

Observations on the Captive Biology of the Southern Stingray

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Abstract.—Complete life history information is essential for effective population management, but little is known about the demographic characteristics of the southern stingray *Dasyatis americana*. We describe life history characteristics of southern stingrays maintained in captivity from birth to 13 years. Size (disc width [DW]) at maturity ranged from 48 to 52 cm in males and from 75 to 80 cm in females; age at maturity was 3–4 years in males and 5–6 years in females. Individual growth was described using three models: the Gompertz function, von Bertalanffy growth function (VBGF), and logistic function. Analyses of DW at age and weight at age indicated that females were significantly larger at birth and reached larger maximum sizes than males. Because of the ability of the VBGF to fit the observed growth and that of previously reported maximum sizes, we favor its use to describe individual growth dynamics for this species. Using this model, we estimated that for males ($n = 20$), the asymptotic DW (DW_{∞}) was 67.4 cm, the von Bertalanffy growth coefficient (k) was 0.44 per year, and the predicted theoretical age at a DW of 0 cm (t_0) was -0.93 years. The corresponding estimates for females ($n = 15$) were a DW_{∞} of 150.9 cm, a k -value of 0.11 per year, and a t_0 of -1.61 years. The oldest southern stingrays in the study were a 12-year-old male and a 13-year-old female, and estimates of longevity were 7.9 years for males and 31.5 years for females. The sex ratio of neonates ($n = 453$) did not differ significantly from 1:1. The life history characteristics derived from captive specimens indicate that southern stingrays are similar to other dasyatids in terms of growth and age at maturity.

The southern stingray *Dasyatis americana* is common in western Atlantic coastal waters from New England to Brazil, including the Caribbean Sea and Gulf of Mexico (Bigelow and Schroeder 1953; McEachran and Fechtel 1998). This species is widely distributed, and although it is not under direct threat of exploitation, it is taken incidentally as bycatch in some trawl fisheries (Graham et al. 2009). An understanding of southern stingray life history characteristics is critical for allowing fisheries managers and biologists to assess potential population-level impacts.

Although information on many aspects of southern stingray biology and behavior is available from studies conducted in the wild and in captivity (Funicelli 1975; Henningsen 2000; Chapman et al. 2003; Corcoran 2006; Semeniuk et al. 2007; Semeniuk and Rothley 2008), little has been reported on the individual growth characteristics of southern stingrays.

The southern stingray is an important resource for some ecotourism operations within the Caribbean (Corcoran 2006; Grubbs et al. 2006; Semeniuk et al. 2007; Semeniuk and Rothley 2008), and additional information describing size-at-age and maturity characteristics would be useful. Some life history characteristics of southern stingrays have been reported: maximum size is 80 cm disc width (DW) for males and 150 cm DW for females (McEachran and Fechtel 1998), and size at maturity ranges from 46 to 51 cm DW for males and from approximately 70 to 80 cm DW for females (Bigelow and Schroeder 1953). Maturity varies within the geographic range and is attained at smaller sizes in the Gulf of Mexico than in the western Atlantic (Bigelow and Schroeder 1953; Funicelli 1975). Litter size in captive southern stingrays ranges from 2 to 10 neonates and is positively correlated with maternal size (Henningsen 2000). An inverse relationship between litter size and mean size of neonates has also been observed (Henningsen 2000). Parturition occurs annually in the wild and biannually in captivity, with gestation in captivity ranging from 4.5 to 7.5 months (Henningsen 2000; Grubbs et al. 2006).

In this study, we describe previously unreported growth and maturity characteristics of captive southern stingrays through ontogeny. This study provides useful life history information to better understand the ecology of this widely distributed species and adds to the knowledge of dasyatids.

Methods

Experimental subjects.—Male ($n = 20$) and female ($n = 15$) southern stingrays born to parents maintained together in a large multispecies exhibit at the National Aquarium in Baltimore (NAIB) were monitored to

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determine individual size (DW) at age, weight at age, size at maturity, and weight at maturity. An additional 453 individuals born at the NAIB from March 1993 to May 2008 were used to determine neonate sex ratio. Relationships between DW (cm) and weight (kg) were determined from 488 individuals. A 1,003,025-L recirculating aquarium system housed the population of wild-caught adult southern stingrays in addition to the captive-born animals used in the study. All southern stingrays maintained for the growth study received 12-mm passive integrated transponder tags injected intramuscularly for individual identification (American Veterinary Identification Devices, Inc., Norcross, California). The fish were fed ad libitum rations, and water temperature was maintained at 24–25°C. Measurements of DW and weight were taken as described by Henningsen (2000), and clasper length in males was measured as inner clasper length (Castro 2000; Gelsleichter et al. 2002). Southern stingrays were measured as close to biannually as possible, with more frequent measurements of DW and weight made opportunistically. Male maturity was assessed according to degree of calcification and rotation of claspers and the presence of spermatozoa in the clasper groove (Conrath 2005). Although the typical indicators of maturity in female batoids (follicular development, nidamental gland width, and uterus width) were not assessed for these captive individuals, pregnancy was used as confirmation of maturity.

