Population Viability Analysis of the Florida Manatee (*Trichechus manatus latirostris*), 1976–1991

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Abstract: *Recent development of age-determination techniques for Florida manatees (*Trichechus manatus latirostris*) has permitted derivation of age-specific data on reproduction and survival of a sample of 1212 carcasses obtained throughout Florida from 1976–1991. Population viability analysis using these data projects a slightly negative growth rate (−0.003) and an unacceptably low probability of persistence (0.44) over 1000 years. The main factors affecting population projections were adult survival and fecundity. A 10% increase in adult mortality would drive the population to extinction over a 1000-year time scale, whereas a 10% decrease in adult mortality would allow slow population growth. A 10% decrease in reproduction would also result in extinction. We conclude that management must focus on retaining and improving the conditions under which manatee demography operates. The major identified agent of mortality is boat-manatee collisions, and rapidly increasing numbers of humans and registered boats portend an increase in manatee mortality. Zoning of manatee-occupied waters for reductions in boating activity and speed is essential to safeguard the manatee population. If boating regulations being implemented by the state of Florida in each of 13 key coastal counties are completed, enforced, and effective, manatees and human recreation could coexist indefinitely. If regulation is unsuccessful, the Florida manatee population is likely to decline slowly toward extinction.*

Análisis de Viabilidad Poblacional del Manatí de Florida (*Trichechus manatus latirostris*), 1976–1991

Resumen: *El reciente desarrollo de técnicas para la determinación de edad para manatís de Florida* Trichechus manatus latirostris *ha permitido la generación de datos sobre reproducción y supervivencia con edad específica de una muestra de 1212 cadáveres obtenidos en Florida de 1976 a 1991. El análisis de viabilidad poblacional de estos datos proyecta una ligera tasa de crecimiento negativa (−0.003) y una inaceptable baja probabilidad de persistencia (0.44) a lo largo de 1000 años. Los factores mas importante que afectan las proyecciones de la población fueron la sobrevivencia de los adultos y la fecundidad. Un incremento del 10% en la mortalidad de los adultos podría derivar en la extinción de la población en una escala de tiempo de 1000 años, mientras que una disminución del 10% en la mortalidad de los adultos podría permitir un crecimiento poblacional lento. Una disminución del 10% en la reproducción podría resultar también en la extinción de la especie. Concluímos que el manejo se debe enfocar en mantener y mejorar las condiciones bajo las cuales la demografia del manatí funciona. La mas importante causa de mortalidad identificada son las colisiones de botes con manatís, aunado a esto, el rápido incremento en el número de humanos y botes registrados augura un incremento en la mortalidad de los manatís. La zonificación de aguas ocupadas por manatís para la reducción de la actividad y velocidad de botes es escencial para salvaguardar la población de manatís. Si la regulación de botes implementada por el Estado de Florida en cada uno de los 13 condados*

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467

*costeros es completa, garantizada y efectiva, manatís y recreación humana pueden coexistir endefinida-
mente. Si la regulación no funciona, la población de manatís de Florida probablemente declinará lentamente
hasta su extinción.*

Introduction

The West Indian manatee (*Trichechus manatus*) is a
large, long-lived, completely aquatic herbivorous mam-
mal inhabiting tropical and subtropical waters of the
New World Atlantic (Lefebvre et al. 1989). It is one of
just four extant species in the order Sirenia. The vulnera-
bilty of sirenians was demonstrated by extirpation of
Steller's sea cow (*Hydrodamalis gigas*) within 27 years
of its discovery in 1741 (Stejneger 1887). A subspecies,
the Florida manatee (*T. manatus latirostris*), has been
protected for over a century (O'Shea 1988), but the pop-
ulation is currently considered endangered. In the
United States, Florida manatees are protected under the
U.S. Endangered Species Act of 1973, the U.S. Marine
Mammal Protection Act of 1972, the Florida Endangered
and Threatened Species Act of 1977, and the Florida
Manatee Sanctuary Act of 1978. Manatee conservation
measures implemented in Florida over the last decade
include designation of sanctuaries, boat speed-limit
zones, regional protection plans, and educational cam-
paigns (O'Shea & Ludlow 1992; O'Shea 1995). A Florida
Manatee Recovery Plan (U.S. Fish & Wildlife Service
1989) details protection, research, and management to
be conducted with the goal of downlisting the species
from endangered to threatened status. Objectives of the
recovery plan include improvement in understanding
manatee demography and construction of population
models to assist in evaluating population status.

The Florida manatee conservation problem is unusual.
Typical threats to wildlife populations—killing animals
for food or as pests and large-scale appropriation of hab-
itat for human use—are absent. Florida manatees oc-
cupy waters that are almost entirely in public ownership
and are regarded favorably by most members of the pub-
lic. The most obvious means for protecting manatees is
to minimize detrimental effects of recreation and other
human activities (O'Shea 1995). This means restricting
boating activity in manatee-populated waters (to reduce
deaths of manatees struck by boat hulls and motors) and
restricting human approach or pursuit of manatees.
When specific regulations to accomplish these objec-
tives are proposed, they are strongly opposed in legisla-
tive and judicial arenas as detrimental to development,
tourism, and boating industries. If controversial conser-
vation policies are to be sustained, it is essential to learn
the extent to which restrictions on human activity are
justified by the actual status and threats to the manatee
population. Manatee natural history and population biol-
ogy, however, operate on an extended time scale,

which also provides an unusual framework for consider-
ing predictions about population status and future per-
sistence.

Age structure, age-specific mortality, and age-specific
reproduction are key factors influencing the ability of a
population to persist. Long-term population studies of
large mammals allowing derivation of estimates for these
factors are rare. The first effort at an integrated analysis
of Florida manatee demography (Packard 1985) used
age-structured Leslie matrix models. Although the data-
base on manatee demography at that time was rudimen-
tary, modeling suggested a low maximum potential rate
of increase and did not discount the possibility of a de-
clining population. Low potential rates of increase have
also been calculated for the closely related dugong
(*Dugong dugon*) (reviewed by Marsh 1995), but recent
advances in knowledge of manatee life history traits sug-
gest the dugong model is not a useful surrogate for Flor-
ida manatees (O'Shea & Ackerman 1995). Quantitative
aspects of population dynamics of the remaining two
species of manatees (*T. senegalensis and T. inunguis*)
are virtually unknown.

