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Osmoregulation of Crocodiles in Everglades National Park

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OSMOREGULATION OF CROCODILES IN EVERGLADES NATIONAL PARK

Report T-599

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ABSTRACT

It is possible that the survival rate of hatchling *C. acutus* in Florida Bay is low and is associated with osmoregulatory problems caused by high salinities near nest sites. Crocodiles show few physiological specializations for life in saline waters in comparison with marine snakes and turtles. Wild *C. acutus* hatchlings have a plasma osmotic pressure near 330 mOsm, a typical level for vertebrates. The osmotic pressure of the cloacal fluid of wild caught *C. acutus* was equal to or less than that of the plasma. The solid portion of the cloacal fluid was mainly uric acid, and contained 1.3 to 450 times more K than Na. The highest levels of these ions were 1111 and 222 μmoles/g dry weight respectively, normal values for carnivorous reptiles. Thus it appears that K is excreted in both the fluid and solid portions of the "urine," whereas Na is conserved. The analysis of Na fluxes of small *C. acutus* submerged in sea water (35 ppt) is complicated by the presence of a sizeable compartment that turns over quite rapidly. There is a second compartment with a long turnover time ($T_{1/2}$ of efflux 29-156 days). I assume that the slow compartment represents the true long-term rate of exchange with sea water. Na influx (11.5 μmoles/100g h) and efflux (2.3 μmoles/100g h) were both quite low, although the influx did exceed the efflux. Thus a net uptake of about 10 μmoles Na/100g h may occur. No passage of Na across small pieces of keratin was observed after one day. It appears that the skin is virtually impermeable to Na, as is the case with most aquatic reptiles. In some plasma samples taken during the first two weeks of life, Na was atypically low, but in others it is near normal (about 150 mM). This discrepancy was not found in plasma samples from mangrove snakes (*Nerodia fasciata compressicauda*) taken and analyzed under identical conditions. The indication that there may be a Na deficiency in some recent hatchlings is supported by the extremely low Na concentrations of cloacal fluid (12-21 mM). In some, but not all cases, Cl and K were much higher than Na. The relationships between snout vent length (L), body weight (W), and surface area (A) are as follows: $A = 1.1550L^{1.8947}$; $W = 0.0263L^{2.9730}$. The head-neck, tail, legs and body regions each account for about one fourth of the total area. After hatching, crocodiles seek out cool, moist, terrestrial microclimates by entering crab holes and wave-cut crevices, or by hiding in clusters of mangrove roots. It might appear that this behavior is advantageous for small crocodiles in avoiding the loss of body weight (about 1.7%/day) that occurs when fasting and immersed in 100% sea water. Such is not the case since a similar amount of evaporative water loss occurs in air at 30°C and 96.5% relative humidity. This is several times the loss of the mangrove snake living in the same habitat. It appears that this obligatory water loss is normally counterbalanced by feeding. When fed *ad lib.* and kept in an aquarium divided into land and water portions, small (100-480g) crocodiles maintain weight at salinities up to at least 17.5 ppt (50% sea water).

INTRODUCTION

There are very few reptiles that carry out their entire life cycles in sea water. The true sea snakes (Hydrophiidae) are the most specialized of these forms, but some members of several other families of snakes have similar habits (Homalopsidae, Acrochordidae, Colubridae; Dunson and Dunson, 1973, 1979; Dunson, 1975, 1980). The sea turtles are of course well adapted for a marine existence, but retain a dependence on land for egg laying. Among crocodilians there are several species which are regularly observed in estuaries and even in the open sea. However it appears that the so-called "salt water" crocodile, Crocodylus porosus, makes its nests along tidal rivers in areas of fresh or brackish water (Messel and Butler, 1977). Tolerance of higher salinities may only be possible as the animals mature (Dunson, 1970). The American crocodile, C. acutus, has similarly been observed in sea water, but there is little evidence establishing its ability to subsist there indefinitely. Hatchlings are intolerant of moderate to high salinities (Dunson, 1970; Evans and Ellis, 1977). Dunson (1970) was unable to demonstrate a salt gland in hatchlings even though a 3.4 kg animal maintained weight in 100% sea water for five months on a diet of whole fish. Thus it would appear that C. acutus is a rather unspecialized estuarine form that may depend heavily on nesting sites near the influence of fresh water. Although the adults can apparently survive in 100% sea water, there are no field data establishing the presence of individual animals under such conditions for extended periods.

The question of the ability of C. acutus to osmoregulate in sea water has become a matter of some importance in the effort to save the vestiges of the population in south Florida. Hunting long ago decimated this species (Dimock, 1926; Simpson, 1932), throughout its very limited range in Florida (Moore, 1953; Ogden, 1978). Yet little recovery of the population appears to have occurred, even in Everglades National Park which is a major part of the historic range. This is in striking contrast to the dramatic comeback of the alligator, raising the suspicion that some recent change in the environment is inhibiting growth of the crocodile population. Since it is likely that hatchling C. acutus require low salinity water, the most obvious relevant environmental factor is the massive change in hydrology of the wetlands that originally drained into Florida Bay. Although the progress of canal and levee construction in southern Florida has been well documented (Leach et al., 1971), it is unfortunate that the quantitative effect on the salinity of Florida Bay is not established. This is due to the lack of hydrologic data for the early 1900's and to the large seasonal variation in salinity of the bay which tends to obscure any long-term trend. There may be a relationship between these hydrologic changes and the contraction of the breeding range of crocodiles, from various outer islands in Florida Bay back towards the mainland (Ogden, 1978).

The purpose of the present study was to examine the physiological effects of high salinity on young C. acutus, and to determine whether mortality in Florida Bay can be attributed to osmoregulatory problems. A full evaluation of this question must await completion of a study of the behavior, movements, and survival of marked hatchlings being carried out by the South Florida Research Center under the direction of James A. Kushlan. In the current investigation measurements were made of the electrolyte composition of plasma and cloacal fluid of wild caught crocodiles in Florida Bay, and of possible hatchling food. Captive hatchlings and subadults of Jamaican origin were used to study Na exchange, weight changes at different salinities, and evaporative water loss.

MATERIALS AND METHODS

Crocodiles were captured in Florida Bay at night with the aid of head lamps (4 volt, Wheat), and in daytime by searching among mangrove roots near nest sites. They were rinsed in fresh water, blotted dry, and blood was then collected by ventral puncture of the caudal vein (Schmidt-Nielsen and Skadhauge, 1967; Gorzula et al., 1976). Cloacal fluid samples were often voided spontaneously upon capture. If not, a blunt probe was inserted into the cloaca and the abdomen was massaged to stimulate excretion. Blood and urine were stored on ice until they could be centrifuged and/or diluted after return to the laboratory, usually within 24 h. The crocodiles were measured, marked with a toe tag and by clipping of the dorsal tail scutes, and released. These same animals were utilized by Mazzotti and Kushlan (unpub. obs.) in a study of population ecology, movements and growth. In one case, hatchlings were removed directly from a nest that was under study by Patty and Kushlan (unpub. obs.). All wild caught crocodiles were released within two hours at their capture sites. Laboratory experiments were carried out on captive crocodiles of Jamaican origin purchased from Cecil Clemons (Gatorama) and Frank Weed. Four recent hatchlings, two six month-old crocodiles, and six subadults of unknown ages were used.