Growth models.—Sex-specific and combined weight-at-size relationships were described with a power function fitted to data using a nonlinear curve-fitting algorithm. Size measured as DW (cm) was related to weight (*W*; kg) using the two-parameter model:

$$W = aDW^b.$$

We employed a sampling algorithm in which the power function was fitted to a set of weight-at-DW estimates. For each set, a single weight-at-DW measurement was randomly sampled from each individual (males: *n* = 20; females: *n* = 15; combined: *n* = 35), and the power function was fitted. The random sampling and power curve fitting were repeated 10,000 times. The mean value of the parameters was determined by fitting a normal distribution to the frequency distribution of the fitted values of *a* and *b*. The 95% confidence intervals (CIs) for the power function parameters were determined as the 2.5 and 98.5 percentiles of the repeated curve-fitting results.

Theoretical growth models were used to describe sex-specific DW at age and weight at age. Three growth models—the von Bertalanffy growth function

(VBGF), Gompertz function, and logistic function—were fitted to observations of size at age. Two of these models, the VBGF and Gompertz function, were used to describe weight-at-age relationships. We assumed that error followed a normal distribution, but we used log transformation when necessary to fulfill the normality criteria of parametric least-squares curve fitting. We analyzed DW-at-age data with a three-parameter VBGF (Ricker 1958):

$$DW_t = DW_\infty[1 - e^{-k(t-t_0)}].$$

Variables used in the above model and in each of the size-at-age models presented below are the observed DW (DW_t) at known age *t* (years). The VBGF model parameters are DW_∞ (defined as the asymptotic maximum DW achieved by an average individual), the growth coefficient *k* (per year; describes the rate at which DW_∞ is achieved), and the predicted theoretical age (t_0) of an individual at a DW of 0 cm. To describe size at age, we also used the Gompertz growth function (Draper and Smith 1981),

$$DW_t = DW_\infty e^{-\beta e^{-kt}},$$

and the logistic growth function (Ebert 1999),

$$DW_t = DW_\infty(1 - \beta e^{-kt})^{-1}.$$

Both the Gompertz and logistic growth functions are three-parameter growth models (parameters are DW_∞ , β , and *k*). The parameter DW_∞ is the asymptotic DW achieved by an individual; β and *k* are not directly comparable between the Gompertz and logistic functions because of the differences in model structure determined by covariation of β and *k* (Ebert 1999). In both models, *k* is a growth rate (per year), and β is defined as

$$\beta = \frac{DW_\infty^{-1/n} - DW_0^{-1/n}}{DW_\infty^{-1/n}},$$

where DW_0 is the DW at *t* = 0 (years) and *n* is a shape parameter; *n* = 1 for the logistic function, and $|n| \rightarrow \infty$ for the Gompertz function (Ebert 1999). Each of the above size-at-age relationships were fitted to size and age data using nonlinear least-squares fitting algorithms to determine the mean and 95% CIs of the parameter estimates.

Weight-at-age model parameters were determined for the weight-based formulations of the VBGF and Gompertz models (presented by Smith et al. 2007) and were fitted to data using nonlinear least-squares criteria. The parameters for the weight-at-age formulations of each model are similar to the size-at-age versions of the VBGF,

$$W_t = W_\infty [1 - e^{-k(t-t_0)}]^3,$$

and the Gompertz function,

$$W_t = W_\infty e^{-ke^{-gt}}.$$

The parameter W_∞ is interpreted as the asymptotic weight achieved by an individual. The parameter k is the growth rate (per year), and g is a shape parameter in the Gompertz function.

Size-at-age and weight-at-age models were analyzed for goodness of fit with Akaike's information criterion (AIC; Burnham and Anderson 2002) and adjusted r^2 . The AIC is defined as:

$$\text{AIC} = 2K + n \log_e(\hat{\delta}^2),$$

where K is the number of model parameters.

The estimated variance ($\hat{\delta}^2$) is equivalent to RSS/n , where RSS is the residual sum of squares of the nonlinear model. The difference in AIC ($\Delta\text{AIC}_{\text{model}}$) between the model under consideration (i.e., Gompertz, VBGF, or logistic) and the best-fitting model (the one with the lowest AIC value) was used as a criterion of comparison among models.

Estimates of longevity were established as at least the maximum age attained during the study, since ages of the wild-caught individuals are unknown. Estimates of longevity were also obtained via the method presented by Ricker (1979) using the parameters from the VBGF for each sex and for both sexes combined. Longevity was estimated as the age at which 95% of DW_∞ was attained and is approximately equal to $5(\log_e 2)/k$ for the VBGF.

Results

Maturity

Male clasper length increased rapidly between 40 and 50 cm DW, with the most rapid increase occurring between 45 and 48 cm, concurrent with calcification of the claspers ($n = 226$; Figure 1). Pregnancy, used to confirm maturity in females, was observed in females of 82.5–90.0 cm DW.

