

Description. Body narrow; mouth large, with strong canine teeth, 16-28 on eyed side (Woolcott et al. 1968) (Fig. 290). Dorsal fin originates opposite forward margin of upper eye. Pelvic fins alike, separated from long anal fin by a considerable space. Caudal fin with rounded margin. Lateral line arched over pectoral fin. Scales small, cycloid, secondary squamation present (Norman 1934). Body proportions: body depth 47% SL; head length 24-34% SL; maxilla length 12-16% SL (Ginsburg 1952b; Gutherz 1967).

Meristics. Dorsal fin rays 80-98; anal fin rays 60-74; pectoral fin rays 18 or 19; lateral line scales 91-108; gill rakers on lower part of anterior arch 14-17; vertebrae 10 or 11 + 30 or 31 = 41 or 42 (Norman 1934; Gutherz 1967; Miller and Jorgenson 1973; Able and Fahay 1998).

Color. Summer flounder are among the most variable flatfishes in color of all the local species and they adapt their pattern most closely to the ground on which they lie. Like most flatfishes they are white on the blind side, with shades of brown, gray, or drab on the eyed side. They can assume a wide range of tints, from nearly white on white sand through various hues of gray, blue, green, orange, pink, and brown to almost black (Mast 1916). Upper surface variegated with pale and dark, with the pattern fine or coarse according to the bottom. They mayor may not be marked with small eyespots, a darker tint than the general ground color. Mast's experiments showed that they are slower in adapting their coloration to actual colors of the bottom than to the general pattern, and that they respond more rapidly to yellows and browns than to reds, greens, or blues. He also observed that the skin simulates the pattern of the background and does not reproduce it.

Incidences of ambicoloration are much rarer than in winter flounder; however, several specimens have been described that were pigmented on both sides, a condition that is often accompanied by incomplete eye migration and a hooked dorsal fin (Gudger 1935a; Dawson 1962; Powell and Schwartz 1972).

Size. Richards (1980) estimated maximum size to be 61 cm in length, 2.6 kg weight for males and 94 cm, 13.4 kg for females. Average size is 40-56 cm and 1-2.3 kg. The all-tackle world record summer flounder weighed 10.17 kg and was caught at Montauk Point, Long Island, in September 1975 (IGFA 2001).

Distinctions. The only Gulf of Maine flatfish with which summer flounder share eyes on the left side, large mouth, and symmetrical pelvic fins are fourspot flounder, but the latter has a distinctive color pattern (four large spots) and fewer dorsal fin rays (72-81) and gill rakers (7-10).

Habits. Summer flounder spend most of their lives on or close to the bottom, as other flatfishes do. During their stay in shoal water they prefer sandy bottom or mud, where they are often seen; it takes them only an instant to bury themselves to the eyes in the sand, although they do not do this as often or as deeply as winter flounder do (Keefe and Able 1993). Summer flounder often lurk in sand patches near eelgrass beds or among dock pilings. In Mid-Atlantic estuaries, they have been found in salt marshes and seagrass beds that have muddy or silty substrates (Dahlberg 1972; Orth and Heck 1980; Rountree and Able 1992a).

Summer flounder are sensitive to oxygen concentrations of less than 3 ppm and may move to avoid these hypoxic areas (Murawski and Festa 1974) or may be killed by such events (Freeman and Turner 1977a; Swanson and Sindermann 1979). Some summer flounder come close inshore during the warm half of the year, where they are caught regularly both along open coasts and in bays and harbors, the smaller sizes often from docks and bridges. Some even run up into freshwater rivers. The great majority of the population, especially of larger ones, lie farther offshore even at that season, in depths of 70-155 m (Grosslein and Azarovitz 1982) and deeper, at least in the northern part of the range.

Food. The main category of food is bony fishes, more than half the food by weight in all size-classes (61.1% by weight over all size-classes of 655 summer flounder, mostly from southern New England south (Bowman et al. 2000: Table B-53a). Cephalopods become important at 31 cm TL and constitute 34.2% of the diet across all size-classes. Crustaceans are important for small size-classes, 43.3% for summer flounder less than 21 cm, decreasing to 22.4% by 36 cm, and then becoming insignificant. Mysids, particularly *Neomysis americana*, and decapods, particularly *Cancer irroratus*, are the most important crustaceans in the diet of smaller summer flounder. Fish prey include a wide assortment of bottom and surface species, with sand lance being most significant starting with summer flounder 26 cm and longer and constituting 22.3% by weight of the total diet. Other fish prey important for particular size-classes

of summer flounder include anchovies, round herring, silver hake, and flatfishes.

