

Size estimation, morphometrics, sex ratio, sexual size dimorphism, and biomass of *Crocodylus acutus* in the coastal zone of Belize

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Abstract. We used morphometric data from 151 *Crocodylus acutus* captured in the Coastal Zone of Belize to develop predictive models for deducing body size (total length [TL] and snout–vent length [SVL]) from measurements of single attributes (dorsal cranial length [DCL], cranial width [CW], snout length [SL] and width [SW], body mass [BM], and rear foot length [RFL]), quantify sexual size dimorphism, examine ontogenetic changes in cranial morphology, and estimate standing crop biomass of crocodiles on an offshore atoll. Strong positive allometric relationships were found between measurements of body length and other morphometric attributes, and provide a reliable means to estimate body length from tracks, skulls, and body parts. The maximum DCL: CW ratio of 2.4 was attained at a body size that coincided with a dietary shift from invertebrates to larger vertebrate prey. The SL: SW ratio of *C. acutus* partially overlapped that of *C. moreletii*, and consequently this attribute was not useful for distinguishing these two morphologically similar, sympatric species. The mean DCL: TL ratio was 0.15 and remained constant across body sizes ranging from hatchlings to large adults. Both overall and adult sex ratio (female: male) were not significantly different from parity. The mean SVL of males (111.3 ± 20.7 cm) was significantly greater than that of females (101.0 ± 6.2 cm). A compressed sexual size dimorphism index (SDI) of 2.10 was calculated for *C. acutus* in coastal Belize. *Crocodylus acutus* in coastal Belize appear to attain a smaller body size than reported for other populations. Standing crop biomass of *C. acutus* in the Turneffe Atoll was estimated to be 0.92 kg/ha.

Key words. Body size, cranial morphology, Crocodylia, *Crocodylus acutus*, morphometrics, ontogenetic change, standing crop biomass.

Introduction

Crocodile research and management rely on knowledge of individual body size and the size-class structure of populations (WEBB & SMITH 1987) because demographic and reproductive variables are functionally dependant on body size rather than age, and population models are generally based on the former (NICHOLS 1987). Collecting morphometric data is therefore recommended during any research project involving crocodylians so that predictive models relating different body dimensions to each other can be derived (WEBB & SMITH 1987). These models allow estimation of body size from skulls and other remains (WEBB & MESSEL 1978, THORBJARNARSON & MCINTOSH 1987, HALL & PORTIER 1994, WOODWARD et al. 1995, PLATT et al. 2006), calibrated photographs (CHOQUENOT & WEBB 1987, STEWART 1988), and tracks (SINGH & BUSTARD 1977, HUTTON 1987a, PLATT et al. 1990, THORBJARNARSON & HERNANDEZ 1993, SEEBACHER et al. 1999, SWANEPOEL et al. 2000, WILKINSON & RICE 2000). Additionally, morphometric models permit detection of ontogenetic changes in cranial morphology (WEBB & MESSEL 1978, CHENTANEZ et al.

1983, HALL & PORTIER 1994, TUCKER et al. 1996), are useful in the study of archaeological material (REITZ et al. 1987), are necessary for calculating individual condition factors (TAYLOR 1979, ELSEY et al. 1992), facilitate the determination of crocodile biomass (HUTTON 1987b, THORBJARNARSON 1988, FUKUDA et al. 2011), and might have some utility for estimating age (WEBB & SMITH 1987). Furthermore, the ability to estimate the body size of crocodiles without actually catching them is a great advantage to wildlife managers and biologists for reasons of logistics, safety, and animal welfare (MONTAGUE 1984). This is particularly true with regard to large adult crocodiles, which not only pose a safety hazard to investigators, but are prone to mortality from severe anoxic acidosis brought on by prolonged struggle during capture (SEYMOUR et al. 1987).

In addition to morphometric data, information on sex ratios among wild populations of crocodylians is readily collected during field studies, and important for understanding patterns of differential growth and survivorship between the sexes, behavioural dynamics, and the role of temperature-dependent sex determination in the evolution of life history strategies (HUTTON 1987, LANG 1987, WOOD-

WARD & MURRAY 1993, RHODES & LANG 1996, THORBJARNARSON 1997, LANCE et al. 2000). Moreover, information on sex ratios is useful for assessing the potential effects of global climate change on crocodylians (JANZEN 1994, THORBJARNARSON & Wang 2010) and designing management strategies for the sustainable harvest of wild populations (PALMISANO et al. 1973, WEBB et al. 1987, JOANEN et al. 1997).

The American crocodile (*Crocodylus acutus*) is widely distributed in the northern Neotropics, occurring from the southern tip of Florida, USA, along the Atlantic and Pacific Coasts of Mexico, Central America, and northern South America, as well as the Caribbean Islands of Cuba, Jamaica, and Hispaniola (THORBJARNARSON 1989). Significant range-wide declines of *C. acutus* have occurred due to over-exploitation and habitat destruction, and despite legal protection, many populations remain small with limited evidence of recovery (THORBJARNARSON et al. 2006). Consequently, *C. acutus* is considered globally “Vulnerable” by the IUCN (IUCN 2010). In Belize and the Yucatan region of Mexico, *C. acutus* is largely confined to offshore islands (cays) and coral atolls (PLATT et al. 1999b, PLATT & THORBJARNARSON 2000a, 2000b, CHARRUAU et al. 2005, RAINWATER & PLATT 2009), possibly as a result of competitive exclusion by the broadly sympatric Morelet’s crocodile (*Crocodylus moreletii*), which occupies freshwater and brackish wetlands on the mainland (MEERMAN 1992, PLATT & THORBJARNARSON 2000c, THORBJARNARSON et al. 2006, ESCOBEDO-GALVÁN et al. 2008). *Crocodylus acutus* is classified as “Threatened” in Belize (McFIELD et al. 1996), and PLATT & THORBJARNARSON (2000a) estimated that no more than 1000 *C. acutus* remained in the country; more recent survey data suggest this population continues to decline (RAINWATER & PLATT 2009).

Although the biology of *C. acutus* is relatively well-studied (THORBJARNARSON 1989), there is a notable paucity of information regarding morphometric relationships, sex ratios of wild populations, and sexual size dimorphism. Herein we address these deficiencies using morphometric data obtained from a large sample of *C. acutus* captured in the Coastal Zone of northern Belize. We develop predictive models for determining body size from measurements of single attributes, examine ontogenetic changes in cranial morphology, and comment on the maximum total length attained by *C. acutus* in coastal Belize. We also report sex ratios and quantify sexual size dimorphism among *C. acutus*. Finally, we use the length–mass relationship and population survey data to estimate the standing crop biomass (total mass of all individuals in a population at a given time) of *C. acutus* in the Turneffe Atoll.

