

TABLE 2. NUMBER OF YEARS TURTLES MARKED IN 1965 WERE PART OF THE POPULATION BEFORE THEY WERE COLLECTED DEAD OR NO LONGER COLLECTED.

Number of years turtles part of the population	Number of turtles collected dead	Number of turtles no longer collected	Number of years turtles part of the population	Number of turtles collected dead	Number of turtles no longer collected
1	2	0	14	0	10
2	9	28	15	0	5
3	7	16	16	0	7
4	14	12	17	0	1
5	9	20	18	0	0
6	12	10	19	2	4
7	12	5	20	0	0
8	17	4	21	0	2
9	4	4	22	0	2
10	0	1	23	0	4
11	2	3	24	0	9
12	2	6	25	0	0
13	2	5			

that a turtle spends in each age class (by definition, age class 1 lasts for nine years; by 1989, classes 2 and 3 each have a known duration of at least 25 years). Of the turtles still alive in 1989, the five class 2 turtles are estimated to be from 27 to 34 years of age; the 17 class 3 turtles range from an estimated 36 to 59 years of age. At last capture, all appeared in good physical condition externally and presumably could live for some time. This is similar to the estimates of 50 to possibly 80 years reported for *T. carolina* (Nichols, 1939; Stickel, 1978; Williams and Parker, 1987).

Dead individuals.—By 1989, 94 turtles (26% of the original population) had been collected dead (Fig. 1). The approximate age classes and sexes are given in Table 1.

How long each turtle was a member of the population before it was collected dead is shown in Table 2. Because we and our dogs covered the study area regularly, we feel that the year the turtle was collected dead indicates the year of death. Except for the two turtles found dead during the year they were marked, the remaining dead turtles are believed to have been permanent residents in the study area.

Transient individuals.—Ninety-two turtles (25% of the original population) are considered transients because they were never collected after the year of marking (Fig. 1). Their approximate age classes and sexes are given in Table 1. Juveniles and young adults predominated; males were more common than females. These age

classes and sex ratios agree with our previous findings that apparently some juvenile turtles move about before establishing a home range and some young adult males (presumably in the early years of sexual activity) undertake extensive movements (Schwartz et al., 1984).

We know that new individuals come into the population as transients, as young produced in the area, or as neighbors that have home ranges along the boundary. We also know that some of these immigrants remain to become permanent residents, some move on through the environment as transients, and some return to that portion of their home range beyond the borders of the study area (Kiestler et al., 1982). There is always the possibility that some of the turtles we assume left the population the year after marking may have died in the study area and were not recovered, but it seems more likely that most represent a transient segment.

Stickel (1978) and Williams and Parker (1987) consider that turtles captured only in the first year of a long-term study are transients; the latter authors report that transients comprise a substantial portion of the population and that many seem to be younger, growing individuals.

Individuals of unknown fate.—By 1989, 158 individuals (43% of the original population) were not accounted for (Fig. 1). The approximate age classes (based on the age at last capture for each turtle) and sexes are given in Table 1. These are more comparable to the age classes and sexes of dead individuals than they are of transients. Because these turtles lived in the study

area for periods varying from two to 24 years (Table 2), they are considered permanent residents.

It is possible that some of these turtles are still alive. To estimate this hypothetical number, we arbitrarily selected all turtles collected in the four years preceding 1989 (that were not taken in 1989) as potential members of the population. However, their actual existence cannot be verified until they are collected again. These 17 potential members occupied home ranges in the study area varying from 1.7 to 9.3 ha—comparable to the size of the home ranges of known members of the surviving population.

The continual loss of turtles to an unknown fate (an average of six per year) appears to represent undetected death. In a previous study (Schwartz and Schwartz, 1974), 68% of known deaths in the study area were related to hibernation; it is possible many turtles died underground during hibernation and were not recovered.

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- ELIZABETH R. SCHWARTZ AND CHARLES W. SCHWARTZ, 3637 Valhalla Road, Coeur d'Alene, Idaho 83814. Accepted 20 Sept. 1990.

