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LOWER SURVIVAL PROBABILITIES FOR ADULT FLORIDA MANATEES IN YEARS WITH INTENSE COASTAL STORMS

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Abstract. The endangered Florida manatee (*Trichechus manatus latirostris*) inhabits the subtropical waters of the southeastern United States, where hurricanes are a regular occurrence. Using mark–resighting statistical models, we analyzed 19 years of photo-identification data and detected significant annual variation in adult survival for a subpopulation in northwest Florida where human impact is low. That variation coincided with years when intense hurricanes (Category 3 or greater on the Saffir-Simpson Hurricane Scale) and a major winter storm occurred in the northern Gulf of Mexico. Mean survival probability during years with no or low intensity storms was 0.972 (approximate 95% confidence interval = 0.961–0.980) but dropped to 0.936 (0.864–0.971) in 1985 with Hurricanes Elena, Kate, and Juan; to 0.909 (0.837–0.951) in 1993 with the March ''Storm of the Century''; and to 0.817 (0.735–0.878) in 1995 with Hurricanes Opal, Erin, and Allison. These drops in survival probability were not catastrophic in magnitude and were detected because of the use of state-of-the-art statistical techniques and the quality of the data. Because individuals of this small population range extensively along the north Gulf coast of Florida, it was possible to resolve storm effects on a regional scale rather than the site-specific local scale common to studies of more sedentary species. This is the first empirical evidence in support of storm effects on manatee survival and suggests a cause–effect relationship. The decreases in survival could be due to direct mortality, indirect mortality, and/or emigration from the region as a consequence of storms. Future impacts to the population by a single catastrophic hurricane, or series of smaller hurricanes, could increase the probability of extinction. With the advent in 1995 of a new 25- to 50-yr cycle of greater hurricane activity, and longer term change possible with global climate change, it becomes all the more important to reduce mortality and injury from boats and other human causes and control the loss of foraging habitat to coastal development.

Key words: climate change; Florida; Gulf of Mexico; hurricanes; manatee; marine mammals; mark–recapture; photo-identification; seagrass; survival probabilities; Trichechus manatus.

Introduction

Ecosystems can be shaped by periodic disturbance from hurricanes and intense storms, which can alter population, community, and ecosystem processes. Much is known about hurricane effects on terrestrial vegetation structure and forest ecosystem processes (Boose et al. 1994, Foster et al. 1997, Cooper-Ellis et al. 1999), but limited information is available on animal populations. Due to the complex interactions of species and habitats, storm effects on animal populations can have important consequences for how habitats and ecosystems respond and recover (Michener et al. 1997). Individuals and populations, however, are differentially affected by hurricanes. Individuals can be killed outright, displaced great distances by a storm, or suffer delayed effects to health and reproduction due to community or ecosystem changes. Some populations may be able to take advantage of the disturbance to increase their numbers or outcompete other species, others may be minimally affected and recover quickly, while others may be impacted substantially. Dispersal ability, population size, life-history strategies, species-specific behaviors to cope with intense storms and their consequences, community dynamics, and damage to food resources or habitat critical to breeding are some of the factors determining impact (Waide 1991, Michener et al. 1997, Spiller et al. 1998).

Understanding how animal populations respond to hurricanes generally has been limited by a lack of critical pre-hurricane data necessary to make post-storm comparisons. Controlled experiments simulating hurricane effects are often precluded for larger vertebrates by their mobility (Tanner et al. 1991). Here we present the first empirical evidence for storm effects on adult survival for a large marine mammal, the Florida manatee (*Trichechus manatus latirostris*). New mark–resighting statistical models now give us the tools to examine annual variation in survival probabilities and to test for effects from environmental factors (Lebreton et al. 1992, Nichols 1992). We previously used these techniques to provide the first estimates of annual survival probabilities for wild, free-ranging manatees us-

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ing photo-identification data of naturally marked individuals that return in winter to warm-water refuges (O'Shea and Langtimm 1995, Langtimm et al. 1998). For a subpopulation along the north Gulf coast of Florida, we reported high annual estimates of adult survival with negligible annual variation from 1982 through 1993 (Langtimm et al. 1998). This result was consistent with the small amount of coastal development in the region, few documented deaths, and expectations based on life-history theory for large, long-lived mammals in a stable environment. However, with six additional years of data (through 1999), we detected significant annual variation with lower survival during years with major storm activity.

Identifying and understanding hurricane effects for this species and others is critical for short- and long-term planning by researchers, managers, and policy makers. In 1995, meteorology researchers identified the beginning of a new dangerous cycle of increased hurricane activity and intensity, which is expected to continue for the next 25–50 yr (Landsea et al. 1996). Earlier (1970 to 1994), the Atlantic basin enjoyed a naturally occurring cycle of mild activity (Gray 1990, Landsea 1993, Landsea et al. 1996) with relatively few land strikes by intense hurricanes. The last seven years of storm data support the predicted long-term increase in major hurricanes (Gray et al. 2001). Longer term changes, beyond this known multi-decade cyclical regime, are possible as well with expected global climate change (McCarthy et al. 2001).

Methods

Ecology of the Florida manatee and the study population in northwest Florida

The Florida manatee inhabits the subtropical waters of the southeastern United States, feeding on seagrass and freshwater vegetation (Hartman 1979). The subspecies is endangered primarily due to small population size, threats to its habitat, and mortality from boat strikes and other human activity (O'Shea et al. 1985, Ackerman et al. 1995). It is 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. Natural mortality events occur periodically from cold stress during extended cold weather (Buergelt et al. 1984) and from toxins inhaled or ingested during red tide blooms (O'Shea et al. 1991, Bossart et al. 1998). Previously, mortality events from hurricanes had only been hypothesized for the Florida manatee (Marmontel et al. 1997) based on the stranding of a single individual near Miami during Hurricane Andrew and the mass strandings of dugongs (Old World relatives of manatees) by cyclones in Australia (Marsh 1989) and India (Jones 1967). Indirect mortality from starvation also was hypothesized with documented periodic hurricane destruction of its food base: seagrass beds (Eleuterius and Miller 1976) and freshwater aquatic vegetation (Mataraza et al. 1999). Similar cyclone destruction of seagrass beds in Australia has resulted in shifts in dugong feeding areas and starvation and death (Heinsohn and Spain 1974, Preen and Marsh 1995).

