ALLIGATOR NEST FLOODING IN THE SOUTHERN EVERGLADES: A METHODOLOGY FOR MANAGEMENT

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Introduction

The management of natural resources in relatively affluent countries such as the United States is generally uncomplicated by a need for the resource to generate revenue. In areas such as Everglades National Park, located in southern Florida, a preservationist policy is mandated by law, such that the Everglades is viewed as a resource to be managed solely for its perpetuation. The American alligator (Alligator mississippiensis) has an important ecological role in the Everglades (Kushlan 1974) and is fundamental to the continuation of the natural processes governing the marsh ecosystem. In that the alligator is not to be viewed as a harvestable resource, ecological rather than economic criteria are crucial for its survival. Management objectives for the Everglades alligator include the preservation of it's role in the ecosystem, in this way maintaining the Everglades ecosystem for future generations.

During our eight-year study of Everglades alligators, fluctuations in environmental conditions have provided us with opportunities for natural experimentation. Research has focused on describing the responses of the alligator to the primary human influence on the system, that of an altered delivery of surface water into the park. With the construction of extensive deep-water canals throughout the Everglades watershed, which drained surface water and halted overland surface flow, the water now entering Everglades National Park is not only of artificial quality, having by-passed the natural filtering processes available in the marsh system, but the flow is entirely controlled by four flood control gates along the park's northern border (Fig. 1). Of concern to this research are the effects of the timing and extent of water flow on the Everglades wetland ecosystem, and in particular on the alligator.

In this short report we discuss one aspect of our study, the flooding of alligator nests, which reached nearly 100% in two years of the study. Of interest was whether nest flooding was a natural occurrence, and in what frequency and extent it was likely to have occurred prior to the alternation of water flow patterns. We undertook a predictive modeling effort geared toward addressing these questions. Here we summarize the results of our analyses, emphasizing the implications for the management of the Everglades ecosystem. This report abstracts the results of a complete report as yet unreleased by the South Florida Research Center (Superintendent, Everglades National Park, Homestead, Fl. 33030, U.S.A.), in which is contained the detailed statistical analyses that support the conclusions drawn here.

Methods

Everglades National Park is located in extreme southwestern Florida, USA, and contains about 1.5 million hectares of Everglades habitat, including freshwater marshes, mangrove estuaries, pinelands, hammocks, and open bays. Information on alligator nesting success was collected in a 10-km2 area in the Shark River Slough, the major drainage area for surface water flow into the park (Fig. 2). Other 10-km2 areas of marsh distributed along the length of Shark Slough were studied with less intensity, as was the lower end of Conservation Area 3A (Fig.2). Although most information was collected in the primary study area, this area reflects average relationships among water conditions and alligator nest flooding throughout Shark Slough, a contention demostrated by the fact that the extent of nest flooding during our study period in the primary study area approximated the average nests flooding in other study areas in the northern and southern parts of Shark Slough.

We determined the number of nests each year from 1975 to 1982 using fixed-wing aircraft, helicopters, and ground searches. In the primary study area, all areas not visible from the air were searched thoroughly on foot to provide complete counts of all nests. These ground searches allowed us to calculate that 13.9 percent of the nests present were not spotted during aerial surveys.

We measured all but five nests built from 1975 to 1982 in the primary study area (n=71). Al one nest an aggressive female prevented us from approaching on the ground, and four other nests were not located prior to hatching. Eggs in each measured nest were counted and examined for viability. The time of egg deposition was estimated from eggs collected from each nest using embryological timing criteria developed by Grabowski et al. (in prep.). At each nest visit we noted the habitat of the nest and took several measurements (Fig.3), including the height of the nest above the prevailing water level at the nest site, the distance from the top of the nest to the top of the egg cavity, and the depth (extent) of the clutch or egg cavity.

From these measurements we calculated the height of the center of the clutch above the water level at the time of measurmement. We then expressed the clutch heights as mean sea level elevations in meters (m MSL) to correspond with the units of stage measurement. Water stage data (m MSL) were recorded daily within the primary study area, and we calculated mean stage values from these daily readings. Water conditions varied over the study period and among the study areas. Such water level variability is an inherent characteristic of the Evenglades system, and each year provided us with a temporal experiment on the effects of water levels on alligator nesting.

Air temperatures were recorded the climatological station located along the northern border of the park. We use the midpoint between the recorded minimum and maximum daily temperature to approximate the daily mean temperature.

Results

NESTING PRODUCTIVITY. Alligators reproduce during a nesting season which is relatively consistent and predictable from year to year. Nesting of the alligator in the Everglades takes place during the boreal summer. From 1975 to 1982, the average date of egg-laying (n=71 nests) was 26 June (s=11 days), with the earliest nesting recorded on 9 June and the latest on 27 July. The average date of egg laying occurred one month after the average beginning of the rainy season as water levels were rising. The nesting season, therefore, seems to reflect a balance in selective pressures. Nesting occurs late enough in the year to coincide with the high ambient temperatures needed for incubation but early enough for hatching to occur before seasonal water levels usually peak, thereby reducing the chances of nest flooding.

