

Salinity Relations of Crocodiles in Florida Bay

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Studies were carried out to determine the importance of high salinity as a limiting factor to the Florida Bay population of *Crocodylus acutus*, since hatchlings in captivity are unable to survive in sea water. Na, K, Cl and osmotic pressure were measured in samples of plasma and cloacal fluid. The ion and uric acid content of solid cloacal excretions was also determined. Na influx and efflux of small crocodiles submerged in sea water and of isolated skin keratin were measured. The relationships between snout-vent length, body mass and surface area were estimated. It was found that the head-neck, tail, legs and body regions each account for about one-fourth of the total area. Studies were conducted on hatchling crocodiles of evaporative water loss, behavioral osmoregulation and on the water and ion content of possible food items. Wild hatchlings have a plasma osmotic pressure near 330 mOsm, a level typical of vertebrates. Body Na influx and efflux are quite low; there is a net uptake in sea water of about 9 μ moles/100 g body mass hr. The skin is probably very low in Na permeability. There is a substantial loss of water from fasting hatchling crocodiles submerged in sea water (35‰) or held in moist air. Feeding is an important means of balancing these water losses. When fed fish ad lib. and kept in an aquarium divided into land and water portions, most small (100-480 g) crocodiles maintained body mass at salinities up to 17.5‰ (50% sea water). Some even gained mass at 26‰. Field data from Florida Bay tend to confirm that *C. acutus* hatchlings are intolerant of 35‰ (100%) sea water.

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 crocodylians there are several species which are regularly observed in estuaries and even in the open sea. However only *Crocodylus porosus* hatchlings have been shown to be capable of growth in sea water (Grigg et al., 1980). *C. porosus* possesses lingual salt glands and these extrarenal organs appear to be extremely important in eliminating excess Na (Taplin and Grigg, 1981; Grigg, 1981). The American crocodile, *C. acutus*, also has lingual salt glands (L. E. Taplin et al., pers. comm.), but their quantitative significance in osmoregulation remains uncertain. Hatchling *C. acutus* in captivity are intolerant of full strength sea water, and there are as yet only fragmentary field data regarding survival and growth in highly saline areas (Dun-

son, 1970; Evans and Ellis, 1977; Ellis, 1981; Moore, 1953; Ogden, 1978). The question of the ability of *C. acutus* hatchlings to osmoregulate in sea water thus assumes considerable importance in the effort to maintain the Florida Bay population.

The purpose of the present study was to examine the physiological effects of high salinity on young *C. acutus*. 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, body mass 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 with 24 hr. 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 F. Mazzotti and J. Kushlan (pers. comm.) in a study of population ecology, movements and growth. In one case, hatchlings were removed directly from a nest that was under study by P. Patty and J. Kushlan (pers. comm.). 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 desiccator (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 mass 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 (84, 87, 100 and 413 g) in 100% sea water. $^{22}\text{NaCl}$ (New England Nuclear) was added to 2 l of sea water at a specific activity of 0.175 mCi/liter. For influx measurements the crocodiles were placed in 2 l radioactive sea water for 5 hr; 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 the 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 l 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. These studies were conducted between 25 Sept. and 7 Oct. 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 (Dunson, 1967) programmed into a HP 67 calculator. The influxes were calculated for the period between one and five hours after placement in radioactive sea water. Effluxes were computed over a four to ten day interval after transfer into non-radioactive sea water.

^{24}Na influx across the skin keratin of *C. acutus* was measured in vitro in glass chambers designed by Dunson (1978). A crocodile (ca 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 cm²) between two glass disks separating 1 ml radioactive sea water (35‰) on the outside and 10 ml reptile Ringers solution (Dunson, 1978) on the inside. $^{24}\text{NaCl}$ was prepared by neutron activation in the Breazeale nuclear reactor and added to sea water at specific activities of 13-20 $\mu\text{Ci/ml}$. Over a 22-23.5 hr period, four 1 ml 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 10⁷ count/min. 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 crocodylians was estimated by carefully skinning 13 specimens of *C. acutus* (4), *C. porosus* (8) and *Caiman* sp. (1), and tracing the outline of the spread skins on graph paper. These outline drawings were cut out and their masses compared with masses of known areas to determine skin surface area. The surface areas were related to a linear dimension, the snout-vent length, which ranged from 11.1 to 38.5 cm. The length-mass relationship for *C. acutus* was determined separately on 12 live specimens (13-62 cm snout-vent length, 57-6,115 g). An HP67 power curve program (SD 03A) was used to calculate the equations.

