacity.

5.6. Variance contributions

The most important contributors to uncertainty varied by response variable and region, and were more numerous than the top contributors to sensitivity and elasticity. In the Atlantic region, uncertainty in population size 100 yr from present was strongly driven by uncertainty in the adult survival rate, the temporal variance of adult survival, calf survival rates, the frequency of Type I catastrophes, and the current and long-term warm-water capacities (Fig. 11). In the Upper St. Johns region, uncertainties in the current and long-term warm-water capacities are the strongest contributors to uncertainty in long-term population size. In the Northwest region, uncertainty about temporal variance in adult survival is the most important contributor, with the warm-water capacity parameters and adult survival also playing a role. In the Southwest, uncertainty in adult survival and its temporal variance are the most important drivers of uncertainty in long-term population size. While the magnitudes of the variance contributions differed among regions, the pattern across parameters was the same. Note that in the Upper St. Johns and Northwest models, the warm-water parameters have slightly different meanings than in the other two regions: k_0 is the long-term warm-water capacity, as a fraction of the current warm-water capacity (k_1), whereas in the Southwest and Atlantic models, k_0 is the long-term capacity expressed on an absolute scale. This difference explains the apparent difference in pattern (Fig. 11).

6. Discussion

The CBM forecasts the population dynamics of the Florida manatee in the four regions, integrating current information on life history, incorporating uncertainty in parameter estimates and applying both demographic and environmental stochasticity. The CBM is an improvement over the IT, 2002 BSR, and SSM models, because it incorporates a greater number of important features of manatee life history and has the flexibility to address a broader range of questions. Like the IT and SSM models, the CBM explicitly accounts for parametric uncertainty; like the BSR and IT models, it incorporates stochasticity. The modular design of the CBM allows it to be customized to answer specific regulatory or management questions. In interpreting the results of the CBM, it is necessary to bear in mind that these results are conditional upon the assumptions of the model, most importantly that threats will remain at their current levels. Specifically, this assumes that watercraft-related mortality will continue indefinitely at its current rate, a significant amount of warm-water capacity will be lost over the next 40 yr as power plants close and spring flows diminish, red tide frequency and magnitude will continue in the future at

the rates estimated, and all other threats will remain at their current levels. Management intervention, as described in the state's management plan and the Federal recovery plan, is intended to improve the status of manatees over time, and if successful, would produce outcomes that differ from the predictions of this model. It is also important to note that the results presented in this paper are based on parameter estimates that were available at the time of the State's 2006 biological status review (Haubold et al., 2006); certainly these results will be superseded as new information becomes available.

6.1.   Population projections

Annual growth rates estimated by the CBM indicate that manatee populations in the Northwest and Upper St. Johns regions are expected to increase at rates of 2.2% and 5.0%, respectively, on average over the next decade; the population in the Atlantic region is expected to remain stable; but the population in the Southwest Region is expected to decrease at a rate of 3.7%. Over time, the growth in the Northwest and Upper St. Johns regions is expected to taper off as the populations approach the warm-water capacity of those regions. In the Southwest, given current parameter estimates and expectations for long-term warm-water capacity, the population is expected to decline over the long-term. In the Atlantic region, any population growth over the next 10-15 yr is expected to taper off, and then turn to a decline as warm-water capacity is lost from the industrial sites (Fig. 4).

Under current levels of threats, including the anticipated loss of warm-water, the statewide manatee population has a low probability of extinction for several reasons: (1) the current population size (>3000 animals) and the longevity of manatees provide a considerable buffer against threats; (2) the CBM treats the regions as independent (if environmental variation among regions is positively correlated, we would expect higher extinction rates; but conversely, migration could provide a rescue effect and lower extinction probability); and (3) the strength of growth in two regions, especially the Upper St. Johns, provides a strong safety net for the statewide population. Analysis of the individual regions, however, reveals vulnerability. There is a high probability of a significant reduction in population size in the two regions that support the most manatees, the Atlantic and Southwest. Thus, the CBM predicts that a substantial shift in the regional distribution of manatees within the state is likely.

The results in this paper appear to emphasize the threat due to the loss of warm water and to exclude consideration of other threats, but that appearance is a consequence of the future emergence of the warm-water threat. In these results, it is fairly easy to see the before and after effects of loss of warm water. In fact, other threats (like watercraft-related mortality) are integrated into these results, but because they are acting currently, their effects are not as apparent. A full analysis of threats could be performed with this model, but would require specific simulations to look at, say, the probability of quasi-extinction as a function of the presence or absence of various threats.

6.2.   *IUCN classification*

This paper does not attempt a full analysis of manatee status with regard to IUCN criteria. It does, however, provide results that can be used to interpret several of the criteria, specifically,

criteria A, C, and E (IUCN, 2001). Criterion A concerns reduction in the population size (either in the past or anticipated in the future); for manatees, the relevant aspect of this criterion is an anticipated future reduction. If the projected or suspected reduction is ≥80% over three generations, the population is classified as critically endangered; ≥50%, endangered; ≥30%, vulnerable. What the IUCN criteria do not specify, however, is the strength of evidence needed for the projected reductions. The CBM predicts a statewide population reduction over three generations of ≥30% with probability 46.5%; ≥50% with probability 12.1%; and ≥80% with probability <0.02% (Table 6). We believe that the precautionary philosophy underlying the IUCN criteria requires fairly strong evidence against any projected decline; thus, we believe Florida manatees do not qualify as critically endangered under this criterion, may qualify as endangered, and at least qualify as vulnerable.

IUCN Criterion C concerns reduction in population size in conjunction with small current population size. To be classified as endangered under this criterion, a population needs to number fewer than 2500 mature individuals and have an estimated continuing decline of ≥20% in two generations. The CBM estimates a 55.5% probability of ≥20% decline over two generations. While current estimates of the statewide population exceed 3200 animals, many of these animals are not of breeding age. The stage distributions predicted by the CBM suggest that the current number of mature individuals is less than 2500. Thus, we believe Florida manatees qualify as endangered under IUCN Criterion C.

IUCN Criterion E concerns the probability of extinction as calculated by a model like the CBM. To be classified as vulnerable, the probability of extinction needs to exceed 10% over 100 yr. Florida manatees do not meet this criterion, based on the results of the CBM.

6.3. *Comparison to other manatee population models*

The CBM model is similar to two previous modeling efforts, the 2002 BSR and IT models, but differs in some important ways. The 2002 BSR model was based on a Leslie matrix as implemented in the software Vortex (Lacy, 1993), and did not account for uncertainty in parameter estimates. Although the CBM, IT, and BSR models all included density dependence and environmental and demographic stochasticity, they differed in their methods. The BSR model truncated population size at carrying capacity (defined as twice the initial population density), while the CBM and IT models applied additional cold weather mortality to the animals exceeding the warm-water refuge capacity. The CBM, IT, and BSR models allowed for two types of catastrophes, virulent disease and red-tide; the BSR model also included a cold weather catastrophe for calves in the Atlantic and Southwest regions. The BSR model was restricted by Vortex to a fixed age at first reproduction, while the other three models contained a pre-reproductive stage allowing age at first reproduction to vary. The BSR was the only model to allow twinning. Because the BSR was written to examine the possibility of population decline across the state of Florida, it was the only model to combine the four regions in a metapopulation structure by estimating movement between the regions. The IT model was written specifically to address the issue of incidental take and therefore separated boat strike mortality from other causes of mortality. Currently, the CBM integrates boat mortality in the survival rates, however adaptive components could be developed to explore the effects of different levels of boat mortality. The IT model applied additional cold mortality to juveniles considered to be inside

the warm-water refugia, in contrast to the CBM which assumed cold mortality as a part of the overall estimate of calf mortality.

The 2002 BSR model and the deterministic stage-structured matrix model (SSM) support the general trends found in the CBM. The one-year growth rates estimated by the CBM are lower than the growth rates estimated by the SSM, because the CBM includes environmental stochasticity, density dependence, and catastrophes, all of which will decrease population growth rates. Estimates from the CBM model run without these components are within 0.2% of the estimates from the SSM model, a difference attributable to rounding.

6.4.   Sensitivity, elasticity, and variance contribution

The sensitivity and elasticity results emphasize the impact of adult survival rates on population growth rates, both short- and long-term (Fig. 8). Population models for other long-lived species, such as killer whales (Brault and Caswell, 1993), cheetahs (Crooks et al., 1998) and sea turtles (Crouse et al., 1987) have also found adult survival to have the largest effect on population growth rate. Population size and quasi-extinction probability are also strongly affected by adult survival rate and its variance (Figs. 9-10). Sensitivity and elasticity should not be equated with management priority, however, because life-history parameters that most influence important demographic results are not necessarily the ones most easily changed through management. Sometimes parameters with lesser influence are easier to change and are thus more useful in evaluating management options (Morris and Doak, 2002). Such an analysis requires a more detailed understanding of how potential management actions might affect life-history parameters.

