Population status of the American alligator (*Alligator mississippiensis*) in Everglades National Park

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ABSTRACT

Studies of population dynamics and monitoring techniques for the American alligator (Alligator mississippiensis) in the Everglades were conducted from 1975 to 1983. Alligator population levels in a 10-km^2 area of Shark Slough remained stable over a four-year period (1977-1980). Stability in population size during this period, however, cannot be extrapolated to evaluate changes in historic patterns or to project future trends. The mortality due to the increased flooding of alligator nests under recent water delivery schedules is compounded by other pressures on population growth. While size-related survivorship rates were comparable to other alligator populations, age-related mortality rates were higher in the Everglades because of low growth rates that hold Everglades alligators at smaller sizes for longer periods. Comprehensive mark-recapture studies that allow sufficient precision in estimates of population size are extremely manpower-intensive and costly, and the data obtained on population size are not enough to allow an assessment of population status. Pond and nest surveys were inadequate techniques for monitoring population levels because environmental and other little understood factors complicated the interpretation of survey results. Line surveys of a deep-water canal bordering the park (L-67) provided the most predictable index to adult population levels although this route is unrepresentative of typical Everglades habitat. Monitoring of reproductive success and survivorship of younger age classes, studies of compensatory mechanisms, and construction of a demographic model of the population are recommended for future studies.

INTRODUCTION

Conflicts with civilization have countered the evolutionary design which once fostered the survival of the crocodilians. A history of overharvesting, encroaching development, and deteriorating habitat quality have reduced many populations to extinction worldwide. Declining population levels of the American alligator (*Alligator mississippiensis*), however, were largely reversed with legal protection in the 1960's. Of current interest is whether the number of alligators is continuing to climb and whether management is necessary in some areas to reduce conflicts with humans. In most areas, however, there is little understanding of how alligator population levels are varying, and of how to best manage for the alligator's future.

Concern for the alligator's preservation, coupled with a limited knowledge of its local ecology, has prompted an evaluation of the status of the alligator population in Everglades National Park. The ecology of alligator populations in various habitats has been documented in other studies (Chabreck 1966, 1971, 1976; Joanen and McNease 1972; Joanen 1974; Fuller 1981; Murphy 1981; Murphy and Fuller 1982). Important differences in climate, habitat, and hydrology, however, suggest that such information is not necessarily applicable to alligators in the Everglades. As a valuable natural resource, the alligator co-exists with wetland habitats that comprise nearly 98 percent of the area of Everglades National Park. The alligator serves as a prime tourist attraction and as an important ecological factor maintaining the balance of nature in the Everglades ecosystem. Understanding the status of the alligator in Everglades National Park is of importance for both the species and the ecosystem that supports it.

In this report we summarize current knowledge of the status of the alligator in the Everglades marsh of Everglades National Park. These results are part of an extensive study aimed at determining the role of water conditions in Shark Slough in maintaining alligator populations. We compare population parameters for Everglades alligators with those reported for alligators in Louisiana, where recovery from previously uncontrolled hunting pressures has been well-documented. We consider how the condition of the Everglades alligator population can be determined in the future. Prior to this study, there were no readily applicable methods for censusing alligators in the Everglades, and a large part of our study has involved the development and testing of monitoring techniques. We present the results of these studies and discuss our recommendations for the institution of a long-term monitoring program for the alligator population.

THE NEED FOR STATUS REVIEW

Despite the widespread loss of wetland habitats, on a regional scale many alligator populations now thrive in protected refuges. In many areas, protection from hunting and preservation of habitat have been sufficient to promote the recovery of the alligator. In Everglades National Park, however, there is an interest beyond the legal aspects of dealing with a threatened species. Single-species management, in fact, is not always in the best interests of natural area preservation. Preserving the Everglades ecosystem suggests a much larger task, that of preserving the role of the alligator in maintaining the ecological relationships it fosters. An ecosystem-level approach has provided the basis for our research and subsequent recommendations with regard to the status of the alligator.

In the Everglades, the trophic impact of the alligator is pervasive, with the wide range of size classes constituting its population consuming different sizes and types of prey. The alligator significantly impacts Everglades habitat. Plant communities are altered by alligator trails and by nest mounds (Craighead 1968). Nest sites afford high ground for other animals, some of which may also use them for nesting (Kushlan and Kushlan 1980). Of the alligator's many influences, its pond maintenance activities may be the most critical to preserving natural ecological function in the southern Everglades (Kushlan 1974, Kushlan and Browder 1976). Ponds provide refugia for aquatic organisms and a food source for the avian predators, whose breeding season occurs at the time of the usual spring dry season. The pervasive dependency of the Everglades ecosystem on the activities of the alligator suggests the importance of its continued persistence. Toward this goal we seek an understanding of the alligator's population dynamics and explore appropriate techniques for the study and monitoring of its status.

METHODS

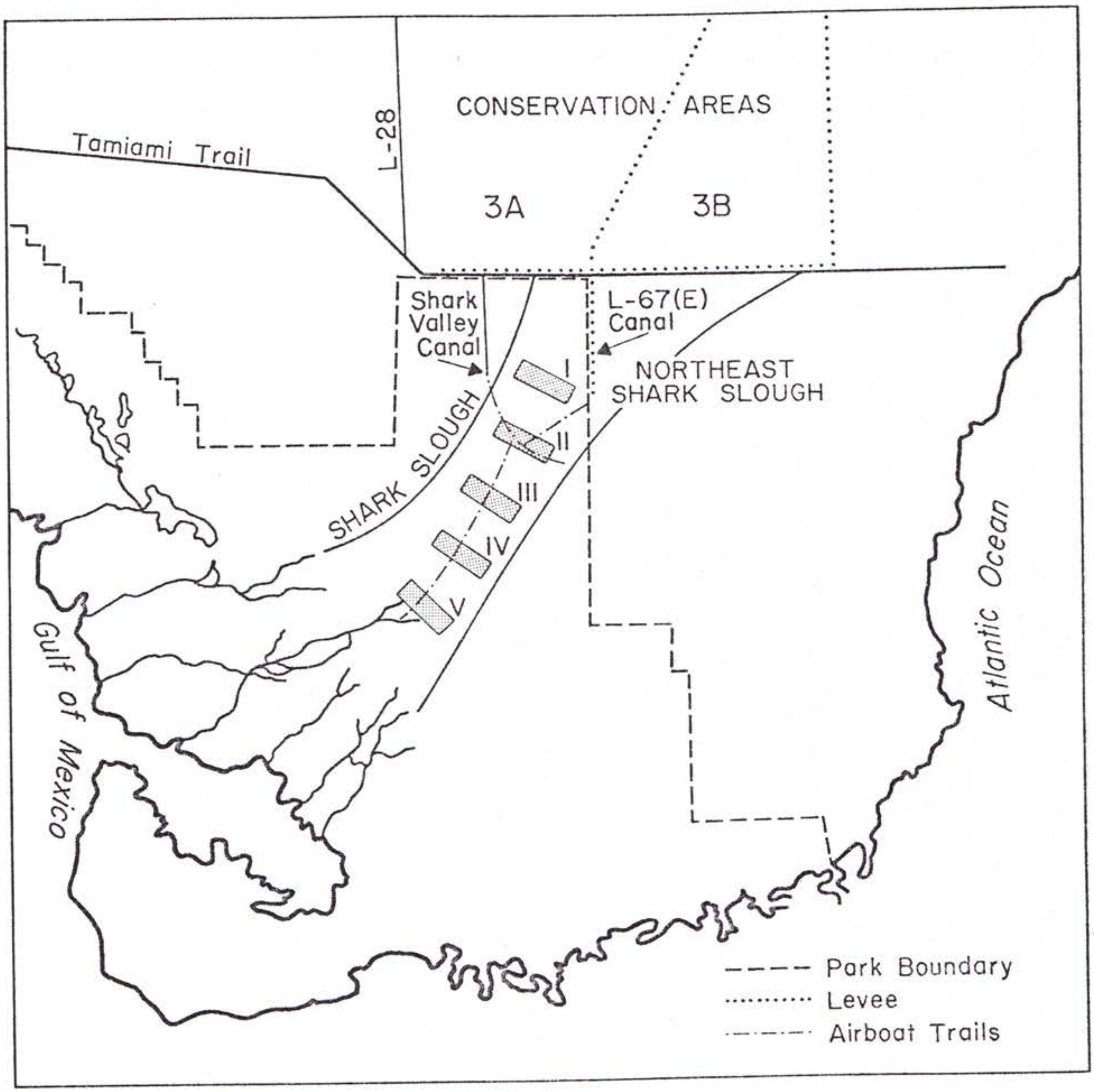
Studies of the status of the alligator population were carried out within the freshwater marshes of Shark Slough in the southern Everglades marsh of Everglades National Park from 1975 to 1983. Information was also gathered from a deep water canal (L-67) along the eastern boundary of the park, from a borrow canal along the Shark Valley

Loop Road which extends for seven miles into the park from its northern boundary, and from a network of three major airboat trails running across and along Shark Slough (Fig. 1).