Materials and methods

We captured crocodiles during 1996–98, 2002, and 2008–09 in conjunction with population surveys (PLATT & THORBJARNARSON 1996, PLATT et al. 1999b, PLATT & THORBJARNARSON 2000a, PLATT et al. 2004, RAINWATER & PLATT 2009), and studies of reproduction (PLATT & THORBJARNARSON 2000b) and population genetics (HEKKALA 2004) conducted in the Coastal Zone of Belize. The Coastal Zone as defined by McFIELD et al. (1996) encompasses the Belize

barrier reef, all offshore cays and atolls, and the mainland within 10 km of the Caribbean Sea. The Belize barrier reef extends north–south for 220 km along the coast, being separated from the mainland by a narrow (18–30 km) stretch of open water known as the inner channel (McFIELD et al. 1996). Within this channel are approximately 450 cays with a combined land area of 689 km² (McFIELD et al. 1996). Three coral atolls are found outside of the barrier reef: the Turneffe, Lighthouse, and Glovers Atolls (STODDART 1962). The Turneffe Atoll is the largest of these with a surface area (open water, land, and mangrove) of 533 km² (STODDART 1962); this total includes 8771 ha of mangrove habitat (McFIELD et al. 1996). Lighthouse and Glovers Atolls consist largely of submerged coral reefs (STODDART 1962, PLATT et al. 1999a). Coastal Belize is described in greater detail elsewhere (STODDART 1962, McFIELD et al. 1996, PLATT et al. 1999a).

Crocodiles were captured at night with the aid of a spotlight; smaller crocodiles (total length [TL] ≤ 100 cm) were taken by hand or dip-net, and a noose-pole was used to capture larger individuals (TL > 100 cm). Hatchlings were captured in nursery lagoons adjacent to communal nesting areas during July–August, shortly after emerging from nests in mid- to late July (PLATT & THORBJARNARSON 2000b, PLATT et al. 2002). Each crocodile was permanently marked for future identification by notching the dorsal edge of a unique series of caudal scutes (JENNINGS et al. 1991, RAINWATER et al. 2007) and released at the site of capture within 12 to 24 hours.

We recorded the following measurements from captured crocodiles (cranial measurements in Fig. 1):

1. Total length (TL): distance from the tip of the snout to the tip of the tail, measured along the ventral surface.
2. Snout–vent length (SVL): distance from the tip of the snout to the anterior margin of the cloacal vent, measured along the ventral surface.
3. Dorsal cranial length (DCL): distance from the tip of the snout to the median posterior edge of the supraoccipital bone.
4. Cranial width (CW): maximum distance between the surangular bones at the level of jaw articulation.
5. Snout length (SL): distance from the tip of the snout to the anterior orbital border, measured medially.
6. Snout width (SW): basal snout width, measured across the anterior orbital borders.
7. Rear foot length (RFL): distance from the posterior-most margin of the heel to the tip of the longest claw (third digit), measured on the right rear foot of crocodiles with a TL ≥ 100 cm.
8. Body mass (BM).

Although in some cases we use a different terminology for clarity, these measurements are consistent with previous morphometric studies of crocodylians (WEBB & MESSEL 1978, MONTAGUE 1984, HUTTON 1987a, HALL & PORTIER 1994). TL, SVL, and RFL were measured with a steel tape to the nearest 0.1 cm. Cranial measurements were taken with dial callipers (±0.1 mm) on smaller crocodiles (DCL < 15 cm), or tree callipers (±0.1 cm) on larger individuals. Hatchling body mass was measured to the nearest 1.0 g with Pesola spring scales. Body mass of small (<1.0 kg), medium (1.0 to 5.0 kg), and large juvenile (5.1 to 10.0 kg) crocodiles was measured with spring scales to

the nearest 0.01, 0.05, and 0.1 kg, respectively. Crocodiles of > 10.0 kg were weighed to the nearest 1.0 lb (0.45 kg) with a spring scale, and this value was converted to kg by dividing it by 2.2; these values were rounded to the nearest 0.5 kg to avoid false precision. With the exception of recent hatchlings, crocodiles were sexed by manual probing of the cloaca (BRAZAITIS 1968).

We fit untransformed morphometric data with least-squares linear regressions to determine predictive relationships. Single attributes (DCL, CW, SL, SW, RFL) were treated as independent variables and regressed separately against body size (SVL and TL). A natural log transformation was used to linearise the relationship between length (TL and SVL) and BM before regressing these variables. To plot ontogenetic changes in cranial morphology we followed TUCKER et al. (1996) and regressed the ratio of DCL: CW against SVL. According to BRAZAITIS (1973), a SL:SW ratio of 1.8 to 2.5 is characteristic of *C. acutus* and useful for distinguishing it from the morphologically similar and broadly sympatric *C. moreletii*. To test this hypothesis, we regressed SL:SW against SVL and compared this relationship to published values for *C. moreletii*. We also calculated the DCL:TL ratio of our sample, and then regressed DCL:TL against TL to determine if this ratio remained constant across size classes of *C. acutus*.

We used a Student's t-test to test the one-tailed hypothesis that SVL of adult male *C. acutus* was significantly greater than that of adult females. In most populations of *C. acutus*, females are thought to become sexually mature at a TL of 210 cm (THORBJARNARSON 1989); however, studies of reproductive ecology in Belize indicate that for reasons as yet unclear, females attain sexual maturity at a somewhat smaller TL of 180 cm (PLATT & THORBJARNARSON 2000b). Similar to most other species of crocodylians (FERGUSON 1985), it is likely that male *C. acutus* become sexually mature at about the same body size as females (THORBJARNARSON 1989).

The degree of size dimorphism (defined as a statistically significant difference in mean length or mass of sexually mature organisms from the same population during a given

time interval) between the sexes was quantified with a compressed sexual size dimorphism index (SDI) (LOVICH & GIBBONS 1992). SDI is a dimensionless number calculated by dividing the mean size of the larger sex by the mean size of the smaller sex and then adding or subtracting one from this value depending on whether males or females, respectively, are the larger sex (LOVICH & GIBBONS 1992). Although SDI may be based on mass or some measurement of length (TL or SVL), we selected SVL as the appropriate variable because body mass in crocodylians often exhibits considerable variation among animals of similar length owing to the presence of eggs in gravid females, recent ingestion of large meals, and overall body condition (WEBB & MESSEL 1978, MONTAGUE 1984). Furthermore, we used SVL rather than TL because the latter is dependent on tail length and distal portions of the tail are occasionally missing or deformed as a result of past injuries (WEBB & MESSEL 1978).

Standing crop biomass of *C. acutus* in the Turneffe Atoll was calculated using an estimate of population size determined during 1996–97 (PLATT & THORBJARNARSON 2000a). Based on nocturnal spotlight counts, PLATT & THORBJARNARSON (2000a) estimated that 220 non-hatchling *C. acutus* inhabited the atoll, including 45 juveniles (TL = 30–90 cm), 83 subadults (TL = 91–180 cm), and 92 adults (TL = 181–320 cm). To estimate biomass we followed THORBJARNARSON (1988) and calculated body mass for the mean value of each size class using the TL–BM relationship, and multiplied this value by the estimated number of individuals in that size class. Biomass values for each size class were then summed to obtain the standing crop biomass of *C. acutus* in the atoll. Statistical references are from ZAR (1996). Mean values are presented throughout as \pm 1 SD and results considered significant at $P \leq 0.05$.

