Species Profile – Summer Flounder (*Paralichthys dentatus*)

Species range/distribution

The geographical range of the summer flounder generally encompasses the shallow estuarine waters and outer continental shelf from Nova Scotia to Florida, although some report their range extending into the gulf of Mexico (Packer et al. 1999).

Habitat Characteristics/Habitat Use

Eggs and larvae

Eggs and larvae are pelagic. Convergence of shelf water flows from the Mid- and South Atlantic Bights (MAB and SAB) upon Cape Hatteras, NC, presents a potential barrier to the exchange of fish larvae between bights. Impinging water often turns northeastward with the Gulf Stream, and larvae of both cool temperate and warm temperate/subtropical shelf fishes suffer expatriation. Transient oceanographic features exist, however, facilitating shelf retention, cross-bight exchange, and return of expatriated larvae. The impact of these features is mitigated by specific distribution with relation to hydrography, resulting in a selective permeability of this barrier. Dynamic oceanography may result in dynamic recruitment success. Grothues et al. (2002) measured the springtime (1996) flux of seven larval fish species assemblages across the confluence by coupling measured water mass/depth specific larval fish concentration with water mass transport values obtained from an extensive moored instrument survey. The assemblage to which summer flounder belonged was the MAB/SAB transition group, and the flow of all the water masses affected this group, which had the widest distribution. This was the only group for which slope water transport played an important role. The larvae from this group were concentrated 2-3 orders of magnitude higher in slope water than in other water masses. Nearshore southward slope water flow accounted for more of the flow south from the study area into the SAB than did MAB or plume water. Gain to the nearshore study area from across the shelf in MAB water did not offset loss across the shelf in SAB and slope water combined. Net flux was out to sea (Grothues et al. 2002).

Selective tidal stream transport is a mechanism by which larval/juvenile summer flounder move into and through estuaries (see Burke et al. 1998, cited and discussed in Packer et al. 1999). Essentially, for larvae moving from the shelf to estuaries, the larvae will move higher into the water column during flood tide and lower into the water column during ebb tide. Hare et al. (2005) considered alternative mechanisms, including passive explanations, for tidal patterns in larval distributions. They examined the biophysical mechanisms responsible for transforming larval to juvenile (G stage, ~ 10 mm) summer flounder ingress into Chesapeake Bay using a Eulerian approach, making flux calculations and partitioned flux estimates among 3 different ingress mechanisms (wind forcing, residual bottom inflow, and tidal). Ingress of the transforming larvae was dominated by tidal mechanisms, and the importance of tides increased with developmental stage. They found little evidence for the hypothesis that tidal patterns in larval distributions resulted from passive processes (water mass-specific distributions, buoyancy, vertical mixing), thereby supporting the hypothesis that tidal patterns resulted from active behaviors (see also Hare et al. 2006).

Source: Packer et al. 1999 and Packer, D.B. 2017.
Summer Flounder Eggs and Larvae

Life Stage	Location	Months/Years	Depth (m)	Mean temperature (0-200 m)
Eggs	Shelf	Oct-Dec, 1978-87	0-100	11-20
Larvae	Shelf	Oct-Dec, 1978-87	0-120	12-20

Juveniles

Juvenile summer flounder were found in the inner continental shelf on Fenwick and Weaver shoals offshore of Maryland and Delaware in habitat dominated by Asabellides occulata (polychaete) tubes; they were not found in other, less spatially complex habitats that were sampled (Diaz et al. 2003).

Nacaise et al. (2005) assessed habitat quality in terms of juvenile fish growth and mortality using basic abiotic factors (temperature, DO, pH) as the major variables. Juveniles (42-59 mm TL) were caged at five sites around Masonboro Is., NC during June and July 1999. Although abiotic conditions varied significantly among sites, no differences in growth rates were detected among sites. Variability in growth rates both within and among sites was high, with one site experiencing total mortality. Although growth rates among sites were not statistically different, there was a trend toward slightly higher growth in mainland creeks than in barrier creeks. Additionally, mortality occurred more often in barrier island enclosures than in mainland enclosures. This pattern seems to contradict the convention, as seen in previous studies, that juveniles preferentially occupy higher salinity habitats near the mouths of estuaries. Nacaise et al. (2005) suggest that basic abiotic conditions, at the levels and durations that occur with a southeastern U.S. estuary during summer, have little impact on juvenile growth, but may influence survival.

Tyler (2005) examined the effect of diel DO fluctuation on habitat usage by summer flounder juveniles, both in the laboratory and in Pepper Creek, a tributary of Indian River Bay, Delaware over the summers of 2001-2003. Bottom DO was measured continuously each summer using multi-parameter sondes. Vertical DO variability was examined in 2001 on nine dates. Summer flounder were monitored at each sonde site in 2001 (3sites, 20 dates) and 2002 (2 sites, 17 dates) using an otter trawl to examine fish abundance and distribution in relation to changes in DO. The laboratory study utilized two-way DO choice experiments at selected levels of temperature and salinity to determine the DO that prompts avoidance behavior. Fluctuation increased in the up-tributary direction during 2001 when severe hypoxia (< 2 mg O2 1-1) occurred at the upper site almost daily between mid-June and early September for periods of 1-4 hours. Severe hypoxia occurred less frequently in 2002 and 2003. Vertical DO variation, and typically concentration were lowest around sunrise. Summer flounder declined during both years around when severe hypoxia events began and their movements in response to DO were unclear. They were most abundant in the upper creek despite lower frequency of severe hypoxia events at the middle and lower sites. In the laboratory, the flounder avoided 1mg O2 1-1 but not 2 mg O2 1-1. Tyler suggests that the sedentary nature of many summer flounder in the laboratory, even at 1mg O2 1-1, suggests that in the natural environment this species might not initiate avoidance behavior until too late to escape a lethal condition. However, this conclusion may contradict other summer flounder DO studies (see discussions in Packer et al. 1999 and Bell and Eggleston 2005, below).

Stierhoff et al. (2006) measured growth and feeding rates in juvenile summer flounder (55-90 mm SL) exposed to sub-lethal hypoxia (low DO) over a range of temperatures, to determine its potential effects on nursery habitat quality. Juveniles were collected from Pepper Creek in the Delaware Coastal Bays, and also from Delaware Bay (near Lewes, DE) between April and June 2001, 2003, and 2004. Growth rates were generally reduced as DO decreased, particularly at DO levels of 50 to 70% air saturation, and as temperature increases. Summer flounder was fairly tolerant of low DO at both 20 and 25°C. At these temperatures, growth was reduced by ~25% (compared to growth at normoxia [7.0 mg O2 l–1]) at 3.5 mg O2 l–1 and by 50 to 60% at 2.0 mg O2 l–1. At 30°C growth was significantly reduced even at 5.0 mg O2 l–1, and was reduced by ~90% at 2.0 mg O2 l–1. A significant relationship between feeding rate and growth suggested reduced consumption to be a major cause of growth limitation under hypoxia. [See also Getchis and Bengtson (2006), who suggest that differences in the rates of food consumption directly influence growth rate variation in newly settled laboratory-reared summer flounder.] There was no evidence of growth acclimation after 7 to 14 d exposure to hypoxia. The effect of hypoxia on growth was reduced at lower salinity (15 vs. 25‰) and was unaffected by the presence of a sand substrate. Similarity between modeled growth under hypoxic conditions, based on their laboratory results, and observed growth of summer flounder in a hypoxic estuarine tributary suggests growth limitation in the wild. Stierhoff et al.

(2006) suggest that these laboratory and field results demonstrate that even moderate hypoxia can adversely affect growth rates, and thus the quality of estuarine nursery habitats for juvenile summer flounder. (See also the later study by Stierhoff et al. (2009), whose results also suggest a strong functional relationship between DO concentration and the growth rate of juvenile summer in the same estuarine nursery. Furthermore, growth rates of wild-caught fishes [estimated from RNA:DNA] appear to be more negatively impacted by diel cycling hypoxia than would be expected from published laboratory data.)

