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ARTICLE

Indication of Density-Dependent Changes in Growth and Maturity of the Barndoor Skate on Georges Bank

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Abstract

Drastic increases or decreases in biomass often result in density-dependent changes in life history characteristics within a fish population. Acknowledging this phenomenon and in light of the recent biomass increase in Barndoor Skate *Dipturus laevis*, the current study re-evaluated the growth rate and sexual maturity of 244 specimens collected from 2009–2011within closed areas I and II on Georges Bank, USA. Ages were estimated using vertebral band counts from skate that ranged from 21 to 129 cm TL. The von Bertalanffy growth function was applied to pooled age-at-length data. Parameter estimates from the current study of $L_\infty = 155$ cm TL and $k = 0.10$ represent a significant decrease from previously reported parameters of $L_\infty = 167$ cm TL and $k = 0.14$. In addition to changes in growth parameters, age at 50% maturity for both males (based on clasper length, testes mass, and percent mature spermatocytes) and females (based on data from shell gland mass, ovary mass, and follicle diameter) increased by 3 years and 4 years, respectively. Based on our results and the 10- to 12-year gap in the collection of samples, it is likely that Barndoor Skate within this region have exhibited pliability in life history parameters.

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Batoids within the family Rajidae are thought to comprise at least 22% of the fishes within the subclass Elasmobranchii (Ebert and Compagno 2007). Like their cartilaginous relatives (sharks and rays), skate exhibit an equilibrium life history strategy (i.e., late sexual maturation, low fecundity), which makes them vulnerable to direct and indirect fishing pressure (e.g., Hoenig and Gruber 1990; Winemiller and Rose 1992; Sulikowski et al. 2003, 2007). In addition, these fishing pressures have been coupled with the common practice of aggregating skate abundance within a region rather than calculating species-specific biomass trends (Dulvy et al. 2000). As a result of fishing pressure and their life history strategy, skate populations worldwide have experienced declines. Examples include the localized extinction of the Common Skate *Dipturis batis* from the Irish Sea and the disappearance of four North Sea skate species from the majority of their distribution (Dulvy et al. 2000). In the United States portion of the northwest Atlantic Ocean, the Northeast Skate Complex (NESC) consists of seven species, five of which occur in the Gulf of Maine (GOM) and southern New England: the Winter Skate *Leucoraja ocellata*, Barndoor Skate *D. laevis*, Thorny Skate *Amblyraja radiata*, Smooth Skate *Malacoraja senta*, and the Little Skate *L. erinacea* (McEachran 2002; NEFMC 2007). Although in the past, skate within this complex were primarily considered bycatch in the groundfish, monkfish, and scallop fisheries, several species have commercial value in the bait and wing industries (NEFMC 2003; Sulikowski et al. 2005a; Sosebee 1998). These directed fisheries place a significant amount of stress on the populations (Casey and Myers 1998; Gedamke et al. 2005; NEFMC 2007). For example, due to declines in their abundance, three species (Thorny Skate, Smooth Skate, and Barndoor Skate) are currently prohibited from commercial landing while the other two species within the complex (Winter Skate and Little Skate) have strict management regulations governing their harvest in accordance with a Skate Fisheries Management Plan (NEFMC 2011).

The Barndoor Skate is the largest skate within the NESC and can reach sizes of over 150 cm TL (McEachran 2002). Within the U.S. portion of the northwest Atlantic Ocean, the distribution of this species is concentrated on Georges Bank and southern New England where it can be found from the tide line to 750 m with a depth preference of greater than 450 m (McEachran 2002; Gedamke et al. 2005). In the late 1960s, Barndoor Skate populations declined to levels far below mandated biomass thresholds (NEFMC 2005). The biomass remained suppressed for the next 30 years, causing speculation that the species was on the verge of localized extinction (Casey and Myers 1998). Although many factors may have contributed to the decline of the Barndoor Skate population, it has been hypothesized that both direct and indirect fishing pressure played a significant role reducing the biomass of this species (Casey and Myers 1998; Gedamke et al. 2005; NEFMC 2007). Survey indices remained at extremely low levels throughout the 1990s indicating a lack of recovery, so managers prohibited retention of the species in 2003 (NEFMC 2011). The NEFSC bottom trawl surveys from 2005 through 2012 suggested that Barndoor Skate populations were no longer overfished, although they still remained below the target biomass level within U.S. waters (NOAA 2012). If the most recent trends in biomass continue, it is likely that the prohibited status will be removed, allowing for commercial harvest of Barndoor Skate to resume (NEFMC 2011). Although a preliminary life history study has been conducted on this species, specimens were collected prior to the biomass increase (1999–2001) and the sample size for age and growth estimates was limited (total $n = 118$, female $n = 51$, male $n = 67$; Gedamke et al. 2005). Results from that study suggest that life history characteristics of the Barndoor Skate are not typical of a large batoid and that the population could be more resilient to fishing pressure than previously thought (Sulikowski et al. 2003; Gedamke et al. 2005).

