Growth rates of the American crocodile (*Crocodylus acutus*): an analysis of regional and habitat related differences

*Tasa de crecimiento del caimán de la costa (*Crocodylus acutus*): un análisis de las diferencias entre regiones y hábitats*

Andrés E. Seijas

Universidad Nacional Experimental de los Llanos Ezequiel Zamora (UNELLEZ)
Guanare, Portuguesa. Venezuela.
Correo electrónico: aeseijas@gmail.com

ABSTRACT

The American crocodile (*Crocodylus acutus*) occupies aquatic environments ranging from freshwater to hypersaline. The current abundance and distribution of the species were affected by commercial exploitation and habitat destruction; which limits their use as criteria for assessing the quality of their habitat. Growth rate (GR) offers an indirect way to assess habitat quality. Herein, I analyzed 286 GR of *C. acutus* from different areas and environmental conditions. For crocodiles < 90 cm of total length (TL), the highest values of GR was found in Venezuelan rivers (0.110 ± 0.011 cm/day), followed for Turkey Point in Florida, USA (0.094 ± 0.012 cm/day). The lowest values of GR were estimated for areas with high salinities in Yucatan (Mexico) and Venezuela (0.050±0.010 and 0.045±0.006 cm/day, respectively). The von Bertalanffy growth model predicted the largest body sizes for two years old crocodiles in rivers of Venezuela and Turkey Point (86.9 and 86.4 cm in TL, respectively) but predicted size at year one was the highest for crocodiles from La Ventanilla, Mexico (73.1 cm), although GR declined sharply during the second year in that locality. The growth model predicts an asymptotic size of 439.0 cm for males in Florida. The asymptotic sizes for females from Florida and mangroves of Venezuela were 261.7 and 227.4 cm, respectively. Females would reach mature size close to 9 years in Florida and more than 16 years in mangroves areas of Venezuela. I discuss the ecological and conservation implications of these results.

Key words: Growth model, habitat quality, von Bertalanffy, sexual maturity, conservation.

RESUMEN

El Caimán de la costa (*Crocodylus acutus*) ocupa ambientes acuáticos que van de desde dulceacuícolas hasta hipersalinos. La abundancia y distribución actual de la especie fue afectada por la explotación comercial y la destrucción de hábitat, lo cual ha limitado el uso de estos dos parámetros poblacionales como criterios para evaluar la calidad de los ambientes que esta especie ocupa. La tasa de crecimiento (TC) ofrece una vía indirecta para evaluar la calidad de los hábitats. Analicé 286 TC de cocodrilos provenientes a diferentes regiones y hábitats. Para individuos <90 cm de longitud total (LT) las mayores TC fue para los ríos de Venezuela (0.110 ± 0.011 cm/día) y Turkey Point en Florida, E.U.A. (0.094 ± 0.012 cm/día). La TC más lenta fue para cocodrilos de áreas de alta salinidad en Yucatán (México) y Venezuela (0.050±0.010 y 0.045±0.006 cm/día, respectivamente). El modelo de crecimiento de von Bertalanffy predice las mayores tallas a los dos años para los cocodrilos de ríos de Venezuela y para Turkey Point (86.9 y 86.4 cm en LT, respectivamente). La mayor talla al año (73.1 cm) fue para los cocodrilos de La Ventanilla (México), aunque la TC decreció abruptamente en esa localidad al segundo año. El modelo de crecimiento predice un tamaño asintótico de 439.0 cm para los machos en Florida. Los valores asintóticos para las hembras de Florida y áreas de manglar en Venezuela es de 261.7 y 227.4 cm, respectivamente. Las hembras requerirían unos 9 años para alcanzar la talla adulta en Florida pero más de 16 para lograrlo en áreas de manglar de Venezuela. Se discute las implicaciones para la conservación de estos resultados.

Palabras clave: Modelo de crecimiento, calidad de hábitat, Von Bertalanffy, madurez sexual, conservación.

INTRODUCTION

The American crocodile (*Crocodylus acutus*) is the most widely distributed crocodilian of its genus in the Neotropics. This species occupies different aquatic environments in both the Pacific and Atlantic sides of the Americas. In the Atlantic drainage the species is found in the tip of the Peninsula of Florida, in southern Gulf of Mexico and the Yucatan Peninsula, and along the Caribbean coast of Guatemala, Belize, Honduras, Nicaragua, Costa Rica, Panamá, Colombia and Venezuela. The species is also found in the Caribbean islands of Cuba, Jamaica, and Hispaniola as well as in offshore cays and coral atolls. Along the Pacific Ocean, the American crocodile extends its distribution from northern Mexico to northern Peru (Ernst, Ross and Ross, 1999; Thorbjarnarson, 2010). The American crocodile inhabits a variety of aquatic environments such as landlocked hypersaline lakes, coastal lagoons of highly fluctuating salinities, estuaries, artificial canals in coastal areas, rivers, and reservoirs (Thorbjarnarson, 1989; Seijas, 2011). It has been mentioned insistently that *C. acutus* is a coastal species that occupies primarily (or even, prefers) mangrove forests, coastal lagoons and estuarine sections of rivers (Brazaitis, 1973; Thorbjarnarson, 1988; Mazzotti, Brandt, Moler and Cherkiss, 2007). Ernst et al. (1999) mentioned that that *C. acutus* is a brackish water crocodile. Although the occupation of freshwater habitats by the American Crocodile is well known, the occurrence of this species in mainland along of the main river courses (Medem, 1981; Thorbjarnason, 1989) has been considered mainly as a curiosity. In the past, the American crocodile was severely affected by unregulated hunting (Álvarez del Toro, 1974; Medem, 1981), and more recently for human-crocodile interactions and habitat fragmentation (Thorbjarnarson, 2010). Unfortunately, there is no detailed information about how abundant *C. acutus* was in each one of the diverse habitat types it is able to occupy, and which could be the optimal environmental conditions. The current abundance and distribution is the result of the presence and pressure of humans who have destroyed or modified high expanses of former areas than were occupied for the species (Thorbjarnarson et al., 2006; Escobedo-Galván, and González-Salazar, 2011). This limits our ability to infer the relationship between distribution and abundance patterns and habitat quality for the American crocodile across of its distribution range.