The timing of larval metamorphosis in summer flounder from the same cohort (i.e., siblings with the same parents) and among cohorts (different parents) is variable due to large differences in individual growth rates. In an effort to understand the energetic basis for growth rate differences, Katersky et al. (2006) measured rates of routine (RR) and specific dynamic action (RSDA) respiration (μg O2/fish/h) in groups of newly metamorphosed summer flounder in the lab (broodstock collected from Long Island Sound) and compared among fish of different sizes (15, 20, 25, and 30 mm TL) and between fast- and slow-growing fish from five cohorts each having a different set of parents. Rates of respiration by fish have been classified into different levels based upon the activity occurring during the measurements; among these, RR corresponds to the energy expended due to routine movements, and RSDA corresponds to energy expended due to feeding, digestion and assimilation of food. Although rates of RR significantly increased with increasing fish size, they were not significantly different between the fastest and slowest growing fish within a cohort. Respiration rates rapidly increased during feeding and the differences in RSDA were noted among fish of different sizes and between fast- and slow-growing fish. However, the results of this study suggest that the energetic basis for growth differences among summer flounder appears to result from processes related to energy intake (e.g., food consumption) rather than those related to routine or feeding energy loss (Katersky et al. 2006).

Source: Packer et al. 1999 and Packer, D.B. 2017.
Juvenile Summer Flounder (<29 cm TL)

Location	Years	Time of Year	Depth (m)	Bottom Temp (°C)	Salinity (ppt)	DO (mg/l)
Shelf	1968-2003	Spring	1-40	6-19	26-31	
Shelf	1963-2003	Fall	1-30	17-28	29-33	
Shelf	1964-1997	Winter	30-60	9-12		
Shelf	1964-1995	Summer	10-20	18-25		
MA	1978-2003	Spring	11-20	10-13		
MA	1978-2003	Fall	6-20	18-22		
Ches Bay	1988-1999	All year	10-18	17-29	17-32	2.5-8.5

Adults

Bell and Eggleston (2005) conducted trawl surveys to examine the avoidance responses of several common estuarine species, including summer and southern flounders, to chronic hypoxia and episodic hypoxic upwelling events in the Neuse River Estuary, NC. Collections were made in three depth strata (3.0–4.6 m, 1.7–3.0 m, and 0.9–1.7 m depth) to quantify changes in the depth-specific distribution and abundance patterns of the six most common estuarine taxa during three dissolved oxygen conditions: normoxia, chronic hypoxia, and episodic hypoxic upwelling events. Flounder abundance increased with increasing dissolved oxygen concentrations, and they exhibited some of the strongest avoidance responses. The flounders displayed a sigmoidal response to decreasing DO, indicating that these species may exhibit a strong threshold avoidance response at DO concentrations < 2–3 mg l-1. Bell and Eggleston (2005) suggest that the primary avoidance mechanism for the flounders is to move laterally towards shallower water, which is further supported by the strong shift in distribution towards shallower water during chronic and episodic hypoxia, relative to other species in the present study.

Lathrop et al. (2006) assessed the efficacy of using sidescan sonar imagery, image classification algorithms, and geographic information system (GIS) techniques to characterize the seafloor bottom of the New York Bight Apex. The resulting seafloor bottom type map was compared with summer flounder trawl survey data to determine whether there were any discernible habitat associations. An unsupervised classification with 20 spectral classes was produced using the sidescan sonar imagery, bathymetry and secondarily derived spatial heterogeneity to characterize homogenous regions within the study area. The spectral classes, geologic interpretations of the study region, bathymetry and a bottom landform index were used to produce a seafloor bottom type map of nine different bottom types. Examination of sediment sample data by bottom type indicated that each bottom type class had a distinct composition of sediments. Analysis of summer flounder presence/absence data from NEFSC trawl surveys did not show evidence of strong associations between the species distributions and seafloor bottom type. However, Lathrop et al. (2006) suggest the absence of strong habitat associations may be more attributable to the coarse scale and geographic uncertainty of the trawl sampling data than conclusive evidence that no habitat associations exist for this species.

Sackett et al. (2007) used ultrasonic telemetry, both passive and active, during 2003-2005 to determine the timing and rate of juvenile and adult summer flounder (268-535mm TL) migrating to and from the Mullica River-Great Bay estuary in southern New Jersey. Seven years of inner continental shelf surveys off New Jersey were also used to assess complementary seasonal movements. The broad seasonal inshore/offshore patterns of movement/migration observed in this study from the inner shelf otter trawl survey and from fish tagged in the estuary were consistent with the general patterns assumed by previous investigations (e.g., see Packer et al. 1999.) Most tagged fish emigrated from the estuary between July and September, though emigration lasted into December and appeared to be influenced by a number of factors. In July 2004, more tagged fish emigrated, at increased rates of movement, at low barometric pressure during a storm event. Trawl collections on the inner shelf demonstrated the same approximate immigration times as seen with telemetry. Later in the fall, increased numbers of tagged summer flounder emigrated from the estuary when dissolved oxygen was decreasing. Fall trawl surveys showed increased numbers of fish on the inner shelf when dissolved oxygen was decreasing in the Mullica River-Great Bay estuary, supporting the telemetry results. Fish emigrated from the estuary during the day and night but nighttime movements were in deeper water at slightly slower rates of movement. Exit and re-entry also occurred during the fall emigration. Ultrasonically tagged individuals demonstrated homing by returning to the same estuary, in March through June, in the second and third year of the study. In summary, immigration may result from homing for a large proportion of summer flounder. Emigration may be associated with storms on an episodic scale, and dissolved oxygen and temperature on a seasonal scale (see continuation of this study, below).

As part of this same passive and active ultrasonic telemetry study on juvenile/adult summer flounder in Mullica River-Great Bay estuary, Sackett et al. (2008) also focused on their temporal and spatial patterns of habitat use during years, seasons, tides, and diel periods. Annual site fidelity was demonstrated by tagged fish that returned to the estuary and frequented locales within 550 m or less of the sites where they were located in previous year(s). Fish resided within the estuary for a mean of 86 d (range: 1-217 d) during summer 2004, the year of the most comprehensive tracking. Fish primarily utilized the lower bay, close to the ocean inlet. Several more mobile individuals moved along the channel of the Intracoastal Waterway in Great Bay numerous times in a single season, while others moved up the bay and into the river in a year when salinity was higher than average. Tagged fish typically used deeper areas of the estuary correlated with high, stable levels of DO and temperature. Over diel and tidal periods, fish resided within small (0.18 km2) areas for 3-6 h but were in motion 74% of that time. Sackett et al. (2008) suggest that together, these observations indicate habitat-use patterns that are stable over long periods (years) but dynamic within shorter time periods (seasons, hours).

Slacum et al. (2008) tested the association between abundance of adult summer flounder and benthic habitat features at two study areas in the Middle Atlantic Bight on the inner continental shelf in summer 2004. The first area was located offshore of Ocean City, MD, and the second was located offshore of Point Judith, R.I. Both of these areas were known to support a nearshore day fishery for summer flounder during the summer months. The study included trawl and remote-sensing surveys that were designed and conducted with the assistance of

commercial fishers. Within each area, a local commercial fisher designated specific locations a priori as productive or unproductive for fishing. Summer flounder abundance, as measured by mean catch per area swept, was significantly greater at sites designated as productive than at sites designated as unproductive (6.5 times greater in Maryland and 4.7 times greater in Rhode Island). The results indicate that summer flounder were attracted consistently to localized habitats that must have had different characteristics than other nearby locations. Habitat variables associated with the substrate (e.g., particle size, bottom shape, and presence of sessile organisms) were measured along trawl paths using underwater video imagery. The measured variables did not explain abundance well, suggesting that microscale characteristics of the substrate did not affect summer flounder distribution. Depth was the best predictor of summer flounder distribution in this study. Most summer flounder were captured between 10- 20 m, which agrees closely with data reported elsewhere in New England and the Middle Atlantic Bight (Packer et al. 1999). However, because in the Slacum et al. (2008) study, both high and low catch rates occurred in this depth range, they suggest that other factors were also important. Slacum et al. (2008) suggest that additional localized variables merit further investigation to determine their importance to summer flounder. The study also demonstrates the importance of combining fishers' knowledge and experience with planned surveys to identify essential habitat features for fish.

Source: Packer et al. 1999 and Packer, D.B. 2017.