Studies of the alligator were designed with the following considerations. When evaluating the status of a large or extensively distributed population it is an economic and logistic impossibility to make observations or measurements of the entire population. Thus only a representative portion of the population can be studied. The selection of a sample unit may be done in a number of ways, depending on statistical, fiscal, or logistic constraints. Measurements taken on this sample may be used to estimate characteristics of the entire population. If this sample is examined over time, the trend observed can be used to estimate the trend of the entire population. Spatial or geographic variability can be evaluated through sampling designs which allow sampling along gradients.

This study follows a systematic sampling design consistent with the above criteria. Five large (10-km^2) study areas (I - V) are equally spaced along the topographic gradient of Shark Slough, each aligned with its long axis perpendicular to surface flow through the main drainage area. Line transects used as survey routes pass through each study area, following a north-south gradient (Fig. 1). Each study area includes primarily marsh habitat except area V, which was located at the interface between marsh and coastal mangrove swamps. One study area, area II, was chosen for high intensity repeated sampling to allow evaluation of temporal variability. The primary study area is located midway along the topographic and hydrologic gradient, and includes all representative marsh habitats. Intensive sampling here permitted higher

Figure 1. Map of boundaries of Everglades National Park showing locations of five 10-km^2 study areas in the major drainage area, Shark Slough. Area II is the primary study area. Also shown are survey locations, including three major airboat trails, Shark Valley Canal, and the L-67 (E) canal.



CONSERVATION AREAS
3A
3B
L-28
Tamiami Trail
Shark Valley Canal
L-67(E) Canal
NORTHEAST SHARK SLOUGH
SHARK SLOUGH
I
II
III
IV
V
Gulf of Mexico
Atlantic Ocean
Park Boundary
Levee
Airboat Trails

precision for estimates of population size and trend than would otherwise be possible. This extra precision within a single, representative area is the trade-off for low precision over more areas.

A mark-recapture program was conducted from 1975 to 1983 in the primary study area. Alligators were measured (snout-vent and total lengths in centimeters) and released at the site of capture. Captures were made from an airboat by hand or using a pole snare, and were trapped in ponds using baited snares (Murphy and Fendley 1973). Sex was determined by cloacal probing (Joanen and McNease 1978). Uniquely-numbered Monel tags were used to identify individuals. During each sampling period, three or four nights were required to search the entire 10-km^2 study area.

Analysis of mark-recapture data for estimates of population size, survivorship, and the respective standard errors were based on estimation formulae first developed by Jolly (1965) and Seber (1965). The standard analyses were provided by a computer software package, POPAN-2, for POPulation ANalysis (Arnason and Baniuk 1978). The program allows analysis of open populations, where births (immigations) and deaths (emigrations) are free to occur ("full model").

Several techniques were explored to allow the future monitoring of alligator population levels. First, we used line survey techniques because they were the most convenient and economical monitoring methods available and have been commonly-used elsewhere for monitoring trends in alligator populations (Chabreck 1976). Censuses along linear transects were conducted along five routes, three in Shark Slough and two along canals. Line surveys were conducted monthly from February, 1977, to September, 1980. The number and sizes of alligators were recorded at night from a slowly moving vehicle (by car for canal surveys and by airboat for marsh surveys). The number of alligators observed was tallied per mile of each survey route, and the total length of each alligator was estimated to the nearest 0.25 meters.

Second, we used censuses of the number of nests constructed each year because in previous studies (Chabreck 1966) these have provided an index of population size. Helicopters and fixed-wing aircraft were used to count nests in the primary study area form 1975 to 1982. Ground searches were made of all places not visible from the air. At each nest we counted the eggs and monitored nesting success. Dimensions of 71 nests were taken for analysis of egg mortality due to flooding.

Third, we conducted aerial censuses of alligators in ponds in the dry season as a potential index of adult alligators. Helicopter surveys were conducted during the dry seasons (winter - spring) of 1976, 1977, 1978, and 1979. All ponds in all five marsh study areas were censused each year and the size of each alligator observed was recorded.

RESULTS AND DISCUSSION

Demographic Studies

Analytic Assumptions. Population size estimates are contingent on the assumptions underlying the Jolly-Seber model, which are:

1. Equal survivorship
2. Equal catchability

3. No tag loss

Assumptions of equal survivorship and equal catchability are addressed by pooling the data by size class. Population parameters are thus based on size rather than age, although size and age can be interconverted using the relation presented in this report. Four size classes are used:

Size Class	Snout-Vent Length (cm)
1	< 30.0
2	30.0 - 60.0
3	60.0 - 80.0
4	> 80.0

These size classes include the smallest and most easily caught segment of the population in class 1, "juveniles" in class 2, "subadults" in class 3, and "adults" in class 4. Pooling assumes that population size and standardized population parameters (ie. survival rate per unit time) are roughly constant within a pooling interval, but changing across intervals (Arnason and Baniuk 1978).

The efficacy of the mark-recapture technique varies among size classes. Adult alligators, for example, were not as likely to be caught as the smallest alligators, because adults spend most of their time in inaccessible, deep-water ponds. Subadult-sized alligators were especially wary and difficult to capture regularly. Thus, our estimates of adult and subadult population levels and survival rates are less accurate than our estimates for smaller size classes.

Annual pooling of capture data standardizes the estimates to give annual rates and increases the precision of the estimates. A total of 346 nights of sampling were conducted, comprising approximately 4 sampling periods in 1975, 6 in 1976, 9 in 1977, 12 in 1978, 11 in 1979, 9 in 1980, 7 in 1981, 1 in 1982, and 1 in 1983. Annual efforts in 1982 and 1983 provided an experiment in the effectiveness of a reduced sampling effort in deriving estimates of population parameters.

Not all years during the mark-recapture study provided an equally accurate assessment of population size. In an extensive area, it requires considerable effort to build up the number of marked alligators in the population. This is important because the ratio of marked to unmarked alligators provides the basis of the estimator of population size. (This has implications for the necessity of maintaining a tagging study over time in order to avoid the costs of reactivation of the project.) In the first two years of the study, 1975 and 1976, the proportion of marked animals in the population was low. As this proportion increased throughout the study, the ratio of marked to unmarked animals became a more accurate reflection of true population size. During the last three years of the study, from 1981 to 1983, the infrequency of recaptures under the reduced sampling effort again reflected an inaccurate ratio of marked to unmarked alligators. Thus, the data derived during the middle years of the study, from 1977 to 1980, provide the more accurate and the most precise estimates of population size.

The Jolly-Seber estimates require that there be no tag loss and that marked animals are correctly identified on recapture (Arnason and Mills 1981). Tag loss does not bias the estimators of population size or its associated standard error (Arnason and Mills 1981), although it can cause over- or under-estimations in some instances (Begon 1979). Importantly, tag loss can be a source of bias for estimates of survivorship and its standard error. When tag loss occurs, the survival estimate is an estimate of the proportion of animals that survive from time I to time I+1 and do not lose their tag in that interval. It is thus an under-estimate of true survival rate (Arnason and Baniuk 1978). Uncorrected estimates can be used if the magnitude of the bias (due to tag loss) in the estimate of survival is less than one-half of the standard error (Arnason and Mills 1981). Thus:

$$(1 - \hat{\theta})\ \hat{\phi} \quad \text{should be less than} \quad S\ (\hat{\phi})/2$$

where $\hat{\phi}$ is the survivorship estimate, $S\ (\hat{\phi})$ its standard error, for all values of $\hat{\theta}$ (tag retention rate).

In our study, tag loss bias does not significantly affect the survival estimates according to this formula. We calculated that the tag retention rates (i.e. 1 - tag loss rate) should be above the following minimum values:

Size Class	Minimum Tag Retention Rate
1	.6955
2	.9020
3	.7310
4	.7650

This means, for example, that a minimum of 69.55 percent of the tags would need to be retained in size class 1 in order to prevent significant bias in the survival estimates. These restrictions are easily met in our study. There were 96 recaptures (over all size classes) for which we were unable to identify the capture histories. This comprises just 4.03 percent of the 2,384 unique tags applied during the study. Thus, tag loss is not a significant factor in this study and will not bias estimates of either survival or population size.