Osmotic pressures of body fluid samples were measured with a Wescor model 5100B vapor pressure osmometer. Na and K were determined in an air propane flame on a Varian Techtron model 1280 atomic absorption spectrometer. Cl was analyzed by hand titration with a Sigma kit. Cloacal uric acid samples were dried at 25°C in a dessicator (over drierite) and measured with a Sigma 292-UV uricase kit. Na and K content were determined after dissolution in concentrated nitric acid. Food samples were dried to a constant weight at 100°C, and then dissolved in concentrated nitric acid, diluted, and analyzed for Na and K.

^{22}Na fluxes were studied in vivo on four fasting crocodiles placed in 100% sea water. ^{22}NaCl (New England Nuclear) was added to 2 liters on sea water (35 ppt) at a specific activity of 0.175 milliCurie/liter. For influx measurements the crocodiles were placed in 2 liters radioactive sea water for 5 hours; they were removed at hourly intervals for counting with a battery powered Eberline SAM-2 assay meter connected to a 10 x 10 cm NaI crystal and photomultiplier. Each crocodile was rinsed in tap water for two minutes, and then positioned in a plastic box on top of crystal so that the counting geometry was repeatable. Samples of the radioactive sea water were counted in the same fashion. After the fifth hourly count, crocodiles were not returned to the radioactive bath but were placed in 2 liters 100% sea water lacking ^{22}Na initially, for measurement of the efflux. They were counted at intervals of one to two days over a 10 to 11 day period. Three of the four crocodiles were transferred to fresh water after six to seven days when they appeared to be weakening from the combined effects of the fast and exposure to sea water. These studies were conducted between September 25 and October 7, 1979, at the Univ. of Miami Pigeon Key Environmental Field Station. Air temperatures varied between 28 and 32°C. Flux calculations were made with a two compartment equation (see Robinson and Dunson, 1976) programmed into a HP 67 calculator.

^{24}Na influx across the skin keratin of C. acutus was measured in vitro in glass chambers designed by Dunson (1978). A crocodile (about 1 kg) kept in dry air to measure evaporative water loss sloughed off small flakes of keratin. These were stored in a sealed plastic bag for seven months. They were then sealed with silicone grease (high vacuum) across a 3 mm opening (area 0.283 cm^2) between two glass disks separating 1 milliliter radioactive sea water (35 ppt) on the outside and 10 milliliters reptile Ringers solution (see Dunson, 1978) on the inside. ^{24}NaCl was prepared by neutron activation in the Breazeale nuclear reactor and added to sea water at specific activities of 13-20 microCuries/milliliter. Over a 22-23.5 hour period, four 1 milliliter samples were removed from the inside solution, counted with a Canberra series 30 multichannel analyzer connected to a NaI crystal, and replaced in the chamber. Comparable volumes of the outside sea water had about 10^7 counts per minute. A total of 14 chambers were used for shed keratin from a single crocodile. Two additional chambers were used to test the flux across a double thickness of cellulose dialysis membrane.

The surface area of crocodilians was estimated by carefully skinning 13 specimens of three species, and tracing the outline of the spread skin on graph paper. These outline drawings were cut out and their weights compared with weights of known areas to determine skin surface area. Some of these specimens were frozen and others were preserved. Thus the surface areas were related to a linear dimension, the snout-vent length. The length-weight relationship for C. acutus was determined separately on the 12 live specimens available. An HP67 power curve program (SD 03A) was used to calculate the equations.

A primitive but effective means of estimating the general fitness of reptiles to survive in a saline environment is to follow weight changes when they are submerged in water of various salinities. In fasting animals this appears to reflect mainly water loss or gain (Dunson, 1979). Several previous studies have followed such changes in fasting, immersed crocodiles (Dunson, 1970; Evans and Ellis, 1977; Ellis, unpub. obs.). In the present study an attempt was made to evaluate the effect of feeding on weight changes of submerged animals and in those allowed a choice between land and water. In the first test, two C. acutus were placed in 50% (18 ppt) or 100% (35 ppt) sea water for about six days and fed live minnows. Later, four crocodiles were placed in either 50 x 27 x 31 cm or 75 x 32 x 48 cm aquaria (length x width x height) depending on their body size. A shallow plastic dish was inserted in the gravel on the bottom of each aquarium. This dish was just large enough to allow each animal to fully immerse itself if it chose to do so. These crocodiles were well acclimated to laboratory life and fed readily from the hand. They were usually offered cut pieces of fish ad lib. every two days; occasionally the diet was supplemented with whole minnows or insects such as grasshoppers and roaches. The salinity of the water in the dish was changed every 7 to 14 days, and the crocodiles were weighed at this time. Air temperatures varied from 24 to 28°C. The relative time spent on land or in water was estimated by recording the position of each animal at various times during the day; consecutive records were not taken at intervals of less than 2 hours.

Evaporative water loss in dry air was measured by the same technique used by Dunson et al. (1978). Small crocodiles (less than 400 grams) were placed in dessicators (20 cm diameter) in a refrigerated incubator. Air from a pump at 300 milliliters/minute passed through a drierite column into the chamber, and then through another drierite column. This second column was weighed to determine water loss. To provide relative humidities of 75 and 96.5%, the initial drierite column was replaced by two flasks of saturated NaCl or K_2SO_4 respectively (Winston and Bates, 1960). Water loss was then estimated by directly weighing the animal each day. Measurements on two larger crocodiles were made in a chamber fashioned from an acrylic cylinder 10 cm in diameter and 60 cm long.

RESULTS

Plasma composition

There was no apparent relationship between plasma concentration and the salinity of water at which an animal was captured (Table 1). Crocodiles were found at salinities ranging from fresh water to hypersaline (0-43 ppt). The latter value for Basin Hills is from a locality outside Everglades National Park, along the shore of Barnes Sound. Although these data document the salinities at the time of capture, such values give little information on the conditions these crocodiles were acclimated to, since the animals move around and salinities may vary considerably over short periods due to rain and wind shifts (which also cause water level changes). Mazzotti and Kushlan (unpub. obs.) will report on long term fluctuations in salinity at these stations. It is important to note, however, that salinities near five nest sites in Florida Bay (Cocoa Point, Alligator Bay, Black Betsy Beach, Trout Cove, Dead Stork) shortly after the time of hatching were fairly high (22-32 ppt; Table 1). However many hatchlings were found on land during the first few weeks, hiding in holes or in clusters of mangrove roots.