We provide new estimates of Florida manatee demo-
graphic parameters based on age-determination studies
of all carcasses recovered during the 16-year period from
1976–1991 (Marmontel 1993, 1995). These data eluci-
date the conservation status of the Florida manatee pop-
ulation in a manner that can guide regulatory policy. We
present a population viability analysis (Lacy et al. 1989;
Seal & Lacy 1990; Lacy 1993) to identify the relative im-
portance of the factors affecting the population and to
assess the merits of possible management alternatives.

Unlike life tables, which make deterministic projec-
tions of population growth, population viability analysis
(PVA) uses stochastic models with fluctuating popula-
tion size and varying demographic parameters to predict
population size and the probability of population persis-
tence for a defined period under specific conditions
(Gilpin & Soulé 1986; Soulé 1986, 1987*a*). By using alter-
native estimates thought to represent the best and worst
cases likely, PVA also can yield probabilistic population
projections for the range of conditions likely to be en-
countered. PVAs have been applied to a number of en-
dangered and threatened species or small populations, in-
cluding marsupials, carnivores, ungulates, primates, birds,
reptiles, amphibians, and plants (Shaffer 1983; Shaffer &
Samson 1985; Menges 1986; Lande 1988; Murphy et al.
1990; Kinnaird & O'Brien 1991; McKelvey et al. 1992;
Lacy 1993). The technique has only recently been ex-
tended to marine mammals (Taylor 1995; Ellis et al. 1993).

Natural History

The Florida manatee is mostly confined to Florida during the winter with similar numbers on either side of the peninsula; some individuals disperse farther north during the warmer months (Lefebvre et al. 1989; Ackerman 1995). The population has relatively high levels of genetic variability (McClenaghan & O'Shea 1988). Manatees inhabit inland rivers or coastal and estuarine waters with access to freshwater sources and deep-water canals (Hartman 1979). They eat a variety of species of aquatic plants (Hartman 1979; Best 1981). Manatees have low metabolic rates and high thermal conductance (Irvine 1983) and as a result seek warm-water sources during the winter in Florida (Reid et al. 1991, 1995; O'Shea & Ludlow 1992), aggregating in large numbers around natural springs or industrial warm-water effluents (Reynolds & Wilcox 1994; Ackerman 1995). Manatees have no regularly reported natural predators except humans (Rathbun 1984).

No reliable technique exists for estimating current population size with accuracy or precision (Lefebvre et al. 1995). Immediately after our period of data collection, however, the Florida Department of Environmental Protection conducted statewide total-count aerial surveys. Following a cold front in January 1992, an uncorrected count of 1856 was obtained, with most located at winter aggregation sites. The count did not estimate variance and is considered a minimum population size (Ackerman 1995).

The annual number of manatees found dead in Florida has increased at a rate of 5.3% per year, averaging 89 per year during 1976–1981 and 153 per year from 1986–1992 (Ackerman et al. 1995). These values could represent unsustainable mortality levels. Collisions with boats were the most important identified cause of mortality, and boat-related mortality has increased 10.3% yearly since 1976 (Ackerman et al. 1995). A greater incidence of collisions with boats occurs in regions that include 13 coastal counties which in 1989 the state of Florida subsequently targeted as "key" counties for mortality-reduction efforts through boat-speed zoning (O'Shea 1995; Ackerman et al. 1995). Other causes of mortality include being crushed in canal locks and flood gates, entanglement in and ingestion of debris and fishing equipment, disease, and natural catastrophes such as exposure to prolonged severe cold spells or biotoxins (Buergelt et al. 1984; O'Shea et al. 1985; Beck & Barros 1991; O'Shea et al. 1991; Ackerman et al. 1995).

Linkage of mortality due to collisions with watercraft and human population growth indicates that human demography may be one of the best predictors of manatee population trends. Florida's human population grew by 32.8% during the period from 1981–1990 and is projected to increase by 20.4% in the succeeding decade (Bureau of Economics and Business Research 1993). Most (86.8%) growth from 1981–1990 was from immigration (net immigration averaged 760 new residents per day). Approximately 80% settled within 16 km of the seacoasts, where boating is a major recreational activity. The number of registered boats increased 3.4% per year from 1976–1992 (Ackerman et al. 1995). In addition, recreational boats are increasing in power and ability to traverse shallow areas (Wright et al. 1995). Unless this pattern of key factors changes, boat-related manatee mortality may continue to rise.

Essential findings from demographic analyses of the manatee carcass sample (Marmontel 1993, 1995) for the 16-year period from 1976–1991 are as follows. Sexual maturation of females occurred at age class 3 (between 3 and 4 years of age), with first calving as early as age class 4. At any one time 33% of the mature females were pregnant, indicating an average calving period of 3.0 years. Age-specific fecundity was stable (0.24 female calves/adult female/year based on both pregnancy and lactation data) from the age of first parturition throughout life. Gross annual recruitment rate was a maximum of 8% (calculated by Marmontel 1995 as [% females in the population] $\times$ [% females mature] $\times$ [annual pregnancy rate], assuming a 12-month gestation). Manatees are long-lived; we found 59 growth layers in bone of 1 manatee, and 75 had counts ranging from 21–39. However, half the carcasses belonged to year classes 0, 1, and 2, and mean age of carcasses was low (5.7 years), with 46% of 460 female carcasses examined reproductively mature. Survival rate was low among the very young, increased up to age class 4, and remained constant (89.9% $\pm$ 0.013 SD) from age class 4 to at least 25. Assuming the carcass sample reflects the age structure of the living population, manatee survival in Florida differed from the normal pattern for large-bodied mammals in lacking a plateau of high rates through middle age (Fig. 1), but instead resembles survivorship curves in exploited populations (Laws 1966; Spinage 1970; Bunnell & Tait 1981). Death from intense cold affected mostly subadults, but mortality by boat collisions was constant across adult age classes. The carcass-based life table indicated approximately zero population growth, with a net reproductive rate $R_0 = 1.09$ and a calculated finite rate of increase $R = 0.005$ (compared with the initial assumption of $r = 0$).