Significant declines in biomass can result in density-dependent changes in life history characteristics within a fish population (Rose et al. 2001; van der Lingen et al. 2006). Populations can respond to a biomass decline with increased growth rates, earlier maturity, and increased fecundity due to decreased intraspecific competition (Sminkey and Music 1995; Rose et al. 2001). Conversely, an increasing population with an elevated density can respond with a reduced growth rate and increasing age and size at maturity (Rose et al. 2001). Although such density-dependent changes have been widely documented in teleost fishes, they have been observed in only a few exploited shark species and never documented in a batoid (Sminkey and Music 1995; Carlson and Baremore 2003; Sosebee 2005). Given the recent changes in the biomass of Barndoor Skate, this species offers a unique opportunity to investigate potential density-dependent changes in life history characteristics in a skate species. In addition, information garnered from such a study would subsequently contribute to a more thorough understanding of potential long-term effects of population depletion in batoids as a whole. Thus, the objectives of the current study were to re-evaluate age, growth, and maturity of the Barndoor Skate and determine whether compensatory changes in these life history parameters have occurred within the sampled population.

METHODS

Sampling

Barndoor Skate were captured opportunistically in collaboration with the Virginia Institute of Marine Science (VIMS) during industry-based, cooperative scallop surveys. Samples were obtained aboard the FV *Celtic* and FV *Endeavor* using a National Marine Fisheries Service (NMFS) sea scallop survey dredge (2.4 m width with 5.1-cm rings) and a Coonamessett Farm turtle deflector dredge (CFTDD) (4.6 m width with 10.2-cm rings) in tandem 15-min tows. Skate were collected within a portion of the Georges Bank closed area I (40°55′–41°26′N, 68°30′–69°01′W) and closed area II (41°00′–41°30′N, 66°24′–67°20′W) between May and October of 2010 and 2011 (Figure 1). The sampling

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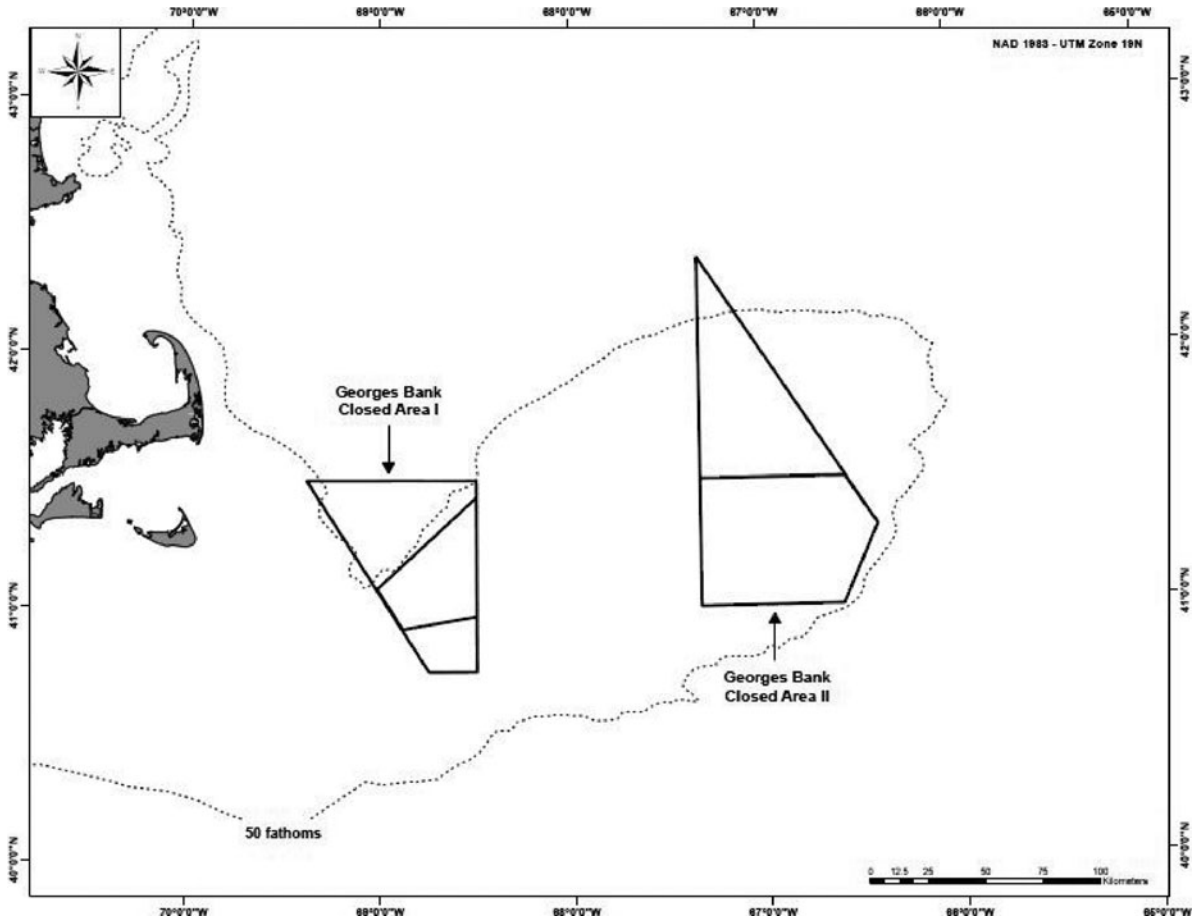


FIGURE 1. Enclosed region represents sampling area within Georges Bank closed area I (40°55′–41°26′N, 68°30′–69°01′W) and closed area II (41°00′–41°30′N, 66°24′–67°20′W) where all Barndoor Skate were collected between May and October of 2010 and 2011.

location and time of year sampled for this study were consistent with those of Gedamke et al. (2005). After capture, specimens were frozen and transported to the Marine Science Center at the University of New England for processing. Prior to dissections, specimens were thawed and all external morphological measurements were recorded including TL, disk width (DW), and wet weight. Total length (cm) was measured from the tip of the rostrum to the end of the tail, and DW (cm) was measured from one pectoral fin apex to the opposite pectoral fin apex. In males, the clasper length (CL; cm) was also measured before dissection.