Growth Models

The DW–weight power curve for both sexes combined fit the observed data well ($r^2 = 0.98$; Figure 2), and parameters were not significantly different between sexes ($P > 0.05$). The DW–weight model for the combined sexes was $W = (3.27 \times 10^{-5})DW^{3.00}$ (95% CI of $a = 1.19 \times 10^{-5}$ to 8.56×10^{-5} ; 95% CI of $b = 2.73$ – 3.29 ; $n = 488$). Sex-specific power curve DW–weight relationships were $W = (4.32 \times 10^{-2})DW^{2.92}$ for males (95% CI of $a = 9.79 \times 10^{-3}$ to 1.85×10^{-1} ; 95% CI of $b = 2.48$ – 3.32 ; $r^2 = 0.96$)

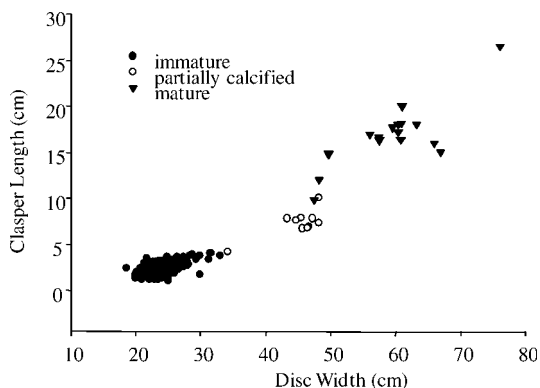


FIGURE 1.—Relationship between clasper length and disc width in captive-born male southern stingrays, with reference to their estimated state of maturity (maturity indicators include calcification of the claspers).

and $W = (2.72 \times 10^{-1})DW^{3.05}$ for females (95% CI of $a = 6.76 \times 10^{-2}$ to 7.72×10^{-1} ; 95% CI of $b = 2.75$ – 3.46 ; $r^2 = 0.99$).

Qualitative data analysis conducted prior to fitting the nonlinear theoretical growth models indicated that there were sex-specific differences in DW at age and weight at age. Parameter estimates and measures of model goodness of fit to the data (adjusted r^2) indicated that sex-specific growth models were appropriate. The lack of overlap in 95% CIs of the parameter estimates for each sex supports the separation of growth curves by sex for each model (Table 1). For the male DW-at-age relationship, each of the three models (Gompertz, VBGF, and logistic) fit the data comparably well. However, for females, the logistic model fit the data better than the Gompertz and VBGF models, as measured by AIC values (Table 1).

Minimum longevity estimates, based upon the age attained by the oldest southern stingrays in the study, were 12 years for males and 13 years for females. Estimates of longevity derived from k (VBGF growth coefficient) were 7.9 years for males (95% CI = 6.2–10.5 years) and 31.5 years for females (95% CI = 23.1–49.5 years).

Neonate Sex Ratio and Size

The sex ratio of neonates did not differ from 1:1 ($\chi^2 = 0.002$, $P > 0.05$). Mean (\pm SE) size of male neonates was 24.27 ± 1.49 cm DW and mean weight was 0.541 ± 0.011 kg. For female neonates, mean size was 24.90 ± 1.62 cm DW and mean weight was 0.585 ± 0.012 kg. Median DW and weight at birth differed significantly between sexes, with females having a greater size and mass than males (Mann–Whitney rank-sum

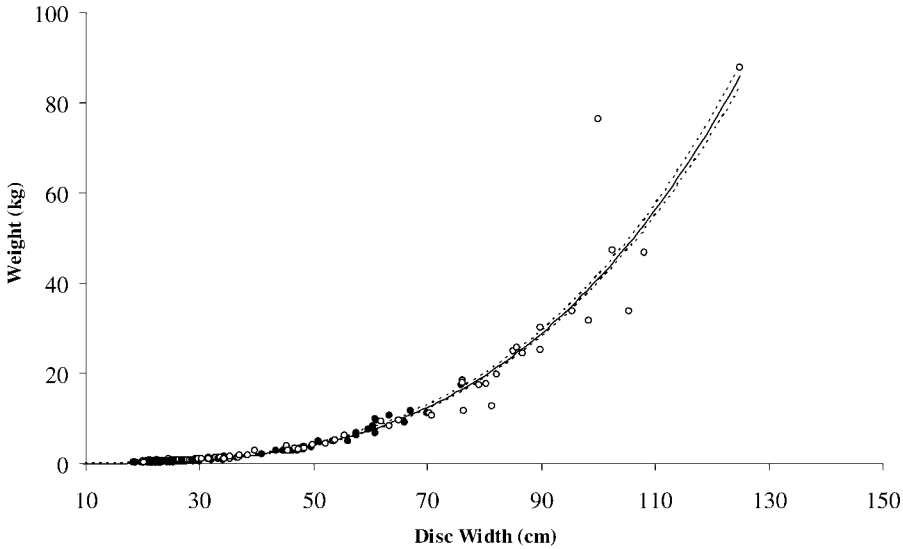


FIGURE 2.—Relationship (solid line) between weight (W) and disc width (DW) and predicted 95% confidence interval (dashed lines) for captive southern stingrays of both sexes (black circles = males; open circles = females), described with a power curve ($W = aDW^b$; $n = 488$).

test: $U = 29,870.5$, $P = 0.002$ for DW ; $U = 30,274$, $P = 0.001$ for weight).

