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Age, growth, and reproduction of tautog *Tautoga onitis* (Labridae: Perciformes) from coastal waters of Virginia*

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Abstract–Tautog *Tautoga onitis* are gaining popularity in Virginia's coastal waters as a recreational and food fish. Adult tautog are seasonally abundant on inshore hard-bottom habitats (1–10 m) and inhabit offshore areas (10–75 m) year-round. Juveniles, especially newly-settled recruits, inhabit vegetated areas in shallow water (usually <1 m). From March 1979 to July 1986, tautog were collected in lower Chesapeake Bay and nearby coastal waters to examine age, growth, and sexual maturation. Age estimates were determined from annular marks on opercle bones: 82% of the fish were age-10 or younger, 18% exceeded age-10, and 1% were age-20 or older. Marginal increment analysis revealed that annuli formed concurrent with a protracted spawning season (April–July). The von Bertalanffy growth equation, derived from back-calculated mean lengths-at-age, was $l_t=742\ [1^{-e-0.085\ (t-1.816)}]$. Tautog are long-lived (25+ yr) and attain relatively large sizes (672 mm TL) slowly (*K* for sexes combined = 0.085). Growth rates of both sexes are similar, although males grow slightly faster (*K*=0.090 vs. 0.085 for females). Maturity occurs at age-3 in both sexes. Growth rates for tautog from Virginia are similar to those reported nearly 25 years ago for tautog in Rhode Island. Growth rates for tautog are similar to those of other reef fishes, such as snappers and groupers. Habitat restriction, slow growth, great longevity, and increasing popularity by user groups may contribute to overexploitation of this species in Virginia waters.

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Tautog *Tautoga onitis* (Linnaeus) range from Nova Scotia (Bleakney 1963, Leim & Scott 1966, Scott & Scott 1988) to South Carolina (Bearden 1961, Sedberry & Beatty 1989) and are one of the northernmost-occurring labrids in the western North Atlantic (only the cunner *Tautogolabrus adspersus* ranges farther northward). Tautog are locally abundant in lower Chesapeake Bay from Gwynn's Island near the mouth of the Rappahannock River south to Sandy Point on the eastern shore (Hildebrand & Schroeder 1928), along hardbottom areas including those associated with the Chesapeake Bay Bridge-Tunnel network (CBBT) at the mouth of the Bay, and along the southern margin of the Bay near Lynnhaven Inlet. This species also occurs in coastal Atlantic waters off Virginia on hardbottom areas around jetties, and reefs and wrecks out to 65 km offshore (Richards & Castagna 1970, Musick 1972, Hostetter 1988). A wide size-range of tautog occurs from spring through late fall in the lower Bay and on the seaside coast; larger individuals occur year-round on suitable habitat offshore to 75 m and deeper. Newly recruited juveniles and young fish to about 100 mm usually inhabit shallow areas (1 m or less) densely vegetated with macrophytic algae (primarily *Ulva lactuca*) or submerged seagrasses including stands of *Zostera* and *Ruppia* (Briggs & O'Connor 1971).

In more northern regions, a marked decrease in activity of tautog has been observed to occur in water temperatures below 10° C (Olla et al. 1974). Smaller individuals overwinter in shallow, rocky areas, whereas when autumn temperatures fall below 10° C, larger and older fish (>25 cm, >3–4 yr old) migrate to offshore, overwintering areas. Adult tautog return from offshore wintering areas to inshore spawning sites with onset of increasing temperatures in the spring (Chenoweth 1963, Cooper 1966, Stolgitis 1970, Olla et al. 1974, Briggs 1977, Olla et al. 1979). In Virginia, tautog populations on nearshore sites also undergo seasonal fluctuations. However, seasonal movements of tautog in Virginia's coastal waters may not be as well defined as the migration patterns noted for tautog in more northern areas. In our study area, not all tautog migrated to inshore areas during

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springtime spawning periods. Tautog in peak spawning condition were collected on both inshore and offshore sites throughout the spring-summer period (late April–early August). Additionally, it was not unusual to observe large fish (>25 cm) at inshore sites during winter, especially in deeper areas. In more northern areas, other researchers (Olla & Samet 1977, Eklund & Targett 1990) have also noted that some adult tautog in the population remain offshore throughout the year.

Tautog are rapidly gaining popularity as a prized food and sport fish with recreational anglers and spearfishermen in Virginia waters (Bain 1984, Arrington 1985). Recreational angling for this species in Virginia has received increased interest since the recent capture of a world record tautog (24 lb, 10.89 kg) by an angler fishing off the eastern shore of Virginia (IGFA 1990). This increasing popularity has also been reflected in the number of awards issued annually to recreational fishermen by the Virginia Salt Water Fishing Tournament for outstanding catches [tautog weighing 4.1 kg (9 lbs) or more]. Awards for outstanding catches of tautog increased from mean values of 122/yr for the period 1976–80 to 282/yr for 1981–86 (C. Bain, Virginia Saltwater Fishing Tournament, VMRC, Virginia Beach VA 23451, pers. commun.). Most recently, however, citations for outstanding catches have decreased to 106/yr (range 91–130/yr) for 1987–91. Commercial catches from 1922 (Hildebrand & Schroeder 1928) to the present (E. Barth, Deputy Chief, Fish. Manage. Div., VMRC, Newport News VA 23607, pers. commun. 3 Jan. 1991) show little annual variation in weight of reported catches in landings for this species. Reported commercial landings of tautog in Virginia from 1973 to 1988, for example, ranged from 234 to 3586 lb/yr ($\bar{x}$=1840 lb/yr). However, these landings are insignificant compared with unreported catches by commercial and recreational rod-and-reel fishermen. According to statistics compiled by the Marine Recreational Fishery Statistics Survey conducted by the National Marine Fisheries Service (NMFS), estimated recreational catches of tautog in the mid-Atlantic Bight from 1979 to 1989 ranged from 70,000 (1982) to 815,000 (1984) fish/yr ($\bar{x}$=383,200 fish/yr). In 1985, landings of tautog taken by recreational anglers in Virginia alone were estimated to be 743,600 lb, representing 3.6% of the total estimated poundage for fishes taken by recreational fishermen in Virginia (VMRC 1985).

Aspects of the tautog's biology, including its association with hardbottom areas (Bigelow & Schroeder 1953, Cooper 1967, Olla et al. 1974, 1977, 1979), which are limited and generally discontinuous in Virginia, and its relatively slow growth (Cooper 1967), render this species susceptible to overexploitation (Briggs 1977). This situation is further exacerbated by recent technological advances in LORAN and recording depth finders used by fishermen that have simplified locating even the smallest, isolated substrates. Populations of slow-growing fish species concentrated in reef areas can be severely depleted by fishing pressure exerted by recreational interests (Briggs 1977, Turner et al. 1983, Manooch & Mason 1984, Matheson and Huntsman 1984, Moore & Labisky 1984, Harris & Grossman 1985). Based on informal surveys of charterboat captains, recent declines in citation awards for large fish, and personal field experiences, the catch-per-unit-effort of tautog has already decreased in Virginia, and the relative abundance of tautog (especially larger-sized individuals) has been detrimentally affected in the more popular fishing areas.

In coastal waters of Rhode Island and New York, Cooper (1966), Olla et al. (1974), and Briggs (1977) noted a seasonal inshore-offshore spawning migration in tautog with no significant north-south component. None of these studies reported the recovery of fish from areas outside the general area in which they were tagged, indicating that little, if any, mixing of adult tautog takes place between fish inhabiting even relatively proximate areas (Rhode Island and New York waters).

This study was undertaken to estimate age structure of the population, growth, longevity, and seasonal patterns of reproduction for tautog occurring in lower Chesapeake Bay and nearby coastal waters of Virginia. Growth parameters estimated for tautog collected in Rhode Island 25+ years ago may not be applicable for the population(s) occurring in more southerly waters. Also, in coastal waters of Rhode Island and Virginia where tautog occur, environmental parameters (primarily seasonal temperature regimes) and habitat availability are different, and these factors may influence growth rates in different populations or segments of the same population. Occurrences of large specimens, such as the current (IGFA 1990) and previous (IGFA 1986) world-record tautogs in coastal waters of Virginia, may also indicate that fish in the lower Mid-Atlantic Bight comprise a separate population, with growth characteristics different from their northern counterparts.