Population Parameters. The size of the alligator population in the primary study area (10-km^2) ranged from 639.2 to 665.7 from 1977 to 1980 (Table 1). Standard errors on population size estimates are low, and population levels were stable with a mean density of 64.76 alligators per square kilometer. Alligators in size class 1 were the most numerous, comprising from 44 to 87 percent of the total population (Fig. 2).

We can express a degree of stability, or extent of fluctuation, based on our measures of population density over four years. The degree of spread of these measurements away from the mean expresses the intensity of fluctuation. Using the logarithms of population size, we can characterize the size of the alligator population in the study area by its geometric mean:

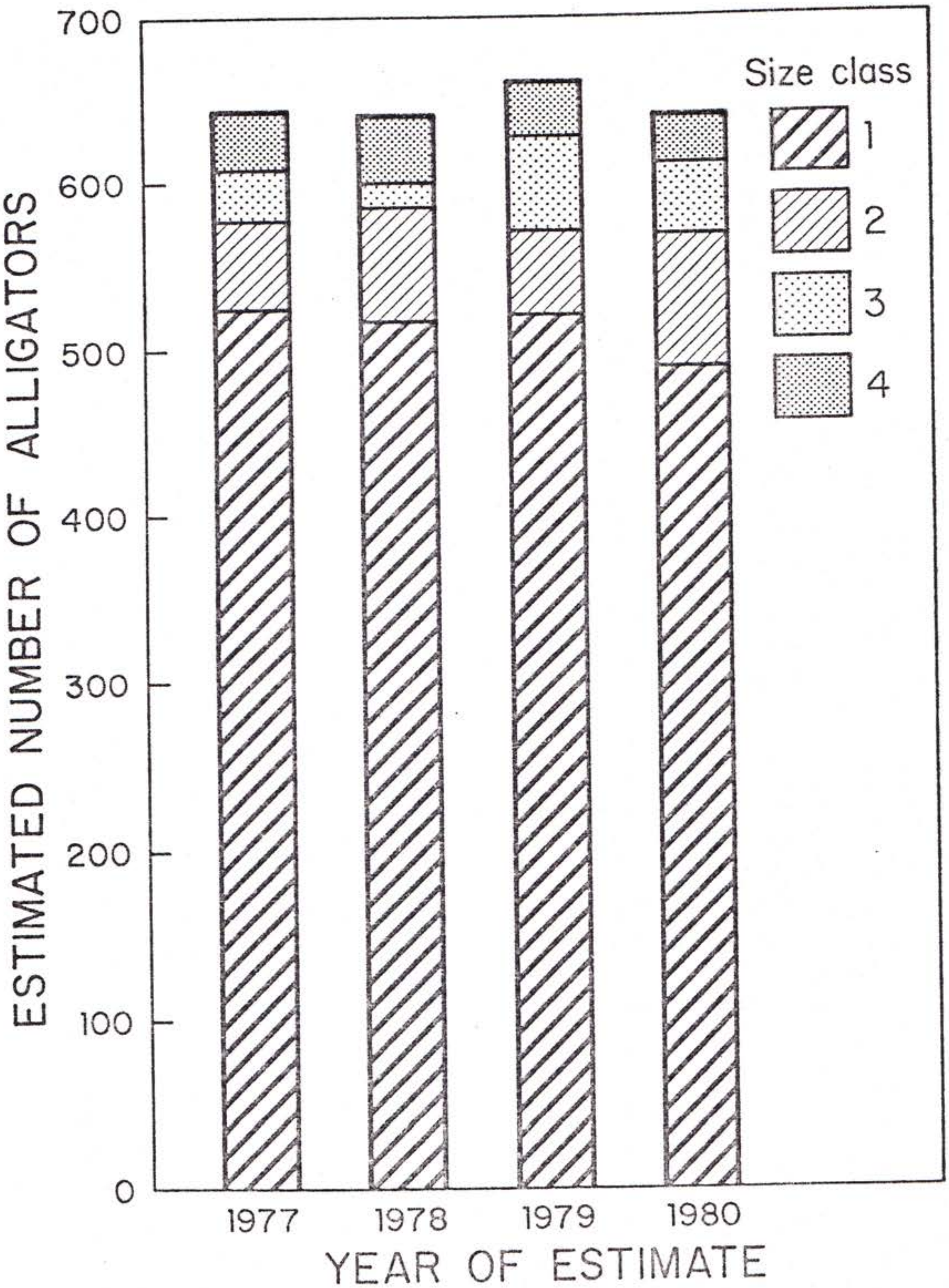
$$\widetilde{N} = \text{geometric mean} = \text{antilog } [(\Sigma \log Nx)/t]$$

where Nx is the population size in year x, and t equals the four years of the study. We use a logarithmic scale because populations grow as fractions or ratios. Using estimated population sizes from 1977 to 1980

Table 1. Population estimates and standard errors in four size classes of Everglades alligators for seven years of mark-recapture data in the primary study area, Shark Slough, Everglades National Park. Numbers represent estimated population levels in a 10-km^2 area of freshwater marsh. Total is the sum of the four estimates. NA = not available, * = unreliable estimates due to small sample sizes.

	Size Class				
Year	1	2	3	4	Total
1976	273.5	143.4	150.0	50.7	617.6
	(40.58)	(80.39)	(NA)	(48.53)	
1977	525.9	51.7	30.0	37.9	645.5
	(79.75)	(7.21)	(9.37)	(22.51)	
1978	517.0	64.6	19.3	39.1	640.0
	(32.03)	(11.84)	(5.31)	(11.45)	
1979	520.0	50.4	38.9	56.4	665.7
	(60.52)	(5.95)	(24.01)	(22.64)	
1980	490.0	78.0	32.5	38.7	639.2
	(39.35)	(19.42)	(21.85)	(34.51)	
1981	436.8	49.0	9.9	8.8	504.5
	(68.12)	(NA)	(NA)	(NA)	
1982	95.7	120.4	3.3	NA	219.4
	(77.23)	(87.88)	(NA)		

Figure 2. Estimated number of alligators in four size classes occurring in a 10-km^2 study area of Shark Slough, Everglades National Park. Figures were derived from Jolly-Seber estimates of population size during four years (1977-1980) of a mark-recapture study conducted from 1975 to 1983. Size classes are discussed in the text.


ESTIMATED NUMBER OF ALLIGATORS
700
600
500
400
300
200
100
0
Size class
1
2
3
4
1977
1978
1979
1980
YEAR OF ESTIMATE

(Table 1) the geometric mean size of the population in the study area is 647.44 alligators per 10-km².

For a dispersion measure, we use a coefficient of fluctuation (CF) (Whittaker 1975) defined as the antilog of the logarithmic deviation around the geometric mean size:

$$CF = \text{coefficient of fluctuation} = \text{antilog} \sqrt{[\Sigma (\log Nx - \log \tilde{N})^2/(t-1)]}$$

where terms are as defined above. CF expresses the range not as a plus or minus value, but as $\tilde{N}/CF$ to $\tilde{N} \times CF$. Applying this equation to the data from 1977 to 1980 (Table 1), the coefficient of fluctuation for the population is 1.019. This means that the densities in different years were mostly not more than 1.9% above or below the mean.

Survivorship rates varied both among size classes and among years (Table 2). For size class 1, survival ranged from 16 to 81 percent, and averaged 39.4 percent (sd = 23.99). Overall estimates for other classes ranged from 53.8 to 65.0 percent. The wide annual variability in survivorship rates reflects either inherent inaccurary in the sampling technique or a responsiveness of these rates to environmental (biotic or abiotic) conditions. The latter is likely to be true, however causes of natural mortality are virtually unknown for wild alligator populations (with the exception of limited data on cannibalism), and in this regard the Everglades is no exception.

Growth Dynamics. In crocodilian populations, parameters such as mortality and age-to-maturity are thought to be more size than age-related. Nevertheless, interconversion of these two types of data

Table 2. Annual survivorship estimates and standard errors in four size classes of Everglades alligators for seven years of mark-recapture data in the primary study area, Shark Slough, Everglades National Park. NA = not available, * = unreliable estimate due to small sample size.