Discussion

The theoretical growth models yielded variable results when fitted to the data (Table 1; Figures 3, 4). Although the VBGF has been conventionally used in elasmobranch aging studies because model parameters are easily comparable among species and populations (Cailliet et al. 2006), recent work has shown that other candidate models may be more appropriate for some species (Mollet et al. 2002; Cailliet and Goldman 2004; Neer and Thompson 2005). The Gompertz, logistic, and VBGF models provided similar fit for male DW at age ($\Delta AIC < 2$, $r^2 \geq 0.91$; Table 1). The mean and 95% CI of DW_{∞} estimated by each of these models underestimated the DW attained by the largest males in the study group (76.0 cm DW) but provided consistent estimates of DW_{∞} among models. Similarly, all of the DW -at-age models underestimated the maximum DW of 80 cm reported in the literature (McEachran and Fechhelm 1998). The logistic model provided the best fit relative to the other candidate models for describing female growth ($\Delta AIC_{\text{Gompertz}}$ and $\Delta AIC_{\text{VBGF}} \geq 17.61$; Table 1). The mean and 95% CI of the DW_{∞} parameter estimated by the logistic model did not predict the DW attained by the largest female in the study group (125.0 cm). Conversely, the Gompertz and VBGF models both predicted DW_{∞} intervals that encompassed the observed maximum size of the largest female in this

study and the previously reported maximum size (McEachran and Fechhelm 1988). For this reason, the VBGF and Gompertz models are preferable to the logistic model for describing female DW at age. Other myliobatid rays that exhibit slow growth are best described by the VBGF, whereas faster-growing species are best described by other models (Cowley 1997; Mollet et al. 2002; Neer and Thompson 2005; Smith et al. 2007). The VBGF model is preferable for describing the individual growth dynamics of southern stingrays because it enables comparison with other taxa. However, the use of the VBGF does not preclude the validity of alternative models, especially the Gompertz growth function, which does a similar job in describing individual growth patterns of both sexes and has become increasingly popular to describe individual growth. The use of alternative models should not be dismissed—especially if, in the future, a larger data set can be analyzed in conjunction with the data reported here.

The estimated VBGF-derived DW -at-age parameters for the southern stingray were greater than those reported for its congeners, the blue stingray *D. chrysonota* (Cowley 1997) and diamond stingray *D. dipterura* (Smith et al. 2007). This is especially notable for males: our mean estimate of k (0.44 per year) was greater than that reported for blue stingrays and diamond stingrays. Because the VBGF parameters k and asymptotic length (L_{∞}) are negatively correlated (Chen et al. 2003), we would expect the value of k

TABLE 1.—Size-at-age (disc width [DW, cm] at age [years]) and weight-at-age (W [kg] at age) parameters determined for captive-born southern stingrays at the National Aquarium, Baltimore, using Gompertz, von Bertalanffy, and logistic growth functions (DW_{∞} = asymptotic DW; β = parameter defined in Methods; k = growth coefficient; t_0 = predicted age at a DW or W of zero; W_{∞} = asymptotic W ; g = shape parameter for the Gompertz function). The mean and 95% confidence interval (CI) for each model parameter are provided for combined sexes as well as for each sex; the associated quality of fit to the data is measured by adjusted R^2 and Aikake's information criterion (AIC). The AIC difference (Δ AIC) values are calculated to determine goodness of model fit among each of the three size-at-age models or two weight-at-age models for each sex.

