2013

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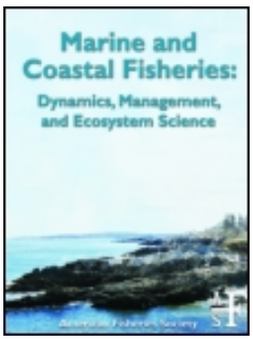
Recommended Citation

Robert A. Fisher , Garrett C. Call & R. Dean Grubbs (2013) Age, Growth, and Reproductive Biology of Cownose Rays in Chesapeake Bay, Marine and Coastal Fisheries, 5:1, 224-235, DOI: 10.1080/19425120.2013.812587



Taylor & Francis
Taylor & Francis Group

Marine and Coastal Fisheries

Dynamics, Management, and Ecosystem Science

ISSN: (Print) 1942-5120 (Online) Journal homepage: http://www.tandfonline.com/loi/umcf20

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To link to this article: https://doi.org/10.1080/19425120.2013.812587

Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science 5:224–235, 2013

ISSN: 1942-5120 online
DOI: 10.1080/19425120.2013.812587

ARTICLE

Age, Growth, and Reproductive Biology of Cownose Rays in Chesapeake Bay

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Abstract

The Cownose Ray *Rhinoptera bonasus* is an opportunistic predator of benthic invertebrates and has had a long history of negative interactions with commercial shellfish industries. Most recently, Cownose Rays have been implicated in negatively affecting the recovery of bay scallop *Argopecten irradians* stocks in North Carolina and oyster restoration and commercial aquaculture efforts in Chesapeake Bay. A mitigation attempt to decrease predation on shellfish has resulted in an unregulated fishery for Cownose Rays. Cownose Ray life history suggests that they are highly susceptible to overexploitation. We determined age, growth, and size at maturity for Cownose Rays collected in Chesapeake Bay. In total, 694 rays were used for the study: 246 males ranging in size from 30.0 to 98.0 cm disc width (DW) and 448 females ranging from 30.0 to 110.5 cm DW. The oldest individual observed was a female (107 cm DW) estimated at age 21. Our data suggested that Cownose Rays grow considerably faster during the first few years than has been previously reported, thus producing higher estimates of the growth coefficient *k*. The best-fit growth models (three-parameter von Bertalanffy models) estimated *k*-values of 0.2741 for males and 0.1931 for females. The large sample size and inclusion of many older animals ($n = 119$ rays over age 10) resulted in theoretical maximum size estimates that matched the observed sizes well. The median size at 50% maturity was 85–86 cm DW for males and females (corresponding to ages of ∼6–7 for males and ∼7–8 for females). Fecundity in Cownose Rays was typically one embryo per mature female, with a gestation period of 11–12 months. Our study confirms that the Cownose Ray is a *K*-selected species with late maturity, long gestation, and low reproductive potential, indicating that it could be highly susceptible to overexploitation.

The Cownose Ray *Rhinoptera bonasus* is a large, coastal-pelagic batoid that migrates in large schools along the U.S. East Coast and in the Gulf of Mexico. Cownose Rays have been noted as abundant in Chesapeake Bay since the early 1600s (Rountree et al. 2008). In the summer, Cownose Rays are seasonal residents in Chesapeake Bay, immigrating into the estuary in May to pup and subsequently mate. In late September, Cownose Rays migrate south to wintering areas, primarily off the Atlantic coast of Florida (Grusha 2005; R. A. Fisher, unpublished data). Cownose Rays are opportunistic predators that are capable of

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Received February 28, 2013; accepted June 3, 2013

durophagous feeding (i.e., consuming hard-shelled prey). Diet studies have indicated that Cownose Rays consume a wide array of prey taxa, including small bivalve mollusks, crustaceans (e.g., amphipods and cumaceans), polychaetes, and even echinoderms (e.g., sand dollars; Smith and Merriner 1985; Collins et al. 2007; Fisher 2010; Ajemian and Powers 2012). Commercial taxa that have been found to be a significant part of the Cownose Ray's diet are weak-valved bivalves, such as bay scallops *Argopecten irradians* in North Carolina only (Powers and Gaskill 2003) and soft-shell clams *Mya arenaria*, historically in Chesapeake Bay (Smith and Merriner 1985). Hard-shelled commercial bivalves, such as hard-shell clams *Mercenaria mercenaria* and eastern oysters *Crassostrea virginica*, have rarely been found in the natural diets of Cownose Rays (Smith and Merriner 1985; Collins et al. 2007; Fisher 2010), and studies have indicated that Cownose Rays display a preference for softer-shelled bivalves (Fisher et al. 2011; Ajemian and Powers 2013).

Wild shellfish stocks have been declining in Chesapeake Bay since the early 1900s (Kennedy and Breisch 1983; Rothschild et al. 1994). In response to the decline in shellfish populations, efforts to restore the bay's habitat began increasing in the 1990s (Kennedy et al. 2011). In the meantime, shellfish aquaculture for human consumption has become a multimillion dollar industry in the Chesapeake Bay region. Since 2005, plantings of eastern oysters in the Virginia portion of Chesapeake Bay have increased nearly tenfold. In 2011, plantings of eastern oysters exceeded 65 million and plantings of hard-shell clams exceeded 450 million in Virginia waters of Chesapeake Bay (Murray and Hudson 2012).

For more than 40 years, Cownose Ray predation on commercial bivalves has been a concern for declining shellfish industries, particularly oyster growers (Merriner and Smith 1979; Smith and Merriner 1985). Recently, Cownose Rays have become a source of controversy and media attention due to increased conflict between Cownose Rays and the restoration and aquaculture efforts in Chesapeake Bay, along with claims that the Cownose Ray population increased dramatically coastwide due to top-down predation release (Myers et al. 2007). Since the turn of the century, oyster restoration and commercial grow-out efforts in Virginia have undoubtedly experienced setbacks due to Cownose Ray consumption of deployed oysters on experimental reefs and commercial grounds. In 2004 and 2006, 1.2 million and 775,500 oysters, respectively, were seeded for reef restoration in Virginia, and anecdotal reports suggest that 95% of the seeded oysters were eaten by Cownose Rays (Wesson 2009). During 2007, an unregulated fishery for Cownose Rays began in Chesapeake Bay in an attempt to decrease predation rates on seed oysters. Although this fishery has been promoted as sustainable, no management plan exists and the Cownose Ray's life history (late maturity and very low fecundity) suggests that these fish are highly susceptible to overexploitation. An early study on the age and growth of Cownose Rays in Chesapeake Bay (Smith and Merriner 1987) and off North Carolina (collected between 1976 and 1978) concluded that males matured at age 5–6 and females matured at age 7–8. Relatively few samples ($n = 61$ males and 54 females) were examined by Smith and Merriner (1987), and the samples were skewed toward younger age-classes. Based on a larger sample size ($n = 227$), Neer and Thompson (2005) estimated that maturity occurred at age 4–5 for Cownose Rays in the northern Gulf of Mexico. These studies suggest that Cownose Rays in the Atlantic and Gulf of Mexico have different life histories; therefore, the results cannot be applied to Cownose Rays that spend their summers in Chesapeake Bay. Updated estimates of life history parameters, such as age and size at maturity, maximum age, fecundity, and reproductive periodicity, are critical for determining susceptibility of the population to overexploitation and for informing future management plans.