Egg deposition generally occurred from late June to early July. The mean laying date differed significantly among the years from 1975 to 1982, and was strongly correlated with spring air temperatures. The mean annual egg-laying date can be predicated by the mean temperature in April and the mean temperature in May-June using the following relationship: $\hat{Y} = 241.62 - 5.45\,X1 - 2.18\,X2$, where $\hat{Y}$ is the estimated laying date expressed as the number of days after May, X1 is the mean daily air temperature in April (°C), and X2 is the mean daily air temperature in May-June (°C). In general, it appears that alligators nest earlier following a warmar spring season and delay nesting in cooler years.

For alligators in the southern Everglades, the average clutch size during our study was 30 eggs (mean=29.7, s=7.52, n=198 nests), and the annual nesting effort from 1975 to 1982 ranged from 16 to 58 percent of the known-breeding females, with an average of 29 percent of the females nesting per year. The clutch size and nesting effort are substantially lower than in Louisiana or North Florida (Joanen 1969, Dietz and Hines 1980, Joanen and McNease 1973). In fact, the annual nesting effort in the Everglades is less than half of what it is in Louisiana. We are studying the possible causes and effects of the lower productivity rate in our ongoing analyses of the population ecology of Everglades alligators.

A lower clutch size means that Everglades alligators have a lower annual reproductive potential than do other populations studied. Given a 25 percent lower clutch size and a 50 percent lower nesting rate, an Everglades alligator appears to produce on average one third as many eggs per year (5.0 viable eggs per mature female per year) as do Louisiana alligators (15.9 viable eggs per mature female per year, Joanen 1969). As a result fewer hatchlings are produced per nest in the Everglades. This may mean that the Everglades alligator population has less ability to buffer the adverse effects of mortality agents effecting nesting success and productivity. A single egg may, therefore, be of a greater value to the stability of the Everglades population than it would be to other populations so far studied. Thus, any factor affecting nesting success would have a relatively greater impact on population levels of Everglades alligators than they would on such other populations.

The single most crucial factor in nest success in the Everglades is nest flooding. The loss of eggs by flooding resulted in an average annual loss from 1975 to 1982 of 27.9 percent ($s=37.1$ percent) and a median loss of 5.4 percent. In years when little or no nest flooding occurred, water levels did not reach relatively high levels during the summer nesting season. In 1975 and 1977, flooding occurred only in two particularly low-lying nests. In two years when flooding was significant, 1978 and 1982, flooding was attributed to an unnatural increase in water discharge levels.

PREDICTING AND MANAGING NEST FLOODING. The ability to anticipate the occurrence and predict the extent of alligator nest flooding would permit appropriate water management decisions by managers of Everglades National Park. To this end, we have developed a method by which we can predicthe extent of nest flooding in a given year. For analytical purposes, we define clutch height as the height of the center of the egg cavity. A nest in considered to be flooded if the ambient water level reaches this point. We can predict with ease whether any particular nest will be flooded in any year during our study by comparing its clutch height to any water level. For our model to be predictive outside of the time of our study, however, we would need to know the clutch heights of all nests constructed each year, and this can be done by means of a predictive relationship.

During the study period, we found that clutch heights differed significantly among years ($F=7.11$, p 0.001, $df=7,63$), and that we could predict the mean annual clutch height by using the water level during the last two weeks of June, the period when nests construction is occurring ($Y = 0.663 X + 0.899$, $r= 0.951$, p 0.001, $n=8$ years). Wha- this relationship implies is that higher water levels during the early summer correlate with nigher clutch heights. The mechanism for this appears to be a multivariate response in nest construction. We can account for 92 percent of the variability in clutch heights during our study and can atribute 46 percent to flexibility in the height of the site chosen for nest construction, 43 percent to the height of the eggs within the nest mound, and 2 percent to the height of the mound itself. Thus, under conditions of higher water levels during the nest construction process, alligators appear to be choosing higher sites, placing eggs higher in the nest mound, and to some extent building higher mounds.

With this information we have constructed a model which includes both the linear response to higher water levels and thresholds beyond which alligators are unable to compensate due to the limitations imposed by the low-lying marsh habitat (Fig. 4). Given this model, we can estimate the clutch height of all nests in any year by inputting water conditions characteristic of early summer. Flooding extent can then be determined by examining the maximum water level achieved during the incubation period.

There are at least four uses of such a model that predicts nest flooding. First, the model can be used after a current nesting season to estimate the amount of nest flooding occurring as a result of the highest water levels reached that year. Second, upon anticipating a rise in summer water levels in the park as a result of a management action or a change in upstream water conditions, a manager could predict the impact on alligator nesting success. Third, if critical water levels were derived from computer simulation using hydrologic models, the effects of simulated hydrologic scenarios on alligator reproductive success could be assessed. And fourth, the model permits estimation of historical nest losses, including those that occurred before intensive water management began.