Manatees occur near shore in estuarine or freshwater habitats. The distribution of manatees in northwest Florida (Powell and Rathbun 1984, Rathbun et al. 1990), and throughout the state, varies seasonally with changes in temperature. In warm months (May through September), the greatest concentrations in northwest Florida occur in the lower Suwannee River and its estuary (Fig. 1). Individuals also frequent the Wakulla, Withlacoochee, Crystal, Homosassa, and Chassahowitzka Rivers, the Cross Florida Barge Canal, and the estuaries of smaller rivers. Manatees are not seen in abundance south of the Chassahowitzka River to Tampa Bay. There are few documented movements between the northwest and southwest subpopulations.

Because manatees are physiologically stressed in cool temperatures (Irvine 1983), during the winter months (November to February) the range contracts and manatees throughout the northwest region converge primarily on two artesian-spring, warm-water refuges near the northern limit of the species' range: the Crystal and Homosassa Rivers (Powell and Rathbun 1984, Rathbun et al. 1990). With the large number of manatees present and the clear water conditions, these rivers have been the focus of manatee research since the late 1960s (Hartman 1979, O'Shea et al. 1995).

Compared to other areas of the state, manatees in this region are less affected by human activities. There are large areas of relatively pristine habitat (Powell and Rathbun 1984), the level of enforcement of boating and diving regulations at the aggregation sites has been high, and the number of known deaths due to boat strikes and other human-related factors has been low (O'Shea et al. 1985, Ackerman et al. 1995). Recent estimates of annual adult survival probabilities were higher in this region than on the more developed Atlantic coast (Langtimm et al. 1998). Analysis of trends in aerial survey counts (Rathbun et al. 1990, Ackerman 1995) and population models incorporating estimates of reproduction and survival rates (Eberhardt and O'Shea 1995) show that this subpopulation has increased since the 1960s.

Data collection and construction of capture histories

A longitudinal study of individuals recognizable by unique scar patterns was begun in the late 1970s (Rathbun et al. 1990). Manatees often acquire distinctive marks in the wild from natural and human-related causes (Fig. 2). Boat-inflicted injuries, fishing line entanglements, and lesions from fungal infections and cold damage can all leave permanent scars and mutilations after they heal. Since 1978, the Sirenia Project (now under the U.S. Geological Survey) has annually pho-

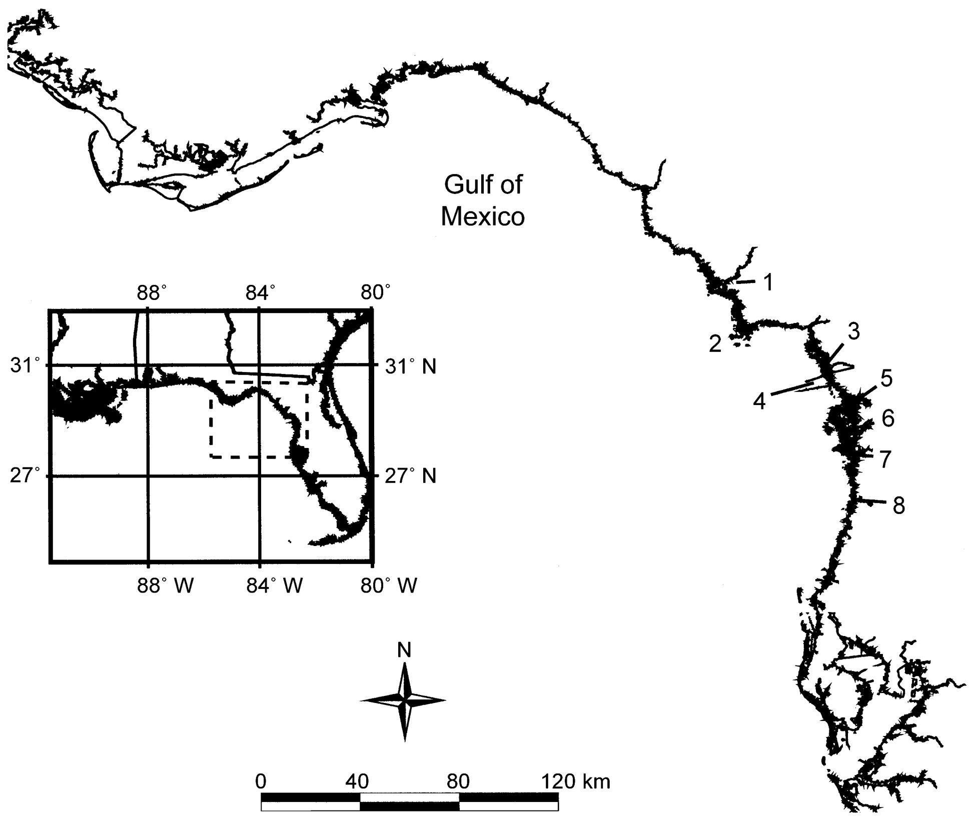

FIG. 1. Map of the study region. On the map showing the enlarged area of northwest region of Florida, sites are numbered as follows: (1) Suwannee River, (2) Cedar Key, (3) Withlacoochee River, (4) Cross Florida Barge Canal, (5) Crystal River, (6) Homosassa River, (7) Chassahowitzka River, and (8) site of 1993 manatee stranding from storm surge.

tographed and documented sightings of scarred individuals at the winter sites. Slide transparencies were taken with underwater cameras fitted with a wide-angle lens as photographers swam near the manatees. Photographs were screened yearly for matches with individuals entered in a photo-catalog, the Manatee Individual Photo-identification System. Digitized images and PC-based search technologies were used to assist researchers in matching photographs to cataloged individuals. To be included in the catalog, an individual had to have healed scars or natural features that were unique and easily recognized, and there had to be complete documentation of the dorsal and lateral views of its body and tail, including those parts without scars. Beck and Reid (1995) described the system and the protocols used to catalog individuals, collect data, and match sightings to cataloged animals.

We believe identification error rate was low and did not bias estimates. We used strict, conservative protocols to catalog animals and to accept data, and the possibility of misidentifications was reduced further by several factors inherent to the identification system. Clear water, the close proximity of photographers to the animals (1–3 m), and the general tolerance of manatees to being approached, allowed the documentation of details of features. Only healed features were used as marks, and there was redundancy in identification information in that nearly all cataloged individuals had multiple scars and features distributed over more than one part of the body. Documentation of newly acquired scars or changes in marking patterns was facilitated by the high return rate of individual manatees each year to the monitored sites (photo-identification data: Rathbun et al. 1990, 1995, Reid et al. 1991, radiotelemetry data: Rathbun et al. 1990) and consistent monitoring of these sites by the same experienced observers. The most likely source of misidentification would have been from losses or changes of original marks, resulting in an underestimation of survival probabilities (Arnason and Mills 1981).