Summer flounder are active in pursuit of prey, often following schools of small fishes up to the surface and jumping clear of the water in their dashes, actions very different from those of the sluggish dab and winter flounder. However, summer flounder also feed on the bottom. They were reported as being active during daytime (Olla et al. 1972) but other studies in the laboratory (Klein-MacPhee 1978) and in the field using telemetry (Szedlmayer and Able 1993) indicated that juveniles, at least, are active at night. Their feeding behavior has been described in detail by Olla et al. (1972). The most important food items for young-of-the-year summer flounder (100-200 mm) in Pamlico Sound, N.C., were mysids (Neomysis americanus), fishes (especially anchovies and sciaenids), amphipods, and crabs (Powell and Schwartz 1979). In New Jersey; young-of-the-year also eat silverside, mummichog, and shrimps such as Palamonetes vulgaris and Crangon septemspinosus (Rountree and Able 1992b). Food consumption generally increases with temperature and falls in winter (powell and Schwartz 1979). Summer flounder move into marsh creeks to feed, and these tidal-mediated movements typically occur up the creeks at night on flood tide and down the creeks following ebb tide (Rountree and Able 1992b). Feeding rates of juvenile summer flounder maintained in the laboratory at various temperature-salinity regimes ranged from 1%.day-1 at 2°C to 24%.day-l at 18°C. Salinity had no apparent effect. Assimilation efficiency averaged 60.3% over a range of temperatures (2°-18°C) and salinities (10-30 ppt). Mean specific growth rates were not significantly different between 2 ° and 10°C (0.14%.day-l) and growth rates ranged from 2.4 to 3.9%.day-l at 14°-18°C (Malloy and Targett 1991).

Feeding habits of pelagic larval summer flounder were examined in relation to larval stage (Grover 1998). Incidence of feeding and gutfullness data indicated that larvae begin feeding near sunrise and continue throughout daylight hours. Incidence of feeding reached its lowest point, 8.3% at 0400- 0559 hours, then dramatically increased to 54.6% at 0600--0759. Maximum gut-ful1ness was seen between 1200 and 1559. Immature copepodites were the primary prey for oceanic larval stages, tintinnids and copepod nauplii made major contributions to the preflexion diet, and large prey such as calanoid copepods and appendicularians were major items in the diets of premetamorphic and metamorphic larvae. At 180(}--1859 and 200(}-2159 hours, the incidence of feeding in estuarine larvae was significantly lower than in oceanic larvae. The estuarine diet was dominated by a calanoid copepod, *remora longicornis*. Incidence of feeding was observed to decline as metamorphosis progressed.

Predators. Summer flounder have been found in the stomachs of spiny dogfish, blue shark, little skate, Atlantic cod, silver hake, goosefish, northern sea robin, spot, bluefish, and winter flounder (Bowman and Michaels 1984; Kohler 1988; Rountree 1999; Bowman et al. 2000), of which spiny dogfish are the most significant predator.

Parasites. The following parasites have been recorded from summer flounder: a protozoan, *Trypanoplasma bullocki* (Sypek and Burreson 1983); an acanthocephalan, *Echinorhynchus sagittiter;* a nematode, immature *Ascaris;* a cestode, *Rhyncobothrium sp.;* two trematodes, *Distomum dentatus,* D. *monticelii;* and a copepod, *Lernaeonema* (Linton 1905). A systematic bacterial infection by *Vibrio sp.* caused an ulcerative disease in summer flounder collected in Connecticut (Robohm and Brown 1978).

Although summer flounder are tolerant of a wide range in temperature, temperature has been indirectly responsible for unusual mortality of summer flounder juveniles in the York River estuary, Chesapeake Bay, Va., and Pamlico Sound, N.C. (Goldstein 1985). A combination of low temperatures and infection by the blood parasite *rrypanoplasma bullocki* is fatal. The parasite is transferred to summer flounder by an estuarine leech, *Calliobdella vivida*. Under normal temperature conditions the juveniles are able to combat the infection and survive but at temperatures below 5°C they succumb (Sypek and Burreson 1983; Burreson and Zwerner 1984).

