Environmental Biology of Fishes (2005) 73: 321–331
DOI 10.1007/s10641-005-2136-5
© Springer 2005

Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits

Julie A. Neer & Bruce A. Thompson
Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803-7503, U.S.A. (e-mail: jneer1@lsu.edu)

Received 6 January 2005 Accepted 23 January 2005

Key words: batoid, elasmobranch, age and growth, reproduction, size at maturity

Synopsis

We determined age and growth, size at maturity, and fecundity for cownose rays, *Rhinoptera bonasus*, collected from the northern Gulf of Mexico. Vertebral age estimates ranged from 0+ to 18+ years for females and 0+ to 16+ years for males. Annual deposition of growth increments was verified with marginal increment analysis. Likelihood ratio tests indicated that the growth of the cownose ray was best described by a combined sexes Gompertz model. Median size at 50% maturity was determined to be 642 mm DW for males and 653 mm DW for females, or 4–5 years of age. Median pup size-at-birth was estimated to be 350 mm DW, with a gestation period of 11–12 months. In all cases, gravid females contained only one pup. Statistically significant differences were detected between growth curves for the Gulf of Mexico and the western Atlantic Ocean. Cownose rays in the Gulf of Mexico had lower estimates of DW_∞ and K, and a higher theoretical longevity than their conspecifics in the western Atlantic Ocean. Cownose rays in the Gulf of Mexico also attain maturity at a smaller size and earlier age than their counterparts in the western Atlantic Ocean.

Introduction

Variability in life history traits for geographically separated populations of the same species has been documented for several species of elasmobranchs. Driggers et al. (2004) found differences in growth parameters and theoretical longevity between the Gulf of Mexico and the western Atlantic Ocean for the blacknose shark, *Carcharhinus acronotus*. Carlson et al. (2003) determined that the finetooth shark, *C. isodon*, obtained a smaller size at maturation in the Gulf of Mexico versus the Atlantic Ocean. Latitudinal variation in life history traits for the bonnethead shark, *Sphyrna tiburo*, in the eastern Gulf of Mexico has also been documented (Parsons 1993, Lombardi-Carlson et al. 2003). To date, no studies examining the variability of life history traits between the Gulf of Mexico and the western Atlantic Ocean have been published on any batoid (skates and rays).

The cow-nosed rays (Family Rhinopteridae) are aplacental viviparous elasmobranchs occurring worldwide in tropical and warm temperate seas, and estuaries (McEachran & Fechhelm 1998). They are semi-pelagic and gregarious, often forming large schools (McEachran & Capapé 1984). Currently, there are five recognized species occupying a single genus (Schwartz 1990).

The cownose ray, *Rhinoptera bonasus*, ranges from southern New England to southern Brazil within the Western Atlantic as well as throughout the Gulf of Mexico and off Cuba (Bigelow & Schroeder 1953, McEachran & Fechhelm 1998). They are most often encountered on continental and insular shelves where they feed primarily on bivalve mollusks and crustaceans (Smith &

Merriner 1985, McEachran & Fechhelm 1998). Information on the age and growth and reproduction of the cownose ray in the Chesapeake Bay can be found in Smith & Merriner (1986, 1987). Additional preliminary information on the reproductive biology of cownose rays in the Atlantic Ocean has been presented by Schwartz (1967) in brief abstract form. Smith & Merriner (1987) and Blaylock (1993) presented information on the distribution and movement of the cownose ray in the Chesapeake Bay, while Schwartz (1990) reported on the migratory movements of several species in the genus.

Whereas information exists regarding geographic variability in life history traits for sharks between the western Atlantic Ocean and the Gulf of Mexico, no evidence is available for batoids. Additionally, no published information is available on the age and growth of any batoid within the Gulf of Mexico. To address this lack of information, we sought to: (1) estimate age and growth for the cownose ray; (2) ascertain size and age at maturity, fecundity, and gestation for the cownose ray; and (3) compare these estimates with those derived for cownose rays from the western North Atlantic Ocean.

Materials and methods

Specimen collection and laboratory processing

We collected cownose ray specimens from fishery-independent sources in the northern Gulf of Mexico. We collected samples from June 1999 through November 2003. Details of the fishery-independent gillnet surveys are in Neer et al. (2005) and Carlson & Brusher (1999).

The senior author conducted external examinations for all specimens. Rays were sexed, weighed to the nearest 0.1 kg, and measured to the nearest disk width (DW, mm). We recorded outer clasper length (from free tip of clasper to where clasper meets the pelvic fin; Compagno 1984) for males. We also completed a detailed internal reproductive examination for all specimens (see Reproduction).

We removed five to seven vertebral centra from vertebrae 15 through 25 and prepared them for age estimation following techniques outlined in Neer & Cailliet (2001). We calculated sex-specific relationships between disk width and centrum diameter (CD) to assess the appropriateness of using vertebrae as an ageing structure. Centrum diameter (mm) was measured using digital calipers for each specimen before sectioning. As no difference was found between sexes (ANCOVA: $F = 3.596$, df = 1, $p > 0.05$), we combined the log transformed data to generate a linear relationship: log DW = 0.779*log CD + log 5.370 ($p < 0.0001$; $r^2 = 0.96$; $n = 227$).

