

**Abstract**—The tautog, *Tautoga onitis* (Linnaeus), ranges from Nova Scotia to South Carolina and has become a popular target for recreational and commercial fisheries. Although tautog are a multiple spawning species, reproductive potential, measured as annual fecundity, has not been estimated previously with methods (batch fecundity, spawning frequency) necessary for a species with indeterminate annual fecundity. A total of 960 tautog were collected from the mouth of the Rappahannock River in the lower Chesapeake Bay to 45 km offshore of Virginia's coastline to investigate tautog reproductive biology in the southern portion of the species range. Tautog did not exhibit a 1:1 sex ratio; 56% were females. Male tautog reached 50% maturity at 218 mm TL, females at 224 mm TL. Tautog spawned from 7 April 1995 to 15 June 1995, at locations from the York River to 45 km offshore. Batch fecundity estimates ranged from 2800 to 181,200 eggs per spawning for female tautog age 3–9, total length 259–516 mm. Mean batch fecundity  $\pm$ SEM for female tautog ages 4–6 was 54,243  $\pm$ 2472 eggs and 106,256  $\pm$ 3837 eggs for females ages 7–9. Spawning frequency was estimated at 1.2 days, resulting in 58 spawning days per female in 1995. Estimates of potential annual fecundity for tautog ages 3–9 ranged from 160,000 to 10,510,000 eggs.

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## Reproductive seasonality, fecundity, and spawning frequency of tautog (*Tautoga onitis*) in the lower Chesapeake Bay and coastal waters of Virginia\*

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The tautog, *Tautoga onitis* (Linnaeus), ranges from Nova Scotia (Bleakney, 1963; Scott and Scott, 1988) to South Carolina (Sedberry and Beatty, 1989; Bearden<sup>1</sup>), although it is most abundant between Cape Cod and New Jersey (Bigelow and Schroeder, 1953). In Virginia, tautog occur within the Chesapeake Bay from Gwynn's Island (mouth of Rappahannock River) and Sandy Point (Eastern Shore) southward to the mouth of the bay (Hildebrand and Schroeder, 1928), and in coastal Atlantic waters out to 65 km offshore (Richards and Castagna, 1970; Musick, 1972; Hostetter and Munroe, 1993). The major habitat requirement for this species is hard-bottom structure that fish can remain under, within, or alongside (Olla et al., 1974). Adult tautog inhabit hard-bottom environments including natural reefs and rock outcroppings,

as well as man-made structures such as jetties, bridge-tunnel networks, artificial reefs, and shipwrecks. Near the southern terminus of the species range suitable hard-bottom habitat to support tautog populations becomes less abundant and may limit population size (Eklund and Targett, 1990; Hostetter and Munroe, 1993).

Tautog are a long-lived, slow-growing species with a maximum recorded age of 34 years in Rhode Island (Cooper, 1967)

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<sup>1</sup> Bearden, C. M. 1961. Common marine fishes of South Carolina. Bears Bluff Lab. Contr., vol 34, 47 p. [Deposited at South Carolina Department of Natural Resources, Marine Resources Library, 217 Fort Johnson Road, P.O. Box 12559, Charleston, SC 29422.]

and 31 years in Virginia (White, 1996). Growth parameters of fish between northern and southern regions (Hostetter and Munroe, 1993) are comparable, except that Virginia tautog have exhibited almost twice the growth increments in young-of-the-year and age 13+ fish. Likewise, growth relationships are similar for tautog from New York (Briggs, 1977) and Virginia (Hostetter and Munroe, 1993).

Within preferred habitats, juvenile and adult tautog develop home sites (Olla et al., 1979). Tagging studies indicate seasonal movements between inshore and offshore habitats, but minimal north-south movement (Cooper, 1966; Briggs, 1977; Lynch<sup>2</sup>; Bain and Lucy<sup>3</sup>). During winter, adult tautog located offshore of Virginia are active at temperatures above 6.1°C (Adams, 1993). Likewise, tautog at inshore locations within Chesapeake Bay (Arendt et al., 2001a, 2001b) remain active at water temperatures of 5°C or above. In northern parts of its range, adult tautog move inshore and spawn when water temperatures increase in the springtime (Chenoweth, 1963; Cooper, 1966; Stolgitis, 1970; Olla et al., 1974, 1979), although some portion of the population remains offshore year-round (Olla and Samet, 1977; Hostetter and Munroe, 1993). Very little is known about the reproductive biology of tautog in Virginia. Tautog begin spawning when water temperatures reach about 11°C (Chenoweth, 1963; Olla et al., 1974, 1980; Eklund and Targett, 1990; Hostetter and Munroe, 1993); thus the spawning season begins later in the spring at higher latitudes. Spawning season extends from mid-April through June in Virginia (Hostetter and Munroe, 1993), mid-May through early August in Massachusetts (Stolgitis, 1970), and from late May to early June in Rhode Island (Chenoweth, 1963). Macroscopic gonad analyses and gonadosomatic indices have indicated that male tautog mature by age 3 and females by age 3–4 throughout the species range (Chenoweth, 1963; Cooper, 1967; Stolgitis, 1970; Briggs, 1977; Hostetter and Munroe, 1993); however, sample sizes of young (age 2–3) fish were small in these studies, and earlier maturation has been noted (Olla and Samet, 1977; Hostetter and Munroe, 1993). To date there has been no histological examination of the reproductive biology of this species in Virginia, or elsewhere.

In laboratory aquaria, tautog have been observed to be a multiple spawning species, spawning as discrete pairs and as groups (Olla and Samet, 1977; Olla et al., 1977). Although hermaphroditism is common among labrids (Warner and Robertson, 1978), tautog are thought to be strictly gonochoristic (Olla and Samet, 1977). However, two color patterns of males exist in samples from Virginia waters; approximately 85% of males exhibit strong dimor-

phism and 15% of smaller males (<550 mm) show external coloration similar to females (Hostetter and Munroe, 1993, this study). Further, histological analysis of 379 male tautog revealed no evidence of hermaphroditism (Munroe and White, unpubl. data)

The reproductive potential of tautog, measured as annual fecundity, has not been addressed to date. To accurately estimate potential annual fecundity for multiple spawning species, batch fecundity must be multiplied by the number of spawnings per year, i.e. spawning frequency multiplied by spawning season length (Hunter and Macewicz, 1985). Chenoweth (1963) and Stolgitis (1970) estimated batch fecundity and length of spawning season but did not measure spawning frequency. The only estimate of number of spawnings per female per year were those of Olla et al. (1977), who observed tautog spawning daily for 68–96 consecutive days in laboratory aquaria; however, results obtained in aquaria studies may not directly apply to natural habitats and have not been used to estimate potential annual fecundity.

Our study, the first to investigate cellular aspects of the reproductive biology of tautog in natural habitats of the lower Chesapeake Bay, was necessary 1) to describe this species as a determinate or indeterminate spawner; 2) to describe annual and spawning season ovarian cycles at the cellular level; 3) to assess age at maturity based on histological sections of gonad tissue; 4) to estimate batch fecundity for females from the southern portion of the species range; 5) to estimate spawning frequency; and 6) to estimate potential annual fecundity.

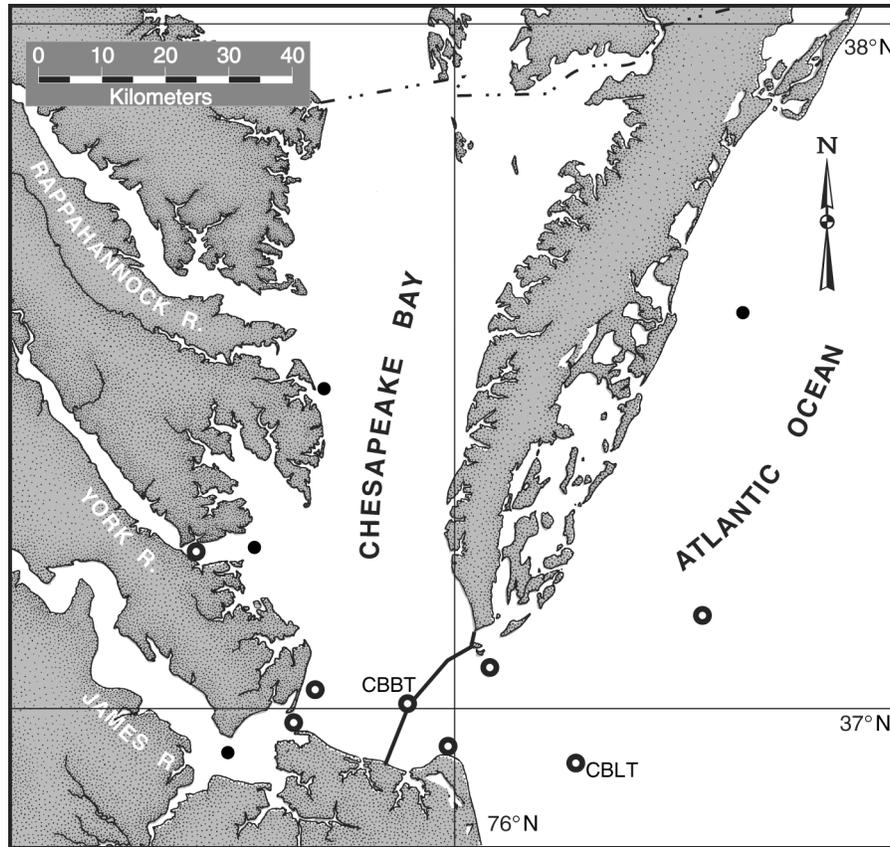
## Materials and methods

A total of 960 tautog (>150 mm total length [TL]) were collected opportunistically between April 1994 and September 1995 from commercial and recreational fishermen (ca. 90%) as well as from research projects (ca. 10%) at Virginia Institute of Marine Science (VIMS). A minimum size of 150 mm TL was selected based on maturity information presented in Hostetter and Munroe (1993). Collection locations ranged from Gwynn's Island at the mouth of the Rappahannock River to 45 km offshore of Virginia's coastline, at depths of 1–35 m (Fig. 1). Approximately one quarter of the fish were taken from within the Chesapeake Bay, one quarter from the Chesapeake Bay Bridge Tunnel (CBBT, depth=5–15 m), and one half from around the Chesapeake Bay Light Tower (24 km offshore, depth=17–20 m).

