Species Profiles: Life Histories and Environmental Requirements of Coastal Fishes and Invertebrates (South Florida)

SOUTHERN, GULF, AND SUMMER FLOUNDERS
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SOUTHERN, GULF, AND SUMMER FLOUNDERS

by

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Performed for
Coastal Ecology Group
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Vicksburg, MS 39180

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National Wetlands Research Center
Research and Development
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Washington, DC 20240

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PREFACE

This species profile is one of a series on coastal aquatic organisms, principally fish, of sport, commercial, or ecological importance. The profiles are designed to provide coastal managers, engineers, and biologists with a brief comprehensive sketch of the biological characteristics and environmental requirements of the species and to describe how populations of the species may be expected to react to environmental changes caused by coastal development. Each profile has sections on taxonomy, life history, ecological role, environmental requirements, and economic importance, if applicable. A three-ring binder is used for this series so that new profiles can be added as they are prepared. This project is jointly planned and financed by the U.S. Army Corps of Engineers and the U.S. Fish and Wildlife Service.

Suggestions or questions regarding this report should be directed to one of the following addresses.

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Attention: WESER-C
Post Office Box 631
Vicksburg, MS 39180
CONVERSION TABLE

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ACKNOWLEDGMENTS

I wish to thank Ms. Rosemarie Mulholland, Florida Department of Natural Resources, Clermont, Florida, for providing access to information she had compiled on the southern and gulf flounders while a graduate student at the University of Florida. I also wish to thank Mr. George H. Burgess, Florida State Museum, University of Florida, Gainesville, for the loan of various reference items used in preparation of this report. I wish to express my appreciation to the journal *Copeia* for permission to reproduce Figures 7 and 8, and to *Estuaries* for permission to reprint Figure 15.
Southern, Gulf, and Summer Flounders

**NOMENCLATURE/TAXONOMY/RANGE**

**Scientific name** ........ Paralichthys leothostigma Jordan and Gilbert
**Preferred common name** .......... Southern flounder (Figure 1)
**Other common names** .......... Mud flounder, southern large flounder, doormat, flounder, fluke, halibut

**Scientific name** ........ Paralichthys albogutta Jordan and Gilbert
**Preferred common name** .......... Gulf flounder (Figure 2)
**Other common names** ........ Sand flounder, flounder, fluke

**Scientific name** ........ Paralichthys dentatus (Linnaeus)
**Preferred common name** .......... Summer flounder (Figure 3)
**Other common names** ........ American turbot, long-toothed flounder, common flounder, flounder, fluke, flounder of New York (New York), plaice (New York, Massachusetts), turbot (Massachusetts), flatfish, turbot (Long Island, New York, Chesapeake Bay), chicken halibut, halibut, brail, puckerbrough (Rhode Island)

**Class** .................. Osteichthyes
**Order** .................. Pleuronectiformes
**Family** .................. Bothidae

Life cycle: reproduction, habitat, marine biology...
Geographic ranges:

Southern flounder: Occurs from Albemarle Sound, North Carolina, south to Loxahatchee River, on lower east coast of Florida; it is absent from there south and around tip of peninsular Florida, but occurs in Caloosahatchee River Estuary, on southwest coast of Florida, and from there around the Gulf of Mexico to northern Mexico (Hoese and Moore 1977; Manooch 1984) (Figure 4). Most common in western half of the Gulf of Mexico. Generally occupies water of lesser average depth than either the gulf flounder or the summer flounder. It is common to depths of 47 m (Nall 1979); the greatest confirmed depth is about 61 m (Stokes 1977). Frequently occurs in water of low salinity or even freshwater (Ross 1980).

Gulf flounder: Ranges continuously in coastal waters from Cape Lookout, North Carolina, to Corpus Christi, Texas (Figure 5), usually in waters less than 92 m deep, but occasionally as deep as 128 m (Ginsburg 1952; Gutherz 1967). Has occasionally been recorded from extreme western Bahamas (Bohlke and Chaplin 1968), and is most common in eastern half of Gulf of Mexico and along eastern coast of Florida. Rarely enters waters of reduced salinities, and never enters freshwater (Ross 1980).

Summer flounder: Ranges from Gulf of Maine (Bigelow and Schroeder 1953) and occasionally Nova Scotia (Leim and Scott 1966) south along Atlantic coast at least to Sebastian Inlet, on southeast coast of Florida (Figure 6). Reports of occurrence in Gulf of Mexico (Poole 1962; Powell 1974; Rogers and Van Den Avyle 1983) are in error (Ginsburg 1952; Gutherz 1967; Topp and Hoff 1972; Hoese and Moore 1977; Wilk et al. 1980; Manooch 1984). Most common between Cape Cod and Chesapeake Bay, usually in waters less than 37 m deep, and occasionally down to 183 m; but occurs at greater average depths to the south. Rarely enters waters of reduced salinities, and never recorded from freshwater.

MORPHOLOGY/IDENTIFICATION AIDS

Adults

All species of Paralichthys are relatively large, robust, darkish, left-eyed flatfishes with large mouths (upper jaw extending to or beyond posterior margin of eye) and well-developed teeth. The bases of both pelvic fins are short and neither extends forward to the urohyal bone.

Southern Flounder

Diffuse dark spots and blotches on pigmented side of body, ocellated spots absent (Figure 1); gill rakers on lower limb of outer arch 8-11 (usually 9-10); anal rays 63-73 (usually 65-71); dorsal rays 80-95 (usually 84-92); scales in straight portion of lateral line 52-69 (usually 56-64); size relatively large: attains a maximum standard length (distance from snout to base of tail) of 660 mm and a weight of over 3 kg (Nall 1979).