Model	Sex	Parameter	Mean	95% CI	Adj. R^2	AIC	Δ AIC
Size at age							
Gompertz	Male	DW_{∞}	64.85	61.19–68.50	0.92	232.34	0
		β	1.03	0.96–1.11			
		k	0.68	0.54–0.82			
	Female	DW_{∞}	123.62	112.67–134.58	0.95	298.31	17.61
		β	1.57	1.47–1.67			
		k	0.26	0.22–0.30			
	Combined	DW_{∞}	116.26	107.56–124.97	0.89	645.58	0
		β	1.54	1.46–1.62			
		k	0.27	0.23–0.30			
von Bertalanffy	Male	DW_{∞}	67.44	62.62–72.26	0.91	233.52	1.18
		k	0.44	0.33–0.56			
		t_0	–0.93	–1.15 to –0.72			
	Female	DW_{∞}	150.86	122.97–178.76	0.94	306.83	26.13
		k	0.11	0.07–0.15			
		t_0	–1.61	–1.97 to –1.25			
	Combined	DW_{∞}	155.02	128.08–181.95	0.89	645.94	0.36
		k	0.10	0.07–0.13			
		t_0	–1.70	–1.97 to –1.43			
Logistic	Male	DW_{∞}	63.24	60.13–66.35	0.92	232.79	0.45
		β	–1.71	–1.91 to –1.52			
		k	0.96	0.79–1.12			
	Female	DW_{∞}	115.26	107.05–123.47	0.95	280.70	0
		β	–3.31	–3.69 to –2.93			
		k	0.41	0.36–0.46			
	Combined	DW_{∞}	105.72	99.85–111.58	0.09	650.35	4.77
		β	–3.16	–3.42 to –2.89			
		k	0.45	0.40–0.49			
Weight at age							
Gompertz	Male	W_{∞}	13.33	10.79–15.87	0.85	53.62	3.12
		k	2.98	2.51–3.44			
		g	0.41	0.29–0.53			
	Female	W_{∞}	134.15	106.16–162.14	0.97	165.88	3.04
		k	4.99	4.59–5.38			
		g	0.18	0.15–0.21			
	Combined	W_{∞}	371.56	–19.81 to 762.93	0.85	477.17	0
		k	5.46	4.70–6.23			
		g	0.10	0.06–0.14			
von Bertalanffy	Male	W_{∞}	14.35	11.1–17.59	0.85	50.5	0
		k	0.3	0.2–0.4			
		t_0	–1.36	–2 to –0.72			
	Female	W_{∞}	238.75	132.17–345.33	0.97	162.84	0
		k	0.08	0.06–0.11			
		t_0	–1.52	–2.34 to –0.69			
	Combined	W_{∞}	520.21	295.33–745.08	0.85	478.46	1.29
		k	0.05	0.04–0.06			
		g	–2.12	–2.55 to –1.69			

estimated from our data to be intermediate to the values estimated for blue stingrays ($DW_{\infty} = 53.2$ cm, $k = 0.175$ per year; Cowley 1997) and diamond stingrays ($DW_{\infty} = 92.4$ cm, $k = 0.05$ per year; Smith et al. 2007). The differences that we observed, especially the elevated growth rate, may be an effect of the captive condition of the individuals as well as the nature of the experimental design; the nonlinear curve was fitted to measurements of individuals that were not indepen-

dently collected (multiple estimates were taken from the same individual). Thus, our results suffer from bias that occurs when estimates of growth are derived from tag–recapture data that are not resampled to ensure independence. Our study did not consider individual variability in growth parameters, which is an important consideration when analyzing tag–recapture data (Sainsbury 1980). These limitations notwithstanding, our estimates do fall within the range of k -values

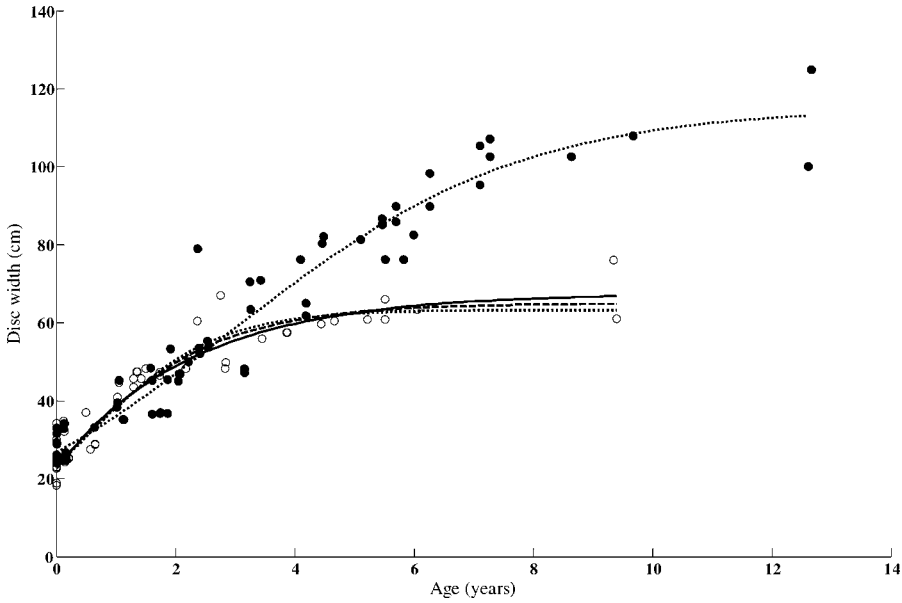


FIGURE 3.—Relationships between disc width and age for male (black lines, open circles) and female (dotted gray line, black circles) southern stingrays described by growth models with an equivalent model fit (i.e., Akaike’s information criterion difference ≤ 2.0). Male growth is described by the Gompertz function (dashed line), von Bertalanffy growth function (solid line), and logistic function (dotted line). Female growth is described by the logistic function.

reported for other viviparous batoids (Cowley 1997; Mollet et al. 2002; Neer and Thompson 2005; Smith et al. 2007).

