

WINTER FLOUNDER / *Pseudopleuronectes americanus* (Walbaum 1792) /

Blackback, Georges Bank Flounder, Lemon Sole, Rough Flounder / Bigelow and Schroeder 1953:276-283

Description. Body oval, about two and a quarter times as long to base of caudal fin as it is wide, thick-bodied, and with a proportionately broader caudal peduncle and tail than any of the other local small flatfishes (Fig. 305). Mouth small, not gaping back to eye, lips thick and fleshy. Blind side of each jaw armed with one series of close-set incisor-like teeth. Eyed *side* with only a few teeth, or even toothless. Dorsal fin originates opposite forward edge of upper eye, of nearly equal height throughout its length. Anal fin highest about midway, preceded by a short, sharp spine (postabdominal bone). Pelvic fins alike on both sides of body, separated from long anal fin by a considerable gap. Gill rakers short and conical. Lateral line nearly straight, with a slight bow above pectoral fin. Scales rough on eyed side, including interorbital space; smooth on blind side in juveniles and mature females, rough in mature males when rubbed from caudal peduncle toward head. An occasional large adult female may also be rough ventrally.

Meristics. Dorsal fin rays 59-76; anal fin rays 44-58; pectoral fin rays 10 or 11; branchiostegals 7; lateral line scales 88-100; gill rakers 7 or 8 on lower anterior arch; vertebrae 36 (Norman 1934; Scott and Scott 1988).

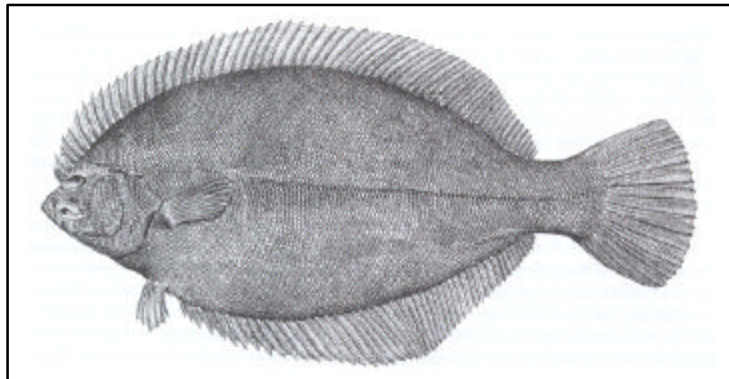
Color. Winter flounder, like other flatfishes, vary in hue according to the bottom on which they lie, but as a rule they are the darkest of the Gulf of Maine flatfishes. Large ones are usually some shade of muddy or slightly reddish brown, olive green, or dark slate above, sometimes almost black. They vary from plain or more or less mottled to definitely marked with smaller and larger spots of a darker shade of the general ground tone. There usually is a wide variation in this respect among any lot of flounders. Fish caught on Georges Bank tend to have a redder hue than those caught inshore.

The blind side is white, more or less translucent toward the edge, where there is often a faintly bluish tinge; the lower side of the caudal peduncle is yellowish in some specimens and pure white in others. Dorsal and anal fins are usually tinged with pink, red, or yellow on the eyed side; the pelvics and pectorals of the eyed side are the general ground tone, but their mates on the blind side are pure white. Small fish are usually paler and more blotched or mottled than large ones.

Various color abnormalities have been recorded, for example, fish that are partially white on the eyed as well as on the blind side (Lux 1973), and it is not uncommon to see specimens with dark blotches on the blind side. In fact, one-third of the fish caught near Providence during the winter of 1897-1998 were these "black-bellies," as fishermen called them (Sherwood and Edwards 1901).

Winter flounder change color to some extent to match their surroundings, usually being very dark on mud and pale on bright sand bottoms, but field experience suggests they have less control than summer flounder over shade and pattern. Pattern related responsiveness of melanophores is neurally controlled and xanthophores are regulated by the pituitary. An overview of color-related changes is given in Burton (1998).