For each fish, total length (mm) and total weight (TW, g) were measured. Sex was assessed externally from several dimorphic characters previously described by Cooper (1967), Olla and Samet (1977), and Hostetter and Munroe (1993). Males were distinguished by their pronounced white chin, blunt forehead, solid black or gray coloration on the upper half of the body and white underneath, and a small white spot (about 15 mm diameter) mid-laterally, below the middle of the dorsal fin. Female tautog have a less pronounced chin, sloped forehead, and a mottled brown coloration. After determination of sex (external examination), gonads were excised, staged macroscopically, and

<sup>2</sup> Lynch, T. R. 1996. Marine finfish investigation, sport fish population survey in Rhode Island marine waters: tautog studies, 1987–1993. Rhode Island Division of Fish and Wildlife performance report project: F-54-R-1, study I-I, reference document TT-396, 55 p. Rhode Island Division of Fish and Wildlife, Marine Fisheries Section, 3 Fort Wetherill Road, Jamestown, RI 02835.

<sup>3</sup> Bain, C. M., and J. A. Lucy. 1996. Virginia Game Fish Tagging Program annual report, 1995. Virginia Mar. Res. Rep. 96-2, 10 p. Virginia Marine Resources Commission, 2600 Washington Ave, Newport News, VA 23067.



**Figure 1**

Map of lower Chesapeake Bay and nearby coastal waters of Virginia. Closed circles indicate sites where tautog were collected; open circles indicate collection sites of tautog in spawning condition. CBBT = Chesapeake Bay Bridge Tunnel. CBLT = Chesapeake Bay Light Tower.

weighed to the nearest 0.01 g (GW). Maturity classification was assigned as outlined in Table 1, based on eight macroscopic stages, modified from Lowerre-Barbieri et al. (1996) for multiple spawning species. One gonad was randomly chosen by coin toss for histological processing and placed in Davidson's fixative. For females staged macroscopically as spawning females, the remaining ovary was placed in 10% neutrally buffered formalin for batch fecundity counts.

Whole unsectioned opercle bones are the accepted method to age tautog (Cooper, 1967; Simpson, 1989; Hostetter and Munroe, 1993). Opercle bones were removed and processed to examine age at maturity and age-related fecundity. Opercles were boiled for 1–3 minutes to remove flesh, scrubbed under warm flowing water, dried for two days, and read with transmitted light. Age of each fish was determined from two readings of both opercles (when possible). An annulus was defined as the transition from a translucent zone to an opaque zone. Annulus formation was previously validated by Hostetter and Munroe (1993). 1 April was used as a birth date to allow maximum growth within the biological year (April to March), and to avoid overlap with fish in the next year class.

Gonads selected for histological processing were placed in Davidson's fixative for two days before transverse sec-

tions of anterior, middle, and posterior ovarian tissue (or anterior and posterior sections of testes) were taken and placed in tissue cassettes. Variation between left and right gonads was accounted for by random selection of one gonad for fixation. Tissue samples were then rinsed overnight with flowing tap water and placed in 70% EtOH. Standard histological processing (tissue embedded in paraffin, sectioned at 5–7  $\mu\text{m}$ , and stained with Harris's hematoxylin and eosin-Y) (Luna, 1968) was performed for all samples. Male gonads were classified microscopically into two stages: sexually mature or immature. Female microscopic gonad stages were assigned based on the occurrence and relative abundance of seven oocyte developmental stages (Wallace and Selman, 1981; West, 1990; Hunter et al., 1992): primary growth, cortical alveoli, partially yolked, advanced yolked, germinal vesicle migration, germinal vesicle breakdown, and hydrated oocytes. Final oocyte maturation (FOM) comprises germinal vesicle migration, germinal vesicle breakdown, and hydrated oocyte stages (Wallace and Selman, 1981; West, 1990). Fully developed ovaries were distinguished from partially spent/redeveloping ovaries by the presence of postovulatory follicles (POFs). Microscopic gonad stages are described in "Description of microscopic gonad stages," ("Results" section), summarized

**Table 1**

Description of macroscopic and microscopic gonad stages (modified from Lowerre-Barbieri et al., 1996) for female tautog. Macroscopic criteria refer to whole fresh ovaries. Gonad stages 4, 5, and 3a comprise the inner spawning cycle. FOM = final oocyte maturation. GSI = gonadosomatic index. GVBD = germinal vesicle breakdown. POF = postovulatory follicle. MA = macrophage aggregate.

Gonad stage	Macroscopic criteria	Microscopic criteria
1 Immature	Ovaries very small, tubular in shape, white to light pink in color; no oocytes visible (mean GSI=0.50)	Oogonia and primary growth oocytes present; high proportion of connective tissue, no atresia or MAs, ovarian membrane thinner than in resting stage.
2 Developing	Ovaries small to medium, tubular shape, dark yellow to light orange in color; yolked (opaque) oocytes begin to appear (mean GSI=2.25 )	Primary growth, cortical alveoli, and some partially yolked oocytes present.
3 Fully developed	Ovaries medium to large, appear slightly grainy, pale mustard in color; yolked oocytes are abundant (mean GSI=3.25 )	Primary growth to advanced yolked oocytes present; no FOM stages, POFs, or remnant HOs.
4 Hydrated	Ovaries large to very large, pink to orange in color; firm, yolked oocytes interspersed with large transparent (hydrated) oocytes (mean GSI=11.74 )	Primary growth to germinal vesicle migration (GVM) and hydrated oocytes present, hydrated oocytes are unovulated; 1-day POFs may be present.
5 Running ripe	Ovaries large to very large; few transparent oocytes in ovarian tissue, transparent oocytes have been ovulated into expanded lumen, and are easily extruded when gonad is excised (mean GSI=10.12)	Primary growth through GVM, and ovulated hydrated oocytes and fresh POFs present; lumen usually seen as separation of ovigerous folds.
3a Partially spent/redeveloping	Ovaries somewhat flaccid, large, slightly more pink than in hydrated stage; lumen has collapsed, occasionally a few remnant hydrated oocytes extruded from excised ovary (mean GSI=8.84); similar to stage 3.	Primary growth through GVBD oocytes present, no unovulated hydrated oocytes, few remnant ovulated hydrated oocytes; lumen collapsed, POFs abundant.
6 Spent/regressing	Ovaries flaccid, small to medium, red to purple; some tissue devoid of yolked oocytes at anterior end of ovary, yolked oocytes visible but less abundant (mean GSI=1.37)	Primary growth through advanced yolked oocytes present; major atresia of all stages except primary growth oocytes.
7 Resting	Ovaries small, purple-opaque to maroon in color; few or no yolked (opaque) oocytes visible (mean GSI=1.50)	Primary growth and cortical alveoli oocytes present, occasional atretic oocytes; MAs abundant, more oogonia tissue, less connective tissue, and thicker ovarian membrane than in immature stage.

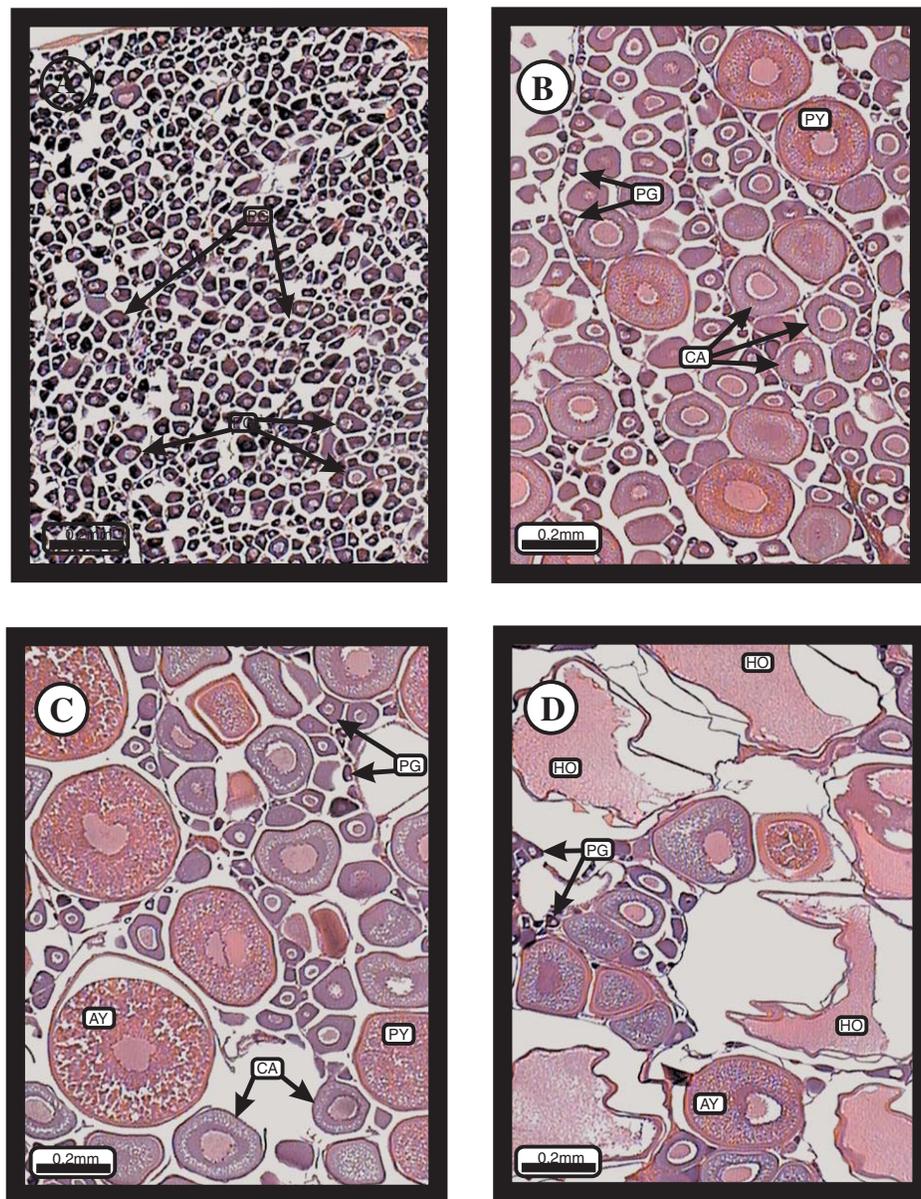
in Table 1, and shown in Figure 2, A–H. Percent agreement between macroscopic and microscopic female gonad stages was calculated to evaluate the accuracy of macroscopic staging (used in all previous studies of tautog reproductive biology). Microscopic stages were assumed to be more accurate because histologic examination provides evidence of differences in cellular development.