TABLE 1. SUMMER (30 JULY–19 AUG. 1978, AND 6–16 AUG. 1979) AND WINTER (11 JAN.–21 FEB. 1979) PLASMA CONCENTRATIONS OF ALLIGATORS AND CROCODILES IN FLORIDA BAY. Mean \pm SD.

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

¹ On northern Key Largo along Barnes Sound.

A primitive but effective means of estimating the general fitness of reptiles to survive in a saline environment is to follow mass 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, 1981). In the present study an attempt was made to evaluate the effect of feeding on mass 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‰) or 100‰ (35‰) sea water for about six days and fed live minnows. Later, four crocodiles were placed in either 50 \times 27 \times 31 cm or 75 \times 32 \times 48 cm aquaria (length \times width \times 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 choose 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.

Evaporative water loss in dry air was measured by the same technique used by Dunson et al. (1978). Small crocodiles (less than 400 g) were placed in desiccators (20 cm diameter) in a refrigerated incubator. Air from a pump at 300 ml/min passed through a drierite column into the chamber, and then through another drierite column. This second column was weighed to determine water loss. Over a six day period at 30 C in dry air, the body mass loss of one crocodile was equal to the amount of water lost and collected in a drierite column. To provide relative humidities of 75 and 96.5%, the initial drierite column was replaced by two flasks of saturated NaCl or K₂SO₄ 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. The actual humidity of the air flowing into the chambers was verified by absorption in a drierite column.

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 (Fig. 1) at salinities ranging from fresh water to hypersaline (0–43‰). 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). F. Mazzotti and J. Kushlan (pers. comm.) have observed 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 (22–34‰; Table 1). However many hatchlings were found on land during the first few weeks, hiding in holes or in clusters of mangrove roots.

The level of plasma Na from hatchlings removed from a nest on Black Betsy Beach (Table 1) was 150 mM and the osmotic pressure 327 mOsm, 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 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).

Hatchling *C. acutus* rapidly disappear from the vicinity of their nest sites. Whether this is

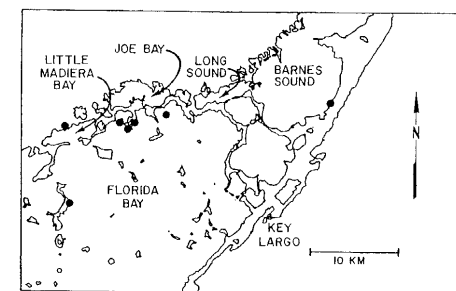


Fig. 1. Locations in southern Florida at which *C. acutus* were captured for blood and cloacal sampling.

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. Its plasma was "normal" as was that of four other animals of similar size from the same locality (Table 1). The single adult sampled and two alligators also had plasma osmotic pressures similar to those of the younger crocodiles sampled.

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. Cloacal fluid osmotic pressure was always equal to or less than that of the plasma (Table 2). A striking result is the extremely low Na concentration (12–21 mM) of cloacal fluid in comparison with plasma (106–166 mM); Cl was usually much higher than Na. Na, Cl and K account for a much smaller percentage of the osmotic pressure in cloacal fluid than they do in plasma.

Fecal 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 liquid and solid portions of the cloacal excretions of *C. acutus* and *C. porosus* (Table 3). There was no apparent relationship to the salinity treatment, at least in the present small sample.

Na exchange in sea water.—Three of the four crocodiles had a mean Na influx in sea water

TABLE 2. A COMPARISON OF CLOACAL FLUID (CF) AND PLASMA (PL) CONCENTRATIONS OF *C. acutus* FROM FLORIDA BAY. Mean \pm SD. Ages 1–180 days.

Water salinity, ‰	N	Sample	Concentrations			
			mM			π , mOsm
			Na	Cl	K	
20–26	5	PL	125 \pm 21	115 \pm 17	5.0 \pm 1.5	325 \pm 10
	5	CF	18 \pm 3	71 \pm 41	9.2 \pm 14.6	278 \pm 49
31–43	2	PL	136 \pm 42	130 \pm 3	5.5 \pm 5.0	350 \pm 10
	3	CF	14 \pm 3	88 \pm 39	25 \pm 23	281 \pm 9

of 11.5 \pm 2.7 μ moles/100 g hr with a fourth higher point of 37 μ moles/100 g hr (mean \pm SD). The Na efflux was 2.3 \pm 1.8 μ moles/100 g hr. Overall rates of Na exchange in *C. acutus* placed in sea water are quite low. The influx exceeds the efflux by about 9 μ moles/100 g hr suggesting that there is a low but significant net uptake of Na when small fasting crocodiles are submerged in sea water. For the purposes of these flux calculations the body Na content of crocodiles was assumed to be 50 μ moles/g wet mass. In one determination on a 56 g hatchling that was killed by a cage mate, the actual value was 39.1 μ moles Na/g wet mass (10.9 μ moles K/g wet mass 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) gave values of 52 and 69 μ moles/g wet mass for two crocodiles in 25‰ sea water.