An indirect way to evaluate the quality of a habitat for a species is through the analysis of growth rates. There is a general agreement among scientists that the growth rate of an individual is a reliable index of its health (Brisbin, 1990). Growth rate could be used as a criterion to assess the response of individuals to different environmental conditions (Brandt, 1989; Charruau, Cedeño, Villegas and Cortés, 2010; Seijas, 2016). The growth rates (GR) of wild crocodiles are affected by several factors such as genetics, food availability, competition, temperature, and water salinity (Coulson, Coulson and Hernandez, 1973; Mazzotti, Bohnsack, McMahon and Wilcox, 1986; Dunson and Mazzotti, 1989; Jacobsen, and Kushlan, 1989). If these characteristics vary from places to place, I expected a geographical variation on growth rates. Crocodiles inhabiting in an environment that offers them the best resources for their development and survival should reach higher GR than those living in environments that have limitations. A fast growth rate translates into a shorter period as a small individual, a stage when crocodiles are more vulnerable to predators, osmotic stress and other environmental pressures (Mazzotti and Dunson, 1989; Platt, Meerman and Rainwater, 1999). It also means that less time is required to reach a reproductive size.

In spite of its wide distribution, there are few available studies on the growth of the American crocodile in the wild. Available information are for populations located in Florida (Mazzotti, Cherkiss and Beauchamp, 2009), Caribbean and Pacific coasts of Mexico (Charruau et al., 2010; García-Grajales, Buenarostro and Charruau, 2012). Some additional studies provide information on growth rates for both captive and wild crocodiles; however most of them are based on limited sample sizes.

In addition, information on the size at which the American crocodile attains sexual maturity is controversial and unclear. Regarding the minimum reproductive size of females, there is an ample spectrum of data ranging from 180 cm to 280 cm in total length (LeBuff, 1957; Thorbjarnarson, 1989; Álvarez del Toro, 1974; Platt and Thorbjarnarson, 1997). In the case of males, mature individuals with only 199 cm of total length have been reported (Balaguera-Reina, Vanegas, Sanjur, Lessios and Densmore III, 2015), but there is a general agreement that males attain sexual maturity at larger sizes than females.

It has been mentioned that large males can exceed 500 cm of total length (Thorbjarnarson, 2010) and there is a record of a female that exceeded 400 cm of total length (Domínguez-Laso, 2009). In any case, both the maximum sizes and the age at which sexual maturity is reached may depend, at least partially, on the available resources and habitat quality.

The purpose of the present work was to analyze and compare growth rates of *C. acutus* in different regions and habitats throughout its range. The analyses were based on both published and unpublished information of mark-recapture studies. The results, along with information on past and current distribution and abundance, will allow drawing conclusions about the quality of the different habitats that the species occupies and would support conservation and management recommendations, with emphasis for the Venezuelan populations.

MATERIALS AND METHODS

I analyzed growth rate records of *C. acutus* from some regions and habitats located in the United States of America (Mazzotti, 1999; Mazzotti et al. 2009; Beauchamp, Cherkiss, Rochford and Mazzotti, 2009), Mexico (Charruau et al., 2010; García-Grajales et al., 2012) and Venezuela (Table 1). In the case of Venezuela, data came from published (Arteaga, 1998; Urdaneta, 2002; Barros, Urdaneta, Lander, López and Gutiérrez, 2005) and unpublished sources (data of my own and other researchers; see acknowledgements).

In Table 2 appears a brief description of the localities where data come from, highlighting the characteristics that, according to my criteria, might help to analyze the results. The most obvious difference among the localities is their geographic locations, spanning more than 15 degrees of latitude from Turkey Point (Florida State, U.S.A.) to Cumaripa (Yaracuy State), a reservoir in Venezuela. One of the localities (La Ventanilla) is in the Pacific coast of Mexico.

Table 1. Total number of Growth data of American crocodiles (*Crocodylus acutus*) from different regions and habitats.

	n	Sex			<90 cm TL
		Males	Females	ND	
Florida, USA	86	36	40	10	19*
Yucatan, Mexico	27	21	6	0	13
La Ventanilla, Mexico	45	35	10	0	30
Reservoirs (Venezuela)	51	22	11	18	29
Mangroves (Venezuela)	37	8	8	21	27
Rivers (Venezuela)	22	4	7	11	19

* Considering only individuals from Turkey Point

Those disparate geographic locations surely determine some climatic differences (temperature fluctuations, rainfall and insolation patterns) that may have an effect in crocodile growing patterns that will not be discussed in this paper. Turkey Point has one peculiar characteristic that is necessary to mention. American crocodile population in this site occupies a series of manmade canals that are part of the cooling system of nuclear and fossil fuel units that operate to generate electricity. Water temperature in the cooling canals range from 34–42 °C and in is warmer (1.9–7.4 °C) than in adjacent canals outside the cooling system (Mazzotti et al., 1986). The predominant vegetation type in the localities of U.S.A. and Mexico is mangrove forest. In the case of Venezuela, data came from *C. acutus* populations inhabiting different habitats such as reservoirs, mangrove areas, and rivers.

Growth rates (GR) of *C. acutus* were expressed as changes in total length (TL, in cm) in the elapsed time (ET, in days) between capture and recapture. GR of *C. acutus* from different regions and habitat types were compared using nonparametric tests (Kruskall-Wallis and Mann-Whitney U tests). Only individuals less than 90 cm in TL at recapture were considered for these analyses, without discriminating by sex, assuming that during the first two years of age differences between male and females are

Table 2. Characteristics of localities and habitats where American crocodiles (*C. acutus*) growth records come from.