Gulf Flounder

Three small, usually conspicuous, ocellated spots on pigmented side of body in a triangular pattern, with the apex of the triangle pointing posteriorly and the posteriormost spot situated astride lateral line (Figure 2); gill rakers on lower limb of outer arch 9-12 (usually 10-11); anal rays 53-63 (usually 56-61); dorsal rays 71-85 (usually 75-81); scales in straight portion of lateral line 47-60 (usually 52-57); size relatively small: attains a maximum standard length (SL) of about 420 mm
Figure 4. Areas of greatest abundance of southern flounder in south Florida.
Figure 5. Areas of greatest abundance of gulf flounder in south Florida.
Figure 6. Areas of greatest abundance of summer flounder in south Florida.
and a weight of about 1.7 kg (Nall 1979). Vick (1964) suggested a maximum length of over 700 mm.

**Summer Flounder**

Five small ocellated spots usually present on pigmented side of body (becoming obscure in larger specimens), with the first two and last two situated on the lateral line (Figure 3); gill rakers on lower limb of outer arch 13-18 (usually 15 or more); anal rays 61-73 (usually 66-70); dorsal rays 80-96 (usually 85-90); scales in straight portion of lateral line 56-76 (usually 62-70); size relatively large: attains a maximum standard length (SL) of about 700 mm and a weight of over 4.4 kg (Powell 1974).

**Postlarvae**

Postlarvae (i.e., individuals that have metamorphosed into an adult-like form) of the summer flounder can be distinguished from those of the southern and gulf flounders by pigmentation pattern (Deubler 1958). Summer flounder at 9-15 mm SL have a well-defined band of black pigment along the border of the anterior four-fifths of the dorsal fin and along the anterior two-thirds of the anal fin (Figure 7); pigment is lacking in these areas in both the southern and gulf flounders (Figure 8). Vertebral differences are also useful for separating postlarval summer flounder from the other two species: *P. dentatus* has 40-42 total vertebrae (usually 41), and the other two species have 36-38, usually 37. Gill rakers are not sufficiently developed at this size to be of aid in identification. Postlarval southern and gulf flounders are difficult to separate at small sizes, inasmuch as no pigmentedary differences have been discovered and vertebral counts for the two species are identical. Number of anal rays is the most diagnostic character, but number of dorsal rays will also separate most specimens (see summary of adult characteristics).

**Figure 7.** Late postlarval pigmentation of summer flounder (Deubler 1958).

**Figure 8.** Late postlarval pigmentation of southern flounder (Deubler 1958).

**REASON FOR INCLUSION IN SERIES**

The three species of *Paralichthys* are important components of both the commercial and sport fishery catches, but since they are combined in catch statistics under the collective name "fluke" (BCF 1964b-1968b; NMFS 1969b-1985b), the exact importance of each species cannot be ascertained. In general, however, the summer flounder is considered the most important of the three species because of its prominence in the sport and commercial fishery catches on the upper Atlantic coast from Cape Hatteras northward. Commercial fishery statistics from 1964 to 1985 indicate
that "fluke" have become an increasingly more important part of the commercial catch in terms of both dollar value and the amount of fish taken.

LIFE HISTORY

Of the three species, the summer flounder has received the greatest attention with regard to studies of its life history and ecology; Powell (1974) and Rogers and Van Den Avyle (1983) have provided the most complete summaries. Topp and Hoff (1972) summarized biological data for the gulf flounder. Stokes (1977) studied the life histories of both the gulf and southern flounders in the Aransas Bay area of Texas, and Hall (1979) studied age and growth of these two species in the northern Gulf of Mexico. Powell (1974), in his study of the summer flounder in North Carolina, also included considerable ecological data on the southern flounder and limited data for the gulf flounder.

Reproduction

Reproductive strategies appear to be similar for the three species of Paralichthys. Adults of each species spend most of the year in bays and estuaries, emigrating into deeper offshore waters during fall and winter as temperatures drop. Spawning occurs at these times; ripe individuals have been collected from September to mid-April (Bigelow and Schroeder 1953; Smith 1973) at depths ranging from 20 to 136 m. Spawning begins earlier at more northerly latitudes (Smith 1973), and occurs progressively later as one proceeds southward. Eggs and newly hatched larvae float at or near the surface, and the developing individuals are carried inshore by winds and currents into nursery areas, where further growth and development take place. Appearance of juvenile (i.e., late postlarval) flounders in bays and estuaries along the Atlantic coast usually peaks when stratification and tidal exchange ratios are at a yearly maximum. Juveniles may move to the surface at night and then be carried by flood tides into tidal creeks (Weinstein et al. 1980). In North Carolina, newly metamorphosed juvenile Paralichthys spp. were captured from December through April in estuarine nursery areas (Powell and Schwartz 1977). Juveniles remain in nursery areas until sexual maturity is reached, and do not move into offshore waters until just prior to spawning (Powell and Schwartz 1977).

Controversy exists with regard to age at which sexual maturity is reached, primarily because of differences in interpretation of aging techniques. Stokes (1977) and Manooch (1984) indicated that both southern and gulf flounders attain sexual maturity at 2 years of age; Powell (1974) reached a similar conclusion for the southern flounder. Powell (1974) and Manooch (1984) also stated that the summer flounder does not achieve sexual maturity until it is 3 years old. However, Nall (1979) reported that the southern flounder does not reach sexual maturity until at least 4 years of age, and that sexual maturity of all individuals was not achieved until they were more than 6 years old.

Stokes (1977) reported adult southern flounder leaving Aransas Bay, Texas, for the Gulf of Mexico from mid-October to mid-December. Emigration peaked during mid-November and seemed to be correlated with a sudden drop (4-5°C) in temperature. Males appeared to leave somewhat earlier than females (Simmons and Hoese 1959; Stokes 1977).

Southern flounder spawn from September to April, although peak
activity is from November to January (Gunter 1945). Spawning apparently occurs at depths of 20-60 m (Benson 1982). Arnold et al. (1977), who observed summer flounder spawning in the laboratory, reported that spawning females swam upward in the water column and released their eggs, which were immediately fertilized by a single attending male.