`Adult Summer Flounder (≥29 cm TL)`

Location	Years	Time of Year	Depth (m)	Bottom Temp (°C)	Salinity (ppt)	DO (mg/l)
Shelf	1968-2003	Spring	1-20+61-140	8-17	34-36	
Shelf	1963-2003	Fall	1-40	15-24	30-32	
Shelf	1964-1997	Winter	40-100	8-12		
Shelf	1964-1995	Summer	10-20	18-23		
MA	1978-2003	Spring	6-25	10-16		
MA	1978-2003	Fall	6-20	15-22		
Narra Bay	1990-1996	Spring	40-110	9-14		
Narra Bay	1990-1996	Summer	30-100	18-23		
Narra Bay	1990-1996	Fall	???	18-23		
Ches Bay	1988-1999	All year	8-22	10-26	16-32	3.5-9.5

Migrations

Summer flounder exhibit strong seasonal inshore offshore movements. Adult and juvenile summer flounder normally inhabit shallow coastal and estuarine waters during the warmer months of the year and remain offshore during the fall and winter.

While information on finer-scale migration patterns is generally unavailable, historical tagging studies suggest that depending on the season and release location, general patterns of "north-south," "east-west," and "inshore-offshore" movements are possible. Murawski (1970) reported that fish tagged from New Jersey in the 1960s moved from inshore waters to offshore wintering grounds, with dispersion to both the south toward Virginia and to the north-east toward southern New England. Lux and Nichy's (1980) tagging results from the 1960s indicated that fish from inshore Southern New England (SNE) waters tagged in September had a broad range of movement, including east and offshore to Veatch Canyon south of Massachusetts, south and offshore to Block and Hudson canyons, and offshore as far southwest as Cape May NJ. Finally, Monaghan's tagging work (1992) on North Carolina fish in the early 1990s showed that fish tagged north of Hatteras mostly moved offshore and north as far as northern New Jersey. Fish tagged south of Hatteras moved to the southwest as far as the North Carolina-South Carolina border.

Food Habits

Summer flounder are opportunistic feeders; their prey includes a variety of fish and crustaceans. The NEFSC trawl survey foods habits database contains information from 18,862 summer flounder stomachs sampled on 5,365 tows, over 70% of which were found to be empty. 'Other fish' (fish which could not be identified to family) were found in about 10% of the stomachs, followed by squids (6%), decapod shrimp (4%), 'animal remains' (3%; partially digested stomach contents), anchovies (2%), and other gadids, porgies, mysids, and other small crustaceans. The data were summarized into 4 multi-year blocks to look for temporal patterns. The frequency of 'Other fish' and decapod shrimp consumption by summer flounder decreased by about 50% over the time series, while the frequency of consumption of squid slightly increased. The frequency of consumption of anchovies peaked in the 1980s. The calculation of total absolute consumption of prey by summer flounder has not been attempted (NEFSC 2013).

Previous studies have inferred that larval and postlarval summer flounder initially feed on zooplankton and small crustaceans (Peters and Angelovic 1971, Powell 1974, Morse 1981, Timmons 1995). Food habits studies on late larval and juvenile estuarine summer flounder reveal that while they are opportunistic feeders and differences in diet are often related to the availability of prey, there also appears to be ontogenetic changes in diet. Smaller flounder (usually less than 4 inches; 100 mm) seem to focus on crustaceans and polychaetes while fish become a little more important in the diets of the larger juveniles (MAFMC 2002).

Adult flounder are most active during daylight hours and may be found well up in the water column as well as on the bottom (Olla et al. 1972). Included in their diet are: windowpane, winter flounder, northern pipefish, Atlantic menhaden, bay anchovy, red hake, silver hake, scup, Atlantic silverside, American sand lance, bluefish, weakfish, mummichog, rock crabs, squids, shrimps, small bivalve and gastropod molluscs, small crustaceans, marine worms and sand dollars (NEFSC 2013; Packer et al. 1999, MAFMC 2002).

The NEFSC trawl survey foods habits database includes summer flounder as a prey item in 65 predator stomachs over the period 1973-2011. Spiny dogfish was the predator in 35 cases (54%), followed by monkfish (11 cases, 17%), winter skate (7 cases, 11%). and bluefish (4 cases, 6%), with other fish species accounting for the other 9 cases and 12%, including 1 case (2%) of summer flounder cannibalism. All of the natural predators of adult summer flounder are not fully documented, and these data are insufficient to calculate total absolute predator consumption of summer flounder (NEFSC 2013).

Using the NEFSC food habits database from Maine to Cape Hatteras for the period 1977-1997, Overholtz et al. (2000) showed that consumption of Atlantic herring by summer flounder was relatively low but consistent during this period.

Bowman et al. (2000), using the same NEFSC food habits database, but only for the years 1977-1980, found that fish dominated the diet for all size classes of summer flounder except for those 56-60 cm, where the squid Loligo pealeii was the dominant prey item (Table 1). Among the more important fish prey are sand lance (Ammodytes dubius) for flounder 26-30 cm, 36-40 cm, and 51-55 cm, and silver hake for flounder < 21 cm. Another major prey item found in the stomachs of summer flounder was crustaceans (e.g, decapods such as Cancer irroratus for flounder < 21 cm). Regionally, Bowman et al. (2000) showed that fish dominated the diet in the Mid-Atlantic, Georges Bank, and inshore north and south of Cape Hatteras (Table 2), with sand lance being important prey in the Mid-Atlantic and Georges Bank, and moustache sculpin (*Triglops murrayi*) being important along inshore south of Cape Hatteras. Other notable regional fish prey included striped anchovy (*Anchoa hepsetus*) along inshore south of Cape Hatteras, and toadfishes, family Batrachoididae, on Georges Bank. Squids were the dominant prey in southern New England, and in the Gulf of Maine, the euphausiid, *Meganyctiphanes norvegica*, was the only prey found in the stomachs of summer flounder examined from that area.

Link and Burnett (2001) also used the NEFSC food habits database and the stomach content data from the Coastal Ocean Program on Georges Bank from 1992-1998 to examine the relationships between feeding and reproduction

in several species, including summer flounder. Some species showed an increase in feeding during the developing, ripe, and running stages of reproduction, indicative of the 'ramper' strategy (or a way of storing energy), while others showed an increase in feeding after spawning in the spent or resting stage of reproduction, indicative of the 'rester' strategy (or a way of restoring energy). However, for summer flounder in the Gulf of Maine, there was no discernable pattern. Summer flounder did show a significant interaction effect between maturity stage and region; stomach contents of ripe and spent stages were highest in southern New England.

Link et al. (2002), again using the NEFSC food habits database from 1973-1998, showed that summer flounder ate primarily fish and cephalopods. Loligo squid, unclassified cephalopods, sand lance, herrings, anchovies, and unidentified or other fish comprised > 80% of the diet. There were significant shifts in diet across the time series, with sand lance unclassified cephalopods, and Illex squids more common in the diet in the 1970s than more recently. Loligo squid, unidentified fish, and herrings have become significantly more prominent in the diet in the 1990s. Major ontogenetic shifts in diet were from anchovies, mysids, Crangon, and similar shrimps, to fish and squids at larger sizes; summer flounder also consumed fewer polychaetes with increasing sizes. The mean stomach contents of summer flounder peaked in the 1986-1990 period, and then declined over the 1990s; the latter also occurred with the other flatfish examined in the study.

Manderson et al. (2000) examined the predator-prey interaction between age 1+ summer flounder (252-648 mm TL) and age-0 winter flounder via laboratory experiments and weekly trammel net surveys in the Navesink River, NJ. Winter flounder were the dominant piscine prey of summer flounder collected in trammel nets, and sand shrimp (Crangon septemspinosa) were the dominant invertebrate prey. Blue crabs (Callinectes sapidus), mysid shrimps, and grass shrimp (Palaemonetes spp.) were also relatively common. They observed a temporal shift in summer flounder diets from sand shrimp and winter flounder, dominant during June and early July, to blue crabs and other fishes (primarily Atlantic silversides, *Menidia menidia* and Atlantic menhaden, *Brevortia tyrannus*) later in the summer. Variations in prey selection appeared to be related to changes in the spatial distribution of predators and spatio-temporal variation in prey availability [as well as the environment; see Manderson et al. (2007)]. In laboratory experiments, summer flounder (271-345 mm TL) preferred demersal winter flounder to a pelagic fish (Atlantic silversides) and a benthic invertebrate (sand shrimp) prey, and the vulnerability of winter flounder increased with increasing prey body size from 20-90 mm TL. Prey vulnerability appeared to be related to the role of vision in the summer flounder's attack strategy and prey activity levels. [See also Scharf et al. (2006) for a discussion of how habitat complexity/type may interact with summer flounder search tactics/strategies for prey such as winter flounder.]