Sexual dimorphism in DW at age is common in batoids, particularly in myliobatids, and in general the females attain a greater size while growing at a slower rate than males (Cowley 1997). The magnitude of difference in maximum size varies among batoid species, often with little difference in skates (Rajidae; Sulikowski et al. 2003). Our results support findings from other studies that report extreme sexual dimorphism in southern stingrays (Bigelow and Schroeder 1953; McEachran and Fechhelm 1998); the mean DW_{∞} estimate for males is 53% that of females based on VBGF estimates. The single report of a significantly larger male (108 cm DW) by Schmid et al. (1988) is contrary to our findings as well as to other published values. The sex-specific differences in maximum size based on the theoretical growth models we examined have biological implications because of the ecological importance of early growth (Osse et al. 1997) and the correlation of life history traits (e.g., age of first reproduction) with growth (Beverton 1992). Juvenile growth rates, in part, determine prey capture efficiency and predator evasion. In the case of male growth, the period of time that they are relatively small is minimized and the period of exposure to predation is reduced. Female size is often attributed to the

accommodation of developing young (Henningsen et al. 2004), and age at maturity is negatively correlated with the instantaneous growth rate. The estimated sizes at maturity of approximately 52 cm DW for males and 75–80 cm DW for females in our study may to some extent be related to differences in the estimated growth patterns. We also note that these estimates of size at maturity are similar to those reported by other authors for the southern stingray (Bigelow and Schroeder 1953; McEachran and Fechhelm 1998) and indicate that captive conditions have little effect on maturity patterns. The exception, however, is the slightly smaller sizes at maturity reported by Funicelli (1975) for southern stingrays from the northern Gulf of Mexico. Differences in life history characteristics are commonly observed for geographically separated populations or subpopulations of elasmobranchs (Henningsen et al. 2004).

The disparity in growth function estimates between sexes results in differing estimates of longevity when using the methods of Ricker (1979). The estimates of longevity in this study were the ages attained by the oldest southern stingrays held at the NAIB. Although data from these individuals were used in the derivation of growth curves, at the time of writing the maximum ages now exceed 17 years for both sexes. The longevity estimates obtained from k were 7.9 years (95% CI = 6.2–10.5 years) for males and 31.5 years

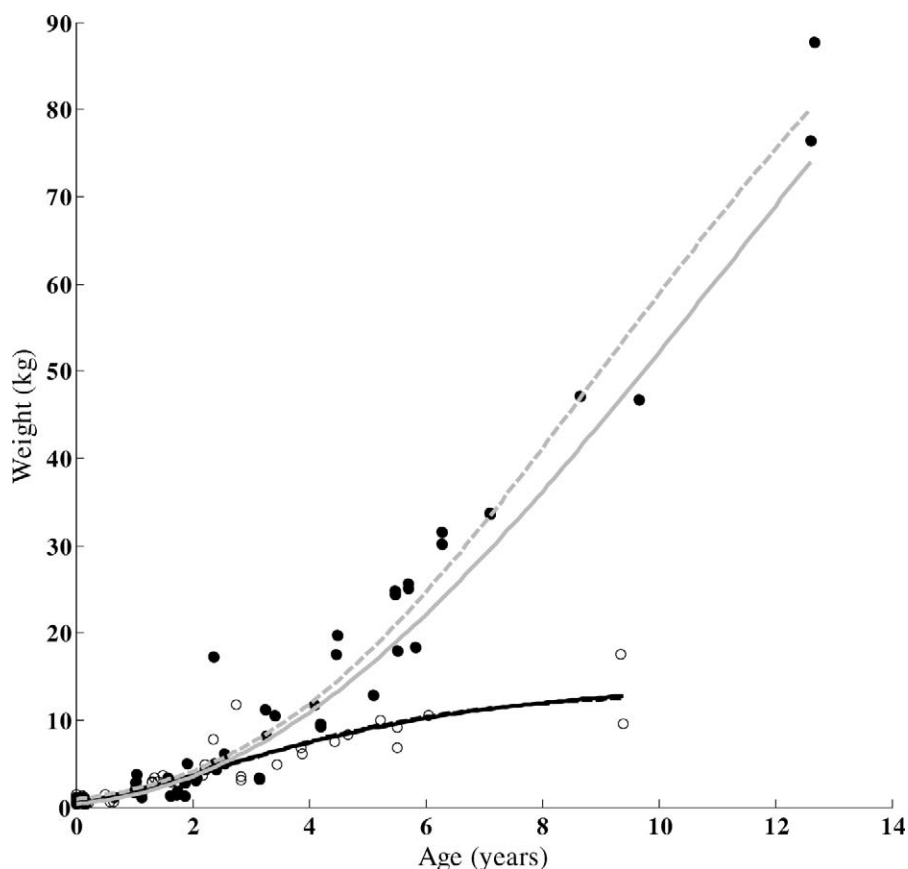


FIGURE 4.—Relationships between weight and age for male (black lines, open circles) and female (gray lines, black circles) southern stingrays described by growth models with an equivalent model fit (i.e., Akaike's information criterion difference ≤ 2.0). For each sex, growth is described by the Gompertz function (dashed line) and von Bertalanffy growth function (solid line).

