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Tautog (*Tautoga onitis*) Life History and Habitat Requirements

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Note on Species Names

The NMFS Northeast Region's policy on the use of species names in all technical communications is generally to follow the American Fisheries Society's lists of scientific and common names for fishes (*i.e.*, Robins *et al.* 1991[a]), mollusks (*i.e.*, Turgeon *et al.* 1998[b]), a decapod crustaceans (*i.e.*, Williams *et al.* 1989[c]), and to follow the Society for Marine Mammalogy's guidance on scientific and common names for marine mammals (*i.e.*, Rice 1998[d]). Exceptions to this policy occur when there are subsequent compelling revisions in the classifications of species, resulting in changes in the names of species (*e.g.*, Cooper and Chapleau 1998[e]).

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[a]Robins, C.R. (chair); Bailey, R.M.; Bond, C.E.; Brooker, J.R.; Lachner, E.A.; Lea, R.N.; Scott, W.B. 1991. Common and scientific names of fishes from the United States and Canada. 5th ed. *Amer. Fish. Soc. Spec. Publ.*20; 183 p.

[b]Turgeon, D.D. (chair); Quinn, J.F.; Bogan, A.E.; Coan, E.V.; Hochberg, F.G.; Lyons, W.G.; Mikkelsen, P.M.; Neves, R.J.; Roper, C.F.E.; Rosenberg, G.; Roth, B.; Scheltema, A.; Thompson, F.G.; Vecchione, M.; Williams, J.D. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks. 2nd ed. *Amer. Fish. Soc. Spec. Publ.* 26; 526 p.

[c]Williams, A.B. (chair); Abele, L.G.; Felder, D.L.; Hobbs, H.H., Jr.; Manning, R.B.; McLaughlin, P.A.; Pérez Farfante, I. 1989. Common and scientific names of aquatic invertebrates from the United States and Canada: decapod crustaceans. *Amer. Fish. Soc. Spec. Publ.* 17; 77 p.

[d]Rice, D.W. 1998. Marine mammals of the world: systematics and distribution. *Soc. Mar. Mammal Spec. Publ.* 4; 231 p.

[e]Cooper, J.A.; Chapleau, F. 1998. Monophyly and interrelationships of the family Pleuronectidae (Pleuronectiformes), with a revised classification. *Fish. Bull. (U.S.)* 96:686-726.

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Acronyms

DO = dissolved oxygen
FDA = [U.S. Department of Health and Human Services'] Food and Drug Administration
FL = fork length
FO = frequency of occurrence
GSI = gonadal-somatic index
MARMAP = [NEFSC's] Marine Resources Monitoring, Assessment, and Prediction Program
NEFSC = [National Marine Fisheries Service's] Northeast Fisheries Science Center
PCB = polychlorinated biphenyl
TL = total length
YOY = young of the year

ABSTRACT

This report compiles and summarizes available information on the tautog (*Tautoga onitis*), covering nomenclature and taxonomy, distribution and habitat, reproduction, development, growth, feeding and diet, behavior, population structure, natural and human-induced environmental factors, and ecological roles. The report also identifies research needs and includes an extensive bibliography.

Recent declines in this species' abundance and certain known aspects of its life history and specific habitat requirements have caused coastal fishery resource and habitat managers to believe the species may need further conservation measures. Essential to developing an effective conservation management strategy for this species is a thorough summary of what is known of the species' life history and of the habitat requirements for all life stages. This information will be important for developing holistic approaches to managing a sustained population and fishery for this species and closely associated members of its ecological community.

This review shows that although much is known about the species, and studies on its life history and ecology are ongoing, there are important gaps and conflicting or unconfirmed results in our understanding of the species, and its needs, which should be addressed.

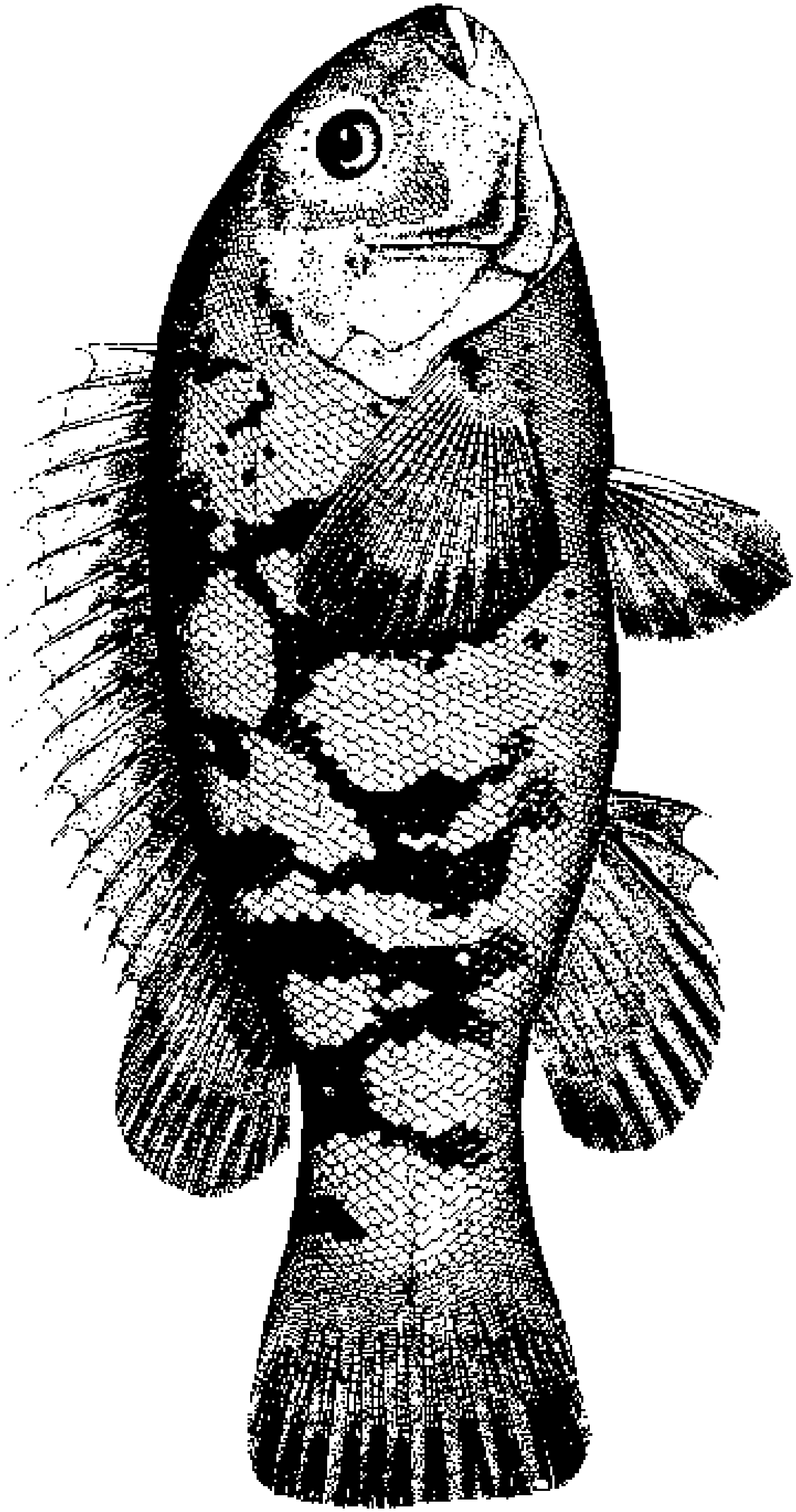

Figure 1. Drawing of tautog by H.L. Todd based on specimen collected by Vinal N. Edwards at Woods Hole, Massachusetts, on December 13, 1875.

INTRODUCTION

The tautog (*Tautoga onitis*) is a valuable recreational and commercial fishery resource from Massachusetts to Virginia in the Northwest Atlantic. It is commonly found on complexly structured, vegetated, or reef-like habitats during post-larval stages. Fishery interest in the species has increased in recent years, and additional management measures for this fishery are being considered. To support the development of information necessary to produce good public policy, an assemblage of existing information on the species is needed (Atlantic States Marine Fisheries Commission 1995). This report compiles and summarizes available information on the life history and habitat requirements of, and natural and human-induced environmental threats to, tautog. It builds upon and substantially expands the previous efforts of Auster (1989), Gray (1992), and others. This review is needed because of: 1) recent increased fishing effort for, and resource user conflicts over, tautog (DiLernia 1993); 2) sensitivity of reef fish such as tautog to exploitation (Hostetter and Munroe 1993); 3) the species' particular habitat needs and the threats to this habitat; and 4) the possible need to exercise additional management of at least certain localized populations of this species (Hostetter and Munroe 1993). Information on regional-level stock abundance, and detailed discussion of state-level populations and harvests, are not included here, but have been compiled by Lazar (1995).

As there are incidental references to this species in many documents and papers, and as there are ongoing studies wholly or partially involving this species, such a review cannot be definitive. It can, however, serve as a stepping stone to adequate knowledge for fishery resource and/or habitat management, or for fishery research planning, as have previous reviews. Because of the scarcity or absence of certain information on tautog, relevant information from studies of the its close labrid relative, the cunner (*Tautogolabrus adspersus*) -- which has similar habitat needs -- has sometimes been considered and discussed as probably an appropriate estimate for tautog.

NOMENCLATURE AND TAXONOMY

NOMENCLATURE

Valid Name

Tautoga onitis (Linnaeus, 1758) is the name recognized by the American Fisheries Society (Robins *et al*. 1991). The generic term is the original name applied to this fish species supposedly by Narragansett Indians. The species term is derived from the Latin, *onitis*, which means "a kind of plant"; but its application by Linnaeus is unclear (Smith 1907).

Synonymy

The species has a rich synonymic history which, following Jordan and Evermann (1896-1900) and Jordan *et al*. (1930), includes: *Labrus onitis* (Linnaeus 1758 and 1766); *L. hiatula* (Linnaeus 1766); *L. carolinus* (Bonnaterre 1788); *L. blackfish* (Schopf 1788); *L. subfuscus* (Walbaum 1792); *L. tesselatus* (Block 1792); *Hiatula gardeniana* (Lacepede 1800); *L. americanus* (Block and Schneider 1801); *L. tautoga rubens* (Mitchill 1814, 1815); *L. tautoga alia* (Mitchill 1814, 1815); *Tautoga niger* (Mitchill 1814, 1815); *L. tautoga fusca* (Mitchill 1815); *T. tessellata* (Cuvier and Valenciennes 1839); *T. americana* (DeKay 1842); *T. onitis* (Gunther 1862; Uhler and Lugger 1876; Yarrow 1877; Jordan and Evermann 1898; Evermann and Hildebrand 1910; Fowler 1912); *H. onitis* (Jordan 1886; Jenkins 1887; Bean 1891); and *H. hiatula* (Goode and Bean 1885).

TAXONOMY

Description and Affinities

This species is a member of the Labridae, a family of lipped fishes commonly called wrasses. This family takes its name from the presence of conspicuous, thick, longitudinally folded lips which, along with other characteristics such as the form of the jaws, give the mouth a peculiar appearance (Smith 1907; Liem and Sanderson 1986). The mouth is terminal and considered of small or moderate size (Hildebrand and Schroeder 1928). Westneat (1995) suggests that tautog may have characteristics which are primitive within the family, mostly based on its hard-prey diet and associated jaw morphology.