Region or habitat type	Data origins	Latitudinal location	Water salinities	Sources of information*
Florida (U.S.A.)	Turkey Point (Canals part of a cooling system of nuclear and fossil fuel units to generate electricity) and other localities of Florida state.	25.40° N	Turkey Point: From fresh to hypersaline and are higher in the cooling system (15-44 ppt) than in other canals in the vicinity.	3; 4; 7; 10; 11; 14.
Yucatan Peninsula (Mexico)	Banco Chinchorro, Cozumel, Canal Zaragoza, Laguna Cementerio, Siete Esteros and Río Huach (Quintana Roo state) Ría Lagarto (Yucatan state).	21.58° N	Marine or hypersaline (>35 ppt) in most localities, except Siete Esteros (estuarine), Ría Lagartos and Río Huach (salinities not reported).	5; 6.
La Ventanilla estuary (Mexico)	Tonameca River estuary (Oaxaca state)	15.68° N	Salinity not reported. The influence of direct and subterranean discharges of the river make me supposed that it is predominantly brackish, particularly during the months of maximum discharges of the river.	8; 9.
Reservoirs (Venezuela)	Pueblo Viejo (Zulia state), Jatira-Tacarigua (Falcón state), and Cumaripa (Yaracuy state).	11.06–10.16° N	Fresh water.	1; 12; 13.
Mangroves (Venezuela)	Los Olivitos (Zulia state), Cuare and Morrocoy (Falcón state) and Turiamo (Aragua state).	10.93–10.45° N	From estuarine to marine (Cuare and Morrocoy) and from marine to hypersaline (Los Olivitos and Turiamo).	2; 12.
Rivers (Venezuela)	Tocuyo (Falcón state), Yaracuy (Yaracuy state) and Rio Chico (Miranda state).	11.04–10.35° N	Fresh water localities, except for Río Chico that is estuarine (up to 16 ppt).	1; 12.

* Sources of information: 1: Arteaga, 1998; 2: Barros et al., 2005; 3: Beauchamp et al., 2009; 4: Brandt, et al., 1995; 5: Charruau et al., 2010; 6: Charruau, 2011; 7: Gaby et al., 1985; 8: García-Grajales et al., 2007; 9: García-Grajales et al., 2012; 10: Mazzotti et al., 1986; 11: Mazzotti, 1999; 12: Seijas et al., 2008; 13: Urdaneta, 2002; 14: Wasilewski and Enloe, 2006.

small or undetectable (Chabreck and Joanen, 1979). Statistical analyses were performed with the statistics software Past, version 3.06 (Hammer, Harper and Ryan, 2001).

In another approach to analyze GR of *C. acutus* from different regions and habitat, I fitted the data to the von Bertalanffy growth model, which is expressed as:

$$TL = TL_\infty (1 - be^{-kd}),$$

Where TL is the predicted size at age d; TL_∞ is the maximum size predicted by the model; b relates both to the asymptotic size and the size at hatching and k is an indication of the rate of proportional growth of the animal (Fabens, 1965).

The model needs to know the age (d) of individuals, information that was not available for most of the crocodiles in our study. Therefore, the parameters TL_∞ and k, were obtained following Fabens (1965). In a first step, data were fit to:

$$TL_{rec} = TL_{inic} + (TL_\infty - TL_{inic}) * (1 - e^{-kt})$$

Where TL_{rec} is the total length at recapture; TL_{inic} is the total length at first capture; and t is the time lapse between initial capture and recapture. Once TL_∞ was known, the parameter b was calculated solving the von Bertalanffy equation when $d = 0$; i.e. $b = 1 - TL_0/TL_\infty$, where $TL_0 = 25.5$ cm, the TL at hatching (Seijas, Urdaneta and Barros, 2008).

The Fabens method is independent of the age of recaptured individuals. Fitting to the model was performed using least square methods and the non-linear fit command of the software JMP IN (2001, SAS Institute Inc.). Fitting the data to the Von Bertalanffy model was performed first for individuals less than 90 cm of TL and without discriminating by sex. This allowed comparing growth pattern of different localities and estimating the size individuals should reach the first two years of life. The whole data set for males and females was also fitted to the growth model. In this case, to increase sample size, individuals for which sex was unknown were added to the males or females alternatively. I also performed an analysis integrating data from Turkey Point with other GR of crocodiles from other areas of Florida (Mazzotti, 1999; Beauchamp et al., 2009).

Once all parameters of Von Bertalanffy model were known, it was possible to get d, the estimated age of a crocodile of a determined size (TL_d), as: $d = k^{-1} \cdot Ln[(TL_\infty - TL_0/TL_\infty - TL_d)]$ where Ln is natural logarithm. That equation was used to estimate the age at which individuals should reach a TL of 200 cm in different localities, a size at which the species is close to adulthood.

RESULTS

For crocodiles < 90 cm in TL, the highest GR was showed by individuals from rivers of Venezuela (0.110±0.11 cm/day), whereas the lowest values were showed for crocodiles in mangroves areas of Venezuela and the Yucatan peninsula in Mexico (Table 3). The differences among regions were highly significant (Kruskal-Wallis test for equal medians. $\chi^2 = 30.3$; $P < =.0001$). A Mann-Whitney pairwise comparison indicated that growth data for Turkey Point and Rivers of Venezuela did not differ between them ($P = 0.051$).

Table 4 shows the parameters of the von Bertalanffy model for small crocodiles (< 90 cm TL). The model predicts the smallest sizes, at one and two years of age, for crocodiles from the Yucatan Peninsula. For 1- year-old crocodiles, the model predicts the largest size at La Ventanilla, whereas 2-year-old crocodiles

Table 3. Growth rates (GR) of *C. acutus* from different regions and habitats. Only individuals <90 cm in TL were considered in the analyses.

	n	Mean Elapsed Time (days)	GR (cm/day)			Diff.*
			Mean ± S.E.	Range	Median	
Turkey Point (USA)	19	330	0.094±0.012	0.010–0.280	0.090	A
La Ventanilla (Mexico)	30	584	0.064±0.009	0.002–0.284	0.047	B
Yucatan (Mexico)	13	293	0.050±0.010	0.013–0.121	0.043	B
Reservoirs (Venezuela)	29	148	0.058±0.007	-0.031–0.141	0.052	B
Mangroves (Venezuela)	27	153	0.045±0.006	-0.002–0.113	0.041	B
Rivers (Venezuela)	19	173	0.110±0.011	0.008–0.193	0.111	A

* Medians with the same letter are not statistically different at the 0.05 alpha level.

from Turkey Point and Rivers of Venezuela were expected to be the largest (Figure 1).

