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THEMED ISSUE

Atlantic Striped Bass Population: Past, Present, and Future Challenges

Female age at maturity and fecundity in Atlantic Striped Bass

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Abstract

Objective: Female age at maturity and fecundity for the Atlantic stock of Striped Bass *Morone saxatilis* were estimated using histological methods and image analysis.

Methods: Ovaries were obtained from surveys encompassing the spring spawning season (March–July; $n=343$), primarily from the Chesapeake Bay, and in the fall months (September–December; $n=85$), primarily from the Atlantic coast. Histological examination of oocytes revealed some Striped Bass in intermediate stages of maturation during the spawning season. These individuals were identified as undergoing pubertal development, defined as the transition from the juvenile stage to first sexual maturity. Pubertal development was characterized by ovaries containing a population of enlarged, lipid-filled oocytes but noticeably lacking vitellogenin-derived yolk globules during the spawning season, and those ovaries were classified as immature. Toward the end of the spawning season, increasing proportions of Striped Bass with unspawned ovaries and oocytes undergoing total atresia were observed.

Result: The female age and length at 50% maturity in Atlantic Striped Bass based on spring samples were 5.5 years and 609 mm total length, respectively. Fecundity was determined gravimetrically via image analysis of ovarian tissue samples from spawning capable individuals ($n=67$). Potential annual fecundity was found to exhibit hyperallometric scaling with respect to body size. Specifically, the scaling exponent for the length–fecundity relationship was 3.24, which was greater than the scaling exponent of 3.05 for the length–body mass relationship. This indicates that large females possess a disproportionately greater reproductive capacity with respect to body mass than the equivalent biomass of smaller females.

Conclusion: Compared with previous studies spanning over a half-century, age at 50% maturity and fecundity were found to be relatively invariant, although variation found between contemporary studies may represent methodological and interpretive differences. Reproductive-related life history traits of female Atlantic Striped Bass are apparently robust to long-term decadal changes in fishing intensity, stock size, habitat alterations, and environmental conditions.

KEYWORDS
life history, management, reproduction

INTRODUCTION

Impact statement

Atlantic Striped Bass are an iconic U.S. East Coast sport fish and a commercially important species. We determined that half of females reach sexual maturity between ages 5 and 6. Additionally, we found that larger (older) females produce more eggs per kilogram body mass than smaller (younger) females. These findings should be considered in future stock management.

The Striped Bass *Morone saxatilis* is a temperate marine species with a native range from the St. Lawrence River, Canada, to the St. Johns River, Florida, and in the Gulf of Mexico from Florida to Louisiana. Although multiple Striped Bass stocks occur within this range, the Atlantic Striped Bass stock, which ranges from coastal areas of North Carolina to Maine, is the foundation for the large-scale and historically important Striped Bass fishery occurring along the northeastern U.S. coast. Recruitment overfishing of Striped Bass during the 1970s led to the eventual collapse of the stock during the following decade (Richards and Rago 1999). After successful fisheries management efforts led to the eventual rebuilding of the stock by 1995, which peaked during the 2010s, poor recruitment and overfishing have led to new declines in the stock. The decline in spawning stock biomass (SSB) over the past decade has resulted in the most recent stock assessment's conclusion that the stock is overfished but no longer experiencing overfishing (Atlantic States Marine Fisheries Commission 2022). In the Chesapeake Bay and for many coastal communities of the northeastern United States, the Atlantic Striped Bass continues to play an outsized role as an iconic fishery species and still supports one of the largest U.S. saltwater recreational fisheries by harvested weight (National Marine Fisheries Service 2022). Detailed information on the reproductive life history traits that translate female Striped Bass biomass into reproductive capacity is crucial for informing future management of the stock.

Striped Bass exhibit a complex life cycle, being long-lived, highly migratory, anadromous, and iteroparous. These factors make it challenging to achieve unbiased sampling of all developmental stages of female Striped Bass for maturity studies. Adult Striped Bass undertake extensive migrations, moving between oceanic feeding grounds off New England states during the summer and then heading southward during the fall and winter months to return to coastal estuaries, where spring spawning occurs. The Chesapeake Bay, which is the largest estuary along the Atlantic coast, is considered the primary production area for the Atlantic Striped Bass stock (Boreman and Austin 1985; Wirgin et al. 1993). Spawning is triggered by water temperature and typically occurs at temperatures above 14°C, peaks at around 18°C, and declines thereafter (Smith and Wells 1977). Mortality of eggs and larvae is water temperature dependent and increases significantly if temperatures are less than 15°C or greater than 20°C (Secor and Houde 1995). The spawning season occurs between late March and June, with peak spawning activity occurring in late April. Striped Bass spawn pelagic eggs, which drift downriver of spawning areas before hatching within 48 h postfertilization (Schilling et al. 2015). Juveniles can remain in estuaries for several years, with the incidence of migration to coastal waters increasing gradually with size (Dorazio et al. 1994). In females, migration can occur in some individuals as early as age 2–3; an increase in the probability of coastal migration occurs between ages 5 and 8 and is associated with female maturity (Secor and Piccoli 2007). To sample all potential developmental stages of female Striped Bass, samples were collected for this study through collaboration with multiple federal and state agencies on both the coast and in the Chesapeake Bay throughout the fall and during the entire spawning season.

Our goals in this study were to improve upon the accuracy of female age-at-maturity and fecundity information for the contemporary Atlantic Striped Bass stock. The female age-at-maturity schedule is used to calculate SSB but was previously estimated during the 1980s, when the stock was considered collapsed, with a contracted age structure. Standardized methods for maturity studies using histological methods have since been developed (Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011). Additionally, aquaculture-focused research has elucidated the complex reproductive development of female Striped Bass, which require multiple years of maturation before functional maturity is attained (Hassin et al. 1999; Holland et al. 2000, 2001). Motivated by the need to control the production and quality of Striped Bass eggs, aquaculture research has also provided insight into the timing and seasonal photothermal cues that stimulate oogenesis and, alternately, ovarian atresia (Mylonas et al. 1997; Sullivan et al. 2003; Clark et al. 2005). Integration of this information into standardized maturity methods can aid in the interpretation of maturity classification. Importantly, failure to account for Striped Bass that are undergoing maturation but that are not yet functionally mature may lead to biased estimates of the age at first maturity and potentially to the overestimation of SSB. Therefore, this study expands upon standardized maturity methodology to provide a more complete picture of Striped Bass-specific histological criteria for distinguishing between immature, maturing, and functionally mature developmental stages.

Potential annual fecundity of Striped Bass in the Chesapeake Bay has been previously estimated by several studies spanning seven decades (Jackson and Tiller 1952; Gervasi et al. 2019). Fecundity in female Striped Bass is strongly related to size and, thus, age, with the largest individuals capable of producing millions of eggs during a single spawning season. However, the allometric relationship between body size and fecundity has not been evaluated. Therefore, we evaluate the assumption that female body mass is proportional to fecundity in Striped Bass. A recent meta-analysis of a wide taxonomic range of marine fish has found that more frequently, reproductive output scales disproportionately with respect to body size (Barneche et al. 2018). This means that larger-sized females (e.g., one 20-kg individual) may be capable of producing disproportionately more eggs per unit body mass than the equivalent aggregate biomass of smaller females (e.g., two 10-kg individuals). If this generality is found to apply in Striped Bass, then the potential reproductive output of the stock may be sensitive to female age structure, which is not currently accounted for in SSB. Finally, we compare our results with previous Striped Bass maturity and fecundity studies to examine temporal variation in female Striped Bass reproductive life history traits.

METHODS

Sample collection

Ovaries were collected from fishery-dependent and fishery-independent surveys during March–July and September–December, both within the Chesapeake Bay and on the Atlantic coast (Table 1). Chesapeake Bay samples were primarily obtained during the Maryland Department of Natural Resources (MDNR) Spring Creel Survey, which is conducted from mid-April to mid-June and encompasses the spring recreational trophy season as well as the start of the summer recreational season. During this survey, the sex and spawning condition (prespawn and postspawn) of the fish are recorded from macroscopic examination of the gonads. Striped Bass ovaries undergo a color shift from orange to green as they ripen (Peer et al. 2012). Prespawn ovaries are typically dark orange to green in color during this time and fill the body cavity. Postspawn ovaries are flaccid, highly vascularized, and pale in color. During the study years (2014–2016), the trophy season opened on the third Saturday in April of each year and ran until May 15, targeting large coastal migrants as they traversed the Chesapeake Bay main stem to and from spawning grounds. The sampled harvest from the trophy season primarily consisted of females (86%) that were in prespawn condition (40%) or had recently spawned (60%) based on macroscopic examination. The summer Striped Bass fishery begins on May 16 and primarily targets smaller premigratory and resident fish, although some migratory fish may still be present within the bay. Determination of spawning condition by macroscopic examination of the ovaries is less certain during this portion of the survey because the ovaries are typically much smaller in size relative to the body cavity and are typically light orange in color. The sampled harvest in this portion of the fishery during the study years was composed primarily of males (79%); females (21% of

TABLE 1 Number of female Striped Bass (*n*) sampled by state and survey, 2014–2016. NEAMAP, Northeast Area Monitoring and Assessment Program; USFWS, U.S. Fish and Wildlife Service.