Chi-square analysis ( $n=489$  fish) was used to test for significant deviations from an expected 1:1 sex ratio for all fish. Deviations from a 1:1 sex ratio among 100-mm length intervals were also analyzed by chi-square to determine if size or age had a significant effect on sex ratio.

Length and age at maturity were analyzed for fish collected from April to mid-June to reduce the possibility of classifying resting, mature fish as immature. Females were considered mature if classified into microscopic stages 2–7

(Table 1). Males were considered mature if spermatocytes or spermatozoa were present in histological sections. Length at maturity was based on 110 females and 79 males (150–350 mm TL). A logistic regression curve was fitted to the data, to estimate length at 50% maturity ( $L_{50}$ ). Age at maturity was based on 135 females and 104 males (ages 1–6).

To determine the annual spawning season, a gonadosomatic index ( $GSI=(\text{gonad weight}/\text{somatic weight}) \times 100$ ) was calculated by using somatic weight ( $SW=TW-GW$ ) for each sex. A more precise estimate of tautog spawning season was determined from microscopic gonad stages. The spawning season was defined by the first and last day that female tautog were collected with ovaries staged as either hydrated, running ripe, or partially spent/redeveloping. Spawning locations were detected by the presence of hy-



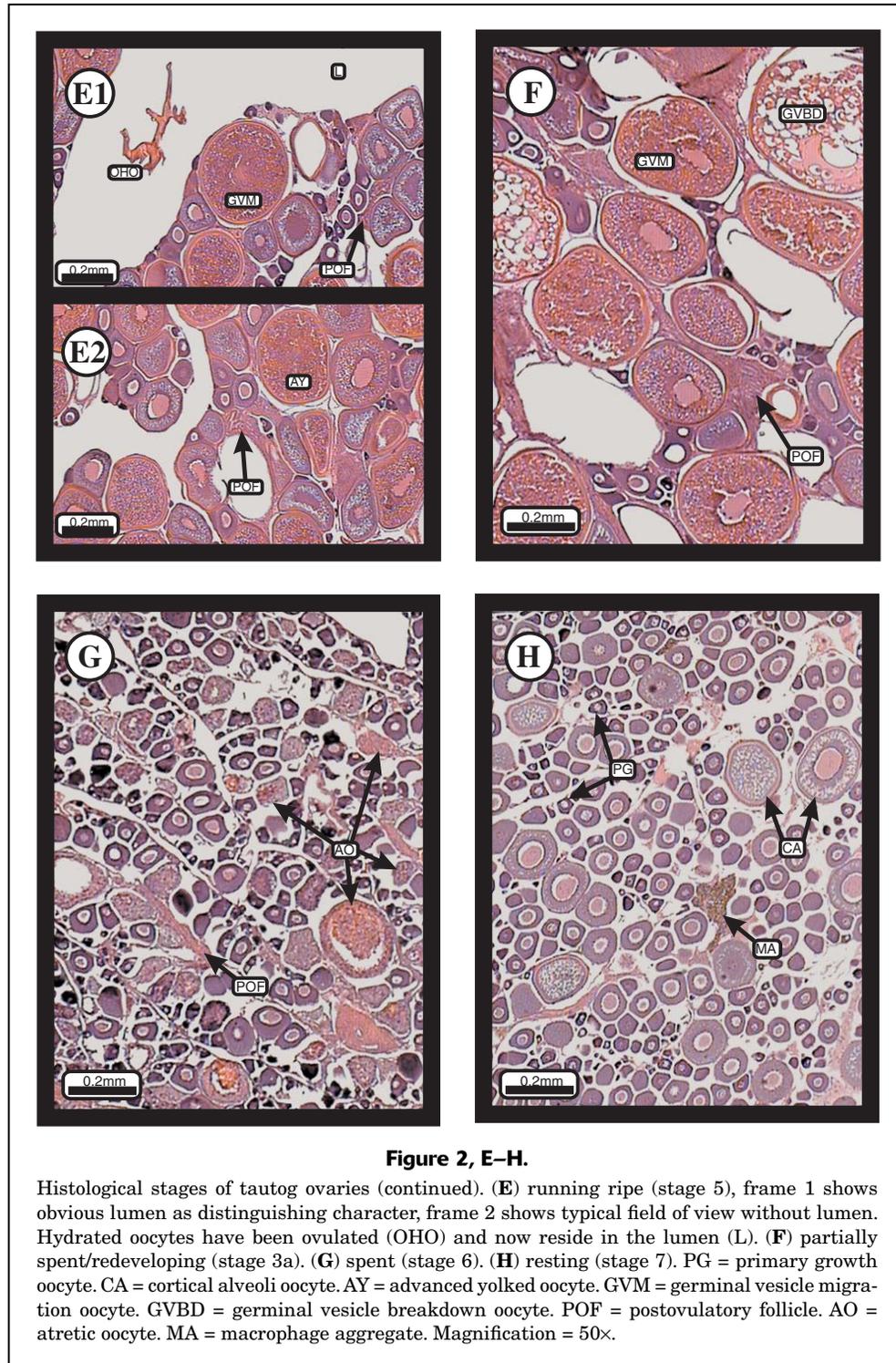
**Figure 2, A–D.**

Histologic stages of tautog ovaries. (A) immature (stage 1). (B) developing (stage 2). (C) fully developed (stage 3). (D) hydrated (stage 4). PG = primary growth oocyte. CA = cortical alveoli oocyte. PY = partially yolked oocyte. AY = advanced yolked oocyte. HO = hydrated oocytes. Magnification = 50 $\times$ .

drated and running ripe fish because those stages have high abundances of hydrated oocytes and fresh POFs, which indicate either imminent or recent spawning activity (Hunter and Macewicz, 1985).

Oocyte development patterns (synchronous, group synchronous, or asynchronous) and type of annual fecundity (indeterminate or determinate) were assessed by oocyte size-frequency distributions (Hunter and Macewicz, 1985) and histology (Hunter and Macewicz, 1985; West, 1990).

Six fish were selected for analysis of oocyte size-frequency distributions; three fish (TL=300, 400, 450 mm ( $\pm 10$  mm)) in April and another three in June, representing gonad development early and late in the spawning season. For each fish, oocytes were hydraulically separated from the ovarian membrane and each other, collected in a 0.1-mm sieve, and preserved in 2% formalin following the method of Low-erre-Barbieri and Barbieri (1993). Preserved samples were stirred to reduce bias due to differential settling of different



stage oocytes, and a 5-mL aliquot was removed and placed in a gridded petri dish. Grids were selected for counting by using a random number table, and maximum diameters of the first 500 oocytes encountered were measured to the nearest 0.001 mm with a Biosonic Optical Pattern Recognition System.<sup>®</sup> Data were grouped in 0.05-mm size

classes for presentation (0.1 mm group=0.075 to 0.124 mm oocytes).

Batch fecundity was determined gravimetrically by using a modification of the hydrated oocyte method (Hunter et al., 1985). The method calls for both ovaries to be fixed in 10% formalin, but we had a formalin wet weight for only

one ovarian lobe. Therefore, we conducted a calibration experiment to determine the percent change in ovarian weight between fresh- and formalin-fixed ovaries. On 25 April 1996, 18 female tautog were collected, fresh ovarian weight was measured to the nearest 0.01 g, and both ovaries were placed in 10% neutrally buffered formalin. Formalin-fixed wet weight was measured to the nearest 0.01 g six times over 30 days to determine when weight stabilized after fixation. Percent change in weight was calculated for each specimen, and regressed against fresh weight of the ovary, thus percent change in weight between formalin-fixed wet weight and fresh ovary weight was calculated with the negative exponential relationship:

$$\text{Percent weight change} = 21.452 e^{(-0.0163GW)} \quad [r^2=0.67];$$

where GW = fresh gonad weight.

Calibrated (formalin fixed) gonad weight (CGW) was calculated as

$$CGW = \text{percent weight change} \times GW.$$

Then, batch fecundity was estimated by using the formula

$$Y = (y/x) CGW,$$

where Y = batch fecundity;

y = number of hydrated oocytes in the tissue sample;

x = formalin wet weight of tissue sample; and

CGW = calibrated formalin-fixed wet weight of ovaries.

Assumptions of the hydrated oocyte method which must be met include 1) all eggs in the most advanced mode are spawned; 2) fecundity is directly proportional to ovary weight; and 3) no bias exists in the estimation of egg abundance within the most advanced mode, in the selection of mature females for analysis, or in the position within and between ovaries from which subsamples were taken (Hunter and Goldberg, 1980; Hunter et al., 1985). The use of hydrated oocytes, which are much larger than the next largest cell size class and are formed only when spawning is imminent, supported acceptance of these assumptions. Following the methods of Hunter et al. (1985), we selected ovaries from 29 females for batch fecundity analysis. These were the only females that had stage-4 (hydrated, Table 1) ovaries without postovulatory follicles as confirmed through histological analysis. If postovulatory follicles were found in histological sections, then that fish was excluded from fecundity analysis.

To test for differential oocyte development between anterior, middle, and posterior sections of ovarian tissue, point counting analyses (Weibel et al., 1966) were performed on histological sections to determine the relative volume of seven cell types and POFs in the ovary. The relative volume of each cell type was calculated by using the number of points within a grid (121 points/grid) overlying each cell type:

$$V_v = P_n / P_{tot},$$

where  $V_v$  = relative volume of one cell type;

$P_n$  = number of points overlying a specific cell type;  
and

$P_{tot}$  = number of points in grid.