Size. The largest winter flounder on record from inshore was 57.8 cm long (Scattergood 1952). Bigelow and Schroeder handled one



Georges Bank fish of 63.5 cm, weighing 3.6 kg. The NEFSC groundfish bottom trawl survey collected two 64-cm females, one on 22 October 1986 at 42°67' N, 67°32' W and a second on 15 April 1997 at 41°01' N, 68°25' W (R. Brown, pers. comm., 25 Sept. 1998). Port samplings of commercial catches by NMFS since 1964 have recorded at least six winter flounder of 67 cm TL. Fish longer than 46 cm or heavier than 1.4 kg are unusual inshore, most being 31-38 cm and 0.7-0.9 kg. They grow larger on Georges Bank, where many fish of 2-3 kg are taken.

Distinctions. Winter flounder are easily separable from yellowtail by the fact that the lateral line is nearly straight, the dorsal profile of the head is less concave, the snout is blunter, the eyes farther apart, there are fewer fin rays, and the fins are less tapered in outline. The most obvious difference between winter flounder and smooth flounder is that winter flounder have more anal fin rays. They differ from witch flounder in that they have only two-thirds as many dorsal rays, they lack the mucous pits that are conspicuous on the left (blind) side of the head of witch, and the tail is proportionately much larger.

Taxonomic Remarks. Winter flounder show some tendency to break up into local races based on the number of fin rays and the size to which the fish grow. The most interesting of these races, from the fisheries standpoint, is the population on Georges Bank, for flounder there tend to grow larger than they do inshore. This fact was first brought to the attention of scientists in 1912, when some of the large flounder from Georges Bank were received by the Bureau of Fisheries and made the basis of a new species, *Pseudopleuronectes dignabilis* Kendall (1912). Kendall felt that the greater number of dorsal and anal fin rays, color, larger size, and different spawning season merited species status. Bigelow and Schroeder concluded that it was just a larger more rusty brown local race of winter flounder. Lux et al. (1970) counted dorsal and anal fin rays on winter flounder from inshore waters off Massachusetts north and south of Cape Cod and from Georges Bank. They then compared historic water temperature records during winter flounder spawning seasons and found them to be higher on Georges Bank. Since environmental conditions influence phenotypic expressions of traits, including fin ray numbers, growth rates, and spawning time, differences in water temperatures might account for the differences in the Georges Bank stock.

Habits. Winter flounder range up into brackish water of river mouths and estuaries and have even been caught in the Susquehanna River, tributary to Chesapeake Bay; in essentially freshwater. They are plentiful at 18-37 m in Cape Cod Bay; Stellwagen Bank, and around Boon Island. Few, if any are caught deeper than this in the inner parts of the Gulf, but in the Bay of Fundy they are taken on soft bottom down to 55-92 m in winter. On Georges Bank they are taken between 46 and 82 m; 143 m is the deepest definite record (McCracken 1954). There appears to be an ontogenetic shift in depth distribution, with larger and older fishes inhabiting deeper water.

Typical inshore habitat consists of muddy sand, especially where this is broken by patches of eelgrass. Winter flounder are also distributed over cleaner sand, on clay; and even on pebbly and gravelly ground. Populations on the offshore banks (Georges Bank and Nantucket Shoals) are on hard bottom. When fish are on muddy bottom, they usually lie buried, all but the eyes, working themselves down into the mud soon

after settling on the bottom. Flounder that live on the flats usually lie motionless over the low tide and actively search for food during flood tide. Tyler (1972) observed that they entered the intertidal zone in the Passamaquoddy Bay region with the rising tide, occupied the area for up to 8 h, then moved back to the sublittoral zone 2.5-0.5 h before the next low tide. Small (4-15 cm) and large (25-49 cm) flounder moved with the same synchrony; intermediate flounder did not move into the intertidal area. These may be responses to light, since intermediate-sized flounder in laboratory and field situations preferred lower light intensities than small flounder or mature ones (McCracken 1963).