The precautionary principle dictates that an assessment of sustainability must be conducted prior to development of a fishery, and the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act of 2006 mandates sustainable catch limits for all U.S. fisheries. Neer et al. (2007) estimated that the maximum rate of population change for Cownose Rays in the Gulf of Mexico was only 2.7% per year. Considering that Cownose Rays have among the lowest reproductive rates of any vertebrate, usually producing a single pup each year (Smith and Merriner 1986; Neer and Thompson 2005; Fisher 2010), and that rhinopterid rays in other parts of the world have been driven to endangered status by relatively small fisheries (Vooren and Lamónaca 2004), data that can be used to inform future stock assessments of Cownose Rays are critical. In this study, we examined age and sexual maturity of Cownose Rays collected from Chesapeake Bay, and we fitted the observed age and growth data with models that could be used in management applications.

METHODS

Cownose Rays were collected from Virginia waters along the western shore of Chesapeake Bay during summer months (from May to early October) in 2006–2010 by using a combination of fishery-dependent methods (e.g., bycatch of commercial haul seines and pound nets) and fishery-independent methods (longline, bowfishing, and experimentally modified Dutch seines). Rays were sexed, weighed (kg), and measured ventrally for straight disc width (DW; cm).

Age assessment.—Starting from the anteriormost vertebrae that can be reached through the exposed abdominal cavity, a section consisting of 6–12 thoracic vertebral centra was removed from each Cownose Ray and was frozen for later age determination. Vertebral sections were thawed, cleaned of excess tissue in a 75% solution of ethanol, and then dried. Individual centra were removed from the vertebral section and mounted onto a cutting block for sectioning. Using a Buehler Isomet low-speed rotary diamond saw, we sectioned each vertebra sagittally through the focus of the centrum. Sections were mounted on a glass microscope slide via mounting medium. Samples were

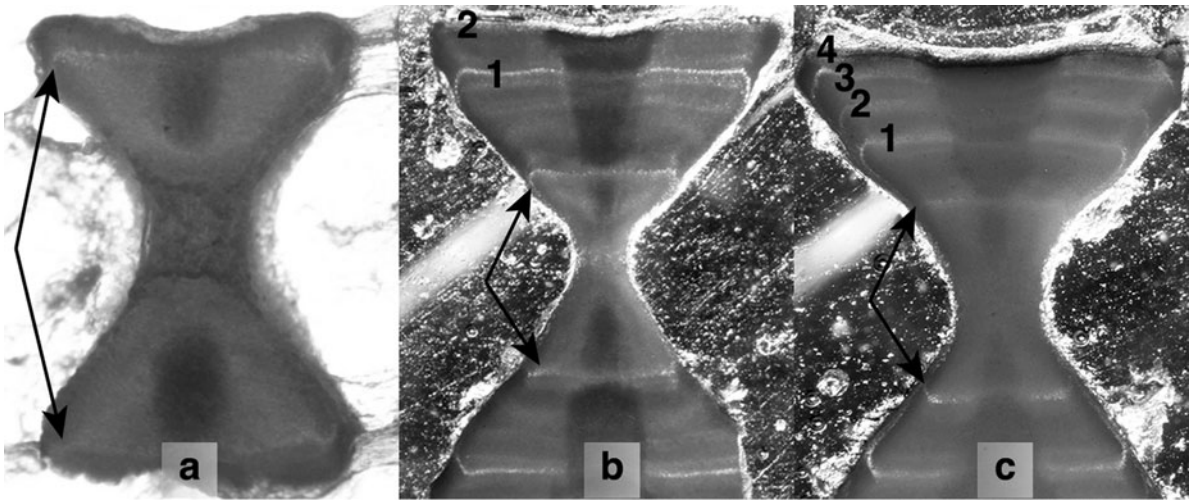

FIGURE 1. Sagittally sectioned vertebrae from Cownose Rays, showing the birth mark (indicated by arrows) and numbered annuli. Ages are as follows: **(a)** near-term embryo, **(b)** 1-year-old ray, and **(c)** 4-year-old ray.

sanded and polished using wet fine-grit sandpaper in a series (grades 320, 400, and 600) until light was readily transmitted through the samples and annuli were distinguishable using a dissection microscope.

To assess age from vertebral sections, we assumed that (1) the birth mark was associated with the change in angle in the intermedialia, (2) the light and dark bands are deposited annually and represent a growth cycle (Cailliet and Goldman 2004), and (3) the light (narrow) bands represent winter periods of slow growth. Age was estimated by counting the number of light bands, but the birth mark was excluded because evidence shows that the birth mark is laid down before birth, as can be seen in the vertebra of a Cownose Ray embryo (Figure 1).

Two readers independently assessed age by counting the winter bands without knowledge of the individual rays' DWs. When disagreement occurred between readers, both readers viewed vertebral sections together to allow for consensus on a final age determination. If readers were still not in agreement on a section, the vertebra sample was eliminated from the study. A McNemar test of symmetry about the main diagonal was used to test the null hypothesis that the readers were interchangeable against the alternative that there were systematic differences between the two readers (see Evans and Hoenig 1998).

Growth assessment.—We fitted five growth models to the observed size-at-age data by using DW. Age-0 Cownose Rays consisted of (1) at-term embryos collected within a 10-d period from the end of June to the first week of July, when parturition was at its peak (half of females sampled had already pupped, and the other half still carried at-term embryos); and (2) free-swimming pups that possessed no winter growth bands. We ran DW–age data through models twice: once including only whole-year age estimates and then using fractional age estimates for young-of-the-year (age-0) rays to better reflect the substantial growth that occurs during the first 3 months of life. Fractional ages were estimated at 0.125 and 0.3 years and defined as follows: age 0.125 represented neonates that were collected during a 2-week period in mid- to late-August, identifiable by a tendency to aggregate with adult females; and age 0.3 represented young that were collected during the second week of October and were identifiable by aggregation with their age-class as they began exiting Chesapeake Bay as a group.

