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Reproductive Biology of Tautog, Tautoga onitis, in the Lower Chesapeake Bay and Coastal Waters of Virginia

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REPRODUCTIVE BIOLOGY OF TAUTOG, *TAUTOGA ONITIS*, IN THE LOWER CHESAPEAKE BAY AND COASTAL WATERS OF VIRGINIA

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by

Geoffrey G. White

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APPROVAL SHEET

This thesis is submitted in partial fulfillment of
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ABSTRACT

The tautog, *Tautoga onitis* (Linnaeus), ranges from Nova Scotia to South Carolina. Tautog are a long lived (34 yrs in RI, 25+ in VA), slow growing, structure associated species that are believed to exhibit only localized movements, therefore they are susceptible to overfishing. The Atlantic States Marine Fisheries Commission (ASMFC) recognizes the need for more research on tautog in the southern portion of the species range.

The reproductive potential of tautog, measured as annual fecundity, has not been previously addressed. Tautog are known to be a multiple spawning species. Previous investigations of tautog fecundity actually estimated batch fecundity, not annual fecundity. To accurately estimate potential annual fecundity for multiple spawning species, estimates of batch fecundity must be multiplied by the number of spawns per year. This study was undertaken in an effort to develop a better understanding of tautog reproductive biology in the lower Chesapeake Bay.

Histological methods were used to describe annual and daily ovarian cycles of tautog to provide insight on reproductive activity and strategy. Annual fecundity was used to estimate reproductive potential and provide fishery managers with data necessary to estimate egg production and spawning stock biomass of tautog resources. Tautog spawned from 7 April, 1995 to 15 June, 1995, at locations from the York River to 45 km offshore. Males attained 100% maturity at age 3, females at age 4. Batch fecundity estimates ranged from 2,754 to 181,190 eggs per spawn for female tautog age 3-9, total length 259-516 mm. Mean batch fecundity for female tautog age 4-6 was 54,243 ± 2,472 eggs and 106,256 ± 3,837 eggs for females age 7-9. Spawning frequency was estimated at 1.14 days. Estimates of potential annual fecundity for tautog age 3-9 ranged from 168,000 to 11,052,606 eggs. Results are presented for fish collected from natural habitats and discussed relative to labrid reproductive biology and fishery management concerns for this species.

REPRODUCTIVE BIOLOGY OF TAUTOG, *TAUTOGA ONITIS*, IN THE LOWER CHESAPEAKE BAY AND COASTAL WATERS OF VIRGINIA

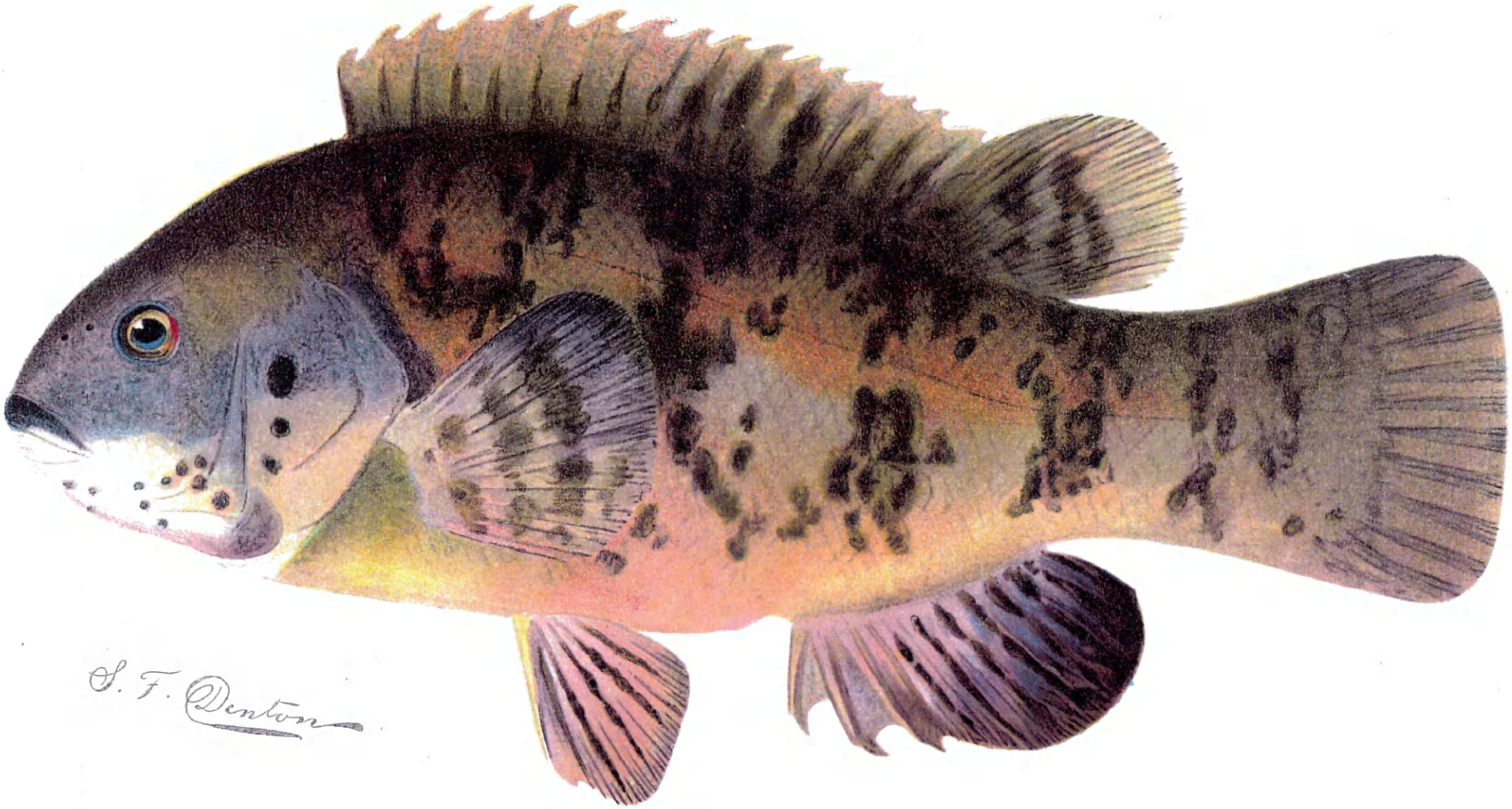
GENERAL INTRODUCTION

The tautog, *Tautoga onitis* (Linnaeus) (Fig. 1), ranges from Nova Scotia to South Carolina, although it is most abundant between Cape Cod and New Jersey (Bigelow and Schroeder, 1953). Tautog are a long lived (25+ years in Virginia, 34 years in Rhode Island), slow growing species that associates with hardbottom habitats (Cooper, 1967; Olla et al., 1977; Hostetter and Munroe, 1993). Tagging studies indicate tautog exhibit seasonal inshore-offshore migrations, but large scale north-south movements have not been recorded (Cooper, 1966; Lynch, 1991; Bain and Lucy, 1996). These life history characteristics make tautog vulnerable to over-exploitation.

Historically, tautog have supported a predominantly (90%) recreational fishery (Moore, 1992). In the last 15 years, tautog have become a popular food and sport fish throughout their range, with a concurrent increase in value as a commercially targeted species. As popularity and fishing effort increased, landings peaked, but more recently have declined (ASMFC, 1996). In northern regions, concern of overfishing has prompted Massachusetts and Rhode Island to set minimum size regulations at 16 inches. Currently, Virginia does not have a management plan for tautog.

The Atlantic States Marine Fisheries Commission (ASMFC) recently passed (April 1996) a coastwide management plan for tautog. For assessment purposes, the stock was divided into two areas: Massachusetts to New York, and New Jersey to Virginia. The definition of overfishing used by ASMFC (F=M=0.15) is similar to mortality reported by Cooper (1967) for healthy tautog stocks. The University of Rhode Island trawl survey has

Figure 1: External appearance of a) male and b) female tautog, *Tautoga onitis*.



TAUTOG (TAUTOGA ONITIS)

shown a decline in abundance of tautog from 40.1 kg per tow during the 1960's to 8.6 kg per tow in the 1990's, which corresponds to an increase of fishing mortality from F=0.15 to F=0.54 (Gibson, 1994). A similar assessment of stock abundance and fishing mortality is not currently possible in the southern range due to lack of data. However, the population structure and growth parameters of tautog in Virginia were recently reported (Hostetter and Munroe, 1993) to be similar to those reported in Rhode Island (Cooper, 1967) over 25 years ago. This observation as well as differences in historic landings between northern and southern regions of the tautog's range, suggest that resource exploitation levels may be vastly different between regions.

ASMFC recognizes the need for more research on tautog in the southern portion of the species range. Topics for research noted in the management plan (ASMFC, 1996) include stock size, fishing mortality, age-length keys, definition of specific spawning areas, definition of offshore egg supply source (i.e. in situ spawning vs. transport of spawned eggs), and estimation of spawning stock biomass. A draft Chesapeake Bay tautog management plan (VMRC, 1994) noted that fecundity estimates are generally lacking for the species, especially in the southern range, and these estimates are critical for understanding size and age related characteristics of females in the population.

This study was undertaken in an effort to develop a better understanding of tautog reproductive biology in Virginia. Histological methods were used to describe annual and daily ovarian cycles of tautog to provide insight on tautog reproductive activity and strategy. Tautog annual fecundity was estimated with methods first published by Lasker (1985) in an attempt to estimate reproductive potential and provide fishery managers with data necessary to estimate egg production and spawning stock biomass of tautog resources.

CHAPTER 1

Reproductive biology

INTRODUCTION

The tautog *Tautoga onitis* (Linnaeus), is one of two temperate labrids which inhabit the northwest Atlantic Ocean, the other is the cunner (*Tautogolabrus adspersus*). Tautog range from Nova Scotia (Bleakney, 1963; Scott and Scott, 1988) to South Carolina (Bearden, 1961; Sedberry and Beatty, 1989). 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).

Tautog are a long lived, slow growing species with a maximum recorded age of 34 years in Rhode Island (Cooper, 1967) and 25 years in Virginia (Hostetter and Munroe, 1993). Hostetter and Munroe (1993) investigated tautog age and growth in the southern portion of the species range and compared growth parameters of fish between northern and southern regions. Growth increments for ages 1-13 were similar to those reported by Cooper (1967) in Rhode Island, but Virginia tautog exhibited almost twice the growth increments in young-of-the-year and age 13+ fish. Comparison of length and weight of tautog from New York (Briggs, 1977) and Virginia (Hostetter and Munroe, 1993) revealed similar relationships.

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. Juvenile tautog

(<100 mm) are commonly found in shallow water (<1 m) areas densely vegetated with *Ulva lactuca*, or *Zostera* sp. and *Ruppia* sp. seagrass beds (Briggs and O'Conner, 1971; Sogard et al., 1992; Dorf, 1994). 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).

Within preferred habitats, juvenile and adult tautog develop home sites (Olla et al., 1979). Tautog less than 25 cm tend to remain within a few meters of the home site while feeding during the day, whereas larger tautog (>30 cm) range up to 300 meters from the home site during daily foraging expeditions (Olla et al. 1974). Fish return to home sites at night and remain there in a quiescent/sleep state (Olla et al. 1974). Tagging studies indicate seasonal movement between inshore and offshore habitats, but minimal north-south movement (Cooper, 1966; Briggs, 1977; Lynch, 1991; Bain and Lucy, 1996). Juveniles typically remain inshore throughout the year and enter a torpid state at water temperatures less than four degrees Celsius during the winter, while adults migrate offshore when water temperatures decline to about 10°C in the fall. In the spring, the majority of tautog return to inshore spawning areas with increasing water temperatures (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).

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. The 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 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 those studies, and precocious maturity has been noted (Olla and Samet, 1977; Hostetter and Munroe, 1993).

Tautog are known to be a multiple spawning species, and have been observed spawn as discrete pairs and as groups in laboratory aquaria (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) with two morphological males present in the population (Hostetter and Munroe, 1993). Dimorphic males tend to be larger, which theoretically improves their ability to set up dominance hierarchies, defend structural territories, and maintain pair spawning (Olla and Samet, 1977). The non-dimorphic males may suggest a different sexual stage in the life history, an indicator of hermaphroditism, or be coincident with a different reproductive behavior (group spawning, interference spawning) used to increase spawning opportunities in the presence of dimorphic males (Olla and Samet, 1977; Olla et al., 1981; Hostetter and Munroe, 1993).

The reproductive potential of tautog, measured as annual fecundity, has not been previously addressed. To accurately estimate potential annual fecundity for multiple spawning species, estimates of batch fecundity must be multiplied by the number of spawns per year, i.e. spawning frequency times spawning season length (Hunter and Macewicz, 1985). Previous research on tautog fecundity by Chenoweth (1963) and Stolgitis (1970) estimated batch fecundity and length of spawning season, but did not measure spawning frequency. The only inference to number of spawns per female per year is Olla et al. (1977),

who observed tautog spawning daily for 68 to 96 days in laboratory aquaria. However, application of results obtained in aquaria are difficult to apply to natural habitats.

This study used recent advances in annual fecundity and histology techniques to investigate reproductive biology of tautog in the lower Chesapeake Bay. Data on spawning season, spawning locations, age at maturity, oocyte size frequency distributions, batch fecundity, spawning frequency, and annual fecundity are presented for fish collected from natural habitats and discussed relative to labrid reproductive biology and fishery management concerns for this species.

METHODS

Fish collection and general biological data

A total of 960 tautog (>150 mm total length (TL)) were collected opportunistically between April 1994 and September 1995 from commercial and recreational fishermen and research activities at Virginia Institute of Marine Science (VIMS). 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 meters (Fig. 2). Approximately one quarter of the fish were taken from within the Chesapeake Bay, one quarter from the Chesapeake Bay Bridge Tunnel, and one half from around the Chesapeake Bay Light Tower (24 km offshore, depth=17m).

For each fish, total length (TL) was measured to the nearest millimeter (mm), and total weight (TW) to the nearest gram (g). External sex was recorded based on 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 with white underneath, and a small white circle (about 15 mm diameter) laterally, immediately ventral to the dorsal fin (Fig. 1b). Female tautog have a less pronounced chin, sloped forehead, and a mottled brown coloration (Fig. 1a). After recording external sex, gonads were excised, staged macroscopically, and weighed to the nearest g (GW). Maturity classification was assigned as outlined in Table 1, based on eight macroscopic stages modified from Lowerre-Barbieri (1994). Eviscerated weight (EW) in grams, of each fish was taken to remove

Figure 2: Map of lower Chesapeake Bay and nearby coastal waters of Virginia. Red circles indicate collection sites. CBBT = Chesapeake Bay Bridge Tunnel. CBLT = Chesapeake Bay Light Tower.

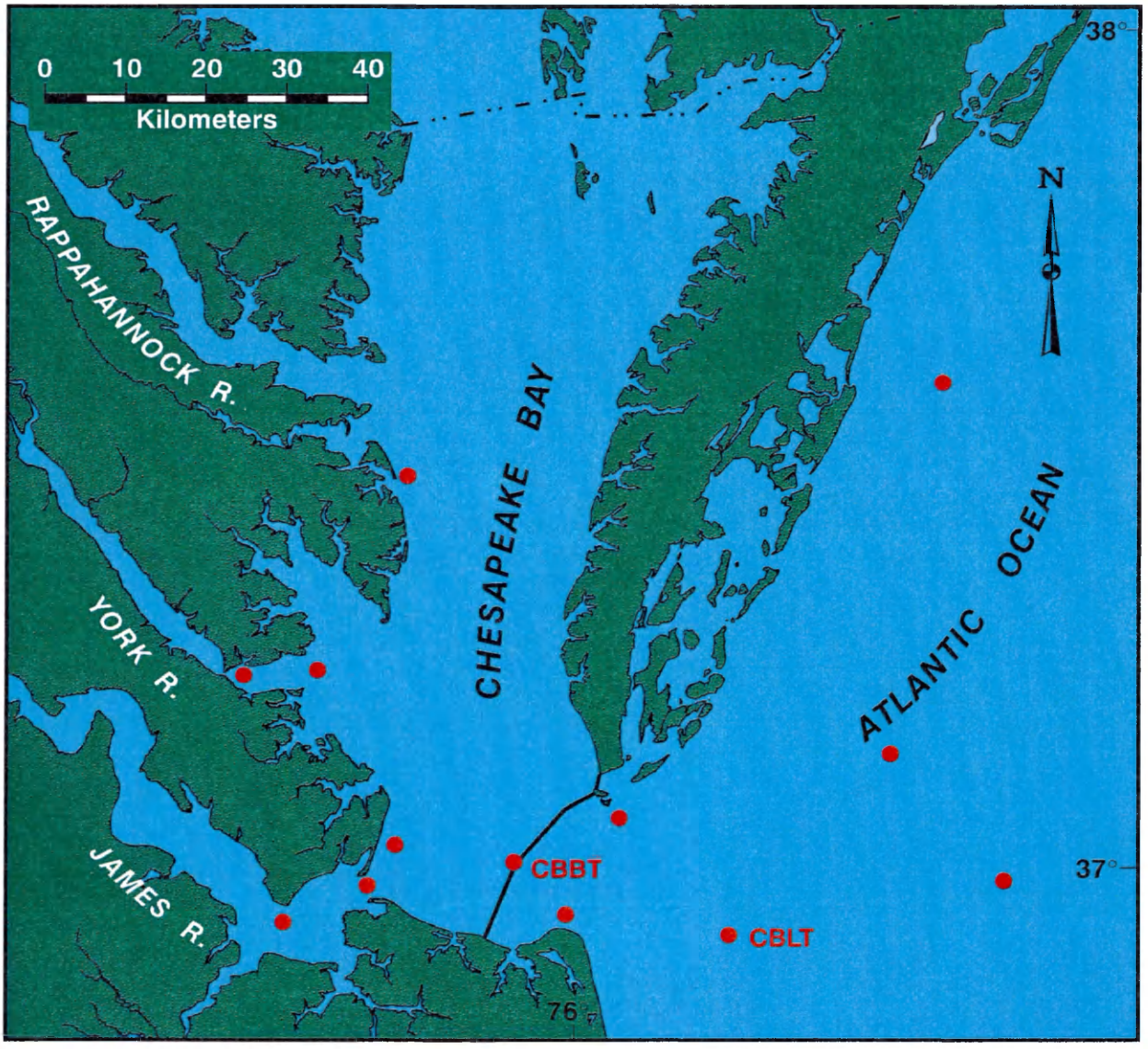

0 10 20 30 40
Kilometers
RAPPAHANNOCK R.
YORK R.
JAMES R.
CHESAPEAKE BAY
ATLANTIC OCEAN
CBBT
CBLT
N
38°
37°
76°

Table 1: Description of macroscopic and microscopic gonad stages for female tautog, *Tautoga onitis*, modified from Lowerre-Barbieri (1994). Macroscopic criteria refer to whole fresh ovaries. Abbreviated gonad stage numbers are in parentheses. Gonad stages 4, 5, and 3a comprise the inner spawning cycle. GSI = gonadosomatic index. POF = post-ovulatory follicles. FOM = final oocyte maturation. GVBD = germinal vesicle breakdown.

Gonad Stage	Macroscopic Criteria	Microscopic Criteria
(1) Immature	ovaries very small, white to light pink in color, no oocytes visible, tubular in shape (mean GSI = 0.50)	only primary growth oocytes present, no atresia, no macrophage aggregates, ovarian membrane thin.
(2) Developing	ovaries small to medium, tubular shape, yolked oocytes begin to appear, dark yellow to light orange in color, (mean GSI = 2.25)	primary growth, cortical alveoli, and some partially yolked oocytes present.
(3) Fully Developed	ovaries medium to large, yolked oocytes abundant, appear slightly grainy, pale mustard in color (mean GSI = 3.25)	primary growth to advanced yolked oocytes present; no remnant hydrated oocytes or POFs.
(4) Hydrated	ovaries large to very large; firm, yolked oocytes interspersed with large transparent (hydrated) oocytes visible, pink to yellow in color (mean GSI = 11.74)	primary growth to germinal vesicle migration and hydrated oocytes present, hydrated oocytes are unovulated, POFs may be present.
(5) Running Ripe	ovaries large to very large, clear oocytes have been ovulated, expand lumen of ovary, and are easily extruded when gonad excised; few clear oocytes in ovarian tissue (mean GSI = 10.12)	primary growth through advanced yolked, and ovulated, hydrated oocytes and fresh POFs present, FOM stages usually absent, lumen usually seen as separation of ovigerous folds.
(3a) Partially spent/ redeveloping	ovaries somewhat flaccid, large, slightly more pink than hydrated; 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	ovaries flaccid, small to medium, red to purple, yolked oocytes visible, but less abundant, and some clearing of tissue at anterior end of ovary (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 opaque (yolked) oocytes visible (mean GSI = 1.50)	only primary growth oocytes and cortical alveoli present, macrophage aggregates abundant, more follicular tissue and thicker ovarian membrane than immature fish.

potential bias caused by fish with full intestinal tracts. One gonad was randomly chosen by coin toss (heads = right gonad) for histological processing and placed in Davidson's fixative. For females staged macroscopically as spawning, 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; ASMFC Tautog Technical Committee). 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 running water, allowed to dry for two days, and read using 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. April 1 was used as a birth date to allow maximum growth within the biological year (April to March), and avoid overlap with fish spawned in the next year class. See Appendix for an age-length plot created from fish aged in this study.

Microscopic gonad analyses

Spawning pattern (synchronous, group synchronous, asynchronous) and type of fecundity (indeterminate or determinate annual fecundity) were assessed by oocyte size frequency distributions (West, 1990; Hunter and Macewicz, 1985) and histology (Hunter and Macewicz, 1985). Six fish were selected for analysis of oocyte size frequency distributions; three fish (TL = 300, 400, 450 mm $^{+}$/- 10mm) 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 and preserved in 2%

formalin following the method of Lowerre-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 using a random number table, and maximum diameter of the first 500 oocytes encountered was measured using the Biosonic Optical Pattern Recognition System®.

Gonads selected for histological processing were placed in Davidson's fixative for two days before transverse sections of anterior, middle, and posterior ovarian tissue, or anterior and posterior sections of testes, were taken and placed in tissue cassettes. Gonad 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 μm, and stained with Harris' Hematoxylin and Eosin-Y) (Luna, 1968) was performed for all samples. Males were classified microscopically as sexually mature or immature by the presence of spermatozoa in histological sections. 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) is comprised of germinal vesicle migration, germinal vesicle breakdown, and hydrated oocyte stages (Wallace and Selman, 1981). Post-ovulatory follicles (POF) were used to distinguish fully developed ovaries from partially spent/redeveloping. Microscopic gonad stages are described in the Results section "Description of microscopic gonad stages", summarized in Table 1, and shown in Figure 4a-h. Percent agreement between macroscopic and microscopic female gonad stages was calculated to evaluate the accuracy of macroscopic staging. Microscopic stages were

assumed to be more accurate, as histology can discern differences in cellular development.

Sex ratios

Chi-square analysis was used to test for significant deviations from an expected one to one sex ratio for all fish. Deviations from a one to one sex ratio among 50 mm length intervals were also analyzed by Chi-square.

Length and age at maturity

Females were considered mature if classified into gonad stages 2-7 (Table 1). Males were considered mature if spermatozoa were present in histological sections. Length at maturity was based on 110 females and 79 males (TL 150-350 mm) collected during the spawning season. The percent of mature fish was analyzed as mean length by 20 mm intervals for each sex. Due to small sample sizes, a logistic regression curve was fitted to the data, and length at maturity (L_{50}) was calculated from the regression equation. Age at maturity was based on 135 females and 104 males (Age 1-6). The percent of mature individuals was plotted against age, and age at maturity was defined as the age at which at least 50% of the fish were mature.

Spawning season and location

A gonadosomatic index (GSI) was calculated for each sex to determine the annual spawning season. GSI was calculated as:

$$GSI = (GW/EW) \times 100$$

and:

$$GSI = (GW/SW) \times 100$$

Eviscerated weight (EW) and somatic weight (SW) were used to calculate different gonadosomatic indices to determine if a bias existed in SW caused by fish with full stomachs (removed in the EW calculation). 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 in spawning condition (hydrated, running ripe, partially spent/redeveloping).

Spawning locations were assessed by the presence of gravid, running ripe, and partially spent/redeveloping fish, since tautog spawn daily (Olla and Samet, 1977; Olla et al., 1977; Chapter 2), and undergo only small localized movements, returning to a home site at night (Olla et al., 1974).

Batch fecundity

Batch fecundity was determined gravimetrically using a modification of the hydrated oocyte method (Hunter et al., 1985). The method, as cited, called for both ovaries to be fixed in 10% formalin to estimate batch fecundity by calculating:

$$Y = (y/x)\ X$$

where:

Y = batch fecundity
y = number of hydrated oocytes in the tissue sample
x = formalin wet weight of tissue sample
X = formalin wet weight of ovaries

Assumptions implicit to the hydrated oocyte method 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 the egg number within the most advanced mode, the selection of mature females for analysis, or position within and between ovaries from which subsamples were taken (Hunter and Goldberg, 1980; Hunter et al., 1985). The use of hydrated oocytes, formed only when spawning is imminent and much larger than the next largest cell size class, supported the acceptance of these assumptions. Histological analyses of females that had recently spawned provided an estimate of the number of hydrated oocytes retained in the ovary (remnant HOs). Hunter et al. (1985) used only hydrated ovaries which had not lost oocytes in storage for batch fecundity counts.

