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# Integration of Manatee Life-history Data and Population Modeling

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**Abstract.** Aerial counts and the number of deaths have been a major focus of attention in attempts to understand the population status of the Florida manatee (*Trichechus manatus latirostris*). Uncertainties associated with these data have made interpretation difficult. However, knowledge of manatee life-history attributes increased and now permits the development of a population model. We describe a provisional model based on the classical approach of Lotka. Parameters in the model are based on data from other papers in this volume and draw primarily on observations from the Crystal River, Blue Spring, and Atlantic Coast areas. The model estimates $\lambda$ (the finite rate of increase) at each study area, and application of the delta method provides estimates of variance components and partial derivatives of $\lambda$ with respect to key input parameters (reproduction, adult survival, and early survival). In some study areas, only approximations of some parameters are available. Estimates of $\lambda$ and coefficients of variation (in parentheses) of manatees were 1.07 (0.009) in the Crystal River, 1.06 (0.012) at Blue Spring, and 1.01 (0.012) on the Atlantic Coast. Changing adult survival has a major effect on $\lambda$. Early-age survival has the smallest effect. Bootstrap comparisons of population growth estimates from trend counts in the Crystal River and at Blue Spring and the reproduction and survival data suggest that the higher, observed rates from counts are probably not due to chance. Bootstrapping for variance estimates based on reproduction and survival data from manatees at Blue Spring and in the Crystal River provided estimates of $\lambda$, adult survival, and rates of reproduction that were similar to those obtained by other methods. Our estimates are preliminary and suggest improvements for future data collection and analysis. However, results support efforts to reduce mortality as the most effective means to promote the increased growth necessary for the eventual recovery of the Florida manatee population.

**Key words:** Florida manatee, *Trichechus manatus latirostris*, population model, population dynamics, life history.

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A population model with life-history data may provide a useful tool for the evaluation of information on trends in counts and annual numbers of recorded deaths of Florida manatees (*Trichechus manatus latirostris*). Thus far, the interpretation of information about population dynamics from the latter two data sets has been difficult. The history of manatee studies in Florida has been dominated by concern about the effect of watercraft-caused mortality on a small population of unknown size. The recovery of carcasses revealed a steady increase in total recorded mortality since

1974 (Ackerman et al. 1995). An increase in public awareness of the problem possibly improved the efficiency of locating carcasses that probably stabilized in many areas because the program has now been of long duration. However, efficiency may continue to increase in other areas as more people continue to settle along the coast and use waterways and where public education and media attention continue to increase. Although the increase in deaths in many areas is clearly not an artifact of data collection, the effect of changing and uneven reporting and recovery rates and the proportion of recovered carcasses remain unknown.

Lack of certainty about the size of the Florida manatee population is similar. Initial efforts to census manatees from the air resulted in an estimated minimum population size of about 1,000 individuals in the 1970's and early 1980's (*[1]Brownell et al. 1981; O'Shea 1988). Counts from subsequent surveys were higher, and 1,200 was given as the minimum population size after 1985 (O'Shea 1988). A large number of aircraft were used in the most recent (beginning 1991) surveys that were conducted after cold fronts, when manatees concentrate in sites where they can be more readily counted. Counts from these surveys were 1,465 in February 1991 and 1,856 in January 1992 (Ackerman 1995). The higher tally was probably due to better conditions, timing, and more intensive coverage rather than a 26% growth in population between 1991 and 1992.

Because manatees reproduce slowly (Hartman 1979; Rathbun et al. 1995), data on manatee numbers from carcass recovery and aerial surveys seem to be inconsistent. Clearly, the mortality during any protracted period was too high for the relatively low tallies from aerial counts (particularly those prior to 1991). In addition to numerous manatees that were killed in collisions with boats and major increases in numbers of registered boats, the high number of individuals that are scarred by propellers (Beck and Reid 1995) made it nonetheless evident that the manatee population was suffering much pressure. The subspecies has been and is currently properly classified as endangered (*U.S. Fish and Wildlife Service 1989), and public education and regulatory efforts to reduce mortality are essential if manatees are to be maintained as a conspicuous and functional component of Florida's fauna.

Because of increased knowledge from research and a longer period of record-keeping, a portion of the increased recorded mortalities may have been due to an increase in the actual numbers of manatees (O'Shea 1988). Such a prospect is encouraging for the conservation of the manatee but increases the complexity and difficulties of planning. This workshop thus served as the initiation of a review of the data and the identification of means to improve an understanding and clarification of the interpretation of the data. Population modeling is one approach for accomplishing such improvements.

