

Abstract.—Spawning patterns, larval distribution, and juvenile growth characteristics for tautog *Tautoga onitis* in New Jersey and the Mid-Atlantic Bight. We analyzed data from plankton surveys (1972–1990) over the continental shelf and in the Great Bay–Mullica River estuarine system. Data on size and abundance of juveniles were derived from throw trap and trawl collections in New Jersey estuaries (1988–89). In addition, we validated the daily deposition of otolith increments and used increment counts to estimate juvenile age and growth patterns. Extensive egg and larval collections indicated that spawning occurs from April through September, with a peak in June and July. Spawning over the continental shelf is concentrated off Long Island and Rhode Island. Based on validated daily increments in sagittal otoliths and the formation of a well-defined settlement mark, tautog larvae spend about 3 weeks in the plankton. Both spawning and settlement occur over a prolonged period, based on otolith back-calculations. Three methods of estimating young-of-the-year growth rates, including length-frequency progressions, otolith age/fish-size comparisons, and direct measurement of growth in caging experiments, indicated an average growth rate of about 0.5 mm/day during the peak midsummer growing season. Length-frequency distributions suggested tautog reach a modal size of about 75 mm SL after their first summer, and 155 mm by the end of their second summer.

Early life history of the tautog *Tautoga onitis* in the Mid-Atlantic Bight*

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The tautog *Tautoga onitis* is one of two labrid wrasses common along the northeast coast of the United States (the other is the cunner *Tautoglabrus adspersus*). Tautog occur in coastal areas from Nova Scotia to South Carolina, but are abundant only from Cape Cod to the Delaware Capes (Bigelow and Schroeder 1953). Adult tautog form a minor component of local commercial fisheries and a major component of the recreational catch. They reach a maximum size of about 90 cm and 10 kg (Bigelow and Schroeder 1953), and an age of 34 years (Cooper 1967). Large juveniles and adults depend on young mussels *Mytilus edulis* for food (Olla et al. 1974), and the diet of recently-settled juveniles consists primarily of copepods and amphipods (Grover 1982). Spawning takes place from May to August, with a peak in June (Kuntz and Radcliffe 1918, Colton et al. 1979, Eklund and Targett 1990). Egg and larval development are described in detail by Kuntz and Radcliffe (1918) and Williams (1967); additional information on life history is

presented in Auster (1989).

Both juvenile and adult tautog are dependent on habitats with structure or cover, which presumably aids in protection from predators (Olla et al. 1974 and 1979, Olla and Studholme 1975). Tautogs typically become quiescent at night, resting in association with some type of shelter (Olla et al. 1974). Smaller fish (subadults <25 cm) may range only a few meters from that shelter during daytime activity, while larger individuals (adults >30 cm) cover a broader area for foraging, returning to the same general shelter area at night (Olla et al. 1974).

Declining water temperatures in the fall trigger an offshore migration of adults (age 4+). An increase in schooling behavior and night activity also occurs (Olla et al. 1980), perhaps related to migratory activity. Laboratory studies indicate that adults attain a dormant state at temperatures <5°C. Juveniles (age 2–3) also become torpid in winter, but they remain inshore, either partially buried or in close proximity to structure (Olla et al. 1974). In spring and summer adults return to inshore habitats. On hard-bottom reefs off Maryland

Table 1Collection sources for *Tautoga onitis* eggs, larvae, and juveniles used in analyses of seasonal distribution and growth comparisons.

Stage	Sampling location	Years sampled	Sampling frequency	No. of tows or samples	Data source
Eggs	Mullica River, Great Bay, Little Egg Inlet	1972-75	monthly or bimonthly	462	Milstein and Thomas 1977
Larvae	Nova Scotia to North Carolina	1977-87	monthly or bimonthly	11,438	MARMAP
	Great Bay, Little Sheepshead Creek	1989-90	weekly	913	Rutgers Marine Field Station Plankton Survey
Early juveniles	Great Bay, Little Egg Harbor	1988-89	biweekly, May-September	436	Sogard and Able 1991
	Great Bay; artificial seagrass	1988	weekly, June-September	54	Sogard 1990
Late juveniles	Great Bay, Little Egg Harbor	1988-89	monthly	808	Rutgers Marine Field Station Trawl Survey

and Virginia (25-35m in depth) fish-trap catches of tautog are lowest in summer (Eklund and Targett 1991), perhaps due to inshore migrations of winter residents. Tagging studies conducted by Cooper (1966) suggest relatively discrete populations of tautog, with adults returning to the same spawning location following their winter residence offshore.

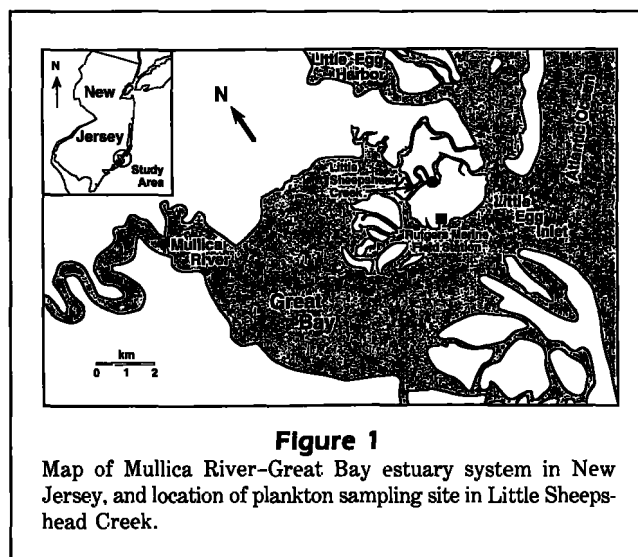
These prior studies of habitat requirements, behavior, and growth have focused primarily on fishes older than 1 year. In this paper we concentrate on life-history aspects for young-of-the-year individuals, particularly larvae and juveniles that have just recently metamorphosed and settled from the plankton. We present information on spatial and temporal distribution of eggs and larvae, larval stage duration, juvenile habitat, daily growth, and otolith-size/fish-size relationships.