The analysis of variance contributions allows identification of research priorities that are expected to most improve precision of projections from the model. In order to improve estimates of long-term population size (Fig. 11) in the Upper St. Johns and Northwest regions, we need better estimates of the long-term warm-water capacity (the product k_1k_0). In the Atlantic region, while estimates of warm-water capacity are important, better estimates of adult survival and its temporal variance, as well as the frequency of catastrophic disease, are required. In the Southwest, the picture is quite different; with an expected decline, long-term warm-water capacity is not particularly relevant—it is much more important to improve estimates of adult survival and its temporal variance. For improving estimates of quasi-extinction (results not shown), the most important research priorities in all regions are better estimates of adult survival and its variance.

Sensitivity analysis of the results to the estimate of initial population size was not performed. Some of the results, particularly those that are stated in terms of absolute population size, may be sensitive to uncertainty in the initial population size, and this sensitivity may be tied as well to uncertainty in the long-term warm-water capacity. Other results, such as those stated in terms of proportional changes to the population (growth rate, quasi-extinction) may be less sensitive to estimates of initial population size.

7. Model Development and Future Work

7.1. *Priorities for model development*

The CBM, like any model, is a simplification of a real system, and is based on a current understanding of ecology and on available data. The CBM should evolve over time, as better estimates for parameters become available, as we acquire a better understanding of the biological mechanisms that affect manatee demography, as the theory of population demography advances, and as the model is applied to new problems. Based on an understanding of what this current CBM omits, and especially relying on the sensitivity and related analyses, we see the following issues as important for future development of this model.

Survival rates. Uncertainty in survival rates, especially for adults, dominates uncertainty in many of the results of interest. Thus, continued focus on improving estimates of survival rate, and tracking changes in survival rate as a function of management actions, is warranted. This is particularly true in the Southwest region, where uncertainty in the survival rates is large enough that it is difficult to know whether the population is currently decreasing or increasing. Langtimm et al. (2004) found an apparent decline in adult survival rates in the Atlantic region at the end of the available time series. Current work is underway to determine whether that trend was due to a real change in survival rates or a bias caused by temporary emigration. Similar work is needed with the Southwest survival rates, but the short time series available in that region is also a limitation. In addition, better estimates of temporal variance in survival rates are needed; this might be especially true in the Upper St. Johns region where the current estimate of variance in adult survival is 0, but the region may experience greater variance in survival over time as the population expands beyond Blue Spring in the winter.

Warm-water capacity. Warm-water capacity is an important element of the CBM and strongly influences the projections of future population size. The models for warm-water capacity were developed by an expert panel in 2002-2003. As empirical data become available, and particularly as the economics and politics of the energy and water industries change, these models will need to be revisited. The very recent dredging to provide manatee access to Homosassa Spring, and the quick response of manatees to that availability, demonstrate the need to update estimates and forecasts of warm-water capacity.

Initial population size. Future versions of the CBM should reconsider how to handle the initial population size. First, the initial population size for these results was based on the state's synoptic survey of 2001 (except in the Upper St. Johns region), which is likely to be an underestimate of the true population size, and is increasingly outdated. Second, no uncertainty in the starting population size was incorporated into the simulations. Third, we assumed that the counts from the synoptic survey did not include first-year calves, so we added first-year calves to the counts to form the initial population; this assumption may be erroneous. We do not believe these assumptions are affecting the general patterns of results, but the results from the model can be refined in the future by revising how the initial population size is estimated. Current efforts to improve the methodology and analytical framework for the synoptic survey will be beneficial to this model.

Red tide. The estimated frequency and magnitude of red-tide mortality were based on the state's 2002 status review (FMRI, 2002), but observed mortality events since then suggest the frequency and perhaps also the magnitude may be increasing, especially in the Southwest region. Thus, the parameter estimates in the CBM need to be revisited. In addition, uncertainty in the estimates of these parameters should be incorporated into the model. If red tide is becoming more regular, then it may be more accurate to model it as a change in the mean and temporal variance of survival rates (i.e., a part of "normal" variation) than as a catastrophic event. At any rate, it is possible that the results in this paper understate the effect of red tide, particularly in the Southwest region.

Cold-related mortality. The primary mechanism for density-dependence in the CBM is additional cold-related mortality in animals that cannot find space in warm-water refugia. This mechanism is not well understood because warm-water capacity has exceeded the population size over recent decades. As manatee populations increase in some areas, and as warm-water capacity is lost, we expect to observe increased cold-related mortality. Research that anticipates when these events will occur, or at least tracks the consequences when they do occur, is important for improving our understanding of the long-term impact of warm-water capacity. We also need a better understanding of the effect of age on cold-related mortality—are calves the most vulnerable, or are subadults more vulnerable because they cannot rely on their mother's experience? Are the age-related effects of cold similar across regions? The juvenile survival rates are based on estimates from the Upper St. Johns region and include the effects of cold, hurricanes, and other factors in that area. The Southwest and Atlantic regions, however, have higher juvenile mortality due to cold than the Upper St. Johns (Deutsch et al., 2000). Finally, the dynamics of cold-related mortality are undoubtedly more nuanced than we have portrayed in the model—distinguishing "cold" from "normal" years may be too simple. For example, there may be winters that are not abnormally cold on average, but are unusual in the timing of cold fronts (e.g., several cold fronts early, before manatees have settled into their winter distributions). These questions should be considered in the future evolution of the CBM.

Hurricanes. There is emerging evidence that hurricanes can affect manatee survival and distribution (Langtimm and Beck, 2003), perhaps in ways that are distinct from "normal" environmental variation. If this is the case, and particularly if climate change affects hurricane frequency and intensity, future versions of the CBM might need to include hurricane effects, perhaps as another form of catastrophe.

Migration and distribution. Florida manatees do move between the four regions, although the common belief is that the movement rates are fairly low. A better understanding of these movement patterns, and how they might change as the regional population sizes and warm-water capacities change, would improve projections of the statewide population.

7.2.   Applications

The manatee core biological model is meant to serve as a flexible projection model for use in assessments relevant to management decision making. We hope it will serve as the core of future modeling efforts; customization for specific applications can occur by controlling various input variables or scenarios and by extracting different response metrics. Several applications

are underway or planned, including: simulations to help develop measurable biological goals for the state's manatee management plan; an analysis of threats to future persistence of Florida manatee populations; evaluation of quantitative recovery criteria; and evaluation of incidental take under the Marine Mammal Protection Act.

Acknowledgments

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Appendix A. Outline of the modeled annual cycle

The components of the model described in the preceding sections are assembled in the manner described below. In this outline, "DEM" refers to an element of demographic stochasticity, "ENV" refers to an element of "normal" environmental stochasticity, and "CAT" refers to a catastrophe.

1. Input: initial population size and structure (mid-winter), warm-water capacity for that winter, correlation coefficient.
2. Calculate effect of exceeding warm-water capacity.
    a. [ENV] Determine if it is a "cold" or "normal" year, based on the standard normal variate used for the annual survival rates (see 3.a. below).
    b. [DEM] If N_{Total} exceeds K, distribute each stage class to "inside" or "outside" the warm-water refugia using a multivariate hypergeometric distribution.
    c. [DEM] Apply the appropriate cold-related mortality rates to the animals in each stage class, depending on whether it is a cold or normal year, whether they are inside or outside refugia, and whether they are calves or older. A binomial distribution is used to determine how many in each stage class survive the winter into spring.
3. Calculate survival and reproductive rates for the remainder of the year
    a. [ENV] Generate annual survival rates and breeding probabilities by sampling from the appropriate logit-normal distributions using correlation coefficient.
    b. [CAT] Determine if a virulent disease strikes the population. If so, reduce the survival and recruitment rates accordingly.
    c. [CAT] Determine if a red tide event strikes the population. If so, reduce the survival and recruitment rates accordingly.
    d. Calculate the density-dependent reduction in breeding probabilities (using the spring population size relative to the warm-water capacity).
4. Apply the life-history parameters
    a. [DEM] Calculate the number of animals in each stage that survive to the next year, using a binomial distribution with the appropriate survival probability.
    b.   [DEM] Calculate the number of the surviving females in each stage that successfully produce young, using binomial distributions.
    c. [DEM] Calculate the number of surviving first-year calves that are female, using a binomial distribution. Calculate the number of males by subtraction.
5. Advance the age classes and make the appropriate stage transitions to produce a resulting population vector.