Worldwide, there are 500-600 species in the Labridae (Nelson 1984). In the United States, there are 12 genera (Robins *et al.* 1991). Five labrid species occur in North Carolina waters (Smith 1907), but only two species are commonly found north of Cape Hatteras: the cunner, *Tautogolabrus adspersus* (Walbaum, 1792), and the tautog, *Tautoga onitis* (Linnaeus, 1758), (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953).

The genus *Tautoga* (Mitchill) consists of a single species: *Tautoga onitis*. The following generic description is from Hildebrand and Schroeder (1928): "Body is elongate, moderately deep and compressed; anterior profile rather strongly arched, head nearly as deep as long; eye small, placed high; mouth rather small; lips quite broad and thick" (Figure 1). "Teeth in the jaws strong, the anterior ones more or less conical and incisor-like." Both the roof of the mouth and the floor of the throat (*i.e.*, pharynx) have a patch of knob-like teeth that are used to crush and grind mollusk and crustacean prey (Bigelow and Schroeder 1953; Liem and Sanderson 1986). The scales are small, with about 70 being in the lateral series, but cheeks and operculums are largely scaleless. The dorsal fin is long and continuous, with the soft part short. The caudal fin is short and round to slightly truncate. The anal fin has three stout spines, with the soft part similar to that of the dorsal fin (Hildebrand and Schroeder 1928).

Normal coloring of this species is variably dull blackish, brownish, blackish green, or blackish blue, with sides irregularly mottled or blotched. The lips, chin, throat, and belly are often lighter. Larger males are gray with white markings on the caudal, pelvic, and dorsal fins, and on the chin -- a very conspicuous characteristic. Females and smaller males are without white markings on fins and chin, and their fins are often plain like the color of the body. Their eyes are green. Juveniles are usually colored green or brown with more distinctive side mottling and three or more darker bars. This coloring can vary with the visual characteristics of the habitat they are using. In some areas, two color patterns are often recognized; one being plain blackish and the other having irregular blackish bars on a pale background. Fish are also observed being dull gray-white. Some of these variations could reflect different environmental factors, such as light or stress. (See the "Color Modulation" section of the "Behavior" chapter.)

The tautog can be distinguished from its close and co-occurring relative, the cunner, in several ways. The adult tautog is longer and stouter than the adult cunner. The dorsal profile of its head is highly arched, while in the cunner it is relatively straight. The caudal peduncle of the tautog is proportionally wider, and the caudal fin is narrower, than those of the cunner (Bigelow and Schroeder 1953; Leim and Scott 1966). Tautog lack scales on the cheeks and operculums, while on cunner they are present (Hildebrand and Schroeder 1928).

Subspecies

No subspecies are recognized. However, the differential juvenile growth rates at the range extremes of the species, discussed in the "Growth" chapter, have been thought possibly to reflect some degree of evolutionary divergence, but this has not been supported in the laboratory (Martin 1993).

Common and Vernacular Names

Tautog is the common name for *T. onitis* accepted by the American Fisheries Society (Robins *et al*. 1991), but "blackfish" is also widely used. Other regional common names include: Canada -- tautogue noir (Leim and Scott 1966); Maine -- white chin (Bigelow and Schroeder 1953); New York -- blackfish (Goode 1887; Hildebrand and Schroeder 1928); New Jersey -- smooth blackfish, tautog, and chub (Goode 1887); Maryland -- black porgy, salt-water chub, chub, and blackfish (Hildebrand and Schroeder 1928); Virginia -- moll and will-george (Goode 1887); and North Carolina -- sea tench (in a 1709 usage) and oyster-fish (Goode 1887; Smith 1907).

The Maine name "white chin" refers to the conspicuous white coloration of the lower jaw of older males (Bigelow and Schroeder 1953; Hostetter and Munroe 1993). Another name used in some places is "slippery bass" which refers to the tautog's mucus covering and rough resemblance to a bass. Jordan *et al*. (1930) also mention the names "cub" and "sea dog" being used for the species.

DISTRIBUTION AND HABITAT

GENERAL DISTRIBUTION

The tautog is a generally a coastal species found on the Atlantic coast of North America, from the outer coast of Nova Scotia to South Carolina (Bigelow and Schroeder 1953). It has been anecdotally, and perhaps dubiously, reported on central Georges Bank from commercial fishery catch data (Chang 1990). The report of tautog on Georges Bank is not reliably supported by Northeast Fisheries Science Center (NEFSC) bottom trawl survey records, although it has been suggested that a few tautog may be collected near the boundaries of the bank every decade (T. Azarovitz, pers. comm.[1]). The tautog may be a "relict" species north of Massachusetts, found in certain, deep, saltwater lakes and protected bays of Nova Scotia that have waters that become warmer in summer and remain slightly warmer in winter (Bleakney 1963).

The tautog is most abundant from Cape Cod to Chesapeake Bay. North of Cape Cod, it is unusual to find tautog more than 6 km from land, or in waters deeper than 18 m. South from Cape Cod to about New Jersey, it can be found to 19 km offshore in up to 24 m of water, and occasionally near the deep Great South Channel between Nantucket Shoals and Georges Bank (Chang 1990). This offshore distance and depth range appear to increase gradually towards the south and near Cape Hatteras (Chang 1990; Hostetter and Munroe 1993). Tautog have been reported in brackish water, but not in freshwater (Bigelow and Schroeder 1953). It has been reported up to 70 km upstream from the mouth of the Hudson River (New York) (Beebe and Savidge 1988), and formerly in the Patapsco River in Baltimore, Maryland (Fowler 1912).

It is uncertain if tautog populations at the northern and southern extremes of its range were introduced by man. To the north, reports that the tautog was introduced to Cape Ann (Massachusetts) in the late 1800s were countered by other reports that it had been abundant many years previous to that time. To the south, reports that it had been introduced to South Carolina were countered by skepticism that its range could be artificially extended southward (Goode 1887). Tautog are currently rarely observed or caught in South Carolina waters (M. Bell, pers. comm.[2]).

In terms of the persistent, overall range of the species, the potential effects of long-term global warming (or cooling) are unknown. Continued global warming could theoretically increase northern coastal water temperatures and potentially the presence of the species (and others) in the Gulf of Maine, and perhaps restrict tautog to north of Cape Hatteras. Such a northern expansion could have occurred since the last glacial period. Empirically, however, it appears that recent warming of air temperatures in the Arctic has hastened the melting of the polar ice cap which has, in turn, increased the flow of cold freshwater into the North Atlantic. This expansion of the North Atlantic "cold pool" has already reduced the habitat for young Atlantic salmon, and may well be, or become, a distribution-reducing factor for cold-intolerant fish species (K. Friedman, pers comm.[3]).

DIFFERENTIAL DISTRIBUTION

Spawning

Adult tautog generally migrate inshore in spring from coastal wintering sites to spawn (Chenoweth 1963; Cooper 1966; Stolgitis 1970; Olla *et al.* 1974; Briggs 1977). Spawning occurs primarily at or near the mouths of estuaries and in inshore waters (Tatham *et al.* 1984; Feigenbaum *et al.* 1989; Sogard *et al.* 1992; Able and Fahay 1998). Inside Narragansett Bay (Rhode Island), mature tautog returned to the same spawning sites each year, usually in the upper estuary, but dispersed throughout the bay after spawning (Cooper 1966; Dorf 1994; Dorf and Powell 1997). Olla *et al.*'s (1980) tagging studies suggested, however, that adult tautog did not always return to the same spawning site in the spring, and that population mixing from different localities occurred.

A portion of the adult population reported to remain offshore throughout the year (Olla and Samet 1977; Eklund and Targett 1990; Adams 1993; Hostetter and Munroe 1993), especially in the southern part of its range, was found seasonally in spawning condition. For example, ripe fish were collected by Eklund and Targett (1990) and Hostetter and Munroe (1993) on hard-bottom sites 25-35 m in depth and 22-37 km off Maryland and Virginia. Collections of eggs and larvae from Georges Bank to North Carolina through the NEFSC's Marine Resources Monitoring, Assessment, and Prediction Program (MARMAP) surveys, suggest that tautog spawning may also occur in continental shelf waters and be concentrated off Southern New England (Sogard *et al.* 1992). Dorf (1994), in contrast, speculates that the occurrence of offshore eggs and larvae can also result from their being flushed from estuarine spawning areas, at least in Southern New England.

Spawning is reported to follow a northward progression through the summer, beginning in April in the southern part of the Middle Atlantic Bight, and extending to the northern areas by May (Able and Fahay 1998). Peak spawning in the central Bight is reported to occur in June and July, and to decline by August (Berrien and Sibunka, in press).

Eggs and Larvae

Tautog eggs and larvae are collected on the inner continental shelf, with highest concentrations being collected off Southern New England and Long Island (New York) (Colton *et al.* 1979; Sogard *et al.* 1992; Malchoff 1993). In the New York Bight (*i.e.*, the continental shelf off Long Island and New Jersey), larvae are reported to be part of a summer coastal fish larval assemblage, perhaps closely associated with spawning areas (Cowen *et al.* 1993). Tautog is the most abundant of any larval species found recently in Narragansett Bay (Keller and Klein-MacPhee 1992). In the Weweantic River Estuary (Massachusetts), the greatest abundances of eggs and larvae were collected over eelgrass (*Zostera marina*)-vegetated sites and near bottom (Stolgitis 1970).

As mentioned earlier, Dorf (1994) believes that eggs and larvae found in offshore coastal waters can result from *ex situ* sources (*i.e.*, flushed out and away from estuaries), but there are inadequate data to support this hypothesis at present. Viable tautog eggs, although lacking oil globules, are buoyant and found in greatest abundance at or near the water surface (Merriman and Sclar 1952; Herman 1963; Stolgitis 1970; Fritzsche 1978; Bourne and Govoni 1988). Nonviable eggs lack or lose buoyancy and probably respond to currents differently, and thus probably become distributed differently (Perry 1994).

Malchoff (1993) reported that tautog larvae migrate vertically in the water column. The larvae, 2-4 mm in length, stay near the water surface (less than 5 m deep) during the day, but go deeper at night. Older and larger larvae spend more time at deeper depths as they grow. Malchoff (1993) also believed the Hudson River plume strongly influences larval tautog transport patterns in that part of the New York Bight. Sogard *et al.* (1992) estimated that larval tautog in coastal New Jersey spend about 3 wk in the plankton before settling to the benthos, but this period can be a short as 17 days (Schroedinger and Epifanio 1997). This is a relatively short planktonic period compared to that of other labrids. This short period could possibly reflect an adaptation to cool-temperate environments and a restricted period of optimum warmer conditions for somatic growth.

Juveniles

Newly settled tautog inhabit shallow areas less than 1 m in depth (Warfel and Merriman 1944; Sogard *et al.* 1992; Hostetter and Munroe 1993), including tide pools (Breder 1922). Bigelow and Schroeder (1953) noted that "fry" were often seined from Southern New England to Virginia. Sogard *et al.* (1992) reported that as young-of-the-year (YOY) tautog grow, they move to areas greater than 1 m deep. Cooper (1964) noted that juveniles (no size range given) in Narragansett Bay were not observed in waters deeper than about 9 m.