Plasma samples were taken from seven hatchlings removed directly from a nest on Black Betsy Beach in the summer of 1979 (Table 1). Plasma Na (150 mM) and osmotic pressure (327 mOsm) were at levels accepted as normal for vertebrates (Dessauer, 1970). The mean plasma osmotic pressure for samples from all recent hatchlings varied from 314 to 353 mOsm. These values are probably within the normal range of variation for this species and provide no evidence for a theory of progressive dehydration during the first two weeks of life. This is especially evident if sequential samples from the same nest site are examined. For example, crocodiles at both Cocoa Point and Black Betsy Beach (summer, 1978) showed fairly stable plasma osmotic pressures over the first two weeks (Table 1). There were irregularities in the plasma electrolyte composition. Despite the rather normal plasma osmotic pressures, some crocodiles had abnormally low plasma Na. Six different groups had means of 111-120 mM, values often exceeded by Cl (Table 1). There is a possibility that this phenomenon is age related in the sense that the first few weeks of life are probably spent fasting and hiding on land. However the present data are insufficient to evaluate this question. Another possibility considered was that of an analytical error. This seems unlikely in view of the fact that the numerous samples taken from mangrove snakes (Table 2) had the expected higher levels of Na and Cl. At present we must consider the possibility that some very young crocodiles actually have a deficiency of Na.

Hatchling C. acutus rapidly disappear from the vicinity of their nest sites. Whether this is due to simple dispersal or death is unclear at present. Only one marked hatchling from the summer of 1978 was recaptured. This animal, marked in Davis Creek and recaptured there, was six months old (Table 3). Its plasma was "normal" as that of four other animals of similar size from the same locality. The single adult sampled and two alligators also had plasma osmotic pressures similar to those of the younger crocodiles sampled. Their plasma Na levels tended to be slightly higher (Table 1).

In contrast to the crocodiles, the effects of dehydration can readily be discerned in plasma samples from mangrove snakes (Table 2). Specimens from Little Pine Island (Lower Florida Keys) and Davis Creek had elevated plasma Na and osmotic pressures when captured. A group of five snakes from Summerland Key (Lower Florida Keys) caught in sea water underwent considerable increases in plasma Na (148 to 194 mM) and Cl (135 to 181 mM), when held 27 days in 35 ppt sea water without feeding. It is also especially interesting that three snakes from Davis Creek had higher plasma Na, Cl, and osmotic pressures than the five crocodiles caught in the same habitat at the same time.

Cloacal excretion

In evaluating these data it is important to remember that the samples collected were expelled prematurely due to handling. Thus the natural processes of reabsorption and secretion in the cloaca and gut may not have been completed. It is evident from Table 3 that cloacal fluid osmotic pressure was always equal to (within experimental error) or less than that of the plasma. A striking result is the extremely low Na concentration (12-21 mM) of cloacal fluid in comparison with plasma (106-166 mM). In five out of six cases Cl was much higher than Na. In only three of seven cases was K present in significant amounts (30-45 mM). Na, Cl and K account for a much smaller percentage of the osmotic pressure in cloacal fluid than they do in plasma.

Faecal samples were not obtained, but analyses were made on the white solid found mixed with the cloacal fluid. In three samples from captive C. acutus and four from C. porosus, 72-95% of the dry white solid material could be accounted for by uric acid. K and small amounts of Na were present in the cloacal fluid solids (Table 4). In four wild hatchlings and two six-months-old animals from Davis Creek, Na and K levels were 11-222 and 87-1111 μmoles/gram dry weight respectively. Captive animals held in dry air, fresh water or sea water had similar amounts of Na and K (2-60 and 62-1003 μmoles/gram dry weight respectively). There was no apparent relationship with the conditions of treatment, at least in the present small sample.

Na exchange in sea water

The three smaller C. acutus used to measure Na fluxes were about two months old; the larger one was about 14 months old. The uptake of ^{22}Na from 35 ppt sea water was most rapid during the first hour, and then leveled off for the next four hours (Table 5). At the end of the five hour influx period, the specific activity of the bath was estimated to still be about 47 times that of the crocodiles. Thus the crocodiles were not nearing equilibrium. The initial (0-1 hour) rapid phase of influx might be due to a rapid absorption of isotope to the body surface and just represent the residual ^{22}Na that cannot be rinsed off within the two minutes allotted. I believe the true influx to be more accurately represented by the value for the 1-5 hour period. Three of the four crocodiles had a mean influx of 11.5 μmoles/100 gram hour, with a fourth higher point of 37 μmoles/100 gram hour (Table 5).

The crocodiles used in the ^{22}Na influx measurements were placed directly into unlabeled sea water for the efflux determinations. A classic two compartment efflux was obtained. However there was a larger "fast" compartment than is usual among aquatic reptiles (Table 5). The rate of loss from this "fast" phase was approximately equal to the accelerated rate of influx during the first hour, suggesting that they might be associated. As with the influx, it is likely that this initial rapid rate of efflux is an artifact of the experimental procedure. The ^{22}Na influx was used as a means of "loading" the body for the subsequent efflux measurement. It is quite possible that the process of equilibrium of ^{22}Na in the body takes several days. A higher specific activity of the tissues that are more accessible to exchange with the environment could have occurred during the first few days of the efflux determination, causing the appearance of a larger than usual fast compartment. This appears to be the most logical explanation at present. Thus the true efflux is best estimated by the mean value of efflux of the "slow" compartment, which was 2.3 μmoles/100 gram hour (Table 5). Three of the four crocodiles were transferred from sea water to fresh water at days 6 and 7, but it appears that this had little or no effect on the efflux.

The overall rates of Na exchange in C. acutus placed in sea water are quite low. The influx exceeds the efflux by about 10 μmoles/100 gram hour, suggesting that there is a low but significant net uptake of Na when small crocodiles are submerged in sea water. Note that the fast phases of influx and efflux differ by approximately the same amount.

For the purposes of these flux calculations the body Na content of crocodiles was assumed to be 50 µmoles/gram wet weight. In one determination on a 56 gram hatchling that was killed by a cage mate, the actual value was 39.1 µmoles Na/gram wet weight (10.9 µmoles K/gram wet weight, and 79.4% water). Since sea water has so much more Na than the body, such slight differences in body Na content have no significant effect on the calculations. Evans and Ellis (1977) give values of 52 and 69 µmoles/gram wet weight for two crocodiles in 25% sea water.

Skin area

The "standard" surface area (A) to weight (W) equation used by many investigators ($A = 10W^{0.67}$) (Minnich, 1979) has not previously been verified for crocodilians. The relations between area and snout-vent length, and weight and snout-vent length were separately determined in this study (Table 6). The calculated surface area to weight relation was then found to be: $A = 11.7384W^{0.6373}$. This and the standard form probably differ by less than the experimental error of the skin area measurements. It is interesting that crocodilians of a given weight have a lower surface area than snakes (Table 6), due a lower y-intercept and slope.