We noted earlier that our model uses data from the primary study area as being indicative of conditions throughout Shark Slough. To support this, we compared the observed nest flooding data in the primary study area with the estimated nest flooding in study areas I and V, located in the northern and southern ends of Shark Slough, respectively (Fig. 2). In one year flooding occurred in all areas, with a 44 percent nest flooding in the primary study area, 79 percent loss of nests in area I, and 25 percent loss of nests in area V. Thus, in years when flooding occurs, results from the primary study area appear to be about average for both upgradient and downgradient areas, and can accurately represent nest flooding throughout Shark Slough.

HISTORIC NEST LOSSES. By extending the use of the flooding model to historic period, we can compare and evaluate the recent effects of water management practices. We calculated the estimated nest loss to flooding that occurred historically beginning in 1953, when hydrologic data first became available (Fig. 5). We found that the extent of nest flooding has increased considerably, from an estimated annual loss of 4 percent under natural, historic conditions, to a recent annual loss of 20 percent, rising by a multiple of five times since active water management began in 1971. By our best estimates derived from our model, it seems that nest losses to flooding did not at any time approach 100 percent during the historic period of data available to us. The estimated maximum flooding reached just 33 percent in 1966. The nearly complete flooding of all nests that we observed in 1981 and 1982 was apparently unprecedented during historic time.

What then is the fundamental cause of the water level conditions that flood alligator nests and how have these conditions changed since scheduled water deliveries began in 1971? We approached this question by evaluating the predictability of the Everglades hydrologic system. We found that during the historic period (1953 to 1962), the maximum summer water level, which was the water level that would potentially flood alligator nests, was highly correlated with two variables - water level in the last two weeks of June, and discharge in June and July. Historically, much of the variability in maximum summer water levels could be attributed to antecedent hydrologic conditions that prevailed in each year, and primarily to water levels in late June, which alone accounted for over 86 percent of the variability ($r=0.928$, p 0.001, $n=10$) (Fig. 6). Thus, the maximum water level that occurred during the risk period for alligator nest was predictable from water conditions during the time of nest construction, the same conditions that correlate significantly with annual clutch heights.

The relationship between water levels during the early summer and the maximum water levels reached during the risk period breaks down after 1971 during the recent water management period (Fig. 6). From 1971 to 1981, the maximum water levels during the incubation period were no longer reliably predictable. Importantly, water level during the last two weeks of June from 1971 to 1981 had no relation to maximum summer water levels. From this analysis several points can be made. First, there was at one time a relationship between water levels during the critical time for initiation of alligator nesting (early summer water levels) and those water levels that threaten flooding of alligator nests (summer maximum water levels). Flooding conditions under contemporary water management practices can no longer be anticipated by water conditions in early summer. The unnatural occurrence of high late summer discharge into Everglades National Park has led to increased nest flooding in recent years, in part through disruption of the natural predictability of the Everglades hydrologic system.

Discussion

Public opinion of the alligator is important to its preservation, a view that is well-recognized by crocodilian biologists. One population view of the alligator is that its status no longer needs to be a matter of concern. Jacobsen and Kushlan (in prep.), in their review of the alligator's status relative to the management of problem alligators in the park, summarized how legal protection for alligators has loosened considerably in recent years. The current popular view of the alligator's status arises because in recent years most populations have benefitted from legal protection from the Endangered Species Act, and have largely recovered from the effects of hunting and their subsequent decline in numbers. Recovery in parts of Florida has been cited in a request by the State Game and Fresh Water Fish Commission as cause to reduce the alligator's status to "threatened by similarity of appearance", thus bringing alligator management completely under the responsibility of the state. Currently, an experimental harvest program in north Florida reflects the state's intention to manage the alligator as a commercially harvestable resource.

There is a temptation to assume that because alligator populations appear to be resilient in some areas, threats to their continued survival no longer exist. A reclassification of alligators throughout Florida includes populations in southern Florida and in Everglades National Park, where threats continue to exist. The long-term effects of limited alligator production in the wetlands of southern Florida are made evident by contrasting the relative size of the alligator nesting population in areas of the Everglades that have had a history of unnaturally high water conditions, such as the southern end of Conservation Area 3a (Fig. 2), with that in southern Shark Slough, using aerial nest censuses as an index for comparison.

In most years, nesting in the deep water marsh of Conservation Area 3a was very limited. On the average the nesting population there was less than 10 percent of that in the shallower and more typically fluctuating marshes in the park. The lack of production in a large geographical area such as Conservation Area 3a reduces considerably the potential size of the total Everglades alligator population. Should high water regimes become prevalent in the park, we could expect that similar dislocations and reduction of the alligator population would follow. The encroachment and subsequent loss of former willow ponds in nearby Conservation Areas reflect in part the loss of adult alligators there. This inadvertent experiment in water management should provide insight into the future of the alligator population in Everglades National Park if productivity is not maintained at historic levels through proper water management.