State	Survey	Months sampled	*n*
Maryland	Spring Creel Survey	Apr–Jun	252
	Spring Spawning Stock Survey	Apr–May	15
	Striped Bass Pound-Net Sampling	Jun–Jul	19
	Nanticoke Spring Pound-Net and Fyke-Net Survey	Mar	2
	Commercial Check Station Sampling	Mar	3
	Fish Health Hook-and-Line Survey	Sep–Nov	5
	Patapsco Gill-Net Survey	Jun	3
	Shad Gill-Net Survey (USFWS)	Apr–May	8
New Jersey	Delaware Bay Gill-Net Survey	Mar–May	15
	Ocean Trawl Survey	Apr–May	9
	Ocean Trawl Survey	Oct	1
	Headboat Sampling	Dec	13
	Herring Survey	May	1
Rhode Island	Fish Trap Survey	Sep–Oct	59
NEAMAP	Ocean Trawl Survey	May	16
	Ocean Trawl Survey	Sep–Oct	7
Total			428

the sample) ranged from immature (14%) to potentially prespawn (38%) and postspawn (49%). Additional samples from the Chesapeake Bay were collected from the Maryland Striped Bass Spawning Stock Survey during April and May. Samples from other surveys in Maryland's portion of the bay and its tributaries were collected in March–July and September–November. Ovary samples from coastal areas were obtained during March–May and September–December. The New Jersey Bureau of Marine Fisheries, the Rhode Island Division of Fish and Wildlife, and the Northeast Area Monitoring and Assessment Program (NEAMAP) contributed samples from their routine surveys.

During sampling, the total length (TL; mm), fish weight (kg), ovary weight (g), visual (macroscopic) maturity stage, and external anomalies were recorded for all fish when possible. Scales were collected to assign ages to sampled fish through the routine scale aging program for Striped Bass conducted by MDNR. Although otolith-based ages from known-age Striped Bass are highly accurate and precise (Liao et al. 2013), comparisons between scale-based and otolith-based ages indicate high agreement up to age 10 and then systematic bias in scale-based ages, which underestimate otolith-based ages (Northeast Fisheries Science Center 2019). Because previous maturity studies have found that all Striped Bass older than age 10 are mature, this bias should have little influence on age-at-maturity estimates. The gonadosomatic index (GSI) was calculated as the ovary weight divided by the total fish weight without the ovary weight and was expressed as a percentage.

Histological procedures

Histological procedures followed the methods from Boyd (2011). Both ovaries were removed from the body cavity and weighed. One ovary was retained in cold, 10% buffered formalin for up to 2 weeks, depending on ovary size. Formalin was used for preservation on all surveys except for NEAMAP surveys, in which Normalin was used. Large ovaries were cut in half and remained in formalin for a longer time to ensure complete fixation. After fixation was complete, a 4-mm-thick cross section of ovary was placed into one or more labeled, standard histological cassettes and stored in 70% ethanol. The MDNR Diagnostics and Histology Laboratory at the Cooperative Oxford Laboratory prepared Mayer's hematoxylin and eosin-stained histological slides of ovary tissues. This combination stain is widely used in histology to differentiate cellular components through blue–red color contrast. Basophilic cellular components take up hematoxylin stain, giving them a purple to blue appearance, whereas eosinophilic components stain light pink to red. For the interpretation of oocyte components, both neutral lipids and cortical alveoli appear transparent; ooplasm is basophilic, appearing light purple; and both vitellogenin-derived yolk globules and the germinal vesicle are eosinophilic, appearing pinkish red.

Reproductive phases

Reproductive phases based upon histological staging of oocytes are described in Table 2 and conceptually diagrammed in Figure 1. Terminology was modified from the standardized description of Brown-Peterson et al. (2011) with the model of oogenesis for temperate Perciformes provided by Reading et al. (2011). In temperate Perciformes that spawn pelagic eggs, such as Striped Bass, oocyte development occurs in three phases: (1) previtellogenic growth, (2) vitellogenic growth, and (3) final oocyte maturation. For this reason, the "developing" phase of Brown-Peterson et al. (2011), which combines previtellogenic growth and vitellogenic growth, was replaced with separate previtellogenic and midvitellogenic phases for Striped Bass in the present study. During previtellogenic growth, which begins in late summer, neutral lipids accumulate throughout the oocyte, eventually forming the prominent oil globule in Striped Bass eggs. Neutral lipids first appear early in oocyte development as small, transparent lipid droplets (Figure 2A), which define the early developing phase (Table 2). To ensure clarity, we refrain from using the term "cortical alveolar oocytes" (Brown-Peterson et al. 2011) when referring to oocytes in the early developing phase in Striped Bass. Unlike many teleost species, in Striped Bass the cortical alveoli are formed in the outer region of the cytoplasm during the postvitellogenesis stage (as depicted in Figure 2F), as indicated by periodic acid–Schiff staining in other moronid species (Mayer et al. 1988). As oocyte lipidation continues (Figure 2B), large lipid vesicles continue to fill the ooplasm (Figure 2C,D), which defines a previtellogenic oocyte. Vitellogenic growth is concurrent with continued oocyte lipidation but is initiated late in the year and entails the deposition of yolk proteins as eosinophilic yolk globules. Vitellogenin-derived yolk globules first appear in the peripheral ooplasm of developing oocytes (Figure 2D), which defines a primary vitellogenic (VTG1) oocyte. Yolk globules continue to accumulate throughout the oocyte centrally toward the germinal vesicle in secondary vitellogenic (VTG2) oocytes. Because VTG1 and VTG2 oocytes represent a continuum of yolk deposition, they are both classified as midvitellogenic. The spawning capable phase is defined by oocytes in the tertiary vitellogenic (VTG3) stage, with yolk globules completely filling the ooplasm (Figure 2E). In the spawning capable phase,

TABLE 2 Histological description of developmental phases in the analysis.

Phase	Histological features	Maturity classification
Immature	Only oogonia and primary growth (PG) oocytes present. No atresia or muscle bundles. Thin ovarian wall and little space between oocytes	Immature
Early developing	Oocytes contain PG and early lipid droplet oocytes only (Figure 2A)	Immature
Previtellogenic	Oocytes enlarge as cytoplasm is filled with transparent lipid vesicles (Figure 2B, 2C). Indicates pubertal development if found in the spring. Occurs in mature adults in the late summer and fall	Immature (pubertal) or Mature (recrudescence)
Previtellogenic atresia	Widespread atresia (up to 100%) of previtellogenic oocytes, gonadosomatic index (GSI) less than 2%. Thin ovarian wall (Figure 3C)	Immature (pubertal)
Midvitellogenic	Oocytes contain the first small acidophilic yolk globules near the oocyte periphery (VTG1, Figure 2D). Yolk globules start to fill the cytoplasm towards the nucleus (VTG2). Lipid vesicles begin to coalesce	Mature
Vitellogenic atresia	Widespread atresia (up to 100%) of vitellogenic oocytes without indications of spawning or GSI >2% with advanced atresia. Thin ovarian wall and no postovulatory follicles (Figure 3D)	Unclassified (skipped spawning or delayed maturity)
Spawning capable	Numerous large yolk globules fill the cytoplasm completely (VTG3, Figure 2E)	Mature
Actively spawning subphase	Lipid vesicles coalesce until filling the center of the oocyte. Oocytes undergoing late germinal vesicle migration or germinal vesicle breakdown (Figure 2F)	
Regressing	Atresia (any stage) and postovulatory follicles present. Some lipid vesicles and/or vitellogenic oocytes present. Thick ovarian wall (Figure 3A)	Mature
Regenerating	Muscle bundles, enlarged blood vessels, thick ovarian wall, and/or gamma/delta atresia or old, degenerating postovulatory follicles may be present (Figure 3B)	Mature

Note: Phases were modified from Brown-Peterson et al. (2011) to accommodate Striped Bass-specific oocyte stages. Photographs accompanying phases found in Figures 2 and 3.

vitellogenic growth is complete and the oocyte is receptive to maturation-inducing hormones (Brown-Peterson et al. 2011). As the spring spawning season nears, oocyte maturation commences with germinal vesicle migration and neutral lipids coalesce centrally, forming an oil globule, which signals the beginning of the actively spawning subphase (Figure 2F). Within less than 24 h, germinal vesicle breakdown occurs and yolk granules coalesce into a mass surrounding the oil globule. When ovulated, Striped Bass eggs contain a prominent oil globule surrounded by a yolk mass with cortical alveoli closely lining the cell wall (Mylonas et al. 1997). The regressing phase occurs directly after spawning and is characterized by a greatly thickened ovarian wall, postovulatory follicles, alpha atresia of unspawned oocytes, and primary growth oocytes (Figure 3A). During the regenerating phase, muscle bundles, enlarged blood vessels, a thick ovarian wall, and/or gamma/delta atresia or old, degenerating postovulatory follicles may be present (Figure 3B).