We cut 0.3 mm thick sagittal sections from the vertebrae using a Buhler Isomet low speed saw. We stained the sections with a 0.01% crystal violet solution following Carlson et al. (2003). Each section was mounted on a glass microscope slide with clear resin and we determined age estimates by examining the sections under a dissecting microscope with transmitted light (Figure 1).

Age assessment and verification

The first author counted each specimen twice without knowledge of its size or sex. Each growth cycle included a broad band representing summer growth and a narrow band representing winter growth (Cailliet & Goldman 2004). We counted the narrow bands for age determination. If the band counts did not agree between the first two readings, the first author counted the specimen a third time to reach a consensus with one of the previous band counts. If no consensus was reached, we discarded that sample. We calculated an index of average percent error (APE; Beamish & Fournier 1981), percent error (D; Chang 1982), and percentage of disagreements by $\pm$i rings (Cailliet et al. 1990) between counts. Only the first two band counts were used as not all specimens were counted a third time.

We verified the annual periodicity of the band formation using relative marginal increment analysis following Natanson et al. (1995):

$$\mathrm{MIR} = (\mathrm{VR} - R_n)/(R_n - R_{n-1}),$$

where MIR is the marginal increment ratio; VR is the vertebral radius; R_n is the last complete narrow band; and $R_{n\text{-}1}$ is the next-to-last complete narrow band. We measured the distances from the centrum origin to the distal edge of the last two growth bands and from the centrum origin to the centrum edge using the Image Tools Version 3 Software Package

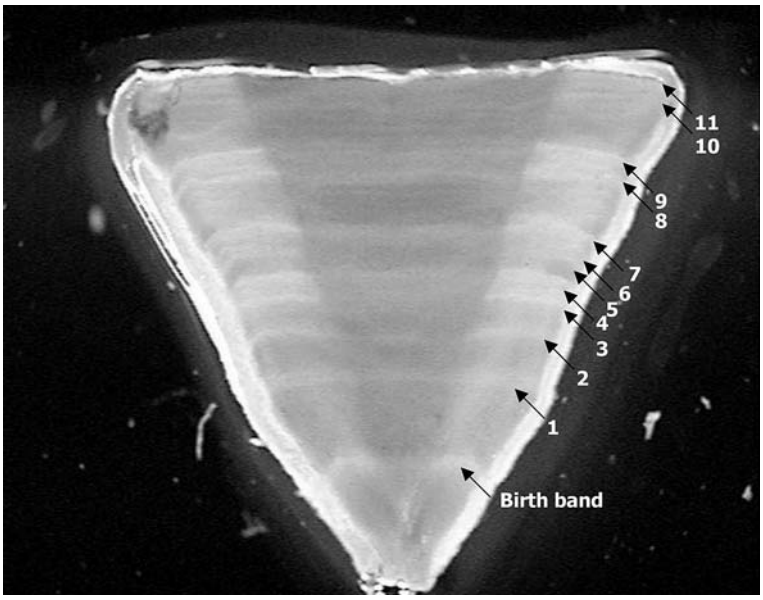

Figure 1. Sagittal vertebral section from a 860 mm female cownose ray. This ray was estimated to be 11+ years-old.

(Department of Dental Diagnostics Science, University of Texas Health Center, Austin, Texas, USA). We plotted mean MIR against month and season (Spring = March–May; Summer = June–August; Fall = September–November; Winter = December–February) to examine trends in band formation. To examine differences between month and season, we used a one-way analysis of variance on the arcsine-transformed MIR data (Zar 1984). We completed this analysis for rays of all size classes and for rays only displaying two bands in the vertebral section to examine potential differences in conducting the analysis over all age classes or restricting it to a single age class, as recommended by Campana (2001).

Growth curve analysis

In using theoretical growth models, we assumed that (1) the birth mark is the band associated with a change in angle in the intermedialia and (2) growth bands are deposited annually. We calculated age estimates using the algorithm presented in Carlson et al. (2003): age = the birth mark + number of narrow bands – 1. If only the birth mark was present, the ray was considered a 0+ year-old individual.

We fitted four growth models to the observed size-at-age data. We fitted the von Bertalanffy growth model (von Bertalanffy 1938) using the equation:

$$\mathrm{DW}_t = \mathrm{DW}_\infty(1 - \mathrm{e}^{-K(t-t_0)}),$$

where DW_t is the mean disk width at time t; DW_∞ is the theoretical asymptotic length; K = growth coefficient; and t_0 is the theoretical age at zero length.

We also fitted a Gompertz growth model (Ricklefs 1967, Ricker 1975), which is an S-shaped double exponential growth model, using the equation:

$$\mathrm{DW}_t = \mathrm{DW}_\infty \mathrm{e}^{-\,e(K(t-t_0))},$$

where DW_t is the mean disk width at time t; DW_∞ is the theoretical asymptotic length; K is the growth coefficient; and t_0 is the theoretical age at zero length.

We also considered a logistic model (Ricker 1975) in the form:

$$\mathrm{DW}_t = \mathrm{DW}_\infty/(1+^{-\mathrm{K}(t-t_0)}),$$

where DW_t is the mean disk width at time t; DW_∞ is the theoretical asymptotic length; K is the growth coefficient; and t_0 is the theoretical age at zero length.