GROWTH OF JUVENILE ALLIGATORS IN PAR POND, SAVANNAH RIVER SITE, SOUTH CAROLINA.—Growth rates and changes in growth with age and size are important life-history characteristics. Growth rates of numerous reptiles including alligators are known to vary geographically as well as by habitat and individual (see Andrews, 1982 for review). In addition to being important for construction of population models, examining patterns of growth within and among populations can help to access the suitability of different habitats.

The American alligator (*Alligator mississippiensis*) occurs in a wide range of aquatic habitats throughout the southeastern United States from North Carolina to Florida and west into Texas. Although the best studied of the crocodylians (Brisbin et al., Savannah River National Environmental Research Park, unpubl.), limited published data are available on patterns of growth of wild individuals. The majority of these studies have been conducted in Louisiana (McIlhenny, 1935; Chabreck and Joanen, 1979) and Florida (Hines et al., 1968; Fogarty, 1974). In addition, a number of unpublished studies have been conducted in North Carolina (Fuller, 1981) and South Carolina (Bara, South Carolina Wildlife and Marine Resources Department, unpubl.; Murphy, 1977). These studies have shown great variability in growth rates and age at maturity of alligators from different geographic areas, and habitats, and among different ages, sizes, and sexes. Because of this variability, population models (and harvest schedules based on these models) based on data from one area may not be applicable to other areas. More detailed information on the extent and pattern of variability in growth rates within and among populations is needed. This study reports on growth of juvenile alligators in Par Pond, Savannah River Site, South Carolina, a location in the northern third of the alligator's range where limited data on alligator growth are available.

Methods.—This study was conducted on Par Pond, an 1120 ha cooling reservoir located on the Department of Energy's Savannah River Site in Barnwell County, South Carolina (Gibbons and Sharitz, 1981). Par Pond received thermal effluent from R-reactor (into the North Arm) from 1961 to 1964 and from P-reactor (into the

TABLE 1. SIZE DATA OF KNOWN-AGE ALLIGATORS FROM PAR POND, SOUTH CAROLINA. Age is in months. Values are means \pm SD (range).

Age	Month	Sample size	TL (cm)	SVL (cm)	°	Mass (g)
0	Sep	220	24.5 \pm 1.42 (20.3–36.6)	11.9 \pm 0.62 (10.0–13.5)		50 \pm 7.1 (27–67)
8	May	7	36.2 \pm 5.40 (24.1–26.9)	17.6 \pm 2.54 (15.0–22.9)		128 \pm 52.0 (86–240)
9	Jun	37	30.7 \pm 5.56 (28.0–36.7)	15.3 \pm 1.13 (13.6–18.3)		73 \pm 22.5 (45–116)
10	Jul	12	33.1 \pm 3.43 (28.0–38.7)	16.2 \pm 1.66 (13.5–18.8)		87 \pm 27.8 (50–134)
11	Aug	28	53.8 \pm 2.41 (47.4–58.0)	25.8 \pm 1.01 (23.5–27.8)		342 \pm 58.4 (250–485)
13	Oct	26	56.2 \pm 7.47 (33.2–65.2)	27.1 \pm 3.52 (16.0–31.7)		424 \pm 137.0 (88–625)
22	Jul	29	70.0 \pm 10.75 (52.5–89.4)	32.5 \pm 3.98 (25.2–44.0)		691 \pm 276.0 (286–1658)
24	Sep	4	69.2 \pm 7.28 (62.0–77.0)	33.6 \pm 3.19 (30.5–36.5)		788 \pm 281.0 (550–1100)
25	Oct	18	69.4 \pm 17.69 (63.2–81.8)	35.5 \pm 2.67 (31.4–39.8)		849 \pm 286.0 (554–1150)
30	Mar	14	74.0 \pm 8.94 (56.0–89.2)	34.6 \pm 4.59 (23.5–39.5)		897 \pm 257.6 (446–1218)
34	Jul	19	79.7 \pm 8.38 (62.4–93.2)	38.6 \pm 4.23 (30.2–45.0)		1090 \pm 369.2 (500–1750)
45	May	9	83.7 \pm 7.89 (69.3–101.1)	40.8 \pm 4.13 (33.5–48.6)		1322 \pm 361.6 (784–2158)

Hot Arm) from 1959 to 1987. When P-reactor was operational, only the Hot Arm (approximately 10% of Par Pond) was affected. The remaining 90% (North Arm, West Arm, and Main Body) is essentially a warm monomictic lake. The effect of thermal effluent on alligators was examined by Murphy and Brisbin (1974) and Murphy (1977). During this study (May 1986–May 1989), thermal effluent was discharged into the Hot Arm only from May 1986–Aug. 1987.