Materials and methods

Reproductive seasonality and larval distribution

Information on timing of spawning and spatial distribution of tautog larvae was obtained from three sources (Table 1). Egg abundances were assessed in plankton collections during December 1972-December 1975 in the Mullica River-Great Bay estuary and adjacent ocean off Little Egg Inlet, New Jersey (Fig. 1). Sampling was conducted with 0.5m and 1.0m diameter plankton nets and 20cm and 36cm diameter bongo samplers with 0.5mm mesh. Surface, midwater, and bottom tows were made with the plankton nets; the bongos were fished obliquely. Data used in this study were reanalyzed from a report by Milstein and Thomas (1977).

Larval occurrences over the continental shelf were determined from collections made on Marine Resources Monitoring, Assessment and Prediction (MARMAP) surveys (Sherman 1988) by the National Marine Fish-

**Figure 1**

Map of Mullica River-Great Bay estuary system in New Jersey, and location of plankton sampling site in Little Sheepshead Creek.

eries Service (NMFS). Surveys were conducted from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia. Sampling stations are shown in Figure 2; sampling methods are described in Sibunka and Silverman (1989).

Our third source of plankton data was obtained from a sampling program at the Rutgers University Marine Field Station. A 1m diameter, 1mm mesh net was fished at the surface and just above the bottom on night flood tides in Little Sheepshead Creek, adjacent to Great Bay (Fig. 1).

Juvenile length-frequency comparisons

Monthly patterns in length-frequency distributions were assessed from collections across several sites in the Little Egg Harbor and Great Bay estuaries (Fig. 1) using throw-trap and otter trawl sampling (Table 1). A throw trap is a 1m² open box that is thrown onto

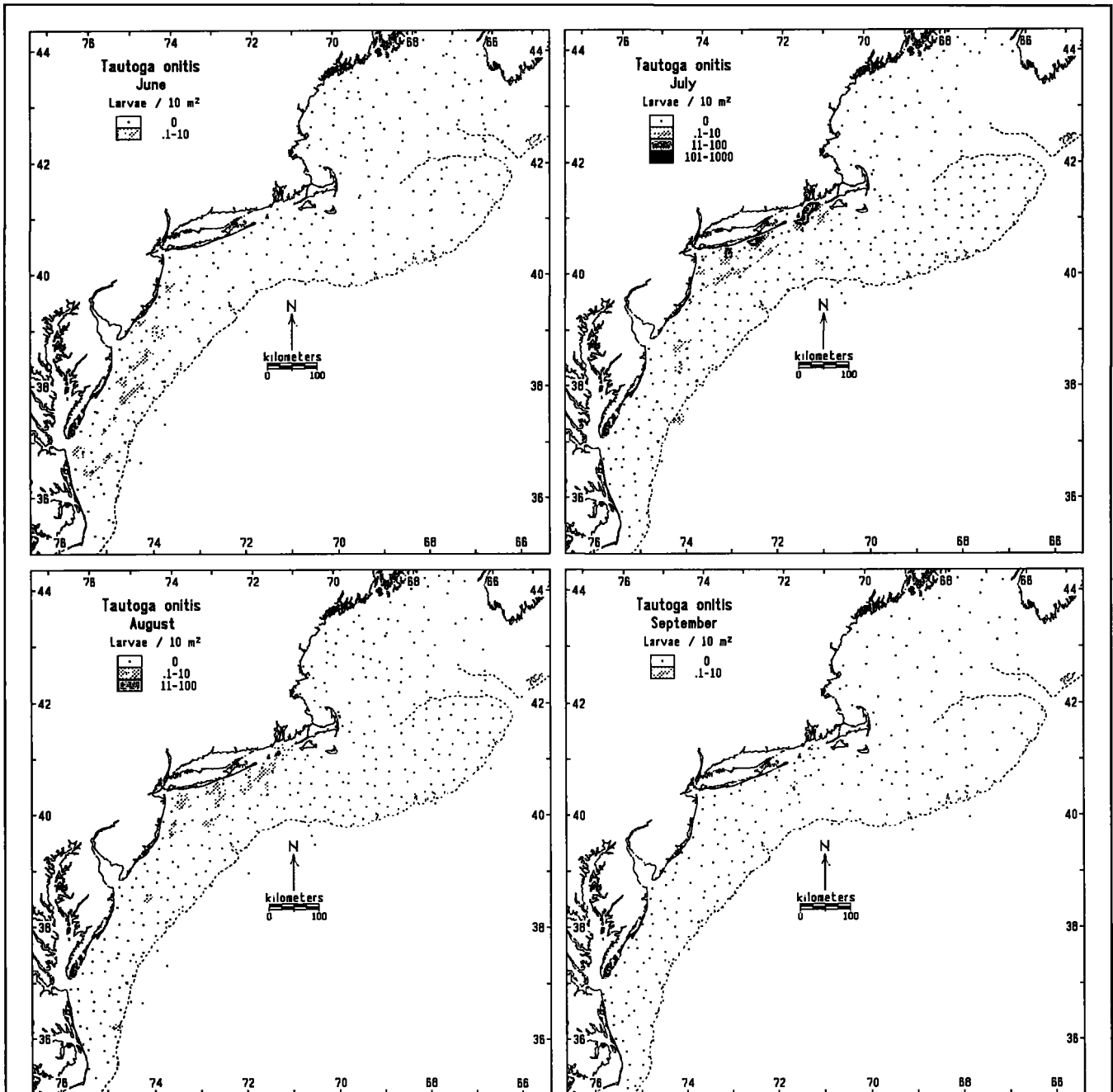


Figure 2

Average monthly distributions of *Tautoga onitis* larvae based on 11 years (1977–87) of sampling in the Mid-Atlantic Bight. Density calculations are based on collections within 1 km² blocks.