In two *C. porosus* the relative contributions of the different body areas to the total surface area were measured. The animals were 36 and 39 cm in snout-vent length, and 71 and 78 cm in total length. The head (13.5%) and neck (7.5%) together comprised 21% of the total. The body, legs, and tail were each 28.5%, 23.2%, and 27.4% respectively. Thus the head-neck, body, legs, and tail regions each account for about one fourth of the total surface area.

Dermal Na permeability

Shed keratin collected from a *C. acutus* that was being dehydrated in dry air appears to be impermeable to Na. A total of 14 pieces of keratin were tested and 11 of these had no influx of ^{24}Na from sea water to Ringer's solution after one day. The remaining three preparations leaked and were discarded. The glass chambers used for this experiment had a diffusion area 3 mm in diameter to accommodate the small pieces of keratin. To test the apparatus and to insure that the silicone grease used to seal the chambers was not blocking Na movement, two cellulose dialysis membranes were measured in the same fashion. A large influx was obtained over one hour (55 µmoles/cm^2 hour), demonstrating the proper functioning of the chambers.

Weight changes in saline water

Hatchling *C. acutus* and *C. porosus* lose weight rapidly (about 1.7%/day) when fasting and immersed in 35 ppt sea water (Dunson, 1970). As size increases, the rate of weight loss diminishes in *C. acutus* (Dunson, 1970; Ellis, unpub. obs.). In *C. porosus* weight loss also decreases in larger animals (Table 7). However the effect rapidly diminshes above 1 kg.

It is important to note that fasting C. porosus as small as 1 kg have rates of loss as low as 0.3%/day when immersed in 35 ppt sea water. If small C. acutus are forced to remain immersed in 35 ppt sea water, they cannot maintain their weight even when fed (Table 7). Yet in 18 ppt they gain weight when fed.

In nature, small crocodiles probably do not remain submerged for long periods, but come out on land. To test the effect of terrestrial activity, four small C. acutus were placed in individual aquaria with dry land and water available as desired, and fed every two days. They were allowed access sequentially to fresh water, 9, 17.5, 26 and 35 ppt sea water for the periods shown in Table 8. Under these conditions weight gains usually occurred with access to 50% sea water (17.5 ppt). Small gains or losses took place with access to 75% sea water (26 ppt). Feeding greatly diminished when the water was changed to 100% sea water (35 ppt) and large amounts of weight were lost. Individual crocodiles differed greatly in the time spent submerged at a given salinity, but data suggest crocodiles may recognize and avoid immersion in water of higher salinities. The mean percentage of time spent in water at 50%, 75% and 100% sea water decreased from 43 to 13 to 8% in one animal, from 62 to 17 to 8% in another and from 95 to 61 to 54% in a third. The largest animal showed a decrease in time spent in water on transfer from 50% to 75% sea water (76 to 57% time), yet an increased amount of time (77%) was spent in 100% sea water. These tests were carried out in a room of fluctuating temperature and humidity, and they should be repeated under constant conditions. Other possible source of errors are the numerous cues for orientation present in the surrounding room. No consistent salinity preference could be demonstrated in a different series of tests with C. acutus placed in tanks divided in half, with fresh water on one side and sea water on the other. Animals often appeared to favor one side or the other depending on the direction of human disturbance in the room.

Salinity at a nest site and composition of potential food

It is difficult to reconcile the intolerance of hatchlings in the laboratory to high salinities with the prevalence of beach nesting sites where salinities are high. At present, survival of three marked hatchlings for 5-6 months has been demonstrated only in two creeks on the edge of Florida Bay (Mazzotti and Kushlan, unpub. obs.). These areas have lower salinities and appear to provide more favorable habitat for growth of the hatchlings than areas near the nest sites on beaches exposed to Florida Bay. Information on one such "outside" or bayside nest site is presented here to illustrate this point. On the north shore of Florida Bay are two small bays, separated by a peninsula. In 1979, three nests were found by Mazzotti and Patty on the seaward sides of the peninsula. One nest (nicknamed Dead Stork) chosen for study was positioned just behind a low beach berm next to a small channel approximately 2 m wide and 79 m long connecting the bay with a shallow lagoon behind the beach. On the nights of August 3-4 approximately 30 eggs hatched (Patty, unpub. obs.). On the night of August 6, eight hatchlings were caught in the nearby channel at a salinity of 32 ppt, marked, and released. On August 16 seven hatchlings, including three unmarked ones, were caught at night in the channel at a salinity of 40 ppt. When released, the young crocodiles often crawled into dense groups of red mangrove roots (Rhizophora mangle) along the edges of the channel. A period of stormy weather followed and water levels were raised. When the area was revisited September 8 during the daytime, a thorough search was made of the mangroves along the channel and no crocodiles were found. Water (30 ppt) had overflowed the banks of the channel and possibly the crocodiles had dispersed. However the salinity had been quite high at this locality and mortality is also a possibility. In the immediate vicinity of this nest there are no areas of low salinity water. A series of large lagoons in the interior of the peninsula were 38-40 ppt on August 16. The elevation of the land is probably too slight to allow formation of brackish water ponds from an underlying lens of fresh water. In contrast, interior nest sites along creek banks may not only be lower in salinity, but are also in closer proximity to pools of brackish water that can form in hammocks and buttonwood (Conocarpus) scrub after rains.

The vicinity of the study nest was well supplied with potential food for hatchling crocodiles. In captivity small crocodiles feed readily on fish or insects and a wild hatchling observed on Key Largo caught and ate a small fish (probably Gambusia). Potential food items were captured and analyzed without rinsing the sea water off since this is the condition in which they would be swallowed by crocodiles. Water, Na, and K contents of these potential prey are shown in Table 9. As expected, fish provide the most free water with the least amount of Na. Beach isopods had four times the Na content of the fish. Na content of the other invertebrates was about twice that of the fish. K and water content of all samples were variable and may not be factors of major importance in determining the osmoregulatory significance of different items.

Evaporative water loss

Immersion in full strength sea water causes a large weight loss in hatchling crocodiles. Thus it would seem advantageous for them to spend most of their time, when not feeding, on land. However the evaporative water loss of C. acutus in air is remarkably large in comparison with the mangrove snake found in the same habitat (Table 10). Indeed the weight loss at a relative humidity of 96.5% of two recent hatchlings was 1.3-1.5%/day, values approaching the figure of 1.7%/day obtained when they are immersed in 35 ppt sea water. A single animal (326 g) was tested in dry air for four days at 30°C, 25°C, and 20°C; the rates of loss declined from 1.24 ± 0.08 to 1.04 ± 0.02 to 0.71 ± 0.07%/day respectively (means ±SD). Thus the rate of evaporative loss decreases with increasing size, increasing relative humidity, and decreasing temperature.