Immigration of juvenile southern flounder into Texas bays begins in January and increases rapidly into February, after which there is a gradual increase in numbers of individuals throughout the spring; abundance peaks during mid-summer (Stokes 1977). Immigration begins when the average water temperature is as low as 13.8°C, and peaks when average water temperature is between 16.0 and 16.2°C. Adult summer flounder return to Texas bays and estuaries from February to April, and remain there until the following fall.

The only available figures on fecundity are those of Arnold et al. (1977), who indicated an average of 40,000 eggs per female in the 1-3 kg weight range. Nall (1979) found developing eggs in all female southern flounder over 6 years old, but in only 5-18% of females 4-6 years old. The smallest maturing female reported by Nall (1979) was 256 mm SL (308 mm total length [tip of snout to tip of tail]). Manooch (1984), who indicated that this species becomes sexually mature at 2 years of age, gave the average total length (TL) of 2 year-old individuals as around 365 mm.

Reproduction in the gulf and southern flounders is similar in most respects. Gulf flounder spawn in the Gulf of Mexico from mid-fall through mid-winter, and Stokes (1977) reported ripe adults leaving Aransas Bay, Texas, from mid-October through December. Spawning evidently occurs offshore, and specimens with ripe gonads have been collected at depths of 20-40 m in the eastern Gulf of Mexico from November through February (Topp and Hoff 1972).

Larval gulf flounder appear in the eastern Gulf of Mexico from December to early March (Topp and Hoff 1972), and juveniles are seen in bays and estuaries in January throughout their range, with peak movement usually occurring in early February (Reid 1954; Springer and Woodburn 1960; Tagatz and Dudley 1961; Stokes 1977). Juvenile gulf flounder, like southern flounder, begin immigrating into Aransas Bay when water temperatures reach 14-16°C (Stokes 1977). Topp and Hoff (1972) reported spent females in Tampa Bay in February.

No fecundity data are available for the gulf flounder. Gonadal examination by Nall (1979) indicated that females mature at sizes as small as 145 mm SL. Manooch (1984) stated that sexual maturity in this species is attained at two years of age. He also indicated the average total length of two-year-old individuals to be around 350 mm, and the average length of three-year-olds to be about 400 mm.

Most information on the summer flounder is based on studies of populations from Pamlico Sound, North Carolina, northward. Smith (1973) observed a seasonal progression in spawning from north to south. He found that peak spawning at the northern limits of its range occurred in early September, spawning north of Chesapeake Bay peaked in October, and spawning south of Chesapeake Bay peaked during November. Bigelow and Schroeder (1953) reported collection of a ripe female in mid-April off Nantucket Island, Massachusetts, but this is unusual. During the 1971-72 season, spawning did not occur until February around Cape Lookout, North Carolina. Powell (1974), on the basis of gonadal development,
reported that most summer flounder in North Carolina waters south of Cape Hatteras spawned from December through February.

As is true of the other two species, summer flounder spend the warmer months in coastal embayments and sometimes in nearshore shelf waters, and migrate offshore during the fall as waters cool. Rogers and Van Den Avyle (1983) reported spawning over a broad depth range (30-200 m). Individuals move into deeper water near the peak of their gonadal development cycle, with the oldest and largest fish apparently moving out first (Morse 1981). The most important nursery areas are located between Long Island, New York, and South Carolina (Powell 1974); the heaviest concentrations are in Virginia and North Carolina (Poole 1966). Summer flounder less than 280 mm TL are uncommon off New England, which suggests that individuals found in those waters have migrated there from the south and that most are about three years old (Lux and Nichy 1981).

Smith (1973) reported that eggs found at or near the surface were most common when bottom temperatures were 12-19°C. Powell (1974) found the most eggs in North Carolina waters when bottom temperatures were about 15°C.

Prior to Smith's (1973) study, it had generally been accepted that currents transport larval summer flounder from the north to major nursery areas farther south, but it now appears that, although eggs and larvae may drift with the current, this is less important than formerly believed.

Female summer flounder appear to reach sexual maturity at 300-330 mm TL and males at 240-270 mm TL. The smallest female examined by Morse (1981) was 250 mm TL, and the smallest mature male was 190 mm TL.

Early Developmental Stages

Balon (1975) defined developmental stages as egg, larva, juvenile, and adult. Transition from egg to embryo occurs when the egg membrane ruptures; the embryo becomes a larva when the individual switches from endogenous to exogenous feeding; and the larva becomes a juvenile upon metamorphosis to an adult-like form. Inasmuch as all three species spawn offshore, the various life stages are adapted for development in full-strength seawater. The onset of metamorphosis in flatfishes appears to be more closely related to environmental temperature and/or size of the individual than to age (Policansky 1982).

Although a detailed description of early developmental stages exists only for the summer flounder (Martin and Drewry 1978: 157-163), one can assume that the characters given apply in large measure to the other two species as well. Martin and Drewry (1978) described the eggs of the summer flounder as "small, spherical, and transparent ... with a rigid shell," and measuring from 0.90 to 1.13 mm (mean - 1.02 mm). The eggs are buoyant (thus, pelagic) and contain a single oil globule in the yolk (Figure 9).

Eggs of the summer flounder have been observed to hatch in from 2 to 9 days (48 to 212 hrs) under laboratory conditions, at temperatures from 21°C down to 5°C (Johns and Howell 1980; Johns et al. 1981). Lengths at hatching were from 2.83 to 3.16 mm (Johns et al. 1981). Although those authors reported hatching at temperatures as low as 5°C, they also indicated that temperatures below 11°C were lethal to larvae during development. Yolk-sac absorption (i.e., transition to larval stage) in this species occurs at about 3.6 mm, and Johns et al. (1981) indicated that this size is
reached approximately 5.7 days after hatching at 11.2°C, or in 2.8 days at 21°C. At this point the eyes are pigmented, the mouth functional, and the digestive tract complete (Figure 10). Hildebrand and Cable (1930) indicated that newly hatched embryos of "Paralichys spp." from Beaufort, North Carolina (the summer flounder is the dominant species in that area) are about 2.5 mm long. At 7 mm the larvae lose their symmetry and the right eye begins to migrate dorsally. Martin and Drewry (1978), however, showed that this change in symmetry occurs at a slightly larger size (ca. 9.5 mm). At 10.5-11 mm, the right eye becomes situated on the ridge of the head (Figure 11), the body becomes increasingly compressed, and the left side of the body is noticeably more pigmented than the right side. At 16 mm, individuals have a form and shape resembling the adult, and pigmentation is almost entirely restricted to the left (i.e., eyed) side of the body. At 77 mm, the body is completely scaled and has the characteristic form and pigmentation of the adult.