Maturity classification

A conceptual diagram of female Striped Bass reproductive development is shown in Figure 1. Striped Bass were classified as immature, pubertal (immature), or mature (Table 2). Aquaculture-focused research into the maturation of Striped Bass has elucidated developmental complexities that have not previously been accounted for in maturity studies but that could bias age-at-maturity estimates. Female Striped Bass undergo a prolonged maturational phase from their second year to at least their fourth year of life, according to longitudinal studies of captive Striped Bass reared under naturally cycling photothermal conditions (Hassin et al. 1999). During this phase, termed “pubertal development,” gonadotropin levels and oocyte diameter profiles display seasonal dynamics similar to those of mature females; however, the oocytes fail to undergo vitellogenic growth, they become atretic toward the end of the spawning season, and they are reabsorbed without being spawned (Holland et al. 2000). This developmental pattern in Striped Bass has been noted before in published field observations (see Chadwick 1965) but has not been accounted for in maturity studies. Similar descriptions of incomplete maturation during the known spawning period in other species have been referred to as “abortive maturation” (McBride et al. 2022); however, we prefer the term “pubertal development,” consistent with previous research on Striped Bass reproductive development. Abortive maturation implies a delay in first functional maturity in reaction to unfavorable internal or external factors, whereas pubertal development is the

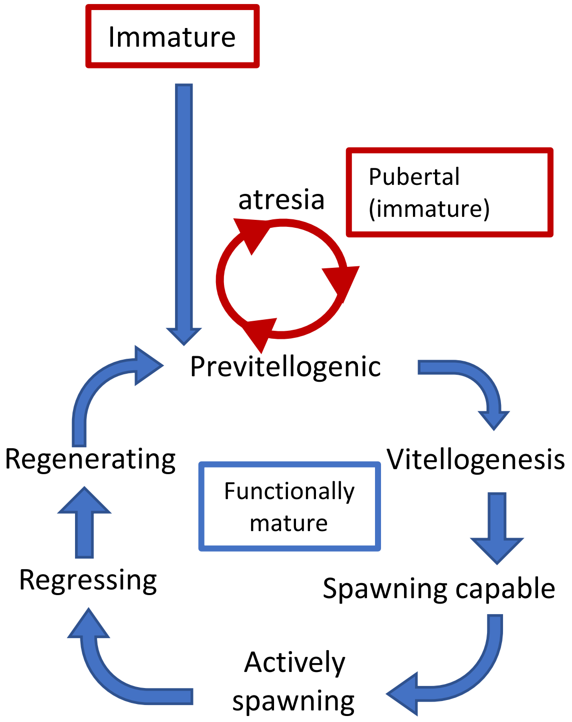

FIGURE 1 The reproductive development of female Atlantic Striped Bass includes multiple annual cycles of maturation (pubertal development) wherein oocytes develop up to the previtellogenic phase before they are reabsorbed at the end of the spawning season. Once functional maturity is achieved, oocytes proceed through vitellogenic growth (spawning capable) and oocyte maturation (actively spawning), leading to spawning. After spawning, ovaries regress and enter recrudescence (regenerating).

physiological process occurring along the brain–pituitary–gonad axis that eventually leads to a competent reproductive system and first functional maturity (Okuzawa 2002). Nevertheless, both abortive maturation and pubertal development indicate that a fish is not functionally mature and should be classified as immature.

In classifying maturity, Striped Bass with ovaries in either the immature phase or the early developing phase were classified as immature (Table 2). Vitellogenesis in mature Striped Bass occurs as early as September (Berlinsky et al. 1995; Clark et al. 2005). Because oocytes develop group synchronously, if the latest stage oocytes in an ovary were previtellogenic in the spring, then oocyte maturation will likely not occur in the current spawning season and developing oocytes will be reabsorbed without spawning when spring water temperatures warm above the upper spawning temperature threshold (Figure 3C). Therefore, Striped Bass entering the spring season with ovaries containing previtellogenic oocytes were considered pubertal and were also classified as immature. Striped Bass assigned to the midvitellogenic and spawning capable phases were considered functionally mature. Fish with ovaries containing a thickened ovarian wall (Figure 3A,B) were considered to have recently spawned and were in either the regressing phase or the regenerating phase and therefore classified as mature.

Different criteria were applied to Striped Bass with ovaries reabsorbing oocytes without indications of having spawned in the current season (thin ovarian wall, absence of postovulatory follicles, etc.). Striped Bass with ovaries in this condition in the spring contained 50% or more oocytes (not including primary growth oocytes) undergoing alpha or beta atresia (Figure 3). If the latest stage oocytes in these ovaries were previtellogenic and the GSI was less than 2%, then a classification of pubertal (immature) was applied. Qualitatively, ovaries undergoing reabsorption and classified as pubertal (immature) tended to have a more heterogeneous population of developing oocytes of varying sizes (Figure 3C). If the most developed oocytes contained within an ovary undergoing resorption showed signs of vitellogenic growth (i.e., yolk globules) or if the GSI was greater than 2%, then the maturity status was considered unknown (Figure 3D–F). It is uncertain whether all Striped Bass within the broad range of ages (4–11 years) found in this state were displaying “skipped spawning” or a prolonged delay in maturity. For this reason, these samples ($n=11$) were subsequently removed from the estimation of the maturity ogives.

Samples collected during the fall months proved difficult to differentiate between pubertal (immature) fish and mature fish that had previously spawned and were undergoing oocyte recruitment for the next spawning season. For this reason, only samples collected during the spring months were considered for maturity analysis, but fall samples are elsewhere reported for descriptive purposes. Based upon the maturity classifications of spring samples, a maturity ogive was estimated from age-at-maturity data through logistic regression by specifying the logit link in a binomial generalized linear model within R (R Core Team 2016).

Fecundity analysis

Striped Bass are considered total spawners with determinate fecundity (Murua et al. 2003). A set number of oocytes is recruited each year into synchronous development, with spawning occurring over a brief period, typically when water temperatures rise above 14°C in the spring (Smith and Wells 1977). Given this reproductive strategy, potential annual fecundity was estimated, which is the total number of maturing yolked oocytes per female per year, not accounting for atretic loss (Murua and Saborido-Rey 2003).

To estimate potential annual fecundity, only the subset of ovaries in the spawning capable phase were utilized for

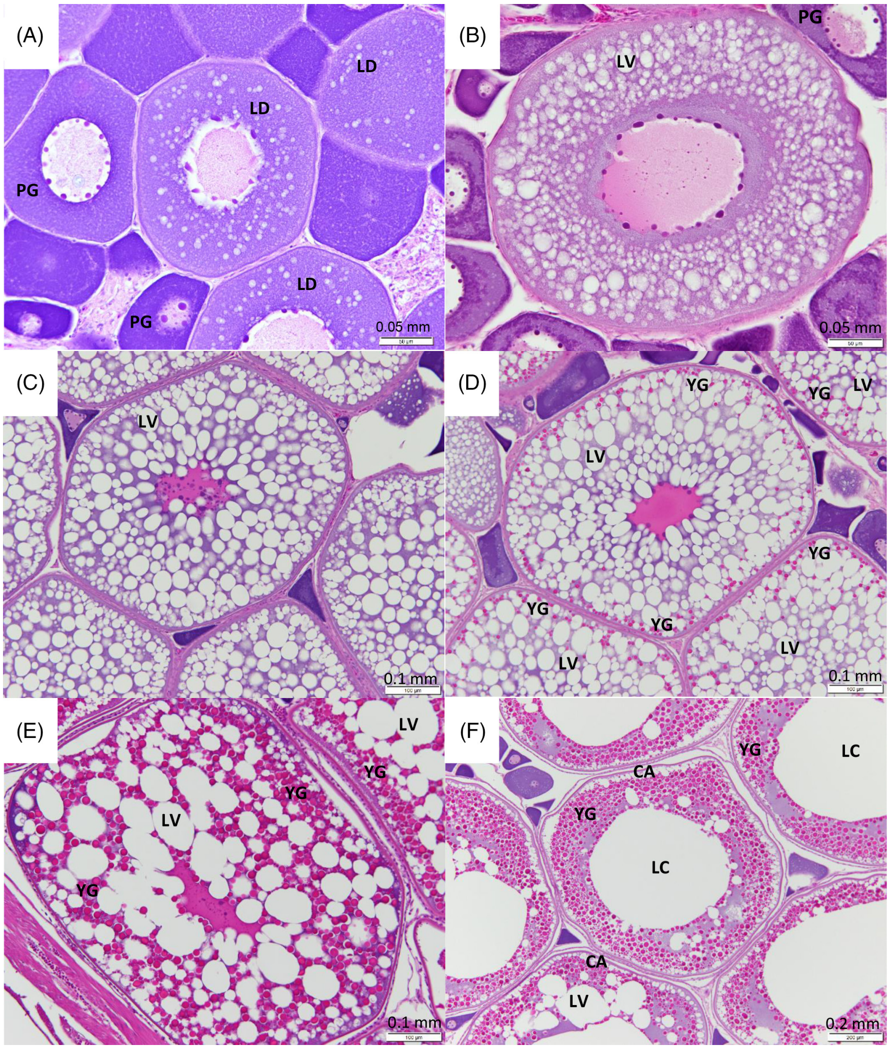

FIGURE 2 Progressive phases of maturing Atlantic Striped Bass oocytes: (A) first appearance of lipid droplets (early developing phase); (B) lipid vesicles accumulate as the oocyte enlarges (early previtellogenic phase); (C) abundant lipid vesicles (previtellogenic phase); (D) first appearance of pinkish-red yolk globules indicates the onset of vitellogenesis (midvitellogenic phase); (E) yolk globules fill the ooplasm and lipid vesicles begin to coalesce, signifying that vitellogenesis is complete (spawning capable phase); and (F) lipid vesicles coalescence centrally, germinal vesicle migration/breakdown occurs, and cortical alveoli line the peripheral cell wall (actively spawning subphase). CA, cortical alveoli; LC, lipid coalescence; LD, lipid droplets; LV, lipid vesicle; PG, primary growth oocyte; YG, yolk globules.

fecundity analysis, with the majority (97%) of those ovaries collected from the Chesapeake Bay. Macroscopically, ovaries in the spawning capable phase fill the body cavity and are highly vascularized, and oocytes are individually distinguishable without magnification. Spawning capable ovaries contain oocytes in the VTG3 stage, which was confirmed through histological examination.