Alligators were captured at night from an airboat by hand (<1.25 m) or by using a self-locking wire noose attached to PVC pipe. Hatchlings were captured at known nest sites within one week of hatching. All animals were weighed, measured (total length, TL, snout-vent length, SVL), given an individual mark by clipping scutes and released at the site of capture. Sex was determined for animals >35 cm by cloacal examination. When possible, animals were assigned a code, indicating the year and nest from which they hatched.

Timing of captures was as follows: prior to Oct. 1986; Oct. 1986; July 1987; March, July,

Sept. 1988; and May 1989. Most of the animals captured prior to July 1987 were less than one year old. Capture periods in July 1987, March 1988, July 1988, and May 1989 consisted of three consecutive nights. The entire surface of Par Pond was searched each night. Animals captured the first and second nights were held until the third night when all animals were released.

Relative condition factor (i.e. Cren, 1951) is a measure of the relative fitness of an individual and can indicate how well an animal is doing in its environment (Taylor, 1979). Condition factors are derived from the relationship between length and weight in the population in the form $K = M \times TL^{-b}$ where M = mass (g) and TL = total length (cm) and b is the slope of the regression of \ln length on \ln mass. If growth is isometric, $b = 3$. For this population $b = 3.2$; therefore, individual condition factors were calculated for all captures using the formula $K = M \times 10^{3/TL^{3.2}}$. A positive correlation has been shown to exist between condition factor and growth in largemouth bass (Cooper et al., 1963; Clugston, 1974), and Gibbons et al. (1978) ob-

TABLE 2. RELATIVE AND ABSOLUTE GROWTH RATES OF ALLIGATORS IN PAR POND. Values are means \pm SD (range). Age is in months.

Age	Sample size	Relative growth	Absolute growth (cm/yr)	
			SVL	TL
0–12	36	0.22 \pm 0.077 (0.02–0.33)	10.6 \pm 5.75 (0.7–19.4)	24.6 \pm 10.84 (6.0–41.2)
12–24	20	0.16 \pm 0.076 (0–0.37)	11.0 \pm 4.31 (3.5–23.8)	25.4 \pm 8.11 (15.0–49.5)
24–36	17	0.10 \pm 0.090 (0.01–0.37)	7.54 \pm 5.85 (0.7–22.9)	18.9 \pm 11.03 (6.0–47.8)
0–36	73	0.18 \pm 0.92 (0–0.37)	10.0 \pm 5.52 (0.7–23.8)	23.5 \pm 10.40 (6.0–49.5)

served seasonal variation in condition of bass as well as lower condition of bass under thermal stress. In addition, Taylor (1979) reported differences in condition of *Crocodylus porosus* from different habitats. If similar relationships exist between condition and growth and condition and habitat for alligators, it may help to explain the variability in growth rates within and among years and populations.

To take into account the difference in size between hatchlings and older animals, relative (or specific) as well as absolute growth rates were calculated for recaptured animals using the equations $(\ln SVL_2 - \ln SVL_1)/\text{days}$ and $(SVL_2 - SVL_1)/\text{days}$, respectively (Andrews, 1982). Days between captures were classified as "growth" (March to Oct.) or "no growth" (Oct. to March) days (Chabreck and Joanen, 1979) and growth expressed as SVL change per growth day. All analyses were done on SVL, but the equation to convert SVL to TL was also calculated ($TL = 1.881[SVL] + 4.673$, $r^2 = 0.996$, $n = 501$).

Results. Hatchling size measurements were based on data from 220 hatchlings from nine nests located during 1981–88. Hatchling sizes (TL, SVL, Mass) were significantly different among nests (Kruskal-Wallis, $P < 0.001$, $H = 153.191$, 159.184, and 166.71 for TL, SVL, Mass, respectively). In addition, sizes of animals of the same age but from different nests were significantly different (Kruskal-Wallis, $P < 0.001$).