For the development of a population model, we apply demographic information from longitudinal field studies that entail direct observations of known individuals through time. Manatee population dynamics have been studied intensively with these methods in two relatively small study areas (Blue Spring and Crystal River) for more than 15 years (O'Shea and Hartley 1995; Rathbun et al. 1995). These are naturally warm waters that attract manatees during winter and to which manatees return at high annual rates (O'Shea and Langtimm 1995). However, these aggregations of manatees are not considered geographic stocks that are separate from manatees in other areas of Florida. Trend data collected at these aggregation sites indicated that the number of manatees increased over the years; 260 manatees were in the Crystal River and 67 were at Blue Spring in January 1992 (Ackerman 1995). Modeling (below) also revealed increases in these two study areas; the joint counts in these areas are about 18% of the total manatee count in Florida in winter. Information from remaining areas in the state is less complete, and trends in counts elsewhere are more ambiguous (Ackerman 1995; Garrott et al. 1995). Consequently, an effort was made to test the model that we describe here in these two study areas. To evaluate the situation in other parts of Florida, we also applied modeling to manatees in the Atlantic Coast study area, where some estimated survival and reproduction data are also now available (O'Shea and Langtimm 1995; Reid et al. 1995). Detailed background information and population data on manatees in these three study areas were provided in Ackerman (1995), Garrott et al. (1995), O'Shea and Hartley (1995), O'Shea and Langtimm (1995), Rathbun et al. (1995), and Reid et al. (1995).

## A Provisional Model

The revised manatee recovery plan (*U.S. Fish and Wildlife Service 1989) calls for the construction of a population model, and one purpose of the workshop was to assemble data for subsequent analysis and modeling. Some initial elements of a new model are included here. Several uncertainties about the best use of the data may ultimately require separate, specialized modeling, and several iterations and versions of a population model will no doubt be useful. We do not anticipate one final and conclusive model for the Florida manatee population. Instead, we believe that the simple model presented here should be regarded only as another tool in population analysis to be used repeatedly as better data become available. This work will serve as the next step beyond Packard's (*1985) initial manatee population model, which was useful but was based on data with greater uncertainty than the data that are now available.

[1] An asterisk denotes unpublished material.

## *Background for Modeling*

The basic model was developed by A. J. Lotka in the early 1900's (Lotka 1907) and was extensively used in demographic studies. Ecological applications of Lotka's model often followed the matrix formulation detailed by Leslie (1945, 1948) that was also independently developed by Bernadelli (1941) and Lewis (1942). In a later paper, Leslie (1966) gave a simplification of the matrix model based on the assumption of constant rates of reproduction and survival rather than on the age-specific rates used in the full matrix model. Various applications of this simplification have since been made. One early use for marine mammals was that of Eberhardt and Siniff (1977).

As better information on survival of adult marine mammals began to accumulate, Leslie's (1966) use of constant adult survival to accommodate the sharp decline in survival accompanying senescence had to be modified. This can most conveniently be accomplished by adopting a truncation point, as done by Eberhardt (1985). Thus far, data on manatee ages (Marmontel 1993, 1995) suggested that manatees may live as long as 50 years. Marsh (1995) reported dugongs that were older than 70 years. For initial purposes, we use a maximum age of 50 to provide a truncation point in lieu of data on senescence. Two other modifications to the basic approach may ultimately be useful for various purposes. First, initial reproduction is spread over several age classes, so that full reproduction is probably not achieved at a single age, as demonstrated by observations in the field (O'Shea and Hartley 1995; Rathbun et al. 1995) and by anatomical studies (Marmontel 1995). Thus, the choice of an appropriate age of first reproduction for use in the simplified model may require more data than are now available. Second, three rates may eventually be useful. One is the survival from birth to weaning, a second is the annual survival of subadults, and the third is the survival of adults.

Thus, several degrees of approximation may be considered. Given a very large sample of reproduction data one may construct a reproduction ($m_x$) curve like that used by Eberhardt (1985) for the Pribilof fur seals (*Callorhinus ursinus*). With less extensive data, that curve may be replaced by a simple rectangle. With better data, a curve could be fitted for the early ages, but the truncation for the right side of the curve should be retained to accommodate senescence. Here, $m_x$ denotes the number of female births per female, so that the usual rate of births per female must be divided by two if sex ratio at birth is approximately even, as seems to be the case in manatees (O'Shea et al. 1985; O'Shea and Hartley 1995; Rathbun et al. 1995).

Similar considerations apply to the survivorship ($l_x$) curve. With a large sample, one can use age-specific rates throughout. With minimal data, one may use only two rates, survival to the age of first parturition ($l_a$) followed by a constant rate of adult survival ($s$) to the truncation age ($w$). Furthermore, the Lotka-Leslie model can be variously formulated, depending on the timing of reproduction. In the original (Lotka) equation, reproduction is considered continuous at a constant rate throughout the year. Consequently, the basic equation is expressed as an integral equation. However, many large mammal populations exhibit what Caughley (1977) termed *birth-pulse reproduction*, in which births are concentrated in a short time period each year. Under these circumstances, the equation may be approximated by a summation:

$$1 = \sum_{a}^{w} \lambda^{-x} l_x m_x \tag{1}$$

Cole (1954) showed that equation (1) provides nearly an exact replacement for the integral equation of Lotka for birth-pulse populations. Reproduction in manatees, however, takes an intermediate form, being distributed over most months of the year with a peak in spring and summer and a marked reduction in winter. Such a seasonal pattern is evident in the reports by Hernandez et al. (1995), Marmontel (1995), O'Shea and Hartley (1995), and Rathbun et al. (1995).