Age Determination

Preparation of vertebral samples.—The vertebral collection process included removal, cleaning, and freezing of the vertebral column (taken from above the abdominal cavity) from 244 individuals. From the vertebrae, three individual centra were cut and excess tissue was removed. A sagittal section of each centrum was cut using a Raytech Jem Saw 45 with 12.7-cm (5 in) saw blades (Raytech Industries, Middletown, Connecticut). All cross sections were then affixed to a glass microscope slide using Cytoseal 60 (Fisher Scientific, Pittsburg, Pennsylvania) and individual centrum diameter (mm) was measured using a digital caliper. If banding was not immediately apparent, prepared vertebrae were sanded with fine grit wet–dry sandpaper until bands could be resolved.

Age analyses.—Age estimates were determined by vertebral band counts following the protocols of Sulikowski et al. (2003). Formation of annual rings was examined digitally using SPOT basic image capture software for microscopy (Diagnostic Instruments) attached to a Nikon SMZ-U stereoscopic zoom microscope (Nikon USA). In most cases banding on the intermedelia was not present; thus, the bands were determined solely by their appearance on the corpus calcareum. Annual band deposition was classified by one opaque band followed by one translucent band (Sulikowski et al. 2003).

In order to remove potential bias, two nonconsecutive band counts were made independently by two readers without knowledge of a specimen's TL or previous counts. Readings were averaged between readers; however, if ages differed by more than 2 years that sample was removed from subsequent analyses. The count reproducibility was calculated using the index of

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average percent error (IAPE) equation (Beamish and Fournier 1981) and an age-bias plot was used to evaluate bias between readers (Campana 2001). The three-parameter von Bertalanffy growth function (VBGF; von Bertalanffy 1938) was fit to size-at-age data using nonlinear regression in Statgraphics Centurion (StatPointTechnologies).

The marginal increment analyses (MIA) method was used to verify the annual periodicity of band-pair formation on 205 specimens, which included immature and mature Barndoor Skate captured in May, July, and October. For MIA, SPOT basic software (Diagnostic Instruments) was used to incorporate point-to-point distance measurements into the digital image spanning the length of the final opaque band and the penultimate opaque band from the edge of the centrum. The ratio of these two values was then calculated as the marginal increment (Sulikowski et al. 2005b, 2007) and plotted by month of capture.

SEXUAL MATURITY

Females.—Sexual maturity in females was assessed by examining developmental changes in the gross morphology of the reproductive tract (Sulikowski et al. 2005b, 2006, 2007). The oviducal gland and ovaries were removed, blotted dry, and weighed to the nearest gram. The largest follicle diameter was measured in millimeters using a digital caliper. Additionally, the presence of egg cases within the uterus was recorded. Females were considered reproductively capable of ovulation and encapsulation, and thus mature, when the oviducal gland measured >30 g and maximum follicle size was >10 mm.

Males.—For each male specimen, the testes were removed, blotted dry, and weighed to the nearest gram. Clasper length (CL), defined as the distance from the posterior of the cloaca to the posterior tip of the clasper, was recorded for each specimen. To further assess maturity, histological analysis of testes was conducted following the protocol of Sulikowski et al. (2005b). After obtaining testes weight, a thin cross section was removed from the medial lobe of the testis and fixed in 10% buffered formalin. Testis cross sections were stained with a standard hematoxylin and eosin staining procedure. Prepared slides were examined under a microscope to observe spermatogenic development. To determine male sexual maturity, the mean proportion of a testes occupied by mature spermatocytes along a straight-line distance across one representative full-lobe cross section of the testis was obtained. Mature spermatocytes were identified by the organization of spermatozoa into tightly shaped packets that were arranged spirally along the periphery of the spermatocytes. Male maturity was classified by specimens having calcified claspers >19 mm, developed testes >12 g, and $>23\%$ mature spermatocytes. We adopted these criteria from previous studies that reported similar characteristics for mature rajid species (Sulikowski et al. 2005b, 2006; Cicia et al. 2009).

Statistical Analysis

For MIA, a multifactor ANOVA was used to test for differences in the length of the marginal increment by sex and maturity to ensure no ontogenetic changes occurred in band deposition and data could thus be combined. Due to nonnormally distributed data with equal variances, a Kruskal–Wallis one-way ANOVA on ranks was then used to test for differences in marginal increment by month (Sulikowski et al. 2003, 2005a). To determine whether there were differences in VBGF parameters between sexes, a likelihood ratio test was employed using Statgraphics Centurion (StatPointTenchnologies; Cerrato 1990). In addition, this comparison was also made between males and females in the Gedamke et al. (2005) study as well as between the combined male and female VBGF parameters of the current study and those of Gedamke et al. (2005). To determine whether a relationship existed between morphological and histological variables, a Pearson correlation analysis was performed for both male and female reproductive parameters. Differences in morphological and histological variables among age-groups were determined using an ANOVA, followed by a Tukey's post hoc test. To determine TL and age estimates at 50% maturity, ogives were fitted to a least-squares nonlinear regression model following the methods of Mollet et al. (2000) and using Statgraphics Centurion (StatPoint Technologies). All statistical tests were considered significant at $\alpha = 0.05$.