In the wild, young crocodiles can seek out relatively cool, moist microclimates. However even under favorable conditions (96.5% relative humidity, 30°C) hatchlings on land are subject to an obligatory evaporative water loss in excess of 1% wt/day. In a 326 gram animal this rate declined markedly to about 0.3%/day. Thus size appears to be an extremely crucial factor associated with problems of water balance during the first three to four months of life.

DISCUSSION

No final answer can be given at this time to the hypothesis that a major portion of the mortality of hatchling C. acutus in Florida Bay is associated with osmoregulatory problems caused by high salinities. Additional field studies of hatchlings during the first four months are needed to establish their fate under the most stringent long term salinity regime ever likely to be naturally encountered. Present data show that the vicinity of many nest sites are saline enough that difficulties in water and salt balance could be encountered. Small C. acutus have few special mechanisms to enable survival in sea water. Hatchlings lose large amounts of water whether submerged in sea water or on land. As yet there is no evidence that C. acutus has a salt gland (Dunson, 1970, 1979). Cloacal fluid is less concentrated than plasma. Cloacally excreted urates contain bound K in excess of Na, but only at about the same level as found in terrestrial carnivorous reptiles. Na exchange in 35 ppt sea water is low, mainly due to the impermeability of the skin, yet a significant net uptake of Na occurs. Young C. acutus seek out protected environments of moderate temperature and high humidity and can feed at night on fish high in water and low in Na content. These and other behavioral strategies can minimize the losses of water and uptake of salt at times when the salinity is high. Despite the lack of specialized physiological mechanisms, an unknown percentage of C. acutus do manage to survive the critical early months of life in northern Florida Bay where the salinities are variable (Mazzotti and Kushlan, unpub. obs.). However it seems highly unlikely that they can do so in areas of sustained high salinities (above 30 ppt). Future field work will have to determine whether the present small rate of recruitment is adequate to maintain a viable population. It is possible that Florida Bay crocodiles are being stressed in part by the marginal ability of young to survive in habitat near present day nest sites.

In contrast with marine snakes and turtles, all crocodilians are poorly adapted to cope with the problems of osmoregulation in sea water. A most cogent comparison can be made between C. acutus and the mangrove snake, Nerodia f. compressicauda. Both live in the same habitat and both apparently lack a salt gland and feed on fish. Yet the mangrove snake has a much lower rate of evaporative water loss and a lower rate of weight loss when immersed in sea water (Dunson, 1980). This occurs in spite of the snake's higher skin surface area. Mangrove snakes are moderately abundant even in highly saline habitat on isolated islets. They are subspecifically distinct from the more widespread fresh-water race N. f. pictiventris, and seem to be well on the way to evolving into a separate estuarine species. This is not an uncommon response for animals living in the estuary, since a suite of highly specialized characters are necessary for survival there. Thus a typical estuary has a low species diversity, and many of the species and subspecies present there will be unique types. C. acutus seems to have undergone a very limited amount of evolutionary specialization for water conservation; it remains basically a terrestrial animal somewhat modified for fresh water life. The so-called "salt water" crocodile, C. porosus, of the western Pacific also remains dependent on the fresh water reaches of tidal rivers for egg laying and rearing of the young (Messel and Butler, 1977).

The first report known to me of the plasma electrolyte concentration of C. acutus is that of Dill and Edwards (1931). Plasma from a single specimen caught in fresh water in Panama was 149 mM Na, 7.9 mM K, and 117 mM Cl. Schmidt-Nielsen and Skadhauge (1967) reported plasma concentrations of Jamaican C. acutus under normal (fresh water), water-loaded, dehydrated, and salt loaded conditions. Plasma osmotic pressures were 294, 278-287, 315-318 and 330-346 mOsm respectively. Evans and Ellis (1977) found plasma Na levels of hatchling C. acutus of Jamaican origin to be 129 mM in fresh water and 142 mM in 25% sea water. Plasma osmotic pressures measured here for hatchling C. acutus along the shores of Florida Bay (Table 1) were in the range reported by Schmidt-Nielsen and Skadhauge (1967) for salt loaded animals. Grigg (1977) found that the plasma of C. porosus was regulated within a narrow range about a mean of 304 mOsm over a wide range of salinities. However values of 330-350 mOsm are not abnormal for vertebrates generally (Dessauer, 1970) and are not here interpreted as evidence for osmoregulatory problems. This is a fair conclusion if these levels are maintained without progressive increases with time. The peculiar feature of these data is the remarkably low plasma Na concentration of many samples, despite the relatively normal osmotic pressure. There is an unaccounted for substance amounting to about 20-30% of the osmotic pressure in many samples from hatchlings. I have no explanation for this at present, except to suggest that more study is needed of Na and water balance of embryos and of hatchlings during the immediate post-hatching period. With the exception of three 16 day-old hatchlings from Black Betsy beach (Table 1), Na levels seem normal (150 mM is a typical vertebrate level). It may be significant that this single case of elevated plasma Na among wild hatchlings (from 120 to 177 mM) occurred at the only nesting site left on an island out in Florida Bay where fresh water influx from the mainland is limited. Note also that the electrolyte contribution to the total osmotic pressure increased from 68 to 91%, even though the absolute osmotic pressure was relatively constant. A similar sequence of measurements among the Cocoa Point hatchlings failed to demonstrate such a rise in plasma Na during the first two weeks (Table 1). It is unfortunate that further plasma samples could not be obtained during the remainder of the first month of life, but hatchling crocodiles become very difficult to find as they disperse from the nest site. Repeated handling of the same animals might pose the hazard of a significant disturbance of normal behavior and physiology. Thus it is problematical whether adequate sequential plasma measurements can ever be made in the wild. Perhaps useful data might instead be obtained by introducing hatchlings into a fenced area that duplicates the natural habitat, and observing any plasma changes in relation to different salinity regimes.

It is interesting that data suggesting dehydration of mangrove snakes at high salinities was obtained in the field (Table 2). Ten animals from Summerland Key and Florida Bay had relatively normal plasma Na levels (means of 148-153 mM). Yet four snakes from Davis Creek and Little Pine Island has much higher concentrations (176-181 mM). In a laboratory simulation, the same five snakes from Summerland Key were placed in 35 ppt sea water for 27 days without food. Mean plasma Na rose from 148 to 194 mM; plasma Cl increased from 135 to 181 mM. A similar effect was noted by Evans and Ellis (1977) when they transferred six hatchling C. acutus from fresh water to 25% sea water; mean plasma Na rose slightly but not significantly from 129 to 142 mM. Total body Na values were only available for three animals, but they increased considerably in 25% sea water.