Macroscopic gonad stages did not distinguish between hydrated, running ripe, and partially spent/redeveloping ovaries, therefore histological analysis of the ovary lobe preserved in Davidson's fixative was used to identify 29 fully hydrated females that fit the criteria for use in batch fecundity analysis. Fish containing hydrated oocytes in the lumen of the ovary in histological samples were not included in fecundity analysis. Possible differences between left and right ovarian lobes were accounted for by randomly selecting one ovarian lobe per fish to be fixed for fecundity analysis.

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

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

V_v = relative volume of one cell type

P_n = number of points overlying specific cell type

P_{tot} = number of points in grid

To ensure that fields of view were chosen randomly, each ovarian section was divided into 5x5 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 5x5 mm area, point counts were made through a gridded reticule (121 points) at 40X magnification. Average relative volume of each cell class was calculated from the three areas as $P_n/363$.

To test if cellular development within the ovary was independent of position within the organ, average relative volumes of cell classes between anterior, middle, and posterior ovarian sections were tested by Multiple Analysis of Variance (MANOVA) (Minitab, 1995). Response variables (8) were average relative volume of each cell class. Differences between fish (10) were removed by blocking on fish. After no positional effects were detected, all hydrated oocytes were counted from three subsamples of approximately 0.3 g from the middle of the formalin fixed ovary.

A final modification to the method was necessary due to possible artifacts created by not fixing both ovaries in formalin. The ratio estimate of batch fecundity calls for formalin wet weight of each tissue sample (x) and formalin wet weight of both ovaries (X). A reliable measure of (x) was available, but the formalin wet weight of both ovaries (X), could not be measured because one ovary was fixed in Davidson's solution for histological processing. Therefore, a calibration experiment was done to determine the percent change in ovarian weight between fresh and formalin fixed paired ovaries. On 25 April 1996, 18 female tautog in spawning condition were collected from the Chesapeake Bay Bridge Tunnel. Fresh ovarian weight was measured to the nearest 0.01 g and whole ovaries (right and left lobes) 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 if weight change stabilized over that

time period. Percent change in weight was calculated for each specimen, and regressed against fresh weight of the ovary (Fig. 3), thus percent change in weight between formalin fixed wet weight and fresh ovary weight can be predicted with the exponential relationship:

$$\text{percent weight change} = 21.452\, e^{(-0.0163GW)} \quad ; R^2=0.67$$

where GW represents fresh gonad weight. Calibrated (formalin fixed) gonad weight (CGW) was then calculated as:

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

The calculation of CGW was necessary to develop the batch fecundity equation.

Finally, batch fecundity was estimated using the ratio estimate:

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

where:

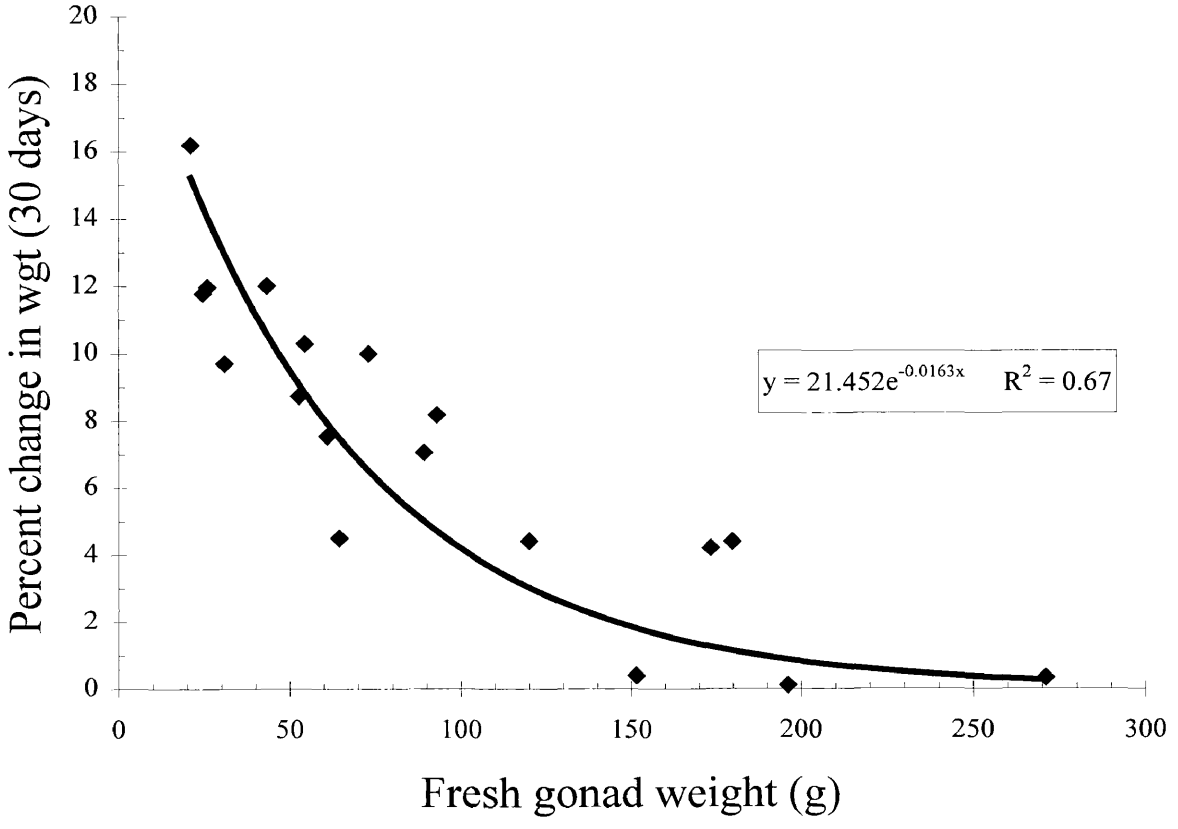
Y = batch fecundity
y = number of hydrated oocytes in the tissue sample
x = formalin wet weight of tissue sample
CGW = Calibrated formalin wet weight of ovaries

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 EW, and regressed against TL, TW, and age.

Spawning frequency

Spawning frequency was estimated using a modified form of the hydrated oocyte method (DeMartini and Fountain, 1981; Hunter and Macewicz, 1985). Spawning frequency is calculated by dividing the percent of females collected with hydrated ovaries during the spawning season into 100% determine the number of days between spawning events for an individual fish. Since it is known that tautog spawn daily (Olla and Samet, 1977; Olla et al.,

Figure 3: Regression of percent weight change of formalin fixed wet weight on fresh weight for tautog ovaries.


Percent change in wgt (30 days)
20
18
16
14
12
10
8
6
4
2
0
0
50
100
150
200
250
300
Fresh gonad weight (g)
y = 21.452e-0.0163x
R2 = 0.67

1977; Chapter 2), hydrated, running ripe, and partially spent/redeveloping fish with fresh POF's were included in the calculation of spawning frequency, since all three indicate spawning was imminent, or had already occurred that day.

Annual fecundity

Annual fecundity was estimated as the number of spawns per female multiplied by the mean batch fecundity for fish divided into 50 mm length intervals. The number of spawns per female was estimated by dividing the number of days in the spawning season by the estimated annual spawning frequency.

RESULTS

Description of microscopic gonad stages

The tautog is a multiple spawning species in which females exhibit annual gonad cycling that can be described by eight microscopic gonad stages (Table 1). Each stage can be differentiated by a unique suite of histological characteristics. Immature ovaries (Fig. 4a) are characterized by the presence of only primary growth oocytes, with a thin ovarian membrane. Developing stage ovaries (Fig. 4b) are characterized by the presence of primary growth, cortical alveoli, and partially yolked oocytes. The fully developed ovary (Fig. 4c) is characterized by the presence of primary growth to fully yolked oocytes but the absence of oocytes in final oocyte maturation (FOM) classes or post-ovulatory follicles (POFs). Hydrated ovaries (Fig. 4d) are distinguished by the overwhelming abundance of hydrated oocytes still inside the ovarian follicles, and may also contain degenerating POFs from an earlier spawn, but noticeably lack oocytes in the germinal vesicle breakdown state. The running ripe stage (Fig. 4e) is classified by the presence of an ovarian lumen, ovulated hydrated oocytes free in the lumen (although many times hydrated oocytes are washed out of the sample during the staining procedure), a large number of fresh POF's and GVM oocytes tend to be the most advanced stage present. Partially spent/redeveloping ovaries (Fig. 4f) are classified by the lack of an ovarian lumen, occasional remnant hydrated oocytes, primary growth to GVBD oocytes, and abundant POFs - some fresh and some beginning to degenerate. The spent stage (Fig. 4g) is characterized by major atresia and resorption of oocytes, and presence of macrophage aggregates (MA), which are groups of cells containing

the pigments lipofuscin, ceroid, and melanin (Wolke, 1992). These cells appear to be a collection of scavenging cells stimulated by excessive degenerating tissue; functioning to remove cellular debris and foreign substances by phagocytosis (Wolke, 1992). In tautog ovaries, MA's are assumed to be associated with the resorption of yolked oocytes after the spawning season. Resting stage ovaries (Fig. 4h) contain only primary growth and cortical alveoli, and can be distinguished from immature stage ovaries by the presence of MA's.

Percent agreement between macroscopic and microscopic gonad stages was 51% overall, with agreement for individual stages varying from 13% to 79% (Table 2).

Spawning pattern and type of fecundity

Oocyte size frequency distributions show no distinct gaps in development, or modes of oocytes, except for hydrated oocytes (0.95 to 1.25 mm), that would indicate synchronous oocyte development (Fig. 5). The presence of oocytes in all developmental stages in histologic sections of fully developed and partially spent ovaries (Fig. 6) also indicates that tautog have asynchronous oocyte development.

Oocyte size frequency distributions were measured at the beginning and end of the spawning season to classify tautog fecundity as seasonally determinate or indeterminate. Since there are no distinct modes of oocyte development, and the number of yolked oocytes (size range 0.30-0.55 mm) did not decrease through the spawning season (Fig. 5), oocytes were continually being yolked and developed from the primary growth and cortical alveoli stages. This type of development defines indeterminate fecundity, as the number of oocytes in the ovary at any one time is insufficient to measure potential annual fecundity (Hunter and Leong, 1981; Hunter et al., 1985)

Figure 4a: Histologic appearance of immature (stage 1) tautog ovary. PG - primary growth oocytes.

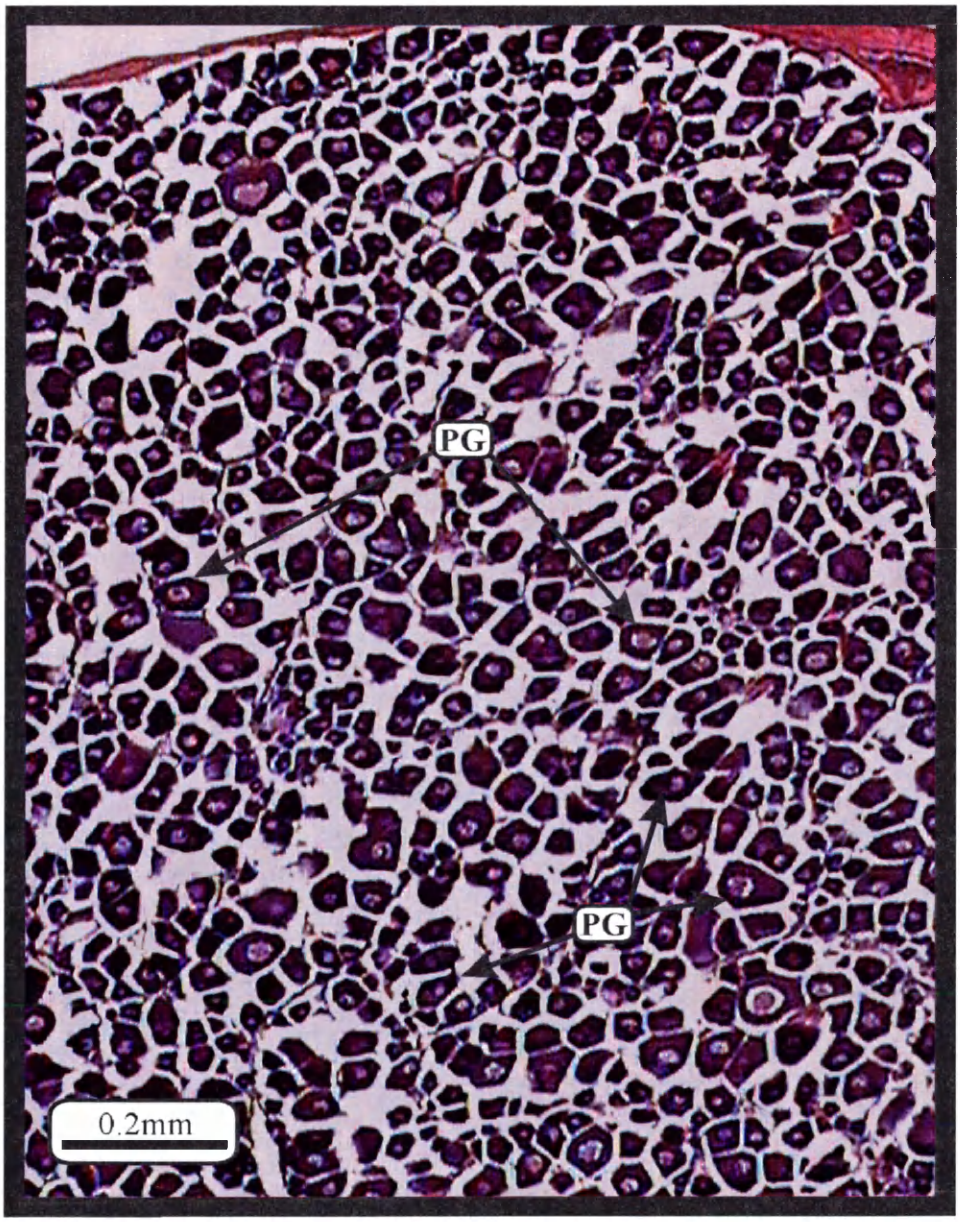

PG
PG
0.2mm

Figure 4b: Histologic appearance of developing (stage 2) tautog ovary. PG - primary growth oocyte. CA - cortical alveoli oocyte. PY - partially yolked oocyte.

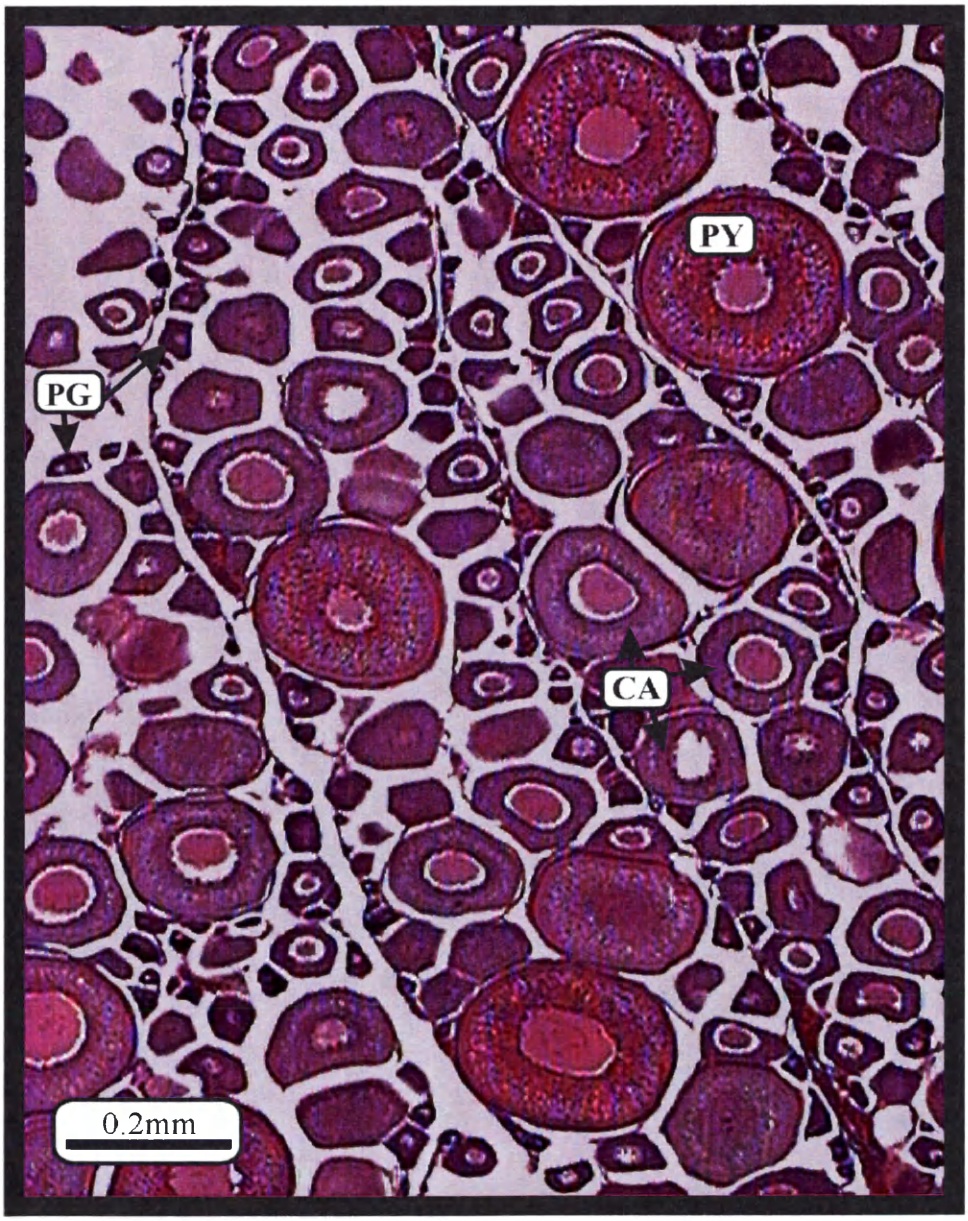

PY
PG
CA
0.2mm

Figure 4c: Histologic appearance of fully developed (Stage 3) tautog ovary. PG - primary growth oocytes. CA - cortical alveoli oocytes. PY - partially yolked oocytes. AY - advanced yolked oocytes.

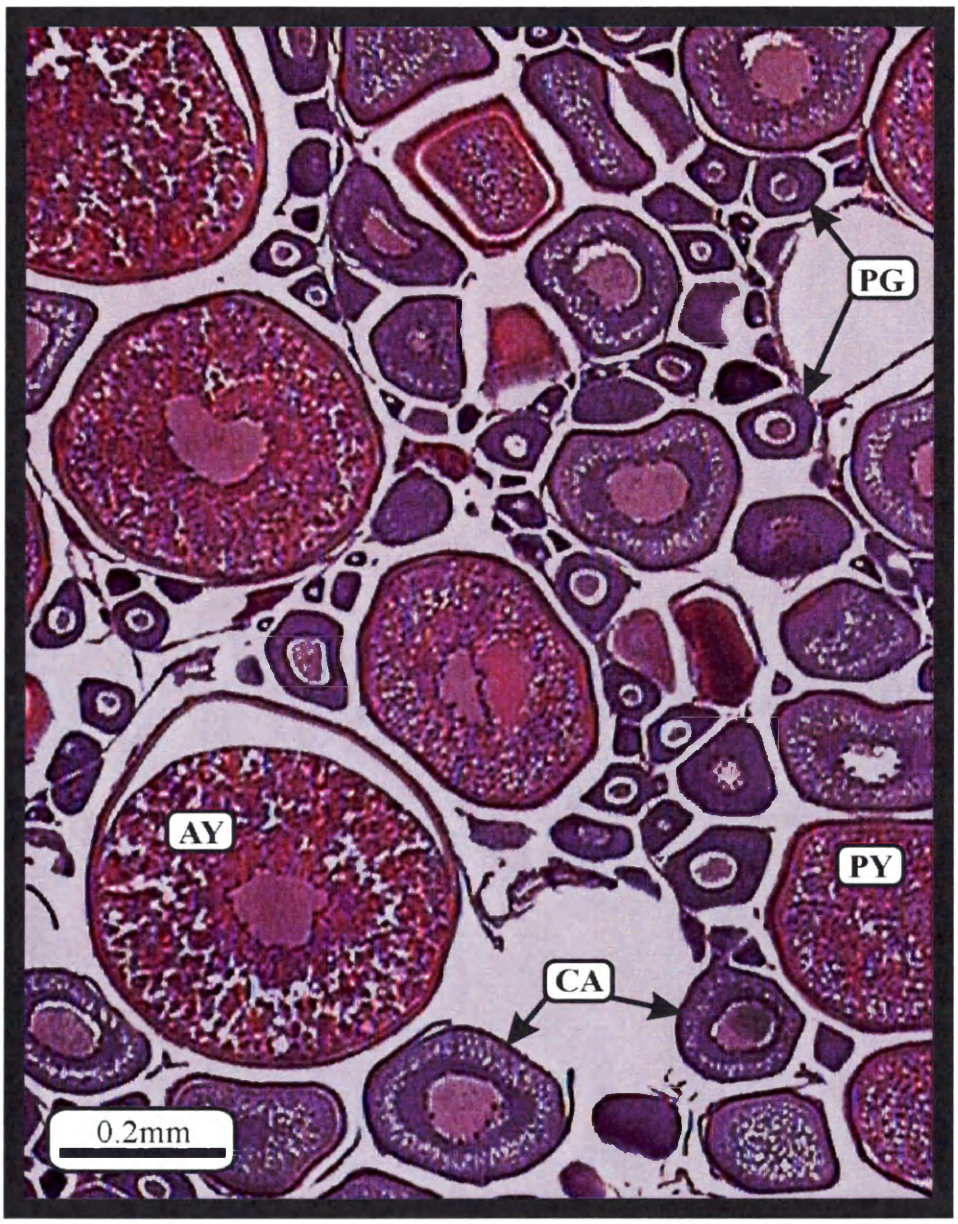

PG
AY
PY
CA
0.2mm

Figure 4d: Histologic appearance of hydrated (Stage 4) tautog ovary. AY - advanced yolked oocyte. HO - hydrated oocytes.