RESULTS

Vertebral Analyses

Comparison of counts between readers indicated no appreciable bias (Figure 2) and minimal error (IAPE of 3.2%) for all sampled vertebrae ($n = 244$). Of the 268 Barndoor Skate sampled 244 individuals were processed for age determination, 139 males and 105 females. After both readings, 53% of the counts agreed, 92% were ± 1 year between counts, and 100% were within ± 2 years. The relationship between TL and centrum

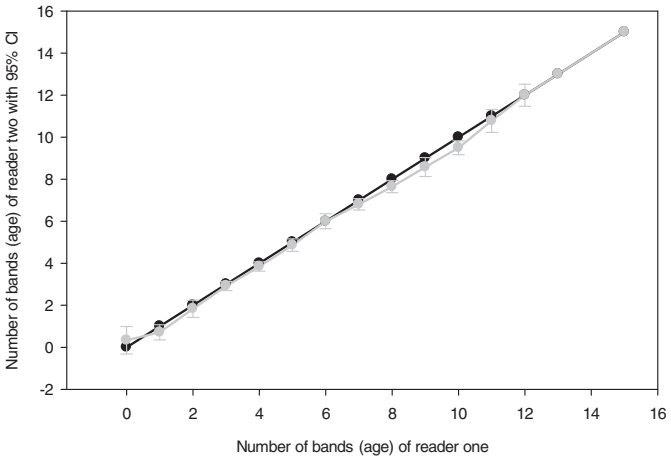


FIGURE 2. Age-bias plot (grey line) for pairwise comparison of 244 Barndoor Skate vertebral counts made by two independent readers. Each error bar represents the 95% CI for the mean age assigned by reader 2 to all specimens assigned a given age by reader 1. The black diagonal line represents the one-to-one equivalence line.

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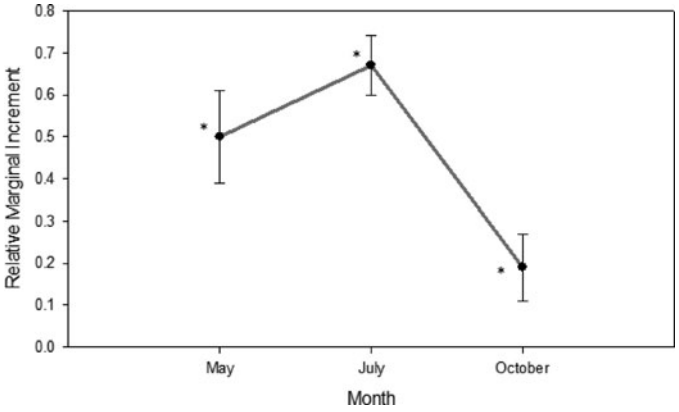


FIGURE 3. Mean monthly marginal increments of opaque bands for 205 sampled Barndoor Skate. Marginal increments were calculated for the sampled months May ($n = 45$), July ($n = 130$), and October ($n = 30$), including both sexes and immature and mature skate. Error bars represent ± 1 SE. Significant difference is represented by an asterisk (*) among months sampled (Kruskal–Wallis test: $P < 0.05$).

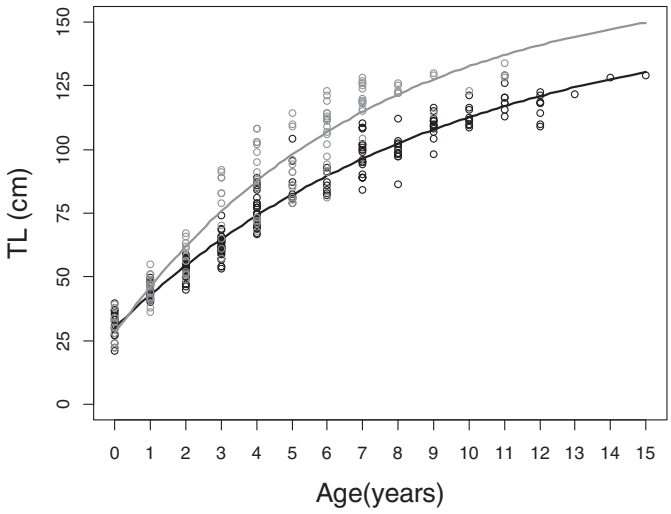


FIGURE 4. Von Bertalanffy growth curves (VBGC) generated from combined Barndoor Skate vertebral data for the current study (black line) and Gedamke et al. (2005) (grey line). Corresponding growth parameters for combined male and female data resulted in $L_\infty = 155$ cm TL, $k = 0.10$, and $L_0 = 28$ cm (current study, lower curve) and $L_\infty = 167$ cm TL, $k = 0.14$, and $L_0 = 27$ cm (Gedamke et al. 2005, upper curve).

diameter was linear ($R^2 = 0.93$, $P > 0.05$) and there were no significant differences in this relationship between males and females. A total of 205 skate ranging from 21 to 129 cm TL were used for MIA. Since no significant differences in marginal increment existed between sexes or maturity stage (multifactor ANOVA: $P > 0.05$), these data were combined. Marginal increment analysis revealed a significant difference existed among months sampled (Kruskal–Wallis ANOVA: $P < 0.05$). The opaque growth band displayed an increasing trend from May to July with a sharp decline in October suggesting the deposition of a new opaque band occurred during this time frame (Figure 3).