In the Everglades, alligators are often seen in artificial ponds and borrow pits in visitor use areas, where concentrations are usually apparent only during dry months. Seasonal numbers reveal little about the biological health of the Everglades alligator popupulation. Even though few animals are being added to the population, the visibility of old adult alligators may distract from what otherwise would be a major concern. Current adverse impacts on the long-term population status of such a long-lived species may take decades to show their effect.

Thus , one should not casually extend reports of alligator population recovery in some parts of Florida to include the status of the alligator in the southern Everglades, and in Everglades National Park in particular. Our studies indicate that alligators in the Everglades marsh may face pressures unusual in other populations. Maintaining an annual pulse of young alligators into the system by avoidance of unnatural nesting failure would seem to be critical to maintaining the adult population. Previous studies modeling hunted crocodilian populations have demostrated that continual production of young is critical to population stability. In fact, those models show that factors that are detrimental to the production of young have a greater effect on long-term population levels than do factors such as hunting and drought that affect all age classes (Blomberg et al. 1980, Nichols et al. 1979). The long-term effect of nest flooding and the loss of young in the Everglade alligator population must be determined in a similar way. It would seem that these model findings may be particularly relevant in the Everglades, where fluctuating water levels potentially threaten the successful production of young alligators by flooding nests. Consequently, managing to prevent unnatural nest failure is crucial to the long-term survival of the alligator population in the Everglades ecosystem, and should such management not be undertaken one can expect continued deterioration of ecosystem processes in the Everglades.

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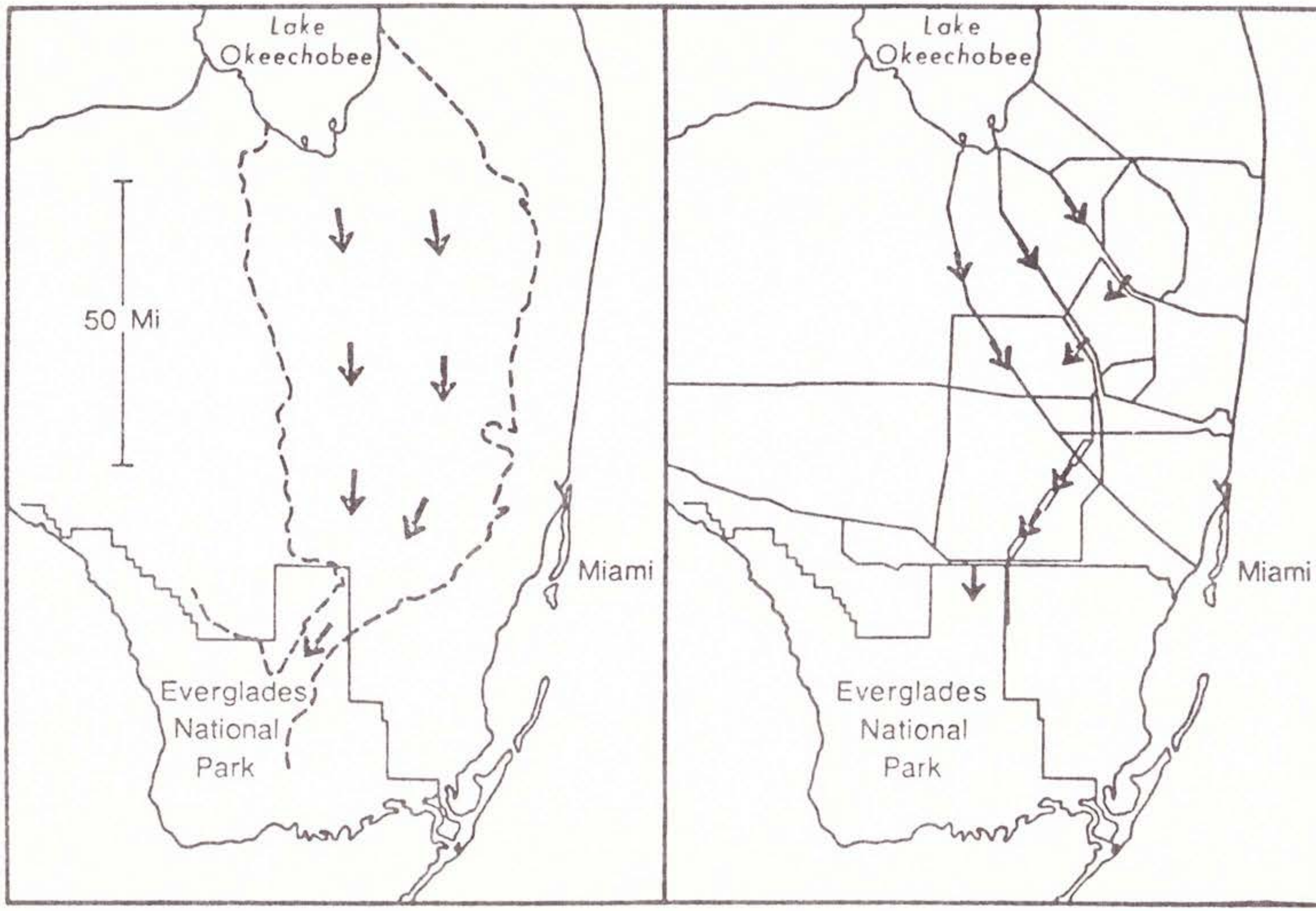

Figure 1: Alteration of water delivery patterns into Everglades National Park due to channelization of Everglades watershed. Left - natural overland flow prior to water management. Right - present situation bypassing natural filtering processes offered by northern marshes and under control of four flood control gates along the northern border of the Park.