Results

We collected morphometric data from 151 *C. acutus* ranging in TL from 26.0 to 301.7 cm, although not all attributes were measured on each crocodile (Fig. 2). Our sample included 38 hatchlings (<30 days old) with a mean TL, SVL, and BM of 28.9 ± 2.0 cm (range = 26.0 to 34.0 cm), 13.7 ± 0.9 cm (range = 12.4 to 16.3 cm), and 62 ± 12 g (range = 50–90 g), respectively. With the exception of RFL ($r^2 = 0.87$), very strong positive allometric relationships ($r^2 \geq 0.98$) were found between measurements of body length (TL and SVL) and other attributes; individual variation was somewhat more pronounced among larger crocodiles (Figs. 3 & 4; Table 1). Log transforming variables other than BM failed to improve the fit of our models. The ratio of dorsal cranial length to cranial width (DCL: CW) ranged from 1.58 to 2.42. Although considerable individual variation was apparent, a scatter plot of DCL: CW against SVL exhibited an overall nonlinear trend described by the equation $DCL: CW = 1.841 + 0.012SVL - 0.00008SVL^2$ ($r^2 = 0.67$; $p < 0.0001$) (Fig. 5). The maximum DCL: CW ratio of 2.4 was associated with a SVL of 42 to 81 cm. The ratio of snout length to snout width (SL: SW) ranged from 1.14 to 2.18. The relationship between SL: SW and SVL was nonlinear and is described by the equation $SL: SW = 1.075 + 0.022SVL - 0.0001SVL^2$ ($r^2 = 0.87$; $p < 0.0001$) (Fig. 6).

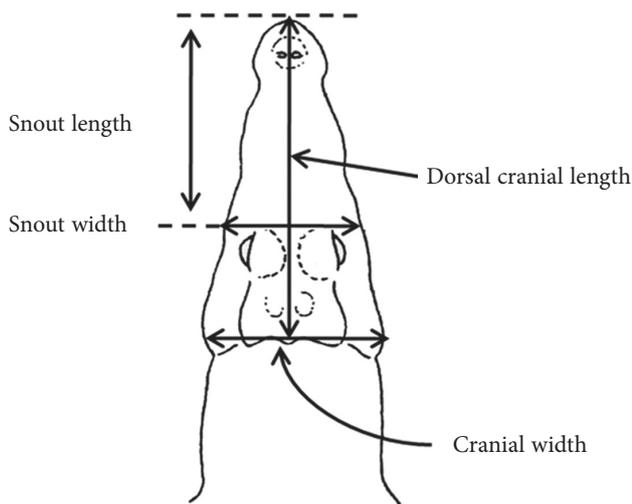


Figure 1. Dorsal view of a *Crocodylus acutus* head showing cranial measurements.

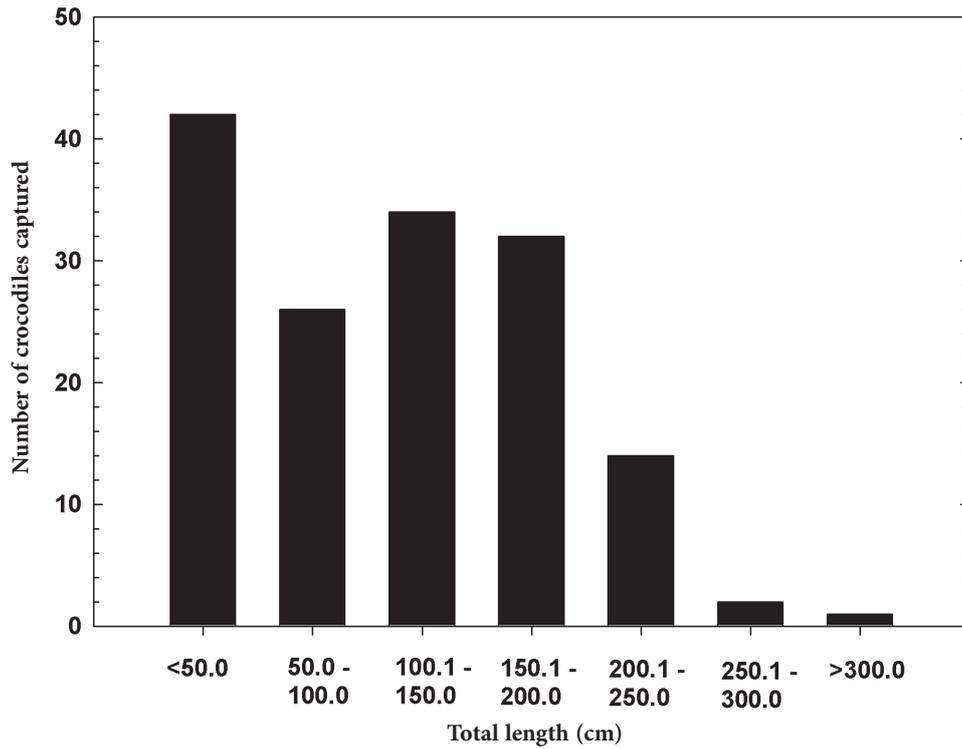


Figure 2. Size class distribution of 151 *Crocodylus acutus* captured in the Coastal Zone of Belize and used to derive equations for predicting body size from single physical attributes.

The ratio of dorsal cranial length to total length (DCL:TL) ranged from 0.14 to 0.17; the mean value was 0.15. The relationship between DCL:TL and TL was not significant ($r^2 = 0.0003$), and DCL:TL remained relatively constant across the range of body sizes in our sample (Fig. 7).

We were able to identify the sex of 107 crocodiles (51 females:56 males) in our sample; 44 hatchlings and small juveniles could not be confidently sexed. The overall sex ratio (female:male) was slightly male-biased (1:1.09), but not significantly different from parity ($\chi^2 = 0.23$, $df = 1$).