To ensure that fields of view were chosen randomly, each ovarian section was divided into 5×5 mm areas with an overlay grid. Three areas per section were chosen with a random number table to ensure that counting fields of view did not overlap. Within each 5×5 mm area, point counts were made through a gridded reticule (121 points) at 4× magnification. Average relative volume of each cell class was calculated from the three areas as  $P_n/363$ , and compared between anterior, middle, and posterior ovarian sections with multiple analysis of variance (MANOVA) (Minitab, 1995). Response variables (8) were the average relative volume of each cell class. Differences between fish (10) were removed by blocking on fish. After no positional effects were detected (Wilk's test value 0.25,  $F=1.35$ ,  $df=16,22$ ,  $P=0.25$ ), it was concluded that oocyte development was evenly distributed throughout the ovaries of tautog. Blocking by fish proved beneficial and effective in removing any artifact caused by differences in kill time between fish, and in increasing the quality of the test by increasing sample size. Nonsignificant positional effects in ovarian development allowed estimation of batch fecundity from only the middle ovarian section. All hydrated oocytes were counted from three subsamples of approximately 0.3 g from the middle of the formalin-fixed ovary.

Simple linear regressions were used to describe relationships between batch fecundity and TL, TW, and age. Relative fecundity was calculated as batch fecundity divided by GW, and regressed against TL, TW, and age.

Diel spawning periodicity estimates for tautog at the mouth of the Chesapeake Bay indicated that spawning occurs during daylight hours but that spawning windows shift with ebb tidal currents (White, unpubl. data). To estimate spawning frequency by the hydrated oocyte method (DeMartini and Fountain, 1981; Hunter and Macewicz, 1985), samples with known kill times must be collected just prior to, and during, the spawning window. Most samples were collected at dockside; thus kill time for individual fish was unknown, and the hydrated oocyte method could not be performed. Therefore, spawning frequency was estimated by the POF method (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985) by using descriptions of fresh (day 0, 0–12 h) and degenerating (day 1, 12–24 h) POFs of tautog (White, unpubl. data). Fresh POFs in tautog ovaries can be identified as a clearly defined, loosely folded ribbons of thecal and granulosa cells that contain visible lumina, similar to "0 day" POFs in anchovies (Hunter and Macewicz, 1985). One-day-old tautog POFs have deteriorated such that individual cell walls are no longer apparent in thecal and granulosa cells, and the structure appears less organized and has a small or indistinguishable lumen similar to that of 24–48 h anchovy POFs (Hunter and Macewicz, 1985). A full description of POF degeneration in tautog ovaries is presented elsewhere (White, unpubl. manscr.).

Annual fecundity was estimated as the number of spawnings per female multiplied by batch fecundity for

**Table 2**

Percent agreement between microscopic and macroscopic ovarian stages assigned to tautog ( $n=484$ ) captured from June 1994 through September 1995. See Table 1 for gonad stage descriptions. Data are expressed as number of ovaries staged.

Microscopic stage	Macroscopic gonad stage								
	1	2	3	4	5	3a	6	7	
1	34	—	—	—	—	—	3	—	
2	3	15	—	—	—	—	—	40	
3	3	18	11	3	—	2	—	5	
4	—	—	—	31	1	—	—	—	
5	—	—	1	38	8	—	—	—	
3a	1	—	4	55	3	11	1	—	
6	1	—	—	—	—	1	6	—	
7	12	3	—	—	—	—	38	132	
Agreement	63%	42%	69%	24%	67%	79%	13%	75%	

each fish. Number of spawnings per female was calculated by dividing the number of days in the spawning season by estimated annual spawning frequency. The relationship between mean annual fecundity per 50-mm length interval and total length was analyzed with both linear and exponential regression.

## Results

### Description of microscopic gonad stages

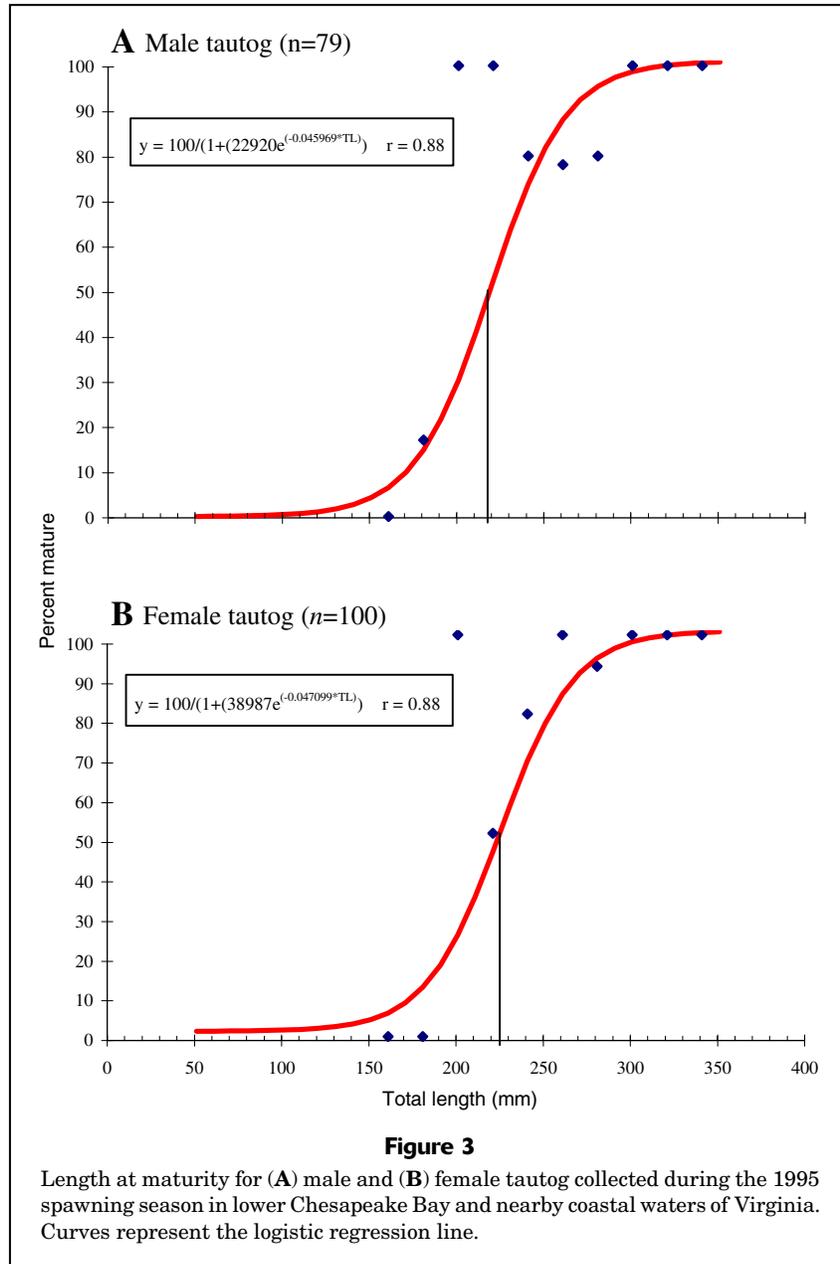
Tautog ovarian development was described by eight microscopic gonad stages (Table 1) characteristic of multiple spawning species. Each stage can be differentiated by a unique suite of histological characteristics. Immature ovaries (Fig. 2A) are characterized by the presence of only oogonia and primary growth oocytes within a thin ovarian membrane and a relatively high volume of connective tissue. Developing stage ovaries (Fig. 2B) are characterized by the presence of primary growth, cortical alveoli, and partially yolked oocytes. The fully developed ovary (Fig. 2C) is characterized by the presence of primary growth to advanced yolked oocytes and the absence of oocytes in final oocyte maturation (FOM) classes, POFs, or remnant HOs. Hydrated ovaries (Fig. 2D) are distinguished by the prominence of hydrated oocytes still inside the ovarian follicles and may also contain degenerating POFs from an earlier spawning, but they noticeably lack oocytes in the germinal vesicle breakdown state (GVBD). The running ripe stage (Fig. 2E) is classified by the presence of an expanded ovarian lumen, ovulated hydrated oocytes free in the lumen (although hydrated oocytes are frequently washed out of the sample during the staining procedure), a large number of fresh POFs, and germinal vesicle migration (GVM) oocytes that tend to be the most advanced stage present within ovigerous folds. Partially spent/redeveloping ovaries (Fig. 2F) are classified by the lack of an ovarian lumen and presence of occasional remnant hydrated oocytes, primary

growth to GVBD oocytes, and an abundance of POFs. The spent stage (Fig. 2G) is characterized by resorption of yolked oocytes (atresia), and sometimes the presence of macrophage aggregates (MAs), which are groups of cells containing the pigments lipofuscin, ceroid, and melanin (Wolke, 1992). These cells appear to be a collection of scavenging cells that remove cellular debris and foreign substances by phagocytosis when stimulated by excessive degenerating tissue (Wolke, 1992). In tautog ovaries, MAs are assumed to be associated with the resorption of yolked oocytes after the spawning season. Resting stage ovaries (Fig. 2H) contain primary growth and cortical alveoli oocytes, and atresia may be present. Resting ovaries can be distinguished from immature stage ovaries by a thickened ovarian membrane, relatively more oogonia than connective tissue and the presence of MAs.

The reliability of macroscopic staging to predict actual reproductive stage as detected by microscopic analysis was examined for 484 females. We considered any level of agreement above 80% to be acceptable. The ability of macroscopic staging to predict actual microscopic stage varied considerably, from 13% to 79% agreement for individual stages (Table 2), indicating that macroscopic staging was generally unreliable for estimating actual reproductive stage for many ovarian stages. Percent agreement between macroscopic and microscopic staging was only 51% overall. The best agreement was for the fully developed, partially spent/redeveloping, and resting ovarian stages (agreement 69%, 79%, 75%, respectively). Intermediate values were obtained for immature, and running ripe stages, (agreement 63% and 67%, respectively). The poorest agreement occurred in assigning developing and spent stages (42%, 13%, respectively).

### Sex ratios

Of the 938 tautog sexed, 522 (56%) were females and 416 were males. Overall, sex ratios varied significantly from an expected 1:1 ratio, with more females than males (1.25:1,  $\chi^2=11.98$ ,  $P<0.01$ ). At lengths  $\leq 400$  mm, females were



more abundant than males, whereas the sex ratios were not significantly different from 1:1 at fish lengths >400 mm (Table 3).