Appendix B. Parameters and their estimates in the CBM

The accompanying spreadsheet (OFR2007-1082AppB.pdf) contains a detailed listing of the parameters in the CBM, the estimates used to generate the results in this paper, and the sources for those estimates.

Appendix C. Outline of the simulation structure
Each simulation consisted of n replicates of x year time series. The structure of each simulation is outlined below.
1. Set the region.
2. Set the hyperparameters (the values that describe the uncertainty distributions for all the parameters), as given in Section 3.
3. Loop over replicates (e.g., $n = 1000$)
   a. Sample all parameters from their uncertainty distributions
      i. Sample warm-water capacity parameters
      ii. Calculate warm-water capacity for $t = 1$ to x years (e.g., $x=100$)
      iii. Sample cold-related mortality parameters, including α and β
      iv. Sample annual survival rates and breeding probabilities
      v. Calculate γ_0 rates from annual breeding probabilities, initial population density, warm-water capacity, and α and β
      vi. Sample standard deviations for temporal variance
   b. Generate variates that govern environmental stochasticity and catastrophes (4 variates for each of x yrs—2 variates from a bivariate normal distribution for the environmental stochasticity in survival rates and breeding probabilities using the correlation coefficient, and two uniform variables for the occurrence of Type 1 and Type 2 catastrophes.
   c. Loop over the specified levels of sensitivity parameter values (optional). For example, replace the sampled annual adult survival rate with one of a set of values within the 95% confidence interval for this region. Loop over the entire set of sensitivity parameter values. The different sensitivity runs will vary only by the sensitivity parameter and the effects of demographic stochasticity.
      i. Set the initial ($t = 0$) population vector by distributing the initial population size across stage classes, using the stable stage distribution predicted from a matrix model of the sampled survival rates and breeding probabilities (or sensitivity parameter values), using a multinomial distribution.
      ii. Loop over time for $t = 1$ to x (e.g., $x=100$)
         1. Adjust survival rates and breeding transition rates to reflect environmental stochasticity, density dependence, and catastrophes.
         2. Apply survival rates and breeding transition rates to population distribution, incorporating demographic stochasticity.
         3. Calculate the one-year change in the population vector
      iii. End loop over time
   d. End loop over levels of sensitivity parameter
4. End loop over replicates
5. Calculate summary metrics.

Table 1. 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. These estimates are largely based on photo-identification mark-recapture methods. Sources: Kendall et al., 2004; Langtimm et al., 2004; Runge et al. 2004.

Parameter	Atlantic		Upper St. Johns		Northwest		Southwest	
	Estimate	Uncertainty	Estimate	Uncertainty	Estimate	Uncertainty	Estimate	Uncertainty
s_1	0.791	(.650, .885)	**0.810**	**(.727, .873)**	0.807	(.673, .895)	0.765	(.616, .869)
s_2	0.893	(.712, .966)	**0.915**	**(.827, .960)**	0.911	(.751, .972)	0.864	(.654, .955)
s_3	0.936	(.923, .949)	**0.961**	**(.915, .983)**	0.956	(.943, .969)	0.906	(.867, .944)
s_4	0.936	(.923, .949)	**0.961**	**(.915, .983)**	0.956	(.943, .969)	0.906	(.867, .944)
s_P	**0.936**	**(.923, .949)**	0.960	(.937, .982)	0.956	(.943, .969)	**0.906**	**(.867, .944)**
s_A	**0.936**	**(.923, .949)**	0.960	(.937, .982)	0.956	(.943, .969)	**0.906**	**(.867, .944)**
γ_4	0.0	(.0, .3)	**0.208**	**(.071, .422)**	**0.000**	**(.000, .285)**	0.0	(.0, .3)
γ_P	0.304	(.132, .529)	**0.610**	**(.505, .709)**	0.381	(.181, .616)	0.304	(.132, .529)
γ_B	**0.381**	**(.292, .470)**	**0.610**	**(.505, .709)**	0.429	(.217, .541)	0.595	(.421, .752)

Table 2. Median and range for temporal standard deviation for the survival rates and breeding probabilities. These values are used to generate the magnitude of normal environmental stochasticity. For s_1 and s_2, the values are on the logit-scale and the range shows the low and high values considered for the standard deviation; for the other parameters, the values are on the nominal scale and the range shows the 95% confidence interval for the standard deviation.

Parameter	Atlantic	Upper St. Johns	Northwest	Southwest
$\sigma(s_1)$	0.104 (0, 0.417)	0 (0, 0.263)	0.128 (0, 0.518)	0.106 (0, 0.851)
$\sigma(s_2)$	0.233 (0, 0.935)	0 (0, 0.589)	0.281 (0, 1.124)	0.184 (0, 1.472)
$\sigma(s_3) = \sigma(s_4)$, $\sigma(s_A) = \sigma(s_P)$	0 (0, 0.039)	0 (0, 0)	0.018 (0, 0.048)	0 (0, 0.082)
$\sigma(\gamma_4)$	0	0	0	0
$\sigma(\gamma_P) = \sigma(\gamma_B)$	0 (0, 0.062)	0	0.076 (0, 0.213)	0.076 (0, 0.213)

Table 3. Probabilities of catastrophes and magnitudes of associated effects. A Type 1 catastrophe is associated with a virulent, infectious disease. Type 2 catastrophes are associated with red tide events. Source: FWRI, 2002.

Parameter	Atlantic	Upper St. Johns	Northwest	Southwest
Type 1				
Probability	0.01	0.01	0.01	0.01
Reduction in s	0.25	0.25	0.25	0.25
Reduction in γ	0.20	0.20	0.20	0.20
Type 2				
Probability	0	0	0.018	0.036
Reduction in s	--	--	0.05	0.10
Reduction in γ	--	--	0.05	0.05

Table 4. Mortality due to cold stress for animals inside and outside warm-water refugia. The numbers in brackets refer to ranges that express uncertainty about the mortality rate. The adult category includes subadults. The calf category includes both first-year and second-year calves. In the model, these parameters do not differ by region. Source: expert panel (Warm Water Task Force).

		Inside Refugia	Outside Refugia
Adults	Normal year	0 %	1 %
	Cold year	0 %	50 % [30-75]
Calves	Normal year	0 %	5 % [2.5-10]
	Cold year	0 %	100 % [90-100]

Table 5. Regional counts from the synoptic aerial survey, January 5-6, 2001, used to set initial population sizes in the CBM. Source: FWC Fish and Wildlife Research Institute.

Region	Count
Atlantic	1447
Upper St. Johns	112[a]
Northwest	377
Southwest	1364
Total	*3300*

[a]In the Upper St. Johns, the initial population size was based on the number of individuals identified throughout the winter of 2000-2001 (141); combined with the other estimates, this gives a total population size of 3329.

Table 6. Probabilities of declines of various magnitudes, as predicted by the Manatee Core Biological Model. The metrics in this table are drawn from the IUCN guidelines for classification of species as vulnerable, endangered, or critically endangered. The metrics are interpreted as follows: for example, "$p(\Delta_3 < -10\%)$" should be read as the probability that the population of mature individuals will decline by more than 10% within 3 generations. There are two metrics under each category; they correspond to the metrics for IUCN criteria A and C, respectively.