Methods

All specimens examined came from manatees that died for reasons unrelated to the study. A multiagency effort began in 1974 to recover all dead manatees found in the southeastern United States (Bonde et al. 1983; O'Shea et al. 1985; Ackerman et al. 1995). Numerous materials were collected for study, and total body length (cm), sex, and cause of death (when possible to determine) were recorded. Procedures appear in Bonde et al. (1983). Each manatee carcass was assigned to an age class based
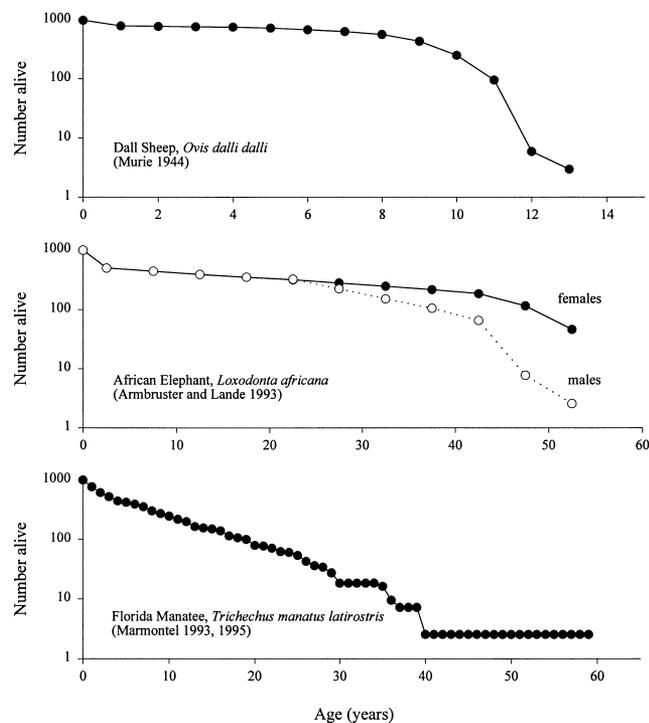
Figure 1. A comparison of survival curves for two other large-bodied mammals (Dall sheep and African elephant) with Florida manatees.

Table 1. Default parameters used in the simulations of Florida manatee demography.*

First age of reproduction: 4
Age of senescence (death): 39
Sex ratio at birth (proportion of males): 0.5
Polygynous mating:
   45% of adult males in the breeding pool
Reproduction (%):
   57.67 (EV = 13.20 SD) produce litters of size 0
   40.64 produce litters of size 1
   1.69 produce litters of size 2
Mortality (%):
   28.02 (EV = 7.70 SD) mortality between years 0 and 1
   18.36 (EV = 10.20 SD) mortality between years 1 and 2
   14.05 (EV = 7.98 SD) mortality between years 2 and 3
   13.90 (EV = 6.74 SD) mortality between years 3 and 4
   9.22 (EV = 1.24 SD) adult mortality (4–60 years)
Frequency of type 1 catastrophe (cold): 1.33%
   with 95% multiplicative effect on reproduction
   with 90% multiplicative effect on mortality
Frequency of type 2 catastrophe (hurricane): 0.5%
   with 95% multiplicative effect on reproduction
   with 90% multiplicative effect on mortality
Frequency of type 3 catastrophe (disease): 2%
   with 95% multiplicative effect on reproduction
   with 90% multiplicative effect on mortality
Initial population size: 2000
Carrying capacity: 5000 (EV = 0.00 SD)

* Simulations were conducted 100 times, each over 1000 years. No inbreeding depression was included. Reproduction was assumed to be density-independent. Environmental variation (EV) in mortality was correlated among age classes, but environmental variation in reproduction was not.

on microscopic examination of growth-layer groups visible in histological preparations of the periotic bone (Marmontel et al. 1996). Estimates of age-specific reproduction and survival used in the PVA (Table 1) were calculated from age assignments for 1212 carcasses. Details on derivation of estimates for reproduction and survival are presented in Marmontel (1993, 1995). A key assumption of the underlying population model was a stable distribution of age classes. Such an age distribution is achieved only if population growth is zero (an assumption of this model), so the model tends to produce a near-zero calculation of population growth rate. A result of growth rate near zero would provide weak evidence of actual population dynamics consistent with the assumed rate of the underlying model, whereas a result markedly different from zero would constitute strong evidence of a non-zero rate for actual dynamics. No fluctuations in age distributions at death were detected among three temporal divisions of the study period (1976–1980, 1981–1985, 1986–1991) (Marmontel 1993), the proportion of calves in year-round aerial surveys appears stable (Rathbun et al. 1995), and fecundity appears constant (Marmontel 1995), generally supporting the assumption of a stable age distribution.

We used the computer program VORTEX51 (Lacy 1993) to calculate the fate of manatee populations under various conditions (Table 1). The VORTEX51 program is

a Monte Carlo simulation of the effects of both deterministic and stochastic events (demographic, environmental, and genetic) on populations. Demographic stochasticity includes random variation in demographic parameters, whereas environmental stochasticity refers to variation in the environment external to a population (Simberloff 1988), although the distinction is somewhat arbitrary (Goodman 1987a). The first affects only very small populations whereas the latter may be significant to larger populations (Leigh 1981; Goodman 1987a, 1987b; Mode & Jacobson 1987). The VORTEX51 program allows input of the proportion of reproducing individuals and the proportion dying in each age class, as well as standard deviations in estimates of birth and death rates to reflect environmental variability. With the variables allowed to change at random within limits, the program predicts risks of extinction at specified intervals (for example, every 100 years during a 1000-year simulation), probability of persistence through the total period, mean time to extinction of those simulated populations that went extinct during the period modeled, and mean final population size. Standard deviation values for extinction time and final population size indicate the range of results across the runs. Standard errors of probability of the

population persisting to 1000 years are small, given by $P(1-P)/\sqrt{1000}$ (Lacy et al. 1989).

We accommodated uncertainty associated with some of the estimates by bracketing values (modeling potential upper and lower bounds), resulting in the evaluation of several different scenarios on the probability of extinction. We considered the possibility that adult mortality might increase by 10% (Ackerman [1995] calculated that mortality from collisions with boats will have increased at 10% per year over the period of study), the possibility that adult mortality might decrease by 10% (by successful reduction of boat speeds in waters with high manatee activity), and the possibility that manatee reproduction might decrease by 10% (from any factor that would lower carrying capacity, such as loss of feeding habitat). We think it unlikely that most factors of manatee reproduction can be increased above present rates because of physiological limits to the currently young ages of first reproduction (conception as early as age class 3) and to the energetic need for extended lactation and maternal care, particularly in winter (O'Shea et al. 1985). Nevertheless, the proportion of reproductive females could increase and such parameter estimates may need to be refined in future analyses.