Only growth data from Turkey Point and from that locality pooled with data from other Florida sites (All Florida), as well as growth data for females from Mangroves areas of Venezuela, allowed modeling growing curves with asymptotic sizes approaching what is expected for a large crocodilian species such as *C. acutus*. The predicted maximum sizes of males and females in Florida increase when large individuals from other localities of that state were added to the ones from Turkey Point. The age at which females are expected to reach a size of 200 cm goes from 8.83 yr in All Florida to 16.60 yr in the mangrove areas of Venezuela (Table 5). Males are expected to reach that size earlier (Figure 2).

DISCUSSION

For a species of an extensive distribution such as the American crocodile, it would be expected to find differences of growth in individuals from geographically distant populations. Unexpectedly, however, GR of juvenile crocodiles inhabiting rivers in Venezuela are very similar to the ones found at Turkey Point, in the subtropical Florida in the USA, localities separated by more of 10° of latitude. Likewise, crocodiles from mangroves areas in Venezuela showed a growth pattern comparable to the one found in distant mangroves areas in the Yucatan Peninsula of México.

Growth data of *C. acutus* analyzed in this paper belong to localities that range from totally freshwater (rivers and reservoirs) to, at least temporarily, hypersaline (Banco Chinchorro, Mexico and Turiamo, Venezuela). Thus, salinity could be one of the main abiotic factors that explain the differences and similarities in growth rates of crocodiles from the localities studied. Low salinity has been associated with higher GR of young crocodiles (Mazzotti et al., 1986; Dunson and Mazzotti, 1989; Mazzotti and Dunson 1989; Mazzotti, 1999) and hatchlings in captivity lose mass and are unable to survive in sea water (Ellis, 1981; Dunson, 1982).

In average, the lowest GRs found in this study were for crocodiles from localities with high salinities, whereas the highest GRs were for crocodiles from rivers. The similarities between the crocodile growth pattern in Turkey

Table 4. Parameters of the von Bertalanffy growth model and predicted size of one and two years old *Crocodylus acutus* from different localities

Data origin	n	LT∞	k	b	Projected size (TL cm) 1 yr.	2 yr.
Turkey Point (USA)	19	208.3	0.2025	0.8776	59.0	86.4
Yucatan (Mexico)	13	86.1	0.6396	0.7038	54.1	69.2
La Ventanilla (Mexico)	30	82.6	1.7963	0.6913	73.1	81.0
Reservoirs (Venezuela)	29	133.5	0.3414	0.8090	56.7	78.9
Mangroves (Venezuela)	27	96.0	0.6699	0.7343	59.9	77.5
Rivers (Venezuela)	19	101.8	0.8153	0.7496	68.1	86.9

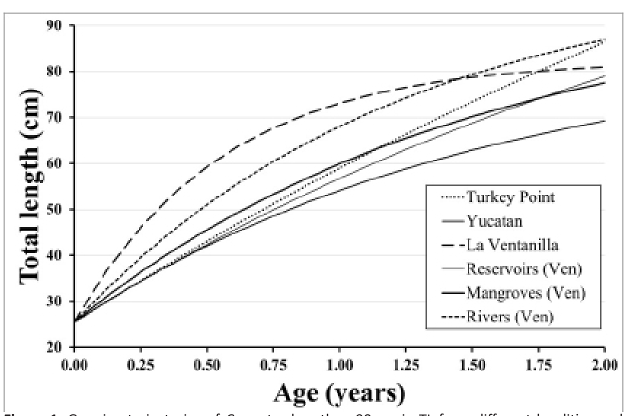

Figure 1. Growing trajectories of *C. acutus* less than 90 cm in TL from different localities and habitats during the first two years according to the von Bertalaffy model.

Table 5. Parameters of the von Bertalanffy growth model and predicted age to reach a TL of 200 cm for *Crocodylus acutus* from different regions or habitats.

	n	LT∞	k	b	Age to reach 200 cm TL
Turkey Point males	38	417.9	0.0788	0.9390	7.46
All Florida (males)	46	439.0	0.0773	0.9419	7.09
Turkey Point females	40	216.2	0.2129	0.8821	11.58
All Florida (females)	50	261.7	0.1521	0.9025	8.83
Mangroves females (Ven)	29	227.4	0.1203	0.8879	16.60

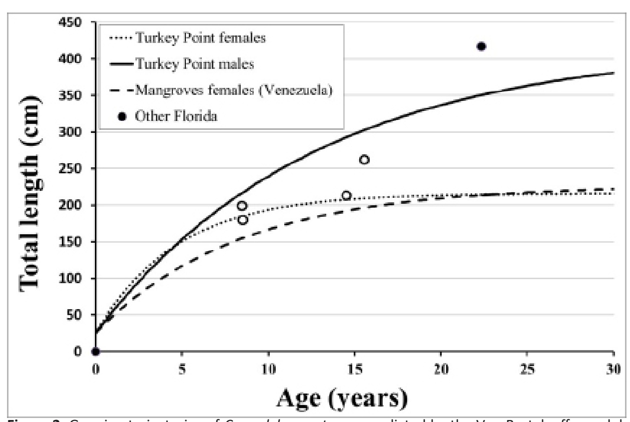

Figure 2. Growing trajectories of *Crocodylus acutus* as predicted by the Von Bertalanffy model. Circles represent crocodiles on known ages from other Florida localities. Close circle: males; open circles: females

Point and that of Venezuelan rivers may seem paradoxical, taking into account no only the latitudinal differences but also that the salinity regimes of these localities are quite different. However, high GRs of *C. acutus* in Turkey Point could be considered anomalous (Thorbjarnarson, 1989), because crocodiles inhabit there cooling canals with elevated temperatures, even during winter (Gaby et al., 1985; Mazzotti et al., 1986) which enhances growing.

Besides the data analyzed in this study, there are not too many figures to compare GR of *C. acutus* from other areas of its range (Table 6). There is a high variability in the GRs reported. However, the low mean value (0.066 cm/day) for crocodiles in a marine environment in Belize (Turneffe Atoll; Platt and Thorbjarnarson, 1997) is comparable to the GRs of crocodiles from the Yucatan Peninsula, most of which came from a similar habitat, Banco Chinchorro atoll. On the other hand, Thorbjarnarson (1988) reported a relatively high mean GR (0.135 cm/day) for crocodiles from an only slightly saline lake in Haiti. It is worth mentioning that even the highest GR reached in the wild fall short when compared to data on growth in captivity reported in Table 6.