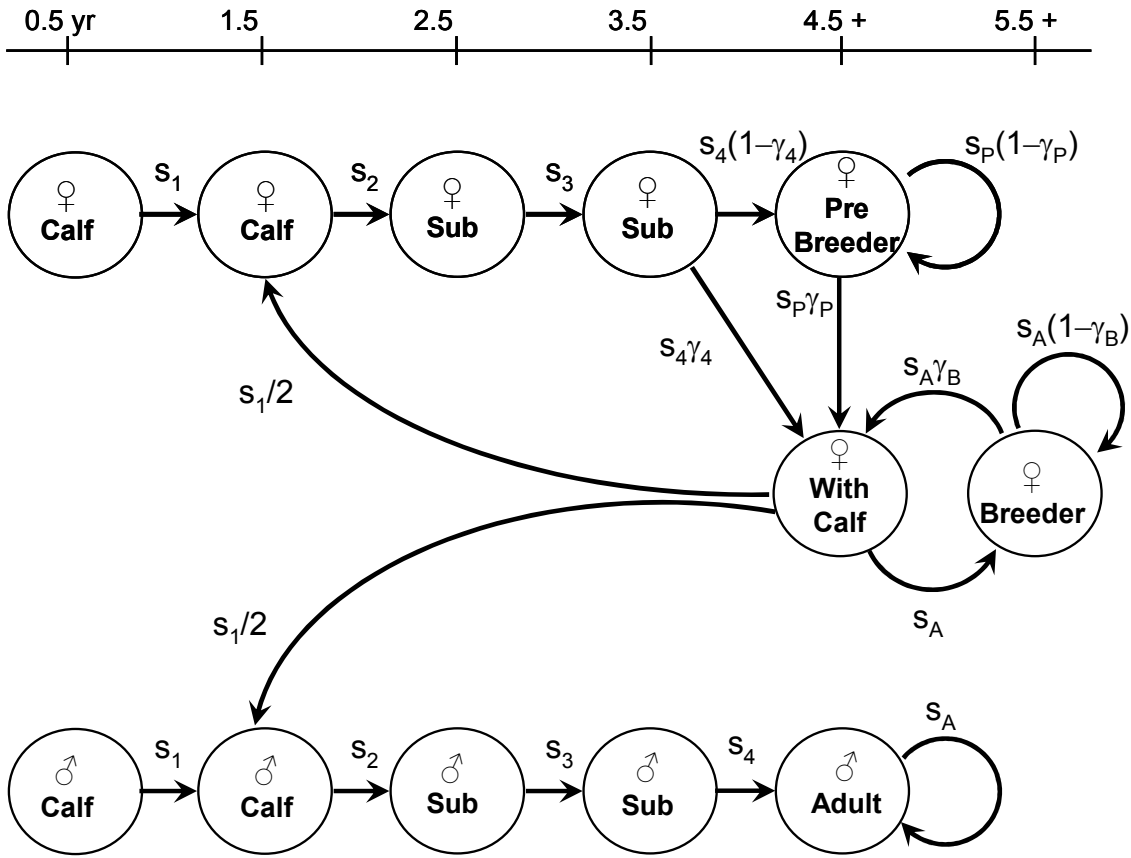|	Atlantic	Upper St. Johns	Northwest	Southwest	Statewide
Vulnerable					
$p(\Delta_3 < -30\%)$	0.7276	0.0042	0.0630	0.9852	0.4650
$p(\Delta_3 < -10\%)$	0.8494	0.0214	0.0862	0.9988	0.7708
Endangered					
$p(\Delta_3 < -50\%)$	0.4192	0.0002	0.0426	0.9256	0.1214
$p(\Delta_2 < -20\%)$	0.7432	0.0044	0.0716	0.9648	0.5554
Critically Endangered					
$p(\Delta_3 < -80\%)$	0.0220	<0.0002	0.0184	0.6070	<0.0002
$p(\Delta_1 < -25\%)$	0.2652	0.0002	0.0518	0.7670	0.1492