When we replace age-specific reproduction ($m_x$) and survivorship ($l_x$) terms in equation (1) by constant rates, the equation can be simplified. When the reproduction curve ($m_x$) is replaced by a rectangular function, we approximate $m_x$ by a constant ($m$) from age $a$ to age $w$. However, this is further complicated because manatees do not reproduce annually but give birth at 2-year or longer intervals (Hartman 1979; Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995; Reid et al. 1995).

If we use two rates for survivorship, the $l_x$ values can be written as $l_x = l_a s^{x-a}$ when $x \geq a$, where $l_a$ denotes survival to age $a$, and $s$ denotes the constant adult rate. With these approximations, equation 1 becomes:

$$1 = \lambda^{-a} l_a m \left[ 1 - (s/\lambda)^{w-a+1} / 1 - (s/\lambda) \right] \tag{2}$$

This equation can be rearranged as a polynomial:

$$\lambda^{a} - s\lambda^{a-1} - m\, l_a \left[ 1 - (s/\lambda)^{w-a+1} \right] = 0 \tag{3}$$

In this form, it can be equated to the *characteristic polynomial* of the Leslie matrix (elements of the matrix are replaced by constants, as described above) with one proviso. The Leslie matrix formulation often is written so that the youngest age class is that of 1-year-olds. We then must write the reproduction term as $m = s_o F$ where $s_o$ is survival from birth to age 1, and $F$ is the number of female births per female as normally used in the Leslie matrix (but expressed as $F_x$ for age-specific rates).

For the data on manatees, equation 3 must be modified to use $l_a = l_k s^{a-k}$ (i.e., we can expect that much of survivor-

ship to age of first parturition will be at the adult rate ($s$) as suggested by observations at Blue Spring [O'Shea and Hartley 1995] and by limited evidence from telemetry in several study areas [O'Shea and Langtimm 1995], rather than at the subadult rate incorporated in $l_k$). We then write equation (3) as:

$$\lambda^a - s\lambda^{a-1} - l_k s^{a-k} m\,[1 - (s/\lambda)^{w-a+1}] = 0 \qquad (4)$$

Inasmuch as a direct expression of $\lambda$ (the finite rate of increase) is not available, the above equations must be solved by iteration.

A necessary assumption for use of the Lotka-Leslie model is that of the stable age distribution. The development of a stable age distribution requires that the population is changing at a constant rate for some period of time. The consequences of a deviation from a stable age distribution are usually not substantial, unless there is a major change in age structure. Such changes may be more probable in small populations, but age-distribution data from manatee-carcass studies seem not to have changed during 1976–91 (Marmontel 1993).

## *Applying the Delta Method to the Model*

An approximation to a variance of $\lambda$ may be obtained by the delta method (Seber 1982:8):

$$V(\hat{\lambda}) \doteq \sum V(x_i)\,[\partial\lambda(x_i)/\partial x_i]^2 \qquad (5)$$

where $x_i$ denotes the three constant values ($s$, $l_k$, $m$) used in equation 4, and $V(x_i)$ the variance of the estimates of these parameters. Seber (1982) includes covariance terms, but these were not included in the present example because separate data sources were used for various components.

Implicit differentiation of equation 4 was used to obtain the several partial derivatives:

$$\partial\lambda/\partial s = -s\lambda^{a+1} - (a-k)l_k\, m\, \lambda s^{a-k}\,[1 - {}^{w-a+1}/_{a-k}\,(s/\lambda)^{w-a+1} - (s/\lambda)^{w-a+1}]/sB$$

$$\partial\lambda/\partial m = -s^{a-k}\lambda^2 l_k\,[1 - (s/\lambda)^{w-a+1}]/B \qquad (6)$$

$$\partial\lambda/\delta l_k = -s^{a-k}\lambda^2 m\,[1 - (s/\lambda)^{w-a+1}]/B$$

where

$$B = s\lambda^a\,(a-1) - a\lambda^{a+1} - (w-a+1)\,l_k m\lambda s^{a-k}(s/\lambda)^{w-a+1}.$$

With the delta method approximation, one can estimate how to best allocate field efforts for estimating $\lambda$ (i.e., how much sampling should be devoted to each component).