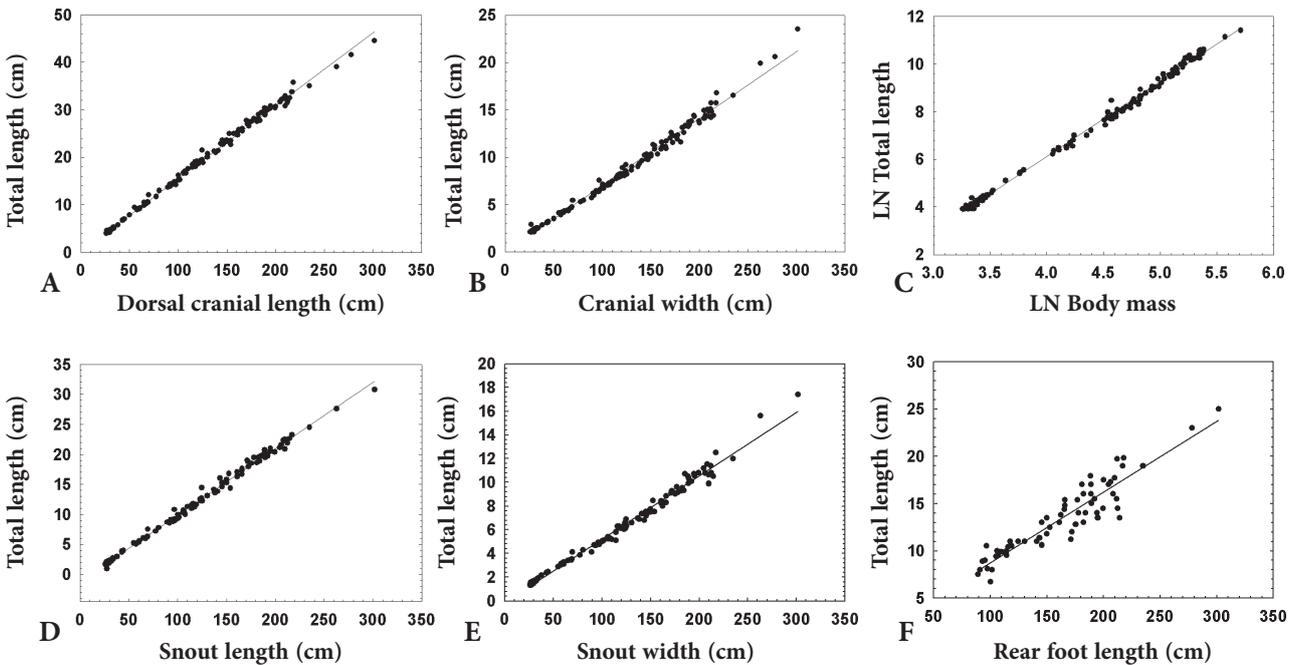


Figure 3. Relationship between total length (TL) and dorsal cranial length (A), cranial width (B), body mass (C), snout length (D), snout width (E), and rear foot length (F) in *Crocodylus acutus* from coastal Belize.

Crocodylus acutus morphometrics

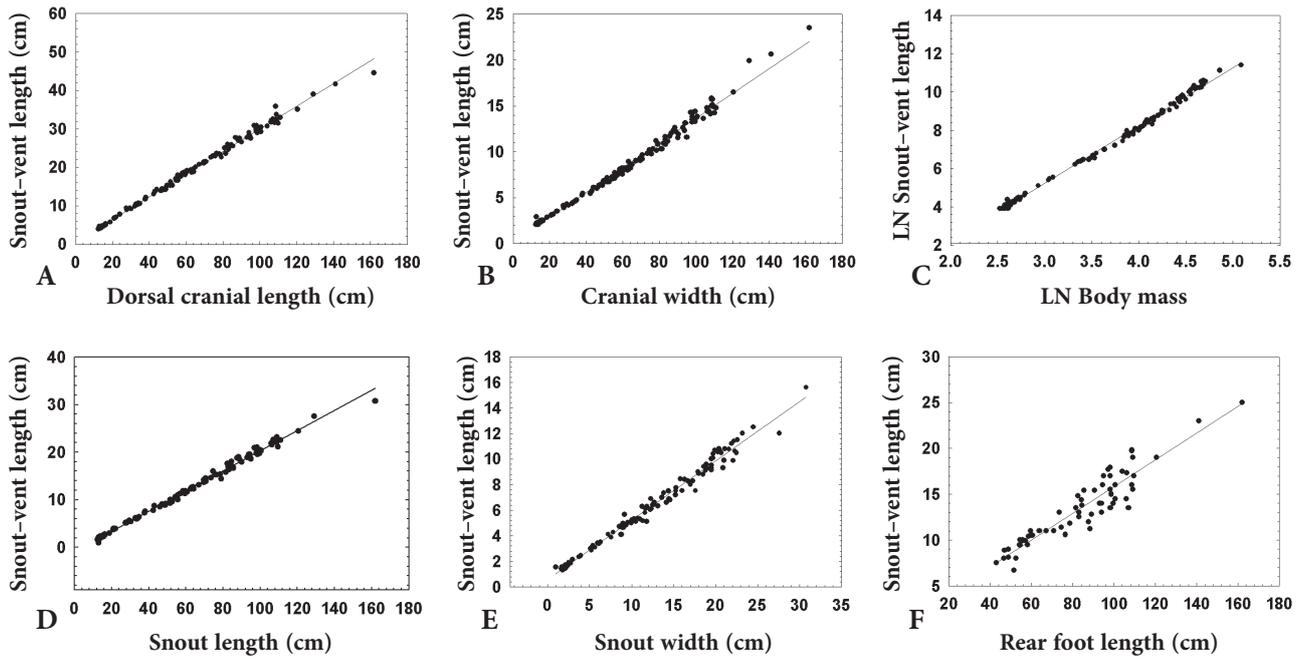


Figure 4. Relationship between snout-vent length (SVL) and dorsal cranial length (A), cranial width (B), body mass (C), snout length (D), snout width (E), and rear foot length (F) in *Crocodylus acutus* from coastal Belize.

Our sample included 37 sexually mature ($TL \geq 180$ cm) crocodiles; 22 females and 15 males. The adult sex ratio was female-biased (1:0.68), but likewise did not differ significantly from parity ($\chi^2 = 1.76$, $df = 1$). The mean SVL of adult male and female *C. acutus* was 111.3 ± 20.7 cm (range = 87.5–162.0 cm), and 101.0 ± 6.2 cm (range = 90.5–111.0 cm), respectively. A frequency distribution indicated that males were larger than females (Fig. 8), and the mean SVL of males was significantly greater than that of females

($t = 1.8$, $df = 14$; $p < 0.05$); a SDI of 2.10 was calculated for this sample.

We used equation 12 (Table 1) to estimate the standing crop biomass of *C. acutus* in the Turneffe Atoll. We divided this value by the area of mangrove habitat (8771 ha; MCFIELD et al. 1996) and km of shoreline (229 km; PLATT & THORBJARNARSON 2000a) in the Turneffe Atoll (Table 2), and present biomass estimates as both kg/ha and kg/km to facilitate comparisons with other studies (Table 3).

Table 1. Regression equations for predicting total length (TL) and snout-vent length (SVL) of *Crocodylus acutus* from other morphometric attributes (DCL = dorsal cranial length; CW = cranial width; SL = snout length; SW = snout width; RFL = rear foot length; BM = body mass). TL, SVL, DCL, CW, SL, SW, and RFL in cm; BM in grams. ** $P \leq 0.001$

Equation no. and predictor X	Estimated value Y	Equation	r ²	n
1. SVL	TL	TL = 1.91SVL + 2.30	0.99**	151
2. DCL	TL	TL = 6.49DCL - 0.82	0.99**	149
3. DCL	SVL	SVL = 3.80DCL - 1.56	0.99**	150
4. CW	TL	TL = 14.08CW + 0.89	0.99**	150
5. CW	SVL	SVL = 7.34CW - 0.64	0.99**	150
6. SL	TL	TL = 9.01SL + 10.80	0.99**	131
7. SL	SVL	SVL = 4.68SL + 4.57	0.99**	131
8. SW	TL	TL = 18.60SW + 3.00	0.98**	132
9. SW	SVL	SVL = 9.63SW + 0.84	0.99**	132
10. RFL	TL	TL = 11.63RFL - 6.35	0.87**	63
11. RFL	SVL	SVL = 6.00RFL - 2.83	0.87**	63
12. BM	TL	lnTL = 0.31lnBM + 2.06	0.98**	123
13. BM	SVL	lnSVL = 0.32lnBM + 1.27	0.98**	123