Each demographic parameter was assigned a distribution with a mean and standard deviation to allow modeling of environmental variation. The VORTEX51 program uses binomial distributions to model annual fluctuations in probabilities of reproduction and mortality (Lacy 1993). Input values for age-specific mortality rates were obtained from the female life table (Marmontel 1993, 1995). In order to approximate the $r = 0$ assumption of VORTEX51, these values were reduced by 11%. Percent mortality for year class 0 was 28.2 (SD = 7.7); for year class 1, the value was 18.36 (SD = 10.2); for year class 2, 14.05 (SD = 7.9); and for year class 3, 13.9 (SD = 6.74) (Table 1). Mean adult mortality (ages 4 and older) was modeled at 9.22% (SD = 1.24). Reproductive values were calculated based on field examination and histological preparation as noted in Marmontel (1995). Maximum litter size was two. The proportion of females producing x offspring per year was recalculated as the proportion of female carcasses observed pregnant plus one-half the proportion observed to be lactating, to correct for those lactating females who had given birth recently. Very few twin births have been observed in manatees (Marmontel 1995; Rathbun et al. 1995). Input values were 57.67% producing 0 offspring, 40.64% producing one offspring, and 1.69% producing two offspring (SD = 13.2). The population was truncated at year class 39 (only one animal in the sample exceeded this age class, but by 20 years) because no data on senescence are available but the likely decline in reproduction accompanying senescence needs to be accommodated (Eberhardt 1985). Manatees are polyandrous, the female mating with a number of males (Hartman 1979). The percentage of males actively reproducing (45%) was based on male age structure and the findings of Hernandez et al. (1995) on sexual maturity, where 93% of mature-sized specimens in non-winter season produced sperm and approximately 50% of males are of mature size. Sex ratio was assumed to be 1:1 based on carcasses (Marmontel 1993, 1995). Internal consistency was checked by comparison with results from the life table. Values for environmental variation associated with mortality and reproductive estimates were calculated based on year-to-year standard deviation of those rates and maintained constant for most schedules (unless specified).

Populations of an initial size of 2000 statewide were modeled to evaluate the impact of changes in different estimates on population growth and persistence. Initial population size was based on the number of manatees (1856) counted during aerial surveys in early 1992 (Ackerman 1995), at the end of our period of study. More recent (February 1996) counts by the Florida Department of Environmental Protection total 2639 manatees. An alternative population size of 4000 was also modeled. There are no estimates of Florida manatee carrying capacity. The subspecies was probably not abundant in historic times (O'Shea 1988), and lack of evidence for current limitations in food supply (extensive seagrass beds and proliferation of exotic aquatic plants beyond the capacity for manatees to control [Etheridge et al. 1985]) indicate that manatees are below carrying capacity. Carrying capacity was therefore arbitrarily modeled at levels of 5000, 8000 and 10,000. Carrying capacity was also modeled with environmental variability (arbitrarily set as 10% of the initial population or 200 individuals), to simulate variations in weather conditions and longer-term habitat changes. When simulating two subpopulations (Atlantic and Gulf coasts), we used the above reproductive parameters and survival rates obtained from the life table based on the entire population (Marmontel 1993). Initial population size was set at 1000 and carrying capacity at 2500 for each coast.

Variability due to periodic cold stress and occasional disease was included in the estimate of environmental variation. Catastrophes not included in this variability were assumed to occur more rarely and with greater impacts on the population. Three catastrophic events were modeled: (1) episodes of extreme cold fronts, (2) high-intensity hurricanes, and (3) disease outbreaks. Data indicate that a major winter freeze (reaching average daily low temperatures of $-6°C$) occurs in Florida every 60 to 90 years (Chen & Gerber 1990). Using an average of 75 years, we modeled the occurrence of an extreme cold event with an annual probability of 1.33%. The severe cold during the winter of 1989–1990 (low temperatures of $-7°C$ at Titusville on the central Atlantic coast of Florida) killed at least 61 manatees (Ackerman et al. 1995), or 3% mortality of a total population of 2000. Considering that an extreme freeze might kill three times as many

manatees, a 10% level was modeled for effects on mortality. Effects on reproduction are unknown, but based on other mammals may be less damaging than effects on survival (Seal & Lacy 1990). For females giving birth in the spring after a severe winter, some proportion of the pregnancies may result in miscarriages, so an arbitrary level of 5% was modeled.

Hurricanes affecting Florida tend to concentrate mostly in the Panhandle and in southern Florida. Of 11 major hurricanes in this century, only one was class 5 (winds of 248+ km/h, storm surge of 5.5+ m) (Johnson & Barbour 1990). Analyzing frequency curves for different intervals (based only on the western coast of Florida), Ho and Tracey (1975) calculated a recurrence of 200 years for storms of such magnitude. Dugongs have been stranded by cyclone tidal surges (Marsh 1989), as was at least one manatee by Hurricane Andrew in 1992. In the future a combination of increased sea-level rise with a class 5 hurricane could have devastating effects (Hine et al. 1987). Destruction of seagrass beds may cause indirect mortality in dugongs (Heinsohn & Spain 1974; Preen & Marsh 1995). Hurricane Camille destroyed 33% of the seagrass beds in Mississippi waters (Eleuterius & Miller 1976). Wave action may also produce upwelling, causing water 5°C colder than normal to remain for days with unknown ecosystem effects (Simpson & Riehl 1981). The population impacts of these factors are hard to judge, but we assumed 10% of the population would be directly affected by the storm and 5% would show reductions in reproduction (Table 1). The model does not allow extended impacts on reproduction.

The impact of disease was modeled as a catastrophe capable of decimating all the animals in one warm-water aggregation, a number varying between at least 200 and 300 manatees at the time of study (Reynolds & Wilcox 1994). A 90% index was given for survival (10% reduction), and 95% for reproduction, with a probability of 2%. The probability of a disease agent spreading to other warm-water concentrations was modeled as 1% with a 70% impact on survival and an 85% impact on reproduction, and 0.75% with a 50% impact on survival and 75% impact on reproduction. These probabilities were projected on a 1000-year period; in reality, in shorter periods such probabilities may be much higher. For example, after our analysis was completed, over 150 manatees died from March to May of 1996 in southwestern Florida from dinoflagellate toxins (Florida Department of Environmental Protection, unpublished data).