Manatees were photographed at all times of the year, but for the analysis, we defined a narrower sample interval of 120 d (1 November through 28 February) when manatees were most readily photographed. Generally, in mark–recapture analysis of this kind, the assumption of equal probability of survival and capture among individuals requires the sample interval to be small compared to the interval between samples (Pollock et al. 1990:18–19). Survival probabilities are estimated for the time between the annual samples. Sightings of adults only were included in the analysis. Each sighting history consisted of the sighting (1) or non-

FIG. 2. Photograph of a scarred manatee cataloged in the sighting database.

sighting (0) of the individual at least once during the winter samples for each year of the study. A full discussion of the criteria for constructing the sighting histories was given in Langtimm et al. (1998). The final dataset consisted of the sighting histories of 311 animals (168 males and 143 females) from winter 1980–1981 through winter 1998–1999. A summary of the time spans over which each individual was monitored is presented in Fig. 3.

Mark–resighting modeling procedures

We used Program MARK (White and Burnham 1999) to model variation in survival and sighting probabilities and to estimate these probabilities under the various models. Our modeling philosophy followed that outlined by Lebreton et al. (1992). We started with the general Cormack-Jolly-Seber model (ϕ_{s*t}, p_{s*t}) [notation for models follows Lebreton et al. 1992], allowing survival (ϕ) and sighting probabilities (p) to vary with sex (s) and time (t). We assessed the goodness-of-fit (GOF) of the data to this global model using Program RELEASE (Burnham et al. 1987), available within Program MARK. We then constructed additional models by successively removing variation from the previous model based on specific biological hypotheses. Our previous analyses for the region (O'Shea and Langtimm 1995, Langtimm et al. 1998) found no differences in survival and sighting probabilities between the sexes, significant annual variation in sighting probabilities, and negligible variation in survival probabilities among years (i.e., essentially constant). Because the annual counts of dead manatees from the Manatee Carcass Recovery Program were low and relatively constant from this region, we hypothesized that the same patterns of variation would hold for this analysis; therefore, we initially utilized the same modeling scheme we employed previously. Subsequently, the analysis led us to the development of an additional hypothesis (see *Results*) that major coastal storms had an effect on annual adult survival probabilities. After testing this hypothesis with data from the National Hurricane Center, we constructed a covariate model in which survival probabilities varied in association with the years when the region experienced major storms.

We chose the best model based on Akaike's Information Criteria (AICc, Anderson et al. 1998, Burnham and Anderson 1998). AICc is an information-theoretic method that assists the researcher in identifying the most parsimonious model with enough parameters to account for the structure of the data without overparameterization and loss in precision (Burnham and

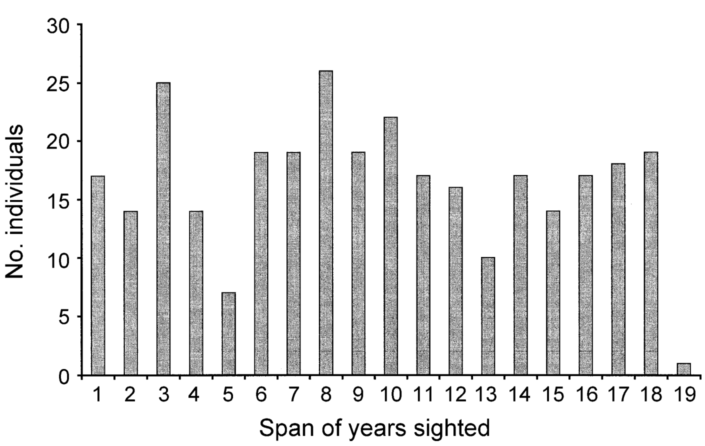

FIG. 3. Summary of the time spans for the individual sighting histories. The mean annual sighting probability estimated for the group was 0.713.

Anderson 1998). Lower AICc values indicate a more parsimonious model. Normalized Akaike weights were used to evaluate the expected likelihood of a given model relative to all the other constructed models (Burnham and Anderson 1998). To further evaluate the fit of the data to the storm covariate model in contrast to our other models, we used an analysis of deviance (ANODEV). ANODEV is analogous to an analysis of variance (ANOVA). It partitions differences between the various models' log likelihoods, whereas ANOVA partitions differences between the models' sums of squares. ANODEV tests for a significant ''treatment'' effect explained by the environmental covariate (Skalski et al. 1993). The best model was then used to obtain maximum-likelihood estimates of annual survival probabilities, sighting probabilities, and approximate 95% confidence intervals (95% CI).

Storm data

Data on timing, strength, and tracks of hurricanes were made available by the National Hurricane Center and National Climatic Data Center (NOAA) and were accessed on the World Wide Web (2 September 1999).[2] The Saffir-Simpson Hurricane Scale was used by these centers to report the relative intensity of each hurricane and is based on wind speed, barometric pressure, and storm surge. Storms are categorized as ''tropical storms'' when wind speeds are low and damage is minor. As the storm intensifies, it can progress from a minor Category 1 hurricane to an extremely strong Category 5. The scale was designed to estimate the potential land damage of a hurricane to the human population (Williams and Duedall 1997) and may not be the most appropriate to assess threats to manatees. Nevertheless, it is widely reported in public weather forecasts and provides a familiar index of storm intensity.

Data on the March 1993 winter storm were available in a report from the National Climatic Data Center (Lott 1993). Winter storms generally are not rated on the Saffir-Simpson Hurricane Scale, but comparisons with the scale based on barometric pressure and storm surge heights were reported by Lott (1993). We used the scale as well to make comparison easier with the summer cyclonic storms.

RESULTS

The general model fits the data satisfactorily for both sexes (Program RELEASE TEST2 + TEST3, males: GOF $\chi^2 = 70.57$, df = 55, $P = 0.08$; females: GOF $\chi^2 = 34.24$, df = 52, $P = 0.97$; total: GOF $\chi^2 = 104.82$, df = 107, $P = 0.54$). Based on AICc values calculated for our preplanned models (Table 1), our hypotheses concerning no sex-specific differences in survival ($\phi_{s*t}\ p_t$ vs. $\phi_t\ p_t$) or capture probabilities ($\phi_{s*t}\ p_{s*t}$ vs. $\phi_{s*t}\ p_t$) were supported. However, contrary to our earlier analysis (Langtimm et al. 1998), the AICc values strongly rejected the constant annual survival model in support of the model in which survival probabilities varied among years. The normalized AICc weight for the time-dependent model ($\phi_t\ p_t$) was 0.934 compared to only 0.066 for the constant survival model ($\phi_{constant}\ p_t$).