Growth rates of *C. acutus* for different habitat types in Venezuela (Table 3) are comparable to those reported by Seijas et al. (2008) which were estimated by the slope of the regression line of total length versus days after hatching of untagged individuals captured along the year. Small crocodiles from rivers reached the highest growth rate (0.119 cm/day), followed for those from reservoirs (0.084–1.04 cm/day), whereas those from hypersaline environments presented the lowest values (0.055-0.057 cm/day). Crocodiles from localities with intermediate salinities showed correspondingly intermediate GR values.

The von Bertalanffy model for small crocodiles (< 90 cm in TL) indicate that during the first two years of age, growth tends to decline slightly with time, except for data from La Ventanilla, where crocodiles seem to stop growing after the first year. The large predicted size for first-year crocodiles from this locality and the sudden decline in growth for the second year may be an artifact caused by the fact that the mean ET capture-recapture was the highest among the samples analyzed. More than one third of the growth data from la Ventanilla are for ET longer than two years. It is well known that as the interval between captures increases the calculated GR decreases. However, the growth pattern in La Ventanilla is similar to the one found in Boca Negra, another estuary in the Pacific coast of Mexico, as I will discuss in the next paragraph.

Cupul-Magaña, Rubio and Reyes (2004) and Charruau (2011) used a different method to get the parameters for the Von Bertalanffy model. The first authors worked at Boca Negra (Jalisco State, Mexico) an estuary with salinities approaching zero, due to the entrance of freshwater from the Ameca River (Cupul-Magaña, Rubi, Reyes and Hernández, 2002). From their equation, it is possible to calculate crocodiles of 64.9 and 70.2 cm TL at one and two years of age, respectively. The first value represents a GR of 0.108 cm/day, only below the growth rates for rivers shown in Table 3. However, crocodiles at Boca Negra seem to stop growing abruptly during the second year, as occurred with crocodiles at La Ventanilla. It is possible that in these estuaries there were abundant food resources for small crocodiles (shrimp, small crabs, small fish, insects), but a relative shortage of larger prey to

Table 6. Additional growth rates (GR) of *C. acutus* from different regions and conditions (in the wild or in captivity).

Data origin and description	Hábitat	Mean GR (cm/day)	n	Source
Panama, Coiba Island	Marine	0.03-0.16	15	1
Mexico, Boca Negra	Barckish, mangrove	0.122	124	2
Venezuela	Captivity (Treatment 1)	0.240	14	3
Venezuela	Captivity (Treatment 2)	0.212	14	3
Cuba	Captivity (Treatment A)	0.288	30	4
Cuba	Captivity (Treatment B)	0.344	30	4
Cuba	Captivity (Treatment C)	0.264	30	4
Belize, Turneffe Atoll	Marine	0.066	3	5
Mexico, Cañon del Sumidero	Reservoir	0.013-0.098		6
Dominican Republic, Enriquillo lake	Brackish to hypersaline	0.107		7
Haiti; Etang Saumatre (0-3 months crocodiles)	Brackish	0.135	13	8

Data source: 1. Balaguera-Reyna et al. 2015; 2. Cupul-Magaña et al. 2004; 3. Hernández et al., 2010; 4. Pérez-Gomez et al., 2009; 5. Platt and Thorbjarnarson 1997; 6. Sigler 2010; 7. Schubert, James, Méndez & Santana, 1996; 8. Thorbjarnarson, 1988.

sustain rapid growth of larger crocodiles. That is a speculation worth investigating.

From equation 5 in Charruau (2011), it is possible to calculate that crocodiles at Banco Chinchorro atoll (Quintana Roo, Mexico) reach a size of 47.1 and 67.3 cm in TL at one and two years of age, respectively. These values are below the ones presented in Table 4 for the Yucatan Peninsula, that were calculated pooling the data from Banco Chinchorro with those from other localities of Yucatan and Quintana Roo states (Charruau et al., 2010). Differences in sample sizes, total length of the crocodiles used in the analyses, and the inclusion in the model of individuals from diverse habitat types may explain the discrepancies.

Only for the data of Florida and for the females of mangrove areas of Venezuela it was possible to get growing models that realistically approached the maximum sizes the species is known to reach. The model is highly sensitive to the presence of large and old animals in the data. In Florida, for example, the asymptotic size for males increased 21.1 cm when a datum of just one individual of 416.6 cm in TL and 22.35 yr old (Beauchamp et al., 2009) was added. The asymptotic size predicted for "All Florida" males is not far from the 442 cm TL of a specimen mentioned by Beauchamp et al., on display at the American Museum of Natural History of New York. Mazzotti (2013) mentioned that males *C. acutus* in Florida can reach up to 460 cm in TL.

The asymptotic size for females in Turkey Point is also below the known maximum length that the species can reach. Five of six nesting females captured by Kushlan and Mazzotti (1989) surpassed the 216 cm and one of them was 306 cm in TL. Predicted maximum size for females increased 45.5 cm when data from Florida Bay (Mazzotti, 1999) were added to the ones from Turkey Point. Even these sizes can be considered as too smalls when compared to the 440 cm for a female from the Grijalba River, in Mexico (Domínguez-Laso, 2009).

The predicted maximum sizes for females are around what has been reported as the necessary to reach sexual maturity (Medem, 1981; Kushlam and Mazzotti 1989; Thorbjarnarson 1988, 1989). Le Buff (1957), based on observations on captive *C. acutus* in Florida, affirmed that the time to reach adulthood is 13 yr, a figure in between the ones estimated in this paper. In good habitats, females might need around nine years to attain maturity. In less favorable habitats, it would take much longer, as for example more than 16 years in mangrove areas of Venezuela. This fact has conservation implications since slow growing individuals are exposed longer to factors that affect their survival before they can reproduce.

If we take into consideration only the GR, crocodiles do poorly in habitats with high water salinities such as the atolls in Belize and Mexico, or the mangrove areas of Venezuela. On the other hand, although based in a limited data set, juveniles from rivers showed the highest GR. Based only in this criterion, I think that the optimal and probably preferred habitat of *C. acutus* is represented by rivers and other freshwater environments. However, Individual GR is not the only criteria that can be used to evaluate the suitability of habitats for the American Crocodile; distribution, abundance, survival, nesting effort, and nesting success are some others (Mazzotti, 1999). Information on those additional population parameters is very limited, particularly outside Florida.