Breeding Habits. Median length at maturity for female and male summer flounder is 28.0 cm and 24.9 cm, respectively (O'Brien et al. 1993) corresponding to ages 2.5 for females and age 2 for males (Penttila et al1989). Based on size at the end of the first year of life, many fish may reach maturity by age 1 (Almeida et al. 1992; Szedlmayer et al. 1992). Spawning occurs during autumn migration to offshore wintering grounds on or near the bottom, where temperatures range from 12° to 19°C (Morse 1981). Fecundity estimates range from 463,000 to 4,188,000 eggs per female for fish between 36.6 and 68 cm total length. Larger fish mature first during the spawning period and produce more eggs (Morse 1981). Females are serial spawners, continuously producing egg batches, which are shed over a period of several months (September to February or March).

Summer flounder have two distinct spawnings each year: intense spawning in autumn and winter over much of the Mid-Atlantic and southern New England regions and a lesser spawning during spring in the southern part of the Mid-Atlantic region (Berrien and Sibunka 1999: Fig. 88). Major spawning begins in September in inshore waters of the Mid-

Atlantic and southern New England. Peak spawning occurs in October when egg distribution broadens to include much of Georges Bank. Spawning in deeper waters continues into November, when eggs occur across the entire breadth of the shelf.

Early Life History. Embryonic development was first described by Smith and Fahay (1970) from artificially reared eggs, which were compared to eggs collected at sea. The eggs are pelagic and contain a single oil globule. The egg diameter ranges from 0.91 to 1.1 mm, mean 1.02 mm, and that of the oil globule from 0.18 to 0.31 mm, mean 0.25 mm (Smith and Fahay 1970). Fertilized eggs are spherical with a rigid transparent shell. The perivitelline space occupies 6% of the egg radius. Eggs hatch between 48 and 71 h postfertilization, depending on incubation temperatures Oohns and Howell 1980). Newly hatched larvae are 2.41-2.82 mm long. The body is thin and long except at the yolk-sac region. The head is flexed downward. Black pigment spots are present on the anterior half of the anal finfold and anterior two-thirds of the dorsal finfold. The posterior quarter of the larva is clear. Pigmented areas on the head include the snout, midbrain, anterior to the yolk, and ventral to the eye. There are a few pigment spots on the upper part of the yolk but the oil globule is clear.

Yolk is absorbed at 3.16 mm NL, at which time the mouth has developed, the eyes become pigmented, and the anus is formed at the margin of the finfold. Dorsal fin rays begin to form at 8.64 mm NL

and the first few are elongate. The eye begins to migrate at 9.5 mm SL and completes migration by about 14-21.4 mm SL. Total time required for metamorphosis of laboratory-reared fish from the start of eye migration to the time the eye reaches its final position is 20-32 days, mean 24.5 days. Details of metamorphosis were described by Keefe and Able (1993).

Duration of metamorphosis in laboratory-reared summer flounder was dramatically affected by temperature, averaging 46.5 days at a mean temperature of 14.5°C and 92.2 days at a mean of 6.6°C (Keefe and Able 1993). Mortality rates during metamorphosis ranged from 17 to 83% and were significantly greater at cold temperatures (4°C). Eggs and larvae of summer flounder are found only at sea, whereas young-of-the-year juveniles are found in or near mouths of estuaries (Smith 1973). Eggs were collected north of Chesapeake Bay from September to December and south of the Bay from November to February at temperatures ranging from 9.1° to 22.9°C. The most productive spawning grounds were off New York and New Jersey in 1965-1966, but during 1980-1986 the center of reproduction was from Massachusetts to New York (Able et al. 1990).