### Length and age at maturity

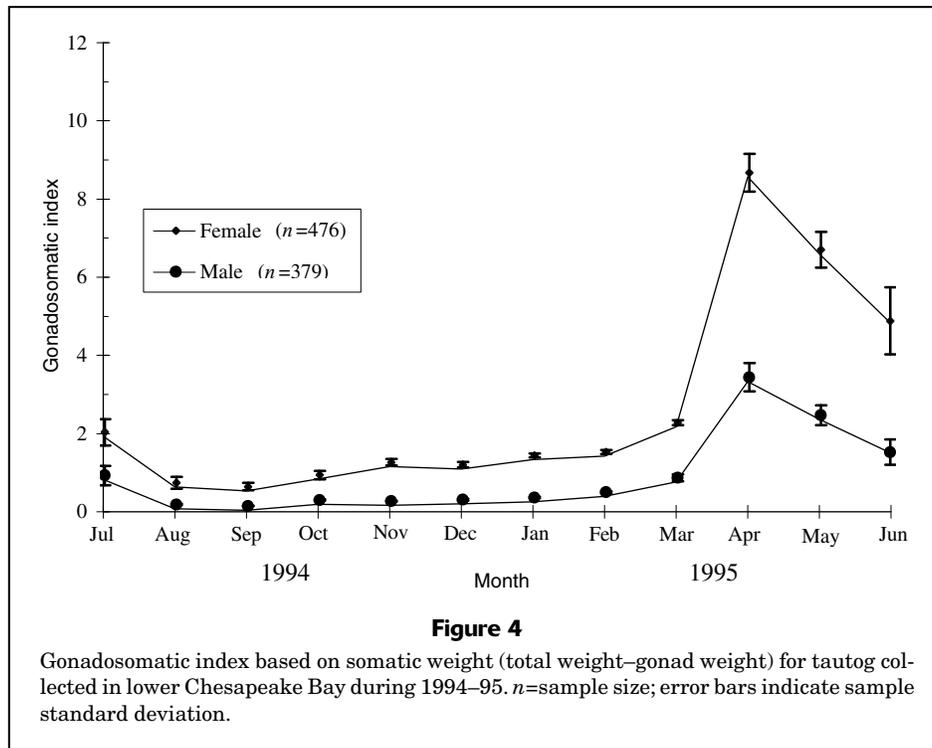
Tautog length at 50% maturity ( $L_{50}$ ) was 218 mm for males ( $n=79$ ) and 224 mm for females ( $n=110$ , Fig. 3). All males and females were mature at 300 mm. No females less than 227 mm had hydrated oocytes or POFs that would have indicated spawning activity.

Age at first maturity was defined as the age at which at least 50% of the fish are mature. Mature gonads were present in 0% of males at age 1, 38% at age 2, and 93% at

age 3. Zero percent of females were mature at age 2, 78% at age 3, and >97% at age 4.

### Spawning season and location

GSI values indicated that tautog spawned from April through June and that peak values occurred in April for the 1995 spawning season (Fig. 4). The 1995 spawning season was more precisely defined as 7 April–15 June based on the presence of females in spawning condition (i.e. staged histologically as hydrated, running ripe). At the beginning of the spawning season, females progressed into spawning condition over approximately two weeks. The end of the spawning season was determined conservatively, based



**Figure 4**

Gonadosomatic index based on somatic weight (total weight–gonad weight) for tautog collected in lower Chesapeake Bay during 1994–95. *n*=sample size; error bars indicate sample standard deviation.

**Table 3**

Sex ratio of tautog by 100-mm length intervals and chi-square values of tests for a 1:1 ratio. \*Significance at  $P=0.05$ . \*\*Significance at  $P=0.01$ . NS = nonsignificant.

Total length (mm)	No. of males	No. of females	No. expected (50%)	% Females	Chi-square
101–00	12	24	18	67	4.00*
201–300	57	88	73	61	6.63*
301–400	147	216	182	60	13.12**
401–00	140	125	133	47	0.85 NS
501–600	38	53	46	58	2.47 NS
601–700	11	14	13	56	0.36 NS
Total	405	520			

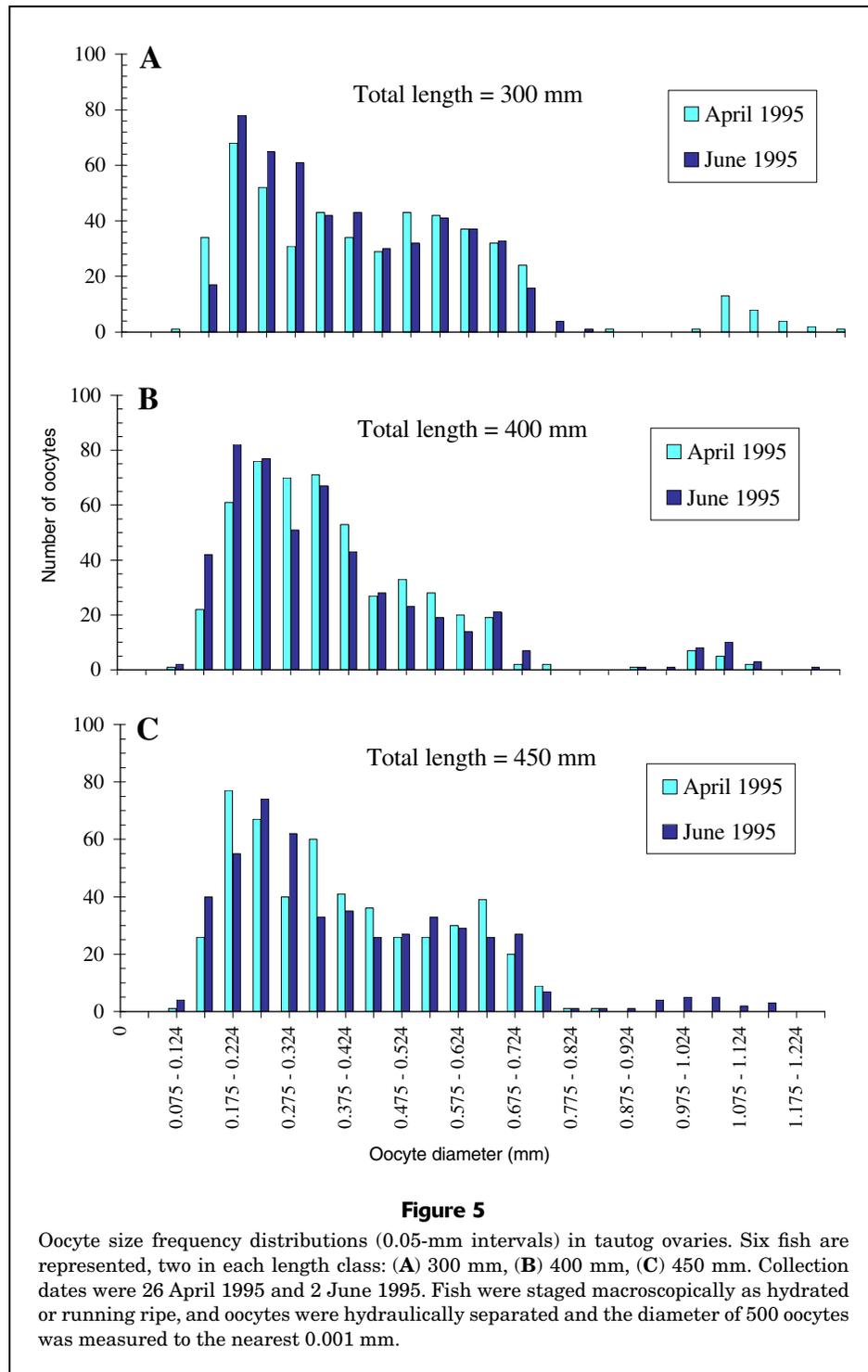
on the last day female tautog were collected in spawning condition (15 June) instead of the first collection date of a spent female (27 June).

Tautog were collected (Fig. 1) in spawning condition within the Chesapeake Bay (York River, Buckroe Beach), at the mouth of the Chesapeake Bay (Chesapeake Bay Bridge Tunnel, Cape Henry wrecks, Anglo-African wreck), and at offshore locations (Chesapeake Bay Light Tower, one site 45 km offshore) and there was no apparent trend in spawning season by location.

#### Ovarian developmental pattern and type of fecundity

Ovarian stages defined for tautog (Table 1) are typical of multiple spawning species. Tautog hydrate and spawn

only a small fraction of the yolked oocytes in the ovary for any one spawning event. Macroscopically, hydrated ovaries appear speckled because of the intermittent occurrence of large, clear hydrated oocytes among the dominant numbers of opaque, yolked oocytes. Further, the lumen of running ripe ovaries was full of ovulated hydrated oocytes, yet there was still a large volume of tissue with maturing yolked oocytes. The occurrence of spawning stage ovaries over a protracted period also suggested a multiple spawning pattern. Tautog were collected in spawning condition (hydrated and running ripe stages) and the partially spent/redeveloping stage throughout the April–June spawning period, but no spent or resting fish were collected until late June, suggesting that individual females were spawning repeatedly during the spawning season.



**Figure 5**

Oocyte size frequency distributions (0.05-mm intervals) in tautog ovaries. Six fish are represented, two in each length class: (A) 300 mm, (B) 400 mm, (C) 450 mm. Collection dates were 26 April 1995 and 2 June 1995. Fish were staged macroscopically as hydrated or running ripe, and oocytes were hydraulically separated and the diameter of 500 oocytes was measured to the nearest 0.001 mm.

Oocyte size-frequency distributions measured at the beginning and end of the spawning season were also used to classify tautog annual fecundity as determinate or indeterminate. Primary growth and cortical alveoli oocytes were continuously yolked, matured, and spawned throughout the spawning season, evidenced by 1) lack of hiatus between advanced yolked oocytes and less mature oocytes, and 2) abundance

of yolked oocytes (size range 0.30–0.55 mm) not decreasing over the spawning season (Fig. 5). This type of development defines tautog as having indeterminate fecundity.