In a related study on predation risk for juvenile winter flounder in the same habitats during July and August, Manderson et al. (2004) found that while winter flounder (18-48 mm SL) occurred in summer flounder (232-555 mm TL) stomachs, Atlantic silverside was the most frequent prey and proportionally dominant by weight and number. This may reflect the mid-summer temporal shift noted above. Sand and grass shrimps were also common in the diet. In addition, they noted that summer flounder were more abundant in the deeper waters (average 256 cm depth) of the study area, where they appeared to represent a predation threat to winter flounder. However, they occurred at depths < 10 cm along an artificial depth gradient in their laboratory and preliminary telemetry studies indicated that the flounder move from deep water onto adjacent sandbars during the morning crepuscular period in the same area where their field experiment was performed (Manderson and Bejda, unpublished data). Because Atlantic silverside, sand shrimp, and grass shrimp were dominant prey for summer flounder and also abundant in the deep habitats in their study, densities of these prey may have been high enough in deep water to eliminate the need for the summer flounder to forage in the shallower habitats.

Witting et al. (2004) examined the rate of isotopic change of nitrogen and carbon and isotopic fractionation at two temperatures during several ontogenetic diet transitions in summer flounder. They examined prefeeding larvae as they metabolize the maternal source of nutrition and evaluated three diet transitions in the early life stages of the species: 1) yolk dependency to first feeding on zooplankton; 2) one zooplankton (rotifers) to another (Artemia); and, 3) zooplanktivity to piscivory. Witting et al. (2004) used experimental results and simulations to contrast

time- versus growth-based models for estimating parameters of isotopic change and fractionation. All rates of isotopic change were lowest for the transition between zooplanktivory and piscivory, most rapid for the transition from yolk dependence to first feeding, and generally lower at cooler temperatures. Estimates of fractionation were greater for N (2.8-3.8%) than for C (0.23-0.91%) but appeared to be unaffected by water temperature or fish life stage. Simulation results suggested that parameter estimates of isotopic change and fractionation may be compromised when growth rates are low unless sampling design is modified to address slow growth rates. Witting et al. (2004) concluded that sampling strategy and the model used can influence the accuracy and precision of estimates of isotopic change and fractionation.

Staudinger (2006) looked at the seasonal and size-based predation of summer flounder on the squids Loligo pealeii and Illex illecebrosus. Flounder from 25-75 cm TL (ave. = 45 cm) were collected for stomach content data from Massachusetts to New Jersey during 2002-2003 in conjunction with the NEFSC bottom trawl survey, the New Jersey Department of Environmental Protection, and an independent survey; diet data was also obtained from the NEFSC food habits database. Overall, diets consisted primarily of fish, squid, and stomatopods. Perciforms and clupeiforms were the dominant piscine prey. The proportion of squid consumed by summer flounder fluctuated significantly among seasons; predation on squid was at its maximum during winter, and elevated during the summer in comparison to spring and fall. Although differences in squid predation among size classes were not significant, squid contributed the greatest relative amount to the diet of medium flounder (40-55 cm). The dominant species of squid identified in all size classes and for all seasons was Loligo [see Bowman et al. (2000) and Link et al. (2002), above]. Illex was found only in the diets of large flounder (> 55 cm) and only during the winter.

Inshore, Bologna (2007) investigated the diet of summer flounder as part of an assessment of the trophic structure of fauna within eelgrass beds (*Zostera marina*) at two sites in Little Egg Harbor, NJ. Summer flounder fed heavily on crustacean prey, including *Palaemonetes spp., Hippolyte spp., Callinectes sapidu*s, and *Crangon septimspinosa*. Pipefish (*Syngnathus fuscus*) was also a major portion of the diet; Atlantic silverside (*Menidia menida*) was another fish prey item.

Latour et al. (2008) analysed diet data of late juvenile and adult summer flounder (14.8-71.2 cm TL) collected from 2002-2006 in Chesapeake Bay. The flounders were statistically grouped into four broad-size categories based on similar diet compostions: < 22.5 cm TL (small), 22.5-37.4 cm TL (small-medium), 37.5-57.4 cm TL (large-medium), and > 57.4 cm TL (large). Nearly half of the diet comprised mysid shrimp (*Neomysis spp.)* and bay anchovy (*Anchoa mitchilli)* accounting for approximately 42% combined (24.1% and 17.9%, respectively) of the diet by weight, and mantis shrimp (*Squilla empusa* — 11.2%) and weakfish (*Cynoscion regalis* — 11.1%) were of secondary and nearly equal importance. Of the remaining prey types, spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), and spotted hake (*Urophycis regia*) were the most important fishes, and sand shrimp (*Crangon septemspinosa*) was the main invertebrate prey. Each of these species represented between 2% and 7% of the diet. All other identifiable prey types each contributed < 2 % to the diet. The amount of fish in the diet increased with increasing size, conforming to previous studies of summer flounder diet [cited and discussed above and in Packer et al. (1999); the absence of squids in the diet of larger summer flounder in the Latour et al. (2008) study is likely due to the lack of this prey in Chesapeake Bay]. Mysid shrimp, sand shrimp, and mantis shrimp accounted for approximately 79% of the diet of summer flounder < 22.5 cm TL. Bay anchovy (9.5%) and weakfish (2.3%) were the main fish prey of these individuals. Mysid shrimp also dominated the diet of summer flounder ranging from 22.5-37.4 cm TL. The contribution of sand shrimp to the diet of these fish was approximately the same as in the smallest size-category, whereas that of mantis shrimp increased. Fishes were again of secondary importance and were represented mainly by bay anchovy, weakfish, and Atlantic croaker. Weakfish was the primary prey of the large-medium summer flounder and, although the contribution of bay anchovy declined, anchovy still represented 15.4% of the diet. The contribution of spot to the diet of summer flounder increased from < 1% in the small-medium fish to 13% in the 37.5-57.4 cm TL size-group. Mantis shrimp was the most important invertebrate prey of the large-medium fish. Sciaenids (i.e., spot, weakfish, and Atlantic croaker) were the main prey of the largest summer flounder and accounted for 67.3% of the diet. Seasonal

changes in summer flounder diet likely mirrored the temporal variability of prey assemblages in Chesapeake Bay. The contribution of sand shrimp and spotted hake peaked in the spring and early summer. Atlantic brief squid (*Lolliguncula brevis*), Atlantic croaker, mantis shrimp, silver perch (*Bairdiella chrysoura*), spot, and weakfish accounted for a greater portion of the diet throughout the summer and autumn. Bay anchovy and mysid shrimp were always two of the top three main prey types in the diet of summer flounder from May to November. Latour et al. (2008) note that the relative importance of specific fish species in the diet of summer flounder has varied across studies, likely because of spatial variations in prey assemblages and perhaps because of differences in study methods, but all the studies indicate that summer flounder are piscivorous within estuarine environments throughout their range. Additionally, there appears to be appreciable similarity in the invertebrate taxa consumed by summer flounder in estuaries because sand and mysid shrimps have been found in the diet in multiple areas across decades (Latour et al. 2008; see also Packer et al. 1999).

Reproduction and Maturity

From https://www.fisheries.noaa.gov/species/summer-flounder#overview.

Summer flounder spawn in the fall and early winter when they migrate offshore. They spawn several times throughout the spawning season, with spawning peaks in October and November when water temperatures change and autumn plankton is most productive. The combination of these elements improves the chance of survival for larval summer flounder. Depending on their size, females have between 460,000 and more than 4 million eggs. They release the eggs into the water column and the eggs hatch in waters of the continental shelf. Newly hatched larvae move with the currents toward coastal areas, where they develop into juveniles.

Smith (1973) found that spawning starts in mid-September between southern New England and New Jersey. As the season progresses spawning moves southward, and by October spawning takes place nearly as far south as Chesapeake Bay. Spawning has been reported to continue into March (Morse 1981). Spawning habitat occurs over the entire shelf between Cape Cod, Massachusetts, and Cape Lookout, North Carolina.

Morse (1981) documented that summer flounder are serial spawners and that egg batches are continuously matured and shed during a protracted spawning season. Morse (1981) also reported a mean maturity index that increased rapidly from August to September, peaked in October- November, then gradually decreased to a low in July. The wide range in the maturity indices during the spawning season indicates nonsynchronous maturation of females and a relatively extended spawning season.