Model parameters were estimated using least-squares estimation for the following models (size refers to DW): (1) a modified (conventional) form of the von Bertalanffy growth function (VBGF), using an estimated age at a size of zero (VBGF_{mod}; Beverton and Holt 1957); (2) the original form of the VBGF, using an empirically derived size-at-birth intercept rather than a theoretical age at size zero (VBGF; von Bertalanffy 1938; Cailliet et al. 2006); (3) a two-parameter form of the original VBGF, with a fixed size at age 0; (4) a Gompertz model (Ricker 1975); and (5) a logistic function (Ricker 1975). We used the residual mean square error (RMSE) and Akaike's information criterion (AIC) as measures of the goodness of fit for all models. Equations for the models are as follows:

$$\text{VBGF}_{mod}\text{: } \text{DW}_t = \text{DW}_\infty\left[1 - \exp^{-k(t-t_0)}\right] \quad (1)$$

$$\text{VBGF: } \text{DW}_t = \text{DW}_\infty - (\text{DW}_\infty - \text{DW}_0)\exp^{-kt} \quad (2)$$

$$\text{Two-parameter VBGF: } \text{DW}_t = \text{DW}_\infty - (\text{DW}_\infty - 45)\exp^{-kt} \quad \text{(mean observed } \text{DW}_0 = 45\text{cm)} \quad (3)$$

$$\text{Gompertz model: } \text{DW}_t = \text{DW}_0\{\exp[G(1 - \exp^{-kt})]\} \quad (4)$$

and

$$\text{Logistic function: } \text{DW}_t = \text{DW}_\infty/\left[1 + \exp^{-k(t-t_0)}\right], \quad (5)$$

where DW_t is the predicted DW at age t; DW_∞ is the asymptotic or theoretical maximum DW; DW_0 is the DW at birth; k is the growth coefficient; t is age; t_0 is the age at which DW theoretically equals zero; and G is equal to $\log_e(DW_\infty/DW_0)$.

Sexual maturity assessment.—Sexual maturity of male Cownose Rays was determined using the following criteria: (1) clasper calcification (uncalcified, partially calcified, or calcified); (2) vas deferens coiling (none, partial, or complete; Neer and Cailliet 2001); (3) presence–absence of seminal fluid (sperm-containing secretion) from the vas deferens and/or expressed through the urogenital papilla; (4) ratio of clasper length to DW (Smith and Merriner 1986); and (5) histological sampling (selected individuals, $n = 24$) of testes and vas deferens for the presence–absence of mature sperm in relationship to vas deferens coiling and the presence of seminal fluid. Males with calcified claspers, enlarged testes, and fully coiled vas deferens were considered mature.

Both lobes of the testes were sampled and weighed for comparison and maturity correlations. Claspers of immature rays are short and flexible, indicating that they are not able to function during copulation. With maturity, internal clasper cartilages calcify and articulate with the pelvic fin cartilage, allowing them to rotate for insertion into female. Outer clasper length (mm) was measured from the free tip of the clasper to the point where the clasper meets the pelvic fin. Presence or absence of seminal fluid was determined by applying slight pressure inward and then caudally along the terminal end of the urogenital tract where the paired sperm sacs converge. Seminal fluid, if present, is expressed through pores in the urogenital papilla. Histological samples for both sexes were initially preserved in 10% neutral-buffered formalin and were later imbedded in paraffin, sectioned, and stained with hematoxylin and eosin by following standard histological procedures. For male testes, tissues from cranial, medial, and caudal portions of the testis lobe were analyzed. As expected for a species with compound testes, no difference was found between lobe sections within a sample; therefore, all subsequent sampling of testis occurred by removing sections from the medial–caudal region of the testis lobe. Given that the testis lobes in male Cownose Rays vary in size, preliminary histological analyses were performed to confirm functionality in both testis lobes. Mature sperm were observed in males with coiled vas deferens and males in which seminal fluid was present. Complete maturity in male Cownose Rays was defined by coiling of the vas deferens and calcification of the claspers; the presence of seminal fluid was used to aid in assigning maturity associated with partially coiled vas deferens, and a clasper–DW ratio greater than 4% was used to aid in correlating maturity with clasper calcification.

Female maturity was largely determined based on the diameter of the largest ova or by confirming that the individual was pregnant. Diameters of the largest three ova within the ovary were measured (mm) to obtain mean maximum ovum diameter (MOD). Cownose Rays with ova larger than 10 mm were considered to be mature (advanced vitellogenic oocytes) per Smith and Merriner (1986). Histological sampling of ovaries was performed to document the stage of vitellogenesis and ova development. Females have one functional oviduct and one nonfunctional oviduct, with the left typically serving as the functional oviduct (Fisher 2010). The uteri are well developed and expanded in females that have recently given birth; uteri are in a transitional development stage in rays that are preparing to gestate for the first time. Left (functional) uterus width (UW; widest point), qualitative assessment of uterine wall thickness, and trophonemata development and color were also used as indications of sexual maturity. Maturing females undergo a rapid expansion in UW, thickening of the uterine wall, and elongation and darkening (from pink to red) of the trophonemata.

Maturity ogives were used to estimate Cownose Ray size at maturity (median DW at which 50% of the individuals are mature) following Mollet et al. (2000) and to estimate age at maturity. The ogives were fitted to a logistic model using binomial maturity determinations (0 = immature; 1 = mature) as described above for both sexes.

Fecundity assessment.—Embryos that were recovered from pregnant female Cownose Rays for fecundity determination were all delivered by necropsy. The recovery of developing embryos and the proper assignment of embryos to respective mothers are sometimes difficult since rays readily abort (slip) their embryos upon death and during subsequent handling. Slipped embryos recovered in this study were used for analyses of embryo size at developmental stage but were not used for fecundity observations. Mating occurs immediately after parturition from mid-June to early July, resulting in gestation periods of 11–12 months (Fisher 2010). Sampling for pregnant females occurred during late gestation (May to early July) and early gestation (July–October) periods. Embryo size at parturition was determined by sampling term embryos during the last week of June and first week of July, when adult females collected within each sample either were still carrying embryos or had recently pupped.