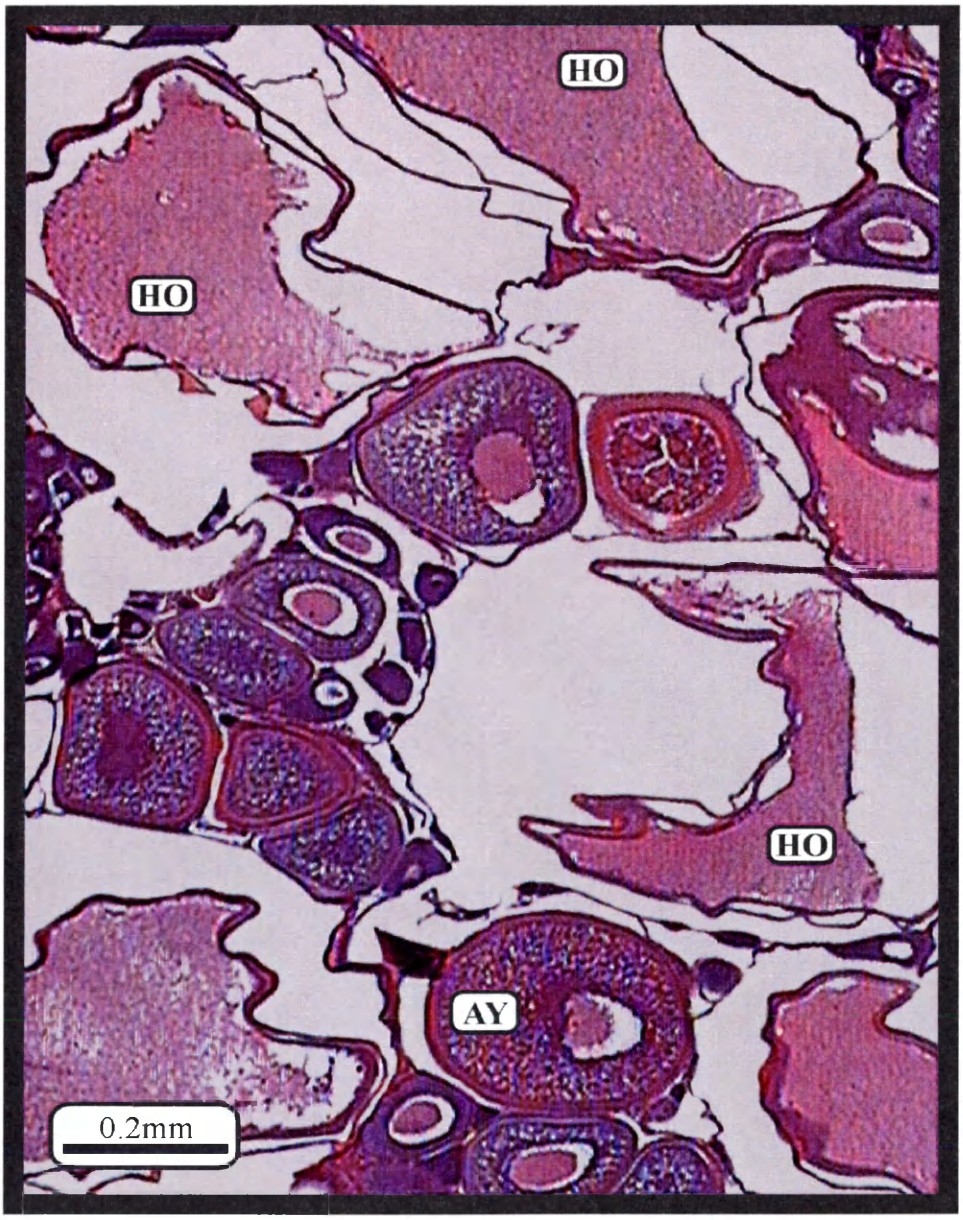
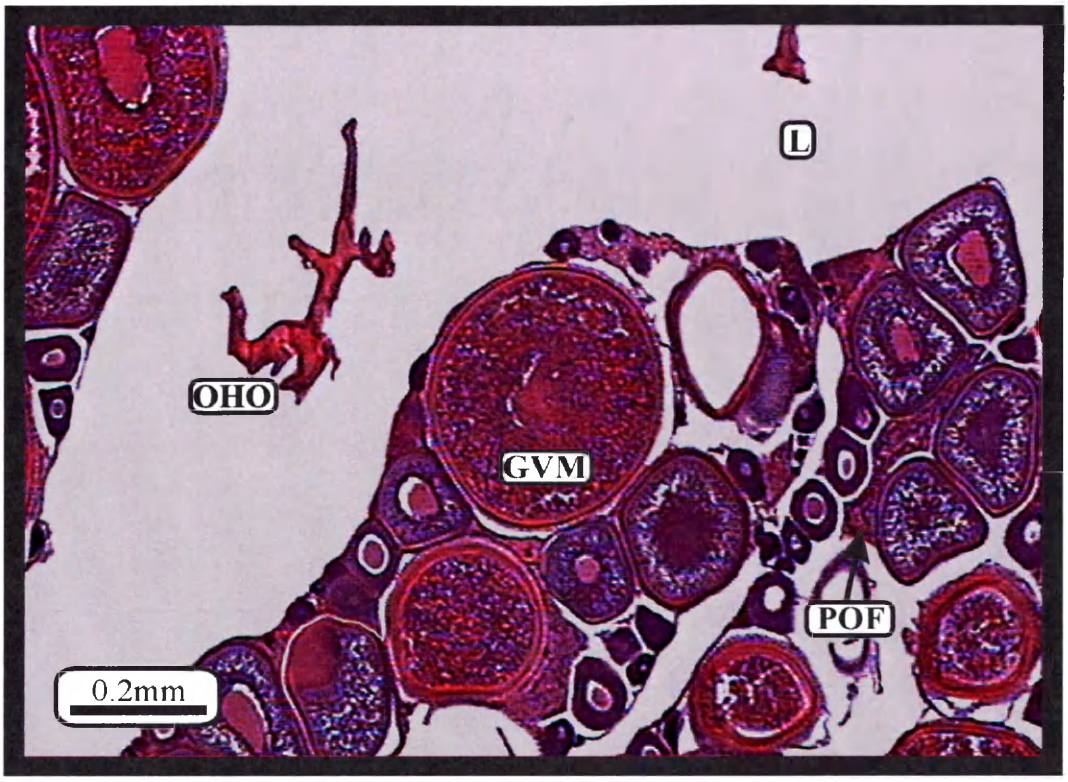

HO
HO
HO
AY
0.2mm

Figure 4e: Histologic appearance of running ripe (Stage 5) tautog ovary. Frame a shows obvious lumen as distinguishing character. Frame b shows typical field of view without lumen. Hydrated oocytes have been ovulated (OHO) and now reside in the lumen (L). AY - advanced yolked oocyte. GVM - germinal vesicle migration oocyte. POF - post-ovulatory follicle.

a)



b)

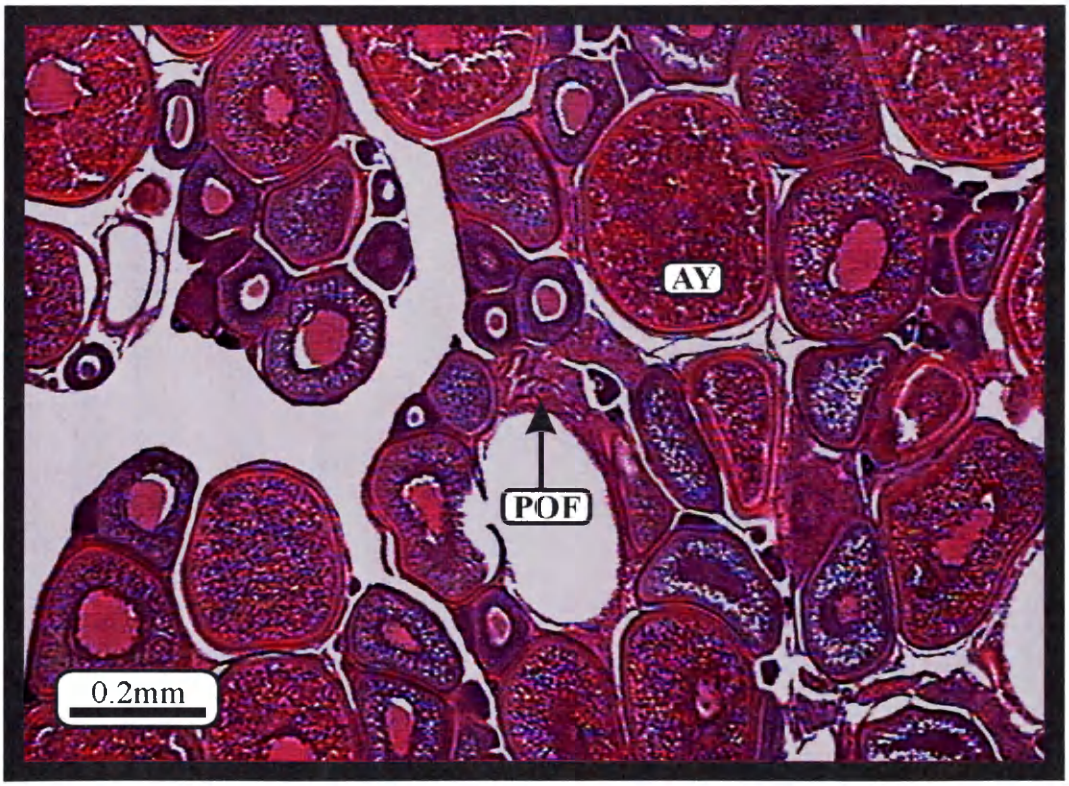


Figure 4f: Histologic appearance of partially spent/redeveloping (Stage 3a) tautog ovary. GVM - germinal vesicle migration stage oocyte. GVBD - germinal vesicle breakdown oocytes. POF - post-ovulatory follicle.

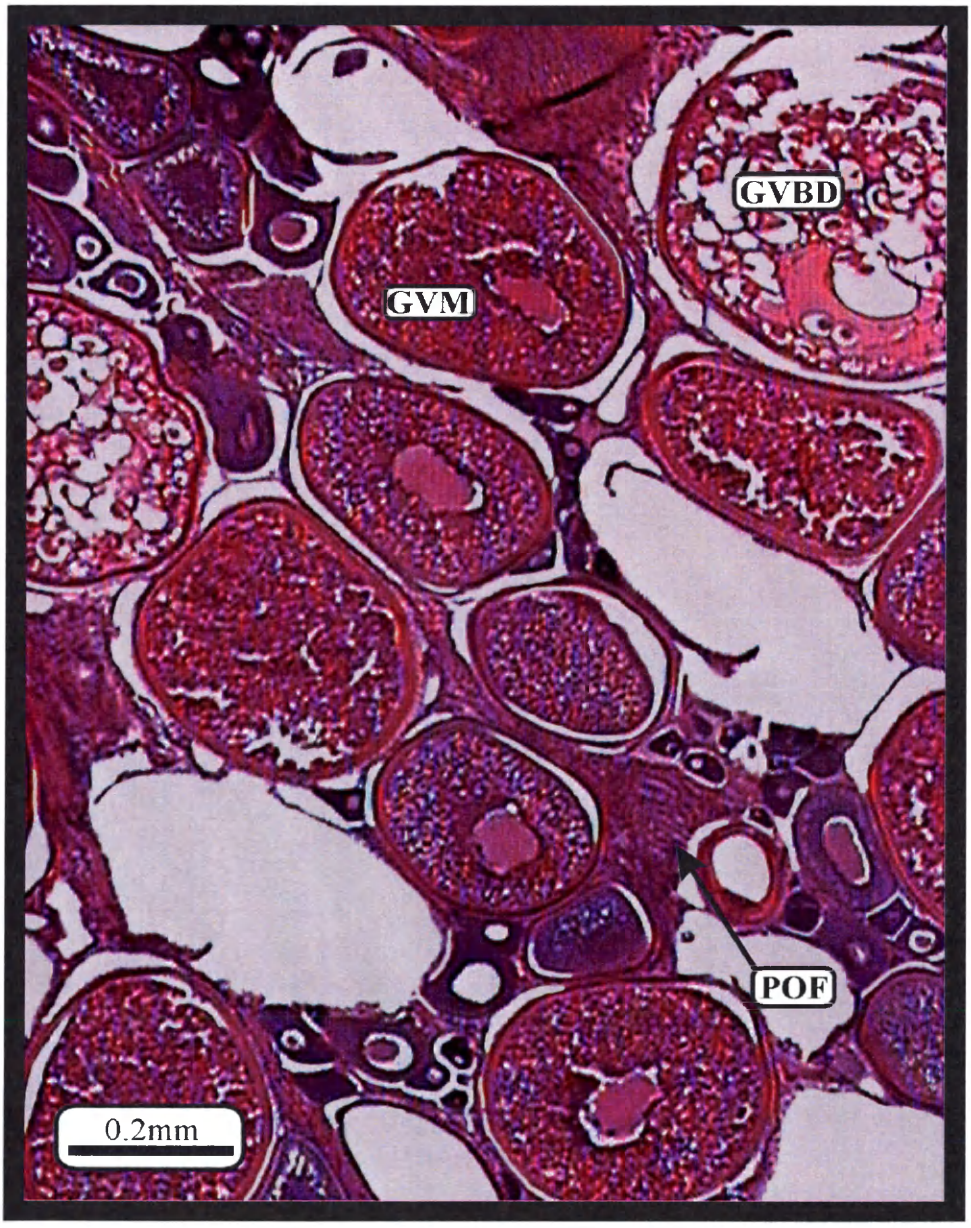

GVBD
GVM
POF
0.2mm

Figure 4g: Histologic appearance of spent (stage 6) tautog ovary. POF - post-ovulatory follicle. AO - atretic oocytes.

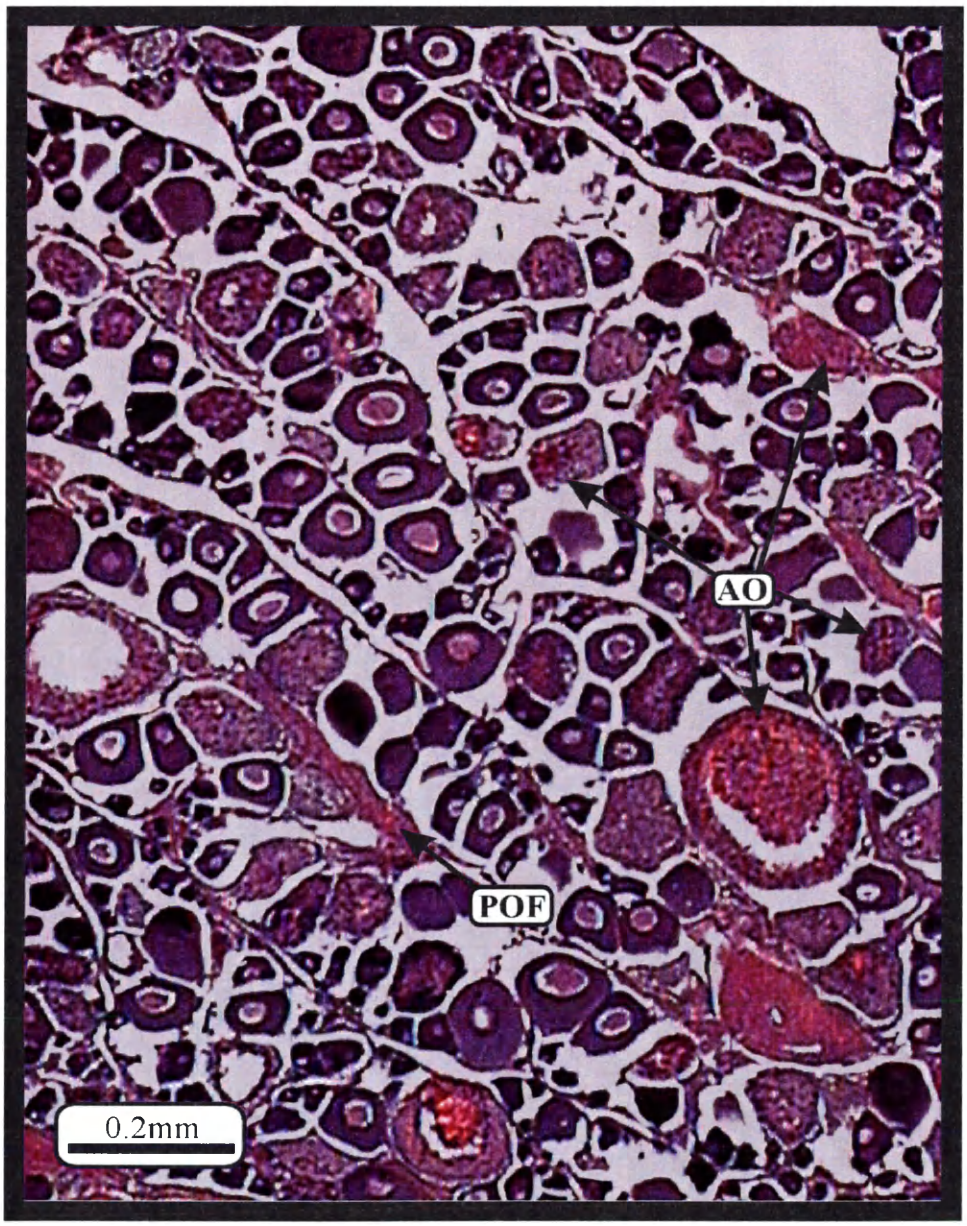

AO
POF
0.2mm

Figure 4h: Histologic appearance of resting (Stage 7) tautog ovary. PG - primary growth oocyte. CA - cortical alveoli oocyte. MA - macrophage aggregate.

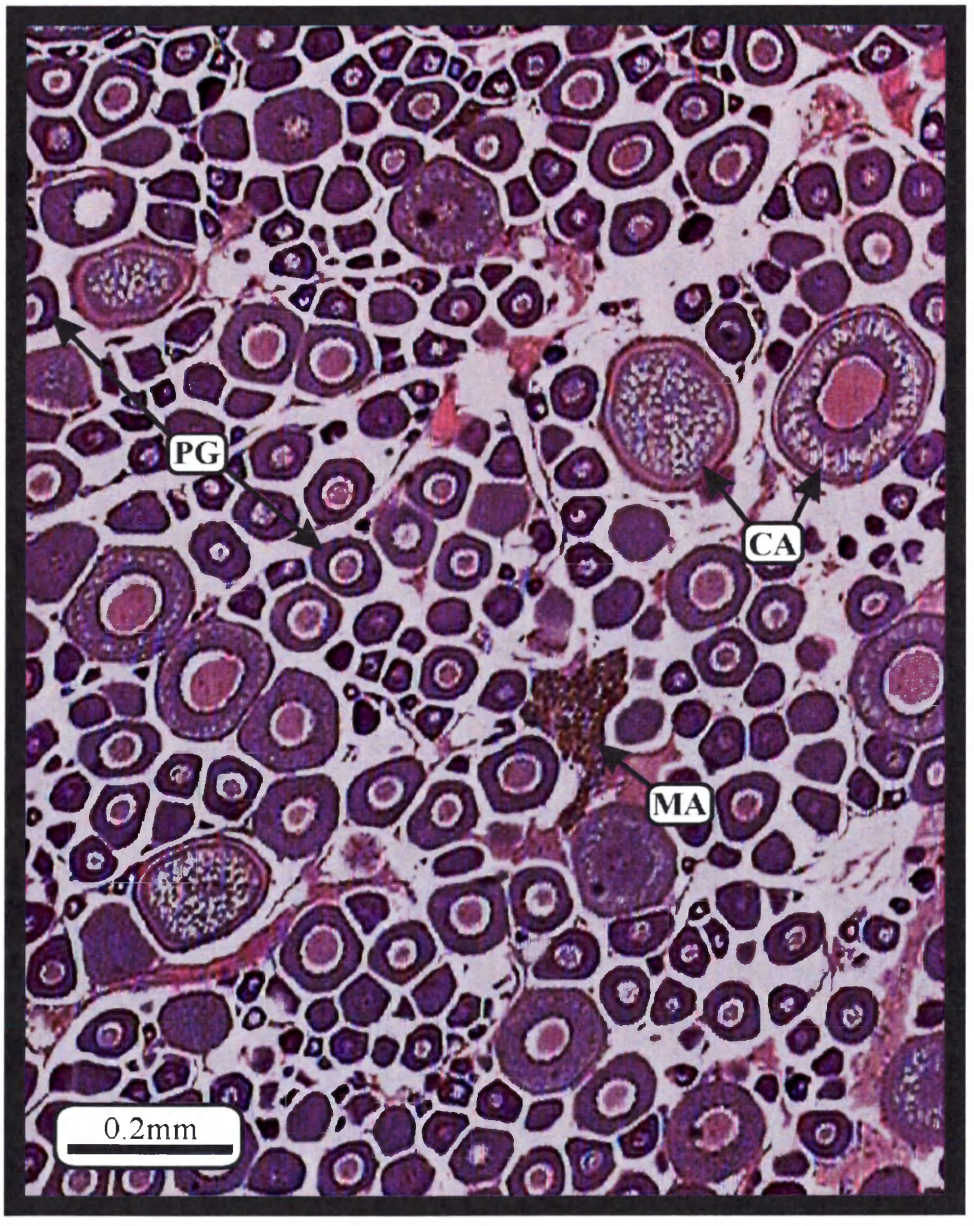

PG
CA
MA
0.2mm

Table 2: Summary of microscopic gonad stages assigned to macroscopically staged tautog ovaries from lower Chesapeake Bay, June 1994-September 1995. See Table 1 for gonad stage names. Microscopic stages were assumed to be correct. Data are expressed as the number of ovaries staged. Percent agreement between gonad staging methods presented below.

	Macroscopic Gonad Stage							
Microscopic 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%

Figure 5: Oocyte size frequency distributions of tautog ovaries. Six fish are represented, two in each length class: a) 300 mm, b) 400 mm, c) 450 mm. Actual collection dates were 26 April 1995 and 2 June 1995. For each fish, ovaries were hydraulically separated and the diameter of 500 oocytes measured in mm.

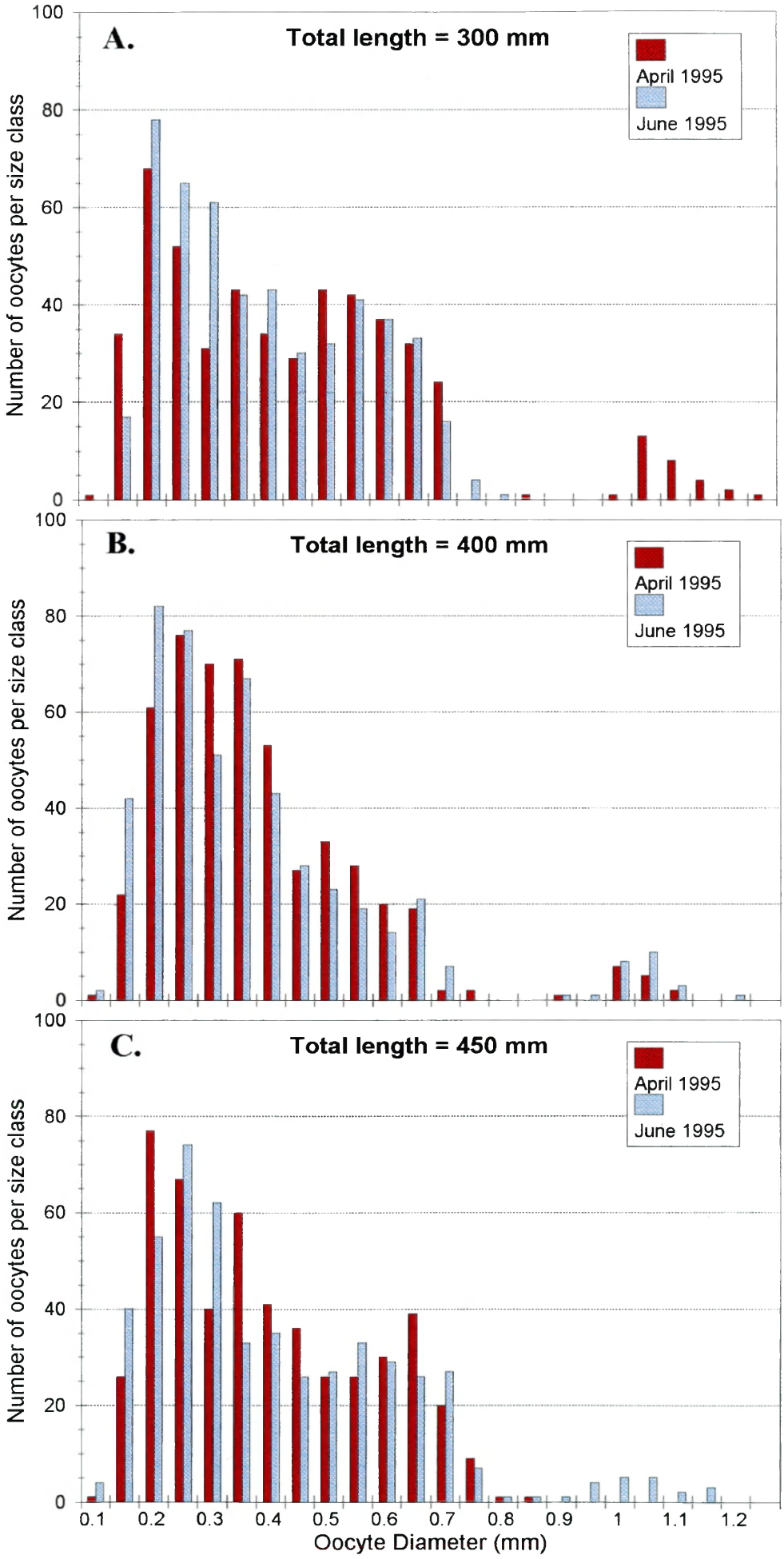
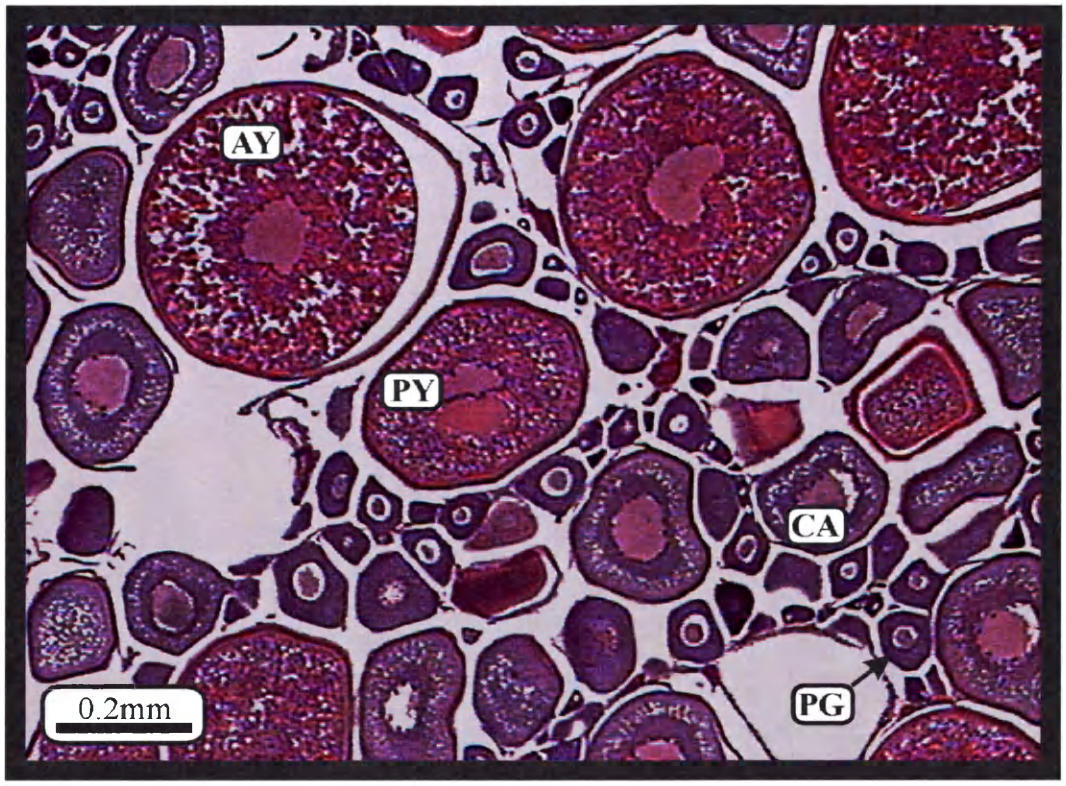
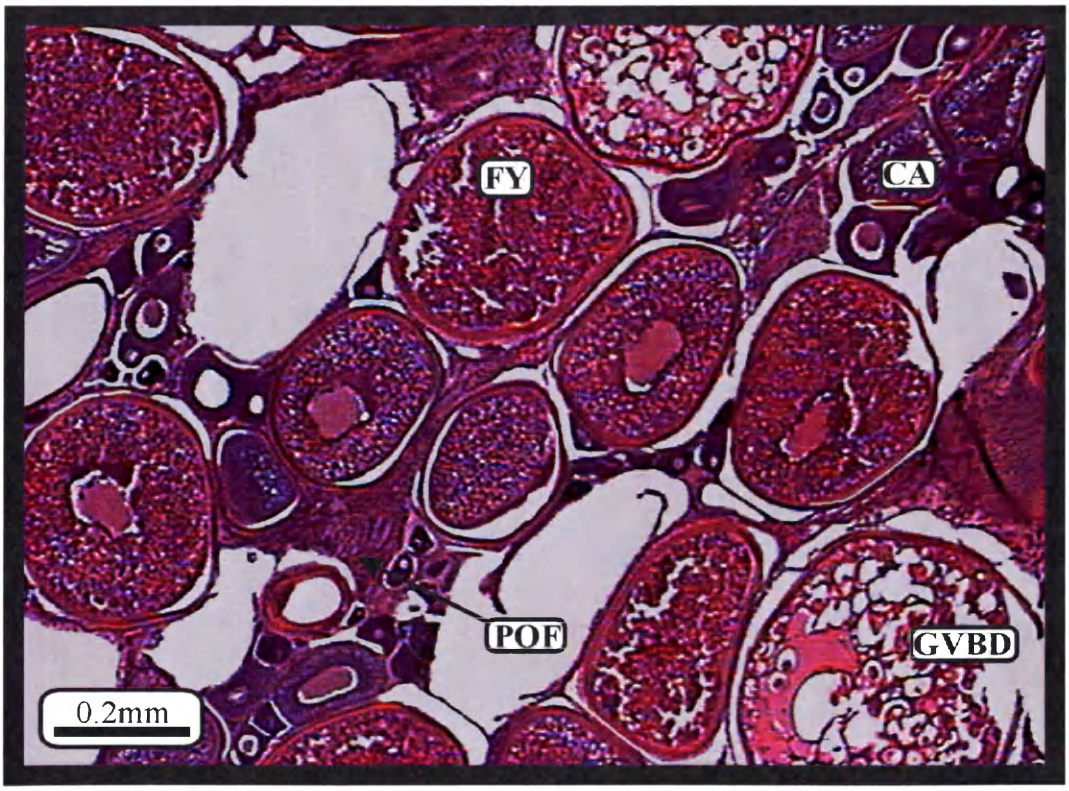