Fecundity of summer flounder is relatively high, ranging from 463,000 to 4,188,000 eggs for fish between 14 inches and 27 inches (Morse 1981). Fertilized eggs are buoyant, floating at or near the surface. Smith (1973) reported that the heaviest concentrations of eggs and larvae were found between Long Island and Cape Hatteras; most eggs were taken within 17 miles of shore and larvae were most abundant 12 to 45 miles from shore. Larvae were found in the northern part of the Middle Atlantic Bight from September to February, and in the southern part from November to May. Mid-Atlantic Region Monitoring and Assessment Program (MARMAP) survey data (Able *et al*. 1990) indicate that peak egg abundance occurs in October through December with October and November being the two months when most eggs were collected.

The reproductive strategy of summer flounder tends to maximize reproductive potential and avoid catastrophe. The strategy is a combination of extended spawning season with variable duration, early maturation (age 1 or 2), high fecundity, serial spawning, and extensive migrations across the continental shelf during spawning. The half year spawning season reduces larval crowding and decreases the impact of predators and adverse environmental conditions on egg and larval survival. The migration pattern disperses the eggs over large areas of the shelf and probably aids in maintaining spawning fish in areas where bottom temperatures are between 54º and 66º F (Smith 1973). The October/November spawning peak coincides with the breakdown of thermal stratification on the continental shelf and the maximum production of autumn plankton which is characteristic of temperate ocean

waters of the northern hemisphere. Thus, the timing of peak spawning assures a high probability of adequate larval food supplies (Morse 1981).

The length-weight relationship for summer flounder was described by Lux and Porter (1966), Wigley et al. (2003), and various benchmark assessments for summer flounder over the years. These studies have shown that there are both seasonal and sex differences in the length-weight relationship. This difference between the sexes was also noted by Smith and Daiber (1977), Eldridge (1962), and Wilk et al. (1978). NEFSC trawl survey data for 1976-2016 for males, females, and sexes combined indicates that female summer flounder attain a significantly larger asymptotic size than males.

The 2018 benchmark assessment examined NEFSC winter, spring and fall trawl survey sample data for trends in mean length and weight by sex and age. The winter and spring series indicate no strong trend in the mean lengths of ages 1-2 for sexes combined. For ages 3-6, there is an increasing trend in mean length from 1976 to about 1990, and a decreasing trend since then. In the fall series, there is no obvious trend for ages 0-1, but there are relatively strong decreasing trends in mean length for combined sexes for ages 2 and older since the mid-1990s. In general, similar trends are observed for mean weight, with a decreasing trend evident for ages 3 and older. Trends in the mean weights at age in the total, combined sexes fishery catch (landings plus discards) exhibit a comparable pattern, with strongest declining trends since the 1990s for ages 3 and older (NEFSC 2019).

For the benchmark assessment of summer flounder (2018), the standard NEFSC fall trawl survey 1982-2016 (35 years) maturity data have been re-examined. The current data set consists of 7,887 males from age 0 to 15 and 6,297 females from age 0 to 14, for a total of 14,184 fish. The 1982-2016 mean percent observed maturities at age (unweighted, simple arithmetic average of annual values at age) are 42% at age 0, 95% at age 1, 99% at age 2, and 100% at ages 3 and older for males; 26% at age 0, 83% at age 1, 96% at age 2, and 100% at ages 3 and older for females; and 36% at age 0, 90% at age 1, 98% at age 2, and 100% at ages 3 and older for sexes combined (NEFSC 2019). The time series value of L50% was estimated to be 26.1 cm for males, 29.8 cm for females, and 27.0 cm for sexes combined (both). The A50% was 0.13 years for males, 0.42 for females, and 0.23 years for sexes combined (i.e. fish about 13-17 months old, based on the actual spawning month and the January 1 aging convention relative to fall sampling). The current L50% and A50% estimates and estimated maturity at age are comparable to those in previous assessments (NEFSC 2019).

Stock structure and status

The assessment found that the black sea bass stock north of Cape Hatteras, NC was not overfished and overfishing (2021). For current details on stock status: https://www.fisheries.noaa.gov/national/status-stocks-reports

Burke et al. (2000) tested the hypothesis that a single phenotypic group of summer flounder exists relative to Cape Hatteras, North Carolina. It is worth quoting their study in detail since it covers several habitat parameter issues beyond stock structure.

They test their hypothesis using several methods:

- Life history parameters of summer flounder from north and south of Cape Hatteras were evaluated by data from peer reviewed literature and state and federal reports.
- To evaluate movement of summer flounder relative to Cape Hatteras they combined data from mark recapture studies conducted by the NC Division of Marine Fisheries between 1973-1996.
- From October 1994-April 1995, immigration of pelagic fish larvae was investigated using a sampling series at Oregon Inlet to the north of Cape Hatteras and to the south at Beaufort Inlet.

- Physiological laboratory experiments were conducted on progeny originating from geographically distant broodstocks in 1998. One group originated from broodstock collected in Long Island Sound, a second group originated from broodstock collected from Onslow Bay, NC. Both groups were raised in the laboratory.

Their results are as follows:

- Life history parameters calculated for summer flounder from South Carolina are quite different from those flounder from the Mid-Atlantic Bight. Calculated natural mortality rates indicate that M is significantly more severe in the south resulting in a shorter life span, smaller maximum size and earlier sexual maturation.
- Size of recaptures varied with season and area. The largest fish in the north were recaptured in the spring and fall and the largest fish in the south in the winter and spring. Fish tagged in the north did not exhibit significant latitudinal movement with the exception of those which were recaptured in the summer, when significantly more fish moved north. In contrast, fish tagged in the south tended to move south in all seasons, with the exception of the spring, when more fish moved north than south: however, this was not considered to be significant.

- Timing of peak larval immigration differed by almost four months between Oregon and Beaufort inlets. Immigration to the north of Cape Hatteras, at Oregon Inlet, rose rapidly to a peak in November and then declined. In contrast, south of Hatteras at Beaufort Inlet, summer flounder first appeared in late December and peaked in late February and March. The range in size at immigration differed between the two inlets. Larger and smaller larvae occurred at Oregon Inlet, where range in length exceeded 6 mm, compared to 4 mm at Beaufort. At Beaufort Inlet, larvae tended to enter at a more advanced stage of development.
- Performance of progeny from the northern and southern broodstocks in the rearing trials was similar at the high (22°C) and low (16°C) temperature but differed at 19°C. Regression analysis indicated that growth was highest at 22°C and that essentially identical linear equations best described growth of both groups. At 16°C, growth of the two groups was also essentially the same and best described by a linear equation. Although growth of the two groups was the same at the high and low temperatures, a difference was apparent at the intermediate temperature. Regression analysis indicated that though linear models were the best fit for growth at 16 and 22°C, curves were required to describe growth at 19°C. These curves described different growth trajectories. The southern group's growth rate increased over time while the northern group rate decreased. Settled juveniles from the growth study were used to compare fin ray development of the two groups, relative to temperature. Fin ray number showed a significant increase for both stocks with temperature. The mean number of rays at a given temperature was consistently lower for fish from the northern group, but differences between groups at a given temperature were not significant. Low salinity tolerance during settlement was different between the two groups, and overall mortality differed between the two groups. Mortality of northern fish was higher, exceeding 50% at 5 ppt and 80% at 2.5 ppt, and differed between the two salinity treatments. Mortality of southern fish was < 40% at both 2.5 and 5 ppt during settlement and did not differ between treatments.

In their discussion, Burke et al. (2000) state that, although Jones and Quattro (1999) (cited and discussed in the original summer flounder EFH source document) show there is no evidence for genetic subdivision of the summer flounder at Cape Hatteras, nevertheless, a number of observations suggest that we should not accept the lack of genetic evidence as proof that the stock is homogeneous north and south of this zoogeographic boundary. The same study did find evidence of genetic structure in the northern portion of the species range where no obvious zoogeographic boundary exists. Burke et al. (2000) suggest that this evidence is difficult to reconcile with the apparent lack of structure relative to Cape Hatteras. Sampling problems could be responsible for the apparent lack of structure as fish samples from the South Atlantic Bight consisted exclusively of juvenile fish. This could bias results if initially mixed groups sort themselves out due to differential mortality or migration. Another alternative explanation advanced by Burke et al. (2000) is that genetic structure does exist relative to Cape Hatteras, but was

not detected due to the resolving power of the molecular techniques used, and given these alternatives, it would seem prudent to consider Jones and Quattro's conclusion of little genetic structure in the summer flounder population as preliminary until studies with adults and higher resolution methods have been tested.