A second aspect for consideration is the relative importance of the three components in management. Changes in adult survival have a large influence on $\lambda$ in marine mammals (as noted of dugongs by Marsh [1995]). This aspect is concisely expressed by the partial derivative,

$$\partial\lambda(x_i)/\partial x_i.$$

These partial derivatives were then used in equation 5 to estimate a variance of $\lambda$ and to examine the relative importance of the three main variance components and the relative effect of changes in survival and rates of reproduction on $\lambda$. Another statistical technique, bootstrapping, provides an alternative estimate of overall variances, as described in a later section of the paper.

## *Parameters in the Model*

Calculation of $\lambda$ from equation 4 requires a choice of the maximum age ($w$), which, as noted above, was set at 50. Use of older ages (e.g., 60) has only a trivial effect on estimates of $\lambda$. Field observations provided 14 records of age at first parturition, seven from Blue Spring (O'Shea and Hartley 1995) and seven from the Crystal River (Rathbun et al. 1995). Age 4 was used for the value of $a$ because in the field studies, four females reproduced at the age of 4 years, four at the age of 5 years, four at the age of 6 years, and two at the age of 7 years. These data are compatible with observations on carcasses; the seven youngest females with anatomical evidence of maturity were between 3 and 4 years old (Marmontel 1995). As noted above, because initial reproduction is spread over several age classes, more data may suggest other options for estimating this parameter.

Rates of reproduction of manatees in the Crystal River were taken from Table 3 of Rathbun et al. (1995) from which records of 147 calves (very young, less-than-1-year-old manatees observed with their mothers; see Rathbun et al. 1995) born in 389 manatee-years (adults only) were used. At Blue Spring (O'Shea and Hartley 1995:Table 2), records of 43 calves in 144 manatee-years were used in our calculations. In both instances, the records are based on long-term observations of individual manatees. Data from the Atlantic Coast population (Reid et al. 1995) are based on similar observations but on lower resighting frequencies. Reid et al. (1995) recorded 254 first-year calves in 664 manatee-years. Because most calves are not born in aggregation sites in winter and are thus not observed until in the winter of their first year, the rate of reproduction ($m$) in equation 4 is calculated at that time and is considerably lower than the actual birth rate. Calf survival from neonatal to about 6 months has been calculated at 0.60 in manatees at Blue Spring and at 0.67 in manatees in the Crystal River (O'Shea and Hartley 1995; Rathbun et al. 1995). Equation 4 thus applies to about 6-months old manatees rather than to true neonates, and the first-year survival ($l_1$) used in the equation is survival

from about 6 months to 1.5 years (first to second winter of life). Survival after age 1.5 has been assumed to be at the adult rate.

Adult survival ($s$) was obtained by the methods of O'Shea and Langtimm (1995). Further assessment of the records resulted in an improved database (C. A. Langtimm, National Biological Service, San Simeon, California, personal communication), which was used for analyses reported here. O'Shea and Hartley (1995:Table 1) reported the survival of 37 of 45 calves to the next winter or an early survival ($l_k$) of 0.82. Rathbun et al. (1995) reported a minimal survival to age 3 of 22 tail-nicked calves but indicated that these data underestimate early survival because observations of calves are less comprehensive in the Crystal River than at Blue Spring. This information is therefore not incorporated in our calculations. Similarly, no satisfactory estimated early survival is available from the Atlantic Coast population. Marmontel (1993:Table 4.8) reported the ages of a large sample of dead manatees and used these data to estimate first-year survival as 0.685. However, this survival was estimated with the classical life-table approach for which a constant population size ($\lambda = 1$) must be assumed. Also, it presumably applies from birth to age 1, whereas here we use a rate from winter to winter or roughly 6–18 months of age. The rate used here would be appreciably higher because it excludes perinatal deaths, which peak in warm months (Marmontel 1995; O'Shea and Hartley 1995; Rathbun et al. 1995).

A crude first-year survival of 0.78 in the Atlantic Coast population can be estimated by applying the ratio of first-year to adult survival at Blue Spring (0.82/0.96) to the estimated adult survival on the Atlantic Coast (0.91). For this calculation, one assumes the ratio of first-year to adult survival is the same on the Atlantic Coast as at Blue Spring, which may not be the case. We believe that this estimate may nonetheless be the best available at present and have used it for illustrative calculations to show the effect of sample sizes on variances. Observations by Reid et al. (1995) do not suggest that survival of young is radically lower on the Atlantic Coast than at Blue Spring.

Estimated parameters in the model included rates of reproduction, adult survival, and early survival of manatees in each of the three areas (Table 1). The age of first reproduction ($a = 4$) and the maximum age ($w = 50$) were assumed to be the same in the different areas. Estimated variances are included for use in equation 6. Variances of rates of reproduction were calculated from the average rates in adult females in the Crystal River and at Blue Spring (where sampled individuals represented a large proportion of the total population of adult females). Because few replicate observations of individual females from the Atlantic Coast were available, an estimated binomial variance was used for those data. Adult survival variances were derived in the same manner as those reported in O'Shea and Langtimm (1995:Table 4), and binomial variances of early survival were calculated. Rates of reproduction were divided by 2 for equation 1, in which the number of daughters per female is used.