Several studies reported that young tautog (less than 10 cm) prefer vegetated over unvegetated bottoms (Briggs and O'Connor 1971; Sogard *et al.* 1992; Dorf 1994; Dorf and Powell 1997). These preferred, vegetated habitats are reported to range from primarily eelgrass beds (Goode 1887; Grover 1982; Orth and Heck 1980; Heck *et al.* 1989; Sogard *et al.* 1992; Szedlmayer and Able 1996) or a mix of eelgrass and algal associates [*i.e.*, sea lettuce (*Ulva lactuca*), *Enteromorpha* sp., and *Polysiphonia*] (Briggs and O'Connor 1971), to beds of mostly *Ulva* (Nichols and Breder 1926; Sogard and Able 1991). In the Great Bay - Mullica River Estuary (New Jersey), early YOY preferred sea lettuce over eelgrass habitats (Sogard 1989). Sogard (1989) reported that juvenile tautog also readily used artificial sea grass as habitat. For YOY and 1-yr-old juveniles, empty oyster and clam shells (Bigelow and Schroeder 1953) and shell and sponge (Szedlmayer and Able 1996) have been reported to be used as habitat. Dixon (1994) added small boulders as a preferred habitat type for juveniles.

The main habitat requirement and distribution factor, however, for juvenile tautog (less than 25 cm) is the availability of cover (*i.e.*, any object that an individual can remain alongside, within, or under) (Olla *et al.* 1974, 1975). Along these lines, Dixon (1994) noted that vertical relief is an important attribute of juvenile habitat. Smith (1907) reported that young fish were abundant around wharves in North Carolina; Able and Fahay (1998) reported the same for New York Harbor. Larger juvenile tautog are closely associated with hard- surface, reef-like habitats (Olla *et al.* 1979). Zawacki (1971) reported that 15-20 cm fish were common around a 1-mo-old, automobile-tire artificial reef in Shinnecock Inlet, Long Island. Adams (1993) reported only juveniles greater than 12 cm total length (TL) recruited to southern, offshore reefs.

In Narragansett Bay, YOY tautog appear from late June through August (Dorf 1994; Dorf and Powell 1997). During winter, juveniles remain inshore (Cooper 1964; Stolgitis 1970; Olla *et al.* 1974). At this time, especially when water temperatures are 5°C or less, YOY and 1-yr-old tautog are found in discarded beverage cans and bottles, eelpots, empty oyster and clam shells, and in crevices of vertical structures; they are also found on their sides in nearby depressions in sediments, either covered with a few millimeters of sand and silt (except head and gill area) or exposed on the sediment surface (Bigelow and Schroeder 1953; Cooper 1964, 1966; Olla *et al.* 1974, 1978, 1979, 1980). Juvenile tautog (3-7 cm TL) were found to select a narrow range of hole sizes (*i.e.*, about 3-4.5 cm in diameter) in structured habitats, and to occur usually near the bottom of any object or structure (Dixon 1994). Dorf (1994) suggested that sheltering habitat could be a limiting distribution factor in Narragansett Bay for juveniles less than 2 yr old. Although the food-producing capability could be surmised as one of the reasons that older juveniles prefer reef-like habitats, Dixon (1994) found that neither the availability of attached food (*e.g.*, small mussels) nor the presence of small but not highly active predators (*e.g.*, toadfish and sculpins) had much effect on habitat use.

Olla *et al.* (1979) reported that young tautog (less than 25 cm) showed an affinity to particular shelters, establishing homesites from which they ranged only a few meters during the day, and to which they returned at night. They also suggested that use of such homesites by some juveniles is seasonal. They observed a perennial homesite -- a basin wall -- which was utilized year-round by part of the juvenile population. At the onset of winter, other young tautog that had possibly dispersed to other nearby summer sites, such as eelgrass or algae beds, rejoined the juvenile colony at the wall to overwinter. In the spring, some of this population again left the wall for other shelter.

The mouths of estuaries or inlets may be especially important habitat areas for juvenile and adult tautog. Briggs (1975) reported that tautog was the most frequently collected fish in traps used on the Kismet artificial reef just inside Great South Bay, Long Island. The species ranked only fourth in abundance on an artificial reef less than 5 km offshore.

Adults

Adult (*i.e.*, mature) tautog (generally greater than 25 cm TL) have the same basic habitat requirements as larger juveniles and are found in vegetation, rocks, natural and artificial reefs, pilings, jetties and groins, mussel and oyster beds, shipwrecks, submerged trees, logs and timbers, and similar complexly structured coastal habitats [*e.g.*, see Smith (1907) and Hildebrand and Schroeder (1928)]. The fish are extremely local, so much so that when fishing for them "a few feet one way or the other may mean the difference between success and failure" (Bigelow and Schroeder 1953). Adams (1993) observed that the species preferred the crest and outer edges of coastal reef habitats.

During summer, adults can be found inshore, co-existing with younger fish. Olla *et al.* (1974) reported adults ranged up to 500 m away from their homesite during the day, but generally returned to the same general shelter area at night. This established a local population during the summer.

In late fall, when water temperatures fall below 11°C, there is an overall migration to perennial offshore areas with rugged topography in waters 25-45 m deep (Cooper 1966). Individual tautog do not appear to return annually to the same sites within an offshore area to overwinter (Olla *et al.* 1979). On the other hand, some adults were found to overwinter inshore, especially in the north.

The seasonal migrations of tautog do not seem to involve great distances [*e.g.*, Briggs (1974) reported that fish from southern Long Island bays winter in deeper coastal waters off northern New Jersey]. Other adult tautog in winter were observed in less than 10 m of water in eastern Long Island Sound (Zawacki and Briggs 1976; Auster 1989), in 10 m of water at an artificial reef 2.4 km off Delaware (Eklund and Targett 1991), and in deeper areas of Chesapeake Bay (Hostetter and Munroe 1993). Eklund and Targett (1990) noted populations in 25-35 m of water 22-37 km offshore of Maryland and northern Virginia, and Hostetter and Munroe (1993) observed populations in 10-75 m of water to 65 km offshore of southern Virginia. At an artificial reef in about 20 m of water 15 km offshore of southern Virginia, Adams (1993) observed that the largest tautog (greater than 75 cm in length) occurred in February when temperatures were about 6°C. He considered tautog to be a "core resident species" on this reef, and to be active year-round.

At very low temperatures, tautog enter a torpor-like state (Cooper 1966; Briggs 1977). Curran (1992) reported that cunner go into true torpor or hibernation during winter, and suggested tautog do likewise, at least in the northern part of their range. She believed the ability of cunner and probably tautog to hibernate may be the key to these two species, of a basically tropical family, being able to tolerate cold water and inhabit cool-temperate waters year-round.

DETERMINANTS OF DISTRIBUTION

Juveniles

Olla *et al.* (1979) suggested that the distribution of habitat use by juvenile tautog was somewhat seasonal and temperature mediated. Juveniles seem to have a perennial site which they use during the winter. In spring, some of the wintering groups dispersed to summer sites. Olla *et al.* (1979) believed this springtime dispersal was possibly due to increased aggression in the population or to other factors which made the perennial winter site suboptimal. If a summer habitat became suboptimal, because of elevated temperatures or inadequate vegetation, juvenile tautog moved to other perennial summer sites.

Young tautog have strong adherence to homesites (Able and Fahay 1998), but if shelter becomes suboptimal, they will move (Olla *et al.* 1979). They will also move if a more attractive habitat is found. In the Great Bay - Mullica River Estuary, Sogard (1989) found that in summer juveniles moved from naturally vegetated homesites to newly planted, artificial seagrass beds. The factors that made the artificial seagrass beds more attractive are not known.

Adults

Adults also show an affinity to homesites, though this is not as strong as for juveniles. Adults have been observed to leave a site readily if suboptimal conditions develop. At an artificial reef in Delaware Bay, tautog which were common in early summer were absent later that year, coincident with a blue mussel (*Mytilus edulis*) kill, probably caused by high water temperatures (personal observation by senior author). Also, at an artificial reef 15 km off Virginia, Adams (1993) noted a decrease in abundance of large tautog when water temperatures were above 20°C for an extended time. He suggested that large fish leave areas with uncomfortably high temperatures for areas with cooler, deeper waters.

The adult fall offshore migration is triggered by bottom water temperature dropping below 10°C (Cooper 1966; Olla *et al.* 1974; Lynch 1994). The spring inshore migration is associated with an increase in bottom water temperatures to 11°C or above (Chenoweth 1963; Cooper 1966; Stolgitis 1970; Olla *et al.* 1974; Briggs 1977; Olla *et al.* 1979). In laboratory experiments, Olla *et al.* (1980) confirmed temperature, not changing photoperiod, as the leading factor in fall migratory movements and distributions.

HABITAT NEEDS

Tautog are specifically associated with complexly structured habitats in all post-larval stages of their life. As juveniles, these habitats include submerged vegetation, shellfish beds, and three-dimensional objects or structures with appropriately-sized crevices and holes for shelter. (See the "Differential Distribution" section in this chapter). As the fish grow, larger complex structures are needed for shelter, and hard substrates are usually required to support the epibenthic or encrusting invertebrates upon which the fish generally feed. (See the "Feeding and Diet" chapter). South of Long Island, beyond where rocks and boulders were deposited during previous glacial periods, there are few natural rock outcroppings in coastal marine waters to provide the "reef" habitat that tautog require, although shellfish beds in euryhaline parts of estuaries serve as habitat (Arve 1960). In this area, the man-made "reef" habitat created by coastal jetties, groins, pilings, accidental shipwrecks, and intentional deposition of solid material as artificial reefs is undoubtedly important to the distribution of the species.

The availability of new macroalgal growth as cover in the late spring to early summer period can be critical to settlement and survival of post-larvae (Dorf 1994; Dorf and Powell 1997). This is especially true for areas that do not support extensive eelgrass beds or complexly structured habitats. Although macroalgae is normally degraded or swept into dense beds later in the season, a healthy, new-growth, spring-summer macroalgal community can be important to the initial survival of juvenile tautog (Dorf 1994; Dorf and Powell 1997). Sogard and Able (1992) reported that juvenile tautog in New Jersey appeared to prefer habitat where sea lettuce (*Ulva*) was present. *Ulva* can have negative effects on certain taxa or species, and the preference or tolerance of *Ulva* by tautog can give it an advantage with competitors or predators (Dorf 1994). In contrast to studies that report the importance of vegetation, Dixon

(1994) reported that YOY tautog preferred small boulders as habitat over cobbles, vegetation, and other structure-based habitat options in an aquarium study.

REPRODUCTION

SEXUALITY

In contrast to most labrids, tautog are not protogynous hermaphrodites (Olla *et al.* 1981). They are heterosexual, but two different morphological males are thought to be present in the population. One type of male is dimorphic with a more pronounced mandible than found on the female, and the other type is nondimorphic and resembles the female (Olla and Samet 1977; Hostetter and Munroe 1993). It has been suggested that the nondimorphic male may be: 1) a sexual stage in the life of the tautog, 2) an indicator of hermaphrodism, 3) a means to increase spawning opportunities, or 4) coincident with a different reproductive behavior than the dimorphic male (Hostetter and Munroe 1993).

