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American Alligator Distribution and Abundance  
in Relation to Landscape Pattern and Temporal  
Characteristics of the Everglades

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Preliminary Draft

December, 1990

UPD-00005572



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## Introduction.

The restoration of wilderness ecosystems in human-dominated landscapes "must involve strategies that have a landscape level of focus, if the natural dynamics of disturbance regimes are to be accommodated by natural populations that fluctuate through time...Large animals with large home ranges, ecological specialists, and species that depend on patchy or predictable resources are most vulnerable to extinctions if functional, landscape mosaics are not protected... Populations of such species that are restricted within landscapes of insufficient size . . .and mosaic composition.... often experience declines related to environmental stochasticity, demographic stochasticity, social dysfunction, or genetic deterioration" (Noss, 1987). Natural areas in such fragmented landscapes are also characterized by " a replacement of native communities in natural abundance patterns by an artificial and impoverished assemblage of species that require explicit conservation strategies" (Noss, 1987).

The reduction by half in the historical area of the Everglades, through drainage and development at accelerated rates over the past 50 years, raises concern as to the viability of populations within the wetland's remaining natural areas. Dramatic declines in higher, trophic-level, consumer populations of the Everglades have been well documented, including regional populations of the Florida panther (a large carnivore with large, home ranges), the Snail kite (an ecologist specialist), wading birds and the American alligator (species dependent on patchy or predictable resources). The need for addressing Everglades restoration strategies to identify the size and mosaic composition of a "minimum dynamic area" ( , 19 ), as well as the restoration of functional, hydrological processes and dynamics within that area, is evident.

Recent, past changes in the natural abundance patterns of the alligator, a keystone species in the Everglades, have been attributed to habitat reduction, degradation, fragmentation of the system, and water management regulation (Craighead, 1968; Neil, 1971; Hines et al, 1968; Kushlan and Jacobsen, 1984,1990). The keystone species status afforded the alligator is defined by its role as a major predator and architect within the system, influencing the structure, distribution and abundance of native plant and animal communities.

The American Alligator is a large, mobile carnivore of the Everglades that represents a versatile and selectively opportunistic predator. An individual feeds on a variety of prey species and sizes during a long, life span of nearly

continuous growth; types and sizes of prey consumed vary by the alligator's size, and include crustaceans, fish, amphibians, reptiles, birds and mammals. Because of its nearly continuous growth over a long life span, alligator populations are characterized by a number of overlapping size classes that function as significant consumer populations at various trophic levels of the system.

An alligator also modifies its environment to meet its life requisites. The "alligator hole" often characterized in popular literature acts as a thermal sink for the animal in regulating its body temperature to diurnal changes in ambient air temperatures, particularly during seasonal declines in surface water and during droughts. This modification of its environment also influences the spatial and temporal characteristics of surrounding plant and animal communities. The excavating and maintenance activities of alligators in preventing the gradual sedimentation of occupied holes or ponds, and the subsequent plant communities that become established within or adjacent to these alligator holes, have been described by several researches (Craighead, 1968; Neil, 1971; Kushlan, 19 ). Alligator holes also serve as dry season refugia for aquatic invertebrates, amphibians, other reptiles, and marsh fish populations (Neil, 1971; Craighead, 1968; Kushlan, 19 ; Loftus and Eckerd, 1989), upon which both breeding and non-breeding wading birds and other predators forage (Craighead, 1968; Robertson and , 19 ; Ogden, 197 ; Kushlan, 19 ; Loftus and Eckland, 1989; Fleming et al, 1989), as dry season watering holes for other semi-aquatic or terrestrial species (otter, raccoon, deer, and panther) (Craighead, 1968; Neil, 1971; Fleming et al, 1989), and as predation traps for these species by alligators (Craighead, 1968; Kushlan, 19 ; Fleming, 1989). The nests of alligators are also used as oviposition sites by other reptiles, including aquatic turtles and snakes, and lizards, particularly during high water periods (Craighead, 1968; Kushlan, 19 ; Fleming, 1989).

Because of its structural and functional role in the system, past changes in landscape characteristics that have affected the species' natural abundance pattern are of importance in the determination of restoration objectives for the Everglades. An understanding of the nature of these changes on a keystone species is also relevant to other wetland systems that have, or are experiencing similar alterations in landscape and temporal characteristics caused by human activities.

The fundamental, environmental characteristics of many aquatic systems occupied by the American alligator within its present range have experienced unprecedented rates of change over the past several decades. The Everglades is an example of one such wetland. Historical, continuous

distributions of this species in the low, coastal plain of the southeastern region of the country are becoming increasingly fragmented into separate, geographical populations. During the past 200 years of human settlement, approximately 42 % of the region's original wetlands within the gulf coastal plain have been lost to development. Within Florida, almost half (46 %) of the state's wetland acreage has been lost during this same period to agricultural and urban settlement. Approximately 60 % of south Florida's original wetland acreage has also been developed (DOI, 1990). Remaining isolated wetlands, inhabited by alligators in these human-dominated landscapes, are also experiencing further habitat reduction and degradation. Recent, accelerated rates of change have occurred within the potential life span of an individual alligator, compared to similar rates of environmental change that occurred in the species' conservative, evolutionary history over geologic periods of time.

#### Review of Published Data.

##### General evolutionary history.

The American Alligator, Alligator mississippiensis, is one of 26 living species of crocodilians that inhabit aquatic ecosystems in both the Old and New Worlds. The earliest representatives of the crocodilians first appeared over 230 million years ago during the Mesozoic Era, a time when amphibians were declining, reptiles obtaining dominance, and birds and mammals rising (Neil, 1971). The crocodilians evolved as a group and show many advanced characteristics for a reptile, including a four-chambered heart, rudimentary diaphragm, and elaborate maternal care and behavior ( , ). The ancestral lineage of these living crocodilians, however, is conservative and generalized. During crocodilian evolution, all divergent lines of descent toward specialization perished (Neil, 1971).

The 26 living crocodilian species have been placed in subfamilies that trace three distinct lines of descent. The crocodilian lineage of blunt-snouted descendants comprise a subfamily, Alligatorinae, that includes the Alligator genus. This genus first arose in North America over 36 million years ago during the Oligocene period of the mid-Cenozoic era. Several lines of descent in the Alligator genus appeared throughout North America during this period, a time when the climate was mild and swamplands widespread across the continent (Neil, 1971).

During the subsequent Miocene period of approximately 25 million years ago, only one line of descent in the Alligator genus entered southeastern North America. This line of

descent occupied the only part of the continent that was not profoundly affected by episodes of drying and cooling during this and the following Pliocene period (25 - 1 million years ago). The other lines of descent in the Alligator genus that occupied the northern, eastern and western parts of the continent did not survive these cooling and drying periods. The modern species, the American alligator, evolved from ancestral stock from this line of descent during the Pliocene and is the only species of the Alligator genus in North America that survived to the present (Neil, 1971). The species' present form has remained essentially unchanged for over 25 million years since its initial evolution from ancestral stock. Present geographic populations are characterized by low, genetic divergence and variability (Mentzies et al, 197 ; et al, 19 ).

#### Geographic range of the American alligator..

The American alligator and its closest living relative, the Chinese Alligator, Alligator sinensis, are the only living crocodilians with geographic ranges that extend into the temperate zone. All other living crocodilians and their ancestors evolved in tropical climes (Neil, 1971).

The geographic range of the American alligator was influenced by interglacial events during the Cretaceous period of 135 million years ago, long before the Alligator genus evolved on the North American continent. Sea level rise during this period formed an arm of the sea inland to central North America and over the present lowlands of eastern North America. The subsequent recession of this inland sea during the same period, exposed the former sea bottom as a low coastal plain, characterized by freshwater swamps, lagoons, and slow moving rivers that developed behind a retreating shoreline of sand dunes. An area or plateau that remained above this submergence, the Piedmont Plateau, delineates the northern boundary of the American alligator's geographic range (Neil, 1971).

Fossil records of the American alligator and its descendants have been recorded only in the coastal plain, from Virginia and the Carolinas south through Florida, westward to eastern Texas, and northward through the lower and central Mississippi Valley. Northern limits of the American alligator's geographic range appear to be determined by the duration of winter temperatures ( , 19 ) and the old Cretaceous shoreline of the coastal plain at the edge of the Piedmont Plateau. Eastern and southern boundaries of its geographic range are limited by the sea, and western boundaries by declining precipitation and local drainages (Neil, 1971).

## Historical to present trends in American alligator distribution and status within its general range.

The historical distribution and abundance of the American alligator are represented from written accounts of European explorers and settlers in the southeastern region of the country during the 1700s and the early 1800s. During this time, the species was reported as abundant in all major river, lake, swamp, and marsh systems within the upper, middle, and lower southeastern coastal plain. By the early 1900s, significant declines in the species' abundance had occurred in the northern and western parts of its range and within the Floridian peninsula. These declines were attributed to unregulated market hunting for the sale of its hide. Commercial hunting of alligators began in the mid-1800's (Smith, 1893), and peak harvests were reached in the late 1800s (McIlhenny, 1935).

Intensive hunting continued into the 1900s, and by the late 1950s, the American alligator had either disappeared, or existed in low numbers only, in most parts of its historical range (Chabreck, 1967). Greatest reductions had occurred throughout the northern and western parts of its range, in the upper and middle reaches of the central, Gulf Coastal Plain, in the central and lower Floridian peninsula, and within the upper Atlantic Coastal Plain of its eastern range limits (Reese, 1915; Neil, 1971). Implementation of harvesting and strict, commercial trade regulations during the 1960s - 1970, combined with restocking efforts, have affected dramatic recovery from hunting and trade-related declines for most populations (Chabreck, 1971; Powell, 1971; Bara, 1971; Schemnitz, 1972; Palmisano, 1972; Joanen and McNease, 1972a, 1972b; Palmisano et al, 1973; McNease and Joanen, 1978; Hines, 198 ).

The present, geographical range of the American alligator includes wetlands within the lower, Atlantic Coastal Plain, from North Carolina southward through the Florida Keys, and within the Gulf Coastal Plain west to eastern Texas, and northward up the Mississippi Valley to southeastern Oklahoma and Arkansas (Figure 1). The regional status of these geographical populations, in an updated 1985 status category listing - as defined under the federal Endangered Species Act of 1973, designates the American alligator as recovered in 46 per cent of its present range, and either endangered (48.1 percent) or threatened (5.9 per cent) in the remaining parts. These categories generally indicate the status of a population based on relative densities within a geographic area. Geographic populations listed as recovered include those of eastern Texas and the coastal marsh populations of south Louisiana in the western parts of its range, and all populations throughout the Floridian peninsula (Joanen and McNease, 1985).

Habitat reduction, degradation and fragmentation of wetland systems presently occupied by the American alligator, however, continue to occur. Wetland systems that support major, geographical populations of the species are presently being threatened by a variety of human activities, including alterations in land cover patterns, sedimentation patterns, and changes in the hydrology and related salinity regimes of these systems through water diversion, oil and gas exploration, and drainage for agricultural and urban development (Constanza et al, 1977 ; Joanen and McNease, 1977 ; McVicar and Johnson, 1989; other papers of this symposium).

Historical to present trends in the distribution and status of the American alligator in the Everglades.

Colonization of the Everglades by the American alligator may have occurred as recently as 2,000 years ago (Craighead, 1968). Human settlement in the region began prior to the 1500s with the migration of native American tribes from west of the Mississippi River to the Gulf shores of the Everglades, followed by European exploration and settlement in the late 17th century. Earliest historical accounts of alligator abundance in the region were recorded with the writings of explorers during the early 1800s.

Major declines in regional alligator populations were first noted after market demands and unregulated, commercial exploitation of the species, begun in the early 1800s, dramatically increased during the late 1800s - early 1900s (Neil, 1971; Hines 1971). Harvests during this period fluctuated in relation to market conditions and declining numbers of alligators. With some legal protection and regulation of harvest in the 1940s, alligator numbers temporarily increased. Despite fluctuations in market demand, hide hunting continued into the 1950s and 1960s, until passage of the federal Endangered Species Act of 1973, and the listing of American alligator populations in Florida as endangered under that Act.

Recent past declines in the Everglades alligator population have been related to accelerated wetland drainage and alterations in the system's natural hydrology through water management regulation (Craighead, 1968 ; Hines, 1971). Estimates by Craighead (1968) of a predrainage era population around the turn of the present century ranged as high as 1,000,000 alligators over 800,000 acres of wet and dry prairie habitats once comprising the freshwater wetlands of the historical, southern Everglades. These estimates were based on the estimated number of pond or solution holes existing in the area at that time, and aerial and ground

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surveys of alligator occupancy rates of these features in remaining areas of suitable habitat during the 1950s. Estimated alligator occupancy rates ranged up to one occupied pond/depression/solution hole per 1.4 hectares of freshwater, wetland habitat during the 1950s. Occupancy was defined as a breeding female and pods of young up to two brood size classes, and included the presence of several subadult and adult animals in adjacent marsh habitat.

~~Craighead's population estimate of one million alligators within the historical southern Everglades represented an average alligator density of approximately 1: 2.75 animals per hectare.~~ This density estimate is within the range of present, observed alligator densities of 1: 1.7 - 7.4 animals per hectare for freshwater wetland habitats reported for Louisiana (Joanen and McNease, 197 ; Taylor, 19 ).

Craighead reported still abundant, but gradually declining, alligator populations within the southern Everglades through the mid-late 1950s. Alligators were described as abundant in prairie habitats of the eastern floodplain, along the edge habitats of the central sloughs, and seasonally abundant throughout the headwater region of downstream, mangrove estuaries along the Gulf of Mexico and Florida Bay coasts, at the southern terminus of the Everglades mainland catchment area. Occupancy of the then deep water, central sloughs was relatively low. The gradual declining trend reported by Craighead was followed by an apparent, but brief, stabilization in numbers over the next five years.

Accelerated wetland drainage of dry prairie habitat comprising the eastern lowlands of the southern Everglades throughout the mid-late 1950s, and the combined effects of: (1) continued poaching throughout the 1950s within Everglades National Park boundaries, (2) a prolonged two year drought (1961 -1962), followed by (3) three more years (1963 - 1965) of blocked, upstream surface water flows during construction of impoundments in the northern Everglades for water retention, concurrent with (4) a period of low rainfall and induced drought conditions, caused a major collapse of the alligator population in the southern Everglades by 1965. Dramatic declines occurred in the number of alligators observed in all formerly occupied habitats within the southern Everglades following this series of natural and man-made events. According to Craighead (1968), total numbers may have declined to as little as one to two percent of the historical, turn of the century, predrainage population. ~~Such reduced numbers would be within the range of estimates for present alligator population size within the southern Everglades.~~ (see New Data).

Changes in the natural abundance patterns of alligators also occurred during this period in response to the impounding and implementation of water regulation schedules in the central and northern reaches of the Everglades

catchment area. The division and impounding of the central and northern Everglades wetlands into three major water retention areas in the early 1960s resulted in an overdrainage of prairie habitats in upstream, and the formation of deep water pools downstream, in each impoundment area. This overdrainage and excessive, deep water impounding degraded formerly prime alligator nesting habitat throughout the northern Everglades (Hines et al, 19 ; Schortemeyer, pers comm).

Unseasonal fluctuations in water depth, related to water management regulation for water supply and flood control, further reduced or degraded remaining nesting habitats in these impounded marsh areas. The perimeter levee system built to impound these marshes completed the fragmentation of most shallow, dry prairie, and edge habitats from the deep water, central sloughs of the system. Accelerated drainage and development of dry prairie habitats east of the impounded areas soon followed and continues to the present (see New Data section of this report).

Estimates of contemporary, alligator distribution and abundance, presented later in this paper, describe a continuing low occupancy of alligators throughout the Everglades. The relative high occupancy of alligators in the eastern, dry prairie habitats, as well as within the freshwater mangrove zones of coastal estuaries, first described by Craighead (1968) in the 1950s, have shifted, following the loss to development or overdrainage of these dry prairies, and reduced freshwater flows into the estuaries. A more restricted distribution now occurs, primarily confined to remaining wet prairie and central slough habitats within the southern Everglades, and to wet prairie habitats in the northern Everglades, along the edges of artificially maintained deep water pools within each impoundment area. Much of the formerly occupied dry prairie habitats of the lowlands along the eastern edge of the northern Everglades have been lost to agricultural and urban developments. Within the southern Everglades, these prairies remain as overdrained marshes, retaining surface water during peak, rainfall periods only (Johnson et al, 198 ; NPS unpublished hydrology data). Present occupancy of these overdrained prairies by alligators is very low compared to that described by Craighead (1968) throughout the 1950s.

#### Life history aspects of the American Alligator.

Most of the recent, scientific literature concerning life history aspects of wild American alligator populations are from studies conducted in the coastal plain regions of North and South Carolina, the Okefenokee Swamp of southeastern

Georgia and north Florida, the lake country of north/central Florida, the Everglades of southcentral and southern Florida, and the coastal prairies of south Louisiana. The geologic origin and age, substrate types, landcover patterns, and the temperature, rainfall, hydrology, and salinity regimes of these systems, as well as their productivity and biomass, differ.

Contingent characteristics of the alligator populations inhabiting these wetlands also differ and provide a comparative basis (1) to relate these contingent characteristics and life history aspects of alligators to the fundamental, environmental characteristics of each wetland, (2) through modeling, to identify alligator population structure and stability attributes in relation to patterns of environmental variability and long-term change in the Everglades that most influence the species' viability, and (3) to discuss restoration and management implications for the Everglades derived from the above-mentioned considerations. The geographical location, areal extent, geologic origin and age, and contemporary environmental characteristics of these wetland systems, that are important to alligator life history aspects reviewed in the following subsections of this paper, are referenced in Table 1.

Daily and seasonal movements, thermoregulatory behavior, circadian rhythms, dispersal and homing instincts.

Alligator population stability attributes and persistence are affected by (1) the ability of alligators to disperse in response to either adverse or favorable seasonal changes in environmental conditions, both from and to a variety of habitats, (2) movements associated with its feeding generality, food partitioning, and food availability in those habitats, and (3) the alligator's ability by thermoregulatory postures, behaviors, and movements to adjust its body temperature to more favorable ranges required for physiological functions, particularly digestion.

Movements of an individual alligator reported in the scientific literature are often related to the animal's sex and age, and seasonality. Within seasonal activity ranges, components of this movement involve travel related to feeding activity, thermoregulatory behaviors and movement, circadian rhythms, movements associated with reproductive activities, predator avoidance, dispersal, and homing instincts ( ). Resource partitioning by size/age classes of individuals occupying shared habitats, social behaviors, territorial defense and dominance hierarchies associated with reproductive activities, also affect the

daily and seasonal movement patterns of individuals ( ).

Documented movements of individual alligators over large areas up to 100 square kilometers (36 square miles) usually involve adult males, nonbreeding adult females, and subadults dispersing from normal activity ranges in response to stochastic events (hurricanes, flooding, and drought). Greater distances of movement up to 13 linear kilometers have been reported for alligators in response to major hurricanes (Chabreck, 1965). Documented travel of up to 60 - 70 linear kilometers by immature and adult alligators, over 1 - 18 months, by individuals captured and released at relocation sites, has also been reported in the direction of original capture areas (Chabreck, 1965; Trops, 19 ; 19 ).

Normal, subadult dispersals from natal sites have also been documented over areas up to 100 square kilometers (Chabreck, 1965). Upon reaching maturity, females usually establish a nesting area from which they seldom move any large distance (Chabreck, 1965). Adult nesting females and pods of young up to two brood size classes do not normally disperse in response to climatic events, but remain near the nesting site throughout the year. Adult females and pods of young up to three brood size classes have also been observed remaining at nesting sites during unusual dry periods or droughts ( ). Non-breeding females and adult males, as well as smaller sized subadults, normally move about a much greater sized activity range than that of a nesting female and her brood of young.

In the coastal prairie marshes of southwestern Louisiana, movements of individual alligators over seasonal activity ranges of up to 25 square kilometers (6000 ha.) have been reported (Joanen and McNease, 19 ). Such movements were associated with adult male travels during the warm weather months. Seasonal activity ranges, however, of adult males during other seasons, and normal seasonal activity ranges of adult female and subadult alligators, occurred within areas of 4 square kilometers or less (500 ha.). Seasonal activity ranges of nesting females, however, were considerably smaller than that occupied by other alligators, and throughout a year averaged only 10 ha., compared to ha. for adult males, and ha. for immature female and male alligators.

Movement patterns of individuals within these activity ranges throughout a year involved an average minimum daily distance traveled of 800 meters for adult males, 25 meters for adult females, 300 meters for immature alligators, and 15 meters for hatchlings (Chabreck, 196 ; Joanen, 19 ; Joanen and McNease, 19 ; McNease and Joanen, 19 ). Normal seasonal movements of alligators include feeding activities

by all individuals during the spring, summer, and autumn, thermoregulatory behaviors throughout the year ( ), restricted movements associated with denning during cold winter or dry periods by all age classes ( ), predator avoidance by hatchlings, juveniles, and subadults ( ), and adult male and female activities associated with reproduction ( ).

Reproductive activities and associated movements included territorial displays and/or defense by adult males during the early spring months, courtship activities by adult males and females during late spring and early summer, and restricted movements of nesting females during and after the nesting season, i.e. nest construction and egg laying period (early - late June), nest attendance during the incubation period (July - early September), and protection of young during the posthatching period (early fall - winter months).

Comparisons of alligator seasonal activity ranges, associated movement parameters, and habitat preferences, by sex and age classes, from a series of studies conducted in coastal prairie marsh habitat of southwestern Louisiana over a six year period, are presented in Table 2. Although each study was conducted for only one year, and surface water conditions varied significantly within some of the same seasons between years, the movements reported by the authors generally described: (1) restricted, daily movements and activity ranges of nesting female alligators within densely vegetated marsh habitats, interspersed with numerous, open water ponds (less than 0.5 hectares in size), throughout the summer and fall months of nest construction and egg laying, incubation, hatching, and posthatching periods, and during winter, dormancy periods. Adult female movements shifted to open, deep water areas during the spring courtship and mating period, in contrast to (2) wide ranging adult male movements occurring primarily in deep, open water habitats during the spring, summer, and fall, with restricted movements associated with denning during winter dormancy periods, and (3) immature male and female movements over a wider range of marsh habitat types throughout the year. However, these movements included less total marsh area than that encompassed throughout a year during normal adult male travels. Use of densely vegetated marsh, interspersed with numerous, small potholes and ponds, was also greater for immature female compared to immature male alligators. Immature males moved about two or more activity centers within their seasonal activity ranges. Most immature females concentrated daily movements about a single activity center within shallow water, natural marsh areas (Joanen and McNease, 19 ).

Extremely high surface water conditions prevailed throughout much of the study period on immature alligators, relative to the surface water conditions that occurred during most

seasons throughout the previous studies, and may have influenced the degree of travel and marsh habitat types utilized by immatures. Chabreck (1965) reported that immature alligators responded more rapidly than adults to normal increases in water depth or moderate flooding events.

Alligator daily movements for most sex and age classes throughout the year were generally greatest during the spring, declining during the hot summer and cooler autumn months, and were minimal on overcast days during the winter. Adult male alligators, however, showed greatest movements during the hot summer period. Joanen (19 ) felt that increased adult male movements during the summer months were related to the extensive use of deep water canals for travel by adult males. He also felt this use may have reflected a preference for the cooler range of water temperatures in the deeper canals, compared to the warmer temperatures, characteristic of shallow, natural marsh habitats, during summer months. Activity periods of adult alligators during the hot summer months also shifted to nocturnal hours. However, no shifts in immature alligator daily activity patterns between daylight and nocturnal hours were noted within a monitored diurnal period throughout the study.

All alligators made extensive use of local topographical features in their daily activities and modes of travel. Ridges and levee berms were used as basking sites, densely vegetated marsh areas interspersed with numerous small ponds as nesting and denning sites, shallow ponds and lakes as centers of feeding activity, and lakes, bayous, and canals as travel lanes within seasonal activity ranges (Joanen, 19 ; Joanen and McNease, 19 ; McNease and Joanen, 19 ).

No comparable, quantified data are available on seasonal activity ranges, daily movements, and habitat utilization of alligators from other major populations within the eastern parts of the species' range, or from the southernmost extension of the species' range in the Everglades. Limited information of general seasonal shifts in alligator occupancy among habitat types have been reported by Hines et al (19 ) for alligator populations in the northern Everglades, and by Craighead (1968) for the southern Everglades.

In the impounded marshes of the northern Everglades, movements of alligators were associated with seasonal fluctuations in water depths (Hines et al, 1968). During periods when the marshes were innudated, stable populations occurred in canals along the perimeter of the impoundments. As water levels dropped, the canals experienced striking increases in numbers. These increases were comprised of immature individuals that had recently left nesting areas, and adult males, moving to the deep water canals as water levels in the interior marshes receded. Individuals

remaining in the interior marshes retreated to holes until the return of surface water. During these drydowns and droughts, females and young up to three size classes were observed concentrating in the interior ponds. Similar fluctuations in alligator numbers have also been reported within canal habitats used by alligators in the southern Everglades (Jacobsen and Kushlan, 19 ; Dalyrample, 198 ).

Pronounced, seasonal water level fluctuations, that occurred during the alligator study in the northern Everglades, resulted from the pumping of excess water from the surrounding agricultural and urban areas into the impoundments during the wet season, in periods of heavy rainfall, and pumping the water out again during the dry season months for distribution to urban and agricultural users. Since rainfall in south Florida is seasonal, all of the storage and natural retention of rainfall-runoff occurred during the wet season months of June through October. Most of this water accumulated in the downstream porportion of each impounded area. Observed alligator populations were low in both overdrained habitats in the upstream area of impounded marshes and in deep water impoundment pools in downstream areas, that had formerly been occupied and used as nesting areas during the years (mid to late 1950s) immediately preceding construction of the impoundments (Hines et al, 1968).

Craighead's (1968) general observations of alligator movements within the southern Everglades during the 1950s, began prior to impoundment of the northern and central Everglades marshes and sloughs. During this period, reduction in seasonal, surface water flows to the southern Everglades was already noticeable, as well as the affects of overdrainage on dry prairie habitats. Craighead's accounts, however, still provide useful descriptions of seasonal shifts in alligator occupancy of habitat types, related to more natural, seasonal fluctuations in surface water conditions, that prevailed in the southern Everglades during this time period, before the construction of an upstream, water control system, and implementation of intensive, water management regulation throughout the region in the early - mid 1960s.

During the high surface water flows of the mid to late wet and early dry seasons, Craighead reported that alligators occurred "in abundant numbers" within the dry prairie habitats of the eastern lowlands and the mangrove flats within the headwater regions of the freshwater estuary zones, along both the Gulf of Mexico and Florida Bay coasts. The eroded, limestone bedrock surface underlying the dry prairies of the eastern lowlands, and the numerous bays, river channels, fingerling creeks, and tributaries of the tidal rivers that intersected extensive mangrove flats, spanning the freshwater mangrove zones, provided stable

surface water pools, or deep water ponds or depressions, occupied by alligators throughout most of the year. Eroded bedrock "ridges" along the edges of central sloughs also provided numerous depressions occupied by alligators. During most dry seasons, and even during droughts, these depressions still retained surface and/or ground water. Alligator occupancy of deep water central sloughs was intermittent, and occurred where deep deposits of muck and dense sawgrass stands were interrupted by large, open ponds with well defined banks, and kept open by the activities of occupying alligators.

With the normal recession of water levels during the dry season months, diminishing freshwater flows through the central flowway of the southern Everglades (Shark River Slough) were attenuated by natural embankments or ancient beach rims, that separated the downstream, freshwater mangrove zone from the more saline and tidal mangrove zones, immediately inland of Gulf coastal beaches and beach rims. Alligators concentrated in the deep water bays, tidal rivers, creeks, and tributaries in the headwater area of this freshwater estuary zone, as upstream freshwater flows through the central sloughs abated during the late dry season months. During drydowns or major drought years, alligators that remained within the dry prairies, and the interior wet prairie or sawgrass marshes of the central sloughs, retreated to ponds or underground caverns, solution holes, or "dens" retaining surface or groundwater in the underlying, eroded limestone bedrock. With the return of seasonal rainfall in the spring, and expanding surface water pools, alligators rapidly dispersed from these dry season refugia to adjacent marsh habitats.

Alligator seasonal occupancy of the freshwater mangrove zones to the southeast, in the headwater areas of these estuaries along the Florida Bay coast, followed a similar pattern of concentrating numbers in tidal creeks, interior bays, and lakes, as upstream freshwater flows diminished during the dry season months. Well established alligator trails or "trekking" paths, however, marked migratory routes of alligators to the deep water interior bays, lakes, and creeks within these estuaries from adjacent dry prairie marshes of the eastern lowlands. Seasonal surface water flows through these high marshes were fed primarily from local rainfall, and the marshes more rapidly drained each dry season, in comparison to the large, lag sheet flows passing through the wet prairie and slough marshes comprising the central flowway of the system (Craighead, 196 ).

During the 1950s, nesting areas of alligators, as described by Craighead (1968), occurred upstream of these freshwater mangrove zones, in the dry prairies and edge habitats to the east and west of the system's central slough or flowway.

Nesting also occurred along the edges of tidal creeks and tributaries that penetrated downstream wet prairie and sawgrass habitats, adjacent to estuarine headwater areas. Nesting areas within the dense, sawgrass dominated upstream reaches of the central flowway were few, and confined to the higher edges of large ponds and tree islands, interspersed within this (then) deep water slough.

By the mid to late 1960s, following the alligator population crash that occurred in response to natural and human-induced drought, Craighead reported a major reduction in alligator occupancy of the eastern dry prairies, and of the headwater regions of the coastal estuaries, concurrent with the reduction in upstream, seasonal flows that occurred during this period throughout the entire southern Everglades. Critical changes in the natural hydrology of the southern Everglades that impacted on the alligator populations at that time included reduced dry season flows that were followed by intense wildfires. Breaches in the natural embankments of the ancient beach rims, that delineated the freshwater mangrove zone from the more saline tidal zone, occurred as a result of the drainage and resultant fires that consumed much of the firm peat comprising the structure of these natural berms (Craighead, 1968).

The natural berms or ancient beach rims had retained upstream, freshwater flows during the dry season. The flat expanse of surface water trapped upstream of these berms had prevented the complete drying down of the numerous depressions, solution holes, and ponds pitting the southern Everglades landscape in all but major drought years. These sites had sustained the alligator's requirement for water during periods of seasonal drying, a time of restricted alligator movement, limited growth, and increased thermal stress (Craighead, 1968).

Thermoregulatory behavior, climate boundaries, and heat energy budgets.

Analyses of the thermoregulatory behaviors of alligators, and modeling of their climate boundaries and heat energy budgets, have highlighted the absolute dependence on water for all life history aspects of this semiaquatic reptile. Size of the alligator, its insulation, metabolic, and evaporative water loss rates, heat conductance to the ground, and maximum and minimum sustainable body temperatures, all determine the range of environmental conditions over which it can exist (Spotila et al, 1972).

Analysis of heat energy budgets in relation to these variables indicated that the standing availability of water was the most important habitat variable upon which the alligator's existence and maximum use of an area depended. Water provided "blackbody conditions" for alligators,

allowing them to maintain relatively constant body temperatures, despite daily cycles in temperature and radiation. Large alligators, capable of large heat storage, could move over wide areas, if such heat could be dumped by returning to blackbody conditions or deep water sites within their normal steady-state regimes/activity range. Small alligators were more closely tied to the physical upper and lower climate limits of their habitat because of their small heat-storage capacity, but could tolerate higher extremes in temperature over short time periods, than adult alligators. All alligators could withstand a wide range of temperatures in a blackbody cavity, or substitute, as that afforded by standing water. Deprived of water, alligator activity was greatly restricted and their chance of survival greatly reduced (Spotila et al, 1972).

As alligators are dependent upon water for their locomotion and their main source of food, drying of an area affects all their behavior patterns, particularly their thermoregulatory behavior. Loss of standing water can not only restrict their activity, but increases the danger of desiccation because of their high rate of evaporative water loss. Analysis of heat energy budgets also supported the need for maintenance of a continuous and stable supply of water in any management strategy, as well as the importance of vegetation as a source of shade for the alligator, and in the maintenance of moderate water temperatures during hot summer months (Spotila et al, 1972).

#### Food habits.

Alligators are versatile, selectively opportunistic predators that utilize a wide variety of prey species. The diet of an alligator influences its growth rate, body and reproductive condition and performance (nesting, fertility, and hatching rates, and clutch size) (Chabreck, 1972; McNease and Joanen, 1981; ). Variation in diets of alligators have been related to alligator size, sex, locality, season, and year. Spatial and temporal changes in prey species relative abundance, prey availability, prey vulnerability, and prey size suitability are believed to be proximal factors related to diet variation in alligators ( ).

#### Variation in diet by alligator size.

The size, types, and variety of prey species consumed by an individual alligator varies with its length ( ). Hatchling alligators feed primarily on insects and small fish ( ). Prey of juveniles includes insects, mollusks, crustaceans, small fish, amphibians, and other small reptiles. Diets of subadult alligators are similar but include a greater proportion of fish in the diet ( ).

). Other reptiles, birds and small mammals may also be eaten. Diets of adult alligators include a greater porportion of vertebrates, including larger fish, reptiles (aquatic turtles and aquatic snakes), as well as other alligators, birds and mammals (primarily rodents and small carnivores, but also animals as large as deer).

#### Variation in diet by season and year.

Diet composition by alligator size class may also vary both seasonally and annually within a habitat type, in response to seasonal or annual changes in relative prey species abundance, prey availability, and prey vulnerability ( , McNease and Joanen, 197 ).

#### Variation in diet by habitat type and geographical area.

Variation in diet by alligators within the same size class, but occupying different habitat types within a locality, has also been documented for adult alligator populations in southwestern Louisiana in relation to marsh salinity zones McNease and Joanen, 19 ; , 19 ), and for adult alligators utilizing shoreline versus open water habitats in the lake systems of north-central Florida ( , 19 ). In the coastal marshes of southwestern Louisiana, mammals were more important in the diets of adult alligators in fresh and intermediate marsh types than in brackish or saline marsh zones. Crustaceans and fish were important foods in the more saline zones. In the lake country of north central Florida, adult alligator in open lake areas feed more exclusively on fish than adults occupying shoreline habitats. The variation in adult alligator diets reported in these studies, with respect to habitat types, reflected differences in the terrestrial and aquatic landscape characteristics between habitats, and related differences in prey species relative abundance. ( ).

Geographic variation in diets of alligators has also been documented. Mammals and crustaceans comprised an important porportion of the diets of adult alligators in the freshwater, coastal marshes of Louisiana, and fish of less importance, compared to that consumed by adult alligators in freshwater, lake systems of north-central Florida. Fish were consumed in greater proportions in the diets of Florida alligators. Fish were important prey for both subadult and adult alligators, while mammals and crustaceans comprised only a small proportion of adult alligator prey items ( , 19 ). A higher relative abundance of mammalian and crustacean prey populations in the more productive prairie marshes of southern Louisiana may account for the differences observed ( ).

## Importance of diet variation to population biology.

The importance of diet variation to alligator population biology has been commented on by Murphy (1981) and other researchers ( ). The potential greater densities of alligators within suitable habitats, compared to any other large carnivore in the subtropical or temperate zones of the continental U.S., can be related to the variation in its diet. High densities of alligators are possible due to resource partitioning by individuals of different size classes. As diet shows a graduation of prey sizes as the alligator increases in length, the consumption of different sized prey items by overlapping size classes of alligators that comprise a population within an area, reduces intraspecific competition. Differences in habitat preferences of adult males and females, and predation avoidance behaviors of immatures, also result in habitat partitioning and a reduction in intraspecific competition (Murphy, 1981).

## Population biology and dynamics.

An alligator's maturation schedule, social and reproductive status, and susceptibility to predation, disease, as well as desiccation and cannibalism during drought, are also related to its size ( ). The rate at which an alligator grows, in terms of changes in its total length and body weight, and its reproductive performance, aggressiveness or activity levels, have been related to the types and amount of food it consumes, and conversion rates of that food to body growth. Food consumption and conversion rates of alligators have been related to several environmental factors, and to its age.

Food consumption, conversion rates, and growth in controlled, environmental conditions.

Food consumption and conversion rates to body growth of alligators in controlled, environmental conditions varied in relation to diet, the temperature and relative humidity of the immediate environment, and to age ( ). Alligators raised in controlled, environmental chambers at a constant temperature ( C) and relative humidity (90%), and fed fish vs red meat diets, demonstrated: (1) decreasing linear growth with increasing consumption of food in relation to increasing age, resulting from (2) a decreasing conversion rate of food consumed to linear growth in relation to increasing age, (3) higher food conversion rates and resulting growth (body weight) for alligators on red meat vs fish diets, and (4) accelerated growth for alligators fed intensively on fish or red meat diets while reared in constant, near optimal temperatures, compared to empirically derived growth rates of alligators in wild

populations (Figure 2). Nesting, fertility, and hatching rates, and mean clutch size for captive alligators kept in outdoor enclosures were also greater for alligators fed red meat vs. fish diets.

#### Other food consumption related factors.

Variation in food consumption capacity by volume and weight for alligators in freshwater compared to saline marsh environments has also been reported. Chabreck (1971) compared stomach capacities of 20 immature alligators taken from both a freshwater marsh (n=10) and an adjacent saltwater canal. Stomach capacities from the freshwater habitat had twice the volume and contained six times the weight of food as stomachs from the saline environment (3 to 19 ppt). He inferred that increased salinities may inhibit feeding and reduce alligator growth.

#### Growth dynamics in wild populations.

The adaptations of the American alligator to the wide variety of aquatic habitats the species occupies, from temperate to subtropical climates within its geographical range, may be best highlighted by its growth dynamics. Growth dynamics of the American alligator in wild populations have been studied in several parts of its range. Variation in the growth rates of alligators in these wild populations have been related to age, sex, season, year, and locality ( ).

Rates of growth of individual alligators in the wild may vary considerably. The amount of growth is generally related to the amount and types of food consumed. Temperature of the immediate environment, however, can also affect the amount of growth with respect to types and amounts of food eaten. Alligator feeding activities and food requirements are higher at higher body temperatures. During inactive periods with no foraging, growth stops. During active periods of low or no food intake, non-positive or even negative periods of growth can occur. When energy from food intake exceeds metabolic costs, growth may resume. (Neil, 19 ; Chabreck and Joanen, 19 ; Jacobsen and Kushlan, 198 ).

#### Size/age relationships.

Studies on the growth of American alligators in south Louisiana, south Florida, and in South and North Carolina reported decreasing linear growth rates of both males and females with increasing age ( ). These observations agree with results obtained in controlled environmental conditions of experimental studies. Growth rates between sexes of immatures did not significantly differ in wild populations of south Louisiana, until animals

attained a total length of 1.0 meter at an approximate age of 3 years, after which growth of females declined sharply. Seasonal growth rates for both sexes varied, and were greatest during the warmer and higher rainfall summer months, declining during the spring and autumn; no growth occurred in winter. Mathematical (regression) growth models indicated that growth of females again declined considerably, after age ten with the onset of sexual maturity, reaching a maximum projected length of 2.73 m at age 45. Males continued to grow fairly rapidly for the first 20 years of life (3.5 m long), and obtained a projected total length of 4.20 m at age 80 (Figure 3). Maximum lengths recorded from individuals shot or captured from wild populations have included 2.9 m for females and 6.7 m for males (Joanen and McNease, 19 ).

Relative growth patterns of alligators from Florida and the Carolinas were similar for the comparable range of sizes investigated, but average growth rates were slower, and predicted maximum body length less than that for Louisiana animals of comparable ages. Alligators in Louisiana grew at rates 2.5 to 3.3 times faster than mean growth rates of alligators in the Carolinas or the Everglades of south Florida (over the range of years compared from hatching to ten years of age (Jacobsen and Kushlan, 1989)). A comparison of predicted total length of alligators of different ages from several parts of its range is presented in Figure 4 (adapted from Jacobsen and Kushlan, 1989).

Periods of indeterminate growth (no positive linear growth and negative growth) in alligators were also reported for south Louisiana (Chabreck and Joanen, 19 ) and south Florida animals (Jacobsen and Kushlan, 19 ). The frequency of non-positive growth occurrences decreased with increasing size of animals in the south Florida population ( ). This pattern of indeterminate growth in Everglades alligators also occurred most frequently during the winter, dry season period of cooler ambient air temperatures and lower water levels for most years of the study (Jacobsen and Kushlan, 1989).

Experimental studies have demonstrated that alligators will usually stop feeding below C ( , 19 ). The increased number of days occurring during the winter months, below this minimum temperature for feeding, would therefore affect feeding activity and resultant growth rates. The slower growth of alligators during the winter period may also be related to other factors besides temperature that influence foraging behaviors of alligators (Coulson and Hernandez, 19 ).....(Neil and circadian rhythms as an adaptative trait to seasonal changes in temperature).

The slower growth of alligators reported for the Carolinas would be expected of ectothermic animals in the northern

parts of their geographic range, where the number of suitable growing months each year is less than that for individuals in more southern parts. Growth rates in these more northern populations, in fact, did not vary appreciably from Louisiana alligators, when compared with respect to sizes reached in relation to cumulative number of growing months available per locality. Alligators in North Carolina reached a total length of 6 feet in 72 - 76 growing months, compared to 72 growing months for Louisiana alligators to reach this same size (Joanen and McNease, 198 ).

Growth rates of Everglades alligators in the southernmost part of the species range, however, were similar to those of alligators in its northernmost range parts, with similar sizes reached at comparable ages, even though the number of suitable growing months based on temperature is greater in the subtropical latitudes of the Everglades. Jacobsen and Kushlan (1989) suggested that higher metabolic costs associated with warmer environments (Parks, 1983) and a lower food base in the Everglades were responsible for the slower growth, i.e. increased metabolic costs that cannot be offset by increased energy intake accounted for the lowered growth rates reported for Everglades alligators. ~~The Everglades alligator population appears to be more food-limited than populations elsewhere in its range.~~

#### Maturation schedule.

The onset of sexual maturity in alligators for distinct populations appears " to depend primarily on size, which reflects environmental factors such as temperature and the availability of food, both of which influence the growth rate. Other factors may also influence the onset of sexual maturity, including age, genetic differences between isolated populations, and the ratio of body fat to protein (Webb et al, 1983)" (Ferguson, 1985). Sexual maturity for female alligators in south Louisiana, the Carolinas, and Georgia occurs at approximately 1.8 m in total body length, after which growth declines considerably. Because the number of growing months for alligators varies in these different range parts, the age of sexual maturity for alligators in these populations also varies, requiring 72 growing months or 10 years in Louisiana (with 7 growing months per year), to 72 -76 growing months or 18 -19 years in North Carolina (with approximately 4 growing months per year), at the northern extremity of the alligator's range (Joanen and McNease, 19 ).

The duration of winter temperatures appears to be the single most important environmental variable influencing growth in these populations, and therefore the approximate age at onset of sexual maturity (Ferguson, 1985). In the Everglades, where other environmental factors appear to more regulate growth, female alligators appear to reach sexual

maturity and breed at smaller body sizes than that reported elsewhere in the species range, and at an older age (15 years) than other southern populations (Jacobsen and Kushlan, 198 ; Fleming, pers. observations).

Murphy (198 ) has suggested that a minimum body mass for alligators may be required before the onset of sexual maturity. This minimum size would be required before an animal can sufficiently thermoregulate its internal body temperature, during the cooler, spring months of each year (March -early April), to that required for normal, early follicle development in adult females and for initiation of spermatogenesis in adult males each spring. Insufficient body size and the failure to maintain an adequate body temperature at this time may prohibit the successful, early development of follicles in adult females and the viability of sperm in adult males. The size at which sexual maturity occurs for alligators in wild populations also appears to correlate with the average or maximum body size obtained from normal growth rates (Ferguson, 1985).

Alligators in the warmer environment of the Everglades, therefore, although reaching sexual maturity at a later age than other southern populations (as a result of a slower mean growth rate, regulated less by the range and duration of winter temperatures and more by apparent energy constraints), could still reach sexual maturity at a smaller, mean body size than that reported for more northern populations. In northern populations, a greater minimum body size for sexual maturity would be required if body mass is critical for the onset of sexual maturity, in relation to the range and duration of lower winter, and subsequent, cooler spring temperatures, that normally prevail at more northern latitudes.

An hypothesis is reviewed in the Discussion section of this paper concerning the differential growth rates of the sexes in relation to differences in the environmental grain and the stability of trophic resources between male and female preferred habitats versus the different reproductive roles and related behaviors and movement patterns of adult males and females in a population, particularly in a warmer, but less productive and more fluctuating (unstable) environment (of the Everglades).

#### Average life spans and longevity.

Present wild alligator populations appear to have few individuals in the oldest age classes that once characterized preharvested populations of the early 1800s, nearly two centuries ago. Due to intensive commercial hunting, average life spans of adult alligators in most populations today appear to be reduced from that obtained in former times. Alligators in captivity have lived up to 35

years for females and up to 50 years for males ( 19 ). During the early 1900s, large individuals shot from wild populations ranged up to 6.7 m in total body length (Joanen and McNease, 19 ). Few alligators in these size classes have been harvested from wild populations during more recent times.

#### Sex ratios.

The number of newborn young in alligator populations each year varies in relation to a wide variety of factors (see Reproductive Biology, Nesting Biology, and New Data sections). The sex ratio of these hatchlings, however, has been related to the role of nest incubation temperature in the sex determination of developing embryos, resulting in biased sex ratios of hatchlings in relation to nest site and related nest temperature characteristics (see Nesting Biology). The sex ratio of hatchlings from a wild population in south Louisiana averaged 83 to 17% females to males over a four consecutive year period (Ferguson and Joanen, 1982, 1983). Adult sex ratios for the same population, however, determined from a previous study during the spring months, when both adult male and female animals are in open water habitats, were 50 to 50 % females to males (Joanen and McNease, 19 ). Differential mortality of young females, sampling errors, or an unknown proportion of adult females remaining in densely vegetated marsh may explain the biased adult sex ratios reported (Joanen and McNease, 1970). Other studies have indicated a surplus of adult males in various alligator populations, ranging from 1.2 to 2.4:1 adult males to females (Carbonneau and Chabreck, 198 ; Chabreck, 1967; Wilkson, 1985; Hines et al, 1968; Bara, 1972; Kinler et al, 1987).

#### Natural mortality sources and survival rates.

Alligator age-specific mortality and resulting survival rates in a locality are primarily size dependent and influence population composition. Sources of natural mortality include predation, cannibalism and dessication from droughts, accidental deaths related to hurricanes, and deaths related to winter freezes, starvation, and disease. Predation and cannibalism on smaller sized alligators (hatchlings and juveniles) account for most of the mortality on populations. Survival rates of alligators are therefore primarily size dependent, reflecting the higher susceptibility of smaller alligators to these two mortality factors (Hines et al, 1968; Nichols et al, 1976; Jacobsen and Kushlan, 1984).

The major mortality factors and rates influencing alligator population structure in south Louisiana have been correlated with changes in marsh water depths ( Nickols et al, 1976). Mathematical functions representing the relationships

between mortality rates for these factors and change in marsh water depths, estimated from empirical data for south Louisiana alligator populations, are presented in Figure 5 (from Nichols et al, 1976). Annual survivorship estimates by size classes of Everglades alligators are presented in Table 3.

A comparison of size/age specific survival rates of south Louisiana alligators to estimated survival rates from a population study conducted over a five year period in the southern Everglades are presented in Table 4 (from Jacobsen and Kushlan, 1984). Although survival rates were similar for size classes between the two populations, the mean ages of Everglades alligators for each size class were significantly greater. Everglades alligators, growing at slower rates, remain at vulnerable sizes much longer than alligators in south Louisiana. The prolonged period of potential higher mortality that adult alligators experience in the Everglades due to slower growth, in the absence of compensating factors, can result in shorter average adult life spans, resultant lower fecundity (based on an increasing size/fecundity relationship and fewer adults reaching larger sizes), and subsequent reduced recruitment rates to breeding age classes for Everglades alligators, compared to other populations elsewhere in the species range with greater, seasonal growth.

#### Population composition.

The population structure resulting from the prevailing size specific survival rates estimated for south Louisiana and Everglades alligators in these studies is composed primarily of hatchlings and juvenile alligators and a small porportion of subadults and adults (Tables 5 and 6). In the age structure generated by a 20 year model simulation of the Louisiana population, hatchlings and yearlings comprised two thirds of the total population. In the Florida field study, these same age classes ranged from 44 to 87 percent of the estimated total population over the four year study period. The total number of alligators in the populations were sensitive to changes in the production and survival of young, that were related to changes in the spatial and temporal characteristics of surface water conditions, causing resulting age class oscillations in the population (Nichols et al, 1976; Jacobsen and Kushlan, 1984).

Simulation model runs for the Louisiana population that included major drydowns during the reproductive season were characterized by significantly reduced nesting effort and related low production of hatchlings, increased hatchling mortality, as well as increased rates of cannibalism on both juveniles and subadults. These drydown affects resulted in age class oscillations and wide fluctuations in total population numbers. Population responses to simulated

hurricanes (100 percent nest flooding) and drought (increased cannibalism, predation, and desiccation) demonstrated dramatic declines, in response to either poor nesting effort (drought) that resulted in low numbers of hatchlings, or to low numbers of surviving eggs or young (hurricanes and droughts). However, recovery over five year simulation runs was rapid, if water depths remained sufficient over the remaining four years of each five year simulation (Figure 6). Alligator numbers in environmentally stochastic simulations also exceeded simulations with constant water levels during some years (Figure 7).

In the Everglades field study, minimum water depths at the end of each dry season during the early reproductive season remained relatively high for most study years, and empirical estimates of total population numbers over the study period also remained relatively stable. Population fluctuations remained within approximately 2 percent of mean population levels. Fluctuations in the numbers of juveniles between some years did occur and appeared to be related to variability in nesting effort between those years and the survivorship of younger animals (Jacobsen and Kushlan, 1984). Undefined, density-dependent compensatory factors apparently regulated the stable population levels observed between these years.

The long life span of adults acted to stabilize oscillations in total numbers during Louisiana population simulation runs, but the proportion of adults in the population was still dependent on prevailing recruitment rates of immature animals into breeding age classes. The proportion of adult females in a simulated, unharvested population in the Louisiana study over a 20 year simulation was small (2.3 percent). In the Everglades field study, the estimated proportion of adult females in the population was also low, averaging approximately 5 percent over a four year period. The number of adult females actually nesting each year in the alligator population also varied in relation to undefined factors in the Everglades study. The number of nesting females each year in a population may also be limited by social behavior factors, affecting individuals in the population competing for resources of space and food in relation to changing environmental conditions.

#### Social behavior.

Alligator activities reflect a complex social system and associated individual behaviors despite the animal's inferior ability to regulate its internal body temperature. Social behaviors and signals share common characteristics with that of birds and mammals, and are the most complex of living reptiles ( ). Territorial behavior,

dominance hierarchies, courtship behaviors, and maternal care have been documented in a number of studies on distinct populations throughout the species range ( ). The social behaviors and communication signals involved in these social interactions of individuals vary by age, sex, social and reproductive status, habitat, and season of the year. ( ).

#### General.

Adult alligators occupy individual areas that vary in size within which intruders may be confronted. The intruder may be another alligator or an individual of a different species. The length of time an adult occupies an area, and the size of the area occupied, varies according to the alligator's sex and age and to seasonal changes in habitat conditions. Shifts in areas occupied can also occur as environmental conditions change, either rapidly in response to droughts or flooding events, or gradually over time in response to slower changing environmental conditions, or as the alligator grows older and becomes more efficient at exploiting available resources ( ). The types of defensive or other behaviors that may be displayed toward other individuals encountered varies according to the sex and age of conspecifics, the season of the year, or the type of threat or danger perceived by the alligator from animals of different species ( ).

For adult males, shifts in seasonal occupancy of areas within its normal activity range have been related to more restricted movements within mating and courtship areas during the reproductive season, and more wide ranging movements throughout its activity range during other times of the year (see Daily and Seasonal Movements, etc). Immatures of both sexes are allowed within general activity ranges of adult males. Antagonistic behaviors are likely, however, when close contact occurs between larger males intruding within the range already occupied by another adult male or within a male's established courtship and mating territory (Neil, 1971; , 19 ). Ritualistic behaviors are often used to establish dominance during these encounters, but actual combat, that may result in serious injury or death, may also occur ( ).

Aggression by American alligators toward conspecifics appears to be greater than that reported for other crocodilian species ( ). This increased aggressiveness may reflect greater competition for available resources in the more rigorous, temperate climates that occur over much of this species' range, compared to the greater number of warm months in tropical zones, characteristic of other crocodilian ranges ( ).

For adult females, shifts away from an established nesting area are believed to be infrequent, but may occur more frequently in younger, nesting females (Chabreck, 196 ; Neil, 1971). Shifts in selection of a nest site, however, may occur between years within an established nesting area as well as related shifts in nursery areas for brooding pods of young (Hunt and Wanatanbe, 19 ). Other adult alligators may be accepted within the general nesting area and are presumably not perceived as a threat to the newborn young (Hopson, 1977). Older and larger juveniles still remaining near the nesting site, that may threaten to eat the very young or compete with them for food, are increasingly confronted by the nesting female, become secretive, and adopt group behaviors that render them less vulnerable to predation upon dispersal from the natal site (Hopson, 1977).

During the courtship period, adult females may move to a nearby, suitable mating area within the activity range of an adult male. After courtship and mating is completed, females return to their established nesting areas (Chabreck, 19 ; Joanen and McNease, 19 ).

#### Territorial behavior and dominance hierarchies.

Territorial behavior of alligators is associated primarily with the reproductive season ( ). Territorial behavior during the reproductive season usually involves males, but has also been described in female alligators ( ). During the breeding season, males become territorial and establish a dominance hierarchy. The dominant males patrol their mating territories, usually located in open, deep water areas ( ). Other large males are excluded, but breeding groups of 6 - 8 females are allowed free movement in and out of defended territories ( ). Small, subdominant males may also be allowed to remain within these territories, but are prevented from courtship displays within the territory of a dominate male ( ).

#### Courtship behaviors.

Courtship is a mutual activity involving elaborate ritualized behaviors that may last hours and may be repeated over several days before mating occurs (Hopson, 19 ). Both sexes are capable of initiating courtship and both males and females are polygamous. Mating activity is believed restricted to open, deep water areas. During mating, females must be mounted and forcefully submerged before they will engage in copulation, and therefore are not receptive to inferior- sized males ( ). Larger females may mate before smaller sized females in the breeding group (Ferguson, 1985). After mating the sexes separate; females return to nesting areas within densely vegetated marsh areas, and males disperse, eventually to overwintering,

denning sites away from females and their young ( ).

#### Parental behavior.

Nest attendance and maternal care of newborn young are highly developed in nesting female alligators. Females remain near their nests during the incubation period in a protective role and continue to guard young throughout their first year of life. The frequency and intensity of nest defense against potential predators and human intruders varies between nesting females within a population, and also between populations in similar, but different localities.

In a study on the function of nest attendance in American alligators, Kushan (1980) concludes that "alligators can distinguish between types of potential predators and have the ability to alter their guardian behaviors under various circumstances. They appear to be able to evaluate the intruder's action during each stage of an encounter and from this experience gauge subsequent responses as well as future responses to similar intruders. Such behavioral plasticity and attendant ability to learn quickly from experience is obviously highly adaptive...Nest attendance behaviors shown by alligators in nature appear to balance benefits in increased reproductive output with potential costs of adult injury to achieve appropriate responses to potential predators...The response of an attending female ( may) include an ordered sequence of up to ten progressively more agonistic behaviors that may terminate in an attack. Attending alligators respond differently to various potential predators depending in part on the intensity of the threat. Several factors, especially experience, modulate the response and determine the behavior of individual alligators."