Potential annual fecundity was estimated with gravimetric methods. Ovaries were previously weighed during initial field sampling. An approximately 10-g sample of fixed ovary tissue was excised and placed onto a 1-mm sieve stacked on top of a 0.21-mm sieve. The sample was vigorously rinsed through the 1-mm sieve onto the 0.21-mm sieve to separate clusters of oocytes and to retain spawning-capable ova based on previous studies of egg size distribution (Jackson and Tiller 1952). Excess water was blotted away from the bottom of the 0.21-mm sieve, and two 1.0-g subsamples were weighed out. Subsamples were placed in petri dishes painted matte black and were covered with 70% ethanol. Petri dishes were then photographed with a 12.3-megapixel digital camera.

Whole counts of oocytes in each subsample were determined from digital images using ImageJ (Abramoff et al. 2004). The image analysis process is illustrated with a sample from the study in Supplemental Figure 1 (available separately online). First, digital images were manually cropped to remove the area outside of the petri dish. The image was then converted to 8 bits, and a threshold was applied to remove the image background, removing any debris such as chorion (which tended to be a light shade

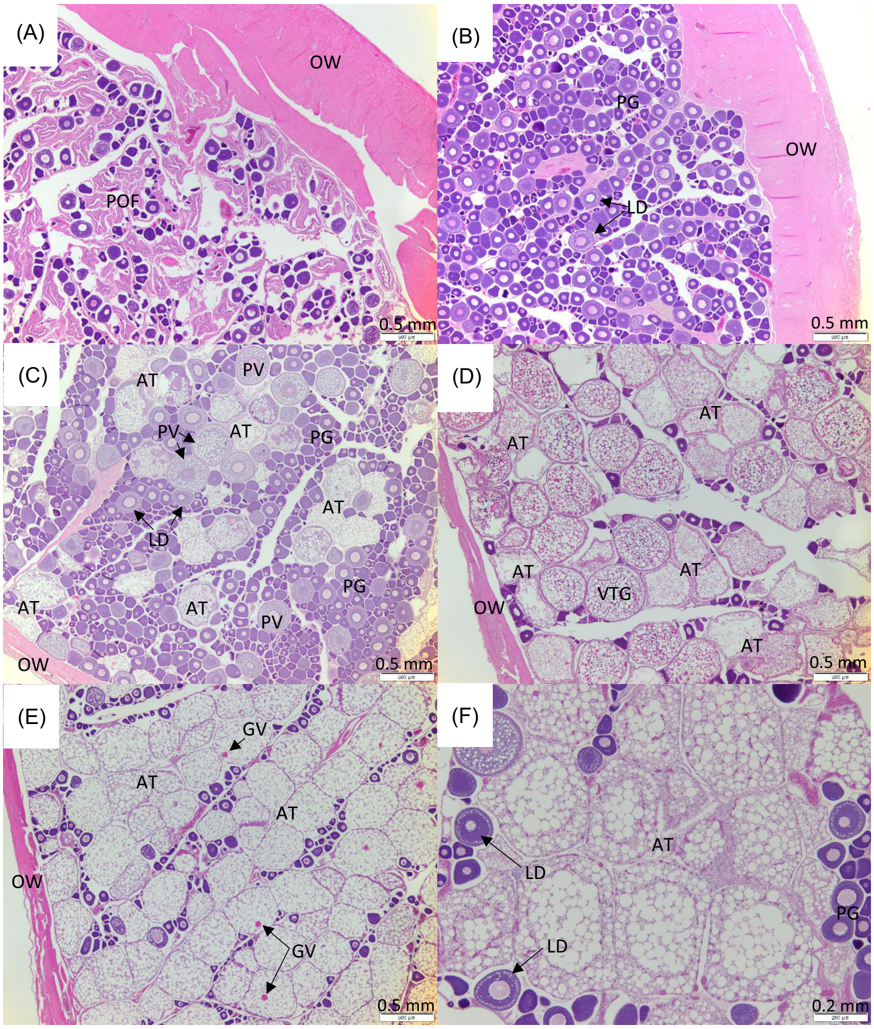

FIGURE 3 Spawned, pubertal, and unspawned ovaries undergoing reabsorption of oocytes in Atlantic Striped Bass that were observed during the spawning season: (A) recently spawned (regressing) ovary containing postovulatory follicles and with a thickened ovarian wall; (B) regenerating ovary containing primary growth and early previtellogenic oocytes and with a thickened ovarian wall; (C) ovary with oocytes undergoing atresia, with a thin ovarian wall and containing a heterogeneous population of previtellogenic oocytes; (D) ovary from an age-11 Striped Bass with a thin ovarian wall containing vitellogenic oocytes undergoing atresia ("skipped spawning"); (E) ovary with a thin wall undergoing total atresia, with displaced and shrunken germinal vesicles visible in some oocytes; and (F) detailed view of atretic oocytes from an unspawned ovary in which the germinal vesicles and yolk globules have been reabsorbed. AT, atresia; GV, germinal vesicle; LD, lipid droplets; OW, ovarian wall; PG, primary growth oocyte; POF, postovulatory follicle; PV, previtellogenic oocyte; VTG, vitellogenic oocyte.

of gray) that separated from an oocyte and thus leaving all oocytes represented as black particles. A binary watershed algorithm available in ImageJ was applied to the image to separate oocytes with touching edges (Papadopulos et al. 2007). Finally, particle analysis was applied, with a minimum particle size of 150–300 pixels depending on oocyte size in images, to identify and enumerate each oocyte while excluding smaller extraneous materials. This process was found to be highly accurate by visually comparing images between steps and adjusting the minimum particle size when necessary.

The precision of egg density estimates (number of oocytes/g) was examined with the coefficient of variation (CV). If the within-sample CV was greater than 10%, a replacement set of subsamples was taken and analyzed. Replacement subsamples were necessary for six samples (9% of the total samples) and tended to result from oocytes that were not sufficiently separated by rinsing and remained in clumps. Potential annual fecundity was calculated as the product of the oocyte density and ovary weight. No attempt was made to account for the weight of tissues not composed of mature oocytes (ovarian wall, primary growth oocytes, etc.), which may overestimate fecundity but was consistent with methods used in previous Striped Bass fecundity studies.

To test the proportionality between fecundity and body size in Striped Bass, we compared the growth allometry between body length and body mass against the scaling relationship between body length and fecundity following the methods of Dick et al. (2017). The relationship between fecundity as a function of body length in fish is commonly expressed as

$$F = aL^b, \tag{1}$$

where F is fecundity, L is the measured fish length, and a and b are constants. The basic length–weight function used for fish follows the same structure:

$$W = cL^d, \tag{2}$$

where W is body weight and c and d are constants. If the exponents are equivalent ($b = d$), then reproductive output (measured as fecundity) scales proportionately to female biomass. However, if b is greater than d, then reproductive output increases disproportionately relative to body size. The constant a determines the magnitude of fecundity (i.e., the scale of the fecundity axis), while the exponent b determines how quickly fecundity changes with increasing female body size. Models were fitted to data with linear least-squares regression on the log-linearized functions through calls to the “lm” function in R (R Core Team 2016). The coefficient of determination (R^2) for each model was calculated with the back-transformed model predictions and original response variable.

The results of fecundity studies can vary due to a variety of factors from methodological differences to spatiotemporal variability. A review of the literature produced five Striped Bass fecundity studies that were conducted in the Chesapeake Bay and estimated potential annual fecundity with similar gravimetric methods. These studies ranged in publication date from 1952 to 2019, and four studies provided length–fecundity function parameters or tabular data from which to determine them, thus facilitating comparison of scaling exponents among studies.

RESULTS

Samples

Over the three study years (2014–2016), 428 ovary samples from 14 surveys were collected for histological analysis (Table 1). Of these, 307 (71.7%) were from Maryland waters of the Chesapeake Bay and 121 (28.3%) were from coastal surveys. Lengths ranged from 350 to 1223 mm TL (mean = 697 mm). Chesapeake Bay fish ranged from 350 to 1223 mm TL (mean = 731 mm), and fish sampled on the coast ranged from 350 to 1030 mm TL (mean = 610 mm). Ages ranged from 2 to 16 years. Most sampled fish were between ages 4 and 6 (54.2%; Table 3), and fish were collected in both spring and fall months (Table 1). Age-9 and older fish were only collected during the spring months. A subset of 60 ovaries in the spawning capable phase from the maturity study were used for fecundity analysis. An additional seven supplemental samples collected in 2017 and 2018 were used for fecundity analysis only, resulting in a total n of 67. These samples were from females ranging in age from 5 to 17 years.

TABLE 3 Number of Striped Bass females (n) that were sampled by age. Ages were calculated relative to the proximate spawning season (e.g., fall-developing fish had their ages advanced by 1 year).