Fig. 1. Life-history diagram for the manatee population model. Note that calves enter the population as separate entities at 1.5 yr. The first circle is shown for completeness.
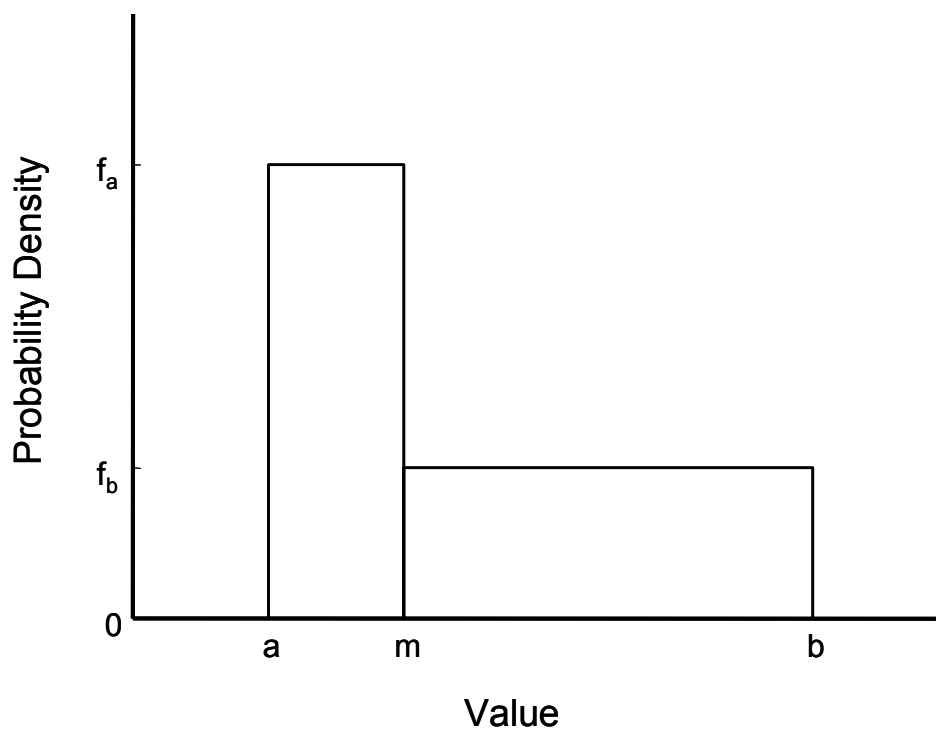
Fig. 2. Two-phase uniform distribution. Half of the density is found between the low value (*a*) and the median (*m*) and half is found between the median and the high value (*b*). Thus, the probability density is f_a for $a < x < m$, and f_b for $m < x < b$; and $f_a(m-a) = f_b(b-m) = 0.5$.
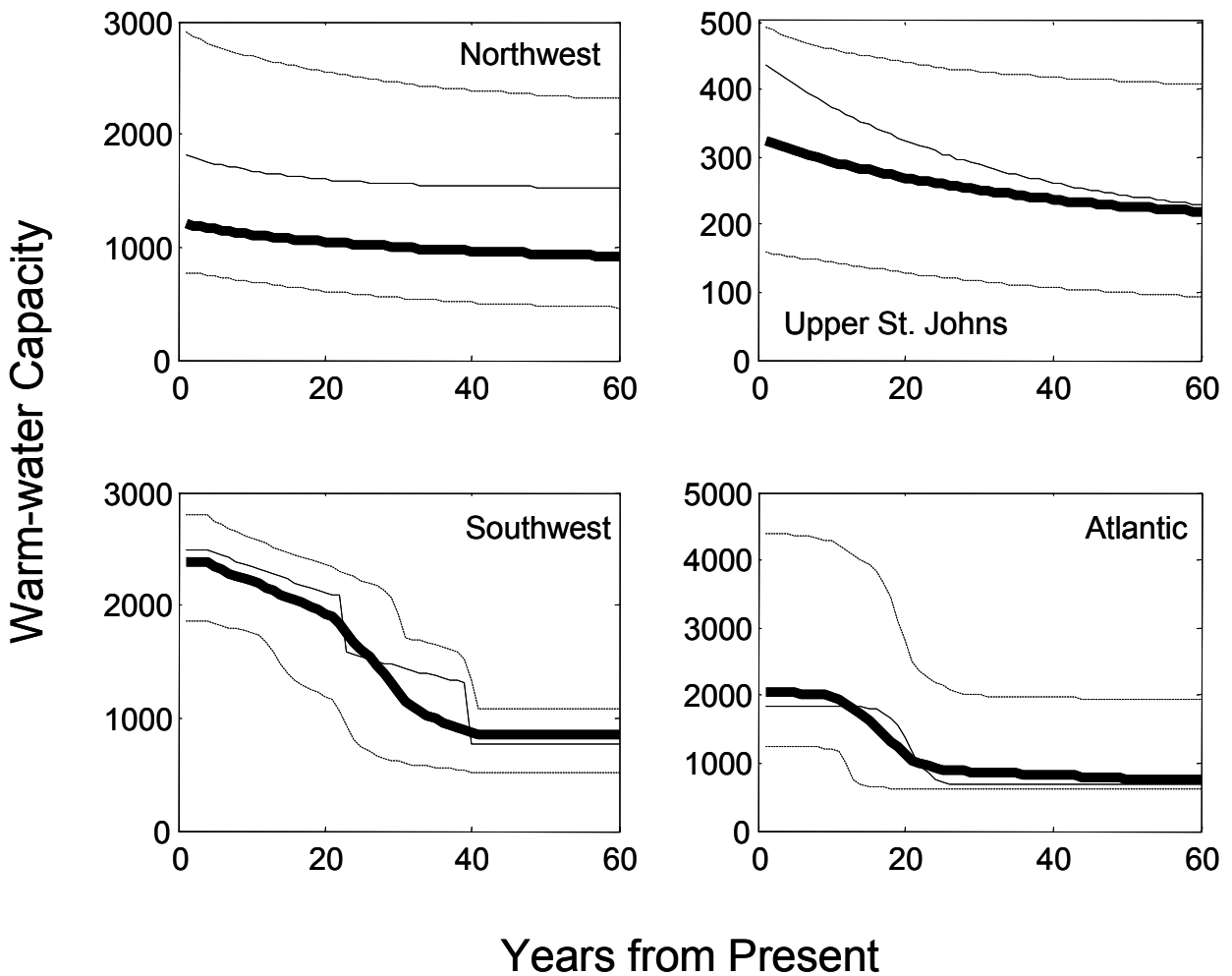
Fig. 3. Projected availability of warm-water habitat for Florida manatees, by region, 0-60 years from present. The bold line shows the median estimate; the dashed lines encompass the 95% prediction interval. In each graph, the thin solid line represents one possible realization of the future trend in warm-water habitat.
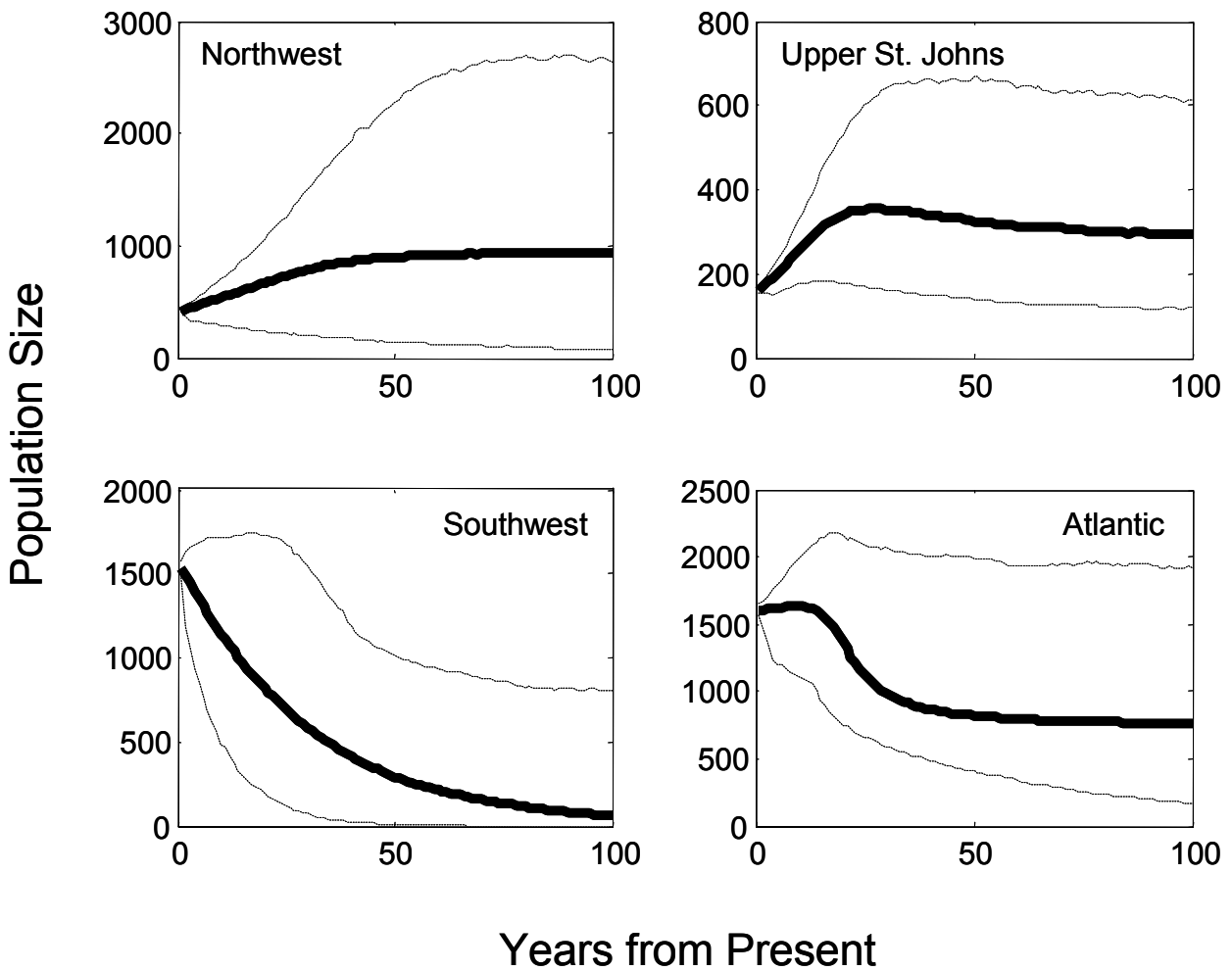
Fig. 4. Projected Florida manatee population size, by region, 0-100 years from present. The bold lines show the median estimate; the dashed lines encompass the 95% prediction interval. These projections are drawn from the Core Biological Model, with 5000 replicates per region.
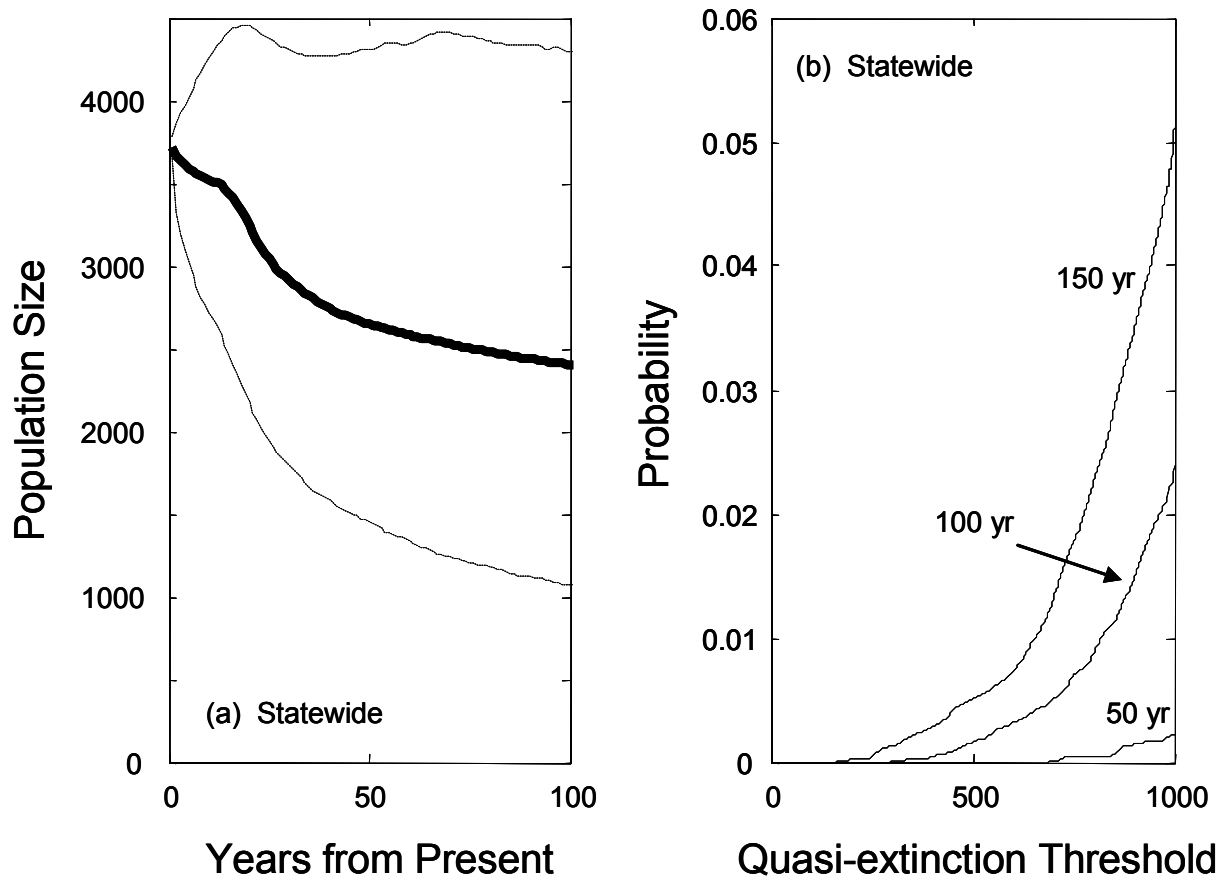