Inasmuch as each of the partial derivatives incorporates all three survival and reproduction terms, the results must be evaluated in terms of specific values of these rates. Because the only satisfactory estimate of early survival was from manatees at Blue Spring, that value was also used for manatees in the Crystal River, where other parameters and conditions in general seemed comparable. Because the early survival value of the Atlantic Coast population is estimated under the assumption that the ratio of early survival to adult survival is the same as at Blue Spring, the calculation of $\lambda$ is uncertain, but the results were included to illustrate probable results from calculations of variance components and the relative importance of the parameters.

## Results From the Model

Estimates of $\lambda$, components of variance, and partial derivatives were obtained (Table 2). Considering the partial derivatives first, changing adult survival clearly has the major effect on $\lambda$ because a change of one percentage point in adult survival results in about the same degree of change in $\lambda$. Reproduction has the next largest partial, and

**Table 1.** Estimated parameters used in the model of population dynamics of Florida manatees (*Trichechus manatus latirostris*) in the Crystal River, at Blue Spring, and on the Atlantic Coast of Florida. Standard errors are in parentheses.

| Area | Rate of reproduction ($m$) | Adult survival ($s$) | Early survival ($l_k$) |
|---|---|---|---|
| Crystal River | 0.189(0.049) | 0.965(0.0060) | [a] |
| Blue Spring | 0.15(0.060) | 0.961(0.0180) | 0.822(0.057) |
| Atlantic Coast | 0.19(0.009) | 0.907(0.0098) | 0.78[b] |

[a] Early survival estimates from Blue Spring used in calculations.
[b] Calculated from ratio of adult and early survival at Blue Spring.

**Table 2.** Values of λ, variance components, and partial derivatives calculated from life-history data of Florida manatees (*Trichechus manatus latirostris*) in the Crystal River, at Blue Spring, and on the Atlantic Coast. Coefficients of variation for λ (standard error/estimate) are in parentheses.

| Study area/ parameter | Estimate of λ | Variance component | Partial derivatives |
|---|---|---|---|
| Crystal River[a] | 1.074(0.009) | | |
| Adult survival | | 0.41 | 1.02 |
| Reproduction | | 0.19 | 0.46 |
| Early survival | | 0.40 | 0.11 |
| | | 1.00 | |
| Blue Spring | 1.057(0.012) | | |
| Adult survival | | 0.82 | 1.02 |
| Reproduction | | 0.11 | 0.51 |
| Early survival | | 0.07 | 0.09 |
| | | 1.00 | |
| Atlantic Coast[b] | 1.01(0.012) | | |
| Adult survival | | 0.63 | 1.03 |
| Reproduction | | 0.10 | 0.43 |
| Early survival | | 0.27 | 0.11 |
| | | 1.00 | |

[a] Using the early survival data from Blue Spring.
[b] Assuming the ratio of early survival to adult survival is the same as that at Blue Spring.

early survival is the smallest. In comparisons of these values with the variance components, the partials indicate the approximate effect of changing a parameter value on the magnitude of λ,whereas the variance components indicate how increasing sample size may reduce the variance of an estimated λ.

In the case of the variance components, the relatively small standard error of adult survival in the Crystal River (Table 1) results in dominance of the variance of early survival. A higher standard error of adult survival results in the dominance of that variance component at Blue Spring. Because trustworthy estimates of early survival in the Crystal River and on the Atlantic Coast are not available, such estimates must be obtained. The same sample size (45) for early survival was used to calculate variances of survival in all sites because the only useful early survival was that of manatees at Blue Spring. If an early survival of manatees on the Atlantic Coast can be estimated, it will probably be done with a larger sample size because of the larger number of observed manatees there.

Because the adult survival at Blue Spring represents most or all of the manatees that use the study area, the sample size cannot be substantially increased by more intensive effort and only increases over time. A large ($n$ = 414) sample of adults was observed for the estimation of survival along the Atlantic Coast, but further improvements in data collection may help improve results from this region by producing an estimate with smaller variance (O'Shea and Langtimm 1995).

The estimates of λ of manatees in the Crystal River (1.07) and at Blue Spring (1.06) are appreciably smaller than rates of increase in counts obtained by Ackerman (1995) from trend data (about λ = 1.10 from the Crystal River and λ = 1.08 from Blue Spring). The coefficients of variation of λ (Table 2) are small enough to suggest that the differences may not be due to sampling errors. The only complete set of reproduction and survival data is that from Blue Spring. As a further check on this seeming disparity, bootstrapping (Efron and Tibishirani 1993) was independently applied to the trend data (bootstrapping deviations from regression) and to the reproduction and survival data (described below in the section on bootstrapping), and the frequency distribution of the differences of the two estimates of λ (one from trend, one from reproduction and survival data) was used to examine the prospect that the observed difference arises from chance alone (Fig. 1). Because few (about 2%) of the differences are less than zero, some real differences in the two data sets are possible.

