



**Description.** Body stout; deep, 2.55-3.00 times in SL; somewhat laterally compressed (Fig. 241). Caudal peduncle deep; head rather short, blunt, with steep upper profile and somewhat rounded snout. Head length 3.25-3.56 in SL, somewhat shorter than body depth. Mouth small, slightly subinferior with thick lips and protractile upper jaw; posterior end of maxilla slightly anterior to vertical through front margin of eye in juveniles, reaching vertical through anterior nostril in adults. Each jaw with two to three series of stout, conical teeth, which gradually decrease in size posteriorly; strong, rounded, crushing pharyngeal teeth at rear of mouth. Snout short, rather rounded, nearly equal to eye diameter. Eye moderate, 3.05-6.00 in HL. Body covered with small, thin, cycloid scales and a tough skin; membrane of dorsal and anal fins partly covered with small scales; top of head, preorbital, maxilla, lower jaw, interopercle, and posterior portions of preopercle naked; series of five to six small scales extend below and posterior to eye and onto anterior region of preopercle; ventral and posterior part of gill cover scaleless; scales on body between gill opening and bases of pectoral and pelvic fins reduced in size. Dorsal fin continuous; originating over upper corner of gill cover at vertical through origin of pectoral fins and continuing posteriorly to caudal peduncle. Antermost four or five dorsal fin rays somewhat graduated in size; others about equal in height; soft-rayed dorsal fin with rays somewhat higher than spines, about a third as long as spiny part, rounded in outline; second dorsal fin ray highest. Anal fin originating somewhat posterior to vertical through midpoint of dorsal fin; rounded in outline. Caudal fin broad, truncate, or slightly rounded. Pelvic fin moderate, at vertical through midpoint of pectoral fin. Pectoral fin relatively large, broad, somewhat rounded. Lateral line complete and continuous, arched anteriorly; Gill rakers short, blunt.

**Meristics.** Dorsal fin rays XVI or XVII, 10 or 11; anal fin rays III, 7 or 8; pectoral fin rays 16; lateral line scales 60-68; gill rakers 9 on lower limb of first arch; branchiostegals 5 or 6; vertebrae (16) 17 + 18 = 34 or 35.

**Color.** Tautog on different bottoms, like cunner, vary greatly in color and in their markings. Adults are often rather darkly colored, ranging from a generally mouse-colored background to one of chocolate gray, deep dusky, olive green, or dull blackish, with the sides irregularly mottled or blotched with

darker pigment. Lateral mottlings are more evident in young fish than in adults and are usually grouped as three pairs of more or less continuous bars or as a series of interconnecting dark blotches. Large fish are often mostly plain brownish or blackish. The belly is only slightly paler than the sides, but the chin is usually white on larger fish, a very conspicuous character. Sexually mature fish vary markedly in coloration. Females and some nondimorphic males tend to be dull mottled brown, usually with a series of lateral blotches. In contrast, dimorphic males are typically grayish or blackish, with prominent white markings on ventral and dorsal margins of pectoral and caudal fins and on the chin, and are often without darkly pigmented lateral markings. Adult males also have a single small, whitish spot on their midsides just posterior to the posterior margin of the pectoral fins (roughly at the height of the lateral line). Newly recruited, young-of-the-year fish, usually those smaller than 35 mm TL, collected in habitats containing large quantities of sea lettuce (*mva lactuca*) are often cryptically mint green in coloration.

**Size.** Tautog grow to about 90 cm and 10.2 kg; most weigh 0.56-1.8 kg (Bigelow and Schroeder; Fahay 1983; Scott and Scott 1988). The all-tackle game fish record (IGFA 2001) is an 11.33-kg fish taken off Ocean City, N.J., in January 1998. Most tautog caught by sport fishermen are 0.9-1.8 kg, and fish 5.4- 6.4 kg are unusual.

**Distinctions.** The body plan of tautog suggests that of an overgrown cunner, but heavier and stouter, about three times as long as deep. The most obvious differences between tautog and cunner are that the tautog head is high-arched, steep, and rounded in dorsal profile vs. not high-arched, more pointed in profile in cunner; the snout is much more blunt, and the lips are much thicker. The cheek region anterior to the gill opening is naked in tautog (scaly in cunner) and velvety to the touch. Tautog are easily distinguished from cunner by counts of fin rays: dorsal spines XVI or XVII vs. XVIII in cunner; anal fin rays 7 or 8 vs. 8 or 9, but rarely 7 or 9. Also, the pelvic fins in tautog are located under the midpoint of the pectoral fins (vs. at a vertical through anterior base of pectorals in cunner). Tautog also grow much larger than cunner.

**Habits.** Tautog are a strictly coastal fish, especially in the northern part of their range. Northward from Cape Cod tautog rarely occur more than 5-6 km from land or deeper than 9-18 m and are unknown from offshore banks (Bigelow and Schroeder). South of New

England, they occur inshore and range farther seaward into deeper waters. They are commonly caught in 18-24 m on Cholera Bank, 18-22 km offshore of Long Island, and on Seventeen Fathom Bank, 13 km off New Jersey. Off Virginia, they occur inshore seasonally and are present in 12-25 m year-round in reetlike areas (*Triangle, Tiger;* and *Fish Haven* wrecks; Chesapeake Light Tower), 33-60 km offshore (Musick 1972; Hostetter and Munroe 1993). At the other extreme, they follow the flood tide up above low-water level around ledges to prey on the abundant supply of blue mussels in the intertidal zone, dropping back into deeper water during ebb tide. Bigelow and Schroeder seined many small tautog close to shore in water less than a meter deep at Provincetown as well as at other southern locations in the Gulf. Newly settled juveniles recruit to shallow waters of the estuary; whereas with increasing size, young-of-the-year fish move from shallow to deeper areas in the estuary (Sogard et al. 1992; Dorf and Powell 1997). Smaller juveniles utilize sea lettuce (*mva*) and other macroalgal habitats, and may be dependent on them (Heck et al. 1989; Sogard and Able 1991; Dorf and Powell 1997), moving to eelgrass and rocky habitats as they grow (Olla et al. 1979; Sogard et al. 1992). The importance of this habitat for young stages of tautog is reflected in the fact that growth rates of young fish were higher in areas where habitat quality (presence of sea lettuce) was also high (Sogard 1992). Young-of-the-year and age-1+ juveniles also utilize empty oyster and clam shells (Bigelow and Schroeder).