Although the frequency and intensity of nest defensive behaviors may vary between individuals and populations, most, if not all, nesting females tend their nests during the incubation period ( ). Hatching of eggs within a nest may be synchronized by vocalization of the young while still in the egg (see Nesting Biology). These vocalizations of the young also illicit nest opening behaviors in attendant females. Nests may be opened by the female either by mounting the nest and scraping away top layers of nest material by using her forefeet, or by tearing away a wedge shape section from one side of the nest by biting actions ( ). Hatchlings may be carried in the female's mouth from the nest to grassy, open-water nursery areas up to m away ( ). Eggs still in various stages of hatching may also be grasped by the female and manipulated within her mouth to assist hatching young from the egg (Kushlan, 19 ). Non-viable, unhatched eggs are frequently eaten by the female (

). Egg-eating by females allows an adult to recover energy and nutrients of nonviable eggs and may also decrease the likelihood of attracting predators that stay near the nest site (Kushlan and Simon, 1981).

Maternal behavior, however, does not terminate with hatching. The post-hatching period appears to initiate a complex relationship between mother and offspring in many crocodilian species. After emerging from the egg, most offspring of alligators remain close to the female for the first year and sometimes into the second or even third year. Mixing of these different size classes of young can result in competition between hatchlings and juveniles for food and maternal care that inversely affects survival of hatchlings. Cannibalism may also occur. Aggressive behaviors toward these older offspring by the female assist in reducing this potential competition. A female may pursue such offspring, or other unknown juveniles in the immediate area and, if caught, hold them in the mouth for a period of time before releasing them unharmed. Older offspring soon become wary of the female, inhibiting their feeding and or movement near hatchlings, and eventually disperse from the nursery and brooding area (Hunt and Watanabe, 1982).

#### Antagonistic behavior and mortality.

Under normal environmental conditions, the social behavior system of alligators, the different habitat preferences of sex and age classes, and the variation in diet of alligators of different sizes, allow large numbers of alligators to occupy shared habitats through partitioning of the available food and space in a locality. During extreme drydown events, however, many alligators are forced to disperse from normal activity ranges within interior, natural marsh habitats and concentrate in high densities in deep water, drought refugia, i.e. unnatural canals, deep water ponds, and in tidal creeks, rivers, pools, and bays. These areas may also undergo drying if the duration of a drought is prolonged. This concentration of alligators in high densities within confined areas, and the inevitable crowding of individuals as a result, often leads to both induced antagonistic behaviors, and an insufficient food supply. High mortality can result from both conditions, resulting in lethal combat between large individuals, and cannibalism by larger sized individuals feeding on smaller alligators (Nichols et al, 1976; Fleming, pers. observ.).

#### Social signals and communication.

Visual signals and/or vocalizations are an important aspect of alligator social behavior from hatchling to adult ( ). When the young are ready to hatch, vocalization from within the egg helps to synchronize hatching (Lee, 1968) and stimulates attendant females to open the nest. Aggregation

and group vocalizations by hatchlings also illicit behaviors by adults that ensure protection during a stage in life when the offspring are small and most vulnerable to predation. Frequent vocalizations occur among young and between young and the adult parent ( ). Disturbance or threats by older offspring toward hatchlings elicit distress calls from the hatchlings and aggressive responses from parent females toward the older young. Other adults may also respond to distress calls of small young ( ). These observations have been suggested to demonstrate an adaptive basis for age-related behaviors of crocodilians (Hopson 1977).

Social signals or signaling behavior of adult alligators include up to eighteen behaviors: eight visual, six vocal, four nonvocal acoustic signals, and composite signals involving elements from all three modalities. The signals vary in their frequency of occurrence, conspicuousness, complexity, and by time of the day and season of the year. Communication over long distances is accomplished by acoustic signals. Visual signals are used more frequently at shorter distances between alligators. The selection of which types of signals are used has been related to several factors: vocal adaptations to the structural characteristics of habitat types occupied (open grassland or more obstructed forested habitat, while on land or in/under water) in relation to the attenuation characteristics of acoustic signals used, the locatability of the signal (in relation to loudness, direction, and time of arrival from the sender to a conspecific), and the purpose or function of the signal. Most signals are given by both sexes ( ).

Long distance signaling is accomplished by two behaviors - bellowing and headslapping, which may carry at least 150 m. Bellowing presumably functions to signal other alligators during the formation of breeding groups, while headslapping and bellowing are both used for advertisement during courtship once the breeding group is formed. Bellowing choruses across the marsh frequently occur during the spring courtship and mating periods, but bellowing may also occur at other times of the year. Bellowing may therefore serve to synchronize reproductive activities. Other acoustic signals, used at shorter distances, include: bellow growl, low growls, coughs, and a hiss. A summary of alligator vocal elements, their physical characteristics, stimulus situation, and probable functions are presented in Table 7 (Garrick et al, 1978).

Visual signals are commonly used for short distance communication and involve movements, postures (which expose variable parts of the body above the water surface), and vibration of body parts. Visual signals include: yawning (to attract other alligators), narial geysering (a precopulatory behavior), submergence (an antisocial

behavior), slimming posture (used to signal assertiveness and as a challenge to a conspecific), tail wagging (used during agnostic situations), head emergent tail arched posture (to signal alertness and readiness to defend territory or nest), inflated posture (a threatening display), and snout lifting (a submissive or conciliatory signal if given in the water). Nonvocal acoustic signals include: inaudible bellow (courtship advertisement), headslapping (to signal presence and location, and promote approach of potential mates to the headslapper), jaw clapping (an element of headslapping also used during interspecific encounters and as a response to the approach of an intruder in the water), and splashing (to emphasize presence). The interrelations among the postural elements of these alligator signaling behaviors is depicted in Figure 8 (Garrick et al, 1978).

As alligators are semi-aquatic, the majority of these visual, acoustic, and nonaudible acoustic signals occur in water. Visual signals include body postures that are modified by increasing or decreasing surface area through inflation of the body or are adjusted by the amount of body surface exposed above the water. Some acoustic signals are transmitted simultaneously through both air and water. Exploiting aquatic communication through signals that carry both in air and water permit alligators to remain concealed and still receive signals through water. Physical advantages of also communicating through the water are the faster speed of sound waves (four times) and greatly increased sound pressures (sixty times) possible in water than in air. The advantage in the use of these types of social signals by alligators is that they may communicate while remaining in water, and the relative safety that affords individuals of this species (Garrick et al, 1978).

The signaling capacity of the alligator communication system reflects its complex social system. Vocal, nonvocal acoustic, and visual elements are similar between alligators and other species of crocodilians which share a common, conservative evolutionary history, but major differences exist between species in the organization of crocodilian signaling systems. Alligator habitat requirements for densely vegetated marsh areas (see Movements) appear to have favored the selection and use of more acoustically than visually conspicuous signals. Purely visual signals are used during close range social contact. The signaling system organization of other crocodilian species which occupy more open habitats are not as vocal as that of the alligator (Garrick et al, 1978).

The reliance on ectothermy by crocodilians in their evolution did not constrain their development of complex social and parallel communication systems, such as that describe above for the alligator. Alligator social and

communication systems share common characteristics with those of birds and mammals. Shared characteristic's of the alligator's signaling system with that of birds and mammals include: (1) the same signal can be used in many contexts, i.e. different meaning to conspecifics dependent upon the season, sex and/or age of the sender, (2) signal elements may be combined in a different order around a basic signal creating a display, i.e. to signal behavioral tendencies or preferences of the sender to conspecifics, and (3) signals may serve to identify individuals, i.e. in the location of possible breeding partners, the choice of mates within breeding groups, the calling of young to the mother or the mother calling the young towards her, etc. The complexity of the alligator social system, and related social signals or behaviors necessitated by this social complexity, also demonstrate the behavioral plasticity or adaptativeness of this species that occurs over a wide range of aquatic habitats and climatic conditions. (Garrick et al, 1978).

## Reproductive biology.

### General.

The basic reproductive biology, as well as the embryology and development chronology of the American alligator, have been studied in several populations within its geographic range (Chabreck, 19 ; Joanen and McNease, 19 ; Hines et al, 19 ; Ferguson, 1985; Grabowski et al, 19 ; ). No significant differences have been observed in these life history aspects between the distinct populations studied. Factors affecting sexual maturity, adult sex ratios, and courtship behavior in wild populations of American alligators have been reviewed in previous sections (see Population Biology and Dynamics, Social Behavior). A chronology of the American alligator's reproductive biology is summarized in Figure 9. The reproductive and nesting biology of alligators have been reviewed in detail by Ferguson (1985). A summary of his review is presented in this section and the following section on Nesting Biology.

### Spermatogenesis.

During February, preceding the courtship period in early spring, testes of adult males start to enlarge and are 11 - 12 times larger by April/May from smallest size occurring during the previous September. Spermatogenesis is advanced by March but mature sperm do not appear in the reproductive tract until late April/early May. Living sperm first appear in the penial groove in early May and are present for a six week period, with maximum production during a 2 week period in late May/early June, coincident with female ovulation. Sperm production varies significantly among reproductive

size classes (1.8 m and above), with large males (over 2.7 m) producing living spermatozoa for a longer time period than smaller males. Ferguson postulated that this reproductive superiority of large bulls may explain why social order in the American alligator favors breeding by males over 2.8 m in length.

Ferguson states that " testicular regression begins in mid - June and is complete by the end of July; testicular weights remain low for the rest of the year. No evidence exists for over winter sperm storage in males. Immature males show no discernable seasonal change in testicular weight, size, thickness, and convolution of the ductus deferens, and have extremely low levels of plasma testosterone...Plasma testosterone levels show a similar seasonal fluctuation to that observed for testicular weight with a peak of 90 ng/ml in April/May (Lance, 1983, 1984) and rapidly decreasing thereafter. The association of elevated testosterone levels with the peak of testicular weight, spermatogenic activity, bellowing intensity, and mating behavior suggests that these functions are androgen dependent...The mechanism initiating gonadal regression is unknown...(and) occurs at a time when temperature and photoperiod appear to be optimal...The plasma testosterone rises slightly in September, when the alligator testes are fully regressed (Lance, 1983). This is difficult to explain, (for) it does not coincide with mating behavior, spermiogenesis or renewed spermatogenesis. The profile is, however, typical of postnuptial spermatogenic cycles (Lance, 1983) and may represent the curtaining of another breeding cycle imposed by the climatic habitat of Alligator mississippiensis, the most northerly ranging crocodilian".

#### Ovulation.

The reproductive system of females also exhibits seasonal variation. In his review of the reproductive events in female alligators, Ferguson states " each ovary contains at least three size classes of follicles: <1mm, 1 - 4 mm, and the crop of preovulatory follicles of the current year, which range from 5 - 45 mm in diameter (Joanen and McNease, 1980; Lance, 1983)...Vitellogenesis (yolk formation) begins in early spring: the 4 - 5 mm follicles grow to about 20 mm by early April, reach 30 mm by early May, and reach a preovulatory diameter of 40 - 45 mm by late May/early June (Lance, 1983; Joanen and McNease, 1980; Giles and Childs, 1949). Developing follicles protrude from the surface of the ovary and are shed through a small opening directly into the...oviduct (Lance, 1983). The time of ovulation varies from year to year depending upon ambient air temperatures during March - May (Joanen and McNease, 1979b). Ovulation usually occurs during the first week in June and shelled eggs appear in the lower end of the oviduct from the second through the last week in June (Joanen and McNease, 1975a, b,

1980; Giles and Child, 1949). Oviposition usually occurs between June 11 to 28 (range June 5 to July 5), and normally it takes two weeks for the entire female population to oviposit (Joanen and McNease, 1980). Following ovulation, the follicle forms a corpus luteum...Whether these corpora lutea are functional is unknown (Lance, 1983). It probably takes 3 years for a differentiated oocyte (immature egg) to grow to a preovulatory diameter. The numbers undergoing atresia (regression) during this period are unknown, but most follicles that reach preovulatory size are ovulated (Lance, 1983)".

"Plasma estradiol levels in females mirror the trends seen for testosterone in males with a peak of approximately 700 pg/ml in early april - the time of preovulatory follicular development and vitellogenesis (Lance, 1983). Plasma from reproducing females in April ...has elevated levels of calcium, magnesium, zinc, iron, total protein, cholesterol, vitamin E, and estradiol - 17B (Lance et al., 1983). These levels correlate with the time of preovulatory follicular development and vitellogenesis, and they return to normal by July (Lance et al., 1983)...As in other oviparous vertebrates, alligator vitellogenesis is probably oestrogen dependent. Estradiol, secreted by the growing ovarian follicles, stimulates the liver to synthesize and secrete vitellogenin (yolk precursor protein), which passes via the blood to the ovary where it is taken up by the follicles (Lance, 1983)...The oviduct is also stimulated by ovarian oestrogen and hypertrophies during the follicular growth phase (Lance, 1983). After oviposition, plasma estradiol levels remain low to nondetectable, and there is no evidence for a prehibernation onset of vitellogenesis (Lance, 1983)" (Ferguson, 1985).

"Nonbreeding females have low to nondetectable estradiol levels (Lance, 1983) and show no evidence of follicular growth (Joanen and McNease, 1980). Likewise, immature females have low estradiol levels and small ovaries...Reproductively senescent or "barren" females (usually over 2.7 m in length) have few growing oocytes, no corpora lutea...and their ovaries frequently contain medium-sized resorbing ovarian follicles and retained oviducal eggs undergoing resorption...The occurrence of senescence in the Crocodilia suggests that there is a limit on the number of oocytes a female can produce, despite the fact that oogonial proliferation ( ) continues throughout much of adulthood" (Ferguson, 1985).

The environmental factors that trigger reproductive behavior, spermatogenesis, ovulation, and egg laying in crocodilians are not well understood. A significant relationship has been determined between peak nesting and average, ambient spring-air temperatures (Joanen and McNease, 1979b; Kushlan and Kushlan, 198 ). Nesting occurs

earliest when spring temperatures are highest. Rainfall has been reported as significant only when nesting effort is reduced during extreme times of drought or high water. However, possible correlations between breeding times and changing water levels have also been reported ( ). Nest construction and oviposition occurs during the time of year when photoperiod is longest while temperature appears to regulate male and female reproductive cycles. The hierarchical order of these extrinsic regulating factors, how alligators perceive changes in these variables, or the physical mechanisms controlling their responses are unknown (Ferguson, 1985).

The hormonal regulation of the alligator reproductive cycle is also poorly understood. No data are available on circulating levels of gonadotropins or follicle stimulating hormones...but glycoproteins similar in molecular weight and amino acid composition to mammalian follicle stimulating hormone (FSH) and luteinizing hormone (LH) have been isolated in the pituitaries of alligators. Irregular reproductive cycles of females in wild populations have been reported, characterized by a variable proportion of adult female alligators nesting each year, and variable intervals between successive nesting of individual females. The operant mechanisms influencing the reproductive cycle are unclear, and may involve metabolic end products either stimulating or inhibiting the endocrine system, behavioral responses to environmental conditions, or genetically determined periodicities in ovulation (Ferguson, 1985).

#### Copulation, fertilization, and egg laying.

Copulation is preceded by an elaborate set of ritualized behaviors. The time period over which these behaviors may occur between a mating pair may last up to two weeks (Joanen and McNease, 1970). Both males and females are polygamous, as multiple matings with different individuals by both sexes may occur within a reproductive season (Chabreck, 1965).

The interval between insemination and egg laying has been reported as three to four weeks in the American alligator (Joanen and McNease, 1975, 1979, 1980; Lance, 1983), but appears to vary widely among crocodilian species (Ferguson, 1985). Sperm can remain viable within the female reproductive tract of American alligators for up to three weeks (Cardielac, per. comm.). A prolonged interval between copulation/ovulation and egg laying may have adaptive advantages for crocodilians that range over a wide variety of aquatic systems and climatic conditions (Webb et al, 1983). During the time interval between copulation and egg laying, sperm storage in the female and delayed fertilization (and)/or a very slow rate of embryonic development may occur while the eggs are still in the oviduct (embryonic hibernation) (Ferguson, 1985).

Variable stages of embryonic development at egg laying, and egg retention within the body of females during adverse environmental conditions (drought, flooding, temperature variations), have also been reported for the American alligator ( ). Female alligators kept in artificial pens with high stocking densities have also exhibited elevated plasma levels of corticosteroids that inhibited ovulation and/or caused egg retention, and thus delayed egg laying (Ferguson, 1983). The interval of time over which eggs can be retained, the rate of embryonic development during this period compared to the "normal" rate within the nest, and whether egg retention affects the viability of the embryo are all unknown (Ferguson, 1985).

#### Nesting biology.

##### Nest construction.

Some crocodilians construct mound-like nests out of vegetation while others dig holes in the ground into which a clutch of eggs is laid (Ferguson, 1985). No well documented occurrences of both nest construction strategies occurring naturally in the same species have been recorded; species-specific nest construction behavior is maintained even in sympatric species (Ferguson, 1985).

The American alligator builds nests constructed from vegetation at the nest site. In the Everglades, nest are less than one meter high ( $65.0 \pm 13.1$  cm;  $n = 213$ ). Attendent females may add additional material to the nest top, but the elevation of the eggs relative to the ground remains unchanged. Compaction and dispersion of nest material after nest construction is not significant for most years (Kushlan and Jacobsen, 1990).

##### Clutch size and age specific fecundity.

Eggs are normally laid during the night or early morning. The female positions her cloaca over an opening in the nest top leading to an egg cavity within the center of the nest, and deposits the entire clutch at one time. Eggs within a clutch are all at comparable stages of development at the time of laying. A significant but highly variable correlation exists between the number of eggs per clutch and body length (age) of the laying female. Maternal age and egg size and egg quality are also related. "Middle-age" females lay more eggs per clutch, and egg size and quality are also greater compared to younger or older aged nesting females. Older females have smaller clutch sizes and more malformed embryos. Young nesting females lay smaller clutches with smaller eggs of inferior quality. Older

females generally lay their eggs earlier in the season than middle aged females which in turn lay earlier than the young females. This temporal progression of egg laying within a season by age of females is consistent with observations of alligator social hierarchy during the mating season. Larger females usually mate earlier with larger males than smaller females (mating with either large or small males). Thus heavier eggs are produced early in the nesting season and light eggs near the end of the season (Ferguson, 1985).

#### Egg fertility and rate of embryonic mortality.

For the American alligator and several other crocodilian species, weight of the eggs is positively correlated with that of hatchlings (Staton and Dixon, 1977; Deitz and Hines, 1980; Webb et al, 1983b, e). Small light eggs laid by young females often result in fetuses of low birth weight with malformations (Ferguson, 198 ). Ferguson (198 ) listed factors that may determine the relationships of egg fertility and rate of embryonic malformation with maternal age of nesting females: (1) reduced ovulation of young and old females, (2) the immaturity of ova in smaller sized females, (3) slight asynchrony between the times of ovulation and copulation in young females, (4) the lower sperm numbers and quality in males near the end of the breeding cycle (when young females mate), and (5) the poorer quality of the large ova released by old females. He also felt that prior to senescence old females either resorb their ova or their eggs, or both, and that young and very old females may contribute little to population recruitment.

Nest temperature and humidity for embryo survival, development, growth, and sex determination.

Nest temperature and humidity are significant factors affecting embryonic survival, development, growth, and sex determination in the American alligator. Nest site selection and construction generally ensure stable thermal and humidity conditions within the egg cavity (Ferguson, 1985).

Primary heat sources for alligator nests include solar heating, decomposition, and embryonic metabolism. Some of the solar heat absorbed in the outer layers of the nest is dissipated to the central egg cavity. Mean nest temperatures, however, are usually 1 - 5 C above the mean air temperature ( ). Additional increases in nest temperature result from decomposition of the nesting vegetation. This source of heat is greatest during the early stages of incubation, and declines during the latter stages. Urination on the nest by females during and after its construction also enhances nest decomposition

and related heating. Embryonic metabolism may also provide a source of heat. Peak weight-specific metabolic rates of other developing crocodilian embryos have been recorded during the early/middle periods of incubation. Temperature rises in nests of American alligators appear to reflect this source of metabolic heat as nests are also warmer during the early/middle incubation period ( ).

Maintenance of nest humidity is also essential for successful embryonic development. The mechanisms for maintaining nest humidity, however, have not been clearly defined. Urination and splashing of the nest by attendant females, as reported in the literature ( ), may indicate that such females are able to monitor nest temperature/humidity through sensory receptors on the jaws (Ferguson, 1979, 1981, 1982). Rainfall and diffusion of marsh water into nests also assist in maintaining nest humidity.

Nest temperatures and humidity outside normal ranges can cause malformed or dead embryos. Incubation temperatures of alligator eggs at 30 to 32 °C produce the highest hatching success (Joanen and McNease, 1977, 1979, 1980, 1981; Ferguson and Joanen, 1982, 1983). Incubation temperatures above or below this optimal range produce lower hatching rates and hatchlings with balance and neuromuscular control problems and other abnormalities resulting in eventual death ( ). Changes in nest humidity may also affect crocodilian eggs and developing embryos. Low levels of humidity dry out the egg shell membrane, killing the embryo. Optimum relative humidities for incubating American alligator eggs ranges from 90 to 92% (Chabreck, 1975; Joanen and McNease, 1977, 1979). At suboptimal humidities, abnormal air sacs form in the egg due to cleavage of the shell membrane away from the calcified eggshell, causing embryonic death if the air space is large. During hot dry years or droughts, this source of egg mortality can be significant, particularly among eggs near the top of alligator nests. Water uptake in crocodilian eggs is considered either essential for normal embryonic development ( ) or as a maintenance source for water gain against lethal levels of water stress during adverse environmental conditions later in the development period ( ). The hydric environment of crocodilian eggs may also influence the sexual differentiation of developing embryos (Ferguson, 198 ).

Data on temperature dependent sex determination in several crocodilian species, including the American alligator, indicate that incubation temperature also determines the sex of hatchlings, and thus adults (Ferguson and Joanen, 1982, 1983; Webb et al, 1983; Webb and Smith, 1984). The apparent lack of heteromorphic sex chromosomes in crocodilian species studied to date makes it likely that all crocodilian species

may have temperature dependent mechanism for sex determination (Ferguson, 1985).

American alligator embryos undergo three phases of gonadal formation: the period of genital ridge formation, the period of bisexuality, and the period of visible sex differentiation. The temperature sensitive period (TSP) for sex determination during incubation is variable, with the TSP between 14 and 21 days (occurring during development stages 13 - 16 out of 28 developmental stages) if egg incubation temperature is shifted from 30 to 34 C, and a TSP between 28 to 35 days (stages 20 - 21) if egg temperatures are shifted from 34 to 30 C. Cooler incubation temperatures act earlier and more rapidly in determining sex. Egg incubation temperature prior to the TSP also influences sex determination but not irreversibly. Higher (run in) temperatures also delays the TSP and embryos remain sexually labile for much longer. Incubation of eggs at 34 C produces only males, while incubation at 30 C or below produces only females. The sex ratio is approximately equal at 31 C, and highly variable at 32 C. Temperature sex determination, however, may correlate with gonadal size-dependent sex determination, which may be a more accurate description of the actual, underlying biological processes (Ferguson, 1985).

Nest site and related nest temperature characteristics and sex ratios of hatchlings at nest sites have been studied in a wild population of American alligators in south Louisiana. Natural nests constructed on levee berms were hotter and produced more males than nests constructed in wet marsh, the preferred habitat of females. Females hatched from eggs at lower incubation temperatures ( $\leq 30$  C) also weighed significantly more than males hatched from eggs incubated at higher temperatures (34 C). The authors hypothesized that this weight difference may constitute a selective evolutionary advantage of temperature-dependent sex determination (TSD) in alligators in that females become large and sexually mature as early as possible.

Additional selective advantages hypothesized included reduced predation risk for being a larger, faster growing female in natural marsh (during the first several years in which an alligator is at a vulnerable size), or a smaller male in the open water. The correlation between the geographical location of male and female producing nests to the preferred habitat of adult males and females was also proposed as another selective advantage of TSD, reducing predation risks further by neither males nor females having to move great distances from "unsuitable" natal sites to the preferred adult habitat (Ferguson and Joanen, 1982).

## Nest flooding and other sources of egg mortality.

Flooding of crocodilian nests also causes embryonic death. An experimental study on simulated flooding affects on hatchability of American alligator eggs, by immersing eggs for different time periods, demonstrated: (1) immersing eggs of any age for single periods of two to six hours had no significant affect on hatchability, nor on eggs submerged for 12 hours if done before day 30 after laying; thereafter, (2) 12 hour submergence killed all embryos and (3) 48 hour submergence killed all embryos at all ages (Joanen et al, 1977). Moisture on the surfaces of crocodilian egg shells greatly reduced their gas conductance and may have totally inhibited oxygen diffusion. Flooding, therefore, inhibits gaseous diffusion and may cause embryonic death, depending on the duration of flooding and the embryo age. Embryos utilize air within the eggshell and so can withstand short periods of flooding; older embryos have higher O<sub>2</sub> requirements, and relatively less air within the eggshell, and therefore cannot withstand as long a period of flooding, as younger embryos (Ferguson, 1985).

The significance of nest flooding on the reproductive success of the American alligator in the Everglades has been investigated in several studies (Hihes et al, 196 ; Nichols et al, 1976; Kushlan and Jacobsen, 1990). Kushlan and Jacobsen (1990) reported a positive correlation between water level at the time of egg laying and height of deposited egg clutches. Egg losses from nest flooding during the study period were related to clutch height above water level at the time of egg laying and subsequent water depth increases during the incubation period.

Regression models were used to estimate the extent of nest flooding over a 30 year period. Prior to water management, the increment of water level rise during the incubation period was predictably correlated with water level at the time of nesting. Water level rise during the incubation period seldom exceeded the height (15 cm.) egg clutches were laid above prevailing spring, water levels at the time of nest construction and egg laying. This predictably disappeared concurrent with the institution of water management in the southern Everglades. Estimated annual nest flooding loss prior to the implementation of water management averaged 4 +/- 4.5%. From 1971 - 1982 during the study period, annual nest flooding losses increased five fold, averaging 20 +/- 32.8 % loss. Present annual rates of nest flooding still remain unnaturally high (see New Data).

The historical pattern of nest flooding and its impacts on alligator reproductive success have been dramatically altered under recent water management. The loss of natural predictability in the hydrological regime of the southern

Everglades has created an additional loss to the annual production of an alligator population already characterized by a smaller, average clutch size (25% lower) and reduced nesting effort (50%) in the naturally fluctuating environment of the Everglades, compared to other alligator populations with higher baseline reproductive potentials (greater clutch size and nesting effort) inhabiting other wetlands (Kushlan and Jacobsen, 1990).

Other sources of egg loss also occur during the incubation period. Predation and the inversion of eggs during egg laying can result in additional, significant losses. Although high egg loss due to predation has been reported for other alligator populations, ranging from 16.5 % in south Louisiana and 56.3% in north Florida to 86.4 % in Georgia ( ), egg loss to predation in the Everglades is relatively low (less than 5 %). A higher occurrence of nest guarding by females in the Everglades (Kushlan and Kushlan, 1979), the remote location of most nests away from upland areas or edge slough habitats , and an apparent lower number of potential predators on alligator eggs may explain the low predation rate.

Death or malformation of embryos may also result if the long axis of the egg during egg deposition is at right angles to the nest base, i.e. eggs laid upright. Ferguson (1983) hypothesized that " the death of embryos following egg inversion may explain why viviparity never evolved in the Crocodilia...During the evolution of viviparity, there is usually an intermediate stage in which the embryo develops inside an egg retained within the oviducts of the female. However, in taxa in which the embryo attaches to the shell membrane and turning or inversion result in embryonic death (as in Crocodilia), this intermediate stage is unlikely to be achieved. The absence of crocodilian viviparity may also be related to increased dependence of embryos on eggshell calcium as compared to the very slight dependence of snakes and lizards (Packard et al, 1977), the absence of biological advantages for prolonged egg retention, and the evolution of nest guarding (Tinkle and Gibbons, 1977)."

#### Hatching.

The mechanics of hatching are similar in all crocodilians. Growth and movement of the developing embryo strain the eggshell, which has already been weakened by the embryo's mobilization of eggshell calcium and extrinsic degradation through bacterial action, until longitudinal cracks develop during the seventh week of incubation, followed by diagonal cracks, and shell flaking just prior to hatching. The embryo later punctures surrounding extraembryonic and shell membranes with a "caruncle", thereby opening the egg (Ferguson, 1985).

Hatching triggers may involve mechanical stimuli and vocalizations. Growth and movement of the embryo bursting the eggshell, increasing levels of waste products, decreasing egg water, the progressive inadequacy of gas exchange, and temperature increases may also stimulate hatching. The hatchling has a distended abdomen full of absorbed yolk that serves as a food supply for the first few weeks until the hatchling begins feeding on small-sized prey within the nesting site (Ferguson, 1985).

#### Nest site selection.

Nest temperature and humidity affects on embryonic development and survival, susceptibility of eggs to flooding and eggs and hatchlings to predation, as well as the sex determination of hatchlings, are all correlated to the nesting site selected by a female. Ferguson (1985) has reviewed the complexity of factors that influence the site selected by females for nest construction and identified several probable factors, including: social interactions with other animals, soil and vegetation characteristics at the nest site, proximity of the site to water, site temperature, degree exposure to sunlight, and height of the site above water level. Although the affect of many of these factors on nest site selection are not well understood, he pointed out that nest site selection is of an immediate importance to a population's fecundity, crocodilian reproductive strategies, and the role of incubation temperature in determining sex ratios of hatchlings.

#### New Data.

##### Introduction.

Continuing declines in higher order, consumer populations within the remaining natural areas of the Everglades have raised wide public concern, particularly for population declines within the downstream reaches of the system included within Everglades National Park (ENP). In response to these declines, an experimental water delivery program to the Park was initiated in 1983. In 1985, the National Park Service (NPS) also initiated an additional series of studies to document and investigate the impacts of these experimental water deliveries on key faunal components of the system, concurrent with other ongoing ecological and hydrological studies and evaluations. These additional studies focused on environmental factors influencing the distribution and abundance of selected keystone and indicator species populations within the central and southern Everglades (Fleming, 1986).

The American alligator, as a keystone species of the system, was included for study. Past research on the alligator in the Everglades and within other geographic populations has demonstrated the sensitivity of alligator population stability to changes in the annual production and survival of young (Nichols et al, 1976; Jacobsen and Kushlan, 1984). Within ENP, recent downstream water management regulation has adversely impacted the reproductive success of nesting alligators, particularly with respect to high egg losses during the late incubation period, resulting from above normal levels of nest flooding (Kushlan and Jacobsen, 1990). A study was therefore initiated in 1985, concurrent with implementation of new rainfall-based, experimental water deliveries to ENP, to continue and expand the NPS's past research efforts on alligator reproductive ecology within the southern Everglades.

Objectives of the study were: (1) to document annual nest abundance patterns and hatching success, (2) to identify and investigate environmental correlates influencing changing nest abundance and egg mortality patterns observed, (3) to relate these findings to experimental, water delivery characteristics, where appropriate, and (4) to provide baseline data for assessment of future water delivery scenarios, as well as (5) to identify hydrobiological relationships for inclusion within an alligator population simulation model, developed for testing hypotheses concerning alligator population stability in relation to changes in the Everglades hydrologic regime.

#### Study Area.

The study area selected (Figure 10) included approximately 1,104 square kilometers (110,400 ha.) of wet prairie and slough marshes comprising the major central flowway of the southern Everglades, Shark Slough (SS). The flowway or slough represents the highest occupancy area of nesting females within the post-drainage, southern Everglades landscape. Previous NPS alligator research was also conducted within this study area (Jacobsen and Kushlan, 1984, 198 ; Kushlan and Jacobsen, 1990).

The slough is bordered on the east by overdrained, high, dry prairie rockland marshes, to the south and west by fresh to slightly brackish mangrove estuaries, to the northwest by a dry prairie rock ridge, and to the north by impounded wet prairie and slough marshes comprising the water conservation areas (WCAs) or impoundments of the central and northern Everglades (Figure 11). Eroded, limestone bedrock underlying the central slough is overlain with muck deposits, graduating to shorter hydroperiod marls along the slough edges. Marl deposits also occur within eroded, bedrock depressions of the dry prairie, rockland marshes to the east of the slough. Sandy marls underlie the dry

prairies to the northwest (Figure 12). Prominent landscape features within the slough include tree islands and numerous small, deep water ponds, interspersed across a mosaic of dense sawgrass stands and open, sedge marshes.

Surface water flows into the slough from an impounded marsh area (WCA3A) immediately upstream are regulated by four water control structures (S12s) located along the western portion of the slough's northern flow section. An additional water control structure (S333) passes a porportion of these flows or discharges to the eastern portion of this flow section (Figure 13). Resultant downstream surface water conditions within the slough are dependent upon the seasonal quantity and flow distribution of these upstream discharges, and local rainfall over the slough.

Under the current rainfall-based deliveries to the Park, seasonal upstream discharges into the slough, during normal rainfall years, and related downstream changes in marsh water depths, usually peak during the late wet season months, decline during the winter dry season, and increase again in the early wet season with the onset of spring rains (Figure 14). Two thirds of the upstream discharges into the slough, however, are delivered through the S12s, outside of the historical or natural channel of the flowway, and drain onto the dry prairie, sandy marl marshes northwest of the historical Shark Slough channel or flowway. Considerable variation in seasonal and annual flows through the slough have characterized recent water management deliveries. These deliveries have resulted in increasingly frequent drydowns of extended duration and magnitude during the dry season, and high seasonal flows during the wet season months, compared to estimated natural flows before intensive, regional water management regulation was initiated in the 1960s (Craighead, 1968; Sikema et al, 198 ; SFWMD, unpublished data; SFWMD, NPS, 1990; Kushlan and Jacobsen, 1990).

#### Methods.

##### Documentation of annual nest abundance patterns.

A systematic experimental design in combination with standard aerial survey transect counting techniques was used to document annual nest abundance patterns of alligators within the slough from 1985 to the present. East - west oriented transects across the topographical gradients of the slough, and systematically spaced at 2 km. intervals north to south, were flown annually, approximately one week following an estimated mean egg laying date, calculated for each year by an egg deposition - ambient air temperature regression relationship developed from previous research

(Kushlan and Jacobsen, 1990). Survey height (40 m), strip width (250m), and groundspeed (50 knots) were standardized for all study years.

Navigation of flight lines and coordinates of all nests located within sampled areas were by reference to a Loran C navigational aid installed aboard a Bell Jet Ranger helicopter. The Loran C was recalibrated over a known ground position before all nest survey flights conducted each year during the study period. Doors were removed from the helicopter for unobstructed observation. The Bell Jet Ranger was also equipped with a radar altimeter used for accurate height control during the nest surveys.

A left and right observer counted nests within a 250 meter strip on either side of predetermined, surveyed flight lines flown across the study area. Operationally, the two strip widths along each flight line were combined and treated as a single, belt transect (500 m wide) during the survey. Each belt transect was searched as a separate block to obtain a total nest count. The area surveyed each year represented a 25 % systematic sample of the total slough area. Loran C coordinates were used to stay within the upper and lower boundaries of each sample belt transect searched for alligator nests. Nest surveys were flown between 0900 - 1500 hours to avoid harsh light conditions during early and late afternoon hours. The nest surveys were conducted during early - mid July of each year, depending upon the estimated mean egg laying date calculated for each study year. Time required to complete a nest survey varied between years, depending upon the number of nests observed, weather conditions, and helicopter availability, averaging approximately 5 days per survey to cover the study area, and ranging from 3 to 8 days over the six year study period.

An initial pilot study was conducted over the study area during the 1985 nesting season to (1) investigate the degree of visibility bias or nest count accuracy, in relation to the height, strip width, and groundspeed survey variable values given above, by comparison of nest counts obtained from both aerial and ground searches of each transect belt, to nest counts from aerial searches only, and (2) to determine the sampling intensity (percent of the total area surveyed) required to obtain repeatable results for mapping alligator nest abundance patterns. The pilot study nest survey was conducted at a 1 km. systematically spaced transect interval over the study area, using the same flight line orientation, strip width, survey height, and groundspeed selected for all subsequent nest surveys during the study period. Nest count data from the pilot study survey were then totaled for each 1 X 1 km. cell of a study area grid. Total nest counts per cell of the grid were converted to nest density estimates per cell to provide a nest density distribution map of the study area.

Repeatability of the nest density distribution documented was then compared at various sampling intensities. The initial pilot study data was used to map nest density distributions and to estimate total nest numbers at 2 - 10 kilometer "resampled" transect intervals and cellular grid resolutions. A 2 km. transect/flight line interval was selected for use in all subsequent nest surveys. This transect interval, combined with the 250 m belt transects searched along both sides of each flight line, provided a 25 per cent systematic sample of the study area. Approximately 85 per cent of the nests counted in this sample area, from combined aerial and ground truth counts, were observed using the aerial survey data only (Fleming et al, in prep).

Documentation of surface water conditions in the study area.

Two sources of data were used to estimate monthly surface water conditions in the study area over the study period. Monthly, water depth distributions were estimated from contouring recorded monthly water levels at 100 hydrological stations and staff gauges located throughout the study area, using a surface contouring software package. A contoured topographical surface plane of the study area was then subtracted from the monthly, water level contours to obtain estimates of monthly, water depth distributions per cell of the study area grid. The accuracy of estimated, monthly water depths was assessed by comparing estimated monthly water depths to recorded water depths for the same months in cells where hydrological stations or staff gauges were located (Portier and Smith, 198 ).

In addition, surface water conditions were also qualitatively described by empirical observations during monthly flights, conducted over the alligator study area, using the same flight lines flown during the alligator nest surveys. From 1985 - 1987, three surface water categories were used to describe and document surface water conditions in the study area: dry - absence of free standing, surface water, (2) transitional - intermittent surface water, and (3) wet - continuous free standing, surface water. Loran C coordinates were recorded along flight lines where changes were observed from one surface water category to another. From 1988 on, a five category classification scheme was employed: (1) dry/dry - absence of free standing surface water with low ground water levels in ponds/depressions occurring in the bedrock or marsh floor, (2) wet/dry - absence of free standing surface water but high water levels in ponds, etc. (3) dry/transitional - intermittent surface water, area mostly dry but with scattered, small surface water pools, (4) wet/transitional - intermittent surface water, but area mostly wet, and (5) wet - continuous, free standing surface water over the area.

Monthly hydropattern maps of the study area were then developed from these data by the following procedures. A monthly surface water condition was assigned to each cell of the study area grid, based on the longitude recorded for changes in surface water conditions along each flight line. The systematically spaced flight lines were oriented east - west across the topographical gradients of the slough (bisecting each row of grid cells), and therefore were of a constant latitude, requiring only longitude recordings to document surface water changes along each flight line (or row of grid cells). Computer files containing these monthly surface water condition code values per cell of the grid were converted to a GIS data format, cell map files, and then mapped using GIS GRASS 3. software.

#### Documentation of reproductive success.

Hatching success, and the sources and extent of egg mortality, were estimated from a representative, subset of nests monitored each year at approximately two week intervals throughout the incubation and hatching periods. The sample size required to obtain repeatable results in monitoring reproductive success was also determined by resampling pilot study data on nest hatching rates at five percent nest sampling intensity increments. A twenty per cent minimum sample of the estimated total number of nests in the study area, from nests initially located in the nest survey sample area, provided repeatable estimates of nest hatching success rates (Fleming et al, in prep). This sampling intensity was used, therefore, to monitor and estimate nest hatching success rates during each year of the study period.

*This is valid to year*

To evaluate nest flooding patterns of nests within the slough, monitored nests were from a systematic subset or sample of the nests located during each year's initial nest survey. Nest were selected in this manner to replicate the observed nest density distribution, mapped from each year's nest survey data. Total number of eggs, and the number of fertile and non-viable eggs (infertile or early embryonic death), per clutch were recorded at the beginning of the incubation period by landing at the nest site during the nest survey, or within the following week. Subsequent, biweekly monitoring flights were conducted to each sample nest to record the number of original eggs lost, by mortality source, throughout the incubation and hatching periods. In 1990, additional weekly flights were also conducted to each nest during the hatching period.

#### Documentation of egg laying dates within sample nests.

During the 1990 nesting season, three viable eggs per clutch were selected from each sample nest during the sixth week of

the normal incubation period. An egg from the top, middle, and lower layer of each egg clutch was selected for examination. Developmental stage and age of each embryo collected were then estimated, following an embryo development key devised from a previous study on the embryology and development chronology of alligators within the southern Everglades (Grabowski et al, in prep). The mean age of the embryos collected from each nest, based on the calendar date on which each embryo age was determined, was then used to estimate the "egg laying date" at each nest site. Estimated egg laying dates based on embryonic ages assume that no significant, oviducal embryonic development has occurred before egg deposition. This assumption and any related bias in the data is discussed in the following Results and Discussion section.

#### Data analyses techniques.

Calculation of annual, alligator nest density distributions and nest population estimates.

Nest count data and coordinates of nest locations were entered into a customized computer program developed by NPS and I.F.A.S., University of Florida, for data processing and analyses of transect count data on I.B.M. compatible microcomputers (I.F.A.S. and N.P.S., 1989). The computer program assigned nest location coordinates to the appropriate cell of a 2 x 2 km. grid calculated by the program for the study area. The program then totals the nest counts per cell of the grid, and converts each total nest count per cell to a nest density estimate, providing a cellular map of the nest density distribution over the study area. Total nest counts along each flight line are also used to calculate a nest population estimate  $\pm$  95 % confidence interval for the study area using the Jolly 2 formula, developed by Jolly (19 ) for analysis of transect count data.

Descriptive statistics for several distribution and abundance parameters are also calculated for the survey area, or by each substratum defined, including a mean nest density  $\pm$  one standard error, maximum and minimum nest densities, and the kurtosis and skewness of the nest density distribution documented over the study area and for each defined substratum. Population estimates for the study area, and/or substrata, occupancy rates (based on the % total number of survey sample nests) for each substratum of the study area, and a chi square test for observed vs expected distribution for each substratum, are also calculated (Fleming et al, in prep). The 2 X 2 km. grid calculated by the program and used for mapping alligator nest density distributions within the study area is depicted in Figure 15.

Landscape classification analysis of the study area to define land element themes, major landscape types, and landscape categories.

To describe annual changes in nest distribution and abundance in relation to landscape patterns and temporal characteristics within the study area, each cell of the grid was first assigned a separate code for its substrate type, dominant ground surface features, dominate vegetation cover type (based on a structural classification), pond density, and an average dry season surface water condition (wetness index of a cell's hydroperiod), calculated from the monthly, surface water condition values previously described. Each of these land element "map layers" or themes were then overlaid and combined into distinct associations, or map layer code combinations per cell of the study area grid, using a Gcross GIS function to classify cells according to varying land facets over the study area. Land facets (cells of similar land element code combinations) were then reclassified using a GIS expert inference system function, Ginfer, to define the boundaries of major landscape types (areas of similar land facets) and landscape categories (areas of similar landscape types) within the study area (Fleming et al, 1990).

Analyses for investigating environmental correlates to nest abundance patterns.

Non-parametric, contingency analyses were then used to relate changes between nest abundance or density associated with each landscape type and varying water depth distributions, occurring during different periods of the reproductive season for each study year.

Analyses for investigating environmental correlates to egg laying dates.

The relationship between mean ambient spring air temperatures to estimated egg laying dates at nest sites and empirically documented, antecedent surface water conditions within each nesting area, prior to the reproductive season, were investigated by: (1) first assigning each nest site to either one of two surface water condition categories (nesting areas retaining surface water versus nesting areas that dried down during the late dry season), and then (2) comparing the distribution of estimated egg laying dates of nests between the two surface water categories using a non-parametric, rank test ( ,19 ).

The 95% confidence interval of the age of an individual embryo is from 8.8 days before to 8.8 days after the estimated age for sample embryos of a mean 25.5 stage. The mean stage of the sample embryos collected during the 1990 nesting season of this study was 28.01. The error about

this mean stage would not exceed 8.8 days as the technique aging error decreases with increasing embryo development stage (Grabowski et al, in prep.).

Using estimates of aging error, the difference in the egg laying dates between the two nest groups was evaluated by a Mann Whitney test. The estimated laying dates within each nest group, based on the estimated embryo ages, were first adjusted to provide a more conservative test. Laying date estimates for the nest group with the smaller mean (smaller values refer to earlier egg laying dates) were increased by a two standard deviation distance for that nest group mean (calculated by dividing the 8.8 days by the square root of the group size). A 95% confidence interval approximates two standard deviations above and below the mean. Laying date estimates for the nest group with the larger mean (later egg laying dates) were decreased by a two standard deviation distance for that nest group. Resulting individual differences in the estimated egg laying dates of nests between each nest group (surface water category) were therefore reduced, decreasing the probability that the test would find a significant difference by chance between the two nest groups.

These data were also plotted and further examined by comparison of each estimated laying date to the mean laying date predicted for all nests based on spring ambient air temperatures only. The distribution of egg laying dates for nests within each surface water category were plotted separately, and each distribution compared to the predicted mean egg laying date for all nests within the study area. The predicted mean egg laying date for all nests was based on a regression relationship previously developed between timing of egg laying and mean ambient, spring air temperatures only (Kushlan and Jacobsen, 19 ).

For verification of predicted laying dates based on estimated embryo ages, these predicted laying dates were also compared to laying dates of each egg clutch, estimated from weekly field nest checks during the hatching period. Egg laying dates, estimated from field hatching dates, were calculated by subtracting 59 days (average incubation period) from each estimated field hatching date. A paired t test was used to determine if the two sets of estimated laying dates differed significantly.

Analyses for investigating the annual variation in total nest numbers observed within the study area.

The relationship of total nest numbers to the annual area of innudation within the study area at different time periods throughout a year was examined through a simple univariate, regression analysis approach.

### Analyses of nest flooding factors.

Factors affecting the frequency and extent of nest flooding within the study area were investigated through the use of descriptive statistics to describe nest flooding patterns in relation to flooding events and water delivery characteristics (flow distribution, volume, and timing parameters) during the incubation period of each study year. Previously developed stage - discharge relationships for the slough (Sikema et al, 1986) were also referenced to relate upstream discharges into the slough, and downstream local rainfall over the slough, to changes in downstream, surface water conditions observed within the study area during the nest construction, egg laying, and incubation periods of each study year.

### Alligator population model simulations.

An alligator population simulation model, developed during a modeling workshop by a collective group of Everglades researchers and system modelers, was also used to examine population stability attributes in relation to proposed water delivery scenarios under consideration as planned, Everglades restoration efforts. The modeling approach, assumptions, and parameters used in the alligator model are presented in a user guide to an evolving, preliminary Everglades ecosystem simulation model initially developed at this workshop (Tait, 1990).

### Results and Discussion.

Results obtained about environmental correlates to nest distribution, abundance, timing of egg laying, and hatching success during the 1985 - 1990 alligator nesting seasons are presented and discussed in relation to alligator reproductive and nesting biology life history aspects summarized in the Review of Published Data. A summary of the annual number of alligator nests estimated within the study area for each study year, and the annual reproductive performance documented, are presented in Table 8. Alligator nest density distributions for selected years with high, moderate, and low surface water conditions during the late dry season, and related hydropattern maps, are presented in Figures 16 - 18. Maps of land element themes, major landscape types, and landscape categories defined within the study area are depicted in Figures 19 - 25. Annual changes in nest abundance patterns associated with these landscape elements and themes are also presented and discussed.

Nest distribution in relation to spatial and temporal characteristics of the study area.

Alligator nest distributions within the study area varied with respect to substrate (Figure 26) and vegetation cover

types (Figure 27), and also varied in relation to water depth distributions occurring during the late dry season (early follicle development period) (Figure 28), and during the nest construction period of each year (Figure 29). Lower limits of water depth that influenced the spatial distribution of alligator nests occurred during the late, dry season months (March - late April) of each year. Upper limits of water depth that influenced nest abundance patterns documented each year usually occurred during the peak nest construction period in the early wet season (mid - June/early July).

Expected nest densities for each landscape category, used to simulate nesting distributions in the alligator population model, were also calculated by (1) pooling nest count data for each landscape category over a range of high, moderate, and low rainfall years and surface water conditions, and then (2) calculating an expected nest density per category, based on the available area within each landscape category (Table 9). Average nest densities over the study period were highest (1.5 - 1.9 nests/km<sup>2</sup>) in central slough habitat types characterized by organic soils, dense vegetation, and long hydroperiods. Lowest average nest densities (0.2 - 0.4 nests/km<sup>2</sup>) occurred in dry prairie or edge habitats characterized by low organic/high marl or sandy marl soils, sparse vegetation, and short hydroperiods. All nest sites were in close proximity to deep water ponds, usually shaded or partially shaded by adjacent, willow or hardwood tree island canopies. Nest occurrence (% of total number of nests in the study area) within each landscape category also varied in relation to relative surface water conditions among years (Table 10).

Mature females apparently remained within established general nesting areas throughout the nesting season during low surface water conditions, even if such areas lost all surface water during the late, dry season months. Nesting in such areas was either absent or in extremely low numbers while the total number of nests throughout the slough was also low. In these drier years, water depth distributions were skewed to shallow water depth classes. Nesting occurred only in areas retaining surface water, and overall nest numbers within the study area declined dramatically from wetter years.

~~In normal rainfall years, water depths during the late dry season months were more evenly distributed, as were nest numbers among the wider range of available, water depth classes. Subsequent total nest numbers within the slough increased during these surface water conditions. In high rainfall years and surface water conditions, nest numbers declined rapidly in areas with marsh water depths exceeding 45 cm during the peak nest construction period of the early wet season (mid- June/early July). Most nesting during high~~

7. water years occurred in areas of shallower, surface water conditions, located along the edges of the slough, and on higher elevated nest sites, within central slough areas.

Nest site selection in relation to relative elevation, soil substrate, vegetation, proximity to permanent water, and related nest site, defensive behaviors.

During years of high rainfall and surface water conditions, a majority of nests ( %) were located on the relatively higher elevated sites within the natural marsh - elevated banks of ponds or edges of tree islands within the slough. During years of moderate surface water conditions, nest locations were more widely distributed among a wider variety of habitat types and relative elevations (Figure 30). In all years, a majority of nest locations ( %) were within close proximity (approximately 10 m) of a pond surrounded by willow shrubs (Salix caroliniana). Craighead (1968) described these willow hedges as the result of early plant invasion on newly disturbed sites. In low rainfall years and surface water conditions, virtually all nests ( percent) were located adjacent to such ponds, predominately shaded either partially or completely by willow or tropical hardwoods, comprising adjacent tree island canopies. Nests in these hot, dry years were noticeably absent from open, wet prairie marsh habitats within the slough.

Substrate type and depth, vegetation cover type, average annual stage duration, and related hydroperiod characteristics of a nesting site are all highly intercorrelated and related to relative elevation differences within the slough (Table 12). Generally, soil depth and organic content, dense vegetation, and deeper ponds are associated with longer hydroperiod sites within the central slough. Burning off of the accumulated vegetation in these areas from wildfires during the study period occurred less frequently than in higher elevated and drier sites. Abundant nesting material was normally available. Attendant females observed in these nesting areas usually remained within densely vegetated marsh (dense sawgrass stands or downstream sawgrass tails of tree islands) or in ponds adjacent to the nesting site.

Under present surface water conditions within the slough, characterized by low flow volumes during most dry season months, such central slough sites represent core nesting habitats and supported the highest average, nest densities in all but high rainfall years and surface water conditions. Such sites were also frequently occupied by larger-sized nesting females that aggressively and consistently defended the nest against human intruders. In the 1988 nesting season, one such female immediately charged the helicopter upon its landing over 45 m away from the nest site, and aggressively pursued any project personnel approaching the

During the 1990 nesting season, however, eggs were absent within 21 per cent (10) of the nests ( $n = 47$ ) located during the initial nest survey (Table 13). Such nests were well developed, with a normal base diameter and height, but lacked a cone-shaped top, characteristic of finished nests in which an egg clutch has already been laid. Of these unfinished nests, four (40%) remained without eggs throughout the nesting and incubation periods. Subsequent egg laying occurred at later dates during the incubation period in the remaining six nests (60%). An additional 7 nests (15 %) of the 47 nests located during the nest survey contained egg clutches that had been recently laid. The nesting areas in which recent or late egg laying occurred had lost all surface water during the late, dry season months (March, April), preceding the 1990 courtship and mating periods. Only one (17%) of these six nesting areas, in which late egg laying occurred, maintained ground water within ponds in the nesting area during the late, dry season months.

In nesting areas that had retained surface water, estimated egg laying dates were normally distributed about the mean egg laying date predicted by mean ambient, spring air temperatures. In contrast, estimated egg laying dates for nests in areas that had previously dried down were highly skewed toward later dates (Figure 31). Simple statistics were used to quantify the difference in estimated egg laying dates between the two nest groups. The distribution of estimated egg laying dates in nests from areas that dried down was compared to the distribution of egg laying dates within areas that retained surface water during these months by a rank test (Table 14). Egg laying dates were significantly later ( $p < 0.05$ ) in nesting areas that had previously dried down compared to nesting areas that retained surface water throughout the preceding late dry season months.

Estimated egg laying dates derived from weekly field nest checks during the hatching period were used to verify the estimated egg laying dates used in the above analysis, and based on the embryo age - predicted egg laying date technique. Predicted egg laying dates based on the mean estimated embryo age from eggs collected ( $n = 3$ ) per nest were plotted against estimated egg laying dates calculated from observed hatching dates or from estimated nest hatching dates, derived from the weekly nest checks during the hatching period (Figure 32). A mid-point value (3.5 days) was used to estimate hatching dates that occurred between these weekly nest checks. Predicted egg laying dates based on the embryo aging techniques did not differ significantly ( $t =$  ,  $p < 0.05$ ) from the estimated egg laying dates calculated from weekly field nest checks. Nest monitoring values derived from weekly nest checks during the hatching period, however, had a smaller 95% confidence interval (6.85

days), compared to the embryo aging technique (8.8 days), but involved weekly field trips to obtain more precise estimates of nest hatching dates.

If egg retention and oviducal embryonic development did occur in monitored nests, then for such nests, actual egg laying dates may have been later than that estimated by the embryo age - predicted egg laying date technique. Such egg retention and delayed egg laying, however, would be expected to occur in nests within dry nesting areas. The difference in egg laying dates between the two nest groups would therefore be even greater than the dates tested, based on egg laying dates estimated from embryonic age. If this bias exists in the test data, then the test would become even more conservative, and further increase the significant difference of the test results obtained.

The 1990 nesting season occurred during drier than normal surface water conditions, but was wetter than the previous year during which a major drought (one in twenty years) occurred. Interannual affects on the productivity and standing crops of alligator aquatic prey can occur during a sequential combination of drier years (Loftus and Eckerd, 1990). Cardeilhac (1988) reported that normal, early follicle development during March - early April is correlated to the amount of protein consumed by a mature female during this time period. Interannual drydown affects, reducing the availability of aquatic prey items during the 1990 winter dry season, may have also reduced the amount of protein intact of mature females during this dry season, below that required for normal early follicle development the following spring. In these conditions, subsequent reproductive activities could also be affected, delaying egg deposition of females in these drier nesting areas during the subsequent nesting season.