(95% CI = 23.1–49.5 years) for females. Additionally, there are southern stingrays at NAIB that were collected from the wild as adults. Males have been kept for as long as 19 years, and the largest female has been kept for 17 years.

The maximum individual weights observed in the captive population were 17.5 kg for males and 87.7 kg for females. Using the DW–weight relationship determined in our study and the maximum DW reported in the literature, W_{∞} is estimated to be 16.7 kg for males and 103.7 kg for females. The estimate for females is far below the estimated W_{∞} from the VBGF weight-based model in the current investigation (Table 1). The estimated k (VBGF) in the current investigation allows life history interpretations because it can be interpreted in terms of longevity (Mollet et al. 2002).

Previously in this captive population, a 1:1 sex ratio at birth was observed, and there was no size discrepancy based upon DW (Henningsen 2000). Here, we report a 1:1 sex ratio at birth based on an increased

sample size; however, we observed significant sexual dimorphism in the DW of neonates. The DW–weight relationships reported in this study are similar to previous reports for this species (Claro 1994; Henningsen 2000; Wigley et al. 2003).

This study expands upon information describing reproduction of a captive southern stingray population at the NAIB (Henningsen 2000) and provides the first known published estimates of age and growth relationships for the southern stingray. Previously, only preliminary growth parameters were available (Cailliet and Goldman 2004). Although growth in captive specimens may differ from that of wild conspecifics, studies of growth in laboratory and aquarium specimens have provided valuable life history information, particularly where none is otherwise available (Cailliet and Goldman 2004; Mohan et al. 2004). Mollet et al. (2002) provide a good discussion of the continuum of growth rates obtained in wild and captive conspecifics.

Although the results obtained in the current investigation suggest that the southern stingray is similar to other myliobatid rays, we suggest that growth in wild conspecifics may be slower. At NAIB, the growth of wild-caught conspecifics conforms fairly well to the parameters presented in our study. For example, a female captured in 1992 grew from nearly 100 cm DW to a size of 130 cm DW over 15 years. The present study adds to existing knowledge of southern stingray biology but also indicates the need for more investigation of the biology of this common species.