Larvae were collected at the same time as eggs from 22 to 83 km offshore. Concentrations occurred off Martha's Vineyard, Long Island, northern New Jersey; and in Delaware Bay at temperatures of 0°-22°C. Larvae have been collected as early as September off Cape Cod and as late as May in North Carolina (Smith 1973; Smith et al. 1975; Bolz et al. 1981; Able et al. 1990; Able and Fahay 1998). Most postlarvae were collected at

night (Smith 1973). It is believed that postlarvae begin to migrate southward and into estuaries during morphological transformation and fin development and that complete metamorphosis and settlement take place in the estuaries (Keefe and Able 1993). Metamorphic summer flounder enter Great Bay-Little Egg Harbor estuary; N.J., prior to completion of metamorphosis and permanent settlement (Keefe and Able 1994). Laboratory experiments indicate a preference by both juvenile and metamorphic summer flounder for sand over mud substrate. Metamorphic individuals do not appear to be capable of burying themselves in the substrate when they enter the estuary; Complete burial was only observed in late metamorphic and juvenile stages. A diel pattern of burying behavior was observed that was dependent upon several environmental variables, including substrate, water temperature, tide, and presence and type of predator. In general, postlarvae begin entering estuaries from New Jersey to North Carolina from October to April, beginning earlier in the northern part of the range, October-April from Long Island Sound to Chesapeake Bay (Olney 1983; Able et al. 1990; Szedlmayer et al. 1992; Norcross and Wyanski 1994), and later in the southern part (December-April in North and South Carolina [Weinstein 1979; Bozeman and Dean 1980; McGovern 1986; Hettler and Chester 1990]). Larval densities outside of Beaufort Inlet, N.C., were correlated with the north component of the wind, nearshore water temperature, and distance to the midshelf front (Hettler and Hare 1998). Differences in larval density across the inlet were significantly correlated with the east component of the wind.

Larvae are eurythermal and euryhaline and have been collected at temperatures ranging from -2.0° (Szedlmayer et al. 1992) to 23.4°C (McGovern and Wenner 1990) and in salinities from 0 (McGovern and Wenner 1990) to 35 ppt (Williams and Deubler 1968). Laboratory-reared summer flounder showed high mortality rates at temperatures less than 2°C and estuarine larvae may suffer increased mortality owing to both severity and duration of cold water temperatures (Malloy and Targett 1991; Szedlmayer et al. 1992). Postlarval *Paralichthys* maintain a preferred position in the Cape Fear River estuary, N.C., by migrating to the surface at night and using tidal drift to enter salt marshes (Weinstein et al. 1980). Youngof-the-year are well adapted to estuaries because they can withstand a wide range of temperatures and salinities (Deubler and White 1962; Szedlmayer et al. 1992), but generally prefer salinities higher than 12 ppt (Powell and Schwartz 1977). During spring and summer in New Jersey marsh creeks (Szedlmayer and Able 1993), they usually remain within narrow limits of temperature (22.3°-24.9°C), salinity (27-31 ppt), and dissolved oxygen (5.9-6.8 ppt). They remain in estuaries until their second year of life in the southern part of their range but to the north move just outside them in winter. A large portion of juveniles tagged in estuaries return to the same

A large portion of juveniles tagged in estuaries return to the same system the next summer (Hamer and Lux 1962; Poole 1962; Jesien et al. 1992). At maturity, they join the adult population in their migration (Grosslein and Azarovitz 1982).

Age and Growth. Summer flounder grow rapidly in their first year. Growth rates of 1.9 mm.day-l have been measured in New Jersey estuaries and young-of-the-year ranged from 200 to 326 mm TL by September (Szedlmayer et al. 1992). Length- at-age was calculated by Poole (1961), Eldridge (1962), and Smith and Daiber (1977) using otoliths, but this proved problematic because of difficulties in interpreting the first opaque zone (Dery 1988d). Poole believed that the first ring was laid down at age 1 when fish were 250-320 mm, whereas Smith and Daiber believed that it was laid down at age 2 and that the fish reached sizes of 170-180 mm at age 1. Poole's interpretation was supported by Szedlmayer et al. (1992). Currently, scales are used for aging and the first distinct annulus measured from the focus is used to represent first-year growth (Almeida et al. 1992). Females grow faster than males and are larger than males after age 2; males attain a maximum age and length of about 7 years and 60 cm, as compared with 12 years and 82 cm for females (Dery 1988d) (Fig. 291).

General Range. Continental waters of eastern North America from Nova Scotia (Vladykov and McKenzie 1935) to South Carolina, possibly to Florida (Wi1k et al. 1980; Gilmore et al. 1981) chiefly south of Cape Cod. Two tag recoveries reported from the Gulf of Mexico (Briggs 1958) seem very unlikely (Wi1k et al. 1980).