Discussion

Smaller crocodiles were somewhat over-represented in our sample when compared to size class distributions derived from population surveys (PLATT & THORBJARNARSON 2000a, PLATT et al. 2004, RAINWATER & PLATT 2009),

which probably reflects their ease of capture (PLATT et al. 2009). Except for extremely large crocodiles, which survey data suggest are rare in coastal Belize (PLATT & THORBJARNARSON 2000a), adults were adequately represented in our sample. The variation noted in morphometric relationships among adult *C. acutus* suggests that larger crocodiles

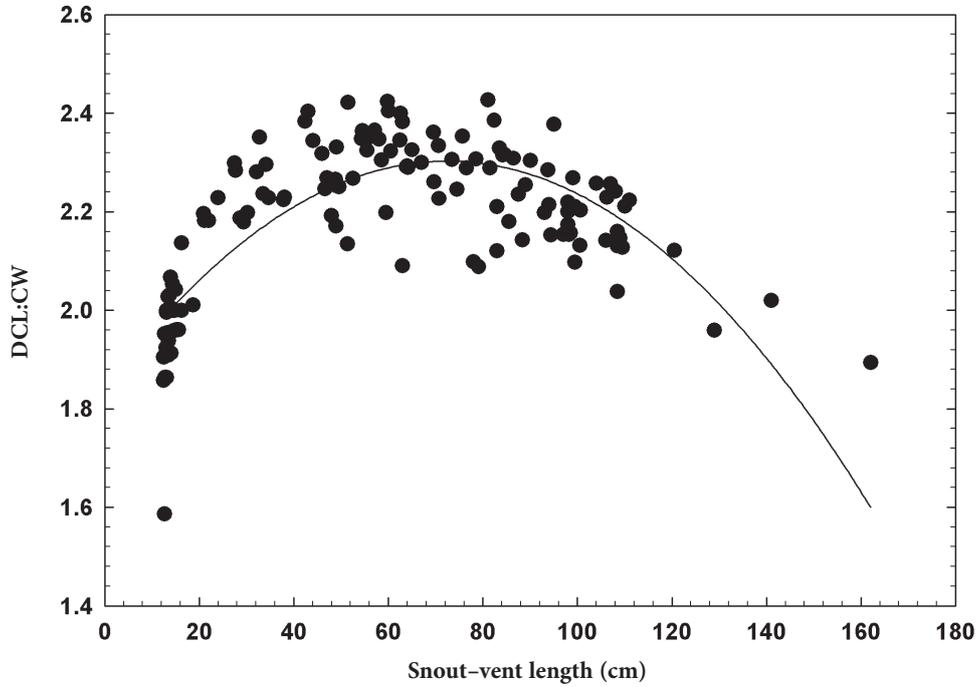


Figure 5. Relationship of the ratio of dorsal cranial length:cranial width (DCL: CW) to snout-vent length (SVL) in *Crocodylus acutus* from coastal Belize.

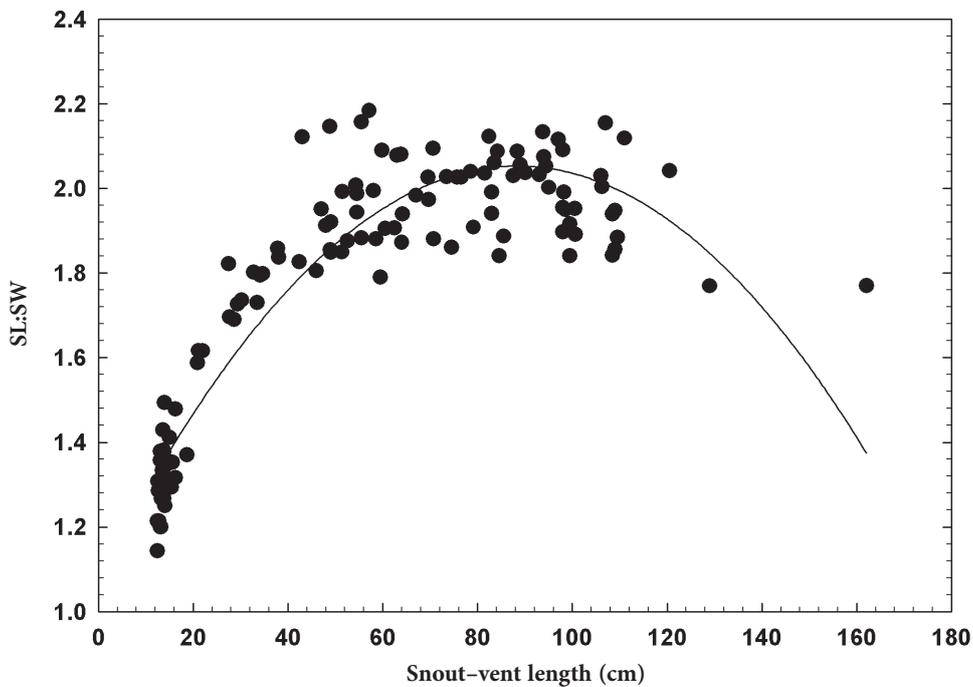


Figure 6. Relationship of the ratio of snout length:snout width (SL: SW) to snout-vent length (SVL) in *Crocodylus acutus* from coastal Belize.

Crocodylus acutus morphometrics

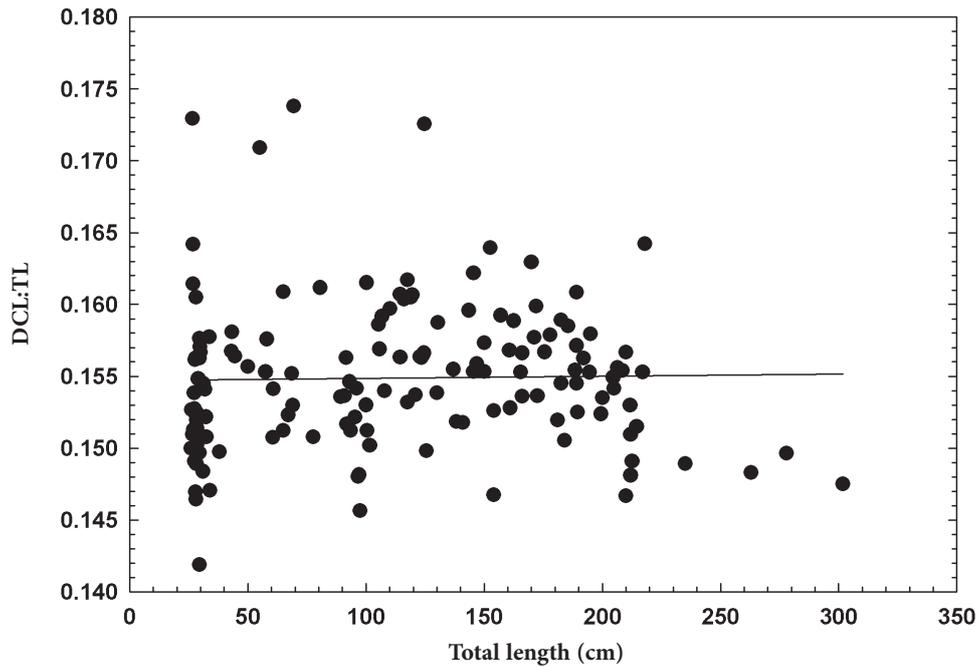


Figure 7. Relationship of the ratio of dorsal cranial length:total length (DCL:TL) to total length (TL) in *Crocodylus acutus* from coastal Belize.