Fig. 5. Projections of the statewide manatee population. (a) Projected Florida manatee population size, 0-100 years from present. The bold line is the median estimate; the dashed lines encompass the 95% prediction interval. (b) Quasi-extinction probability. The probability of the statewide population falling below any particular absolute threshold is shown for 50 yr, 100 yr, and 150 yr time horizons.
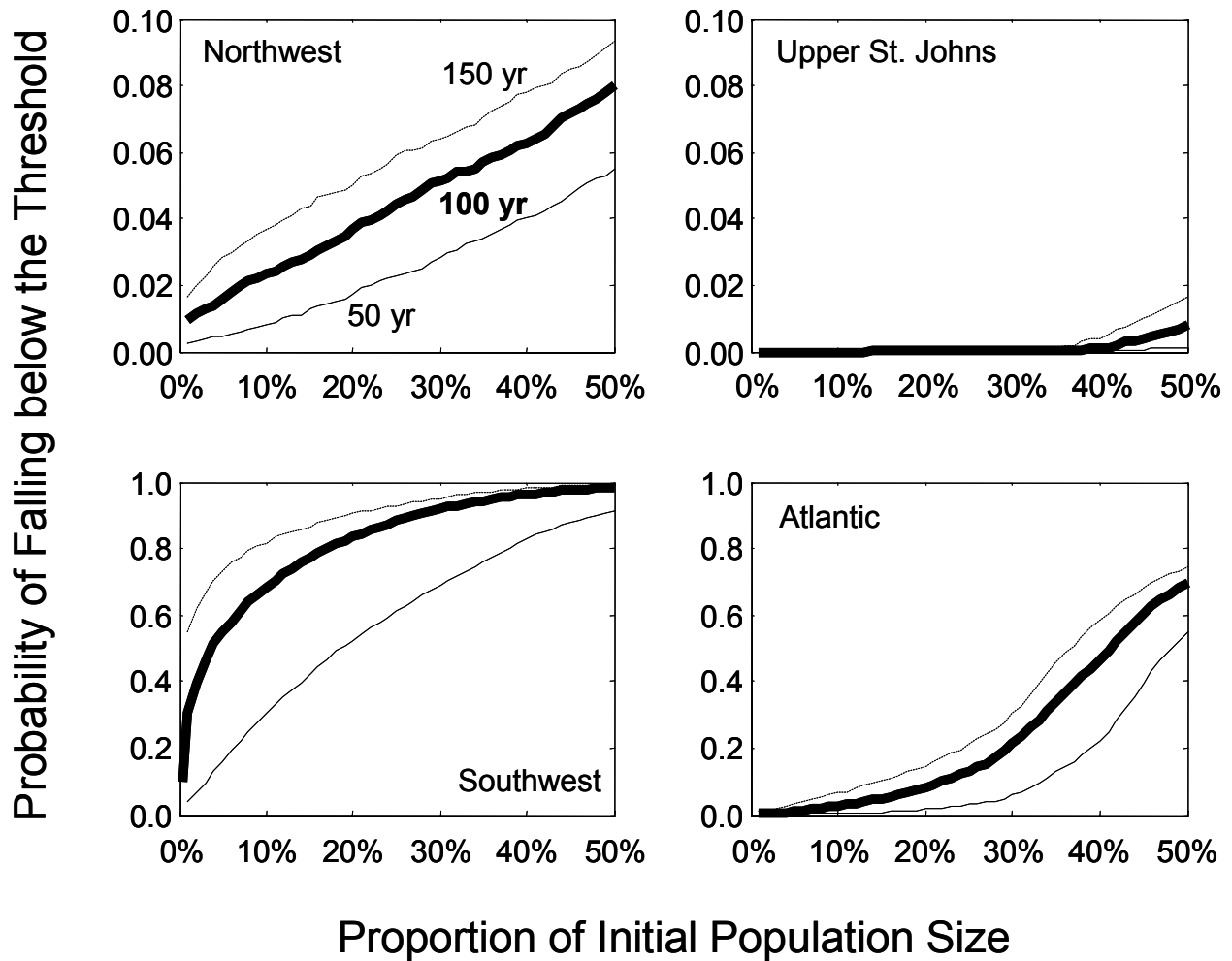
Fig. 6. Quasi-extinction probability by region. The graphs show the probability of a regional population falling below various fractions of the initial population size over 50 yr (thin solid line), 100 yr (bold line), and 150 yr (dashed line) time horizons. Note that the scale of the y-axis on the top two graphs is different from the scale on the bottom two graphs.
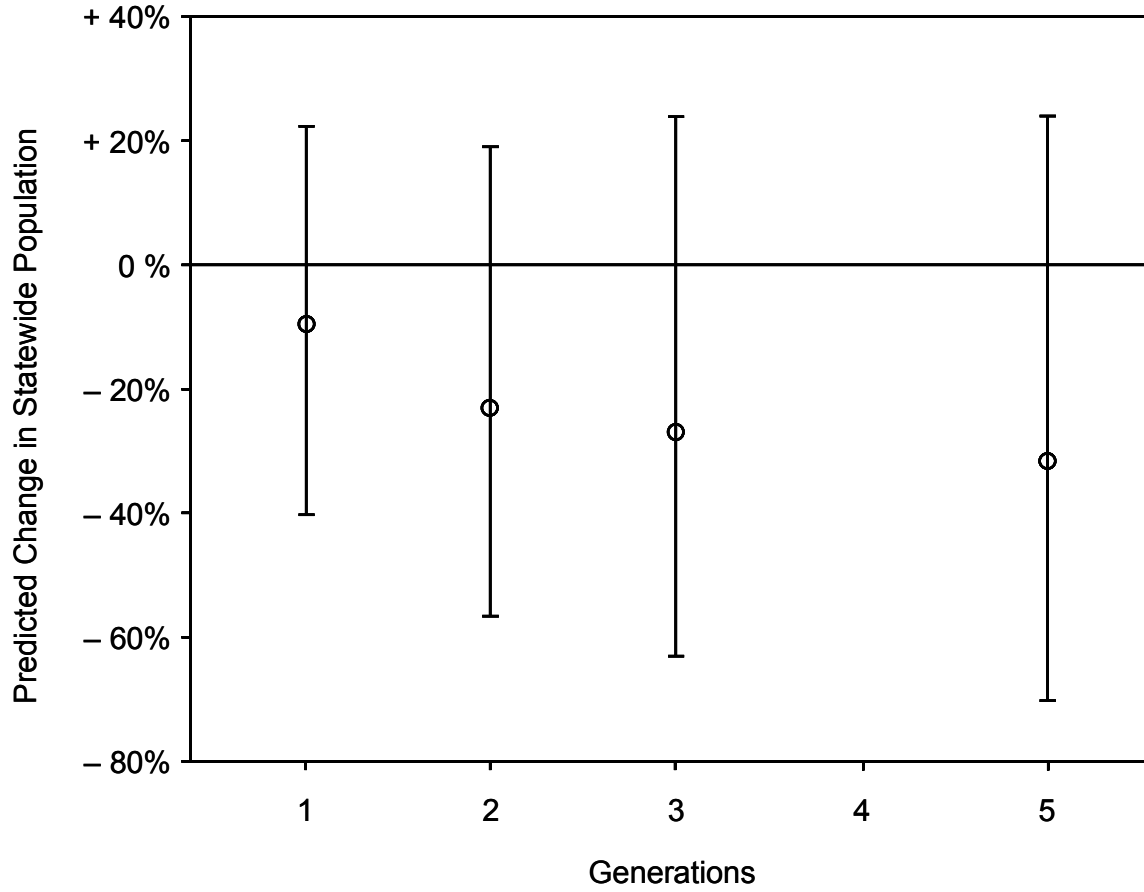
Fig. 7. Predicted statewide change in the population size of mature manatees after 1, 2, 3, and 5 generations. The open circles show the mean change; the errors bars are 95% confidence intervals.
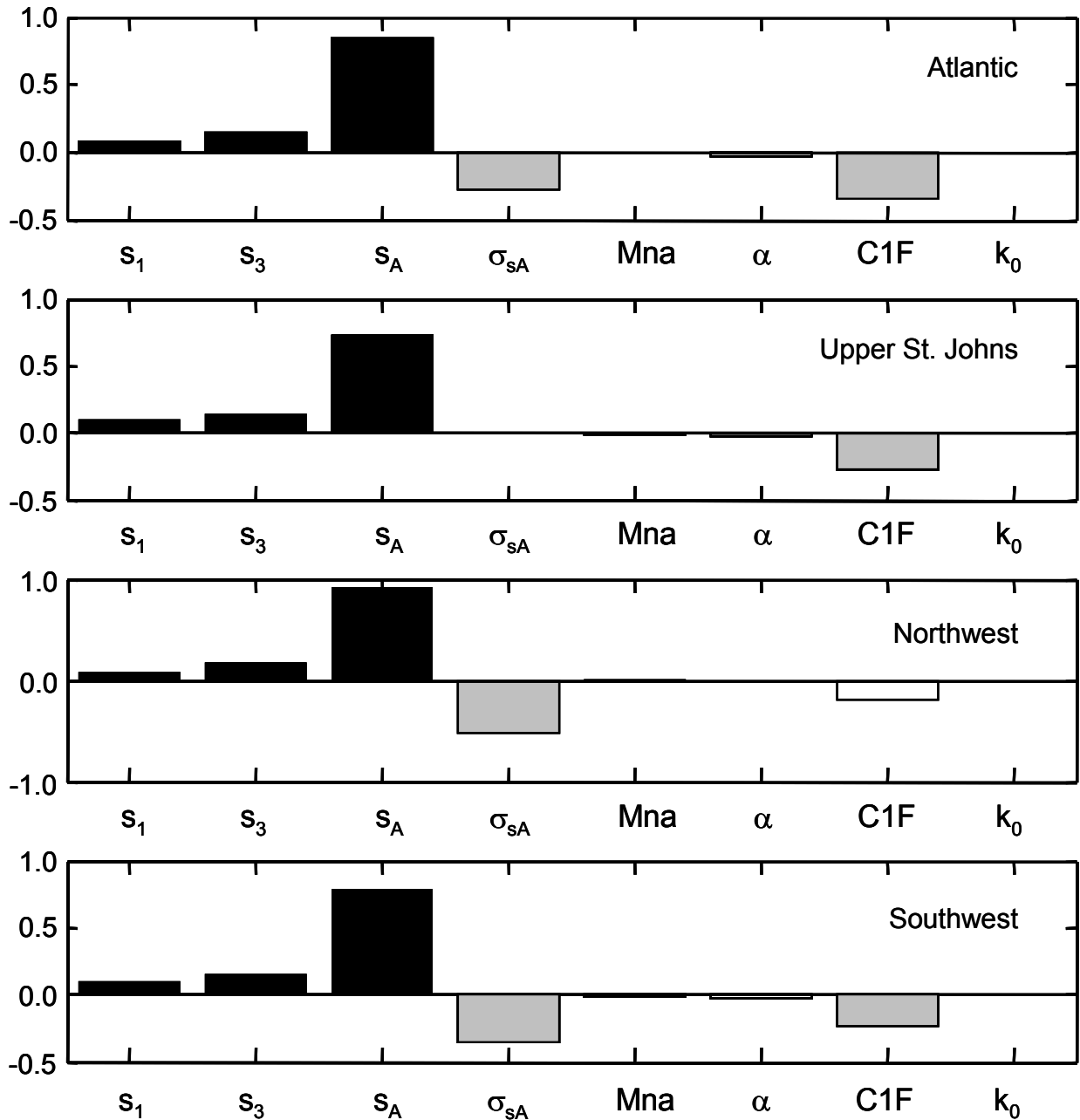