Age	*n*	Percent
2	3	0.7
3	13	3.0
4	45	10.5
5	131	30.6
6	56	13.1
7	32	7.5
8	36	8.4
9	13	3.0
10	28	6.5
11	44	10.3
12	14	3.3
13	8	1.9
14	4	0.9
16	1	0.2
Total	428	

Reproductive phases

Striped Bass were classified as immature if ovaries were in the immature, early developing, or previtellogenic phase. Striped Bass with ovaries in the immature phase ranged in age from 2 to 7 years (Figure 4). Ovaries in the immature phase were observed in all age-2 Striped Bass females, over 90% of age-3 females, and 30% of age-4 females. The immature phase comprised 3% or less of the total for each age from 5 to 7 years. Although not shown in Figure 5, Striped Bass in the immature phase were observed in all months sampled except December. It should be noted, however, that samples from fish younger than age 5 were not obtained during December from any of the surveys.

Striped Bass with ovaries in the early developing phase (Figure 2A) ranged from 3 to 8 years old (Figure 4) and occurred throughout the year, without apparent seasonality (Figure 5). The single age-3 Striped Bass that was not in the immature phase was in the early developing phase. The early developing phase was most prominent in ages

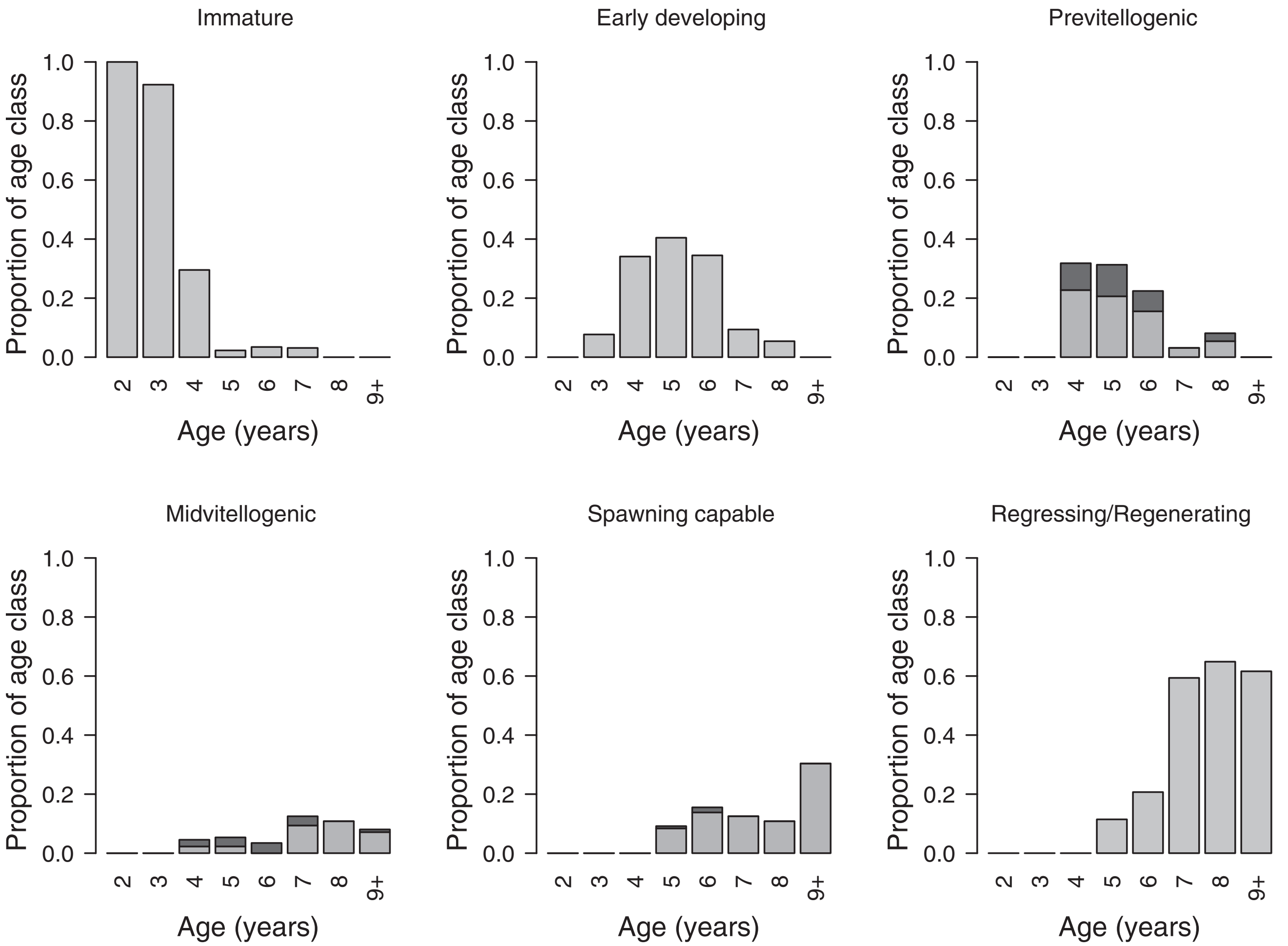

FIGURE 4 The proportion of each age-class observed in each reproductive phase for Atlantic Striped Bass. Ages 9–16 are grouped together as age 9+. Dark shading indicates the occurrence of widespread atresia. The spawning capable phase includes the actively spawning subphase, which was directly observed in ages 5, 6, 7, 10, and 12.

4–6 and from samples that were collected in October. This reflects the heavy sampling of these ages from the coast in October, as older and larger fish were mostly sampled in the spring. Among the Striped Bass that were sampled on the coast in the fall, all individuals that were not in the immature phase or the previtellogenic phase were in the early developing phase. As noted previously, the fall samples were excluded from the estimation of maturity ogives.

The previtellogenic phase (Figure 2C) was observed in ages 4–8 (Figure 4). Previtellogenic phase ovaries were observed in both spring and fall months (Figure 5). Widespread atresia in ovaries containing previtellogenic oocytes appeared toward the end of the spawning season in May and June and in fish ranging from ages 4 to 8. In May, 20% of previtellogenic phase ovaries were undergoing widespread atresia, which increased to 89% in June. Because these fish had not initiated vitellogenic growth by the spring, they were classified as immature.

Striped Bass were classified as mature if ovaries contained oocytes undergoing vitellogenesis (midvitellogenic phase) or more advanced stages (spawning capable, regressing, and regenerating phases). Striped Bass containing ovaries in the midvitellogenic phase (Figure 2D) were only observed during the spring months (Figure 5). Striped Bass in the spawning capable phase (Figure 2E) were observed from March through June but were overwhelmingly present during April and May (Figure 5). The spawning capable phase was observed in age-5 and older Striped Bass (Figure 4). Among the spawning capable phase samples, 12 were in the actively spawning subphase (Figure 2F) and ranged from ages 5 to 12. All except one were collected on the spawning grounds during the Maryland Spawning Stock Survey in April and May.

Toward the end of the spring spawning season, increasing proportions of ovaries with oocytes containing yolk globules were observed undergoing atresia and resorption (Figure 5). Of these samples, we observed one age-11 Striped Bass in late April with ovaries undergoing resorption of VTG2 oocytes, a thin ovarian wall, and no evidence of postovulatory follicles (Figure 3D). Additionally, in May and June, 10 ovaries from age-4–7 fish with oocytes containing yolk globules were undergoing widespread atresia.

Given the age range of Striped Bass that were observed undergoing this condition, it is possible that these individuals represent a potential delay in maturity in younger-aged fish and skipped spawning in older fish. Because of this uncertainty, these samples were not given a maturity classification or included in the maturity ogives.

Striped Bass with ovaries in the regressing and regenerating phases were observed during April–July but predominantly were present at the end of the spawning season in May and June (Figure 5). Sequentially, spawning capable phase ovaries peaked in April, followed by a peak in regressing phase ovaries during May and then a peak in regenerating phase ovaries in June. Regressing and regenerating phases, which indicate that spawning had recently occurred, were observed in age-5 and older Striped Bass (Figure 4). Although we observed an age-4 Striped Bass in the midvitellogenic phase, we did not observe any age-4 Striped Bass in the spawning-capable, regressing, or regenerating phase.