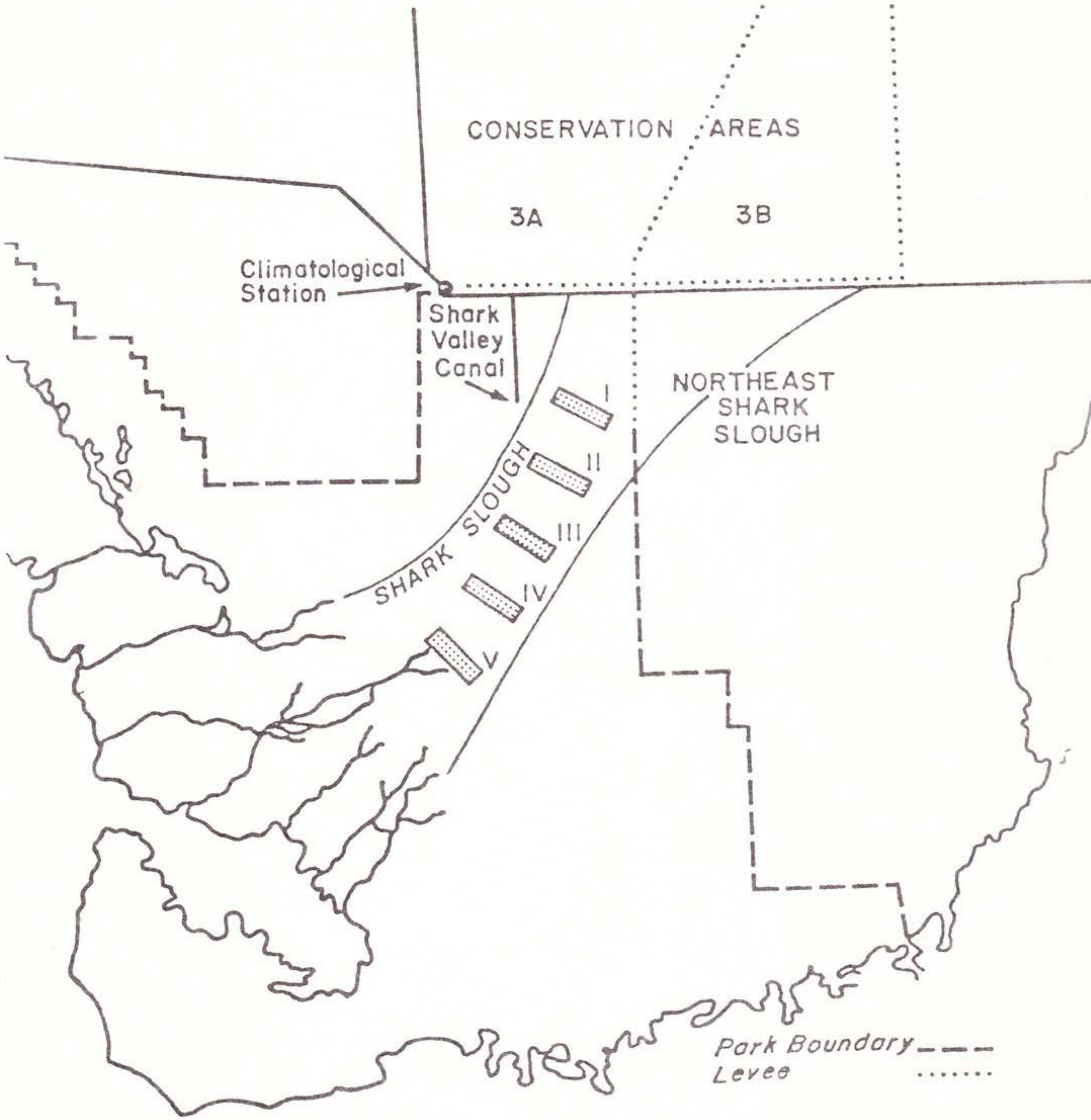

Figure 2: Map of south Florida showing the location of five alligator study areas (numbered rectangles) in Shark Slough, Everglades National Park, and nearby locations. Conservation areas 3A and 3B to the north are separated from Shark Slough in the Everglades National Park by levees.