Finally, we fitted a four parameter Richards or "Generalized von Bertalanffy" (Richards 1959, Gulland 1969) growth model to the observed size at age data in the form:

$$DW_t = DW_\infty[(1 - L_0(e^{-k*t}))]^P,$$

where DW_t is the mean disk width at time t; DW_∞ is the theoretical asymptotic length; K is the growth coefficient; and L_0 is the y-intercept (e.g. size at birth), and p is a shape parameter. This model is useful as a selection tool and can generate the other three models by varying the value of p: von Bertalanffy if $p = 1$, logistic if $p = -1$, and Gompertz as p goes to infinity.

We estimated all growth model parameters using Marquardt least-squares non-linear regression in the SAS statistical software (SAS V.8, SAS Institute, Inc). We assessed the goodness-of-fit of each model by examining residual mean square error (MSE), coefficient of determination (r^2), and level of significance ($p < 0.05$; Neer & Cailliet 2001, Carlson & Baremore 2005). To aid in model selection, we used likelihood ratio tests implemented using SAS (Kimura 1980, Devore 2000). We also used a likelihood ratio test implemented using the solver add-in in Excel (Haddon 2001) to determine whether growth models differed between sexes (Kimura 1980, Cerrato 1990). We estimated theoretical longevity as the age at which 95% of DW_∞ is reached (5*(ln 2)/K (Fabens 1965, Cailliet et al. 1992).

To investigate the potential of geographic variability in growth parameters, we compared data obtained from the current study for the Gulf of Mexico with the original data of Smith & Merriner (1987) from the western Atlantic Ocean. We fitted growth models to observed size at age data for the sexes separately and combined, with the resulting models compared using a likelihood ratio test (Kimura, 1980, Cerrato, 1990). We then used a likelihood ratio test to compare the Smith & Merriner growth curves to those generated in the current study.

Reproduction

We assigned male reproductive status based on three criteria: (1) the ratio of clasper length to disc width (Smith & Merriner 1986); (2) clasper calcification (Yano 1993); and (3) vas deferens coiling (none, partial, or complete; Neer & Cailliet 2001). We measured outer clasper length as the distance from the free tip of clasper to where the clasper meets the pelvic fin (Compagno 1984). We subjectively assigned clasper calcification to one of three categories based on ease of clasper bending: not calcified, partially calcified, and calcified. We considered a specimen mature if it met at least 2 of the three following criteria: calcified claspers, coiled vas deferens, and a clasper length–disc width ratio, expressed as a percentage, greater than or equal to 4%.

We based the reproductive status of female specimens on two criteria: (1) diameter of ova (Smith & Merriner 1986), and (2) uterine width (Neer & Cailliet 2001). We considered females mature if they contained ovarian ova >10 mm in diameter or the uteri were differentiated from the oviducts and measured at least 10 mm in width at its widest point. We measured the diameter of the largest ova to the nearest 0.1 mm and considered gravid females mature, regardless of ova size. We recorded the number, size, weight, and sex for all pups observed.

We determined median disc width at maturity (MDW) following Mollet et al. (2000). We fitted a logistical model $Y = [1 + e^{-(a+bX)}]^{-1}$ to our binomial maturity data (immature = 0, mature = 1) for males and females separately and calculated median disk width-at-maturity (MDW) using the equation MDW = $-a/b$.

Results

Specimen collection

We examined a total of 227 cownose rays during this study. Males ranged in size from 338 to 960 mm DW ($n = 106$), while females ranged from 336 to 1025 mm DW ($n = 121$; Figure 2). The total length-weight relationship for rays collected during this study was best described by a power curve of the form: $y = 5E\text{-}09x^{3.1936}$($r^2 = 0.99$; $n = 122$).

We collected rays from all months except December, January, and February, although not from all months every year. Temperature at time of collection ranged from 20 to 32°C, and salinity ranged from 22.1 to 36 ppt.

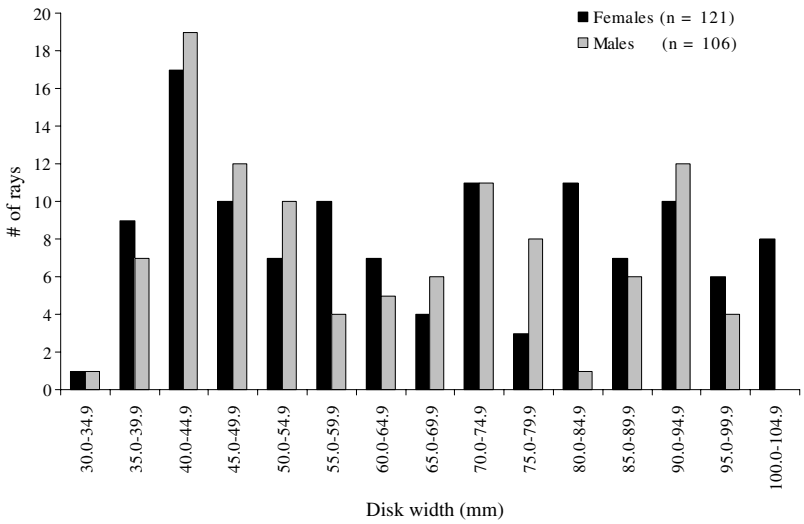

Figure 2. Length frequency histogram for cownose rays examined during this study (n = 227).