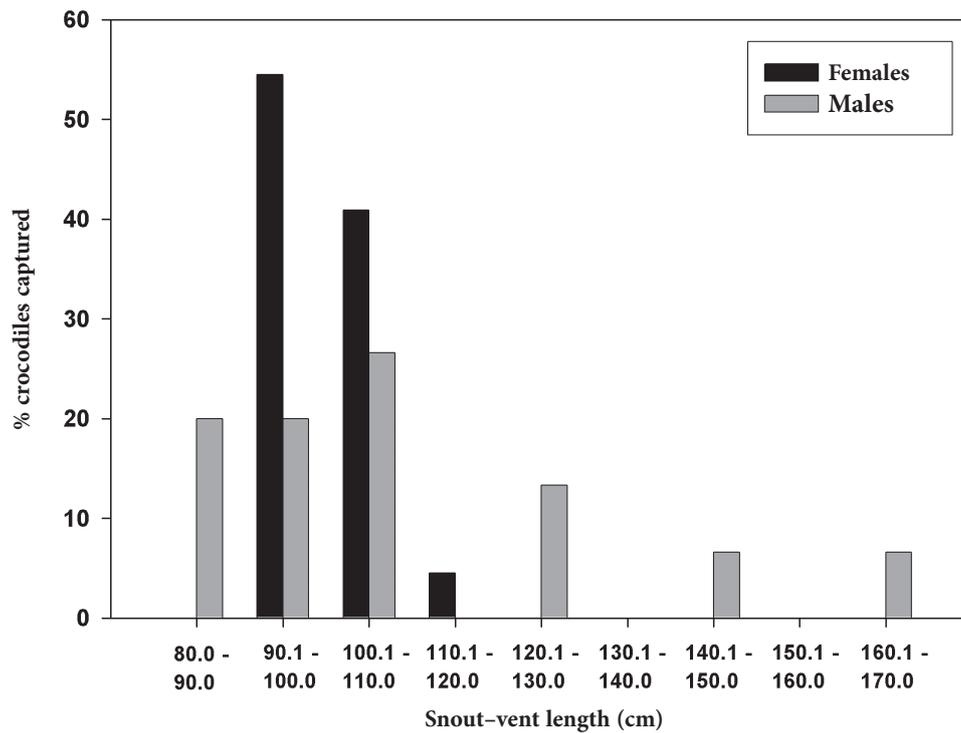


Figure 8. Size class distribution (snout-vent length) of adult male (n = 15) and female (n = 22) *Crocodylus acutus* captured in coastal Belize.

are more variable in body form than smaller size classes (WEBB & MESSEL 1978, MONTAGUE 1984, HUTTON 1987a, PLATT et al. 2009); however, this is probably also due in part to the difficulty of measuring large adults (HUTTON 1987a, RAINWATER et al. 2010). Similar to our results, oth-

ers have likewise found highly significant allometric relationships between measurements of body length and various morphometric attributes of crocodylians (WEBB & MESSEL 1978, CHENTANEZ et al. 1983, MONTAGUE 1984, HUTTON 1987a, PLATT et al. 2009). Because these morpho-

Table 2. Estimated standing crop biomass of non-hatchling *Crocodylus acutus* in the Turneffe Atoll, Belize. Population and size class data from PLATT & THORBJARNARSON (2000a). Individual body mass estimated from equation 12 in Table 1. Biomass estimates based on 8771 ha of mangrove habitat (McFIELD et al. 1996) and 229 km of shoreline (PLATT & THORBJARNARSON 2000a) in the Turneffe Atoll.

Size class	Total length (cm)	Median length (cm)	Predicted individual body mass (g)	Number of individuals	Estimated biomass (g)
Juveniles	30 – 90	60	779	45	35,055
Subadults	91 – 180	135	10,614	83	880,962
Adults	181 – 320	250	77,808	92	7,158,336
Total standing crop biomass (g)					8,074,353
Biomass/ha (kg/ha)					0.92
Biomass/km shoreline (kg/km)					35.2

metric attributes display strong allometric relationships, it is possible to reliably estimate TL and SVL from measurements of skulls, tracks, body parts, and calibrated photographs (WEBB & MESSEL 1978, CHOQUENOT & WEBB 1987, HUTTON 1987a, HALL & PORTIER 1994, PLATT et al. 2006).

Measurements of rear foot tracks are useful in calculating the body size of crocodylians (particularly nesting females) and have been used to this end with a variety of species (e.g., SINGH & BUSTARD 1977, WEBB et al. 1977, THORBJARNARSON & HERNANDEZ 1993, PLATT et al. 1990, WILKINSON & RICE 2000, PLATT et al. 2008a). When crocodylians walk, the rear feet carry a large proportion of the body weight and leave deeper and more distinct imprints than the much smaller forefeet (HUTTON 1987a). Importantly, measurement error is minimal because the track length differs little (± 0.1 cm) from the actual rear foot length (PLATT et al. 1990, WILKINSON & RICE 2000). We used measurements of rear foot tracks found at nesting beaches to estimate the body size of nesting females during a study of *C. acutus* reproductive ecology in coastal Belize (PLATT & THORBJARNARSON 2000b). The damp, compact sand where females exited the water and emerged onto nesting beaches provided an excellent substrate for capturing measurable quality tracks. However, because tracks are ephemeral and rapidly degraded by wind and water, finding measurable quality tracks generally proved difficult.

The change in the DCL: CW ratio of *C. acutus* reflects a reversal in the relative growth rates of these two cranial measurements; as the skull begins to broaden relative to length, the ratio declines. Similar ontogenetic changes in relative cranial dimensions are common among crocodylians (DODSON 1975, WEBB & MESSEL 1978, HUTTON 1987b, HALL & PORTIER 1994, TUCKER et al. 1996, PLATT et al. 2009), and probably result from selective pressures to strengthen the skull and increase gape capacity for capturing larger prey as crocodiles mature (DODSON 1975, HALL & PORTIER 1994). As such, these ontogenetic changes in skull structure are generally accompanied by dietary shifts to meet the energetic demands of rapid growth (HUTTON 1987b, TUCKER et al. 1996). In crocodylians studied to date, larger vertebrates are incorporated into the diet when the DCL: CW ratio reaches 2.4 to 2.6 (WEBB & MESSEL 1978, HUTTON 1987b, TUCKER et al. 1996). Because this cranial ratio is similar among different species of crocodylians, TUCKER et al. (1996) posit the existence of a common structural threshold for taking on large prey. Among

our sample, 2.4 was the maximum value of the DCL: CW ratio, and only six crocodiles had a ratio ≥ 2.4 (range = 2.40–2.42). This maximum DCL: CW ratio was attained in the mid-range of body sizes (TL ca. 85–160 cm), and thereafter moderately declined with increasing body size as CW broadened relative to DCL. As in other crocodylians, broadening of the skull in *C. acutus* occurs at a body size that coincides with a dietary shift from invertebrates to larger vertebrate prey (THORBJARNARSON 1988, VILLEGAS & SCHMITTER-SOTO 2008).