TABLE 1. Comparison of fit for the preplanned survival models.

Model	AIC_c	ΔAIC_c	AIC_c weight	No. para-meters	Deviance
$\phi_t p_t$	**3838.882**	**0.00**	**0.93376**	**33**	**2352.469**
$\phi_{constant}\ p_t$	3844.174	5.29	0.06624	18	2388.574
$\phi_{s*t}\ p_t$	3862.169	23.29	0.00001	50	2340.249
$\phi_{s*t}\ p_{s*t}$	3884.068	45.19	0.00000	66	2328.146

Notes: Models were constructed by successively removing variation (reducing the number of parameters) from the more general model beginning with the global model $\phi_{s*t}\ p_{s*t}$. Model notations indicate variation in survival (ϕ) and capture (p) probabilities by time (t), sex (s), or negligible over time (constant). Models are ranked according to lowest AIC_c (Akaike Information Criterion). The best model is in bold. Deviance is a relative measure of fit. ΔAIC_c is the difference in AIC_c values between the given model and the model with the lowest AIC_c.

This variation was unexpected, and we examined the annual survival estimates (Fig. 4) in search of a pattern. We looked for any point estimates below 0.95 (this was the lower bound of the approximate 95% confidence interval in our earlier analysis [Langtimm et al. 1998]). Three years showed dips in apparent survival below 0.95: 1985, 1993, and 1995. Two of the years, 1985 and 1993, were years in which surges from major storms had inundated the headwaters of Crystal River with saltwater and killed freshwater aquatic vegetation (Mataraza et al. 1999). However, no storm surge occurred at Crystal River in 1995, the year with the lowest estimated survival probability. Manatees that overwinter at Crystal River range throughout the northern Gulf coast at other times of the year. Strong storms in the region could directly impact a significant portion of the population even if the Crystal River area did not take a direct hit. If storms did impact survival, we hypothesized that we would find an association of storm occurrences with survival probabilities. To test this we examined the annual storm tracks plotted by the National Climatic Data Center. We expected to find at least one large, high-intensity storm during each of the three years with lower estimated survival and none or only low-intensity storms during the remaining years of higher survival estimates.

We tallied the number of storms tracking through the Gulf of Mexico in a rectangle defined at the northwest corner by New Orleans, Louisiana (30.0° N, 90.1° W), to Clearwater, Florida (28.0° N, 82.8° W) at the southeast corner (Fig. 1) and confirmed our hypothesis. No storms, or only minor tropical storms and Category 1 hurricanes occurred in the years with high estimated survival probabilities. However, during the three years

[2] URL: ⟨http://weather.unisys.com/hurricane/atlantic/index.html⟩

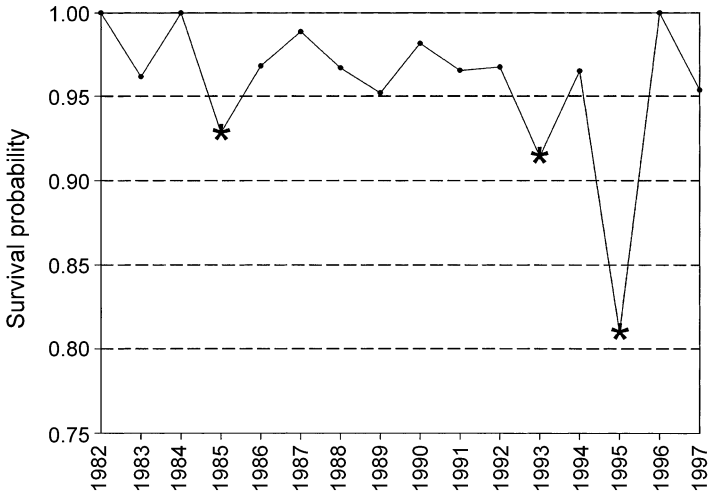

FIG. 4. Graph depicting annual variation in survival probabilities estimated under the time-dependent model (ϕ_t p_t). Estimates below 0.95 represented unusual years as they fell below the estimated lower 95% confidence limit for an analysis conducted six years earlier. Asterisks indicate years with intense storms.

with lower survival probabilities, strong storms classified as Category 3 and 4 on the Saffir-Simpson Hurricane Scale, in addition to minor hurricanes or tropical storms, had made landfall or skirted the north Gulf coast: Hurricanes Elena (Category 3), Kate (Category 3), and Juan in 1985 (Case 1986) (Fig. 5a), the March ''Storm of the Century'' (Category 3) in 1993 (Lott 1993) (Fig. 5b), and Hurricanes Opal (Category 4), Erin, Allison, and Tropical Storm Jerry in 1995 (Lawrence et al. 1998) (Fig. 6).

Because we were interested in accurately estimating survival probabilities and associated variance, we sought the best model to calculate the estimates. Therefore, after the results of the storm track analysis, we constructed one additional post hoc model that included a covariate with storm years. Years without major storms were constrained as constant among years (based on the results of Langtimm et al. 1998), while each storm year was allowed to vary independently from the other years. We did not constrain the storm years to the same survival probability, as the number, intensity, and location of storms varied each year and most likely would have impacted survival differently.

The low AICc value and normalized AICc weights strongly supported the storm covariate model (ϕ_{storm} p_t) with a weight of 0.99961 as compared to 0.00036 for the time-dependent model (ϕ_t p_t), the best preplanned model (Table 2). The storm covariate model was also supported by a highly significant ANODEV (Table 3).

The annual apparent survival estimates under the storm model are presented in Table 4. The magnitude of the storm effect varied among the different storm years, with the largest drop in apparent survival occurring in 1995 when Hurricane Opal and three lesser storms impacted the region. The estimated mean annual sighting probability under the storm covariate model was 0.713 (95% CI = 0.689–0.735).

DISCUSSION

Our analysis identified three years in which survival probabilities dropped below the essentially constant probabilities normally experienced by adults during the 19-yr study. Because human impact is generally low in the region and no increases in deaths from boats were documented, the sudden decreases most likely were due to natural or unusual causes. No red-tide blooms or extended cold spells occurred during years with low survival, and we knew of no events that affected habitat quality resulting in the movement of individuals out of the region. Rather, the highly significant ANODEV for the storm covariate model showed a strong association of lower survival with intense storms. It is extremely improbable that this association occurred by chance alone over the 19-yr period and strongly supports a cause–effect relationship. Further research is needed, but as major storms will continue to strike northwest Florida, we should be able to predict and test for storm-related changes in survival in a more definitive study. This is the first empirical evidence for storm effects on manatee survival. Even though there were no catastrophic die-offs, we were successful in detecting smaller magnitude effects from relatively rare storms by monitoring known individuals over a long period of time with state-of-the-art analytical techniques. Because individuals of this small population range extensively along the north Gulf coast, it was possible to resolve storm effects on a larger regional scale than the site-specific local scale common to studies of more sedentary species.