Based on the previously presented statistical analysis, a hierarchical, conceptual approach to understanding the environmental factors controlling the timing of egg laying in the American alligator may provide a more useful model for relating the affects of seasonal photoperiod, ambient spring air temperatures, antecedent seasonal and annual surface water conditions ( and related affects on prey availability, protein intact, and subsequent body and reproductive condition of nesting females) to spatial and temporal patterns of egg laying during a nesting season (Figure 33). During wetter years and in nesting areas in which surface water conditions remain within normal ranges, when dry conditions are not adversely affecting the reproductive physiology of nesting females, ambient spring air temperatures may be the controlling factor determining the timing of egg laying. In drier years or nesting areas, other environmental factors, such as low water depth and associated suboptimal feeding and high (stressful) thermal

conditions, may have a greater influence on the body and reproductive condition of potential nesting females, and subsequent egg laying dates. Such a model could provide a greater degree of predictability than a univariate model, based on ambient, spring air temperatures alone.

Annual nest abundance and length frequency distributions of nesting females in relation to spatial and temporal innudation characteristics during and antecedent to the reproductive season.

The total number of alligator nests observed within the study varied each year (Figure 33), as did surface water conditions during and antecedent to the reproductive seasons of those years. Changes in total nest numbers within the slough each year were significantly related to the porportion of the area retaining surface water during the late, dry season months of the early, follicle development period (Figure 34). Nesting occurred most frequently in the core, central habitats of the slough that retained surface water during most years of the study period. Nest numbers within the general study area increased exponentially in relation to the innudation of additional, wet and dry prairie habitats during higher rainfall years and surface water conditions. Nests were thirteen times as numerous in 1986 as in 1985. Extremely low surface water conditions prevailed throughout the late dry and early wet season months of the reproductive season in 1985, in contrast to high, surface water conditions sustained throughout the slough during the following dry season months that preceded the 1986 reproductive season.

No evidence of genetically determined periodicities in ovulation of nesting females within the study area is confirmed by these data. The variable porportion of mature females nesting from year to year can be explained by annual changes in the areal extent of innudation preceding each nesting season. The annual variation in the area of innudation, and related influences such changes in surface water conditions have on the metabolic processes affecting the reproductive condition and/or behavior of potential nesting females in the slough, may account for the changes in nest production observed between years, particularly when food and thermal stress conditions may become limiting. In south Florida, rainfall follows a repeat frequency of high annual rainfall once in every five to seven years, usually declining each year thereafter until the next high rainfall year ( , 19 ). If genetically determined periodicities in ovulation do exist, then such periodicities could be adapted to this rainfall repeat frequency, and correlated with the associated changes in surface water conditions each year within the slough.



nesting site or the helicopter for several hours. In the 1990 nesting season, a very large female aggressively defended her nest throughout the incubation period even though no eggs were ever laid in the nest.

The occurrence of nest defense against a human intruder was not limited, however, to such females, and also occurred in a wide range of size classes of nesting females encountered during the study period. On several monitoring trips, the ~~smallest nesting females~~ encountered exhibited highly aggressive, nest defensive behaviors. Nest defense appeared to have a strong, individual innate component, as the frequency and intensity of such behaviors varied widely both between and within size classes of attendant nesting females.

The frequency of nest defense by attendant females at other nest site locations within the slough was more variable, averaging approximately per cent over the study period, and ranging from a ~~high of 40 percent~~ in the drier years to a ~~low of 10 per cent~~ in some wetter years. Nest defense did occur more frequently than that typically reported in the northern Everglades, where nest defense by attendant females is infrequent and human disturbance more common ( , 19 ), and for that reported in populations occurring in other wetlands ( ). Nest defense was also highly variable within a nesting season by individual females, and appeared to occur most frequently on overcast, rainy, and cooler days during the summer incubation period. In comparison, the occurrence of nest defense by attendant females was lowest on clear, hot days, suggesting that environmental conditions at the nest site may affect the activity levels, and related defensive behaviors of some less innately aggressive, nesting females.

Timing of egg laying in relation to mean ambient, spring air temperatures and surface water conditions.

Egg laying can be shown to depend on both water level and ambient spring air temperatures. ~~Major drydowns occurred during the 1985, 1989, and 1990 late dry seasons.~~ During ~~wetter years of the study period, 1986, 1987, 1988,~~ most nests (98%) located during the initial nest surveys each year already contained eggs. Hatching dates of over 85% of monitored nests for these years occurred within +/- one week of a predicted annual, mean hatching date based on ambient spring air temperatures. The estimated mean hatching date each year was calculated by adding 59 days (average incubation period), to the estimated mean egg laying date, predicted from a (regression) relationship between time of egg laying and ambient spring, air temperatures (Kushlan and Jacobsen, 1990).

~~During the driest (most stressful) years of the study period, in slough areas that either lost surface water or retained only low surface water conditions during the late, dry season months, length frequency distributions of attendant nesting females observed during the subsequent nesting season, appeared more highly skewed to smaller size classes. During wetter years, when higher surface water conditions were maintained in the same slough areas, length frequency distributions of nesting females observed appeared to be more normally distributed among a wider range of adult, nesting female size classes.~~

~~If a more normal distribution of larger sized females do nest in wetter years, and an increasing size - fecundity relationship exists, then the mean nest clutch size for these years should be greater than during drier years.~~ During the drier than normal 1990 nesting season, following a major drought year, the mean clutch size was significantly lower than that documented for previous years ( ,  $p < 0.$  ). No significant inverse relationship was also found between nest clutch size and estimated egg laying dates during the 1990 nesting season (Figure 35). If an increasing size - fecundity relationship exists for females within the slough, and larger females nest earlier than smaller sized females, according to social order factors (Ferguson, 1985 ), then clutch size should have decreased in relation to later egg laying dates. These data suggest that such social ordering factors were not operative during the stressful conditions existing during the 1990 reproductive season.

x A stronger, but weak ~~inverse correlation~~ (Figure 36) between egg mass and estimated egg laying dates during the 1990 nesting season was found, suggesting that selective pressures on nesting females ~~may be for increased egg quality, and not increased clutch size,~~ during stressful years and/or in environments with pronounced seasonal water level fluctuations. Nest in which latest egg laying occurred after nest construction also had increased egg mass relative to other nests in which late egg laying also occurred. If these latest egg laying dates resulted from prolonged egg retention, then oviducial embryonic development (occurring before egg deposition) may account for the increased egg mass observed. Late egg laying by larger sized nesting females could also account for the increased egg mass observed in these clutches.

The antecedent surface water conditions in the nesting area, that were significantly related to estimated egg laying dates within each nesting area during the 1990 nesting season, and favoring an apparent increased frequency of smaller sized nesting females in drier years, best explains the temporal pattern of estimated egg deposition dates observed during the 1990 nesting season. In consecutively,

wetter years, social order may then be a more influential factor affecting the temporal pattern of mating and egg laying of females, when environmental conditions again become favorable.

Larger-sized adult females within the slough also appear to suffer greater, proportional weight losses during dry years of lower food availability, and increased thermal stress, than smaller sized adult females (Dalyrample, pers. comm.). Higher energy maintenance requirements for larger sized alligators with a greater body mass and increased thermal stress (under the high temperature extremes that occur during these dry years), compared to smaller sized alligators (in relation to a smaller ratio of skin surface area to body mass for larger sized animals), may explain this differential weight loss. Under such stressful conditions, larger-sized adult females may actually have a smaller energy reserve to invest in reproduction, during and immediately following such dry years or seasonal conditions, compared to smaller sized adult females.

Under recent water management, characterized by increasing frequencies of major drydowns, the resulting low surface water conditions, reduced prey availability associated with and following drydowns, and increased thermal stress in drier years, could favor an increased nesting frequency of smaller sized females during such years, compared to that of larger size classes, particularly in a population that appears to be food limited. Given the increasing size - fecundity relationship reported for alligators, such selective pressures favoring smaller sized females to nest more frequently, particularly in drier years, could also result in a decrease in the population's fecundity, in response to the increased frequency, magnitude, and duration of drydowns occurring under present water management practices.

Major drydowns do appear to be extremely stressful on large sized adult females that remain in established nesting areas during low surface water or drought conditions. Several dead, large sized females were observed in the late, dry season months during the drought of 1989. These females had remained within interior, central slough ponds that dried down completely. These same females had been observed in these isolated ponds during the previous months, buried in the still moist muck at the exposed bottom of the drying ponds. Other occupied ponds were apparently abandoned after drying out. Alligator tracks from these dried out ponds were observed leading in the general direction of drought refugia areas. Both an adult male and adult female were also found sharing an underground den beneath another pond, that had also dried down during this same period.

With the drying of the marsh floor, alligators occupying ponds in slough areas of exposed, eroded bedrock appeared to retreat to underground dens or caverns in the eroded bedrock that provide a black body cavity. Alligators occupying ponds in areas of bedrock, overlain with dried and cracking muck, either dispersed in the general direction of drought refugia areas, or remained for unknown reasons within the dried out ponds, and died. No smaller sized subadult or adult alligators were observed remaining above ground in these ponds during monthly flights over the study area. The higher extreme body temperatures that smaller sized alligators can tolerate over a short time period (Spotila et al, 19 ) may partially explain the apparent, greater dispersal tendency of these smaller-sized animals, from isolated, central slough habitats to adjacent drought refugia areas during the drought conditions observed.

During the remaining, late dry season months of the 1989 drought, increasingly greater numbers of subadult and adult sized alligators were observed concentrating in drought refugia habitat provided by canals along the eastern and western edges of north Shark Slough, and downstream within the numerous tidal rivers, creeks, tributaries, and inland bays within or adjacent to the estuary headwater areas, immediately south and west of the slough. During late dry season flights over these headwater areas during the months of April through June, alligators observed were still concentrated in these drought refugia. Several occurrences of agnostic mortality or cannibalism were also observed between large sized alligators during each flight. Few large sized alligators were observed aboveground, however, in the remaining ponds of the central slough still retaining some ground water during this period. The reduced reproductive performance of nesting females within the slough, during low water conditions or following such major drydown events, is discussed in the following section.

#### Reproductive success in relation to spatial and temporal characteristics of the study area.

The major environmental variable influencing the annual production of hatchlings within the study area was the antecedent surface water condition preceding each nesting season. High or low surface water conditions influenced the number of females nesting each year, and the resultant total production of eggs (see previous section).

The greatest source of egg loss over the study period ~~resulted from nest flooding~~. Other sources of egg mortality included egg infertility or early embryonic death, arrested embryonic development, and the dessication, crushing, or predation of eggs. These mortality sources were relatively constant and small for wetter years of the study, compared to egg loss from nest flooding. Total egg loss from all

sources of mortality, however, only modified the number of hatchlings produced each year, compared to the influence of antecedent, surface water conditions during the late dry season months on subsequent alligator annual nest and related total egg production within the slough.

#### Egg loss to nest flooding.

Nest flooding within the study area was related to both local flooding events and to upstream water management regulation and related water delivery characteristics to the slough. Nest flooding-related egg loss was highly variable among study years, ranging from 6 - 51 %. Egg loss to natural flooding events was relatively small for most years, while ~~water management related nest flooding~~ resulted in losses of over half (51 %) of the total production of eggs within the slough during some nesting seasons (Table 8).

~~Most nest flooding events occurred in the high rainfall and surface water flow periods of the late, wet season months each year, during the last two - three weeks of the normal incubation period (Figure 37).~~ Water delivery characteristics for three years of the study period, 1985 - 1986, in relation to local rainfall and downstream changes in surface water depths during the alligator nesting and incubation periods, are depicted in Figures 38 - 40. The three years selected represent low (1985), high (1986), and moderate (1987) rainfall years and related surface water flows.

During the normal high rainfall and surface water flow months of the late wet season, an increasing porportion of the total volume of water discharged into the slough (up to 100 % in some study years) was delivered through the four water control structures (S12s) along the western porportion of the slough's main flow section, and discharged outside of the historical channel of the slough onto higher elevated, dry prairie marshes. Rapid and large increases in water depths, related to these discharges, occurred immediately downstream of these structures, flooding most nests to the southeast and south of the control structures, when discharges were excessively high.

In 1988, following a high period of rainfall during the late incubation period, nest flooding increased throughout the slough. Egg flooding occurred in the lower layers only of egg clutches within nests in the eastern and extreme southern areas of the slough, away from the S12 structures. Entire egg clutches within nests immediately south and southeast of the S12 structures, however, were completely innudated, resulting in a 51% egg loss due to nest flooding within the slough during the 1988 nesting season. In other study years, when wet season rainfall was more normally distributed, and upstream discharges into the slough can be

more evenly distributed across the entire northern flow section, egg loss from nest flooding was much lower, averaging 14 %, and ranging from 6 to 23 %. Egg loss to flooding during these years was also more evenly distributed among the sample nests monitored throughout the study area.

Since construction of the water conservation areas to the north of this central flowway, predictability of the system's hydrology regime has been decreased (Kushlan and Jacobsen, 1990). Current "natural" levels of alligator nest flooding remain much higher than that estimated to occur by Kushlan and Jacobsen (1990) prior to the construction of these water retention areas during the 1960s and subsequent, intensive regional water management. Estimated egg loss to nest flooding averaged only 4 +/- 4.5 % over a ten year period (1953 - 1962) preceding recent water management regulation, compared to an average 20 +/- 32.8 % of nest flooding-related egg loss (a five fold increase) experienced under recent water management (1971 - 1982). An average egg loss of 17 +/- % to nest flooding has been documented during the six year period (1985 - 1990) of this study.

The loss of the hydrologic regime's predictability between peak early wet season water levels and late wet season maximum water level rise, the inadequate flexibility of existing water control structures to distribute high, late wet season flows in relation to the topographical contours of the historical flowway, and normal upstream discharge and flow distribution operational procedures (related to flooding concerns of agricultural interests and private land owners to the east of the slough), are intercorrelated and contribute to nest flooding. Such constraints have prevented the restoration of a more natural hydrological regime through this central flowway of the southern Everglades.

#### Other egg mortality sources.

Egg infertility and/or early embryonic death was relatively constant and low during wetter years of the study period, compared to egg mortality from nest flooding (Table 8). During wetter years, egg loss due to infertility and/or early embryonic death averaged approximately 8 per cent, and ranged from 7 to 9 per cent. During drier study years, such rates were more variable, averaging 14 per cent and ranging from 3 - 25 per cent.

Annual egg losses from crushing, by female movements over nests during the incubation period, or cracking during egg deposition, were low (less than 1 per cent). Desiccation of eggs was also low (less than 1 per cent), and occurred most frequently in the top egg layers of the clutch. Annual egg desiccation rates, however, did not increase during the drier years of this study. In dry years, low water levels usually

occur during the nest construction and egg deposition periods. Egg clutch heights are closer to ground surface elevation than in wetter years. The height of nests constructed do not significantly differ between such years (Kushlan and Jacobsen, 1990). The increased amount of nesting material above the egg clutches in drier years, and the shifting of nest site locations to more shaded areas and to lower elevated (wetter) sites, apparently prevented excessive drying of nests during the driest years of the study. Predation on eggs was not common, and only occurred in a few nests that were located on the drier edges of the slough. Annual predation rates over the study period averaged 2 percent, ranging from 0 - 4 per cent. Combined egg mortality from crushing, cracking, dessication, and predation was also low and relatively constant, averaging only two percent over the study period, and ranging from 0 - 5 percent annually.

Reduced nest production and lower hatching rates were documented in relation to the drought conditions of 1989, and reduced nest production, mean clutch size, and lower hatching rates during the low surface water conditions still prevailing throughout the 1990 nesting season (table 8). During the nesting season of the 1989 drought, and in the following year, egg mortality from egg infertility or early embryonic death, and arrested development, average 35 %, a five fold increase over the average egg loss (7%) recorded from these sources during the previous wetter years of the study. The average clutch size (24.4) in the 1990 nesting season was also lower than that recorded (27.0 - 29.7) for previous wetter years.

The hatching rate was also low for nests in which late egg laying occurred during the 1990 nesting season, averaging 47 percent, compared to higher average hatching rates (67 %) of nests in previous wetter years (1986 - 1988), during which more favorable nesting conditions occurred. This average hatching rate (47 %) for nests in which late egg laying occurred was also lower than the average hatching rate (59 %) of other nests during the 1990 nesting season in which earlier egg laying occurred. Nests in which late egg laying occurred had similar rates of infertility or early embryonic death, an apparent increased rate of arrested development, but decreased rates of egg loss from flooding, compared to nests with earlier egg laying dates (Figure 41). Later egg laying in nests occurred during higher marsh water depths of late July that resulted in higher egg clutch heights above ground elevation. These higher egg clutch heights and subsequent, low water level rise during the remainder of the 1990 incubation period, may explain the reduced rates of flooding for nests in which later egg laying occurred.

Based upon these data, adaptative advantages of late nesting (delayed mating) or delayed egg deposition within nests (sperm storage and delayed fertilization and/or egg retention) appear limited as a reproductive strategy for alligators in the slough in relation to drought. The estimated production of hatchlings ( ) during the 1990 nesting season was less than one third of the average ( ) for previous wetter years of the study, and represented approximately half of the average number of hatchlings produced each year ( ) over the study period. Nests in which late egg laying occurred contributed only % (240) to the estimated total production of young ( ) during the 1990 nesting season.

Late nesting or delayed egg laying, however, as a reproductive strategy in response to drought, may have other benefits beyond the limited number of young produced. Such late nests, or nests in which delayed egg deposition may occur, could have a greater probability of producing a higher female to male ratio of hatchlings by delaying egg laying in dry nesting areas. During the 1990 nesting season, females deposited egg clutches at later dates, in nesting areas that had previously dried down, after low marsh water depths in these nesting areas had significantly increased. Nests in wetter conditions could be expected to have lower internal temperatures than during previous dry conditions at the nesting site. Later mating and egg laying and/or delayed egg deposition in these nests during wetter conditions may produce more female hatchlings than would earlier egg laying during drier (hotter) conditions at the nesting site.

Although late nesting and egg laying, or delayed egg deposition, in drier years produces fewer young, a female is insured of producing a greater number of female progeny, compared to earlier egg laying in drier nesting sites, or if potential nesting females did not mate at all during these dry years. The normal small proportion of adult females (5% or less) comprising most alligator populations makes the continued production of biased female hatchling sex ratios an adaptative advantage, particularly for nesting females in alligator populations inhabiting wetlands such as the Everglades, with unstable or fluctuating environments, and irregular reproductive output. Nesting females that produce a greater number of female hatchlings each year would have an increased probability of passing their genetic inheritance to latter generations, compared to the production of biased male hatchling ratios in a population with surplus adult males.

Another reproductive strategy that potential nesting females could adapt in relation to drought is to reduce nesting effort (no mating or egg absorption) to conserve energy in adverse conditions (to improve their survival chances and/or

nesting attempts during the following nesting season). During the 1989 drought, and during other dry years of the study, nest numbers were low. Nest numbers in subsequent nesting seasons, however, increased significantly if higher surface water conditions prevailed during the intervening dry season months. Most potential nesting females within the slough, therefore, apparently reduced their nesting effort, as an adaptative strategy in response to drought or major drydown events.

Alligator population model responses to simulated surface water flows within the central and southern Everglades.

The NPS restoration goals and objectives for the Everglades are based on the assumption that an ecosystem management approach is best achieved through reestablishment of a more natural hydrological regime than is possible by current water management practices. The basis for this assumption was tested for the alligator population within the central and southern Everglades by use of an alligator population simulation model (see Methods of this section) to compare the model responses to a simulated natural Everglades hydrological regime (no water control structures or wellfield diversions) versus simulated surface water conditions resulting from four different water delivery management alternatives, under consideration by local, state and federal agencies, involved in restoration plans for Shark Slough, the central flowway of the system (NPS, 1990).

#### Natural or "restored" model scenario.

The "natural" simulation or scenario estimates surface water flow distributions, volumes, and timing of these flows for wet prairie and slough marshes that comprise the central and southern Everglades under pre-flood control conditions of the system (SFWMD, unpublished data) with the same rainfall database (1969 - 1982) used to model the four other water delivery management alternatives. This natural simulation was used as a scientific control or model of hydrological conditions that provided: (1) a complete inundation of the evaluated area at the end of most peak wet season flows for the 14 year period; (2) distribution of seasonal surface water flows in accordance with natural topographical contours, and (3) lag, dry season volumes of flow from northern reaches of the Everglades catchment area (outside of the evaluated area) flowing into the central and southern Everglades. These lag flows maintained continuous dry season, surface water flows throughout the central and southern Everglades for most dry seasons of the 14 year period.

In contrast to natural simulated flows, the other four management alternatives did not maintain these continuous dry season, surface water flows through the slough. Major drydowns occurred on the average of once in every three years, compared to only one major drydown under the natural simulation, modeled for the same area and using the same 14 year period of rainfall data. Flow distributions of these other simulated alternatives were also not in accordance with natural topographical contours, but maintained deep water impounded marsh areas and overdrained marsh areas, characteristic of the present system, during most years of the 14 year simulation runs.

#### Alligator population simulation model parameters.

Population parameters used in the alligator model for comparing model responses to seasonal and annual inundation characteristics of these water delivery alternatives are listed in Table 15. Cohort survival rates used in the simulations were estimated from both published and unpublished data sources (Kushlan and Jacobsen, 198 ; Dalrymple, 1989). Antagonistic mortality estimates were based on field observation and from the general literature. The model assumes a stable age distribution at the beginning of each 14 year simulation run. Annual nesting effort is based upon expected nest densities previously presented in this section, and adjusted within the model for proportional increases/decreases in the available female nesting population, estimated by the model for each simulated year. Nesting success is based upon both constant (infertility, predation, dessication, etc,) and variable sources of egg mortality (nest flooding) as documented by Kushlan and Jacobsen (1990) and by data previously presented in this section.

#### Alligator population simulated responses.

A comparison of simulated alligator population parameters resulting from the natural and the four other water delivery alternatives is presented in Table 16. Average alligator population size for the 14 year evaluation period was approximately one third greater for modeled natural flows than for any of the proposed alternatives. Peak population sizes resulting from natural flows were also greater than twice that of maximum population sizes obtained for the other water delivery alternatives. Nesting success with natural flows was also significantly greater and the frequency of significant nest flooding events only one-fourth that of the other proposed deliveries.

The difference in predicted alligator population sizes for the natural simulation runs compared to any of the four alternatives was related to increased nesting effort and success and reduced drought-related mortality of smaller

size classes. Dry season lag flows from northern reaches of the Everglades catchment area maintained greater downstream, dry season stage durations in the evaluated area, particularly within Shark Slough, for most years. Alligator nest production and survival rates of younger alligators are correlated to these late dry season stage durations.

The natural distribution of flows also provided an increased area of habitat suitable for nesting (Figure 42). Under the other management alternatives, deep water depths maintained in the impounded marshes of WCA3A reduced the overall area of suitable nesting habitat within the evaluated area during most simulated years. A significant reduction in the frequency and magnitude of nest flooding under the natural simulation runs also resulted in higher rates of nesting success compared to any of the other modeled alternatives. Under the natural simulation, a better correlation existed between the timing of early and late wet season peak flows compared to the modeled alternatives. The peak nest construction and egg laying period for alligators in the Everglades occurs during early wet season peak flows (late June/early July). Egg clutches within the nest are deposited approximately one-half foot above prevailing water levels at the time of egg deposition (see Review of Published Data). Increases in water depths during the following incubation period in the natural simulation rarely exceeded that height, significantly reducing occurrences of nest flooding, when compared to the other alternatives. Consistent and significant flooding of alligator nests occurred within WCA3A and downstream of the S12s for most years of the simulation period with all the management alternatives (Figure 43).

Alligator population stability attributes demonstrated by these simulation runs, and biotic instabilities in relation to frequent drydown events, are reviewed in the following Discussion section of this paper. Major and frequent drydowns adversely impact aquatic prey populations that are important food sources for alligators. Interannual effects of major drydowns require several years for recovery of aquatic food webs (Loftus and Eklund, 1989). Major drydown intervals, occurring as frequently as that predicted for the modeled management alternatives, would prevent such recovery and lead to a downward trend in the system's overall aquatic productivity and capacity to support higher order consumer populations, represented in this case by the alligator.

The alligator population simulation model used to compare population responses to these water delivery alternatives predicts responses based on correlations with surface water conditions only. The model does not consider, therefore, decreasing standing crops of prey bases resulting from interannual affects of frequent and major drydowns as modeled for the proposed water delivery alternatives. If

the model was modified to assess the effects of declining prey bases on alligator population sizes and stability, the predicted responses to the four proposed water delivery alternatives would have been even lower, compared to natural simulated flows. Egg loss to arrested development was also treated as a constant in the model. Increased egg loss from arrested development does occur, however, during major drydown events, and should be modeled as a variable. Reproductive success would have been even lower for the four management alternatives, compared to the natural scenario, due to the increased rate of arrested development that would result from the greater frequency of drydowns that occur with these alternatives.

The innudation patterns that were characteristic of the four management alternatives did not provide natural improvements to restoring downstream, dry season flows within the central and southern Everglades. Water deliveries under the two base alternatives were a function of regulatory schedules. Resultant flows through the S12s were not into the main channel of the central flowway, and were inefficient in establishing downstream surface water pools that traditional occurred in the area prior to recent water management regulation. Past actual flows under modified minimum deliveries (NPS, 1990), similar to these modeled base condition alternatives, did not in fact restore functional downstream surface water conditions within this central flowway.

The two rainfall based alternatives did not adequately produce the natural, dry season lag flows to the central and southern reaches of the Everglades catchment area. This deficiency could be corrected through the development of better estimates of rainfall-runoff relationships that more closely approximate lag, dry season flow volumes of the natural simulation. The basic rain-driven alternative included planned modifications to water control structures to allow for more natural flow distributions across the central flowway. Modeled flow distributions for this alternative did provide approximate flow distributions as represented in the natural system simulation.

The ACE hydrology model used to simulate flows under all these alternatives did not include monthly water depth distributions for the downstream mangrove estuaries or the short, hydroperiod marshes along the eastern edge of the system. Historically, these areas were also important to alligators within the southern Everglades (see Review of Published Data). The freshwater zones of these estuaries provide important drought refugia to the alligator population. The dry prairie marshes along the system's eastern edge once provided extensive alligator nesting habitat. Future hydrological modeling efforts need to include these areas, if alligator population modeled

responses are to have the level of realism required to properly evaluate population responses to simulated system flows.

#### General Discussion.

Contingent characteristics of alligator populations are dependent upon both fundamental environmental and fundamental species characteristics (DeAngelis, 1989). Fundamental environmental characteristics of wetlands such as soil types and depths, inundation characteristics, and resultant impacts on aquatic food webs and prey species abundance and availability, as well as the number of suitable months available for feeding activity and growth, influence differences in fundamental species characteristics between distinct alligator populations. These differences, or contingent characteristics, between distinct alligator populations are represented by variable growth rates, maximum body sizes obtained, ages at onset of sexual maturity, etc., and vary for populations in different areas of the species geographical range.

#### Fundamental environmental characteristics of wetlands in relation to the American alligator.

Fundamental environmental characteristics of wetlands are comprised of both abiotic and biotic factors important to crocodilian life history aspects and population stability and persistence. A summary of these factors are listed in Table 17.

#### Abiotic factors or conditions.

The thermal, hydrological, salinity, and fire regimes of wetlands, as well as the topographical and landscape pattern or features of a system, are major determinants to the contingent characteristics of alligator populations. Spatial and temporal characteristics of these environmental factors and their effects on the basic life history aspects of the American alligator are summarized below.

#### Thermal regime.

The thermal regime of a wetland influences the energy budgets of alligators in relation to the amounts of food consumed, metabolic expenditures, and resulting growth patterns and rates. Growth patterns and rates also influence the time period required for alligators to reach sizes required for the onset of sexual maturity, population size - fecundity and size/age-specific survival rates, population composition, and habitat utilization. Temperature characteristics at nest sites also determine the sex ratio of hatchlings, that also influence population structure.

Energy budgets of alligators in relation to the thermal regime have been proposed as a limiting factor on growth rates, or indeterminate growth patterns, of alligators in the Everglades. Minimum temperatures required to initiate feeding, and the duration of winter temperatures either above or below this threshold, as well as seasonal temperature extremes, particularly during droughts, affect the metabolic rates, growth and reproductive patterns of alligators. Limitations on growth or reproduction also influence the population's rate of increase or decrease, and resulting changes in alligator population size or stability.

#### Hydrology regime.

The affect of these thermal parameters on the demographic patterns of an alligator population are also correlated to the spatial and temporal characteristics of the wetland's hydrologic and related salinity regimes. The frequency, magnitude, and duration of drydowns within the Everglades are a major driving variable affecting the alligator population's annual productivity, survival rates of sex and age classes, and recruitment of subadults into adult age classes (see Review of Published Data and New Data). These demographic parameters affect the population's persistence, both in terms of alligator seasonal and long-term occupancy of an area, and the actual, minimum viable, or genetically effectively population sizes sustained within an area over time.

Reduction in the distribution and areal extent of core alligator habitat within the Everglades since the 1950s, and resultant declines in the alligator's overall numbers, may be attributed to fundamental changes in the system's hydrologic regime. Changes in occupancy rates of formerly extensive dry and wet prairie habitats, and of downstream estuaries of the system, have been related to the changes or reduction in the maximum area of innudation, seasonal flow volumes and distribution, and the timing of seasonal flows within the Everglades catchment area. Changes in these hydrological parameters during the recent past have altered the hydroperiods of formerly occupied dry prairie habitats, as well as the predictability of seasonal surface water flows through the system's central flowway, and the quantity and timing of freshwater flows into downstream estuaries (see Review of Published Data and New Data).

#### Salinity regime.

Reduced upstream, freshwater sheet flow into downstream estuaries also influences estuarine salinity regimes. Salinity ranges affect alligator feeding rates and food consumption, the suitability of freshwater estuarine zones as nesting habitat and for juvenile survival, as well as the

use of tidal rivers, creeks, tributaries, and inland bays within this zone as drought refugia by alligators during times of extreme thermal and food - related stress.

#### Topographical and landscape patterns/features.

Reduction in freshwater flows to the downstream reaches and estuaries of the system during the 1960s, and resultant, intensive wild fires that occurred concurrent with these reduced flows, breached old, inland coastal beach rims or natural berms bordering the headwater areas of these estuaries. Seasonal drydown characteristics of the hydrologic regime that were attenuated by large, surface water pool formations, maintained in upstream, freshwater habitats within the southern Everglades by the impoundment effect of these natural berms, were subsequently reduced, increasing the severity of seasonal drydowns, while simultaneously reducing the effectiveness of these drought refugia for alligators during drydown events. Salinity regimes within these freshwater estuarine zones were also affected by the reduction in the size, areal extent, and duration of these downstream pool formations. Such alterations in landscape features of a system may have far reaching affects on resident alligator populations.

The topography and ground surface features of a system are important to all life history aspects of alligators. Open, deep water areas are required for courtship and mating. Nest sites are located in close proximity to ponds or permanent water areas, particularly during low surface water conditions or during drought. These permanent or persistent deep water areas offer drought refugia, as well as do depressions, solution holes, or caverns in eroded limestone bedrock, that provide underground dens or black body conditions (thermal sinks) during dry and thermally stressful periods. Canals, rivers, creeks, tributaries, and open water areas or shallow lakes are also used as travel routes by feeding alligators; particularly by adult males, and as staging and courtship areas for breeding groups.

The ponds occupied and kept open by alligators are also important landscape features affecting marsh fish survival during droughts, and subsequent recruitment rates within marsh areas following major drydown events (Loftus and Eckland, 1989; Loftus, per. comm). The diversion of sheet flow from the northeastern section of the historical Shark Slough flowway, from the early 1960s through the early 1980s, contributed to a decline in alligator occupancy of the area. Ponds formerly occupied by alligators have silted in, following invasion by hydric plant species, and no longer provide drought refugia for marsh fish populations.

Attempts at restoration of sheet flow to this area, beginning during the early 1980s, have not resulted in significantly increased marsh fish populations and wading bird foraging within the area. Alligator occupancy also remains extremely low, as does the occurrence and associated density of ponds, resulting in reduced recruitment rates and standing crops of marsh fish populations following seasonal drydowns, and an associated reduction in wading bird foraging within this area, compared to adjacent slough habitat (Figure 44). The importance of topography and landscape features to alligator occupancy of an area, also affects the role of the alligator in the continuance of ecological processes important to other biological components of the system. These fundamental, biotic components of the system are also important to the contingency characteristics of alligators within the Everglades.

#### Biotic conditions.

Fundamental biotic components of the system that are important to alligator life history aspects include: landscape heterogeneity, prey species availability, interspecific competition for prey, as well as intraspecific, density dependent factors or competition for food and space, that affect an individual's growth, cannibalism rates within a population, and vulnerability of individuals to predation.

#### Landscape heterogeneity.

Aspects of landscape heterogeneity that influence alligator occupancy and habitat utilization are important at both the micro and mesohabitat scales. As an ectotherm, the ability of an alligator to regulate its internal body temperature in response to lower and upper temperature extremes is critical to its survival. This ability is dependent upon several landscape features and related environmental conditions within its normal activity range. The presence of a permanent or stable body of water (used as a heat source or thermal sink), a blackbody cavity or den for use during major drydown events, shade or shaded water areas from radiation during the hot summer months (provided by dense, grass vegetation or tree canopies), and a basking site during cool periods, are critical landscape features enabling the alligator to maintain its body temperature within tolerable limits during high or low temperature extremes, through normal thermoregulatory behaviors.

In the Everglades, several, small open water ponds with well defined banks, often connected by trails through the marsh grass, a high interspersed of dense and open grass cover types, and the presence of tree islands, characterize high density areas of "resident" nesting females and pods of

young. At the mesohabitat scale, proximity to a major, permanent body of water also appears important to alligator occupancy of marsh areas that are without exposed, eroded bedrock to provide denning sites required by alligators for survival during major drydown events or drought.

#### Prey species availability.

The availability of alligator prey species is apparently higher within shallower water marsh, or the edge of deep water habitats, in relation to other life requirements of alligators. Proximal factors affecting alligator prey vulnerability and prey suitability also appear greater. Alligators within lake habitats frequently inhabit lake littoral zones, declining in number with increasing distance from the shoreline. In the Everglades, occupancy of the edges of deep water impoundments also appears highest (Schortemeyer, pers. comm.), with nesting restricted to edge habitats during most moderate to high water years. During dry season declines in marsh water level, however, both small and large aquatic prey species, and terrestrial prey, are increasingly concentrated within or adjacent to deeper water bodies, including interior marsh ponds, tidal rivers, creeks, and tributaries, and within artificial canal habitats.

During the drought of 1989, a number of adult alligators that remained within interior marsh ponds and/or canals were observed each month of the dry season feeding on large turtles, as well as wading birds and river otters, that frequented these ponds. Ponds of alligator young in interior ponds were also observed feeding on increasing concentrations of small fish within these ponds as the dry season progressed. Wading bird foraging about ponds also increases as the dry season progresses, providing potential prey for subadult/adult sized alligators; the larger wading bird species also represent potential predators on hatchling alligators, confined within interior marsh ponds during seasonal water level declines.

#### Predation, Inter- and intraspecific competition.

Predation on eggs, cannibalism rates on smaller sized alligators, and antagonistic mortality also increase during drydown events (see Review of Published Data and New Data). Periods of indeterminate growth occur more frequently during these events, as the marsh floor dries, and alligators concentrate in drought refugia; predation by wading birds and alligators on increasingly concentrated marsh fish populations eventually reduce prey availability, limiting food intake, as thermal stress and metabolic costs increase.

Predators that frequent these ponds, particularly during drydown events, either compete with alligators for declining populations of prey, or prey on alligator pods of young confined within these drought refugia or ponds during the dry season months. Interspecific predators observed preying on alligator young include large fish, bullfrogs, turtles, wading birds, hawks, river otters, raccoons, bobcats, and panther (Craighead, 1968; Neil, 1971; Fleming, 1975; Bass, pers. comm.; Schortemeyer, 198 ; ). Such predators may also be consumed by larger alligators that normally reside in these ponds (Craighead, 1968; Neil, 1971; Fleming, 1975; Fleming, pers. observ.).

#### Fundamental species characteristics of the American Alligator.

Crocodylians descended from ancestral forms over 230 million years ago. Their evolutionary lineage is conservative, with all lines of descent toward specialization perishing during their long evolutionary history. Present morphology of the American alligator has remained essentially unchanged since the Miocene period over 25 million years ago. Present alligator populations are characterized by low genetic variability and divergence (see Review of Published Data).

Fundamental species characteristics of the American alligator are summarized in Table 18 and discussed below. Fundamental species characteristics of alligators appear adapted for coevolution in stable, aquatic systems.

#### Longevity, maturation schedule, maximum body size, and fecundity.

Individuals in wild populations have long life spans of up to 50 years, characterized by nearly continuous growth, resulting in large adult sizes. The maturation schedule is very long, requiring from 10 - 18 years before the onset of sexual maturity. Potential fecundity is moderately low (ranging from an average of 28 - 39 eggs/clutch within distinct populations), increasing with age until senesce at old ages.

#### Habitat generality.

Habitat generality is related to the permanency of water and/or the occurrence of suitable drought refugia. Highest population densities occur in marshes in which such drought refugia are numerous, or where drydown intervals are long and drought refugia nearby in adjacent habitats.

### Feeding generality.

Alligators are also versatile and selectively opportunistic predators, feeding on a wide variety of prey types and sizes. Diet composition varies with increasing size through a long life span of nearly continuous growth. This variation in diet of different sized alligators within an area allows for high potential numbers of individuals among overlapping size classes to share suitable habitat.

### Dispersal ability.

Alligators are also capable of responding rapidly to changes in marsh water depths, by dispersing to drought refugia during seasonal declines in water levels or during drought, and by rapid dispersal from such refugia with the return of normal seasonal rainfall and increasing marsh water depth (see Review of Published Data).

### Maternal care.

Behavior of nesting females, exhibiting complex nest site selection choices in relation to varying environmental conditions, and the guardarian role of attendant nesting females of the nest during incubation and of the young following hatching, also increases reproductive performance, particularly in fluctuating or unstable environments where potential predation may be high. Maternal protection occurs at a size or age in life when the young are extremely vulnerable to such predation.

### Environmental tolerances.

Environmental tolerances of alligators to changes in thermal, hydrologic, and salinity conditions also determines the upper and lower limits, or environmental characteristics, of habitats occupied by different size classes of alligators.

### Thermal tolerances.

In terms of thermal conditions, the frequency, magnitude, and duration of summer or winter droughts and temperature extremes associated with these events, as well as winter freezes in the northern parts of its range, influence energy expenditures or metabolic costs of activity in relation to the availability of prey populations, the amount of food consumed, the available number of months for growth, and resultant growth rates. Lower limits to survival occur at approximately 4 - 5 C ( 32 - 41 F) (Brisbin et al, 1982) and upper limits at 34 C (93 F) (Wilber, 1960) of body temperature. Feeding activity of laboratory animals is not initiated at body temperatures below 22 C (72 F) (Coulson et al, 1973). Feeding activity and the amount of food consumed and

converted to body growth in free ranging individuals is dependent on external air and water temperatures, in relation to the thermoregulatory behaviors and age of the individual, and prey availability.

#### Hydrologic tolerances.

The hydrologic regime of an aquatic system also determines seasonal occupancy rates and utilization of marsh habitat types by size classes of alligators. Upper and lower climate boundaries of seasonal activity ranges are related to changes in marsh water depths. Short term occupancy of an area will depend on seasonal water depth extremes, while long term occupancy may be related to annual average stage duration and intervals between major drydowns. Too frequent drydown intervals (less than once in every five - seven years) may limit the occupancy and nesting frequency within an area, if numerous drought refugia are not available or nearby, as will excessive water depths (greater than 45 cm) for occupancy and for nesting during the nest construction period. The duration of ground water in drought refugia is also important within short hydroperiod areas throughout the dry season months. Maintenance of adequate ground water levels allows for more continuous occupancy and nesting within these marsh habitat types (see Review of Published Data and New Data).

#### Salinity tolerances.

Occupancy and utilization of marsh habitat types are also determined by salinity tolerances of alligators. Salinity tolerances vary by the size/age of individuals. High salinity ranges affect habitat types used for nesting, with most nesting limited to marshes with salinities less than 9 ppt. Upper salinity ranges are particularly important for hatchling survival. Exposure to salinities exceeding ppt for up to two months can be lethal to hatchlings (Joanen, 19 ). Salinities greater than 3 ppt may also affect food consumption rates and capacities of alligators, retarding growth rates and maximum body sizes obtained (Chabreck, 19 ). Marshes with salinities greater than 10 ppt are not normally utilized by alligators (Joanen and McNease, 198 ).

#### American Alligator contingent population characteristics and persistence in a changing Everglades.

The fundamental environmental characteristics of major wetlands occupied by the American alligator within several areas of its geographic range are summarized in Table 1. A comparison of Everglades alligator contingent population characteristics to other geographic populations within these wetlands is presented in Table 19. Differences in these contingent characteristics are compared in terms of mean

population density, growth or body size at comparable ages, age to maturity, clutch size, the frequency and intensivity of nest defense and maternal care, and measures of mean levels of genetic variability.

Generality, differences in these contingent population characteristics are greatest between populations in the northeastern extremities of the species range (within the Atlantic coastal plain) and the more southern populations located in wetlands within the western Gulf coastal plain of the southeastern United States. The southernmost population of the American alligator, occurring within the Everglades, is an exception to the directional trend in differences between most contingent characteristics of these populations. Everglades alligators grow at slower rates and reach sexual maturity at an older age, produce smaller clutch sizes, and adults also remain longer in size classes having higher rates of size - specific mortality, than other southern populations (see Review of Published Data).

Everglades alligators, however, demonstrate the most aggressive nest site defensive behaviors, and resulting average egg loss to predation is the lowest reported for any geographic population. Lowest nest defense and the highest predation rates on eggs (50 - 87 %) are reported for the more northern populations that inhabit relatively more stable wetland systems. The occurrence of nest defense increases as average predation rates decline to approximately 16 percent in wetland systems in north central Florida and south Louisiana ( systems characterized by moderate water level fluctuations). Nest defense is highest and predation lowest (averaging only 2 percent) in the Everglades (a system characterized by pronounced, seasonal water level fluctuations).

Differences in egg losses to predators within these range parts appear related to the relative stability of water levels among wetlands and subsequent differences in predation patterns and alligator nest defense. Raccoons are an important predator on alligator eggs within these systems. The frequency and intensity of raccoon predation on alligator eggs and young has been related to seasonal differences in water level fluctuation and subsequent raccoon movement patterns and food habits (Fleming et al, 1976, Nichols et al, 1976). Predation rates on alligator eggs within nests in coastal Louisiana and the Everglades generally increase during drier years in which water levels fluctuate below normal ranges. Increased parental care by nesting females in the Everglades, particularly increased nest defense during drier years, appears to be an adaptative response to compensate for constraints on reproductive performance and juvenile survival in a more fluctuating, unstable, and stressful environment.

Other contingent characteristics of the Everglades alligator population are more closely associated with those of northern populations, where a limited number of suitable growing months are available each year. Alligators in the Everglades remain active for longer periods throughout the winter dry season than alligators in these northern populations. Frequent periods of indeterminate growth, decreasing with increasing size class, however, characterize the more active winter dry season period of the Everglades. Increased metabolic costs during the mild winter period, and a lower prey base than that occurring in other Gulf coastal plain wetlands, has been proposed as the basis for an apparent food limited population within the Everglades (see Review of Published Data). Past and present human alterations in the system's natural hydrologic and related salinity regimes have further decreased the stability of trophic resources availability to Everglades alligators (see Review of Published Data and New Data).

#### Stability attributes of the Everglades alligator population.

The historical or predrainage Everglades of southern Florida once covered an area of approximately 4000 square miles, and extended a distance of over 90 miles from its headwaters to the estuaries of Florida Bay and the Gulf of Mexico. Since the late 1940's, almost half (1960 square miles) of the original area of this wetland system has been lost to urban and agricultural development, or to overdrainage and invasion by exotic vegetation. The remaining natural areas of the Everglades have been furthered altered by construction of a massive system of canals, levees, and water storage impoundments. Only 20 percent (800 square miles) of the historical Everglades remains undeveloped and outside of impounded marsh areas, and occurs in the downstream reaches of the Everglades catchment area within Everglades National Park and a portion of the Big Cypress National Preserve (Johnson et al, 1990). Water management practices have also altered the distribution and timing of seasonal flow volumes from northern to downstream reaches of the catchment area, reducing the persistence of downstream dry season pools and increasing drydown frequencies, compared to estimated natural and past actual flows (SFWMD, unpublished data; NPS, unpublished data; Craighead, 1968).

Everglades alligator contingent population characteristics are influenced by such fundamental changes in spatial and temporal characteristics of the system, and by related impacts such changes have on the wetland system's productivity and the availability of important alligator prey populations. Fundamental species characteristics of the American alligator that provide resistance and structural stability to such perturbations or disturbance, and recoverability or resilience from these perturbations,

well as the documented occurrence of mercury concentrations in the aquatic food webs of the system and in the alligator population, represent present trends in habitat reduction and degradation.

Long term changes in the system's hydrologic regime are also detrimental to alligator population stability. Simulated alligator population responses to an increased frequency, magnitude, and duration of drydown events, in relation to the present seasonal timing of flows and increasing wellfield diversions modeled for all restoration proposals currently under consideration, portray a population that demonstrates increasing biotic instability in relation to abiotic events (drydowns and droughts), intensified by density-dependent biotic factors (increased food competition, cannibalism, and significantly reduced reproductive effort and success).

#### Life strategies.

Alligator populations are capable of rapid rates of increase related to the relative large clutch sizes of potential nesting females and the long life spans of adults in the population. This potential rate of increase and long life spans of adults reduces the interval of time to extinction in relation to demographic or environmental variability. The increased frequency, magnitude, and duration of drydowns, however, experienced since recent water management, and future increased drydown frequencies predicted as future water consumption demands necessitate additional well field diversions from the system, represent long term changes in periodicity, and not seasonal patterns of variability, in environmental conditions. Such directional changes in long term periodicity of seasonal flows represent alterations in the system's natural hydrologic regime that threaten the species population stability and long term persistence within the Everglades ecosystem.

Characteristic alligator population structures and rapid rates of increase are dependent on stable resources (food and water) for reproductively active females, that have highly restricted activity ranges throughout a year, and comprise only a small porportion of the total population (less than 5%). Adverse, directional impacts on this subsegment of the population can cause rapid and dramatic population declines. The unrestricted harvesting of adult females during the first half of this century contributed to rapid population declines ( ). Simulated harvesting strategies of alligator populations in south Louisiana also demonstrated the need to protect this subsegment of the population (Nichols et al, 19 ). Oscillation in age class structures in simulated south

Louisiana and Everglades alligator populations and rapid declines in overall population numbers, in relation to simulated drydowns, also resulted from drydown impacts on the reproductive performance of nesting females within each population (see Review of Published Data and New Data).

Sufficient data are not available to provide meaningful estimates of actual, minimum viable, and (genetically) effective population sizes for the Everglades alligator population (see Conclusions). Alligator population model responses to simulated water delivery flows in the post - drainage Everglades landscape indicate that estimated population sizes may be approaching the lower limits of minimum viable population sizes. A minimum viable population size requires spatial and temporal characteristics within an Everglades landscape that allows for the alligator population to recover from natural disturbance regimes. The occurrence of major drydowns throughout the system are perturbations or disturbances once associated with five to seven year rainfall repeat frequencies, characteristic of south Florida's climate and rainfall regime ( , 19 ).

Declines in surface water flows and drydown intervals associated with these rainfall patterns now occur with greater frequency than that expected, based on these rainfall repeat frequencies. The biotic instability demonstrated by the alligator population's modeled responses to these increased drydown frequencies are indicative of a population with wide population fluctuations and associated age class oscillations. Populations with widely fluctuating numbers and unstable age distributions are themselves unstable and subject to possible drastic declines in relation to abiotic events, requiring management intervention before recovery is achieved.

Reduced upstream, dry season flows have also altered the salinity balance of the system's downstream estuaries that are used as drought refugia by alligators in the southern Everglades during major drydown events or droughts (Craighead, 1968). Increased dry season estuarine salinities reduce the estuaries' effectiveness as drought refugia for dispersing alligators. In the estuaries, increased salinities related to reduced upstream, freshwater flows further concentrate dispersing alligators, resulting in increased cannibalism rates, competition for suitable space and for food, that further intensifies the biotic instability of the alligator population to drydown events.

Everglades restoration goals should not only seek to maintain a minimum viable population size for such keystone species, but also to maintain the genetic variability of the population, its effective population size, over greater time periods spanning generations. The

Everglades has created an additional loss to the annual production of an alligator population already characterized by a smaller, average clutch size (25% lower) and reduced nesting effort (50%) in the naturally fluctuating environment of the Everglades, compared to other alligator populations with higher baseline reproductive potentials (greater clutch size and nesting effort) inhabiting other wetlands (Kushlan and Jacobsen, 1990).

Other sources of egg loss also occur during the incubation period. Predation and the inversion of eggs during egg laying can result in additional, significant losses. Although high egg loss due to predation has been reported for other alligator populations, ranging from 16.5 % in south Louisiana and 56.3% in north Florida to 86.4 % in Georgia ( ), egg loss to predation in the Everglades is relatively low (less than 5 %). A higher occurrence of nest guarding by females in the Everglades (Kushlan and Kushlan, 1979), the remote location of most nests away from upland areas or edge slough habitats , and an apparent lower number of potential predators on alligator eggs may explain the low predation rate.

Death or malformation of embryos may also result if the long axis of the egg during egg deposition is at right angles to the nest base, i.e. eggs laid upright. Ferguson (1983) hypothesized that " the death of embryos following egg inversion may explain why viviparity never evolved in the Crocodilia...During the evolution of viviparity, there is usually an intermediate stage in which the embryo develops inside an egg retained within the oviducts of the female. However, in taxa in which the embryo attaches to the shell membrane and turning or inversion result in embryonic death (as in Crocodilia), this intermediate stage is unlikely to be achieved. The absence of crocodilian viviparity may also be related to increased dependence of embryos on eggshell calcium as compared to the very slight dependence of snakes and lizards (Packare et al, 1977), the absense of biological advantages for prolonged egg retention, and the evolution of nest guarding (Tinkle and Gibbons, 1977)."

#### Hatching.

The mechanics of hatching are similar in all crocodilians. Growth and movement of the developing embryo strain the eggshell, which has already been weakened by the embryo's mobilization of eggshell calcium and extrinsic degradation through bacterial action, until longitudinal cracks develop during the seventh week of incubation, followed by diagonal cracks, and shell flaking just prior to hatching. The embryo later punctures surrounding extraembryonic and shell membranes with a "caruncle", thereby opening the egg (Ferguson, 1985).

Hatching triggers may involve mechanical stimuli and vocalizations. Growth and movement of the embryo bursting the eggshell, increasing levels of waste products, decreasing egg water, the progressive inadequacy of gas exchange, and temperature increases may also stimulate hatching. The hatchling has a distended abdomen full of absorbed yolk that serves as a food supply for the first few weeks until the hatchling begins feeding on small-sized prey within the nesting site (Ferguson, 1985).

#### Nest site selection.

Nest temperature and humidity affects on embryonic development and survival, susceptibility of eggs to flooding and eggs and hatchlings to predation, as well as the sex determination of hatchlings, are all correlated to the nesting site selected by a female. Ferguson (1985) has reviewed the complexity of factors that influence the site selected by females for nest construction and identified several probable factors, including: social interactions with other animals, soil and vegetation characteristics at the nest site, proximity of the site to water, site temperature, degree exposure to sunlight, and height of the site above water level. Although the affect of many of these factors on nest site selection are not well understood, he pointed out that nest site selection is of an immediate importance to a population's fecundity, crocodilian reproductive strategies, and the role of incubation temperature in determining sex ratios of hatchlings.

#### New Data.

##### Introduction.

Continuing declines in higher order, consumer populations within the remaining natural areas of the Everglades have raised wide public concern, particularly for population declines within the downstream reaches of the system included within Everglades National Park (ENP). In response to these declines, an experimental water delivery program to the Park was initiated in 1983. In 1985, the National Park Service (NPS) also initiated an additional series of studies to document and investigate the impacts of these experimental water deliveries on key faunal components of the system, concurrent with other ongoing ecological and hydrological studies and evaluations. These additional studies focused on environmental factors influencing the distribution and abundance of selected keystone and indicator species populations within the central and southern Everglades (Fleming, 1986).

The American alligator, as a keystone species of the system, was included for study. Past research on the alligator in the Everglades and within other geographic populations has demonstrated the sensitivity of alligator population stability to changes in the annual production and survival of young (Nichols et al, 1976; Jacobsen and Kushlan, 1984). Within ENP, recent downstream water management regulation has adversely impacted the reproductive success of nesting alligators, particularly with respect to high egg losses during the late incubation period, resulting from above normal levels of nest flooding (Kushlan and Jacobsen, 1990). A study was therefore initiated in 1985, concurrent with implementation of new rainfall-based, experimental water deliveries to ENP, to continue and expand the NPS's past research efforts on alligator reproductive ecology within the southern Everglades.

Objectives of the study were: (1) to document annual nest abundance patterns and hatching success, (2) to identify and investigate environmental correlates influencing changing nest abundance and egg mortality patterns observed, (3) to relate these findings to experimental, water delivery characteristics, where appropriate, and (4) to provide baseline data for assessment of future water delivery scenarios, as well as (5) to identify hydrobiological relationships for inclusion within an alligator population simulation model, developed for testing hypotheses concerning alligator population stability in relation to changes in the Everglades hydrologic regime.

#### Study Area.

The study area selected (Figure 10) included approximately 1,104 square kilometers (110,400 ha.) of wet prairie and slough marshes comprising the major central flowway of the southern Everglades, Shark Slough (SS). The flowway or slough represents the highest occupancy area of nesting females within the post-drainage, southern Everglades landscape. Previous NPS alligator research was also conducted within this study area (Jacobsen and Kushlan, 1984, 198 ; Kushlan and Jacobsen, 1990).

The slough is bordered on the east by overdrained, high, dry prairie rockland marshes, to the south and west by fresh to slightly brackish mangrove estuaries, to the northwest by a dry prairie rock ridge, and to the north by impounded wet prairie and slough marshes comprising the water conservation areas (WCAs) or impoundments of the central and northern Everglades (Figure 11). Eroded, limestone bedrock underlying the central slough is overlain with muck deposits, graduating to shorter hydroperiod marls along the slough edges. Marl deposits also occur within eroded, bedrock depressions of the dry prairie, rockland marshes to the east of the slough. Sandy marls underlie the dry

prairies to the northwest (Figure 12). Prominent landscape features within the slough include tree islands and numerous small, deep water ponds, interspersed across a mosaic of dense sawgrass stands and open, sedge marshes.

Surface water flows into the slough from an impounded marsh area (WCA3A) immediately upstream are regulated by four water control structures (S12s) located along the western portion of the slough's northern flow section. An additional water control structure (S333) passes a porportion of these flows or discharges to the eastern portion of this flow section (Figure 13). Resultant downstream surface water conditions within the slough are dependent upon the seasonal quantity and flow distribution of these upstream discharges, and local rainfall over the slough.