Even though large mammals have density-dependent regulatory functions (reproductive rate of adult females, age of first reproduction, immature mortality rates, and adult mortality rates) (Charnov 1986; Eberhardt 1977; Fowler 1981, 1987), no density-dependence was chosen because (1) populations with numbers reduced by human activities are typically far below carrying capacity (K), so it is reasonable to model them without density

Table 2.   Population viability analysis for Florida manatees under various scenarios of mortality, reproduction, sources of variation, and risk.*

Scenario*	Rate of increase (r)	Probability of persistence (p)	Mean time to first extinction	Mean final population size
1. Deterministic scenario, no EV, no catastrophes	0.0004	1.00	none	2994 ± 1289
2. No catastrophes, with EV	0.000	0.94	679 ± 187	1250 ± 1283
3. No EV, with catastrophes	−0.003	0.61	843 ± 121	85 ± 67
4. Basic scenario with EV and catastrophes (Table 1 and scenarios 5–20, below)	−0.003	0.44	756 ± 165	161 ± 184
5. −10% reproduction	−0.012	0.00	411 ± 95	0
6. +10% age class 0 mortality	−0.007	0.09	606 ± 149	31 ± 26
7. +10% age class 1 mortality	−0.005	0.15	684 ± 161	38 ± 30
8. +10% age class 2 mortality	−0.005	0.19	714 ± 170	52 ± 64
9. +10% age class 3 mortality	−0.005	0.24	675 ± 170	108 ± 205
10. +10% adult mortality	−0.010	0.00	452 ± 104	0
11. +10% overall mortality	−0.018	0.00	289 ± 66	0
12. −10% adult mortality	0.003	1.00	none	3073 ± 1231
13. Disease: 1.0/0.85/0.70	−0.005	0.21	668 ± 182	141 ± 362
14. Disease: 0.75/0.75/0.50	−0.005	0.12	565 ± 188	67 ± 64
15. N = 2000; K = 5000; 2 EV in reproduction, mortality	−0.003	0.15	542 ± 202	113 ± 143
16. N = 2000; K = 3500	−0.003	0.38	713 ± 163	138 ± 191
17. N = 2000; K = 8000	−0.003	0.49	755 ± 160	106 ± 200
18. N = 4000; K = 10000	−0.003	0.64	816 ± 139	193 ± 241
19. 10% EV in K (= 200)	−0.003	0.44	735 ± 170	157 ± 297
20. +10% males reproducing	−0.003	0.34	679 ± 168	188 ± 233

**Average from 100 simulations over 1000 years. Basic scenario represents the best estimates of demographic variables from carcass-derived database under 1976–1991 conditions. EV = environmental variation, N = initial population size, K = carrying capacity.*

Table 3. Results of 100 simulations for 1000 years of Florida manatee populations under different levels of migration and catastrophes.*

Scenario	r_1	p_1	r_2	p_2	$p_{1,2}$	MTFE	MFPS
1. Single population							
$\quad$ N = 1000; K = 2500							
$\quad$ Default survival, catastrophes	−0.003				0.22	695 ± 166	81 ± 103
2. Two subpopulations							
$\quad$ Migration = 0.0001							
$\quad$ $N_1 = N_2 = 1000$							
$\quad$ $K_1 = K_2 = 2500$							
$\quad$ Default survival, catastrophes	−0.003	0.26	−0.003	0.30	0.44	754 ± 153	88 ± 101
3. Two subpopulations							
$\quad$ Migration, survival, N and K as above							
$\quad$ Effects of cold and disease 50%							
$\quad$ higher in population 1, hurricanes							
$\quad$ 50% higher in population 2 (than default)	−0.004	0.15	−0.005	0.13	0.25	740 ± 155	76 ± 77

*r, rate of increase; p, probability of persistence; subscript 1, Atlantic coast population; subscript 2, Gulf coast population; MTFE, mean time to first extinction; MFPS, mean final population size for successful cases.

dependence (Ferson & Akçakaya 1990) and (2) models without density dependence usually are conservative estimators of extinction risks, generally giving higher estimates of risks of extinction than the more realistic models with density dependence (Ferson et al. 1989; Ginzburg et al. 1990), even though this is not always the case (Boyce 1992).

A summary of the default parameters used in the simulations is presented in Table 1. For each set of parameters, we set the program to run for 1000 years and replicated the simulation 100 times. The scenario with carcass-based estimates believed closest to manatees' current demography and minimum population size was considered the basic scenario. Subsequently we altered values of the various estimates one at a time by 10% and repeated the process (Table 2). Table 3 shows simulation results for the evaluation of a manatee metapopulation, modeling two subpopulations (Atlantic and Gulf coast) and low levels of migration (0.01% per year).

We also simulated the basic scenario for 100 years, 100 times, to evaluate the status of the manatee population under Mace and Lande's (1991) system. That system uses as criteria broad categories of population size, immigration rate between population fragments, percentage decline in a number of generations, and probability of catastrophes.

Results

Deterministic and Stochastic Scenarios

The simulated schedule with calculated average mortality and reproductive rates and without environmental variation or catastrophes (scenario 1, Table 2) yielded a growth rate of nearly 0, consistent with the assumed rate of the underlying demographic model. The probability of persistence through 1000 years was 1.0, and the

final population was approximately 1.5 times as large as the initial. In a more realistic schedule, approximating 1976–1991 conditions (scenario 4, Table 2), inclusion of year-to-year environmental variation in the demographic parameters and the predicted frequency and severity of extreme cold fronts, high-intensity hurricanes, and disease resulted in a slightly negative growth rate ($r = -0.003$), but a much lower probability of persistence in 1000 years was predicted ($p = 0.44$) and the mean final population size projected was only 10% of the original value (Fig. 2).

Sensitivity to Variation in Demographic Parameters

The most important factors for the prospects of the population were mortality and fecundity, and the model was most sensitive to changes in adult survival. The mean
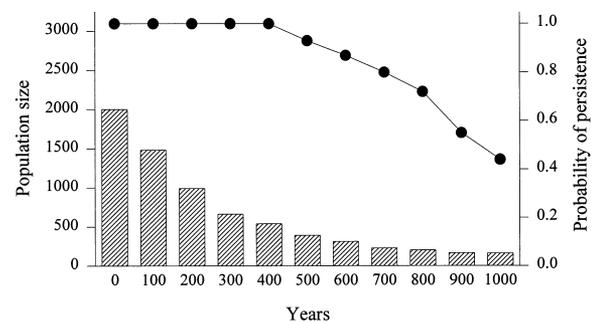

Figure 2. Projection of the Florida manatee population under the basic scenario ($r = -0.003$) (Table 1, scenario 4 in Table 2) over 1000 years, average of 100 simulations, initial population size 2000, including environmental variation and catastrophes. Bars represent population size, line represents probability of persistence.

time to extinction, under most schedules, was less than 600 years for populations simulated to go extinct within 1000 years with probabilities of persistence ranging from 9% to 44% (Table 2). The persistence probability became null and the ultimate population size was reduced to 0 when adult mortality was simulated to increase (scenario 10, Table 2). A 10% increase in adult mortality had twice as large an impact on *r* as mortality of any of the juvenile age classes except year class 0 (scenarios 6–9, 10; Table 2), resulting in extinction (mean final population size = 0; Fig. 3). Similarly, if all

Figure 4. Projection of the Florida manatee population with adult mortality reduced by 10% (r = 0.003) (scenario 12, Table 2) over 1000 years, average of 100 simulations, initial population size 2000. This scenario could be achieved by management of boating activity. Bars represent population size, line represents probability of persistence.

age classes suffer a 10% increase in mortality, the population growth rate would decline to −1.8%/year and final population size would be reduced to zero (scenario 11, Table 2; Fig. 3). In contrast, if adult manatee mortality could be reduced by 10%, population growth rate would improve from slightly negative to slightly positive (*r* = 0.003, scenario 12, Table 2; Fig. 4) and population size would increase. The growth rates markedly less than zero, calculated in scenarios 10 and 11, show that the assumed zero rate of the underlying demographic model does not mask the consequences of higher mortality.