Age assessment and verification

We derived age estimates for all 227 specimens processed for age assessment. Age estimates ranged from 0^+ to 18^+ years for females (n = 121) and from 0^+ to 16^+ for males (n = 106). The precision of band counts was high between the first two sets of band counts, resulting in an APE of 3.81% and D (percent error) of 3.45%. Percent agreement between the first two sets of band counts was 62.6% exact count, 89.9% within 1 band, and 99.6% within 2 bands.

We found significant differences in the marginal increment analysis between seasons for all cownose ray age classes combined (single factor ANOVA by season: F-ratio = 3.721, df = 2, $p < 0.05$, n = 169; Figure 3). *Post-hoc* pairwise comparisons found Spring was significantly different from Fall (Bonferroni pairwise *Post-hoc* test: $p < 0.05$). Spring and Summer were not significantly different (Bonferroni pairwise *Post-hoc* test: $p > 0.1$) nor were Fall and Summer (Bonferroni pairwise *Post-hoc* test: $p > 0.1$). We also found significant differences in the analysis by month for all cownose ray age classes combined (single factor ANOVA by month: F-ratio = 2.422, df = 8, $p < 0.05$, n = 169; Figure 3). All monthly pairwise comparisons were not different with the exception of April and November (Bonferroni pairwise *Post-hoc* test: $p < 0.05$).

Although monthly and seasonal changes in marginal increment analysis observed in the YOY-only analysis followed a similar trend as all age classes combined, we determined the peaks were

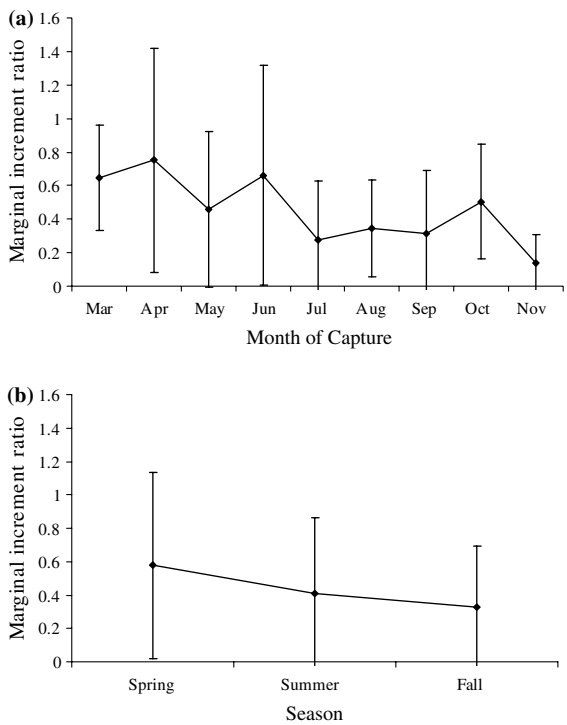

Figure 3. Mean marginal increment analysis for cownose rays (n = 169) by (a) month and (b) season. Vertical bars are ± standard deviation.

not statistically different (single factor ANOVA by month: F-ratio = 0.754, df = 4, $p > 0.10$; by season: F-ratio = 0.794, df = 2, $p > 0.10$). This lack of significance may be due to the small sample size available for analysis ($n = 20$).

Growth curve analysis

All four growth models fitted the observed size-at-age data well and were highly significant ($p < 0.0001$; Table 1). According to our criteria, the Gompertz model best described the data. The model had the lowest MSE and the highest r^2 value of the three parameter models, and the same r^2 value as the four parameter Richards model (Table 1). The likelihood ratio test also indicated that the Gompertz model provides the best reduction from the four parameter Richards model, without being significantly different from it ($\chi^2 = 0.049$, df = 1, $p > 0.10$; Table 1). In order to allow for comparison to the literature, we are presenting results for both the Gompertz and von Bertalanffy growth models.

Likelihood ratio tests indicated that our observed size at age data are best described as one combined-sexes model than for the sexes separately (Gompertz: $\chi^2 = 3.23$, df = 3, $p > 0.10$; von Bertalanffy: $\chi^2 = 3.27$, df = 3, $p > 0.10$; Figure 4). The combined sexes Gompertz model predicted a DW_∞ of 1100.2 mm DW, a K value of 0.1332 per year and a t_0 of −0.2573 years. The von Bertalanffy model for sexes combined predicted a DW_∞ of 1238.3 mm DW, a K value of 0.0746 per year and a t_0 of −5.4799 years. Theoretical longevity was estimated to be 26.1 years for the Gompertz model and 46.2 years for the von Bertalanffy model.

Likelihood ratio tests indicated that the Smith & Merriner data are also best described using one model for the sexes combined (Gompertz: $\chi^2 = 5.52$, df = 3, $p > 0.10$; von Bertalanffy: $\chi^2 = 4.50$, df = 3, $p > 0.10$). The von Bertalanffy

Table 1. Summary of goodness-of-fit of four models fit to observed size at age data for the cownose ray from the Gulf of Mexico.