Larval immigration and movement data from North Carolina indicate that spawning of summer flounder from south of Cape Hatteras may be distinct from spawning of resident and southward migrating fish north of Cape Hatteras. The mark recapture data indicated that significant movement of northern fish was only evident in summer, when the expected movement north was apparent. In contrast, fish tagged south of Hatteras showed movement south during the period, a trend that apparently continues through the fall and winter. Burke et al. (2000) suggest that these differences in movement patterns of adults may explain the difference in the timing of spawning and peak recruitment of larvae in the two regions. The pattern of larval immigration observed at Oregon Inlet in 1994-1995 is consistent with larval data from the shelf of North Carolina north of Cape Hatteras (Able et al. 1990) (cited and discussed in the original summer flounder EFH source document) and supports the finding that peak spawning north of Hatteras occurs in the fall (Berrien and Sibunka 1999) (cited and discussed in the original summer flounder EFH source document). Examination of seasonal variability of summer flounder ingress at Beaufort Inlet shows that peak immigration generally occurs in the spring and may result from spawning of southern fish during late winter and spring (Burke et al. 2000).

Burke et al. (2000) go on to say that phenotypic variation between summer flounder from regions north and south of Hatteras might be expected based on environmental, habitat, and faunal differences and may be responsible for observed differences in life history parameters and movement patterns of adults. Differences in larvae entering the sounds of North Carolina through Oregon and Beaufort Inlets may result from differences in environmental conditions under which larvae develop and differences in the parent stock. Differences in temperature and currents north and south of Hatteras would be expected to influence growth, development, and transport of larvae. The increasing trend in size at Oregon Inlet and in dorsal ray count at Beaufort Inlet over the season might be expected given the different temperature regimes during the spawning season in the two regions. Size at a given developmental stage increases as growth rate decreases and consequently generally increases as temperature decreases (Seikai et al. 1986; cited in Burke et al. 2000). At Oregon Inlet, where immigration started during the fall when coastal waters were warm and continued as water temperature fell, larval size would be expected to increase as the season progressed since the range of development at immigration of summer flounder is limited to metamorphosing larvae (Burke et al. 1998; cited and discussed in the original summer flounder EFH source document). The number of fin rays increases with increasing environmental temperature during larval development (Kinoshita et al. 2000; cited in Burke et al. 2000). At Beaufort Inlet immigration commenced in the winter though the major portion of recruitment occurred in spring and the number of fin rays would be expected to increase over the season as the coastal waters warmed during spring.

Burke et al. (2000) performed the laboratory experiments with northern and southern groups under the assumption that adaptation to regional environmental and habitat differences have occurred so that one group would be expected to perform better on a given trial; e.g., it was expected that growth of the northern group would be better than the southern group in the low temperature treatment; the opposite at high temperature. That didn't happen, however. The pattern of growth at 19oC suggests a difference in growth rate may develop after settlement and transformation to the juvenile stage, a possibility supported by the work of Malloy and Targett (1994) (cited and discussed in the original summer flounder EFH source document) with juvenile summer flounder. Results of the salinity trials indicated that the southern group was more tolerant of low salinity conditions during metamorphosis than the northern group. This supported the assumption that the southern group was more likely to use estuarine nurseries where exposure to low salinity during settlement was probable. Water temperatures in Mid-Atlantic Bight estuaries may fall below 0oC, which can be lethal to summer flounder. It has been speculated that larvae may settle on the shelf and immigrate to estuaries as juveniles in the spring (Able et al. 1990). Temperature had a similar effect on fin formation of both groups. The significance of consistently higher numbers of rays in the southern group is not clear since this may relate to variability among individuals rather than stocks. In contrast to these results, Ginsburg (1952) (cited in the original summer flounder EFH source document) compared meristics

of summer flounder from Chesapeake Bay and from North Carolina waters and found lower numbers in North Carolina flounders. Rearing conditions had a strong effect on fin ray development in both groups as they exhibited much lower ray numbers than wild summer flounder. It is unlikely that this is an effect of temperature since spawing appears to occur between 12-19oC (Smith 1973) (cited and discussed in the original summer flounder EFH source document). A more likely cause of low fin ray numbers is nutrition, which has been shown to affect other developmental processes such as pigmentation development in flatfish (Seikai et al. 1987; cited in Burke et al. 2000). The clear morphological difference in fin ray number between the hatchery-reared flounder and wild summer flounder probably reflects a variety of physical and behavioral differences between wild and hatchery-reared fish.

Burke et al. (2000) conclude that these results support earlier studies, which concluded that different stocks exist relative to the zoogeographic boundary at Cape Hatteras. At present, the northern and southern groups should be considered functional stocks since currently there is no evidence that they are genetically distinct (Jones and Quattro 1999).

Kraus and Musick (2001) revisit the question of summer flounder stock structure. In their review, they present an interpretation of various morphometric, meristic, biochemical, and tagging studies, published and unpublished, that indicate the presence of two, or possibly three, distinct stocks in the management area. They also include new data from a tagging study that was conducted on juveniles form Virginia that aids in defining the stock(s) north of Cape Hatteras. It appears that juveniles from Virginia can recruit to New England estuaries as adults; in addition, there is no evidence to suggest that juveniles from Virginia are part of the group of summer flounder that occurs in the inshore areas of North Carolina.

The Fishery

There is a recreational and commercial fishery for summer flounder. Total U.S. commercial landings of summer flounder from Maine to North Carolina (based on NMFS data) peaked in 1979 at around 18,000 mt. Landings in the commercial fishery in 2019 were approximately 9.06 million pounds (4,109 mt), about 83% of the adjusted commercial quota (after overage deductions) of 10.98 million pounds (4,981 mt). Commercial dead discards were estimated at 1.73 million pounds (783 mt). Total commercial catch (10.79 million pounds or 4,892 mt) was estimated at about 20% below the commercial ACL. This is likely due to the mid-year revisions of the commercial quota, and the fact that not all states were able to adjust their management measures mid-year to encourage full quota utilization.

Recreational harvest in 2019 was 7.80 million pounds (3,537 mt), about 101% of the revised 2019 RHL of 7.69 million pounds (which was set based on the 2018 assessment incorporating revised MRIP estimates). Recreational dead discards were estimated at 3.04 million pounds (1,379). Total recreational catch (10.84 million pounds or 4,916 mt) was approximately 6% below the recreational ACL of 11.51 million pounds (5,218 mt).

Management

Summer flounder are jointly managed by the Mid-Atlantic Fishery Management Council (MAFMC)/NOAA Fisheries and the Atlantic States Marine Fisheries Commission (ASMFC). The MAFMC and ASMFC cooperatively develop fishery regulations, with the National Marine Fisheries Service (NMFS) serving as the federal implementation and enforcement entity within the United States (U.S.) Department of Commerce. Cooperative management was developed because significant catch is taken from both state (0-3 miles offshore) and federal waters (>3-200 miles offshore). Additional management actions and all FMP documents can be viewed at http://www.mafmc.org/fisheries/fmp/sf-s-bsb and http://www.asmfc.org/species/summer-flounder.

References

Able, K.W., R.E. Matheson, W.W. Morse, M.P. Fahay, and G. Shepherd. 1990. Patterns of summer flounder Paralichthys dentatus early life history in the Mid-Atlantic Bight and New Jersey estuaries. Fish. Bull. (U.S.) 88: 1-12.

Bell, G.W. and D.B. Eggleston. 2005. Species-specific avoidance responses by blue crabs and fish to chronic and episodic hypoxia. Mar. Biol. 146 (4): 761-770.

Bologna, P. 2007. Impact of differential predation potential on eelgrass (Zostera marina) faunal community structure. Aquat. Ecol. 41 (2): 221-229.

Bowman, R. E., C. E. Stillwell, W. L. Michaels, and M. D. Grosslein. 2000. Food of Northwest Atlantic fishes and two common species of squid. NOAA Tech. Memo. NMFS-F/NE-155. 138 p.

Burke, J.S., J.P. Monaghan Jr., and S. Yokoyama. 2000. Efforts to understand stock structure of summer flounder (Paralichthys dentatus) in North Carolina, USA. J. Sea Res. 44: 111-122.

Diaz, R.J., G.R. Cutter, Jr., and K.W. Able. 2003. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 26: 12-20.