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References

- Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology* 41:137–160.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition. Springer-Verlag, New York.
- Bigelow, H. B., and W. C. Schroeder. 1953. Fishes of the western North Atlantic part II: sawfishes, guitarfishes, skates and rays; chimaerids. Yale University, Memoirs of the Sears Foundation of Marine Research, New Haven, Connecticut.
- Cailliet, G. M., and K. J. Goldman. 2004. Age determination and validation in chondrichthyan fishes. Pages 399–447 in J. C. Carrier, J. A. Musick, and M. R. Heithaus, editors. *Biology of sharks and their relatives*. CRC Press, Boca Raton, Florida.
- Cailliet, G. M., W. D. Smith, H. F. Mollet, and K. J. Goldman. 2006. Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes* 77:211–228.
- Castro, J. 2000. The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. *Environmental Biology of Fishes* 58:1–22.
- Chapman, D. D., M. J. Corcoran, G. M. Harvey, S. Malan, and M. S. Shivji. 2003. Mating behavior of southern stingrays, *Dasyatis americana* (Dasyatidae). *Environmental Biology of Fishes* 68:241–245.
- Chen, Y., M. Hunter, R. Vadas, and B. Beal. 2003. Developing a growth-transition matrix for the stock assessment of the green sea urchin (*Strongylocentrotus droebachiensis*) off Maine. *U.S. National Marine Fisheries Service Fishery Bulletin* 101:737–744.
- Claro, R. 1994. Características generales de la ictiofauna [General characteristics of the ichthyofauna.] Pages 55–71 in R. Claro, editor. *Ecología de los Peces Marinos de Cuba* [Ecology of the marine fishes of Cuba.] Instituto de Oceanología Academia de Ciencias de Cuba Y Centro de Investigaciones de Quintana Roo, Quintana Roo, Mexico.
- Conrath, C. L. 2005. Reproductive biology. Pages 103–126 in J. A. Musick and R. Bonfil, editors. *FAO (Food and Agriculture Organization of the United Nations) Fisheries Technical Paper* 474.
- Corcoran, M. J. 2006. The influence of supplemental feeding on the movement patterns of the southern stingray, *Dasyatis americana*, at Grand Cayman, Cayman Islands. Master's thesis. Nova Southeastern University, Dania, Florida.
- Cowley, P. D. 1997. Age and growth of the blue stingray, *Dasyatis chrysonota chrysonota* from the southeastern cape coast of South Africa. *South African Journal of Marine Science* 18:31–38.
- Draper, N., and H. Smith. 1981. *Applied regression analysis*, 2nd edition. Wiley, New York.
- Ebert, T. A. 1999. *Plant and animal populations: methods of demography*. Academic Press, San Diego, California.
- Funicelli, N. A. 1975. Taxonomy, feeding, limiting factors, and sex ratios of *Dasyatis sabina*, *Dasyatis americana*, *Dasyatis sayi* and *Narcine brasiliensis*. Doctoral dissertation. University of Southern Mississippi, Hattiesburg.
- Gelsleichter, J., L. E. L. Rasmussen, C. A. Manire, J. Tyminski, B. Chang, and L. Lombardi-Carlson. 2002. Serum steroid concentrations and development of reproductive organs during puberty in male bonnethead sharks, *Sphyrna tiburo*. *Fish Physiology and Biochemistry* 26:389–401.
- Graham, L. J., B. R. Murphy, and D. Hata. 2009. Using species composition data from a trawl survey to determine potential bycatch of the commercial trawl fishery for Horseshoe crab *Limulus polyphemus* in the Middle Atlantic Bight. *North American Journal of Fisheries Management* 29:478–487.
- Grubbs, D. R., F. Snelson, A. Piercy, R. S. Rosa, and M. Furtado. 2006. *Dasyatis americana*. In 2007 IUCN Red List of Threatened Species. Available: iucnredlist.org. (November 2009).
- Henningsen, A. D. 2000. Notes on reproduction in the southern stingray, *Dasyatis americana* (Chondrichthyes: Dasyatidae), in a captive environment. *Copeia* 2000:826–828.
- Henningsen, A. D., M. Smale, R. Garner, and N. Kinnunen. 2004. Reproduction, embryonic development, and reproductive physiology of elasmobranchs. Pages 227–236 in M. Smith, D. Warmolts, D. Thoney, and R. Hueter, editors. *Elasmobranch husbandry manual*. Ohio Biological Survey, Columbus.
- McEachran, J. D., and J. D. Fechtel. 1998. *Fishes of the Gulf of Mexico*. University of Texas Press, Austin.
- Mohan, P. J., S. T. Clark, and T. H. Schmid. 2004. Age and growth of captive sharks. Pages 201–226 in M. Smith, D. Warmolts, D. Thoney, and R. Hueter, editors. *Elasmobranch husbandry manual*. Ohio Biological Survey, Columbus.
- Mollet, H., J. M. Ezcurra, and J. B. O'Sullivan. 2002. Captive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832). *Marine and Freshwater Research* 53:531–541.
- Neer, J. A., and B. A. Thompson. 2005. Life history of the

- cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. *Environmental Biology of Fishes* 73:321–331.
- Osse, J. W. M., J. G. M. Van den Boogaart, G. M. J. Van Snik, and L. Van der Sluys. 1997. Priorities during early growth of fish larvae. *Aquaculture* 155:249–258.
- Ricker, W. E. 1958. Handbook of computation for biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin Number 119.
- Ricker, W. E. 1979. Growth rates and models. Pages 677–743 in W. S. Hoar and D. J. Randall, editors. *Fish physiology*, volume VIII. Academic Press, New York.
- Sainsbury, K. J. 1980. Effect of individual variability on the von Bertalanffy growth equation. *Canadian Journal of Fisheries and Aquatic Sciences* 37:241–247.
- Schmid, T. H., L. M. Ehrhart, and F. F. Snelson Jr. 1988. Notes on the occurrence of rays (Elasmobranchii, Batoidea) in the Indian River lagoon system, Florida. *Florida Scientist* 51:121–128.
- Semeniuk, C. A. D., and K. D. Rothley. 2008. Costs of group-living for a normally solitary forager: effects of provisioning tourism on southern stingrays *Dasyatis americana*. *Marine Ecology Progress Series* 357:271–282.
- Semeniuk, C. A. D., B. Speers-Roesch, and K. D. Rothley. 2007. Using fatty-acid profile analysis as an ecologic indicator in the management of tourist impacts on marine wildlife: a case of stingray-feeding in the Caribbean. *Environmental Management* 40:665–677.
- Smith, W. D., G. M. Cailliet, and E. M. Melendez. 2007. Maturity and growth characteristics of a commercially exploited stingray, *Dasyatis dipterura*. *Marine and Freshwater Research* 58:54–66.
- Sulikowski, J. A., M. D. Morin, S. H. Suk, and W. H. Howell. 2003. Age and growth estimates of the winter skate (*Leucoraja ocellata*) in the western Gulf of Mexico. U.S. National Marine Fisheries Service Fishery Bulletin 101:405–413.
- Wigley, S. E., H. M. McBride, and N. J. McHugh. 2003. Length-weight relationships for 74 fish species collected during NEFSC research vessel bottom trawl surveys, 1992–1999. NOAA Technical Memorandum NMFS NE-171.