Age and Growth Estimates

Captured males ranged between 0 and 15 years (21–129 cm TL) and females between 0 and 11 years (30–126 cm TL).When the VBGF were fitted to length-at-age data, model results indicated a reasonable fit for males ($R^2 = 0.96$), females ($R^2 = 0.95$) and sexes combined ($R^2 = 0.96$). Von Bertalanffy growth parameters between sexes had the same k value (0.10) but a slightly higher L_∞ for females than for males (male $L_\infty = 158$ cm; female $L_\infty = 167$ cm). Although a significant difference was found between sexes (likelihood ratio = 12.41, chi-square $P < 0.01$), these data were combined to allow for a direct comparison between the VBGF of the current study ($L_\infty = 155$ cm, $k = 0.10$, $L_0 = 28$ cm) and the VBGF calculated from Gedamke et al. (2005: $L_\infty = 166$ cm, $k = 0.14$, $L_0 = 27$ cm). This comparison revealed a significant difference in the VBGF parameters existed between the two studies (likelihood ratio = 340.63, chi-square $P < 0.01$) (Figure 4).

Maturity

Males.—In males, as TL and age increased reproductive development was observed in testis mass, CL, and percent mature spermatocytes (Table 1). In addition, all measured parameters were strongly correlated with an increase in TL (all r^2 values were greater than 0.75) over the course of maturation. The presence of mature spermatocytes was first observed in a 7-year-old, 98-cm-TL skate, and an abrupt increase in spermatocytes occurred between ages 8 (9%) and 9 (20%). This corresponded with testis development where a significant increase in testis mass occurred during maturation between ages 8 and 9 years and again between 11 and 12 years (ANOVA: $P < 0.05$). Additionally, there was a significant increase in CL between ages 10 and 11 years (ANOVA: $P < 0.05$). Maturity ogives predicted 50% maturity occurs at a TL of 108 cm and an estimated age of 9 years. This is in agreement with morphological measurements, which suggest maturity occurs at 9–10 years and a TL occurs between 106 and 109 cm (Figure 5). The smallest sexually mature male measured 102.5 cm TL and was 8 years old, and the largest immature male measured 109.5 cm TL and was 10 years old. According to the observed data set, maturity in males occurs at 84% of their maximum observed TL and 60% of their maximum observed age.

Females.—In females, the increase in TL and age corresponded with reproductive development in ovary mass, oviducal gland mass, and follicle size (Table 2). All measured reproductive parameters were strongly correlated with TL (all r^2 values were greater than 0.68) over the range of maturation. However, of the 131 females sampled only three were found to be mature. Follicular development (all follicles < 1 mm in diameter) was not observed until the onset of maturity at 7 years in age. There was a significant increase in ovary mass and shell gland mass between ages 8 and 9 years, while significant increases in all of the measured reproductive parameters in females occurred between 9 and 11 years of age and 100–118 cm TL (ANOVA: $P < 0.05$). Maturity ogives indicated 50% maturity in females

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TABLE 1. Morphological measurements and reproductive parameters for male Barndoor Skate. Values are given as mean ± SE; NA denotes no fish sampled in this category; CL = clasper length. For each column an asterisk represents significant differences (ANOVA followed by a Tukey's post hoc test: $P < 0.05$) between skates in consecutive age-groups.

Age (years)	*n*	TL (cm)	CL (cm)	Mass (kg)	Testes mass (g)	% mature spermatocytes
0	14	33 ± 6	2.19 ± 0.85	0.11 ± 0.08	0.09 ± 0.09	0 ± 0
1	11	45 ± 3	3.42 ± 0.70	0.42 ± 0.23	0.41 ± 0.21	0 ± 0
2	17	53 ± 3	4.54 ± 0.53	0.69 ± 0.17	0.73 ± 0.25	0 ± 0
3	17	61 ± 4	5.38 ± 0.84	1.08 ± 0.26	1.26 ± 0.25	0 ± 0
4	13	73 ± 4	6.58 ± 0.98	1.82 ± 0.65	2.77 ± 0.90	0 ± 0
5	6	85 ± 7	9.18 ± 3.25	5.05 ± 1.18	5.38 ± 3.02	0 ± 0
6	6	92 ± 14	13.66 ± 8.81	3.48 ± 0.73	9.32 ± 12.07	0 ± 0
7	11	98 ± 10	14.79 ± 6.16*	5.14 ± 1.73	11.31 ± 5.14	4 ± 10
8	11	100 ± 6	19.10 ± 7.50*	5.18 ± 1.28	14.86 ± 10.03*	9 ± 15*
9	4	107 ± 8	23.38 ± 8.86	7.11 ± 2.324	22.43 ± 15.10*	20 ± 16*
10	10	113 ± 4	26.5 ± 4.71*	8.41 ± 1.13	25.46 ± 10.81	20 ± 17
11	6	119 ± 6	32.18 ± 2.63*	10.58 ± 1.13	44.78 ± 7.44	32 ± 6
12	8	116 ± 5	31.80 ± 2.03	9.4 ± 1.30	46.99 ± 8.65	25 ± 11
13	1	122 ± 0	34.70 ± 0	9.73 ± 0	51.0 ± 0	50 ± 0
14	1	128 ± 0	33.50 ± 0	11.36 ± 0	61.0 ± 0	NA
15	1	129 ± 0	35.50 ± 0	10.86 ± 0	57.54 ± 0	35 ± 0

occurs at a TL of 100 cm and an age of 10 years (Figure 6). The smallest mature female measured 118 cm TL and was aged 11 years, and the largest immature female measured 114.5 cm and was aged 9 years. According to the observed data set, maturity in females occurs at 79% of the maximum observed TL and 91% of their maximum observed age.