Arnold et al. (1977) reported that eggs of the southern flounder hatched at 61 to 76 hrs under laboratory conditions. Time at which transition from embryo to larva occurred was not indicated, but time required for metamorphosis to begin in the laboratory was 40 to 46 days after hatching (at 8 to 11 mm), and this process was completed in 50 to 51 days.

![Figure 9. Egg development and yolk-sac larva of summer flounder, from less than 32 h after fertilization to 75 h after fertilization. Lengths expressed in standard length (SL) or notochord length (tip of snout to end of notochord) (NL) (Martin and Drewry 1978).](image)

![Figure 10. Yolk-sac larva to larval stages of summer flounder: (A) 12 h after hatching, (B) 96 h after hatching, and (C-E) subsequent stages (Martin and Drewry 1978).](image)
Middle Atlantic Bight (i.e., from Cape Hatteras northward) indicated an overall movement of this species toward the northern limits of the Bight as the fish grow older.

The only published results of tagging studies involving the southern flounder are those by Stokes (1977) from Texas, who reported 28 returns out of a total of 1,298 individuals tagged (2.2%) between early 1974 and late 1975. He reported some movement between and within Texas bays, although no consistent patterns were evident. Returns showed movement of from 0 to 18.2 km over periods of 3 to 212 days; the most rapid movement was 9.3 km in 3 days. One individual tagged in November 1973, in Aransas Bay, was recovered 1 year later 451 km to the east.

The only tagging study of gulf flounder was by Stokes (1977), who reported no returns out of a total of 33 individuals tagged.

Although the above data seem to indicate more extensive movements of the summer flounder than the other two species, this may be, at least in part, a result of the greater number of summer flounder tagged, as well as the longer period of time during which studies on the summer flounder were carried out.

Subpopulations

Analysis of morphometric and meristic characters in 1,214 specimens of summer flounder from New York to central Florida indicate two distinct subpopulations, one in the Middle Atlantic Bight north of Cape Hatteras, North Carolina, and the other in the South Atlantic Bight (Wilk et al. 1980). Discriminant analysis coefficients indicate these subpopulations are separable at a level of 93%. These results are partly confirmed by tagging.

Migration and Movement of Adults

Seasonal inshore-offshore movements of adult Paralichthys are related to spawning activities, as discussed earlier. Tagging studies of summer flounder show that latitudinal movement occurs along the Atlantic coast. Of a total of 6,679 individuals tagged off New Jersey during 1960-67, 2 were recaptured south of Cape Hatteras, North Carolina (Murawski 1970). Poole (1962) reported 1 return from below Cape Hatteras out of 5,845 individuals tagged in New York waters during 1956-59. Lux and Nichy (1981) reported 1 return (out of 2,839) in early 1963 from off southern Maryland; the individual had been tagged in New York waters the preceding September. Lux and Nichy (1981) and Rogers and Van Den Avyle (1983), however, said that in general tagging studies in the

Figure 11. Larval stages of summer flounder, showing transition of eyes from symmetrical to asymmetrical position (Martin and Drewry 1978).
studies by Poole (1962) and Murawski (1970), who found little evidence of movement of individuals between these two areas, as well as Smith's (1973) studies of distribution patterns of eggs and larvae. Smith (1973) had also suggested that the subpopulation in the Middle Atlantic Bight could be further subdivided, with one group occurring in New York and New Jersey and the other from Delaware Bay to Cape Hatteras; but Wilk et al. (1980) could neither confirm nor deny this hypothesis on the basis of their work.

There is insufficient data to indicate whether or not distinct subpopulations of southern and gulf flounders exist; however, the wide distributional break of the southern flounder around the tip of peninsular Florida (Figure 4) suggests that this is a reasonable possibility.

GROWTH CHARACTERISTICS

Almost all age-growth studies of Paralichthys have used otoliths to determine age. Analyses of yearly size classes, even at small sizes, have been shown to be of limited value because of variable individual growth rates and protracted spawning seasons. Body lengths may be expressed either as standard length or total length. Sometimes method of measurement is not indicated, although in such cases one can usually assume this to be total length. Since the tail makes up about 17% of the total body length, one can subtract this percentage, when necessary, to obtain approximate standard length. Sex of individuals analyzed is not always indicated, despite evidence that Paralichthys females reach a larger size than males.

Controversy exists regarding results of various otolith aging studies on the species of Paralichthys. Different investigators have ...variously indicated the first 'annulus' in the summer flounder to form at ages II through VII, indicating that length-at-age information is subject to considerable error" (Rogers and Van Den Avyle 1983). Poole (1961) and Powell (1974), working on New York and North Carolina populations, respectively, determined that the first opaque ring on the otoliths of summer flounder was a valid first annulus. Poole also concluded that the species attains a maximum age of no more than 5 years, but he did not attempt to estimate maximum longevity. Eldridge (1962), Smith (1969), Daiber and Smith (1969), and Smith and Daiber (1977) determined that the first distinct opaque ring does not represent the first annulus, and concluded that this species lives as long as 8 or 9 years. Smith et al. (1981) concluded that estimates of greater longevity are more likely correct.