Model	df	SS	MSE*	r^2	P	Ratio	−ln(ratio)*n	df	$p > \chi^2$
Von Bertalanffy	224	747222	3291.7	0.920	<0.0001	0.998	0.555	1	0.456
Gompertz	224	745559	3284.4	0.921	<0.0001	1.000	0.049	1	0.824
Logistic	224	749427	3301.4	0.920	<0.0001	0.995	1.224	1	0.269
Richards	223	745397	3283.7	0.921	<0.0001				
Corrected total	226	9380890							

*Calculated with total number of observations, not df.

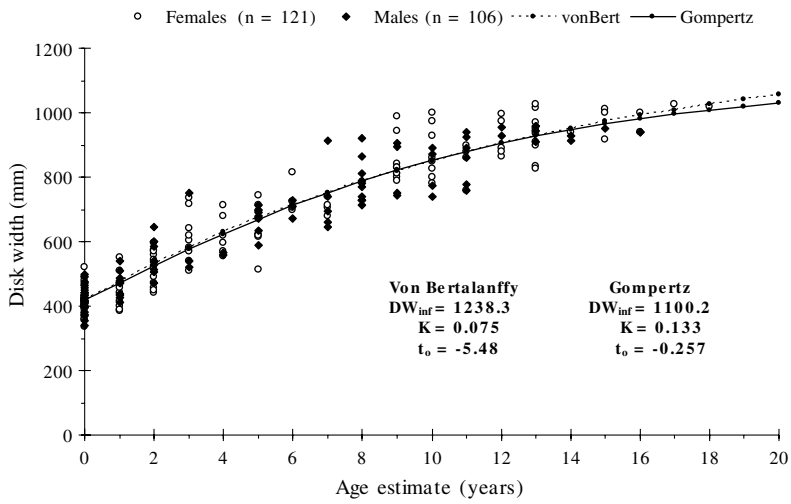

Figure 4. Growth functions fitted to the combined sexes observed size-at-age data for cownose rays ($n = 227$).

model for combined sexes predicted a DW_∞ of 1389.6 mm DW, a K value of 0.0878 per year and a t_0 of −4.6530 years. The combined sexes Gompertz model predicted a DW_∞ of 1195.1 mm DW, a K value of 0.1667 per year and a t_0 of −0.3990 years. Theoretical longevity was estimated to be 39.5 years for the von Bertalanffy model and 20.8 years for the Gompertz model. Significant differences were found between growth models for the Gulf of Mexico and the western Atlantic Ocean ($\chi^2 = 216.17$, df = 3, $p < 0.0001$).

Reproduction

We determined reproductive status for 218 rays during this study (104 males, 114 females). Median disk width at maturity (MDW) for male cownose rays was 642 mm (Figure 5), which corresponds to an age at maturity of ~4–5 years. An abrupt change in the clasper length–disk width relationship begins at ~600 mm DW (Figure 6). Seventy-one percent of males > 642 mm DW (n = 45) displayed complete coiling of the vas deferens and 77% (n = 47) had calcified claspers. The smallest mature male observed was 635 mm DW and the largest immature male was 750 mm DW.

Female cownose rays had a MDW at maturity of 653 mm (Figure 5). The smallest mature female was 623 mm DW and the largest immature female was 713 mm DW. Ninety-eight percent of females > 653 mm DW (n = 53) displayed a uterine width greater than 10 mm. For females larger than 653 mm DW for which ova size data were available (n = 42), fifty percent possessed ovarian ova greater than 10 mm diameter. Age of MDW at maturity was estimated to be approximately 4–5 years.

We observed 33 gravid females during this study. The smallest gravid female we collected measured 760 mm DW. In all cases, we observed only one pup in the left uterus. No ovary or uterine development was observed in the right reproductive tract in any of the females rays we examined (n = 108), thus only the left reproductive tract is functional in cownose rays. Embryos ranged in size from 205 to 395 mm DW and were observed in April, May, and September through November. The sex ratio of embryos was 1 to 1 (males to females). The smallest free swimming individual we observed measured 336 mm DW and was collected in July. The largest embryos we collected were in mid-April through mid-May (285–395 mm DW), indicating that pupping may be occurring at this time. Gestation appears to take 11–12 months based on embryos sizes collected throughout the year, however lack of samples from every month precludes further examination.

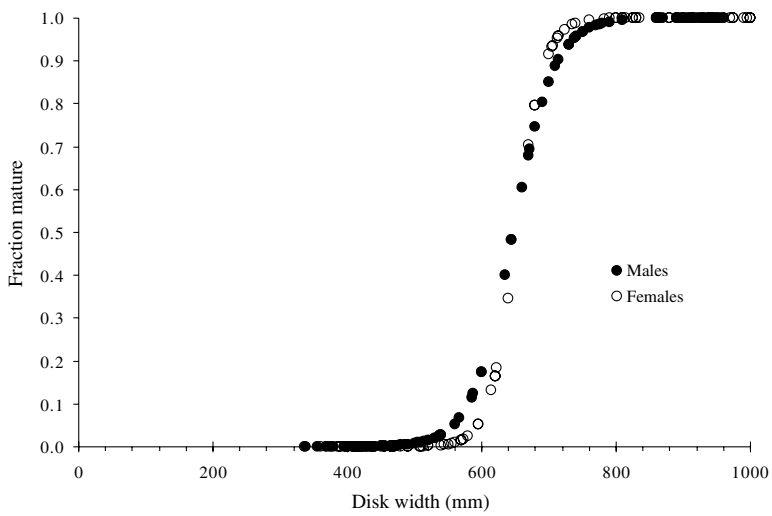

Figure 5. Relationship between maturity and disk width for the cownose ray. A logistic model was fitted to the binominal maturity data (0 = immature, 1 = mature).