If adverse effects on the population decreased reproductive output by 10%, population growth would become *r* = −0.012, and 1000-year persistence probability would be 0 (Fig. 5). Similarly, if age-specific fecundity

Figure 3. Projections of the Florida manatee population over 1000 years, average of 100 simulations, initial population size 2000, showing the effect of a 10% increase in mortality rate for age class 0 manatees (r = −0.007) (a); adult manatees (r = −0.010) (b); and manatees of all age classes (r = −0.018) (scenarios 6, 10, and 11, Table 2) (c). Initial population size 2000. Bars represent population size, line represents probability of persistence.
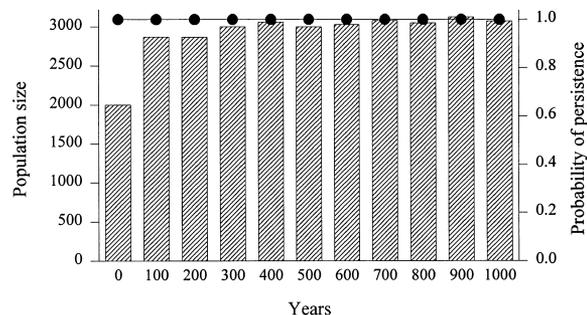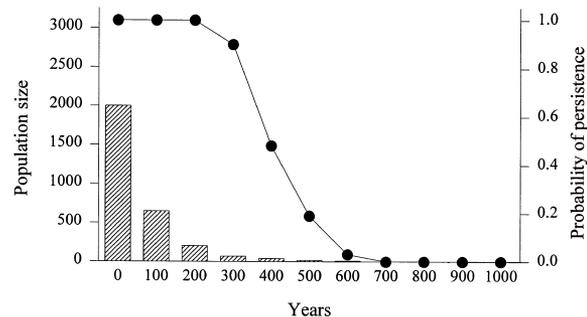

Figure 5. Projection of the Florida manatee population with reproduction reduced by 10% (r = −0.012) (scenario 5, Table 2) over 1000 years, average of 100 simulations, initial population size 2000. This scenario could result from degradation of feeding habitat or sublethal effects of widespread debilitating injuries. Bars represent population size, line represents probability of persistence.

decreased after a certain age, the probability of persistence would be reduced.

Simulation results indicate that a population of an initial size of 2000 has a 44% chance of persistence in 1000 years (scenario 4, Table 2), but if the initial size is twice as large, probability of persistence increases by 50% (scenario 18, Table 2). Carrying capacity (K) did not affect the growth rate, but the probability of persistence and the size of the persisting population increased with increasing K (scenarios 4, 16, and 17; Table 2). Increasing the magnitude of disease decreased the projected persistence time of the population. For example, scenarios 13 and 14 simulated a disease spreading to more than one aggregation (occurring with a lower probability but with higher impact on the population).

If the populations on both coasts of Florida were completely isolated (and assuming equal probability of catastrophes), overall probability of persistence would decrease (p = 0.22, scenario 1, Table 3). However, persistence probability reflects the default value for the total population (scenario 2, Table 2) when a small amount of migration (0.01% per year) is allowed between the east and west coasts. If the probability of cold events and epidemic disease were higher than the default value for total population on the east coast (where more artificially warmed aggregation sites occur and are farther north), and the probability of a hurricane strike is larger on the west coast (based on historical data), population growth rate would decrease to −0.004% and persistence probability would fall to 25%, despite migration.

Discussion

The inferences from this study are simple, and their meaning for conservation is clear. The Florida manatee population during the study period was inferred to be approximately stable relative to the short-term context in which policy decisions are normally made, but slowly declining in the longer-term scale more appropriate to this long-lived species. The 1976–1991 scenarios (1–4, Table 2) described a small range of uncertainty from an increasing to a decreasing population. The most reasonable scenario 4, which included environmental variation and was based on demographic estimates from carcasses collected state-wide and incidences of known or likely catastrophes, had a slightly negative growth and an unacceptably low probability of persistence over 1000 years. Thus management must focus on retaining and improving the conditions under which manatee demography operates. Our sensitivity analysis shows that if adult manatee mortality decreases by 10%, the manatee population should grow. If manatee mortality increases by 10%, the population should trend toward extinction, although the probability of persistence varies depending on the age class most affected. Manatee reproduction is

unlikely to be increased (Marmontel 1995; O'Shea & Hartley 1995; Rathbun et al. 1995) unless the proportion of reproductive females can be elevated, but it might possibly be decreased by changes such as loss of feeding habitat and increases in the numbers of females with debilitating injuries. If manatee reproduction is decreased by 10%, the population should trend toward extinction. Thus priorities for management policies should be to reduce manatee mortality and protect manatee habitat. Because the main identifiable agent of mortality is boat-manatee collisions, creating zones for managing boating activity and speed to reduce probabilities of collisions is the policy most likely to ensure manatee survival.

Caveats

The manatee PVA simulations suffer from some of the same uncertainties identified for the grizzly bear model (Shaffer 1983). The period of data collection is not lengthy in relation to longevity, so long-term patterns cannot be detected. Despite the fact that it is an excellent data set, it is not error-free, and sampling variation cannot be separated from true variation in the basic parameters. The model does not include genetics or density dependence.

Inferences from this study apply to the Florida manatee population for the 16-year time period from 1976–1991. Our inferences also assume that the carcass sample represents without bias the population living in that period. This assumption cannot be evaluated unless a reliable, independent method is developed to document the age structure of the living population.

With these caveats, however, we believe the demographic characterization of this PVA reliably depicts the population for the period of study. Our interpretations of future status for the manatee population are less certain, but we believe they serve as a reasonable if approximate guide to the prospects for the population.