Materials and methods

Tautog were collected opportunistically from March 1979 to July 1986 by spearfishing, rod-and-reel, commercial fish pots, and as bycatch in trawl tows from other research studies. During the course of the study, fish were taken at 19 different locations, at depths of 2–35 m and representing a wide variety of ecological conditions characteristic of tautog habitat within

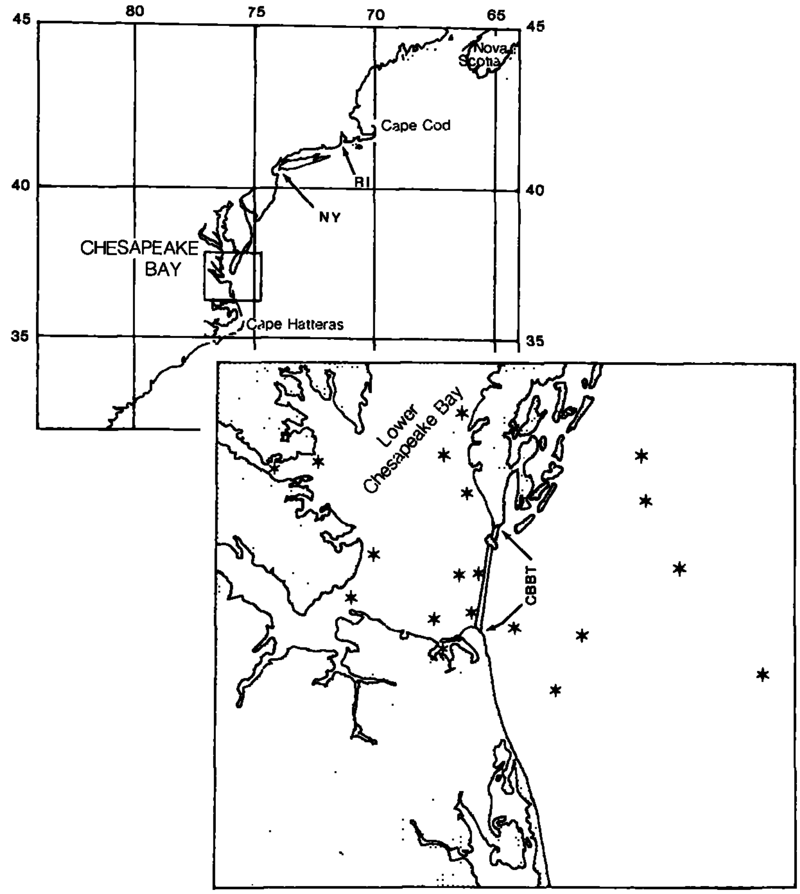

Figure 1

Collection localities (marked by stars) in lower Chesapeake Bay and Virginia coastal waters where *Tautoga onitis* were collected for age, growth, length, and weight parameters. Stars indicate general collecting areas, with most indicating more than one collection per area. Arrows indicate locations of the Chesapeake Bay Bridge Tunnel (CBBT) and of previous studies on tautog from Rhode Island (by Cooper, see Citations) and from New York and northern New Jersey (by Briggs & Olla and co-workers, see Citations).

Chesapeake Bay and offshore hardbottom areas (CBBT, wrecks, artificial reefs) of coastal Virginia (Fig. 1).

Each specimen was measured to the nearest 1 mm for standard length (SL) and total length (TL), and weighed (WT) to the nearest 5 g. Length data from both sexes were combined to generate a regression equation for SL on TL (TL = 4.78+1.20 SL). High correlation (r^2=0.98) between these measurements prompted the use of TL in analyses, since this was the more easily and reliably obtained measurement.

For each fish, an initial determination of sex was made by examining several external characters that have been previously shown to be dimorphic (Cooper 1967, Olla & Samet 1977). Adult males usually have a blunt forehead with a more massive mandible, compared with that of adult females which have a less massive mandible and more anteriorly-tapered profile of the head. Larger males are typically gray and have distinctly visible (especially underwater) white markings on the caudal, pelvic, and dorsal fins, and also on the chin region. Females (all sizes) and smaller males tend to have a mottled brown coloration without white markings on the fins and chin region.

After initial determination of sex based on external characteristics, gonads were then excised, staged macroscopically for maturity state, and weighed (gonad weight = GW) to the nearest 0.1 g (gonad weights were not available for all fish). Maturity stages were defined as follows: **Immature**—gonads undifferentiated; **Mature**—gonads obviously differentiated; **Ripe**—gonads enlarged, containing sperm or ova; **Running ripe**—sperm or ova expressed when slight pressure applied to abdomen; **Spent**—large, flaccid gonads, often bloody in appearance, with no obvious signs of sperm or ova upon dissection. A gonadosomatic index (GSI) for females for all years combined was calculated using the formula GSI=GW × 100/WT.

Scales, saccular otoliths, and opercles were collected and compared to determine the best method for ageing tautog. Whole unsectioned opercles (Fig. 2) were prepared following procedures used by Cooper (1967). The articular apical center, as defined by Le Cren (1947), McConnell (1952), Bardach (1955), and Cooper (1967), is the center of the high ridge projecting from the medial surface of the opercle. Opercular radius (OR), defined as the distance from the articular apex center to the midpoint of the posterior margin of the opercle, was measured with dial calipers to 0.1 mm (Fig. 2). Similarly, measurements (to 0.1 mm) were made along this axis to each annulus to determine annual growth increments. An annulus was defined as the sharp transition from a translucent (hyaline) to an opaque zone on the opercle. Only discernible annuli continuous from

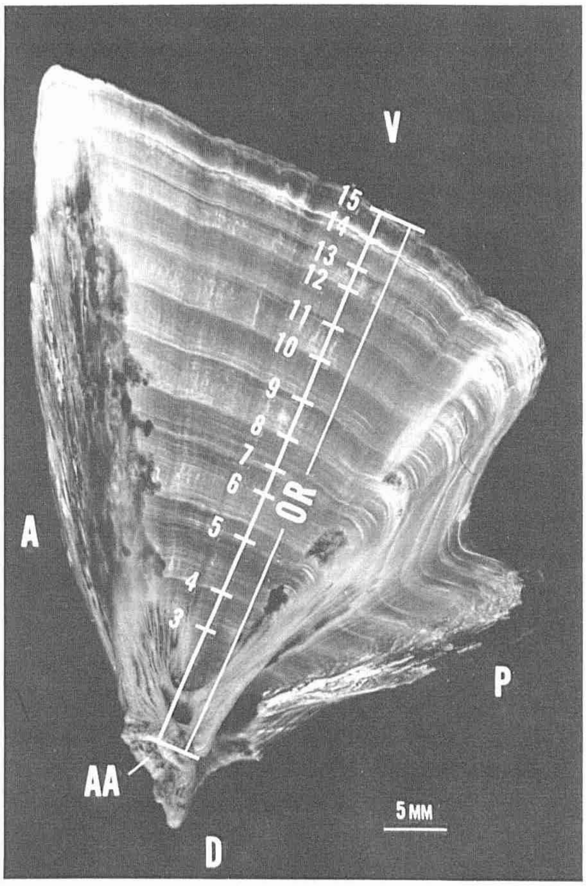

Figure 2
Measurements on each opercle of *Tautoga onitis* used in age analyses. Illustration depicts whole left opercle from *Tautoga onitis*. Orientation of the opercle is: **(A)** anterior; **(P)** posterior; **(D)** dorsal; **(V)** ventral. Successive annuli (3–15; first two annuli obscured by articular apex) are indicated; **OR** is the opercular radius; **AA** is the articular apex of the opercle.

anterior to posterior margins of the bone were considered to be annuli and counted to determine age. Other horizontal marks such as incomplete bands (= false checks) were not included in the annuli counts. All annuli continuous within contours of the opercle were counted on both right and left opercles using transmitted light. Initially, annuli on both opercles from each fish were counted with 90% agreement between counts. If differences were noted, the age estimate from the opercle with the most clearly defined annuli was used. All age estimates were made by the senior author, then a subset (n=100) of those opercles were re-read by the second author. All initial estimates by both readers were in agreement, thus age estimates (by Hostetter) were used in subsequent analyses.

Annuli were counted for both right and left opercles using transmitted light. A total of 24% (167/706) of the opercles were counted six times; four counts were made at 1× and two were made at 6× magnification. Since there was close agreement between all counts regardless of magnification, the remaining 76% of opercles were aged twice under 1× magnification. Marginal increment, the seasonal growth of the opercle, was measured by plotting increment width from the last annulus (A) against date of capture (Fig. 3).