The mechanisms responsible for the lower survival probabilities are unknown. Somehow, storms prevented the return of marked individuals to the winter sites either as a consequence of death or voluntary or forced emigration from the study area. At least four processes in a storm as described by Simpson and Riehl (1981) could be responsible: (1) storm surges, which push sea

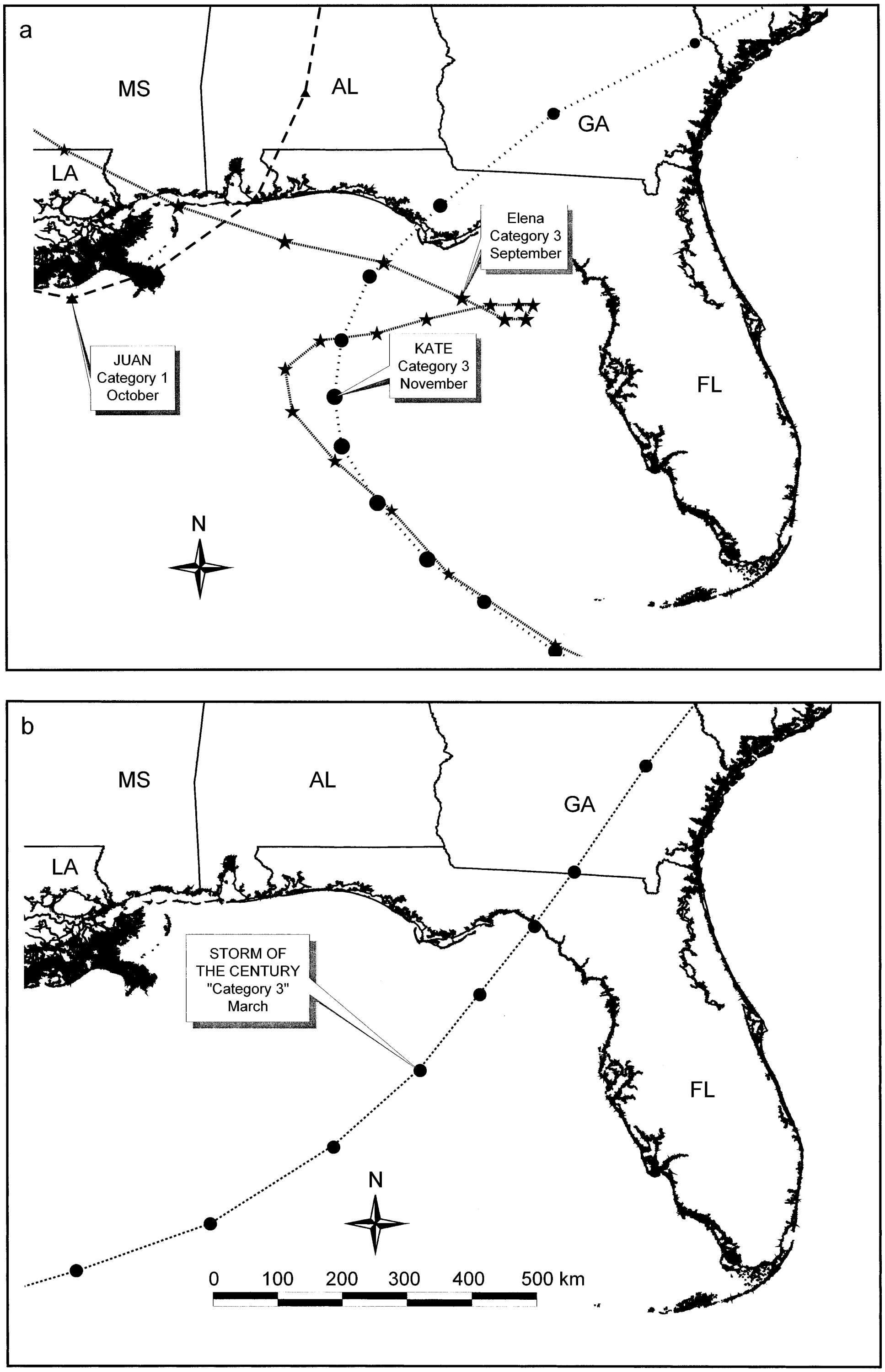

FIG. 5. Tracks of the major storms affecting the study area in (a) 1985 and (b) 1993. Abbreviations are: FL, Florida; GA, Georgia; AL, Alabama; MS, Mississippi; LA, Louisiana; Cat., category.

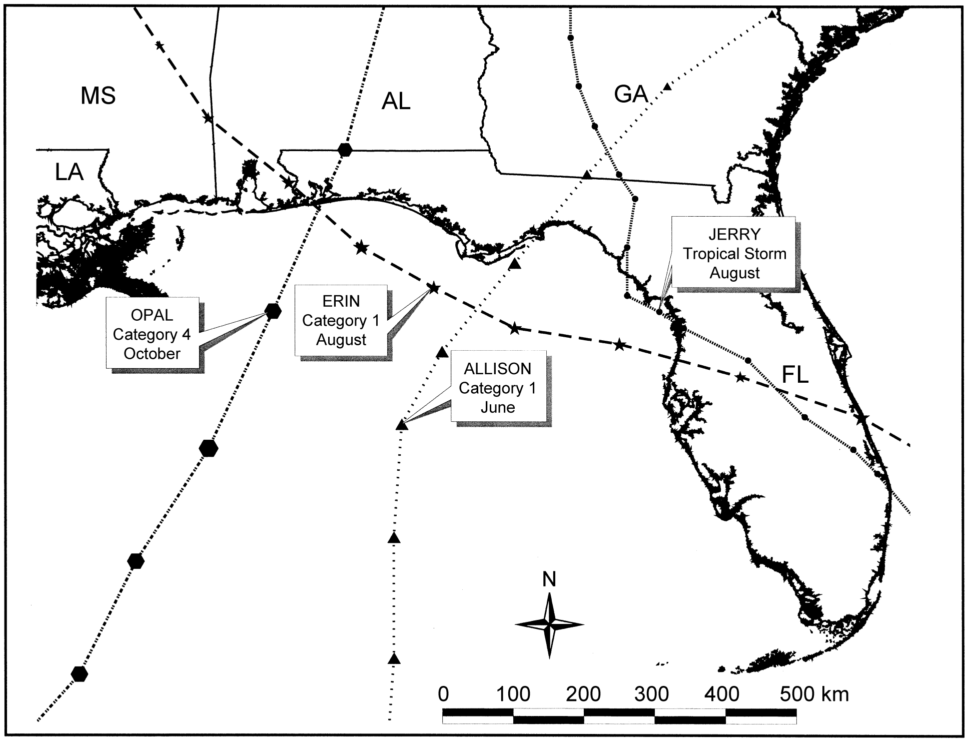

FIG. 6. Tracks of the major storms affecting the study area in 1995. See Fig. 5 for abbreviations.