The range of values that we calculated for SL: SW (1.14–2.18) partially overlapped with the lower range (1.8–2.5) given for *C. acutus* by BRAZAITIS (1973). In our sample, a SL: SW ratio of > 1.8 was typical of the larger size classes (SVL ca. 55–140 cm), although considerable individual variation was evident. Additionally, the SL: SW ratios we found among *C. acutus* from coastal Belize overlapped considerably with SL: SW ratios (1.06–1.86) of *C. moreletii* from the same region (PLATT et al. 2009). Consequently, we consider this attribute to be of little use in distinguishing these two morphologically similar species, in particular as they occasionally hybridise (HEKKALA 2004, RAY et al. 2004). These findings further support our earlier conclusion (PLATT & RAINWATER 2005, PLATT et al. 2009) that the best diagnostic character for distinguishing the two species is the presence of irregular scale groups among the subcaudal scutes of *C. moreletii*, which are lacking in *C. acutus* (ROSS & ROSS 1974).

It is widely assumed that a DCL: TL ratio of 1:7 (0.14) is typical of most crocodylians, and this ratio is thought to remain constant over a range of body sizes, from hatchlings to large adults (BANKS 1931, SCHMIDT 1944, WERMUTH 1964, BELLAIRS 1969, DANIEL & HUSSAIN 1973, GREER 1974). This standard DCL: TL ratio has been used to estimate the size of animals encountered during spotlight surveys, and the TL of crocodiles from measurements of large skulls (BARBOUR 1924, BARBOUR 1933, DANIEL & HUSSAIN 1973, WHITAKER & WHITAKER 2008). However, because interspecific variation in body form exists among crocodylians, WHITAKER & WHITAKER (2008) question the universal applicability of this ratio to all species. Furthermore, intraspecific changes in relative growth rates make the application of this ratio across a range of body sizes problematic (MONTAGUE 1983). While individual variation in this ratio was apparent in our sample, the mean DCL: TL ratio among *C. acutus* from coastal Belize was slightly greater

Table 3. Estimates of standing crop biomass (kg/ha and kg/km of shoreline) for crocodylian populations.

Species	Estimated biomass	Source
<i>Crocodylus acutus</i>		
Lake Étang Saumâtre (Haïti)	66.6 kg/km	THORBJARNARSON (1988)
Turneffe Atoll (Belize)	35.2 kg/km	This study
Turneffe Atoll (Belize)	0.92 kg/ha	This study
<i>Crocodylus moreletii</i>		
Gold Button Lagoon (Belize)	187.2 kg/km	PLATT et al. (2009)
Gold Button Lagoon (Belize)	9.5 kg/ha	PLATT et al. (2009)
<i>Crocodylus niloticus</i>		
Victoria Nile (Kenya)	397.5 kg/km	GRAHAM (1968)
Lake Turkana (Uganda)	350.0 kg/km	PARKER & WATSON (1970)
Lake Ngezi (Zimbabwe)	172.0 kg/km	HUTTON (1987b)
Lake Ngezi (Zimbabwe)	9.4 kg/ha	Calculated from HUTTON (1987b)
<i>Crocodylus porosus</i>		
Blyth River (Australia)	203.6 kg/km	FUKUDA et al. (2011)
Cadell River (Australia)	109.1 kg/km	FUKUDA et al. (2011)
Liverpool River (Australia)	104.5 kg/km	FUKUDA et al. (2011)
South Alligator River (Australia)	304.4 kg/km	FUKUDA et al. (2011)
West Alligator River (Australia)	146.1 kg/km	FUKUDA et al. (2011)
Wildman River (Australia)	370.3 kg/km	FUKUDA et al. (2011)

than the ratio of 1:7 reported for other species. Moreover, this ratio remained relatively constant across body sizes from hatchlings to large adults. These results suggest that a DCL:TL ratio of 1:7 can yield a close approximation of TL in *C. acutus*, at least within the range of body sizes that we sampled. Because DCL becomes proportionally shorter in relation to TL near the upper asymptotic body size (MONTAGUE 1983), using a ratio of 1:7 to estimate TL may not be appropriate for *C. acutus* beyond the size range of our sample (WEBB & MESSEL 1978).

Maximum body size is relevant from both an evolutionary and ecological perspective, and upper asymptotic size is important when describing growth patterns in crocodylians (WOODWARD et al. 1995). *Crocodylus acutus* ranks among the largest New World crocodylians (THORBJARNARSON 1989) and specimens measuring 6.25 to 7.0 m long have historically been reported (SCHMIDT 1924, BEARD et al. 1942, SCHMIDT & INGER 1957, ALVAREZ DEL TORO 1974), although individuals > 4.0 m are now rare (VARONA 1987, THORBJARNARSON 1989, PEREZ-HIGAREDA et al. 1991, DOMÍNGUEZ-LASO 2009). There are few reliable historic reports of large crocodiles from Belize, and owing to the similarity between *C. acutus* and *C. moreletii*, it is generally impossible to conclude which species is being referenced. For instance, GANN (1925) observed a crocodile estimated to be 4.8 m long in the Rio Grande River of southern Belize that was probably *C. acutus* because this region lies beyond the (ill-defined) southern distributional limit of *C. moreletii* (PLATT et al. 1999c). However, such reports must be interpreted with caution as visual estimates of TL are unreliable and even experienced researchers encounter difficulties when estimating the size of large crocodylians (MAGNUSSON 1983). FROST (1974) reported crocodile skins measuring 14 to 15 feet (TL ca. 426–457 cm) listed in government trade statistics, but these records make no dis-

inction between *C. moreletii* and *C. acutus*. Furthermore, reptile skins often stretch considerably during preparation; in snake skins this may be up to 25% (OLIVER 1958). Therefore, size estimates based on the length of dried skins must be regarded as ambiguous at best.

This study and size data from population surveys (PLATT et al. 2004, PLATT & THORBJARNARSON 2000a) collectively suggest that *C. acutus* in coastal Belize have a smaller body size in comparison to other populations (RAINWATER et al. 2010, 2011). Whether this is due to past over-hunting, which selectively removed large adult crocodiles, or genetic and environmental factors remains unresolved. Crocodile populations in Belize were decimated by unregulated commercial skin hunting that ceased only after legal protection was afforded in 1981 (PLATT & THORBJARNARSON 2000a, 2000b). Few adult crocodiles remained by the late 1970s (ABERCROMBIE et al. 1980), and populations may have yet to recover from this period of intense over-exploitation. Alternatively, the small body size of crocodiles in coastal Belize could be the consequence of reduced growth rates, which preliminary data suggest are among the lowest reported for any population of *C. acutus*, possibly because of osmoregulatory costs entailed by dwelling in a marine environment (PLATT & THORBJARNARSON 1997).

The sex ratio that we found among *C. acutus* in coastal Belize is consistent with our earlier reports based on less extensive sampling (PLATT & THORBJARNARSON 1996, 2000a). Although biased sampling is a major impediment to analysing sex ratios of crocodylian populations (THORBJARNARSON 1997), we are unaware of any obvious source of potential bias in our study and believe that sampling was essentially random; captures occurred throughout the year, in many locations, and in a variety of habitats throughout the Coastal Zone. Although male- (THORBJARNARSON 1989, CHARRUAU et al. 2005) and female- (LANCE et al.