Standard least-squares linear regression (Sokal & Rohlf 1981) was used in Lotus-R spreadsheet format (Jeanty 1984) to describe TL:SL, TL:OR, and TL:WT relationships. Determination of time of annulus formation was adopted from Nose et al. (1955) and Cooper (1967). Mean back-calculated TL-at-age (Table 1) was computed for males and females separately and for sexes combined, following Bagenal & Tesch (1978). Slope and intercept values from these equations were used in the back-calculated length equation of Ricker (1975). Calculated lengths by sex were independently determined through substitution of logarithmic values for average TL and OR by age-class. Analysis of covariance (ANCOVA) using SPSS-X (Norusis 1985) was used to compare age-at-length between sexes. Back-calculated mean lengths-at-age were used to develop von Bertalanffy curves (Gulland 1976).

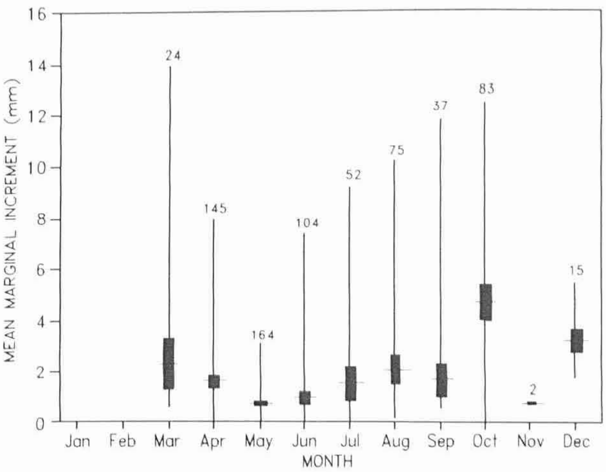

Figure 3
Mean seasonal incremental growth (in mm) of opercles of *Tautoga onitis* from coastal waters of Virginia. Vertical bars represent the range; middle horizontal bars are the mean; darkened portions represent the standard deviation; and numbers at top of each line are sample sizes.

Table 1

Back-calculation formulae for male and female *Tautoga onitis* from coastal waters of Virginia (TL=mm total length; OR=mm opercular radius); L_n=total length at year n; R_n=opercle radius at year n; R_t=opercle radius at capture; b=slope of body-bone regression; where $L_n = \log TL + b(\log R_n - \log R_t)$.

(males) $\log TL = 1.2916 + 0.860 \log OR$ (n=398; r^2=0.968)
(females) $\log TL = 1.2889 + 0.864 \log OR$ (n=281; r^2=0.967)

Results

Ageing technique and validation

Opercles were found to be the best structure for estimating age of tautog. In fish with less than four annuli, there was close agreement between annuli on scales and those on opercles. However, abrasion, surface-area damage, and ring compaction along the outer margin of scales precluded using scales for ageing older fish. Comparisons of age estimates from otoliths and opercle bones from 27 fish indicated close agreement in readings of annuli from each structure, especially in younger fish. However, otoliths from larger fish had a thickened nuclear core, which made it difficult to discern any microstructure in this region. Sanding and sectioning of otoliths proved difficult because of the small size of the otoliths, and in most cases these procedures also blurred or removed annuli on the outer edge of the otolith. The first annulus is also sometimes difficult to detect on opercles of large tautog because of thickening of the buttress zone at the articular apex. In these instances (<5% of the fish aged), we assigned a distance to the first annulus (7.4 mm) based on mean measurements from opercles with clearly defined first annuli.

Opercle radius and TL (Fig. 4) were linearly related (r^2=0.97; sexes combined). Age estimates based on the first and fourth readings (at 1×) of individual opercles were in close agreement (81%, 135/167). All age disagreements were within 1yr (n=31), except one (2 yr).

Marginal increment analysis (Fig. 3) revealed minimum growth distal of the last annulus during May, June, and early July for all age-groups. There was no indication of formation of a second mark during the year for any fish examined.

Age and growth

A total of 712 tautog measuring 51–765 mm TL was collected (Fig. 5). Of these, 701 (398 males, 282 females, and 21 immature fish of unknown sex) were used to estimate age distribution and growth rates. Specimens not included in age analyses had missing data or damaged opercles, which precluded their use in the analyses. Mature males (n=364) ranged in size from 198 to 765 mm TL, weighed 138–6895 g, and were aged 3–25 yr. Mature females (n=247) were comparable in size (232–750 mm TL) and weight (130–7392 g), and were aged 3–21. Few males (9%, n=32) and females (5%, n=14) in our samples were older than age-13. Immature fish ranged from 51 to 265 mm TL, weighed 5–410 g, and were aged 0–3 yr. Length-weight relationships (Figs. 6,7), calculated separately for males and females, indicated that mean total lengths and

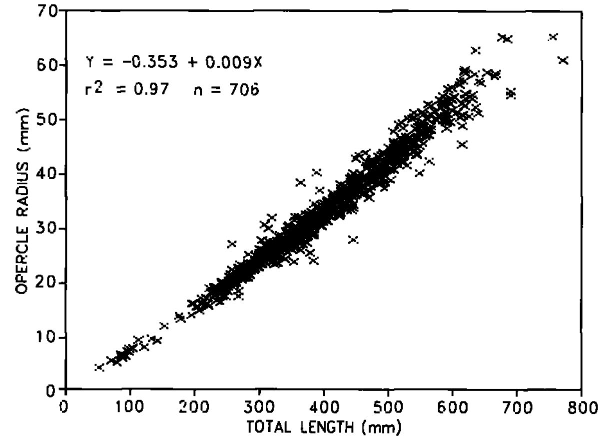

Figure 4

Relationship of opercular radius (OR) on total length (TL) for *Tautoga onitis* (sexes combined) from coastal waters of Virginia, 1979–86.

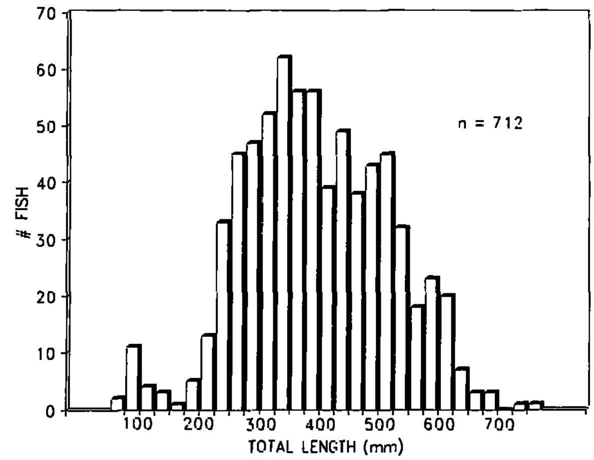

Figure 5

Length-frequencies of *Tautoga onitis* within 25 mm TL size-classes collected in coastal waters of Virginia, 1979–86.

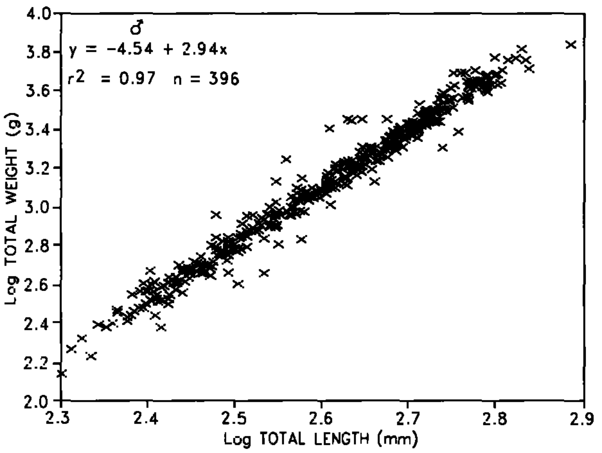

Figure 6

Length-weight relationship for male *Tautoga onitis* collected in coastal waters of Virginia, 1979–86.

weights (Tables 2,3) increased with age for both sexes ($P<0.01$).

Estimates of mean back-calculated size-at-age (Tables 4,5) suggest that growth for male and female fish is similar. However, we analyzed the data by sex to compare with previously reported values. Greatest incremental growth in TL for both sexes occurred during the first year and then declined rapidly. Growth in the second year was only 40–49% of that recorded for the first year for both sexes (Tables 4,5). Only small differences in back-calculated lengths-at-age occurred between the sexes to age-13 (Tables 4,5), and these were not statistically significant. Males usually had a slightly larger growth increment at each successive age throughout the life span.