water and objects in its path high onto shores and into estuaries and rivers; (2) high-energy waves generated by high winds, which increase the storm tide and produce large swells and breaking waves; (3) strong longshore currents running parallel to the shore; and (4) cooled surface waters, which follow in the wake of a hurricane and can persist for days.

Manatees could be killed outright by any of these processes. Stranding in a storm surge may be most likely, and although drowning seems a remote possibility for a marine mammal, blunt injury from debris in turbulent water could result in death. Indirect death is also possible. Animals could become disoriented and either swim or get swept out to sea. Unless they find their way back they would die from lack of food and/or freshwater. The orientation and navigational skills of manatees are untested, and unfamiliar waves, currents, and debris could obscure navigation cues; exhaustion and debilitating cold water could dull the senses and the integration of information. Death from cold stress in the colder waters following hurricanes could be possible if late in the fall, as ambient temperatures remained cold.

Mortality, however, may not be the only process operating. Individuals may be alive, but gone from the study area. They could voluntarily leave if the food base is degraded or destroyed, as has been documented with dugongs and seagrasses in Australia (Heinsohn and Spain 1974, Preen and Marsh 1995), or they could be forced from the area if caught in longshore currents pushing them south or west. Mark–resighting statistical models cannot discern true mortality from permanent emigration, although additional monitoring can document the eventual return of displaced individuals.

Little information and data are available to evaluate these mechanisms, primarily because of contingency, remoteness, and post-storm priorities on human impact. Only two live-stranded manatees in heavily populated areas were found and rescued after past storms: one in 1993 in Hernando County after the March Storm of the Century and the other in 1992 near Miami after Hurricane Andrew (C. A. Beck, *personal observation*). The Manatee Carcass Recovery Program has not reported

TABLE 2. Comparison of fit for the storm covariate model and the preplanned survival models.

Model	AIC_c	ΔAIC_c	AIC_c weight	N0. parameters	Deviance
$\boldsymbol{\phi_{storm} p_t}$	**3823.027**	**0.00**	**0.99961**	**21**	**2361.302**
$\phi_t p_t$	3838.882	15.86	0.00036	33	2352.469
$\phi_{constant} p_t$	3844.174	21.15	0.00003	18	2388.574
$\phi_{s*t} p_t$	3862.169	39.14	0.00000	50	2340.249
$\phi_{s*t} p_{s*t}$	3884.068	61.04	0.00000	66	2328.146

Notes: Model notations indicate variation in survival (ϕ) and capture (p) probabilities by time (t), sex (s), or negligible over time (constant). Models are ranked according to lowest AIC_c (Akaike Information Criterion). The best model is in bold. Deviance is a relative measure of fit. ΔAIC_c is the difference in AIC_c values between the given model and the model with the lowest AIC_c.

TABLE 3. Results of the Analysis of Deviance (ANODEV) testing the impact of the storm covariate in explaining the variation.

Source	df	Deviance	Mean deviance	F	P
Uncorrected total	33	2388.574			
Grand mean	18	2352.469			
Corrected total	15	36.105			
Total covariate	3	27.272	9.091	12.3501	0.0006
Error	12	8.833	0.736		

an increase in the number of carcasses in the northwest in years with large storms. Nonetheless, extensive salt marshes dominate the coast, making it difficult to find a stranded manatee on the coast or at sea without specially designed aerial surveys. Survival probability only dropped from 0.97 to 0.94 in 1985 and to 0.91 in 1993. The drop in survival in 1995, the year of Hurricane Opal, was larger (from 0.97 to 0.82), but given the small size of the population, this would mean the death of a relatively small number of individuals spread over a large area. Available evidence for emigration is lacking as well. Photo-identification studies in southwest Florida have reached a sustained effort only recently and none are ongoing west of Florida, where manatees are only rarely seen.

One, several, or all of the above mechanisms could contribute to the observed decreases in survival. The magnitude of impact to the population will vary with the destructiveness of the storm, which depends on storm intensity, size, speed of forward motion, proximity to the coast, track direction relative to the coast, and coastal and ocean bottom topography (Simpson and Riehl 1981). Other factors can then exacerbate or ameliorate risk, such as density of manatees in the strike area, the number of storms within a season, or coincidence with other mortality factors. As a tropical species, one would expect that manatees would have evolved behaviors to cope with violent tropical storms, but Florida manatees, endangered and living at the northern limit of their natural range, are subject to multiple sublethal stresses (e.g., injury and maiming from boat collisions [O'Shea et al. 2001], cold weather [Buergelt et al. 1984], variable winter refuges [Packard et al. 1989], degraded feeding areas [Sargent et al. 1995]). These can have chronic and debilitating effects, making individuals more vulnerable to storm death.

The implications for the conservation and sustainability of the species are not trivial. If a major storm struck in the fall or spring where manatees are amassed near the winter aggregation sites, a significant segment of the population could be killed. The ability of the population to quickly recover would be impeded by its small population size, long generation time, and low reproductive rate. Catastrophic events can lead to population decline, greatly increasing the chance of extinction (Mangel and Tier 1994). Periodic smaller drops in adult survival, such as those detected in this study, lower the rate of population growth and slow recovery (Eberhardt and O'Shea 1995, Marmontel et al. 1997). Furthermore, we have no reason to believe that subadults and calves fared any better than adults during the storms. Long-term studies of large terrestrial mammals are providing evidence that immatures are most adversely affected by harsh climatic conditions and that changes in their numbers make the largest contribution to changes in population growth rate (Gaillard et al. 2000, Coulson et al. 2001).