RESULTS

In total, 694 Cownose Rays were examined in this study, including 246 males ranging in size from 30.0 to 98.0 cm DW and 448 females ranging from 30.0 to 110.5 cm DW. The samples included (1) 325 individuals exceeding 47 cm DW ($n = 117$ males and 208 females), which were used for both age estimation and maturity assessment; (2) 212 juvenile rays less than 47 cm DW, which were only used for the age and growth assessments; (3) 127 rays greater than 80 cm DW ($n = 28$ males and 99 females), which were only used in maturity assessments; and (4) 30 pregnant females, which were added to an existing pool of pregnant rays and used for fecundity assessment ($n =$ 196 total pregnant rays). In total, 537 Cownose Rays were used for age and growth assessment (Figure 2). Age estimates ranged from 0 to 21 years, with no significant difference between the ages estimated by the two readers ($\chi^2 = 2.112$, df = 1, $P =$ 0.146). Percent agreement between the readers was as follows: ages were in complete agreement for 32.5% of samples, agreed

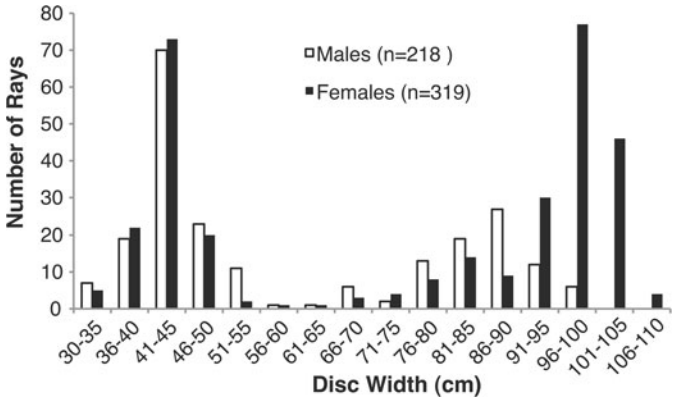

FIGURE 2. Numbers and sizes of male and female Cownose Rays used in the age and growth study.

within ±0–1 years for 72.6% of samples, agreed within ±0–2 years for 87.4% of samples, and differed by 3 years or more for 12.6% of samples. Despite intensive sampling throughout Chesapeake Bay, 51–75-cm DW rays were largely absent.

Age and Growth

The oldest Cownose Ray observed was a female (107 cm DW) estimated to be age 21. The largest individual was a 110.5-cm DW female estimated to be age 19. The oldest male Cownose Ray (97 cm DW) was estimated to be age 18. The largest male was 98 cm DW and was estimated to be age 16. In total, 115 at-term embryos (55.6% female; 44.4% male) were collected and averaged 42.14 cm DW and 1.28 kg. Female at-term embryos averaged 42.3 cm DW (1.32 kg), and male at-term embryos averaged 41.9 cm DW (1.24 kg). Free-swimming neonates were observed during late July in each sampling year (2006–2010).

Samples for neonate growth assessment were obtained in early August 2007, when aggregations of neonates with mature females were observed. In total, 109 neonates were collected during the first week of August; 46% were females averaging 42.47 cm DW (SD = 0.78) and 1.06 kg, and 54% were males averaging 42.53 cm DW (SD = 4.38) and 1.04 kg. Neonate growth within the first 4–6 weeks postparturition was negligible; a nominal increase in DW but a considerable decrease in weight (16–18%) were observed. Initial weight loss of 6.4% was observed in captive Cownose Rays ($n = 5$) during the first 9 d after birth (Fisher 2010). The smallest and largest free-swimming Cownose Rays observed were males, measuring 30 and 50 cm DW. At the time of their migration southward (late September to early October), age-0 Cownose Rays were routinely observed to aggregate together and left Chesapeake Bay after the adults had already done so. Sampling with pound nets at the mouth of the bay in early October resulted in only the collection of age-0 rays ($n = 67$); 38.5% were females averaging 55.5 cm DW (2.14 kg), and 61.5% were males averaging 51.4 cm DW (2.05 kg). Relative to at-term embryos, these sizes represent 13.2- and 9.5-cm increases in DW and 61.7% and 60.5% increases in weight for age-0 females and males, respectively.

The DW–weight relationships for Cownose Rays in this study ($n = 448$ females and 246 males) were similar between the sexes and are described by the following power functions:

$$\text{Females: weight} = 5 \times 10^{-6}(\text{DW}^{3.2587}) \quad (R^2 = 0.9881)$$

and

$$\text{Males: weight} = 6 \times 10^{-6}(\text{DW}^{3.2061}) \quad (R^2 = 0.99).$$

Growth Models

The size-at-age data indicated that male Cownose Rays grew faster and reached a smaller maximum size than females; a likelihood ratio test (Kimura 1980) confirmed significant differences between the VBGF curves for males and females (likelihood ratio = 451.1, df = 3, $P < 0.0001$). Therefore, we analyzed data for each sex separately. All growth models that were fitted to observed size-at-age data were significant ($P < 0.0001$), and the results based on fractional age estimates were similar to those based on the use of only whole-year age estimates (Tables 1, 2).

The two forms of the three-parameter VBGF had the lowest RMSEs and the lowest AIC values, suggesting that they provided the best fit to the observed size-at-age data for male and female Cownose Rays (Tables 1, 2). Model parameters and growth rates further illustrated differences between the sexes (Figure 3). The Gompertz model and the two-parameter VBGF model produced the worst fit to our data for both males and females. The estimates for DW_∞ were biologically reasonable for all models (males and females) except the logistic growth model, which underestimated this parameter for both sexes. The maximum observed DW was 110 cm for females and 98 cm for males, and all models except the logistic model produced DW_∞ estimates of 104–106 cm for females and 95–97 cm for males. Observed sizes at age of both sexes are given in Tables 3 and 4.

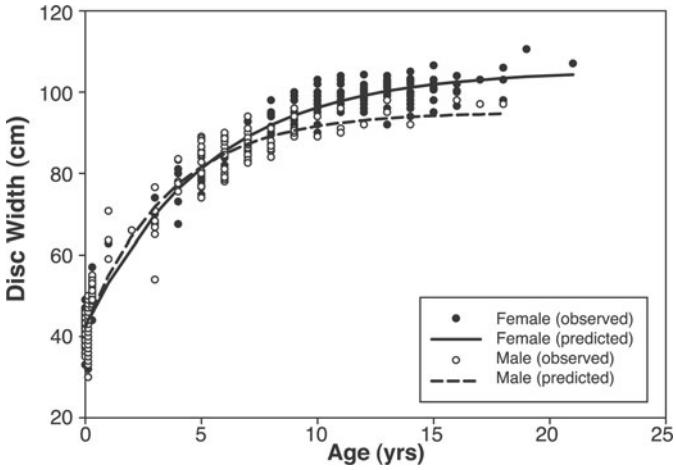

FIGURE 3. The von Bertalanffy growth curves (using fractional age-0 observations) for male ($n = 218$) and female ($n = 319$) Cownose Rays sampled in Chesapeake Bay.

TABLE 1. Five models used to evaluate growth of Cownose Rays ($n = 260$ females, 140 males), without fractional age estimates for young-of-the-year rays (VBGF = von Bertalanffy growth function; $VBGF_{mod}$ = modified VBGF [see Methods]; DW_∞ = asymptotic maximum disc width [mean ± SE]; k = growth coefficient [mean ± SE]; t_0 = theoretical age at which DW equals zero; DW_0 = DW at birth; AIC = Akaike's information criterion; RMSE = residual mean square error). Values from the best-fitting models are in bold italics.