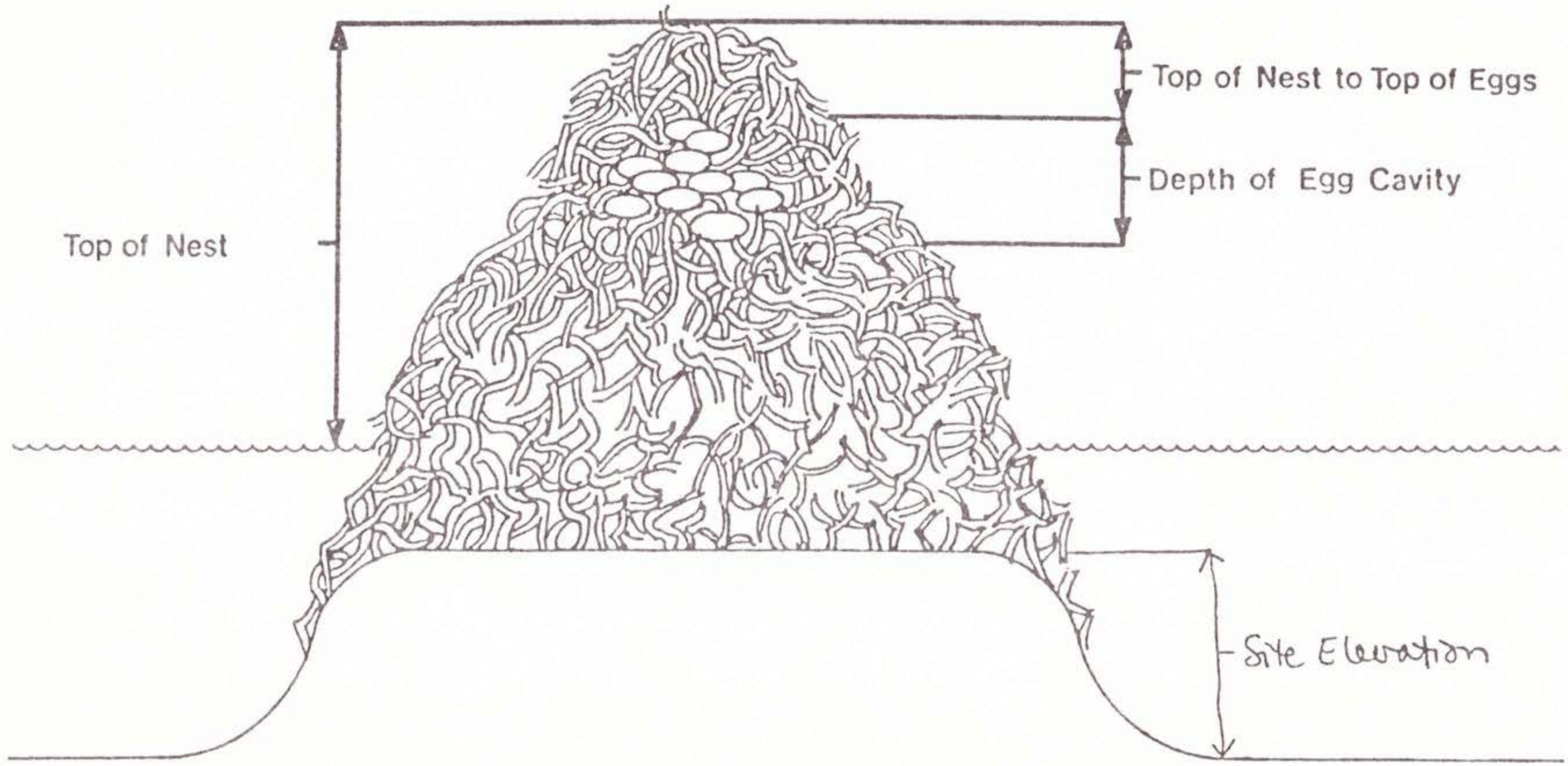

Figure 3: Field measurements typically taken of alligator nests in Everglades National Park including the height of the top of the nest above prevailing water level, the distance from the top of the nest to the top egg in the egg cavity, and the depth (extent) of the egg cavity containg the clutch. All measurements are taken in centimeters.