Gonadosomatic index

The GSI was found to vary over 34-fold between the immature phase and the actively spawning subphase (Table 4). The mean GSI was less than 1% for the immature and early developing phases. Previtellogenic phase ovaries had a mean GSI close to 1%, which did not differ when the ovaries were found with widespread atresia. Midvitellogenic phase ovaries, which contained noticeably larger oocytes in the VTG1 and VTG2 stages, had a mean GSI close to 4%. Ovaries containing atretic vitellogenic oocytes were also close to a mean GSI of 4%. The largest increase in GSI between reproductive phases was observed in the spawning capable phase, which increased to a mean GSI of 10.4%. The GSI peaked during the actively spawning subphase, ranging up to 25.7%, with a mean of 17.2%. Regressing ovaries ranged in GSI from 0.1% to 3.2% depending on the exact state of the ovary, including whether postovulatory follicles were

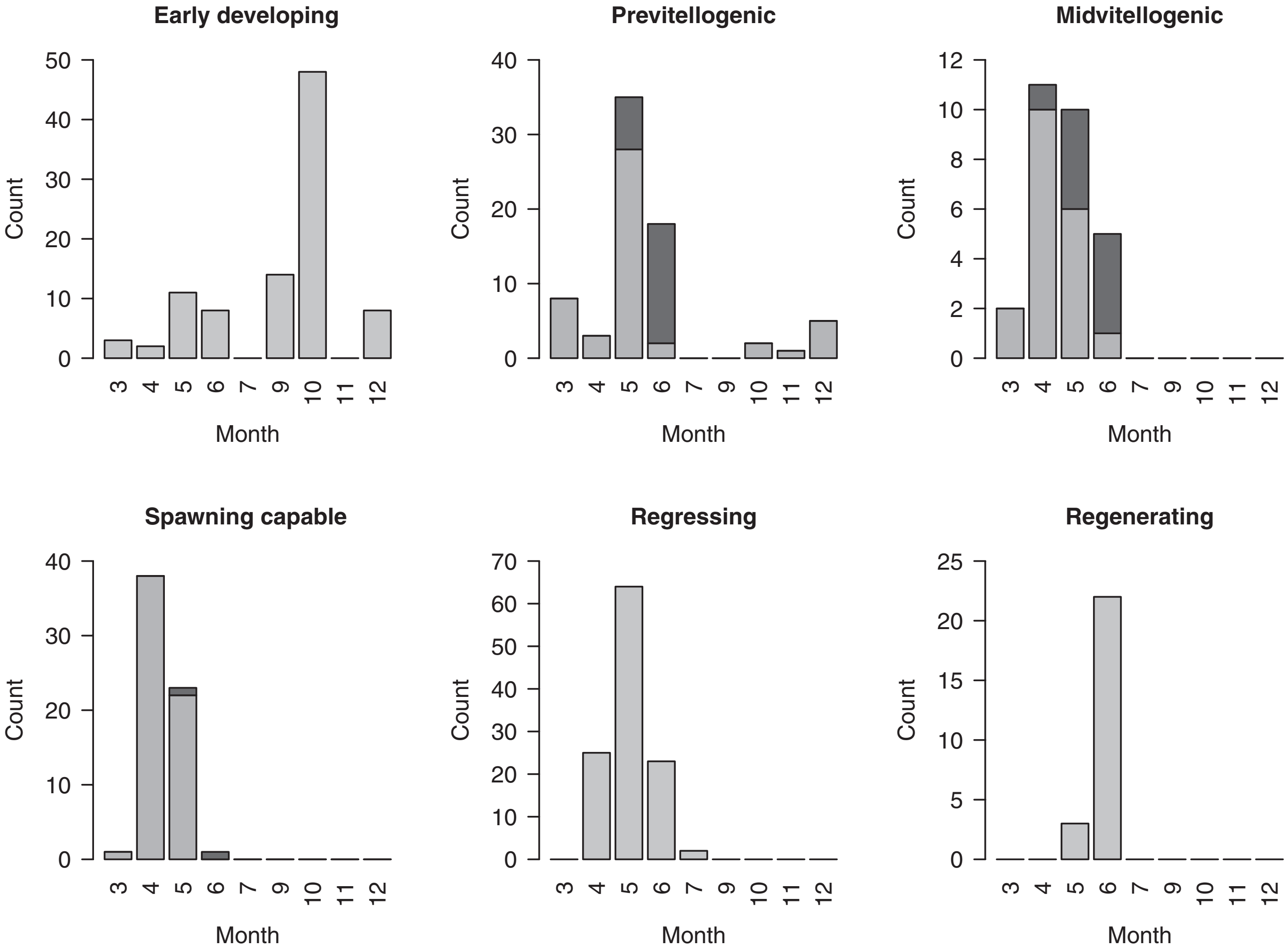

FIGURE 5 Numbers of Atlantic Striped Bass that were observed in each reproductive phase by month. Dark shading indicates the occurrence of widespread atresia. The spawning capable phase includes the actively spawning subphase, which was observed in April ($n=5$) and May ($n=7$). The immature phase is not depicted here but was encountered in all months except December. Reproductive phases are described in Table 2. Note the difference in *y*-axis scales.

TABLE 4 The gonadosomatic index (GSI; %) of female Striped Bass varied over 34-fold between reproductive phases. Ovary weights for calculating the GSI could not be obtained for all ovary samples.

Phase	Mean GSI	SD	*n*	Maturity classification
Immature	0.5	0.2	18	Immature
Early developing	0.7	0.1	88	Immature
Previtellogenic	1.1	0.4	43	Immature (pubertal)
Previtellogenic atresia	1.0	0.5	21	Immature (pubertal)
Midvitellogenic	3.9	1.3	17	Mature
Vitellogenic atresia	3.7	1.1	11	Unclassified
Spawning capable	10.4	2.6	45	Mature
Actively spawning	17.2	4.2	9	Mature
Regressing	1.4	0.4	105	Mature
Regenerating	0.9	0.2	21	Mature

still present, the number of oocytes that did not undergo ovulation, and the advancement of atresia. The mean GSI of the regressing phase declined to 1.4%, representing a 92% decrease relative to the actively spawning subphase. The regenerating phase returned to a mean GSI of less than 1%, similar to the GSI of the early developing phase.

Maturity ogives

Both age- and length-based maturity ogives for the spring data set derived from a generalized linear model with binomial error and logit link functions had statistically significant model coefficients ($p \leq 0.05$). The age at 50% maturity was estimated to be 5.5 years, and the length at 50% maturity was 609 mm TL (Figure 6). The largest immature female was 843 mm TL and 8 years old, whereas the smallest mature female was 488 mm TL and 5 years old.

Fecundity

Fecundity analysis was performed on 67 Striped Bass ranging in length from 499 to 1139 mm TL and ranging in age from 5 to 17 years. For the remainder of this section, when we use the term "oocytes" we are referring to spawning-capable (yolked) oocytes (see Methods). Precision of within-sample oocyte density counts as measured by the CV was maintained below 10%, with a mean of 3.65%. Potential annual fecundity ranged from 187,558 oocytes in an age-5 individual to 4,141,424 oocytes in an age-13 individual.

Power functions were fitted to data using simple linear regression on log–log-transformed data such that the slope coefficient in the log-linear regression was equivalent to the scaling exponent of the power function. The log-linear regression of body mass as a function of body length (Figure 7A) was significant ($F_{1,59} = 6943$, $p < 0.000$) and highly precise ($R^2 = 0.98$). The estimated scaling exponent d was 3.05 [95% confidence interval (CI) = 2.98–3.12]. This establishes that allometric scaling between body

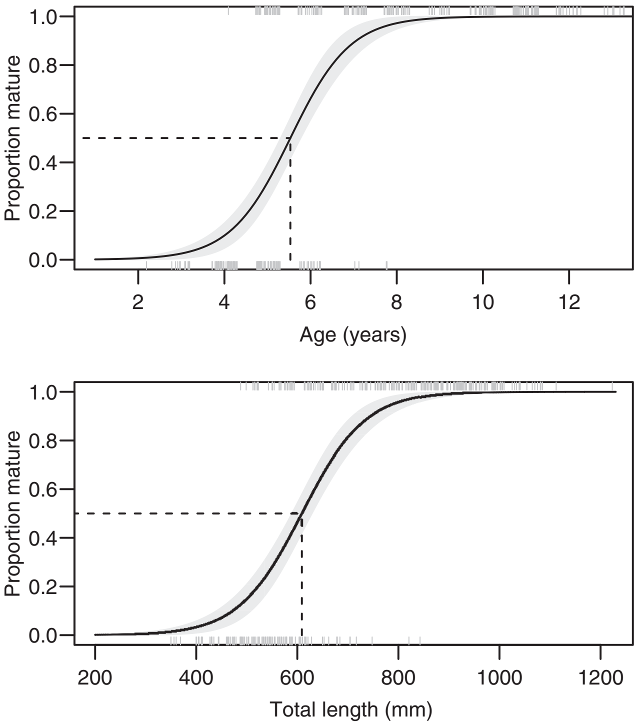

FIGURE 6 Maturity ogives by age (top) and total length (bottom) for female Atlantic Striped Bass sampled from the Chesapeake Bay and along the Atlantic coast in spring (March–July). Ogives were derived from a generalized linear model with binomial error and logit link functions. Shaded polygons indicate 95% confidence intervals. Dashed lines indicate the age and length at 50% maturity, which were 5.5 years and 609 mm TL, respectively, for the spring data. The x-axis rug plot indicates the ages (jittered) and total lengths sampled.