Occurrence in the Gulf of Maine. Summer flounder are plentiful offshore in the southern Gulf of Maine, eastward to Nantucket Shoals, and to the western part of the South channel. NMFS surveys and commercial catch records show that they are present on the westernmost edges of Georges Bank and in shallow waters on Georges Bank (Able and Kaiser 1994). They are rare north of Cape Cod, but occasionally occur north as far as Brown's Bank, and to outer Nova Scotia waters on La Have Bank and Passamaquoddy Bay; N.B. (Scott and Scott 1988).

Movements. In inshore waters of the New York Bight, summer flounder appear in April and continue to move inshore during May and June to reach peak numbers in July or August (Grosslein and Azarovitz 1982). They appear in early May near Woods Hole (Bigelow and Schroeder). Those that come close inshore from Chesapeake Bay northward move offshore again during autumn, presumably to escape winter chilling, although some overwinter in Delaware Bay (Smith and Daiber 1977). They begin offshore migrations in September and are usually gone from the northern part of their range by October or November. Tagging on both inshore and offshore grounds (Hamer and Lux 1962), showed that fish tagged in New Jersey inshore waters moved northward along the coast and eastward along Long Island toward Martha's Vineyard. They scattered over the Mid-Atlantic Bight during their offshore migration. Summer flounder tagged on offshore grounds east of Hudson Canyon were recaptured between lower New York Bay and Cape Cod and seldom strayed south or west of Hudson Canyon. This is probably the source of fish summering in Rhode Island and Massachusetts waters.

Importance. This is the most commercially important flatfish to the west and south of Rhode Island and the most sought after by sportsmen there. They occur in commercial quantities sporadically on Georges Bank. They were landed in the 1940s and 1950s but were essentially absent from 1963 to 1973. Numbers then increased but only to low levels compared to other areas (Henderson 1979). Georges Bank-Mid-Atlantic commercial landings peaked at about 15,000 mt from 1976 to 1988 and then declined to about 5,000 mt (Fig. 292). The otter trawl is the most common commercial gear used (accounting for about 90% of the commercial landings), but handlines, haul seines, various traps and nets, and spears are also used (Byrne and Azarovitz 1982). Summer flounder are an important by-catch and discard in the small-mesh fishery for squid in Nantucket and Vmeyard sounds (Glass et al. 1999).

The recreational fishery probably accounts for more than half the total catch and considerably exceeds it from New York to Maine (McHugh and Ginter 1978). Most fishermen are anglers fishing from shore, piers, docks, and small boats, but in the southern part of the range they use spears as well (Byrne and Azarovitz 1982; Manooch 1984). This is the gamest of the local flatfishes, biting freely on almost any bait, even taking artificial lures at times, and large ones put up a strong resistance when hooked.

Commercial aquaculture of summer flounder began in 1996 (Bengston 1999). Both the research leading to commercialization and the production itself have been heavily oriented toward the hatchery phase. Producers are experimenting with both recirculation systems and net pens to identify the equipment that optimizes grow-out production. Current operations are located in New England and New York.

Stocks. There have been three interpretations of stock structure of summer flounder. (1) Two distinct populations, one in the Mid-Atlantic Bight between Cape Cod and Cape Hatteras and the other between Cape Hatteras and Florida, based on meristic and morphological differences (Smith and Daiber 1977; Wilk et al. 1980; Fogarty 1981). This is the concept currently accepted for stock assessment and management purposes (Terceiro 1998b). (2) Two Mid-Atlantic Bight stocks, one of which appears to make a consistent offshore migration in summer and another that appears to spend the summer in estuaries and inner-shelf areas from Virginia to Maryland, but overwinters near Cape Hatteras. This trans-Hatteras stock is supported by electrophoretic (Van Housen 1984), meristic and morphometric (Delaney 1986) analyses and by tagging studies (Able and Kaiser 1994). (3) Three stocks, Mid-Atlantic Bight, South

Atlantic Bight. and trans-Hatteras. Support for distinction of local populations north and south of Cape Hatteras comes from tagging studies (Mercer et al. 1987; Monaghan 1992). A recent mitochondrial DNA study (Jones and Quattro 1999) of summer flounder from Massachusetts to South Carolina evaluated the effect of Cape Hatteras on gene flow and found no significant population subdivision centered around Cape Hatteras.