the desired substrate, with all animals subsequently removed with a 1 m wide net scraped across the bottom substrate. All throw-trap sampling was conducted at low tide in shallow (<0.5 m at low tide) vegetated and unvegetated habitats. Further details on the throw-trap method and sampling schedule are presented in

Sogard and Able (1991). Additional length data were obtained from tautog collected with throw traps from artificial seagrass habitats on a shallow sandflat in Great Bay (Sogard 1990).

Tautog in deeper waters (1–8 m) of the Great Bay–Little Egg Harbor estuarine system were collected

during the Rutgers Marine Field Station trawl survey. A 4.9-m otter trawl (6.3 mm mesh cod end, 19 mm mesh wings) was towed for 2 minutes at a total of 14 stations, which were representative of a variety of habitat types. Four replicate trawls were taken at each station.

Otolith increment analysis

More detailed information on planktonic stage duration, settlement patterns, and growth of young-of-the-year tautog was derived from analysis of otolith increments. To validate a daily rate of increment formation, the number of increments following a tetracycline-induced fluorescent mark on the sagitta was compared with the actual number of days elapsed. Juvenile tautog (19–63 mm SL) were immersed for 24 h in a 500 mg/L solution of oxytetracycline dihydrate in natural seawater (20–25 ppt) diluted with distilled water to about 17 ppt. They were then held in laboratory aquaria, fed daily with *Artemia*, and preserved in 95% ethanol after 6–30 days. The sagittae of these individuals were removed, embedded in Spurr resin, and polished in the sagittal plane to the central primordium on both sides, using a series of 400–1500 grit sandpaper and alumina powder (0.3 μm), following the methods of Secor et al. (1991). The number of increments following the tetracycline mark was counted with UV microscopy at 400–1000 \times magnification.

The degree of correspondence between otolith size and fish size was determined for 55 juvenile tautog by comparing radial measurements of the rostrum, postrostrum, and antirostrum (Fig. 3) with standard lengths. Radial measurements were made with an image analysis system attached to an Olympus BH-2 microscope, using a magnification on the monitor of 160 \times or 410 \times , depending on the size of the otolith. The relationship between otolith radial measurements and length (SL) of the fish was determined by regres-