Tautog do not school but many individuals often congregate in the same habitat. Tautog, like cunner, live near the bottom, strongly associated with cover. They are most numerous along steep, rocky shores; around breakwaters, off-lying ledges, and submerged wrecks; around piers, docks, and jetties; over boulder-strewn bottoms; and on mussel beds in shallow water (usually well under 30 m). However, in some places (e.g., the eastern side of Cape Cod Bay) considerable numbers are caught on smooth bottom, away from any structure or relief (Bigelow and Schroeder; Schwartz 1964b). Small juveniles, 19-155 mm long, are sometimes seined on sandy beaches, but young tautog usually inhabit vegetated areas such as *Zostera* beds or mats of macrophytic algae (Tracy 1910; Bigelow and Schroeder; Briggs and O'Connor 1971; Sogard 1989; Heck et al. 1989; Sogard and Able 1991; Able and Fahay 1998). In Narragansett Bay, R.I., juvenile abundances varied significantly with submerged vegetation cover density (Dorf and Powell 1997), with high and medium cover densities harboring significantly greater numbers of tautog than sites with low cover densities. Tautog usually enter polyand mesohaline regions of estuaries, but as yet are unrecorded from freshwater. Tautog produce deep thumps and barklike grunts in the field, probably in response to alarming stimuli (Fish 1954). They also produce escape sounds and thumps during feeding in the laboratory. The sonic mechanism is their large swim bladder vibrated by contraction of skeletal muscle, striking or rubbing of the ribs, and drum-beating motions of the opercles (Fish and Mowbray 1970). Tautog exhibit a typical labrid diet behavioral pattern of high activity during daylight hours and nearly complete inactivity at night (Olla et al. 1974; Arendt et al. 2001a). From ultrasonic tracking studies, Olla et al. (1974) found that initiation and cessation of activity varied somewhat relative to morning and evening civil twilight. Activity began from 10 min before to 69 min after the start of morning twilight. Cessation of activity was more variable, ranging from 222 min before to 69 min after the end of evening twilight. In Chesapeake Bay, mean daily activity began at sunrise and ceased at sunset, with

daily peaks in activity occurring during slack tide in the early morning or late afternoon (Arendt et al. 2001a). Tautog of all sizes require a suitable physical structure (home area or shelter) during their quiescent (sleep) nighttime phase (Olla et al. 1974), and up to the age of 3 years are totally dependent upon the home area at all activity levels.

Daily movements consist of fish leaving a home area and moving to a feeding area. They remain at the feeding area (usually a mussel bed) until the approach of twilight, whereupon they return to the home area, settle in one location, and remain there throughout the night in an inactive state (Olla et al. 1974). Tautog smaller than 25 cm do not venture further than 2-3 m from their home area to forage and, unlike the larger fish, feed within proximity of the shelter.

Adult tautog undertake seasonal inshore-offshore migrations, at least in northern regions of the range. Migration occurs when water temperatures approach 8°-12°C. Throughout the northern parts of their range tautog are seldom observed inshore before late April or after November (Bigelow and Schroeder; Cooper 1966; Briggs and O'Connor 1971). Tagging studies off Rhode Island (Cooper 1966) and New York (Olla et al. 1974; Briggs 1977b) indicated marked seasonal inshore-offshore migrations of adults depending on temperature. There was little if any north-south component to this migration. Juvenile tautog overwinter in inshore areas (Bigelow and Schroeder; Olla et al. 1974; Briggs 1977b) and are inaccessible to most conventional collecting gear during this time. In some regions, a portion of the adult population remains offshore in deep water throughout the year (Olla and Samet 1977; Hostetter and Munroe 1993). In Chesapeake Bay adult tautog occupy inshore habitats year-round (Arendt et al. 2001b). Some fish in this region evidently do not make seasonal inshore-offshore movements.

Tautog are not usually caught in Massachusetts Bay or at Duxbury in Cape Cod Bay before late April or early May (Bigelow and Schroeder). In 1950, which appears to have been an early season, they were reported as biting well in Cape Cod Bay by 25 May and at Duxbury by the last days of the month. Further up the Bay, however, at Cohasset and Swampscott, very few were caught before July. In most years the best catches are made in August, September, and into October, and Bigelow and Schroeder reported that tautog are not usually taken anywhere in the Gulf after early November at the latest. Based upon field observations and tag returns, Cooper (1966) showed that adult tautog inhabited Narragansett Bay from early May until late October. Offshore migration of adults began in late October or early November. With onset of colder temperatures, adults migrated approximately 3 km offshore to areas of rugged bottom topography 24-60 m in depth.

Seasonal movements of adults and juveniles in an inshore area near Long Island, N. Y., were observed by ultrasonic tracking and diving studies (Olla et al. 1974) over a 2-year period (two autumns, one spring). In August (water temperature 17°C), tautog of varying sizes inhabited the study area. By November (water temperature 10°C), many small tautog were observed, but none of the larger ones was seen in the study area. When water temperatures decreased below about 6°C (2.00-5.5°C), small tautog overwintering inshore were lethargic or torpid and partially covered with silt. The following spring (May), with water temperatures about 10°C, active tautog of all sizes were again observed inshore.