Model	DW_∞ (cm)	k (year^{-1})	t_0	DW_0 (cm)	AIC	RMSE
		Males				
Two-parameter VBGF	97.095 ± 1.73	0.2333 ± 0.019	na	45	1,295.6	21.704
VBGF	94.983 ± 1.40	0.2742 ± 0.021	na	42	1,251.3	17.554
$VBGF_{mod}$	***94.983 ± 1.40***	***0.2741 ± 0.021***	***−2.14***	***na***	***1,251.3***	***17.554***
Gompertz	95.224 ± 1.44	0.3070 ± 0.021	na		1,295.9	21.740
Logistic	92.713 ± 1.11	0.4330 ± 0.025	0.363	na	1,269.2	19.061
		Females				
Two-parameter VBGF	106.34 ± 0.93	0.1778 ± 0.008	na	45	1,775.0	14.995
VBGF	105.34 ± 0.76	0.1931 ± 0.008	na	42	1,702.4	11.865
$VBGF_{mod}$	***105.34 ± 0.76***	***0.1931 ± 0.008***	***−2.64***	***na***	***1,702.4***	***11.865***
Gompertz	104.26 ± 0.70	0.2364 ± 0.008	na		1,766.6	14.605
Logistic	102.30 ± 0.49	0.3226 ± 0.009	1.059	na	1,707.5	12.056

TABLE 2. Five models used to evaluate growth of Cownose Rays ($n = 319$ females, 218 males), with fractional age estimates for young-of-the-year rays. Models and parameters are defined in Table 1. Values from the best-fitting models are in bold italics.

Model	DW_∞	k (year^{-1})	t_0	DW_0	AIC	RMSE
		Males				
Two-parameter VBGF	96.446 ± 1.57	0.2422 ± 0.019)	na	45	808.5	17.072
VBGF	95.685 ± 1.34)	0.2622 ± 0.018)	na	42	785.6	15.122
$VBGF_{mod}$	***95.685 ± 1.33)***	***0.2622 ± 0.018)***	***−2.22***	***na***	***785.6***	***15.122***
Gompertz	94.920 ± 1.33)	0.3125 ± 0.020)	na		811.7	18.482
Logistic	93.061 ± 1.04)	0.4253 ± 0.023)	0.411	na	798.5	16.585
		Females				
Two-parameter VBGF	105.99 ± 0.82)	0.1814 ± 0.007	na	45	1,388.2	11.921
VBGF	105.48 ± 0.71)	0.1911 ± 0.007	na	42	1,350.3	10.223
$VBGF_{mod}$	***105.48 ± 0.71)***	***0.1911 ± 0.007***	***−2.69***	***na***	***1,350.3***	***10.223***
Gompertz	104.09 ± 0.62)	0.2387 ± 0.007	na		1,383.7	11.716
Logistic	102.36 ± 0.46)	0.3207 ± 0.008	1.052	na	1,351.4	10.269

TABLE 3. Mean size at ages 0–8 (including fractional ages for young of the year) for male and female Cownose Rays sampled in Chesapeake Bay (DW = disc width).

	Age (years)										
Variable	0	0.12	0.30	1	2	3	4	5	6	7	8
					Males						
Mean DW (cm)	41.9	41.7	50.9	64.5	66.0	67.0	79.5	82	83.6	86.3	87
SD	2.45	4.05	2.06	5.92	na	6.82	3.61	4.14	3.90	2.47	2.07
Predicted DW	42.1	43.9	46.3	54.8	64.5	71.7	77.3	81.6	84.8	87.2	89
N	51	58	20	3	1	7	5	16	14	14	9
					Females						
Mean DW (cm)	42.4	42.3	50.5	62.8		70.7	75.4	79.1	83.3	85.8	92.4
SD	2.75	3.78	3.78	na		2.94	5.49	3.18	3.60	1.18	2.21
Predicted DW	42.2	43.6	46.5	53.2		69.9	76.1	81.2	85.5	89	91.8
N	63	51	9	1	0	3	5	8	7	13	10

TABLE 4. Mean size at ages 9–21 for male and female Cownose Rays sampled in Chesapeake Bay (DW = disc width).

	Age (years)												
Variable	9	10	11	12	13	14	15	16	17	18	19	20	21
Males													
Mean DW (cm)	91.7	92.8	92.3	92	96.5	92		98	97	97			
SD	2.67	2.50	3.21	na	2.12	na		na	na	na			
Predicted DW	90.5	91.5	92.4	93	93.5	93.8		94.3	94.5				
N	6	4	3	1	2	1	0	1	1	1	0	0	0
Females													
Mean DW (cm)	94.4	97.8	99.7	98.8	99.8	100.1	101.6	100.5	103	103	110.5		107
SD	3.36	3.29	2.96	2.86	2.84	2.99	2.99	2.49	na	3.31	na		na
Predicted DW	94.2	96.2	97.8	99.1	100.2	101.1	101.8	102.4	103	103.4	103.7		104.2
N	15	25	22	23	23	17	11	6	1	4	1	0	1

The best-fit models (three-parameter VBGF models) estimated *k*-values of 0.2741 for males and 0.1931 for females.

Reproductive Maturity

In male Cownose Rays, the earliest coiling of vas deferens was observed at estimated age 3 and 75.5 cm DW. Testes were not present in any significant mass and sperm was not found through histological sampling until the DW reached approximately 75 cm. Weight of the left (largest) testis grew rapidly as males attained 80 cm DW and progressed through maturity (Figure 4). Sperm and seminal fluid were first observed in a ray with an estimated age 4 and a DW of 78 cm and were concurrent with coiled vas deferens, but the claspers were not calcified. The smallest ray in which mature sperm were found had a DW of 78.25 cm but possessed immature claspers. Outer clasper length increased rapidly as DW approached 80 cm (Figure 5), at which point a clasper length–DW ratio greater than 4% became indicative of the onset of sexual maturity. In one male (83.25 cm DW), coiled vas deferens was analyzed via histology to verify presence or absence of mature sperm. In this immature male, mature sperm were present but no seminal fluid was expressed, and although the clasper length–DW ratio was 4.5%, the male possessed uncalcified claspers. At an estimated age of 5 years and a DW of 81 cm, the smallest ray exhibiting complete sexual maturity was observed to possess mature sperm in the left and right enlarged testes, coiled vas deferens, expressed seminal fluid, fully calcified claspers, and a clasper length–DW ratio of 4.4%. The next-smallest ray observed to be fully mature was 83.5 cm DW.