Some of the differences between demographic estimates of population growth rates and trend counts in the Crystal River and at Blue Spring may be due to an influence of immigration on trend counts. Rathbun et al. (1995) suggested possible immigration into the Crystal River study area, and immigrant manatees from southeastern Florida have overwintered at Blue Spring (National Biological Service and Florida Park Service, unpublished data). Protection of these areas as manatee refuges may play a role in attracting immigrants. Furthermore, because the estimated rate of reproduction from Blue Spring is

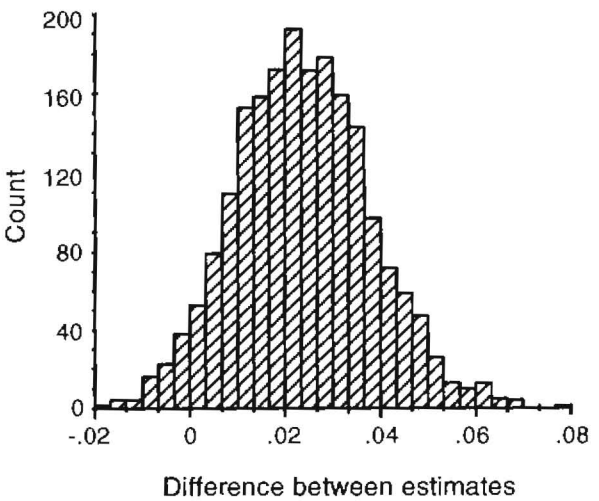


**Fig. 1.** Frequency distribution of differences between values of λ of Florida manatees (*Trichechus manatus latirostris*) obtained from bootstrap samples. Bootstrap samples were separately derived from trend data from aerial counts and from reproduction and survival data obtained by direct observation.

lower than the nearly equal rates from the other two sites (Table 1), this estimate may also be assumed responsible for part of the lower estimate of λ. A calculation with $m$ set equal to the value from the other two sites ($m = 0.38$) gives $\lambda = 1.07$, which is appreciably closer to the value from trend data (1.08). Another prospect for underestimation comes from the early survival data, which depend on reidentification of surviving individuals in some future year. Pollock et al. (1990) pointed out that such estimates can be biased because an individual may survive to the next year but may subsequently not be seen and die and thus may never be seen again and is assumed to have died in the year subsequent to marking. Pollock et al. (1990) recommended the Jolly-Seber method in such cases because that method corrects for the probability of resighting. However, at Blue Spring, many surveys are conducted in each year, and the probability of sighting an individual, if it is present, approaches unity (only one individual of 37 was not seen in the year after recruitment as a calf but was then seen in subsequent years and is believed to have wintered elsewhere during the interim; O'Shea and Hartley 1995).

As previously pointed out here, the estimate of λ from the Atlantic Coast is uncertain because of the need to assume an early survival value with the same ratio to adult survival as observed at Blue Spring. An indirect estimate may be obtained from the state-wide age data of Marmontel (1993:Table 4.8). Applying the method of Chapman and Robson (1960) to data from 4-year-old and older manatees gives an estimated survival of 0.896. Because the Chapman-Robson methods also require the assumption that $\lambda = 1$, this estimate is biased, but the bias is of the form $s^* = s/\lambda$ (c.f., Eberhardt 1988), where $s^*$ is the Chapman-Robson estimate and $s$ is the true survival. Because the estimated survival (Table 2) is relatively precise and presumably unbiased, we can calculate

$$\lambda = s/s^* = 0.907/0.896 = 1.01.$$

This is the same rate as obtained by the delta method. Lambda from the Atlantic Coast data indicates a slow rate of increase. The only trend data from that region (Garrott et al. 1995) also suggested an increase in the manatee population size.

## *Bootstrapping for Estimating Variances*

As noted previously, the only complete set of reproduction and survival data is from Blue Spring. Using the delta method (equation 5) with equation 4 provides an estimate of the coefficient of variation for the estimate of λ (1.06) from these data. This estimate is 0.012 with 95% confidence limits of about 1.02–1.10. Because calculations of this kind in the study of large-mammal population dynamics are relatively new, a cross-check of the results with the bootstrapping technique seemed desirable (Efron and Tibishirani 1993). Three estimated parameters were examined. Rate of reproduction ($m$) was evaluated by using data from Blue Spring of O'Shea and Hartley (1995; Table 3). Records of number of years of observation and number of young born to each of 20 individual adult female manatees were entered into a file, samples of 20 were drawn with replacement, and a rate of reproduction was calculated.