In defense of my suggestion that rivers and other freshwater environments represent the best habitats for *C. acutus*, as the growth data seems to support, I will discuss briefly about past distribution and abundance of the species. That discussion is difficult due to the lack of data on the status of the species before the commercial exploitation took place. Schmidt (1924) for example, was amazed about how abundant the species was in Lake Ticamaya of Honduras. Alvarez del Toro (1974) refers to *C. acutus* as "Cocodrilo de Río" and commented about how abundant this species was in several rivers of Mexico. In Colombia *C. acutus* was abundant along the valleys of large rivers like the Sinú, San Jorge, Cauca and Magdalena (Medem, 1981; Ulloa-Delgado, 2011). What seems to be the most important population of *C. acutus* in Costa Rica is found in the Río Tárcoles, with reported abundances of 9.2–30.1 ind/km (Porras, 2004).

In Venezuela *C. acutus* has been reported in several rivers of the Maracaibo Lake basin (Santa Rosa, Negro, Aricuaisá, Chama, Birimbay, Motatan) and the Caribbean coast basin (Tocuyo, Aroa, Yaracuy, Neverí) to mention just the best known cases (Seijas 1986; De Sola et al., 2004, Lander and Bermúdez, 2005). Beside rivers, the American crocodile seem to do well in other types of freshwater habitats: the reservoirs.

Despite the past and current distribution and abundance of *C. acutus* in rivers and other freshwater habitats, most studies have been conducted in coastal environments, where many protected areas are located. That is particularly so regarding studies on growth rate. In Costa Rica, for example, where the population status of the species in several rivers have been studied in some detail (Porras et al., 2008; Sánchez et al., 1997; Sasa and Chaves, 1992) there is not a single record available on growth in natural conditions.

The emphasis of studying *C. acutus* populations mostly found in mangrove areas, coastal lagoons and other places close or under the influence of the sea, has probably contributed to seed the idea that this crocodile is mostly an inhabitant of estuaries and other coastal environments, which is only a reflect of its current status.

Taking into consideration the GRs analyzed in this study, together with the information (rather scarce and incomplete) on current distribution and abundance, it is possible to conclude that most mangrove areas that the species occupies are marginal habitats. If *C. acutus* is still found in some of them it is no because they are the preferred habitat but because populations in other areas have been exterminated. In the past, when populations of this species were not as fragmented and depleted as they are today, perhaps the bulk of populations were found in rivers and there was a permanent exchange of individuals, in a metapopulation dynamics, with subpopulations in estuaries and coastal lagoons.

In Venezuela there are several coastal areas that are legally protected (National parks, and wildlife refuges and Reserves) that contain populations of *C. acutus*. Only two full freshwater localities (Tacarigua-Jatira reservoirs, in Falcón state) are included in one of those areas (Tucurere Wildlife Reserve, Falcon state). There is no a program for the continuous assessment of the status of *C. acutus* populations in any area of the country. The conservation activities have focused mainly on population reinforcement in protected areas, which, as already mentioned, are neither the optimal habitat nor the localities where the largest population of the species are found. The future of the *C. acutus* in Venezuela (and probably other countries) will depend, to a large extent, on the conservation of the populations of rivers and other freshwater localities where the species is present.

ACKNOWLEDGEMENTS

Some of the data analyzed in this study were provided by Alfredo Lander (†), Carlos Chávez, Bethina Vargas, and Alvaro Velasco. Sara and Andres Seijas Falkenhagen helped me with English, but the grammatical errors that remain are of my complete responsibility.

REFERENCES

Álvarez del Toro, M. (1974). Los Crocodylia de México (Estudio comparativo). México, D.F.: Instituto Mexicano de los Recursos Naturales Renovables, A.C.

Arteaga, A. (1996). Conservación y manejo del caimán de la costa en la cuenca baja del rio Yaracuy: Informe de avance 1995-1996: Fundación para la Defensa de la Naturaleza (FUDENA), Caracas.

Arteaga, A. (1998). Aspectos bioecológicos de *Crocodylus acutus* liberados en el embalse Tacarigua (Falcón, Venezuela). Unpublished Maestría, Universidad Simón Bolívar.

Balaguera Reina, S.A., Venegas Anaya, M., Sanjur, O.I., Lessios, H.A., & Densmore III, L.D. (2015). Reproductive Ecology and Hatchling Growth Rates of the American Crocodile (*Crocodylus acutus*) on Coiba Island, Panama. South American Journal of Herpetology, 10(1), 10-22.

Barros, T., Urdaneta, A., Lander, A., López, R., & Gutiérrez, T. (2005). Reforzamiento y seguimiento de la población de caimanes de la costa (*Crocodylus acutus*) en la Ciénaga de los Olivitos, estado Zulia, Venezuela. Ciencia, 13(2), 162-181.

Beauchamp, J.S., Cherkiss, M.S., Rochford, M.R., & Mazzotti, F.J. (2009). A recent capture of a large American Crocodile (*Crocodylus acutus*) in Florida. Florida Field Naturalist, 37(4), 149-150.

Brandt, L. (1989). The status and ecology of the American alligator (*Alligator mississippiensis*) in Par Pond, Savannah River site. Florida International University.

Brandt, L.A., Mazzotti, F.J., Wilcox, J.R., Barker, P.D.J., Hasty, G.L.J., & Wasilewski, J. (1995). Status of the American crocodile (*Crocodylus acutus*) at a power plant site in Florida, USA. Herpetological Natural History, 3, 29-36.

Brazaitis, P. (1973). The identification of living crocodilians. Zoologica, 58(3), 59-101.

Brisbin, I.L., Jr. (1990). Growth curve analyses and their application to the conservation and captive management of crocodilians. Paper presented at the Proceedings of the Ninth Working Meeting of Crocodile Specialist Group.

Chabreck, R., & Joanen, T. (1979). Growth rates of American alligators in Louisiana. Herpetologica, 35(1), 51-57.