	Size Class			
Year	1	2	3	4
1976	.250	.502	.500	.792
	(.0421)	(.1146)	(.2529)	(.4965)
1977	.453	.501	.469	.508
	(.0376)	(.1069)	(.1596)	(.2132)
1978	.462	.490	1.000*	.778
	(.0551)	(.0917)	(.5332)	(.2145)
1979	.233	.619	.741	1.000*
	(.0291)	(.1418)	(.5393)	(.3881)
1980	.814	.412	.351	.707
	(.1277)	(.0813)	(.2020)	(.6600)
1981	.156	.705	.182	.118*
	(.1281)	(.4474)	(NA*)	(.1046)
1982	NA	NA	NA	NA
Mean	.394	.538	.540	.650
	(.2399)	(.1052)	(.2907)	(.3051)

is of great value. The difficulty has been in finding reliable measures of age in such a long-lived species. The use of osteological growth zones has been proposed to age alligators, however this technique requires destructive sampling, an option not available in Everglades National Park. The use of morphological characters that vary continuously with age (such as size) is the best option for aging alligators, and this requires that a size-age relation be established. For this purpose, we gathered morphological data during our mark-recapture study. These data enabled us to derive a size-age relation which we present here.

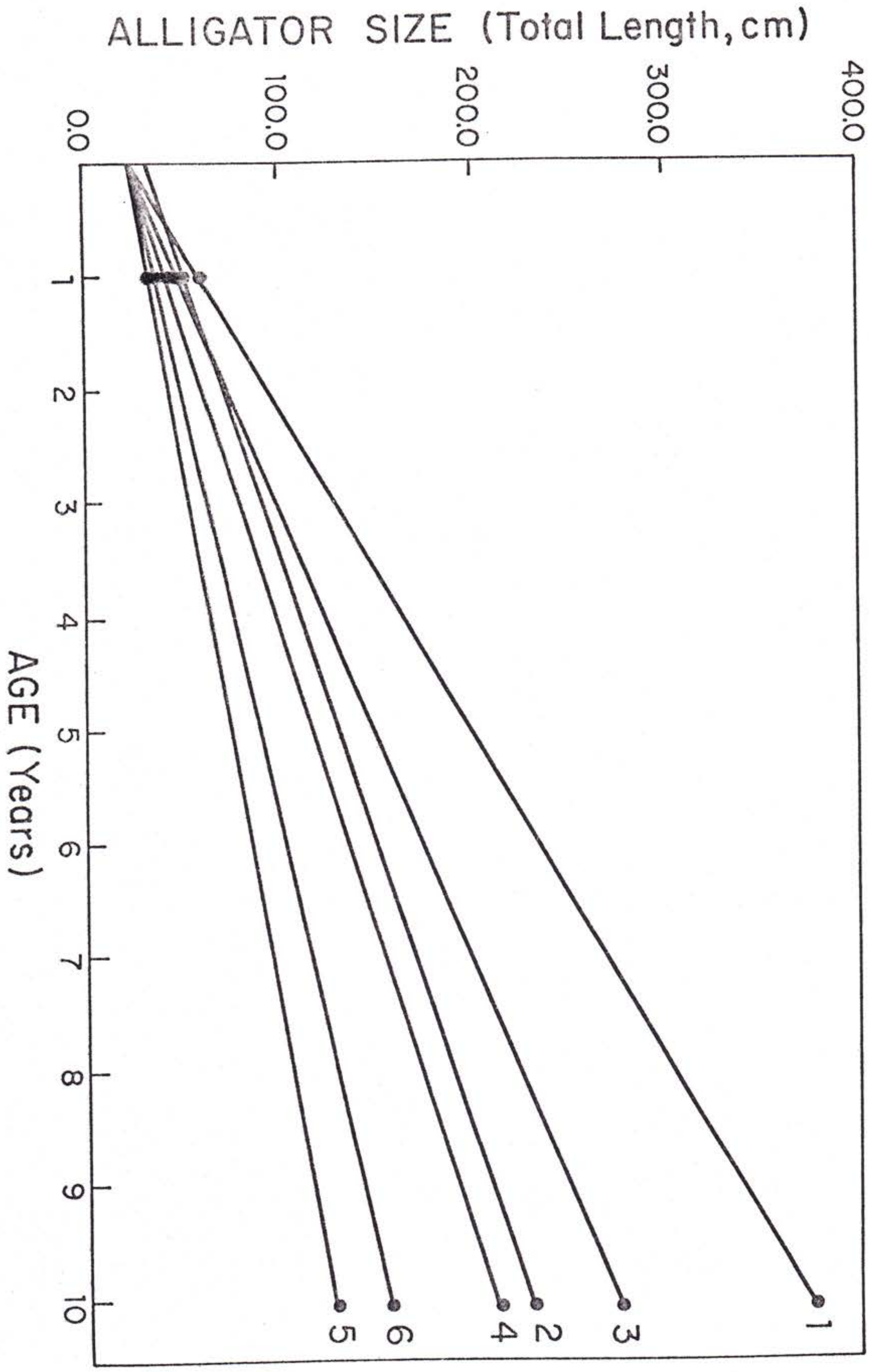
We have analyzed 2015 records of alligator growth, and evaluated growth rate using seven models conventionally used in growth studies, including the logistic, Bertalanffy, exponential, Gompertz, and Richards models. We found that the power curve was the best predictor of the growth of Everglades alligators. Size is best estimated from age using the model:

Snout-vent length (cm) = ((.0021*(Age(days) +473.844))**0.758)*12.3

(*=multiplication, **=exponentiation).

Using this relationship, we can compare the growth curves of alligators in the Everglades with those reported for populations in other areas (Fig. 3). The best way to consider this is to compare lengths at specific ages, for example at ages of one and ten years. At both ages, Everglades alligators are smaller than those in Louisiana or South Carolina, and are generally almost half the size. Their growth, in fact, more closely parallels that observed in North Carolina, at the

Figure 3. Size-age curves for six alligator populations. Linear functions are used to approximate the actual nonlinear functions for purposes of comparison. 1-Louisiana (from Murphy 1981), 2-Louisiana (Chabreck and Joanen 1975), 3 and 4-South Carolina (Murphy 1981), 5-Everglades (this study), 6-North Carolina (Fuller 1981).


ALLIGATOR SIZE (Total Length, cm)
0.0
100.0
200.0
300.0
400.0
AGE (Years)
1
2
3
4
5
6
7
8
9
10
1
3
2
4
6
5

northernmost extent of the alligator's range. Everglades alligators are extremely slow-growing, and may be exposed to more stressful environmental conditions than would be expected given the subtropical qualities of Everglades habitat.

Monitoring Studies

Nest Counts. Nest surveys are thought to provide an index to the number of nesting females in the area. Chabreck (1966) proposed that the total population size (P) can be estimated using the formula: $P = (N/(A*F*E))*100$, where N = the total number of alligator nests in the area, A = the percent of the population over six feet long, F = the percent of females among alligators over six feet long, and E = the percent of adult females nesting. This technique has been used for alligator populations in Louisiana (Chabreck 1966) and for a population of the American crocodile (*Crocodylus acutus*) in Everglades National Park (Kushlan and Mazzotti, in prep.).

The number of nests in the 10-km^2 primary study area varied from 4 to 18 per year from 1975 to 1982. Annual nesting effort was variable (coeficient of variation = .498), suggesting that the population of nesting females in the study area fluctuated, or alternatively, that not all females nested every year. The latter appears to be true. From a combination of tagging studies and nest locations over all years we estimate that the average number of females in the nesting population in the primary study area from 1975 to 1982 was 31. Nesting effort is estimated to have ranged from 12.9 to 58.1 percent per year. On the average only one-third (33.0%) of the adult females nested in any year.

The nest census technique is not suitable for monitoring the population size of Everglades alligators. Nesting effort fluctuates in an unpredictable manner, and is unlikely to reflect an actual change in the number of adult alligators in the population.

Pond Census. An assumption of the pond survey technique is that as water levels recede during the dry season, alligators concentrate in ponds and are more easily observed and counted than if they were scattered and submerged in the surrounding marshes. Thus it is likely that the number of alligators observed in ponds may depend in part on water levels, with drier conditions forcing alligators to concentrate more densely in ponds.

The total number of adult alligators observed in all study areas varied annually from 74 to 322 (Table 3). Since the adult population is unlikely to fluctuate to this extent, the wide range in counts suggests that the pond census technique is highly imprecise. Counts differed significantly among years ($F = 4.13$, $p < 0.05$, $df = 3,12$), primarily because few adults were observed in 1976 (total of 74) as compared with 1977 (total of 322) (SNK, $p < 0.05$). The number of adults counted did not differ among study areas ($F = 2.16$, ns), despite the fact that more ponds were censused in some areas than in others (Table 4). In fact, the number of ponds surveyed accounts for only 24.4% of the variability in the number of adults observed (linear regression, $r=.494$, $df=19$). Thus, the number of adult alligators observed on pond surveys is not readily explained, and may result from a combination of pond density and other factors apart from alligator density. As in the nest censuses, the high degree of variability in counts among years suggests that some factor is preventing the counts from being an accurate index of adult population size.