Under the current rainfall-based deliveries to the Park, seasonal upstream discharges into the slough, during normal rainfall years, and related downstream changes in marsh water depths, usually peak during the late wet season months, decline during the winter dry season, and increase again in the early wet season with the onset of spring rains (Figure 14). Two thirds of the upstream discharges into the slough, however, are delivered through the S12s, outside of the historical or natural channel of the flowway, and drain onto the dry prairie, sandy marl marshes northwest of the historical Shark Slough channel or flowway. Considerable variation in seasonal and annual flows through the slough have characterized recent water management deliveries. These deliveries have resulted in increasingly frequent drydowns of extended duration and magnitude during the dry season, and high seasonal flows during the wet season months, compared to estimated natural flows before intensive, regional water management regulation was initiated in the 1960s (Craighead, 1968; Sikema et al, 198 ; SFWMD, unpublished data; SFWMD, NPS, 1990; Kushlan and Jacobsen, 1990).

#### Methods.

##### Documentation of annual nest abundance patterns.

A systematic experimental design in combination with standard aerial survey transect counting techniques was used to document annual nest abundance patterns of alligators within the slough from 1985 to the present. East - west oriented transects across the topographical gradients of the slough, and systematically spaced at 2 km. intervals north to south, were flown annually, approximately one week following an estimated mean egg laying date, calculated for each year by an egg deposition - ambient air temperature regression relationship developed from previous research

(Kushlan and Jacobsen, 1990). Survey height (40 m), strip width (250m), and groundspeed (50 knots) were standardized for all study years.

Navigation of flight lines and coordinates of all nests located within sampled areas were by reference to a Loran C navigational aid installed aboard a Bell Jet Ranger helicopter. The Loran C was recalibrated over a known ground position before all nest survey flights conducted each year during the study period. Doors were removed from the helicopter for unobstructed observation. The Bell Jet Ranger was also equipped with a radar altimeter used for accurate height control during the nest surveys.

A left and right observer counted nests within a 250 meter strip on either side of predetermined, surveyed flight lines flown across the study area. Operationally, the two strip widths along each flight line were combined and treated as a single, belt transect (500 m wide) during the survey. Each belt transect was searched as a separate block to obtain a total nest count. The area surveyed each year represented a 25 % systematic sample of the total slough area. Loran C coordinates were used to stay within the upper and lower boundaries of each sample belt transect searched for alligator nests. Nest surveys were flown between 0900 - 1500 hours to avoid harsh light conditions during early and late afternoon hours. The nest surveys were conducted during early - mid July of each year, depending upon the estimated mean egg laying date calculated for each study year. Time required to complete a nest survey varied between years, depending upon the number of nests observed, weather conditions, and helicopter availability, averaging approximately 5 days per survey to cover the study area, and ranging from 3 to 8 days over the six year study period.

An initial pilot study was conducted over the study area during the 1985 nesting season to (1) investigate the degree of visibility bias or nest count accuracy, in relation to the height, strip width, and groundspeed survey variable values given above, by comparison of nest counts obtained from both aerial and ground searches of each transect belt, to nest counts from aerial searches only, and (2) to determine the sampling intensity (percent of the total area surveyed) required to obtain repeatable results for mapping alligator nest abundance patterns. The pilot study nest survey was conducted at a 1 km. systematically spaced transect interval over the study area, using the same flight line orientation, strip width, survey height, and groundspeed selected for all subsequent nest surveys during the study period. Nest count data from the pilot study survey were then totaled for each 1 X 1 km. cell of a study area grid. Total nest counts per cell of the grid were converted to nest density estimates per cell to provide a nest density distribution map of the study area.

Repeatability of the nest density distribution documented was then compared at various sampling intensities. The initial pilot study data was used to map nest density distributions and to estimate total nest numbers at 2 - 10 kilometer "resampled" transect intervals and cellular grid resolutions. A 2 km. transect/flight line interval was selected for use in all subsequent nest surveys. This transect interval, combined with the 250 m belt transects searched along both sides of each flight line, provided a 25 per cent systematic sample of the study area. Approximately 85 per cent of the nests counted in this sample area, from combined aerial and ground truth counts, were observed using the aerial survey data only (Fleming et al, in prep).

Documentation of surface water conditions in the study area.

\* Hydro

Two sources of data were used to estimate monthly surface water conditions in the study area over the study period. Monthly, water depth distributions were estimated from contouring recorded monthly water levels at 100 hydrological stations and staff gauges located throughout the study area, using a surface contouring software package. A contoured topographical surface plane of the study area was then subtracted from the monthly, water level contours to obtain estimates of monthly, water depth distributions per cell of the study area grid. The accuracy of estimated, monthly water depths was assessed by comparing estimated monthly water depths to recorded water depths for the same months in cells where hydrological stations or staff gauges were located (Portier and Smith, 198 ).

\* Hydro patterns

In addition, surface water conditions were also qualitatively described by empirical observations during monthly flights, conducted over the alligator study area, using the same flight lines flown during the alligator nest surveys. From 1985 - 1987, three surface water categories were used to describe and document surface water conditions in the study area: dry - absence of free standing, surface water, (2) transitional - intermittent surface water, and (3) wet - continuous free standing, surface water. Loran C coordinates were recorded along flight lines where changes were observed from one surface water category to another. From 1988 on, a five category classification scheme was employed: (1) dry/dry - absence of free standing surface water with low ground water levels in ponds/depressions occurring in the bedrock or marsh floor, (2) wet/dry - absence of free standing surface water but high water levels in ponds, etc. (3) dry/transitional - intermittent surface water, area mostly dry but with scattered, small surface water pools, (4) wet/transitional - intermittent surface water, but area mostly wet, and (5) wet - continuous, free standing surface water over the area.

Monthly hydropattern maps of the study area were then developed from these data by the following procedures. A monthly surface water condition was assigned to each cell of the study area grid, based on the longitude recorded for changes in surface water conditions along each flight line. The systematically spaced flight lines were oriented east - west across the topographical gradients of the slough (bisecting each row of grid cells), and therefore were of a constant latitude, requiring only longitude recordings to document surface water changes along each flight line (or row of grid cells). Computer files containing these monthly surface water condition code values per cell of the grid were converted to a GIS data format, cell map files, and then mapped using GIS GRASS 3. software.

#### Documentation of reproductive success.

Hatching success, and the sources and extent of egg mortality, were estimated from a representative, subset of nests monitored each year at approximately two week intervals throughout the incubation and hatching periods. The sample size required to obtain repeatable results in monitoring reproductive success was also determined by resampling pilot study data on nest hatching rates at five percent nest sampling intensity increments. A twenty per cent minimum sample of the estimated total number of nests in the study area, from nests initially located in the nest survey sample area, provided repeatable estimates of nest hatching success rates (Fleming et al, in prep). This sampling intensity was used, therefore, to monitor and estimate nest hatching success rates during each year of the study period.

To evaluate nest flooding patterns of nests within the slough, monitored nests were from a systematic subset or sample of the nests located during each year's initial nest survey. Nest were selected in this manner to replicate the observed nest density distribution, mapped from each year's nest survey data. Total number of eggs, and the number of fertile and non-viable eggs (infertile or early embryonic death), per clutch were recorded at the beginning of the incubation period by landing at the nest site during the nest survey, or within the following week. Subsequent, biweekly monitoring flights were conducted to each sample nest to record the number of original eggs lost, by mortality source, throughout the incubation and hatching periods. In 1990, additional weekly flights were also conducted to each nest during the hatching period.

#### Documentation of egg laying dates within sample nests.

During the 1990 nesting season, three viable eggs per clutch were selected from each sample nest during the sixth week of

the normal incubation period. An egg from the top, middle, and lower layer of each egg clutch was selected for examination. Developmental stage and age of each embryo collected were then estimated, following an embryo development key devised from a previous study on the embryology and development chronology of alligators within the southern Everglades (Grabowski et al, in prep). The mean age of the embryos collected from each nest, based on the calendar date on which each embryo age was determined, was then used to estimate the "egg laying date" at each nest site. Estimated egg laying dates based on embryonic ages assume that no significant, oviducal embryonic development has occurred before egg deposition. This assumption and any related bias in the data is discussed in the following Results and Discussion section.

#### Data analyses techniques.

Calculation of annual, alligator nest density distributions and nest population estimates.

Nest count data and coordinates of nest locations were entered into a customized computer program developed by NPS and I.F.A.S., University of Florida, for data processing and analyses of transect count data on I.B.M. compatible microcomputers (I.F.A.S. and N.P.S., 1989). The computer program assigned nest location coordinates to the appropriate cell of a 2 x 2 km. grid calculated by the program for the study area. The program then totals the nest counts per cell of the grid, and converts each total nest count per cell to a nest density estimate, providing a cellular map of the nest density distribution over the study area. Total nest counts along each flight line are also used to calculate a nest population estimate  $\pm 95\%$  confidence interval for the study area using the Jolly 2 formula, developed by Jolly (19 ) for analysis of transect count data.

Descriptive statistics for several distribution and abundance parameters are also calculated for the survey area, or by each substratum defined, including a mean nest density  $\pm$  one standard error, maximum and minimum nest densities, and the kurtosis and skewness of the nest density distribution documented over the study area and for each defined substratum. Population estimates for the study area, and/or substratum, occupancy rates (based on the % total number of survey sample nests) for each substratum of the study area, and a chi square test for observed vs expected distribution for each substratum, are also calculated (Fleming et al, in prep). The 2 X 2 km. grid calculated by the program and used for mapping alligator nest density distributions within the study area is depicted in Figure 15.

Landscape classification analysis of the study area to define land element themes, major landscape types, and landscape categories.

*map scale*  
To describe annual changes in nest distribution and abundance in relation to landscape patterns and temporal characteristics within the study area, each cell of the grid was first assigned a separate code for its substrate type, dominant ground surface features, dominate vegetation cover type (based on a structural classification), pond density, and an average dry season surface water condition (wetness index of a cell's hydroperiod), calculated from the monthly, surface water condition values previously described. Each of these land element "map layers" or themes were then overlaid and combined into distinct associations, or map layer code combinations per cell of the study area grid, using a Gcross GIS function to classify cells according to varying land facets over the study area. Land facets (cells of similar land element code combinations) were then reclassified using a GIS expert inference system function, Ginfer, to define the boundaries of major landscape types (areas of similar land facets) and landscape categories (areas of similar landscape types) within the study area (Fleming et al, 1990).

Analyses for investigating environmental correlates to nest abundance patterns.

*surface water + abundance*  
Non-parametric, contingency analyses were then used to relate changes between nest abundance or density associated with each landscape type and varying water depth distributions, occurring during different periods of the reproductive season for each study year.

Analyses for investigating environmental correlates to egg laying dates.

The relationship between mean ambient spring air temperatures to estimated egg laying dates at nest sites and empirically documented, antecedent surface water conditions within each nesting area, prior to the reproductive season, were investigated by: (1) first assigning each nest site to either one of two surface water condition categories (nesting areas retaining surface water versus nesting areas that dried down during the late dry season), and then (2) comparing the distribution of estimated egg laying dates of nests between the two surface water categories using a non-parametric, rank test ( ,19 ).

The 95% confidence interval of the age of an individual embryo is from 8.8 days before to 8.8 days after the estimated age for sample embryos of a mean 25.5 stage. The mean stage of the sample embryos collected during the 1990 nesting season of this study was 28.01. The error about

this mean stage would not exceed 8.8 days as the technique aging error decreases with increasing embryo development stage (Grabowski et al, in prep.).

Using estimates of aging error, the difference in the egg laying dates between the two nest groups was evaluated by a Mann Whitney test. The estimated laying dates within each nest group, based on the estimated embryo ages, were first adjusted to provide a more conservative test. Laying date estimates for the nest group with the smaller mean (smaller values refer to earlier egg laying dates) were increased by a two standard deviation distance for that nest group mean (calculated by dividing the 8.8 days by the square root of the group size). A 95% confidence interval approximates two standard deviations above and below the mean. Laying date estimates for the nest group with the larger mean (later egg laying dates) were decreased by a two standard deviation distance for that nest group. Resulting individual differences in the estimated egg laying dates of nests between each nest group (surface water category) were therefore reduced, decreasing the probability that the test would find a significant difference by chance between the two nest groups.

These data were also plotted and further examined by comparison of each estimated laying date to the mean laying date predicted for all nests based on spring ambient air temperatures only. The distribution of egg laying dates for nests within each surface water category were plotted separately, and each distribution compared to the predicted mean egg laying date for all nests within the study area. The predicted mean egg laying date for all nests was based on a regression relationship previously developed between timing of egg laying and mean ambient, spring air temperatures only (Kushlan and Jacobsen, 19 ).

For verification of predicted laying dates based on estimated embryo ages, these predicted laying dates were also compared to laying dates of each egg clutch, estimated from weekly field nest checks during the hatching period. Egg laying dates, estimated from field hatching dates, were calculated by subtracting 59 days (average incubation period) from each estimated field hatching date. A paired t test was used to determine if the two sets of estimated laying dates differed significantly.

Analyses for investigating the annual variation in total nest numbers observed within the study area.

The relationship of total nest numbers to the annual area of innudation within the study area at different time periods throughout a year was examined through a simple univariate, regression analysis approach.

## Analyses of nest flooding factors.

Factors affecting the frequency and extent of nest flooding within the study area were investigated through the use of descriptive statistics to describe nest flooding patterns in relation to flooding events and water delivery characteristics (flow distribution, volume, and timing parameters) during the incubation period of each study year. Previously developed stage - discharge relationships for the slough (Sikema et al, 1986) were also referenced to relate upstream discharges into the slough, and downstream local rainfall over the slough, to changes in downstream, surface water conditions observed within the study area during the nest construction, egg laying, and incubation periods of each study year.

## Alligator population model simulations.

An alligator population simulation model, developed during a modeling workshop by a collective group of Everglades researchers and system modelers, was also used to examine population stability attributes in relation to proposed water delivery scenarios under consideration as planned, Everglades restoration efforts... The modeling approach, assumptions, and parameters used in the alligator model are presented in a user guide to an evolving, preliminary Everglades ecosystem simulation model initially developed at this workshop (Tait, 1990).

## Results and Discussion.

Results obtained about environmental correlates to nest distribution, abundance, timing of egg laying, and hatching success during the 1985 - 1990 alligator nesting seasons are presented and discussed in relation to alligator reproductive and nesting biology life history aspects summarized in the Review of Published Data. A summary of the annual number of alligator nests estimated within the study area for each study year, and the annual reproductive performance documented, are presented in Table 8. Alligator nest density distributions for selected years with high, moderate, and low surface water conditions during the late dry season, and related hydropattern maps, are presented in Figures 16 - 18. Maps of land element themes, major landscape types, and landscape categories defined within the study area are depicted in Figures 19 - 25. Annual changes in nest abundance patterns associated with these landscape elements and themes are also presented and discussed.

Nest distribution in relation to spatial and temporal characteristics of the study area.

Alligator nest distributions within the study area varied with respect to substrate (Figure 26) and vegetation cover

types (Figure 27), and also varied in relation to water depth distributions occurring during the late dry season (early follicle development period) (Figure 28), and during the nest construction period of each year (Figure 29). Lower limits of water depth that influenced the spatial distribution of alligator nests occurred during the late, dry season months (March - late April) of each year. Upper limits of water depth that influenced nest abundance patterns documented each year usually occurred during the peak nest construction period in the early wet season (mid - June/early July).

Expected nest densities for each landscape category, used to simulate nesting distributions in the alligator population model, were also calculated by (1) pooling nest count data for each landscape category over a range of high, moderate, and low rainfall years and surface water conditions, and then (2) calculating an expected nest density per category, based on the available area within each landscape category (Table 9). Average nest densities over the study period were highest (1.5 - 1.9 nests/km<sup>2</sup>) in central slough habitat types characterized by organic soils, dense vegetation, and long hydroperiods. Lowest average nest densities (0.2 - 0.4 nests/km<sup>2</sup>) occurred in dry prairie or edge habitats characterized by low organic/high marl or sandy marl soils, sparse vegetation, and short hydroperiods. All nest sites were in close proximity to deep water ponds, usually shaded or partially shaded by adjacent, willow or hardwood tree island canopies. Nest occurrence (% of total number of nests in the study area) within each landscape category also varied in relation to relative surface water conditions among years (Table 10).

Mature females apparently remained within established general nesting areas throughout the nesting season during low surface water conditions, even if such areas lost all surface water during the late, dry season months. Nesting in such areas was either absent or in extremely low numbers while the total number of nests throughout the slough was also low. In these drier years, water depth distributions were skewed to shallow water depth classes. Nesting occurred only in areas retaining surface water, and overall nest numbers within the study area declined dramatically from wetter years.

In normal rainfall years, water depths during the late dry season months were more evenly distributed, as were nest numbers among the wider range of available, water depth classes. Subsequent total nest numbers within the slough increased during these surface water conditions. In high rainfall years and surface water conditions, nest numbers declined rapidly in areas with marsh water depths exceeding 45 cm during the peak nest construction period of the early wet season (mid- June/early July). Most nesting during high



water years occurred in areas of shallower, surface water conditions, located along the edges of the slough, and on higher elevated nest sites, within central slough areas.

Nest site selection in relation to relative elevation, soil substrate, vegetation, proximity to permanent water, and related nest site, defensive behaviors.

During years of high rainfall and surface water conditions, a majority of nests ( %) were located on the relatively higher elevated sites within the natural marsh - elevated banks of ponds or edges of tree islands within the slough. During years of moderate surface water conditions, nest locations were more widely distributed among a wider variety of habitat types and relative elevations (Figure 30). In all years, a majority of nest locations ( %) were within close proximity (approximately 10 m) of a pond surrounded by willow shrubs (*Salix caroliniana*). Craighead (1968) described these willow hedges as the result of early plant invasion on newly disturbed sites. In low rainfall years and surface water conditions, virtually all nests ( percent) were located adjacent to such ponds, predominately shaded either partially or completely by willow or tropical hardwoods, comprising adjacent tree island canopies. Nests in these hot, dry years were noticeably absent from open, wet prairie marsh habitats within the slough.

Substrate type and depth, vegetation cover type, average annual stage duration, and related hydroperiod characteristics of a nesting site are all highly intercorrelated and related to relative elevation differences within the slough (Table 12). Generally, soil depth and organic content, dense vegetation, and deeper ponds are associated with longer hydroperiod sites within the central slough. Burning off of the accumulated vegetation in these areas from wildfires during the study period occurred less frequently than in higher elevated and drier sites. Abundant nesting material was normally available. Attendant females observed in these nesting areas usually remained within densely vegetated marsh (dense sawgrass stands or downstream sawgrass tails of tree islands) or in ponds adjacent to the nesting site.

Under present surface water conditions within the slough, characterized by low flow volumes during most dry season months, such central slough sites represent core nesting habitats and supported the highest average, nest densities in all but high rainfall years and surface water conditions. Such sites were also frequently occupied by larger-sized nesting females that aggressively and consistently defended the nest against human intruders. In the 1988 nesting season, one such female immediately charged the helicopter upon its landing over 45 m away from the nest site, and aggressively pursued any project personnel approaching the

During the 1990 nesting season, however, eggs were absent within 21 per cent (10) of the nests ( $n = 47$ ) located during the initial nest survey (Table 13). Such nests were well developed, with a normal base diameter and height, but lacked a cone-shaped top, characteristic of finished nests in which an egg clutch has already been laid. Of these unfinished nests, four (40%) remained without eggs throughout the nesting and incubation periods. Subsequent egg laying occurred at later dates during the incubation period in the remaining six nests (60%). An additional 7 nests (15 %) of the 47 nests located during the nest survey contained egg clutches that had been recently laid. The nesting areas in which recent or late egg laying occurred had lost all surface water during the late, dry season months (March, April), preceding the 1990 courtship and mating periods. Only one (17%) of these six nesting areas, in which late egg laying occurred, maintained ground water within ponds in the nesting area during the late, dry season months.

① In nesting areas that had retained surface water, estimated egg laying dates were normally distributed about the mean egg laying date predicted by mean ambient, spring air temperatures. In contrast, estimated egg laying dates for nests in areas that had previously dried down were highly ② skewed toward later dates (Figure 31). Simple statistics were used to quantify the difference in estimated egg laying dates between the two nest groups. The distribution of estimated egg laying dates in nests from areas that dried down was compared to the distribution of egg laying dates within areas that retained surface water during these months by a rank test (Table 14). Egg laying dates were significantly later ( $p < 0.05$ ) in nesting areas that had previously dried down compared to nesting areas that retained surface water throughout the preceding late dry season months.

Estimated egg laying dates derived from weekly field nest checks during the hatching period were used to verify the estimated egg laying dates used in the above analysis, and based on the embryo age - predicted egg laying date technique. Predicted egg laying dates based on the mean estimated embryo age from eggs collected ( $n = 3$ ) per nest were plotted against estimated egg laying dates calculated from observed hatching dates or from estimated nest hatching dates, derived from the weekly nest checks during the hatching period (Figure 32). A mid-point value (3.5 days) was used to estimate hatching dates that occurred between these weekly nest checks. Predicted egg laying dates based on the embryo aging techniques did not differ significantly ( $t =$  ,  $p < 0.05$ ) from the estimated egg laying dates calculated from weekly field nest checks. Nest monitoring values derived from weekly nest checks during the hatching period, however, had a smaller 95% confidence interval (6.85

days), compared to the embryo aging technique (8.8 days), but involved weekly field trips to obtain more precise estimates of nest hatching dates.

If egg retention and oviducal embryonic development did occur in monitored nests, then for such nests, actual egg laying dates may have been later than that estimated by the embryo age - predicted egg laying date technique. Such egg retention and delayed egg laying, however, would be expected to occur in nests within dry nesting areas. The difference in egg laying dates between the two nest groups would therefore be even greater than the dates tested, based on egg laying dates estimated from embryonic age. If this bias exists in the test data, then the test would become even more conservative, and further increase the significant difference of the test results obtained.

The 1990 nesting season occurred during drier than normal surface water conditions, but was wetter than the previous year during which a major drought (one in twenty years) occurred. Interannual affects on the productivity and standing crops of alligator aquatic prey can occur during a sequential combination of drier years (Loftus and Eckerd, 1990). Cardeilhac (1988) reported that normal, early follicle development during March - early April is correlated to the amount of protein consumed by a mature female during this time period. Interannual drydown affects, reducing the availability of aquatic prey items during the 1990 winter dry season, may have also reduced the amount of protein intact of mature females during this dry season, below that required for normal early follicle development the following spring. In these conditions, subsequent reproductive activities could also be affected, delaying egg deposition of females in these drier nesting areas during the subsequent nesting season.

Based on the previously presented statistical analysis, a hierarchical, conceptual approach to understanding the environmental factors controlling the timing of egg laying in the American alligator may provide a more useful model for relating the affects of seasonal photoperiod, ambient spring air temperatures, antecedent seasonal and annual surface water conditions ( and related affects on prey availability, protein intact, and subsequent body and reproductive condition of nesting females) to spatial and temporal patterns of egg laying during a nesting season (Figure 33). During wetter years and in nesting areas in which surface water conditions remain within normal ranges, when dry conditions are not adversely affecting the reproductive physiology of nesting females, ambient spring air temperatures may be the controlling factor determining the timing of egg laying. In drier years or nesting areas, other environmental factors, such as low water depth and associated suboptimal feeding and high (stressful) thermal

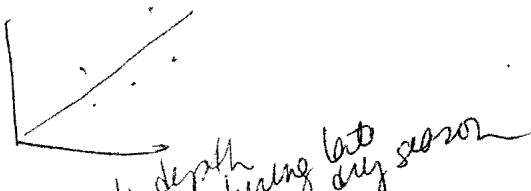
conditions, may have a greater influence on the body and reproductive condition of potential nesting females, and subsequent egg laying dates. Such a model could provide a greater degree of predictability than a univariate model, based on ambient, spring air temperatures alone.

Annual nest abundance and length frequency distributions of nesting females in relation to spatial and temporal innudation characteristics during and antecedent to the reproductive season.

\* The total number of alligator nests observed within the study varied each year (Figure 33), as did surface water conditions during and antecedent to the reproductive seasons of those years. Changes in total nest numbers within the slough each year were significantly related to the porportion of the area retaining surface water during the late, dry season months of the early, follicle development period (Figure 34). Nesting occurred most frequently in the core, central habitats of the slough that retained surface water during most years of the study period. Nest numbers within the general study area increased exponentially in relation to the innudation of additional, wet and dry prairie habitats during higher rainfall years and surface water conditions. Nests were thirteen times as numerous in 1986 as in 1985. Extremely low surface water conditions prevailed throughout the late dry and early wet season months of the reproductive season in 1985, in contrast to high, surface water conditions sustained throughout the slough during the following dry season months that preceded the 1986 reproductive season.

No evidence of genetically determined periodicities in ovulation of nesting females within the study area is confirmed by these data. The variable porportion of mature females nesting from year to year can be explained by annual changes in the areal extent of innudation preceding each nesting season. The annual variation in the area of innudation, and related influences such changes in surface water conditions have on the metabolic processes affecting the reproductive condition and/or behavior of potential nesting females in the slough, may account for the changes in nest production observed between years, particularly when food and thermal stress conditions may become limiting. In south Florida, rainfall follows a repeat frequency of high annual rainfall once in every five to seven years, usually declining each year thereafter until the next high rainfall year ( , 19 ). If genetically determined periodicities in ovulation do exist, then such periodicities could be adapted to this rainfall repeat frequency, and correlated with the associated changes in surface water conditions each year within the slough.

# nests



depth increasing late dry season

dry years smaller size ♀ nesting

During the driest (most stressful) years of the study period, in slough areas that either lost surface water or retained only low surface water conditions during the late, dry season months, length frequency distributions of attendant nesting females observed during the subsequent nesting season, appeared more highly skewed to smaller size classes. During wetter years, when higher surface water conditions were maintained in the same slough areas, length frequency distributions of nesting females observed appeared to be more normally distributed among a wider range of adult, nesting female size classes.

dry years smaller size ♀ nesting

⊗ If a more normal distribution of larger sized females do nest in wetter years, and an increasing size - fecundity relationship exists, than the mean nest clutch size for those years should be greater than during drier years. During the drier than normal 1990 nesting season, following a major drought year, the mean clutch size was significantly lower than that documented for previous years ( ,  $p < 0.05$  ). No significant inverse relationship was also found between nest clutch size and estimated egg laying dates during the 1990 nesting season (Figure 35). If an increasing size - fecundity relationship exists for females within the slough, and larger females nest earlier than smaller sized females, according to social order factors (Ferguson, 1985 ), then clutch size should have decreased in relation to later egg laying dates. These data suggest that such social ordering factors were not operative during the stressful conditions existing during the 1990 reproductive season.

A stronger, but weak inverse correlation (Figure 36) between egg mass and estimated egg laying dates during the 1990 nesting season was found, suggesting that selective pressures on nesting females may be for increased egg quality, and not increased clutch size, during stressful years and/or in environments with pronounced seasonal water level fluctuations. Nest in which latest egg laying occurred after nest construction also had increased egg mass relative to other nests in which late egg laying also occurred. If these latest egg laying dates resulted from prolonged egg retention, then oviducial embryonic development (occurring before egg deposition) may account for the increased egg mass observed. Late egg laying by larger sized nesting females could also account for the increased egg mass observed in these clutches.

The antecedent surface water conditions in the nesting area, that were significantly related to estimated egg laying dates within each nesting area during the 1990 nesting season, and favoring an apparent increased frequency of smaller sized nesting females in drier years, best explains the temporal pattern of estimated egg deposition dates observed during the 1990 nesting season. In consecutively,

wetter years, social order may then be a more influential factor affecting the temporal pattern of mating and egg laying of females, when environmental conditions again become favorable.

Larger-sized adult females within the slough also appear to suffer greater, proportional weight losses during dry years of lower food availability, and increased thermal stress, than smaller sized adult females (Dalyrample, pers. comm.). Higher energy maintenance requirements for larger sized alligators with a greater body mass and increased thermal stress (under the high temperature extremes that occur during these dry years), compared to smaller sized alligators (in relation to a smaller ratio of skin surface area to body mass for larger sized animals), may explain this differential weight loss. Under such stressful conditions, larger-sized adult females may actually have a smaller energy reserve to invest in reproduction, during and immediately following such dry years or seasonal conditions, compared to smaller sized adult females.

Under recent water management, characterized by increasing frequencies of major drydowns, the resulting low surface water conditions, reduced prey availability associated with and following drydowns, and increased thermal stress in drier years, could favor an increased nesting frequency of smaller sized females during such years, compared to that of larger size classes, particularly in a population that appears to be food limited. Given the increasing size - fecundity relationship reported for alligators, such selective pressures favoring smaller sized females to nest more frequently, particularly in drier years, could also result in a decrease in the population's fecundity, in response to the increased frequency, magnitude, and duration of drydowns occurring under present water management practices.

Major drydowns do appear to be extremely stressful on large sized adult females that remain in established nesting areas during low surface water or drought conditions. Several dead, large sized females were observed in the late, dry season months during the drought of 1989. These females had remained within interior, central slough ponds that dried down completely. These same females had been observed in these isolated ponds during the previous months, buried in the still moist muck at the exposed bottom of the drying ponds. Other occupied ponds were apparently abandoned after drying out. Alligator tracks from these dried out ponds were observed leading in the general direction of drought refugia areas. Both an adult male and adult female were also found sharing an underground den beneath another pond, that had also dried down during this same period.

With the drying of the marsh floor, alligators occupying ponds in slough areas of exposed, eroded bedrock appeared to retreat to underground dens or caverns in the eroded bedrock that provide a black body cavity. Alligators occupying ponds in areas of bedrock, overlain with dried and cracking muck, either dispersed in the general direction of drought refugia areas, or remained for unknown reasons within the dried out ponds, and died. No smaller sized subadult or adult alligators were observed remaining above ground in these ponds during monthly flights over the study area. The higher extreme body temperatures that smaller sized alligators can tolerate over a short time period (Spotila et al, 19 ) may partially explain the apparent, greater dispersal tendency of these smaller-sized animals, from isolated, central slough habitats to adjacent drought refugia areas during the drought conditions observed.

During the remaining, late dry season months of the 1989 drought, increasingly greater numbers of subadult and adult sized alligators were observed concentrating in drought refugia habitat provided by canals along the eastern and western edges of north Shark Slough, and downstream within the numerous tidal rivers, creeks, tributaries, and inland bays within or adjacent to the estuary headwater areas, immediately south and west of the slough. During late dry season flights over these headwater areas during the months of April through June, alligators observed were still concentrated in these drought refugia. Several occurrences of agnostic mortality or cannibalism were also observed between large sized alligators during each flight. Few large sized alligators were observed aboveground, however, in the remaining ponds of the central slough still retaining some ground water during this period. The reduced reproductive performance of nesting females within the slough, during low water conditions or following such major drydown events, is discussed in the following section.

Reproductive success in relation to spatial and temporal characteristics of the study area.

The major environmental variable influencing the annual production of hatchlings within the study area was the antecedent surface water condition preceding each nesting season. High or low surface water conditions influenced the number of females nesting each year, and the resultant total production of eggs (see previous section).

The greatest source of egg loss over the study period resulted from nest flooding. Other sources of egg mortality included egg infertility or early embryonic death, arrested embryonic development, and the dessication, crushing, or predation of eggs. These mortality sources were relatively constant and small for wetter years of the study, compared to egg loss from nest flooding. Total egg loss from all

sources of mortality, however, only modified the number of hatchlings produced each year, compared to the influence of antecedent, surface water conditions during the late dry season months on subsequent alligator annual nest and related total egg production within the slough.

#### Egg loss to nest flooding.

Nest flooding within the study area was related to both local flooding events and to upstream water management regulation and related water delivery characteristics to the slough. Nest flooding-related egg loss was highly variable among study years, ranging from 6 - 51 %. Egg loss to natural flooding events was relatively small for most years while water management related nest flooding resulted in losses of over half (51 %) of the total production of eggs within the slough during some nesting seasons (Table 8).

51%  
nest flooding  
vs  
rainfall  
S12's

Most nest flooding events occurred in the high rainfall and surface water flow periods of the late, wet season months each year, during the last two - three weeks of the normal incubation period (Figure 37). Water delivery characteristics for three years of the study period, 1985 - 1986, in relation to local rainfall and downstream changes in surface water depths during the alligator nesting and incubation periods, are depicted in Figures 38 - 40. The three years selected represent low (1985), high (1986), and moderate (1987) rainfall years and related surface water flows.

During the normal high rainfall and surface water flow months of the late wet season, an increasing porportion of the total volume of water discharged into the slough (up to 100 % in some study years) was delivered through the four water control structures (S12s) along the western porportion of the slough's main flow section, and discharged outside of the historical channel of the slough onto higher elevated, dry prairie marshes. Rapid and large increases in water depths, related to these discharges, occurred immediately downstream of these structures, flooding most nests to the southeast and south of the control structures, when discharges were excessively high.

In 1988, following a high period of rainfall during the late incubation period, nest flooding increased throughout the slough. Egg flooding occurred in the lower layers only of egg clutches within nests in the eastern and extreme southern areas of the slough, away from the S12 structures. Entire egg clutches within nests immediately south and southeast of the S12 structures, however, were completely innudated, resulting in a 51% egg loss due to nest flooding within the slough during the 1988 nesting season. In other study years, when wet season rainfall was more normally distributed, and upstream discharges into the slough can be

More 2  
S12's  
nature

more evenly distributed across the entire northern flow section, egg loss from nest flooding was much lower, averaging 14 %, and ranging from 6 to 23 %. Egg loss to flooding during these years was also more evenly distributed among the sample nests monitored throughout the study area.

Since construction of the water conservation areas to the north of this central flowway, predictability of the system's hydrology regime has been decreased (Kushlan and Jacobsen, 1990). Current "natural" levels of alligator nest flooding remain much higher than that estimated to occur by Kushlan and Jacobsen (1990) prior to the construction of these water retention areas during the 1960s and subsequent, intensive regional water management. Estimated egg loss to nest flooding averaged only 4 +/- 4.5 % over a ten year period (1953 - 1962) preceding recent water management regulation, compared to an average 20 +/- 32.8 % of nest flooding-related egg loss (a five fold increase) experienced under recent water management (1971 - 1982). An average egg loss of 17 +/- % to nest flooding has been documented during the six year period (1985 - 1990) of this study.

The loss of the hydrologic regime's predictability between peak early wet season water levels and late wet season maximum water level rise, the inadequate flexibility of existing water control structures to distribute high, late wet season flows in relation to the topographical contours of the historical flowway, and normal upstream discharge and flow distribution operational procedures (related to flooding concerns of agricultural interests and private land owners to the east of the slough), are intercorrelated and contribute to nest flooding. Such constraints have prevented the restoration of a more natural hydrological regime through this central flowway of the southern Everglades.

#### Other egg mortality sources.

Egg infertility and/or early embryonic death was relatively constant and low during wetter years of the study period, compared to egg mortality from nest flooding (Table 8). During wetter years, egg loss due to infertility and/or early embryonic death averaged approximately 8 per cent, and ranged from 7 to 9 per cent. During drier study years, such rates were more variable, averaging 14 per cent and ranging from 3 - 25 per cent.

Annual egg losses from crushing, by female movements over nests during the incubation period, or cracking during egg deposition, were low (less than 1 per cent). Desiccation of eggs was also low (less than 1 per cent), and occurred most frequently in the top egg layers of the clutch. Annual egg desiccation rates, however, did not increase during the drier years of this study. In dry years, low water levels usually

measure clutch height  
canopy cover  
nest parameters to success by 5

occur during the nest construction and egg deposition periods. Egg clutch heights are closer to ground surface elevation than in wetter years. The height of nests constructed do not significantly differ between such years (Kushlan and Jacobsen, 1990). The increased amount of nesting material above the egg clutches in drier years, and the shifting of nest site locations to more shaded areas and to lower elevated (wetter) sites, apparently prevented excessive drying of nests during the driest years of the study. Predation on eggs was not common, and only occurred in a few nests that were located on the drier edges of the slough. Annual predation rates over the study period averaged 2 percent, ranging from 0 - 4 per cent. Combined egg mortality from crushing, cracking, dessication, and predation was also low and relatively constant, averaging only two percent over the study period, and ranging from 0 - 5 percent annually.

nest production drought

Reduced nest production and lower hatching rates were documented in relation to the drought conditions of 1989, and reduced nest production, mean clutch size, and lower hatching rates during the low surface water conditions still prevailing throughout the 1990 nesting season (table 8). During the nesting season of the 1989 drought, and in the following year, egg mortality from egg infertility or early embryonic death, and arrested development, average 35 %, a five fold increase over the average egg loss (7%) recorded from these sources during the previous wetter years of the study. The average clutch size (24.4) in the 1990 nesting season was also lower than that recorded (27.0 - 29.7) for previous wetter years.

The hatching rate was also low for nests in which late egg laying occurred during the 1990 nesting season, averaging 47 percent, compared to higher average hatching rates (67 %) of nests in previous wetter years (1986 - 1988), during which more favorable nesting conditions occurred. This average hatching rate (47 %) for nests in which late egg laying occurred was also lower than the average hatching rate (59 %) of other nests during the 1990 nesting season in which earlier egg laying occurred. Nests in which late egg laying occurred had similar rates of infertility or early embryonic death, an apparent increased rate of arrested development, but decreased rates of egg loss from flooding, compared to nests with earlier egg laying dates (Figure 41). Later egg laying in nests occurred during higher marsh water depths of late July that resulted in higher egg clutch heights above ground elevation. These higher egg clutch heights and subsequent, low water level rise during the remainder of the 1990 incubation period, may explain the reduced rates of flooding for nests in which later egg laying occurred.

Based upon these data, adaptative advantages of late nesting (delayed mating) or delayed egg deposition within nests (sperm storage and delayed fertilization and/or egg retention) appear limited as a reproductive strategy for alligators in the slough in relation to drought. The estimated production of hatchlings ( ) during the 1990 nesting season was less than one third of the average ( ) for previous wetter years of the study, and represented approximately half of the average number of hatchlings produced each year ( ) over the study period. Nests in which late egg laying occurred contributed only % (240) to the estimated total production of young ( ) during the 1990 nesting season.

Late nesting or delayed egg laying, however, as a reproductive strategy in response to drought, may have other benefits beyond the limited number of young produced. Such late nests, or nests in which delayed egg deposition may occur, could have a greater probability of producing a higher female to male ratio of hatchlings by delaying egg laying in dry nesting areas. During the 1990 nesting season, females deposited egg clutches at later dates, in nesting areas that had previously dried down, after low marsh water depths in these nesting areas had significantly increased. Nests in wetter conditions could be expected to have lower internal temperatures than during previous dry conditions at the nesting site. Later mating and egg laying and/or delayed egg deposition in these nests during wetter conditions may produce more female hatchlings than would earlier egg laying during drier (hotter) conditions at the nesting site.

Although late nesting and egg laying, or delayed egg deposition, in drier years produces fewer young, a female is insured of producing a greater number of female progeny, compared to earlier egg laying in drier nesting sites, or if potential nesting females did not mate at all during these dry years. The normal small proportion of adult females (5% or less) comprising most alligator populations makes the continued production of biased female hatchling sex ratios an adaptative advantage, particularly for nesting females in alligator populations inhabiting wetlands such as the Everglades, with unstable or fluctuating environments, and irregular reproductive output. Nesting females that produce a greater number of female hatchlings each year would have an increased probability of passing their genetic inheritance to latter generations, compared to the production of biased male hatchling ratios in a population with surplus adult males.

Another reproductive strategy that potential nesting females could adapt in relation to drought is to reduce nesting effort (no mating or egg absorption) to conserve energy in adverse conditions (to improve their survival chances and/or

nesting attempts during the following nesting season). During the 1989 drought, and during other dry years of the study, nest numbers were low. Nest numbers in subsequent nesting seasons, however, increased significantly if higher surface water conditions prevailed during the intervening dry season months. Most potential nesting females within the slough, therefore, apparently reduced their nesting effort, as an adaptative strategy in response to drought or major drydown events.

#### Alligator population model responses to simulated surface water flows within the central and southern Everglades.

The NPS restoration goals and objectives for the Everglades are based on the assumption that an ecosystem management approach is best achieved through reestablishment of a more natural hydrological regime than is possible by current water management practices. The basis for this assumption was tested for the alligator population within the central and southern Everglades by use of an alligator population simulation model (see Methods of this section) to compare the model responses to a simulated natural Everglades hydrological regime (no water control structures or wellfield diversions) versus simulated surface water conditions resulting from four different water delivery management alternatives, under consideration by local, state and federal agencies, involved in restoration plans for Shark Slough, the central flowway of the system (NPS, 1990).

#### Natural or "restored" model scenario.

The "natural" simulation or scenario estimates surface water flow distributions, volumes, and timing of these flows for wet prairie and slough marshes that comprise the central and southern Everglades under pre-flood control conditions of the system (SFWMD, unpublished data) with the same rainfall database (1969 - 1982) used to model the four other water delivery management alternatives. This natural simulation was used as a scientific control or model of hydrological conditions that provided: (1) a complete innudation of the evaluated area at the end of most peak wet season flows for the 14 year period; (2) distribution of seasonal surface water flows in accordance with natural topographical contours, and (3) lag, dry season volumes of flow from northern reaches of the Everglades catchment area (outside of the evaluated area) flowing into the central and southern Everglades. These lag flows maintained continuous dry season, surface water flows throughout the central and southern Everglades for most dry seasons of the 14 year period.

In contrast to natural simulated flows, the other four management alternatives did not maintain these continuous dry season, surface water flows through the slough. Major drydowns occurred on the average of once in every three years, compared to only one major drydown under the natural simulation, modeled for the same area and using the same 14 year period of rainfall data. Flow distributions of these other simulated alternatives were also not in accordance with natural topographical contours, but maintained deep water impounded marsh areas and overdrained marsh areas, characteristic of the present system, during most years of the 14 year simulation runs.

#### Alligator population simulation model parameters.

Population parameters used in the alligator model for comparing model responses to seasonal and annual inundation characteristics of these water delivery alternatives are listed in Table 15. Cohort survival rates used in the simulations were estimated from both published and unpublished data sources (Kushlan and Jacobsen, 198 ; Dalrymple, 1989). Antagonistic mortality estimates were based on field observation and from the general literature. The model assumes a stable age distribution at the beginning of each 14 year simulation run. Annual nesting effort is based upon expected nest densities previously presented in this section, and adjusted within the model for proportional increases/decreases in the available female nesting population, estimated by the model for each simulated year. Nesting success is based upon both constant (infertility, predation, dessication, etc,) and variable sources of egg mortality (nest flooding) as documented by Kushlan and Jacobsen (1990) and by data previously presented in this section.

#### Alligator population simulated responses.

A comparison of simulated alligator population parameters resulting from the natural and the four other water delivery alternatives is presented in Table 16. Average alligator population size for the 14 year evaluation period was approximately one third greater for modeled natural flows than for any of the proposed alternatives. Peak population sizes resulting from natural flows were also greater than twice that of maximum population sizes obtained for the other water delivery alternatives. Nesting success with natural flows was also significantly greater and the frequency of significant nest flooding events only one-fourth that of the other proposed deliveries.

The difference in predicted alligator population sizes for the natural simulation runs compared to any of the four alternatives was related to increased nesting effort and success and reduced drought-related mortality of smaller

size classes. Dry season lag flows from northern reaches of the Everglades catchment area maintained greater downstream, dry season stage durations in the evaluated area, particularly within Shark Slough, for most years. Alligator nest production and survival rates of younger alligators are correlated to these late dry season stage durations.

The natural distribution of flows also provided an increased area of habitat suitable for nesting (Figure 42). Under the other management alternatives, deep water depths maintained in the impounded marshes of WCA3A reduced the overall area of suitable nesting habitat within the evaluated area during most simulated years. A significant reduction in the frequency and magnitude of nest flooding under the natural simulation runs also resulted in higher rates of nesting success compared to any of the other modeled alternatives. Under the natural simulation, a better correlation existed between the timing of early and late wet season peak flows compared to the modeled alternatives. The peak nest construction and egg laying period for alligators in the Everglades occurs during early wet season peak flows (late June/early July). Egg clutches within the nest are deposited approximately one-half foot above prevailing water levels at the time of egg deposition (see Review of Published Data). Increases in water depths during the following incubation period in the natural simulation rarely exceeded that height, significantly reducing occurrences of nest flooding, when compared to the other alternatives. Consistent and significant flooding of alligator nests occurred within WCA3A and downstream of the S12s for most years of the simulation period with all the management alternatives (Figure 43).

Alligator population stability attributes demonstrated by these simulation runs, and biotic instabilities in relation to frequent drydown events, are reviewed in the following Discussion section of this paper. Major and frequent drydowns adversely impact aquatic prey populations that are important food sources for alligators. Interannual effects of major drydowns require several years for recovery of aquatic food webs (Loftus and Eklund, 1989). Major drydown intervals, occurring as frequently as that predicted for the modeled management alternatives, would prevent such recovery and lead to a downward trend in the system's overall aquatic productivity and capacity to support higher order consumer populations, represented in this case by the alligator.

The alligator population simulation model used to compare population responses to these water delivery alternatives predicts responses based on correlations with surface water conditions only. The model does not consider, therefore, decreasing standing crops of prey bases resulting from interannual affects of frequent and major drydowns as modeled for the proposed water delivery alternatives. If

the model was modified to assess the effects of declining prey bases on alligator population sizes and stability, the predicted responses to the four proposed water delivery alternatives would have been even lower, compared to natural simulated flows. Egg loss to arrested development was also treated as a constant in the model. Increased egg loss from arrested development does occur, however, during major drydown events, and should be modeled as a variable. Reproductive success would have been even lower for the four management alternatives, compared to the natural scenario, due to the increased rate of arrested development that would result from the greater frequency of drydowns that occur with these alternatives.

The inundation patterns that were characteristic of the four management alternatives did not provide natural improvements to restoring downstream, dry season flows within the central and southern Everglades. Water deliveries under the two base alternatives were a function of regulatory schedules. Resultant flows through the S12s were not into the main channel of the central flowway, and were inefficient in establishing downstream surface water pools that traditional occurred in the area prior to recent water management regulation. Past actual flows under modified minimum deliveries (NPS, 1990), similar to these modeled base condition alternatives, did not in fact restore functional downstream surface water conditions within this central flowway.

The two rainfall based alternatives did not adequately produce the natural, dry season lag flows to the central and southern reaches of the Everglades catchment area. This deficiency could be corrected through the development of better estimates of rainfall-runoff relationships that more closely approximate lag, dry season flow volumes of the natural simulation. The basic rain-driven alternative included planned modifications to water control structures to allow for more natural flow distributions across the central flowway. Modeled flow distributions for this alternative did provide approximate flow distributions as represented in the natural system simulation.

The ACE hydrology model used to simulate flows under all these alternatives did not include monthly water depth distributions for the downstream mangrove estuaries or the short, hydroperiod marshes along the eastern edge of the system. Historically, these areas were also important to alligators within the southern Everglades (see Review of Published Data). The freshwater zones of these estuaries provide important drought refugia to the alligator population. The dry prairie marshes along the system's eastern edge once provided extensive alligator nesting habitat. Future hydrological modeling efforts need to include these areas, if alligator population modeled

responses are to have the level of realism required to properly evaluate population responses to simulated system flows.

#### General Discussion.

Contingent characteristics of alligator populations are dependent upon both fundamental environmental and fundamental species characteristics (DeAngelis, 1989). Fundamental environmental characteristics of wetlands such as soil types and depths, inundation characteristics, and resultant impacts on aquatic food webs and prey species abundance and availability, as well as the number of suitable months available for feeding activity and growth, influence differences in fundamental species characteristics between distinct alligator populations. These differences, or contingent characteristics, between distinct alligator populations are represented by variable growth rates, maximum body sizes obtained, ages at onset of sexual maturity, etc., and vary for populations in different areas of the species geographical range.

#### Fundamental environmental characteristics of wetlands in relation to the American alligator.

Fundamental environmental characteristics of wetlands are comprised of both abiotic and biotic factors important to crocodilian life history aspects and population stability and persistence. A summary of these factors are listed in Table 17.

#### Abiotic factors or conditions.

The thermal, hydrological, salinity, and fire regimes of wetlands, as well as the topographical and landscape pattern or features of a system, are major determinants to the contingent characteristics of alligator populations. Spatial and temporal characteristics of these environmental factors and their effects on the basic life history aspects of the American alligator are summarized below.

#### Thermal regime.

The thermal regime of a wetland influences the energy budgets of alligators in relation to the amounts of food consumed, metabolic expenditures, and resulting growth patterns and rates. Growth patterns and rates also influence the time period required for alligators to reach sizes required for the onset of sexual maturity, population size - fecundity and size/age-specific survival rates, population composition, and habitat utilization. Temperature characteristics at nest sites also determine the sex ratio of hatchlings, that also influence population structure.

Energy budgets of alligators in relation to the thermal regime have been proposed as a limiting factor on growth rates, or indeterminate growth patterns, of alligators in the Everglades. Minimum temperatures required to initiate feeding, and the duration of winter temperatures either above or below this threshold, as well as seasonal temperature extremes, particularly during droughts, affect the metabolic rates, growth and reproductive patterns of alligators. Limitations on growth or reproduction also influence the population's rate of increase or decrease, and resulting changes in alligator population size or stability.

#### Hydrology regime.

The affect of these thermal parameters on the demographic patterns of an alligator population are also correlated to the spatial and temporal characteristics of the wetland's hydrologic and related salinity regimes. The frequency, magnitude, and duration of drydowns within the Everglades are a major driving variable affecting the alligator population's annual productivity, survival rates of sex and age classes, and recruitment of subadults into adult age classes (see Review of Published Data and New Data). These demographic parameters affect the population's persistence, both in terms of alligator seasonal and long-term occupancy of an area, and the actual, minimum viable, or genetically effectively population sizes sustained within an area over time.

Reduction in the distribution and areal extent of core alligator habitat within the Everglades since the 1950s, and resultant declines in the alligator's overall numbers, may be attributed to fundamental changes in the system's hydrologic regime. Changes in occupancy rates of formerly extensive dry and wet prairie habitats, and of downstream estuaries of the system, have been related to the changes or reduction in the maximum area of innudation, seasonal flow volumes and distribution, and the timing of seasonal flows within the Everglades catchment area. Changes in these hydrological parameters during the recent past have altered the hydroperiods of formerly occupied dry prairie habitats, as well as the predictability of seasonal surface water flows through the system's central flowway, and the quantity and timing of freshwater flows into downstream estuaries (see Review of Published Data and New Data).

#### Salinity regime.

Reduced upstream, freshwater sheet flow into downstream estuaries also influences estuarine salinity regimes. Salinity ranges affect alligator feeding rates and food consumption, the suitability of freshwater estuarine zones as nesting habitat and for juvenile survival, as well as the

use of tidal rivers, creeks, tributaries, and inland bays within this zone as drought refugia by alligators during times of extreme thermal and food - related stress.

#### Topographical and landscape patterns/features.

Reduction in freshwater flows to the downstream reaches and estuaries of the system during the 1960s, and resultant, intensive wild fires that occurred concurrent with these reduced flows, breached old, inland coastal beach rims or natural berms bordering the headwater areas of these estuaries. Seasonal drydown characteristics of the hydrologic regime that were attenuated by large, surface water pool formations, maintained in upstream, freshwater habitats within the southern Everglades by the impoundment effect of these natural berms, were subsequently reduced, increasing the severity of seasonal drydowns, while simultaneously reducing the effectiveness of these drought refugia for alligators during drydown events. Salinity regimes within these freshwater estuarine zones were also affected by the reduction in the size, areal extent, and duration of these downstream pool formations. Such alterations in landscape features of a system may have far reaching affects on resident alligator populations.

The topography and ground surface features of a system are important to all life history aspects of alligators. Open, deep water areas are required for courtship and mating. Nest sites are located in close proximity to ponds or permanent water areas, particularly during low surface water conditions or during drought. These permanent or persistent deep water areas offer drought refugia, as well as do depressions, solution holes, or caverns in eroded limestone bedrock, that provide underground dens or black body conditions (thermal sinks) during dry and thermally stressful periods. Canals, rivers, creeks, tributaries, and open water areas or shallow lakes are also used as travel routes by feeding alligators, particularly by adult males, and as staging and courtship areas for breeding groups.

The ponds occupied and kept open by alligators are also important landscape features affecting marsh fish survival during droughts, and subsequent recruitment rates within marsh areas following major drydown events (Loftus and Eckland, 1989; Loftus, per. comm). The diversion of sheet flow from the northeastern section of the historical Shark Slough flowway, from the early 1960s through the early 1980s, contributed to a decline in alligator occupancy of the area. Ponds formerly occupied by alligators have silted in, following invasion by hydric plant species, and no longer provide drought refugia for marsh fish populations.

Attempts at restoration of sheet flow to this area, beginning during the early 1980s, have not resulted in significantly increased marsh fish populations and wading bird foraging within the area. Alligator occupancy also remains extremely low, as does the occurrence and associated density of ponds, resulting in reduced recruitment rates and standing crops of marsh fish populations following seasonal drydowns, and an associated reduction in wading bird foraging within this area, compared to adjacent slough habitat (Figure 44). The importance of topography and landscape features to alligator occupancy of an area, also affects the role of the alligator in the continuance of ecological processes important to other biological components of the system. These fundamental, biotic components of the system are also important to the contingency characteristics of alligators within the Everglades.

#### Biotic conditions.

Fundamental biotic components of the system that are important to alligator life history aspects include: landscape heterogeneity, prey species availability, interspecific competition for prey, as well as intraspecific, density dependent factors or competition for food and space, that affect an individual's growth, cannibalism rates within a population, and vulnerability of individuals to predation.

#### Landscape heterogeneity.

Aspects of landscape heterogeneity that influence alligator occupancy and habitat utilization are important at both the micro and mesohabitat scales. As an ectotherm, the ability of an alligator to regulate its internal body temperature in response to lower and upper temperature extremes is critical to its survival. This ability is dependent upon several landscape features and related environmental conditions within its normal activity range. The presence of a permanent or stable body of water (used as a heat source or thermal sink), a blackbody cavity or den for use during major drydown events, shade or shaded water areas from radiation during the hot summer months (provided by dense, grass vegetation or tree canopies), and a basking site during cool periods, are critical landscape features enabling the alligator to maintain its body temperature within tolerable limits during high or low temperature extremes, through normal thermoregulatory behaviors.

In the Everglades, several, small open water ponds with well defined banks, often connected by trails through the marsh grass, a high interspersed of dense and open grass cover types, and the presence of tree islands, characterize high density areas of "resident" nesting females and pods of

young. At the mesohabitat scale, proximity to a major, permanent body of water also appears important to alligator occupancy of marsh areas that are without exposed, eroded bedrock to provide denning sites required by alligators for survival during major drydown events or drought.

#### Prey species availability.

The availability of alligator prey species is apparently higher within shallower water marsh, or the edge of deep water habitats, in relation to other life requirements of alligators. Proximal factors affecting alligator prey vulnerability and prey suitability also appear greater. Alligators within lake habitats frequently inhabit lake littoral zones, declining in number with increasing distance from the shoreline. In the Everglades, occupancy of the edges of deep water impoundments also appears highest (Schortemeyer, pers. comm.), with nesting restricted to edge habitats during most moderate to high water years. During dry season declines in marsh water level, however, both small and large aquatic prey species, and terrestrial prey, are increasingly concentrated within or adjacent to deeper water bodies, including interior marsh ponds, tidal rivers, creeks, and tributaries, and within artificial canal habitats.