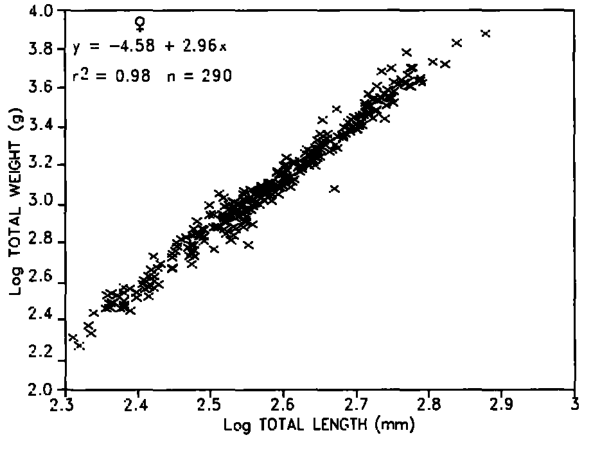

Figure 7

Length-weight relationship for female *Tautoga onitis* collected in coastal waters of Virginia, 1979–86.

Estimates of empirical length-at-age (Table 6) compared favorably with both back-calculated estimates (Tables 4,5) and observed growth (Tables 2,3). K-value for male tautog (0.090) was greater (Table 6) than that calculated for females (K=0.085). Males were also larger in size (TL) when compared with females of comparable age (Fig. 8), although the differences were not statistically significant. Males and females achieved 50% of L_∞ between ages 6 and 7, and 75% between ages 14 and 15. ANCOVA analyses indicated no significant differences between slopes of regression equations of length-at-age for male and female tautog (F=2.600, $P>0.05$) or for homogeneity of means around regression slopes (F=2.979, $P>0.05$).

Derived length-at-age estimates from von Bertalanffy growth equations were later used in regression equations to calculate weight-at-age. Although correlation coefficients were high (r=0.81) in the analysis of WT on TL, variation in weight-at-age within age-groups was considerable, and estimates of growth based on weight were less reliable than estimates based on TL.

Sexual dimorphism and reproductive biology

We observed two different morphological males in fish we examined. Approximately 15% of the fish we classified initially as females, based on external characteristics, were later determined upon dissection to be males. Generally, these non-dimorphic males were fish smaller than 550 mm TL and less than age-10. However, several approached the largest sizes observed for other males. Pigmentation of non-dimorphic males was a dull mottled brown, with remnants of disrupted lateral bands, and was similar to that noted for females. In contrast, dimorphic males were typically grayish with distinctive white markings on ventral and dorsal margins of pectoral and caudal fins and on the chin. The anterior skull and rostral region were also blunter and more massive in dimorphic males than for those noted in females and non-dimorphic males. Both types of morphological males were considered as males in analyses of age and growth and sex ratios.

Gonadal maturation was evident in both sexes by age-3. Age-2 fish, collected only in late March and early April, were immature with undeveloped gonads. GSI values for females plotted against date of capture (Fig. 9) indicated peak spawning from April through June, with the highest GSI recorded in May. GSI values declined rapidly after July. Although not shown, the GSI of tautog collected inside and at the mouth of Chesapeake Bay peaked somewhat earlier, in mid-May, and started to decrease by mid-June, whereas a small percentage (usually ~20%) of running ripe fish were

Table 2

Sample sizes (n), means ($\bar{x}$), and standard deviations (SD) for total and standard lengths (mm), and weight (g) by age for male *Tautoga onitis* from coastal waters of Virginia.

	Total length			Standard length			Weight		
Age	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
1	11	246	21	11	201	17	11	306	98
2	23	276	33	23	225	28	22	491	156
3	52	292	40	52	240	33	51	542	261
4	38	329	42	38	273	41	34	740	306
5	29	357	57	29	295	47	27	982	459
6	30	375	46	30	313	43	30	1145	447
7	31	414	52	31	340	52	31	1577	711
8	40	443	42	40	364	34	40	1795	511
9	39	481	47	39	398	47	39	2397	694
10	30	501	48	30	416	48	30	2693	794
11	18	533	41	18	438	36	18	2911	731
12	20	564	47	20	466	38	20	3663	839
13	6	545	22	6	451	22	6	3410	466
14	7	574	25	7	474	23	7	3861	573
15	1	595	0	1	491	0	1	4340	0
16	5	586	29	5	489	30	5	4202	777
17	2	587	27	2	479	20	2	4860	30
18	8	655	48	8	532	31	7	5549	766
19	3	614	15	3	504	10	3	4452	62
20	1	550	0	1	460	0	1	3090	0
21	1	613	0	1	508	0	1	4750	0
22	2	655	25	2	538	22	2	4995	725
23	0	—	—	0	—	—	0	—	—
24	0	—	—	0	—	—	0	—	—
25	1	672	0	1	577	0	1	6568	0

Table 3

Sample sizes (n), means ($\bar{x}$), and standard deviations (SD) for total and standard lengths (mm), and weight (g) by age for female *Tautoga onitis* from Virginia.

	Total length			Standard length			Weight		
Age	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
1	12	224	33	12	185	28	12	256	107
2	23	268	37	23	222	32	23	444	182
3	31	286	40	31	236	33	31	526	240
4	34	334	30	34	274	26	34	822	226
5	27	350	35	27	284	33	27	910	245
6	23	378	47	23	317	44	23	1205	468
7	37	401	38	37	334	33	37	1395	479
8	16	425	43	16	351	38	16	1551	438
9	20	453	58	20	375	46	20	1960	700
10	13	519	42	13	428	37	13	3114	876
11	13	524	54	13	436	46	13	3033	873
12	11	545	42	11	451	35	11	3660	1063
13	8	525	39	8	437	31	8	3227	643
14	3	551	64	3	464	54	3	3677	1188
15	2	518	30	2	429	20	2	2715	395
16	1	485	0	1	395	0	1	2530	0
17	1	575	0	1	479	0	1	4220	0
18	5	628	80	5	517	47	5	4961	1700
19	0	—	—	0	—	—	0	—	—
20	1	557	0	1	485	0	1	3385	0
21	1	660	0	1	570	0	1	5100	0

Table 4

Back-calculations of growth (mm) for male *Tautoga onitis* from coastal waters of Virginia.

Age (yr)	No. of Specimens	Mean length at capture	Mean back-calculated lengths at preceding annuli																								
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1	11	174	123																								
2	23	252	144	219																							
3	52	288	147	216	268																						
4	38	325	141	203	262	308																					
5	29	353	141	199	253	303	341																				
6	30	379	144	202	254	296	332	362																			
7	31	418	152	210	254	301	342	377	409																		
8	40	440	151	204	251	292	329	367	404	431																	
9	39	477	152	203	257	300	340	375	409	441	469																
10	30	501	145	204	251	298	337	370	403	433	464	491															
11	18	519	171	197	242	279	310	346	375	404	433	460	502														
12	20	560	139	194	248	295	338	376	412	444	476	509	533	554													
13	6	561	147	195	250	284	316	344	370	400	432	465	499	528	551												
14	7	566	145	188	241	294	329	362	391	421	447	473	497	523	546	562											
15	1	592	154	204	226	264	307	348	368	400	433	459	486	514	552	570	586										
16	5	578	153	201	260	286	313	328	358	383	406	435	462	490	511	532	550	569									
17	2	593	147	203	259	287	321	344	363	394	417	445	460	481	510	531	554	574	588								
18	8	668	154	209	244	275	310	344	377	413	449	485	512	542	570	595	614	636	652	664							
19	3	615	127	173	229	264	298	330	352	373	397	423	446	472	502	521	543	558	574	597	612						
20	1	578	131	156	209	239	272	300	326	352	374	394	418	445	467	492	514	533	544	553	564	575					
21	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
22	2	622	118	165	218	243	268	289	327	358	390	431	452	473	495	508	528	546	564	579	593	606	614	622			
23	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
24	1	679	164	204	232	267	290	311	349	380	411	437	463	481	505	529	561	586	605	616	629	643	650	658	666	673	
25	1	672	119	182	236	272	296	322	339	357	375	393	406	435	465	491	519	558	586	611	631	641	648	655	662	668	672
Weighted mean			146	204	254	296	331	364	397	425	452	475	499	522	531	547	563	581	599	616	602	608	632	639	664	671	672
Growth increment			146	58	50	41	36	33	33	28	28	23	24	23	9	16	16	18	18	18	–14	6	24	7	26	7	1

Table 5

Back-calculations of growth (mm) for female *Tautoga onitis* from coastal waters of Virginia.