2000) biased populations of *C. acutus* have been reported, the sex ratio of most populations does not significantly deviate from 1:1 (GABY et al. 1985, THORBJARNARSON 1988, KUSHLAN & MAZZOTTI 1989, BRANDT et al. 1995, CEDEÑO-VAZQUEZ et al. 2006). This is not unexpected as THORBJARNARSON (1997) found that neutral, and male- and female-biased sex ratios are evident at the intraspecific level among the Crocodylia. Assuming unbiased sampling, deviations from a 1:1 adult sex ratio in crocodylian populations could result from differential patterns of temperature-dependent sex determination, annual variation in weather, and differences in survivorship and growth between males and females (GIBBONS 1990, RHODES & LANG 1996, THORBJARNARSON 1997, LANCE et al. 2000).

While it has long been recognized that males are the larger sex in *C. acutus* (ALVAREZ DEL TORO 1974, NEILL 1971), our study is the first to quantify this size differential. Interestingly, the SDI value we calculated for *C. acutus* is almost identical to that of *C. moreletii* (2.12) from the same region (PLATT et al. 2009). To our knowledge, these are the only two attempts to quantify sexual size dimorphism in crocodylians using the compressed SDI, although this index is being increasingly applied to turtles (e.g., GIBBONS & LOVICH 1990, FORSMAN & SHINE 1995, BROPHY 2006, PLATT et al. 2008b). The compressed SDI is a simple and universally applicable index that allows meaningful interpretations of sexual size differences across all phylogenetic groups (LOVICH & GIBBONS 1992), and we reiterate our earlier suggestion (PLATT et al. 2009) that it henceforth be adopted in studies of crocodylians.

Sexual size differences appear ubiquitous among the Crocodylia (FITCH 1981), with males being approximately 20% larger than females (PLATT et al. 2009). Sexual size dimorphism is thought to result from different selective pressures faced by females and males (BERRY & SHINE 1980, SHINE 1989). Female growth trajectories slow upon reaching sexual maturity as energy is diverted from growth and allocated to reproduction (JACOBSEN & KUSHLAN 1989, TUCKER et al. 2006), while males must compete for females in a polygynous breeding system (LANG 1987) where large body size undoubtedly confers a fitness advantage in aggressive male-to-male encounters (HOWARD 1978).

Other causal mechanisms that have been invoked to explain differences in body size among the sexes are probably unimportant in crocodylians. Selection may favour larger male body size if males must overpower and forcibly inseminate females during courtship (GHISELIN 1974), but forced insemination is not part of the crocodylian courtship sequence (LANG 1987). Ecological models that attempt to explain sexual size differences suggest that males and females consume different foods as a means of avoiding potential intraspecific competition (SLATKIN 1984). However, we are unaware of any studies that demonstrate intersexual dietary differences among *C. acutus* or any other crocodylian, and as SHINE (1989) cautions, ecological differences between the sexes are likely a consequence rather than a cause of the observed patterns of size dimorphism. Finally, it is important to recognize that the degree of sexual size dimorphism can vary among populations of the same species due to population-specific growth patterns, size-specific mortality, and food availability, and also within the same population over time (LOVICH & GIBBONS 1992).

Therefore, additional studies of sexual size dimorphism in *C. acutus* throughout its extensive distribution and over longer periods are warranted.

Biomass estimates are important in understanding the role of organisms in community organization, energy flow, and ecosystem productivity (DODD 1998). Owing to their lower energetic demands, reptiles often have a standing crop biomass several orders of magnitude greater than populations of similar-sized endothermic vertebrates (POUGH 1980, IVERSON 1982, SHINE 1986). There are few estimates of standing crop biomass for aquatic vertebrates other than fish and salamanders (GIBBONS et al. 2006), and to our knowledge, biomass estimates are available for only four species of crocodylians at 11 locations. Contrary to the standard convention of presenting biomass estimates as body mass per unit of area (e.g., IVERSON 1982, SHINE 1986, DODD 1998), estimates for crocodile populations are often given as body mass per unit of shoreline distance (GRAHAM 1968, PARKER & WATSON 1970, HUTTON 1987b, THORBJARNARSON 1988, FUKUDA et al. 2011). Presumably, this is because crocodiles are most abundant in the shallow littoral zone while avoiding the deeper, open waters of the rivers and lacustrine habitats where these studies were conducted. Consequently, biomass estimates based on the total surface area of these waterbodies are much lower than those based on shoreline distances (e.g., HUTTON 1987b, THORBJARNARSON 1988, PLATT et al. 2009).

Our estimate of *C. acutus* biomass (kg/km) in the Turneffe Atoll is about half the value calculated for Lake Étang Saumâtre by THORBJARNARSON (1988); notably, both populations occur in mangrove habitats characterized by brackish or saline conditions. Regardless of whether values for kg/km or kg/ha are considered, biomass estimates for *C. acutus* are among the lowest reported for any crocodylian. These results are somewhat surprising as crocodylian biomass is ultimately determined by primary productivity, which is generally high in mangrove habitats and often comparable to freshwater systems (MITSCH & GOSSELINK 2000). Additionally, mangrove habitats support a diverse prey base of crustaceans, gastropods, fish, and wading birds. The depressed biomass characteristic of *C. acutus* in both Étang Saumâtre and Turneffe Atoll might be an artefact of past over-exploitation and could increase if populations recovered. In northern Australia, *C. porosus* biomass began to increase immediately after legal protection became effective in the early 1970s, and continues to increase even as population densities have stabilized, presumably because large crocodiles continue to grow even larger (FUKUDA et al. 2011). Because crocodylians are territorial (LANG 1987), social constraints could also be important in determining densities and hence biomass. If foraging areas are defended as suggested by LANG (1987), territory size may decrease (with a concomitant increase in crocodile density) in response to increasing prey abundance in more productive habitats. Although studies suggest this to be the case among many species of birds (reviewed by GILL 1995), the interplay between resource availability and territory size in crocodylians has not been investigated.

In conclusion, we found highly significant, positive allometric relationships between measurements of body length (TL and SVL) and single morphometric attributes of *C. acutus* from coastal Belize. The consistently high

r^2 -values of these relationships indicate all attributes are suitable estimators of body size. Importantly, equations relating single attributes to body size can be used to reliably estimate TL and SVL from tracks, skulls, other body parts, and calibrated photographs. For example, because crocodiles are rarely observed at nesting beaches and trapping at these sites could potentially cause nest abandonment, measurements of rear foot tracks proved especially useful for estimating the body size of nesting females (PLATT & THORBJARNARSON 2000b). We also used skulls obtained from fishermen to estimate the body size of crocodiles that drowned in fishing nets (PLATT & THORBJARNARSON 1997), and most crocodiles observed during nocturnal spotlight surveys were assigned to body size categories on the basis of DCL (PLATT & THORBJARNARSON 2000a). Finally, our data on the sex ratio of *C. acutus* in coastal Belize lend further support to the contention of THORBJARNARSON (1997) that blanket claims of female-biased sex ratios among the Crocodylidae (e.g., DEEMING & FERGUSON 1989, WOODWARD & MURRAY 1993) are unwarranted.

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