During the drought of 1989, a number of adult alligators that remained within interior marsh ponds and/or canals were observed each month of the dry season feeding on large turtles, as well as wading birds and river otters, that frequented these ponds. Ponds of alligator young in interior ponds were also observed feeding on increasing concentrations of small fish within these ponds as the dry season progressed. Wading bird foraging about ponds also increases as the dry season progresses, providing potential prey for subadult/adult sized alligators; the larger wading bird species also represent potential predators on hatchling alligators, confined within interior marsh ponds during seasonal water level declines.

#### Predation, Inter- and intraspecific competition.

Predation on eggs, cannibalism rates on smaller sized alligators, and antagonistic mortality also increase during drydown events (see Review of Published Data and New Data). Periods of indeterminate growth occur more frequently during these events, as the marsh floor dries, and alligators concentrate in drought refugia; predation by wading birds and alligators on increasingly concentrated marsh fish populations eventually reduce prey availability, limiting food intake, as thermal stress and metabolic costs increase.

Predators that frequent these ponds, particularly during drydown events, either compete with alligators for declining populations of prey, or prey on alligator pods of young confined within these drought refugia or ponds during the dry season months. Interspecific predators observed preying on alligator young include large fish, bullfrogs, turtles, wading birds, hawks, river otters, raccoons, bobcats, and panther (Craighead, 1968; Neil, 1971; Fleming, 1975; Bass, pers. comm.; Schortemeyer, 198 ; ). Such predators may also be consumed by larger alligators that normally reside in these ponds (Craighead, 1968; Neil, 1971; Fleming, 1975; Fleming, pers. observ.).

#### Fundamental species characteristics of the American Alligator.

Crocodylians descended from ancestral forms over 230 million years ago. Their evolutionary lineage is conservative, with all lines of descent toward specialization perishing during their long evolutionary history. Present morphology of the American alligator has remained essentially unchanged since the Miocene period over 25 million years ago. Present alligator populations are characterized by low genetic variability and divergence (see Review of Published Data).

Fundamental species characteristics of the American alligator are summarized in Table 18 and discussed below. Fundamental species characteristics of alligators appear adapted for coevolution in stable, aquatic systems.

Longevity, maturation schedule, maximum body size, and fecundity.

Individuals in wild populations have long life spans of up to 50 years, characterized by nearly continuous growth, resulting in large adult sizes. The maturation schedule is very long, requiring from 10 - 18 years before the onset of sexual maturity. Potential fecundity is moderately low (ranging from an average of 28 - 39 eggs/clutch within distinct populations), increasing with age until senesce at old ages.

#### Habitat generality.

Habitat generality is related to the permanency of water and/or the occurrence of suitable drought refugia. Highest population densities occur in marshes in which such drought refugia are numerous, or where drydown intervals are long and drought refugia nearby in adjacent habitats.

#### Feeding generality.

Alligators are also versatile and selectively opportunistic predators, feeding on a wide variety of prey types and sizes. Diet composition varies with increasing size through a long life span of nearly continuous growth. This variation in diet of different sized alligators within an area allows for high potential numbers of individuals among overlapping size classes to share suitable habitat.

#### Dispersal ability.

Alligators are also capable of responding rapidly to changes in marsh water depths, by dispersing to drought refugia during seasonal declines in water levels or during drought, and by rapid dispersal from such refugia with the return of normal seasonal rainfall and increasing marsh water depth (see Review of Published Data).

#### Maternal care.

Behavior of nesting females, exhibiting complex nest site selection choices in relation to varying environmental conditions, and the guardarian role of attendant nesting females of the nest during incubation and of the young following hatching, also increases reproductive performance, particularly in fluctuating or unstable environments where potential predation may be high. Maternal protection occurs at a size or age in life when the young are extremely vulnerable to such predation.

#### Environmental tolerances.

Environmental tolerances of alligators to changes in thermal, hydrologic, and salinity conditions also determines the upper and lower limits, or environmental characteristics, of habitats occupied by different size classes of alligators.

#### Thermal tolerances.

In terms of thermal conditions, the frequency, magnitude, and duration of summer or winter droughts and temperature extremes associated with these events, as well as winter freezes in the northern parts of its range, influence energy expenditures or metabolic costs of activity in relation to the availability of prey populations, the amount of food consumed, the available number of months for growth, and resultant growth rates. Lower limits to survival occur at approximately 4 - 5 C ( 40 - 45 F) (Brisbin et al, 1982) and upper limits at 34 C (93 F) (Wilber, 1960) of body temperature. Feeding activity of laboratory animals is not initiated at body temperatures below 22 C (72 F) (Coulson et al, 1973). Feeding activity and the amount of food consumed and

converted to body growth in free ranging individuals is dependent on external air and water temperatures, in relation to the thermoregulatory behaviors and age of the individual, and prey availability.

#### Hydrologic tolerances.

The hydrologic regime of an aquatic system also determines seasonal occupancy rates and utilization of marsh habitat types by size classes of alligators. Upper and lower climate boundaries of seasonal activity ranges are related to changes in marsh water depths. Short term occupancy of an area will depend on seasonal water depth extremes, while long term occupancy may be related to annual average stage duration and intervals between major drydowns. Too frequent drydown intervals (less than once in every five - seven years) may limit the occupancy and nesting frequency within an area, if numerous drought refugia are not available or nearby, as will excessive water depths (greater than 45 cm) for occupancy and for nesting during the nest construction period. The duration of ground water in drought refugia is also important within short hydroperiod areas throughout the dry season months. Maintenance of adequate ground water levels allows for more continuous occupancy and nesting within these marsh habitat types (see Review of Published Data and New Data).

#### Salinity tolerances.

Occupancy and utilization of marsh habitat types are also determined by salinity tolerances of alligators. Salinity tolerances vary by the size/age of individuals. High salinity ranges affect habitat types used for nesting, with most nesting limited to marshes with salinities less than 9 ppt. Upper salinity ranges are particularly important for hatchling survival. Exposure to salinities exceeding ppt for up to two months can be lethal to hatchlings (Joanen, 19 ). Salinities greater than 3 ppt may also affect food consumption rates and capacities of alligators, retarding growth rates and maximum body sizes obtained (Chabreck, 19 ). Marshes with salinities greater than 10 ppt are not normally utilized by alligators (Joanen and McNease, 198 ).

#### American Alligator contingent population characteristics and persistence in a changing Everglades.

The fundamental environmental characteristics of major wetlands occupied by the American alligator within several areas of its geographic range are summarized in Table 1. A comparison of Everglades alligator contingent population characteristics to other geographic populations within these wetlands is presented in Table 19. Differences in these contingent characteristics are compared in terms of mean

population density, growth or body size at comparable ages, age to maturity, clutch size, the frequency and intensivity of nest defense and maternal care, and measures of mean levels of genetic variability.

Generality, differences in these contingent population characteristics are greatest between populations in the northeastern extremities of the species range (within the Atlantic coastal plain) and the more southern populations located in wetlands within the western Gulf coastal plain of the southeastern United States. The southernmost population of the American alligator, occurring within the Everglades, is an exception to the directional trend in differences between most contingent characteristics of these populations. Everglades alligators grow at slower rates and reach sexual maturity at an older age, produce smaller clutch sizes, and adults also remain longer in size classes having higher rates of size - specific mortality, than other southern populations (see Review of Published Data).

Everglades alligators, however, demonstrate the most aggressive nest site defensive behaviors, and resulting average egg loss to predation is the lowest reported for any geographic population. Lowest nest defense and the highest predation rates on eggs (50 - 87 %) are reported for the more northern populations that inhabit relatively more stable wetland systems. The occurrence of nest defense increases as average predation rates decline to approximately 16 percent in wetland systems in north central Florida and south Louisiana ( systems characterized by moderate water level fluctuations). Nest defense is highest and predation lowest (averaging only 2 percent) in the Everglades (a system characterized by pronounced, seasonal water level fluctuations).

Differences in egg losses to predators within these range parts appear related to the relative stability of water levels among wetlands and subsequent differences in predation patterns and alligator nest defense. Raccoons are an important predator on alligator eggs within these systems. The frequency and intensity of raccoon predation on alligator eggs and young has been related to seasonal differences in water level fluctuation and subsequent raccoon movement patterns and food habits (Fleming et al, 1976, Nichols et al, 1976). Predation rates on alligator eggs within nests in coastal Louisiana and the Everglades generally increase during drier years in which water levels fluctuate below normal ranges. Increased parental care by nesting females in the Everglades, particularly increased nest defense during drier years, appears to be an adaptative response to compensate for constraints on reproductive performance and juvenile survival in a more fluctuating, unstable, and stressful environment.

Other contingent characteristics of the Everglades alligator population are more closely associated with those of northern populations, where a limited number of suitable growing months are available each year. Alligators in the Everglades remain active for longer periods throughout the winter dry season than alligators in these northern populations. Frequent periods of indeterminate growth, decreasing with increasing size class, however, characterize the more active winter dry season period of the Everglades. Increased metabolic costs during the mild winter period, and a lower prey base than that occurring in other Gulf coastal plain wetlands, has been proposed as the basis for an apparent food limited population within the Everglades (see Review of Published Data). Past and present human alterations in the system's natural hydrologic and related salinity regimes have further decreased the stability of trophic resources availability to Everglades alligators (see Review of Published Data and New Data).

#### Stability attributes of the Everglades alligator population.

The historical or predrainage Everglades of southern Florida once covered an area of approximately 4000 square miles, and extended a distance of over 90 miles from its headwaters to the estuaries of Florida Bay and the Gulf of Mexico. Since the late 1940's, almost half (1960 square miles) of the original area of this wetland system has been lost to urban and agricultural development, or to overdrainage and invasion by exotic vegetation. The remaining natural areas of the Everglades have been furthered altered by construction of a massive system of canals, levees, and water storage impoundments. Only 20 percent (800 square miles) of the historical Everglades remains undeveloped and outside of impounded marsh areas, and occurs in the downstream reaches of the Everglades catchment area within Everglades National Park and a portion of the Big Cypress National Preserve (Johnson et al, 1990). Water management practices have also altered the distribution and timing of seasonal flow volumes from northern to downstream reaches of the catchment area, reducing the persistence of downstream dry season pools and increasing drydown frequencies, compared to estimated natural and past actual flows (SFWMD, unpublished data; NPS, unpublished data; Craighead, 1968).

Everglades alligator contingent population characteristics are influenced by such fundamental changes in spatial and temporal characteristics of the system, and by related impacts such changes have on the wetland system's productivity and the availability of important alligator prey populations. Fundamental species characteristics of the American alligator that provide resistance and structural stability to such perturbations or disturbance, and recoverability or resilience from these perturbations,

enable populations to persist in a fluctuating environment. The fundamental species characteristics contributing to these stability properties for alligator populations are listed in Table 20.

Alligator population persistence in relation to environmental variability.

Alligator population persistence in relation to environmental variability and disturbance regimes in the Everglades requires adaptative responses of individuals to seasonal changes in environmental conditions and to stochastically occurring events (drought, hurricanes, wild fires, etc.), as well as adaptation to long term changes (increased frequencies of drydowns, sea level rise and related changes in estuarine salinity regimes, etc).

Alligator responses to seasonal changes in the thermal, hydrologic and salinity regimes involve adjustments in thermoregulatory behaviors in response to seasonal temperature changes, indeterminate growth patterns and/or rapid dispersal from or to more favorable habitats in relation to drydown events or the reinnudation of preferred habitats following such events, and seasonal occupancy and utilization of estuarine habitats for feeding activities during peak, upstream wet season freshwater flows. Freshwater flows and associated salinity ranges in the downstream estuaries of the Everglades, that affect alligator occupancy and utilization of these estuaries, are related to changes in upstream seasonal flow volumes and distributions, and variability in the timing of these flows in relation to rainfall patterns, upstream water management practices, and seasonal changes in sea level or wind driven tides.

Adaptative responses of alligators to major stochastic events (hurricanes, drought, wildfires, etc.) appear limited. Density independent mortality resulting from hurricanes and drought are frequently reported after such events and may be significant (see Review of Published Data).

Long-term changes in periodicities of seasonal events or environmental conditions within the Everglades, however, appear to have the most significant affects on alligator population stability and persistence. Sea level rise, related to global warming, that may result in inundation of the central slough or flowway within the southern Everglades ( , 1989), would eliminate the present highest occupancy area of alligator nesting habitat. Other directional changes in habitat characteristics, including the invasion of exotics in overdrained marshes, the accumulation of nutrient loads related to runoff from agricultural areas and related habitat structure changes, as

well as the documented occurrence of mercury concentrations in the aquatic food webs of the system and in the alligator population, represent present trends in habitat reduction and degradation.

Long term changes in the system's hydrologic regime are also detrimental to alligator population stability. Simulated alligator population responses to an increased frequency, magnitude, and duration of drydown events, in relation to the present seasonal timing of flows and increasing wellfield diversions modeled for all restoration proposals currently under consideration, portray a population that demonstrates increasing biotic instability in relation to abiotic events (drydowns and droughts), intensified by density-dependent biotic factors (increased food competition, cannibalism, and significantly reduced reproductive effort and success).

#### Life strategies.

Alligator populations are capable of rapid rates of increase related to the relative large clutch sizes of potential nesting females and the long life spans of adults in the population. This potential rate of increase and long life spans of adults reduces the interval of time to extinction in relation to demographic or environmental variability. The increased frequency, magnitude, and duration of drydowns, however, experienced since recent water management, and future increased drydown frequencies predicted as future water consumption demands necessitate additional well field diversions from the system, represent long term changes in periodicity, and not seasonal patterns of variability, in environmental conditions. Such directional changes in long term periodicity of seasonal flows represent alterations in the system's natural hydrologic regime that threaten the species population stability and long term persistence within the Everglades ecosystem.

Characteristic alligator population structures and rapid rates of increase are dependent on stable resources (food and water) for reproductively active females, that have highly restricted activity ranges throughout a year, and comprise only a small porportion of the total population (less than 5%). Adverse, directional impacts on this subsegment of the population can cause rapid and dramatic population declines. The unrestricted harvesting of adult females during the first half of this century contributed to rapid population declines ( ). Simulated harvesting strategies of alligator populations in south Louisiana also demonstrated the need to protect this subsegment of the population (Nichols et al, 19 ). Oscillation in age class structures in simulated south

Louisiana and Everglades alligator populations and rapid declines in overall population numbers, in relation to simulated drydowns, also resulted from drydown impacts on the reproductive performance of nesting females within each population (see Review of Published Data and New Data).

Sufficient data are not available to provide meaningful estimates of actual, minimum viable, and (genetically) effective population sizes for the Everglades alligator population (see Conclusions). Alligator population model responses to simulated water delivery flows in the post - drainage Everglades landscape indicate that estimated population sizes may be approaching the lower limits of minimum viable population sizes. A minimum viable population size requires spatial and temporal characteristics within an Everglades landscape that allows for the alligator population to recover from natural disturbance regimes. The occurrence of major drydowns throughout the system are perturbations or disturbances once associated with five to seven year rainfall repeat frequencies, characteristic of south Florida's climate and rainfall regime ( , 19 ).

Declines in surface water flows and drydown intervals associated with these rainfall patterns now occur with greater frequency than that expected, based on these rainfall repeat frequencies. The biotic instability demonstrated by the alligator population's modeled responses to these increased drydown frequencies are indicative of a population with wide population fluctuations and associated age class oscillations. Populations with widely fluctuating numbers and unstable age distributions are themselves unstable and subject to possible drastic declines in relation to abiotic events, requiring management intervention before recovery is achieved.

Reduced upstream, dry season flows have also altered the salinity balance of the system's downstream estuaries that are used as drought refugia by alligators in the southern Everglades during major drydown events or droughts (Craighead, 1968). Increased dry season estuarine salinities reduce the estuaries' effectiveness as drought refugia for dispersing alligators. In the estuaries, increased salinities related to reduced upstream, freshwater flows further concentrate dispersing alligators, resulting in increased cannibalism rates, competition for suitable space and for food, that further intensifies the biotic instability of the alligator population to drydown events.

Everglades restoration goals should not only seek to maintain a minimum viable population size for such keystone species, but also to maintain the genetic variability of the population, its effective population size, over greater time periods spanning generations. The

50 per cent reduction in the system's original or historical area, and the overdrainage of much of this remaining area, also restricts movements of individuals in the population within the remaining undeveloped or "natural" areas of the system. Restricted movements in relation to overdrained wetland and increasing drydown frequencies within these remaining natural areas may also affect the normal outbreeding roles of adult males, and increase the future likelihood of greater inbreeding or allele fixation within the population, intensified by wide fluctuations in population sizes.

Hypotheses concerning adaptative strategies of species with low, genetic variation and large body size.

Alligator mississippiensis has been described (et al, 19 ) as a species composed of a series of populations with differing allele frequencies and low genetic variation (comparable values of P for other vertebrates but lower values of H than expected for nonmammalian vertebrates). Several hypotheses have been proposed concerning low genetic variation in species with large, body size. Hypotheses advanced to explain the low genetic variation documented in American alligator populations include: bottleneck ( ), random genetic drift in isolated populations ( ), environmental grain ( ), stability of trophic resources ( ), the genetic strategy of adaptation ( ), and an environmental amplitude hypothesis ( ).

The hypotheses concerning bottleneck and random genetic drift in isolated populations, as applied to the historical distribution and status of American alligator populations, do not explain the low genetic variability, characteristic of the species' present populations ( , 19 ). Despite dramatic past declines in the historical abundance of this species, sufficient numbers of alligators (greater than 300) are believed to have survived to maintain the genetic variability of the distinct populations for which mean levels of heterozygosity have been estimated and compared.

Hypotheses concerning the species perception of environmental grain, the stability of trophic resources, genetic strategies of adaptation, and environmental amplitude have relevance to documented alligator life history aspects and population structures. The relationship of these hypotheses needs to be clarified, however, in terms of: (1) the differential growth rates of the sexes, in relation to (2) differences in the environmental grain and stability of trophic resources between male and female preferred habitats, and (3) the different behaviors

associated with the reproductive roles and genetic contributions of adult males and females that influence the effective population size of alligators in a locality.

Strong, directional selection for a slower growth rate in female versus male alligators appears to occur both at dispersal age (3 years) and at maturity, in relation to the habitat preference of females for a more course, environmental grain, but less stable (more stressful) habitat (shallow water marsh areas required for nesting), and restricted movements within that habitat (related to a guardian role for nest defense during the incubation period, and maternal care or protection for newborn young), in contrast to wider ranging male movements within habitat of a finer environmental grain (open, deep water areas) that provides a relatively more stable local environment. Declines in growth curves for females are significant, both at dispersal age and at the onset of sexual maturity, while growth continues for males at these ages. Habitat preferences of the sexes also begin to differ following dispersal, with immature female daily movements more focused within a single activity center, compared to several activity centers of immature males, and at sexual maturity with adult female activity ranges highly restricted, compared to that of adult males.

Both immature and adult females use the same course grained, habitat type (densely vegetated marsh interspersed with numerous small potholes and ponds) versus open, deep water areas used more frequently by wider ranging immature and adult males. This differential habitat use may be reflected not only in the different growth rates or mean body sizes of each sex at comparable ages, but has also been proposed as a basis for the role of incubation temperature sex determination in the biased sex ratios of alligator hatchlings. Nest site and nest thermal characteristics that favor biased female hatchling sex ratios (wetter conditions) also enable a nesting female to produce progeny (female hatchlings) that are scarce in the population. The chances of a female to pass on her genetic inheritance to future generations would actually increase with the increased production of female hatchlings, compared to the production of hatchling males in alligator populations with a surplus of adult males.

In the Everglades, particularly in the postdrainage landscape, directional selection may be greater for slower growth or a smaller mean body size for all alligators, compared to other southern populations that inhabit more stable wetland systems. The higher metabolic rates and lower food availability in a tropical (warmer), but more fluctuating environment, characterized by lower productivity (low trophic resources), and an increased frequency, duration, and magnitude of drydown events (unstable

resources) would favor slower growth. However, the accumulated effects or stress of these environmental factors is greater on female energetic budgets, as the females occupy a more unstable and stressful local environment, compared to males. The differential growth rates of the sexes may reflect this difference in stress between the different habitats occupied by the sexes.

Slower growth or a mean body size in adult nesting females would be potentially more advantageous in terms of a greater nesting frequency, due to reduced energy requirements (lower maintenance energy requirements relative to smaller body mass), resulting in greater energy reserves for reproduction, compared to larger females during stress periods of lower rainfall, and during drought years (when females remain in established nesting areas and restricted activity ranges centered about a pond. This slower growth would provide a better short-term "goodness of fit" to a more coarse, environmental grain and allow an increased frequency of reproduction in fluctuating (stressful) environments.

In more stable and productive wetland systems, a relatively larger body size is an advantage for increased reproductive performance - an earlier onset of sexual maturity, occupancy of core nesting habitat, and for early mating (social order). The local environment within the restricted activity ranges of nesting females in such systems would also be more stable and less stressful. Attenuated drydown characteristics of the natural hydrological regime of the predrainage Everglades landscape provided a more stable environment (infrequent drydowns) that would foster faster growth in nesting females and a resultant average, higher fecundity over the life time of an individual.

Directional trends and selective pressures over the past 50 - 75+ years in the postdrainage Everglades landscape, characterized by an increasing frequency, magnitude and duration of drydowns, that favors an increased frequency of smaller-sized nesting females, could foster the establishment of a deleterious trait in the Everglades alligator population, in terms of the cost of short-term fitness versus long-term adaptability. Potential genetic deterioration of the population could also occur, in relation to both habitat reduction and degradation, resulting from fewer size classes of nesting females able to reproduce regularly (decreasing chance of offspring from all generations to contribute equally for all generations), resulting in a lower effective population size, and low individual fecundity within the population, as a result of smaller-sized females nesting more frequently over most years, in the post-drainage Everglades landscape.

Other potential contributions to reduced genetic variability in the Everglades alligator population, in terms of individual responses to habitat degradation and fragmentation, include a greater probability of inbreeding of the restricted population within a reduced movement dynamic of the post-drainage Everglades landscape (reduction in area and drier conditions), particularly for adult males with more restricted movement patterns, and a subsequently reduced outbreeding role within the population. These potential responses to habitat reduction, degradation, and fragmentation could contribute to a lower mean level of heterozygosity in the post-drainage Everglades alligator population, following a sufficient period of time and/or generations. Periods of drying and cooling over parts of the North American continent that once supported ancestral forms of the modern American alligator, may have created similar selective pressures for short-term fitness versus long term adaptability of reproductively active females. In combination with a reduced movement dynamic area, these selective pressures may also have resulted in low levels of genetic variability within these now extinct ancestral forms of Alligator mississippiensis.

#### Everglades Restoration and Management Recommendations.

Ongoing and proposed restoration plans for the Everglades have primarily addressed experimental water delivery alternatives to downstream reaches of the Everglades catchment area. Ecological benefits of these alternatives are assessed by comparison to existing base conditions. Restoration elements involving a more fundamental return to preflood control environmental conditions throughout the entire catchment area, and requiring major alterations or removal of existing networks of canals, impoundment perimeter and internal levees, and the elevating of roads crossing the central sloughs of the system by construction of causeways, have to date largely remained in the background of restoration efforts. Modeled responses of keystone, indicator, and endangered species within the system to simulated natural system flows (predrainage and water management), from upper to lower reaches of the Everglades catchment area, compared to water delivery management alternatives that involve only relatively minor changes in selected water control structures and present water management practices, however, demonstrate the need to pursue far more fundamental restoration elements and changes, than that proposed in present plans, if system restoration goals and objectives are to be achieved (NPS, 1990).

## A landscape mosaic approach to restoration.

A landscape mosaic approach to restoration is required if the seasonal, surface water parameters and dynamics of modeled natural system flows, more characteristic of the historical system, are to be achieved. Artificial replication of historical water depths, however, at selected sites within the system without regard to natural topographical gradients and flow patterns, and related monthly proportions of shallow to deep water areas created throughout the entire catchment area, will not restore the functional dynamics of the historical Everglades system. Selection of a minimum dynamic area, comprised of a functional landscape composition, and managed for more natural patterns of spatial and temporal water depth distributions, is required to provide the monthly proportions of shallow to deep water areas that characterized the predrainage Everglades landscape.

The skewed water depth distributions that create extremes in hydroperiod conditions, and an increased frequency, magnitude and duration of drydowns, characteristic of all proposed water delivery management alternatives modeled within a truncated, (postdrainage) Everglades landscape, have not provided the surface water conditions required for stable cycling populations of keystone, indicator, and endangered species within the system (NPS, 1990).

As a keystone species of the system, American alligator habitat requirements may serve as an example of the inadequacies of present proposed restoration alternatives, based primarily on existing flood control and water supply constraints that prohibit restoration of more natural, seasonal surface water flow volumes and distributions within the system. Present water delivery alternatives provide only 32 to 64  $\text{km}^2$  of core freshwater habitat for alligators within the central Everglades (WCA3A and WCA3B); no core freshwater habitat, however, is maintained at all within the southern Everglades, including Everglades National Park.

In comparison, approximately  $\text{km}^2$  of core, dry season, freshwater wetland habitat for alligators is maintained in the central and southern Everglades (  $\text{km}^2$  in southern Everglades alone) under the natural system scenario, modeled for the same total area, and using the same rainfall data used to simulate flows in the other intensive, management oriented restoration alternatives (NPS, 1990). Volumes of annual flows required to maintain these core, dry season habitats for alligators within the southern reaches of the catchment area, under the natural system scenario, were no greater than that of the other alternatives, and were less than actual annual volumes of flow delivered to the southern

Everglades under past water delivery formulas (NPS unpublished data).

Natural flow distributions and the seasonal timing of surface water flows under the natural system scenario also resulted in more diverse habitat conditions and a greater interspersed of habitat types, important to food partitioning requirements of the alligator population, compared to the artificial impounding or overdrainage of marsh habitats (exceeding critical, upper and lower limits of key habitat variables for alligators) that occurs within impounded marshes, managed with fixed, regulatory target schedules in the northern and central reaches of the Everglades catchment area. Greater spatio-temporal variation in water depth distributions, modeled under the natural system scenario, also avoids the potential overcoupling of predator-prey populations, characteristic of systems with artificially reduced patterns of environmental variability (DeAngelis et al 198 ).

More suitable alligator habitat was also available per unit area of wetland, based on modeled water depth distributions and ranges of the natural system scenario, in which flow distribution was in accordance with natural topographical contours. Alligator population stability attributes in relation to these simulated flows were also more responsive. Modeled alligator population responses demonstrated stable, cycling characteristics under the natural system scenario, compared to the biotic instability demonstrated under simulated flows for all other restoration alternatives. Such flows led to greater population demographic stochasticity, in relation to an increased frequency, duration, and magnitude of drydown events that occurred once in every three years under the management alternatives.

The "alligator hole" as a critical land element of the Everglades.

The importance of the "alligator hole" as a critical land element of the Everglades is defined by the habitat requirements of this keystone species, and the importance of keystone species to the ecological dynamics of a system. Alligator life history aspects, population ecology and persistence are dependent on both the topographical/land surface features of its habitat and the functional need of this species to regulate and maintain its internal body temperature by exploiting the thermal gradients provided by these features in relation to changing marsh water depths. Human alterations in these landscape features, particularly overdrainage of marsh habitats, or the maintenance of excessive water depths in impounded marsh areas, have restricted alligator movements and adversely affected their ability to survive in these extreme

hydroperiod conditions. Such changes have eliminated or reduced alligator occupancy of dry and wet prairie/slough habitats over much of the postdrainage Everglades landscape.

The structural and functional role of this species in maintaining deep water, drought refugia within shallow water marsh habitats has importance to a wider variety of species dependent upon such refugia, particularly within a system characterized by seasonal fluctuations in water depth. The loss of such keystone species has lead to drastic reordering and simplification of ecosystem functioning in other aquatic systems ( , 19 ). Changes in the spatial and temporal characteristics of the Everglades landscape that have affected the abundance patterns of the alligator, therefore, need to be identified and considered as critical elements required within any Everglades restoration plan.

#### Critical restoration elements.

A comparison of simulated, alligator population responses between the "natural" system scenario and present water management scenarios within the postdrainage Everglades landscape demonstrate: (1) the importance of an increased flow section across the principal flowway of the central and southern Everglades (Shark Slough) and restoration of sheet flow in eastern lowlands to provide a greater minimum dynamic area of suitable wetland habitat within downstream reaches of the system; (2) the dependence of alligator annual productivity and population stability on lag, dry season flows from northern reaches of the Everglades catchment area to central and southern reaches of the system during the dry season months, (3) the importance of a more natural or wider distribution of peak wet season flows to a reduction in nest flooding for increased reproductive success within downstream reaches of the system, and (4) the need for legally, proscribed rainfall-based water delivery formulas to provide seasonal flows in ranges needed to restore overdrained wetland areas within these downstream reaches.

Restoration objectives for the system can be best achieved by implementing: (1) the lowest management intensive restoration strategy that provides (2) the greatest minimum dynamic area, comprised of a functional landscape mosaic, with (3) spatial and temporal characteristics of flow distributions within that area in accordance with natural, topographical contours, and (4) rainfall-based, lag dry season flows, from upper to lower reaches of the Everglades catchment area, (5) in sufficient volume to maintain dry season pool formations and persistence within the downstream reaches of the system, (6) as expected in relation to the rainfall repeat frequencies that occur within the region, and (7) in relation to local, natural topographical characteristics of the catchment area.

Present classification status of the American alligator population in the Everglades under the Endangered Species Act of 1973.

A reexamination of the present classification status of the American alligator population occurring within the Everglades appears warranted. Classification status reviews involve habitat evaluations, effectiveness of State research, management and enforcement programs, natural mortality factors, the adequacy of regulatory mechanisms, and other miscellaneous factors (Joanen and McNease, 198 ). The need for a classification status review for the American alligator population within the Everglades is based on the paucity of data that actually exists on the life history aspects of the American alligator within the Everglades, the biotic instability demonstrated by the Everglades alligator population, based on the best available data on the population and modeling expertise, the continuing habitat loss and degradation within the south Florida area, and the non-recovered status of the alligator population in terms of reasonable, biological standards, based on stability attributes of the population in relation to current declining trends in its habitat quantity and quality.

The determination of a population's status, without sufficient data, is a difficult task. Contingent population characteristics, however, need to be assessed in comparison to the stability attributes of the population, where sufficient data exist to do so. The determination of a population's status by contingent, population characteristics alone may overlook changes in population stability attributes in relation to concurrent changes in landscape and temporal characteristics of the environment that affect the population's continued viability over the long term.

Contingent density estimates, relative to a geographical area, in which natural areas remain only as fragmented components of an otherwise human-dominated landscape, will provide a low predictive value for monitoring the real status of populations, particularly for populations inhabiting wetland systems that are undergoing rapid changes in fundamental, environmental characteristics caused by human activities. Such an approach establishes a conservative, contingent baseline to monitor future population change. As a result, the approach may fail to recognize induced stability problems, instead of identifying appropriate, habitat restoration/management strategies for the species.

Both past and present directional trends in habitat fragmentation, reduction, and degradation within the Everglades and south Florida area represent such a case.

The present Threatened Status (by Similarity of Appearance) of the American alligator population within the Everglades needs to be reviewed. A Threatened Status classification would more accurately describe the present status of the American alligator population within the Everglades, particularly for that porportion occurring within the southern Everglades, included within both Dade and Monroe counties.

#### Conclusions.

"The order Crocodilia survived for 200 million years, an immense span of time during which the major land masses of the earth were rearranged, mountain chains thrown up and leveled again, vast areas drowned beneath the waves or uplifted from the sea bottom...But the Crocodilia are not likely to survive much beyond the end of the present century...Parks and "preserves" will not save the alligator. Such places, even though theoretically inviolate, and set aside for the enjoyment and edification of all, in practice are encroached upon more and more by commercial interests. Also, a park is not immune to the effects of commercialization outside its boundries...Other conditions mitigate against the preservation of the alligator for very long...The reptile could not be saved unless expanses of suitable habitat were also saved, along with a selection of the prey animals on which the alligator feeds...But today it is comparatively easy to drain or fill such tracts, and this is being done rapidly as the human population multiplies and so requires more living space" (Neil, 1971).

"Probably no phenomenon better typifies man's desecration of the southern Florida wilds than the disappearance of the alligator through his unknowledgeable attempts to manipulate nature's plan of watering the Everglades. These reptiles were present in unbelievable numbers when the white man appeared. The alligator, like the buffalo of the plains, once dominated the ecology of the Everglade Swamps" (Craighead, 1968).

The resource management issues that dominate "the Everglade Swamps" of today are the same problems first voiced by Craighead and Neil in the late 1960s and early 1970s. In the intervening two decades over people, each requiring both living space and potable water, have settled within the south Florida landscape. Increasing wellfield diversions of water from the Everglades to supply estimated water consumption demands of the 1990s, and the planned development of another wellfield adjacent to the central flowway of the system on the Parks eastern boundary, are critical issues to planned Everglades restoration

initiatives. The biotic instability demonstrated by modeled alligator population responses to major drydown events, and the frequency of these major drydown events, as simulated to occur in all present restoration plans under consideration in which estimated water supply demands for the 1990s have been included, will not sustain viable alligator populations in a functional, keystone species role in a future Everglades landscape.

The priority conservation concerns in the 1990s must address this central issue of water availability and use. Growth management, alternate water sources, more efficient water management and regulated use of the water resource, particularly during low rainfall and drought years, are required if system restoration objectives are to be achieved. The restoration of lag, dry season flows from upstream to downstream reaches of the catchment area in natural flow patterns, the acquisition, protection, and restoration of sheet flow to remaining dry prairie habitats of the eastern lowlands of the system, restoration of water quality, and control of exotic plant invasions in presently overdrained wetlands, are critical system restoration objectives to be implemented, if core habitat requirements of this keystone species are to be preserved within a postdrainage Everglades landscape.

Funding commitment by land management agencies involved in Everglades restoration plans is also required to provide the continuing research still required on this keystone species. No quantitative data are available on alligator seasonal activity ranges, daily movements, and habitat preferences for sex and age classes within the Everglades. No data are also available on the food habits of this species within the Everglades, even though available growth data indicates that the population is food limited. Data on the basic relationship between seasonal marsh water depths, prey availability, environmental temperature, food intake and resulting body and reproductive condition and growth rates of Everglades alligators is also lacking.

Other critical aspects of alligator population biology within this system remain undefined, including the effects of population density and marsh water depth on cannibalism rates, the relationship between marsh water depth and dessication rates of alligators, and the effects of predator density on predation rates of hatchling and young alligators as a function of water level change. These relationships profoundly affect changes in alligator population size, particularly in relation to major drydown events.

Modeling of energetic constraints in relation to alligator population size is also required to better understand the affects spatial and temporal changes in marsh water depths have on alligator population stability and persistence.

Such information would assist in providing meaningful estimates of minimum viable alligator population sizes, as well as the minimum dynamic area and water requirements to support a viable Everglades population, in relation to proposed wellfield developments, experimental water delivery characteristics, and other issues critical to fundamental system restoration proposals or scenarios. No funds, however, are available to support these research efforts.

## Acknowledgements.

I would like to thank sincerely David Buker, Computer Specialist, South Florida Research Center, Everglades National Park, for his technical assistance, advice and programming contributions to this project. Frank Draughn, GIS specialist with the research center, also provided technical assistance. I would also like to thank Dr. Ken Portier and Art Smith, I.F.A.S., University of Florida, Gainesville, who assisted in the pilot phase of the study, the development of customized computer programs for processing and analyses of study data, and statistical assistance in various phases of data analyses. I am grateful to Bob Johnson, David Sikema, and Dr. David Moon, Hydrologists, South Florida Research Center, for the assistance provided in analyses and interpretation of large, hydrological data bases.

Dr. R. Gabowski, Chairman, Department of Biology, University of Miami, generously helped with estimating embryonic stages and ages of specimens collected.

I am particularly indebted to Dr. D. L. DeAngelis, Senior Ecologist, Oak Ridge National Laboratories, Oak Ridge, Tennessee, for informative and valuable guidance in the presentation and interpretation of study results. Useful discussions with Dr. G. . Dalyrample, Professor of Ecology, Florida International University, Miami, Dr. R. . Chabreck, Professor of , Louisiana State University, Baton Rouge, and Jim Schortemeyer, Biologist, Florida Game and Freshwater Fish Commission, Naples, also contributed to a better understanding of alligator life history aspects.

Many individuals assisted in data processing/ management and field aspects of the study. I would like to thank them all, but particularly Annette Cordano, Kira Janssen, Kristi Link, Natasha Kline and Su Jewell, all of whom assisted as technicians during various phases of the study. Special appreciation is also extended to Su Jewell for timely efforts in locating, obtaining, and compilation of a list of the publications either cited or referenced in this paper. Claudette Doffermeyer provided professional editorial assistance and preparation of the final manuscript.

I would also like to acknowledge Ted Joanen, Research Biologist, Louisiana Department of Wildlife and Fisheries, and Alistair Graham, both crocodile specialist, who have provided inspiration to me and others involved in crocodilian research and conservation.

Literature Cited.

in the process of compilation

**Table 1. A comparison of the geographical location, areal extent, geologic origin and age, and fundamental environmental characteristics of selected wetlands occupied by the American alligator within the coastal plain of the southeastern United States.**

| Locality                                                | Latitude   | Physiography                            | Mainland Area (km <sup>2</sup> ) | Geologic Origin                                                                           | Geologic Surface Age (Y.B.P.) | Elevation (MSL) m | Dominant Substrate                                               | Dominant Landscape                                                                   |
|---------------------------------------------------------|------------|-----------------------------------------|----------------------------------|-------------------------------------------------------------------------------------------|-------------------------------|-------------------|------------------------------------------------------------------|--------------------------------------------------------------------------------------|
|                                                         | Longitude  |                                         |                                  |                                                                                           |                               |                   |                                                                  |                                                                                      |
| northeastern<br><br>(coastal North Carolina)            | 35° 09.1'N | riverine, lacustrine, estuarine         | 20,270                           | Recent and Pleistocene sedimentary <sup>1</sup>                                           |                               | 0-                | Non-resistant rocks; soils variable from mucks to marls          | coastal plain, pocosins                                                              |
|                                                         | 76° 46.0'W |                                         |                                  |                                                                                           |                               |                   |                                                                  |                                                                                      |
| east-central<br>(Okefenokee Swamp in southeast Georgia) | 30° 46.5'N | shallow water swamp                     | 1,775                            | rock basin within marine terrace formed during Pleistocene                                | 6000 to 7000                  |                   | sands, marls                                                     | open, shallow water areas, numerous forested islands                                 |
|                                                         | 82° 17.6'W |                                         |                                  |                                                                                           |                               |                   |                                                                  |                                                                                      |
| south-central<br><br>(north-central Florida)            | 29° 40'N   | lacustrine                              |                                  |                                                                                           |                               |                   | mucks                                                            | large, shallow lakes and fringing marsh areas with floating islands                  |
|                                                         | 82° 25'W   |                                         |                                  |                                                                                           |                               |                   |                                                                  |                                                                                      |
| southwestern<br><br>(central south Louisiana)           | 29° 50.0'N | wet prairie, estuarine                  | 4,880                            | deltic and long-shore deposition of sediments from Mississippi River during recent period | 4,000 to 5,000                | 0-0.3             | deep mucks                                                       | numerous small potholes, shallow water areas, and bayous; stranded beach rims        |
|                                                         | 91° 30.6'W |                                         |                                  |                                                                                           |                               |                   |                                                                  |                                                                                      |
| southern<br><br>(Everglades in south Florida)           | 25° 45'N   | wet prairie, dry prairie, and estuarine | 8,280                            | coral reef formed by marine sediment deposition during recent period                      | 4,000 to 5,000                | 0-5.5             | mucks in north, graduating to marls and eroded rockland in south | numerous solution holes, ponds, three islands, tidal creeks, rivers, and inland bays |
|                                                         | 80° 45'W   |                                         |                                  |                                                                                           |                               |                   |                                                                  |                                                                                      |

<sup>1</sup> Department of the Interior, 1970.

Table 1, continued.

| Temperature (ambient)         |                          |                                      | Hydrology                       |                                 |                                 |                                   |                                              | Salinity                                    |                   |                         |                         |
|-------------------------------|--------------------------|--------------------------------------|---------------------------------|---------------------------------|---------------------------------|-----------------------------------|----------------------------------------------|---------------------------------------------|-------------------|-------------------------|-------------------------|
| Avg. Monthly Max. °C          | Avg. Monthly Min. °C     | No. Months $\geq 22^{\circ}\text{C}$ | Avg. Total Annual Rainfall (cm) | Max. Avg. Monthly Rainfall (cm) | Min. Avg. Monthly Rainfall (cm) | % Total Annual Rainfall (Jun-Sep) | Normal Inundation Characteristics            | Proportion (%) total area by salinity zones | Annual Avg. (ppt) | Avg. Monthly Max. (ppt) | Avg. Monthly Min. (ppt) |
| 27 <sup>1</sup><br>(Jul)      | 8 <sup>1</sup><br>(Jan)  | 4                                    | 135.5 <sup>1</sup>              | 18.9 <sup>1</sup><br>(Jul)      | 7.6 <sup>1</sup><br>(Apr)       | 48                                | low to moderate water depth fluctuations     | Freshwater                                  | NA                | NA                      | NA                      |
|                               |                          |                                      |                                 |                                 |                                 |                                   |                                              | Brackish                                    | NDA               | NDA                     | NDA                     |
| 27 <sup>3</sup><br>(Jul, Aug) | 10 <sup>3</sup><br>(Jan) | 6                                    | 132.5 <sup>3</sup>              | 19.0 <sup>3</sup><br>(Jul)      | 5.8 <sup>3</sup><br>(Nov.)      | 50                                | relatively stable water depths               | acidic freshwater 100%                      | NA                | NA                      | NA                      |
| 28 <sup>4</sup><br>(Aug)      | 14 <sup>4</sup><br>(Jan) | 6                                    | 136.6 <sup>4</sup>              | 21.6 <sup>4</sup><br>(Jul)      | 5.3 <sup>4</sup><br>(Nov)       | 53 <sup>4</sup>                   | moderate water depth fluctuations            | Alkaline freshwater 100%                    | NA                | NA                      | NA                      |
| 5                             | 5                        | 7 <sup>4</sup>                       | 142.5 <sup>5</sup>              | 5                               | 5                               | 40 <sup>6</sup>                   | moderate water depth fluctuations            | freshwater (41%)                            | NA                | NA                      | NA                      |
|                               |                          |                                      |                                 |                                 |                                 |                                   |                                              | intermediate <sup>6</sup> (22%)             |                   |                         |                         |
|                               |                          |                                      |                                 |                                 |                                 |                                   |                                              | brackish <sup>6</sup> (37%)                 |                   |                         |                         |
| 28 <sup>6</sup><br>(Aug)      | 19 <sup>6</sup><br>(Jan) | 8 <sup>6</sup>                       | 136.8 <sup>6</sup>              | 24.1 <sup>6</sup><br>(Jun)      | 3.2 <sup>6</sup><br>(Dec)       | 80 <sup>6</sup>                   | pronounced seasonal water depth fluctuations | freshwater <sup>7</sup> (70%)               | NA                | NA                      | NA                      |
|                               |                          |                                      |                                 |                                 |                                 |                                   |                                              | brackish <sup>7</sup> (30%)                 | 24.0              | 35.9<br>(Oct/Nov)       | 9.9<br>(May/Jun)        |

<sup>1</sup> Data for Wilmington, NC; courtesy of National Weather Service (1950-1980 average)

<sup>2</sup> Data for Waycross, GA; courtesy of National Weather Service (1950-1980 average)

<sup>3</sup> Data for Okefenokee Swamp;

<sup>4</sup> Data for Ocala, FL; courtesy of National Weather Service (1950-1980 average)

<sup>5</sup> Chabreck (197 )

<sup>6</sup> Data for Tamiami Trail Ranger Station, FL; Climatological Data, NOAA (1951-1980 average)

<sup>7</sup> Robblee, unpublished data

Table 2. A comparison of seasonal activity ranges, daily distance traveled, and habitat utilization by sex and age classes of the American alligator in coastal prairie marshes of southwestern Louisiana (adapted from Joanen and McNease 196 , Joanen and McNease 197 , McNease and Joanen 19 ).

| Sex and Age      | Sample Size (n) | Date of Study | Environmental Conditions       |                  |       | Activity Range (ha) |        |       | Average Daily Distance Traveled (m)** |        |       | Habitat Utiliz.***                    |
|------------------|-----------------|---------------|--------------------------------|------------------|-------|---------------------|--------|-------|---------------------------------------|--------|-------|---------------------------------------|
|                  |                 |               | Avg. Surface Water Depth* (cm) | Avg. Temperature |       |                     |        |       |                                       |        |       |                                       |
|                  |                 |               |                                | Air              | Water |                     |        |       |                                       |        |       |                                       |
|                  |                 |               |                                | (C°)             |       | Avg.                | Max.   | Min.  | Avg.                                  | Max.   | Min.  |                                       |
| SPRING           |                 |               |                                |                  |       |                     |        |       |                                       |        |       |                                       |
| Adult Females    | 4               | 5/69          | Moderate (5)                   | N.D.             | N.D.  | 3.6                 | 4.1    | 2.7   | greatest daily movements              |        |       | deep water areas                      |
| Adult Males      | 10              | 4-5/71        | Normal (-2.5 to 5.0)           | N.D.             | N.D.  | 373.2               | 784.6  | 44.6  | 770.2                                 | 1297.8 | 234.2 | deep water areas                      |
| Immature Females | 8               | 3-5/73        | Extreme (17.5+)                | 22.5             | 23.0  | 317.3               | 784.6  | 70.9  | 296.9                                 | 583.4  | 123.1 | marsh & potholes                      |
| Immature Males   | 8               | 3-5/73        | Extreme (17.5+)                | 22.5             | 23.0  | 295.9               | 679.1  | 75.0  | 280.9                                 | 476.9  | 214.8 | shallow water areas                   |
| SUMMER           |                 |               |                                |                  |       |                     |        |       |                                       |        |       |                                       |
| Adult Females    | 3               | 6-8/69        | Normal (-2.5 to 5.0)           | N.D.             | N.D.  | 1.8                 | 2.7    | 1.4   | restricted daily movement             |        |       | marsh & potholes                      |
| Adult Males      | 6               | 6-8/71        | Normal (-2.5 to 5.0)           | N.D.             | N.D.  | 1323.6              | 1666.4 | 153.6 | 863.1                                 | 1723.1 | 456.3 | deep water areas                      |
| Immature Females | 8               | 6-8/73        | Extreme (17.5+)                | 28.3             | 29.2  | 93.2                | 159.6  | 44.1  | 291.4                                 | 769.2  | 75.1  | marsh & potholes and deep water areas |
| Immature Males   | 8               | 6-8/73        | Extreme (17.5+)                | 28.3             | 29.2  | 205.4               | 383.6  | 27.7  | 243.1                                 | 413.5  | 192.3 | deep water areas                      |

\* Expressed as cm above mean marsh floor level

\*\* Defined as linear distance traveled during a 24-hour period

\*\*\* Marsh  $\bar{c}$  potholes - marsh with dense vegetation, interspersed with numerous small potholes, ponds, and shallow marsh lakes

Marsh  $\bar{c}$  bayous - marsh with dense vegetation intersected by natural bayous

Shallow water areas - impounded marsh characterized by large, open water areas and regulated water levels

Deep water areas - natural bayous and canals characterized by relatively deep water

Table 2, continued.

| Sex and Age      | Sample size (n) | Date of Study | Environmental Conditions       |                  |       | Activity Range (ha) |        |      | Average Daily Distance Traveled (m)** |       |       | Habitat Utiliz.***                    |
|------------------|-----------------|---------------|--------------------------------|------------------|-------|---------------------|--------|------|---------------------------------------|-------|-------|---------------------------------------|
|                  |                 |               | Avg. Surface Water Depth* (cm) | Avg. Temperature |       |                     |        |      |                                       |       |       |                                       |
|                  |                 |               |                                | Air              | Water |                     |        |      |                                       |       |       |                                       |
|                  |                 |               |                                | (C°)             |       | Avg.                | Max.   | Min. | Avg.                                  | Max.  | Min.  |                                       |
| AUTUMN           |                 |               |                                |                  |       |                     |        |      |                                       |       |       |                                       |
| Adult Females    | 3               | 9-11/69       | Low (0)                        | N.D.             | N.D.  | 0.9                 | 1.4    | <0.5 | highly restricted daily movement      |       |       | marsh c potholes                      |
| Adult Males      | 6               | 9-11/71       | Extreme (17.5+)                | N.D.             | N.D.  | 500.0               | 1151.4 | 66.4 | 592.6                                 | 134.2 | 109.5 | deep water areas                      |
| Immature Females | 8               | 9-11/73       | Extreme (17.5+)                | 25.5             | 25.8  | 42.7                | 87.3   | 13.6 | 213.8                                 | 288.6 | 121.8 | marsh c potholes and deep water areas |
| Immature Males   | 6               | 9-11/73       | Extreme (17.5+)                | 25.5             | 25.8  | 47.3                | 47.3   | 47.3 | 187.1                                 | 232.6 | 238.5 | deep water areas                      |
| WINTER           |                 |               |                                |                  |       |                     |        |      |                                       |       |       |                                       |
| Adult Females    | 0               | N.A.          | N.A.                           | N.A.             | N.A.  | N.D.                | N.D.   | N.D. | N.D.                                  | N.D.  | N.D.  | N.D.                                  |
| Adult Males      | 3               | 12/71 to 2/72 | Extreme (17.5+)                | N.D.             | N.D.  | No movement         |        |      | No movement                           |       |       | marsh c potholes                      |
| Immature Females | 5               | 12/73 to 2/74 | Extreme (17.5+)                | 15.3             | 17.5  | N.D.                | N.D.   | N.D. | 171.1                                 | 172.9 | 169.2 | marsh c potholes                      |
| Immature Males   | 1               | 12/73 to 2/74 | Extreme (17.5+)                | 15.3             | 17.5  | No movement         |        |      | No movement                           |       |       | marsh c bayous                        |

\* Expressed as cm above mean marsh floor level

\*\* Defined as linear distance traveled during a 24-hour period

\*\*\* Marsh  $\bar{c}$  potholes - marsh with dense vegetation, interspersed with numerous small potholes, ponds, and shallow marsh lakes

Marsh  $\bar{c}$  bayous - marsh with dense vegetation intersected by natural bayous

Shallow water areas - impounded marsh characterized by large, open water areas and regulated water levels

Deep water areas - natural bayous and canals characterized by relatively deep water

**Table 3. Annual survivorship estimates and standard errors by size classes of Everglades alligators in Shark Slough, Everglades National Park, 1976-1981 (from Jacobsen and Kushlan 1984).**

| Year              | Size Class        |                   |                    |                    |
|-------------------|-------------------|-------------------|--------------------|--------------------|
|                   | 1<br>(<60.0 cm)   | 2<br>(60.0-120.0) | 3<br>(120.0-160.0) | 4<br>(>160.0)      |
| 1976              | 0.250<br>(0.0421) | 0.502<br>(0.1146) | 0.500<br>(2.529)   | 0.792<br>(0.4965)  |
| 1977              | 0.453<br>(0.0376) | 0.501<br>(0.1069) | 0.469<br>(0.1596)  | 0.508<br>(0.2132)  |
| 1978              | 0.462<br>(0.0551) | 0.490<br>(0.0917) | 1.000*<br>(0.5332) | 0.778<br>(0.2145)  |
| 1979              | 0.233<br>(0.0291) | 0.619<br>(0.1418) | 0.741<br>(0.5393)  | 1.000*<br>(0.3881) |
| 1980              | 0.814<br>(0.1277) | 0.412<br>(0.0813) | 0.351<br>(0.2020)  | 0.707<br>(0.6600)  |
| 1981              | 0.156<br>(0.1281) | 0.705<br>(0.4474) | 0.182<br>(NA*)     | 0.118*<br>(0.1046) |
| AVERAGE           | 0.394             | 0.538             | 0.540              | 0.650              |
| STANDARD<br>ERROR | (0.2399)          | (0.1052)          | (0.2907)           | (0.3051)           |

NA = Not available

\* = Unreliable estimate due to small sample size

**Table 4. A comparison of size/age specific survival rates of American alligator populations in the coastal chenier plain of south Louisiana and the Everglades of south Florida, (from Jacobsen and Kushlan 1984).**

| Size Class           | South Louisiana |             | Everglades    |             |
|----------------------|-----------------|-------------|---------------|-------------|
|                      | Survival Rate   | Age (years) | Survival Rate | Age (years) |
| 1 (<60.0 cm)         | 0.350           | <1          | 0.394         | 1-3         |
| 2 (60.0 - 120.0 cm)  | 0.600-0.788     | 2-3         | 0.538         | 4-8         |
| 3 (120.0 - 160.0 cm) | 0.788           | 4           | 0.540         | 9-15        |
| 4 (>160.0 cm)        | 0.750-0.875     | >5          | 0.650         | >15         |

**Table 5. Age structure generated by a 20-year model simulation of the American alligator population in south Louisiana (from Nichols et al. 197 ).**

| Age Class             | MALES  |                    | FEMALES |                    | TOTAL   |                    |
|-----------------------|--------|--------------------|---------|--------------------|---------|--------------------|
|                       | Number | % Total Population | Number  | % Total Population | Number  | % Total Population |
| Juveniles (1-3 years) | 44,246 | 44                 | 29,375  | 29                 | 73,621  | 73                 |
| Subadults (4-9 years) | 12,449 | 12                 | 8,266   | 9                  | 20,715  | 21                 |
| Adults (>10 years)    | 2,485  | 3                  | 3,179   | 3                  | 5,664   | 6                  |
| TOTAL                 | 59,180 | 59                 | 40,820  | 41                 | 100,000 | 100                |

**Table 6. Age structure estimated from empirical data collected during a population study (1977-1980) of the American alligator in the southern Everglades (from Jacobsen and Kushlan 19 ).**

| <b>Age Class</b>           | <b>No. of Alligators</b> | <b>Percent Total Population</b> |
|----------------------------|--------------------------|---------------------------------|
| Juveniles<br>(1-3 years)   | 512                      | 78                              |
| Sub-adults<br>(4-15 years) | 102                      | 16                              |
| Adults<br>(>15 years)      | 39                       | 6                               |
| <b>TOTAL</b>               | <b>653</b>               | <b>100</b>                      |