Local physical conditions appear to determine inshore distribution patterns, whereas offshore movements appear to be associated with extreme summer and winter conditions. In general, in summer months adult winter flounder stay in the shallow shore zone when water temperature is not excessive and food availability is adequate. If these conditions are not met, they may move into deeper channels or offshore, or may take evasive action (see the discussion under temperature tolerance). In the fall, as gonads ripen, adult winter flounder remain in or move into shallow water to spawn in southern locations in winter and northern locations in spring. During winter in the southern parts of their range they remain or move into shallow water to spawn, whereas in northern regions they remain inshore in protected areas and move offshore in exposed areas to avoid turbulence and drifting pack ice (Van Guelpen and Davis 1979). Winter flounder in deeper waters such as Georges Bank remain at these depths year-round.

The normal distribution of winter flounder covers a wide range of temperatures in one season or another: a minimum close to the freezing point of saltwater around Newfoundland, in Nova Scotian waters, and in the Gulf of Maine in late winter; a maximum of about 18°-19°C in shallow water in the southwestern part of the Gulf in summer; and 20°-21°C in the southern part of the range.

Lethal temperatures appear to be -1.4°C (Duman and De Vries 1974b) and 19.3°C. Winter flounder often recover from cold shock, but never from heat shock (Hoff and Westman 1966). Their blood contains an AFP (antifreeze protein) that helps protect them against freezing (Duman and De Vries 1974b, 1976). This protein is produced seasonally; and the cycles differ in populations from different geographical areas (Fletcher and Smith 1980). Both shorthorn sculpin and winter flounder secrete AFP into the blood serum, which serves to depress the freezing temperature of their

extracellular fluid and both produce skin-type AFPs that act as the first line of defense against freezing (Low et al. 1998). Winter flounder bury in sediment when water temperatures are below 0°C and ice crystals are present in the water but may succumb to anchor ice in winter if overtaken in very shoal water in a severe freeze. Divers observing flounder in Great South Bay; Long Island, where bottom temperatures ranged from 17° to 24°C reported that flounder were active up to 22°C and became inactive at 23°C. Temperatures measured 50-60 mm below the sand were 2°-3°C below ambient (Olla et al. 1969), so the flounder could avoid the heat by burying themselves. If they are trapped in shallow enclosed bays they can perish by the thousands during spells of very hot summer weather, as happened in Moriches Bay; Long Island, in 1917, when temperatures rose to about 30°C (Nichols 1918).

Winter flounder are sensitive to dissolved oxygen (DO) concentrations lower than 3 mg.liter⁻¹. They were present in significantly lower numbers in Long Island Sound, where the DO concentration was 2-2.2 mg.liter⁻¹, and showed reduced lengths at DO concentrations higher than 2 mg.liter⁻¹. There was a 4-cm difference in mean lengths between fish taken between concentrations less than 2 mg.liter⁻¹ and greater than 5 mg.liter⁻¹ (Howell and Simpson 1994). Although this might indicate a sorting by size-class differential to DO, winter flounder growth rates in the laboratory were twice as high in fish held at high DO (6.7 mg.liter⁻¹) than in those held at low DO (2.2 mg.liter⁻¹) and reduced at fluctuating levels of DO compared to high levels (Bejda et al. 1992). It has long been believed that winter flounder are among the most stationary fishes, apart from seasonal movements of the sorts just mentioned and a general tendency for the young that are produced in bays and estuaries to work offshore as they grow older (Perlmutter 1947). This essentially stationary nature has been demonstrated by extensive marking experiments in Long Island Sound, along southern New England, and on the coast of Maine: about 94% of the recaptures were made in the general areas where the fish had been tagged (Lobell 1939; Perlmutter 1947). In a 10-year tagging study at 21 locations off Massachusetts (Howe and Coates 1975), winter flounder showed the following movements: north of Cape Cod they were localized and confined to inshore waters and south of Cape Cod they were seasonally dispersed in a southeast direction with little mixing between Georges Bank and inshore areas. These movements appear to be related to water temperature. In Passamaquoddy Bay, mature winter flounder leave the shore zone only in areas where temperatures rise above 15°C (McCracken 1963). This movement is restricted to depths at which the temperature does not go below 12°C. They return to the shore zone in fall after the temperature falls below 15°C. In spring, both immature and mature fish are found along the shore, with spawning fish concentrated in shallow water where the temperature has warmed to 3 o-4 . In the southern Gulf of St. Lawrence, winter flounder move into the Miramichi estuary during October and November and remain there until spring (Hanson and Courtenay 1996). Thus the population consists of many independent localized stocks inhabiting bays and estuaries along the coast, with fish tending to scatter from population centers, although a few may move considerable distances.