Time Scale for Population Projections

Time to extinction provides a measure of the population's susceptibility to demographic challenges (Lacy et al. 1989). For most endangered species, a risk of extinction of less than 5% in 100 years is taken as a goal for preservation of the species from extinction (Seal & Lacy 1990). In line with this goal, a proposed reevaluation of World Conservation Union–International Union for the Conservation of Nature (IUCN) criteria to list species believed appropriate for most vertebrates examines levels of probability of extinction (critical, endangered, and vulnerable) in a 100-year period (Mace & Lande 1991). The criteria proposed suggest that 100 years is realistic in terms of prediction accuracy and legal expectations. Manatees do not meet the minimum criterion of 10% probability of extinction in 100 years for the lowest level (vulnerable) defined by

Mace and Lande (1991), yet our results show they would still trend toward a crisis. For the long-lived manatee, however, 100 years spans only a few generations, and individual longevity can be more than half of this time. A millennium is a more appropriate time scale to evaluate population trends and enable adaptive and evolutionary processes to operate. Similarly, Shaffer (1981) adopted a 99% persistence probability for 1000 years as a viability criterion for grizzly bears.

With an initial population size similar to uncorrected high counts from aerial surveys at the end of the study as a basis for comparison (N = 2000, Table 1), only three of the scenarios (1, 2, and 12) we considered likely to occur yielded a manatee population of more than 1000 animals after 1000 years (Table 2). The Florida manatee population was projected to grow only under constant conditions (no environmental variation or catastrophes, scenario 1, Table 2), which is an unrealistic assumption. Scenario 2 (Table 2) assumed environmental variation but no extremes; though more optimistic than real conditions, this scenario slightly reduced the probability of persistence, leading to some predictions of extinction and to a population size reduced by 40% after 1000 years. Only the prospect of reducing adult mortality by 10% (scenario 12) led to an increase over current population size. All other scenarios led to mean final population sizes that would be quite vulnerable to extinction.

Suggested guidelines for minimum viable population size of large mammals range from a few thousand (Soulé 1987b) to many thousands (Lacy et al. 1989; Thomas 1990). Calculated persistence times less than the time scale of interest are grounds for concern (Lacy et al. 1989; Seal & Lacy 1990; Stacey & Taper 1992) because they imply that the population has some probability of going extinct prior to the calculated mean. Furthermore, the small mean final populations remaining are easily affected by environmental variation and may be geographically isolated and thus have very low probability of persistence. A desirable population level is one that is unlikely to fall into an extinction vortex (Lacy 1993), given natural fluctuations. The IUCN (1987) recommends emergency measures such as captive breeding programs for populations that decline below 1000 individuals. Although these guidelines are based on theory and modeling, Berger (1990) confirmed the prediction of greater vulnerability of smaller populations by examining historical data on over 100 populations of bighorn sheep (*Ovis canadensis*).

Normal and Extreme Environmental Variation

Environmental variation routinely changes population survivorship and fecundity even in the absence of other factors (Caughley 1966; Murphy & Whitten 1976; Beissinger 1986). Such variation may reduce populations but seldom causes extinction unless numbers are already de-

pleted (Gilpin & Soulé 1986). Because populations of large iteroparous organisms are physiologically protected against short-term environmental change (Gilpin & Soulé 1986), populations of such species vulnerable to extinction are likely to have moderate (not low) levels of mean persistence time. Projections from the manatee PVA were consistent with these expectations. Probable effects of catastrophes on manatee demography (scenario 3, Table 2) decisively destabilized the population and led to severe population decline. Catastrophes have been implicated in the extinction or near extinction of populations of other mammals and endangered species (Whooping Crane [*Grus americana*], Doughty 1989; reindeer [*Rangifer tarandus*], Klein 1968; black-footed ferret [*Mustela nigripes*], Seal et al. 1989; and Puerto Rican parrot [*Amazona vittata*], Lacy et al. 1989). A disease spreading among manatees could reduce the population to a level at which chance variations in demographic parameters could cause extinction. New problems also might appear at low population levels, such as loss of genetic variability or difficulty in finding mates.

Unusually cold weather mainly affects young manatees (O'Shea et al. 1985; Ackerman 1995), but prolonged, severe cold might affect a wider range of age classes and, hence, more of the population. Manatees have learned to rely on sources of warm water during the winter, and warm effluents from electricity-generation plants have affected manatee distribution and movement (Packard et al. 1989). Sudden shutdown of a power plant operation may jeopardize manatees using its artificially warmed outflow, and wildlife managers should be consulted on proposed changes in operating schedules of power plants during winter (Packard et al. 1989). Large aggregations of manatees around warm-water sources during the winter also set the stage for catastrophes of other kinds (O'Shea & Ludlow 1992). An oil or chemical spill, the introduction of an epizootic agent to which the population is naive, or destruction of the local winter food supply could produce calamitous mortality. There are no records of disease epizootics in manatees, so they are modeled with great uncertainty. If their effects are not devastating, then the population has a reasonable level of security; however, if catastrophes have a strong effect (scenario 14 with 50% mortality, Table 2) or occur with higher frequency than modeled, then the population would face a much greater risk of extinction. Harwood and Hall (1990) estimated that disease outbreaks elevate average mortality of marine mammals by roughly 15–30%. An epizootic associated with a red tide episode (O'Shea et al. 1991) showed that one factor acting in a restricted area could affect a considerable proportion of a region's manatees. If the count of 338 manatees at the Fort Myers power plant in the winter of 1984–1985 (Reynolds & Wilcox 1994) is an accurate indication of manatee abundance in southwestern Florida, the red tide incident killed about 10% (*n* = 37) of the an-

imals using that area. The recent, highly publicized deaths of over 150 manatees in the period from March–May of 1996 in southwestern Florida also from exposure to red-tide dinoflagellate biotoxins rather than a disease, is about 35% of the total count of 427 made at the Fort Myers site in winter 1996 (Florida Department of Environmental Protection, unpublished data).

Manatees are very mobile (Reid et al. 1991, 1995) and live in an environment with few barriers to long-distance movements. Therefore it is hard to envision a metapopulation structure (Harwood & Hall 1990), except perhaps for the eastern and western coasts of Florida. If a disaster were to decimate the population on either coast, replacement would be limited mainly by the low potential growth rate. Replacement through migration would be slow because manatees are uncommon in the Florida Bay and Keys (Lefebvre et al. 1989) and are believed to not travel regularly around the southern portion of the peninsula. Movement across the state via Lake Okeechobee may occur but has never been recorded (O'Shea 1988). Furthermore, the Florida manatee population is unlikely to receive migrants from the Antillean subspecies. Strong currents in the Florida Straits and cooler temperatures in the northern Gulf of Mexico are believed to have promoted isolation between the two subspecies of West Indian manatees (Domning & Hayek 1986).