**Table 7. A summary of American alligator social signals and their vocal elements, physical characteristics, stimulus situations, and probable functions (from Garrick et al. 1978).**

| Vocalization     | Median & range of no. units                                                                                       | Sex     | Mean & (range) call duration (seconds)                        | Median & range of durations(s) of intercall intervals | Fundamental or dominant frequency Hz                                                                                       | Estimated distance vocalization carries in air (m) |
|------------------|-------------------------------------------------------------------------------------------------------------------|---------|---------------------------------------------------------------|-------------------------------------------------------|----------------------------------------------------------------------------------------------------------------------------|----------------------------------------------------|
| Bellow           | (1-11)<br>5/bout                                                                                                  | M<br>F  | 1.83 (1.23-2.79)<br>1.71 (1.23-2.67)                          | 3.94 (2.92-6.70)<br>2.60 (1.76-4.83)                  | 50-250                                                                                                                     | 150                                                |
| Bellow Growl     | (1-6)<br>2/bout                                                                                                   | F       | 0.91 (0.36-1.43)                                              | 2.86 (1.76-5.38)                                      | 125-200                                                                                                                    | 75                                                 |
| Deep Grunt       | 1                                                                                                                 | unknown | 1.04                                                          | —                                                     | 50 with harmonics                                                                                                          | ~5                                                 |
| Low Growl        | 1                                                                                                                 | M,F     | 0.68                                                          | —                                                     | 100 with harmonics                                                                                                         | <10                                                |
| Growl = Chumpfs  | 3<br>2 forms                                                                                                      | M,F     | 0.20<br>0.29                                                  | 1.0                                                   | 75 with harmonics                                                                                                          | <5                                                 |
| Hiss             | 1 or 2                                                                                                            | M,F     | 1-30                                                          | 3.5                                                   | 50-250 and 550-650                                                                                                         | ~5                                                 |
| Vocalization     | Stimulus Situation                                                                                                |         | Post-vocal Responses                                          |                                                       | Probable Functions                                                                                                         |                                                    |
| Bellow           | <u>External</u><br>Bellow<br>Headslap<br>Bellow Growl<br>Nonbiological sounds<br><u>Internal</u><br>"Spontaneous" |         | Bellowing<br>Approach of Bellow<br>Nonspecific movement       |                                                       | Signals presence and location<br>Synchronize group activity<br>Individual recognition<br>Attract conspecifics for breeding |                                                    |
| Bellow-Growl     | Approach by male<br>Nearby male-male agonistic encounter                                                          |         | Female swims off, submerges or leaves water<br>Female remains |                                                       | Inhibits mating attempt by male<br>Identifies vocalizer as a female;<br>inhibits attack                                    |                                                    |
| Deep Grunt       | Playbacks of juvenile grunts                                                                                      |         |                                                               |                                                       | Signal to young; recognition                                                                                               |                                                    |
| Low Growl        | During headslapping, yawning and inflated posture                                                                 |         | Females bellow-growl                                          |                                                       | Signal modification                                                                                                        |                                                    |
| Coughs = Chumpfs | Initial phase of courtship                                                                                        |         | More courtship, usually                                       |                                                       | Initial identification; facilitates further contact                                                                        |                                                    |

Table 8. A comparison of American alligator reproductive performance in Shark Slough, Everglades National Park, for 1985-1990.

| Year | Late Dry Season Surface Water Condition <sup>1</sup> | Nest. Pop. <sup>2</sup> Estimate<br>$\bar{Y} \pm 95\%$ C.L. | Monitored Nests (n) | Avg. Clutch Size (# eggs) | Hatching Rate <sup>3</sup> (%) | Infertility Rate <sup>4,5</sup> (%) | Arrested Dev. Rate <sup>6</sup> (%) | Flooding Rate <sup>7</sup> (%) | Predation Rate <sup>7</sup> (%) | Other <sup>7,8</sup> Mortality (%) | Avg. No. <sup>9</sup> Hatchlings per Clutch | Estimated <sup>7</sup> Total No. Hatchlings |
|------|------------------------------------------------------|-------------------------------------------------------------|---------------------|---------------------------|--------------------------------|-------------------------------------|-------------------------------------|--------------------------------|---------------------------------|------------------------------------|---------------------------------------------|---------------------------------------------|
| 1985 | Low                                                  | $28 \pm 50\%$                                               | 9                   | 28.2                      | 74                             | 3                                   | 0                                   | 23                             | 0                               | 0                                  | 20.9                                        | 585                                         |
| 1986 | High                                                 | $368 \pm 30\%$                                              | 75                  | 27.0                      | 85                             | 7                                   | 0                                   | 6                              | 1                               | 1                                  | 23.0                                        | 8464                                        |
| 1987 | Moderate                                             | $208 \pm 38\%$                                              | 51                  | 29.7                      | 73                             | 8                                   | 0                                   | 14                             | 4                               | 1                                  | 21.7                                        | 4514                                        |
| 1988 | Mod.Low                                              | $108 \pm 50\%$                                              | 25                  | 29.2                      | 44                             | 9                                   | 0                                   | 47                             | 0                               | 0                                  | 12.8                                        | 1382                                        |
| 1989 | Low                                                  | $40 \pm 68\%$                                               | 10                  | 30.1                      | 58                             | 25                                  | 17                                  | 0                              | 0                               | 0                                  | 17.4                                        | 696                                         |
| 1990 | Mod.Low                                              | $156 \pm 40\%$                                              | 27                  | 24.4                      | 55                             | 9                                   | 19                                  | 13                             | 4                               | 0                                  | 13.4                                        | 2090                                        |
| AVG  | ---                                                  | $151 \pm ( )$                                               | 33                  | 27.9                      | 74                             | 6                                   | 2                                   | 15                             | 2                               | <1                                 | 20.6                                        | 3111                                        |

- 1 Relative to a 40-year period of record average at Hydrological Station P33, Shark Slough
- 2 Ninety-five percent confidence limits expressed as a percentage of the estimated population mean
- 3 Rates (%) based on pooled egg counts/category divided by total number eggs/year
- 4 Includes both infertile and early embryonic death
- 5 Includes desiccation, crushing, or breakage during egg deposition
- 6 Calculated by multiplying average clutch size for each year by average hatching rate
- 7 Calculated by multiplying nest population estimate for each year by average number of hatchlings/clutch

**Table 9. Expected American alligator nest densities (#/km<sup>2</sup>) by major landscape categories and water depth classes within Shark Slough, Everglades National Park (based on pooled nest counts over low (1985), high (1986), and moderate (1987) surface water conditions during the late dry season).**

| Landscape Category         | Average water depth (cm) during peak mating period |            |             |             |       |
|----------------------------|----------------------------------------------------|------------|-------------|-------------|-------|
|                            | 0                                                  | 0.1 - 15.0 | 15.1 - 30.0 | 30.1 - 45.0 | >45.0 |
| Outcrop & ridges; lowlands | 0.2                                                | 0.3        | 0.4         | 0.0         | 0.0   |
| Upper Central Sloughs      | 0.2                                                | 1.1        | 1.2         | 0.5         | 0.0   |
| Lower Central Sloughs      | 1.5                                                | 1.7        | 1.9         | 1.1         | 0.0   |

**Table 10. A comparison of American alligator nest occurrence by major landscape categories during low (1985), high (1986), and moderate (1987) rainfall years and related surface water conditions.**

| Landscape Category   | Environmental Characteristics                                                                                    | Proportion (%) of Total Area | Proportion (%) Total Nest Counts |                           |                               | Average Proportion (%) Total Nest Counts <sup>1</sup> |
|----------------------|------------------------------------------------------------------------------------------------------------------|------------------------------|----------------------------------|---------------------------|-------------------------------|-------------------------------------------------------|
|                      |                                                                                                                  |                              | 1985 (low surface water)         | 1986 (high surface water) | 1987 (moderate surface water) |                                                       |
| Ridges and Rockland  | High relative elevation; rockland, marls, mixed marls and mucks; sparse vegetation; short hydroperiods (< 6 mo)  | 39                           | 0                                | 9                         | 13                            | 3                                                     |
| Upper Central Slough | Moderate relative elevations; mixed marls and mucks; sparse-dense vegetation; intermediate hydroperiods (6-9 mo) | 25                           | 0                                | 31                        | 9                             | 31                                                    |
| Lower Central Slough | Low relative elevation; mucks; dense vegetation; Long hydroperiods (> 9 mo)                                      | 36                           | 100                              | 60                        | 78                            | 67                                                    |

<sup>1</sup> Pooled for 1985-87

Table 11. American alligator average nest occurrence (% total number) by major landscape categories and water depth classes within Shark Slough, Everglades National Park (based on pooled nest counts over low (1985), high (1986), and moderate (1987) surface water conditions during the late dry season).

| Water Depth Class (cm)                 | Alligator Nest Frequency Occurrence | Landscape Type   |         |                | % Total Nests in Water Depth Class |
|----------------------------------------|-------------------------------------|------------------|---------|----------------|------------------------------------|
|                                        |                                     | Ridge & Rockland | Lowland | Central Slough |                                    |
| 0.0                                    | Total Percent                       | 0.00             | 2.78    | 5.56           | 8.33                               |
|                                        | Row Percent                         | 0.00             | 33.33   | 66.67          |                                    |
|                                        | Column Percent                      | 0.00             | 9.09    | 8.33           |                                    |
| 0.1 - 15.0                             | Total Percent                       | 2.78             | 2.78    | 5.56           | 11.11                              |
|                                        | Row Percent                         | 25.00            | 25.00   | 50.00          |                                    |
|                                        | Column Percent                      | 100.00           | 9.09    | 8.33           |                                    |
| 15.1 - 22.5                            | Total Percent                       | 0.00             | 2.78    | 2.78           | 5.56                               |
|                                        | Row Percent                         | 0.00             | 50.00   | 50.00          |                                    |
|                                        | Column Percent                      | 0.00             | 9.09    | 4.17           |                                    |
| 22.6 - 30.0                            | Total Percent                       | 0.00             | 2.78    | 8.33           | 11.11                              |
|                                        | Row Percent                         | 0.00             | 25.00   | 75.00          |                                    |
|                                        | Column Percent                      | 0.00             | 9.09    | 12.50          |                                    |
| 30.1 - 37.5                            | Total Percent                       | 0.00             | 2.78    | 13.89          | 16.67                              |
|                                        | Row Percent                         | 0.00             | 16.67   | 83.33          |                                    |
|                                        | Column Percent                      | 0.00             | 9.09    | 20.83          |                                    |
| 37.6 - 45.0                            | Total Percent                       | 0.00             | 2.78    | 5.56           | 8.33                               |
|                                        | Row Percent                         | 0.00             | 33.33   | 66.67          |                                    |
|                                        | Column Percent                      | 0.00             | 9.09    | 8.33           |                                    |
| 45.1 - 52.5                            | Total Percent                       | 0.00             | 5.56    | 5.56           | 11.11                              |
|                                        | Row Percent                         | 0.00             | 50.00   | 50.00          |                                    |
|                                        | Column Percent                      | 0.00             | 18.18   | 8.33           |                                    |
| 52.6 - 60.0                            | Total Percent                       | 0.00             | 2.78    | 11.11          | 13.89                              |
|                                        | Row Percent                         | 0.00             | 20.00   | 80.00          |                                    |
|                                        | Column Percent                      | 0.00             | 9.09    | 16.67          |                                    |
| >60.0                                  | Total Percent                       | 0.00             | 5.56    | 8.33           | 13.89                              |
|                                        | Row Percent                         | 0.00             | 40.00   | 60.00          |                                    |
|                                        | Column Percent                      | 0.00             | 18.18   | 12.50          |                                    |
| Percent Total Nests/<br>Landscape Type |                                     | 2.78             | 30.56   | 66.67          | 100.00                             |

**Table 12. Proportion (%) of the area within each one-foot elevation class occurring within Shark Slough that is comprised of high vs low organic soils, dense vs sparse vegetation cover, and mostly wet vs mostly dry average, dry season surface water condition.**

| Elevational Class (NGV) | Landscape Type                              | Dominant Soil Type |       |            | Dominant Vegetation Cover Type |                   | Average Dry Season Surface Water Condition |                    |            |
|-------------------------|---------------------------------------------|--------------------|-------|------------|--------------------------------|-------------------|--------------------------------------------|--------------------|------------|
|                         |                                             | Mucks              | Marls | Rock-lands | Dense Vegetation               | Sparse Vegetation | Mostly Wet                                 | Moderately Wet-Dry | Mostly Dry |
| 1'                      | Lower Central Slough and Estuary Headwaters | 0                  | 100   | 0          | 25                             | 75                | 65                                         | 35                 | 0          |
| 2'                      |                                             | 9                  | 82    | 9          | 21                             | 79                | 14                                         | 83                 | 3          |
| 3'                      |                                             | 44                 | 44    | 12         | 38                             | 62                | 48                                         | 52                 | 0          |
| 4'                      | Central Slough                              | 58                 | 23    | 19         | 27                             | 73                | 23                                         | 69                 | 8          |
| 5'                      |                                             | 39                 | 28    | 33         | 15                             | 85                | 33                                         | 64                 | 3          |
| 6'                      |                                             | 61                 | 6     | 33         | 8                              | 92                | 32                                         | 63                 | 5          |
| 7'                      | Lowlands and Ridges                         | 29                 | 41    | 30         | 4                              | 96                | 20                                         | 73                 | 7          |
| 8'                      |                                             | 0                  | 0     | 100        | 0                              | 100               | 0                                          | 100                | 100        |
| 9'                      |                                             | 0                  | 0     | 100        | 0                              | 100               | 0                                          | 100                | 100        |

**Table 13. American alligator reproductive performance for individual sample nests monitored during the 1990 nesting season in Shark Slough, Everglades National Park.**

| Nest Identity Number | Surface Water Condition in Nesting Area (late March-early April) | Estimated Egg Laying Date | Egg Laying Date Relative to Initial Nest Check | Clutch Size (no. of eggs) | Hatching Rate (%) | Infertility Rate (%) | Arrested Dev. Date (%) | Flooding Rate (%) | Other Mortality (%) |
|----------------------|------------------------------------------------------------------|---------------------------|------------------------------------------------|---------------------------|-------------------|----------------------|------------------------|-------------------|---------------------|
| 27                   | dry-transitional                                                 | 6-26-90                   | > 7 days before                                | 27                        | 96                | 4                    | 0                      | 0                 | 0                   |
| 36                   | dry-transitional                                                 | 6-26-90                   | > 7 days before                                | 25                        | 68                | 0                    | 0                      | 32                | 0                   |
| 29                   | dry-transitional                                                 | 6-30-90                   | > 7 days before                                | 31                        | 72                | 14                   | 14                     | 0                 | 0                   |
| 34                   | dry-transitional                                                 | 6-30-90                   | > 7 days before                                | 30                        | 96                | 4                    | 0                      | 0                 | 0                   |
| 1                    | dry-dry                                                          | N.D.                      | > 7 days before                                | 18                        | 0                 | 100                  | 0                      | 0                 | 0                   |
| 18                   | dry-dry                                                          | N.D.                      | > 7 days before                                | 36                        | 94                | 6                    | 0                      | 0                 | 0                   |
| 32                   | dry-dry                                                          | N.D.                      | > 7 days before                                | 21                        | 0                 | 9                    | 0                      | 91                | 0                   |
| 38                   | dry-dry                                                          | N.D.                      | > 7 days before                                | 22                        | 82                | 0                    | 14                     | 4                 | 0                   |
| 46                   | dry-dry                                                          | 7-4-90                    | 1-3 days before                                | 20                        | 0                 | 7                    | 0                      | 0                 | 0                   |
| 25                   | dry-dry                                                          | 7-5-90                    | 1-3 days before                                | 25                        | 100               | 0                    | 0                      | 0                 | 0                   |
| 26                   | dry-dry                                                          | 7-6-90                    | 1-3 days before                                | 32                        | 90                | 3                    | 7                      | 0                 | 0                   |
| 5                    | wet-dry                                                          | 7-8-90                    | 1-3 days before                                | 27                        | 95                | 5                    | 0                      | 0                 | 0                   |
| 7                    | dry-dry                                                          | 7-8-90                    | 1-3 days before                                | 20                        | 0                 | 6                    | 0                      | 94                | 0                   |
| 40                   | dry-dry                                                          | 7-8-90                    | 1-3 days before                                | 24                        | 91                | 9                    | 0                      | 0                 | 0                   |
| 16                   | wet-dry                                                          | 7-10-90                   | 1-3 days before                                | 29                        | 0                 | 7                    | 83                     | 0                 | 0                   |
| 20                   | dry-dry                                                          | 7-14-90                   | > 7 days before                                | 25                        | 14                | 14                   | 0                      | 72                | 0                   |
| 9                    | dry-dry                                                          | 7-18-90                   | > 7 days before                                | 23                        | 70                | 0                    | 30                     | 0                 | 0                   |
| 19                   | dry-dry                                                          | 7-18-90                   | 5-15 days after                                | 27                        | 92                | 0                    | 4                      | 0                 | 4                   |
| 22                   | dry-dry                                                          | 7-20-90                   | 3-15 days after                                | 23                        | 5                 | 10                   | 75                     | 10                | 0                   |
| 44                   | wet-dry                                                          | 7-26-90                   | 9-10 days after                                | 7                         | 100               | 0                    | 0                      | 0                 | 0                   |
| 45                   | dry-dry                                                          | 7-30-90                   | 9-10 days after                                | 26                        | 75                | 0                    | 25                     | 0                 | 0                   |
| 10                   | dry-dry                                                          | N.D.                      | 3-16 days after                                | 24                        | 11                | 6                    | 83                     | 0                 | 0                   |
| 21                   | dry-dry                                                          | N.D.                      | 3-15 days after                                | 20                        | 0                 | 12                   | 88                     | 0                 | 0                   |
| 12                   | dry-dry                                                          | N.A.                      | no eggs laid                                   | 0                         | --                | --                   | --                     | --                | --                  |
| 14                   | wet-dry                                                          | N.A.                      | no eggs laid                                   | 0                         | --                | --                   | --                     | --                | --                  |
| 37                   | dry-transitional                                                 | N.A.                      | no eggs laid                                   | 0                         | --                | --                   | --                     | --                | --                  |
| 43                   | dry-dry                                                          | N.A.                      | no eggs laid                                   | 0                         | --                | --                   | --                     | --                | --                  |

Table 14. Mann Whitney rank test analysis used to compare the distribution of estimated egg clutch laying dates by surface water categories at nest sites within Shark Slough during the 1990 nesting season.

|        |                                                                                                                  |                |                |                |                |                |                |                |                |                |                |                 |                  |                  |                  |                  |                  |                  |
|--------|------------------------------------------------------------------------------------------------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|-----------------|------------------|------------------|------------------|------------------|------------------|------------------|
| Step 1 | Estimated egg laying dates (8 days from April 1) for nest sites with surface water during the late dry season    | 87.00          | 87.00          | 88.00          | 88.00          |                |                |                |                |                |                |                 |                  |                  |                  |                  |                  |                  |
| Step 2 | Two standard deviation value                                                                                     | +4.40          | +4.40          | +4.40          | +4.40          |                |                |                |                |                |                |                 |                  |                  |                  |                  |                  |                  |
| Step 3 | Adjusted egg laying dates                                                                                        | 91.40          | 91.40          | 94.40          | 94.40          |                |                |                |                |                |                |                 |                  |                  |                  |                  |                  |                  |
| Step 4 | Estimated egg laying dates (8 days from April 1) for nest sites without surface water during the late dry season | 95.00          | 95.00          | 96.00          | 96.00          | 98.00          | 98.00          | 100.00         | 103.00         | 106.00         | 106.00         | 110.00          | 112.00           | 121.00           |                  |                  |                  |                  |
| Step 5 | Two standard deviation value                                                                                     | -2.44          | -2.44          | -2.44          | -2.44          | -2.44          | -2.44          | -2.44          | -2.44          | -2.44          | -2.44          | -2.44           | -2.44            |                  |                  |                  |                  |                  |
| Step 6 | Adjusted egg laying dates                                                                                        | 92.56          | 92.56          | 93.56          | 95.56          | 95.56          | 95.56          | 97.56          | 100.56         | 106.56         | 106.56         | 107.56          | 115.56           | 118.56           |                  |                  |                  |                  |
| Step 7 | Ranks                                                                                                            | 91.40<br>(1.5) | 91.40<br>(1.5) | 93.56<br>(3.5) | 93.56<br>(3.5) | 93.56<br>(5.5) | 94.40<br>(6.5) | 94.40<br>(6.5) | 95.56<br>(8.5) | 95.56<br>(8.5) | 95.56<br>(8.5) | 97.56<br>(11.0) | 100.56<br>(12.0) | 106.56<br>(13.5) | 106.56<br>(13.5) | 107.56<br>(15.0) | 115.56<br>(16.0) | 118.56<br>(17.0) |
| Step 8 | Test Statistics                                                                                                  | $T_1 = 16$     |                |                |                | $T_2 = 56$     |                |                |                | $T = 16$       |                |                 |                  | $T_{adj} = 16$   |                  |                  |                  |                  |

**Table 15. Alligator population model parameter values used in simulation runs to compare model responses to water delivery alternatives for the central and southern Everglades.**

| Survival Rates | Age Classes |     |     |     |     |     |     |
|----------------|-------------|-----|-----|-----|-----|-----|-----|
|                | 1           | 2   | 3   | 4   | 5   | 6   | 7   |
|                | 0.7         | 0.7 | 0.8 | 0.8 | 0.8 | 0.8 | .95 |

| Number of Alligator Nests/1000 Acres |                     |     |     |     |
|--------------------------------------|---------------------|-----|-----|-----|
| Soil Type                            | Water Depth Classes |     |     |     |
|                                      | 1                   | 2   | 3   | 4   |
| 1                                    | 2.0                 | 2.2 | 6.3 | 4.0 |
| 2                                    | 4.5                 | 8.9 | 9.9 | 6.5 |

| Cannibalism Parameters                         |     |
|------------------------------------------------|-----|
| Max. rate per year =                           | 0.2 |
| Half saturation rate =                         | 1.0 |
| Exponent for sigmoid cannibalism response =    | 4.0 |
| Healthy adult monthly food requirements (kg) = | 4.5 |

**Table 16. A comparison of simulated alligator population parameters resulting from a natural vs four water delivery management alternatives for the central and southern Everglades.**

| Water Deliveries  | Population Estimates |         |         | Average % Nesting Success | % Frequency Occurrence of Significant Nest Flooding |
|-------------------|----------------------|---------|---------|---------------------------|-----------------------------------------------------|
|                   | Average              | Maximum | Minimum |                           |                                                     |
| Natural           | 178000               | 350000  | 125000  | 93                        | 7                                                   |
| Base              | 116300               | 152000  | 925000  | 81                        | 19                                                  |
| Modified Base     | 124600               | 155000  | 95000   | 72                        | 28                                                  |
| Rainfall          | 131750               | 155000  | 92500   | 69                        | 31                                                  |
| Modified Rainfall | 125250               | 155000  | 92500   | 68                        | 32                                                  |

**Table 17. Fundamental environmental characteristics of wetlands important to crocodilian life history aspects and population stability and persistence.**

| Abiotic Conditions                       | Biotic Conditions                                                                                                        |
|------------------------------------------|--------------------------------------------------------------------------------------------------------------------------|
| (1) Thermal regime                       | (1) Landscape heterogeneity                                                                                              |
| (2) Hydrologic regime                    | (2) Prey Species availability                                                                                            |
| (3) Salinity regime                      | (3) Competition:<br>a) interspecific (for prey)<br>b) intraspecific<br>i) growth (for space and prey)<br>ii) cannibalism |
| (4) Topography and land surface features |                                                                                                                          |
|                                          | (4) Predation                                                                                                            |

**Table 18. Fundamental species characteristics of the American Alligator.**

| <u>Characteristic</u>                   |                                                                                                                                                                                                                                                                                                                                                                              |
|-----------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Longevity                               | long life spans (up to 50 years).                                                                                                                                                                                                                                                                                                                                            |
| Maximum growth rates & sizes            | slow but nearly continuous over long life spans, resulting in large adult sizes (up to 6.7 m).                                                                                                                                                                                                                                                                               |
| Maturation schedule                     | very long (10-18 years).                                                                                                                                                                                                                                                                                                                                                     |
| Fecundity                               | moderately low (average clutch sizes from 30-40 eggs).                                                                                                                                                                                                                                                                                                                       |
| Habitat generality                      | related to permanency of water and availability of drought refugia.                                                                                                                                                                                                                                                                                                          |
| Feeding generality                      | versatile and selectively opportunistic; feed on wide variety and size of prey; diet related to alligator size (total body length).                                                                                                                                                                                                                                          |
| Dispersal ability                       | capable of rapid response to drydowns or flooding.                                                                                                                                                                                                                                                                                                                           |
| Reproductive behavior and maternal care | complex nest site selection and material protection of young during period in life of high predation vulnerability related to small size of hatchlings and juveniles.                                                                                                                                                                                                        |
| Environmental Tolerances                |                                                                                                                                                                                                                                                                                                                                                                              |
| Thermal                                 | lower limit of 4-5°C (- °F) and upper limit of 34°C (93°F) of core body temperature; feeding activity not initiated below 22°C (72°F) of core body temperature.                                                                                                                                                                                                              |
| Hydrological                            | long-term occupancy highest in marsh areas with 5-7 year drydown interval; nesting occupancy limited to seasonal water depths less than approximately 45 cm during nest construction period; availability of drought refugia and maintenance of ground water important to both short- and long-term use of an area, particularly during dry periods or major drydown events. |
| Salinity                                | upper limits of 10 ppt for regular occupancy and utilization of marsh habitat types; upper limit of approximately 9 ppt for nesting habitat; salinities greater than ppt for longer than 2 months are lethal to hatchlings; increasing salinities (> 3 ppt) also adversely affect food consumption and stomach capacities, retarding growth rates.                           |

Table 19. A comparison of American alligator contingent population characteristics for selected wetlands within the coastal plain of the southeastern United States.

| Locality within Species Geographic Range   | Average Estimated Population Size by Salinity Marsh Types |          | Average Density by Salinity Marsh Types | Average Total Length (cm) Reached in 10 Years | Average Age to Sexual Maturity (Years) | Clutch Size (# of eggs) |          | Maternal Care (nest defense is indexed by predation ratio on eggs) (%) | Genetic Variability*                   |                               |                                    |
|--------------------------------------------|-----------------------------------------------------------|----------|-----------------------------------------|-----------------------------------------------|----------------------------------------|-------------------------|----------|------------------------------------------------------------------------|----------------------------------------|-------------------------------|------------------------------------|
|                                            |                                                           |          |                                         |                                               |                                        | Avg.                    | Range    |                                                                        | Mean $\pm$ 2 S.E. Heterozygosity (H)   | Avg. No. of Alleles/Locus (A) | Proportion of Polymorphic Loci (P) |
| Northeastern (coastal NC)                  | freshwater                                                | ND       | .02 alligators/km of shoreline          | 135.7                                         | 18                                     | 35.5                    | 27 to 40 | low (50%)                                                              | $0.034 \pm 0.006$<br>$0.033 \pm 0.008$ | 1.15<br>1.18                  | 1.186<br>0.235                     |
|                                            | brackish                                                  | ND       | 0.2 alligators/km of shoreline          |                                               |                                        |                         |          |                                                                        |                                        |                               |                                    |
| East-Central (Okefenokee Swamp in s.e. GA) | freshwater                                                | 15,000   | 9 alligators/km <sup>2</sup>            | ND                                            | ND                                     | 30.0                    | ND       | very low (86%)                                                         | ND                                     | ND                            | ND                                 |
| South-Central (north-central FL)           | freshwater                                                |          | alligators/km <sup>2</sup> of shoreline |                                               |                                        | 37.5                    | 21 to 54 | low to moderate (16%)                                                  | ND                                     | ND                            | ND                                 |
| Southwestern (coastal so. LA)              | freshwater                                                | 164,280  | 100 alligators/km <sup>2</sup>          | 231.6                                         | 10                                     | 39.5                    | 20 to 60 | low to moderate (18.5%)                                                | $0.012 \pm 0.004$<br>$0.019 \pm 0.006$ | 1.07<br>1.18                  | 0.074<br>0.118                     |
|                                            | intermediate                                              | 214,760  | 140 alligators/km <sup>2</sup>          |                                               |                                        |                         |          |                                                                        |                                        |                               |                                    |
|                                            | brackish                                                  | 109,020  | 70 alligators/km <sup>2</sup>           |                                               |                                        |                         |          |                                                                        |                                        |                               |                                    |
| Southernmost (Everglades in so. FL)        | freshwater                                                | <200,000 | 33 alligators/km <sup>2</sup>           | 128.8                                         | >15                                    | 27.9                    | 1 to 45  | High (2%)                                                              | $0.022 \pm 0.006$<br>$0.014 \pm 0.005$ | 1.19<br>1.12                  | 0.191<br>0.118                     |
|                                            | brackish                                                  | ND       | ND                                      |                                               |                                        |                         |          |                                                                        |                                        |                               |                                    |

\*no data are available for N. Carolina populations; data presented are from S. Carolina populations.

**Table 20. Population stability attributes influencing contingent population characteristics of the American alligator.**

| <b>Resistance and Structural Stability Attributes to Perturbations or Disturbance</b> |                      |
|---------------------------------------------------------------------------------------|----------------------|
| Longevity                                                                             | structural stability |
| Large body size                                                                       | structural stability |
| Maternal care                                                                         | resistance           |
| Habitat generality                                                                    | resistance           |
| Feeding generality                                                                    | resistance           |
| <b>Resilience and Recoverability Attributes from Perturbations or Disturbance</b>     |                      |
| Fecundity                                                                             | resilience           |
| Dispersal ability                                                                     | resilience           |
| Landscape heterogeneity (spatial and temporal characteristic)                         | recoverability       |

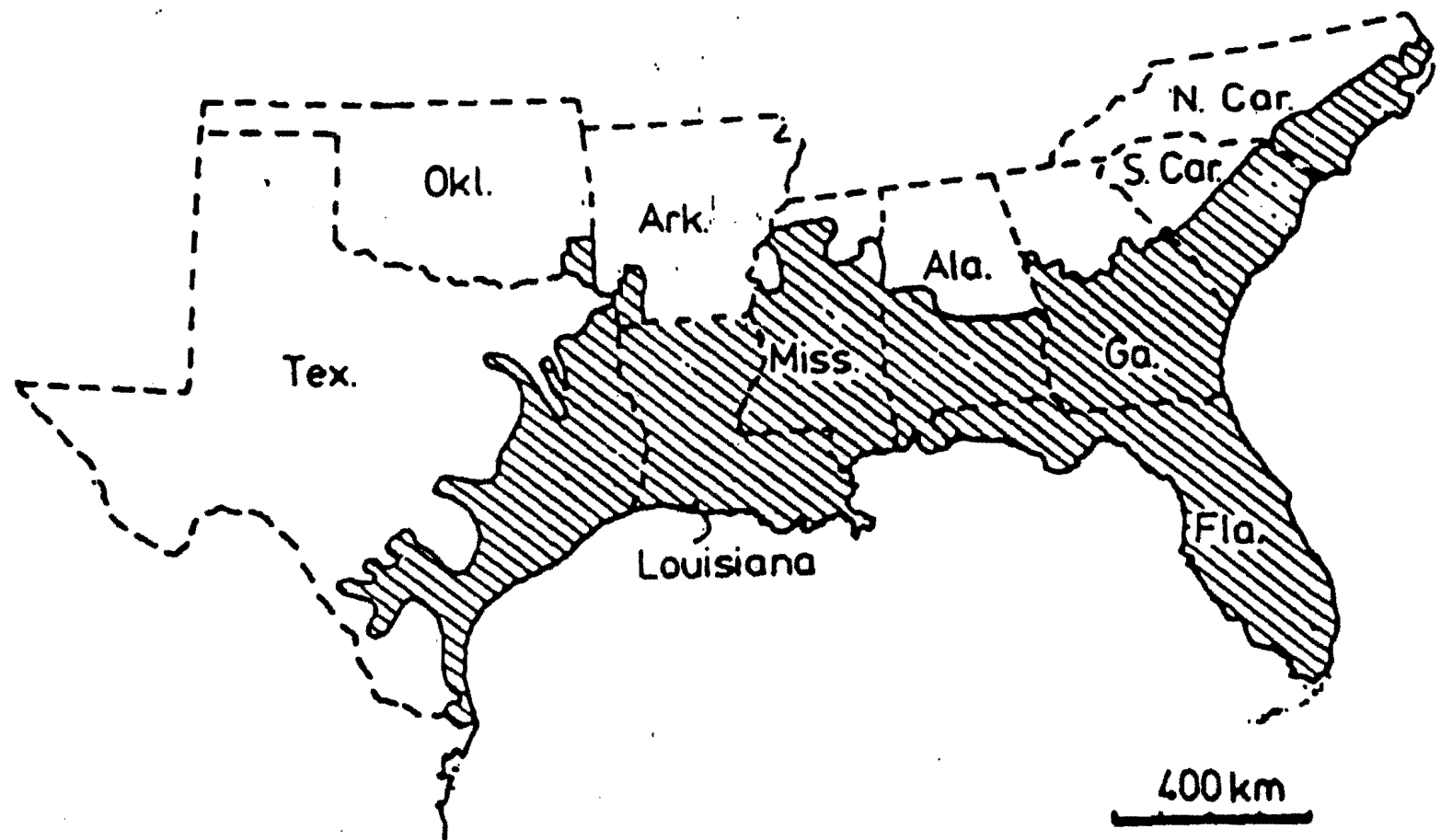


Figure 1. Present geographical range of the American alligator (from Joanen and McNease, 19 ).

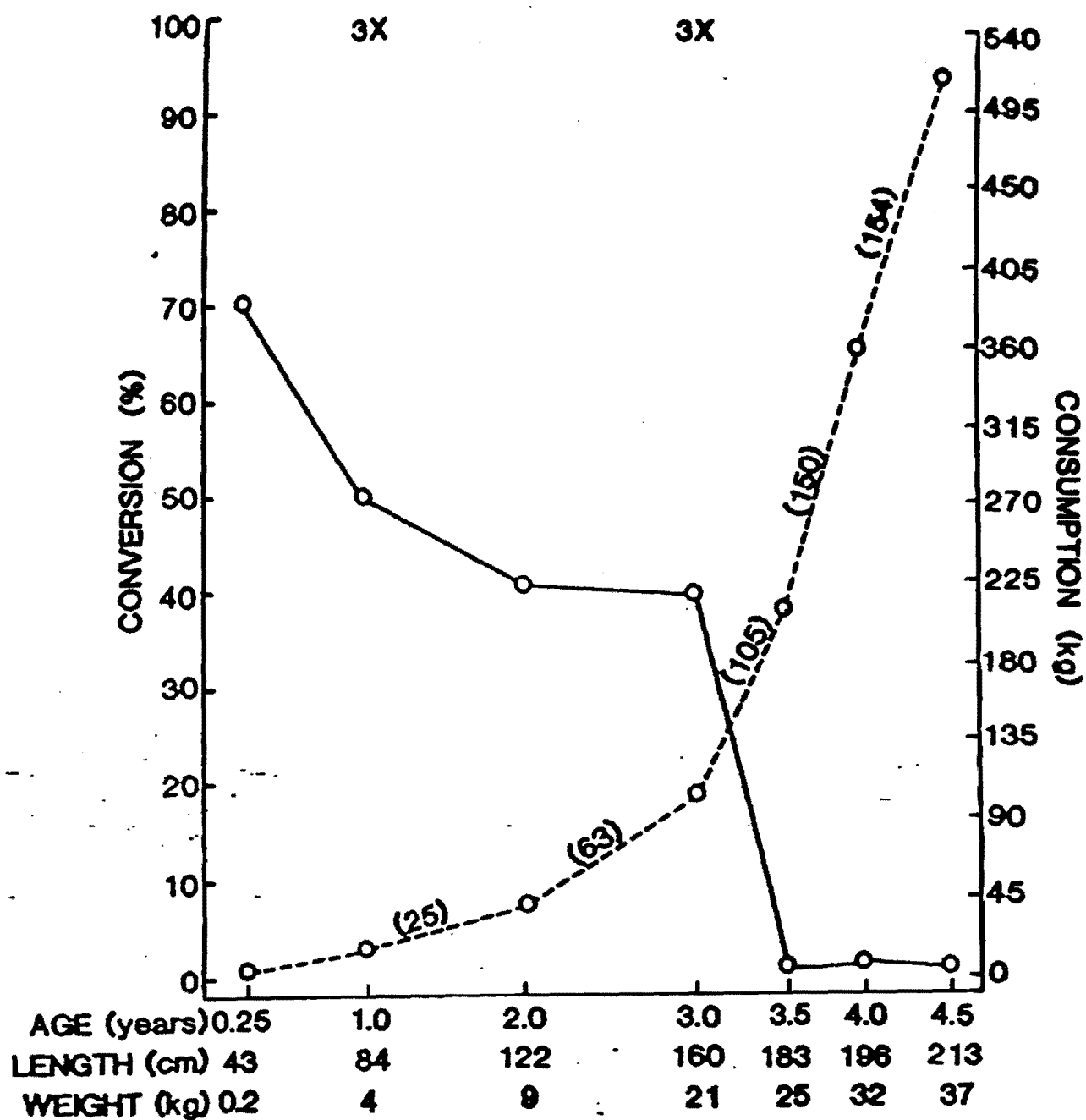


Figure 2. Food consumption, conversion, and growth rates versus age for alligators raised in controlled environmental conditions (from Joanen and McNease, 19 ).

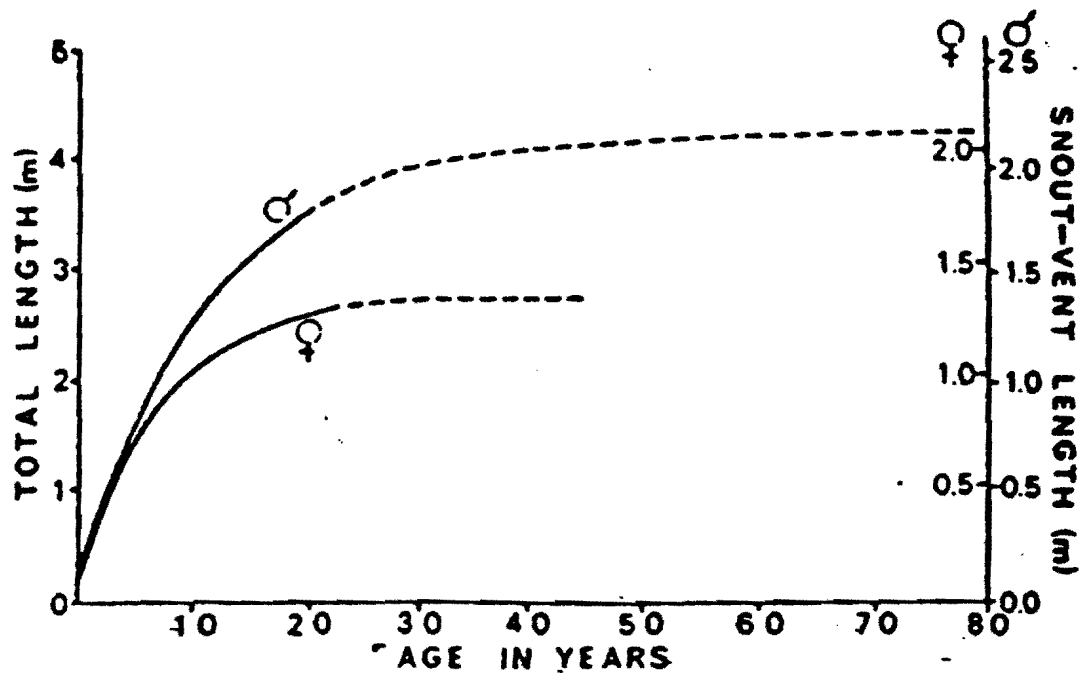


Figure 3. Growth curves for male and female alligators estimated by regression models from data collected from a wild population in south Louisiana (from Chabreck and Joanen, 19 ).

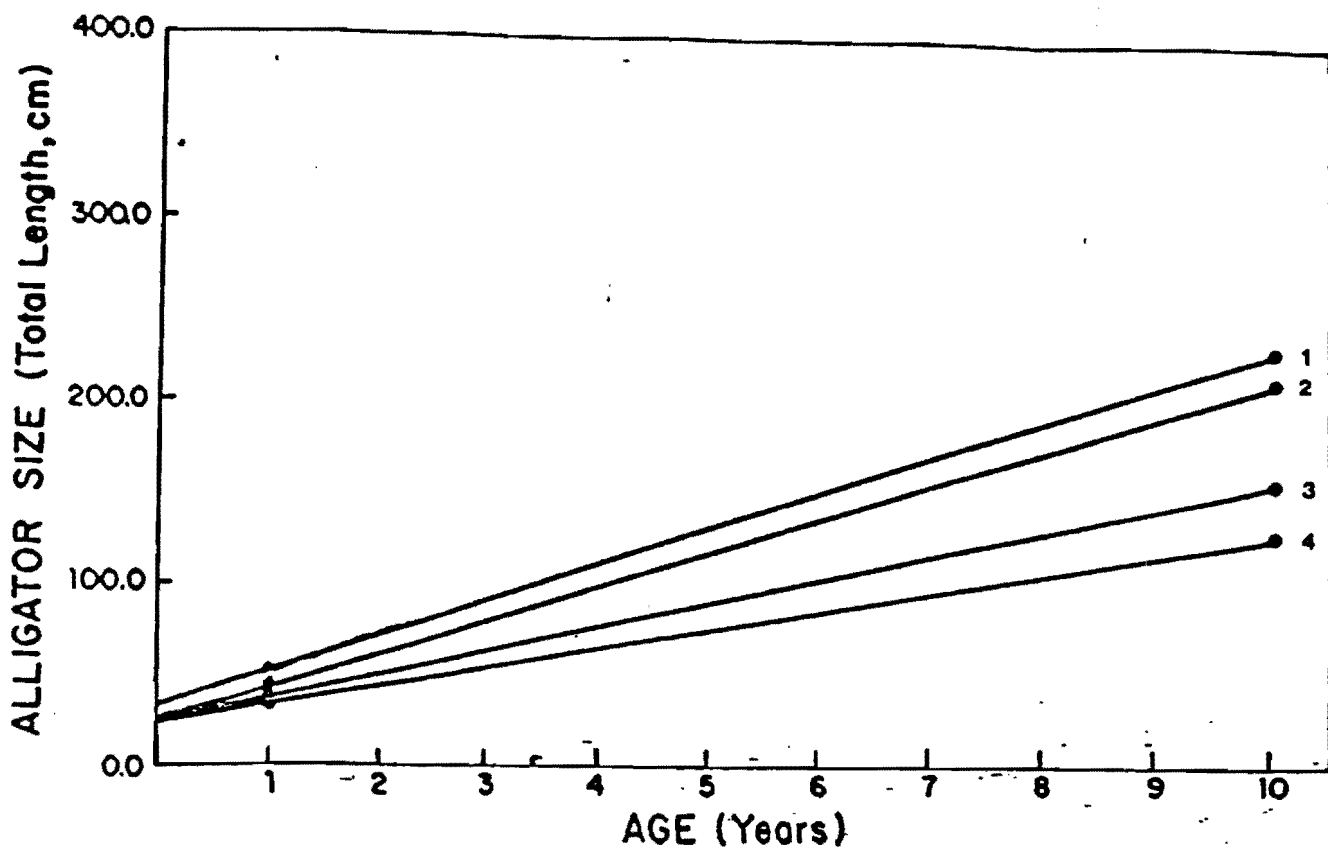


Figure 4. A comparison of predicted total length of the American alligator at different ages from several areas within its range. 1 = south Louisiana (Chabreck and Joanen, 1975), 2 = South Carolina (Murphy, 1981), 3 = North Carolina (Fuller, 1981), 4 = Everglades (Jacobsen and Kushlan, 1989).

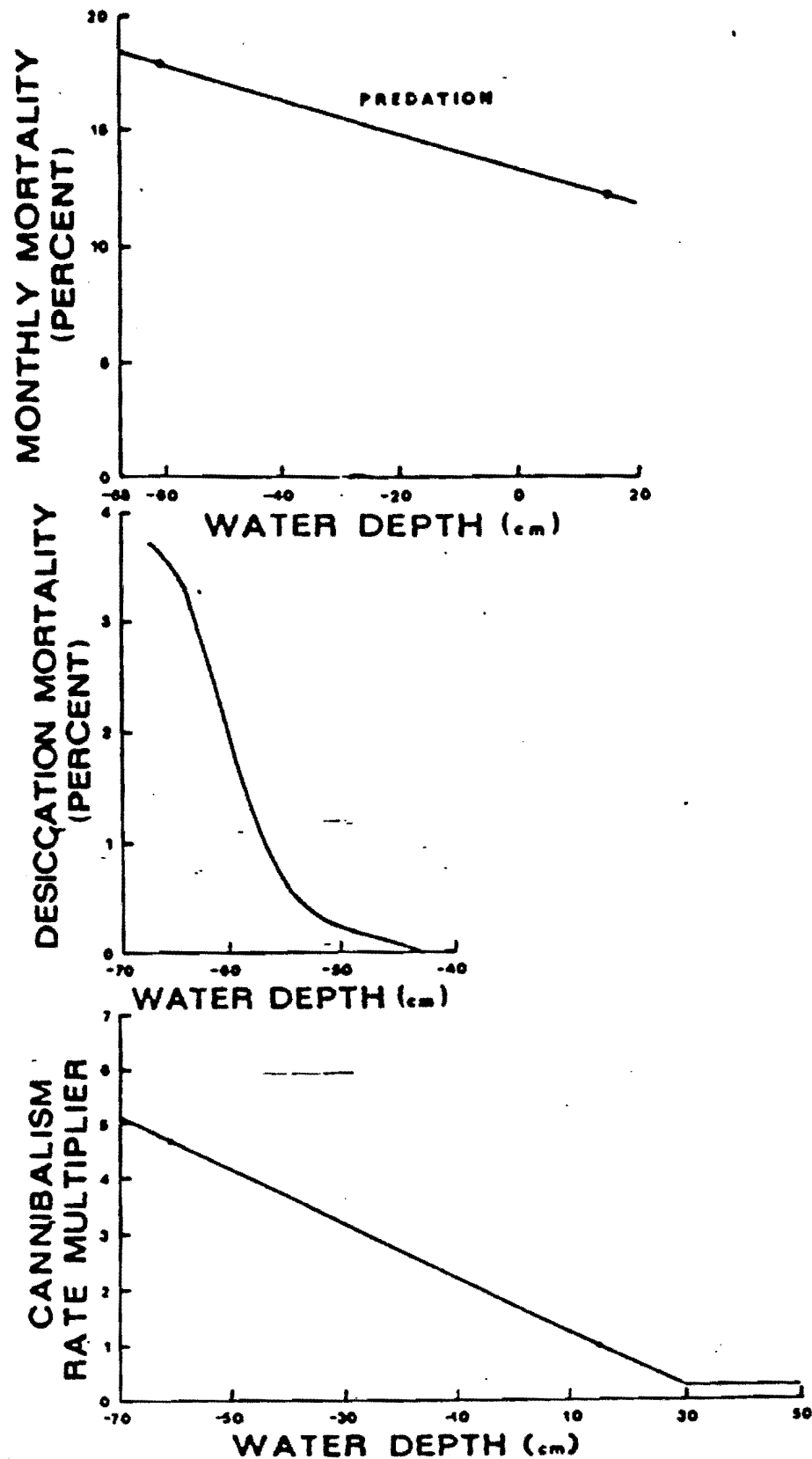


Figure 5. Major mortality factors and rates in relation to changes in marsh water depths influencing alligator population structure in south Louisiana (adapted from Nichols et al, 19 ).

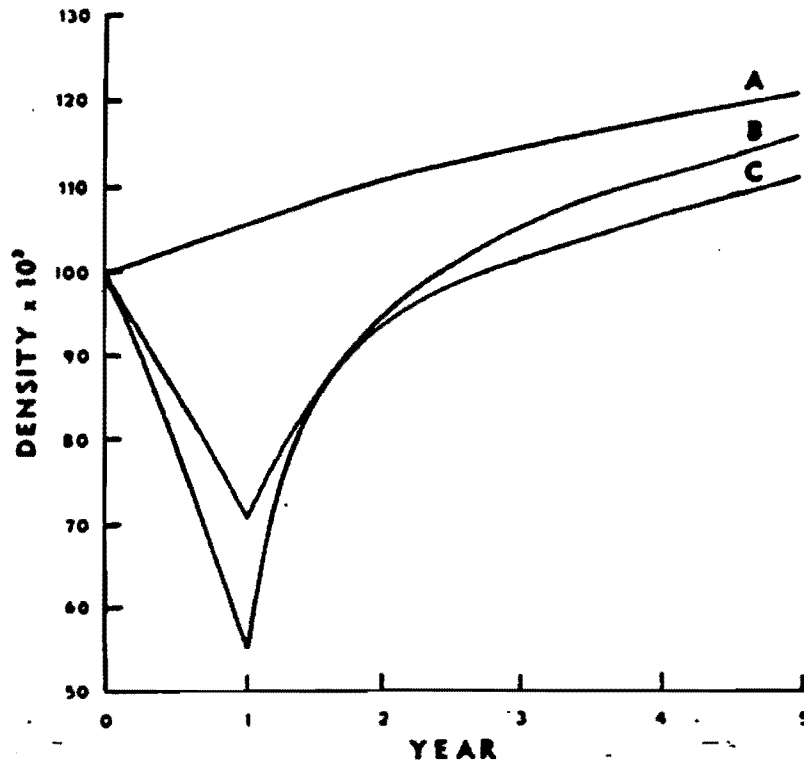


Figure 6. Simulated alligator population response to an August hurricane (plot B), severe summer drought (plot C), and constant water depth (plot A) in south Louisiana coastal marshes (from Nichols et al, 1976).

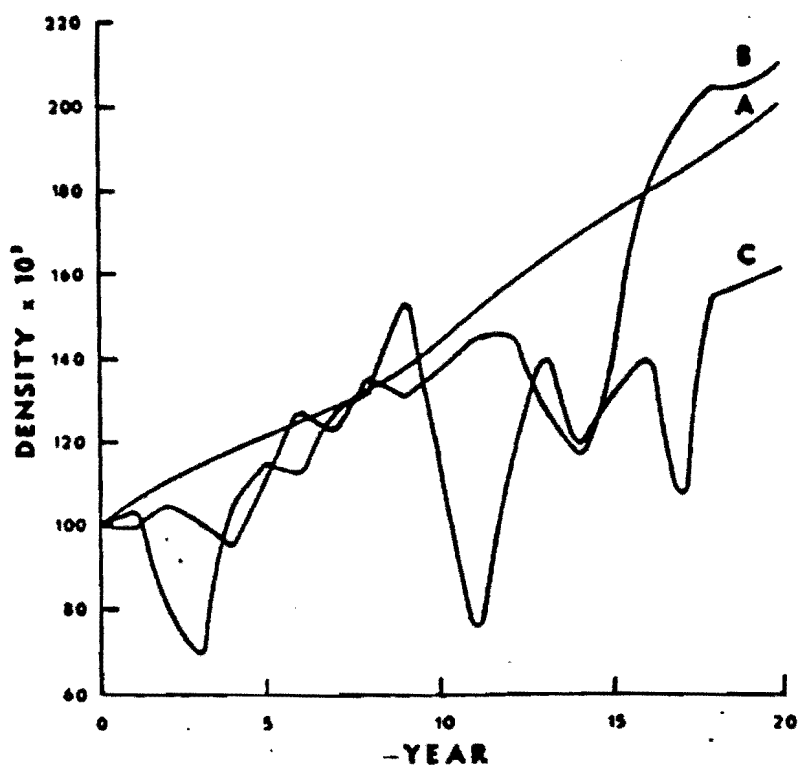


Figure 7. Simulated alligator population response to constant (plot A) and stochastic (randomly generated - plots B and C) marsh water depths and winter freezes in south Louisiana coastal marshes (from Nichols et al, 1976).

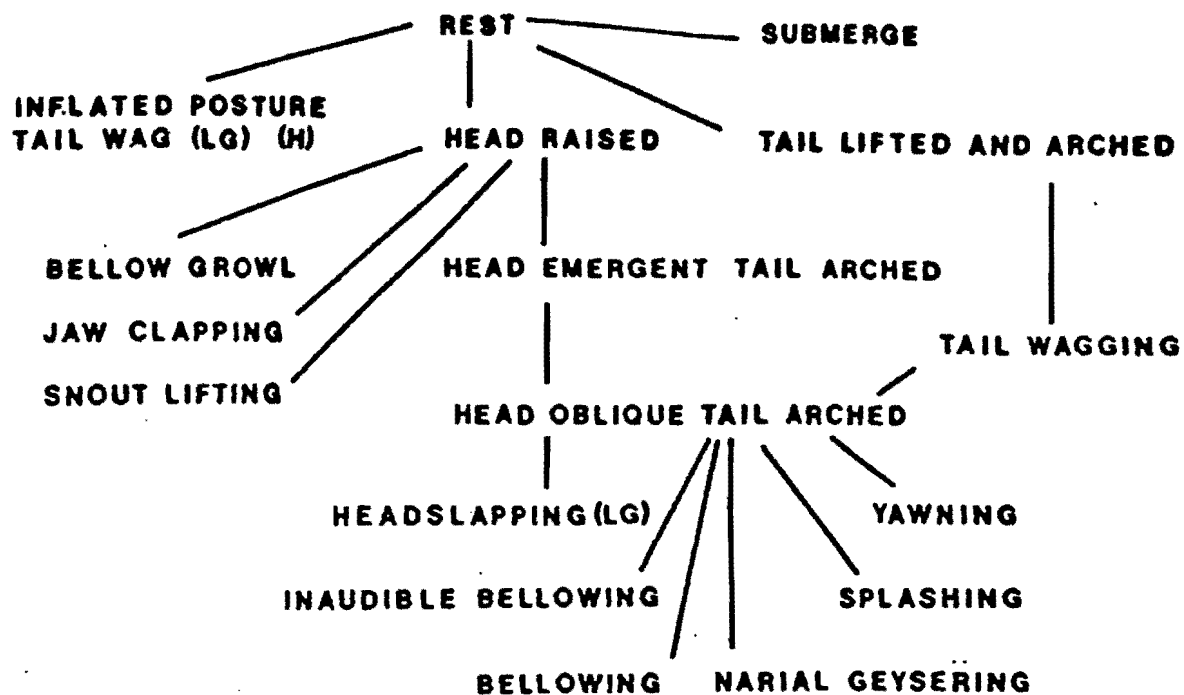


**Figure 8. Interrelations of postural elements of alligator signaling behaviors (from Garrick et al, 1978).**

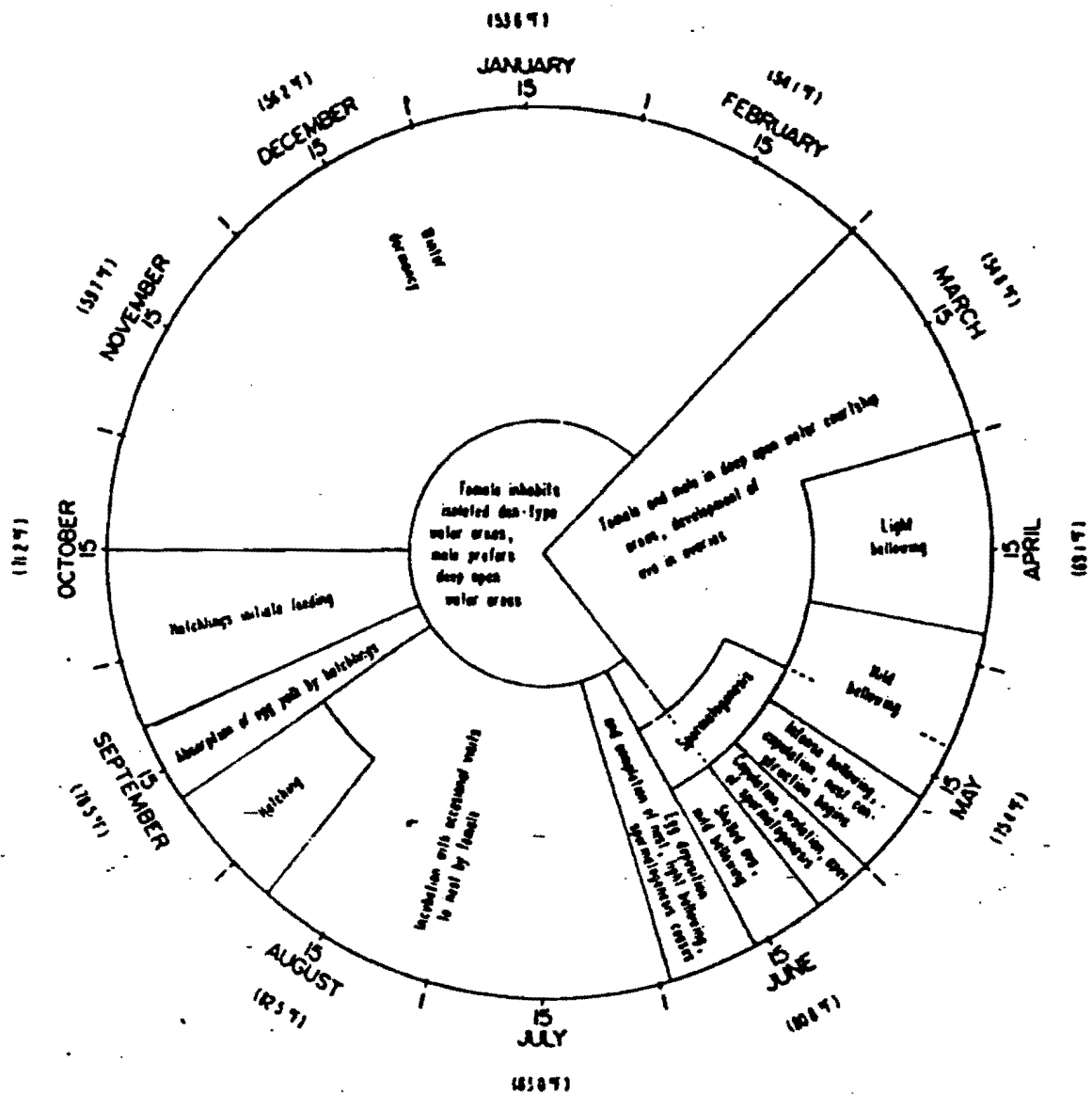


Figure 9. Chronology of the American alligator's reproductive biology (from Joanen and McNease, 19 ).