Food. Adult winter flounder are limited by their small gape to a diet of small invertebrates and, rarely, fishes such as sand lance. Principal

stomach contents of 1,746 winter flounder (Bowman et al. 2000) included polychaetes (35.6% by weight), anthozoans (33.4%), and amphipods (6.7%). Other food items included shrimps, small crabs, and other crustaceans; ascidians; holothurians; squids; and bivalve and univalve mollusks. They often break off clam siphons that protrude from the sand. Feeding habits, with a comprehensive list of food organisms found in their stomachs, were summarized by Klein-MacPhee (1978). More recent studies of offshore fish indicate they eat more hydrozoans and anthozoans than inshore fish (Langton and Bowman 1981; Bowman 1988; Bowman et al. 2000). Frank and Leggett (1984) described the importance of capelin eggs in the diet of winter flounder from Conception Bay, Nfld.

Winter flounder are sight feeders and are diurnally active in both inshore and offshore waters (Pearcy 1962; Bowman 1988). At night they lie flat, heads resting on the bottom and eye turrets retracted, becoming active at sunrise. While feeding, a winter flounder lies with its head raised off the bottom and 12-17 dorsal fin rays braced vertically into the substrate. The left pelvic fin and several anal fin rays are used to support the head. Eye turrets are extended and the eyes move independently of one another. After sighting prey, the fish remains stationary; pointed toward the target, and then lunges forward and downward to seize the prey. Debris is expelled from the right gill covering. The fish then resumes the feeding position. If no food is sighted it swims to another location less than a meter away (Olla et al. 1969).

Daily ration estimates in the field vary from 1.27% body weight per day for a spring population from a Rhode Island salt pond (Worobec 1984), to 1.3-1.5% for a late-fall population from Georges Bank (Huebner and Langton 1982), to 1.77% for a spring population from Passamaquoddy Bay (MacDonald and Waiwood 1987).

Diatoms are the first food larvae take after yolk-sac absorption (Sullivan 1915; Pearcy 1962; and Klein-MacPhee, unpubl. data). Later, they feed on rotifers, tintinnids, and invertebrate eggs and finally on bivalve and polychaete larvae, copepod nauplii, and copepodites. Newly metamorphosed juveniles eat small isopods, amphipods, polychaetes, other crustaceans, annelids, and mollusks (Linton 1921; Pearcy 1962). With a progressive increase in size, young winter flounder tend to prefer larger prey organisms (Pearcy 1962; Richards 1963b; Mulkana 1966).

Predators. Winter flounder were found in stomachs of 11 species of fishes in the NEFSC food habits survey, of which four species had multiple occurrences: Atlantic cod, spiny dogfish, goosefish, and winter skate, in order of number of occurrences (Rountree 1999). Other known fish predators include little skate, smooth dogfish, hakes (spotted, white, and silver), sea raven, striped sea robin, striped bass, bluefish, and wrymouth (Willey and Huntsman 1921; Dickie and McCracken 1955; Derickson and Price 1973; Bowman and Michaels 1984; Manderson et al. 1999; Rountree 1999; Bowman et al. 2000). They are also eaten by harbor, harp, and gray seals (Fisher and Mackenzie 1955; Seizer et al. 1986; Bowen et al. 1993), and osprey (Scott and Scott 1988). Young winter flounder are eaten by blue heron and cormorant (Tyler 1971b), sand lance and moon jellies (Grove 1982), and toadfish and summer flounder (Pearcy 1962).

Parasites. Winter flounder are host to a wide variety of parasites (summarized by Klein-MacPhee [1978] and Margolis and Arthur [1979]): 7 species of protozoans, 2 myxosporidians, 18 trematodes, 5

cestodes, 13 nematodes, 6 acanthocephalans, 4 branchiurans, 4 copepods, and an isopod.