**Table 3.** Bootstrapping estimates of λ, rates of reproduction, and adult survival in Florida manatees (*Trichechus manatus latirostris*) in the Crystal River and at Blue Spring in comparison with direct estimates. Standard errors are in parentheses.

| | Blue Spring | | Crystal River | |
|---|---|---|---|---|
| Parameter | Bootstrap | Direct | Bootstrap | Direct |
| λ | 1.057(0.012) | 1.051(0.019) | 1.074(0.009) | 1.074(0.010) |
| Reproduction | 0.15(0.010) | 0.15(0.060) | 0.19(0.008) | 0.189(0.049) |
| Adult survival | 0.967(0.009) | 0.961(0.018) | 0.963(0.006) | 0.965(0.006) |

Bootstrapping the adult survival ($s$) was more complicated. The file of capture records of manatees at Blue Spring (similar to that in Appendix A-2 of O'Shea and Langtimm [1995]) contains 68 survival records (from more than 15 years). This file was also sampled by drawing 68 samples with replacement, and the resulting sample was used to estimate survival with the Jolly-Seber method (and the formulation by Pollock et al. 1990). Results of an execution of 2,000 bootstraps provided a mean survival of 0.967 with a standard error of 0.009 (Table 3). With the methods of O'Shea and Langtimm (1995), the rate was 0.961 with a standard error of 0.018.

The remaining parameter in the bootstrapping was that of early survival ($l_k$). O'Shea and Hartley (1995) observed 45 calves and noted that 37 survived from one winter to the next. Bootstrapping these data was simple and was based on a file containing 8 zeros and 37 ones, which was sampled with a sample size of 45 with replacement. Results from such sampling essentially follow the binomial distribution, which was assumed in the delta method.

The final bootstrapping contained the described four subprograms; each was set up to return an estimate of the appropriate parameter in each bootstrapping execution of the main program. An execution of 2,000 bootstraps gave a mean of 1.057 for $\lambda$ with a standard error of 0.012, whereas the delta method gave $\lambda = 1.051$ with a standard error of 0.019. Bootstrapping results can be used to obtain approximate 95% confidence limits by tabulating such limits from a frequency distribution of outcomes. Such a frequency distribution (Fig. 2) gave approximate limits of 1.03–1.08, appreciably narrower than those from the delta method.

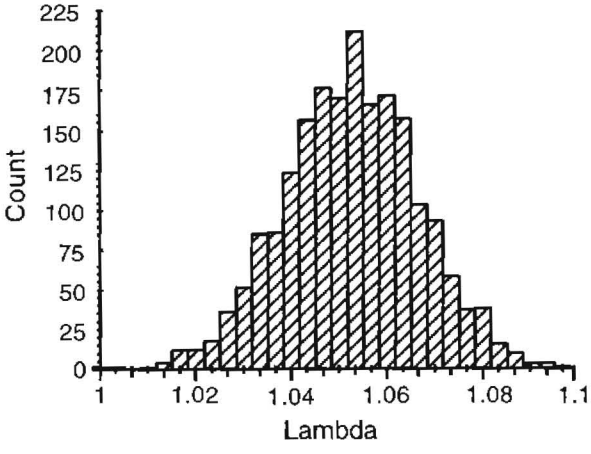


**Fig. 2.** Frequency distribution of 2,000 bootstrap estimates of $\lambda$ of Florida manatees (*Trichechus manatus latirostris*) at Blue Spring on the upper St. Johns River, Florida.

Bootstrapping the data on manatees from the Crystal River was based on using early survival data on manatees at Blue Spring. A larger sample of survival data of manatees in the Crystal River was available (234 records). The calculated survival of O'Shea and Langtimm (1995) was obtained with Model B of Jolly (1982), who used a rather complex method to obtain a weighted estimate of $s$ from the estimates from each year. A simple average was used for the bootstrapping, rather than attempting to program this complex procedure. Various estimates from bootstrapping and the delta method generally agreed (Table 3).

## Integrating Life-history Data and Population Models

The major question about Florida manatee populations is simply how well they will persist into the future. The evidence thus far is ambiguous. Carcass-recovery data show a trend of increasing boat-related deaths, and this trend significantly correlated with increasing boat registrations (Ackerman et al. 1995). Regarded as a crude catch-effort relation, this suggested that manatee numbers may have been keeping up with losses, but the manatee population cannot indefinitely sustain such losses. Manatee counts from two study areas (Blue Spring and Crystal River) show annual rates of increase of about 8% and 10% (Ackerman 1995), and the analysis of manatee counts at power plants on the Atlantic Coast (Garrott et al. 1995) also suggested an increasing population. However, the analyses of survival data from the Atlantic Coast population indicated appreciably lower adult survival there than in the Blue Spring and Crystal River study sites.