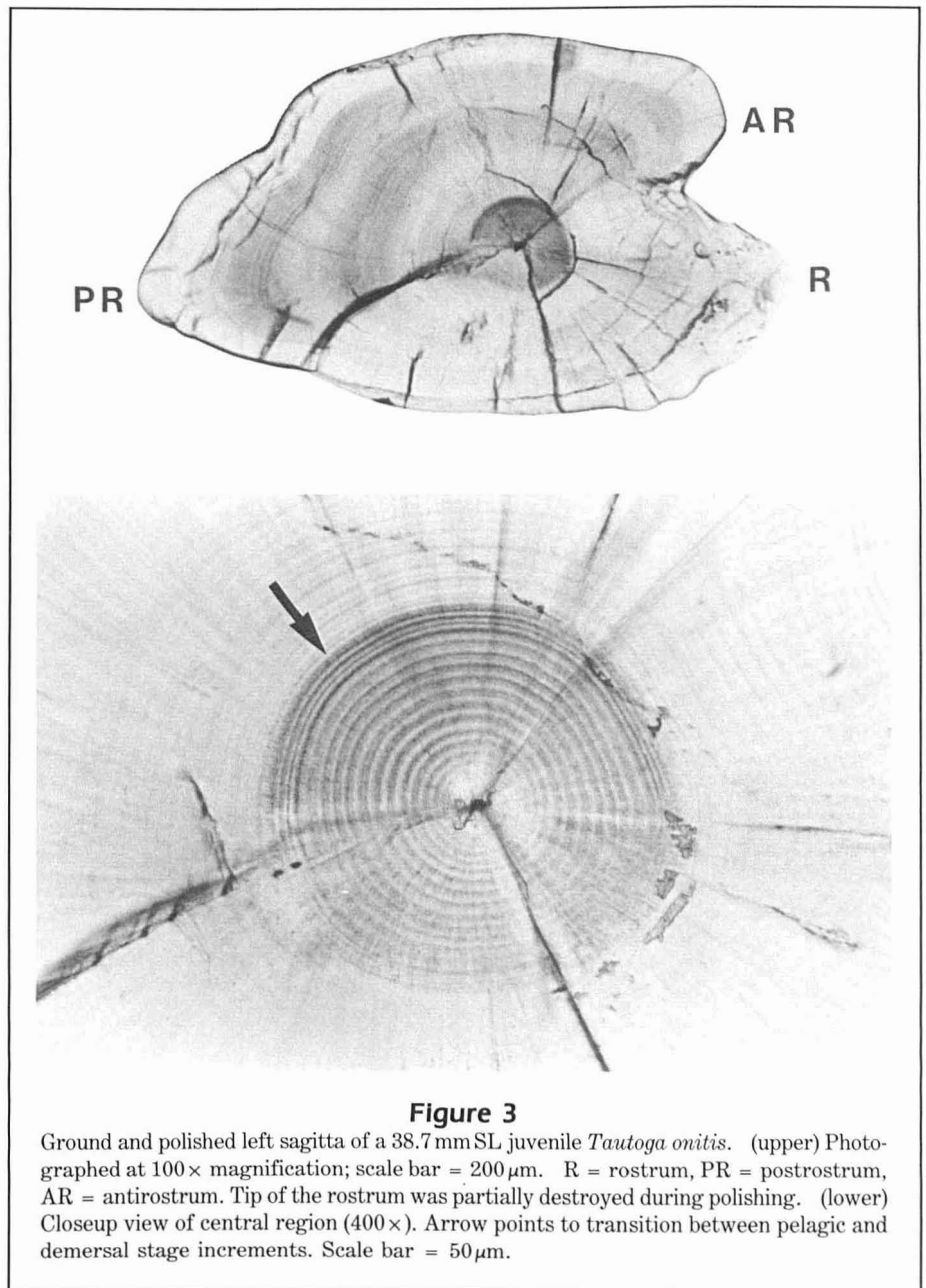


Figure 3
Ground and polished left sagitta of a 38.7 mm SL juvenile *Tautoga onitis*. (upper) Photographed at 100 \times magnification; scale bar = 200 μm . R = rostrum, PR = postrostrum, AR = antirostrum. Tip of the rostrum was partially destroyed during polishing. (lower) Closeup view of central region (400 \times). Arrow points to transition between pelagic and demersal stage increments. Scale bar = 50 μm .

sion analysis. Because preliminary analysis of a matched set of sagittae found no significant differences between left and right radius measurements (paired comparisons *t*-tests: n 8, $P > 0.10$ for all three radii), either sagitta was used in subsequent analyses.

Increments were counted for a series of tautog (n 37, 7.6–62.8 mm SL) collected from early-July through late-September in 1988. Larval and juvenile increments were distinguished on the basis of an apparent settlement mark in the sagittae (see below). Increments were counted independently on three different dates by the same reader, and the results were averaged. Preliminary counts of matched sagittae found no difference

between left and right (paired comparisons *t*-test: $P > 0.10$), with the two sides differing by $< 2\%$. Thus, either sagitta could be used for increment counts.

The mean duration of the planktonic stage was estimated by the mean number of increments preceding the settlement mark. Birth and settlement dates were estimated by subtracting the number of total increments and juvenile increments, respectively, from the date of capture. Assuming that initial increment formation occurred at about the time of hatching, as in other wrasses (Victor 1982), our estimates of birthdates should correspond within a few days to the date of hatching.

Juvenile growth rates

We used three independent methods to estimate growth rates of young-of-the-year juveniles during the summer. The relationship between otolith age (total increments) and standard length was fit to a linear equation, using the slope as an estimate of daily growth. We also examined the progression of mean lengths for tautog collected on a weekly basis in 1988 (primarily from artificial seagrass experiments). Weekly mean lengths were determined and regressed on time, with the slope of the resulting equation used as a second estimate of daily growth. Growth rates based on these two indirect estimates were compared with a third, direct measurement of individual tautog growth in field caging experiments by Sogard (In press).

Results

Reproductive seasonality and larval distribution

In the Great Bay–Mullica River estuarine system, tautog eggs occurred in plankton collections from April through August, with peak abundances in June and July (Table 2). Initial occurrence and peak abundance of eggs were earlier in the Mullica River than in the bay and adjacent inlet, suggesting that spawning began earlier in the season in the upper part of the estuary, and continued later in the summer in the lower estuary and offshore waters. Tautog larvae in weekly plankton collections in Great Bay (Table 1) occurred in July and August of 1989 ($n = 12$) and July of 1990 ($n = 9$). Larvae were collected

in the offshore MARMAP surveys from May through October, with a peak in July (Table 3, Fig. 2).

Based on geographic distribution of larvae, spawning was concentrated in southern New England waters (Fig. 2). Spawning activity in continental shelf waters appeared to follow a northward progression through the summer, beginning as early as May in the southern part of the region (Table 3).

Daily increment validation

Results of the validation tests indicated that increments on sagittae of juvenile tautog were deposited on a daily basis. The slope of the regression comparing the actual number of days elapsed with the number of increments following tetracycline marks did not differ from 1 ($P > 0.05$, $r^2 = 0.86$, Fig. 4). Comparison of sagittal

Table 2
Monthly mean densities (no./1000 m³) of *Tautoga onitis* eggs in Mullica River, Great Bay, and adjacent Atlantic Ocean off Little Egg Inlet, New Jersey, December 1972–December 1975. Plankton sampling was conducted throughout the year, but eggs were not collected in months not appearing in the table.

	Mullica River	Great Bay	Atlantic Ocean
April	66	3	0
May	116	726	853
June	169	165	1259
July	22	2221	1984
August	0	13	20

Table 3
Abundance of *Tautoga onitis* larvae (\bar{x} no./100 m³) collected during MARMAP survey cruises, 1977–87, by subarea and month. Mean abundance is followed by number of occurrences (2d line) and total number of stations sampled (3d line).