Two patterns of oocyte development are common among multiple spawning fishes: group synchronous and asynchronous oocyte development. Tautog oocyte size-frequency distributions (Fig. 5) show no distinct gaps in develop-

ment, or modes of oocytes, except for hydrated oocytes (0.95 to 1.25 mm)—a finding that indicates asynchronous oocyte development. The presence of primary growth through advanced yolked oocytes, as well as oocytes in FOM and POFs in histologic sections of fully developed and partially spent ovaries (Fig. 2, C and F), is evidence that tautog exhibit a multiple spawning pattern.

### Ovarian cycle

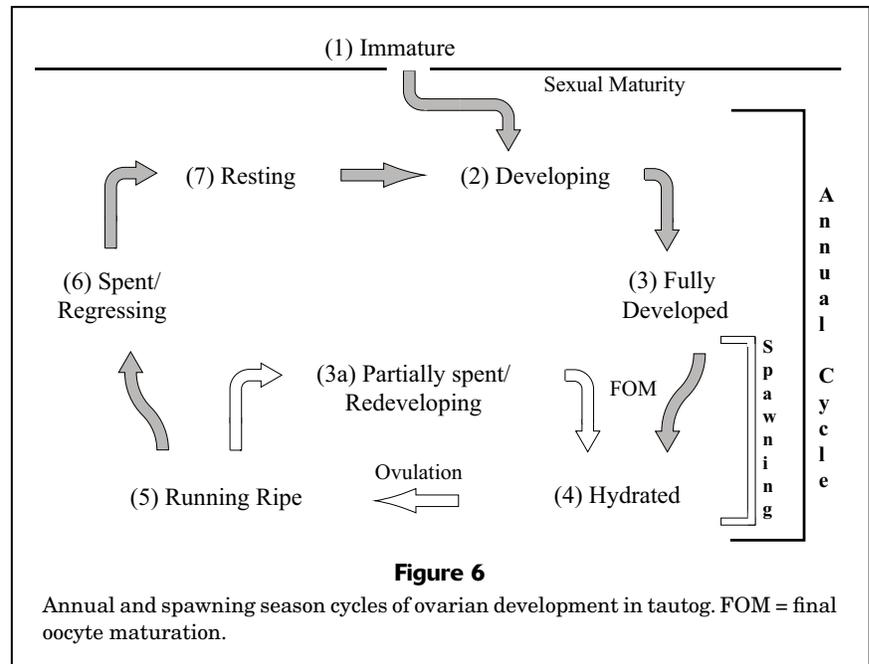
Egg maturation in tautog is a complex process comprising both seasonal and annual components. This complex pattern of multiple spawning exhibited by an inner spawning cycle (made up of hydration, ovulation, spawning, and redevelopment) within the annual ovarian developmental cycle, is summarized for tautog in Virginia in Figure 6. In the spring, fully developed ovaries contain primary growth to advanced yolked oocytes, but lack POFs. Fish enter the spawning cycle by hydration and ovulation of the first batch of oocytes. After the first spawning event, partially spent/redeveloping ovaries contain fresh POFs (indicating recent spawning during the previous 24 hours) and another batch of oocytes in FOM in preparation for the next spawning event. Thereafter, the inner spawning cycle is repeated throughout the spawning season. Histological examination of hydrated ovaries during the spawning season revealed the co-occurrence of hydrated oocytes (indicating an imminent spawn) and degenerating POFs, suggesting that some tautog are capable of repeating the inner spawning cycle on a daily basis. At the end of the spawning season, ovaries progress to the spent-regressing stage, where, through the process of oocyte atresia, the remaining stock of yolked oocytes are resorbed before the ovary enters the resting stage.

### Batch fecundity

Batch fecundity was determined for 29 female tautog ranging in total length from 260 to 520 mm, total weight 475 to 3,500 g, and ages 3–9 (Fig. 7). Although there was a high degree of variation in batch fecundity between individual fish, significant relationships were found between batch fecundity and fish length, weight, and age. Batch fecundity was more closely related to total length and total weight than to age. Batch fecundity (BF) increased significantly with total length (ANOVA,  $n=29$ ,  $F=16.92$ ,  $P<0.0005$ , power=0.97), following the regression equation (Fig. 7A)

$$BF = 425.76(TL) - 84,534 \quad [r^2=0.39].$$

Batch fecundity increased significantly with total weight (ANOVA,  $n=29$ ,  $F=16.80$ ,  $P<0.0005$ , power=0.99), the regression equation being (Fig. 7B)



$$BF = 56,066 \ln(TW) - 322,091 \quad [r^2=0.50].$$

Batch fecundity also increased significantly with age (ANOVA,  $n=29$ ,  $F=10.22$ ,  $P<0.004$ , power=0.88), following the regression equation (Fig. 7C)

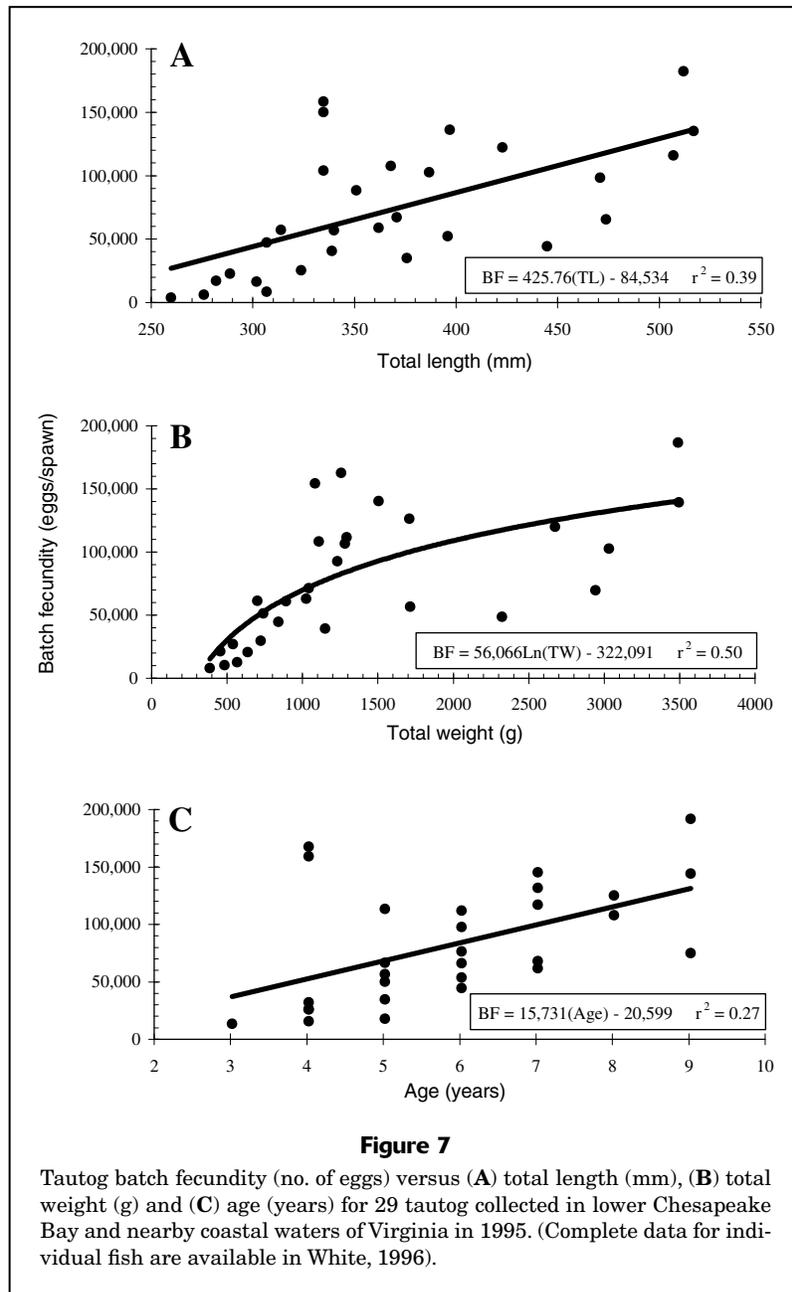
$$BF = 15,731(AGE) - 20,599 \quad [r^2=0.27].$$

Tautog relative fecundity (BF/GW) did not increase significantly with fish length (ANOVA,  $n=29$ ,  $F=1.98$ ,  $P=0.17$ ) or age (ANOVA,  $n=29$ ,  $F=1.72$ ,  $P=0.20$ ), but there was a significant increase in relative fecundity with total fish weight (ANOVA,  $n=29$ ,  $F=4.46$ ,  $P=0.044$ ).

### Spawning frequency

Histological examination of 169 tautog collected from 7 April 1995 to 15 June 1995 revealed some variation in the abundance of three reproductive states that were indicative of imminent or recent spawning. Forty-four percent of female tautog had HOs, 32% had fresh POFs without any HOs, and 84% of females collected had 1-day-old POFs (Table 4). Tautog spawning frequency was calculated as 1.2 days based on the percentage of fish with 1-day-old POFs following the methods of Hunter and Goldberg (1980). Number of spawnings per female tautog in 1995 was calculated as the spawning season (70 days) divided by spawning frequency (1.2 days/spawning), yielding 58 spawnings per female.

Individual tautog in natural habitats were capable of spawning daily after entering the spawning season. Evidence of daily spawning was provided by the rapid ovarian development observed in histological sections: 1) 70 fish with HOs and degenerating POFs; 2) 90 fish with both fresh and degenerating POFs; and 3) partially spent/



redeveloping females with both GVBD oocytes and fresh POFs (Fig. 2F).