Prior to mating (May to early July; Fisher 2010), the ova of mature females were over 10 mm in diameter (Figure 6). The two smallest females with ova larger than 10 mm were 83.75 and 84 cm DW and had an estimated age of 6 years. The functional (left) uterus of both females was 25 mm in width

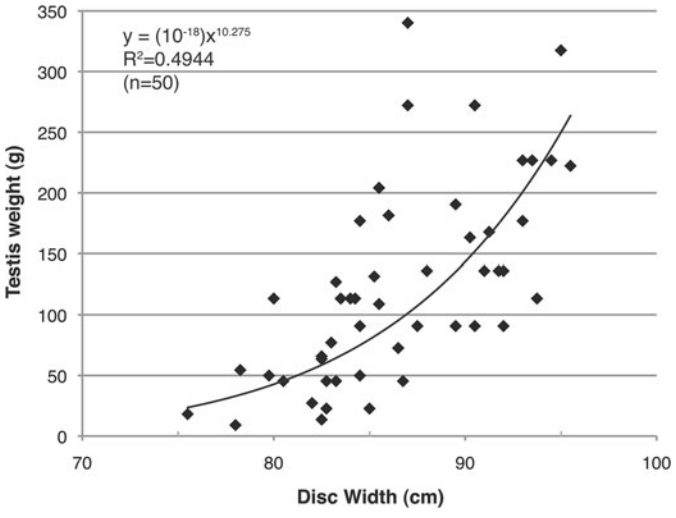

FIGURE 4. Relationship between disc width and the weight of the left testis in male Cownose Rays.

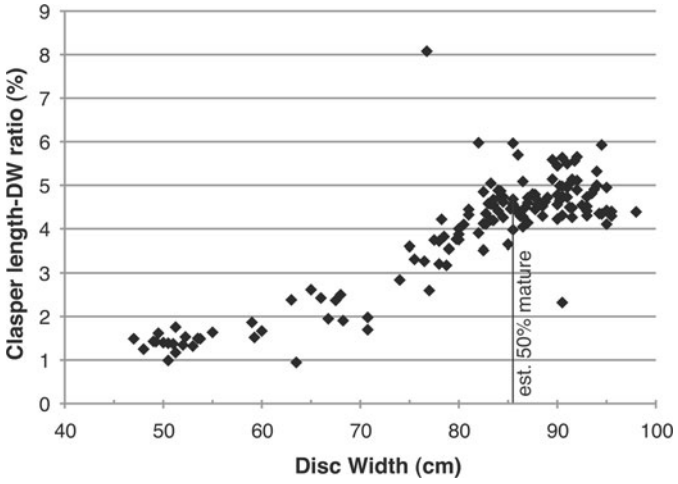

FIGURE 5. Relationship between disc width (DW) and the outer clasper length–DW ratio in male Cownose Rays sampled from Chesapeake Bay (n = 148).

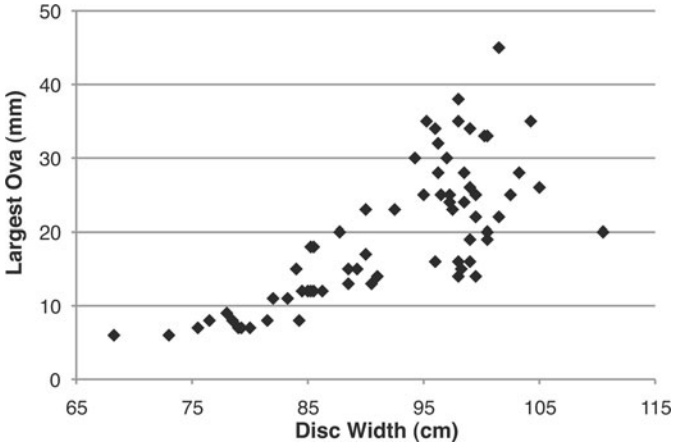

FIGURE 6. Relationship between disc width and the largest ova in female Cownose Rays captured from Chesapeake Bay between May and early July (pre-mating period).

but was thin walled, with trophonemata at the initial stage of development (short, light pink in color). The uteri also contained a caramel-colored, highly viscous, gelatinous material (high-molecular-weight phosphoprotein) in rays that had not previously been pregnant (Fisher 2010). For these females, this may have been the first year at sexual maturity and preparation for a first breeding event.

The UW (left uterus) began to increase as rays approached 80 cm DW, and a distinct widening of the uterus was observed beginning at 82–84 cm DW (Figure 7). Doubling of the UW in females reaching sexual maturity was observed between 82 and 88 cm DW. Mean UW was 11.9 mm in 79–82-cm DW females, 24 mm in 84–88-cm DW females, and 38 mm in 88.5–92-cm DW females. The first occurrence of UW doubling was noted for an individual with a DW of 82 cm.

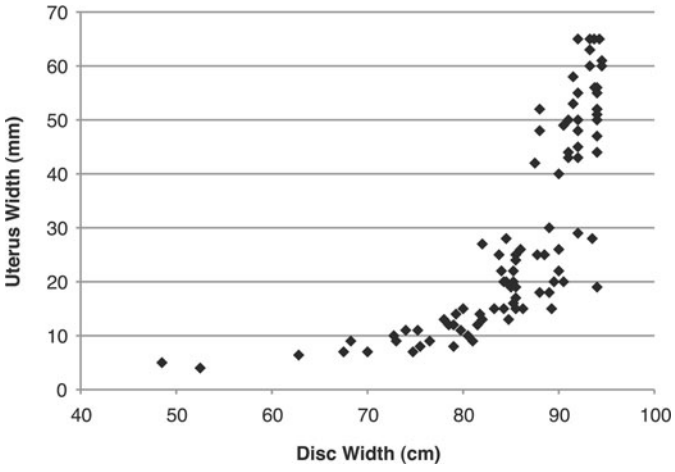

FIGURE 7. Relationship between disc width and the width of the left (functional) uterus in female Cownose Rays ($n = 91$; with disc widths of no more than 95 cm) captured from Chesapeake Bay during the pre-mating period (May and June).