Age (yr)	No. of Specimens	Mean length at capture	Mean back-calculated lengths at preceding annuli																				
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	23	174	123																				
2	28	249	131	212																			
3	31	288	130	202	263																		
4	32	333	138	208	260	312																	
5	29	345	133	200	249	296	332																
6	24	379	137	196	251	294	340	368															
7	34	401	135	192	244	283	322	360	387														
8	19	422	134	195	248	292	326	358	389	412													
9	21	450	146	207	254	293	328	358	388	420	443												
10	10	522	144	206	261	298	340	378	409	445	481	508											
11	14	522	137	193	245	294	335	373	404	430	460	486	513										
12	9	527	134	189	240	278	311	349	379	404	431	461	492	515									
13	12	540	134	196	250	285	319	344	370	397	426	452	483	508	530								
14	2	558	157	205	246	312	368	400	422	447	466	489	506	525	542	555							
15	2	513	126	169	235	265	286	316	339	363	385	404	434	455	474	490	505						
16	2	516	122	164	227	245	263	284	304	331	360	384	416	434	455	476	497	512					
17	1	575	112	193	237	259	281	309	340	367	380	414	432	467	490	508	535	548	566				
18	4	614	127	175	222	251	288	320	347	373	402	430	458	484	507	534	554	577	592	608			
19	1	685	150	223	275	325	384	413	440	452	470	504	530	565	585	608	626	643	662	676	683		
20	1	557	164	192	230	245	258	279	297	313	336	355	371	393	413	433	456	487	506	527	543	550	
21	1	660	148	180	216	266	310	354	390	437	476	502	526	545	560	572	588	594	600	621	634	645	660
Weighted mean			134	200	251	292	327	359	386	413	440	466	486	499	515	521	536	560	587	608	620	598	652
Growth increment			134	65	51	41	34	32	27	27	28	26	19	13	16	7	14	25	27	21	12	–22	55

Table 6

Estimated parameters and standard errors (SE) of the von Bertalanffy growth equation for *Tautoga onitis* from coastal waters of Virginia (L_t=mean asymptotic total length in mm; K=growth coefficient; t_0=time (yr) at which total length would theoretically be zero).

Parameter	Estimate	Asymptotic SE
Males		
L_t	732.24	9.124
K	0.090	0.003
t_0	−1.64	0.132
Females		
L_t	733.61	28.362
K	0.085	0.009
t_0	−1.74	0.324
Sexes combined		
L_t	742.37	9.051
K	0.085	0.003
t_0	−1.816	0.144

present in samples from offshore collecting sites until late July and early August. Fish occurring on wrecks further offshore (and usually deeper) generally had higher GSI values later into the season (early July–early August) than those collected from inshore areas.

Chi-square analysis of sex ratios for 701 tautog divided into 10 cm length-groups indicated significant deviations (χ^2=18.87; df=1) from a 1:1 sex ratio in the larger size-classes (Table 7). The larger size-classes and older fishes were comprised predominantly of males.

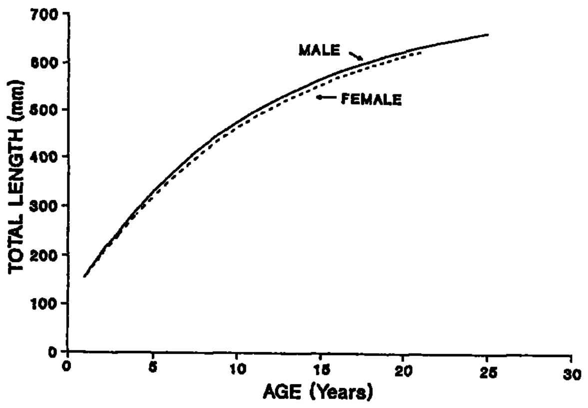

Figure 8

von Bertalanffy growth curves for male and female *Tautoga onitis* collected in coastal waters of Virginia, 1979–86.

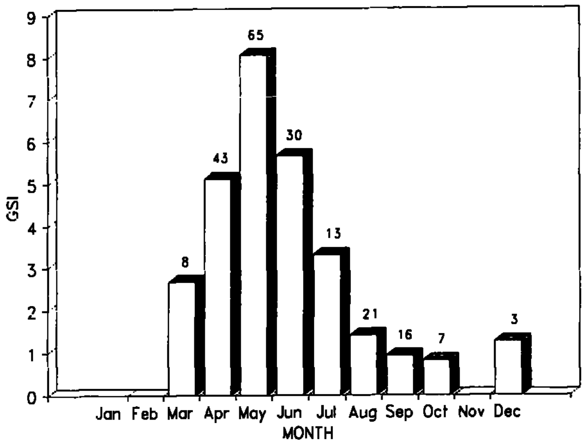

Figure 9

Seasonal gonadal development (gonadosomatic index, GSI) for female *Tautoga onitis* collected in coastal waters of Virginia, 1982–84. Numbers over bars are sample sizes.

Discussion

Age and growth

The only previously published study on age, growth, and longevity of tautog was from samples collected in and near Narragansett Bay, Rhode Island (Cooper 1967). Cooper's (1966) tag and recapture data verified that continuous rings on opercle bones in tautog represented annuli and that these marks were indicative of rate of growth over the year. High level of agreement between opercle readings, high linear correlation between TL and OR, and consistent time of annulus formation for fish examined in this study were similar to results reported by Cooper (1967).

Our study is the first to present information on growth and longevity for tautog from southern portions of the species range. Our results agree with those of Cooper (1967) on tautog from Rhode Island that the

Table 7

Chi-square analysis of sex ratios for different size-classes of *Tautoga onitis* captured in coastal waters of Virginia (*P 0.05= 3.84; **P 0.01=6.63).

Standard length (mm)	Male	Females	χ^2	*P*
0–100	16	24	1.60	NS
101–200	137	110	2.95	NS
201–300	128	94	5.21	*
301–400	103	57	13.23	**
401–500	24	8	8.00	**

tautog is a long-lived species that reaches relatively large sizes slowly. Seasonal growth, reflected by annular growth increments on opercles (Fig. 3), is one of rapid somatic growth following spawning, with maximum yearly growth achieved from July to December. Slower rates of somatic growth during January to March may be attributed to decreased feeding during colder winter temperatures (Cooper 1966, Olla et al. 1974). From March to June, the rate of somatic growth is less than that observed in other seasons and most likely results from energy expenditure associated with gonadal maturation and spawning.

In Virginia and Rhode Island, annual growth in length was rapid during the first three years (~33% and 38% of the total in Virginia and Rhode Island, respectively) and declined steadily with increasing age. Except for age-1, annual growth increments between populations were roughly similar to about ages 12–13, after which yearly increments (TL) in Rhode Island fish declined rapidly; whereas growth rates for tautog of the same age-groups from Virginia's coastal waters did not diminish as rapidly. In fact, from about ages 12–13 onward, annular growth increments of tautog from Virginia were nearly double those of their counterparts from Rhode Island (compare Tables 4&5 with Cooper 1967). Other differences between this study and Cooper's (1967) are that tautog in Virginia reach twice the TL of those in Rhode Island at time of first annulus formation. Annular growth estimated by back-calculations indicated that in tautog from Virginia, the greatest average yearly increment in growth occurred during the first year. In contrast, Cooper found that both sexes had their largest yearly increase in TL during their second year of life. Observed differences in first-year growth of tautog from Virginia and Rhode Island result either from our missing the first annulus, or from differences in environmental factors between study areas. We discounted missing the first annulus, because we believe we had adequate numbers of fish in these younger age-groups (*n*=204), from both seasonal and size perspectives, to consider this a reasonable estimate of opercle size at age-1. Additionally, back-calculated lengths-at-age-1 for all tautog aged closely matched actual observations of TL at the end of the first year (compare Tables 2,3 and 4,5).