Skin area.—The “standard” surface area (A) to mass (M) equation used by many investigators

($A = 10M^{0.67}$) (Minnich, 1979) has not previously been verified for crocodilians. The relations between area and snout-vent length (L), and mass and snout-vent length were separately determined in this study $A = 1.16L^{1.89}$; $M = 0.026L^{2.97}$; $r^2 > 0.98$). The calculated surface area to mass relation was then found to be: $A = 11.7M^{0.64}$. 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 mass have a lower surface area than snakes (Dunson, 1978), due to 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.

TABLE 3. SODIUM AND POTASSIUM CONTENT OF CROCODILE CLOACAL EXCRETIONS. Mean \pm SD.

Salinity, ‰	N	Mass, g	Days acclimated	Ion content of urates, μ moles/g dry mass		[Fluid] mM	
				Na	K	Na	K
<i>C. acutus</i> caught in Florida Bay:							
In nest	4	~65	—	96 \pm 85	240 \pm 186	—	—
20	1	355	—	11	478	—	—
31	1	470	—	39	1,111	—	—
<i>C. acutus</i> in captivity:							
0	4	3,416 \pm 1,879	>50	24 \pm 16	401 \pm 344	4 \pm 2	29 \pm 18
35	1	5,780	28–38	20 \pm 14	532 \pm 64	5 \pm 2	45 \pm 16
<i>C. porosus</i> in captivity:							
0	3	2,672 \pm 951	>50	43 \pm 48	393 \pm 1	2 \pm 2	28 \pm 17
35	2	3,928 \pm 392	13–34	7 \pm 4	671 \pm 501	2 \pm 1	45 \pm 16

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. 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 μ moles/cm²hr), demonstrating the proper functioning of the chambers.

Mass changes in saline water.—Hatchling *C. acutus* and *C. porosus* lose mass rapidly (about 1.7%/day) when fasting and immersed in 35‰ sea water (Dunson, 1970). As size increases, the rate of mass loss diminishes in *C. acutus* (Dunson, 1970; Ellis, 1981). In six *C. porosus* mass losses of fasting animals between 1.2 and 11.3 kg were similar (0.34 \pm 0.09%/day). One larger animal (29 kg) has a lower rate of loss (0.16%/day). If small *C. acutus* are forced to remain immersed in 35‰ sea water, they cannot maintain their mass even when fed. Two animals weighing 220 and 290 g lost 1.5 and 1.4%/day respectively. Yet in 18‰ they gained mass when fed (0.2 and 0.4%/day).

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‰ sea water. Under these conditions mass gains usually occurred with access to 50‰ sea water (17.5‰) (Fig. 2). Small gains or losses took place with access to 75‰ sea water (26‰). Feeding greatly diminished when the water was changed to 100‰ sea water (35‰) and large amounts of mass were lost.

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 often 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 (F. Mazzotti and J. Kushlan, pers. comm.). These areas have lower salinities and appear to provide more favorable

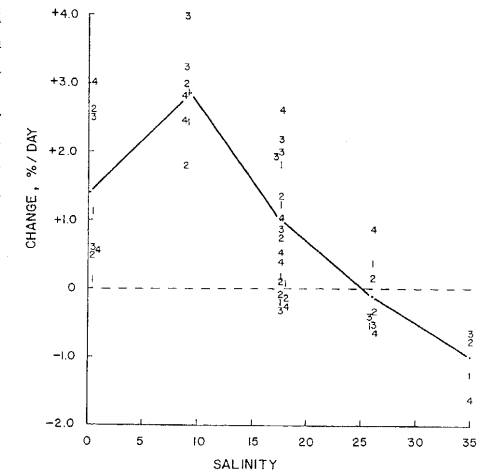


Fig. 2. Changes in body mass by four small *C. acutus* offered a choice between land and water of different salinities (in ‰) and fed fish. Crocodile 1 was initially 484 g; the other three were 98–116 g. The solid line connects mean values for observations on individuals 1 through 4.