FECUNDITY

Chenoweth (1963) found that tautog that were 21-68 cm in fork length (FL), weighed 170-5207 g, and were between 3 and 20 yr old, contained 5000 to 637,500 mature eggs. He found that the number of eggs (Y) were related to fork length (X) in millimeters by the regression: $Y = -6.00307 + 3.0960(X)$. The number of eggs (Y) was also related to weight (Z) in grams by the regression: $Y = 0.31492 + 1.07993(Z)$. The number of eggs produced per unit of weight per ovary reaches a maximum in 7-9 yr old fish which are about 34-39 cm TL (Cooper 1967). Thereafter, egg production stabilizes until an age of about 16 yr, after which it declines (Chenoweth 1963; Cooper 1967).

SPAWNING

The ratio of the mass of gonadal tissue to the mass of all body tissues [*i.e.*, the gonadal-somatic index (GSI)] can be an indicator of a fish's reproductive state, with the highest indices just prior to spawning, and the lowest indices just after spawning. The GSIs for female and male tautog off the coast of Maryland and Virginia were reported to peak between April and June (Eklund and Targett 1991; Hostetter and Munroe 1993).

Spawning begins when water temperatures reach 9°C or above, generally peaks about June, and continues throughout summer (Kuntz and Radcliffe 1918; Nichols and Breder 1926; Perlmutter 1939; Bigelow and Schroeder 1953; Wheatland 1956; Chenoweth 1963; Cooper 1964; Colton *et al.* 1979; Eklund and Targett 1990; Monteleone 1992; Sogard *et al.* 1992; Hostetter and Munroe 1993; Malchoff 1993). Sogard *et al.* (1992) used NEFSC-MARMAP larval distribution (Berrien and Sibunka, in press) and other data to show spawning began in May-June south of New York, and reached its peak in June-

July off Southern New England. Dorf (1994) reported finding hatching eggs in late May to late July in Narragansett Bay. Sandine (1984) reported the occurrence of tautog eggs in Barnegat Bay (New Jersey) from March to August, and questionably in October.

COURTSHIP

Tautog spawn in heterosexual pairs or in a group with a single female being active simultaneously with several males (Olla and Samet 1977; Dixon 1997). The mode of spawning is reported to depend on the number of mates available for the female, the presence of a male-dominance hierarchy, and environmental factors such as availability of shelter and food (Olla and Samet 1977). In laboratory studies with two active males (one of which was dominant) one female, and one shelter, mating occurred only between the dominant male and the female (Olla and Samet 1977). Group spawning was observed when there was either an increase in the number of males, a lack of a dominant male, an increase in the male:shelter ratio, an inability to control a territory, or an elevated temperature (Olla and Samet 1977; Olla *et al.* 1981).

Several weeks before spawning, male aggressiveness toward females noticeably decreased and was replaced by "rushing" (*i.e.*, males quickly approached females then veered off) (Olla and Samet 1977). Coincident with this change in male behavior, females increased their girth with enlargement of their ovaries.

In laboratory studies, courtship activity prior to spawning was observed to continue for several hours. In paired spawning, the male rushed the female frequently (Olla and Samet 1977), and male pigment bars darkened while those of the female lightened (Bridges and Fahay 1968). Physical contact between the sexes, including nuzzling and rubbing flanks, was observed (Bridges and Fahay 1968). Courtship culminated with the paired fish moving rapidly together within 1 m of the water's surface. The fish then turned toward each other, arched their bodies, and released their gametes near, or as they broke, the water surface (Olla and Samet 1977). Spawning usually occurred in the afternoon, with as many as three spawnings daily (Olla and Samet 1977, 1978). Spawning often continued into evening in the wild (Ferraro 1980).

Olla and Samet (1977) observed slight differences in courtship during group spawnings. The males did not rush the female as frequently, and "contact-clustering behavior" occurred (*i.e.*, two or more males clustered near the female and contacted her with their flanks).

DEVELOPMENT

OVA

The development of the ova was described by Chenoweth (1963):

> *The ova arise from the germinal epithelium that lines the interior wall of the ovary and fills a large part of the organ through convolutions. At first the developing ova are opaque, relatively hard, and average 0.36 mm in diameter. As development proceeds the ovary enlarges and transparent, soft, mature ova appear interspersed with the immature ova. These ova average 0.79 mm in diameter.*

There are corresponding changes in the appearance of the ovary as the eggs mature.

EGGS AND EMBRYOS

Spawned tautog eggs are about 1 mm in size, highly transparent, and spherical in form (Herman 1963). The egg membrane is thin but tough and the yolk sphere does not contain an oil globule (Kuntz and Radcliffe 1918). Egg size varies from year to year, with diameters of 0.70-1.18 mm being reported (Nichols and Breder 1926; Richards 1959; Chenoweth 1963; Lebida 1969). Egg size also decreases with an increase in water temperature, and as the spawning season progresses (Williams 1967). Therefore, it has been suggested that annual variation in egg diameter reflects differences in sampling times. Eggs that were reported in the literature with variable diameters could be explained by their being collected at different times during the spawning season in different years (Auster 1989).

Incubation of fertilized eggs at temperatures of about 20-22°C in the laboratory was reported to take 42-48 hr to hatching (Kuntz and Radcliffe 1918; Merriman and Sclar 1952; Perry 1994), but at 14.2-16.8°C, it took about 81 hr (Perry 1994). Kuntz and Radcliffe (1918) and Fahay (1983) described embryonic development.

D. Perry (pers. comm.[4]) reports that the proportion of normally developing, viable embryos among all tautog embryos collected in central Long Island Sound near New Haven, Connecticut, declined as the spawning season progressed. This decline had no significant locality variance, nor appeared to be related to differences in habitat quality. This progressive decline was also noted in laboratory spawned eggs and reared embryos (Perry 1994). Olla and Samet (1978) found higher ambient temperatures affected normal development of tautog embryos.

LARVAE

Newly hatched embryos, or yolk-sac larvae, are approximately 2.2 mm in length, but can be slightly less. [Some variance in the lengths of specimens reported in the literature and reported here can be the results of preservation which usually causes some shrinkage. This shrinkage can vary with developmental stage (*e.g.*, degree of ossification).] The head is slightly deflected and the yolk sac is relatively large, elliptically ovate, and unpigmented. The vent is located about mid-length of the body. The depth of either dorsal or ventral fin fold is less than the depth of the body just posterior to the vent. The fin folds and the posterior caudal region of the body remain free of pigment.

One day after hatching at temperatures of 20-22°C, tautog larvae are about 2.0-3.0 mm in length. The yolk sac is greatly reduced and the head is no longer deflected. The chromatophores increase in size and show well developed pigment processes, but are fewer in number than in the newly hatched larvae; individual pigment cells merge to form large chromatophores. The larvae have a distinct blackish color (Able and Fahay 1998).

Four days after hatching is a critical period for this species. The yolk sac has been absorbed and the mouth has been formed and is functional (Bigelow and Schroeder 1953). These post-yolk-sac larvae, which are now 3.2-3.5 mm in length, must begin planktonic feeding. Black chromatophores are uniformly distributed over the dorsal and lateral aspects of the body, but the posterior caudal region is free of pigment.

Larvae which are 5.0 mm in length show a relatively greater increase in body depth and thickness than in length. The distribution of pigment remains essentially the same as 4 days after hatching; however, the chromatophores increase in size and number. Larvae which are 10 mm in length display well differentiated dorsal, anal, and caudal fins. Pigment distribution remain the same as in earlier ontogenetic stages of development, but the number of chromatophores and quantity of pigment increase.

Malchoff (1993) found that larvae in the New York Bight ranged from about 2.0 to 7.0 mm TL. From his time-series collections, he developed a larval age-length relationship: $A = -1.877 + 8.535\,L$, where A = age in days, and L = length in millimeters.

The mean duration of the larval phase of tautog was reported to be 25.4 ± 3.4 (SD) days for an undefined area of the Northwest Atlantic (Victor 1986). Sogard *et al.* (1992) and Malchoff (1993), however, reported the larval phase to be only about 20 days in the New York Bight and Great Bay - Mullica River Estuary. Dorf (1994) and Dorf and Powell (1997) reported the same period for Narragansett Bay, but it can be less (Schroedinger and Epifanio 1997).

JUVENILES

After the larval phase, settlement to benthic habitats occurs and an epibenthic lifestyle begins. The transition between the larval pelagic and juvenile demersal stages is evident in the otolith sagitta; inner increments are higher in contrast, darker in appearance, and more circular than those outside the transition area (Sogard *et al.* 1992).

At 30 mm TL, the fish are generally considered to be juveniles and show the general morphological characteristics of adults, except for their often greenish background color. The black chromatophores form heavily pigmented areas which give the body a transversely banded appearance as well (Kuntz and Radcliffe 1918).

The fish lay down their first visible bone annulus in the spring of the following year, usually in May. For example, in the opercular bone, this is evident as a sharp transition from a translucent to an opaque zone. Annuli of this type are formed on bony structures each spring (Cooper 1967).

ADULTS

Most male tautog mature by age 3, females by age 4 (Chenoweth 1963; Cooper 1967; Stolgitis 1970; Briggs 1977; Hostetter and Munroe 1993). Chenoweth (1963) observed that 55% of males were already mature by age 2, and 90% were mature by age 3, in Rhode Island. This latter age corresponds to a tautog length of about 26 cm, as determined by Hostetter and Munroe (1993). The latter authors found that few females were mature by age 2, but 80% were mature by age 3. Precocious females, approximately 2 yr old, were observed in New York waters (Olla and Samet 1977) and in Mt. Hope Bay, (Massachusetts) (Hostetter and Munroe 1993).

The influence of heavy fishing mortality on the genetic selection process for sexual maturity is unknown at present; this pressure can favor the portion of the population with genes for early maturation and spawning, although with lower gamete production.

AGE AND GROWTH

LARVAE

Malchoff (1993) reported larval growth rates for this species to be 0.30 mm/day in the New York Bight. This rate is lower than a mean 0.75 mm/day, back-calculated rate reported for Narragansett Bay fish by Dorf (1994). Martin (1993) reported that larval growth rates varied with latitude and were directly related to water temperature.

JUVENILES

Sogard *et al.* (1992) used length-frequency progressions, otolith age - fish size comparisons, and direct measurements of growth in cage experiments to determine that YOY tautog grew at an average rate of about 0.5 mm/day during the summer in the Great Bay - Mullica River Estuary. The same rate was found in Narragansett Bay (Dorf 1994). In the Great Bay - Mullica River Estuary study, mean growth rates varied slightly among different methods of estimation and with habitat types where the fish were collected. Sogard *et al.* (1992) also found minor growth also occurred in other seasons. Martin (1993) reported that YOY grew up to 0.7 mm/day when fed mysids in the laboratory.

During the 2-3 yr of the juvenile phase of this species, annual growth is usually rapid (Cooper 1967). Annual growth is reported to increase progressively from northern to southern regions (Martin 1993). For example, in Narragansett Bay, Cooper (1967) reported first-year growth in tautog to be 60-62 mm. This was less than half the first-year growth of 134-146 mm by YOY tautog in southern Virginia waters (Hostetter and Munroe 1993). Tracy (1910), however, reported first-year growth to range between 72 and 288 mm in Rhode Island; the larger value is obviously questionable (Fritzsche 1978).