Tautog of all sizes become lethargic and even torpid in low water temperatures. The lack of escapement behavior in their behavioral

repertoire, other than to move offshore (adults only), makes this species susceptible to injury or death from cold-shock. Mass mortalities, presumably owing to cold-shock, were reported (1841, 1857, 1875, 1901, and probably others) for populations off Rhode Island and Massachusetts (Bigelow and Schroeder), and tautog mortalities were reported in a major anoxia-hypoxia event off New Jersey (Azarovitz et al. 1979).

In the northern parts of their range, tautog apparently do not feed during seasonal thermal minima. Young fish overwintering inshore remain in a nonfeeding, dormant state at their home site (Olla et al. 1974). Adults observed in waters 24-28 m deep off Rhode Island during winter (water temperature 7.5°C) were torpid, with some lying on their sides and others upright in bottom crevices (Cooper 1966). Intestinal tracts of three captured specimens were greatly reduced in size and devoid of food. Of 12 additional adults that Cooper obtained from commercial fishermen during December, only two had food in their digestive tracts (remains of *Cancer irroratus*). Further south, for example, off Virginia, where winter temperatures are not as cold, tautog at offshore sites actively feed throughout much of the winter (Hostetter and Munroe 1993). In inshore areas of Chesapeake Bay, adult tautog were seasonally not active for 1-7 days during annual minimum temperatures (5°-7°C) (Arendt et al. 2001a)

Sublethal thermal stress studies (Olla and Studholme 1975; Olla et al. 1975a, 1978) indicated that feeding behavior for both juvenile and adult tautog is depressed at elevated temperatures, and activity, aggression, and feeding are reduced, whereas association with shelter is increased. Upper lethal temperatures are about 31°-33°C (Pearce 1969; McCormack 1976).

**Food.** Tautog are opportunistic sight feeders (Olla et al. 1974, 1975a), feeding throughout the day on a variety of invertebrates, chiefly mollusks (both univalves and bivalves), especially mussels (*Mytilus edulis* in northern parts of the range, *Brachiodontes exustus* at Masonboro Inlet, N.C. [Lindquist et al. 1985]); barnacles that they pick off rocks and pilings; various other crustaceans including amphipods, isopods, and decapods, echinoderms; and occasionally small fishes. Feeding begins shortly after morning twilight and continues up to evening twilight. With the approach of evening they become inactive, and they cease feeding during night time.

Tautog jaws are equipped with large canine teeth on both the premaxillae and dentaries. The primary function of these jaw teeth is to capture and manipulate prey; not mastication of prey items. Tautog possess a highly evolved pharyngeal jaw apparatus for crushing and grinding their hard-shelled prey (Lime and Sanders 1986).

Food habit studies conducted in the New York area indicate that blue mussels (*Mytilus edulis*) were the principal prey item of tautog of all sizes (Olla et al. 1974, 1975a). Tautog (3453 cm) held in an aquarium fed on clumps of mussels by grasping them from the substrate using their canine teeth, and if the shell clump was too large, the shells were separated using the canines (Olla et al. 1974). Initial ingestion of mussels did not involve any crushing by the canines. Instead, shells were crushed after ingestion by the pharyngeal teeth. The average size of ingested mussels was 11.9 mm (1-2 years old). All fish observed in the field and aquariums selected young, small-sized mussels, although the mouth could accommodate much larger ones. Preference for small mussels results from size limitations imposed by the pharyngeal jaw apparatus. Fish 34-53 cm could crush mussels in

the pharyngeal apparatus that were only 0.47 times the maximum size of mussels that could be accommodated in the buckle region (Olla et al. 1974).

Other food items in the tautog diet include rock crabs, hermit crabs, mud crabs, sand dollars, gammarid amphipods (sand fleas), scallops, clams, shrimps, isopods, and lobsters (Hildebrand and Schroeder 1928; Steimle and Ogren 1982; Lindquist et al. 1985). Rock crabs constituted 78% of the diets of tautog at an artificial reef off New York (Steimle and Ogren 1982). Small lobsters are generally swallowed whole, but shells of larger ones are first cracked by using the pharyngeal crushing teeth. It is also likely that tautog living in shallow bays (e.g., Duxbury) prey to a considerable extent on sea worms (*Nereis*); certainly they take these freely as bait (Bigelow and Schroeder). Young-of-the-year fish feed on copepods (mostly harpacticoids), amphipods, isopods, and small decapod crustaceans (Dorf 1994). Beyond lengths of about 120 mm, tautog gradually change their diets to include greater numbers of small mussels.

**Predators.** No species is known to preferentially feed on tautog. Juveniles are preyed upon by piscivorous birds such as cormorants (Nichols and Breder 1927) and undoubtedly by piscivorous fishes. In a laboratory study of predator avoidance, Dixon (1994) showed that juvenile tautog avoided an active predator (juvenile bluefish), but did not react to the presence of inactive, camouflaged predators (toadfish) or to a moderately active predator (longhorn sculpin). Bigelow and Schroeder reported the following fish species as predators on juvenile or adult tautog: smooth dogfish, barn-door skate, red hake, sea raven, and goosefish. Schaefer (1960) reported tautog in the diet of silver hake collected off northern New Jersey.

**Parasites.** Linton (1901b) noted that tautog, unlike other benthic omnivorous fishes in the Woods Hole region, did not host large or diverse populations of helminth parasites. He suggested that the low helminth parasite loads he observed may have resulted from the "antihelminthic" diet of tautog, which includes the abrasive fragments from barnacles, decapod crustaceans, and blue mussels crushed and macerated during feeding. These sharp fragments may prevent establishment, or may actually destroy, the delicate larval stages of helminths ingested with the food supply. Despite this potentially difficult environment, five helminth species have been recovered from the alimentary tract of tautog: the cestode *Bothrimonus intermedius* (Linton 1941) and digenetic trematodes *Zoogonoides laevis*, *Homalometron pallidum*, *Opecoeloides vitellosus* from fishes at Woods Hole (see Yamaguti 1958), and the acanthocephalan *Echinorhynchus gadi* from tautog at Narragansett Bay (T. A. Munroe, unpubl. data).