The excretion of electrolytes by the kidney of Jamaican C. acutus has been considered in an excellent paper by Schmidt-Nielsen and Skadhauge (1967). The osmotic urine to plasma ratio only changed slightly (0.7 to 0.9) between states of hydration and dehydration. The glomerular filtration rate varied but slightly in comparison with most amphibious reptiles. The renal tubules have little or no capacity for regulation of the urine composition. The cloaca has an important role in ion balance; Na and Cl are almost completely reabsorbed. Crocodiles are ammono-uricotelic (excrete ammonia and uric acid but little urea) and their kidney function is more characteristic of terrestrial forms than that of typical amphibious reptiles such as turtles. In normal C. acutus cloacal fluid (251 mOsm) was 5.9 mM Na, 16.5 mM Cl, and 2.7 mM K. After salt loading all these ions increased; Na was 38 mM, Cl was 77 mM and K was 35 mM (Schmidt-Nielsen and Skadhauge, 1967). In cloacal fluid samples from Florida Bay hatchlings, a similar effect was found, although there was some variation in the relative amounts of Na, Cl and K. In cloacal fluid samples of osmotic pressure above 300 mOsm, there was little K (Table 3). Cl was always present greatly in excess of Na, with one exception. Na levels were generally below those found by Schmidt-Nielsen and Skadhauge (1967), whereas Cl was often higher. The fact that most Na is reabsorbed from the cloacal fluid tends to confirm the plasma evidence that many hatchlings were hyponatremic.

Schmidt-Nielsen and Skadhauge (1967) found large amounts of ammonia in the cloacal fluid, but they did not measure uric acid. Khalil and Haggag (1958) had previously shown that crocodilians excrete their nitrogenous wastes as ammonia and uric acid. In the present study the white solids mixed in with the cloacal fluid were found to be 72-95% uric acid. In other reptiles cations are also excreted in this material, bound to urates (see review by Minnich, 1979). The content of Na is generally low; K is much higher and varies from about 1000 µmoles/gram dry weight in carnivorous reptiles to about 4000 µmoles/gram in certain herbivorous ones. In this study wild C. acutus had urate Na contents as high as 222 µmoles/gram, and K contents up to 1111 µmoles/gram. Captive crocodiles similarly had a maxmimum Na level of 60 µmoles/gram and K 1003 µmoles/gram. Longer term studies need to be carried out of the effects of dehydration and salt loading on urate cations. However at present there seems no reason to suppose that C. acutus has an ability different from that of a typical carnivorous reptile to excrete Na and K in this fashion.

The only previous study of Na fluxes of *C. acutus* is that of Evans and Ellis (1977). They found an efflux of 2.5 µmoles/100 gram hour in fresh water and 5.6 µmoles/100 gram hour in 25% sea water (125 mM Na). These are very low values and indicate a slow turnover of body Na in exchange with media of low salinities. In the present study the efflux in 100% sea water (470 mM Na) was 2.3 µmoles/100 gram hour (Table 5). Thus it appears that changes in the external salinity have little effect on Na efflux. Since the crocodiles had been in 100% sea water for more than a week and were dehydrated, such a low efflux also indicates that there is no salt gland. The smallest functional salt gland yet described in reptiles is that of the snake *Cerberus rhynchops*, which secretes Na at about 16 µmoles/100 gram hour (Dunson and Dunson, 1979). More specialized sea snakes and turtles have rates in excess 100 µmoles Na/100 gram hour (Dunson, 1979).

Na influx of *C. acutus* in 100% sea water was higher than the efflux (Table 5). It appears that a substantial net uptake of about 10 µmoles/100 gram hour is occurring in 100% sea water. In comparison, the fasting sea snake *Pelamis* has a Na influx and efflux of 8.2 and 7.1 µmoles/100 gram hour respectively (Dunson and Robinson, 1976). When the salt gland is stimulated, the efflux can jump to 140 µmoles/100 gram hour. Since *C. acutus* lacks a salt gland or the renal ability to excrete excess Na, it must then avoid exposure to sea water. However a great deal more information is needed to properly evaluate Na balance at various salinities. We especially need a series of influx and efflux determinations at intermediate salinities (50 and 75% sea water), a study of the effects of salt loading, and an examination of changes in plasma Na and body Na content of crocodiles held at various salinities. There is also the problem of compartmental analysis of these fluxes as discussed in the methods section. All of these experiments require large numbers of captive hatchlings, a commodity not available for the present study.

It appears likely that the skins of most aquatic reptiles are essentially impermeable to Na (Dunson, 1978, 1979). *C. acutus* is no exception to this general rule. Small pieces of shed keratin were impermeable to Na *in vitro*, and the living skin with the intact keratin covering it is probably equally so. This should be confirmed (as has been done for *Cerberus* by Dunson, 1978) by placing crocodiles in radioactive sea water (^{24}Na or ^{22}Na) with the head alternately held in and out of the water.

Apparently the skin surface area of crocodilians has never previously been measured. It is common practice to use the equation $A = 10\ W^{0.67}$ (Schmidt-Nielsen and Skadhauge, 1967; Bentley and Schmidt-Nielsen, 1965, 1966). In this study the actual relation was found to be $A = 11.7384W^{0.6373}$ (Table 6); agreement of these two equations is remarkably close. It is interesting that two species of snakes measured in the same way have greater surface areas than crocodiles of the same weight (Table 6).

The first measurements of weight loss of *C. acutus* immersed in sea water were made by Dunson (1970). Small animals (mean wt 86 gram) lost

1.7% weight/day over a four day period in 100% sea water. Evans and Ellis (1977) got an identical figure for a single hatchling in full strength sea water. Since typical marine reptiles lose only about 0.1-0.4% weight/day (Dunson, 1979), small crocodiles do not appear capable of surviving long in 100% sea water. Small (101g) Caiman sclerops do even poorer; they lost 6.8% weight/day in 3.3% NaCl (Bentley and Schmidt-Nielsen, 1965). Even when fed, two young C. acutus (220 and 290g) still lost 1.5 and 1.4% weight/day (Table 7) when completely immersed. However as size increases, weight loss of fasting C. acutus decreases; Evans and Ellis (1977) report rates of 0.4 and 0.7%/day in two 1-2 kg specimens in 100% sea water. Dunson (1970) kept a 3.4 kg C. acutus immersed for five months in 100% sea water: it remained healthy and fed on trout. Fasting C. porosus as small as 1.2 kg also show a diminished rate of water loss when immersed in full strength sea water (Table 7). Ellis (unpub. obs.) has also measured rates of loss in a large range of body sizes of C. acutus; body weight was inversely related to the rate of weight loss.