In Narragansett Bay and the Great Bay - Mullica River Estuary, the greatest annual growth increment, 200%, occurred during the second year for both sexes (Cooper 1967; Sogard *et al.* 1992). In southern Virginia waters, the greatest annual growth increment occurred in the first year, and the second year's growth was only a 30% increase (Hostetter and Munroe 1993). It has been hypothesized that the faster initial growth rates in southern waters reflect the longer duration of warmer water temperatures, which may provide optimal conditions for tautog growth during the first juvenile year, but for some reason not the second year (Sogard *et al.* 1992; Hostetter and Munroe 1993).

Sogard (1992) observed that the mean seasonal growth in length of juvenile tautog in New Jersey was higher in vegetation, but growth in mean weight was higher on bare sand. Growth rates were higher in sea lettuce beds than in eelgrass beds, and seemed to be directly related to prey density and not shelter type.

ADULTS

Although Cooper (1967) noted that Rhode Island females attained a slightly greater mean length than males (62 mm compared to 60 mm) during their first juvenile year, by age 3, as they became adults, males had faster annual growth rates. At age 7 in Rhode Island, the male tautog's mean length was 348 mm, while the female's mean length was 301 mm. Faster adult male annual growth rates were also found by Simpson (1989) in Long Island Sound. In southern Virginia waters, males also grew faster than females at all ages (*i.e.*, K = 0.090 for males compared to K = 0.085 for females[5]) (Hostetter and Munroe 1993).

Hostetter and Munroe (1993) found that tautog attained a relatively large size slowly, and that their growth varied seasonally. These authors reported that in southern Virginia's coastal waters, maximum somatic growth occurred after spawning, from July to December. Slower growth occurred from January to March because of decreased feeding associated with cool water temperatures and the fish's associated torpor condition in colder northern waters. In northern waters, this period of slower winter growth is also probably longer because these waters cool sooner and remain cold longer. In southern Virginia waters, the least somatic growth in adults occurred from March to June during gonadal maturation and spawning.

Mean annual growth rates in length were similar for tautog in northern and southern waters until about age 13, then growth rates decreased more rapidly in northern waters. For males in Rhode Island, annual growth increments decreased to less than 12 mm after age 12, and further declined to 2-4 mm after age 20. For females in Rhode Island, annual growth increments decreased to less than 11 mm after age 13, and to 3-4 mm after age 17 (Cooper 1967). In southern Virginia waters, increments in annual growth declined after age 13, but growth rates were nearly double those of tautog in northern waters (Hostetter and Munroe 1993). The von Bertalanffy growth equation for tautog from both areas support this finding: in northern waters, L = 506 mm for females and 664 mm for males (Cooper 1966), compared with L = 733 mm for females and 732 mm for males in southern waters (Hostetter and Munroe 1993).

Several studies reported variable length-weight relationships for whole and eviscerated tautog from Narragansett Bay to southern Virginia waters (Table 1).

Tautog are a relatively long-lived fish, with the oldest fish examined by the scientific community estimated to be a 34-yr-old male (Cooper 1967). A 91-cm (36.5-inch), 10.1-kg (22.5-lb) fish, caught off New York in 1876 and reported by Goode (1887), could have been older. Hostetter and Munroe (1993) reported that the world's record weight for the species is 10.9 kg (24 lb) for an 81.9-cm fish caught recently off Virginia; the authors estimated the fish to be about 30 yr old. Simpson (1989) suggested that males can live more than 30 yr, and females about 25 yr.

FEEDING AND DIET

FEEDING BY LIFE STAGE

Larvae

No specific data were found; larval tautog probably feed on small motile crustaceans in the water column such as small copepods [which were part of the diet of small juvenile (30-40 mm) tautog reported by Grover (1982) and Dorf (1994)] and other larval fish. D. Perry (pers. comm.[6]) reported some success in getting larvae to eat dried food.

Table 1. Reported length-weight relations for tautog. [W = weight (g); L = length (mm); W_o = weight (oz); L_i = length (inches); and (E) = eviscerated weight.]

Area	Sex	Relationship	Source
Rhode Island	male	Log W(E) = -4.357 + 2.776 log L	Cooper (1967)
	female	Log W(E) = -4.804 + 3.016 log L	Cooper (1967)
Long Island	both	Log W_o = -5.992 + 2.916 log L_i	Briggs (1969a)
New York Bight	male	Log W = -5.203 + 3.206 log L	Wilk *et al.* (1978)
	female	Log W = -5.444 + 3.230 log L	Wilk *et al.* (1978)
	both	Log W = -4.721 + 3.020 log L	Wilk *et al.* (1978)
Virginia	both	Log W = -4.632 + 2.979 log L	Hostetter and Munroe (1993)

Juveniles

The diets of juvenile tautog are discussed below by arranging the available information from north to south to best fit the gradual zoogeographical shifts in diet that occur on this axis. Dorf (1994) found the diets of juveniles in Narragansett Bay to consist of amphipods and copepods, with the copepods being mostly harpacticoids. Richards (1963) notes that YOY and 1-yr-old juvenile tautog in a sand-shell area of Long Island Sound ate pycnogonids (sea spiders), razor clams (*Ensis directus*), and decapod and amphipod crustaceans. Nichols and Breder (1926) also report "seaweed" as part of the diet of juvenile tautog in this area.

Grover (1982) found that both caprellid and gammarid amphipods and small copepods constituted 95% of the diet of YOY (31-71 mm TL) tautog in southern Long Island waters. Frequency of occurrence (FO) in the digestive tract was 98% for amphipods, 94% for copepods, 29% for polychaetes, and 25% for isopods. This diet indicated that juvenile tautog forage on benthic, as well as planktonic, prey. As they grow, juvenile tautog rely less on planktonic food resources and feed primarily on benthic prey, although the prey remain primarily crustaceans, such as decapods. The general form and location of the tautog's mouth suggest that benthic organisms would be a primary component of the adult's diet (Grover 1982). In Great South Bay (New York), 2-3 yr old tautog (105-206 mm) did not feed mostly on crustaceans throughout the year, but on blue mussels (Olla *et al.* 1975). This diet difference is partially consistent with the laboratory prey selection findings reported by Lankford *et al.* (1995) that juvenile tautog gradually shift their diet from small crustaceans (*e.g.*, amphipods) to small mussels as the fish grow to and beyond a length of about 120 mm. Mussels that were about half of their maximum size were primarily eaten.

In the Great Bay - Mullica River Estuary, Sogard (1992) found that copepods were the preferred prey, with a 78% FO, in 31-85 mm YOY fish. Amphipods were a close second in importance (FO = 75%), followed by other crustaceans (FO = 40%), polychaetes (FO = 5%), and mollusks (FO = 5%). Festa (1979) reported that isopods (*Idotea* sp. and *Erichsonnella* sp.), xanthid (mud) crabs, and (to a lesser degree) several species of amphipods were the prey of 60-160 mm tautog from Great Egg Harbor (New Jersey). He also reported that larger subadult tautog, greater than 200 mm in length, ate predominantly xanthid crabs.

In eelgrass beds of Chesapeake Bay, juvenile tautog (90-170 mm) fed on penaeid shrimp, blue crabs (*Callinectes sapidus*), isopods, grass shrimp (*Paleomontes* sp.), and detritus (Orth and Heck 1980).

Lindquist *et al.* (1985) reported that mytilid mollusks and gammarid and caprellid amphipods dominated the diets of 22 tautog (95-270 mm) examined from rock jetties near Wrightsville Beach (North Carolina); they also noted the occurrence of algae in the stomachs. Troutman (1982) reported that the dominant prey in these North Carolinian diets varied seasonally, and included a venerid clam. MacKenzie (1977) also reported juvenile tautog to prey on a juvenile venerid, the northern quahog (*Mercenaria mercenaria*).

Adults

Adult tautog are durophagous and feed chiefly on blue mussels and other shellfish throughout the year. Barnacles (*Balanus* sp.), brachyuran crabs, hermit crabs, sand dollars, (bay?) scallops, amphipods, decapod shrimp, isopods, lobsters, and probably nereid polychaetes were reported by Bigelow and Schroeder (1953) to be part of the tautog's diet. Consistent with this broad summary, Osburn (1921) reported that "tautog feed on bryozoa along with other hard shelled organisms to which it was attached," and Verrill (1873) reported that tautog fed on benthic tunicates. Bleakney (1963) reported tautog from Nova Scotia to feed not on blue mussels, but on horse mussels (*Modiolus modiolus*) and periwinkles (*Littorina littorea*). Linton (1899) and Scott and Scott (1988) also listed gastropods in the tautog diet. Auster (1989) included the softshell (clam) (*Mya arenaria*) as a diet item.

South of Cape Cod, examination of digestive tracts of tautog in New York estuarine waters showed that 70% of the fish contained 78-100% mussels by volume (Olla *et al.* 1974). Steimle and Ogren (1982), however, found that Atlantic rock crabs (*Cancer irroratus*) constituted greater than 78% by volume of the diet of tautog collected from a coastal New York artificial reef. They also found that sand dollars (*Echinarachnius parma*) (38%), Atlantic rock crabs (28%), and blue mussels (9%) dominated the tautog diet on a volumetric basis at a northern New Jersey artificial reef. Festa (1979) reported that xanthid crabs dominated the diet of small adults (about 300 mm) in Great Egg Harbor Estuary.

Unpublished data collected by the senior author showed that besides blue mussels (54%), *Metridium* anemones (11%), Atlantic rock crabs (5%), and razor clams (4%) dominated overall definable prey in 358 tautog stomachs, by volume, in a 1990-94 Delaware Bay artificial reef study; these fish ranged from 110 to 580 mm, with a mean length of 320 mm. The proportional composition of the diet varied among years (*e.g.*, the mussels varied from 13 to 87% of total diet volume). Various small mollusks, barnacles, decapod crabs, and other crustaceans of suitable size were reported also to be the food of this species in the Chesapeake Bay area (Hildebrand and Schroeder 1928).

Richards (1992) confirmed Smith's (1907) note that tautog will eat commercially important Jonah crabs (*Cancer borealis*) and small American lobsters (*Homarus americanus*). Predation on these species occurred, however, when they were without shelter in aquaria.

Chao (1973) reports that the cunner lacks a well defined stomach, which is a characteristic of most labrids, including tautog. The tautog's gastro-intestinal tract is semitransparent and remarkably thin for containing the broken shells of its prey as it moves through to evacuation.

FEEDING BEHAVIOR

Tautog feed throughout the daytime. Beginning soon after sunrise, tautog were reported to leave their shelters to forage for food, which involved scan-and-pick feeding (Briggs 1969b; Olla *et al.* 1975). This activity sometimes took the adults up to 500 m from their homesites (Wicklund 1966; Olla *et al.*1974). Bigelow and Schroeder (1953) observed that tautog followed the flood tide up above low water levels, around ledges, to prey on mussels in the intertidal zone, and returned to deeper water during the ebb tide. Feeding continued to evening twilight (Olla *et al.* 1974). Olla *et al.* (1974) reported that tautog required about 8 hr to process and evacuate food.