A.
Total length = 300 mm
April 1995
June 1995
Number of oocytes per size class
0
20
40
60
80
100
B.
Total length = 400 mm
April 1995
June 1995
Number of oocytes per size class
0
20
40
60
80
100
C.
Total length = 450 mm
April 1995
June 1995
Number of oocytes per size class
0
20
40
60
80
100
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
Oocyte Diameter (mm)

Figure 6: Histologic appearance of a) fully developed and b) partially spent/redeveloping stage tautog ovaries. Note presence of most oocyte stages in each picture as evidence of asynchronous oocyte development and indeterminate annual fecundity. PG - primary growth oocytes. CA - cortical alveoli oocytes. PY - partially yolked oocytes. AY - advanced yolked oocytes. GVBD - germinal vesicle breakdown oocytes. POF - post-ovulatory follicle.

a)



b)



Spawning season/location

Tautog were collected 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).

Gonadosomatic indices indicate that tautog spawn from April through June, with peak spawning in April for the 1995 spawning season (Fig. 7). No bias in GSI was caused by use of somatic weight (Fig. 7a), as the pattern of mean GSI-SW by month is similar to mean GSI-EW by month (Fig. 7b). Both male and female GSI values decreased through the spawning season. Mean GSI was lower for males and females from August through February.

The 1995 spawning season was more precisely defined as 7 April - 15 June by the presence of females staged histologically as hydrated, running ripe, and partially spent/redeveloping. 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 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).

Sex ratios

Overall sex ratios varied significantly from an expected one to one ratio with more females than males (1.28:1, χ^2=14.21, n=931). Sex ratios per 100 mm size class (Table 3) were significantly different than the expected one to one ratio for fish under 400 mm, and did not vary significantly for fish over 400 mm.

Figure 7: Gonadosomatic indices for tautog collected in lower Chesapeake Bay (1994-1995). a) GSI based on somatic weight (GSI-SW), b) GSI based on eviscerated weight (GSI-EW), sample sizes given in legend.

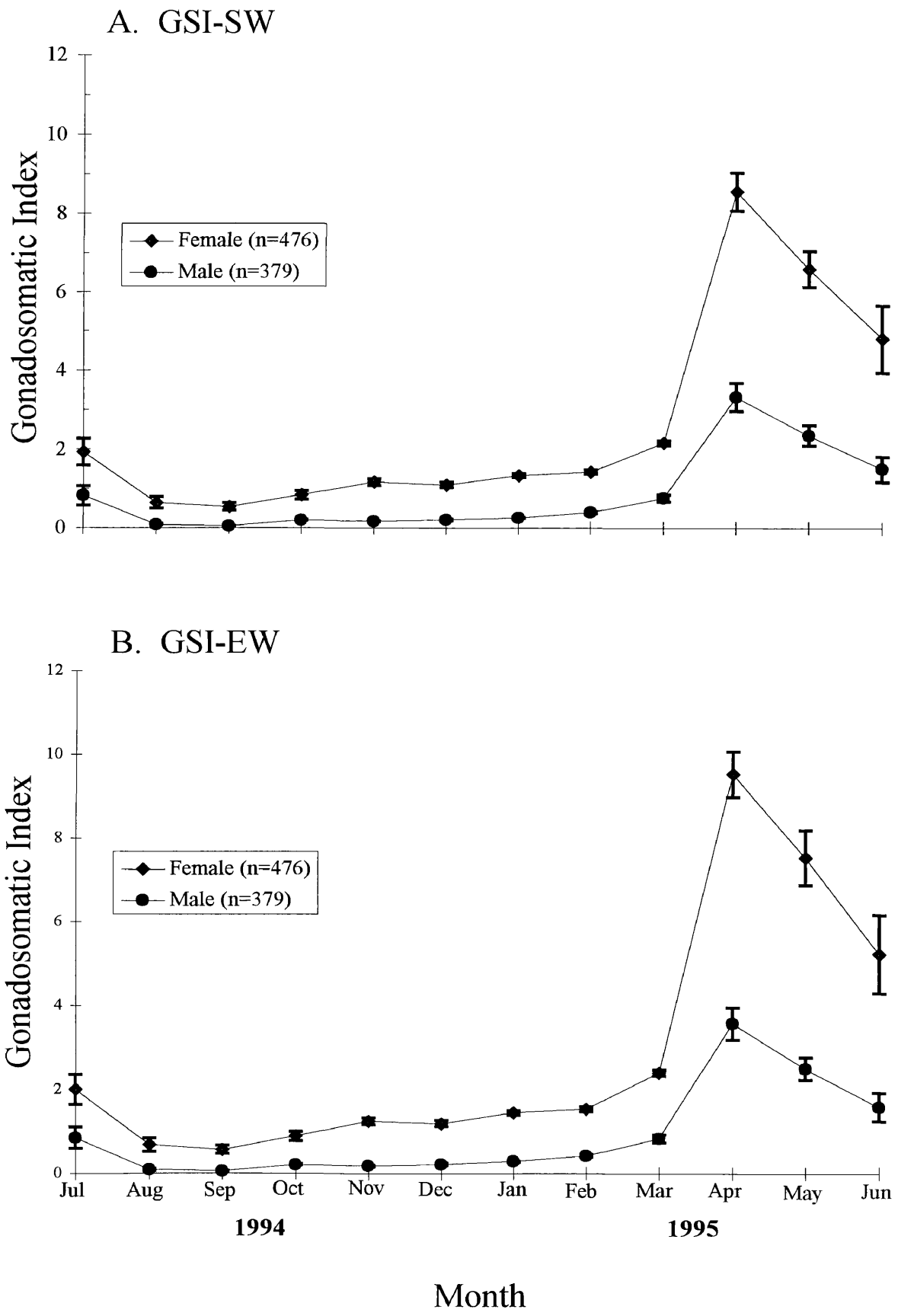

A. GSI-SW
Gonadosomatic Index
12
10
8
6
4
2
0
Female (n=476)
Male (n=379)
B. GSI-EW
Gonadosomatic Index
12
10
8
6
4
2
0
Female (n=476)
Male (n=379)
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
1994
1995
Month

Table 3: Chi square analyses of tautog sex ratios by 50 mm length intervals. Significant deviations from an expected one to one relationship are noted with an (*). Significance was set at p=0.05 a priori.

Total length (mm)	# Males	# Females	# expected	% females	Chi-Square
150-199	11	23	17	68	4.24*
200-249	22	20	21	48	0.10
250-299	35	68	52	66	10.57*
300-349	71	110	91	61	8.40*
350-399	77	105	91	58	4.31*
400-449	73	76	75	51	0.06
450-499	65	50	58	43	1.96
500-549	23	31	27	57	1.19
550-599	17	23	20	58	0.90
600-649	7	11	9	61	0.89
650-799	5	3	4	38	0.50
total	408	523	466	56	14.21*

Length and age at maturity

Tautog length at first maturity (L_{50}) was 193 mm for males and 206 mm for females (Fig. 8). All males and females were mature at 300 mm. There were no females less than 227 mm that had hydrated oocytes or POFs to indicate spawning activity.

Age at maturity was defined as the age at which at least 50% of the fish are mature. No male tautog were mature at age 1, 38% were mature at age 2, and 93% were mature at age 3. No females were mature at age 2, 78% were mature at age 3, and all females were mature at age 4 (Fig. 9).

Batch fecundity

Oocyte development was evenly distributed throughout the ovaries of tautog in spawning condition. MANOVA results (Table 4) testing the effect of individual fish and position within the ovary for 8 cell classes showed a significant difference between fish (alpha = 0.05). Therefore, blocking by fish proved beneficial and effective in removing any artifact caused by differences in kill time between fish, while increasing the quality of the test by using more fish. Non-significant positional effects in ovarian development allows estimation of batch fecundity from middle ovarian sections (3 tissue samples), thus saving analysis time.

Batch fecundity was determined for 29 female tautog ranging in total length from 260-520 mm, total weight from 475-3500 g, and ages 3-9 (Table 5). Although there was a high degree of variation in batch fecundity between individual fish, there were significant relationships between batch fecundity and fish length, weight, and age. Batch fecundity

Figure 8: Length at maturity for a) male and b) female tautog collected during the spawning season in lower Chesapeake Bay and nearby coastal waters of Virginia (1995). Curves indicate logistic regression line.

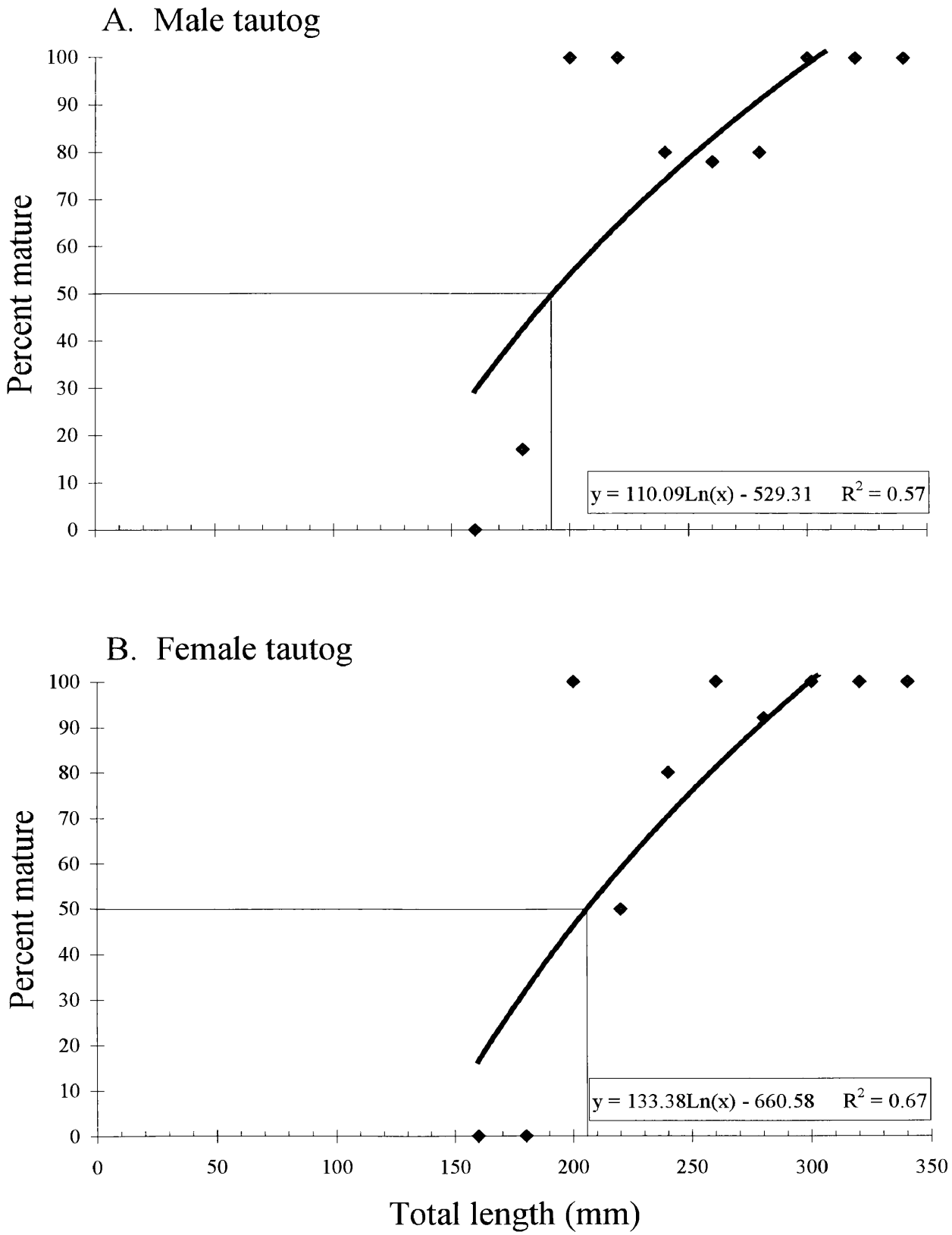

A. Male tautog
Percent mature
100
90
80
70
60
50
40
30
20
10
0
y = 110.09Ln(x) - 529.31 R2 = 0.57
B. Female tautog
Percent mature
100
90
80
70
60
50
40
30
20
10
0
y = 133.38Ln(x) - 660.58 R2 = 0.67
0
50
100
150
200
250
300
350
Total length (mm)

Figure 9: Age at maturity for a) male and b) female tautog collected during the 1995 spawning season in lower Chesapeake Bay and nearby coastal waters of Virginia.

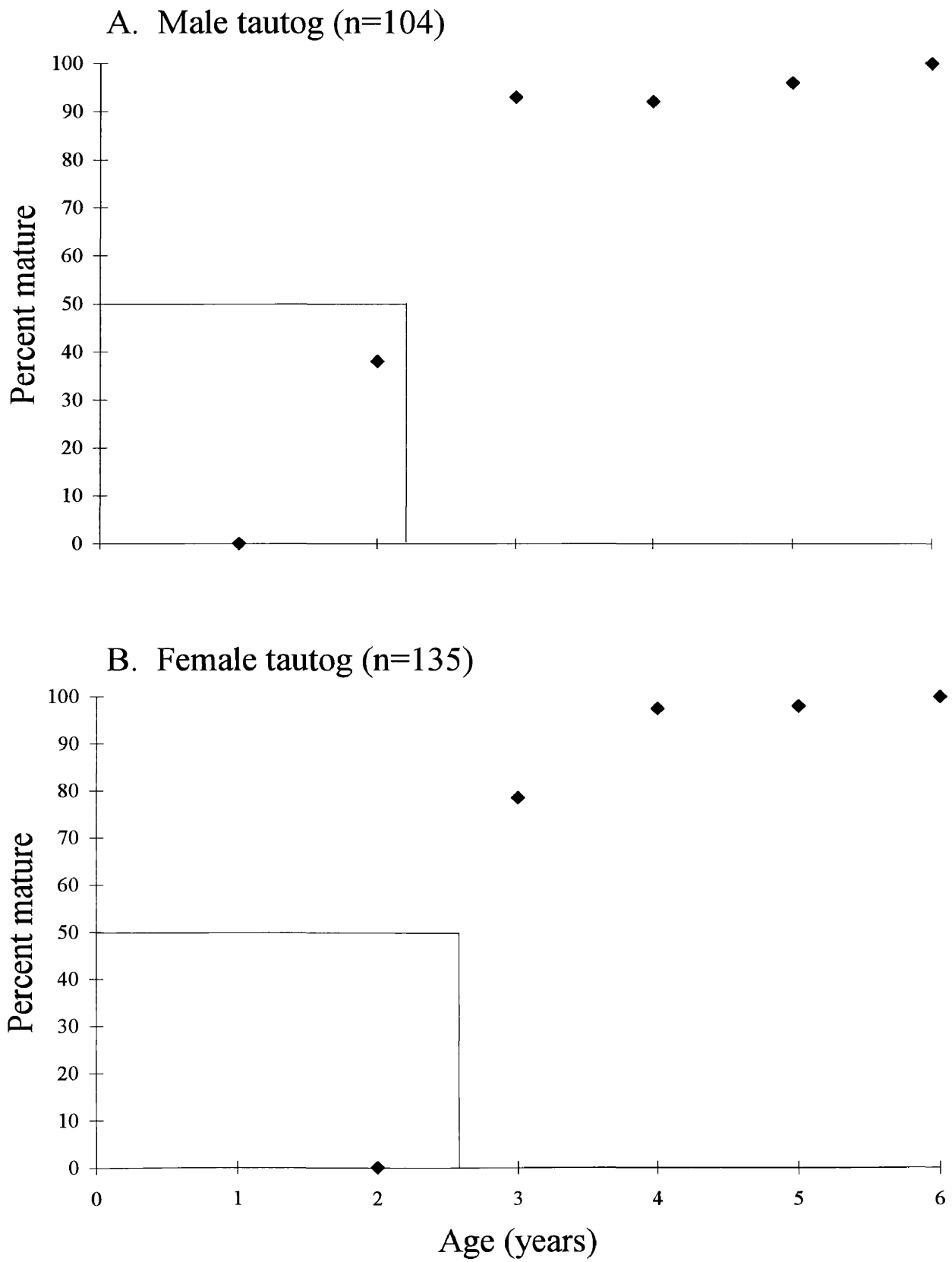

A. Male tautog (n=104)
Percent mature
100
90
80
70
60
50
40
30
20
10
0
B. Female tautog (n=135)
Percent mature
100
90
80
70
60
50
40
30
20
10
0
0
1
2
3
4
5
6
Age (years)

Table 4: MANOVA testing for variation in oocyte development between ovarian positions. Measurements tested were relative cell volumes for eight cell classes from three ovarian positions (anterior, middle, posterior) within ten individual fish.
* indicates significance at alpha = 0.05.

	Between Tautog		Ovarian Position within Tautog	
s value	8		2	
	Wilk's	Lawley-Hotelling	Wilk's	Lawley-Hotelling
test value	0.00	77.92	0.25	2.12
F value	4.61	10.01	1.35	1.32
df	72, 74	72, 74	16, 22	16, 20
p value	0.00*	0.00*	0.25	0.27

Table 5: Batch fecundity estimates for 29 tautog collected during the 1995 spawning season. Corrected gonad weight is a calculated formalin fixed wet weight used in the batch fecundity equation.

Date	Total Length (mm)	Total Weight (g)	Eviscerated Weight (g)	Age opercle	Gonad Weight (g)	Corrected GW (g)	Batch Fecundity
950422	259	373	340	3	10.90	12.85	2,754
950426	275	472	422	4	25.40	28.99	4,959
950601	281	445	394	4	21.20	24.41	15,857
950422	288	528	452	4	35.90	40.17	21,687
950422	301	626	534	4	31.50	35.53	15,231
950509	306	555	491	5	20.00	23.09	7,204
950426	306	728	582	5	85.40	89.91	46,122
950601	313	689	560	5	63.70	68.50	56,124
950422	323	711	593	5	48.50	53.19	24,256
950426	334	1,096	796	5	206.40	207.89	102,903
950426	334	1,071	798	4	187.20	189.06	148,854
950426	334	1,246	916	4	240.00	241.00	157,197
950601	338	829	722	5	51.80	56.55	39,388
950601	339	879	723	6	79.90	84.51	55,734
950426	350	1,220	926	6	171.40	173.60	87,171
950601	361	1,012	833	7	96.40	100.65	57,625
950426	367	1,280	954	7	205.00	206.52	106,416
950601	370	1,031	887	6	79.50	84.12	66,014
950509	375	1,138	1,011	6	77.90	82.55	33,952
950601	386	1,271	1,077	6	108.90	112.81	101,445
950407	395	1,702	1,370	7	184.20	186.12	51,222
950426	396	1,494	1,144	7	208.80	210.25	134,900
950509	422	1,698	1,577	7	205.80	207.30	121,092
950407	444	2,311	1,839	6	249.00	249.89	43,279
950407	470	3,021	2,439	8	335.50	335.79	97,305
950407	473	2,930	2,423	9	269.20	269.89	64,297
950509	506	2,662	2,239	8	224.00	225.21	114,631
950407	511	3,477	2,757	9	413.70	413.80	181,190
950407	516	3,483	2,728	9	398.40	398.52	133,882

increased significantly with total length (ANOVA, n=29, F=16.92, P<.0005), following the regression equation (Fig. 10):

$$BF = 425.76 - 84{,}534(TL) \quad ; \ R^2 = 0.39$$

Batch fecundity increased significantly with total weight (ANOVA, n=29, F=16.80, P<.0005), the regression equation being (Fig. 11):

$$BF = 56{,}066Ln(TW) - 322{,}091 \quad ; \ R^2 = 0.50$$

Batch fecundity also increased significantly with age (ANOVA, n=29, F=10.22, P<.004), following the regression equation (Fig. 12):

$$BF = 15{,}731(AGE) - 15{,}731 \quad ; \ R^2 = 0.27$$

Batch fecundity was more closely related to total length and total weight than to age.

Tautog relative fecundity did not increase significantly with length (ANOVA, n=29, F=1.98, P=0.17) or age (ANOVA, n=29, F=1.72, P=0.20), although there was a significant increase in relative fecundity with total weight (ANOVA, n=29, F=4.46, P=.044).

Spawning frequency

During the 1995 spawning season, 87% of female tautog caught were in spawning condition, corresponding to a spawning frequency of once every 1.1 days. The occurrence of females with both GVBD oocytes and POFs (Fig. 4f) - signifying daily spawning (see chapter 2) - indicates tautog are capable of spawning at such high frequencies.

Figure 10: Regression of tautog batch fecundity on total length (mm) for 29 tautog collected in lower Chesapeake Bay and nearby coastal waters of Virginia in 1995.