Subarea	May	June	July	Aug	Sept	Oct
Georges Bank	—	0.01	—	—	—	—
	0	1	0	0	0	0
	332	152	213	312	144	396
Southern New England	—	—	1.75	0.19	0.08	0.01
	0	0	26	18	4	1
	225	131	231	191	103	224
New Jersey	—	0.07	0.06	0.03	—	—
	0	4	9	4	0	0
	209	139	176	174	120	143
Delmarva Peninsula	—	0.16	0.02	0.01	—	—
	0	6	3	1	0	0
	163	82	104	140	126	45
Virginia and North Carolina	0.08	0.09	0.01	0.01	—	—
	7	3	1	1	0	0
	135	66	76	122	103	37

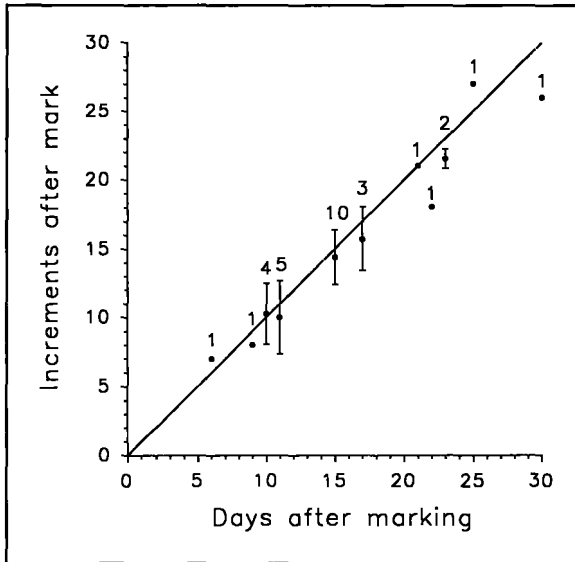


Figure 4
Validation of daily deposition of otolith increments in *Tautoga onitis*, comparing the number of increments outside a tetracycline-induced mark with the number of days since marking. Numbers above data points are numbers of fish tested; error bars are SD's. Resulting regression line does not deviate significantly ($P > 0.05$) from a line of one-to-one correspondence.

radius measurements with standard length demonstrated a strong correspondence for all three radii (Fig. 5). For all three cases, a square-root equation provided the best fit.

Settlement marks and larval stage duration

An obvious transition in the appearance of increments occurred in the sagittae (Fig. 3). Inner increments were generally more distinct because they were higher in contrast, darker in appearance, and more circular than increments outside the transitional area. In the sagittal plane, outer increments diverged in morphology, with increased deposition along the eventual axes of rostrum, postrostrum, and antirostrum. Sagittae of larval tautog ($n = 5$) were comprised of only the darker, inner increments. Thus, we believe this transition in increment contrast and shape takes place at or near the time of settlement, when the individual has completed transformation and moved from a planktonic to epibenthic lifestyle. Settlement marks are a common feature of labrid otoliths, allowing ready distinction of larval and juvenile increments (Victor 1986).

The total number of increments (separated into larval and juvenile stages) was counted for 37 individuals collected in the Great Bay and Little Egg Harbor sampling. The number of increments deposited during the

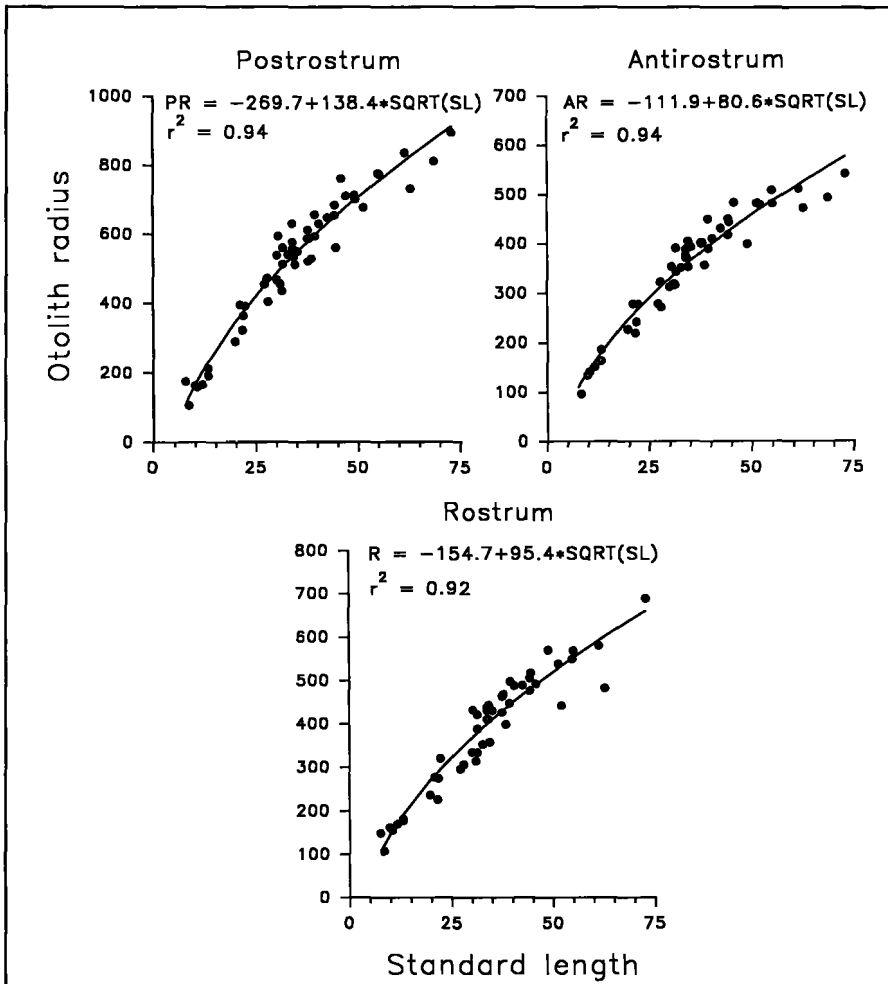


Figure 5

Regressions comparing otolith radial measurements (see Fig. 3) with standard length of juvenile *Tautoga onitis*. Displayed curves fit the square-root equations derived in regression analysis.