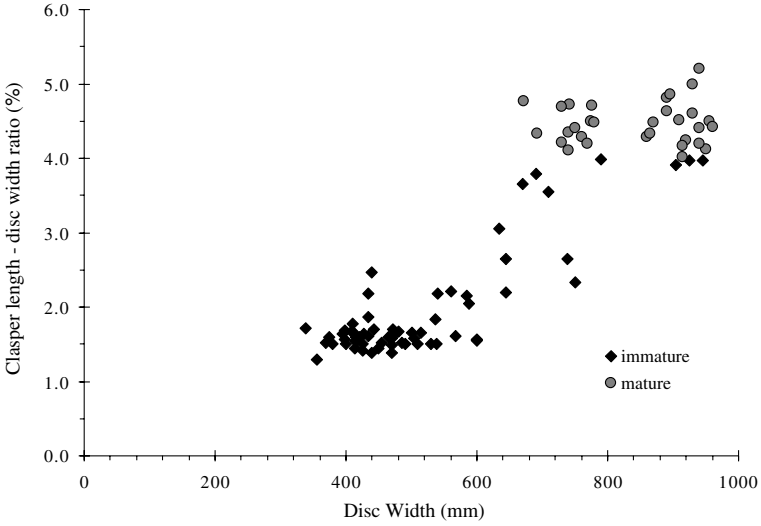

Figure 6. Relationship between outer clasper length and disk width for the cownose ray (n = 99).

Discussion

The Gompertz growth curve best described the growth of the cownose ray. Traditionally, the von Bertalanffy growth function (VBGF) has been applied to describe the growth of elasmobranch species (see review in Cailliet & Goldman 2004). However, more recent studies have indicated that the Gompertz function may better describe the growth of animals who continue to increase in weight and bulk over time, but not greatly in length once they reach large size (Cailliet & Goldman 2004). This may be especially true for the batoids. Mollet et al. (2002) suggested that the Gompertz model best described the captive growth of the pelagic stingray, *Dasyatis violacea*, indicating that it provided more realistic estimates of size at birth and growth rate than the VBGF. Neer & Cailliet (2001) also suggested that the Gompertz model provided the best fit for the size at age data for the Pacific electric ray, *Torpedo californica*. However, they did not provide parameters estimates for the Gompertz model but rather those from the VBGF to allow comparison to the published literature.

The Gompertz model also produced the more biologically realistic parameter estimates than the von Bertalanffy for the cownose ray. The largest ray we encountered during the study was a 1025 mm DW female, close to the DW_∞ of 1100.2 mm predicted by the Gompertz model. The DW_∞ predicted using the VBGF (1238 mm) seems to be an overestimate, based on the size of rays observed during this study. The estimates of longevity produced using the parameter estimates of K from the two models also indicate that the Gompertz model is more biologically realistic. The oldest animal aged in this study was a 18+ year-old female. The theoretical longevity estimate of 26.1 years determined from the Gompertz model is possible, while it seems doubtful that this species lives to 46 years based on the data currently available.

Our results verified of our assumption that narrow bands are formed annually in the winter months in the cownose ray. Smith & Merriner (1987) also concluded annual band formation based on the lack of what they termed a "hyaline band" in neonates and the presence of only one hyaline band in rays they determined to by approximately 1 year-old. These findings lead them to suggest that this "hyaline" band is formed in the winter months. Despite this corroboration, further validation of the annual periodicity of the banding pattern observed in the cownose ray is necessary through techniques such as chemical marking or tag-recapture studies.

Results of this study indicate that geographic variation in life history traits does occur for the cownose ray. The observed differences in growth

model parameters between the Gulf of Mexico and the Atlantic Ocean may be due to several factors. The Smith & Merriner age estimates were determined using cross-sectioned vertebrae while those determined in the current study used sagittally thin sectioned samples. Differences in preparation technique may confound results (Cailliet et al. 1990). Differences may also be due to the age classes included in the models. The oldest rays included in the western Atlantic Ocean data set were a 13-year-old female and an 8-year-old male. The oldest female we observed was 18+ years-old, while the oldest male was 16+ years-old. The lack of older individuals can greatly affect growth model parameter estimates (Cailliet & Goldman 2004). Although researchers have suggested that changes in life history parameters over time many be the result of compensatory changes in response to anthropogenic factors such as fishing (Walker & Hislop 1998, Carlson & Baremore 2003), we do not believe that is the case for the cownose ray as no directed fishery exists for this species. Finally, these results may truly reflect differences in regional growth patterns. Driggers et al. (2004) found statistically significant differences in growth models between the western Atlantic Ocean and the Gulf of Mexico for the blacknose shark, and Carlson et al. (2003) found similar results for the finetooth shark.