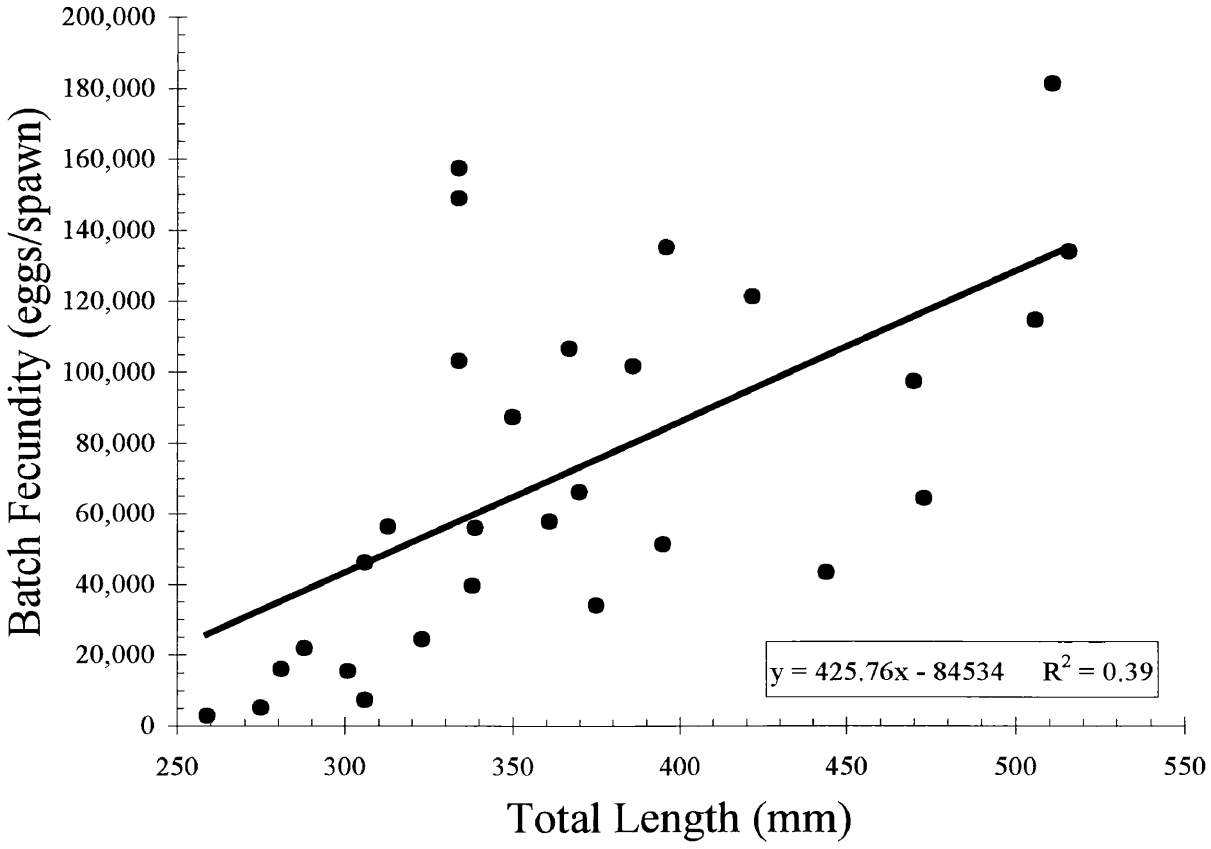

Batch Fecundity (eggs/spawn)
200,000
180,000
160,000
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
250
300
350
400
450
500
550
Total Length (mm)
y = 425.76x - 84534
R2 = 0.39

Figure 11: Regression of tautog batch fecundity on total weight (g) for 29 tautog collected in lower Chesapeake Bay and nearby coastal waters of Virginia in 1995.

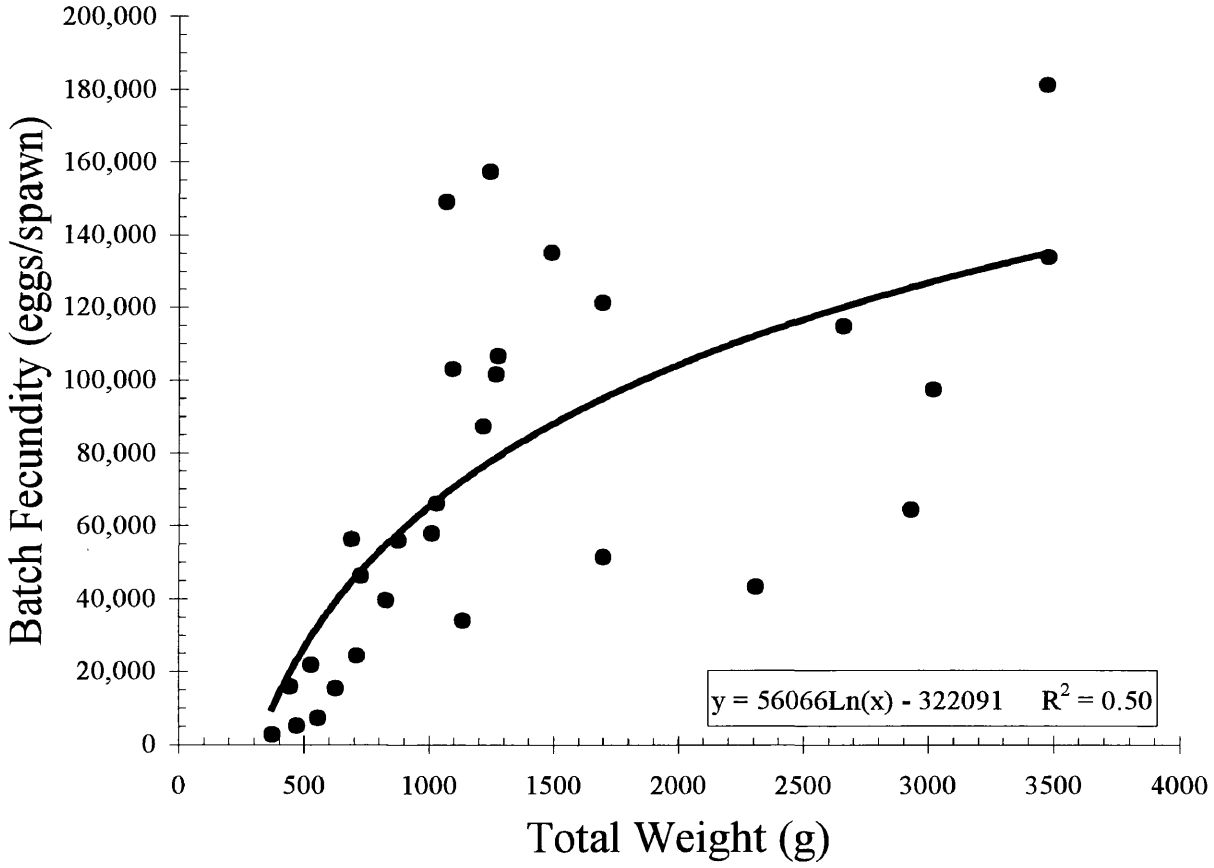
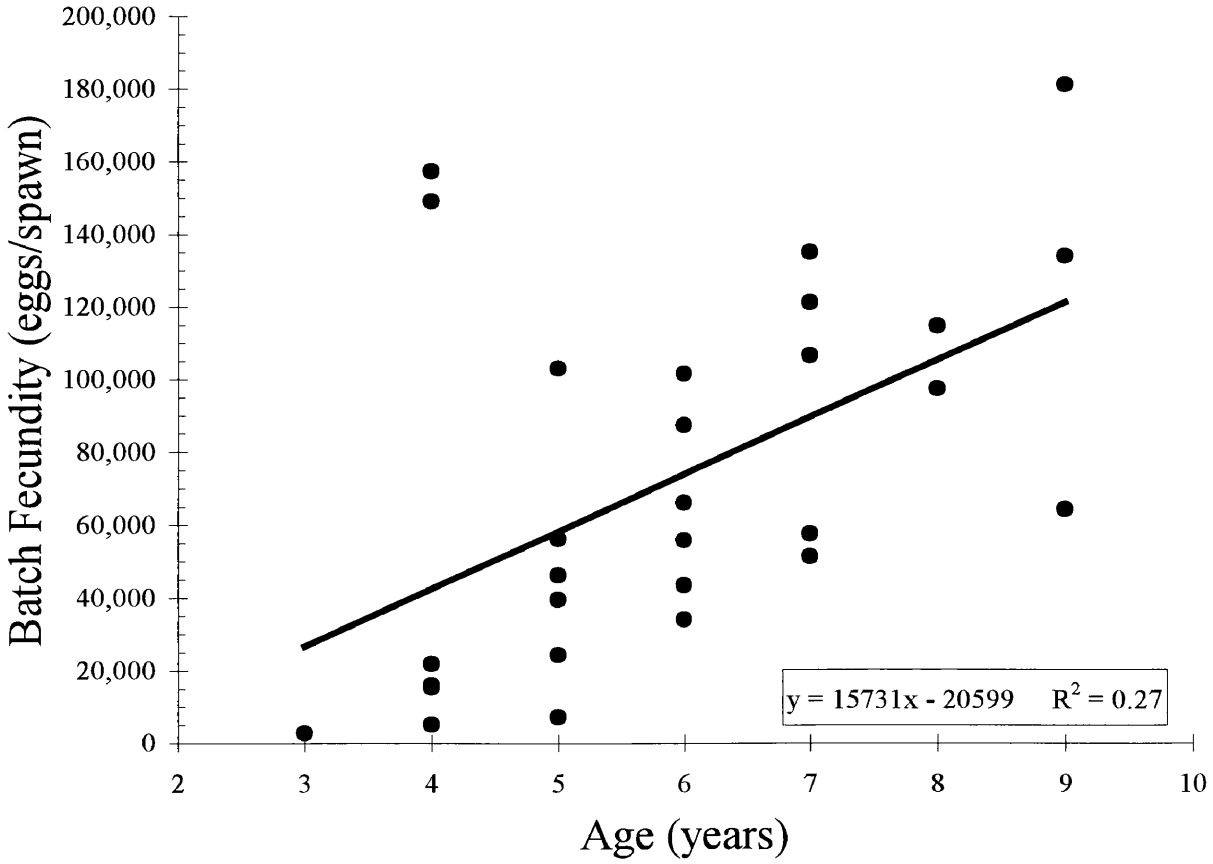

Batch Fecundity (eggs/spawn)
200,000
180,000
160,000
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
0
500
1000
1500
2000
2500
3000
3500
4000
Total Weight (g)
y = 56066Ln(x) - 322091
R2 = 0.50

Figure 12: Regression of tautog batch fecundity on age (years) for 29 tautog collected in lower Chesapeake Bay and nearby coastal waters of Virginia in 1995.


Batch Fecundity (eggs/spawn)
200,000
180,000
160,000
140,000
120,000
100,000
80,000
60,000
40,000
20,000
0
2
3
4
5
6
7
8
9
10
Age (years)
y = 15731x - 20599
R2 = 0.27

Annual fecundity

The spawning season, defined earlier as April 7 - June 15 (70 days), was used to estimate tautog annual fecundity. The number of spawns per year was calculated as the spawning season (70 days) divided by spawning frequency (1.14 days/spawn) yielding 61 spawns per season per female. Annual fecundity was calculated as 61 spawns/female multiplied by batch fecundity. Annual fecundity varied from 167,970 eggs (259 mm, age-3 fish), to 11,052,606 eggs (511 mm, age-9 fish).

Mean annual fecundity was regressed 50 mm size classes, following the exponential relationship (Fig. 13a):

$$\text{Mean AF} = 178{,}086e^{0.0076} \quad ; R^2 = 0.67,$$

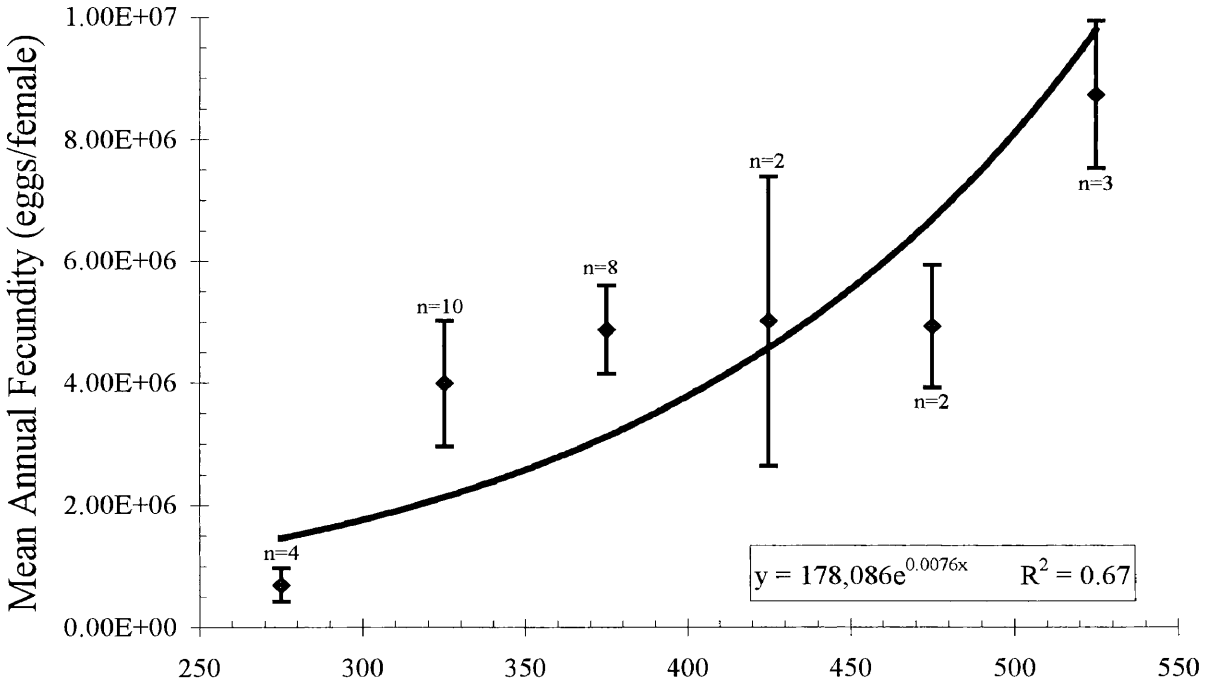
and the linear relationship (Fig. 13b):

$$\text{Mean AF} = 24{,}694(\text{TL}) - 5.17 \times 10^6 \quad ; R^2 = 0.81.$$

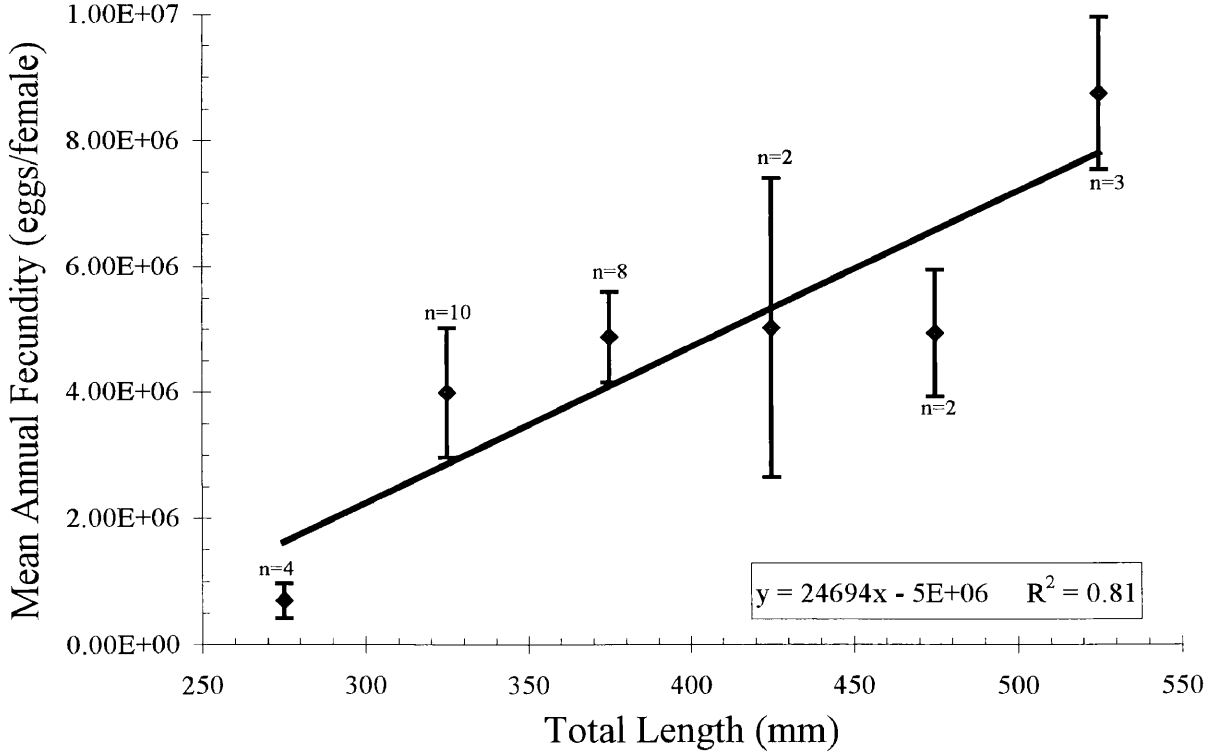
The exponential curve was fitted to the data based on a theoretical logistic curve for potential annual fecundity of tautog, reaching an asymptote at older ages (approaching 20 years for females). However, the linear regression provided a better empirical relationship for this Data set. Mean annual fecundity increased significantly with fish size (ANOVA, n=5, F=16.69, P=0.015).

Figure 13: Mean annual fecundity for tautog divided into 50 mm length classes following a) exponential relationship and b) linear relationship. Sample sizes are noted above each data point. Error bars indicate standard error of the mean.

A.


Mean Annual Fecundity (eggs/female)
1.00E+07
8.00E+06
6.00E+06
4.00E+06
2.00E+06
0.00E+00
250
300
350
400
450
500
550
n=4
n=10
n=8
n=2
n=2
n=3
y = 178,086e^0.0076x
R^2 = 0.67

B.


Mean Annual Fecundity (eggs/female)
1.00E+07
8.00E+06
6.00E+06
4.00E+06
2.00E+06
0.00E+00
250
300
350
400
450
500
550
Total Length (mm)
n=4
n=10
n=8
n=2
n=2
n=3
y = 24694x - 5E+06
R^2 = 0.81

DISCUSSION

Gonad staging and spawning pattern

Tautog are a multiple spawning species with a complex reproductive cycle. Female gonadal development, defined by eight microscopic stages, follows a pattern typical of multiple spawners (Hunter et al., 1985) which includes 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), this study defines oocyte development and type of fecundity using recently improved methodologies (Lowerre-Barbieri and Barbieri, 1993) and histological techniques on fish taken from natural environments. Therefore it is 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 indicate that tautog have asynchronous oocyte development and indeterminate annual fecundity. Therefore, the number of eggs in the ovary at any one time during the spawning season is inadequate to measure potential annual fecundity, as new batches of eggs are continuously matured from primary growth oocytes through hydrated oocytes and 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, which supports the classification of

regressing stage ovaries in this study, based on the histological occurrence of partially yolked oocytes in various stages of atresia. The similarity between oocyte size frequency distributions of spawning tautog widely separated by date and location (Chenoweth, 1963; This study), observations of tautog spawning daily in laboratory aquaria (Olla et al., 1977), and histological analysis of ovarian tissue supports the classification of tautog as a multiple spawning species with indeterminate annual fecundity.

Percent agreement between macroscopic and microscopic ovarian staging techniques found macroscopic staging to be inadequate to assess ovarian development in eight stages. Although there were many misclassifications by macroscopic staging, errors were usually only one developmental stage away (Table 2). Errors in macroscopic staging were most likely due to the rapid development of ovarian tissue required to sustain daily spawning events. Macroscopic ovarian staging of multiple spawning fishes can be difficult, as subtle differences at the cellular level may not be detectable at the gross gonadal level (Parrish et al., 1986). For example, macroscopic analysis cannot determine the occurrence of POFs, atretic oocytes, and macrophage aggregates; the cellular structures that help distinguish partially spent/redeveloping, spent, and resting females. However, macroscopic analysis provides rapid maturity estimates and a description of spawning seasons at a lower cost than time consuming histological methods. Although macroscopic staging described the annual gonad cycle, it did not separate fully developed (stage 3) and partially spent (stage 4) ovaries, thus could not provide evidence for the inner spawning cycle. The use of histological techniques in this study was necessary to accurately describe the annual and the inner spawning ovarian developmental cycles of tautog, and identify fully hydrated ovaries for batch fecundity estimation.

The low percent agreement (51% overall) between macroscopic and microscopic classification of eight ovarian stages suggests combining some of the microscopic stages based on cellular development into fewer macroscopic stages which are more reliably distinguished at the gross gonadal level. Five macroscopic gonad stages (described in Table 6) can be created based on the distribution of data in Table 2: immature, developing, spawning, running ripe, and spent. Classification of immature ovaries remains unchanged. Mature ovarian classifications were grouped as follows: revised developing stage now includes previous developing and fully developed stages; revised spawning stage includes hydrated and partially spent ovaries; and the revised spent stage includes previous spent and resting stages (Table 6). Previous studies of tautog reproductive biology used five macroscopic stages, similar to the revised macroscopic stages presented in Table 6, to assess ovarian development (Chenoweth, 1963; Stolgitis, 1970; Hostetter and Munroe, 1993).

Spawning season and location

Tautog spawn over a two month period throughout the species range, with the initiation of spawning activity occurring later in the spring to early summer in more northern regions (Chenoweth, 1963; Stolgitis, 1970; Briggs, 1977; Hostetter and Munroe, 1993). In this study, the spawning season occurred from 7 April through 15 June 1995 (70 days). Hostetter and Munroe (1993) also reported late April through June as the tautog spawning season in Virginia. In Rhode Island, tautog have been recorded to spawn from early June through late July (Chenoweth, 1963). Spawning seasons have been reported as long as three months (mid-May through early August) for fish in Massachusetts (Stolgitis, 1970), and four months (early May through early September) for tautog in New York waters (Austin, 1973).

Abundance of tautog eggs in plankton collections also show tautog spawning seasons occur 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), but it is interesting to note that the length of tautog spawning seasons is similar throughout the species range. Increasing water temperature during springtime is a major cue to initiate spawning, but termination of spawning activity has not been related to environmental cues. 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. On 9 May 1995, fish collected 20 km offshore changed ovarian stage from running ripe to partially spent, indicating that spawning had occurred (see Chapter 2). Field observations of tautog daily movements found 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. Tagging studies indicate that discrete spawning groups exist at sites in Narragansett Bay (Cooper, 1966), however movement between sites was not quantified. Although most tautog migrate inshore in the spring to spawn (Cooper, 1966), some portion of the population remains offshore year round (Eklund and Targett, 1990; Hostetter and Munroe, 1993). However, there is not sufficient data available to determine if tautog exhibit spawning site fidelity throughout the spawning season, or use multiple spawning sites within general inshore and offshore classifications. Although

Table 6: Suggested macroscopic gonad stages for future research on tautog. Macroscopic stages are revised from 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. (Immature stage from Table 1)
Developing Fully Developed	**Developing**	ovaries medium to large, yolked oocytes present, appears slightly grainy, pale mustard in color, no hydrated oocytes visible through ovarian membrane. (Developing and Fully developed stages from Table 1)
Hydrated	**Spawning**	ovaries large to very large, yolked oocytes interspersed with large transparent (hydrated) oocytes, occasionally a few remnant hydrated oocytes. (Hydrated and Partially spent/ redeveloping stages from Table 1)
Running Ripe	**Running Ripe**	ovaries large to very large, clear oocytes have been ovulated and expand lumen of ovary, are easily extruded from excised ovary; few clear oocytes in ovarian tissue. (Running Ripe stage from Table 1)
Partially spent/ redeveloping		
Spent Resting	**Spent**	ovaries flaccid, small to medium, red to purple in color, few yolked (opaque) oocytes visible, some or all of ovary clear with no oocytes visible. (Spent and Resting stages from Table 1)

spawning occurs at both inshore and offshore locations, spawning success in these areas, as well as larval drift and recruitment patterns, are unknown at this time.

Sex ratios

Sex ratios vary greatly between published studies on tautog life history. This variability may be due to true differences in the composition of local populations, or an artifact of sampling strategies rooted in collection seasons or gear biases. In this study, sex ratios were skewed towards females for fish under 400 mm TL, and did not differ significantly from a one to one ratio for tautog greater than 400 mm TL. 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 of 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 7 years, collected primarily with fish traps and hook and line. Eklund and Targett (1990) found a 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 between May and September 1961. Aspects of tautog behavior and migration may influence the sex ratios of landed fish, depending on time of year, gear use, and social behavior of individual fish. However, data are insufficient to evaluate the effects of these factors.

Length and age at maturity

Published reports of tautog length and age at maturity are similar throughout the

species range. This study found tautog length at maturity (L_{50}) to be 193 mm for males and 206 mm for females. Seventy-eight percent of females age 3 (199-274 mm) were mature. Thirty-eight percent of males were mature at age 2 (162-193mm) and 93% mature at age 3 (206-310 mm). Hostetter and Munroe (1993) also reported that females reach 100% maturity at age 4 and males at age 3 in Virginia. Age and length at maturity for tautog collected in Massachusetts (Stolgitis, 1970) are also similar; 40% of age 2 (149-175) males and 87% age 3 (171-239 mm) males were mature, while females attain 71% maturity at age 3 (187-206 mm) and 100% maturity at age 4. In Rhode Island, Cooper (1966) found males mature at 300 mm (age 3) and females at 190 mm (age 3).

Hostetter and Munroe (1993) suggested that precocious development may be occurring in tautog as a response to fishing pressure, based on a small number of fish sampled in northern areas. No clear trend exists in the smallest female collected in spawning condition between studies that suggests female tautog are maturing at smaller sizes; 227 mm in Virginia (this study), 261 mm in Massachusetts (Stolgitis, 1970), and in Rhode Island, 216 mm (Chenoweth, 1963) and 180 mm (Hostetter and Munroe, 1993). A definitive answer on precocious development is not possible at this time, as data on small fish are limited in all studies.