Observed differences in first-year growth between tautog occurring in Virginia and Rhode Island may result from environmental factors in more southern waters that favor growth over a longer season (Fig. 10). For example, temperatures in shallow-water areas below which juvenile tautog become inactive (~10°C) occur earlier and persist longer in inshore coastal waters of Narragansett Bay, Rhode Island than in the lower York River in Chesapeake Bay. On average, water temperatures in springtime remain below 10°C nearly a full month longer in Narragansett Bay (not until mid-April) than in the York River (usually mid-March). And in the fall, temperatures again decline below 10°C during mid- to late October in Narragansett Bay, whereas in Virginia temperatures remain above 10°C usually well into mid-November or early December. These temperatures, which are conducive for somatic growth in juvenile tautog, are extended seasonally in coastal waters of Virginia compared with those of more northern areas. Recently, D.L. Martin and T.E. Targett (Grad. Coll. Mar. Stud., Univ. Delaware, Lewes DE 19958, unpubl. data) found in laboratory growth experiments that young-of-the-year tautog from high-latitude populations (Rhode Island) show no genetic compensation for a shorter growing season when compared with tautog from Delaware Bay and Virginia waters. These data further support our hypothesis that observed differences in growth of young tautog from northern (Rhode Island) and southern (Virginia) areas of the species range are due primarily to environmental factors between the two areas (i.e., duration of optimal temperatures for growth is longer in Virginia coastal waters compared with those of coastal areas in the northern end of the species range).

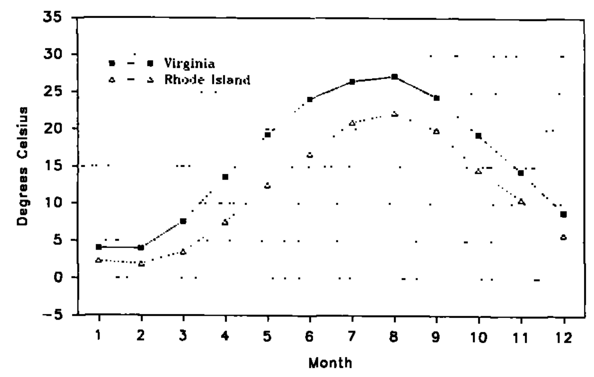

Figure 10

Average monthly water temperatures (1979–86) for lower York River, Virginia (VIMS oyster pier, taken 1m below surface at 2.0–2.5m depth; G. Anderson, Coll. William & Mary, VIMS, Gloucester Point VA, pers. commun.), and for bottom-water temperatures at Fox Island, Narragansett Bay, Rhode Island (H.P. Jeffries, Univ. Rhode Island, Grad. School Oceanogr., Narragansett RI, pers. commun.). Solid squares and open triangles represent mean monthly values for York River and Narragansett Bay, respectively.

Estimated values of L_∞ for tautog from Virginia are also considerably higher than those estimated for tautog from Rhode Island (Table 8). A calculated L_∞ of 733 mm TL (data for sexes combined; 733 mm for females, 732 mm for males) as derived from the von Bertalanffy equation in our study is close to the observed maximum TL of 765 mm. Growth equations es-

Table 8

von Bertalanffy growth functions derived for *Tautoga onitis* collected in Virginia (1979–86) and Rhode Island (from Cooper 1965).

Virginia tautog			
(males, *n*=398)	K	=	0.090, $L_\infty = 732$
	t_0	=	-1.644
	L_t	=	$732\,[1-e^{-0.090(t+1.644)}]$
(females, *n*=281)	K	=	0.085, $L_\infty = 733$
	t_0	=	-1.743
	L_t	=	$733[1-e^{-0.085(t+1.743)}]$
Rhode Island tautog			
(males, *n*=1041)	L_t	=	$664[1-e^{-0.09108(t+1.66238)}]$
(females, *n*=1119)	L_t	=	$506[1-e^{-0.15189(t+0.95220)}]$

timated for tautog in Rhode Island (Cooper 1965) indicated appreciably smaller L_∞ values (506 mm and 664 mm) for both sexes compared with those estimated for tautog in Virginia.

The present study also found that males grow at a somewhat faster rate than females. Cooper (1965) found a slightly faster growth rate in females when compared with males (Table 8). However, in both studies estimated *K*-values are comparable. Similarities in *K*-values between tautog occurring in Rhode Island and Virginia support the contention that growth rate (*K*) is an intrinsic value for the species, largely independent of geographic location.

Although Cooper (1965) found that females initially grew at a faster rate than males, he reported divergence in growth between sexes favoring faster growth in males after age-3. We also found similar divergence in growth of males, but unlike Cooper's study, this difference was apparent for males at all ages.

In our study area, males live longer than females. The oldest fish examined were a male estimated to be age-25 and a female estimated to be age-21. Cooper (1967) indicated a life span of 34 yr for males and 22 yr for females in the population he studied in Rhode Island, and suggested that females may reach senescence at an earlier age than males. Although longevity estimates of tautog based on actual data range between 25 and 34 yr, most fish aged were considerably younger than this, and it seems that claims of fish more than a half century old (Reiger 1985) are exaggerated. Average age for tautog in this study was just over 7 yr; 82% of the fish were age-10 or younger, only 1% were age-20 or older. Cooper (1967) found a similar age structure in the population of tautog residing in Narragansett Bay just over 25 yr ago, where approximately only 15% and 8% of males and females, respectively, were older than age-13. The current world record for tautog (IGFA 1990) was a fish taken by rod-and-reel off Virginia measuring 819 mm TL (~10.89 kg). Within constraints of the von Bertalanffy equation and length-weight relationship derived for tautog from Virginia waters, we estimate an age for this fish of ~30 yr, which is comparable to the maximum age (34 yr) reported for the species (Cooper 1967).

Weight-at-age estimates for tautog, as a measure of growth, were much more variable than length estimates. This variation is attributed to different stages in ontogenetic development, as well as differences in sex, maturity, and age. Geographic location and associated environmental conditions, such as seasonality (date and time of capture), stomach fullness, disease and parasite loads (Le Cren 1951, Bagenal & Tesch 1978), can also affect weight-at-age estimates. Since these factors contribute significant variation to regression relationships of WT on TL, interpretation of differences in these data between populations must be viewed with caution.

Direct comparisons of our length-weight data with those of Cooper (1967) were not feasible due to sampling differences (Cooper used eviscerated weights of fish). However, in a study of tautog from coastal waters off New York, Briggs (1969) calculated a length-weight relation based on uneviscerated weights of over 3000 fish collected during several seasons (May–November) over a 3 yr period. Although Briggs did not present data for individual sexes, comparisons of data combined for both sexes are still possible (Table 9). From these comparisons, it is evident that the length-weight relationship for tautog from Virginia waters is similar to that estimated for tautog from off New York.

Table 9

Comparison of estimated length-weight relationships between *Tautoga onitis* collected in Virginia (uneviscerated weights, sexes combined; Log W (g)= –4.632+2.979 Log L; *n*=687) and New York (from Briggs 1969; uneviscerated weights, sexes combined; Log W (oz) = –5.992+2.916 Log L; *n*=3156).

	Estimated weight (g)	
Length (mm)	New York	Virginia
150	76.5	70.9
200	119.1	112.2
250	334.4	324.7
300	567.0	558.9
350	890.2	884.7
400	1215.4	1316.8
450	1854.1	1870.3
500	2520.3	2560.0
550	3328.3	3400.5
600	4289.4	4406.7
650	4941.4	5096.1

Reproduction and growth

Maximum GSI values calculated in the present study indicate that spawning commences in late April and continues to early June for tautog taken at inshore sites in Virginia. Finding fish in spawning condition in Virginia in late April is somewhat earlier than reported previously for tautog from more northern inshore areas, and undoubtedly reflects the warmer temperatures in coastal waters of Virginia in early spring. Based on laboratory (Olla et al. 1980) and field observations (Chenoweth 1963, Olla et al. 1974, Eklund & Targett 1990, this study) of ripe fish, spawning in tautog generally commences when water temperatures reach 11° C or above. In Massachusetts, tautog spawn from mid-May to early August (Stolgitis 1970), while peak spawning was reported to occur from late May to early June in tautog collected within shallow waters of Narragansett Bay, Rhode Island (Chenoweth 1963). Near Long Island, tautog eggs have been collected in the plankton from May through early September (Perlmutter 1939, Wheatland 1956, Austin 1973); however, the effective spawning season may be somewhat shorter since few larvae were collected when water temperatures exceeded 21.0° C (Austin 1973).