Sizes of known-age alligators (Table 1) and growth rates (relative and absolute) of recaptured animals were based on 521 records for 177 nonhatchling and 220 hatchling alligators. Of these, 288 records were from 101 known-

age animals. Of the animals used for growth analysis, 54.4% were captured twice, 22.8% three times, 13.9% four times, 5.0% five times, 3.0% six times, 0% seven times, and 0.9% eight times. Capture intervals ranged from five to 2414 days with 26.8% of the capture intervals between five and 100 d, 11.5% between 101 and 200, 21.3% between 201 and 300, 15.8% between 301 and 400, 8.2% between 401 and 500, and 16.4% after more than 501 days.

Relative growth rates of animals one year of age or less were significantly different from those of animals one to two and two to three years (Kruskal-Wallis, $P < 0.0001$, $H = 23.254$), but absolute growth rates were not (Table 2). Relative and absolute growth decreased with average age and average size between captures until approximately 3.5–4 years of age or 40 cm SVL (80 cm TL) when absolute growth rates appear to increase slightly but relative growth rates appear to level off (Fig. 1).

There was no significant difference in relative or absolute growth rates of males and females ≤ 48 months (≤ 1 m TL). No comparisons between males and females older than 48 months were made because only four males older than 48 months were recaptured.

There was a significant linear relationship between age and size of animals of both sexes ≤ 36 months ($SVL = 0.852[\text{age}] + 11.967$, $P < 0.0001$, $df = 379$, $r^2 = 0.876$). The slope of the regression equation for animals ≤ 36 mo fell between the values reported by Murphy (1977) for the Hot and North arms of Par Pond and was not significantly different from either. The regression equation for females 0–103 months ($SVL = 0.725[\text{age}] + 14.643$, $P < 0.0001$, $df = 34$, $r^2 = 0.960$, Fig. 2) predicts that, if the size-age relationship remains the same, females

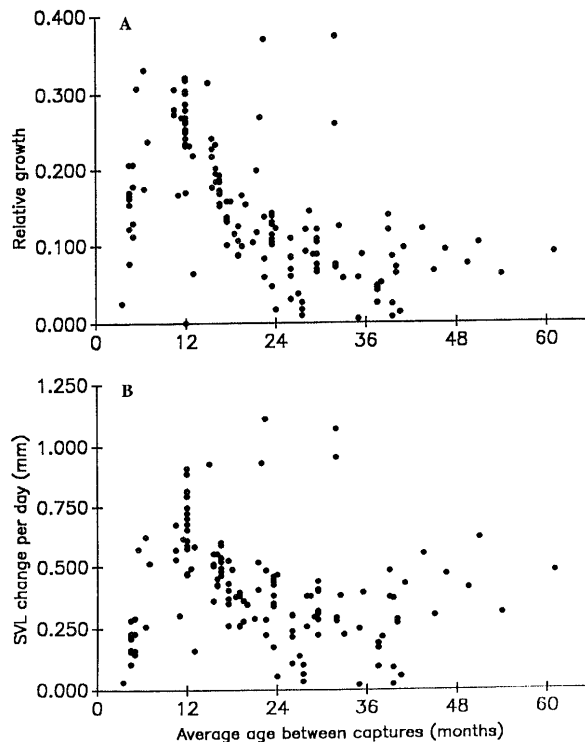


Fig. 1. Relationship between average age between captures and relative (A) and absolute (B) growth rates of juvenile alligators in Par Pond, South Carolina ($n = 202$).

will reach maturity (1.8–2 m; Joanen and McNease, 1975) at about 9–10 yr of age (predicted size at nine yr 184.6 ± 8.9 cm, at 10 yr 201.6 ± 10.1 cm). Condition factors for non-hatchling animals < 2 m were significantly different by month (ANOVA, Scheffe's multiple comparison, $P < 0.05$, $df = 232$, $F = 2.138$, Fig. 3) with June significantly higher than all other months and May significantly greater than July.