Tautog also host a variety of external parasites, including a monogenetic trematode, *Microcotyle hiatulae*, which has been reported in heavy infections at Woods Hole (Linton 1940), Newport, R.I. (Goto 1900), and coastal Virginia (Thoney and Munroe 1987). Tautog apparently are also parasitized by the leech *Calliobdella vivida*, because blood samples from tautog in Chesapeake Bay revealed infestations with a hemoflagellate, *Trypanoplasma bullocki*, which is transmitted to fish via feeding of a marine leech (Burrison and Zwerner 1982). The most conspicuous and frequent external parasites of tautog are the encysted metacercariae of a digenetic trematode *Cryptocotyle lingua*. Linton (1901b, 1928, 1940) recorded heavy and pervasive infestations of these metacercarial cysts in

tautog collected at Woods Hole, noting that it was unusual to find a fish not infected with this larval trematode. Cheung et al. (1979) reported tautog lethally infected with an intestinal coccidian parasite.

**Reproductive Biology.** Tautog are gonochoristic (Bigelow and Schroeder; Chenoweth 1963; Cooper 1967). The sex of adults can easily be recognized by the strong dimorphism in mandible structure and dichromatic coloration; males have more pronounced mandibles than females (Cooper 1967). Little is known concerning reproductive biology of populations in the Gulf of Maine and further north so information presented is based on studies conducted in more southern parts of the range.

Sexual maturation in tautog occurs at the beginning of the third year of life for males and at the beginning of the fourth year for females, corresponding to sizes of approximately 14-25 cm (Chenoweth 1963; Cooper 1967; Stolgitis 1970; Hostetter and Munroe 1993). Males off Long Island (Briggs 1977b) were ripe at 215 mm (Cooper's age 3) and the smallest ripe female was 230 mm (age 4). Briggs concluded that females may mature somewhat later in the more southerly waters of New York.

Olla and Samet (1977) reported capturing small (sizes unstated), reproductively mature individuals in which the distinctive dimorphism in mandible structure characteristic of older, larger fishes was not developed. It is not known whether these smaller fish participate in or contribute to the reproductive success of the population.

Tautog are indeterminate serial spawners with a protracted spawning season (Hostetter and Munroe 1993; White 1996), and estimating fecundity poses several problems. Fecundity data for this species contained in unpublished theses (Chenoweth 1963; Stolgitis 1970; White 1996) indicate that they are relatively prolific. However, as White (1996) has shown, previous fecundity estimates were for batch, not total, fecundity.

Batch fecundity estimates for tautog from these three studies provide the following range of estimates by age-group: females age 3 produced 3,400–24,000 eggs per batch; age 4-6, 46,000–54,000; age 7-9, 103,000–117,000; age 13-16, 209,000– 457,000; and age 20, about 150,000-483,000. Maximum batch fecundity was observed in females ages 7-9 with reduced fecundity in fishes older than age 16 (Chenoweth 1963). Stolgitis found that batch fecundity for 49 females he studied was more closely related to length and weight than to age. Fecundity increased in proportion to the weight of the fish and to the cube of its length. White (1996) estimated a spawning frequency of about 1.2 days, resulting in 58 spawning days per female per season. Based on batch fecundity and spawning frequency estimates, potential annual fecundity for tautog ages 3-9 ranges from 160,000 to 10,500,000 eggs.

Spawning in a natural environment has never been described for tautog primarily because these fish are easily disturbed by diver intrusions (Olla and Samet 1977). Bridges and Fahay (1968) observed possible courtship behavior of two laboratory- held tautog. Olla and Samet (1977) believed that the tautog observed by Bridges and Fahay were exhibiting aggressive behavior and not courtship displays, either because the fish were not in complete reproductive synchrony or because the confines of the aquarium produced behavioral artifacts.

Olla and Samet (1977) successfully spawned tautog in the laboratory and provided the following observations concerning the behavior of the spawning fish. Two separate groups of tautog, each with two males and one female, were studied over an entire spawning season. The larger male was dominant over the other two fish and, once reaching reproductive readiness, was the primary spawning partner of the female. The subordinate male did spawn with the female, although only infrequently: Each day the female exhibited dynamic and transient shading changes that became maximally developed as the time of each spawning approached in the afternoon. Actual gamete release occurred after 6-8 h of courtship, as male and female moved upward in synchrony and spawned at or near the surface. Often, both fish broke the surface while simultaneously releasing gametes. Breaking of the water's surface at gamete release may be critical for maximizing fertilization.

During one set of observations, Olla and Samet (1977) observed 37 spawnings, and in a second set noted 23 spawnings. Laboratory spawning took place almost exclusively in pairs, but whether or not a true pair bonding between mates occurs in nature is still unclear. Other spawning behaviors, such as aggregate spawning, were infrequently observed in this species, but cannot be eliminated because spawning has not been observed under natural conditions. In some areas, tautog were reported to begin spawning in the afternoon (Olla and Samet 1977; Perry 1994). Based on the ages of eggs collected in ichthyoplankton samples, Ferraro (1980) reported that tautog apparently spawn into the night. However, more accurate estimates of egg release based on hydrated oocyte methods (White 1996) indicated that age estimates based on ichthyoplankton samples are not reliable. Based on hydrated oocytes in the ovaries, White (1996) reported that tautog daily ovarian development followed a general pattern of hydration early in the day (0700-0930 EST), running ripe (spawning) midday (0930-1530 EST), and partially spent/redeveloping in late afternoon and early evening (1430-1830 EST). Differences in spawning windows among groups of tautog sampled on different days indicated that changes in environmental conditions such as water depth, ambient light, or tidal stage may also influence ovarian cycles.