The microsporidian *Glugea stephani* is a common parasite that primarily infects the intestinal wall and pyloric caeca (Stunkard and Lux 1965). The infection is temperature dependent (above 15°C) and probably enters the host by way of a crustacean vector (Takvorian and Cali 1981, 1984). It can be fatal, especially in young-of-the-year; it also causes a decline in immunoglobulin levels and suppresses the host's immune response to other antigens (Laudan et al. 1987).

Breeding Habits. Winter flounder breed in the winter and early spring, spawning from January to May (inclusive) in New England. Spawning activity peaks during February and March south of Cape Cod and in the Massachusetts Bay region, but later along the coast of Maine. Near Boothbay; spawning commences in early March and continues until mid-May; with peak egg deposition occurring in early to mid-April (Bigelow and Schroeder). Spawning occurs earlier in the southern part of the range: November to April in the Indian River Bay; Del. (Fairbanks et al. 1971). On Georges Bank, the timing of spawning is unclear but it has been reported to take place in April and May (Bigelow and Schroeder).

Spawning occurs in inshore waters at close to minimal seasonal water temperatures: 00 to 1.7°C in the Woods Hole region, 0° to 2.8°C near Gloucester, and -0.5° to 1.7°C near Boothbay. Most egg deposition occurs before the water has warmed above 3.3°C, with about 4.4° - 5.6°C as the maximum for any extensive spawning in the inner parts of the Gulf of Maine. Spawning on Georges Bank occurs at higher water temperatures, ranging from about 3.3°C to perhaps 5.5°C.

Winter flounder spawn on sandy bottom and algal mats (Anonymous 1972; Grove 1982) often in water as shoal as 1.8-5.4 m, but as deep as 45-72 m off Georges Bank. Most eggs are deposited at salinities of 31-32.3 ppt in the inner parts of the Gulf to somewhere between 32.7-33 ppt on Nantucket Shoals and Georges Bank. Estuary spawning occurs in more brackish water, in salinities as low as 11.4 ppt near Woods Hole.

Winter flounder in the New York region mature at age 2 for males and age 3 for females, when they are 20-25 cm TL (Perlmutter 1947). There is a clinal gradient in maturity with later maturation occurring in more northerly latitudes, at age 3 for females and males south of Cape Cod, age 3.3 for males and 3.5 for females north of Cape Cod, and 6 for males and 7 for females in Newfoundland (Kennedy and Steele 1971). Maturity appears to be a function of size rather than age. The Georges Bank stock has a mean age of 1.9 years for both sexes (O'Brien et al. 1993). Maturation of winter flounder on the Scotian Shelf and in the southern Gulf of St. Lawrence was found to be highly variable from year to year (Beacham 1982) and large numbers of nonreproductive individuals were found in any given year (Burton and Idler 1984). This appears to result from restricted feeding prior to and immediately subsequent to the current spawning period, which indicates a nutritionally sensitive critical period (Burton 1994). There is a 2- to 3-year cycle in oocyte maturation (Burton and Idler 1984). Individual females produce an average of 500,000 eggs annually, but 3,329,000 were taken from a 5-year-old (40-cm) fish (Topp 1968).

Sex ratios tend to favor males, especially older ones, but vary with the population examined. Ratios were 7:3 female to male in Green Hill Pond, R.I. (Saila 1961), 3:2 in Narragansett Bay (Saila 1962), 3:1 on fishing grounds south of Rhode Island and Massachusetts (Lux

1969), 2.3:1 in Massachusetts (Howe and Coates 1975), and 1:1 in Long Pond, Nfld. (Kennedy and Steele 1971). Explanations for this vary from catch selectivity for larger fish, which favors larger, faster-growing females (Saila 1962) to higher mortality rates for males (Witherell and Burnett 1993).