Fecundity

The tautog is a multiple spawning species with asynchronous oocyte development and indeterminate annual fecundity. Therefore, the only way to assess potential annual fecundity is to multiply batch fecundity by spawning frequency (Hunter and Macewicz 1985, Hunter et al. 1985). 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 (see Appendix; Cooper 1967; Hostetter and Munroe, 1993). Batch fecundity ranged from 2,754 eggs to 181,190 eggs in 29 females age 3-9 (Table 5). The oldest tautogs collected in this study were a 31 year old male, and an 17 year old female. After 100% maturity at age 4, individual females may spawn up to 60 times per year for as many as 14 years. A mean batch fecundity for the species does not adequately describe egg production between size or age groups. Although significant statistical relationships were found between batch fecundity and total length, total weight, and age, there were no distinct gaps in fecundity levels to divide fish into natural groups. Mean batch fecundity was calculated for two age groups, 4-6 and 7-9, since all females were mature by age 4 and over 90% of all tautog sampled in this study were less than 10 years old. Mean batch fecundity for female tautog age 4-6 was 54,243 ± 2,472 eggs and 106,256 ± 3,837 eggs for females age 7-9 (Table 7).

Previous estimates of tautog fecundity by Chenoweth (1963) and Stolgitis (1970) are not annual fecundity estimates. Both studies counted mature, transparent eggs in the ovary, currently referred to as hydrated oocytes; but they did not distinguish tautog as having seasonally indeterminate annual fecundity, and had no measure of spawning frequency. By counting only the most advanced oocytes, i.e. the hydrated oocytes, Chenoweth and Stolgitis actually estimated batch fecundity. Mean batch fecundity calculated for ages 4-6 and 7-9 from data presented by Chenoweth (1963) and Stolgitis (1970) are presented in Table 7. It is interesting to note the similarity of batch fecundity estimates over the period of 30 years between studies, and wide geographic areas, i.e. Chesapeake Bay to Narragansett Bay (550 km).

Table 7: Comparison of batch fecundity estimates for tautog.

	Mean Batch Fecundity ± SEM			
Study	Age 4 - 6	n	Age 7 - 9	n
Chenoweth (1963)	49,967 ± 1,032	29	103,214 ± 4,005	14
Stolgitis (1970)	46,833 ± 4,500	6	117,478 ± 2,488	23
White (1996)	54,243 ± 2,472	18	106,256 ± 3,837	10

Spawning frequency has not been previously calculated for tautog using methods developed by Hunter and Macewicz (1985). Spawning frequency in this study was estimated at 1.14 days, thus over the 70 day spawning window, female tautog are estimated to spawn on 61 days. Under artificial conditions, Olla et al. (1977) observed tautog spawning on 68-96 consecutive days in laboratory aquaria. Therefore the estimate of 61 spawning days in natural habitats is not unrealistic. Chenoweth (1963) raised the question, but could not answer whether 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 tautog are capable of such activity in natural habitats under appropriate environmental conditions (temperature, day length, etc.).

Estimates of potential annual fecundity for Virginia tautog age 3-9 ranged from 168,000 to 11,052,606 eggs. However, net annual fecundity may be lower due to remnant hydrated oocytes, atresia, nutritional status of adult females, or environmental conditions (McEvoy and McEvoy, 1992). Regression of mean annual fecundity (eggs/female) on total length was analyzed with both exponential and linear relationships (Fig. 13). The exponential curve was fitted to the data (Fig. 13a) based on a theoretical logistic curve for potential annual fecundity of tautog, reaching an asymptote at older ages (approaching 20 years for females) similar to increases in total length. Annual fecundity estimates were only possible for females between age 3 and age 9, thus only the exponential portion of the logistic curve is visible. The linear regression equation (Fig. 13b) has a better fit and predictive power ($R^2 = 0.81$) than the exponential regression. Although annual fecundity estimates were not possible over the entire size range of mature females sampled in this study

(ages 3-17), over 90% of the fish sampled were younger than age 10. Therefore, the linear regression equation is the best predictor of potential annual fecundity for the most abundant size range of tautog sampled in the lower Chesapeake Bay and coastal waters of Virginia.

Fecundity estimates by Chenoweth (1963) ranged from 5,000 to 673,500 eggs. Stolgitis (1970) presented a similar range for tautog fecundity, 7,000 to 483,000 eggs. Although analysis of their methods clearly shows those are batch fecundity estimates, data are presented here for comparison, since results of Chenoweth and Stolgitis are commonly cited as representing annual fecundities. For theoretical comparison, by combining batch fecundity ranges of Chenoweth (1963) and Stolgitis (1970) to between 6,000 and 550,000 eggs, and multiplying by the 68 day "spawning season" observed in laboratory aquaria by Olla et al. (1977), the calculated potential annual fecundity would be 408,000 to 37,400,000 eggs per female, depending on size and/or age of the individual. This estimate is higher than the estimated potential annual fecundity of Virginia tautog (168,000 to 11,053,000 eggs), and may be due to the fact that fish older than age 9 were lacking in the Virginia fecundity estimates.

Overview

Tautoga onitis is the only labrid species for which potential annual fecundity has been estimated. This research was one step necessary to more fully understand tautog reproduction and life history. Although spawning season length and batch fecundity estimates are similar between southern and northern portions of the tautog's range, previous estimates date back 30 years. Estimates of annual fecundity in the northern regions of the species range should be pursued to determine if tautog annual fecundity varies with latitude.

Even if batch fecundity and spawning frequency remain relatively constant over latitude, the size structure of the stock will dictate estimates of total egg production, thus continued research is necessary to clarify the size structure of tautog populations throughout the species range.

Hostetter and Munroe (1993) found that tautog age at maturity was similar to that measured in Rhode Island by Cooper (1966) almost 30 years previous and suggested it may be the result of sampling relatively healthy populations. Similarities in age at maturity between this study and Stolgitis (1970), and batch fecundity estimates with Chenoweth (1963) and Stolgitis (1970), may also indicate healthy populations, as juvenescence has not been observed. Many aspects of tautog life history affect recruitment but require further investigation, including: egg dispersal, egg mortality, larval drift, larval mortality, hatching success, first feeding success, pre-settlement mortality, post-settlement mortality, juvenile mortality, recruitment, stock structure, and spawning stock biomass (ASMFC, 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, 1996). In April 1997, ASMFC will impose a 13 inch, or 325 mm size limit on tautog, effective from Delaware through North Carolina, and 14 inches (350 mm) north of Delaware. Proposed size limits are supported by data from this study as a 325 mm size limit will allow tautog in the southern region to spawn for at least one spawning season, and most likely two, therefore contributing a mean annual fecundity of 3.02 million eggs per female calculated from the linear regression equation (Fig. 13b).

CHAPTER 2

Daily spawning incidence

INTRODUCTION

Marine teleost fishes have evolved a variety of reproductive strategies. Presumably, the strategy employed by each species is tuned to provide maximum survivorship to the offspring. For example, multiple spawning species release gametes over a protracted spawning season each year. Therefore, egg release and larval development (growth, transport, and settlement) occur over a range of environmental conditions, which enhances the probability that some spawning products will coincide with favorable recruitment conditions (Johannes, 1978; Doherty, 1983). Ferraro (1980) suggested that annual spawning seasons dependent upon temperature, annual production, or a period of low predation (Nikolsky, 1963; Cushing, 1969; Hoar, 1969) provide coarse adjustment, while diel spawning periodicity acts to fine tune gamete release with temporally changing environmental conditions.

Diel spawning periodicity estimates for many marine finfish have been used to investigate factors which regulate reproductive behavior. In addition to behavioral studies, estimates of annual fecundity in multiple spawning species require knowledge of spawning time (Hunter and Macewicz, 1985; Hunter et al., 1985). Diel periodicity in spawning has been hypothesized to synchronize reproduction between sexes (Aschoff, 1964), increase reproductive isolation between related and morphologically similar species (Marshall, 1967), and minimize predation on eggs and larvae (Nikolsky, 1963; Johannes, 1978). Aspects of a species life history, such as behavioral cues (spawning aggregations, visual courtship

displays) and environmental cues (tidal stage, tidal current, and/or lunar cycles), may also limit its spawning periodicity(Robertson, 1981).

Previous estimates of diel spawning periodicity for marine fish have relied on both laboratory and field techniques. Spawning has been observed in laboratory aquaria maintained under simulated light regimes (Marshall, 1967; Leong, 1971; Olla and Samet, 1977). Field estimates of diel periodicity include back calculation from naturally spawned and fertilized planktonic eggs (Ahlstrom, 1943; Simpson, 1971; Smith and Lasker, 1978; Ferraro, 1980; Holt et al., 1985), analysis of gonad tissue from fish collected with known kill times (Hunter and Macewicz, 1980; DeMartini and Fountain, 1981; Alheit et al., 1984; Goldberg et al., 1984; Clarke, 1987; Fitzhugh and Hettler, 1993; Taylor and Villoso, 1994), and diver observations of behavior (Randall and Randall, 1963; Hobson, 1965; Reinboth, 1973; Thresher, 1979; Robertson, 1981, 1983).

Four patterns of diel periodicity have been observed in marine species which spawn pelagic eggs. Morning spawning occurs in the surgeonfish *Acanthurus lineatus*, when competition for food and territory defense activities are at a minimum (Robertson, 1983). Midday/afternoon spawning is common for scarids, labrids and acanthurids which require daylight for visual courtship displays (Randall and Randall, 1963; Robertson, 1981, 1983). Dusk spawning of some acanthurid and serranid species has been attributed to daylight courtship displays and decreased egg predation at night (Randall, 1961; Colin, 1992). Nocturnal spawning fishes are not light limited, and take advantage of decreased egg predation at night (Hobson and Chess, 1978; Ferraro, 1980).

Tropical labrids commonly restrict diel spawning activity to the period between noon and dusk as observed in *Bodianus rufus*, *Halichoeres bivittattus*, *H. poeyi*,

H. maculipinna, and *Thalassoma bifasciatum* (Warner and Robertson, 1978) and *H. garnoti* (Robertson, 1981). Observations of afternoon spawning in temperate labrids are restricted to cunner (*Tautogolabrus adspersus*) (Wicklund, 1970; Pottle and Green, 1979) and tautog, *Tautoga onitis* (Olla and Samet, 1977), although Ferraro (1980) estimated that the majority of tautog spawning activity occurs at night.

The tautog is a multiple spawning labrid (Olla and Samet, 1977) that inhabits nearshore hard-bottom habitats from Nova Scotia (Bleakney, 1963) to South Carolina (Sedberry and Beatty, 1989). Tautog begin spawning activity when water temperature reaches approximately 11°C (Chenoweth, 1963; Olla et al., 1974; Eklund and Targett, 1990; Hostetter and Munroe, 1993), thus the spawning season begins later at higher latitudes. Spawning seasons extend 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). Male tautog attain 100% maturity by age 3 and females by age 4 throughout the species range (Chenoweth, 1963; Cooper, 1967; Stolgitis, 1970; Briggs, 1977; Hostetter and Munroe, 1993; Chapter 1). Observations of tautog reproductive behavior include visual courtship displays, pair spawning, group spawning, and a night time quiescent/sleep state (Olla and Samet, 1977). Published estimates of tautog diel spawning periodicity are contradictory. Under laboratory conditions, tautog have been observed to spawn between 1300 and 1600 (EST) (Olla and Samet, 1977), while back calculation from field fertilized planktonic eggs (Ferraro, 1980) estimated tautog spawning occurred between 1800 and 0100 (EST).

To determine diel spawning periodicity of tautog in Virginia, ovarian development was analyzed for tautog collected from natural habitats. Objectives of this study were to 1)

relate ovarian developmental cycle to daily spawning time, 2) determine optimal collection time of tautog ovaries for fecundity estimates in Virginia, and 3) compare previous estimates of tautog spawning periodicity with ovarian developmental data.

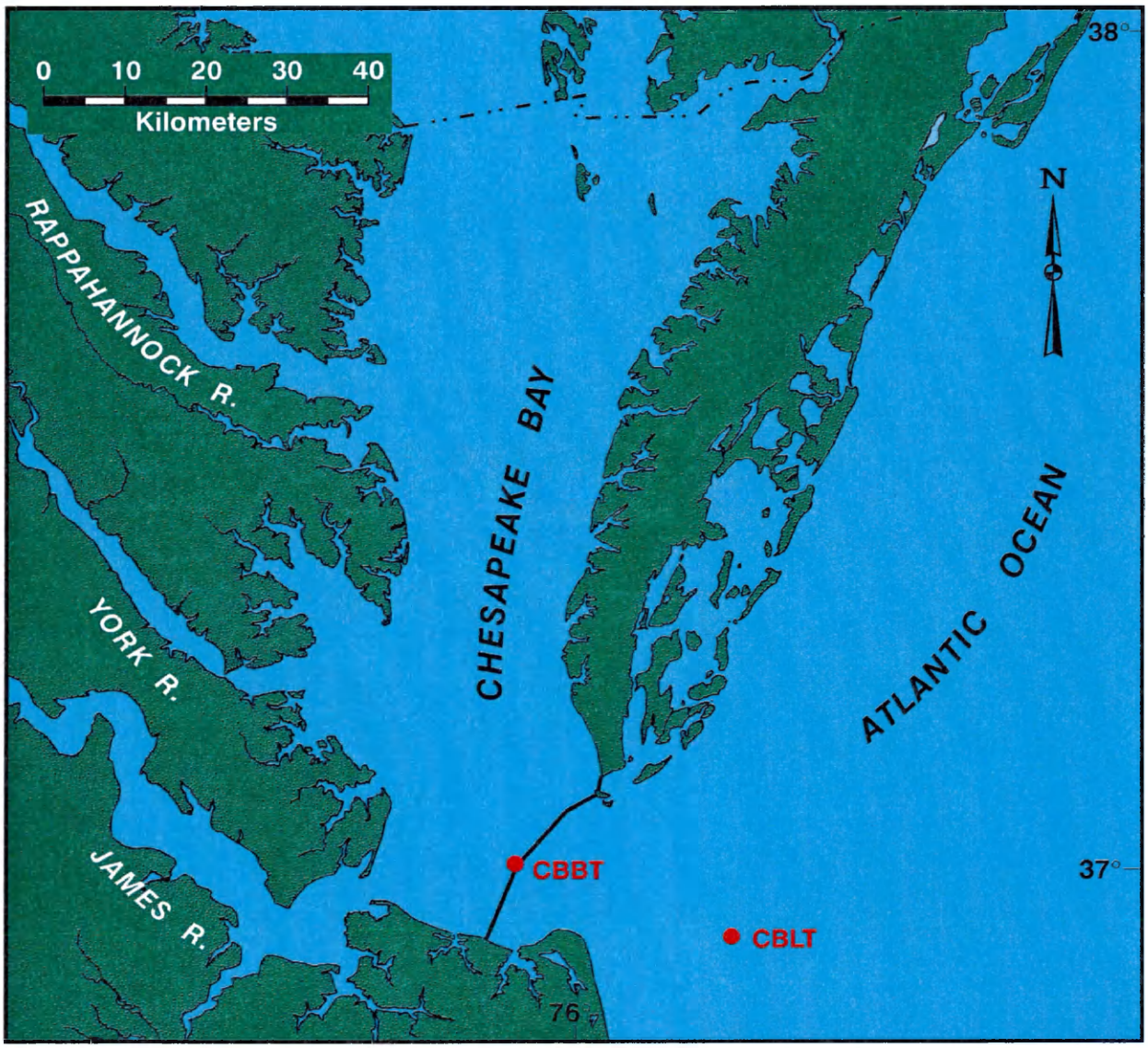
METHODS

Field collections and processing

Tautog were collected at two stations near the mouth of the Chesapeake Bay; the Chesapeake Bay Bridge Tunnel (CBBT) on 26 April 1995, and the Chesapeake Bay Light Tower (CBLT) on 9 May 1995. Multiple sites around each structure were sampled aboard a commercial hook and line vessel (Fig. 14). Female fish were field sacrificed from 0745 to 1820 (EST). Kill time, collection location, depth, and tidal stage were recorded for each field sacrificed female. Ovarian tissue was excised and staged macroscopically as fish were landed. One ovary was randomly selected by coin toss (heads = right ovary) and placed in Davidson's fixative for histological processing; the remaining ovary was fixed in 10% neutral buffered formalin for batch fecundity analysis (Chapter 1).

All male and female tautog which were not field sacrificed (unknown kill times) were retained for laboratory analysis of total length (mm), total weight (g), eviscerated weight (g), sex determination (externally and internally), gonad weight (0.1g), and age. One gonad was randomly selected by coin toss (heads = right gonad) and placed in Davidson's fixative for histological analysis and opercle bones were removed for aging. After two days in Davidson's fixative, transverse sections of anterior, middle, and posterior ovarian tissue were placed in tissue cassettes, rinsed overnight with flowing tap water, and placed in 70% ETOH. Standard histological processing (tissue embedded in paraffin, sectioned at 5-7 μm, and stained with Harris' Hematoxylin and Eosin-Y)(Luna, 1968) was performed for all samples.

Figure 14: Map of collection locations for daily spawning incidence in the lower Chesapeake Bay. CBBT = Chesapeake Bay Bridge Tunnel. CBLT = Chesapeake Bay Light Tower.


0 10 20 30 40
Kilometers
RAPPAHANNOCK R.
YORK R.
JAMES R.
CHESAPEAKE BAY
ATLANTIC OCEAN
CBBT
CBLT
N
38°
37°
76°

Ovary developmental stage classification

Studies of annual gonadal developmental cycle in multiple spawning fishes typically include eight ovarian stages (Barbieri, 1993; Lowerre-Barbieri, 1994): 1) immature, 2) developing, 3) fully developed, 4) hydrated, 5) running ripe, 3a) partially spent/redeveloping, 6) spent, and 7) resting (Table 8 = Table 1, placed again here for the readers convenience). These ovarian stages describe both the annual gonadal cycle and the internal spawning cycle (Fig. 15). The internal spawning cycle involves developmental stage 4, 5, and 3a gonadal tissue and directly correlates with diel periodicity of spawning.

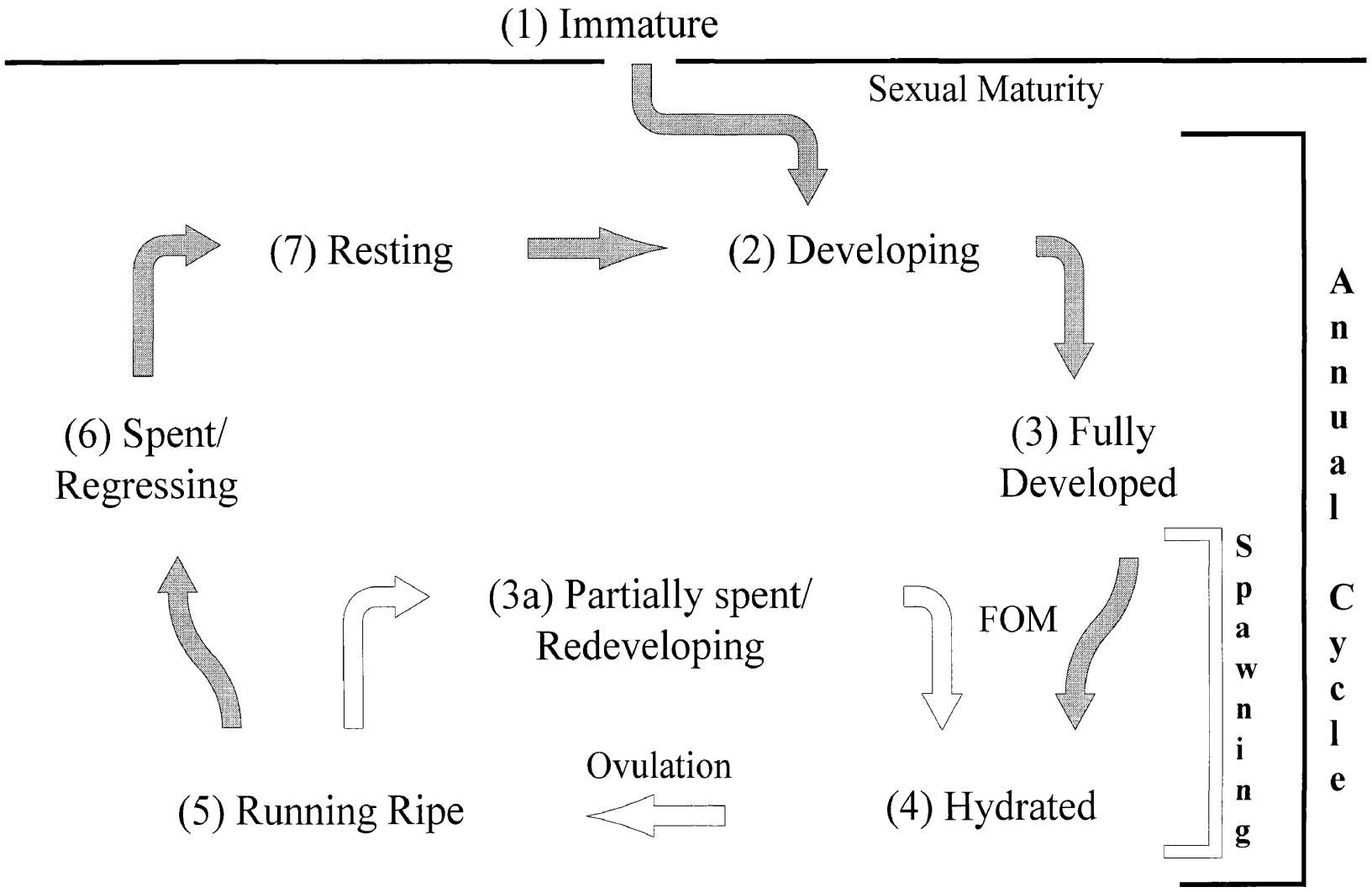
Initial macroscopic field examination assessed ovarian developmental stage as hydrated (stage 4), running ripe (stage 5), or partially spent/redeveloping (stage 3a). Hydrated ovaries were identified by the abundance of unovulated transparent oocytes, absence of a lumen, and lack of oocyte extrusion from the posterior of the excised ovary. Running ripe ovaries lacked visible transparent oocytes in ovarian tissue, contained an obvious lumen full of ovulated oocytes, and oocytes could be extruded from the posterior of the excised ovary. Partially spent/redeveloping ovaries were slightly flaccid, few, if any, transparent oocytes were visible in the ovarian tissue, and lacked a distinct lumen.

Histological classification of ovary stage was based on eight developmental cell types (Wallace and Selman, 1981; Hunter et al., 1992): primary growth, cortical alveoli, partially yolked, advanced yolked, germinal vesicle migration (GVM), germinal vesicle breakdown (GVBD), hydrated oocytes (HO), and post ovulatory follicles (POF). Final oocyte maturation (FOM) is comprised of GVM, GVBD, and HO classes. An ovary stage classification was developed for tautog based on the approximate abundance of cell types (especially FOM classes) and presence/absence of the lumen (see Chapter 1).

Table 8: Description of macroscopic and microscopic gonad stages for female tautog, *Tautoga onitis*, modified from Lowerre-Barbieri (1994). Macroscopic criteria refer to whole fresh ovaries. Abbreviated gonad stage numbers are in parentheses. Gonad stages 4, 5, and 3a comprise the inner spawning cycle. GSI = gonadosomatic index. POF = post-ovulatory follicles. FOM = final oocyte maturation. GVBD = germinal vesicle breakdown.

Gonad Stage	Macroscopic Criteria	Microscopic Criteria
(1) Immature	ovaries very small, white to light pink in color, no oocytes visible, tubular in shape (mean GSI = 0.50)	only primary growth oocytes present, no atresia, no macrophage aggregates, ovarian membrane thin.
(2) Developing	ovaries small to medium, tubular shape, yolked oocytes begin to appear, dark yellow to light orange in color, (mean GSI = 2.25)	primary growth, cortical alveoli, and some partially yolked oocytes present.
(3) Fully Developed	ovaries medium to large, yolked oocytes abundant, appear slightly grainy, pale mustard in color (mean GSI = 3.25)	primary growth to advanced yolked oocytes present; no remnant hydrated oocytes or POFs.
(4) Hydrated	ovaries large to very large; firm, yolked oocytes interspersed with large transparent (hydrated) oocytes visible, pink to yellow in color (mean GSI = 11.74)	primary growth to germinal vesicle migration and hydrated oocytes present, hydrated oocytes are unovulated, POFs may be present.
(5) Running Ripe	ovaries large to very large, clear oocytes have been ovulated, expand lumen of ovary, and are easily extruded when gonad excised; few clear oocytes in ovarian tissue (mean GSI = 10.12)	primary growth through advanced yolked, and ovulated, hydrated oocytes and fresh POFs present, FOM stages usually absent, lumen usually seen as separation of ovigerous folds.
(3a) Partially spent/ redeveloping	ovaries somewhat flaccid, large, slightly more pink than hydrated; 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	ovaries flaccid, small to medium, red to purple, yolked oocytes visible, but less abundant, and some clearing of tissue at anterior end of ovary (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 opaque (yolked) oocytes visible (mean GSI = 1.50)	only primary growth oocytes and cortical alveoli present, macrophage aggregates abundant, more follicular tissue and thicker ovarian membrane than immature fish.

