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Research article

Using growth rates to estimate the minimum age and size at sexual maturity in a captive population of the critically endangered Central American river turtle *Dermatemys mawii*

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Abstract

The Central American river turtle *Dermatemys mawii* is a critically endangered species that has incurred substantial losses over the last several decades due to overhunting. This species is now being considered for head-starting programmes (i.e., captive breeding of turtles for wild release). However, relatively little is known about their life history characteristics, especially with respect to growth and sexual maturation. A robust knowledge of *D. mawii* life history traits is important in developing conservation management plans. This research is the first known study to maintain hatchlings, juveniles and adults in captivity with regular morphometric data collection. Growth rates were quantified (cm yr^{-1}) and growth parameters were calculated (e.g., growth coefficients) to estimate body size and age at onset of sexual maturity in a group of wild-caught but captive-held and captive-bred *D. mawii* in Belize. Sizes at the onset of sexual maturity were inferred by segmented linear regressions that identified changes in growth rate by body size. Asymptotic sizes and growth coefficients were calculated using the Fabens method and the Wang method. Parameters from these models were then applied to a modified von Bertalanffy growth equation to estimate age at the onset of sexual maturity. Male and female *D. mawii* begin sexual maturation at approximately 38.0 cm and 40.0 cm straight-line carapace length, respectively. Ages associated with these sizes were estimated at 13.5–16.9 years (males) and 13.6–17.3 years (females). No previous literature on growth rates or age at maturation for wild or captive *D. mawii* has been reported, so these results serve as a starting point in conservation management. Given the life history trait of delayed sexual maturity (>10 years), *D. mawii* may be more sensitive to losses of the adult population; therefore, captive breeding and head-starting programmes may be beneficial with concomitant protection of wild, adult populations.

Introduction

The Central American river turtle *Dermatemys mawii* is found in coastal lowlands of southern Mexico, northern Guatemala and Belize (Vogt et al. 2011) and is the lone surviving species within the family Dermatemydidae (Iverson and Mittermeier 1980). It is a relatively large freshwater turtle characterised by a smooth, broad carapace and webbed feet with robust claws. *Dermatemys mawii* is highly aquatic; generally only females come ashore (to nest), and neither sex basks (Vogt et al. 2011). The Central American river turtle has been intensely harvested for its meat (Moll 1986; Polisar and Horwich 1994; Polisar 1994; 1995) throughout its restricted range. As a result, *D. mawii* has been virtually eliminated from much of its former range in southern Mexico (Gonzales-Porter et al. 2011; Vogt et al. 2011). Populations continue to decline in Belize (Moll 1986; Polisar and Horwich 1994; Rainwater et al. 2012) and its status in Guatemala remains unclear (Polisar 1994). Currently, *D. mawii* is considered one of the world's most heavily exploited turtles and is classified as Critically Endangered by the International Union for the Conservation of Nature (IUCN), Endangered under the US Endangered Species Act, listed on Appendix II of the Convention on International Trade in Endangered Species of Faina and Flora (CITES), and is the 15th most endangered

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turtle species in the world (CITES 2009; IUCN 2009; USFWS 2009; Turtle Conservation Coalition 2011). Conservation efforts for *D. mawii* have been multi-faceted and captive breeding and rearing of individuals for wild release into protected areas (i.e., 'head-starting') have been identified as potential means of restoring wild populations (Rainwater et al. 2012). Currently, 15 *D. mawii* captive breeding centres are officially recognised by governments in Mexico (14) and Belize (1) (Rangel-Mendoza et al. 2014). Despite these facilities, relatively little is known about the life history characteristics of *D. mawii*, specifically those related to growth and size/age of sexual maturity.

In general, the life history of turtles is characterised by delayed sexual maturity, an iteroparous reproductive strategy and a long lifespan (Congdon and Gibbons 1990). As such, specifics on longevity, reproductive output, age/size-specific survivorship, and age at maturity, along with an understanding of how these traits interact to influence population parameters, are important in developing effective species-specific management plans (Congdon and Gibbons 1990; Frazer 1992; Congdon et al. 1993; Heppell 1998). Therefore, a better understanding of *D. mawii* life history traits is vital in developing conservation management plans for this critically endangered species. Although some studies have reported demographics on wild *D. mawii* populations such as mature sizes of each sex (Polisar 1996; Vogt et al. 2011) and morphometrics and sex ratios of geographic populations (Rainwater et al. 2012), important growth parameters that could inform captive breeding management, such as age at sexual maturity, growth rates and temporal duration of early life stages, are lacking in the published literature. To address this data gap, the purpose of the present study was to use a group of wild-caught, captive-held and captive-bred *D. mawii* to quantify patterns of growth and estimate the sizes and ages of sexual maturity to inform conservation management, captive breeding and head-starting efforts for *D. mawii*.