pelagic larval stage was remarkably similar, with a mean of 20.4 (SD 2.7). Assuming that the first increment is deposited at about the time of hatching, tautog spend 3 weeks in the plankton before settling to the benthos. Subtraction of total increments from the date of collection resulted in a wide spread of estimated birth (hatch) dates, with a mean of 4 June and a range of 17 April–22 July. These dates are consistent with the general timing of the collection of eggs and larvae (Tables 2, 3). Settlement dates, estimated by subtracting only the juvenile-stage increments from the date of capture, were correspondingly wide-spread, with a mean of 25 June and a range of 6 May–13 August.

Juvenile habitat, size composition, and growth

In throw-trap samples collected in the shallow waters of Great Bay and Little Egg Harbor, juvenile tautog were collected only on vegetated substrates, and were more abundant in sea lettuce (*Ulva lactuca*, $n = 19$) than in eelgrass (*Zostera marina*, $n = 2$) (Sogard and Able 1991). Juveniles <40 mm in length were rare in the deeper waters sampled by trawls, but the larger young-of-the-year and 1-year-old tautog collected by trawling were most abundant in eelgrass beds. Of 14 sampling stations throughout Great Bay and Little Egg Harbor, two were in eelgrass habitats. These two stations accounted for 69% of the 235 tautog collected by trawling in 1988 and 1989.

Combined length-frequency data from throw-trap sampling and trawling efforts suggested that most tautog in the Great Bay–Little Egg Harbor system, based on these sampling techniques, belonged to one of two year-classes (Fig. 6). Young-of-the-year first appeared in July, primarily in the shallower (<1 m) habitats sampled by throw trapping. In the deeper areas (>1 m) sampled by otter trawl, larger young-of-the-year fishes in-

creased in number in August collections. By September, the young-of-the-year dominated the trawl samples while decreasing in throw-trap sampling.

Modal progression of length-frequency distributions demonstrated relatively rapid growth for both young-of-the-year and 1-year-old tautog during the summer months. In contrast, comparison of young-of-the-year sizes in October with 1-year-old lengths in June indicated only minor growth during the fall, winter, and spring. Juvenile tautog attained a size of 40–100 mm

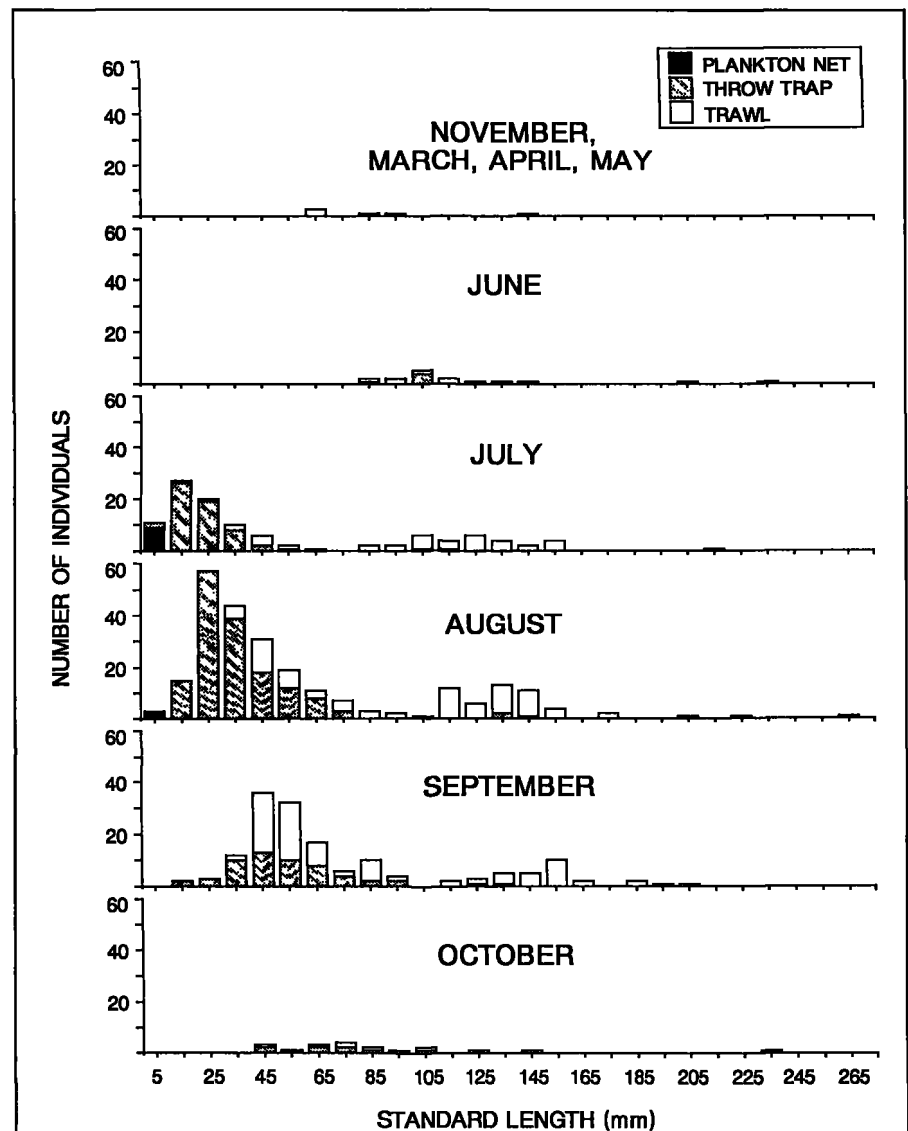
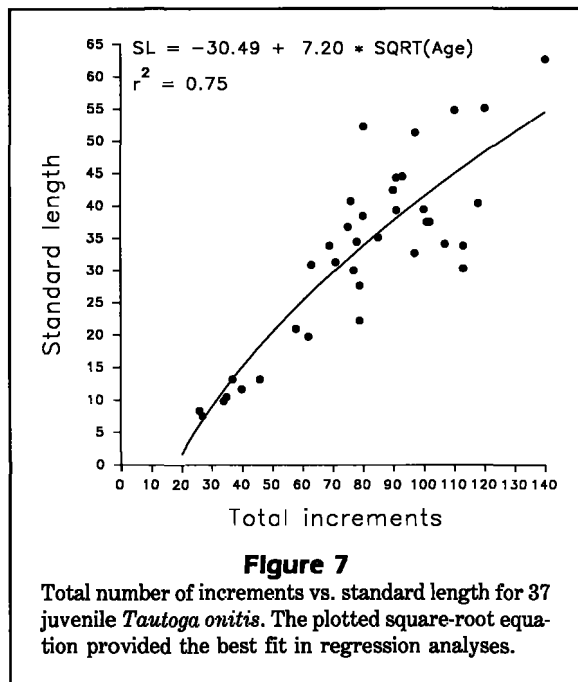