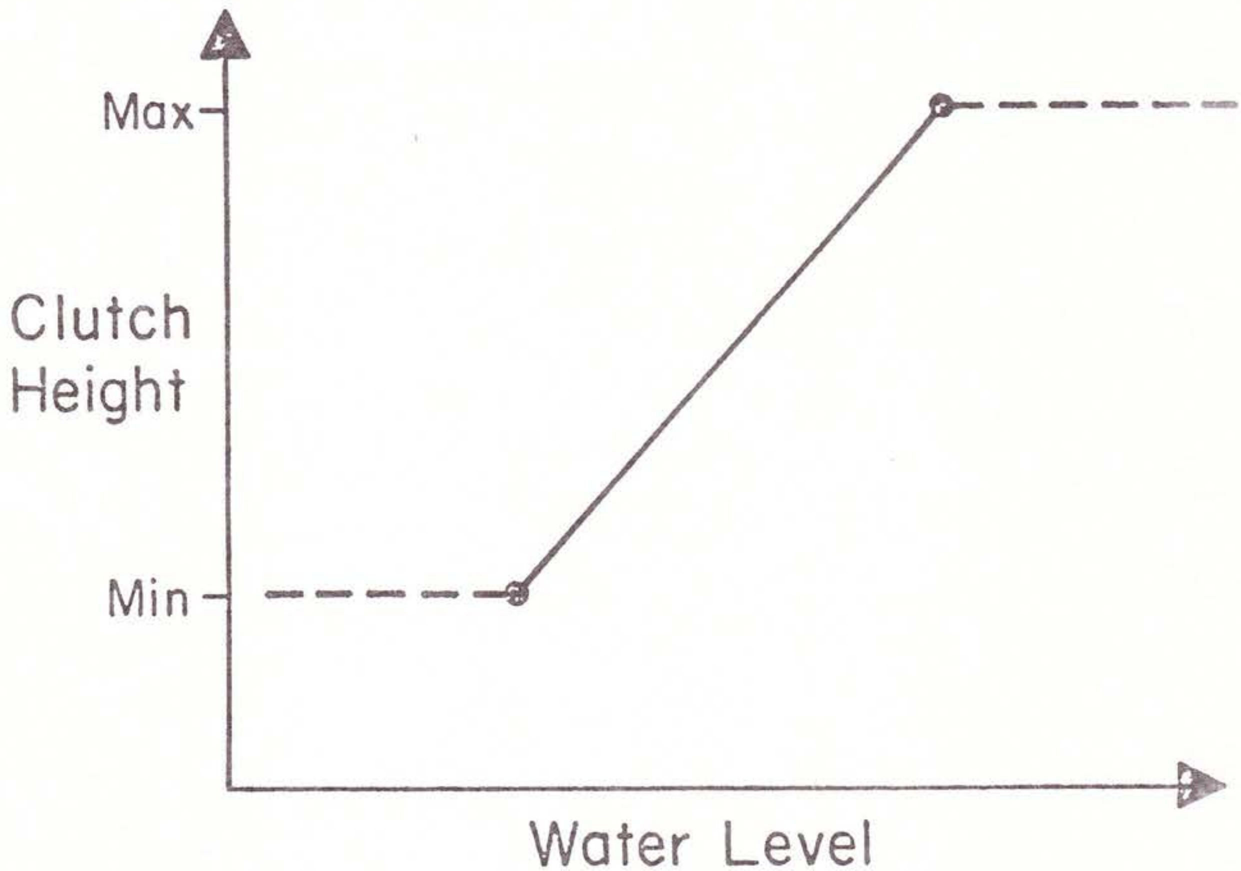

Figure 4: Schematic diagram of nest flooding, illustrating linear compensation in clutch height for water level during the last two weeks of June, bounded by thresholds which delimit the compensatory ability. At the lower threshold, nests are constructed at the level of the marsh, and at the upper threshold at the highest elevation provided by the available habitat.