Differences in reproduction also exist between cownose rays from the Gulf of Mexico and the western Atlantic Ocean. Smith & Merriner (1986) suggested that male cownose rays <75 cm DW were immature while males >80 cm were mature while females begin sexual maturation at 85–90 cm and are mature at disk widths >90 cm. This study found the median disk width at maturity for males in the Gulf of Mexico to be roughly 10 cm smaller and 1–2 years earlier than those in the Atlantic Ocean. Female cownose rays in the Gulf of Mexico also reach the median disk width at maturity at a smaller size ($\sim$20 cm smaller) and earlier age (2–3 years earlier) than their counterparts in the western Atlantic Ocean. Carlson et al. (2003) reported similar trend for the finetooth shark. Holden (1974) suggested that elasmobranchs mature after reaching approximately 60% of their theoretical asymptotic size. This assumption is supported by our data. Male and female cownose rays mature at $\sim$58% of their estimated maximum disc width. Smith & Merriner (1986) suggested that cownose rays in the western Atlantic Ocean mature after reaching 70–75% of their predicted maximum DW.

Size-at-birth and timing of parturition may differ between the Atlantic Ocean and Gulf of Mexico populations. We estimated a mean size-at-birth to be approximately 350 mm DW, although our smallest free swimming individual measured 336 mm DW. This estimate falls within the previous estimates of size-at-birth of approximately 400 mm DW from Smith and Merriner (1986) and approximately 300 mm DW proposed by Schwartz (1967). Schwartz (1967) further defined the parturition and breeding cycle to occur June through October in the Chesapeake Bay. Smith & Merriner (1986) reported a similar seasonal reproductive cycle. Our study supports this protracted pupping and mating season, although the pupping season may begin slightly earlier in the Gulf of Mexico. We observed young-of-the-year individuals less than or equal to 400 mm DW from May through November. Additionally, we observed gravid females with embryos greater than 400 mm DW in April and May. This longer pupping season may be due to the warmer waters of the Gulf of Mexico relative to the Chesapeake Bay.

Fecundity and gestation estimates for the Gulf of Mexico population are similar to the published literature. Smith & Merriner (1986) reported a fecundity estimate of 1 pup per litter and suggested an 11–12 month gestation period, which agrees with the current study. The possibility that cownose rays may have two litters per year has been suggested (Smith & Merriner 1986) however the current data and information on reproductive hormonal cycling in captive animals do not support this (Alan Henningsen, Baltimore Aquarium, personal communication).

This study provides the first published age and growth estimates for a batoid from the Gulf of Mexico. Cownose rays appear to be similar to other elasmobranchs in being relatively long-lived, having low fecundity, and a late age at sexual maturity. However, more detailed information regarding age validation, parturition season, reproductive cycles, and migration patterns is needed to refine the estimates presented here.

Acknowledgements

Thanks to I.E. Baremore, D. Bethea, J.K. Carlson, and all the Shark Population Assessment Group interns with assistance in collection of the animals in Florida. Thanks also to J.K. Blackburn, G.W. Peterson, and K.P. Barry for collection assistance in Louisiana. Additional thanks go to the National Marine Fisheries Service, Panama City, Florida for providing logistical support without which this project would not have been possible. J.K. Carlson reviewed an early version of this work and provided valuable insight. Special thanks to J.W. Smith for providing the original data for the western Atlantic Ocean population. The first author received support for this research from the National Marine Fisheries Service/National Sea Grant Joint Fellowship Program in Population Dynamics and Marine Resource Economics. This study was conducted under the guidelines set forth and approved by the Louisiana State University Institutional Animal Care and Use Committee, Protocol #00-112.

References

Beamish, R.J. & D.A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Can. J. Fish Aquat. Sci. 38: 982–983.

Bigelow, H.B. & W.C. Schroeder. 1953. Fishes of the Western North Atlantic. Part I, Lancets, cyclostomes and sharks. Memoir Sears Foundation for Marine Research. Allen Press, Lawrence. 576 pp.

Blaylock, R.A. 1993. Distribution and abundance of the cownose ray, Rhinoptera bonasus, in lower Chesapeake Bay. Estuaries 16: 255–263.

Cailliet, G.M. & K.J. Goldman. 2004. Age determination and validation in chondrichthyan fishes. pp. 399–447. *In*: J.C. Carrier, J.A. Musick & M.R. Heithaus, (eds), Biology of Sharks and Their Relatives, CRC Press, Boca Raton.

Cailliet, G.M., K.G. Yudin, S. Tanaka & T. Taniuchi. 1990. Growth characteristics of two populations of Mustelus manazo from Japan based on cross-readings of vertebral bands. pp 167–176. *In*: H.L. Pratt Jr., S.H. Gruber & T. Taniuchi (eds) Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries, U.S. Department of Commerce. NOAA Technicial Report NMFS 90.

Cailliet, G.M., H.F. Mollet, G.G. Pittenger, D. Bedford & L.J. Natanson. 1992. Growth and demography of the Pacific angel shark (*Squatina californica*), based upon tag returns off California. Aust. J. Mar. Freshwater Res. 43: 1313–1330.

Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. J. Fish Biol. 59: 197–242.

Carlson, J.K. & J.H. Brusher. 1999. An index of abundance for coastal species of juvenile sharks from the northeast Gulf of Mexico. Mar. Fish. Rev 61: 37–45.

Carlson, J.K. & I.E. Baremore. 2005. Growth dynamics of the spinner shark, *Carcharhinus brevipinna*, off the Southeast United States and Gulf of Mexico: a comparison of methods. Fish Bull. 103: 208–291.