Discussion.—The mean yearly growth increment for all animals ≤ 36 mo (23.5 cm/yr TL) was similar to that reported by Murphy (1977)

for the same population (19.0 and 25.4 cm/yr for animals in the North and Hot arms, respectively). It was higher than that reported by Fuller (1981) in North Carolina (12.4 cm/yr), Bara (South Carolina Wildlife and Marine Resources Department, unpubl.) in South Carolina (16.1 cm/yr), and Deitz (1979) in north Florida (11.9–21.1 cm/yr), about the same as the 22.0 cm/yr reported by Chabreck and Joanen (1979) in Louisiana, and lower than yearly growth reported by McIlhenny (1935) in Louisiana (34.1 cm/yr) and Hines et al. (1968) in south Florida (31.0 cm/yr). The variation in yearly growth rates observed among popula-

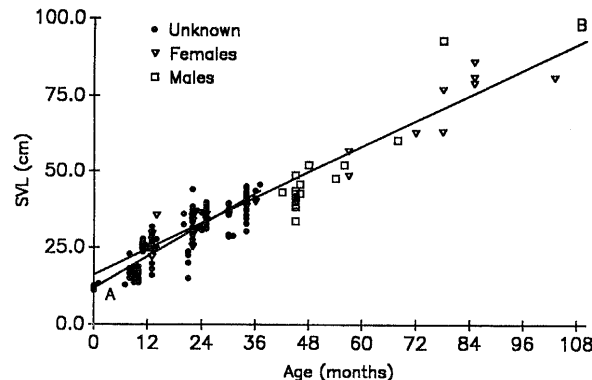


Fig. 2. Relationships between age and SVL for alligators in Par Pond, South Carolina ($n = 233$). Regression equations are for A, all animals ≤ 36 months, and B, female alligators 0–103 mo.

tions may be related to the geographic location, time of year of captures, size of the animals followed, clutch, yearly variation in density, and quality of the habitat.

Animals in northern areas experience a shorter annual activity period, and growth rates during this period may vary. Chabreck and Joanen (1979) reported that animals in Louisiana grew very little if at all from Oct. to March and had

highest growth rates during June and July. Animals in this study showed a similar pattern with average growth rates varying from 0 to 6.9 cm/mo depending on the time of year, with highest growth rates observed between May and Sept.

Condition factors are also variable with lowest values in the spring. The low spring values probably reflect the replenishment of energy reserves after the winter to a point at which

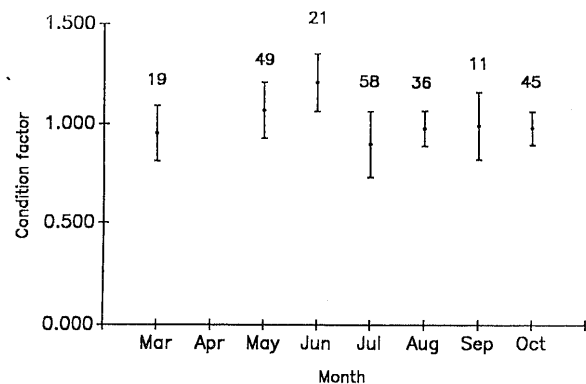


Fig. 3. Condition factor of nonhatchling alligators < 2 m captured in Par Pond from May 1986 to Oct. 1988. Number above values are sample sizes.

energy can be put into growth in length. The decrease in the condition factor in July reflects a combination of growth and a higher metabolic cost because of higher temperatures (Coulson and Hernandez, 1964). In the fall, as temperatures and metabolic cost begin to decrease, but food availability and consumption do not, condition again increases. A greater mass in the fall should increase the probability of winter survival and decrease the period in the spring when growth in length does not occur.

Undoubtedly, the number of days that an animal can grow will affect its yearly growth rate. It would be interesting to compare monthly patterns of growth of animals from areas with growing seasons of different lengths. Animals in areas with less extreme temperature fluctuations may show similar fluctuations in growth rates, or they may exhibit constant growth throughout the year.