Fig. 8. Sensitivity of first-year population growth rate to absolute change in various model parameters. The parameters listed are: first-year survival rate (s_1), sub-adult survival rate (s_3), adult survival rate (s_A), the temporal standard deviation of adult survival rate (σ_{sA}), the mortality of adults outside warm-water refugia in normal years (Mna), one of the parameters describing density-dependence (α), the frequency of Type I catastrophes (C1F), and the long-term warm-water capacity (k_0). For the Upper St. Johns region, no sensitivity analysis was done for σ_{sA}.
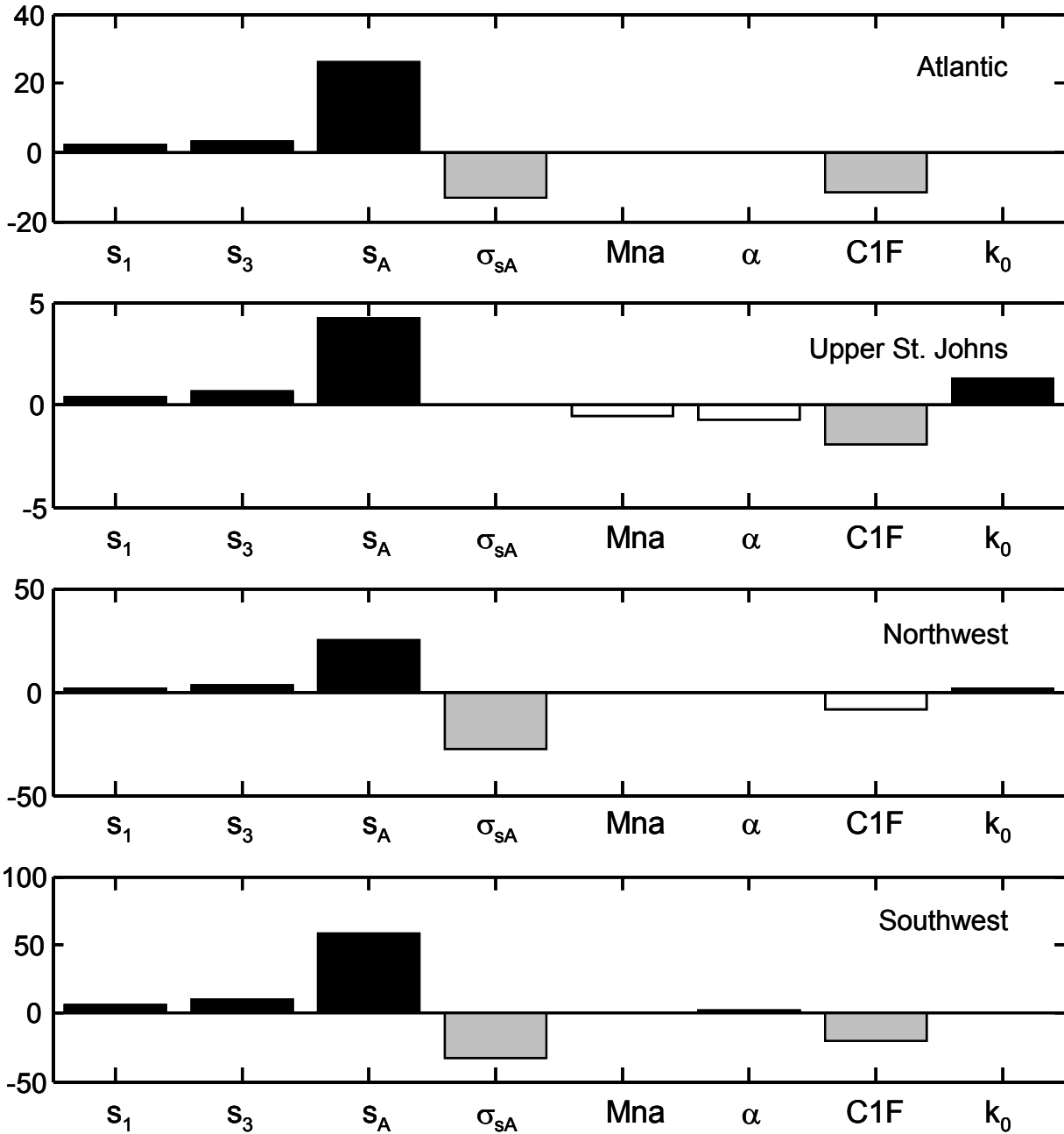
Fig. 9. Sensitivity of population size (log-scale) at 100 years to absolute change in various model parameters. The parameters listed are: first-year survival rate (s_1), sub-adult survival rate (s_3), adult survival rate (s_A), the temporal standard deviation of adult survival rate (σ_{sA}), the mortality of adults outside warm-water refugia in normal years (Mna), one of the parameters describing density-dependence (α), the frequency of Type I catastrophes (C1F), and the long-term warm-water capacity (k_0). For the Upper St. Johns region, no sensitivity analysis was done for σ_{sA}.
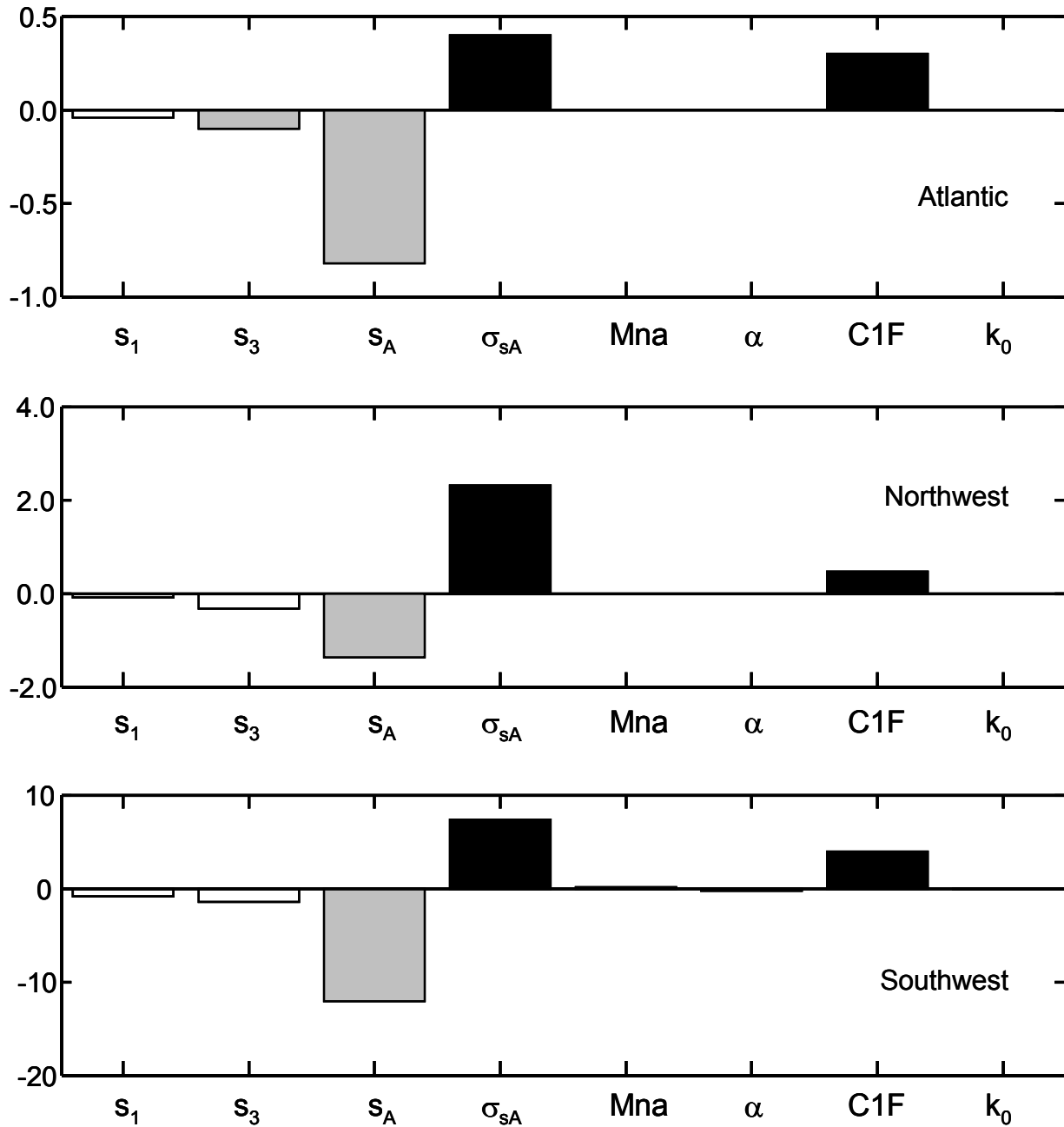