Implications for Conservation Policy

The inferred marginal stability of the Florida manatee population, high rate of mortality, collisions with boats as the dominant mortality agent, and the rapidly increasing human population and number of registered boats portend an increase in adult manatee mortality. Diminishing survival of adult manatees would lead inexorably to extinction (scenario 10, Table 2).

These results justify current policy-making efforts to reduce mortality as a limiting factor in manatee demography, which would improve the apparent situation of zero growth and maintain the population in the face of environmental variation. In view of severe conflict over proposed regulations, only full use of democratic processes and institutions may acceptably balance the responsibility for life advocated by proponents of manatee conservation and the rights of boaters, divers, and landowners advocated by coastline developers, dive shop and marina owners, and the boat and motor industry. The Florida Department of Environmental Protection has implemented boat speed zones and a preliminary marina-siting rule in each of the 13 coastal counties with greatest manatee usage and greatest current mortality, intended to allow continued human use and safe occupation by manatees (Ackerman 1995; Ackerman et al. 1995; O'Shea 1995). Meanwhile, the affected counties are crafting their own Manatee Protection Plans, with input from local citizens and approval from locally elected

officials. These plans vary in constitution but may include boat speeds, siting of marinas, ramps, and multiple boat slips at condominiums, habitat protection, and public education. County plans that are considered sufficiently protective are approved by the state agency, the state rule may be modified to eliminate minor discrepancies, and the state rule and the local plan are administered jointly.

Our study indicates that if these regulations are completed, enforced, and effective, conditions of manatee demography should improve. More females would survive to enter older age classes and produce young for longer periods. Mortality would diminish, the population would grow, and the probability of population persistence would increase. People and manatees should be able to coexist indefinitely. Conversely, if regulation is unsuccessful, the Florida manatee population is likely to decline slowly toward extinction.

As these regulations and plans are developed, anti-regulation advocates often argue that no scientific basis for regulation exists because there have been few manatee deaths in the waters of a municipality or county in the past year (or for the 4-year term of current elected officials). Our study, however, shows that the modeled scenario of 10% more adult mortality would be nearly imperceptible on a local, short-term basis; the 14–17 manatee deaths per year guaranteeing extinction (scenario 10, Table 2) would be an increase of only about 1 in each of the 13 key coastal counties. A local geographic and short temporal scale are not a reliable basis for evaluating the prospects of long-lived, mobile species like the Florida manatee.

Similarly, the high long-term risk of manatee extinction documented here shows that the interim goal of the manatee recovery plan (U.S. Fish and Wildlife Service 1989), to downlist the species from endangered to threatened by maintaining viable populations on both Atlantic and Gulf coasts, is not likely to be attainable under current conditions. Given the slow demographics of this population, it would be especially inappropriate to modify listing status under the brief 100-year framework of Mace and Lande (1991) without extended monitoring. If a reliable means of estimating population size is developed, the minimum time scale appropriate for evaluating population trend would be several decades (Lefebvre et al. 1995).

Research Needs

Our PVA was an initial approach based on an extensive carcass-derived database. Additional analyses of this database should be carried out to refine projections. In addition, the use of an expanding amount of information on manatee demographics based on longitudinal studies of living animals in the field also should be considered in future PVA modeling. Our findings of high model sensitivity to changes in adult survival have been verified by a

classical, deterministic population dynamics modeling approach (Eberhardt & O'Shea 1995) using sight-resight estimates of adult survival and observational records of reproductive traits among identifiable free-ranging manatees (O'Shea & Hartley 1995; O'Shea & Langtimm 1995; Rathbun et al. 1995; Reid et al. 1995). The latter approach also revealed higher adult survival in study areas where manatees have a long history of rigorous protection efforts, including boat speed restrictions, and sufficient high quality habitat (Crystal River and Blue Spring). Corresponding trend counts show notable increases in these limited regions (Ackerman 1995), supporting our conclusion that conservation efforts reducing adult mortality will lead to manatee population growth. Somewhat higher reproductive rates were also obtained using these alternative methods and should be taken into account in future PVA modeling. However, the carcass analysis is the only database that currently allows estimation of traits over the entire range of the subspecies. Sight-resight survival estimates for manatees sampled over the Atlantic Coast, for example, approach those used in our statewide PVA (Eberhardt & O'Shea 1995). Further reconciliation and combination of these two sources of demographic information should be attempted to allow development of more robust and refined PVA models.

We also recommend that analysis of future carcass samples consider the method of Van Sickle et al. (1987), using ages-at-death to calculate population growth rate and survivorship schedules (Tait & Bunnell 1980), because the approach appears applicable to this kind of data and robust to sampling errors. The method requires an estimate of first-year survival and consists of the calculation of rate of increase through the solution of a high-order polynomial. The rate of increase may then be used to calculate survivorship values. Study of salvaged carcasses and living populations will enable detection of demographic change. However, such indications of changing conditions occur long after the fact, enabling correction but not avoidance of problems.

PVAs are inherently speculative and predictions are only probabilistic (Shaffer 1990). Because all the factors are neither incorporated into the model (for example, genetics, density dependence or other feedback processes such as extended impacts on reproduction as noted in dugongs [Marsh 1995; Preen & Marsh 1995]) nor totally understood, the viability analysis may inaccurately estimate the true probabilities of extinction. Because the interaction of the various forces may be more than additive (Gilpin & Soulé 1986), several authors have called for the inclusion of all parameters in a comprehensive model (Samson et al. 1985; Ewens et al. 1987; Soulé 1987*a*; Boyce 1992), although Boyce (1992) also made the point that efforts should nevertheless be made to do the best with whatever limited information one has. It is essential to obtain accurate estimates of

means and variances of population parameters, which underscores the need for long-term studies and extensive field research. It is advisable to continue monitoring the status, rates, and variability of Florida manatee population parameters and to conduct further viability analyses. Attempts at developing indices of population size and trend using aerial survey and other methods should be continued (Lefebvre et al. 1995). It is also necessary to develop a methodology and program to monitor the condition of essential manatee habitats. Because it is possible that future coastal development will degrade habitat that provides manatee food, ecosystem effects of coastal development need to be evaluated. Areas important for reproduction and feeding should be identified and protected to ensure realization of the full reproductive potential (e.g., Sadleir 1969; Widdowson 1981; Knight & Eberhardt 1985). Although wildlife disease is seldom considered a population-limiting factor (Scott 1988), disease can be catastrophic to small populations. Intensified work to identify exposure and vulnerability of manatees to disease could prevent its potential effects from being overlooked.

Acknowledgments

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