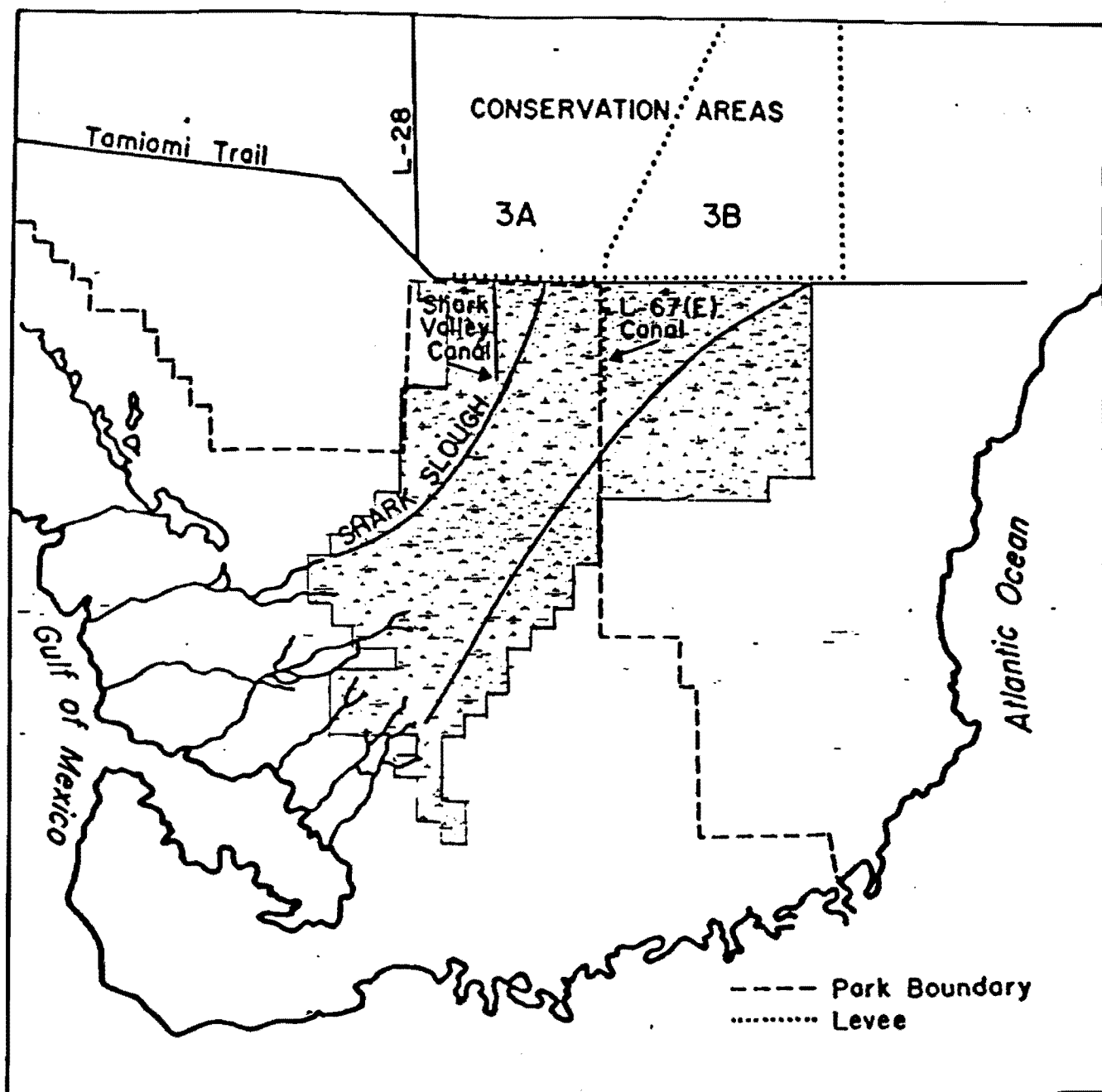
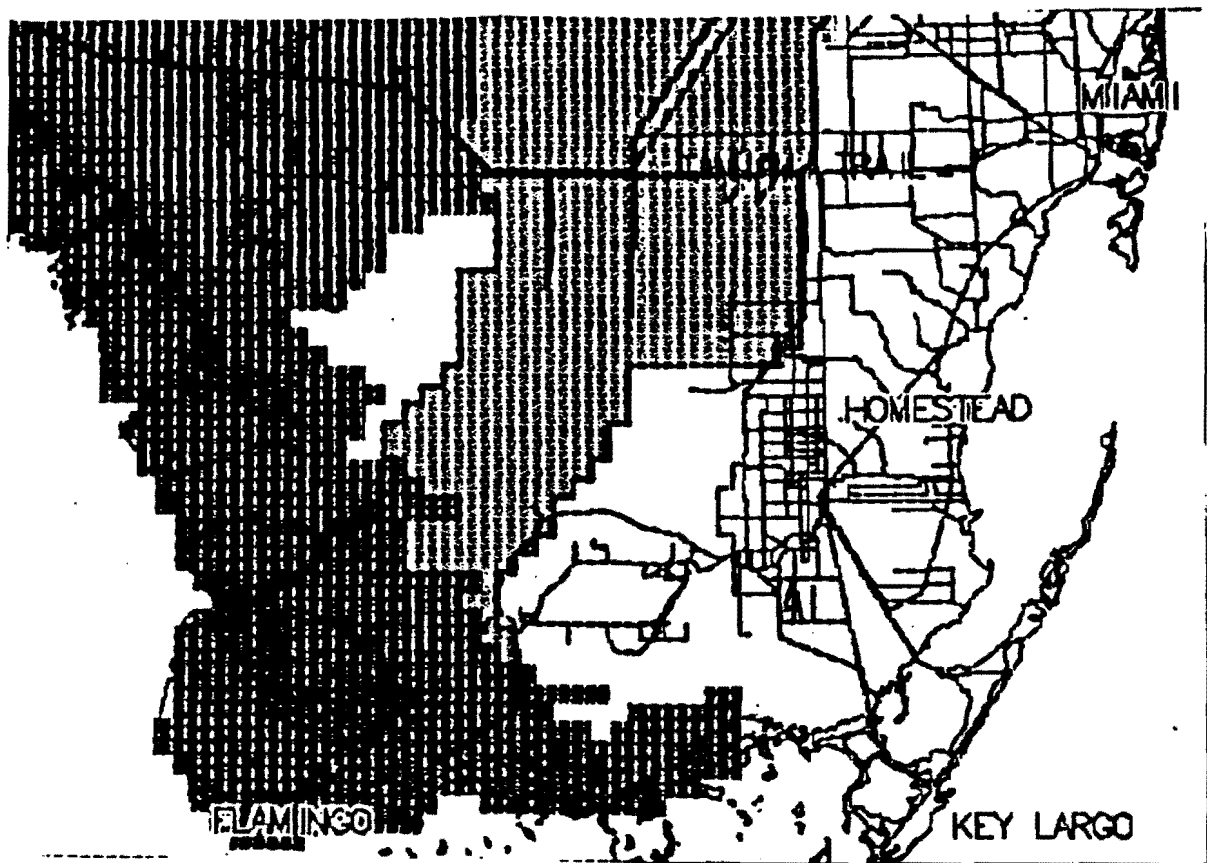


Figure 10. Alligator study area comprising the central flowway, Shark Slough, of the southern Everglades.



Cypress Swamp



Wet Prairie Savannah,  
Slough



Dry Prairie  
Savannah



Mangrove Estuary

8 more  
for Alligator  
paper - JCU

Figure 11. Physiographic regions of south Florida in relation to the alligator study area and Everglades National Park.

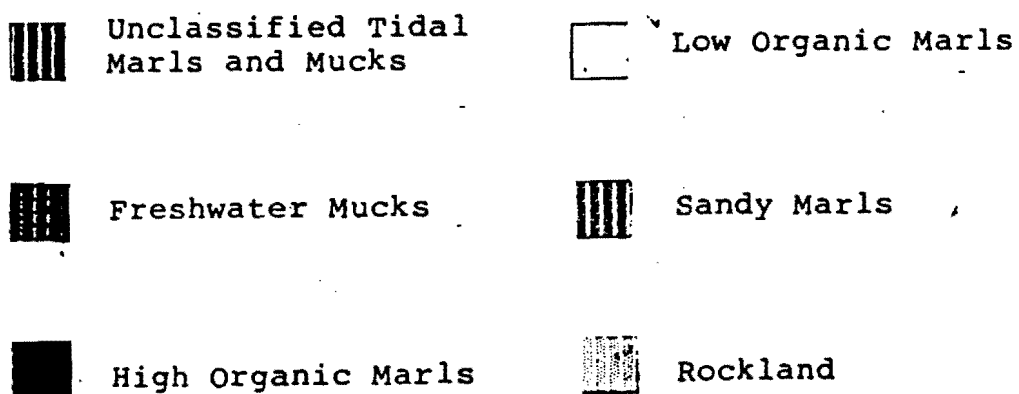
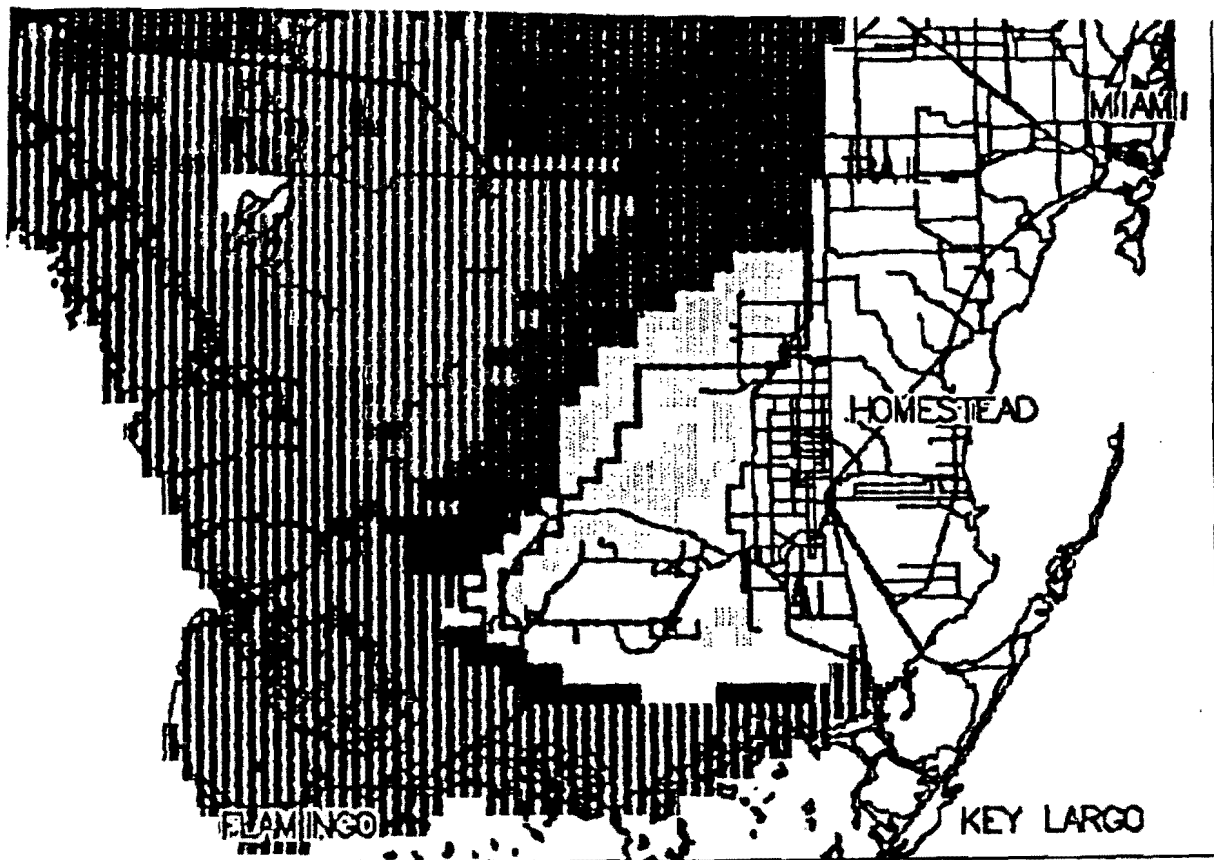


Figure 12. Soil associations of south Florida in relation to the alligator study area and Everglades National Park.

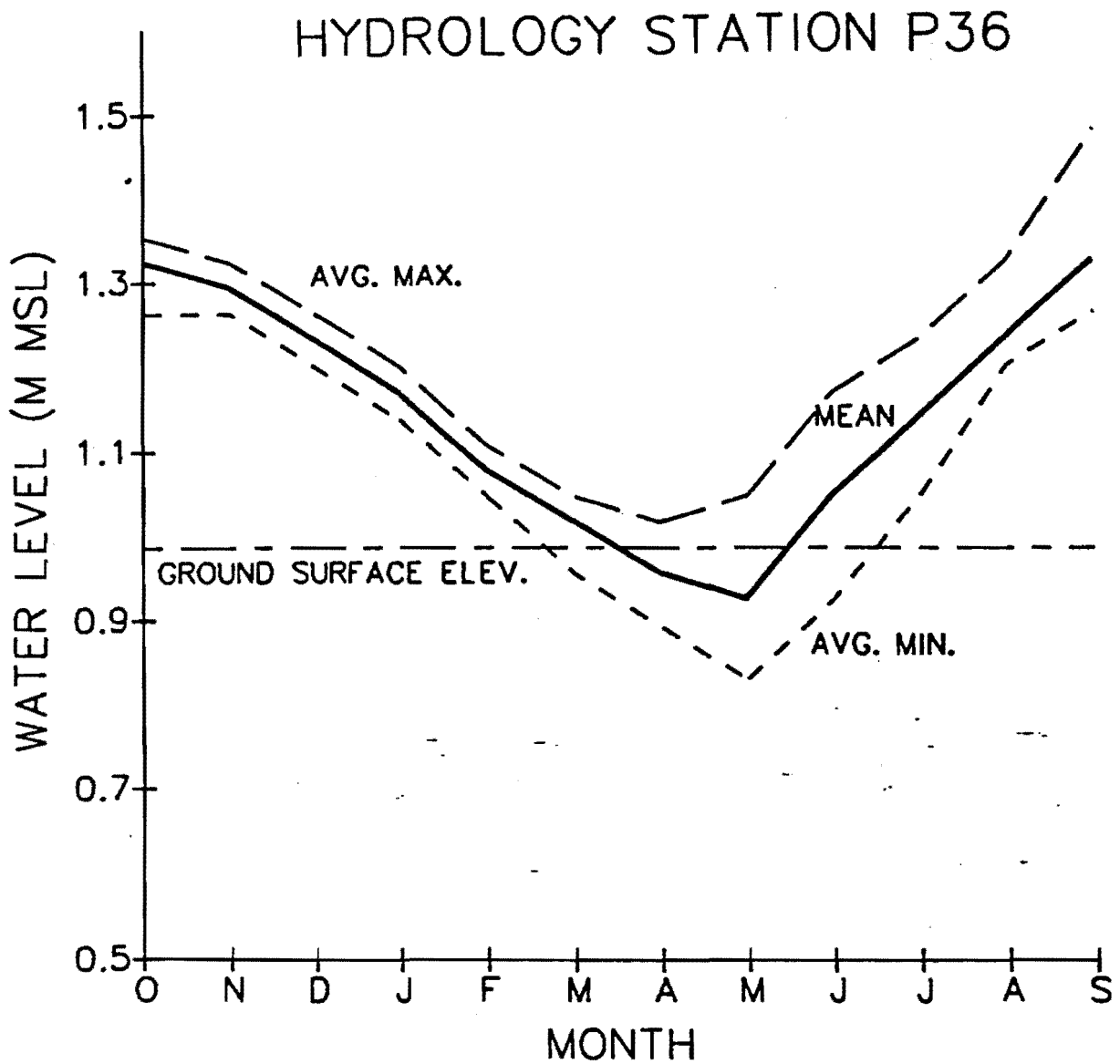


Figure 14. Average monthly, marsh water depths within Shark Slough in relation to rainfall - based water deliveries during the study period, 1985 - 1990.

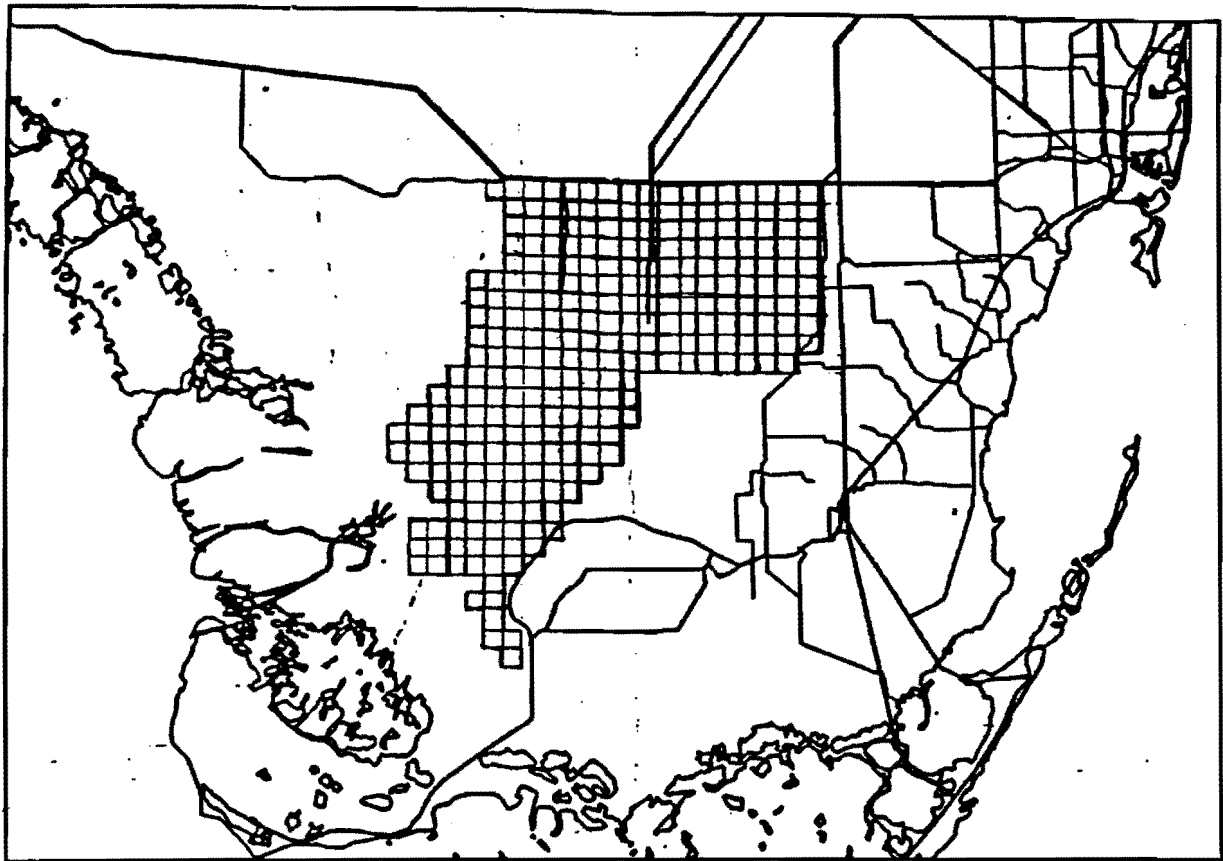


Figure 15. The 2 X 2 km. grid of the alligator study area.

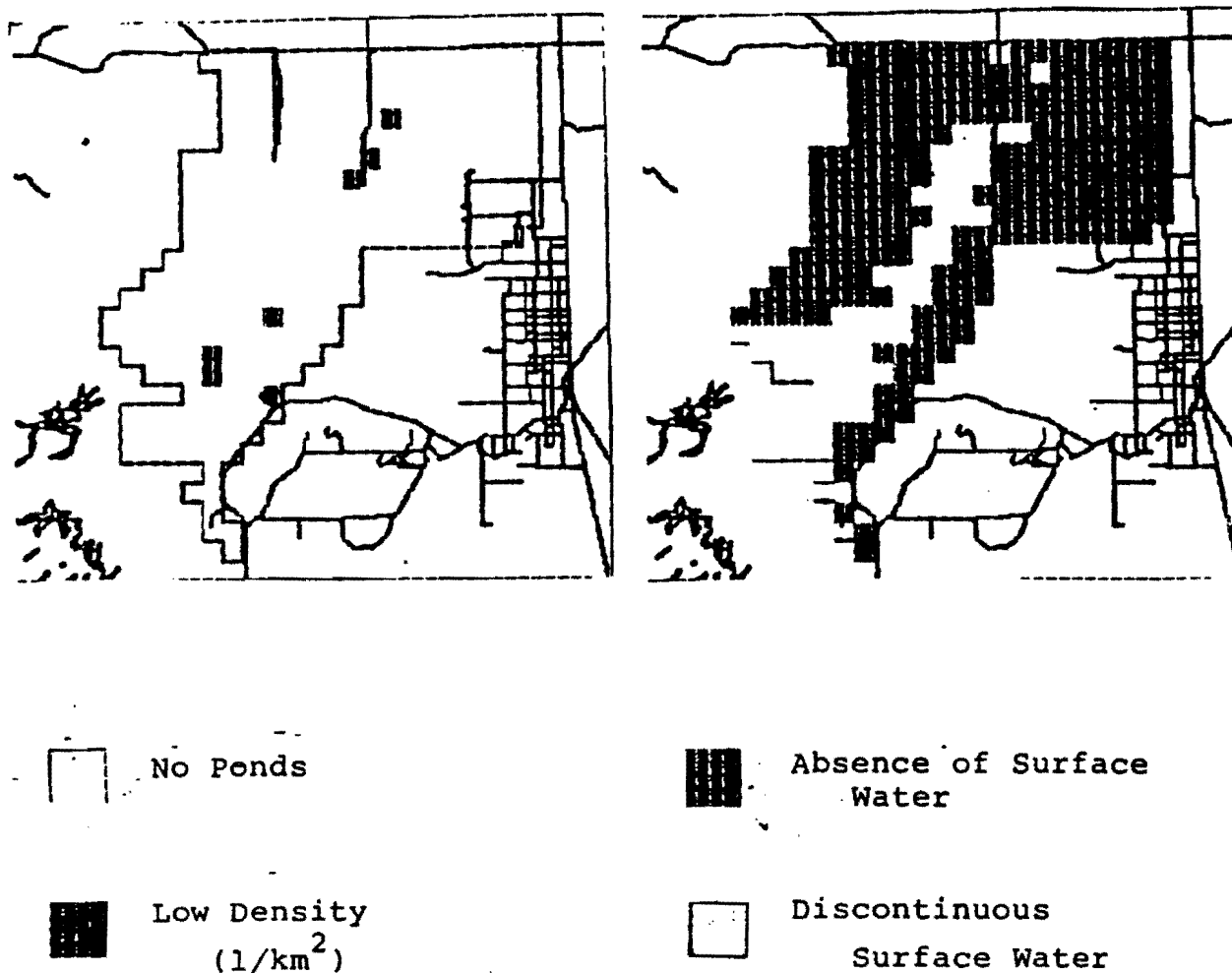
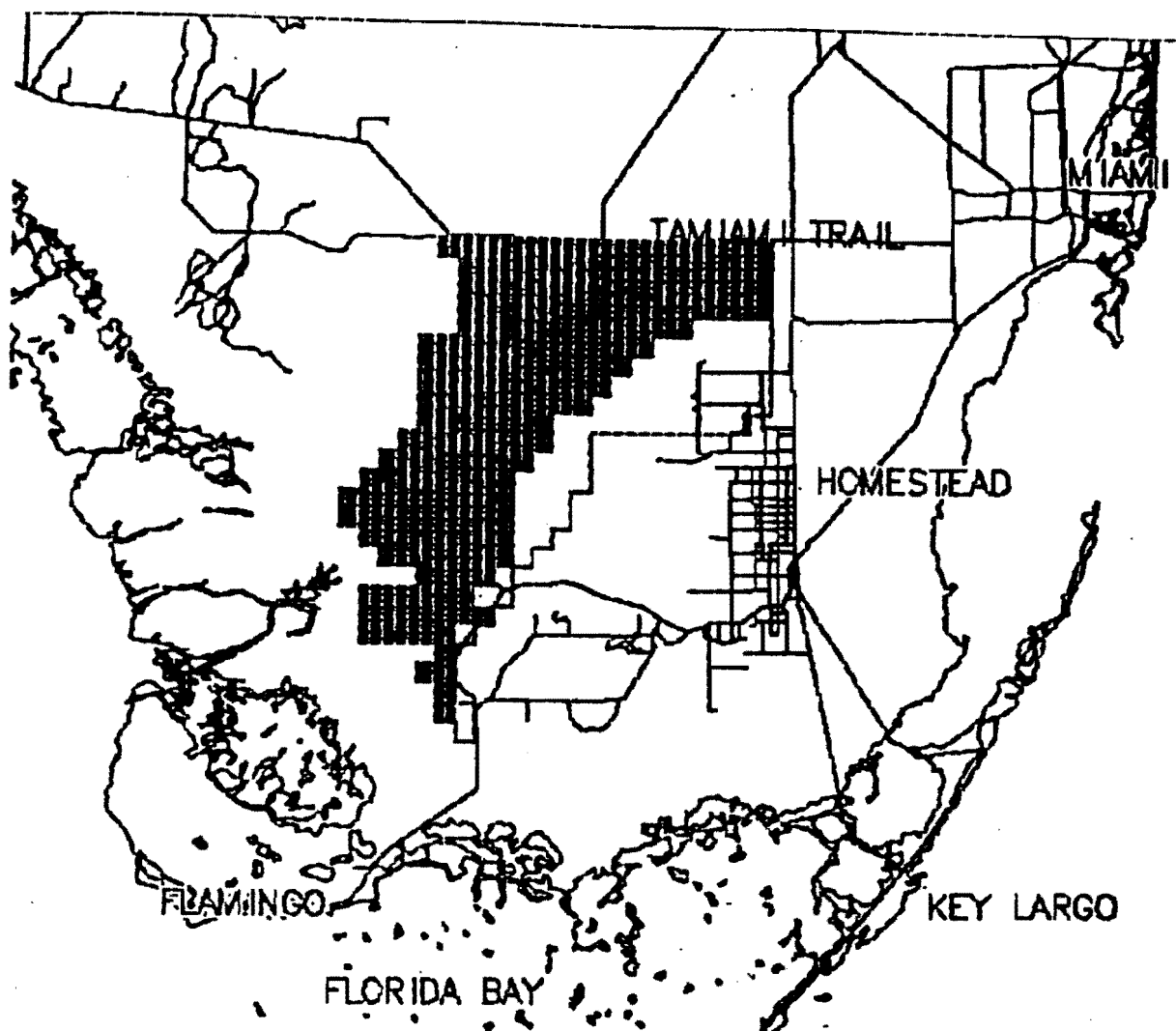


Figure 16. Alligator nest density distribution (A) for the study area, and associated hydropattern map (B), documented during a low rainfall year (1985).



 Ridge and Rock Outcrop

 Lowland

 Central Slough

Figure 19. Dominate ground surface features per 2 x 2 km. cell of the alligator study area grid.

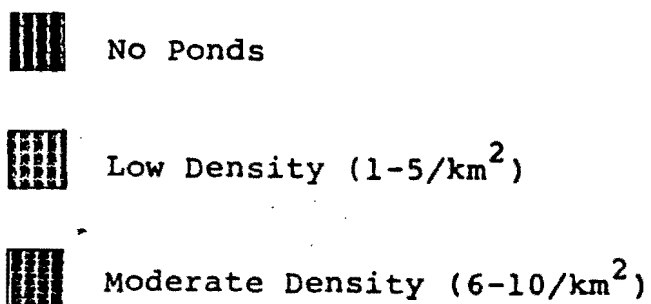
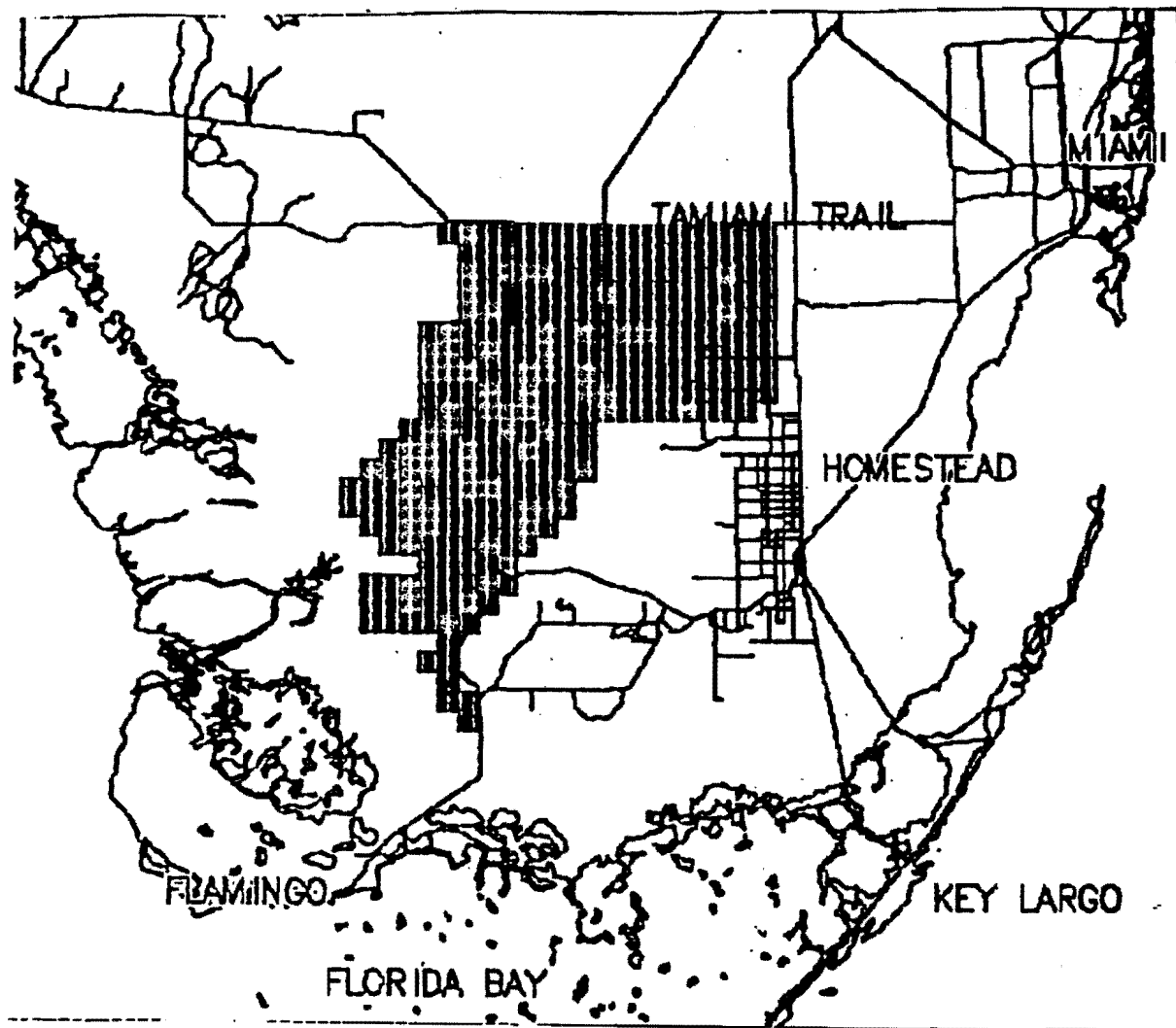


Figure 20. Open water pond density per 2 x 2 km. cell of the alligator study area grid.

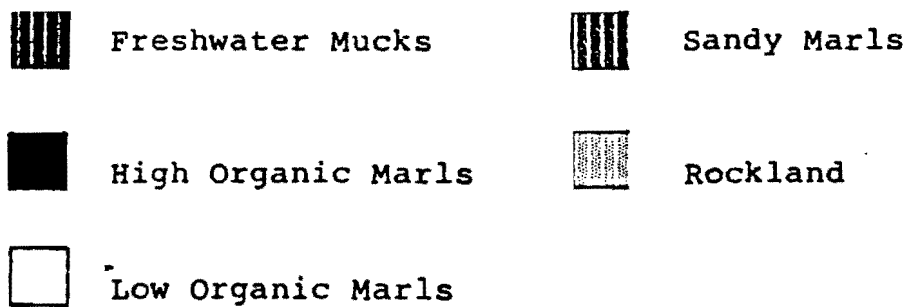
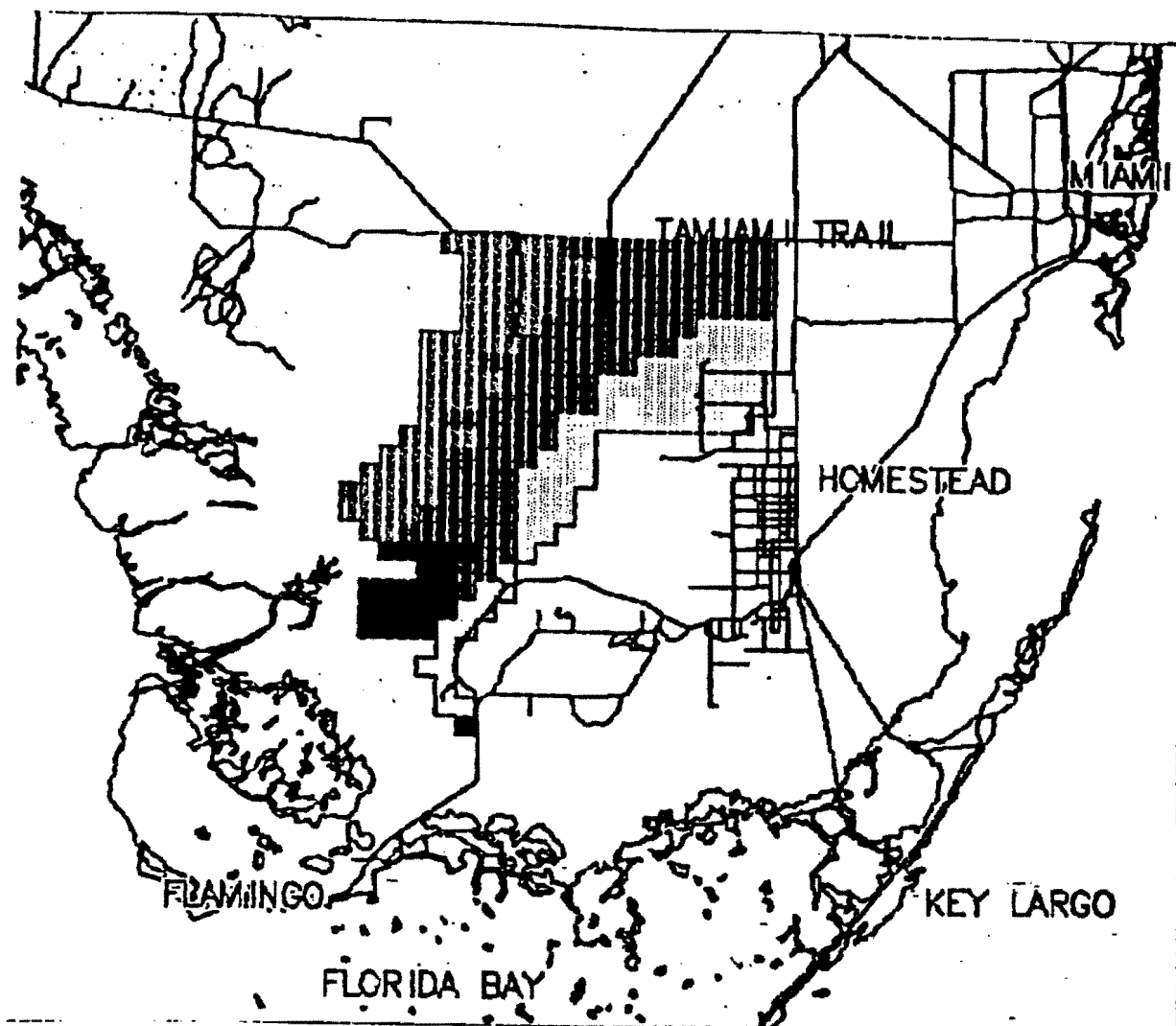


Figure 21. Dominate soil association per 2 x 2 km. cell of the alligator study area cellular grid.

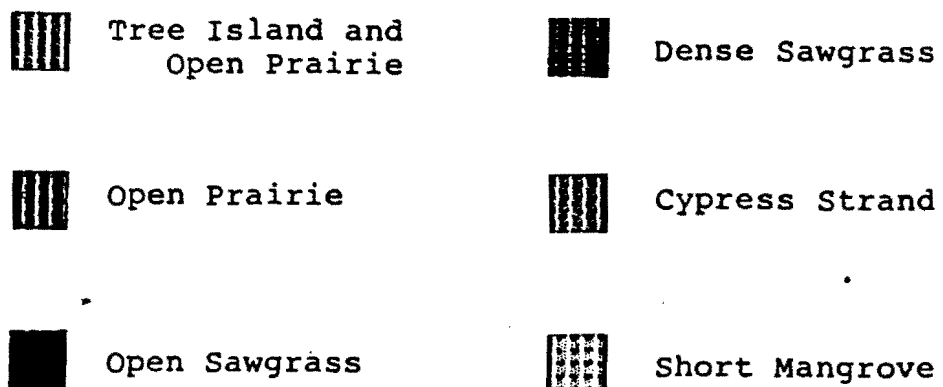
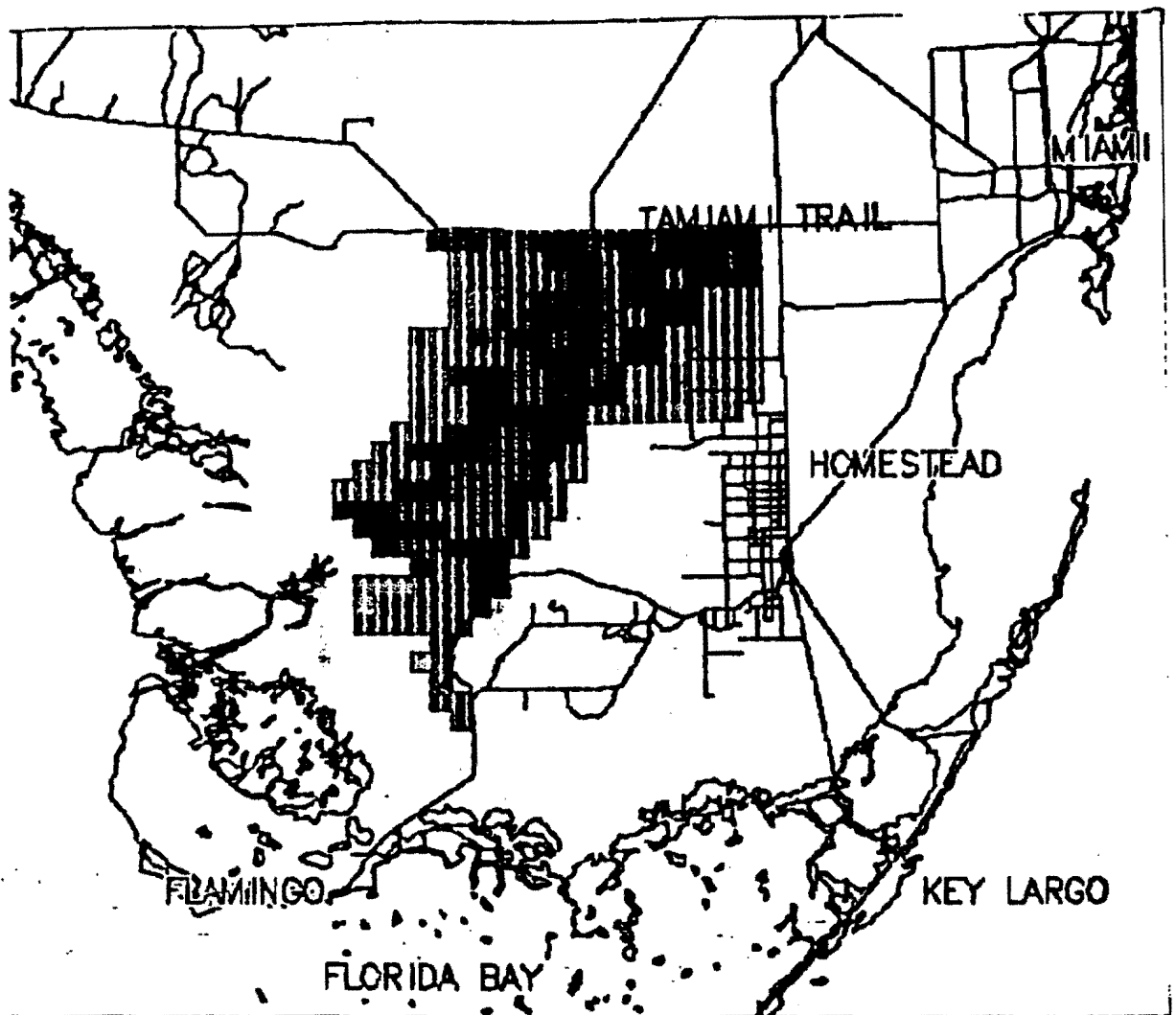


Figure 22. Dominate vegetation cover type per 2 x 2 km. cell of the alligator study area cellular grid.

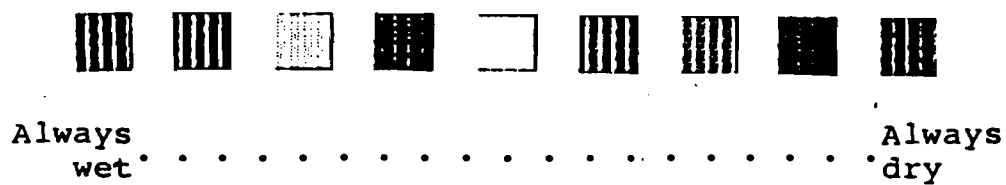
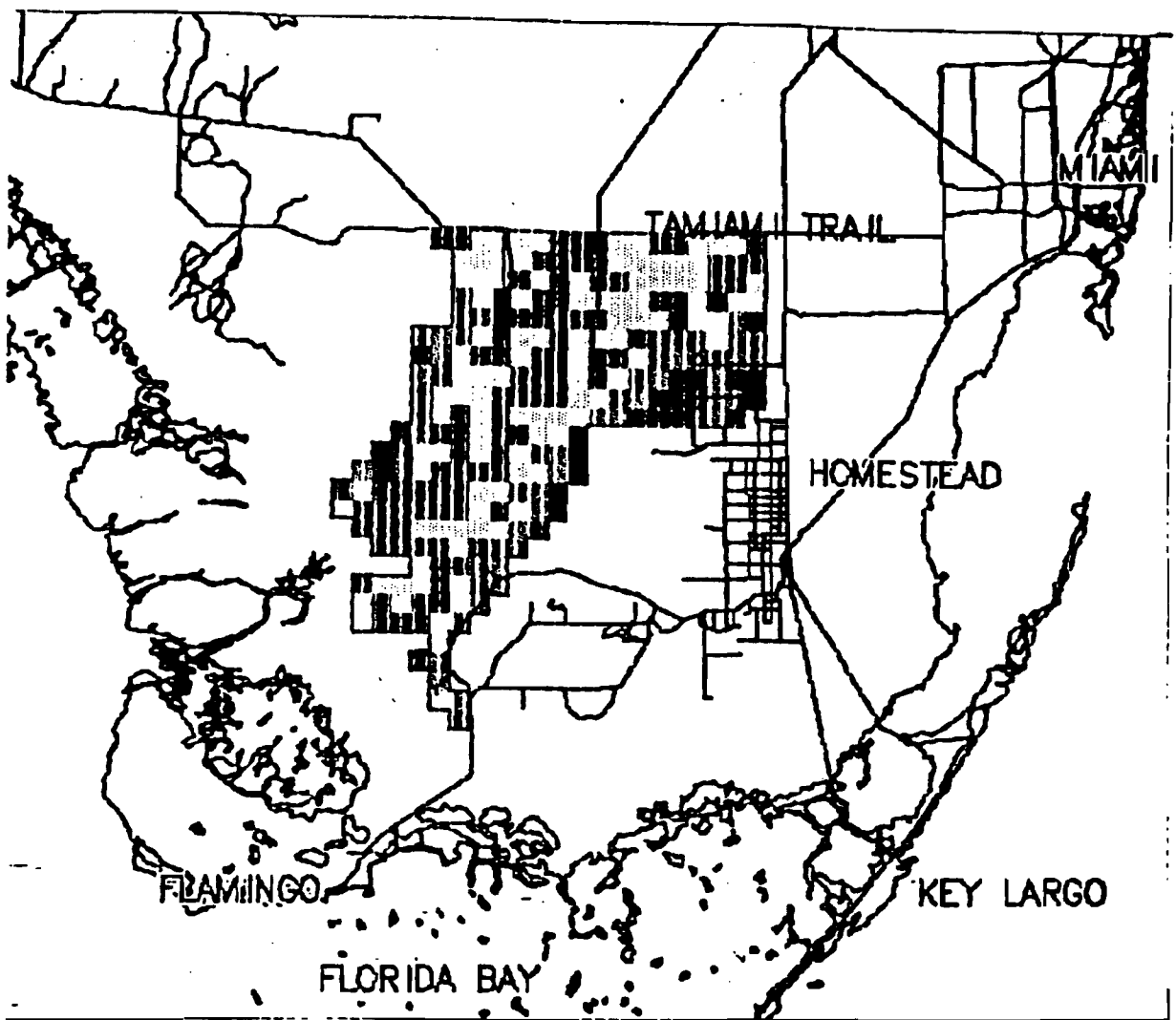


Figure 23. Average dry season surface water condition per 2 x 2 km. cell of the alligator study area grid.

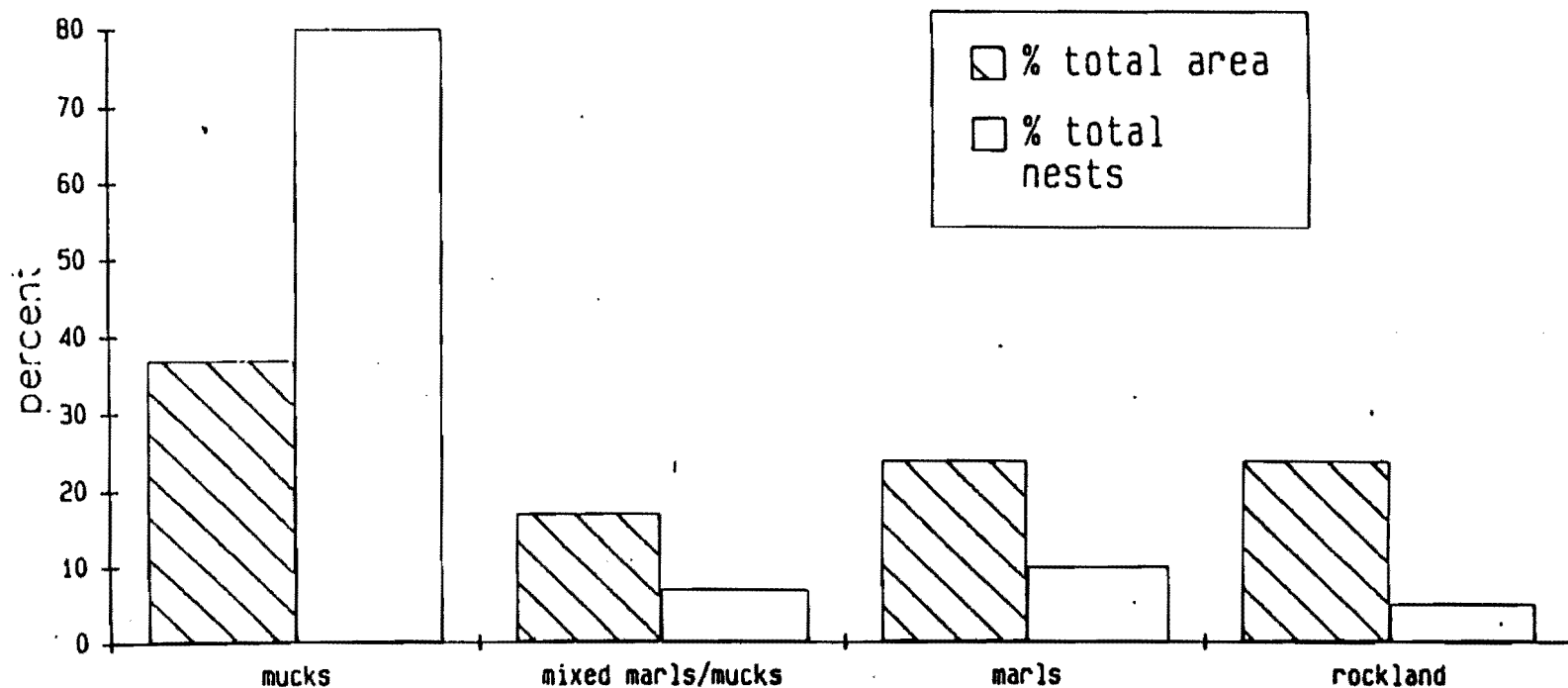


Figure 26. Average frequency of occurrence (%) of alligator nests in relation to dominate soil associations within the alligator study area (based on pooled nest counts over low (1985), high (1986), and moderate rainfall years and related surface water conditions).

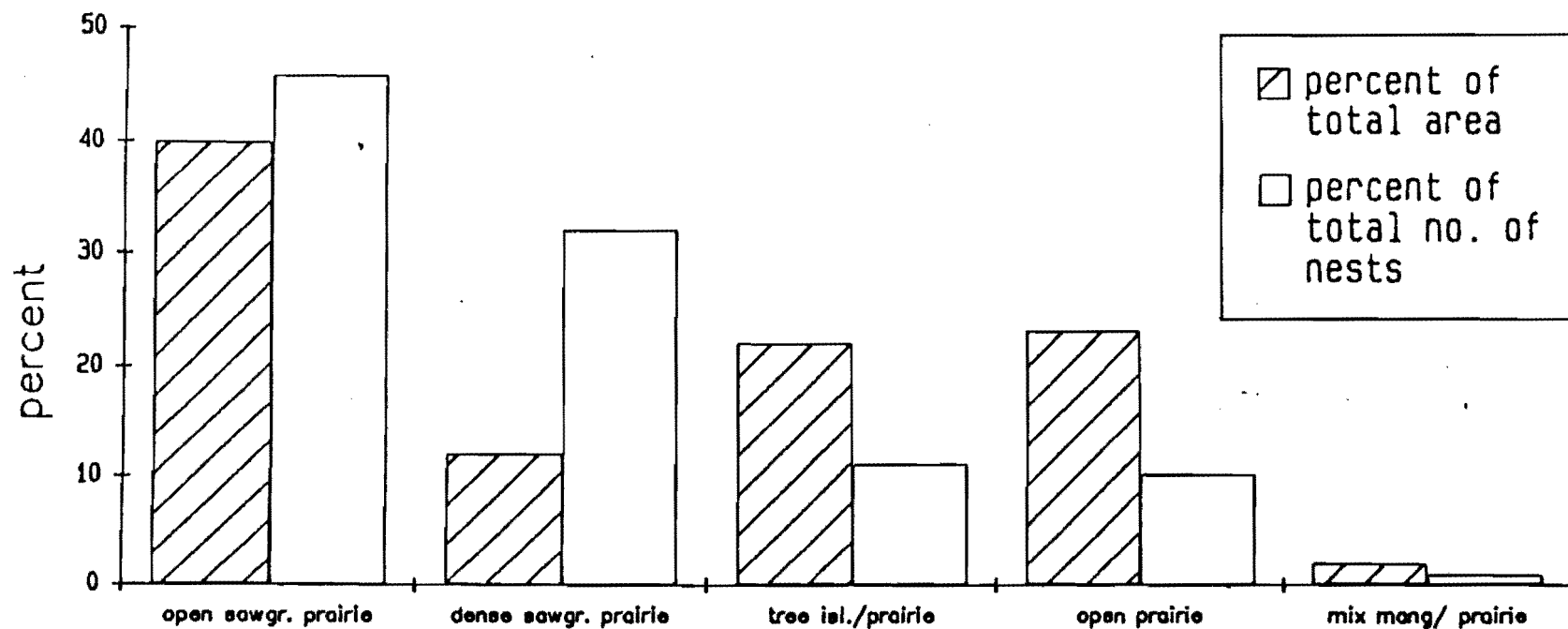


Figure 27. Average frequency of occurrence (%) of alligator nests in relation to dominate vegetation cover types within the alligator study area (based on pooled nest counts over low (1985) high (1986), and moderate (1987) rainfall years and related surface water conditions).