DISCUSSION

Age and maturity information is essential for the calculations of growth rates, mortality rates, and reproductive productivity, making these two of the most important variables for estimating a population's status and assessing the effects of overfishing (Cailliet and Goldman 2004; Walker 2005; Sulikowski et al. 2007). Due to the plasticity of these and other life history parameters, this information should be frequently revaluated and monitored for subsequent changes if accurate stock assessments are to be conducted for commercially exploited species (Dulvy et al. 2000; Hutchings and Reynolds 2004). Density-dependent shifts in life history parameters have been widely observed in commercially important teleosts such as Haddock *Melanogrammus aeglefinus* in the North Atlantic Ocean (Rose et al. 2001) and Pacific Sardine *Sardinops sagax* populations in the southern

TABLE 2. Morphological measurements and reproductive parameters for female Barndoor Skate. Values are given as mean ± SE. For each column an asterisk represents significant differences (ANOVA followed by a Tukey's post hoc test: $P < 0.05$) between skates in consecutive age-groups.

Age (years)	*n*	TL (cm)	Mass (kg)	Ovary mass (g)	SG Mass (g)	Largest follicle (mm)
0	5	32 ± 2	0.22 ± 0.15	0.07 ± 0.10	0 ± 0	<1
1	8	45 ± 3	0.60 ± 0.46	0.30 ± 0.14	0.02 ± 0.02	<1
2	8	52 ± 4	0.76 ± 0.41	0.79 ± 0.58	0.03 ± 0.05	<1
3	21	62 ± 4	0.98 ± 0.43	1.30 ± 0.45	0.05 ± 0.05	<1
4	18	78 ± 6	2.40 ± 1.02	3.13 ± 1.34	0.17 ± 0.14	<1
5	3	92 ± 10	3.81 ± 1.50	5.93 ± 3.04	0.66 ± 0.80	<1
6	3	92 ± 1	4.71 ± 0.30	7.44 ± 2.57	1.08 ± 0.20	<1
7	11	97 ± 4	5.59 ± 1.05	11.50 ± 7.69	6.15 ± 15.18	3 ± 5
8	1	100 ± 0	5.18 ± 0	6.63 ± 0*	2.19 ± 0*	5 ± 0
9	10	110 ± 2	7.62 ± 2.27	18.48 ± 6.11*	15.27 ± 11.09*	9 ± 5*
11	3	122 ± 6	12.32 ± 6.03	42.85 ± 10.03*	37.97 ± 4.68*	24 ± 15*

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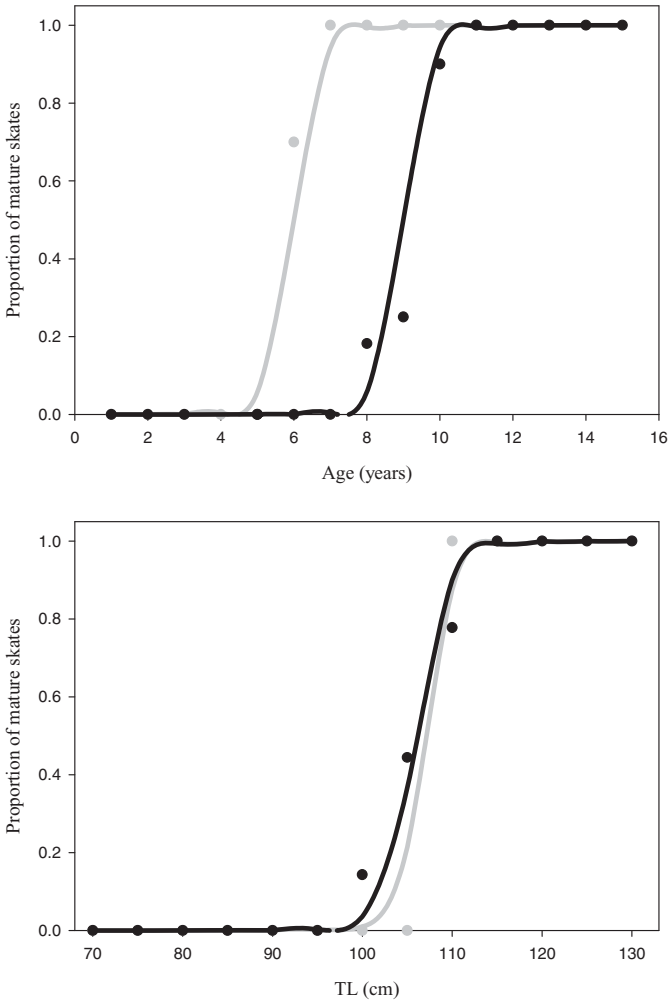


FIGURE 5. Maturity ogives for (upper panel) age and (lower panel) TL of the male Barndoor Skate based on morphological and histological parameters collected from the current study (black) and Gedamke et al. (2005) (grey).