Figure 6

Length-frequency distributions of *Tautoga onitis* collected in the Little Egg Harbor–Great Bay estuarine system. Plankton samples were collected on a weekly basis throughout the year. Throw-trap samples were collected from shallow habitats (<1 m at low tide), May–October; trawl samples were collected from deeper habitats (1–8 m) monthly, with no tautog collected during December–February.



SL in their first growing season, with a modal size of 75 mm in October (Fig. 6). One-year-old fish reached a size of 110–170 mm SL by the end of their second summer, with a modal size in September of 155 mm.

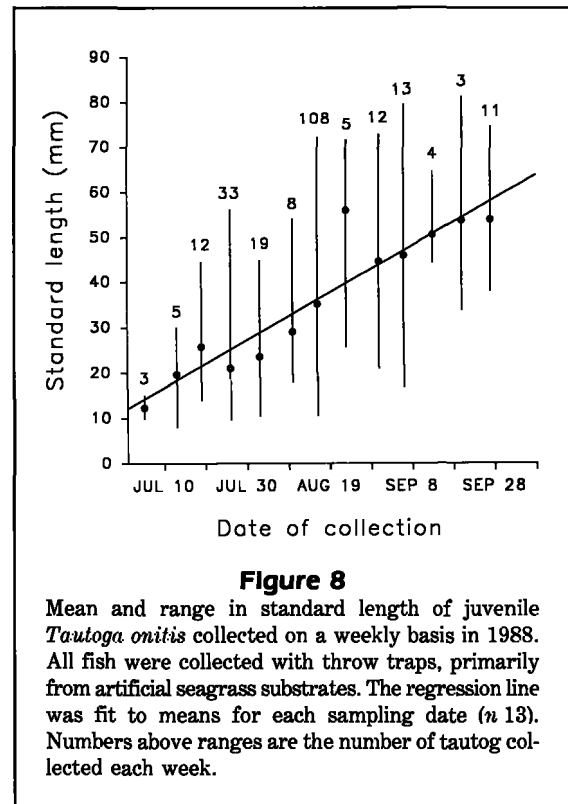
Comparison of otolith ages (total increment counts) with standard lengths provided a general estimate of juvenile growth. The resulting relationship was best described by a square-root equation (Fig. 7), indicating a slight decline in absolute growth rate with age. If the data are fit to a linear equation, a slope of 0.47 results, thus estimating an average rate of 0.47 mm/day during the early juvenile stage. Substantial variability was evident, especially among older individuals (Fig. 7).

To obtain an estimate of growth based on length-frequency distributions, we compared length with the date of capture for 236 juveniles collected only by throw traps in 1988. When the mean length each week was regressed on time (Julian date), the resulting slope provided an estimated growth rate of 0.52 mm/day (Fig. 8).

Discussion

Spawning patterns

Based on the seasonal occurrence of eggs and larvae, the peak spawning period for tautog in the Mid-Atlantic Bight and inshore New Jersey waters is during the summer. Spawning appears to follow a geographical progression, beginning earlier in the southern part of the region. Consistent with this pattern, Eklund and Targett (1990) report that gonosomatic indices of adult



tautog off Maryland and northern Virginia are highest in May.

The egg collections in New Jersey and high egg and larval abundances in areas such as Narragansett Bay (Bourne and Govoni 1988) demonstrate that tautog spawn primarily inside estuaries or nearshore waters. The MARMAP collections indicate that spawning activity involves offshore continental shelf waters as well, since all of the tautog larvae obtained during MARMAP surveys were preflexion stage.

Otolith deposition patterns

Otolith increments of juvenile tautog can be reliably used to obtain valuable age and growth information. The strong correspondence of otolith size (based on radial measurements) with fish size suggests that accurate back-calculation of size-at-age is possible. Increments on the sagittae are deposited on a daily basis and can be readily separated into planktonic and demersal stages, due to the distinct contrast in microstructure at the time of settlement. We did not, however, test increment deposition rates under conditions of poor or negative growth. These conditions have resulted in less than daily increments in other species (Geffen 1982, Lough et al. 1982, McGurk 1984, Alhos-saini and Pitcher 1988, Siegfried and Weinstein 1989,

Sogard 1991, Szedlmayer and Able In press), and we caution that this may also be the case for tautog otoliths.