Winter flounder migrate into shallow water or estuaries and coastal ponds to spawn, and tagging studies show that most return repeatedly to the same spawning grounds (Lobell 1939; Saila 1961; Grove 1982). Winter flounder are batch spawners. Continuous observations in a large research aquarium monitored their behavior during and after the spawning season. Fish spawned over a 60-day period, with an average of 40 spawns per female and 147 spawns per male. Males initiated all observed spawning events, which occurred throughout the night, but primarily between sunset and midnight. Spawning by one pair frequently elicited sudden convergence and spawning by secondary males; consequently, strictly paired spawning was uncommon. Male and female activity patterns were almost entirely nocturnal during the reproductive season but became increasingly diurnal during the postspawning season. Field and laboratory results indicate that male spawning strategy is adapted to maximize the number of eggs fertilized. There is probably high genetic diversity in the offspring from any one female, owing to frequent spawning and to multiple males participating in individual spawning events (Stoner et al. 1999).

The pattern of sperm release and changes in sperm quality were investigated throughout the normal spawning season of male winter flounder caught in Conception Bay. Whereas a lengthy period of spermiation, lasting about 6 months (December-July), can be detected in some males, the major period for sperm release was from May to July in the summer spawning season. By late July, sperm production fell rapidly along with a notable deterioration in sperm motility (Shangquan and Crim 1999).

Early Life History. This species is peculiar among Gulf of Maine flatfishes in that their eggs are not buoyant but sink to the bottom, where they stick together in clusters, usually so closely matted that individual eggs are forced into irregular outlines. They are 0.74-0.85 mm in diameter, and newly shed eggs have no oil globule. Eggs vary in color, with most pale to bright yellow, but some are pink to salmon-colored (pers. obs.). A description of developmental events is given in Martin and Drewry (1978).

Incubation occupies 15-18 days at a temperature of 2.8°- 3.3°C, which is about what they encounter in nature. Young larvae, which are about 3-3.5 mm long at hatching, are marked by a broad vertical band of pigment cells that subdivides the postanal part of the body; a characteristic feature; the end of the gut is also heavily pigmented. In water of about 3.8°C larvae grow to 5 mm in length, and the yolk is absorbed in 12- 14 days. Vertical fin rays begin to appear 5-6 weeks after hatching, at a length of about 7 mm, and the left eye has moved upward by then until about half of it is visible above the dorsal outline of the head, while the whole left eye shows from the right side and the fins are fully formed in larvae of 8 mm. Metamorphosis continues rapidly. The left eye moves from this position to the right side of the head, pigment fades from the blind side, the eyed side becomes uniformly pigmented, and the little fish now lies and swims with the blind side down, its metamorphosis complete when it is only 8-9 mm long.

The youngest larval stages are identifiable as winter flounder by the pigment bar just mentioned. They are distinguished from smooth flounder by the lack of pigment in the eyes of yolk-sac larvae and the presence of internal pigment spots over the notochord in larvae larger than 3.2 mm. The presence of dark pigment cells on the fins of yolk sac preflexion and flexion larvae, and a lower snout to anus length-standard length ratio (Laroche 1981). After the fin rays appear, the winter flounder's small mouth separates them from any of the large-mouthed flounders; their short, deep body; combined with small number of fin rays, separates them from witch; and the number of fin rays marks them off from yellowtail. Winter flounder also complete metamorphosis at a smaller size than either of these other small-mouthed flatfishes. A large series of larvae from newly hatched through metamorphosis is illustrated in Laroche (1981).

Rate of larval development is governed by temperature, occupying 2.5-3.5 months, and larvae that hatch later may exhibit compensatory growth. Average age at metamorphosis is 59.5 days but may vary by as much as 25 days. Larvae that metamorphose late do so at a larger size. Length at metamorphosis is significantly less variable than age at metamorphosis and both length and age at metamorphosis are positively correlated (Chambers and Leggett 1987).