**Spawning Seasonality.** Tautog eggs were collected by the MARMAP surveys from April to September in coastal and midshelf waters (Berrien and Sibunka 1999: Fig. 64). Spawning begins as early as April in the southern portion of the Mid-Atlantic and by May progresses northward into southern New England waters. Peak spawning occurred in inshore waters from Chesapeake Bay to Nantucket Shoals in June and July; Based on egg and larval occurrences in plankton collections, it is evident that tautog begin spawning at water temperatures of 9.0°-10.0°C and continue throughout the summer until early October.

Austin (1976) noted that developing embryos were absent and no larvae were taken from ichthyoplankton samples in waters warmer than 21°C. He suggested that effectual spawning of tautog may therefore be restricted to a narrower, early summer range of temperatures and that conceivably tautog do not spawn in any numbers when temperatures exceed 22°C. It is interesting to note that from a larval energetics study; Laurence (1973) also found that 22°C approaches the upper temperature limit for normal metabolism of embryonic and prolarval tautog. He demonstrated that tautog prolarvae may encounter a potential energy deficit at higher

temperatures (19°-22°C) within their spawning range. Larvae produced at a lower spawning temperature (16°C) did not appear to be as susceptible to a potential energy deficit as those produced at the higher temperatures. Also, prolarvae hatched at 16°C were larger at completion of yolk absorption and had a longer period between hatching and the initiation of feeding. In the laboratory; when incubation temperatures were gradually raised from 20.0°C, anatomical deformities, including stunted embryos and/or abnormal body curvatures, as well as increased mortality; occurred between 24.2° and 26.3°C (Olla and Samet 1978).

**Spawning Location.** Tagging studies in Rhode Island (Cooper 1967) and New York (Briggs 1977b) indicate that tautog form discrete, localized groups that spawn in the same areas for several seasons. North of Cape Cod, tautog eggs have been collected in Salem Harbor from May to September

(Elliott and Jimenez 1981), but it is uncertain to what degree tautog populations in the Gulf of Maine are maintained by local spawning vs. immigration of fishes spawned further south (Bigelow and Schroeder). Bigelow and Schroeder did not collect eggs, larvae, or juvenile tautog north of Cape Cod Bay, and other authors have also noted the absence of eggs and larvae in areas north of Massachusetts Bay (Nova Scotia [Dannevig 1919] and Central Maine [Chenoweth 1973; Berrien and Sibunka 1999]). It seems likely that some limited spawning probably does occur in northern portions of range, at least during periods of favorably warm temperatures. Hauser (1973), for example, collected two larval tautog from the Sheepscott River estuary-Montsweag Bay, Maine, and Bleakney (1963b) collected a gravid female in Nova Scotia, although little is known of tautog spawning activities in Canadian waters (Scott and Scott 1988). Spawning occurs in inshore and nearshore waters, at the mouths of estuaries, and offshore on wrecks and reefs on the continental shelf (Herman 1963; Cooper 1966; Eklund and Targett 1990; Sogard et al. 1992; Hostetter and Munroe 1993), at temperatures of 9°-26°C in Long Island Sound (in salinities of 26-29 ppt) and 13°-14°C (in polyhaline water) in Rhode Island (Fritzsche 1978).

**Early Life History.** Detailed descriptions of tautog eggs and larvae appear in Kuntz and Radcliffe (1917), Fritzsche (1978), and Fahay (1983). Laboratory culturing of tautog has been accomplished successfully (Perry 1994; Mercaldo-Allen et al. 1997; Perry et al. 1997a,b, 1998) and described in detail (Schoedinger and Epifanio 1997).

Tautog eggs are pelagic, buoyant, spherical, lack an oil globule, and have a diameter of 0.9-1.0 mm (Able and Fahay 1998). Identifying them in ichthyoplankton samples is complicated by the fact that eggs of cunner and tautog are similar in size and seasonal occurrence and both decrease in diameter during the course of the spawning season (Williams 1967). However, the decreases in size are parallel in the two species, with the smaller eggs being those of cunner. Eggs of the two species can also be distinguished by immunodiffusion (Orlowski et al. 1972).

Hatching occurs in 42-45 h at 20°-21°C (Kuntz and Radcliffe 1917), whereas at 16°C it takes 7 days (Laurence 1973), compared with 5 days at 19°C and 4 days at 22°C. Larvae hatch at 1.7-2.2 mm with unpigmented eyes and unformed mouth parts (Schoedinger and Epifanio 1997; Able and Fahay 1998). Yolk-sac absorption occurs at 3.2-3.5 mm (Fritzsche 1978) and the mouth is fully formed at 4 days

(temperature ca. 20°-22°C). At 5 mm, the first traces of caudal fin rays are evident. At 10 mm, dorsal and anal fins are differentiated. By about 30 mm, the fins, body form, deep caudal peduncle, and blunt nose of adult tautog are evident. Prey density has a strong effect on growth of tautog larvae (Schoedinger and Epifanio 1997), with mean growth at high prey density (1,000 liter-!) approximately four times that at low prey density (100 liter-!). Sogard et al. (1992) estimated that tautog larvae are planktonic for about 3 weeks before settling. Larvae and small juveniles of tautog and cunner resemble each other closely in general form. However, the arrangement of pigment on the body offers a ready means for identification at all but the very earliest stages, for black pigment cells remain more or less uniformly scattered over the whole trunk in tautog, whereas they soon cluster into two definite patches in cunner.

**Age and Growth.** No aging studies have been published for tautog populations from the Gulf of Maine. Cooper (1967) successfully used opercular bones for aging tautog in Narragansett Bay; and Hostetter and Munroe (1993) examined age-growth characteristics of tautog occurring off Virginia. Scales were not used to age tautog in these studies because annuli were difficult to discern and scales were often pitted by metacercariae of a digenetic trematode (*Cryptocotyle*) and regenerated. Otoliths can be used to age fish during their first few years of life, but beyond that there are difficulties with interpretation of annuli on the outer margin of these structures (Hostetter and Munroe 1993).