Table 3. Density of alligators (number per pond) in five 10-km^2 study areas observed during four years of aerial pond censuses in Shark Slough, Everglades National Park.

Number of Alligators Per Pond

Year	I	II	III	IV	V	Overall
1976	.11	.29	.17	.18	.04	.17
1977	.30	.86	.83	.33	.33	.53
1978	.15	.40	.38	.29	.18	.28
1979	.42	.16	.21	.33	.21	.27
Mean	.24	.43	.40	.38	.29	.31
St.Dev.	.142	.304	.302	.709	.119	.153

Table 4. Number of ponds surveyed within each of five 10-km^2 study areas during aerial censuses of alligator ponds in Shark Slough, Everglades National Park. Two-way Anova evaluates the effects of year and study area.

	Year			
Area	1976	1977	1978	1979
I	24	35	43	44
II	36	46	53	53
III	48	60	64	67
IV	34	40	41	43
V	24	40	44	47

ANALYSIS OF VARIANCE

Source	SS	DF	MS
Year	937.80	3	312.600
Area	1442.70	4	360.675
Error	81.70	12	6.808
Total	2462.20	19	

F (year) = 45.914 **

F (area) = 52.976 **

The four annual pond censuses allow us to evaluate the effect of water level on counts, since each census was conducted under different water conditions. A significant negative correlation was found between the water level recorded at the time of the survey and the number of alligators counted ($r=.543$, $p < 0.05$, $n=20$). Water level at station NP-203 accounts for 42% and 30% of the variability in alligator density and total numbers, respectively (Table 6), thus accounting for part of the year-to-year variability in the aerial census data. Pond census counts appear to depend on factors other than change in the population size of adult alligators even if water conditions are accounted for. As a result, this technique does not provide an index by which the size of the alligator population can be monitored over time.

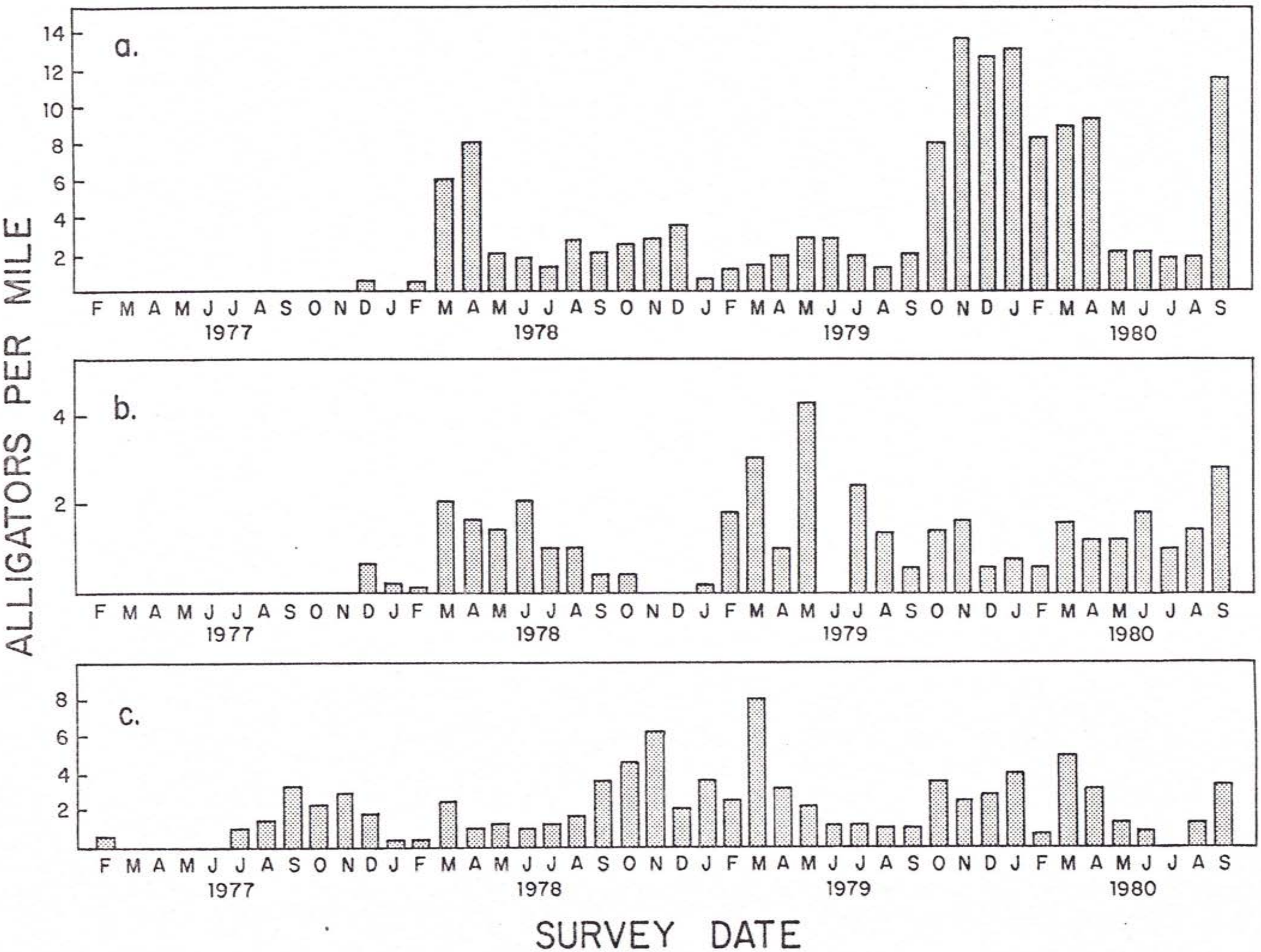
Line Census. Night survey counts are an efficient survey technique because of the presence of a tapetum layer in the crocodilian eye. This tapetum layer produces a characteristic "eyeshine" when illuminated by a beam of light, resulting in a high efficiency for counting alligators (Murphy 1981). Night-time alligator surveys of marsh communities in the Everglades provided relative density information from an undisturbed glades-type alligator habitat. Marsh survey routes were run along major airboat trails; across Shark Slough from the airboat landing to station P-33 (approximately 5 miles), and down Shark Slough from L-67 canal to station P-35 at the junction of the sawgrass marsh and mangrove swamp (approximately 8 miles). Canal surveys provided relative density information from unnatural deep-water habitats. One canal survey was conducted along L-67 for approximately 9.5 miles south of Structure 12-D. A second canal survey was conducted along the Shark Valley Loop Road for seven miles of the west road from the Tamiami Trail to the

Shark Valley Tower. The Shark Valley west road surveys provided information on alligator use of an unnatural, deep-water habitat in an area of human presence.

The cross-slough route showed total counts ranging from 0 to 21 alligators (Fig. 4b), with mean counts per mile ranging from 0 to 4.2. The overall mean for the cross-slough route was 1.55 (±1.97) alligators per mile. The down-slough census route was divided into two segments; from L-67 to the P-33 airboat trail and from the airboat trail to station P-35. Along the northern segment of the down-slough survey route, the total count ranged from 0 to 58 alligators (Fig. 4a), with mean counts per mile ranging from 0 to 14.5. The overall mean for the northern segment was 4.35 (± 4.32) alligators per mile. Along the southern segment of the down-slough survey route, the total count ranged from 4 to 113 alligators (Fig. 4c), with mean counts per mile ranging from 0.29 to 8.07. The overall mean for the southern segment was 2.32 (± 2.26) alligators per mile.

The number of alligators counted during line surveys of natural marsh habitat over the three-year sampling period showed no long-term pattern. Much of the variation in abundance appears to be attributable to seasonality. For example, the data for the cross-slough route consistently peaked during the period from in March to June, with the lowest numbers reached during winter months. Such variation was not related to water conditions ($r = -.186$, ns). On the southern down-slough route, the fluctuation in counts appeared to be a result of the seasonal appearance of hatchlings, which comprised 51% of all animals observed. Counts along the southern down-slough route were also uncorrelated with water levels ($r = 0.306$, ns). It appears that the

Figure 4. Mean number of alligators observed per mile of monthly night-time marsh surveys in Shark Slough, Everglades National Park. a. Northern segment of down-slough survey (December 1977 to September 1980). b. Cross-slough survey (December 1977 to September 1980). c. Southern segment of down-slough survey (February 1977; July 1977 to September 1980).