The measurements of weight loss in sea water reported above have two serious flaws: (1) the animals are forced to remain in sea water and (2) they are usually not fed. To provide a better simulation of conditions in the wild, four small C. acutus were placed individually in tanks with land and water sections. Salinity of the water was varied and the crocodiles were fed every two days. Three of four animals gained small amounts of weight at salinities as high as 26 ppt (75% sea water). Larger weight gains occurred at 17.5 ppt (50% sea water). About 1% weight/day was lost at 35 ppt (Table 8). Further work is necessary to determine the long term effects of maintenance at such salinities on recent hatchlings, since the crocodiles do enter the water frequently and might slowly accumulate deleterious Na loads. However it now appears that young (3.5 month) C. acutus are capable of good growth in salinities approaching 20 ppt if they are fed regularly and allowed to choose between land and water environments. In these tests crocodiles were fed mainly on pieces of marine fish flesh with the skin attached. Whole fish provides the same amount of water as most invertebrates, with about half the amount of Na (Table 9).

Observations of hatchling crocodiles in Florida Bay shows that they spend considerable amounts of time out of water (Mazzotti, Kushlan and Dunson, unpub. obs.). Thus it is surprising to find that large amounts of evaporative water loss (1.3 to 1.6%/day) occur in air at a relative humidity of 96.5% and 30°C (Table 10). This is about three to seven times the evaporative loss rates of mangrove snakes. Despite their high rate of terrestrial water loss, crocodiles gain the advantage on land of avoiding net uptake of Na that occurs when immersed in 100% sea water. C. acutus also appears to be better adapted for a terrestrial existence than two of its close relatives. Caiman lost 13.3% weight/day at 23°C and a relative humidity of 25%, about 75% of which is dermal (Bentley and Schmidt-Nielsen, 1965, 1966). An Alligator (668 g) at 38°C lost 20% weight/day at 27% relative humidity and 12.5%/day at 46%

relative humidity (Bogert and Cowles, 1947). As *C. acutus* increases in size, its rate of evaporative water loss rapidly decreases. A 326 g animal had a loss rate of only 0.27%/day (Table 10). Thus size appears to be a most crucial determinant of the ability of *C. acutus* to maintain water balance in air as well as when immersed in sea water.

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Table 1. Summer (July 30-August 19, 1978, and August 6-August 16, 1979) and winter (January 11-February 21, 1979) plasma concentrations of alligators and crocodiles in Florida Bay. Mean ±SD.

			Water	Plasma				
	Age,		salinity,	mM			mOsm	$\frac{Na+Cl+K}{\pi}\cdot 100$
Locality	days	N	ppt	Na	Cl	K	π	
Alligators: summer, 1978								
Florida Bay		2	0-3	170 ±12	123 ±18	3.9	326 ±21	91
Crocodiles: summer, 1978								
Taylor River	Adult	1	0	169	129		321	93
Cocoa Point	1	6	23-26	155 ±9	123 ±18	4.4 ±0.7	324 ±10	87
	7	3	26	113 ±6	117 ±6	2.9 ±2.2	353 ±25	66
	14	2	25-27	111 ±8	106 ±6	2.6 ±1.8	327 ±4	67
Alligator Bay	1.5	2	23	116 ±4	125 ±0	3.9 ±0	348 ±12	70
Black Betsy Beach	<1	7	26	120 ±13	101 ±16	4.5 ±2.5	331 ±12	68
	16	3	25-28	177 ±23	127 ±10		335 ±16	91
Trout Cove	<7	1	22	118	128	4.6	320	78
Basin Hills[1]	10	2	43	110 ±6	128 ±0	3.0 ±1.5	334 ±13	72
Crocodiles: summer, 1979								
Black Betsy Beach	0	7	In nest	150 ±5		8.4 ±1.8	327 ±13	
Dead Stork	2-3	6	32	151 ±5		7.4 ±4.0	314 ±5	
Crocodiles: winter, 1979								
Davis Creek	180- 360	5	19-31	157 ±7	123 ±16	8.3 ±2.1	337 ±19	86

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[1] On northern Key Largo along Barnes Sound

Table 2. Plasma concentrations of freshly captured mangrove snakes (*Nerodia f. compressicauda*). Mean ±SD. Partly from Dunson (1980).

Locality	N	Water salinity, ppt	Plasma				
			mM			$\frac{\text{mOsm}}{\pi}$	$\frac{\text{Na+Cl+K}}{\pi}\cdot 100$
			Na	Cl	K		
Summerland Key	5	35	148 ±15	135 ±15	6.9 ±0.8		
Summerland Key[1]	5	35	194 ±6	181 ±18	7.2 ±1.6	482 ±47	79
Little Pine I.	1	40	176	136	7.6	409	78
Florida Bay	5	23-28	153 ±21	124 ±5	5.6 ±3.4	371 ±37	76
Davis Creek	3	20-31	181 ±8	135 ±20	5.6 ±0.5	379 ±30	85

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[1] Same group as above but held 27 days in 35 ppt sea water without feeding

Table 3. A comparison of cloacal fluid (CF) and plasma (PL) concentrations of individual *C. acutus* from Florida Bay.

		Water		Concentrations				
	Age,	salinity		mM			mOsm	$\frac{Na+Cl+K}{\pi} \cdot 100$
Locality	days	ppt	Sample	Na	Cl	K	π	
Black Betsy Beach	<1	26	PL	113	102	3.9	313	70
			CF	21	86	3.1	272	40
	<1	26	PL	126	94	3.6	323	69
			CF	15	94	0		
Cocoa Point	7	26	PL	109	120	5.4	340	69
			CF				306	
Trout Cove	<7	22	PL	118	128	4.6	320	78
			CF	18	94	2.6	322	36
Basin Hills	10	43	PL	106	128	1.9	343	69
			CF	12	60	0		
Dead Stork[1]	13	40	CF	17.1 ±3.0		29.9 ±33.2	287 ±30	
Davis Creek	~180	31	PL	166	132	9.0	357	86
			CF	13	115	45.0	274	63
Davis Creek[2]	180	20	PL	161	132	7.3	328	92
			CF	17	<10	31.0	212	27

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[1] Mean values ±SD for 5 crocodiles. No plasma taken.

[2] Marked as a hatchling and known to be 6 months old.

Table 4. Sodium and potassium content of the solid portion of the cloacal fluid excretion from _C. acutus_ held in fresh water in the laboratory or freshly captured in Florida Bay.

Animal No.	Salinity, ppt	Weight g	Days acclimated	Content, µmoles/g dry wt Na	K	K/Na
Caught in Florida Bay:						
1	In nest	~65		76	487	6.4
2	In nest	~65		45	108	2.4
3	In nest	~65		44	87	2.0
4	In nest	~65		222	279	1.3
5	20	355		11	478	43.5
6	31	470		39	1111	28.5
In captivity:						
7	Dehydrated in air	326	9	60		
7	"		5	16	1003	62.7
7	"		8	30	478	15.9
8	0	3110	>50	2	901	450.5
8	0			19		
8	0			44	316	7.2
9	0	1800	>50	17	142	8.4
10	0	2640	>50	18	62	3.4
11	0	6115	>50	43	585	13.6
12	35	5780	28	9	483	53.7
12	35		29	14	508	36.3
12	35		38	36	604	16.8

Table 5. Sodium fluxes of <u>C. acutus</u> in 35 ppt sea water.