Highest GSI values for tautog from Virginia occurred over a longer seasonal period than reported for tautog collected inside Narragansett Bay (Chenoweth 1963). We attribute this to the fact that we collected fish over a broad range of sites spread over a much wider geographic area, including many deepwater offshore stations. On hardbottom areas 22–37 km offshore of Maryland and northern Virginia, Eklund & Targett (1990) noted significantly higher GSI values for female tautog (24–50 cm TL) from May through the beginning of August, with spawning taking place during summer (May–July). This time schedule is similar to what we observed in tautog collected at offshore habitats in southern Virginia, and, as was pointed out by Eklund and Targett, this seasonality also corresponds with the occurrence of tautog eggs and yolksac larvae in Mid-Atlantic Bight plankton samples (Colton et al. 1979).

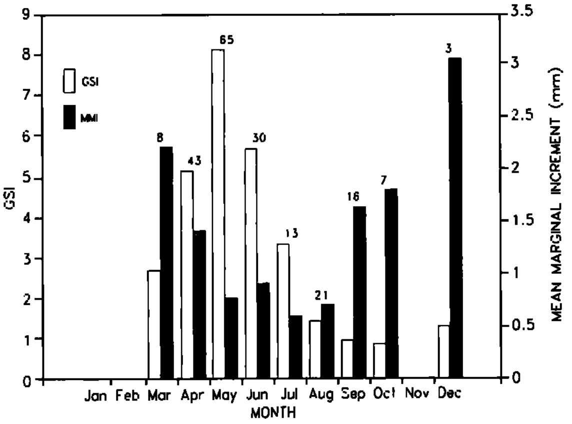

Figure 11

Relationship demonstrating co-occurrence of time of annulus formation (mean marginal increment, MMI) and peak spawning season (gonadosomatic index, GSI) for *Tautoga onitis* from coastal waters of Virginia.

Annulus formation in tautog collected in Virginia occurs in May or June commensurate with gonadal maturation (Fig. 11). Formation of an annulus on the opercle concomitant with spawning was noted also by Cooper (1967) for tautog from Rhode Island. Decline in physiological condition during gonadal development, presumably representing disruption in somatic growth, was observed in tautog by Chenoweth (1963). Such disruption in somatic growth could contribute to the slow-growth phase observed on opercles during this time. However, annulus formation occurs in sexually immature fish during this same time, indicating that inherent physiological factors other than those associated with spawning also influence annulus formation in these fish.

Annulus formation in tautog collected in Rhode Island occurred in late or middle May at the start of the spawning season (Cooper 1967). In Virginia, we observed that annuli formed over a longer time-period (May–July). Warmer water temperatures earlier in spring in Virginia may cause smaller fish to form annuli slightly earlier than larger fish. This growth pattern would agree with observations that younger and smaller fish are more active than larger fish at lower water temperatures (Olla et al. 1974, 1980). Also, since these smaller fish do not usually participate in spawning activities, all growth during spring would be reflected as increases in somatic rather than gonadal growth.

Variation in the estimate of time of annulus formation may have resulted from analyzing data independent of year of collection. Interannual differences in environmental conditions would be expected when these data are combined. Also, we sampled tautog from various geographically separated inshore and offshore locations, and small-scale variations in time of annulus formation may be expected in fish collected from these diverse areas. One other source of variation could result from annulus formation during the spawning period. Since spawning commences earlier and is apparently more protracted for fish in southern areas of the species range, the period for annulus formation would also be extended in tautog occurring in Virginia compared with those occurring further north.

Growth and sexual strategy

The present study, and previous ones conducted in more northern waters (Chenoweth 1963, Cooper 1967, Stolgitis 1970, Briggs 1977), found that male tautog mature by age-3 and females by age-4. Similar age-at-maturation for tautog from different portions of the species range for the present population of tautog living in Virginia's coastal waters, and that reported by Cooper 25 years ago (1967) for tautog from Narragansett Bay, may reflect demographics of populations that have not sustained intensive exploitation. It would be valuable to compare age-growth data for the present-day population of tautog residing in Narragansett Bay with historical data in Cooper (1967) to test this hypothesis.

It is unknown what percentage of tautog in a population mature precociously, under what environmental or social situations, or even if smaller fish are sexually active and reproduce successfully. In May 1985, the second author collected a 180 mm TL, age-2 gravid female north of the confluence of the Taunton River and Mount Hope Bay, Massachusetts. In the present study, no sexually mature females smaller than 230 mm TL or younger than age-3 were found. We note, though, that our data are limited for age-2 fish, especially for fish of this age-group during their second summer and fall. Olla & Samet (1977) also reported collecting sexually mature tautog "which were of a much smaller size and younger age [no sizes or ages reported] than has previously been reported" from coastal waters of New York and northern New Jersey. It is interesting to note that precocious individuals have only recently been reported, and these were tautog occurring in northern waters where sport and localized commercial fisheries have operated historically since the 1800s (Goode 1884) and have undoubtedly intensified since that time. Earlier maturation is a common compensatory response in fish populations subjected to intensive exploitation (Goodyear 1980) and may explain the appearance of precocious individuals in tautog populations inhabiting northern portions of the species range where exploitation has occurred for a longer time.

Sex ratios for tautog divided into 10 cm length-groups were found to deviate significantly from a 1:1 ratio in the larger size-classes, with larger (and older) size-classes of tautog being comprised predominantly of males. Based on a smaller sample size, Eklund and Targett (1990) also reported a sex ratio (0.86:1) skewed in favor of males. Small sample size in their study, however, precluded breakdown of sex ratios over the size range studied. Among other factors, skewed sex ratios in larger (and older) fish may be attributed to differential growth and longevity of males or slowing of growth (measured as TL) with age in females, or possibly as a result of sex reversals. Faster growth coupled with greater longevity for male tautog found in Virginia's coastal waters may reflect the higher energetic costs of reproduction and subsequent earlier senescence and differential mortality for females, as suggested by Cooper (1967). Larger size may also be selected for in males. Observations of courtship and spawning reveal that a size-related male dominance hierarchy is one reproductive mode (group spawning without a dominance hierarchy is the other) occurring in tautog with dominant males exhibiting strong territoriality and performing a protracted courtship with females, culminating in pair-spawning (Olla & Samet 1977). In reproductive strategies involving pair-spawning, territoriality, and dominance social hierarchies, size selection for large males would be advantageous. Such strong size and sexual selection is known in other labrids, including bluehead wrasse *Thalassoma bifasciatum* (Warner et al. 1975), California sheepshead *Semicossyphus pulcher* (Warner 1975), cunner *Tautogolabrus adspersus* (Johansen 1925, Pottle & Green 1979a,b), and others (Warner & Robertson 1978), where females primarily select larger (older) males as spawning partners.

Although diandric male phases are prevalent in both tropical and temperate labrids (Robertson & Choat 1974, Warner & Robertson 1978, Dipper & Pullin 1979), diandric male tautog were not reported in earlier studies (Chenoweth 1963, Cooper 1967). Olla & Samet (1977), following Cooper (1967), noted in their study on spawning behavior that "tautog were easily identifiable with respect to their gender by the sexually dimorphic mandible, which is more pronounced in males." However, in that same paper, unpublished data of Olla & Bejda noted the occurrence of sexually-mature young tautog of both sexes, without any sexual dimorphism. Olla & Samet (1977) suggested that mandibular dimorphism in tautog may develop ontogenetically, becoming apparent only in older, larger fish. In contrast, we found wide overlap (up to ~50 cm TL) in body size between the two male forms, rendering it unlikely that age alone controls development of secondary male characteristics in tautog.

Olla & Samet (1977) also discussed the possibility that younger, mature fish may represent a different sexual stage than that of older fish. They pointed out that nothing was known of behavior or gonadal development of these young fish, and that it was even remotely possible that tautog might be hermaphroditic.

Since two spawning strategies have been observed in male tautog (Olla et al. 1977, 1981), it is possible that diandric males are those that utilize different reproductive strategies. Since non-dimorphic males have coloration patterns reminiscent of females, they may increase spawning opportunities through sneak or interference spawning during activities of territorial males. Reproductive behavior of individual male tautog is flexible and influenced by both size and sexual composition of the population. For example, in some situations with co-dominant males, or when males greatly outnumbered females, group spawning occurred even among dimorphic males that in previous experiments exhibited strong territoriality and more typically attempted only exclusive pair-spawning with females (Olla et al. 1981). Diandric males, each with different reproductive behaviors, have been reported for hermaphroditic labrids (Robertson & Choat 1974, Warner 1975, Warner & Robertson 1978, Dipper & Pullin 1979, Pottle & Green 1979a) and scarids (Warner & Downs 1977, Robertson & Warner 1978). However, diandric males not resulting from sexual inversions, but with different reproductive strategies, have also been reported (Pottle & Green 1979a,b) in cunner *Tautogolabrus adspersus*, another temperate species of wrasse co-occurring throughout most of the geographic range of the tautog.