Methods

Study site

This study was conducted from September 2014 to April 2018 at the Hicatee Conservation Research Center (HCRC) at the Belize Foundation for Research and Environmental Education (BFREE) in the Toledo District of southern Belize. A captive population of *D. mawii* (locally known as 'hicatee'; Briggs-Gonzalez et al. 2018) was established at HCRC between 2014 and 2016 from wild-caught individuals from various water bodies throughout the country, as well as confiscations from illegally harvested individuals. Only adult and large juvenile turtles were collected from the wild, and all hatchlings were produced in captivity by these animals. The HCRC facility includes two ponds which are approximately 30 m long, 25 m wide and 4 m deep in the centre, and lined with pond liner. A freshwater well and solar-powered pumping system provided fresh water to the ponds on a continuous basis during daylight hours. A 3×3 m floating island covered in vegetation was located in each pond to provide additional cover for turtles. A 3.5 m electrified fence surrounded the perimeter of the ponds. The density of turtles in the two ponds was similar (Pond A: 22 individuals; Pond B: 23 individuals). Turtles were separated into ponds based on sexual maturity (Pond A: no secondary sexual characteristics present; Pond B: secondary sexual characteristics present such as dorsal head colouration and tail size). Diet of the captive turtles consisted of native vegetation (e.g., *Inga* spp., *Paspalum* spp.) that grew within the enclosure and was supplemented four times weekly with other plant material (e.g., foliage, fruits, etc.) collected from the surrounding jungle based on Moll's (1989) dietary analysis of *D. mawii*. Sex of turtles was determined by the presence of eggs or follicles using ultrasound (Sonosite Micromax 5–8 Hz vascular/abdominal probe) or by manually probing the cloacal vent for the presence of a penis in individuals that were large enough. Turtles <1 year old were classified as hatchlings, and turtles >1 year old whose sex could not be determined were classified as juveniles. All turtles were marked with a passive integrated transponder (PIT) tag and by notching the marginal scutes of the carapace in a unique numerical sequence. All capture and handling methods used in this study were approved by the University of Florida IACUC (protocol 201810297).

Calculating growth rates

Morphometric data for all *D. mawii* destined for the HCRC were collected upon capture in the field and then measured during annual or bi-annual health checks. Straight-line carapace length (SCL) was measured (to nearest 0.1 cm) using aluminum tree calipers or dial calipers (hatchlings, small juveniles) (Rainwater et al. 2012). To examine growth differences in the early stages of life, SCL for turtles of unknown sex (n=49) were measured weekly during the first year and monthly to bi-annually in subsequent years. Individual growth rates were calculated for hatchlings (age <1 year) and for turtles whose sex could not be determined (i.e., juveniles). Growth rates were calculated as change in SCL from one time interval to the next. Growth rates were then divided into 10 mm categories (e.g., 50–59 mm SCL, 60–69 mm SCL, etc.) based on the SCL at the midpoint of the growth rate interval similar to methods in Jones et al. (2011). Differences in growth rates among categories were determined by one-way ANOVA with a Tukey post-hoc test.

Size at onset of sexual maturity

Individual growth rates from all turtles were used to estimate body size at the onset of sexual maturity. In previous studies of freshwater turtles, changes in growth rates have indicated the onset of sexual maturity, where growth slowed as resources were allocated to reproduction (Gadgil and Bossert 1970; Bury 1979; Georges 1985; Kennett 1996). When growth rates are plotted against carapace length at the midpoint of the growth rate interval, a segmented linear regression can be used to determine if, and at what size, a change in slope occurs indicating the onset of sexual maturity (Kennett 1996; Toms and Lesperance 2003).

Growth rates were determined by measuring the change in SCL at approximately 12-month intervals according to methods from Kennett (1996). Growth rates were then plotted against SCL at the midpoint of the growth rate interval for each individual of each sex. Separate segmented linear regression analyses were conducted for males and females to determine at which point the slope of the regression line changed. Individual turtles were included in the regression more than once (Kennett 1996). A total of 78 growth intervals for 16 males and 73 growth intervals for 26 females were used to calculate the growth rate and size at the onset of sexual maturity. Individuals whose sex was not determined by the end of the study were not included in this portion of the study. All graphs and segmented linear regression analyses were completed with the software R 3.1.2 (segmented package, R Core Team 2014).