In laboratory studies, Olla *et al.* (1974) observed that tautog grasped mussels with their anterior teeth and tore them from their attached substrate with a lateral shaking of the head. Small prey were swallowed whole (Bigelow and Schroeder 1953), while larger, hard-shelled ones were crushed by pharyngeal teeth before swallowing (Bigelow and Schroeder 1953; Olla *et al.* 1974). The anterior teeth were not involved in the crushing process (Olla *et al.* 1974, Liem and Sanderson 1986). It was observed that the tautog's mouth can accommodate larger clumps of mussels than the pharyngeal teeth can process efficiently. In this case, the fish ingests and egests the clump from its mouth, separating it in the process into smaller, crushable sizes. The feeding and mastication methods of this species are specialized and typical of labrids and cichlids only (Liem and Sanderson 1986).

In the southern part of its range (*i.e.*, below New Jersey), the blue mussel, a dominant prey in colder waters, is at its warm-temperature limits and has wide variability in recruitment and abundance (Foster *et al.* 1994). Without strong periodic recruitment, mussel populations in these areas can be preyed upon by tautog to near extirpation, as reported for Virginia (Chee 1977; Chesapeake Executive Council 1994). This near extirpation creates a change in the prey field available to tautog in this habitat, and can cause at least some of the tautog population to seek alternate or better foraging areas. This change in prey field can be a factor in the local distribution of the population. (See the "Adults" subsection, "Differential Distribution" section of the "Distribution and Habitat" chapter.)

FACTORS AFFECTING FEEDING

Tautog find prey visually and were reported not to feed at night (Olla *et al.* 1974; Deacutis 1982). Neither do they actively feed in northern waters during the coldest part of the year (Cooper 1966; Curran 1992). In Narragansett Bay, Cooper (1966) observed that of 15 tautog, 13 had shrunken and emptied digestive tracts in winter. The other two fish had remains of Atlantic rock crabs in their stomachs. Curran (1992) found all feeding stopped in the closely related cunner (and probably tautog) when water temperatures reached the low levels that induce torpor and hibernation. Cunner, at least, survived up to 6 mo without food, using glycogen, lipids, and proteins stored in their livers (Curran 1992); tautog may do likewise.

In laboratory experiments, a decrease in feeding was observed with an increase in water temperature above certain levels. Tautog which had been acclimated to temperatures of 19°C and 21°C, respectively, decreased their ingestion of food, when water temperatures were increased to 28.7-33.0°C over a certain amount of days (Olla and Studholme 1975; McCormack 1976; Olla *et al.* 1978). McCormack (1976) also reported that it required up to 7 days for field-collected fish to begin feeding in laboratory aquaria. (For other environmental effects on feeding, see the "Habitat Modification and Loss" section of the "Natural and Human-Induced Environmental Factors" chapter.)

Tautog were observed to vary, to some extent, their feeding in association with their place in a group dominance hierarchy. In one laboratory study with three fish, the dominant fish of the moment ate the greatest amount of food, followed by the subordinate fish, in some order of rank (Olla *et al.* 1978). In a related tank study, McCormack (1976), however, found no difference in consumption of Atlantic surfclam (*Spisula solidissima*) meats between the dominant and subordinate individuals of paired 160-280 mm tautog.

Food intake in tautog may decrease during spawning. Bridges and Fahay (1968) reported possible courtship behavior of tautog in a laboratory study during which no spawning occurred. In this study, 1 day prior to courtship behavior, the male and female daily food (undefined) intake decreased from 40 to 1g. During courtship behavior, which lasted 2 wk, the 300-mm female ceased eating, but the 270-mm male increased food intake to 10 g/day. After courtship behavior ceased, the female resumed eating, but less than 10 g/day. The time period that this reduced level of feeding persisted, or if it changed, was not reported. It is possible that some of this behavior was an artifact of the fish's confinement in aquaria, as it has not been documented in the wild.

Deacutis (1982) found tautog did not have an acute sense of smell for detecting prey, compared to red hake (*Urophycis chuss*), and were hesitant to explore open bottom to find food they could not see.

BEHAVIOR

MIGRATION AND LOCAL MOVEMENTS

Many studies report limited, seasonal, onshore and offshore movements of this species. (See the "Differential Distribution" section of the "Distribution and Habitat" chapter.) Channels may be important pathways of migration into coastal areas for spawning and out again to deeper or offshore wintering areas (Cooper 1966). As noted previously, Briggs (1977) reported that part of the southern Long Island tautog population migrated to the area off northern New Jersey when water temperature declined in the late fall; Nichols and Breder (1926) called this movement "heavy." At a more local level, Merriman (1947) reported that small tautog do not move with the high-tide levels into intertidal areas; this contrasts with Bigelow and Schroeder's (1953) report of intertidal-associated movements of presumably adults for feeding on tidally submerged mussels, as noted earlier.

SCHOOLING

Some degree of schooling is thought to occur as tautog are reported to congregate during or just prior to spawning (Bigelow and Schroeder 1953; Cooper 1964; Stolgitis 1970). Briggs (1969b) believed that tautog also congregate into some type of a school before and during their movement to deeper water in the fall off New York. This is supported by laboratory studies where tautog schooling was observed when water temperatures declined to 6.3°C (Olla and Studholme 1975).

DAILY AND SEASONAL ACTIVITY LEVELS

In laboratory studies, tautog showed a high level of activity (*i.e.*, movement) within the first hour of daylight (Olla *et al.* 1978). This activity decreased toward mid-morning, when the fish rested on the sand or within shelters between bouts of activity (Frey 1963). Bigelow and Schroeder (1953) noted that when tautog were not feeding, they gathered in holes or crevices, being still or lying on their side, often grouped together, until a rising tide stirred them to activity (for intertidal feeding, presumably). In field investigations at night, Olla *et al.* (1974) found tautog to be inactive in a shelter of some type, and in a state of such low responsiveness that individuals were readily touched by divers. Curran (1992) suggested that this state represents true sleep in cunner (and probably in tautog), and can be for energy conservation.

Tautog in northern waters overwinter in a torpid state within shelter (Nichols and Breder 1926). Olla *et al.* (1974) observed small fish (less than 250 mm TL) in a torpid condition at water temperatures less than 6°C. Cooper (1966) observed adult tautog being dormant, either lying on their sides or in upright positions in crevices, at a water temperature of 7.5°C. In laboratory studies, tautog activity decreased as temperatures declined to 5.2°C, then tautog aggregated around shelters or burrowed under objects on the bottom (Olla *et al.* 1980). At water temperatures of 2.1°C or below, activity ceased and tautog remained in torpor. Curran (1992) considered this torpid state to be true hibernation in cunner. Emergence from torpor occurred when temperature increased to 4.0°C (Olla and Studholme 1975). In southern Virginia waters, tautog were observed to remain active despite water temperatures as low as 7°C (Adams 1993). In laboratory studies, young and adult tautog responded to an increase in temperature, from 19.1°C or 21.3°C to 28.7°C, with a decrease in aggressiveness and activity, and an increase in the tendency to aggregate (McCormack 1976; Olla *et al.* 1978). This lowered response to stimuli at temperature extremes was supported by the sound-detection-threshold experiments of Offutt (1971).

HIERARCHICAL DOMINANCE

In laboratory studies, a dominance hierarchy was observed among variably sized pairs or a group of tautog (Olla and Studholme 1975; McCormack 1976; Olla *et al.* 1978). In these studies, the larger, most aggressive or dominant fish caused a less aggressive, usually smaller subordinate to assume a submissive posture, tilting its dorsal surface toward the dominant fish at an angle. This behavior usually occurred within 1-3 m of the dominant male. Field studies have not confirmed these observations.

VOCALIZATION AND RESPONSE TO SOUND

Fish (1954) found that tautog produced deep thumping, grunting, or barking sounds, as well as sounds from crushing shells of their prey when feeding. The nonfeeding sounds were heard in aquaria when fish were startled or exposed to experimental electrical impulses, and were not thought to be produced commonly. The air bladder was thought to be involved in this sound production. The purpose of producing these sounds was unknown, but could be defensive. Parker (1910) reported that tautog avoided sources of loud sounds. Offutt (1971) used conditioned, cardiac responses to show that fish can respond to sound impulses.

COLOR MODULATION

Behre (1933) reported that small tautog responded to changes in light intensity and color by changes in their body color or shading. Absence of light reduced the intensity of body color, while high-intensity light enhanced the body's dark coloration. Differently colored light and sequential combinations of colored lights caused different responses in body coloration. These responses suggested to Behre some ability by tautog to distinguish colors or shading. Regan *et al.* (1982) reported that the photoreaction capacity of tautog was markedly different from its close, but shorter-lived relative, the cunner. No reason for this was suggested, however. McCormack (1976) reported that there were body color or shading patterns evident during the interaction between dominant and subordinate fish in an aquarium. Dominant fish often exhibited darker shading, and submissive fish paled, during confrontations. Mallet (1972) reports color changes from mottled-dark to pallid, gray-white as a stress response to hypoxia. (For other stress responses, see the "Hydrographic" subsection, "Habitat Modification and Loss" section of the "Natural and Human-Induced Environmental Factors" chapter.)

MUTUALISM

Although many tropical and some temperate wrasses (*e.g.*, European wrasse) clean external parasites from larger fish of other species (Darwall *et al.* 1992), this behavior has not been reported for any lifephase of tautog.

POPULATION STRUCTURE

SEX RATIO

Chenoweth (1963) noted that about 53% of the tautog he collected in Narragansett Bay were female. In northern Virginia waters, however, the slightly skewed sex ratio (0.86:1) was in favor of males (Eklund and Targett 1990). A significant deviation from a 1:1 ratio was also observed in larger fish by Hostetter and Munroe (1993), possibly because the older fish (greater than 18 yr old) were predominantly males (Cooper 1967; Hostetter and Munroe 1993).

AGE COMPOSITION

As noted previously for Narragansett Bay, the oldest male fish found by Cooper (1966) was estimated to be 34 yr, and the oldest female 22 yr. In southern Virginia waters, the oldest male fish collected was estimated to be 25 yr, and the oldest female 21, although the age of the oldest fish taken by rod and reel from Virginia waters was estimated to be approximately 30 yr (Hostetter and Munroe 1993).

In the early 1960s, 5- and 6-yr-old tautog were the most abundant age classes in the Narragansett Bay population (Cooper 1967). The recent average age for tautog in Virginia waters was 4 yr (Hostetter and Munroe 1993). In 1960s in Narragansett Bay, 79% of the tautog were less than 10 yr old (Cooper 1967). This population structure remained similar for Massachusetts to New York into the mid-1990s (Lazar 1995). This age structure is also similar to southern Virginia waters where 82% of the population was recently noted as being less than 10 yr old (Hostetter and Munroe 1993).