### Potential annual fecundity

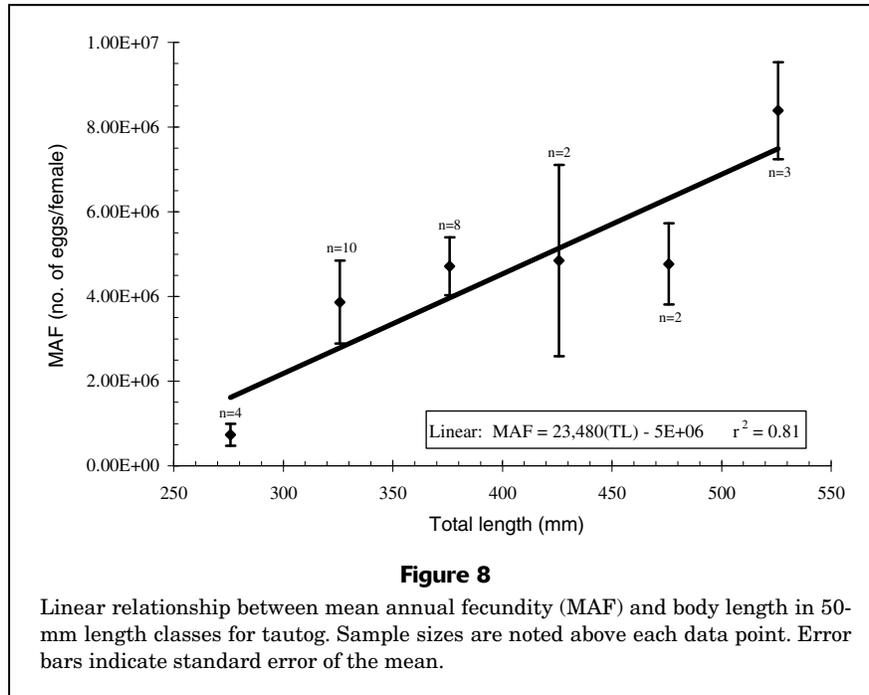
Annual fecundity was calculated as 58 spawnings/female multiplied by batch fecundity. Annual fecundity varied from 160,000 eggs (259 mm, age-3 fish), to 10,510,000 eggs (511 mm, age-9 fish). Mean annual fecundity increased significantly (ANOVA,  $n=5$ ,  $F=16.69$ ,  $P=0.015$ ) with fish size. A linear regression of mean annual fecundity on fish length (50 mm size classes, Fig. 8), was described by the following relationship:

$$\text{Mean } AF = 23,480(TL) - (5 \times 10^6) \quad [r^2 = 0.81].$$

### Discussion

#### Macroscopic and microscopic gonad staging

Macroscopic ovarian staging of multiple spawning fishes can be difficult because subtle differences at the cellular level may not be detectable macroscopically (Parrish et al., 1986). However, macroscopic analysis does provide a rapid estimate of maturity and results in a general description of spawning seasons at a reduced cost compared to

**Table 4**

Reproductive state of female tautog collected during 1995 spawning season. HO = hydrated oocyte. POF = postovulatory follicle.

Date (1995)	No. with HOs	No. with fresh POFs, no HOs	No. with 1-day POFs	No. mature, not spawning	Total no. of mature females
7 April	11	0	11	1	13
8 April	11	4	12	13	29
15 April	1	0	1	0	1
22 April	9	2	10	4	14
26 April	12	23	47	1	49
9 May	15	16	33	2	35
24 May	0	0	1	0	1
31 May	5	6	11	0	11
1 June	10	33	14	0	14
2 June	1	0	1	0	1
15 June	0	0	1	0	1
Total	75	54	142	21	169
Total %	44.4	32.0	84.0	—	—

time-consuming histological methods. West (1990) noted that there have been few attempts to assess the accuracy of macroscopic gonad staging with histological analysis. Most scientists attempting to assess reproductive stage of female tautog will most likely use macroscopic criteria. Given that all eight microscopic stages cannot be identified in a macroscopic context, a revised macroscopic gonad staging was developed (Table 5) with validated agreement against microscopic analysis. The validated stages (Table 5) generally agree with previous studies of tautog reproductive biology (Chenoweth, 1963; Stolgitis, 1970; Hostetter

and Munroe, 1993). However, even with this revised, simplified staging criteria, we caution others that agreement between the new criteria and microscopic staging is still low for some ovarian stages, rendering this method less reliable than microscopic analysis.

Despite these limitations, macroscopic staging errors were usually off by only one developmental stage (Table 2). Errors in macroscopic staging were most likely due to the rapid development of ovarian tissue required to sustain daily spawning events. The low percent agreement (51% overall) between macroscopic and microscopic classifications of tautog ovar-

**Table 5**

Revised macroscopic gonad stages for future research on tautog. These revised macroscopic stages are based on the gonad stages seen in Table 1.

Gonad stage (Table 1)	Revised gonad stage	Macroscopic appearance
Immature	Immature	Ovaries very small, tubular in shape, white to light pink in color, no oocytes visible. (Same as "immature stage" from Table 1.)
Developing and Fully developed	Developing	Ovaries medium to large with slightly grainy appearance, pale mustard in color, yolked (opaque) oocytes present, no hydrated (transparent) oocytes visible through ovarian membrane. (This stage is a combination of "developing" and "fully developed" stages from Table 1.)
Hydrated and Partially spent/redeveloping	Spawning	Ovaries large to very large, pink to orange in color, may be dotted with transparent oocytes, yolked oocytes interspersed with large transparent (hydrated) oocytes, occasionally a few remnant hydrated oocytes. (This stage is a combination of "hydrated" and "partially spent/redeveloping" stages from Table 1.)
Running ripe	Running ripe	Ovaries large to very large, pink to orange in color, hydrated oocytes have been ovulated, expand lumen of ovary and are easily extruded from excised ovary; few hydrated oocytes in ovarian tissue. (Same as "running ripe" stage from Table 1.)
Spent and Resting	Spent	Ovaries flaccid, small to medium, red to purple in color, few yolked (opaque) oocytes visible, some or all of ovary having no oocytes visible. (This stage is a combination of "spent" and "resting" stages from Table 1.)

ian stages is similar to that of studies on *Lutjanus vittus*, which found the accuracy of macroscopic staging for ripe gonads to be only 61% (CSIRO data, cited in West, 1990).

Macroscopic staging of tautog ovaries functioned to describe the annual gonad cycle, yet it did not separate the fully developed (stage-3) and partially spent (stage-3a) ovaries. Macroscopic analysis does not yield proof of POFs, atretic oocytes, and macrophage aggregates—cellular structures that help distinguish fully developed, partially spent/redeveloping, spent, and resting females. Thus, macroscopic analysis could not provide evidence of multiple spawning in tautog. Histological techniques used in this study were necessary to accurately describe the annual cycle and the inner (multiple spawning) spawning cycle of ovarian development for tautog. Histological staging also permitted identification of fully hydrated ovaries that could then be used for batch fecundity estimation. Further, histology slides were used for point-counting analyses to test for positional differences in development between anterior, middle, and posterior regions within the ovary.

### Sex ratios

Sex ratios vary greatly among published studies on tautog life history. This variability may be due to true differences in the composition of local populations, or it may be an artifact of sampling strategies rooted in collection seasons or gear biases. In our study, sex ratios were skewed towards females for fish under 400 mm and did not differ significantly from a 1:1 ratio for tautog greater than 400 mm. Collections were primarily made by hook-and-line angling

throughout the year, although sample sizes were low between July and September. Hostetter and Munroe (1993) found no significant difference in sex ratios for fish less than 200 mm, but significantly more males than females for fish between 201–500 mm in Virginia. Their sampling occurred over a period of seven years, and fish were collected primarily with fish traps and hook and line. Eklund and Targett (1990) found a female-to-male sex ratio of 0.86:1 in the trap fishery between April and December 1987. Chenoweth (1963) collected more females than males with an otter trawl at three stations in Narragansett Bay, RI, between May and September 1961. Factors that affect sex ratios of tautog from fishery-dependent collections are still unknown and provide an opportunity for further research into the sex ratios and reproductive success of this species.

### Length and age at maturity

Published reports of tautog length and age at maturity (from studies with macroscopic techniques and GSI) are similar for the entire species range. Estimates of tautog lengths and ages at maturity in our study were similar to results reported by Hostetter and Munroe (1993) for tautog captured off Virginia. Hostetter and Munroe (1993) reported that both sexes show evidence of gonadal maturation at age 3 in Virginia. Likewise, age and length at maturity for tautog collected in Massachusetts (Stolgitis, 1970) are also similar; 40% of age-2 (149–175 mm) males and 87% of age-3 (171–239 mm) males were mature, and females attained 71% maturity at age 3 (187–206 mm) and 100% maturity at age 4. In Rhode Island, Cooper (1966)

found that males matured at 200 mm (age 3) and females at 190 mm (age 3).

For a small number of fish sampled in northern areas, Hostetter and Munroe (1993) suggested that precocious development may be occurring in tautog as a response to fishing pressure. The smallest females collected in spawning condition have been 227 mm in Virginia (this study), 261 mm in Massachusetts (Stolgitis, 1970), 216 mm (Chenoweth, 1963) and 180 mm (Hostetter and Munroe, 1993), in Rhode Island. A definitive answer on precocious development is not possible at this time because data on small fish are limited in all studies. Detailed histological analysis should be performed on tautog from 100 to 250 mm TL to discern maturity schedules for specimens in this size range.

### Spawning season and location

Tautog spawn over at least a two-month period throughout the species range, and the initiation of spawning activity occurs later in the spring to early summer in more northern regions (Chenoweth, 1963; Stolgitis, 1970; Briggs, 1977; Hostetter and Munroe, 1993). In our study, spawning occurred from 7 April through 15 June 1995 (70 days), similar to the time interval reported by Hostetter and Munroe (1993) for tautog in Virginia. In New York waters, tautog have been recorded to spawn for four months (early May through early September; Austin, 1973). In Rhode Island, tautog spawn from early June through late July (Chenoweth, 1963), and spawning seasons as long as three months (mid-May through early August) have been reported for fish in Massachusetts (Stolgitis, 1970). Abundance of tautog eggs in plankton collections also shows that the spawning season occurs progressively later in more northern regions (Sogard et al., 1992). The earlier spawning season in Virginia has been attributed to differences in water temperature (Hostetter and Munroe, 1993). Increasing water temperature during springtime is a major cue to initiate spawning, but termination of spawning activity has not been related to environmental cues. However, Austin (1973) suggested that the effective spawning season may be shorter than the season of egg release for this species, based on a decrease in larval abundance as water temperature exceeded 21.0°C in Long Island Sound.