Estimating age of sexual maturity

The von Bertalanffy growth curve (Equation 1) has been used to calculate growth parameters and model size and age relations. The equation used for the von Bertalanffy growth curve was:

$$L_t=a(1-be\^(-kt)) \quad (1)$$

where L_t is the length (SCL) at time t, a is the asymptotic size, b is a parameter related to size at hatching, e is Euler's constant and k is the growth coefficient. Once the parameters were calculated, age was estimated using the following rearranged von Bertalanffy equation (Zug et al. 1997; equation 2):

$$age=\ln|((a-L)/ab)|/-k \quad (2)$$

where *L* is the SCL of interest, in this case, the SCL for males and females at the onset of sexual maturity as indicated by the segmented linear regression analyses. It should be noted that this method does not allow for the calculation of ages for individual turtles (Zug et al. 1997).

Growth models for calculating parameters

The same data used to calculate size at the onset of sexual maturity were used to calculate growth model parameters in addition to data from hatchlings and juveniles of unknown sex (males: 80 growth intervals from 27 individuals; females: 61 growth intervals from 37 individuals). Model parameters (e.g., asymptotic sizes and growth coefficients) were calculated for the von Bertalanffy growth curve using two models that were appropriate for mark-recapture data. When calculations of asymptotic size were different than literature values, asymptotic size was fixed according to methods in Martins and Souza (2008) which modeled growth using published sizes of large, wild-caught individuals in lieu of calculated asymptotic size. Once model parameters were calculated, age at the onset of sexual maturity was estimated by using the rearranged von Bertalanffy equation (Equation 2) that replaced time with age and substituted length with the SCL indicated by the segmented linear regression analyses. Growth parameters were calculated using capture-recapture data from regular health checks and were compared to parameters and age at maturity between models developed by Fabens (1965) and Wang (1998). All model parameters were calculated with the software R 3.1.2 (FSA and nlstools packages, R Core Team 2014).

The Fabens (1965) method uses length at captures and time between captures to develop the growth model. The Fabens growth curve is a rearranged form of Equation 1 and is:

$$L_r=a-(a- L_c) e^{(-kd)} \quad (3)$$

where L_r is recapture length (SCL), L_c is initial capture length (SCL), and *d* is the time interval between the two measurements. The parameters *k* and *a* were calculated according to Fabens (1965) and were used to estimate *b* (Frazer et al. 1990) to complete the von Bertalanffy equation,

$$b=e^k (1-h/a) \quad (4)$$

where *h* is the mean SCL of hatchlings. A limitation of the Fabens growth method is that it does not account for differences in growth among individuals (Wang 1998; Laslett 2002). The model developed by Wang (1998) reduces parameter estimate bias by allowing for individual variation in respect to asymptotic size. Additionally, the Wang method is not as sensitive to variability in the growth coefficient (i.e., individual growth can vary).

Results

Growth rate

The growth of *D. mawii* can be characterised by a von Bertalanffy growth curve with younger individuals exhibiting rapid growth that exponentially decays with time. The hatchlings in the present study had an average growth rate of 56.8 mm SCL yr^{-1} (n=12, SE=0.21) and doubled their hatching size within their first year. When growth rate was assessed by bin size, turtles within the 80–89 mm SCL (corresponding to the end of their first year) had significantly faster growth rates (59.0±7.1 mm yr^{-1}; P<0.001) than

Table 1. Growth rates for turtles of unknown sex based on 10 mm SCL bin sizes; *indicates significantly different from other SCL bin sizes at α ≤0.001; SCL=straight-line carapace length.

SCL bin (mm SCL)	Avg mid-body size (mm SCL±SD)	Avg growth rate (mm year^{-1}±SD)	n
60–69	69.0±0.7	44.0±1.3	4
70–79	74.7±3.3	50.4±7.1	13
80–89	83.7±2.7	59.0±7.1*	8
90–99	96.0±3.0	42.2±6.8	3
100–109	104.5±3.4	39.1±5.7	9
110–119	115.4±1.7	43.5±7.4	4
130–139	136.5±4.6	33.1±2.3*	5
160–169	163.1±1.7	38.7±0.4	3