Charruau, P. (2011). Estimación de la edad de los cocodrilos (*Crocodylus acutus*) de Banco Chinchorro, Quintana Roo, México. Quehacer Científico en Chiapas, 2011(11), 36-43.

Charruau, P., Cedeño-Vásquez, J., Villegas, A., & González Cortés, H. (2010). Tasas de crecimiento del Cocodrilo Americano (*Crocodylus acutus*) en estado silvestre en la Península de Yucatán, México. Revista Latinoamericana de Conservación, 1(2), 63-72.

Coulson, T., Coulson, R., & Hernandez, T. (1973). Some observations on growth of captive alligators. Zoologica, 58, 47-52.

Cupul-Magaña, F.G., Rubio-Delgado, A., Reyes-Juárez, A., & Hernández-Hurtado, H. (2002). Sondeo poblacional de Crocodylus acutus (Cuvier, 1807) en el Estero Boca Negra, Jalisco. Ciencia y Mar, 6(16), 45-50.

Cupul-Magaña, F.G., Rubio-Delgado, A., & Reyes-Juárez, A. (2004). Crecimiento en talla y peso del cocodrilo americano (*Crocodylus acutus*) durante su primer año de vida. Revista Española de Herpetología, 18, 55-61.

De Sola, R., Quero, M., Colomine, G., Velasco, A., Villarroel, G., Lander, A., et al. (2004, 24-29 May 2004). Evaluation of wild populations and habitats of American crocodile (*Crocodylus acutus*) in Venezuela. Paper presented at the Crocodiles. Proceedings of the 17th Working Meeting of the Crocodile Specialist Group, Darwin, Nothern Territory of Australia.

Domínguez-Laso, J. (2009). Record size for a female *Crocodylus acutus* in the Grijalba River, Chiapas, Mexico. Crocodile Specialist Group Newsletter, 28(2), 14-15.

Dunson, W.A. (1982). Salinity relations of crocodiles in Florida Bay. Copeia, 1982(2), 374-385.

Dunson, W.A., & Mazzotti, F. (1989). Salinity as a limiting factor in the distribution of reptiles in Florida Bay: A theory for the estuarine origin of marine snakes and turtles. Bulletin of Marine Science., 1989(1), 229-244.

Ellis, T.M. (1981). Tolerance of sea water by the American crocodile, *Crocodylus acutus*. Journal of Herpetology, 15(2), 187-192.

Ernst, C.H., Ross, F.D., & Ross, C.A. (1999). *Crocodylus acutus* (Cuvier) American Crocodile. Catalogue of American Amphibians and Reptiles, 700, 1-17.

Escobedo-Galván, A.H., & González-Salazar, C. (2011). Aplicando modelos de nicho ecológico para predecir áreas potenciales de hibridación entre *Crocodylus acutus* y *C. moreletii*. Quehacer Científico en Chiapas, 2011(11), 27-35.

Fabens, A.J. (1965). Properties and fitting of the Von Bertalanffy growth curve. Growth, 29, 265-289.

Gaby, R., McMahon, M., Mazzotti, F., Gillies, W.N., & Wilcox, J.R. (1985). Ecology of a population of *Crocodylus acutus* at a power plant site in Florida. Journal of Herpetology, 19(2), 189-198.

García-Grajales, J., Aguirre-León, G., & Contreras-Hernández, A. (2007). Tamaño y estructura poblacional de *Crocodylus acutus* (Cuvier 1807) (Reptilia: Crocodylidae) en el estero La Ventanilla, Oaxaca, México. Acta Zoológica Mexicana, 23(1), 53-71.

García-Grajales, J., Buenarostro-Silva, A., & Charruau, P. (2012). Growth and age of juvenile American crocodiles (*Crocodylus acutus*) in La Ventanilla estuary, Oaxaca, Mexico. Herpetological Conservation and Biology, 7(3), 330-338.

Hammer, O., Harper, D.A.T., & Ryan, P.D. (2001). PAST: Paleontological statistical software package for education and data anaysis. Paleontologia Electronica, 4(1), 9.

Hernández, O., Espín, R., Boede, E.O., & Rodríguez, A. (2010). Algunos factores que afectan el crecimiento en cautiverio de crías de caimanes (*Crocodylus intermedius*, *Crocodylus acutus* y *Podocnemis expansa*). In A. Machado Allison (Ed.), Investigación y Manejo de la Fauna Silvestre en Venezuela. Caracas.

Jacobsen, T., & Kushlan, J.A. (1989). Growth dynamics in the American alligator (*Alligator mississippiensis*). Journal of Zoology of London, 219, 309-328.

Kushlan, J., & Mazzotti, F. (1989). Population biology of the American crocodile. Journal of Herpetology, 23(1), 7-21.

Lander-García, A., & Bermúdez, S. (2005). Evaluación de las poblaciones del caimán de la costa (*Crocodylus acutus*) en la cuenca del Lago de Maracaibo. Informe de avance: MPPA. Oficina Nacional de Diversidad Biológica, MSBRG, Maracay.

LeBuff, C.R. (1957). Observations on captive and wild North American crocodilians. Herpetologica, 13, 28.

Mazzotti, F. (1999). The American Crocodile in Florida Bay. Estuaries, 22(2B), 552-561.

Mazzotti, F. (2013). American Crocodile (*Crocodylus acutus*) in Florida (No. WEC 38): IFAS Extension, University of Florida.

Mazzotti, F., Bohnsack, B., McMahon, M., & Wilcox, J. (1986). Field and laboratory observations on the effects of high temperature and salinity on hatchling *Crocodylus acutus*. Herpetologica, 42(2), 191-196.

Mazzotti, F., Brandt, L., Moler, P., & Cherkiss, M.S. (2007). American Crocodile (*Crocodylus acutus*) in Florida: Recommendations for endangered species recovery and ecosystem restoration. Journal of Herpetology, 41(1), 121-131.

Mazzotti, F., Cherkiss, M.S., & Beauchamp, J.S. (2009). American crocodile monitoring program for the Turkey Point uprate: Florida Power and Light Company.

Mazzotti, F.J., & Dunson, W.A. (1989). Osmorregulation in crocodilians. American Zoologist 29, 903-920.