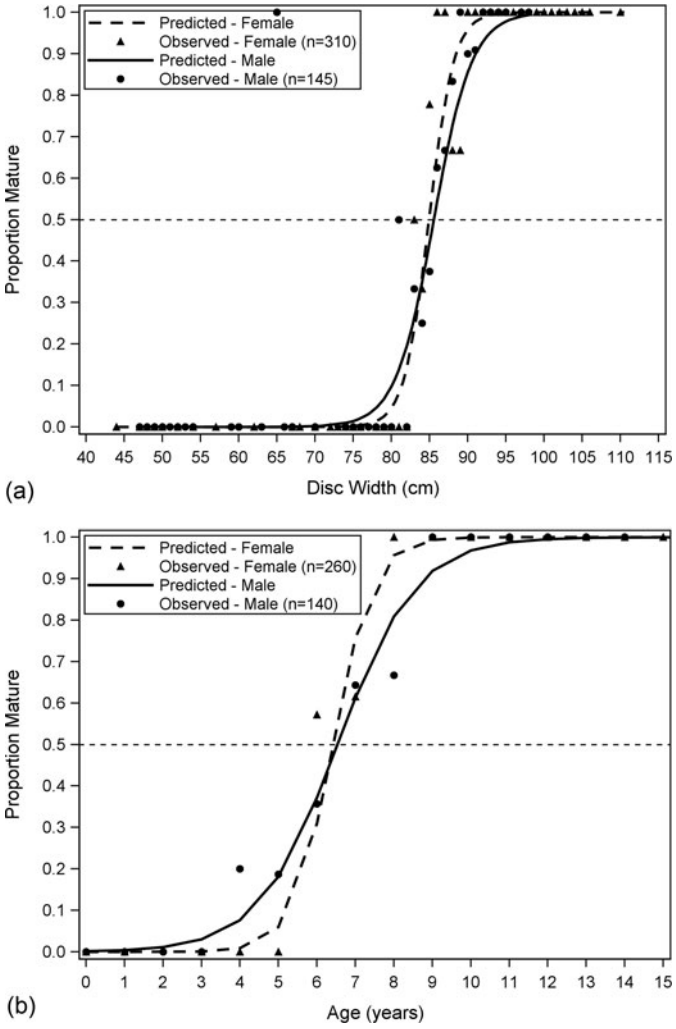

FIGURE 8. Maturity ogives for (upper panel) median disc width and (lower panel) age of male and female Cownose Rays.

The relationship between size and maturity is best indicated by maturity ogives for male and female Cownose Rays (Figure 8). The predicted median DW at 50% maturity was 85.5 cm (bootstrap 95% confidence interval [CI] = 83.84–86.71 cm; CI calculated by the method of Efron and Tibshirani 1993) for males and 85.0 cm (bootstrap 95% CI = 83.80–86.09 cm) for females. Predicted median age at 50% maturity was 6.5 years (bootstrap 95% CI = 5.92–7.12 years) for males and 6.4 years (bootstrap 95% CI = 5.91–6.90 years) for females. Fecundity in Cownose Rays was typically one embryo per mature female. Cownose Rays are only accessible to sampling in Chesapeake Bay from May to October, the period during which gestation is completed for one year-class (late June to early July) and quickly begins for the next. The smallest pregnant females observed were 89 cm DW (in June) and 88 cm DW (in September) and likely represented females that were gestating for the first time but within separate breeding cycles.

TABLE 5. Comparison of observed maximum disc width (DW_{max}), model-derived theoretical maximum DW (DW_∞), and observed maximum estimated age of Cownose Rays across three studies.

Source	n	Observed DW_{max} (cm)	DW_∞ (cm)	Observed max age (years)
Males				
Smith and Merriner (1987)	51	98.1	119.2[a]	8
Neer and Thompson (2005)	106	96	123.8[b]; 110[c]	16+
Present study	140	98	97.1[a]	18
Females				
Smith and Merriner (1987)	40	107	125[a]	13
Neer and Thompson (2005)	121	102.5	123.8[b]; 110[c]	18+
Present study	260	110.5	106.3[a]	21

[a]Determined with the von Bertalanffy growth model (sexes separate).
[b]Determined with the von Bertalanffy growth model (sexes combined).
[c]Determined with the Gompertz model (sexes combined).

DISCUSSION

Two previous studies have modeled age and growth for Cownose Rays: one study in Chesapeake Bay, and the other in the Gulf of Mexico (Table 5). Smith and Merriner (1987) provided the first age and growth estimates for Cownose Rays in Chesapeake Bay; however, predicted maximum sizes for males and females were far greater than observed sizes in that study. This discrepancy was likely due to small sample sizes and the inclusion of only one animal older than 10 years. Lacking these older age-classes, the growth curves did not reach an asymptote, leading to DW_∞ estimates of 119.2 cm for males and 125.0 cm for females (Smith and Merriner 1987). The largest animals observed in the Smith and Merriner (1987) study were a 98.1-cm male and a 107.0-cm female. By contrast, our study's sample size was much larger ($n = 537$) and included many animals over age 10 ($n = 119$), resulting in DW_∞ estimates (95.7 cm for males; 105.5 cm for females) that matched the observed sizes (98 cm for males; 110.5 cm for females) very well (Table 5).

Neer and Thompson (2005) examined 227 Cownose Rays from the Gulf of Mexico; the rays in their study matured more quickly (4–5 years) and at smaller sizes (64 cm for males; 65 cm for females) than the Chesapeake Bay Cownose Rays we sampled. Estimated k and maximum observed ages in our study were higher than those estimated by Neer and Thompson (2005; Table 6). However, maximum sizes were comparable between the two studies. The differences in age, growth, and maturity patterns could indicate separate Gulf of Mexico and Atlantic Ocean stocks of Cownose Rays. Our estimates of k were higher than those previously reported. However, values of k tend to be highly variable in batoids (Frisk 2010), and values comparable to ours are relatively common in the literature. These differences are summarized in Table 6. Lack of samples for certain size-classes and age-classes in the study by Smith and Merriner (1987) and in the current study may have contributed to the variability in k. In addition, the criteria used to discern age-1 individuals may have differed between the studies, thereby producing the 10-cm discrepancy in size at age 1. Collection of multiple samples through the first summer of growth in the current study indicated higher growth for this period than was reported by Smith and Merriner (1987).

Many studies do not fully explore alternative models for estimating age and growth of elasmobranchs. Historically, most of the growth studies on elasmobranch fishes have only fitted data with variations of the VBGF (Cailliet et al. 2006). However, studies that employ multiple models often have shown that alternative models provide a better fit to the data (e.g., Killam and Parsons 1989; Zeiner and Wolf 1993; Neer and Thompson 2005). This has been especially true of fishes such as batoids that grow relatively quickly early in life but continue to grow in weight after growth in length or DW has slowed considerably. For example, Neer and Thompson (2005) reported that the Gompertz growth model best fit the data for Cownose Rays in the Gulf of Mexico, and Zeiner and Wolf (1993) found that the logistic growth model yielded the best fit for TL growth in the Big Skate *Raja binoculata*. In our study, we compared five

TABLE 6. Comparison of model-derived growth coefficients (k) across multiple studies of Cownose Rays and other batoid fishes, indicating that k can be highly variable across species and between sexes.

Source	Species	k (combined sexes)	$k_{females}$	k_{males}
This study	Cownose Ray		0.19	0.26
Smith and Merriner (1987)	Cownose Ray		0.119	0.126
Neer and Thompson (2005)	Cownose Ray	0.075; 0.133[a]		
Martin and Cailliet (1988)	Bat Ray *Myliobatis californica*		0.0995	0.229
Jacobsen and Bennet (2010)	Plain Maskray *Neotrygon annotata*		0.20	0.31
White et al. (2002)	Western Shovelnose Stingaree *Trygonoptera mucosa*		0.241	0.493

[a]Determined with the Gompertz model; other k-values for Cownose Rays were based on the von Bertalanffy growth model.

different growth models, and the three-parameter VBGF model produced the best fit for the data.