Weight, g	Influx µmoles/100g h		Efflux, µmoles/100g h "Fast" phase		"Slow" phase		
	0-1h	1-5h	Flux	$T_{1/2}$ days	Flux	$T_{1/2}$ days	% total activity
87	59.6	12.6	95.7	0.4	4.6	29	57.5
84	86.3	37.3	43.3	1.6	2.4	53	51.8
100	88.4	13.5	53.2	1.2	0.3	156	61.0
413	44.0	8.4	44.5	1.1	1.7	74	66.7
mean ±SD	69.6 ±21.5	11.5[1] ±2.7	59.2 ±24.8		2.3 ±1.8		

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[1] Mean calculated without the highest value.

Table 6. The relation between snout-vent length (L), weight (W), and body surface area (A) in crocodilians and snakes.

Species (N)	Range in snout vent length, cm	Range in body weight, g	Equation	r^2
Crocodilians:				
C. acutus (4) *C. porosus* (8) *Caiman* sp. (1)	11.1-38.5		$A = 1.1550L^{1.8947}$	0.981
C. acutus (12)	13.4-61.8	57-6115	$W = 0.0263L^{2.9730}$	0.995
Calculated from above relationships			$A = 11.7384W^{0.6373}$	1.0
Snakes:				
Nerodia sipedon[1]			$A = 14.17W^{0.679}$	
Pelamis platurus[1]			$A = 12.78W^{0.717}$	

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[1] From Dunson (1978)

Table 7. Weight changes of crocodiles completely immersed in sea water.

Species	Salinity, ppt	Days	Body weight, kg	Weight change, %/day
C. porosus:	fasting			
	35	14	28.6	-0.16
	35	14	11.3	-0.26
	35	14	1.9	-0.23
	35	14	1.8	-0.38
	35	14	1.6	-0.38
	35	9	1.2	-0.46
	35	14	1.2	-0.31
C. acutus:	fed live minnows			
	35	6.4	0.29	-1.39
	35	6.4	0.22	-1.52
	18	5.7	0.29	+0.21
	18	5.7	0.22	+0.37

Table 8. Maintenance of body weight by small *C. acutus* offered a choice between land and water. Fed every two days with fish, starting October 31, 1979. 100% sea water is 35 ppt.

Salinity, ppt	Days	Change in body weight, %/day no. 1	no. 2	no. 3	no. 4	Mean
0	8	+0.14	+0.55	+0.59	+0.49	+0.44
9	14	+2.45	+1.83	+3.25	+2.45	+2.50
17.5	14	+0.18	-0.07	-0.31	+0.42	+0.06
17.5	14	+1.83	+1.36	+2.19	+2.60	+2.00
26	14	+0.40	+0.18	-0.39	+0.88	+0.07
35	7	-1.25	-0.69	-0.61	-1.62	-1.04
9	14	+2.89	+3.00	+3.99	+2.83	+3.18
26	14	-0.47	-0.35	-0.52	-0.62	-0.49
17.5	14	+1.27	+0.65	+2.01	-0.27	+0.92
17.5	14	-0.22	+0.15	+0.88	+1.07	+0.47
17.5	14	+0.12	-0.16	+1.98	+0.55	+0.62
0	6	+1.17	+2.63	+2.55	+3.03	+2.35
Initial age, months		15.5	3.5	3.5	3.5	
Initial weight, grams		484	116	98	115	
Final weight, grams		1054	240	293	273	

Table 9. Water and cation content of possible hatchling crocodile food items collected near the study nest site, Florida Bay. Mean ±SD.

Item	N	Individual weight, g	% water	Cation content, µmoles/g wet wt	
				Na	K
Invertebrates					
Isopod	4	0.042 ±0.008	80.0 ±1.7	402 ±38	99 ±67
Adult dragonfly (*Erythrodiplax berenice*)	3	0.054 ±0.004	70.5 ±1.3	205 ±38	106 ±7
Fiddler crab (*Uca* sp.)	1	1.47	69.9	195	54
Earwig	3	0.049 ±0.023	74.9 ±3.0	186 ±106	76 ±43
Earthworm	6	0.247	85.3	190	36
Fish:					
Sailfin molly (*Poecilia latipinna*)	6	0.355	76.6	103	117
Silverside (*Menidia beryllina*)	10	0.180	78.0	90	97
Sheepshead minnow (*Cyprinodon variegatus*)	5	0.336	77.5	111	54
Gulf killifish (*Fundulus grandis*)	2	1.0	75.0	98	89

Table 10. Total evaporative water loss of crocodiles (*C. acutus*) and mangrove snakes (*N. f. compressicauda*) (expressed as % initial weight lost/day) in air (at 30°C) pumped at 300 ml/min. Mean ±SD (days tested).

Body weight, g	Evaporative loss at relative humidities listed		
	0%	75%	96.5%
C. acutus			
81			-1.55 ± 0.17(4)
84			-1.33 ± 0.32(6)
326	-1.24 ± 0.08(4)	-0.63 ± 0.13(3)	-0.27 ± 0.02(4)
995	-0.69 ± 0.13(7)		
1544	-0.47 ± 0.05(5)		
N. f. compressicauda			
55			-0.55 ± 0.45(4)
69			-0.35 ± 0.13(6)
152			-0.21 ± 0.11(5)

Appendix 1. Crocodilians handled in Florida Bay.

Table	Item	Identification	Date
1	<u>Alligators: summer, 1978</u>		
		MN873	7/26/78
	Taylor River	MN827	8/19/78
1	<u>Crocodiles: summer, 1978</u>		
	Taylor River	ME421	8/19/78
	Cocoa Point	A9-12,15-16	7/26/78
	"	A13-14,A20	8/1/78
	"	A20-21	8/8/78
	Alligator Bay	B3-4	7/30/78
	Black Betsy Beach	H1,3,4,6,7,11,14	7/30/78
	"	H10,16,17	8/15/78
	Trout Cove	K1	8/8/78
1	<u>Crocodiles: summer, 1979</u>		
	Black Betsy Beach	H19-25	8/7/79
	Dead Stork	M1,3-7	8/6/79
1	<u>Crocodiles: winter, 1979</u>		
	Davis Creek	SE42,55,65,78; ME251	2/6-2/21/79
3	<u>Crocodile cloacal fluid composition</u>		
	Black Betsy Beach	H3,11	7/30/78
	Cocoa Point	A13	8/1/78
	Trout Cove	K1	8/8/78
	Dead Stork	M4,6,8,10; 317	8/16/78
	Davis Creek	SE78	2/15/79
	"	SE42	2/21/79
4	<u>Crocodile urate ion content</u>		
	Black Betsy Beach	H18-25	
	Davis Creek	SE42	2/21/79
	"	SE78	2/15/79