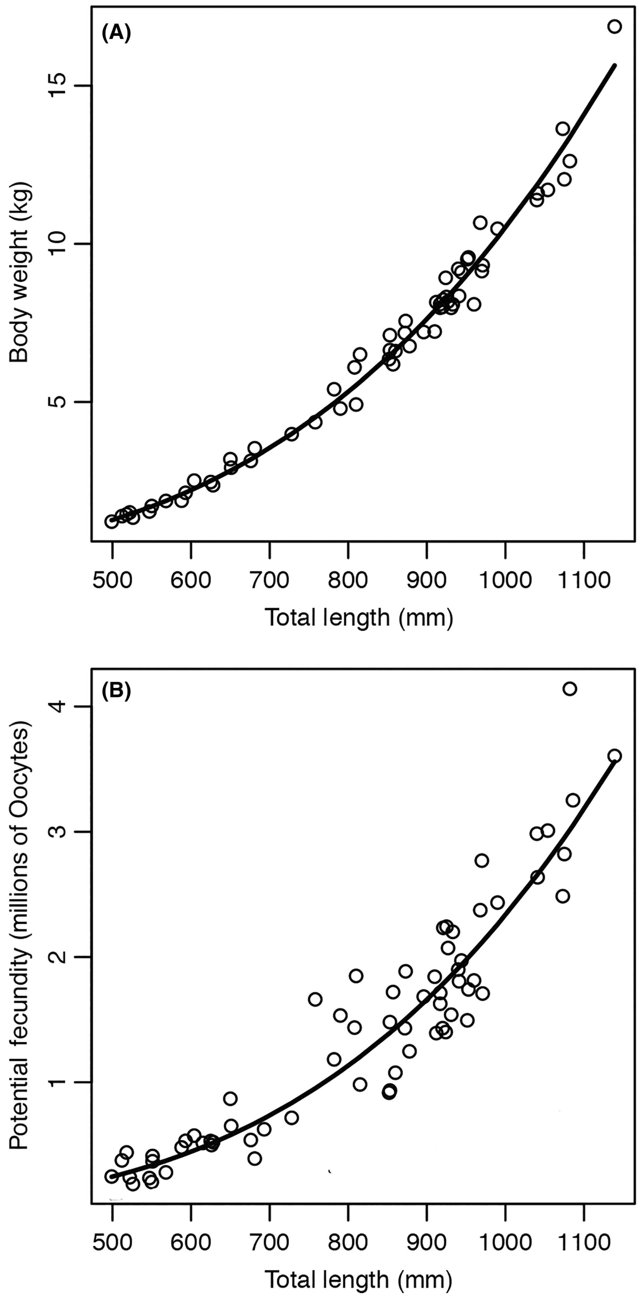

FIGURE 7 Allometry in Atlantic Striped Bass body length, weight, and potential annual fecundity was assessed by fitting power law functions to log–log-transformed data using ordinary least-squares regression and comparing the scaling exponents. (A) The scaling relationship between total length (L; mm) and body weight (W; kg) was estimated as $W = \exp(-18.72) \times L^{3.05}$ ($R^2 = 0.98$). (B) Potential annual fecundity (F; millions of eggs) increases with total length (mm) according to the relationship $F = \exp(-7.72) \times L^{3.24}$ ($R^2 = 0.89$).

length and weight in adult female Striped Bass is slightly higher than but not dissimilar to the theoretical value of 3.0, which is the isometric mass-scaling exponent. The log-linear regression of potential annual fecundity as a function of body length (Figure 7B) was significant ($R^2 = 0.89$; $F_{1,65} = 659$, $p < 0.000$), with a slope b of 3.24 (95% CI = 2.99–3.49). The highest measured potential annual fecundity was not from the largest fish and deviated strongly from the expected value. However, the length–fecundity exponent was relatively insensitive to exclusion of this data point (3.21 vs. 3.24). When comparing scaling exponents, b was greater than d, providing some evidence that reproductive output scales disproportionately in Striped Bass, but the estimates had overlapping 95% CIs.

DISCUSSION

Age at maturity

To accurately assess the age at maturity of female Striped Bass, it is crucial to have a comprehensive understanding of the species' reproductive development and oogenesis. This study differentiated between maturing and fully mature Striped Bass based on a review of aquaculture-focused research into the reproductive development of female Striped Bass. This research proved to be invaluable for interpreting histological observations of oocyte stages and determining maturity status.

Striped Bass ranging in age from 4 to 8 years were sometimes identified as maturing but not yet functionally mature. Previous maturity studies of wild Striped Bass populations have made similar observations but have not accounted for this developmental pattern when determining age at maturity. In Striped Bass caught in San Francisco and San Pablo bays, Chadwick (1965) described “a complete intergradation [sic] of intermediate stages” and recognized signs of gonadal development occurring a year or more before spawning. Berlinsky et al. (1995) also documented early secondary growth oocytes in Striped Bass during February in Long Island Sound and during April in the Hudson River and suspected that these oocytes would not have matured enough for spawning in the upcoming season. This developmental pattern is consistent with pubertal development in Striped Bass, which is the physiological process occurring along the brain–pituitary–gonad axis that leads to first sexual maturity (Okuzawa 2002). Pubertal development in female Striped Bass has been studied from juveniles up to the beginning of the fourth year in captive-reared Striped Bass from broodstock of Chesapeake Bay origin (Hassin et al. 1999; Holland et al. 2000, 2001). These studies found that in Striped Bass, female pubertal development encompasses multiple annual cycles of incomplete ovarian growth stimulated by pituitary gonadotropins, displaying seasonal dynamics concurrent with the adult reproductive cycle. Our observations of ovaries containing previtellogenic oocytes undergoing preovulatory atresia by the end of the spawning season in May and June further confirm incomplete maturation in these fish.

In experiments manipulating the natural photothermal cycle of adult Striped Bass, photoperiod has been noted to exert a significant influence on the growth of oocytes during previtellogenic growth. However, for vitellogenesis to occur, the fish must be exposed to cold water temperatures (Clark et al. 2005). If the environmental cue of seasonally fluctuating water temperatures is not received, the oocytes will only undergo previtellogenic growth and will not initiate vitellogenesis. The similarity of this phenomenon to partial oocyte development during puberty suggests that the brain–pituitary–gonad axis of pubertal individuals may not yet be fully developed and receptive to the proper environmental signals that stimulate the vitellogenic growth phase of the reproductive cycle.

Oocyte degradation is impacted by warm water temperatures and can be delayed for several months in gravid Striped Bass if kept at abnormally low temperatures (Sullivan et al. 2003). During the time when water temperatures can often rise above the upper threshold for Striped Bass spawning (i.e., from late May into June), we observed a rise in mass atresia both in pubertal (previtellogenic) female Striped Bass and in females with oocytes undergoing vitellogenesis. The resorption of oocytes arrested at the previtellogenic phase in pubertal Striped Bass toward the end of the spawning season is a characteristic of this stage of development. In older Striped Bass, such as the observed age-11 individual, the resorption of vitellogenic oocytes could be classified as "skipped spawning" (Rideout et al. 2005). Studies using telemetry on individual Striped Bass from the Chesapeake Bay population have documented nonannual or skipped spawning, in which the fish do not return to their spawning areas during the spawning season (Secor et al. 2020). Jackson and Tiller (1952) observed several age-10 and older Striped Bass during the spring that had greatly reduced ovarian weights relative to their body size and contained few enlarged oocytes. Factors contributing to nonannual spawning in Striped Bass, such as age or body condition, and the impact of nonannual spawning on lifetime reproductive capacity, deserve further attention. However, modeling exercises exploring the influence of skipped spawning on egg production per recruit suggest that this would have minor effects (Secor 2008). Additionally, preliminary investigation into the energetic status of female Striped Bass and the incidence of skipped spawning was inconclusive (Peer 2012).

Striped Bass in the midvitellogenic phase with weakly yolked oocytes were observed throughout the spawning season and were tentatively classified as mature. Although these females were classified as functionally mature in this study, it is possible that there are additional phases of reproductive development during adolescence in Striped Bass that involve varying degrees of advanced vitellogenesis before consistently viable eggs are produced. Additionally, younger Striped Bass (as young as age 4) were observed to enter vitellogenesis but failed to spawn and were undergoing atresia. This may represent a type of abortive maturation (McBride et al. 2022) or an additional step in pubertal development. Hassin et al. (1999) observed that Striped Bass reaching sexual maturity for the first time had a lower GSI and lower accumulation of yolk than known-adult age-6 females. Striped Bass maternal size affects both egg size and larval growth rates; however, it does not appear to impact larval survival rates (Monteleone and Houde 1990). Further research into female adolescence and first functional maturity in Striped Bass could provide a more nuanced understanding of the species' reproductive biology.

Compared with previous studies utilizing histological methods to estimate maturity, the results of the current study were very similar to those of Berlinsky et al. (1995) but differed from those reported in the most contemporary study by Gervasi et al. (2019). Berlinsky et al. (1995) estimated the age at 50% maturity at 5.3 years for migratory Striped Bass from coastal Rhode Island waters, which were considered representative of the Atlantic Striped Bass stock. However, based on Striped Bass sampled from the Chesapeake Bay, Gervasi et al. (2019) estimated an age at 50% maturity of 2.84 years, which is substantially lower than our estimate.

Age-at-maturity estimates for the current study were highly similar to estimates from Berlinsky et al. (1995) despite differences in methodology, sampling location, and time period. Both studies estimated a similar age at 50% maturity (age 5.3 vs. age 5.5), with first maturity occurring at age 4 and over 90% maturity obtained by age 7. Berlinsky et al. (1995) sampled migratory Striped Bass from the coastal waters of Rhode Island during the spring and fall of 1985–1987, and they used an oocyte diameter size threshold of 150 μm and the presence of cytoplasmic inclusions to classify maturity. During that period, the stock was considered collapsed and the age structure had greatly contracted. The Atlantic Striped Bass stock recovered and maintains a diverse age structure but has since declined below the SSB threshold indicating that the stock was overfished during the current study period (Northeast Fisheries Science Center 2019). The results of studies conducted when the population was considered collapsed and after the population was recovering indicate that age at maturity in Striped Bass is a life history characteristic that has not responded rapidly to fishing-induced changes in abundance and age structure.