ALLIGATORS PER MILE
a.
14
12
10
8
6
4
2
F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1977
1978
1979
1980
b.
4
2
F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1977
1978
1979
1980
c.
8
6
4
2
F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S
1977
1978
1979
1980
SURVEY DATE

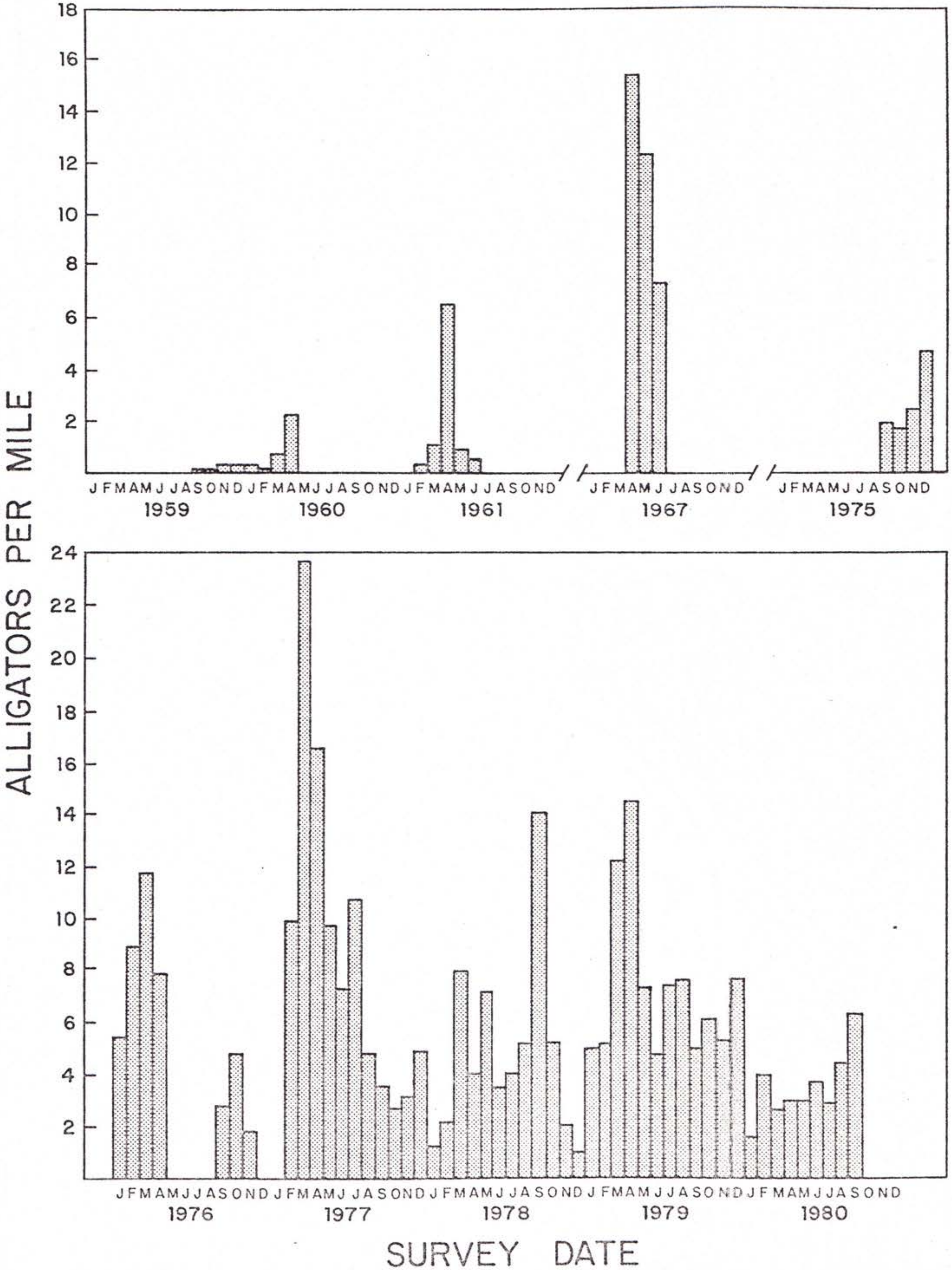
lack of trend along these survey routes is due in part to inconsistent and as yet unpredictable seasonal fluctuations.

A major difficulty with the line surveys of natural marsh habitat is the low number of adult alligators observed, making the determination of trend difficult. The size classes censused consisted primarily of juvenile and subadult animals. For example, along the southern segment of the down-slough route, an average of 0.32 (± 0.656) alligators (longer than 1.5 meters, total length) were counted. This is equivalent to only 0.02 large alligators per mile, far too low a density to be useful in monitoring population change.

Canal surveys showed a higher density of alligators than did marsh surveys, and may therefore be more useful as monitoring sites despite the unnaturalness of the habitat. Line censuses along two canals in Everglades National Park have a long, although interrupted, history with censuses prior to our studies being conducted by biologists with the state of Florida and with the National Park Service.

The canal adjacent to the Tower road at Shark Valley was censused four times in 1959, nineteen times in 1960 and 1961, three times in 1967, and monthly from September, 1975, to September, 1980, for a total of 92 censuses. The early intermittant records are based on counts made during daylight hours, with counts at night, totaling 46 censuses, beginning in 1977. Total counts along the Shark Valley Canal survey route ranged from 0 to 166 alligators (Fig. 5), with mean counts per mile ranging from 0 to 23.7. The overall average along this route was 4.77 (± 4.56) alligators per mile. No overall trend is apparent in census data taken along the Shark Valley Tower survey route. Substantial seasonal variation shows alligator numbers peaking during March and April. Unlike

Figure 5. Mean number of alligators observed per mile of monthly night-time surveys of the Shark Valley west road canal. Surveys were run intermittently from September, 1959, to June, 1967, and monthly from September, 1975, to September, 1980.



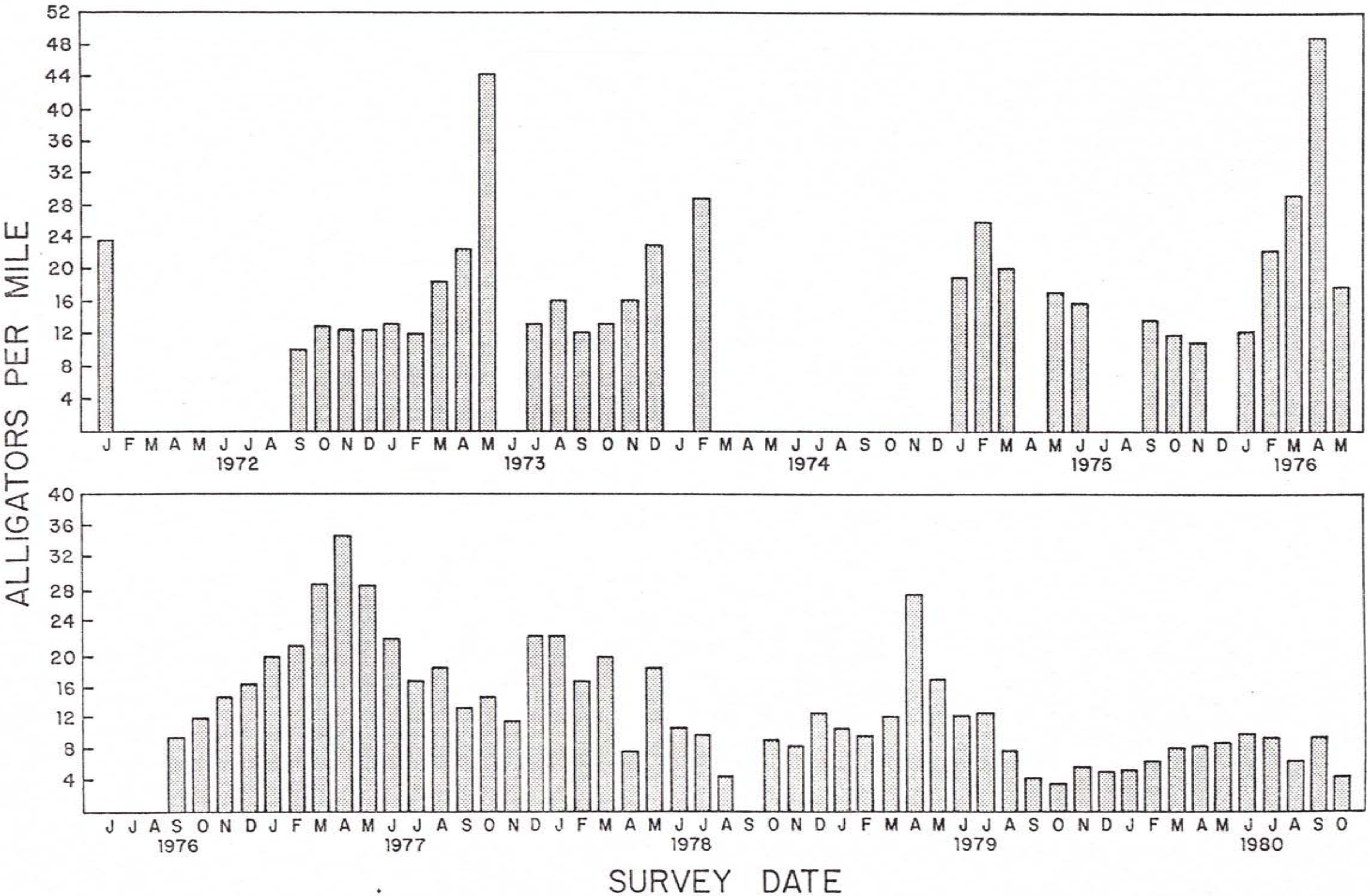
ALLIGATORS PER MILE
18
16
14
12
10
8
6
4
2
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1959
1960
1961
J F M A M J J A S O N D
1967
J F M A M J J A S O N D
1975
24
22
20
18
16
14
12
10
8
6
4
2
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1976
1977
1978
1979
1980
SURVEY DATE