Larvae have been taken in bays, estuaries, and salt ponds from Delaware to Newfoundland (Frank and Leggett 1983). The larvae are less at the mercy of the tide and current than other Gulf of Maine flatfishes, for they have been described as alternately swimming upward then sinking (Percy 1962), instead of remaining constantly adrift near the surface, as the larvae of most of the flatfishes do at a corresponding stage in their development. Larval, metamorphosing, and newly metamorphosed swimming behavior observed in the laboratory showed constant upright swimming after yolk-sac absorption to slower decreased swimming in a canted position during metamorphosis to a final horizontal swimming using rippling of fins for propulsion at metamorphosis. After metamorphosis there was a decrease in overall activity level (Jearld et al. 1993).

Young-of-the-year winter flounder exhibit little movement from the areas where they settle, although this may be site-specific. Winter flounder collected during the first 2 months of settlement in Waquoit Bay, Mass., and marked with acrylic paint were mostly recaptured (98%) within 100 m of their release site (Saucerman and Deegan 1991), indicating limited movement after settlement during their first summer. Age-O+ individuals in Point Judith Pond, R.I., were also recaptured within the area they were marked during the first summer postsettlement (O'Connor 1997). On the other hand, age-O+ juveniles in Great Salt Pond, Block Island, R.I., appeared to move out of certain locations in the late summer, perhaps in response to high temperatures (Neuman 1993). Age-O+ winter flounder in Great South Bay appeared to be relatively stationary until they reached a size of 30-50 mm, at which time they began to move into the upper estuary. They exhibited little segregation by depth, but few were found on the intertidal mud flats (Armstrong 1997). In a New Jersey estuary, age-O+ juveniles were more abundant in unvegetated areas than in vegetated locations (eelgrass beds and macro algae accumulations) and showed better growth when caged in unvegetated habitat (Sogard 1992). In contrast, in the Damariscotta River estuary, winter flounder abundance was greater in eelgrass beds than in unvegetated areas and they dominated fish collections at night when the invertebrate epifaunal abundance was also higher (Mattila et al. 1999). In Connecticut, abundance of young-of-year winter flounder in

habitat types within nursery areas was correlated with sediment type in shallow embayments. Highest densities occurred in mud-shell litter habitat, and sites with mud combinations had higher densities than sandy sites. This may reflect an abundance of prey in these areas (Howell et al. 1999).

A large series from Casco Bay, measured by Welsh, and others seen near Boothbay Harbor and at Mt. Desert indicate that off southern New England juveniles of the previous winter grow to an average length of 4-8 cm by August, are 5-10 cm long by the end of September, and 10-15 cm long in January and February, when they are almost 1 year old; this is probably true north of Cape Cod as well. They may grow somewhat faster in more southern (warmer) waters, as in Chesapeake Bay, where young-of-the-year are 11-18 cm long in January and February. Daily growth rates of young-of-the-year were 0.18 mm.day⁻¹ in a Rhode Island salt pond (O'Conner 1997) and 0.09-0.11 mm.day⁻¹ in a New Jersey estuary (Sogard 1992).

Age and Growth. Winter flounder are relatively long-lived, reaching a maximum age of about 15 years and a length of 58 cm (Fields 1988). Scales and otoliths have been used for determining age and growth (Fields 1988). Age verification of winter flounder in Narragansett Bay using sectioned otoliths showed that age determination was probably accurate for ages 1-4 but that fish up to 11 years could also be aged. There was no significant difference in aging by otolith section, whole otoliths, and scales, so any of these techniques can be used (Haas and Recksiek 1995). Growth rate up to age 5 is the same for both sexes, after which females grow faster and live longer than males (Fig. 306). Witherell and Burnett (1993) determined that total length for female flounder in Massachusetts calculated from scale samples was 19.9 mm at age 2, 26.8 mm at age 3, 32 mm at age 4, 36.1 mm at age 5, 39.1 mm at age 6, 41.4 mm at age 7, and 43.2 mm at age 8. Their findings are consistent with those of Lobell (1939) and Perlmutter (1947). Winter flounder on Georges Bank grow faster than fish from inshore areas (Lux 1973).

General Range. Atlantic coast of North America from Windy Tickle, Labrador, 55°45' N (Backus 1957b) south to North Carolina and Georgia. They are most abundant from the Gulf of St. Lawrence to Chesapeake Bay.