The classification of maturity varies among studies and species based upon the reproductive strategy of the study species and the objective of the maturity studies. It is typical to classify ovaries containing enlarged previtellogenic oocytes—referred to elsewhere as cortical alveolar oocytes—as mature since secondary growth has been initiated (Lowerre-Barbieri et al. 2011). In their histological study of Striped Bass maturity, Gervasi et al. (2019) considered that the early developing phase (the phase preceding vitellogenesis in the standard terminology) could be either immature or mature but assumed that “females with CA [cortical alveolar] oocytes typically continue to press through vitellogenesis and spawn in the upcoming season.” Due to the classification of early developing fish as “mature” in the Gervasi et al. (2019) study, their estimate of the age at 50% maturity may be interpreted as the age when female Striped Bass begin to undergo physiological maturation rather than the age at which they achieve functional maturity. They estimated the age at 50% maturity at 2.84 years, which is substantially lower than our estimate (5.5 years) and which is below age 4, the age at which we first observed maturity to occur in any individual. In laboratory studies with Striped Bass reared under naturally cycling annual photothermal conditions for the first 4 years of life, 65% of individuals first entered the pubertal phase by age 3 and tentatively reached first functional maturity (adolescence) at age 4 (Hassin et al. 1999). If their estimate was for functional maturity, it would not align with results from the long-term Maryland Spawning Stock Survey, which employs experimental drift gill nets on the major spawning grounds in the Potomac River and the upper Chesapeake Bay. Age-3 or younger females have not been encountered on the spawning grounds since 1994, and age-4 females have been encountered only sporadically since then. Typically, less than three—and usually zero—age-4 female Striped Bass have been captured on the spawning grounds during the Maryland Spawning Stock Survey each year since 1995, where on average 157 females are captured per year.

To accurately differentiate between individuals that have reached puberty and those that are functionally mature, it is recommended to collect ovaries throughout the spawning season. In the limited size range of Striped Bass that were collected along the coast during the fall, we observed the early developing and previtellogenic phases. However, the present study was limited in the breadth of Striped Bass ages sampled in every month and was unable to determine when vitellogenic growth begins in different size-classes. In captive rearing studies using an annual photothermal cycle, yolk globules were observed in Striped Bass oocytes as early as September (Hassin et al. 1999; Clark et al. 2005). In the wild, Berlinsky and Specker (1991) reported observing vitellogenic phase Striped Bass in Rhode Island as early as September in larger fish (947 mm fork length) and by November in fish with a mean fork length of 690 mm. In the current study, the Striped Bass that were sampled during the fall had a limited size range, with a mean of 604 mm TL. To enhance future research on the maturity of Striped Bass, it would be beneficial to sample a wider range of size-classes from coastal waters throughout the year.

The timing of vitellogenesis as it relates to ontogeny, migratory behavior, and photothermal period should receive further attention in future studies of Striped Bass reproductive development. We are uncertain whether vitellogenesis alone is an accurate indicator of functional maturity or whether there is an additional period of quasi-competent adolescence after pubertal development during which the oocytes are weakly yolked and potentially unviable.

Fecundity

In Figure 8, results of previous studies of Striped Bass fecundity that were conducted in the Chesapeake Bay region are summarized and compared to the results of the current study. Four studies either fit a power function to length–fecundity data or provided tabular data to estimate a scaling exponent (Table 5). All four estimated exponents were greater than 3.0 and ranged from 3.14 (Sadler et al. 2006) to 3.78 (Richards et al. 2003), providing further support for hyperallometric scaling of fecundity in Striped Bass. Two studies (Jackson and Tiller 1952; Mihursky et al. 1987) shared scaling (3.24 and 3.20, respectively) that was very similar to scaling in the present study. The most contemporary study by Gervasi et al. (2019) used model selection based on Akaike's information criterion and found more support for a simple linear model instead of a power function; they did not report the scaling exponent, although a linear model implies a scaling exponent close to 1.0. Empirically, Gervasi et al. (2019) had the lowest measured potential annual fecundity, especially for larger individuals. A length–fecundity scaling exponent of 1.0 would be considered low for a marine fish and implies that potential annual fecundity continually declines with respect to body mass as fish grow larger.

Our length-based estimates of the potential annual fecundity were consistent with most previous studies conducted over a period of seven decades in the Chesapeake Bay region. Two studies (Jackson and Tiller 1952; Mihursky et al. 1987) were highly similar to the current study. This is surprising given that Jackson and Tiller (1952) was the earliest study conducted and the Mihursky et al. (1987) study was conducted during the Atlantic Striped Bass stock collapse in the 1980s. Like age at maturity, fecundity seems to be a temporally invariant life history trait in Striped Bass, although future studies incorporating a broader range of

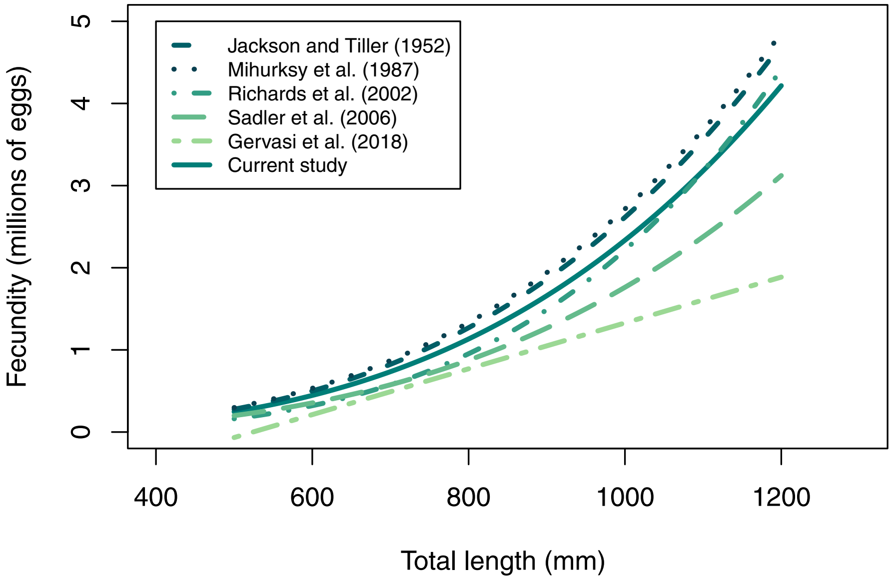

FIGURE 8 The relationship between Atlantic Striped Bass total length (mm) and potential annual fecundity (millions of eggs) from the current study compared with relationships reported in five previous studies conducted in the Chesapeake Bay region.

TABLE 5 Power model coefficients estimating the scaling relationship between body length and potential annual fecundity in Striped Bass from studies conducted within the Chesapeake Bay region using similar gravimetric methods. *a*, intercept; *b*, scaling exponent; na, not available; TL, total length.

Source	Log(*a*)	*b*	*n*	Length range (mm TL)	Chesapeake Bay location(s)
Present study	−7.72	3.24	67	499–1139	Main stem and upper bay
Jackson and Tiller (1952)	−7.58	3.24	32	530–1105	Chesapeake Bay
Mihursky et al. (1987)	−7.21	3.20	235	456–1249	Upper bay, Potomac River, Choptank River, and C&D Canal
Richards et al. (2003)	−11.51	3.78	142	750–1190	Choptank River spawning grounds
Sadler et al. (2006)	−7.06	3.14	na	na	James and Rappahannock rivers

year-classes are needed to explore interannual variability in fecundity and its potential drivers.

The greatest difference between our study and the other fecundity studies was with the most contemporary study (Gervasi et al. 2019), which reported the lowest fecundity-at-length values. These results may have been affected by the sampling period for larger, older fish in their study. Most larger fish in the study were sampled in February and March, and few fish older than age 5 were sampled in April (Gervasi 2015). Oocytes that are recruited for the upcoming spawning season change drastically in size from early spring leading up to spawning, almost doubling in diameter (Jackson and Tiller 1952). Depending on how the ovarian samples were processed and the methods used to enumerate oocytes, the small size of oocytes undergoing secondary growth in February and March may result in an undercount of putative vitellogenic oocytes.

Scaling exponents from the current study and all other previous studies that fit a power function to the length–fecundity data were greater than 3.0, providing some evidence that potential annual fecundity scales disproportionately with body size in Striped Bass. This finding indicates that the potential reproductive capacity of the Atlantic Striped Bass stock may be dependent not only on female spawning biomass, but also on the age structure and size structure of mature females in the population. Although our length–fecundity scaling exponent was not statistically different from the length–weight exponent owing to the large variance in fecundity, the additional sampling of larger fish in future studies may help to improve the precision of the scaling exponent. We suggest that future Atlantic Striped Bass stock assessments should explore the management implications of using SSB versus alternate measures of reproductive capacity that incorporate disproportionate scaling in reproductive output with body size.

The results of this maturity and fecundity study were mostly consistent with the results of studies spanning seven decades. The greatest variation between our study and the other studies was with the most contemporary study (Gervasi et al. 2019) and may be attributable to methodological differences and differing interpretations of maturity (physiological maturation vs. functional maturity) rather than spatiotemporal variation. Overall, these findings suggest that the reproductive-related life history traits of female Striped Bass are robust to long-term decadal changes in fishing pressure, population size, and environment.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this study may be available upon request from the state data collectors for the individual datasets. Data contacts can be provided by the corresponding author.

ETHICS STATEMENT

Most samples for this study were obtained dockside from deceased fish harvested by recreational anglers returning from charter trips. Samples obtained from fishery independent surveys were collected under the guidelines of the acting institution or agency.

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SUPPORTING INFORMATION

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