The potential destruction of feeding grounds by hurricanes also has bearing on sustainability of the species. Past storms in the southeastern U.S. have damaged both seagrasses and freshwater aquatic plants through wave action, sediment deposition, and changes in water salinity (Eleuterius and Miller 1976, Mataraza et al. 1999). To date, there are no documented effects to manatees from previous small-scale disturbances, but the likelihood of large-scale habitat destruction and its consequences are clear from research in Australia on dugongs. Important seagrass communities can be severely

TABLE 4. Estimates of annual survival probabilities under the storm covariate model (ϕ_{storm} p_t).

Years	Major storms (Category 3 and 4)	Lesser storms	Estimate of survival	95% CI
1982–1984	(none)	0	0.972	0.961–0.980
1985	Hurricanes Elena and Kate	1	0.936	0.864–0.971
1986–1992	(none)	6	0.972	0.961–0.980
1993	''Storm of the Century''	0	0.909	0.837–0.951
1994	(none)	2	0.972	0.961–0.980
1995	Hurricane Opal	3	0.817	0.735–0.878
1996–1998	(none)	4	0.972	0.961–0.980

damaged by tropical storms (Preen et al. 1995, Poiner and Peterken 1996), and although freshwater plants may recover quickly (Mataraza et al. 1999), seagrasses may take up to a decade or more to recover (Poiner and Peterken 1996). Given the die-off of dugongs from starvation after cyclone destruction (Preen and Marsh 1995), the same outcome to manatees under a similar scenario is entirely plausible. Decreased reproduction would also be likely given that emaciation would impair the ability of reproductive females to bear healthy calves.

Natural disasters cannot be deflected or managed to the benefit of manatees, but human-related risks can be managed. To insure the long-term viability of the population in the face of episodic die-offs from hurricanes, it becomes all the more important to control and reduce the level of mortality and injury from boats and other human causes, and the loss of foraging habitat to coastal development. Conservative management in favor of greater protection to manatees is warranted until we have a clearer understanding of storm effects, future threats, and the resiliency of the population. Studies designed to monitor death, emigration, and reproduction after storms, to document manatee behavior in response to storm forces, and to model various storm attributes and storm frequency with impact to the population and habitat will be crucial. The Florida Manatee Recovery Plan (U.S. Fish and Wildlife Service 2001) has implemented recovery tasks to reduce human-related mortality and debilitating injury and to protect manatee habitat. Nonetheless, more stringent regulations may be required to offset losses from natural causes. Reclassification and delisting criteria also should be reconsidered. Benchmarks of recovery based on data and analyses from 20 yr of research in a mild hurricane cycle may not be adequate to meet challenges posed with the new active cycle and long-term global climate change.

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Literature Cited

Ackerman, B. B. 1995. Aerial surveys of manatees: a summary and progress report. Pages 13–33 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report **1**.

Ackerman, B. B., S. D. Wright, R. K. Bonde, D. K. Odell, and D. J. Banowetz. 1995. Trends and patterns in mortality of manatees in Florida, 1974–1992. Pages 223–256 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report **1**.

Anderson, D. R., K. P. Burnham, and G. C. White. 1998. Comparison of AIC and CAIC for model selection and statistical inference from capture-recapture studies. Journal of Applied Statistics **25**:263–282.

Arnason, A. N., and K. H. Mills. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark–recapture experiments. Canadian Journal of Fisheries and Aquatic Sciences **38**:1077–1095.

Beck, C. A., and J. P. Reid. 1995. An automated photo-identification catalog for studies of the life history of the Florida manatee. Pages 120–134 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report **1**.

Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs **64**:369–400.

Bossart, G. D., D. G. Baden, R. Y. Ewing, B. Roberts, and S. D. Wright. 1998. Brevetoxicosis in manatees (*Trichechus manatus latirostris*) from the 1996 epizootic: gross, histologic, and immunohistochemical features. Toxicologic Pathology **26**:276–282.

Buergelt, C. D., R. K. Bonde, C. A. Beck, and T. J. O'Shea. 1984. Pathologic findings in manatees in Florida. Journal of the American Veterinary Medical Association **185**:1331–1334.

Burnham, K. P., and D. R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph **5**:1–437.

Case, R. A. 1986. Annual summary. Atlantic hurricane season of 1985. Monthly Weather Review **114**:1390–1405.

Cooper-Ellis, S., D. R. Foster, G. Carlton, and A. Lezberg. 1999. Forest response to catastrophic wind: results from an experimental hurricane. Ecology **80**:2683–2696.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. T. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science **292**:1528–1531.

Eberhardt, L. L., and T. J. O'Shea. 1995. Integration of manatee life-history data and population modeling. Pages 269–279 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report **1**.

Eleuterius, L. N., and G. J. Miller. 1976. Observations on seagrasses and seaweeds in Mississippi sound since Hurricane Camille. Journal of the Mississippi Academy of Science **31**:58–63.

Foster, D. R., J. D. Aber, J. M. Melillo, R. D. Bowden, and F. A. Bazzaz. 1997. Temperate forest response to natural catastrophic disturbance and chronic anthropogenic stress. BioScience **47**:437–445.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31**:367–93.

Gray, W. M. 1990. Strong association between West African rainfall and U.S. landfall Atlantic seasonal hurricane frequency: Part II. Forecasting its variability. Monthly Weather Review **112**:1669–1683.

Gray, W. M., C. W. Landsea, E. Blake, P. W. Mielke, Jr., and K. J. Berry. 2001. Summary of 2001 Atlantic tropical cyclone activity and verification of authors' seasonal activity forecast. The Tropical Meteorological Project. Colorado State University. [Online, URL: ⟨http://typhoon.atmos.colostate.edu/forecasts/2001/nov2001/⟩, accessed on 11 March 2002.]

Hartman, D. S. 1979. Ecology and behavior of the manatee (*Trichechus manatus*) in Florida. American Society of Mammalogists Special Publication **5**:1–153.

Heinsohn, G. E., and A. V. Spain. 1974. Effects of a tropical cyclone on littoral and sub-littoral biotic communities and on a population of dugongs (*Dugong dugon* (Müller)). Biological Conservation **6**:143–152.

Irvine, A. B. 1983. Manatee metabolism and its influence on distribution in Florida. Biological Conservation **25**:315–334.

Jones, S. 1967. The dugong, *Dugong dugon* (Müller), its present status in the seas around India with observations on its behaviour in captivity. International Zoo Yearbook **7**:215–220.

Landsea, C. W. 1993. A climatology of intense (or major) Atlantic hurricanes. Monthly Weather Review **121**:1703–1713.

Landsea, C. W., N. Nicholls, and L. A. Avila. 1996. Downward trends in the frequency of intense Atlantic hurricanes during the past five decades. Geophysical Research Letters **23**:1697–1700.