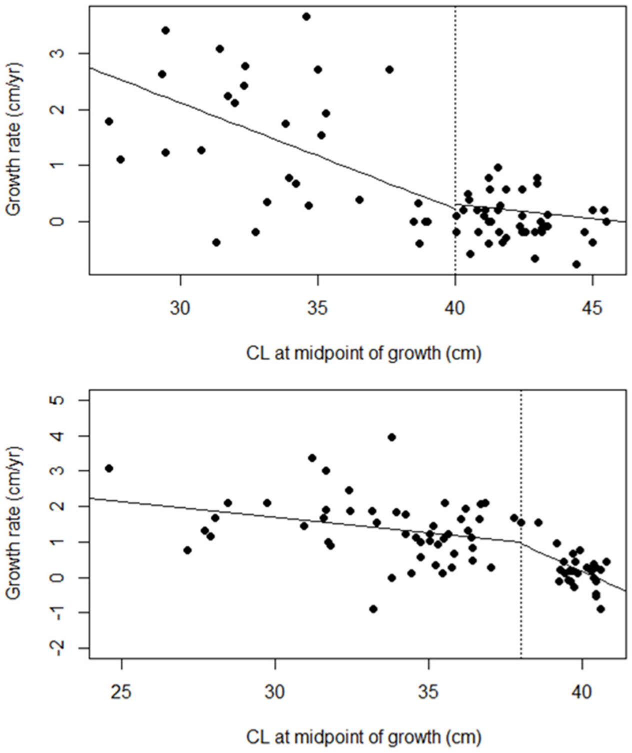

Figure 1. Segmented linear regression analyses indicating the sizes at which growth changes (vertical dashed lines) in females (40.0 cm SCL, 34.4-45.7 95% CI, P<0.001; top) and males (38.0 cm SCL, 35.2-40.7 95% CI; P<0.0001; bottom) associated with the onset of sexual maturity; SCL straight-line carapace length.

Table 2. Straight-line carapace length (cm) at the onset of sexual maturity for *Dermatemys mawii* as determined by segmented linear regression analyses; 95% confidence intervals are indicated in parentheses. [a]basis of sexual maturation was not disclosed. [b]sexual maturity for females based on presence of oviductal eggs, corpora lutea, corpora albicans and/or enlarged vitellogenic follicles; for males head colouration and tail length exceeding 10 cm (Polisar 1992); distinction made between lagoons and rivers.

	Male	Female
This study	38.0 (35.2–40.7)	40.0 (34.4–45.7)
Vogt et al. 2011[a]	36.5–38.5	39.5–42.0
Polisar 1992, 1996[b]	38.0–39.0 lagoon 37.0–39.0 river	41.0–42.0 lagoon 40.0–42.0 river

Table 3. Comparison of parameters calculated from Fabens (1965) and Wang (1998) growth models; 95% confidence intervals are indicated in parentheses for *a* and *k*. Age in parentheses used estimates from literature values of largest individuals (males: 45.0 cm SCL, females: 48.0 cm SCL; Polisar 1995) *a*s asymptotic size. a asymptotic size (cm straight-line carapace length [SCL]); k growth coefficient; age (years) at onset of sexual maturity using SCL indicated by the segmented linear regression."

	a		*k*		age		R^2	
	Male	Female	Male	Female	Male	Female	Male	Female
Fabens 1965	43.2 (41.5–45.1)	44.5 (42.3–47.2)	0.139 (0.125-0.154)	0.133 (0.117–0.149)	15.3 (13.5)	17.3 (13.6)	0.99	0.99
Wang 1998	46.7 (44.6–49.1)	49.0 (46.1–52.4)	0.109 (0.098–0.120)	0.104 (0.092–0.116)	15.3 (16.9)	16.2 (17.1)	0.99	0.99

turtles of other bin sizes (Table 1). Turtles within the 130–139 mm SCL bin (age 2.5 years) had significantly slower growth rates (33.1±2.3 mm yr^{-1}; P<0.001). Growth was most rapid within the first year and declined by 56% by 2.5 years.

Estimated size at onset of sexual maturity

The segmented linear regression analyses indicated males begin to sexually mature at 38.0 cm SCL (35.2–40.7 95% CI, n= 78, P<0.0001), and females begin at 40.0 cm SCL (34.4–45.7 95% CI, n= 73; P<0.0001; Table 2, Figure 1). Estimates were considered significantly different if the 95% CI did not overlap (Aresco and Guyer 1999). Therefore, there was no difference in size at the onset of sexual maturity between males and females.