Occurrence in the Gulf of Maine. Winter flounder are the most common shoal-water flounder and perhaps the most familiar of all the groundfishes of the Gulf of Maine. Most of the winter flounder population of the inner parts of the Gulf live shoaler than 55 m (Map 39); the zone occupied around the coast north of the elbow of Cape Cod is about 13-16 km wide, measured from the outer headlands or islands, except for Stellwagen Bank, which lies several kilometers farther out, and off Cape Sable, where their outer-depth limit is 24 km offshore. Their range extends out along the offshore rim of the Gulf in somewhat deeper water, to include the Nantucket Shoals region as a whole and the shoaler parts of Georges Bank.

Importance. Winter flounder are the thickest and meatiest of all the Gulf flatfishes. Most of today's commercial catch is made by otter trawlers, with a small part taken with hook and line or various types of nets. The commercial fishing grounds include the inner parts of the Gulf, from the tip of Cape Cod around to Cape Sable, Nantucket

Shoals, and Georges and Browns banks. In Canadian waters, they are caught off the Scotian Shelf and at the mouth of the Bay of Fundy: The fishing season generally begins in the spring after adults spawn and ends in late fall. The peak is in spring and early summer (Klein-MacPhee 1978).

Recreational fishing for winter flounder occurs in harbors, estuaries, and other sheltered situations all around the shores of the Gulf, from bridges, piers, and small boats. Most anglers bottom fish with small hooks baited with sea worms, clams, snails, squid, and other bait. When they are not actively feeding, flounders can sometimes be attracted by stirring the bottom.

Commercial landings in the Gulf of Maine increased from 1,000 mt in 1961 to nearly 3,000 mt in 1982 and then declined. The recreational catch almost equals the commercial landings. In 1979 the combined catch totaled 7,100 mt. This dropped to 3,100 mt in 1983 owing to a 70% reduction in recreational catches and a 25% reduction in commercial landings. Since 1989 landings in both fisheries have trended downward. Bottom trawl survey indices decreased from 1983 to 1988 and reached a record low in 1994 (Fig. 307). Low landings and CPUE and survey indices show that winter flounder abundance has been substantially reduced, and the stock is considered overexploited and at a low biomass level (Brown and Gabriel 1998).

Commercial landings from Georges Bank increased from 1,900 mt in 1976 to 3,800 mt during 1980-1984. They began to decline in 1985-1988, averaging 2,400 mt, and from 1991 to 1992 averaged 1,700 mt. In 1993 landings were near the lowest on record (1,700 mt) and CPUE indices were also low. The autumn survey stock biomass has trended downward since 1977. The stock has declined to record lows and is overexploited. No recreational catches have been reported from the Georges

Bank stock (Brown and Gabriel 1998). The southern New England-Mid-Atlantic stock is also at low biomass levels and remains overexploited (Brown and Gabriel 1998).

By-catch of winter flounder occurs in the Gulf of Maine shrimp fishery; and there is an 11% discard (by number) in the size range of 17-28 cm TL (Howell and Langan 1992). Mortality of winter flounder discarded is estimated at 10%, which is lower than that for other fish species (Ross and Hokenson 1997). In the spring inshore fishery for squid in Nantucket and Vineyard sounds, high catches and discards of undersized flounder occur. By-catch rates vary spatially and temporally but over 30% by weight of the total catch is discarded at sea, 3% of which is winter flounder (Glass et al. 1999).

Winter flounder have been identified as a candidate for aquaculture in Atlantic Canada. Their resistance to low temperatures provides an opportunity for aquaculture development in some of the colder waters along the Atlantic Canadian coast previously deemed unsuitable for fish culture. The focus is on development of techniques and technology for larval rearing and juvenile grow-out. Recent advances have been summarized by Litvak (1999).

Stocks. Winter flounder appear to form relatively discrete local groups (see Habits). For assessment purposes these are divided into three groups: Gulf of Maine, southern New England-Mid-Atlantic, and Georges Bank but additional studies of stock structure are needed (Brown and Gabriel 1998).