Estimates of daily growth using otolith increments were provided for juveniles by Sogard et al. (1992), who found that young tautog in New Jersey grow relatively rapidly; at an average rate of 0.5 mm.day-!, during the summer. They reach a modal size of about 75 mm SL (40-100 mm SL) after their first summer and 155 mm (110-170 mm SL) by the end of their second summer. Only minor growth was evident during fall, winter, and spring. Based on formation of a settlement mark, it was estimated that young tautog spend about 3 weeks in the plankton before settling to the benthos. In one study, growth rates of juveniles were also affected by habitat quality (Sogard 1992), with highest rates occurring in areas with abundant quantities of sea lettuce, whereas Phelan et al. (2000) reported that growth was relatively independent of whether a habitat was vegetated or adjacent to vegetation.

Annulus formation for tautog in Rhode Island waters occurs during middle or late May (spawning season) and only one annulus is formed per year. Age estimates for tautog populations off Rhode Island and Virginia reveal that tautog are relatively long-lived, with estimates of longevity ranging up to 34 years (Cooper 1965b, 1967; Hostetter and Munroe 1993). Tautog grow slowly and attain relatively large sizes. Males grow faster and bigger than females (*Loo* = 655 mm for males; *Loo* = 506 mm for females). Hostetter and Munroe (1993) estimated parameters of the von Bertalanffy growth equation for tautog (both sexes) in Virginia waters as:  $L_{\infty} = 742(1 - e^{-t/3.16})$ , with *L* in mm and *t* in years.

Using eviscerated weights of tautog collected in June 1961, Cooper derived the following length-weight relationships for tautog collected in Rhode Island:  $\log W = 4.35670 + 2.77660 \log L$  for males;  $\log W = -4.80357 + 3.01607 \log L$  for females.

Back-calculated length increments agreed well with observed increments for tagged fish. The largest annual increments in growth occurred during years 1-4. Males (average length 73 mm) and

females (66 mm) grew the most in length during their second year of life. Annual increments of 12- 36 mm occurred in years 6-12; increments decreased to 23 mm (males) and 22 mm (females) in year 10; and after age 12 growth of both sexes continued, but at much slower rates (11~ 2 mm.year<sup>-1</sup>).

Briggs and O'Connor (1971) measured seasonal size progression of young-of-the-year tautog in Long Island. Young-of- the-year (19-35 mm TL) first appeared in the study area in July. By November these fish had grown to 76-134 mm, and these lengths lie within back-calculated values for age-1 tautog from Rhode Island (Cooper 1967). With derived length-weight relationships (see above), Cooper calculated annual increments of weight for males and females. He found that females were heavier than males at a given size. Body weight (eviscerated) increased approximately as the cube of the length for females and less rapidly for males. Annual increments increased to a maximum of 169.9 for males age 9 and 208.9 for females age 11, despite the fact that the greatest annual increments in length were attained during the second year. Males required 10 years and females 9 years to reach a body weight (excluding viscera) of 908.9 (2lb). From his length-weight formula, Cooper calculated that tautog reach 1,820.9 (4lb) in approximately 25 and 15 years for males and females, respectively.

A length-weight relationship based on uneviscerated weights was derived by Briggs (1969b) for tautog from Long Island:  $\log W = -5.99220 + 2.916210 \log L$ . This relationship represents data from 3, 156 fish sampled from sport catches during May through November for the period 1964-1966. This equation differs from those provided by Cooper primarily because fish were unsexed, uneviscerated, and collected throughout the season. From his growth equation (assuming growth rates to be similar for tautog from Rhode Island and Long Island) a more reasonable estimate can be made for age at entry into the recreational fishery: From Briggs's weight data, a 908-g fish corresponds to a 7- to 8-year-old and a 1,820-g fish to a 9- to 11-year-old.

**General Range.** Tautog occur along the eastern coast of North America from Halifax, N.S. (Scott and Scott 1988), to northern South Carolina (Bearden 1961), but are most abundant between Cape Cod and Chesapeake Bay (Hildebrand and Schroeder 1928; Bigelow and Schroeder; Hostetter and Munroe 1993). Previous to 1957, tautog were rarely reported from Canadian waters (Bleakney 1963b; Leim and Scott 1966), and they are not usually taken in commercial numbers north of Massachusetts or south of Chesapeake Bay (Bigelow and Schroeder; Scott and Scott 1988; Hostetter and Munroe 1993).

**Occurrence in the Gulf of Maine.** Tautog are extremely local, perhaps more so than any other Gulf of Maine fish that are of interest either to the angler or to the commercial fisherman. Apart from Mitchell's statement that by 1814 the Boston market had a full supply (which may have come from south and not north of Cape Cod), the first positive record in Massachusetts Bay is of several that were caught along the Cohasset rocks in 1824, which local fishermen said was a species new to them (Bigelow and Schroeder). By 1839 tautog were caught in numbers in inner parts of Massachusetts Bay (e.g., Lynn, Nahant, Boston Harbor), were even more abundant around Manomet Headland in Plymouth, and supported a considerable hook-and-line fishery at Wellfleet. A few

years later their presence was established for the coast of Maine, and in 1851 they were reported as common (according to Perley) in Saint John Harbor, N.B., though these Bay of Fundy fish were introduced (not native). In 1876, weirs north of Cape Cod took 1,034 kg of tautog, and in 1879 Goode and Bean described them as abundant in many localities around Cape Ann.