Similar controversy results from the age-growth studies on southern flounder by Stokes (1977) and Nall (1979) on Texas and northern Gulf of Mexico populations, respectively. Stokes concluded that this species lives a maximum of 5 years, as opposed to the 9 (occasionally 10) years projected by Nall (1979). The only age-growth studies on the gulf flounder were also conducted by Stokes (1977), who indicated that they live a maximum of 3 years. Assuming that Stokes (1977) was consistent in his aging techniques for southern and gulf flounder, one may presume that the latter species has the shorter life span of the two, although it may be longer than that indicated by Stokes.

Manooch (1984) summarized age-growth data for all three species. He indicated a maximum age of 9 years for the summer flounder, and listed the following average yearly total lengths in mm for age groups I-IX (females only): 215, 288, 377,
428, 488, 511, 531, 564, and 597 mm. These data are comparable to those provided for females of this species by Eldridge (1962) and Smith and Daiber (1977), who gave the following yearly average total lengths (also in mm) for age groups I-VII: 170, 250, 332, 377, 415, 446, and 456 mm. As indicated from the above, females not only reach a larger size but also apparently live longer, inasmuch as all individuals examined by Eldridge (1962) that were over 7 years of age were females. In all studies but one it was concluded that females live 1 year longer than males; the exception was reported by Smith (1969), who determined that male summer flounder achieve a maximum age of only 5 years, as opposed to 8 for females.

Daiber and Smith (1969) found the respective maximum sizes for female and male summer flounder from Delaware to be 661 and 517 mm TL. Powell (1974) found that only two individuals from North Carolina (out of a total of 1,029) exceeded 650 mm TL, with the largest being 750 mm. Poole (1966) determined the maximum size of females from New York to be around 800 mm TL and 5.5 kg, and for males 600 mm TL and 2.2 kg. DeSylva (1965) reported that although this species occasionally reaches 11-13.6 kg, a weight of 7 kg is unusual; he indicated that most adults weigh between 0.9-2.3 kg. Powell (1974) presented a graph showing length-weight relationships based on 1029 specimens (sexes combined) from North Carolina (Figure 12).

Manooc (1984) indicated life spans of only 5 and 3 years for the southern and gulf flounder, respectively. This information is in accord with, and may partly have been based upon, Stokes' (1977) studies from Texas. However, Nall (1979), based on examination of 152 specimens from the northern Gulf of Mexico, calculated a life span of 9 (occasionally 10) years for the southern flounder, and provided the following average standard lengths in mm (sexes combined) for each year of life approximated (total lengths indicated in parentheses): Age 0 = 63 (76), I = 102 (122), II = 145.5 (175), III = 190.5 (250), IV = 230.5 (278), V = 272 (327), VI = 320 (384), VII = 351.5 (423), VIII = 382 (460). Stokes (1977), in studies of Texas populations of the southern flounder, found differences in size and life span between males and females similar to those reported earlier for the summer flounder. He reported that females live up to 5 years and reach a total length of up to 620 mm, whereas males live only up to 3 years and reach a maximum total length of 320 mm. Although Stokes may have

![Figure 12. Length-weight relationship with fitted curve for summer flounder. Weight expressed in grams; length in total length (Powell 1974).](image-url)
underestimated the overall life span of this species, his data clearly indicate that females live longer and attain a larger size than males.

The largest individual southern flounder (620 mm TL) reported by Stokes (1977) is slightly larger than that examined by Nall (1979) (493 mm SL, or ca. 595 mm TL). Ginsburg (1952), however, reported a maximum size for this species of 630 mm SL (= 762 mm TL). Nall (1979) presented a graph showing length-weight relationships based on 152 specimens (sexes combined; Figure 13).

Stokes (1977) conducted the only age-growth study of the gulf flounder, although Nall's (1979) study contained limited data. Both studies were conducted in conjunction with work on the southern flounder, which is much more common in the respective study areas (Texas and the northern Gulf of Mexico); the small number of specimens available to Nall (33) precluded his attempting any aging estimates. Stokes (1977) concluded, based on a total of 123 specimens, that female and male gulf flounder live only 3 and 2 years, respectively, and these figures were repeated by Manooch (1984). Although the gulf flounder may live longer than indicated by Stokes, his data nevertheless strongly suggest a shorter life span for this species as compared to both the southern and summer flounders. The largest female and male gulf flounders examined by Stokes were 420 and 290 mm TL, respectively. This is substantially smaller than the 710 mm TL (5 kg) individual (sex not indicated) reported by Vick (1964) from St. Andrews Bay, Florida. The markedly greater size of Vick's specimen suggests the possibility of species misidentification (most likely with the southern flounder), and thus this record requires confirmation. Nall (1979) presented a graph showing length-weight relationships of gulf flounder, based on 33 specimens (sexes combined) (Figure 14).

There is some evidence that southern flounder from different areas grow at different rates, independent of differing interpretations of aging techniques (Etzold and Christmas 1979; Nall 1979). This may be due to combinations of differences involving genetic stock, prey availability, temperature and salinity (Deubler 1960; Stickney and White 1973; Peters and Kjelson 1975; Laurence 1977).

**Figure 13.** Length-weight relationship with fitted curve for southern flounder. Weight expressed in grams; length in standard length (Nall 1979).

**ECOLOGICAL ROLE**

**Food and Feeding**

The three species of Paralichthys under consideration consume animal
A wide variety of animal organisms, with copepod nauplii predominating. Plankton density is an important factor in larval survival, particularly since it affects the growth rate of the individual and length of the larval period, which is the time during which these fish are most vulnerable to predation (Houde and Schekter 1980).