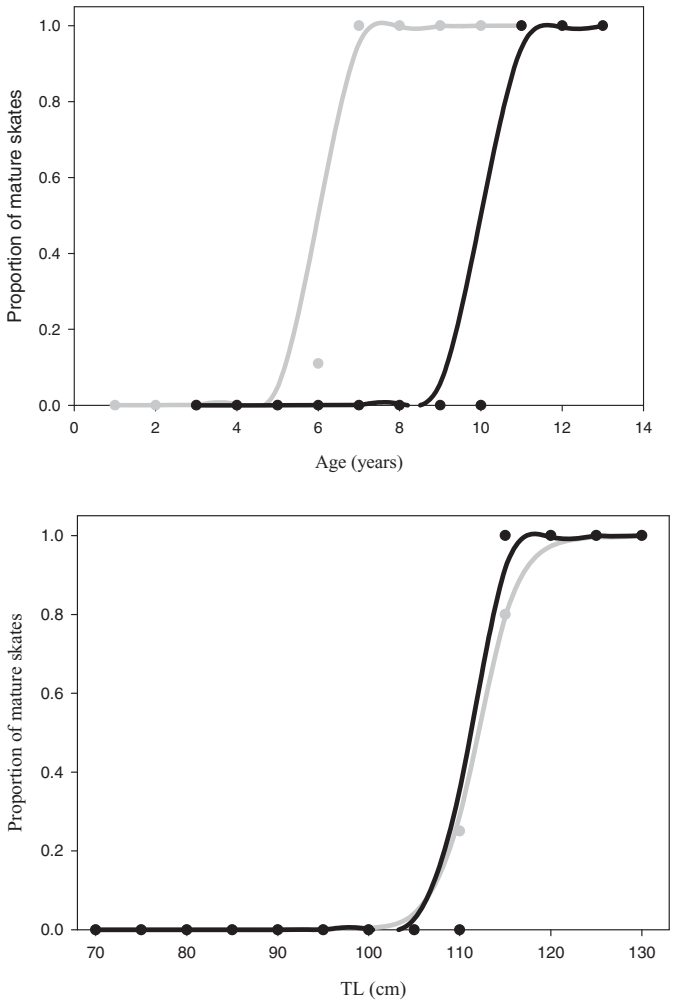


FIGURE 6. Maturity ogives for (upper panel) age and (lower panel) TL of the female Barndoor Skate based on morphological parameters collected from the current study (black) and Gedamke et al. (2005) (grey).

Atlantic Ocean (van der Lingen et al. 2006). Although most research has focused on teleosts, evidence for density-dependent change has been documented in a few elasmobranchs after commercial exploitation had occurred (Sminkey and Music 1995; Carlson and Baremore 2003; Sosebee 2005). For example, increases in juvenile growth rates of two sharks, Sandbar Shark *Carcharhinus plumbeus* and Atlantic Sharpnose Shark *Rhizoprionodon terraenovae*, were documented after a drastic reduction in adult biomass in the 1980s (Sminkey and Music 1995; Carlson and Baremore 2003). In addition, Sosebee (2005) described a 9-cm decline in size at first maturity in female Spiny Dogfish *Squalus acanthias* in the U.S. northwest Atlantic Ocean after significant biomass declines in their respective adult populations. Although limited, the aforementioned studies indicate that compensatory changes can occur in shark species. However, these changes have never been studied in batoids after substantial changes in their population abundance. This lack of understanding is problematic, particularly in skate, because this group of elasmobranchs appears to be susceptible to fishing pressures and exhibit variable rates of recovery after management plans have been enacted (Dulvy et al. 2000, 2003; Cicia et al. 2012). To date, the current study is the first to suggest observable density-dependent changes in the life history characteristics of a batoid species.

When the VBGFs of Gedamke et al. (2005) were compared with those of the current study a significant difference in growth coefficient was observed ($k = 0.14$ in Gedamke et al. 2005 versus 0.10 in the current study). The 10–12-year gap between sampling intervals (1999–2001 versus 2009–2011) is comparable with the time frame of collections from other elasmobranch studies where density-dependent changes were also observed (Sminkey and Music 1995; Carlson and Baremore 2003; Sosebee 2005). Although variation exists in life history characteristics, in general larger skate species, such as the Thorny Skate (TL, ~130 cm; k, ~0.1), exhibit slower growth rates, while smaller skate, such as the Roundel Skate

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TABLE 3. Comparison of calculated VBGF parameters for male, female, and combined sexes, as well as male and female age (years) and TL (cm) at maturity estimates between the current study and that of Gedamke et al. (2005). Likelihood ratio comparisons were performed between males and females as well as between combined sexes of Barndoor Skate between the studies (Cerrato 1990).