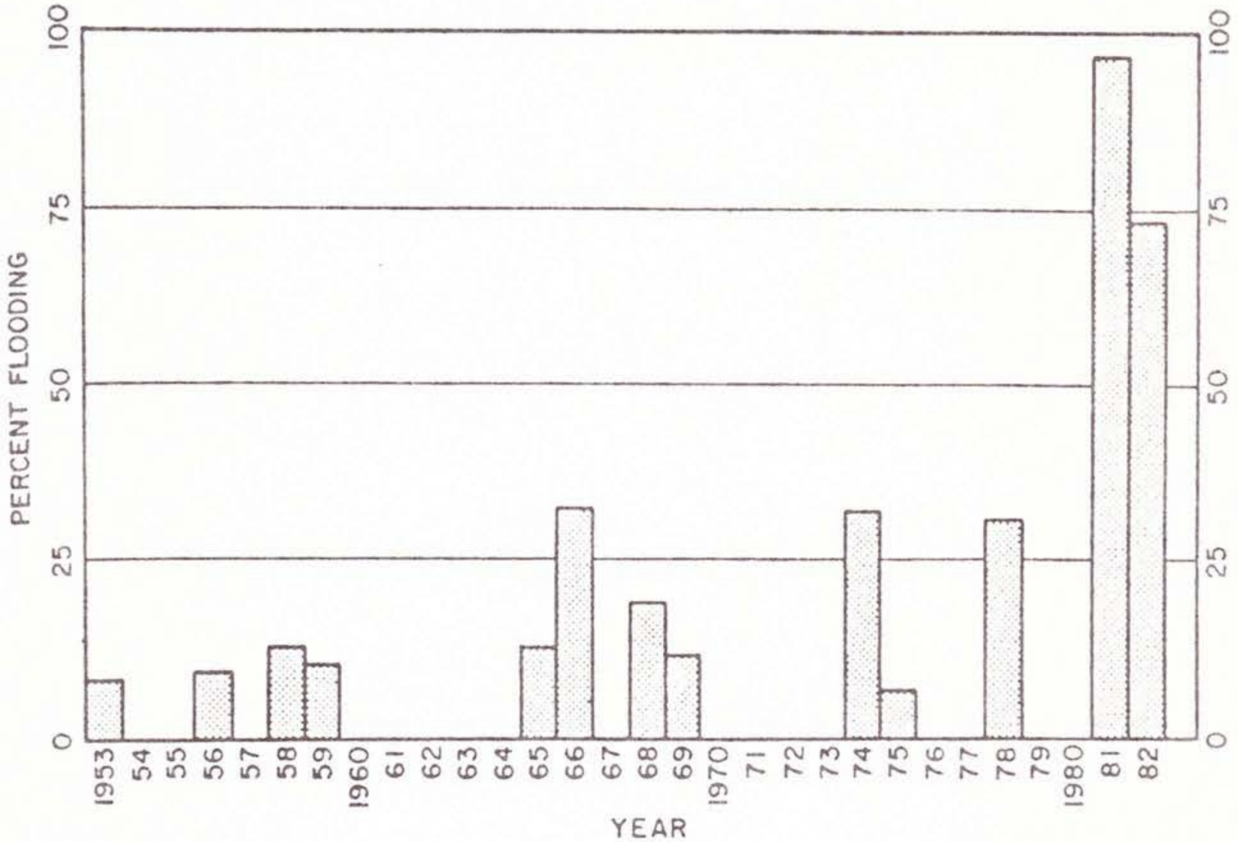

Figure 5: Percent of alligator nests flooded in the Everglades from 1953 to 1982. Values prior to the study period, which began in 1975, were estimated using the nest flooding model. From 1975 to 1982, nest flooding extent was measured in the primary study area. The nearly complete flooding observed in 1981 and 1982 was apparently unprecedented under historic conditions.

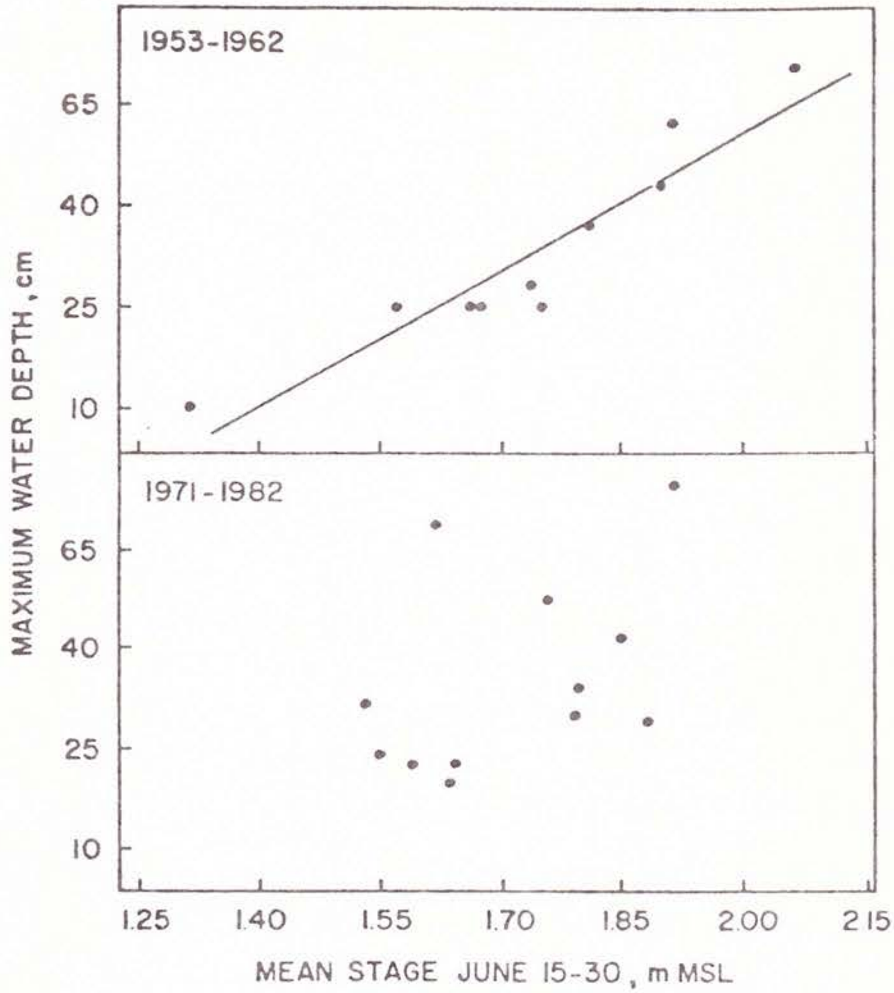

Figure 6: Relation of the maximum water depth (cm) in the primary study area, Everglades National Park, during the estimated incubation period and the mean water level (m MSL) from June 15 to 30. These figures illustrate the breakdown in predictability of the Everglades hydrologic system in recent years. a (top) - Historic period, 1953 - 1962, r=0.928, p 0.05, n=10. b (bottom) - Recent period, 1971-1982, r=0.465, p 0.05, n=12.

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