Reid (1954) reported that gulf flounder under 45 mm TL feed primarily on amphipods and other small crustaceans; above this size they begin to feed on fish, which subsequently become the main item in their diet. Stokes (1977) found that, numerically, 95% of the food items of juvenile southern flounder (10-150 mm TL) from Texas consists of invertebrates. Juvenile southern flounder over 80 mm TL consume progressively larger food items as the fish increases in size, but there is no indication that large adult flounders eat larger prey than subadults (Darnell 1958; Fox and White 1969). Powell and Schwartz (1979) compared the year-long diets of young (100-200 mm TL) summer and southern flounder from Pamlico Sound, North Carolina (Figure 15). A much higher percentage of empty stomachs was noted during the winter months. Powell and Schwartz (1979) found the two species to feed on basically the same food items. Fish and mysids (malacostracan crustaceans) formed the bulk of their diet at all seasons; however, they found the relative percentages of food items to be consistently different, with the southern flounder feeding more heavily on fish. They considered that this most likely resulted from differing food availability in the different habitats occupied by the two species (i.e., the summer flounder prefers higher salinities and a sand bottom, whereas the southern flounder occurs in lower-salinity water over a mud-silt-clay bottom); however, they did not discount the possibility of selective

Figure 14. Length-weight relationship with fitted curve for gulf flounder. Weight expressed in grams; length in standard length (Nall 1979).

Figure 15. Length-weight relationship for gulf flounder. Weight expressed in grams; length in standard length (Nall 1979).

matter throughout life. Postlarvae feed on zooplankton and adults feed on benthic and pelagic fishes, as well as crustaceans.

Peters and Angelovic (1971) reared postlarval summer flounder on a diet of zooplankton (mostly copepods) and Artemia nauplii. Deubler (1958) raised postlarvae of summer, southern, and gulf flounder "to a definitive size" on brine shrimp (Artemia), white worms (Enchytraeus), and cut shrimp (Penaeus). Lasswell et al. (1971) reared the bulk of their diet at all seasons; however, they found the relative percentages of food items to be consistently different, with the southern flounder feeding more heavily on fish. They considered that this most likely resulted from differing food availability in the different habitats occupied by the two species (i.e., the summer flounder prefers higher salinities and a sand bottom, whereas the southern flounder occurs in lower-salinity water over a mud-silt-clay bottom); however, they did not discount the possibility of selective

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Frequency of occurrence of different fish species in the diet appears to depend more on local and/or seasonal prey abundance than on specific prey selection (Darnell 1958; Fox and White 1969).

Feeding behavior has only been described for the summer flounder, but presumably is similar for all three species. The summer flounder is primarily a diurnal feeder that can capture its prey equally well on the bottom or in the water column (Olla et al. 1972; Powell and Schwartz 1979). Although it may bury itself in bottom sediments, it does not ambush passing prey, but rather stalks its quarry along the bottom before striking at speeds of 40 to 50 cm/sec (Olla et al. 1972).

ENVIRONMENTAL REQUIREMENTS

Substrate

The three species of Paralichthys under discussion apparently prefer specific substrates. Most studies indicate that the summer flounder prefers a hard and/or sandy substrate (Hildebrand and Schroeder 1928; Bigelow and Schroeder 1953; Powell and Schwartz 1979), as does the gulf flounder (Ginsburg 1952; Stokes 1977; Nall 1979), but the southern flounder is most abundant on soft bottoms comprised of rich organic mud, clay, or silt (Ginsburg 1952; Stokes 1977; Nall 1979; Powell and Schwartz 1979). The contrasting relative abundance of southern and gulf flounder in the eastern Gulf of Mexico may reflect these habitat preferences, inasmuch as the western gulf (where the southern flounder predominates) is substantially muddier, on the average, than the eastern gulf (Lynch 1954).
Tabb and Manning (1961) reported that southern flounder from southwestern Florida occur over shell and firm marl bottoms, but Topp and Hoff (1972) questioned their species identifications, since the area where these observations were made is outside the known geographic range of this species. Dahlberg and Odum (1970) reported southern flounder in Georgia from bays with primarily sand bottoms. Springer and Woodburn (1960) collected gulf flounder over a wide variety of habitats in the Tampa Bay area of Florida. Moe and Martin (1965) collected a few gulf flounder near rocky offshore reefs, and this species occasionally has been found around coral reefs in the extreme western Bahamas (Bohlke and Chaplin 1968). Nall (1979), based on observations of 152 specimens, never found southern flounder over an exclusively sand bottom, but noted that gulf flounder were somewhat less specific with regard to bottom type. Of 33 specimens analyzed, 12 were collected over a sand bottom, 16 came from a combination sand-mud bottom, and 5 were from a strictly mud bottom.

**Salinity**

Adult southern flounder, in contrast to adult gulf and summer flounder, are highly euryhaline, as indicated by their frequent occurrence in rivers (Ross 1980). Analyses of collections of adult southern and gulf flounders from a wide geographic area (Florida to Texas) usually indicate a strong preference by the former species for salinities less than 20 ppt (Gunter 1945; Tagatz 1968; Stokes 1977) and by the latter species for salinities greater than this (Reid 1954; Springer and Woodburn 1960; Stokes 1977). Perret (1971), however, reported samples of southern flounder (totaling about 800 individuals) taken from Louisiana estuaries to be equally distributed over salinities ranging from 0 to slightly over 30 ppt. Powell (1974), in his analysis of the relative numbers of adult southern and summer flounder in a North Carolina estuary, found an inverse relationship between the two species with regard to salinity; southern flounder predominated at salinities up to 11 ppt (85% of the total), but above 11 ppt the summer flounder predominated (65% of the total). Another sharp change in relative percentages of individuals of these two species was noted as salinity increased from 17 to 18 ppt; at this point the relative abundance of summer flounder increased from 65% to 94%.