Fig. 10. Sensitivity of quasi-extinction over 100 years to absolute change in various model parameters. The parameters listed are: first-year survival rate (s_1), sub-adult survival rate (s_3), adult survival rate (s_A), the temporal standard deviation of adult survival rate (σ_{sA}), the mortality of adults outside warm-water refugia in normal years (Mna), one of the parameters describing density-dependence (α), the frequency of Type I catastrophes (C1F), and the long-term warm-water capacity (k_0). For the Upper St. Johns region, population size did not fall below quasi-extinction levels for any sensitivity analyses.
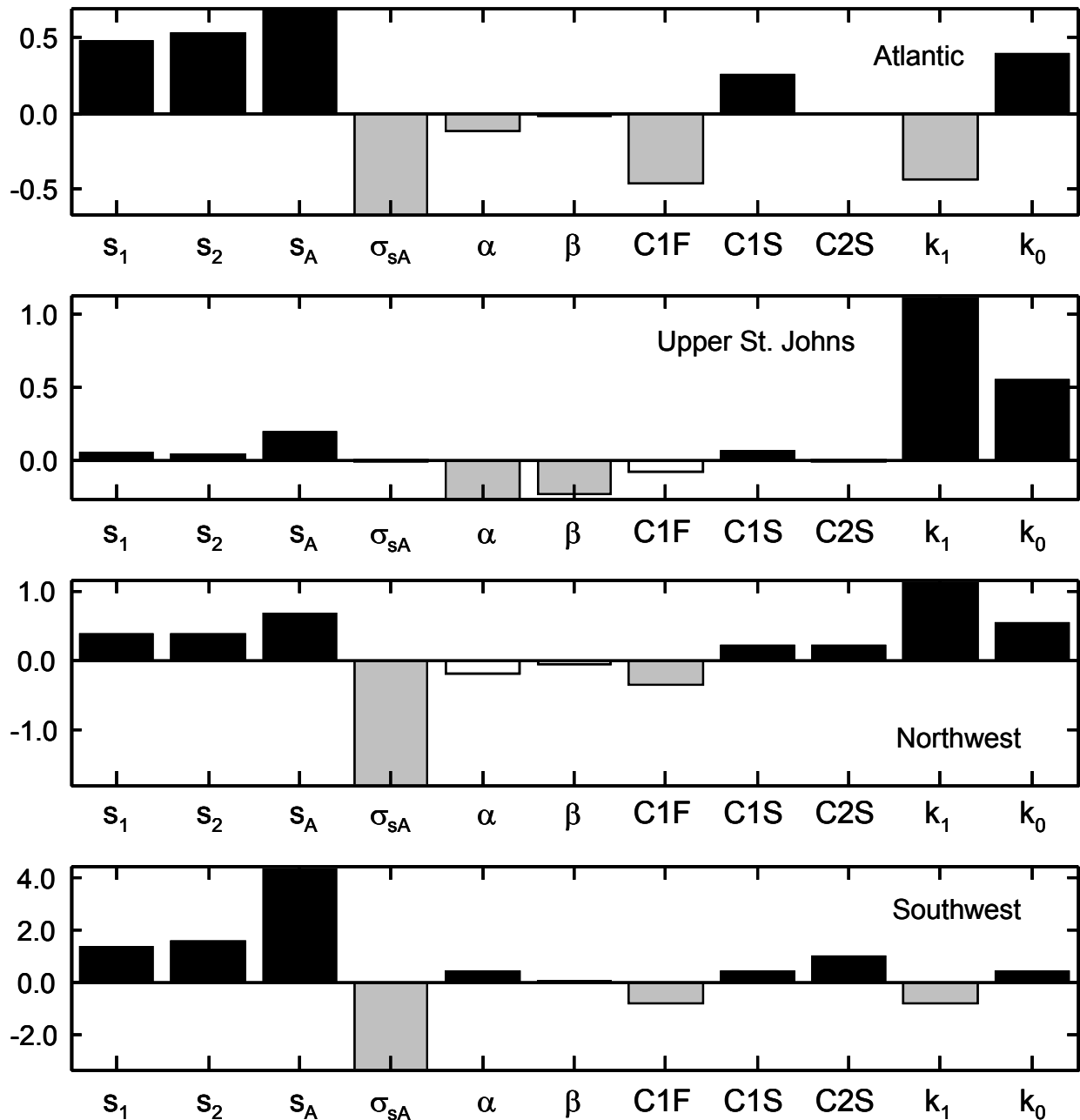
Fig. 11. Relative contributions to uncertainty in population size (log-scale) at 100 years from uncertainty in the life-history parameters. The parameters listed are: first-year survival rate (s_1), second-year survival rate (s_2), adult survival rate (s_A), the temporal standard deviation of adult survival rate (σ_{sA}), both of the parameters describing density-dependence (α, β), the frequency and severity of Type I catastrophes (C1F, C1S), the severity of Type II catastrophes (C2S), the current warm-water capacity (k_1), and the long-term warm-water capacity (k_0). For the Upper St. Johns region, no sensitivity analysis was done for σ_{sA}.