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 F. Mazzotti and P. 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 3–4 Aug. approximately 30 eggs hatched (P. Patty, pers. comm.). On the night of 6 Aug., eight hatchlings were caught in the nearby channel at a salinity of 32‰, marked and released. On 16 Aug. seven hatchlings, including three unmarked ones, were caught at night in the channel at a salinity of 40‰. 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 8 Sept. during the daytime, a thorough search was made of the mangroves along the channel and no crocodiles were found. Water (30‰)

TABLE 4. WATER AND CATION CONTENT OF POSSIBLE HATCHLING CROCODILE FOOD ITEMS COLLECTED NEAR THE STUDY NEST SITE, FLORIDA BAY. Mean \pm SD.

Item	% water	Cation content, μ moles/g wet mass	
		Na	K
Invertebrates:			
Isopod	80.0 \pm 1.7	402 \pm 38	99 \pm 67
Adult dragonfly (<i>Erythrodiplax berenice</i>)	70.5 \pm 1.3	205 \pm 38	106 \pm 7
Fiddler crab (<i>Uca</i> sp.)	69.9	195	54
Earwig	74.9 \pm 3.0	186 \pm 106	76 \pm 43
Earthworm	85.3	190	36
Fish:			
Sailfin molly (<i>Poecilia latipinna</i>)	76.6	103	117
Silverside (<i>Menidia beryllina</i>)	78.0	90	97
Sheepshead minnow (<i>Cyprinodon variegatus</i>)	77.5	111	54
Gulf killifish (<i>Fundulus grandis</i>)	75.0	98	89

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‰ on 16 Aug. 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 4. 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 mass 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 5). Indeed the mass 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‰ 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 to 1.04 to 0.71%/day respectively. 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

TABLE 5. TOTAL EVAPORATIVE WATER LOSS OF CROCODILES (*C. acutus*) AND MANGROVE SNAKES (*N. f. compressicauda*) (EXPRESSED AS % INITIAL MASS LOST/DAY) IN AIR (AT 30 C) PUMPED AT 300 ML/MIN. Mean \pm SD (days tested).

Body mass, g	Evaporative loss at relative humidities listed		
	0%	75%	96.5%
<i>C. acutus</i>			
81			-1.55 \pm 0.17 (4)
84			-1.33 \pm 0.32 (6)
326	-1.24 \pm 0.08 (4)	-0.63 \pm 0.13 (3)	-0.27 \pm 0.02 (4)
995	-0.69 \pm 0.13 (7)		
1,544	-0.47 \pm 0.05 (5)		
<i>N. f. compressicauda</i>			
55			-0.55 \pm 0.45 (4)
69			-0.35 \pm 0.13 (6)
152			-0.21 \pm 0.11 (5)

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% mass/day. In a 326 g 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

Fasting *C. acutus* lose large amounts of water whether submerged in sea water or on land. Cloacal fluid and urates contain little Na. Na excretion in 35‰ sea water is low, mainly due to the impermeability of the skin, yet a significant net uptake of Na may occur. This is surprising in view of the recent finding that *C. acutus* has a lingual salt gland (L. E. Taplin et al., pers. comm.). 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. However it seems highly unlikely that hatchling *C. acutus* can live and grow in areas with sustained salinity levels above 30‰.

Recent studies by W. Magnusson (pers. comm.), Grigg (1977, 1981), and Grigg et al. (1980) have shown that *C. porosus* live both in fresh water and in highly saline regions in northern Australia. A lingual salt gland allows excretion of excess NaCl, but the actual secre-

tory capacity of the glands remains to be quantified (Taplin and Grigg, 1981). L. E. Taplin et al. (pers. comm.) have succeeded in stimulating the lingual glands of *C. acutus* to secrete approximately 0.5 M NaCl by the injection of mecholyl. The lingual glands of *C. acutus* may secrete at a relatively slow rate. Preliminary measurements of secretory rates gave a value of about 14 μ moles/100 g hr (L. E. Taplin et al., pers. comm.), a figure near the lower end of the range for marine reptiles (Dunson, 1979). It is possible that the lingual salt glands in *C. acutus* are of limited significance in overall ion balance. Otherwise it is hard to understand why Na effluxes obtained by Evans and Ellis (1977) and in the present study were so low. A similar situation occurs in some terrestrial birds where nasal salt glands appear to be functional, but of little osmoregulatory significance (Johnson, 1969; Dunson et al., 1976). Considerably more study is needed of the routes of loss of Na from *C. acutus* of different ages exposed to various levels of dehydration and to Na loading.

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. Ellis (1981) reports plasma Na of three subadult *C. acutus* caught in 91–100% sea water to be 141–174 mM. 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, 1981) 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 ob-

tained by introducing hatchlings into a fenced area that duplicates the natural habitat, and observing any plasma changes in relation to different salinity regimes.