Tautog were collected in spawning condition within the Chesapeake Bay and as far as 56 km offshore in this study and by Hostetter and Munroe (1993). Eklund and Targett (1990) sampled tautog in spawning condition 22–37 km off the coast of Maryland and Virginia. Field observations of daily movements showed that tautog exhibit fidelity to a home site which they return to each night (Olla et al., 1974, 1975), suggesting that tautog remain at one location throughout the spawning season. Arendt et al. (2001b) found that tautog tended to move between sites during the winter and early spring as the spawning season began and remained at a single site throughout the summer. Tagging studies indicate that discrete spawning groups exist at sites in Narragansett Bay (Cooper, 1966); however, movements between sites were not quantified. Sufficient data are not available to determine if tautog exhibit spawning-site fidelity throughout the spawning sea-

son, or if multiple spawning sites are used within general inshore and offshore classifications. It is generally believed that most tautog migrate inshore in the spring to spawn (Cooper, 1966) and some portion of the population remains offshore year round (Eklund and Targett, 1990; Hostetter and Munroe, 1993). Although we have documented adult spawning activity at both inshore and offshore locations, spawning success in these areas, as well as larval drift and recruitment patterns, are unknown at this time.

### Spawning pattern and type of fecundity

Histological analysis of ovarian tissue supports the classification of tautog as a multiple spawning species with a complex reproductive cycle. The complexity of ovarian maturation (Fig. 6) in this species has not been recognized in previous studies on its reproductive biology. The typical cycle of female development for multiple spawning species is defined by eight microscopic gonad stages (Lowerre-Barbieri et al., 1996) which include an annual cycle (5 stages) and an inner spawning cycle (3 stages). Although tautog have been observed to be multiple spawners in laboratory aquaria (Olla and Samet, 1977; Olla et al., 1977), we define oocyte development and type of fecundity using recently improved methods (Lowerre-Barbieri and Barbieri, 1993) and histological techniques on fish taken from natural environments; therefore, they are directly comparable to other studies of reproductive biology without artifacts associated with aquarium conditions. Analysis of oocyte size-frequency distributions and histological sections of ovarian tissue indicates that tautog have asynchronous oocyte development and indeterminate annual fecundity. Therefore, counting the number of oocytes in the ovary prior to the spawning season is inadequate to measure potential annual fecundity because new batches of eggs continuously mature from primary growth oocytes through hydrated oocytes and are released during spawning events (Hunter et al., 1985). Chenoweth (1963) analyzed oocyte size-frequency distributions of three tautog collected over the course of the spawning season in Rhode Island and noted that the number of mature yolked oocytes did not decline through the spawning season. He suggested that not all yolked oocytes were spawned and that some portion remained in the ovary and were resorbed after the spawning season. This observation is consistent with asynchronous oocyte development.

### Fecundity

This is the first study on tautog reproduction for which potential annual fecundity has been estimated by multiplying batch fecundity by spawning frequency. Batch fecundity was more closely related to total length and total weight than to age. This result makes sense when one considers the extreme variability in length at age exhibited by tautog (Cooper, 1967; Hostetter and Munroe, 1993). Batch fecundity ranged from 2800 eggs to 181,200 eggs in 29 females age 3–9 (Fig. 7). The oldest tautogs collected in this study were a 31-year-old male and a 17-year-old female. After reaching maturity, individual females may spawn up to 58 times a year for at least 14 years.

**Table 6**

Comparison of batch fecundity estimates for tautog from three different studies. Mean batch fecundity was calculated for two age groups, 4–6 and 7–9, because all females were mature by age 4 and over 90% of all tautog sampled in White (1996) were less than 10 years old.

Study	Mean batch fecundity $\pm$ SEM			
	Age 4–6	<i>n</i>	Age 7–9	<i>n</i>
Chenoweth (1963) <sup>1</sup> Rhode Island	49,967 $\pm$ 1032	29	103,214 $\pm$ 4005	14
Stolgitis (1970) <sup>1</sup> Massachusetts	46,833 $\pm$ 4500	6	117,478 $\pm$ 2488	23
White (1996) <sup>1</sup> Virginia	54,243 $\pm$ 2472	18	106,256 $\pm$ 3837	10

<sup>1</sup> Mean batch fecundity for age groups 4–6 and 7–9 was calculated from the raw data presented in the reference.

Previous estimates of tautog fecundity by Chenoweth (1963) and Stolgitis (1970) were not annual fecundity estimates (Table 6). They counted mature, transparent eggs in the ovary, currently referred to as hydrated oocytes, but they did not distinguish tautog as having indeterminate annual fecundity and had no measure of spawning frequency. By counting only the hydrated oocytes, these investigators actually estimated batch fecundity. However, it is interesting to note the similarity of batch fecundity estimates (Table 6) over the period of 30 years between studies and wide geographic areas, i.e. from Chesapeake Bay to Narragansett Bay (550 km).

Spawning frequency had not been previously calculated for tautog with methods developed by Hunter and Macewicz (1985). Although the hydrated oocyte method is less expensive, it requires collection of females just prior to spawning. With the hook-and-line collection method, it is difficult to collect sufficient samples in a short period of time. Therefore spawning frequency was estimated in our study by using the POF method to read histologic preparations of ovarian tissue. A female spawning every 1.2 days over the 70-day spawning window would spawn on an estimated 58 days in 1995. Under artificial conditions, Olla et al. (1977) observed tautog spawning on 68–96 consecutive days in laboratory aquaria. Therefore, an estimate of 58 spawning days in natural habitats is not unrealistic. Chenoweth (1963) raised, but could not answer, the question of whether individual tautog spawn throughout the entire spawning season. The spawning-frequency estimate presented here, and observations of tautog spawning on 68–96 consecutive days in laboratory aquaria (Olla et al., 1977), indicate that tautog are capable of spawning daily throughout the spawning season in natural habitats under appropriate environmental conditions (temperature, day length, etc.).

Estimates of potential annual fecundity for Virginia tautog age 3–9 ranged from 160,000 to 10,510,000 eggs. However, net annual fecundity may be lower because of remnant hydrated oocytes, atresia, nutritional status of adult females, or environmental conditions (McEvoy and McEvoy, 1992). Based on our samples (females age 3–9), a linear regression provided the most predictive power ( $r^2=0.81$ ) to estimate mean annual fecundity (Fig. 8). Although female tautog live to be 17+ years old, it is

estimated that 90% of tautog in Virginia waters are age 10 or younger (Hostetter and Munroe, 1993). Therefore, as the data range in this study is similar to the age structure of the resource, we suggest that the regression equation ( $Mean AF=23,480(TL) - (5 \times 10^6)$ ) is the most appropriate formula for use by fishery managers for estimating annual fecundity of tautog in the southern portion of its range.

We have made a theoretical comparison of potential annual fecundity for tautog (ages 4–9) between the northern and southern areas by combining results from several studies in the northern range of tautog. Although commonly cited as representing annual fecundity estimates, the methods of Chenoweth (1963) and Stolgitis (1970) clearly show that their results are batch fecundity estimates. For our comparison, we selected the lowest value for age-4 and the highest for age-9 tautog as the sampled range of batch fecundity estimates. We averaged northern data from Chenoweth (1963: age 4, 265 mm TL, 6000 BF and age 9, 401 mm TL, 224,000 BF) and Stolgitis (1970: age 4, 261 mm TL, 7000 BF and age 9, 486 mm TL, 260,000 BF) to create a batch fecundity range of 6500–242,000 eggs. This range was multiplied by the 68-day “spawning season” observed in laboratory aquaria by Olla et al. (1977) to calculate a range for potential annual fecundity of 442,000 to 16,456,000 eggs per female in northern areas. Our samples from the southern range (age 4: 275 mm TL, 5000 BF and age 9: 511 mm TL, 181,200 BF) multiplied by 58 spawning events in 1995 results in potential annual fecundity of 290,000 to 10,510,000 eggs per female. Differences in these estimates of potential annual fecundity are primarily due to the number of spawnings per year and are questionable because the spawning frequency estimate based on aquarium studies may not apply for naturally spawning fish. This comparison indicates that we still lack adequate information on the spawning frequency and annual fecundity for fish from the northern part of the species range.

Although batch fecundity estimates appear similar between southern and northern portions of the tautog’s range, previous batch fecundity estimates from northern populations are 30 years old. Reported spawning seasons between areas also vary in length from two to four months, which could greatly affect potential annual fecundity estimates with this method. Estimates of annual fecundity in

the northern regions of the species range should be pursued to determine if tautog annual fecundity varies with latitude. Evidence of different growth rates (Cooper, 1965, 1966, 1967; Stolgitis, 1970; Hostetter and Munroe, 1993; White, 1996), seasonality of occurrence in coastal waters, and winter activity cycles between tautog in southern versus northern regions (Olla et al., 1974; Hostetter and Munroe, 1993; Arendt et al., 2001a, 2001b) strongly point to considering latitudinal effects when analyzing and comparing any biological features of this species. Even if batch fecundity and spawning frequency remain relatively constant over latitude, size structure of the stock will dictate estimates of total egg production: thus continued research is necessary to monitor size structure and abundance of tautog resources throughout the species range. Additional data on larger, older females is necessary to evaluate the relative contribution of older females to population fecundity and egg production. Because many aspects of tautog life history affect recruitment, further investigation is required on egg dispersal, egg mortality, larval drift, larval mortality, hatching success, first feeding success, pre- and postsettlement mortality, juvenile mortality, recruitment, stock structure, and spawning stock biomass (ASMFC<sup>4</sup>).

Historically, tautog have supported a predominantly (90%) recreational fishery throughout their range (ASMFC<sup>4</sup>). Over the past 15 years, this popular food and sport fish has increased substantially in value as a commercially targeted species. As popularity and fishing effort increased, landings peaked in 1993 but have declined more recently, prompting the Atlantic States Marine Fisheries Commission (ASMFC<sup>4</sup>) to pass a coastwide management plan for tautog in April 1996.

Tautog annual fecundity is a key piece of data necessary for egg production models and estimates of spawning stock biomass, and there are no reliable estimates of tautog spawning stock biomass to date (ASMFC<sup>4</sup>). In April 1998, the ASMFC imposed a 14-inch (350-mm) minimum size limit, effective for tautog caught from Massachusetts to Virginia. The benefits of instituting a size limit for tautog are well supported by data from this study. A minimum size limit allows tautog in the southern regions of the species' distribution to have at least one spawning season, and most likely two, thereby affording the opportunity for each female to contribute on average 3.22 million eggs (calculated from the linear regression equation, Fig. 8) towards the annual population fecundity.

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