Figure 15: The ovarian cycle of tautog, showing the annual gonadal development and the inner spawning cycle, typical of multiple spawning species.


(1) Immature
Sexual Maturity
(2) Developing
(3) Fully Developed
(3a) Partially spent/ Redeveloping
(4) Hydrated
(5) Running Ripe
(6) Spent/ Regressing
(7) Resting
FOM
Ovulation
Spawning
Annual Cycle

Hydrated ovaries (stage 4) were dominated by unovulated HOs and the absence of a lumen (Fig. 16a). Running ripe ovaries (stage 5) were distinguished by a large proportion of GVM, few GVB, some unovulated HOs, and the presence of a lumen full of ovulated oocytes (Fig. 16b). Partially spent/redeveloping ovaries (stage 3a) were classified by a high percentage of GVM cells, absence of HOs, and absence of a lumen (Fig. 16c).

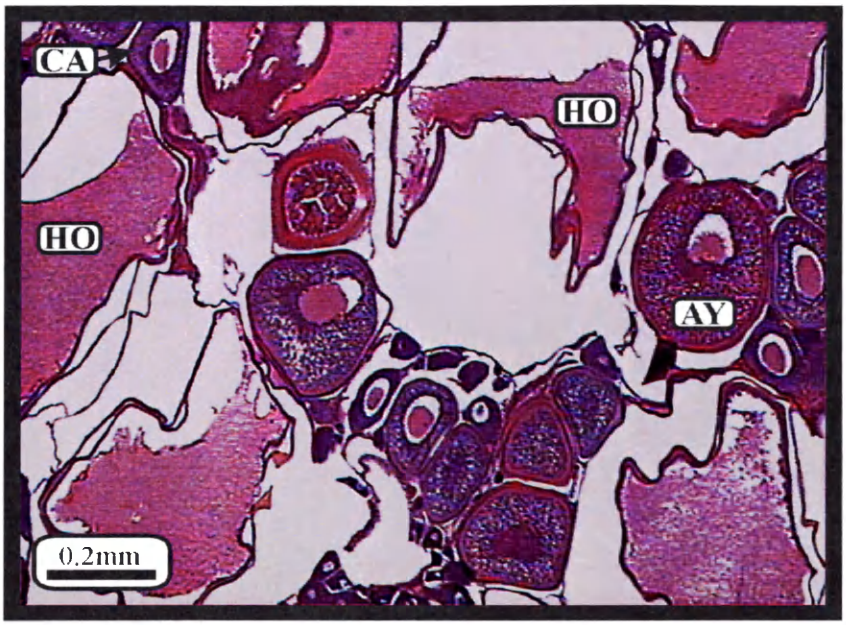
Diel Periodicity

Histological and macroscopic ovarian stages from female tautog with known kill times were used to estimate daily spawning windows, defined as the time of day that fish were capable of releasing oocytes in a spawning event. Daily physiological spawning windows were determined by the first and last occurrence of running ripe fish (stage 5) containing ovulated oocytes in the lumen. The actual spawning window may be shorter in duration if spawning is behaviorally controlled by courtship displays after females reach physiological readiness.

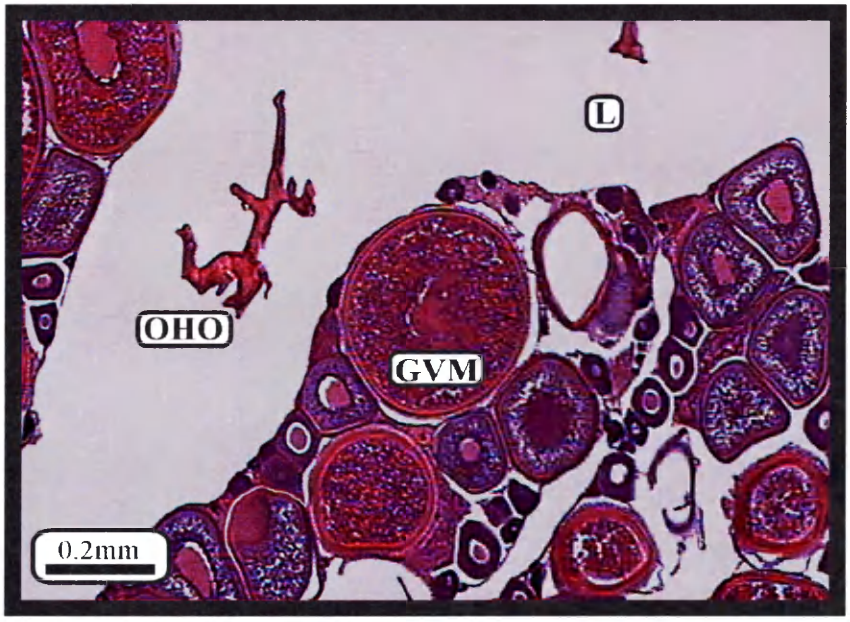
Batch fecundity estimation requires hydrated females, best sampled just prior to spawning (Hunter and Macewicz, 1985). The principal of optimal collection time attempts to maximize quantity of useable samples for batch fecundity analysis while reducing total sampling time. Optimal collection times for tautog to be used in batch fecundity analyses were defined by the presence of hydrated females (stage 4).

Figure 16: Histological appearance of: (A) a hydrated (stage 4) ovary from 26 April 1995 with hydrated oocytes (HO) and advanced yolked oocytes (AY); (B) a running ripe (stage 5) ovary from 26 April 1995 with germinal vesicle migration oocytes (GVM), ovulated hydrated oocytes (OHO) in the lumen (L), and post-ovulatory follicles (POF); (C) a partially spent/redeveloping (stage 3a) ovary from 26 April 1995 with germinal vesicle migration oocytes (GVM), germinal vesicle breakdown oocytes (GVBD) are the most advanced oocytes, and post-ovulatory follicles (POF).

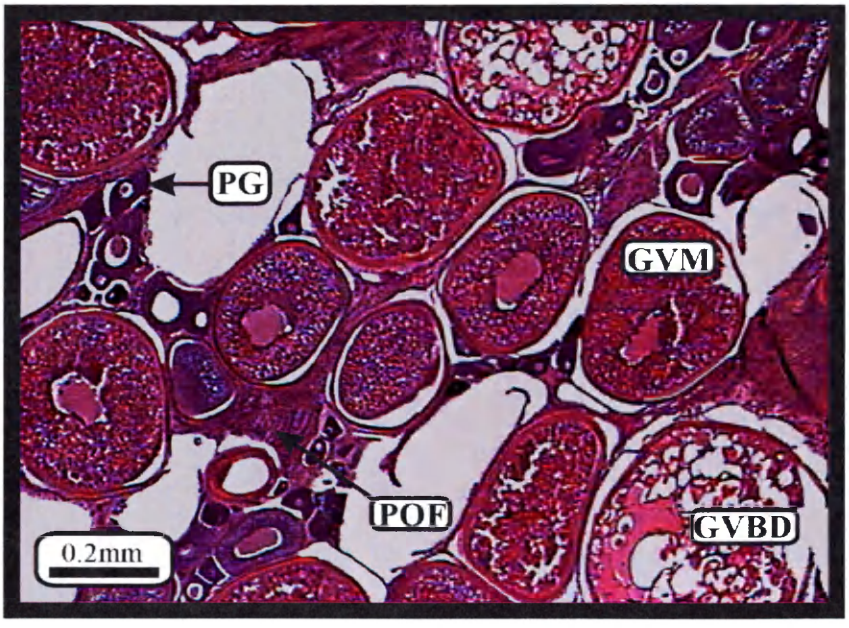
a)



b)



c)



Statistical analyses

Length frequency distributions, age structure, and sex ratios were analyzed for all fish landed on each sampling day to determine if a difference in the composition of local spawning groups existed between stations. Length and age distributions were compared between stations with the Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1981). Chi Square sex ratios were calculated for each station and compared. Significance level of alpha = 0.05 was set a priori.

Percent agreement between macroscopic and histological stages was used to verify the ability to distinguish ovarian stages in the field. Ovarian developmental stage was compared with collection time, tidal stage, and current flow for each sampling date.

RESULTS

Field collections

On 26 April 1995, 60 tautog were collected at sites along the Chesapeake Bay Bridge Tunnel (depth = 3-12 meters). Between 1100 and 1300 (EST), no fish were captured, presumably due to strong currents which lifted the bait off the bottom. On 9 May 1995, 55 tautog were collected at sites near the Chesapeake Bay Light Tower (depth = 20-25 meters).

Sex ratios differed significantly from the expected 1:1 relationship with more females than males collected at both sampling sites. The sex ratio was 2.75:1 ($\chi^2 = 13.06$, $\chi^2_{\alpha = 0.05} = 3.84$) at CBBT sites, and 1.89:1 ($\chi^2 = 5.26$, $\chi^2_{\alpha = 0.05} = 3.84$) at CBLT sites. Length frequency distributions for fish sampled at CBBT and CBLT stations were not significantly different ($D=0.2136$, $D_{0.05}= 0.2535$) using the Kolmogorov-Smirnov two-sample test. Although there was a similar range in total length of fish collected at both stations, there were more large males (410-510 mm) collected at the CBLT, while collections at the CBBT were dominated by smaller (310-400 mm) females (Fig. 17). Age frequency distributions (Fig. 18) were not significantly different between the two sites.

Daily oocyte development analyzed from histological ovarian sections verifies and clarifies macroscopic field classification of ovarian stage. Percent agreement between macroscopic and histological gonad staging of field sacrificed female tautog was 91%. Thus macroscopic ovarian staging is accurate in the field, but fixation of ovarian tissues concurrent with fish kill time increased sample quality for histological and batch fecundity analyses.

Figure 17: Length frequency distributions by 10 mm size classes for all fish landed on 26 April at CBBT sites and 9 May 1995 at CBLT sites. Sample sizes are indicated in figure legend.

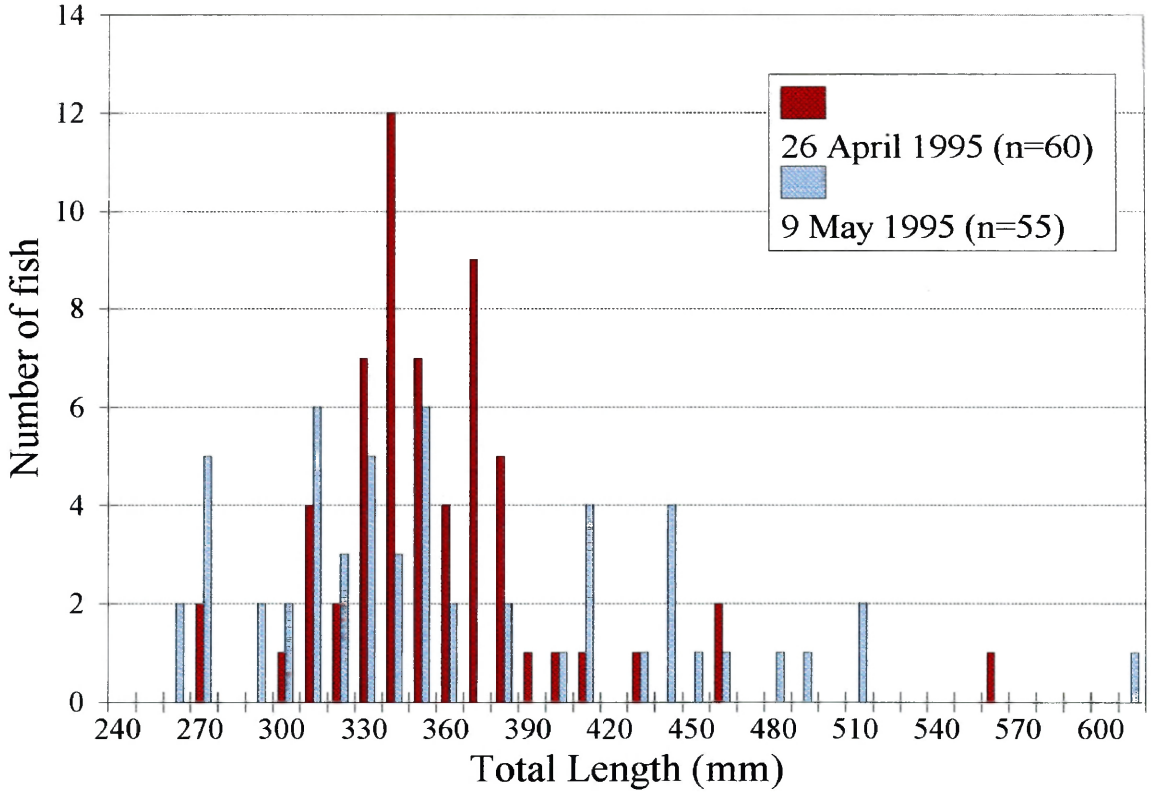
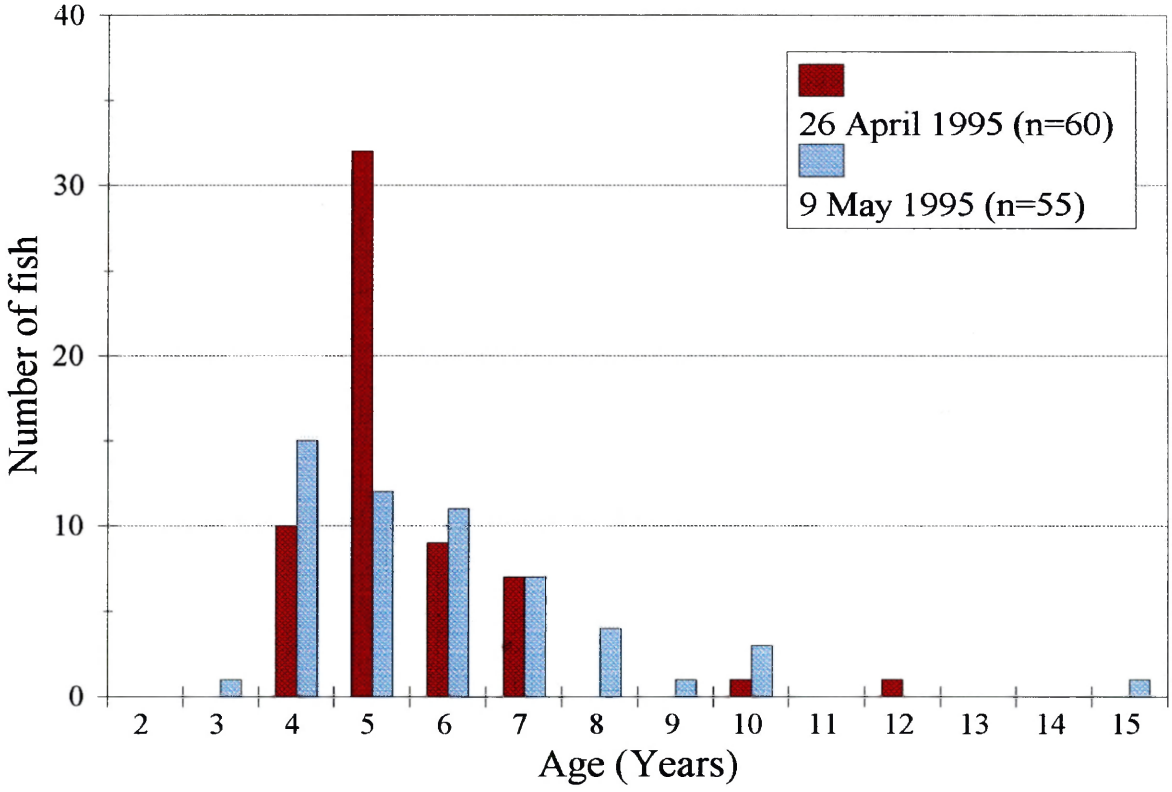

14
12
10
8
6
4
2
0
Number of fish
26 April 1995 (n=60)
9 May 1995 (n=55)
240
270
300
330
360
390
420
450
480
510
540
570
600
Total Length (mm)

Figure 18: Age frequency distributions for all fish landed on 26 April at CBBT sites and 9 May 1995 at CBLT sites. Sample sizes are indicated in figure legend.


40
30
20
10
0
Number of fish
26 April 1995 (n=60)
9 May 1995 (n=55)
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Age (Years)

Diel periodicity

On 26 April 1995, 16 females were collected at the CBBT with known kill times: six hydrated females between 0815 and 1045, four running ripe females between 1400 and 1530, and six partially spent/redeveloping were collected - one at 1010 and five between 1700 and 1820 (Fig. 19, Table 9). On 9 May 1995, 18 females were sampled with known kill times at the CBLT: four hydrated females collected between 0745 and 1045, five running ripe females collected between 0925 and 1330, and nine partially spent/ redeveloping were collected - one at 0845 and eight between 1700 and 1820 (Fig. 19, Table 9). Ovarian stages 4 and 5 overlapped during the beginning of spawning windows, but the end of spawning was clearly defined by a sharp change from stage 5 to 3a on both sampling days.

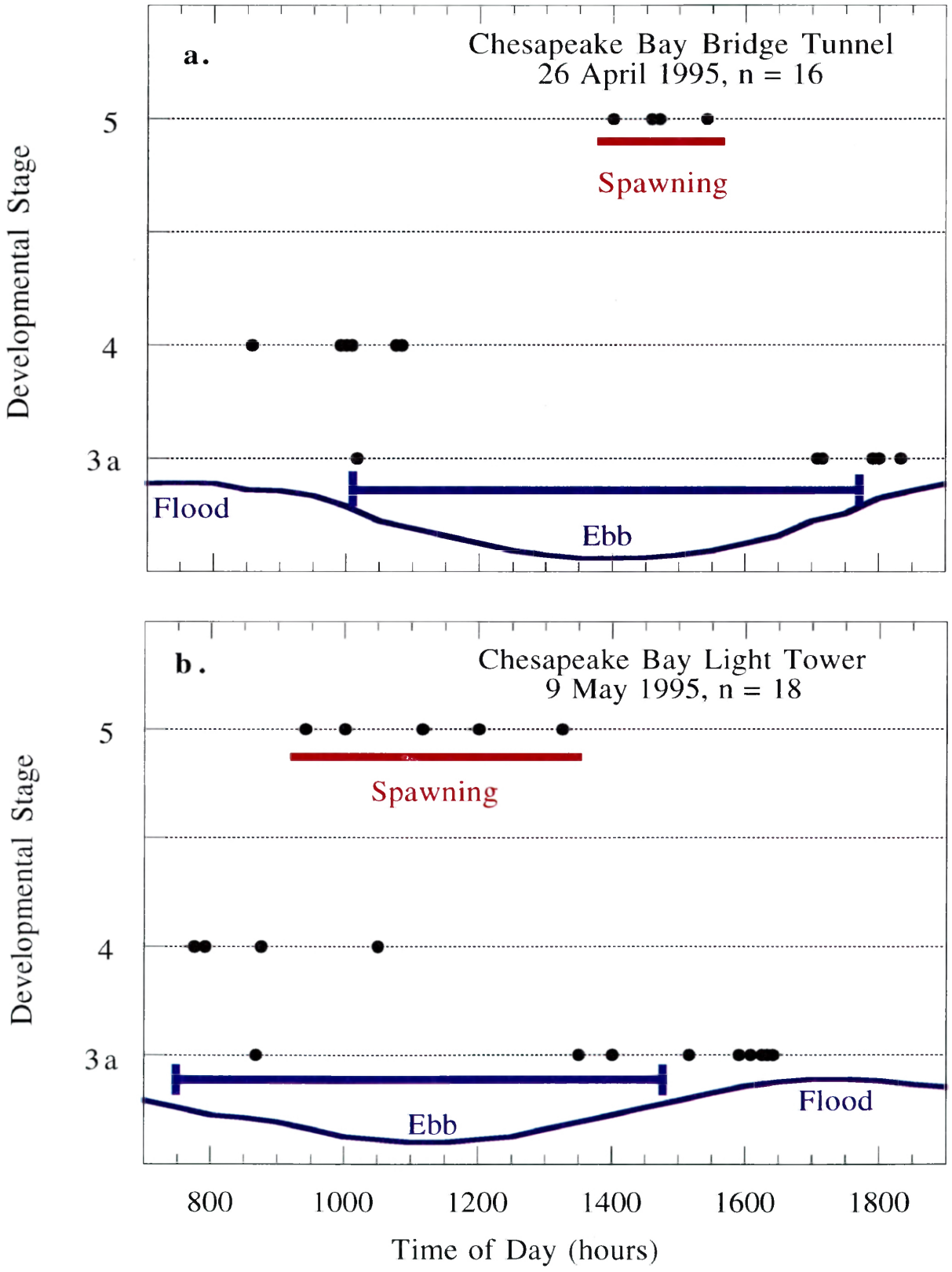
The occurrence of running ripe females was directly translated to physiological spawning windows of 1400-1530 EST on 26 April 1995 and 0925-1330 EST on 9 May 1995. The spawning window on 26 April was most likely longer, but due to difficulties in collecting fish between 1100-1400, and 1530-1630, exact limits could not be identified.

The presence of hydrated females between 0745 and 1100 EST defined optimal collection time for tautog ovarian samples to be used in batch fecundity analyses.

Table 9: Summary of field collections on 26 April 1995 at Chesapeake Bay Bridge Tunnel (CBBT) and 9 May 1995 at Chesapeake Bay Light Tower (CBLT). Sample sizes given in parentheses.

	26 April 1995 (CBBT)		9 May 1995 (CBLT)	
Ovary Stage	Time (n)		Time (n)	
4 - Hydrated	0845-1045	(n=6)	0745-1045	(n=4)
5 - Running Ripe	1400-1530	(n=4)	0925-1315	(n=5)
3a - Partially spent/ redeveloping	1010 1700-1820	(n=1) (n=5)	0845 1330-1820	(n=1) (n=8)

Figure 19: Tautog ovary developmental stage and time of day: a) 26 April 1996 and b) 9 May 1996. Red line depicts physiological spawning window. Blue curve represents tidal stage. Blue bar represents ebb current flow. Time is given as Eastern Standard Time.


a.
Chesapeake Bay Bridge Tunnel
26 April 1995, n = 16
Developmental Stage
5
4
3 a
Spawning
Flood
Ebb
b.
Chesapeake Bay Light Tower
9 May 1995, n = 18
Developmental Stage
5
4
3 a
Spawning
Ebb
Flood
800
1000
1200
1400
1600
1800
Time of Day (hours)

DISCUSSION

Tautog daily ovarian development followed a general pattern of hydration early in the day (0730-0930 EST), running ripe (spawning) mid-day (0930-1530 EST), and partially spent/redeveloping in late afternoon and early evening (1430-1830 EST). Physiological spawning windows on 9 May 1995 occurred about two hours earlier than on 26 April (Fig. 19, Table 9). Observed differences in spawning windows between sampled groups of tautog may reflect different spawning behavior or changes in environmental conditions (depth, ambient light, tide).

Two modes of reproduction have been observed in tautog, pair and group spawning. Pair spawning has occurred when territorial males maintained dominance hierarchies, and involved extensive courtship displays with females (Olla and Samet, 1977). Group spawning without a dominance hierarchy has also been observed (Olla and Samet, 1977, Olla et al. 1977, 1981). The flexibility of tautog reproductive behavior (pair vs group spawning) has been linked to size and sexual composition of the spawning group (Olla et al. 1977). These investigators found that changes in the number of mates and availability of shelter in laboratory aquaria determined the occurrence of pair or group spawning behavior. Olla et al. (1977) also reported that 99% of spawning events (pair and group) occurred within the same spawning window - between 1300 and 1600 (EST).

In this study, differences in the composition of spawning groups were compared by sex ratios, length frequencies, and age frequencies of landed fish. Although length and age distributions were not significantly different between CBBT and CBLT stations, sex ratios

did show significant differences between sampling locations in this study. However, length distributions, age distributions, and sex ratios only apply to those fish landed by the sampling gear. Hook and line sampling is not 100% efficient at removing fish from an area and is biased for fish that are actively feeding. Also, tautog courtship displays and spawning behavior may alter the feeding activities of local spawning groups.

Olla et al. (1981) observed spawning groups of tautog in aquaria. In experiments with five males and three females, males spent more time establishing and defending dominance hierarchies than courting females. Females typically swam around the aquaria in the morning and began visiting males territories and associated with structure in the early afternoon, in the hour prior to spawning. When females received little attention from males, they developed a stronger coloration pattern (white saddle) presumably to attract more attention from the males.

It is possible that many males were present at sampling sites in this study, but were not sampled because they were involved in dominance displays instead of feeding activities. Further, if females were present, but not actively involved in courtship, they may continue to feed, becoming vulnerable to hook and line sampling gear. The skewed sex ratios (more females than males) seen in this study may be caused by sampling bias due to differential feeding activity of male and female tautog during courtship. However, in controlled situations where the spawning behavior was altered by artificial changes in the composition of spawning groups, the diel periodicity of spawning events remained constant. Therefore, variation of spawning behavior (pair or group) may occur in natural habitats based on size and sexual composition of local spawning groups, but shifts in tautog diel spawning periodicity are more likely caused by differences in environmental factors such as light levels

at depth, tidal stage, or tidal currents.