Presently; the regular range of tautog includes the whole coastline from Cape Cod around to Cape Ann, in suitable localities (Bigelow and Schroeder). They are less regular northward from Cape Ann, less abundant, and more local. There are some tautog grounds around the Isles of Shoals, off Cape Porpoise, and around Casco Bay; where Kendall (1931) reported them as having been locally numerous for some time. Tautog were also taken along the ledges near Boothbay Harbor and in Penobscot Bay. They are uncommon east of Penobscot Bay and so scarce in the Passamaquoddy region (they have long since vanished from Saint John Harbor) that only three specimens are known to have been taken there within recent years: one near the head of the Bay of Fundy on the Nova Scotian side (Scotts Bay; Kings County), one on the Nova Scotian shore of the open Gulf of Maine (Cranberry Head, Yarmouth County), and one on the outer coast of Nova Scotia near Halifax (Petpeswick Harbor, Halifax County), the most northerly record for tautog.

The more productive tautog grounds north of the elbow of Cape Cod are the Cape Cod Bay shore southward from Wellfleet; the Sandwich-Sagamore shore with the jetties at the mouth of the Cape Cod Canal; boulder habitat around Manomet headland and nearby; Gurnet Point at Duxbury; ledges off Scituate and Cohasset, and especially those off Swampscott; the Nahant, Marblehead, and Magnolia Rocks; and along the rocky shore from Gloucester Harbor around Cape Ann. The Cape Cod Bay grounds are exceptional for tautog are caught there on smooth bottom, not among ledges, which are their usual haunts. Bigelow and Schroeder also reported that good-sized tautog were taken inside of Nauset Inlet (where there are scattered boulders only), one in a lobster pot during the summer of 1949, and quite a number, large and small, within Duxbury Bay; especially around the pilings of Powder Point Bridge.

Bigelow and Schroeder questioned whether or not the stock north of Cape Cod is maintained wholly by local reproduction or is reinforced by recruitment from fish produced further south. Bleakney (1963b) suggested that because of their rarity in Nova Scotia and New Brunswick, tautog may exist only in relict, disjunct populations in more protected (with regard to temperature) bays of Nova Scotia. Evidence

supporting Bleakney's hypothesis of disjunct populations includes the sporadic nature of catches of this species in the northern regions of the species range, including the rare capture of a single gravid female and other unusual sightings in Mahone Bay; N.S. (Bleakney 1963b); sport fish catches in 1957 of over 2,000 tautog from Eel Brook Lake, N.S. (Leim and Day 1959); and collection of only two larval tautog from the Sheepscot River estuary-Montsweag Bay (Hauser 1973). Tagging studies of tautog from Rhode Island and Long Island (Cooper 1966; Briggs 1977b) provide estimates of population sizes and indicated that tautog apparently form localized populations that mix very little with adjacent coastal populations. Analysis of mitochondrial and nuclear genes (Orbacz and Gaffney 2000), however, suggests that tautog from Rhode Island to Virginia represent a single genetic stock.

**Importance and Utilization.** Unlike most labrids, tautog are a highly valued recreational species and an excellent table fish. A small commercial fishery has existed for at least the past 100 years (Goode 1884), although, until only recently; they were never a primary target species of commercial fishermen. Historically; the tautog fishery resulted from by-catches of other commercial fisheries, with the greatest numbers of fish being landed in inshore and nearshore fisheries utilizing nonselective gear such as handlines, weirs, and fyke, pound, and floating trap nets. Although this species has traditionally supported a small commercial fishery, especially south of Cape Cod, harvesting was done primarily by rod-and-reel fishermen and spear fishermen (Cooper 1966; Briggs 1969a, 1975, 1977b). In recent years, however, a directed commercial fishery has developed, primarily in Massachusetts (south of Cape Cod), Rhode Island, Connecticut, and New York. Fish are now taken commercially by a number of gear types including gill nets, trawls, and fish pots. Although tautog are harvested in commercial quantities from Massachusetts to Virginia, the greatest numbers are landed in the area extending from Massachusetts to New York. Rhode Island generally has the highest reported landings. Few if any tautog are taken commercially north of Cape Cod or south of Virginia, primarily because the species is never abundant enough to support directed fisheries in these areas. Within the Gulf of Maine, historical fluctuations have occurred in commercial catches for various areas. Bigelow and Schroeder noted in particular that the average yield per pound from net or trap was from 2 to 20 times as great from Cape Cod Bay as from the north shore of Massachusetts Bay. Other areas along the coast from Boston Harbor to Gloucester reported catches of tautog from time to time, and the chief center of abundance for tautog for Cape Cod Bay in some years has been along the Sagamore shore. In other years, unusual concentrations appeared at Sandwich and Brewster, whereas in some years some of the best tautog fishing was reported from the Wellfleet region.

As early as 1884, Goode reported that annual catches of tautog were difficult to estimate because, on the one hand, they were generally landed as by-catch of other, more valuable fisheries and, on the other, much of the catch was consumed locally: In 1883 about 90,909 kg of tautog, landed by 200 fishermen, was shipped to New York, but the total catch for 1883 was estimated to have been between 182,000 and 227,000 kg (Goode 1884). Annual fishery statistics from 1883 to 1919 are scattered and incomplete. Most tautog taken commercially have been landed in Massachusetts, Rhode Island, and Connecticut. Annual landings from Massachusetts to Virginia for 1919-1974 were highest during the 1920s and 1930s, peaking at about 408,219 kg in 1930. Landings declined to about 136,986 kg in 1935 and to 91,324 kg in 1950. Prior to 1950, annual landings reported from Massachusetts, Rhode Island, and Connecticut combined ranged from 41,552 kg (1919) to a peak of 252,968 kg in 1930. Since 1950, 60,731-95,434 kg of tautog have been landed yearly: According to the most recent Fishery Management Plan for Tautog, spawning stock biomass and landings appear to be declining. The annual recreational catch peaked in 1986 at 7.6 million kg and declined to 2.4 million kg in 1990 and 1993. Annual commercial landings peaked in 1987 at 0.5 million kg and began declining in 1991. The 1993 commercial harvest of 0.2 million kg was the lowest since 1983 (ASMFC 1996).