Estimating age at maturity is important for resource managers interested in understanding recruitment. For the purposes of this study, we identified age at maturity as the age at which 50% of the animals were sexually mature. Smith and Merriner (1986) reported that males reached maturity at 82 cm DW or at ages 5–6. Although these ages and sizes are comparable to those of the youngest fully mature males we observed (81 cm DW at age 5; 83.5 DW at age 6), maturity of 50% of the males did not occur until age 6–7 in our study. One likely reason why our determination differs from that of Smith and Merriner (1986) is that we used multiple measures of sexual maturity in the present study. This methodology revealed that reproductive structures mature at different rates within an individual male Cownose Ray. In some cases, we observed the presence of seminal fluid and functional sperm but uncalcified claspers, indicating that the individual may have been physiologically mature but not physically mature or capable of copulation. The proportion of mature individuals increased more gradually among males than among females. This maturation period was observed in 75–86-cm DW rays, which spanned multiple age-classes. Of the observed male rays between 75 and 86 cm DW ($n = 57$), 47.3% expressed seminal fluid but only 8.8% possessed fully calcified claspers. Using multiple measures of maturity, we found that 50% of males were mature between ages 6 and 7 (at least 85 cm DW).

Maturity of female Cownose Rays was largely determined based on MOD, UW, and pregnancy. Of the female rays that were collected in May and June (prior to breeding), none of the 84–86-cm DW females ($n = 18$) was pregnant (mean UW = 19.7 mm; MOD = 13.3 mm); eight of the fifteen 88–90-cm DW females were pregnant (mean UW = 24.62 mm; MOD = 17.4 mm); and twenty-four of the twenty-five 91–93-cm DW females were pregnant. From these observations and from tracking the expansion of UW (Figure 7) and MOD (Figure 6), we estimated that female Cownose Rays in Chesapeake Bay reached sexual maturity between 85 and 88 cm DW and between ages 7 and 8 (Table 3). A difference between age at sexual maturity and age at first reproduction should be considered for Cownose Rays given their 11.5–12.0-month gestation period. Female Cownose Rays that become sexually mature and mate for the first time at age 7 (85.8 cm DW) do not complete gestation—and therefore do not contribute to recruitment—until age 8 (92.4 cm DW). If a Cownose Ray fishery management plan is established for the Chesapeake Bay region, minimum size requirements for females should reflect this delay in recruit contribution.

Throughout sampling from various locations in Chesapeake Bay, rays of ages 2–4 (60–80 cm DW) were scarce. Because the gear types that were largely employed for sampling (haul seines and pound nets) are not size selective (i.e., they capture smaller juvenile rays and adult rays), the absence of these age-classes suggests that the older juvenile Cownose Rays are not present in Chesapeake Bay or do not widely use this estuary. Other studies have also indicated that older juveniles might not use Chesapeake Bay. Trawl surveys conducted in the bay by the Chesapeake Bay Multispecies Monitoring and Assessment Program at the Virginia Institute of Marine Science from 2002 to 2010 collected 161 Cownose Rays ranging in size from 24.0 to 111.8 cm; however, no rays between 54.7 and 71.9 cm were recorded (Bonzek et al. 2010). Young-of-the-year rays emigrate from Chesapeake Bay after the adults leave. In October, only age-0 rays were captured, indicating that the adults had already fully emigrated. This pattern is consistent with patterns observed for other elasmobranch fishes in Chesapeake Bay, such as the Sandbar Shark *Carcharhinus plumbeus* (Grubbs et al. 2007). Such ontogenetic shifts in habitat use patterns are probably a function of growth-mediated reductions in predation risk (Grubbs and Kraus 2010; Grubbs 2010). Remaining in the semiprotected waters of the estuary longer than the adults allows the age-0 Cownose Rays to maximize their growth before the onset of the first energetically demanding climatic migration south and also allows them to avoid the bulk of the migrating predators, such as large sharks, that are present during September.

It is possible that Cownose Rays also show an ontogenetic shift in the magnitude of climatic migrations. Juvenile rays younger than at least age 3 may not participate in the springtime northerly migration, which is gametic (reproductive) in function, and instead may remain in estuaries to the south. Future studies should attempt to assess the age-classes of Cownose Rays, if present, in waters to the south during summer months. Of particular interest would be assessing whether estuaries in North Carolina and South Carolina contain a migratory adult component that is ephemeral and a resident large-juvenile component that is missing from Virginia waters.

Our study confirms that the Cownose Ray is a typical *K*-selected species with late maturity. The lack of observations of age-2–4 individuals demonstrates a lack of knowledge about juvenile migration and life history, which must be determined in order to formulate a responsible fishery management plan. This study reinforces the differences in life history patterns between the Chesapeake Bay population and the Gulf of Mexico population, indicating the need for further investigation to determine whether these are two different stocks. Considering that females mature at age 8 and the oldest female in our study was estimated to be age 21, the average lifetime fecundity is likely less than 14 offspring. Reproductive potential is low in Cownose Rays (typically one offspring per year), but the presence of two developing in utero embryos, the live birth of twins, and infrequent gestation in the right uterus are reported (Fisher 2010). This life history renders Cownose Rays particularly susceptible to overexploitation. For comparison, large sharks with similar ages at maturity have very low intrinsic rates of natural increase (0.04–0.06) and estimated population doubling times of between 10 and 20 years (Smith et al. 1998), yet the lifetime fecundity for these sharks is many times greater than that for Cownose Rays. Cownose Ray populations may therefore be much more susceptible to overexploitation and have lower rebound potential than large sharks. Indeed, Neer et al. (2007) estimated the

intrinsic rate of increase for Cownose Rays in the Gulf of Mexico to be 0.027 per year, which is likely higher than that of Cownose Rays in Chesapeake Bay given the differences in life history between the populations in these regions. Given the slow growth and extremely low fecundity of Cownose Rays, current harvests of this species and any future fisheries that may develop should be monitored very closely.

ACKNOWLEDGMENTS

We are grateful to Janet Krenn for editorial review of drafts of this paper and to David Rudders for statistical analysis assistance. We also thank the many Virginia fishermen and seafood processors for assistance with the collection and processing of rays. This work is a result of research sponsored by National Oceanic and Atmospheric Administration (NOAA) Award Number NA07NMF4570324 and in part by NOAA Award Number NA10OAR4170085 to Virginia Sea Grant. This is Virginia Institute of Marine Science Contribution Number 3252.

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