the marsh surveys, water levels in the Shark Valley Canal correlated significantly with total survey counts ($r = .499$, $p < 0.05$, $n=70$). It appears that the canal draws alligators from other areas as the surrounding marshes dry, although most of the canal dries even during normal dry periods. During wet years and under persistent high water conditions, fewer alligators were observed in the canal. The wide variability in alligator abundance and habitat availability makes the Shark Valley canal of limited value as a site for long-term monitoring of Everglades alligators.

The most extensive line survey information comes from the L-67 canal. As a deep canal, L-67 does not dry seasonally. Daytime surveys of L-67 began in January, 1972, and were run intermittently until September, 1976, when a standard monthly census, conducted at night, was implemented. Total counts along the L-67 canal ranged from 36 to 467 alligators (Fig. 6), with mean counts per mile ranging from 3.6 to 44.2. The overall mean for this survey route was a relatively high 17.24 ($\pm$ 10.12) alligators per mile.

Although early censuses run during the day and over only five miles of the canal are not strictly comparable to the night, full-canal counts, the long history of survey data at this site requires that we attempt to in some way adjust the early data to be comparable with more recent data. We did this by running a series of paired surveys, each conducted within one day and using both methods. We found a significant linear relation between the 5-mile day and 9.5-mile night counts. ($r = 0.968$, $p < 0.01$, $\hat{Y} = 0.603 X + 8.73$), which permits conversion of the early counts into the equivalent standard counts, thereby creating a consistent 8-year record. This record includes data on alligator sizes

Figure 6. Mean number of alligators observed per mile of monthly, night-time surveys of the L-67 (E) canal located along the eastern boundary of Everglades National Park. Survey data from September, 1972, to February, 1976, are shown as corrected night-time counts (see text).


ALLIGATORS PER MILE
52
48
44
40
36
32
28
24
20
16
12
8
4
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M
1972
1973
1974
1975
1976
40
36
32
28
24
20
16
12
8
4
J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O
1976
1977
1978
1979
1980
SURVEY DATE

as well. Alligators censused in L-67 were relatively large, with the mean size being 1.81 meters total length (±0.30), which is over adult size (1.75 m). Small animals were relatively infrequent, whereas subadult animals were the most abundant, comprising 36 percent of the total number of alligators observed. Because of the dominance of large alligators and the long-term record available, the L-67 survey route potentially provides the best opportunity for using line censuses to monitor population trends.

As has occurred on other survey routes, the numbers of alligators surveyed in L-67 fluctuated seasonally, with the highest densities occurring during the dry season. The number of alligators in the canal were in part determined by water depths in the adjacent marsh, with the maximum alligator counts in any year significantly correlated with water level ($r = -0.886$, $p < 0.05$). The consistent dependence of alligator counts on water level in L-67 suggests that surveys here could be adjusted for water level effects and subsequently used for monitoring. Alligator counts conducted at the lowest water levels of the year could be compared with the densities predicted using the relationship $\hat{Y} = -90.0\ X + 214.59$, where X is the water level in L-67 (at Richmond Heights).

ASSESSING POPULATION STATUS

Although gifted with a certain intuitive understanding, the term "status" suffers from a lack of rigorous definition and from the lack of a "standard error" in its assessment. Thus it remains an elusive concept in the realm of quantitative science. In addition, crocodilian populations are notoriously difficult to study due to the inaccessibility of the habitat and the fundamental lack of knowledge of the response of population parameters to changing environmental conditions. As a result of these factors, assessing the status of the Everglades alligator is a complex and difficult task.

We discuss four areas to be addressed in considering the status question (Murphy 1981):

1. Historical causes of population decline.
2. Current pressures that limit recovery or persistence.
3. Population numbers and distribution necessary to ensure maintenance of a recovery objective, based on a knowledge of population attributes.
4. Monitoring procedures that are adequate to document the attainment and maintenance of recovery.

Our "recovery objective" for the alligator in the Everglades is that it be a self-regulating population freed from unnatural constraints on population growth. Here we discuss the contribution of these four approaches to the achievement of that objective.

Historical Information. In south Florida, hide records suggest that alligator population levels were extremely high prior to man's encroachment (Hines 1979). Based on the number of ponds in Shark Slough, Craighead (1968) estimated that as many as one million alligators historically occupied this area. Population levels were already very low in the late 1930's due to overharvesting when Beard (1938) made his reconnaissance of the future Everglades National Park.

During the 1940's, protection apparently allowed levels to increase, and with the establishment of the Park in 1947, a "good but gradually declining" alligator population was reported in the Everglades. Early writings report alligators still abundant in the early and mid-1950's, when "it was not uncommon to sight 50-100 alligators while running a skiff for 5 or 6 hours on the fresh water tributaries of the Shark, North East, and Rodgers Rivers" (Craighead and Holden 1965, Stegner 1967, Craighead 1968).

Hurricanes, natural droughts, and the impacts of the altered water regime in the early 1960's combined to effect a second great decline in alligator numbers in the Park, bringing considerable national publicity (e.g. Carr 1967). In 1965 and 1966, Craighead (1968) traveled the four freshwater tributaries of Whitewater Bay "without seeing a single alligator." Craighead further suggested that between 1960 and 1965, alligator numbers in the area were reduced by as much as 98 percent. The problem of maintaining alligator populations in the southern Everglades became sufficiently acute during these years to cause the park to counteract the effects of low water by excavating artificial alligator ponds in Shark and Taylor Sloughs. An intensive law enforcement effort called the "Gator Guard" was instituted to discourage hunting. With the return of surface discharge in the late 1960's and the listing of the alligator as an endangered species in the early 1960's, populations had an opportunity to increase in Shark Slough despite some years of apparent nesting failure caused by high water levels.

Sporadic studies of alligators were conducted in the Everglades prior to our study. In 1965, The Florida Game and Fresh Water Fish

Commission conducted surveys and a limited tagging study (Hines et. al. 1968). In 1966, the U.S. Geological Survey measured the bathymetry of about 12 alligator ponds, and sampled water quality at their primary study site, Cottonmouth Pond (Kolipinski and Higer 1969). In the early 1970's, the National Park Service sponsored a small study of alligator nesting success for three seasons, with information on clutch size and nest size collected at 5 to 10 nests each year (J. Ogden, pers. comm.). In the mid-1970's, two studies near the Park provided some baseline data on alligator biology (Fogarty 1974, Kushlan 1973, 1974).

Because of their restricted intensity and duration, these studies provided little useful information on natural factors affecting alligator population status. Although historic fluctuations in alligator numbers in the Everglades have been described as "dramatic" (Stevenson 1904), our knowledge of an adequate recovery is limited by a lack of baseline historic data. To what extent recovery has occurred is unknown and cannot be evaluated since only qualitative and speculative estimates of historical abundance exist. Lessons from historical causes of population decline, however, are critical in charting a future course of management. The sparseness of willow ponds in the Conservation Areas and the successional closure of former alligator ponds evident in northeast Shark Slough foretell the effects of a lack of adult alligators. This may be due to a lack of resilience following hunting, the continuance of human presence through recreational activities, or a response to the altered water regimes in these areas. It is evident in any case that the alligator is not adaptable to high and persistent levels of disturbance.