Carlson, J.K. & I.E. Baremore. 2003. Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity. Mar Freshwater Res. 54: 227–234.

Carlson, J.K., E. Cortès & D. Bethea. 2003. Life history and population dynamics of the finetooth shark, *Carcharhinus isodon*, in the northeastern Gulf of Mexico. Fish. Bull. 101: 281–292.

Cerrato, R.M. 1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. Can. J. Fish. Aquat. Sci. 47: 1416–1426.

Chang, W.Y.B. 1982. A statistical method for evaluating the reproducibility of age determination. Can. J. Fish. Aquat. Sci. 39: 1208–1210.

Compagno, L.J.V., 1984. FAO Species Catalogue. Vol. 4. Sharks of the World. An Annotated and Illustrated Catalogue of Sharks Species Known to Date. Part 1. Hexanchiformes to Lamniformes. FAO Fisheries Synopsis 125, part 1. Rome. 249 pp..

Devore, J.L. 2000. Probability and Statistics for Engineering and the Sciences. 5 ed.Duxbury, Australia. 775 pp.

Driggers, W.B. III, J.K. Carlson, D. Oakley, G. Ulrich, B. Cullum & J.M. Dean. 2004. Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth rates. Environ. Biol. Fish. 71: 171–178.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29: 265–289.

Gulland, J.A. 1969. Manual of Methods for Fish Stock Assessment. Part 1. Fish Population Analysis. FAO of the United Nations, Rome. 154 pp.

Haddon, M. 2001. Modelling and Quantitative Methods in Fisheries. Chapman & Hall–CRC, Boca Raton. 406 pp.

Holden, M.J. 1974. Problems in the rational exploitation of elasmobranch populations and some suggested solutions. pp. 117–137. *In*: F.R. Harden-Jones, (eds), Sea Fisheries Research, John Wiley and Sons, New York.

Kimura, D.K. 1980. Likelihood methods for the von Bertalanffy growth curve. Fish. Bull. 77: 765–776.

Lombardi-Carlson, L.A., E. Cortés, G.R. Parsons & C.A. Manire. 2003. Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo*, (Carcharhiniformes:Sphyrnidae) from the eastern Gulf of Mexico. Mar. Freshwater Res. 54: 875–883.

McEachran, J.D. & C. Capapé. 1984. Rhinopteridae. pp. 208. *In*: P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen & E. Tortonese (eds) Fishes of the North-eastern Atlantic and Mediterranean. Vol. 1, UNESCO.

McEachran, J.D. & Fechhelm, J.D. 1998. Fishes of the Gulf of Mexico. Vol. 1, University of Texas Press. 192 pp.

Mollet, H.F., G. Cliff, H.L. Pratt Jr. & J.D. Stevens. 2000. Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. Fish. Bull. 98: 299–318.

Mollet, H.F., J.M. Ezcurra & J.B. O'Sullivan. 2002. Captive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832). Mar. Freshwater Res. 53: 531–541.

Natanson, L.J., J.G. Casey & N.E. Kohler. 1995. Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. Fish. Bull. 93: 116–126.

Neer, J.A., J.K. Blackburn & B.A. Thompson. In press. Shark nursery areas of central Louisiana's nearshore Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States. American Fisheries Society.

Neer, J.A. & G.M. Cailliet. 2001. Aspects of the Life history of the Pacific electric ray, *Torpedo californica* (Ayres). Copeia 2001: 842–847.

Parsons, G.R. 1993. Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. Environ. Biol. Fish. 38: 25–35.

Richards, J. 1959. A flexible growth function for empirical use. J. Exp. Bot. 10: 290–300.

Ricker, W.E. 1975. Computation and Interpretation of Biological Statistics of Fish Populations. Bulletin of the Fisheries Research Board Canada 191, Ottawa. 382 pp.

Ricklefs, R.E. 1967. A graphical method of fitting equations to growth curves. Ecology 48: 978–983.

Schwartz, F.J. 1967. Embryology and feeding behavior of the Atlantic cownose ray, *Rhinoptera bonasus*. Association of Island Marine Laboratories of the Caribbean – 7th Meeting, Barbados, West Indies. 000 pp .

Schwartz, F.J. 1990. Mass migratory congregations and movements of several species of cownose rays, Genus *Rhinoptera*: A world-wide review. J. Elisha Mitchell Sci. Soc. 106: 10–13.

Smith, J.W. & J.V. Merriner. 1985. Food habits and feeding behavior of the cownose ray, *Rhinoptera bonasus*, in lower Chesapeake Bay. Estuaries 8: 305–310.

Smith, J.W. & J.V. Merriner. 1986. Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. Fish. Bull. 84: 871–877.

Smith, J.W. & J.V. Merriner. 1987. Age and growth, movements and distribution of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. Estuaries 10: 153–164.

Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II.). Human Biol. 10: 181–213.

Walker, P.A. & J.R.G. Hislop. 1998. Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and present day. ICES J. Mar. Sci. 55: 392–402.

Yano, K. 1993. Reproductive biology of the slender smoothhound, *Gollum attenuatus*, collected from New Zealand waters. Environ. Biol. Fish. 38: 59–71.

Zar, J.H. 1984. Biostatistical Analysis. 2 ed.Prentice-Hall, New Jersey. 243 pp.