Sex	Study	k	L_∞	Age at maturity (years)	TL at maturity (cm)	Likelihood ratio	χ^2 P-value
Male	Current study	0.10	158.34	9	108	149.68	<0.001
	Gedamke et al.	0.12	184.61	6	110		
Female	Current study	0.10	167.20	10	110	115.10	<0.001
	Gedamke et al.	0.17	154.12	7	116		
Sexes combined	Current study	0.10	155.24			340.63	<0.001
	Gedamke et al.	0.14	166.60				

Raja texana (TL, ~70 cm; k, ~0.30), typically display faster growth rates (Dulvy et al. 2000; Sulikowski et al. 2005a, 2007). The slower growth rate in our study is more characteristic of larger batoid species, suggesting the barndoor skate may be more susceptible to fishing pressure than previously thought (Dulvy et al. 2000; Gedamke et al. 2005; Cavanagh and Damon-Randall, 2009). Prior studies have suggested that after depletion and subsequent depression of a population's biomass, resources become more readily available (Rose et al. 2001). An artifact of this depressed biomass is decreased competition between the remaining individuals, which ultimately contributes to an increased growth rate exhibited by the population as a whole (Lorenzen and Enberg 2002; Rose et al. 2001; Carlson and Baremore 2003). Additionally, laboratory-based studies corroborate the changes in life history observed in the field. For example, under controlled laboratory conditions an increase in individual growth rate was observed when a higher quantity of food was made available to juvenile Blacktip Reef Sharks *Carcharhinus melanopterus* and juvenile Lemon Sharks *Negaprion brevirostris* (Taylor and Wisner 1988; Cortes and Gruber 1994). Based on the collective field and laboratory studies, it is possible that the increased availability of food and other resources was a contributing factor in the higher growth rate observed by Gedamke et al. (2005) when compared with the current study. While no elasmobranch studies have assessed the compensatory changes associated with a population increase, elevated biomass levels in teleost species can cause density-dependent decreases in growth rates. For example, reductions in growth rates were observed in Brown Trout *Salmo trutta*, Coho Salmon *Oncorhynchus kisutch*, and steelhead O. mykiss *after* population densities were arbitrarily increased over a 3-month time period in riverine environments (Bohlin et al. 1994). The estimated biomass (NEFMC 2007) of the Barndoor Skate population sampled by Gedamke et al. (2005) was far below the estimated biomass levels from which the current growth rates were calculated (NEFMC 2011). The slower growth observed in the current study supports the hypothesis that the lower k values presented herein may be the result of increased competition for resources. However, further research is needed to determine the mechanism responsible for the observed changes in growth rates between Gedamke et al. (2005) and the current study.

Comparisons of reproductive parameters between Gedamke et al. (2005) and the current study revealed that the age at maturity for both male and female Barndoor Skate had increased from 6 to 9 years and from 7 to 10 years, respectively. In males, due to opportunistic sampling in summer and fall, continuous production of sperm after the onset of sexual maturity was assumed based on previous skate studies (Sulikowski et al. 2005b; Cicia et al. 2009). It is important to note that only three mature female specimens were obtained, suggesting the largest and oldest females were not represented in this study. The small number of large individuals within sampled females could result in an overestimated growth rate for their population, causing a potential further slowing of growth and age and size at maturity in Barndoor Skate that is not reflected in the current study (e.g., Sulikowski et al. 2003). Although age at maturity increased, TL at maturity experienced very little change between studies, suggesting that the current population requires an additional 3 years to reach maturity at that size (Table 3). The maturation process of Barndoor Skate reported in the current study is similar to those observed in other large skate, such as the Alaska Skate *Bathyraja parmifera* (TL ~120 cm), which reaches maturity at approximately 9 years in males and 10 years in females. Several studies on elasmobranchs have observed changes in size at maturity after biomass depletion. For example, Carlson and Baremore (2003) observed that the Atlantic Sharpnose Shark experienced a decrease both in age and TL at maturity, while Sosebee (2005) reported a large decrease (9 cm) in size at sexual maturity in Spiny Dogfish. Although previous elasmobranch studies have not addressed changes in maturity as a result of a biomass increase, several studies in teleosts have suggested that increased competition for fewer available resources can result in delayed maturation and lower reproductive potential, creating an overall compensatory shift in the population (Rose et al. 2001). For example, the percentage of mature age-1 male Walleyes *Sander vitreus* in Lake Erie declined from 99% after drastic population depletion to 32% after the population had recovered in Lake Erie (Muth and Wolfert 1986). In addition, studies on Silver Hake *Merluccius bilinearis* in the northwest Atlantic Ocean suggest

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that sexual maturity can be delayed when stock abundance is increased due to added competition (Helser and Almeida 1997). Based on the collective information of the aforementioned studies, it appears that the onset of maturity in elasmobranchs can be altered as a function of density-dependent changes in biomass. Thus, the delayed maturity observed in the current study supports the notion that the observed phenomenon may indeed be the result of increased competition for resources. However, further research is needed to determine the mechanism responsible for the observed changes in size at maturity between Gedamke et al. (2005) and the current study.

Accounting for density-dependent changes is essential in management measures that involve long-term predictions of fish population dynamics (Rose et al. 2001). Due to opportunistic sampling, specimen collections were limited to trips in the summer and fall for both studies. Although 268 skate were used to assess maturity, we lack data for the largest mature females. It is also possible that observed changes in life history parameters were influenced by other factors such as natural variability. Despite these limitations, based on the results presented herein and the 10- to 12-year gap between the collections of data it is likely that the Barndoor Skate sampled within closed areas I and II on Georges Bank have undergone significant changes in their life history parameters. Historically, the closures on Georges Bank have benefitted many benthic and demersal species, particularly those exhibiting minimal movement in and out of the closed area (Murawski et al. 2000). This appears to be the case for Barndoor Skate sampled in the current study. Thus, the life history characteristics presented herein should be considered when new management measures for this species are implemented.

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