Table 4. Comparison of growth parameters and age at maturity in chelonian species with a minimum of a decade to reach maturity. k = intrinsic rate of growth; all data female, unless otherwise noted. Table modified from Shine and Iverson 1995.

Species	age at maturity (years)	*k*	Source
Dermatemys mawii	Male 14–17, Female 14–17	Male 0.14, Female 0.14	averages from this study
Caretta caretta	20	0.08	Frazer 1983, 1986; Casale et al. 2009
Chelonia mydas	25	0.07	Bjorndal 1980; Bjorndal et al. 1995; Zug et al. 2002
Chelydra serpentine	20	0.05	Galbraith and Brooks 1987; Galbraith et al. 1989
Kinosternon flavescens	11	0.11	Iverson 1991
Terrapene ornata	11	0.09	Legler 1960; Metcalf and Metcalf 1985
Gopherus agassizii	16	0.07	Turner et al. 1987
Gopherus polyphemus	11	0.12	Iverson 1980; Cox 1989
Geochelone gigantea	23	0.05	Bourn and Coe 1978
Testudo graeca	12	0.09	Hailey 1990; Hailey and Loumbourdis 1990
Podocnemis voglii	10	0.11	Ramo 1982

Growth models

The Fabens model estimated asymptotic lengths of 43.2 cm SCL and 44.5 cm SCL for males and females respectively; the Wang model asymptotic length estimates were 46.7 cm SCL (male) and 49.0 cm SCL (female). Both models appeared to be accurate estimates of parameters for males and females given the coefficients of determination of 99%. Model parameters were considered significantly different ($P<0.05$) if the 95% CI did not overlap (Aresco and Guyer 1999). Therefore, differences between the estimates of asymptotic SCL for males and females were not significant between sexes or between models (Table 3). Both models estimated asymptotic sizes appropriate for our captive population, as our largest captive individuals (males=41.0 cm SCL; females=45.5 cm SCL) fell within or below the 95% confidence intervals. The Fabens model exhibited faster growth coefficients (males: k=0.139; females: k=0.133) with no differences between the sexes. The parameters from the Fabens model estimated the age at onset of sexual maturity for females at 17.3 years and for males at 15.3 years; the Wang model parameters estimated the age at onset of sexual maturity in females at 16.2 years and males at 15.3 years (Table 3).

Discussion

This study is the first to report growth rates and estimates of asymptotic size and growth coefficients for *D. mawii*. The results suggest that *D. mawii* exhibits rapid juvenile growth followed by reduced growth rates in adults as the species conforms to a von Bertalanffy growth curve generally exhibited by chelonians (Bury 1979; Kennett 1996). Hatchlings doubled their size at hatching within the first year and the rate of growth decreased with size as turtles aged. The Wang model estimated asymptotic SCL slightly larger than mean adult sizes for wild individuals with the upper limits of 95% confidence intervals exceeding maximum reported sizes of 45 cm SCL for males and 48 cm SCL for females (Polisar 1995). Previous studies suggest realistic estimates of asymptotic length should be slightly larger than the mean adult size (Frazer et al. 1990; Schmid and Witzell 1997). Although there were not significant differences in asymptotic size between the Fabens and Wang models, the Wang model may be better when calculating parameters for estimating age at maturity as it accounts for individual variation in length asymptote.

The estimates for sizes at the onset of sexual maturity for *D. mawii* are corroborated by previous field studies based on *D. mawii* populations throughout Belize (Table 2). Polisar (1992; 1996) reported sizes of sexually mature *D. mawii* based on secondary sexual characteristics such as yellow to orange dorsal head colouration and enlarged tail size. His estimates ranged between 37.0–39.0 cm SCL for males and 40.0–42.0 cm SCL for females. Vogt et al. (2011) estimated *D. mawii* males reach sexual maturity between 36.5–38.5 cm SCL and females between 39.5–42.0 cm SCL.

While other studies have reported sizes of sexually mature turtles, the present study is the first to estimate an age for the onset of sexual maturity in *D. mawii*. The number of years it takes an individual to be able to produce offspring is important in determining extinction risk (Turtle Expert Working Group 2009; Bjorndal et al. 2013), generation time (Congdon et al. 1994), and long-term population growth (Heppell et al. 2003). The delayed sexual maturity displayed by *D. mawii* makes the species more sensitive to losses of adults in populations (Crouse et al. 1987; Congdon et al. 1993; Congdon et al. 1994; Heppell et al. 1996; Zug and Parham 1996; Heppell and Crowder 1998). Because turtles have evolved to withstand high hatchling mortality, increasing first year survival does not have a significant impact on the population growth if survival rates are not increased in subsequent years (Heppell et al. 1996). Therefore, head-starting may be an important component of *D. mawii* conservation, but any captive management also needs concomitant protection of wild juveniles and adults to be effective (Congdon et al. 1994).