NATURAL AND HUMAN-INDUCED ENVIRONMENTAL FACTORS

PREDATORS

Perry (1994) reported from laboratory experiments that typical coastal copepods, such as *Acartia tonsa*, can prey upon newly hatched, yolk-sac tautog larvae. Bigelow and Schroeder (1953) reported the following fish species were known to eat juvenile or adult tautog: smooth dogfish (*Mustelus canis*), barndoor skate (*Raja laevis*), red hake, sea raven (*Hemitripterus americanus*) and goosefish (*Lophius americanus*). In analysis of 123 New York striped bass (*Morone saxatilis*) stomachs, one tautog was found in a greater-than-60-cm fish (Schaefer 1970). Striped bass were observed pursuing young tautog in the same general area at a later time (Olla *et al.* 1974). Zawacki (1971) reported that live small tautog were commonly used for surf fishing for striped bass on Long Island, suggesting that the bass were familiar with this prey. Schaefer (1960) reported that silver hake (*Merluccius bilinearis*) ate tautog in the "Mud Hole" off northern New Jersey. Wilk (1977) added bluefish (*Pomatomus saltatrix*) to the list of tautog predators. Dixon (1994) reported that toadfish (*Opsanus tau*) and longhorn sculpin (*Myoxocephalus octodecemspinosus*), small cryptic predators common in coastal waters, as well as larger YOY bluefish, preyed upon YOY tautog confined in aquaria. Other demersal piscivorous fish, such as conger eel (*Conger oceanicus*), summer flounder (*Paralichthys dentatus*), and various sharks, can be expected to prey upon small tautog. Although American lobsters share the same habitat with tautog, and are active at night when tautog are inactive, there are no reports of lobster predation on tautog.

It is also likely that diving or stalking piscivorous birds, such as cormorants, grebes, loons, herons, and egrets, also prey upon juvenile tautog in shallow estuarine or coastal areas during daylight and the warm seasons when the fish are outside their shelters (Whoriskey 1983). Bent (1919, 1922, 1923, 1926) noted that small estuarine fish were eaten by these birds, with labrids being specifically mentioned in the diets of the black-crowned night-heron (*Nycticorax nycticorax*) and the double-crested cormorant (*Phalacrocorax auritus*). Nichols and Breder (1926) noted a small tautog in the stomach of a red-throated loon (*Gavia stellata*). Another observation of this predation can be recorded, with an approximately 12-15 cm tautog being observed in the beak and swallowed by a cormorant near a rocky sea wall in Sandy Hook Bay (New Jersey) (personal observation by the senior author in July 1992). The relative importance of this predation on population structure, habitat use, and growth or mortality rates is unreported or unknown.

Humans as fishermen are also predators. Simpson (1989) estimated fishing mortality for a Long Island Sound population to be F = 0.12, and to be about equal per sex. He estimated natural adult mortality to be lower in males (M = 0.15) than females (M = 0.20) for this population.

COMPETITORS

Competition between tautog on the one hand and cunner, sheepshead (*Archosargus probatocephalus*), and American lobster on the other hand has been suggested because all four species use the same habitat and prey commonly on blue mussels, other small mollusks, and crustaceans, and because the latter three species have ranges that overlap that of tautog (Hildebrand and Schroeder 1928; Weiss 1970; Olla *et al.* 1975). Botton and Ropes (1989) suggest that horseshoe crabs (*Limulus polyphemus*) can consume large quantities of shellfish, including mussels, and thus may also be a competitor for food. Sea stars, such as *Asterias*, that prey heavily on mussels when they are available near the seabed, will compete trophically with tautog for this food resource too (Richards 1963). Other invertebrate predators of mussels, other shellfish, and barnacles can be substantial tautog trophic competitors when present in abundance. Species that eat copepods and decapod crustaceans should also be considered potential competitors of juvenile tautog for this essential prey resource (Dorf 1994).

Competition with cunner was thought to be restricted to May and June, after which cunner change their diet (Olla *et al.* 1975). In a laboratory study, cunner seemed to be aggressively territorial in excluding similarly sized juvenile tautog from certain habitats where they co-occur (McErlean 1963). The competition between tautog and cunner can only seriously exist with juvenile tautog; larger tautog use larger shelter and prey that are well beyond the range of cunner. Dixon (1994) suggests, however, that YOY cunner and tautog have differing, but overlapping, preferences in the location and use of their microhabitats that can reduce competition.

DEFORMITIES AND ABNORMALITIES

Briggs (1966) reported on a mature female, estimated to be 9+ yr old, that was pugheaded (*i.e.*, exophthalmic eyes, shortened and broadened maxilla, steep forehead, pushed-in snout, incomplete closure of jaws, extended mandibles). Several 250-300 mm tautog collected by hook-and-line in Delaware Bay had notable sigmoid vertical curvatures of their spines that compressed their body length (personal observation by the senior author in June 1994). No ecological nor environmental factor has been implicated in these deformities.

Tautog have been reported with small black spots within their muscle tissue. Microscopic examination found that these spots were actually associated with blood vessels, not the muscle tissue itself (I. Sunila, pers. comm.[7]). These spots were found to be deposits of dark pigment surrounded by fibrosis. This pigment originates from their high use of blue mussels as prey. These spots are considered harmless to the fish and to consumers.

PATHOGENS, PARASITES, AND BIOTOXINS

Tautog exposed to water in the apex of the New York Bight, near the then-active dredged material and sewage sludge disposal sites, were found to have antigenic responses to certain human enteric bacteria. These responses indicate that tautog are immunologically responsive to exposure to sewage bacteria (Stolen *et al.* 1983).

Finrot disease, thought to be caused by some microbial agent and anthropogenic stress, was not found on tautog in the New York Bight, although the disease was reported on 22 other common fish species in a study by Mahoney *et al.* (1973). However, a subsequent study did report, without supporting details, this condition on tautog (Murchelano and Ziskowski 1982).

Cooper (1964) observed that 10% of the tautog in his survey had scales that were either pitted or regenerated. He considered this pitting or regeneration to be due either to metacercaria of the trematode *Cryptocotyl* sp., or to physical abrasions. Laird and Bullock (1969) found no positive evidence of hematozoan parasites in New England and Canadian tautog. Cheung *et al.* (1979) reported tautog to be infected lethally with a coccidian intestinal parasite. Linton (1899) found immature trematode distomes to be encysted in abundance on the skin, fins, and eyes of a tautog collected off Woods Hole (Massachusetts), and also reported cestodes, nematodes, and trematodes to occur in cunner.

Perlmutter (1952) reported summer mortalities of "blackfish" along the ocean side of Jones Beach, southern Long Island. These mortalities were speculated to be related to a nearly concurrent, offshore bloom of the dinoflagellate *Noctiluca* sp. A number of other fish species were reported affected at this time as well.

HABITAT MODIFICATION AND LOSS

Structure

The dependence of tautog on specific coastal and estuarine habitats can make any degradation or loss of these habitats a serious threat to the tautog resource (Chesapeake Executive Council 1994). The loss of vegetated estuarine habitats can impair the habitat value of estuaries as juvenile tautog (and other species) nurseries. However, juvenile tautog have been observed using other habitats and a variety of substrates, including artificial (*e.g.*, pilings), that provide shelter or concealment and access to food.

(See the "Habitat Needs" section of the "Distribution and Habitat" chapter.) Rocky reef habitats used by tautog are very limited south of Long Island, and shipwrecks and other subtidal, manmade material placed in this area have expanded the distribution of this habitat into the common, open sandy habitats of the Middle Atlantic coasts (Hastings 1978; Lindquist *et al.* 1985). Tautog were collected around a sewer outfall under construction off southern Long Island; their peak abundance was during October through December when bottom water temperatures were 7-13°C (Briggs 1984). None of the tautog were found with any obvious pathological conditions or other possible effects from this physical habitat alteration and disturbance.

In the past, salvaging of certain metal shipwrecks or lowering of wreck heights if they might be navigation hazards, reduced the value of shipwrecks as tautog habitat. Before 1900, some wrecks off New Jersey were even dynamited to stun and collect reef fish (Smith 1892). Recently, the use of certain, heavy, "rock-hopper-roller," bottom trawl gear over many older, more fragile wrecks, lower-profile reefs, and mussel beds (DiLernia 1993) also threatens habitat quality, including the destruction of slow-growing colonies of the northern star coral (*Astrangia* sp.) which provide biogenic reef habitat for tautog.

Reef habitats that lose structural height are more prone to siltation (Rothschild *et al.* 1994) or burial by sediment movement. Briggs and O'Connor (1971) report that tautog avoided estuarine areas that were sandfilled, as from shoreline sand replenishment. The decline in the number, distribution, and structure of oyster beds (Rothschild *et al.* 1994) is another threat to the estuarine habitat needs of juvenile tautog and other species with similar habitat needs (Chesapeake Executive Council 1994). The creation of new "reef" habitat by the artificial reef programs of most states (McGurrin 1989) where the species occurs may be mitigating this habitat degradation to some degree.

Hydrography

Auster (1989) reported that current velocity can affect small-scale spatial distribution and can change foraging behavior in tautog and other species. The high hydrographic energy caused by passage of a hurricane was reported to disrupt juvenile tautog distributions in Narragansett Bay (Dorf 1994; Dorf and Powell 1997).

Howell and Simpson (1994) reported that tautog are not tolerant of dissolved oxygen (DO) concentrations below 2 mg/l, and prefer DO levels above 3 mg/l. This intolerance is supported by the cardiac and preliminary respiration response results of Mallet (1972) who showed that tautog are oxygen conformers under normal conditions, and that there is no inflection threshold. He also showed that these response rates increase with temperature and cadmium exposure, and that hypoxia responses can then be detected at higher oxygen concentrations. Mallet also observed several tautog stress responses to hypoxia. These responses included a change in mottled-dark body color to a pallid white-gray, attempts to jump out of experimental tanks, regurgitation of food, mucus secretion (especially around the gills), and milt ejaculation in ripe males. Baldwin (1923) reported some degree (undefined) of hypoxia "tolerance" at an unreported temperature for this species.

In a fish kill off the northern New Jersey coast in 1968, possibly caused by hypoxia, tautog were present in the area, but not found affected, although its smaller relative, the cunner, were found dead or dying (Ogren and Chess 1969). Tautog mortalities, however, were reported by commercial fishers and were observed on the beach during a major anoxia-hypoxia episode off New Jersey in 1976 (Azarovitz *et al.* 1979).

Smith *et al.* (1980) reported that high water temperatures were incrementally lethal in the laboratory for tautog gastrula-stage eggs: 10% mortality at 16.8°C after 26 min, 50% mortality at 21.3°C after 50 min, and 90% mortality at 31.4°C after 55 min. These authors suggested that tautog eggs enduring 15 min of a once-through cooling system of a power plant, with a 10°C temperature rise from a base temperature of 15°C, would suffer 10-50% mortality. Olla and Samet (1978) reported that tautog eggs incubated above 20°C resulted in embryos with anatomical deformities, and that those eggs incubated above 24°C resulted in increased mortalities. Normal embryonic development resumed when water temperature decreased to 20°C or lower. Laurence (1973) reported that tautog yolk-sac larvae ("prolarvae") may develop an energy deficit at water temperatures above 19°C because of increased metabolic rate and use of their yolk. This higher-than-normal rate of yolk use can result in smaller larvae just when those larvae need to start feeding on plankton. He believed these smaller larvae can be at a competitive disadvantage with larger siblings and other plankton predators, and may be less successful in obtaining suitable prey. This potential competitive disadvantage could affect survival or lead to slower larval growth rates and lowered capacity to reach protected inshore nursery habitats.

As noted in the "Eggs and Embryos" section of the "Development" chapter, the viability of tautog embryos has been reported to decline as the spawning season progresses. The cause of this decline is not known, but could be environmental, such as high temperatures (Olla and Samet 1978).