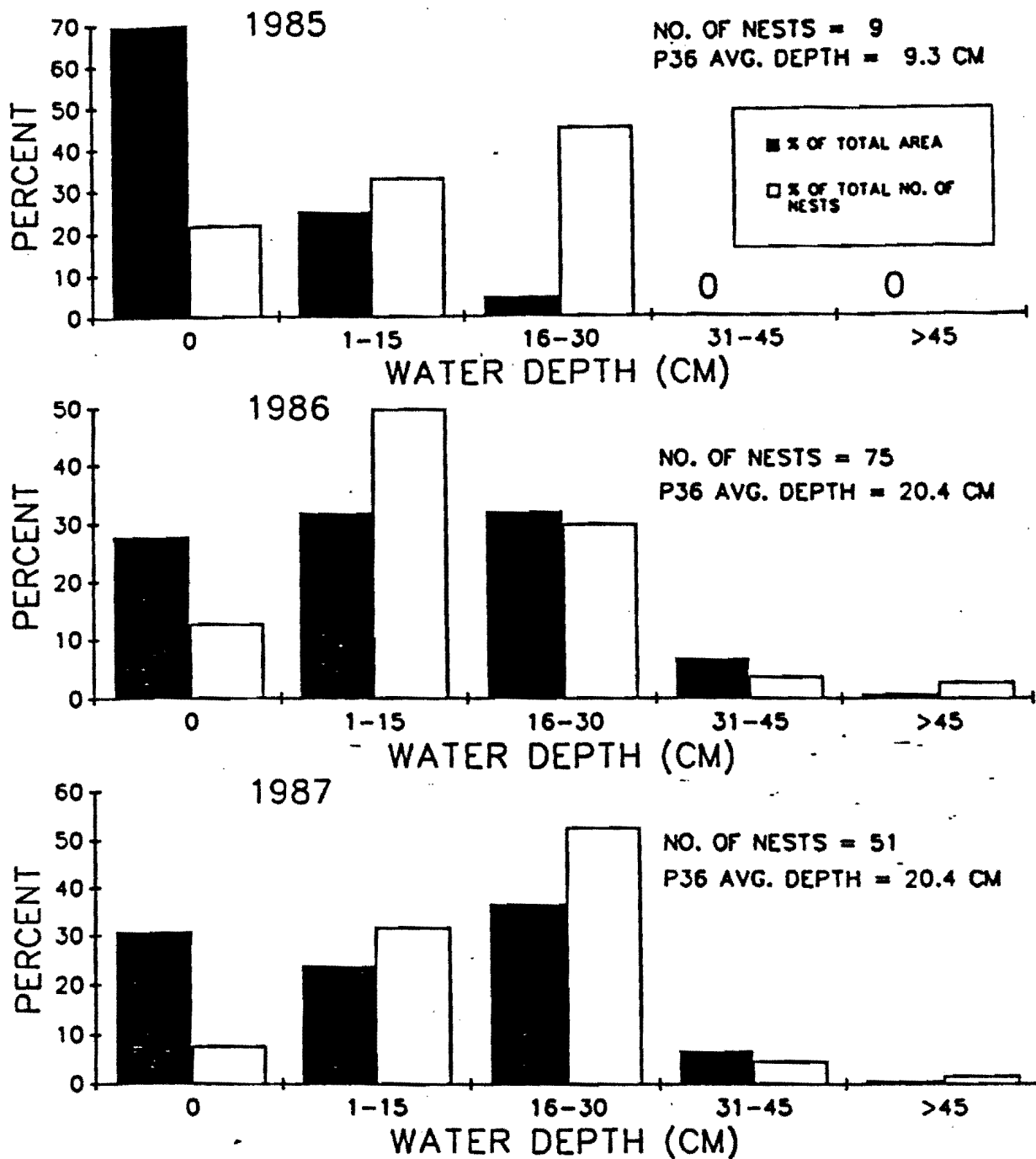


Figure 28. Frequency of occurrence (%) of alligator nests in relation to antecedent, water depth distribution within the study area during the late dry season for low (1985), high (1986) and moderate (1987) rainfall years and related surface water conditions.

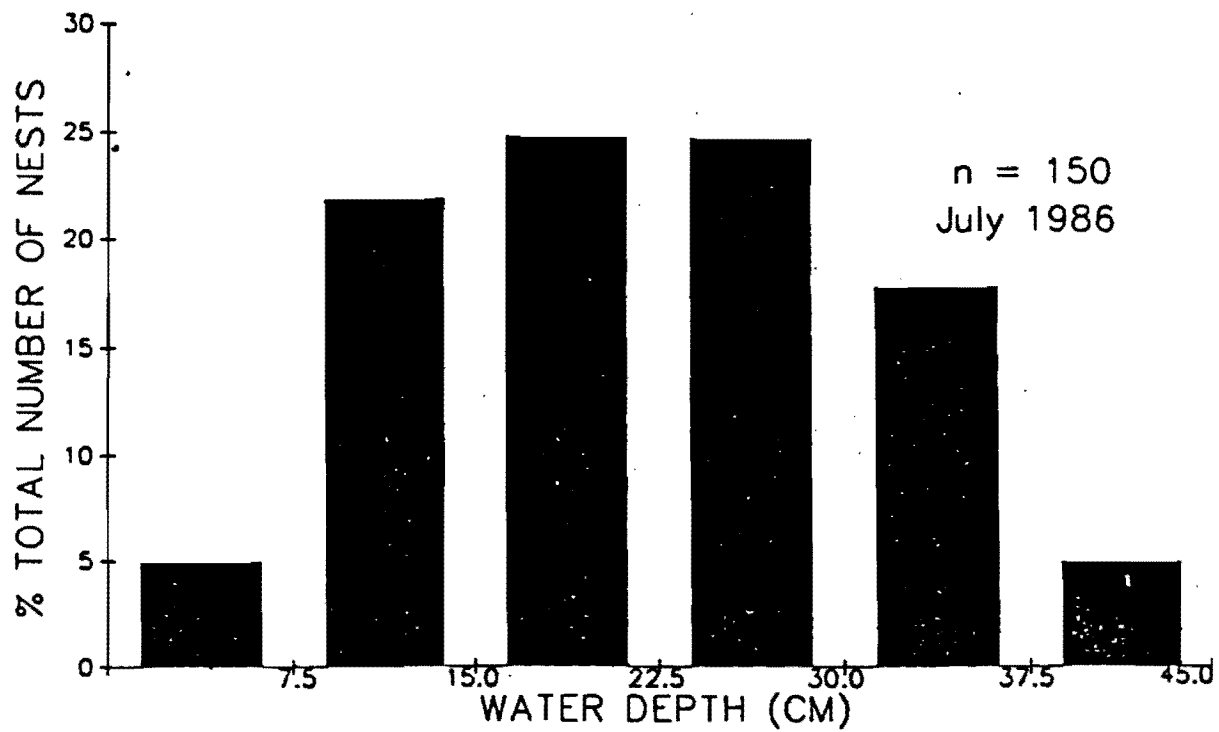


Figure 29. Frequency of occurrence (%) of alligator nests in relation to water depth distribution within the alligator study area during the nest construction period (June), 1986.

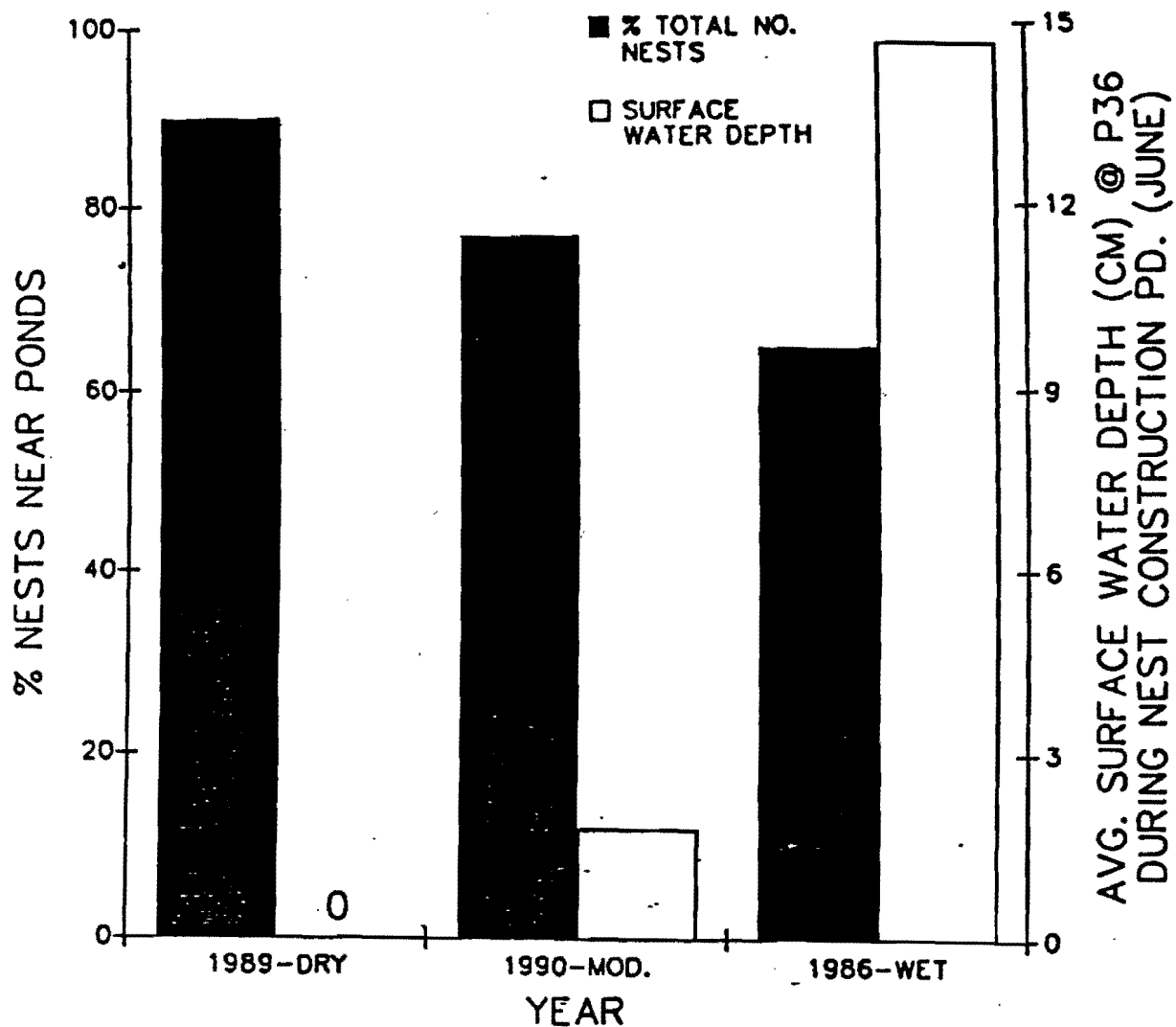


Figure 30. Alligator nest site selection versus surface water condition during the nest construction period (June) for low, moderate, and high rainfall years.

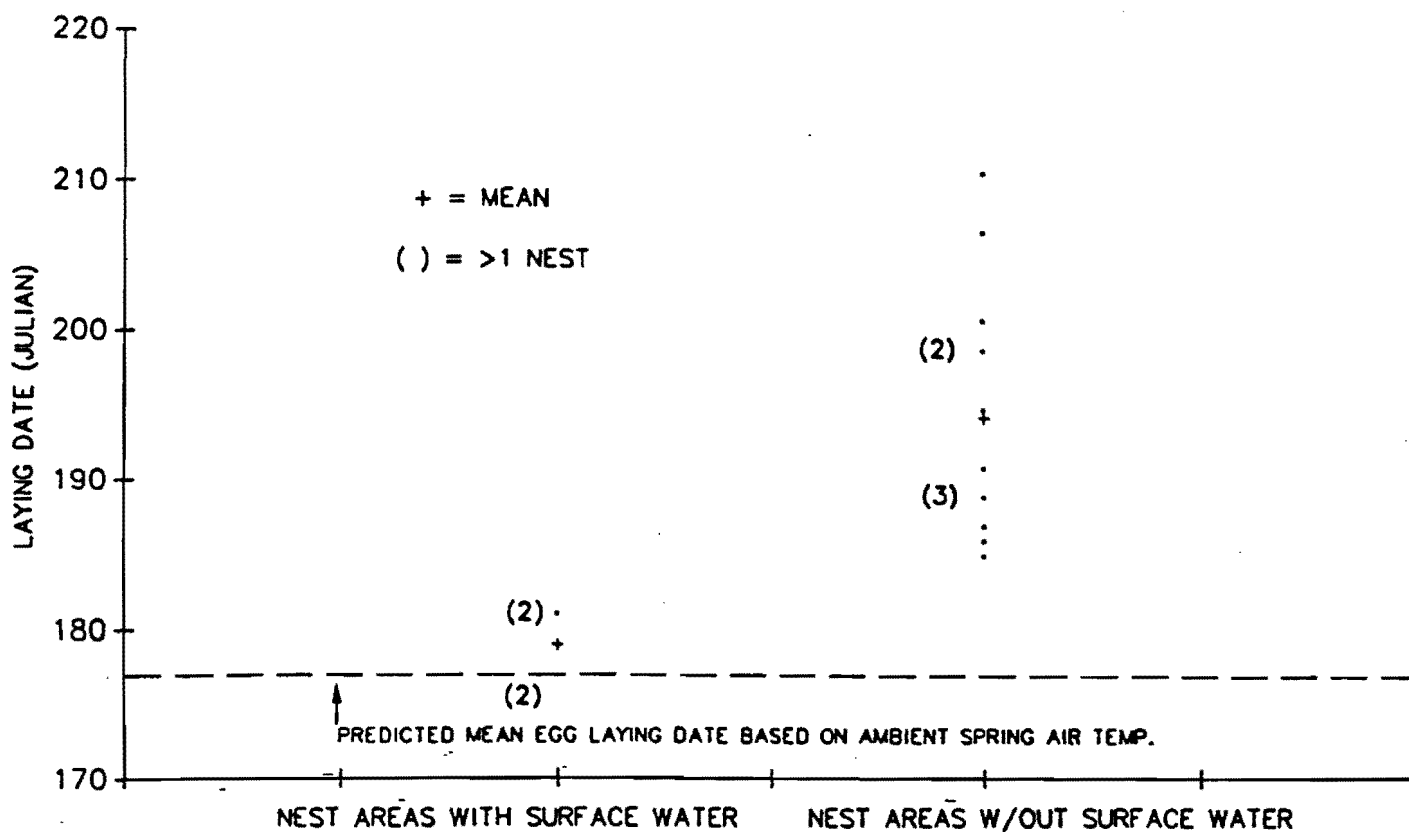


Figure 31. Distribution of estimated egg laying dates in sample nests during the 1990 alligator nesting season in relation to antecedent, late dry season surface water conditions and the predicted mean egg laying date based on ambient spring air temperatures only.

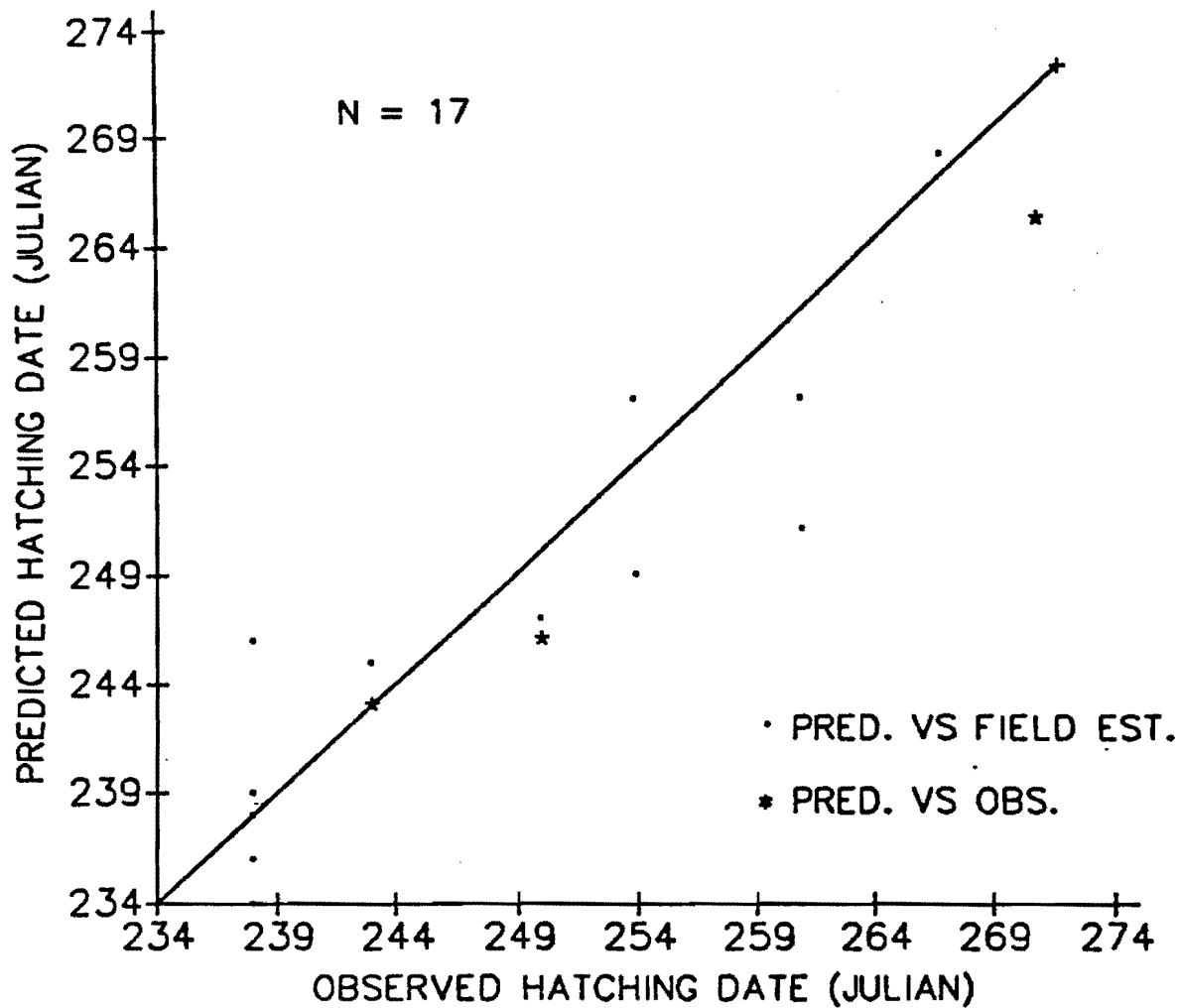


Figure 32. A plot of predicted versus observed alligator egg clutch hatching dates for the 1990 alligator nesting season.

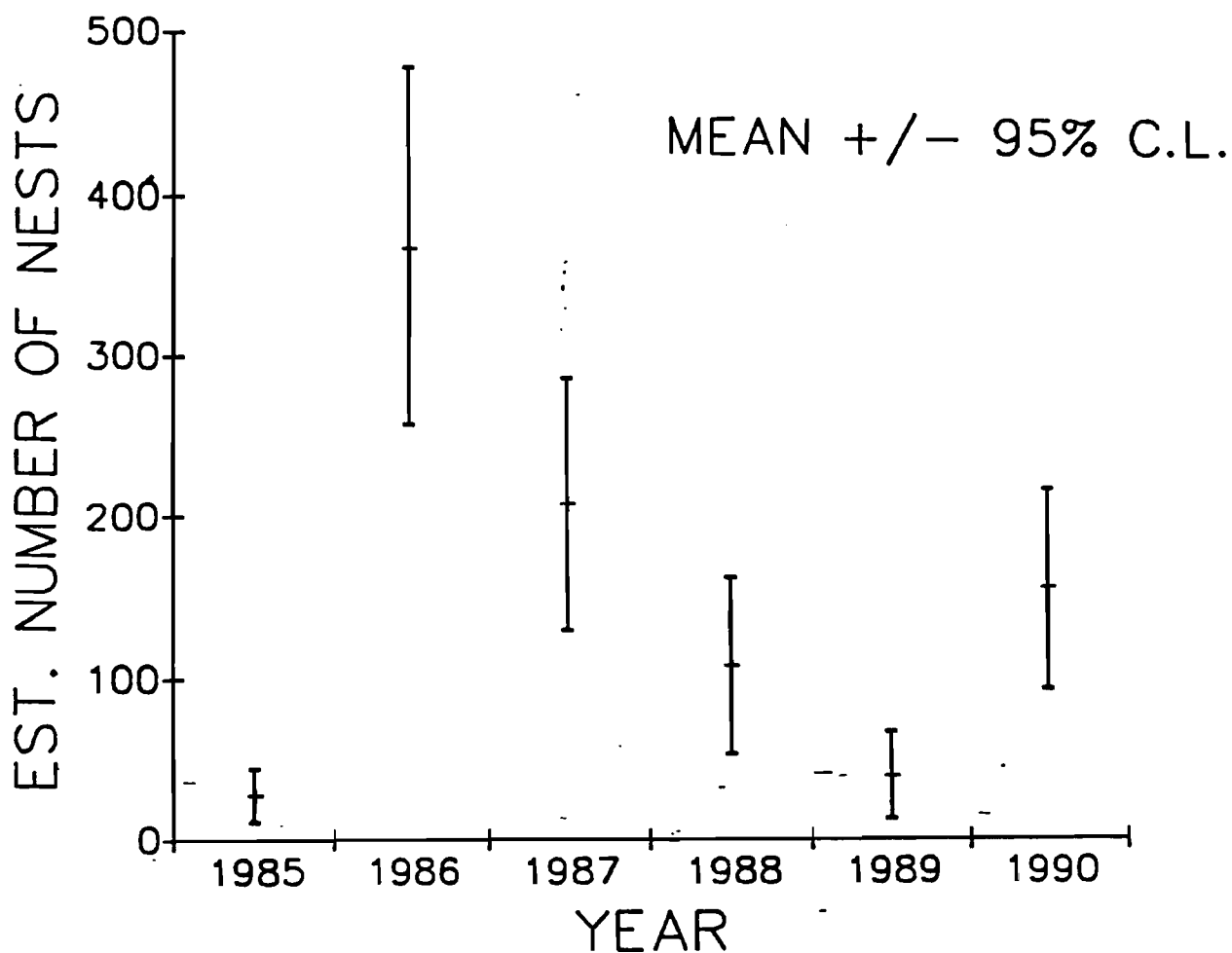


Figure 33. The total number of alligator nests estimated each year within the study area, 1985 - 1990.

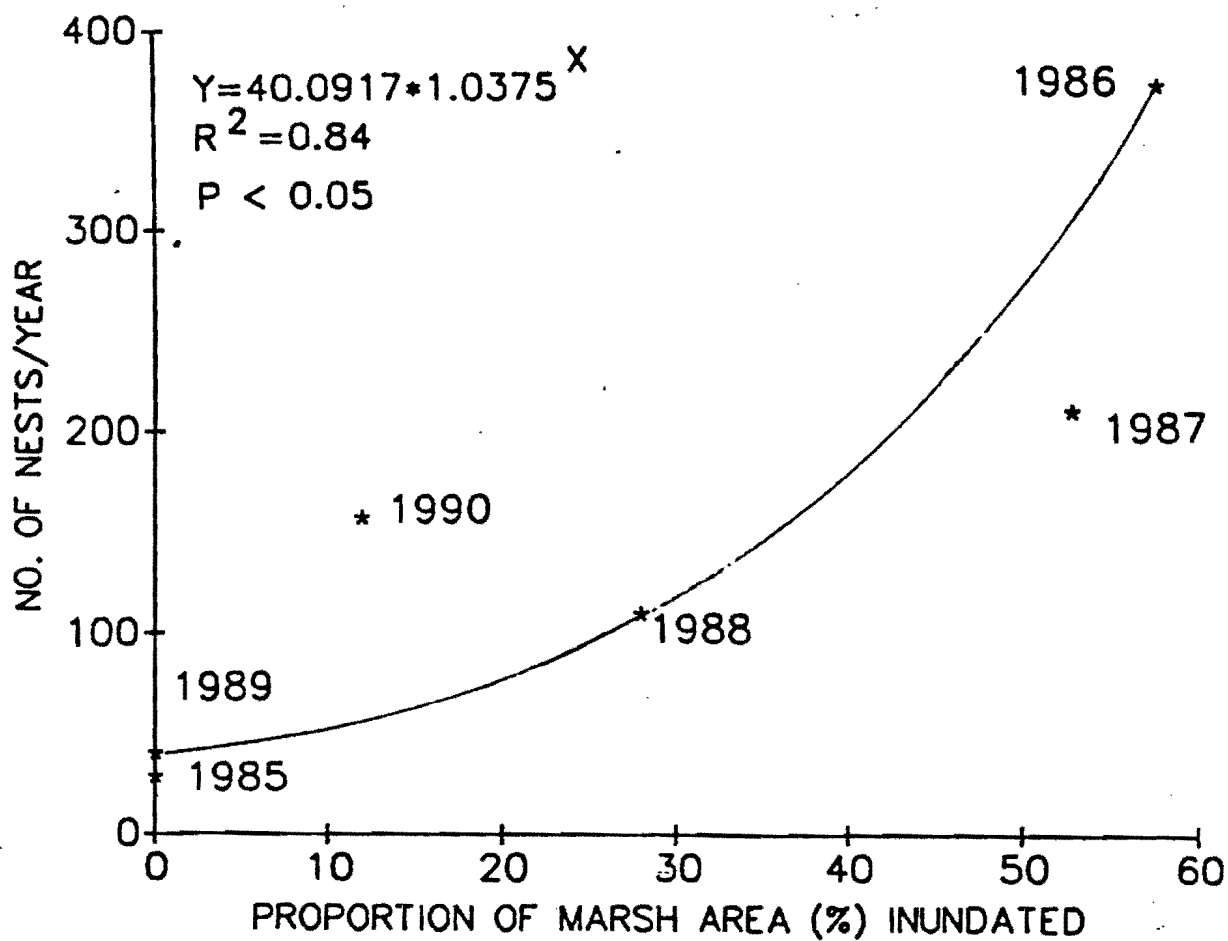


Figure 34. Relationship between annual number of alligator nests and antecedent surface water conditions during the late dry season (April) each year within the alligator study area, 1985 - 1990.

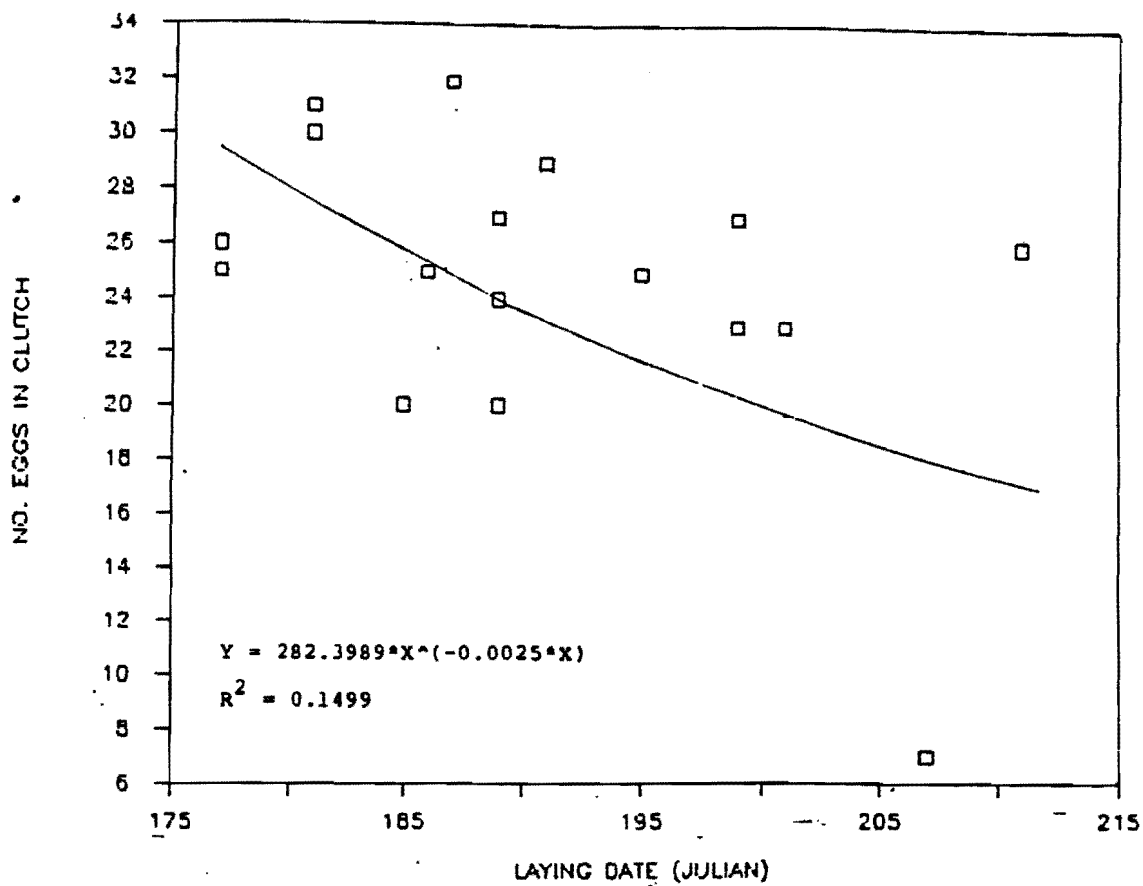


Figure 35. Relationship between nest clutch size and estimated laying date during the 1990 alligator nesting season.

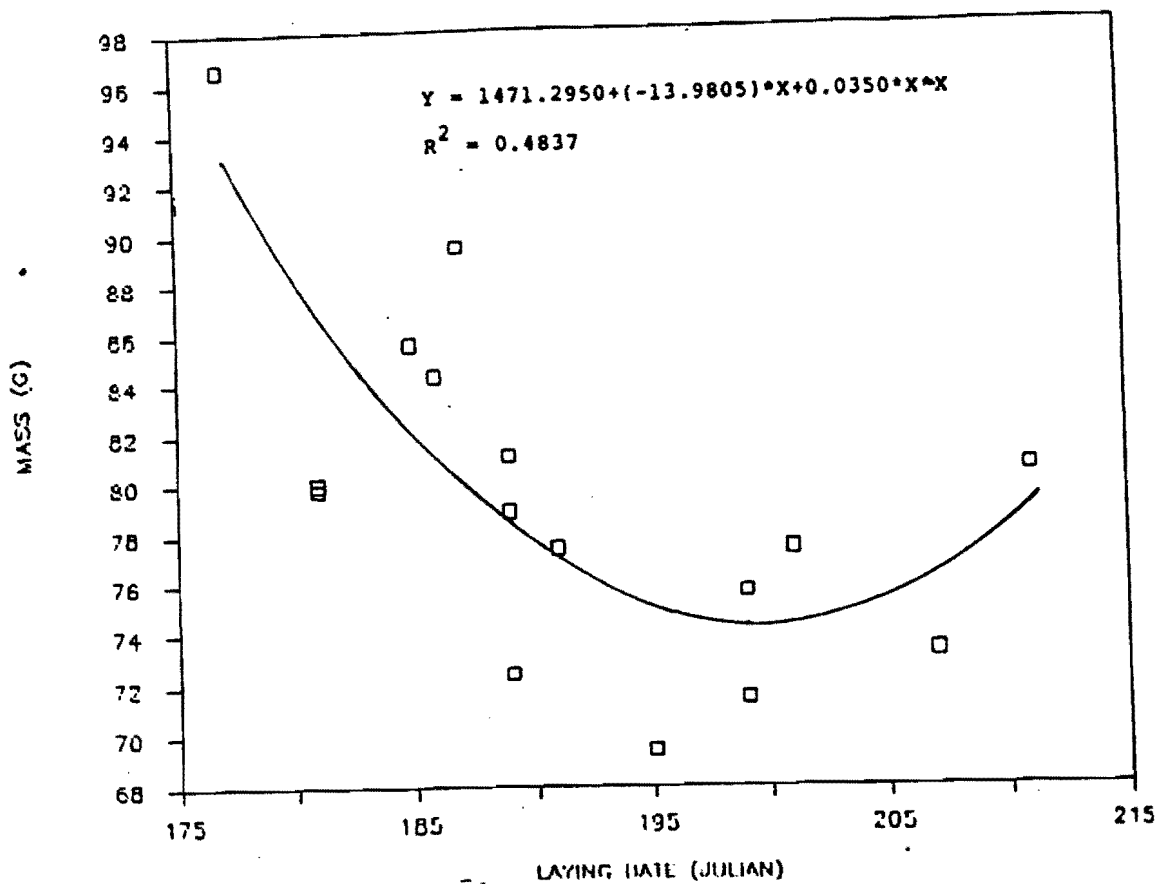


Figure 36. Relationship between average egg mass per clutch and estimated laying date during the 1990 alligator nesting season.

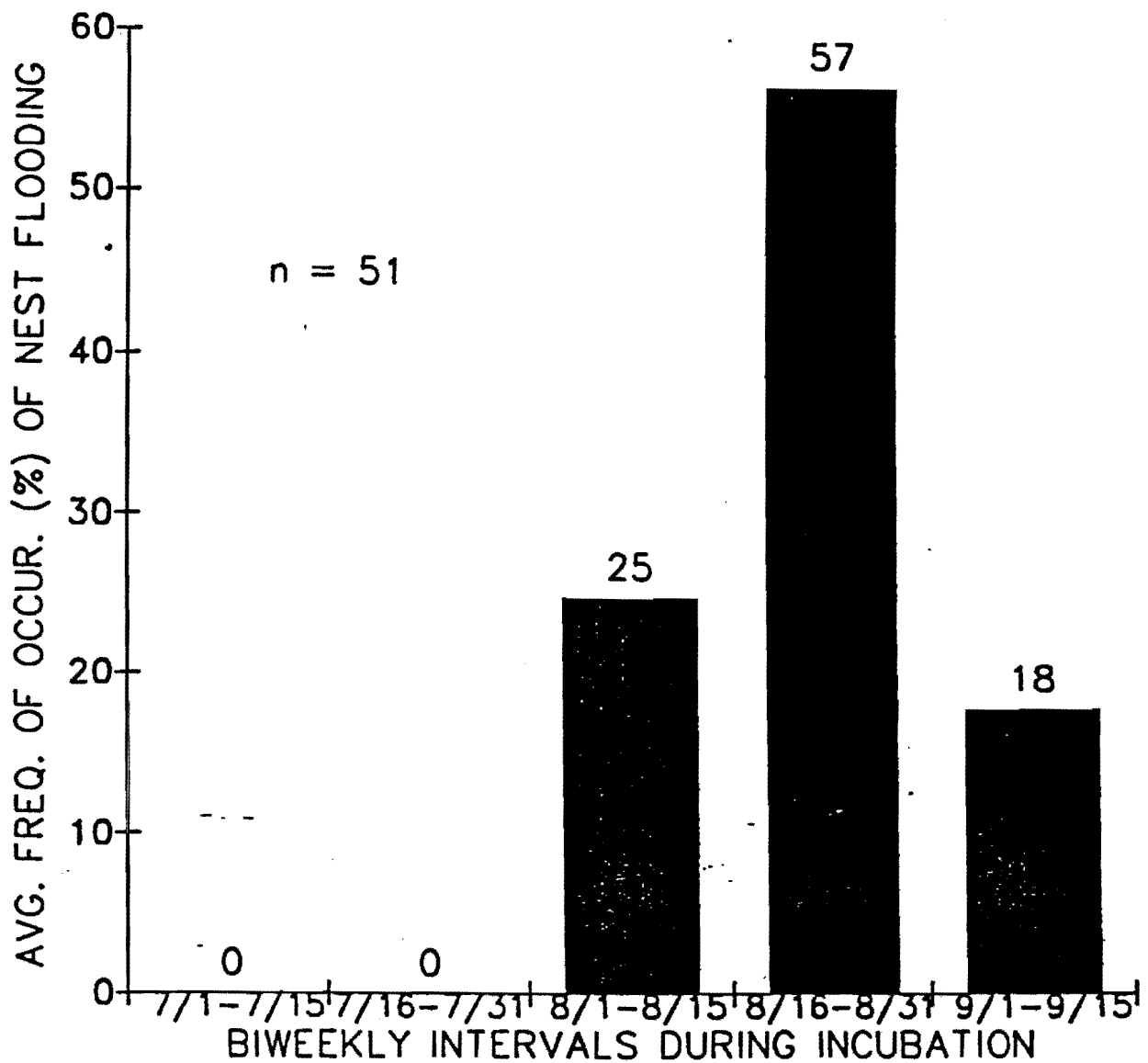


Figure 37. Frequency of occurrence (%) of nest flooding events within the alligator study area during the incubation period, 1985 - 1990.

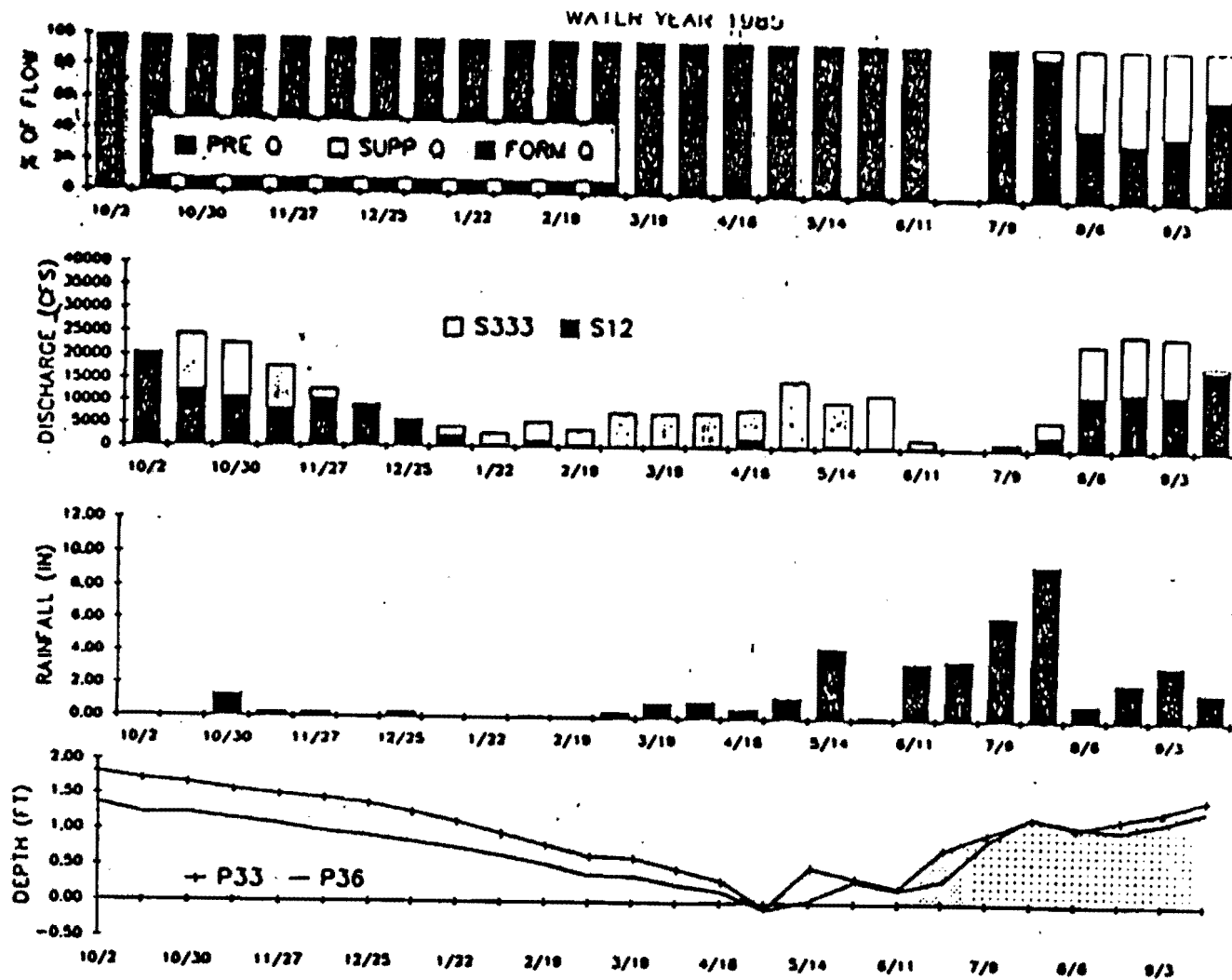


Figure 38. Water delivery characteristics for a low rainfall year (1985) in relation to local rainfall and downstream changes in marsh water depths within the study area.

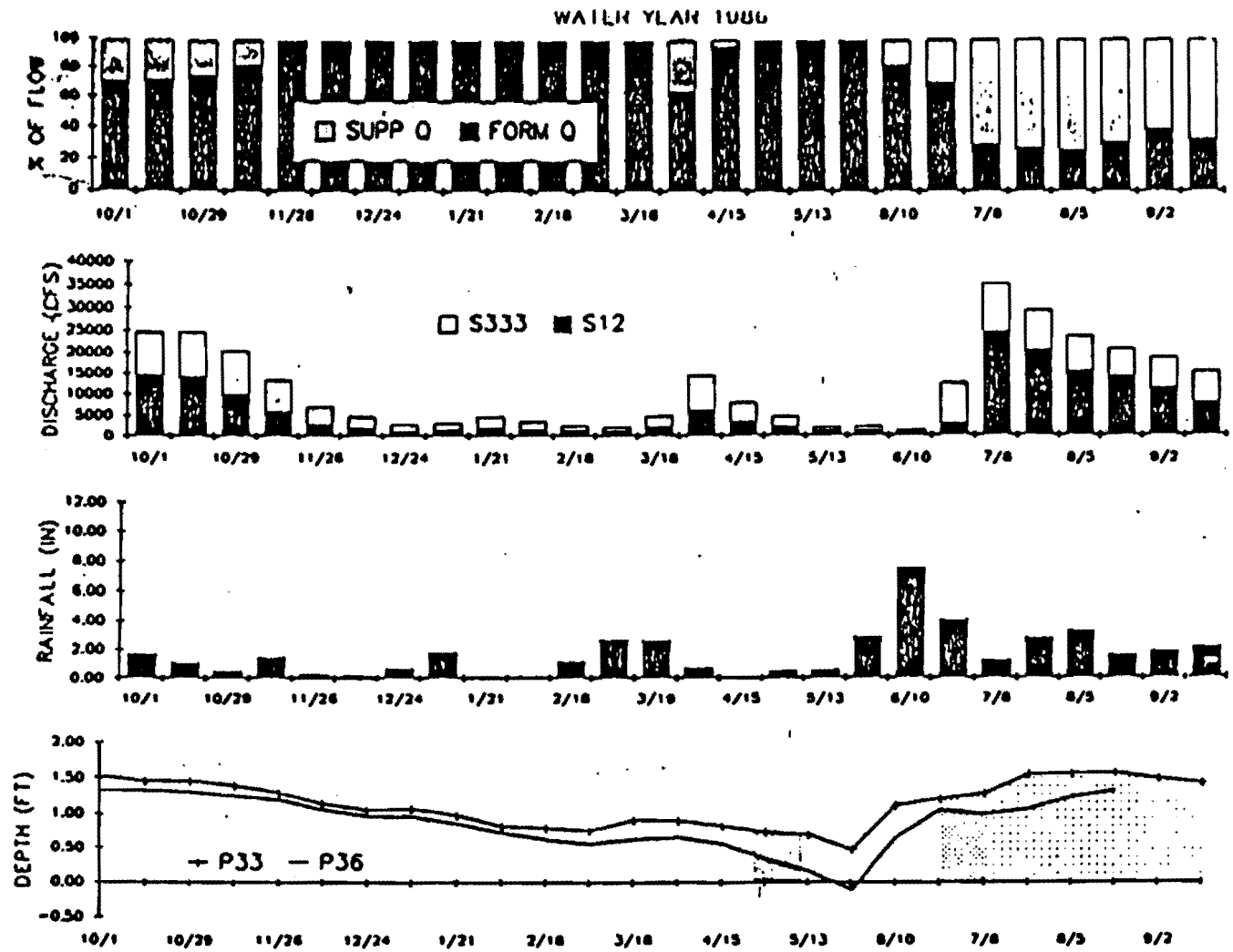


Figure 39 Water delivery characteristics for a high rainfall year (1986) in relation to local rainfall and downstream changes in marsh water depths within the study area.

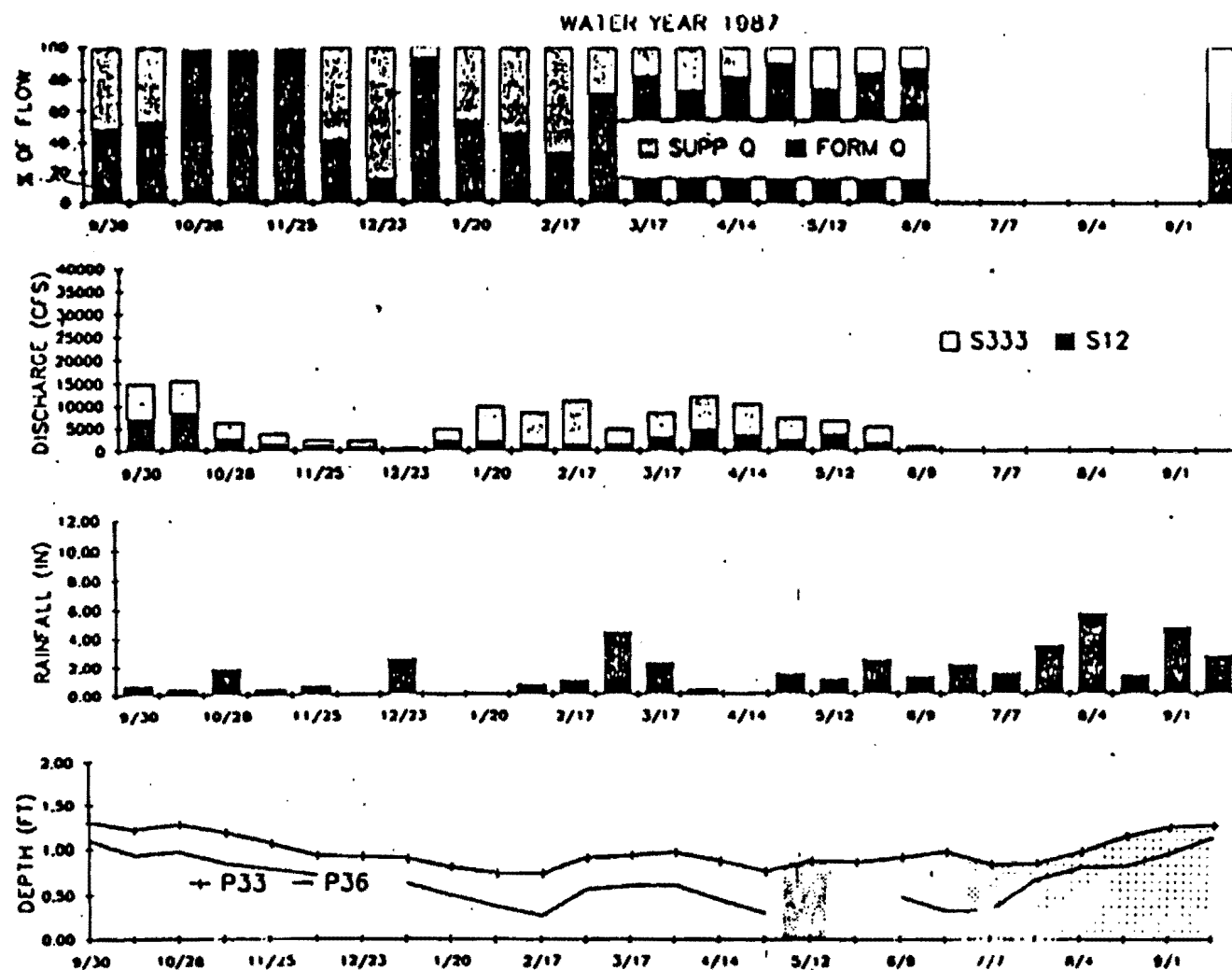


Figure 40. Water delivery characteristics for a moderate rainfall year (1987) in relation to local rainfall and downstream changes in marsh water depths within the study area.

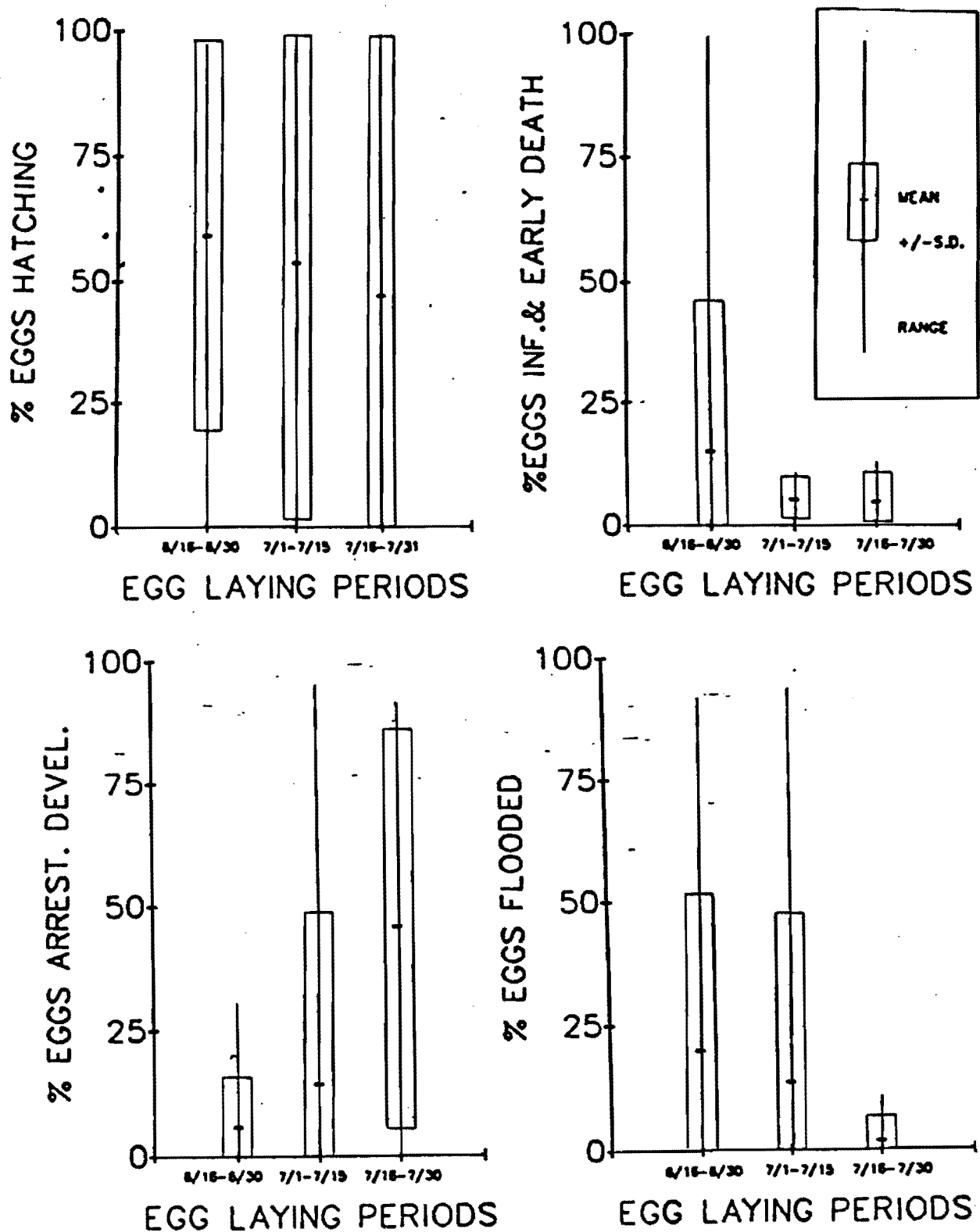


Figure 41. A comparison of nest egg clutch hatching, infertility, arrested development, and flooding rates for early, mid, and late egg laying periods during the 1990 nesting season.

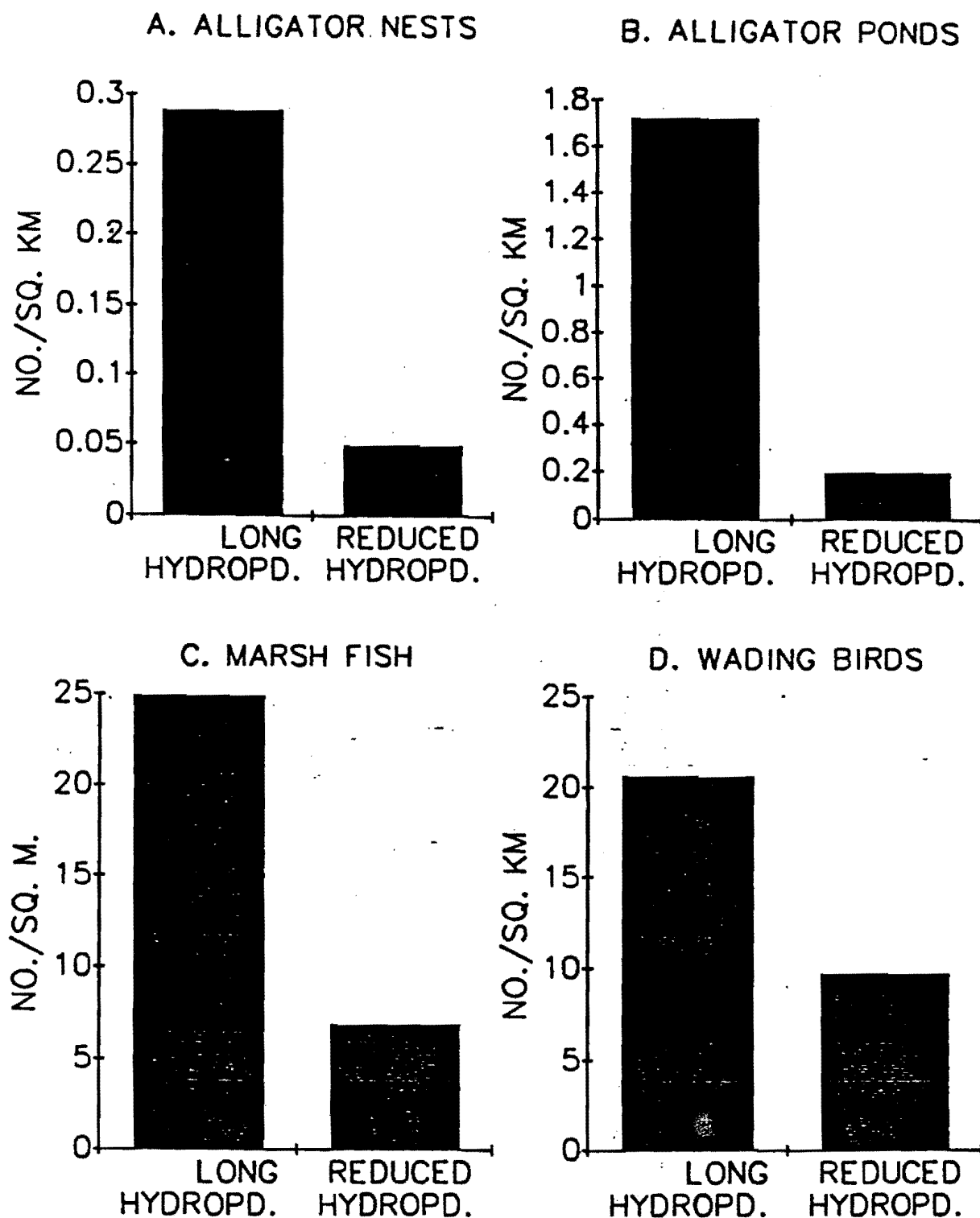


Figure 44. A comparison of alligator nest, pond, marsh fish, and foraging wading bird average densities between adjacent wet prairie habitat with long versus reduced hydroperiods within Shark Slough, Everglades National Park.