Eldridge, PJ. 1962. Observations on the winter trawl fishery for summer flounder, Paralichthys dentatus.MS thesis, College of William and Mary, Virginia Institute of Marine Science, Gloucester Point, VA.

Geer, P.J. 2002. Summary of essential fish habitat description and identification for Federally managed species inhabiting Virginia waters of Chesapeake Bay 1988-1999. Virginia Mar. Res. Rep. VMRR 2001-03, Jan. 2001, Revised June 2002. 169 p.

Getchis, T.S. and D.A. Bengtson. 2006. Food consumption and absorption efficiency by newly settled summer flounder, Paralichthys dentatus (Linneaus, 1766). Aquaculture 257 (1-4): 241-248.

Gottschall, K., M.W. Johnson, and D.G. Simpson. 2000. The distribution and size composition of finfish, American Lobster, and long-finned squid in Long Island Sound based on the Connecticut Fisheries Division Bottom Trawl Survey, 1984-1994. NOAA Tech. Rep. NMFS 148. 195 p.

Grothues, T.M., R.K. Cowen, L.J. Pietrafesa, F. Bignami, G.L. Weatherly, and C.N. Flagg. 2002. Flux of larval fish around Cape Hatteras. Limnol. Oceangr. 47: 165-175.

Hare, J.A., S. Thorrold, H. Walsh, C. Reiss, A. Valle-Levinson, and C. Jones. 2005. Biophysical mechanisms of larval fish ingress into Chesapeake Bay. Mar. Ecol. Prog. Ser. 303: 295-310.

Hare, J.A., H.J. Walsh, and M.J. Wuenschel. 2006. Sinking rates of late-stage fish larvae: Implications for larval ingress into estuarine nursery habitats. J. Exp. Mar. Biol. Ecol. 330 (2): 493-504.

Hurst, T.P., K.A. McKown, and D.O. Conover. 2004. Interannual and long-term variation in the nearshore fish community of the mesohaline Hudson River estuary. Estuaries 27: 659-669.

Katersky, R.S., M.A. Peck, and D.A. Bengtson. 2006. Oxygen consumption of newly settled summer flounder, Paralichthys dentatus (Linnaeus, 1766). Aquaculture 257 (1-4): 249-256.

Kraus, R.T. and J.A. Musick. 2001. A brief interpretation of summer flounder, Paralichthys dentatus, movements and stock structure with new tagging data on juveniles. Mar. Fish. Rev. 63: 1-6.

Lathrop, R.G., M. Cole, N. Senyk, and B. Butman. 2006. Seafloor habitat mapping of the New York Bight incorporating sidescan sonar data. Estuar. Coast. Shelf Sci. 68 (1-2): 221-230.

Latour, R.J., J. Gartland, C.F. Bonzek, and R.A. Johnson. 2008. The trophic dynamics of summer flounder (Paralichthys dentatus) in Chesapeake Bay. Fish. Bull. 106 (1): 47-57.

Link, J.S., K. Bolles, and C.G. Milliken. 2002. The feeding ecology of flatfish in the Northwest Atlantic. J. Northw. Atl. Fish Sci. 30: 1-17.

Link, J.S. and J. Burnett. 2001. The relationship between stomach contents and maturity state for major northwest Atlantic fishes: new paradigms? J. Fish. Biol. 59: 783-794.

Lux, F.E. and Nichy, F.E. (1980) Movements of tagged summer flounder, Paralichthys dentatus, off southern New England. Northeast Fisheries Center Laboratory Reference Document No. 80-34, 20 pp.

Lux FE, Porter LR. 1966. Length-weight relation of the summer flounder (Paralichthys dentatus (Linneaus). US Bur Comm Fish. Spec Sci Rep Fish. No 531. 5 p.

MAFMC. 1999. Amendment 12 to the Summer Flounder, Scup, and Black Sea Bass Fishery Management Plan. Available at: www.mafmc.org.

MAFMC (Mid-Atlantic Fishery Management Council). 2002. Amendment 13 to the Summer Flounder, Scup, and Black Sea Bass Fishery Management Plan. Dover, DE. Available at: https://mafmc.squarespace.com/s/SFSCBSB_Amend_13_Vol_1compressed.pdf

Manderson, J.P., B.A. Phelan, A.W. Stoner and J. Hilbert. 2000. Predator-prey relations between age-1+ summer flounder (Paralichthys dentatus, Linnaeus) and age-0 winter flounder (Pseudopleuronectes americanus, Walbaum): predator diets, prey selection, and effects of sediments and macrophytes. J. Exp. Mar. Biol. Ecol. 251: 17-39.

Manderson, J.P., J. Pessutti, J.G. Hilbert, and F. Juanes. 2004. Shallow water predation risk for a juvenile flatfish (winter flounder; Pseudopleuronectes americanus, Walbaum) in a northwest Atlantic estuary. J. Exp. Mar. Biol. Ecol. 304: 137-157.

Manderson, J.P., J. Pessutti, P. Shaheen, and F. Juanes. 2007. Dynamics of early juvenile winter flounder predation risk on a Northwest Atlantic estuarine nursery ground. Mar. Ecol. Prog. Ser. 328: 249-265.

Monaghan, J.P., Jr. (1992) Migration and population dynamics of summer flounder (Paralichthys dentatus) in North Carolina, Study 3A. Transactions of the North Carolina Division of Marine Fisheries. In Marine Fisheries Research, Completion Report for Project F-29, 36 pp.

Morse, W.W. 1981. Reproduction of the summer flounder, Paralichthys dentatus (L.). J. Fish Biol. 19: 189-203.

Murawski, W.S. (1970) Results of tagging experiments of summer flounder, (Paralichthys dentatus), conducted in New Jersey waters from 1960–1967. New Jersey Division of Fish, Game, and Shellfisheries, Nacote Research Station. Miscellaneous Report No. 5M, 72 pp.

Necaise, A.M.D., S.W. Ross, and J.M. Miller. 2005. Estuarine habitat evaluation measured by growth of juvenile summer flounder Paralichthys dentatus in a North Carolina estuary. Mar. Ecol. Prog. Ser. 285: 157-168.

NEFSC (Northeast Fisheries Science Center). 2013. 57th Northeast Regional Stock Assessment Workshop (57th SAW) Assessment Report. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 13-16; 967 p. Available from: National Marine Fisheries Service, 166 Water Street, Woods Hole, MA 02543-1026, or online at http://nefsc.noaa.gov/publications/.

Northeast Fisheries Science Center (NEFSC). 2019. 66th Northeast Regional Stock Assessment Workshop (66th SAW) Assessment Report. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 19-08; 1170 p. Available from: http://www.nefsc.noaa.gov/publications/

Overholtz, W.J., J.S. Link, and L.E. Suslowicz. 2000. Consumption of important pelagic fish and squid by predatory fish in the northeastern USA shelf ecosystem with some fishery comparisons. ICES J. Mar. Sci. 57: 1147-1159.

Packer, D.B., S.J. Griesbach, P.L. Berrien, C.A. Zetlin, D.L. Johnson, and W.W. Morse. 1999. Essential fish habitat source document: Summer flounder, Paralichthys dentatus, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-151. 88 p. Available at: http://www.nefsc.noaa.gov/nefsc/habitat/efh/

Packer, D.B. 2017. Unpublished Essential Fish Habitat Source Document, Update Memo.

Peters, D.S. and J.W. Angelovic. 1971. Effect of temperature, salinity, and food availability on growth and energy utilization of juvenile summer flounder, Paralichthys dentatus. In D.J. Nelson ed. Proc. 3rd Natl. Symp. Radioecology USAEC Conf.,-710501-PI. p. 545-554. National Technical Information Service, Springfield, VA.

Powell AB. 1974. Biology of the summer flounder, Paralichthys dentatus, in Pamlico Sound and adjacent waters, with comments on P. lethostigma and P. albigutta. M.S. Thesis. University of North Carolina, Chapel Hill, NC. 145 p.

Sackett, D.K., K.W. Able, and T.M. Grothues. 2007. Dynamics of summer flounder, Paralichthys dentatus, seasonal migrations based on ultrasonic telemetry. Estuar. Coast. Shelf Sci. 74 (1-2): 119-130.

Sackett, D.K., K.W. Able, and T.M. Grothues. 2008. Habitat dynamics of summer flounder Paralichthys dentatus within a shallow USA estuary, based on multiple approaches using acoustic telemetry. Mar. Ecol. Prog. Ser. 364: 199-212.