The size of an animal followed will also affect the measured rate of growth. In this study, both absolute and relative growth rates decreased with age and size. Hatchlings had the highest relative growth. This was expected because it would be advantageous to grow as rapidly as possible during the first year to get to a less vulnerable size. The decrease in the rate of absolute growth from hatching to about 80 cm TL and the apparent increase after this point may be related to the availability and quality of food as well as physiological changes related to growth. Webb et al. (1978) and Abercrombie (IUCN Crocodile Specialist Group, unpubl.) reported a similar pattern of growth for *C. porosus* in Australia and *A. mississippiensis* in north central Florida, respectively. Abercrombie (IUCN Crocodile Specialist Group, unpubl.) speculated that at about 85 cm TL juvenile alligators may be able to exploit new/larger food resources, the result being an increase in the amount or quality of food and hence more fuel for growth.

It was not possible to directly access the affect of condition on growth rates. However, it would be interesting to examine this relationship particularly for animals of different ages. Do animals at four yr/80 cm TL size have a higher condition factor than animals in the next smaller size group? A positive relationship between condition factor and growth, and a higher condition factor of the larger animals, would support the idea that the larger animals have access to more or higher quality food.

It was also not possible to separate clutch affect in these analyses. However, preliminary in-

spection of available data on growth of animals from different clutches indicate that there are probably significant differences in growth rates among clutches, possibly related to incubation conditions or hatching size.

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- LAURA A. BRANDT, *Department of Biological Sciences, Florida International University, Miami, Florida, and Savannah River Ecology Laboratory, Aiken, South Carolina. Current address: Department of Wildlife and Range Sciences, University of Florida, Southwest Florida Research and Education Center, PO Drawer 5127, Immokalee, Florida 33934. Accepted 19 Sept. 1990.*

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RATHKE'S GLAND SECRETION BY LOG-GERHEAD (*CARETTA CARETTA*) AND KEMP'S RIDLEY (*LEPIDOCHELYS KEMPI*) SEA TURTLES.—Many aquatic turtles possess paired exocrine organs called Rathke's glands that open through pores in the axillary, inframarginal, and/or inguinal regions (Waagen,

1972; Ehrenfeld and Ehrenfeld, 1973). Predator repulsion, intraspecific communication, and shell maintenance are among the functions discussed for Rathke's gland secretions (Ehrenfeld and Ehrenfeld, 1973; and others). Weldon and Tanner (1990) suggested that these glands excrete metabolites such as lactic acid, which was found in high concentrations in the exudates of hatching loggerhead sea turtles (*Caretta caretta*). Other compounds, including lipids (Eisner et al., 1978; Weldon and Tanner, 1990; Weldon et al., 1990) and glycoproteins (Radhakrishna et al., 1989), have been characterized from the secretions of various species.

Rathke's gland fluids are reported to be released when turtles are injured or disturbed (Neill, 1948a; Goode, 1967), but little else is known of secretion discharge. We report here on two aspects of Rathke's gland secretion in marine turtles: (1) the volume of secretions released by hatching *C. caretta* and Kemp's ridley (*Lepidochelys kempi*) sea turtles, along with estimates of the amounts of some secretion components discharged; and (2) possible evidence of glandular discharge by adult turtles in the form of clearings on the shell around the gland duct openings.

Methods.—*Caretta caretta* and *L. kempi* hatched in July 1987 from eggs collected at Clearwater, Florida, and Rancho Nuevo, Mexico, respectively. Turtles were maintained as described in Radhakrishna et al. (1989).

Hatching *C. caretta* generally possess two Rathke's gland pores in the axillary/anterior inframarginal region and one in the inguinal region (Stromsten, 1917; cf. Waagen, 1972; Rainey, 1981; Fig. 1A). The two anterior pores receive secretions from one bilobed gland; the inguinal pore receives secretions from a separate gland (Stromsten, 1917). Hatching *L. kempi* possess six Rathke's gland pores, five on the posterior margins of inframarginal scutes, and one in the inguinal region (cf. Waagen, 1972; Fig. 1B). Each pore in *L. kempi* receives secretions from a separate gland.

The volume of Rathke's gland fluids discharged in response to electrical stimulation was measured individually in 10 *C. caretta* and 10 *L. kempi*, 39- and 36-weeks old, respectively. Turtles were removed from their containers, and their shells were lightly wiped with a paper towel. Individuals discharging secretions after wiping were not used as subjects. An electrical probe (described in Radhakrishna et al., 1989) was