The recovery plan (*U.S. Fish and Wildlife Service 1989:21) indicates that "Downlisting should be considered when population modeling indicates that the population is growing or is stable, when mortality factors are controlled at acceptable levels or are decreasing, and when habitats are secure and threats are controlled or are decreasing".

Quite clearly, modeling cannot indicate the status of the population, but it is a means to integrate the several sources of population data in a way that supplies an approximation to a test of a null hypothesis that the population is decreasing. Given a valid estimate of the total population size, the population-dynamics analyses may also serve to indicate the level of mortality that the population can sustain. However, the difficulties of accurately and precisely estimating total population size (Lefebvre et al. 1995) are such that perhaps the best prospect is the testing of the null hypothesis that $\lambda$ is less than unity because it does not need to involve absolute population size. Doing this for the Atlantic Coast

population requires early-survival data, which are not currently available.

## *Implications for Future Research and Management*

For about the last 15 years, the annual number of manatee deaths raised concerns about the future of the population. Many observers pointed to the relative size of the kill and maximum aerial counts as evidence of a catastrophic state of affairs. Others noted that a relatively small population could not support such a large loss, suggesting that the actual population must be much larger. In addition, all dead manatees are probably not found, so that the recorded mortality and the aerial counts are below their true magnitudes. Thus, Eberhardt (*1982) speculated that the population at that time may actually have contained 3,000 manatees. O'Shea (1988), however, advanced reasons to believe that the increasing number of deaths could have been due, in part, to increases in population size.

An understanding of the situation would be considerably improved if reliable estimates of losses and population size were available. Such estimates may in fact be possible with further advances in the use of scar-pattern recognition of individuals. Careful scrutiny of dead manatees should make the identification of previously sighted individuals possible. Because estimates of survival are now available (O'Shea and Langtimm 1995), the total mortality may be estimated by a simple proportionality. Similarly, recording the number of live manatees scrutinized for identity may make possible the use of the data from which survival is now estimated to also estimate population size.

In the absence of useful estimates of total mortality or total population size, estimates of needed reductions in mortality to achieve management goals are not definitive. In a previous section, $\lambda$ was estimated as being about unity in the Atlantic Coast population. This suggests that the population may have been holding its own or slightly increasing in the past. However, the future course of the population cannot be forecast without key improvements in data collection. Important segments of the Florida manatee population have been omitted from our analyses simply because corresponding life-history data do not exist. Unlike manatees in the three study areas for which reproduction and survival data are available, the number of manatees in southwestern Florida has not increased (Garrott et al. 1995) despite extensive suitable habitat that may be able to support large numbers of manatees. At the same time, manatees in southwestern Florida seem to be suffering from increased mortality (Ackerman et al. 1995; Wright et al. 1995). In addition, the largest number of manatees in our three study areas is on the Atlantic Coast, but manatee population attributes from this area include the lowest estimate of $\lambda$ and are based on weaker reproduction and survival data than those of manatees in the Crystal River and at Blue Spring. Current management aimed at mortality reduction should continue as the most effective means of promoting population growth, as indicated by the sensitivity of our model to adult survival. Future researchers should focus on obtaining improved estimates of life-history and survival parameters of larger segments of the statewide population and of manatees in the existing study areas.

Although we compared trend data with our calculations of population growth rates based on demography and found concurrence in the positive growth in three study areas, we did not carry out extensive formal hypothesis testing about manatee population growth rates. We had several reasons for not doing so. First, although substantial improvements in knowledge of manatee life-history traits have been made since previous modeling attempts, we identified significant gaps that must be filled by additional research. Some key input parameters in our models from some areas were not based on direct measurements in those areas but were substitute values or estimates derived from data from other study areas; some are based on small data sets. Despite 15 or more years of sampling in some areas, the sampling interval remains shorter than the manatee lifespan and possible year-to-year changes in the environment that could affect birth and death rates. For example, the extent of variability in reproduction or survival based on stochasticity in weather patterns or disease episodes may not be adequately reflected in sampling efforts. Finally, we recommend that future researchers who attempt to test hypotheses about population growth rates based on either demography or trend data also consider statistical power, the probability of rejecting a null hypothesis when it is false.

An eventual decrease in population size should be accompanied by a decrease in total observed mortality. However, extensive experience with over-fishing in fishery management revealed that this is often not true. Ackerman et al. (1995) showed a steady increase in recorded manatee mortality with increasing boat registrations. Additionally, Wright et al. (1995) indicated that changes in propulsion arrangements made operating boats at high speeds in shallow water with heavy vegetation growth possible. One can thus argue that such information reflects a catch-effort relation and that more efficient effort may well keep the catch (accidental kill) at high levels until the affected population ultimately collapses, as it has in many commercial fisheries where declines in catch are accompanied by increasing fishing efficiency and continued high yields, to the point where the fish population virtually disappears.

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