Scharf, F.S., J.P. Manderson, and M.C. Fabrizio. 2006. The effects of seafloor habitat complexity on survival of juvenile fishes: Species-specific interactions with structural refuge. J. Exp. Mar. Biol. Ecol. 335 (2): 167-176.

Slacum, H.W., Jr., J.H. Voelstad, E.D. Weber, W.A. Richkus, R.J. Diaz, and C.O.Tallent. 2008. The value of applying commercial fishers' experience to designed surveys for identifying characteristics of essential fish habitat for adult summer flounder. N. Am. J. Fish. Manage. 28 (3): 710-721.

Smith, W.G. 1973. The distribution of summer flounder, Paralichthys dentatus, eggs and larvae on the continental shelf between Cape Cod and Cape Lookout, 1965-66. Fish. Bull. (U.S.) 71: 527-548.

Smith, R.W. and F.C. Daiber. 1977. Biology of the summer flounder, Paralichthys dentatus, in Delaware Bay. Fish. Bull. (U.S.) 75: 823-830.

Staudinger, M.D. 2006. Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf. Fish. Bull. 104 (4): 605-615.

Stierhoff, K.L, T. E. Targett, and K. Miller. 2006. Ecophysiological responses of juvenile summer and winter flounder to hypoxia: experimental and modeling analyses of effects on estuarine nursery quality. Mar. Ecol. Prog. Ser. 325: 255-266.

Stierhoff, K.L, T. E. Targett, and J.H. Power. 2009. Hypoxia-induced growth limitation of juvenile fishes in an estuarine nursery: assessment of small-scale temporal dynamics using RNA:DNA. Can. J. Fish. Aquat. Sci. 66 (7): 1033-1047.

Timmons, M. 1995. Relationships between macroalgae and juvenile fishes in the inland bays of Delaware. Ph.D. dissertation, Univ. Delaware, Newark, DE. 155 p.

Tyler, R.M. 2005. Distribution and avoidance patterns of juvenile summer flounder (Paralichthys dentatus) and weakfish (Cynoscion regalis) in relation to hypoxia: Field studies in a temperate coastal lagoon tributary and laboratory choice experiments. Ph.D. dissertation, Univ. Delaware, Newark, DE. 183 p.

Wigley SE, McBride HM, McHugh NJ. 2003. Length-weight relationships for 74 fish species collected during NEFSC research vessel bottom trawl surveys, 1992-99. NOAA Technical Memorandum NMFS-NE-171.

Wilk SJ, Smith WG, Ralph DE, Sibunka J. 1980. The population structure of summer flounder between New York and Florida based on linear discriminant analysis. Trans Am Fish Soc. 109: 65-271.

Wilber, D.H., D.G. Clarke, M.H. Burlas, H. Ruben, and R.J. Will. 2003. Spatial and temporal variability in surf zone fish assemblages on the coast of New Jersey. Estuar. Coast. Shelf Sci. 56: 291-304.

Witting, D.A., R.C. Chambers, K.L. Bosley, and S.C. Wainright. 2004. Experimental evaluation of ontogenetic diet transitions in summer flounder (Paralichthys dentatus), using stable isotopes as diet tracers. Can. J. Fish. Aquat. Sci. 61: 2069-2084.

Table 1. Diet composition of summer flounder by fish length category. Data expressed as percentage of stomach content by weight. Squared brackets indicate major taxon subtotal; parentheses indicate minor taxon subtotal. Source: Bowman *et al*. (2000); from NEFSC groundfish surveys, 1977-1980.

Stomach Contents	\<21	21-25	26-30	31-35	36-40	41-45	51-55	56-60	\>60	Total
CEPHALOPODA	-	-	[4.9]	[27.1]	[1.5]	[19.1]	[26.2]	[64.5]	[38.3]	[34.2]
Illex sp.	-	-	-	10.2	-	-	-	-	31.5	9.4
Loligo pealeii	-	-	-	3.8	-	12.2	12.7	51.1	-	16.3
Loligo sp.	-	-	-	-	-	2.3	-	3.4	-	1.2
Lolliguncula brevis	-	-	-	2.4	-	-	-	-	-	0.1
Cephalopoda unid.	-	-	4.9	10.7	1.5	4.6	13.5	10.0	6.8	7.2
CRUSTACEA	[43.3]	[41.8]	[18.6]	[22.4]	[6.5]	[8.8]	[1.1]	-	[0.9]	[4.4]
Stomatopoda	-	(5.5)	-	(0.3)	-	-	-	-	-	(\<0.1)
Amphipoda	-	-	(1.6)	(0.7)	(1.0)	-	-	-	-	(0.2)
Mysidacea	(0.6)	(24.1)	(12.3)	(12.1)	(2.2)	(0.7)	(0.3)	-	(0.9)	(2.0)
Neomysis americana	0.6	24.1	12.3	12.1	2.2	0.7	0.3	-	0.9	2.0
Euphausiacea	-	-	-	(6.0)	-	-	-	-	-	(0.3)
Meganyctiphanes norvegica	-	-	-	6.0	-	-	-	-	-	0.3
Decapoda	(42.7)	(12.0)	(4.7)	(2.8)	(3.3)	(7.3)	(0.8)	-	-	(1.8)
Dichelopandalus leptocerus	-	-	-	-	-	1.9	-	-	-	0.2
Crangon septemspinosa	9.0	4.3	0.3	0.3	0.2	\<0.1	-	-	-	0.1
Cancer irroratus	33.2	2.1	1.8	2.5	1.3	3.0	-	-	-	0.8
Cancridae	-	-	1.7	\<0.1	-	-	0.8	-	-	0.1
Ovalipes ocellatus	-	-	-	-	1.8	2.4	-	-	-	0.5
Decapoda unid.	0.5	5.6	0.9	-	-	-	-	-	-	0.1
Crustacea unid.	(\<0.1)	(0.2)	-	(0.5)	-	(0.8)	-	-	-	(0.1)
OSTEICHTHYES	[56.6]	[58.2]	[75.7]	[49.8]	[91.9]	[70.9]	[72.7]	[35.5]	[60.6]	[61.1]
Batrachoididae	-	-	-	-	-	-	-	-	5.5	1.6
Etrumeus teres	-	35.1	-	-	12.5	4.0	-	-	-	2.9
Clupeidae	-	-	-	-	-	5.5	-	13.4	-	4.2
Anchoa hepsetus	-	-	7.6	-	-	1.9	-	-	-	0.4
Anchoa mitchilli	-	-	-	-	-	-	-	-	1.3	0.4
Anchoa sp.	-	6.4	-	-	-	-	-	-	-	0.1
Engraulidae	-	-	-	-	-	-	0.3	2.1	-	0.6
Cyprinodon variegatus	-	-	-	-	-	-	2.2	-	-	0.2
Merluccius bilinearis	54.0	-	-	4.6	-	-	-	-	-	0.3
Gadidae	-	-	-	-	-	0.7	-	-	-	0.1
Ophidiidae	-	-	-	-	-	7.6	-	-	-	0.8
Ammodytes dubius	-	-	34.0	12.1	58.2	27.3	43.2	12.8	4.5	22.3
Triglops murrayi	-	-	-	-	1.9	-	-	-	-	0.3
Cynoscion regalis	-	-	-	6.0	-	2.4	-	-	-	0.6
Ulvaria subbifurcata	-	-	-	1.3	-	-	-	-	-	0.1
Macrozoarces americanus	-	2.9	-	-	-	-	-	-	-	\<0.1
Paralichthys sp.	-	-	-	3.5	-	-	-	-	-	0.2
Scophthalmus aquosus	-	-	-	4.9	-	-	-	-	-	0.2
Bothidae	-	-	5.4	0.8	-	\<0.1	-	-	-	0.2
Osteichthyes unid.	2.6	13.8	28.7	16.6	19.3	21.5	27.0	7.2	49.3	25.6
ANIMAL REMAINS AND MISC.	[0.1]	[\<0.1]	[0.8]	[0.7]	[0.1]	[1.2]	-	-	[0.2]	[0.3]
Number sampled	22	76	135	113	111	80	52	44	22	655
Number empty	16	53	84	74	66	44	30	25	10	402
Mean stomach content (g)	0.167	0.363	0.427	0.881	2.828	2.659	3.503	12.155	25.717	3.050
Mean fish length (cm)	18	23	27	32	38	42	47	53	64	35