The observed change in spawning windows does correlate with a shift of tidal ebb currents between sampling dates. On 26 April, the spawning window occurred from 1400-1530 (EST) while the ebb current flowed from 1030-1715 (EST) (Figure 19). On 9 May 1996, the spawning window was 0930-1315 (EST), while the ebb current flowed from 0730-1445 (Fig. 19). Additional observations while collecting females for batch fecundity estimates (Chapter 1) from CBLT sites on 1 June 1995 found four hydrated females between 0855 and 0935 (EST), and one running ripe female at 1345 (EST), while ebb currents were predicted to be 0230-0915 and 1345-2100. The absence of running ripe females during the early morning ebb tide on 1 June, and collection of running ripe females only during midday to afternoon ebb tides suggests a combination of daylight and ebb tidal currents as environmental cues for tautog diel spawning activity in the lower Chesapeake Bay.

Other labrid and acanthurid species have been observed to release pelagic eggs during daylight ebb or "off-reef" currents (Table 10) (Randall, 1961; Thresher, 1979; Robertson, 1981, 1983). In addition to the basic correlation with tidal currents, the strength of tidal signals may determine spawning time (Robertson, 1981, 1983). For example, two wrasses, *Halichoeres garnoti* and *H. maculipinna* spawn from late morning to early afternoon during ebb tidal currents in Florida (Thresher, 1979), but in Panama where the tidal range is small and most currents are generated by wind, spawning is restricted to the period between 1300-1530 for *H. garnoti* and 1400-1700 for *H. maculipinna*, regardless of tidal stage (Robertson, 1983).

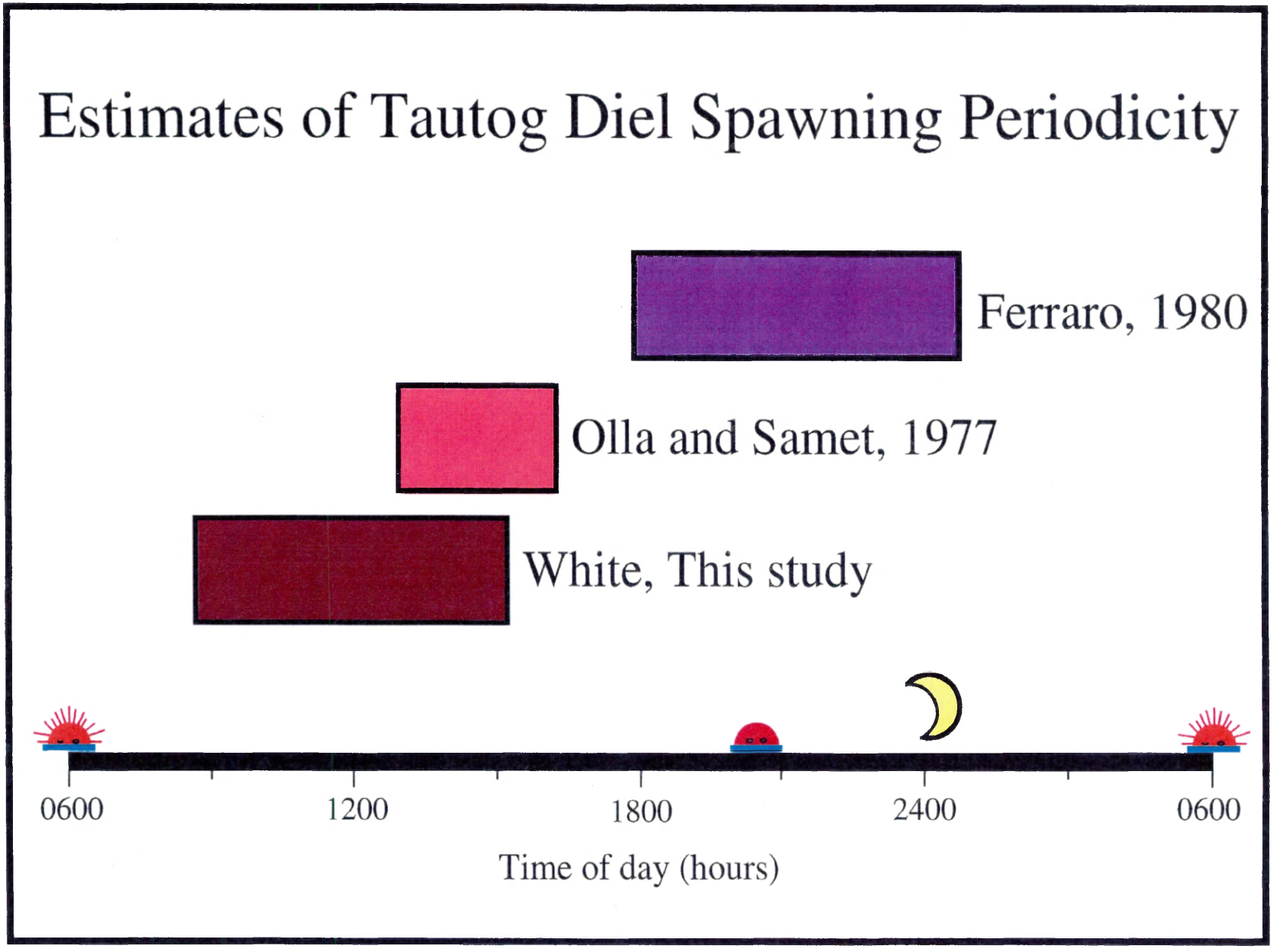
Table 10: Diel spawning periodicity of several reef dwelling species. Spawning time standardized to EST, spawning strategy P=pair, G=group, I=interference spawning, Tide symbols Ebb=ebb current, None=no relationship to tidal cycles, (-)=no data available.

Family and species	Spawning time	Strategy	Tide	Reference
Labridae				
Bodianus rufus	late afternoon	P		Warner and Robertson 1978
Halichoeres bivittattus	mid afternoon	P, G, I	-	Warner and Robertson 1978
	late morning to early afternoon	P, I	Ebb	Thresher 1979
H. garnoti	late morning to early afternoon	P, I	Ebb	Thresher 1979
	1300 - 1530	P, I	None	Robertson 1981
H. maculipinna	mid afternoon	P, G, I	-	Warner and Robertson 1978
	late morning to early afternoon	P, I	Ebb	Thresher 1979
	1400 - 1700	P, I	None	Robertson 1981
H. poeyi	mid afternoon	P, G, I		Warner and Robertson 1978
Tautoga onitis	1330 - 1600	P, G	-	Olla and Samet 1977
	1800 - 0100	-	-	Ferraro 1980
Tautogolabrus adspersus	1200 - 1700	G	-	Wicklund 1970
	1300 - 2100	P	-	Pottle and Green 1979
Thalassoma bifasciatum	mid-day	P, G, I		Warner and Robertson 1978
Scaridae				
Scarus croicensis	mid-day to late afternoon	G	-	Colin 1978
Sparisoma rubripinne	afternoon	G	None	Randall and Randall 1963
Acanthuridae				
Acanthurus lineatus	morning	P, G	Ebb	Robertson 1983
A. nigrofuscus	afternoon	P, G	Ebb	Robertson 1983
A. triostegus	dusk	-	Ebb	Randall 1961
		G	Ebb	Robertson 1983
Ctenochaetus striatus	afternoon	P, G	Ebb	Robertson 1983
	dusk	G	Ebb	Randall 1961
Zebrasoma spp	mid-morning to dusk	P	Ebb	Robertson 1983
	-	P	-	Robertson et al. 1979
	dusk	G	Ebb	Randall 1961

Comparison of diel spawning periodicity estimates for tautog (Fig. 20) shows a similarity between Olla and Samet's (1977) laboratory observations (1330-1600 EST) and this study (0925-1315 and 1400-1530). The difference between this study and Olla and Samet's (1977) may be due to the ability to include tidal influence in natural habitats, a factor which is absent in laboratory experiments. Tautog spawning periodicity estimates in environments with tidal influence (this study) and without tidal influence (Olla and Samet, 1977), may parallel the difference in spawning activity of *Halichoeres* sp. at two natural sites (Florida and Panama) with different tidal amplitudes described above. The occurrence of spawning periodicity shifts under similar environmental cues in other labrids supports the relationship between spawning windows and tides observed for tautog in this study. Ferraro's (1980) estimation of evening spawning (1800-0100 EST) by aging field fertilized planktonic eggs contradicts ovarian development (this study), behavioral observations of visual courtship displays, and a quiescent state at night (Olla and Samet 1977; Olla et al. 1974), and therefore appears to be a less reliable method of defining spawning periodicity of tautog.

Wide spawning windows with overlapping ovarian stages suggests that spawning behavior may be controlled by several factors. Individual variation was observed as an overlap of ovarian stages 4, 5, and 3a at the beginning of tautog spawning windows. Multiple spawning events per day have been observed for tautog (Olla and Samet, 1977), cunner (Pottle and Green, 1979), and the bluehead wrasse (Reinboth, 1963). Observations of prolonged courtship, but limited spawning in tautog and cunner indicate females may retain oocytes after becoming physiologically ready to spawn. Although ovarian stages overlap at the beginning of spawning windows, the cessation of spawning was clearly evident on both days (Fig. 19). Cues to terminate spawning behavior seem more distinct than

Figure 20: Comparison of published estimates for tautog diel spawning periodicity with this study. Hours listed as Eastern Standard Time.


Estimates of Tautog Diel Spawning Periodicity
Ferraro, 1980
Olla and Samet, 1977
White, This study
0600
1200
1800
2400
0600
Time of day (hours)

those initiating spawning. Spawning behavior may terminate in response to a decrease in tidal currents, ambient light levels, or depletion of gametes. The length of tautog spawning windows (2-4 hours) observed in the lower Chesapeake Bay seem to be caused by multiple factors: variability in individual spawning time, multiple spawning events per day for individual females, and the ability to retain ovulated hydrated oocytes in the lumen until favorable spawning conditions (physical environment and courtship behavior) are met.

Theoretically, spawning on ebb tides has evolved in tropical reef fish in order to avoid predation on offspring within the reef system (Nikolsky, 1963; Johannes, 1978; Robertson, 1981, 1983). Larval drift patterns have not been studied for tautog, thus we do not know how a correlation between spawning time and ebb current flow might factor into larval survivorship, settlement, and recruitment to juvenile habitats. Variability in habitat, currents, and tidal regimes throughout the species range presumably affect reproductive strategies, therefore one cannot assume similar behavior across environmental conditions (Johannes, 1978). Future analysis of diel spawning periodicity of tautog, including measurement of light levels at depth and concurrent plankton tows, should be pursued to verify the coupling of daylight and ebb current flow as determinants of tautog spawning periodicity in this and other regions of the species range.

Estimation of diel spawning periodicity from field collected ovarian tissue avoids logistical difficulties and costs associated with maintaining large aquaria or SCUBA diving in areas of low visibility and high current speeds. Furthermore, analysis of ovarian tissue precludes the need to back-calculate spawning time from estimated embryo ages, and adds information on local spawning areas and environmental conditions. Daily spawning windows can be delimited by macroscopic gonad staging and/or histological analyses of field

collected females with known kill times (DeMartini and Fountain, 1981; Goldberg et al., 1984; Alheit et al., 1984). The use of histological techniques also provides data to verify macroscopic gonad stages, age post-ovulatory follicles for use in spawning frequency analysis (Hunter and Goldberg, 1980; Hunter et al., 1985), and to accurately determine optimal gonad collection time for batch fecundity counts (Hunter and Macewicz, 1985).

The use of ovarian stage of females with known kill times, caught from natural habitats, is a strong tool to estimate diel spawning periodicity of fishes. By pinpointing diel periodicity, researchers can maximize sampling effort for fecundity estimation, investigate relationships with environmental cues, determine differences in spawning patterns within a species range, and gain insight to several selective pressures governing spawning behavior.

APPENDIX

Age and growth parameters of tautog, *Tautoga onitis*

Length - weight relationships
TW = total weight (g), TW = total length (mm), EW = eviscerated weight (g)

White (This study) - see graphs on following page:

Males (n=388)	Log(TW) = -4.78 + 3.04Log(TL)	$R^2 = 0.98$
Females (n=490)	Log(TW) = -4.84 + 3.08Log(TL)	$R^2 = 0.98$

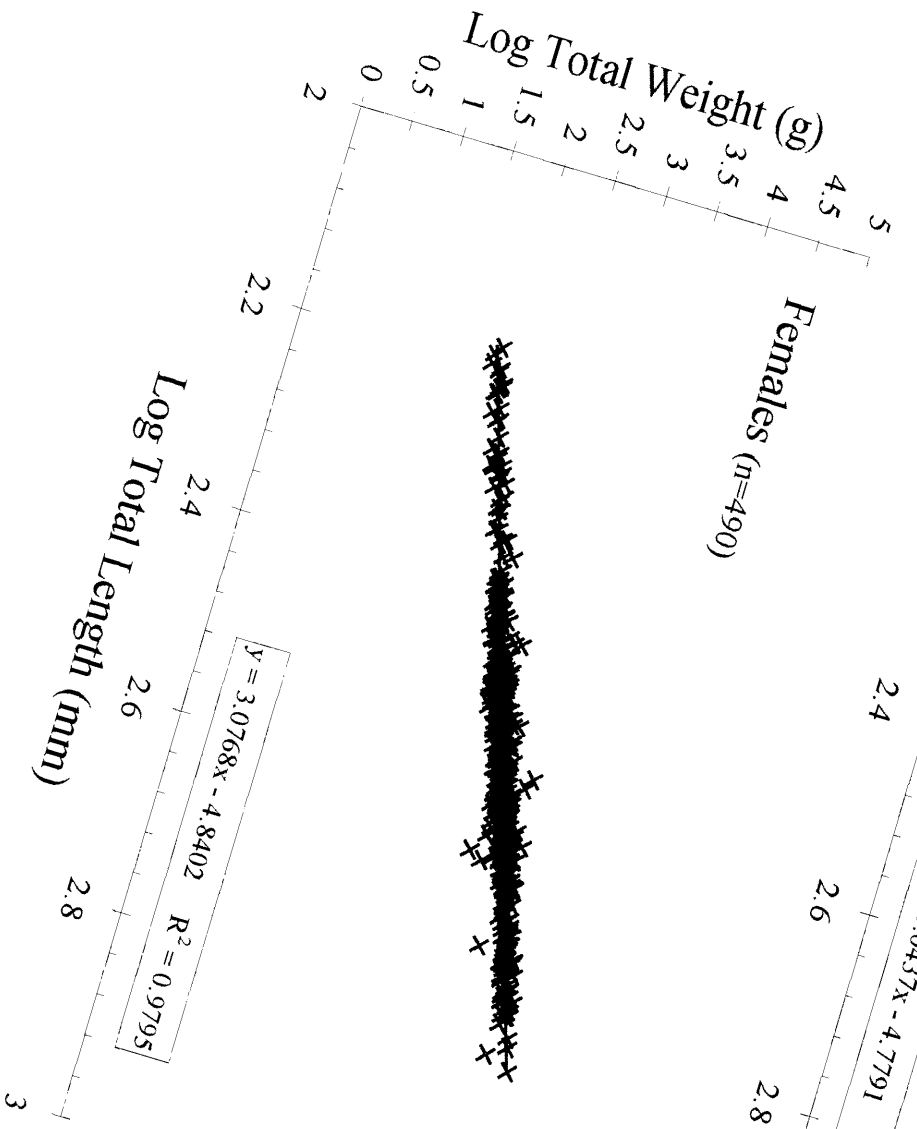
Hostetter and Munroe (1993):

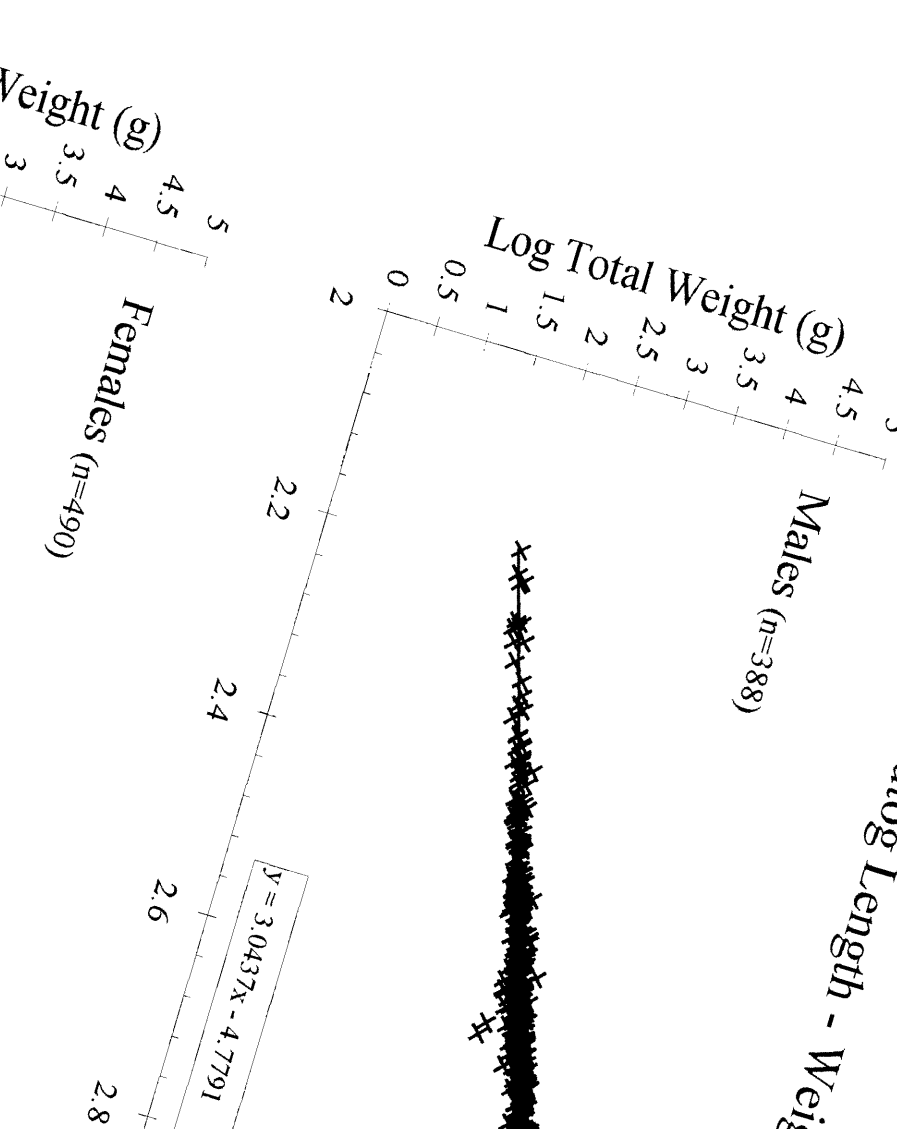
Males (n=396)	Log(TW) = -4.54 + 2.94Log(TL)	$R^2 = 0.97$
Females (n=290)	Log(TW) = -4.58 + 2.96Log(TL)	$R^2 = 0.98$

Cooper (1967):

Males (n=81)	Log(EW) = -4.36 + 2.78Log(TL)
Males (n=102)	Log(EW) = -4.80 + 3.02Log(TL)

Tautog Length - Weight



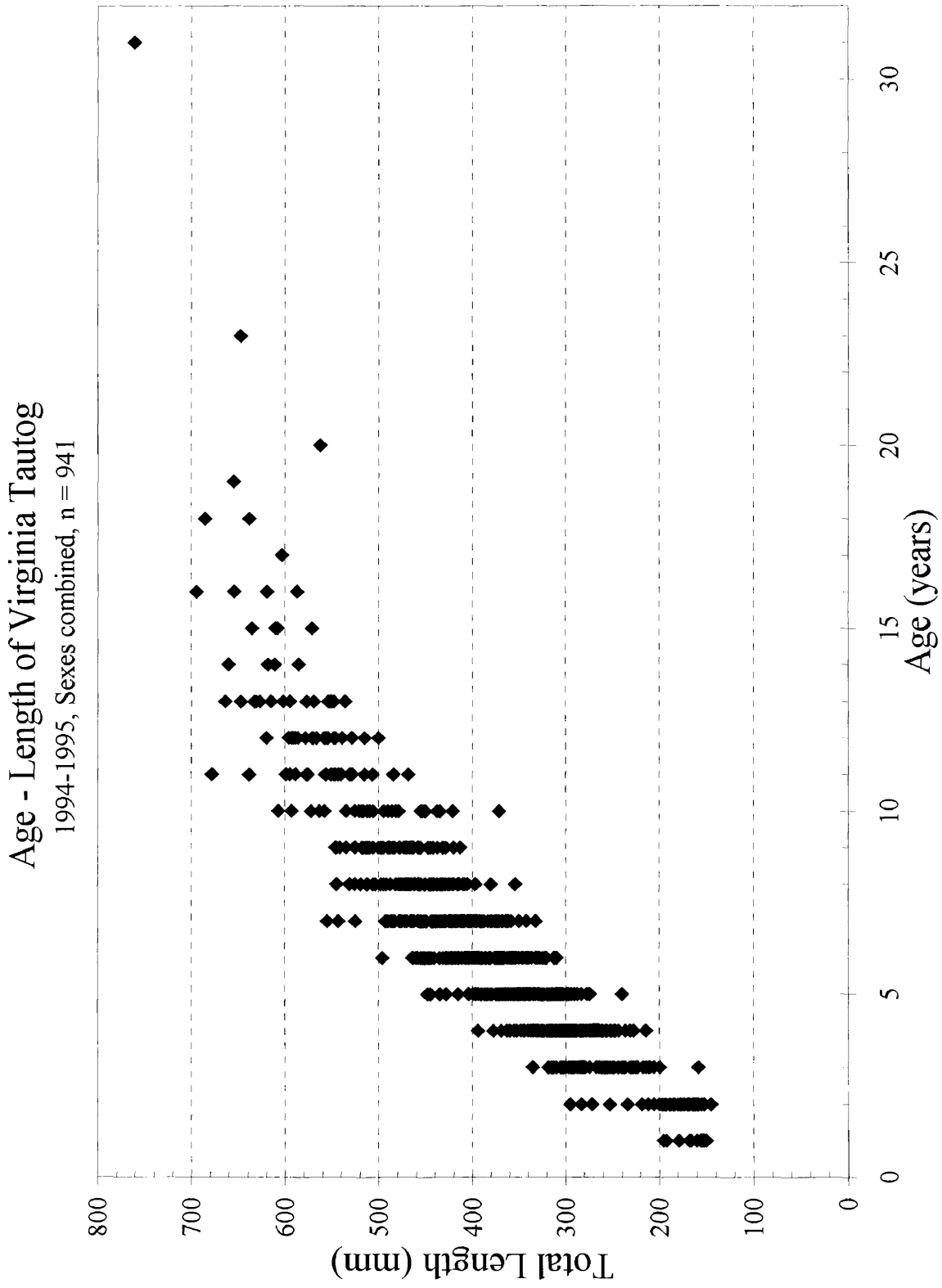


APPENDIX: Age and growth parameters of tautog

Von-Bertalanffy growth parameters ($L_t = L_\infty[1-e^{-k(t-t0)}]$
Estimates of L_∞ = mean asymptotic length in mm, K = growth coefficient, and t_0 = time (yr) at which total length would theoretically be zero are listed, ± Asymptotic Standard Error.

	L_∞	K	t_0
White (this study)			
Males (n=402)	762.0±27.92	.099±0.009	-1.20±0.24
Females (n=509)	911.0±65.18	0.072±0.009	-1.60±0.27
Combined (n=942)	791.9±22.6	0.093±0.006	-1.13±0.135
Hostetter and Munroe (1993)			
Males (n=398)	732.0±9.124	0.090±0.003	-1.64±1.32
Females (n=282)	733.6±28.36	0.085±0.009	-1.74±3.24
Combined (n=701)	742.37±9.05	0.085±0.003	-1.82±0.144
Cooper (1965)			
Males (n=1041)	664	0.091	-1.67
Females (n=1119)	506	0.151	-0.95

APPENDIX: Age and growth parameters of tautog



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VITA

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GEOFF'S FAVORITE TAUTOG RECIPES

1.) Blackened, served with red beans + rice, and/or garden salad

2.) Grilled - with whatever spices and side dishes you are in the mood for tonight

3.) Baked tautog over rosemary potatoes and vegetables

Ingredients:
4 Tautog fillets, skinned
5 large baking potatoes - cut into 8 sections
1-2 green peppers (add red or yellow if wish) - large cubes
1 Bermuda onion, sliced thick, slices cut in 1/2
handful of baby carrots (optional)
1/2 tsp dried rosemary
olive oil
garlic - to taste, up to 4 cloves

Protocol:
Preheat oven to 350° C, oops, °F, spread 1 tbls olive oil in 9x13 pan
Steep rosemary in 2-3 tbls water for 3-5 min
Mix potatoes, peppers, onion and rosemary in baking pan
-bake for 30 min, mixing once or twice
Dip tautog fillets in olive oil, place on top of potatoes and vegetables, and top with sliced or diced garlic.
-bake another 10 min, until fillets flake with a fork

Serve immediately with an expensive Chardonnay or Johannisberg Riesling