Langtimm, C. A., T. J. O'Shea, R. Pradel, and C. A. Beck. 1998. Estimates of annual survival probabilities for adult Florida manatees (*Trichechus manatus latirostris*). Ecology **79**:981–997.

Lawrence, M. B., B. M. Mayfield, L. A. Avila, R. J. Pasch, and E. N. Rappaport. 1998. Atlantic hurricane season of 1995. Monthly Weather Review **126**:1124–1151.

Lebreton, J.-D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs **62**:67–118.

Lott, N. 1993. The big one! A review of the March 12–14 1993 ''Storm of the Century. '' NOAA National Climatic Data Center Publication TR 93–01. Washington, D.C., USA.

Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. Ecology **75**:607–614.

Marmontel, M., S. R. Humphrey, and T. J. O'Shea. 1997. Population viability analysis of the Florida manatee (*Trichechus manatus latirostris*), 1976–1991. Conservation Biology **11**:467–481.

Marsh, H. 1989. Mass stranding of dugongs by a tropical cyclone in northern Australia. Marine Mammal Science **12**:54–88.

Mataraza, L. K., J. B. Terrell, A. B. Munson, and D. E. Canfield, Jr. 1999. Changes in submersed macrophytes in relation to tidal storm surges. Journal of Aquatic Plant Management **37**:3–12.

McCarthy, J. J., O. F. Canziani, N. A. Leary, D. J. Dokken and K. S. White, editors. 2001. Climate change 2001: impacts, adaptation and vulnerabilty. Contributions of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK.

Michener, W. K., E. R. Blood, K. L. Bildstein, M. M. Brinson, and L. R. Gardner. 1997. Climate change, hurricanes, and tropical storms, and rising sea level in coastal wetlands. Ecological Applications **7**:770–801.

Nichols, J. D. 1992. Capture–recapture models: using marked animals to study population dynamics. BioScience **42**:94–102.

O'Shea, T. J., B. B. Ackerman, and H. F. Percival, editors. 1995. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report **1**.

O'Shea, T. J., C. A. Beck, R. K. Bonde, H. I. Kochman, and D. K. Odell. 1985. An analysis of manatee mortality patterns in Florida, 1976–1981. Journal of Wildlife Management **49**:1–11.

O'Shea, T. J., and C. A. Langtimm. 1995. Estimation of survival of adult Florida manatees in the Crystal River, at Blue Spring, and on the Atlantic coast. Pages 194–222 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report **1**.

O'Shea, T. J., L. W. Lefebvre, and C. A. Beck. 2001. Florida manatees: perspectives on populations, pain, and protection. Pages 31–43 *in* L. A. Dierauf and F. M. D. Gulland, editors. CRC handbook of marine mammal medicine. Second edition. CRC Press, Boca Raton, Florida, USA.

O'Shea, T. J., G. B. Rathbun, R. K. Bonde, C. D. Buergelt, and D. K. Odell. 1991. An epizootic of Florida manatees associated with a dinoflagellate bloom. Marine Mammal Science **7**:165–179.

Packard, J. M., R. K. Frohlich, J. E. Reynolds, and J. R. Wilcox. 1989. Manatee response to interruption of a thermal effluent. Journal of Wildlife Management **53**:692–700.

Poiner, I. R., and C. Peterken. 1996. Seagrasses. Pages 40–45 *in* L. P. Zann and P. Kailola, editors. The state of the marine environment report for Australia. Technical Annex: 1. Great Barrier Reef Marine Park Authority, Townsville, Australia.

Pollock, K. H., J. D. Nichols, C. Brownie, and J. E. Hines. 1990. Statistical inference for capture–recapture experiments. Wildlife Monographs **107**:1–97.

Powell, J. A., and G. B. Rathbun. 1984. Distribution and abundance of manatees along the northern coast of the Gulf of Mexico. Northeast Gulf Science **7**:1–28.

Preen, A. R., W. J. Lee Long, and R. G. Coles. 1995. Flood and cyclone related loss, and partial recovery, of more than 1000 km^2 of seagrass in Hervey Bay, Queensland, Australia. Aquatic Botany **52**:3–17.

Preen, A. R., and H. Marsh. 1995. Response of dugongs to large-scale loss of seagrass from Hervey Bay, Queensland, Australia. Wildlife Research **22**:507–519.

Rathbun, G. B., J. P. Reid, R. K. Bonde, and J. A. Powell. 1995. Reproduction in free-ranging Florida manatees. Pages 135–156 *in* T. J. O'Shea, B. B. Ackerman, and H. F. Percival, editors. Population biology of the Florida manatee. U.S. Department of the Interior, National Biological Service, Information and Technology Report **1**.

Rathbun, G. B., J. P. Reid, and G. Carowan. 1990. Distribution and movement patterns of manatees (*Trichechus manatus*) in northwestern peninsular Florida. Florida Marine Research Publications **48**:1–33.

Reid, J. P., G. B. Rathbun, and J. R. Wilcox. 1991. Distribution patterns of individually identifiable West Indian manatees (*Trichechus manatus*) in Florida. Marine Mammal Science **7**:180–190.

Sargent, F. J., T. J. Leary, D. W. Crewz, and C. R. Kruer. 1995. Scarring of Florida's seagrasses: assessment and management options. Florida Marine Research Institute Technical Reports TR-1:1–43.

Simpson, R. H., and H. Riehl. 1981. The hurricane and its impact. Louisiana State University Press, Baton Rouge, Louisiana, USA.

Skalski, J. R., A. Hoffmann, and S. G. Smith. 1993. Testing the significance of individual- and cohort-level covariates in animal survival studies. Pages 9–28 *in* J.-D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhauser Verlag, Basel, Switzerland.

Spiller, D. A., J. B. Losos, and T. W. Schoener. 1998. Impact of a catastrophic hurricane on island populations. Science **281**:695–697.

Tanner, E. V. J., V. Kapos, and J. R. Healey. 1991. Hurricane effects on forest ecosystems in the Caribbean. Biotropica **23**:513–521.

U.S. Fish and Wildlife Service. 2001. Florida manatee recovery plan. Third revision, U.S. Fish and Wildlife Service, Atlanta, Georgia, USA.

Waide, R. B. 1991. Summary of the response of animal populations to hurricanes in the Caribbean. Biotropica **23**:508–512.

White, G. C., and K. P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study **46** Supplement:120–138.

Williams, J. M., and I. W. Duedall. 1997. Florida hurricanes and tropical storms. University Press of Florida, Gainesville, Florida, USA.