Reasons for declines in landings of tautog since 1930 are difficult to assess because there are no historical data on size or age composition

of commercially caught fish. Tautog are a slow-growing species that forms localized populations (Cooper 1966, 1967; Briggs 1977b), which are vulnerable to commercial overexploitation. It is possible that overfishing occurred during the 1920s and 1930s and that tautog populations were not able to recover to former levels. It is also possible that the eelgrass decline during the early 1930s severely affected populations of young tautog.

Another explanation for earlier declines in landings is that fisheries that employ the most successful gears for taking tautog (handlines, fykes, weirs, trap nets) have declined since the 1920s and 1930s. For example, in 1905 about 265 fish traps were operated in Rhode Island waters, whereas in 1958 there were fewer than a dozen (Gordon 1960). About a dozen traps are still in operation in Rhode Island. There have been similar declines in fishing effort in the other New England states as well as in the Mid-Atlantic and Chesapeake states. The effects of recent extensive harvesting on stocks of a long-lived, slow-growing species such as tautog can be particularly significant (Hostetter and Munroe 1993). In fact, once the recent directed fishery for tautog began, negative impacts on tautog populations were noted almost immediately: In response to the dramatic impacts on tautog stocks, a coastwise management plan was adopted by the Atlantic States Marine Fisheries Commission in an attempt to restore stock to prefishery levels by imposing size limits and catch restrictions for both commercial and recreational fishermen. Availability of tautog to the commercial fishery generally corresponds to periods of high activity during seasons of inshore-offshore migrations (in the north) of adults (including the spring spawning migration). Most of the commercial catch is landed

from May to July and from late September to early November in New England and south to New Jersey. Further south, tautog are caught earlier in the spring and later into the fall and during the winter, depending upon water temperatures. Few tautog are taken offshore by commercial trawlers during the winter, primarily because these fish seek out areas of rugged bottom topography and are dormant within crevices within this structure. Little information is available on size-at-entry and size-age composition of commercially landed fish.

Cooper (1966) reported that tautog entered the sport and commercial fisheries in Rhode Island at about 275 mm. Bigelow and Schroeder estimated that fish landed in the Gulf of Maine and Massachusetts Bay averaged about 0.9-1.8 kg.

Recently, interest has developed in investigating the suitability of tautog as a candidate for aquaculture (Perry 1994; Mercaldo-Allen et al. 1997; Perry et al. 1998), especially as a year-round source of live or fresh fish for ethnic markets. With enhanced nutrition and elevated water temperature, they might be cultured to market size, which is a 0.5-1.0 kg or "wok-sized" fish, within a 2-year period (Perry et al. 1998). Suggestions to release cultured tautog into the wild to enhance diminished natural populations (Perry et al. 1998) should be carefully considered before implementation.

South of the Gulf of Maine, tautog are among the most important game fishes sought by shore fishermen along rocky areas (Migdalski 1958; Wilcoxson 1975), and they are also a primary species at artificial reefs in the northeast (Zawacki 1969; Briggs 1975). Active sport fisheries for tautog exist along the coast south to Virginia. The sport fishing season tends to be bimodal (May-July and September-October) in New York and northward. Tautog are generally available to nearshore fishermen throughout the spring, summer, and fall seasons, but many of the larger fish apparently move to deeper water

during periods of summer high temperatures and winter low temperatures in inshore waters (Briggs 1969a), and move inshore again with the onset of favorable temperatures. In 1990 and 1991, tautog were the most frequently caught fish in the recreational fishery in the North Atlantic, with an estimated catch of 1.1 million fish, of which some 289,000 were caught in Massachusetts (Voorhees et al. 1992). The principal mode of capture was by anglers on private and rental boats, *followed* by party / charter and shore fishing anglers. Along the stretch from Manomet Headland, Plymouth, to Cape Ann, tautog are caught either from a boat at anchor over submerged ledges or bottoms covered with boulders or by casting with a long rod from dry ledges or from the rocky coastline. **In** either case, the fish are so local and irregular in distribution (depending on food supply and the contour of the rocks) and so stationary that it is worth fishing for them only in certain spots. Tautog are a challenge to sport fishermen. A few feet from their structure one way or the other may mean the difference between success and failure. **In** Cape Cod Bay; however, where the tautog occur on smooth bottom, they lie in little openings among eelgrass (whenever there is any), and, if a fiddler or hermit crab is lowered in a clear spot in front of them, they can be caught in very shallow water.

Fishing the Cohasset rocks, Bigelow and Schroeder found green crabs (*Carcinus maenas*) the most attractive bait, whole if small enough, cut if larger; rock crabs (*Cancer*) or hermit crabs second best; and large snails or cockles (*Polynices*) fairly good. They also noted that lobster would perhaps be best of all, were it not so expensive. Mussels are often successful bait for capturing tautog, but are difficult to keep on the hook. Small, whole clams, hooked through the siphon with the shell cracked so as to let the juices escape, are also a good bait. However, mussels and clams are next to worthless if shelled because they are stolen almost immediately by the swarms of cunner frequenting the same habitats as tautog. **In** Cape Cod Bay; where tautog are caught on smooth bottom, the baits most used are hermit and fiddler crabs. Bigelow and Schroeder also noted that tautog will occasionally strike sea worms (*Nereis*) as well.

Tautog are not the easiest fish to catch on hook and line. When a tautog bites, it passes the bait back to the pharyngeal teeth to crush the shells before swallowing them, and in doing so it gives several distinctive jerks or twitches. This is the time to hook it. Many fish are missed by being struck too soon by anglers not experienced in the ways of the tautog.