Pearce (1969) reported 31°C to be lethal to adult tautog in a 1-hr change from ambient during an aquarium study. McCormack (1976), though, reported that tautog do not lose equilibrium until about 33°C when water temperature was raised more gradually. At above-ambient temperatures, tautog behavior is altered; these alterations included changes in activity, dominance, habitat use, and posture that suggest stress (Olla and Studholme 1975; McCormack 1976); Olla and Studholme (1975) reported that the fish recover normal behavior when water temperatures return to a normal ambient range.

Olla *et al.* (1980) found tautog to survive in waters as cold as 1.9°C. The tautog's relative, the cunner, is reported to tolerate seawater temperatures slightly below 0°C (Green and Farwell 1971). Temperature extremes have been shown to reduce response thresholds in tautog (Liem and Sanderson 1986).

Tautog are sometimes killed if caught in shoal water by a quick drop to subfreezing air temperatures. This type of mortality was reported for 1841, 1857, 1875, and 1901 along Rhode Island and Massachusetts coasts (Bigelow and Schroeder 1953).

Water pH levels below 7.8 were reported stressful to this species, and prolonged exposure to these levels can result in death (Behre 1933).

Contaminants

Metals

Mears and Eisler (1977) determined concentrations of chromium, copper, iron, manganese, nickel, and zinc in tautog liver tissue. Their results suggested patterns of concentrations of these metals that were related to body length and sex. In males, chromium and copper concentrations decreased with length; in both sexes, nickel concentrations decreased. In both sexes, iron, manganese, and zinc concentrations were not related to body length. Hall *et al.* (1978) also examined 15 metals in this species (collection location not defined) and found low to average levels in muscle samples.

A recent study (National Marine Fisheries Service 1995) found muscle concentrations of nine metals (*i.e.*, silver, cadmium, chromium, copper, nickel, lead, zinc, arsenic, and mercury) to be well below U.S. Food and Drug Administration (FDA) action levels in tautog collected off Manasquan Inlet (New Jersey). Mercury levels in tautog were higher than those in bluefish, black sea bass (*Centropristis striata*), and summer flounder, but still well below FDA action levels.

Mallet (1972) reported that acute, sublethal (*i.e.*, 20 ppm) cadmium exposures and intoxication caused a change in tautog cardiac response to gradual hypoxia; this response included higher variability in heart rates and lowered rate-response sensitivity to oxygen levels, which suggest that the metal interferes with the cardiac regulatory mechanism for hypoxia. Lethal cadmium exposures (*i.e.*, 400 ppm) resulted in death in about 5 hr, but produced no significant histological damage to gills, liver, kidney, or intestine. In another study, Mallet noted that cadmium levels on gill tissue can be very high.

Studies of the effect of longer-term experimental exposure of cadmium on the closely related species, cunner, found that this metal did cause pathological changes to a number of organs and tissues (National Marine Fisheries Service 1974; MacInnes *et al.* 1977).

Organics

Tautog fillets from the Hudson River - Raritan Bay Estuary, collected between 1980 and 1985, were examined for Chlordane, DDT, DDD, DDE, dibenzoanthracine, Endine, Heptachlor, hexachlorobenzene, Lindane, and total polychlorinated biphenyls (PCBs). Concentrations of these organics were found to be low, relative to concentrations in some other fish species examined (New York State Department of Environmental Conservation 1987). This general result was confirmed in a recent study by the National Marine Fisheries Service (1995) which also found that all concentrations of PCBs and pesticides in tautog tissue were below an FDA action level of 2.0 ppm. Polycyclic aromatic hydrocarbons were largely undetected in the tautog tissue.

No information was found of the effects of exposure to organics on tautog. Several studies are available for cunner, however, the other labrid in the Northeast, the results of which could be similar for tautog. Payne *et al.* (1978) found little pathological effect in cunner from a 6-mo exposure to petroleum hydrocarbons. Payne and May (1979) further reported that cunner were able to metabolize petroleum hydrocarbons. Williams and Kiceniuk (1987) reported that a prolonged exposure to crude oil is required to suppress feeding by cunner, and that recovery can occur in a few weeks. Deacutis (1982) found, however, that tautog would not hesitate to consume hard clam or mussel meats that were contaminated with #2 fuel oil, and that tautog made little effort to avoid oil-contaminated feeding areas. An environmental threat to tautog can exist in petroleum-hydrocarbon-contaminated areas because bivalve mollusks, a common prey, cannot metabolize polycyclic hydrocarbons and can accumulate petroleum hydrocarbons to high levels and lose it slowly, maintaining a reservoir for continued induction (Vandermeulen and Penrose 1978).

Klein-MacPhee *et al.* (1993) reported larval tautog survived, but had significantly reduced feeding and growth, in an experimental exposure to starch blended with vinyl alcohol copolymers (*i.e.*, a biodegradable, potential substitute for plastic packaging). The low nutritional value of starch to carnivorous fish and a low DO concentration were suggested as being involved in these results.

ECOLOGICAL ROLES

The tautog is an important member of the resident, coastal, three-dimensionally structured habitat community in the Northeast's marine environment. Although the species' overall ecological role in the community has not been well studied, we do have some information, such as their predative and competitive interactions as discussed in the "Feeding and Diet" chapter and in the "Competitors" section of the "Natural and Human-Induced Environmental Factors" chapter, or we can suggest reasonable probabilities. These probable roles require more study, verification, and quantification, if possible. Some consideration should be given also to the species that could irreversibly replace tautog in the north-temperate-reef ecosystem, if tautog abundance is reduced to the point where the species loses its ability to compete for its former habitats and ecological role.

One example of this role is the species' predation on mussels and other encrusting and epifaunal organisms found in reef-like habitats, as discussed in the "Feeding and Diet" chapter. This predation can be important to the biodiversity of the invertebrate community of these habitats, and to the mesoscale landscape ecology of these habitats. Tautog grazing on dense sets of mussels and barnacles can help to reopen habitat space for renewed colonization by other species necessary for maintaining biodiversity and habitat patchiness. That is, the tautog may be a "keystone" species in the same manner as Paines' (1969) sea star was in defining the concept. Its occasional feeding on anemones, sponges, bryozoans, and other long-lived, relatively unproductive, surface-encrusting taxa can also open space for colonization by more productive species, such as mussels or oysters, that can also be used as food by other fisheries resources or be harvested by humans. The tautog's feeding can be important in controlling certain predators or competitors, such as crabs, gastropods, or tunicates, of juvenile harvestable shellfish. Heavy tautog predation on shellfish beds or other encrusting fauna can also increase the rate of recycling of nutrients, which accumulate in these filter-feeding organisms, back into the water. Its preference for mussels and shellfish can be a problem, however, if it feeds on shellfish populations that are cultured or harvested by humans.

Tautog will resort to shellfish prey from the surface of open habitats, such as small clams in muddy or sandy areas near and away from shelter, when epifaunal food resources of the shelter become scarce. This alternate use of off-reef prey can thus affect soft-bottom community ecology, as well, in the vicinity of a reef habitat with a tautog population.

By crushing the shells of their molluscan prey during feeding, tautog also contribute to available habitat types and use by altering a coarse, empty-whole-shell-rich habitat that would remain if mussels only died of adverse environmental conditions or age, to a finer, shell-hash-sediment habitat. The coarse shell or the shell hash creates different habitats used or favored by different invertebrate or post-larval fish and epifaunal species assemblages.

Some indirect effects of tautog populations on habitats, such as that of certain harvesting gear targeting tautog, are discussed in the "Structure" subsection, "Habitat Modification and Loss" section of the "Natural and Human-Induced Environmental Factors" chapter.

Although small tautog are preyed upon (see the "Predators" section of the "Natural and Human-Induced Environmental Factors" chapter), it does not appear that any predator is highly dependent on them as food, or that tautog serve as a key forage species. Their localized populations, slow growth, and relatively long life can provide stability to resident fish communities within which they occur.

RESEARCH NEEDS

This review shows that there is much known about the life history and habitat requirements of the tautog, although there are still many weak areas or gaps that need attention before it can be claimed that we know enough. Some of our knowledge of the species comes from laboratory studies; some effort must be made to confirm these controlled-environment results in the field before they are used, without question, in planning. In turn, some field observations need to be examined in the laboratory to define better the cause-and-effect relationships. The variations or differences in some results from multiple studies also need to be resolved, or the reasons for the differences understood.

This review suggests there are areas for which life history and habitat requirement information is nonexistent or weak for tautog. Some of these key areas that require special research attention are presented below, noting in many cases the implications for fishery resource and habitat managers:

1. Defining specific prespawning and spawning aggregation areas used by all major local populations, as well as defining the criteria for, or times of, use of these areas. It will be critical to protect these areas from degradation, and to protect these populations against excessive exploitation during their use of these areas.

2. Defining specific wintering areas used by juveniles and adults of all major local populations, as well as defining the criteria for, or times of, use of these areas. It will be critical to protect these areas from degradation, and to protect these juveniles and adults against excessive exploitation during their use of these areas.

3. Defining specific migration routes used by tautog to get to and from spawning and wintering areas. It will be critical to protect these migration routes from degradation, and to protect these fish against excessive exploitation during their use of these routes.

4. Defining sources of offshore eggs and larvae -- are the eggs and larvae from *in situ* sources, or have they been washed out of coastal spawning areas? If offshore eggs and larvae do come from coastal spawning areas, then weather may be a critical factor in recruitment.

5. Defining the extent, condition (*e.g.*, optimum, suitable), and trends of juvenile habitats. It will be critical to protect these habitats, or to stimulate their restoration or enhancement, if required.

6. Exploring possible genetic differences within the overall tautog population, noting their geographical distribution and trends, and relating them to recruitment, growth, and exploitation rates. Such knowledge of different/local genetic components within the overall population could support more effective regional management of this species.

7. Confirming that tautog, like cunner, “hibernate” in the winter, and if they do, determining in what areas, for how long, and with what special habitat needs. It would be important to understand such behavior, particularly as it might affect harvesting availability and vulnerability.

8. Defining susceptibility of juveniles to coastal contamination and contaminant effects. Such knowledge would be important for assessing and managing habitat/population damage.

9. Defining the role of prey type and availability in local juvenile/adult population dynamics. Such knowledge could help to explain differences in local abundance, movements, growth, fecundity, contaminant burdens, etc.

10. Defining larval tautog diets and prey availability requirements.

11. Better defining and quantifying the ecological role of tautog in coastal “reef,” or grass bed, communities.

ENDNOTES

1. NEFSC, Woods Hole, MA; October 1995.

2. South Carolina Wildlife and Marine Resources Commission, Charleston, SC; 1995.

3. NOAA-UMass Cooperative Marine Education and Research Program, Amherst, MA; May 1999.

4. NEFSC, Milford, CT; 1995.

5. The “K” term is a component of the von Bertalanffy growth equation: $l_t = L\,[1-e^{-K(t-t0)}]$, where l_t = length at age t, L = ultimate length associated with a particular stock or population, K = coefficient of growth, e = base of natural logarithms, and t_0 = age when length would theoretically be zero.

6. NEFSC, Milford, CT; 1995.

7. Bureau of Aquaculture, Connecticut Department of Agriculture, Milford, CT; 1998.

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