Current Pressures. Both protective legislation and the establishment of the National Park have contributed to the preservation of the alligator population in south Florida. Poaching occurs only rarely within the Park today (Jacobsen and Kushlan 1983), and is unlikely to become of future concern as long as legislation and market incentives provide a sufficient deterrent. Hunting pressures on the alligator do not pose a direct threat to the immediate future of the alligator in Everglades National Park. The increasingly accepted tendency of viewing the alligator as a harvestable resource, however, and the establishment of experimental and operational harvest programs in Louisiana and north Florida may indirectly threaten the Everglades population if only to change public appreciation of the important ecological role of the alligator.

Prevailing circumstances that place pressure on the alligator are not unprecedented historically. The consequences of interfering with the natural delivery of surface water into the park have clearly been shown by actions taken by the park in the early 1960's. More recently, we have reported (Kushlan and Jacobsen 1984) the deleterious affects of altered water regimes in the park and in other areas of formerly-natural Everglades habitat such as the Conservation Areas. An altered water delivery schedule has increased the flooding of alligator nests from an estimated 4 to 20 percent following the institution of water management in the 1960's (Kushlan and Jacobsen 1984). Flooding of alligator nests and the subsequent reduction in productivity are a direct consequence of an alteration of the predictability of the hydrologic regime. These issues, which revolve around water levels, are undoubtedly of current and future concern.

Population Attributes. On a rangewide basis, geographic variability, disjunct populations, and the lack of established techniques and historic information have impeded completion of a comprehensive recovery plan for the alligator. Documenting the number of alligators necessary for a self-sustaining population and thus ensuring recovery has proven difficult (Murphy 1982). As yet no standards for recovery exist, and interpretations of local population levels are limited to interpretations based on conventional demographic theory and comparisons among studies conducted in different areas.

From 1977 to 1980, alligator population levels in the primary study area remained constant. Fluctuations of 2% about a mean population level are relatively conservative, implying remarkable stability during the four-year period under study. Such stability is characteristic of K-selected species such as crocodilians. This strategy, however, relies on a long-term co-evolution with natural environmental conditions. The period of study, 1977 to 1980, does not include the two years (1981 and 1982) of nearly 100% reproductive failure due to nest flooding. Although an estimated 35% loss of eggs occurred in 1978, the absolute number of hatchlings surviving was large due to a peak in nesting activity that year (Kushlan and Jacobsen 1984). Whether stability is maintained during years of low productivity as a result of compensatory factors is unknown. Whether stability is characteristic over long time periods and is critical to be maintained are also unknown.

The nature and limitations of the mark-recapture study deserve further consideration. First, the time interval over which population estimates were derived, four years, is short compared to the average life span of the alligator, and these results say little about long-term population dynamics. Thus, we are unable to extrapolate this stability to either future or historical trends. Second, little is known about natural fluctuations in alligator population levels, except that hatchling production can be extremely variable, producing wide changes in total population numbers. And third, we cannot estimate how many alligators there "should be" in the Everglades, so that setting a recovery objective based on population levels is not feasible at this time.

Some demographic theory can be cautiously invoked. With stable population levels, the rate of change in population size (dN/dt) is zero. The net reproductive rate (Ro), the number of female offspring that replace each female of the previous generation, is one, such that each female is replaced by only one female (Kormondy 1984). (If Ro were equal to 2, each female would be replaced by two and so the population would increase. Conversely, failure to replace oneself would lead to population decline.) The natural patterns of reproductive success and survivorship maintain current population levels. If the patterns are altered, current levels will not be maintained unless the action of compensatory mechanisms can be demonstrated. Such mechanisms, which might include density-dependent survival, are notoriously difficult to study, and are a focus of current research in crocodilian ecology.

Estimates of survivorship allow comparison of these parameters with comparable estimates from studies of Louisiana alligators (Nichols et. al. 1976). Comparable annual survivorship rates are shown below.

	Nichols (1976)		This Study	
Size Class	Surv. Rate	Age (years)	Surv. Rate	Age (years)
1 (< 60.0 cm)	.350	<1	.394	1-3
2 (60 - 120.0)	.600 - .788	2-3	.538	4-8
3 (120 - 160.0)	.788	4	.540	9-15
4 (> 160.0)	.750 - .875	>5	.650	>15

Survivorship estimates are similar in Louisiana and in the Everglades among size classes. However,size- and age-related mortality figures differ considerably between the two areas. Because of their relatively slow growth rates, Everglades alligators remain in smaller size classes much longer than Louisiana alligators. Since survival is strongly size-related, with higher mortality at small size classes, Everglades alligators are subject to higher mortality for a longer portion of their lifespan. This may be reflected in the low replacement rate and zero growth rate observed in this study.

For a population adapted to high early age class mortality, these changing survivorship patterns may not be significant to overall population stability. However, we currently have no understanding of the mechanisms involved in the widely varying annual survivorship rates reported in this study. We don't know, for instance, if mechanisms that compensate for the higher age-related mortality continue to operate under current environmental conditions. It is possible that the alteration of water delivery into the park has changed the selective factors associated with the alligator's life history and that conventional demographic theory can no longer be used to assume that the population can adapt. Pre-hatching juvenile mortality has gone from variably low and predictable to high and unpredictable due to nest flooding (Kushlan and Jacobsen 1984), leading to different evolutionary expectations with respect to the alligator's reproductive effort.

Monitoring. A final aspect of assessing status is to develop and recommend future monitoring procedures. Night counts have been shown in other studies to vary widely in accuracy due to the strong influence of environmental factors on the number of alligators observed (Woodward and Marion 1980). Similarly, we found that no one monitoring technique gives a reliable and representative index of trends in population size for Everglades alligators due to the confounding effects of survey technique, habitat type, time of year, water conditions, and the apparent size-class specificity of each route.

If there is one exception to the problems encountered with night counts, it is to be found in the survey of the L-67 canal, a deep-water, artificial canal bordering the park. The L-67 survey offers a highly predictive relationship between water levels and baseline population levels, although there are two problems with this route. First, it is not possible to pre-determine the lowest water level that will be reached in any year, such that surveys would need to be conducted throughout the drying season. Second, the number of alligators in the canal is not necessarily an indication of population levels in the interior marshes. Tagging studies have shown that most alligators in the L-67 canal are subadult males and are transients. As a result, using the L-67 canal as a monitoring site would potentially result in a highly unrepresentative index of the Everglades alligator population. In addition, because of the long time required for hatchlings to reach subadult size, factors operating on early age classes would not be detectable for many years if only adults or subadults were monitored. During this lag time between the occurrence of a disturbance and its identification, much damage to the population structure may already have occurred before corrective action could be instituted.

SUMMARY

Line surveys may measure a non-target segment of the alligator population, and thus their use as a monitoring technique is not sufficient in itself for assessing the future status of the Everglades alligator population. The determination of population levels is not adequate for at least two reasons. First, little is known about natural fluctuations in population size. Second, only intensive, monthly tagging could provide data comparable to the baseline levels reported here, since annual tagging efforts give insufficient precision in population estimates. Annual samples in this study were unrepresentative of population size and structure on comparison to the intensive sampling period (1977-1980). Given the amount of information obtained for the intensity of effort required, an extensive mark-recapture study is not an economical or feasible approach to establishing a long-term monitoring program.

Monitoring survivorship of the earliest age classes may provide the most feasible approach in future studies. This eliminates both a time lag in detection of adverse factors and the methodological difficulties inherent in monitoring adults. Ecosystem-level changes, such as the timing and extent of flood and drought conditions and effects on water quality, first target either the smallest alligators or their prey base, i.e. they are likely to act at a low trophic level. Adequate (natural) survival of early age classes will ultimately ensure maintenance of population levels given no additional mortality in the population. A mark-recapture study combined with nesting success surveys, both conducted at reduced levels of effort relative to the present study, may be satisfactory in monitoring the survivorship of the smallest size classes. Our analyses suggest that mark-recapture studies may yield precise estimates of survivorship for the easily-caught segment of the alligator population, while if necessary, larger alligators may be more easily censused using a line survey technique.

Maintainence of the natural hatching rate is critical to the life history strategy of the alligator, especially if the replacement of females under natural conditions is occurring at such a low rate that it allows little flexibility in mortality rates. Thus the extent of nest flooding each year is an important parameter to be monitored in the future. Validation and refinement of the nest flooding model (Kushlan and Jacobsen 1984) would provide a tool to save field time and personnel costs. Validation might include two additional years (under differing water conditions) of agreement between actual flooding (observed using nesting success surveys) and predicted nest flooding (using hydrological conditions as input into the model). Finally, a population model that includes the demographic parameters presented in this paper may provide the best tool for predicting the consequences of any observed changes in survivorship rates.

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