Plasticity of male reproductive behavior, presence of diandric males in the population, and skewed size and sex-ratios indicate that reproduction in tautog is more complex than recognized previously. Many of these same characteristics are paralleled in protogynous hermaphroditic labrids. In fact, protogynous hermaphroditism is one of the more common reproductive strategies utilized by labrids (Roede 1972, Warner & Robertson 1978). Earlier researchers (Chenoweth 1963, Cooper 1967) did not consider that tautog might be hermaphroditic; others (Olla & Samet 1977) recognized such possibilities, but, as yet, no evidence based on histological examination of gonads exists to prove or disprove the occurrence of hermaphroditism in this species. In view of the complex reproductive biologies of other labrids, further study on reproductive biology of tautog is warranted and is currently under investigation.

Growth rates of tautog, other labrids, and reef fishes

Few published age-growth studies on labrids exist, undoubtedly because most are tropical species that have proven difficult to age reliably and few have commercial or recreational value. However, growth rates available for temperate labrids from the eastern and western Atlantic and eastern Pacific indicate slow growth rates and generally extended longevities in these species (Fig. 12), similar to those reported for tautog. It is possible that slow growth and extended longevities are characteristic not only of relatively large-sized temperate labrids, but also may be an inherent feature of growth patterns in large-sized labrids in general.

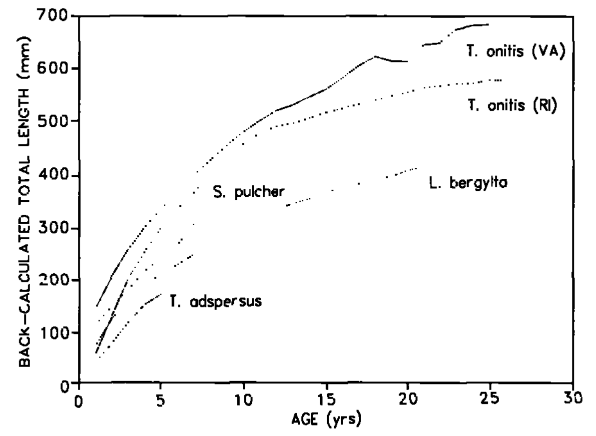

Figure 12

von Bertalanffy growth curves for selected species of temperate and subtropical species of wrasses (Family Labridae). Species represented and information sources for data presented in figure are: *T.*(=*Tautoga*) *onitis*, Rhode Island (Cooper 1965), Virgina, this study; *S.*(=*Semicossyphus*) *pulcher*, Warner 1975; *L.*(=*Labrus*) *bergylta*, Dipper et al. 1977; *T.*(=*Tautogolabrus*) *adspersus*, Serchuk & Cole 1974.

Coefficients derived from the von Bertalanffy growth equation provide insights into ecological strategies, especially in direct comparisons among diverse taxa (Table 10). Manooch (1979) considered fishes such as the bluefish *Pomatomus saltatrix*, Atlantic menhaden *Brevoortia tyrannus*, and king mackerel *Scomberomorus cavalla*, which have relatively high *K*-values (0.23–0.39) indicative of fast growth rates, as the coastal pelagic guild. Species with slower growth rates (K usually <0.22) and generally longer lived, on the other hand, were grouped together as the snapper-grouper guild. These fishes represent a wide spectrum of distantly related taxa including temperate labrids, reef-dwelling snappers and groupers, and other demersal fishes such as tilefish *Lopholatilus chamaelonticeps* which inhabits burrows on the continental shelf. Based on categories of growth coefficients adopted by Manooch (1979), we include the tautog in the snapper-grouper guild. This type of comparison, which crosses phylogenetic and demographic lines, suggests similarities in selection patterns for growth rates among species inhabiting areas where spatial resources may be limited.

Conclusions and management considerations

Growing recreational and commercial fisheries for tautog, limited amounts of natural habitat available in

Table 10

Comparison of growth coefficients (K-values) and longevity for selected species of labrids and other coastal fishes (age in years; L_∞ in mm).

Species	Source	Age	L_∞	K
Snowy grouper *Epinephelus niveatus*	Matheson & Huntsman (1984)	17	1255	0.07
Tautog *Tautoga onitis*	this study (males)	25	732	0.09
	this study (females)	22	733	0.09
	Cooper (1965) (males)	27	664	0.09
	(females)	22	506	0.15
Ballan wrasse *Labrus bergylta*	Dipper et al. (1977)	29	405	—
Calif. sheepshead *Semicossyphus pulcher*	Warner (1975)	>20	800	—
Lane snapper *Lutjanus synagris*	Manooch & Mason (1984)	10	501	0.13
Speckled hind *Epinephelus drummondhayi*	Matheson & Huntsman (1984)	15	967	0.13
Mutton snapper *Lutjanus analis*	Mason & Manooch (1985)	14	862	0.15
Tilefish *Lopholatilus chamaeleonticeps*	Turner et al. (1983)	35	960	0.16
Red snapper *Lutjanus campechanus*	Nelson & Manooch (1982)	16	975	0.16
Scamp *Mycteroperca phenax*	Matheson et al. (1986)	21	985	0.17
Cunner *Tautogolabrus adspersus*	Serchuk & Cole (1974)	6	285	0.20
Black sea bass *Centropristis striata*	Wenner et al. (1986)	10	341	0.23
Bluefish *Pomatomus saltatrix*	Wilk (1977)	9	—	0.23
Blue runner *Caranx crysos*	Goodwin & Johnson (1986)	11	412	0.35
King mackerel *Scomberomorus cavalla*	Normura & Rodriques (1967)	14	—	0.35
Atlantic menhaden *Brevoortia tyrannus*	Schaaf & Huntsman (1972)	—	—	0.39

the southern Mid-Atlantic Bight, and the slow growth and reproductive characteristics of this species, suggest a need for a fisheries management plan to maintain the present stocks of tautog in Virginia's coastal waters (and elsewhere). It has been shown that intense fisheries directed at species exhibiting slow growth rates and a habitat-restricted ecology affect populations detrimentally (Manooch & Mason 1984, Matheson & Huntsman 1984, Moore & Labisky 1984, Harris & Grossman 1985, Matheson et al. 1986). Strong habitat preferences (hardbottom with structural relief), slow growth rates, extended longevities (to 25+yr), and relatively long time to reach sexual maturity (3+ yr), indicate that strategies applied to reef species—the snapper-grouper cohort of Manooch (1979)—may be applicable in managing tautog populations as well.

We suggest as a first step in managing stocks of tautog in Virginia the imposition of size limits on fish taken by recreational as well as commercial fishermen, since the recreational fishery is the primary harvestor of tautog. A minimum size limit of approximately 300 mm TL (12 in.) is recommended for fish taken by recreational or commercial fisheries to insure that all females have at least one opportunity to spawn before being harvested (Briggs 1977). Imposing a 12 in. size limit for tautog should also insure the maintenance of a quality recreational fishery. Currently, a 12 in. minimum size limit is required for tautog taken by recreational and commercial fishermen in Rhode Island, Massachusetts, and Connecticut waters.

To maximize any management plan for this species, it is also critical that the reproductive biology of tautog be well understood. Directed fishing pressure, disruptive to size or sex ratios by the selective removal of dominant pair-spawning males (usually larger individuals), could affect reproductive success in localized populations. Musick & Mercer (1977) concluded that heavy fishing pressure on black sea bass *Centropristes striata* may impact reproduction through changes in sex ratios in the population.

Tautog populations in Virginia and elsewhere can also be enhanced by continued development of artificial reefs (Feigenbaum & Blair 1986). Reef development is especially important in Virginia since suitable, naturally-occurring substrate appears to be limited both in size and occurrence. Placement of artificial structures over wide geographic areas also disperses fishing pressure, since competition for fishing space on presently-available isolated wrecks can at times be intense.

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