Juvenile southern flounder appear to be more strongly euryhaline than juveniles of the other two species, and have been shown to survive abrupt transfer from nearly full-strength seawater (30 ppt) to freshwater (Deubler 1960). Although juvenile southern flounder have been collected from North Carolina estuaries at salinities ranging from 0.2 to 35.0 ppt (Powell and Schwartz 1977), it appears that a change in salinity tolerance occurs during development from early postlarval to a more advanced postlarval stage. Early postlarvae of this species grow most rapidly at higher salinities (ca. 30 ppt), but individuals of this size (0.1 g) are not very tolerant of extremely low salinities; however, advanced postlarvae do best at salinities of 5-15 ppt (Stickney and White 1973). Deubler and White (1962) showed that advanced postlarval summer flounder, by contrast, exhibit the greatest percentage weight gain at salinities between 20 and 30 ppt. The differing salinity levels at which optimal development of southern and summer flounder occurs during laboratory experiments reflect the different natural environmental conditions under which these two species are found.
Powell and Schwartz (1977) reported collecting juvenile gulf flounder from North Carolina estuaries at salinities ranging from 6 to 35 ppt, whereas Williams and Deubler (1968) reported taking them only over a salinity range from 22 to 35 ppt. In both cases, however, it was indicated that greatest abundance was found near mouths of estuaries, where salinities were highest.

Hickman (1968) found that adult southern flounder exhibit seasonal changes in osmoregulatory processes that correspond to spawning migrations between estuarine and offshore waters.

Temperature

Adults of the three species of Paralichthys under discussion have been reported over comparable temperature ranges. Perret (1971) reported collecting adult southern flounders from Louisiana estuaries over a temperature range of 5.0-34.9°C (41.0-94.8°F). These figures represent both the minimum and maximum temperatures reported for adults of this species throughout its range, and exceed the temperature ranges reported by Barrett et al. (1978) from Louisiana, and by Gunter (1945) and Stokes (1977) from Texas. All temperature data on adult gulf flounders are based on observations from Florida, and range from 8.3°C (46.9°F) (Reid 1954) to 32.5°C (90.5°F) (Springer and Woodburn 1960). Powell (1974) reported the minimum and maximum temperatures at which summer flounders were collected in Pamlico Sound, North Carolina, to range from 7°C (44.6°F) in February to 29°C (84.4°F) in July and August.

Stokes (1977) found that adults of both the southern and gulf flounders left Aransas Bay, Texas, during the period when the mean water temperature dropped from 23.0°C (73.4°F) in October to 14.1°C (57.4°F) in December. Maximum emigration often (though not always) coincided with the passage of cold fronts, when sudden drops in temperature (up to 4-5°C) occurred.

Williams and Deubler (1968) reported the capture of juvenile southern and gulf flounders in Atlantic estuaries at water temperatures as low as 2-4°C (35.6-39.2°F), and Gunter (1945) found juvenile southern flounder (17-40 mm) in Texas estuaries at temperatures from 14.5 to 21.6°C (58.1-70.9°F). Stokes (1977) found that juvenile southern and gulf flounders began to immigrate into Texas estuaries from the Gulf of Mexico at water temperatures as low as 13.8°C (56.8°F), but peak movement occurred between 16.0 and 16.2°C (60.8-61.2°F). Williams and Deubler (1968) reported the capture of juvenile summer flounder over a temperature range of 2-22°C (35.6-71.6°F); most individuals were found in the 8-16°C (46.4-60.8°F) temperature range.

Temperature is important in the life histories of these species, and affects such things as time of spawning, movement of adults and larvae into different habitats, availability of preferred food items, maximal efficiency of food conversion, and rapidity of growth.

Vegetation

Aquatic vegetation does not appear important to the basic ecology of adult Paralichthys, but is utilized by juveniles. Adams (1976) and Orth and Heck (1980) reported that juvenile summer flounder occur in eelgrass (Zostera marina) beds during daylight hours, either to take advantage of the cover afforded or to feed on small fish and invertebrates that congregate there. Stokes (1977) found juveniles of both southern and gulf flounders to be most abundant in those areas of
estuaries where dense patches of shoal grass (Diplanthera wrightitii) were present and covered 30% to 60% of the total area. Reid (1954) reported juvenile gulf flounder to be abundant on shallow grass flats around Cedar Keys, on the gulf coast of northern peninsular Florida.

Dissolved oxygen

Deubler and Posner's (1963) laboratory study of juvenile southern flounder apparently is the only work published on oxygen requirements of any Paralichthys species. They found that juvenile southern flounder actively moved into more highly oxygenated water when the dissolved oxygen concentration fell below 3.7 mg/liter. Although they noted increased general activity with an increase in water temperature, there was no increase in sensitivity to oxygen depletion at temperature levels of 6.1°, 14.4°, and 25.3°C (43.0°, 57.9°, and 77.5 °F, respectively).

FISHERY

Quality and Value of Commercial Fishery

The three species of Paralichthys under discussion are highly prized North American food fishes; the relative importance of each species is greatest in the area of its highest abundance. From late spring into the fall most commercial catches of these fish are made by shrimp trawlers fishing close inshore or in estuaries, and smaller numbers are caught by individual fishermen "gigging" (i.e., spearing) in the shallows at night. Lesser numbers of summer flounder are caught at this time in fyke nets, weirs, traps, and pound nets (Manooch 1984). During the winter months, most are caught by vessels fishing with otter trawls in deeper waters offshore.

The three species are lumped together (either as "fluke" or "flounder") in Federal commercial catch statistics (BCF 1939a-1968a; NMFS 1969a-1977a; BCF 1964b-1968b; NMFS 1969b-1985b). In some cases they were distinguished from other commercially important flatfish species living along the upper Atlantic coast (i.e., north of North Carolina), such as "blackback," or winter flounder (Pseudopleuronectes americanus) and yellowtail flounder (Limanda ferruginea), whereas in other cases these species were combined in catch statistics. Unfortunately, in those cases in which the above taxa were separated, catch statistics were combined for the entire Atlantic coast and Gulf of Mexico (BCF 1964b-1968b; NMFS 1969b-1985b); alternately, when this broad geographic region was broken down into smaller subregions, these taxa were combined (BCF 1939a-1968a; NMFS 1969a-1977a). This greatly complicates interpretation of catch statistics from the upper Atlantic coast, and allows meaningful comparison only for the lower Atlantic coast and Gulf of Mexico.