Medem, F. (1981). Los Crocodylia de Sur América. Los Crocodylia de Colombia (Vol. 1). Bogotá: Universidad Nacional de Colombia y Fondo Colombiano de Investigaciones Científicas y Proyectos Especiales "Francisco José de Caldas", COLCIENCIAS. Vol. I. Editorial Carrera 7a. Ltda.

Pérez Gómez, M., Naranjo López, C., Reyes Tur, B., & Vega Ramírez, I. (2009). Influencia de dos tipos de dietas sobre la talla y el peso corporal en neonatos de *Crocodylus acutus* Cuvier, 1807 (Crocodylidae: Crocodylia) del Zoocriadero de Manzanillo, Cuba. Acta Zoológica Mexicana (n.s.), 25(1), 151-160.

Platt, S.G., Meerman, J.C., & Rainwater, T.R. (1999). Diversity, observations, and conservation of the herpetofauna of Turneffe, Liaghthouse, and Glovers atolls, Belize. British Herpetological Society Bulletin, 66, 1-13.

Platt, S.G., & Thorbjarnarson, J.B. (1997). Status and Life History of the American crocodile in Belice: Final Project Report to United Nations: United Nation Development Programme. Global Environmental Facility.

Porras, L.P. (2004). Situación actual del cocodrilo americano (*Crocodylus acutus*) en los ríos Jesús María, Tárcoles y Tusubres: estructura poblacional e intercambio genético. Universidad Nacional, Heredia.

Porras, L.P., Bolaños, J.R., & Barr, B. (2008). Variación genética y flujo de genes entre poblaciones de *Crocodylus acutus* (Crocodylia: Crocodylidae) en tres ríos del Pacífico Central, Costa Rica. Revista de Biología Tropical, 56(3), 1471-1480.

Sánchez, J.J., Bolaños, J.R., & Piedra, L. (1997). Población de *Crocodylus acutus* (Crocodylia: Crocodylidae) en dos ríos de Costa Rica. Revista de Biología Tropical, 44, 835-840.

Sasa, M., & Chaves, M. (1992). Tamaño, estructura y distribución de una población de *Crocodylus acutus* (Crocodylia:Crocodilidae) en Costa Rica. Revista de Biología Tropical, 40(1), 131-134.

Schubert, A., James, W., Mendez, H., & Santana, G. (1996). Headstarting and translocation of juvenile *Crocodylus acutus* in Lago Enriquillo, Dominican Republic. Paper presented at the Crocodiles. Proceedings of the 13th Working Meeting of Crocodile Specialist Group, Santa Fe, Argentina.

Seijas, A.E. (1986). Situación actual del caimán de la costa, *Crocodylus acutus*, en Venezuela. Paper presented at the Crocodiles. Proceedings of the 7th Working Meeting of Crocodile Specialist Group, Caracas, Venezuela.

Seijas, A.E. (2011). Los Crocodylia de Venezuela: Ecología y Conservación. Caracas: Academia de Ciencias Físicas, Matemáticas y Naturales.

Seijas, A.E. (2016). Regional differences in growth rates of Orinoco crocodiles (*Crocodylus intermedius*) from the Venezuelan llanos. Herpetological Journal, 26(October 2016), 263-269.

Seijas, A.E., & Chávez, C. (1991). Conservación del caimán de la costa (*Crocodylus acutus*) en el río Yaracuy y el Parque Nacional Laguna de Tacarigua: Informe para FUDENA. Estudio avalado por la UNELLEZ (código 23190106).

Seijas, A.E., & Chávez, C. (1991). Conservación del caimán de la costa (*Crocodylus acutus*) en el río Yaracuy y el Parque Nacional Laguna de Tacarigua: Informe para FUDENA. Estudio avalado por la UNELLEZ (código 23190106).

Seijas, A.E., Urdaneta, A., & Barros, T. (2008). Tasas de crecimiento durante primer año de vida y la temporada de eclosión de caimán de la costa (*Crocodylus acutus*) en Venezuela Boletín del Centro de Investigaciones Biológicas, 42(4), 445-459.

Sigler, L. (2010). La historia natural del Cocodrilo Americano *Crocodylus acutus* en el Parque Nacional Cañón del Sumidero, Chiapas, México. Revista Latinoamericana de Conservación, 1(2), 73 - 82.

Thorbjarnarson, J., Mazzotti, F., Sanderson, E., Buitriago, F., Lazcano, M., Minkowski, K., et al. (2006). Regional habitat conservation priorities for the American crocodile. Biological Conservation, 128(2006), 25-36.

Thorbjarnarson, J.B. (1988). The status and ecology of the American crocodile in Haiti. Bulletin of Florida State Museum Biologica Sciences, 33(1), 1-86.

Thorbjarnarson, J.B. (1989). Ecology of the American crocodile, *Crocodylus acutus*. In Crocodiles, Their Ecology Management and Conservation. (pp. 228-259). Gland, Switzerland: UCN: International Union for the Conservation of Nature and Natural Resources.

Thorbjarnarson, J.B. (2010). American Crocodile *Crocodylus acutus*. In C. Manolis & C. Stevenson (Eds.), Crocodiles. Status Survey and Conservation Action Plan. (pp. 46-53): Crocodile Specialist Group: Darwin.

Ulloa-Delgado, G.A. (2011). Plan de manejo preliminar para la conservación de las poblaciones del caimán de aguja *Crocodylus acutus* (Cuvier, 1807) en los ríos Sardinata, San Miguel, Nuevo Presidente y Tibú. Departamento Norte de Santander, Cuenca del Catatumbo de Colombia: CORPONOR, ECOPETROL.

Urdaneta, A. (2002). Evaluación poblacional del caimán de la costa (*Crocodylus acutus*) en el R.F.S.R.P Ciénaga de Los Olivitos y el embalse Pueblo Viejo, Estado Zulia, Venezuela. Unpublished Tesis de pregrado, Universidad del Zulia, Maracaibo.

Wasilewski, J.A., & Enloe, B. (2006). The status of the American crocodile (*Crocodylus acutus*) at Turkey Point Nuclear Power Plant, Florida, USA. Paper presented at the Crocodiles. Proceedings of the 18th Working Meeting of the Crocodile Specialist Group, Montélimar, France.