Although the present estimates of size at sexual maturity in captive *D. mawii* are similar to those for wild populations, caution should be taken when extrapolating these parameters and growth rates for captive animals to wild populations. Turtle densities in the captive ponds used in this study well exceed wild population densities reported in the 1980s of 2.3 *D. mawii* ha^{-1} (Moll 1986) in lagoon habitats of Belize. Bjorndal et al. (2000) reported density-dependent effects on somatic growth in green turtle juveniles with a significant inverse correlation between density and growth in wild populations. Bjorndal et al. (2000) suggested that growth was slowed under high densities due to nutrient limitations. Although the turtles in the present study were held at high population densities, they were fed ad libitum so that nutrients were not limited. It is therefore assumed that the growth rates observed in this study are probably faster than those occurring wild populations and values for asymptotic size from the captive population are probably an underestimate. When asymptotic size is substituted with literature values (Polisar 1995) of wild populations (slightly larger SCL), the age at the onset of sexual maturity was reduced to 13.6 years for females and 13.5 years for males (Table 3). Unfortunately, no reports of growth rates are available for wild *D. mawii*.

Implications for conservation and captive breeding

Time to maturity is fundamental for developing conservation and management plans as it strongly correlates with fecundity, adult life span and adult annual survival when compared across taxa (Stearns 1992; Shine and Iverson 1995; Heppell 1998). For captive breeding, the age of maturity is important in genetic management given that longer generation times generally lose heterozygosity at a slower rate (Balmford et al. 1996). Furthermore, time to maturation, along with captive population size, has also been implicated in reducing the accumulation of deleterious mutations that often coincide with the relaxed pressures of natural selection found in captive populations (Rodriguez-Ramilio et al. 2006).

The practice of head-starting, or rearing hatchling turtles until they are large enough to be released into the wild with a high probability of surviving, is often not practical due to slow growth rates and the associated costs and time involved in rearing turtles to an appropriate size of release. Given the age to maturity in *D. mawii*, rearing turtles for over a decade until they are sexually mature may not be feasible. Because turtle survival is positively correlated to size (Iverson 1991), the longer hatchlings are maintained in captivity (healthy and protected) (>1 year) the greater odds of post-release survival and subsequent recruitment into the adult population. Heppell et al. (1996) showed that head-starting programs for turtle species released into the wild at one year of age and that take 10-15 years to reach maturity may not be effective. However, *D. mawii* exhibits faster overall growth rates than other chelonians (Table 4), and therefore head-starting with this species may be successful if turtles are maintained in captivity for approximately two years post-hatching. For example, juveniles in this study demonstrated a significant ($P<0.001$; Table 1) decrease in growth rate after reaching 13.0 cm SCL, associated with the end of their second year of age, in which growth decreased by 56%. Keeping *D. mawii* hatchlings in captivity for two years (thereby capitalising on their fastest growth period) should not pose as great a challenge (e.g., infrastructure/space, husbandry personnel) as keeping them in captivity until sexually mature, but may offer increased survival rates compared to animals released at one year of age.

Conclusions

Dermatemys mawii appear to follow a von Bertalanffy type growth curve with rapid growth rates early in life that decrease with age. Males and females begin to sexually mature between 38.0–40.0 cm SCL with no significant difference in sizes between males and females. Fabens growth models estimate that males and females undergo the onset of sexual maturity at approximately 15 years old and 17 years old, respectively. This pattern of delayed sexual maturity is typical among chelonians and makes many turtle species, including *D. mawii*, more sensitive to losses in adult populations (Crouse et al. 1987; Congdon et al. 1993; 1994; Heppell et al. 1996; Zug and Parham 1996; Heppell and Crowder 1998). Captive breeding for *D. mawii* has been identified as a possible way to restore wild populations and this study has shown that relatively rapid growth among hatchlings and juveniles makes this species a potentially successful candidate for captive breeding. However, captive breeding alone is not enough to protect *D. mawii*. Congdon et al. (1994) demonstrated that programs focusing solely on increasing hatchling survival may not have an appreciable effect without a concomitant protection of adults. Therefore, captive breeding with the protection of wild adult *D. mawii* may be necessary for the success of any conservation program for the species.

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