For the South Atlantic region, the total poundage of flounders remained relatively low until 1945, ranging from 132,000 lb in 1918 to 1.5 million lb in 1936 (BCF 1939a-1968a). In 1945, there was an increase to about 2.1 million lb, a circumstance likely related in part to cessation of the war. Catches dropped during the late 1950's, but subsequently increased and reached a peak of slightly over 5.1 million lb in 1965, for a total value of just over 1 million dollars. By 1977 (the last year for which data are available for this specific area), the total catch had risen to 11.4 million lb, for a total value of 5.1 million dollars. (Keep in mind that dollar values are biased by inflation.) Over 90% of the "flounder" catch for the South Atlantic area comes from North Carolina, and can
be attributed in large degree to the substantially greater abundance of summer flounder in that area, as opposed to farther south.

Total catches of "flounder" from the Gulf of Mexico area are substantially less, but show a similar upward trend. Commercial catches ranged from a low of 192,000 lb in 1888 to over 1.1 million lb in 1945, and had increased slightly to 1.2 million lb by 1965, for a value of $231,000. By 1977 the total catch amounted to slightly over 1.5 million lb, for a value of $561,000. In contrast to the situation in the South Atlantic area, no one State bordering the Gulf of Mexico was dominant in terms of the number of pounds harvested.

The relative importance of "flounder" in commercial catches has increased substantially in comparison to most other commercially important marine food species. Prior to 1945, for example, catches of "flounder" along the South Atlantic coast were substantially less than those for "croakers" or "drums" (several species, but predominantly the Atlantic croaker), bluefish, king mackerel, Spanish mackerel, kingfish or king mackerel, striped mullet, sea trout, and spot. By 1965, the total poundage of "flounder" exceeded the total for each of the above except mullet. By 1977, the total poundage exceeded that for each of the other species (most by a substantial amount) except croakers, and the total dollar value was greater than for each of the above in both 1965 and 1977 (comparative dollar values are not available prior to 1945).

Recent total poundage and dollar value figures for "flounder" from the Gulf of Mexico are well below those for a number of other commercial fish species, but nevertheless show an upward trend comparable to that seen for the South Atlantic coast.

Commercial catch data for flounder from Florida during the period 1964-1983 (Fla. Dep. Nat. Res., unpub. Florida landings) show results somewhat different from those given above. Although total poundage of flounder increased during this period, from a low of 336,600 lb in 1967 to a high of 775,400 lb in 1982, the overall importance of flounder in relation to other edible commercial marine species in Florida has stayed about the same. It ranks about 15th behind such fishes as groupers (several species, the most important of which is the red grouper); several species of snapper, including mangrove, red, and yellowtail; Spanish mackerel; king mackerel; striped mullet; sheepshead; Florida pompano; Jack crevalle; spotted seatrout; king whiting; spot; and several species of "croakers" or "drums," such as Atlantic croaker and redfish.

Data from Florida also include a breakdown of commercial catches of flounder according to location (i.e., Atlantic and Gulf of Mexico coasts). These show consistently higher catches for the gulf coast. In 1969, the catch for the Atlantic coast was less than 50% of that for the gulf coast (120,000 vs. 268,600 lb), but for most years the relative percentages ranged above 70%, with a high of 88% in 1981 (276,900 vs. 313,200 lb). Extremes in yields for the Atlantic coast ranged from 120,000 lb in 1969 to 322,500 lb in 1979; for the gulf coast these figures ranged from 182,800 lb in 1967 to 404,200 lb in 1979.

Sport Fishery

Flounder are caught by sport fishermen using various techniques, such as still fishing, drift fishing, casting from shore, and angling from piers and banks using live, fresh, or frozen baits cast 6 to 18 inches above the bottom (Wisner 1965).
Another popular method for catching these fish in some areas is by "gigging" at night in shallow water, using a long-handled, three-pronged spear and a torch or flashlight (DeSylva 1965). Sport fishing usually begins in the spring (when the fish return from deeper waters offshore, where they have spent the winter), and continues into the fall.

Sport catch statistics for the Atlantic and gulf coasts (NMFS 1969b-1985b) are more informative than commercial catch statistics because individual species are identified. These data indicate that the summer flounder is one of the most important game fishes, in terms of numbers caught, along the mid-Atlantic coast between Cape Hatteras and Cape Cod, together with winter flounder, bluefish, white perch, spot, scup, and various searobins. In 1980, it ranked second only to bluefish, but in 1979 it ranked about fifth in number. Based on average size of individuals caught, it would rank well ahead of all of the above except winter flounder and bluefish. Along the south Atlantic and gulf coasts, however, the numbers of flounder caught are well below those for many other sport species.
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Species Profiles are literature summaries of the taxonomy, morphology, range, life history, and environmental requirements of coastal species. The southern, gulf, and summer flounders live most of their lives in or near estuaries. Adults migrate into offshore waters during fall and winter, where spawning occurs from September to April. Eggs and newly-hatched larvae are carried inshore into estuaries, where further growth takes place. Age at sexual maturity for the three species has been estimated from 2 to 4 years, and maximum longevity from 3 to 10 years. Females apparently live slightly longer than males. Southern and summer flounders are estimated to live slightly longer than the smaller gulf flounder. Postlarvae eat mostly zooplankton, and larger individuals feed on fish and crustaceans. The summer and gulf flounders prefer a hard and/or sandy substrate, whereas the southern flounder is more common in a soft bottom of rich organic mud, clay, or silt. The southern flounder, unlike the other two species, is highly euryhaline, and frequently occurs in fresh water. Commercial catch statistics lump the three species together under the name "flounder." Peak commercial catch in the Gulf of Mexico (in 1977) was 1.5 million lb, for a value of $561,000; peak catch in the south Atlantic region (also in 1977) was 11.4 million lb, for a value of $5,100,000.