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 only 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. 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 (Minnich, 1979). The content of Na is generally low; K is much higher and varies from about 1,000 μ moles/g dry mass in carnivorous reptiles to about 4,000 in certain herbivorous ones. 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 μ moles/100 g hr in fresh water and 5.6 μ moles/100 g hr 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 μ moles/100 g hr. 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 no salt gland is secreting. The smallest functional salt gland yet described in reptiles is that of the snake *Cerberus rhynchops*, which secretes Na at about 16 μ moles/100 g hr (Dunson and Dunson, 1979). More specialized sea snakes and turtles have rates in excess of 100 μ moles Na/100 g hr (Dunson, 1979).

Na influx of *C. acutus* in 100% sea water was higher than the efflux. It appears that a substantial net uptake of about 9 μ moles/100 g hr 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 μ moles/100 g hr respectively (Dunson and Robinson, 1976). When the salt gland is stimulated, the efflux can rise to 140 μ moles/100 g hr. *C. acutus* has salt glands but their overall role in osmoregulation is yet to be determined. We need a series of influx and efflux determinations on *C. acutus* 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.

It appears likely that the skins of many aquatic reptiles are very low in permeability to Na (Dunson, 1978, 1979; Dunson and Robinson, 1976). *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 crocodil-

ians has never previously been measured. It is common practice to use the equation $A = 10M^{0.67}$ (Schmidt-Nielsen and Skadhauge, 1967; Bentley and Schmidt-Nielsen, 1965, 1966). In this study the actual relation was found to be $A = 11.7M^{0.64}$; agreement of these two equations is remarkably close.

The first measurements of mass loss of fasting *C. acutus* immersed in sea water were made by Dunson (1970). Small animals (mean mass 86 g) lost 1.7%/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% mass/day (Dunson, 1979), small fasting crocodiles do not appear capable of surviving long in 100% sea water. Small (101 g) *Caiman crocodilus* do even poorer; they lost 6.8% mass day in 3.3% NaCl (100% sea water is approximately equivalent to 3.5% NaCl) (Bentley and Schmidt-Nielsen, 1965). Even when fed, two young *C. acutus* (220 and 290 g) still lost 1.5 and 1.4% mass/day when completely immersed. However as size increases, mass 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 mass loss when immersed in full strength sea water. Ellis (1981) has also measured rates of loss in a large range of body sizes of *C. acutus*; body mass was roughly inversely related to the rate of mass loss.

To provide a 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 mass at salinities as high as 26‰ (75% sea water). Larger mass gains occurred at 17.5‰ (50% sea water). About 1% mass/day was lost at 35‰ (Fig. 2). 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‰ 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 4).

Observations of hatchling crocodiles in Florida Bay show that they spend considerable amounts of time out of water. Thus it was 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 5). 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% mass/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% mass/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 5). 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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Buoyancy Studies of Notothenioid Fishes in McMurdo Sound, Antarctica

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Measurements of buoyancy on 11 species of notothenioid fishes from McMurdo Sound, Antarctica indicate that they range from neutrally buoyant to relatively heavy. Since these fishes lack a swim bladder, reduction in body weight is accomplished primarily through low levels of skeletal mineralization and lipid deposition. Neutrally buoyant species have ash contents of less than 1% of the body weight. There is no reduction in the percentage of body weight occupied by musculature. Lipid (triglyceride) deposits provide static lift in neutrally buoyant species; these deposits are contained in large connective tissue sacs or in typical adipose cells located subcutaneously as well as intermuscularly. As judged by low percentage weight and negative buoyancy, the liver is not an organ of buoyancy. Measurements of buoyancy and morphological studies allow recognition of species associated with pelagic, cryopelagic, benthopelagic and benthic habitats.

AT 77° south latitude, McMurdo Sound, Antarctica is the most isolated and uniformly cold marine environment in the world, with a mean annual water temperature of -1.87°C (Littlepage, 1965). A unique group of 90-100 species of perciform fishes is found in this environment (DeWitt, 1971). These fishes of the Notothenioidei are highly endemic with 86% of the genera and 95% of the species confined to Antarctic waters (DeWitt, 1971). No-

tothenioids are hypothesized to have been derived from a bottom dwelling perciform approximately 40 million years ago (Regan, 1914; Norman, 1938; DeWitt, 1971). Paleontological study of planktonic foraminiferal assemblages indicates that about this time substantial Antarctic sea ice began to form resulting in a rapid drop in water temperature (Kennett, 1978). Low water temperatures, extreme geographic isolation and lack of south