Settlement

Increment counts preceding the settlement mark averaged 20.4, suggesting larvae spend approximately 3 weeks in the plankton before settling to the benthos. This estimate of larval stage duration is similar to that derived by Victor (1986) for a sample of five tautog (\bar{x} 25.4). The planktonic stage for tautog is relatively short compared with other labrids; Victor (1986) estimated average larval durations of 17–104 days for other wrasse species.

The earliest estimated date of settlement, based on otolith increments, was earlier than the first collections of juveniles with throw traps, suggesting that tautog were not available to the collecting gear during and immediately after settlement. The smallest juveniles for which we have otolith information were 7.6–13.2 mm SL and had 11–23 increments (\bar{x} 16.3) deposited after the settlement mark. Victor (1983) reported that newly settled wrasses of the species *Halichoeres bivittatus* bury in sediments immediately following settlement from the plankton and remain buried for an average of 5 days. We do not know if a similar behavior occurs in *Tautoga onitis*.

Juvenile habitat utilization

Our collection of juvenile tautog primarily in vegetation is in accord with prior studies, which demonstrated an association with structured habitats (Olla et al. 1974, Olla et al. 1979). Several studies comparing eelgrass vs. unvegetated substrates noted significantly higher densities of tautog in grassbeds, with few or no tautogs collected on bare substrates (Briggs and O'Connor 1971, Orth and Heck 1980, Weinstein and Brooks 1983, Heck et al. 1989). The importance of sea lettuce as a nursery habitat has received only limited attention, although Nichols and Breder (1926) mentioned its attraction to small juvenile tautog. In a separate study that also quantitatively compared sea lettuce and eelgrass habitats in New Jersey, using suction sampling, Able et al. (1989) also noted higher abundances of early juvenile tautog in sea lettuce patches than in eelgrass, although the total catch was relatively small. Larger juveniles make extensive use of rocky reef habitats (Olla et al. 1979). The importance of hard substrates for newly settled tautog has not been examined.

All of the smaller juvenile tautog (<35 mm SL) that we collected were from sea lettuce patches or artificial seagrass plots. These individuals were a brilliant green

in color. As noted by Nichols and Breder (1926), this color closely matches that of *Ulva lactuca*, but presumably would be conspicuous on a bare sand substrate. In our sampling, these early juveniles were absent from eelgrass beds. The larger juveniles collected during trawl sampling (in eelgrass and other habitats) had a dark, mottled coloration similar to that of the adults as depicted by Bigelow and Schroeder (1953).

Over the course of our summer sampling, we observed a shift in concentration of young-of-the-year from the shallow areas sampled by throw traps to deeper waters sampled by otter trawl (Fig. 6). This shift suggests that newly-settled juveniles concentrate in shallow waters, moving to deeper sections of the estuary with growth.

Although trawling was conducted year round, individuals of age 1 or older were common only from June through September. This pattern could result from inaccessibility to the gear. Some individuals may move out of shallow habitats in the fall to deeper areas of the estuary with more stable sheltering refuges. Behavioral responses displayed by tautog in cold temperatures, i.e., dormancy and remaining in close contact with sheltering structure (Olla et al. 1974) or burying in sediments (Olla et al. 1979), would also reduce capture rates in winter. In addition, some individuals may leave the estuary to winter offshore, although Olla et al. (1974) suggest that most tautogs less than 4 years old remain inshore.

Tautogs older than 1 year may be more abundant in the estuary than trawl catches would indicate. Larger individuals inhabit holes and crevices of eroding salt marsh banks, and other physical structures such as pilings and rock jetties, where they would not be available to trawling gear.

Juvenile growth

Our estimates of sizes attained by juvenile tautog at the end of the first and second summers are larger than the mean lengths (TL) at ages 1 and 2 calculated for Rhode Island tautog from opercular bone annuli (Cooper 1967). Warmer temperatures in New Jersey may support faster mean growth rates than in Rhode Island. In addition, more southern estuaries in the tautog's range have an extended summer season, allowing both earlier spawning in the spring and continued rapid growth prior to declining water temperatures in the fall.

Analysis of length progressions and otolith ages resulted in two similar estimates of natural growth rates for juvenile tautog (0.52 mm/day and 0.47 mm/day). Individual growth rates of juvenile tautog were also measured in the field in caging experiments (Sogard In press). To summarize results of Sogard

(In press), growth rates varied significantly, depending on location in the estuary and habitat type (vegetated or unvegetated). Across four experiments and a total of 141 tautog, growth averaged 0.18 mm/day, with a range of -0.47 to +0.84 mm. At the site (Great Bay 1) and habitat (sea lettuce) supporting the fastest growth, the mean rate was 0.45 mm/day. Thus, length-frequency patterns and otolith ages reported in this study provided growth estimates that were higher than the overall average in caging experiments but comparable to rates for tautog caged in the best habitats. Based on throw-trapping results, juvenile tautog were rare at those sites and habitats where growth in cages was poor (Sogard In press). Thus, for the areas where tautog were likely to be common, the directly measured growth rate in cages was comparable to rates indirectly calculated for unrestrained fishes. The three methods together estimated a rapid growth rate of about 0.5 mm/day for southern New Jersey estuaries during the first summer.

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